ASSESSING THE CHANGE IN LAKE WHITEFISH *(COREGONUS CLUPEAFORMIS)* MATURITY SCHEDULES FROM 1976-2013 IN THE UPPER GREAT LAKES

By

Marissa Lynn DeCosta

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ABSTRACT

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Maturation schedules often vary within a given fish species, between individuals, and among different stocks within a population. These variations in maturation schedules can usually be linked to plastic or adaptive responses as a result of changes within the environment.

This study assessed the change in Lake Whitefish maturity schedules in the U.S. waters of lakes Huron, Michigan, and Superior from 1976 to 2013 to better understand how maturity schedules have changed over time in order to help inform the future management of the Lake Whitefish fishery. To do this, I evaluated fishery independent and fishery dependent biological data from Lake Whitefish managers by performing a logistic regression using 'R' software's 'glm' function, which is a general linear model that produced estimates for length and age at 50% maturity.

Results indicated that Lake Whitefish population maturation schedules varied through time, temporally, spatially, and sexually among populations in all three lakes. Females generally matured at older ages and longer lengths (5.0 years-old and 439 mm) than males (4.6 years-old and 419 mm). I found that the L_{50} for both sexes declined significantly in lakes Huron and Michigan after the year 1990, and both sexes in Lake Superior matured at larger lengths (F= 458 mm, M= 447 mm) for given ages than fish in lakes Huron and Michigan. These finding are likely a result of plastic responses due to ecological changes in the food web coupled with Lake Whitefish abundance. Continued monitoring of maturity schedules could help fishery managers to better understand how Lake Whitefish response mechanisms occur due to changes within the environment as a way to help inform future management decisions surrounding the harvest of Lake Whitefish..

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Introductory Summary

In the upper Great Lakes, Lake Whitefish *(Coregonus clupeaformis)* represent the most economically valuable commercial fishery, having an average catch valued at U.S.$16.6 million from 1994-2004 (Ebener et al. 2008). Lake Whitefish became an important food source incorporated into the diets of aboriginal people and European settlers following the late 1700's when the commercial harvest of Lake Whitefish began (Kinietz 1965; Cleland 1982; Ebener et al. 2008). Thus, Lake Whitefish are not only economically important, but also culturally significant in the Great Lakes region (Ebener et al. 2008). Since the 1990's Lake Whitefish growth and condition has declined within lakes Huron and Michigan, which has been attributed to declines in *Diporeia* and increased abundance in Lake Whitefish populations (Madenjian et al. 2002). Understanding how Lake Whitefish maturity schedules may fluctuate in response to such changes within the ecosystem could help fishery managers enhance the predictive capabilities of the models that are used to estimate future recruitment and yield as a way to ensure the continued sustainability of the Lake Whitefish fishery by.

Fish maturation schedules can vary within a given species, between individuals, and among different stocks within a population, as is the case with Lake Whitefish. These variations in maturation schedules can often be attributed to plastic or adaptive responses as a result of changes that occur in the environment, such as changes in mortality (natural and fishing), physical habitats, or competition between species or individuals.

The goal of this thesis was to assess the change in Lake Whitefish maturity schedules in the U.S. waters of lakes Huron, Michigan, and Superior from 1976 to 2013 to better understand how maturity schedules may have changed as the ecosystem in the Great Lakes was impacted by invasive species, which could help to enhance the inputs of population models used by fishery managers to estimate Lake Whitefish population abundance and set harvest quotas. To achieve this goal, I used a logistic regression to calculate estimates of length and age at 50% maturity over this time period using both fishery independent and fishery dependent biological data obtained from Lake Whitefish managers and commercial fishing operators. Perhaps the most important finding of this study was that Lake Whitefish length and age at 50% maturity did fluctuate significantly over time, and those fluctuations happened relatively quickly, sometimes within five years. Lake Whitefish managers currently set regulations based on a population model that predicts maturity as a constant; as evidence by this study, that is not the case. As such, this information could be useful for future management discussions regarding the population models that are used to predict Lake Whitefish abundance and set harvest quotas.

Introduction

Maturation Schedules and the Mechanisms that Influence Variation

Analysis of maturation schedules (the timing and size at which fish reach sexual maturity), can help us to better understand changes in fishery population dynamics in response to environmental conditions (Trippel 1995; Ficker 2014)**.** Maturation schedules often vary within a given species, between individuals, and among different stocks within a population (Jensen 1981; Ficker et al. 2014); variations in maturation schedules can be linked to plastic and adaptive responses to changes within the environment (Wang 2009). Plastic responses in maturation can result from maturation schedules that might vary because of fluctuations in growth or mortality rates, and adaptive responses can result from maturation schedules that might vary because of selection-induced circumstances (Wang et al. 2008).

Maturation schedules vary across Lake Whitefish populations within the Great Lakes region because sexual maturity is directly related to growth potential (Wang et al. 2008), which is generally the expected growth rate of individual stocks living in a specific body of water with known biological and physical characteristics (Budy et al. 2011). There is also a direct relationship between the age and length at which Lake Whitefish become mature; stocks that have a higher growth potential are likely to reach maturity at a larger size because they grow faster, whereas stocks with a lower growth potential reach maturity at a smaller size because they grow more slowly (Jensen 1985; Taylor et al. 1992; Wang et al. 2008). In general, Lake Whitefish in the upper Great Lakes typically achieve sexual maturity between 370 to 550 mm and 4-12 years of age with males usually reaching sexual maturity before females (Ebener et al. 2008).

Influence of Maturation Schedules on Recruitment and Yield of Fish Populations

Maturation schedules can affect the recruitment and subsequent yield of fish populations through impacts on a fish’s lifetime reproductive success, along with the overall productivity of the population (Jensen 1981). Recruitment of Lake Whitefish in the Great Lakes (the number of fish that survive to enter the fishery each year) relies on adult stock size and water temperatures that are optimal for spawning, incubation, and development of new individuals, all of which depend on abiotic and biotic variables (Brown et al. 1993). Therefore, the overall yield of a population depends on the successful recruitment of fish. When fish mature earlier, lifetime egg production can increase as long as environmental conditions, such as temperature, competition, food source availability, and commercial harvest are suitable for fish growth and survival (Jensen 1981; Brown et al. 1993). However, when environmental conditions are not suitable for fish growth and survival, fish may need to expend less energy on either growth or reproduction so maturation occurs earlier and at smaller sizes (Kratzer 2006; Kratzer et al. 2007). Having less energy available for growth and/or reproduction can lead to potential negative impacts on a fish's lifetime reproductive output through potentially decreased egg production, and therefore, recruitment and population yield (Kratzer 2006; Kratzer et al. 2007).

In addition, fluctuations in maturation schedules that lead to declines in Lake Whitefish growth rates can have negative impacts on recruitment because body size and fecundity have been shown to be positively correlated (Kratzer et al. 2007). Under circumstances when fish have less energy available for growth, even less energy may be available to expend on egg production and the development of larger lipid stores for each egg, thus potentially decreasing both the egg quantity and quality (Kratzer et al. 2007). If fish produce lower quality eggs, year-class strength and recruitment can be negatively impacted because a large lipid store has been shown to be an important factor for the survival of developing larval Lake Whitefish before they switch to exogenous feeding (Pothoven et al. 2001; Kratzer et al. 2007). However, Muir et al. (2009) found no evidence to show that parental conditions were critical to the survival of larval/juvenile individuals. It is possible that female condition can impact fish on an individual basis, but at the stock level, Muir et al. (2009) suggest that environmental conditions or density-dependent growth dynamics have more of an impact on recruitment than parental condition. Nevertheless, because changes in maturation schedules have been shown to influence recruitment and yield through fecundity and reproductive success, it is important for fishery managers to understand what biological mechanisms may be influencing variations in maturation schedules as way to help predict year-class strength and changes in Lake Whitefish population dynamics years in advance should egg quality and quantity decline as a result of fluctuating maturity schedules.

Impacts of Size-Selective Fishery Exploitation on Maturation Schedules

Because Lake Whitefish are highly economically valued within the Great Lakes region, it is also important to understand how fishery exploitation could impact maturation schedules. In previous studies of exploited Lake Whitefish stocks, it has been suggested that Lake Whitefish will compensate for exploitation by maturing at smaller sizes and at younger ages. Because of this, Lake Whitefish could have potentially higher fecundity over a lifetime than Lake Whitefish from unexploited stocks because individuals may have more years to reproduce (Wang 2009) as long as environmental conditions, such as temperature, competition, and food source availability support increased fecundity (Jensen 1981; Brown et al. 1993).

Lake Whitefish have been shown to exhibit density-dependent growth dynamics, meaning that growth rates can depend on the density of the population. For example, Kratzer et al. (2007) found that declines in Lake Whitefish growth rates during the 1990's were more closely linked to the increase in abundance of Lake Whitefish than to the availability of *Diporeia*, which had declined in density around the same time. Even though Lake Whitefish abundance increased, less food and therefore, energy for growth was available per individual. Because density-dependent growth dynamics exist among Lake Whitefish populations, growth rates can also be elastic in response to factors such as fishery exploitation, which directly impacts Lake Whitefish densities (Kratzer et al. 2007; Claramunt et al. 2010). Some authors have suggested that increasing growth rates in the case of fishery exploitation (maturing at smaller sizes and at younger ages) is a compensatory response due to declines in population density and intraspecific competition (Henderson et al. 1983; Wang et al. 2008).

Maturing at smaller sizes and at younger ages has implications for populations because it has been hypothesized that prolonged exploitation can have impacts on the genetic make-up of populations, especially related to changes in growth rates (Nalepa et al. 2005; Kratzer 2006). Prolonged changes to growth rates occur under heavy exploitation because fish that grow faster tend to be harvested at a higher rate than fish that grow slower because they generally reach the minimum length limit for harvest sooner. This in turn can minimize the chances that faster growing fish have to spawn before being harvested, unless they reach sexual maturity before reaching the minimum size limit for harvest. Slower growing fish can then be left making up the majority of the spawning stock and will produce offspring that typically display slower growth (Conover and Munch 2002; Nalepa et al. 2005; Kratzer 2006). If Lake Whitefish are growing more slowly and are maturing earlier or at smaller sizes in response to size-selective fishery exploitation, then their offspring are more likely to grow slower and mature earlier or at smaller sizes, which can again, have impacts on recruitment because body size and fecundity have been shown to be positively correlated (Kratzer et al. 2007).

Importance of Understating Lake Whitefish Maturation Schedules in the Great Lakes

It has been shown that Lake Whitefish exhibit slower growth rates, and therefore reach sexual maturity later in Lake Superior than in lakes Huron and Michigan (Taylor et al. 1992). These slower growth rates have been attributed to the fact that Lake Superior is colder, has fewer invasive species, and has lower primary production than lakes Huron and Michigan (Barbiero and Tuchman 2001; Ebener et al. 2008; EPA 2013). Although Lake Whitefish in lakes Huron and Michigan have historically had higher growth rates, and therefore reach sexual maturity earlier than Lake Whitefish in Lake Superior, there have been recently noted declines in their growth (Schneeberger et al. 2005). This decline in growth rate has been attributed to two factors: 1) density-dependent responses as a result of increases in Lake Whitefish abundance in recent years, coupled with declines in body condition (Mohr and Ebener 2005; Schneeberger et al.

2005), and 2) declines in the density of Lake Whitefish's preferred nutrient dense and energy rich food source, *Diporeia* (McNickle et al. 2006; Pothoven et al. 2001). The decline in *Diporeia* that occurred during the 1990's when invasive zebra mussels *(Dreissena polymorpha)* spread throughout lakes Huron and Michigan (Nalepa et al. 2005) led to direct competition for food between zebra mussels and D*iporeia,* more so than in Lake Superior (Mills et al. 2005).

In addition to zebra mussels, invasive sea lamprey *(Petromyzon marinus)* predation and fishing mortality have also been linked to the decline in growth rate, along with earlier sexual maturation of Lake Whitefish in lakes Huron and Michigan (Baldwin et al. 2002; Ebener et al. 2005; Schneeberger et al. 2005). The sea lamprey invaded the upper Great Lakes region in the late 1930's, and by the 1950's and 1960's their predation on Lake Whitefish in lakes Huron and Michigan became widespread and intense (Nalepa et al. 2005). In addition to increased mortality rates due to sea lamprey, lakes Huron and Michigan also had historically larger commercial fisheries for Lake Whitefish than Lake Superior (D. Caroffino, Fisheries Biologist, Michigan Department of Natural Resources, personal communication). Lake Whitefish in lakes Huron and Michigan have therefore experienced more size-selective mortality on adult fish due to fishery exploitation and sea lamprey predation than Lake Whitefish in Lake Superior (Baldwin et al. 2002; Mohr and Ebener 2005; Schneeberger et al. 2005). Size-selective mortality on adults tends to cause an adaptive response where overtime, fish begin to mature earlier and at smaller sizes. This adaptive response can ultimately help to improve lifetime reproductive success. For example, in the case of size-selective sea lamprey predation and fishery exploitation, maturing earlier and at a smaller size might increase the chance that an individual has to spawn before being harvested or preyed upon (Wang 2009).

Lake Whitefish Management

At present, the Lake Whitefish fishery in the upper Great Lakes is cooperatively managed according to the terms of the 2000 Consent Decree, which is a court-ordered agreement between the Michigan Department of Natural Resources (MDNR), the United States Fish and Wildlife Service (USFWS), and five Native American tribes with regard to the management and allocation of the Lake Whitefish fishery in order to ensure the future sustainability of Lake Whitefish populations. The Decree applies to areas covered by the 1836 Treaty of Washington and the 1842 Treaty of LaPointe. This court-ordered agreement dictates that Lake Whitefish populations will be cooperatively managed through harvest quotas that are estimated annually based on catch-at-age models, along with a 17 inch (432mm) legal length limit (Ebener et al. 2005; Modeling Subcommittee, Technical Fisheries Committee 2013). The catch-at-age models forecast Lake Whitefish recruitment based on a stock-recruitment function that does not include empirical data on pre-recruits, or other environmental factors that may influence recruitment, such as variation in food abundance or temperature. In addition, the models used to manage the Lake Whitefish fishery also incorporate maturity schedules as something that is constant through time. These factors make it difficult to accurately forecast Lake Whitefish year-class strength years before they recruit to the fishery (Brown 1991; Claramunt et al. 2010).

Because the Lake Whitefish fishery is managed based on models that use a constant rate for maturity, no information on pre-recruits, a 17 inch (432mm) legal length limit, and harvest quotas (Ebener et al. 2005; Modeling Subcommittee, Technical Fisheries Committee 2013), it is essential that fishery managers understand fluctuations in Lake Whitefish maturity schedules as a way to enhance the predictive capabilities of the models that are used to estimate future recruitment and yield of Lake Whitefish to ensure that the fishery remains viable in the future.

Goals and Objectives

The goal of this study was to evaluate changes in the maturity schedules of Lake Whitefish from 1976 to 2013 in the U.S. waters of lakes Huron, Michigan, and Superior to better understand how Lake Whitefish maturity schedules have changed over time, along with the possible contributing factors, in order to enhance the future management of the Lake Whitefish fishery.

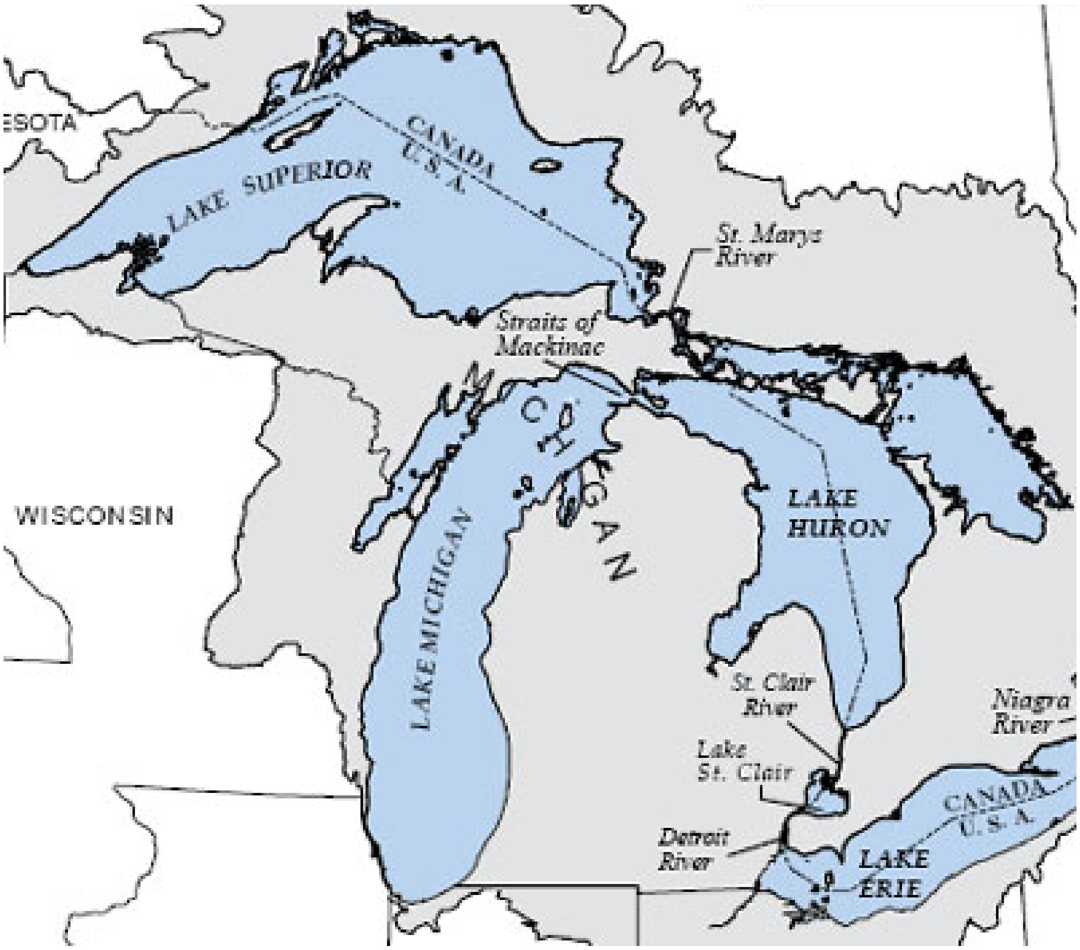
The main objectives of this study were to 1) use fishery independent and fishery dependent Lake Whitefish biological data obtained from fishery managers and associated commercial operators to evaluate any change in length and age at maturity from 1976 to 2013 in lakes Huron, Michigan, and Superior; 2) determine if there is a significant difference between the overall trend in length and age at maturity when comparing results from fishery independent and fishery dependent data, and 3) present future management implications surrounding the commercial Lake Whitefish fishery.

Methods

Site Selection

This study focused on the U.S. waters of lakes Huron, Michigan, and Superior, all of which are managed cooperatively by the States of Michigan, Minnesota, Wisconsin, and the Tribes of the 1836 and 1842 Treaty areas of Washington and LaPointe. The location of the U.S. waters within lakes Huron and Superior (all of Lake Michigan is comprised of U.S. waters) are illustrated on Figure 1 by the dotted line that passes through lakes Huron and Superior.

