**MIXED-STOCK ANALYSIS OF LAKE MICHIGAN'S LAKE WHITEFISH
(*COREGONUS CLUPEAFORMIS*) COMMERCIAL FISHERY**

By

Ryan T. Andvik

A Thesis

Submitted in partial fulfillment of the requirements of the degree

MASTER OF SCIENCE
IN
NATURAL RESOURCES (FISHERIES)

College of Natural Resources
UNIVERSITY OF WISCONSIN
Stevens Point, WI

January 30, 2012

APPROVED BY THE GRADUATE COMMITTEE OF

Dr. Brian L. Sloss, Committee Chair
Assistant Unit Leader
U.S. Geological Survey
Wisconsin Cooperative Fishery Research Unit
College of Natural Resources
University of Wisconsin-Stevens Point

Dr. Daniel A. Isermann
Assistant Professor
College of Natural Resources
University of Wisconsin-Stevens Point

Dr. Les P. Werner
Associate Professor
College of Natural Resources
University of Wisconsin-Stevens Point

ABSTRACT

Six genetic stocks of lake whitefish have been described in Lake Michigan. Concerns exist about the mixed-stock characteristics of Lake Michigan's lake whitefish commercial fishery. The genetic stock-structure model and microsatellite reference database for lake whitefish spawning aggregates in Lake Michigan provide a framework for addressing some key information gaps. These gaps include determining if a mixed-stock fishery exists and what level of exploitation each of the six stocks is experiencing. The objectives of this research were: (1) to determine if differential stock harvest occurs in the total commercial catch, (2) determine if spatial differences in genetic composition are present in the harvest, and (3) determine if seasonal differences are present in the commercial harvest. Mixed-stock analysis was conducted on 18 commercial harvest samples collected from spring 2009 to fall 2010. Results showed considerable variability in composition of genetic composition throughout the lake. The samples consisted of 2 to 4 genetic stocks contributing relatively large proportions. The predominant stocks observed in the samples of harvested fish were the North and Moonlight Bay stock (NMB), Big Bay de Noc stock (BBN), the Northern stock (NOR; Epoufette and Naubinway), and the Northeastern stock (NOE; Grand Traverse Bay and Hog Island). For most samples, significant admixture of stocks was present; however, the majority of the samples showed the dominant harvested stock represented <60% of the total sample. Samples from WFM-08 were the most homogeneous, with 80.3% of the sample comprised of the Southern stock (SOU; Saugatuk, Ludington, Muskegon, MI). Multiple samples from WI-2 and WFM-01 across spring, summer, and fall of both sample years showed seasonal differences within in some years, and between years. Interestingly,

samples from zone WI-2 were consistently comprised of a majority of BBN fish as opposed to the geographically proximate, NMB stock. In many cases, the data showed $\leq 50\%$ of the sampled fish were from the most geographically proximate stock. These findings have implications for stock-specific management and the allocation of fish to various quotas as geographic location of harvest does not correlate to genetic stock harvest.

ACKNOWLEDGMENTS

I would like to thank the Great Lakes Fishery Commission for providing funding and insight throughout the process of this project. I am indebted to my academic advisor, Dr. Brian L. Sloss for his commitment to guiding and continually challenging me to go above and beyond the requirements of class work and research. Without his guidance I would not have made it through my first year. I would also like to thank my committee, Dr. Daniel A. Isermann and Dr. Les P. Werner for their suggestions on class work, review and revisions of my project, and guidance on continuing my career in fisheries.

A very special thanks goes out to my dear friend Dr. Justin A. VanDeHey. He has always been a call or an e-mail away with suggestions and good direction. It has been a real pleasure to know and work with him. Although we do not agree on preferences on hunting dogs or baseball teams he has proven time and time again to be a model for many young professionals.

I would like to thank all of the managers and staff that work with Lake Michigan including Scott Hansen, Ken Royseck, Paul Peeters, Steven Lenart, Mark Ebener, Eric Olsen, and the Lake Michigan Technical Committee.

Enough thanks cannot be given to all of the commercial fishers. Without their willingness to help out I would never have been able to collect my samples. Further, the commercial fishers taught me about their perspectives on commercial fishing (through good times and bad), women, politics, and life in general (a true education that you cannot learn in a classroom). These commercial fishers include Ben And Joel Peterson, Greg Ruleau, Mo Hermes, Charlie Hendricksons, Mark and Jeff Weberg, Dennis Hickey,

Bill King, Bill Folwer, Bill, Allen, Eric, and Joel Petersons in southern Lake Michigan, Rick Johnson, and George ‘Skip’ Duhamel. I would also like to thank the Wisconsin Commercial Fishers Committee for allowing me to share my research with them and hear their input.

I cannot forget to thank my fellow graduate students, Justin Haglund, Pat Wherley, Kyle Mosel, Matt Faust, Joe Ditrieck, and Matt Waterhouse for their help in the field, discussion of my project, and willingness to have a cold beverage at the end of the day to help unwind and reflect on life.

Without the help of my technicians in the field and the lab I would not have been able to complete this project on time. I couldn’t have asked for an easier going technician than Rebecca Pawlak. Her willingness to work inclement weather with a wide variety of personalities and her quality of work speaks volumes about her as a person. Lucas Nathan has been a valued individual whose hard work and dedication to work weekends and late evenings did not go unnoticed. Both their efforts are greatly appreciated.

Without the support of my family, completing my Master’s degree would have been ten-fold more difficult, if not impossible to do. I have been very fortunate to have my parents, Jeff and Linda Andvik, who instilled many values and a strong work ethic that define me today. I have been very blessed to have my older siblings, Marc and Molly Andvik. They have set a high standard for quality of work. Their achievements in life have driven me to be more successful than I could have been in their absence.

I will always be in debt to my good friends who have been willing to make the trip to Wisconsin to visit me, call to see how life was treating me, or listen to my endless

complaints about the most futile frustrations in life. My friends Weston Wise, Mike Blaaid, Karl Nyberg, and Luke Schultz have had many a good time that will not be forgotten. Last, but certainly not least I would like to thank Pete and Sally Beito and the rest of the Blue Goose Gang for all of the wonderful November days spent deer hunting.

DEDICATION

My father Jeff, brother Marc, and uncles Mike and Kevin, and great-uncle Dave have spent countless days in fields, swamps, and on the water and have spurred my interest in a career in the natural resources. This compilation of work is in dedication to these individuals who have inspired and supported me to pursue my interest in fisheries.

TABLE OF CONTENTS

TITLE PAGE	i
APPROVED BY THE GRADUATE COMMITTEE OF	ii
ABSTRACT	iii
ACKNOWLEDGMENTS	v
DEDICATION	viii
TABLE OF CONTENTS.....	ix
LIST OF TABLES	xi
LIST OF FIGURES	iii
INTRODUCTION	4
LITERATURE REVIEW	7
<i>Commercial fishery</i>	7
<i>Great Lakes commercial fishery management</i>	8
<i>Stock concept</i>	9
<i>Mixed-stock analysis</i>	11
<i>Genetic stock management and Lake Michigan lake whitefish</i>	12
MATERIALS AND METHODS.....	15
Experimental Design and Sampling	15
Genetic Analysis	16
Mixed Stock Analysis	17
Statistical Analysis.....	18
<i>Proportional stock harvest across all samples</i>	18
<i>Geographic distribution of harvested stocks</i>	19
<i>Temporal comparisons of stock contributions</i>	19
RESULTS	22
<i>Proportional stock harvest across the whole commercial harvest</i>	24
<i>Geographic distribution of harvested samples</i>	24
<i>Temporal comparisons of stock contributions</i>	25

DISCUSSION	26
<i>Spatial differences in proportional stock harvest</i>	26
<i>Temporal comparisons of stock contributions</i>	29
<i>Management implications and future research</i>	30
LITERATURE CITED	35

LIST OF TABLES

Table 1. Great Lake commercial fish harvest by kgs and value (U.S. Dollars) in the year 2009.....	41
Table 2. Yield (kg) and value (U.S. Dollars) of the lake whitefish commercial harvest in the Great Lakes during 2009.....	41
Table 3. Lake Michigan commercial fish harvest by kgs and value in the year 2009 (USGS Report).....	42
Table 4. Microsatellite and primers, primer sequences, observed allele size range in base pairs (microsatellites), number of alleles observed (A), and references. Locus code refers to the specific microsatellite locus.	43
Table 5. PCR reaction concentrations and fluorescent labels. Multiplex indicates loci amplified in the same PCR reaction with the corresponding thermal cycling profiles provided as footnotes.	44
Table 6. Reference location and reporting stocks from VanDeHey et al. (2007).....	45
Table 7. Results of mixed-stock analysis of the 18 commercial harvest samples from 2009-2010 including and the number of genetic samples (N). Grid represents the commercial fishing grid that the sample was collected. Values for each stock represent the proportion of that stock. The numbers below estimates represent the 95% confidence interval of the estimate.	46
Table 8. Two-way chi-square results for spatial and temporal comparisons of 2009 samples.....	49
Table 9. Two-way chi-square results for spatial and temporal comparisons of 2010 samples.....	50
Table 10. Chi-squared tests of equal stock proportions for all 18 samples collected from the Lake Michigan commercial catch.	51
Table 11. Two-way chi-square results for temporal analysis of WI-2 (NMB) samples...	52
Table 12. Two-way chi-square results for temporal analysis of WFM-01 (BBN) samples.....	53

LIST OF FIGURES

Figure 1. Commercial management units used to monitor population dynamics of lake whitefish in Lake Michigan. Zones in Wisconsin waters include WI-1, WI-2, and WI-3. All other zones are in Michigan waters (WFMs) and were originally established by the 1836 Consent Decree	54
Figure 2. The six genetic stocks of lake whitefish identified in Lake Michigan by VanDeHey et al. (2009). North and Moonlight Bays (NMB), Big Bay de Noc (BBN), Northern (NOR), Northeastern (NOE), Elk Rapids (ER), and Southern (SOE).....	55
Figure 3. Lake Michigan statistical commercial fishing grids.....	56
Figure 4. Proportional stock harvest of the six randomly chosen commercial fishing samples.	57
Figure 5. Proportional stock harvest of the two primary commercial sample zones, WFMI-01 and WI-02. Relative size of the gray circle is indicative of the range of locations sampled from these two management units.....	58

INTRODUCTION

The stock concept is an approach to conservation and fisheries management that is aimed at protecting productivity and evolutionary potential by maintaining abundance and diversity of each individual stock (Shaklee & Currens 2003). Typically, fish species are composed of multiple stocks and therein populations (Shaklee & Currens 2003). Ihssen et al. (1981b) defined a stock as “an intraspecific group of randomly mating individuals with temporal or spatial integrity.” Adaptations to local environments, in combination with differences in population dynamics, make stocks independent and identifiable from other stocks; thus, making a stock the basic biological unit of a fishery. A goal of stock-based management programs is to protect the genetic variability and maintain the functional identity of component stocks (Spangler et al. 1981). For stock-based management of a commercial fishery to be effective it is critical to identify all component stocks, their population dynamics, and their contribution to the total harvest (Utter & Ryman 1993).

