

ECOSYSTEM BASED MANAGEMENT FOR MILLE LACS LAKE, MINNESOTA  
UNDER CHANGING ENVIRONMENTAL CONDITIONS

by

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## Abstract

Single-species and multi-species modelling was employed to seek options for sustainable management of Mille Lacs Lake, the second largest lake within Minnesota, known primarily for its walleye (*Sander vitreus*) fisheries. Managers of the lake face challenges in adapting to changes that include changing temperature of the water body, changing community structure, growing number of piscivorous birds, and an invasion of zebra mussels leading to greater water clarity. The lake experienced a historical decline in the population of cisco (*Coregonus artedii*)—a cold-water stenothermic forage species. Surplus production models of cisco population suggested that temperature explained 36-40% of change in cisco abundance and that the decline in the species was due to a combination of temperature increase and high fishing pressure. To rebuild the depleted stock, I concluded that strong restriction was required on cisco fisheries especially in warmer years.

For multi-species analysis, I built an ecosystem model with the Ecopath with Ecosim (EwE) modelling suite using extensive field data on organism parameters and diet. The EwE model was fitted to abundance and catch data for the period 1985 to 2006. Influence of temperature on the model predictions were simulated by adding temperature data as forcing function in the EwE model. The model was driven forward 25 years to evaluate the ecosystem-wide predictions for prevailing harvesting strategies and other possible fisheries scenarios of interest to the lake managers. The ecosystem model was used to estimate single-species and ecosystem-level reference points for thirteen fished species in the lake with and without including the effects of temperature change. The analysis helped

comparison of ecosystem effects and temperature effects on the estimated reference points. The EwE model successfully forecast most of the changes seen in the lake after the period of fitted-data from 2007 to 2012. The model was extended for evaluation of ecosystem-wide impact of zebra mussels invasion. The model predicted that the mussels population would stabilise in the lake after attaining maximum density. But during this period several species, including the important walleye, could be negatively affected by the filtration of phytoplankton by zebra mussels.

# Preface

A version of Chapter 2 is published. [Rajeev Kumar], Martell, S. J., Pitcher, T. J., & Varkey, D. A. (2013). Temperature-Driven Decline of a Cisco Population in Mille Lacs Lake, Minnesota. *North American Journal of Fisheries Management*, 33(4), 669-681. I worked on the modelling and the writing of the manuscript. Steve Martell helped with building the model structure. Tony Pitcher provided guidance with the writing of the manuscript. Divya Varkey assisted me with the modelling.

I constructed the model presented in Chapter 3. Chapters 4 used the model developed in Chapter 3. Tony Pitcher provided me guidance in building the model and helped me with the layout of the chapters. Tony Pitcher and Minnesota Department of Natural Resource (MNDNR) staffs provided assistance in designing the fisheries scenarios to be evaluated in Chapter 3.

An extended abstract from Chapter 5 is published. [Rajeev Kumar], Varkey, D. A., & Pitcher, T. J. (2014). Simulation of zebra mussels invasion and evaluation of impacts on the Mille Lacs Lake, Minnesota: an ecosystem model, p. 86. In: Steenbeek *et al.* (eds.), *Ecopath 30 Years Conference Proceedings: Extended Abstracts*, pp. 86. Fisheries Centre Research Reports 22(3). University of British Columbia. The modelling in Chapter 5 is an extension of the model developed in Chapter 3. Tony Pitcher and Divya Varkey provided me support with building the simulations and writing the manuscript, while Tom Jones and Eric Jensen from MNDNR provided me the required data used in the model.

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*To my parents*

# 1 Introduction

In this human-dominated world, it's rare to find an ecosystem in its pristine state (Vitousek *et al.*, 1997); most natural ecosystems have several resource management issues that need to be addressed. A coalescence of ecological understanding and modelling approaches may provide answers to questions such as (1) what are the effects of anthropogenic activity, (2) how does the changing environment affect the ecosystems, and (3) how to achieve the management goals of setting fishery yields and quotas while maintaining fish populations and biodiversity, taking into account the effect of environmental changes. Apropos of their restricted boundaries, lakes often serve as ideal locations for modelling; research on lakes has contributed to fundamental understanding of energy flows in the ecosystem (Odum, 1968), trophic cascades (Brett and Goldman, 1996; Carpenter and Kitchell, 1996), and the more recent concept of foraging arena theory (Ahrens *et al.*, 2012; Biro *et al.*, 2004; Walters and Juanes, 1993). The current study is a modelling endeavor towards the holistic aim of sustainable and ecosystem-based management of a lake ecosystem, in particular, Mille Lacs Lake, Minnesota, which is especially valuable for recreational fishing but also provides a fishery for native people. The lake and its management issues are described below.

## 1.1 Study site: Mille Lacs Lake, Minnesota

Mille Lacs Lake (MLL), the second largest lake in Minnesota, is located in Aitkin, Crow Wing, and Mille Lacs counties in the east-central Minnesota (46.23°N, 93.64°W) (Figure 1.1). An Eco-region approach is used by the U.S. Environmental Protection Agency (EPA)

for lake classification; lakes in Minnesota are mainly found in 4 of the 7 eco-regions, namely northern lakes and forests, northern central hardwood forests, western cornbelt plains, and northern glaciated plains. Based on ecoregions classification criteria, Mille Lacs Lake falls under the northern lakes and forests eco-region which typically have lakes with trophic states ranging from oligotrophic to mesotrophic (MPCA, 2014a).

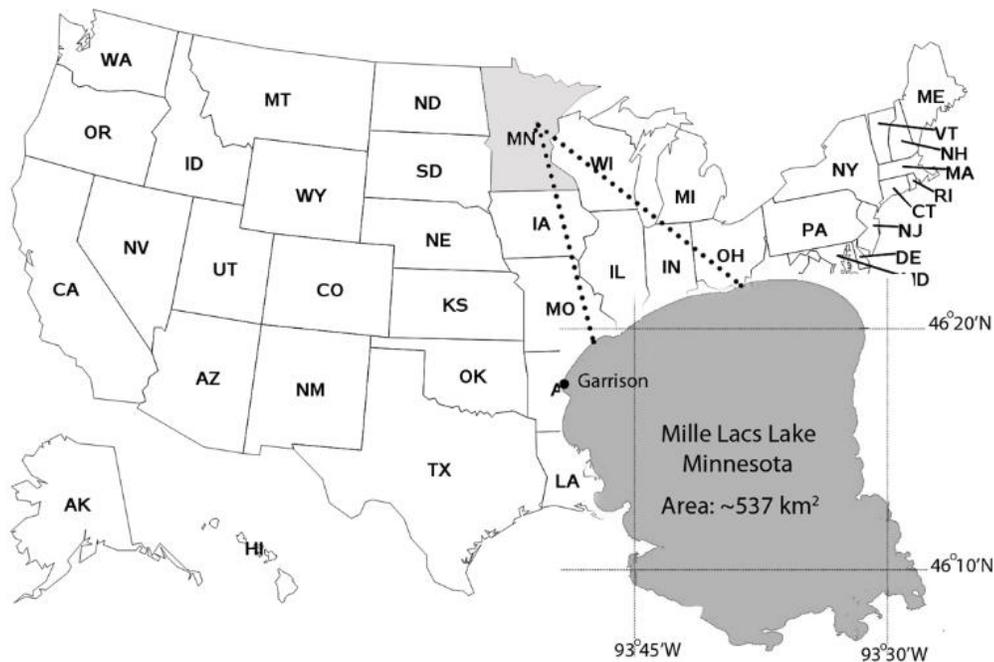


Figure 1.1. Mille Lacs Lake, Minnesota, USA.

*Inset lake map also shows the location of the city of Garrison on the north-west side. (Source: Background US map-generated using SAS/GRAPH map datasets; the inset for Mille Lacs Lake was obtained from Minnesota Department of Natural Resources).*

Mille Lacs is a glacial lake that covers an area approximately 537 km<sup>2</sup> with about 1,080 km<sup>2</sup> of watershed area (Heiskary *et al.*, 1994). It has 14 perennial inlets and single outlet, Rum River, which flows into the Mississippi River. The northern half of the lake has most of the lake's mud flats while the southern half of the lake has more gravel and rock bars. The mean annual water temperature of the lake was estimated as 8.8°C (Bruesewitz, 1995). Maximum

depth of the lake is 12.8 m while average depth is 8.8 m. This is a polymictic lake and has virtually no thermocline due to wind-driven mixing of water freely from top to bottom.

A large portion of the lake shoreline (137 km) is suitable for walleye (*Sander vitreus*) spawning (Jones, 2006), and the lake is one of the most productive large lakes for walleye fisheries in the state (Radomski, 2003). Apart from walleye, other principal game fish targeted by sport fishers are yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), and muskellunge (*Esox masquinongy*). In addition, largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), rock bass (*Ambloplites rupestris*), burbot (*Lota lota*), bullheads (*Ameiurus* spp.), bowfin (*Amia calva*), common carp (*Cyprinus carpio*), black crappie (*Pomoxis nigromaculatus*), and sunfish (*Lepomis* spp.) are also present in the lake. Yellow perch, cisco (also called tullibee locally) (*Coregonus artedii*), different species of shiners (*Notropis* spp.), darters (*Etheostoma* spp.), and minnows (*Pimephales* spp.) are the main forage fish species of the lake (MNDNR, 1997). A list of fish species used in the model with their scientific names is included in Appendix C.

The lake also has the two islands (Spirit Island and Hennepin Island) which harbor a number of bird species such as double-crested cormorant (*Phalacrocorax auritus*), common tern (*Sterna hirundo*), and two species of gulls (*Larus* spp.)—ring-billed gull and herring gull. Common terns are restricted to Hennepin Island and cormorants to Spirit Island.

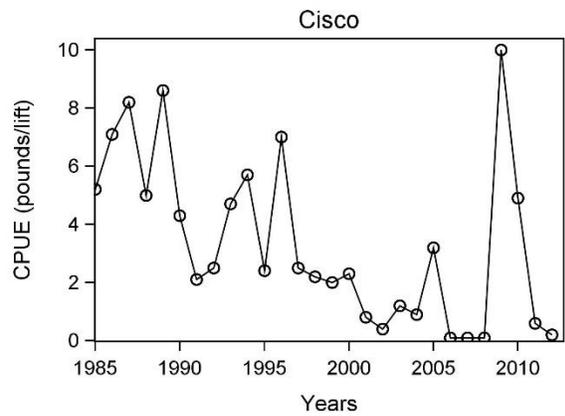
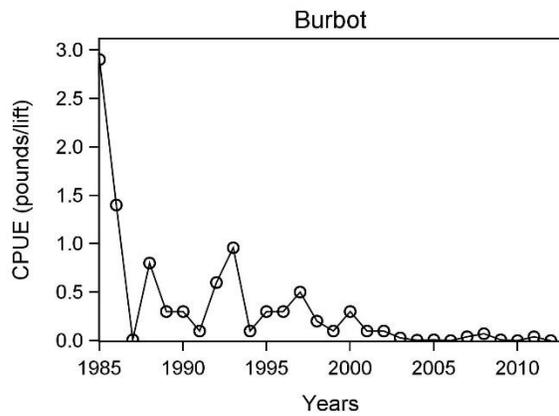
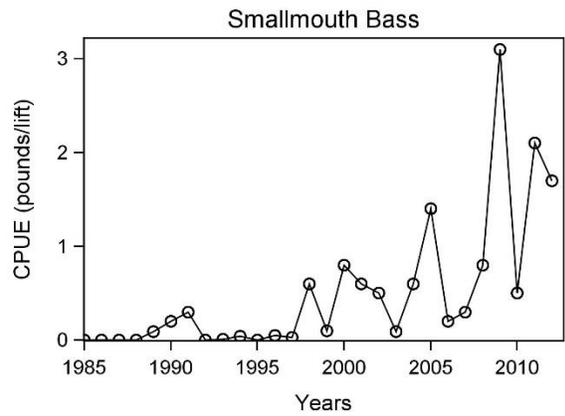
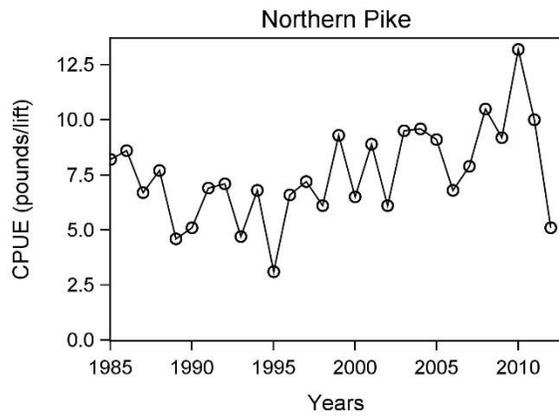
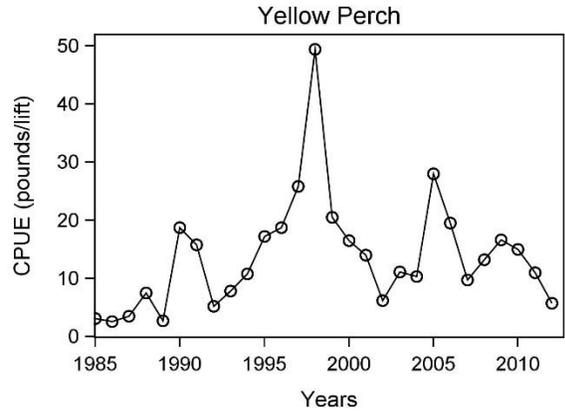
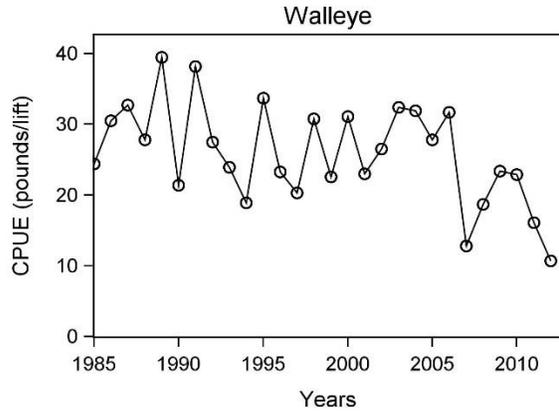
## **1.2 Current management in Mille Lacs Lake**

Current annual monitoring and management of Mille Lacs lake entails the following 7 steps (MNDNR, 1997): “(1) collection and evaluation of biological information as benchmarks of

the status of fish stocks, (2) estimation of abundance of important species, (3) calculation of target harvest levels based on state regulations, (4) decision on tactics to restrict the target harvest levels, (5) monitoring and enforcement of the regulations, (6) protection of critical habitats and reclamation of those lost due to degradation and (7) annual evaluation of management actions”.

Mille Lacs Lake fish populations are monitored by test netting (gill netting, trawling), electro-fishing, tagging, scuba diving and creel survey. Most of the sampling is done in September each year (Jones, 2006). Standard experimental gill nets have 5 panels of following mesh sizes: 0.75 in, 1.0 in, 1.25 in, 1.5 in, and 2.0 in. The gill nets are set overnight at 32 inshore locations, and the data such as catch per unit of effort (CPUE), length and weight of all the fish sampled are recorded (Jones, 2006).

State-licensed anglers and Native American tribal (Mille Lacs Band of the Chippewa/Ojibwe tribe) netters, spearers, and anglers are the two major resource users of the lake (Figure 1.3). Catch quota allocation between them are allocated after evaluation of stock status and target harvest level of important fish. Bag limits, size based restrictions (minimum and maximum size limit or protected slots), gear-based restrictions, seasonal restrictions, night-closures, and no-killing at all are the conventional regulations imposed on fisheries to keep the fishing levels within management targets (MNDNR, 2014) (further details about the lake management is provided in the section “Managing recreational fisheries: walleye” in Chapter 1).



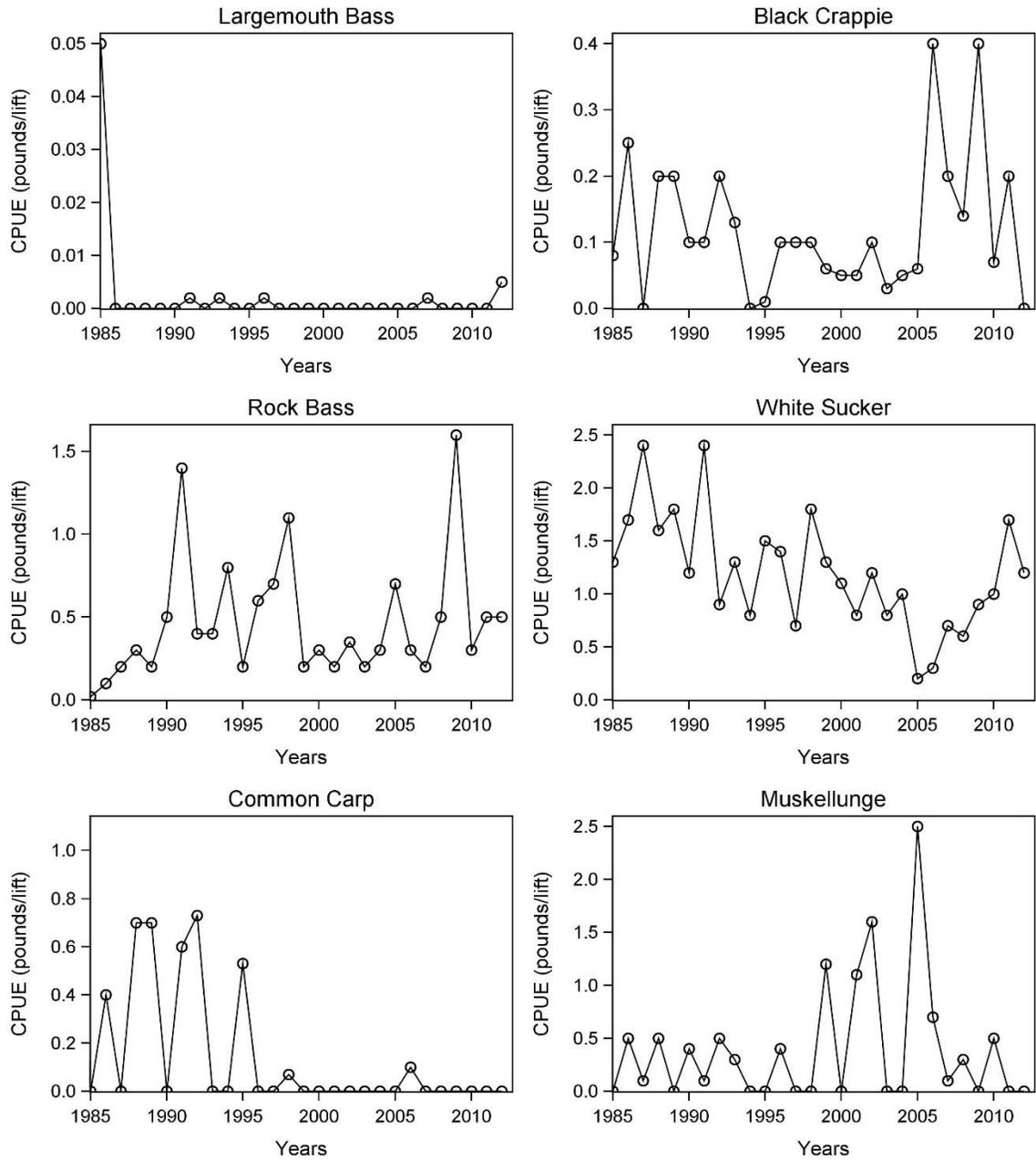
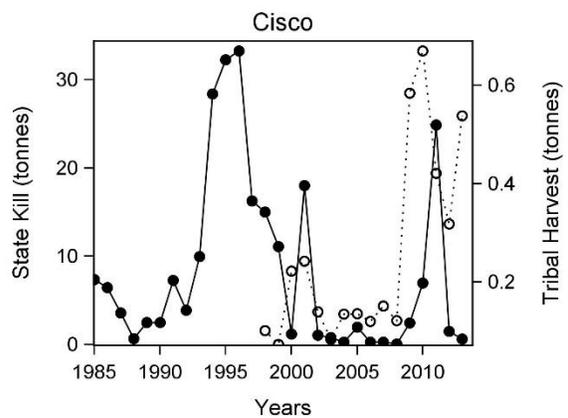
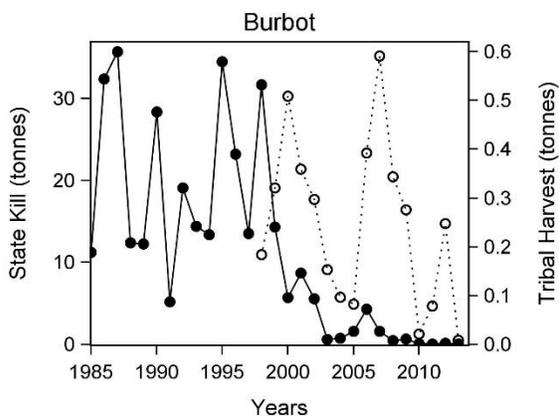
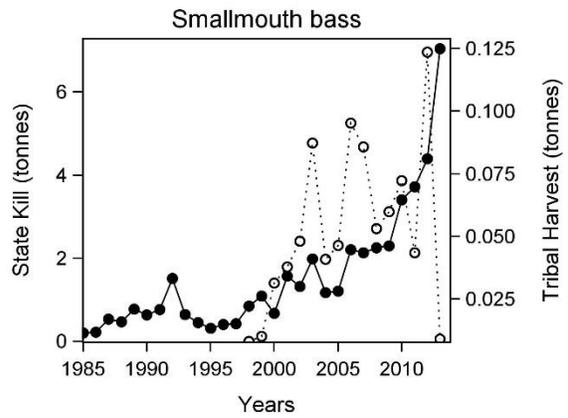
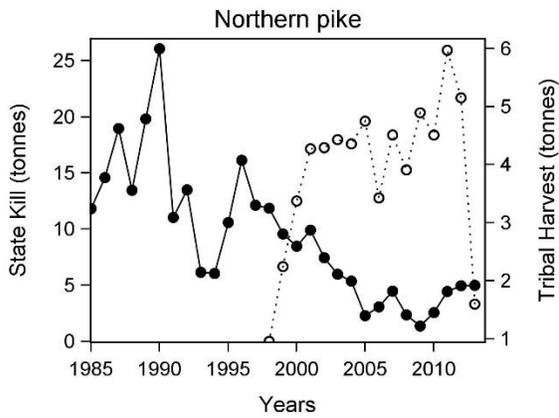
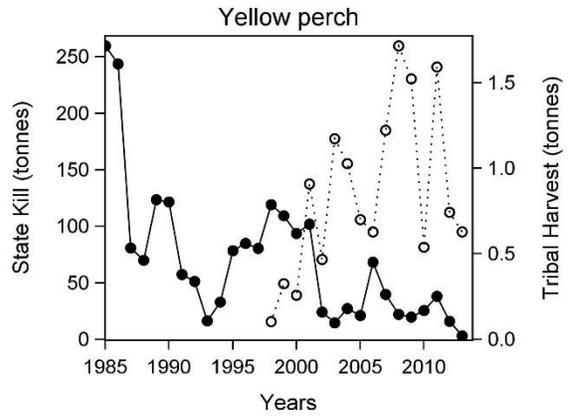
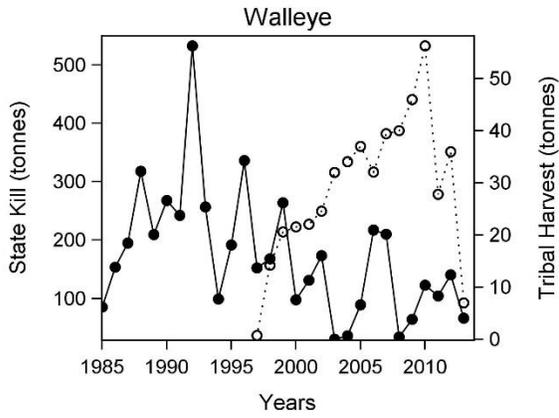
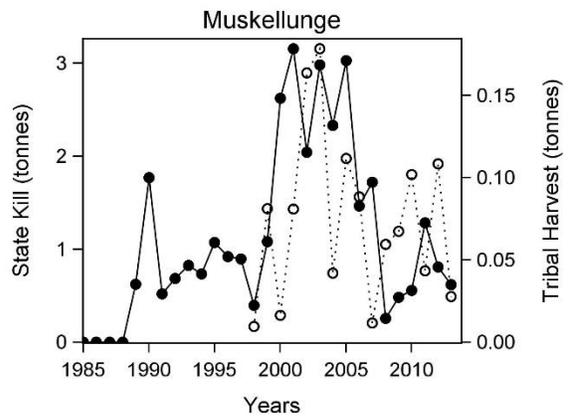
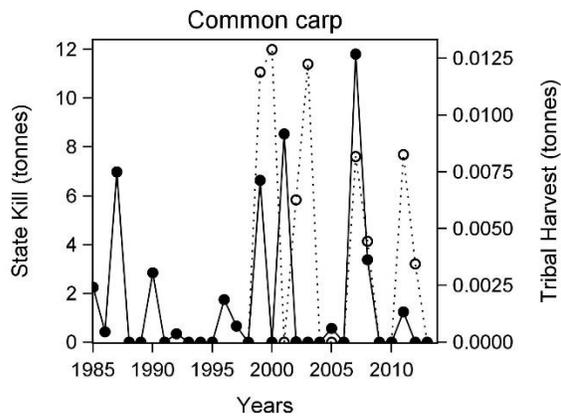
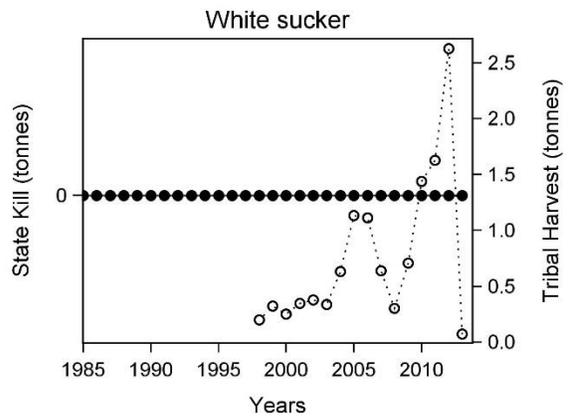
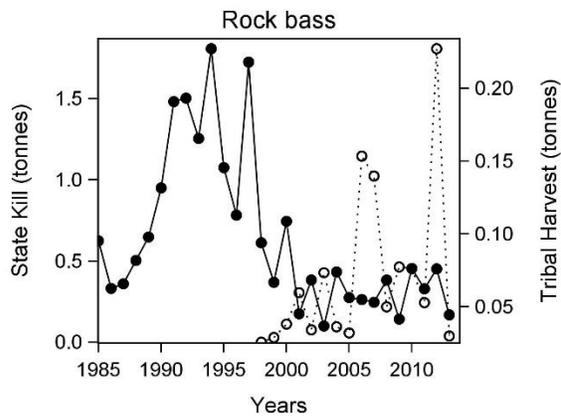
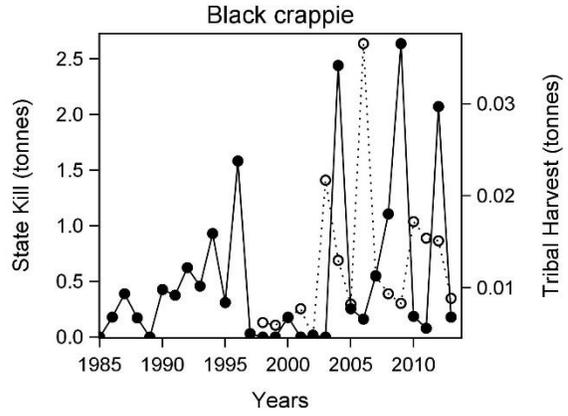
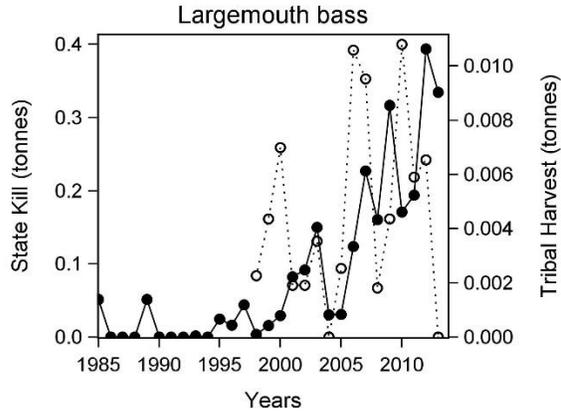


Figure 1.2. Average catch per unit of effort (CPUE) trend from the 32-location assessment gill netting program on Mille Lacs Lake.

—●— State Kill  
 - - -○- - Tribal Harvest





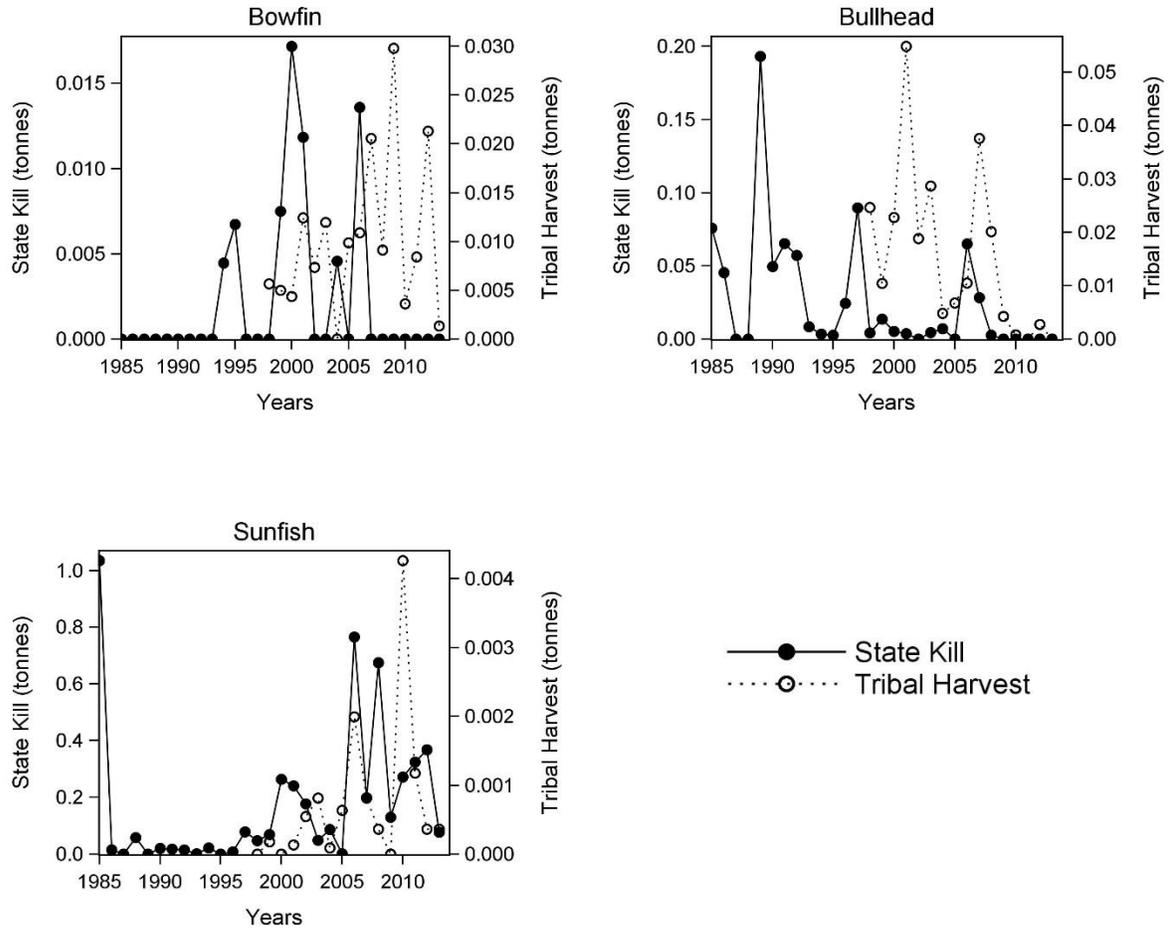


Figure 1.3. Catch time-series of Mille Lacs Lake, Minnesota.

Mille Lacs Lake fisheries are shared between State-licensed anglers and North American native tribes.

### 1.3 Issues in lake management

A prime goal of any kind of fisheries management is to ensure that benefits are maximized within the constraint that fisheries are sustainable, which could be described as taking benefit from any natural resources only up to the level that would allow future generations to take the same level of benefit from the resources. This goal has been articulated in many different ways by different authors. Garcia (2003) states that the Ecosystem Approach to Fisheries (EAF) “recognizes the need to maintain productivity of ecosystems for present

and future generations”. In the 1990s, the main goal of the Great Lakes fisheries managers, closely associated with the managers of Mille Lacs in Minnesota, was to restore the native communities to levels that existed prior to overexploitation, habitat degradation, and sea lamprey invasion (Kitchell *et al.*, 2000); i.e., to restore the degraded system as close as feasible to the historical level and maintain the level is a goal of sustainable management. But another important goal of sustainable management is to prevent and minimise degradation because in the process of degradation, the ecological, social, and economic benefits that can be obtained from an ecosystem decline. Further, restoration from the degraded state has been a daunting task for management authorities and even after spending millions of dollars, in particular because of invasions of organisms to these ecosystems was a major stressor (Smith *et al.*, 2014), in the Great Lakes the success of the “remedial action plans” has been mixed (Makarewicz and Bertram, 1991; Sproule-Jones, 2002). Invasive species and attempts to mitigate the impacts of invading species constrain the optimization of fisheries.

Sustainable management requires a thorough understanding of the interactions within biotic components; between biotic and abiotic components, and human effects on the ecosystem (Sissenwine and Mace, 2003). It is important to identify the ecological, human, and environmental issues that affect those interactions (Griffith *et al.*, 2012).

Over the last 3 decades Mille Lacs Lake has gone through several noticeable changes such as over 90% reduction in the biomass of cisco and burbot, introduction of new species such as Muskellunge in the system, increased abundance of piscivorous birds, and more recently, establishment of zebra mussels, and decline of its most important fish, the walleye (Figure

1.2). Paying attention to these changes and evaluation of their ecosystem-wide impacts are vital in sustainable management planning for Mille Lacs Lake.

In the following sections, I will present a review of some common issues in lakes with reference to the Mille Lacs Lake ecosystem.

### *1.3.1 Environmental change: Rising temperature*

Climate change such as rising temperature can negatively affect water quality (Murdoch *et al.*, 2000) and increasing surface water temperature leading to a reduction in dissolved oxygen (DO) level, a stronger lake stratification and sometimes increased eutrophication (Ficke *et al.*, 2007). Since fish are poikilotherms, elevated water temperature could severely impede their physiological processes. An assessment of impact of climate change on freshwater species in the US found that “suitable thermal habitat” for cold water species would decrease leading to a shrinkage in the distribution of these species and in turn reduce opportunities for recreational fisheries (Jones *et al.*, 2013). Maximum air temperature recorded in the months of July and August near Mille Lacs Lake fluctuated between 29°C and 37°C, and was over 35 °C in several years (NCDC, 2014) (Figure 1.4a). The average temperatures have increased by over 1°C since 1990: average temperature between 2000-2005 was 0.6 °C higher than the previous decade (1990-1999), with a further increase of 0.44 °C during 2006-2013 period (Figure 1.4b).

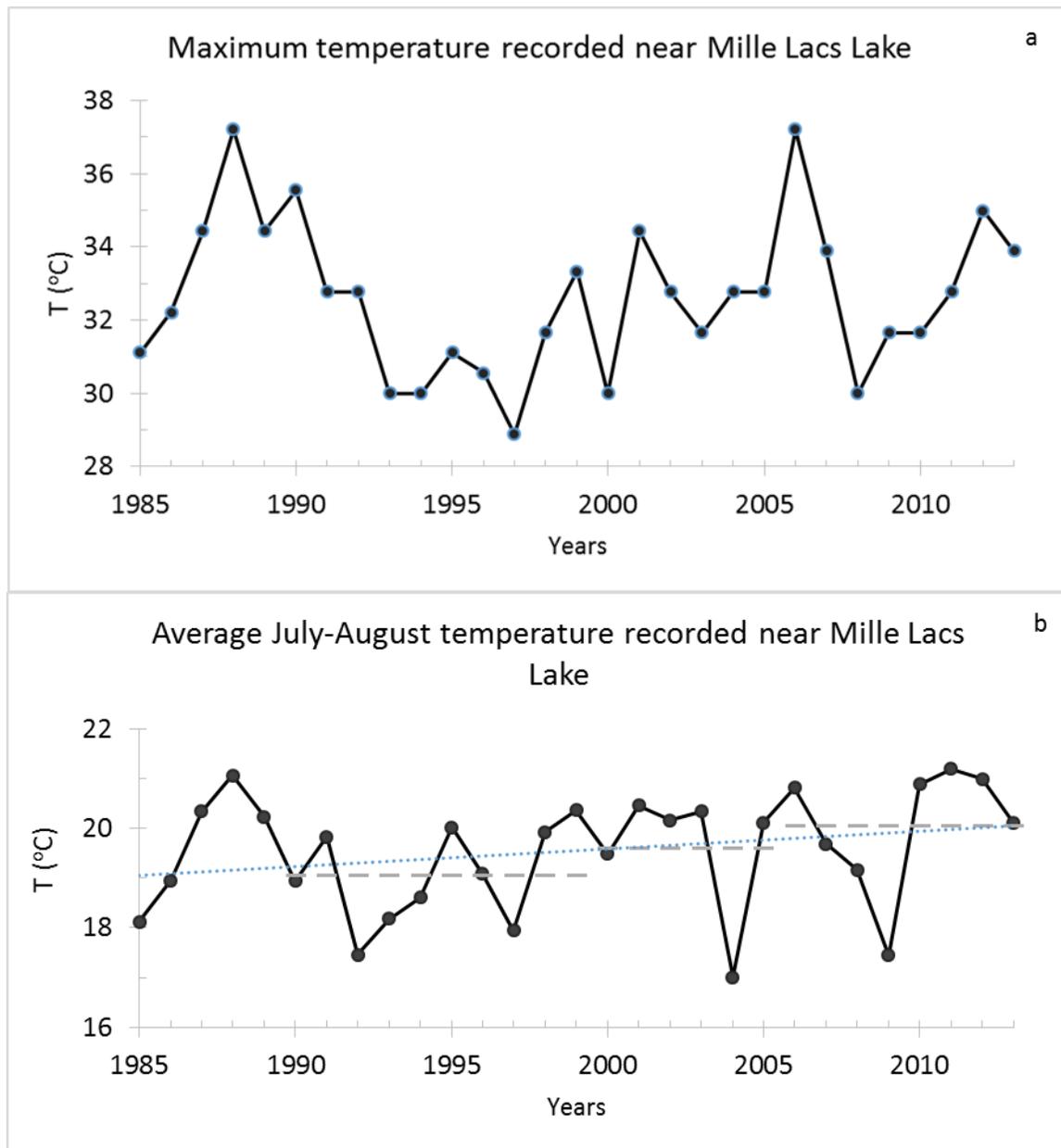


Figure 1.4. Maximum and average air temperature in July-Aug recorded at Isle station, near Mille Lacs Lake. Panel a shows maximum temperatures. Panel b shows average temperatures. In panel b the dashed grey lines show the average temperature for the corresponding time-frame (1990-1999, 2000-2005, and 2006-2013, and the blue dotted line is the trend line through the data.

Mass mortalities of ciscoes, a cold-water stenotherm, because of high temperature and low DO level in several Minnesota lakes (including Mille Lacs) have been well documented

(Jacobson *et al.*, 2008; Kumar *et al.*, 2013; Latta, 1995). Sharma *et al.* (2011) concluded that around 25-70% of the cisco population would be wiped out from the waters of Wisconsin by AD 2100 mainly because of climate change. Burbot, the another cold-water stenotherm, are widespread in Minnesota, but in several lakes including Mille Lacs Lake, declines have been reported by fisheries biologists and anglers (Stapanian *et al.*, 2010). This decline in the southern reaches of its distribution are also hypothesized to be related to the level and duration of rising temperature (Jackson *et al.*, 2008; Stapanian *et al.*, 2010). On the other hand, higher temperatures appear to be beneficial for species like smallmouth bass, especially the younger bass (Dunlop and Shuter, 2006; Wuellner *et al.*, 2010). Food-web dynamics of the lake in response to the direct effect of temperature changes on cisco, burbot and smallmouth bass were assessed in this study.

### 1.3.2 Eutrophication

Eutrophication is a nutrient-enrichment process in an aquatic ecosystem and is considered as one of the most prevalent challenges for many aquatic ecosystems (Lampert and Sommer, 2007; Schindler, 1974; Smith, 2003). Though eutrophication is a “natural and slow” process, human influence significantly increases its rate; it renders the system undesirable by affecting the water quality (Smith, 2003). Most of the freshwater systems in US have elevated concentrations of total phosphorus (TP) and total nitrogen (TN) (Dodds *et al.*, 2009), the main nutrients responsible for eutrophication. The nutrients trigger the abundance of algae and macrophytes (Smith, 2003) which augment the decomposition rate of organic materials and significantly reduce DO level especially at the lake bottom (hypolimnion).

In general, trophicity of a lake determines its water clarity: an oligotrophic lake has more clear water than a eutrophic lake. The most common method for determining the trophic condition of a lake is Trophic State Index (TSI) (Carlson, 1977). Based on average 10 years (2004-2013) summer sample, mean TSI for combined parameters (TP, Chl-a, and Transparency) for Mille Lacs Lake is 49 (MPCA, 2014b) which indicates the lake is mesotrophic with “moderately clear” water in most of the summer (RMBEL, 2013). Further, I assembled the available environmental parameters to explore if there is any correlation between these observations (Figure 1.5).

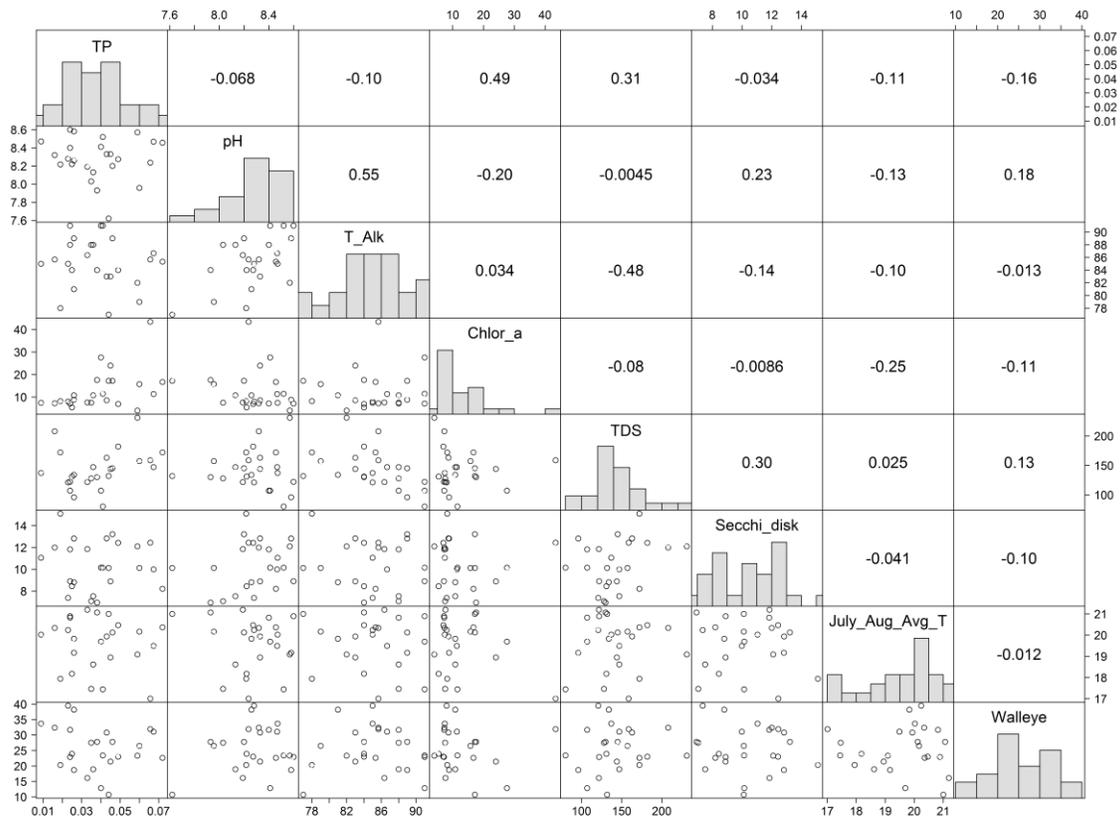


Figure 1.5. Correlation matrix between environmental variables (source: MPCA).

The lower panels show the correlation plots, and upper panels show the corresponding correlation coefficients. Units: Total Phosphorous (TP), Total Alkalinity (T\_Alk), and Total Dissolved Solids (TDS) in ppm. Chlorophyll a (Chlor\_a) in ppb and Secchi Disk transparency in feet. Average Walleye CPUE in lb/lift.

No significant correlation was found between the environmental parameters apart from the obvious one (such as pH vs Alkalinity). As discussed in the following sections that water clarity of the lake increased especially after 2010 that coincides with the invasive species zebra mussels expansion in the system; thus, I was expecting a strong inverse relationship between TP and water clarity, but no trend were observed in TP level. This is probably because of the role of zebra mussels that caused increase water clarity level without affecting the TP level.

Historically, Mille Lacs transparency time-series data in the form of Secchi disk readings were recorded by Minnesota Pollution Control Agency (MPCA) from around 40 sub-stations across the lake. However, the data collected from different sub-stations were highly discontinuous: around 65% of the station were sampled only a single year, and only two stations namely station 206 (southern side of lake) and 213 (north-eastern side of the lake) had the data recorded for 10 years or more. Further, there were no data recorded after year 2002 from station 206. Based on the data recorded at station 213, Mille Lacs Lake transparency seems to be very stable at around 12 feet (3.65 m) from the Secchi disk readings (Figure 1.6) until the zebra mussels invasion.

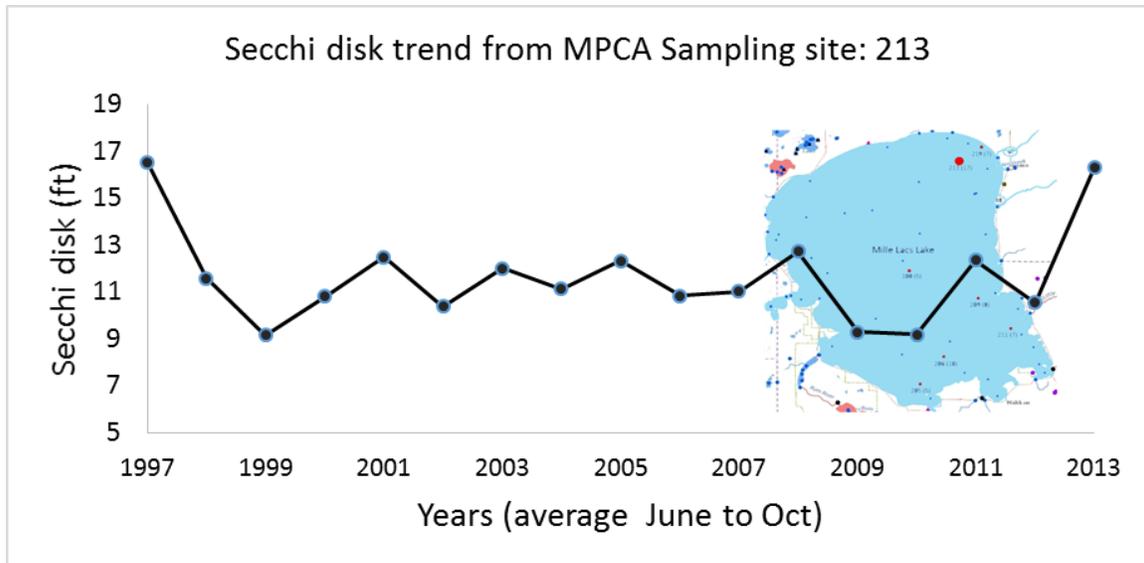


Figure 1.6. Mille Lacs transparency trend shown by Secchi disk readings at station 213 (source: MPCA). A red point in N-Eastern side of the inset lake map shows the location of sampling station 213

Starting from year 2005 MNDNR also began to collect Secchi disk data consistently at 9 offshore stations across the lake. The data collected by MNDNR also showed the transparency of the lake was quite stable across all the 9 stations from 2005, but a sharp rise in the transparency trends was observed starting from year 2010 (Figure 1.7). The rise in transparency in the lake in later years coincides with the establishment of the the invading zebra mussels—the species was first sighted in the lake in year 2005 (please see the section 1.3.3). Increased water clarity can promote the growth of aquatic vegetation, thereby altering fish habitat: for example the change might be favorable for muskellunge and smallmouth bass which prefer clear water but undesirable for walleye which prefers turbid water (Vanderploeg *et al.*, 2002).