FIGURE 1. A map of the U.S. waters of lakes Huron, Michigan, and Superior that are cooperatively managed by the States of Michigan, Minnesota, Wisconsin and five Native American Tribes. U.S. waters are illustrated by the dotted line that passes through lakes Huron and Superior (Wilcox et al. 2007).



Lake Whitefish Data Used for Analysis

The data used for evaluating the change in Lake Whitefish maturity schedules in lakes Huron, Michigan, and Superior from 1976-2013 came from datasets that are maintained by the Michigan Department of Natural Resources (MDNR), the Wisconsin Department of Natural Resources (WDNR), the United States Fish and Wildlife Service (USFWS), the Little Traverse Bay Bands of Odawa Indians (LTBB), the Grand Traverse Band of Ottawa and Chippewa Indians (GTB), and the Chippewa Ottawa Resource Authority (CORA). Each of the data sets that were acquired contained Lake Whitefish biological information that included the following: total length (mm), age, sex, and maturity status. In addition to biological data, sample collection date, Lake Whitefish management unit, the aging structure used for aging (scale, otolith, or fin ray), gear type, and survey type classified as either fishery independent or fishery dependent were obtained. Fishery dependent data is defined as data collected on fish harvested as part of the commercial fishery, and fishery independent data is defined as data collected on fish harvested by fishery managers as part of their yearly monitoring efforts.

Aging fish using scales can be biased for slow growing Lake Whitefish that are older than 7 years-old because annuli can be hard to identify, but scales are typically accurate for exploited, fast growing Lake Whitefish younger than 7 years-old (Mills and Beamish 1980; Wang 2009). Because the Lake Whitefish populations in lakes Huron, Michigan, and Superior are exploited, I decided not to exclude Lake Whitefish records when scales were used for aging.

I chose to incorporate fishery independent and fishery dependent data into the evaluation of Lake Whitefish maturity schedules for two reasons. The first reason is size selectivity. Fishery independent data are capable of sampling Lake Whitefish of all sizes due to the utilization of varying catch methods and mesh sizes, which provide data on fish that are both smaller and larger than fish that would be harvested by commercial fishing gear (fishery dependent data). Including fishery independent data in this analysis allowed me to evaluate maturity schedules using a wider range of fish sizes. Even though fishery independent data can tell us about all fish sizes, it is still important to understand what is happening with the population of fish that is actually being harvested by commercial fishermen. The second reason that I chose to incorporate both types of data into my evaluation of Lake Whitefish maturity schedules was to determine if there was a difference between the conclusions regarding the change in maturity schedules based on data type (fishery independent vs. fishery dependent). Making this determination would allow me to make management suggestions surrounding the future need and/or use for fishery independent and fishery dependent sampling in Lake Whitefish research and management.

I evaluated each of the three lakes (Huron, Michigan, and Superior) separately because of their ecological differences as outlined: 1) Of the three lakes, Lake Superior is the largest by volume, deepest, and coldest, Lake Michigan is the second largest by volume, and Lake Huron is the third largest by volume (EPA 2012), 2) Over the time period studied, lakes Michigan and Huron both had larger commercial fisheries than Lake Superior, and 3) Lake Superior has been least impacted by invasive species in comparison to lakes Huron and Michigan (Ebener et al. 2008). Because of these known ecological differences, along with the fact that each lake is managed separately in terms of harvest quotas, it made the most sense to perform this analysis on a lake-by-lake basis. I did not have access to data that would allow me to perform the analysis for each management unit; therefore, the analysis was performed on the whole fishery by lake.

I also evaluated the change in length and age at 50% maturity by sex because males and females exhibit different maturity schedules (Ebener et al. 2008). Because the sexes are known to display differing maturity schedules, I felt it made the most sense to separate them when analyzing the data to avoid skewing the results.

Description of Lake Whitefish Biological Data

The fishery independent data that were used to evaluate lakes Huron, Michigan and Superior came from the USFWS, LTBB, GTB, WDNR, and MDNR. The data were collected between January and December from 1971 to 2013, using graded mesh gill nets ranging in size from 2-6 inches, trap nets with 4.5 inch mesh size, bottom gill nets, and a bottom trawl survey with an unspecified mesh size. Scales, otoliths, and fin rays were taken from fish collected and later used for aging.

The fishery dependent data that were used came from the MDNR, CORA's Inter-Tribal Fisheries Assessment Program (ITFAP), LTBB, and WDNR. The data were collected from the commercial fishery between January and December from 1976 to 2013, using both large (4.5 inch) and small (2.5 inch) mesh commercial trap nets, and large mesh gill nets ranging in size from 4.5 to 6 inches. Scales, otoliths, and fin rays were used as aging structures.

Tables 1, 3, and 5 summarize the data sources, timing of data collection, and gear types from both fishery independent and fishery dependent data obtained for lakes Huron, Michigan and Superior. Tables 2, 4, and 6 show the total number (N) of Lake Whitefish records that were used for the evaluation of Lake Whitefish maturity schedules in lakes Huron, Michigan, and Superior based on the data summarized in Tables 1, 3, and 5.

TABLE 1. Summary of data sources (United States Fish and Wildlife Service (USFWS), Little Traverse Bay Bands of Odawa Indians (LTBB), Michigan Department of Natural Resources (MDNR), and Chippewa Ottawa Resource Authority's Inter-Tribal Fisheries Assessment Program (CORA ITFAP)), timing of data collection, and gear types used in Lake Huron.

Fishery Independent			
Source	**Months**	**Years**	**Gear Types Used**
USFWS	May - Oct	2002 - 2012	Graded mesh gill net, mesh size ranges 2-6"
LTBB	May - Aug	2005 - 2013	Graded mesh gill net, mesh size ranges 2-6"
Fishery Dependent			
Source	**Months**	**Years**	**Gear Types Used**
MDNR	April - Dec	1981 - 2013	Commercial trap net, mesh size 4.5"
CORA ITFAP	Jan - Dec	1988 - 2013	Commercial trap net, mesh size 4.5" Commercial trap net, mesh size 2.5"
LTBB	May - Aug	2005 - 2013	Commercial gill net, mesh size 4.5"

TABLE 2. Total number (N) of Lake Whitefish records used to determine A_{50} and L_{50}'s over time in Lake Huron sorted by sex and data source type. The N for each year includes data that has been compiled from all data sources.

	Fishery Independent		Fishery Dependent	
Year	**Females**	**Males**	**Females**	**Males**
1975			278	
1976			345	
1977			1025	1115
1978			487	568
1979			372	389
1980			527	542
1981			422	455
1982			618	581
1983			353	346
1984			269	294
1985			277	310
1986			399	442
1987	44		497	669
1988	39		521	
1989	33		716	
1990	32	67	900	1134
1991	72	82	1219	1604
1992	58	75	1295	
1993	70	83	1494	
1994	100	134	1853	2241
1995	139	126	1836	2400
1996	99	143	1631	1894
1997	124	145	1146	1329
1998	232	265	917	1006
1999	147	206	658	743
2000	143	173	566	638
2001	114	160	469	531
2002	47	88	393	439
2003	31	57	298	396
2004	25	33	217	287
2005	47	38		163
2006		9		72
2007		10		

TABLE 3. Summary of data sources (Grand Traverse Band of Ottawa and Chippewa Indians (GTB), Little Traverse Bay Bands of Odawa Indians (LTBB), Michigan Department of Natural Resources (MDNR), Wisconsin Department of Natural Resources (WDNR), and Chippewa Ottawa Resource Authority's Inter-Tribal Fisheries Assessment Program (CORA ITFAP)), timing of data collection, and gear types used in Lake Michigan.

Fishery Independent			
Source	**Months**	**Years**	**Gear Types Used**
GTB	Jan - Dec	1985 - 2012	Graded mesh gill net, mesh size ranges 2-6" Trap net, mesh size 4.5" Trawl, unspecified mesh size
LTBB	April - Dec	1998 - 2013	Graded mesh gill net, mesh size ranges 2-6"
MDNR	April - Oct	1978 - 2012	Graded mesh gill net, mesh size ranges 2-6"
WDNR	Aug - Sept	2009 - 2012	Bottom gill net, unspecified mesh size Bottom trawl net, unspecified mesh size
Fishery Dependent			
Source	**Months**	**Years**	**Gear Types Used**
MDNR		2002 - 2012	Commercial gill net, mesh size 4.5"
WDNR	Aug - Sept	2009 - 2012	Commercial trap net, mesh size 4.5"
CORA ITFAP	Jan - Nov	1980 - 2013	Commercial trap net, mesh size 4.5" Commercial trap net, mesh size 2.5" Commercial large mesh gill net, mesh size ranges 4.5-6"
LTBB	April - Dec	1998 - 2013	Commercial gill net, mesh size 4.5"

TABLE 4. Total number of Lake Whitefish records used to determine A_{50} and L_{50}'s over time in Lake Michigan sorted by sex and data source type. The N for each year includes data that has been compiled from all data sources.

	Fishery Independent		Fishery Dependent	
Year	**Females**	**Males**	**Females**	**Males**
1974	304	374		
1975	796	924		
1976	543	738		
1977	694	920		
1978	357	484		
1979	159	269	260	290
1980	224	309	286	307
1981	508	555		425
1982	336	552	1032	1007
1983	121	140	749	
1984	36	41	545	655
1985	22		523	589
1986			643	743
1987			530	547
1988			655	594
1989			594	
1990			639	624
1991			819	
1992			603	528
1993			561	
1994	126	111		624
1995	183	211	960	921
1996	149	228	1208	1175
1997	214	284	1476	1499
1998	302	394	1367	1489
1999	200	330		
2000	205	298	748	878
2001	225	355	681	880
2002	213	273	588	688
2003	187	247	761	754
2004	113	146	559	
2005	92	111	445	402
2006	69	90	304	247
2007	83	68	172	79
2008		46	35	

TABLE 5. Summary of data sources (Michigan Department of Natural Resources (MDNR), and Chippewa Ottawa Resource Authority's Inter-Tribal Fisheries Assessment Program (CORA ITFAP)), timing of data collection, and gear types used in Lake Superior.

Fishery Independent			
Source	**Months**	**Years**	**Gear Types Used**
MDNR	May - Oct	1971 - 2013	Graded mesh gill net, mesh size ranges 2-6"
Fishery Dependent			
Source	**Months**	**Years**	**Gear Types Used**
CORA ITFAP	Jan - Dec	1966 - 2013	Commercial trap net, mesh size ranges 4.5-6" Commercial large mesh gill net, mesh size ranges 4.5-6"

TABLE 6. Total number of Lake Whitefish records used to determine A_{50} and L_{50}'s over time in Lake Superior sorted by sex and data source type. The N for each year includes data that has been compiled from all data sources.

	Fishery Independent		**Fishery Dependent**	
Year	**Females**	**Males**	**Females**	**Males**
1972	49			
1973	107			
1974	107	91		
1975		49	197	337
1976			105	232
1980			106	93
1981		32	67	81
1982			33	
1983	61	60		
1984		69		
1985	25			
1986		108		
1987	18			
1989			467	
1990	92	98	584	779
1991	100	179	726	932
1992	59		460	559
1993			401	502
1994		40	513	669
1995			437	488
1996			251	340
1997			248	332
1998	140	168	183	211
1999		85	76	98
2000		57		73
2001		19		
2003		1		
2004		3		42

Data Preparation

The first step of this analysis was to evaluate the change in Lake Whitefish maturity schedules from 1976 to 2013 in lakes Huron, Michigan, and Superior by examining each dataset to exclude the following: entries with no recorded length or age, or unknown sex. Any years that did not have at least 20 records each of Lake Whitefish determined by fishery managers to be immature and mature were also excluded in an effort to eliminate any potential biases as a result of having a small sample size, which could minimize the precision of estimates surrounding the change in maturity schedules of Lake Whitefish (Gustafson 1988).

The second step was to obtain a cohort year for each Lake Whitefish record in order to perform this study using a cohort analysis. I decided to evaluate Lake Whitefish maturity schedules using a cohort-based approach because my study follows research similar to that conducted by Wang et al. (2008). Their study used a cohort-approach to assess Lake Whitefish maturity schedules from 1971-2005, and for my study and results to be comparable I choose to follow their methodology. To determine the cohort year, the recorded age of each fish was subtracted from the sample year in which the biological data were collected. For example, if a fish was recorded to be 5 years old in the data set and was sampled in 1995, the cohort year for that fish was 1990 (i.e. the year it was born). Performing a cohort analysis makes it easier to relate the success or year-class strength of one year-class, to environmental conditions, even if only temporary, that may have impacted their growth and condition overtime.

The final step for preparing the biological data for analysis was to standardize the data from multiple agencies as follows: sex was assigned a 1 (representing female) or a 2 (representing male), gear type was assigned a 1 (representing fishery independent) or a 2 (representing fishery dependent), and maturity was assigned a 0 (representing immature) or a 1 (representing mature). Categorizing the sex, gear type, and maturity status numerically allowed me to import and use the data in the statistical package R (V.2.15.1) to perform the logistic regression (Schluter 2014).

Analysis

To determine the age (A_{50}) and length (L_{50}) at 50% maturity for lakes Huron, Michigan, and Superior, I used the same methods as those performed by Wang et al. (2008) for studying the maturity schedules of Lake Whitefish within the upper Great Lakes – a cohort analysis done by lake, sex, and data source (fishery independent vs. fishery dependent). Wang et al. (2008) conducted their study using a logistic regression over two time frames: cohorts before 1990 and cohorts after 1990. I decided to conduct my analysis on a yearly basis for two reasons: I wanted to look at the change in length and age at 50% maturity on a yearly scale, and I was able to obtain additional data that allowed me to do so.

The first phase of my analysis was to estimate the age (A_{50}) and length (L_{50}) at 50% maturity, or the age and length at which 50% of the Lake Whitefish population within a cohort is mature. Because there can be both plastic and adaptive responses to changes in the environment within a cohort (Law 2000; Beauchamp et al. 2004; Wang et al. 2008), some individuals may mature early, while others may mature late, therefore, using ages or lengths when the first (less than 50%) or all Lake Whitefish (100%) are mature may not represent the majority of the cohort. Estimating changes in maturity schedules based on when 50% of the Lake Whitefish population within a cohort was mature can provide a better representation of the 'average' Lake Whitefish within each cohort (D. Caroffino, Fisheries Biologist, Michigan Department of Natural Resources, personal communication). I performed a logistic regression using R Software's 'glm' function (Rodriguez 2014) to determine the A_{50} and L_{50}'s. This is a general linear model function that performs a logistic regression and allows for a binary response to account for the fact that this study investigated maturity, which has two responses (immature or mature). The following equation was used to determine the A_{50} and L_{50}'s for four categories: 1) females from fishery dependent data, 2) females from fishery independent data, 3) males from fishery dependent data, and 4) males from fishery independent data within lakes Huron, Michigan, and Superior:

1. glm(formula, family=binomial(link=logit))

Within this equation, maturity status was set as 0=immature or 1=mature, the age or length of each individual fish was the predictor and was specified in the 'formula'. Once the logistic regression was performed, the A_{50} and L_{50}'s were calculated by dividing the negative intercepts by the slopes of the estimated logistic curves (Wang et al. 2008).

After obtaining the estimates for the A_{50} and L_{50}'s, a 95% confidence interval was estimated for each of the four data categories using bootstrap techniques (Wang et al. 2008). This procedure was also used by Wang et al. (2008) to determine the significance of the results for both A_{50} and L_{50}. To bootstrap the data, a boot function was developed where individual fish samples were randomly selected with replacement so that 1000 sets of data were created. The 'glm' function was again used to fit a logistic regression on the bootstrapped data to generate new estimates for A_{50} and L_{50}'s (Wang et al. 2008). The following function and equations were used to bootstrap Lake Whitefish biological data to obtain new estimates for A_{50} and L_{50}'s:

1. ```
   boot.reg.fx<-function(data,indices) {
   Y<-data[indices,]
   reg.boot<-glm(formula, family=binomial(link=logit))
   -reg.boot$coefficients[1]/reg.boot$coefficients[2]
   }
   ```

2. boot(data, statistic=boot.regfx,R=1000)

3. boot.ci(data)
   ```

To evaluate differences among the A_{50} and L_{50}'s for the four categories of data (as previously described) in lakes Huron, Michigan, and Superior, the A_{50} and L_{50}'s were plotted over time, and the 95% confidence intervals were compared visually (Wang et al. 2008). If the 95% confidence intervals for two estimates of either A_{50} or L_{50} did not overlap, then the estimates were determined to vary significantly (Wang 2009).

Results

Summary of Findings

Variation in maturation schedules based on estimates of A_{50} and L_{50}

The age and length at 50% maturity (A_{50} and L_{50}) differed over time between males and females and among lakes Huron, Michigan, and Superior. In general, males matured before females based on both fishery independent and fishery dependent data (Figures 6 – 29 in Appendices 1.1, 1.2, and 1.3). The A_{50} and L_{50} varied among all three lakes, with Lake Whitefish in Lake Michigan having generally younger A_{50}'s by one year on average, and shorter L_{50}'s by 20 mm on average than fish in lakes Huron and Superior based on both fishery independent and fishery dependent data. Lake Whitefish in Lake Superior often had the oldest A_{50}'s (2.7 – 7.5 years-old) and longest L_{50}'s (310 mm – 525 mm) compared to lakes Huron (2.9 – 6.9 years-old and 374 mm – 512 mm) and Michigan (1.5 – 5.9 years-old and 370 mm – 477 mm) based on both fishery independent and fishery dependent survey data (Figures 6 – 29 in Appendices 1.1, 1.2, and 1.3).

Among Lake Whitefish populations in lakes Huron and Michigan, similar increasing or decreasing trends over time were seen between A_{50} and L_{50}'s for both fishery independent and fishery dependent data. For example, if the L_{50} followed a declining trend for two to three years, the same declining trend could be seen in the L_{50}'s among both lakes when looking at fishery independent and fishery dependent data from the same years. During the year 1990, the values for L_{50} decreased significantly and the values for A_{50} increased significantly (Figures 6 – 21 in Appendices 1.1 and 1.2) for Lake Whitefish in lakes Huron and Michigan. In Lake Superior, the values for A_{50} and L_{50} did not change significantly around the year 1990 (Figures 22 – 29 in Appendix 1.3), as was seen in lakes Huron and Michigan.

