AN ASSESSMENT OF HARVEST POLICIES FOR A MULTI-SPECIES FISHERY IN LAKE
HURON USING A FOOD-WEB MODEL

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ABSTRACT

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Lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) are important species to commercial fisheries in Lake Huron. Lake trout dominated harvest until their near extirpation in the 1950s, and lake whitefish are currently the primary commercially harvested species in the lake. Lake trout are currently stocked in the lake with the goal of re-establishing self-sustaining populations. Fishery management objectives include continued harvest of lake whitefish and restoration of lake trout. Bycatch of lake trout in the commercial lake whitefish fishery creates potential tradeoffs for managers in reaching both objectives. Changes in the food web of Lake Huron may influence interactions between lake trout, lake whitefish, and the lake whitefish fishery in unforeseen ways. The research described herein assesses tradeoffs in objectives for lake whitefish harvest and lake trout restoration in Lake Huron by simulating harvest policies for the commercial lake whitefish fishery using the food-web modeling software Ecopath with Ecosim. Chapter 1 provides background information on biological changes within Lake Huron's food web as well as on Ecopath with Ecosim, Chapters 2 and 3 describe questions encountered while constructing the model, Chapter 4 describes the results of policy simulations, and Chapter 5 provides overall conclusions. Two critical questions arose during construction of the food-web model: 1) what is the effect of adjusting for imbalances in data inputs on simulation results, and 2) how to include invasive species in dynamic model simulations. I examined the effect on simulation results in Ecosim resulting from different approaches of adjusting data inputs to meet the requirements of mass balance in

Ecopath (Chapter 2). I found that reasonable changes in data inputs had less effect on simulation results than did changes in vulnerability parameters in Ecosim, and that the effect was smaller when the food web had changed substantially. I compared four methods for including species invasion in Ecosim models (Chapter 3). I found that all four methods allowed the model to reasonably reproduce observed biomass patterns; however they differed in terms of their complexity to implement. Harvest policies were simulated after the questions in balancing and species invasion were addressed (Chapter 4). As expected, I found that, among the policies I considered, policies where bycatch rates of lake trout were reduced in the lake whitefish fishery performed best at simultaneously meeting management objectives for both species. Indirect interactions between lake trout and lake whitefish were minimal; the two species interacted primarily via harvest in the lake whitefish fishery. Future levels of environmental productivity substantially influenced both the magnitude of expected biomass and harvest of lake trout and lake whitefish, as well as the relative performance of management options. Furthermore, the simulation results were sensitive to alternative assumptions about the strength of trophic interactions between predators and their prey (vulnerabilities). In summary, although environmental productivity and vulnerability parameters influenced the forecasted performance of management options, policies where lake trout bycatch rates were reduced invariably performed best. Under original best-fit values for vulnerabilities, indirect interactions between lake trout and lake whitefish were minimal and the two species remained linked primarily by interactions within the fishery, however under alternative and plausible values of vulnerabilities the magnitude of indirect interactions increased.

ACKNOWLEDGEMENTS

PREFACE

The material presented in Chapters 2-4 was intended for submission to peer-reviewed journals. I therefore wish to acknowledge the contributions of my coauthors: Drs. Michael L. Jones, Stephen C. Riley, Mark Rogers, and Hongyan Zhang. Due to the collaborative work involved in Chapters 2-4, I have used first-person plural narratives. First-person singular narratives were used elsewhere. Although Chapters 2-4 were included in manuscript form, there will undoubtedly be differences between the material presented herein and in their eventual published form.

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CHAPTER 1

Introduction

This dissertation seeks to inform managers about decisions for the commercial lake whitefish fishery in Lake Huron, as managers seek to balance lake whitefish (*Coregonus clupeaformis*) harvest and lake trout (*Salvelinus namaycush*) recovery, while accounting for potential effects of changes within the food web. To meet my objectives, I simulated harvest policies for the commercial lake whitefish fishery using a food-web model, Ecopath with Ecosim (EwE). To better understand the biological and modeling processes involved in my research, I describe both my model system and model software in this introduction, and then describe the process I used to address my research objectives, which are described in more detail in later chapters.

Biological introduction:

The Laurentian Great Lakes represent the largest freshwater system in the world. A total of 244,160 km^2 and 22,781 billion m^3 of water are spread across the five main lakes: Superior, Huron, Michigan, Ontario, and Erie (Beeton et al. 1999). Each lake is ranked among the seventeen largest lakes in the world (Beeton et al. 1999). The Great Lakes basin is connected to the Mississippi River drainage through the Chicago canal and flows into the Atlantic Ocean through the St. Lawrence River.

Lake Huron is the second largest Laurentian Great Lake by surface area (Beeton et al. 1999). It drains Lake Superior through the St. Marys River and Lake Michigan through the Straits of Mackinac, and flows into Lake Erie through the Detroit River via Lake St. Clair. Given the proximity and inflow of water from lakes Michigan and Superior, Lake Huron shares characteristics of both lakes in terms of species composition (Barbiero and Tuchman 2001a; Barbiero et al. 2001), fisheries (Bence and Smith 1999, Brown et al. 1999), and water quality

(Beeton et al. 1999). Historically, little scientific attention was given to Lake Huron (Ryder 1995), but recent ongoing research surveys by federal, state, and academic institutions have improved understanding of the lake.

Three distinct basins comprise Lake Huron; the main basin, Georgian Bay, and the North Channel. The main basin is the deepest, largest, and best studied of the three basins. The main basin also contains Saginaw Bay, a large shallow embayment, which has distinct limnological characteristics from the rest of the lake (Beeton and Saylor 1995). Whereas the three primary basins are considered oligotrophic, Saginaw Bay is considered eutrophic (Beeton et al. 1999).

Lake Huron lies on the border between the state of Michigan and province of Ontario. The relatively few management authorities for Lake Huron compared to lakes Superior, Michigan, and Erie simplify the management process, although it still remains complex. Management authority for fisheries in Lake Huron is shared among Michigan and Ontario, as well as with multiple tribal groups (Dochoda and Jones 2002; Ebener et al. 2008a). Communication, research, and management structure for the Great Lakes, including Lake Huron, are facilitated by the Great Lakes Fishery Commission (Dochoda and Fetterolf 1987; Gaden et al. 2008). Management objectives are outlined in the Joint Strategic Plan for all Great Lakes (GLFC 2007), and the Fish Community Objectives for Lake Huron (DesJardine et al. 1995), and although legally non-binding, form the guiding principles upon which management actions are to be based.

The food webs of the Great Lakes have been shaped substantially from the time species were able to colonize beginning with the end the last ice age. In Lake Huron at least two morphotypes of lake trout and a suite of deepwater ciscoes developed to utilize the full extent of the deep cold waters (Eshenroder et al. 1995, Eshenroder and Burnham-Curtis 1999). The current

composition of Lake Huron is a mixture of glacial relict species and those introduced from other sources (Dobiesz et al. 2005). Lake trout, lake whitefish, cisco (*Coregonus artedi*), and deepwater chubs (*Coregonus hoyi*) comprised a mature native fish-community, which was supported by an invertebrate community of *Mysis*, *Diporeia spp.*, and other species (Eshenroder and Burnham-Curtis 1999).

Human populations around the Great Lakes have expanded, and have adapted the lakes to fit their needs. Rainbow trout (*Oncorhynchus mykiss*) were intentionally stocked for recreational fishing opportunities in 1895 in Lake Superior, and the species established spawning populations by the 1930s in Lake Huron (Berst and Spangler 1973). Rainbow smelt (*Osmerus mordax*) were introduced in Lake Michigan in 1912 and found in Lake Huron beginning in 1925 (Berst and Spangler 1973). In addition to intentional introductions, unintentional introductions also occurred. Alewife (*Alosa psuedoharengus*), an Atlantic coast planktivore was originally found in Lake Ontario in 1873, and nearly six decades later was found in Lake Huron (Berst and Spangler 1973). Sea lamprey (*Petromyzon marinus*), a parasitic fish native to the Atlantic coast made a similar journey into the Great Lakes as did alewife; sea lamprey were abundant in Lake Ontario by 1875 (Smith 1995), but were not seen in Lake Huron until 1937 (Berst and Spangler 1973).

The addition of new species contributed to changes in the native fish community. The primary fisheries in Lake Huron were for lake trout and lake whitefish. Lake whitefish constituted the majority of harvest prior to 1880, but was surpassed by lake trout beginning in the 1880s and continuing until the 1940s (Eshenroder et al. 1995, Baldwin et al. 2002). Ciscoes and chubs were also extensively harvested during the early 1900s. Although the exact relative role of invasive species and fishing pressure on the existing fish community in the mid 1900s is uncertain (Berst and Spangler 1973, Eshenroder et al. 1995), the changes during and following

species invasions are not. Lake trout drastically declined and by the 1950s the lake trout fishery in Lake Huron had collapsed. Lake trout were nearly extirpated from the lake with remnant populations remaining in remote areas of Georgian Bay and the North Channel (Eshenroder et al. 1995). The fishery for ciscoes collapsed shortly thereafter (Eshenroder and Burnham-Curtis 1999).

The collapse of the lake trout fishery led to greater cooperation among Great Lakes management agencies, and increased focus on managing fish communities for public benefit, including lake trout restoration (Dochoda 1991, Hansen 1999). The number of parasitic-stage sea lamprey in the lake was an impediment to lake trout restoration, so substantial control efforts were developed (Smith and Tibbles 1980). Although not fully eradicated, sea lamprey populations were substantially reduced and the success of control measures led to the initiation of stocking programs for lake trout in 1969 (Eshenroder et al. 1995). Recently, natural reproduction of lake trout has been observed, suggesting some success in restoration efforts (Nester and Poe 1984; Riley et al. 2007).

Control of sea lamprey opened the door for stocking of other non-native recreational species. To help control the increases of alewife in the 1960s and to establish recreational fishing opportunities, the state of Michigan decided to begin a stocking program of large piscivores in addition to lake trout stocking (Johnson et al. 2010). Pacific salmonines (Chinook (*Oncorhynchus tshawytscha*) and Coho (*Oncorhynchus kisutch*) salmon) were chosen as suitable species, and when supply of fry became available, they were stocked into Lake Michigan in 1966 (Tody and Tanner 1966) and thereafter in lakes Huron, Superior, and Ontario (Johnson et al. 2010). Stocking of large Pacific salmonines has continued in the Great Lakes and has helped

reduce prey fish populations and support valuable recreational fishing opportunities (Talhelm 1988, Johnson et al. 2010).

Multiple impediments to lake trout restoration have been identified in addition to sea lamprey predation. Key issues include lack of sufficient spawner density in suitable spawning habitats, and high mortality from a combination of egg and larval predation, early mortality syndrome (EMS), and harvest (Eshenroder et al. 1995, Ebener 1998). The stocking program was established to increase spawner densities at critical spawning sites, although stocking locations have not always overlapped with prime spawning habitat since some areas are deferred to reduce the amount of restrictions on local fishers (Ebener 1998). Early mortality syndrome is caused by a thiamine deficiency, resulting in impaired movement once fry emerge, making the fry more vulnerable to predators or less capable of feeding (Fitzsimons et al. 1999). Alewife have high concentrations of thiaminase, a compound that breaks down thiamine and can lead to impaired reproductive success for lake trout (Tillit et al. 2005). Consequently, lake trout consuming a diet primarily of alewife can suffer from EMS. Alewife also prey on lake trout larvae directly (Madenjian et al. 2008).

Lake trout harvest occurs in both the recreational fishery and as bycatch in the lake whitefish fishery. Lake whitefish harvest has grown substantially since the 1970s, and reached a record high in 1998 (Baldwin et al. 2002). The majority of lake whitefish harvest comes from Canadian waters (Ebener et al. 2008a). Growth of the lake whitefish fishery has been attributed to both conservative management and good environmental conditions (Ebener 1997). Regardless of the mechanism for increased lake whitefish harvest, increased bycatch of lake trout will continue to be an issue while lake whitefish harvest remains high, and restoration of lake trout remains a priority. To reduce bycatch mortality of lake trout, Michigan banned non-tribal large-

mesh gill nets in its waters, functionally causing all gill nets to be replaced with impoundment gear during the 1970s (Johnson et al. 2004a, Ebener et al. 2008a). In addition, lake trout refuges were established to protect some lake trout from harvest in recreational and commercial fisheries (Ebener et al. 2008a). Tribal groups were allowed to retain their right to fish commercially for lake trout in waters outlined by the 1836 treaty, however large-mesh gill net effort was substantially reduced (Ebener et al. 2008a). Even with Michigan's transfer from gill nets to trap nets, and reductions in gill net mesh sizes and establishment of refuges as part of tribal negotiations, bycatch mortalities are still substantial (Johnson et al. 2004a,b).

In the past three decades a new wave of invasive species has entered the Great Lakes and been implicated in substantial ecological changes (Vanderploeg et al. 2002). Abundance of prey fish, and in particular alewife, has declined to record lows (Riley et al. 2008). Low abundance of prey fish is thought to be a consequence of altered food-web structure caused by dreissenid mussel invasion (Riley et al. 2008), however greater than expected predation by wild Chinook salmon could also have contributed to declines (Johnson et al. 2010). Dreissenids have also been implicated in the decline of *Diporeia*, a primary prey item of lake whitefish (Nalepa et al. 2009) which has led to changes in lake whitefish growth (Pothoven and Madenjian 2008). Increased abundance of round gobies (*Neogobius melanostomus*) has raised concerns about the amount of egg predation on and competition with native species (Jude et al. 1992, Schaeffer 2005). Additional changes include shifts in the community structure of zooplankton from smaller-bodied cladocerans and copepods preferred by fish, to large-bodied copepods (Barbiero et al. 2009). Also, concerns have been expressed about a possible reduction in the spring diatom bloom within the phytoplankton community (Barbiero et al. 2009). Although the exact causes of ecological changes within Lake Huron are unknown, it is certain that many invasive species have

altered processes within the lake throughout the past century. Despite uncertainty about causes and mechanisms, fishery managers must continue to make decisions based on the information they have available.

Changes within Lake Huron provide opportunities for restoration of lake trout and other native species, but present with them challenges to maintain harvest levels for lake whitefish that have been experienced over the past two decades. As lake trout abundance increases, bycatch of lake trout will likely increase as well. In the presence of bycatch quotas in the lake whitefish fishery, greater lake trout bycatch would limit yields for lake whitefish. Declines in alewife affect lake trout abundance; fewer alewife in the diet of lake trout reduces the probability of EMS and predation on and consumption with lake trout larvae, however fewer alewife also means less available food for adult lake trout. Increased densities of dreissenid mussels raise concerns that Lake Huron's energy pathways have changed, leading to uncertain consequences for growth and production of harvested fish populations, especially lake whitefish. Clearly, improved understanding of food-web interactions becomes even more important in light of the recent changes in Lake Huron, as does appreciation for their implications in the performance of harvest policies applied to the commercial lake whitefish fishery in Lake Huron.

Model introduction:

Given the potentially important effects that changes in the food web may have on lake trout and lake whitefish populations, a food-web model was needed in which harvest policies for the commercial lake whitefish fishery could be explored. Many food-web models have been constructed to explore the effects of changes to harvest policies on targeted species from both the direct effects of harvest, as well as the indirect effects of changes in trophic interactions

(Hollowed et al. 2000; Whipple et al. 2000). Ecopath with Ecosim (EwE) was chosen from among many models capable of being used to explore the effects of changes in harvest policies on lake whitefish and lake trout in Lake Huron. Ecopath with Ecosim is freely and easily available, is continually being developed, and is used by many across the world (Christensen and Walters 2004; Morisette 2007). I chose Ecopath with Ecosim primarily due to its ability to assess the direct and indirect effects of harvest policies (Whipple et al. 2000; Latour et al. 2003), which was the primary objective of my research, and its performance compared to other modeling approaches (Latour et al. 2003; Robinson and Frid 2003). Latour et al. (2003) identified EwE, along with multispecies production, multispecies virtual population, and multispecies bioenergetic models as all having great potential for fisheries management based on its ability to quantitatively model important processes across temporal and spatial scales. Similarly, Robinson and Frid (2003) identified EwE and the European Regional Seas Ecosystem Model, which is a type of multispecies bioenergetics model (Latour et al. 2003), as top performing models based on the inclusion of important groups, simulation capabilities, physical and environmental forcing, spatial dynamics, and the ability to assess effects of fishing on food-web dynamics. Ecopath with Ecosim models of the Laurentian Great Lakes have been constructed for lakes Ontario (Halfon et al. 1996, Jaeger 2006, Stewart and Sprules 2011) and Superior (Kitchell et al. 2000, Cox and Kitchell 2004), and models for the other great lakes are currently being developed (Bo Bunnell, USGS, pers. comm.; Ed Rutherford, University of Michigan, pers. comm.; Sarah Adlerstein, University of Michigan, pers. comm.).

Ecopath with Ecosim consists of two modules, Ecopath and Ecosim. The first module, Ecopath, is used to construct a static mass-balance description of a food web for a particular year. Ecopath originated out of a desire to describe the connections and flows within entire

ecosystems, not just parts of ecosystems, and was originally applied to a well studied coral reef ecosystem in the Hawaiian Islands (Polovina 1984, Polovina 1993). Ecopath consists of a system of linear equations that describe abundance, consumption, and production of modeled groups based on data inputs for biomass, production to biomass and consumption to biomass ratios, diet, and harvest (Polovina 1984, Christensen and Pauly 1992, Christensen et al. 2005). Overall, Ecopath provides a useful tool for simplifying complicated process within a food web into easy to understand descriptions of flows and interactions.

The second module, Ecosim, is used to run time-dynamic simulations from which the effects of ecosystem changes on biomass, mortality, and consumption of modeled groups can be assessed. Ecosim is particularly useful for fisheries applications where changes in the ecosystem can be caused by changes in harvest policies. Ecosim consists of a series of differential equations, relating changes in biomass to gains from growth, reproduction (if age structure is included), and immigration, and losses from predation, harvest, emigration, and senescence at each time step (Walters et al. 1997). Consumption of prey by predators is calculated based on foraging arena theory, which assumes that prey are in one of two states: vulnerable, and thus able to be preyed on, and invulnerable, or unable to be preyed on (Christensen and Walters 2004; Ahrens et al. 2012). Important parameters in Ecosim include indicators of how great an effect changes in predator biomass may have on prey mortality (vulnerabilities), yearly variations in the level of primary production in the system (production anomalies), and indicators of how much prey will adjust their feeding time to maintain consumption rates (feeding time adjustment rates).

Constructing EwE models occurs in a series of five steps. The first step is to choose the groups to include in the model. Groups can be either individual species if species-specific data are available, or aggregations of similar species (functional groups) if data are unavailable.

Fulton et al. (2003) suggested that balancing model complexity with model effectiveness should guide which groups go into the model, and also stressed the importance of including important components. Age-structure can be included in the model, which is useful for modeling groups with different trophic ontogeny or mortality schedules, and provides a way to assess recruitment processes within the model (Walters and Martell 2004; Walters et al. 2008). Once groups are chosen, the second step is to compile the necessary data inputs for each group in a specific initial year.

Data inputs are rarely balanced, and therefore the third step is to balance the Ecopath model. Ecopath is a mass-balanced model, meaning that the sum of modeled mortality sources affecting any one group must be less than the total mortality rate for that group. When data inputs do not meet the criterion of mass-balance, inputs are adjusted until balance occurs. Little description of the balancing process is provided for most published Ecopath models, however work has been done on automating the balancing procedure (Kavanaugh et al. 2004) and on describing which inputs have the greatest effect on model balance (Essington 2007; Morissette 2007).

Once the Ecopath model is constructed and balanced, Ecosim can be used for policy simulation. An important component of simulating policies in the future is being able to have confidence that the model can reproduce the past. The fourth step in model construction is to tune the model (estimate vulnerability and production anomaly parameters) based on fits to observed biomass time series. The estimation process is done automatically in Ecosim, and is based on minimizing the sum of squared residuals, calculated on a *log* scale, between model-predicted biomass values and observed biomass time series. After estimating Ecosim parameters,

and assuring that the model is able to reproduce past dynamics, the fifth and final step is to simulate harvest policies.

Two questions arose while going through the steps of constructing the Lake Huron EwE model, and were addressed prior to simulating harvest policies. As was expected, initial data inputs resulted in model imbalance. To achieve mass-balance, adjustments to data inputs were required; however the effect of these adjustments on Ecosim results was uncertain. Attempts have been made to determine the effects of changes in data inputs to achieve mass-balance on Ecopath results (Essington 2007; Morissette 2007), but as far as I know, no attempts have been made to assess effects on Ecosim results. Consequently, prior to simulating harvest policies, I wanted to assess whether changing data inputs in order to achieve mass balance would affect policy results in Ecosim, and address the topic in Chapter 2.

The second question which arose during model construction was how to include species invasion in EwE models. Ecopath models are required to be constructed and balanced with all groups included. Species that invade after the initial Ecopath year (the year for which data inputs are based) must therefore be included in the model, even though they are actually not yet present in the food web. Methods for modeling species invasions exist in the literature (e.g. Cox and Kitchell 2004) however they have not been compared. Consequently, prior to simulating harvest policies for Lake Huron, I wanted to compare methods for modeling species invasions that have occurred during the past three decades, and address the topic in Chapter 3.

Once the two questions about model construction were adequately addressed, I was able to simulate harvest policies within the Lake Huron EwE model. The research in Chapter 4 describes the results of harvest policy simulations for the commercial lake whitefish fishery in Lake Huron on biomass and harvest of lake trout and lake whitefish, which was the impetus for

my dissertation. The effect of including alternative assumptions for key uncertainties in the understanding of the food web in Lake Huron, as well as in model parameters (vulnerabilities and production anomalies) is also considered in Chapter 4. I conclude my dissertation in Chapter 5, with thoughts and comments from the results of the harvest policy analysis interpreted within the context of my findings from earlier chapters.

I construct different EwE models for Chapters 2-4, each building on the previous model. I include 36 groups in all models, representing 21 species or groups of species, eight of which were modeled with age structure. Data inputs are based in 1999 for the model in Chapter 2 (with details on sources in Appendix 2B), and in 1981 for Chapters 3 and 4 (with details on sources in Appendix 4B). Data were more readily available in 1999, and therefore were used to assess the effects of changes in data inputs. When simulating species invasion (Chapter 3) and harvest policies (Chapter 4), longer time series of data were preferable and thus an earlier initial start year was chosen. Although the balancing process is only described in detail in Chapter 2, adjustments in data inputs were required for all models. Vulnerability and production anomalies were set to specific values in Chapter 2, whereas values were estimated from fits to observed biomass time series in Chapters 3 and 4.

CHAPTER 2

The effect of different approaches to achieve mass balance on a food-web model of Lake Huron

Abstract:

The Ecopath with Ecosim (EwE) software is an increasingly popular modeling tool in fishery research and management. Ecopath requires a mass-balanced snapshot of a food-web at a particular point in time, which Ecosim then uses to simulate biomass through time. Initial inputs to Ecopath, including available estimates of biomass, production, consumption, and diets, rarely produce mass balance, and thus changes to the inputs are required to balance the model. There has been little discussion of whether these changes to achieve mass balance affect model results. We constructed two EwE models for the offshore community of Lake Huron, balanced in two contrasting but realistic ways. One placed more confidence in estimates of consumption; levels of production were increased to achieve mass balance. The other placed more confidence in estimates of production; levels of predation were decreased. To assess the effect of choice of balancing approach on model results, we compared ecosystem metrics within Ecopath (ascendency and system omnivory index (SOI)), as well as biomass dynamics within Ecosim. Within Ecosim, we compared simulations given alternative assumptions about the type of control (top-down or bottom-up) under two scenarios of (1) increased fishing mortality or (2) increased environmental production. Ascendency for the first balancing approach was approximately four times that of the second, and was mostly due to greater assumed production in planktonic groups. Values of SOI were nearly identical, suggesting very little difference between the two approaches. Differences in overall biomass between the two balancing approaches were greatest under scenarios assuming top-down control, and differed by at most a factor of 1.15. When expressed relative to the overall change in biomass for each scenario, the differences between balancing approach represented at most 41%, but were much lower for scenarios where biomass changed substantially. The importance of these differences appears to be small, and similar

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results from other EwE models would be helpful to evaluate the generality of this conclusion. Our findings suggest that approaches to balancing Ecopath models have the greatest effect on model results when top-down control is prevalent in the system and when simulated biomass dynamics are stable through time.

Introduction:

Mathematical models are tools to explain complex processes in simple and understandable ways. Trophic interactions within most aquatic ecosystems are complex, and attempts to understand these interactions for applications to fisheries management can be aided by models. A variety of modeling frameworks have been used to describe ecosystem processes, and even within an individual framework, the processes themselves can be described in multiple ways (e.g. alternative assumptions about the strength of trophic interactions). When models are used to inform decisions, and thereby influence management actions, it is important to determine whether alternative descriptions of ecosystem processes within a modeling framework affect conclusions.

The use of models to inform fisheries management decisions is likely to increase in the future. This is due partly to increased computing power, which allows for more explicit accounting of multiple species and the processes that govern their interactions (Hilborn and Walters 1992; Robinson and Frid 2003), and also to greater awareness of the need to base management on an understanding of the ecosystems within which fisheries operate (Bundy 2001; Walters et al. 2008). These have contributed towards the progression from single-species management to ecosystem-based fisheries management (EBM), which incorporates objectives for many components within an ecosystem, not just for harvested species (Marasco et al. 2007). Examples of ecosystem objectives include prey availability for non-human components of the ecosystem, maintaining important habitats, and managing bycatch (Ruckelshaus et al. 2008). Ecosystem models are a valuable tool for the assessment of EBM policies in meeting desired objectives (Pikitch et al. 2004; Smith et al. 2007; Walters and Martell 2004). Policies for Laurentian Great Lakes fisheries have incorporated attributes of EBM, such as the Fish

Community Objectives for Lake Huron (DesJardine et al. 1995) and the Joint Strategic Plan (Gaden et al. 2008). As the use of ecosystem models increases, the value of understanding their sensitivity to alternative process descriptions within the model will as well.

A variety of ecosystem models have been used for fisheries applications (Hollowed et al. 2000; Latour et al. 2003; Robinson and Frid 2003; Whipple et al. 2000), all with strengths and weaknesses. The modeling framework used here is the Ecopath with Ecosim (EwE) software. Ecopath with Ecosim consists of two modules, Ecopath and Ecosim. Ecopath allows for a mass-balanced description of a food-web at a single point in time, which is parameterized with biomass, growth, and consumption data for each modeled group (Christensen and Walters 2004). The Ecopath model, along with values reflecting the strength of interspecific interactions is then used as input to Ecosim, which simulates the dynamics of the modeled groups through time (Christensen and Walters 2004). Published Ecopath models in the Great Lakes exist for Lake Superior (Cox and Kitchell 2004; Kitchell et al. 2000) and Lake Ontario (Halfon et al. 1996; Koops et al. 2006; Stewart and Sprules 2011), while unpublished work exists for Lake Michigan (Ann Krause, University of Toledo (UT), pers. comm.). Work is also underway on building models for other Great Lakes (David Bunnell, United States Geological Survey (USGS), pers. comm.; Sara Adlerstein and Ed Rutherford, University of Michigan, pers. comm.).

A challenge when constructing Ecopath models is obtaining representative average data inputs across a year and system that meet the physical constraints of mass balance. Mass balance is a requirement in Ecopath models; the amount of food consumed must be less than what is available, and the gain in weight from consumption must be less than the weight of food consumed. Achieving mass balance in Ecopath models invariably requires modifying input parameters (Christensen et al. 2005), but EwE users rarely discuss this process. Modifying input

parameters can be done in many ways, and thus multiple descriptions of the food web are possible as a result of the balancing process. Studies that used Ecosim models of the Great Lakes focused on time dynamic simulations and only briefly discussed balancing procedures (Cox and Kitchell 2004; Kitchell et al. 2000). Studies without time dynamic simulations focused on ecosystem descriptions, and discussed the balancing process only briefly (Halfon et al. 1996; Koops et al. 2006), with the exception of Stewart and Sprules (2011).

There are two primary procedures to balance Ecopath models. Model inputs can be adjusted subjectively by the modeler, based on their judgment of which inputs are least reliable or most likely to achieve mass balance (Christensen et al. 2005). Alternatively, changes can be made objectively by the software, based on a quantification of user-perceived reliability for input parameters and a formal objective function, such as minimizing changes to initial inputs (Kavanagh et al. 2004). In one of the few publications in which the impact of balancing was discussed, Essington (2007) found that randomly balancing a model produced a balanced model as close to the "true" model (one in which all parameters were known) as when balancing was done using an objective function. Although Essington (2007) found that the overall variation in input parameters among balanced models was similar when using either balancing procedure, the differences in model outputs such as ecosystem metrics or simulated biomasses in Ecosim were not assessed. When using the subjective procedure, the modeler, rather than the software, makes changes to input parameters which can provide a better understanding of the linkages within the system. Although more time consuming, consideration of such linkages may reveal unexpectedly important groups or gaps in the understanding of the system.

Subjective balancing was used to balance the model described herein. Through iterative attempts to achieve mass balance, a major source of imbalance was found to be due to a

perceived overconsumption of intermediate trophic-level groups. Conversations with other EwE modelers suggest this is a common problem, but the observation has not been discussed in standard balancing documentation and has only recently been discussed in the Ecopath literature (Stewart and Sprules 2011).

The objective of this research was to assess how alternative strategies for balancing an Ecopath model affected EwE results. An Ecopath model of the offshore fish community of Lake Huron was constructed and subjectively balanced using two approaches. The first approach assumed data for upper trophic-level groups were more reliable than data for lower trophic-level groups, whereas the second assumed the opposite. Differences in model outputs of ecosystem metrics in Ecopath and time dynamic simulation results in Ecosim were used to compare the two balancing approaches. The strength of trophic interactions, and the level of environmental productivity and fishing mortality were adjusted within Ecosim to assess the impact of ecosystem conditions on model results. Possible reasons for observed imbalances in the model are also described.

Methods:

Study site

Lake Huron is the second largest of the Laurentian Great Lakes with a surface area of 59,570 km^2 (DesJardine et al. 1995), and is divided by the border between the United States and Canada (Figure 2.1). Both commercial and recreational fisheries exist in the lake; the majority of commercial effort occurs in Canadian waters, whereas the majority of recreational activity occurs in US waters. Management responsibilities for the fisheries are shared among Michigan, Ontario, and Native American agencies. These agencies collect information pertinent to fisheries

management, and are assisted in collection and coordination by the USGS, US Fish and Wildlife Service, Environmental Protection Agency, Canadian Department of Fisheries and Oceans, and Great Lakes Fishery Commission. Data to parameterize the model were provided by these agencies as well as from published sources, and are described in detail in appendix 2B (Table 2.6).

The model

Ecopath with Ecosim (EwE) version 6.1.1 was used to construct a food-web model of the offshore fish community in the main basin of Lake Huron (Figure 2.2). It is a freely downloadable software package that describes a snapshot of an ecosystem at a particular point in time (Ecopath), and simulates the dynamics of modeled groups through time (Ecosim). Details of the modeling software have been discussed previously (Christensen and Pauly 1992; Christensen and Walters 2004), but a summary of key equations and parameters is provided below. The mass balance equation in Ecopath for each group *i* is

$$P_i = Y_i + E_i + (BA)_i + B_i(M2)_i + B_i(M0)_i \,, \tag{1}$$

where P is production; Y is total harvest; E is net migration (emigration - immigration); BA is biomass accumulation; B is biomass; $M2$ is predation mortality rate; and $M0$ is other mortality rate, which represents sources of mortality not included in the model. For simplicity, both E and BA were assumed to be zero for this research. The Ecopath user does not provide estimates for all parameters in equation (1) directly, but rather provides inputs from which parameters in equation (1) are calculated. When expressed in terms of Ecopath user inputs, equation (1) becomes

$$EE_i = \frac{Y_i + \sum_j (Q/B)_j B_j (DC)_{ij}}{(P/B)_i B_i},$$ (2)

where *EE* is ecotrophic efficiency, which equals $1\text{-}M0_i/(P/B)_i$ and represents the proportion of total mortality explained by sources in the model; *Q/B* is the consumption to biomass ratio; DC_{ij} is the percent contribution of prey *i* to the diet of predator *j*; and *P/B* is the production to biomass ratio. Allen (1971) found that under standard assumptions of exponential mortality and von Bertalanffy growth, *P/B* is equivalent to the total instantaneous mortality rate, assuming *BA* is zero. It is assumed that all components of mortality are included in equation (1), and thus conservation of matter requires that the sum of these terms equals the assumed level of production. In relation to equation (2), this means total production (denominator) must be greater than the loses due to consumption and fishing described in the model (numerator) so that EE<1. When this occurs, the Ecopath model is said to be balanced and can be used as input into Ecosim.

Ecosim is governed by two primary equations. For groups with a single age stanza, the change in biomass of each group is modeled as

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - \left((M0)_i + F_i + e_i\right)B_i,$$ (3)

where *t* is time in months; *g* is the gross food-conversion efficiency ratio (GCE), which is the ratio of *P/B* to *Q/B*; Q_{ij} is consumption of prey *i* by predator *j*; *I* is immigration; *e* is the emigration rate; and *F* is the fishing mortality rate. The solution to the differential equation is estimated using an Adams-Bashford method (Christensen et al. 2005). More complicated versions of equation (3) are used for groups with multiple age stanzas (see Walters et al. 2008 for

details). The second Ecosim equation defines the value of consumption, which in its simplest form is modeled as

$$Q_{ij} = \frac{a_{ij} v_{ij} B_i B_j}{2v_{ij} + a_{ij} B_j},$$ (4)

where a_{ij} is the effective search rate of predator j for prey i, and v_{ij} is the vulnerability of prey i to predator j. Vulnerabilities define the strength of trophic interaction between a predator and its prey and can be adjusted within Ecosim. The user does not actually adjust v_{ij}, but rather a constant (k_{ij}) from which v_{ij} is calculated using $v_{ij} = k_{ij}(Q_{ij}/B_i)$ (Walters and Christensen 2007).

Vulnerabilities have been described with respect to their effect on predation mortality rates of prey and consumption to biomass rates of predators (Walters et al. 1997; Ahrens et al. 2012). Dividing Q_{ij} in equation 4 by B_i or B_j provides an equation for the predation mortality rate on prey i, or the consumption to biomass ratio of predator j, respectively. As v_{ij} becomes large compared to $a_{ij}B_j$ in the denominator of equation 4, Q_{ij}/B_i (predation mortality on prey i) approaches a rate ($B_j a_{ij}/2$) proportional with predator biomass. On the other hand, as v_{ij} becomes small, predation mortality approaches a constant rate (v_{ij}), independent of predator biomass. Consequently, vulnerabilities have been described in terms of the effect that changes in predator biomass have on prey. When vulnerabilities are low, changes in predator biomass have little effect on prey mortality, and control is considered to be "bottom-up", whereas when vulnerabilities are high, changes in predator biomass have greater effects on prey mortality, and control is considered to be "top-down" (Walters et al. 1997).