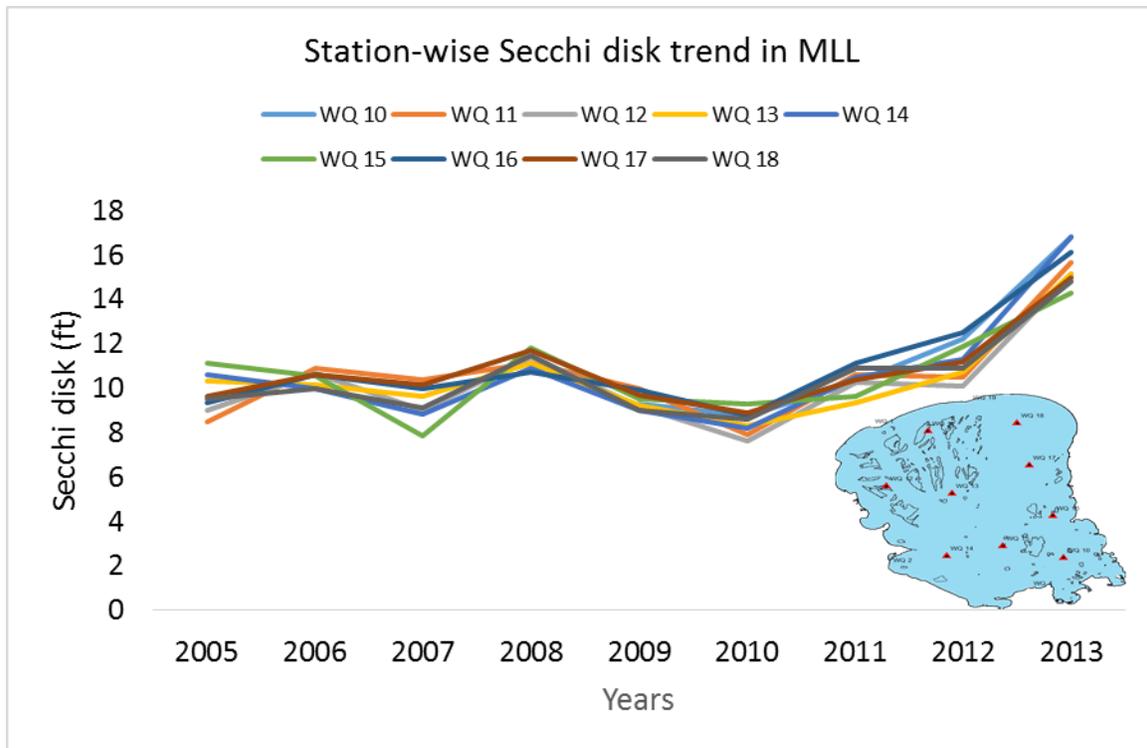


Figure 1.7. Mille Lacs transparency trend shown by Secchi disk readings at 9 stations (source: MNDNR). The red spots in the inset map show the location of the 9 sampling stations (WQ10 to WQ18) the data were sampled from.

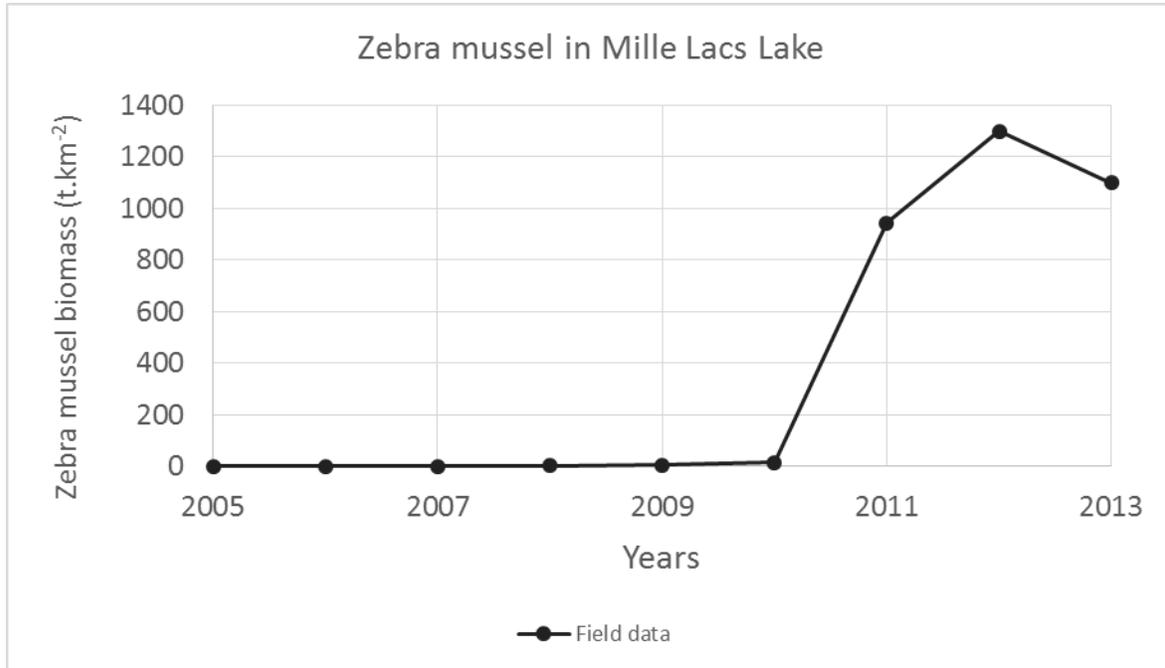
### 1.3.3 Invasive species

Infestation with invasive species is another substantial threat to ecosystem function caused by increased human intervention (Mills *et al.*, 1993, 1994). Once the invasive species become established in the system, they interfere with the natural food-web, create risk to native species by outcompeting them and modifying fundamental ecological structure (Gozlan *et al.*, 2010). Invasive species apply a variety of strategies to compete with native species (Vojtkovska *et al.*, 2014). As reported in Pimentel *et al.* (2005), overall 138 fish species have been introduced in the US States and around 40 of them negatively affect the indigenous species, and the country has to sustain economic losses of \$5.4 billion per annum.

Mille Lacs Lake has been infested with several invasive species such as: common carp, zebra mussels (*Dreissena polymorpha*), Chinese mystery snail (*Bellamy chinensis*), banded mysterysnail (*Viviparus georgianus*), spiny water flea (*Bythotrephes longimanus*), Eurasian watermilfoil (*Myriophyllum spicatum*), and curly-leaf pondweed (*Potamogeton crispus*) (MNDNR, 2012a). Among those, zebra mussels have shown the most rapid spread in the lake: Zebra mussels were first noticed in the lake in 2005, and the density increased from less than 0.5 t.km<sup>-2</sup> in 2008 to over 1000 t.km<sup>-2</sup> by the year 2013 (Figure 1.8). Three factors that can contribute to this rapid spread are (i) high rates of reproduction (Mackie, 1991), (ii) high rates of filter feeding (Kryger and Riisgård, 1988), and (iii) the presence of few predators in the North American fresh waters (Strayer, 1999). For these reasons, zebra mussels are considered “aggressive invaders” (Karatayev *et al.*, 2007) that are likely to induce substantial changes in the Mille Lacs Lake ecosystem. Effective filtration of phytoplankton by zebra mussels has been observed to cause decreased productivity, improved clarity (Fahnenstiel *et al.*, 2010) and changes to the plankton community (Allinger and Reavie, 2013; Fahnenstiel *et al.*, 1995; Fishman *et al.*, 2010). However, the species may also have some beneficial effects such as improving the water quality as observed in highly eutrophied Lake Erie (Allinger and Reavie, 2013).

The ecosystem modelling approach in Chapter 5 of the thesis will model zebra mussels invasion in MLL and will allow the exploration of potential effects of reduced productivity on the native species in the lake. Considering the rapid spread and high density of zebra mussels in Mille Lacs Lake, the focus of Chapter 5 is only on zebra mussels invasion. However, it is possible that the effects of other invasive species such as spiny water fleas

could interact with the effects caused by zebra mussels. The results from Chapter 5 and the potential impacts of other invasions are discussed in the concluding chapter.



*Figure 1.8. Zebra mussels biomass trend observed in Mille Lacs Lake, Minnesota. The species was first spotted in year 2005, and within 6-7 years it attained enormous biomass.*

#### *1.3.4 Managing recreational fisheries: Walleye*

Recreational fishing or angling usually is not a “primary source” of subsistence (Arlinghaus and Cooke, 2009) and mostly is for “fun” (Pitcher and Hollingworth, 2002). The game fish communities principally targeted by anglers are walleye, yellow perch, northern pike, smallmouth bass, and muskellunge (MNDNR, 1997). Size-based catch restrictions and possession limits are imposed on catch of walleye, northern pike, smallmouth bass, muskellunge, and cisco. Since Mille Lacs Lake is one of the best walleye lakes in Minnesota, the most important management goal in the lake is maintaining the recreational harvest of this species. The estimates of the safe harvest level for walleye are calculated

using statistical catch-at-age modelling (Drake, 2007). The model integrates survey information obtained from electrofishing, trawling, and gill netting with catch information on angler kill and tribal harvest into a dynamic age-structured model. After completing an annual population estimate, a Safe Harvest Level (SHL) of walleye is estimated by the MNDNR as “catchable walleye” biomass times 24% based on a “constant – exploitation strategy” (Radomski, 2003). The rate ‘24%’ was originally based on an  $F_{0.1}$  reference point (Don Pereira, MNDNR, pers. comm.) Once SHL is determined, regulations such as bag limits, protected slot, and night closures are imposed to regulate the catch. Since 1997, annual quotas have been set for sharing of total harvest by state licensed recreational anglers and Ojibwe Indian netters and spearers (Figure 1.3: walleye). Penalties are imposed if the quotas are transgressed. Before the quota management systems were implemented, the annual average exploitation rate of older walleye (age 3+) was 19%. After 1997, the average annual exploitation rate has been reduced to 11% (Drake, 2007).

The Mille Lacs walleye population, which was more stable than any other walleye population in the larger lakes in Minnesota (Radomski, 2003), has dropped to historically low levels in the last 5 years (2007-2012). Assessment gill net data indicates that on average walleye dropped to 5 fishes (10.7 lb) per net in year 2012 from the historical median level of 13 fishes (27 lb) per net (MNDNR, 2012b) (Figure 1.2: walleye). The nearly one-third drop is certainly an alarming situation for managers, causing them to contemplate over different aspects of the lake ecosystem starting from ecological imbalances to current modelling practices and policy implementation. MNDNR has already established a panel of experts to review the walleye crisis (Pereira, 2014).

### 1.3.5 Other issues

#### **Piscivorous bird populations**

A rising population of fish-eating birds such as double-crested cormorants, common terns and others can affect the fish population in the ecosystem. Diet observations from different independent studies (Hobson *et al.*, 1989; Kozie and Anderson, 1991; Manuel, 1931; Rudstam *et al.*, 2004) indicate that birds are able to consume a wide-array of fishes in lakes. From just 3 nesting colonies reported in 1925, the population of double-crested cormorants reached around 16,000 nesting pairs in Minnesota (Erika, 2005). As far as Mille Lacs Lake is concerned, the birds became established at Spirit Island from just 2 nesting pairs in 1998 to a total of 195 nesting pairs in 2006 (McDowell, 2007). Common terns and Ring Billed Gulls are mostly occupants of Hennepin Island. Efforts are being made to confine the gull population to the island in order to lessen competition faced by common terns, which are listed as a threatened species in Minnesota.

#### **Fluctuations in abundance**

There are several species in the lake whose abundances have either declined drastically or boomed to the record high levels, and in most of the cases, managers have none or few certain explanations for the observations. The lake experienced a historical decline of the forage fish cisco by nearly 90%, and on the other hand the population of yellow perch, a most important forage fish, has approached almost its carrying capacity during the modelled period (based on a production model: Appendix B ). Similarly, assessment-net

data suggest that the abundance trends of northern pike and smallmouth bass reached a record high level in recent years while burbot declined (Figure 1.2).

#### **1.4 Ecosystem based advice necessary? Why?**

Ecosystem Based Management (EBM) can be defined in various ways; in essence, it considers interactions of species with their physical environment, the complex feeding and competing interactions among species, and the impacts of fishing and climate change on the system (EPAP, 1999). Single-species modelling methods are, undoubtedly, widely used in fisheries management; paradoxically, fisheries have been unsustainable historically, and the models have been criticized for not being able to represent interactions between fish populations (Pauly *et al.*, 2002). One of the reasons is that the single-species models inherently assume stability in “recruitment and natural mortality rate”, and are not capable of adjusting for changes in those parameters consequent to variation in predator-prey abundance or other ecological patterns (Walters *et al.*, 2008). To improve the current fisheries management, there is a need of an ecosystem-based management (EBM) that particularly takes trophic interactions into account and considers management targets for the whole ecosystem rather than being confined to a select few species (Francis *et al.*, 2007; Minns, 2013; Pikitch *et al.*, 2004).

As mentioned above, the walleye population has shown a decline in recent years in Mille Lacs Lake in spite of MNDNR’s management efforts starting from population assessment to determination and implementation of safe-harvest level. Then what happened to walleye? Is this a result of disruption in natural complex food-web of the system? Ecosystem approaches could probably provide an answer to the question. Further, the dynamics of

yellow perch and cisco populations are important to understand because they are the important prey species of walleye and other important predators in the lake. Mille Lac's cisco population has declined over the last two decades and during the same time period the yellow perch population has increased. It is hypothesized that temperature increase has caused cisco decline. An ecosystem model with temperature effects could be a useful approach to investigate the hypothesis.

Increasing densities of zebra mussels are capable of clearing water efficiently by filtering phytoplankton out of the system; the negative effect on phytoplankton creates a bottom-up control in the food-web, and an ecosystem approach would be best suited for analysing these bottom-up effect. Similarly, the effect of consistent rise in the fish-eating bird population and artificial stocking of muskellunge can ideally be investigated using ecosystem approaches.

Addressing the above questions require an understanding of the complexity of the interactions between the species in the lake. Further, being confined in nature, making the ecosystem model and implementing the ecosystem approach to fisheries management on a lake offers more reliability than open-systems such as rivers and marine ecosystems.

However, it doesn't imply that challenges in a lake ecosystem are small: in aspects such as infestation with alien species and increasing abundance of piscivorous birds, the adverse effects are more substantial and conspicuous in a confined water body. For the same reason, the anthropogenic effects could have considerable impacts on a lake ecosystem. It is generally understood that human impacts on water quality and fisheries were small before European contact in North America. It is believed that in the past few hundred years, Mille

Lacs Lake ecosystem would have changed considerably owing to changes in land use patterns in the lake watershed, fisheries, stocking, migration, and invasive species. In this thesis, I have chosen ‘1985’ as the baseline year for all analyses because data on Mille Lacs Lake fisheries, surveys, and environmental variables were mostly available from 1985. In the final concluding chapter of thesis, I present a summary of the possible major ecosystem changes experienced by North American lakes in the past few hundred years and discuss the results from the thesis within the longer term context of the lake ecosystem changes.

But increasing the capacity from the conventional target-species based management to Ecosystem-wide sustainable management is not an easy task because of various levels of complexities involved in ecosystem process as well as in the human influences on the system (Emlen, 2013; Moss, 1999). Incorporation of all the aforesaid issues of the lake in the ecosystem context are fraught with challenges. Besides, the emergence of challenges or threats to ecosystem is a continuous process, and EBM should be able to keep integrating those; thus EBM is not a “short-term” planning exercise (Minns, 2013).

## **1.5 Thesis focus: Ecosystem-based management under changing environmental conditions**

The current study is a modelling effort to improve the understanding of Mille Lacs Lake ecosystem (especially as the lake responds to change in temperature and invasion by zebra mussels) and explore the ecosystem-based management options for the lake. An overview of the topics explored in the thesis is listed below:

- to quantify the role of temperature changes in driving a decline of the cisco population (for details: see Chapter 2),
- to build an ecosystem-model, incorporate the direct effect of temperature changes to the species such as cisco, burbot and smallmouth bass, and fit the model with the historical time-series data such as catch and CPUE (for details: see Chapter 3),
- to drive the ecosystem model forward in time to anticipate and understand changes in the ecosystem as a function of prevailing management practices such as a  $F_{0.24}$  strategy for walleye management and other management scenarios that are related to the current issues in the lake and/or are requested by the Minnesota DNR managers of the lake (for details: see Chapter 3),
- to estimate the ecosystem based maximum sustainable yield for most of the exploited fish species in the lake (for details: see Chapter 4), and
- to evaluate the ecosystem impact of an invasive species, the zebra mussels (for details: see Chapter 5).

To address the topics listed above, an ecosystem model was built for the lake using the Ecopath with Ecosim (EwE) version 6 modelling framework (Christensen and Pauly, 1992; Christensen and Walters, 2004; Christensen *et al.*, 2008). The following sections discuss the pros and cons of the EwE ecosystem modelling framework along with other available ecosystem modelling suites.

### *1.5.1 Ecopath with Ecosim modelling approach*

The core idea of the Ecopath with Ecosim (EwE) modelling approach was developed approximately 30 years ago (Polovina, 1984). As the interest in ecosystem modelling and

the use of EwE models grew, the modelling platform faced several challenges in responding to challenges presented by real data, ecology, and management questions. The capacity enhancements of the EwE approach, together with testing and documentation have been in continuous development since then in order to address the emerging challenges (Christensen and Walters, 2004). Following section provides a brief review of the strengths and weakness of EwE modelling approach.

Ecopath is based on the fundamental principles of an energy budget (Christensen and Pauly, 1992; Christensen and Walters, 2004; Pauly *et al.*, 2000; Polovina, 1984). Species are aggregated into functional groups based on the functional roles in the ecosystem and/or the management/commercial importance. The multi-stanza feature of Ecopath enables modelling of age-structure dynamics of important functional groups. The calculations for the individual stanzas are obtained from a fully age-structured simulation based on the input parameters (Christensen and Walters, 2004). This feature can be used to model ontogenetic shift in trophic behavior or the selectivity of a functional group to different fleets (for example a trawl gear may capture smaller age groups of a commercially important species but more selective gear might target only the adults). The flexibility of the multi-stanza set up (i.e. the delineation of the age groups into stanzas) allows this feature to be a highly useful for ecosystem modellers in parameterizing a model to be parsimonious while attempting to build a realistic representation of the ecosystem.

Ecosim allows time-dynamic simulation that allows the actual consumption in the food web to respond dynamically to predator and prey abundance as well as the diet matrix (see Figure 3.6). In addition to including predator and prey production and consumption rates in

the calculation of biomass dynamics, a key strength of Ecosim is the inclusion of prey behavior through the foraging arena concept (Walters *et al.*, 1997) which allows the description of a ‘distinct feeding niche’ for predator-prey interactions; the vulnerability parameters govern vulnerability of prey to the predator groups (Ahrens *et al.*, 2012; Christensen and Walters, 2004). This simulation of prey behavior was a major advancement in the ability of the EwE model to “realistically” represent complex ecosystems that did not suffer from “pathological instabilities” in predator-prey interactions (Walters and Christensen, 2007) and in practice allows the vulnerability parameters to be adjusted to obtain the best fit by least squares to time series data on abundance and biomass.

Ecosim allows the users to explore the response of the ecosystem to different management options. This is probably one of the most popular applications of the software. Another feature that makes Ecosim highly valuable as a modelling approach is the capacity to incorporate environmental effects through forcing functions. The forcing functions can be applied to the predator-prey interactions or to the production rates of the functional groups. It enables the modeller to investigate the impact of historical environmental changes or develop projections for ecosystem response to future environmental change.

A critical analysis of the value of EwE modelling approach (Plaganyi and Butterworth, 2004) concluded that ecosystem approaches like EwE complemented management based on single-species approaches by providing better “understanding of ecosystem functioning”. This was mainly achieved by incorporating the effects of fisheries on non-target species, identifying trophic cascades, quantifying non-linear responses such as cultivation depensation (Plaganyi and Butterworth, 2004; Walters and Kitchell, 2001). EwE is also

useful in understanding ecosystem-scale changes (i.e. regime shifts) that occur due to changes in productivity.

One of the challenges of using ecosystem models is the uncertainty in predictions arising from the large number of parameters incorporated into the model (Fulton *et al.*, 2003). The Monte Carlo routine in Ecosim allows the user to specify confidence intervals around the basic input parameters. Ecosim takes random draws from the provided distributions for parameters and repeats Ecosim runs for 'n' number of times, and these results can be used to provide a band of confidence around the Ecosim results (Christensen *et al.*, 2008).

Secondly, when time series are available for comparison, the Monte Carlo routine produces the 'sums of squares' estimate for each run allowing the user to explore the parameter combinations that lead to the lowest sums of squares (Christensen and Walters, 2004).

There are several other features of the EwE modelling software which can be used for further exploration based on the model developed in the thesis (for example spatial analysis using Ecospace; non-trophic mediation interactions between organisms).

Several weaknesses of the EwE approach have been pointed out, the most important being that the energy content of the prey is not part of the calculation of predator consumption, and the sensitivity of Ecosim simulations to the vulnerability parameters (Plaganyi and Butterworth, 2004), and uncertainty in the diet preference matrix. Other criticisms which would be applicable to any ecosystem model are the amounts of data required, the dangers of using parameters estimated for similar species based on studies of a different ecosystem (Plaganyi and Butterworth, 2004), model resolution for optimal complexity and the reconciliation of the model outputs with management objectives (Fulton *et al.*, 2003).

As the interest in ecosystem approaches increased in the field of fisheries, the availability of methods for multispecies analyses has also increased. New models are continuously in development. Some recent developments are the following: Length-based multispecies model (LeMans) which was originally developed by Hall *et al.* (2006) has recently gained lot of attention for modelling the size structure of populations in multispecies context (Collie *et al.*, 2013; Rochet *et al.*, 2011). NEMURO.FISH (Megrey *et al.*, 2007) has been applied to understanding Pacific herring and plankton dynamics. NEMURO.FISH has been applied to several other species (Kishi *et al.*, 2011) and has also been coupled with EwE (Aydin *et al.*, 2005). Models of Intermediate Complexity in Ecosystems (MICE) have been designed based on data availability and management question (Plagányi *et al.*, 2014). Further, MICE can be implemented within the Management Strategy Evaluation framework with the capability to incorporate different stakeholders and the economic and social drivers for the system (Plagányi *et al.*, 2014). Similarly Ecotroph modelling approach (Gascuel *et al.*, 2005; Gascuel *et al.*, 2011) has been applied to several real case studies —it is a minimum realistic ecosystem model that uses trophic spectra to describe ecosystems (Gasche and Gascuel, 2013). But it is powerful enough to include low and high trophic groups and is able to assess fisheries impacts; for this reason, it is also a ‘whole ecosystem model’ (Gasche and Gascuel, 2013; Gasche *et al.*, 2012). Further EcoTroph R Package has been developed to offer an interface between EcoTroph and EwE (Colleter *et al.*, 2013).

Plagányi (2007) compared and evaluated 20 approaches for multispecies modelling and service to ecosystem-based management. The 20 approaches were classified as follows (1) Whole ecosystem models (Ecopath with Ecosim), (2) Dynamic system models (Atlantis, Invitro, Osmose), (3) Dynamic multi-species models which have also been referred to as

minimum realistic models (MRM) because these models try to effectively model the most essential components (MSVPA, Gadget, etc), and (4) Extensions of single-species models (ESAM). Among all the approaches evaluated, only three, namely EwE, Atlantis, and Invitro were capable of modelling all the trophic levels in the ecosystem. These models are also referred to as end to end models (Fulton, 2010; Rose *et al.*, 2010) because they try to incorporate physical drivers, low trophic levels and high trophic levels. Dynamic multi-species models are suitable for modelling fish species but these have poor resolution at the lower trophic levels (Plagányi, 2007). EwE, Atlantis, ERSEM, Invitro, and Osmose were the only ones that could handle more than 10 species groups efficiently. While EwE has capacity to incorporate environmental affects, Atlantis, Invitro and several others are more powerful in this respect with possibility for detailed representation of light, nutrients, temperature etc. Atlantis was evaluated to be the most powerful after consideration of capacities to incorporate age-structure of species, three-dimensional spatial structure, ocean circulation, functionality to incorporate management goals and multiple stakeholders; at the same time, EwE was evaluated to be the most widely applicable based on the number of applications (Plagányi, 2007). The biogeochemical ecosystem model of Atlantis requires very large amounts of time and work (typically several postdocs are needed to build one model) and is generally not suitable for a PhD thesis project.

Following are some examples of how the EwE approach has been used. EwE has been used to understand various aspects of ecosystem based management such as historical changes in ecosystem structure (Heymans *et al.*, 2004; Hoover *et al.*, 2013a); important trophic linkages in ecosystems ranging from freshwater estuarine, coastal, to deep sea habitats (Harvey *et al.*, 2012; Kitchell *et al.*, 2000; Tecchio *et al.*, 2013; Tsagarakis *et al.*, 2010);

and ecosystem-wide impacts of fishing strategies (Ainsworth *et al.*, 2008; Bundy, 2004; Hoover *et al.*, 2013b; Lassalle *et al.*, 2012; Pitcher and Ainsworth, 2010). EwE approach has also been used for evaluating the effects of environmental change (Coll *et al.*, 2009; Coll *et al.*, 2006; Mackinson *et al.*, 2009; Wolff *et al.*, 2012) and for large scale comparisons based on models of component ecosystems (Coll and Libralato, 2012) and models of large marine ecosystems (Christensen *et al.*, 2009). Besides, the approach has also been used for the modelling of invasive species (Langseth *et al.*, 2012; Miehls *et al.*, 2009).

Given that the key changes in Mille Lacs lake and their effects on food web structure are not directly testable, the Ecopath and Ecosim (EwE) ecosystem modelling suite (Christensen *et al.*, 2008), provides the researcher with a powerful tool for the examination of these otherwise inaccessible events using quantitative thought-experiments.

While other modelling frameworks may be viable, in this thesis I have chosen to concentrate my research effort and time on the Ecosim dynamic ecosystem simulation approach, fitting the parameters of the model to best represent extensive time series of abundance data from the lake, using considerable field data on diets and temperature change, and covering invading species while assessing uncertainty in the results using the Monte Carlo approach. After fitting the ecosystem model to data up to 2005, I then compared forecasts of the model with further field data from 2006 to 2013.

## 1.5.2 Chapter outlines

### 1.5.2.1 Chapter 2: Temperature-driven decline of cisco population in MLL

Cisco is a one of the forage species in the lake, and their summer die-offs are well-studied in the literature (Edsall and Colby, 1970; Jacobson *et al.*, 2008). Several hypotheses have been put forward to delineate the cause of this decline in Mille Lacs Lake *viz.* introduction of muskellunge, increase in lake water temperature due to climate change and decreasing dissolved oxygen level. A study based on 41 lakes in Minnesota where muskellunge were stocked compared abundances of cisco and other principal species including walleye, northern pike and yellow perch before and after stocking of muskellunge; the study did not find any evidence of muskellunge causing the decline of any of these species (Knapp *et al.*, 2012). Therefore, the hypothesis about muskellunge's influence on cisco is not supported by evidence. Suitability of lake habitat has been described for cisco as a combination of temperature and oxygen profile, and the summer die-off of cisco has been attributed to high temperatures and hypoxic hypolimnion (Jacobson *et al.*, 2008). Mille Lacs Lake does not provide an ideal milieu for the thriving of its cisco population and is identified as “nonrefuge lake” for the species (Fang *et al.*, 2012). Similarly, burbot is another species in the lake that has experienced stress from increase in temperature and numbers of days of exposure in high temperature (Jackson *et al.*, 2008) through mechanisms such as depression in metabolic activity (Binner *et al.*, 2008) and movement (Hofmann and Fischer, 2002; Paragamian and Wakkinen, 2008). The temperature effects were predominant on adult burbot (Hofmann and Fischer, 2002). Mille Lacs Lake historic abundance data suggests that cisco and burbot declined by nearly 98% and 90% respectively over the years 1985-2006.

At this point it became important to analyse whether temperature alone was responsible for the summer die-off of cisco and decline of burbot or if fishing pressure also contributed to this decline. To address this question, I built a temperature-influenced single-species surplus production model to test the effect of temperature. Using the model, I quantified the decline caused by the temperature, and how carrying capacity and maximum sustainable yield varied under changing temperature (Kumar *et al.*, 2013). Since the analysis for burbot was very similar to the model developed for cisco, the findings for burbot are presented in Appendix B.

### **1.5.2.2 Chapter 3: Ecosystem simulations for ecosystem based fisheries management in MLL**

While Chapter 2 quantifies the influence of temperature on cisco, the approach did not include any consideration of ecosystem trophic-dynamics. In Chapter 3 building an ecosystem model enabled me to investigate multispecies interactions in Mille Lacs. Considering the importance of cisco as a forage fish, in Chapter 3, I was able to investigate the effects of cisco decline on the other species in the lake. Additionally, I was able to use the model to analyse various scenarios relevant to the management of the lake, and investigate how different strategies of lake management would affect the lake ecosystem.

The ecosystem drivers ranging from producers to top-order predators were first classified into relevant functional groups. Key species such as walleye, northern pike, yellow perch, smallmouth bass, muskellunge, and cisco were modelled with life history stanzas to accommodate ontogenetic shift and recreational fishing pressure on adults. A total of 50 functional groups were formed and parameterized using the information on abundance,

production, consumption, diet composition and fisheries catch. The base Ecopath model represented an ecosystem snapshot of Mille Lacs Lake in 1985. It was a challenging task to gather model parameters and the vast network of predator-prey interactions to trophically interlink nearly 50 functional groups. The parameter information was obtained from various sources such as field-estimates, published literature, standard single-species modelling exercise for many species (Appendix B), and, professional inputs from experienced MNDNR biologists working on the lake.

The static mass-balance Ecopath model was used to initiate a time-based dynamic simulation (Ecosim) for tracking changes in the biomass of species with temporal changes in catch patterns, food-web (predator-prey interactions), and environmental condition. The dynamic Ecosim model was tuned with the historic time-series data of catch and abundance of the lake over a 22-year period from 1985-2006; the process is called model-fitting, and it required repeated adjustments of many parameters of Ecosim—vulnerability was the most important one—until the deviations between observed data and model predictions were minimised. The fitted Ecopath with Ecosim model was then driven forward to see how the ecosystem would behave under different scenarios. A set of scenarios were selected carefully so that managers would be able to foresee the lake ecosystem in response to the prevailing management practices and plausible challenges.

Thus, building the ecosystem model, incorporating temperature forcing functions, tuning/fitting the model to observed data, and simulating a chain of effects on important species in response to changes in fishing pattern, species abundance, and climatic variation such as rising temperature are the key aspects of this chapter.

### **1.5.2.3 Chapter 4: Ecosystem and single-species maximum sustainable yield (MSY) for major species of MLL**

Reference points are popular metrics used in marine fisheries management for understanding and communicating the status of a stock (Portley and Geiger, 2014; Worm *et al.*, 2009). These metrics are less commonly used in freshwater fisheries management, but there is potential to improve freshwater fisheries management by establishing reference points for freshwater species (Cooke *et al.*, 2014). The concept of Maximum sustainable yield (MSY) and the corresponding fishing mortality level ( $F_{msy}$ ) are popular in fisheries science as limit reference points (Mace, 2001). The single-species MSY became a popular tool in fisheries management especially after the “surplus production model” (Schaefer, 1954) was introduced in the 1950s but this popularity was followed by severe criticisms owing to several weaknesses (Larkin, 1977). The weaknesses include the inability to adjust to changes in recruitment, the dangers of overfishing substocks, and the denial of multispecies interactions in an ecosystem (Larkin, 1977). Weaknesses on the management side include difficulty of estimation due to inaccuracies in fisheries statistics and the possibility that in several years MSY could be exceeded thereby weakening the stock status. The rebirth of MSY has been based on the recognising its weaknesses as a target reference point and the philosophy of using it as a limit reference point (Mace, 2001).

As noted as one of its weaknesses previously, the estimation of MSY is only for the target species and it doesn't take into account of responses of other ecosystem players (non-target species in the food web). Gislason (1999) showed that reference points calculated in a single-species framework may be different from those obtained in a multispecies framework. Implementation of ecosystem based management will be aided by the

availability of ecosystem level reference points (Levin *et al.*, 2013; Voss *et al.*, 2014). In this chapter, I calculate the ecosystem level MSY (ESmsy) for most of the fished species in Mille Lacs Lake. Further, to make comparison, single-species (SSmsy) of all the corresponding species were also estimated. Additionally environmental effects can affect species productivity (Holsman *et al.*, 2012; Mangel *et al.*, 2002), and the analyses in Chapter 2 showed that cisco and burbot (see Appendix B for burbot) were sensitive to the temperature change. So, the estimations (SSmsy and ESmsy) were repeated under two settings—(1) with a temperature forcing function and (2) temperature effects were not included. Finally, the importance of incorporating uncertainty in fisheries analyses is being increasingly recognised (Charles, 1998; Harwood and Stokes, 2003; Link *et al.*, 2012) and so I performed Monte Carlo simulations to estimate the uncertainties around the estimates.

#### **1.5.2.4 Chapter 5: Simulation of zebra mussels invasion and evaluation of impacts on MLL**

Zebra mussels are recognised as one of the most destructive exotic species in lakes; it damages the ecosystem mainly through bottom-up effects (North *et al.*, 2013; Strayer, 1999). It is capable of hugely modifying an ecosystem by virtue of its tremendous reproductive potential, fast colonization, habitat alteration and high water-filtration rate. It clears the water by siphoning off phytoplankton; the effect of lessening density of the primary producer ripples through the complex food-web and threatens the top-order fishes (Cuhel and Aguilar, 2013; Mills *et al.*, 2003).

It is an unfortunate coincidence that the species boomed in Mille Lacs during my PhD program when a preliminary ecosystem model of the lake was already built. In the later part

of my research, this potentially devastating species was included in the ecosystem model. The model then simulated the invasion to assess the ecosystem-wide impact on the native species. A number of scenarios were simulated to capture the explosion of zebra mussels in the lake; for each scenario I explored the consequences for phytoplankton, zooplankton, forage fish, and top predators in the lake.

#### **1.5.2.5 Chapter 6: Conclusion**

Finally, Chapter 6 relates the findings to the issues taken up in the thesis. I expect that findings from various chapters would be helpful for managers by providing an ecosystem perspective and by improving their understanding of important functions in the ecosystem. Ideally the work in the thesis will help the management in making better decisions.

## 2 Temperature-Driven Decline of a Cisco Population in Mille Lacs Lake, Minnesota<sup>1</sup>

### 2.1 Introduction

Cisco (*Coregonus artedii*) is a forage salmonid species widely distributed in central and northern Minnesota. This coldwater stenotherm is vulnerable to environmental stress, and its survival is often related to temperature-oxygen profile of lake (Jacobson *et al.*, 2008). Frey (1955) (as cited in Colby and Brooke, 1969) defined habitat suitable for cisco, termed as “cisco layer”, based on their lethal temperature-oxygen tolerance level as a portion of the water column at temperatures less than or equal to 20°C with dissolved oxygen (DO) levels higher than or equal to 3 ppm. Younger cisco can survive higher temperature levels than adults; Edsall and Colby (1970) reported an upper lethal temperature of age-0 cisco as 26°C.

Sampling data from Mille Lacs Lake suggest a substantial decline of cisco abundance over the last two decades. An increase in temperature over the years is hypothesized as a causative factor for this decline (Colby and Brooke, 1969; Jacobson *et al.*, 2008). However, this species was also fished over the same time period: cisco catch varied from ~7 tonnes in 1985 to ~0.5 tonnes in 2007 with a peak of ~30 tonnes in mid-1990s (Figure 2.1e). The

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<sup>1</sup> A version of this chapter has been published. Kumar, R., Martell, S. J., Pitcher, T. J., & Varkey, D. A. (2013). Temperature-Driven Decline of a Cisco Population in Mille Lacs Lake, Minnesota. *North American Journal of Fisheries Management*, 33(4), 669-681.

average summer temperature of the lake is over 16 °C and rises to around 23°C (MNDNR, 1995). Jacobson *et al.* (2008) recorded a maximum temperature 26.1°C in year 2006.

Several Minnesota lakes, including Mille Lacs Lake, experience mass mortality of ciscoes especially during summer when the “cisco layer” is relatively small. Pelagic ciscoes, mostly adults, move to cooler deeper water (hypolimnetic zone) in summer (Scott and Crossman, 1973); mortality occurs when the prevailing hypoxic condition in the hypolimnion forces the cisco to move up in the water column having lethal temperature. Mille Lacs Lake is a shallow lake with a mean depth of 8.8m and a maximum depth of 12.8m. And because the lake is quite shallow, wind-driven mixing of water occurs freely from top to bottom; consequently, ciscoes do not get enough thermal refuge in the deeper parts of the lake. My objective through this modelling exercise was to investigate and quantify the influence of temperature on cisco carrying capacity and abundance in Mille Lacs Lake, Minnesota.

## **2.2 Methods**

### *2.2.1 Data*

I used time-series data of catch per unit effort (CPUE), temperature, and catch from 1985 through 2007 (Figure 2.1). The data were obtained from the Minnesota Department of Natural Resources (MNDNR). State-licensed anglers and tribal/band fishers (netters, spearers, and anglers) are the two groups that engage in fisheries on the lake (Figure 2.1e). CPUE data was from standard experimental gill netting conducted by MNDNR to monitor the fish populations in Mille Lacs Lake.

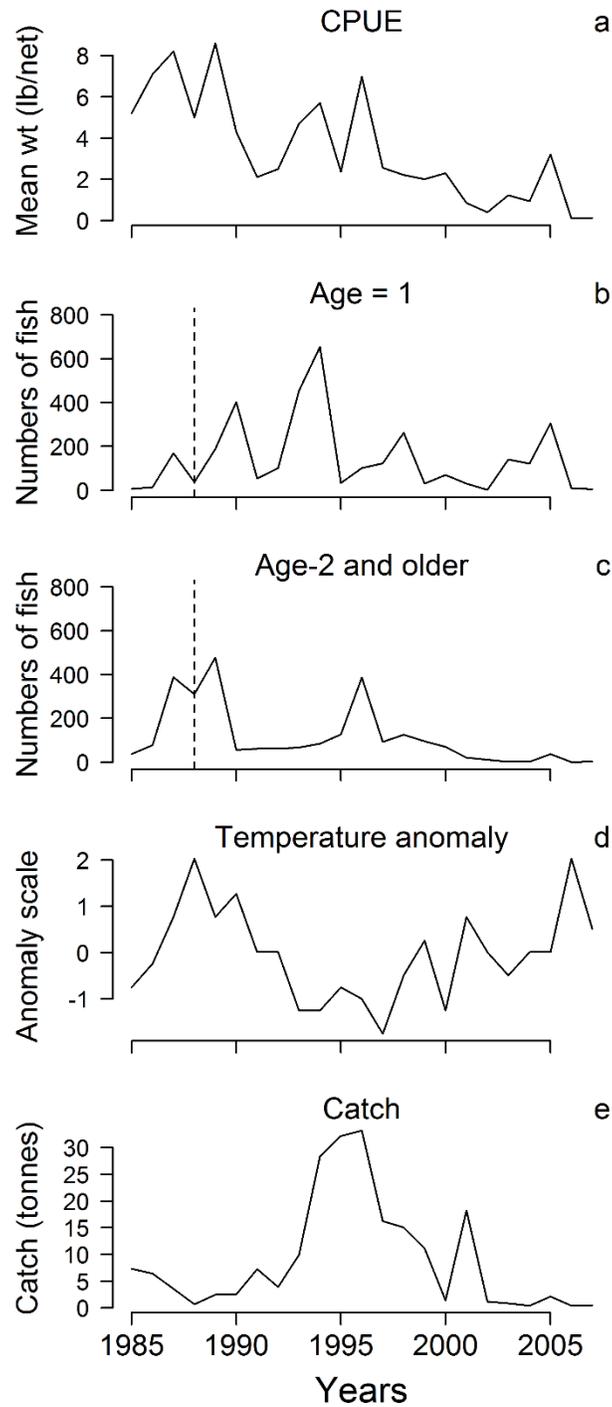


Figure 2.1. Time-series data from 1985 to 2007

(a) average observed CPUE data (pounds/gill-net lift) from 32 experimental gillnets, (b) average CPUE (numbers/gill-net lift) of age 1 fish, (c) average CPUE (number/gill-net lift) of age 2+ fish, (d) temperature anomaly for maximum temperatures in months July-August, and (e) total catch in metric tons.

Every year, usually in the last week of September, gill nets are set overnight at 32 inshore locations widely spread around the lake (Jones, 2006). The CPUE data for each year is the average gill net fish catch. Since the same types of nets are set at the same location and time every year, I assume that capture probabilities are relatively consistent across years and should not bias CPUE as an index of biomass. CPUE data show a decline of the cisco population in the lake (Figure 2.1a): the decline was observed in fish age-2 and older but not in the number of age-1 recruits suggesting that the decline in CPUE has followed the decline in adult cisco (Figure 2.1b and Figure 2.1c).

Air temperature data were recorded at Garrison, Minnesota (Figure 1.1) for the time period 1985 to 2007 (Melissa Drake, MNDNR, personal communication). Water temperature data from Mille Lacs Lake was not available for the 23-year time period for which CPUE information was available. For the few years where I had water temperature data, I checked if the monthly average Garrison air temperature data was correlated with the monthly average water temperature data from Mille Lacs Lake. I found that the two temperature series were highly correlated except during the winter months with ice cover on the lake. In the analysis, I used records only from July and August ( $r=0.88$  for temperature records in July and August; see Appendix A for more details). I used the air temperature series to calculate an anomaly factor, thus taking into account only the trend and not the absolute temperature records. The summer temperature anomaly was calculated based on the maximum temperatures (Figure 2.1d) observed every year in July-August for the 23-year period. For any data series, the anomaly denotes the deviation from the mean, in other words, it is the distance of data points from the mean relative to the standard deviation. The

temperature anomaly ( $Ta$ ) was calculated by standardizing the time-series of maximum temperature using Equation 1:

$$Ta_t = \frac{(T_t - \mu)}{\sigma}$$

*Equation 1*

where,  $Ta_t$  denotes the temperature anomaly in year  $t$ ,  $T_t$  is the maximum temperature for year  $t$ , and  $\mu$  and  $\sigma$  represent the mean and standard deviation of the temperature time-series. Maximum temperatures increased from 1985 to 1987 then declined till 1997. From 1997, the temperatures maintained an increasing trend. Additionally, as a sensitivity analysis, a temperature anomaly based on accumulated degree days in July-August for the 23-year period was also calculated. I used this alternate description of temperature anomaly in the temperature dependent surplus production models and explored the results. The additional data and models are provided in Appendix A.

### *2.2.2 Model formulation*

Three model formulations were used to examine the effect of temperature on cisco population decline.

Model 1: Surplus production model (SPM) with observation error

Model 2: SPM with a temperature anomaly and observation error

Model 3: SPM with a temperature anomaly, observation error, and random effects process error (state-space model).

*Model 1: SPM with observation error.*—The ‘surplus production’ refers to “the difference between increase in biomass due to growth and recruitment to the fishable population, and the loss in biomass due to natural mortality” (Punt and Smith, 2001). In the presence of a fishery, if catch is equal to surplus production, stock biomass is maintained at equilibrium; higher catch leads to decrease in stock biomass, and catch lower than surplus production leads to an increase in stock biomass (Jacobson *et al.*, 2001). The Schaefer SPM (Schaefer, 1954) is based on a logistic population growth model, and it has density dependence such that growth and survival are faster at lower population biomasses than at levels close to the unfished biomass (Punt and Smith, 2001). When fisheries catch is incorporated into the logistic population growth, the model can be modified for next year’s biomass as in Equation 2 (Hilborn and Mangel, 1997)

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K}\right) - C_t$$

*Equation 2*

where,  $K$  is the carrying capacity of the population;  $r$  is the intrinsic rate of population increase;  $B_t$  describes the biomass at any point in time  $t$ ; and  $C_t$  is the catch at time  $t$ . Equation 2 was reformulated as:

$$P_{t+1} = P_t + rP_t(1 - P_t) - \frac{C_t}{K}$$

*Equation 3*

where,  $P$  is the biomass expressed as a proportion of the carrying capacity. The subscript  $t$  and  $t+1$  denote time and time a year later respectively. This formulation of the model

enables easier control of the biomass falling below an unrealistic ‘zero’ value during the fitting process. Since direct annual estimates of fish biomass are not available, a compromise is to study the trends in the population biomass by conducting regular (usually annual) sampling surveys. Sampling survey CPUEs are commonly used as indices of abundances or biomass. The observation model assumes that any change in biomass will be reflected in CPUE:

$$CPUE = qB_t$$

*Equation 4*

where, parameter  $q$  is the catchability of the sampling net. Catchability expresses the index of abundance (CPUE) as a proportion of the biomass. Thus, if I know the values of parameters  $r$ ,  $K$ ,  $q$ , and have data on catch trends, then Equation 3 and Equation 4 allow me to predict the CPUE for the same years. The CPUE predicted by the model was fitted to the observed CPUE obtained from assessment gill net surveys.

Carrying capacity  $K$  was estimated as  $\log_e(K)$  in the fitting process so that the estimated parameters had similar magnitude, and the log scale also keeps the estimate positive. If fisheries data were available from the beginning or very early history of the fisheries, then it would have been credible to assume the first year biomass at or close to the carrying capacity, but in many instances data are collected only after fisheries have existed for some length of time. Since it was difficult to make valid assumptions on the biomass of cisco in the first year of the time-series (1985), the model also estimated  $P_0$ , the biomass in the first

year of simulation expressed as a fraction of  $K$ . The final parameter that the model estimated was the standard deviation ( $\sigma$ ) in the measurement error of CPUE.

*Model 2: SPM with a temperature anomaly and observation error.*—To incorporate the influence of temperature, carrying capacity is allowed to vary every year as a function of the temperature anomaly as in Equation 5:

$$K_t = K * \exp(\lambda * Ta_t)$$

*Equation 5*

where,  $K_t$  is time varying carrying capacity,  $Ta_t$  denotes the temperature anomaly in year  $t$  and  $\lambda$  is an additional parameter to be estimated. The parameter  $\lambda$  describes the relationship between  $K_t$  and temperature anomaly. If  $\lambda=0$ , then the multiplier on carrying capacity is equal to 1. A value of  $\lambda < 0$  has a negative influence on  $K_t$  (carrying capacity in year  $t$  is lower than the average carrying capacity  $K$ ), while a value of  $\lambda > 0$  has a positive influence on  $K_t$ .

The production function (Equation 3) in the surplus production model was modified to incorporate  $K_t$  as in Equation 6:

$$P_{t+1} = P_t + rP_t(1 - P_t) - \frac{C_t}{K_t}$$

*Equation 6*

*Model 3: State-space SPM with temperature anomaly.*— Process error was incorporated into the model 2 as a random effect on the  $P_t$  (Equation 7)

$$P_t = P_t * \exp(X_t * \tau)$$

*Equation 7*

where,  $X_t$  is the random effect added to the  $P_t$  estimated from Equation 6, and parameter tau ( $\tau$ ) is the standard deviation of the random effects process error.

### 2.2.3 Objective functions

The criteria to fit the models was to minimize the negative log-likelihood (NLL) of the predicted versus observed CPUE values. NLL for model 1 and model 2 was calculated as:

$$NLL = \frac{1}{2} \log(2\pi) + n \log(\sigma) + \sum_{t=1}^n \frac{\epsilon_t^2}{2\sigma^2}$$

*Equation 8*

where,  $NLL$  is summed over all the years ( $n$ ) for which CPUE data were available. Epsilon ( $\epsilon$ ) is the difference between the observed and predicted CPUE. The standard deviation of the observation error is denoted by the parameter  $\sigma$ .

The NLL for model 3 was the sum of the Equation 8 and Equation 9. Equation 9 describes the NLL for the process error component:

$$NLL = \frac{1}{2} \log(2\pi) + n \log(\tau) + \sum_{t=1}^n \frac{[\log(X_t)]^2}{2\tau^2}$$

Equation 9

where, tau ( $\tau$ ) is the standard deviation of the process error.