Lake whitefish *Coregonus clupeaformis* are one of the remaining viable, Great Lakes commercial fisheries (Madenjian et al. 2002; Ebener et al. 2008; Modeling Subcommittee 2009). In addition to commercial harvest, lake whitefish play an important ecological role as keystone benthivores and are socially valued as sport and subsistence fisheries. The Great Lakes commercial fisheries have changed dramatically since the early 1800's (Ebener 1997; Pothoven et al. 2001; Madenjian et al. 2002; Ebener et al. 2008), with many fisheries, including lake whitefish, experiencing dramatic population declines. In Lake Michigan, overfishing, habitat destruction, and varying year class strength contributed to dramatic population declines (Wells & McLain 1973;

Healy 1975; Ebener 1997; Madenjian et al. 2002). Lake whitefish have subsequently rebounded, in part due to sea lamprey control, water quality measures, and improved fisheries management, and continue to be the dominant commercially harvested species in Lake Michigan (Ebener 1997; Schneeberger et al. 2005).

Current Lake Michigan lake whitefish management practices monitor the population dynamics of the species within composite management units (Figure 1). It is unknown what contributions each putative stock makes to the total harvest within and between these management units. However, it is likely that all stocks are not experiencing the same exploitation rate (Rowe 1984). Managing lake whitefish based on current management units and geographic allocation of harvest could lead to over-exploitation of some stocks and under-utilization of others. For example, even if the catch in WFM-03 is actually composed of 20% Big Bay de Noc (BBN; WFM-02), 30% North and Moonlight Bay (NMB; WI-2), 50% Naubinway and Epoufette (NOR; WFM-03) all harvested fish are regardless allocated to WFM-03.

To maintain a sustainable commercial fishery in Lake Michigan, each component stock needs to be identified, their specific population dynamics understood, and subsequent quotas and strategies developed to ensure sustainability in light of realized harvest levels. Recently, six genetically distinct stocks of lake whitefish within Lake Michigan were identified (Figure 2) (VanDeHey et al. 2009). VanDeHey et al. (2010) investigated the usefulness of the microsatellite genetic data originally used to identify the stock structure of lake whitefish to serve as a reference data set for a mixed-stock analysis (MSA) of Lake Michigan's commercial fishery. VanDeHey et al. (2010) examined the accuracy of individual assignment and MSA of realistic commercial

harvests using the microsatellite reference data, simulated genotypes of the resolved spawning stocks from VanDeHey et al. (2009), and maximum likelihood-based MSA algorithms (Anderson et al. 2008) to predict overall proportions of harvested stocks. Initial tests showed high accuracy of assigning sampled lake whitefish back to their known stock of origin (96 to 100%). Moderate levels of resolution were observed when simulated individuals (assuming Hardy-Weinberg equilibrium and gametic equilibrium among loci) from a single population/stock were assigned to their putative stock of origin. The results showed a mean stock self-assignment of 82.34% ranging from 73.94% (BBN) to 91.63% (SOE). This suggested MSA with an incorporation of error rates was feasible (VanDeHey et al. 2010). The results of 10 realistic mixed-stock simulations confirmed the usefulness of the microsatellite database for MSA. Therefore, MSA using commercially harvested samples and the VanDeHey et al. (2009) baseline microsatellite data is capable of estimating proportional stock harvest in Lake Michigan's commercial lake whitefish fishery. Assessing and understanding the relationships between these genetically differentiated stocks and their exploitation rates are a critical component of managing the Lake Michigan lake whitefish fishery on a stock basis.

The goal of this study was to provide a better understanding of stock-specific harvest in the lake whitefish commercial fishery occurring in Lake Michigan. Therefore, this study aimed to determine if genetically delineated stocks of lake whitefish are being differentially harvested in the Lake Michigan commercial fishery. Three specific objectives were addressed to better understand the implication and distribution of harvested stocks. These were to (1) determine if stocks were differentially harvested in the total commercial catch, (2) determine if spatial differences in the genetic stock

composition of harvested fish are present, and (3) determine if seasonal differences in genetic stock composition exist in the stock harvest at WI-2 and WFM-01.

Literature Review

Commercial fishery.—Historically, Great Lakes fisheries have been important for both cultural purposes and economic activity in the surrounding communities. Targeted species included lake trout *Salvelinus namaycush*, chubs *Couesius plumbeus*, and lake whitefish (Brown et al. 1999). Due to many disturbances, the Great Lakes fisheries have changed dramatically since the 1800's resulting in commercial fisheries crashes (Ebener 1997; Pothoven et al. 2001; Madenjian et al. 2002; Ebener et al. 2008). Changes in food web dynamics, invasive species, habitat destruction, and over exploitation are a few of the many factors that likely contributed to these declines (Ebener 1997; Pothoven et al. 2001; Madenjian et al. 2002; Ebener et al. 2008). Today, the Great Lakes have relatively few remaining commercial fisheries, but those that remain still play an important role in economic and cultural activities across the region.

Since the mid-1800's, lake whitefish have supported one of the largest freshwater commercial fisheries in North America (Baldwin 1979). Currently, lake whitefish comprise the majority of the Great Lakes harvest in terms of both total biomass and total value of any species (Table 1) (Kinnunen 2003; Ebener et al. 2008). In 2008, the United States' share of the Great Lakes lake whitefish commercial fishery produced 4.68 million kg of lake whitefish with an estimated value of U.S. \$11.11 million (USGS 2009). Lake Michigan hosts the majority of the United States' Great Lakes lake whitefish harvest (Table 2) (USGS 2009). Although the Lake Michigan ecosystem has experienced many changes (Madenjian et al. 2002; Nalepa et al. 2005), lake whitefish harvest levels are

near historic records (Ebener 1997). The harvested biomass of lake whitefish in Lake Michigan is greater than all other species combined from the lake (Table 3). In 2009, 2.52 million kg of lake whitefish were harvested from Lake Michigan with an estimated value of U.S. \$5.90 million for the flesh alone (USGS 2009). Currently, concerns exist regarding the health and status of the Great Lakes lake whitefish populations.

Great Lakes commercial fishery management.—Commercial fisheries in the Great Lakes are licensed and monitored through multiple state agencies, federal agencies, tribal nations, and the province of Ontario (Kinnunen 2003; Ebener et al. 2008). Season closures, permanent and seasonal refuge areas, minimum size restrictions, gear restrictions, and quotas are implemented to maintain sustainable harvest (Kinnunen 2003; Ebener et al. 2008). Statistical catch-at-age (SCAA) models are used to estimate age- and year-specific population abundances and mortality rates. These estimates provide an understanding of how abundance and mortality rates change over time. Population abundances for a given year are calculated as the proportion of the previous age-class surviving from the start of the previous year. Mortality rates are estimated by the combination of natural and fishing mortality rate estimates (Ebener et al. 2008).

Commercial harvest of lake whitefish on Lake Michigan is co-managed between Wisconsin and Michigan agencies (Ebener et al. 2008). Currently, concerns exist over the proper allocation and management of this resource. The Wisconsin commercial fishery consists of only state licensed commercial fishers. The total annual harvest is divided among the three management units on a fixed percentage basis. Annually, WI-1 receives 9.1%, WI-2 receives 82.2%, and WI-3 receives 8.7% of the total harvest. Each management unit's share is then divided among the number of licenses within that unit.

Michigan has both a state licensed and tribal commercial fishery. A combination of the five tribes of the Chippewa Ottawa Resource Authority (CORA), the United States Department of Interior's U.S. Fish and Wildlife Service, and the Michigan's Department of Natural Resources and Environment (MIDNRE) use the 1836 Ceded Territory treaty and the 2000 Consent Decree to determine harvest levels for waters shared between commercial and state licensed fishers. The 2000 Consent Decree addressed the shared resource aspect of the lake whitefish harvest by providing guidelines to set harvest limits in management units shared between tribal and state licensed commercial fishers. Additionally, the 2000 Consent Decree provided a means for committees, consisting of tribal, state, and federal biologists, to calculate harvest limits. Statistical catch-at-age models are used to estimate age and year-specific population abundances and mortality rates in each management unit (Modeling Subcommittee 2009). Unlike Wisconsin, the total harvest is not distributed to management units based on a fixed percentage basis. Instead, quotas are distributed to both tribal and state license holders based on five-year average catch rates.

Stock concept.—Fisheries managers are faced with many concerns regarding long term management and sustainability of resources. In addition, many concerns revolve around identifying and evaluating genetic risks associated with current management plans (Shaklee & Currens 2003). Rarely are fish species entirely panmictic, instead they are generally composed of multiple stocks and therein populations (Shaklee & Currens 2003). Ihssen et al. (1981b) define a stock as “an intraspecific group of randomly mating individuals with temporal or spatial integrity.” These stocks have local adaptations largely due to limited gene flow via spatial and temporal isolation (MacLean & Evans

1981). Many of these local adaptations have not been identified. Further examination of these adaptations would aid in implementing the stock concept. The combination of temporal and spatial isolation with limited gene flow provides the basis for the stock concept.

The stock concept is an approach to fisheries management that is aimed at protecting productivity and evolutionary potential by maintaining abundance and diversity of each individual stock (Shaklee and Currens 2003). Stocks are comprised of populations that generally exhibit similar population dynamics, such as growth rates, morphological features, and mortality rates (Shaklee & Currens 2003). Adaptations to local environments in combination with differences in population dynamics make a given stock independent and identifiable from other stocks, making a stock the basic biological unit of a fishery. The goal of most stock-based management programs is to protect genetic variability and sustainability (Spangler et al. 1981). Stock-based management provides grounds for evaluating the success of management actions, and allows for a more effective and efficient means for management of a resource.

Baseline data such as stock identification, life history characteristics, and population dynamics are necessary for any stock-based management program (Shaklee & Currens 2003). Long-term management for sustainability requires an assessment of all component stocks and continual maintenance of genetic integrity, variability, and diversity (Shaklee & Currens 2003). In general, stock-based management provides protection for smaller stocks that are most susceptible to overexploitation. The more diverse and subdivided a species is, the more important it is to manage for productivity and evolutionary potential via maintaining component stocks (i.e., stock-based

management) (Shaklee & Currens 2003). Defining and understanding these relationships between stocks is critical for effective management (Shaklee & Currens 2003). Stock-based management can be accomplished with the use of MSA.

Mixed-stock analysis.—A MSA is an estimate of the contributions of each component stock to the total fishery (Shaklee & Currens 2003). The three requirements of any genetic-based mixed stock analysis include (1) baseline data (i.e., genetic data from all component stocks), (2) samples of the mixed fishery (i.e., harvested individuals), and (3) genotypes of sampled individuals. A sample of the mixed fishery is necessary to determine the contributions of the component stocks harvested. The size of the sample is dependent on the degree of differentiation of stocks and number of loci utilized (Fabrizio 2005). Typically, simulations are run to determine the optimal sample size. Mixed stock analysis assumes there is more than one stock with detectable differences in the fishery, all component stocks are accounted for in the baseline data, and the degree of gene flow between component stocks is limited (Fabrizio 2005).

After samples of harvested fish have been collected they need to be genotyped and analyzed. Two common approaches for a stock component analysis include classification models and mixture models (Fabrizio 2005). Classification models assign individuals back to a specific stock, whereas mixture models assign the most likely combination of stocks (Fabrizio 2005). Typically classification models are used for phenotypic data and mixture models are used for genetic data (Fabrizio 2005). Mixture models generally tend to have more statistical power. Mixture models perform best when all stocks contribute equally to the harvest (Mulligan et al. 1988). Most mixture models underestimate the dominant stocks contributions, conversely, overestimating

minor stocks (Wood et al. 1987).

