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TEMPORAL AND SPATIAL TRENDS IN SISCOWET (*SALVELINUS NAMAYCUSH*) ABUNDANCE AND BIOLOGY FOR MICHIGAN WATERS OF LAKE SUPERIOR

presented by

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has been accepted towards fulfillment
of the requirements for the

M.S. degree in Fisheries and Wildlife

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May 4, 2009
Date

TEMPORAL AND SPATIAL TRENDS IN SISCOWET (*SALVELINUS NAMAYCUSH*) ABUNDANCE AND BIOLOGY FOR MICHIGAN WATERS OF LAKE SUPERIOR

By

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Fisheries and Wildlife

2009

ABSTRACT

TEMPORAL AND SPATIAL TRENDS IN SISCOWET (*SALVELINUS NAMAYCUSH*) ABUNDANCE AND BIOLOGY FOR MICHIGAN WATERS OF LAKE SUPERIOR

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The siscowet form of lake trout (*Salvelinus namaycush*) is the most abundant of three lake trout morphotypes found in Lake Superior of the North American Laurentian Great Lakes, but published information on their population dynamics and biology is limited. I investigated spatial patterns, temporal patterns, or both, in abundance and life history attributes of siscowet lake trout across Michigan waters of Lake Superior based on data collected during 1970 through 2006. I assessed temporal patterns in siscowet lake trout abundance based on data from a long-term survey that targeted the lean lake trout morphotype, because data from a survey targeting siscowet was more limited. In order to develop an index of siscowet abundance from these data, I used delta-lognormal models. I emphasize both the abundance results and the modeling methodology, which is generally applicable for non-target species. My results agree with previous reports that siscowet densities increased substantially during the 1980-2006 period, and show that the rate of increase decreased since about 2000. The most striking spatial and temporal differences in life history were for length-at-maturity and condition (mass at length). In eastern Michigan waters, siscowets matured at smaller sizes and were in better condition than in waters further to the west. In most areas there was a decline in condition and length-at-age, and an increase in length-at-maturity after 1999, coinciding with when the rate of increase in siscowet density appeared to be decreasing.

ACKNOWLEDGEMENTS

Thank you Shawn Sitar (MDNR), Mark Ebener (CORA), Bill Mattes (GLIFWC), Matt Symbal (Red Cliff Fisheries Department), and all other personnel that collected and provided data for this project. This project wouldn't have started without your collaboration and efforts in creating a siscowet database and finding all available data for siscowet lake trout. I thank my committee members Mike Jones and Andrew McAdam who contributed their thoughts and guidance throughout my academic career and during the development of this thesis.

To my advisor Jim Bence, I don't even think there are words to describe how lucky and grateful I am to have you as an advisor. Even though, I may have floundered a bit by taking on little more than I can chew from time to time. You never tried to change my mind, and let me venture into several different areas while attending Michigan State University (MSU). I'm grateful that you allowed me to figure my way out and discover my limits. Once again, thank you for finally emailing me back and giving me this opportunity to work with you and attend MSU. This will be one of the few defining moments in my life. Thank you.

Finally I would like to thank my family, which consists of my fiancé Eric and our dog Honey. This has been an adventure for the both of us, while struggling to find employment to be close or working long distance. They have both endured through many of my departures while I further my academic career and I'm grateful for their patience. If there were times I felt discouraged, Eric was always there to pick me up when I truly needed encouragement and support.

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THESIS INTRODUCTION & SUMMARY

Lake Superior is the largest of the Laurentian Great Lakes and is the only one to contain lake trout (*Salvelinus namaycush*) morphotypes other than the lean. Three morphotypes are widely distributed in Lake Superior: the lean, the siscowet or "fat", and the humper (Khan and Qadri 1970; Lawrie and Rahrer 1973; Pycha and King 1975). These morphotypes are distinguished by facial characteristics, body fat content, habitat depth, and spawning time.

The siscowet morphotype of lake trout, the focus of this study, usually inhabit offshore water at depths greater than 80 m and have a deep, stout body high in fat content making them less desirable to commercial fisheries (Eschmeyer and Phillips 1965; Khan and Qadri 1970; Pycha and King 1975; Burnham-Curtis 1993; Moore and Bronte 2001; Bronte 1993). Nevertheless, siscowet contributed 27% of the lake trout harvest from 1929 to 1961, with the lean form making up most of the remainder (Bronte and Sitar 2008). Lean lake trout tend to inhabit inshore water at depths less than 80 m, have a salmon-like appearance, and are currently the only commercially targeted lake trout (Eschmeyer and Phillips 1965; Pycha and King 1975). Humper lake trout are distinguished from the other forms by inhabiting deep offshore reefs and through their deep-bodied shape with thin abdominal walls (Eschmeyer and Phillips 1965). Several additional variants have been reported as being extant, but only near Isle Royale in the north-central part of the lake (Moore and Bronte 2001). Significant genetic differences exist among these three morphotypes, but they do not warrant species or subspecies distinctions (Burnham-Curtis 1994; Krueger and Ihssen 2005). Phenotypic differences appear to be adaptations to their respective environments (Henderson and Anderson 2002).

Historically, lake trout were a dominant predator in the Lake Superior fish community, and they supported a substantial commercial fishery that yielded an annual average of 2.0 million kg from 1913 to 1950 (Hansen et al. 1995). During the 1950s, lake trout abundance declined drastically because of excessive commercial fishing and predation by sea lamprey (*Petromyzon marinus*). Sea lamprey invaded Lake Superior in the 1940s, and their abundance increased in the late 1950s, reaching peak levels in 1961 (Smith 1971). Commercial yield of lake trout declined by more than 90% from 1952 to 1962, which resulted in closure of lake trout commercial fisheries in 1962 (Pycha and King 1975).

Lake trout rehabilitation and management efforts focused primarily on lean lake trout populations, despite the ecological importance of both siscowet and humper morphotypes of lake trout (Horns et al. 2003). Lean lake trout stocks increased rapidly in the 1970s and 1980s, in response to the commercial fishery closure, stocking of yearling hatchery-reared lean lake trout, and sea lamprey control. Commercial lake trout fisheries reopened in Wisconsin and Michigan in 1970 and 1980, respectively, as their stocks increased (Hansen et al. 1995). Although not the focus of restoration efforts, siscowet and humper lake trout stock levels increased in the 1980s, primarily due to sea lamprey control.

Recent reports indicate that siscowet densities have been much higher than those of lean lake trout for the past 30 years. Commercial catch per unit effort (CPUE) data indicate that siscowet densities increased steadily from >20 $kg \cdot km^{-1}$ net in the early

1950s to about 250 kg·km^{-1} net in the late 1990s (Bronte et al. 2003). In addition, increases in by-catch of siscowet lake trout in the sport fisheries, which targeted lean lake trout, has also been observed since the early 1990s (Bronte et al. 2003). Based on both spring and summer lean lake trout surveys, Sitar et al. (2007) showed that siscowet lake trout relative abundance, doubled during 1993-2000 from surveys during 1985-1992. In contrast, lean lake trout relative abundance during 1993-2000 was below their average relative abundance during 1983-1992. Ebener (1995) also showed that in 1995 siscowet lake trout made up 72% of the total predator biomass in western Lake Superior compared to 21% for lean lake trout.

Given the previous emphasis of research and management on lean lake trout populations and evidence of the high abundance and potential ecological importance of the other forms, there is a growing recognition of a need to develop objectives for each of the three lake trout forms that were historically (1929 – 1943) widely distributed in Lake Superior (Burhnam-Curtis 1993; Burnham-Curtis and Smith 1994). Concerns have been expressed about potential ecological effects of the siscowet form on the lean form (Bronte et al. 2003; Bronte and Sitar 2008), and recently their has been a renewal of interest in harvesting siscowet (Bronte and Sitar 2008) because they contain high levels of omega-3 fatty acids (Wang et al. 1990; Bronte and Sitar 2008), which could be used for pharmaceutical needs. Additional knowledge of their biology and population dynamics could be useful in defining sustainable harvest levels. There is also some interest in re-introducing deep water forms, such as siscowet lake trout, to other Great Lakes. Improved understanding of their biology could be informative for such efforts.

In this thesis I explore both temporal trends in relative abundance of siscowet lake trout in different areas of Michigan's waters of Lake Superior (chapter 1), and spatial and temporal patterns in their life-history and biology (chapter 2). In fisheries management information on year-specific abundance is often crucial for making decisions. In addition to evaluating trends in abundance, it is also important to understand the life history and biology of a fish. For example information on maturity at age, mass-at-length, and length-at-age could be used in calculations of per recruit reference points and could be informative on sustainable levels of fishing (Quinn and Deriso 1999). Furthermore, it would be useful to evaluate the extent to which life-history characteristics vary spatially and over time as this might provide clues to whether stocks in Lake Superior are approaching biological limits or whether if the siscowet form were introduced into other lakes its biology might differ from what has been seen in particular areas of Lake Superior. This latter topic points out the usefulness of evaluating both relative abundance and life history of a fish.

Summary of Chapter 1

CPUE is widely used as an index of abundance, in part because time series of catch and effort information are frequently available from commercial, recreational or assessment fisheries. For instance, in Michigan's waters of Lake Superior a spring gill-net survey that targets lean lake trout has collected catch and effort information since 1959 and a gill net survey that targets siscowet form lake trout has collected catch and effort information for five survey years (but with many fewer sites sampled each year than the survey targeting lean lake trout) during 1996-2006 in most areas.

In chapter 1, I report on efforts to develop an index of abundance based on fitting statistical models to "standardize" CPUE data from the spring gill-net survey that targets lean lake trout. I chose not to use the survey that targeted siscowet form lake trout because of its shorter time-series, fewer sampled years, and fewer sample sites for each year. Catch and effort standardization methods are widely used to account for factors other than abundance that influence CPUE through the use of statistical models, such as general linear models or generalized linear models. Such catch and effort standardization generally should be used in developing an index of abundance based on data unless the data arise from a fully randomized design. When using raw CPUE (a ratio of total catch to total effort or a simple average of the ratio over samples for annual or longer periods) as an index of abundance in such situations, instead of estimates based on statistical modeling, it is known that there are various factors other than abundance that could influence the expected CPUE. Changes in such factors, when not accounted for, could either add unnecessary noise to the index or lead to a violation of the basic assumption for using CPUE as an index of abundance, that CPUE is directly proportional to abundance.

For the spring lean lake trout survey, catches of siscowet form lake trout are essentially by-catch. By-catch species tend to have CPUE data that are highly skewed to the left with a high proportion of zero catches. Such data are common for non-target species in both surveys and fisheries. This type of data leads to difficulty in modeling CPUE and alternative statistical methods are needed to address such problems. A modern method that is commonly used in marine systems to analyze such CPUE data is called the delta approach (Lo et al. 1992; Vignaux 1996; Ortiz et al. 2000; Ortiz et al.

2004). This method essentially involves modeling both the probability of a non-zero catch and the CPUE given a positive catch and then taking the product of these as an index of abundance. I adopted this approach and the delta-lognormal model specifically, to analyze the siscowet form CPUE observations from the lean lake trout survey.

In chapter 1, I emphasize both the modeling methodology and what the results tell us about changes in siscowet relative abundance over time. My approach illustrated the usefulness of statistical standardization, random effects to account for correlations, and information theoretic model selection methods, as well as the value of the delta approach for analyzing by-catch data where zeros are common.

My results agree with previous reports that siscowet densities increased substantially during the 1980-2006 period, and show that the rate of increase decreased since about 2000. Given the use of statistical modeling for CPUE standardization and the use of the lean lake trout survey data, my results provide further evidence of substantial increases in siscowet densities during the 1980-2006 period, based on a different suite of data and assumptions than previous assessments based primarily on raw CPUE from fishery data. My results also show a decrease in the rate of increase since about 2000. My analyses were done separately for five different lake trout management areas in Michigan's waters, and roughly similar patterns were seen across areas.

Summary of Chapter 2

In chapter 2, I focused on biological characteristic that would be important to fisheries management in the future. The biological characteristics I chose were age and size composition, mortality, maturation, condition, and growth. These are key demographic factors that can influence spawning stock biomass, recruitment, and yield potential. Some limited basic biology and life history attributes of siscowet form lake trout have been described in previous studies, for example, siscowet lake trout have an estimated Brody growth coefficients (*K*) ranging from (0.053-0.080), first maturity near age 8, and mass-specific fecundity has been estimated at 1025 eggs/kg (Carlander 1970; Peck 1988; Kitchell et al. 2000; Miller and Schram 2000). However, there is still much more to be learned about their life history. My study is the most comprehensive investigation of siscowet life history and the first to look simultaneously at age and size composition, condition, growth, maturation, and mortality of siscowet in Lake Superior.

The objective for this chapter was to examine all these aspects of biology/life history together, and for each biological measure describe temporal and spatial variation and determine whether the measures are related to siscowet density. The sources of information for this chapter included several fish surveys primarily targeting leans or siscowets that use gill-nets with either fixed or varying mesh sizes. Available siscowet data I used start as early as 1990 and extend through 2006, where for most analyses I created time periods: period 1 is a time block for the 1990s and period 2 is a time block for the 2000s. During the1990s there was general increase in siscowet abundance, whereas during the 2000s, increases were still occurring but at a declining rate potentially approaching an asymptote (Chapter 1, Bence et al. manuscript). Therefore, one objective of my study was to identify whether siscowet biology has changed during these periods when large changes in abundance took place. In addition, I was interested in identifying whether there were spatial differences in siscowet biology within the Michigan waters represented in the survey data I used (Management units MI2 through MI7, Chapter 1,

Figure 1.1). To evaluate this I looked for differences among zones consisting of one or more management units.

Various statistical techniques were used to evaluate temporal and spatial patterns in life history and biological parameters, in addition I looked at several different gear types that targeted either lean or siscowet lake trout. While the details differ among analyses and from Chapter 1, again I rely on statistical models, incorporation of appropriate random effects, and information theoretic methods for model selection. Regardless of the type of gear used, the temporal and spatial trends observed were consistent. In general, I saw a shift toward older and longer siscowet from period 1 to period 2. Siscowet lake trout are pre-dominantly maturing at larger sizes and both condition and growth were declining over time. A particularly interesting finding was for siscowet lake trout in zone 4 (MI7), the most eastern part of the lake I evaluated, which had different results compared to the other areas. Siscowet lake trout in zone 4 matured at smaller size, were in better condition, and were longer at younger ages.

Concluding Remarks and Connection Between Chapters 1 and 2

In general, I found that both the population dynamics and several life history attributes for siscowet lake trout have been changing through time. Several life history attributes underwent substantial changes of the type one would expect as compensatory responses as siscowet densities approached their highest levels. This may be an indication of a cause and effect relationship between siscowet densities and the growth and condition declines and the associated changes in the maturity schedule. These results provide a new in depth look at siscowet abundance and siscowet biology, considering spatial and temporal differences and will contribute to furthering our knowledge of siscowet lake trout.

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CHAPTER 1

ABSTRACT

DEVELOPING AN INDEX OF ABUNDANCE FOR SISCOWET LAKE TROUT (*SALVELINUS NAMAYCUSH*) USING A NON-TARGET SURVEY FOR MICHIGAN WATERS OF LAKE SUPERIOR

By

Melissa T. Mata

Siscowet lake trout are the most abundant form of lake trout in Lake Superior. Published information on siscowet population dynamics is largely based on commercial fishery data. A survey to specifically sample siscowet lake trout was not started until 1996, is done only every third year, and samples relatively few locations within each management unit in Michigan waters. In this paper we assess temporal patterns in siscowet form lake trout abundance in Michigan waters of Lake Superior based on data from a long-term lake trout survey that targeted the lean form. Although siscowets are regularly caught in the lean lake trout survey, there were high proportions of zero catches in some years and highly skewed positive catch data. In order to develop an index of siscowet abundance from these data, we used delta-lognormal models. This approach involves fitting two submodels, one for the proportion of non-zero (positive) catches, and one for the catch per unit effort (CPUE) conditional on the catch being non-zero, and estimating the unconditional CPUE for each year as the product of the estimated proportion of non-zero catches and the conditional CPUE. We developed these statistical models for five of the eight management units within Michigan, with the other units not having sufficient data to estimate a useful time-series of indices. We considered year, grid (a fixed sample site), and depth of the gill-net as potential factors to include in the

models and selected among alternative models using Akaike Information Criterion (AIC). We emphasize both modeling methodology as an example of such methods for fish species of interest from a non-target survey, and the results that provide further evidence of substantial increases in siscowet densities during the 1980-2006 period, with a decrease in the rate of increase since about 2000.

Introduction

Lake Superior is the largest of the Laurentian Great Lakes and is the only one to contain lake trout (*Salvelinus namaycush*) morphotypes other than the lean. The siscowet morphotype of lake trout, the focus of this study and one of the three morphotypes distributed lake-wide, usually inhabit offshore water at depths greater than 80 m and have a deep, stout body high in fat content making them less desirable to commercial fisheries (Eschmeyer and Phillips 1965; Khan and Qadri 1970; Pycha and King 1975; Burnham-Curtis 1993; Moore and Bronte 2001; Bronte 1993). Nevertheless, siscowet contributed 27% of the lake trout harvest from 1929 to 1961 (Bronte and Sitar 2008).

Historically, lake trout were a dominant predator in the Lake Superior fish community, and they supported a substantial commercial fishery that yielded an annual average of 2.0 million kg from 1913 to 1950 (Hansen et al. 1995). During the 1950s, lake trout abundance declined drastically because of excessive commercial fishing and predation by sea lamprey (*Petromyzon marinus*). Sea lamprey invaded Lake Superior in the 1940s, and their abundance increased in the late 1950s, reaching peak levels in 1961 (Smith 1971). Commercial yield of lake trout declined by more than 90% from 1952 to 1962, which resulted in closure of lake trout commercial fisheries in 1962 (Pycha and King 1975).

Lake trout rehabilitation and management efforts focused primarily on lean lake trout populations, despite the ecological importance of both siscowet and humper morphotypes of lake trout. Lean lake trout stocks increased rapidly in the 1970s and 1980s, in response to the commercial fishery closure, stocking of yearling hatchery-reared lean lake trout, and sea lamprey control. Commercial lake trout fisheries reopened in Wisconsin and Michigan in 1970 and 1980, respectively, as their stocks increased (Hansen et al. 1995). Although not the focus of restoration efforts, siscowet and humper lake trout stock levels increased in the 1980s, primarily due the sea lamprey control efforts. Observations of increasing catch per unit effort (CPUE) of siscowet lake trout for commercial lake trout and whitefish fisheries during the 1980s and early 1990s led to the development of the Lake Superior Technical Committee (LSTC) lake-wide siscowet surveys. These surveys were initiated in 1996 and 1997 throughout Lake Superior and are conducted every three years in an attempt to document siscowet densities and verify that the observed increasing catch per unit effort in the commercial fishery was in fact reflecting increases in siscowet stocks.

In addition to data from this survey, there is substantial biological and catch per unit effort information on siscowet lake trout obtained by various standardized assessment fisheries throughout Michigan waters of Lake Superior. These standardized surveys primarily targeted the inshore lean lake trout; siscowet and humper lake trout were considered incidental catch. However, siscowet lake trout have been caught commonly in these surveys for several decades, providing relevant information on time trends of abundance for siscowet lake trout.

Evaluations of relative abundance, based largely on (CPUE) in fishery and survey samples, suggest that siscowet densities have been increasing since the 1960s and have been much higher than those of lean lake trout for the past 30 years (Bronte et al. 2003; Sitar et al. 2007; Bronte and Sitar 2008). Ebener (1995), based on commercial fishery data, concluded that siscowet lake trout made up 72% of the total predator biomass in western Lake Superior compared to 21% for lean lake trout in 1995. CPUE for siscowet increased from >20 kg·km^{-1} net in the early 1950s to about 250 kg·km^{-1} net in the late 1990s (Bronte et al. 2003). In addition, by-catch of siscowet lake trout increased after the early 1990s in the sport fisheries, which targeted lean lake trout (Bronte et al. 2003). Sitar et al. (2007) reported that CPUE of siscowet lake trout doubled from 1985-1992 to 1993-2000, based on a summer survey that targets smaller sizes of lean lake trout. In comparison, lean lake trout CPUE from this survey during 1993-2000 was below the average CPUE for 1983-1992.

There is now a need to broaden lake trout management efforts and develop specific objectives for siscowet and humper morphotypes as well as for lean lake trout (Horns et al. 2003). All three of these lake trout morphotypes were historically (1929 – 1943) caught in substantial numbers in Lake Superior (Burnham-Curtis 1993; Burnham-Curtis and Smith 1994), and are currently widely distributed in the lake. Given the high abundance of siscowet lake trout in Lake Superior, interest in their biology and population dynamics has increased.

The purpose of this paper is to i) develop an index of abundance for siscowet lake trout utilizing the spring lean lake trout survey data and ii) describe trends in relative abundance over time and space. The siscowet survey provides samples from only five sample years starting in 1996, and thus provides limited information on long-term trends. In contrast, the spring lean lake trout survey contains catch and effort information since 1959, and siscowet lake trout have been consistently caught in these surveys since the late 1970s. Our approach contrasts with and builds upon past efforts in evaluating trends in siscowet abundance in several ways. Results presented by Bronte et al. (2003 and 2008) are based upon commercial fishery data, and such trends can be influenced by changing fishing power and fishing behavior (Hilborn and Walters 1992). In addition, Bronte et al. (2003 and 2008) and Sitar et al. (2007) based their evaluations of temporal changes in siscowet abundance upon raw CPUE (a ratio of total catch to total effort for annual or longer periods). Such aggregate measures of CPUE can be influenced by changes in fishing or sampling locations or other factors. Although sampling locations tend to be more constant for surveys than for a fishery, there have been some inter-annual differences in sampling locations for the lean lake trout surveys due to logistics (e.g., weather conditions) and to intentional design changes. Patterns resulting from such changes can be confounded with actual abundance changes. Fortunately, a "catch-effort standardization" approach based upon statistical modeling can account for some variation due to such factors and produce less biased estimates of relative abundance and a more reliable assessment of uncertainty (e.g., Maunder and Punt 2004).

One challenge for developing a statistically-based index of abundance for non-target catch and effort is that the data are skewed to the left with a high proportion of zero catches (Stefansson 1996; Ortiz et al. 2000). This adds to the usual need to account for variation due to factors such as changes in sampling locations. Such standardization of catch and effort is most commonly accomplished through the use of general linear models, generalized linear models, or related approaches on catch and effort data (Maunder and Punt 2004), and here we applied both of these types of models to CPUE data. In addition, we implemented a delta approach to address statistical issues stemming from the relatively high frequency of zero catches. The delta approach is widely used in modeling CPUE where there is a high proportion of zero catches, as is often the case for non-target species in both survey and fishery data (Lo et al. 1992; Vignaux 1996; Ortiz et al. 2000; Ortiz et al. 2004).