#### 2.2.4 Model priors

*Prior on  $r$  for cisco.*— This prior was calculated using a demographic method suggested in McAllister *et al.* (2001) and later updated in Stanley *et al.* (2009). The demographic method uses inputs of natural mortality, stock-recruitment steepness, and growth parameters for establishing a stable age structure and then numerically solves the Euler-Lotka equation to estimate  $r$ . The methodology is detailed in Appendix A. The density of the estimated prior closely resembled a normal probability density function with a mean of (0.40) and standard deviation of (0.09) (Figure 2.2). Hence, a normal distribution with the same mean and standard deviation was used to describe the prior.

*Prior on  $\lambda$ .*—A rescaled beta function was used to provide an uninformative uniform prior on  $\lambda$  to confine its value between -1 to 1 ( $-1 \leq \lambda \leq 1$ ); values 1.1 was chosen for both shape parameters of the beta distribution to keep distribution shape nearly uniform (Equation 10).

$$0.5(\lambda + 1) = \text{Beta}(1.1, 1.1)$$

Equation 10

*Prior on  $\sigma$  and  $\tau$ .*— A fairly uninformative gamma prior (conjugate prior on precision for normal distribution) was placed on the precision of observation and process error (Equation 11).

$$1/\sigma^2 = \text{Gamma}(3.01, 0.51)$$

*Equation 11*

Since the estimates of  $q$  were converging in model 1 and model 2, a prior for  $q$  was not required in the formulation of these models. In model 3, a penalty  $-\log_e(q)$  was added to the likelihood function to prevent the  $q$  from approaching very small magnitudes. The models were written in AD Model Builder (ADMB Project, 2009) software. The fitting procedure depended on taking derivatives of the negative log-likelihood across the parameter space.

### *2.2.5 Management variable: Maximum Sustainable Yield (MSY)*

MSY was calculated as a function of intrinsic rate of population growth ( $r$ ) and carrying capacity of the system ( $K$ ). For model 1, MSY is calculated as:

$$MSY = rK/4$$

*Equation 12*

For models 2 and 3, the estimates of carrying capacity (Equation 5) and MSY (Equation 13) varied depending on the annual temperature anomaly:

$$MSY_t = \frac{r * K_t}{4}$$

Equation 13

where,  $K_t$  and  $MSY_t$  are the time-varying carrying capacity and the MSY respectively.

## 2.3 Results

Under all SPM formulations, the posterior mean for the parameter  $r$  was estimated to be lower than the prior mean of  $r$  (Figure 2.2; Table 2.1).

Table 2.1. Parameter estimates across the 3 models with 95% confidence limits.

$r$  = intrinsic rate of population growth,  $K$  = carrying capacity,  $q$  = catchability,  $\lambda$  = correlation coefficient of temperature with carrying capacity,  $\sigma^2$  = observation error variance, and  $\tau^2$  = process error variance

Parameters	Models	Estimates	95% confidence limits	
			Lower	Higher
$r$	1	0.30	0.12	0.49
	2	0.32	0.13	0.50
	3	0.38	0.26	0.54
$K$ (tonnes)	1	133.24	106.80	203.70
	2	96.97	72.01	155.53
	3	124.22	94.59	233.35
$q(1000*q)$	1	0.03	0.01	0.05
	2	0.03	0.02	0.04
	3	0.02	0.01	0.04
$\lambda$	2	-0.36	-0.70	-0.10
	3	-0.40	-0.65	0.02
$\sigma^2$	1	0.64	0.41	1.44
	2	0.53	0.36	1.22
	3	0.25	0.12	0.67
$\tau^2$	3	0.28	0.11	0.87

Parameter  $r$  consistently approached the lower bound to capture the population decline when the prior was not used; the informative prior used here rectified this problem. Since  $r$  and  $K$  are correlated, providing a prior for  $r$  also to some extent addressed the problem related to scale of the biomass estimates.

If mean of  $\lambda$  was '0', it would indicate no correlation of temperature with carrying capacity. Posterior mean  $\lambda$  was estimated as -0.36 for model 2 and -0.40 for model 3 indicating that approximately 36-40% of the change in carrying capacity was a result of change in temperature. The posterior densities of  $\lambda$  estimated by the model 2 and model 3 almost overlapped each other (Figure 2.2) and supported a negative correlation of temperature with carrying capacity. Correlation plots of the parameters are presented in Appendix A.

The model fits to the CPUE data were very similar in the period 1995-2007, but in the period before 1995 the fits of models 2 and 3 seemed to follow the trends in CPUE better than model 1 (Figure 2.3a). And compared to models 2 and 3, model 1 estimates a lower biomass in 1985 (Figure 2.3b). Depending on model formulations, estimated biomass ranged from 82-147 tonnes in year 1985 to 4-10 tonnes in year 2007. Carrying capacity estimates varied 37% between the models; model 2 had the lowest estimates while model 1 had highest estimates. The estimated time-varying carrying capacity for model 2 and model 3 varies as function of temperature anomaly. The estimates from model 3 were consistently higher than the estimates of model 2, but on the relative scale the patterns were very similar and both the models showed more than 3 fold difference in carrying capacity between low and high temperature years (Figure 2.3c).

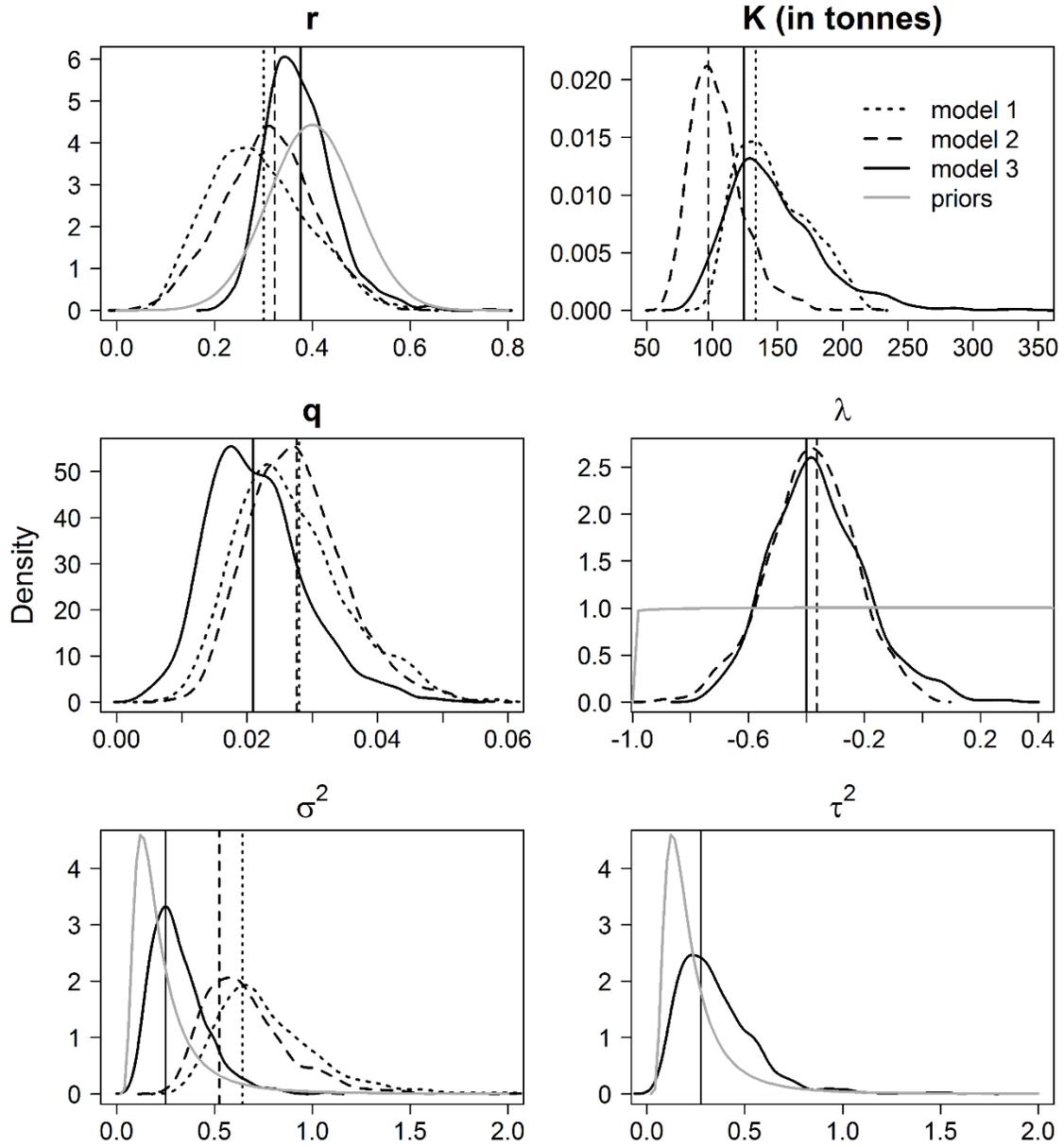


Figure 2.2. Parameter densities from all surplus production model formulations.

The prior and posterior densities of parameters from model 1, model 2, and model 3 are superimposed in each panel. The magnitude of  $q$  presented in the figure is  $1000 \cdot q$ .

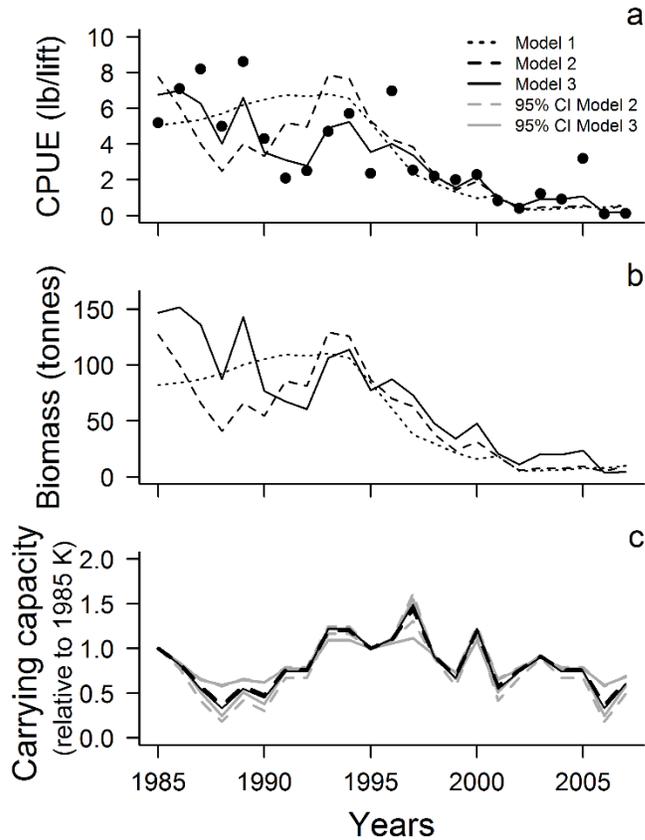


Figure 2.3. Time-series of (a) fitted CPUE, (b) estimated biomass, and (c) temperature-influenced time-varying carrying capacity estimates.

Dotted lines in panel c indicate 95% confidence interval of the estimates for respective models.

I compared the model predictions for stock status and fishery status and found that all three models gave similar predictions about current depletion and the trajectory of fishing mortality (Figure 2.4). All the models suggested that the harvest rate was higher than MSY in several years after 1995 (Figure 2.4). However, the models estimated substantially different base year (1985) biomasses. Model 1 estimated the fraction of biomass to carrying capacity at base year ( $P_0$ ) as 0.61 while models 2 and 3 estimated it to be nearly at carrying capacity (Figure 2.4), suggesting a stronger decline in biomass caused by temperature change.

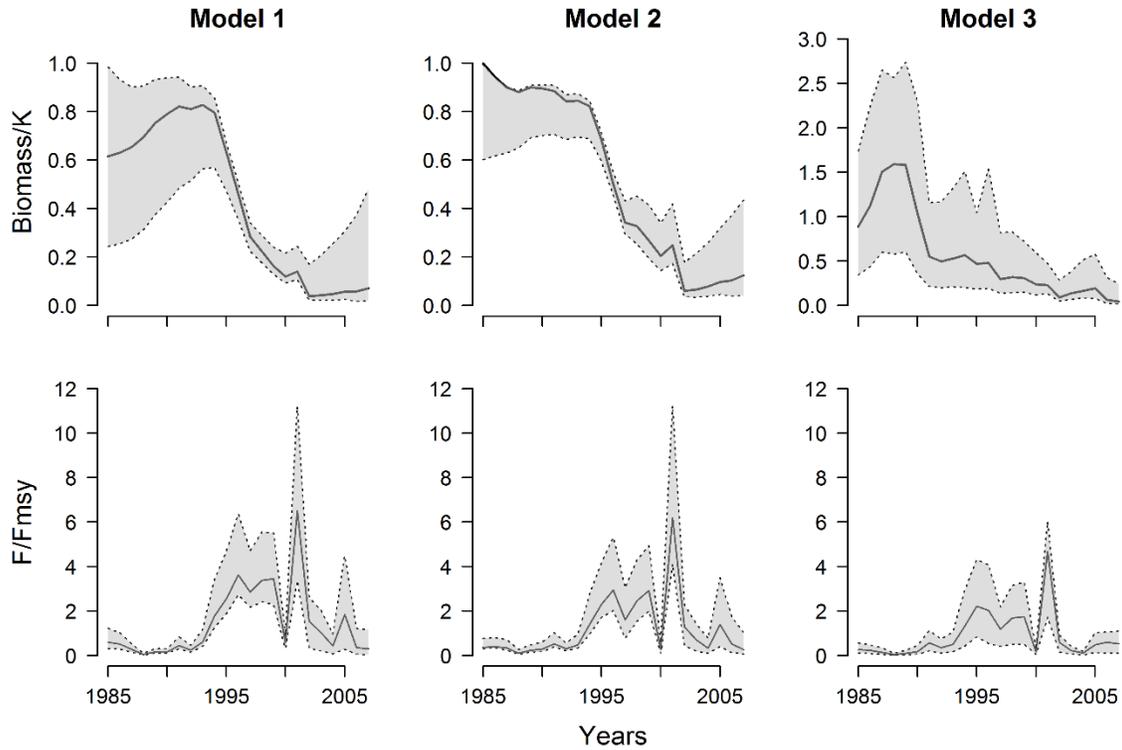


Figure 2.4. Biomass relative to carrying capacity ( $K$ ), and fishing effort ( $F$ ) relative to  $F_{msy}$  across all the models' formulations.

Dotted lines show 95% confidence interval for respective models.

Based on the Akaike's Information Criterion (AIC) statistic, which measures the goodness of fit while adjusting for the addition of parameters, model 2 was judged to best describe the given data (Table 2.2).

Table 2.2. Comparison of the 3 models based on AIC statistics.

Models	Objective function ( $-\log_e$ -likelihood)	$\log_e$ -likelihood	Number of parameters	AIC	$\Delta$ AIC
Model 1	30.55	-30.55	5	71	4
Model 2	27.54	-27.54	6	67	0
Model 3	35.60	-35.60	29	129	62

## 2.4 Model forecast: Comparison with observation

The model was fitted to data from 1985 to 2007. The observations from 2008 to 2012 were used to evaluate the forecast from the model using the SPmodel parameters estimated for Model 2. The model was able to successfully predict the increase in biomass in 2009 to 2010 and the decline in 2011 and 2012. Temperatures were below average in 2008, 2009, and 2010; in fact, the temperature observed in 2008 and 2009 was the lowest after 2000. The model predicted an increase in biomass which was lower than the peak observed in 2009. However, this period also saw slow increase in catch (2008, 2009, and 2010: 0.17, 3.04, 7.65 tonnes respectively). The temperature increased to near average levels in 2011, but the catch was high, 25.28 tonnes. Temperatures increased to above average levels in 2012, this combined with the catch taken in 2012 (~1.79 tonnes) and the previous year led to the decline in cisco biomass.

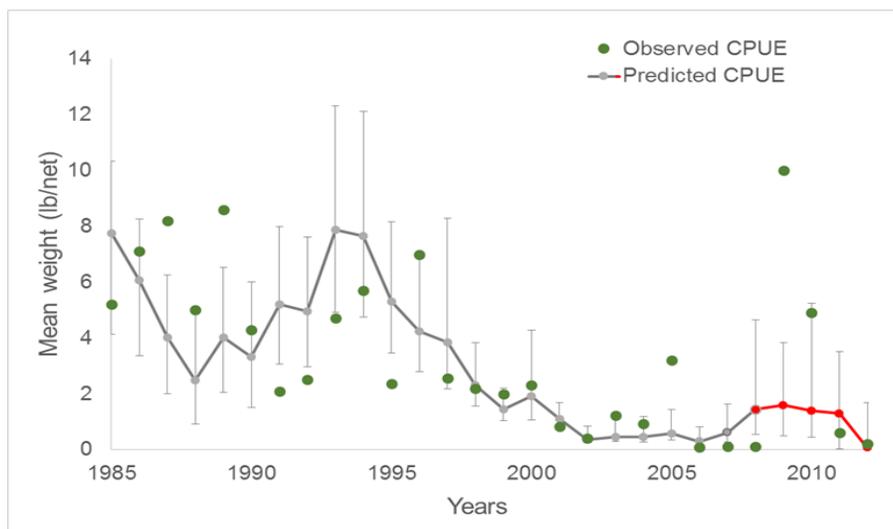


Figure 2.5. Model forecast: comparison with data.

Dot represents observed CPUE trend. Grey part of line is fitted to CPUE data (1985-2007) while red part of line is model prediction starting from year 2008. The trend of predicted line is in close agreement with observed data

## 2.5 Discussion

### 2.5.1 Model formulation

It's not uncommon to incorporate environmental variables to assess the climatic effects on population dynamics in various fields. In a study of the California sardine (*Sardinops sagax*), Jacobson *et al.* (2005) investigated the environmental effects on the fish productivity (productivity was correlated with El Niño related variation in habitat area) using an “environmentally dependent surplus model (EDSP)”. A study on predicted effect of temperature increase on a songbird (*Cinclus cinclus*) population in Norway related net recruitment rate to temperature effect and estimated the change in carrying capacity (Sæther *et al.*, 2000). The response of a cod (*Gadus morhua*) population under various climate change scenarios was explored by relating recruitment to temperature variables (Clark *et al.*, 2003). In this model, the parameter  $\lambda$  was used to define a correlation between carrying capacity and temperature. Since summer kill was observed for cisco, I hypothesized that cisco survival in Mille Lacs Lake decreased in years of high temperature thus affecting the carrying capacity in any given year. The current model formulation could be altered to include parameter  $\lambda$  as a correlation with intrinsic rate of growth  $r$ , if it were expected that juvenile survival rate was associated with the environmental covariate. The alternate parameterization would lead to different parameter estimates, but the resulting population biomass dynamics predictions would be very similar because  $r$  and  $K$  parameters are correlated with each other. However, I believe that it was more appropriate to relate temperature to carrying capacity because recent studies (Fang *et al.*, 2012) that have explored the effect of temperature on cisco in detail have related it to the available refuge volume in the lake. Further, temperature caused mortality mostly in the adult population;

therefore, the impact of temperature was more on the carrying capacity of the population rather than the intrinsic rate of growth.

Including process error in the model did not alter the estimate of the temperature decline parameter, thus showing that process error in the model could not explain the decline in cisco population. I explored additional model formulations including alternate descriptions of temperature anomaly using accumulated degree days, an asymmetric surplus production model (modified Fox model), and process error only models. Model 2 provided a better fit to the data than any of the additional models explored. For the purpose of clarity, the additional models are not included here, but are provided in Appendix A.

I consider that my modelling approach is the first step towards quantifying the effect of temperature on cisco. Given the data limitations, I was not able to explore an age-structured model to capture the effect of temperature on age specific cohorts of the population. Since several lakes have exhibited cisco mortality (Colby and Brooke, 1969; Jacobson *et al.*, 2008), it might be possible to undertake a large-scale meta-analytic modelling of lake specific and age specific effects of temperature on cisco populations.

### *2.5.2 Temperature, management, and ecosystem implications*

Many cold water fish species move to cooler, deeper waters of lakes in the summer months. Deeper waters, however, might present constraints associated with lower oxygen concentration. Jacobson *et al.* (2008) described that cisco mortality was generally observed in lakes with high temperatures in the epilimnion and hypoxic conditions in the metalimnion and hypolimnion. In Amisk Lake in Alberta, Canada, after lake aeration

ciscoes were found in deeper waters (Aku *et al.*, 1997) showing an increase in available habitat when the oxygen concentrations improved in the hypolimnion. Mille Lacs Lake is located at the southern extent of cisco distribution and is a relatively shallow lake. As stated earlier, a thermocline does not develop in this lake, and cisco do not have an opportunity to find a thermal refuge in deeper cooler waters. This further establishes the importance of temperature as a driving factor for cisco mortality.

All the three models were able to explain the cisco population decline ( $B_{2007}/K < 0.1$ ). It is not possible to rule out whether the relationship of the stock size with temperature is causal or accidental. Previous observations of summer kill in the lake and the results from model 2 and model 3 indicate that cisco decline is a combined effect of temperature and fisheries. In 1985, the temperatures were low and the biomass of cisco was high. However, temperature increased from 1985 to 1988 but cisco biomass remained high from 1985 to 1989. During this period, the cisco catch was low, with a continuous decrease in catch from 7.3 tonnes in 1985 to 0.7 tonnes in 1988 (Figure 2.1e). The model estimates a decline in carrying capacity between 1985 and 1988 (Figure 2.3c), but suggests that the biomass did not decline because the catch was low. After 1990, temperatures declined and stayed low till 1997. This period saw an increase in carrying capacity of cisco in the lake. The same period recorded some of the historical highest catch of cisco obtained from Mille Lacs Lake (Figure 2.1e). Catch decreased after 1997 but the fishing mortality considerably exceeded the  $F_{MSY}$  in years following 1995 (Figure 2.4). Following the high harvest rate in high temperature year 2001, the biomass fell to less than 10% of the carrying capacity. Temperatures in 2002 were similar to the temperatures in 1991-92, but biomass levels were much lower. The main reason was that in years preceding 1991, fishing mortality was lower

than  $F_{MSY}$  while in years preceding 2002, fishing mortality was higher than  $F_{MSY}$ . Thus increase in temperature was a major cause in decline of cisco, but fishing ( $F/ F_{MSY} > 2$ ) was also an important contributor to the decline.

Results of models 2 and 3 suggested that increase in temperature in future years would lead to increased stress on Mille Lacs Lake cisco and could lead to further population decline. Catch in 2006 was low (<5 tonnes compared to historic catch levels of >20 tonnes), and the fishing mortality was lower than  $F_{MSY}$ . As a result, biomass in 2007 showed a 2% increase. In order to ensure species recovery, the study suggests that strong restrictions on cisco catch be made in warmer years, especially in light of the current depletion level.

In this research, I did not explore change in predatory pressure as a possible cause for cisco decline. The abundance of the major predator species of cisco—walleye (*Sander vitreus*)—has remained consistent over the study period, and another forage species—yellow perch (*Perca flavescens*)—contributes to more than 75% of the walleye diet. However, I cannot ignore the possibility of walleye being a driver in the decline of cisco, and this question could be explored further in ecosystem-wide models of Mille Lacs Lake.

## 3 Ecosystem Simulations for Ecosystem Based Fisheries Management in Mille Lacs Lake, Minnesota<sup>2</sup>

### 3.1 Introduction

Mille Lacs Lake (MLL), Minnesota is a complex freshwater food-web ecosystem that harbors around 50 fish species along with other vertebrates and invertebrate species. Fishes such as walleye (*Sander vitreus*) and northern pike (*Esox lucius*) are top-order predators; yellow perch (*Perca flavescens*), shiners (*Notropis* spp.), darters (*Etheostoma* spp.) and cisco (*Coregonus artedi*) are prey species of the lake. Besides, mammals, growing numbers of piscivorous birds like double-crested cormorants (*Phalacrocorax auritus*) might have important influences on the lake food-web. Apart from direct prey-predator effects, in a complex-food web one may expect a number of indirect effects such as trophic cascades, compensation, and cultivation depensation (Walters and Kitchell, 2001). Temperature is one of the most significant abiotic components of ecosystems because it plays dominant roles in determining the rate of physiological process of organisms, especially coldwater species in the northern hemisphere, (Shuter *et al.*, 2012) and therefore affects the functioning of food-web. Species such as cisco and burbot (*Lota lota*) are cold-water stenotherms and therefore are highly sensitive to the changes in lake water temperature. The optimum temperature for cisco is below 20 °C while for burbot is below 18.2 °C (Scott and

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<sup>2</sup> A version of this chapter will be submitted for publication.

Crossman, 1973). The average Mille Lacs Lake water-temperature between 2000-2005 was measured to be mostly higher than 19° C during the period of July to August, and the daily temperature on several days reached to over 23° C in August; 2006 was a warmer year, and the average daily temperature was recorded as high as 26.1° C (Jacobson *et al.*, 2008). The summer temperature may cause stress to burbot; the species reduces its feeding rate at higher temperature (Hardewig *et al.*, 2004). On the contrary, the phase of high temperature has a positive influence on the growth of smallmouth bass (Wuellner *et al.*, 2010) especially young smallmouth bass (Dunlop and Shuter, 2006). The preferred temperature of adult bass is in the range of 21-27°C; however the preference range was even higher in the laboratory measurements (Edwards *et al.*, 1983).

Further, fisheries play an important role in determining the dynamics of food-web because the fished-species are integral component of the ecosystem in which they live. The lake offers fisheries for multiple species (mainly walleye, yellow perch, northern pike, smallmouth bass, cisco) with walleye contributing more than 70% of the total harvest. More detail including figures showing catch trends for MLL fisheries was provided in section 1.2 and so is not repeated here. For addressing such complex food-web interactions coupled with the impact of fishing and temperature changes, an efficient ecosystem-wide modelling exercise is required.

As discussed in section 1.5.1, I used Ecopath and Ecosim (EwE) ecosystem modelling software (considered to be one of the top ten breakthroughs by National Oceanic and Atmospheric Administration (NOAA) to build the Mille Lacs Lake ecosystem model. EwE is a food web based model that works on the principle of energy balance in the

ecosystem (Christensen and Pauly, 1992; Christensen and Walters, 2004). In section 1.5.1 in Chapter 1, I discussed details of the strengths and weaknesses of EwE; the various fields where the EwE has been used; the features of alternative available ecosystem modelling frameworks; and my reasons for adopting this modelling approach.

As mentioned, the effect of temperature changes on the sensitive species cited above may have significant direct or indirect effects on the food-web. Thus, simulating the trophic model with a temperature driver linked to such species could enhance its prediction performance. The EwE modelling approach can incorporate environmental effects by constructing forcing functions and applying these to various input parameters in the model. The impacts of temperature and fisheries on the cisco population was explored in Chapter 2. The ecosystem model here allows the exploration of interspecies interactions on cisco and many questions related to species biomass dynamics and fisheries management in Mille Lacs Lake within an ecosystem context.

By building the Mille Lacs Lake ecosystem model, this chapter aims to:

- (i) quantify the predator-prey interactions in Mille Lacs Lake
- (ii) use the model to reproduce the historical dynamics of the principal lake species
- (iii) perform temporal simulations for analyzing scenarios for fisheries management purposes.

## 3.2 Methods

### 3.2.1 Ecopath

EwE version 6 was used to build the Mille Lacs Lake ecosystem model (Christensen *et al.*, 2008) with the aim to study the food-web dynamics of Mille Lacs Lake. Each functional group in the static mass-balance model (Ecopath) was parameterized using life-history, production, consumption, and diet matrix parameters. The details of Ecopath and Ecosim can be found in Christensen and Walters (2004); however, the following section presents the key aspects of the modelling routine. The mass-balance constraint ensures that the extraction of energy (by predation, fishing etc.) from a functional group is replenished through consumption by the group; the two master equations of Ecopath explains this energy balance. The first equation ensures energy balance among the groups as (Equation 14):

$$B_i * (P/B)_i = Y_i + \sum_j (B_j * (Q/B)_j * DC_{ji}) + E_i + BA_i + B_i * (P/B)_i * (1 - EE_i)$$

Equation 14

where subscript  $i$  and  $j$  indicates prey and predator group respectively;  $B$  stands for biomass,  $P$  for production,  $Y$  for total fishery catch,  $Q$  for consumption, and  $E$  for net migration rate;  $DC_{ji}$  is the fraction of prey  $i$  in the diet of predator  $j$ ;  $BA$  accounts for biomass accumulation; and  $EE$  explains ecotrophic efficiency *i.e.* fraction of group mortality explained in the model.

The second equation explains the energy balance within a functional group using Equation 15 as:

$$\textit{Consumption} = \textit{Production} + \textit{Respiration} + \textit{Unassimilated food}$$

*Equation 15*

The Ecopath model built here characterised the ecosystem condition of the lake in the year 1985. Ecosystem drivers such as producers, consumers, and detritus were combined into 50-functional groups in the ecosystem model: 21 groups of fish; 2 groups of birds; 8 groups of invertebrates; 1 group each for otters and minks, turtles, frogs, and zooplankton; 3 groups of producers; and 1 group for detritus (Figure 3.1). The functional groups and dietary interactions in the model have been developed through an extensive process of consultation and interaction with Minnesota Department of Natural Resources (MNDNR).

Age-structure in Ecopath is modelled using a multi-stanza setup: 6 species of fish are modelled with multi-stanza; walleye was sub-divided into 4 stanzas (age 0, age 1, age 2 and age 3+); yellow perch, northern pike and cisco into 3 stanzas (age 0, age 1, and age 2+); muskellunge and smallmouth bass into 2 stanzas (age 0 and 1+). The biomass dynamics between juveniles and adults group is governed based on Deriso-Schnute delay-difference model (Christensen and Walters, 2004; Walters *et al.*, 2000). The stanza feature allows the model to account for differences between juvenile and adult in the diet composition (many juveniles are planktivorous while adults are piscivorous), in the vulnerability to predation, and in the fishing mortality. In MLL, the recreational fisheries catches for many important species like walleye, northern pike, and smallmouth bass are regulated by size based

restrictions; so, the fishing mortality on juveniles and adults is different. This is the reason for the incorporation of the multi-stanza framework for the important fish species.

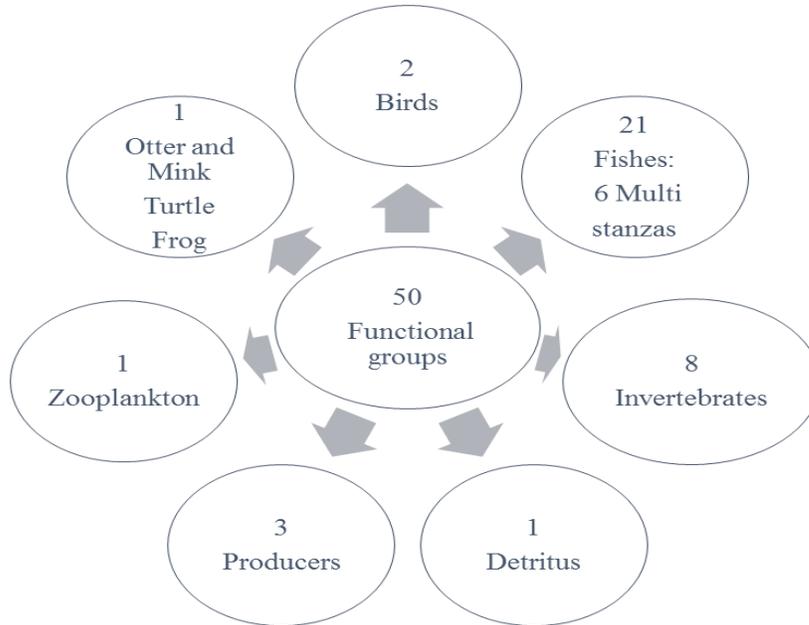


Figure 3.1. Summarised representation of functional groups in Mille Lacs Lake EwE model. The complete list of species, scientific names, input parameters are presented in Appendix C.

### 3.2.1.1 Data sources

An Ecopath model essentially requires the data of diet interactions and any 3 parameters among the 4 of B, P/B, Q/B and EE; it estimates the 4<sup>th</sup> one using its mass-balance assumption (Christensen and Walters, 2004; Christensen *et al.*, 2008). In the case of availability of the 4 parameters, Ecopath can estimate either biomass accumulation or net migration rate. The data for those parameters were obtained from various sources; however most of the data used in the model were collected by MNDNR for the lake. To determine the stock-status, MNDNR has been carrying out various sampling programs for years such as setting of standard inshore and offshore gill nets, hauling trawl net, performing tagging,

and using electro-fishing techniques. Samples of some important fish species are also brought in for gut-content analysis.

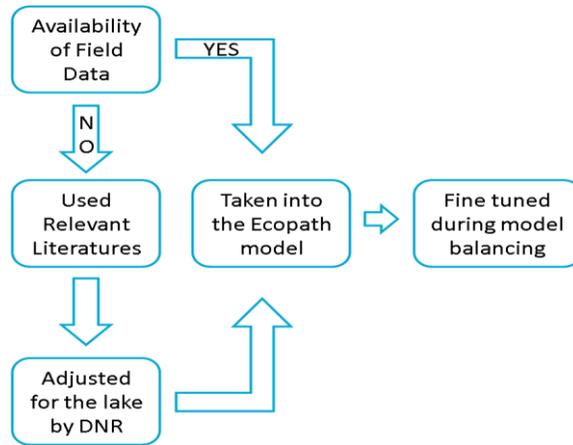
Besides MNDNR, other sources of parameters were relevant published literature and length-weight and surplus production analysis using the field data. Simple surplus production (SP) models were used to estimate the historic biomass trends starting from year 1985 for many species for which gill net CPUE data was available (see Appendix B for SP model). For walleye the biomass estimate was taken from the Statistical Catch At Age model (Drake, 2007). The SP models were also used to calculate the fishing mortality estimates for the 1985 Ecopath model. For the functional groups of fishes for which biomass values were not estimated by the SP model because of unavailable or uninformative CPUE data, the biomass was estimated by the Ecopath mass-balance approach, usually by providing a reasonable EE value. In some cases professional guess values were also used to approximate biomass.

Details about the definition of the 50 functional groups and sources of all data (B, P/B, Q/B, diet etc) used in the Ecopath model can be found in Appendix C of the thesis.

### **Diet matrix**

For the diet selection, preferences were given to field estimates based on gut-content analysis conducted by MNDNR. However, these data were available for only the major species. In the absence of field data, relevant literature was used and adjusted to make it congruent for the lake. The diet matrix thus created was reviewed several times in

consultation with the MNDNR staff, and some alterations were made during the process of balancing the model. Figure 3.2 depicts the processes for diet selection for the EwE model.



*Figure 3.2. Process of parameterising the diet matrix*

*The direction of arrows show the process of finalising the diet matrix of the Ecopath with Ecosim model*

Mille Lacs Lake complex food-web representation (Figure 3.3) was developed by Kumar and Varkey (2009) using Statistical Analysis System (SAS) software. The diagram with over 2000 linkages (interactions) shows the complexity of the Mille Lacs Lake food-web.

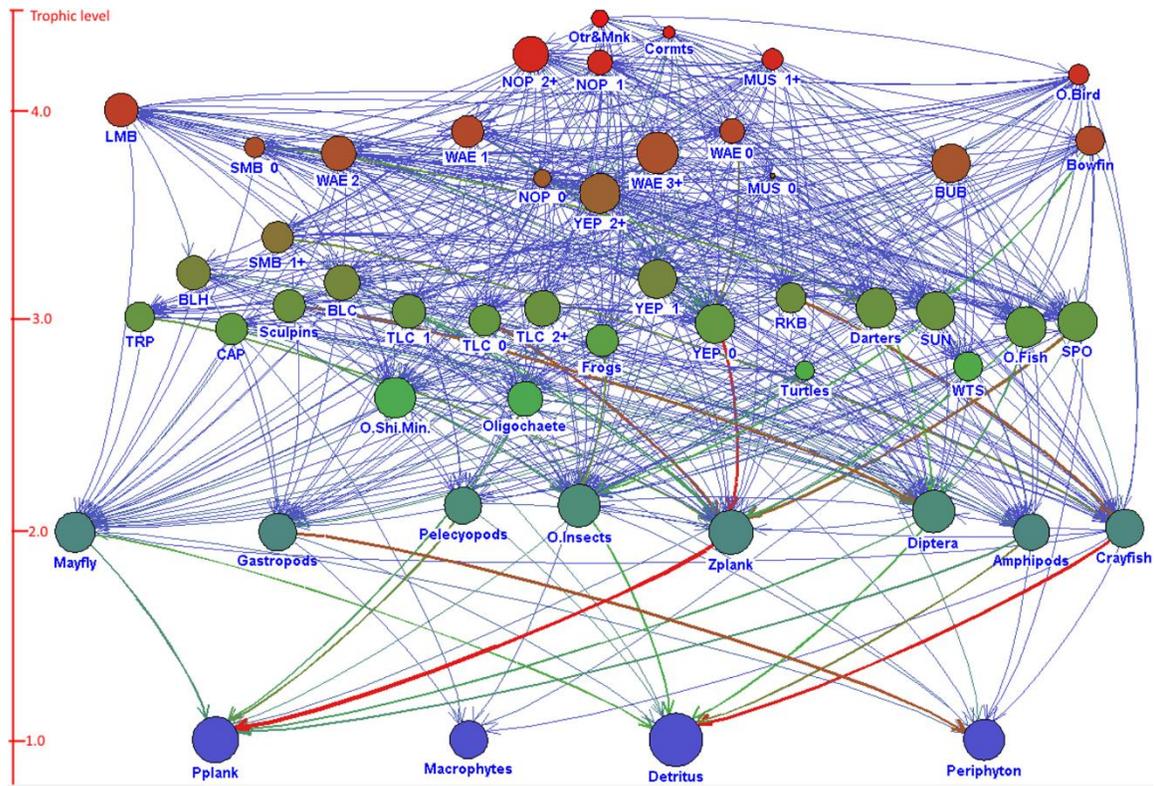


Figure 3.3. Mille Lacs Lake food-web.

Each circle (node) represents a functional group of the model. The sizes of circles are scaled logarithmically to the biomass of the functional groups that the circles represent. The positions of the circles are set according to their trophic level in the model. Connecting lines (link lines) show the predator-prey interactions. The color coding of link lines are mapped between red for highest interaction and blue for the least interactions; remaining colors of link lines represent intermediate interactions. The color coding for circles reflects the trophic level of the species, the primary producers are shown in blue, the top predators are shown in red and the intermediate trophic levels are represented in intermediate colors. Name coding: BLH=bullhead, BUB=burbot, CAP=common carp, Cormts=cormorants, LMB=largemouth bass, MUS=muskellunge, NOP=northern pike, RKB=rock bass, SMB=smallmouth bass, SPO=spottail shiner, SUN=sunfish, TLC=cisco, TRP= trout-perch, WAE=walleye, WTS=white sucker, YEP=yellow perch.

### 3.2.2 Ecosim

The static mass-balance Ecopath model is then used to initiate a time-based dynamic simulation (Ecosim) for tracking changes in the biomass of species with temporal changes in catch patterns, food-web (predators-preys interaction), and environmental condition. The

dynamic change is assessed using Equation 16 derived from the first master equation of Ecopath:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i) * B_i$$

Equation 16

where,  $dB_i/dt$  is the biomass growth rate of group  $i$  in time-interval  $dt$ ;  $g_i$  denotes net growth efficiency (production/consumption) of group  $i$ ;  $Q_{ji}$  is the consumption by group  $i$  while  $Q_{ij}$  is for group  $i$  consumed by predators;  $I_i$  is the immigration rate;  $MO_i$  explains other mortality excluding fishing and predation and  $F_i$  is the fishing mortality. Note that the actual consumption in the Ecosim diet responds dynamically through time to predator and prey biomasses as constrained by the diet preference matrix of probabilities provided by Ecopath (see Figure 3.6)

Consumption by a group highly depends on available biomass of prey and its exchange rate between unavailable and available states (foraging arena theory: Walters *et al.*, 1997). The theory says the prey population is split into ‘vulnerable’ and ‘invulnerable’ fraction, and the transfer rate between the two fractions is defined as vulnerability (Ahrens *et al.*, 2012; Christensen and Walters, 2004; Walters *et al.*, 2000). Each predator-prey trophic interaction is assigned a vulnerability ( $v$ ) value, from one to infinity. If  $v=1$ , a bottom up or donor driven relationship is implied. Assigning a high value, implies a predator driven interaction, in which predation mortality is proportional to the product of prey and predator abundance (i.e., Lotka-Volterra). This implies a high flux rate for prey species in and out of vulnerable biomass pools. For a high value for vulnerability parameter, if the predator biomass

doubles, the increase in predation mortality would be approximately 2 times. If vulnerability ( $v=1$ ), a similar increase in predator biomass will not have a large effect on the predation mortality.

### 3.2.2.1 Forcing functions

Ecosim version 6 (Christensen *et al.*, 2008) has the capability to incorporate the temperature tolerance of a species in calculation of the biomass dynamics. Forcing functions are automated routines in Ecosim used to incorporate environmental effects, like effects of temperature change. Here the shape of the function follows the change in the environmental variable. The user provides the optimum temperature for a species and upper and lower bounds of its temperature tolerance—the upper tolerance level for cisco was obtained from the literatures of Edsall and Colby (1970) for younger cisco and Colby and Brooke (1969) for adult cisco. In the next step, the temperature time-series is entered as a forcing function, and within Ecosim the forcing function is applied to the P/B ratio of the functional group. When the temperature in the time-series deviates from the optimum temperature provided for the species, the P/B of the species is affected; consequently, the biomass trend is affected. To explain how temperature change is related to the P/B ratio of a species, I present Figure 3.4. At the optimum temperature, the P/B of the group is equal to the Ecopath base P/B. As the temperature changes (increases or decreases) from the optimum, the P/B rate decreases. The rate of decrease is reflected by the slope of the curves (Figure 3.4). For a eurythermal species, the difference between the critical temperature and the optimum temperature is larger than for a stenothermal species. As shown in Figure 3.4, the farther the critical temperature is from the optimum, the shallower the slope of the curve. The user is allowed to separately parameterize the limbs to right and left of the

optimum (i.e. there is no limitation to assume a symmetric tolerance to temperature above and below the optimum temperature).

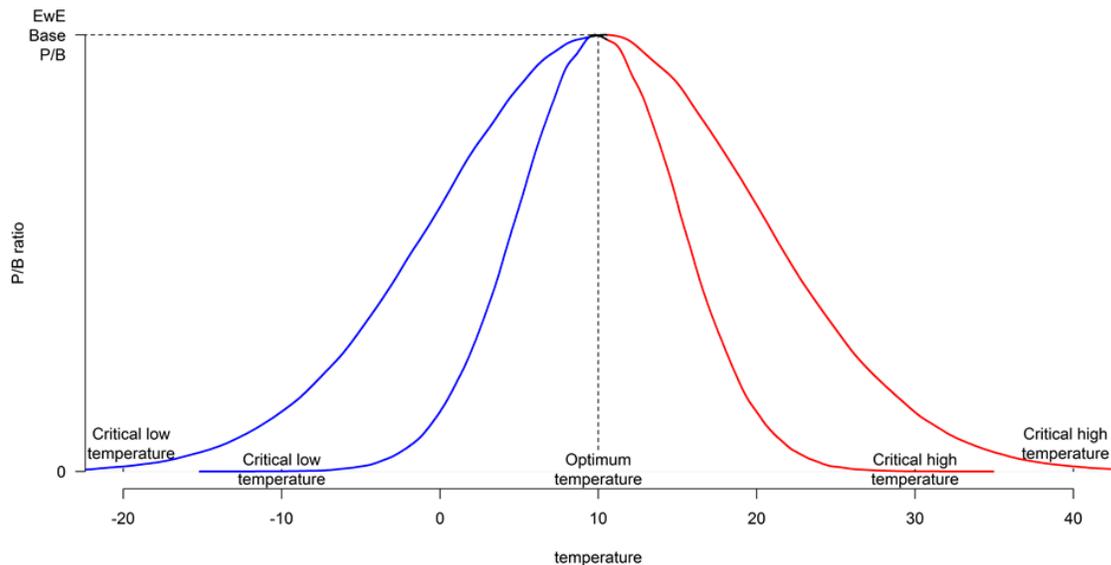


Figure 3.4. Change in  $P/B$  as temperature deviates from the optimum.

The slope of the decline of  $P/B$  value depends on the difference between the optimum and the critical temperature: for a species with small tolerance range the  $P/B$  decreases sharply compared to a species with wide tolerance range. Also,  $EwE$  allows the user to parameterise the temperature tolerance below optimum (blue) and above optimum (red) separately (i.e. there is no restriction that the tolerance map should be symmetric around the mean).

The average temperatures observed in July and August from 1985 to 2006 were used to build the forcing function because, as discussed in Chapter 2, cisco mortalities were commonly observed in July and August (Jacobson *et al.*, 2008). I assumed that temperatures of the lake in other months were at not a significant source of mortality.

The same temperature forcing function was applied to model burbot, and the temperature tolerance levels for burbot were adjusted according to the findings in Hofmann and Fischer

(2002). The temperature forcing function was also applied to smallmouth bass; it was applied such that the vulnerability of prey to the juveniles of smallmouth bass increased at high temperature. Several studies have indicated that smallmouth bass, especially young immature fish have higher growth and survival in warmer waters (Dunlop and Shuter, 2006).

#### **3.2.2.2 Ecosim: Fitting to time-series**

The base Ecosim model with 50 functional groups was tuned with historic time-series data of catch and abundance from 1985 to 2006 in order to reconstruct the historical trends; the process is termed model-fitting. The first step in the fitting process was to identify the most critical vulnerability interactions in the model. The sensitivity of the sum of squares of differences between model predictions and time-series data points with change in vulnerability values were analysed using an automated routine in Ecosim, and the vulnerability interactions which highly influenced the sum of squared differences between the observed and predicted time-series were selected. However, the goal of fitting was not to simply reduce the sum of square deviations as some time-series have scarce or erratic values while other series have more representative information—it is up to the judgement of the modeller to decide which time-series are key to explaining the dynamics in the system. Ecosim allows the modeller to assign different weights to different series; time-series which were erratic (for example, common carp CPUE series) could be assigned low weights during the fitting—thus the Ecosim model in its automated routines would not assign the same importance to reduce the sum of squares of the common carp series as for the walleye series. There are two approaches to search for vulnerabilities: (1) where all the vulnerability values associated with one predator are searched in one set, and (2) each

selected predator prey interaction is searched independently. The first approach assumes that interactions of a predator with its entire prey species are similar, and the second approach assumes that the interaction of the predator with each of its prey could be unique. When all the prey of a predator are expected to be equally vulnerable to the predator (similar biomass and behaviour) then the first approach is appropriate. During the fitting process, the search was first conducted by predators and then several manual adjustments were made to fit the time-series.

There is a regular stocking program for muskellunge in the lake; hence, the resultant biomass every year is not entirely dependent on the biomass changes due to food-web and fisheries interactions. Therefore, for muskellunge, the biomass was forced using absolute biomass values. The biomass vector for cormorants and other piscivorous birds were also forced in the model. The bird population was composed of birds settled on the two islands of Mille Lacs Lake and birds migrating from other areas around the lake; their relative composition cannot be captured in the functional group dynamics of the model; except in the case where the lake experiences a constant inflow every year in which case a constant rate of immigration could be used to model the group. This was the reason behind forcing the bird functional groups in the simulation.

The Ecosim model was able to reasonably predict the dynamics of the walleye and northern pike population; walleye population is stable while northern pike shows an increasing trend (Figure 3.5). The model reproduced the decline of cisco and burbot biomass observed over the time period. The model predicted an increase in yellow perch and smallmouth bass population in the lake but not to the levels indicated in the observed CPUE trends. The

model predicts an increase in rock bass but a decrease in white sucker and black crappie. The period of cisco decline also saw the increase of yellow perch which became the most important forage species in the lake.