Vulnerabilities also influence consumption to biomass ratios of predators. As v_{ij} becomes large compared to $a_{ij}B_j$ in the denominator of equation 4, Q_{ij}/B_j (the consumption to biomass ratio of predator j) approaches a value ($a_{ij}B_i$) independent of predator biomass. As v_{ij} becomes small, the consumption to biomass of predator j approaches an inverse relationship ($a_{ij}B_i/B_j$) with predator biomass. Vulnerabilities therefore influence the extent to which density dependence affects predator consumption rates, so have also been described more recently in terms of the proximity of a group to its carrying capacity, where low vulnerabilities suggest a group is near its carrying capacity (strong density dependence) and high vulnerabilities suggest a group is far from its carrying capacity (Ahrens et al. 2012).

Building an Ecopath model

The Ecopath model of Lake Huron was constructed in a series of three steps: choice of groups, choice of time period, and choice of data sources. For choosing which groups to include in the model, Lake Huron biologists were consulted, and 21 species or groups of species were identified based on their assumed importance to the offshore community (Table 2.1). Individual species were further separated into age stanzas when appropriate data were available. Each age stanza consisted of a set of age classes and reflected a difference in trophic ontogeny or mortality schedule. The total number of modeled groups increased from 21 to 36 when age stanzas were included (Table 2.1).

Special considerations were required for modeling stocked and semelparous species. Ecopath requires the age of the first stanza for each group to begin at 0 months. Species are stocked into Lake Huron at either six months (fingerlings) or 12 months (yearlings) so a pre-stocking stanza with age either 0-6 or 0-12 months was included in the model with a very low

mortality rate and import-only diet. An import-only diet represents feeding outside the modeled system and allows a stanza that is not actually in the system, but is required by the model, to be included without affecting other species. Within Ecosim, the biomass of the first age stanza for stocked species (lake trout (*Salvelinus namaycush*), steelhead (*Oncorhynchus mykiss*), and Chinook salmon (*Oncorhynchus tshawytscha*)) was set to the initial Ecopath value for each simulation year. This was also done for sea lamprey (*Petromyzon marinus*), whose recruitment is heavily influenced by management (pest control). Ecopath also assumes that all species are iteroparous. Therefore, the semelparous Chinook salmon was modeled with a terminal age stanza (age 6+) that had an import-only diet. A terminal age stanza (age 6+) for steelhead was also included in the model.

The second step was to choose a representative time period, which was dictated by the availability of data. Biomass estimates for nearly all modeled groups were available for 1999. The choice of time period should reflect a period of stability in the food-web. Lake Huron has undergone substantial changes in recent years; zebra (*Dreissena polymorpha*) and quagga mussels (*D. bugensis*) have proliferated in the 1990s and early 2000s (Nalepa et al. 2007) and alewife (*Alosa pseudoharengus*) abundance collapsed in 2003 (Riley et al. 2008). Despite the proximity of these events, 1999 was chosen as the modeled year due to the greater availability of biomass estimates, particularly for lower trophic-level groups.

Step three was to find estimates for Ecopath parameters centered around 1999 for the chosen groups. Ecopath requires estimates of *B*, *P/B*, *Q/B*, and diet for all groups. For groups with age stanzas, *B* and *Q/B* are needed for only one stanza. Ecopath then calculates *B* and *Q/B* for all other age stanzas based on an age-structured model that assumes a stable age distribution and von Bertalanffy growth (Walters et al. 2008). Consequently, von Bertalanffy growth

coefficients (K) were also required for groups with multiple age stanzas. When estimates of parameters were not available for Lake Huron in 1999, estimates were obtained from as similar a system and time period as possible. Recent time periods in Lake Huron are generally divided by the invasion of dreissenid mussels in the early 1990s and the collapse of alewife in 2003. Consequently, when data were not available explicitly for 1999, sources from 1990-2003 were preferentially used. When estimates were not available for Lake Huron, estimates for other Great Lakes were used. Given the geographical and biological similarities between Lake Huron and Lake Michigan, parameter estimates were preferentially taken from Lake Michigan data, and as near to 1999 as possible. When Lake Michigan estimates were not available, preference was given to studies on Lake Ontario, Lake Superior, and finally Lake Erie. When estimates were not available from studies within the Great Lakes, estimates were taken from Ecopath models built for Lake Michigan (Ann Krause, UT, pers. comm.), Lake Superior (Cox and Kitchell 2004; Kitchell et al. 2000), or from regression relationships (e.g. Pauly 1980).

Balancing an Ecopath model

Once the Ecopath model was built, parameter estimates were adjusted so that the model was balanced. We are not aware of any Ecopath model that met the requirement of mass balance without some adjustment to initial parameter estimates. To achieve mass balance, initial parameter estimates were changed by an iterative process following recommended practices (Christensen et al. 2005). Christensen et al. (2005) recommend that to achieve mass-balance, diet inputs for predators of unbalanced groups be adjusted first, followed by consumption to biomass ratios for predators of unbalanced groups and production to biomass ratios for unbalanced groups, and then lastly biomass values of unbalanced groups. Estimates of *P/B*, *Q/B*, and diet

from other Great Lakes and other time periods were consulted to supply a range of plausible

parameter estimates as additional guidelines to inform the balancing process. Lake Huron

biologists were consulted throughout the balancing process to ensure that only plausible

estimates of parameters were considered.

The order in which parameters were changed to achieve mass balance reflected their

assumed reliability. Diet studies for Lake Huron species are not common, and studies within the

Great Lakes themselves range over many years, particularly for lower trophic-level groups. The

inherent nature of diet studies also results in poor reliability. Diet varies both temporally and

spatially, and thus diet observations may differ substantially among samples, even within the

same system and year. Consequently, diet information was assumed to be least reliable and was

changed first during balancing. After reasonable adjustments to diets were made, Q/B and P/B

ratios, and B were changed. Changing Q/B ratios was particularly relevant when many groups

consumed by the same predator were all unbalanced.

The balancing process can produce many different, but balanced, models. Two

contrasting but realistic approaches to balancing were compared. The first approach was based

on the assumption that data for top trophic-level groups were most reliable. Therefore, to achieve

mass balance, production (P/B or B) of lower trophic-level groups was preferentially increased to

meet the consumption demands of their predators. This approach will be referred to as the

"consumption-based" approach throughout this paper, reflecting the confidence placed on the

estimates of consumption by top trophic-level groups. The second approach was based on the

assumption that data for prey fish and other lower trophic-level groups were most reliable.

Consumption (Q/B or B) by predators was therefore lowered to meet the production of their prey.

This approach will be referred to as the "production-based" approach, reflecting the confidence placed on estimates of production by lower trophic-level groups.

Assess impacts of balancing approaches

Ecosystem metrics within Ecopath and biomass dynamics within Ecosim were used to compare the two balancing approaches. Measures of ecosystem maturity (*sensu* Odum 1969) have been used to compare ecosystem models (Christensen 1995). For this research, ascendency (as described in Christensen and Pauly 1992) was used to assess ecosystem maturity. Ascendency describes the size and organizational structure of an ecosystem, and is argued to reflect ecosystem maturity where high values represent a mature ecosystem and low values represent an immature ecosystem (Ulanowicz 1986). The second ecosystem metric was system omnivory index (SOI) which is the average of each consumer's omnivory index weighted by the logarithm of their food intake (Christensen et al. 2005). This index also describes the structure of the food web while accounting for the magnitude of consumption for each group, and is therefore influenced by changes to parameters that define either food-web structure (diet) or food intake (B, Q/B).

Ecosim dynamics were also used to compare the two balancing approaches. Ecosim was run for a duration of 40 years, and the proportional difference in biomass between the two balancing approaches was calculated as

$$\text{index } 1 = med_i \left[med_t \left(\frac{\max_m \left(B_{i,t,m} \right)}{\min_m \left(B_{i,t,m} \right)} \right) \right], \tag{5}$$

where med_i is the median value taken over the index (in this case i groups); $\max_m$ and $\min_m$ are the maximum and minimum values between the $m = 2$ balancing approaches, respectively; and

$B_{i,t,m}$ is the biomass of group i in month t for balancing approach m. To assess the sensitivity of balancing, the median change in relative biomass across balancing approach, time, and then groups was calculated as

$$\text{index } 2 = med_i\left[med_t\left(med_m\left[\left(relB_{i,t,m}\right)^{\zeta_{i,t,m}} \right] \right) \right], \tag{6}$$

where $relB_{i,t,m}$ is the biomass of group i in month t for balancing approach m relative to the biomass in month 1, and $\zeta_{i,t,m}$ is an indicator variable that was 1 if $relB_{i,t,m} > 1$ and -1 if $relB_{i,t,m} < 1$, and then the ratio of the two indices (adjusted to reflect percentage changes) was calculated as

$$\text{index } 3 = (\text{index } 1 - 1)/(\text{index } 2 - 1). \tag{7}$$

For all indices, sea lamprey and the first age stanza for stocked species were not included in the calculations because the biomasses of these groups were forced at their initial Ecopath values. The last age stanzas for steelhead and Chinook salmon were also excluded because they were modeling artifacts and were not of interest.

In the absence of any perturbation and with biomass accumulation rates equal to zero, the biomass of each group in Ecosim does not change from its initial Ecopath value. Therefore, to compare the two balancing approaches, either the underlying productivity of the environment (modeled as the *P/B* ratio of phytoplankton) or the total fishing mortality on all groups was doubled during simulations. This caused the biomass for each group to vary across years in both balancing approaches. The changes made to environmental productivity and fishing mortality were based on observed variability from past estimates. Estimates based on chlorophyll *a* suggest that primary production during the late 1980s and early 1990s was approximately twice that during 1999 (Barbiero et al. 2009). Similarly, estimates of fishing mortality for lake whitefish

Coregonus clupeaformis (Adam Cottrill, Onatrio Ministry of Natural Resources, unpublished data) and other salmonines have varied more than two-fold through time, although doubling fishing mortality produced greater values than those observed in the past for lake trout (Ji He, Michigan Department of Natural Resources, unpublished data) and Chinook salmon (Travis Brenden, Michigan State University, unpublished data).

Ecosim dynamics are heavily influenced by assumptions about the strength of species interaction (vulnerabilities; Christensen and Walters 2004). Therefore, three different values for the vulnerabilities of prey to their predators were also used: 1.01, 2, and 10. These values reflect low (1.01), intermediate (2), and high (10) effect of predators on their prey. Low vulnerabilities can be thought to represent bottom-up control, whereas high vulnerabilities can be thought to represent top-down control. Each vulnerability value was used on both types of forcing (environmental or fishing) for a total of six different Ecosim scenarios.

Results:

As expected, the initial Ecopath model was unbalanced. Unbalanced groups included age 0 bloater (*Coregonus hoyi*; *EE*=2.1) and rainbow smelt (*Osmerus mordax*: *EE*=3.2); less abundant prey fish including round goby (*Neogobius melanostomus*; *EE*=28.4), ninespine stickleback (*Pungitius pungitius*; *EE*=7.4), and slimy (*Cottus cognatus*; *EE*=60) and deepwater sculpins (*Myoxocephalus thompsoni*; *EE*=1.2); yearling lake trout (*EE*=2.1); age 1+ alewife (*EE*=1.5); and phytoplankton (*EE*=3.2). Except for phytoplankton, these groups occupied intermediate trophic levels, where demand on them was entirely predatory. Groups with demand from commercial or recreational harvest, on the other hand, were all balanced.

To achieve mass balance, simple changes in diet contributions were made first. The final diet matrix for the "consumption-based" approach describes the changes made during balancing (Table 2.2). The diet matrix for the "production-based" approach was similar and is not shown. Predation on age 0 bloater was nearly entirely (99%) from benthic prey-fish. Consumption of bloater eggs by slimy sculpin, deepwater sculpin, and ninespine stickleback was modeled as consumption of age 0 bloater. Removing the contribution of age 0 bloater from the diets of these three species resulted in mass balance for bloater (Table 2.2). Slimy sculpin had the largest pre-balance value of *EE*, and thus was the most unbalanced group. Approximately 80% of slimy sculpin predation mortality was from age 1+ rainbow smelt. Lantry and Stewart (1993) assumed that rainbow smelt consumed slimy sculpin, and although supported by Brandt and Madon (1986), few other studies report predation on this species (Storch et al. 2007; Walsh et al. 2008). Consequently, slimy sculpin was removed from the diet of age 1+ rainbow smelt (Table 2.2). This change alone, however, did not result in mass balance.

Changes to more than just diet were required for balancing some species. Values of *B*, *P/B*, and *Q/B* for all species are provided for models balanced with both the "consumption-based" (Table 2.3) and "production-based" (Table 2.4) approaches. Slimy sculpin were particularly difficult to balance. Once predation by age 1+ rainbow smelt was removed, the remaining mortality was from steelhead and burbot (*Lota lota*). Moderate changes to slimy sculpin in the diet of these species were made (Table 2.2), but slimy sculpin were still unbalanced. Balance was achieved by either increasing slimy sculpin biomass (Table 2.3), or reducing consumption by its predators (Table 2.4). Ninespine stickleback and round gobies also required more than just changes in diet to balance. Most consumption of ninespine stickleback (94%) and all consumption of round goby was by adult lake whitefish. Although contributions

of round goby and ninespine stickleback to the diet of lake whitefish were small, the large

biomass of lake whitefish resulted in high levels of consumption. Changes to the diet of lake

whitefish lowered the *EE* of these groups, but, as was the case for slimy sculpin, balance was

achieved only after either increasing biomass of round goby and ninespine stickleback (Table

2.3) or decreasing consumption by lake whitefish (Table 2.4). Changes in diet were not used to

balance phytoplankton. Zooplankton were responsible for 99% of mortality of phytoplankton,

and because they fed nearly exclusively on phytoplankton, balance was achieved by either

increasing phytoplankton production (Table 2.3) or decreasing zooplankton consumption (Table

2.4).

Values for the ecosystem metrics showed some difference between the two balancing

approaches. Ascendency was 28,884 for the "consumption-based" approach and 7840 for the

"production-based" approach. The nearly four-fold difference in ascendency between the two

models was mostly due to the different levels of production of phytoplankton and zooplankton.

For the "consumption-based" and "production-based" balancing approaches, phytoplankton and

zooplankton contributed 56 and 47% of the total ascendency, respectively. Detritus made up an

additional 40% for each approach. Although the scale of the models as estimated by ascendency

was different, the structure was nearly identical; SOI was 0.085 for the "consumption-based"

approach and 0.084 for the "production-based" approach.

Differences in biomass dynamics between the two balancing approaches (index 1) also

suggested that balancing affected model results. The magnitude of the difference depended on

the assumed strength of interaction (vulnerabilities) between predators and prey. Ecosim

dynamics in the two balancing approaches were least similar under high vulnerabilities and most

similar under low vulnerabilities (Figure 2.3). Although this pattern was maintained under both

types of forcing, it was more pronounced when environmental productivity was doubled than when fishing mortality was doubled. At most, the difference was 15% (Figure 2.3).

Median changes in relative biomass (index 2) followed a similar trend as index 1. Doubling environmental productivity produced the greatest change in relative biomass, especially when vulnerabilities were high (Figure 2.4). Although index 2 reflected both decreases and increases from initial biomass levels, biomass of nearly all groups increased when productivity was doubled. Doubling fishing mortality resulted in much smaller changes, but these were still greatest when vulnerabilities were high (Figure 2.4). Index 2 was used to calculate index 3, which expressed the difference in biomass between the balancing approaches relative to the change in biomass due to other sources of perturbation. Values for index 3 were at most 41% and were again greatest under high vulnerabilities (Table 2.5), but in contrast to other indices, were greatest when fishing mortality was doubled than when environmental productivity was doubled (Table 2.5).

Indices were also calculated for each modeled group. The largest values for indices 1 and 2 were observed when environmental productivity was doubled and vulnerabilities were high. Under these conditions, index 1 was greatest for dreissenids (7.39) and ninespine stickleback (5.31), and followed by slimy sculpin (1.60). Index 2 was greatest for age 3+ and age 0-3 burbot (21.2 and 21.0, respectively), and followed by dreissenids (12.3). In scenarios with low vulnerabilities, index 1 was greatest for age 0 alewife when environmental productivity and fishing mortality were doubled (1.19 and 1.27, respectively) and was followed by age 0.5 Chinook salmon (1.06 and 1.12, respectively). In scenarios with intermediate vulnerabilities, index 1 was greatest for age 1-5 Chinook salmon (1.10) when fishing mortality was doubled, and ninespine stickleback (1.19) when environmental productivity was doubled.

Values for index 3 were greatest when fishing mortality was doubled, but contrary to the pattern in overall medians, the greatest individual group value occurred under intermediate vulnerabilities. Under intermediate and high vulnerabilities, respectively, age 0 whitefish (203 and 161%) and *Diporeia spp*. (200 and 170%) had the greatest values when fishing mortality was doubled. Under low vulnerabilities, age 0 alewife (12.7 and 119%) and age 0.5 Chinook salmon (3.3 and 102%) had the greatest values when both environmental productivity and fishing mortality were doubled, respectively. Ninespine stickleback had the greatest values (8.65 and 70%) under intermediate and high vulnerabilities, respectively, when environmental productivity was doubled.

Biomass dynamics for age 4+ lake whitefish, *Diporeia*, age 1+ alewife, and ninespine stickleback illustrate the general patterns observed among modeled groups (Figure 2.5). Lake whitefish represent 80% of commercial harvest in Lake Huron (Ebener et al. 2008b), *Diporeia* has been their primary prey, and alewife are a major component of Chinook salmon and lake trout diets. Ninespine stickleback was included because of its large values for index 1 and 3. Because indices were greatest when vulnerabilities were high, biomass dynamics are shown only for these scenarios (Figure 2.5).

Discussion:

Effect of balancing approach

The effect of balancing depended on the strength of trophic interactions and the magnitude of biomass change in the system. Under both types of forcing, all indices were greatest when vulnerabilities were high. Although the overall difference between balancing approaches (index 1) was smallest when fishing mortality was doubled (Figure 2.3), the effect of

balancing when expressed relative to the overall change in biomass (index 3) was greatest (Table 2.5). This occurred because changes in relative biomass were small when fishing mortality was doubled (Figure 2.4), and therefore differences between the two balancing approaches were also small in absolute terms (Figure 2.3). When expressed relative to the change in biomass, however, the effect of these differences appeared greater (Figure 2.5). In other words, when small changes to biomass occurred in the system, the effect of changes produced by differences in balancing becomes more important. Based on these results, we conclude that the way in which our Ecopath model was balanced most affected model conclusions when vulnerabilities were high and when biomass dynamics in the system were stable.

The significance of our results remains difficult to determine. Although the effect of balancing is different among the six scenarios, and influenced by whether absolute or relative effects were considered, the question remains; "Is a 41% effect important?". Based on our results, the answer to this questions appears to be no. Under scenarios with greater biomass change (i.e. environmental productivity was doubled) the absolute difference between balancing approaches was at most 1.15 (Figure 2.3). When put into the context of the overall change in biomass, the difference between balancing approaches was 3.5% (Table 2.5). Although a 41% effect is greater than a 3.5% effect, the overall change in biomass when fishing mortality was doubled was at most 1.08 and therefore small in absolute terms (Figure 2.4). We understand that our findings reflect a single ecosystem, and that other ecosystems may have greater changes in biomass, or require more contrast between balancing approaches when modeled. Additional comparisons would be helpful to determine the significance of these results, and whether the general patterns we indentify hold.

Indices for some individual species (i.e. not averaging over i groups) were larger than those when averaging over all groups. Age 0 lake whitefish, *Diporeia*, age 0 alewife, age 0.5 Chinook salmon, and dreissenids were often the groups with the greatest values in various scenarios. Biomass dynamics of age 0 alewife and age 0.5 Chinook salmon were highly oscillatory when vulnerabilities were low. A similar pattern existed for age 0 lake whitefish at all vulnerabilities when environmental productivity was doubled, and can also be seen for age 4+ lake whitefish (Figure 2.5). A slight shift in phase for oscillating biomass trajectories inflated the difference between the two balancing approaches, and thus these indices were large. Similarly, as biomass dynamics from either balancing approach neared zero, the differences between the two approaches increased greatly. This occurred for dreissenids, and to a lesser extent ninespine stickleback (Figure 2.5), when vulnerabilities were high and environmental productivity was doubled. Although biomass dynamics for ninepsine stickleback did approach zero briefly, the large effect of balancing was likely because of high predation mortality by lake whitefish. Under high vulnerabilities, oscillations in lake whitefish biomass likely amplified oscillations in ninespine stickleback biomass.

Ecopath metrics were less informative in determining the effects of balancing on model results than indices within Ecosim. Of the two Ecopath metrics that were used, ascendency changed the most. Values of ascendency for both models were within the range (approximately 1000-10,0000) of those for 41 other Ecopath models (Christensen 1994), and similar to Lake Superior (5221.3; Kitchell et al. 2000) and Lake Ontario (25,630; Halfon and Schito 1993). Christensen (1994) found that ascendency was highly correlated with total system throughput, which is a measure of ecosystem size. Because production by lower trophic-level groups was increased in the "consumption-based" approach, and consumption of higher trophic-level groups

was decreased in the "production-based" approach, the sizes of the models balanced by the two approaches were expected to be different. However, much of the difference in size was due to differences in biomass of planktonic and detrital groups. Although the sizes of the Lake Huron models were different, the values for SOI were very similar. This was likely because SOI is a metric for consumers, and thus does not account for differences in biomass estimates of phytoplankton and detritus, which were substantial. The values of SOI for Lake Huron were between those for Lake Ontario (0.0633; Halfon and Schito 1993) and Lake Superior (0.108; Kitchell et al. 2000), and less than two models of the Bay of Quinte in Lake Ontario (0.114 and 0.147; Koops et al. 2006).

Effect of vulnerabilities

Vulnerability parameters influenced the effect of balancing on Ecosim results. Values for each index were greatest under scenarios with high vulnerabilities, and smallest under scenarios with low vulnerabilities. When vulnerabilities are high, the effect that a predator can have on its prey is greater, and small changes to predator biomass can cause large changes in the biomass of their prey. It makes sense then that differences in biomass dynamics between the balanced models would be amplified when vulnerabilities were high. Vulnerabilities are known to influence results when exploring management scenarios within Ecosim (Cox and Kitchell 2004), but have not previously been examined for their influence on balancing.

Vulnerabilities are commonly associated with the type of control in the food web, either top-down, bottom-up, or a combination of the two. Because high vulnerabilities reflect top-down control, Ecopath models of systems where predators control overall dynamics would be most affected by the way in which balancing is achieved. There is no consensus on the type of control

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operating in Great Lakes food-webs (Bence et al. 2008). Lake trout were historically the top-piscivore within the Great Lakes and were believed to exert strong top-down control on the food web (Ryder et al. 1981). Through a combination of increased fishing mortality and predation mortality from the invasive sea lamprey, lake trout were nearly extirpated from the Great Lakes (Eshenroder et al. 1995). Ongoing stocking of introduced Pacific salmonines and lake trout has increased the number of species occupying top trophic levels in several Great Lakes and has raised concerns about levels of consumption (Dobiesz et al. 2005; Jones et al. 1993). This concern continues today, especially given the high level of wild Chinook salmon recruitment in Lake Huron (Johnson et al. 2010) and because predation by salmonines was found to be an important factor in alewife recruitment in Lake Michigan (Madenjian et al. 2005). Evidence of top-down control also exists at lower trophic levels. Increased predation mortality by predatory zooplankton has been suggested by Bunnell et al. (2011) to have caused declines in zooplankton abundance in Lake Huron (Barbiero et al. 2009).

Bottom-up control has also been hypothesized as a driver of recent changes in Lake Huron. Dreissenid mussels, which are hypothesized to remove nutrients from the offshore community and bind them in nearshore areas (Hecky et al. 2004) have been implicated in the decline of *Diporeia* (Nalepa et al. 2007) and consequently the reduction in lake whitefish growth (Pothoven and Madenjian 2008). The clearing of the water column by mussels has also been suggested as a possible driver for large declines in cladoceran zooplankton biomass (Barbiero et al. 2009; 2011). Significant declines in primary production have been observed in Lake Michigan (Fahnenstiel et al. 2010) and Lake Erie (Depew et al. 2001), and both have been attributed to filtering of dreissenids. The declines in zooplankton are implicated in the decline in the abundance of alewife as well as other deepwater prey-fish in Lake Huron (Riley et al. 2008).

Consequently, community dynamics within Lake Huron are likely a combination of top-down and bottom-up control.

Model imbalance

A common observation in Ecopath models is that based on initial input values, consumption of intermediate and lower-trophic groups often exceeds production by those groups, and that various adjustments must be made to achieve mass balance. The model presented here supports these observations. Stewart and Sprules (2011) discuss trophic imbalances in an Ecopath model of Lake Ontario and compare this to observations from stream ecology (see Huryn 1996). An informal poll of other EwE modelers revealed that they had imbalances in the lower-trophic groups in their models. Apart from Stewart and Sprules (2011), little has been discussed in the EwE literature about whether these common observations reveal a larger issue with the modeling framework or with sampling of aquatic ecosystems in general.

If intermediate and lower trophic-level groups are commonly overconsumed in Ecopath models, it makes sense to discuss possible reasons for why this should occur. An obvious reason is uncertainty in input parameters. A critical assumption of sampling is that it is both spatially and temporally representative of the system being modeled. Biomass estimates of prey fish were taken from area-swept methods based on bottom trawl surveys. These surveys are best suited for benthopelagic species, and are likely to underestimate biomass of benthic species, such as deepwater and slimy sculpins, and pelagic species such as rainbow smelt (Riley et al. 2008). Comparisons with acoustic surveys however, suggest that trawl estimates are generally similar (Roseman and Riley 2009; Warner et al. 2009). Biomass estimates of phytoplankton were taken within the top 20 m of the water column and therefore ignored the contribution in the deep

chlorophyll layer, which has been estimated to provide a substantial contribution to primary production (Barbiero and Tuchman 2001b). Biomass estimates of zooplankton were taken from surveys done once in August, which likely captured a peak in consumptive demand on phytoplankton (Barbiero et al. 2009). Increasing biomass of benthic and pelagic fish and phytoplankton (Table 2.3), or decreasing biomass of zooplankton (Table 2.4) addressed some model imbalances as reflected by the two balancing approaches.

Although spatial and temporal constraints on sampling can be addressed by more representative techniques, there still exist challenges that may contribute to imbalances when combining parameter estimates into a single model. Often, the offshore zone is less productive than the nearshore, although some studies have found the opposite (Depew et al. 2001). Estimates taken only from offshore sites ignore the greater contribution of food resources provided in the nearshore zone. Consequently, resources are available to predators in the system that are not included in an offshore model. In addition, predators rarely feed within an average area of a system, so predation is likely to be concentrated in areas were food resources are at their highest. Thus, although a sampler sees an average value of food availability, a predator may see an above-average value.

Subjective balancing

We elected to balance the Ecopath model using the subjective balancing procedure, despite the ease at which balancing can be reproduced by the objective procedure (Kavanagh et al. 2004). Although two different objective functions could have been used to perform the analyses for this research, we chose to balance the model in ways with more biological appeal. Initial discussions with Lake Huron biologists about ways to address model imbalance often

focused on increasing production or decreasing consumption, and thus were used as the two approaches. While subjectively balancing the model, problems in the modeling of diet contributions were found such as the consumption of bloater eggs being attributed as age 0 bloater, and consumption of slimy sculpin by age 1+ rainbow smelt. These balancing problems could have also been noticed when using the objective procedure, however, because changes can be made automatically within the software it does not assist in their possible discovery.

Conclusions

Estimates used to parameterize Ecopath models commonly result in imbalance. The process of balancing an Ecopath model is rarely described in the literature, especially with respect to its effect on simulations in Ecosim. This research assessed the effect of contrasting but realistic approaches to balancing on biomass dynamics in Ecosim and ecosystem metrics in Ecopath. Indices in Ecosim were more informative at assessing differences between balancing approaches than were metrics in Ecopath. The difference in biomass dynamics between the two balancing approaches was greatest when control of the ecosystem was top-down, providing further evidence that vulnerabilities are important parameters in Ecosim. The effect of balancing was also greatest when changes in biomass caused by other perturbations in the model were small. We encourage EwE modelers to consider the sensitivity of their models to balancing when dynamics within their system are stable through time or when top-down control is expected, but otherwise to focus their efforts on understanding the sensitivity of model results to vulnerability parameters rather than alternative ways to achieve mass balance.

APPENDICES

APPENDIX 2A

Tables and Figures

Table 2.1: Names of species (with scientific names) or groups of species that were included in the Ecopath model, and their corresponding group numbers. Specific age stanzas are listed for groups modeled with age structure.

Group name	Scientific Name	Group number
Sea lamprey	*Petromyzon marinus*	1
Lake whitefish	*Coregonus clupeaformis*	
age 0, age 1-3, age 4+		2, 3, 4
Lake trout	*Salvelinus namaycush*	
age 0, age 1, age 2-4, age 5+		5, 6, 7, 8
Chinook salmon	*Oncorhynchus tshawytscha*	
age 0, age 0.5, age 1-5, age 6+		9, 10, 11, 12
Steelhead	*Oncorhynchus mykiss*	
age 0, age 1, age 2-5, age 6+		13, 14, 15, 16
Burbot	*Lota lota*	
age 0-3, age 3+		17, 18
Alewife	*Alosa pseudoharengus*	
age 0, age 1+		19, 20
Rainbow smelt	*Osmerus mordax*	
age 0, age 1+		21, 22
Bloater	*Coregonus hoyi*	
age 0, age 1+		23, 24
Round Goby	*Neogobius melanostomus*	25
Slimy sculpin	*Cottus cognatus*	26
Deepwater sculpin	*Myoxocephalus thompsoni*	27
Ninespine Stickleback	*Pungitius pungitius*	28
Diporeia	*Diporeia spp.*	29
Mysis	*Mysis diluviana*	30
Benthic invertebrates		31
Dreissenid mussels	*Dreissena polymorpha*	32
	Dreissena bugensis	
Predatory zooplankton	*Bythotrephes longimanus*	33
Zooplankton		34
Phytoplankton		35
Detritus		36

Table 2.2: Contributions of prey (rows) to the diet of predators (columns) from the model balanced with the "consumption-based" approach. When changed, initial contributions are provided in parenthesis and bolded. Numbers in the leading row and column correspond to group numbers provided in Table 2.1. Groups not preyed on, or predators that fed outside the system are not shown.

		Predator group numbers												
		1	2	3	4	6	7	8	10	11	14	15	17	18
Prey group numbers	2												0.004	0.015
	4	0.05												
	6							0.01 (0.029)						
	8	0.50												
	11	0.20												
	15	0.10												
	18	0.10												
	19					0.44	0.54	0.16	0.66 (0.19)		0.37	0.15 (0)	0.16	
	20						0.28	0.70		0.74		0.50 (0.85)		0.26
	21					0.50	0.08		0.19 (0.81)		0.03			
	22						0.04	0.031 (0.012)		0.26 (0.24)		0.32 (0.09)	0.14	0.35
	23						0.015							
	24	0.05					0.015	0.083						0.03
	25			0.001 (0.032)										
	26					0.03	0.009	0.005				0.005 (0.03)	0.04 (0.115)	0.02 (0.06)
	27					0.025	0.018	0.011					0.19 (0.115)	0.10 (0.06)
	28			0.005 (0.01)	0.005 (0.048)	0.01				0.01 (0.03)			0.004	0.004
	29			0.015 (0.01)	0.074 (0)									
	30		0.02	0.06			0.003							

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Table 2.2 (cont'd)

31		0.11	0.36	0.34				0.15 **(0)**		0.60	0.03	0.40	0.19
32			0.24	0.56								0.07	0.031
33			0.12	0.02									
34		0.87	0.20										
35													
36													

Table 2.2 (cont'd)

Prey group numbers		Predator group numbers														
		19	20	21	22	24	25	26	27	28	29	30	31	32	33	34
	2															
	4															
	6															
	8															
	11															
	15															
	18															
	19				0.01											
	20															
	21				0.05 **(0.18)**											
	22															
	23							0 **(0.064)**	0 **(0.057)**	0 **(0.02)**						
	24															
	25															
	26				0 **(0.09)**											
	27							0 **(0.064)**	0 **(0.057)**							
	28															
	29	0.035	0.09	0.065	0.20	0.095	0.024	0.72 **(0.63)**	0.37 **(0.32)**	0.65		0.03				
	30	0.21	0.31	0.18	0.56 **(0.28)**	0.40	0.009	0.17 **(0.15)**	0.62 **(0.55)**	0.22						
	31	0.015	0.02	0.015	0.02	0.004	0.034	0.11	0.011	0.026			0.05			
	32						0.93									
	33	0.13	0.05	0.006	0.02 **(0.017)**		0.005									

Table 2.2 (cont'd)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
34	0.61	0.53	0.73	0.14	0.50				0.10		0.67			1.0	0.05
35										0.01	0.30		0.30 **(0.51)**		0.95
36										0.99		0.95	0.70 **(0.49)**		

Table 2.3: Parameter values from the Ecopath model balanced with the "consumption-based" approach. Proportional adjustments from initial parameter estimates that were changed are in parentheses and bolded. Names of group numbers are provided in Table 2.1.

Group number	B (g/m2)	P/B (/yr)	Q/B (/yr)	EE	Harvest (g/m2)
1	0.000470	0.860	16.0	0	
2	0.0116	2.00	18.4	0.09	
3	0.464	0.355	5.09	0	
4	0.96	0.500	2.80	0.19	0.090
5	0.000398	0.00100	13.2	0	
6	0.00363	0.410	6.91	0.72	
7	0.00782	0.330	4.81	0.30	0.001
8	0.0318	0.600	3.35	0.53	0.006
9	0.00167	0.00100	27.1	0	
10	0.0101	3.60	14.2	0	
11	0.0500	1.40	6.22	0.29	0.019
12	0.000321	1.40	3.48	0	
13	0.00166	0.00100	16.5 (**0.75**)	0	
14	0.0122	0.500	9.16 (**0.75**)	0	
15	0.142	0.106	5.50 (**0.75**)	0.10	0.001
16	0.475	0.106	4.49 (**0.75**)	0	
17	0.00357	0.745	5.02	0	
18	0.0647	0.149	2.00	0.08	
19	0.263	4.00	33.7	0.31	
20	0.667	1.25	13.6	0.88	
21	0.0751	2.64	12.9	0.77	
22	0.462	1.17	4.60	0.70	
23	0.0147	2.33	31.9	0.02	
24	0.309	1.02	8.60	0.06	0.004
25	0.0096 (**2**)	0.640	4.70	0.44	
26	0.0113 (**2.5**)	1.00 (**1.18**)	7.50 (**0.63**)	0.78	
27	0.117	0.850 (**1.42**)	7.50 (**0.75**)	0.19	
28	0.0240 (**2**)	1.77	12.0	0.66	
29	14.7	1.43	25.0	0.25	
30	3.53	2.80	25.0	0.80	
31	3.92	2.50	8.60	0.40	
32	11.0	0.315	8.60	0.60	
33	0.610	10.0	86.0	0.33	
34	67.8	26.3	110	0.28	
35	23.8 (**3**)	365 (**1.31**)		0.82	
36	147			0.08	

Table 2.4: Parameter values from the Ecopath model balanced with the "production-based" approach. Proportional adjustments from initial parameter estimates that were changed are in parentheses and bolded. Names of group numbers are provided in Table 2.1.