Currently, management is concerned with levels of exploitation on individual components of mixed-stock fisheries. To manage each component stock it is necessary to estimate the contribution of each stock to the total fishery (Shaklee & Currens 2003). Implementation of stock-based management can prove to be very difficult due to many uncertainties, including population size, lack of readily identifiable morphological features, and instantaneous contributions to the total harvest (Utter & Ryman 1993). However, stock-based management provides the means for sound based science and management. Understanding the contributions of each component stock provides the grounds for management based on the stock concept.

Genetic stock management and Lake Michigan lake whitefish.—Stock identification is necessary to assess each individual component stock (Waldman 2005). In the most basic sense, stock identification recognizes components that are discrete either spatially or temporally; that is, they have unique life histories and experience unique demographic influences (Waldman 2005). Stock identification provides the baseline data necessary for a mixed stock analysis.

Identifying stocks can be accomplished through the use of life history characteristics, artificial marking, morphometric characteristics, meristic counts, parasite infestations, or genetic markers (Pella and Milnar 1987; Utter & Ryman 1993; Cardin 2005; Waldman 2005). The major downfall of natural marks is that environmental conditions can strongly influence these characters, thus they must be examined regularly to monitor any changes (Pella and Milnar 1987). Similarly, artificial tagging can require much effort and expense (Utter & Ryman 1993). Fortunately, genetic marks have

proven highly effective because they occur naturally, are transferred from adults to offspring, are expressed throughout lifecycles (e.g., both juvenile and adults can be identified), do not require initial marking, and genotypes can be identified at a reasonable cost and effort (Pella & Milnar 1987).

Prior to the use of genetic markers, determining taxonomic relationships among lake whitefish was difficult largely due to variation in morphometric and meristic characteristics (Scott & Crossman 1973). Lake whitefish display a high degree of phenotypic plasticity across their range, largely due to different environments and community dynamics; however, this variability is more limited within the Great Lakes (Lindsey et al. 1970; Ihssen et al. 1981a; Bernatchez 2005). These discrepancies have required the use of genetic markers to accurately determine degree of speciation of lake whitefish.

Previous research has used a variety of methods to determine life history, biological, and behavior characteristics of lake whitefish in Lake Michigan. These studies indicated the potential for multiple stocks and therein a mixed-stock fishery (Ebener 1980; Ebener & Copes 1985, Walker et al 1993). In Lake Michigan, lake whitefish have shown site fidelity by returning to natal spawning areas (Ebener 1980; Rowe 1984; Ebener & Copes 1985; Walker et al. 1993). Observations from tagging studies have shown differences in population dynamics including age composition, mean age in the fishery, annual length increments, instantaneous growth rates, mortality rates, and year class abundance between geographically separated spawning aggregates of lake whitefish (Ebener & Copes 1985; Scheerer & Taylor 1985). These tagging studies showed lake whitefish were highly vagile throughout the majority of the year; often

crossing established management unit boundaries. However, tagged fish consistently returned to spawning areas (Rowe 1984; Ebener & Copes 1985). Genetic research also showed temporal and spatial overlap among populations/stocks (Imhoff 1980; Leary 1979) consistent with the presence of discrete stocks and the likelihood of a mixed-stock fishery during non-spawning times. This combination of site fidelity, mobility, and differences in population dynamics provided strong evidence for the presence of stocks and, subsequently, a mixed-stock fishery (Rowe 1984; Ebener & Copes 1985; Scheerer & Taylor 1985).

Recently, an in-depth analysis of genetic structure among lake whitefish spawning aggregates identified six genetically distinct stocks of lake whitefish throughout Lake Michigan (VanDeHey et al. 2009). Known spawning aggregates of lake whitefish were sampled in the late fall during the lake whitefish spawn. Only fish with ripe, running gametes were used as samples to maximize the probability of sampling fish from a specific aggregate. Genetic stock identification (Shakelee and Currens 2003) was used in combination with 11 microsatellite loci to delineate these stocks. These six resolved stocks corresponded to geographically separate spawning aggregates (VanDeHey et al. 2009). The 11 microsatellite loci and six genetically differentiated stocks provide the necessary baseline information for a mixed stock analysis.

MATERIALS AND METHODS

Experimental Design and Sampling

Lake whitefish from the Lake Michigan commercial fishery were sampled based on both targeted and random sampling efforts. Two locations, WI-2 and WFM-01, were sampled three times per year (2009 and 2010) corresponding to spring, summer, and fall samples. Three samples per year were taken from the remaining zones in Michigan and Wisconsin waters using a random stratified design with season as the first strata (spring, summer, and fall) and management zone, excluding WI-2 and WFM-01, as the second strata. Once a zone was sampled in a given season, it could not be re-sampled. All 18 sampling events were used to address objectives one and two. Alternatively, only the 12 sampling events from WI-2 and WFM-01 (seasonal samples) were used to test the temporal focus of objective three.

Samples were collected in spring, summer, and fall during the 2009 and 2010 commercial fishing seasons. Spring samples were collected from May 15th-31st, summer samples were collected from July 15th-31st, and fall samples were collected prior to the lake whitefish spawn from October 1st-15th. All samples were collected in coordination with tribal and state commercial fishers, state biologist (WDNR and MIDNRE), and tribal biologists (CORA). A random selection of harvested fish (target n = 150) was sampled for each selected location (i.e., per sample). Anal or caudal fin clips were taken from all fish for DNA extraction. Fin clips were preserved in individually labeled tubes with 95% non-denatured ethanol.

Genetic Analysis

Genetic diversity data from all sampled fish were collected at 12 microsatellite DNA loci (Table 4; Bernatchez 1996; Patton et al. 1997; Rogers et al. 2004). Eleven of these loci were used in the stock delineation study of VanDeHey et al. (2009). An additional locus (C2-157; Turgeon et al. 1999) was added in an effort to increase the confidence of stock estimation.

Genomic DNA was extracted from fin samples using the Promega Wizard[®] Genomic DNA purification kit¹ (Promega Corp., Madison, WI) with a 96-well modification. DNA was quantified using a Nanodrop[®] ND-1000 spectrophotometer (Nanodrop Technologies, Wilmington, Delaware) and the concentration was normalized to a standard concentration of 20 ng/μl. Minor adjustments were made to the PCR reaction conditions found in VanDeHey et al. (2007) (Table 5). Following amplification, individuals were genotyped on an ABI 3730 DNA Analyzer (Applied Biosystems Inc., Foster City, CA). Allele sizes were determined using an internal size standard (GeneFlow[™] 625, Chimerx Inc., Milwaukee, WI) and GeneMapper[®] software (Applied Biosystems Inc.). Allele calls were manually confirmed resulting in multi-locus genotyping data. A random subset of samples (10%) was genotyped a second time to ensure the accuracy and consistency of allele calls.

All data was standardized to ensure consistency with allele calls in VanDeHey et al. (2009). Standardization was necessary because that study used an ABI Prism[®] 377XL DNA sequencer and this study used an ABI 3730 DNA Analyzer. Differences in sizing can occur when different platforms are used. A subset of samples from that study

¹ The use of trade and product names does not imply endorsement by the U.S. Government or the University of Wisconsin-Stevens Point.

was re-genotyped and allele scores were compared to the VanDeHey et al. (2009) allele scores (Stott et al. 2010). When discrepancies occurred, scores were examined to determine if a consistent correction factor was available (i.e., if there was a systemic bias in allele sizing). The original data of VanDeHey et al. (2009) were considered the ‘correct’ scores and all correction factors were directionally applied to match those values.

The C2-157 locus was added to the original reference data from VanDeHey et al. (2009). All samples from VanDeHey et al. (2009) were genotyped for this locus and the new data was examined for consistency with the previous findings in terms of divergence values and stock identification. In brief, AMOVA results and the un-rooted neighbor joining tree from VanDeHey et al. (2009) were reassessed with the new locus included to ensure the addition of this locus did not change the previous findings. In no case did results differ in terms of significance. Therefore, the new locus was included in this study to provide additional discrimination of the putative genetic stocks.

Mixed Stock Analysis

The collected genotype data was used in conjunction with the reference/baseline data from VanDeHey et al. (2009) to conduct MSA whereby the proportional contribution of the *a priori* identified stocks were estimated in a given sample of the commercial fishery. This approach required a reference file of genotype data from sample locations (i.e., reference), reporting groups, and a sample file of suspected mixed stock genotypes. The reference and reporting groups (Table 6) were modified from VanDeHey et al. (2009). The reference data was modified by the aforementioned

inclusion of locus C2-157 and the reporting groups were modified by the elimination of the Menominee River and the Cedar River samples. These two samples are suspected of being of mixed origin given the relatively recent origin/re-colonization or rejuvenation of the two rivers (Paul Peeters, WDNR, personal communication).

Mixed stock analysis was performed on all 18 samples of the commercial harvest using a maximum likelihood approach employed in ONCOR (Anderson et al. 2008) consistent with the methods of VanDeHey et al (2010). This maximum-likelihood estimate (MLE) predicts the most likely proportional stock distribution of each component stock (reference data and reporting groups) in a given sample. Confidence intervals (95%) were estimated via bootstrapping with 1,000 pseudoreplicates.

Statistical Analysis

Proportional stock harvest across all samples.—The initial objective reflected a null hypothesis that all stocks contributed equally to harvest at each location and season. This hypothesis was tested two ways: (1) using an equal harvest assumption wherein the six stocks were expected to be equally represented (16.7% each), and (2) a more analogous approach to the SCAA models wherein the expected stock contributions were determined based on proximity of the sampled region to a specific stock. For example, at WI-2 the NMB stock would represent 100% of the harvest. A two-way chi-squared test in MiniTab15[®] Statistical Software (Minitab, Inc., State College, PA) was used to test the goodness of fit of the observed and expected samples. The degrees of freedom were calculated by multiplying the number of rows minus one by the number of column minus one, $df = (r - 1)(c - 1)$.

To calculate the expected values for the first approach the number of fish per sample was multiplied by 16.7%. In the second approach, NMB and BBN were expected to have higher contributions since they were sampled six total times each compared to only one or two samples from any other stock. As a result, the expected values were weighted based on the proportion of total samples from each management zone. To calculate the expected values for the second approach the proportion of fish from a specific management unit was multiplied by the total number of fish collected. For example, if 35% of all sampled fish were acquired from landings in WFM-01, the expected BBN proportion was 35%. In both test scenarios, observed values were derived from the MSA-estimated stock proportions multiplied by the number of sampled fish for a given site. A chi-squared goodness of fit test in MiniTab® v15 (Minitab, Inc., State College, PA) was used to tests differences between the observed and expected values with the expected values being either (1) the equal harvest assumption or (2) the weighted values based on sampling intensity. Alpha was corrected for multiple pairwise comparisons using a sequential Bonferroni approach (Rice 1989).

Geographic distribution of harvested stocks.—The first spatial objective was to determine if spatial differences in stock contributions occurred among the commercial samples. The critical question related to this was if the stocks being harvested in each management unit differed. Because there were no expected values for this objective, two-way chi-squared goodness of fit tests were used to test for significant difference within a season during a given year. For example, in summer 2009, three samples were collected from WI-2, WFM-01, and WFM-04 and pairwise, two-way chi-squared tests were conducted between these three samples.