Methods

Assessment Fishery Data

We analyzed data based on samples collected in Michigan's waters of Lake Superior by the Michigan Department of Natural Resources (MDNR), Chippewa Ottawa Resource Authority (CORA), and Great Lakes Indian Fish and Wildlife Commission (GLIFWC) (Figure 1.1). These data came from a standardized spring gill-net survey that has been conducted since 1959. Only data archived electronically were used, limiting our analysis to 1975 through 2006 overall. Michigan (MI) waters of Lake Superior are divided into eight management units, and the end year for individual management units was either 2005 or 2006. The primary purpose for this survey was to provide an index of abundance for lean lake trout. Sampling occurred during April through June at fixed stations, using large mesh gill-nets (4.5 inch stretched mesh), and set on the bottom across contours targeting depths from 30 – 250 feet (ft). Data collected for each gill-net set include: date, length of gill-net set, water depth at start and end of the set, management unit, number by species of fish caught, and other descriptive and quantitative biological variables.

The catch of siscowet represented 4.6% of the total lake trout catch by numbers for this assessment period. There was a total of 3310 gill-net sets conducted, of which 1211 captured at least one siscowet. The proportion of lake trout catch that was siscowet ranged over years from 2% to 86%, showing a generally increasing pattern (Figure 1.2).

Siscowet were regularly caught in the surveys, however there were a large proportion of zeros catches, especially in earlier years, and the positive catch data were highly skewed. To achieve our objective of developing an index of siscowet abundance from these data, we needed to account for the distribution of the data. To this end we used a delta approach, which involved fitting two "submodels".

Delta Approach Overview

We applied the delta approach separately for five of the eight management units. At this spatial scale the populations are likely to be experiencing different recruitment and survival patterns over time. Thus a combined analysis was not considered, because we believed that complex interactions involving management unit would make the results of such an analysis difficult to interpret and reduce or preclude statistical benefits such as increased power to detect common patterns. For two units, MI1 and MI2, we did not develop models because there were no siscowet catches. We did not include a third management unit (MI8) because data were available for only four years, which we found to be insufficient for describing temporal trends in abundance. Briefly, the idea is to model CPUE as the product of the probability of occurrence for a non-zero catch and CPUE for positive catches, and use estimates of these two components for a given year to obtain indices of abundance. CPUE is expressed as the number of fish caught per kilometer of gill-net set. Duration of gill-net sets varied, and thus CPUE was standardized to account for varying soak time and the influence of net saturation prior to analysis (Hansen et al. 1998).

More specifically, we used a delta-lognormal model to estimate annual indices of abundance for siscowet lake trout. This involved developing statistical submodels for the two components (probability of occurrence for a non-zero catch and CPUE for positive catches). The probability of occurrence for a non-zero catch naturally follows a Bernoulli distribution. For the second component, CPUE given positive catches was assumed to follow a lognormal distribution because positive CPUE data were highly skewed. Parameters for each submodel were estimated using either generalized linear models or generalized linear mixed models (GLMs or GLMMs), by using "lm", "glm" or "lmer" procedures in R version 2.4.0.

Our statistical submodels for the probability of occurrence for a non-zero catch or CPUE given positive catches potentially included year, grid (a fixed sample site), and depth of the gill-net set as fixed effects. Depth was treated as a fixed categorical effect. A gill-net is classified as shallow if the maximum of the start and end depths of a gill-net set was <=150 ft, as deep if the minimum was > 150 ft, and as intermediate if otherwise (i.e., if 150 ft was between the maximum and minimum). We defined depth as a categorical variable with just three levels because typical gill-net sets spanned a broad range of depths. Our models also potentially included all possible interactions of these fixed effects as random effects. Grid is treated as a fixed effect because the fixed sampling locations represented by these grids were chosen based on historical fishing, in a non-random fashion. Depths of samples were also not randomly selected and fish in general tend to have defined depth distributions, hence this factor was treated as fixed. Our focus here is to estimate relative abundance in each year, and identify potential systematic trends over the study period. Hence we also model year as a fixed effect, but recognize that modeling year as a random but temporally correlated effect is a reasonable alternative. Our modeling of the interactions of fixed effects as random, contrasts with the more usual treatment of these as fixed in the context of a manipulative experiment. The idea here is that these interactions reflect short-term and/or smaller spatial scale variations in distribution that are unpredictable and thus can be viewed as if random. For example, we are treating the year by grid interactions as reflecting chance variations in the distribution of fish that influenced CPUE at the specific grid and time of sampling. Note that another way of viewing these random interactions is that including them is equivalent to imposing non-independence in the residual error among the gill-net sets representing the combination of factors represented by the interaction, for a model that does not include such random interactions. Our final submodels and associated indices did not include all these potential fixed and random effects, as we first went through a model selection process to avoid an over-parameterized model.

Modeling the probability of occurrence for a non-zero catch

Parameters for the submodel for the probability of occurrence for a non-zero catch were estimated based on data for each gill-net set, where observations were classified as "1" if at least one siscowet was caught or "0" if no siscowet caught. The analysis assumes that the classified observations are independent realizations of Bernoulli random variables, with probability p of success of catching a siscowet for a given combination of years, grid and depth as defined by effects in the model. There were often multiple observations (n) for each combination of effects and hence we modeled the number of non-zero catches as binomial, using a generalized linear mixed effect model and a logit link function (McCullagh and Nelder 1989; Schall 1991; Venables and Dichmont 2004). The fully (saturated) mixed effects model for the logit [g()] of the probability [p_i] of non-zero catches for the ith observation from year y, grid g, and depth stratum d is:

[1] $g(p_i) = \log_e(p_i/(1-p_i)) = \alpha_y + \beta_g + \omega_d + \delta_{yg} + \gamma_{yd} + \lambda_{gd} + \rho_{ygd}$

where α_y is the effect for year, β_g is the effect for grid, ω_d is the effect for depth, δ_{yg} is the random interaction for year and grid, γ_{yd} is the random interaction for year and depth, λ_{gd} is the random interaction for grid and depth, and ρ_{ygd} is the random interaction for year by grid by depth. All random effects were assumed to be normally distributed with a mean of zero and a variance estimated by the model.

Sparse data are known to cause convergence issues and unreliable estimates for this type of model (Collett 2003), which we found to be true for these data also in preliminary analyses. Consequently we restricted our analysis to years where both zero and non-zero (positive) catches were made for a management unit, and to grids that were sampled in at least three years (Table 1.1).

Modeling the catch rate for positive catches

A second submodel was constructed using data for gill-net sets that caught at least one siscowet. The response variable is the catch rate, which we also refer to as catch per unit effort (CPUE), for an individual (*i*th) gill-net set for a given year y, grid g, and depth stratum d. Given our assumption of lognormal CPUE for positive catches, data were log-transformed, and the fully (saturated) mixed effects model is:

[2] $\log_e(CPUE_i) = \mu + \alpha_y + \beta_g + \omega_d + \delta_{yg} + \gamma_{yd} + \lambda_{gd} + \rho_{ygd} + \varepsilon_i$

where μ is the overall mean, α_y is the effect for year, β_g is the effect for grid, ω_d is the effect for depth, δ_{yg} is the random interaction for year and grid, γ_{yd} is the random interaction for year and depth, λ_{gd} is the random interaction for grid and depth,

ρ_{ygd} is the random interaction for year and grid by depth, and ε_i is the unexplained residual error.

Model selection procedure

We considered models simpler than the fully saturated one. To this end we fit all possible models that allowed any combination of fixed effect and random effect terms included in the fully saturated model, provided the fixed effect of year was included. We focused on models that included a year effect because our objective was to calculate an annual index of abundance, and this is only possible for models that included such an effect. We also considered an intercept only model, with no fixed effects, in order to assess whether there was evidence for changes in CPUE from year to year. There were 16 different candidate models for random effects (Table 1.2), and five different candidate models for fixed effects (Table 1.3), leading to a total of 80 possible models. However, many random effects had variances that converged on zero, and hence a number of models became effectively identical to more parsimonious models. We only report results for those models that are unique and also do not report results for the intercept only model, which was always the worst based on AIC (see below).

Final models for each management unit were selected using Akaike's information criterion (AIC) (Burnham and Anderson 1998):

$$[3] \qquad \mathrm{AIC} = -2 \log L(\theta) + 2\mathrm{K},$$

where $\log L(\theta)$ is (maximum) log-likelihood, and K denotes the number of parameters in the model. Model selection was accomplished using R 2.4.0, using both AIC and log-likelihood built in function. For models that included random effects we used the R lmer functions, and for fixed effect models we used the glm function for the binomial component and the lm function for the CPUE for positive catches component (the lmer function requires at least one random effect). We subtracted two from the AIC results obtained using lm because the residual variance is counted as a parameter for K in the AIC calculation for lm, but is not included in the calculation of K by lmer. Maximum likelihood (ML) techniques were used for model fitting when comparing all models. All models were comparable within each management unit because there was no missing data and all models used the same response variable. In addition, for each model we calculated $\Delta\mathrm{AIC}_i$ ($\Delta\mathrm{AIC}_i = \mathrm{AIC}_i - \mathrm{AIC}_{\mathrm{min}}$), where i is the model index, and Akaike weights (Burnham and Anderson 1998). The model selection procedure was applied separately for both the probability of occurrence for a non-zero catch and the catch rate (CPUE) given positive catches, resulting in one best overall model (with two separately selected components).

We conducted a comparative analysis to evaluate how an alternative data selection procedure would influence results. Our alternative data selection procedure was to again require that each year contain both zero and non-zero catches, but that each grid needed to be sampled in at least eight different years (instead of the three years we required in the base analysis). Only three of the five management units were re-analyzed based on this procedure (MI5 thru MI7), because for the other units all grids that were sampled at least three times were also sampled at least eight times. Once we had applied the alternative data selection procedure we repeated the complete model selection process and compared both the selected model and the resulting trends in abundance indices with those that resulted from the base analysis.

For the best CPUE for positive catches model, a frequency histogram of the residuals and a quantile-quantile plot were examined to evaluate whether there were substantial departures from the assumed normal error distribution (on the transformed scale).

Constructing indices of abundance and standard errors

An index of annual abundance was defined based on combining least square means (LSMs) for year obtained from the best submodels for the probability of occurrence for a non-zero catch and catch rate given a positive catch. The index of abundance is defined as:

[4] Index of annual abundance = $\log_e(\hat{p}) + \log_e(\text{CPUE}|\text{positive catches})$,

where $\hat{p}$ is the estimated probability of occurrence for a non-zero catch (capturing a siscowet = "success") and CPUE|positive catch is the catch per unit effort (catch rate) given a positive catch. Both of these components are estimated for each year for average values of the explanatory variables (other than year). The $\log_e(\hat{p})$ component of the annual index of abundance was constructed by first converting the LSMs from the binomial model, which was on the logit scale, to a probability scale. From equation 1 we have:

[5] $LSM = g(\hat{p}) = g(p(\hat{\theta}, X)) = \log_e\left(\dfrac{p(\hat{\theta}, X)}{1 - p(\hat{\theta}, X)}\right) = \hat{\alpha} + X\hat{\beta}$

Where $g()$ is the logit link function, $\hat{\theta}$ is the vector of estimated parameters (α and β), α is the intercept, and β is a vector of slope coefficients, and it is understood that this equation is for a given year. By defining $\hat{p} = p(\hat{\theta}, X)$ we are emphasizing that the estimated probability depends upon the estimated parameters and the row vector of explanatory values. Here, for calculation of LSMs, X represents average values of the explanatory variables, except for year which is set to the year of interest. Solving equation 5 for the estimated probability leads to:

[6] $\hat{p} = p(\hat{\theta}, X) = \frac{\exp(LSM)}{1+\exp(LSM)}$.

Variances for estimates of $\log_e(p)$ (squared standard errors) were calculated using a simplified form of the delta method (Seber, 1982, p. 8):

$Var(\log_e(\hat{p})) = Var(h(LSM)) = \left(\frac{\partial h(LSM)}{\partial LSM}\right)^2 Var(LSM)$, where

$h(LSM) = \log_e\left(\frac{\exp(LSM)}{1+\exp(LSM)}\right)$, $\frac{\partial h(LSM)}{\partial LSM} = \frac{1}{1+\exp(LSM)}$, and Var($LSM$) was obtained by squaring the standard errors for the LSMs.

The standard errors for the final standardized CPUE estimates are just the square root of the variances for the index, and these variances are obtained as the sum of the variances for the two components: Var(Index) = Var($\log_e(\hat{p})$) +Var($\log_e(CPUE \mid$ positive catches)). Var($\log_e(\hat{p})$) is obtained as described above, and Var($\log_e(CPUE \mid$ positive catches)) is the squared standard error for the LSMs for GLMs or GLMMs for the positive catches.

LSMs for both submodels and their standard errors were constructed in SAS version 9.1 (SAS 2003), because within R's lmer function you can not extract the mean square error that is needed to calculate the standard errors for the LSMs. SAS was not used for model selection because PROC GLIMMIX uses a pseudo-likelihood and associated pseudo AIC values which should not be compared across models (Schabenberger personal communication, 2007). The conversion from the logit to the p scale (expression [5]) is done automatically within SAS (with appropriate specification of options), but is not automatically calculated within R. We verified that the results matched what we obtained by our own calculations for the same model using R.

Results

Model Selection for the probability of occurrence for a non-zero catch (p)

The final models that best explained the probability of occurrence for a non-zero catch varied slightly across all management units (Tables 1.4-1.8). In general, however, the best model included both year and depth fixed effects. Models for MI4 and MI5 differed from the other units by also including a year by grid by depth random interaction (Table 1.5 and 1.6). Each management unit had at least one competing model that was within 2 AIC units, indicating that these models also had substantial support (Tables 1.4-1.8). These competing models did not share a common model structure across management units, in contrast to what we saw for the best models.

Model Selection for the catch rate for positive catches (ln(CPUE))

The best model for the catch rate for positive catches included year, grid, and depth fixed effects for three out of five management units. The models for the remaining two management units did not include the grid fixed effect (Tables 1.4-1.8). Four of the management units also had at least one competing model that received substantial support, and 50% of those models also included year, grid, and depth fixed effects. In the second data selection procedure, where we required that a grid be sampled in at least eight years, two management units (MI5 and MI6) that previously included both year and depth fixed effects in the best model for the first data selection procedure, now also included a grid fixed effect as the overall best model (Tables 1.9-1.10).

Important fixed and random effects

Year was present in all the models and all these models were better (lower AIC) than an intercept only model with no fixed effects. Based on AIC we were able to conclude that depth was an important factor, since all the best models included a depth fixed effect. Most models that included a depth fixed effect were within six AIC units of the best model, except for two probability of occurrence of non-zero catch models in MI4. Alternatively, models that did not include a depth fixed effect had an AIC from 6 to 85 units more than the AIC for the best model. The grid fixed effect was included in four out of 10 best models, and two additional best models in management units MI4 and MI5 (one for each unit) included random interactions involving grid, although grid was not included as a fixed effect in those models. Overall, however, relatively few random effects were included in the best models, with 80% of the best models including no such effects.

Trends in the probability of occurrence for a non-zero catch (p)

We describe these trends on the probability scale (*p*) instead of on the log-scale to aid in the interpretation. In 82% of the year by management unit combinations during the period 1975 through 1985 siscowet were not captured and the probability of occurrence for 50% of those years when siscowet was captured was less than 0.1. The probability of occurrence during 1986-1995 varied across management units but there was generally a trend of increase during the early 1990s. The probability of occurrence for a non-zero catch was highest in MI3 and MI5, with an average probability of 0.58. During the 1996 through 2006 period the probability of non-zero catch increased and then leveled off in all management units, with an average upper level of 0.75 (Figure 1.3). In MI4, the average probability during this period was 0.88. The average probability of occurrence increased from 0.30 in the 1975-1985 period to 0.97 in the 1996-2006 period.

Trends in the catch rate for positive catches (ln(cpue))

The trends observed for the catch rate for positive catches (on a log-scale) was slightly different from the trends observed in the probability of occurrence for a non-zero catch. The first (1975-1985) period was similar, in that it had the lowest average of -0.23. The general patterns of increase and leveling off for the catch rate resembled trends observed for the probability occurrence (Figure 1.4). However, patterns for catch rate diverged for some units during 1986-1995 from the patterns seen for the probability of occurrence. The year with the maximum catch rate (for positive catches) occurred during this middle period for MI3 and MI5 (Figure 1.4). In contrast, catch rates for MI4 and MI6 have their highest averages during the last period (1996-2006) (Figure 1.4). The increase in siscowet catch rate between the first (1975-1985) and last (1996-2006) periods averaged 1.60 on a natural log-scale, corresponding to nearly a five-fold increase.

Trends in Standardized Catch Rate (Index of annual abundance = (ln(p)+ln(cpue))

In Michigan waters of Lake Superior, our siscowet index of abundance was near zero or siscowets were not caught at all between 1975 and 1985, except for MI6 (Figure 1.5). The trends in the index varied across management units, but there was a general pattern of increase from 1986-1995 and a leveling off at a higher level from 1996-2006 (Figure 1.5). In MI6 our abundance index average was higher than in the other units and did not show the same temporal pattern. From 1975 to 1985, the index was higher than in the other management units and declined from 1979 to 1985 (Figure 1.5). As seen previously in other management units between 1996 and 2006, there was a general increase followed by leveling off in siscowet abundance.

Comparative Analysis

Even though we usually found one or more models that were within two AIC units of the best (lowest AIC) model, we did not resort to model averaging. We did not use model averaging because the differences among the competitive models in the resulting annual estimates for the probability of occurrence for a non-zero catch and the catch rate for positive catches were slight, and thus differences among the models do not suggest substantial differences in the trends nor add much uncertainty. We illustrate the similarities between the best model and its closest competitor by plotting the estimated probability of occurrence for a non-zero catch and catch rate for positive catches over time for each management unit (Figures 1.6-1.8).

Discussion

When catch and effort data are used to estimate standardized indices of abundance, sometimes zero catches are observed. These zeros are often either dropped or a small constant is added (to zeros or to all observations) to apply normal-based parametric methods following log-transformation. This approach can be useful when there is a low proportion of zeros and the assumptions of normality and constant variance can be approximated. Other approaches commonly used include modeling catches as count data, or using zero-inflated models. These methods also work best when the proportion of zeros is low because when the proportion of zeros is high, because dispersion tends to be higher than these methods allow for (Maunder and Punt 2004). Despite the usefulness of the above methods in some situations, alternative approaches need to be sought given that some catch data include high proportions of zero catches. An alternative standardization method for catch and effort data, when dealing with such data, is called the delta approach (Lo et al. 1992; Stefansson 1996; Punt et al. 2000; Ortiz and Arocha 2004). In the delta approach the probability of non-zero catches and the catch rate given a positive catch are modeled separately. This methodology is especially useful for analyzing data from non-target surveys, where a particular fish of interest is caught by accident ("by-catch"), and zero catches are common.

In this study we applied delta models to standardized siscowet catch and effort data from non-target (lean lake trout) surveys in Michigan waters of Lake Superior and produced a standardized index of abundance for siscowet lake trout. We used both generalized linear models and generalized linear mixed models to model both the non-zero catch and the catch rate given a positive catch. This is one of just a few attempts to apply the delta approach to develop an index of fish abundance in the Great Lakes (see Haeseker (2001) for another example) and the first applied to a salmonid.

During 1975-1985 in most years no siscowet lake trout were recorded as caught, and our standardized index was low. More siscowet lake trout were recorded in the catch during 1986-1995, where our index was higher. Around 1995, there was a substantial increase in catch and the index, but the period of increase generally ended around 2000. The analysis strongly suggests that siscowet lake trout were increasing in abundance as early as 1995 and reached a leveling off period starting in 2000 through 2006. Our annual estimates from the standardized catch rates confirmed concerns about increases in siscowet catches in lean lake trout habitat.

There is little information documenting trends in abundance for siscowet lake trout in Lake Superior, and the information that is available is recent. Bronte (2003) looked at commercial gill-net catch and effort data from both U.S. and Canadians waters to evaluate abundance from 1950-1998 and the results indicated that siscowet had generally increased over that entire period. More recently Bronte and Sitar (2008) used fishery data to estimate relative abundance during three different fishing periods: early modern (1929-1939), pre-collapse (1941-1949) and collapse (1953-1961). Their results indicate that siscowet abundance was declining before the 1940s and that the sea lamprey likely contributed to the near extirpation of siscowet lake trout.

Our analysis provided limited information on trends prior to the mid-1980s, but suggests a continuing increase in abundance from then until 2006, and in the years that overlap between our study and that of Bronte et al. (2003), Bronte et al. reported a similar temporal pattern to what we report (Figure 1.9). Although the temporal patterns turned out to be similar, we believe our use of survey data and a rigorous statistical approach can allow managers and biologists to now be more confident about the patterns. Bronte et al. (2003) used commercial fishery data to develop a raw index of abundance by using the ratio of siscowet catch to effort for each year in Lake Superior from 1950 to 1998. Shifts in who fishes and where they fish, as well as other factors have been shown in many circumstances to distort the relationship between the ratio of aggregate catch to effort (Maunder and Punt 2004; Deroba and Bence 2009). Use of survey data, with more limited temporal changes in how fish were collected, and adjustments for what changes did occur, provide stronger basis for inferring that CPUE reflected abundance changes, at least in the depth ranges covered by the survey.

We believe that the standardized catch rate for siscowet lake trout, which can be obtained from the spring lean lake trout survey, is one useful way to monitor trends, especially in shallower waters of the lake. Although the siscowet morphotype has been more abundant in waters deeper than those covered by the lean survey, the survey does overlap with their depth distribution. Furthermore, our analyses (including preliminary ones not reported here) showed no indication for a shift in siscowet depth distributions over time. We suspect that this index provides a meaningful measure correlated with siscowet abundance across their entire depth range. We cannot rule out, however, the possibility that changes in the relative abundance of siscowet within the lean survey depths versus deeper waters could make the lean index less reflective of total abundance. Ebener et al. (in preparation), however, did not find evidence of such a change between 1996 and 2006 in survey results that covered the entire siscowet depth range.

It is also important to note that we standardized catch and effort data to account for factors that may affect the assumption that catch rate is proportional to abundance. We did our best to account for such factors by using general and generalized linear mixed effect models in developing indices of abundance, however such models are always subject to refinement or change as additional information becomes available or conditions change. At this point, given the available data, our analyses indicate that the delta approach can be used to standardize catch rates of siscowet in lean lake trout surveys.

It appears that siscowet were the most abundant lake trout morphotype in Lake Superior during the 1990s and early 2000s (Ebener 1995; Kitchell et al. 2000; Bronte et al. 2003; Sitar et al. 2007), and it is also possible that siscowet were the dominant morphotype historically (Bronte and Sitar 2008). It has been hypothesized that siscowet densities are higher than lean densities in the more extensive deep areas of the lake because siscowet lake trout are better adapted to the deepwater habitat (Sitar et al. 2008). Sitar et al. (2008) also noted that lean lake trout were primarily caught at depths of 200 m (~656 ft) or less, whereas siscowets were caught at depths of 40 m (~163 ft) and greater. Thus there is substantial overlap in depth distributions between lean and siscowet morphotypes, suggesting that an index of siscowet abundance within lean lake trout habitat (as was developed here) is of interest.