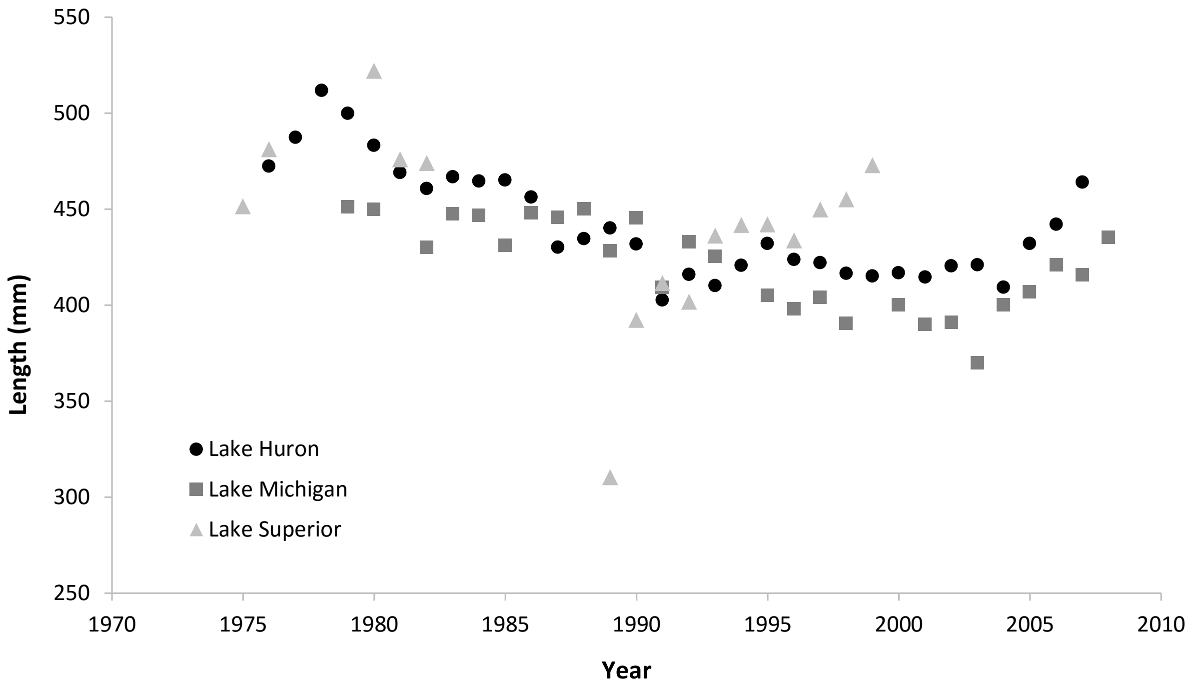
In general, at least 50% of the Lake Whitefish populations in lakes Huron and Michigan were observed to reach sexual maturity as early as 370 mm, before reaching the minimum length limit (432 mm) for harvest; whereas, at least 50% of the Lake Whitefish populations in Lake Superior generally did not reach sexual maturity before reaching the minimum length limit for harvest. Instead, females were maturing between 434 mm and 522 mm, and males were maturing between 444 mm and 479 mm (Figures 6 – 29 in Appendices 1.1, 1.2, and 1.3). For lakes Huron and Michigan, Lake Whitefish became sexually mature before reaching the legal length limit for harvest after the year 1990. Prior to the year 1990, the length at 50% maturity for Lake Whitefish was, in general, greater than the legal length limit for harvest in lakes Huron (433 mm to 476 mm) and Michigan (431 mm – 438 mm) (Figures 6 – 21 in Appendices 1.1. and 1.2).

Among all lakes, A_{50} ranged from 2 to 8 years-old for both sexes, but was most frequently observed between 3 and 6 years old (Figures 6 – 29 in Appendices 1.1, 1.2, and 1.3). The L_{50} ranged from 370 to 550 mm, but was most frequently observed between 400 and 500 mm (Figures 6 – 29 in Appendices 1.1, 1.2, and 1.3). The 95% confidence intervals for the A_{50} and L_{50}'s were generally wider for fishery independent data than fishery dependent data in lakes Huron and Superior, while the 95% confidence intervals for the A_{50} and L_{50}'s were wider for fishery dependent data than fishery independent data in Lake Michigan, potentially due to the difference in the amount of data available. The variability in confidence intervals can be seen in Figures 6 – 29 in Appendices 1.1, 1.2, and 1.3.

Comparing Trends for Estimates of L_{50} Among all Lakes over the Time Frame Studied

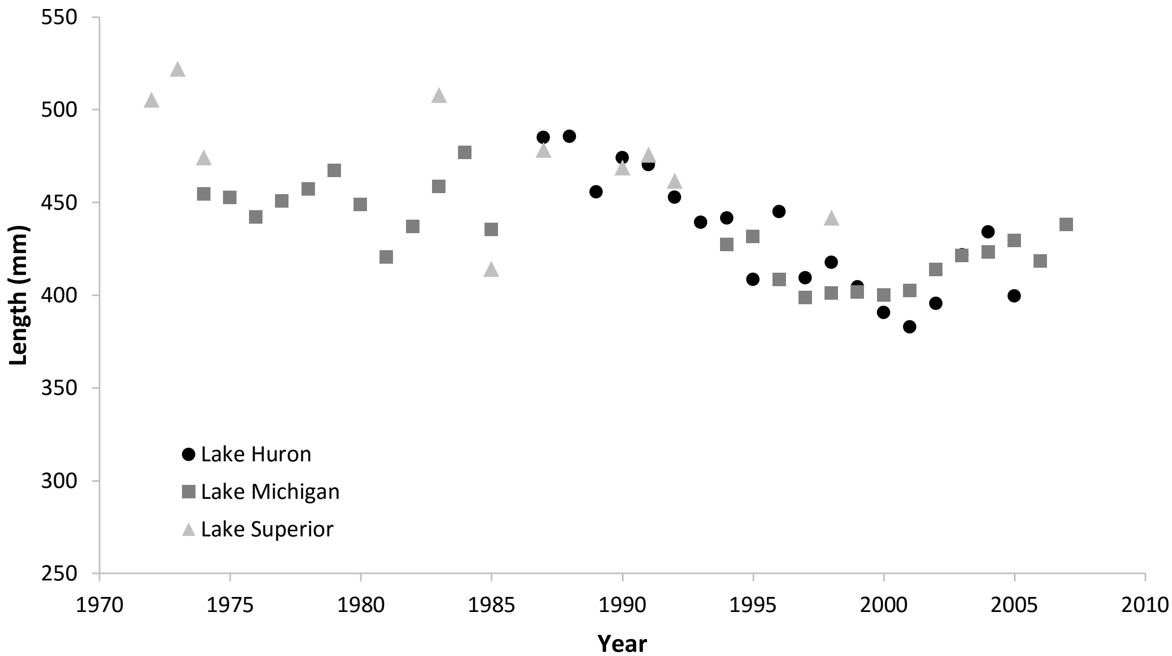
The length at 50% maturity for female Lake Whitefish among lakes Huron, Michigan, and Superior based on fishery independent data are shown in Figure 2. As depicted in the figure, lakes Huron (black dots) and Michigan (gray squares) followed a similar pattern over the time frame studied, with L_{50} being generally greater, with differences in L_{50} ranging from 9 to 48 mm, in Lake Huron than in Lake Michigan. Lake Superior (light gray triangles) followed a pattern similar to that seen in lakes Huron and Michigan from 1975 to 1993. After 1993, the L_{50} increased from 435 mm to 472 mm in Lake Superior through 1999, whereas it decreased from 425 mm to 390 mm throughout this timeframe in lakes Huron and Michigan when Lake Whitefish abundances increased and invasive species impacted the availability of food sources.

FIGURE 2. Length at 50% maturity for female Lake Whitefish among lakes Huron, Michigan, and Superior based on commercial fishery monitoring data.



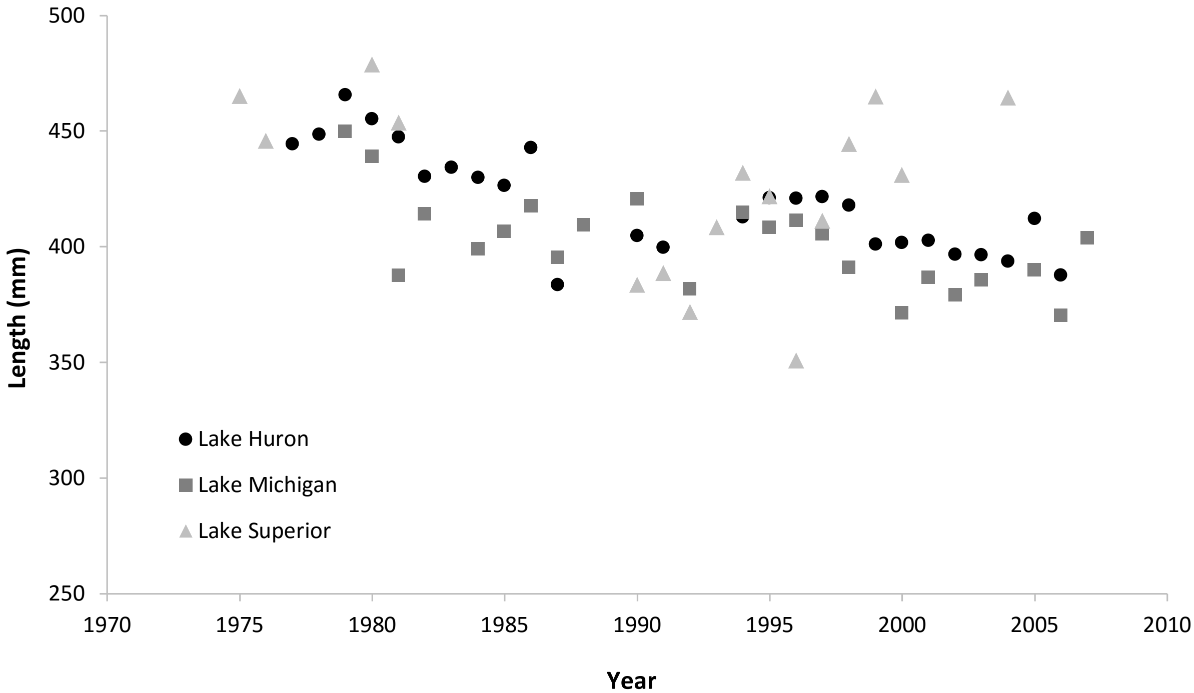
The length at 50% maturity for female Lake Whitefish among lakes Huron, Michigan, and Superior based on fishery independent survey data are shown in Figure 3. As depicted in the figure, the L_{50}'s for lakes Huron (black dots) and Michigan (gray squares) followed a similar declining pattern over the time frame studied, with differences between the L_{50}'s ranging from as little as 1 mm to 30 mm. Lake Superior's (light gray triangles) L_{50}'s were more variable prior to 1985, with values that ranged from 414 to 522 mm, but from 1987 to 1998, they declined, similar to those of lakes Huron and Michigan (478 mm to 400 mm). The patterns in the L_{50}'s over the time frame studied for females from fishery dependent data (Figure 3) and fishery independent data (Figure 2) are similar. This finding suggests that the results from fishery independent and fishery dependent survey data are be comparable to one another when thinking about the future use of both in Lake Whitefish management.

FIGURE 3. Length at 50% maturity for female Lake Whitefish among lakes Huron, Michigan, and Superior based on fishery independent survey data.



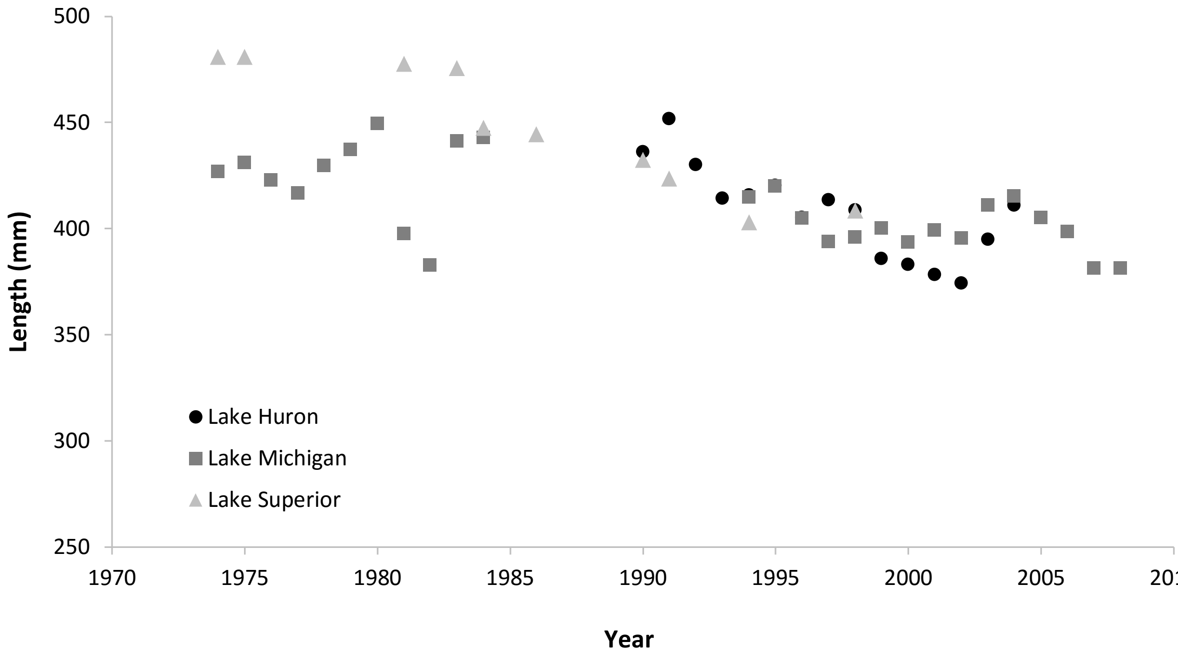
The length at 50% maturity for male Lake Whitefish among lakes Huron, Michigan, and Superior based on commercial fishery monitoring data are shown in Figure 4. As depicted in the figure, the length at 50% maturity for lakes Huron (black dots) and Michigan (gray squares) follow a similar declining trend over the course of the time frame studied. Prior to 1990, the difference between the values of the lengths at 50% maturity seen in lakes Huron and Michigan ranged anywhere from 10 to 50 mm. After 1990, the ranges between the values of the lengths at 50% maturity in both lakes declined, and were not more than 30 mm different. Lake Superior (light gray triangles) did not follow the same overall declining trend that was observed throughout the study period in lakes Huron and Michigan; the lengths at 50% maturity fluctuated over time, ranging from 351 to 465 mm. However, prior to 1992 in Lake Superior, the length at 50% maturity followed a declining trend (465 to 372 mm), but after 1992, the length at 50% maturity began following an increasing trend and reached a value of 464 mm in 2004.

FIGURE 4. Length at 50% maturity for male Lake Whitefish among lakes Huron, Michigan, and Superior based on commercial fishery monitoring data.



The length at 50% maturity for male Lake Whitefish among lakes Huron, Michigan, and Superior based on fishery independent data are shown in Figure 5. The length at 50% maturity for lakes Huron (black dots) and Michigan (gray squares) followed similar fluctuating patterns to one another after 1990. Prior to 1990, data was not available for Lake Huron. In general, Lake Michigan had slightly larger lengths at 50% maturity, with values for L_{50} that were only 5-15 mm greater than values for L_{50} in Lake Huron. Lake Superior did not follow the same pattern as Lake Michigan prior to 1990; the lengths at 50% maturity were greater, sometimes by 100 mm or more, in Lake Superior than they were in Lake Michigan. After 1990 however, the L_{50} in all three lakes decreased from 451 mm in 1991 to 381 mm in 2008. When comparing the patterns in the L_{50}'s over the time frame studied in Figure 4 (males from fishery dependent data) to the patterns seen in the L_{50}'s depicted in Figure 5 (males from fishery independent data), it can be concluded that the results from fishery independent and fishery dependent survey data could be comparable to one another when thinking about the future use of both in Lake Whitefish management.

FIGURE 5. Length at 50% maturity for male Lake Whitefish among lakes Huron, Michigan, and Superior based on fishery independent survey data.



Recent Trends

Estimates of A_{50} and L_{50} in Lake Huron

The L_{50} for females evaluated by fishery independent data decreased insignificantly over the last 10 years of the data set (1995: 408 mm to 2005: 399 mm), while the L_{50} for females evaluated by fishery dependent data increased significantly (1997: 422mm to 2007: 464mm). The estimates for A_{50} from females evaluated by both fishery independent and fishery dependent data did not have a discernable trend (Table 7).

The L_{50} for males evaluated by fishery independent and fishery dependent data both showed an insignificant decreasing trend over the last 10 years of the data set (1994: 416 mm to 2004: 411 mm and 1996: 421 mm to 2006: 388 mm). The A_{50} for males evaluated by fishery independent data increased insignificantly over the last 10 years of the data set (1994: 5.8 years-old to 2004: 6.9 years-old), while the A_{50} for males from fishery dependent data decreased insignificantly (1996: 5.1 years-old to 2006: 3.7 years-old). All estimates for L_{50}, excluding females evaluated by fishery dependent data in 2007, were less than the 432 mm minimum length limit for commercial harvest, meaning that at least 50% of the Lake Whitefish population in Lake Huron reached sexual maturity before becoming fully vulnerable to the commercial fishery.

TABLE 7. Recent trends in estimates of A_{50} and L_{50} for females and males from Lake Huron based on fishery independent and fishery dependent data sources.

Females					
Fishery Independent			**Fishery Dependent**		
	L_{50} (mm)	**A_{50} (years-old)**		**L_{50} (mm)**	**A_{50} (years-old)**
Trend	Decreasing	None	**Trend**	Increasing	None
Value in 1995	408	5.7	**Value in 1997**	422	5.0
Value in 2005	399	5.3	**Value in 2007**	464	5.0
Males					
Trend	Decreasing	Increasing	**Trend**	Decreasing	Decreasing
Value in 1994	416	5.8	**Value in 1996**	421	5.1
Value in 2004	411*	6.9	**Value in 2006**	388	3.7

*Increased from lower value in last few years of dataset.

Estimates of A_{50} and L_{50} in Lake Michigan

The L_{50} for females evaluated by both fishery independent and fishery dependent data increased over the last 10 years of the data set, with the increase for fishery independent data being significant (1997: 398 mm to 2007: 438 mm and 1998: 390 mm to 2008: 435 mm). The estimates for A_{50} from females evaluated by both fishery independent and fishery dependent data also showed an increasing trend over the last 10 years of the data set, with the increase for fishery dependent data being significant (1997: 4.7 years-old to 2007: 5.3 years-old** and 1998: 2.4 years-old to 2008: 4.0 years-old) (Table 8).

The L_{50} for males evaluated by both fishery independent and fishery dependent data show an insignificant decreasing trend over the last 10 years of the data set (1998: 396 mm to 2008: 381 mm and 1997: 405 mm to 2007: 404 mm*). The A_{50} for males evaluated by fishery independent data decreased significantly over the last 10 years of the data set (1998: 4.4 years-old to 2008: 3.9 years-old), while the A_{50} for males evaluated by fishery dependent data increased insignificantly (1997: 2.8 years-old to 2007: 3.6 years-old). All estimates for L_{50}, excluding females evaluated by both fishery independent and fishery dependent data in 2007 and 2008, were less than the 432 mm minimum length limit for commercial harvest, which means that at least 50% of the Lake Whitefish population in Lake Michigan reached sexual maturity before becoming fully vulnerable to the commercial fishery.

TABLE 8. Recent trends in estimates of A_{50} and L_{50} for females and males from Lake Michigan based on fishery independent and fishery dependent data sources.

