A COMPARISON OF RECENT AND HISTORICAL TIME PERIODS: CHANGES IN THE SMALLMOUTH BASS POPULATION OF WAUGOSHANCE POINT, NORTHERN LAKE MICHIGAN

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ABSTRACT

A COMPARISON OF RECENT AND HISTORICAL TIME PERIODS:
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WAUGOSHANCE POINT, NORTHERN LAKE MICHIGAN

by Emily Kristen Martin

Smallmouth bass (*Micropterus dolomieui*) populations in nearshore waters of northern Lake Michigan were historically considered a premier sport fishery. Since the 1950's, regulations, including season and length limits, have changed. Previous research on the movement, abundance, reproduction, and growth of a smallmouth bass population in Lake Michigan was performed in the 1950s at Waugoshance Point in northern Lake Michigan. The objective of this study was to assess the smallmouth bass population to determine if and how the fishery at Waugoshance Point has changed since the 1950's. Smallmouth bass were captured via trap nets and tagged for individual identification in June 2009-2011 and May and July 2012. Length and weight were recorded, and scale samples were collected for aging. Catch-per-unit-effort, length distributions, length-at-age, growth of juvenile smallmouth bass, and condition factor increased since the historical time period. Smallmouth bass also had high relative weights indicating good condition of individuals captured. Estimates of apparent survival were higher than those of the nearby Beaver Archipelago, and temporary emigration and immigration estimates indicate that movement into and out of the Waugoshance Point population was also high. Given the potential for movement between Waugoshance Point and the Beaver Archipelago, the two fisheries are likely part of a metapopulation. Tag returns for smallmouth bass tagged at Waugoshance Point also indicate that the smallmouth bass fisheries of Lake

Michigan, and potentially Lake Huron, have some connectivity, which is an important consideration for management and monitoring efforts.

The smallmouth bass population at Waugoshance Point has changed since the historic time period, which is likely a result of ecosystem and management changes. Increased length limits may have altered length frequencies, while the invasive round goby (*Neogobius melanostomus*) may contribute to increased length-at-age, growth increments, and condition. An understanding of potential connections and how management and ecosystem changes in the Great Lakes have affected smallmouth bass fisheries are important to managing smallmouth bass as a recreational resource.

Due to the importance of smallmouth bass age estimates in this study to determine age structure, growth rates, and length-at-age, the precision of age estimates for the species was also investigated. Precise age estimates are critical due to their use in management decisions. The objective of the second study was to determine and compare the precision of two non-lethal aging structures, anal spines and scales, for smallmouth bass in northern Lake Michigan. Because known-age smallmouth bass were unavailable for this study, only precision, rather than accuracy, could be evaluated. Coefficient of variation, average percent error, and standard deviation indicated scales were the most precise aging structure. For smallmouth bass in northern Lake Michigan where harvesting individuals for lethal aging structures is not possible, scales should be the nonlethal structure of choice due to greater precision and less error in processing.

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A COMPARISON OF RECENT AND HISTORICAL TIME PERIODS: CHANGES IN THE
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Introduction

Population assessments in fisheries management are routinely performed to provide

managers with information on a fishery's current status. The status of population growth, age

structure, overall size, and abundance among other factors are important to management

decisions (Ault and Olson, 1996; Post et al., 2002 Pope et al., 2010). Unlike assessments which

focus on the exploitable part of the population (termed stock assessments), population

assessments are more inclusive because they include the portion of the population not exploited

in a fishery (Pope et al., 2010). The knowledge gained through population studies is influential

in management or regulation decisions and helps support appropriate decisions (Colby and

Nepszy, 1981; Elliot, 1985; Mills and Mann, 1985; Haro et al., 2000; Pope et al., 2010; Alp et

al., 2011). The changes that occur in a population over time are especially important for

managers to consider. Population structure and size can fluctuate from year to year and with

environmental and anthropogenic disturbance (McRae and Diana, 2005; Pope et al., 2010).

Population assessment data can be used to compare characteristics of the same population over

time and reveal the significance of these changes (Van Den Avyle and Hayward, 1999). When

significant amounts of time pass between population assessments, current trends and

comparisons to previous information is important (Van Den Avyle and Hayward, 1999; Pope et

al., 2010).

Population assessments have been an important tool for managers in evaluating the status of many species. Species that are either threatened or endangered can be monitored, and the success of rehabilitation efforts analyzed using population assessments (e.g., lake sturgeon *Acipenser fulvescens*; Galarowicz, 2003). Without population assessments or monitoring, at-risk populations may not receive the rehabilitation efforts or proper management necessary for survival. However, species that are not threatened also require population assessments. Popular sportfish such as walleye (*Sander vitreus*) and lake trout (*Salvelinus namaycush*) are Great Lakes species that require monitoring to assess the impact of environmental and anthropogenic disturbance and management efforts (Bronte et al., 2008; Kayle, 2008; Haas and Thomas, 2009).Productivity of walleye, specifically in Lake Erie, has been affected by food web shifts, urban development, pollution, warmer winters, and river barriers since the 1980's (Locke et al., 2005; Kayle, 2008). Rehabilitation efforts of lake trout are underway after the negative impacts of overfishing, invasive species such as alewife (*Alosa pseudoharengus*) and sea lamprey (*Petromyzon marinus*), and habitat degradation (Bronte et al., 2008). The effects of management, regulations, and rehabilitation efforts on a sportfish population can be evaluated through regular assessments (Van Den Avyle and Hayward, 1999).

Smallmouth bass (*Micropterus dolomieu*) are both ecologically and economically important in the Great Lakes due to their role as a predator and their popularity as a sportfish, especially in nearshore regions (Bremigan et al., 2008; Kaemingk, 2008). Historical research on the movement, abundance, reproduction, and growth of a smallmouth bass population in northern Lake Michigan was performed in the 1950's at Waugoshance Point, Michigan (Latta, 1963). Located approximately18 km west of Mackinac City, Waugoshance Point is a popular

site with smallmouth bass anglers. Since the 1950's, no further population assessments have been performed at Waugoshance Point; however, a study of a nearby smallmouth bass fishery indicated changes within the fishery since the 1970's (Kaemingk et al. 2012). Ecosystem and regulation changes in Lake Michigan and at Waugoshance Point may have influenced the smallmouth bass population, and a population assessment would allow researchers to evaluate the consequences of these changes.

Smallmouth bass are typically found in the nearshore areas (< 30-m depth) of Lake Michigan (Bremigan et al., 2008; Kaemingk et al., 2011b). Changes in Lake Michigan since the 1950's include a reduction in densities of certain macroinvertebrate species, which have declined the most in nearshore areas, in part due to filtering of the water column by zebra mussels (*Dreissena polymorpha*) (Nalepa et al., 1998; Madenjian et al., 2002) and declines in phosphorus levels (Nalepa et al., 1998; Mida et al., 2010). Invasive round gobies (*Neogobius melanostomus*) also alter nearshore areas and are a predator of both the dreissenid mussels and macroinvertebrates (Lederer et al., 2006). As a result of round goby interactions, numbers of mottled sculpin (*Cottus bairdii*) and johnny darter (*Etheostoma nigrum*), prey species of smallmouth bass, have declined (Janssen and Jude, 2001; Lauer et al., 2004), but round goby are also a potential prey source for smallmouth bass (Corkum et al., 2004; Steinhart et al., 2004b). Currently, Kaemingk et al. (2012) is the only study to document the impacts of ecosystem changes on a smallmouth bass population in the northern Great Lakes. Due to its importance as a sportfish in Lake Michigan, especially in easily accessible nearshore habitats, understanding the impacts of ecosystem changes on smallmouth bass populations is essential(Kaemingk et al., 2012).

Smallmouth bass size limit and season regulations at Waugoshance Point have also changed since the historical (1950's) time period. In the 1950's, the size limit for smallmouth bass was 254 millimeters (mm) (Latta, 1963). Size limits were increased in 1976 to 305 mm and to 355 mm in 1995 (Bremigan et al., 2008); a change in size limit has the potential to alter the characteristics of the smallmouth bass population (Philipp et al., 1997; Slipke et al., 1998; Steinhart et al., 2004a). The opening day of smallmouth bass season was also moved from the third Saturday in June to June 1 in 1962 and then to the Saturday of Memorial Day weekend in 1968 (Bremigan et al., 2008). The purpose of closed seasons during the spring is to reduce total annual mortality and protect spawning males that are vulnerable to fishing (Bremigan et al., 2008). Smallmouth bass typically begin spawning activity in late May to mid-June in nearshore areas of Lake Michigan (Ridgway et al., 1991; Kaemingk et al., 2011a). As a result, the population has the potential to be fished heavily during the earlier spawning season. Due to the effect of weather conditions on spawning, cooler years are a threat to smallmouth bass recruitment from a combination of late spawning, decreased nest success, and fishing mortality (Bremigan et al., 2008; Steinhart, 2004; Kaemingk et al., 2011a; Landsman et al., 2011). However, a size limit of 355 mm theoretically allows the majority of smallmouth bass to spawn at least once before being at risk of harvest (Bremigan et al., 2008). This combination of regulation changes on the smallmouth bass population has the potential to alter the population dynamics at Waugoshance Point.

The interaction of ecosystem and regulation changes could be extremely important for smallmouth bass. For example, use of round goby as a prey item increases young-of-year growth rates in smallmouth bass, which may result in greater survival and earlier maturity

(Wootton 1990; Stearns, 1992; Steinhart et al., 2004a). However, the potential positive effects of round goby as a food source may be outweighed by their impacts as an egg predator on nest success and recruitment (Steinhart, 2004; Steinhart et al., 2004a, b).Additionally, catch-and-release angling affects smallmouth bass populations due to the physiological response of individuals. Immediate physiological responses, such as decreased physical activity after release of smallmouth bass, may decrease fitness as low physical activity affects spawning behavior and nest guarding (Cooke et al., 2002). Increased minimum size limits may result in greater numbers and biomass of smallmouth bass, especially in the portion of the population below the minimum size (Newman and Hoff, 2000). The combination of these ecosystem and management changes may result in more and larger smallmouth bass due to increased growth rates, greater survival, earlier maturity, and greater biomass.

Given the potential impacts of ecosystem and management changes and the importance of the Waugoshance Point smallmouth bass fishery, an assessment of the smallmouth bass population would provide valuable information about the past, present, and future of the fishery. The objective of this study was to determine if population characteristics of the smallmouth bass at Waugoshance Point in the recent (2009-2012) time period are different than the historical (1953-1955) time period. Specifically, do the smallmouth bass at Waugoshance Point exhibit improved length-at-age, condition factor, growth, and length frequencies in comparison to the historical population? In addition, does population abundance differ between the recent and historical time periods?