Group number	B (g/m2)	P/B (/yr)	Q/B (/yr)	EE	Harvest (g/m2)
1	0.000470	0.860	16.0	0	
2	0.00886 (**0.75**)	2.00	13.8 (**0.75**)	0.06	
3	0.348 (**0.75**)	0.355	3.82 (**0.75**)	0	
4	0.72 (**0.75**)	0.500	2.10 (**0.75**)	0.25	0.090
5	0.000398	0.00100	13.2	0	
6	0.00363	0.410	6.91	0.72	
7	0.00782	0.330	4.81	0.30	0.001
8	0.0318	0.600	3.35	0.53	0.006
9	0.00125 (**0.75**)	0.00100	20.3 (**0.75**)	0	
10	0.00756 (**0.75**)	3.60	10.6 (**0.75**)	0	
11	0.0375 (**0.75**)	1.40	4.66 (**0.75**)	0.39	0.019
12	0.000241 (**0.75**)	1.40	2.61 (**0.75**)	0	
13	0.000832 (**0.5**)	0.00100	16.5 (**0.75**)	0	
14	0.00611 (**0.5**)	0.500	9.16 (**0.75**)	0	
15	0.0710 (**0.5**)	0.106	5.50 (**0.75**)	0.20	0.001
16	0.238 (**0.5**)	0.106	4.49 (**0.75**)	0	
17	0.00179 (**0.5**)	0.745	5.02	0	
18	0.0324 (**0.5**)	0.149	2.00	0.16	
19	0.263	4.00	33.7	0.17	
20	0.667	1.25	13.6	0.63	
21	0.0751	2.64	12.9	0.70	
22	0.462	1.17	4.60	0.22	
23	0.0147	2.33	31.9	0.02	
24	0.309	1.02	8.60	0.05	0.004
25	0.00480	0.630	4.70	0.50	
26	0.00450	1.00 (**1.18**)	7.50 (**0.63**)	0.78	
27	0.117	0.850 (**1.42**)	7.50 (**0.75**)	0.11	
28	0.0120	1.77	12.0	0.90	
29	14.7	1.43	25.0	0.24	
30	3.53	2.80	25.0	0.79	
31	3.92	2.50	8.60	0.32	
32	11.0	0.315	8.60	0.34	
33	0.610	10.0	86.0	0.31	
34	16.8 (**0.25**)	26.3	100 (**0.91**)	0.48	
35	7.94	278		0.75	
36	80.6			0.27	

Table 2.5: Values of index 3 for each scenario. Index 3 is the percentage change in biomass due to balancing, averaged across all groups, relative to the percentage change in biomass due to other sources, averaged across all groups. Ranges of values for individual groups are provided in parentheses. Details of vulnerabilities and forcing type are explained in Figure 2.2.

Vulnerabilities	Forcing type	Index 3 (%) (range)
Low	Environ	0.059 (0.00-12.7)
Med	Environ	1.40 (0.11-8.65)
High	Environ	3.46 (0.19-70.0)
Low	Fishing	21.1 (0.00-119)
Med	Fishing	23.1 (0.00-203)
High	Fishing	41.3 (1.79-170)
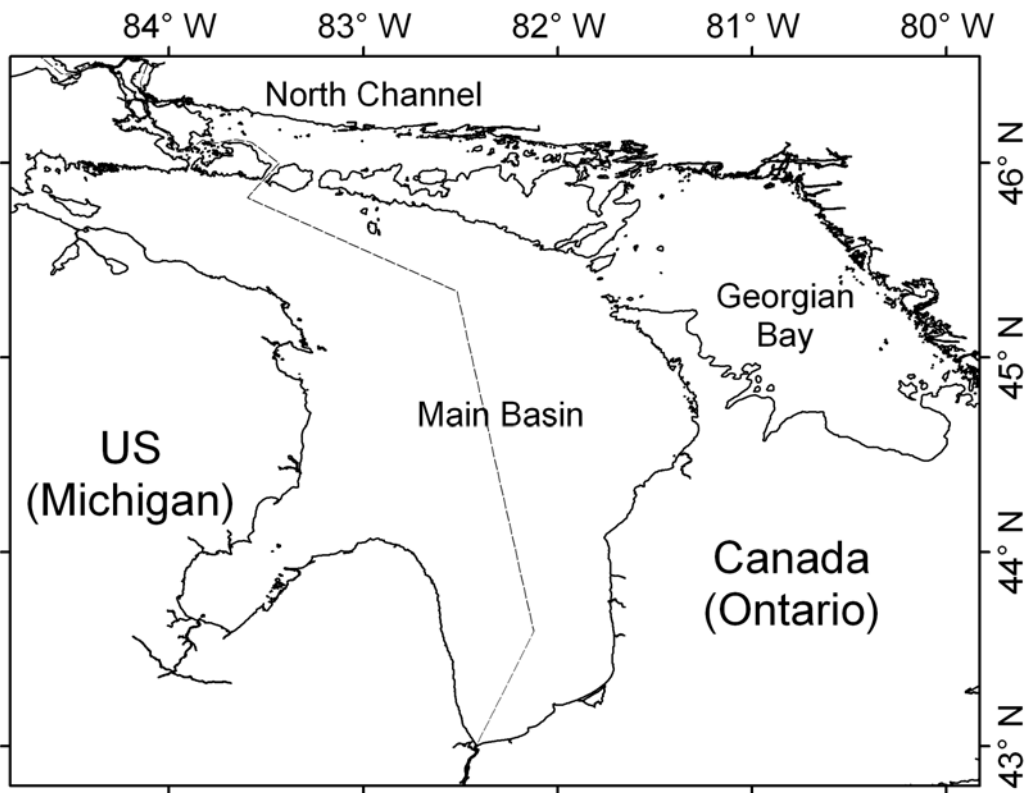
Figure 2.1: Map of Lake Huron with neighboring countries and lake basins labeled.
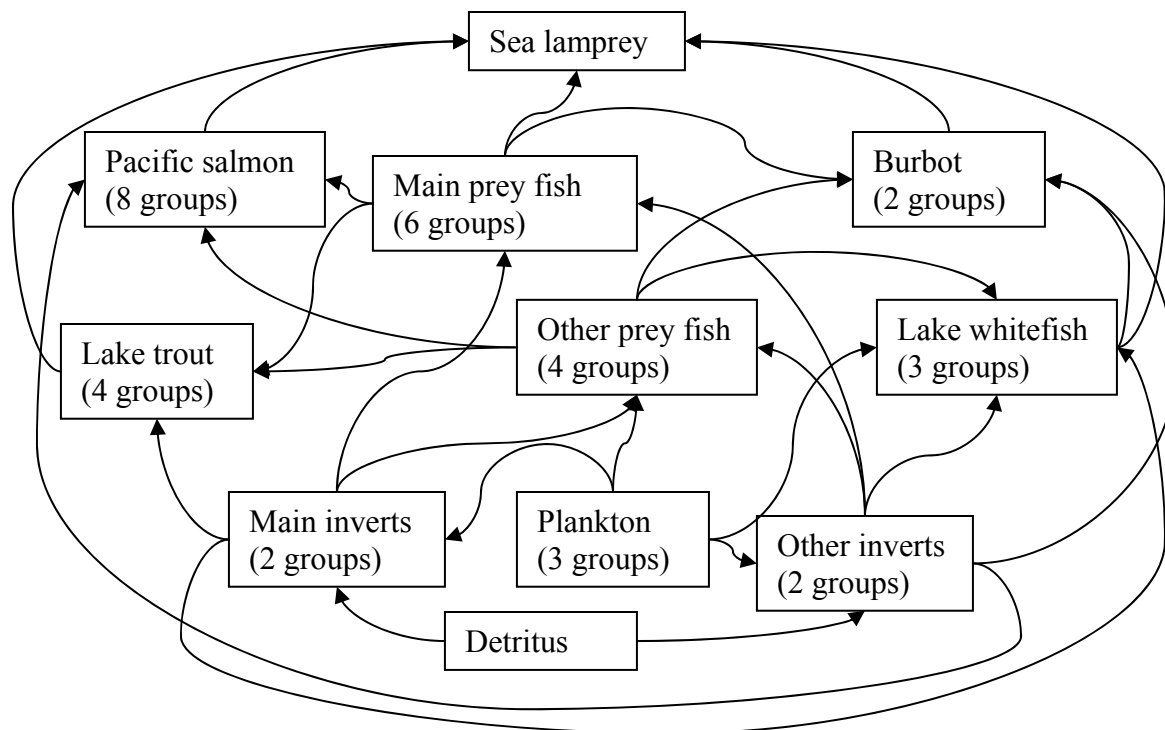
Figure 2.2: Simplified food-web of the offshore community in the main basin of Lake Huron. "Pacific salmon" represent groups 9-16 in Table 2.1, "Main prey fish" groups 19-24, "Other prey fish" groups 25-28, "Main inverts" groups 29-30, "Other inverts" groups 31-32, and "Plankton" groups 33-35.
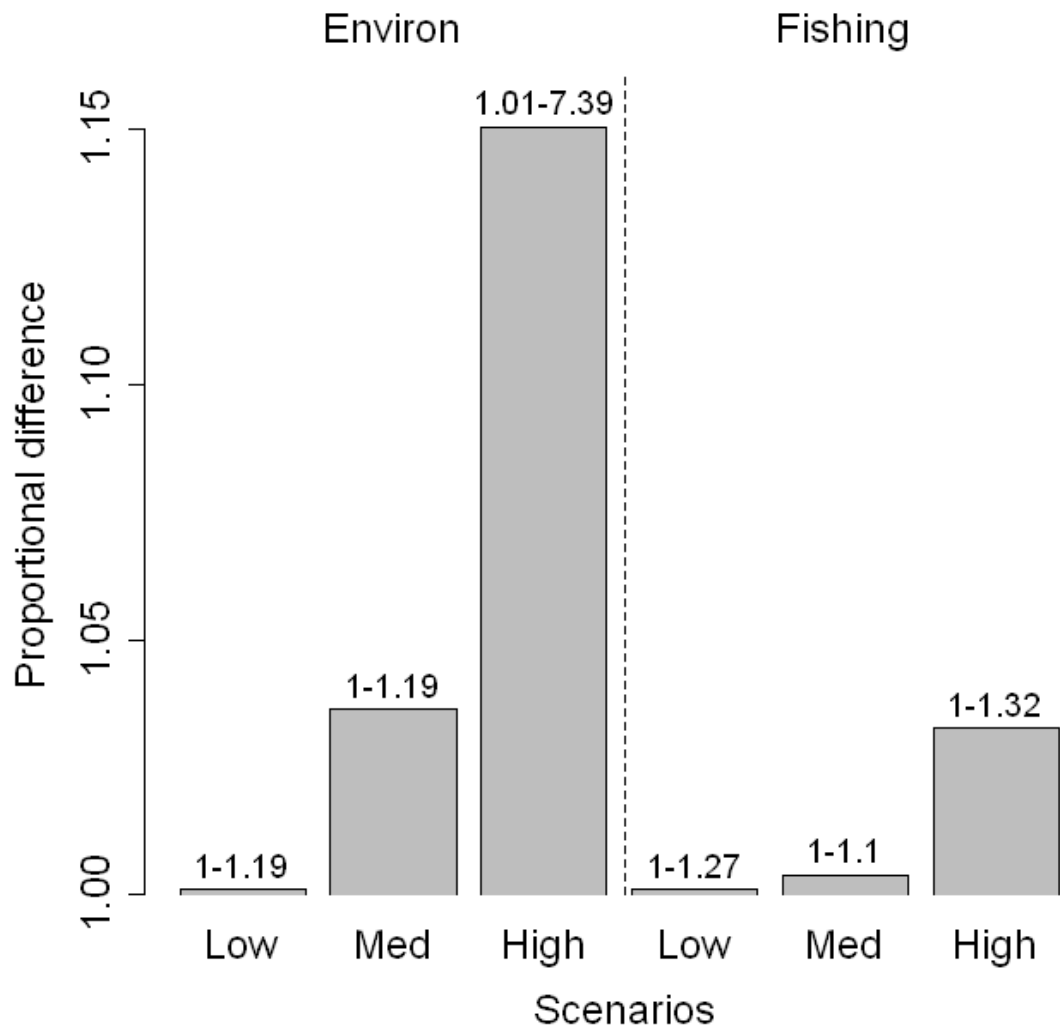
Figure 2.3: Median proportional differences in biomass between the two balancing approaches taken across groups and 40 years of simulation (index 1) for each of six scenarios. Values above the bars reflect the range of proportional differences over groups. "Low", "med", and "high" represent the magnitudes of trophic interactions (vulnerabilities) used in each scenario (1.01, 2, and 10, respectively). "Environ" and "Fishing" represent scenarios where environmental productivity was doubled and fishing mortality was doubled, respectively. The vertical dashed lines separates scenarios between "Environ" and "Fishing".
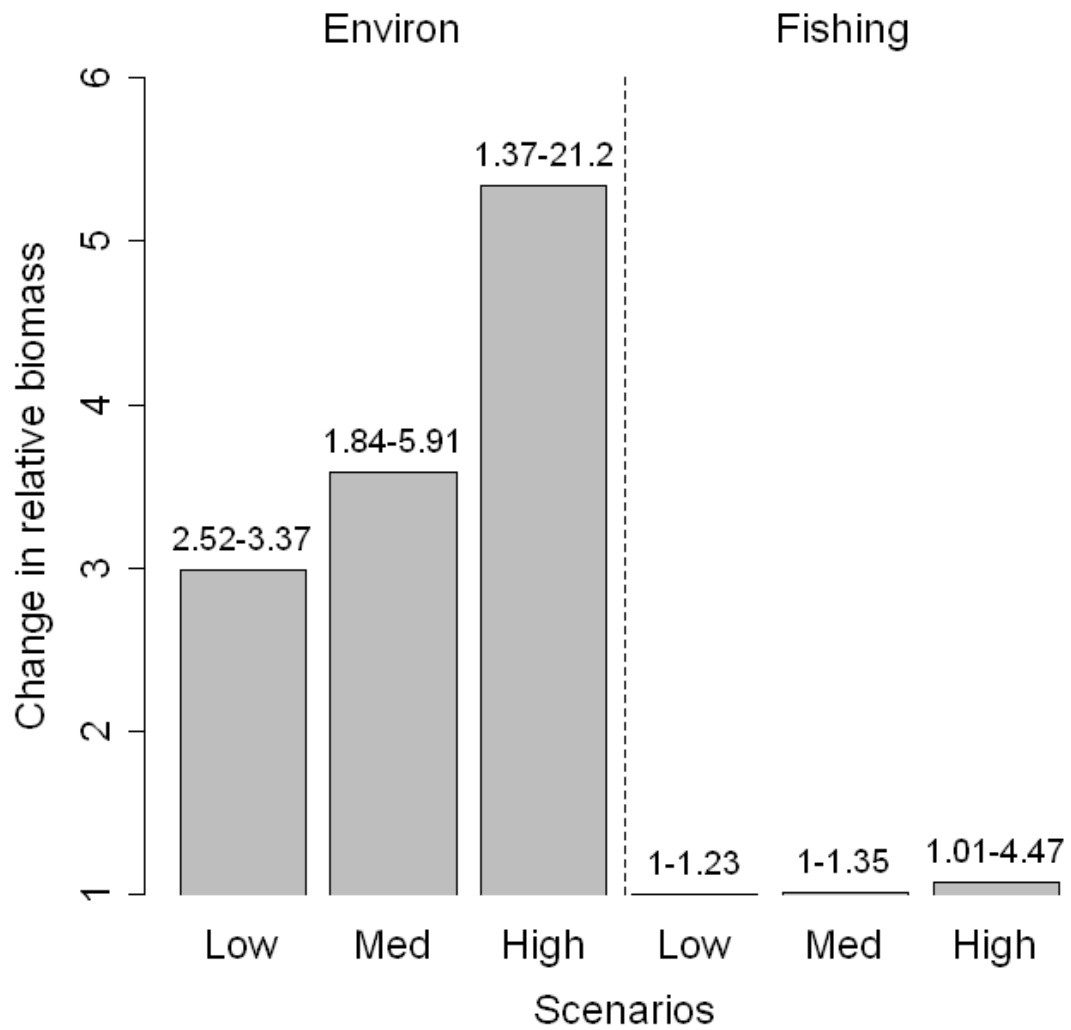
Figure 2.4: Median change in relative biomass taken across groups, 40 years of simulation, and balancing approach for each of six scenarios. Values above the bars reflect the range of proportional differences over groups. Details of each scenario are explained in Figure 2.2.
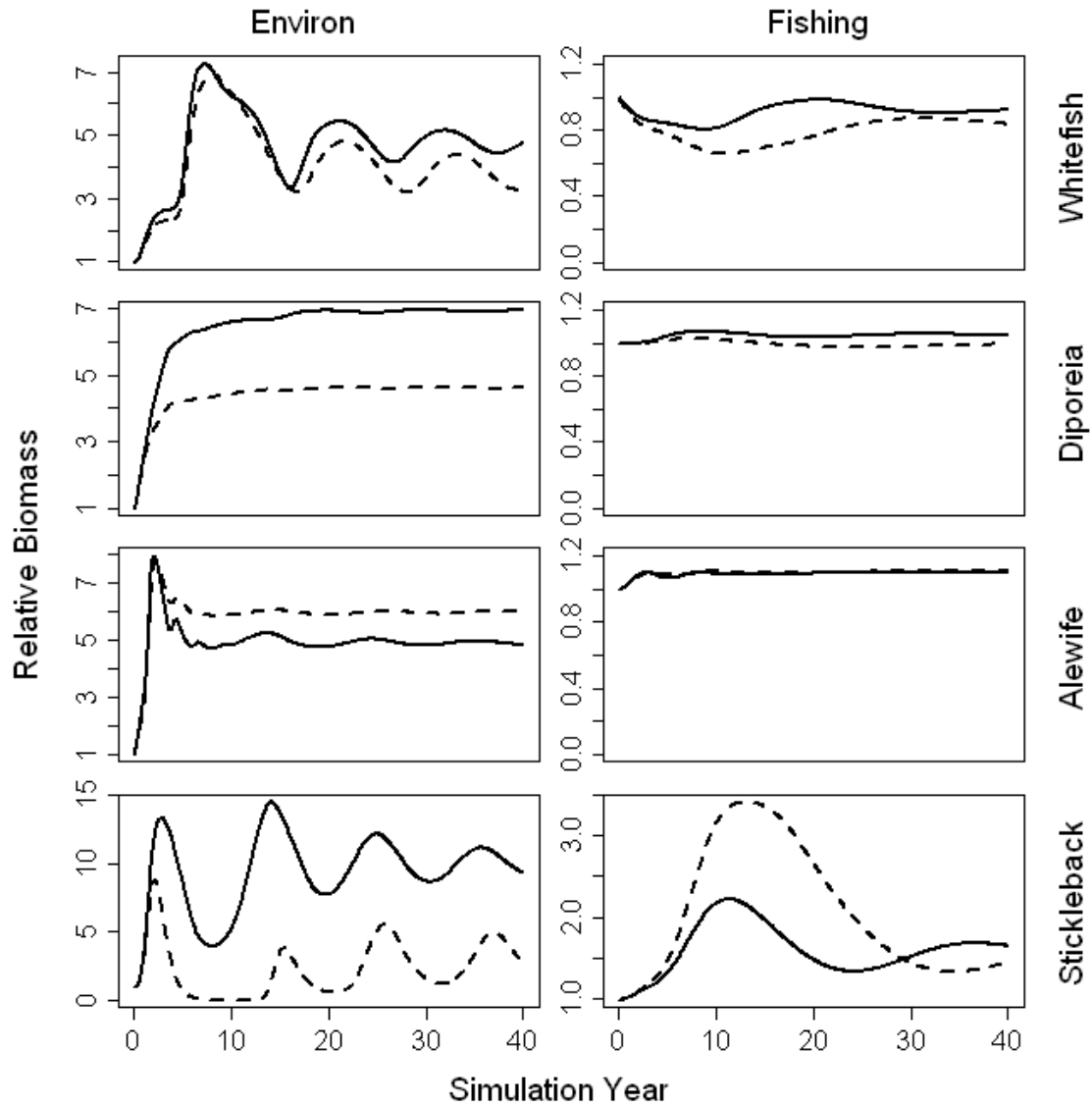
Figure 2.5: Relative biomass for 40 years of simulation from the "consumption-based" (solid line) and "production-based" (dashed line) balancing approaches for age 4+ lake whitefish, *Diporeia*, age 1+ alewife, and ninespine stickleback, under high vulnerabilities and environmental (Environ) and fishing (Fishing) forcing types. Note the different scales.

APPENDIX 2B

Explanation of data input used in the Ecopath model

Table 2.6: Sources of data for biomass (B), production to biomass (P/B) and consumption to biomass (Q/B) ratios, diet, and when appropriate commercial or recreational harvest inputs. Von Bertalanffy growth coefficients (K) and age of 50% maturity (Amat) are given for multistanza groups. When applicable, location of data is listed, LH = Lake Huron, LM = Lake Michigan, LS = Lake Superior, LE = Lake Erie, LO = Lake Ontario, and RE = estimates taken from published regression relationships. Group numbers (#) for pre-stocking stanzas for lake trout (5), Chinook salmon (9), and steelhead (13), as well as age 6+ stanzas for Chinook salmon (12) and steelhead (16) are not included. Names of group numbers are provided in Table 2.1.

#	Input	Data description	Years	Source
1	B	LH number of spawners	1999	Mike Siefkes (Great Lakes Fishery Commission, pers. comm.)
		Survival of parasite to spawning = 0.75		Jones et al. (2009)
		Average wet weight (WW) of parasitic phase		Bergstedt and Swink (1994)
	P/B	LM ecopath model estimate		Ann Krause (University of Toledo-UT, pers. comm.)
	Q/B	Great Lakes bioenergetics study		Madenjian et al. (2003)
	Diet	LM ecopath model estimate		Ann Krause (UT, pers. comm.)
2	P/B	Assumed value		
	Diet	LH spring-summer sampling	2000, 2003	Nalepa et al. (2009)
3	P/B	LH Ontario catch-at-age (SCA) models	1999	Adam Cottrill (Ontario Ministry of Natural Resources-OMNR, pers. comm.)
		LH 1836 treaty waters SCA models	1999	Ebener et al. (2005), Modeling subcommittee (2009)
	Diet	LH spring summer sampling	2000, 2003	Nalepa et al. (2009)
	Harvest	LH Ontario catch-at-age (SCA) models	1999	Adam Cottrill (OMNR, pers. comm.)
		LH 1836 treaty waters SCA models	1999	Ebener et al. (2005), Modeling subcommittee (2009)
4	B	LH Ontario catch-at-age (SCA) models	1999	Adam Cottrill (OMNR, pers. comm.)
		LH 1836 treaty waters SCA models	1999	Ebener et al. (2005), Modeling subcommittee (2009)
	P/B	LH Ontario catch-at-age (SCA) models	1999	Adam Cottrill (OMNR, pers. comm.)
		LH 1836 treaty waters SCA models	1999	Ebener et al. (2005), Modeling subcommittee (2009)
	Q/B	Bioenergetics on laboratory fish		Madenjian et al. (2006b)
	Diet	LH spring summer sampling	2000, 2003	Nalepa et al. (2009)

Table 2.6 (cont'd)

	Harvest	LH	Ontario catch-at-age (SCA) models	1999	Adam Cottrill (OMNR, pers. comm.)
		LH	1836 treaty waters SCA	1999	Ebener et al. (2005), Modeling subcommittee (2009)
	K	LH	Canadian index sampling = 0.229	1999-2008	Adam Cottrill (OMNR, pers. comm.)
	Amat	LH	Canadian index sampling = 6 yrs	1999-2008	Adam Cottrill (OMNR, pers. comm.)
6	P/B	LH	SCA models	1999	Ji He (Michigan Department of Natural Resources-MDNR, pers. comm.)
	Diet	LH	bioenergetics model	1984-1998	Dobiesz (2003)
7	P/B	LH	SCA models	1999	Ji He (MDNR, pers. comm.)
	Diet	LH	offshore spring/summer diet	1998-2003	Madenjian et al. (2006a)
	Harvest	LH	SCA models	1999	Ji He (MDNR, pers. comm.)
8	B	LH	SCA models	1999	Ji He (MDNR, pers. comm.)
	P/B	LH	SCA models	1999	Ji He (MDNR, pers. comm.)
	Q/B	LH	bioenergetics model	1998	Dobiesz (2003)
	Diet	LH	offshore spring/summer diet	1998-2003	Madenjian et al. (2006a)
	Harvest	LH	SCA models	1999	Ji He (MDNR, pers. comm.)
	K	LH	sampling = 0.303	1975-2007	Ji He (MDNR, pers. comm.)
	Amat	LH	SCA models = 7 yrs	1984-2008	Ji He (MDNR, pers. comm.)
10	P/B	LH	stocking model	1999	Travis Brenden (Michigan State University–MSU, pers. comm.)
	Diet	LM	spring-fall diet	1973-1982	Jude et al. (1987)
11	B	LH	stocking model	1999	Travis Brenden (MSU, pers. comm.)
	P/B	LH	stocking model	1999	Travis Brenden (MSU, pers. comm.)
	Q/B	LH	bioenergetics model	1998	Dobiesz (2003)
	Diet	LH	spring-fall diets	1984-1998	Dobiesz (2003)
	Harvest	LH	US recreational and tribal commercial harvest estimates	1999	Jim Johnson (MDNR, pers. comm.)
	K	LH	stocking model = 0.37		Travis Brenden (MSU, pers. comm.)
	Amat		Assumed value = 3 yrs		
14	P/B	LH	stocking model	1999	Travis Brenden (MSU, pers. comm.)
	Diet	LM	spring-fall diet	1973-1982	Jude et al. (1987)
15	B	LH	stocking model	1999	Travis Brenden (MSU, pers. comm.)
	P/B	LH	stocking model	1999	Travis Brenden (MSU, pers. comm.)

Table 2.6 (cont'd)

	Q/B	LM bioenergetics study	1978-1988	Stewart and Ibarra (1991)
	Diet	LM spring-fall diet	1973-1982	Jude et al. (1987)
	Harvest	LH US recreational estimates	1999	Jim Johnson (MDNR, pers. comm.)
	K	LH stocking model = 0.466		Travis Brenden (MSU, pers. comm.)
	Amat	Assumed value = 3 yrs		
17	P/B	LH bioenergetics model	1998	Dobiesz (2003)
	Diet	LH bioenergetics model	1984-1998	Dobiesz (2003)
18	B	LH bioenergetics model	1998	Dobiesz (2003)
	P/B	LH bioenergetics model	1998	Dobiesz (2003)
	Q/B	LH bioenergetics model	1998	Dobiesz (2003)
	Diet	LH bioenergetics model	1984-1998	Dobiesz (2003)
	K	LH sampling = 0.238	1987-2008	Ji He (MDNR, pers. comm.)
	Amat	Assumed value = 3 yrs		
19	P/B	LM bioenergetics model	1987	Rand et al. (1995)
	Diet	LM spring-fall diet study	1998-2004	Pothoven and Madenjian (2008)
20	B	LH bottom trawl estimates with fishing power correction (FPC)	1999	Stephen Riley (United State Geological Survey-USGS, pers. comm.)
	P/B	LM bioenergetics model	1987	Rand et al. (1995)
	Q/B	LM bioenergetics model	1987	Rand et al. (1995)
	Diet	LM spring-fall diet study	1998-2004	Pothoven and Madenjian (2008)
	K	LH index survey = 0.625	1999-2004	Adam Cottrill (OMNR, pers. comm.)
	Amat	Assumed value = 2 yrs		
21	P/B	LH bioenergetics model	late 1980s	Lantry and Stewart (1993)
	Diet	LH bioenergetics model	late 1980s	Lantry and Stewart (1993)
22	B	LH bottom trawl estimates with FPC	1999	Stephen Riley (USGS, pers. comm.)
	P/B	LH bioenergetics model	late 1980s	Lantry and Stewart (1993)
	Q/B	LH bioenergetics model	late 1980s	Lantry and Stewart (1993)
	Diet	LH bioenergetics model	late 1980s	Lantry and Stewart (1993)
	K	LH bioenergetics model = 0.477	late 1980s	Lantry and Stewart (1993)

Table 2.6 (cont'd)

	Amat	Assumed value = 2 yrs	
23	P/B	LM bioenergetics model	1987	Rand et al. (1995)
	Diet	LM fall diet study	1979-1980	Crowder and Crawford (1984)
24	B	LH bottom trawl estimates with FPC	1999	Stephen Riley (USGS, pers. comm.)
	P/B	LM bioenergetics model	1987	Rand et al. (1995)
	Q/B	LM bioenergetics model	1987	Rand et al. (1995)
	Diet	LM august sampling	1995-1996	TeWinkel and Fleischer (1999)
	Harvest	LH fishery harvests	1999	Baldwin et al. (2002)
	K	LH Canadian index sampling = 0.147	1999-2008	Adam Cottrill (OMNR, pers. comm.)
	Amat	Assumed value = 2 yrs	
25	B	LH bottom trawl estimates with FPC	1999	Stephen Riley (USGS, pers. comm.)
	P/B	RE estimates		Pauly (1980)
		Lmax = 11.8 from Detroit River	1996	MacInnis and Corkum (2000)
		K = 0.4 from Detroit River	1996	Fishbase (www.fishbase.org)
		T = 6 from LH SCA model for group 8		Ji He (MDNR, pers. comm.)
	Q/B	LE bioenergetics study	2000-2001	Lee and Johnson (2005)
	Diet	LH fall diet study by number	2000-2001	Schaeffer et al. (2005)
		WW for zooplankton		Hawkins and Evans (1979)
		WW for benthic invertebrates		Nalepa and Quigley (1980), Nalepa et al. (2002)
		WW for dreissenids		Mills et al. (1999)
		WW for *Diporeia*		Landrum (1988)
		WW for *Mysis*		Sell (1982)
		WW for *Bythotrephes*		Barbiero and Tuchman (2004), Johannsson et al. (2000)
26	B	LH bottom trawl estimates with FPC	1999	Stephen Riley (USGS, pers. comm.)
	P/B	LS ecopath model		Kitchell et al. (2000)
	Q/B	LS ecopath model		Kitchell et al. (2000)

Table 2.6 (cont'd)

	Diet	LM diet study in dry weights (DW)	2000-2001	Hondorp et al. (2005)
		DW:WW for *Diporeia* = 0.2		Landrum (1988), Johnson (1988)
		DW:WW for *Mysis* = 0.15		Landrum et al. (1992)
		DW:WW for other (chironomids) = 0.14		Smit et al. (1993)
		DW:WW for fish eggs (standard zoobenthos) = 0.166		Jørgensen (1979)
27	B	LH bottom trawl estimates with FPC	1999	Stephen Riley (USGS, pers. comm.)
	P/B	LS ecopath model		Kitchell et al. (2000)
	Q/B	LS ecopath model		Kitchell et al. (2000)
	Diet	LM diet study		Hondorp et al. (2005)
28	B	LH bottom trawl estimates	1999	Stephen Riley (USGS, pers. comm.)
	P/B	RE with		Pauly (1980)
		Lmax = 7.6 from Canada		Fishbase (www.fishbase.org)
		K = 1.6 from England		Fishbase (www.fishbase.org)
		T = 6 from LH SCA model for group 8		Ji He (MDNR, pers. comm.)
	Q/B	Assumed the same as group 26		
	Diet	LS diet study	1968-1969	Griswold and Smith (1973)
29	B	LH sampling study in numbers	1999	Richard Barbiero (Environmental Protection Agency-EPA, pers. comm.)
		Average WW per individual		Landrum (1988)
	P/B	LH sampling study in profundal zone	1980-1982	Johnson (1988)
	Q/B	LS ecopath model		Kitchell et al. (2000)
	Diet	LM spring-fall sampling	1986-1987	Evans et al. (1990)
30	B	LH sampling study	1971	Sell (1982)
	P/B	LH sampling study	1971	Sell (1982)
	Q/B	LS ecopath model		Kitchell et al. (2000)
	Diet	LO diet study	1995	Johannsson et al. (2001)
31	B	LH numbers	2000	Nalepa et al. (2007)
		Conversions to WW	1987-1996	Nalepa et al. (2002)
	P/B	LO study	1967-1968	Johnson and Brinkhurst (1971)
	Q/B	LM ecopath model		Ann Krause (UT, pers. comm.)
	Diet	LM ecopath model		Ann Krause (UT, pers. comm.)

Table 2.6 (cont'd)

32	B	LH numbers	2000	Nalepa et al. (2007)
		LO WW	1995	Mills et al. (1999)
		LE conversion to shell free WW	1993-1994	Johannsson et al. (2000)
	P/B	LO and LE study	1992-1994	Chase and Bailey (1999)
	Q/B	LO network model		Jaeger (2006)
	Diet	LM ecopath model		Ann Krause (UT, pers. comm.)
33	B	LH sampling in DW	1999	Richard Barbiero (EPA, pers. comm.)
		DW:WW ratio = 0.1		Makarewicz (1988) for rotifers
		Average depth = 76 m		based on Barbiero et al. (2001)
	P/B	LE RE	1993-1994	Johannsson et al. (2000)
		LH sampling for average length	1983-1999	Barbiero and Tuchman (2004)
		LH surface temperature data		www.ndbc.noaa.gov
	Q/B	LM ecopath model		Ann Krause (UT, pers. comm.)
	Diet	LH summer diet study	1988	Vanderploeg et al. (1993)
34	B	LH sampling in DW	1999	Richard Barbiero (EPA, pers. comm.)
		DW:WW ratio = 0.1		Makarewicz (1988) for rotifers
		Average depth = 76 m		based on Barbiero et al. (2001)
	P/B	LE RE	1993-1994	Johannsson et al. (2000)
		RE		Shuter and Ing (1997)
		LH surface temperature data		www.ndbc.noaa.gov
	Q/B	LM ecopath model		Ann Krause (UT, pers. comm.)
	Diet	LM ecopath model		Ann Krause (UT, pers. comm.)
35	B	LH sampling	1999	Richard Barbiero (EPA, pers. comm.)
		Depth of sampling = 20 m		Richard Barbiero (EPA, pers. comm.)
	P/B	LM ecopath model		Ann Krause (UT, pers. comm.)
36	B	RE		Pauly et al. (1993)
		LH spring euphotic depth = 26	1993-1995	Fahnenstiel et al. (2000)
		WW:Carbon (C) for phytoplankton = 42		Cushing et al. (1958)
		DW:C for detritus = 2.22		Jørgensen (1979)
		DW:WW for detritus = 0.08 (assuming same as for phytoplankton)		Cushing et al. (1958)

CHAPTER 3

Modeling species invasions in an Ecopath with Ecosim model of Lake Huron.