Females					
Fishery Independent			**Fishery Dependent**		
	L_{50} (mm)	**A_{50} (years-old)**		**L_{50} (mm)**	**A_{50} (years-old)**
Trend	Increasing	Increasing	**Trend**	Increasing	Increasing
Value in 1997	398	4.7	**Value in 1998**	390	2.4
Value in 2007	438	5.3**	**Value in 2008**	435	4.0
Males					
Trend	Decreasing	Decreasing	**Trend**	Decreasing	Increasing
Value in 1998	396	4.4	**Value in 1997**	405	2.8
Value in 2008	381	3.9	**Value in 2007**	404*	3.6

* Increased from lower value in last few years of dataset.

**Decreased from higher value in last few years of dataset.

Estimates of A_{50} and L_{50} in Lake Superior

The L_{50} for females evaluated by fishery independent data decreased insignificantly over the last eight years of the data set (1990: 469 mm to 1998: 442 mm), while the L_{50} for females evaluated by fishery dependent data increased significantly (1989: 310 mm to 1999: 437 mm). The estimates for A_{50} from females evaluated by fishery independent data decreased insignificantly over the last eight years of the data set (1990: 7.4 years-old to 1998: 6.4 years-old), while the A_{50} for females evaluated by fishery dependent data increased insignificantly (1989: 3.9 years-old to 1999: 4.9 years-old) (Table 9).

The L_{50} for males evaluated by fishery independent data decreased insignificantly over the last eight years of the data set (1990: 432 mm to 1998: 408 mm), while the L_{50} for males evaluated by fishery dependent data increased significantly (1994: 432 mm to 2004: 464 mm). The A_{50} for males evaluated by fishery independent data decreased insignificantly over the last eight years of the data set (1990: 7.4 years-old to 1998: 5.4 years-old), while the A_{50} for males evaluated by fishery dependent data showed no discernable trend. All estimates for L_{50}, excluding females evaluated by fishery dependent data in 1989 and males evaluated by fishery independent data in 2008, are greater than the 432 mm minimum length limit for commercial harvest, meaning that at least 50% of the Lake Whitefish population in Lake Superior had not reached sexual maturity before becoming fully vulnerable to the commercial fishery.

TABLE 9. Recent trends in estimates of A_{50} and L_{50} for females and males from Lake Superior based on fishery independent and fishery dependent data sources.

Females					
Fishery Independent			**Fishery Dependent**		
	L_{50} (mm)	**A_{50} (years-old)**		**L_{50} (mm)**	**A_{50} (years-old)**
Trend	Decreasing	Decreasing	**Trend**	Increasing	Increasing
Value in 1990	469	7.4	**Value in 1989**	310	3.9
Value in 1998	442	6.4	**Value in 1999**	437	4.9
Males					
Trend	Decreasing	Decreasing	**Trend**	Increasing	None
Value in 1990	432	7.4	**Value in 1994**	432	4.2
Value in 1998	408	5.4	**Value in 2004**	464	4.1

Summary of Recent Trends in Estimates of A_{50} and L_{50}

In lakes Huron, Michigan, and Superior, males generally reached sexual maturity at shorter lengths and at younger ages than females (Tables 7, 8, 9). When observing the last 10 years of each data set, it can be noted that there are some significant increasing trends in the estimates for L_{50} in lakes Huron and Michigan that follow the decline in L_{50} that occurred around the year 1990, suggesting that the L_{50} could be increasing again in both lakes. Although some increasing trends in the estimates of L_{50} can be noted over the last 10 years of the data set, males and females, in general, still achieved sexual maturity before reaching the minimum length limit of 432 mm for commercial harvest in lakes Huron and Michigan. In Lake Superior, males and females, in general, continue to achieve sexual maturity after reaching the minimum length limit for harvest.

Discussion

Based on the results of this study, it can be concluded that maturity schedules vary temporally, spatially, and by sex among the Lake Whitefish populations in lakes Huron, Michigan, and Superior, which is consistent with the overall findings of Wang et al. (2008). The temporal, spatial, and sexual variations in Lake Whitefish maturation schedules are discussed in depth in the following sections, and are depicted on Figures 6-29 in Appendices 1.1, 1.2, and 1.3.

Temporal Variation in Lake Whitefish Maturation Schedules

Influence of a Changing Diet on Maturation Schedules

For lakes Huron and Michigan, the significant declining trend observed in L_{50} began with the 1990 cohort for Lake Whitefish evaluated using both fishery independent and fishery dependent data, which followed a time of significant ecological change coupled with increases in Lake Whitefish abundance within the upper Great Lakes (Nalepa et al. 2005; Ebener et al. 2008; Wang et al. 2008). This trend can be seen in Figures 6-21 in Appendices 1.1. and 1.2, and is not consistent with the findings of Wang et al. (2008) who found no difference between before 1990 and after 1990 cohorts.

Prior to the 1990's, a number of invasive species had become established within the Great Lakes region, however, it wasn't until the establishment of zebra *(Dreissena polymorpha)* and quagga mussels *(Dreissena bugensis)* in the late 1980's and early 1990's that Lake Whitefish began to show signs of having been impacted by dreissenid mussels in both lakes Huron and Michigan (Nalepa and Schloesser 1993). The recent decrease in Lake Whitefish growth rates and body condition in lakes Huron and Michigan (Madenjian et al. 2002) has been attributed to intra-specific competition for a food source (Pothoven et al. 2001; Mohr and Ebener 2005), along with a diet change. Lake Whitefish went from eating mainly *Diporeia*, their historically preferred nutrient dense and energy rich food source, to dreissenid mussels and other prey items that are less nutrient dense and energy rich (Kratzer et al. 2007), all while experiencing increased population abundance due to strong year-classes in previous years (Mohr and Ebener 2005; Schneeberger et al. 2005)

With the establishment of zebra mussels throughout the Great Lakes region, a new competitor was introduced into the food wed. Zebra mussels are filter feeders that consume algae that live in the water column, whereas *Diporeia* live in the sediment and consume algae that settle on the lake bottom (McNickle et al. 2006; Kratzer 2006; Kratzer et al. 2007; DeBruyne et al. 2008). With less algae building up on the lake bottom for *Diporeia* to consume, the density of *Diporeia* populations declined within lakes Huron and Michigan (Pothoven et al. 2001; Mills et al. 2005; Nalepa et al. 2005). Traditionally, Lake Whitefish selectively fed on *Diporeia* because they are nutrient dense and energy rich (Kratzer et al. 2007); however, with a decline in their abundance due to the increased competition with zebra mussels over algae, Lake Whitefish have been forced to seek alternative food sources (Nalepa et al. 2005; Kratzer 2006; Ebener et al. 2008). Although other food sources, like mussels, gastropods, and shrimp, were and are still available for Lake Whitefish, they are not as nutrient dense and energy rich (Kratzer et al. 2007). This has likely contributed to the declines that have been seen in the growth rate and body condition of Lake Whitefish within lakes Huron and Michigan because fish had less energy available to expend on growth (Pothoven et al. 2001; Pothoven 2005; Kratzer et al. 2007; Wang 2009).

Additionally, because growth rates declined in lakes Huron and Michigan, the age structure of sexually mature Lake Whitefish increased (Mohr and Ebener 2005). Although Lake Whitefish are now reaching sexual maturity at smaller sizes, it is taking them longer to reach it. This means that the likelihood of natural mortality occurring could potentially increase before Lake Whitefish are able to reproduce. Mohr and Ebener's (2005) findings regarding the age structure of sexually mature Lake Whitefish were supported by the results of this study, which showed that the A_{50} in lakes Huron and Michigan did not decline while the L_{50} decreased (Figures 6-21 in Appendices 1.1 and 1.2). Because the nutrient and energy intake for Lake Whitefish had declined (Kratzer et al. 2007), it may also be possible that plastic response mechanisms are responsible for fluctuations in Lake Whitefish growth rates, thus making it so more energy could be expended on reproductive growth instead of somatic growth (Nalepa et al. 2005; Kratzer 2006; Wang 2009). If plastic response mechanisms are at play, it could help to explain why Lake Whitefish began to reach sexual maturity at smaller sizes in lakes Huron and Michigan following the 1990's.

Influence of Size-Selective Mortality on Maturation Schedules

Size-selective mortality on adult fish tends to produce an adaptive response where fish will evolve to mature earlier and at smaller sizes. For example, maturing younger and at a smaller size could be an adaptation that occurs over time, and could help minimize the impact of sea-lamprey predation on an adult fish's ability to reproduce (Wang 2009). Predation on adult Lake Whitefish in lakes Huron and Michigan following the introduction of the invasive sea lamprey *(Petromyzon marinus)* in the late 1930's became prevalent by the 1950's and 1960's (Nalepa et al. 2005). Over the past decade, the impacts of sea lamprey predation on Lake Whitefish have declined, due to control methods that were implemented throughout the mid to late 1900's (Ebener et al. 2008).

It has also been found that by having a long-standing fishery that is size-selective, Lake Whitefish exhibit adaptive responses where they evolve to mature at smaller sizes and at younger ages (Henderson et al. 1983; Rochet et al. 2000; Wang 2009). This response mechanism likely acts as a way to ensure reproductive success before fish are harvested. During the time period studied, lakes Huron and Michigan had larger commercial fisheries for Lake Whitefish than Lake Superior (D. Caroffino, Fisheries Biologist, Michigan Department of Natural Resources, personal communication), so Lake Whitefish in lakes Huron and Michigan have experienced more size-selective mortality on adult fish over time as a result of fishery exploitation than fish in Lake Superior (Baldwin et al. 2002; Mohr and Ebener 2005; Schneeberger et al. 2005).

Although size-selective mortality can influence maturation schedules by producing an adaptive response where fish evolve to mature at shorter lengths and at younger ages (Henderson et al. 1983; Rochet et al. 2000; Wang 2009), the results of this study do not show that an adaptive response has caused the age at which Lake Whitefish reach sexual maturity to decrease (Figures 6 – 29 in Appendices 1.1, 1.2 and 1.3). However, Lake Whitefish in lakes Huron and Michigan did appear to reach sexual maturity at shorter lengths. This can likely be attributed to the fact that when pressured with size-selective mortality (or with a change in diet), Lake Whitefish populations have been shown to compensate via plastic responses that can cause sexual maturation to occur at shorter lengths (Wang 2009).

Like Wang et al.'s (2008) study, this research only evaluated approximately 40 years of Lake Whitefish biological data (1976-2013), which is a relatively short time frame in comparison to the length of time that commercial harvest has been going on in the Great Lakes (since the 1700's; Ebener et al. 2008). Therefore, there may not be enough evidence to conclude that size-selective fishing pressure played a role in adaptive responses leading to the variation of maturity schedules in lakes Huron and Michigan (Wang 2009). The relationship between the timing of the decline in L_{50} with the ecological changes in the food web that occurred prior to and around the 1990's coupled with increased Lake Whitefish abundance provides a more compelling argument for plastic responses playing a role in influencing Lake Whitefish maturation schedules because of the short-time frame in which Lake Whitefish populations began to reach sexual maturity at shorter lengths than years past.

Spatial Variation in Lake Whitefish Maturation Schedules

Influence of Ecosystem Differences among Lakes on Maturation Schedules

Lake Superior is the largest of the three upper Great Lakes, and is the coldest (EPA 2013). The prevalence of invasive species in Lake Superior is less than in lakes Huron and Michigan. The abundance of dreissenid mussels in Lake Superior is also lower (Ebener et al. 2008), so they have not had the same impact on *Diporeia* densities, and therefore, have not impacted the diet of Lake Whitefish in Lake Superior as much as they have in lakes Huron and Michigan (Ebener et al. 2008). Lake Whitefish in Lake Superior have historically displayed slower growth rates than fish in lakes Huron and Michigan, potentially a result of cold water and less food availability due to low primary production (Taylor et al. 1992; Barbiero and Tuchman 2001; Wang 2009). Cold waters, fewer invasive species, less food availability, and historically slower growth rates likely explain why the results of this study showed that for both fishery independent and fishery dependent data, the L_{50} in Lake Superior was larger than in lakes Huron and Michigan, and that it also did not decline around the year 1990, as it did in the other two lakes, and did not display a discernable trend. Additionally, since the growth rates in Lake Superior have remained relatively stable over time, unlike those seen in lakes Huron and Michigan (Schorfhaar and Schneeberger 1997), the age structure of sexually mature fish did not shift upward as it did in the other two lakes, as illustrated by the results of this study which showed no clear pattern for variations in A_{50} over time in Lake Superior (Figures 6-29 in Appendices 1.1, 1.2, and 1.3).

The results of this study also indicated that at least 50% of the population of Lake Whitefish were reaching sexual maturity after becoming fully vulnerable to the commercial fishery (432 mm) for both fishery independent and fishery dependent data in Lake Superior, whereas at least 50% of the population of Lake Whitefish in lakes Huron and Michigan were reaching sexual maturity before becoming fully vulnerable to the commercial fishery (Figures 6-21 in Appendices 1.1, 1.2, and 1.3). Because Lake Whitefish in Lake Superior were reaching sexual maturity after becoming fully vulnerable to the commercial fishery, it could mean that at times, a portion of the Lake Whitefish population in Lake Superior has not had the opportunity to spawn, or reproduce before being harvested. This is an important factor to consider when making management decisions surrounding the minimum legal length limit (432mm) for harvest because recruitment of Lake Whitefish relies in part on adult stock size (Brown et al. 1993). The collapse of many fish stocks has been attributed to overfishing younger individuals (FAO 1998). Therefore, if Lake Whitefish do not reach sexual maturity before becoming fully vulnerable to the commercial fishery, they cannot spawn, or produce and fertilize eggs that could become recruits for the next cohort, potentially leading to negative impacts on population growth.

However, these findings, along with those of Barbiero and Tuchman (2001) and Wang (2009), suggest that Lake Whitefish in Lake Superior have historically reached sexual maturity at larger lengths and older ages than Lake Whitefish in lakes Huron and Michigan, potentially as a result of lower fishery exploitation. This could imply that although food availability is less and their growth is slower, body sizes at maturity are larger, and therefore, fish in Lake Superior may be more fecund than Lake Whitefish in lakes Huron and Michigan, since body size and fecundity have been shown to be positively correlated (Kratzer et al. 2007). If Lake Whitefish are in fact more fecund in Lake Superior, and recruitment depends in part on adult spawning stock (Brown et al. 1993), it is possible that the Lake Whitefish that do avoid being harvested before reaching sexual maturity (and therefore are able to spawn) are enough to sustain the population of Lake Whitefish in Lake Superior.

Lastly, although Lake Whitefish have been reaching sexual maturity at sizes greater than the 432 mm minimum length limit in Lake Superior, population trends show that it has been the most stable lake over time, having consistent recruitment, low mortality, and conservative harvest quotas (D. Caroffino, Fisheries Biologist, Michigan Department of Natural Resources, personal communication). Therefore, fish reaching sexual maturity after becoming fully vulnerable to the commercial fishery is not alarming. Given current environmental and fishing conditions, it is likely that Lake Whitefish in Lake Superior will continue to sustain themselves. However, should fishing pressure or environmental conditions change in a way that could directly impact recruitment, such as invasive species, increased fishing effort, or temperature fluctuations it would be important for managers to monitor the maturity schedules to ensure the length limit still made sense.

Sexual Variation in Lake Whitefish Maturation Schedules

<u>Influence of Reproductive Costs on Maturation Schedules</u>

The results of this study indicated that for fishery independent and fishery dependent data evaluated among lakes Huron, Michigan, and Superior, females matured at longer lengths and older ages than males, which is consistent with the reproductive life history characteristics displayed by Lake Whitefish (Ebener et al. 2008; Ficker et al. 2014) and is consistent with the findings of Wang et al. (2008) (Figures 6-29 in Appendices 1.1, 1.2 and 1.3). The energy needed for reproduction is generally greater for females than males due to the energy required for developing lipid stores, and egg size and body size have been shown to be positively correlated

(Wang 2009). Fecundity is greater when fish are able to expend more energy on growth and delay maturity (Ihssen et al. 1981). Therefore, Lake Whitefish are likely to produce more fish over their lifetime if they can grow larger and mature later (Ihssen et al. 1981).

Although this study indicated that females were maturing at older ages than males, the actual length at which both sexes were maturing had declined in lakes Huron and Michigan over the timeframe studied (Figures 6 – 21 in Appendices 1.1 and 1.2). This finding is important because if both sexes are maturing at smaller sizes, they may actually be expending less energy on both reproductive and somatic growth (Nalepa et al. 2005; Kratzer 2006). Since egg size has been positively correlated with female body size, reaching sexual maturity at smaller sizes could have negative impacts on the fecundity of female Lake Whitefish because smaller fish cannot produce as many eggs at once as larger fish (Kratzer et al. 2007). This could limit the potential for recruitment of new fish if fewer eggs are produced and survival rates are not high.

Additionally, if smaller body size is a result of a diet that is not nutrient dense and energy rich, fewer, lower quality eggs could be produced (Kratzer et al. 2007). Some studies suggest that if the quality of eggs is reduced, in that lipid stores within each egg are smaller, larval survival could decline because lipid stores are important for the development of larval individuals before they begin feeding exogenously (Pothoven et al. 2001; Kratzer et al. 2007). Having access to a readily abundant food source to begin feeding exogenously is important, therefore, if zooplankton blooms are not in sync with larval emergence, having a larger lipid store could mean the difference between life and death. However, Muir et al. (2009) found that parental body condition may not be critical to the survival of larval/juvenile individuals at the stock level, and rather, environmental conditions or density-dependent growth dynamics may have more of an impact on recruitment of Lake Whitefish than female body size.

In summary, increased Lake Whitefish abundances coupled with ecological changes in the food web, along with size-selective mortality have likely caused Lake Whitefish maturity schedules to change temporally and spatially, among both males and females in the upper Great Lakes. These changes in maturity schedules are likely a result of plastic responses due to changes within the environment because they occurred over a relatively short time frame (5 – 10 years).

Considerations for the Future

The fishery independent and fishery dependent data used for this analysis came from different management agencies, and one agency may or may not collect and process Lake Whitefish samples using comparable methods as other agencies. Collecting fishery independent and fishery dependent survey data can occur at different times of the year, which could introduce seasonal-based biases in that more data is sometimes collected during different times of the year than others. Data collection occurs with different sampling gear, introducing gear-based biases in that fishery independent data samples all sizes of fish, whereas fishery dependent data does not. Although protocol-, seasonal-, spatial-, and gear-based biases may have been introduced into the data set used for this study, the results suggest that both fishery independent and fishery dependent data led to the same conclusions surrounding the temporal, spatial, and sexual variation in Lake Whitefish maturity schedules, which suggests that maturation schedules actually do differ among lakes Huron, Michigan, and Superior and between sexes within each lake (Figures 6 – 29 in Appendices 1.1, 1.2, and 1.3).