Methods

Study Site

Sampling was conducted in Lake Michigan at multiple sites near Waugoshance Point, Michigan. Waugoshance Point is located in the northern lower peninsula of Michigan within Wilderness State Park and extends into Lake Michigan approximately 5 kilometers (km) (Figure 1). The Beaver Archipelago is located roughly 27 km to the west of Waugoshance Point. There was limited access to Waugoshance Point until 1947, when the road to the point was improved and anglers learned of the smallmouth bass fishery (Latta, 1963). A historical study of the smallmouth bass at Waugoshance Point from 1953-1955 was prompted by angler interest in smallmouth bass fishing and concern that the population was declining (Latta, 1963).
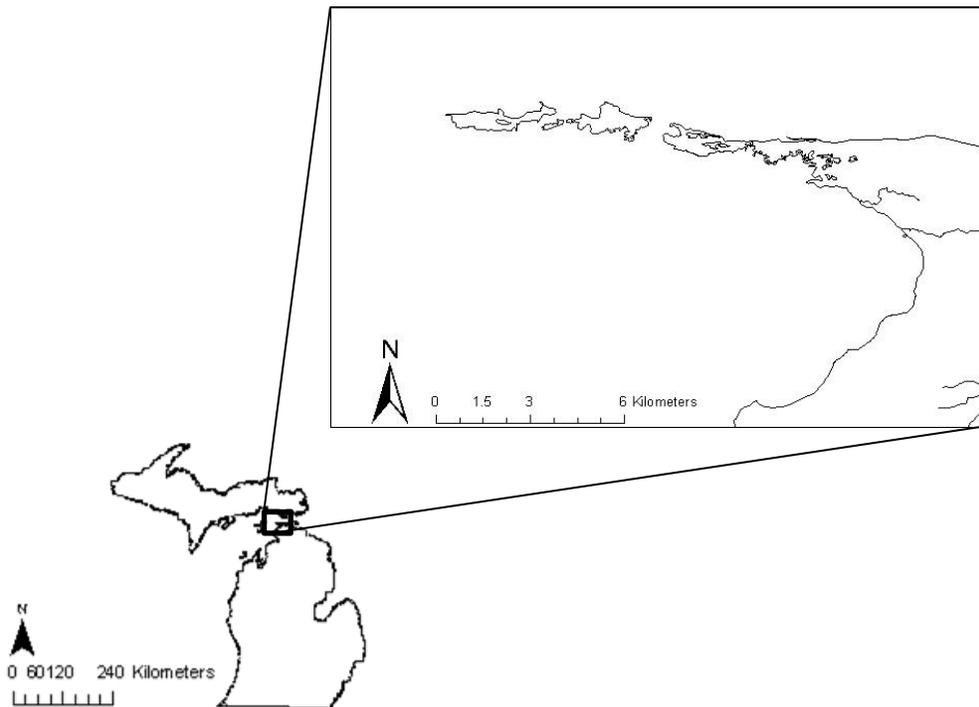
Figure 1. The sampling area, Waugoshance Point, located within Wilderness State Park, northern Lake Michigan.

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Field Sampling

Trap nets (1.5 meter (m) wide x 2.5 m long x 0.9 m depth with 2 cm mesh) were used to sample adult smallmouth bass in 2009-2012. Depending on water depth, a 20 m or 40 m lead was set towards shore. Six to seven trap nets were set around the southern side of Waugoshance Point (Figure 2), and each fished for 24 hours on June 16-19 of 2009, June 22-25 of 2010, June 14-17 of 2011, and May 21-25 and July 17-20 of 2012. Two to three modified fyke nets (0.6 m x 0.9 m with 0.6 m diameter hoops and 0.6 cm mesh) were used to sample young-of-year (YOY) and juvenile smallmouth bass for 4-6 days in June 2010 and July 2012; each net fished for 24 hours.

Total length (mm) and weight (nearest 10 g) were recorded for each adult smallmouth bass captured. All smallmouth bass over 250 mm were tagged using individually numbered monel jaw tags in the upper mandible. Scales were removed from all smallmouth bass (except YOY) below the lateral line distal to the pectoral fin when it was pressed against the body (Everhart, 1950). The first two to three anal spines were also clipped as close to the body as possible. Fin clips served as a secondary mark if jaw tags were lost or a primary mark if smallmouth bass were too small to receive a jaw tag.
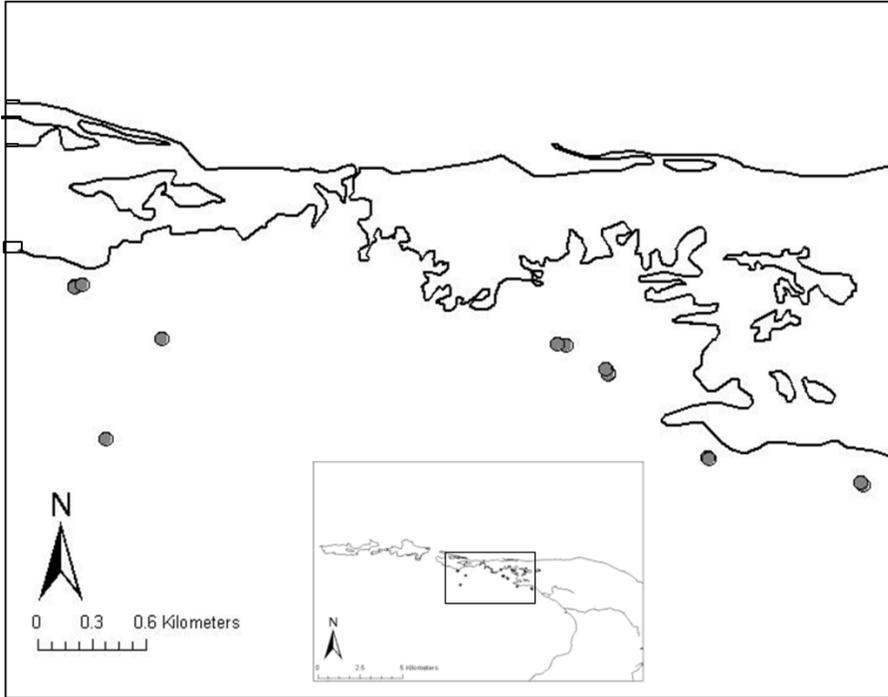
Figure 2. The sampling sites (circles) for trap nets at Waugoshance Point, Wilderness State Park, northern Lake Michigan.

Preparation and Aging of Scales and Anal Spines

Scales collected from each smallmouth bass were used for aging. Scales were pressed between two acetate slides using a scale press. The scale impressions were imaged using a Nikon SMZ800 microscope and Image-Pro Plus 5.1 software. At least three scales per individual were pressed and imaged. Annuli on scales were marked, and the distance from the center measured using the Image-Pro Plus 5.1 software. Scales were aged by counting where annuli "cut over" at each annulus (Latta, 1963; Kaemingk, 2008). Scales were aged by two readers, and only scales with agreed upon ages were used. If agreement was less than 75% for any year, a third reader was used.

Historical Data

In addition to the published report from Latta (1963), unpublished data was also accessed and used to recalculate certain parameters (W. C. Latta, unpublished data; Michigan DNR file data). Catch-per-unit effort, length-at-age, length frequencies, and age frequencies could be recalculated for comparison with the recent time period. The length-weight equation, condition factor, and population size could not be recalculated, but the estimates from the published report were used for comparison. Species composition of bycatch and relative weights could not recalculated and were not estimated in the historical study, so comparisons to the recent time period were not possible.

Program MARK Models and Population Estimates

Population estimates were calculated in Program Mark (version 6.1) using the Robust Design model (Kendall and Nichols, 1995; Kendall et al., 1997). The robust design uses primary and secondary sampling periods, in which primary periods are intervals between sampling periods where births and deaths may occur while secondary periods are a shorter interval within the sampling period. The population is considered closed during the shorter secondary periods, which is when the population estimates were made. Since trapping locations are not in isolated bays and movement between sites is likely, the population estimates were based on data compiled from all trapping sites within a sampling period. The population estimate was only for smallmouth bass large enough to be tagged (>250 mm) (Kaemingk 2008), similar to the historical study (Latta 1963).

The robust design also estimates apparent survival (S), recapture probability (c), capture probability (p), temporary immigration (γ'), and temporary emigration (γ''). Apparent survival is

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the probability that a member of the population in the first trapping session (i) survives and is available for capture in the next trapping session ($i+1$). Capture probability, or the apparent encounter probability, is the probability that an individual survives from one time period to the next, remains in the study area, is available for capture and is encountered alive. The recapture probability is the probability that an individual will be encountered alive, survives to the next trapping session, and is encountered alive for a second time. Temporary immigration is the probability of an individual being off the study area and unavailable for capture during a primary trapping session (i), given that it was not present on the study area during the previous primary trapping session ($i-1$) and has survived to the current trapping session (i). Temporary emigration is the probability of being off the study area and unavailable for capture during the current trapping session given that the individual was present during the previous primary session and has survived to the current trapping session (Kendall et al., 1995; Kendall et al., 1997).

Random, Markovian, and no emigration types of temporary emigration were analyzed. In random emigration models, the probability of an individual moving between being available or unavailable between primary trapping sessions is independent of the previous state (Kendall et al., 1997). When there is random emigration, $\gamma' = \gamma''$, and the probability of the individual leaving equals the probability of the individual staying in the study area. In Markovian models, the probability of an individual moving between being available and unavailable between primary trapping sessions is conditional on the state at time $i-1$. In other words, the individual will "remember" that it is off the study area in the Markovian model (Kendall et al., 1997). In the Markovian model, $\gamma_k' = \gamma_{k-1}'$ and $\gamma_k'' = \gamma_{k-1}''$ so that γ' and γ'' are equal to an earlier period when

k = time period. The no emigration model is the null model where all γ' parameters are set to

zero and no individuals may leave or stay away from the study area. Estimates for all parameters

were made for June 2009-2011 and May 2012. The data for July 2012 was excluded from the

Program MARK analysis because there is greater movement of smallmouth bass in Lake

Michigan at this time than in late May and June (Kaemingk et al., 2011b).

A Schnabel population estimate was also calculated for smallmouth bass at Waugoshance

Point. Because Latta (1963) performed a Lincoln-Peterson estimate, a third population estimate

was calculated using this method for direct comparison. In addition to apparent survival,

estimates of survival and mortality were calculated from catch curve data using the Chapman-

Robson model (Chapman and Robson, 1960; Robson and Chapman, 1961).

Data Analyses

Catch-per-unit-effort (CPUE) was calculated as:

$$\text{CPUE} = \frac{\text{Number of smallmouth bass captured}}{\text{Unit effort}} \qquad \text{(Equation 1)}$$

for trap nets in 2009-2012.The same method was used to calculate fyke net CPUE of smallmouth

bass and the CPUE for all species combined in fyke nets was also calculated. One way analyses

of variance (ANOVA) tests were used to compare trap net CPUE among years of the recent time

period (R Development Core Team, 2011).Trap net CPUE from the recent time period was

compared to historical CPUE at Waugoshance Point using a two-sample t-test(R Development

Core Team, 2011). July 2012 was excluded from the ANOVA and two sample t-test analysis

due to differences in temperature and the fact that all other sampling occurred in late May to

mid-June. One unit effort for all gear types was one net night (24 hours). The species

composition from trap nets was also calculated for all bycatch or non-target species.

Mean length-at-age was calculated for each age group for June (2009-2011), May (2012),

and July (2012) sampling periods. Calculating length-at-age for each sampling period in 2009-

2012 allowed for comparisons between the recent sampling years using pairwise comparisons

from a repeated measures ANOVA (RMANOVA). The RMANOVA was also used to determine

if length-at-age differed by year(R Development Core Team, 2011). A paired t-test was used to

determine if there was a significant difference between the historical and recent time periods(R

Development Core Team, 2011). Length frequency distributions were calculated for comparison

with the historical time period and between individual years during the recent time period using a

Kolmorgorov-Smirnoff test(R Development Core Team, 2011).

The length-weight relationship for smallmouth bass greater than 200 mm was calculated

using:

$$\log W_s = \log a + b(\log L) \qquad \text{(Equation 2)}$$

Where a and b are derived, L is total length (mm), and W_s is the length-specific standard weight

(Murphy et al., 1990; Murphy et al., 1991). Both a and b were determined using linear regression

for smallmouth bass greater than 200 mm. Because the historical length-weight equation was

calculated using standard length, the standard length to total length conversion values from the

historical time period were used to convert total length of smallmouth bass from the current

study to standard length values (Latta 1963). Weight data used for estimating the historical time

period length-weight equation was not available, so the equations were compared qualitatively.