Abstract:

Invasive species affect the structure and processes of ecosystems they invade. Invasive species have been particularly relevant to the Laurentian Great Lakes, where they have played a part in both historical and recent changes to Great Lakes food webs and the fisheries supported therein. There is increased interest in understanding the effects of ecosystem changes on fisheries within the Great Lakes, and ecosystem models provide an essential tool from which this understanding can take place. A commonly used model for exploring fisheries management questions within an ecosystem context is the Ecopath with Ecosim (EwE) modeling software. Incorporating invasive species into EwE models is not a straightforward process and methods for doing so have not been compared nor described thoroughly. We compared four methods for incorporating invasive species into an EwE model for Lake Huron based on the ability of the model to reproduce patterns in observed biomass time series. The methods differed in whether invasive species biomass was forced in the model, the initial level of invasive species biomass at the beginning of time dynamic simulations, and the approach to cause invasive species biomass to increase at the time of invasion. The overall process of species invasion could be reproduced by all methods, but fits to observed time series were best when time series of invasive species were forced. Among methods where invasive species time series were not forced, starting invasive species biomass at high values and artificially removing biomass until the time of invasion performed best, but was more complicated to implement than other methods. We recommend forcing invasive species biomass when model objectives are to understand ecosystem impacts in the past and when time series of invasive species biomass are available. For understanding the effect of invasive species on future fisheries management actions, we

recommend initiating invasive species biomass at low levels based on the simplicity and realism

of the method.

Introduction:

Non-native species are a continual threat to the maintenance of Great Lakes ecosystems. Approximately 185 non-native species have invaded the Laurentian Great Lakes (Ricciardi 2006) with effects ranging from mild to severe. Non-native species that become established, increase in abundance, and alter system processes are termed "invasive" (Williamson and Fitter 1996) and are the focus of policy, research, and restoration efforts within the Great Lakes.

Several non-native species from the Ponto-Caspian region of Eurasia have recently invaded the Great Lakes. The spiny-water flea (*Bythotrephes longimanus*), zebra (*Dreissenia polymorpha*) and quagga (*D. bugensis*) mussel (hereafter referred to as dreissenids), and round goby (*Neogobius melanostomas*) have all received extensive attention for their perceived ability to alter Great Lakes food-webs. *Bythotrephes* invaded the Great Lakes during the 1980s (Vanderploeg et al. 2002), and preys heavily on mesozooplankton (Bunnell et al. 2011). Dreissenids were first observed in Lake St. Clair in 1988 (Vanderploeg et al. 2002), and have been suggested to contribute to shifts in the zooplankton community (Barbiero et al. 2009; Bunnell et al. 2011), declines in prey fish abundances (Riley et al. 2008), reductions in the spring phytoplankton bloom (Barbiero and Tuchman 2004), and declines in abundance of native benthic amphipods (*Diporeia spp.*; Nalepa et al. 2007). Round goby were first observed in the St. Clair River in 1990 (Vanderploeg et al. 2002) and compete with other benthic fish, predominantly sculpins (Jude et al. 1992).

Developing ecosystem models can facilitate with assessment of recent changes to Great Lakes food-webs, including the effect of invasive species. Ecosystem model development also supports ecosystem based approaches to fisheries management, which are becoming more prevalent (Pikitch et al. 2004). A popular tool for exploring food-web dynamics and assessing

multi-species management objectives is the Ecopath with Ecosim (EwE) computer software (Halfon and Schito 1993; Halfon et al. 1996; Kitchell et al. 2000; Cox and Kitchell 2004; Stewart and Sprules 2011). Ecopath with Ecosim requires a mass-balance description of a food web at an initial point in time (Ecopath; Christensen and Pauly 1992), which is then used as the initial conditions for forward-projecting time-dynamic simulations (Ecosim; Christensen and Walters 2004).

Simulating species invasions in EwE models is not straightforward. Species included in Ecosim time-dynamic simulations must have positive biomass when the model is initialized and balanced in Ecopath. This presents a problem for invasive species that invaded the system after the initial Ecopath year. One solution to account for invasive species effects has been to construct separate pre-invasion and post-invasion Ecopath food-web models (e.g., Jaeger 2006; Stewart and Sprules 2011). Such an approach only utilizes Ecopath, and precludes opportunity to explore dynamic simulations in Ecosim. A solution that utilizes Ecosim is to run simulations in Ecosim based on an Ecopath model initialized in a year after all invasive species were present, and therefore when biomass values were truly positive. Time-series of data are used by Ecosim to tune model parameters and evaluate model performance, and therefore initializing Ecopath in a later year excludes available time-series data from the model-fitting process that could inform species interactions prior to the invasion.

Another approach to simulate species invasions in Ecosim models has been used, and does not reduce the length of data time series. With this approach, invasive species are initialized at some positive biomass value in Ecopath, prior to actual invasion, artificially maintained at negligibly low biomasses until the year of invasion, and then afterwards allowed to proliferate. For example, Pine et al. (2007) simulated the invasion of flathead catfish (*Pylodictis olivaris*)

into an inland reservoir by artificially increasing fishing mortality on catfish, to explore what the system might have looked like prior to invasion, and then reducing fishing mortality to allow catfish to invade. Similarly, Espinosa-Romero et al. (2011) initially suppressed biomass of sea otters (*Enhydra lutris*) by applying high artificial fishing mortality, and then released fishing mortality in order to simulate reintroductions across a spatial gradient. Forcing biomass of an invasive species (i.e. specifying a time series rather than dynamically modeling it) has also been successfully employed to model lionfish (*Pterois volitans*) invasion in the Caribbean (V Christensen, Fisheries Centre, University of British Columbia, pers. comm.). Cox and Kitchell (2004) describe that changes to data inputs for the prey and predators of invasive species are also needed when attempting to model invasion dynamics. Although, the methods described above are ad-hoc, they represent practical attempts to account for the effects of invasive species.

To date, methods for modeling invasive species in EwE models have not been compared to determine their effectiveness for capturing food-web dynamics through time. Furthermore, trade-offs among methods or required assumptions for methods have not been elucidated. In this study, we explored the relative performance of four methods for incorporating invasive species into EwE models. All methods used both Ecopath and Ecosim components of the modeling framework. For each method, we evaluated the model's ability to capture the biomass time-dynamics for both invasive and non-invasive species. We present a quantitative comparison as to which method best reproduced observed data time series and provide advantages and disadvantages to using each method.

Methods:

Ecopath with Ecosim models

Data inputs taken primarily from Lake Huron were used to construct an Ecopath model. The model was parameterized from data collected around 1981 for 20 unique species or groups of species. When data were available, multiple age-stanzas were included for biologically important species as well as those targeted by fisheries, which increased the total number of modeled groups to 36 (Table 3.1). This model focused on the offshore fish community, so important nearshore groups were excluded. Sea lamprey (*Petromyzon marinus*) biomass was forced at observed levels because much of its biological control occurs outside the model in the form of chemical treatments.

Invasive species in the model included *Bythotrephes*, round goby, and dreissenids. The modeled year of invasion was based on the first year in the observed biomass time series with positive biomass. Even though actual invasion occurred earlier, *Bythotrephes* were assumed to invade in 1998, round goby in 1997 (S. Riley, United State Geological Survey, Ann Arbor, unpublished data), and dreissenids in 1997. Dreissenids data were available beginning in 2000 (Nalepa et al. 2007, French et al. 2009), but because dreissenids are the primary prey for round goby, the same year of "invasion" as round goby was chosen for dreissenids.

Estimates of biomass (*B*), production to biomass ratio (*P/B*), consumption to biomass ratio (*Q/B*), diet components (*DC*), harvest, and biomass accumulation rates (*BA*) were taken from published and non-published sources and used to define interactions among modeled groups and fisheries within Ecopath. Data inputs were used in Ecopath to calculate search rates of predators on every modeled group, and other mortality rates (*M0*) for each group. Other mortality is the mortality not explained by modeled sources and is the difference between total mortality entered into the model, which is a group's *P/B* ratio, and the sum of predation mortality, fishing mortality, and *BA* for each group. If any *M0* was negative, the model was

unbalanced, and data inputs were adjusted following recommended practices (Christensen et al. 2005). Greater details on Ecopath model equations are available in Christensen and Pauly (1992), and greater details on balancing can be found in Chapter 2 of this dissertation.

After species interactions were defined in Ecopath, Ecosim was used to predict biomasses for each modeled group through time. Descriptions of Ecosim calculations are outlined in Christensen and Walters (2004). Perhaps the most important parameters governing interactions in Ecosim are vulnerabilities (Plagányi and Butterworth 2004; Ahrens et al. 2012), which control the strength of the trophic interaction between a predator and its prey. Although unique vulnerabilities for each predator-prey interaction are possible, using a single value for all prey to a single predator is recommended (V. Christensen, Fisheries Centre, University of British Columbia, pers. comm.). Ecosim has a fitting procedure to estimate vulnerability parameters based on minimizing differences between predicted model outputs and observed biomass time series (Christensen and Walters 2004). The fitting procedure also provides a way to either idependently or simultaneously estimate inter-annual variability in primary producer *P/B* (i.e., production anomalies). Estimating production anomalies often greatly reduces deviations between model predicted biomasses and observed biomasses relative to estimating vulnerabilities alone (C. Walters, Fisheries Centre, University of British Columbia, pers. comm.).

Alternative methods for incorporating invasive species:

We compared four methods of incorporating invasive species into EwE models. The methods included: 1) forcing biomass dynamics of invasive species through time (forcing biomass); 2) starting biomass of invasive species at low levels, and allowing biomass to increase at the time of invasion (low initial Ecopath biomass); 3) starting biomass of invasive species at

high levels, reducing biomass until the time of invasion, and then allowing biomass to increase

afterwards (high initial Ecopath biomass); and 4) starting biomass of invasive species at high

levels, and reducing and then increasing biomass by adjusting the strength of predator-prey

interactions through time (mediating vulnerabilities). The methods differed in terms of the

assumed initial values of biomass for invasive species, either low or high; the approach used to

maintain and "release" invasive species biomass, either forcing biomass, using an artificial

fishery, or changing vulnerabilities; and whether observed invasive-species biomass time-series

were forced or fit in the fitting procedure. A summary of each method is provided (Table 3.2),

with details described in the sections below.

Method 1 – Forcing biomass

A simple way in which to model invasive species was via biomass forcing. Time series of

invasive species biomass were used to overwrite predicted values from Ecosim equations for

years when data were available. Time series for dreissenids and *Bythotrephes* did not contain

data from the earliest years of invasion, nor was data available for every year once the time series

began. As there was no way to know the biomass of dreissenids and *Bythotrephes* prior to when

data were available, we assumed that biomass was zero in years prior to the first data point. Any

gaps in the forcing time series were automatically filled in with Ecosim estimates.

The way in which Ecosim filled in gaps in the time series was found to be affected by the

choice of initial biomass estimates. Low initial biomass estimates in Ecopath resulted in lower

Ecosim biomass predictions than were observed in the time series. On the other hand, high initial

biomass estimates in Ecopath resulted in Ecosim predictions that more closely matched the

observed biomasses for years adjacent to the period where the gap occurred. We therefore chose

to use high initial biomass estimates when forcing invasive species biomass, and describe the process more in our description of method three.

Method 2 – Low initial Ecopath biomass

In contrast to method 1, methods 2-4 used deviations between Ecosim predictions and observed biomass time-series of invasive species in the fitting procedure to estimate vulnerability parameters and production anomalies. Initial biomass inputs for invasive species were set at low values in method 2, which were arguably more representative of a pre-invasion state. However, entering biomass or diet of invasive species at arbitrary low levels led to grossly incorrect descriptions of trophic interactions between groups.

To more accurately describe interactions between invasive species and their prey and predators when invasive species biomass was initialized at low levels, we used the following approach. We picked a recent year (2002) for each invasive species in which biomass was high and diet information for their predators was available. The biomass value for each invasive species from the chosen year was then divided by 1000 and used as the initial biomass value in Ecopath. The 1/1000th scaling factor was small enough to make initial biomass estimates for the invasive species small, but also large enough so that when diet contributions were scaled downward, Ecopath would not round the contributions to zero. To maintain search rates as calculated in Ecopath, diet contributions of invasive species to their predators in recent years were reduced by the same scaling factor. By down-scaling the invasive species component of the predator's diet, we assumed that predator search rates for invasive species did not change over time. To allow diet contributions of predators to sum to one, non-invasive components of their diets, taken in the initial Ecopath year, were adjusted proportionally.

Once invasive species were entered into Ecopath at low levels, they tended to remain at low levels within Ecosim. To simulate an increase in biomass during the time at which invasion was assumed to occur, fishing mortality was applied to each invasive species initially, and then removed in the year of invasion. The year of invasion corresponded to the first year in which positive biomass data were available. The level of fishing mortality was chosen to reflect the instantaneous rate of population increase (r), as calculated from observed increases in the biomass time series of invasive species during the early years of invasion. We fit a model, $B_t = B_0 e^{rt}$, to the years of initial biomass increase, where B_0 was the first biomass estimate in the time series, and B_t was the biomass estimate t years after the year for B_0. The number of data points used to estimate r was 3 and 5 for dreissenids and round goby, respectively. The biomass time series for *Bythotrephes* did not cover a period of biomass increase, and so we used the slope of the line connecting the initial biomass input used in Ecopath to the value of the first data point in the time series, calculated on a *log* scale, as our estimate of r. To offset the added fishing mortality rate, initial *P/B* ratios of the invasive species were increased by an amount equivalent to the level of fishing mortality. Increasing *P/B* ratios ensured that estimates for *M0* were taken only from trophic interactions with other species, and that when fishing mortality was removed, Ecosim estimates of *P/B* ratios were appropriate.

Method 3 – High initial Ecopath biomass

An alternative to initializing invasive species biomass to low levels was to initialize invasive species biomass at high recently observed levels, similar to what was done for method 1, and then artificially reduce biomass (by applying fishing mortality) until the year of invasion. As for method 2, biomass estimates of invasive species and diet contributions of invasive species

to their predators were taken from 2002 and used as initial data inputs in Ecopath. Contributions of other groups to the diet of predators of invasive species during the initial Ecopath year were proportionally adjusted so that total diet summed to one. In contrast to method 2, diet and biomass values of invasive species were not reduced by a scaling factor.

We encountered a problem when initializing the model with high invasive species biomass values. Recent observed biomass values for dreissenids were substantial and caused imbalance for groups that dreissenids consumed. To correct the additional (artificial) predation mortality caused by dreissenids, as well as by other invasive species, we added negative BA to prey items that was equivalent to the initial level of consumption of the prey item by the invasive species. Adding negative BA allowed Ecopath to calculate appropriate levels of $M0$ that were based on only non-invasive species (species actually present in the system in the initial Ecopath year).

Once invasive species were appropriately entered into the initial Ecopath model, artificial fishing mortality was applied to each invasive group in Ecosim so that biomass would become zero within the first year. Reducing invasive species biomass with fishing allowed invasive species to be present in the time dynamic simulations prior to their actual invasions, but without having any effect on the rest of the food web. Negative BA equivalent to the level of fishing was added to each invasive group so that estimates of $M0$ remained unchanged by the addition of fishing mortality. As in method 2, the artificial fishing mortality was released in the year of invasion.

Method 4 – Mediating vulnerability

We used the same approach for method 4 as for method 3 for setting initial biomasses

and diets, but used a different approach for simulating the process of invasion. In contrast to

methods 2 and 3, where the process of invasion was simulated by the addition and then removal

of artificial fishing mortality, assumptions about changes in the strength of trophic interactions

(i.e., vulnerabilities) were used to simulate species invasion for method 4. Two forcing functions

were used in Ecosim to mediate vulnerabilities; one to mediate the vulnerabilities of prey to

invasive species predators (Figure 3.1a), and the other to mediate vulnerabilities of invasive

species to their predators (Figure 3.1b). In both instances, vulnerabilities were forced to zero in

years prior to the actual invasion, which implies no effect of the invasive species on either their

predators or their prey. Prey species were assumed to become more susceptible to the invasive

species predator once invasion occurred, and was simulated by having vulnerabilities increase to

a peak (Y in Figure 3.1a). Over time, we assumed that prey defense mechanisms would be

developed and vulnerabilities to invasive species predators would reach stable levels (i.e. would

return to a relative value of one by year $X2$ in Figure 3.1a). Similarly, in the initial stages of an

invasion (prior to year $X1$ in Figure 3.1b), predators on invasive species may not have developed

a search image, and therefore vulnerabilities of invasive species to their predators were assumed

to be low. Over time during the invasion, the vulnerabilities of invasive species to their predators

were assumed to increase to stable levels (i.e. would return to a relative value of one by year $X2$

in Figure 3.1b). The shapes (Figure 3.1) of the vulnerability forcing functions were based on the

shape of the round goby biomass time series. Parameters values for the shape of vulnerabilities

of prey to invasive species predators were $Y = 5$; $X1 = 1997$ for dreissenids and round goby, and

1998 for *Bythotrephes*; and $X2 = 7$ years after $X1$ (Figure 3.1a). The same parameter values for

X1 were used for the shape of vulnerabilities of invasive species to predators, however *X2* = 6 years after *X1* (Figure 3.1b).

Assessment of Invasive Species methods

Fits of predicted Ecosim dynamics to observed time series provided objective criteria to compare the four methods of incorporating invasive species into EwE models. Ecosim calculates residual sum of squared deviations (RSS) between the Ecosim predicted and the observed data values, calculated on a *log* scale. Observed data values can be either relative or absolute values. We used absolute biomass time series for invasive species and a mixture of absolute and relative time series for non-invasive groups. Seventeen time series of biomasses for some modeled groups were available from published and unpublished sources in 1981-2008 and were used in the Ecosim fitting procedure (Table 3.3). Unique vulnerability parameters for every modeled predator and production anomalies for every modeled year were simultaneously estimated for each method.

Results:

Our analysis revealed that the overall process of species invasion could be reproduced in an Ecopath with Ecosim model, but the exact timing and magnitude of changes in invasive species biomass differed among the methods considered. Timing depended both on whether invasive species biomass increased from low levels at the appropriate year, and whether invasive species biomass was quickly reduced to, or maintained at low levels prior to the time of invasion. As expected, method 1 fit the timing of biomass changes for invasive species perfectly (Figure 3.2). Timing of biomass increases of invasive species between methods 2-4 was comparable,

although biomass of *Bythotrephes* increased sooner in method 2 than in methods 3 and 4 (Figure 3.2). The primary difference in timing between methods 2-4 was reflected prior to the time of invasion, when biomass levels of round goby and dreissenids declined more slowly for methods 3 and 4 (Figure 3.2).

The magnitude of species invasion depended on whether invasive species biomass increased to observed levels once invasion occurred. As expected, biomass values of invasive species fitted perfectly in method 1 (Figure 3.2). Apart from method 1, few patterns were present when comparing estimated invasive species biomass to observed biomass values across methods. Although method 3 appeared to underestimate the magnitude of invasive species biomass, fits to *Bythotrephes* were nearly as good as for method 1, and biomass levels for dreissenids were lower in method 2 than method 3 (Figure 3.2).

In addition to fitting the dynamics of invasive species, we also wanted our methods to adequately fit non-invasive groups. Fits of non-invasive groups were adequate, but varied depending on the group and method employed. With the exception of method 2 for lake whitefish, fits to *Diporeia* and lake whitefish were most similar to observed biomass values (Figure 3.2). Estimated biomass values for lake whitefish were greater than observed biomass values in method 2 than for other methods (Figure 3.2). Fits of alewife were similarly poorest among the methods considered for method 2, however, estimated biomass values were lower than observed biomass values rather than higher, like for lake whitefish (Figure 3.2). Fits of estimated lake trout biomass varied the most from observed values, but fits were comparable across methods (Figure 3.2).

Residual sum of squared deviations provided a way to quantitatively assess the performance of each method. Not all RSS values could be directly compared among methods

because the number of time-series used to fit the models differed. Time series of invasive species biomass were forced in method 1, and therefore did not contribute towards the RSS, whereas in methods 2-4 these time series contributed to the RSS. Consequently, only RSS between methods 2-4 could be compared among each other.

Quantitative performance of each method based on observed fits varied between the methods considered. Among methods 2-4, methods 4 had the lowest RSS, followed closely by method 3 and less closely by method 2 (Table 3.4). Method 2 performed poorer in part because of poorer fits to dreissenids, lake whitefish, and alewife than the other methods. Time series for invasive species did not include early years, and therefore the slow declines for invasive species biomass in methods 3 and 4 did not contribute to overall fit.

The presence of invasive species in the diet of their predators was a second important attribute that we wanted the model to capture. In addition to reasonably reproducing biomass time series, estimated diet proportions for predators of invasive species reproduced observed data for all methods (but are not shown). As expected, the increase in contributions of invasive species to their predators' diet matched increases in abundance.

Discussion:

The ability to incorporate species invasions into time-dynamic ecosystem models is helpful in understanding system dynamics. Many creative methods can be employed for modeling species invasions, however the task of comparing methods and considering their trade-offs can be challenging given model complexity. Our analysis provided a first step in comparing methods of incorporating invasive species into a time-dynamic EwE model without limiting the length of available time series. Rather than providing a rule that all other EwE modelers should

use, we instead hoped to provide guidance about the strengths and weaknesses of our four proposed methods and help future EwE modelers decide how to include invasive species in models of their systems.

The performance of each method as based on RSS depended on the model used (Table 3.4). With the exception of the slow decline in invasive species biomass for method 4, the methods generally captured the basic biomass dynamics of invasive species (Figure 3.2), suggesting any method could possibly be used for future EwE models. Although RSS for method 1 was much lower in both models considered, we could not compare method 1 with the other methods because different time series were used. Comparisons might be made among non-invasive species only, but we felt that because the invasive species time series contributed to RSS in methods 2-4, thereby affecting the fits for other groups, comparing RSS for non-invasive groups only would still be incomplete. How best to compare the performance of method 1 to the performance of methods 2-4 based on RSS remains uncertain.

Caution with RSS is warranted even when the number of time series used during fitting is the same. When multiple time series are used, the weighting of time series to the overall sum of squares can be important. Although scales in Ecosim are relative, and the RSS are on a *log* scale, differences among groups in the magnitude of change in the biomass time series can bias the fitting procedure toward fitting one group over another. A method that fits well for important groups but poorly for a single unimportant group may have a poorer RSS than a method that fits not quite as well for all groups. In general, careful attention should be given to judging which data sources are most informative about food-web dynamics and how such data sources may influence RSS, and which groups warrant priority in model fitting given the modeling objective.

To help other EwE modelers make their own assessments about which method to use, we summarize advantages and disadvantages of each method below.

Method 1 - Forcing biomass:

The primary advantage of method 1 was that forcing biomass of invasive species was the best way to match observed dynamics of invasive species. Ecosim can predict future biomass levels of invasive species even when forcing occurs, so method 1 does not remove the ability of the model to simulate future scenarios. As described in the methods, predictions of future biomass levels of invasive species depended heavily on initial biomass inputs in Ecopath. We recommend that if simulations in Ecosim are used, and invasive species biomass is forced, that recent biomass estimates be used to initialize invasive species biomass in Ecopath. A secondary advantage of method 1 was its simplicity, in that forcing was a direct way to keep calculated biomass levels low until the time of invasion and did not require artificial fishing mortality or adjustments to trophic interactions.

The major disadvantage of method 1 was that because invasive species were forced, estimates of invasive species vulnerabilities (vulnerabilities of prey to invasive species) were not informed by the biomass time series of invasive species themselves. Rather, estimates of invasive species vulnerabilities were only informed by the effect of invasive species on the biomass time series of other modeled groups. Although the exact effect is unknown, having vulnerabilities be estimated based on biomass fits to other groups may influence future projections of invasive species. A secondary disadvantage was that method 1 required a fairly complete time series of observed biomass data for invasive species. Missing data in time series could be addressed by interpolating missing points before entering the time series into the model,

or by allowing the model itself to estimate biomass dynamics in years when data are missing during Ecosim simulations. Alternatively, if a large continuous portion of the time series is missing (e.g. the first five years of invasion) the invasion can be assumed to start later than it actually occurred, as was the case for *Bythotrephes* and dreissenids.

Method 2 – Low initial Ecopath biomass:

The primary advantage of method 2 was in its realism. Starting biomass of invasive species at low levels best mirrors the process of actual invasion in which invasive species enter a system at low biomass levels and then proliferate to higher levels. A secondary advantage of method 2 was its simplicity. Contrary to the other three methods, method 2 did not require the removal of high initial biomass before the time of invasion. Similarly, because invasive species biomass was initialized in Ecopath at low levels, fewer adjustments to the diet of predators of invasive species, and $M0$ of prey of invasive species were required than for methods 1, 3, and 4.

The primary disadvantage of method 2 was that invasive species dynamics had to be maintained by an artificial fishery. Dynamics of invasive species were influenced by the time of release from fishing and by the level of fishing mortality, and both affected the estimated vulnerabilities of prey to invasive species. Under higher fishing mortality rates, invasive species biomass increased quickly and estimated vulnerabilities of prey to invasive species were lower in order to match observed dynamics. Our approach of applying fishing mortality equivalent to the rate of biomass increase (as described in the methods) at the time when data began provided a standardized approach for including artificial fishing mortality.

Method 3 – High initial Ecopath biomass:

Method 3 was a complicated method to implement, however it performed well for the Lake Huron model (Table 3.4). The primary advantage was that invasive species were able to reach high levels of biomass very quickly due to the high initial biomass and removal of substantial fishing mortality at the time of invasion (Figures 3.2 and 3.3). Higher fishing mortalities, contrary to the lower calculated rates used in method 2, were used in method 3 to drive down the high initial biomass of invasive species so that the effect of invasive species on other modeled groups would be minimal prior to invasion.

The primary disadvantage for method 3 was its complexity. The level of fishing mortality and BA adjustment influenced how quickly and to what level invasive species biomass declined, and also influenced the estimation of vulnerabilities of prey to invasive species. If fishing mortality rates were not high enough, biomass values for invasive species did not reach low levels prior to the time of invasion after vulnerabilities were estimated. Consequently, the approach we used of iteratively trying values of fishing mortality and BA and then estimating vulnerabilities to achieve an overall best fit was more subjective than methods 1 and 2.

Method 4 – Mediating vulnerabilities:

The primary advantage of method 4 was that it used biological interactions (mediating vulnerabilities) to adjust biomass of invasive species rather than using artificial fishing. Although biomass of invasive species were slower to decline than when artificial fishing was used, dynamics after the time of invasion were captured by the method (Figure 3.2). Method 4 reflects an attempt to account for theoretical trophic responses rather than using artificial modeling methods to control species invasion.

The greatest disadvantage for method 4 was in the sensitivity of invasive species biomass to adjustments in vulnerability and the lack of empirical knowledge about the shape of our adjustments. The overall shape of the mediation functions we used made theoretical sense, but there was no way to know whether the shape was correct. The time over which vulnerabilities stabilized (the difference between *X1* and *X2* in Figures 3.1a and 3.1b) and the overall magnitude of the effect of invasive species on their prey (*Y* in Figure 3.1a) influenced the estimated biomass values of invasive species. Although changing the shape could improve biomass fits, doing so would be similar to forcing biomass fits for invasive species. Consequently, we did our best to standardize the shapes for our analyses when using method 4 (as described in the methods and Figure 3.1), but without empirical evidence other than the biomass time series, these reflect one hypothesis about the shapes of the process.

Conclusions

Invasive species modeling approaches we tested exhibited characteristics of alternative modeling philosophies. Of the four methods we examined, one was based on forcing invasive species, and the other three involved using past data on the invasive species to fit the model. The choice between forcing and fitting depends on the objectives for which the model was developed. We suggest that the forcing method (method 1) may be the best approach if 1) complete time series of data on invasive species biomasses are available and 2) if objectives of the work are primarily to assess effects of invasive species on the system, rather than to predict future interactions. If the objectives of the work are to account for the effect of invasive species and consider future outcomes of management strategies, then using one of three fitting methods may be preferable. Choosing among the three fitting methods should depend on model objectives

and data availability. If information on how species invasion may influence the strength of predator-prey interactions were available, then method 4 may be preferred, but if not, then the simplicity of method 2 may be preferred.

The methods we examined here emerged from a working group discussion of options for including invasive species in EwE models. Our list is not exhaustive, but we suspect other methods will be related to one or more of the methods examined here, or reflect a combination of the methods examined here. As the EwE software moves towards more user-developed plug-ins (Christensen and Lai 2007), additional ways to include invasive species will likely be developed and are encouraged. Our comparison was not meant to be a single recommendation for all modelers, but instead will hopefully foster new approaches to including invasive species in food-web models.

APPENDIX

APPENDIX 3

Tables and Figures

Table 3.1: Species or groups of species used in the Lake Huron Ecopath with Ecosim model. Age stanzas for multi-stanza groups are provided in years.

Group/species name (age stanzas)	Scientific name
Sea lamprey	*Petromyzon marinus*
Lake whitefish (0, 1-3, 4+)	*Coregonus clupeaformis*
Lake trout (0, 1, 2-4, 5+)	*Salvelinus namaycush*
Chinook salmon (0, 0.5, 1-5, 6+)	*Oncorhynchus tshawytscha*
Steelhead (0, 1, 2-5, 6+)	*Oncorhynchus mykiss*
Burbot (0-3, 3+)	*Lota lota*
Alewife (0, 1+)	*Alosa pseudoharengus*
Rainbow smelt (0, 1+)	*Osmerus mordax*
Bloater (0, 1+)	*Coregonus hoyi*
Round Goby	*Neogobius melanostomus*
Slimy sculpin	*Cottus cognatus*
Deepwater sculpin	*Myoxocephalus thompsoni*
Ninespine Stickleback	*Pungitius pungitius*
Diporeia	*Diporeia spp.*
Mysis	*Mysis diluviana*
Benthic invertebrates	
Dreissenid mussels	*Dreissena polymorpha*
	Dreissena bugensis
Predatory zooplankton	*Bythotrephes longimanus*
Zooplankton	
Phytoplankton	
Detritus	

Table 3.2: Biomass time series used for comparing performance of methods to incorporate invasive species into the Lake Huron Ecopath with Ecosim model.

Time series group	# of data points
Sea lamprey	25
Age 3 lake whitefish	26
Age 4+ lake whitefish	26
Age 2-4 lake trout	25
Age 5+ lake trout	25
Age 1-5 Chinook salmon	28
Age 1-5 steelhead salmon	25
Age 1+ alewife	23
Age 1+ rainbow smelt	23
Age 1+ bloater	23
Round goby	9
Slimy sculpin	23
Deepwater sculpin	23
Ninespine stickleback	12
Diporeia	10
Dreissenids	8
Bythotrephes	8
Zooplankton	8

Table 3.3: Summary of each method for incorporating invasive species into the Lake Huron Ecopath with Ecosim models. Details of each method are described in the text.

Method	Time series of invasive species	Initial biomass of invasive species	Approach used maintain and release invasive species	Reasoning
1 – Forcing	Forced	High	Forced time series	Forcing time series allows fitting routine to match dynamics to other species while invasive species dynamics are fit without error.
2 – Low initial Ecopath biomass	Fit	Low	Artificial fishery	Invasive species begin their invasion at low biomass levels, and thus should be initialized as such.
3 – High initial Ecopath biomass	Fit	High	Artificial fishery	Starting biomass at levels more similar to recent years allows invasive species to reach high biomass levels more easily
4 – Mediating vulnerabilities	Fit	High	Changes to vulnerabilities	Biological processes keep invasive species biomass suppressed until the time of invasion

Table 3.4: Residual sum of squared deviations between observed biomass time series and Ecosim predicted biomass values for each method of incorporating invasive species into the Lake Huron Ecopath with Ecosim model.

	Method			
Model	1 - Forcing	2 – Low initial Ecopath biomass	3 – High initial Ecopath biomass	4 – Mediating vulnerabilities
Lake Huron	103.3	146.5	130.7	129.2
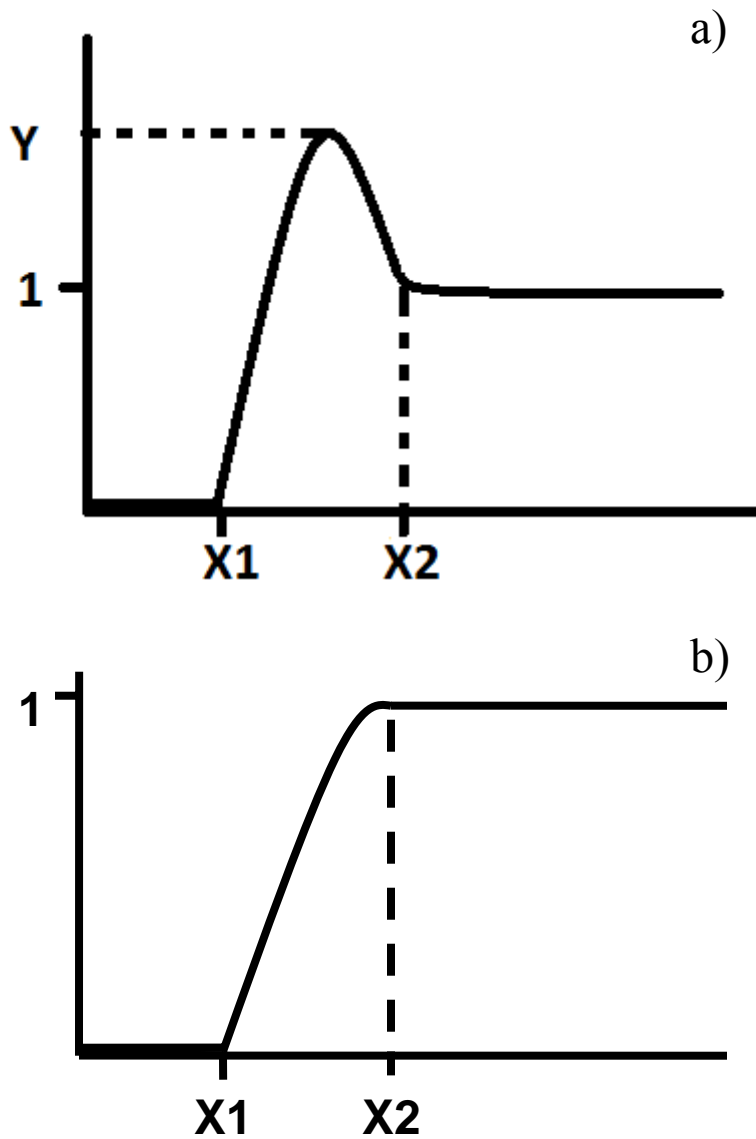
Figure 3.1: Shapes of vulnerability forcing function for a) prey of invasive species, and b) invasive species to their predators. For vulnerabilities of prey to invasive species, vulnerabilities began very low for the early simulation years, and increased to a peak (Y) after the species invaded (time period X1), then stabilized to one once the species began to become established (time period X2). For vulnerabilities of invasive species to their predators, vulnerabilities began very low for the early simulation years, and increased to one once the species invaded.
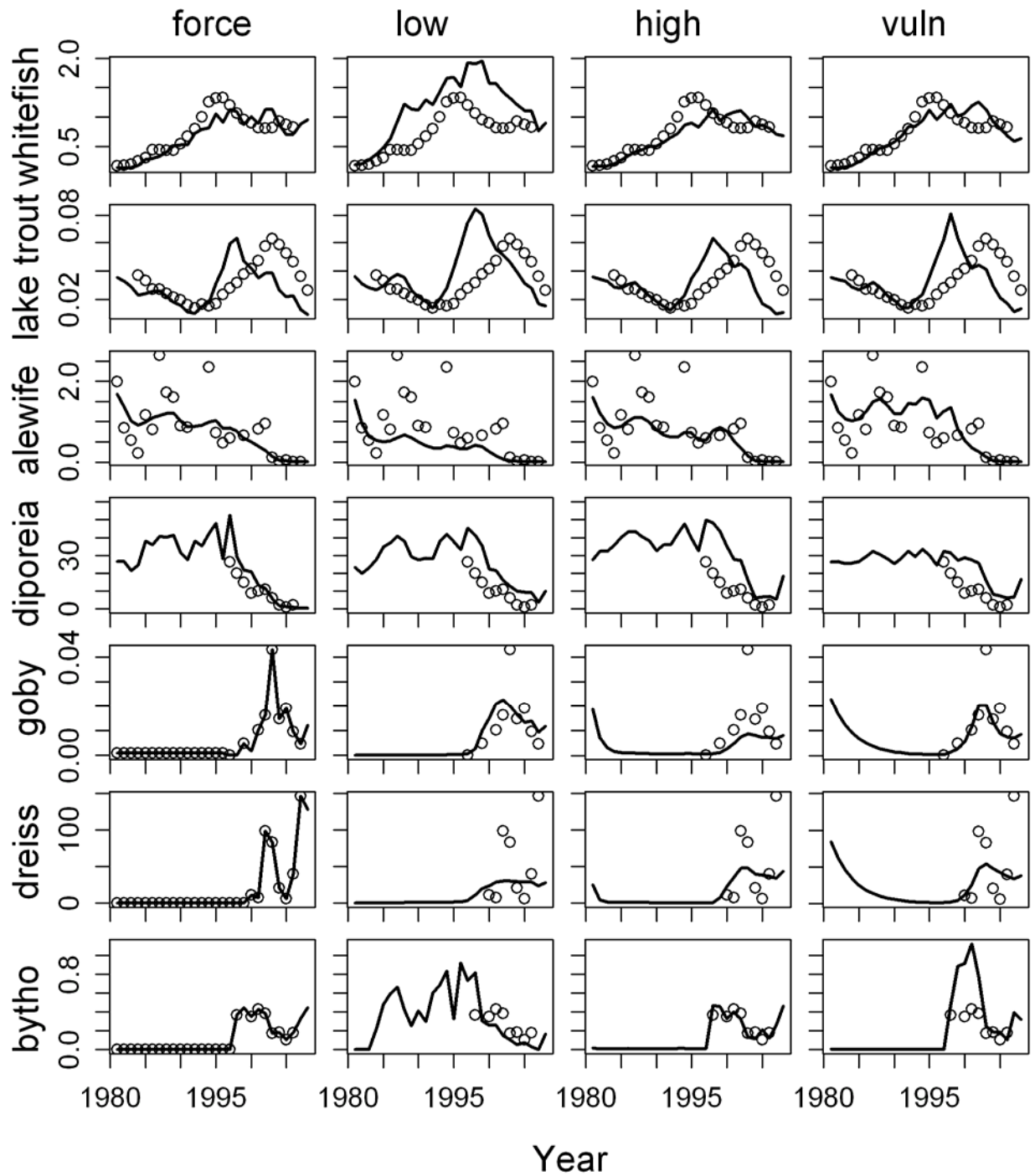
Figure 3.2: Fits to a subset of modeled groups for each method from 1981-2008 for the Lake Huron Ecopath with Ecosim model. The solid black line represents model predicted biomass, and the open circles represent observed biomass. Groups include age 4+ lake whitefish (whitefish), age 5+ lake trout (lake trout), age 1+ alewife (alewife), *Diporeia* (diporeia), round goby (goby), dreissenids (dreiss), and *Bythotrephes* (bytho). *Bythotrephes*, round goby, and dreissenids were modeled as invasive species.

