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William W. Taylor
Major Professor's Signature

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CHANGES IN GROWTH, CONDITION, FECUNDITY, AND EGG LIPID CONTENT OF LAKE WHITEFISH IN THE UPPER GREAT LAKES BETWEEN 1986-87 AND 2003-05

By

Jud Fisher Kratzer

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ABSTRACT

CHANGES IN GROWTH, CONDITION, FECUNDITY, AND EGG LIPID CONTENT OF LAKE WHITEFISH IN THE UPPER GREAT LAKES BETWEEN 1986-87 AND 2003-05

By

Jud Fisher Kratzer

Lake whitefish (*Coregonus clupeaformis*) support the single largest and most valuable commercial fishery in the Laurentian Great Lakes. In recent years, fishery managers have reported declining growth and condition of lake whitefish in the upper Great Lakes. Proposed causes of the observed declines in individual growth rates include changes in: 1) lake whitefish density, 2) food quality and abundance, 3) population genetics, and 4) climatic conditions. I evaluated the relationships between each of these factors and lake whitefish growth in selected regions of the upper Great Lakes (i.e., Lakes Michigan, Huron, and Superior). I found that lake whitefish growth declines began with the development of a very strong 1991 year class due to favorable climatic conditions, leading to density dependent growth dynamics, which were exacerbated by a dramatic decline in the high-energy, benthic prey item (*Diporeia* spp.) toward the latter part of the 1990's.

Additionally, I described the changes in lake whitefish growth, condition, fecundity, egg lipid content, and total ovary lipid content in selected regions of the upper Great Lakes in 1986-87 and 2003-05, two time periods with different lake whitefish and diporeia densities. Lake whitefish grew more slowly in 2003-05 than in 1986-87 at all sites. The condition of these fish was also generally lower during 2003-05. Under conditions of high lake whitefish density and low diporeia density, female lake whitefish

generally produced fewer eggs. Individual egg lipid content, however, increased at all sites from 1986-87 to 2003-05, regardless of changes in lake whitefish or diporeia densities. I found that total ovary lipid content and lake whitefish abundance were inversely related, while there was no significant relationship between total ovary lipid content and diporeia density.

Growth, condition, and egg production of lake whitefish is lower now than it was 20 years ago at most of the sites studied. This study provides evidence that growth of lake whitefish in these regions of the upper Great Lakes is influenced by the abundance of young lake whitefish that are not yet recruited to the fishery and that condition and total ovary lipid content are more strongly affected by lake whitefish abundance than by diporeia density. Despite recent changes to the Great Lakes foodweb that have occurred as a result of dreissenid mussel invasion, managers may be able to use harvest regulations that result in reduced lake whitefish densities to increase lake whitefish condition, which should result in a plumper, more marketable fish, and to increase total ovary lipid content, which should benefit reproductive dynamics. Fisheries managers likely have less control over lake whitefish growth because growth rate appears to be more influenced by the abundance of pre-recruits, which can not be readily manipulated by managers, as their abundance is largely determined by density independent factors.

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CHAPTER ONE

Introduction to the Dissertation:

Lake Whitefish Production Dynamics in the Upper Great Lakes

Lake whitefish (*Coregonus clupeaformis*) are native to northern North America, with the southernmost portion of their range being the Laurentian Great Lakes (Hubbs and Lagler 2004). Adult lake whitefish are generally benthivores, eating mollusks, crustaceans, and insects, but they have been reported to occasionally eat plankton and small fish (Walden 1964, Ihssen et al. 1981, Pothoven 2005). Lake whitefish are deep water fish, preferring to live in 15-50 m of water during much of their life history (Walden 1964). They migrate to the shallows of lakes or connecting rivers in late October and November to spawn by broadcasting eggs and milt over gravel or cobble substrate in less than five meters of water (Hart 1930). As such, they are important integrators of offshore and nearshore energy dynamics in the Great Lakes.

Lake whitefish are also important economically in the Great Lakes region. Currently, this species supports the single largest and most valuable commercial fishery in the Laurentian Great Lakes, accounting for approximately 40% of total weight and value of fish harvested from the Great Lakes (Daniels 2003). Lake whitefish are harvested using large mesh trap nets and gill nets and must be at least 432 mm in length (typically age-2 to 4) to be legally harvested in most regions of the upper Great Lakes (Bence and Ebener 2002). Nearly 11,000 metric tons of lake whitefish were harvested from all Great Lakes combined in 1879, and yields declined to all time lows in the 1960s and 1970s (Figure 1.1). This decline in lake whitefish abundance has been attributed to

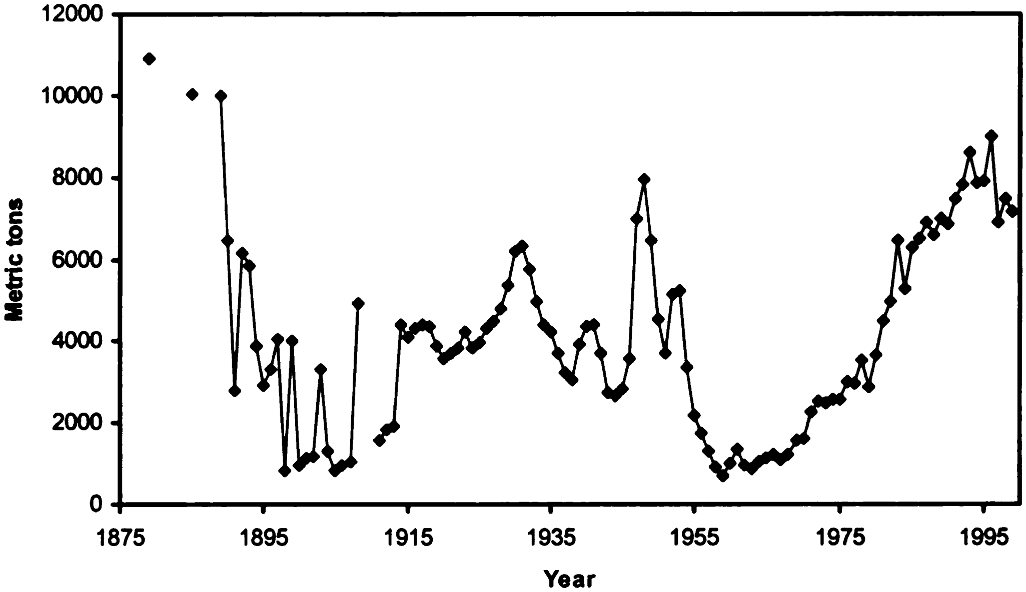

Figure 1.1 Commercial yield of lake whitefish from all Great Lakes combined, 1879-1999 (data from Baldwin et al. 2000).

overfishing, predation on adults by the invasive sea lamprey (*Petromyzon marinus*), predation on larvae and competition with larvae by the invasive alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), and degradation of water quality and habitat (Nalepa et al. 2005). Lake whitefish abundance has since rebounded as a result of sea lamprey control, better management of the commercial fishery, phosphorus abatement, and the introduction and recovery of large bodied piscivores, which suppressed alewife and rainbow smelt numbers and deflected sea lamprey predation away from lake whitefish (Cook et al. 2005, Mohr and Ebener 2005, Schneeberger et al. 2005). Yield of lake whitefish from Lake Michigan generally increased starting in the 1960s, reaching a peak of nearly 4,000 metric tons in the mid-1990s, a yield that was the highest recorded in over 100 years (Schneeberger et al. 2005). Similarly, in the main basin of Lake Huron, catch-per-unit-effort of lake whitefish increased steadily starting in the 1970s, peaking in the mid to late 1990's (Mohr and Ebener 2005).

Although the commercial harvest of lake whitefish from the Great Lakes continues to be large, there have been concerns regarding recent declines in growth and condition of lake whitefish in parts of the upper Great Lakes. During the 1990s, there were widespread reports from commercial fishermen on Lake Michigan that lake whitefish girth was declining, and they were returning legal-length fish to the water because they were not heavy enough to be marketable (Schneeberger et al. 2005). Madenjian et al. (2002) reported that lake whitefish growth declined during the 1990s and that condition factor dropped rapidly from 1995 to 1998 in Lake Michigan. Pothoven et al. (2001) showed that growth and condition of lake whitefish in southern Lake Michigan were lower during 1992-1999 than during 1985-1991. In Lake Huron's main basin, growth and condition of lake whitefish have declined over the past 10 to 15 years (Mohr and Ebener 2005). Several possible causes of these declines in growth and condition have been suggested, including changes in lake whitefish population abundance, climate change, changes in the composition and quality of the food-web, changes in population genetics, and parasitism or disease (Law 2000, Conover and Munch 2002, Nalepa et al. 2005).

The density of lake whitefish has been found to affect their growth and condition through intraspecific competition for food. More fish in an area means less food available for each individual fish, which can cause decreased growth and condition (Van Den Avyle and Hayward 1999). Healey (1980) and Mills et al. (1995) experimentally subjected lake whitefish populations to different levels of exploitation, and demonstrated that growth increased as population densities decreased. Bidgood (1973) and Henderson et al. (1983) also reported density dependent growth of lake whitefish. Density dependence has been cited as at least part of the reason that lake whitefish growth and condition have declined in Lakes Michigan and Huron (Schneeberger et al. 2005, Mohr and Ebener 2005).

Climate change has also been implicated as a possible cause of decreasing lake whitefish growth and condition because climate influences year class strength, which in turn affects growth and condition though density dependent mechanisms. Year class strength of lake whitefish is strongly dependent on weather conditions during spawning, egg incubation, and larval stages. Freeberg (1985) noted that year class strength was much higher when ice formed over spawning beds before the first winter storms (generally by late December) and hypothesized that strong wind generated currents that destroyed developing eggs in suboptimal habitats on the spawning grounds. Ice generally begins to melt by mid- to late March in the upper Great Lakes (Assel 2003). In years that experience rapid warming in the spring, investigators reported the development of relatively large year classes; a function of increasing available food for newly hatched larval lake whitefish, which was hypothesized to increase the growth and survival at this life history stage (Brown et al. 1993).

Recently, research scientists have also hypothesized that a possible cause of decreased growth and condition of lake whitefish is the changing Great Lakes food-web, in particular recent declines in *Diporeia* spp. Diporeia are crustaceans belonging to the order Amphipoda (Nalepa et al. 2000). Maximum diporeia densities occur between 30 and 70 m of depth, where they live on and in the bottom sediments of deep, cold lakes and feed on diatoms and organic particles that sink to the lake bottom (Dermott and Kerec 1997, Nalepa et al. 1998, Lozano et al. 1999, Dermott 2001, Dittman and Owens 2001, Lozano et al. 2001, Nalepa et al. 2001a, Nalepa et al. 2001b, Pothoven et al. 2001). By eating organic matter that settles from the pelagic regions of lakes and by serving as prey for fish, diporeia has historically represented a major link between pelagic primary production, the benthos, and upper trophic levels (Madenjian et al. 2002, Scharold et al. 2004). Benthic biomass production in the upper Great Lakes has historically been dominated by diporeia (Cook and Johnson 1974), which have been reported to be a significant component of the lake whitefish diet in this region (Pothoven et al. 2001, Pothoven 2005).

Diporeia abundance has declined in all Great Lakes except Lake Superior over the past decade, and a likely explanation is food limitation brought on by competition with the invasive dreissenid mussels (Nalepa et al. 2005). Zebra and quagga mussels (*Dreissena polymorpha* and *D. bugensis*) are natives of the Ponto-Caspian region and were introduced into the Great Lakes via the ballast water of commercial shipping vessels (Vanderploeg et al. 2002). Dreissenid mussels filter algae from the water column, and it has been hypothesized that as algal consumption by dreissenid mussels increases, the quantity of settled algae available for diporeia consumption decreases, leading to decreased diporeia production (Lozano et al. 2001, Dermott 2001, Vanderploeg et al. 2002, Nalepa et al. 2005). During the 1990s diporeia have declined while dreissenids have increased in Lake Erie (Dermott and Kerec 1997), Lake Ontario (Lozano et al. 1999, Dermott 2001, Dittman and Owens 2001, Lozano et al. 2001), Lake Michigan (Nalepa et al. 1998, Nalepa et al. 2001a, Pothoven et al. 2001), and Lake Huron (Nalepa et al. 2001b). Many parts of the Great Lakes are now totally devoid of diporeia, which historically occurred at densities of over 10,000/m^2 in some areas (Nalepa et al. 2005, T. Nalepa, Great Lakes Environmental Research Lab, unpublished data).

Declines in the biomass of the relatively energy rich diporeia (4,429 J/g wet mass) and increases in the biomass of the relatively energy poor dreissenid mussels (1,047-2,478 J/g wet mass of soft tissue) have been hypothesized to have lowered the quality of the lake whitefish diet (Schneider 1992). Changes in lake whitefish diet have been demonstrated near Muskegon, Michigan (Lake Michigan), where diporeia nearly disappeared between 1998 and 2000, and the proportion, by weight, of lake whitefish diet comprised by diporeia fell from 70% to 25% (Pothoven *et al.* 2001). With fewer diporeia available, lake whitefish shifted their diet to include dreissenid mussels and other lower energy prey (e.g., chironomids, zooplankton), resulting in decreased individual somatic growth of these fish. Pothoven (2005) discovered a similar trend in small (<430 mm) lake whitefish during the late 1990's in southeastern Lake Michigan, where diporeia went from 57% to 1% (dry weight) of their diet. In shallow (< 60 m) waters of Lake Ontario, lake whitefish diet shifted to include more dreissenids, sphaeriids, and *Mysis relicta* following the loss of diporeia (Owens et al. 2005). In Lake Huron and Lake Ontario, fishing effort for lake whitefish has shifted further offshore (Hoyle 2005, Mohr and Ebener 2005). For example, in one region of southern Lake Huron, average fishing depth increased from 30 m in 1992 to 61 m in 1999, where diporeia still exist, although in reduced numbers (Mohr and Ebener 2005). The shifting of fishing effort to deeper waters suggests that the fish have shifted to deeper waters, possibly in response to loss of diporeia in nearshore areas due to the establishment of dreissenids in those areas (Hoyle 2005, Mohr and Ebener 2005).