The condition factor K was calculated for direct comparison with the historical time period using

converted standard length values because K in the historical time period was calculated using standard length (Latta 1963). Condition factor was calculated for 25.4 mm increments (1 inch), following the methods of the historic study. The condition factor equation used was:

$$K = (W/L^3) \times 10^5$$ (Equation 3)

Where W is the weight of the individual and L is the standard length (mm). The relative weight (W_r) was calculated using:

$$W_r = (W/W_s) \times 100$$ (Equation 4)

W_s is the standard weight, and W is the weight (g) of individual fish (Wege and Anderson, 1978; Murphy et al., 1991). W_r was the primary measure of condition for this study since the condition factor K does not allow comparison within the species if fish are of disparate lengths (Murphy et al., 1991).

The growth rate for the Waugoshance Point population was estimated using the Fraser-Lee method of back-calculation in FishBC 2.0(Doll and Lauer, 2007, with the formula:

$$L_i = \frac{L_c - a}{S_c} S_i + a$$ (Equation 5)

where L_c is the length of the fish captured, S_c is the radius of the age structure, S_i is the radius of the hard part at increment i, and L_i is the back-calculated length of the individual fish when increment i was formed (Devries and Frie, 1996). The formula

$$L_i = \frac{L_c - a}{S_c}$$ (Equation 6)

is the estimate of the slope of a regression line to estimate L_i, and a is the intercept of the regression line (Devries and Frie, 1996). The regression line has two points, $(0, a)$ and (S_c, L_c), and the slope was calculated from the line connecting these two points. The standard intercept,

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a, of 14 mm used by Latta (1963) in historical time period calculations was also used instead of the intercept of 35 mm (Carlander, 1982; Willis et al., 1990).Since smallmouth bass were collected in the spring, the outside edge was tagged as an annuli, but only growth up to the last visible annulus was included in growth estimation.

Growth increments were calculated to allow for a direct comparison with the historical time period (Latta 1963). For growth increments, the average total length at the end of each year of life was calculated for each age-group, and age groups were arranged by year of capture and year class (Latta, 1963); growth increments were calculated by subtracting the average length of a year of life from the average length of the next year (Latta, 1963). For example, the total length for Age 1 was subtracted from that of Age 2 to estimate the average growth increment from Age 1 to Age 2. Wilcoxon-Signed-Rank tests were used to evaluate differences between time periods for each age group, depending on if growth increments were normally distributed or not.

The von Bertalanffy growth models were used to evaluate differences in growth between the recent and historical time periods. The models were generated using

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) + \varepsilon \qquad \text{(Equation 7)}$$

where L_t is the total length (mm) at age t, L_∞ is the asymptotic maximum length (mm), K is the growth coefficient, t_0 is the hypothetical age at which length equals zero, and ε is the residual error. The age-at-length zero, or t_0, was set equal to zero for both models so that more realistic parameter estimates would be produced (Beauchamp et al. 2002).The models were generated using subsamples of length-at-age data (25 individuals per 25 mm increment) to prevent an effect of population size structure on parameter estimates. To initially determine if growth differed

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between time periods, data from both time periods was compiled and a model was generated, resulting in a model with no time factor. A model with the data separated into two time periods was then generated. The model with no time factor and the time factor model were compared using an ANOVA to determine which model explained more variation in the data; more variation explained by the time factor model would indicate a difference in growth between the two time periods. The confidence intervals, calculated by bootstrapping, of L_∞ and K were compared to determine if parameter estimates differed between the two time periods. All growth models and related statistics were completed using R (R Core Development Team, 2011).

Results

The number of smallmouth bass captured in trap nets from 2009 – 2012 ranged from 271 individuals in 2009 to 1121 individuals in May 2012, with an average of 466 smallmouth bass tagged each year. In all sampling periods expect July 2012, less than 5% of the smallmouth bass captured were recaptures from a previous year. In July 2012, 35 (12.6%) of the smallmouth bass were recaptured from a previous year. Within week recaptures made up 1.4 – 10.1% of the total smallmouth bass catch. Recaptures from previous years and within the week combined comprised less than 15% of the smallmouth bass captured in all sampling events at Waugoshance Point.

Temperatures in July 2012 were significantly different than temperatures in 2010-May 2012, so July 2012 was excluded from catch-per-unit-effort analyses (F = 133, df = 3, $P < 0.001$). Catch-per-unit-effort (CPUE) of smallmouth bass caught in trap nets in 2009-12 was greater in the recent time period relative to the historical time period ($t = -2.30$, $P = 0.05$; Figure 3). CPUE also differed among individual years of the recent time period (ANOVA; F = 3.80; df = 3; $P =$

0.03; Figure 4); the lowest CPUE occurred in 2009, while the highest CPUE was documented in 2012.

The species composition of the bycatch from trap nets at Waugoshance Point could not be compared to historic time period. The bycatch consisted of common white sucker (*Catostomus commersonii*; 43.2%), rock bass (*Ambloplites rupestris*; 25.5%), bluegill (*Lepomis macrochirus*; 14.4%), two species of turtles (3.2%), northern pike (*Esox lucius*; 2.5%), freshwater drum (*Aplodinotus grunniens*, 2.1%), walleye (1.7%), channel catfish (*Ictalurus punctatus*; 1.0%), and 10 other fish species (6.4%).

Catch-per-unit-effort

Mean CPUE for all species in fyke nets in 2010 and 2012 was 25.75 ($\pm$10.20 SE) and 9.65 ($\pm$ 3.6 SE) individuals per fyke net night. The fyke net catch in 2010 was comprised of round goby (88.24%), rock bass (4.2 %), crayfish (*Orconectes* spp.; 6.72 %), and johnny darter (0.84%). Young-of-year smallmouth bass comprised the highest percentage of the catch in 2012 (34.7%; CPUE=3.91(($\pm$ 1.68 SE)) followed by round goby (29.6%), *Orconectes* spp. (26.5%), rock bass (9.2 %).
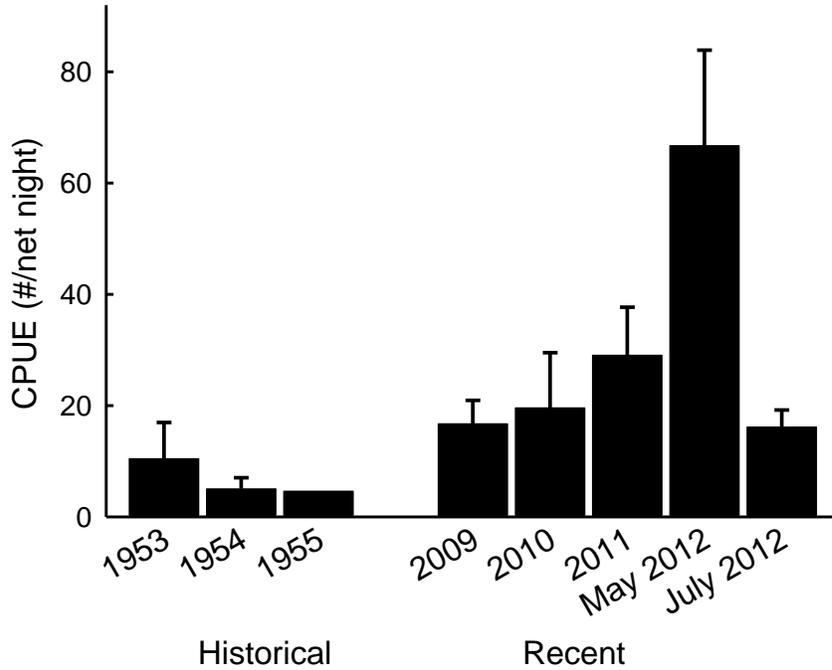
Figure 3. Catch-per-unit-effort (smallmouth bass caught per net night; CPUE + SE) for smallmouth bass from 1953-1955 (Latta, 1963) and 2009-2012 at Waugoshance Point, northern Lake Michigan. July 2012 is shown, but was excluded from the statistical analysis.
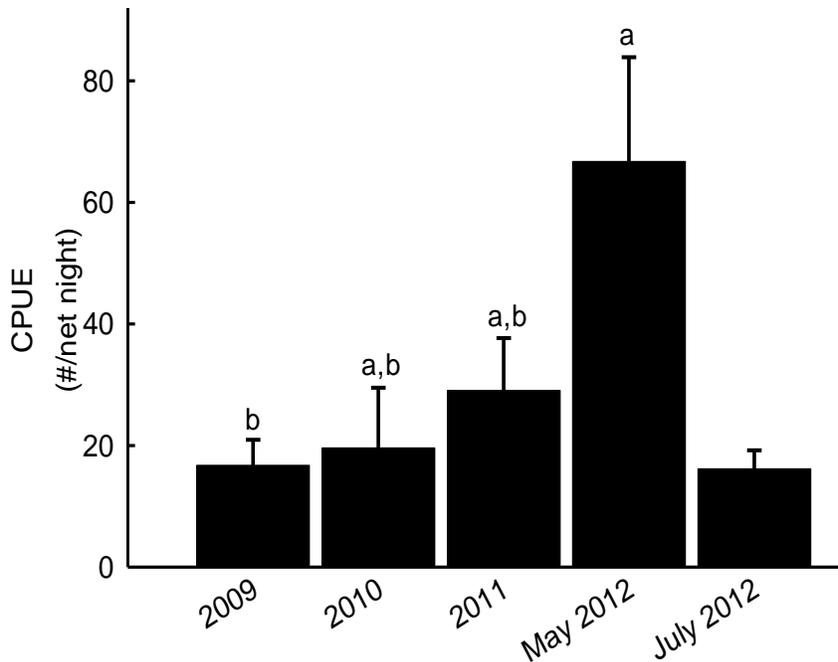
Figure 4. Catch-per-unit-effort (CPUE + SE) for smallmouth bass from 2009-2012 at Waugoshance Point, northern Lake Michigan. Similar letters indicate no significant difference. July 2012 was excluded from the statistical analysis.

Program Mark, Population Estimates, and Survival Estimates

Model weights from Program MARK did not reveal one overall best model, so model averaging was used for parameter estimates (Burnham and Anderson, 2004). Population size varied over time in all of the models receiving weight, but capture (p) and recapture (c) probability were held constant (Table 1). No particular type of emigration model was best for the smallmouth bass population; of the five models receiving weight, two were Markovian emigration models and two were random emigration models (Table 1). Estimates of population size from model averaging were lower than those from the historical time period (Latta, 1963), with the largest estimated number of smallmouth bass in May 2012 and lowest in 2010 (Table 2). The estimated population sizes in 1954 and 1955 were 6,007 and 4,920 smallmouth bass, respectively, based only on trap net recoveries, while the estimates on the basis of angler recoveries were 5,264 (1954) and 4,184 (1955) smallmouth bass (Latta, 1963). Population estimates using the same method were 7,100 to 33,100 smallmouth bass in 2009-2012. Capture probability estimates were greater than those found in the Beaver Archipelago in 2006-2008, while recapture probability estimates were lower (Kaemingk, 2008). Apparent survival (S) varied in 2009-2011 and was lowest between 2010 and 2011, consistent with the low population estimate in 2010. Estimates of survival from the Chapman-Robson model from 2009-2012 catch data (55.88 ± 1.68) were similar to apparent survival estimates in 2010-2011, but a direct comparison cannot be made since apparent survival also incorporates the probability of remaining in the sampling area. Temporary emigration and immigration were high for all time periods, but both were lowest between 2010 and 2011.

Table 1. All models created in Program MARK for the smallmouth bass population at Waugoshance Point using Akaike's information critieria. Akaike's information criteria includes the Akaike information criterion that is corrected for small-sample bias (AIC_c), the differences in AIC_c (Δ_i), the weight of each model (w_i), and the number of parameters (K). Parameters with "t" change over time in the model. Parameters with "·"are held constant in the model. Models named "Random" are models in which temporary emigration is random, or $\gamma' = \gamma''$. Models named "Markovian" are models in which individuals "remember" they are off the study area, or when $\gamma_k' = \gamma_{k-1}'$ and $\gamma_k'' = \gamma_{k-1}''$. Models named "No Movement" have γ' and γ'' set to zero, so individuals cannot leave or enter the study.