CHAPTER 4

Performance of harvest policies for a mixed lake whitefish lake trout commercial fishery in Lake Huron

Abstract

Lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) are integral members of the offshore fish community in Lake Huron. Both species have supported, and in the case of lake whitefish, still support extensive commercial fisheries. Overfishing and intense predation by the invasive sea lamprey *(Petromyzon marinus)* led to the collapse of the lake trout fishery in Lake Huron by the 1950s. Rehabilitation of lake trout is a priority for fisheries managers, and stocking programs have been in place since the early 1970s. Lake whitefish now support the primary commercial fishery in Lake Huron, but these fisheries capture lake trout as bycatch, potentially impeding rehabilitation efforts. Large changes to the Lake Huron food-web have occurred over the past two decades, including declines in key prey items of lake whitefish and lake trout. There is substantial uncertainty about how management actions may influence lake whitefish harvest and lake trout rehabilitation within a dynamic and altered food web. Potential management options were simulated using an Ecopath with Ecosim food-web model to assess the direct and indirect effects of management actions on lake whitefish and lake trout. Management options included changes in fishing mortality targets for lake trout and lake whitefish, and changes in the allowable amount of bycatch of lake trout in the lake whitefish fishery. Although simulated biomass dynamics did not perfectly match observed biomass time series for 1981-2008, general trends in species biomass were reflected in model predictions. When forward projections were made using best-fit parameter values, management options where bycatch rates of lake trout were adjusted in the lake whitefish fishery performed best at meeting objectives for both species. Among the options considered, forecasted lake whitefish harvest increased by at most 63% without declines in forecasted lake trout biomass. Alternatively, forecasted lake trout biomass increased by at most 37% without declines in

forecasted lake whitefish harvest. The sensitivity of management options to alternative assumptions about model parameters (future productivity and strength of predator-prey interactions) and diet compositions were also simulated. Alternative assumptions about future levels of primary production had a greater effect on the magnitude of harvest and biomass than alternative assumptions about diet or parameters affecting the strength of predator-prey interactions, and affected both the overall magnitude of biomass and harvest and the relative performance of policies. Alternative assumptions about parameters affecting the strength of predator-prey interactions also affected the ranking of management options, but the magnitude of the effect was less than alternative assumptions about primary production. Consequently, values for primary production and parameters affecting predator-prey interaction strength remain important factors in assessing policy performance and influencing expectations about future levels of biomass and harvest. Under original values for diet and the strength of predator-prey interactions, indirect interactions between lake trout and lake whitefish had limited effects on outcomes. Under plausible alternative values for vulnerabilities, the effect of lake whitefish on lake trout increased, suggesting there are scenarios where the interaction may be important, and providing further evidence for the importance of vulnerability parameters.

Introduction

Lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) are important members of the offshore fish community in Lake Huron. Lake trout were historically the dominant piscivore in Lake Huron, and supported an extensive commercial fishery representing the majority of harvest from the 1880s to the late 1940s (Eshenroder et al. 1995; Baldwin et al. 2002). A combination of overfishing and predation by sea lamprey (*Petromyzon marinus*) resulted in the collapse of the fishery and the near extirpation of lake trout from Lake Huron except for a few isolated populations (Eshenroder et al. 1995). Lake whitefish harvests have also varied widely through time. Lake whitefish were the primary harvested species prior to the 1880s, when lake trout became dominant (Eshenroder et al. 1995, Baldwin et al. 2002). Harvests declined in the early half of the 1900s before steadily increasing to records levels in 1998 (Baldwin et al. 2002). Lake whitefish now support the primary commercial fishery in the lake (Ebener et al. 2008a).

A defined set of fish community objectives (FCOs) guides management actions in Lake Huron (DesJardine et al. 1995). The FCOs for Lake Huron include sustained harvest of coregonine species, of which lake whitefish are dominant, and continued harvest of salmonines with lake trout being the dominant species. Given the near extirpation of lake trout populations in the past, their rehabilitation has been an important goal of fisheries managers (Ebener 1998). Controlling lake trout mortality has been necessary for rehabilitation of lake trout populations. Mortality by sea lamprey was a critical concern in the years following the collapse of the commercial fishery and substantial effort was taken and remains ongoing to control sea lamprey populations with chemical treatments (Eshenroder et al. 1995). Stocking of lake trout began in the 1970s after sea lamprey abundance was reduced and continues to the present (Ebener 1998).

Natural reproduction has been observed in Lake Huron (Nester and Poe 1984) and is increasing, especially recently (Riley et al. 2007), however catch rates of wild fish have not reached the levels experienced in Lake Superior, which led to the cessation of stocking in that lake (Riley et al. 2007).

A potential impediment to lake trout rehabilitation is bycatch within the lake whitefish fishery. Bycatch in the lake whitefish fishery is largely from gill nets during periods where lake trout and lake whitefish overlap (Johnson et al. 2004a,b). Lake trout are not generally targeted by the fishery due to their lesser value compared to lake whitefish and also to their greater handling time in nets. Adjustments to regulations for the lake whitefish fishery could be made to reduce lake trout bycatch but such changes would likely reduce the potential to achieve and maintain objectives for lake whitefish. Fisheries managers are therefore faced with tradeoffs in how best to attain both lake whitefish and lake trout objectives. Possible actions of fisheries managers are fairly limited, with changes to stocking rates for lake trout; sea lamprey control; harvest rates; and areas, times, and gears used to fish as the primary levers that can be adjusted.

Changes in the food web of Lake Huron have complicated the ability of fisheries managers to achieve FCOs for Lake Huron's offshore fish community. Changes in the abundance of certain species in the food web may influence interactions among lake trout, lake whitefish, and the lake whitefish fishery. The increase in abundance of recent invasive species, and in particular dreissenid mussels (Nalepa et al. 2007), has caused concern about the productivity in the offshore food-web and effects on current species (Vanderploeg et al. 2002; Heckey et al. 2004). Prey fish abundance in Lake Huron has declined to all time lows, presumably due to increases in dreissenid mussels (Riley et al. 2008), which raises concerns about the sustainability of piscivores such as lake trout and Pacific salmonines (Roseman and

Riley 2009). On the other hand, declines in alewife (*Alosa psuedoharengus*), which are an important prey fish for piscivores but a strong competitor with other prey fish, may provide increased opportunity for native prey species to rebound (Madenjian et al. 2008). Abundance of *Diporeia* spp. in Lake Huron has also declined to low levels, and is similarly presumed to be related to increases in abundance of dreissenid mussels (Nalepa et al. 2009). Declines in *Diporeia* have been found to reduce condition of lake whitefish because of the importance of *Diporeia* to lake whitefish diets (Pothoven and Madenjian 2008, Nalepa et al. 2009). Changes in abundance of key prey items may influence lake trout and lake whitefish in unexpected ways, increasing the importance for understanding potential effects to fisheries management.

Food-web models provide opportunity to explore the effects of changes in the food web and of potential management actions on harvest and abundance of lake whitefish and lake trout. The software package Ecopath with Ecosim (EwE) is a food-web model that performs well compared to other ecosystem/food-web models (Latour et al. 2003; Robinson and Frid 2003) but is not without its shortcomings (Aydin 2004; Plaganyi and Butterworth 2004; Koen-Alonso and Yodzis 2005). Ecopath with Ecosim models have been constructed for some of the Great Lakes and have been used to explore ecosystem effects of invasive species (Cox and Kitchell 2004; Stewart and Sprules 2011) and of management actions (Kitchell et al. 2000).

Results from Ecopath with Ecosim models are known to be sensitive to estimates of vulnerability parameters (Chapter 2; Christensen and Walters 2004; Ahrens 2012). Given the importance of vulnerabilities, it is prudent to describe them in more detail. Vulnerabilities describe the strength of predator-prey interactions. Specifically, vulnerabilities influence how predation mortality exerted on prey by a predator changes as biomass of the predator changes (Walters et al. 1997). Vulnerabilities are described on a continuum; when vulnerabilities are high

changes in predator biomass result in greater effects on their prey, whereas when vulnerabilities are low the effect is less. Consequently, vulnerabilities have been related to "top-down" (high vulnerability) or "bottom-up" (low vulnerability) control (Walters et al. 1997). Vulnerabilities also affect the extent to which density dependence affects predator consumption rates. Consumption to biomass ratios of a predator are more dependent on the predator's biomass when vulnerabilities are low than when vulnerabilities are high (Christensen and Walters 2004). Consequently, Ahrens et al. (2012) describe vulnerabilities in terms of the proximity of a group to its carrying capacity, where low vulnerability suggests a group is near its carrying capacity and high vulnerability suggests a group is far from its carrying capacity.

Our objective in this paper was to explore the potential effects of a range of possible management options on lake whitefish and lake trout both directly through interactions with the fishery, and indirectly through trophic interactions within the food web. We used an EwE model to describe the Lake Huron food-web, and developed simulations, in consultation with Lake Huron stakeholders, to explore the effect of potential harvest policies on the biomass and harvest of lake trout and lake whitefish. We simulated three management approaches representing changes to fishing mortality targets of lake trout and lake whitefish, and changes in bycatch rates of lake trout in the lake whitefish fishery. Plausible alternative assumptions in future levels of primary production, strength of predator-prey interactions (vulnerabilities), and the level of dietary overlap between lake trout and lake whitefish were also considered for each management approach. Lastly, we assessed the indirect effects of lake trout and lake whitefish on one another via trophic interactions within the food web.

Methods

Study site

Lake Huron is the second largest of the five Laurentian Great Lakes by area at 59,600

km^2, and second shallowest with an average depth of 59 m (Beeton et al. 1999). Lake Huron

consists of three unique spatial areas: the main basin, the North Channel, and Georgian Bay. The

lake is primarily oligotrophic, although Saginaw Bay, which is a large shallow embayment

within the main basin is eutrophic (Beeton et al. 1999). The main basin is the largest and best

studied of the three spatial areas and contains the majority of fishery harvests, so was the focus

of our modeling efforts. Our analysis focused on the offshore fish community, so we excluded

the fisheries and species of Saginaw Bay.

Modeling approach

Ecopath with Ecosim version 6.2 was used to construct a model of the offshore food-web

in the main basin of Lake Huron. Ecopath with Ecosim is a freely downloadable software

program (www.ecopath.org) widely used for modeling the effect of fishing policies on

freshwater and marine systems (Christensen and Pauly 2004). The software consists of two

modules: the first module (Ecopath) is used to construct a mass-balanced description of the food

web at a single point in time (Christensen and Pauly 1992, Walters et al. 1997, Pauly et al. 2000),

while the second module (Ecosim) is used to simulate time-dynamics of the food web as

described in Ecopath in response to modeled management scenarios (Christensen and Walters

2004). Although static, Ecopath models need not be at equilibrium; rates of biomass

accumulation (BA) can be added or subtracted to reflect population growth or decline.

Ecopath requires data inputs for biomass, consumption, and production for each modeled

group for the specific time period. If available, harvest and biomass accumulation rates can also

be entered into Ecopath. Groups can represent individual species or groups of species, and can represent separate age classes to reflect differences in trophic ontogeny or mortality patterns (Walters et al. 2008). We parameterized an Ecopath model using data from as near to 1981 as possible for 36 total groups, representing 20 living species/groups of species and one group of detritus. Age structure was included for eight species. Groups were chosen to reflect important contributors to the offshore food-web in Lake Huron. In addition, six fisheries were included in the model: lake whitefish gill net fishery in Canadian waters, lake whitefish trap net fishery in Canadian and US waters, lake whitefish gill and trap net fishery in treaty ceded waters, recreational fishery, bloater gill net fishery, and the commercial Chinook salmon fishery. Not all required data inputs were available from Lake Huron, or from 1981, in which case inputs from other years and other systems were used. When Lake Huron-specific data were not available, we preferentially used data from Lake Michigan studies, but also used data inputs from previously published (Kitchell et al. 2000) and unpublished (Ann Krause, University of Toledo, personal communication) Ecopath models, which had used data from a variety of sources.

Ecopath requires that data inputs be balanced (Christensen et al. 2005). Mass balance rarely occurs with initial data inputs, so ad-hoc adjustments were made so that production for every group was greater than the sum of mortality components on that group. Previous model explorations revealed that reasonable ad-hoc adjustments to data inputs had limited effect on resultant Ecosim simulations when compared to the effect of alternative assumptions about vulnerabilities (see Chapter 2). Due to the limited effect of ad-hoc adjustments on model simulations, we followed recommended practices to achieve mass balance (Christensen et al. 2005). Greater details on balancing can be found in Chapter 2. Data inputs for the balanced model, with the exception of diet proportions, are provided in Table 4.1. The biomass

accumulation rate for any group with trends in observed biomass time series beginning in 1981 was included in Ecopath. The biomass accumulation rate was calculated as the slope in relative (to 1981) biomass over the duration of the trend. The trend extended for nine years for lake trout, four years for alewife, 15 years for rainbow smelt, and six years for bloater, lake whitefish, and slimy and deepwater sculpin.

Ecosim uses observed biomass time series to estimate parameters so that modeled species dynamics reproduce dynamics actually observed in the system. Parameters estimated in Ecosim include vulnerabilities, and production anomalies, which define changes over time in the magnitude of primary production relative to the initial production entered in Ecopath. Parameters are estimated based on minimizing the sum of squared residuals between the *log* of Ecosim biomass estimates and the *log* of observed biomass estimates (Christensen et al. 2005). Time series of observed biomass from 1981-2008 for 17 groups were used during the fitting procedure. Observed time series were also used in place of model estimated values for some groups. Model estimates of sea lamprey biomass were set to observed values from 1981-2008, as were fishing mortality rates for ages 1-3 and 4+ lake whitefish, ages 2-4 and 5+ lake trout, and age 1-5 Chinook salmon. Observed biomass and mortality time series were obtained from either survey estimates or estimates from single-species catch-at-age models.

A question arose during model construction of how best to include invasive species that were not present in Lake Huron in 1981 but which invaded the lake thereafter and became important components in the system. Round goby, dreissenid mussels, and predatory zooplankton were modeled as invasive species. We modeled invasive species with low initial biomasses, scaled downward from actual biomass estimates in years when the invasive species were established, and with artificial fishing mortality, which was released when the actual

establishment occurred. Given that invasive species were not actually present in Lake Huron in 1981, but were included in the model, predation mortality by invasive species on their prey was removed using negative biomass accumulation rates. This approach was found to be effective in a comparison of multiple tactics for modeling invasive species in Ecosim (see Chapter 3).

Modeling lake trout dynamics posed a challenge when constructing the Ecosim model. Between 1981 and 2008, lake trout recruitment has been primarily supported by stocking. A stocking function based on observed stocking rates was initially entered into Ecosim to overwrite production of age 0 lake trout. For future simulations, we initially assumed that lake trout stocking would continue, and so assigned values to the stocking function for future years. We found that stocking removed the chance for recruitment overfishing to occur, and that lake trout could persist in the system regardless of the intensity of fishing. Recently, natural recruitment of lake trout in Lake Huron has increased, and discussions about cessation of stocking have begun. To better emulate the direction of lake trout stocking in Lake Huron, and to increase the sensitivity of lake trout recruitment to harvest, we modeled future lake trout production without stocking.

To model future lake trout production without stocking, we had to adjust the way we modeled lake trout stocking. We simulated past stocking rates by multiplying Ecosim-calculated lake trout egg production for each year from 1981-2008 by a factor which represented the relative (to 1981) rate of stocking. Ecosim calculates egg production as the product of spawning stock biomass and an effective fecundity parameter (Walters et al. 2008). The effective fecundity parameter is calculated from the initial biomass and survivorship data inputs, which were entered in Ecopath, and is used to scale the absolute numbers of eggs produced to reflect actual biomass data inputs (Walters et al. 2008). Consequently, we allowed Ecosim to calculate the amount of

recruitment occurring, but then altered the level based on changes in stocking rate. In other words, we supplemented the amount of recruitment predicted by the model to simulate the general increase in stocking observed during 1981-2008. For years after 2008, when we wanted to simulate a cessation of stocking, we set the factor used to multiply model-predicted recruitment to one, which implies that model-predicted lake trout recruitment would not be supplemented by additional production. We admit that our approach for modeling lake trout stocking is a work around. However, our method allowed past stocking rates to influence lake trout dynamics, which we considered important. This method also provided a way to remove stocking in future simulations, which would allow recruitment to be vulnerable to changes in fishing mortality, which we also considered important.

Simulations

Our goal was to simulate a range of harvest strategies using the Ecosim model, and compare their performance at meeting management objectives. The harvest strategies and the objective-based performance measures were developed in consultation with Lake Huron fishery stakeholders (i.e. biologists, managers, industry representatives, and fishers) at two two-day workshops in April 2009 and 2010. Two types of harvest strategies were simulated: 1) increasing or decreasing target fishing mortality rates for lake whitefish in the lake whitefish fishery (and correspondingly for lake trout, as bycatch), which will hereafter be referred to as "incremental policies"; and 2) reducing bycatch rates of lake trout within the lake whitefish fishery, and then considering different lake whitefish harvest scenarios, which will be hereafter referred to as "bycatch policies". The bycatch policies were intended to represent possible changes to fishing practices that would affect bycatch rates, including modifications to gear or adjustments to the

fishing season. Gear modifications include either reducing the amount of net near the bottom of the gear, adjusting the type of gear used, or adjusting mesh size in the net.

For the incremental policies, commercial fishing mortalities for harvested ages of lake whitefish (age 1-3, 4+) and lake trout (age 2-4, 5+) were adjusted. Seven sub-policies were simulated: -100%, -50%, -25%, 0%, +25%, +50%, and +100% changes from 2006 fishing mortalities, which was the most recent year for which we had estimates of fishing mortality for lake whitefish. Fishing rates were changed equally for both lake whitefish and lake trout, because commercial lake trout harvest is derived from bycatch in targeted lake whitefish fisheries.

For the bycatch policies, the rate of lake trout bycatch in the lake whitefish fishery was reduced. Six sub-policies were simulated for the bycatch policies, spanning two distinct but similar scenarios (Table 4.2). In the first two sub-policies, representing the first scenario, lake trout bycatch rates were assumed to be reduced by 25% or 50% from 2006 rates, but lake whitefish harvest was assumed to remain the same. This first scenario was intended to represent changes in fishing gear from gill nets to trap nets. The first sub-policy of the scenario reflected a 50% conversion of gill nets to trap nets for Canadian waters only while the second sub-policy reflected a 100% conversion. In the remaining four sub-policies, representing the second scenario, lake trout bycatch rates were assumed to be reduced by 28% or 49% from 2006 levels. For each reduction in lake trout bycatch rates for the second scenario, one of two conditions was simulated. First, we assumed that fishing effort for lake whitefish would remain the same, causing lake whitefish harvest to remain the same but reducing lake trout harvest because of reduced lake trout bycatch rates. Second, we assumed that fishing effort for lake whitefish would increase up to the point where lake trout harvest would be maintained at levels prior to when bycatch rates were reduced, causing lake whitefish harvest to increase. The second scenario was

intended to represent changes to fishing seasons. A reduction in bycatch rates of 49% from 2006 rates represented harvest levels if fishing occurred only in winter, as calculated from Canadian commercial harvest data from 2004-2008 (Adam Cottrill, OMNR, personal communication). A reduction in bycatch rates of 28% from 2006 rates represented a less extreme case, and reflected harvest levels if fishing did not occur in summer.

Harvest and biomass were identified by stakeholders as the most important performance metrics for distinguishing among sub-policies regarding their success at meeting management objectives. Other performance metrics were noted by stakeholders, including profit, species composition in the harvest, and variability in harvest, but were not included in favor of the more direct and easily interpretable biomass and harvest. Simulations were run for 50 years and harvest and biomass values were averaged over the last 5 years of simulation and used to assess policy performance.

Simulations of the incremental and bycatch policies assessed direct effects of changes to fishing targets on lake trout and lake whitefish biomass and harvest. Another objective of this research was to assess the indirect effects among lake trout, lake whitefish, and the lake whitefish fishery. Indirect effects were assessed by changing fishing mortality rates in the model on either lake trout or lake whitefish alone, and assessing the change in biomass for the other group. Fishing mortality rates for either species were adjusted by -50%, 0, and 50% of 2006 levels, and the change in biomass of the other species was compared. As before, simulations were run for 50 years and biomass values were averaged over the last five years of simulation. This analysis allowed us to separate direct (bycatch) and indirect (food web) effects of harvesting in the model, recognizing that these effects are not separable in the actual fishery because bycatch cannot, for all practical purposes, be eliminated.

Uncertainties

Important uncertainties about Lake Huron's food-web were also discussed during stakeholder workshops. We assessed sensitivity of simulation results to alternative assumptions about three key areas of uncertainty: 1) the amount of future primary production in Lake Huron, 2) the extent of trophic (diet) interactions between lake trout and lake whitefish, and 3) the strength of predator-prey interactions (vulnerabilities) between lake whitefish and their prey, as well as lake trout and their prey. Three possible levels of future primary production were considered: the first (low), second (med.) and third (high) quartiles of estimated production anomalies from 1981-2008. Alternative assumptions about trophic interactions between lake whitefish and lake trout were considered. We increased interaction between lake trout and lake whitefish by increasing the amount of piscivory by lake whitefish by adding 10% of age 0+ rainbow smelt to the diet of age 4+ lake whitefish, and by adding direct predation (2%) of age 5+ lake trout on age 1-3 lake whitefish. Added diet percentages represented a balance between anecdotal observations of piscivory by lake whitefish and consumption of lake whitefish by lake trout from stakeholders, and values reported in the literature. Finally, two alternative assumptions about vulnerabilities for age 5+ lake trout and age 4+ lake whitefish were considered: 1) vulnerabilities estimated from the fitting routine in Ecosim, and 2) a 10x increase in vulnerabilities from the values estimated in Ecosim. Vulnerabilities were increased, as opposed to being decreased, because initial estimated vulnerabilities were low, and low values of vulnerabilities for exploited species tend to result in less change in biomass dynamics of those species than when vulnerabilities are greater (Ahrens et al. 2012).

Each of the harvest strategies described earlier was simulated for each of the above alternative assumptions. The effect of alternative assumptions on the indirect interactions between lake trout, lake whitefish, and the lake whitefish fishery were also assessed. For alternative assumptions about trophic interactions (diet) or the values of vulnerabilities, the model was re-fit, resulting in different estimated production anomalies and vulnerabilities (except for lake trout and lake whitefish vulnerabilities when they were forced). Thus the model parameters were re-estimated as if the chosen assumption about diet or vulnerability was the true state of nature.

Results

Predicted biomass values in Ecosim captured overall trajectories of observed biomass time series for the majority of modeled groups (Figure 4.1). Fits of exploited fish groups were reproduced better than other groups, likely due to additional time series for fishing mortalities (for lake trout, lake whitefish, and Chinook salmon), total mortality (age 1 lake trout), or stocking functions (lake trout, Chinook salmon, and steelhead). Fits of fished groups had sum of squared residuals per data point (SS/n) of 0.24, compared to values of 0.60 for non-fished and non-invasive groups. Fits to invasive species were poorest among modeled groups, in part due to short time series of biomass as well as to large relative changes within the time series. Sum of squared residuals per data point for invasive groups were 1.17. Increases and decreases over time in age 4+ lake whitefish biomass was captured, although increases in biomass were greater in the model than those observed in later years (Figure 4.1). Similarly, the decline in age 5+ lake trout biomass during the 1980s, increase during the 1990s, and decline during the later 2000s was captured, although predicted biomass was lower than what was observed during the 2000s

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(Figure 4.1). Predicted declines in Chinook biomass were similar to observed declines, and were largely driven by declines in alewife (Figure 4.1). Although variability in observed alewife biomass was not captured by the model, the overall decline in biomass, and low levels after 2003 were captured (Figure 4.1). Predicted declines in *Diporeia* were not as extreme as those observed, however the short length of the biomass time series made comparing the two more difficult (Figure 4.1). Predicted changes in invasive species biomass did not match all observed values, however the basic dynamics of species invasion, where biomass remained low until the time of invasion and increased afterwards, were captured (Figure 4.1).

Not all predicted biomass dynamics for non-invasive groups matched observed values. Fits to observed biomass time series of age 1-3 lake whitefish, age 2-5 steelhead, age 1+ rainbow smelt, and age 1+ bloater were poor. Fits for steelhead could likely be improved if time series of fishing mortalities were available. Instead, a constant fishing mortality of steelhead in the recreational fishery was assumed, which is unlikely. The decline in age 1+ rainbow smelt, increase in age 1+ bloater biomasses during the late 1980s, and increase in age 1-3 lake whitefish biomasses during the early 1990s were not captured during the fitting process. Bloater, rainbow smelt, lake whitfish, and steelhead biomass dynamics were matched if time series were fit one at a time, however could not be fit as well when other time series were included in the fitting process. Time series for burbot, age 0 rainbow smelt, age 0 alewife, and age 0 bloater were also originally included in the model, but excluded for final analysis because fits to them were poor. Observed time series of age 0 prey fish biomasses were highly variable, likely reflecting variation in recruitment. Although variability in recruitment for age 0 prey fish would have been valuable to capture, estimates of production anomalies were very sensitive to age 0 prey fish time series, resulting in poor fits for other groups. Consequently, fits to adult prey fish time series

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were preferred. Burbot time series were similarly difficult to fit. Biomass estimates of burbot could not be fit even when burbot were the only time series included in the fitting process. This suggested that either Ecopath data inputs for burbot were inaccurate (not capturing the actual interactions between burbot and other species) or that the observed biomass time series for burbot was inaccurate. Both factors likely contributed to poor burbot fits.

Vulnerability parameters and production anomalies were estimated by the model during the fitting routine. Both high and low vulnerabilities values were estimated, depending on the group, with a vulnerability of 4.7 being the median. Age 0 and 1+ alewife had the highest vulnerability allowed by the fitting process, which was 1.0×10^{10}. In contrast, age 1-5 Chinook salmon, age 2-5 steelhead, and non-invasive lower trophic groups had estimated vulnerabilities of their prey to them near one (the lowest possible value). Production anomalies showed strong declines in primary production in recent years (Figure 4.2), likely driven by the overall declining trend in most biomass time series (Figure 4.1).

Policies

Patterns in performance metrics for the incremental and bycatch policies were as expected. Policies where bycatch rates of lake trout were adjusted performed best at meeting performance metrics for both species. As commercial fishing mortality targets were increased from estimated rates in 2006 in the incremental policies, harvest of lake whitefish increased by 65% (Figure 4.3). Gains in harvest of lake whitefish were offset by 39% and 68% reductions in biomass of lake whitefish and lake trout, respectively, from conditions without commercial harvest (Figure 4.3). Lake trout harvest was non-zero, even at a 100% reduction in commercial harvest because recreational harvest still occurred (Figure 4.3).

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In contrast to the incremental policy, the bycatch policies achieved increases in lake trout biomass without reductions in lake whitefish harvest (Figure 4.3, sub-policies 1-4), or similarly, achieved increases in lake whitefish harvest without reductions in lake trout biomass (Figure 4.3, sub-policies 5-6). The largest reduction in lake trout bycatch rates (50% reduction in fishing mortality in 2006 for sub-policy 2) resulted in a 37% increase in biomass from simulated 2006 levels (Figure 4.3). Similar increases in biomass were observed for sub-policy 4 (Figure 4.3). The largest increase in lake whitefish targets (192% of fishing mortality in 2006 for sub-policy 6) resulted in a 63% increase in lake whitefish harvest from simulated 2006 levels (Figure 4.3).

The magnitude of estimated harvest for lake trout in both the incremental and bycatch policies was lower than expected. Average harvest quotas for lake trout in Lake Huron from 2003-2008 were approximately 0.3 million kg (Adam Cottrill, OMNR, personal communication) however simulated harvest was an order of magnitude lower (Figure 4.3). Although the absolute biomass of lake trout was not comparable to recent estimates, we felt that proportional changes in lake trout biomass and harvest were appropriate. Low harvest of lake trout occurred because biomass of lake trout was lower than expected, which in turn was a function of how we handled lake trout stocking. Lake trout were not stocked in future simulations to allow the possibility of recruitment overfishing of lake trout to occur. If stocking of lake trout were continued past 2008, biomass, and consequently harvest of lake trout would be nearer to observed values from 2003-2008. Harvest and biomass for lake whitefish were similar to values from 2003-2008 regardless of whether lake trout were stocked in the future.

Levels of biomass and harvest for lake trout and lake whitefish did not show signs of overfishing among the policies considered. Harvest of both species increased steadily as fishing mortality targets increased (Figure 4.3). Had either recruitment or growth overfishing occurred,

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harvest would have been expected to decline as fishing mortality targets were increased. The policy under which the greatest amount of fishing occurred reflected a fishing mortality rate of 0.32 for age 5+ lake trout and 0.193 for age 4+ lake whitefish. Adding predation by sea lamprey and other mortality from the model resulted in total instantaneous mortality rate under this scenario of 0.83 for lake trout and 0.58 for lake whitefish; higher than the mortality rate corresponding to stock decline for lake trout (0.69, or 50% annual mortality; Healey 1978), and lower than the rate at which lake whitefish stocks become depleted (1.2, or 70% annual mortality; Ebener et al. 2005).

Our simulation results indicated limited indirect interaction occurred between lake trout and lake whitefish. Changes in lake trout biomass due to changes in fishing mortality had negligible effect on biomass of lake whitefish (Figure 4.4). Changes in lake whitefish biomass had a larger effect on biomass of lake trout, however the effect was still small. Interactions between lake trout and lake whitefish were largest when vulnerability parameters were adjusted and small when diet compositions were adjusted. Under changes in vulnerability parameters and diet compositions, 50% changes to the fishing mortality rate of lake whitefish resulted in at most a 17% and 0.5% change in lake trout biomass, respectively (Figure 4.4)

Uncertainties

Alternative assumptions about future levels of environmental productivity resulted in the greatest changes in harvest and biomass for lake trout and lake whitefish. As expected, higher productivity resulted in higher biomass and harvest of both species, across a wide range of fishing mortality rates (Figure 4.5). Changes in lake whitefish biomass and harvest across sub-policies were similar among productivity values (decreasing by about 40% from unfished

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conditions for biomass and increasing by about 65% from estimated 2006 levels for harvest),

however biomass and harvest of lake trout were especially sensitive to higher productivity

(Figure 4.5). When productivity was high, biomass of lake trout declined from unfished

conditions as fishing mortality targets increased more (81%) than under low (50%) or median

(68%) productivities (Figure 4.5). Under high productivity, biomass declined at a faster rate than

the increase in fishing mortality and therefore harvest declined as fishing mortalities targets were

increased from 2006 levels (Figure 4.5). The decline in harvest was unexpected, and it shows

that the ability of lake trout to compensate from increased fishing mortality is reduced when

productivity within the system increases.

Changes in diet did not greatly alter biomass and harvest of lake whitefish or lake trout

across sub-policies. In general, biomass and harvest of lake trout and lake whitefish when diets

were adjusted were similar to values from the model with original diet compositions (Figure 4.6).

The small differences in results were the result of refitting vulnerabilities and production

anomalies more so than due to changes in diet. When diets were changed without re-fitting the

model (i.e., without adjusting vulnerabilities and production anomalies), the performance metrics

showed little difference from the results when original diet and vulnerability values were used;

results not shown), implying that changes in vulnerability (when the model was re-fitted) had a

greater effect on performance metrics than did changes to diet.

Changes in vulnerabilities had a small effect on the biomass and harvest of lake whitefish

across sub-policies, and had a much larger effect on the biomass and harvest of lake trout (Figure

4.6). Lake whitefish biomass decreased across sub-policies more (51%) when vulnerabilities

were changed than when original vulnerabilities were used (~35%; Figure 4.6). In contrast,

biomass of lake trout was less sensitive to increased fishing mortality rates under higher values

of vulnerability, and declined by 14% from unfished conditions when vulnerabilities were changed, compared to the 68% decline when original vulnerabilities were used (Figure 4.6). Vulnerabilities of prey to lake whitefish were the major reason for the effect, because changes in vulnerabilities of prey to other groups in the model, including lake trout, had less influence on the performance metrics than did changes to vulnerabilities of prey to lake whitefish. With higher vulnerabilities for their prey, decreased lake whitefish biomass allowed prey of lake whitefish to increase as fishing mortalities increased, thereby providing additional food to younger lake trout. Increased growth of and reduced predation on younger lake trout reduced the effect of fishing on older lake trout biomass. The strength of the compensation was surprising, and suggests that under high vulnerabilities of prey to lake whitefish, lake trout biomass remains relatively unaffected by changes in fishing mortality. In other words, decreases in lake trout biomass due to fishing were mitigated by increases in lake trout biomass due to greater prey availability and survival for younger ages.