Delines in diporeia have been associated with declines in growth and condition of lake whitefish in regions of the Great Lakes. For instance, decreases in growth and condition of lake whitefish were at least partially attributed to declines in diporeia abundance in Lake Ontario and Lake Michigan (Pothoven et al. 2001, Hoyle 2005, Schneeberger et al. 2005). Researchers noted a 53% decrease in lipid content of lake whitefish in Lake Michigan between 1983-1993 and 1996-1999, which they attributed to decreases in diporeia abundance (Wright and Ebener 2006). Growth and condition of lake whitefish, however, have remained high in Lake Erie, despite the total disappearance of diporeia, presumably because these fish are able to feed heavily on an abundant and diverse benthic invertebrate community (Cook et al. 2005).

Potential changes in the genetic make-up of lake whitefish populations have also been implicated in the changes noted in the individual growth of lake whitefish over the past decade. During the 1990's, the harvest of lake whitefish was at all time highs in many parts of the Great Lakes (Nalepa et al. 2005). It has been documented in other fish species that intense fishing efforts through many generations of fish can exert powerful selective forces that can have lasting effects on the genetics of fish populations, resulting in slower individual growth rates (Law 2000, Conover and Munch 2002). The proposed mechanism for this phenomenon is that faster growing fish are harvested more heavily because they reach the minimum length of the fishery more quickly than slower growing members of their cohort, thus reducing the probability that the faster growing fish will reproduce before being harvested. This ultimately leaves predominately slower growing fish to spawn and produce offspring that on the average exhibit slower growth than before the fishery exerted heavy mortality pressures on the population. Such a phenomenon was demonstrated by Conover and Munch (2002), who experimentally harvested large, fast growing fish from a population of *Menidia menidia*, which eventually led to lower yields and slower growth of individuals because the "fishery" severely reduced the faster growing genotypes. The commercial lake whitefish fishery that has existed on the Great Lakes since the early 1800s (Brown et al. 1999) would tend to remove faster growing individuals from the population and could potentially result in slower growing fish being more likely to pass their genes on to succeeding generations. As such, if the fishery has been causing a change in lake whitefish genetics, the expected outcome would be a reduction of growth rate through time.

Decreases in growth and condition of lake whitefish could also affect other aspects of their population dynamics, such as the number of eggs produced or the amount of energy incorporated in each egg, both of which are important to development of year class strength in lake whitefish (Brown and Taylor 1992). Fecundity is clearly related to fish growth because larger fish have the capacity to produce more eggs (Bell et al. 1977, Jude et al. 1987, Smale 1988). Fish with higher quality (more energy dense) diets produce higher quality (more energy dense) eggs (Leray *et al.* 1985, Hardy *et al.* 1990, Corraze *et al.* 1993). Eggs with larger lipid stores provide more energy to developing larval fish, which allows for faster somatic growth and a longer time before larval fish must begin consuming prey (Brown and Taylor 1992). A key point in the early life history of fish occurs during the critical period, when larval fish switch from endogenous to exogenous food (Cushing 1990). In lake whitefish, this critical period generally occurs approximately 20 days after they hatch in mid-March to mid-April (Freeberg et al. 1990). During the egg and early larval stages, the developing fish depends on endogenous energy, which is stored as yolk by the mother. Once this endogenous food supply is expended, larval fish must switch to eating exogenous food, such as zooplankton (Taylor and Freeberg 1984). Thus, sufficient exogenous food of the right size and nutritional value is critical for larval survival (Brown and Taylor 1992). Weather conditions often determine year class strength in lake whitefish because warm spring conditions allow for high abundances of zooplankton, which are needed when the larval fish expend their endogenous energy stores (Brown et al. 1993). Larvae from larger, more yolk-filled, eggs have a survival advantage because they are able to survive longer before they need to switch to exogenous food, and more food is available to them because of their larger size, which enables them to consume a wider size range of food and a faster swimming speed to find their prey and to avoid predators (Miller *et al.* 1988, Brown and Taylor 1992). Decreases in lake whitefish reproductive success, as measured by year class strength, were associated with the disappearance of diporeia in Lake Ontario, presumably because changes in the food-web reduced the quality of the lake whitefish diet, resulting in reduced nutritional status and egg quality (Hoyle 2005).

The overall goal of this research was to describe the changes in growth, condition, fecundity, and egg and ovary lipid content from 1986-87 to 2003-05 in seven regions of the upper Great Lakes and to relate these changes to changes in lake whitefish abundance, diporeia abundance, population genetics, and climatic conditions. My dissertation consists of 5 chapters, including this introduction and a summary. In chapter two, I evaluate the possible causes for the noted changes in lake whitefish growth dynamics in the upper Great Lakes. My objectives for this chapter were to assess the effects of lake whitefish abundance, diporeia abundance, population genetics, and climatic conditions on lake whitefish individual growth in four regions of the upper Great Lakes which differed in lake whitefish abundance, food energy availability, and fishing mortality over time. In chapter three, I specifically describe the changes in lake whitefish growth and condition between 1986-87 and 2003-05 in my study areas. The objectives of this chapter were to evaluate the changes in length-at-age, body weight-at-length, and liver weight-at-length in seven regions of the upper Great Lakes that exhibited different combinations of changes in lake whitefish and diporeia densities, in order to ascertain the relative importance of the influence of lake whitefish and diporeia abundances on growth and condition of lake whitefish. In chapter four, I describe changes in the reproduction dynamics of lake whitefish in seven regions of the upper Great Lakes between 1986-87 and 2003-05. Specifically, I evaluated the changes in fecundity, egg lipid content, and total ovary lipid content of lake whitefish in my study areas, where lake whitefish and diporeia densities have changed during the past 20 years. In chapter five, I summarize the key findings of my research and make suggestions for enhanced management of this fishery in the future.

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CHAPTER TWO

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Jud F. KRATZER[1], William W. TAYLOR[1], C. Paola FERRERI[2], Mark P. EBENER[3]

[1]Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, USA

[2]School of Forest Resources, Pennsylvania State University, University Park, PA, USA

[3]Chippewa Ottawa Resource Authority, Sault Ste. Marie, MI, USA

Factors Affecting Growth of Lake Whitefish in the Upper Laurentian Great Lakes

Abstract

Lake whitefish support the single largest and most valuable commercial fishery in the Laurentian Great Lakes. Recently, fishery managers have reported declining growth and productivity of lake whitefish in the upper Great Lakes. Several causes for the declines noted in individual growth rates have been proposed. These include changes in: 1) lake whitefish density, 2) food quality and abundance, 3) population genetics, and 4) climatic conditions. We evaluated the relationships between each of these factors and lake whitefish growth in selected regions of the upper Great Lakes. Specifically, we examined the timing of the changes in the environment with lake whitefish growth to determine causal relationships. Lake whitefish growth declines began with the development of a very strong 1991 year class due to favorable climatic conditions, leading to density dependent growth dynamics, which were exacerbated by a significant decline in the high-energy, benthic prey item (*Diporeia* spp.) toward the latter part of the 1990's. It appears that declines in *Diporeia* density, which are related to the introduction of two invasive species (*Dreissena* spp.) have resulted in a lower carrying capacity for lake whitefish in the upper Great Lakes. As such, managers need to implement conservative harvest strategies that protect the viability of these stocks under lower productivity conditions.

[1]Department of Fisheries and Wildlife, Michigan State University, 12 Natural Resources Building, East Lansing, MI 48824, USA

[2]School of Forest Resources, Pennsylvania State University, 207 Ferguson Building, University Park, PA 16802, USA

[3]Chippewa Ottawa Resource Authority, 179 W. Three Mile Rd., Sault Ste. Marie, MI 49783, USA

Introduction

Lake whitefish (*Coregonus clupeaformis*) are native to northern North America, with the southernmost portion of their range being the Laurentian Great Lakes (HUBBS & LAGLER 2004). Adult lake whitefish are generally benthivores, eating mollusks, crustaceans, and insects, but they have been reported to occasionally eat plankton and small fish (WALDEN 1964, IHSSEN et al. 1981, POTHOVEN 2005). These deepwater fish prefer to live in depths of 15 to 50 m during much of their life history (WALDEN 1964). Lake whitefish are broadcast spawners, migrating to the shallows of lakes or connecting rivers in late October and November to spawn over gravel or cobble substrate in less than five meters of water (HART 1930). These life history traits make lake whitefish important integrators of offshore and nearshore energy dynamics in the Great Lakes. Year class strength of lake whitefish is strongly dependent on weather conditions during spawning, egg incubation, and larval stages. FREEBERG (1985) noted that year class strength was much higher when ice formed over spawning beds by late December, before the first winter storms, and hypothesized that strong wind generated currents and destroyed developing eggs in marginal habitats on the spawning grounds. Ice generally begins to melt by mid to late March in the upper Great Lakes (ASSEL 2003). In years that experience rapid warming in the spring, investigators have reported the development of relatively large year classes; a function of increasing available food for newly hatched larval lake whitefish, which was hypothesized to increase the growth and survival at this life history stage (BROWN et al. 1993).

Lake whitefish support the single largest and most valuable commercial fishery in the Laurentian Great Lakes. In 2002, lake whitefish accounted for approximately 40% of total weight and total value of fish harvested from all the Great Lakes (DANIELS 2003). Recently, concerns have arisen regarding declining growth and productivity of lake whitefish in regions of the upper Great Lakes. For example, during the 1990's, declining growth of lake whitefish was observed in northern Lake Michigan (MADENJIAN et al. 2002), southern Lake Michigan (POTHOVEN et al. 2001), and Lake Huron (MOHR & EBENER 2005). Several possible causes of recent declines in lake whitefish growth have been proposed, including 1) density dependent growth due to relatively high lake whitefish abundance; 2) declines in the food base due to reduced nutrient loadings and impact of invasive species on the food web, particularly the loss of the high-energy and important food resource *Diporeia* spp., a benthic amphipod; 3) a change in the population genetics of lake whitefish due to fisheries harvest regimes; 4) the presence of parasitism/disease; and finally 5) the impact of changes in climatic conditions (NALEPA et al. 2005, LAW 2000, CONOVER & MUNCH 2002). Lake whitefish growth rates are known to be elastic, given differing population densities and environmental conditions. Studies by BIDGOOD (1973), HEALEY (1980), and MILLS et al. (1998) demonstrated that lake whitefish growth is related to the amount of food available per fish and that density dependent changes in growth can occur because of changes in lake whitefish abundance or forage availability.

Over the last decade, lake whitefish abundance has been relatively high compared to historic abundances in Lakes Michigan, Huron, and Superior (NALEPA et al. 2005). The food base in Lakes Michigan and Huron has changed dramatically over the last decade, and primary production has decreased over the past 30 years due to reduced nutrient loadings from the surrounding watersheds (MADENJIAN et al. 2002, DOBIESZ et al. 2005). As such, the amount of food energy available to lake whitefish has declined in Lakes Michigan and Huron while abundance of these fish has increased. The food-web changes noted in the upper Great Lakes, especially the declines in the benthic amphipod diporeia, are believed to have caused significantly lower food quantity and quality for lake whitefish in these regions (POTHOVEN et al. 2001). The decline of diporeia, a historically important, high-energy prey item for lake whitefish, has been associated with the establishment of the invasive zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*). Dreissenid mussels are natives of the Ponto-Caspian region and were introduced into the Great Lakes via the ballast water of commercial shipping vessels (VANDERPLOEG et al. 2002). The exact mechanism by which dreissenid mussels inhibit diporeia abundance is unknown, but a likely explanation is competition for algae (LOZANO et al. 2001, DERMOTT 2001, VANDERPLOEG et al. 2002, NALEPA et al. 2005). Dreissenid mussels filter algae from the water column, and diporeia eat algae that fall to the lake-bottom. It has been hypothesized that as algal consumption by dreissenid mussels increases, the quantity of settled algae available for diporeia consumption decreases, leading to decreased diporeia production. Declines in diporeia biomass (energy rich – 4,429 J/g wet mass) and increases in zebra mussel biomass (energy poor – 1,047-2,478 J/g wet mass of soft tissue) have been proposed to result in a lower quality of prey available to lake whitefish (SCHNEIDER 1992), as these fish now consume less energy-rich items than before the decline of diporeia. As an example, POTHOVEN et al. (2001) found that diporeia in Lake Michigan near Muskegon, Michigan nearly disappeared between 1998 and 2000, resulting in a decrease in the proportion of diporeia, by weight, in lake whitefish diet from 70% to 25%. Thus, with fewer diporeia available in this region, lake whitefish were forced to shift their diet to include dreissenid mussels and other lower energy prey, which made less energy available for growth.