Model	AICc	Δ_i	w_i	K
$\gamma'. \gamma'.S_tp. c. N_t$	-16879.1	0	0.384	9
Random $S_tp. c.N_t$	-16878.6	0.468	0.305	10
Markovian $S. p.c.N_t$	-16877.2	1.883	0.150	10
Markovian $S_t p. c.N_t$	-16876.8	2.251	0.124	11
Random $S. p. c.N_t$	-16874.5	4.584	0.039	10
No Movement $S_tp.c.N_t$	-16785.3	93.764	0	9
Random $S_tp_t = c_tN_t$	-16680.5	198.562	0	12
Markovian $S_tp_t = c_tN_t$	-16678.9	200.1943	0	13
Random $S.p_t = c_tN_t$	-16676.4	202.6775	0	12
Markovian $S.p_{t = c_t}N_t$	-16669.1	209.9193	0	13
No Movement S_tp_t	-16658.5	220.5433	0	11

Table 2. Parameter estimates from model averaging for the smallmouth bass population of Waugoshance Point, northern Lake Michigan including standard error (SE), 95% upper and lower confidence intervals for apparent survival (S), temporary emigration (γ''), temporary immigration (γ'), capture probability (p), recapture probability (c), and population size (N).

Parameter and Period	Estimate	SE	Lower 95%	Upper 95%
Apparent survival (S) 2009-2010	0.988	0.007	0.001	0.999
Apparent survival (S) 2010-2011	0.531	0.143	0.119	0.904
Apparent survival (S) 2011-2012	0.884	0.109	0.205	0.995
Temporary emigration (γ'') 2009-2010	0.954	0.014	0.913	0.975
Temporary emigration (γ'') 2010-2011	0.939	0.023	0.821	0.981
Temporary emigration (γ'') 2011-2012	0.950	0.008	0.922	0.969
Temporary immigration (γ') 2010-2011	0.938	0.027	0.808	0.982
Temporary immigration (γ') 2011-2012	0.956	0.009	0.900	0.982
Capture probability (p) 2009	0.338	0.016	0.307	0.369
Capture probability (p) 2010	0.338	0.016	0.307	0.369
Capture probability (p) 2011	0.338	0.016	0.307	0.369
Capture probability (p) 2012	0.338	0.016	0.307	0.369
Recapture probability (c) 2009	0.066	0.004	0.058	0.075
Recapture probability (c) 2010	0.066	0.004	0.058	0.075
Recapture probability (c) 2011	0.066	0.004	0.058	0.075
Recapture probability (c) 2012	0.066	0.004	0.058	0.075
Population size (N) 2009	373	17	341	406
Population size (N) 2010	300	11	279	322
Population size (N) 2011	712	21	671	753
Population size (N) 2012	1542	52	1440	1644

Population estimates calculated using the Schnabel method were over twice the estimated number of smallmouth bass from Program MARK (Figure 5). The smallest population size was in 2010 and the highest was in May 2012, based on both the Schnabel and Program MARK estimates. The Lincoln-Peterson population estimates (Figure 6; 7,100-33,100 individuals) were higher than both Schnabel and Program MARK estimates (Figure 5); the Lincoln-Peterson estimates greatly exceeded estimates from the historical time period (Latta 1963).
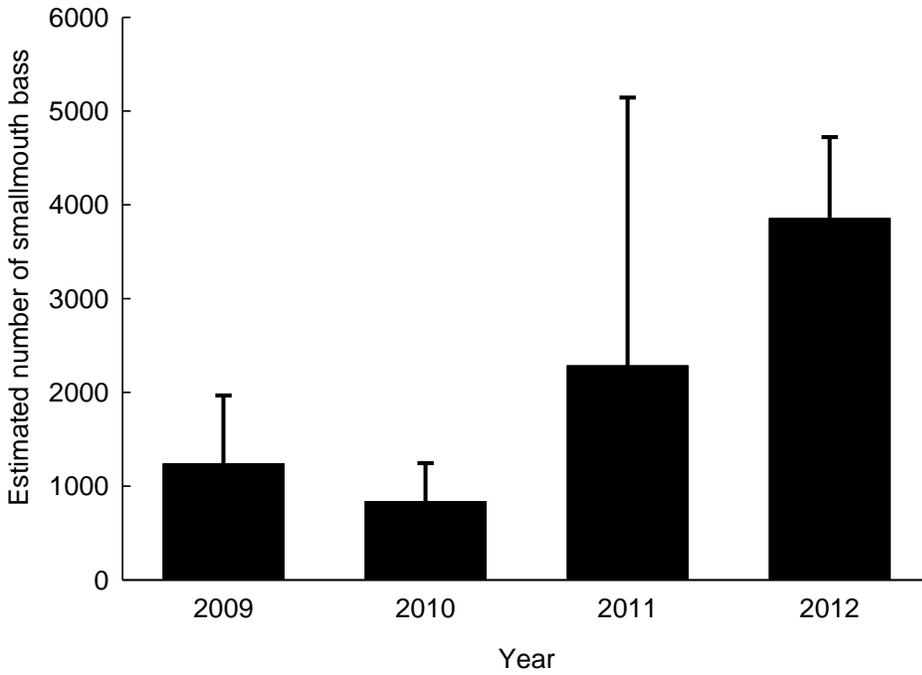
Figure 5. Population estimates calculated using the Schnabel method for the smallmouth bass population at Waugoshance Point, northern Lake Michigan, with 95% upper confidence intervals.

Figure 6. Population estimates calculated using the Lincoln-Peterson method for the smallmouth bass population at Waugoshance Point, northern Lake Michigan, with 95% upper confidence intervals in the historical (Latta 1963) and recent time period.

Length-at-age and Length Frequencies

Mean length-at-age was higher in the recent time period relative to the historical time period for ages 3-7(df = 4; P = 0.002; Figure 7). In addition, the length-at-age for ages 3-6differed among all years (F= 3.50; df= 7; P = 0.02).
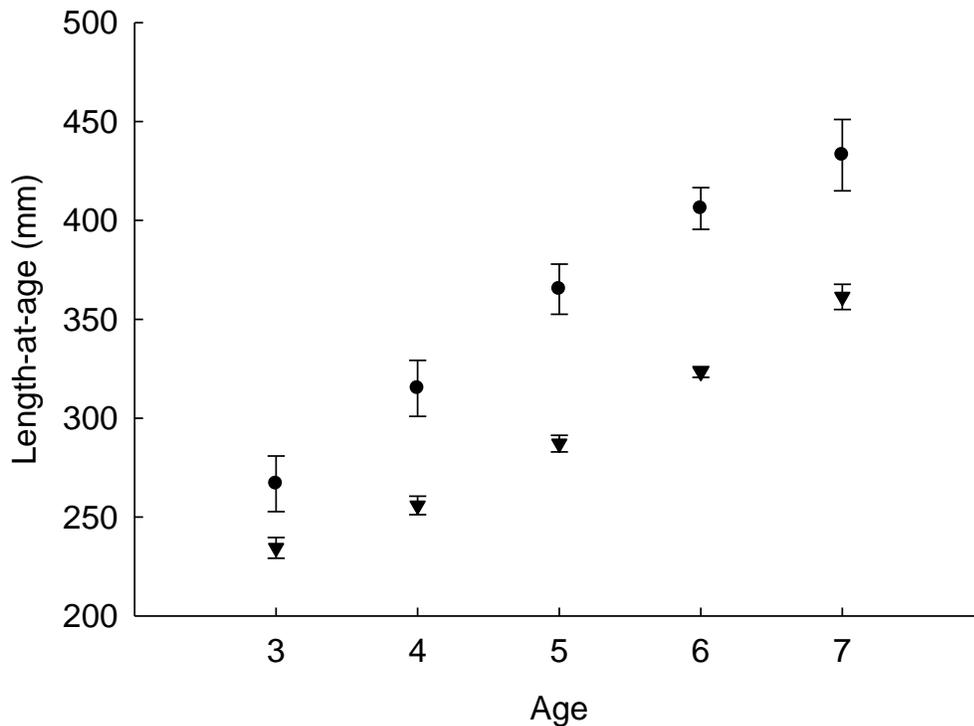
Figure 7. Mean age-at-length (mm ± SE) for age 3-7 smallmouth bass for at Waugoshance Point, northern Lake Michigan, for historical (triangles, 1953-1955) and recent (circles, 2009-2012) time periods.

Length frequency distributions shifted from smaller to larger smallmouth bass from the historical to the recent time period (D = 0.372; P <0.001), with higher proportions of individuals from 400-500 mm in the recent time period (Figure 8). Length frequency distributions for individual years within the recent time period differed from each other, with higher proportions

of 400-500 mm smallmouth bass in 2009 – May 2012 than in July 2012 (P <0.001). July 2012

also had higher proportions of 100-200 mm smallmouth bass than any other year in the recent

time period.
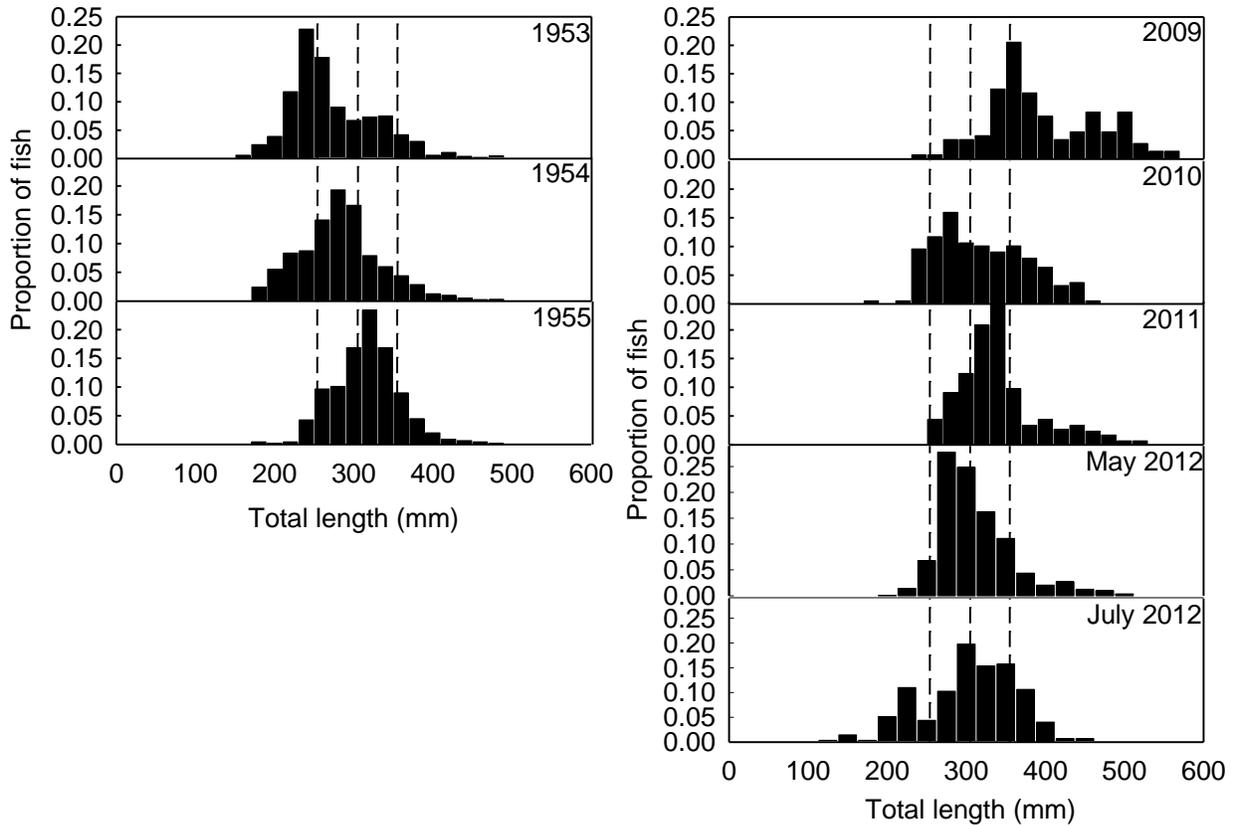
Figure 8. Total length (mm) frequency of smallmouth bass caught using trap nets at
Waugoshance Point, northern Lake Michigan, from the historical (1953-1955; Latta 1963) and
recent (2009-2012) time periods. Dashed lines indicate previous minimum size limits (254 mm
<1976, 305 mm – 1976-1996, 355 mm > 1996) for smallmouth bass.