Another consideration surrounding the data used for this study is that there were not always the same ratios of males to females sampled, because fish are randomly sampled, and there are not always the same ratios of fishery independent to fishery dependent data records. This could have contributed to the variation in the width of the upper and lower bounds of the

95% confidence intervals shown in Figures 6 – 29 in Appendices 1.1, 1.2, and 1.3. If there are more records with age and length for males then there are for females, or if there are more records for fishery independent data than there are for fishery dependent data, the data set may provide a more holistic representation of the male population evaluated using fishery independent data, for example. Having a larger sample size helps to reduce the potential error in the estimates of length and age at 50% maturity (Gustafson 1988), thus allowing for a confidence interval with tighter upper and lower bounds. The width of the upper and lower bounds of the 95% confidence intervals might be smaller if more data were available, which could either increase or decrease the significance of the results based on the amount of remaining overlap between the 95% confidence intervals. In addition, the variability in confidence intervals could also be due to the fact that fishery dependent data is more size-selective than fishery independent data, so there may be less variability in the size of fish sampled (tighter confidence intervals) than would be seen in fish sampled independent of the commercial fishery where sampling is less size-selective and therefore more variable (wider confidence intervals).

The amount of fishery independent and fishery dependent data available for lakes Huron and Michigan were greater than the amount of data available for Lake Superior because there was more commercial fishing occurring in lakes Huron and Michigan over the time frame studied. Therefore, there was more sampling effort from management agencies in lakes Huron and Michigan. This could have introduced larger spatial biases into the data set surrounding the conclusions about the temporal, spatial, and sexual variation in maturity schedules between the lakes if the data available for Lake Superior did not provide a holistic representation of the Lake Whitefish population. Although the data evaluated for Lake Superior may have provided a holistic representation of the Lake Whitefish population, the difference in the amount of data available for Lake Superior may help to explain why the 95% confidence intervals for both A_{50} and L_{50} were more frequently wider, than in lakes Huron and Michigan, which could have impacted the significance of change over time, in Lake Superior. This also reflects the idea that with a larger sample size, the error in the estimates of length and age at 50% maturity may be reduced (Gustafson 1988), thus producing tighter confidence intervals. Although varying amounts of data were used to evaluate all lakes, this study did show that there was a difference between the temporal, spatial, and sexual variation in maturity schedules among all three lakes, and that Lake Whitefish in Lake Superior tend to grow slower and mature at older ages than fish in lakes Huron and Michigan (which is supported by previous studies; Schorfhaar and Schneeberger 1997; Ebener et al, 2008; Wang 2009). Therefore the potential biases introduced because of the amount of data available for Lake Superior compared to lakes Huron and Michigan may not have influenced the results.

Management Implications

Sexual Maturity and the Minimum Legal Length Limit

When evaluating the current management structure for Lake Whitefish in lakes Huron, Michigan, and Superior, it is important to recognize the potential consequences of the current minimum legal length limit for harvest on Lake Whitefish populations. The results for Lake Superior indicated that at least 50% of the Lake Whitefish population has been reaching sexual maturity after becoming fully vulnerable to the commercial fishery (432 mm). When observing the time series evaluated for Lake Superior, it is evident that this pattern is not new. Lake Whitefish in Lake Superior have, in general, been reaching sexual maturity after becoming fully vulnerable to the commercial fishery from 1976 to 2013. Alternatively, at least 50% of the Lake Whitefish populations in lakes Huron and Michigan have been reaching sexual maturity before becoming fully vulnerable to the commercial fishery. During the time frame studied, fishery exploitation was greater in lakes Huron and Michigan than in Lake Superior, therefore, the difference in the timing of sexual maturity between the three lakes is likely a result of fishery exploitation and the subsequent impacts of size-selective fishing mortality on growth rates. In addition, the difference in maturity schedules is likely a plastic response due to ecological changes that occurred within the food web in lakes Huron and Michigan. Even though at least 50% of the fish in lakes Huron and Michigan have been reaching sexual maturity before becoming fully vulnerable to the commercial fishery, the results of this study indicated that they have been maturing at smaller sizes, which is important to consider since body size and fecundity have been positively correlated (Kratzer et al. 2007; Wang 2009), especially in light of the recently noted declines in growth and condition of Lake Whitefish in lakes Huron and Michigan (Schneeberger et al. 2005).

However, given the current environmental conditions, along with the fishery management structures in place, it is likely that Lake Whitefish in all three lakes will continue to be able to sustain themselves regardless of when they reach sexual maturity. In addition to the minimum legal length limit, zone closures, harvest quotas, and gear restrictions all work towards ensuring a fishery that does not over harvest the Lake Whitefish population, therefore protecting the spawning stock. Nevertheless, should fishing pressure or environmental conditions ever change in a way that could directly impact recruitment, such as introductions of new invasive species, increased fishing effort, or warming temperatures as a result of climate change, it would be imperative for fishery managers to continue monitoring Lake Whitefish maturity schedules as a way to help ensure that the current length limit, amongst other management tools, still made sense.

Further Investigation of Recent Trends

When evaluating the results for Lake Whitefish sampled in lakes Huron and Michigan, the L_{50} followed a declining trend during the 1990's that in some instances, ended between 2002 and 2004. After this time period, the L_{50} began to increase throughout 2010. As Lake Whitefish populations are monitored over the next few years, it would be very interesting to repeat this study to see if the L_{50} continues approaching the legal length limit for harvest (432mm), and to investigate what changes might have been going on ecologically to cause this change. If this increasing trend in L_{50} does continue to occur in lakes Huron and Michigan, it could mean that Lake Whitefish populations may be responding to new ecological surroundings, such as changing temperatures, and plastic responses are influencing their growth rates and maturity schedules. If the increasing trend in L_{50} in lakes Huron and Michigan does continue, it could also mean that Lake Whitefish are maturing after becoming fully vulnerable to the commercial fishery, similar to fish in Lake Superior, which again may not be an issue as long as fishing pressure and environmental conditions continue to support recruitment.

Future Need for Fishery Dependent and Fishery Independent Data

Because the findings of this study indicated that the temporal, spatial, and sexual variations among all three lakes were similar for both fishery independent and fishery dependent data, fishery managers may be able to discuss the need for continuing to conduct both fishery independent surveys and commercial fishery monitoring to determine maturation schedules and harvest regulations. Since the Modeling Subcommittee of the upper Great Lakes uses fishery dependent data to populate the catch-at-age models that serve as the basis for setting harvest quotas and managing the Lake Whitefish fishery, continuing to consistently collect fishery dependent data makes the most sense, otherwise the entire modeling process and management structure would have to be recrafted. Fishery independent data allows managers to assess the entire Lake Whitefish population within each lake, not just what is being harvested by the commercial fishery. Fishery managers may be able to consider using fishery independent data as supplemental information useful for answering specific questions if they are ever faced with limited resources and have to choose between which dataset to consistently continue collecting.

Maturity Schedules are not Constant over Time

Perhaps the most important finding for fishery managers to consider as they manage Lake Whitefish populations into the future is the plasticity and short-time frame in which maturity schedules seem to have fluctuated in response to environmental conditions within all three lakes, especially lakes Huron and Michigan.

Currently, fishery managers are using models to manage Lake Whitefish populations that define maturity rates as a constant through time. However, as evidenced by this study, that is not the case, especially in lakes Huron and Michigan. In these two lakes, maturity schedules varied significantly through time, likely due to declines in *Diporeia* abundance during the 1990's, coupled with increases in Lake Whitefish abundance around the same time. When larger Lake Whitefish year-classes occurred in the 1990's, the amount of *Diporeia* available to each individual was reduced. Even though Lake Whitefish had other food options available, they were not as nutritionally dense and energy rich as *Diporeia*. Therefore, it is highly probable that plastic response mechanisms played a role in ensuring that any available energy and nutrients went toward sexual maturation processes instead of somatic growth. The absence of a huge decline in Lake Whitefish year-class strength throughout the 1990's can probably be attributed to these plastic response mechanisms. The rapid change in nutrient and energy availability, both due to declines in *Diporeia* and increases in Lake Whitefish abundance, could be the main cause for declining growth and condition of Lake Whitefish, along with the significant variation in maturation schedules through time. Because Lake Whitefish maturation schedules changed within such a short time frame in response to these two factors, it will be important for fishery managers to consider incorporating Lake Whitefish maturity schedules into the models as something that is not constant through time.

Climate Change and Maturity Schedules

Within the Great Lakes region, it is estimated that climate change will alter the distribution, growth, year-class strength and trophic dynamics of freshwater fishes (Lynch 2013). Climate projections for the region suggest that warming temperatures may allow fish to move deeper and further north to stay within their thermal habitat (Lynch 2013). Warmer temperatures are also likely to support increased growth and survival for most species (Shutter and Post 1990). With increasing temperatures, decreased levels of dissolved oxygen are also a possibility, and can limit the amount of habitat available to Lake Whitefish (Lynch 2013). Zooplankton biomass is projected to increase with warming temperatures (Regier et al. 1990), but because zooplankton are especially sensitive to temperature ques that guide their maturity stages, some zooplankton species may become more sensitive to lower dissolved oxygen levels and warmer summer temperatures (Lynch 2013). Should warming temperatures within the Great Lakes support increased growth and survival of Lake Whitefish, coupled with more optimal habitat and increased abundances of zooplankton, their growth and condition could improve, and maturity could occur at older ages and longer lengths due to decreased environmental pressures. However, if zooplankton does not emerge in sync with larval Lake Whitefish, if growth and survival increases and optimal habitat does not, or if new invaders enter and disrupt the Great Lakes ecosystem, maturity could occur at shorter lengths due to sub-optimal environmental conditions.

Fishery managers are faced with managing Lake Whitefish populations within the upper Great Lakes during a time of unknown and unpredictable ecological change, and it may be challenging to predict how Lake Whitefish will respond to such changes due to the plastic and adaptive nature of the population's response to change. Because the study indicated that Lake Whitefish maturity schedules varied temporally, spatially, and sexually from 1976-2013, likely as a result of ecological changes in the food web, size-selective fishing mortality, and increases in Lake Whitefish abundance, it will be important for fishery managers to continue monitoring the maturity schedules of Lake Whitefish over time as a way to ensure that the current management structure, which uses catch-at-age models to set harvest quotas for a size-selective fishery (Ebener et al. 2005; Modeling Subcommittee, Technical Fisheries Committee 2013), can be adjusted appropriately in order to ensure the viability of Lake Whitefish populations with lakes Huron, Michigan, and Superior.

APPENDICES

Appendix 1.1. Plots depicting estimates of A_{50} and L_{50} for Lake Whitefish (Coregonus clupeaformis) evaluated by fishery dependent and fishery independent data in Lake Huron

Plots Depicting Estimates of A_{50} and L_{50} Based on Fishery Dependent Data

FIGURE 6. Age at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Huron based on commercial fishery monitoring data.

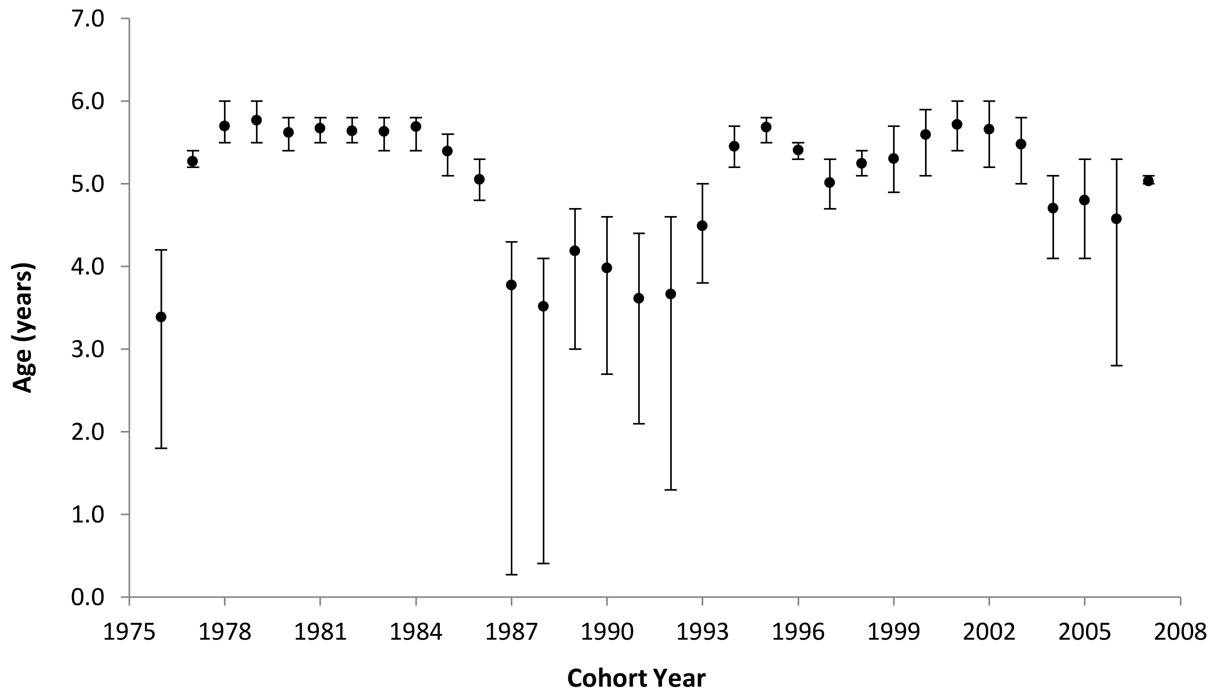


FIGURE 7. Length at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Huron based on commercial fishery monitoring data. Solid line indicates 432mm, the current commercial harvest length limit.

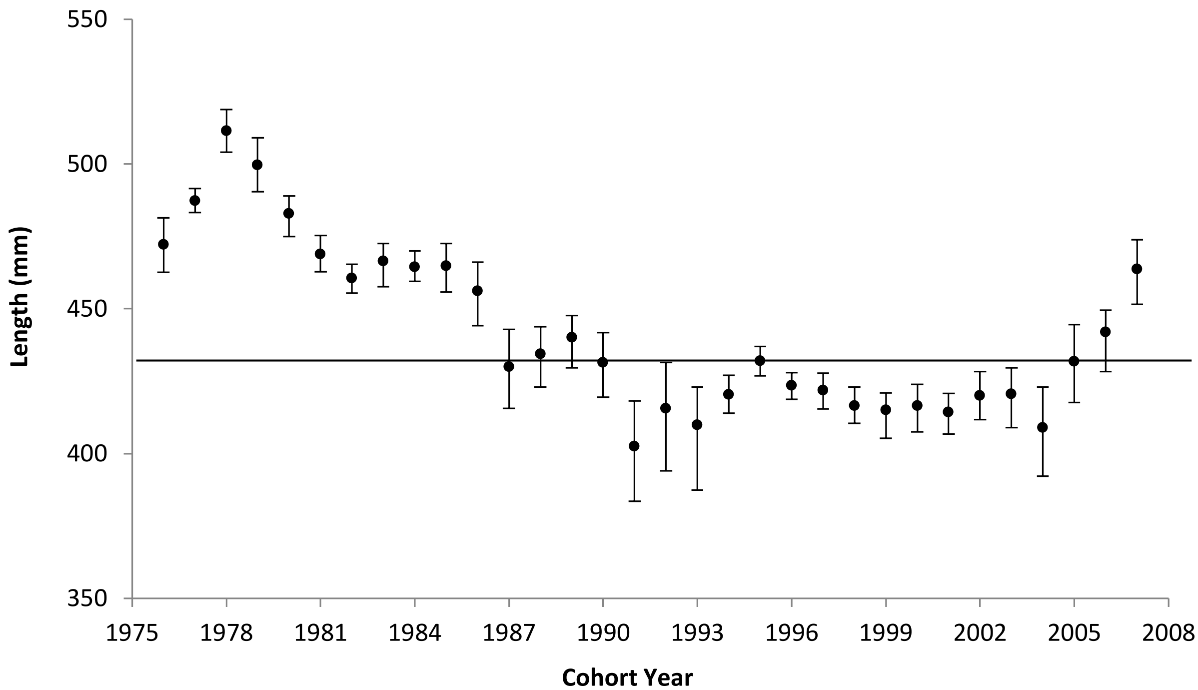


FIGURE 8. Age at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Huron based on commercial fishery monitoring data.

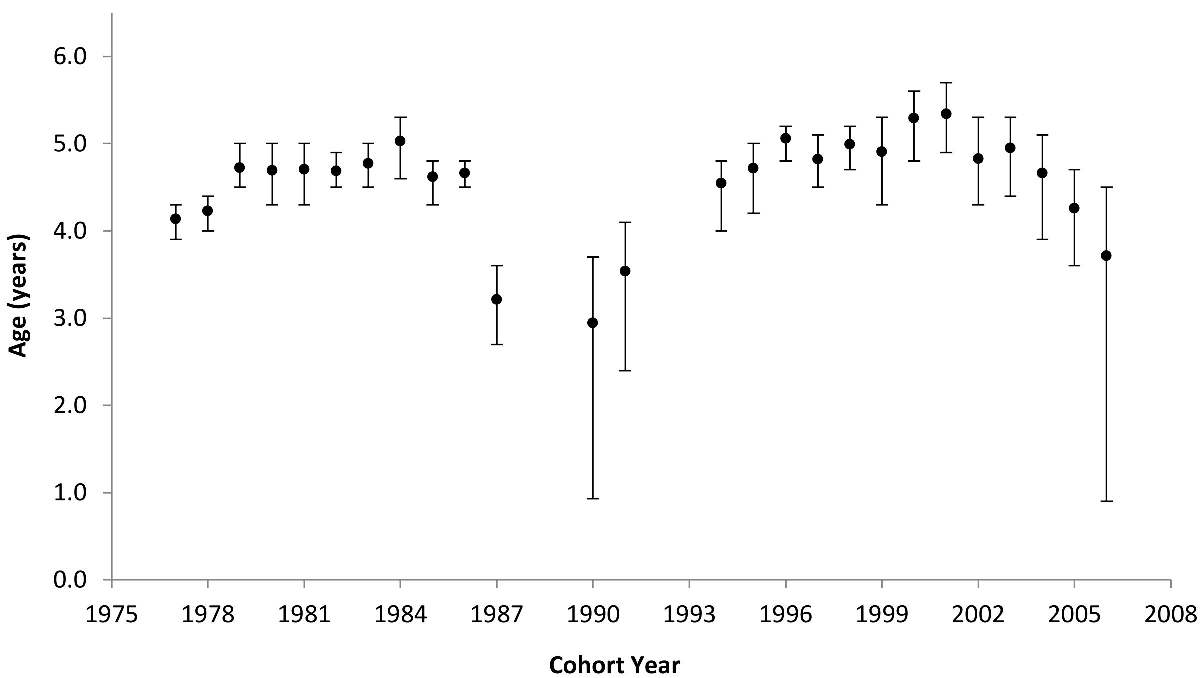
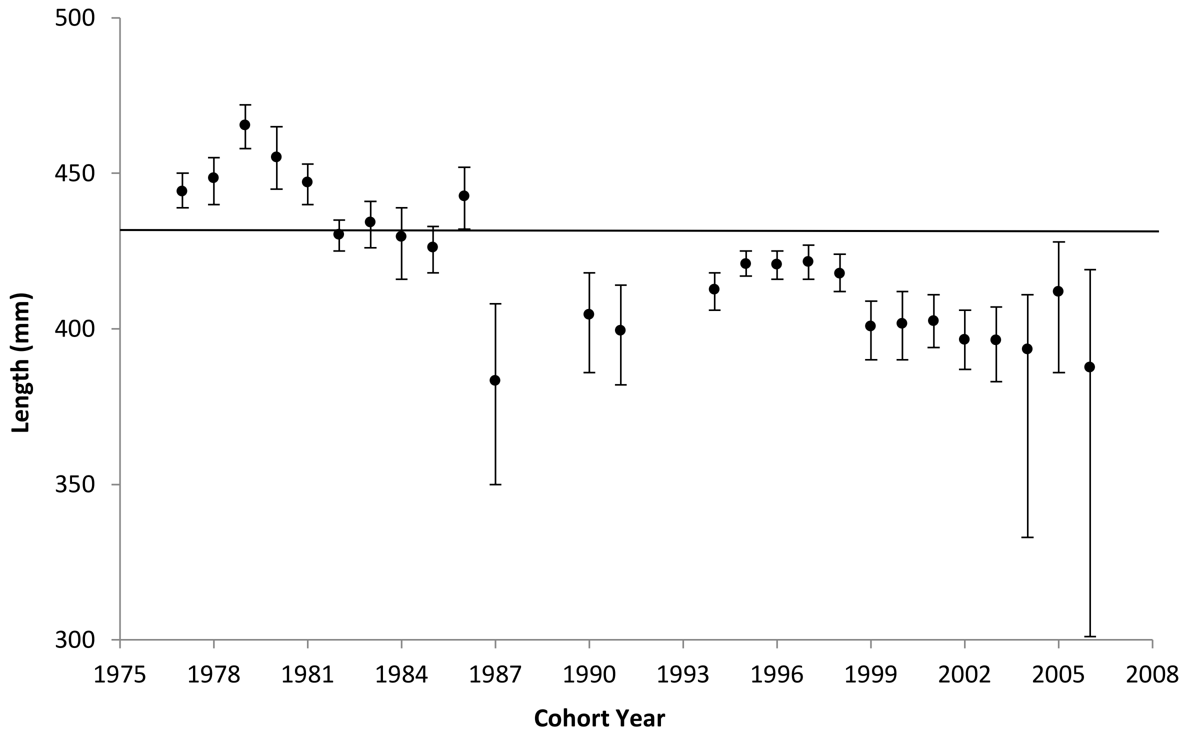


FIGURE 9. Length at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Huron based on commercial fishery monitoring data. Solid line indicates 432mm, the current commercial harvest length limit.