In addition to the effects of changing environmental factors, the potential changes in the genetic make-up of lake whitefish populations have also been implicated in the changes noted in the individual growth of lake whitefish over the past decade. During the 1990's, the harvest of lake whitefish was at all time highs in many parts of the Great Lakes (NALEPA et al. 2005). It has been documented in other fish species that intense fishing efforts over a sustained period of time can exert powerful selective forces that can have lasting effects on the genetics of fish populations, resulting in slower individual growth rates (LAW 2000, CONOVER & MUNCH 2002). The proposed mechanism for this phenomenon is that faster growing fish are harvested more heavily because they reach the minimum length requirement more quickly than slower growing members of their cohort, thus reducing the probability that the faster growing fish will reproduce before being harvested. This ultimately leaves predominately slower growing fish to spawn and produce offspring that on the average exhibit slower growth than before the fishery exerted heavy mortality pressures on the population. Such a phenomenon was demonstrated by CONOVER & MUNCH (2002), who experimentally harvested large, fast growing fish from a population of *Menidia menidia*, which eventually led to lower yields and slower growth of individuals because the "fishery" weeded out faster growing genotypes.

The goal of this study was to evaluate the causes for changing lake whitefish individual growth rates in four regions of the upper Great Lakes which differed in lake whitefish abundance trends, food energy availability, and fishing mortality.

Materials and Methods

Study Sites

We selected four sites in the upper Great Lakes in which to evaluate lake whitefish growth (Figure 2.1). Lake whitefish are found throughout the upper Great Lakes, and stocks are roughly delineated by spawning sites and defined as whitefish management units (BENCE & EBENER 2002). The four sites used in this study correspond to whitefish management units: northwestern Lake Huron (WFH-01), northern Lake Michigan (WFM-03), northeastern Lake Michigan (WFM-05), and eastern Lake Superior (WFS-07). Lake whitefish in these sites are recognized as distinct stocks for fishery management purposes (EBENER et al. 2005). These sites have historically been productive fishing grounds for lake whitefish and differ in lake whitefish abundance, food energy availability, and fishing mortality trends over the past 30 years (Table 2.1). We selected these four sites because they were geographically located near each other, thus experiencing similar climatic variables, while the whitefish populations within these sites are reproductively isolated from one another (BENCE & EBENER 2002).

Data Sources

Information on lake whitefish growth, biomass, and fishing mortality came from data derived from the annual Chippewa/Ottawa Resource Authority (CORA) assessments of the commercial fishery and the statistical catch-at-age (SCAA) models that are used to manage the lake whitefish fisheries in these waters (QUINN & DERISO 1999, EBENER et al. 2005). In particular, SCAA provided us with the abundance and weight-at-age data needed to calculate biomass-at-age statistics for the fishery.

Figure 2.1. Approximate locations of study sites within the Laurentian Great Lakes: 1) northwestern Lake Huron, 2) northern Lake Michigan, 3) northeastern Lake Michigan, and 4) eastern Lake Superior.

Table 2.1. Average instantaneous fishing mortality (F) from 1976 to 2003, mean fishable biomass of lake whitefish from 1990-1999 (EBENER et al. 2005), and diporeia density at depths less than 60 m for the Lakes Huron and Michigan sites and diporeia density for the eastern quarter of Lake Superior (T. NALEPA & S. LOZANO, Great Lakes Environmental Research Lab, NOAA, unpublished data).

	Mgmt.		Fishable	Mean (± SE) *Diporeia* Density (#/m^2)		
Site	Unit	F	Biomass (kg)	1994	2000	2003
NW Lake Huron	WFH-01	0.34	1,477,350	NA	1031 ± 551	457 ± 262
N Lake Michigan	WFM-03	0.35	1,451,495	1961 ± 1904	40 ± 34	NA
NE Lake Michigan	WFM-05	0.21	566,083	2174 ± 2038	142 ± 38	NA
E Lake Superior	WFS-07	0.38	NA	2714 ± 771	881 ± 504	NA

The index of growth we used in this study was the sum of the mean weights-at-age for ages three, four, and five for each cohort. Age-three was the first age we used for the Lakes Michigan and Huron sites, as lake whitefish recruit to the fishery at an average age of three years in these regions, while in Lake Superior, they recruit to the fishery at age-four, on average (BENCE & EBENER 2002). To be legally harvested by commercial fishermen in the upper Great Lakes, lake whitefish must be longer than 430 mm TL (POTHOVEN 2005). As the fishery at each of these three sites is predominantly composed of three age classes, we used ages three, four, and five in Lakes Michigan and Huron and ages four, five, and six in Lake Superior to assess growth and density at each site. These age classes composed at least 75% of the total abundance of recruited fish during the time period evaluated, although fish older than age-ten were infrequently harvested.

Data on diporeia abundance and primary production (phosphorus loadings) for Lakes Michigan, Huron, and Superior came from T. NALEPA and S. LOZANO (Great Lakes Environmental Research Lab, NOAA, unpublished data), MADENJIAN et al. (2002), BRONTE et al. (2003), and DOBIESZ et al. (2005).

Evaluation of factors affecting lake whitefish growth

We evaluated potential causes of the decreased growth of lake whitefish by comparing the observed changes in growth to outcomes predicted by the hypothesized causes. We assessed the hypothesis that lake whitefish abundance changes were responsible for the growth declines in these regions by performing linear regression of each cohort's growth index on the mean total biomass of lake whitefish in the fishery. It was expected that if lake whitefish abundance was causing reduced growth at any given

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location and time, growth would be relatively high when biomass was low for that location and time, while growth would be relatively low when biomass was high.

We evaluated the possibility that food energy availability was responsible for changes in growth dynamics of lake whitefish by assessing several hypotheses. First, we evaluated the impact of the declining diporeia resource on lake whitefish growth by comparing the timing and location of lake whitefish growth declines to the timing and location of declining diporeia abundance. Evidence in support of the hypothesis that diporeia abundance determined lake whitefish growth dynamics would be simultaneous declines of diporeia abundance and lake whitefish growth. We also evaluated the effects of declining primary productivity on lake whitefish growth rate. Evidence in support of the primary production hypothesis would be decreasing lake whitefish growth during declines in phosphorus loadings into the upper Great Lakes (MADENJIAN et al. 2002, DOBIESZ et al. 2005).

We evaluated the hypothesis that changes in lake whitefish population genetics led to slower growing fish by determining if growth declines in these fish were most evident at sites where fishing mortality was highest and least evident where fishing mortality was lowest. This pattern would be consistent with what would be predicted for lake whitefish growth based on this hypothesis because the four study sites represent four largely non-interbreeding stocks of lake whitefish (BENCE & EBENER 2002).

We evaluated the impact of climate-related variables on lake whitefish growth dynamics by analyzing the timing of declining lake whitefish growth. While the four sites occur in three different Great Lakes, they are spatially close enough together that they should be exposed to similar air temperatures and wind speeds, both of which have

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been shown to affect year class strength (BROWN et al. 1993), which in turn affects growth via intraspecific competition for food (BIDGOOD 1973, HEALEY 1980). Evidence in support of the hypothesis that climatic conditions are the key drivers in lake whitefish growth would be a decline in lake whitefish growth at all four sites at the same time, as only weather variables, which are density independent, would be expected to have the same impact at all sites, at the same time. We also used data on ice cover, wind speed, and air temperature (ASSEL 2003, NOAA 2005) to evaluate this hypothesis because we expected strong year classes when ice cover, wind speeds, and spring temperatures were favorable for maximum egg survival (BROWN et al 1993).

Results and Discussion

Climate variables and lake whitefish abundance

At all four sites, lake whitefish growth was found to decline starting with the 1991 year class and remained low thereafter (Figure 2.2). Of the hypotheses listed in this study, only the influence of climate variables was expected to cause the same pattern in growth at all four sites, at the same time. As such, we believe that climate variables are the key factors driving the decreased growth observed in these fish during this time period. Interestingly, there was no significant relationship between abundance of fish in the fishery and individual growth rates at any of the sites (Table 2.2). Of the four sites, the highest percentage of variation in growth rate that could be explained by abundance was only 19% (northern Lake Michigan).

The mechanism by which climate variables affected the growth of lake whitefish in the upper Great Lakes is likely through the development of year class strength and its

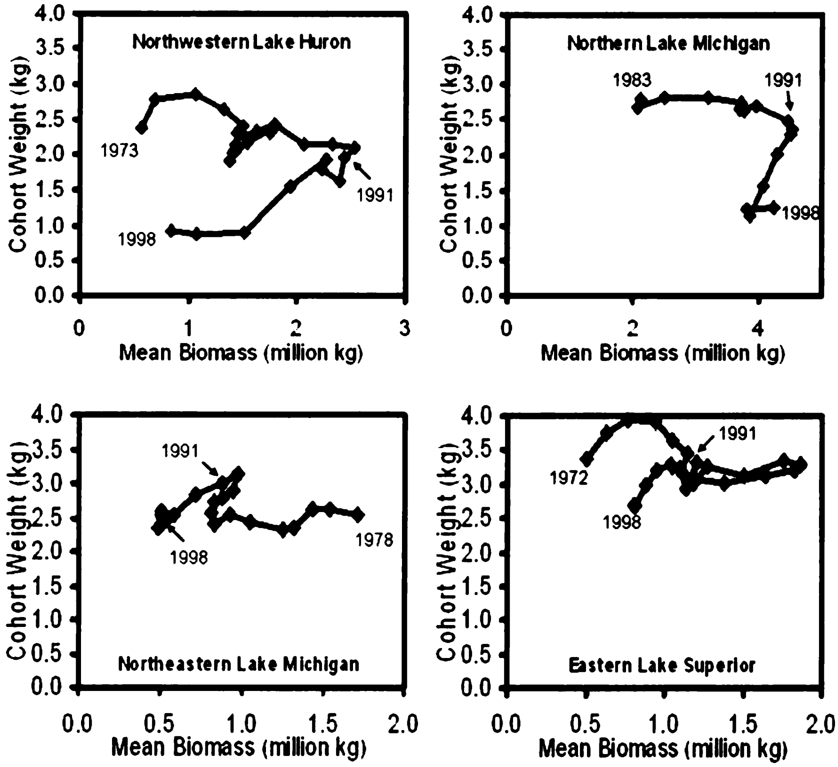

Figure 2.2. Plots of growth index (sum of the mean weights-at-age for the three youngest recruited ages) against mean biomass in time. Dates correspond to the first, last, and 1991 year classes.

Table 2.2. Results of linear regression of growth index on biomass and changes in growth index between the 1991 and 1998 year classes.

	Regression			Growth Index		
Site	R^2	Slope	P	1991	1998*	% change
NW Lake Huron	0.008	-0.09	0.67	2.0	0.9	-53%
N Lake Michigan	0.193	-0.34	0.09	2.5	1.2	-50%
NE Lake Michigan	0.000	-0.01	0.94	3.0	2.5	-18%
E Lake Superior	0.028	-0.15	0.42	3.2	2.7	-16%

* WFS-07 data only goes to the 1997 year class, so it was substituted for 1998.

relationship to density dependent growth. The 1991 year class was one of the strongest year classes in the past 20 years across Lakes Michigan, Huron, and Superior (M. EBENER, unpublished). In lake whitefish, strong year classes are generally a function of favorable climatic conditions in the winter and early spring, which impact egg survival and larval growth and survival, respectively. FREEBERG (1985) found that larval survival of lake whitefish was higher when ice formed before the first winter storms occurred over the spawning area because the ice reduced wind-generated currents and allowed eggs to successfully incubate and hatch in sub-optimal rearing habitats. Spring warming before hatching is important, as rapid warming contributes to favorable planktonic food resources for larval lake whitefish, which sustain good growth and survival during the critical period (LJUNGREN 2002), thus making for the establishment of a large year class (BROWN et al. 1993). Weather data from the National Oceanic and Atmospheric Administration (NOAA) indicated that the timing of early winter ice formation and wind conditions were not especially favorable for a strong 1991 year class, but that May temperatures were warmer than average during 1991 (Table 2.3, ASSEL 2003, NOAA 2005). Warm air temperatures in May suggest that spring water temperatures may have risen relatively rapidly, which would favor the development of a strong year class due to very positive larval growth and survival dynamics (BROWN & TAYLOR 1992). The development of this strong year class in 1991 resulted in a high density of young lake whitefish, which in turn negatively impacted individual growth rates of this, and successive, cohorts. The fact that growth rates of lake whitefish were generally not affected by biomass of adult lake whitefish but were affected by climatic conditions

Table 2.3. Ice, wind, and mean May air temperature (°C) conditions during years of low, moderate, and high recruitment of lake whitefish as estimated by BROWN et al. (1993). The long-term average May air temperature was 9.7 °C.

Year	Ice[a]	Wind[b]	Temperature
Low Recruitment			
1976	9-Jan	12	8.7
1982	7-Jan	10	13.4
Moderate Recruitment			
1973	5-Jan	8	7.9
1983	15-Jan	10	7.4
High Recruitment			
1977	22-Dec	13	12.9
1991	9-Jan	18	13.2

[a] Date when 40% ice cover first occurred

[b] Number of days of two-day average wind speed above 10 knots prior to the formation of 40% ice cover.

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suggests that growth rates were determined by year class strength, before the fish were recruited to the fishery.

It is difficult to predict the effects that global warming could have on year class strength and individual growth rates of lake whitefish because warmer temperatures would cause later ice formation, which would tend to decrease egg survival in marginal habitats, thereby potentially reducing year class strength. However, the warmer climatic conditions would also result in better larval food resources in the spring, which would tend to increase the growth and survival of larval lake whitefish, thereby potentially increasing year class strength. The relative importance of ice cover/wind speed and spring warming rates in determining year class strength of lake whitefish may be site-dependent. BROWN et al. (1993), in a study that compared an index of lake whitefish recruitment to weather conditions over a 24-year time period, found that the influence of ice cover and wind speed on lake whitefish recruitment was stronger than the influence of spring warming rates in Big Bay de Noc, Lake Michigan, but that the opposite was true near Naubinway, Lake Michigan. As such, it is unclear at this time what the overall effect of global warming would be on lake whitefish population abundance and growth dynamics in the upper Great Lakes.