Age Frequency

　　　　Age frequency distributions also differed between the recent and historical time periods

(Kolmorgorov-Smirnoff: P<0.04). The historical time period age frequencies indicated one

strong year class in the smallmouth bass population from 1953-1955 while other year classes

comprised relatively small proportions of the population (Figure 9; Latta, 1963). In contrast, the

age frequencies during the recent time period had relatively similar proportions of individuals in

each year class, and no particularly strong year classes were evident (Figure 9).
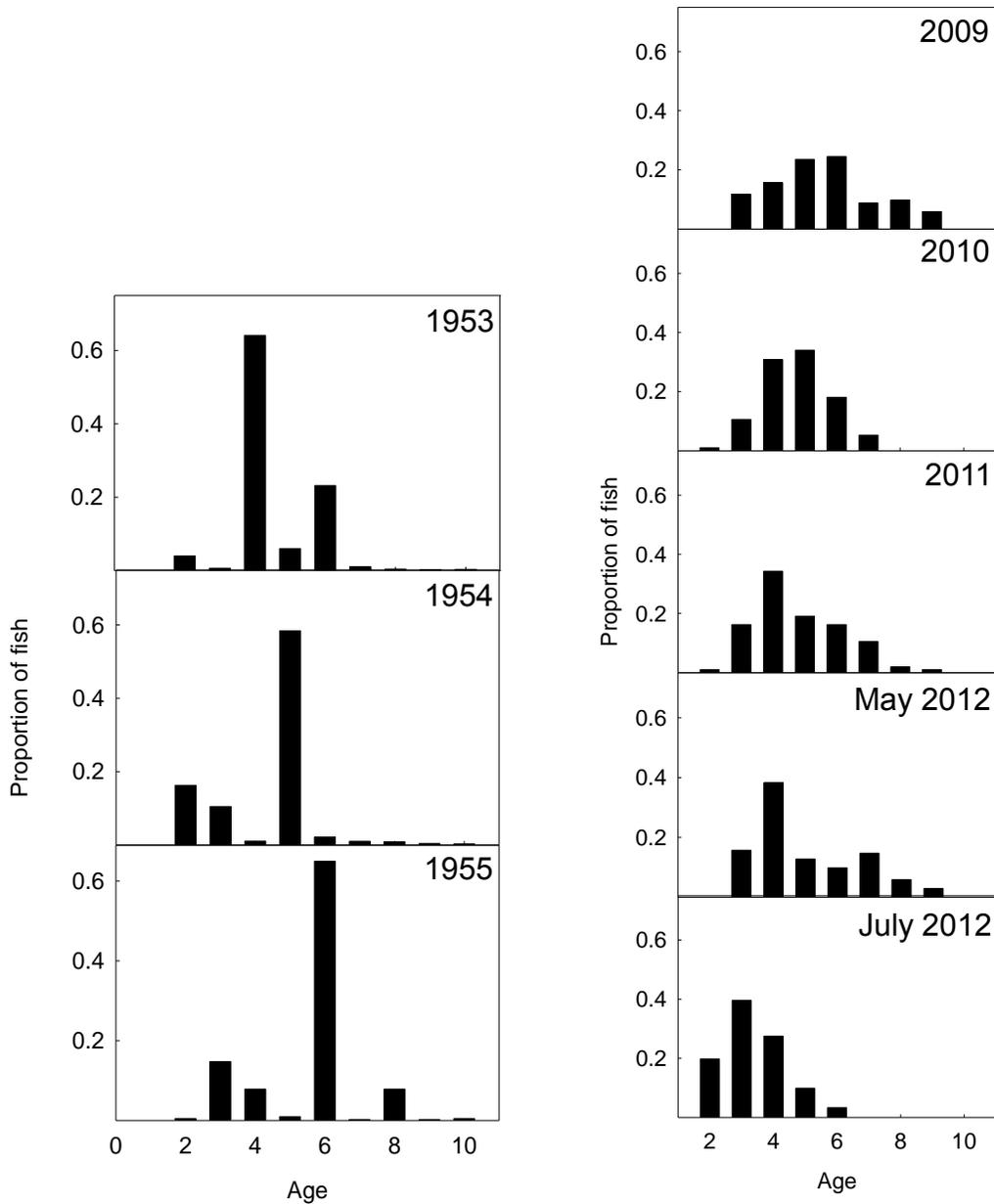
Figure 9. Smallmouth bass age frequency histograms at Waugoshance Point, northern Lake Michigan, during the historical (1953-1955) and recent (2009-2012) time period.

Length-Weight Relationship and Condition

The total lengths of smallmouth bass from the recent time period were converted to standard lengths using conversion factors developed by Latta (1963); log W_s = -3.76292 + 2.7249 log (SL). For smaller size classes, the lines appear to have similar slopes. The lines converge in the larger side classes and intersect at just below 400mm (Figure 10).
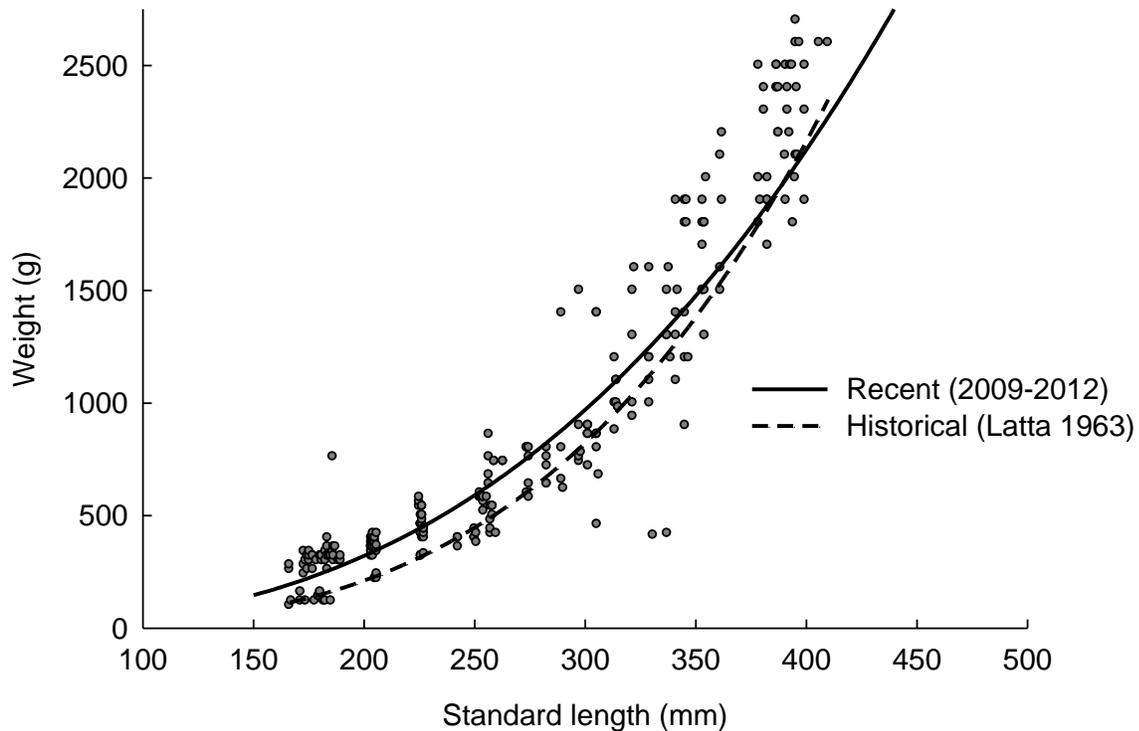
Figure 10. Smallmouth bass standard length and weight (circles) from the recent smallmouth bass population at Waugoshance Point, northern Lake Michigan, with length-weight relationship curves of the historical (Latta, 1963) and recent time periods.

The total length-weight relationship calculated during the recent time period was log W = -4.16106 + 2.78068 log (TL). Using this equation, calculated relative weights differed by 50-mm length increment, and all values were near or above 100 (t = 5.85; *P* <0.00; Figure 11). The lowest W_r was for the 300-349 and 350-399 mm sizes with values of 97.5 and 98.5, respectively,

while the highest W_r was the 200-249 size group with a value of 117.3. Condition factor (K) was

higher in the recent time period relative to the historical time period ($P = 0.0007$; Figure 12).
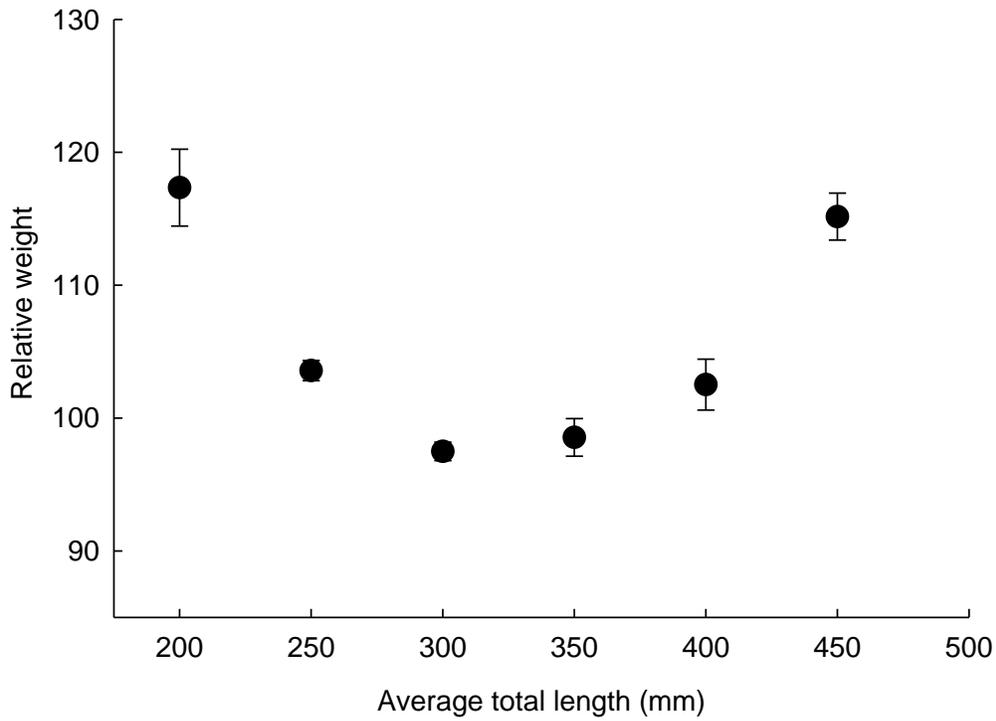
Figure 11. Relative weights (±SE) for smallmouth bass at Waugoshance Point, northern Lake Michigan, during the recent time period (2009-2012).
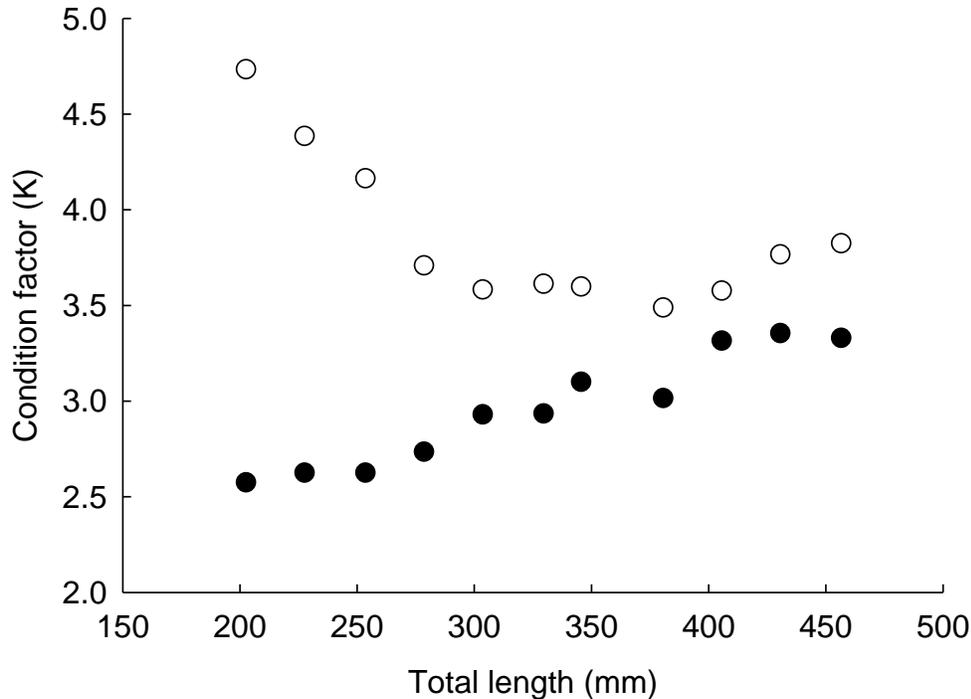
Figure 12. Condition factor (K) for smallmouth bass at Waugoshance Point, northern Lake Michigan by length. Solid circles represent the historical time period (1953-1955) and open circles represent the recent time period (2009-2012).