Plots Depicting Estimates of A_{50} and L_{50} Based on Fishery Independent Data

FIGURE 10. Age at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Huron based on fishery independent survey data.

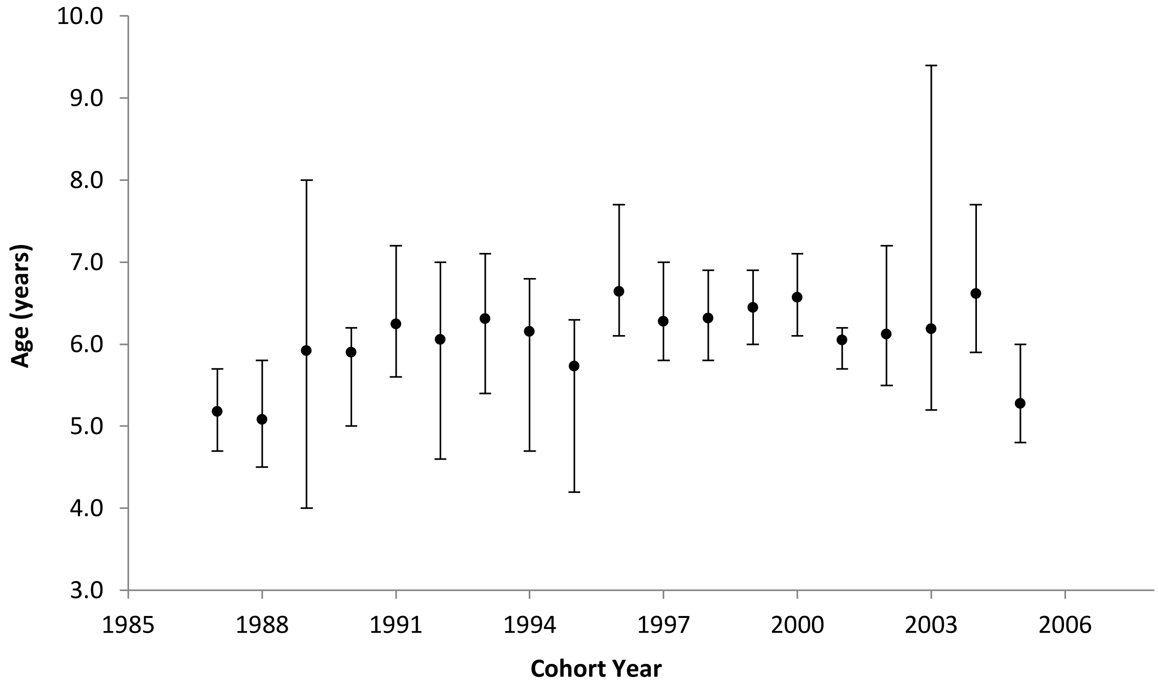


FIGURE 11. Length at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Huron based on fishery independent survey data. Solid line indicates 432mm, the current commercial harvest length limit.

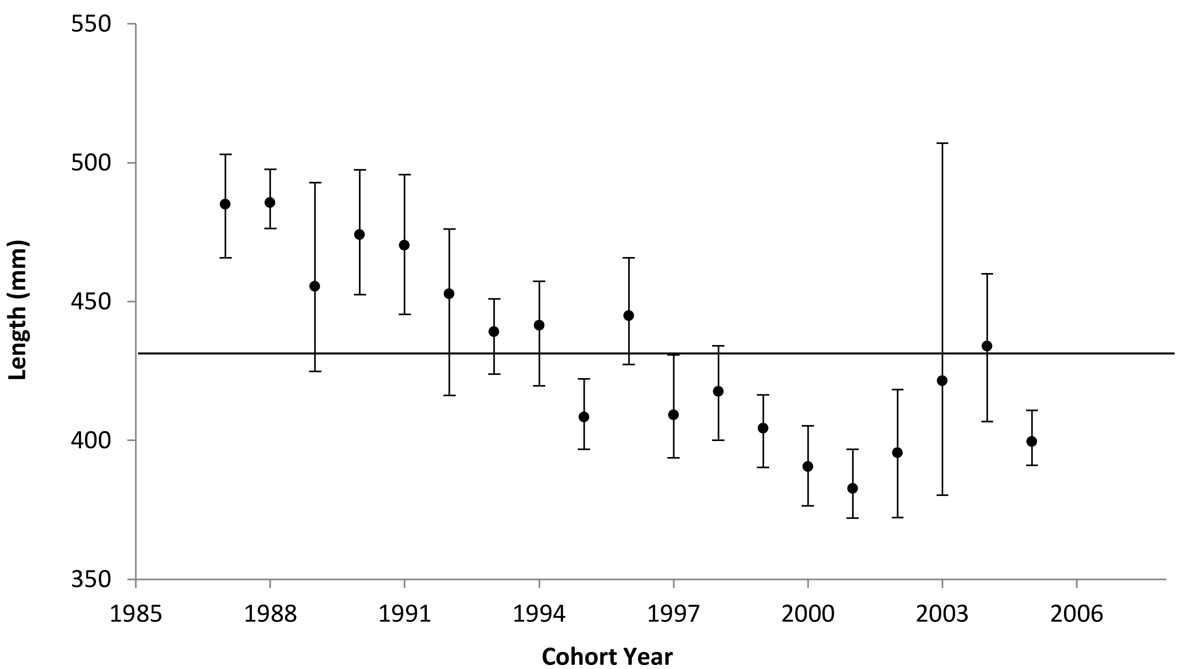


FIGURE 12. Age at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Huron based on fishery independent survey data.

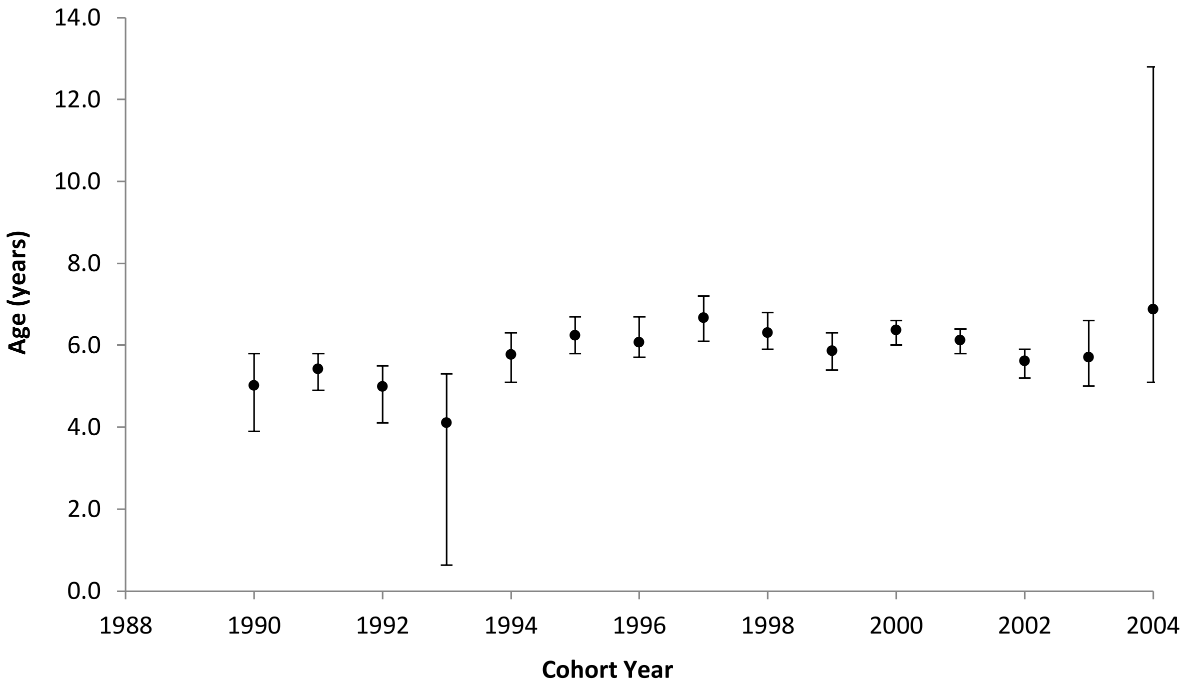
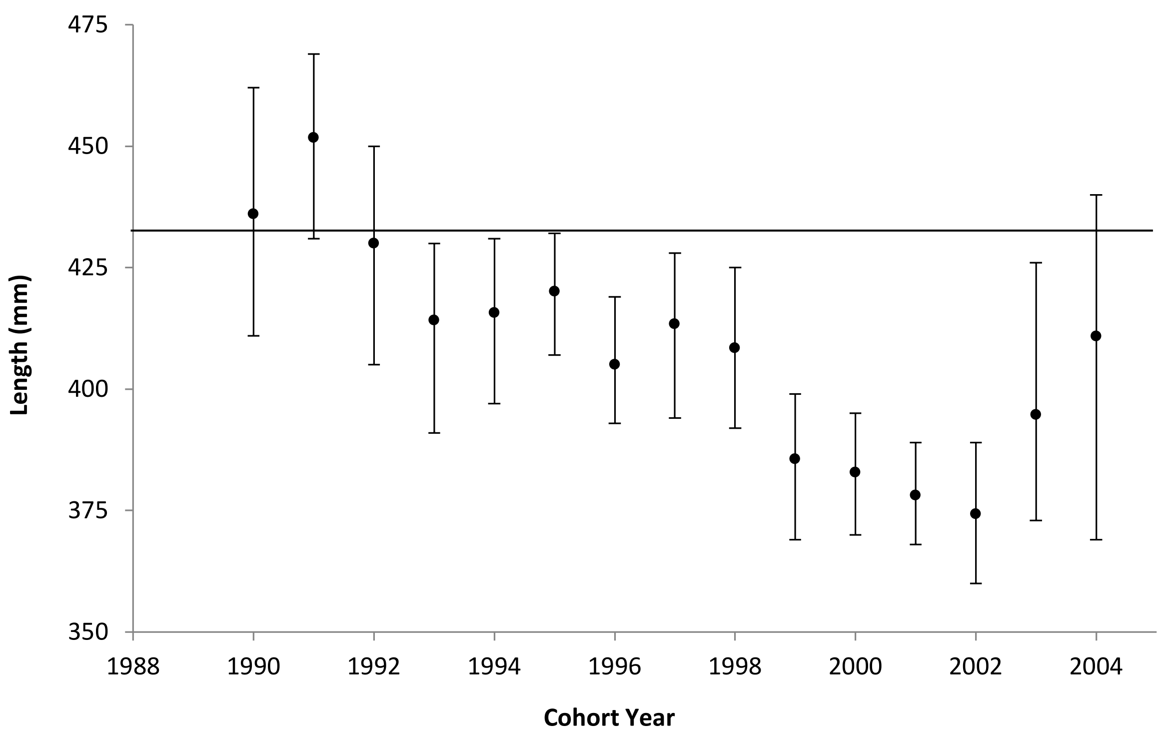


FIGURE 13. Length at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Huron based on fishery independent survey data. Solid line indicates 432mm, the current commercial harvest length limit.



Appendix 1.2. Plots depicting estimates of L_{50} and A_{50} for Lake Whitefish (Coregonus clupeaformis) evaluated by fishery dependent and fishery independent data in Lake Michigan

Plots Depicting Estimates of A_{50} and L_{50} Based on Fishery Dependent Data

FIGURE 14. Age at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Michigan based on commercial fishery monitoring data.

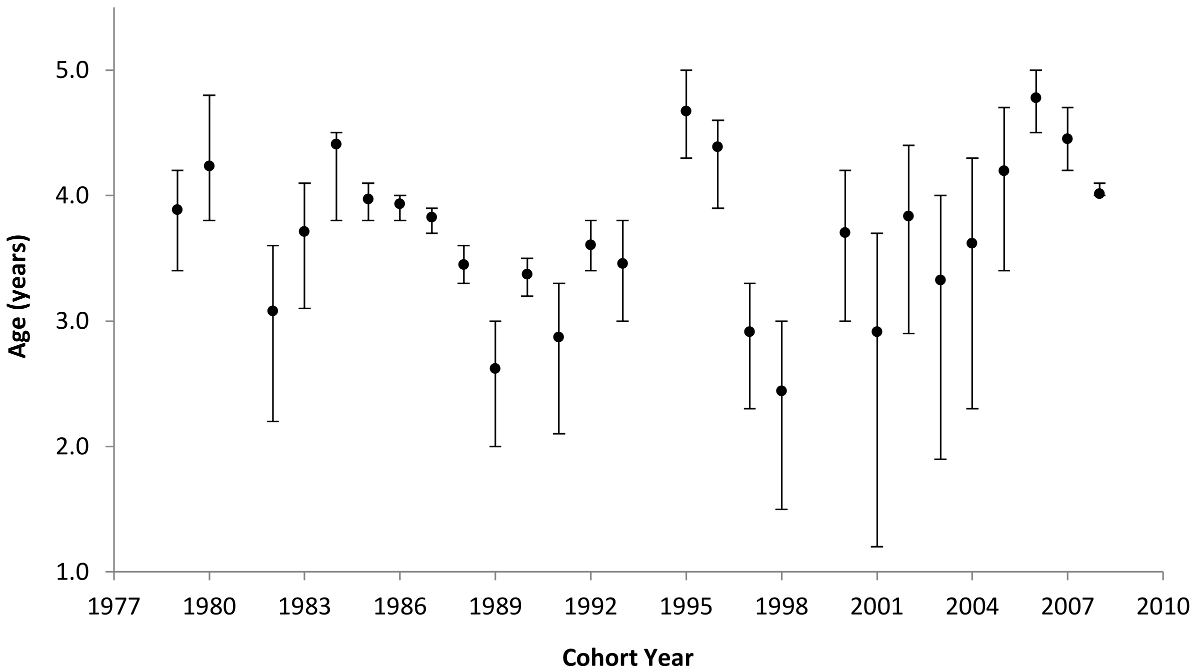


FIGURE 15. Length at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Michigan based on commercial fishery monitoring data. Solid line indicates 432mm, the current commercial harvest length limit.

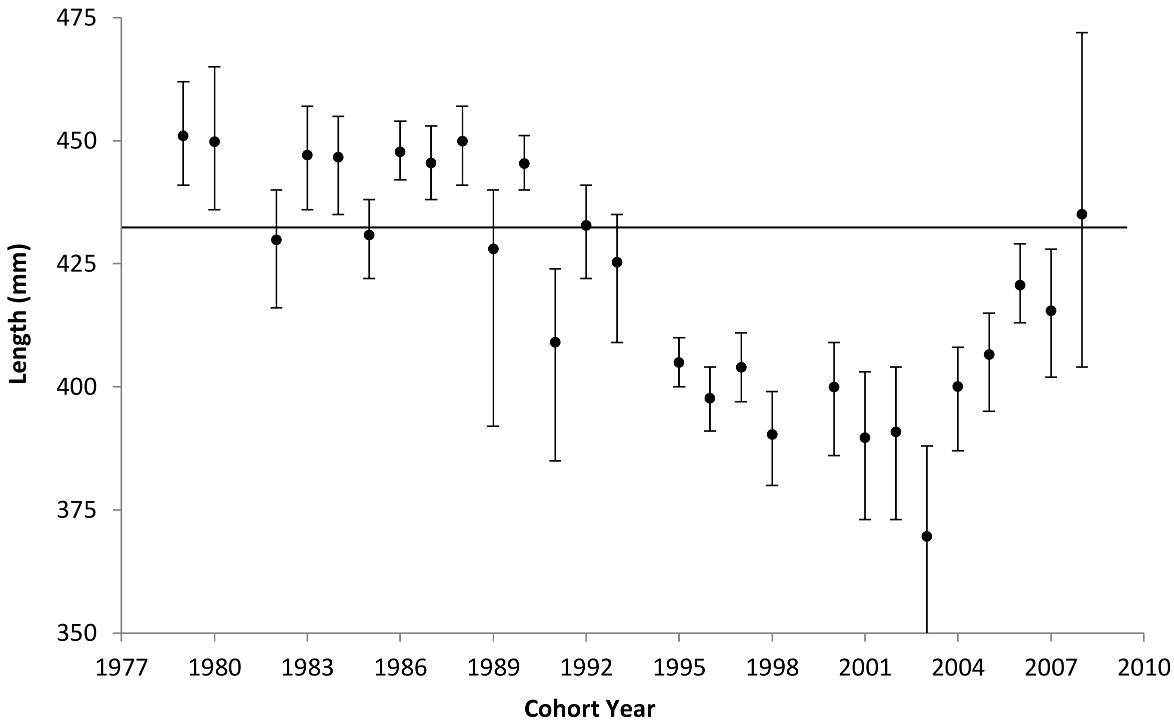


FIGURE 16. Age at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Michigan based on commercial fishery monitoring data.