There is interest in developing a commercial fishery for siscowet to extract fish oils for dietary-supplement purposes, because of the high amount of lipids in their bodies (Wang et al. 1990). Development of such a fishery needs to be done cautiously. Both modeling and empirical studies suggest that siscowet lake trout may only be able to tolerate relatively low levels of fishing (Kitchell et al. 2000; Bronte et al. 2003; Bence et al. manuscript). If such a fishery develops it will be important to monitor stock status using fishery independent data, and the existing lean lake trout survey provides a means of assessing future changes relative to patterns since the 1980s.

Acknowledgments

We thank Shawn Sitar (MDNR), Mark Ebener (CORA), Bill Mattes (GLIFWC), Matt Symbal (Red Cliff Fisheries Department, and all other personnel that collected and provided data for this project. Mike Jones and Andrew McAdam contributed their thoughts and guidance during the conduct of this research and on earlier versions of this paper. In addition, thank you to our colleagues at Quantitative Fisheries Center (QFC), Michigan State University for technical and modeling advice. This work was funded by the USFWS Restoration Act program (under cooperative agreement # 301814J260) and by the Michigan DNR Fisheries Division, and GLIFWC was the agency sponsor for the Restoration Act Project.

Table 1.1. Specific years, number of years, number of grids, and number of gill-net sets included in this analysis for siscowet lake trout index of abundance for Michigan water of Lake Superior.

Management Unit	Years Included	# of years	# of grids	# of gill-net sets
MI3	1975, 1987, 1988, 1990-2006	20	2	429
MI4	1977, 1987, 1990-2006	19	6	519
MI5	1986, 1988, 1990-1995, 1999, 2000, 2003-2006	14	5	243
MI6	1977, 1980-1985,1988, 1990-1996, 1998-2006	24	9	430
MI7	1977, 1985-1988, 1990-1991, 1993-1995, 1997-2005	19	4	299

Table 1.2. Combinations of random effects considered in models for both the probability of occurrence for non-zero catch and catch rate (CPUE) for positive catches. The random terms are defined as follows: δ_{yg} year by grid interaction, γ_{yd} year by depth interaction, λ_{gd} grid by depth interaction and ρ_{ygd} year by grid by depth interaction.

Model Number	**Model Structure for random effect**
1	No random effects
2	$\delta_{yg} + \gamma_{yd} + \lambda_{gd} + \rho_{ygd}$
3	$\delta_{yg} + \gamma_{yd} + \lambda_{gd}$
4	$\delta_{yg} + \gamma_{yd} + \rho_{ygd}$
5	$\delta_{yg} + \lambda_{gd} + \rho_{ygd}$
6	$\delta_{yg} + \gamma_{yd}$
7	$\delta_{yg} + \lambda_{gd}$
8	$\delta_{yg} + \rho_{ygd}$
9	$\gamma_{yd} + \lambda_{gd}$
10	$\gamma_{yd} + \rho_{ygd}$
11	$\lambda_{gd} + \rho_{ygd}$
12	δ_{yg}
13	γ_{yd}
14	λ_{gd}
15	ρ_{ygd}
16	$\gamma_{yd} + \lambda_{gd} + \rho_{ygd}$

Table 1.3. Combinations of fixed effects considered in models for both the probability of occurrence for a non-zero catch and catch rate (CPUE) for positive catches. The fixed effects are defined as α_y is the year effect, β_g is the grid effect, and ω_d is the depth effect.

Model Number	**Model Structure for fixed effect**
1	$\alpha_y + \beta_g + \omega_d$
2	$\alpha_y + \beta_g$
3	$\alpha_y + \omega_d$
4	α_y
5	μ intercept/means model

Table 1.4. Unique candidate models with number of estimated parameters (*K*), Akaike's information criterion differences (ΔAIC, 0 = best model) and AIC weights for both the probability of occurrence for a non-zero catch and catch rate for positive catches submodels for MI3.

Model Structure	***K***	**ΔAIC**	**Weights**
	Probability of occurrence		
year + depth	22	0.00	0.730
year + grid + depth	23	2.00	0.370
year + grid x depth	21	14.94	0.000
year + grid + grid x depth	22	16.88	0.000
year + grid + year x depth	22	31.36	0.000
year + year x depth	21	32.07	0.000
year + grid + year x depth x grid	22	33.39	0.000
year + grid	21	34.12	0.000
year + year x depth x grid	21	34.82	0.000
year	20	35.87	0.000
	Catch rate for positive catches		
year + depth	22	0.00	0.641
year + grid + depth	23	1.17	0.356
year + grid x depth	21	12.54	0.001
year + grid + grid x depth	22	14.49	0.000
year + grid x depth + year x grid x depth	22	14.53	0.000
year + grid + grid x depth + year x grid x depth	23	16.48	0.000
year + year x grid x depth	21	25.60	0.000
year	20	25.97	0.000
year + grid + year x grid x depth	22	26.81	0.000
year + grid	21	27.20	0.000
year + year x depth	21	27.38	0.000
year + grid + year x depth	22	28.89	0.000

Table 1.5. Unique candidate models with number of estimated parameters (*K*), Akaike's information criterion differences (ΔAIC, 0 = best model) and AIC weights for both the probability of occurrence for a non-zero catch and catch rate for positive catches submodels for MI4.

Model Structure	***K***	**ΔAIC**	**Weights**
	Probability of occurrence		
year + depth + year x grid x depth	22	0.00	0.603
year + depth + year x grid + year x grid x depth	23	1.41	0.298
year + depth + year x grid	22	4.04	0.080
year + depth	21	8.59	0.008
year + grid + depth + year x grid x depth	27	9.06	0.006
year + grid + depth + year x grid + year x grid x depth	28	10.61	0.003
year + grid + depth + year x grid	27	13.06	0.001
year + grid + depth	26	15.78	0.000
year + grid x depth + year x grid x depth	21	23.85	0.000
year + year x grid + grid x depth + year x grid x depth	22	25.71	0.000
year + year x grid x depth	20	28.28	0.000
year + year x grid + grid x depth	21	29.09	0.000
year + grid x depth	20	32.13	0.000
year + grid + grid x depth + year x grid x depth	26	32.89	0.000
year + grid + year x grid + grid x depth + year x grid x depth	27	34.75	0.000
year + grid + year x grid x depth	25	36.61	0.000
year + grid + year x grid + grid x depth	26	38.20	0.000
year + year x grid	20	38.95	0.000
year + year x grid + year x depth	21	40.21	0.000
year + grid + grid x depth	25	41.03	0.000
year	19	43.05	0.000
year + year x depth	20	45.04	0.000
year + grid + year x grid	25	47.01	0.000
year + grid + year x grid + year x depth	26	48.57	0.000
year + grid	24	48.76	0.000
	Catch rate for positive catches		
year + grid + depth	26	0.00	0.694
year + grid + depth + grid x depth	27	1.98	0.258
year + depth + grid x depth	22	5.35	0.048
year + grid x depth	20	19.00	0.000
year + grid + grid x depth	25	25.59	0.000
year + depth + year x grid	22	27.54	0.000
year + depth	21	28.92	0.000

Table 1.5 (cont'd).

Model Structure	***K***	**ΔAIC**	**Weights**
	Catch rate for positive catches		
year + depth + year x grid x depth	22	29.42	0.000
year + grid + year x depth	25	52.06	0.000
year + grid	24	59.89	0.000
year + grid + year x grid x depth	25	60.17	0.000
year + year x depth + year x grid x depth	21	75.14	0.000
year + year x grid x depth	20	75.98	0.000
year + year x grid + year x depth	21	76.12	0.000
year + year x grid + year x depth + year x grid x depth	22	77.12	0.000
year + year x depth	20	78.34	0.000
year	19	84.83	0.000
year + year x grid	20	85.41	0.000

Table 1.6. Unique candidate models with number of estimated parameters (*K*), Akaike's information criterion differences (ΔAIC, 0 = best model) and AIC weights for both the probability of occurrence for a non-zero catch and catch rate for positive catches submodels for MI5.

Model Structure	***K***	**ΔAIC**	**weights**
	Probability of occurrence		
year + depth + year x grid x depth	17	0.00	0.250
year + depth + year x grid	17	0.55	0.190
year + depth + year x grid + year x grid x depth	18	1.67	0.109
year + depth	16	2.41	0.075
year + depth + year x grid + grid x depth	18	2.46	0.073
year + grid + depth	20	2.98	0.056
year + depth + grid x depth	17	3.24	0.049
year + grid + depth + year x grid	21	3.61	0.041
year + grid + depth + year x grid x depth	21	3.77	0.038
year + year x grid _ grid x depth	16	4.18	0.031
year + grid x depth + year x grid x depth	16	4.53	0.026
year + grid x depth	15	4.85	0.022
year + grid + depth + year x grid + year x grid x depth	22	5.42	0.017
year + year x grid + grid x depth + year x grid x depth	17	5.93	0.013
year + year x grid x depth	15	9.19	0.003
year + grid + year x grid + grid x depth	20	10.28	0.001
year + grid + grid x depth	19	10.47	0.001
year + grid + grid x depth + year x grid x depth	20	10.57	0.001
year + grid + year x grid x depth	19	11.69	0.001
year + grid + year x grid + grid x depth + year x grid x depth	21	12.09	0.001
year + year x grid	15	13.57	0.000
year + grid	18	14.04	0.000
year + grid + year x grid	19	14.35	0.000
year + grid + year x depth	19	15.45	0.000
year + year x depth	15	17.14	0.000
year	14	17.85	0.000

Table 1.6 (cont'd).

Model Structure	***K***	**ΔAIC**	**Weights**
		Catch rate for positive catches	
year + grid + depth	20	0.00	0.851
year + depth	16	4.05	0.112
year	14	8.29	0.013
year + grid x depth	15	8.61	0.011
year + grid	18	9.98	0.006
year + grid + grid x depth	19	10.83	0.004
year + grid + year x depth	19	11.79	0.002

Table 1.7. Unique candidate models with number of estimated parameters (*K*), Akaike's information criterion differences (ΔAIC, 0 = best model) and AIC weights for both the probability of occurrence for a non-zero catch and catch rate for positive catches submodels for MI6.

Model	***K***	**ΔAIC**	**Weights**
	Probability of occurrence		
year + depth	26	0.00	0.513
year + grid + grid x depth	27	1.96	0.192
year + depth + year x grid + grid x depth	27	2.00	0.189
year + depth + year x grid + grid x depth	28	3.34	0.096
year + grid + depth	36	8.50	0.007
year + grid + depth + year x grid	37	10.46	0.003
year + grid x depth	25	26.85	0.000
year + year x grid + grid x depth	26	28.33	0.000
year + year x depth	25	35.20	0.000
year	24	35.60	0.000
year + grid + year x grid + year x depth	26	36.51	0.000
year + year x grid	25	37.26	0.000
year + year x grid x depth	25	37.52	0.000
year + grid + year x grid + grid x depth	36	41.27	0.000
year + grid	34	44.73	0.000
year + grid + year x depth	35	44.92	0.000
year + grid + year x grid x depth	35	46.57	0.000
year + grid + year x grid	35	46.73	0.000
year + grid + year x grid + year x depth	36	46.76	0.000
year + grid + year x depth + year x grid x depth	36	46.92	0.000
	Catch rate for positive catches		
year + depth	26	0.00	0.508
year + grid + depth	36	0.06	0.492
year + grid x depth	25	18.87	0.000
year + grid + grid x depth	35	26.35	0.000
year	24	28.39	0.000
year + year x depth	25	29.82	0.000
year + grid	34	30.28	0.000
year + grid + year x depth	35	31.55	0.000

Table 1.8. Unique candidate models with number of estimated parameters (*K*), Akaike's information criterion differences (ΔAIC, 0 = best model) and AIC weights for both the probability of occurrence for a non-zero catch and catch rate for positive catches submodels for MI7.

Model Structure	***K***	**ΔAIC**	**Weights**
	Probability of occurrence		
year + depth	21	0.00	0.929
year + grid + depth	24	5.13	0.071
year + grid x depth	20	22.44	0.000
year + grid + grid x depth	23	27.90	0.000
year + year x depth	20	61.47	0.000
year + grid + year x depth	23	64.29	0.000
year + grid	22	65.03	0.000
year	19	65.47	0.000
year + grid + year x grid x depth	23	66.97	0.000
year + year x grid x depth	20	67.20	0.000
	Catch rate for positive catches		
year + grid + depth	24	0.00	0.624
year + depth	21	1.67	0.271
year + depth + grid x depth	22	3.56	0.105
year + grid x depth	20	17.68	0.000
year + grid + grid x depth	23	22.73	0.000
year	19	37.68	0.000
year + year x depth	20	37.94	0.000
year + year x grid x depth	20	38.57	0.000
year + grid	22	39.52	0.000
year + year x depth + year x grid x depth	21	39.75	0.000
year + grid + year x depth	23	40.16	0.000
year + grid + year x grid x depth	23	40.89	0.000
year + grid + year x depth + year x grid x depth	24	42.11	0.000

Table 1.9. Unique candidate models with number of estimated parameters (*K*), Akaike's information criterion differences (ΔAIC, 0 = best model) and AIC weights for both the probability of occurrence for a non-zero catch and catch rate for positive catches submodels for MI5 for the second data selection procedure.

Model Structure	***K***	**ΔAIC**	**Weights**
	Probability of occurrence		
year + depth + year x grid x depth	17	0.00	0.195
year + depth + year x grid	17	0.34	0.164
year + grid + depth	19	0.86	0.127
year + grid + depth + year x grid	20	1.45	0.094
year + depth + year x grid + year x grid x depth	18	1.54	0.090
year + grid + depth + year x grid x depth	20	1.66	0.085
year + depth	16	2.33	0.061
year + depth + year x grid + grid x depth	18	2.34	0.060
year + grid + depth + year x grid + year x grid x depth	21	3.26	0.038
year + depth + grid x depth	17	3.66	0.031
year + year x grid + grid x depth	16	5.58	0.012
year + grid + depth + year x depth + grid x depth + year x grid x depth	22	5.66	0.011
year + grid x depth + year x grid x depth	16	5.89	0.010
year + grid x depth	15	6.11	0.009
year + year x grid + grid x depth + year x grid x depth	17	7.33	0.002
year + grid + year x grid + grid x depth	19	9.71	0.001
year + grid + grid x depth	18	9.75	0.001
year + grid + grid x depth + year x grid x depth	19	9.97	0.001
year + year x grid x depth	15	10.38	0.001
year + grid + year x grid x depth	18	11.02	0.001
year + grid + year x grid + grid x depth + year x grid x depth	20	11.52	0.001
year + grid	17	13.20	0.000
year + grid + year x grid	18	13.60	0.000
year + grid + year x grid + year x depth	19	14.28	0.000
year + grid + year x depth	18	14.39	0.000
year + year x grid	15	14.62	0.000
year + year x depth	15	17.99	0.000
year	14	18.92	0.000
	Catch rate for positive catches		
year + depth	16	0.00	0.909
year + grid + depth	19	4.92	0.078
year	14	10.01	0.006

Table 1.9 (cont'd)

Model Structure	***K***	**ΔAIC**	**Weights**
	Catch rate for positive catches		
year + grid x depth	15	10.71	0.004
year + year x depth	15	11.65	0.003
year + grid	17	15.73	0.000
year + grid + grid x depth	18	16.54	0.000
year + grid + year x depth	18	17.28	0.000

Table 1.10. Unique candidate models with number of estimated parameters (*K*), Akaike's information criterion differences (ΔAIC, 0 = best model) and AIC weights for both the probability of occurrence for a non-zero catch and catch rate for positive catches submodels for MI6 for the second data selection procedure.

Model Structure	***K***	**ΔAIC**	**Weights**
	Probability of occurrence		
year + depth	26	0.00	0.599
year + depth + depth + year x grid	27	0.85	0.392
year + grid + depth	34	9.31	0.006
year + grid + depth + year x grid	35	10.61	0.003
year + grid x depth	25	21.58	0.000
year + year x grid + grid x depth	26	22.24	0.000
year	24	25.13	0.000
year + year x grid	25	26.19	0.000
year + year x grid x depth	25	27.05	0.000
year + year x grid + year x depth	26	28.16	0.000
year + grid + grid x depth	33	34.24	0.000
year + grid + year x grid + grid x depth	34	35.03	0.000
year + grid	32	36.75	0.000
year + grid + year x grid	33	38.03	0.000
year + grid + year x grid x depth	33	38.58	0.000
year + grid + year x grid + year x depth	34	40.01	0.000
	Catch rate for positive catches		
year + grid + depth	34	0.00	0.435
year + depth	26	1.16	0.244
year + grid + depth + year x depth	35	2.00	0.160
year + grid + depth + grid x depth	35	2.00	0.160
year + grid x depth	25	16.54	0.000
year + grid + grid x depth	33	23.16	0.000
year	24	25.67	0.000
year + year x depth	25	26.54	0.000
year + grid	32	27.36	0.000
year + grid + year x depth	33	27.94	0.000

Table 1.11. Unique candidate models with number of estimated parameters (*K*), Akaike's information criterion differences (ΔAIC, 0 = best model) and AIC weights for both the probability of occurrence for a non-zero catch and catch rate for positive catches submodels for MI7 for second data selection procedure.

Model Structure	***K***	**ΔAIC**	**Weights**
	Probability of occurrence		
year + depth	21	0.00	0.847
year + grid + depth	23	3.43	0.153
year + grid x depth	20	19.82	0.000
year + grid + grid x depth	22	23.50	0.000
year + year x depth	20	60.59	0.000
year + grid + year x depth	22	62.05	0.000
year + grid	21	62.50	0.000
year	19	64.13	0.000
year + grid + year x grid x depth	22	64.19	0.000
year + year x grid x depth	20	65.49	0.000
	Catch rate for positive catches		
year + grid + depth	23	0.00	0.808
year + depth	21	3.53	0.138
year + depth + grid x depth	22	5.43	0.053
year + grid x depth	20	20.36	0.000
year + grid + grid x depth	22	23.57	0.000
year	19	40.66	0.000
year + grid	21	40.77	0.000
year + year x depth	20	40.91	0.000
year + grid + year x depth	22	41.39	0.000
year + year x grid x depth	20	41.46	0.000
year + grid + year x grid x depth	22	42.08	0.000
year + year x depth + year x grid x depth	21	42.66	0.000
year + grid + year x depth + year x grid x depth	23	43.31	0.000

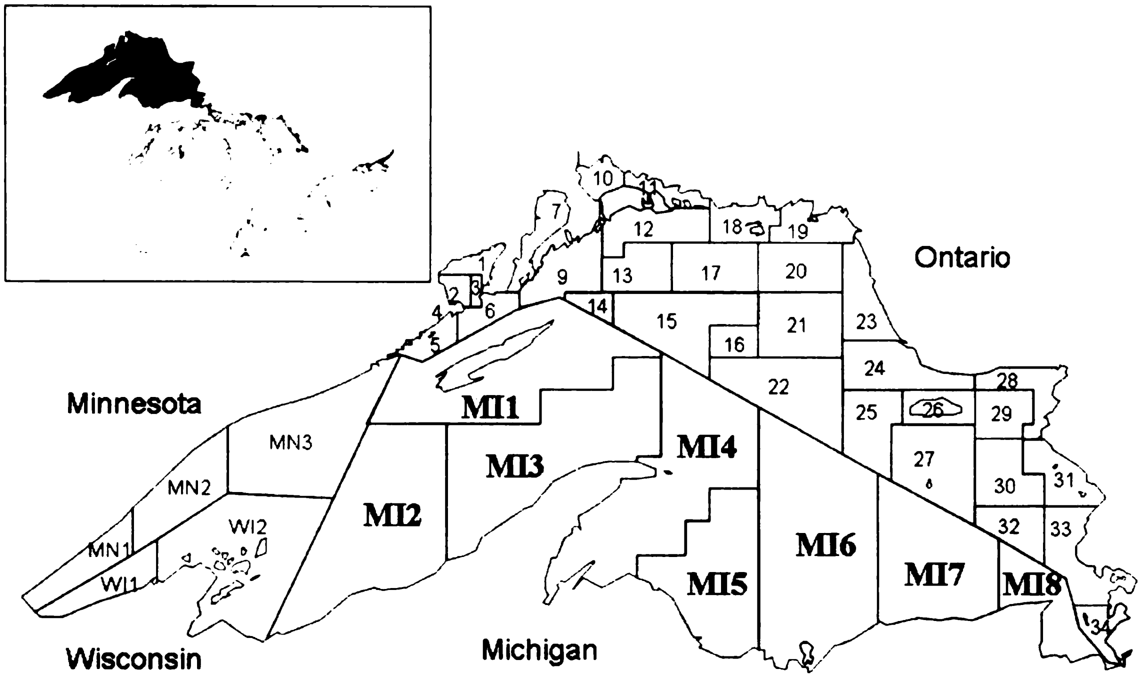

Figure 1.1. Lake trout management units of Lake Superior (Hansen et al. 1995). The letter abbreviations denote U. S. waters by state MN – Minnesota, MI – Michigan, and WI – Wisconsin, and numbers represent Canadian waters. Bolded management units were the ones that supplied data used in this paper.

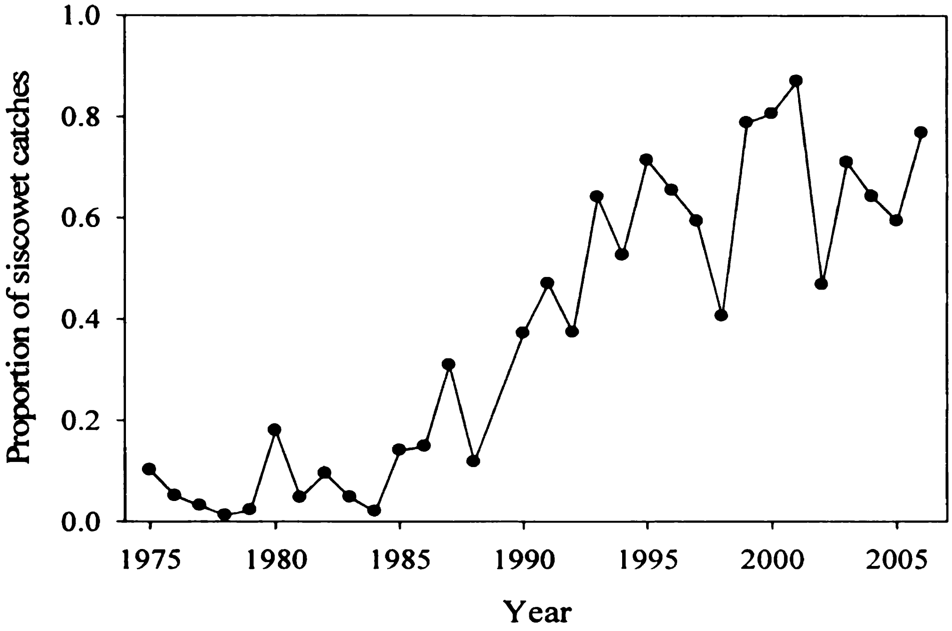

Figure 1.2. Proportion of gill-net sets that caught at least one siscowet from the standardized spring lean lake trout survey from 1975-2006.