Food energy availability

The original decline in lake whitefish growth in the 1990's could not be attributed to declining diporeia densities because the timing of declining growth of these fish did not coincide with the timing of declining diporeia. At all four sites, the growth index for lake whitefish started to decline with the 1991 year class, when diporeia were still relatively abundant in the upper Great Lakes (Table 2.1). As such, our study does not

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support the hypothesis proposed by other researchers (POTHOVEN et al. 2001, HOYLE 2005, NALEPA et al. 2005) that declining diporeia abundances were responsible for declines in lake whitefish growth observed during the mid to late 1990's in the Great Lakes. However, it is possible that the changes in food base of the Great Lakes may be responsible for the continued relatively slow growth and reduced lipid content of lake whitefish throughout the past decade (WRIGHT & EBENER 2006, this issue). This decline in diporeia in the latter half of the 1990's likely exacerbated the already poor growing conditions in these areas due to high competition for food among an abundant lake whitefish population. Such a scenario would lead to intense density dependent growth suppression, something that we observed in all regions evaluated. The fact that growth remained low at all four sites even in later year classes, some of which were below average in density, may be evidence that low diporeia densities, while not responsible for the initial collapse of lake whitefish growth rates, are inhibiting their recovery.

Our analysis does not support the hypothesis that declines in primary production have affected lake whitefish growth. MADENJIAN et al. (2002) showed that phosphorus loadings to Lake Michigan generally declined from the 1970's to 1995, and most of this decline occurred early in this time span, while DOBIESZ et al. (2005) showed that phosphorus loadings to the main basin of Lake Huron decreased during the 1970's and have remained low ever since. In contrast, growth of lake whitefish in the Lakes Michigan and Huron sites did not decline through the time period coinciding with the reduction in phosphorus levels, but rather decreased abruptly starting with the 1991 year class (Figure 2.2). Additionally, lake whitefish growth declined at the same time in Lake

Superior as it did in Lakes Michigan and Huron, even though phosphorus loadings have been relatively low and stable there over the past century (BRONTE et al. 2003).

Population genetics

In our study, there was no evidence in support of the hypothesis that the slower growth rates of lake whitefish in the regions studied were related to changes in the genetics of these populations. During the period of study, fishing mortality rates were similar for the northwestern Lake Huron, northern Lake Michigan, and eastern Lake Superior sites, but were lower in northeastern Lake Michigan (Figure 2.3), the latter area having been closed to commercial harvest of lake whitefish from the 1950's to the late 1970's (EBENER 2002). Thus, if growth dynamics were solely determined by the genetics of these fish, the northeastern Lake Michigan fish would be expected to exhibit no or a lesser decline in growth than the other three sites. Instead, we found that lake whitefish in Lake Superior exhibited the smallest decline in their growth over the time studied, yet had the highest fishing mortality (Table 2.2).

One additional hypothesis for the declining growth of lake whitefish in the upper Great Lakes is that disease or parasites were impacting the bioenergetics of these populations (PICKERING 1993). While this hypothesis cannot be totally eliminated by the data we analyzed, neither parasitism nor disease appear to be the main cause of declining growth index, as excessive symptoms of parasite or disease infection were not reported by the commercial fisheries or assessment biologists during this time.

Summary

Given the spatial and temporal patterns in lake whitefish growth in the areas of the upper Great Lakes studied, it appears that climatic variables and density dependent

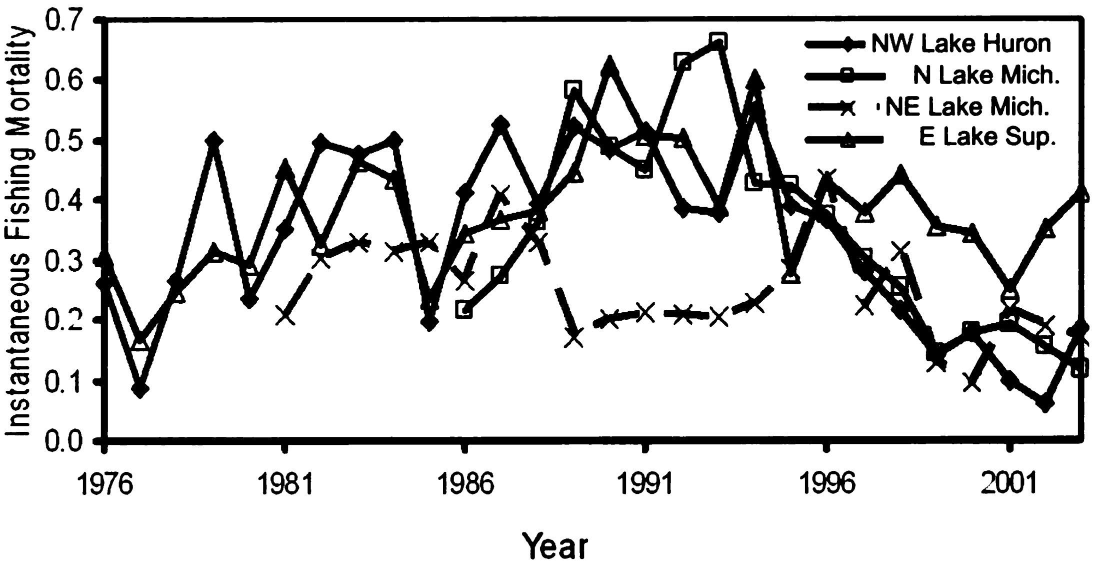

Figure 2.3. Historical fishing mortalities, averaged for all recruited ages, at each of the four sites.

growth dynamics were responsible for the decline in lake whitefish growth. This decline began with the development of a very strong 1991 year class and was exacerbated by a significant decline in the high energy prey item, diporeia, toward the latter part of the 1990's, which appears to have prevented the recovery of lake whitefish growth rates in spite of reduced lake whitefish abundance (POTHOVEN et al. 2001, HOYLE 2005, NALEPA et al. 2005). As such, it appears that the carrying capacity for lake whitefish in the upper Great Lakes has been diminished due to a changing food web caused by invasive species, and managers must implement conservative harvest strategies that protect the viability of these stocks under lower productivity conditions.

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CHAPTER THREE

Changes in growth, condition, and liver weights of lake whitefish (*Coregonus clupeaformis*) in the upper Laurentian Great Lakes between 1986-87 and 2003-05

INTRODUCTION

Lake whitefish (*Coregonus clupeaformis*) are harvested from the Laurentian Great Lakes with large mesh trap nets and gill nets (Bence and Ebener 2002). These fish support the single largest and most valuable commercial fishery in the these waters, accounting for approximately 40% of total weight and value of fish harvested from the Great Lakes in 2002 (Daniels 2003).

In recent years, concern has been expressed about declining growth and condition of lake whitefish in many regions of the upper Great Lakes (Figure 3.1, Madenjian *et al.* 2002, Pothoven *et al.* 2001, Mohr and Ebener 2005). Growth of lake whitefish has been shown to be directly related to the amount of food available per fish, and density dependent changes in growth occur because of changes in lake whitefish abundance or forage availability (Bidgood 1973, Healey 1980, Mills *et al.* 1998). As such, two of the more commonly suggested causes of declines in lake whitefish growth in the Great Lakes have been increases in lake whitefish density and decreases in the density of the amphipod, *Diporeia* spp., an energy-rich and historically important part of the lake whitefish diet (Nalepa *et al.* 2005).

Lake whitefish abundance is currently high relative to 20 years ago in many parts of the upper Great Lakes. Annual yield of lake whitefish, a surrogate measure of

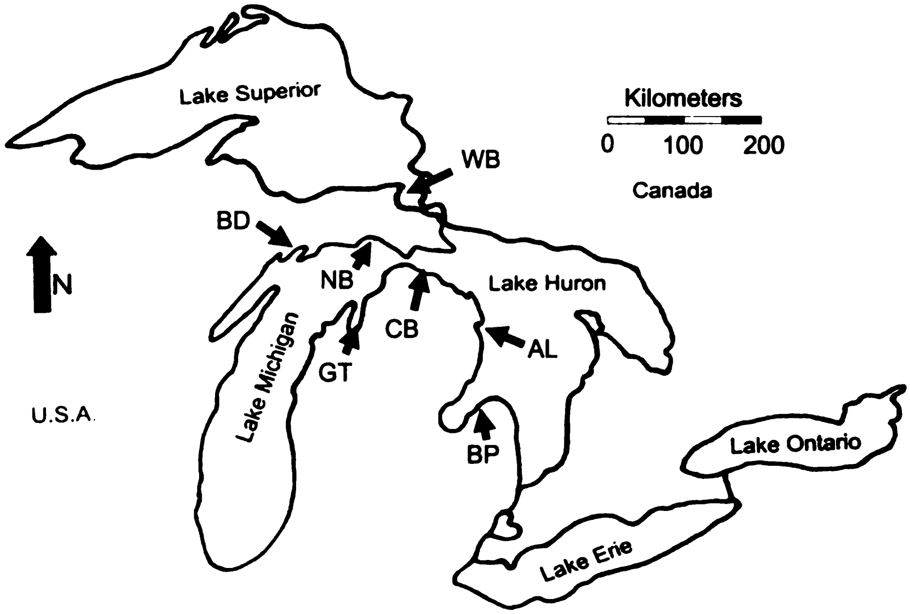

Figure 3.1. Map of the Great Lakes with study sites. AL=Alpena, BD=Big Bay de Noc, BP=Bay Port, CB=Cheboygan, GT=Grand Traverse Bay, NB=Naubinway, WB=Whitefish Bay

abundance, increased from a low of less than 1.5 million kg in 1977 to a high of over four million kg in 1998 in waters of northwestern Lake Huron, northern and eastern Lake Michigan, and southeastern Lake Superior (Figure 3.1). In contrast, lake whitefish abundance during the 1950's and 1960's was less than half of current numbers due to the effects of invasive species, overexploitation, and habitat degradation (Nalepa *et al.* 2005).

While lake whitefish abundance increased in the upper Great Lakes, forage availability also changed. From 1980 to 1993, primary production decreased in nearshore waters of Lake Michigan because of stricter water quality standards, which resulted in reduced nutrient input into the Great Lakes, thus contributing to the decreased abundance of benthic invertebrates, including diporeia (Madenjian *et al.* 2002). Additionally, food-web changes due to invasive species, especially dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*), have been correlated with declines in diporeia, resulting in lower food quantity and quality for lake whitefish (Pothoven *et al.* 2001). Furthermore, declines in the abundance of diporeia have been associated with reduced growth and condition of lake whitefish in Lake Michigan (Pothoven *et al.* 2001) and Lake Ontario (Hoyle 2005).

The exact mechanism by which dreissenid mussels inhibit diporeia abundance is unknown, but a likely explanation is via competition for algae (Nalepa *et al.* 1998, Nalepa *et al.* 2000, Dermott 2001, Lozano *et al.* 2001, Nalepa *et al.* 2001, Vanderploeg *et al.* 2002). Dreissenid mussels filter algae from the water column, and diporeia eat algae that settle to the lake-bottom. It has been hypothesized that as algal consumption by dreissenid mussels increases, the quantity of algae available for diporeia consumption decreases, thereby reducing diporeia production. Thus, declines in the biomass of the

relatively energy rich diporeia (4,429 J/g wet mass) and increases in the biomass of the relatively energy poor dreissenid mussels (1,047-2,478 J/g wet mass of soft tissue) have lowered the quality of prey available to lake whitefish (Schneider 1992). This change in lake whitefish diet has been demonstrated near Muskegon, Michigan (Lake Michigan), where diporeia nearly disappeared between 1998 and 2000, with the result being that the proportion, by weight, of lake whitefish diet comprised by diporeia declined from 70% to 25% (Pothoven *et al.* 2001). With fewer diporeia available, lake whitefish shifted their diet to include dreissenid mussels and other lower energy prey (e.g., chironomids, zooplankton), resulting in an observed decrease in somatic growth. Pothoven (2005) discovered a similar trend in small (<430 mm) lake whitefish during the late 1990's in southeastern Lake Michigan, where diporeia went from 57% to 1% (dry weight) of their diet.

The combined effects of increased lake whitefish abundance and decreased high energy prey sources would be expected to contribute to reduced growth and condition. The goal of this study was to determine the combined influence of changes in lake whitefish and diporeia densities on lake whitefish growth and condition. The specific objectives were to evaluate the changes in length-at-age, body weight-at-length, and liver weight-at-length in seven regions of the upper Great Lakes that have exhibited different combinations of changes in lake whitefish and diporeia densities and to determine the relative importance of lake whitefish and diporeia densities in determining the growth and condition of female lake whitefish.

METHODS

Study sites

Growth and condition were assessed at seven locations in the upper Great Lakes (Figure 3.1). These locations correspond to seven lake whitefish management units in the three upper Great Lakes: Alpena (WFH-05), Bay Port (WFH-07), Big Bay de Noc (WFM-01), Cheboygan (WFH-01), Grand Traverse Bay (WFM-05), Naubinway (WFM-03), and Whitefish Bay (WFS-07) (Bence and Ebener 2002). These sites were chosen because they have experienced different directions and magnitudes of changes in lake whitefish abundance and diporeia density since the 1980's (Table 3.1) and because lake whitefish growth and condition had been assessed in these management units in 1986 and 1987, a time prior to the establishment of dreissenid mussels in these regions.