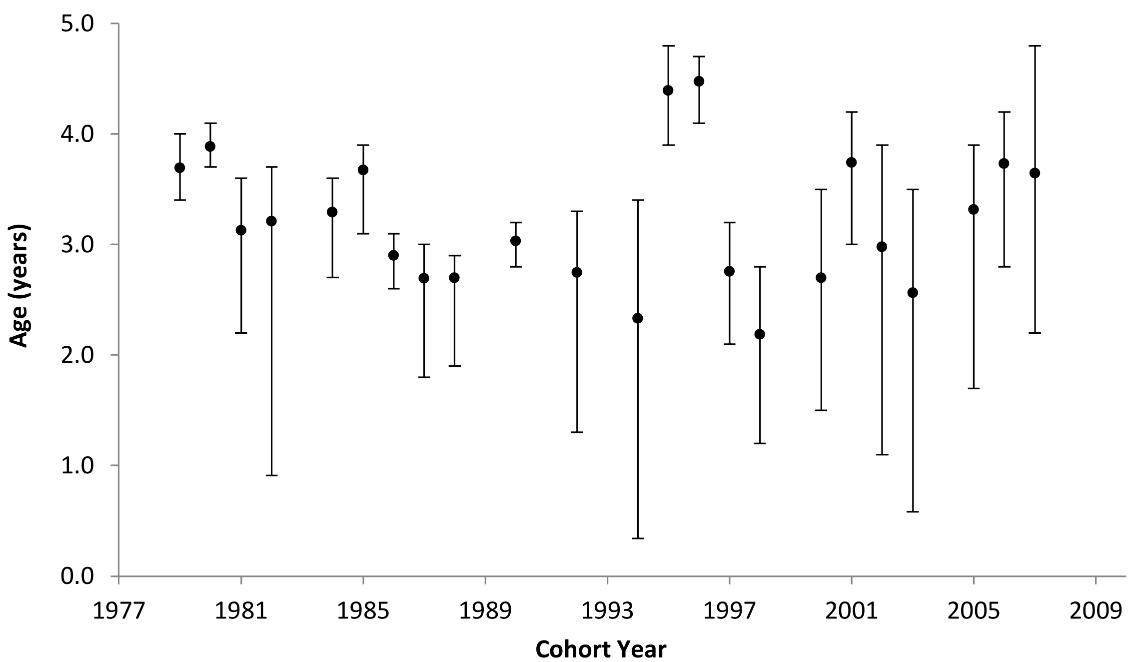
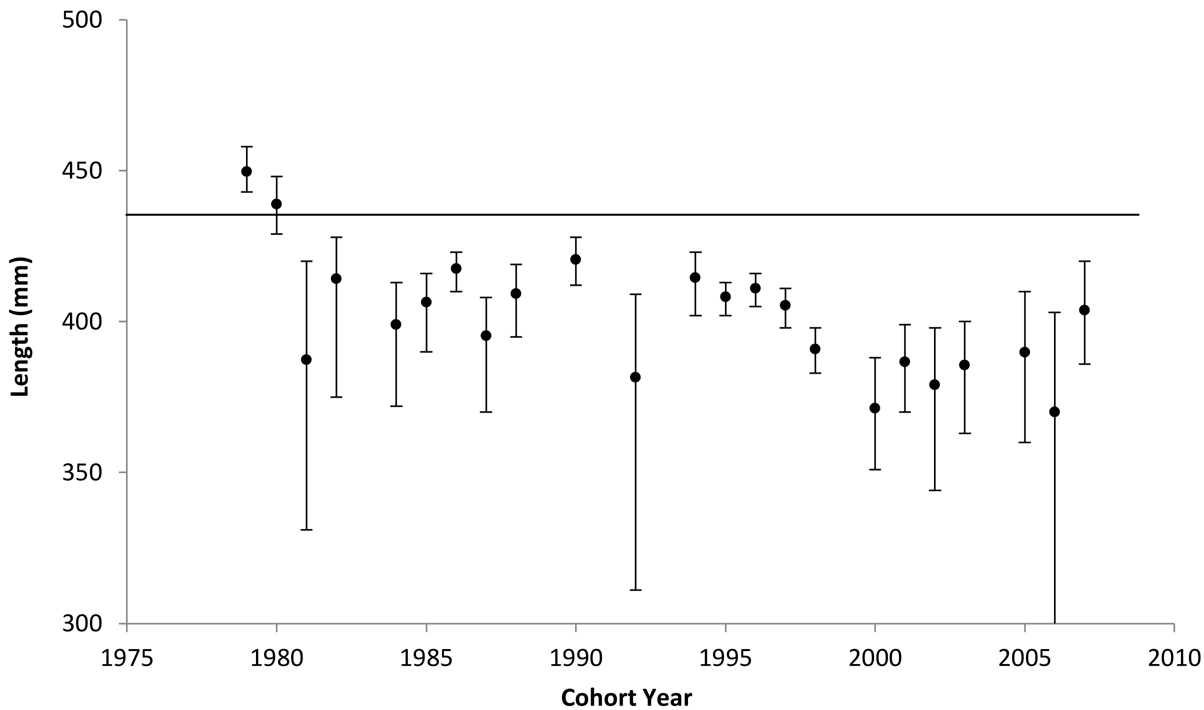


FIGURE 17. Length at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Michigan based on commercial fishery monitoring data. Solid line indicates 432mm, the current commercial harvest length limit.



Plots Depicting Estimates of A_{50} and L_{50} Based on Fishery Independent Data

FIGURE 18. Age at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Michigan based on fishery independent survey data.

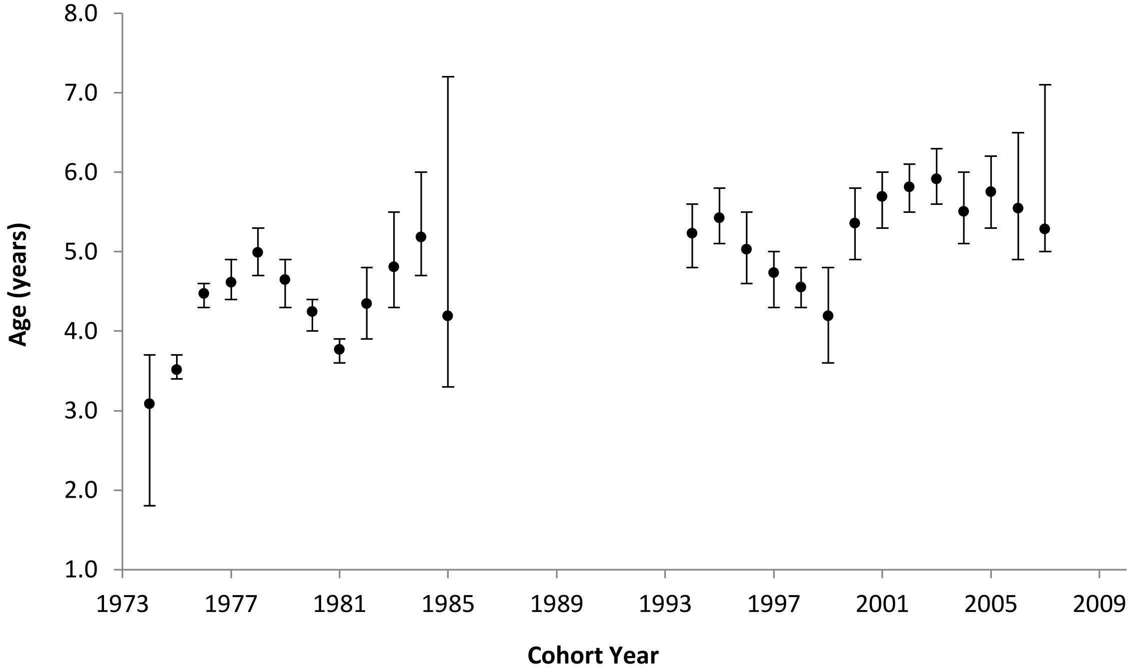


FIGURE 19. Length at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Michigan based on fishery independent survey data. Solid line indicates 432mm, the current commercial harvest length limit.

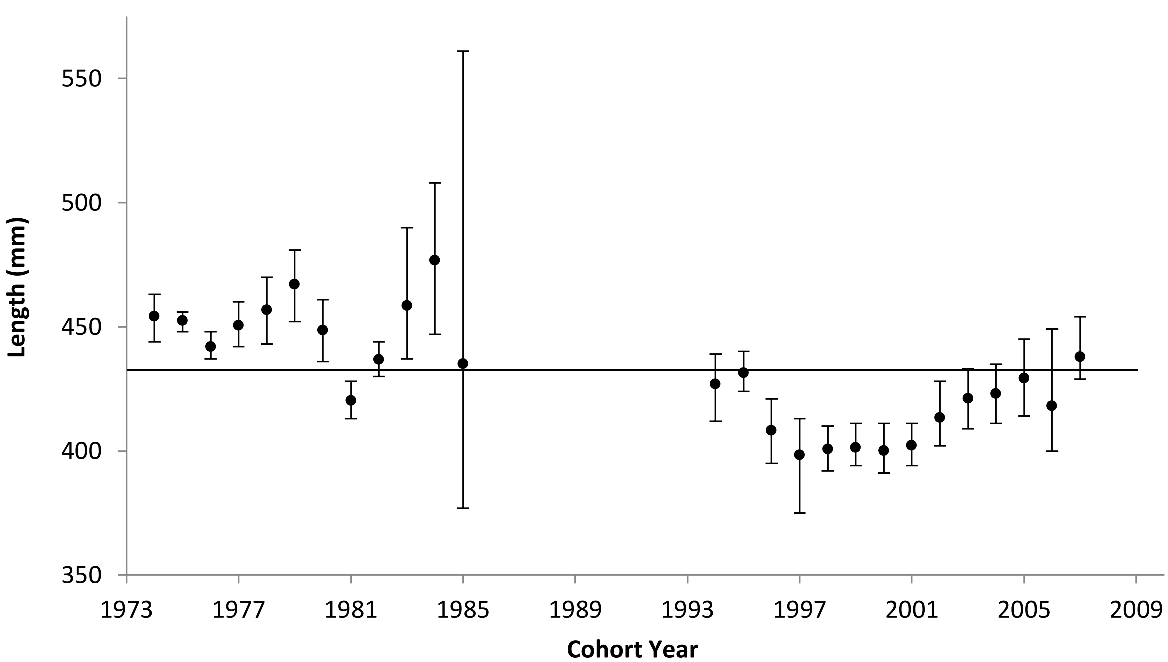


FIGURE 20. Age at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Michigan based on fishery independent survey data.

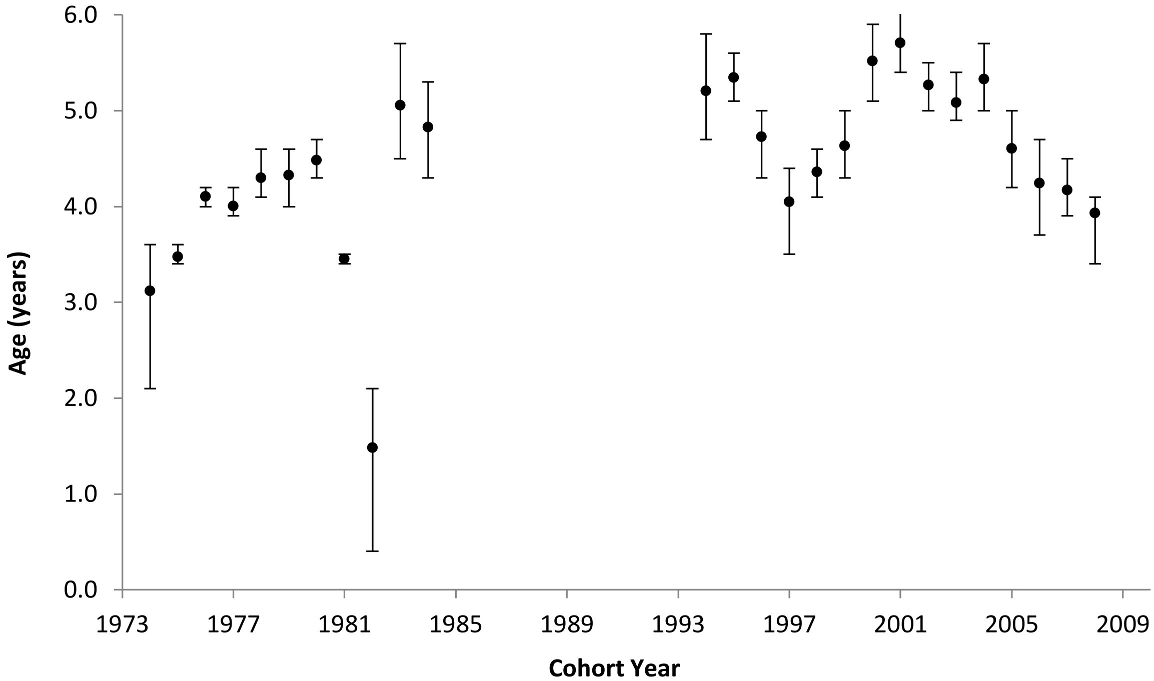
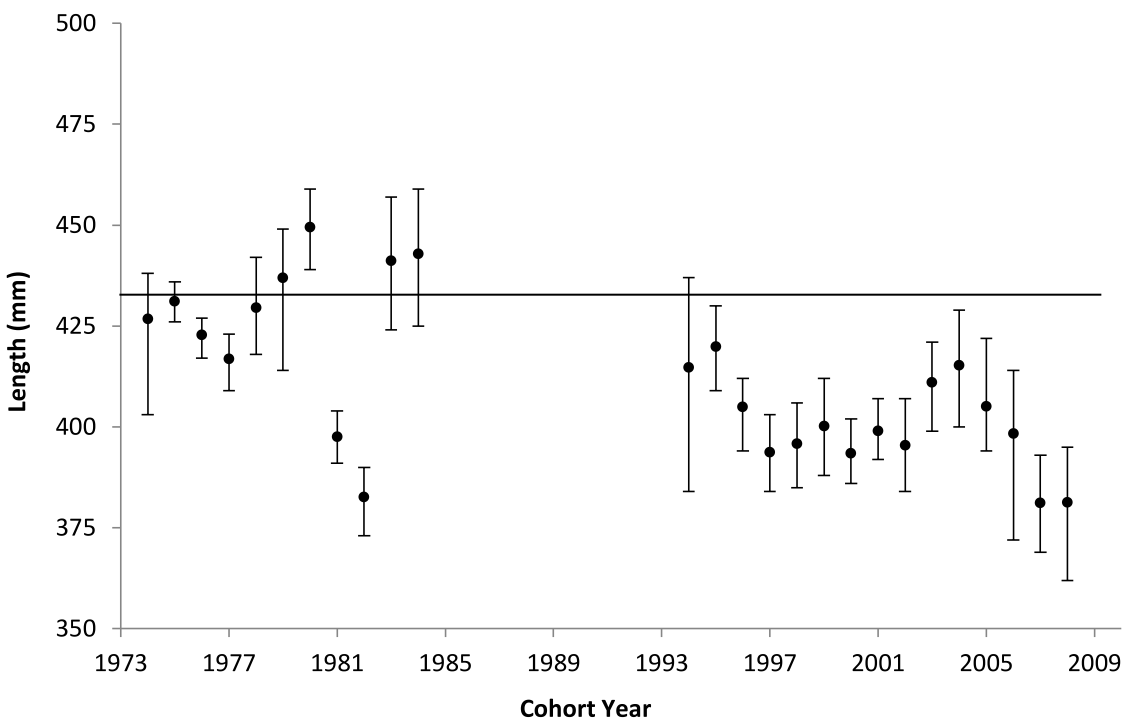


FIGURE 21. Length at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Michigan based on fishery independent survey data. Solid line indicates 432mm, the current commercial harvest length limit.



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Appendix 1.3. Plots depicting estimates of L_{50} and A_{50} for Lake Whitefish (Coregonus clupeaformis) evaluated by fishery dependent and fishery independent data in Lake Superior

Plots Depicting Estimates of A_{50} and L_{50} Based on Fishery Dependent Data

FIGURE 22. Age at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Superior based on commercial fishery monitoring data.

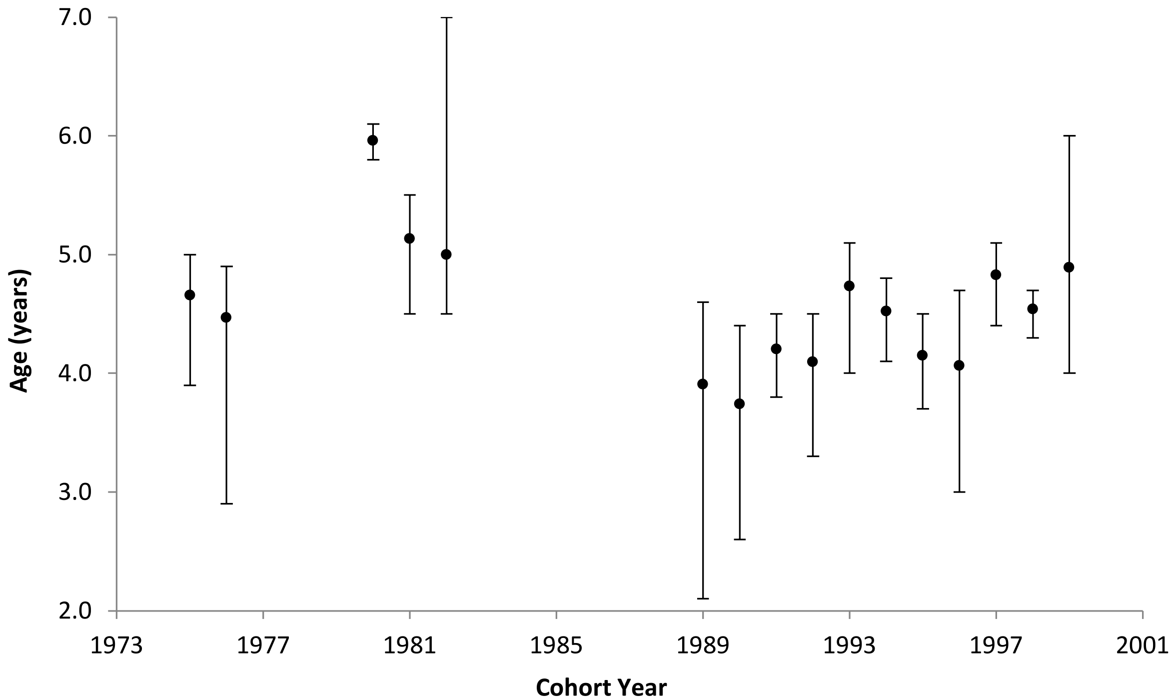


FIGURE 23. Length at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Superior based on commercial fishery monitoring data. Red line indicates 432mm, the current commercial harvest length limit.