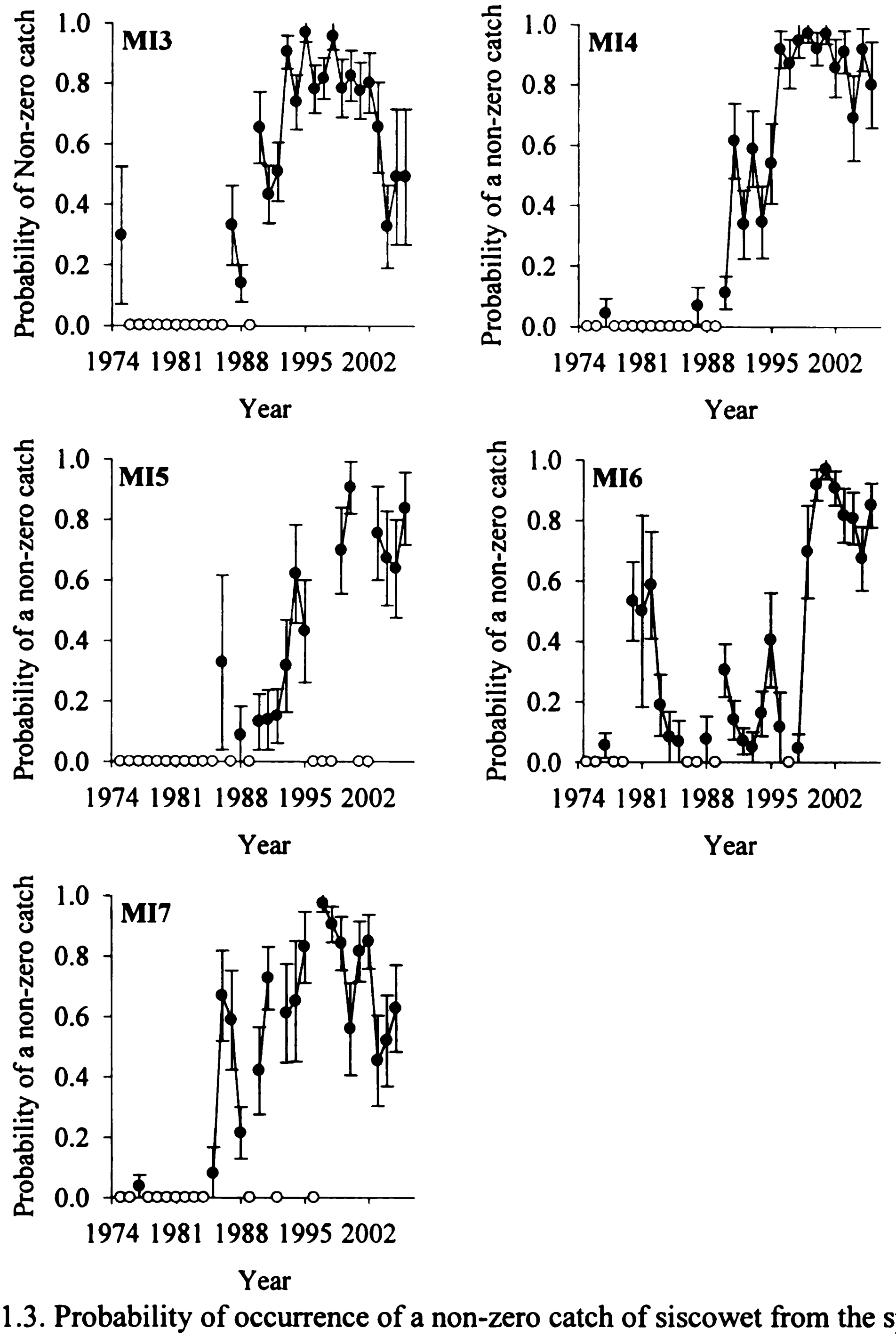

Figure 1.3. Probability of occurrence of a non-zero catch of siscowet from the spring lean lake trout survey for five Michigan management units in Lake Superior during 1975-2006 (solid circles joined by dashed line). The open circles show years that did not catch any siscowet for each unit.

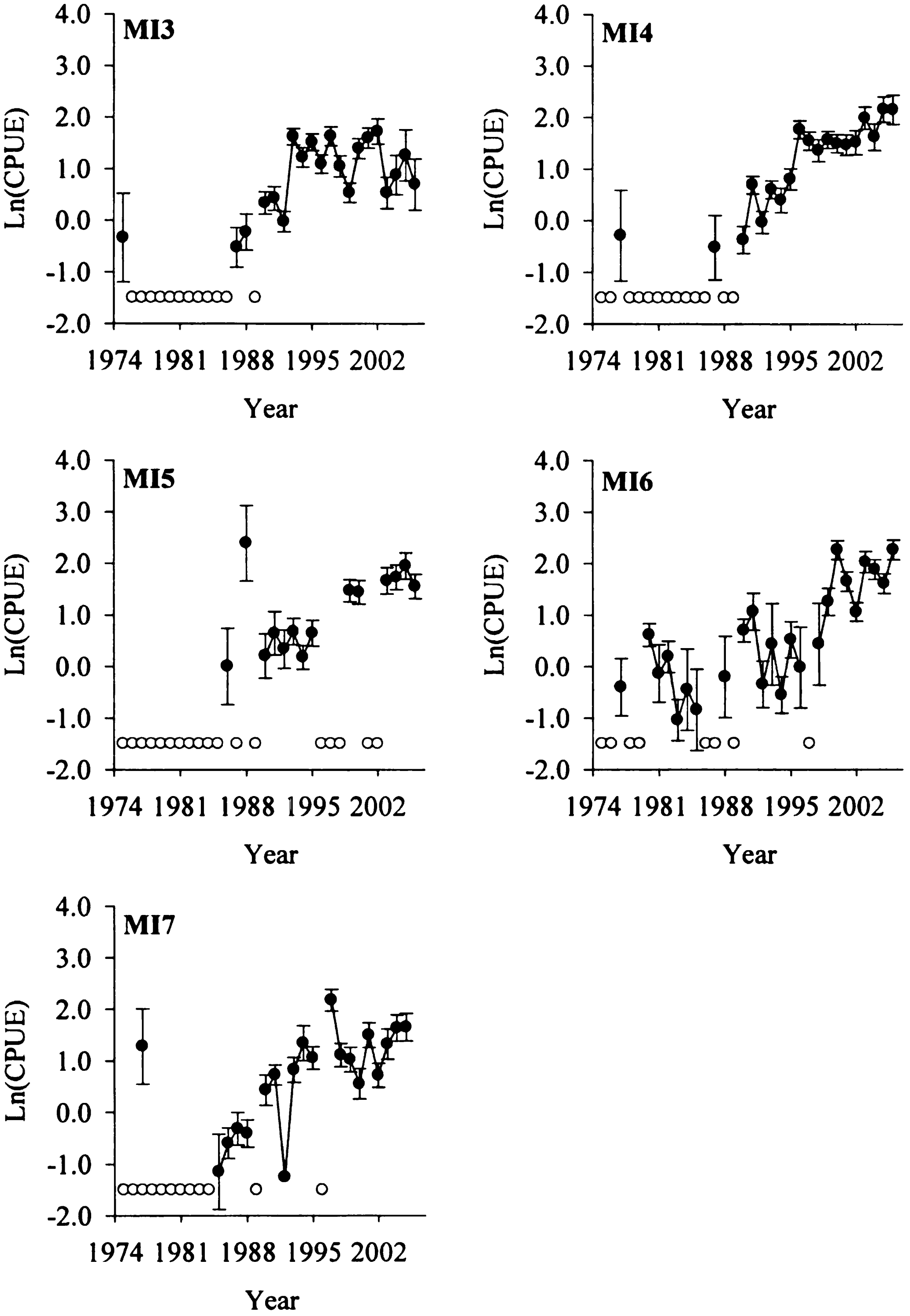

Figure 1.4. Estimated log-scale catch per unit effort (CPUE) for siscowet positive catches from the lean lake trout survey for five Michigan management units in Lake Superior during 1975-2006 (solid circles joined by dashed line). The open circles show years that did not catch any siscowet lake trout.

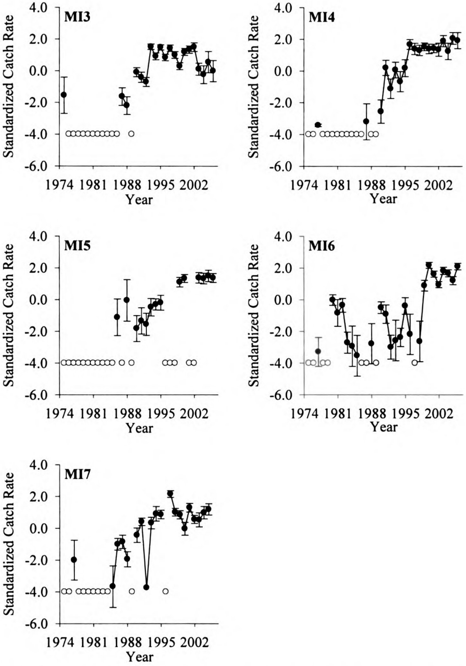

Figure 1.5. Estimated standardized catch rates (log$_e$ scale) of siscowet lake trout from the spring lean lake trout survey for five Michigan management units in Lake Superior during 1975-2006 (solid circles joined by dashed line). The open circles show years that did not catch any siscowet lake trout.

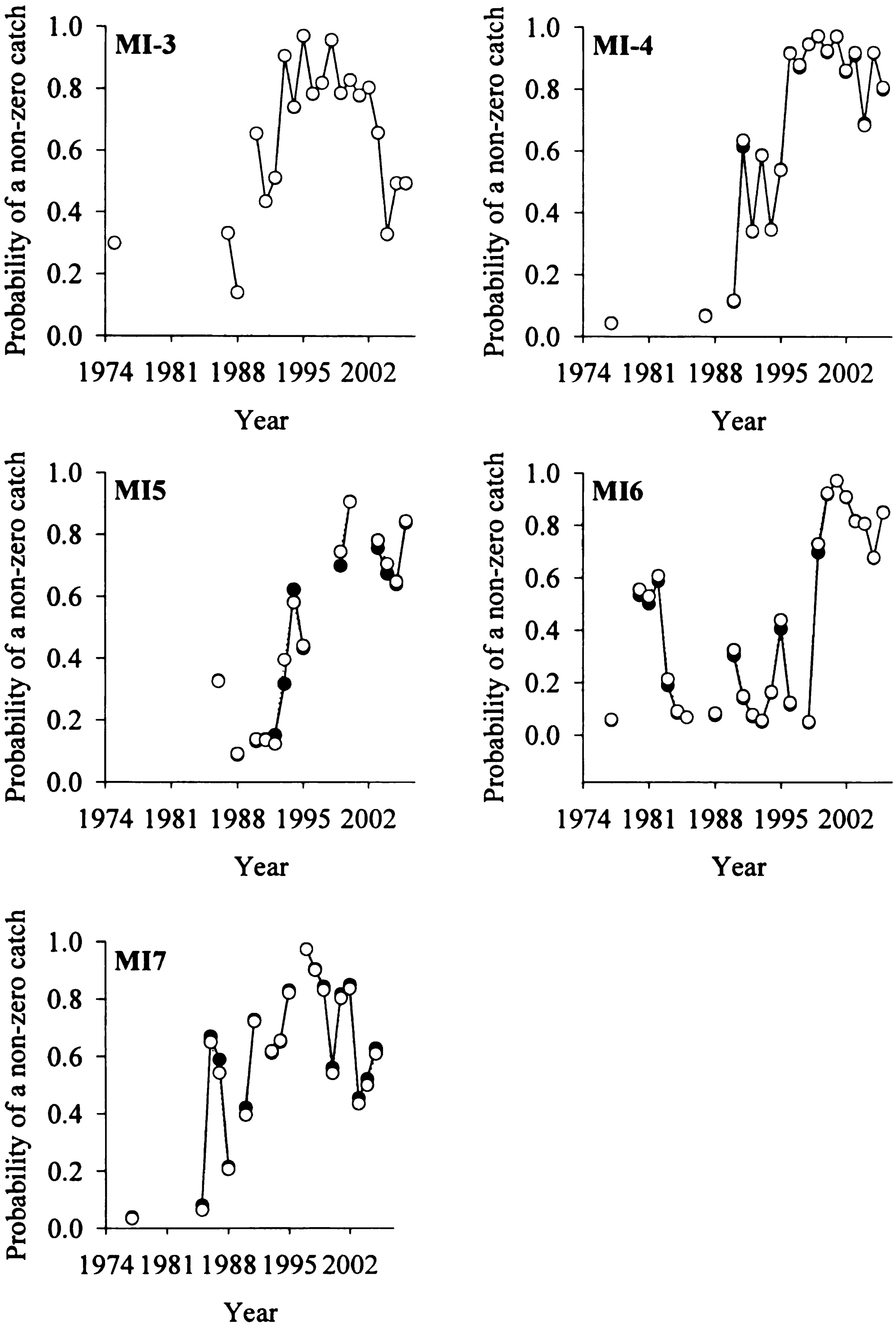

Figure 1.6. Estimated probability of occurrence of a non-zero catch of siscowet from the spring lean lake trout survey for five Michigan management units in Lake Superior during 1975-2006 for best (filled circles) and second best (open circles) selected models using AIC. When only one symbol is visible for a year (open circle) then the two estimates are identical.

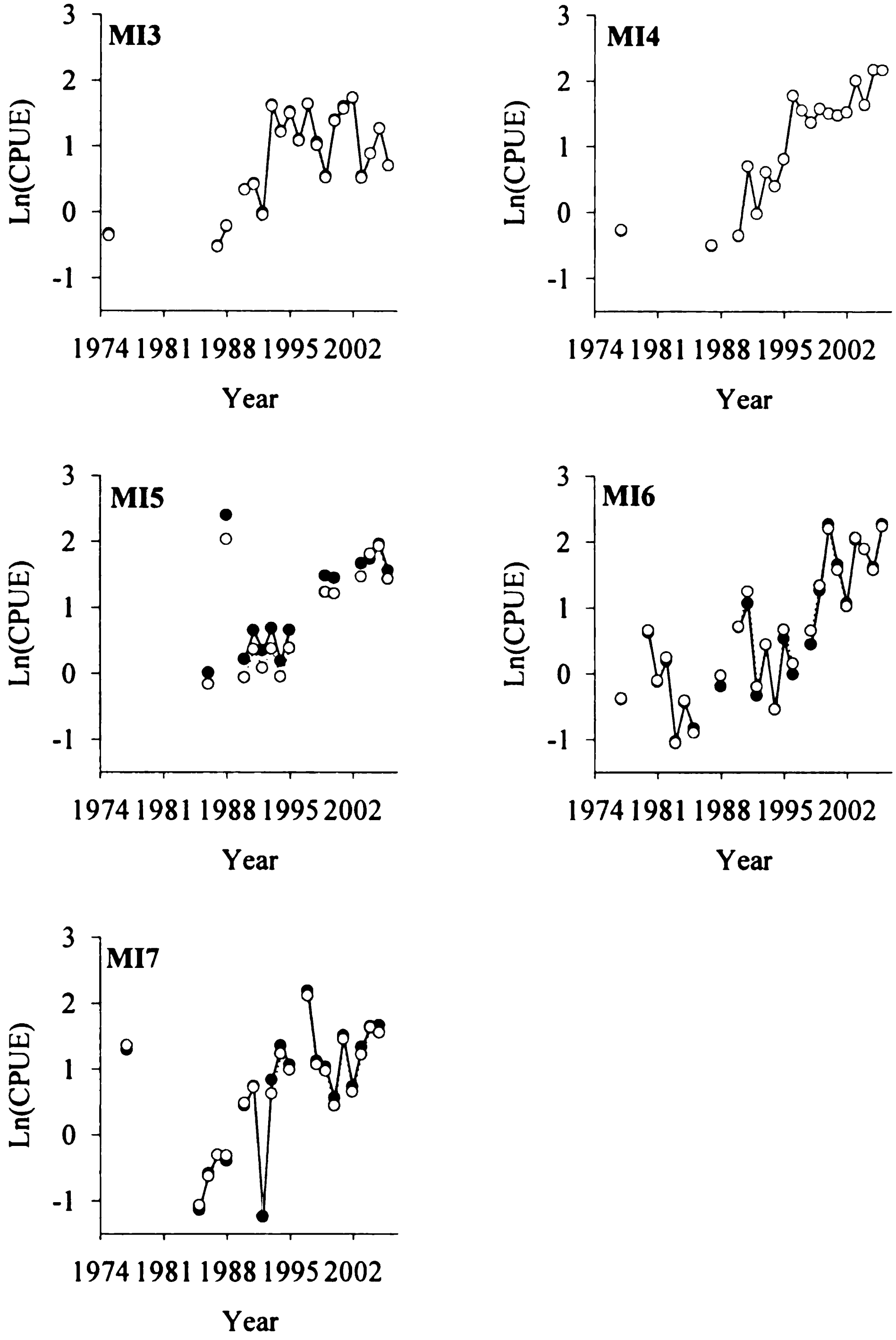

Figure 1.7. Estimated log-scale catch per unit effort for siscowet from the spring lean lake trout survey for five Michigan management units in Lake Superior during 1975-2006 for best (filled circles) and second best (open circles) selected models using AIC. When only one symbol is visible for a year (open circle) then the two estimates are identical.

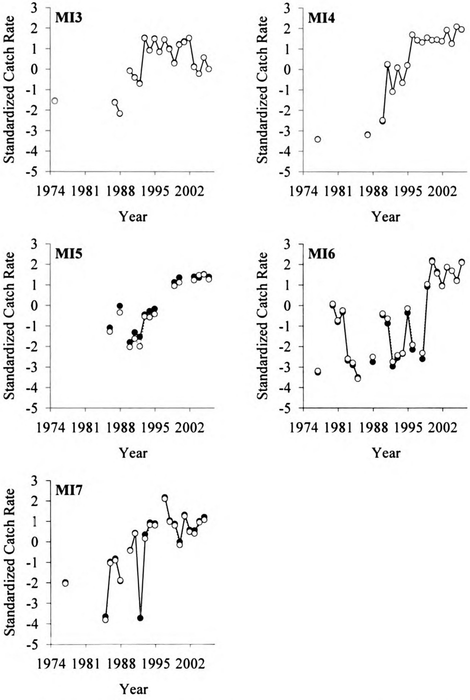

Figure 1.8. Estimated standardized catch rates for siscowet from the spring lean lake trout survey for five Michigan management units in Lake Superior during 1975-2006 for best (filled circles) and second best (open circles) selected models using AIC. When only one symbol is visible for a year (open circle) then the two estimates are identical.

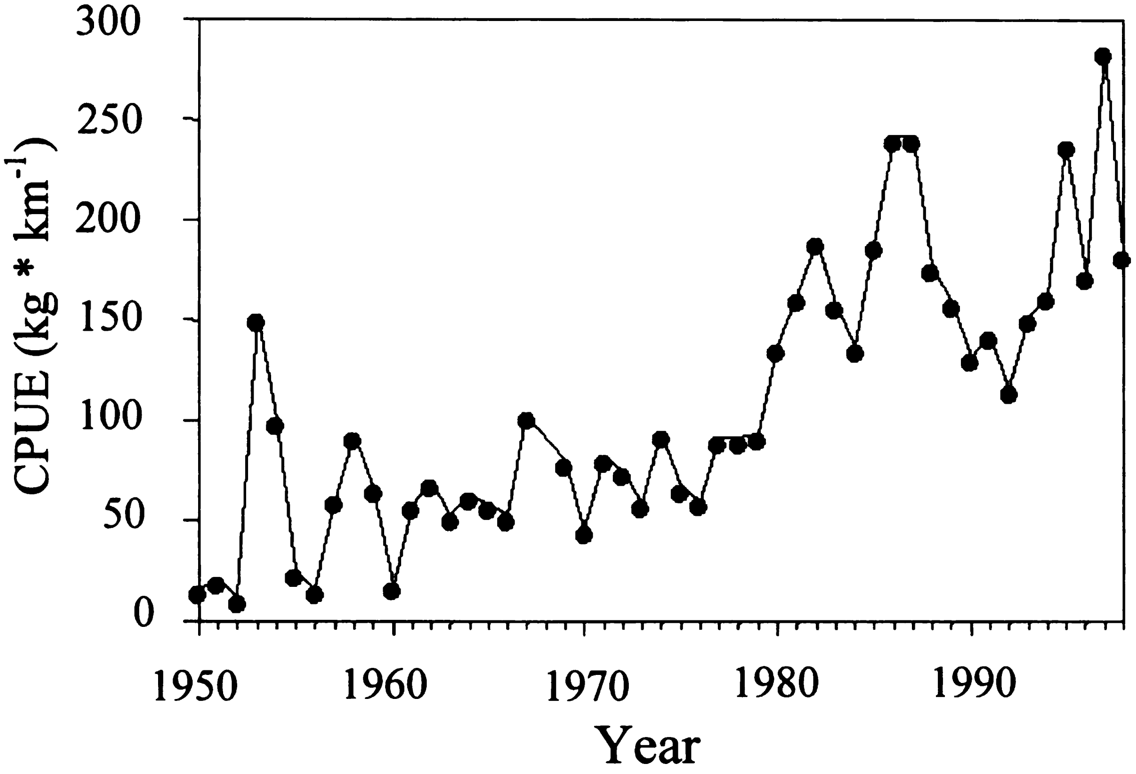

Figure 1.9. Relative abundance (CPUE) of siscowet lake trout in commercial fisheries in all area U.S. and Canadian waters of Lake Superior during 1950-1989 (from Bronte et al. 2003).

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CHAPTER 2

ABSTRACT

SISCOWET BIOLOGY ACROSS REGIONS AND OVER TIME IN MICHIGAN WATERS OF LAKE SUPERIOR

By

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The siscowet form of lake trout (*Salvelinus namaycush*) is the most abundant of three lake trout morphotypes found in Lake Superior of the North American Laurentian Great Lakes, but its biology has been little studied. We investigated spatial and temporal patterns in life-history attributes of siscowet lake trout across Michigan waters of Lake Superior from 1990 through 2006. The most striking spatial and temporal patterns we saw were for length-at-50% maturity and condition (mass-at-length). In the eastern most spatial zone of Michigan waters of Lake Superior considered in our analysis (corresponding to lake trout management unit MI7) siscowets matured at smaller sizes and were in better condition than in waters west of that zone. In this eastern zone length-at-maturity did not show striking changes over time, whereas in Michigan waters west of MI7 fish matured at greater lengths after 1999. There was a general pattern for condition to decline over time and for larger sizes of siscowet lake trout to make up a larger proportion of the populations after 1999. The life history and biological characteristics found in this study could be used as a basis for calculating per-recruit reference points to help identify possible levels of sustainable fishing, and also suggest what sort of spatial variation and changes over time might be expected for the siscowet form of lake trout if they were introduced in other lakes.