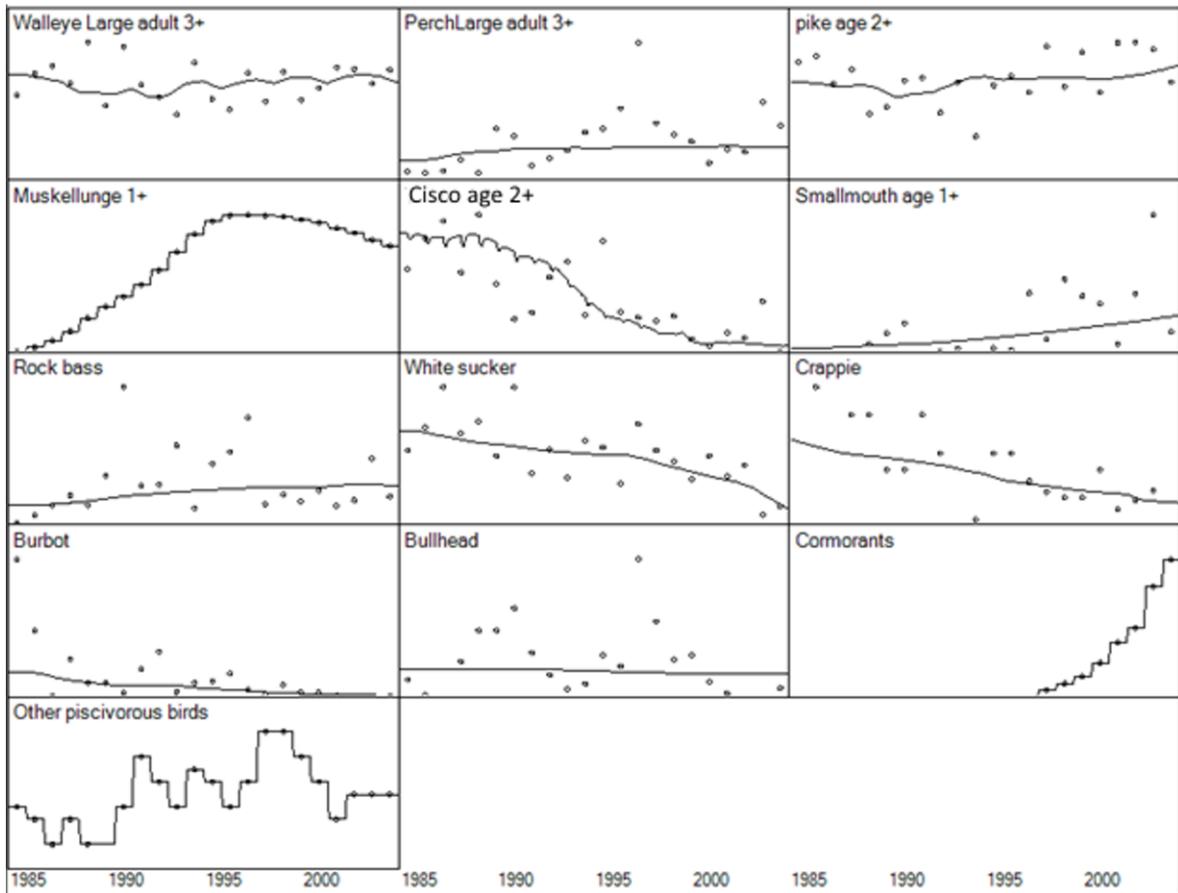


Figure 3.5. Ecosim fitting from 1985-2006.

The dots are the observations and the lines are the Ecosim predictions. Prediction lines that exactly follow the dots are forced biomasses.

I present the changes in diet for some predator-prey interactions over the time period of fitting (Figure 3.6): cisco became less important in the diet of walleye (panel a); yellow perch seemed to essentially fill the gap for a forage species left by cisco decline as can be judged from the increased contribution of yellow perch in the diet of northern pike. There

were other changes in diet too but here the purpose is to show that diet for a species changes during the fitting period within the Ecosim simulation as a response to changes in predator and prey biomass and foraging arena calculations. The trends in observed data for bullhead were highly erratic, and the model predicted no change in bullhead biomass during the 21-year period.

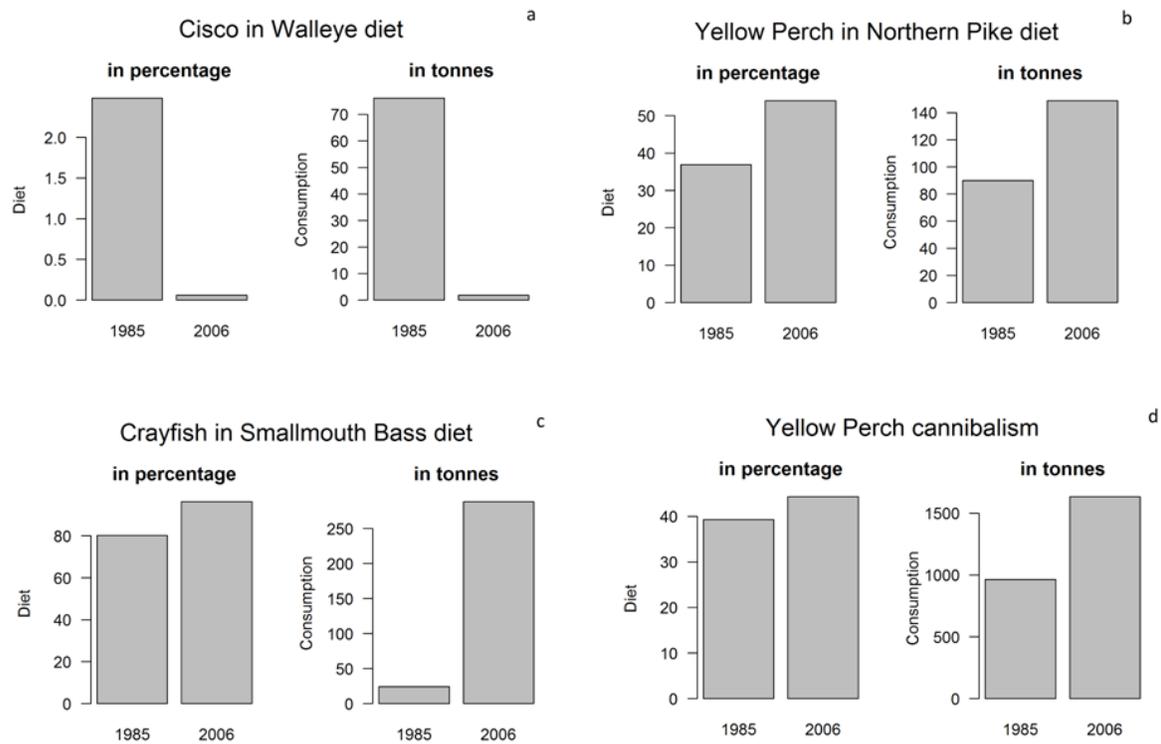


Figure 3.6. Diet changes within Ecosim during fitting period

The figure demonstrates that diet changes within Ecosim with changes in prey and predator biomass, and foraging arena calculations. The bars on the left show the percentage of prey in predator diet and the bars on the right panel show the resultant consumption in biomass.

### 3.2.3 *Ecosim scenarios*

It is not possible to conduct adaptive experiments on a lake of this size to understand the strength of interactions between species for managing the system based on ecosystem approach to fisheries. In this situation, one of the best options available is to test alternate scenarios with greater confidence by using a fitted-ecosystem model. As has been highlighted by several authors (Fulton et al 2003; Plaganyi 2007), ecosystem models are helpful in comparing strategic management options. The Ecosim representing Mille Lacs Lake ecosystem was dynamically simulated forward in time under various fisheries management scenarios to gain understanding on how the ecosystem could possibly respond to change from current management. Temperature effects were extended into the scenario period; in other words, all the drivers that were part of fitting the model to the historical time series were also extended into the scenario period. For the scenario period, for July and August, I chose the average temperatures for 2000 to 2005 (Figure 1.4b); a period that showed higher temperature than the previous decade. As applied to the fitting of the model, temperature was applied to the P/B of cisco and burbot and to the vulnerability parameters for smallmouth bass. The list of alternative scenarios was developed in conjunction with requests from the biologists at MNDNR. These are the management scenarios, the ecosystem implications of which the management was interested to explore as part of the ecosystem-based management initiative, of which this modelling was also a part. The specific rationale behind each management scenario is presented together with the description of the results for each scenario. All the scenarios were driven by the historical time-series data of fishing mortality (F) till the year 2006, then it was driven another 25 years (till 2031) using the F values related to objective of the given scenario.

The following scenarios were explored using the Ecosim model:

- (i) Status quo: the fisheries were held at the current levels of fishing mortality;
- (ii) Managing walleye: four scenarios for walleye management were explored—
  - a. the impacts of small levels of fishing mortality on age 2 walleye,
  - b. the impacts of small levels of fishing mortality on age 1 and age 2 walleye,
  - c. doubling fishing pressure on walleye age 3+, and
  - d. doubling fishing on all species other than walleye;
- (iii) Managing cisco: two scenarios for cisco management were explored—
  - a. closing fisheries on cisco and
  - b. extirpation of cisco,
- (iv) Impact of increase in cormorants;
- (v) Fishing all species at their Fmsy levels: the estimation of Fmsy values are presented in Chapter 4.

### *3.2.4 Monte Carlo analysis*

I performed Monte Carlo (MC) simulations explored the Ecosim fitting and scenarios to obtain confidence intervals around the results presented in the chapter. MC analysis in Ecosim allows the modeller to provide coefficient of variation (CV) for the biomass, P/B, Q/B, EE, and biomass accumulation (BA). A 10% coefficient of variation was allowed on biomass, P/B, Q/B, EE and 5% on BA. The MC routine selects random values for the parameters with the given CV but discards any runs that do not achieve mass balance. However, the MC routine in EwE allows a small relaxation above mass balance.

### 3.3 Results

To make the results intuitive and easy to comprehend, the end-results for each scenario are presented in comparison to ecosystem condition of the year 2006, and in the following sections, I referred to year 2006 as baseline. Results are scaled in terms of percentage gain or loss in biomass at the end of simulations in 2031 relative to the biomass in 2006. For each scenario, only those functional groups were described whose biomass changed by more than 20% or the groups deserving special attention for fisheries management purposes. For easy comparison of scenario predictions against current management, I presented the status quo result in the figure for each scenario.

#### 3.3.1 Scenario 1: Status quo

The status quo scenario was analogous to the ‘control’ unit of any experiment; the rationale behind the simulation was to foresee the species composition if 2006 fishing levels were maintained until the end of simulation (2031). This scenario would aid in planning the possible management options and providing an evaluation of their outcomes with reference to the prevailing condition.

Smallmouth bass, northern pike, largemouth bass were the major fish groups which were expected to get substantial benefits under the status quo scenario: their population increased by 85%, 59%, and 37% respectively from the baseline (Figure 3.7). Trout-perch, forage fishes such as shiners/minnows and spottail shiners also benefited. In contrast, walleye biomass was expected to decline by 17% between 2006 and 2031. Other species species such as white sucker, burbot, black crappie and cisco declined by more than 80% while darters and bullhead declined by nearly 25%.

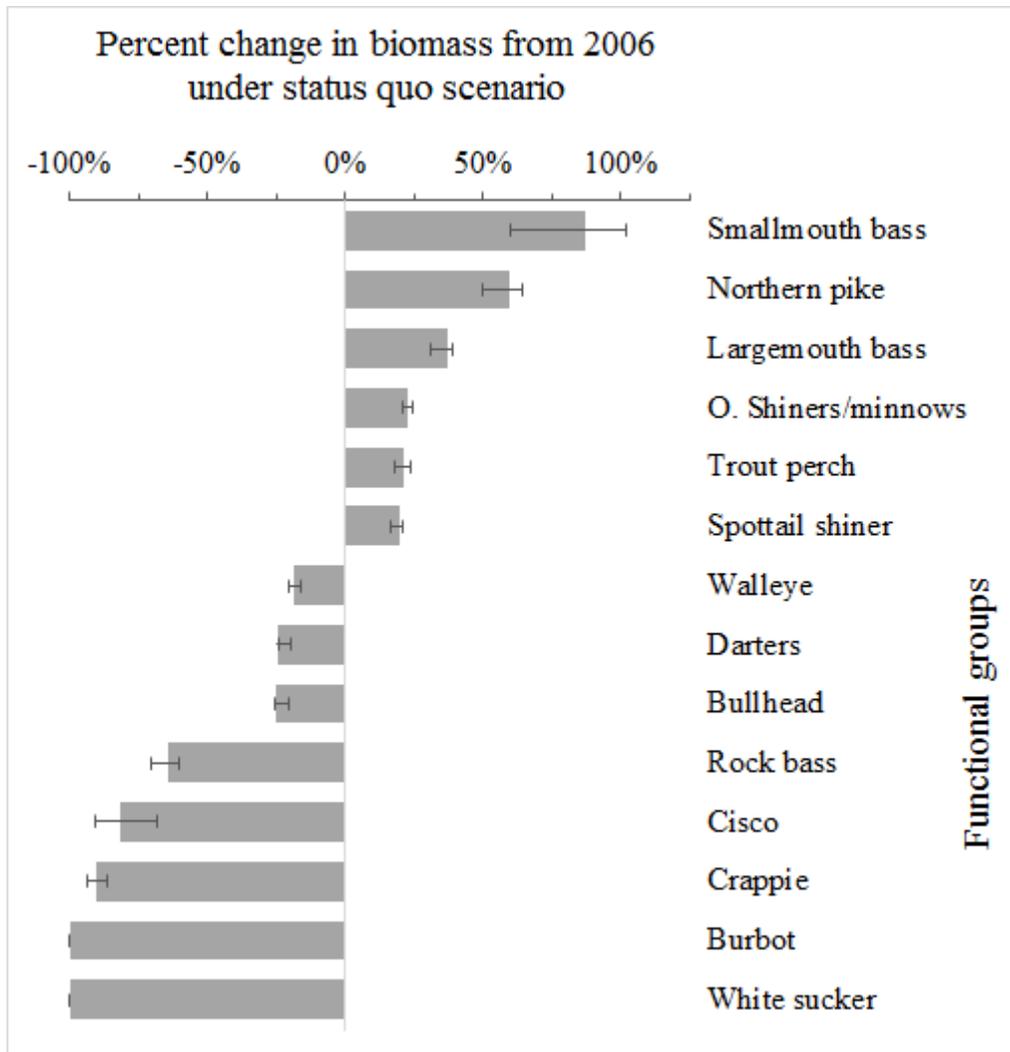


Figure 3.7. Percentage change in biomass observed in the status quo scenario. No change from 2006 biomass of the species would be indicated by 0%.

### 3.3.2 Scenario 2: Managing walleye

Walleye is the most preferred fish in Mille Lacs lake recreational fisheries and so its management has key importance. I investigated 4 alternative scenarios involving increases in fishing pressure over different stanzas of walleye. All the scenarios represent realistic questions for walleye management that could be posed at the model. The scenarios were (2a) Fishing pressure on age 2 walleye equivalent to 10% of walleye age 3+ harvest; (2b)

Fishing pressure on both age 1 and age 2 walleye: 10% of walleye age 3+ harvest on age 2 and 1% of walleye age 3+ harvest on age 1; (2c) increase F (double) on adult walleye (age 3+); and (2d) heavy fishing on all the fished species except walleye.

### **3.3.2.1 2a. Adding fishing pressure on age 2 walleye**

Anglers often release substantial quantities of walleye which are either too small to eat or because of bag limits and size-based regulation prohibits them from keeping the fish (numbers of walleye age 2 and younger released is approximately equal to 20% of total number of walleye harvested). A significant percentage of the released fish die because of injuries inflicted by hooks (hooking mortality). Mille Lacs Lake based study found that hooking mortality of walleye was associated with temperature among other factors such as bleeding and hook location (Reeves and Bruesewitz, 2007). Hooking mortality estimates ranged from 0% in May to 12% in July and August especially when temperature increased above 20°C. It is therefore possible that hooking mortality could increase with lake temperature increase. I simulated the scenario by adding fishing pressure on age 2 walleye equivalent to 10% of the adult harvest while fishing the adult walleye at their SHL. Overall, the walleye biomass decreased by 26% from baseline; the decline was higher than the decline from status quo condition. At the level of individual stanzas compared to the status quo, walleye age 3 and older decreased by 11%, walleye age 2 decreased by 7%, walleye age 1 improved by 4% because of lower predation pressure from larger walleye, and negligible difference was observed for walleye age 0 (Figure 3.8).

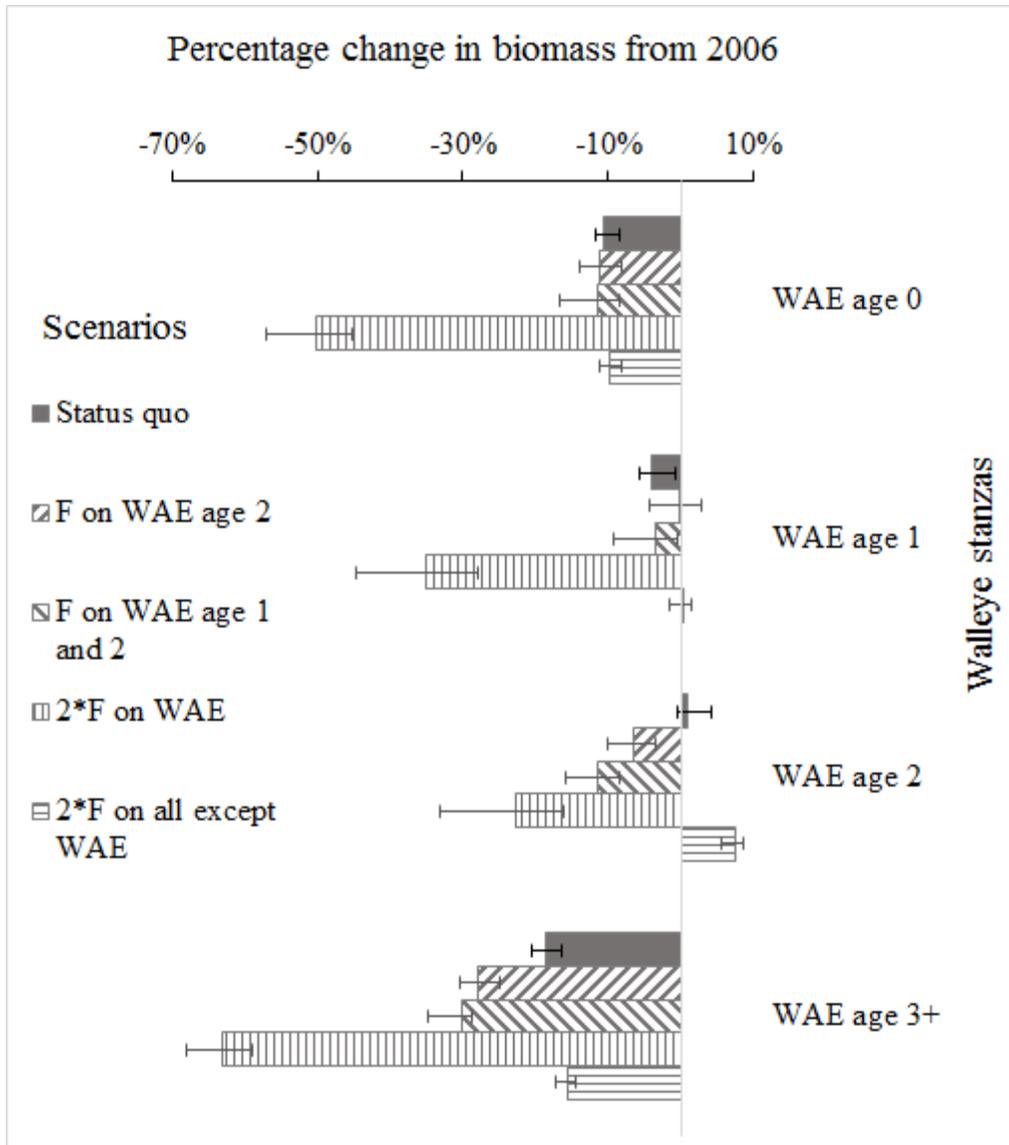


Figure 3.8. Change in biomass observed in walleye stanzas across all the 4 scenarios of walleye. The bar filled with grey color indicates status quo result against which the four walleye scenarios can be compared. 0% indicates 2006 reference line. F indicates fishing mortality, and WAE indicates Walleye.

### 3.3.2.2 2b. Adding fishing pressure on age 2 and age 1 walleye

This scenario could be seen as an extension of the previous scenario. In addition to fishing pressure on age 2 from previous scenario, a very small fishing pressure (equivalent to 1% of adult harvest) was also applied on age 1. All the other conditions were kept same such as

maintaining adult walleye at their SHL. Overall 28% reduction (2% more than previous scenario where fishing pressure only on age 2 walleye was applied) was observed in walleye biomass; the decline was 11% more compared to the condition in status quo (Figure 3.8).

Thus adding fishing pressure on age 1 too, as expected, slightly higher decline were observed at individual stanzas compared to the previous scenario: walleye age 3 and older decreased by 2%, walleye age 2 decreased by 5%, walleye age 1 decreased by 3%, and walleye age 0 decreased by 1%. (Figure 3.8).

### **3.3.2.3 2c. Increase F twice to large adult walleye age 3+**

Walleye management in Mille Lacs Lake states that the exploitation rate of “catchable walleye” (walleye of size around 14 inch or longer) should not be more than of 24% of its biomass; referred to as the “safe harvest level” (SHL). The rationale behind the scenario was to investigate the effect of overexploiting walleye population on walleye stock and other fish populations in the lake. As expected, the effect of the higher fishing pressure reflected directly on walleye biomass. All stanzas of walleye population declined substantially from baseline (age 0, age1, age 2, and age 3 and older decreased by 50%, 35%, 23%, and 63% respectively) (Figure 3.8); the average loss including all stanzas were 60% from the baseline (2006). Conspicuously, the decline was much higher than that of status quo, where the average decline was merely 17% from the baseline. The flip side of the effect was a boost (~100% better) in northern pike, largemouth bass, and sculpin populations. Besides, abundance of bowfin also increased by 44% which was in loss in

status quo. A better performance by cisco was observed compared to status quo, though it still continued to decline.

#### **3.3.2.4 2d: Heavy fishing on all species except walleye**

Recent lake assessment data by MNDNR suggest an increasing trend of abundance for some species such as smallmouth bass and northern pike. As mentioned, the lake is a premiere walleye lake, and its management is largely focused on sustainability of walleye population. Hence, the rationale behind the scenario is to explore the opportunities for improving fishing from the system while aiming to maintain the walleye population.

Fishing mortality on all species except walleye was doubled ( $2 \cdot F_{2006}$ ),  $F$  on walleye was held at SHL. I explored if fishing the other species had any negative impacts on the walleye population. All walleye stanzas performed either slightly better or almost equal compared to status quo, and overall the walleye population biomass increased by 4% from status quo (Figure 3.8).

A major change was noticed in the abundance of common carp; the species, which was improving by 18% from the baseline under the status quo scenario, was reduced by over 80% under this scenario. The species such as northern pike, smallmouth bass, and largemouth bass still had an increasing trend, though not to the same levels as under status quo. The biomass of northern pike increased by only 12% which was much lower compared to the status quo (59%) (Figure 3.9).

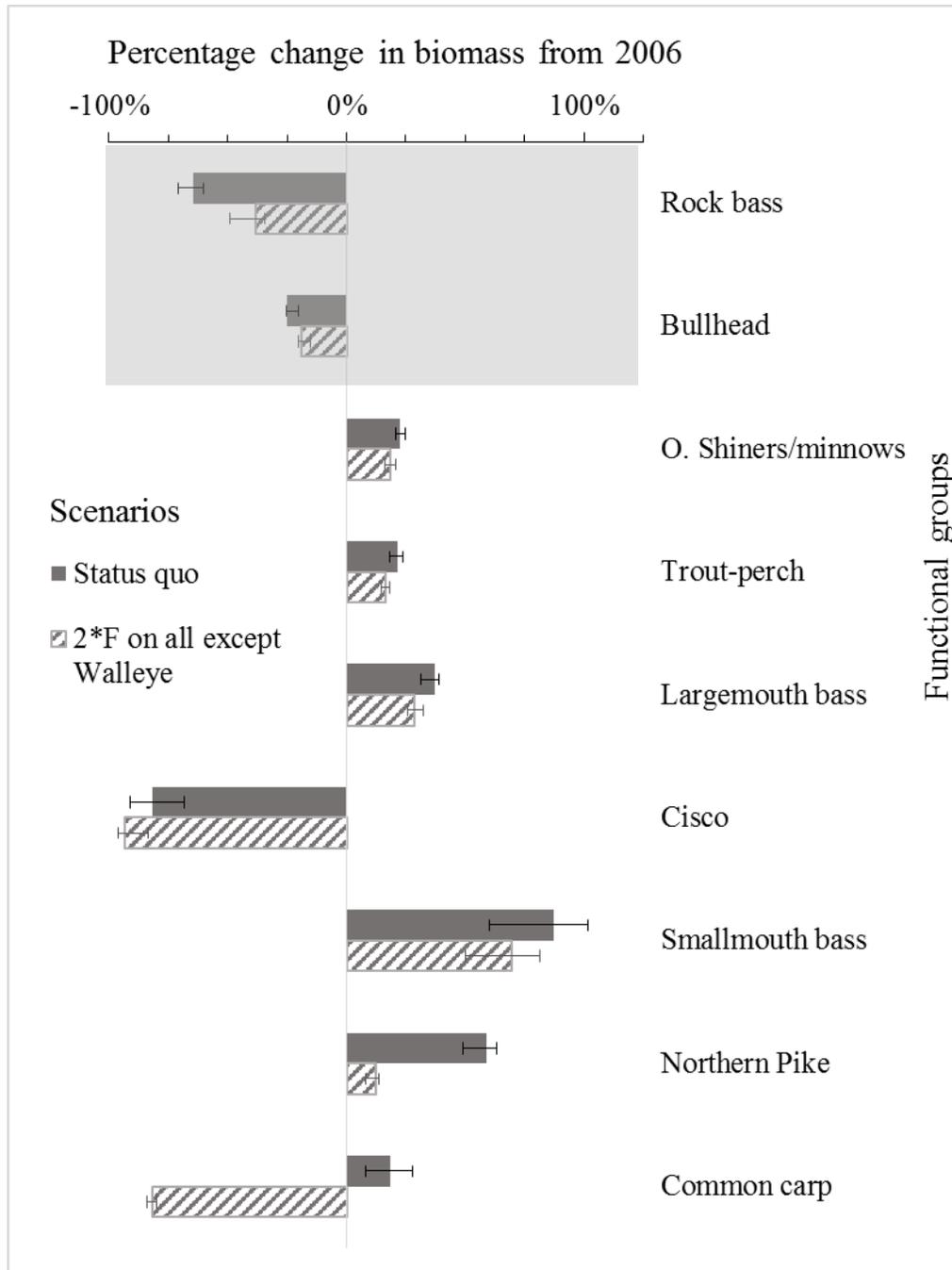


Figure 3.9. Change in biomass observed for scenario: heavy fishing on all species except walleye  
 The results are presented against the model prediction for status quo. The grey shaded box shows species for which the predicted biomass at the end of the heavy fishing scenario was higher than the status quo prediction

### 3.3.3 Scenario 3: Managing cisco

Cisco is a forage fish in the lake. Its historical decline in the lake is a cause of serious concern for MNDNR. I tested two scenarios on cisco: (3a) absolute no-fishing cisco and (3b) extirpation of cisco.

#### 3.3.3.1 3a: Absolute no-fishing on cisco

The objective behind the scenario was to investigate the options for restoration of cisco population. Cisco continued to decline. However, it performed much better—a 45% reduction in cisco biomass from baseline was observed under this scenario, while the reduction was 82% under status quo (Figure 3.10). It is worthwhile to mention here that even after complete closure of fishing, cisco biomass remained at merely at 3% from model base year (1985).

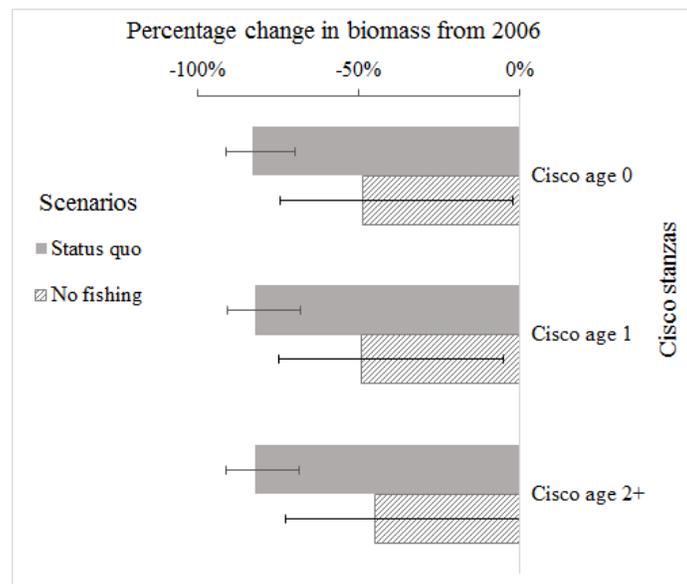


Figure 3.10. Percentage change in cisco biomass after complete closure of fishing on cisco.

The result can be seen in comparison with status quo (bar filled with grey color) when 2006 fishing level was maintained till the end of simulation.

### 3.3.3.2 3b: Extirpation of cisco from the system

The rationale behind second cisco scenario was to explore how the ecosystem would behave if the threats for cisco such as temperature, fishing and predatory pressure rise continuously and cause the cisco population to completely collapse. Since cisco had already declined by over 95% in last few decades, the case for cisco extirpation from the lake was quite plausible if no protective measures were undertaken. As expected, this scenario indicates negligible changes in species abundances of the lake from their status quo conditions.

### 3.3.4 Scenario 4: Impact of cormorants

Abundance of double-crested cormorants increased in North America in 1990s, and the population of this fish-eating bird is considered “overabundant” (Wires and Cuthbert, 2006). In Mille Lacs Lake, from merely 2 nests observed on Spirit Island of the lake in 1998, the numbers increased to 303 nests in 2009 (McDowell, 2009). Owing to its potential threat to fisheries, especially walleye and yellow perch, a locally threatened waterbird common tern (*Sterna hirundo*), and local revenue, the state took initiative to keep the species under control by killing them (Hundt *et al.*, 2013). I performed this scenario to examine the impacts of the rising population of cormorants on fish communities of the lake. Cormorant biomass in the model was forced to increase gradually at the rate of 25% every year till the biomass reached 5 times to the current biomass. To add stochasticity in the population, a 10% variation was allowed in the forced biomass.

As discussed in the methods section, during the fitting process, the biomass of cormorants was forced in the Ecosim simulation. Considering that when the biomass of a group is

forced, it is not possible to evaluate the quality of fit for that group; hence, I conducted a sensitivity analysis of the results to the vulnerability parameter of fish prey to cormorants. In the fitted model, the vulnerability parameter was set to 2 which indicates mixed bottom-up and top-down control (mixed control). I found that when the relationship was top-down (vulnerability = 50) smallmouth bass showed a large decline (Figure 3.11). Some other species such as cisco and black crappie also showed a reduction in their biomass compared to the mixed control. Cascading effect of smallmouth bass reduction was seen in the increment of northern pike, largemouth bass, and bowfin; smallmouth bass feeds on crayfish, hence crayfish increased which benefited its predators, rockbass and yellow perch. With increase in yellow perch, northern pike, largemouth bass and bowfin increased. When the relationship was bottom-up (vulnerability = 1), the results were very similar to those obtained under mixed control.

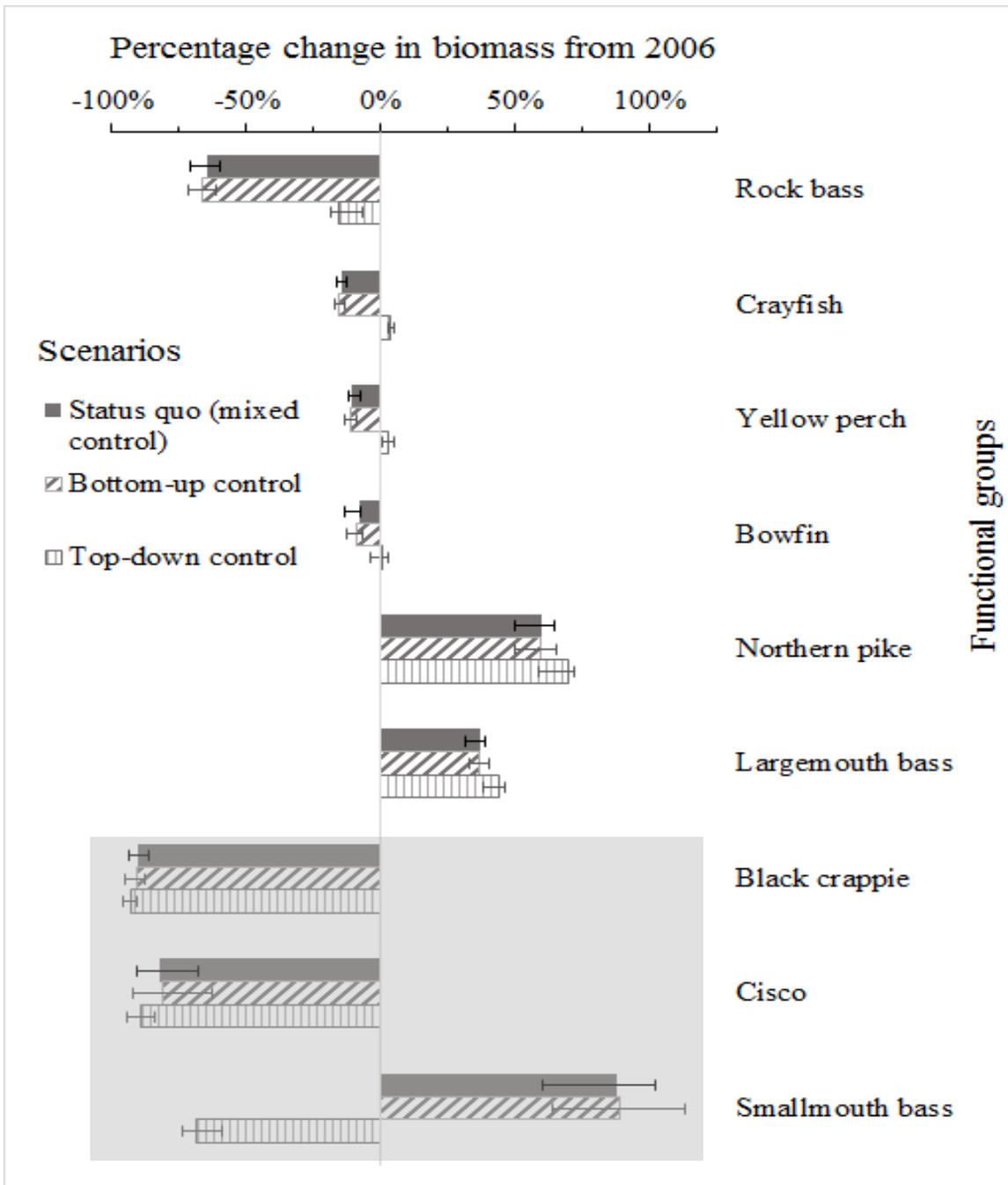


Figure 3.11. Change in biomass observed for scenario: increase in cormorants

The results show sensitivity of biomass changes to the vulnerability parameter (all species which showed atleast 3% or more change are shown). The grey shaded box shows species for which the predicted biomass at the end of the top-down control was lower than the status quo prediction.

### 3.3.5 Scenario 5: Fishing all the species at their ecosystem $F_{msy}$

The aim of performing this scenario was to investigate the potential changes in fish-community structure when all species were fished at their  $F_{msy}$  level, a fishing rate at which, conceptually, the stock has maximum growth rate. I estimated ecosystem- $msy$  ( $ES_{msy}$ ) for more than a dozen species of Mille Lacs Lake using the same ecosystem model in Chapter 4. The  $F_{msy}$  values used as inputs in this scenario are presented in Table 4.1 in Chapter 4. The following major fished species decreased from baseline: walleye by 35%, yellow perch by 70%, northern pike by 29%, largemouth bass by 74%, and darters by 13%. On the contrary, gains were observed in the abundance of cisco, burbot, and black crappie. As usual, some minor changes were also observed in some of the other species.

## 3.4 Discussion

### 3.4.1 Ecosim scenarios

In any trophic simulation model, prey-predators interactions are important factors in determining the ecosystem dynamics as these interactions “link” all the functional groups (Board, 2006; Christensen and Pauly, 1993). Even the sensitivity of a particular species to climatic factor such as temperature propagates upward to predators and (or) downward to prey through the prey-predator interaction. Thus, implementation of an EBM approach requires a careful consideration of “tradeoffs” between harvesting strategies and stock status of target and non-target species (Board, 2006). This study delivers valuable information about plausible shift in fish-community structure under the influence of fisheries management strategies as well as environmental change.

### 3.4.1.1 Scenario 1: Status quo

Lake temperature and temperature preference of a species, especially in the temperate latitudes, has a strong effect on ‘duration of optimal preference’ of a species (Shuter *et al.*, 2012). Direct effects of temperature could be seen on the model’s prediction for smallmouth bass, cisco, and burbot. Dunlop and Shuter (2006) studied the influence of climatic variables on the growth of different age groups of smallmouth bass within the native range of the species and found a significant positive correlation between temperature and growth of young smallmouth bass. In Mille Lacs Lake, smallmouth bass is close to the northern edge of its native range (see Figure 1 in Dunlop and Shuter (2006)) where it would be expected that an increase in temperature would be most beneficial. This positive effect of temperature was simulated by applying the temperature forcing function between younger smallmouth bass and its prey species. When the temperature forcing was not implemented, the population growth dropped from ~85% to ~38%, but still the population had a positive trend. In a separate analysis (Chapter 5) while simulating the impact of zebra mussels invasion on the same lake, I investigated that the invasion benefitted the abundance of smallmouth bass population through trophic interactions via crayfish, “zebra mussels-crayfish-smallmouth bass interaction” (Chapter 5: submitted for publication). The status quo results suggest that the lake will experience an unprecedented high population of smallmouth bass in future, which is partly because of general rising of the lake water temperature and partly because of zebra mussels-crayfish interaction. For the last few years, the lake’s assessment gill-net data also suggest a rising CPUE trend of the bass species (Figure 1.2: smallmouth bass), which further supports the status quo prediction.

Unlike smallmouth bass, rising-temperature negatively affected the cisco and burbot in the lake. These results are also supported by recent assessment data. Moreover, maintaining a higher fishing pressure on burbot compared to its  $F_{msy}$  level imposed an additional stress to the species. Effect of temperature on cisco well-documented in the literature (Fang *et al.*, 2012; Jacobson *et al.*, 2008; Kumar *et al.*, 2013). The lake assessment data supports a substantial decline of the cisco population from the lake over the few decades (Chapter 2); and there was support for the hypothesis that temperature was a major cause of this decline. However, Kumar *et al.* (2013) findings implied that not only the temperature but high fishing pressure in many years in the past also contributed to this decline. None of the above studies involves the impact of trophic linkages; the present analysis indicates that cisco population faces an added predatory pressure from rising population of northern pike. Thus, the species faces major pressures in the form of rising temperature, fishing pressure, predation and competition.

Northern pike and largemouth bass populations increased because they experienced a significantly lower fishing pressure compared to their  $F_{msy}$  and a consistent abundance of their major prey yellow perch and some other prey such as, spottail shiners, other shiners/minnows, other fishes (“other fishes” is a functional group in the model which includes some tiny fishes which were not represented by individual groups in the model, see Appendix C for functional groups). The rise in largemouth bass, a predator on bullhead, caused bullhead to decline by a quarter. Black crappie was affected by the rise of northern pike, smallmouth bass and largemouth bass together.

### 3.4.1.2 Scenario 2: Managing walleye

Walleye decreased from reference line across all the scenarios performed; however, the biomass level remained higher than the biomass at msy (Bmsy) except in the scenario when fishing pressure on adult was raised to two times the SHL. Using the equilibrium analysis tool in EwE the mean ecosystem Bmsy of walleye was estimated to be 968 tonnes at Fmsy 0.29. When adult walleye was fished at  $F = 0.48$  ( $2 * SHL$ ), the simulated walleye biomass ended up at a level much lower than the Bmsy estimates. However, in remaining scenarios, maintaining  $F$  at SHL—which was slightly lower than the Fmsy—allowed the stock biomass to remain higher than Bmsy. I also tried several experimental scenario and found that walleye stock could be maintained at 2006 level by fishing at  $F=0.17$  provided other ecological conditions remained the same.

The loss caused by hooking mortality is integral to the size-based management approach of recreational fisheries, though the mortality rates varied depending upon several factors such as water temperature, type of hooks used, body-location, and severity of injuries etc. (Muoneke and Childress, 1994; Reeves and Bruesewitz, 2007). The mean walleye hooking mortality rate for Mille Lacs Lake was estimated to be around 12% in summer when the lake temperatures were at or above 20°C (Reeves and Bruesewitz, 2007). After adding the fishing pressure on younger walleye (age 1 and age 2), the responses by other species maintained the similar trend with the responses at status quo. However, the species preyed upon by walleye performed slightly better than that of under status quo, and biomass of the walleye approached to its Bmsy.

On doubling the fishing pressure on adult walleye, the species declined and caused some forage species to increase resulting in benefits for northern pike and largemouth bass. Largemouth bass also benefited by release of predation pressure from walleye which had a trace amount of largemouth bass in its diet. Sculpins improved following reduction in walleye and burbot. An improvement in forage fish such as sunfish considerably favoured bowfin. Cisco and yellow perch did not get as much benefit as expected after the reduction in walleye abundance; release of predation pressure from walleye on cisco was mostly balanced by rising population of northern pike, while northern pike and largemouth bass together controlled yellow perch. The result is interesting as yellow perch constitutes the bulk of walleye diet in every stanza, and conversely, yellow perch was not getting benefit from the decline of walleye.

Under the heavy fishing condition on all species except walleye, substantial reduction of common carp was caused by the F-level ( $F=0.18$ ) which was more than twice its ecosystem  $F_{msy}$  ( $0.07$ ). As expected the upsurge of northern pike was significantly controlled by the high fishing pressure. A further increased fishing level caused already stressed-cisco to be almost collapsed from the system. The ecosystem impact of heavy fishing on all species except walleye only slightly affected the walleye population.

#### **3.4.1.3 Scenario 3: Managing cisco**

The scenario's outcome indicates that "no-fishing" alone is not sufficient to build the population to the historic level. I expected cisco to better rebound but unfavourable climatic condition, and continued pressure on adult cisco from northern pike and walleye and on cisco age 0 from adult yellow perch did not allow cisco to rebuild. The model results had a

very wide confidence interval. However, in almost all cases, the prediction was higher than status quo. The positive error bars were wider and in some cases almost approached the biomass levels in 2006.

The reason for no major changes in MLL ecosystem after cisco extirpation was that the model/ecosystem had adjusted to the cisco decline. The species had already declined ~95% by 2006 and further decline did not cause any noticeable change. In Mille Lacs Lake, yellow perch now is the most important forage species. Research in Oneida lake showed that yellow perch and its abundance moderate the levels of predation by walleye on other species (Forney, 1974). When cisco declined in Lake Superior (Cox and Kitchell, 2004; Selgeby, 1982), the niche for a prey species was fulfilled by rainbow smelt (*Osmerus mordax*) (Mason *et al.*, 1998). Later, studies reported cisco recovery (MacCallum and Selgeby, 1987), but there was not much discussion on the impact of cisco decline on the ecosystem (Stockwell *et al.*, 2009).

#### **3.4.1.4 Scenario 4: Impacts of cormorants**

Cormorants eat a wide variety of fish species, though yellow perch contributes a substantial quantity in its diet (Hundt *et al.*, 2013; Rudstam *et al.*, 2004). At the end of the cormorant increase scenarios, the biomass of yellow perch in the lake was about 300 times higher than the biomass of cormorants, and the predation mortality generated on yellow perch by cormorants was small compared to the influence of walleye and other yellow perch predators. When the vulnerability represented a bottom-up relationship, all prey became available to cormorants according to their abundance, and large prey groups such as yellow perch, crayfish, and darters showed a minor decline compared to mixed trophic

control in status quo. When the relationship between cormorants and its prey was made top-down, all prey became vulnerable to cormorants. Thus compare to bottom-up scenario, species such as smallmouth bass, cisco and black crappie experienced more predation pressure from cormorants. This distribution of predation pressure released some of the predation pressure on yellow perch from cormorants.

Under mixed trophic control, smallmouth bass continued to increase till about year 2020 and then started levelling off, but under top down control, cormorants exerted high predation pressure that arrested the smallmouth bass increase. Considering that smallmouth bass continues to show increasing trends in the assessment gillnets, there seems more support for mixed control or bottom-up trophic control.

#### **3.4.1.5 Scenario 5: Fishing all the species at their ecosystem Fmsy**

The reductions observed in major species were the consequence of direct fishing; for most species the actual fishing level in 2006 were lower than their Fmsy. Cisco increased because of decline in its predators walleye and northern pike and increased abundance of prey species such as pelecypods, zooplankton; these prey became more available because of reduction in yellow perch. Burbot was present in trace amounts in walleye diet. The decline in walleye released predatory pressure from burbot and the species showed gains. However, reduction in yellow perch, one of the major prey of burbot, was supposed to negatively affect the species, but increase in crayfish, a prey of both yellow perch and burbot, because of reduction in yellow perch was able to sustain the burbot population.

### 3.5 Conclusion

Building the ecosystem model, especially parameterising the diet preference matrix, balancing the Ecopath model and simulating the Ecosim model temporally was a new departure in understanding the trophic dynamics of Mille Lacs Lake as the lake was never studied before by accounting for all the interactions together. While the diet matrix helped me understand the diversity of prey-predator interactions, the estimates of predation mortality and balancing process revealed the complexity of these interactions. Simulating the ecosystem effect of different fishing strategies provided interesting information about the ecosystem dynamics of species such as yellow perch, cisco, burbot, walleye, and others which had not been investigated previously in the lake.

Walleye is being managed well using the Safe Harvest Level approach with the biomass levels remaining consistently above  $B_{msy}$ . The model suggests that overfishing the walleye population would lead to increases in northern pike, largemouth bass, cisco, and sculpins. Interestingly, overfishing walleye would not result in increase in the yellow perch population, the major prey of walleye. However, recent field estimations point towards a decline in the walleye, and this is coincident with the boom of zebra mussels in the lake. In Chapter 5, I explore the impact of zebra mussels invasion.

Continuing *status quo* management is predicted to lead to increase in biomass of northern pike and smallmouth bass. The scenario analyses showed that there was potential to increase the fisheries for several species (such as northern pike and smallmouth bass) without negatively affecting the walleye population. The abundance trends of black crappie showed a decline, and the analysis suggested that increase in fishing pressure on smallmouth

bass would provide additional fishing opportunity and also positively affect black crappie (because it is preyed upon by both northern pike and smallmouth bass.). The model did not predict large effects from increasing cormorants on the lake.

For cisco, the predictions of the fitted Ecosim were similar to the results obtained in Chapter 2—temperature was an important contributing influence in the decline of cisco. Cisco has declined in the lake and the model predicted further decline if *status quo* is maintained: when no fishing was allowed on cisco, the population showed better performance than status quo. Surprisingly, the Ecosim model did not predict large ecosystem-wide repercussions of cisco extirpation. However, the EwE model does not incorporate any possible energetic advantage (as mentioned as one of the weaknesses of the EwE model), of cisco over yellow perch as forage for certain predatory species, and this caveat has not been explored here.

The capabilities of the Mille Lacs lake ecosystem model built in the study are not restricted to the scenarios tested in the chapters. Scenarios tested in the thesis were conceptualized based on the current condition of the lake. In future the base model can be used for making various strategical decision pertaining to that point of time. The model can also be enhanced by adding more functional group especially at the lower trophic level, as may be required in a lake invaded by zebra mussels. The model can also be used for spatial analysis that was not part of the present study. Further, the model can be adapted for ecosystem based analysis in other similar lakes in Minnesota, a State that is known as “the land of 10,000 lakes”.

# **4 Ecosystem and Single-Species Maximum Sustainable Yield Using an Ecosystem Model for Major Species of Mille Lacs Lake, Minnesota<sup>3</sup>**

## **4.1 Introduction**

Management of fisheries exploitation and maintenance of healthy and sustainable ecosystem are aided by modelling exercises that take into account the multitude of interactions among biotic, abiotic, and anthropogenic drivers of an ecosystem (Pikitch *et al.*, 2004). In spite of the popularity of sophisticated single-species stock assessment models in fisheries, these models have drawn criticism for their inability to incorporate predator-prey trophic interactions (Pauly *et al.*, 2002). Management based on single-species models that do not consider species interactions may lead towards unexpected and undesirable ends; even a perfectly managed single-species management is not immune to risks such as by-catch of endangered or protected species (Hilborn, 2011). While reviewing multispecies models, Hollowed *et al.* (2000) stressed the need for multispecies models to assess the impact of energy flows in an ecosystem; they argued that competition, predation, and environmental effects were the three fundamental factors determining the ecosystem dynamics that should form a “framework” for multispecies modelling. However, Mace (2001) suggested using an integration of both single-species and multispecies approaches.

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<sup>3</sup> A version of this chapter will be submitted for publication.