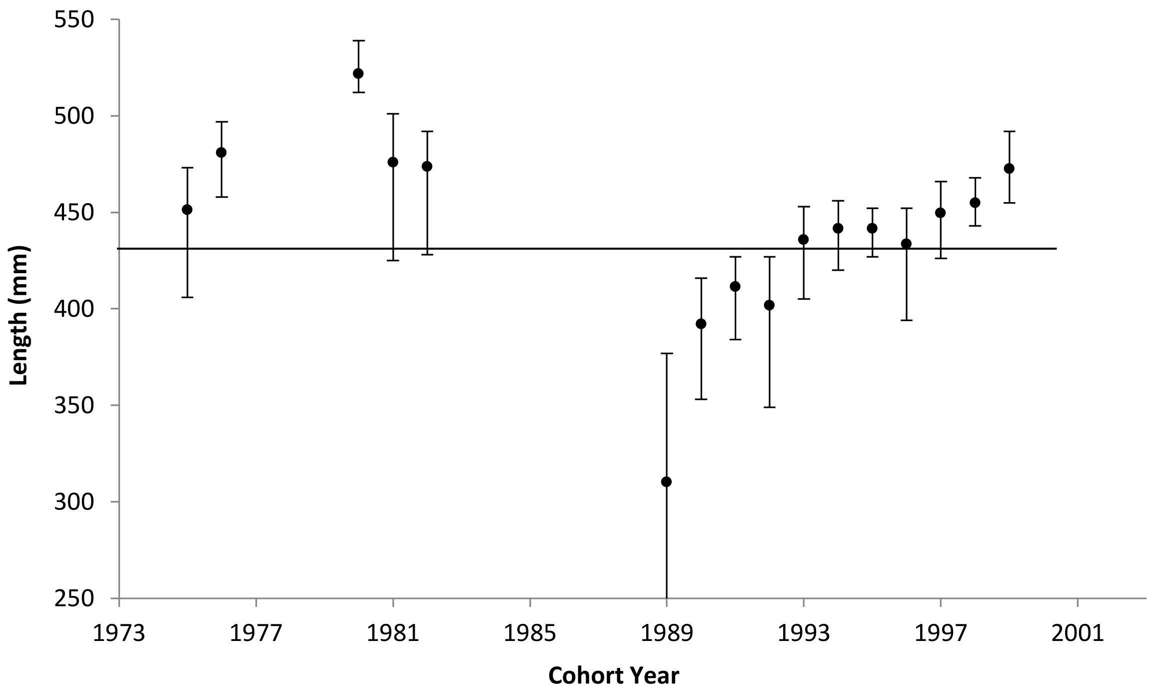


FIGURE 24. Age at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Superior based on commercial fishery monitoring data.

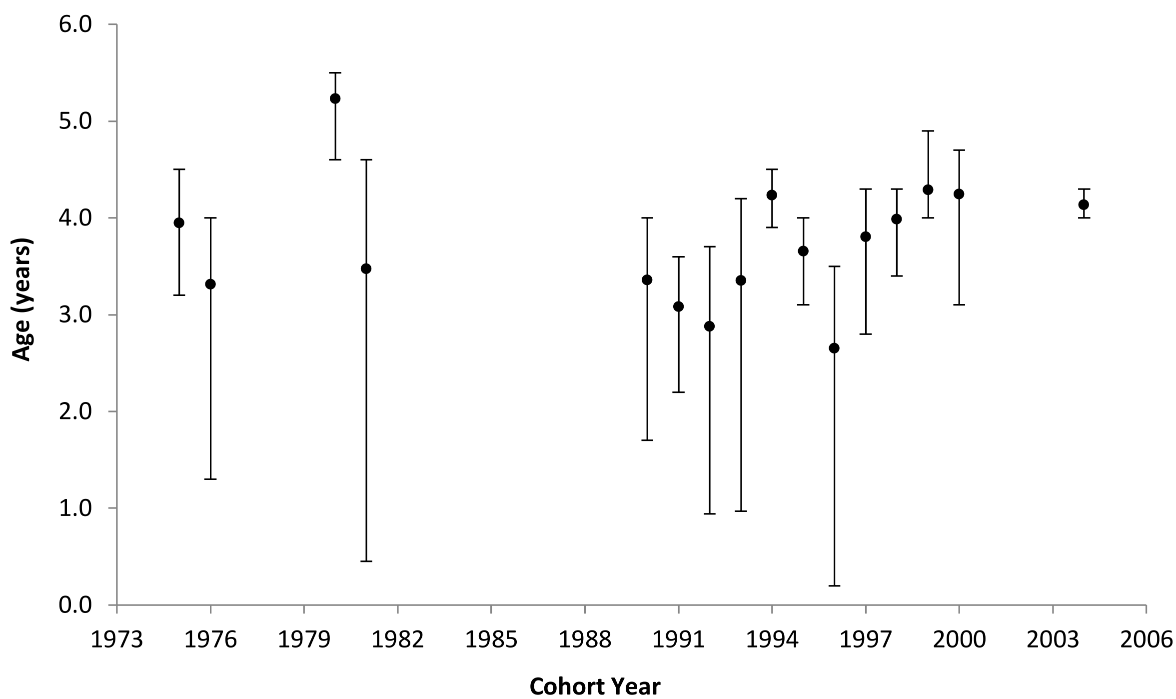
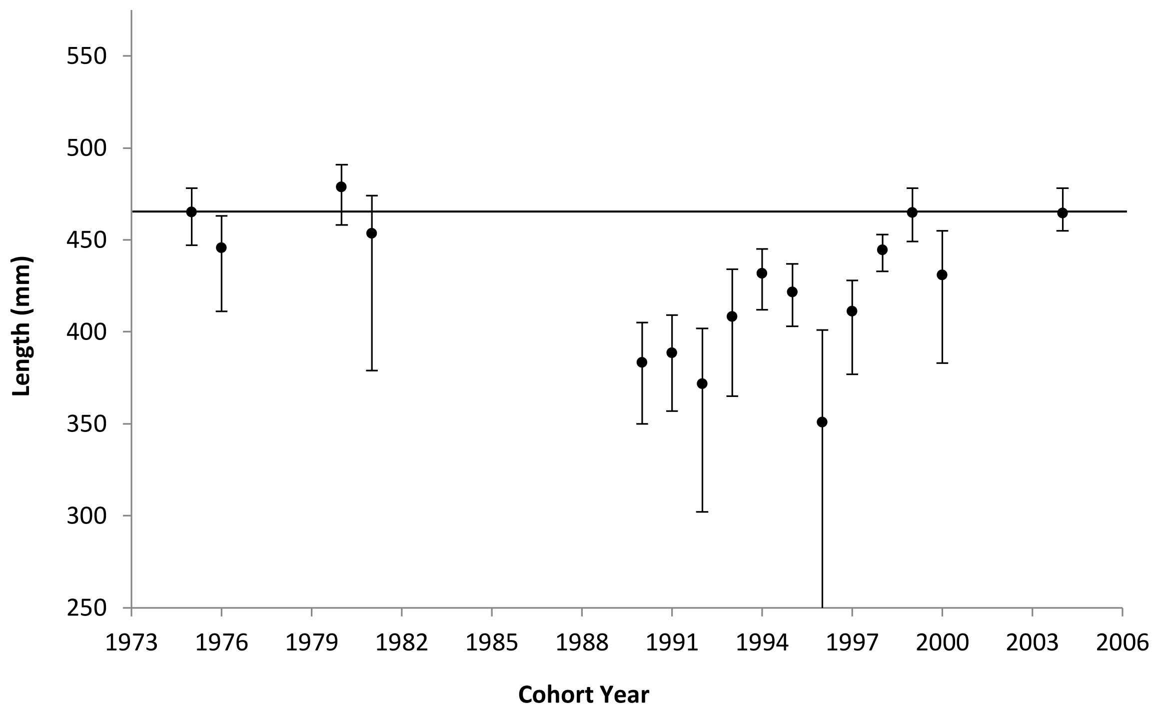


FIGURE 25. Length at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Superior based on commercial fishery monitoring data. Solid line indicates 432mm, the current commercial harvest length limit.



Plots Depicting Estimates of A_{50} and L_{50} Based on Fishery Independent Data

FIGURE 26. Age at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Superior based on fishery independent survey data.

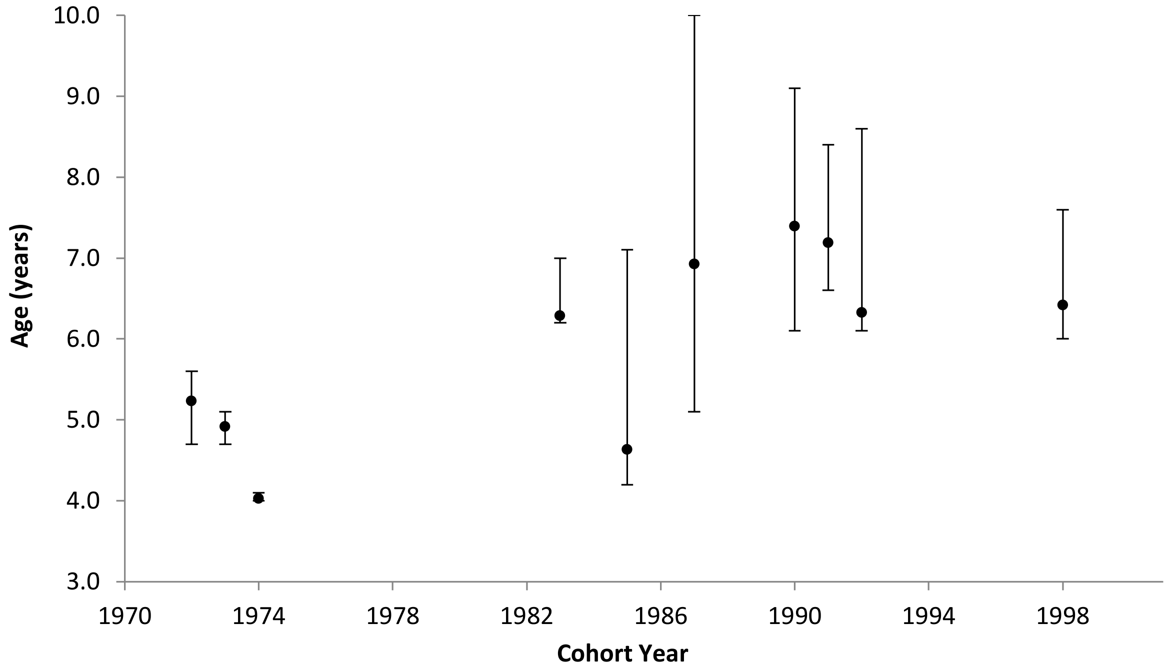


FIGURE 27. Length at 50% maturity with 95% confidence interval of female Lake Whitefish among Lake Superior based on fishery independent survey data. Solid line indicates 432mm, the current commercial harvest length limit.

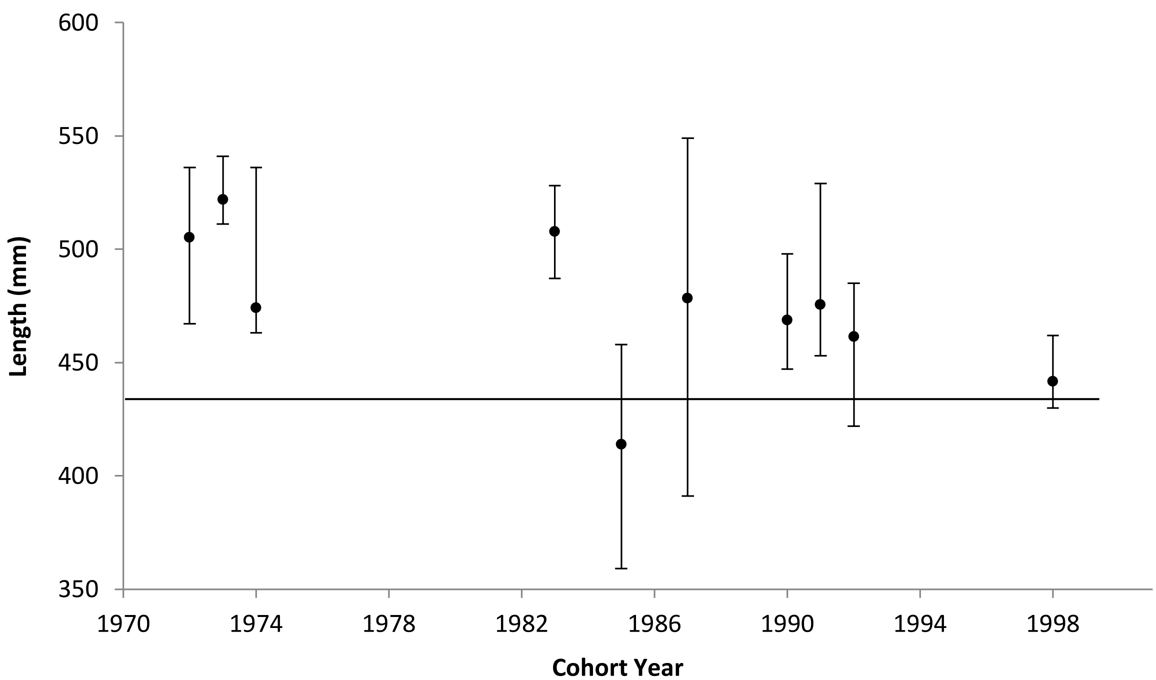


FIGURE 28. Age at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Superior based on fishery independent survey data.

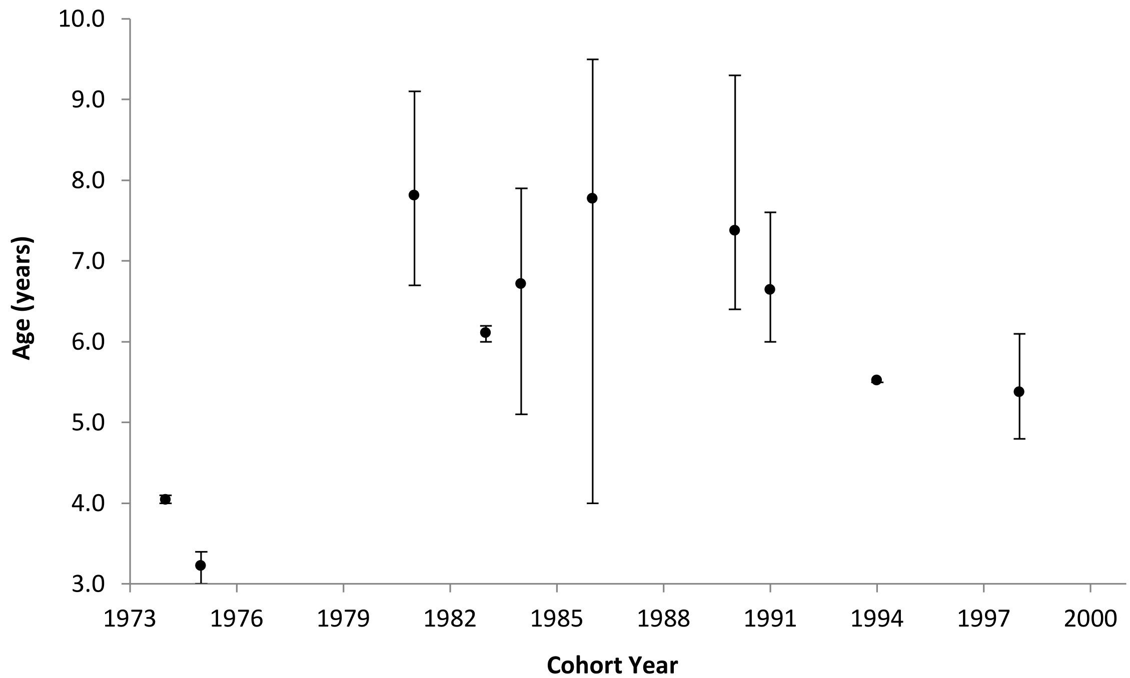
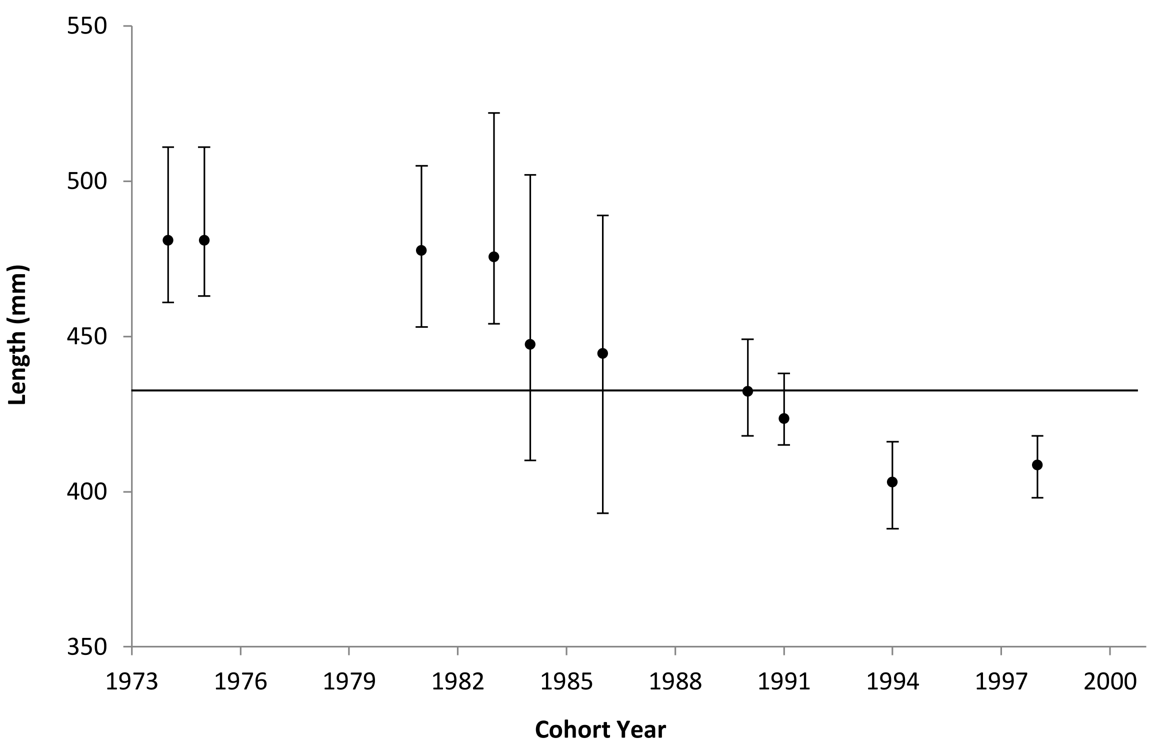


FIGURE 29. Length at 50% maturity with 95% confidence interval of male Lake Whitefish among Lake Superior based on fishery independent survey data. Solid line indicates 432mm, the current commercial harvest length limit.



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