Sampling

Lake whitefish females were collected from the commercial fishery during the spawning season (late October and early November) in 1986, 1987, 2003, 2004, and 2005. Most fish were purchased from the local fish processing facilities where commercial operators sell their catch, while some fish from the Big Bay de Noc, Cheboygan, and Naubinway sites were provided by other fisheries researchers who were using trap nets to collect lake whitefish for a mark-recapture study. Workers at fish processing facilities process each fisherman's catch separately and know the timing and location of each fisherman's catch. Target sample sizes were 40 to 50 randomly selected, mature females from each location.

Table 3.1. Estimated lake whitefish abundances and diporeia densities at the study sites. Lake whitefish data were provided by M. Ebener (Chippewa Ottawa Resource Authority, unpublished data, 2005) and T. Goniea (Michigan Department of Natural Resources, unpublished data, 2004). Diporeia data were provided by T. Nalepa (NOAA, Great Lakes Environmental Research Lab, unpublished data, 2004) and Scharold et al. (2004).

	Past			Present			Percent Change in Density	
	Lake Whitefish	Diporeia		Lake Whitefish	Diporeia			
Location	Abundance[a]	Year(s)	Density (#/m^2)	Abundance[b]	Year	Density (#/m^2)	Lake Whitefish	Diporeia
Alpena	459 kg/net lift	1972	4,637 - 11,259	550 kg/net lift	2000	7 - 4,204	20%	-75%
Naubinway	9.0 kg/m^2	1994, 1995	1,000 - 2,000	21.5 kg/m^2	2000	0	138%	-100%
Bay Port	82 kg/net lift	1972	3,232 - 7,252[c]	168 kg/net lift	2000	0	104%	-100%
Big Bay De Noc	134 kg/net lift	NA	NA	201 kg/net lift	2000	0	50%	NA
Cheboygan	15.0 kg/m^2	1972	4,637 - 11,259[d]	5.3 kg/m^2	2000	0 - 2,000	-64%	-75%
Grand Traverse Bay	4.8 kg/m^2	1994, 1995	5,000 - 6,000	2.1 kg/m^2	2000	0	-56%	-100%
Whitefish Bay	11.7 kg/m^2	1973, 1994	350, 2714	4.8 kg/m^2	2000	881 ± 504[e]	-59%	0%

[a] Mean kg per trap net lift from 1985 to 1987 for Alpena and Big Bay de Noc, mean kg per trap net lift from 1986 to 1987 for Bay Port, and kg/m^2 for 1987 as estimated by statistical catch at age models for Naubinway, Cheboygan, Grand Traverse Bay, and Whitefish Bay.

[b] Mean kg per trap net lift from 2001 to 2003 for Alpena and Big Bay de Noc, mean kg per trap net lift from 2001 to 2002 for Bay Port, and kg/m^2 for 2003 as estimated by statistical catch at age models for Naubinway, Cheboygan, Grand Traverse Bay, and Whitefish Bay.

[c] Sample location at mouth of Saginaw Bay.

[d] Alpena values applied to Cheboygan.

[e] Mean ± standard deviation for eastern quarter of Lake Superior.

The fish were transported, on ice, back to Michigan State University campus, where total length (mm) and wet weight (g) were recorded and reproductive condition was recorded as either ripe or running. Running fish, those that very easily lost eggs when squeezed, were not used in condition analysis because not all eggs were present in the fish at time of capture. Fish were sampled and processed on the same day that they were harvested.

I compared growth and condition of lake whitefish at each site during two time periods, 1986-87 and 2003-05. I back-calculated length-at-age using scale annuli, fit von Bertalanffy curves with t_0 set to zero, and plotted growth curves (Quinn and Deriso 1999). Condition was described with weight-at-length, with plumper fish having better condition (Anderson and Neumann 1996), and with liver weight (Strange 1996, Dutil and Lambert 2000). The liver stores energy reserves, thus a smaller liver suggests that a fish has lower energy reserves (Dutil and Lambert 2000), which could be as a result of low amounts of food energy available per fish. I compared both measures of condition using ANCOVA, with total body or liver wet weight as the dependent variable, time as the categorical variable, and total length as the covariate. If there was no time by length interaction for a given site, the interaction term was dropped and ANCOVA was run again to test for the time effect.

RESULTS

Growth

The average age at which female lake whitefish reached the minimum legal length (432 mm) increased from 1986-87 to 2003-05 at all sites (Table 3.2), suggesting slower

Table 3.2. Average age (in years) at which female lake whitefish reached the minimum legal length (432 mm) at each site during the two time periods.

Site	1986-87	2003-05
Alpena	3.6	5.9
Naubinway	3.1	5.5
Bayport	2.9	5.0
Big Bay de Noc	4.5	5.3
Cheboygan	4.0	5.6
Grand Traverse Bay	4.6	5.1
Whitefish Bay	3.7	4.8

growth rates during the current time period. The average increase was 1.6 years, with the largest increase observed at Naubinway, where average age at the minimum legal length increased from 3.1 to 5.5 years of age. This change in growth rate was further evidenced by evaluating the von Bertalanffy parameter, K, which was significantly lower (t-test, $p < 0.05$) during 2003-05 than during 1986-87 at all sites (Table 3.3). The values of K observed at each site decreased from a range of 0.25-0.65 in 1986-87 to 0.15-0.21 in 2003-05. While growth rates were lower in 2003-05 than in 1986-87 at all sites, L_∞ was significantly higher (t-test, $p< 0.05$) at all sites during 2003-05. Additionally, length-at-age of fish older than age-7 during 2003-05 was observably higher than that of similarly aged fish during 1986-87 at Cheboygan, Grand Traverse Bay, and Whitefish Bay (Figure 3.2).

Condition

Condition, as described by total body wet weight-at-length, was significantly different between the two time periods at all sites except Grand Traverse Bay (Figure 3.3). Mean weight-at-length was consistently lower in 2003-05 than in 1986-87 at Alpena, Bayport, Cheboygan, and Naubinway. Mean weight-at-length was higher for most lengths in 2003-05 than in 1986-87 at Whitefish Bay. Mean liver weight-at-length was significantly lower during 2003-05 at Bayport but significantly higher in 2003-05 at Cheboygan, Naubinway, and Whitefish Bay (Figure 3.4). At Grand Traverse Bay, liver weight-at-length was higher in 2003-05 than in 1986-87 for fish smaller than 550 mm.

Table 3.3. Von Bertalanffy growth parameters (K and L_∞), their standard errors, and the number of fish used to back-calculate length at age.

	1986-87					2003-05				
Site	K	SE	L_∞	SE	n	K	SE	L_∞	SE	n
Alpena	0.36	0.02	594	9	73	0.16	0.02	707	35	50
Naubinway	0.25	0.01	632	12	121	0.21	0.02	651	24	99
Bayport	0.42	0.02	614	7	93	0.18	0.02	724	31	45
Big Bay De Noc	0.65	0.04	496	7	77	0.18	0.01	690	24	50
Cheboygan	0.33	0.02	554	10	61	0.18	0.01	702	29	72
Grand Traverse Bay	0.34	0.02	574	7	100	0.15	0.01	758	23	101
Whitefish Bay	0.32	0.02	623	10	35	0.17	0.01	762	18	96

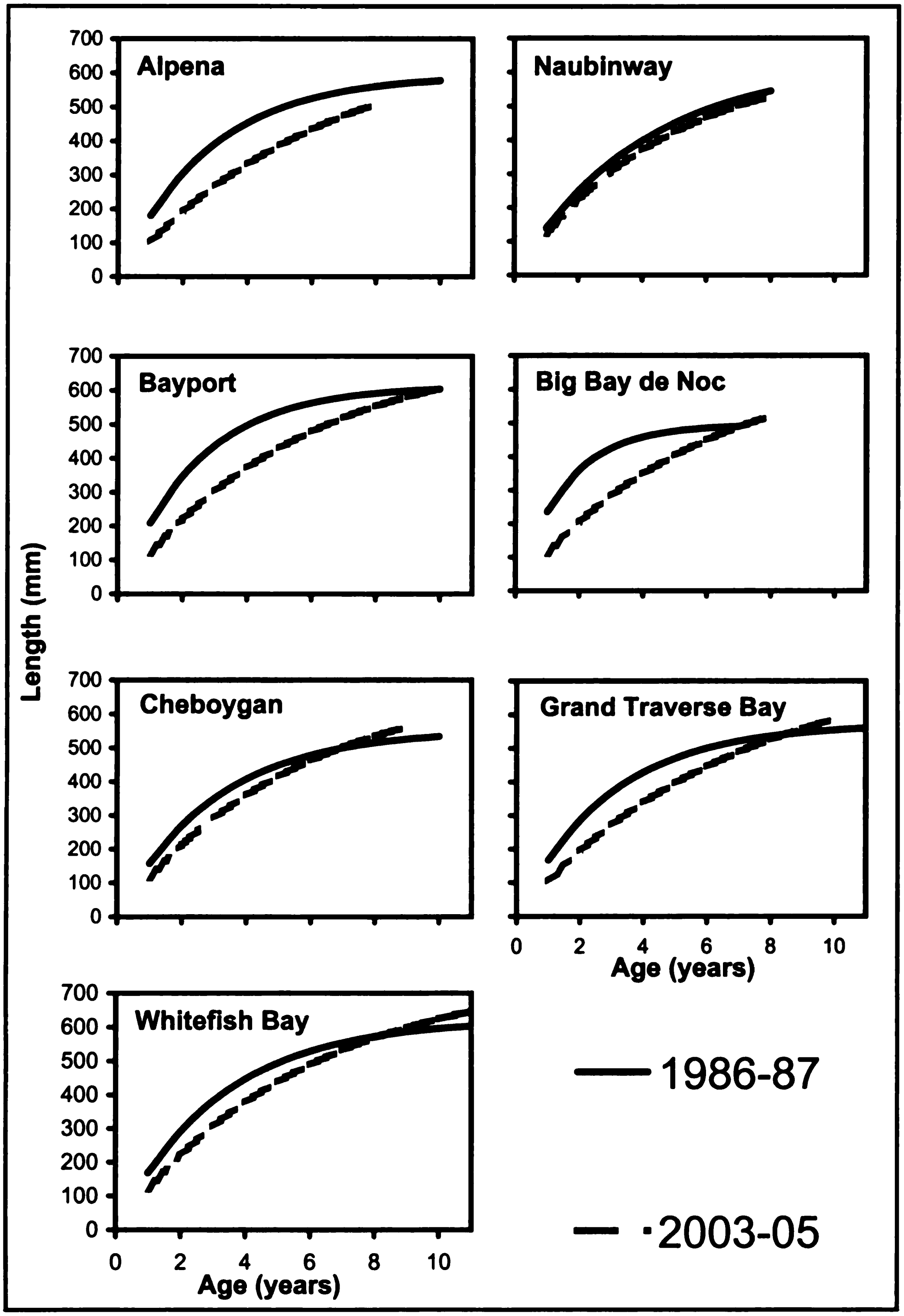

Figure 3.2. Von Bertalanffy growth curves for lake whitefish during the two time periods.

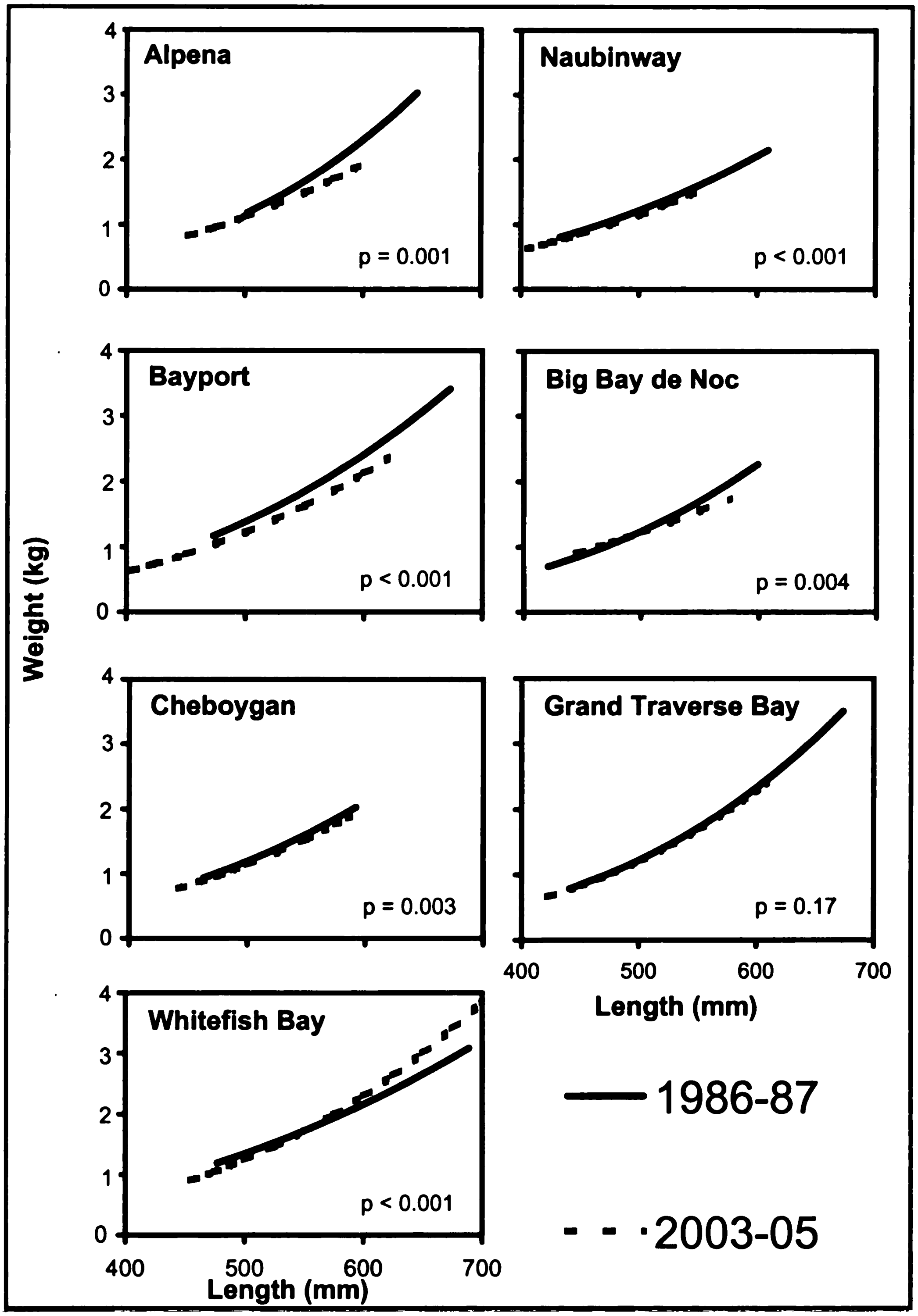

Figure 3.3. Mean total weight-at-length during the two time periods with p-values for the time effect in ANCOVA.