An individual stock had to contribute a proportion greater than zero to be used to calculate the degrees of freedom. In some cases, predicted individual stock contributions were low (<5 fish) resulting in an error in the calculation of the chi-squared statistic. The chi-squared test has two assumptions: (1) the sample must be randomly selected, and (2) the sample size must be large enough so the expected count in each cell is ≥ 5 (Technical Support by Minitab™ <http://www.minitab.com/support/documentation/Answers/Chi-Square%20Test%20Assumptions.pdf>; Date accessed: 28 November 2011). Assumption 1 was met for all samples; however, in some cases Assumption 2 was violated. When samples violated Assumption 2, individual sample values were changed to zero. The only exception to this was if a specific stock contribution was low in both samples (a situation that did not invalidate the chi-square assumptions). In these situations, sample values were not changed. For example, at the Spring WFM-06 2010 and Summer WFM-08 2010 samples the NOE stock only found two and four observed fish, respectively. As a result, there was no need to change these values to zero before running the chi-squared test.

Temporal comparisons of stock contributions.—The third objective was to determine if the proportion of harvested stocks differed temporally in commercial management units WI-2 and WFM-01. This objective was tested in three ways (1) between seasons within a year (e.g. WI-2 Spring 2009 vs. WI-2 Summer 2009), (2) within seasons between year (e.g. WI-2 Spring 2009 vs. WI-2 Spring 2010), and (3) across years and seasons (e.g. WI-2 Spring 2009 vs. WI-2 Fall 2010). Observed values were calculated by multiplying the number of fish per sample by the proportional MSA estimates. As described previously, two-way chi-squared

goodness of fit tests were used between samples to compare proportions of stocks harvested. Any violations of the statistical assumptions followed the previously described approach. All values and degrees of freedom were calculated as stated previously.

RESULTS

Samples were collected from 9 of 13 commercial fishing/lake whitefish management units in Wisconsin and Michigan waters of Lake Michigan. Management units WI-1, WI-3, WFM-00, WFM-07 and WFM-09 were the only units not targeted in the study. For a majority of the samples, the commercial fishing grid(s) were available allowing for a relatively fine scale identification of where fish were captured (Figure 3). Nine samples were collected from both 2009 and 2010. The number of samples collected from spring, summer, and fall in 2009 was two, three, and four samples, respectively. The number of samples collected from the spring, summer, and fall in 2010 was three, four, and two, respectively. Four samples did not meet the target sample size of 150 randomly selected fish: Spring 2009 WFM-01 ($n = 144$), Summer 2009 WFM-01 ($n = 144$), Fall 2009 WFM-02 ($n = 90$), and Summer 2010 WFM-08 ($n = 120$), but were still used in subsequent analysis.

Temporal samples were collected from WI-2 and WFM-01 in the spring, summer, and fall of both 2009 and 2010. The WFM-01 Spring 2009 sample was a split sample of fish from WFM-00 (Grid number 604) and WI-1 (Grid number 804) but were included in WFM-01 since this was the location these fish were landed. The number of samples for each targeted site were nearly equal with a total of 784 and 797 fish collected and used in the final analysis from WI-2 ($n = 6$ samples) and WFM-01 ($n = 6$ samples), respectively.

In total, 2,610 lake whitefish were sampled from 18 different commercial harvest sampling events over the 2009 and 2010 commercial seasons. Attempts were made to genotype all samples with 12 microsatellite loci but as a result of low quality/quantity of

DNA and other reasons, some samples did not amplify at all loci. Each sample had to have ≥ 8 microsatellite loci successfully genotyped to be included in the final analysis; 2,331 sampled fish (89.3%) met the eight locus minimum requirement for inclusion (Table 7). As a results, four samples, WI-2 Fall 2009 (n = 120), WFM-01 Fall 2009 (n = 121), WFM-02 Fall 2009 (n = 78), and WFM-08 Summer 2010 (n = 115), failed to meet the targeted 125 genotyped individuals (VanDeHey et al. 2010 but were still included in the final analysis. Following quality assurance and quality control procedures, the random subset of samples (10%) showed <1% error rate, consistent with other studies using microsatellite typing (Pompanon et al. 2005).

Significant mixed-stock contributions were observed in all samples. Results showed considerable variability in stock composition across the harvest samples with 2-4 genetic stocks contributing large proportions to all harvest samples (Figures 4 and 5). The spatial distribution of harvested stocks differed significantly across the lake in each season (Table 7; Figures 4 and 5). The predominant stocks observed in the harvest were the North and Moonlight Bay stock (NMB), Big Bay de Noc stock (BBN), the Northern stock (NOR; Epoufette and Naubinway), and the Northeastern stock (NOE; Grand Traverse Bay and Hog Island). For most samples, the dominant stock harvested composed <60% showing significant admixture in most samples (10 of 18 samples; Table 7). In most cases, two stocks were major contributor to a harvested sample with only three samples being 70% or greater one stock (WI-2 Spring 2009-BBN, WFM-01 Fall 2010-BBN, and WFM-08 Summer 2010-SOU). Samples from WFM-08 were the most homogeneous of all harvest samples with 80.3% of the sample estimated to be from the Southern stock (SOU; Saugatuk, Ludington, Muskegon, MI).

Proportional stock harvest across the whole commercial harvest.—Differential harvest of the six genetic stocks occurred in all samples during both 2009 and 2010. Significant differences were observed in the proportion of harvested stocks across the study sites when a baseline 16.7% expected value was used. Differences were detected when all samples were pooled together for 2009 ($\chi^2 = 493.150$, $df = 5$, $p < 0.001$), 2010 ($\chi^2 = 410.496$, $df = 5$, $p < 0.001$), and 2009 and 2010 combined ($\chi^2 = 784.63$, $df = 5$, $p < 0.001$) (Table 10). Additionally, significant differences were also observed with the more analogous approach to the SCAA models where expected values were weighted based on sampling intensity of a given site in 2009 ($\chi^2 = 124.89$ $df = 4$, $p < 0.001$), 2010 ($\chi^2 = 100.42$, $df = 4$, $p < 0.001$), and across both sample years ($\chi^2 = 327.52$, $df = 5$, $p < 0.001$) (Table 10).

Geographic distribution of harvested samples.—Spatial sampling showed considerable variability in stock composition. Nineteen of the 20 sample comparisons within a specific season and a given year showed significant differences in the proportions of stocks harvested. The Spring 2009 WI-2 versus WFM-01 chi-square test was the only comparison that did not differ in stock composition ($\chi^2 = 7.78$ $df = 4$, $p = 0.051$) (Table 8). All spatial comparisons for the spring, summer and fall of 2010 were significantly different (Table 9). Despite the differences between spatial samples, three stocks, NMB, BBN, and NOR were consistently observed in most of the collected samples with the exceptions of WFM-08 Summer 2010 and WFM-06 2010 Spring samples. In general, geographic proximity was a reasonable predictor of what stocks were observed in the harvest. However, key disagreements in terms of predominant

stock existed. For example, BBN comprised the majority of harvested fish for five of the six samples from WI-2, yet the NMB stock was geographically closer (Table 7).

Temporal comparisons of stock contributions.—Temporal samples at WI-2 and WFM-01 showed similarities and dissimilarities between seasons and years (Tables 11 and 12; Figure 5). All the 2009 WI-2 samples were significantly different across seasons. However, all at the 2010 WI-2 samples were not different. In WFM-01, all across season comparisons for 2009 were not different; however, all 2010 comparisons were different. The BBN stock contributed the most of any stock to harvest in WI-2 and WFM-01 in 11 of the 12 sampling events. At both WI-2 and WFM-01, the spring 2009 sample was not significantly different from the spring of 2010. All other within season between comparisons were different. Further, the Spring 2009 sample from WI-2 was not different from the Summer or Fall sample from 2010. At WFM-01 the Spring 2010 sample was not different from either the Summer or Fall samples in 2009. Despite the differences among stocks harvested at these target areas, three stocks, NMB, BBN, and NOR were consistently observed in all temporal samples from both WI-2 and WFM-01. No distinguishable patterns within or across years were apparent in either WI-2 or WFM-01.

DISCUSSION

Spatial differences in proportional stock harvest.—The Lake Michigan lake whitefish commercial fishery in Lake Michigan is a mixed-stock fishery during all non-spawning seasons and at all locations and harvest does not include a homogeneous mixture of stocks at all locations or at all seasons. Mixed-stock estimates showed variability in the number of stocks harvested in a specific management unit and across the 18 sampling locations. In general, 2-4 stocks were major contributors to the commercial samples in this study: NMB, BBN, NOR, and NOE. At most, five of the six stocks were represented in a single commercial sample (WFM-01 Summer 2010) with the minimum number of harvested stocks found in the WFM-08 Summer 2010 sample (two stocks).

The majority of harvested fish in a specific location were expected to come from the nearest stock, with all six stocks expected to be major contributors to the commercial harvest in the vicinity of their respective spawning aggregates. Mixed-stock estimates generally demonstrated that geographic proximity was a relative predictor for which stocks would contribute to the sampled location. However, the dominant stock was often <60% of the total harvest. The consistent mixed-stock nature of the commercial harvest poses a challenge to stock-based management of the fishery, considering harvest allocations are currently based on management units that mostly assume stocks are confined to their respective management units (Ebener et al. 2010).

The relatively weak correlation between geographic location of harvest and dominant stock harvested shows lake whitefish are highly mobile throughout the commercial season. The derivation of management units could attribute to these weak correlations. The management units in Michigan waters were originally designed to

account for suspected stocks of lake whitefish (M. Ebener, CORA, personal communication). The Wisconsin management units were designed for multi-species fisheries, and did not necessarily account for spawning stocks of lake whitefish (S. Hansen, WDNR, personal communications). Regardless of how management units were originally established, they are management boundaries and do not account for the actual delineation of biological stocks or the mixing of these stocks.

The NMB and BBN stocks were expected to be major contributors to the commercial harvest given their perceived abundance, the level of exploitation in WI-2 and WFM-01, and suspected movement patterns. Previous studies (Ebener and Copes 1985 and Ebener et al. 2010) suggested fish from these two regions exhibited differing levels of movement between stocks. Ebener and Copes (1985) used tagging data to suggest BBN fish were more sedentary compared to other lake whitefish spawning aggregates. However, the study of Ebener et al. (2010) found a different pattern of movement with BBN fish found extensively in Wisconsin waters in and around Green Bay. A potential explanation for these differences could be the result of various ecological and environmental changes in Lake Michigan, causing lake whitefish to seek habitats that will optimize growth, survival, and reproduction (Ebener et al. 2010). For example, the introduction of zebra mussels *Dreissena polymorpha* is linked to a major reduction in *Diporeia* species, which was a primary food source for lake whitefish. Consequently, lake whitefish may have altered their movement patterns as a result of this food-web shift. Haugen et al. (2006) has documented northern pike *Esox lucius* acting in a similar fashion, changing movement patterns in relation to habitat quality and quantity consistent with model predictions to maximize their fitness.