Discussion

Ecopath with Ecosim was able to capture the overall biomass dynamics within Lake Huron's food-web (Figure 4.1). When aggregated into a single fitting routine, it was clear that many biomass time series for Lake Huron declined in recent years. Individual variations in observed biomasses were not always matched however. For example, peaks in age 1+ bloater, deepwater and slimy sculpin, round goby, and dreissenid time series were not reproduced as well as for other groups in the model. Furthermore, fits of steelhead and patterns in age 1+ rainbow smelt biomass were poor. Imperfect fits were in part to be expected, because the fitting routine made tradeoffs in fits among groups.

The primary purpose for time series fitting was to estimate vulnerability parameters. Although critically influential on simulation outcomes, vulnerabilities are very difficult to estimate in the field (Christensen et al. 2005). Fitting modeled biomass dynamics to observed time series is therefore more important because it is one of a few ways to estimate vulnerability parameters for Ecosim models (Ahrens et al. 2012). Given the importance of time series fitting in estimating vulnerability parameters, consistent and reliable time series of biomass are valuable to the construction of Ecosim models.

Policies

Bycatch policies best balanced tradeoffs between harvest of lake whitefish and lake trout biomass. Results of the bycatch policies should be considered in the context of practical considerations for the existing fisheries. Current management practices for Canadian commercial fisheries in Lake Huron limit changes to fishery quotas to be no more than 10% per year, except under extreme cases (Ebener et al. 2008a), so changes of greater than 10% may not be easily implemented. Similarly, the bycatch sub-policies were developed to reflect possible changes in gear and season. Complete conversion of gill nets to trap nets in Canadian waters of Lake Huron would be challenging in some locations depending on depths and habitat conditions. Gill nets are viewed by many commercial fishers as easier to handle and more suitable for smaller fishing operations, and can be more easily fished in deeper waters and above variable substrate types than can trap nets (Ebener et al. 2008). Consequently, there may be areas and fishers that would not be able to easily convert entirely from gill nets to trap nets. Restricting fishing to a single season or eliminating fishing for an entire season would also present significant challenges. Winter fishing is physically demanding and dangerous, and thus is likely more costly for the

same level of effort. In addition, removing a summer fishing season would affect access to local markets created by seasonal resort users in areas where fishing occurs. Stakeholders emphasized the value of this specialty market during our workshops. More generally, markets for fresh lake whitefish exist year-round, so seasonal restrictions on fishing could have economic consequences not considered in our analysis.

Despite the challenge of actually implementing some of our simulated policies, they still provided valuable insight into management tradeoffs. Rather than implement smaller scale adjustments to lake trout bycatch rates, which may be more feasible, we chose to use policies that would elicit greater changes in biomass and harvest. Based on our analysis, complete conversion from gill nets to trap nets in the Canadian fishery or allowing harvest only in winter, both substantial undertakings, would provide a 36% increase in lake trout biomass and 63% increase in lake whitefish harvest from estimated 2006 values, respectively. More conservative, but feasible, policies would most likely yield lesser changes in bycatch rates, and subsequently lesser increases in lake trout biomass and lake whitefish harvest.

Simulation-based management strategy evaluations of harvest policies using single-species statistical models have been performed for lake trout in Lake Superior (Nieland et al. 2008) and lake whitefish stocks in parts of Lake Huron (Molton 2011; Deroba and Bence 2012). Ecopath with Ecosim models do not have the level of detail or statistical rigor employed in single-species statistical models, and thus exact comparisons with previous studies are difficult, but general comparisons are warranted given the similarities in species and location. Our results are not at odds with previous findings for lake whitefish. Deroba and Bence (2012) compared alternative harvest control rules for lake whitefish stocks in the 1836 Treaty waters of Lake Huron and found that among constant fishing mortality harvest control rules, which were most

similar to our analysis, the current management target of 65% total annual mortality rate resulted in maximum yields and low reductions in spawning stock biomass. Molton (2011) found that if mixing occurred between productive and less productive lake whitefish stocks, a 45% total annual mortality rate resulted in less risk of overexploitation than a 65% rate. Under a 100% increase in fishing mortality rates in our simulations, lake whitefish total annual mortality rate was 44%, and therefore our finding that this resulted in the maximum harvest among the policies we considered is not unreasonable. Our total annual mortality rate is calculated using a aggregated fishing mortality rate over ages four and above, and thus harder to compare with the management target, which is to be applied for fully selected ages.

What is surprising about our results is that they suggest that lake trout can withstand greater harvest pressure than previous studies. Nieland et al. (2008) found that the currently accepted 42% annual total mortality rate for lake trout in Lake Superior was sustainable when assessed using dynamic simulation models, and that rates higher than 74% total annual mortality rate should be avoided. Under a 100% increase in fishing mortality rates, lake trout total annual mortality rate was 56%, and therefore between sustainable and unstable rates found by Nieland et al. (2008). Lake trout biomass reached 32% of unfished levels at our highest fishing rate (Figure 4.3) and therefore was near the threshold of sustainability used by Nieland et al. (2008). Nonetheless, at 32% of unfished levels, lake trout harvest was increasing (Figure 4.3). A possible reason for why our model suggested greater ability of lake trout to withstand harvest than do either Nieland et al. (2008) or Healy (1978) could be that we used age 5+ lake trout biomass and harvest as our performance metric. Nieland et al. (2008) found that if age 4+ lake trout were used, higher rates of harvest would not indicate declines in abundance. Using an older age to

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assess lake trout performance for our analysis might therefore result in policy outcomes more similar to conventional wisdom.

Uncertainties

Our analysis also revealed that future management scenarios are heavily influenced by future environmental productivity, which affected the magnitude of performance metrics more than when alternative assumptions about diet or vulnerabilities were included. Future primary productivity had a greater influence on the magnitude of performance metrics than on the relative performance of management actions considered (Figure 4.5). Future productivity was increased 27% from low to high levels, however lake trout harvest (which changed the most among lake trout and lake whitefish performance metrics) increased by at most 47-fold from low to high levels of production (at unfished levels). Lake trout biomass was affected by increases in productivity more than lake whitefish likely because lake trout vulnerability was higher than that of lake whitefish. Higher vulnerability implies a further distance from carrying capacity (Ahrens et al. 2012), which means that lake trout consumption to biomass ratios would be less density dependent than those of lake whitefish, so greater lake trout biomass was not offset by reduced consumption to biomass ratios as much as for lake whitefish.

Lake trout biomass was also more sensitive to changes in fishing mortality under high levels of primary production than under low levels (Figure 4.5). An alternative interpretation of our results is that lake trout were less sensitive to changes in fishing mortality under low levels of primary production than under high levels (Figure 4.5). At 2006 fishing mortality rates, annual total mortality of lake trout was 49%, which was similar to the rate corresponding to stock decline found by Healey (1978) and supported by Nieland et al. (2008). Consequently, patterns

for lake trout harvest under high levels of production may be more reflective of what is known about lake trout than under low and median levels of production. The exact mechanism for why lake trout were less able to compensate for increased fishing mortality under higher levels of production (or more able to under lower and median levels) is unknown. Potential mechanisms could be increased competition with other piscivores (steelhead, Chinook salmon, and burbot biomass increased more under high levels of production than median levels as fishing mortality rates increased), or decreased recruitment of age 0 lake trout (mortality rates of age 0 lake trout increased more under high levels of production than median levels as fishing mortality rates increased). Although no obvious reason for the difference in compensation between the levels of production was apparent, it is possible that multiple less obvious differences (e.g. increased competition and decreased recruitment) could compound with one other and result in the pattern observed (Figure 4.5).

The large changes that have occurred to the Lake Huron food web in recent years point to considerable uncertainty about what commercial fishery yields and coldwater fish biomasses can be expected in the future. Productivity was variable in the 1990s (Figure 4.2), likely following spikes in biomass for deepwater and slimy sculpin, age 1+ bloater, and ninespine stickleback (Figure 4.1). Estimates of production after 1995 declined to their lowest levels in 2006. If productivity remains low, expectations for future yields should be adjusted downward to reflect this. Dreissenid mussels are hypothesized to remove nutrients from the offshore community and bind them in near shore areas (Hecky et al. 2004), so continued expansion of dreissenids would suggest future production in the offshore fish community to be even lower. Alternatively, low estimated production anomalies might be an artifact of the fitting routine, and instead reflect the common decline in biomass time series. Increased production in the final year of simulation may

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similarly be an artifact of increases in some biomass time series during that year (Figure 4.2). Trends in observed phosphorous loadings declined in recent years (Barbiero et al. 2009), but not to the extent of our estimated production anomalies. Similarly, trends in observed chlorophyll α did not reveal strong declines in recent years (Barbiero et al. 2009). Consequently, increased productivity in the future may not be unreasonable.

Alternative assumptions about diet or vulnerabilities did not change the magnitude of performance metrics as greatly as did changes in environmental productivity, however the ranking of policies was affected. Changing vulnerabilities of lake trout and lake whitefish affected the performance of policies for lake trout. With increased vulnerability for both species, lake trout biomass remained nearly unchanged across fishing mortality rates (Figure 4.6). Increased lake whitefish vulnerabilities were responsible for reduced sensitivity of lake trout biomass to fishing. As fishing mortality rates were reduced, lake whitefish biomass increased (Figure 4.6). With higher vulnerabilities, as lake whitefish biomass increased, predation mortality on prey increased even more, and therefore biomass of lake whitefish prey declined. Young lake trout, and prey of older lake trout, feed on prey of lake whitefish. Consequently, as prey of lake whitefish declined, prey of lake trout declined as well. Reduced growth of young lake trout resulted in greater foraging time, which resulted in greater mortality because foraging time is proportional to natural mortality for younger age groups (Walters and Juanes 1993; Christensen and Walters 2004). Therefore, as fishing mortality declined, biomass of older ages of lake trout did not increase as much as was expected. Although the decreased biomass of younger ages of lake trout was not enough to offset the increased biomass of older ages due to less fishing pressure as fishing mortality rates were reduced, it did alter dynamics more than when either diet was changed or when original diets and vulnerabilities were used (Figure 4.6). Changes in diet

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reduced the rate of increase in lake whitefish biomass as fishing mortalities were decreased (Figure 4.6). Although different trophic interactions can not be ruled out as having an effect, when diets were changed and vulnerabilities were not refit, the results were very similar to when original diets and vulnerabilities were used. From this we concluded that different values for vulnerabilities were likely more responsible than changes in diets for the slower increase in lake whitefish biomass as fishing mortality rates were decreased.

If lake trout biomass was sensitive to lake whitefish vulnerabilities, then it is important to assess the likelihood that lake whitefish vulnerabilities could be higher than our model estimates would suggest. Evidence for determining the values of lake whitefish vulnerabilities can be taken from results of the fitting procedure. Fits to time series had residual sum of squares of 160 for the original model and 156 for the model where vulnerabilities were increased. Difference in sum of squares between the original model and the model with higher vulnerabilities were small compared to the initial sum of squares for both models of 942 and 1225, respectively, prior to fitting. Therefore, based on the fitting routine, lake whitefish vulnerabilities were more likely to be higher, and therefore lake whitefish would have greater influence on lake trout restoration.

Evidence for the likelihood that lake whitefish vulnerabilities could be higher can also be taken from the biological interpretation of vulnerabilities. Discussions of top-down or bottom-up control have rarely included lake whitefish (Bence et al. 2008), so its difficult to say whether lake whitefish vulnerabilities would be low or high based on the type of control. Lake whitefish abundance may have been greater in the past based on high harvest in the late 1800s (Baldwin et al. 2002), however the influx of dreissenids likely has reduced carrying capacity in Lake Huron. There is criticism about the feasibility of the FCOs in Lake Huron (Bence et al. 1999) given the declines in prey fish (Riley et al. 2008) and *Diporeia* abundances (Nalepa et al. 2009), and

increases in dreissenid abundance (Nalepa et al. 2007). A reduced carrying capacity in the lake combined with record harvest would suggests lake whitefish to be near carrying capacity, and therefore have low vulnerability.

As might be expected from the results of Figure 4.6, differences in vulnerabilities influenced the strength of indirect interactions between lake trout and lake whitefish. Indirect effects were greatest when alternative assumptions about vulnerability parameters were included in the model (Figure 4.4). The primary mechanism for differences in indirect interactions was differences in vulnerabilities. Under low vulnerabilities, lake whitefish were unable to exert greater predation mortality on their prey as their biomass changed. Any changes in the biomass of lake whitefish therefore limited changes in the biomass of their prey, and indirectly the biomass of other groups in the model. When vulnerabilities of lake whitefish were altered, changes in lake whitefish had larger effects on other groups. Using original model-estimated values for vulnerabilities, we would conclude that that the commercial fishery is the primary factor that links these two groups, and that future work on balancing tradeoffs in the commercial fisheries should therefore focus on direct interactions with the fishery (i.e. bycatch management), rather than on indirect interactions through the food web. However, there were scenarios where the indirect interactions between lake whitefish and lake trout were more substantial. Differences between these scenarios point to increased importance of improved estimation of vulnerability parameters in EwE models.

Future directions

Some future directions for research were revealed in this analysis. First and foremost was the ongoing discussion on the importance of vulnerabilities in Ecosim models. Indirect

interactions were mediated by changes in lake whitefish vulnerabilities, as were policy outcomes for lake trout. Both values used for lake whitefish vulnerability were reasonable and were supported by either model fits or biological interpretations of vulnerabilities. When lake whitefish vulnerabilities were low, the indirect interactions between lake trout and lake whitefish were minimal, however the magnitude of the interaction increased as vulnerabilities for lake whitefish increased. Consequently, improved understanding on the likelihood of lake whitefish to have high vulnerabilities would be valuable. Secondly, future productivity in the system is uncertain. Although not done in our analysis, future work would assess the ability for dreissenids to account for declines in biomass time series for most groups in the absence of changes in production anomalies. In other words, research could be performed on the extent to which dreissenids are responsible for declines in biomass of modeled groups. Modeling the effect of dreissenids could provide evidence on future levels of primary production, that if high were found to affect preferred targets of fishing mortality rates for lake trout, in particular.

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APPENDICES

APPENDIX 4A

Tables and Figures

Table 4.1: Biomass, production to biomass ratios (P/B), consumption to biomass ratios (Q/B), biomass accumulation rates (BA), and total harvest (Y) for the balanced Ecopath model. Round goby, dreissenids, and predatory zooplankton were modeled as invasive species, and so were artificially harvested. Predation mortality by invasive species on prey (*Diporeia*, *Mysis*, benthic invertebrates, zooplankton, and phytoplankton) was offset using negative BA rates. Values of BA for age-structured groups are given for the oldest age stanza, but are applied by Ecosim to all ages of the group.

Group	Biomass (g/m^2)	P/B (yr^{-1})	Q/B (yr^{-1})	BA (yr^{-1})	Y(g/m^2)
Sea lamprey	0.000284	0.860	80.0		
Age 0 lake whitefish	0.0549	2.00	17.1		
Age 1-3 lake whitefish	0.526	0.587	6.55		0.000132
Age 4+ lake whitefish	0.177	0.483	4.41	0.289	0.0171
Age 0 lake trout	0.00452	5.48	22.4		
Age 1-2 lake trout	0.00588	0.729	7.95		0.00429
Age 2-4 lake trout	0.0435	0.411	4.50		0.000388
Age 5+ lake trout	0.0369	0.678	3.35	-0.081	0.00592
Age 0-0.5 Chinook salmon	0.00045	0.001	25.0		
Age 0.5-1 Chinook salmon	0.00474	1.23	12.4		
Age 1-5 Chinook salmon	0.0990	0.888	5.00		0.00669
Age 6+ Chinook salmon	0.00584	0.888	3.17		
Age 0-1 steelhead	0.000934	0.001	22.1		
Age 1-2 steelhead	0.00686	0.500	12.2		
Age 2-5 steelhead	0.0790	0.110	7.35		0.000333
Age 6+ steelhead	0.253	0.110	5.99		
Age 0-3 burbot	0.00118	0.667	7.65		
Age 3+ burbot	0.0101	0.263	3.38		
Age 0 alewife	0.468	4.00	29.2		
Age 1+ alewife	1.99	1.25	11.0	-0.282	
Age 0 rainbow smelt	0.369	2.64	14.3		
Age 1+ rainbow smelt	2.46	1.17	5.50	-0.044	
Age 0 bloater	0.0390	2.33	20.4		
Age 1+ bloater	0.186	1.02	7.00	0.681	0.00540
Round goby	0.0000260	1.97	4.70		0.0000283
Slimy sculpin	0.00835	1.50	12.0	-0.091	
Deepwater sculpin	0.218	0.900	10.0	-0.070	
Ninespine stickleback	0.00720	2.45	12.0		
Diporeia	26.0	2.00	15.0	-0.00000168	
Mysis	4.00	3.00	12.0	-0.00000410	
Benthic invertebrates	3.17	2.36	8.14	-0.0000190	
Dreissenid mussels	0.0980	1.39	8.60		0.105
Predatory zooplankton	0.000366	25.5			0.000168
Zooplankton	5.76	21.1		-0.00647	
Phytoplankton	7.40	278		-0.0228	
Detritus	73.6				

Table 4.2: Details on the percentage of reduction in bycatch rate from 2006 fishing mortality rates and the targeted fishing mortality rates (F) for age 5+ lake trout in the 6 sub-policies of the bycatch policies. Sub-policy 0 is the status quo simulation where the fishing mortality rates for lake trout and lake whitefish were set to 2006 rates. Sub-policies 1-6 were intended to represent one of two scenarios: changes in gear from gill to trap nets (gear), or changes to fishing seasons (season). Of the seasonal scenario sub-policies, one of two conditions were met; either age 5+ lake trout (LT) or age 4+ lake whitefish (WF) fishing mortality rates were maintained at 2006 levels.

Sub-policy number	Scenario	Condition	Reduction in bycatch rate	F
0	-	-	0%	0.161
1	Gear	-	25%	0.0823
2	Gear	-	50%	0.122
3	Season	WF	28%	0.116
4	Season	WF	49%	0.0826
5	Season	LT	28%	0.161
6	season	LT	49%	0.161
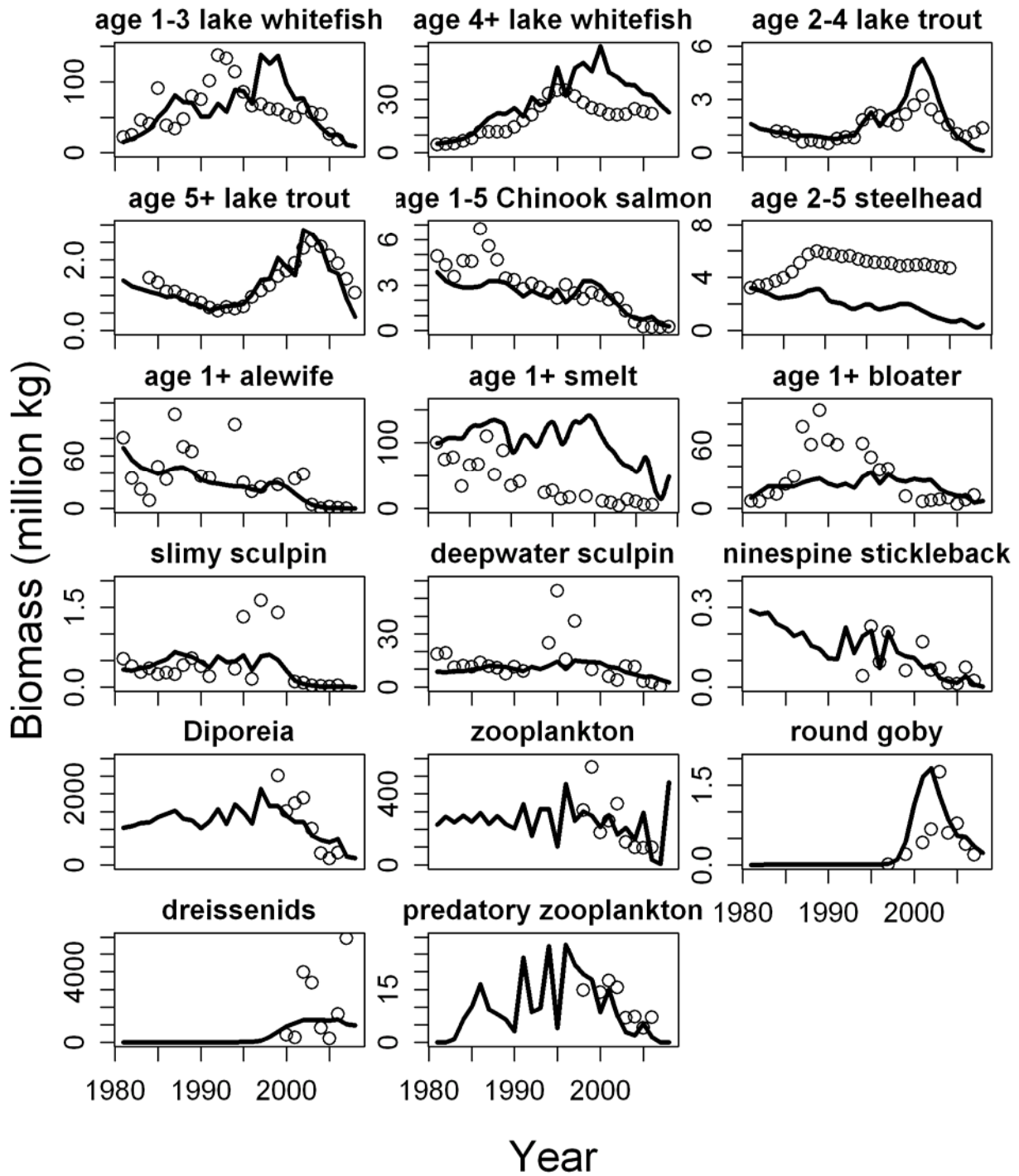
Figure 4.1: Fits to observed biomass time series. Open circles are observed yearly data, solid line is Ecosim monthly estimate. Age 4+ lake whitefish, age 5+ lake trout and invasive species groups (round goby, dreissenids, and predatory zooplankton) were fit using absolute time series. All other groups were fit with relative time series.
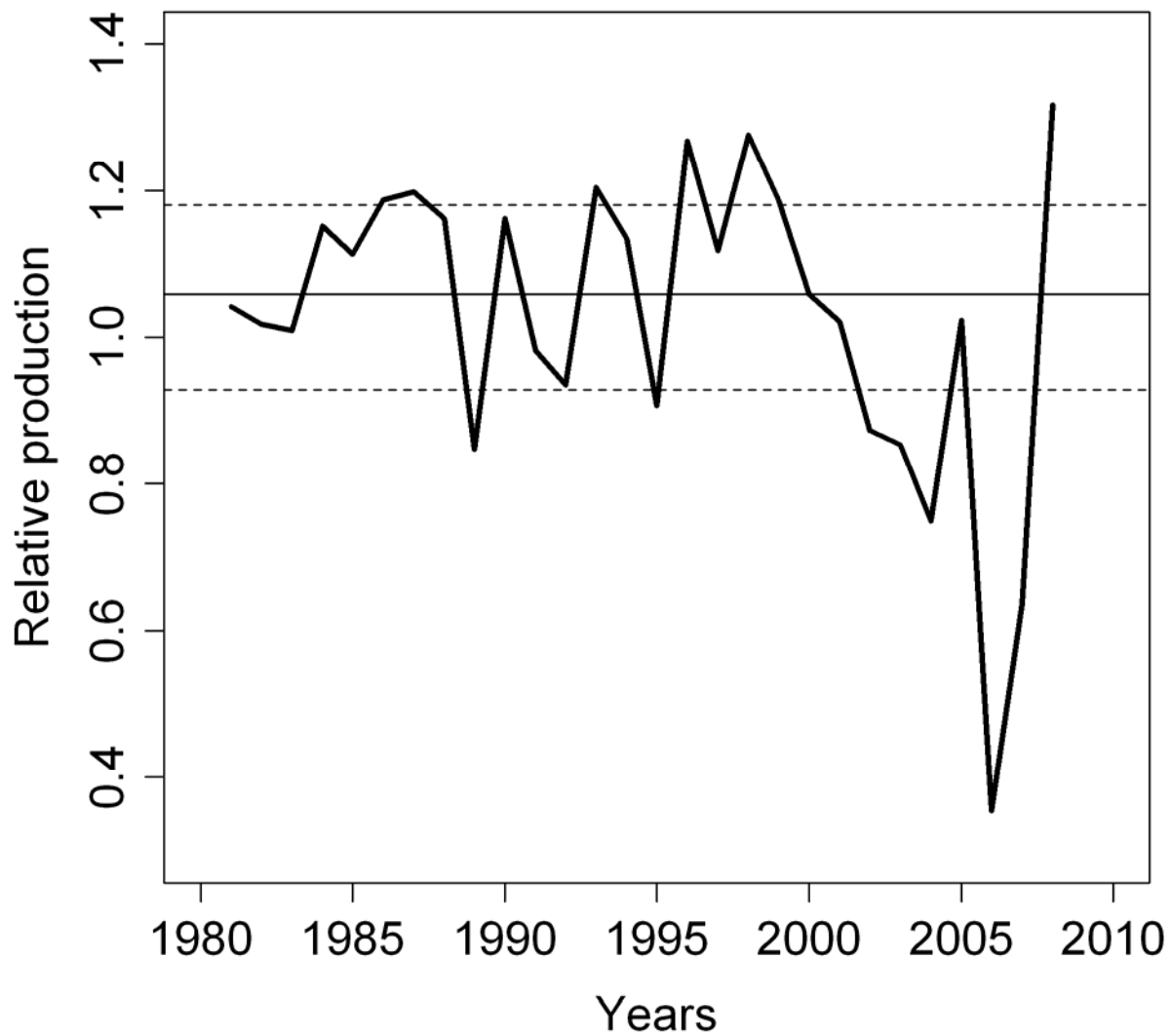
Figure 4.2: Time series of yearly estimates (production anomalies) of relative production for phytoplankton from 1981-2008, where values are relative to the initial Ecopath value. Dotted horizontal lines represent the 1st (lower) and 3rd (upper) quartiles of the time series, and the solid horizontal line represents the median value of the time series.
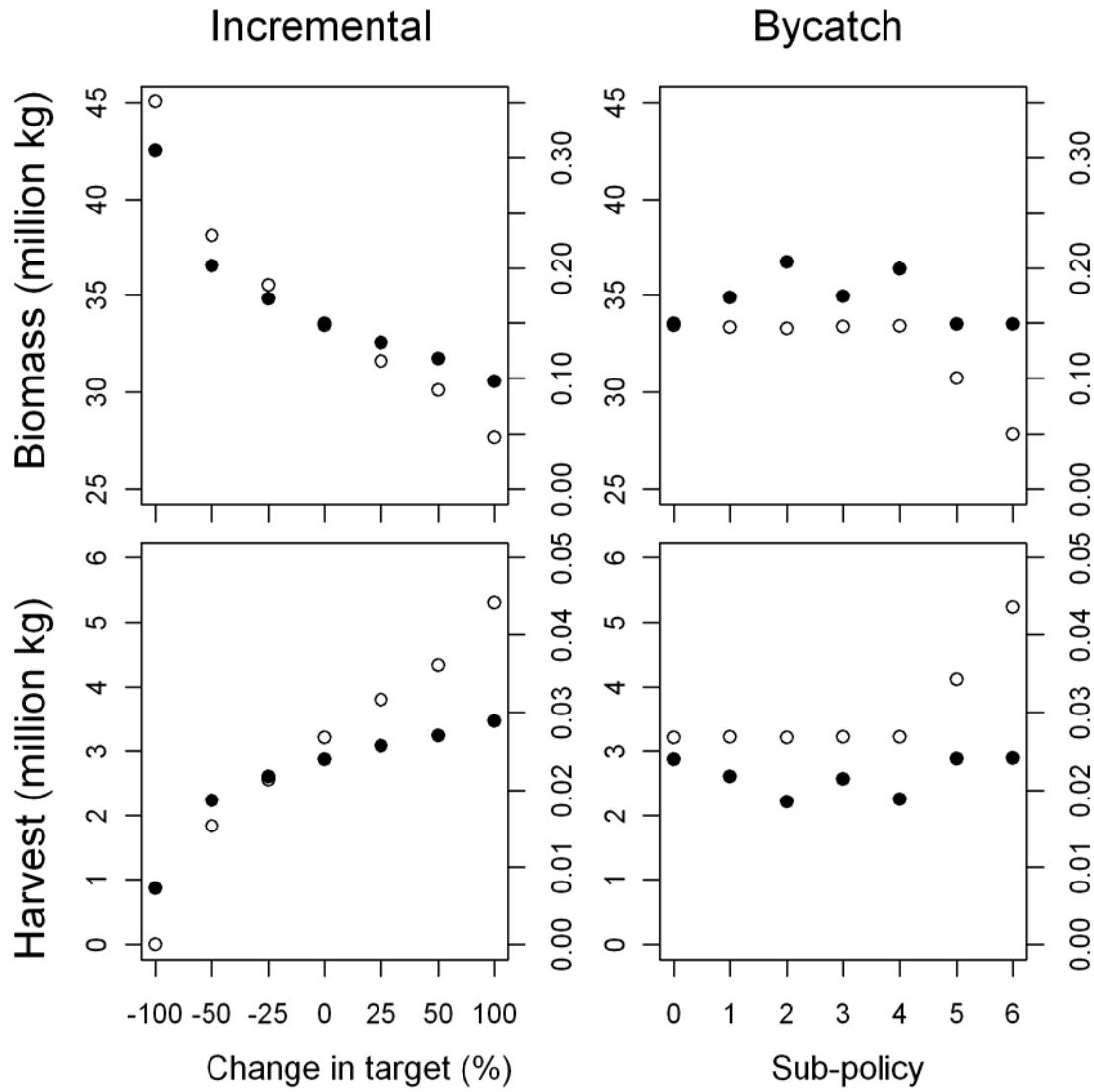
Figure 4.3: Average biomass and harvest from the last five years of simulations for age 4+ lake whitefish (open circles) and age 5+ lake trout (solid circles) for the "incremental" and "bycatch" policies. Biomass and harvest values for age 4+ lake whitefish are on the left y-axis, while values for age 5+ lake trout are on the right y-axis. Changes in target for the "incremental" policy are based on 2006 fishing mortality levels for both species, and sub-policies for the "bycatch" policy are outlined in Table 4.2.
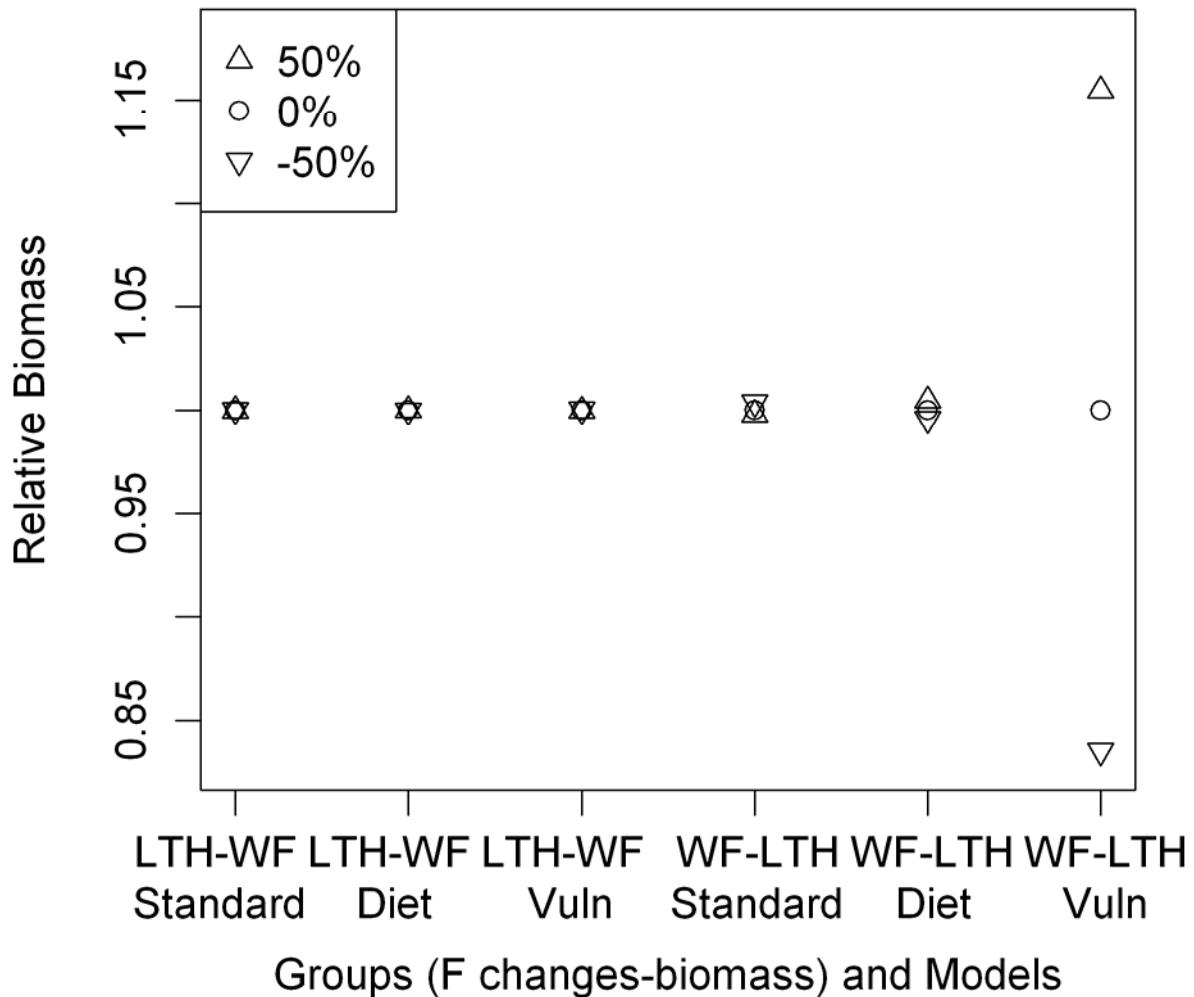
Figure 4.4: Average relative biomass in the last five years of simulation for age 4+ lake whitefish at various levels of fishing mortality on age 5+ lake trout (LTH-WF) and of age 5+ lake trout at various levels of fishing mortality on age 4+ lake whitefish (WF-LTH). Biomass values were plotted relative to the biomass when fishing mortalities were unchanged (0%). The level of fishing mortality was expressed as a percentage of fishing mortality in 2006. The second row of the x-axis reflects the model under standard assumptions for diet and vulnerabilities (Standard), with adjustments to diet (Diet), or with greater vulnerability values for age 4+ lake whitefish and age 5+ lake trout (Vuln).
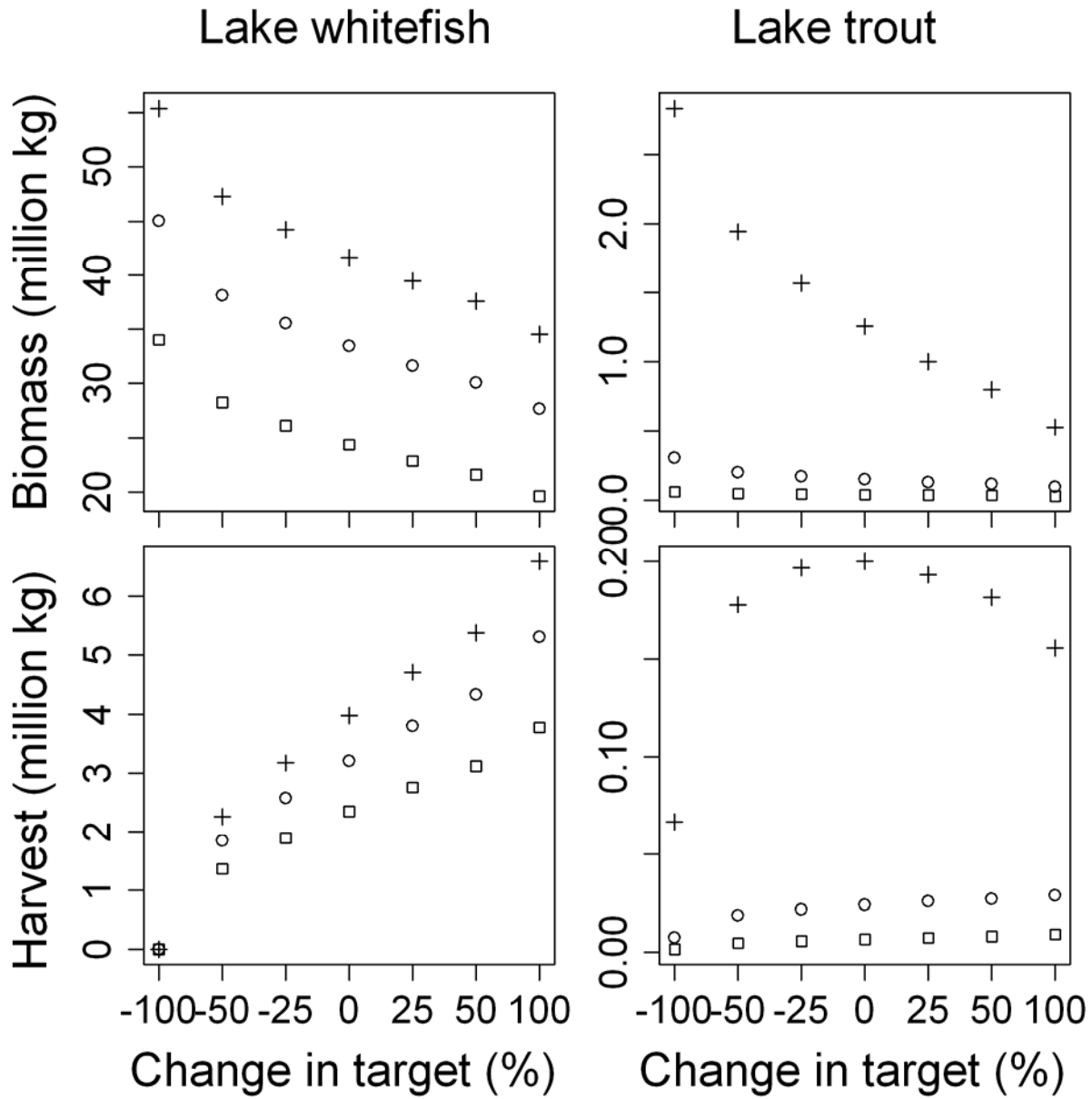
Figure 4.5: Average biomass and harvest of age 4+ lake whitefish (whitefish) and age 5+ hatchery lake trout (lake trout) from the last five years of simulation for three levels of environmental productivities in the standard model for the "incremental" policy. Levels were based on the 1st quartile (square), median (circle), and 3rd quartile (plus sign) from estimated production anomalies (see Figure 4.2).