Growth

Annual growth increments, calculated for ages 1-7, differed between the historical and recent time periods for age 1 ($P = 0.0002$), age 2 ($P = 0.0001$), and age 3 ($P = 0.001$) smallmouth bass (Appendix A; Figure 12). Growth increments for age 4 ($P = 0.10$), age 5, ($P = 0.20$), age 6 ($P = 0.09$), and age 7 ($P = 0.56$) smallmouth bass did not differ between time periods.

For smallmouth bass ages 4-7, growth increments in the historical time period were similar with almost identical growth in the early 1950's (Figure 13). In contrast, smallmouth bass ages 3-7 in the recent time period had more variation in growth between age groups (Figure 13). Growth increments increased for all ages in 2010and appear to decline into 2011. In 2008, growth increments declined slightly for ages 4, 6, and 7 (Figure 13).

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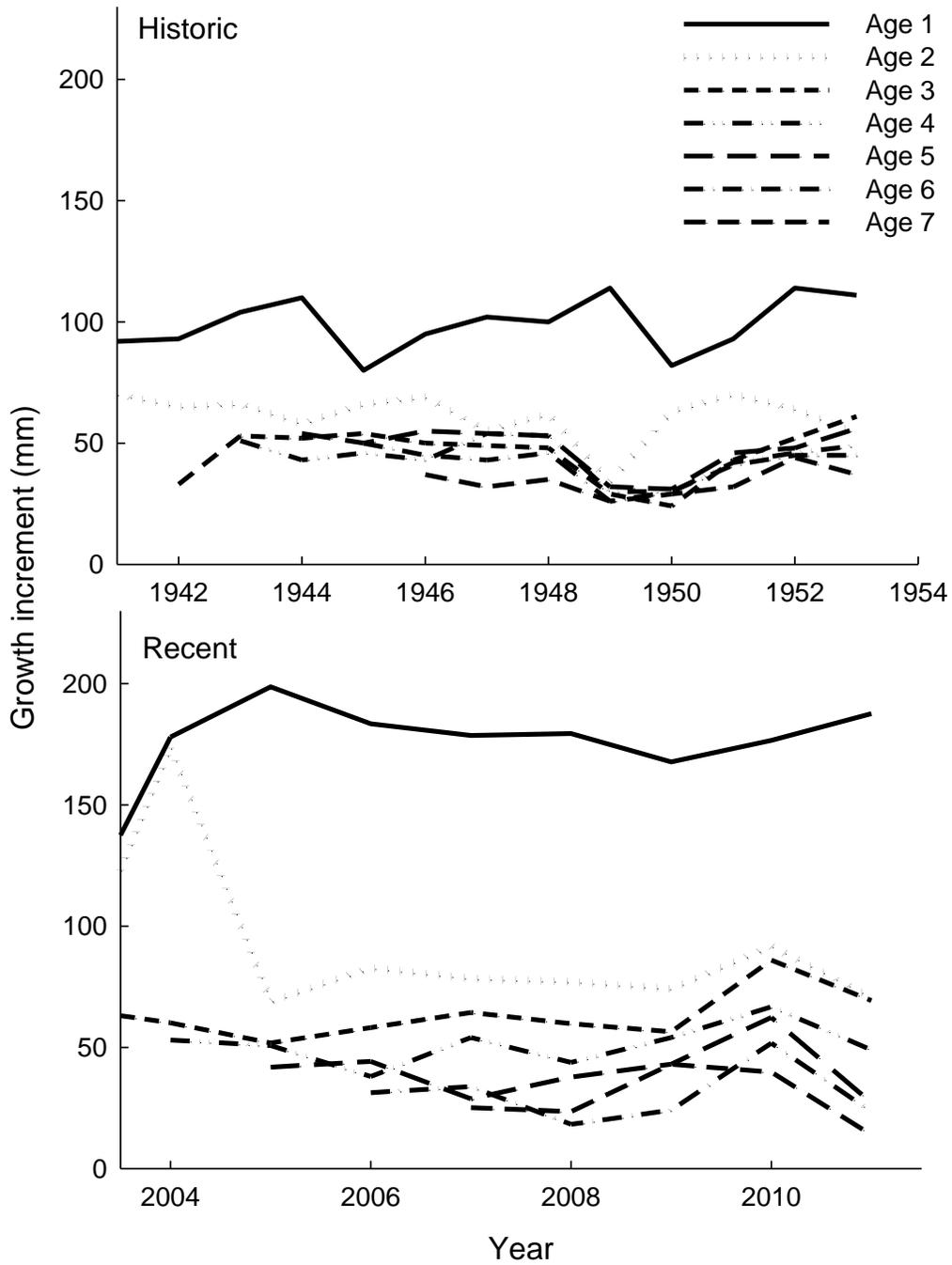
Figure 13. Growth increments (mm) by calendar year for smallmouth bass at Waugoshance Point, northern Lake Michigan, in the historical (top, Latta, 1963) and recent (bottom) time period.

The von Bertalanffy growth model generated with a time factor explained more variation in length-at-age data than the model without a time factor ($F = 147.67$, df = 1, $P < 0.001$), which supported separate growth models for the two time periods (Figure 14). Parameter estimates of L_∞ and K were not significantly different between time periods based on overlapping confidence intervals (Table 3), which contrasts with differences in growth increments.

Table 3. Von Bertalanffy growth model estimates for the asymptotic maximum length, L_∞, and the growth coefficient, K, for both time periods at Waugoshance Point, northern Lake Michigan when $t_0 = 0$ with 95% upper (UCI) and lower (LCI) confidence intervals.

Time period	L_∞	LCI	UCI	K	95% CI	UCI
Historical (1953-1955)	499.8	475.6	529.9	0.19	0.18	0.22
Recent (2009-2012)	565.4	526.6	620.7	0.21	0.18	0.24
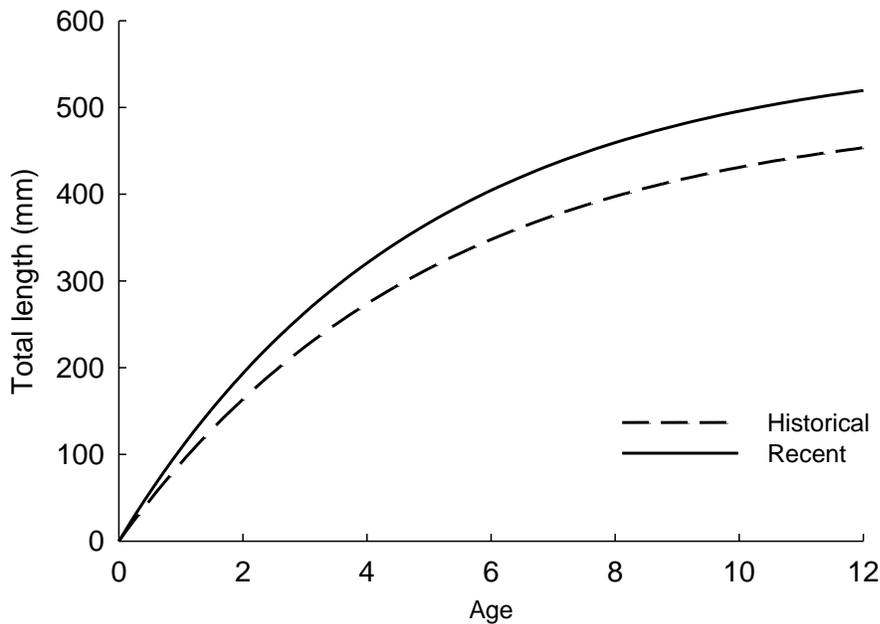
Figure 14. Von Bertalanffy growth models for the historical and recent time periods generated using length-at-age data from the current study and Latta (1963) at Waugoshance Point, northern Lake Michigan. Estimates of L_∞ and K between the two time periods did not differ.

Discussion

The smallmouth bass population at Waugoshance Point has increased and individual smallmouth bass are larger, have better condition, and grew faster in juvenile stages in recent years relative to the 1950's. The increased catch rates of smallmouth bass at Waugoshance Point and comparisons of Lincoln-Peterson population estimates between historical and recent time periods indicate a larger population size. Although the Lincoln-Peterson population estimates are likely overestimated and are not recommended for extended sampling periods (Pine et al., 2003), a relative increase of the smallmouth bass population has occurred. A similar increase in catch rates was documented in the nearby Beaver Archipelago smallmouth bass fishery (Kaemingk et al., 2012; T. Galarowicz, unpublished data). A change in bycatch species from primarily rock bass in addition to yellow perch, white sucker, and brown bullhead to bycatch dominated by common white sucker, with no brown bullhead or yellow perch in the recent time period, also indicates community changes (Latta, 1963). Similar shifts in the assemblage have been seen in the Beaver Archipelago fishery (Kaemingk, 2008), which in addition to increases in catch rates, suggest that broad ecosystem or regulation changes may be positively affecting this population.