In addition to WI-2 and WFM-01, the MSA results also suggested that the NOE and NOR stocks were moving more than previously expected. In a mark-recapture study, Scheerer and Taylor (1985) examined the distribution of tag returns from the Northeastern portion of Lake Michigan and found fish from this region did not move extensively to other parts of the lake. Of their recaptured fish, the majority were originally tagged in the same area they were recaptured. Ebener et al. (2010) also examined the NOR stock and found the majority of tagged fish stayed in local waters with a small percentage of fish migrating into Lake Huron. Both the NOR and NOE stocks were harvested in proportions greater than expected based on previous research; especially their contribution to commercial harvest landings in the WI-2 and WFM-01 regions. As these stocks move into neighboring management units during the commercial season, the impact is more variable mixed stock harvest and less accurate SCAA models. Based on the consistent recovery of these stocks in commercial harvest samples virtually throughout this study, these stocks represent a critical producer of fish harvested in the commercial fishery.

The small contribution of the ER and SOE stock to the commercial fishery was not surprising given previous research. A tagging study showed this stock to be highly sedentary within the eastern lobe of Grand Traverse Bay (Walker et al. 1993). This lack of movement into the lake proper was attributed to shoreline complexity and water depth (Walker et al. 1993). They hypothesized that deep troughs thermally separated the inner and outer bays acting as a barrier to movement. The SOE stock similarly showed minimal to no contribution to harvested samples outside of its respective region. The Southern stock is the most geographically distant stock from all other stocks, as a result,

distance alone could explain its relatively small contribution to harvest in other management units. These reasons not only explain the small contributions of ER and SOE to harvest in other regions of the lake but also explain the relatively low contribution of other stocks to harvest in and around these two stocks.

Temporal comparisons of stock contributions.—Significant changes in the composition of the commercial harvest occurred through the course of a given season and between years. The replicated samples from the WI-2 and WFM-01 showed seasonal shifts occurred in some year and not in others. The contribution of the BBN stock to WFM-01 appeared to increase from the spring to the summer to the fall. A plausible explanation of this could be that these fish are getting closer to their spawning aggregates as the spawning season approaches. However, when confidence intervals were examined this pattern was less clear. Of the six samples from WI-2, the NOR stock ranged from a low of 0.06% (lower 95% CI = 0.00) to a high of 19.3%. Similarly, the NOE stock comprised 6.8% to 16.7% of the harvest within WI-2. For WFM-01 harvest estimates, NOR stock ranged from 3.7-10.6% and NOE stock ranged from 0-17.6%. Given the size of the commercial harvest in WI-2 and WFM-01, these estimates suggest a significant harvest of these two stocks in this region regardless of harvest location. The commercial harvest yield is not consistent across seasons, understanding these season variations in proportional stock harvest coupled with predicted patterns of yield could provide critical data for the further development of more effective management approaches.

The samples used in this study were opportunistic samples and, as such, did not always represent the ideal or preferred location and time of harvest. The temporal results may be influenced by this limited control over location of catch within a given zone

resulting in, the comparisons of profoundly different locations at different times of the year. For example, the location of harvest within WI-2 changes throughout the commercial season. In the spring and part of the summer most of the commercial harvest occurs in Green Bay. However, as the commercial season progresses the commercial fishers begin to set their nets on the lakeside of the Door County Peninsula (S. Hansen, WDNR, personal communication). Conversely, the commercial fishery in WFM-01 harvests the relatively same location, until after the sampling dates of this study, when they move deeper into Big Bay de Noc. Nevertheless, results showed significant differences associated with time of capture and location of landing and confirmed the mixed-stock nature of the fishery. Therefore, this study stands as an example of the variability that is present in the harvest across a moderate coverage of the commercial harvest over a two year period.

Management implications and future research.—Stock-based management was originally developed for Pacific salmonid commercial fisheries. The goal of stock management was to better estimate the contributions of each harvested stock to the commercial harvest, thus decreasing the chances of overharvest (Grant et al. 1980). As a result, stock-based management has become an increasingly important management tool that has expanded beyond Pacific salmonid fisheries. Successful, long-term sustainability requires the use of genetic and demographic data (i.e., stock based management). Currently, management agencies have set up standard sampling of the commercial fishery to collect demographic data. Incorporating the genetic data from this study would provide a more comprehensive understanding of this mixed-stock fishery.

The resulting estimates of mixed-stock proportions found in this study stress the need for further development and refinement of genetic approaches and harvest sampling if quota-based stock management is to be employed. First, to increase the level of understanding/resolution necessary to use this type of data to its full potential, a more intensive sampling regime would be necessary aimed at more accurately identifying spatial and temporal trends. Second, the observed variability between seasons suggests within season variability in stocks harvested at a given location exists. To address this, replicate within season sampling at key sites would allow the levels of seasonal variance in stocks harvested to be predicted. Third, management agencies could consider disregarding or de-emphasizing the *a priori* designation of management units with incorporation of an MSA monitoring or predictive allocation. This approach would provide a more accurate assessment of the commercial harvest in terms of specific location of harvest. It would also provide a more realistic explanation of stock harvest based on location because harvest from grids that lie near the border of two zones (e.g., the border of WI-2 and WFM-01) get allocated to the specific management zone of capture.

Fine-scale differences in stock composition could be the result of distance or time. For example, if a single commercial fisher tends their nets one day and tends them a day or two later, are the stock compositions significantly different? Likewise, if two commercial fishers are tending their nets in the same management units 5 km apart, are the stock contributions significantly different? If so, the prospects of genetic monitoring are not encouraging because the level of effort necessary to parse out that fine-scale level of variability is likely too high for current conservation and fisheries genetics

laboratories in the Great Lakes region. Further, the cost of such an effort would be prohibitive. However, if the variation across time and space can be accounted for through further studies and predictive modeling, the level of effort may not be such an impediment.

A more refined approach examining specific, single stock contribution to the harvest at a given site or during a specific season may provide better predictive data for incorporation in current SCAA or future models for stock harvest. The current study was not designed to specifically address this issue. However, if the contribution of a single stock does not differ at a given location and season, a predictive model could be developed to allow for a more refined allocation of stock harvest. Given a proportional estimate and knowing the variability of harvest in a given location through time (i.e., some seasons have more intense harvest than others), these data can improve contemporary allocations of harvest. Examining these individual stock contributions may better reveal stock-specific patterns than looking for patterns of the total combination of stock contributions in the fishery.

Finally, advances in molecular genetic tools and markers to estimate within and between population diversity and mixed-stock analysis models have resulted in finer levels of resolution and a higher confidence in stock allocation. For example, advances in single nucleotide polymorphism (SNP) techniques and Bayesian admixture analysis has provided for more confident resolution in Cooper River (AK) MSA of sockeye salmon (*Oncorhynchus nerka*) (Ackerman et al. 2011). The reference microsatellite data of VanDeHey et al. (2009) provided adequate estimates of MSA in the current study. Confidence intervals and standard deviation estimates for the lake whitefish mixed-stock

estimates are similar to those reported for Chinook salmon (*O. tshawytscha*) (DeCovich and Templin 2009), chum salmon (*O. keta*) (Flannery et al 2010), and lake sturgeon (*Acipenser fulvescens*) (Bott et al. 2009); but these studies recovered slightly more precise estimates likely attributable to their having a larger suite of markers and a larger reference dataset. These similarities suggest the microsatellite data is sufficient for resolution of stock identification of harvested samples, assuming the level of expectation is kept at 80-85% accuracy as found in VanDeHey et al. (2010). If higher resolution is required, more refined approaches such as the techniques and markers being developed by the Bernatchez Laboratory (Université Laval, Quebec City, Quebec, CN; Rogers and Bernatchez 2006; 2007) may be necessary.

If lake whitefish continue to do well in Lake Michigan, historical spawning areas are likely to be repopulated with spawning lake whitefish. Future research should aim to provide a better understanding of the re-colonization and genetic composition of these re-colonized spawning aggregates. For example, lake whitefish historically spawned in the Menominee River. However, lake whitefish were extirpated from this area, in part, because of a variety of anthropogenic stressors (S. Hansen, WDNR, personal communication). Over the past decade, the WDNR has documented increasing numbers of spawning lake whitefish in this river system. Initially, questions revolved around whether this was a rejuvenated, unique genetic lineage (repressed and never fully extirpated), or if this new spawning aggregates was founded with one or more neighboring stocks. A secondary study (data not shown) has shown this spawning aggregate is an admixture of multiple neighboring stocks. The dynamics of recolonization and the implications to the contemporary distribution of genetic diversity

in Lake Michigan are important considerations of continuing this research and/or monitoring of the lake whitefish resource. Monitoring these systems could help provide a better understanding of population abundances, stream versus lake spawning success, and potential mixing of stocks.

LITERATURE CITED

- Ackerman, M.W., C. Habicht, and L.W. Seeb, 2011. Single-nucleotide polymorphisms (SNPs) under diversifying selection provide increased accuracy and precision in mixed-stock analyses of sockeye salmon from the Copper River, Alaska. *Transactions of the American Fisheries Society* 140:865-881.
- Anderson, E.C., R.S. Waples, and S.T. Kalinowski. 2008. An improved method for estimating the accuracy of genetic stock identification. *Canadian Journal of Fisheries and Aquatic Sciences* 65:1.
- Baldwin, N.S., R.W. Saalfeld, M.S. Ross, and J.J. Buettner. 1979. Commercial fish production in the Great Lakes, 1867-1977. Great Lakes Fishery Commission, Technical Report 3, Ann Arbor, Michigan.
- Bernatchez, L. 2005. On the role of natural selection in promoting population divergence in lake whitefish (*Coregonus clupeaformis*): relevance for population management in the Great Lakes. Pages 21-46 in L.C. Mohr and T.F. Nalepa, editors. Proceeding of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. Great Lakes Fisheries Commission Technical Report 21, Ann Arbor, Michigan.
- Bernatchez, L., J.A. Vuorinen, R.A. Bodaly, and J.J. Dodson. 1996. Genetic evidence for reproductive isolation and multiple origins of sympatric trophic ecotypes of whitefish (*Coregonus*). *Evolution* 50(2):624-635.
- Bott, K., G.W. Kornely, M.C. Donofrio, R.F. Elliott, and K.T. Scribner. 2009. Mixed-stock analysis of lake sturgeon in the Menominee River sport harvest and adjoining waters of Lake Michigan. *North American Journal of Fisheries Management* 29:1636-1643.
- Brown, R.W., M.P. Ebener, and T. Gorenflo. 1999. Great Lakes commercial fisheries: historical overview and prognosis for the future. Pages 307-354 in W.W. Taylor and C. Paola Ferreri editors. Great Lakes fisheries policy and management a binational perspective. Michigan State University Press, East Lansing, Michigan.
- Cardin, S. X., K.D. Friedland, and J.R. Waldman. 2005. Stock identification methods: an overview. Pages 3-6 in S.X. Cardin, K.D. Friedland, and J.R. Waldman, editors. Stock identification methods application in fishery science. Elsevier Academic Press, Burlington, Massachusetts.
- DeCovich, N.A., and W.D. Templin. 2009. Genetic stock identification of Chinook salmon harvest on the Yukon River 2007. Alaska Department of Fish and Game, Fishery Data Series No. 09-39, Anchorage, AK.