Introduction

The siscowet lake trout (*Salvelinus namaycush*), also known as a "fat", is one of three lake trout morphotypes widely distributed in Lake Superior of the North American Laurentian Great Lakes (hereafter Great Lakes, Khan and Qadri 1970; Lawrie and Rahrer 1973; Pycha and King 1975). They primarily inhabit deep water (~80 m and greater) (Sweeny 1890; Eschmeyer 1955; Lawrie and Rahrer 1973; Goodier 1981; Bronte et al. 2003) and siscowet densities are higher, or at least the catch rates for them are, in deeper water (Sitar et al. 2008). However, siscowet lake trout are known to utilize both shallow and deep waters of the lake throughout their life (Bronte et al. 2003). It is also believed that they were once abundant in all the other Great Lakes (except Lake Erie), from which they are now extirpated (Brown et al. 1981).

Siscowet lake trout are the most abundant lake trout morphotype and make up most of the biomass of lake trout in Lake Superior (Ebener 1995; Bronte et al. 2003; Bence et al. manuscript). Siscowet lake trout have become increasingly abundant inshore as a consequence of an increase in overall abundance and possibly also because of a change in depth distribution (Bronte and Moore 2007; Bronte and Sitar 2008; Chapter 1). There have been concerns among biologists, anglers, and commercial fisherman that increased abundance, particularly in shallower depths inhabited by leans, will have detrimental effects on leans and/or other deepwater species (Bronte and Moore 2007; Bronte and Sitar 2008). To address such concerns, additional basic information on siscowet biology, life history, and population dynamics is needed to supplement the limited information now available. Therefore, during the early 1990s the Lake Superior

Technical Committee initiated research and a survey to focus on siscowet lake trout so as to gain an improved understanding of both their biology and life history.

As part of the initiative, researchers evaluated potential effects siscowet would have on lean lake trout abundance and diet, by examining the extent of overlap in distribution and diet. It is well established that lean lake trout have been successfully rehabilitated in Michigan waters of Lake Superior, and there is evidence that their abundance has exceeded historic levels in some areas of Lake Superior (Hansen et al. 1995; Bronte et al. 2003; Wilberg et al. 2003; Richards et al. 2004; Sitar et al. 2007). The increased abundance of siscowet has not obviously affected lean lake trout, as indicated by similar trends in abundance (rather than a negative correlation), albeit at different magnitudes, for the two morphotypes (Bronte et al. 2003; Wilberg et al. 2003; Sitar et al.2007; Chapter 1). Recent studies have also indicated there is very little dietary overlap between the two lake trout morphotypes (Kitchell et al. 2000; Harvey and Kitchell 2000; Harvey et al. 2003; Ray et al. 2008), and this may explain why there has not been an obvious detrimental effect on lean lake trout of the increased abundance of siscowet lake trout in depths occupied by lean lake trout. Kitchell et al. (2000) also used system modeling to predict that if a fishery was directed toward siscowet, siscowet abundance would decline rapidly, but their decline would not lead to an increase in lean lake trout abundance. Thus far, there are no indications that siscowet lake trout are impeding lean lake trout populations.

While biologists are still cognizant that there could be as yet undetected detrimental effects of siscowet on lean lake trout, interest in siscowet recently shifted more toward two other objectives: 1) in part, because of failure to achieve similar rehabilitation of lean lake trout in the other Great Lakes, managers have become interested in exploring the possible reestablishment of deepwater morphotypes of lake trout in those lakes, and 2) there is interest in whether siscowet, which are high in omega-3 fatty acids (Wang et al. 1990), can be harvested to extract these fatty acids for pharmaceutical purposes (Bronte and Sitar 2009). An improved basic understanding of the biology, life history, and population dynamics of the siscowet form will facilitate addressing these objectives. Some limited basic biology and life history attributes have been described in previous studies, for example, siscowet lake trout have an estimated Brody growth coefficients (*K*) ranging from (0.053-0.080), first maturity near age 8, and mass-specific fecundity has been estimated at 1025 eggs/kg (Carlander 1970; Peck 1988; Kitchell et al. 2000; Miller and Schram 2000). However, there is still much more to be learned about their life history, biology, and population dynamics. Our study is the first to look simultaneously at age and size composition, condition, growth, maturation, and mortality of siscowet in Lake Superior.

The objective of this study was to examine all these aspects of biology/life history together, and for each biological measure describe temporal and spatial variation and assess whether the measures are related to siscowet density. The sources of information for this study were derived from several fish surveys, primarily targeting leans or siscowets that use gill-nets with either fixed or varying mesh sizes. Reliable siscowet biological data start as early as 1990 and continue through 2006; for most analyses we created two time periods: period 1 included1990-1999 and period 2 includes 2000 through 2006. The 1990s represent a period of substantial increase in siscowet abundance, whereas during the 2000s, increases were still occurring but at a declining rate, potentially approaching an asymptote (Chapter 1, Bence et al. manuscript). Our study sought to identify whether there is evidence that siscowet biology has changed between these periods when large changes in abundance took place. In addition, we were interested in identifying whether there were spatial differences in siscowet biology within the Michigan waters represented in the survey data we used (Management units MI2 through MI7 (Figure 2.1)). To evaluate this we looked for differences among zones consisting of one or more management units (described in Methods). Spatial zones will identify whether geographic areas of Lake Superior contain stocks or populations of siscowet that differ in biological characteristics that may be used for future management efforts in potential harvesting siscowet lake trout.

Methods

Assessment fishery data

We analyzed data obtained from samples collected in Michigan waters of Lake Superior by the Michigan Department of Natural Resources (MDNR), Chippewa Ottawa Resource Authority (CORA), and Great Lakes Indian Fish and Wildlife Commission (GLIFWC) (Figure 2.1). These data come from three different bottom-set gill-net surveys that date back to as early as 1959: a siscowet/deepwater survey, a spring lean lake trout survey, and a summer recruit survey. Only biological data archived electronically were used, limiting our analysis to 1990 through 2006. This also corresponds to the time period when focus shifted to siscowet lake trout so that more biological data started to be collected on this morphotype. Michigan waters of Lake Superior are divided into eight management units, and the ending years for available data were either 2005 or 2006 depending upon management unit and survey.

The primary purpose for the spring lean lake trout survey was to provide an index of abundance for lean lake trout. This survey will be referred to as survey 1 throughout the rest of the paper. Sampling occurred during April through June at fixed stations, using large mesh gill-nets (4.5 inch stretched mesh), and set across contours targeting depths from 30 – 250 feet (ft). This survey has been described in detail by Hansen et al. (1994).

The summer recruit survey used graded mesh to assess the abundance of juvenile lake trout. This survey will be referred to as survey 2 throughout the rest of the paper. This survey was conducted during July and August. The survey used multifilament nylon gill nets with a net size 6 ft high by 300 ft long per mesh size, with mesh sizes ranging from 2 inches to 3 inches in ¼ inch increments, with an additional mesh size of 3.5 inches, for a total gang length of 1800 ft. The net was set across depth contours ranging from 90 ft to 240 ft in depth.

The siscowet/deepwater survey was designed to assess siscowet populations to gain an understanding of their current abundance and to define their population dynamics based on sampling that covers the deeper waters where they are most abundant. This survey will be referred to as survey 3 throughout the rest of the paper. Sampling for this survey was conducted in June, with the exception of 1997 when sampling was in August. The survey was initiated in some areas in 1996 and in others in 1997. Starting in 2000 the survey has been done once every three years in each area, with additional sampling in a number of intervening years in MI4. Sampling gear used was a graded mesh (2 to 6 in mesh by ½ in increments) set across contours at six different depth intervals (0-19, 20-

39, 40-59, 60-79, 80-99, 100-119 fathoms). The overall survey design has been described by Sitar et al. (2008).

Data collected for each gill-net set include: date, length of gill-net set, water depth at start and end of the set, management unit, number by species (or morphotype) of fish caught, mass, length, age and maturation status. For analyses that made use of age data we only used ages based on otoliths, and such ages were first recorded in 1994. Otoliths ages were used rather than scale ages because scale ages tend to be biased low for lake trout (Schram and Fabrizio 1998). Sex and maturity status of a fish were determined by internal examination of the gonads.

To evaluate spatial patterns we adopted the idea of zones. Zones were delineated based on an understanding of similar bathymetry in each management unit area and observed biological differences of siscowet lake trout in these areas. Agency biologist, Shawn Sitar, MDNR, has used a similar spatial delineation. There are four different zones: zone 1 combines management units MI2 and MI3, zone 2 is management unit MI4, zone 3 combines management units MI5 and MI6, and zone 4 is management unit MI7 (Figure 2.1). Management units MI1 and MI8 were not included because there were insufficient data for analyses. The amount of data available for analyses varied among zones and surveys for each analysis (age-size composition, condition, length-at-maturity, mortality and growth) (Table 2.1).

Temporal changes were identified either through evaluating differences among years or between the two defined time periods. The data were insufficient to obtain annual estimates for analyses that depended on age determinations or for length-at-maturity.

General Analysis Procedures

Model diagnostics were evaluated to determine whether there were gross violations of the normality and constant variance assumptions for each analysis, when applicable. Model diagnostics consisted of evaluating a frequency histogram of the residuals, a quantile-quantile plot, and plotting residuals against the predicted values. The maturation analysis was done using R version 2.4.0, the growth analysis using AD Model builder, other analyses were done using SAS version 9.1 (SAS 2003).

Age and size composition

Age and size composition was estimated with length frequency histograms and summary statistics of the data for each survey, zone, and temporal period. Length frequency histograms were constructed using 10 mm increments in length, and age frequency histograms were constructed reporting the frequency of age in annual increments. Age and length frequency histograms were constructed from sample data collected during 1994 through 2006. Sample statistics included sample size, minimum (length, mm or age, year), maximum, mean, and standard deviation. To determine if both size and age differed between period and/or zone, we compared length or age between period and zone using a general linear model:

$$[1] \qquad Y_{epi} = \mu + \alpha_e + \beta_p + \gamma_{ep} + \varepsilon_{i.}$$

where the response variable (Y) is either $\log_e$(length) or age, μ is the overall mean (intercept), α_e is the effect of zone, β_p is the effect for period, γ_{ep} is the interaction effect of zone and period, and $\varepsilon_{i.}$ is the unexplained residual error. The error term is assumed to be normally distributed with a mean of zero and variance estimated by the model. For both size and age, least square means were generated by SAS Proc Mixed to compare mean size or age by period and zone separately for each survey (SAS Institute 2003). Significance tests were done using the Tukey-Kramer procedure for multiple comparisons for least-square means (Kutner et al. 2005) with results with $P < .05$ declared statistically significant. We excluded survey 1 in zone 3 from analysis of both age and size because siscowet were not captured in period 1 for that survey and zone, precluding a comparison between periods.

Mortality

The instantaneous rate of mortality (Z) was estimated for each survey, zone, and temporal period using age-based catch curves (Ricker, 1975). The basic approach was to conduct a linear regression of the natural logarithm of number of fish in an age class versus age. The slope of the regression provides an estimate of mortality (Z). The first fully recruited age of siscowet caught by each survey, zone, and period was estimated by visually examining the dome and descending limb of the catch curve (e.g., Ricker 1975). We assume that siscowets caught from that particular age are fully recruited to the survey and older fish are equally likely to be captured. Also based on visual inspection of the catch curves, we omitted ages above an upper age at which abundance reached low values and it was judged that log abundance provided little information on mortality. Mortality estimates were not calculated for survey 1 in zone 3 and period 1, because siscowets were not captured during this period or zone.

Length-at-50% maturation

Maturity was based on visual examination of the gonads and classifications were placed into two categories: mature and immature. A mature fish is defined as a fish that was going to reproduce or has physical indications that it has reproduced in previous years. An immature fish has no physical indication of reproducing in the past or present (Sitar and He 2006). We use estimated length-at-50% maturity (L_{50}) as our maturation schedule index, which is defined as the length at which 50% of the fish population is mature (Beauchamp et al. 2004). For each survey, zone, and period, we fitted a logistic regression model to data with maturity status (1=immature; 0=mature) as a binary response with length as the response variable. The logistic regression model for the ith observation is:

[2] $$\mathrm{logit}(p_i) = \log_e(p_i/(1-p_i)) = \alpha + \beta \times L$$

where p is the probability of being mature, α is the intercept, and β is the slope for length (L) the explanatory variable, and L_{50} was estimated as the negative of the ratio of estimates intercept/slope.

We calculated 95% confidence intervals (CIs) for the L_{50} estimates by using a bias-corrected bootstrap technique using 1000 bootstrap samples (Efron 1987). Statistical differences for L_{50} were evaluated by comparing the 95% CIs. During preliminary analysis we determined that both survey 1 and 3 provided inadequate data in identify length-at-50% maturity (L_{50}) for some zone and period combinations due to low proportions of mature siscowet or missing information on maturity status. Therefore, only maturation results for survey 2 are presented in the results section. In cases where length-at-50% maturity could be ascertained for the other surveys, qualitative patterns among zones and between periods were consistent with those for survey 2.

Mass-Length Relationship – Condition Indices

We modified the usual mass-length power model [3] to be a linear mixed-effects model so as to evaluate spatial and temporal changes in the mass-length relationship for siscowet lake trout. As a starting point we linearized the power function:

[3] $W = aL^{b}$,

by taking logarithms of both sides to obtain

[4] $\log_e(W) = \log_e(a) + b\log_e(L) = \mu + \alpha * \log_e(L)$. Here W is the observed fish mass in grams (g), L is observed fish length in mm, $\log_e(a) = \mu$ is the intercept, and $b = \alpha$ is the slope. We then modified this model so that the slope and intercept could potentially depend upon year and zone to obtain the fully (saturated) mixed effects model for the mass-length relationship:

[5] $\log_e(W)_{yei} = \mu + \beta_y + \omega_e + [\alpha + \phi_e + \gamma_y + \rho_{ye}] * \log_e(L) + \lambda_{ey} + \varepsilon_{yei}$

where μ is the overall mean (intercept), α is the effect for $\log_e$(length), β_y is the effect for year, ω_e is the effect for zone, ϕ_e is fixed interaction for $\log_e$(length) and zone, γ_y is the random interaction for $\log_e$(length) and year, λ_{ey} is the random interaction for zone and year, ρ_{ye} is the random interaction for $\log_e$(length) by year by zone and ε_{yei} is the unexplained residual error. All random effects and error term are assumed to be normally distributed with a mean of zero and variance estimated by the model.

All main effects were fixed. Log_e(length) is a continuous variable, whereas year and zone were categorical variables. Interactions that involved year were treated as random effects. Log_e(length) is treated as a fixed effect because fish have a defined power relationship between weight and length. Our goal here is to estimate mass for each year and zone so as to identify potential systematic patterns over the study period. Thus, we treat year as fixed. Zone is treated as a fixed effect, because zones represent a small number of specific areas of interest, which cannot be reasonably viewed as a random sample of a larger population.

Our modeling of the interactions between the fixed year effect and other fixed effects were random, contrasts with the more usual treatment of these as fixed in the context of a manipulative experiment. The idea here is that these interactions reflect relatively short-term and/or smaller spatial scale variations about overriding spatial and temporal patterns that are essentially unpredictable and thus can be viewed as if random. For example, we are treating the year by zone interactions as reflecting chance variations that are transient and not region-wide and hence not systematic effects of interest.

Our final model and associated predicted masses did not include all these potential fixed and random effects, as we first went through a model selection process to avoid an over-parameterized model. Our approach was to first select which random effects to include based on the model that produced the lowest Akaike's information criterion (AIC), by comparing models with all possible random effect combinations in models that contained all fixed effects (Burnham and Anderson 2003). Restricted maximum likelihood techniques were used for model fitting when comparing random effect models (Ngo and Brand 1997; Bolker et al. 2009). Once the best random effects were selected, the best fixed effects model was also selected based on AIC. Here we selected from among the fixed-effect models representing all combination of these effects provided that $\log_e$(length) was in each model, plus the model that included no fixed effects (intercept only). Maximum likelihood techniques were used for model fitting when making comparisons among fixed effect models (Ngo and Brand 1997; Bolker et al. 2009). There were eight different candidate models for random effects (Table 2.2), and seven different candidate models for fixed effects (Table 2.3). However, many random effects had variance components that converged on zero, and hence a number of models were effectively identical to more parsimonious models. We only report results for those models that are unique and also do not report the intercept model, which was always the worst based on AIC (see below).

Once the best model was selected, predicted masses for two different size classes, 450 mm and 700 mm, were used to assess fish condition over time by zone for each survey. The two size classes were chosen based on a preliminary examination of length distributions for each survey. These sizes were well within the length distributions but represented relatively small and large siscowet. We selected a small and large size to evaluate possible differences in the magnitude of spatial or temporal differences in fish condition between fish of different sizes. In addition to evaluating predicted mass-at-length from our best model, we also made such predictions for other models with AIC within 2 of the best model. We only present results for the best model because predicted temporal and spatial patterns from these other competitive models were similar to those from our best model.

Modeling time-vary growth

Growth was evaluated by fitting an incremental version of the von Bertalanffy growth model to a time-series of length-at-age data. For pragmatic reasons, we used a Bayesian hierarchical approach implemented in AD Model Builder rather than a nonlinear mixed-model fit by maximum likelihood to evaluate changes in growth. Given the complexity of the dynamic model, the analysis was not easily implementable in standard packages such as R or SAS. Attempts to fit this model using a version of AD Model Builder designed for nonlinear random effects led to point estimates for parameters that produced years where growth was negative. Attempts to force positive growth (see below) led to numerical problems when the software attempted to integrate out the random effects.

Data used in this analysis were all observed lengths-at-age from 1996-2006 across zones and surveys. For this analysis we looked at two scenarios: 1) we pooled data over zones and surveys and 2) we fit models separately by zone (with surveys still pooled). We pooled surveys given the limited numbers of aged fish. The full model we considered was:

$$\begin{aligned} & L_{a,y} = L_{a-1,y-1} + (L_{\infty y} - L_{a-1,y-1})(1-\exp(-K_y) \\ [6]\quad & L_{a,y,i} = L_{a,y}\exp(\varepsilon_i) \\ & \varepsilon_i \sim N(0,\sigma_i^2) \end{aligned}$$

Where $L_{a,y}$ is the median length at age a in year y, L_{∞} and K are the year specific asymptotic length and Brody growth coefficients, $L_{a,y,i}$ is the length of the ith observation for a fish of age a in year y, and ε_i represents among fish variation in length about the year and age specific median, assumed to be lognormally distributed. Initial median length at age-3 was assumed constant for all years based on an initial examination of observed mean lengths. Median lengths-at-ages over age 3 in the first year (1996) were obtained as:

[7] $$L_{a,1996} = L_{a-1,1996} + (L_{\infty 1996} - L_{a-1,1996})(1 - \exp(-K_{1996})) \text{ ,}$$

which effectively assumes that the initial length-at-ages could have arisen from von Bertalanffy growth under constant growth conditions. In models that allowed L_∞ or K to vary the values were estimated for 1996 as separate parameters, rather than from the random walk process (see below). When a parameter was assumed to be constant over time the 1996 value was set to the same value estimated for subsequent years.

We considered alternative models in which both K and L_∞ varied over years, K only varied over years, L_∞ only varied over years, or where both growth parameters were constant. In our base analysis we modeled temporal variation in growth parameters as arising from a random walk on a log-scale:

[8] $$\begin{aligned} &\ln\theta_y = \ln\theta_{y-1} + \eta_{y-1} \\ &\eta \sim N(0, \sigma_\theta^2) \\ &\theta = \{L_\infty, K\} \end{aligned}$$

using methods similar to those of Szalai et al. (2003) and He and Bence (2007). The observation error variance was estimated for each modeling scenario prior to model fitting based on an empirical measure of among fish variation in $\log_e$(length) about the average for that age and year, using only ages and years that contributed ten or more observations. The resulting values ranged from 0.013 to 0.019 (Table 2.4), these values were fixed when other parameters were estimated. The vectors of deviations influencing year specific values through the random walks are random effects, and their variances (on log scale) were estimated along with other parameters. The random walks are defined by the initial value of the particular growth parameter in 1996, and the associated variance parameter for subsequent deviations.

To avoid negative growth when L_∞ was allowed to vary, any negative increment was assumed to be zero. Technically, to ensure differentiability required by the model fitting method, this was done by multiplying all growth increments by the output from a logistic function that rapidly went from zero to 1.0 as growth increments went from negative to positive. In additional preliminary analyses we also considered models where the von Bertalanffy model parameters were estimated as separate parameters for each year, rather than being modeled as random walks (see results).

When using a Bayesian approach, inferences about parameters (or quantities calculated from them) are based on the posterior distribution of the parameters. These posterior distributions depend both on the likelihood of the data given the parameters and prior distribution assumed for the parameters. We specified the priors for each parameter and the likelihood for the data and then we used MCMC simulations to approximate the posterior distribution. Most parameters were given a diffuse/non-informative prior, which effectively adds a constant to the log posterior density and thus does not need to be incorporated into the calculations used to generate the posterior distribution. One exception to the use of diffuse priors was the random deviations (which in a Bayesian context are considered parameters), which were assumed to be normally and identically distributed with mean zero. The standard deviations for these deviations were also estimated parameters on a log scale, and these were given normal priors, with distributional parameters (mean= -2.919, sd= 1.04) that allowed a wide range of possible levels of inter-annual variation. Diagnostics of trace plots for several scenarios and model combinations determined that the posterior distribution of the standard deviation for the inter-annual changes in *K* sometimes did not converge to a stable solution. When this occurred the value at the peak of the posterior occurred at very small values for the standard deviation (<.001), and all values in the MCMC chain were also near zero. We interpret this result as indicating for these cases that temporal variation in *K* was negligible and thus dropped those models from consideration. Initially we had assumed diffuse priors for the log standard deviation parameters also, but had implemented modestly informative priors in an attempt to address the problem with the MCMC chains for the standard deviation associated with K. Implementation of these priors did not fully resolve the problem but did help us better determine that the problem was occurring because of a tendency for the standard deviations to converge toward zero. Reliable model fits obtained with and without the informative priors for the standard deviations were similar.