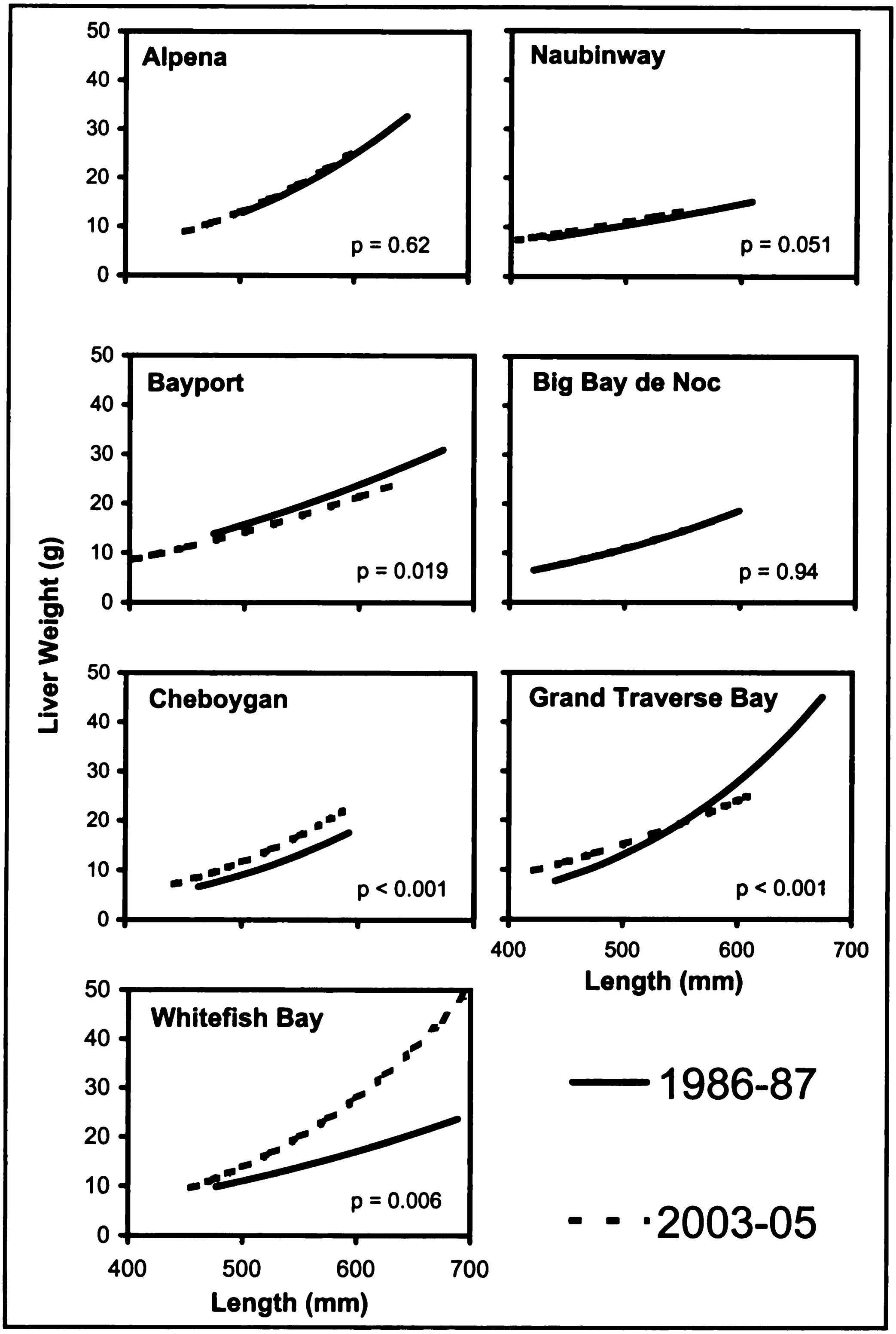

Figure 3.4. Liver weight-at-length of lake whitefish during the two time periods with p-values for the time effect in ANCOVA.

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Environmental changes

Between the two time periods for which lake whitefish growth and condition were evaluated, lake whitefish and diporeia densities changed in varying ways at the sites sampled (Table 3.1). Lake whitefish density increased at Alpena, Big Bay de Noc, Bayport, and Naubinway, while it decreased at Cheboygan, Grand Traverse Bay, and Whitefish Bay. It was unclear what changes if any occurred in diporeia density at Big Bay de Noc due to insufficient data. However, diporeia density decreased at all other sites in Lakes Michigan and Huron, where dreissenid mussels had become established between 1987 and 2003. Whitefish Bay, where dreissenid mussels had not become established, did not exhibit a decrease in diporeia abundance between the two time periods.

DISCUSSION

Growth rate (K) was lower at all sites in 2003-05 than in 1986-87, and lake whitefish reached the minimum legal length of 432 mm at older ages in 2003-05 than in 1986-87 at all sites. The fact that growth rate decreased to similar values ranging from 0.15-0.21 at all sites suggests that a density independent factor, such as climate, has acted on all sites. Kratzer et al. (2006) observed a decrease in the growth rate of lake whitefish at four sites in the upper Great Lakes (northwestern Lake Huron, northern and northeastern Lake Michigan, and eastern Lake Superior) and theorized that climatic conditions that were favorable for survival of eggs and larvae of lake whitefish allowed

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for the production of strong year classes, which in turn reduced growth rates through intraspecific competition for food (Brown and Taylor 1992, Brown *et al.* 1993).

While growth rate was likely affected by density of pre-recruit lake whitefish, the length of fish older than age-7 and condition may be more sensitive to density of lake whitefish that are recruited to the fishery. Length-at-age of fish older than age-7 increased from 1986-87 to 2003-05 at the three sites where lake whitefish density decreased between those two time periods, and decreased at the four sites at which lake whitefish density increased between the two time periods (Table 3.4). Whitefish Bay was the only site at which diporeia densities did not decrease, but lake whitefish densities decreased through time (Table 3.4). The increase in condition of longer fish observed at Whitefish Bay is evidence that changes in lake whitefish density alone, regardless of changes in diporeia density, can affect condition of lake whitefish. Estimates of lake whitefish abundance used in this study included only those fish that were recruited to the fishery. The relationship we observed between lake whitefish abundance and the length-at-age of older fish and condition suggests that intraspecific competition among lake whitefish that are recruited to the fishery can reduce the lengths of older fish and the condition of fish that are recruited to the fishery. These findings agree with those of Bidgood (1973) and Healey (1980), who observed that lake whitefish growth was higher for highly exploited lake whitefish populations, which had lower densities of fish that were recruited to the fishery.

Additionally, there was evidence that diporeia density alone can affect condition of lake whitefish. At Grand Traverse Bay, there was no change in condition of lake whitefish between the two time periods, despite the decrease in lake whitefish and

Table 3.4. Direction of change in lake whitefish and diporeia densities and length-at-age of fish older than age-7, total weight-at-length, and liver weight-at-length of lake whitefish between 1986-87 and 2003-05. (↑↓ indicates changes were not consistent for all lengths)

Site	Lake Whitefish	Diporeia	Length at Age-8+	Weight at Length	Liver Weight at Length
Alpena	↑	↓	↓	↓	no change
Naubinway	↑	↓	↓	↓	↓
Bayport	↑	↓	↓	↓	↓
Big Bay de Noc	↑	NA	↓	↑↓	no change
Cheboygan	↓	↓	↑	↓	↑
Grand Traverse Bay	↓	↓	↑	no change	↑↓
Whitefish Bay	↓	no change	↑	↑↓	↑

diporeia densities. An increase in growth and condition would be expected as the lake whitefish population declined, but there was no change in condition between 1986-87 and 2003-05. As such, it is likely that the disappearance of diporeia that occurred between 1986-87 to 2003-05 prevented lake whitefish from increasing their condition even though intraspecific competition decreased. Reduced growth and condition of lake whitefish associated with declines in diporeia densities have been reported for Lakes Michigan, Huron, and Ontario (Pothoven *et al.* 2001, Nalepa et al. 2005). Although we observed evidence for a relationship between diporeia density and lake whitefish condition, we did not observe a relationship between diporeia density and lake whitefish growth.

Grand Traverse Bay provides additional evidence that lake whitefish density is more important than diporeia density in determining overall growth dynamics and condition of lake whitefish. Lake whitefish density decreased by 56% and diporeia density decreased by 100% between the two time periods, resulting in no change in lake whitefish condition. If these changes in lake whitefish and diporiea densities actually counterbalanced one another, the fact that the smaller percent change was observed in lake whitefish density suggests that lake whitefish condition was more sensitive to lake whitefish density than to diporeia density.

Liver weight was not a good indicator of fish condition in this study. Liver weight-at-length and body weight-at-length were significantly correlated for all sites and times combined ($p < 0.001$), but changes in liver weight-at-length were not related to changes in lake whitefish condition as described by weight-at-length (Table 3.4). Additionally, changes in liver weight-at-length were not related to changes in lake whitefish or diporeia densities in any consistent way (Table 3.4). Dutil and Lambert

(2000) and Lambert *et al.* (2000) were able to use livers weights to describe condition of Atlantic cod (*Gadus morhua*) that were starved for food. It is possible that fish must be very close to starvation before liver size starts to noticeably decrease. Thus, although growth and condition of lake whitefish in the upper Great Lakes have been affected by lake whitefish and diporeia densities, they do not show any physiological evidence of suffering severe starvation at this time.

Conclusion

Growth and condition of lake whitefish have changed over the past twenty years in the upper Great Lakes. These changes have been affected by changes in the densities of lake whitefish and diporeia. Growth rates were lower in 2003-05 than in 1986-87 at all sites. We found lake whitefish growth and condition to be more sensitive to changes in lake whitefish density than to changes in diporeia density. Despite recent changes to the Great Lakes foodweb that have occurred as a result of dreissenid mussel invasion, managers may be able to affect lake whitefish condition through harvest regulations that result in reduced lake whitefish densities. Managers likely have less control over lake whitefish growth because growth rate is likely affected by the abundance of pre-recruits, which can not be readily manipulated by managers. While length-at-age of lake whitefish older than age-7 may be related to the abundance of lake whitefish that are recruited to the fishery, fish older than age-7 make up a small proportion of the harvest (typically 25% or less), and high fishing mortalities would further reduce this proportion.

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CHAPTER FOUR

At the time of submission of this dissertation, this chapter was in review for publication in the Journal of Great Lakes Research. The formatting follows the guidelines for the Journal of Great Lakes Research, but I did renumber the tables and figures for this dissertation.

Changes in Fecundity and Egg Lipid Content of Lake Whitefish (*Coregonus clupeaformis*) in the Upper Laurentian Great Lakes between 1986-87 and 2003-05

Jud F. Kratzer[1*], William W. Taylor[1], and Mark Turner[2]

[1]*Department of Fisheries and Wildlife, Michigan State University,*
13 Natural Resources Building, East Lansing, MI 48824 U. S. A.

[2]*Department of Natural Resources, Division of Wildlife,*
Lake Erie Fisheries Unit, Sandusky, OH 44870 U. S. A.

*Corresponding author: Jud Kratzer, Michigan State University, 12 Natural Resources Building, East Lansing, MI 48824 USA, Phone 1-(517)-353-6697, Fax 1-(517)-432-1699, email: kratzer1@msu.edu

William Taylor, Michigan State University, 14 Natural Resources Building, East Lansing, MI 48824 USA, Phone 1-(517)-353-3048, Fax 1-(517)-432-1699, email: taylorw@msu.edu

Mark Turner, Department of Natural Resources, Division of Wildlife, Lake Erie Fisheries Unit, Sandusky, OH 44870 USA, email: Mark.Turner@dnr.state.oh.us

Running title: Fecundity and egg lipids in lake whitefish

ABSTRACT. Lake whitefish (*Coregonus clupeaformis* Mitchill), an important commercial species in the Laurentian Great Lakes, have experienced decreased growth and condition in parts of the upper Great Lakes over the past 20 years. Increases in lake whitefish density and decreases in the density of *Diporeia* spp., an energy rich and historically important part of the lake whitefish diet, have been implicated in the recent declines in lake whitefish growth and condition. The goal of this study was to describe lake whitefish fecundity, egg lipid content, and total ovary lipid content in selected regions of Lakes Huron, Michigan, and Superior in 1986-87 and 2003-05, two time periods with different lake whitefish and diporeia densities. Under conditions of high lake whitefish density and low diporeia density, female lake whitefish in the upper Laurentian Great Lakes generally produced fewer eggs. Egg lipid content, however, increased at all sites from 1986-87 to 2003-05, regardless of changes in lake whitefish or diporeia densities. Total ovary lipid content and lake whitefish abundance were inversely related, while there was no significant relationship between total ovary lipid content and diporeia density. Lake whitefish abundance had a stronger influence on the amount of energy that lake whitefish invested in egg production than did diporeia density, thus managers may be able to influence the reproductive dynamics of lake whitefish in the upper Great Lakes through harvest regulations that affect population density.