- Ebener, M.P. 1980. Population dynamics of lake whitefish, *Coregonus clupeaformis*, in Green Bay and Lake Michigan east of Door County, Wisconsin. Master's thesis. University of Wisconsin-Stevens Point, Stevens Point, WI.
- Ebener, M.P. 1997. Recovery of lake whitefish populations in the Great Lakes: a story of successful management and just plain luck. *Fisheries* 22:18-20.
- Ebener, M.P., T.O. Brendon, G.M. Wright, M.L. Jone, and M. Faisal. 2010. Spatial and temporal distributions of lake whitefish spawning stocks in northern Lakes Michigan and Huron, 2003-2008. *Journal of Great Lakes Research* 36(Supplement 1):38-51.
- Ebener, M.P., and F.A. Copes. 1985. Population statistics, yield estimates, and management considerations for two lake whitefish stocks in Lake Michigan. *North America Journal of Fisheries Management* 5:435-488.
- Ebener, M.P., R.E. Kinnunen, P.J. Schneeberger, L.C. Mohr, J.A. Hoyle, and P.J. Peeters. 2008. Management of commercial fisheries for lake whitefish in the Laurentian Great Lakes of North America. Pages 99-143 in M.F. Schechter, N.J. Leonard, and W.W. Taylor, editors. *International governance of fisheries ecosystems: learning from the past, finding solutions for the future*. American Fisheries Society, Bethesda, Maryland.
- Fabrizio, M.C. 2005. Experimental design and sampling strategies for mixed-stock analysis. Pages 467-498 in S.X. Cardin, K.D. Friedland, and J.R. Waldman, editors. *Stock identification methods application in fishery science*. Elsevier Academic Press, Burlington, Massachusetts.
- Flannery, B.F., R.R. Holder, G.F. Maschmann, E.J. Kretschmer, and E.J. Wenburg. 2010. Application of mixed-stock analysis for Yukon River fall chum salmon, 2008. U.S. Fish and Wildlife Service, Office of Subsistence Management, Fisheries Resource Monitoring Program, Annual Report for Study 06-205, Anchorage, Alaska.
- Grant, W.S., G.B. Milner, P. Krasnowski, and F.M. Utter. 1980. Use of biogeochemical genetic variants for identification of sockeye salmon (*Oncorhynchus nerka*) stocks in Cook Inlet, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 37:1236-1247.
- Haugen, T.O., I.J. Winfield, L.A. Vøllestad, J.M. Fletcher, J.B. James, N.C. Stenseth. 2006. The ideal free pike: 50 years of fitness-maximizing dispersal. *Proceedings of the Royal Society B: Biological Sciences* 273:2917-2924.
- Healy, M. C. 1975. Dynamics of exploited whitefish populations and their management, with special reference to the Northwest Territories. *Journal of the Fisheries Research Board of Canada* 32:427-448.

- Imhoff, M.A., R.F. Leary, and H.E. Booke. 1980. Population stock structure of lake whitefish, *Coregonus culpeaformis*, in northern Lake Michigan as assessed by isozyme electrophoresis. *Canadian Journal of Fisheries and Aquatic Sciences* 37:783-793.
- Ihssen, P.E., H.E. Brooke, J.M. Casselman, J.M. McGlade, N.R. Payne, and F.M. Utter. 1981b. Stock identification: materials and methods. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1838-1855.
- Ihssen, P.E., D.O., Evans, and W.J. Christie, J.A. Reckahn, and R.L. DesJardine. 1981a. Life history, morphology, and electrophoretic characteristics of five allopatric stocks of lake whitefish (*Coregonus clupeaformis*) in the Great Lake region. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1790-1807.
- Kinnunen, R.E. 2003. Great Lakes commercial fisheries. Michigan Great Lakes Fisheries Leadership Institute Technology Report. Available <http://www.miseagrant.umich.edu/downloads/fisheries/GLCommercialFinal.pdf>. (June 2009).
- Leary, R. 1979. Population or stock structure of lake whitefish, *Coregonus culpeaformis*, in northern Lake Michigan as assessed by isozyme electrophoresis. Master's Thesis. University of Wisconsin-Stevens Point, Stevens Point, WI.
- Lindsey, C.C., J.W. Clayton, and W.G. Franzin. 1970. Zoogeographic problems and protein variation in the *Coregonus culpeaformis* whitefish species complex. Pages 124-147 in C.C. Lindsey and C.S. Woods, editors. *Biology of Coregonid fishes*. University of Manitoba Press, Winnipeg, Manitoba.
- MacLean, J.A. and D.O. Evans. 1981. The stock concept, discreteness of fish stocks, and fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1889-1898.
- Madenjian, C.P., G.L. Fahnenstiel, T.H. Johengen, T.F. Nalepa, H.A. Vanderploeg, G.W. Fleischer, P.J. Schneeberger, D.M. Benjamin, E.B. Smith, J.R. Bence, E.S. Rutherford, D.S. Laves, D.M. Robertson, D.J. Jude, and M. P. Ebener. 2002. Dynamics of the Lake Michigan food web, 1970-2000. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Modeling Subcommittee, Technical Fisheries Committee. 2009. Technical Fisheries Committee Administrative Report 2009: Status of Lake Trout and Lake Whitefish Populations in the 1836 Treaty-Ceded Waters of Lakes Superior, Huron and Michigan, with recommended yield and effort levels for 2009. D.C. Caroffino and S.J. Lenart, editors. Available: http://www.michigan.gov/documents/dnr/2009-status-report_303561_7.pdf (June 2010).

- Mulligan, T.J., S. McKinnell, and C.C. Wood. 1988. Uncertainty in stock composition estimates of oceanic steelhead trout using eletrophoretic characteristics: comments on a recent study. *Canadian Journal of Fisheries Management* 7:459-474.
- Nalepa, T.F., L.C. Mohr, B.A. Henderson, C.P. Madenjian, and P.J. Schneeberger. 2005. Lake whitefish and *Diporeia* spp. in the Great Lakes: an overview. Pages 21-46 in L.C. Mohr and T.F. Nalepa, editors. *Proceedings of a Workshop on the Dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the Amphipod *Diporeia* spp. in the Great Lakes*, Ann Arbor, Michigan.
- Patton, J.C., B.J. Gallaway, R.G. Fechhelm, and M.A. Cronin. 1997. Genetic variation of microsatellite and mitochondrial DNA genetic markers in broad whitefish (*Coregonus nasus*) in the Colville and Sagavanirktok rivers in northern Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1548-1556.
- Pella, J.J., and G.B. Milner. 1987. Use of genetic marks in stock composition analysis. Pages 247-276 in N. Ryman and F. Utter, editors. *Population genetics & fishery management*. University of Washington Press, Seattle, Washington.
- Pompanon, F., A. Bonin, and P. Taberlet. 2005. Genotyping errors: causes, consequences, and solutions. *Nature Reviews Genetics* 6:847-856.
- Pothoven, S.A., T.F. Nalepa, P.J. Schneeberger, and S.B. Brandt. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. *North American Journal of Fisheries Management* 21:876-833.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223-225.
- Rogers, S.M. and L. Bernatchez. 2006. The genetic basis of intrinsic and extrinsic post-zygotic reproductive isolation jointly promoting speciation in the lake whitefish species complex (*Coregonus clupeaformis*). *Journal of Evolutionary Biology* 19:1979-1994.
- Rogers, S.M and L. Bernatchez. 2007. The genetic architecture of ecological speciation and the association with signatures of selection in natural lake whitefish (*Coregonus* sp. Salmonidae) species pairs. *Molecular Biology and Evolution* 24:1423-1438.
- Rogers, S.M., M.H. Marchand, and L. Bernatchez. 2004. Isolation, characterization and cross-salmonid amplification of 31 microsatellite loci in lake whitefish (*Coregonus clupeaformis*, Mitchill). *Molecular Ecology Notes* 4:89-92.

- Rowe, M. 1984. Population dynamics of lake whitefish in the Big Bay de Noc, Bark and Cedar Rivers, and Portage Bay areas of Lake Michigan. Master's thesis. University of Wisconsin Stevens Point, Stevens Point, Wisconsin.
- Scheerer, P.D., and W.W. Taylor. 1985. Population dynamics and stock differentiation of lake whitefish in northeastern Lake Michigan with implication for their management. *North American Journal of Fisheries Management* 5:526-536.
- Schneeberger, P.J., M.P. Ebener, M. Toney, and P.J. Peeters. 2005. Status of lake whitefish (*Coregonus clupeaformis*) in Lake Michigan. Great Lakes Fisheries Commission Technical Report 66:67-86.
- Scott, W.B., E.J. Crossman. 1973. Freshwater fishes of Canada. Crown Copyrights, Ottawa, Canada.
- Shaklee, J.B., and K.P. Currens. 2003. Genetic stock identification and risk assessment. Pages 291-328 in E.M. Hallerman, editor. Population genetics: principles and application for fisheries scientists. American Fisheries Society, Bethesda, Maryland.
- Spangler, G.R., A.H. Berst, J.F. Koonce. 1981. Perspectives and policy recommendations on the relevance of the stock concept to fishery management. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1908-1914.
- Stott, W., J.A. VanDeHey, B.L. Sloss. 2010. Genetic diversity of lake whitefish in lakes Michigan and Huron; sampling, standardization, and research priorities. *Journal of Great Lake Research* 36:59-65.
- Technical Support by Minitab. Technical Support Document Chi-square Test Assumptions. Available: <http://www.minitab.com/support/documentation/Answers/Chi-Square%20Test%20Assumptions.pdf>. (November 2011).
- Turgeon, J., A. Estoup, and L. Bernatchez. 1999. Species flock in the North American Great Lakes: molecular ecology of Lake Nipigon ciscoes (Teleostei: Coregonidae: *Coregonus*). *Evolution* 55:2274-2286.
- United State Geological Survey 2009. Commercial fishing reports: total pounds and dollar value of commercial catch in U.S. waters of the Great Lakes by year, state, lake and species. Available: http://www.glsc.usgs.gov/_files/cfreports/noaa07.txt. (June 2010).
- Utter, F. and N. Ryman. 1993. Genetic markers and mixed stock fisheries. *Fisheries* 18:11-21.

- VanDeHey, J.A. 2007. Genetic structure among Lake Michigan's lake whitefish spawning aggregates. Master's thesis. University of Wisconsin Stevens Point, Stevens Point, Wisconsin.
- VanDeHey, J.A., B.L. Sloss, P.J. Peeters, and T.M. Sutton. 2009. Genetic Structure of lake whitefish (*Coregonus clupeaformis*) in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 66(3):382-393.
- VanDeHey, J.A., B.L. Sloss, P.J. Peeters, and T.M. Sutton. 2010. Determining the efficacy of microsatellite DNA-based mixed stock analysis of Lake Michigan's lake whitefish commercial fishery. Journal of Great Lakes Research 36:52-58.
- Waldman, J.R. 2005. Meristics. Pages 197-210 in S.X. Cardin, K.D. Friedland, and J.R. Waldman, editors. Stock identification methods application in fishery science. Elsevier Academic Press, Burlington, Massachusetts.
- Walker, S.H., M.W. Prout, W.W. Taylor, and S.R. Winterstein. 1993. Population dynamics and management of lake whitefish stocks in Grand Travers Bay, Lake Michigan. North American Journal of Fisheries and Aquatic Sciences 13:73-85.
- Wells, L., and A.L. McClain. 1973. Lake Michigan: man's effects on native fish stocks and other biota. Great Lakes Fishery Commission, Technical Report 20.
- Wood, C.C., S. McKinnell, T.J. Mulligan, and D.A. Fournier. 1987. Stock identification with the maximum-likelihood mixture model: sensitivity analysis and application to complex problems. Canadian Journal of Fisheries and Aquatic Science 44:866-881.

Table 1. Great Lake commercial fish harvest by kgs and value (U.S. Dollars) in the year 2009.