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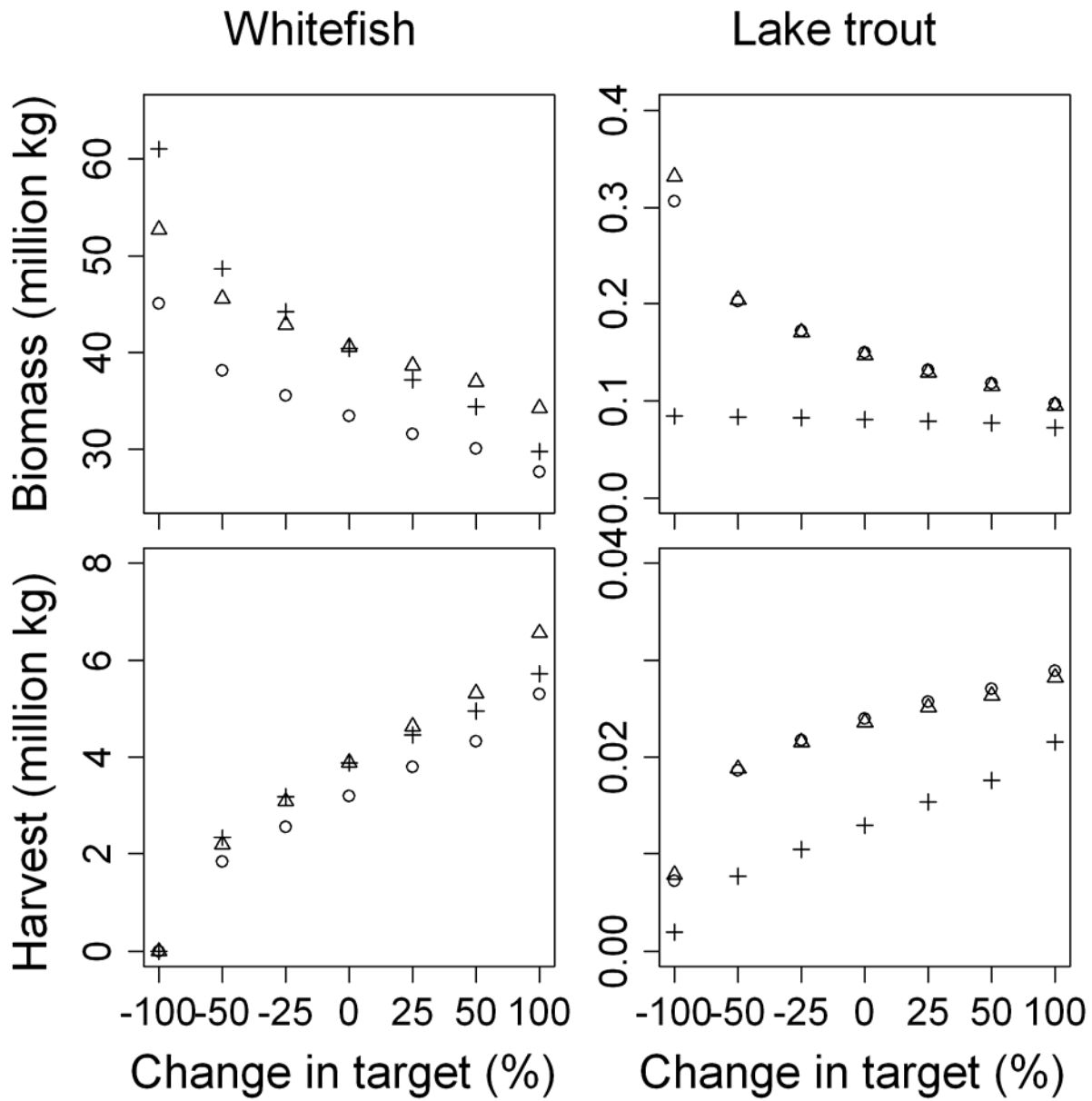
Figure 4.6: Average biomass and harvest of age 4+ lake whitefish (whitefish) and age 5+ lake trout (lake trout) from the last five years of simulation under standard assumptions (circle), with adjustments to diet (triangle), and with greater vulnerability values for age 4+ lake whitefish and age 5+ lake trout (plus sign) for the "incremental" policy.

APPENDIX 4B

Explanation of data inputs used for the Ecopath models in Chapters 3 and 4.

This document outlines the process for obtaining data inputs for 21 individual species or functional groups in the Ecopath models described in Chapters 3 and 4 of this dissertation (Table 3.1). It is my hope that this document will provide assistance to future Ecopath modelers during model parameterization. The descriptions are formatted the same for each group, with ordered categories numbered below. All groups have descriptions about biomass, production to biomass (P/B) and consumption to biomass (Q/B) ratios, diet contributions, and other categories are described as needed. I also include a description for how the management strategy evaluation (MSE) simulations for lake whitefish and lake trout harvest were structured which also includes adjustments to harvest of Chinook salmon, and so is located after the description for Chinook salmon. After the descriptions for data inputs for all groups, I include an overall description for the feeding time adjust rates used in Ecosim, and a description for the proportion of unassimilated to consumed food used in Ecopath. Values for these two data inputs were adjusted slightly from default values.

Listed values for each data input, with the exception of diet contributions, are those entered into the model prior to balancing and therefore do not necessarily reflect final data values. When pre-balanced values are listed, adjustments made during balancing are described. Diet contributions consist of more values than other data inputs, and therefore were provided as post-balanced values to simplify their description. Changes made during balancing are provided for diets as well.

1. Species name or group name

2. Age-structure (if included)

3. Socking (if included)

4. Biomass

5. P/B

6. Q/B

7. Diet

8. Harvest (if targeted by fisheries)

9. Time series (if available)

10. Biomass accumulation (if trend in biomass time series)

Sea lamprey (*Petromyzon marinus*)

Biomass

Biomass estimates for parasitic stage sea lamprey were calculated from the product of number of spawners based on weir returns (Mike Siefkes, Great Lakes Fishery Commission (GLFC), personal communications) and yearly average wet weight of parasites (81.7 g; Bergstedt and Swink 1994). Sea lamprey prey on other species during the parasitic stage of their lifecycle, and so the number of parasitic stage sea lamprey was calculated from spawner numbers. The number of parasitic stage sea lamprey in 1981 was calculated by assuming a 75% survival rate to the spawning phase (Jones et al. 2009). Spawner numbers in 1982 were divided by 0.75 to produce parasite numbers in 1981.

$B = 0.000284$ g/m^2

P/B

Production to biomass values were available from data inputs calculated for a preliminary Lake Michigan EwE model (Ann Krause, University of Toledo (UT), personal communication).

The value of *P/B* from regression relationships using Linf = 50 cm (Bergstedt and Swink 1994), K = 0.16 (fishbase), and temperature of 6 C (based on similar temperature assumptions of catch at age models for lake trout) was 0.23, and was 0.6 from the Lake Superior Ecopath model (Cox and Kitchell 2004).

$$P/B = 0.86 \text{ yr}^{-1}$$

Q/B

The consumption to biomass ratio was originally based on blood consumption from a Lake Huron bioenergetics study and was 16 (Madenjian et al. 2003). This value resulted in low predation mortality on prey of sea lamprey, and so was increased five fold. An increased *Q/B* ratio would reflect consumption of the entire prey item by sea lamprey. Assuming the feeding event resulted in death of the prey item, then functionally that prey items biomass was removed from the food web. Sea lamprey only consume blood, so I allowed only a portion of the "consumed" biomass to go towards growth by setting the fraction of unassimilated food to be high, which I describe at the end of the appendix. The adjusted *Q/B* ratio was more similar to estimates from a Lake Superior Ecopath model (78; Cox and Kitchell 2004) and from a preliminary Lake Michigan Ecopath model (42; Ann Krause, UT, personal communication).

$$Q/B = 80 \text{ yr}^{-1}$$

Diet

Diet estimates for sea lamprey were sparse. Although sea lamprey predation on lake trout is well established, predation of sea lamprey on other species is often ignored. Chinook salmon, burbot, bloater, and lake whitefish have all been suggested to make up some component of sea

lamprey diet (Morse et al. 2003). Estimates from an unpublished Lake Michigan Ecopath model were used as the basis for sea lamprey diets (Ann Krause, UT, personal communication). Contributions of burbot were reduced from 20% to 10%, with the difference being added equally to age 2-4 and age 5+ lake trout, and contributions of salmon were assumed to be primarily from Chinook salmon.

Age 4+ lake whitefish	0.05
Age 2-4 lake trout	0.25
Age 5+ lake trout	0.35
Age 1-5 Chinook salmon	0.15
Age 2-5 steelhead	0.05
Age 3+ burbot	0.1
Age 1+ bloater	0.05

Time series

Biomass time series for sea lamprey from 1981-2007 were calculated from numbers of returning spawners in Lake Huron (Mike Siefkes, GLFC, personal communications). The same procedure for calculating biomass for the initial Ecopath model was repeated for each year in the time series. The time series for sea lamprey biomass was forced into Ecosim as an absolute time series because I assumed the majority of factors influencing sea lamprey biomass were due to pest management, which was outside the scope of the model. Ecosim requires forced biomass time series to have information for all years, so biomass values in 2008 were assumed to be same as the value in 2007.

Lake whitefish (*Coregonus clupeaformis*)

Age structure

Lake whitefish were divided into three age groups in the model: age 0, age 1-3, and age 4+ years. The final age stanza was the leading stanza and was chosen based on targeted ages

within statistical catch-at-age (SCA) models (Adam Cottrill, Ontario Ministry of Natural Resources (OMNR), personal communication). Age 1-3 was chosen based on groupings used for published diet studies (Pothoven and Madenjian 2008, Nalepa et al. 2009) as based on fork lengths from offshore index surveys (Adam Cottrill, OMNR, personal communication). Age data in the SCA models began mostly at age three, so information on biomass and mortality were not available for younger ages. Age 0 was assumed to have a unique diet in published studies (Nalepa et al. 2009) and so was modeled separately from other age groups.

Incorporating age groups into Ecopath required additional data inputs. The von Bertalanffy growth coefficient (K), and the point at which maturity occurred, specified as a proportion of the maximum weight (W_{mat}/W_{inf}), were required. The W_{mat}/W_{inf} ratio defines the age at which a fish matures, and is set to 0.09. The value of 0.09 assumes that length at maturity occurs at $0.09^{1/3}$ or 45% of maximum length. Actual values for W_{mat}/W_{inf} were difficult to obtain. Although values for age at maturity at which 50% of the population was mature (A_{mat}) were readily obtainable, I chose to use the default value for W_{mat}/W_{inf} for all age-structured groups. Estimates of K were based on length and age data from offshore indices done by the OMNR in Canadian waters between 1965-2008 over ages 0 to 24 (Adam Cottrill, OMNR, personal communication). The von Bertalanffy growth model was used to calculate K.

$K = 0.44$

Biomass

Biomass estimates for 1981 were available from SCA models in Lake Huron (Adam Cottrill, personal communication, Modeling subcommittee 2009). The SCA models were divided into seven lake whitefish management units, which accounted for treaty ceded (WFH 01, 02, and

04), Canadian (aa 123, 45, and 89), and parts of Michigan (WFH 05) waters. Models for Canadian management units combined assessment areas (aa) one, two, and three, areas four and five, and areas eight and nine. Data in the SCA models extended from 1981-2006 for ages 3-10+ for Canadian management units, ages 4-10 for treaty ceded management units, and ages 3-9+ for management units for Michigan waters.

A significant contribution of lake whitefish biomass and harvest occurs in Michigan waters (WFH 04). Models for WFH 04 were not complete and unavailable for analysis. I did not include data from WFH 04 in my analysis, but instead assumed that densities of biomass and harvest for other areas of the lake would be comparable to WFH 04. Consequently, I calculated areal estimates for Ecopath inputs based on an area of 26505 km^2, which is the area of the main basin excluding WFH 04 (Christine Joseph, Great Lakes GIS, personal communication).

Biomass estimates averaged across the year were used to reflect a representative yearly value that was more similar to sampling of other species done in the spring and fall. Biomass in each management unit was calculated using equation 1,

$$\overline{B}_{y,a,i} = \frac{N_{y,a,i}}{Z_{y,a,i}}\left(1 - e^{-Z_{y,a,i}}\right)W_{y,a,i} \qquad \text{(eq. 1)}$$

where $N_{y,a,i}$ was number of age a fish in year y and management unit i, $Z_{y,a,i}$ was total instantaneous mortality of age a fish in year y and management unit i, and $W_{y,a,i}$ was weight of an individual age a fish in year y for management unit i. All parameters for equation 1 were provided in the SCA model output. Weight at age in the SCA model was assumed to represent an average weight across the year.

The overall biomass estimate was calculated by summing over the i management units and ages for the leading stanza only from equation 1. Ecopath requires biomass to be entered for

only the leading stanza of each group. Biomass estimates for other stanzas are calculated by Ecopath internally.

$$\bar{B}_{y=1981,a=4+} = 0.177 \text{ g/m}^2$$

P/B

Production to biomass ratios were calculated from estimates of total instantaneous mortality (Z) in 1981 from SCA models for Lake Huron (Adam Cottrill, OMNR, personal communication). Age and year specific estimates of Z were provided in SCA models for each of seven management areas in Lake Huron. Total mortality was averaged across management units using

$$\bar{Z}_{y,a} = -\ln\left[\sum_{i=1}^{7} \bar{B}_{y,a,i} e^{-Z_{y,a,i}} \Big/ \sum_{i=1}^{7} \bar{B}_{y,a,i}\right] \tag{eq. 2}$$

and then averaged across appropriate ages for each age stanza using

$$\bar{Z}_{y,a} = -\ln\left[\sum_{s=1}^{2} \bar{B}_{y,j} e^{-Z_{y,j}} \Big/ \sum_{s=1}^{2} \bar{B}_{y,j}\right] \tag{eq. 3}$$

where j was the ages in stanza s, and $B_{y,j}$ was the biomass summed over ages j in stanza s in year y. Values for only the oldest two stanzas were available. Each age stanza in the EwE model is required to have an estimate of P/B. In the absence of estimates of P/B for age 0-1 lake whitefish, I assumed a value of 2.0 based on smoothness of biomass estimates at age given in the Ecosim multistanza editing pane, and on similarities to P/B values for age 0 prey fish. For the age 1-3 stanza, mortality estimates for only ages 3 were available from SCA output. I used estimates of Z for age 3 lake whitefish for age 1-3 P/B ratios in the model. This assumption is likely to be low given that younger ages tend to have higher mortality rates.

$$\bar{Z}_{y=1981,a=0-1} = 2.0 \text{ yr}^{-1}$$

$$\bar{Z}_{y=1981,a=1-3} = 0.587 \text{ yr}^{-1}$$

$$\bar{Z}_{y=1981,a=4+} = 0.483 \text{ yr}^{-1}$$

Q/B

Consumption to biomass ratios were calculated from a bioenergetics study on lake whitefish for lakes Huron and Michigan (Pothoven and Madenjian 2008). Daily Q/B ratios were available for lake whitefish prior to dreissenid invasion (Figure 5, Pothoven and Madenjian 2008; data from Steve Pothoven, National Oceanographic and Atmospheric Administration (NOAA), personal communication). Daily ratios were averaged across northern, central, and southern samples by age, and then averaged over ages and multiplied by 365 to obtain a yearly overall value.

Estimates were also available from other sources for the Great Lakes. Daily Q/B ratios were available from a Lake Huron bioenergetics study for lake whitefish after dreissenid invasion (Madenjian et al. 2006b). Total consumption over 133 days by lake whitefish were divided by the average of beginning and ending weights to obtain Q/B ratios for four separate tanks (Table 1; Madenjian et al. 2006b). The average of each tank was taken and used as the overall Q/B ratio for 133 days, and was multiplied by $365/133 = 2.74$ to obtain a yearly estimate. A preliminary Ecopath model for Lake Michigan used a value of 14.2 (Krause pers. comm.), while Lake Superior models used values of 15 (Kitchell et al. 2000), and 4.8 and 2.8 for lake whitefish younger and older than age 4, respectively (Cox and Kitchell 2004).

$$Q/B_{4+} = 4.41 \text{ yr}^{-1}$$

Diet

Lake whitefish diet information was available from a variety of Lake Huron surveys. Diet contributions for age 4+ lake whitefish were based on values used for a Lake Huron bioenergetics model for years (1983-1994) prior to dreissenid invasion (Table 3; Pothoven and Madenjian 2008). Even though ages in the study ranged from 2-8, I assumed that the diet contributions would be indicative of adult populations. Contributions of "other" were ignored and the additional contributions were added to *Diporeia*. Diet contributions were also available for large-sized lake whitefish (350-688 mm) in years after dreissenid invasion and revealed additional dietary components such as fish and invasive species contributions (Nalepa et al. 2009). Nalepa et al. (2009) used 350 mm as the length metric to distinguish size classes of lake whitefish. Based on index surveys, approximately 90% of fish with fork lengths < 350 mm were ages 0-3, and about 70% of fish with fork lengths > 350 mm were ages 4+ (Adam Cottrill, OMNR, personal communication). Contributions from both studies were combined to form an overall diet. Half of fish contributions in years after dreissenid invasivion were of ninespine stickleback while about a fourth were of gobies (Nalepa et al. 2009). The majority of overall diet contributions were of dreissenids while a smaller amount was of *Bythotrephes* (Nalepa et al. 2009). Diet proportions from Nalepa et al. (2009) of invasive species (dreissenids, gobies, and *Bythotrephes*) were reduced by a 1/1000th scaling factor and then added to the diet of age 4+ lake whitefish while contributions of ninespine stickleback were also added to the diet but without the scaling factor reduction. For a description of why the scaling factor was used, see the individual descriptions of each invasive species, or Chapter 3. The final diet contribution was

obtained by reducing the contributions of non-invasive groups (excluding ninespine stickleback) so that the total proportions summed to one.

Diet contributions for age 1-3 lake whitefish for years prior to dreissenid invasion were based on a Lake Huron study (Table 4; McNickle et al. 2006). Although McNickle et al. (2006) claim diets proportion were for adult lake whitefish, I assumed values were for juvenile lake whitefish mainly because I assumed that adults would have a broader array of diet items than was presented. Diet contributions were also available for medium-sized lake whitefish (<350 mm excluding age 0) in years after dreissenid invasion and revealed additional dietary components such as zooplankton and invasive species (Nalepa et al. 2009). I assumed medium-sized lake whitefish reflected ages 1-3. Contributions from both studies were used to generate an overall diet. I added 10% of zooplankton to the diet contributions of McNickle et al. (2006), which was the average of zooplankton estimates between the two studies, and adjusted contributions of *Diporeia* down to 75% and of benthic invertebrates down to 15% to sum to one. I then added contributions of invasive species (dreissenids and *Bythotrephes*) from Nalepa et al. (2009), reduced by a scaling factor of 1/1000th, as well contributions of *Mysis* and fish. I assumed the same proportion of ninespine stickleback in "fish" as for large lake whitefish (i.e. 50% of fish contributions), but unlike large-sized lake whitefish did not add round gobies to the diet. After adding contributions from Nalepa et al. (2009), I made proportional adjustments to contributions of *Diporeia*, zooplankton, and benthic invertebrate so that the overall proportions summed to one.

Diet contributions for age 0 lake whitefish were based on a Lake Huron study of diets after invasion of dreissenids (Nalepa et al. 2009). Contributions were primarily of zooplankton, which was in agreement with another study in Lake Huron (Pothoven and Nalepa 2006) and a

study in Lake Ontario (Hoyle et al. 2011). Nalepa et al. (2009) found little evidence of *Diporeia* consumption by older lake whitefish, which is normally a primary prey item (Owens and Dittman 2003) largely because of reduced abundance of *Diporeia*. I assumed that a pre-invasion diet for age 0 lake whitefish would contain *Diporeia*, both because adults consume *Diporeia*, and because age 0 lake whitefish were found to consume *Mysis*, which is a larger prey item than *Diporeia* (Pothoven and Nalepa 2006). I added 5% of *Diporeia* to the diet contributions of Nalepa et al. (2009) and reduced contributions of zooplankton and *Mysis*, and removed contributions of other smaller prey items. The 5% value for *Diporeia* was an assumption, however estimates from the other age 0 studies suggest the contribution to be small.

During balancing, both ninespine stickleback and round goby were unbalanced, so contributions of both groups to the diet of lake whitefish were reduced until balance occurred. Contributions of ninespine stickleback were reduced to 0.5% for age 4+ lake whitefish, and to 0.15% for age 1-3 lake whitefish, and contributions of round goby were reduced to 0.1%. After adjustments were made, the remaining contributions were proportionately adjusted so that diets summed to one. A greater reduction of round goby was used for age 4+ lake whitefish because I assumed that lake whitefish would be less of a source of round goby predation than for other prey items.

	Age 0	Age 1-3	Age 4+
Round Goby	0	0	1.00×10^{-6}
Slimy sculpin	0	0	0
Deepwater sculpin	0	0	0
Ninespine stickleback	0	0.0015	0.005
Diporeia	0.05	0.711	0.477
Mysis	0.01	0.05	0.318
Benthic invertebrates	0.10	0.142	0.199
Dreissenids	0	0.00024	0.00056
Predatory Zooplankton	0	0.00012	2.00×10^{-5}
Zooplankton	0.84	0.0947	0

Harvest

The primary gears used to harvest lake whitefish in Lake Huron include gill nets and trap nets. The state of Michigan only allows commercial trap netting in its waters, so gill nets were solely in tribal and Canadian waters. The fisheries included in the model that captured lake whitefish were Canadian gill nets, Canadian trap nets, and treaty fisheries which included both trap and gill nets. Small lake whitefish were also captured in the bloater fishery and accounted for as bycatch.

Harvest in 1981 was available from the SCA report files (Adam Cottrill, OMNR, personal communication, Modeling subcommittee 2009). Harvest at age was calculated as the product of observed landings in numbers, observed proportions-at-age in numbers for the gill and trap nets, and weight at age values. When observed data were not available predicted data were used instead. Harvest for each management unit, gear type, and age were calculated, and then summed across management units and ages within modeled age classes to obtain a lake wide estimate of harvest for each gear and each age class. As was the case for biomass, harvest from management unit WFH 04 was unavailable (see biomass section).

Commercial fishery bycatch data were used to calculate harvest of lake whitefish in the bloater gill net fishery (Lloyd Mohr, OMNR, unpublished data). Values were average landings from 1985-2009 for all Canadian waters of Lake Huron, which includes the North Channel and Georgian Bay. Gill net mesh size is smaller in the bloater fishery than the lake whitefish fishery (L. Mohr, personal communication), so I assigned bycatch in the bloater fishery to be age 1-3 lake whitefish.

Ecopath estimates biomass values for non-leading age stanzas. Biomass estimates of Ecopath for age 1-3 lake whitefish were greater than values calculated from the SCA models,

primarily because the SCA models were mostly for age three or older fish. Data inputs in Ecopath were used to appropriately account for mortality sources, so in order to have the same estimate of fishing mortality for age 1-3 lake whitefish, harvest and bycatch of age 1-3 lake whitefish was increased by a factor of 9.81, which was the ratio of Ecopath estimated biomass to that of the biomass estimated from the SCA model. The values below for harvest and bycatch of age 1-3 lake whitefish used for Chapter 3 include the 9.81 proportional increases. Landings for Chapter 4 were modeled differently and are described in the MSE simulations section below.

$$\text{Bycatch}_{y=1985\text{-}2009,a=1\text{-}3,\text{bloater}} = 0.00043 \text{ g/m}^2$$

$$\text{Landings}_{y=1981,a=1\text{-}3,\text{gill}} = 0.112 \text{ g/m}^2$$

$$\text{Landings}_{y=1981,a=1\text{-}3,\text{trap}} = 0.0116 \text{ g/m}^2$$

$$\text{Landings}_{y=1981,a=1\text{-}3,\text{treaty}} = 0.000569 \text{ g/m}^2$$

$$\text{Landings}_{y=1981,a=4+,\text{gill}} = 0.0209 \text{ g/m}^2$$

$$\text{Landings}_{y=1981,a=4+,\text{trap}} = 0.000669 \text{ g/m}^2$$

$$\text{Landings}_{y=1981,a=4+,\text{treaty}} = 0.016 \text{ g/m}^2$$

Time series

Biomass and fishing mortality time series for age 1-3 and 4+ lake whitefish from 1981-2006 were available from SCA models for Lake Huron (Adam Cottrill, OMNR, personal communication; Modeling subcommittee 2009). The same procedure for calculating biomass for the initial Ecopath model was repeated for each year in the biomass time series. Fishing mortality values for age 1-3 and age 4+ lake whitefish from the SCA models were averaged across ages in the age stanza using equation 4

$$\bar{F}_{y,a} = \frac{\hat{C}_{y,a}\bar{Z}_{y,a}}{\hat{B}_{y,a}\left(1-e^{-\bar{Z}_{y,a}}\right)}$$ (eq. 4)

where $\hat{C}_{y,a}$ was the total predicted harvest of ages a lake whitefish in year y summed over all

management units, $\bar{Z}_{y,a}$ was the total mortality of ages a lake whitefish in year y averaged

across management units (as calculated with equation 3), and $\hat{B}_{y,a}$ was the biomass of ages a

lake whitefish in year y, calculated as the product of numbers and weight, summed across

management units. Predicted harvest of ages a lake whitefish in year y ($\hat{C}_{y,a}$) was calculated as

the sum of predicted harvest for each management unit and ages within the age stanza, where

predicted harvest for each management unit was calculated using the Baranov catch equation,

$$\hat{C}_{y,a,i} = \frac{F_{y,a,i}N_{y,a,i}\left(1-e^{-Z_{y,a,i}}\right)}{Z_{y,a,i}}$$ (eq. 5)

where $F_{y,a,i}$ is the sum of fishing mortality rates for all gears, $N_{y,a,i}$ is numbers, and $Z_{y,a,i}$ is

total mortality rate, and are provided as outputs from the SCA files for year y, age a, and

management unit i.

Time series for ages 1-3 lake whitefish were based solely on data from age 3, which was

the youngest age available for most management units, and thus I assumed that trends in age 3

fishing mortality and biomass were similar for ages 1-3. Biomass for ages 1-3 would be greater

than biomass for age 3 alone, and it is very likely that fishing mortality for ages 1-3 would be

lower than age 3 alone because lake whitefish below age 3 were rarely captured in the fishery.

Time series of harvest were not included for lake whitefish because matching biomass and

fishing mortality time series would result in matches to harvest. The time series for age 1-3 lake

whitefish biomass was used in Ecosim as a relative time series, relative to the initial biomass input, whereas the time series for age 4+ lake whitefish biomass was used in Ecosim as an absolute time series. For time series where information for all years was required (i.e. fishing mortality time series), values in 2007-2008 were assumed to be same as the value in 2006. Time series of Z, although available, were not used to validate estimates generated in Ecosim, nor were they used to drive species interactions.

Biomass accumulation

Time series suggested an increasing trend in age 4+ lake whitefish biomass from 1981-1986. A biomass accumulation rate of 0.289 yr^{-1} was calculated by dividing the slope of the increase by the initial biomass estimate in 1981.

Lake trout (*Salvelinus namaycush*)

Age structure

Lake trout were divided into four age groups in the model: age 0, age 1, age 2-4, and age 5+. These ages are in years. The final age stanza was the leading stanza and was chosen based on a combination of diet and fishing information. Age 5 was used in SCA models as the beginning age at which to apply a targeted maximum total-mortality rate. Furthermore, diet information for a bioenergetics study by the Michigan Department of Natural Resources (MDNR) was divided into length bins and length-at-age data within the study suggested the age of separation between two of the bins was age 5 (Ji He, MDNR, personal communication). The first two age groups, age 0 and age 1, were chosen because age 1 has time-varying mortality in the SCA models, and because Ecopath requires all groups to begin at age 0.

Estimates of K were based on length data taken by the MDNR for use in a bioenergetics model (Ji He, MDNR, personal communication). Estimates were available for lake trout management units one and two combined, and unit three. A weighted average of the two values was taken, weighted by the biomass at the middle of the year for ages 1-15 (see biomass section). Only estimates of K from 1984-2007 were included in the average, although 1975-2007 were available, because lakewide estimates for lake trout biomass began in 1984. A single value of K was used over time because EwE assumes K remains constant, however the actual estimates varied between 0.4 and 0.25 (Ji He, MDNR, personal communication).

$K = 0.303$

Stocking

Ecosim incorporates stocking by replacing calculated recruitment levels of the modeled group with time series of relative stocking rates. Ecosim applies the stocking time series to the first age stanza in the model, which begins at age 0, and for lake trout extends to age one. Lake trout stocking data are reported as yearling equivalents, so the year of stocking for yearling (age 1) lake trout was reduced by one for input into the model to represent the stocking rate for age zero lake trout. Stocking numbers from 1982-2008 were used from the SCA models, multiplied by the weight at age for age 1 lake trout in each management unit, and then reduced by one year to obtain a final stocking weight (Ji He, MDNR, personal communication). Stocking for 2008, which after reducing the year by one was unknown, so was assumed to be the same as for 2007. Although there is evidence of wild recruitment of lake trout in Lake Huron (Nestor and Poe 1984, Johnson and VanAmberg 1995, Desorcie and Bowen 2003, Riley et al. 2007), particularly

in recent years, stocking rates were assumed to be the primary drivers of lake trout abundance and thus wild recruitment was ignored.

I encountered a problem when running policy simulations for lake trout (in Chapter 4). Lake trout stocking influenced the extent to which lake trout could support fishing. Further, if stocking were removed (i.e. set to zero), lake trout would quickly die off because the stocking value of 0 would be used to overwrite recruitment. Thus, I could not model any sort of natural reproduction by lake trout themselves, independent of stocking, by replacing recruitment with a stocking function. Furthermore, I wanted lake trout recruitment to be affected by changes in fishing mortality. Thus, in Chapter 4 I incorporated a work around for lake trout stocking for 1981-2008, but removed the additional production from stocking in years after 2008. Stocking was simulated in 1981-2008 by multiplying Ecosim-calculated egg production during those years by relative (to 1981) stocking rates in each year. For years after 2008, the increased production from stocking was removed by setting the relative stocking rate to one. Consequently, only egg production calculated by Ecosim was used.

Biomass

Biomass estimates for 1984 were available from SCA models in Lake Huron (Ji He, MDNR, personal communication). The SCA models were divided into three lake trout management units, MH1, MH2, and MH3 (which is an aggregate of MH3-MH6). Although US management units are named, data used in the SCA models included harvest and efforts from Ontario and treaty waters. Data in the SCA models extended from 1984-2008 for ages 1-15+ for all management units.

Biomass estimates averaged across the year were used to reflect a representative yearly value that was more similar to sampling of other species done in the spring and fall. Biomass in each management unit was calculated using equation 1 (shown in the lake whitefish biomass section), except that $W_{y,a,i}$ was the weight of an individual age a fish in year y for management unit i in the middle of the year for management units MH1 and MH2. For MH3, $W_{y,a,i}$ was the weight at the beginning of the year.