INDEX WORDS: *Coregonus clupeaformis*, *Diporeia*, fecundity, egg lipid, ovary

INTRODUCTION

Lake whitefish (*Coregonus clupeaformis* Mitchill) are native to northern North America, with the southernmost portion of their range being the Laurentian Great Lakes (Hubbs and Lagler 2004). These fish are generally deepwater benthivores, preferring to live in depths of 15 to 50 m during much of their life history (Walden 1964, Ihssen *et al.* 1981, Pothoven 2005), migrating to the shallows in late October and November to spawn over gravel or cobble substrate in less than 5 m of water (Hart 1930, Taylor and Freeberg 1984). Today, lake whitefish support the single largest and most valuable commercial fishery in the Laurentian Great Lakes, accounting for approximately 40% of total weight and value of fish harvested from these waters in 2002 (Daniels 2003). Annual yield of lake whitefish over the past 30 years has increased from a low of less than 1.5 million kg in 1977 to a high of over four million kg in 1998 in waters of northwestern Lake Huron, northern and eastern Lake Michigan, and southeastern Lake Superior (Fig. 4.1).

Recently, concerns have arisen regarding declining growth and condition of lake whitefish in many regions of the upper Great Lakes (Fig. 4.2). During the 1990's, declining growth rates of lake whitefish were observed in northern Lake Michigan (Madenjian *et al.* 2002), southern Lake Michigan (Pothoven *et al.* 2001), and Lake Huron's main basin (Mohr and Ebener 2005). Previous studies by Bidgood (1973), Healey (1980), and Mills *et al.* (1998) demonstrated that lake whitefish growth is directly related to the amount of food available per fish, and that density dependent changes in growth occur because of changes in lake whitefish abundance or forage availability. The two most commonly suggested causes of the recent declines in lake whitefish growth and condition observed in the upper Great Lakes have been increases in lake whitefish

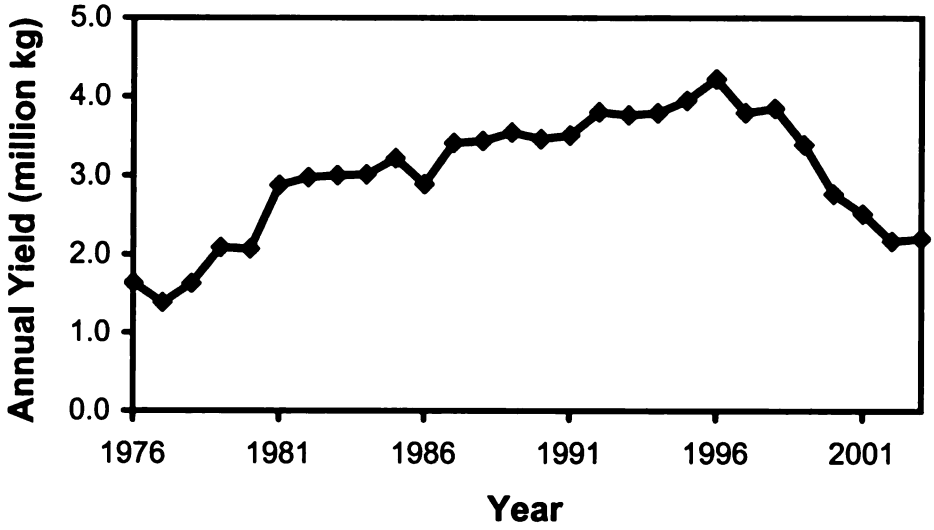

Figure 4.1. Annual yield of lake whitefish from selected waters of northwestern Lake Huron, northern and eastern Lake Michigan, and southeastern Lake Superior 1976 to 2003, all gear types combined.

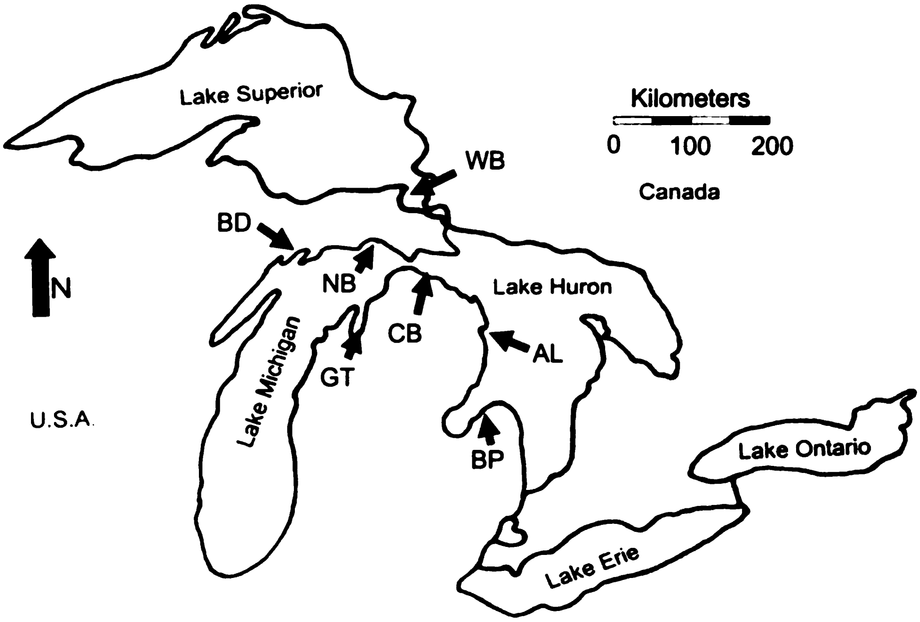

Figure 4.2. Map of the Great Lakes with study sites. AL=Alpena, BD=Big Bay de Noc, BP=Bay Port, CB=Cheboygan, GT=Grand Traverse Bay, NB=Naubinway, WB=Whitefish Bay

density and decreases in the density of *Diporeia* spp., an energy-rich and historically important component of the lake whitefish diet (Nalepa *et al.* 2005). Diporeia are thought to be suppressed through competition for food with the invasive dreissenid mussels, which were first discovered in the Great Lakes ecosystem in 1988 (Vanderploeg *et al.* 2002).

Decreases in growth and condition of lake whitefish could affect their population dynamics and future production via changes in the number of eggs produced or the amount of energy incorporated in each egg, both of which are important to the development of year class strength (Brown and Taylor 1992). Fecundity is directly related to fish growth, as larger fish produce more eggs (Bell *et al.* 1977, Jude *et al.* 1987, Smale 1988). Fish with higher quality diets, which allow for higher growth rates and condition, produce a larger number of eggs that are generally of higher quality (Leray *et al.* 1985, Hardy *et al.* 1990, Corraze *et al.* 1993). These eggs have larger lipid stores, which provide more energy to developing larval fish than lower quality eggs, and thus allow for faster somatic growth and a longer time interval before larval fish must begin consuming prey exogenously (Brown and Taylor 1992). A key point in the early life history of lake whitefish occurs during the critical period when larval fish switch from endogenous to exogenous food (Cushing 1990). During the egg and early larval stages, the developing fish depends on endogenous energy, which is stored as yolk by the mother. Once this endogenous food supply is expended, the larval fish must switch to eating exogenous food, such as zooplankton (Taylor and Freeberg 1984), thus sufficient exogenous food of the right size and nutritional value is critical for larval survival (Brown and Taylor 1992). Larvae from larger, more yolk-filled eggs have a survival advantage because they are able to survive longer before they need to switch to exogenous food in early spring, when food conditions are often unpredictable due to weather conditions (Taylor and Freeberg 1984). Additionally, more food types are available to these larvae because of their larger size (Miller *et al.* 1988, Brown and Taylor 1992).

The goal of this study was to describe the reproduction dynamics of lake whitefish through an assessment of their fecundity, egg lipid content, and total ovary lipid content in seven areas of the upper Great Lakes (Fig. 4.2) in 1986-87 and 2003-05; two time periods with differing densities of these fish and their primary food source, diporeia. The locations from which lake whitefish were sampled corresponded to seven whitefish management units that have been defined by the managers of these fisheries: Alpena (WFH-05), Bay Port (WFH-07), Big Bay de Noc (WFM-01), Cheboygan (WFH-01), Grand Traverse Bay (WFM-05), Naubinway (WFM-03), and Whitefish Bay (WFS-07) (Bence and Ebener 2002).

MATERIALS AND METHODS

Female lake whitefish were collected from the commercial fishery during the spawning season in late October and early November in 1986, 1987, 2003, 2004, and 2005. In general, 40 to 50 randomly selected dead female lake whitefish were purchased from the local fish processing facilities where commercial operators sell their catch. Workers at these facilities process each fisherman's catch separately and know the timing and location of each fisherman's catch.

Lake whitefish collected from the commercial fishery were transported, on ice, back to Michigan State University campus, where total length (mm), wet weight (g), and reproductive condition were recorded. Fish were sampled and processed on the same day that they were harvested. Ovaries were removed and frozen in air-tight freezer bags for later determination of fecundity and egg lipid content. Running fish, those that very easily lost eggs when squeezed, were not used in fecundity calculations because not all eggs were present in the fish at time of capture, but eggs from these fish were used in lipid content analysis.

Fecundity

In the laboratory, fecundity of each fish was determined. The ovaries were first thawed and weighed, providing the mass composite of each fish's eggs (wet weight, g). Then, three sub-samples of 100 eggs were counted, and wet weight (g) of each sub-sample was determined. Fecundity was calculated for each fish (total number of eggs per female) based on total ovary wet weight and average wet weight per 100 eggs (Crim and Glebe 1990). These 100-egg samples were dried at 70-80°C for 24 hours and weighed to determine dry weight of eggs. As fecundity increases with fish size (Strange 1996), analysis of covariance (ANCOVA) was used to compare fecundities during the two time periods with log(fecundity) as the dependent variable, time period (1986-87 or 2003-05) as the categorical variable, and log(length) as the covariate.

Egg and Ovary Lipid Content

Egg lipid content was measured using a Foss Tecator Soxtec HT6 solvent extraction system (AOAC International 2000). For each fish, three 0.7 g sub-samples of dried eggs, which had been finely ground, were placed in individual cellulose thimbles for lipid analysis. Petroleum ether was used to dissolve the lipids from the sub-samples and deposit them in pre-weighed aluminum cups. After the ether was evaporated, the weight of lipids in the sample was calculated by subtracting the original weight of the cup from the final weight. We calculated the mg of lipid per egg based on the mean dry weight per egg and mean percent lipid in the dried egg samples. Lipid content of eggs during the two time periods was compared with a two sample t-test because we found no significant correlation between fish size and egg lipid content.

Finally, to assess the total amount of energy that fish invested in egg production, the number of eggs in each female was multiplied by the amount of lipid per egg to calculate the total amount of lipid in the ovaries of each fish. The two time periods were compared using ANCOVA with log(g of lipid in the ovary) as the dependent variable, time period as the categorical variable, and log(length) as the covariate.

RESULTS

For all sites and dates combined, lake whitefish fecundity ranged from a minimum of 1,689 eggs in a 631 mm female from Whitefish Bay in 1986-87, to a maximum of 107,548 eggs in a 640 mm female from Grand Traverse Bay in 1986-87. Mean fecundity was lowest (15,265) at Cheboygan in 1986-87 and highest (39,699) at Bay Port during the same time period. The only site where fecundity increased significantly from 1986-87 to 2003-05 was Whitefish Bay (Fig. 4.3), where the average fecundity of a 550 mm fish (based on ANCOVA) increased by 5.7%. Fecundity significantly decreased between the two time periods at Alpena, Bay Port, Big Bay de Noc, and Grand Traverse Bay (Fig. 4.3), where average fecundity of a 550 mm fish