Apparent survival was low in 2010-2011, which could have been due to multiple factors such as high natural mortality, angling mortality, and emigration from Waugoshance Point (Kaemingk, 2008). Waugoshance Point is a popular sport fishery, but angling mortality does not likely affect apparent survival as these estimates are not low across all years. Increased growth rates and high relative weights indicate that smallmouth bass at Waugoshance Point are not experiencing high natural mortality (Willis et al., 1991; Kaemingk, 2008). Increased abundances

and greater length-at-age in the recent time period are also indicative of a population with low natural mortality (Kaemingk, 2008). In addition, angler tag returns for smallmouth bass tagged at Waugoshance Point have revealed movement to the south (Charlevoix and Petoskey), as well as northeast to the Cheboygan River in Lake Huron (T. Galarowicz, unpublished data); suggesting emigration is the likely cause of low apparent survival in 2010-2011, while angling and natural mortality are low. Emigration in 2010 could be due to higher water temperatures observed in the summer of 2010. The movement of smallmouth bass also indicates that the smallmouth bass fisheries of Lake Michigan, and potentially Lake Huron, have some connectivity, which is an important consideration for management and monitoring efforts.

Shifts in length frequencies to a higher proportion of large (400-500 mm) smallmouth bass could result from regulation or ecosystem changes. Increases of the minimum size limit in other smallmouth bass populations have resulted in increased average length of individuals as well as increased biomass and population size (Hoff, 1995; Newman and Hoff, 2000). Changes in regulations for bluegill (*Lepomis macrochirus*) have also caused population responses, such as a decrease in the number of large individuals when there is no minimum length limit (Goede and Coble, 1981; Coble, 1988). While changes in the minimum size limit can affect the average lengths, length distribution, population size, and biomass of a population or fishery, fishing season changes can also influence smallmouth bass (Goede and Coble, 1981; Coble, 1988; Hoff, 1995; Newman and Hoff, 2000). Male smallmouth bass are vulnerable to angling pressure while guarding a nest and removal of the male from the nest can negatively impact guarding behavior (Cooke et al. 2002) and nest success (Steinhart, 2004; Steinhart et al., 2004a). Currently, smallmouth bass at Waugoshance Point do not appear to be negatively affected by angling

during spawning. However, if round goby numbers continue to increase, nest predation may become a more prevalent issue for smallmouth bass nest success. Since Waugoshance Point is a popular sport fishery in Lake Michigan, the impacts of management changes must be considered if continued use of this resource is desired. In addition, increased growth at a younger age due to predation on round goby may also contribute to increased length-at-age and a higher proportion of large smallmouth bass (Steinhart et al., 2004b).

The increase in age 1 growth increments for smallmouth bass may result from the availability of round goby as a prey source and their transition to piscivory may also be aided by this abundant prey source (Wootton 1990; Stearns, 1992; Steinhart et al., 2004a, b). Other vertebrates, such as the Lake Erie water snake (*Nerodia sipedon insularum*), have increased growth and attain larger body sizes when preying on round goby (King et al., 2006). Though growth differs for younger smallmouth bass, this may be obscured by similarities in older smallmouth bass growth in the von Bertalanffy parameter estimates (He and Stewart, 2002).

Smallmouth bass condition, both in terms of condition factor and relative weights, has increased since the 1950's, indicating that prey is readily available and environmental conditions are favorable (Porath and Peters, 1997; Blackwell et al., 2000). The increase in condition may have resulted in higher reproductive potential and recruitment, similar to other freshwater species (Willis, 1987; Neumann and Murphy, 1992; Neumann and Willis, 1995). A slight decrease in condition in the recent time period of the 300-350 mm size class, in comparison to other size classes, is within the typical size range at which smallmouth bass sexually mature, when energy reserves are likely invested in sexual maturation or reproduction instead of growth (Wiegmann et al., 1992).

The significant changes in the smallmouth bass population at Waugoshance Point highlight the importance of monitoring populations when ecosystem and management changes occur. Current ecosystem alterations may negatively affect many species, but smallmouth bass appear to be a resilient species in the Great Lakes. In addition, smallmouth bass are moving to the southern edge of the Upper Peninsula, Lake Huron, and south in Lake Michigan based on angler returns from both the Beaver Archipelago and Waugoshance Point.

Movement between the Beaver Archipelago and Waugoshance Point indicates that though these locations hold two separate fisheries with different management regimes, they may not be two separate populations. The possibility that Waugoshance Point and the Beaver Archipelago may be subpopulations of one larger metapopulation needs to be considered. Differences in connectivity, habitat quality, and demography can be dramatic within a metapopulation and it is possible that these differences exist between the two fisheries (Lipcius et al., 2008). Connectivity differences are apparent, given that only one-way dispersal has been observed. Smallmouth bass differ in abundance between the two locations, but the size structure and relative weights are similar, which does not indicate demographic differences (Kaemingk et al., 2012; T. Galarowicz, unpublished data). Habitat quality could also differ between the two sites. Though quality spawning habitat exists in the Beaver Archipelago, smallmouth bass appear to primarily spawn in only two bays around Garden Island (Kaemingk et al., 2011a). In contrast, Waugoshance Point may have more continuous quality spawning habitat, which may explain higher abundances during pre-spawn, and the retention of smallmouth bass from the Beaver Archipelago. Habitat continuity influences genetic mixing in Chinook salmon (*Oncorhynchus tshawytscha*), because females are more likely to move freely in search of

nesting sites than females in areas with patchy spawning habitat (Neville et al., 2006). Though

continuous and connected habitat can benefit genetics, more suitable habitat for smallmouth bass

would allow greater numbers of individuals to spawn at Waugoshance Point than in the Beaver

Archipelago (Isaak et al., 2007).

If the fisheries of the Beaver Archipelago and Waugoshance Point are connected and are

two separate fisheries of a metapopulation, this must be a consideration of fisheries management.

In one way dispersal, the Beaver Archipelago could be a source for the Waugoshance Point

fishery and these populations should be managed with this relationship in mind. Waugoshance

Point does not appear to be a sink habitat for smallmouth bass. However, it is possible that a

source-pseudosink relationship may exist in which Waugoshance Point is a viable fishery, but

appears to be a sink (i.e. pseudosink) due to the dispersal of individuals from the Beaver

Archipelago (Watkinson and Sutherland, 1995). The potential connectivity of other smallmouth

bass fisheries in the Great Lakes is also important to consider, as is the potential that other

species within the region could have connected fisheries. The structure of a population needs to

be defined in order for management to be effective, indicating these possibilities warrant further

investigation (Meffe, 1995).

Though information regarding the smallmouth bass population at Waugoshance Point

between the 1950's and the current time period is not available, this population assessment

provides information on the current status of the population as well as the possible impacts of the

ecosystem and management changes. Changes in the smallmouth bass population at

Waugoshance Point are likely a result of both ecosystem and management alterations. Although

the ability to link any population shifts over a 50 year period to a specific management or

ecosystem alteration is limited, this evaluation of the smallmouth bass population at Waugoshance Point provides managers with information on their current status. An understanding of these connections and how management and ecosystem changes in the Great Lakes have affected each fishery are important to managing smallmouth bass as a recreational resource.

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CHAPTER II

AGING PRECISION OF SMALLMOUTH BASS ANAL SPINES AND SCALES

Introduction

Precise and accurate age estimates are an important part of fisheries research, especially for understanding population dynamics. Age estimates are used to determine age structure, growth rates, age at maturity, mortality, and survival as well as other demographic parameters used to make management decisions and set regulations (Davis-Foust et al. 2009; Hoxmeier et al. 2001; Jackson et al. 2007). Errors in age estimates will influence these age-based parameters and can lead to mismanagement of a species (Campana 2001).

Hard structures such as otoliths (Campana et al. 1995), scales (Maceina and Sammons 2006), vertebrae (Maraldo and MacCrimmon 1979), fin rays (Ihde and Chittenden 2002), and spines (Isermann et al. 2003) can be used to age fish. Otoliths are a widely used structure for aging many species of fish over a broad range of ages (Campana 2001) and are typically considered more accurate and precise than other structures (Devries and Frie 1996; Maceina and Sammons 2006). Scales are also sufficient aging structures though not as precise or accurate as otoliths and can lead to age underestimation especially of fish over age 7 (Maraldo and MacCrimmon 1979; Maceina and Sammons 2006). Underestimation in age with scales likely results from the decreasing annual growth increments as fish age (Maraldo and MacCrimmon 1979). Otoliths also show variation of precision and accuracy between older and younger fish (Isermann et al. 2003). For example, whole otoliths may be used for younger walleye (*Sander vitreus*), while individuals over age 5 are typically aged with sectioned otoliths (Isermann et al. 2003). In largemouth bass (*Micropterus salmoides*), differences in length-at-age from otolith

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and scale ages can be seen as early as age 2 (Besler 1999). Ages from vertebrae, fin rays, and

dorsal spines have low levels of agreement with otolith and scale ages indicating they are

imprecise and inaccurate (Isermann et al. 2003; Maceina and Sammons 2006; Maraldo and

MacCrimmon 1979). However, collection of scales, fin rays, and anal spines is non-lethal, while

collection of otoliths and vertebrae involves sacrificing the fish. For some species or

populations, the sacrifice of fish for aging or other purposes is an accepted practice. In popular

recreational fisheries, sacrifice of fish for research is not always as feasible (Isermann et al.

2003). Removal of adult fish could be a problem in certain populations, but public scrutiny is

another reason managers avoid the use of lethal age structures (Hoxmeier et al. 2001). In these

situations, it is important to determine which non-lethal structure is best for age estimates.

Smallmouth bass (*Micropterus dolomieu*) are an important part of the recreational fishery

in northern Lake Michigan. Smallmouth bass popularity as a sport fish warrants the need for

evaluation of non-lethal aging structures. Sacrifice of fish in these smallmouth bass fisheries

could be avoided if an appropriate non-lethal aging structure was determined. Age estimates for

smallmouth bass are important for determining growth rates and length-at-age for individuals as

well as evaluating the population status as a whole. The objective of this study was to determine

the precision of two non-lethal aging structures, anal spines and scales, for smallmouth bass in

northern Lake Michigan. In addition, whether or not there is a certain age at which one structure

is better than the other will be investigated. Because known age smallmouth bass were

unavailable for this study, only precision, rather than accuracy, between aging structures could

be evaluated.

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Methods

Study Area

Collection of smallmouth bass anal spines and scales was conducted in Lake Michigan near Waugoshance Point. Waugoshance Point is located in the northern lower peninsula of Michigan within Wilderness State Park and extends into Lake Michigan about 5 kilometers (km) (Latta 1963). The age structures used in this study were collected in June 2009-2011 during annual sampling at multiple sites around Waugoshance Point.

Structure Collection

Scales were collected from midbody just above the lateral line, stored in scale envelopes, and dried (Devries and Frie 1996). Anal spines were removed as close to the body as possible using fin clip scissors. Only the first two to three anal spines were removed. Anal spines were stored in a scale envelope and dried (Devries and Frie 1996).

Structure Preparation

Once dried, scales were pressed between two acetate slides using a scale press. The scale impressions were imaged using a microscope equipped with a Nikon SMZ800 camera and Image-Pro Plus 5.1 software. Images were initially saved with unique file names to allow for specific identification for use in another study. Anal spines were sectioned using a Dremmel tool and 7/8" x 0.005" blade. The first section of the spine was discarded, and the second section of the spine was kept for aging. Only the first anal spine was sectioned unless damaged, in which case the second anal spine was sectioned. Anal spine sections were placed in mineral oil and imaged using a microscope equipped with a Nikon SMZ800 camera and Image-Pro Plus 5.1

software. Initially, spine images were saved with unique file names similar to scales. The time

for the preparation of scales and spines from 20 individuals was recorded and averaged so that

processing time could be considered.

Aging

A subsample of the collected age structures was aged for this study. The subsample

included structures from five individuals from each ten millimeter (mm) length increment from

the range of captured smallmouth bass lengths (200-530 mm). The subsample was randomly

selected from the collected age structures, but paired anal spines and scales were used. For

example, if smallmouth bass #53 was selected, both the anal spine and scale were used. In some

cases, five individuals were not available for a length increment. As a result, the total sample

size was 146 anal spines and 146 scales. To avoid bias from unique file names, the ten structure

images from each interval were given randomized file names. The entire subsample was aged

twice each by three readers with a total of six reads for each structure. Both reads by an

individual reader on a specific structure were performed within a two week period to avoid any

potential bias. Scales were aged by counting where annuli "cut over" at each annulus (Latta

1963; Kaemingk 2008). When anal spine sections were aged, the translucent bands were

counted as annuli (Welch et al. 1993).