Several criticisms have been leveled against single-species maximum sustainable yield (MSY) estimations. The main criticisms against this metric are the challenges of estimation especially responding to changes in recruitment and multispecies influences in the ecosystem, and its suitability as a management target (Larkin, 1977; Punt and Smith, 2001). Adopting MSY as the target resulted in managers treating the metric as the ‘maximum average catch’ and allowed the real fisheries catch to sometimes overshoot resulting in overfishing (Mace, 2001). The value of MSY was eventually “reborn” with a new face as a limit reference point (Mace, 2001). And MSY and associated reference points continue to be very popular (Sissenwine *et al.*, 2014). In this Chapter, I estimated and compared Single-species ‘maximum sustainable yield’ (SSmsy) and ecosystem-based MSY (ESmsy) for exploited species of Mille Lacs Lake, Minnesota. With ESmsy I refer to the estimation of sustainable yield for target species as a function of fishing mortality (F) while accounting for the continual responses of non-target species as a result of fishing on the target species, because in ecosystem perspective, their dynamics are linked mostly through food-web. Here I calculated MSY not because it was necessarily the best reference point with which to manage fisheries but because it was one of the most widely understood metrics that could be used to effectively compare the productivity of multiple species in a system against fishing pressure.

Few works have actually compared single-species (SS) and ecosystem (ES) estimates. After a comparison of SSmsy and ESmsy estimates, Walters *et al.* (2005) using an Ecopath with Ecosim based analysis concluded that focus on single-species methods alone could be detrimental to fisheries for higher trophic level species. Comparison of reference points generated in a virtual population analysis (VPA) and multi-species VPA (MSVPA),

Gislason (1999) showed that multispecies calculations provided highly valuable information, though management based on ecosystem reference points was complicated because the value generated by the predator (cod) and its prey species (herring and sprat) were different. ‘Balanced harvesting’ is a new strategy that has been proposed to manage multispecies fisheries (Garcia *et al.*, 2012; Kolding and van Zwieten, 2014)—this strategy recommends that fish species are fished in proportion to their productivity. This strategy aims to enhance sustainability by structuring the fishing mortality similar to the distribution of natural mortality on all species and sizes of fish using a variety of harvest mechanisms (Kolding and van Zwieten, 2014).

The expected ecosystem outcomes become more uncertain when environmental changes and fishing pressure occur concurrently. From a SS perspective, Wayte (2013) showed that not adjusting reference points in the wake of environmental changes could lead to erroneous management recommendations. Within a ES perspective, Large *et al.* (2013) showed that estimates of ecosystem indicators changed in response to environmental fluctuations and provided improved understanding of changing ecosystem status. In Chapter 2 based on surplus production modelling, I found that rising phase of temperature in the summer months diminished the carrying capacity of the lake for cisco and therefore significantly affected the MSY estimates of the species. (Kumar *et al.*, 2013). Similar evidence was also available from data and preliminary modelling exercise for Burbot (Appendix B). Further, as it was mentioned in Chapter 3 that smallmouth bass, especially young immature fish have higher growth and survival in warmer waters (Dunlop and Shuter, 2006). Optimum temperatures for smallmouth bass range from 20 to 27°C (Scott and Crossman, 1973). Adding the effects of temperature while accounting for trophic

interactions would help to make the MSY estimates more realistic. Thus, using the Mille Lacs Lake ecosystem model developed in Chapter 3, this chapter aims:

- (i) to estimate the biological reference points of MSY and  $F_{msy}$  for the principal fished species of the lake under two frameworks—(a) Ecosystem MSY (ES<sub>msy</sub>) where food-web dynamics were accounted for while estimating the MSY of target species and (b) traditional single-species MSY (SS<sub>msy</sub>) where it was assumed that non-target species were not affected by fishing on target species,
- (ii) to explore the reasons for different values, if any, obtained for SS<sub>msy</sub> and ES<sub>msy</sub> i.e., the compensation that resulted in higher estimates of ES<sub>msy</sub> or the costs, for example competition, that results in higher SS<sub>msy</sub> levels,
- (iii) to explore the influence of temperature on the SS<sub>msy</sub> and ES<sub>msy</sub> estimates when the temperature forcing function was applied on species such as cisco, burbot and smallmouth bass, and
- (iv) to conduct sensitivity analysis on MSY estimates.

## **4.2 Methods**

### *4.2.1 Summary of Ecopath model and forcing function*

As mentioned above, I used EwE model built for Mille Lacs Lake ecosystem in chapter 3. Details of EwE modelling approach can be found in published literature (Christensen and Pauly, 1992; Christensen and Walters, 2004), and Chapter 3 can be consulted about parameterization and temporal simulation of the lake ecosystem model.

The effect of temperature changes on MSY estimates were achieved by applying a temperature forcing function in the Ecosim model. An average of July temperature and average of August temperature from year 2000 to 2005 were used to represent the temperature forcing of month July and August respectively for each year of simulation; I assumed that temperature in remaining months were not a cause of mortality for the cold-water stenothermal species such as cisco and burbot. Temperatures in July and August of 2000-2005 were on average higher than the temperatures observed in 1985 when the Ecopath model was initialized. It was expected that the higher temperature would have a negative effect on the cisco and burbot and positive effect on food availability for smallmouth bass. Setting the forcing function this way allowed me to simulate the ecosystem at the higher temperature level observed in recent years. Besides, same as in Chapter 3, the both species were provided with temperature tolerance ranges, and the temperature forcing function was applied to this tolerance range; during the simulation when the temperature deviated from optimum, the P/B ratios were negatively affected. For the details about how the forcing function affects the P/B ratios, please refer to the section 3.2.2.1. I simulated the effect of temperature changes on smallmouth bass by applying the same temperature forcing as applied with cisco and burbot, though in a different way—here the temperature forcing function was applied on vulnerability parameter between the juvenile smallmouth bass and all its prey such that the higher temperatures were advantageous for the predator.

In summary, I estimated the reference points with and without including the temperature forcing function, and this allowed me to estimate how much the lake ecosystem and the fisheries reference points were affected by the changes in temperature.

#### 4.2.2 Estimation of MSY and Fmsy

EwE has a built in function to estimate SSmsy and ESmsy. The function works under two different conditions depending biomass state of non-target species (Walters *et al.*, 2005):

1. SSmsy: while estimating the MSY of target species, biomass of non-target species (i.e. rest of functional groups) were frozen (forced to be static) at their base ecopath value (1985 biomass).
2. ESmsy: on the contrary, biomasses of non-target species were allowed to respond dynamically to changing target species biomass.

Uncertainty is an integral part of estimates that may arise from the uncertainty in data, input parameters and complexity of models simulating the natural process. Monte Carlo (MC) simulation is a widely used method to assess uncertainty (Haddon, 2001). The built in functions in EwE do not provide uncertainty around the SSmsy and ESmsy estimates; however, the functionality for MC analysis is available within the Ecosim Scenario component of EwE. In order to estimate MSY with uncertainty, I constructed a time-series and simulated it through the Ecosim scenario with MC to estimate MSY with uncertainty around the estimates. The time-series extended for 500 years; in the time-series, the fishing mortality ( $F$ ,  $\text{yr}^{-1}$ ) values of target species was incremented step by step (25 steps) and the ecosystem was allowed to equilibrate for 20 years at each incremental  $F$  value. The  $F$  values for the non-target species were held at their base ecopath value (i.e., unchanged). The  $F$  value which resulted in maximum yield was recorded as  $F_{\text{msy}}$  and the corresponding yield as  $\text{MSY}$ . This method was applied to estimating  $\text{ESmsy}$  under temperature forcing function.

I performed MC simulation through 80 successful-runs of Ecosim for each MSY estimation. For each run, MC simulation randomly selected a set of parameters within a 10% coefficient of variation (CV=0.1) for the B, P/B, Q/B, EE parameters. Some sets of parameters did not satisfy Ecopath mass-balance (EE, the fraction of production of functional groups that goes to their predator's diet or fished out from the system, exceeds 1.0 plus some tolerance); in that case the trial was considered unsuccessful, and the MC routine drew another set of parameters values.

### **4.3 Results**

SSmsy and ESmsy for 13 species with and without the temperature forcing function were estimated (Table 4.1). To make reading and writing easier, in the following paragraph I used abbreviations as:

1. SSmsy for single-species MSY without temperature forcing function,
2. SSmsyT for single-species MSY with temperature forcing function,
3. ESmsy for ecosystem MSY without temperature forcing function, and
4. ESmsyT for ecosystem MSY with temperature forcing.

#### *4.3.1 Trophic and temperature effects on MSY*

When temperature forcing was not included, except smallmouth bass, bowfin and common carp, for 10 out of 13 species evaluated, the ESmsy estimated was nearly equal or higher than the SSmsy. As expected, implementation of temperature directly influenced the ESmsyT estimates for burbot, cisco, and smallmouth bass (Table 4.1). Temperature forcing also led to indirect effects on the estimates for several other species; the ESmsyT estimates

were lower than that of ESmsy as well as SSmsy for many species such as yellow perch, northern pike, and rock bass.

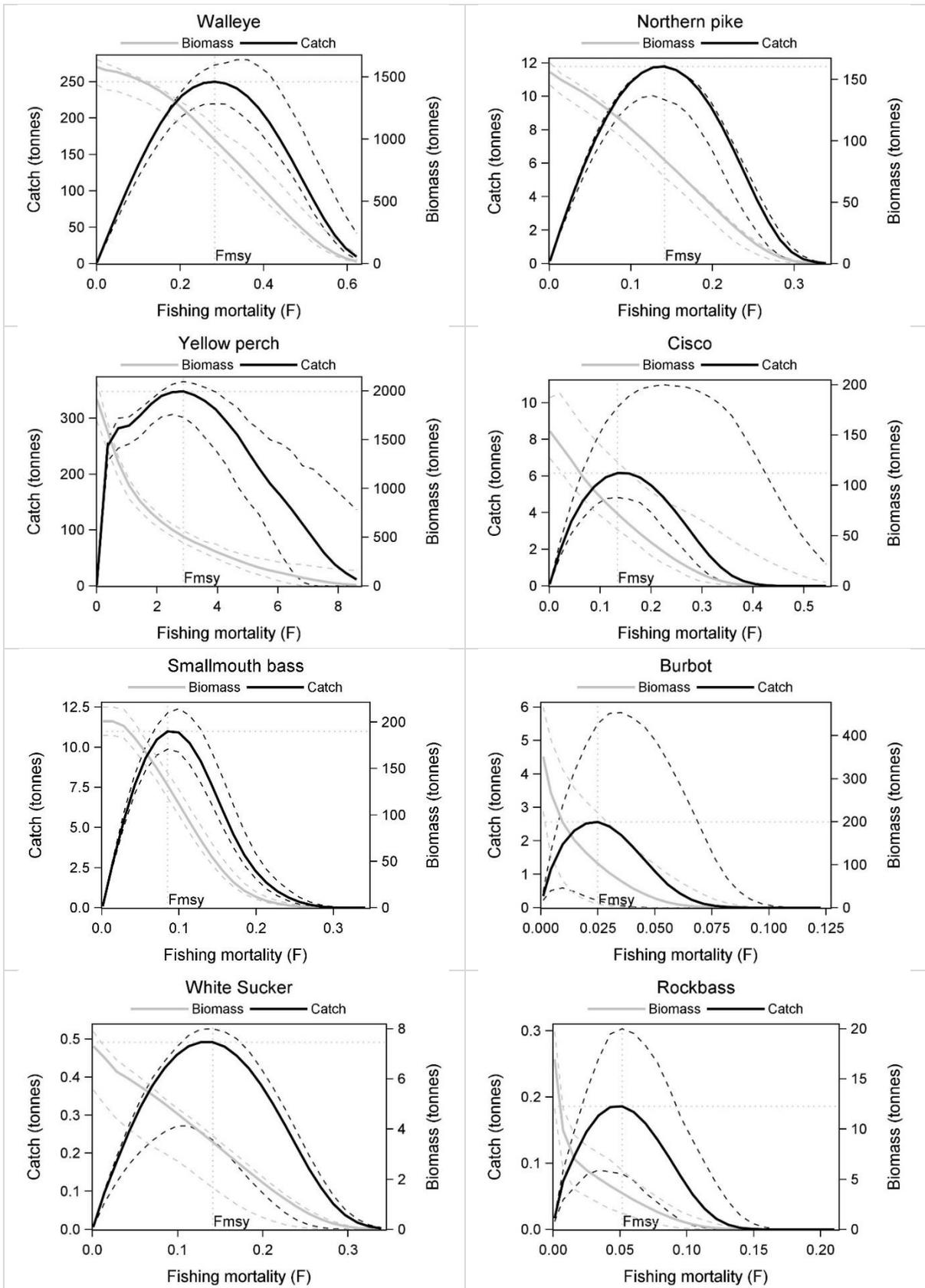
*Table 4.1 MSY (tonnes) and corresponding Fmsy (yr<sup>-1</sup>) estimates for 13 species of Mille Lacs Lake, Minnesota.*

Species	With temperature forcing function				Without temperature forcing function			
	Single-species		Ecosystem		Single-species		Ecosystem	
	MSY	Fmsy	MSY	Fmsy	MSY	Fmsy	MSY	Fmsy
Walleye	170.25	0.22	249.80	0.28	174.27	0.21	221.77	0.27
Yellow perch	336.86	1.08	347.82	2.87	357.11	1.23	399.93	2.86
Northern pike	12.38	0.13	11.77	0.14	12.43	0.14	12.65	0.14
Cisco	11.46	0.22	6.17	0.13	18.71	0.27	18.86	0.27
Smallmouth bass	14.87	0.08	10.99	0.09	0.41	0.07	0.34	0.07
Rock bass	0.48	0.06	0.19	0.05	0.62	0.06	0.64	0.07
White sucker	0.25	0.07	0.26	0.07	0.25	0.07	0.27	0.07
Black crappie	0.17	0.02	0.48	0.04	0.33	0.03	0.45	0.04
Burbot	4.04	0.03	2.56	0.02	11.59	0.04	12.25	0.04
Common carp	2.70	0.07	2.77	0.07	2.67	0.06	2.63	0.06
Largemouth bass	1.15	0.05	1.91	0.07	1.23	0.05	1.89	0.08
Bowfin	0.10	0.03	0.11	0.03	0.11	0.03	0.10	0.03
Bullhead	2.16	0.08	3.27	0.11	2.15	0.07	3.14	0.10

The key reason for getting higher ESmsy corresponding to SSmsy was a consequence of gradual increases in availability of the prey to the target species as the target species was fished down; the biomass of the target species decreased, and this released predation pressure from their prey. I also noticed several other trophic effects propagating through ecosystem: in some cases trophic interactions enhanced compensation in the targeted species while in others trophic interactions weakened the compensation. In the following section on species-wise comparison, I first describe the differences between ESmsy and SSmsy estimates due to trophic interaction only (without temperature effect); then I describe differences between ESmsy and ESmsyT estimates with and without implementation of temperature effects (combined trophic and temperature effect). Figure 4.1 provides the temperature-influenced ESmsy estimates (ESmsyT) for all the species. A summary of all types of MSYs estimates are provided in Table 4.1 above.

#### **4.3.1.1 Walleye**

The higher ESmsy of walleye was supported by an increase in its prey such as cisco, shiners and minnows, and hex mayflies. Yellow perch was the major prey of the species, and I expected an increase in its abundance as F was increased on walleye. But that was not the case, a decline in yellow perch was observed mainly because of increased predation from burbot and northern pike. Burbot was benefited by increase of its prey such as shiners and minnow and weakening of the trace amounts of predatory pressure by walleye on itself. This was an interesting example of indirect-influence observed in the ecosystem model. When the temperature forcing was implemented, the results were very similar except a better performance of shiners and minnows which probably contributed to slightly higher ESmsyT (13%) estimate for walleye.



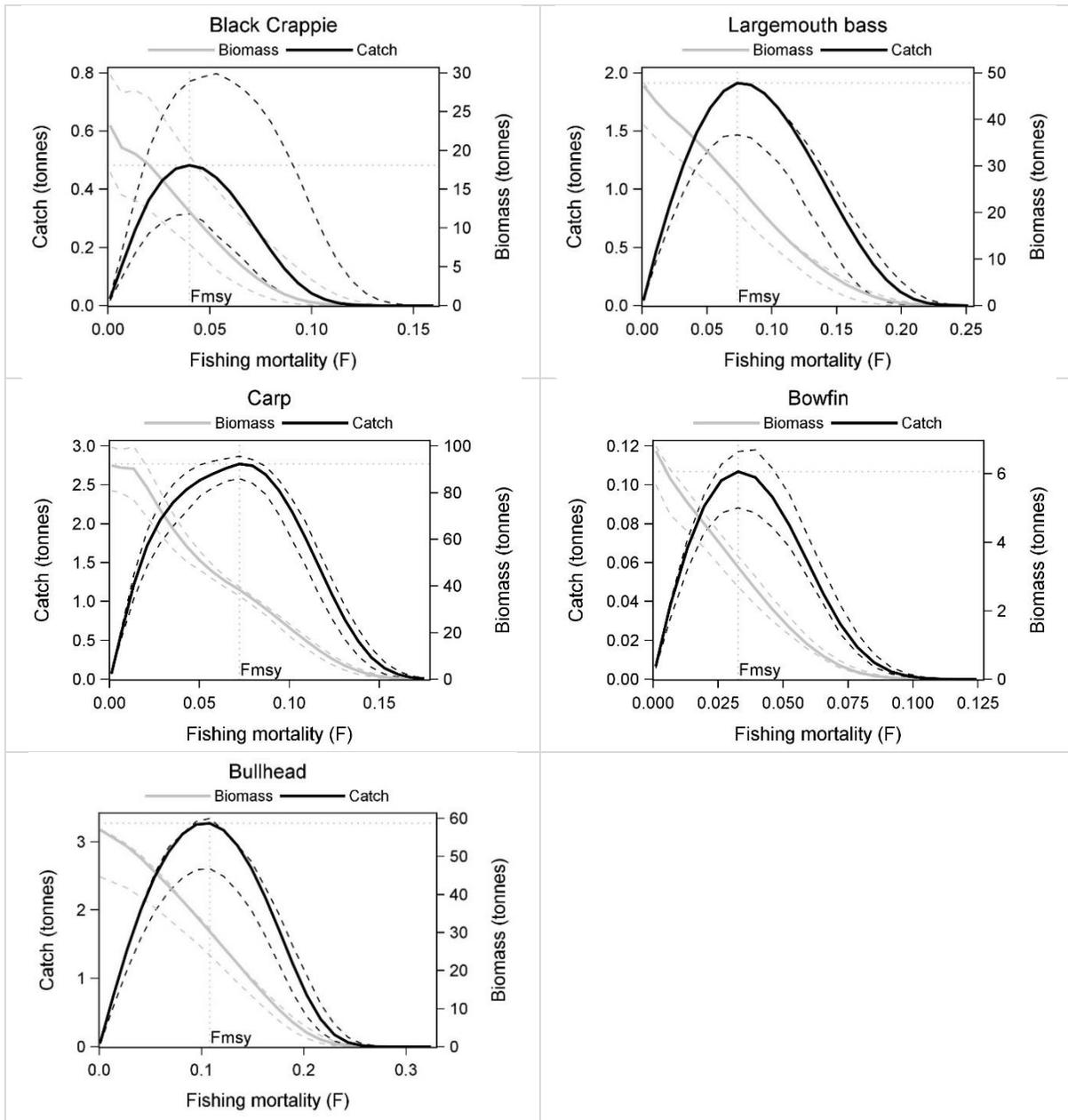


Figure 4.1. Temperature influenced ecosystem MSY ( $ES_{msyT}$ ) for key recreational species in Mille lacs Lake. The black solid lines show predicted catch and the dashed black lines show the inter quartile range for catch. The grey solid lines show predicted biomass and the dashed grey lines show the inter quartile range for biomass.

#### **4.3.1.2 Yellow perch**

Yellow perch is a radial point in the food web of the lake; it constitutes a major portion in the diet of almost all the piscivores. The instability in its abundance as a consequence of increased F contributed to numerous minor and major fluxes in the food-web. As a direct consequence of its decline, its prey such as darters, pelecypods, crayfish, and gastropods improved, and predators, especially walleye and burbot, declined. After an initial decline, northern pike stabilized in the later years of simulation as availability of crayfish and darters increased in the system. Improved trend in the biomass of smallmouth bass and cisco were also observed; healthier population of crayfish contributed to the former while pelecypods and zooplankton to the latter. I also expected a dwindling in the abundance of fish-eating birds such as cormorants as yellow perch contributes to the diet of these birds, but an augmented cisco and smallmouth bass balanced the loss of yellow perch. When the temperature forcing was in-effect, the ESmsyT estimate for yellow perch was 13% lower than the ESmsy. Increase in smallmouth bass due to temperature caused increased pressure on crayfish population which in turn was not able to provide the same level of compensation to yellow perch population.

#### **4.3.1.3 Northern pike**

Fishing was a major component of mortality on northern pike; thus the ESmsy estimated was merely 2% higher than the SSmsy. This small advantage was probably due to increase in prey species such as rock bass and yellow perch. With temperature forcing function, I got 7% lower estimate of ESmsyT compared to ESmsy due to lower performance of yellow perch and rock bass and temperature influenced decline in cisco. Northern pike exerts some

predatory pressure on younger walleye; therefore, the walleye population showed a minor improvement when the biomass of northern pike declined slightly under temperature forcing.

#### **4.3.1.4 Cisco**

For cisco, the estimates for ESmsy and SSmsy were very close when temperature-forcing was not incorporated in the model. Cisco biomass declined in response to a gradual rise in F, which triggered an increase in the biomass of prey such as zooplankton, pelecypods, and gastropods and a decline predator northern pike. Both the effects would have been conducive for a higher ESmsy estimate for cisco if the decline of burbot and northern pike had not triggered yellow perch to increase. Rise in yellow perch added extra predatory pressure on zooplankton which constituted a large percentage of cisco diet. These positive and negative effects counterbalanced each other, and ESmsy for cisco was not altered by these compensatory responses. Since yellow perch is the most important prey of walleye, walleye was not affected by the decline of cisco. When temperature forcing function was in effect, cisco ESmsyT was half of the SSmsyT, and both the estimates were reduced by around 67% and 39% respectively compared to their corresponding estimates with no temperature effect (ESmsy and SSmsy). Burbot also declined under temperature forcing consequently causing increase in yellow perch and walleye. In addition to factors discussed above, under temperature forcing the compensation from pelecypods (a prey of yellow perch and cisco) and crayfish (a prey of yellow perch and smallmouth bass) was lower than the simulation without temperature, and this was probably the reason for a much smaller ESmsyT estimate for cisco. The SSmsyT estimate obtained here was within the range of the

estimates from surplus production modelling in Chapter 2 while the ESmsyT estimate here was lower (Figure 4.2).

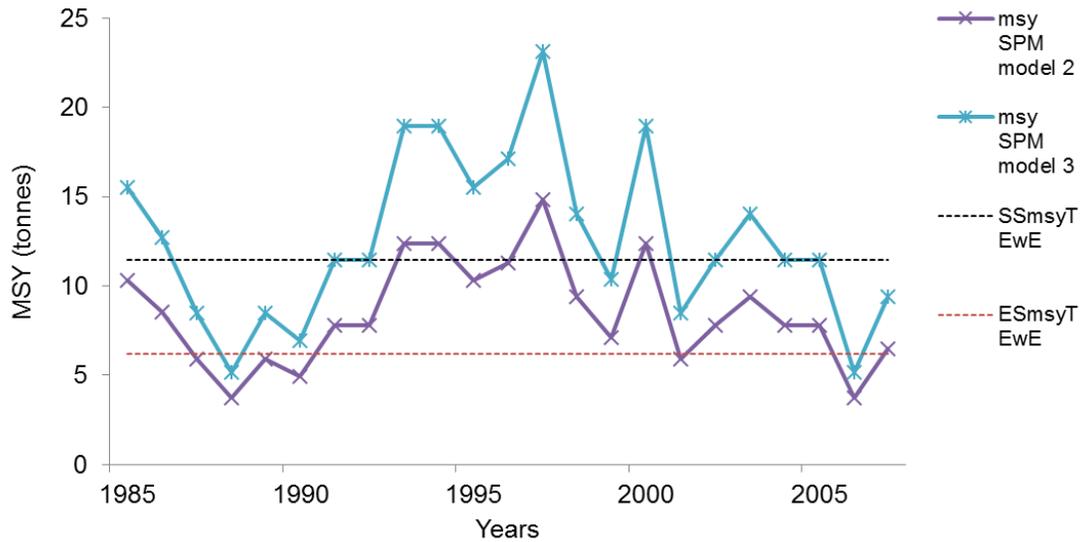


Figure 4.2. Cisco SSmsyT and ESmsyT comparison shown against temperature varying MSY estimates from Chapter 2.

#### 4.3.1.5 Burbot and white sucker

The ESmsy for burbot was higher (6%) than SSmsy, and that was mainly because of improvement in its prey such as juvenile yellow perch and crayfish. Incorporating temperature negatively affected burbot resulting in lower MSY estimates— ESmsyT dropped by 79% and SSmsyT by 65%. The greater differences in ESmsy estimates were due to be increased competition for yellow perch and crayfish. For white sucker, I got very similar estimates across all the cases of MSY estimations—differences were not more than 5%. Burbot and white sucker equally contributed (17% each) in the diet of otters and minks. The decline of burbot under temperature forcing condition and fishing white sucker

at MSY led to decrease in the biomass of otters and minks. Decrease in otters and minks also favored cormorants and other piscivorous birds.

#### **4.3.1.6 Smallmouth bass and rock bass**

The ESmsy for smallmouth bass was 17% lower than SSmsy (0.34 vs. 0.41) (Table 4.1), the decrease was mostly due to competition for prey such as black crappie and crayfish from other predators such as northern pike and yellow perch. When the temperature acted on the vulnerability of smallmouth bass to its prey, both SSmsyT and ESmsyT were high, but the ESmsyT was about 26% lower than the SSmsyT. Competition from yellow perch and higher predation from walleye was probably the cause for this difference. For rock bass, the SSmsy and ESmsy estimates were very similar. However, ESmsyT was lower than SSmsyT because of the rising population of smallmouth bass. The latter competes with rock bass for crayfish which is a major item in the diet for both smallmouth and rock bass.

#### **4.3.1.7 Bullhead and largemouth bass**

The higher ESmsy estimates for Bullhead and Largemouth bass were the result of direct prey-predator interactions. Bullhead was benefitted by invertebrates and decrease in biomass of its main predator, largemouth bass. Largemouth bass was benefitted by increase in its prey, bullhead. Not much difference was observed between ESmsy and ESmsyT estimates for bullhead and largemouth bass.

#### **4.3.1.8 Other species: Bowfin, black crappie, and common carp**

The ESmsy for Bowfin was slightly lower (6%) than SSmsy. Bowfin consumes black crappie and trace amounts of largemouth bass along with other prey. When bowfin was

fished heavily, a small improvement in largemouth bass was observed, but this had a large negative impact on black crappie. The reduction in black crappie resulted in a lower ESmsy for Bowfin. Under temperature forcing, the negative impacts were not as strong and the ESmsyT for bowfin was slightly higher compared to ESmsy. For black crappie, the ESmsy was greater than the SSmsy for due to losses in its predators' abundance such as largemouth bass, northern pike, bowfin and smallmouth bass. The ESmsy and ESmsyT estimates for black crappie were very similar. For common carps, there was less than 5% difference between the different MSY estimations.

#### *4.3.2 Sensitivity analysis*

For cisco and burbot, the MSY estimates were highly sensitive to uncertainty in Ecopath parameters; the confidence interval around ESmsyT varied widely between 5 to 11 tonnes for cisco and between 0.6 to 5.8 tonnes for burbot. Similarly, wide confidence intervals were also obtained for rock bass and black crappie.

### **4.4 Discussion**

#### *4.4.1 Trophic and temperature effects on MSY*

In many cases especially when the temperature forcing was not in effect, the SSmsy estimates were more conservative than the ESmsy estimates. When the temperature effects were accounted for, the model predicted a mixed response (Figure 4.3); for some species the ESmsy was larger and for others it was smaller. As expected, the reference point estimates for cisco and burbot were lower when the temperature effects were considered. For smallmouth bass, temperature effects led to higher reference point estimates. However,

indirect effects on the estimates were also observed on several other species. For example, increased competition with smallmouth bass for crayfish led to lower reference point estimates for rockbass and yellow perch. Similarly, the lower performance of cisco and yellow perch led to a lower reference point estimate for northern pike.

Species	Trophic effect	Trophic and temperature effect
Cisco		
Burbot		
Smallmouth bass		
Rockbass		
Yellow perch		
Walleye		
Northern pike		
White sucker		
Black crappie		
Carp		
Largemouth bass		
Bowfin		
Bullhead		

	Increase >5%
	Decrease >5%
	Change <5%

Figure 4.3. Trophic and temperature effects on MSY estimates

For each species the figure shows the difference in reference point estimates after including trophic and temperature effects. The legend for the figure is shown on the right.

In a similar analysis, Walters *et al.* (2005) found that ESmsy estimates increased as a result of compensation from predator and/or prey species. Similar results favoring higher effort levels under multispecies calculations were found in Gislason (1999) and Jacobsen *et al.* (2014) mainly through adjustments in competition, predation, and cannibalism. In a complex food-web it is not always easy to identify all the direct-indirect influences responsible for such compensation, but this analysis identified several major linkages in the system and showed how these linkages influenced the reference point estimates. The analysis showed that the compensatory response of prey influenced the ecosystem MSY estimates; thus, exploitation of prey species needs to take into account the contribution of same species to the predator diets. This kind of information would not be available from a single-species based analysis. Global analysis of contribution of prey species to fisheries found that in addition to direct benefits from catch, the total value generated by prey species was much higher due to their contribution to catch from higher trophic groups (Pikitch *et al.*, 2014; Smith *et al.*, 2011). It is also possible that based on the similarity of trophic function, forage fish be managed as a pool of species (Dickey-Collas *et al.*, 2014), but this could be problematic in a situation where differences exist between the forage species with respect to how they respond to environmental changes (for example it would not be appropriate to group cisco with yellow perch).

As mentioned, yellow perch is the leading prey species in the lake and the explanation of food-web dynamics of the lake without understanding the perch population dynamics is inconceivable. The major factors regulating its dynamics were walleye and cannibalism within the yellow perch population. When walleye was under exploited, the yellow perch population was controlled by direct predatory pressure from walleye. However, the effects

were not always straightforward: when walleye biomass was reduced by fishing at MSY, contrary to expectations, yellow perch biomass declined. The decline of yellow perch was due to predation pressure from species which were released from walleye predation. Direct compensation was not observed indicating that walleye-perch relationship is highly complicated (Ivan *et al.*, 2011); walleye exerts predation pressure on yellow perch but also controls the other predators of yellow perch.

This analysis enhances the understanding on interspecies interaction in the system and provides reference points which could serve to improve the current management plan that is largely based on single-species studies. Previous to this analysis, reference points for catch/stock status for Mille Lacs Lake were limited to a few species only such as walleye (Drake, 2007), northern pike (Schwarz, 2006) and yellow perch (Madsen, 2005). This analysis has laid out the reference limits for more than a dozen key species of the lake, a contribution that could serve as a strategic step in implementation of EBM (Large *et al.*, 2013; Levin *et al.*, 2013). The analysis showed that there is an opportunity to increase fishing on smallmouth bass and northern pike (Figure 4.4). Fishing mortality on cisco appears to be restricted successfully but the catch for burbot in 2006 was higher than the model ES<sub>msy</sub>T estimate. For rock bass, level of harvest was lower than the SS<sub>msy</sub>T but higher than the ES<sub>msy</sub>T; this indicates the species, possibly, is being overfished.

Further, my approaches allow the integration of temperature and trophic effects. I am able to identify sources of ecosystem pressure that caused lower ES<sub>msy</sub> for cisco, rock bass and other species under temperature forcing. Temperature has a strong influence on the decline of cisco (Jacobson *et al.*, 2008). In Chapter 2, I found that temperature accounted for 36%

change in cisco population in Mille Lacs Lake by correlating “temperature anomaly” with carrying capacity in the SP model. I obtained a very similar result for cisco from the EwE based analysis in this chapter: SSmsyT was 39% lower than SSmsy. Further, the analysis here suggests that in addition to the direct effects of temperature, cisco also faced indirect effects of temperature rise in the form of stronger competition from yellow perch and smallmouth bass which led to a lower estimates of limit reference points for cisco. The indirect effects contributed to further 30% reduction for the ESmsyT estimate.

Several studies have reported instances where increase in temperature has favored smallmouth bass (Funnell, 2012). The present analysis shows that projected increase of productivity of smallmouth bass would create competition for crayfish in Mille Lacs Lake. This competition for crayfish could negatively affect rock bass, cisco, and yellow perch. However, temperature rise also led to decline of burbot which is predatory on yellow perch; this released some predation pressure from yellow perch. The analysis here, therefore, lays out several hypotheses of how the ecosystem would respond under changing temperature. The analysis re-emphasizes that estimates of reference points could change with environmental changes, and it is important to re-estimate the reference points when it is expected that such changes could affect the productivity of a species.

#### *4.4.2 Mille Lacs Lake harvesting compared to ESmsy estimates*

I compared the fisheries catch from Mille Lacs Lake during the period from 2000 to 2006 against their ESmsy obtained with temperature effects. The comparison gives an intuitive idea about potential for increasing or the need for controlling the fishing intensity for each species under the changing environmental conditions.

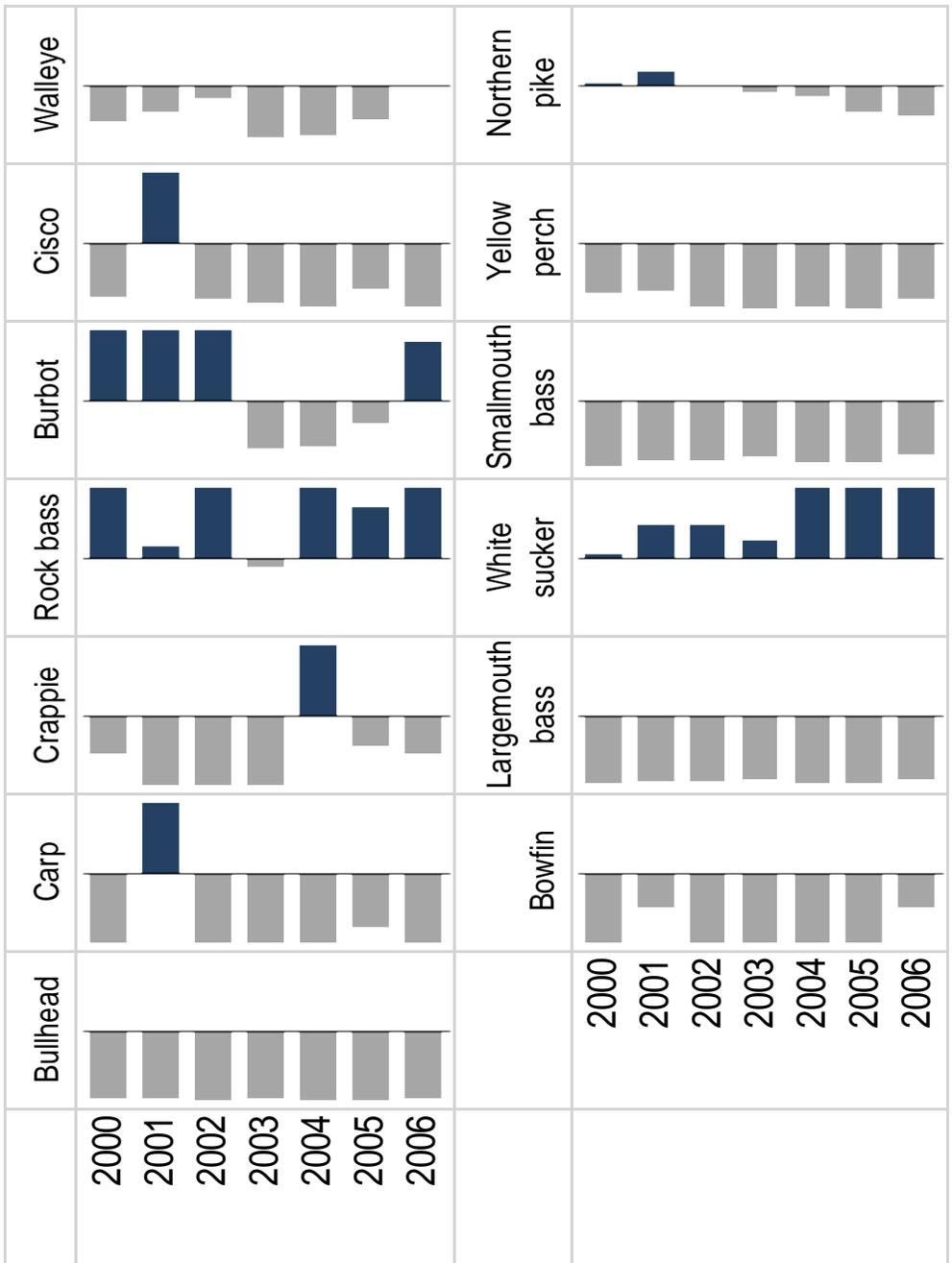


Figure 4.4. Comparison of catch against ESmsy

The horizontal bar represents the species ecosystem MSY with temperature forcing function (ESmsyT). The blue bar above the horizontal line indicate years when the catch was higher than ESmsyT and the grey bars below the horizontal line indicate the years when catch was lower than ESmsyT. The panels on the left show the names of the species.

Most of the species estimated were fished below their ESmsy levels (Figure 4.4). Walleye catch was below ESmsy from 2000-2005, but was equal to ESmsy in 2006. Northern pike, cisco, and burbot catch exceed their MSY estimate in 2001, but the catch was consistently lower than MSY in the following years. Exploitation for white sucker and rock bass were above the corresponding ESmsy levels. I also expect that the improved understanding of the inter-species interactions and comparison of exploitation levels against reference points will help develop management policy that will improve ecological sustainability of the lake.

#### 4.4.3 Fisheries selectivity

This research also highlights the importance of species-selective fishing, which is one of the major advantages of angling as a harvest technique. An evaluation of the Fmsy estimates (Figure 4.5) reveals how widely the sustainable fishing mortality levels vary between the species.

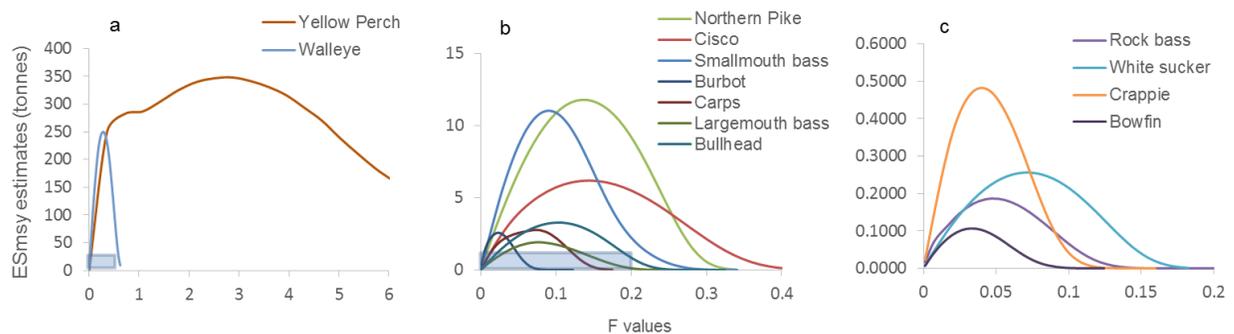


Figure 4.5. ESmsy plots for 13 species.

The figure is shown in 3 panels because of the wide range in ecosystem MSY ( $ESmsyT$ ) and corresponding Fmsy estimates. The blue rectangle area in the lower left corner of graph in panel a has been magnified in panel b; similarly the rectangle in the lower left corner of graph in panel b has been magnified in panel c.

Model results predict a population collapse for all species except yellow perch if all species were harvested at the walleye Fmsy. The results highlight the importance of multispecies analyses especially where non-selective fishing methods are more prevalent.

#### *4.4.4 Sensitivity analysis*

In a 50 functional group model, where four of every functional group parameters are allowed to vary within the Monte Carlo routine, I consider our results are quite encouraging. There were several cases where the inter-quartile limit varies by several tonnes, but the uniformity in species response under the different simulations points to model stability. One can argue that the Monte Carlo analysis does not vary the diet matrix parameters which help in calculating the mass-balance constraint of functional groups in Ecopath. However, the strength of the predatory-prey relationship (i.e. predation mortality estimates within the model) and the consumption varies depending on the biomass, P/B, and Q/B values of the predator and the prey species. Therefore, all the important predator-prey linkages will be affected by the Monte Carlo routine on the  $4 \times n$  (number of functional groups) parameters in the model (~200 parameters in the MLL model). Further, adding Monte Carlo on diet preferences has not yet been possible within the EwE software on account of the complexity required. In this Mille Lacs Lake EwE model, which attempts to model 50 functional groups, there are more than 2,000 diet interactions. Allowing a sensitivity analysis on each of these interactions, while constraining for mass-balance will be a highly computationally intensive task (because of the number and complexity of interactions among parameters to achieve mass balance for each Monte Carlo choice). In terms of structural uncertainty, a direct temperature effect was included for three species, but it might be possible that temperature had direct effects on other species too that I did

not explore. So there is scope to investigate other effects of temperature in future. Moreover, other sources of structural uncertainty related to spatial complexity (Charles, 1998), could be explored through spatial extensions of the model using Ecospace.

## **4.5 Conclusion**

I estimated single-species and ecosystem based reference limits with and without the influence of temperature for 13 species; reference points available previously were limited single-species analysis for few species. The analysis re-emphasised that reference points are not stationary estimates, but they change when environmental conditions alter species productivity. To prevent overexploitation, it is necessary for management to re-estimate or re-evaluate the reference points when environmental changes occur. Direct effects of temperature were incorporated into the dynamics of cisco, burbot, and smallmouth bass. The analysis showed that the ESmsyT for cisco and burbot were lower and for smallmouth bass was higher. But, the impact of temperature on the first three species also led to lower ESmsyT estimates for yellow perch, northern pike, and rock bass. The analysis showed that for these six species in the lake, it was important for the management to consider the combined effects of food-web interactions and temperature. From the perspective of ongoing management, a comparison of the catch records against the estimated ESmsyT showed that except burbot, rock bass and white sucker, most of the species were being fished below this reference level, and there is scope to increase fishing pressure on other species such as northern pike and smallmouth bass. The results suggest that taking into account ecosystem considerations are most important when the prey species in the ecosystem have a commercial fishery on them. There is some preliminary indications that when there is fishing on prey species, the recovery of over-exploited predator groups might

be difficult. I also present the importance of fishery selectivity; I show that if fisheries are managed for one productive species and fishing is using non-selective gear (i.e., lots of bycatch), then there is potential for several species to be overfished.

# 5 Simulation of Zebra Mussels Invasion and Evaluation of Impacts on the Mille Lacs Lake, Minnesota: An Ecosystem model<sup>4</sup>

## 5.1 Introduction

Zebra Mussels (*Dreissena polymorpha*) are freshwater, sessile, filter-feeding mussels which are known for its tremendous reproductive potential (Mackie, 1991), high water-filtration rate (Kryger and Riisgård, 1988), and fast colonization of the bottom substrate (Berkman *et al.*, 1998; Ludyanskiy *et al.*, 1993). After infestation, zebra mussels rapidly attain high densities: Lake Erie was reported to have a density of more than  $3 \times 10^5$  individuals.m<sup>-2</sup> during 1990 (MacIsaac *et al.*, 1991); average abundance of zebra mussels in Oneida Lake in 2001-2008 was 6,000 individuals.m<sup>-2</sup> (Naddafi and Rudstam, 2013). Their high level of planktivory affects the availability of nutrients and food for other species in the system. On account of their ability to modify benthic habitat structure and their effect on ecosystem function, invasive molluscs have often been referred to as ‘ecosystem engineers’ (Crooks, 2002; Gestoso *et al.*, 2013; Gutiérrez *et al.*, 2003).

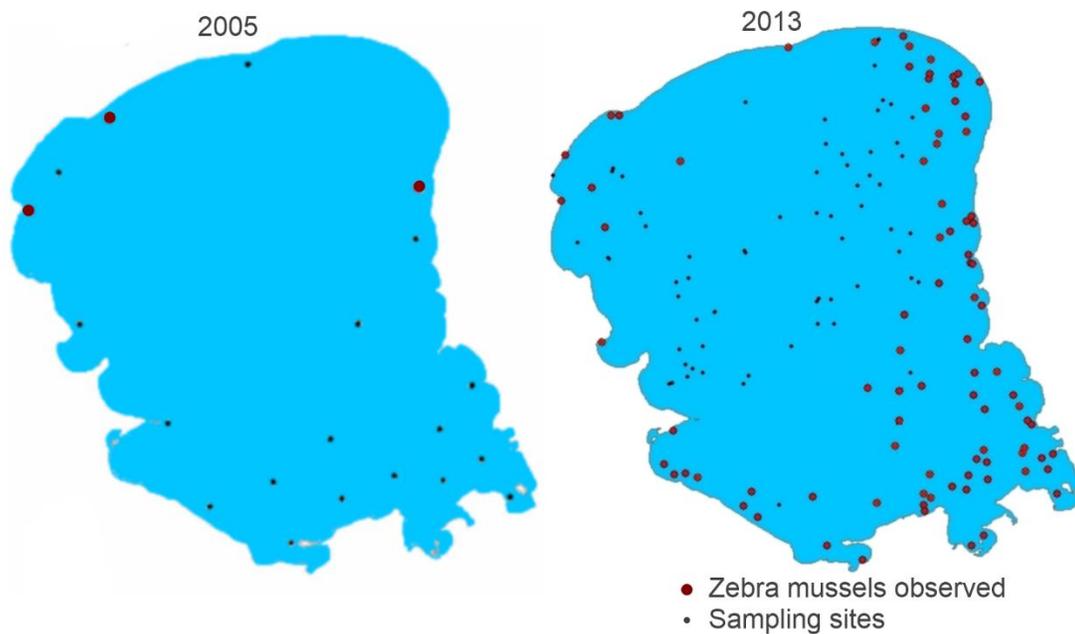
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<sup>4</sup> A version of this chapter has been submitted for publication and extended abstract was published. “Kumar, R. et al. 2014. Simulation of zebra mussel invasion and evaluation of impacts on the Mille Lacs Lake, Minnesota: an ecosystem model, p. 86. In: Steenbeek, J., Piroddi, C., Coll, M., Heymans, J. J., Villasante, S., Christensen, V. (eds.), Ecopath 30 Years Conference Proceedings: Extended Abstracts, pp. 86. Fisheries Centre Research Reports 22(3). Fisheries Centre, University of British Columbia [ISSN 1198-6727]. 237 p.”

Human-aided dispersal made possible the spread of this prolific species native to the Ponto-Caspian region (Black, Caspian, and Azov seas) through various regions of Europe—observed in England in 1824 (Karatayev *et al.*, 1997)—and from Europe to North America (Karatayev *et al.*, 1997; Ricciardi and MacIsaac, 2000). Lake St Clair was the first to witness the existence of zebra mussels in North America in 1988; later, it spread throughout the Great Lakes region (Mellina and Rasmussen, 1994) and eventually dispersed to lakes in Eastern US and Canada (Benson, 2014). Many factors could be implicated in the swift proliferation of the species in North American waters (McMahon, 1996) such as: absence of effective predators like round goby (*Neogobius melatostomus*), a predator in its native waters (Naddafi and Rudstam, 2014); having high fecundity and growth rate; early maturity and short lifespan; and high temperature tolerance—can tolerate temperatures in the range of 27-28°C or even bit higher in North American waters (Allen *et al.*, 1999; McMahon, 1996).

Mille Lacs, the premier walleye lake, has also been infested with several invasive species such as: common carp (*Cyprinus carpio*), zebra mussels, Chinese mystery snail (*Bellamya chinensis*), banded mysterysnail (*Viviparus georgianus*), spiny water flea (*Bythotrephes longimanus*), Eurasian watermilfoil (*Myriophyllum spicatum*), and curly-leaf pondweed (*Potamogeton crispus*) (MNDNR, 2012a). Among those, zebra mussels have shown the most rapid spread in the lake: scuba divers first sighted zebra mussels in 2005 at merely 3 sites (Figure 5.1). The average density increased from just 5 individuals.m<sup>-2</sup> in 2008 to 11,540 individuals.m<sup>-2</sup> in 2013 (Tom Jones, MNDNR, Pers. Comm.). The species have spread across the eastern shore of the lake as well as along few sites on the western shore (Figure 5.1).