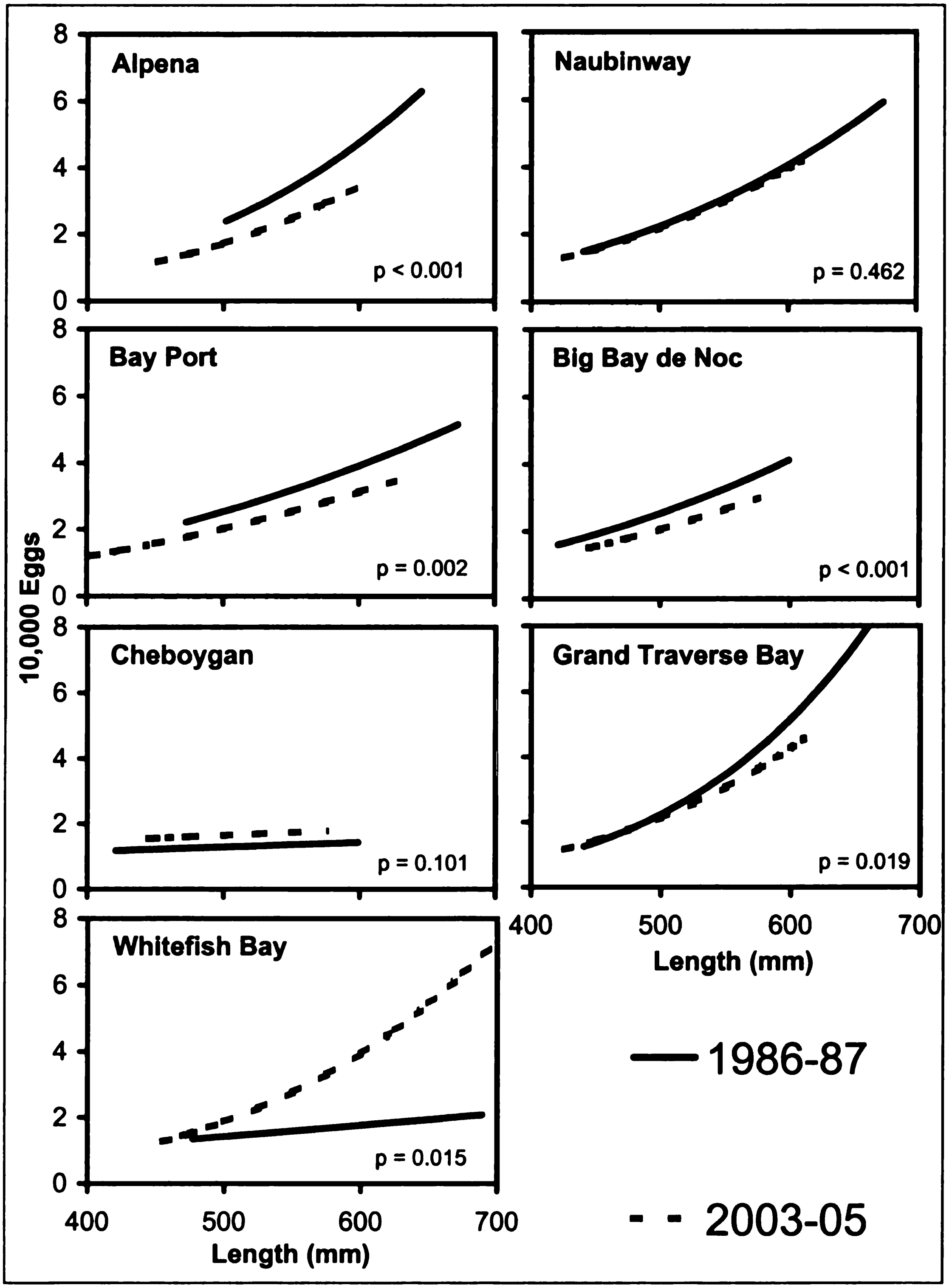

Figure 4.3. Mean fecundity at length of lake whitefish collected from the study sites during 1986-87 and 2003-05 with p-values for time effect in ANCOVA.

decreased by 3.0%, 2.2%, 2.0%, 1.1%, respectively. There was no significant difference between time periods at Naubinway and Cheboygan.

For all sites and dates combined, milligrams of lipid per egg ranged from a minimum of 0.251 mg in a 436 mm female from Naubinway in 1986-87 to a maximum of 0.988 in a 733 mm female from Whitefish Bay in 2003-05. Mean mg lipid per egg was highest at Whitefish Bay in 2003-05 (0.655) and lowest at Naubinway in 1986-87 (0.458, Table 4.1). The amount of lipid per egg was significantly higher for all populations during 2003-05 than in 1986-87 ($p < 0.005$).

The total amount of lipid in the ovaries was significantly lower in 2003-05 than in 1986-87 at Alpena and Naubinway, while it was significantly higher in 2003-05 at Cheboygan, Grand Traverse Bay, and Whitefish Bay. No significant difference between time periods was observed in the lake whitefish sampled at Bay Port or Big Bay de Noc (Table 4.2).

DISCUSSION

Between the two time periods for which we evaluated lake whitefish fecundity and egg lipid content, there were different combinations of changes in lake whitefish and diporeia densities at the different sites (Table 4.3). Lake whitefish density increased at Alpena, Big Bay de Noc, Bay Port, and Naubinway, and it decreased at Cheboygan, Grand Traverse Bay, and Whitefish Bay. Dreissenid mussels have become well established in all of the Great Lakes except Lake Superior between the two time periods (Vanderploeg *et al.* 2002, Scharold et *al.* 2004), and diporeia densities declined between the two time periods at all sites except for Whitefish Bay. As such, lake whitefish in parts of the upper Great Lakes have experienced decreased food energy available per fish

TABLE 4.1. Egg lipid content (mg per egg) of lake whitefish collected during the two time periods with p-values from t-tests.

	1986-87			2003-05			
Site	Mean	St. dev.	n	Mean	St. dev.	n	p
Alpena	0.464	0.052	73	0.569	0.129	86	<0.001
Naubinway	0.458	0.092	121	0.564	0.107	144	<0.001
Bay Port	0.504	0.068	93	0.569	0.162	65	0.003
Big Bay de Noc	0.507	0.069	77	0.606	0.098	88	<0.001
Cheboygan	0.517	0.059	51	0.549	0.118	74	<0.001
Grand Traverse Bay	0.484	0.087	129	0.527	0.093	135	<0.001
Whitefish Bay	0.581	0.067	25	0.655	0.102	137	<0.001

TABLE 4.2. Predicted (ANCOVA) ovary lipid content of a 550 mm fish in 1986-87 and 2003-05 and p-value of time effect in ANCOVA.

	Ovary Lipid Content (g)			
Site	1986-87	2003-05	Percent Change	p
Alpena	15.4	13.3	-14%	0.036
Naubinway	16.1	12.2	-24%	<0.001
Bay Port	15.3	14.5	-5%	0.510
Big Bay de Noc	16.8	16.1	-4%	0.436
Cheboygan	7.9	12.2	54%	0.002
Grand Traverse Bay	16.4	17.9	9%	<0.001
Whitefish Bay	9.4	18.0	91%	<0.001

TABLE 4.3. Estimated lake whitefish abundances and diporeia densities at the study sites. Lake whitefish data were provided by M. Ebener (Chippewa Ottawa Resource Authority, unpublished data, 2005) and T. Goniea (Michigan Department of Natural Resources, unpublished data, 2004). Diporeia data were provided by T. Nalepa (NOAA, Great Lakes Environmental Research Lab, unpublished data, 2004) and Scharold et al. (2004).

	Past			Present			Percent Change	
	Lake Whitefish	Diporeia		Lake Whitefish	Diporeia		in Density	
Location	Abundance[a]	Year(s)	Density (#/m^2)	Abundance[b]	Year	Density (#/m^2)	Lake Whitefish	Diporeia
Alpena	459 kg/net lift	1972	4,637 - 11,259	550 kg/net lift	2000	7 - 4,204	20%	-75%
Naubinway	9.0 kg/m^2	1994, 1995	1,000 - 2,000	21.5 kg/m^2	2000	0	138%	-100%
Bay Port	82 kg/net lift	1972	3,232 - 7,252[c]	168 kg/net lift	2000	0	104%	-100%
Big Bay De Noc	134 kg/net lift	NA	NA	201 kg/net lift	2000	0	50%	NA
Cheboygan	15.0 kg/m^2	1972	4,637 - 11,259[d]	5.3 kg/m^2	2000	0 - 2,000	-64%	-75%
Grand Traverse Bay	4.8 kg/m^2	1994, 1995	5,000 - 6,000	2.1 kg/m^2	2000	0	-56%	-100%
Whitefish Bay	11.7 kg/m^2	1973, 1994	350, 2714	4.8 kg/m^2	2000	881 ± 504[e]	-59%	0%

[a] Mean kg per trap net lift from 1985 to 1987 for Alpena and Big Bay de Noc, mean kg per trap net lift from 1986 to 1987 for Bay Port, and kg/m^2 for 1987 as estimated by statistical catch at age models for Naubinway, Cheboygan, Grand Traverse Bay, and Whitefish Bay.

[b] Mean kg per trap net lift from 2001 to 2003 for Alpena and Big Bay de Noc, mean kg per trap net lift from 2001 to 2002 for Bay Port, and kg/m^2 for 2003 as estimated by statistical catch at age models for Naubinway, Cheboygan, Grand Traverse Bay, and Whitefish Bay.

[c] Sample location at mouth of Saginaw Bay.

[d] Alpena values applied to Cheboygan.

[e] Mean ± standard deviation for eastern quarter of Lake Superior.

as a result of decreased diporeia density and increased lake whitefish density, and these changes could be expected to affect lake whitefish reproduction dynamics.

Smith and Fretwell (1974) found that fish tend to produce fewer, high quality eggs rather than a constant number of lower quality eggs when food energy is limited because this life history strategy maximizes their fitness, or likelihood of passing genetic material onto successive generations. Lake whitefish sampled in this study behaved similarly with respect to fecundity by generally producing fewer eggs during periods of high lake whitefish densities and low diporeia densities (Table 4.4). Similarly, Healey (1978) observed increased fecundity of lake whitefish after exploitation by the fishery reduced population density.

The observed increase in egg lipid content during the current time period, regardless of changes in lake whitefish and diporeia densities, was not expected, and it is possible that increases in egg lipid content could compensate for decreases in fecundity, resulting in no net loss of recruitment. Brown and Taylor (1992) showed that egg lipid content is positively correlated with larval length at hatch and endogenous growth rate, and higher lipid stores allow larval fish to live longer before having to consume external sources of energy. Based on their data, we calculated that the higher lipid content of eggs during 2003-05 should result in significantly larger larvae at the time when they switch from endogenous to exogenous food. While the calculated increase in size of larval lake whitefish from 1986-87 to 2003-05 was statistically significant, it is unclear whether this difference is biologically significant, as the greatest increase in expected length at any site was only 0.16 mm or 1.3% (Naubinway). Additionally, it is unlikely that this change in lipid content has had any observable affect on lake whitefish recruitment because their

TABLE 4.4. Direction of change in lake whitefish and diporeia densities and fecundity, egg lipid content, and total ovary lipid content of lake whitefish between 1986-87 and 2003-05.

Site	Lake Whitefish	Diporeia	Fecundity	Egg Lipid	Ovary Lipid
Alpena	↑	↓	↓	↑	↓
Naubinway	↑	↓	not sig.	↑	↓
Bay Port	↑	↓	↓	↑	not sig.
Big Bay de Noc	↑	no data	↓	↑	not sig.
Cheboygan	↓	↓	not sig.	↑	↑
Grand Traverse Bay	↓	↓	↓	↑	↑
Whitefish Bay	↓	no change	↑	↑	↑

year class strength is largely determined by density independent factors, particularly weather (Taylor and Freeberg 1984, Brown *et al.* 1993).

Lake whitefish abundance appears to have influenced the total amount of lipid in the ovaries of lake whitefish in the upper Great Lakes. The three sites that experienced decreased lake whitefish abundance from 1986-87 to 2003-05 (Cheboygan, Grand Traverse Bay, and Whitefish Bay) had increased total lipid content of the ovaries (Table 4.4). At sites where lake whitefish abundance increased, ovary lipid content decreased (Alpena and Naubinway) or did not change significantly (Big Bay de Noc and Bay Port). Changes in diporeia density were not consistently related to total ovary lipid content, as ovary lipid content increased, decreased, and remained the same at sites where diporeia density decreased (Table 4.4). Especially noteworthy in this case, is Grand Traverse Bay, where total ovary lipid content increased significantly, despite the total disappearance of diporeia.

Conclusion

Reproduction dynamics of lake whitefish changed between 1986-87 and 2003-05 in parts of the upper Great Lakes. Female lake whitefish produced fewer eggs in 2003-05 than in 1986-87 at four sites, and fecundity only increased at one site. Fish at all sites produced eggs with higher lipid content in 2003-05 than they did in 1986-87. It is unclear whether increases in egg lipid content have been high enough to cause an increase in age-0 survival sufficient to compensate for the reduced fecundity that has occurred in parts of the upper Great lakes, although current abundances of lake whitefish remain high, implying high age-0 survival (Brown *et al.* 1993, Nalepa *et al.* 2005). Density of lake whitefish had a stronger influence on the amount of energy that lake whitefish invested in egg production than did diporeia density because ovary lipid content and lake whitefish abundance were inversely related, and this relationship was not affected by changes in diporeia density. Thus, managers may be able to influence the reproductive dynamics of lake whitefish in the upper Great Lakes through harvest regulations.

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CHAPTER FIVE

Summary and Management Implications

Lake whitefish of the upper Great Lakes have experienced changes in growth, condition, fecundity, egg lipid content, and total ovary lipid content between 1986-87 and 2003-05. The overall density of lake whitefish appears to be the dominant causal agent of changes noted in lake whitefish production dynamics over the past two decades, as demonstrated by the declines in lake whitefish growth that began with the unusually strong 1991 year class. This was further substantiated by my findings that lake whitefish abundance influenced their condition and the amount of energy they invested into egg production. Unlike other investigators (i.e., Pothoven et al. 2001, Hoyle 2005, Schneeberger et al. 2005), this study provides only limited evidence that declines in diporeia have affected lake whitefish production dynamics. Although changes in growth, condition, fecundity, and egg and ovary lipid content were not consistently related to changes in diporeia density, the fact that growth rates remain low even in areas where lake whitefish density has declined suggests that declines in diporeia may have lowered the carrying capacity of lake whitefish in the Great Lakes by decreasing the amount of food energy available to them.

Because the density of lake whitefish directly affects their condition, it also affects the marketability of the commercial harvest. If abundance is too high, the fillets produced by harvested fish tend to be smaller, leading to reduced profits and dissatisfaction with the fishery. Managers can reduce the abundance of lake whitefish through harvest regulations that would result in an increase in the condition and marketability of these fish. Managers have less control over lake whitefish growth, as growth rate appears to be more influenced by the abundance of pre-recruits, which is largely determined by density independent factors (i.e., weather conditions).

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