Species	Scientific Name	Total kg	Total Value
Lake Whitefish	<i>Coregonus clupeaformis</i>	4,682,742	\$ 11,112,595
Cisco	<i>Coregonus artedii</i>	563,791	\$ 714,863
Chubs	<i>Coregonus hoyi</i>	166,726	\$ 833,216
Lake Trout	<i>Salvelinus namaycush</i>	389,315	\$ 858,293
Yellow Perch	<i>Perca flavescens</i>	737,895	\$ 2,802,428
Walleye	<i>Sander vitreus</i>	22,134	\$ 81,868
Channel Catfish	<i>Ictalurus punctatus</i>	276,290	\$ 230,920
Rainbow Smelt	<i>Osmerus mordax</i>	25,914	\$ 126,990

Table 2. Yield (kg) and value (U.S. Dollars) of the lake whitefish commercial harvest in the Great Lakes during 2009.

Great Lakes	Total kg	U.S. Dollars	Percent of Great
			Lakes Harvest
Lake Erie	135,136.96	\$ 301,136	3%
Lake Superior	729,757.09	\$ 1,576,194	16%
Lake Huron	1,294,489.12	\$ 3,335,961	28%
Lake Michigan	2,523,358.85	\$ 5,899,304	54%
Lake Ontario	-	-	-
Total	4,682,742.02	\$ 11,112,595	

Table 3. Lake Michigan commercial fish harvest by kgs and value in the year 2009 (USGS Report).

Species	Scientific Name	Total kgs	U.S. Values
Rainbow smelt	<i>Osmerus mordax</i>	20,239	\$ 120,490
Burbot	<i>Lota lota</i>	5,539	\$ 4,325
Lake Whitefish	<i>Coregonus culpeaformis</i>	2,523,359	\$ 5,899,304
Round Whitefish	<i>Prosopium cylindraceum</i>	4,074	\$ 6,101
Chubs	<i>Coregonus hoyi</i>	139,334	\$ 717,964
Lake Trout	<i>Salvelinus namaycush</i>	177,509	\$ 163,215
Yellow Perch	<i>Perca flavescens</i>	28,252	\$ 155,084
Walleye	<i>Sander vitreus</i>	5,044	\$ 17,692

Table 4. Microsatellite and primers, primer sequences, observed allele size range in base pairs (microsatellites), number of alleles observed (A), and references. Locus code refers to the specific microsatellite locus.

Locus		Primer Sequence (5'-3')	Allele size (bp)	A	Reference
Locus	Code				
Cocl-23	C23	gctgatgagatagcattc gcattaggtcgtttgtg	250-278	16	Bernatchez 1996
Bwf-1	B1	gatcagagaaatacacacaacgcatcaa cagcgggtccattactgagcac	187-225	14	Patton et al. 1997
Bwf-2	B2	gggatacatcggcaacctctg agacagtcccaatgagaaaa	139-165	12	Patton et al. 1997
Cocl-lav 18	C18	aacaaactaaaacatcccaagtc ttagattggggcctacctg	142-160	7	Rogers et al. 2004
Cocl-lav 68	C68	gtgtgttacaagtggctatg gtgatggctttcagaggc	173-183	6	Rogers et al. 2004
Cocl-lav 4	C4	tggtgtaatggctttctctg gggagcaacattggactctc	146-154	5	Rogers et al. 2004
Cocl-lav 41	C41	aaacaacagtggaggagtg gccagcactctctcatgctttt	180-230	19	Rogers et al. 2004
Cocl-lav 6	C6	gccatcatctcccaggaac cagggaatctgcactggagc	126-147	19	Rogers et al. 2004
Cocl-lav 45	C45	gagtgacagcaggagcag ggctcgggtgaaagttgaga	239-259	10	Rogers et al. 2004
Cocl-lav 28	C28	acaatagcaggccattcagg ccaatcttcaaagccatttca	166-178	7	Rogers et al. 2004
Cocl-lav 52	C52	ggcgattgggagagtgatta acagagccccagatggtaac	90-164	36	Rogers et al. 2004
C2-157	C157	cttagatgatggctgctcc ggtgcaatcactcttacaacacc	119-191	28	Turgeon et al 1999

Table 5. PCR reaction concentrations and fluorescent labels. Multiplex indicates loci amplified in the same PCR reaction with the corresponding thermal cycling profiles provided as footnotes.

Locus Code	Multiplex	10X Buffer (Conc.)	dNTPs (mM)	MgCl ₂ (mM)	Primer F (Conc.)	Primer R (Conc.)	Taq (U)	Label
C28	1	2.0X	0.20	2.00	0.20	0.20	0.50	Hex
C41	2	1.5X	0.20	1.50	0.20	0.20	0.50	Ned
C23	3	1.0X	0.20	2.00	0.10	0.10	0.50	6-Fam
B2					0.03	0.30		6-Fam
C18	4	2.0X	0.20	2.10	0.32	0.32	0.50	Hex
C68					0.25	0.25		Ned
C4					0.08	0.08		6-Fam
C45	5	1.0X	0.20	1.50	0.10	0.10	0.50	Hex
C52					0.10	0.10		6-Fam
B1	6	1.4X	0.20	1.4	0.22	0.22	0.25	Ned
C157					0.10	0.10		Hex
B1	7	1.4X	0.20	1.70	0.25	0.25	0.50	Ned
C6					0.08	0.08		Ned
1	95° C for 3 min. 8 series of 5 cycles each at 94° C for 30s, then 63, 62.5, 62, 61.5, 61, 60.5, 60, and 59° C annealing for 30s. 72° C for 30s then a final elongation of 72° C for 7 min.							
2	94° C for 5 min. 2 series of 5 cycles each at 94° C for 30 s, then 63, and 62° C annealing for 30 s, then 72° C for 30 s. Then 2 series of 8 cycles each at 94° C for 30 s, then 61, and 60.5° C annealing for 30 s, then 72° C for 30 s. Then a final series of 5 cycles of 94° C for 30 s, then 60° C annealing for 30 s, then 72° C for 30 s and a final elongation of 72° C for 7 min.							
3	94° C for 3 min. 6 series of 5 cycles each at 94° C for 30 s, then 60, 59, 58, 57, 56, and 55° C annealing for 30 s. 72° C for 1 min then a final elongation of 72° C for 7 min.							
4	95° C for 3 min. 1 series of 35 cycles each at 95° C for 30 s, then 57° C annealing for 30 s. 72° C for 1 min then a final elongation of 72° C for 7 min.							
5	95° C for 1 min. 1 series of 35 cycles each at 94° C for 1 min, then 62° C annealing for 1 min. 72° C for 50 s then a final elongation of 72° C for 7 min.							
6	95° C for 3 min. 1 series of 35 cycles each at 95° C for 30 s, then 60° C annealing for 30sec. 72° C for 1 min then a final elongation of 72° C for 30 min.							
7	95° C for 3 min. 1 series of 35 cycles each at 95° C for 30 s, then 60° C annealing for 30sec. 72° C for 1 min then a final elongation of 72° C for 7 min.							

Table 6. Reference location and reporting stocks from VanDeHey et al. (2007).

Location	Stock	Stock Abbreviation
Epoufette	Northern	NOR
Naubinway	Northern	NOR
Grand Traverse Bay	Northern	NOR
Hog Island	Northeastern	NOE
Elk Rapids	Elk Rapids	ER
Saugatuck	Southern	SOE
Muskegon	Southern	SOE
Ludington	Southern	SOE
North and Moonlight Bays	North and Moonlight Bays	NMB
Big Bay de Noc	Big Bay de Noc	BBN

Table 7. Results of mixed-stock analysis of the 18 commercial harvest samples from 2009-2010 including and the number of genetic samples (N). Grid represents the commercial fishing grid that the sample was collected. Values for each stock represent the proportion of that stock. The numbers below estimates represent the 95% confidence interval of the estimate.

Location	Grid	Season	Year	N	Genetic Stocks					
					NOR	NOE	EKR	SOU	NMB	BBN
WI-2	507	Spring	2009	137	0.096	0.127	0	0	0.3822	0.3952
					0.026-0.351	0.029-0.264	0.000-0.022	0.000-0.101	0.140-0.518	0.137-0.535
WFM-01	604	Spring	2009	129	0.106	0.176	0.000	0.012	0.226	0.481
	804				0.025-0.352	0.036-0.317	0.000-0.031	0.000-0.076	0.057-0.386	0.228-0.605
WI-2	506	Summer	2009	122	0.1925	0.0676	0	0.0001	0.2967	0.4431
					0.026-0.363	0.005-0.248	0.000-0.000	0.000-0.114	0.110-0.458	0.215-0.590
WFM-01	408	Summer	2009	135	0.0577	0.1143	0	0	0.3306	0.4974
					0.001-0.280	0.010-0.256	0.000-0.024	0.000-0.063	0.125-0.498	0.250-0.650
WFM-04	316	Summer	2009	145	0.2154	0.6906	0	0.015	0.0395	0.0395
					0.074-0.444	0.409-0.741	0.000-0.060	0.000-0.092	0.000-0.221	0.000-0.181
WI-2	706	Fall	2009	120	0.1137	0.121	0	0.0003	0.0696	0.6954
					0.016-0.343	0.009-0.284	0.000-0.032	0.000-0.092	0.000-0.320	0.323-0.737

Table 7. Continued.

Location	Grid	Season	Year	N	Genetic Stocks					
					NOR	NOE	EKR	SOU	NMB	BBN
WFM-01	408	Fall	2009	121	0.1028	0.0854	0	0	0.1964	0.6154
					0.001-0.356	0.008-0.266	0.000-0.006	0.000-0.042	0.023-0.367	0.332-0.723
WFM-02	409	Fall	2009	78	0.0568	0.1261	0	0	0.5293	0.2879
					0.000-0.357	0.004-0.330	0.000-0.016	0.000-0.167	0.162-0.668	0.015-0.526
WFM-03	N/A	Fall	2009	132	0.4041	0.3401	0	0	0.1712	0.0847
					0.194-0.584	0.149-0.451	0.000-0.045	0.000-0.135	0.001-0.310	0.000-0.280
WI-2	605	Spring	2010	127	0.0599	0.1192	0	0	0.4764	0.3445
					0.000-0.265	0.018-0.285	0.000-0.052	0.000-0.088	0.158-0.632	0.118-0.563
WFM-01	408	Spring	2010	128	0.0521	0.1066	0	0	0.2206	0.6207
					0.003-0.299	0.019-0.255	0.000-0.012	0.000-0.061	0.031-0.364	0.342-0.717
WFM-06	912	Spring	2010	142	0.0129	0.18	0	0.6806	0.1265	0
					0.000-0.184	0.036-0.303	0.000-0.025	0.496-0.785	0.000-0.230	0.000-0.156

Table 7. Continued.