Determination of Precision

To determine the precision of age estimates from anal spines and scales, three statistical

methods were used. Average percent error (APE), coefficient of variation (CV), and standard

deviation were calculated for anal scales and spines separately. Higher APE, CV, and standard

deviation would indicate lower precision of the aging structure estimates. APE is:

$$APE_j = 100 \times \frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} - X_j|}{X_j}$$

where R is the number of times each fish is aged, and X_{ij} is the ith age of the jth fish and X_j is the

mean age of the jth fish (Campana et al. 1995; Campana 2001).The coefficient of variation was

calculated as (Rien and Beamesderfer 1994):

$$CV_j = 100\% \times \frac{\sigma}{\mu}$$

where σ is the standard deviation of age estimates and μ is the mean of age estimates. A

comparison of APE and coefficient of variation for the two structures was performed to

determine the more precise structure. Wilcoxon rank-sum or Mann Whitney tests were used to

determine if the APE, CV, and standard deviation of anal spines and scales were significantly

different. The APE and CV were compared between and within readers. Within reader

comparisons were done using the APE and CV calculated for the two reads by each individual

reader. Between-reader comparisons were done using the APE, CV, and standard deviation

calculated from all reads by the three readers combined. In addition, the APE and CV of age

estimates under age 5 and age estimates over age 5 for both structures were compared using

Wilcoxon-rank sum or Mann Whitney tests to determine if precision changes significantly after

smallmouth bass reach age 5. Age 5 was chosen based on personal communication and the fact

that precision differs between whole and sectioned otoliths of walleye between these two age

groups (Isermann et al. 2003). Though for largemouth bass differences can be seen in precision

starting at age 2 (Besler 1999), there were very few individuals under age 2 in the sample. The

standard deviation of age estimates from both structures was correlated with total length using a Spearman rank correlation in order to determine if fish size affects aging precision (Welch et al. 1993). All statistical analysis was performed in R (R Development Core Team 2011)

Results

Mean processing times of three scales (150.6 s ± 8.73 SE) and one anal spine (147.6 s ± 8.35 SE) were not significantly different ($P = 0.81$). Processing time for scales was for three structures since several scales for each individual are typically collected and processed. Between reader APE differed for scales and anal spines ($P = 0.009$), but between reader CV ($P = 0.09$) and standard deviation ($P = 0.36$) did not differ between the structures (Table 4). For within reader comparisons, only one reader had significant differences in APE and CV between the two structures (Reader 1: $P < 0.0001$). APE and CV did not differ for the other readers (Reader 2: $P = 0.78$; Reader 3: $P = 0.07$).

APE and CV did not differ between age groups (≤ 5 and > 5 years) for scales or anal spines (Table 4; $P > 0.1$). Standard deviation of age estimates was significantly different between the two age groups for scales ($P < 0.0001$) but not for spines ($P = 0.07$). Standard deviations were lower for smallmouth bass under age 5 ($\sigma^2 = 0.875$) than those over age 5 ($\sigma^2 = 1.185$), indicating higher precision. CV ($P = 0.46$), APE ($P = 0.72$), and standard deviation ($P = 0.72$) did not differ between scales and anal spines for the ≤ 5 age group. As age of smallmouth bass increased, aging precision changed. For smallmouth bass > 5 years old, CV ($P < 0.0001$), APE ($P < 0.0001$), and standard deviation ($P < 0.0001$) of age estimates were significantly different between scales and spines. Scale values of APE and CV were lower and indicated greater precision than aging with spines in smallmouth bass > 5.

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Table 4. Estimates of average percent error (APE), coefficient of variation (CV), and standard deviation (SD) for ≤age 5 and > age 5 smallmouth bass and within reader age estimates.

	APE		CV		σ	
	Scale	Spine	Scale	Spine	Scale	Spine
Between Reader	27.69	24.80	0.19	0.21	1.04	1.11
≤ Age 5	24.43	25.90	0.20	0.22	0.88	1.02
> Age 5	23.42	26.61	0.19	0.22	1.19	1.19

The standard deviation of age estimates for anal spines was correlated with length ($P =$ 0.003, $r = 0.25$), but the correlation coefficient indicated a week correlation (Figure 15). The standard deviation of age estimates for scales were not correlated with total length of smallmouth bass ($P = 0.41$, $r = -0.07$, Figure 15). Since there was no correlation between aging precision and length for scales and a weak correlation of precision with length for anal spines, it does not appear that aging precision is strongly affected by smallmouth bass length.
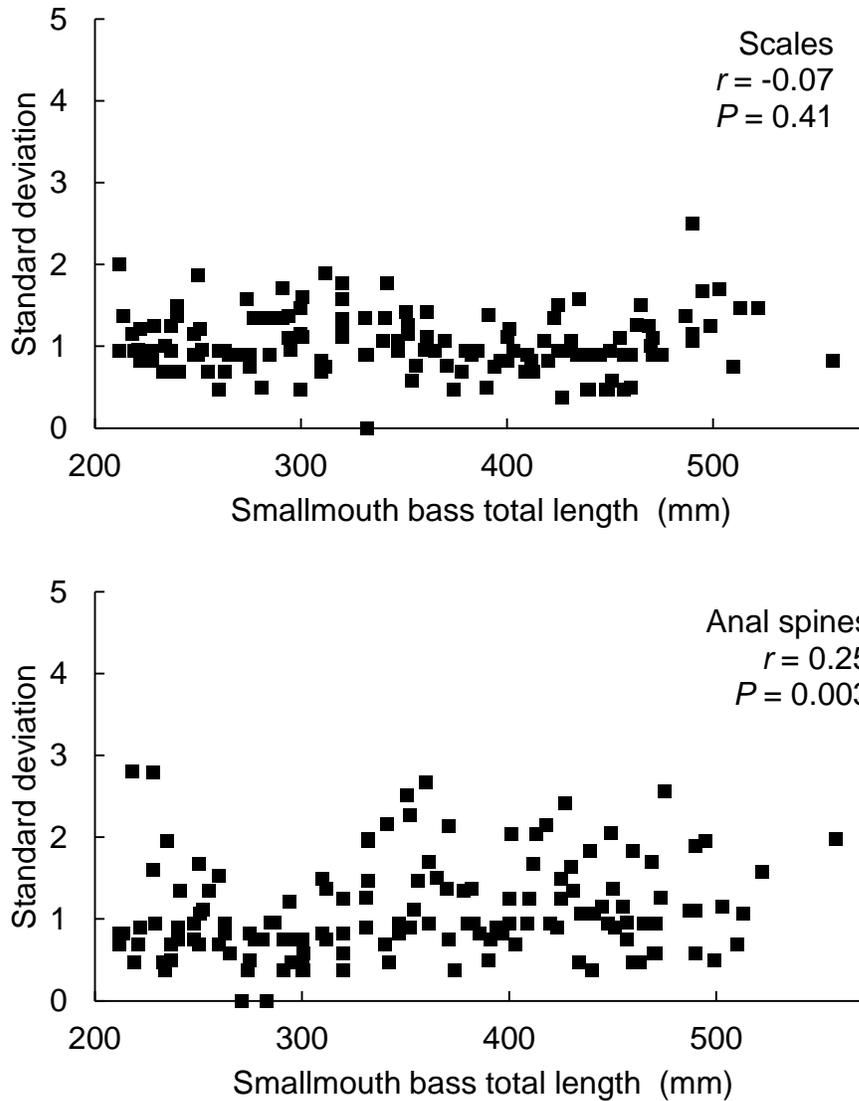
Figure 15. Standard deviation of age estimates from smallmouth bass scales (top) and anal spines (bottom) as correlated with total length (Spearman rank correlation).

Discussion

The aging structure that best suits the objectives of a study or is most precise can depend

on location, species, individual size, and individual age (Maraldo and MacCrimmon 1979;

Welch et al. 1993; Hoxmier et al. 2001; Isermann et al. 2003; Maceina and Sammons 2006).

The purpose of this study was to determine the most precise aging structure for smallmouth bass in northern Lake Michigan, taking into consideration the possibility that one structure may be better than another after fish reach a certain age. Aging precision of smallmouth bass by scales is greater than or equal to aging precision by anal spines. Although scales took slightly longer to process than anal spines, the scales were subject to less processing error. In addition, scale removal may be less stressful for smallmouth bass than anal spine removal. For largemouth bass aging structures, CV for whole otoliths is higher than the CV of both anal spines and scales in our study, indicating greater precision of age estimates for both anal spines and scales in this study (Besler 1999). Smallmouth bass pectoral fin rays in previous studies also had similar APE values to scales in our study (Rude et al. 2012). Precision differs between aging structures for other species, including pectoral fin rays and sphenoids for shovelnose sturgeon (*Scaphirhynchus platorynchus*; Jackson et al. 2007), and sectioned otoliths, whole otoliths, dorsal spines, and scales in spotted sea trout (*Cynoscion nebulosus*; Ihde and Chittenden 2002).

In studies examining otoliths and scales, otoliths are more precise for smallmouth bass aging (Long and Fisher 2011), but in a sport fishery like Waugoshance Point, northern Lake Michigan, a nonlethal structure may be preferred. Sacrifice of smallmouth bass for aging structures is not possible at Waugoshance Point because of the current and historical popularity of the fishery. Based on this comparison between scales and anal spines, in addition to precision values reported in previous studies, it appears that scales are the best structure to use for aging the smallmouth bass in northern Lake Michigan.

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APPENDIX

SMALLMOUTH BASS AVERAGE CALCULATED TOTAL LENGTH (MM) AND
GROWTH INCREMENTS (IN BOLD), WAUGOSHANCE POINT, NORTHERN
LAKE MICHIGAN, 2009-2012. AN ASTERISK (*) INDICATES A YEAR WHERE
GROWTH INCREMENT WAS NEGATIVE.

Year Class	Year of life							
	1	2	3	4	5	6	7	8
2001	159.3	237.8	303.8	356.8	398.7	430.0	455.2	475.7
	159.3	**78.5**	**66.0**	**53.0**	**41.8**	**31.3**	**25.2**	**20.5**
2002	162.3	234.9	295.0	345.7	389.9	423.7	447.2	
	162.3	**72.6**	**60.1**	**50.7**	**44.2**	**33.8**	**23.5**	
2003	137.8	311.3	363.1	401.0	429.8	448.0	491.0	498.0
	137.8	**173.5**	**51.8**	**37.9**	**28.8**	**18.2**	**43.0**	**7.0**
2004	166.3	235.2	293.3	347.4	385.1	409.2	449.0	427.5
	166.3	**68.9**	**58.1**	**54.1**	**37.7**	**24.1**	**39.8**	*****
2005	168.5	251.2	315.6	359.3	402.3	454.1	468.0	
	168.5	**82.7**	**64.4**	**43.7**	**43.1**	**51.8**	**13.9**	
2006	156.9	235.3	295.0	349.1	411.4	434.8		
	156.9	**78.3**	**59.7**	**54.1**	**62.3**	**23.4**		
2007	162.1	239.2	295.6	362.2	389.3			
	162.1	**77.0**	**56.4**	**66.6**	**27.1**			
2008	161.5	235.6	321.6	370.6				
	161.5	**74.1**	**86.0**	**49.0**				
2009	156.0	247.8	317.0					
	156.0	**91.7**	**69.2**					
2010	176.6	247.1						
	176.6	**70.5**						
2011	187.7							
	187.7							