There are some ecosystem model studies that explore zebra mussels impacts in Bay of Quinte, Canada, and Oneida Lake, USA (Miehls *et al.*, 2009) and Lake Huron and Lake Michigan (Langseth *et al.*, 2012). This is the first ecosystem modelling study on Mille Lacs Lake to assess the potential impacts of zebra mussels on native species. Following sections describe the process of inclusion of zebra mussels functional group in the ecosystem model, the simulation of the invasion, and the ecosystem-wide implication of the infestation.



*Figure 5.1. Spreading of zebra mussels in Mille Lacs Lake, Minnesota.*

*The species was first noticed in 2005 at 3 sites, and by 2013, it spread into large regions of the lake.*

## **5.2 Methods**

The base Ecopath model with 50 functional groups built in Chapter 3 was used for the simulation of the invasion. The Ecopath model represented an ecosystem snapshot of Mille

Lacs Lake in 1985, therefore the model lacked the representation (functional group) of zebra mussels, because this invasive species was first sighted in the lake in 2005.

### *5.2.1 Parametrization of zebra mussels in Mille Lacs Lake EwE model*

The EwE modelling approach requires that all functional groups be included in the Ecopath model from the start of the simulation; hence, zebra mussels were included as an additional functional group (51<sup>st</sup>) in the EwE model. Zebra mussels obtain their food by filtering the water—an adult can filter around a litre/day, and phytoplankton constitutes most of their diet (Benson *et al.*, 2012; Snyder *et al.*, 1997). Langseth *et al.* (2012) used (80%) phytoplankton in the diet of zebra mussels in the Lake Huron model; however, Jaeger (2006) indicated to higher detritus consumption by zebra mussels. Based on the literatures, diet of zebra mussels was adjusted as 70% phytoplankton and 30% detritus in the model. The consumption per unit biomass (Q/B), 4.1/year, was obtained from an energetics based estimate (Schneider, 1992). Production over biomass (P/B) value was obtained from the study of Jaeger (2006) as 1.35/year.

The biomass estimates of zebra mussels were available from annual monitoring by scuba diving at 250 sites in the Lake. In 2013, zebra mussels were observed in 88 out of the 250 sites monitored (Figure 5.1), indicating that the mussels had spread to about 34% of the lake locations (Tom Jones, MNDNR, pers. comm.). The density at the various sites ranged from 538 to 32,292 individuals/m<sup>2</sup> with an average of 11,540 individuals/m<sup>2</sup>. Based on the samples obtained at two sites (Spider Island and Deep Cove) in the lake, on an average, each zebra mussel weighs 0.28g. By multiplying the weight and density, the current

biomass was estimated as 1,100 tons.km<sup>-2</sup>, and 95% confidence limit for the estimate were 600 to 1,600 tons.km<sup>-2</sup>.

### 5.2.2 *Simulating the invasion*

The newly added functional group zebra mussels was set up with a very high initial biomass of zebra mussels (1,100 tons.km<sup>-2</sup>) in 1985. The biomass was constrained to be very low until 2005 by putting high fishing pressure on it. The simulations were run on the fitted-model (fitted from 1985-2006) to the year 2036. At the onset of 2005, the fishing pressure was gradually released allowing zebra mussel biomass to increase; the rate of relaxation was calibrated in such a way that the dynamics of observed density matched with the trend of predicted density during the initial period of invasion. To satisfy the ecopath mass-balance principle, a negative biomass accumulation of the magnitude equal to the amount of phytoplankton consumed by the zebra mussels was applied onto the phytoplankton (Langseth *et al.*, 2012).

Based on a comparison across multiple lakes infested with zebra mussels, Burlakova *et al.* (2006) suggested that availability of suitable substrate limited zebra mussels population size. Extended periods of high temperature (29 to 30°C) in summer affected growth and tissue condition and caused mortality of zebra mussels in Lower Mississippi River (Allen *et al.*, 1999). Mille Lacs Lake also experienced higher temperature in few years after zebra mussels' invasion, so there was possibility for this change to cause stress for the zebra mussels population. In an effort to mimic these sort of non-nutritional challenges zebra mussels could have faced in invading and colonising an ecosystem, I used different trajectories for releasing fishing pressure from zebra mussels. The non-nutritional

challenges in the lake may include: substrate limitation, high summer temperatures, and others for which I do not have much information such as presence of predators that were not accounted for in the model or calcium levels in water.

### *5.2.3 Effects on zebra mussels predators*

Analysis of stomach contents of major fish predators in Mille Lacs Lake provided evidence of very low predation on zebra mussels: 118 smallmouth bass, 115 northern pike, and 677 walleye diets were analysed, and the quantities of zebra mussels in their diets were 0.0616%, 0.0048%, and 1.030% respectively (pers comm. Tyler Ahrenstorff, Fisheries Research Biologist, MNDNR). I incorporated these diet estimates in the model and explored the impact on zebra mussels and its predators. Though not observed in Mille Lacs Lake, several field experiment based studies have reported that crayfish feed on zebra mussels (Goote and Bergman, 2012; Love and Savino, 1993; Macisaac, 1994); so, I also explored scenarios with zebra mussels constituting (i) 20% , (ii) 30% and, (iii) 50% of crayfish diet.

## **5.3 Results**

### *5.3.1 Zebra mussels biomass*

The model was able to reproduce the explosion of zebra mussels reasonably well in the lake. When fishing pressure was completely released and zebra mussels were allowed to grow freely; their biomass increased rapidly and plateaued at  $\sim 700\text{t.km}^{-2}$ , which was lower than the observed biomass, but the estimate was within confidence interval (CI) of observed biomass (95% CI, 600-1,600). In the model, the biomass at which zebra mussels levelled-

off depended on the amount of fishing pressure released. As mentioned before, by applying different trajectories of fishing mortality, I simulated non-nutritional challenges for spread of zebra mussels in the system, and the lowest value at which the biomass stabilized was  $\sim 300\text{t.km}^{-2}$  (Figure 5.2).

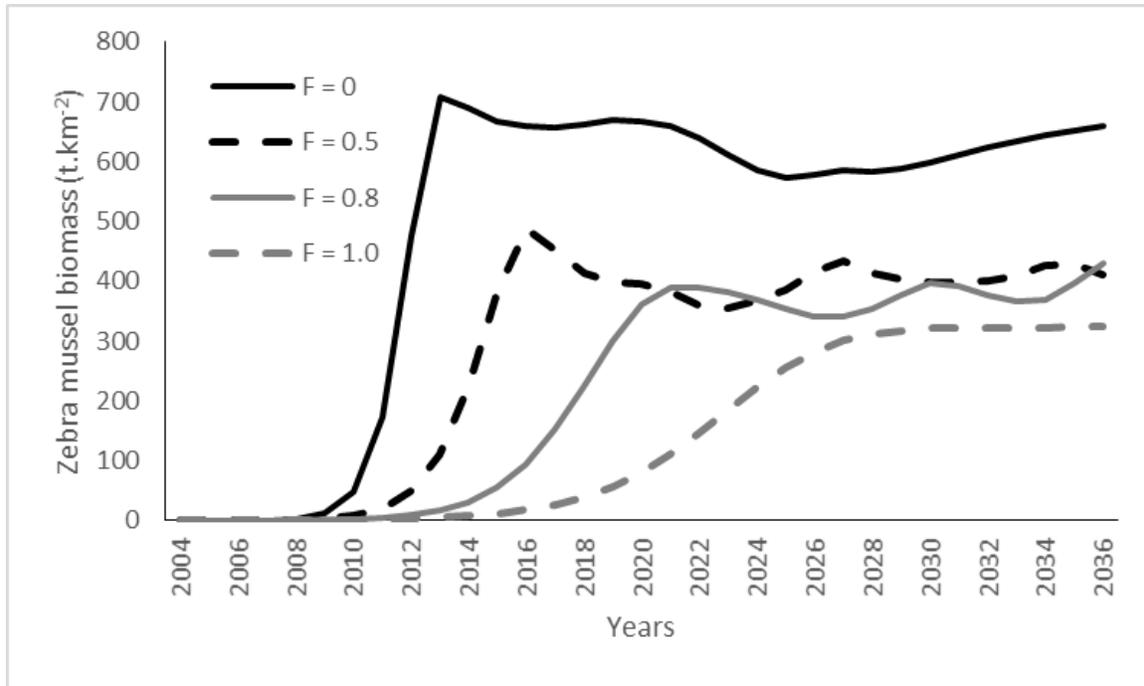


Figure 5.2. Zebra mussels trajectories at different fishing mortalities.

The solid black line shows the simulation of invasion when there is no pressure on the zebra mussels population, and the other lines show the projection when there are some pressures on the zebra mussels population.

Further, I also conducted a simple test of the sensitivity of the zebra mussels biomass trajectory in response to the consumption to biomass ratio (Q/B) parameter, and found that the level to which zebra mussels would increase was sensitive to their consumption rate (Q/B) (Figure 5.3). At higher Q/B levels, the mussels biomass plateaued at a lower level;

this was because at higher Q/B more phytoplankton was consumed to achieve the same level of production.

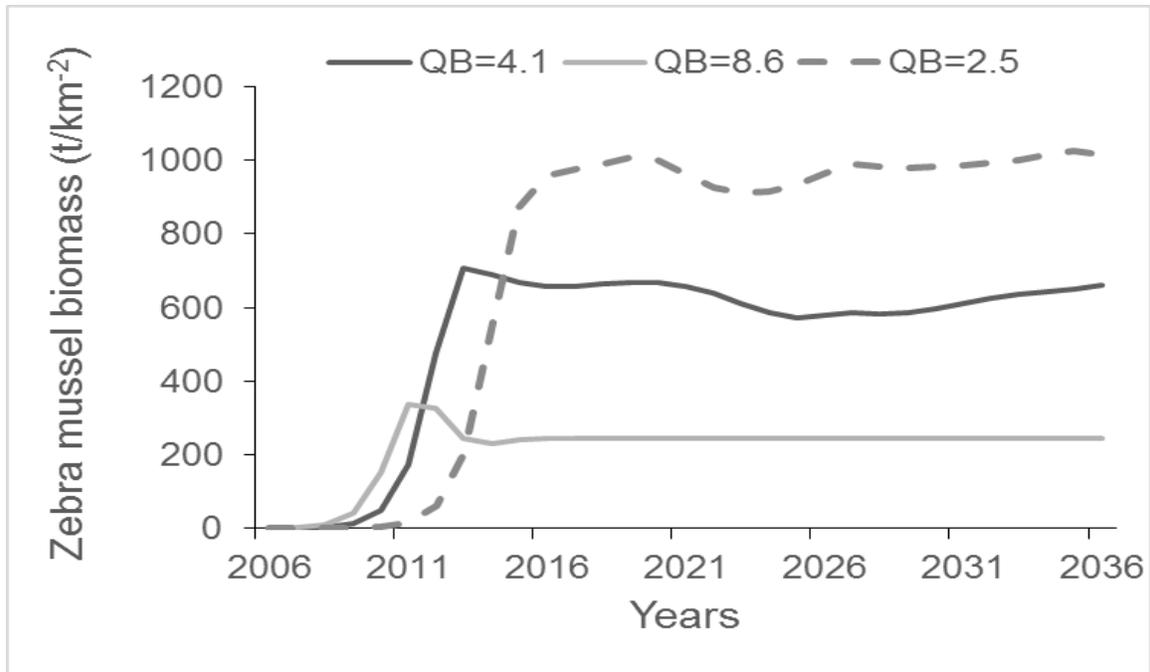


Figure 5.3. Sensitivity test on zebra mussels trajectories to  $Q/B$  parameter.  
 $Q/B = 4.1$  represents the base value chosen for the Ecopath model

### 5.3.2 Effects on food chain: bottom-up trophic control

It was found that increases in zebra mussels caused phytoplankton to decline drastically (Figure 5.4: phytoplankton) which resulted in a decline in zooplankton population. Besides, the plankton groups also constitute a bulk of the diet of numerous insect species; their abundance also declined in response to plankton decline. Zooplankton and insects together form a large proportion of young yellow perch diet; hence, a decline in yellow perch was observed. Zooplankton is also a major food item for many juvenile fish, and yellow perch is a central forage species of top-order piscivores; their depletion badly affected the apex predators such as walleye and northern pike. Thus, invasion of zebra mussels caused the

decline of the primary and secondary producers in the lake; this effect moved up the food chain and major fish species declined (Figure 5.4).

On the other hand, some species showed increases in biomass (Figure 5.4). The model predicted an increase in periphyton which led to an increase in sunfish (*Lepomis* spp.), other shiners and minnows (the functional group comprised a number of tiny forage species (Appendix C). Macrophytes remained at their base levels in the models, and gastropods which consume macrophytes increased because their main predators declined while food remained continuously available.

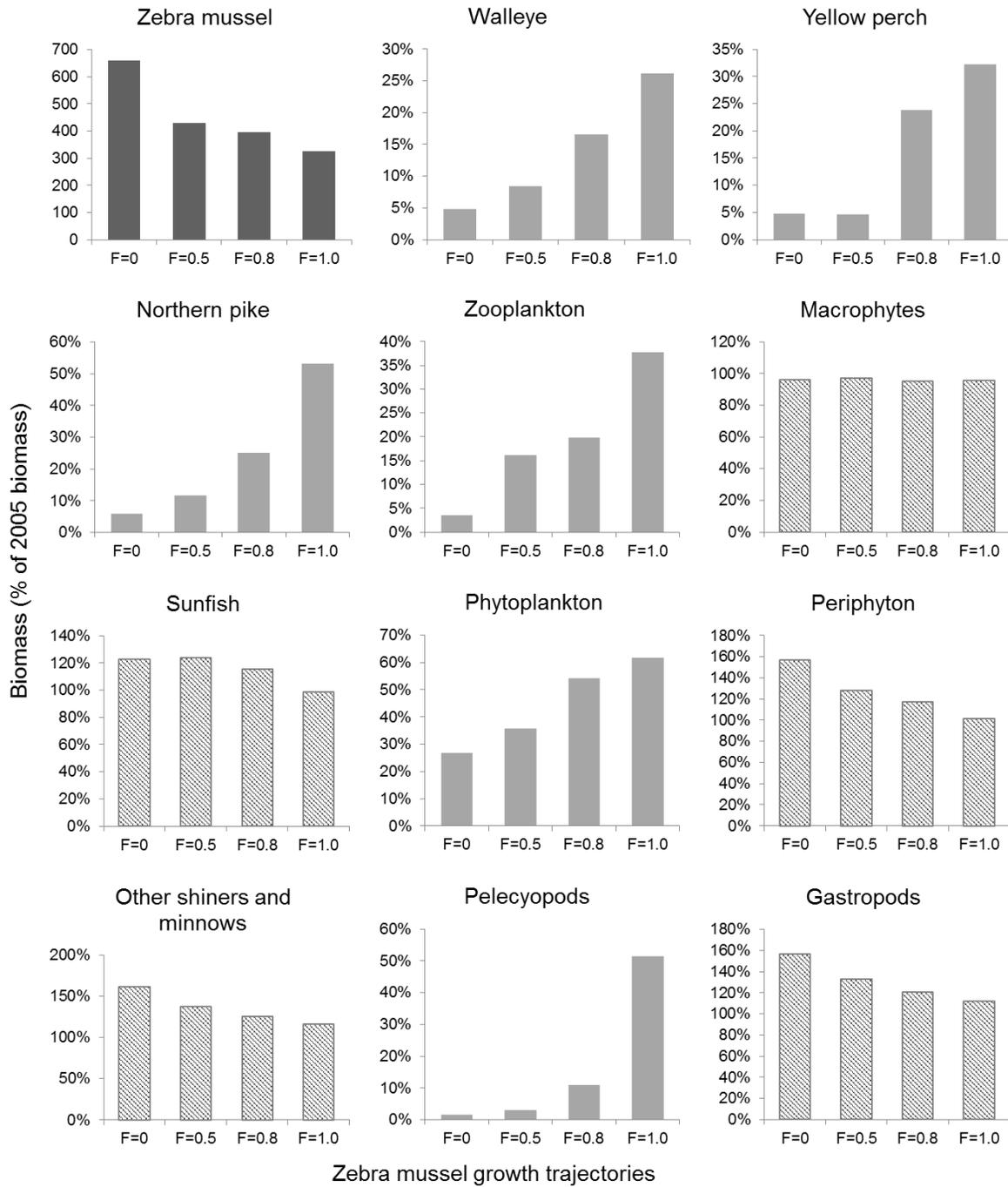


Figure 5.4. Biomass of various species at the end of simulation.

The end biomasses are expressed as a percentage of their corresponding 2005 biomasses (except zebra mussels for which the absolute biomass is shown). *F* values indicate the level of fishing pressure applied on zebra mussels from the year of invasion 2005 onwards. The grey bars represent species which are negatively impacted by zebra mussels; the shaded bars show species that are either positively affected or unaffected by zebra mussels.

### 5.3.3 Effects on zebra mussels predators

The effects of adding small amounts of zebra mussels (~1%) to the diets of walleye, northern pike, and smallmouth bass made no observable difference to the dynamics of zebra mussels or other species in the lake. On the other hand, adding zebra mussels to crayfish diets led to increase in crayfish biomass. Since smallmouth bass mostly consumes crayfish in the lake, increase in the latter also led to increase in biomass of smallmouth bass. As the proportion of zebra mussels in crayfish diet was increased, crayfish biomass continued to increase and smallmouth bass also steadily increased. The increased predation had a very small impact on zebra mussels densities (Figure 5.5).

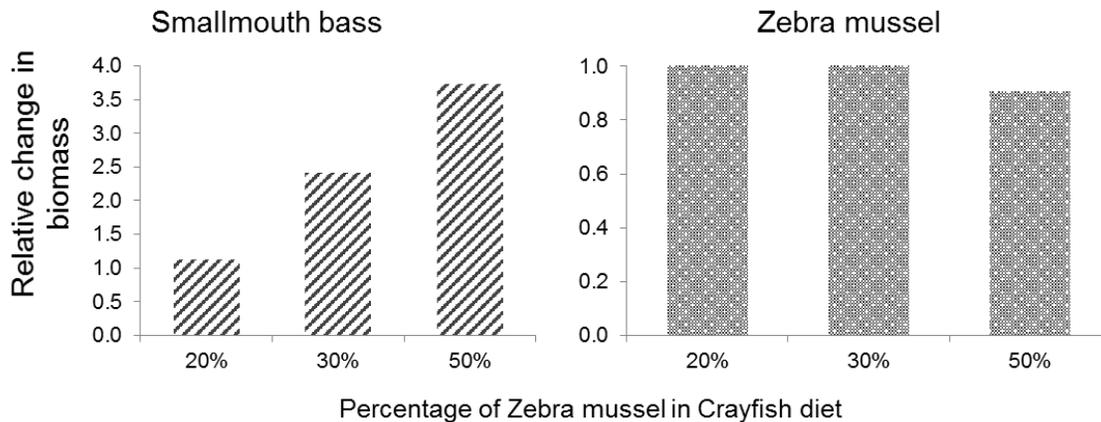


Figure 5.5. Zebra mussels-crayfish-smallmouth bass interactions.

The graph shows biomass levels for smallmouth bass and zebra mussels at the end of simulation year when zebra mussels were included in the diet of crayfish by 20%, 30%, and 50%. The changes are shown relative to not including zebra mussels in diet of crayfish.

## 5.4 Confronting model prediction to field data

As mentioned the EwE model was fitted to the historical catch and abundance data from 1985 to 2006, and the fitted model was driven for another 30 years (till 2036). The model

prediction performances were compared to the available field data of zebra mussels' biomass, water clarity in the form of Secchi disk readings, zooplankton density, and the abundance of many fish functional groups from 2007 to 2012. In most cases, model predictions were consistent with trends in field data as shown in the following sections.

#### *5.4.1 Zebra mussels biomass vs water clarity*

Both observed and predicted biomass trend of zebra mussels included rapid population growth, though field estimates were higher than the model's prediction (Figure 5.6). That zebra mussels attained maximum density within few years of invasion was observed in several lakes in North America (Burlakova *et al.*, 2006), and the findings from Mille Lacs Lake further support the typical rapid growth pattern of the mussels. Zebra mussels are a filter-feeding species that is known for its capacity to clarify water by filtering phytoplankton out of system. Mille Lacs transparency trend (Secchi disk readings) has also increased rapidly as zebra mussels increased in the system (Figure 5.6): the transparency trend which was almost stable around 12 feet historically (Figure 5.6 and Figure 1.6), increased after 2010 and reached as high as 15 feet. A 3 foot increment in transparency of the lake in merely 3 years reflects its tremendous presence in the lake as well as its filtration rate.

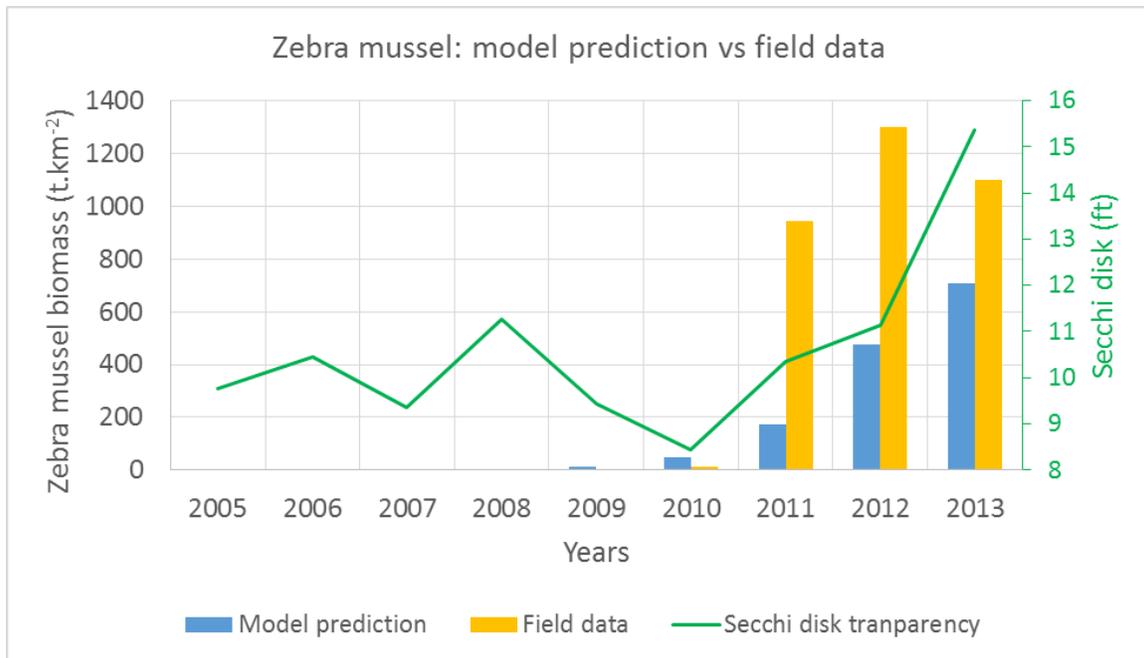


Figure 5.6. Zebra mussels observed biomass vs predicted biomass from invasion (2005) to 2013. Water transparency in the form of Secchi disk readings range during the same time period were also overlaid on the graph (green line).

#### 5.4.2 Zooplankton: model prediction vs observed density

In the model, zooplankton solely feeds on phytoplankton; thus a reduction in phytoplankton biomass because of zebra mussels caused zooplankton to decline substantially. Total observed zooplankton density declined from nearly 70 per litre in the beginning of invasion to nearly 25 per litre by the year 2013. The model predicts a similar declining trend (Figure 5.7). However, with regards to the proportion of different types of zooplankton, the observed data indicates that copepods were least affected compared to the cladocerans. Since the model included a single group for zooplankton species, it is unable to capture this difference. The changes in zooplankton community structure indicate that different community of zooplankton interact differently with phytoplankton community, and that there may be some phytoplankton components that were less affected by zebra mussels'

irruption and supported zooplankton like copepods from declining. This is perhaps a major limitation of by the present model with single phytoplankton and zooplankton group, especially with regards to using the model for future prediction. This suggests that future work on zebra mussels impacts should include a higher resolution of plankton at these lower trophic levels.

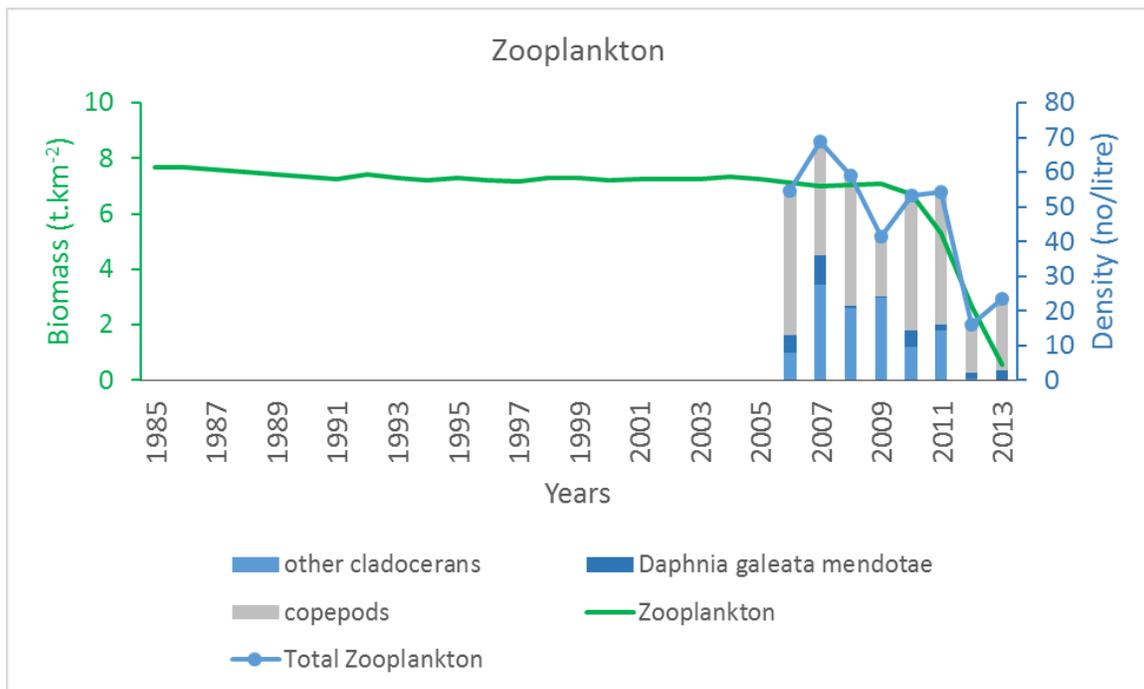


Figure 5.7. Zooplankton biomass prediction vs observed density. Green line represents zooplankton biomass predicted by model while Columns represent observed density. Each column also shows the relative proportion of different species of zooplankton.

#### 5.4.3 Fish species: model prediction vs observed CPUE

To keep track of changes in fish species abundance, Mille Lacs Lake is monitored by test netting at 32 locations across the lake. The pattern of average CPUE time-series observed from these nets were compared from the model predictions for a number of species given

below (Figure 5.8). Model prediction were in quite good agreement with the observed trend in most of the cases.

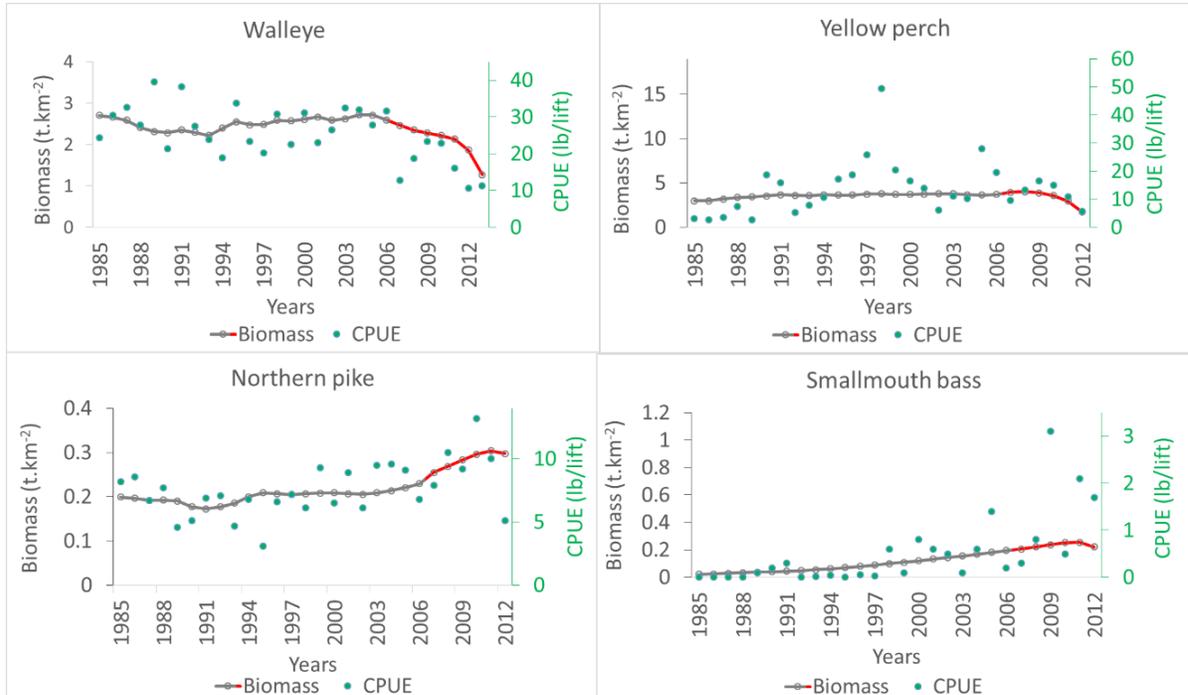


Figure 5.8. Model prediction of biomass against assessment gill net CPUE.

Dot represents observed CPUE trend. Grey part of line is from the ecosystem model fitted to CPUE data (1985-2006) while red part of line is ecosystem model predictions starting from year 2007. The trend of the predicted line is in close agreement with observed data.

## 5.5 Discussion

### 5.5.1 Zebra mussels biomass

The rapid increase in zebra mussels followed by levelling-off of the population is a response that has been recorded across several instances of zebra mussels infestation. In a study across multiple lakes infested with zebra mussels, it was observed that zebra mussels populations increased rapidly and then stabilized; it took approximately 3 years to reach

maximum density from detection of its presence and about 7 to 12 years from the first date of invasion (Burlakova *et al.*, 2006). In Saginaw Bay in Lake Huron and Long Point Bay in Lake Erie, zebra mussels populations reached their maximum levels within two years of being detected (reviewed in: Burlakova *et al.*, 2006). In Mille Lacs Lake, as stated earlier, three sites recorded the presence of zebra mussels in 2005 and by 2012, the population had achieved very high densities and since then the population has remained relatively stable

The model predicted similar trends across all the scenarios explored using the different fishing pressure trajectories. The sensitivity analysis indicated that the biomass at which zebra mussels population stabilised could vary depending on Q/B parameter for zebra mussels: a lower Q/B (than used in the model) predicted much higher biomass levels. The sensitivity of the model prediction to the Q/B parameter and stabilization at a biomass level lower than the field estimate indicates towards a nutrient limitation for zebra mussels in Mille Lacs Lake. If the model prediction of stable biomass was reached at a level higher than the field estimate, I would have had more confidence in a non-nutrient limitation.

### 5.5.2 *Effects on food web*

Studies across various lakes established a consistent decline in chlorophyll level after zebra mussels invasion (Cha *et al.*, 2013; Higgins *et al.*, 2011; Mida *et al.*, 2010). Huge declines in various phytoplankton species, especially diatoms in Lake Michigan were recorded following invasion by mussels (Fahnenstiel *et al.*, 2010; Vanderploeg *et al.*, 2010).

Reduction in phytoplankton negatively affected zooplankton (Watkins *et al.*, 2013), and this was linked to decline of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes (Herbst *et al.*, 2013).

The model prediction about system-wide collapse of forage and predatory fish species at the end of simulation (2036) may be an overestimation of zebra mussels' influence. Some weaknesses in the model could have created a simple pathway for predicted declines—the model was constrained by the inclusion of a single phytoplankton group and a single zooplankton group. Hence it was not able to explore the shift in phytoplankton composition such has been recorded: shift from larger to smaller diatoms in Lake Erie (Barbiero *et al.*, 2009) and sometimes to less desirable groups like cyanobacteria and *Microcystis* (Fishman *et al.*, 2010). Different phytoplankton groups might be differently vulnerable to zebra mussels consumption, thus not totally limiting the availability for all zooplankton. This is reflected in the sampling data (Figure 5.7) where total zooplankton in the lake declined after the invasion, but the copepods were less affected compared to that of *Daphnia* and other cladocerans. Similarly the model cannot capture change in zooplankton communities such as observed in Lake Huron: amphipod *Diporeia* and cladocerans were replaced by copepods (Barbiero *et al.*, 2009). Ecopath models of Lake Ontario representing pre and post-invasion time periods showed decline in the biomass and production of several invertebrate and fish species; the decline in *Diporeia* led to increased contribution of mysis (*Mysis diluviana*) in the diets of smelts, sculpins, and alewives (Stewart and Sprules, 2011). While in Lake Ontario, mysis contributed to the prey base for fish species, in Lake Michigan and Lake Huron alewife population declined following *Diporeia* declines (Snyder *et al.*, 2011). For Bay of Quinte, Ecopath model was used to evaluate targets for remedial action plans especially in relation to ecosystem capacity to support the different species (Blukacz-Richards and Koops, 2012)—the analysis found that reduction in zebra mussels was necessary to “accommodate all the predatory demands on phytoplankton”.

Similar decline in *Diporeia* population was not observed in the New York finger lakes and studies based on fatty acid tracers concluded that this observation was related to the access to food sources (of terrestrial detritus origin) not “intercepted” by zebra mussels (Watkins *et al.*, 2012). Plankton community shifts would affect different fish groups differently based on their dependence on specific phytoplankton and zooplankton groups.

The response of Mille Lacs Lake food web to zebra mussels invasion is governed by at least three factors: (1) How do the juveniles of different fish groups respond to shifts in plankton community; (2) How does the invertebrate community respond to zebra mussels; and lastly but perhaps most importantly from Mille Lacs Lake perspective (3) Is yellow perch able to use alternate pathways for obtaining energy (i.e., an altered plankton community or an altered invertebrate community). But, this would not be a trivial exercise. Even if I split the different phytoplankton and zooplankton groups, the model will not be strengthened unless these new groups are parameterized differently. Spiny water fleas invasion was observed in Mille Lacs Lake in 2009; from the perspective of plankton dynamics, it is also important to consider the effects of spiny water on the zooplankton in the lake (MNDNR 2013).

Additionally, round goby invasion in several lakes in the Great Lakes region including Duluth harbour in Lake Superior (USGS 2015) creates a potential for its spread to Mille Lacs Lake. In the concluding chapter, I extensively discuss the potential effects of spiny water flea and possible round goby invasion in Mille Lacs Lake.

### 5.5.3 *Effects on zebra mussels predators*

Crayfish densities and smallmouth bass densities have reportedly increased in the last few years in Mille Lacs Lake. The analysis suggests that a possible cause for this could be an

increase in crayfish owing to zebra mussels consumption. In addition, crayfish foraging on other invertebrates is not affected negatively by zebra mussels because of its ability to “burrow under zebra mussel colonies” (Beekey *et al.*, 2004). In Lake Erie round goby (predator of zebra mussels in its native waters) invasion occurred in 1990; its population increased, and it became an important prey for smallmouth bass (Hogan *et al.*, 2007) and introduced salmon.

## **5.6 Conclusion**

The model is the first attempt at predicting ecosystem-wide impacts of zebra mussels invasion in Mille Lacs Lake. Model predictions were in close-agreement with the field data when compared with them from year 2006-2012. It predicts severe declines in phytoplankton and zooplankton densities followed by system-wide collapse of forage fish and top predators such as walleye. The model predicted increases in species such as shiners and minnows and sunfish which depend on periphyton. Model predictions of system-wide collapses by the end of simulation year are probably overestimated owing to a limited resolution of the model at the level of primary and first-order secondary consumers. The work predicts a steady increase in smallmouth bass population subsequent to a possible crayfish-zebra mussels interaction in the lake. Finally I conclude that zebra mussels populations would probably stabilize after the initial population boom already recorded based on predictions from the different scenarios explored in the model.

## **6 Conclusion**

### **6.1 Chapter 1**

Ecosystem wide sustainable management, control of alien species, and restoration of depleted species in the face of changing temperature and high fishing pressure are the cardinal research questions that were addressed in this thesis. Mille Lacs Lake in Minnesota is a lake managed rigorously for recreational fisheries, especially walleye. A statistical catch at age (SCAA) model (Drake 2007) is used to quantify the status of the walleye stock and to set the limits for the recreational anglers. The status of walleye and other fish populations in the lake is expected to respond to management regulations and environmental conditions. Every year the MNDNR conducts gillnet sampling surveys to monitor the population status of most of the different fish species in the lake. However, before this research, all the varied data have not been incorporated into analyses that estimate the status of the different fish populations. My thesis built an ecosystem model (a food web model in the Ecopath with Ecosim (EwE) framework) which was tuned to the observed abundances of the various species observed in the gill-net sampling assessments and the catch records maintained by MNDNR. The ecosystem model was used for (1) quantifying the ecosystem structure (Chapter 3), (2) exploring scenarios for recreational fisheries management (Chapter 3), and (3) calculation of management reference points for the fished-species (Chapter 4). I used temperature data to explore environmental effects on the MLL ecosystem: in Chapter 2, I studied the influence of temperature on the cisco and in Chapter 4 on management reference points. The complexity of ecosystem based management of Mille Lacs Lake was exacerbated by the invasion of zebra mussels during

this research. In Chapter 5, I included zebra mussels in the ecosystem model and explored the ecosystem-wide impacts of zebra mussels invasion.

When the findings from the ecosystem model which was built using extensive amounts of field data were presented to MNDNR, managers and biologists considered many model predictions to be credible based on their experience of the ecosystem. This feed-back from the managers and the field biologists is mentioned here because of the applied research context of the thesis, but here the intention is not to use the positive feed-back for validation purposes. The model will be presented to the MNDNR for continued use in exploring ecosystem effects of various scenarios, and the staff expressed interest in training members from their group in using the model.

### *6.1.1 Historical perspective*

The baseline for all the analyses in the thesis is the year 1985 mainly because consistent fisheries and environmental data were available from this year. However, Mille Lacs Lake and the adjoining regions are understood to have undergone many changes over the past few hundred years following European settlement. West shore of Lake Superior was one of the regions of first contact between the Ojibwe Native tribes (also known as the Chippewa or Anishinabe) and French fur traders in the late 1600s (USDA, 2015). As early as 1733, a Henry Popple map shows Mille Lacs Lake as "Lake Mifsifsucaigan or Baude" and the name "Mini Sagaigonin or Mille Lacs" emerges in government records in 1843 (Wikipedia, 2015). Approximately 27 million acres of land (current geographical regions of Wisconsin, Minnesota, and Michigan) were held by the Ojibwa in the 1800s (Newhouse, 2000). The

1837 treaty negotiations between the Ojibwa and the United States granted hunting, fishing, and gathering rights to the natives in the 'ceded lands' (Newhouse, 2000).

Records indicate that approximately 24 aboriginal tribes occupied lands within the native range of walleye and sauger (*Sander canadensis*). In the lower Great Lakes, native fishing using spears, hook and line, wiers, and probably even nets were as old as 2500 B.C.

(Schmalz *et al.*, 2011). Written records of walleye fishing in Lake Huron are as early as 1695. In the 1830s, the Ojibwe used gillnets and hook and line gears for fishing.

Quantifying the impact of native subsistence harvest on the fisheries is difficult but is generally understood to be of low impact mainly because of lack of facilities to preserve and transport large amounts of fish, the spiritual importance attached to fish, and the fact that Europeans recorded large individual fish and high abundance of fish (Schmalz *et al.*, 2011). In the current times, tribal fisheries is understood to take approximately 4 to 5% of walleye age 3 and higher in Mille Lacs Lake (Schmalz *et al.*, 2011).

Many ecological changes followed the European settlement in the Great Lakes region. Logging and fire suppression led to changes in forest community structure and land use patterns (Friedman and Reich, 2005; Schulte *et al.*, 2007). The clearcutting probably also led to water-table fluctuations and increases in stream flow leading to nutrient enhancement (Veny, 1986). Diatom stratigraphic profiles used to study human impact on lake ecosystems in Minnesota and Dakota showed signs of enrichment following "land clearance and cultivation" in the late 19<sup>th</sup> century (Bradbury, 1975). Before settlement the water quality changes in Minnesota lakes were small, but post settlement chloride and total phosphorus levels in the lakes increased; the level of increase was related to the extent of development

in the watershed areas (Ramstack *et al.*, 2004). Lake shore development in the late 19<sup>th</sup> and the early 20<sup>th</sup> centuries were predominantly seasonal and probably did not cause large changes to the lakeshore but when the settlements changed to year round use nutrient loading in the lakes increased (Garrison and Wakeman, 2000). Further, the evolution of the American Midwest into the “nation’s breadbasket” through intensive agriculture led to further changes in water quality through soil erosion and use of fertilizers (Turner and Rabalais, 2003). The Federal Water Pollution Control Act of 1948 was the first law to control pollution of streams in the United States. The Clean Water Act of 1972 was more powerful and is believed to have improved water quality (i.e. reduced the nutrient loading) in several lakes in Minnesota (including Mille Lacs Lake) though much data on Mille Lacs Lake water clarity is not available prior to 1988 (MNDNR pers comm).

Mille Lacs Lake is understood to have higher turbidity before the implementation of the Clean Water Act in 1972 (Don Pereira, MNDNR, pers. comm.). Greater environmental awareness among private citizens also led to improvement in water quality (Eric Jensen, MNDNR, pers. comm). Minnesota Pollution Control Agency (MPCA) has been historically collecting the MLL water clarity data from 40 different locations across the Lake since 1974. Unfortunately, data availability was not consistent between the stations across all years: 65% stations were even sampled for only a single year during 1974-2013 (Figure 6.1); further, even those 65% stations were not consistent over the years (Figure 6.1). Only 7 out of 40 sampling sites that MPCA collected the data for at least 5 years. Sampling location 213 was the only station that was sampled more than 10 years; location 206 had 10 years of data, and all other stations had fewer than 10 years of data. Considering the

inconsistency in the data across stations, it is difficult to come to a conclusion changes in lake water clarity.

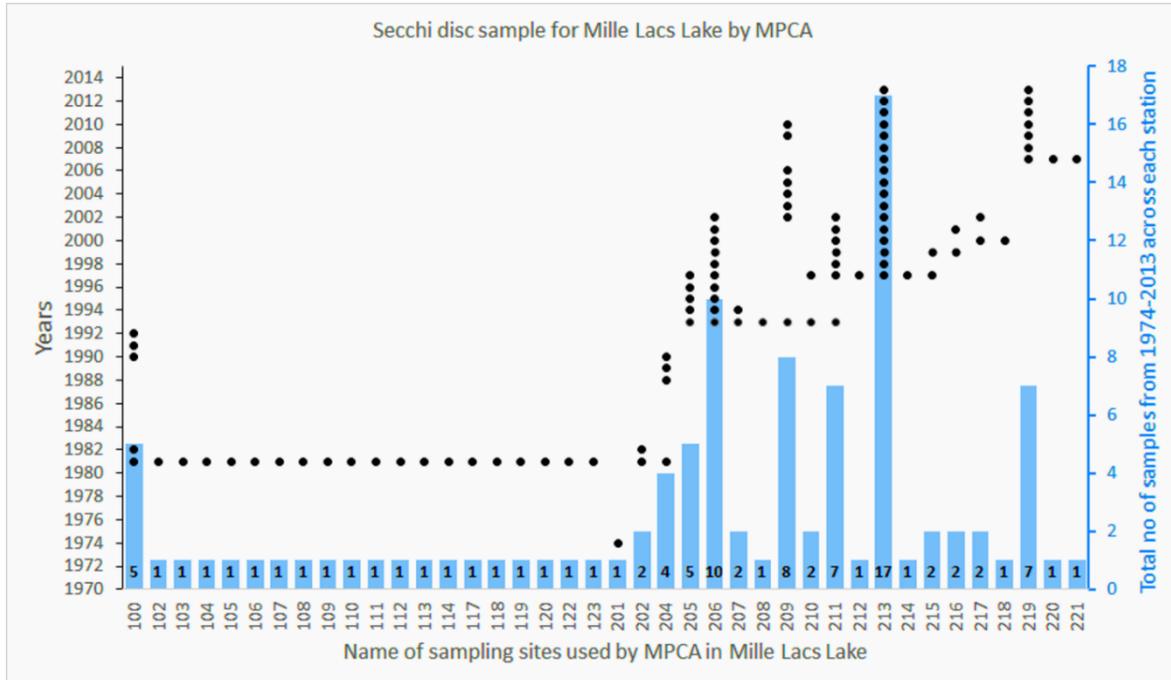


Figure 6.1. Summary of Mille Lacs Lake water clarity (source:MPCA).

X-axis represent the name of sampling station (sites) in Mille Lacs Lake used by MPCA. The dots represent the years when data are available at each sampling station. Height of bars are relative to the number of year(s) data are available at each station from 1974-2013. For example, sampling site 213 has continuous data from year 1997 to 2013 (total 17 years data), and most of the stations has data for just one year.

Recent data consistently collected across 9 stations in Mille Lacs Lake by MNDNR shows an increase in clarity from 2010 following the establishment of zebra mussels population in the lake (Figure 1.7). From a long term perspective, it seems that nutrient loading increased in the 1900s but in the recent time period water clarity is increasing following zebra mussels invasion. The lake water quality especially water clarity in the current time period is probably more similar to the status of the lake pre-European settlement but the species composition is definitely very different. Zebra mussels and spiny water flea have altered the

phytoplankton and zooplankton food webs in the lake. Cisco and burbot are lower than they were in 1985, but it is not possible to comment on the importance of these species in the lake food web hundred years ago. While from an environmental perspective, the baseline for the lake could be in the pre-settlement time period but from a management perspective, the baseline is ought to be much more recent owing to the many changes that have happened in the watershed and within the lake itself.

## **6.2 Chapter 2**

Cisco is a cold-water stenotherm, and annual monitoring revealed that this coregonid forage fish species has undergone severe declines in the past two decades. There was also a fishery for this species over the last 20 years. Similar declines have also been recorded in other Minnesota lakes, and several studies have pointed to temperature increase as the cause for cisco mortality (Fang *et al.*, 2012; Jacobson *et al.*, 2008; Jiang *et al.*, 2012). However, the influence of temperature has not been quantified previously. Hence, in Chapter 2, I developed three surplus production models with different levels of complexity for the cisco population: (1) generic surplus production model, (2) surplus production model with temperature influence, and (3) surplus production model with temperature influence and process error. The main goal was to investigate if temperature was a causative factor for cisco decline; the model with observation error and process error was used to explore if the decline could be explained away as process error. Data on catch per unit effort (CPUE) of sampling gill nets from 1985 to 2007 were used as an index of fish abundance for the lake population. The model parameters were estimated by fitting the predicted CPUE to the observed CPUE. Temperature-influenced time-varying carrying capacity and maximum sustainable yield (MSY) were also estimated. Based on the models evaluated, I concluded

that the causes of cisco decline were a combination of temperature and fishing pressure. Additionally, I also tested other model formulations (models with only process error) and data (accumulated degree days instead of temperature). After the in-depth evaluation of structural uncertainty, I concluded that temperature changes were responsible for approximately 36 to 40% of change in ecosystem carrying capacity for cisco.

Frey (1955), as cited in Colby and Brooke (1969), described the summer habitat suitability as cisco-layer—water where the temperature was lower than 20°C and the dissolved oxygen level was higher than 3ppm. MLL is a shallow lake allowing full mixing of water and is characterised by the absence of a thermocline thus providing little thermal refuge in deeper waters. If the modelling approach were extended to other lakes, the refuge volume (“cisco layer”) could be used as a covariate rather than temperature alone to quantify the influence of temperature. Using temperature and oxygen profile, Fang *et al.* (2012) estimated the “oxythermal” habitat for cisco lakes in Minnesota and found that cisco in only about a third of these lakes would have habitat suitable for survival under future warmer conditions. This work opened up the opportunity for a population wide (North America) meta-analysis of temperature effects on cisco based on the modelling approach used in Chapter 2 (Kumar *et al.*, 2013).

I assumed that temperature was directly correlated with carrying capacity, but physiological studies (Beauchamp *et al.*, 2007; Pörtner and Peck, 2010) and observational (Eriksen *et al.*, 2012) point towards a dome-shaped response curve to temperature. Future studies could explore an alternate parameterization of the cisco temperature dependent surplus production model wherein the carrying capacity had a dome shaped response to temperature change.