					Genetic Stocks					
Location	Grid	Season	Year	N	NOR	NOE	EKR	SOU	NMB	BBN
WI-2	606	Summer	2010	146	0.0762	0.1514	0	0	0.3624	0.41
					0.496-0.270	0.029-0.273	0.000-0.030	0.000-0.093	0.163-0.507	0.206-0.533
WFM-01	408	Summer	2010	145	0.0467	0.1329	0	0.0918	0.0658	0.6628
					0.001-0.277	0.022-0.268	0.000-0.028	0.010-0.194	0.000-0.248	0.366-0.714
WFM-05	716	Summer	2010	138	0.0632	0.6429	0.0392	0.1294	0.0363	0.0889
					0.000-0.285	0.371-0.7001	0.000-0.132	0.045-0.273	0.000-0.216	0.000-0.218
WFM-08	1810	Summer	2010	115	0.0375	0.1541	0.0054	0.803	0	0
					0.000-0.239	0.017-0.304	0.000-0.049	0.577-0.877	0.000-0.119	0.000-0.083
WI-2	706	Fall	2010	132	0.0984	0.1667	0	0.02	0.3164	0.3985
					0.018-0.364	0.036-0.305	0.000-0.036	0.000-0.119	0.089-0.472	0.175-0.560
WFM-01	408	Fall	2010	139	0.0371	0	0	0.0334	0.2263	0.7032
					0.000-0.276	0.000-0.145	0.000-0.027	0.000-0.113	0.060-0.441	0.340-0.784

Table 8. Two-way chi-square results for spatial and temporal comparisons of 2009 samples.

	WI-2 Spring	WFM-01 Spring	WI-2 Summer	WFM-01 Summer	WFM-04 Summer	WI-2 Fall	WFM-01 Fall	WFM-02 Fall
WFM-01 Spring	$\chi^2 = 7.78$ 3 df p = 0.051							
WI-2 Summer	$\chi^2 = 8.08$ 3 df p = 0.044	$\chi^2 = 10.56$ 3 df p = 0.014						
WFM-01 Summer	$\chi^2 = 3.21$ 3 df p = 0.360	$\chi^2 = 6.79$ 3 df p = 0.079	$\chi^2 = 11.05$ 3 df p = 0.011					
WFM-04 Summer	$\chi^2 = 141.04$ 3 df p < 0.001	$\chi^2 = 115.38$ 3 df p < 0.001	$\chi^2 = 138.51$ 3 df p < 0.001	$\chi^2 = 157.09$ 3 df p < 0.001				
WI-2 Fall	$\chi^2 = 37.72$ 3 df p < 0.001	$\chi^2 = 16.40$ 3 df p < 0.001	$\chi^2 = 28.27$ 3 df p < 0.001	$\chi^2 = 28.39$ 3 df p < 0.001	$\chi^2 = 135.17$ 3 df p < 0.001			
WFM-01 Fall	$\chi^2 = 14.35$ 3 df p = 0.002	$\chi^2 = 6.55$ 3 df p = 0.088	$\chi^2 = 9.20$ 3 df p = 0.027	$\chi^2 = 7.68$ 3 df p = 0.053	$\chi^2 = 149.77$ 3 df p < 0.001	$\chi^2 = 9.67$ 3 df p = 0.022		
WFM-02 Fall	$\chi^2 = 5.43$ 3 df p = 0.143	$\chi^2 = 20.35$ 3 df p < 0.001	$\chi^2 = 18.53$ 3 df p < 0.001	$\chi^2 = 10.17$ 3 df p = 0.017	$\chi^2 = 120.74$ 3 df p < 0.001	$\chi^2 = 57.58$ 3 df p < 0.001	$\chi^2 = 28.59$ 3 df p < 0.001	
WFM-03 Fall	$\chi^2 = 76.50$ 3 df p < 0.001	$\chi^2 = 66.10$ 3 df p < 0.001	$\chi^2 = 68.63$ 3 df p < 0.001	$\chi^2 = 95.50$ 3 df p < 0.001	$\chi^2 = 37.68$ 3 df p < 0.001	$\chi^2 = 99.76$ 3 df p < 0.001	$\chi^2 = 94.49$ 3 df p < 0.001	$\chi^2 = 63.02$ 3 df p < 0.001

Table 9. Two-way chi-square results for spatial and temporal comparisons of 2010 samples.

	WI-2 Spring	WFM-01 Spring	WFM-06 Spring	WI-2 Summer	WFM-01 Summer	WFM-05 Summer	WFM-08 Summer	WI-2 Fall
WFM-01 Spring	$\chi^2 = 22.30$ 3 df $p < 0.001$							
WFM-06 Spring	$\chi^2 = 170.65$ 4 df $p < 0.001$	$\chi^2 = 184.29$ 4 df $p < 0.001$						
WI-2 Summer	$\chi^2 = 3.65$ 3 df, $p = 0.301$	$\chi^2 = 11.85$ 3 df, $p = 0.008$	$\chi^2 = 180.81$ 4 df $p < 0.001$					
WFM-01 Summer	$\chi^2 = 68.69$ 4 df $p < 0.001$	$\chi^2 = 22.97$ 4 df $p < 0.001$	$\chi^2 = 166.29$ 4 df $p < 0.001$	$\chi^2 = 51.76$ 4 df $p < 0.001$				
WFM-05 Summer	$\chi^2 = 141.34$ 5 df $p < 0.001$	$\chi^2 = 143.05$ 5 df $p < 0.001$	$\chi^2 = 117.53$ 5 df $p < 0.001$	$\chi^2 = 135.25$ 5 df $p < 0.001$	$\chi^2 = 118.33$ 5 df $p < 0.001$			
WFM-08 Summer	$\chi^2 = 205.08$ 4 df $p < 0.001$	$\chi^2 = 206.32$ 4 df $p < 0.001$	$\chi^2 = 16.00$ 2 df $p < 0.001$	$\chi^2 = 215.60$ 4 df $p < 0.001$	$\chi^2 = 170.88$ 4 df $p < 0.001$	$\chi^2 = 117.36$ 5 df $p < 0.001$		
WI-2 Fall	$\chi^2 = 9.76$ 4 df $p = 0.045$	$\chi^2 = 14.41$ 4 df $p = 0.006$	$\chi^2 = 159.21$ 4 df $p < 0.001$	$\chi^2 = 4.28$ 4 df $p = 0.370$	$\chi^2 = 39.33$ 4 df $p < 0.001$	$\chi^2 = 111.82$ 5 df $p < 0.001$	$\chi^2 = 191.32$ 4 df $p < 0.001$	
WFM-01 Fall	$\chi^2 = 50.64$ 4 df $p < 0.001$	$\chi^2 = 21.11$ 4 df $p < 0.001$	$\chi^2 = 211.70$ 4 df $p < 0.001$	$\chi^2 = 44.01$ 4 df $p < 0.001$	$\chi^2 = 33.55$ 4 df $p < 0.001$	$\chi^2 = 188.50$ 5 df $p < 0.001$	$\chi^2 = 229.77$ 4 df $p < 0.001$	$\chi^2 = 41.01$ 4 df $p < 0.001$

Table 10. Chi-squared tests of equal stock proportions for all 18 samples collected from the Lake Michigan commercial catch.

Location	Season	Year	Chi-square	df	P-Value
WI-2	Spring	2009	72.548	5	<0.0001
WFM-01	Spring	2009	60.463	5	<0.0001
WI-2	Summer	2009	65.542	5	<0.0001
WFM-01	Summer	2009	83.548	5	<0.0001
WFM-04	Summer	2009	111.685	5	<0.0001
WI-2	Fall	2009	58.747	5	<0.0001
WFM-01	Fall	2009	76.718	5	<0.0001
WFM-02	Fall	2009	47.984	5	<0.0001
WFM-03	Fall	2009	68.398	5	<0.0001
WI-2	Spring	2010	76.467	5	<0.0001
WFM-01	Spring	2010	85.030	5	<0.0001
WFM-06	Spring	2010	111.592	5	<0.0001
WI-2	Summer	2010	79.256	5	<0.0001
WFM-01	Summer	2010	86.137	5	<0.0001
WFM-05	Summer	2010	72.228	5	<0.0001
WFM-08	Summer	2010	114.819	5	<0.0001
WI-2	Fall	2010	57.815	5	<0.0001
WFM-01	Fall	2010	116.814	5	<0.0001
Global	All	2010	493.150	5	<0.0001
Global	All	2010	410.496	5	<0.0001
Global	All	2009 & 2010	784.634	5	<0.0001
Weighted Global	All	2009	124.89	4	<0.0001
Weighted Global	All	2010	100.42	4	<0.0001
Weighted Global	All	2009 & 2010	327.52	5	<0.0001

Table 11. Two-way chi-square results for temporal analysis of WI-2 (NMB) samples.

	Spring 2009	Summer 2009	Fall 2009	Spring 2010	Summer 2010
Summer 2009	$\chi^2 = 8.08$ 3 df p = 0.044				
Fall 2009	$\chi^2 = 37.72$ 3 df p < 0.001	$\chi^2 = 28.27$ 3 df p < 0.001			
Spring 2010	$\chi^2 = 2.81$ 3 df p = 0.421	$\chi^2 = 16.67$ 3 df, p = 0.001	$\chi^2 = 54.12$ 3 df p < 0.001		
Summer 2010	$\chi^2 = 0.78$ 3 df p = 0.854	$\chi^2 = 12.10$ 3 df p = 0.007	$\chi^2 = 36.39$ 3 df p < 0.001	$\chi^2 = 3.654$ 3 df p = 0.301	
Fall 2010	$\chi^2 = 4.68$ 4 df p = 0.322	$\chi^2 = 12.24$ 4 df p = 0.016	$\chi^2 = 33.52$ 4 df p < 0.001	$\chi^2 = 9.76$ 4 df p = 0.045	$\chi^2 = 4.28$ 4 df p = 0.370

Table 12. Two-way chi-square results for temporal analysis of WFM-01 (BBN) samples.

	Spring 2009	Summer 2009	Fall 2009	Spring 2010	Summer 2010
Summer 2009	$\chi^2 = 6.79$ 3 df p = 0.079				
Fall 2009	$\chi^2 = 6.55$ 3 df p = 0.088	$\chi^2 = 7.68$ 3 df p = 0.053			
Spring 2010	$\chi^2 = 6.59$ 3 df, p = 0.086	$\chi^2 = 4.86$ 3 df, p = 0.182	$\chi^2 = 2.20$ 3 df p = 0.532		
Summer 2010	$\chi^2 = 31.35$ 4 df p < 0.001	$\chi^2 = 40.66$ 4 df p < 0.001	$\chi^2 = 23.57$ 4 df p < 0.001	$\chi^2 = 22.97$ 4 df p < 0.001	
Fall 2010	$\chi^2 = 40.05$ 4 df p < 0.001	$\chi^2 = 29.04$ 4 df p < 0.001	$\chi^2 = 20.84$ 4 df p < 0.001	$\chi^2 = 21.11$ 4 df p < 0.001	$\chi^2 = 33.55$ 4 df p < 0.001

Figure 1. Commercial management units used to monitor population dynamics of lake whitefish in Lake Michigan. Zones in Wisconsin waters include WI-1, WI-2, and WI-3. All other zones are in Michigan waters (WFMs) and were originally established by the 1836 Consent Decree.

Figure 2. The six genetic stocks of lake whitefish identified in Lake Michigan by VanDeHey et al. (2009): North and Moonlight Bays (NMB), Big Bay de Noc (BBN), Northern (NOR), Northeastern (NOE), Elk Rapids (ER), and Southern (SOE).

Figure 3. Lake Michigan statistical commercial fishing grids.

Figure 4. Proportional stock harvest of the six randomly chosen commercial fishing samples.

Figure 5. Proportional stock harvest of the two primary commercial sample zones, WFM-01 and WI-2. Relative size of the gray circle is indicative of the range of locations sampled from these two management units.