Deviance information criterion (DIC), which for Bayesian modeling is analogous to AIC, was used separately for each scenario to compare models making different assumptions about temporal variation in growth (Gelman et al. 2004; He and Bence 2007). We selected the model with the lowest (best) DIC value and report the result for all models that produced reliable estimates of the posterior distribution. Predicted values of length-at-age (presented for the best model) are calculated using posterior averages of parameters. We present these predictions for ages 6, 12, and 20 to illustrate how changes in length at age differ among a range of ages. We used MCMC simulations with a Metropolis-Hastings algorithm to calculate the posterior distribution using AD Model Builder. The chain length for the MCMC simulations was 100,000 cycles for each model, where we saved every 100th cycle for analysis. We dropped the first 25% of each chain as a burn-in period, so all analyses and inferences are based on a saved chain of 750 values.

Results

Age and size composition

A total of 13,588 of siscowet lake trout were examined for both age and size for all surveys combined, where surveys 1-3 contributed 2937, 6183 and 4468 samples, respectively. The length-frequency distributions were mostly unimodal, regardless of the survey, zone, and temporal period (Figure 2.2-2.4). There were no clear spatial patterns in length distributions across all surveys, but for surveys 1 and 2, there was a general increase in mean length (Table 2.5) and the frequency of larger fish (Figures 2.2 & 2.3) from period 1 to period 2. The increase in mean length for survey 2 from period 1 to period 2 in zones 1, 2, and 4 were the only statistically significant ($P < .05$) changes. In contrast to those surveys, changes in size distributions from period 1 to period 2 were inconsistent among the zones for survey 3 (Table 2.5, Figure 2.4). For example, for survey 3 mean lengths were significantly ($P < .05$) larger in period 2 than in period 1 for zone 3, whereas in zone 4 there was a significant change in the opposite direction. Both surveys 1 and 3 had the smallest mean lengths in zone 4 in each temporal period (Table

2.5). In contrast, for survey 2 mean lengths were larger in zone 4 than in the other regions (Table 2.5).

There were more than 20 age groups in each survey, zone and period combinations, and very few siscowet younger than age 5 or older than age 25 (Figure 2.5-2.7). The age composition of siscowet lake trout differed substantially among zone/period combinations and the spatial-temporal pattern for age-compositions was not obviously related to the pattern seen for length compositions. Overall, the youngest siscowet captured was an age-3 fish in survey 2 (pre-recruit survey) and the oldest siscowet, 43 years of age, was captured by survey 1 (Table 2.6). Average age was significantly less ($P < .05$) in zone 4 than in the other regions, regardless of survey or temporal period (Table 2.6). In addition, for survey 3 average age increased from period 1 to period 2 for every zone (Table 2.6), and these changes were significant except in zone 4. Even though on average younger fish were captured in zone 4, 66% of the time the oldest fish were also found in this region (Table 2.6).

Mortality

We did not calculate mortality estimates for survey 3 in zone 4 and period 1 because the age composition did not have a range of ages that seemed to be consistent with an exponential drop off due to mortality (there was essentially no drop off from a broad dome of the catch curve). The estimates of Z varied between 0.16 in for survey 2 in zone 2 during period 2 to 0.59 for survey 3 in zone 2 during period 1 (Table 2.7). Estimates of mortality based on survey 1 and 2 were substantially lower than those estimated using survey 3 data (Table 2.7). Individual mortality estimates were very uncertain and there was no obvious pattern of differences between periods that was consistent across zones.

The results shown here for mortality should be interpreted with caution; the different mortality estimates derived from each survey suggest that the catch data are highly variable. We would have expected that our best mortality estimates would be based on data from survey 3, given that this survey better covers the depth range of this form, but we do not have an obvious explanation for why these estimates should be higher than those of the other surveys. These highly variable results may be an artifact of the assumption of traditional catch curves being violated. One assumption when evaluating catch curves is that recruitment is varying without trend. The fact that we know that siscowet abundance has been increasing through time (Chapter 1) suggests that this may not be true.

Length-at-50% maturity

Length-at-50% maturity (L_{50}) (in survey 2) varied between zone and temporal periods. Siscowet L_{50} increased from period 1 to period 2 in zones 1 through 3, but the difference was significant ($P < .05$) only zones 1 and 3 based on non-overlapping confidence intervals between periods for those zones (Table 2.8). In zone 4 the L_{50}s were lower than in all other zones, and the difference with zone 2 during period 1 and with all zones during period 2 were statistically significant ($P < .05$) (Table 2.8).

Model Selection for the mass-length relationship

The best random effects were selected prior to selecting the best fixed effects portion of the model to combine with them. This was done by evaluating alternative random effect models with all fixed effects included in the model (Table 2.9). This analysis identified, in addition to the best random effects model, a plausible alternative for both surveys 1 and 3 (ΔAIC < 4, Table 2.9). We then considered unique combination of fixed effects in association with the best random effects (ΔAIC = 0) model from Table 2.9 (Table 2.10), as well as for the plausible alternative random effects models for surveys 1 and 3 (results not shown).

The final models that best explained the mass-length relationship for siscowet lake trout were different for each survey (Table 2.10). For both survey 1 and 3, a final model that included all four fixed effects was far superior to any other fixed effect options. For survey 2, the final model included the main fixed effects but did not include the fixed interaction of $\log_e$(length) with zone, but a model that added this effect was somewhat plausible (ΔAIC < 4) (Table 2.10). Thus, there is compelling evidence that $\log_e$(length), year, and zone are useful for predicting mass.

Predicted Mass at 450 mm and 700 mm as condition indices

Predicted masses are shown only for the best model because predictions from plausible alternative models (based on the best or alternative random effect portions of the model) yielded similar qualitative patterns (see Methods). Siscowet lake trout predicted mass at 450 mm TL for survey 1 was highest in zone 4 and lowest in zone 1. Most annual predicted masses at 450 mm were below the lake-wide predicted average of 6.60 g, starting from 1997 through 2006 for zones 1 and 3. In contrast, in zone 4 annual predictions were above the predicted average from 1990-2006, except for 2002 (Figure 2.8). The average predicted masses for zone 2 fell below the lake-wide predicted average in 2000 through 2005. Siscowet predicted mass at 700 mm TL was also highest in zone 4 and lowest in zone 1. Temporal and spatial patterns in annual predicted masses for siscowet at 700 mm were similar to patterns for siscowet at 450 mm (Figure 2.8).

Siscowet lake trout predicted mass at 450 mm TL for survey 2 were also highest in zone 4 of Lake Superior and the ranking of predicted masses in the other zones varied over time. Most annual predicted masses from 1999 to 2005 were below the lake-wide predicted average (6.60 g) for zones 1-3, whereas predicted values for zone 4 fell below the average once in 2002 (Figure 2.8). Qualitative spatial and temporal patterns for predicted masses at 700 mm TL for survey 2 were the same as was observed for 450 mm TL in that survey (Figure 2.8). On average, zone 3 predicted masses were greater than predicted masses in zone 1 and 2, except in 2002-2004, when predicted masses for zone 3 fell below those of zones 1 and 2 (Figure 2.8).

There were some modest differences in patterns observed for siscowet lake trout predicted mass at 450 mm TL for survey 3 in comparison with surveys 1 and 2. In this survey predicted masses at 450 mm TL were also highest in zone 4, but the lowest predicted masses were in zone 3. Most annual predicted masses from 1999 to 2005 were below the lake-wide predicted average (6.60) for zones 1-3, whereas predicted values for zone 4 fell below the average once in 2002 (Figure 2.8). Spatial and temporal patterns for predicted masses at 700 mm TL for survey 3 were generally qualitatively the same as was observed for 450 mm TL fish in that survey (Figure 2.8). An exception to the above generalization was that the lowest predicted masses at 700 mm were found in zone 1 versus the lowest being found in zone 3 at 450 mm. The temporal pattern of variation was similar for these larger fish in zones 1-3, with predictions below the lake-wide predicted average from 2000 through 2006 (Figure 2.8) and zone 4 predictions never fell below the lake-wide predicted average.

Despite the differences in predicted mass among the surveys, likely caused by gear selection, there was an overall pattern of predicted masses for a given length declining over time. In our analysis the pattern was similar across zones but this may be a result of our treatment of interactions involving year and zone as being random. For each survey, predicted masses at 450 mm TL suggested a declining temporal trend and a linear trend was statistically significant ($P < .05$), except in the cases of zones 1 and 2 for survey 1. The pattern for predicted mass at 700 mm also suggested a decline over time, and the linear trend was significant ($P < .05$) for all zones and surveys.

Growth and length-at-age

In our combined zone analyses, the model that allowed both L_∞ and K to vary over time according to random walks was superior (lower DIC) to the alternatives, and all the models that allowed temporal changes in growth were superior to a constant growth model (Table 2.11). These results run counter to preliminary comparisons among alternative models in which growth parameters were estimated separately by year. In this case, given that there were no random effects, we were able to fit the models by maximum likelihood and compare models by AIC. The constant growth model produced the lowest AIC. While it is not legitimate to directly compare a model in which an effect is modeled as random versus as fixed, our results suggest there is some evidence for growth parameters changing with some inertia, but the data do not provide enough information to freely estimate year specific growth parameters without such an assumption. Results from our best model, with time varying parameters, suggest modest changes in growth over time, most notably declines in length-at-age after 2001, with some increases in 2006 for younger ages (Figure 2.9).

When analyzing growth by zone the model allowing only L_∞ to vary through time was far superior to any other model for zones 1, 3, and 4 (Table 2.10). For zone 2, although the model with only L_∞ varying had the lowest DIC, the model that allowed both L_∞ and K to vary over time had nearly as low a DIC (Table 2.10). Results from our best model for each zone (with only L_∞ varying); suggest that in general there have been modest changes in growth over time. Most notable changes are declines in length-at-age in zones 1 and 3 after 2001, for younger fish with a less notable change in zone 4 (Figure 2.10). Changes in growth for older aged siscowet (20 years of age) the declines are very modest compared to those observed for 6 year old siscowets (Figure 2.10). Similar to age 6 growth trends, these declines in length-at-age are only observed in zones 1, 3, and 4 after 2001 (Figure 2.10). For both younger and older fish length-at-age in zone 2 did not change as much through time as was the case in the other zones (Figure 2.10). Siscowet lake trout found in zone 4 are larger in size at younger ages and smaller at older ages compared to other zones (Figure 2.10).

Discussion

Our analysis of age and size composition, mortality, maturation, and condition demonstrated that the survey used to sample siscowet could influence the overall representation of siscowet biology. Even though results across surveys were not completely congruent, there were some important temporal and spatial patterns that were consistent. The unexplained differences among surveys may reflect differences in gear selectivity and sampling design (particular depth at which gill-nets were set). Gear selectivity can be a problem when describing biological attributes of a population because different gears could exclude specific size classes that could be used in analysis (Potts and Manooch III 2002; Jones et al 2008; Colombo et al. 2008). For two of the three surveys, siscowets were collected by gill-nets set in shallow water depths, which is not their primary habitat. The siscowet survey was designed to include sampling at deeper depths. Therefore, when interpreting results from a specific survey, care should be taken to consider the potential sampling biases, in particular those associated with habitat preferences and behavior of organisms.

The general patterns in our results show that siscowet lake trout in zone 4, which is the eastern part of the lake, have different characteristics than those found elsewhere. In zone 4 siscowet were on average smaller, younger, in better condition, and matured at lower lengths compared to other zones. It has been suggested that regional differences in siscowet characteristics is associated with availability of bathymetric habitat. Bronte and Moore (2007) suggest that there may be smaller local stocks located in the eastern region of the lake, where the bathymetry is highly variable compared to other parts of the lake and this may contribute to difference seen in siscowet morphology. Bathymetry is likely to be important in contributing to the differences between siscowet in zone 4 and other zones, but we cannot rule out the importance of other habitat and environmental factors, and relatively little is known about how these other factors influence siscowet.

Our analysis demonstrates that biological characteristics of siscowet lake trout were changing through the 1990s and 2000s. These changes may be related to changes in siscowet densities from the 1990s to the 2000s (Figure 2.11; Chapter 1). Across all surveys, the frequency of older and larger siscowet increased between periods 1 and 2. In addition, siscowets were maturing at smaller sizes compared to those observed in the 1990s. Siscowet condition and length-at-age declined over time, with the largest rate of decrease during the 2000s. Declines in length-at-age were modest compared to changes in condition. Similar declines for lean lake trout in Lake Huron were associated with changes in prey availability (He et. al 2008). Decreases in prey biomass (rainbow smelt *Osmerus mordax* and cisco *Coregonus artedi artedi*) may also be the reason for declines in growth rates of lean lake trout in Lake Superior during the 1970 through 2003 period (Bronte et al. 2003; Sitar and He 2006). In addition, lean lake trout length-at-50% maturity (L_{50}) declined during a period when lean lake trout abundance was increasing and prey fish abundance was low (Sitar and He 2006). Our result for maturation indicate a general increase in siscowet L_{50} over time, which can possibly be explained by the same reasons Sitar and He (2006) proposed for lean lake trout. Siscowets were increasing in abundance during the 1990s and the rate of increase decreased in the early 2000s moving towards an asymptote (Figure 2.11; Chapter 1). Siscowet lake trout feed primarily upon coregonines (cisco, bloater *Coregonus hoyi*, kiyi *Coregonus kiyi kiyi*), sculpins, burbot *Lota lota* and rainbow smelt (Conner et al. 1993; Kitchell et al. 2000; Bronte et al. 2003; Ray et al. 2007). Rainbow smelt abundance has been decreasing since the 1970s and coregonine abundance began decreasing in the 1990s (Bronte et al. 2003; Eby et al. 1995). Therefore, both changes in abundance of siscowet and several of their principal prey suggest that food limitation and intraspecific competition may be playing an important role in causing the changes we observed in maturation and condition.

Our mortality estimates varied greatly among surveys, zones, and temporal periods, and no obvious general spatial or temporal patterns were evident. The most obvious pattern was that mortality estimates from the siscowet survey were higher than for the other surveys, and this clearly must be a consequence of differences in survey designs as the mortality estimates differed for the same zone and periods, although we have not been able to formulate a more specific hypothesis that can explain the difference.

Overall our results support speculations that siscowet are experiencing density dependent life history responses similar to what has been found with lean lake trout (Bronte et al. 2003; Sitar and He 2006). While different data sources suggest some different responses in the details, we saw pervasive patterns across three different surveys differing in mesh size configurations, sampling locations, depths, and time of year of sampling. Therefore, we believe these results provide important information on real changes that are occurring and actual zone differences in siscowet populations, and provide an important baseline about siscowet biology. This information provides a basis for better understanding possible interactions between leans and siscowet, as well as the critical information needed to make informed judgments about the per recruit contributions of siscowet both in response to changes in mortality in Lake Superior (e.g., due to changes in a sea lamprey control or fishery harvest) and under conditions that might exist if siscowet are reintroduced to the lower Great Lakes (Eshenroder et al. 1999; Janssen et al. 2007). The manner in which these life-history characteristics vary spatially and over time might provide clues to whether stocks in Lake Superior are approaching biological limits or whether if the siscowet form were introduced into other lakes its biology might differ from what has been seen in particular areas of Lake Superior. Further studies that provide detailed understanding of intraspecific variation in siscowet biology through time and space, and connecting these observed changes to either environmental changes or behavior would improve our ecological understanding of siscowet lake trout in Lake Superior.

Acknowledgments

We thank Shawn Sitar, Michigan (MDNR), Mark Ebener (CORA), Bill Mattes (GLIFWC), and Matt Symbal, Red Cliff Fisheries Department for their advice and assistance in assembling and interpreting their agency data, and all personnel that collected and provided data for this project. We also thank Mike Jones and Andrew McAdam for their thoughts and guidance during the course of this research and on earlier drafts of this manuscript. In addition, we thank our colleagues at the Quantitative Fisheries Center (QFC) at Michigan State University for technical and modeling advice. Funding was provided by the U.S. Fish and Wildlife Service Restoration Act Program under cooperative agreement #301814J260 and by the Michigan Department of Natural Resources. We are grateful to the GLIFWC who acted as the agency sponsor for this Restoration Act project.

Table 2.1. Number of observations (*N*) on individual siscowet included for each analysis by survey and zone for Michigan waters of Lake Superior.

			Zone			
Analysis	**Survey**	***N***	**1**	**2**	**3**	**4**
Age and Size Composition, Mortality, Growth	1	2937	379	611	694	1253
Age and Size Composition, Mortality, Growth	2	6183	1916	1509	2197	561
Age and Size Composition, Mortality, Growth	3	4468	1212	1042	1554	660
Condition	1	4983	418	988	1369	2208
Condition	2	9467	2792	2560	3266	849
Condition	3	5952	1552	1207	1984	1209
Maturation	1	7481	1226	2317	1642	2296
Maturation	2	11251	3567	3153	3617	914
Maturation	3	6714	2159	1290	2055	1210

Table 2.2. All possible combinations of random effects considered in models for mass-length relationship that included all fixed effects. Model shorthand notation is used to indicate which random effects are included in the model (e.g., length*year indicates that a random interaction of length and year was included). For the actual model see equation 3.

Model Number	All Possible Random-Effect Models for Mass-Length Relationship
1	$\log_e$(length)*year zone*year $\log_e$(length)*year*eco*region
2	$\log_e$(length)*year zone*year
3	$\log_e$(length)*year $\log_e$(length)*year*zone
4	zone*year $\log_e$(length)*year*zone
5	$\log_e$(length)*year
6	zone*year
7	$\log_e$(length)*year*zone
8	No effects (intercept only)

Table 2.3. All possible combinations of fixed effects for mass-length relationship that were considered and used with best random effects model. Model shorthand notation is used to indicate which effects are included in the model (e.g., year indicates an effect of year was included, and length*zone that an interaction of length and zone was included). For the actual model see equation 3.

Model Number	**All Possible Random-Effect Models for Mass-Length Relationship**
1	$\log_e$(length) year zone $\log_e$(length)*zone
2	$\log_e$(length) zone year
3	$\log_e$(length) zone $\log_e$(length)*zone
4	$\log_e$(length) year
5	$\log_e$(length) zone
6	$\log_e$(length)
7	No effects (intercept only)

Table 2.4. Estimated observation error (among individual variation not explained by age or year) used for each analysis for modeling time varying von Bertalanffy growth model. Zones are defined as combination of management units: zone 1 is MI2 and MI3, zone 2 is MI4, zone 3 is MI5 and MI6 and zone 4 is MI7.

Model Scenario	**Observation error**
Combined zones	0.019
Zone 1	0.015
Zone 2	0.019
Zone 3	0.018
Zone 4	0.013

Table 2.5. Length distribution (mm) summary statistics for siscowet lake trout for each survey, time period, and zone from samples collected during 1996-2006. Statistics are denoted by: sample size (*N*), minimum (min), maximum (max), mean, and standard deviations (std).

Survey	**Zone**	**Period 1**				
		N	**min**	**max**	**mean**	**std**
1	1	169	341	815	594.94	76.47
1	2	175	317	798	569.53	86.40
1	4	819	334	755	524.92	53.33
		Period 2				
1	1	210	140	834	576.86	99.22
1	2	436	327	949	578.12	91.48
1	3	694	388	938	561.27	74.56
1	4	434	406	775	534.64	56.26
		Period 1				
2	1	677	234	772	442.82	88.14
2	2	631	231	805	425.89	97.68
2	3	891	221	778	457.43	98.56
2	4	306	261	730	462.73	70.74
		Period 2				
2	1	1239	160	803	480.14	108.81
2	2	878	251	815	461.28	106.93
2	3	1306	215	829	463.25	94.53
2	4	255	339	675	489.24	63.28
		Period 1				
3	1	895	203	853	536.75	101.19
3	2	400	260	831	517.04	111.67
3	3	1078	236	922	521.96	105.08
3	4	401	302	770	508.60	105.21
		Period 2				
3	1	317	287	787	535.65	97.22
3	2	642	178	859	509.58	129.80
3	3	476	250	943	542.72	118.62
3	4	259	248	715	475.64	94.70

Table 2.6. Age (years) distribution summary statistics for siscowet lake trout for each survey, time period, and zone from samples collected during 1996-2006. Statistics are denoted by: sample size (*N*), minimum (min), maximum (max), mean, and standard deviations (std).

Survey	**Zone**	**Period 1**				
		N	**min**	**Max**	**mean**	**std**
1	1	169	5	26	16.56	3.48
1	2	175	5	23	14.63	3.58
1	4	819	5	43	10.75	3.49
		Period 2				
1	1	210	4	32	15.54	4.66
1	2	436	5	27	14.16	4.77
1	3	694	5	36	13.53	4.30
1	4	434	5	37	11.00	3.74
		Period 1				
2	1	677	3	26	11.57	3.67
2	2	631	3	24	10.67	3.99
2	3	891	3	28	11.49	4.40
2	4	306	4	31	9.51	3.58
		Period 2				
2	1	1239	3	31	12.79	5.13
2	2	878	3	33	11.27	4.78
2	3	1306	3	26	10.87	4.19
2	4	255	4	26	9.50	2.94
		Period 1				
3	1	895	4	27	14.18	3.75
3	2	400	5	28	13.77	4.02
3	3	1078	3	30	13.41	3.72
3	4	401	4	32	12.63	4.69
		Period 2				
3	1	317	6	37	15.45	4.24
3	2	642	5	29	15.57	4.92
3	3	476	4	31	15.89	5.10
3	4	259	4	29	12.82	5.24

Table 2.7. Estimates of instantaneous rates of total mortality (*Z*) for each survey by zone and period and 95% confidence intervals (denoted by lower and upper bounds for intervals).

Survey	**Zone**	**Period 1**			
		Ages	**Estimated *Z***	**lower bound**	**upper bound**
1	1	>=19	0.324	0.046	0.602
1	2	>=19	0.450	0.124	1.022
1	4	14-20	0.463	0.357	0.569
		Period 2			
1	1	18-26	0.360	0.126	0.487
1	2	>=12	0.210	0.132	0.289
1	3	>=13	0.199	0.156	0.242
1	4	12-21	0.383	0.242	0.523
		Period 1			
2	1	12-22	0.297	0.202	0.392
2	2	10-21	0.270	0.158	0.381
2	3	13-24	0.294	0.189	0.398
2	4	11-20	0.294	0.127	0.371
		Period 2			
2	1	15-27	0.323	0.221	0.424
2	2	12-25	0.156	0.120	0.193
2	3	13-35	0.307	0.199	0.416
2	4	11-20	0.270	0.225	0.514
		Period 1			
3	1	18-24	0.584	0.356	0.811
3	2	17-21	0.592	0.139	1.049
3	3	17-25	0.506	0.321	0.690
3	4				
		Period 2			
3	1	18-27	0.330	0.244	0.416
3	2	21-28	0.547	0.429	0.665
3	3	21-28	0.552	0.412	0.692
3	4	14-25	0.183	0.087	0.278

Table 2.8. The number of siscowet sampled (*N*) and length-at-50% maturity (L_{50}, mm) with 95 % confidence intervals in parentheses for each zone and temporal period for survey 2. Zones are defined as combination of management units: zone 1 is MI2 and MI3, zone 2 is MI4, zone 3 is MI5 and MI6 and zone 4 is MI7. Period 1 includes years < 2000 and period 2 includes years > 1999.