### 6.3 Chapter 3

While the analysis using surplus production models for cisco improved our understanding of the influence of temperature, there still was a gap in understanding the ecosystem effects through the lake food web, such as the impact of decline of cisco on other fish species in the lake. To explore these interactions for cisco and other important species in MLL, in Chapter 3, I built an ecosystem model. However, a model can only be a close approximation of the natural process (Haddon, 2001), but there are several benefits of engaging in this process. The first and foremost benefit of building an ecosystem model was that it quantified the important interactions in the ecosystem and built a ‘quantitative picture’ of the ecosystem. It presented the abundance, predation mortality, and fishing mortality of one species against another in the larger ecosystem context. In Ecosim, which dynamically tracks changes in biomass due to changes in mortality, the accuracy in prediction about natural process largely depends on how much the model was capable of reconstructing past patterns. Hence, this model was tuned to observed abundance time-series and catch records from the year 1985 to 2006.

Fitting the model to observed time-series data led to the following major conclusions: (1) temperature and fisheries had an impact in the decline of cisco as found in Chapter 2, (2) walleye biomass had not seen major changes over the time period, (3) yellow perch and smallmouth bass populations had increased. One can argue that the increase of smallmouth bass was the result of temperature forcing, but even after I removed the effect of temperature forcing on smallmouth bass, biomass still increased, though not to the same levels. From a future management perspective, I found that there is opportunity to increase fishing (doubling fishing from current levels) on other recreational species (such as

northern pike, smallmouth bass) without having a negative influence on the walleye population. The increased level of fishing could also induce the recovery of cisco and improvement of black crappie.

Managing walleye at safe harvest levels (SHL) does not cause unsustainable reduction in the population and the biomass continued to be higher than  $B_{msy}$ . However hooking mortality on walleye juveniles (age 0, age 1, and age 2) could lead to approximately 10% decline in walleye population compared to status quo. This showed that there was opportunity to strengthen the walleye population by controlling the fisher-induced mortality on the juveniles.

A very healthy stock of yellow perch played an important role as the key forage fish species in the lake—for example it constituted a bulk of the cormorant diet, and the continued increase in yellow perch population had absorbed the pressure generated by the increase in cormorants. The model includes separate stanzas to capture the dynamics (especially cannibalism) of different life-stages of yellow perch, yet the model may not be able to address “within-cohort” differences that have emerged in experimental studies (Roswell *et al.*, 2013). In terms of future analysis, and especially because yellow perch is cannibalistic, some new approaches could be developed to capture such interactions.

For many species the model biomass predictions fitted with time-series of field data reasonably well (walleye, northern pike, cisco); however in some cases, despite various efforts, the model did not predict the historic trends (bullhead). Since in an ecosystem model every species is linked through predator prey interaction, the effects of insufficiently fitting a group can ripple into other trophic groups and affect their predictions. Due to these

reasons, it was important to explore the uncertainty in the predictions. For this reason, I performed Monte Carlo (MC) simulations for all the scenario analyses. MC analysis in Ecosim allows uncertainty on P/B, Q/B, biomass, and EE parameters in the model. However, the MC routine does not allow uncertainty on the diet matrix. When trace amounts of a prey with small biomass in the ecosystem are found in the diets of a relatively highly abundant predator (walleye, yellow perch), these interactions can have major effects on the biomass dynamics of the prey species, for example including trace amounts of burbot in walleye diet affected burbot dynamics in the model. Though the MC analysis does not allow uncertainty analysis on the diet matrix, I feel that during MC analysis, when P/B, Q/B, and biomass of prey and predator species changed in different proportions and directions, the net predation mortality could change in unpredictable manner thereby to some extent compensating the lack of MC functionality on diet matrix. On the other hand, a very thorough gut-content analysis could enhance the accuracy of input data and thereby the fitting and resulting predictions. While MC analysis allowed an exploration of parameter uncertainty in Ecosim, it did not allow an exploration of structural uncertainty. Model prediction also depends on model complexity; Pinnegar *et al.* (2005) showed a significant difference in model predictions when a complex Ecosim model was aggregated into models of various sizes (in terms of number of functional groups) after comparing the trophic links and removing the weak trophic links. Since the research in my thesis identifies the important trophic links in MLL, in future there is opportunity to build a less complex model of the same ecosystem that focusses on the important species and linkages (for example, a walleye-focused condensed model).

A valuable extension of the current modelling exercise would be a development of a spatially explicit Ecospace model since some species are predominantly found in the inshore areas. Ecospace would capture the nuances in predator-prey linkages arising from the differential overlap of predators and their prey. However, this exploration was not possible within the context of the current thesis because at present Ecospace cannot be driven by external factors like temperature.

## **6.4 Chapter 4**

Chapter 3 allowed the exploration of different fishing scenarios for Mille Lacs Lake. I felt that a comparison of the current exploitation levels against reference points would add information for management. As discussed in Chapter 4, though maximum sustainable yield (MSY) has been criticised on various counts, I used MSY and the corresponding fishing mortality ( $F_{msy}$ ) as a metric to compare the production of and fishing pressure on the fished-species in MLL. I estimated single-species MSY ( $SS_{msy}$ ) and ecosystem MSY ( $ES_{msy}$ )—under  $SS_{msy}$  no changes were allowed in the ecosystem when the species were fished while for  $ES_{msy}$ , the ecosystem was allowed to respond to changes in mortality on the target fish species. A comparison of  $SS_{msy}$  against  $ES_{msy}$  allowed the understanding of effects of ecosystem interactions on the reference points. Since the previous chapters emphasized the importance of temperature on the ecosystem dynamics, here I estimated  $SS_{msy}$  and  $ES_{msy}$  under two states: with and without considering the effect of temperature. These estimations helped understand how the fisheries potential changed following the increase in temperature. Several modelling studies have explored the influence of environmental changes on dynamics of individual species (Brunel *et al.*, 2010; Hurtado-Ferro *et al.*, 2010) but few have explored ecosystem-wide impacts (Mackinson *et al.*, 2009;

Travers-Trolet *et al.*, 2014; Wolff *et al.*, 2012). Travers-Trolet *et al.* (2014) explored how the plankton and fish populations would respond to simultaneous effects of fishing and change in upwelling conditions, and they found that the response of the forage fish groups was key to understanding the ecosystem-wide effects of the different drivers. Similarly, Wolff *et al.* (2012) found that bottom up effects of El Nino were felt primarily by plankton groups and secondary consumers and then these effects cascaded up the higher trophic levels of the ecosystem.

The temperature effects modelled in the chapter were based on average July-August temperatures observed from year 2000 to 2005. ESmsyT is probably the most valuable estimate for the management especially in years when higher than average temperatures are recorded: the fisheries pressure should be evaluated against the reference points that include temperature effects especially for species like cisco and burbot. When temperatures in a year are lower than the 2000 to 2005 average, the management could also consider the reference points without temperature effects. However, in this context, it is important to evaluate the temperature, the fishing pressure, and the abundance trends in the preceding few years. For example, it would be unrealistic to assume that one year with good temperature would be sufficient to lead to recovery of the species from negative effects of temperature in the previous years.

To some extent, the results in the thesis are in agreement with the above results— I found that yellow perch dynamics was important to the dynamics of most other fish species in the lake. Yellow perch has emerged as the single most important forage fish in the lake after the decline of cisco. The other important forage species are shiners and minnows, crayfish,

darters, and so on. All changes that led to an improvement in the biomass of the forage species benefitted its predators and, vice versa, interactions that negatively affected these forage species negatively affected the predator species. In majority of the cases, the higher ESmsy was obtained as a result of compensation from the prey species. I believe that Mille Lacs Lake ESmsy estimates were higher than SSmsy for several species because the exploitation rate on the important prey species like yellow perch, spottail shiners, minnows etc. was low. The model results indicates that in other systems, where forage species are heavily exploited, the compensation from the forage base would probably not be available to support the predatory species, but a conclusion in this regard would require more analysis. The results suggested that taking into account ecosystem considerations were important when the prey species in the ecosystem had a commercial fishery on them. The results also provided some preliminary indication that when there is fishing on prey species, the recovery of over-exploited predator groups might be difficult. Mackinson *et al.* (2009) found that expected compensation was sometimes delayed or diminished due to “tradeoffs in competition and predation interactions”. I found that when the ESmsy was lower than the SSmsy, it was mostly a result of competition for prey (as in the case of smallmouth bass) or an increase in predation (as in the case of black crappie).

Similar to the results in Chapter 2, when temperature effects were incorporated in Chapter 4 the SSmsyT estimates for cisco and burbot were much lower than SSmsy estimates. I found that the SSmsy estimates under temperature influence were similar to the values obtained from the surplus production modelling in Chapter 2. However, the ESmsy estimates were lower indicating that there were ecosystem pressures on cisco and burbot that exerted further pressure on these populations thus exacerbating the effect of temperature change. I

expected that the ESmsy of smallmouth bass would be higher than the SSmsy owing to the application of temperature to the vulnerability of prey to smallmouth bass juveniles. On the contrary, I found that smallmouth bass faced competition from yellow perch for its prey crayfish and as a result ESmsy was lower than the corresponding SSmsy. Similarly rock bass also had a lower ESmsy estimate owing to competition for its prey crayfish. This result was also unexpected considering that crayfish biomass had remained consistent through the fitting process when fluctuations in several species were observed.

## **6.5 Chapter 5**

In less than a decade after being first noticed in 2005, Zebra mussels (*Dreissena polymorpha*) became fully-established in Mille Lacs Lake, Minnesota. I used the ecosystem model built in Chapter 3 to explore the ecosystem-wide impact of this invasion in Mille Lacs Lake. Zebra mussels functional group was added in the EwE model and given a high initial biomass. Simulating invasions of alien species using the EwE framework was not straightforward and so an innovative work around was adopted to drive explosion of zebra mussels biomass (Langseth *et al.*, 2012). The biomass was held low till 2005 using an artificial fishing pressure—adequate fishing pressure was applied on it with an aim to neutralize the effect on ecosystem caused by the inclusion of zebra mussels. At the onset of 2005, the fishing pressure was released and the functional group (zebra mussels) was allowed to ‘invade’ the model ecosystem. The result also indicated that the population of zebra mussels in the lake stabilized after attaining the maximum density within a few years, a prediction that appears to agree with recent observed data. The model predictions also showed good agreement with trends in observed data for zooplankton and fish groups. Furthermore, the model predicted increase in smallmouth bass population when zebra

mussels were incorporated in the diet of the crayfish. The results from Chapter 3 and Chapter 5 indicated that conditions were becoming favorable for smallmouth bass, and this was also supported by the higher abundances of this species reflected in the assessment surveys.

Empirical models based on zebra mussels invasion history showed some similarities in impacts observed at several locations (impacts on macro-invertebrates, native mussels, and phytoplankton) (Ricciardi, 2003; Ward and Ricciardi, 2007). Zebra mussels were observed to have negative effects on native clams in Lake Erie (Haag *et al.*, 1993) and several other locations in North America (Nalepa *et al.*, 1996; Ricciardi *et al.*, 1995; Schloesser and Nalepa, 1994; Sherman *et al.*, 2013). Community analysis of mollusc abundance in Oneida Lake showed that nutrient loading and zebra mussels invasion were the main drivers of biodiversity (Karatayev *et al.*, 2014). The present study on Mille Lacs Lake ecosystem also predicted decline in native bivalves mainly through the effects of competition for food.

Alarmingly, the long term simulation end results indicated system-wide collapse of major predators including walleye due to the effect of bottom-up control as zebra mussels efficiently filter out the phytoplankton from the system. The observed data for zooplankton show that though all zooplankton groups showed a decline after zebra mussels invasion, all groups were not affected to the same extent. It is possible that the model overestimated the predictions of system-wide collapses because phytoplankton and zooplankton in the model were large aggregate groups that did not allow the model to capture the differential impacts of zebra mussels over different plankton groups. Using a bioenergetics model simulated for individual zebra mussels, Schneider (1992) found that zebra mussels growth rate varies as

per environmental temperature and availability of phytoplankton. Filtration rate of zebra mussels can be as high as  $132\text{m}^3\text{m}^{-2}\text{day}^{-1}$  (MacIsaac *et al.*, 1992) leading to overgrazing of phytoplankton (Barbiero *et al.*, 2006; Howell *et al.*, 1996). Further, zebra mussels are selective in phytoplankton consumption leading to an increased proportion of larger and colonial forms of alga in Lake Erken in Sweden (Naddafi *et al.*, 2007). In Lake Ontario transfer of energy to the benthic food chain was understood to be responsible for ‘disproportionate declines’ in zooplankton compared to the total decline in productivity following zebra mussels invasion (Stewart *et al.*, 2010). These changes lead to an overall decrease in food availability for zooplankton. Predatory effects of zebra mussels also extend to veligers and other microzooplankton (MacIsaac *et al.*, 1995).

Ecological network analysis (ENA) of the Lake Erie and Lake Ontario (Bay of Quinte) fish and invertebrate community before and after zebra mussels invasion showed that zebra mussels diverted energy from the pelagic to the benthic food chain (Miehls *et al.*, 2009a, 2009b) through detrital and microbial pathways. The ENA predicted that the altered energy pathways in general had negative effects on pelagic fish species like walleye, yellow perch, and shiners and positive effects on benthic fish such as bullhead and catfish in Oneida Lake (Miehls *et al.*, 2009a). In addition to strengthening of the detrital and microbial pathways, an evaluation of photosynthetic rate data showed that the increase in clarity was found to improve benthic primary production in Oneida Lake (Cecala *et al.*, 2008).

The model capability to predict the response of the Mille Lacs Lake to zebra mussels invasion in the long term would largely depend on the dynamics of plankton groups, the response of juveniles of higher trophic fish species like walleye to the changing dynamics

of plankton groups, and the response of yellow perch population. The limitations of the model are further complicated by the invasion of spiny water fleas in Mille Lacs Lake because this species is also capable of changing the zooplankton community structure (Yan *et al.*, 2001) thereby affecting the food availability for the juvenile fish communities. Spiny water fleas were first sighted in the Great Lakes in 1980s (Lake Huron in 1984; Lake Ontario and Lake Erie in 1985; Lake Michigan in 1986) (USGS, 2015). The most probable source of invasion of this species (native to Northern Europe and Asia) was through ballast water from ships. Though not as widespread as the zebra mussels, spiny water fleas are now found in several lakes in the Great Lakes and adjoining regions. In Mille Lacs Lake, the spiny water fleas were first recorded in 2009, and the abundance fluctuates seasonally with lower densities in summer zooplankton tows (2 individuals per tow) compared to fall zooplankton tows (10 individuals per tow) (MNDNR, 2013).

Spiny water fleas feed directly on small cladocerans (*Diaphanosoma* spp., *Bosmina* spp., *Chydorus* spp., *Daphnia retrocurva*) and are considered one of the important causes of decline in small cladocerans in Mille Lacs Lake (Hirsch and Staples, 2014; MNDNR, 2013). By causing decline of small cladocerans, the spiny water fleas compete with cyclopoid copepods and juvenile fish (Evans, 1988; Strecker *et al.*, 2006). In Harp Lake, Canada, following spiny water fleas invasion cladocerans declined and therefore the zooplankton community structure changed (Yan *et al.*, 2001). Zebra mussels consumption of phytoplankton also negatively affects the zooplankton population as observed in several Great Lakes therefore making it difficult to separate the effects of the two invasive species in Mille Lacs Lake (Hirsch and Staples, 2014).

On the other hand, spiny water fleas are protected from predation by very young fish by its sword like tail (LeDuc, 2012). Recent sampling data from Mille Lacs Lake shows that age 1+ cisco and age 1+ yellow perch ingest spiny water fleas (MNDNR, 2013), but it was not clear if these fish are able to successfully digest their spiny prey. Study of stomach contents of adult walleye and yellow perch in the Lake Michigan showed that these species consume spiny water fleas, but some reports suggested that young yellow perch “cough up” the spiny water fleas (Berg, 1992). In experimental settings, pumpkinseed sunfish (*Lepomis gibbosus*) was found to be able to successfully remove the spine and ingest the body of the spiny water fleas (LeDuc, 2012). Cisco stomachs from Rainy Lake in Minnesota contained large proportion of spiny water fleas, and the spines were “tangled into large masses” in cisco stomachs (LeDuc, 2012). Thus, understanding the impacts of spiny water fleas are complicated because of the interactions through competition with juvenile fish and some reports of predation by adults. Since the spiny water fleas were first recorded in 2009 and the main focus of chapter 5 was to understand the influence of zebra mussels, spiny water fleas were not incorporated in the model. However, a deeper understanding of the impact of invasive species would require inclusion of spiny water fleas in the model to improve understanding of the plankton and fish juvenile dynamics as a result of zebra mussels filtration of phytoplankton and spiny water fleas predation on zooplankton.

It is probably also necessary to consider the effects of potential invasion by round goby in Mille Lacs Lake ecosystem. Round gobies (*Neogobius melanostomus*) are predators of zebra mussels in their native range (Naddafi and Rudstam, 2014). Round gobies were first detected in St. Clair River (Jude *et al.*, 1992) in 1990 and then spread into Lake St. Clair, Lake Erie, and Lake Michigan in subsequent years. By 1998 the goby made their presence

in all the Great Lakes (USGS, 2015): Considering the rapid rate of spread of round goby, and the fact that it has been spotted in Duluth/Superior Harbour, it can't be ruled out that the species could potentially enter into Mille Lacs Lake. However, considering the extensive sampling program and high angler use of Mille Lacs Lake, it is highly unlikely that its presence would go unnoticed for long (Don Pereira, MNDNR, pers. comm.). Round gobies are the native predators of zebra mussels and even in the North American systems, their diets can be composed of up to 80% Dreissenids (Zebra and Quagga mussels) (Johnson *et al.*, 2005). In a study based in Bay of Quinite ecosystem, using a bioenergetics model, Taraborelli *et al.* (2010) estimated the Q/B of round gobies in the upper and lower bay (~11-16 tonnes per year); they established that round gobies had become an important component Bay of Quinite ecosystem. The gobies contributed to the diets of fish species such as walleye (Jude *et al.*, 1992), smallmouth bass, northern pike, burbot, yellow perch and largemouth bass (Taraborelli *et al.*, 2010). Since round gobies are bottom dwelling fish and shares habitat with other smaller benthic fish such as sculpins (*Cottus* spp.), darters (*Etheostoma* spp), and logperch (*Perchina caprodes*), they can directly predate on juveniles of those species (Jude *et al.*, 1992). Round gobies along with the mussels are also found to modify the structure of benthic invertebrate communities (Kuhns and Berg, 1999). In Lake Erie, it has been reported that round gobies heavily consume smallmouth bass eggs (nests) and therefore affect smallmouth bass recruitment (Steinhart *et al.*, 2004). It is possible that if introduced into Mille Lacs Lake, round gobies could have negative effects on the smallmouth bass population in Mille Lacs Lake. However, in Lake Ontario following the invasion and establishment of round gobies, a shift in cormorant diets was observed from predominantly yellow perch, alewives, and sticklebacks (~60% combined) to invasive

round gobies (~80%) taking predation effects away from yellow perch and smallmouth bass (Johnson *et al.*, 2010). In Lake Huron and Lake Michigan, burbot diets were observed to shift from native species to round gobies (~ 50%) but the burbot predominantly consuming the gobies also showed lower growth rates compared to those that depended predominantly on native species (Hensler *et al.*, 2008). Therefore, potential spread of round gobies to Mille Lacs Lake can have mixed impacts on the lake food web.

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# Appendices

## Appendix A: Additional details of model and data used in Chapter 2

### A.1: Specification of prior $r$ <sup>5</sup>

The demographic method (McAllister *et al.*, 2001; Stanley *et al.*, 2009) numerically solves the Euler-Lotka equation to estimate  $r$  using inputs of natural mortality, stock-recruitment steepness, and growth parameters. Equation A 1 is a modification from the original Euler-Lotka equation where the integration is performed from age-0; when there is no reproduction in the age-0 class of individuals, the integration starting either at age-0 or at age-1 is equivalent (Stanley *et al.*, 2009). The initial guess for  $r$  in the calculation was 0.4 based on a surplus production model for cisco in Lake Superior.(Jensen, 1984).

$$\sum_{t=1}^T l_t m_t e^{-tr} = 1$$

Equation A 1

where,  $t$  denotes age,  $T$  is the maximum age of the species,  $l_t$  denotes survivorship at age, and  $m_t$  is the number of age-1 recruits expected to be produced by females of age  $t$ . For further details on equations for calculation of  $l_t$  and  $m_t$ , please see Stanley *et al.* (2009).

Monte Carlo sampling of 10,000 combinations from distributions of natural mortality and stock-recruitment steepness was done to obtain a distribution around the

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<sup>5</sup> This material in the appendix has been published as an online appendix with the manuscript paper based on Chapter 2 of this thesis.

estimate of the prior for  $r$ . The distribution of  $M$  was uniform with a lower bound of 0.30 and an upper bound of 0.65 based on mortality profiles and resulting  $M$  estimates of Cisco year-classes from 1998 to 2004 in the Mille Lacs Lake (Tom Jones, MNDNR, personal communication).

Steepness information was not available for the Mille Lacs Lake Cisco population—the steepness (normal distribution mean 0.53 and standard deviation 0.06) used was based on estimates of steepness for salmonid species from Myers *et al.* (1999) meta-analysis of stock recruitment relationships. The starting values of  $r$  were also varied during the estimation. The density of the estimated prior closely resembled a normal probability density function so a normal distribution with mean (0.40) and standard deviation (0.09) was used to describe the prior in fitting the surplus production model.

### A.2: Parameter correlation plots for models used in Chapter 2

Supplementary figures: Parameter correlation plots for models 1, 2 and 3:

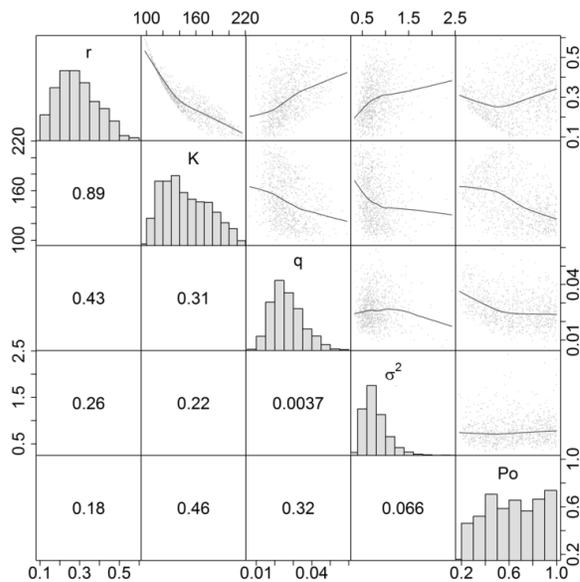


Figure A 1. Parameter correlation plots for model 1 in Chapter 2.

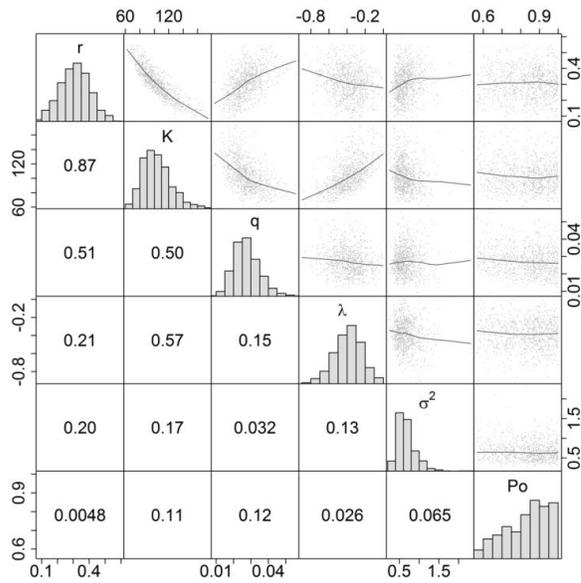


Figure A 2. Parameter correlation plots for model 2 in Chapter 2.

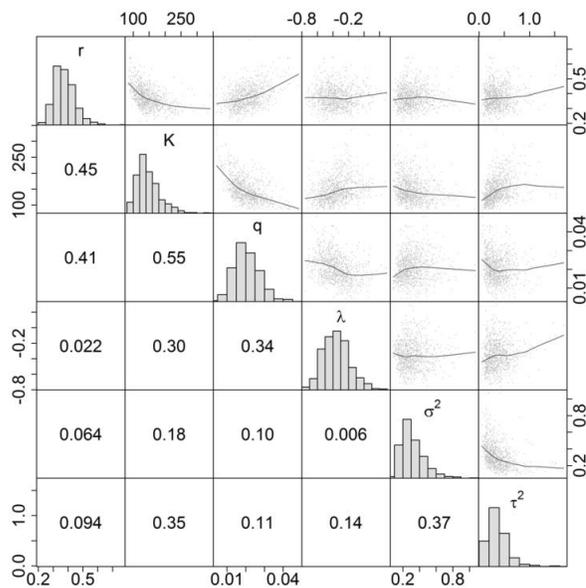


Figure A 3. Parameter correlation plots for model 3 in Chapter 2.

### A.3: Additional data and models

#### Temperature data

Table A 1. Temperature data and corresponding anomaly estimates.

Column 2 shows the maximum air temperatures attained at Garrison, Minnesota, in the July-August months every year. Column 3 shows the anomaly calculated based on the temperature in Column 2. This is the anomaly data used in the main text. Garrison air temperature data were also used to calculate accumulated degree-days (ADD; column 4). The ADD data was used in additional models presented later in the Appendix

A

Year	July-Aug maximum temperature	Anomaly based on maximum temperatures	Accumulated degree-days	Anomaly based on ADD
1985	88	-0.75	439.55	-0.81
1986	90	-0.24	449.05	-0.51
1987	94	0.77	492.65	0.89
1988	99	2.03	529.25	2.06
1989	94	0.77	507.80	1.37
1990	96	1.27	459.55	-0.17
1991	91	0.01	453.05	-0.38
1992	91	0.01	437.30	-0.88
1993	86	-1.25	431.05	-1.08
1994	86	-1.25	441.55	-0.75
1995	88	-0.75	442.30	-0.72
1996	87	-1.00	427.90	-1.18
1997	84	-1.76	434.05	-0.99
1998	89	-0.49	439.05	-0.83
1999	92	0.26	477.05	0.39
2000	86	-1.25	435.80	-0.93
2001	94	0.77	518.55	1.71
2002	91	0.01	456.80	-0.26
2003	89	-0.49	467.55	0.08
2004	91	0.01	442.30	-0.72
2005	91	0.01	487.55	0.72
2006	99	2.03	517.05	1.67
2007	93	0.52	495.05	0.96

## Correlation of air temperature and water temperature data

Water temperature data from Mille Lacs Lake were not available for the 23 year time period for which CPUE information was available. For the few years where I had water temperature data, I checked if the monthly average Garrison air temperature data was correlated with the monthly average water temperature data from Mille Lacs Lake. I found that the two temperature series were in close agreement except the winter months with ice cover on the lake. In the analysis, I used temperatures only from July and August where the temperatures were in agreement. Additionally, I used the air temperature series to calculate the anomaly, thus taking into account only the trend and not the absolute temperature records.

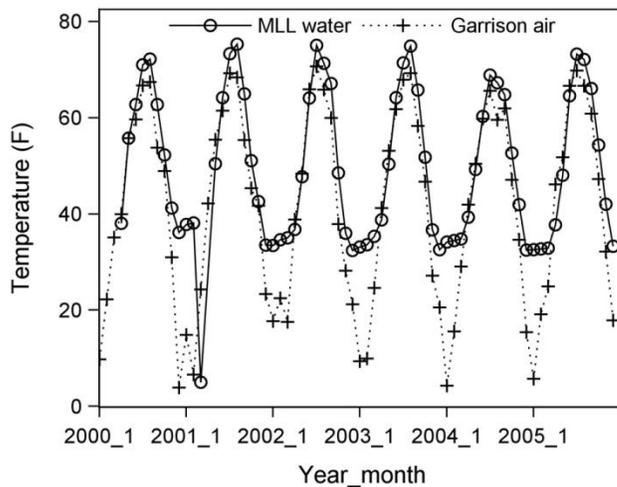


Figure A 4. Time-series of Garrison air temperature and MLL water temperature from 2000 to 2005. The number following the year in the horizontal axis denotes the month.

## CPUE data

Table A 2. CPUE data from Mille Lacs Lake with CV (for years when available)

Year	Mean weight (lb/net)	CV
1985	5.20	
1986	7.10	
1987	8.20	
1988	5.00	
1989	8.60	
1990	4.30	
1991	2.10	
1992	2.50	
1993	4.71	
1994	5.70	
1995	2.37	
1996	6.98	
1997	2.55	
1998	2.20	
1999	2.00	2.21
2000	2.30	1.86
2001	0.84	2.32
2002	0.40	2.47
2003	1.23	1.08
2004	0.93	1.38
2005	3.21	1.75
2006	0.09	2.39

## Additional models

Seven other models, listed as follows, were explored in addition to the three models presented in the Chapter 2.

1. Degree days Model 2
2. Degree days Model 3

3. Process error only Model 1
4. Process error only Model 2
5. Fox Surplus production Model 1
6. Fox Surplus production Model 2
7. Fox Surplus production Model 3

Table A 3. Model performance compared based on AIC statistic.

Models	Objective function (negative log-likelihood)	Log-likelihood	Number of parameters	AIC score	$\Delta$ AIC
Model 1	30.55	-30.55	5	71	4
Model 2	<b>27.54</b>	-27.54	6	67	0
Model 3	35.60	-35.60	29	129	62
Degree days Model 2	28.83	-28.83	6	70	3
Degree days Model 3	37.20	-37.20	29	132	65
Process error only Model 1	32.76	-32.76	5	76	8
Process error only Model 2	29.92	-29.92	6	72	5
Fox Surplus production Model 1	35.69	-35.69	5	81	14
Fox Surplus production Model 2	32.39	-32.39	6	77	10
Fox Surplus production Model 3	36.14	-36.14	29	130	63

The performance of models including degree days was very similar to the models presented in the manuscript. The values of the AIC statistic were slightly higher than the models based on maximum temperature anomaly. The estimate of  $\lambda$  parameter less certain with the models based on degree days. The objective functions for the process error models indicate that the model performance approaches the other models, but the standard deviations on the parameter estimates for  $K$  were very high ranging into a few thousand tonnes. The modified Fox versions of the surplus production models did not perform as

well as the Schaefer surplus production models. However, the parameter estimates were very similar.

### Model parameter densities

In the figure below for parameter densities, densities in dotted lines represent Process error only Model 1 and Fox Surplus production Model 1; densities in dashed lines represent Degree days Model 2, Process error only Model 2, and Fox Surplus production Model 2; and densities in solid lines represent Degree days Model 3 and Fox Surplus production Model 3.

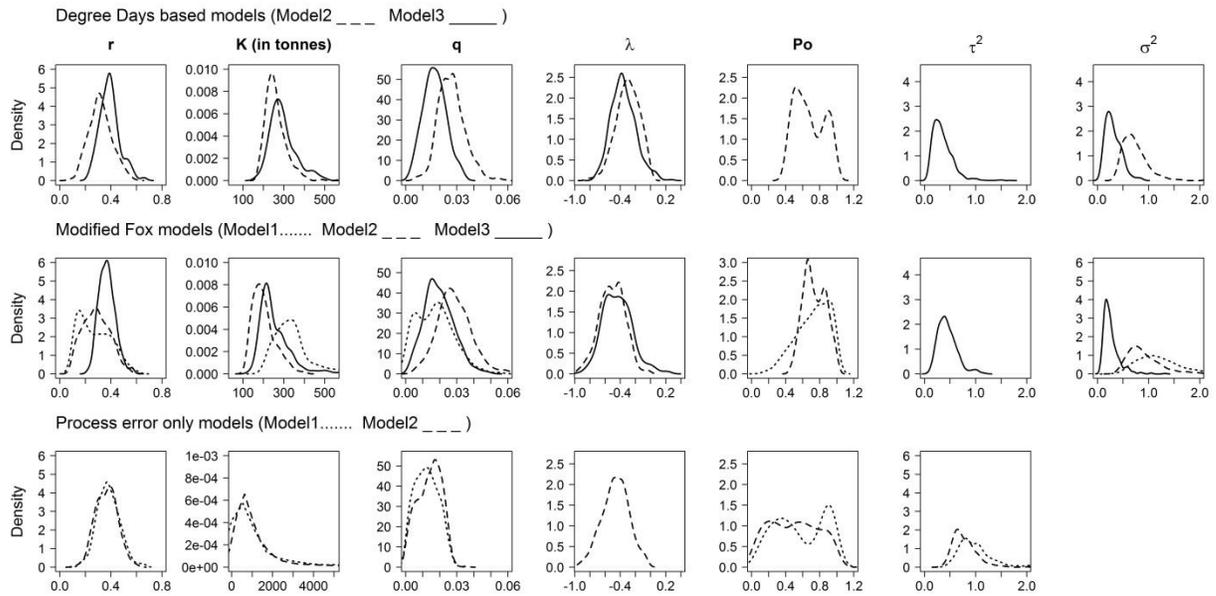


Figure A 5. Parameter density plots for additional models described in Appendix A

## Model details

### Degree Days based models

Additional models, degree-days model 2 and degree-days model3, simply replaced the temperature anomaly data in Model 2 and Model 3 with the temperature anomaly calculated based on ADD.

### Process error only models

I do not think it is appropriate to apply a process error only version of any fisheries model as it is never possible to obtain perfect data for abundances. However, for exploratory purposes only, we developed an alternate versions of model 1 and model 2 process error only. The model formulations are based on Hilborn and Mangel (1997). Here I assumed that the CPUE observations were perfect representations of the population biomass and all the error observed was a result of model process error. The details are as follows:

Process error only Model 1 (Equation A 2):

$$B_{t+1} = \frac{1}{q} CPUE_t + r \frac{1}{q} CPUE_t \left( 1 - \frac{1}{Kq} CPUE_t \right) - C_t$$

*Equation A 2*

Process error only Model 2, the above equation was modified to include the lambda ( $\lambda$ ) parameter (Equation A 3):

$$B_{t+1} = \frac{1}{q} CPUE_t + r \frac{1}{q} CPUE_t \left( 1 - \frac{1}{K \exp(-\lambda * Ta_t) q} CPUE_t \right) - C_t$$

*Equation A 3*

### **Fox version of the surplus production model**

The Schaefer Surplus production is represented as (Equation A 4):

$$SP = rB_t \left( 1 - \frac{B_t}{K} \right)$$

*Equation A 4*

The Fox Surplus production model is represented as (Equation A 5):

$$SP = \ln(K)rB_t \left[ 1 - \frac{\ln(B_t)}{\ln(K)} \right]$$

*Equation A 5*

The Pella and Tomlinson Surplus production model is represented as (Equation A 6):

$$SP = \frac{r}{p} B_t \left[ 1 - \left( \frac{B_t}{K} \right)^p \right]$$

*Equation A 6*

Haddon (2001) suggests if the  $p$  term in the Equation A 6 is close to zero, then the parameters from the Fox model (Equation A 5) and the Pella-Tomlinson model (Equation A 6) are directly comparable. I used Equation A 6 with  $p$  fixed at 0.01 for modelling the Fox surplus production equation.

## Appendix B: Surplus production model for some species

The details about the methodology I used for fitting the data to surplus production model (SPM) can be found in Chapter 2 (about cisco). Here I mainly presented the results of the fitting for some more species other than cisco with a recap of the methodology.

### *B.1: Recap of methodology*

Using the AD Model Builder (ADMB Project, 2009) software, I fit the Schaefer SPM with the time-series data of catch and abundance (CPUE) of many species using Equation B 1 and Equation B 2 (Hilborn and Mangel, 1997):

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K}\right) - C_t$$

*Equation B 1*

$$CPUE = qB_t$$

*Equation B 2*

where  $K$  is the carrying capacity of the population,  $r$  is the intrinsic rate of population increase,  $B_t$  describes the biomass at any point in time  $t$ ,  $C_t$  is the catch at time  $t$ , and  $q$  is the catchability of the sampling gear.

In the case of Burbot the carrying capacity in Equation B 1 was modelled as a function of temperature as  $Kt$  (Equation B 3) since the survival of burbot, similar to cisco (Chapter 2), is also sensitive to the rise in lake water temperature.

$$K_t = K * \exp(\lambda * Ta_t)$$

*Equation B 3*

where,  $Ta_t$  denotes the temperature anomaly in year  $t$  and  $\lambda$  is the additional parameter to be estimated in this formulation of the model. The parameter  $\lambda$  is the correlation coefficient between carrying capacity and temperature anomaly.

The fitting criterion was to minimize the negative log-likelihood (NLL) function using Equation B 4:

$$NLL = \frac{1}{2} \log(2\pi) + n \log(\sigma) + \sum_{t=1}^n \frac{\epsilon_t^2}{2\sigma^2}$$

*Equation B 4*

where  $\epsilon_t$  is the difference between ‘observed CPUE’ and ‘predicated CPUE’ which assumed to be normally distributed with mean ( $\mu$ ) = 0 and standard deviation ( $\sigma$ ) i.e.  $\epsilon \sim N(0, \sigma)$ .

Reference point such as MSY is estimated as:

$$MSY = r * k/4$$

*Equation B 5*

and for burbot,

$$MSY_t = \frac{r * K * \exp(\lambda * T a_t)}{4}$$

*Equation B 6*

## *B.2: Data used in the model*

### **B.2.1: Gill net CPUE**

In Mille Lacs Lake inshore sampling using gill nets is done usually in the last week of September every year. Standard experimental gill nets have 5 panels of following mesh sizes: 0.75 in, 1.0 in, 1.25 in, 1.5 in, and 2.0 in. The gill nets are set overnight at 32 inshore locations, and the length and weight of all the fish sampled are recorded (Jones, 2006).

Time-series of CPUE from 32-gill nets sampling is available from 1985 to 2006 for many species. The same types of nets are set at the same location and time every year (overnight in fall sampling season), so I assume that capture probabilities are relatively consistent across years and are not a cause of concern in using CPUE as an index of biomass.

Since these are sampling gill nets, there are no concerns of improved knowledge of fishers leading to alteration in CPUE trends. The CPUE data used in the model fitting is an average of gill net CPUE estimates from 32 broadly spread inshore locations in the lake; therefore, the issue of aggregation or range contraction leading to hyperstability of CPUE values is not of much concern. If there are changes in fish distribution triggered by schooling behaviour of fish or by other reasons, then it will be reflected in the average CPUE (because some stations where greater than usual abundance is noticed will be counter-

balanced by other stations where the abundance is lower). Considering the aforesaid reasons, it is expected, for the purposes of the surplus production model, the CPUE trends reflect a proportional change in biomass of the species in the lake.

### **B.2.2: Fisheries catch**

The catch time-series for harvest from the Mille Lacs lake ecosystem were provided by MNDNR for 15 species spanning a time period of 1985 to 2007, and surplus production models were built for 5 species. Surplus production models were not built for the rest of the species mainly because of scanty CPUE data (except walleye for which I borrowed biomass estimates from the report of Drake (2007) and muskellunge which is a species with ongoing stocking input into the population).

State licensed anglers and tribal netters, spearers, and anglers are the two fisher groups who engage in fisheries on the Mille Lacs Lake. The graph of catch time-series data for the year 1985 to 2007 is given in Figure 1.3. Prior to 1998 (1997 for walleye only), tribal contribution to the total catches was negligible—state anglers were the main resource users. The estimates of hooking mortality were available for walleye; for the other species, an additional 5% (10% in case of muskellunge) of total fish released by anglers was added to the total catches as a hooking mortality.

### *B.3: Results and Discussion*

The results of the fitting exercise, estimated biomass trends and sensitivity analysis of MSY are shown in the figures in their respective sections, and the results are explained by species. A sensitivity analysis was conducted for the parameter estimates and MSY using

the MCMC routine in ADMB. Sensitivity analyses search for parameter values within the parameter bounds specified in the model and give an idea of parameter uncertainty. The MCMC resampling was conducted 10,000 times and the results were used to plot the density of MSY.

### **B.3.1: Burbot**

The estimated biomass trend for burbot shows a decline from  $\approx 365$  tonnes to 8 tonnes in the time period from 1985 to 2007 (Figure B 1d). The intrinsic rate of growth  $r$  is estimated to be 0.1 which seems reasonable considering that burbot is a relatively slow growing long lived species. In Mille Lacs Lake, burbot lives at the higher end of its temperature tolerance and has relatively shorter life span. In recent years Mille Lacs Lake has experienced an increase in temperature. Research shows that the most optimum temperatures for survival of burbot are in the range from 15.6 to 18.2° C (Scott and Crossman, 1973). Burbot are reported to show first response to temperature stress at temperatures 23.7° C, and temperatures above 27.5 ° C are found to be critical (Hofmann and Fischer, 2002). It is not only the temperature level but also the duration of warm temperatures that is understood to cause stress for burbot (Keith Reeves, MNDNR, pers. comm.). Consequently, Accumulated Degree Days (ADD) was incorporated into the surplus production model. Degree Days were calculated for the temperatures in July-August above the critical temperature value using Equation B 7.

$$\text{Degree Day (DD)} = \frac{T_{max} + T_{min}}{2} - T_{base}$$

*Equation B 7*

where  $T_{max}$  is the maximum temperature in the day,  $T_{min}$  is the minimum temperature in the day and  $T_{base}$  is the critical temperature for burbot.

Any temperature below  $T_{base}$  was set to  $T_{base}$  in the calculation. For each year in the time-series, the degree days were accumulated (ADD) for the period from July to August. To explore if the decline in burbot was due to an increase in temperature, the ADD were converted to an anomaly and used as temperature anomaly ( $T_{at}$ ) in the surplus production model Equation B 3

The fitted versus observed CPUE are shown in Figure B 1a. The parameter  $\lambda$  which denotes the correlation coefficient between surplus production and temperature was estimated to be -0.50 indicating that temperature explained 50% of the variation. Figure B 1b shows the ADD temperature anomaly and Figure B 1c shows how carrying capacity follows the change in temperature. There were two periods of high temperature that caused a decline in burbot carrying capacity, one in the period 1985 to 1988 and the other in the period from 1996 to 2006. Burbot biomass (Figure B 1d) also shows decline in 1985 to 1988, then an improvement in lower temperature years from 1989 to 1994, and a decline afterward. Further increases in duration of high temperatures would affect burbot negatively.

Catch also contributed to the decline in burbot in the lake; till 1999 the catch was higher than the estimated MSY (Figure B 2). Estimated MSY ranged widely from  $\approx 13$  tonnes to  $\approx 3$  tonnes between lower and higher temperature years respectively. The lowest catch was recorded in 2003 (0.79 tonnes) but the catch increased again to 4.71 tonnes in next 3 years. In recent years burbot catch was considered incidental to walleye catch (MNDNR, pers. comm.); burbot catch was higher than 10% of walleye catch in several years prior to 1999,

and in recent years it declined to about 1% of walleye catch. However, even these low catch levels approach the MSY in high temperature years (Figure B 2, years 2004 to 2007) because MSY itself is low in high temperature years; improving the biomass of burbot requires strong restriction on catch especially in years with high temperature.

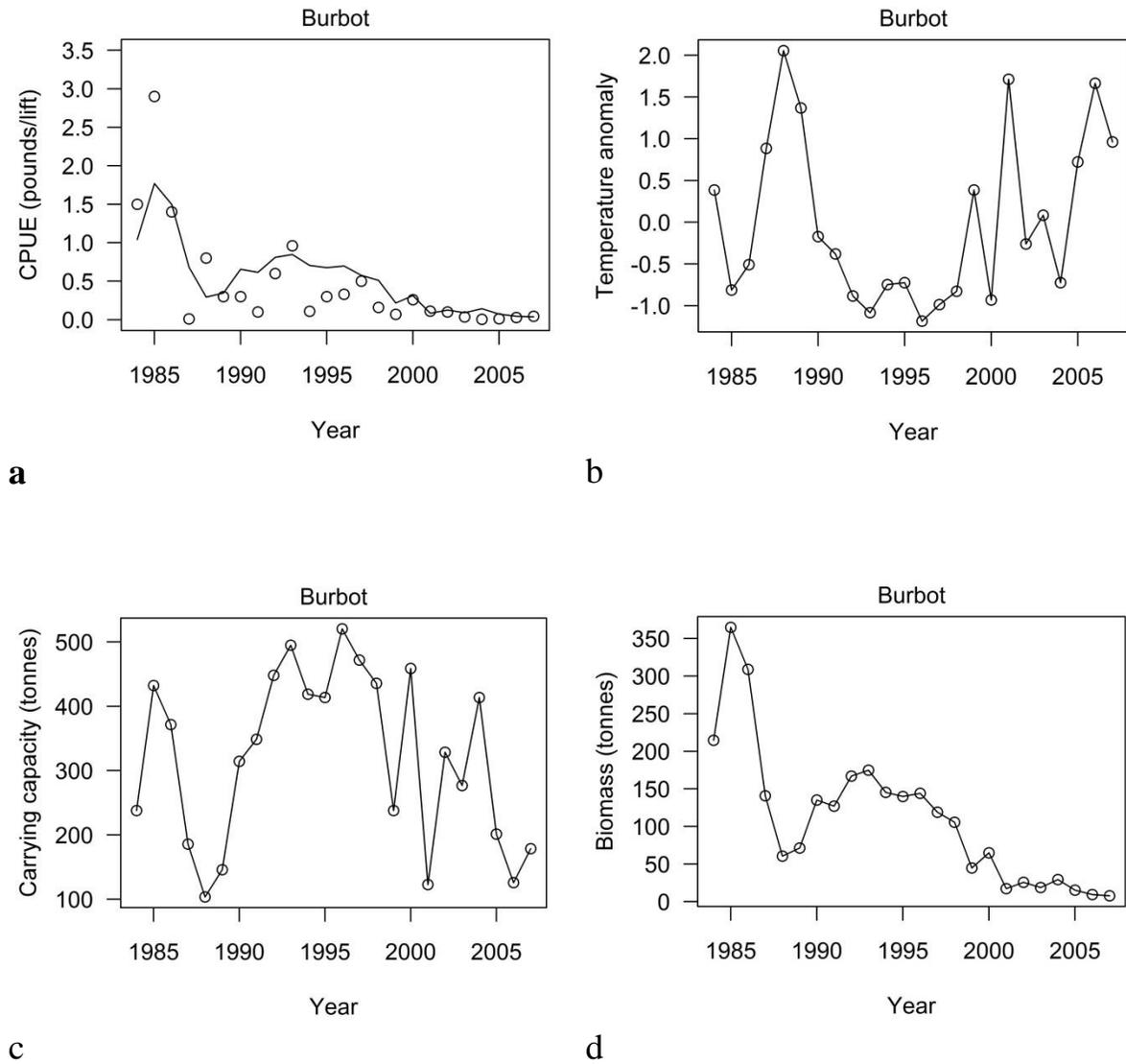


Figure B 1. Fitted CPUE, temperature anomaly, estimated carrying capacity and biomass for burbot

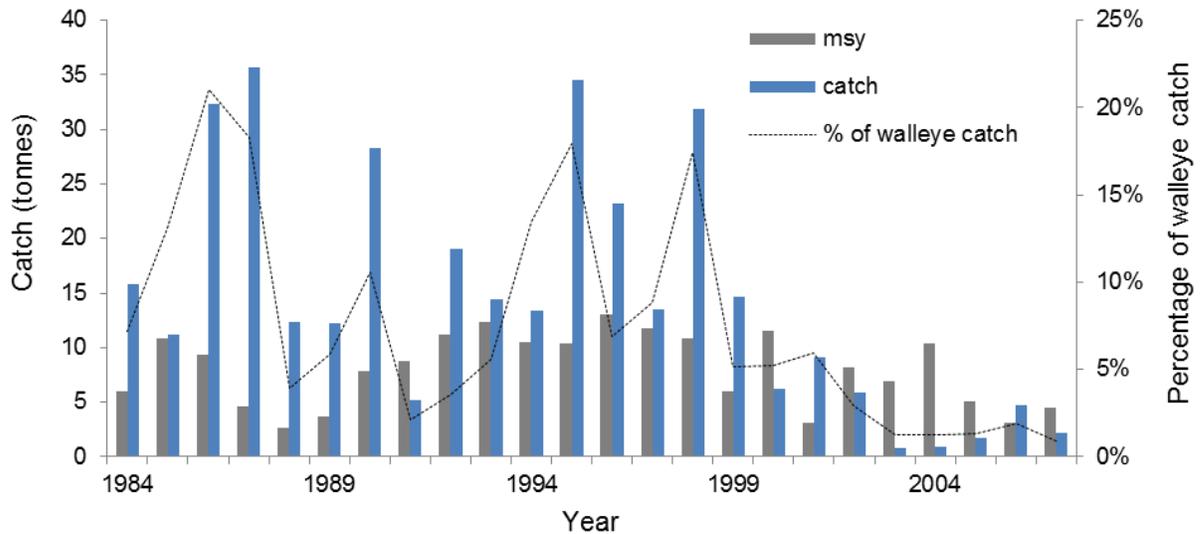


Figure B 2. Comparison of catch and estimated MSY for burbot.