	Period 1		**Period 2**	
Zone	*N*	L_{50}	*N*	L_{50}
1	1667	571 (563, 579)	1900	594 (586, 602)
2	1305	579 (571, 590)	1848	589 (578, 601)
3	1466	569 (561, 577)	2150	600 (590, 615)
4	464	544 (527, 565)	450	524 (512, 542)

Table 2.9. Unique candidate models for random effects in mass-length models with number of estimated parameters (N_p), AIC differences (ΔAIC, 0 = best model), and AIC weights for the mass-length relationship model for each survey. All fixed effects were included in all models.

Model Structure	N_p	**ΔAIC**	**Weights**
	Survey 1		
*$\log_e$(length)*year*zone*	2.0	0.0	0.562
*zone*year*	2.0	0.5	0.438
No random effects	1.0	51.4	0.000
	Survey 2		
*$\log_e$(length)*year + zone*year*	3.0	0.0	0.948
*$\log_e$(length)*year + $\log_e$(length)*year*zone*	3.0	5.8	0.052
*zone*year*	2.0	25.1	0.000
*$\log_e$(length)*year*zone*	2.0	28.9	0.000
*$\log_e$(length)*year*	2.0	148.4	0.000
No random effects	1.0	167.2	0.000
	Survey 3		
*$\log_e$(length)*year + zone*year*	3.0	0.0	0.760
*$\log_e$(length)*year + $\log_e$(length)*year*zone*	3.0	2.3	0.240
*zone*year*	2.0	38.7	0.000
*$\log_e$(length)*year*zone*	2.0	39.4	0.000
*$\log_e$(length)*year*	2.0	72.8	0.000
No random effects	1.0	94.9	0.000

Table 2.10. Unique candidate mass-length models containing fixed effects and the best random effects model (lowest AIC in Table 2.1) with number of estimated parameters (N_p), AIC differences (ΔAIC, 0 = best model), and AIC weights for the mass-length relationship model for each survey. Fixed effects are not italicized and random effects are italicized.

	Survey 1		
Model Structure	N_p	**ΔAIC**	**Weights**
log_e(length) + year + zone + log_e(length)*zone + _log_e(length)*year*zone_	23	0.0	1.000
log_e(length) + year + zone + _log_e(length)*year*zone_	20	34.1	0.000
log_e(length) + zone + log_e(length)*zone + _log_e(length)*year*zone_	10	50.3	0.000
log_e(length) + zone + _log_e(length)*year*zone_	7	86.6	0.000
log_e(length) + year + _log_e(length)*year*zone_	17	101.4	0.000
log_e(length) + _log_e(length)*year*zone_	4	112.2	0.000
Intercept + _log_e(length)*year*zone_	3	626.8	0.000
	Survey 2		
log_e(length) + year + zone + _log_e(length)*year + zone*year_	19	0.0	0.786
log_e(length) + year + zone + log_e(length)*zone + _log_e(length)*year + zone*year_	22	2.6	0.214
log_e(length) + zone + _log_e(length)*year + zone*year_	8	22.4	0.000
log_e(length) + zone + log_e(length)_*zone + log_e(length)*year + zone*year_	11	24.7	0.000
log_e(length) + year + _log_e(length)*year + zone*year_	16	32.9	0.000
log_e(length) + _log_e(length)*year + zone*year_	5	43.8	0.000
Intercept + _log_e(length)*year + zone*year_	4	191.3	0.000

Table 2.10 (cont'd).

Model Structure	N_p	**ΔAIC**	**Weights**
		Survey 3	
log_e(length) + year + zone + log_e(length)*zone + log_e(length)*year + zone*year	20	0.0	0.966
log_e(length) + zone + log_e(length)*zone + log_e(length)*year + zone*year	11	6.7	0.034
log_e(length) + year + zone + log_e(length)*year + zone*year	17	96.1	0.000
log_e(length) + zone + log_e(length)*year + zone*year	8	104.6	0.000
log_e(length) + year + log_e(length)*year + zone*year	14	105.6	0.000
log_e(length) + log_e(length)*year + zone*year	5	107	0.000
Intercept + log_e(length)*year + zone*year	4	246.6	0.000

Table 2.11. List of alternative growth models for model comparison based on deviance information criteria (DIC), number of estimated parameters n_e, and ΔDIC is the differences between DICs with the best model (lowest DIC). When parameters were allowed to vary over time they followed a random walk model (see text).

Model (Time varying parameters)	**DIC**	n_e	**ΔDIC**
	Zones Combined		
L_∞ and K	12378.38	14.14	0.00
K*	-	-	-
L_∞	12409.10	14.07	30.73
Constant	12896.97	2.98	518.59
	Zone 1		
L_∞ and K*	-	-	-
K	2337.94	3.39	16.09
L_∞	2321.85	0.73	0.00
Constant	2439.23	3.07	117.39
	Zone 2		
L_∞ and K	2250.76	8.69	0.24
K	2258.63	5.00	8.10
L_∞	2250.53	7.84	0.00
Constant	2403.53	2.95	153.01
	Zone 3		
L_∞ and K*	-	-	-
K*	-	-	-
L_∞	3208.83	8.74	0.00
Constant	3551.62	2.99	342.80
	Zone 4		
L_∞ and K*	-	-	-
K*	-	-	-
L_∞	510.29	11.08	0.00
Constant	851.41	2.93	341.12

* indicates that the variance component of K converged toward zero and is a more parsimonious model

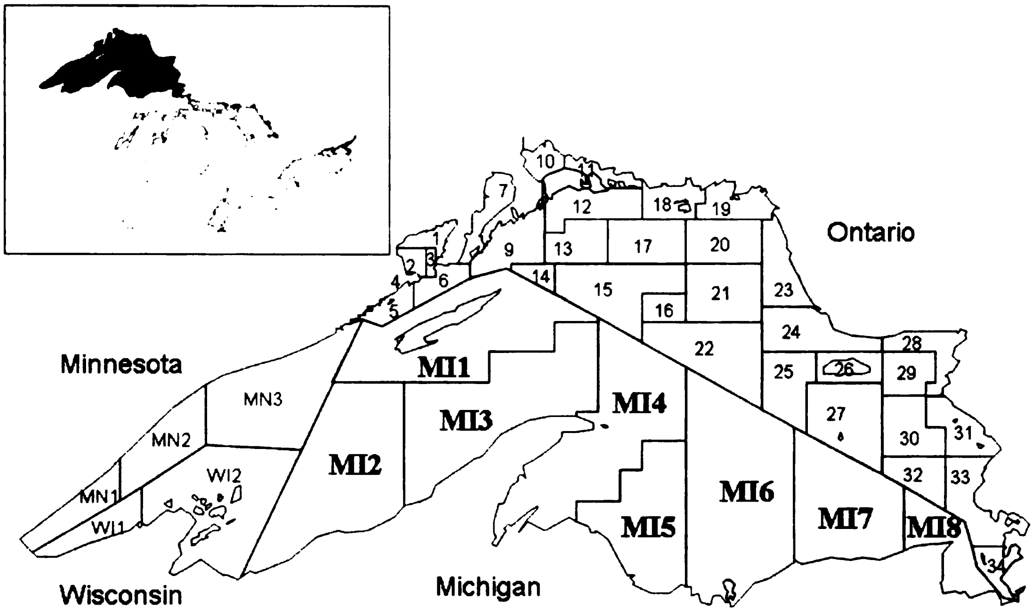

Figure 2.1. Lake trout management units of Lake Superior (Hansen et al. 1995). The letter abbreviations denote U. S. waters by state MN – Minnesota, MI – Michigan, and WI – Wisconsin, and numbers represent Canadian waters. Bolded management units were the ones that supplied data used in this paper.

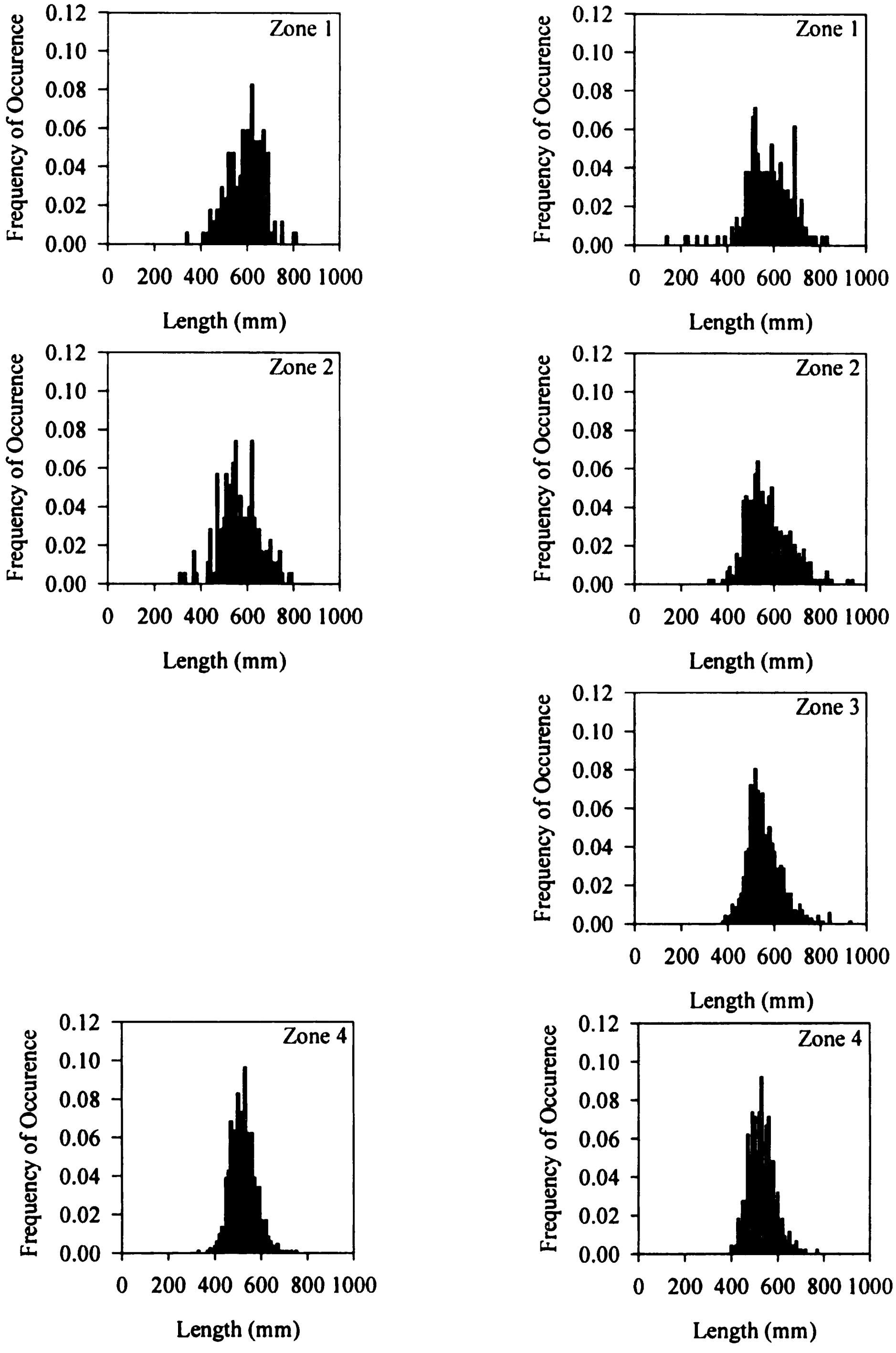

Figure 2.2. Length-frequency distributions for siscowet lake trout sampled in survey 1 for each period and zone. Left panels are for period 1 and right panels are for period 2. Zones are defined as combination of management units: zone 1 is MI2 and MI3, zone 2 is MI4, zone 3 is MI5 and MI6, and zone 4 is MI7. Period 1 includes years < 2000 and period 2 includes years > 1999.

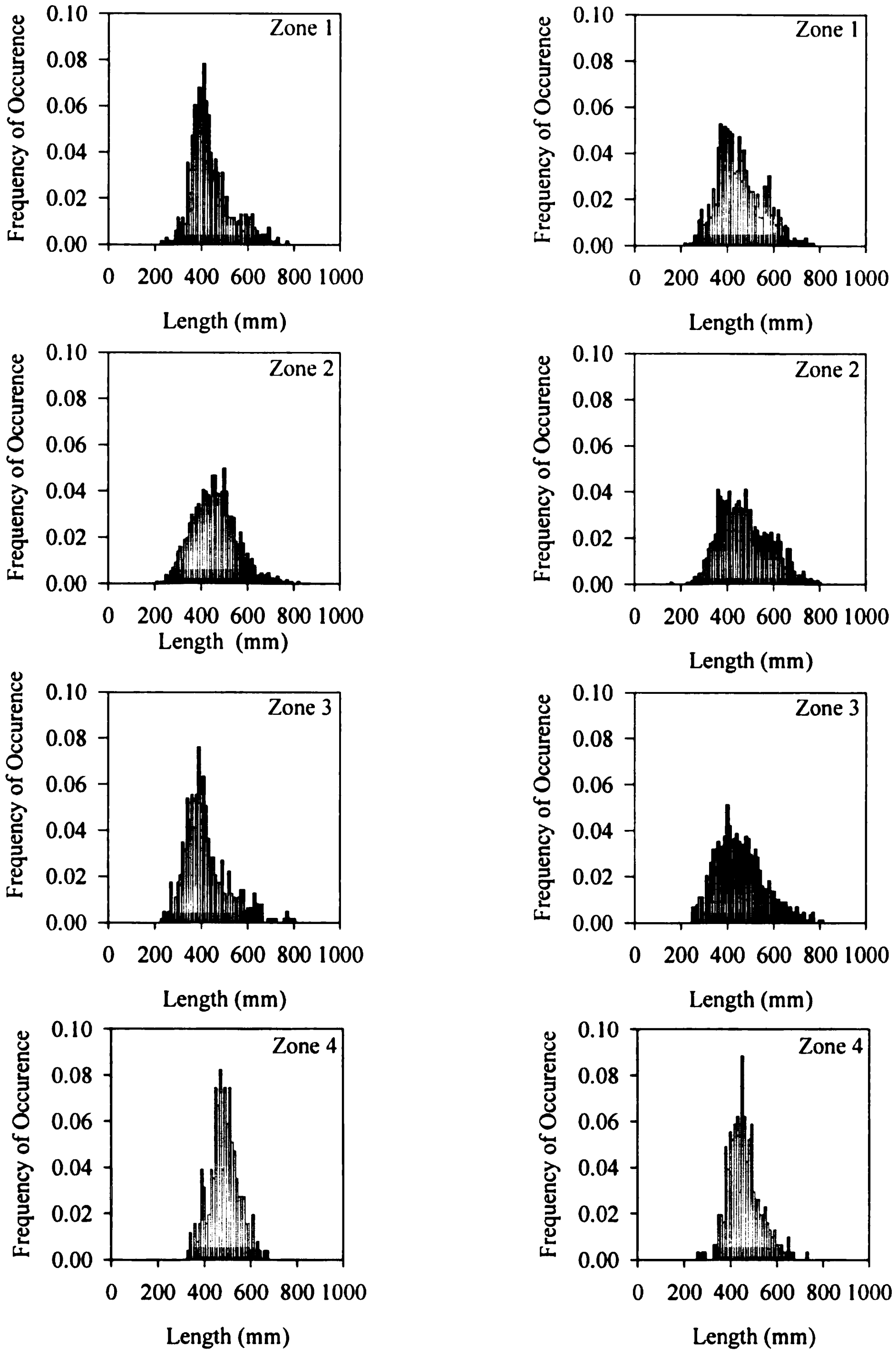

Figure 2.3. Length-frequency distributions for siscowet lake trout sampled in survey 2 for each period and zone. Left panels are for period 1 and right panels are for period 2. Zones are defined as combination of management units: zone 1 is MI2 and MI3, zone 2 is MI4, zone 3 is MI5 and MI6, and zone 4 is MI7. Period 1 includes years < 2000 and period 2 includes years > 1999.

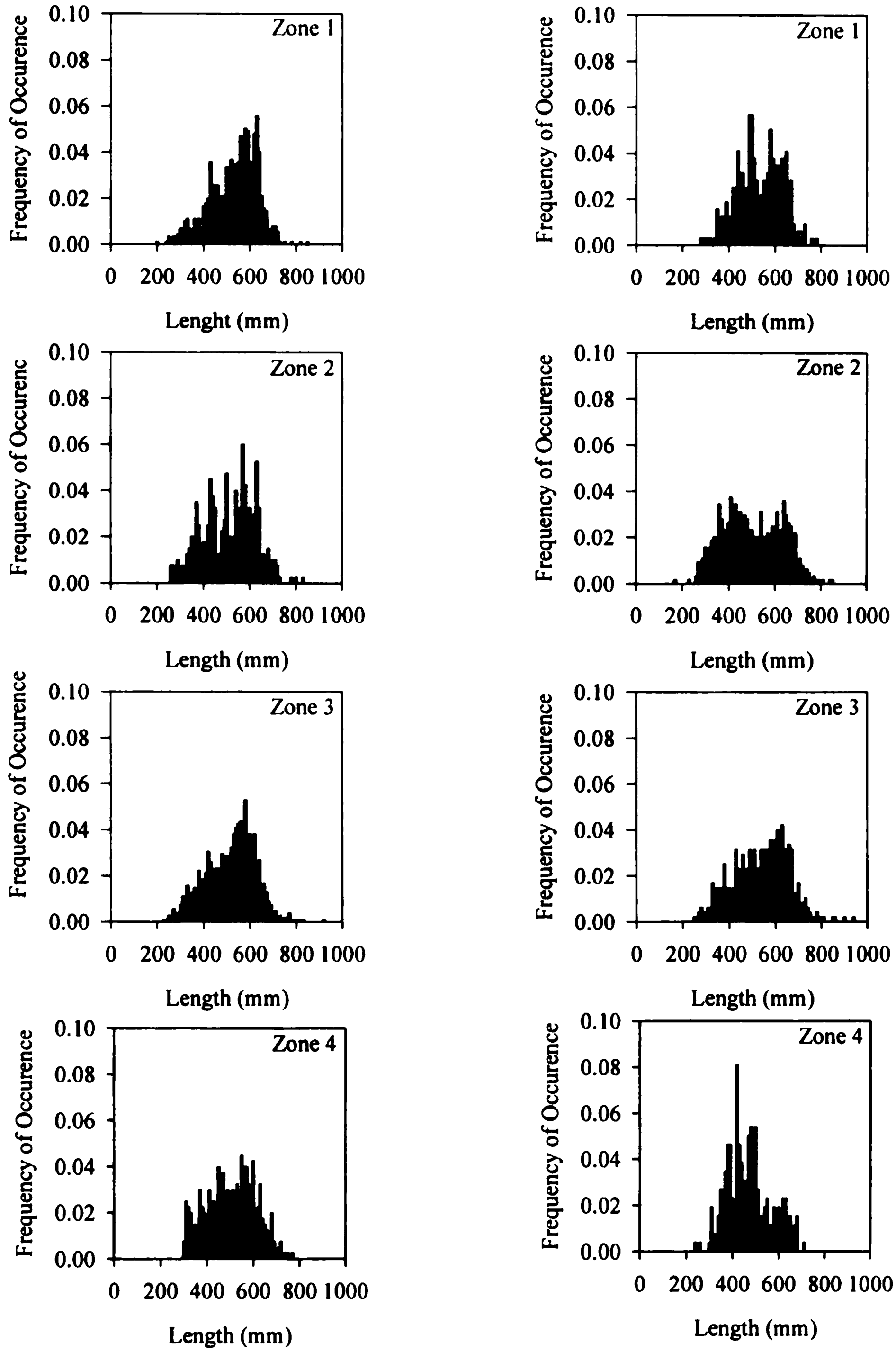

Figure 2.4. Length-frequency distributions for siscowet lake trout sampled in survey 3 for each period and zone. Left panels are for period 1 and right panels are for period 2. Zones are defined as combination of management units: zone 1 is MI2 and MI3, zone 2 is MI4, zone 3 is MI5 and MI6, and zone 4 is MI7. Period 1 includes years < 2000 and period 2 includes years > 1999.

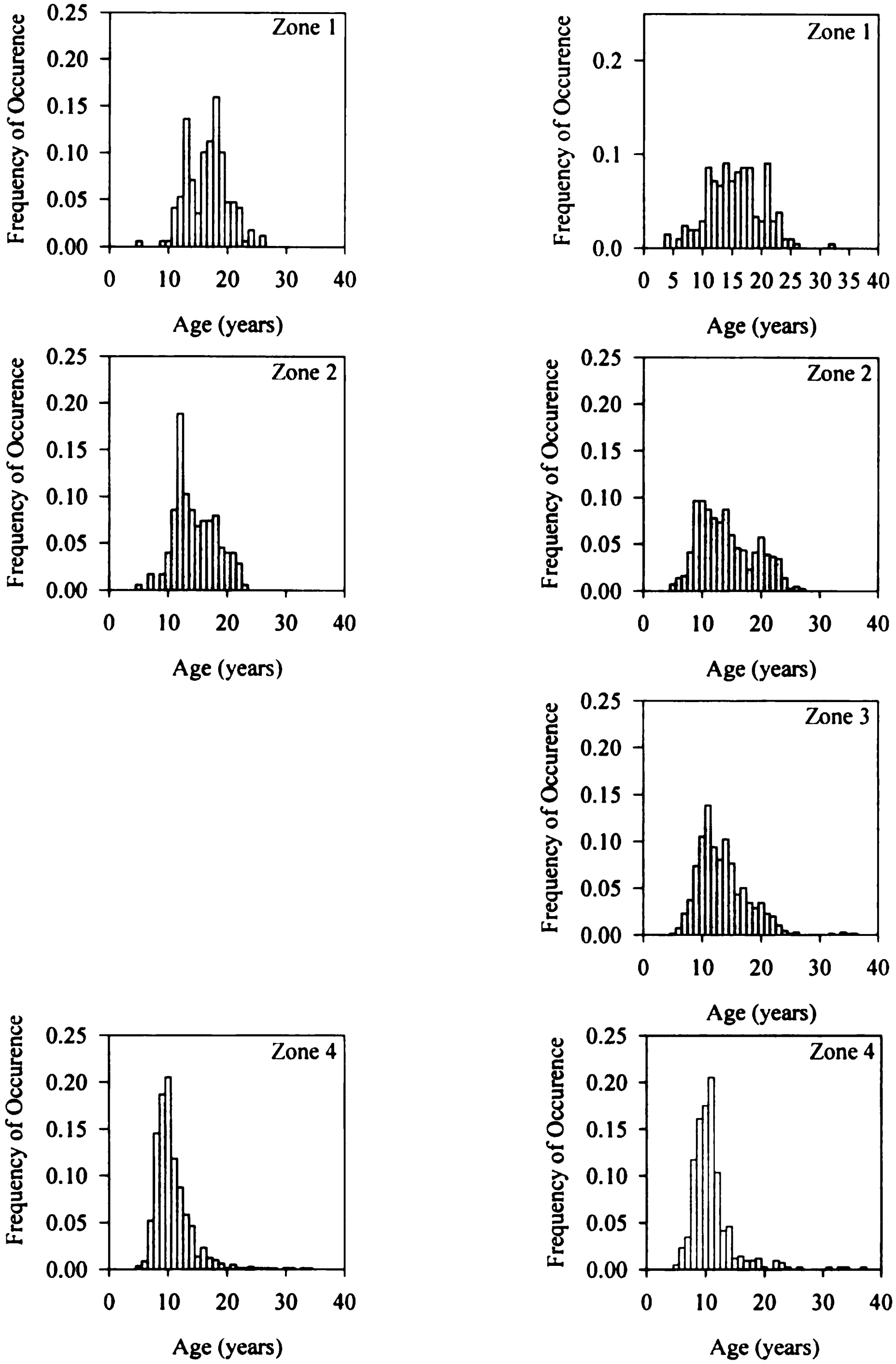

Figure 2.5. Age-frequency distributions for siscowet lake trout sampled in survey 1 for each period and zone. Left panels are for period 1 and right panels are for period 2. Zones are defined as combination of management units: zone 1 is MI2 and MI3, zone 2 is MI4, zone 3 is MI5 and MI6, and zone 4 is MI7. Period 1 includes years < 2000 and period 2 includes years > 1999.