### B.3.2: Yellow perch

Figure B 3a shows the plot of fitted CPUE. The model predicts that biomass of yellow perch increased from 725 tonnes to 2805 tonnes from the year 1985 to 2006 (Figure B 3b). MSY of yellow perch was estimated as 321 tonnes (Figure B 3d), and total annual harvest of this species never exceeded the MSY. The catch of yellow perch was highest ( $\approx 260$  tonnes) in the years 1985-86 and after 1987 the catch was always below 125 tonnes (Figure B 3c). The decrease in catch was followed by an increase in the biomass of perch. It seems that the average CPUE of 49 pounds per lift in 1998 is an outlier in the data (Figure B 3a) since none of the preceding or subsequent years has recorded similar high levels of CPUE. It is possible to interpret this high CPUE value to be the result of an exceptionally high recruitment event, but that is relatively unlikely because the consequences of this high recruitment are not apparent in the subsequent years. This extreme value does not affect the model prediction because predicted CPUE line does not chase that point during the fitting

process. The intrinsic rate of growth  $r$  was estimated to be 0.44. The model estimates that the current biomass (year 2006) of perch is 97% of its carrying capacity in the lake. From a management perspective, the result indicates that the biomass of perch is approaching to its carrying capacity and would not increase much higher than the current level.

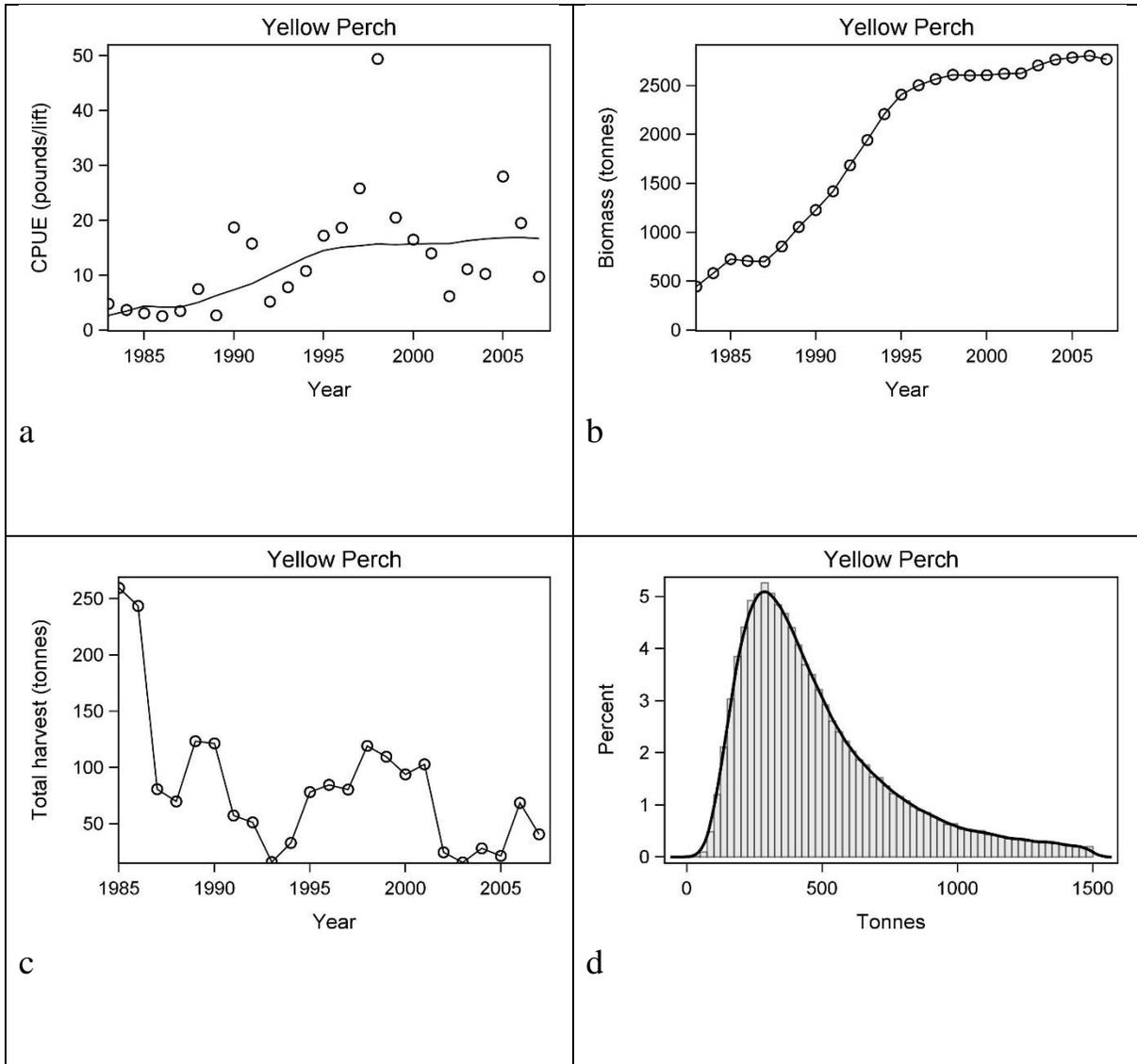


Figure B 3. Fitted CPUE, estimated biomass, catch, and MSY profile for yellow perch

### **B.3.3: Northern pike**

This was one of the better fits obtained using the surplus production model in this report. A distinct feature of the observed CPUE series for northern pike was the presence of a descending limb and an ascending limb (Figure B 4a). Catch of northern pike increased from 12 tonnes to 26 tonnes during 1980s (Figure B 4c); the same time period showed a decrease in the CPUE (a descending limb). The catch decreased drastically in early 1990s from around 26 tonnes in 1990 to around 6 tonnes in 1993, and this period showed a reversal of the CPUE trend. Catch peaked again in 1996 at around 16 tonnes and since then declined to around 9 tonnes in 2007. The model estimated the MSY around 14 tonnes (Figure B 4d). The estimated biomass time-series shows this species maintains an almost steady biomass trend (Figure B 4b). Estimated biomass increased from 105 tonnes to 125 tonnes during 1985 to 2006. The model estimates that at the current level of catch, the population of northern pike is at about 55% of its carrying capacity in the lake.

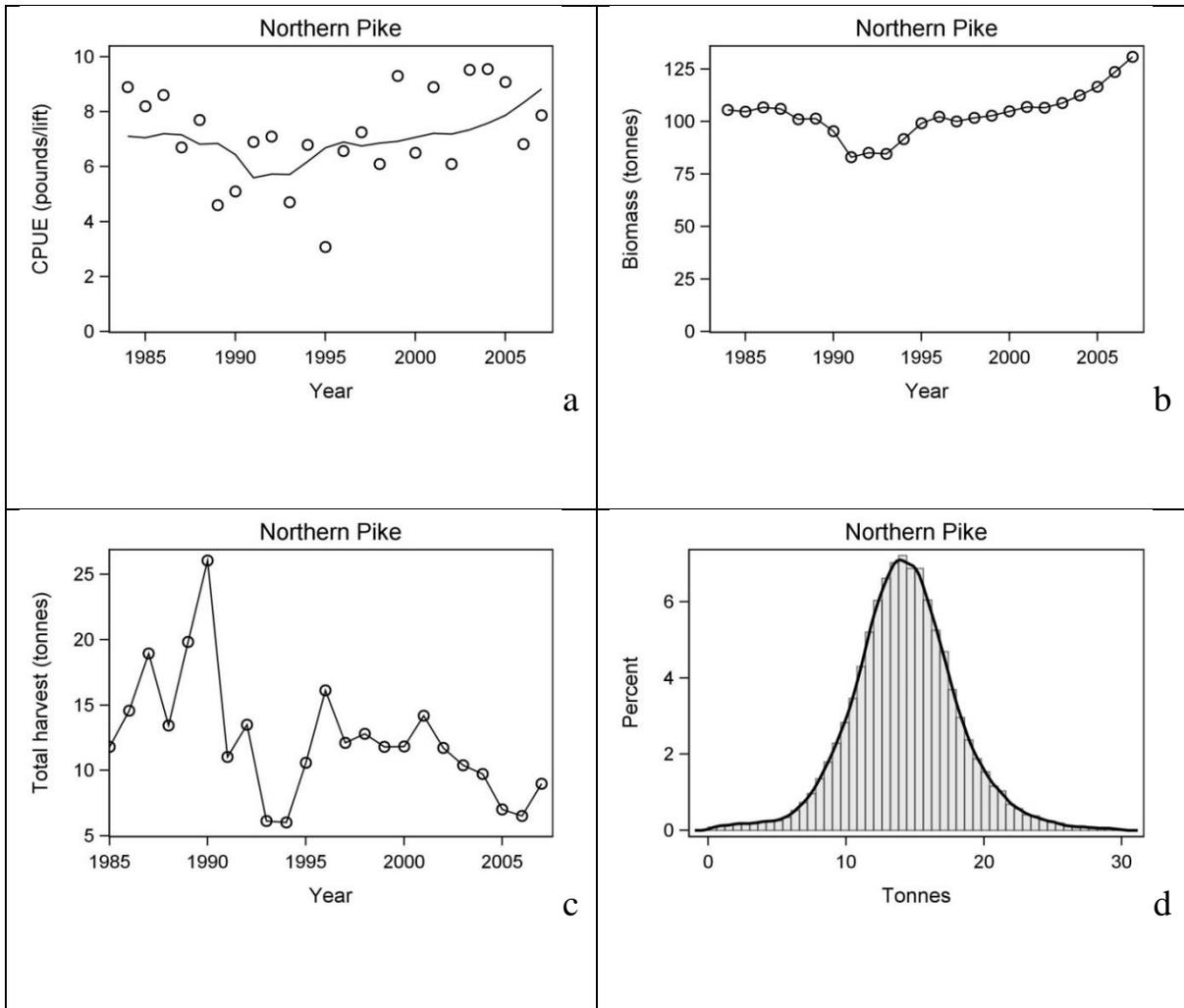


Figure B 4. Fitted CPUE, estimated biomass, catch, and MSY profile for northern pike

### B.3.4: White sucker

There was no state kill on this species; the catch was comprised only by tribal harvest.

There was no catch prior to 1998. The fitted CPUE and estimated biomass time-series is given in Figure B 5a and Figure B 5b respectively. The estimated biomass was almost around 4 tonnes from mid of 1980s to onset of catch (year 1998), then began to decline.

MSY was estimated around 0.4 tonnes (Figure B 5d). During mid of 2000s, the 2 to 3 times hike in harvest (Figure B 5c) above the MSY, caused a sharp decline in the estimated

biomass. Based on the estimated trend, it is likely that biomass will recover if the fishing pressure in subsequent years is reduced.

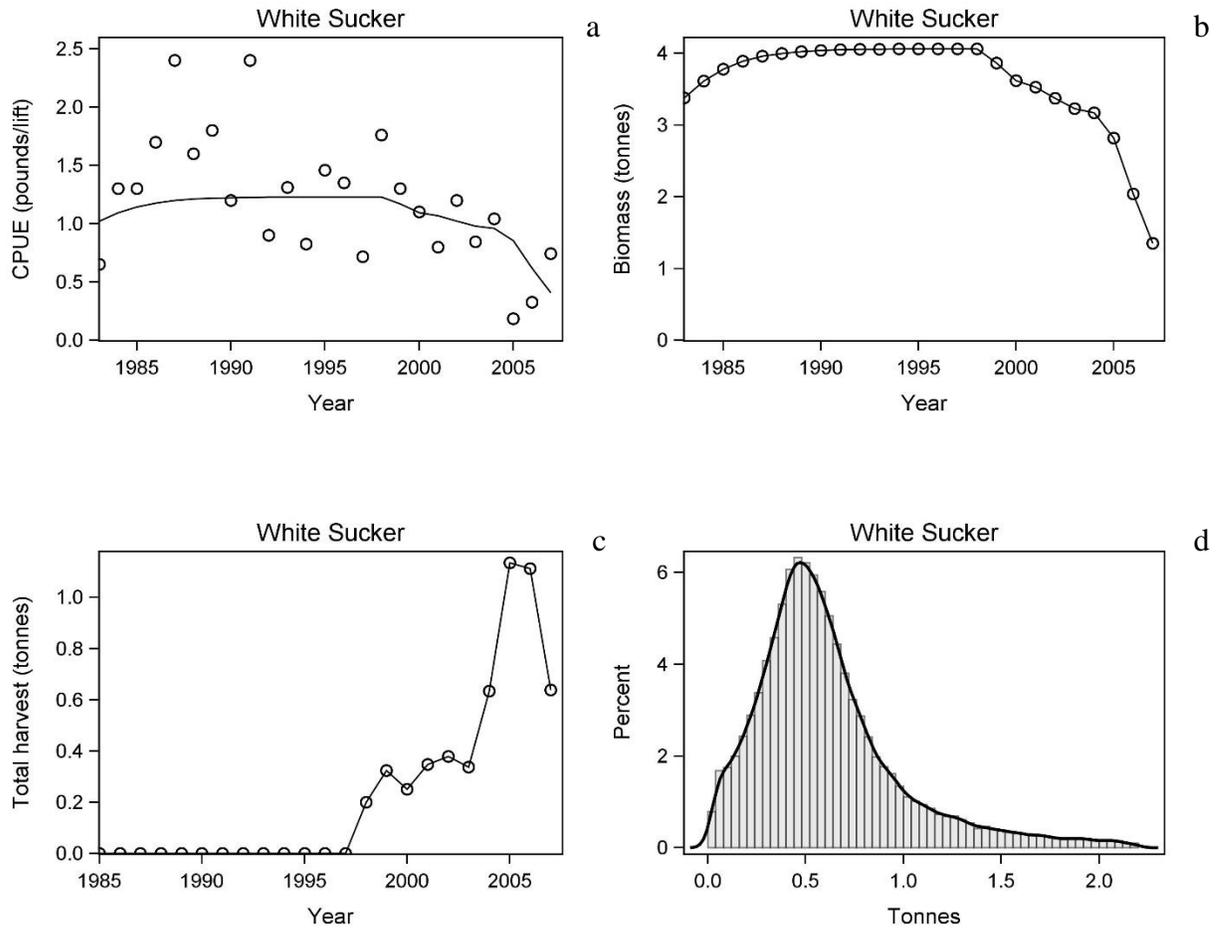


Figure B 5. Fitted CPUE, estimated biomass, catch, and MSY profile for white sucker.

#### B.4: Summary of results

Table B 1 summarises the results of the analysis using single-species surplus production models—the table lists the estimates for carrying capacity  $K$ , intrinsic rate of growth  $r$ , catchability coefficient  $q$ , variance of observation error distribution  $\sigma$ , and the correlation coefficient between surplus production and temperature anomaly  $\lambda$  for burbot. The table

also shows the estimated MSY for each species. Since the carrying capacity and MSY for burbot change with the temperature anomaly, the carrying capacity values in the first year of the simulation is shown in the table. The MSY for burbot in the last year of simulation is shown in the table. Catchability coefficient is the scaling factor between observed gill net CPUE and the carrying capacity. Thus a species with high carrying capacity relative to the CPUE could have a smaller estimate of catchability while for species with lower carrying capacity, the estimate of catchability could be higher.

The MSY estimates are single-species estimates and do not take into account the role a species plays as a predator or prey in the ecosystem. The estimates of ecosystem MSY from the Ecopath with Ecosim equilibrium analysis will therefore provide an alternate estimate of MSY under the predatory pressure experienced by a species.

*Table B 1. Summary of estimated parameters and MSY from the surplus production model*

Species	K (tonnes)	r	q	$\tau$	P <sub>0</sub>	$\lambda$	MSY (tonnes)
Burbot	238	0.10	2.2E-06	0.57	0.90	-0.50	4.47
Yellow Perch	2882	0.45	2.7E-06	0.56	0.15	-	320.71
Northern Pike	224	0.25	3.1E-05	0.12	0.47	-	13.97
White Sucker	4	0.41	1.4E-04	0.44	0.83	-	0.42

## Appendix C: Supplemental information of chapter 3, 4, and 5

### C.1: Ecopath functional groups and data sources

Table C 1. Parameterization of Mille Lacs Lake ecosystem model.

Ecopath functional groups and their parameters: values and data sources. Abbreviation: B=Biomass, P=Production, Q=Consumption, EE=Ecotrophic Efficiency, ME=Model estimates (value in bold represents the estimation by the model). Note: the diet information for some cases in the model was adjusted from their actual sources at the diet matrix workshop with Minnesota Department of Natural Resource (MNDNR) staff at Aitkin, Minnesota and during the Ecopath balancing process.

SN	Functional groups and parameters	Value	Source of data and general comments
1	Walleye ( <i>Sander vitreus</i> ) age 0		
	B	0.003	ME for stanza (Christensen and Walters, 2004)
	P/B	1.000	Adjusted during the model balancing
	Q/B	17.172	ME for stanza (Christensen and Walters, 2004)
	Major preys	5,19,28,30	Gut-content analysis and workshop with MNDNR
2	Walleye age 1		
	B	0.053	ME for stanza (Christensen and Walters, 2004)
	P/B	0.600	Adjusted during the model balancing
	Q/B	6.993	ME for stanza (Christensen and Walters,

			2004)
	Major preys	5,28,32,6,13	Gut-content analysis
3	Walleye age 2		
	B	0.149	ME for stanza (Christensen and Walters, 2004)
	P/B	0.400	Adjusted during the model balancing
	Q/B	4.337	ME for stanza (Christensen and Walters, 2004)
	Major preys	5,28,6,39,13	Gut-content analysis
4	Walleye age 3+		
	B	2.496	Drake (2007)
	P/B	0.303	Drake (2007)
	Q/B	2.284	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	5,28,6,39,14,15	Gut-content analysis
5	Yellow perch ( <i>Perca flavescens</i> ) age 0		
	B	0.952	ME for stanza (Christensen and Walters, 2004)
	P/B	5.000	Adjusted during the model balancing
	Q/B	15.047	ME for stanza (Christensen and Walters, 2004)

	Major preys	46	Gut-content analysis
6	Yellow perch age 1		
	B	0.676	ME for stanza (Christensen and Walters, 2004)
	P/B	2.100	Adjusted during the model balancing
	Q/B	6.036	ME for stanza (Christensen and Walters, 2004)
	Major preys	39,38,43,41,5,40	Based on gut-content analysis and study by Tarby (1974)
7	Yellow perch age 2+		
	B	1.350	Surplus production model (SPM) using time-series of catch and assessment gill net CPUE data of the lake (Hilborn and Mangel, 1997)
	P/B	0.783	M estimated by an empirical equation (Pauly, 1980); $F=C/B$ ; and $F+M=Z=P/B$ (Allen, 1971)
	Q/B	3.378	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	5,38,30,43	Based on gut-content analysis and study of Tarby (1974)
8	Northern pike ( <i>Esox Lucius</i> ) age 0		
	B	0.000	ME for stanza (Christensen and Walters, 2004)
	P/B	1.000	Adjusted during the model balancing

	Q/B	15.492	ME for stanza (Christensen and Walters, 2004)
	Major preys	5,46,39,30,38,13	Gut-content analysis and workshop with MNDNR
9	Northern pike age 1		
	B	0.003	ME for stanza (Christensen and Walters, 2004)
	P/B	0.400	Adjusted during the model balancing
	Q/B	6.383	ME for stanza (Christensen and Walters, 2004)
	Major preys	7,5,6,2,32,19,21,15,14	Gut-content analysis and workshop with MNDNR
10	Northern pike age 2+		
	B	0.195	SPM using time-series of catch and assessment gill net CPUE data of the lake (Hilborn and Mangel, 1997)
	P/B	0.210	M estimated by an empirical equation (Pauly, 1980); $F=C/B$ ; and $F+M=Z=P/B$ (Allen, 1971)
	Q/B	2.322	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	7,32,19,2,15,28,14,3,4,5,6	Gut-content analysis and workshop with MNDNR
11	Muskellunge ( <i>Esox masquinongy</i> ) age 0		

	B	0.000	ME for stanza (Christensen and Walters, 2004)
	P/B	0.810	Adjusted during the model balancing
	Q/B	11.732	ME for stanza (Christensen and Walters, 2004)
	Major preys	5,46,20,39,38,30,13	Adjusted based on study of Hourston (1952)
12	Muskellunge age 1+		
	B	0.001	"Muske life table" data sheet (Tom Jones, MNDNR, pers. Comm.
	P/B	0.344	Assumed equivalent to M which was estimated using Pauly's formula (Pauly, 1980)
	Q/B	2.110	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	7,20,15,17,24,14,30	Based on study of Hourston (1952)
13	Cisco ( <i>Coregonus artedi</i> ) age 0		
	B	0.038	ME for stanza (Christensen and Walters, 2004)
	P/B	2.000	Adjusted during the model balancing
	Q/B	12.001	ME for stanza (Christensen and Walters, 2004)
	Major preys	46,40	Engel (1976)
14	Cisco age 1		

	B	0.095	ME for stanza (Christensen and Walters, 2004)
	P/B	1.000	Adjusted during the model balancing
	Q/B	6.508	ME for stanza (Christensen and Walters, 2004)
	Major preys	46,40,39,41,43,44	Workshop with MNDNR
15	Cisco age 2+		
	B	0.237	Estimated from sampling data (Kumar <i>et al.</i> , 2013)
	P/B	0.650	M estimated by an empirical equation (Pauly, 1980); $F=C/B$ ; and $F+M=Z=P/B$ (Allen, 1971)
	Q/B	4.622	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	46,40,39,41,43,44	Workshop with MNDNR
16	Smallmouth bass ( <i>Micropterus dolomieu</i> ) age 0		
	B	0.000	ME for stanza (Christensen and Walters, 2004)
	P/B	1.500	Adjusted during the model balancing
	Q/B	11.869	ME for stanza (Christensen and Walters, 2004)
	Major preys	30,21,29,40,41	From Pelham <i>et al.</i> (2001)
17	Smallmouth bass age 1+		

	B	0.020	Guesstimate
	P/B	0.530	M estimated by an empirical equation (Pauly, 1980); $F=C/B$ ; and $F+M=Z=P/B$ (Allen, 1971)
	Q/B	2.765	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	38,29,41,5,6	From Frey <i>et al.</i> (2003)
18	Rock bass ( <i>Ambloplites rupestris</i> )		
	B	0.022	SPM using time-series of catch and assessment gill net CPUE data of the lake (Hilborn and Mangel, 1997)
	P/B	0.430	M estimated by an empirical equation (Pauly, 1980); $F=C/B$ ; and $F+M=Z=P/B$ (Allen, 1971)
	Q/B	2.514	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	38,39,28,30,41	Based on the work of Roth (2001)
19	Spottail Shiner ( <i>Notropis hudsonius</i> )		
	B	1.052	Mass-balance approach with $EE = 0.9$ (Christensen and Walters, 2004)
	P/B	0.940	Randall and Minns (2000)
	Q/B	22.265	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	46,40,41,48	Based on Hartman <i>et al.</i> (1992)

20	White sucker ( <i>Catostomus commersonii</i> )			
	B	0.014		SPM using time-series of catch and assessment gill net CPUE data of the lake (Hilborn and Mangel, 1997)
	P/B	0.254		M estimated by an empirical equation (Pauly, 1980); $F=C/B$ ; and $F+M=Z=P/B$ (Allen, 1971)
	Q/B	2.821		Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	41,46,49,40,42,47,39,43		Based on Becker (1983)
21	Black crappie ( <i>Pomoxis nigromaculatus</i> )			
	B	0.077		Mass-balance approach with $EE = 0.9$ (Christensen and Walters, 2004)
	P/B	0.230		Randall and Minns (2000)
	Q/B	2.346		Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	46,40,42,19,41,5,39		Adjusted based on Pearse (1918)
22	Burbot ( <i>Lota lota</i> )			
	B	0.679		SPM using time-series of catch and assessment gill net CPUE data of the lake (Hilborn and Mangel, 1997). The model also included Accumulated Degree Days (ADD) in the estimation.
	P/B	0.317		M estimated by an empirical equation (Pauly, 1980); $F=C/B$ ; and $F+M=Z=P/B$ (Allen, 1971)

	Q/B	2.317	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	5,38,6,30,28,19	From Persell and Ware (1982)
23	Trout perch ( <i>Percopsis omiscomaycus</i> )		
	B	0.019	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	0.690	Randall and Minns (2000)
	Q/B	6.275	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	46,40,39,42	Based on study of Nelson and Dick (2002)
24	Carp ( <i>Cyprinus carpio</i> )		
	B	0.047	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	0.110	Randall and Minns (2000)
	Q/B	10.703	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	41,40,39,47,42,44	Based on a couple of studies (Becker, 1983; Pearse, 1918)
25	Largemouth bass ( <i>Micropterus salmoides</i> )		
	B	0.090	Mass-balance approach with EE = 0.8 (Christensen and Walters, 2004)
	P/B	0.160	Randall and Minns (2000)

	Q/B	2.386	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	29,5,7,27,6,21,37	Excerpted from the study of Pearse (1922), Pearse (1924), and Snow (1971)
26	Bowfin ( <i>Amia calva</i> )		
	B	0.013	Mass-balance approach with EE = 0.6 (Christensen and Walters, 2004)
	P/B	0.080	Randall and Minns (2000)
	Q/B	1.971	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	29,38,5,21,32,6	From the study of Lagler and Applegate (1942)
27	Bullhead ( <i>Ameiurus nebulosus</i> )		
	B	0.103	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	0.290	Randall and Minns (2000)
	Q/B	2.244	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	42,45,40,28,41,44	Excerpt from the studies of Pearse (1924) and Kline and Wood (1996)
28	Others Shiners/minnows <sup>i</sup>		
	B	1.802	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)

	P/B	1.006	Average of 5 species of Shiners, 4 species of Dace and 3 species of Minnows taken from Randall and Minns (2000)
	Q/B	13.000	Average Q/B of mimic shiners, bluntnose minnows and pearl dace estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	40,50,41,48,46	Based on analysis of Moyle (1973)
29	Sunfish ( <i>Lepomis spp.</i> ) <sup>ii</sup>		
	B	0.702	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	0.577	Average of bluegill, pumpkinseed and green sunfish taken from the study of Randall and Minns (2000)
	Q/B	3.710	Average Q/B of bluegill, pumpkinseed, and green sunfish estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	41,44,39,42,46,40	Based on Etnier (1971) and Phillips <i>et al.</i> (1982)
30	Darters ( <i>Etheostoma spp.</i> ) <sup>iii</sup>		
	B	1.381	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	1.200	Randall and Minns (2000)
	Q/B	10.720	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	40,41,39,46	Based on Martin (1984)

31	Sculpins ( <i>Cottus spp.</i> ) <sup>iv</sup>		
	B	0.053	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	0.770	Average of mottled and slimy sculpin from Randall and Minns (2000)
	Q/B	5.910	Estimated by an empirical formula (Palomares and Pauly, 1998)
	Major preys	40,42,41,46	Based on Hershey (1985) and Hondorp <i>et al.</i> (2005)
32	Other fishes <sup>v</sup>		
	B	1.621	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	0.596	Average of P/B of seven species that comprised the group taken from Randall and Minns (2000)
	Q/B	5.311	Q/B estimated for all the seven species using (Palomares and Pauly, 1998) and the average was taken
	Major preys	46,40,39,48,41	Obtained from a number of studies (Johnson and Dropkin, 1993; Keast, 1985; Markley, 1940)
33	Otter and Mink		
	B	0.000	Guesstimate
	P/B	0.080	Guesstimate

	Q/B	41.975	Based on the data of Environment Protection Division, BC (Warrington, 1996)
	Major preys	22,20,3,7,51,29,9,10,32	Based on Knudsen and Hale (1968) and Erlinge (1969) <u>ENREF_6</u>
34	Double-crested cormorants		
	B	0.000	Assumed a negligible biomass as a placeholder
	P/B	0.100	Database (Nelson, 1979)
	Q/B	61.056	Database (Nelson, 1979)
	Major preys	7,6,17,19,14,15,22,2	Based on the study of Hobson <i>et al.</i> (1989) and Rudstam <i>et al.</i> (2004)
35	Other piscivorous birds		
	B	0.000	Based on McDowell (2007) and Patrick Schmalz, MNDNR, pers. comm.
	P/B	0.100	Assumed to be same as double-crested cormorants
	Q/B	74.000	Based on the data of Environment Protection Division, BC (Warrington, 1996)
	Major preys	22,32,19,28,51,7,3,23	Mainly based on Manuel (1931) and Kozie and Anderson (1991)
36	Turtle ( <i>Chrysemys picta</i> )		
	B	0.000	Mass-balance approach with EE = 0.8 (Christensen and Walters, 2004)

	P/B	0.100	Guesstimate
	Q/B	3.500	Guesstimate
	Major preys	41,44,48,40,39	Based on Cooley <i>et al.</i> (2003) <u>ENREF 4</u>
37	Frog		
	B	0.055	Mass-balance approach with EE = 0.8 (Christensen and Walters, 2004)
	P/B	3.139	Based on Deutschman and Peterka (1988)
	Q/B	10.463	ME by providing P/Q=0.3
	Major preys	41,51,48,47,40	Based on Linzey (1967)
38	Crayfish		
	B	1.350	Mass-balance approach with EE = 0.4 (Christensen and Walters, 2004)
	P/B	5.500	Adopted from Momot and Gowing (1975) and Momot (1984)
	Q/B	36.000	From Ecopath model (Mavuti <i>et al.</i> , 1996)
	Major preys	50	Based on Harris (1988) and Madden <i>et al.</i> (1989)
39	Hex mayflies		
	B	1.380	Based on Mille Lacs Lake survey
	P/B	6.400	Based on (Persell and Ware, 1982)
	Q/B	54.600	Adjusted based on study by Cummins and

			Klug (1979) and Ross and Wallace (1983)
	Major preys	50,49,48	Based on Koslucher and Minshall (1973)
40	Diptera		
	B	3.447	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	9.000	Based on Breys's database (Brey, 2001)
	Q/B	54.600	Assumed to be same as other insects
	Major preys	50,49,46	Based on Koslucher and Minshall (1973)
41	Other insects		
	B	3.310	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	4.225	Based on Breys's database (Brey, 2001)
	Q/B	54.600	Adjusted based on (Ross and Wallace, 1983)
	Major preys	50,49,46,48	Adjusted from several studies (Koslucher and Minshall, 1973; Mecom, 1972; Monson <i>et al.</i> , 1995)
42	Amphipoda ( <i>Gammarus spp.</i> )		
	B	0.291	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	9.000	From Persell and Ware (1982)
	Q/B	21.000	Based on Poepperl (2003)

	Major preys	50,49	Based on the study of Koslucher and Minshall (1973) and Marchant and Hynes (1981)
43	Pelecypods		
	B	0.410	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	4.000	From Persell and Ware (1982)
	Q/B	8	From Brey (2001) for bivalve of Ohio River
	Major preys	49,50,56	Adjusted from Nichols and Garling (2000)
44	Gastropods		
	B	0.513	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	4.000	From Persell and Ware (1982)
	Q/B	14.554	Based on Brey's database (Brey, 2001)
	Major preys	48,50,47	Loosely based on Madsen (1992)
45	Oligochaete ( <i>Hirudinea</i> )		
	B	0.152	Mass-balance approach with EE = 0.9 (Christensen and Walters, 2004)
	P/B	3.000	From Persell and Ware (1982)
	Q/B	40.000	Based on Poepperl (2003)
	Major preys	49,40,44,42,45	Based on Bradley and Reynolds (1987)

46	Zooplankton		
	B	7.700	Estimated from the Lake survey data
	P/B	12.000	From the range suggested by (Wetzel, 2001)
	Q/B	124.228	Based on Gulati <i>et al.</i> (1982)
	Major preys	49	Considered solely herbivorous
47	Macrophytes		
	B	0.588	Mass-balance approach with EE = 0.5 (Christensen and Walters, 2004)
	P/B	1.780	Based on Rich <i>et al.</i> (1971)
48	Periphyton		
	B	1.906	Mass-balance approach with EE = 0.5 (Christensen and Walters, 2004)
	P/B	40.000	From Angelini <i>et al.</i> (2006)
49	Phytoplankton		
	B	38.000	Approximated based on Chlorophyll a data
	P/B	113.000	Mean P/B from fresh water ecosystem (Wetzel, 2001)
50	Detritus		
	B	300.000	From Ontario food web model Halfon and Schito (1993)

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<sup>i</sup> This group includes Mimic shiner *Notropis volucellus*, Golden shiner *Notemigonus crysoleucas*, Blacknose shiner *Notropis heterolepis*, Blacknose dace *Rhinichthys atratulus*, Pearl dace *Semotilus margarita*, Northern redbelly dace *Phoxinus eos*, Finescale dace *Phoxinus neogaeus*, Bluntnose minnow *Pimephales notatus*, Brassy minnow *Hybognathus hankinsoni*, Fathead minnow *Pimephales promelas*, Central mudminnow *Umbra lima*

<sup>ii</sup> This group includes Bluegill *Lepomis macrochirus*, Pumpkinseed *Lepomis gibbosus*, Green sunfish *Lepomis cyanellus*

<sup>iii</sup> This group includes Bluegill *Lepomis macrochirus*, Pumpkinseed *Lepomis gibbosus*, Green sunfish *Lepomis cyanellus*

<sup>iv</sup> This group has Mottled sculpin *Cottus bairdi*, Slimy sculpin *Cottus cognatus*

<sup>v</sup> This group includes all those fish species in the lake which were not included in any other functional group in the model such as Banded killifish *Fundulus diaphanus*, Tadpole madtom *Noturus gyrinus*, Shorthead redhorse *Moxostoma macrolepidotum*, Brook stickleback *Culaea inconstans*, Brook silverside *Labidesthes sicculus*, Silver redhorse *Moxostoma spp.*, Logperch *Percina caprodes*

C.2: Fitting of von Bertalanffy Growth Function (VBGF)

VBGF model was fitted to the observed age-length data for a number of species of Mille Lacs Lake. The model predicts the length of a fish as a function of its age using parameters used in the equation below: the using Equation

$$L_t = L_\infty(1 - \exp(-K(t - t_0)))$$

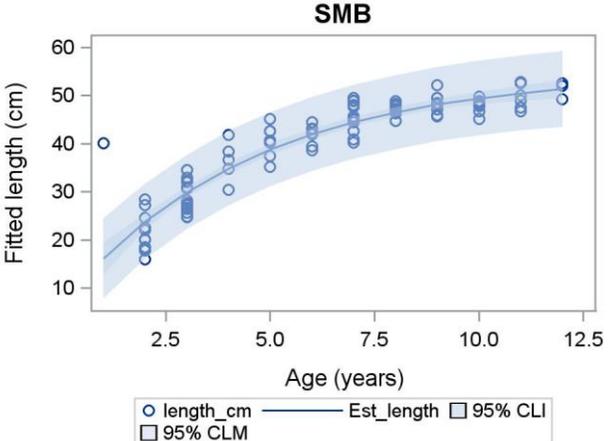
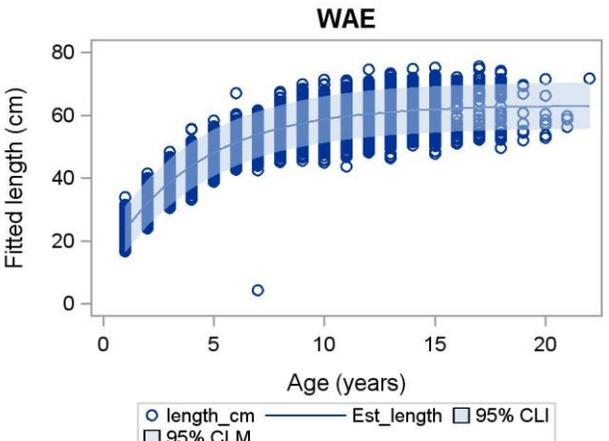
Equation C 1

where,  $L_t$  is length of fish at age  $t$ ,  $L_\infty$  is the asymptotic length,  $K$  is growth coefficient, and  $t_0$  is the hypothetical age when length of fish is zero also called initial condition parameter.

Table C 2. Fitting of VBGF model with Mille Lacs Lake age-length data for 5 species.

$P$ =parameter estimated,  $Est.$ =value of estimated parameters,  $SE$ =standard error. Species name:  $NOP$ =northern pike,  $SMB$ =smallmouth bass,  $WAE$ =walleye,  $YEP$ =yellow perch,  $TLC$ =cisco

P	Est.	SE	95% Conf. limits		Fitted curve
$t_0$	-1.82	0.42	-2.65	-0.99	
$l_{inf}$	90.63	2.76	85.21	96.05	
$k$	0.30	0.05	0.21	0.40	

P	Est.	SE	95% Conf. limits		Fitted curve
to	-0.57	0.37	-1.31	0.17	 <p><b>SMB</b></p> <p>Fitted length (cm)</p> <p>Age (years)</p> <p>○ length_cm — Est_length □ 95% CLI □ 95% CLM</p>
Linf	54.66	2.32	50.07	59.26	
K	0.22	0.04	0.15	0.30	
to	-0.95	0.02	-0.99	-0.92	 <p><b>WAE</b></p> <p>Fitted length (cm)</p> <p>Age (years)</p> <p>○ length_cm — Est_length □ 95% CLI □ 95% CLM</p>
Linf	63.19	0.14	62.91	63.47	
K	0.24	0.00	0.24	0.24	

P	Est.	SE	95% Conf. limits		Fitted curve
to	0.00	0.00	0.00	0.00	
Linf	31.72	0.15	31.42	32.02	
K	0.37	0.00	0.37	0.38	
to	-0.29	0.05	-0.38	-0.19	
Linf	36.40	0.20	35.99	36.80	
K	0.72	0.03	0.66	0.78	

### C.3: Diet matrix of Ecopath with Ecosim model

Table C 3. Diet matrix used in the EwE model.

SrN Prey/Predators	1	2	3	4	5	6	7	8	9	10	11	12
1 Walleye age 0			0.000	0.000				0.020	0.005	0.001	0.020	0.008
2 Walleye age 1			0.003	0.001					0.095	0.050		0.020
3 Walleye age 2				0.004						0.030		0.020
4 Walleye age 3+				0.004						0.029		0.008
5 Yellow perch age 0	0.650	0.441	0.345	0.242		0.070	0.364	0.320	0.188	0.025	0.312	0.005
6 Yellow perch age 1		0.098	0.148	0.108			0.029	0.011	0.150	0.020	0.011	0.011
7 Yellow perch age 2+				0.010					0.225	0.325		0.231
8 Northern pike age 0										0.000		0.009
9 Northern pike age 1				0.000								0.027
10 Northern pike age 2+												0.009
11 Muskellunge age 0								0.000	0.000			
12 Muskellunge age 1+												
13 Cisco age 0		0.015	0.015	0.003			0.007	0.038	0.005	0.005	0.038	0.004
14 Cisco age 1				0.011					0.020	0.040		0.054
15 Cisco age 2+				0.010					0.025	0.049		0.119
16 Smallmouth bass age 0	0.000			0.000			0.000	0.001	0.000	0.000	0.005	
17 Smallmouth bass age 1+										0.001		0.080
18 Rock bass	0.001	0.001	0.000	0.000				0.032	0.010	0.009	0.017	0.034
19 Spottail shiner	0.100	0.027	0.099	0.080		0.001	0.001	0.020	0.050	0.099	0.001	0.001
20 White sucker	0.000	0.000	0.000					0.001	0.001	0.001	0.079	0.161
21 Black crappie								0.001	0.050	0.010	0.010	0.010
22 Burbot				0.013						0.001		0.001
23 Trout-perch		0.020		0.000				0.001	0.001	0.001	0.001	0.001
24 Common carp								0.035			0.028	0.056
25 Largemouth bass				0.002				0.010			0.010	0.020
26 Bowfin										0.001		
27 Bullhead												0.001
28 O. Shiners/minnows	0.100	0.246	0.171	0.187		0.001	0.001	0.037	0.038	0.048	0.037	
29 Sunfish	0.034	0.022	0.017	0.050				0.015	0.005	0.005	0.015	0.030
30 Darters	0.070	0.020	0.002	0.004		0.097	0.187	0.070	0.038	0.034	0.056	0.040
31 Sculpins			0.001	0.005								
32 Other fishes		0.098	0.044	0.080				0.008	0.075	0.206	0.008	
33 Otter and Mink												
34 D.C. cormorants												
35 O. piscivorous birds												
36 Turtles												0.017
37 Frogs				0.021				0.020	0.010	0.010	0.020	0.011
38 Crayfish	0.000	0.001	0.015	0.048		0.243	0.260	0.066	0.010		0.065	0.013
39 Hex mayflies	0.005	0.004	0.132	0.105		0.250	0.019	0.075			0.074	
40 Diptera	0.002	0.002	0.002	0.005	0.045	0.054	0.019	0.025			0.025	
41 Other insects	0.000	0.000	0.001	0.001	0.001	0.071	0.004	0.025			0.025	
42 Amphipoda	0.000	0.000	0.004	0.004	0.013	0.000	0.001					
43 Pelecypoda			0.000			0.186	0.102	0.010			0.010	
44 Gastropoda	0.000	0.003	0.000	0.001		0.009	0.005	0.010			0.010	
45 Oligochaete	0.001	0.001	0.000	0.001				0.040			0.040	
46 Zooplankton	0.036				0.941	0.018	0.001	0.108			0.084	
47 Macrophytes												
48 Periphyton												
49 Phytoplankton												
50 Detritus												
51 Import												

contd.

SrN	Prey/Predators	13	14	15	16	17	18	19	20	21	22	23	24
1	Walleye age 0												
2	Walleye age 1												
3	Walleye age 2												
4	Walleye age 3+												
5	Yellow perch age 0		0.020	0.020		0.020	0.020			0.080	0.299	0.012	
6	Yellow perch age 1					0.020	0.020				0.155		
7	Yellow perch age 2+												
8	Northern pike age 0												
9	Northern pike age 1												
10	Northern pike age 2+												
11	Muskellunge age 0												
12	Muskellunge age 1+												
13	Cisco age 0												
14	Cisco age 1												
15	Cisco age 2+												
16	Smallmouth bass age 0												
17	Smallmouth bass age 1+												
18	Rock bass												
19	Spottail shiner				0.001	0.001	0.001			0.090	0.060		
20	White sucker										0.000		
21	Black crappie				0.165								
22	Burbot					0.010							
23	Trout-perch										0.000		
24	Common carp												
25	Largemouth bass				0.001								
26	Bowfin												
27	Bullhead												
28	O. Shiners/minnows				0.001	0.003	0.025			0.001	0.071		
29	Sunfish				0.080	0.090	0.010						
30	Darters				0.515	0.002	0.025				0.120		
31	Sculpins										0.005		
32	Other fishes				0.002	0.003					0.040		
33	Otter and Mink												
34	D.C. cormorants												
35	O. piscivorous birds												
36	Turtles												
37	Frogs												
38	Crayfish		0.015	0.030	0.002	0.802	0.788				0.219	0.008	0.001
39	Hex mayflies		0.147	0.158	0.018	0.003	0.087		0.086	0.060		0.082	0.150
40	Diptera	0.200	0.172	0.158	0.072		0.000	0.220	0.133	0.200	0.010	0.247	0.150
41	Other insects		0.147	0.158	0.066	0.033	0.024	0.031	0.171	0.080	0.010		0.349
42	Amphipoda				0.043				0.121	0.110	0.011	0.069	0.069
43	Pelecypoda		0.052	0.158					0.063				
44	Gastropoda		0.041	0.158					0.040				0.069
45	Oligochaete				0.002	0.013							0.050
46	Zooplankton	0.800	0.407	0.158	0.032		0.000	0.737	0.142	0.380		0.582	0.050
47	Macrophytes								0.102				0.113
48	Periphyton							0.012					
49	Phytoplankton								0.142				
50	Detritus												
51	Import												

contd.

SrN Prey/Predators	25	26	27	28	29	30	31	32	33	34	35	36
1 Walleye age 0	0.001									0.010	0.003	
2 Walleye age 1	0.001									0.030	0.008	
3 Walleye age 2									0.100	0.010	0.040	
4 Walleye age 3+									0.045	0.010	0.016	
5 Yellow perch age 0	0.163	0.099								0.001	0.001	0.001
6 Yellow perch age 1	0.102	0.045								0.253	0.027	0.001
7 Yellow perch age 2+	0.143	0.001							0.066	0.312	0.094	0.002
8 Northern pike age 0											0.001	
9 Northern pike age 1									0.060	0.007	0.001	
10 Northern pike age 2+									0.060	0.007	0.010	
11 Muskellunge age 0									0.000	0.000		
12 Muskellunge age 1+									0.010			
13 Cisco age 0										0.020		
14 Cisco age 1										0.061		
15 Cisco age 2+									0.030	0.060		
16 Smallmouth bass age 0												
17 Smallmouth bass age 1+									0.002	0.099		
18 Rock bass											0.033	
19 Spottail shiner	0.010		0.011							0.061	0.134	
20 White sucker									0.120		0.010	
21 Black crappie	0.060	0.080								0.020		0.001
22 Burbot									0.223	0.035	0.144	
23 Trout-perch										0.001	0.040	
24 Common carp		0.001									0.010	
25 Largemouth bass		0.001										
26 Bowfin	0.001	0.001										
27 Bullhead	0.120	0.032							0.021			0.001
28 O. Shiners/minnows	0.027	0.001	0.097						0.043		0.130	
29 Sunfish	0.168	0.464							0.060		0.001	0.001
30 Darters										0.000		
31 Sculpins												
32 Other fishes	0.015	0.077							0.052	0.001	0.144	
33 Otter and Mink												
34 D.C. cormorants									0.000			
35 O. piscivorous birds									0.002			0.001
36 Turtles												
37 Frogs	0.057	0.014							0.012			0.001
38 Crayfish	0.003	0.182	0.010		0.010				0.001	0.000	0.005	0.001
39 Hex mayflies	0.001		0.012	0.010	0.100	0.190	0.005	0.075				0.023
40 Diptera	0.046		0.216	0.268	0.041	0.500	0.760	0.378				0.023
41 Other insects	0.036	0.001	0.065	0.166	0.484	0.220	0.050	0.049	0.032		0.015	0.365
42 Amphipoda	0.026		0.326	0.033	0.051	0.029	0.120				0.010	
43 Pelecypoda			0.001		0.010	0.001	0.010		0.001			
44 Gastropoda			0.036		0.254	0.001	0.010					0.296
45 Oligochaete	0.001	0.001	0.226			0.001	0.010					
46 Zooplankton	0.020		0.001	0.123	0.050	0.059	0.035	0.438				
47 Macrophytes												
48 Periphyton				0.143				0.056				0.283
49 Phytoplankton												
50 Detritus				0.258								
51 Import								0.004	0.060		0.125	

contd.

SrN	Prey/Predators	37	38	39	40	41	42	43	44	45	46
1	Walleye age 0										
2	Walleye age 1										
3	Walleye age 2										
4	Walleye age 3+										
5	Yellow perch age 0										
6	Yellow perch age 1										
7	Yellow perch age 2+										
8	Northern pike age 0										
9	Northern pike age 1										
10	Northern pike age 2+										
11	Muskellunge age 0										
12	Muskellunge age 1+										
13	Cisco age 0										
14	Cisco age 1										
15	Cisco age 2+										
16	Smallmouth bass age 0										
17	Smallmouth bass age 1+										
18	Rock bass										
19	Spottail shiner					0.001					
20	White sucker										
21	Black crappie										
22	Burbot										
23	Trout-perch										
24	Common carp										
25	Largemouth bass										
26	Bowfin										
27	Bullhead										
28	O. Shiners/minnows					0.001					
29	Sunfish										
30	Darters										
31	Sculpins										
32	Other fishes					0.001					
33	Otter and Mink										
34	D.C. cormorants										
35	O. piscivorous birds										
36	Turtles										
37	Frogs										
38	Crayfish										
39	Hex mayflies	0.002	0.010								
40	Diptera	0.035	0.007			0.010				0.291	
41	Other insects	0.602	0.001			0.010					
42	Amphipoda									0.100	
43	Pelecypoda										
44	Gastropoda	0.018								0.140	
45	Oligochaete	0.010								0.050	
46	Zooplankton				0.100	0.100		0.128			
47	Macrophytes	0.070	0.001						0.050		
48	Periphyton	0.080	0.001	0.136		0.098			0.800		
49	Phytoplankton			0.341	0.410	0.291	0.350	0.614		0.419	1.000
50	Detritus		0.980	0.523	0.490	0.489	0.650	0.258	0.150		
51	Import	0.183									