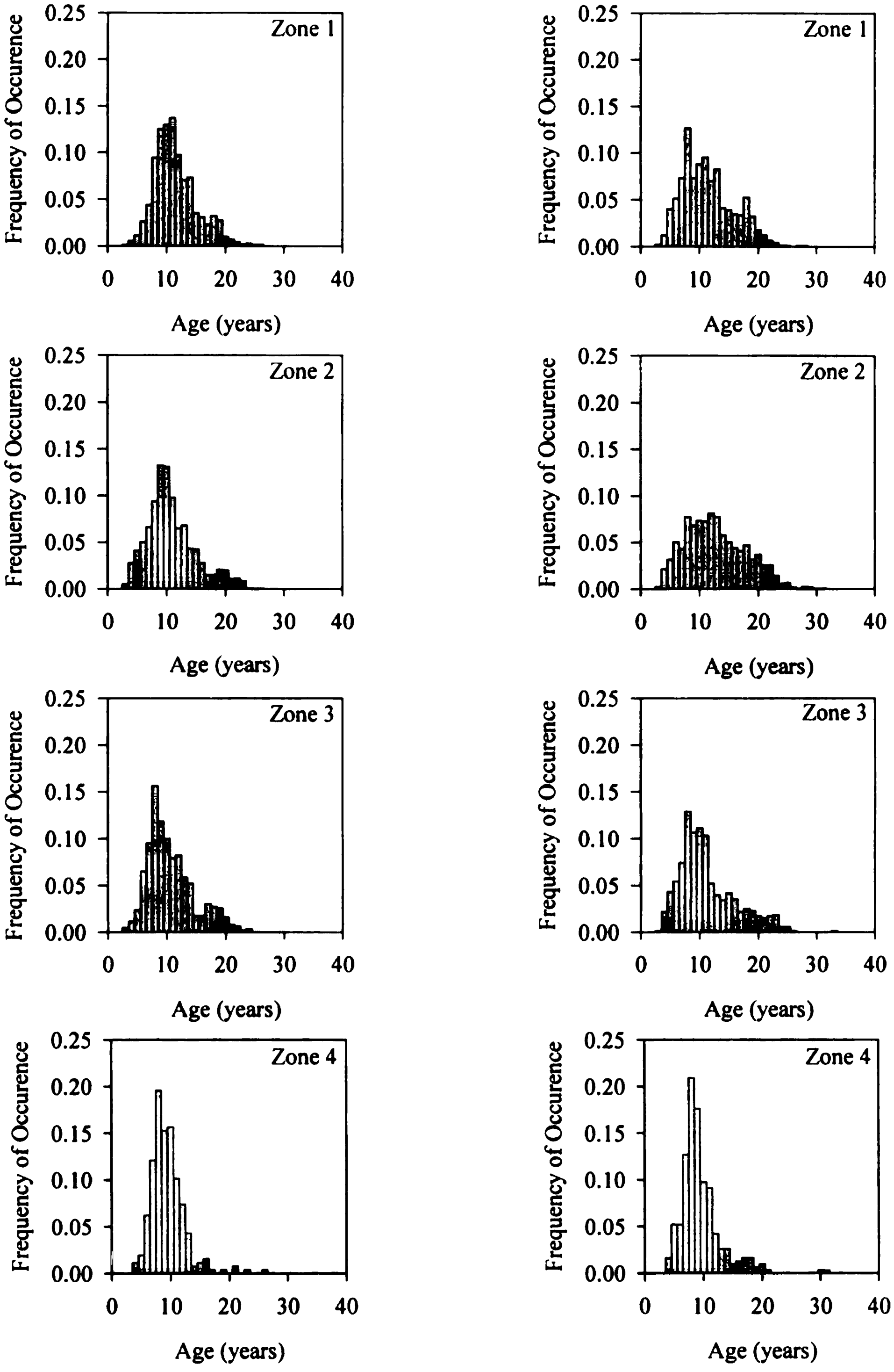

Figure 2.6. Age-frequency distributions for siscowet lake trout sampled in survey 2 for each period and zone. Left panels are for period 1 and right panels are for period 2. Zones are defined as combination of management units: zone 1 is MI2 and MI3, zone 2 is MI4, zone 3 is MI5 and MI6, and zone 4 is MI7. Period 1 includes years < 2000 and period 2 includes years > 1999.

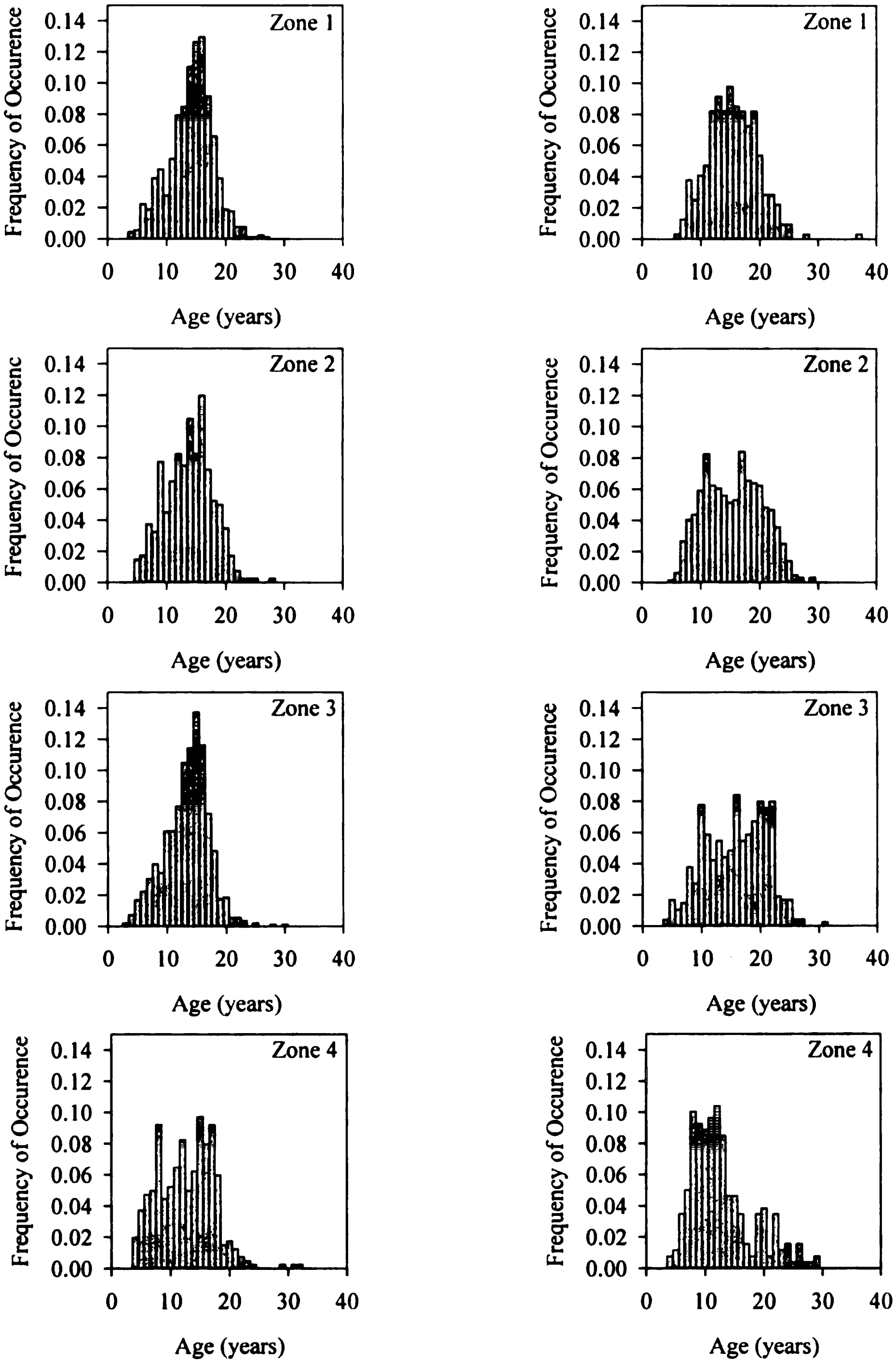

Figure 2.7. Age-frequency distributions for siscowet lake trout sampled in survey 3 for each period and zone. Left panels are for period 1 and right panels are for period 2. Zones are defined as combination of management units: zone 1 is MI2 and MI3, zone 2 is MI4, zone 3 is MI5 and MI6, and zone 4 is MI7. Period 1 includes years < 2000 and period 2 includes years > 1999.

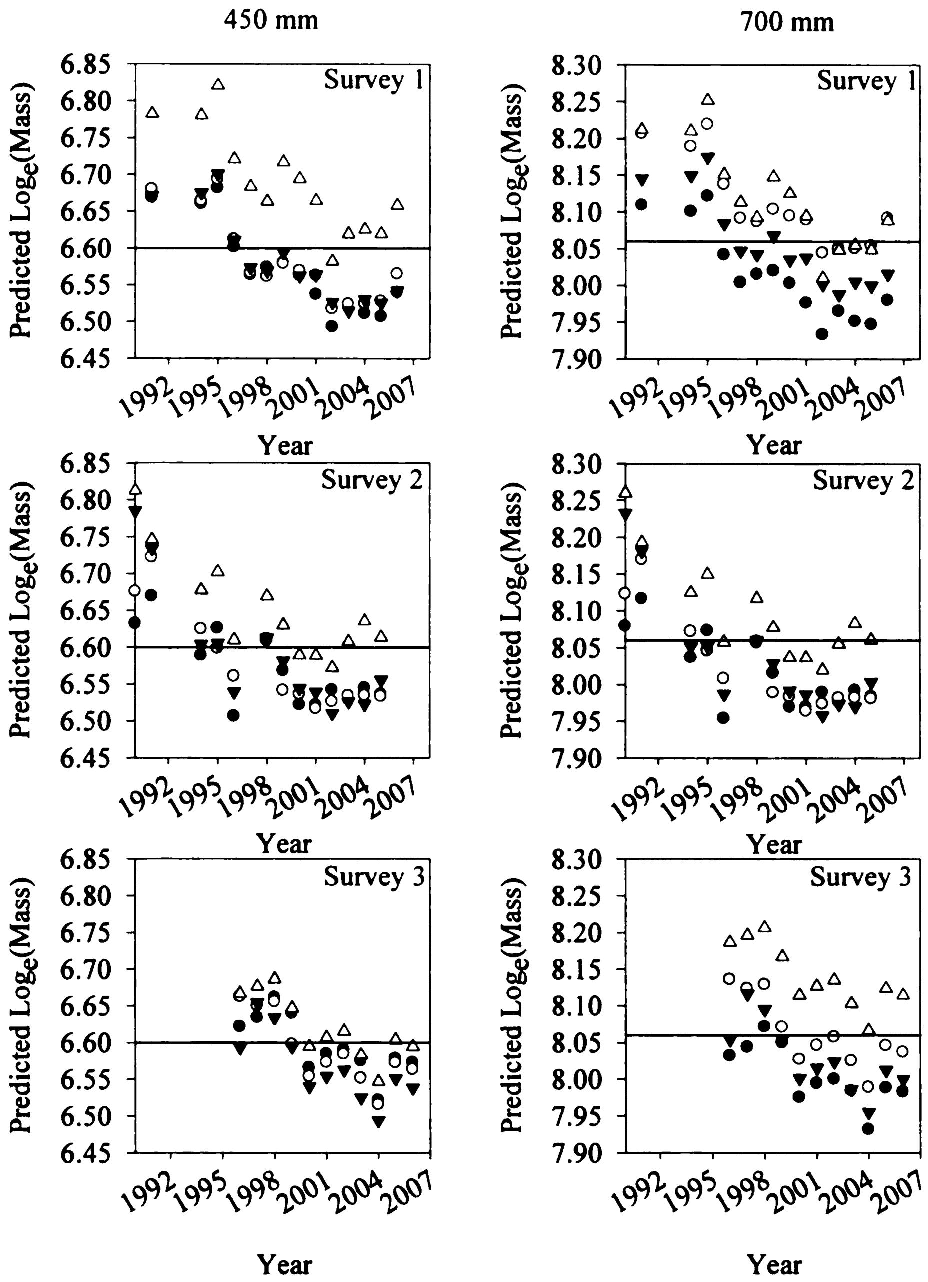

Figure 2.8. Predicted logarithm of masses at 450 (on left) and 700 mm (on right) total length for siscowet lake trout in three different surveys for each zone from 1990 to 2006. The zones are denoted by: solid circle zone 1; open circles zone 2; solid upside-down triangle zone 3; open triangle zone 4. The vertical line represents the lake-wide average of log$_e$(mass) within each survey and length class.

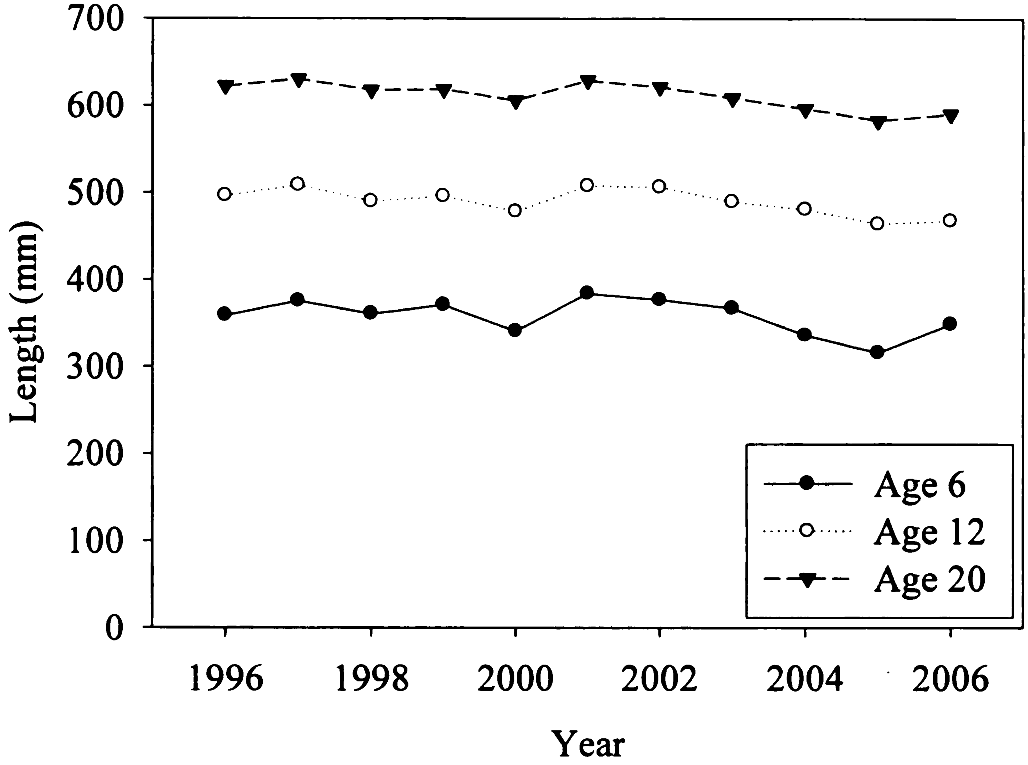

Figure 2.9. Length at age (mm) estimated by (mean of posterior distribution) nonlinear von Bertalanffy model that allowed parameters to vary over time (see text) for three selected ages.

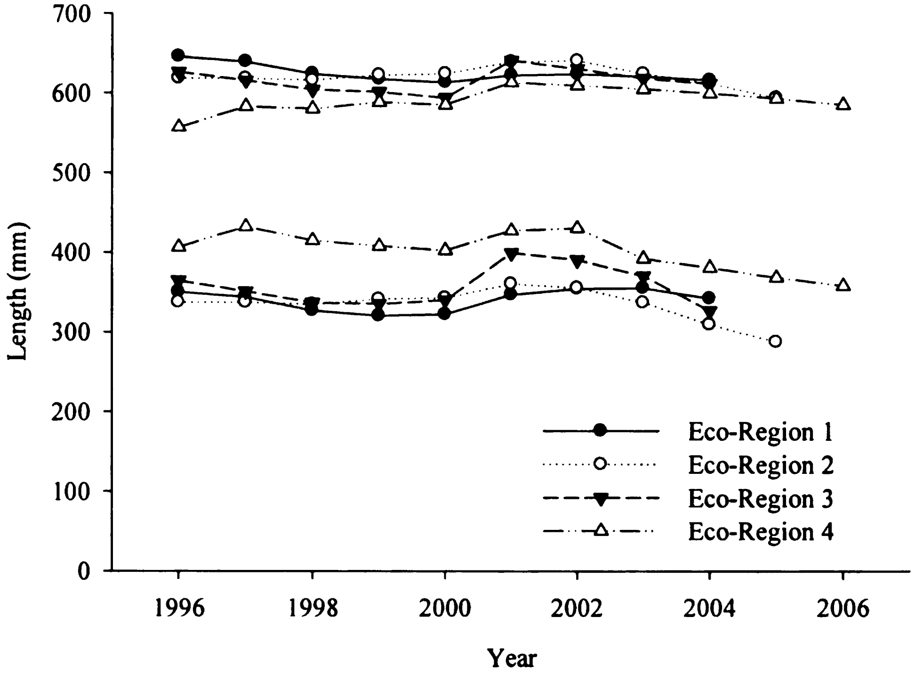

Figure 2.10. Length at age (mm) estimated (mean of posterior distribution) by nonlinear von Bertalanffy model that allowed parameters to vary over time (see text) for age 6 and age 20. The first four lower lines are predicted values for age 6 and top four lines correspond to age 20 siscowet.

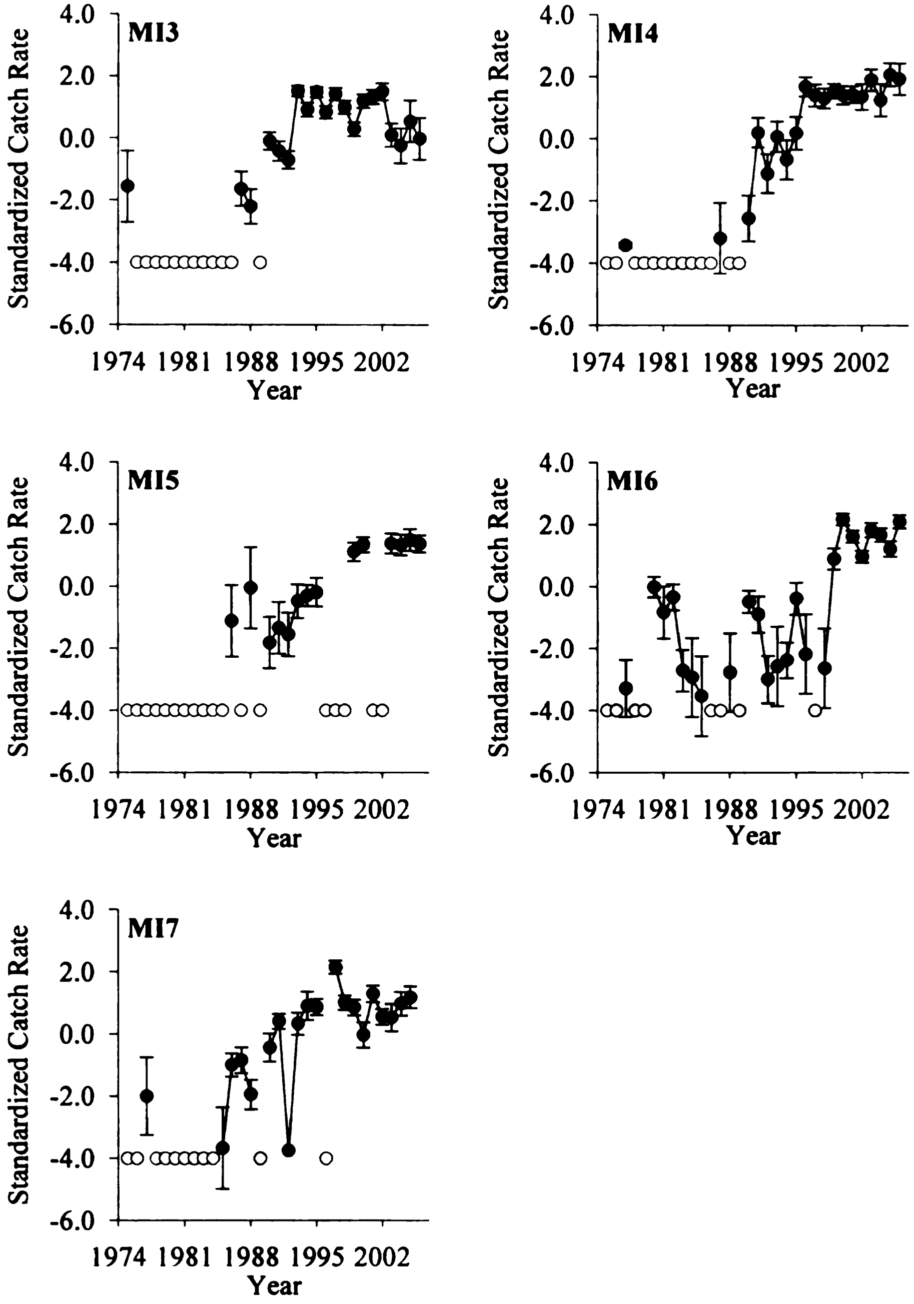

Figure 2.11. Estimated standardized catch rates ($\log_e$ scale) of siscowet lake trout from the spring lean lake trout survey for five Michigan management units in Lake Superior during 1975-2006 (solid circles joined by dashed line). The open circles show years that did not catch any siscowet lake trout (reproduced from Chapter 1).

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