The overall biomass estimate was calculated by summing over management units and ages for the leading stanza only. Ecopath requires biomass to be entered for only the leading stanza of each group. Biomass estimates for other stanzas are calculated by Ecopath internally.

$$\overline{B}_{y=1984,a=5+} = 0.0369 \text{ g/m}^2$$

P/B

Production to biomass ratios were calculated from estimates of Z in 1984 from SCA models for Lake Huron (Ji He, MDNR, personal communication; Modeling subcommittee 2009). Age and year specific estimates of Z were estimated in SCA models for each of three management areas in Lake Huron. Data were available for all management areas from 1984-2008. Estimates from 1984 were therefore used as 1981 values. Total mortality was averaged across management units using equation 2, but with three management units instead of seven, and across age stanzas using equation 3, but with three age stanzas instead of two. Total mortality estimates for age 0 lake trout were available from survival estimates for age 0 lake trout during a sea lamprey dominated time period for Lake Michigan (Table 4; Ferreri et al. 1995).

$$\overline{Z}_{y=1984,a=0} = 5.48 \text{ yr}^{-1}$$

$$\overline{Z}_{y=1984,a=1} = 0.729 \text{ yr}^{-1}$$

$$\overline{Z}_{y=1984,a=2-4} = 0.411 \text{ yr}^{-1}$$

$$\overline{Z}_{y=1984,a=5+} = 0.678 \text{ yr}^{-1}$$

Q/B

Consumption to biomass ratios were available from a bioenergetics studies on lake trout in Lake Huron (Bence and Dobiesz 2000). At the time of model construction, values were only available for 1998. A longer time series from 1984-1998 of consumption and biomass data summed across ages (one through 15+) were provided later based on figures in Dobiesz (2003). Values ranged from 2.72 in 1984 to 3.56 in 1993.

Estimates were also available from other sources in the Great Lakes. Summing consumption and biomass estimates across ages for a Lake Michigan bioenergetics study produced an estimate of 2.78 (Madenjian et al. 1998). A preliminary Ecopath model for Lake Michigan used a value of 2.41 and 2.49 for adult and juvenile lake trout, respectively (Ann Krause, UT personal communication), while a Lake Superior model used values of 4.8 and 2.8, respectively (Cox and Kitchell 2004).

$$Q/B_{5+} = 3.35 \text{ yr}^{-1}$$

Diet

Lake trout diet was taken primarily from surveys from Lake Huron from 1984 (Ji He, MDNR, unpublished data). Diet summaries were reported in length categories, <400 mm, 400-600 mm, and >600 mm. Based on length-at-age data from catch-at-age models, I assumed that

the categories < 400 mm corresponded to ages 2-4, whereas the categories >400 mm

corresponded to ages 5 and above (Ji He, MDNR, personal communication; Modeling

subcommittee 2009). Only diet contributions from the >600 mm category were used for ages 5+.

Prey categories included alewife, rainbow smelt, sculpin, stickleback, coregonines (assumed to

be bloater), and round goby. Based on proportions reported in Madenjian et al. (1998), I assumed

that 66% of the alewife consumed by lake trout <400 mm (age 2-4) were age 0, and 10% of the

alewife consumed by lake trout >600 mm (age 5+) were age 0. Contributions of coregonines

were zero until 1994, but were included based on findings from others (Madenjian et al. 2006a),

and entered at an assumed value of 5%. *Mysis* have also been reported as diet items for age 2-4

lake trout (Madenjian et al. 1998), but were not included. Contributions of sculpin were divided

equally between deepwater and slimy sculpin. Following the age groupings in Dobiesz (2003)

and the length-at-age classifications in Madenjian et al. (2006a), age 1 lake trout were assigned

the same diet as ages 2-4.

   Contribution of round goby to age 5+ lake trout was taken as the average contribution

from 400-600 mm and >600 mm lake trout in 2002, the year used as input for round goby

biomass. Contributions of round goby to lake trout dramatically increased after 2002 however. I

reduced contributions of round goby by a scaling factor of 1/1000th, and made proportional

adjustments to contributions of other prey contributions so that the overall proportions summed

to one.

   Dry weight diet proportions for age 0 lake trout were available from a Lake Huron study

(Figure 2; Roseman et al. 2009). A weighted average (based on the number of stomachs) of each

prey item across all sampling periods was calculated. No corrections were used to convert dry

weight to wet weight diet proportions. Contributions of predatory zooplankton (*Bythotrephes*)

were recued by a 1/1000th scaling factor and contributions reapportioned to other groups,

proportional to the existing contributions of each group. Contributions of zooplankton were low,

and thus *Mysis* were reduced and 10% was added to zooplankton.

	Age 0	Age 1 and Age 2-4	Age 5+
Age 0 alewife	0	0.335	0.03545
Age 1+ alewife	0	0.165	0.319
Age 1+ rainbow smelt	0	0.47	0.5855
Age 1+ bloater	0	0	0.05
Round goby	0	0	0.000075
Slimy sculpin	0	0.013	0.002
Deepwater sculpin	0	0.012	0.003
Ninespine stickleback	0	0.005	0.005
Mysis	0.81	0	0
Benthic invertebrates	0.085	0	0
Predatory zooplankton	0.000027	0	0
Zooplankton	0.105	0	0

Harvest

Lake trout harvest occurs in Lake Huron primarily as bycatch in the commercial lake

whitefish fishery, but also occurs in the recreational fishery. Harvest in 1981 was available from

the SCA report files (Ji He, MDNR, personal communication). Harvest at age was calculated as

the product of observed landings, observed proportions-at-age for commercial (gill and trap nets

assumed to have the same proportions) and recreational fisheries, and observed weight at age

values mid-way through the year. When observed data were not available, predicted data were

used instead. Observed numbers and proportion-at-ages by number were used to calculate

recreational landings while values based on weight were used for commercial landings. The

exception to this was bycatch in Michigan licensed trap-nets, which were only reported in

numbers. Trap nets had an assumed bycatch mortality rate of 5.4 percent. I assumed that bycatch

mortality of landings in the tribal trap net fishery, which allow for retention of captured lake

trout were 100 percent. Misreporting by commercial fisheries was assumed to occur for

management units MH-1 and MH-2. Harvests were scaled by an assumed proportion up to and including 2002 in MH-1 and up to and including 2008 in MH-2 to account for misreporting.

Ecopath estimates biomass values for non-leading age stanzas. Biomass estimates of Ecopath for age 2-4 lake trout were greater than values calculated from the SCA models. Data inputs in Ecopath were used to appropriately account for mortality sources, so in order to have the same estimate of fishing mortality for age 2-4 lake trout, harvest and bycatch of age 2-4 lake trout was increased by a factor of 3.19 in Chapter 3, which was the ratio of Ecopath estimated biomass to that of the biomass estimated from the SCA model. The value of the ratio of Ecopath estimated biomass to that of the biomass estimated from the SCA model was slightly different (2.46) for Chapter 4 because biomass accumulation was used in Chapter 3, which changed the modeled biomass estimate for age 2-4 lake trout. The values below for harvest of age 2-4 lake trout used for Chapter 3 include the 3.19 proportional increases. Landings for Chapter 4 were modeled differently and are described in the MSE simulations section.

$$\text{Bycatch}_{y=1984,a=2\text{-}4,\text{trap}} = 0.0000169 \text{ g/m}^2$$

$$\text{Landings}_{y=1984,a=2\text{-}4,\text{gill}} = 0.0002725 \text{ g/m}^2$$

$$\text{Landings}_{y=1984,a=2\text{-}4,\text{treaty}} = 0.001943 \text{ g/m}^2$$

$$\text{Landings}_{y=1984,a=2\text{-}4,\text{rec}} = 0.0008044 \text{ g/m}^2$$

$$\text{Bycatch}_{y=1984,a=5+,\text{trap}} = 0.000016 \text{ g/m}^2$$

$$\text{Landings}_{y=1984,a=5+,\text{gill}} = 0.000553 \text{ g/m}^2$$

$$\text{Landings}_{y=1984,a=5+,\text{treaty}} = 0.0022 \text{ g/m}^2$$

$$\text{Landings}_{y=1984,a=5+,\text{rec}} = 0.00319 \text{ g/m}^2$$

Time series

Biomass and fishing mortality time series for ages 2-4 and 5+ lake trout and time series of total mortalities for age 1 lake trout from 1984-2008, and stocking time series for age 1 lake trout from 1981-2008 were available from SCA models for Lake Huron (Ji He, MDNR, personal communication). The same procedure for calculating biomass for the initial Ecopath model was repeated for each year in the biomass time series. The fishing mortality time series was calculated using equation 4, following the procedure outlined in the lake whitefish time series section. Time series of harvest were not included for lake trout because matching biomass and fishing mortality time series would result in matches to harvest. The time series for age 2-4 lake trout biomass was used in Ecosim as a relative time series, relative to the initial biomass input, whereas the time series for age 5+ lake trout biomass was used in Ecosim as an absolute time series. For time series where information for all years was required (i.e. fishing mortality and stocking time series), values in 1981-1983 were assumed to be same as the value in 1984. Yearling lake trout were modeled with time varying natural mortality in the SCA models, and were forced into the Ecosim model. This was done with fishing, because of limitations in the modeling software. Little consumption of yearling lake trout was available from diet studies, and thus no predation mortality was included in the EwE model. Time series of Z, although available, were not used to validate estimates generated in Ecosim, nor were they used to drive species interactions for age 2-4 or age 5+ lake trout.

Biomass accumulation

Biomass accumulation rates were not calculated for stocked species. I assumed that changes in the stocking function would cause increases or decreases in biomass. Lake trout were stocked in the model used for Chapter 3, and therefore no biomass accumulation rate was used. Lake trout however were not stocked in the model used for Chapter 4, so biomass accumulation was used. Time series suggested a decreasing trend in age 5+ lake trout biomass from 1984-1992. A biomass accumulation rate of -0.081 yr^{-1} was calculated by dividing the slope of the decrease by the initial biomass estimate in 1984.

Chinook salmon (*Oncorhynchus tshawytscha*)

Age-structure

Chinook salmon were divided into four age groups in the model: ages 0, 0-0.5, 1-5, and age 6+. Biomass estimates were available for ages 1-5 and so was chosen as the leading age group. The first two age groups, age 0-0.5 and age 0.5-1, were chosen based on how Ecopath accounts for stocking. Chinook salmon stocking data are reported in fingerling equivalents (assumed to be age six months), so to include stocking in the model an age stanza of age 0.5-1 was included. Ecopath requires all groups to begin at age 0, and so this age stanza was also included. I used an import only diet for age 0-0.5 Chinook salmon so that ages prior to stocking would not influence trophic dynamics. The age 6+ age group represented fish assumed to have died from spawning because Ecosim doesn't have capabilities for modeling semelparous species such as Chinook salmon. To include semelparity in the model, I used an import only diet for age 6+ Chinook salmon so that they would not have an effect on trophic interactions. Another option would be to apply high mortality to the age group but this was not done. Estimates of *K* were

based on calculated values from the salmon stocking model for Lake Huron (Travis Brenden,

Michigan State University (MSU), personal communication).

$K = 0.37$

Stocking

Ecosim incorporates stocking by replacing calculated recruitment levels of the modeled

group with time series of relative stocking rates. Ecosim applies the stocking time series to the

first age stanza in the model, which begins at age 0, and for Chinook salmon extends to age six

months. Chinook salmon stocking data are reported as fingerling equivalents, and the year of

stocking was not adjusted like it was for lake trout and steelhead. Stocking numbers from 1981-

2005 were used from the salmon stocking model for Lake Huron (Travis Brenden, MSU,

personal communication), and numbers in years 2006-2008 were assumed to be the same as for

2005.

Wild reproduction of Chinook salmon has increased substantially since the mid 1980s

The first recorded year of wild recruitment was 1985, in 1991-1993 an estimated 30% of

Chinook salmon was wild, and in 2000-2003 the estimate was 80% (Johnson et al. 2010).

Therefore, I multiplied the stocking time series by a multiplier (1-the proportion wild) to account

for wild Chinook salmon contributions. The proportion wild was assumed to be 0 in 1984,

linearly increase to 0.3 in 1991, and then again to 0.8 in 2000. After 2000, the proportion wild

was assumed constant at 0.8. The time series with wild recruitment multipliers was then divided

by stocking in 1981 to generate a relative time series.

Biomass

Biomass estimates were available for 1981 from a Lake Huron stocking model (Travis Brenden, MSU, personal communication). Biomass at the beginning of each year was calculated as the product of number-at-age in the beginning of each year, and weight-at-age for each age and year. The overall biomass estimate was calculated by summing over individual ages for the leading stanza.

$B_{1-5} = 0.09898$ g/m^2

P/B

Production to biomass was calculated from estimates of total mortalities from a Lake Huron stocking model for ages 0-5 in 1981 (Travis Brenden, MSU, personal communication). An overall total mortality estimate for age 1-5 Chinook salmon in 1981 was calculated by averaging individual mortalities at age across ages using equation 3. The total mortality estimate from the model for age 0 Chinook salmon in 1981 was used for age 0.5-age 1 P/B, and mortality for age 0-0.5 was set to an arbitrarily low value.

Other P/B ratios were available from bioenergetics models and other Ecopath models. A bioenergetics model of Chinook salmon in Lake Michigan estimated P/B to be 1.6 (Stewart and Ibarra 1991) while one in Lake Huron estimated P/B to be 1.05 in 1981 (Dobiesz 2003, data provided by Norine Dobiesz, University of Minnesota, personal communication). The Lake Superior Ecopath model estimated P/B to be 1.22 (Kitchell et al. 2000).

$P/B_{0-0.5} = 0.001$ yr^{-1}

$P/B_{0.5-1} = 1.23$ yr^{-1}

$P/B_{1-5} = 0.888$ yr^{-1}

$P/B_{6+} = 0.888 \text{ yr}^{-1}$

Q/B

A consumption to biomass ratio was available from a Lake Huron bioenergetics study for 1981 (Dobiesz 2003, data provided by Norine Dobiesz, University of Minnesota, personal communication). Dobiesz (2003) estimated ratios from 1968-1998, which were similar to the value for 1981. Estimates were also available from other sources in the Great Lakes. Rand et al. (1993) estimated a value of 8.2 based on estimated P/B and gross food conversion efficiency values. A preliminary Ecopath model for Lake Michigan used a value of 5.5 (Ann Krause, UT, personal communication), while Lake Superior models used a value of 2.1 (Cox and Kitchell 2004) and 7.1 (Kitchell et al. 2000).

$Q/B_{1-5} = 5.00 \text{ yr}^{-1}$

Diet

Diets by percent weight were available from a Lake Michigan study from 1973-1982 (Figure 2; Jude et al. 1987). Jude et al. (1987) reported diets for Chinook salmon <30 cm and >30 cm, which I assumed reflected fish age 0.5 and age 1-5, respectively. For both age groups, I assigned contributions from unidentified fish to fish groups identified in stomachs based on the proportion of fish that were identified. I applied miscellaneous diet contributions of Chinook salmon < 30 cm to rainbow smelt. For age 0.5 diets, alewife and rainbow smelt contributions were assumed to be age 0, where as for age 1-5 diets, alewife and rainbow smelt contributions were assumed to be age 1+. Contributions of invertebrates were assumed to be benthic

invertebrates. Diets for age 0-0.5 and age 6+ Chinook salmon were set as import only to ensure these groups did not affect other groups in the model.

Other diet studies in the Great Lakes showed similar diets, although in some studies rainbow smelt made up a greater contribution than from Jude et al. (1987). Due to greater rainbow smelt contributions for Chinook salmon in some studies, the contribution of age 0 and age 1+ alewife were reduced slightly and the differences given to age 0 and age 1+ rainbow smelt. For Lake Huron, Dobiesz (2003) presented contributions by weight while Diana (1990) presented contributions by number. For Lake Michigan, Stewart and Ibarra (1991) have Chinook salmon consuming fish at young ages. Age 0 alewife were unbalanced and therefore contributions of alewife were reduced and added to contributions of rainbow smelt, as suggested by other diet studies.

	Age 0.5	Age 1-5
Age 0 alewife	0.55	0
Age 1+ alewife	0	0.80
Age 0 rainbow smelt	0.3	0
Age 1+ rainbow smelt	0	0.20
Benthic invertebrates	0.15	0

Harvest

Estimated harvest of Chinook salmon was available from the Lake Huron stocking model (Travis Brenden, MSU, personal communication). Harvests in the stocking model were estimated beginning in 1973, and fit to expanded creel estimates in Michigan waters beginning in 1986. I used estimated recreational harvest from the stocking model in 1981 as input for harvest of Chinook salmon. Commercial harvest of Chinook salmon is allowed in tribal waters, and thus observed commercial harvests for 1986 were entered into the model with the assumption that harvest in 1986 would be comparable to 1981 (Jim Johnson, MNDR, personal communication). I

assumed harvest of Chinook salmon was only of ages 1-5. Chinook salmon are also captured as bycatch in the lake whitefish gill net fishery. Commercial fishery bycatch data were used to calculate bycatch of Chinook salmon (Lloyd Mohr, OMNR, unpublished data). Values were average landings from 1985-2009 for all Canadian waters of Lake Huron, which includes the North Channel and Georgian Bay. I assumed bycatch of Chinook salmon was only of ages 1-5. The landings below were used for Chapter 3. Landings for Chapter 4 were modeled differently and are described in the MSE simulation section.

$$\text{Bycatch}_{y=1985-2009, a=1-5, \text{gill}} = 0.000063 \text{ g/m}^2$$

$$\text{Landings}_{y=1981, a=1-5, \text{rec}} = 0.00656 \text{ g/m}^2$$

$$\text{Landings}_{y=1986, \text{age}=1-5, \text{com}} = 0.000129 \text{ g/m}^2$$

Time series

Biomass and fishing mortality time series for age 1-5 Chinook salmon from 1981-2005 were available from a Lake Huron stocking model (Travis Brenden, MSU, personal communication). Time series of harvest were not included for Chinook salmon because matching biomass and fishing mortality time series would result in matches to harvest. The time series for Chinook salmon biomass was used in Ecosim as a relative time series, relative to the initial biomass input. For time series where information for all years was required (i.e. fishing mortality), values in 2006-2008 were assumed to be same as the value in 2005.

Biomass accumulation

Biomass accumulation rates were not calculated for stocked species. I assumed that changes in the stocking function would cause increases or decreases in biomass.

MSE simulations

The management strategy evaluation tool in Ecosim adjusts efforts for desired fisheries so that user-inputted fishing mortality targets are achieved for the species caught by the fishery. Ecosim bases the changes to fishing effort on initial fishing mortality rates in Ecosim, calculated as the ratio of harvest to biomass. Fishing mortality rates for individual species have changed from 1981-2008, as have the fishing mortality rates of each fishery on individual species. For species harvested by multiple gears (lake whitefish, lake trout, and Chinook salmon), I chose to base initial fishing mortality rates and distributions of harvest for each gear on fishing mortality rates in 2006 rather than in 1981, so that changes in gear would reflect more recent fishing practices. The MSE tool was only used for policy simulations (Chapter 4) so changes from harvests provided in the lake whitefish, lake trout, and Chinook salmon species sections were only applied to the model in Chapter 4, and are described in this section.

I adjusted landings in Ecopath for age 1-3 and 4+ lake whitefish and age 2-4 and 5+ lake trout so that initial Ecopath calculated fishing mortality rates (in 1981) reflected actual fishing mortality rates for 2006. I also adjusted landings for each gear so that proportions that each gear contributed to the overall fishing mortality matched those in 2006. Adjustments to landings for age 1-3 lake whitefish and age 2-4 lake trout included an increase in harvest by factors of 9.81 and 2.46, respectively, which was the ratio of EwE estimated biomass of the two age groups to the estimates from the SCA models. I set landings in Ecopath for age 1-5 Chinook salmon to reflect fishing mortality rates for 1981, but adjusted the harvest of Chinook salmon in gears capturing them to reflect gear distributions in 2006. I used 1981 because contrary to lake

whitefish and lake trout, fishing mortalities rates for Chinook salmon were smaller in 1981 than in 2006.

Lake whitefish harvests

$Bycatch_{y=1985\text{-}2009,a=1\text{-}3,bloater} = 0.00045$ g/m^2

$Landings_{y=1981,a=1\text{-}3,gill} = 0.000086$ g/m^2

$Landings_{y=1981,a=1\text{-}3,trap} = 0.000046$ g/m^2

$Landings_{y=1981,a=1\text{-}3,treaty} = 0$ g/m^2

$Landings_{y=1981,a=4+,trap} = 0.000618$ g/m^2

$Landings_{y=1981,a=4+,gill} = 0.0104$ g/m^2

$Landings_{y=1981,a=4+,treaty} = 0.00602$ g/m^2

Lake trout harvests

$Landings_{y=1984,a=2\text{-}4,gill} = 0.000269$ g/m^2

$Bycatch_{y=1984,a=2\text{-}4,trap} = 0.00000169$ g/m^2

$Landings_{y=1984,a=2\text{-}4,treaty} = 0.000059$ g/m^2

$Landings_{y=1984,a=2\text{-}4,rec} = 0.000060$ g/m^2

$Bycatch_{y=1984,a=5+,trap} = 0.0000167$ g/m^2

$Landings_{y=1984,a=5+,gill} = 0.0029$ g/m^2

$Landings_{y=1984,a=5+,treaty} = 0.0022$ g/m^2

$Landings_{y=1984,a=5+,rec} = 0.0008696$ g/m^2

Chinook salmon harvests

$Bycatch_{y=1985\text{-}2009,a=1\text{-}5,gill} = 0.00011$ g/m^2

$Landings_{y=1981,a=1\text{-}5,rec} = 0.00285$ g/m^2

$Landings_{y=1986,age=1\text{-}5,com} = 0.00379$ g/m^2

Fishing mortality rates of age 1-3 and 4+ lake whitefish and age 2-4 and 5+ lake trout were greater in 1981 than in 2006, so to ensure that the total mortality rates for age 1-3 and 4+ lake whitefish and age 2-4 and 5+ lake trout matched estimates for 1981, I added additional

mortality in the form of an additional "predator fishery" group. Because Chinook salmon fishing

mortalities rates were set to 1981 levels, I did not need to add additional mortality.

The predator fishery was entered in Ecopath with a low *P/B* ratio of 0.001, and a *Q/B*

estimate that simplified calculations of predation mortality ($Q/B = 10$). Biomass and diet

contributions were entered so that the predation mortality of the predator fishery group matched

the difference in mortality between fishing mortality rates in 1981 and 2006 for age 1-3 and 4+

lake whitefish and age 2-4 and 5+ lake trout. Biomass was set to be the sum of consumption

required for fishing mortalities to match, and diet contributions were scaled appropriately for

each "prey" item. Only age 1-3 and 4+ lake whitefish and age 2-4 and 5+ lake trout were

"preyed" upon by the predator fishing because the management strategy evaluation was based on

using these groups.

Age 1-3 lake whitefish	0.848
Age 4+ lake whitefish	0.1387
Age 2-4 lake trout	0.01321
Age 5+ lake trout	0.00013

Between 1981-2008, lake trout, lake whitefish, and Chinook salmon fishing mortalities

were overwritten by time series from SCA models. Therefore, predation mortality by the

predator fishery was only needed to initialize starting conditions in Ecopath. A high fishing

mortality rate of 1000 g/m^2 was applied to the predator fishery to drive biomass to zero once

Ecosim simulations began. A biomass accumulation of -1000 g/m^2/yr was applied to the

predator fishery group so that balance could be achieved.

Steelhead (*Oncorhynchus mykiss*)

Age-structure

Steelhead were divided into four age groups in the model: ages 0, 1, 2-5, and age 6+. Biomass estimates were available for ages 2-5 and so was chosen as the leading age group. Biomass are also available for age 1 steelhead, however because steelhead stocking data are reported as yearling equivalents, I included age 1-2 separately. Ecopath requires all groups to begin at age 0, and so age 0-1 was also included. I used an import only diet for age 0-1 steelhead so that ages prior to stocking would not influence trophic dynamics. The age 6+ group represented fish assumed to have died from spawning. Steelhead are iteroparous, however I included them in the model as semelparous because I assumed that age 6+ steelhead represented only a small proportion of steelhead in the lake. Age 5 steelhead made up a fairly large proportion of total biomass (Travis Brenden, MSU, personal communication) so my assumption may not be accurate, however I have no way of knowing exactly how much biomass age 6+ steelhead represent. To include semelparity in the model, I used an import only diet for age 6+ steelhead so that they would not have an effect on trophic interactions. Another option would be to apply high mortality to the age group but this was not done. Estimates of K were based on calculated values from the salmon stocking model for Lake Huron (Travis Brenden, MSU, personal communication).

$K = 0.466$

Stocking

Ecosim incorporates stocking by replacing calculated recruitment levels of the modeled group with time series of relative stocking rates. Ecosim applies the stocking time series to the first age stanza in the model, which begins at age 0, and for steelhead extends to age one. Steelhead stocking data are reported as yearling equivalents, so the year of stocking for yearling

(age 1) steelhead was reduced by one for input into the model to represent the stocking rate for age zero steelhead. Stocking numbers from 1982-2005 were used from the stocking model for Lake Huron (Travis Brenden, MSU, personal communication). Stocking for 2005-2008, which after reducing the year by one was unknown, was assumed to be the same as for 2004. Stocking was assumed to be the primary drivers of steelhead abundance even though there is speculation about wild recruitment.

Biomass

Biomass estimates were available for 1981 from a Lake Huron stocking model (Travis Brenden, MSU, personal communication). The overall biomass estimate was calculated by summing over individual ages for the leading stanza.

$B_{2-5} = 0.079$ g/m^2

P/B

Production to biomass ratios were available from total mortality estimates from a Lake Huron stocking model for 1981 (Travis Brenden, MSU, personal communication). Estimates were very near 0.11 for ages 2-5 so no averaging was needed. Mortality for age 1 steelhead was used to set P/B for age 1 in Ecopath, and mortality for age 0 was set to an arbitrarily low value. Estimates were also available from a Lake Michigan bioenergetics model (0.83; Rand et al. 1993). Although steelhead are stocked so total mortality may not reflect production to biomass ratios, because biomass values were taken from the stocking model, mortality estimates were taken from there as well. Estimates for the age 6+ group affected estimates of biomass and Q/B in younger groups, so I used the same P/B value as for age 2-5.

$P/B_{6+} = 0.11$ yr^{-1}

$P/B_{2-5} = 0.11$ yr^{-1}

$P/B_1 = 0.5$ yr^{-1}

$P/B_0 = 0.001$ yr^{-1}

Q/B

Consumption to biomass estimates were calculated from a Lake Michigan bioenergetics model as the product of P/B and gross conversion efficiency (Figure 7; Rand et al. 1993). Thus, I assumed that the overall P/B ratio in Rand et al. (1993) was appropriate for age 2-5 steelhead in Lake Huron. The Q/B ratio of ages 6+ were adjusted so that the Q/B ratio of ages 2-5 was equal to the calculated value.

$Q/B_{2-5} = 7.345$ yr^{-1}

Diet

Diets by percent weight were available from 1973-1982 in Lake Michigan (Figure 2; Jude et al. 1987). Jude et al. (1987) reported diets for steelhead <30 cm and >30 cm, which I assumed reflected fish age 1 and age 2-5, respectively. For both age groups, I assigned contributions from unidentified fish to fish groups identified in stomachs based on the proportion of fish that were identified. For age 1 diets, alewife and rainbow smelt contributions were assumed to be age 0, where as for age 2-5 diets, alewife and rainbow smelt contributions were assumed to be adults. Contributions of sculpin were assumed to be slimy sculpin, and contributions of invertebrates were assumed to be benthic invertebrates, even though reported

invertebrates were more terrestrial insects (Jude et al. 1987). Contributions of miscellaneous

items and shiners were not included, and the proportions were reapportioned to other prey items,

proportional to the existing contributions of each group, so that total contributions summed to

one. Contributions of age 1+ alewife were reduced and differences divided between age 0

alewife (5%) and age 1+ rainbow smelt (21%). Slimy sculpin were unbalanced so contributions

were reduced by 2% and differences added to age 1+ rainbow smelt as well.

	Age 1	Age 2-5
Age 0 alewife	0.37	0.05
Age 1+ alewife	0	0.6
Age 1+ rainbow smelt	0	0.3
Slimy sculpin	0	0.005
Benthic invertebrates	0.63	0.026

Harvest

Estimated harvest of steelhead was based on expanded creel estimates in Michigan waters

beginning in 1986 (Jim Johnson, MDNR, personal communication). Expanded estimates

included extrapolations for ports not used in some years. I used the landings in 1986 as estimates

for harvest in 1981, and assumed that harvest in 1986 would be comparable to 1981. I assumed

harvest of steelhead was only for ages 2-5. Harvest of steelhead occurs in Ontario waters of Lake

Huron, and estimates are available every five years from angler surveys. Based on estimated

harvest numbers in the 2005 survey, which included harvest from Georgian Bay (OMNR 2009),

and an average steelhead weight of 2.46 kg in 2005 from Michigan creel surveys (Tracy Kolb,

MDNR, personal communication) harvest of steelhead in Ontario waters was substantially higher

compared to harvest in Michigan waters for the same year; 221000 kg compared to 6161 kg. I

am unsure how large the differences are between Michigan and Ontario harvests for 1986. Even

though harvest in Ontario waters is substantial, estimates were not available on a yearly basis and

therefore were not included in the model. Fishing mortality on steelhead in the model was low, and therefore greater harvest is not unlikely. Nonetheless, ignoring Ontario steelhead harvest is likely not to influence models fits, primarily because harvest time series was not used in the fitting procedure. Adding Ontario harvest may result in better harvest time series however, and thus may be result in improved fits to steelhead biomass if included in the fitting procedure.

$$\text{Landings}_{y=1986,a=2\text{-}5,\text{rec}} = 0.000333 \text{ g/m}^2$$

Time series

Biomass time series for age 2-5 steelhead and stocking time series for yearling steelhead for 1981-2005 were available from a Lake Huron stocking model (Travis Brenden, MSU, personal communication). Harvest time series for steelhead for 1986-2008 were ultimately not used in the Ecosim fitting procedure, but were available from expanded Michigan creel estimates for Lake Huron (Jim Johnson, MDNR, personal communication). I did not use harvest time series to drive fishing mortalities for steelhead because I believed the resulting estimates would be imprecise. Rather, estimates of fishing mortality from the recreational fishery remained constant over time, which is also imprecise, but I initially included harvest time series in the Ecosim fitting procedure. Patterns in harvest did not match patterns in biomass, and because steelhead represent a lesser component than Chinook salmon of the overall recreational harvest, I excluded the harvest time series from the fitting routine and instead focused of fitting biomass. The time series for steelhead biomass was used in Ecosim as a relative time series, relative to the initial biomass input.

Biomass accumulation

Biomass accumulation rates were not calculated for stocked species. I assumed that changes in the stocking function would cause increases or decreases in biomass.

Burbot (*Lota lota*)

Age structure

Burbot were divided into two age groups in the model: ages 0-3, and ages 3+ years. Age groups were chosen based on data availability of biomass and diet. Rudstam et al. (1995) assumed maturity to occur at age 3, and data from MNDR surveys show the age at 50% maturity to be between age 3 and 4 (Ji He, MNDR, unpublished data). Therefore, the separation also reflected distinction between juvenile and mature individuals. Estimates of K were based on length data taken by the MDNR from 1996-2008 for use in a bioenergetics model (Ji He, MNDR, personal communication). Ages ranged from 2-18. Estimates of K were calculated by assuming growth followed a von Bertalanffy growth equation.

$K = 0.238$

Biomass

Biomass estimates were available for 1983 from a consumption model based on bioenergetics for Lake Huron (Figure 3.5, Dobiesz 2003; data provided by Norine Dobiesz, University of Minnesota, personal communication). Limited biological data were available for burbot, so Dobiesz (2003) used estimates of lake trout abundance and survey ratios of observed burbot to lake trout numbers to calculate burbot biomass, however earlier admitted that doing so was based on "tenuous assumptions" (Bence and Dobiesz 2000). Biomass estimates were presented as an aggregate estimate across years in Dobiesz (2003) which I used for the leading

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stanza (age 3+) in Ecopath. Other available estimates were from bottom trawl surveys done by the United State Geological Survey (USGS) (Stephen Riley, USGS, personal communication) but an absolute biomass estimate from the trawl survey was not used for the initial biomass data input.

$$B_{3+} = 0.0101 \text{ g/m}^2$$

P/B

Production to biomass ratios were available from a bioenergetics model for Lake Huron for 1983 (Dobiesz 2003, data provided by Norine Dobiesz, University of Minnesota, personal communication). For ages 0-3, P/B was estimated as the simple average of total mortality for age 1 and age 2 burbot (Bence and Dobiesz, 2000, Tables A1 and A2). Intensity of sea lamprey predation was only given for years after 1996, so I assumed that predation intensity for 1981 would be the same as in 1998 because sea lamprey biomasses were similar in 1981 and 1998 (Mike Siefkes, GLFC, personal communication).

$$P/B_{0\text{-}3} = 0.667 \text{ yr}^{-1}$$

$$P/B_{3+} = 0.263 \text{ yr}^{-1}$$

Q/B

Consumption to biomass ratios were available from a bioenergetics model of Lake Huron for 1983 (Dobiesz 2003, data provided by Norine Dobiesz, University of Minnesota, personal communication). Consumption to biomass ratios were estimated for a bioenergetics model of Green Bay, Lake Michigan (2.87; Rudstam et al. 1995), and an Ecopath model of Lake Michigan (2.587; Ann Krause, UT, personal communication).

Q/B_{3+} = 3.38 yr^{-1}

Diet

Burbot consumed round gobies and dreissenids, and therefore diets from Dobiesz (2003), which were assumed to represent a mostly pre-invasion diet, were adjusted. Diets from Dobiesz (2003) for ages 4-7 and 8+ were averaged to generate diets for age 3+ burbot. Approximate post-invasion diet contributions of round goby and dreissenids were taken from estimates from surveys in Lake Huron and were added to diets of burbot (Ji He, MNDR, personal communication). The contribution of gobies to the diet of age 0-3 burbot was assumed to be 0.2 for juveniles and 0.1 for adults. The average of contributions of round goby in 2001-2003 were approximately 0.2 from the surveys. Contributions of round goby greatly increased in the survey, up to an average of 75% in 2004-2008 in the surveys. Estimates from 2002 were taken because they reflected a year where biomass estimates of round goby and dreissenids were entered into the model. Other studies similarly show high contributions of round goby to burbot of around 60% (Hensler et al. 2008). The contribution of dreissenids to the diet of age 0-3 burbot was assumed to be 0.1, and to the diet of age 3+ burbot 0.05, which were higher than the MDNR surveys. Lower contributions of round goby and dreissenids to adults compared to juveniles were chosen to reflect a shift from these diet items to larger prey items as burbut grow, as evidenced by diet contributions for juveniles and adults from Dobiesz (2003). Biomass estimates of invasives were reduced by a 1/1000th scaling factor, so diet contributions of invasives to predators were as well. Therefore, diet contributions for other groups were proportionally adjusted upwards. Crayfish comprised a large contribution of the diet of burbot, however because they were not included in the model, diet contributions for crayfish were reapportioned

to other groups, proportional to the existing contributions of each group, so that total contributions summed to one. Contributions of alewife to age 0-3 burbot were assumed to be of age 0 alewife, based on statements from Fratt et al. (1997) that most alewife in diets of burbot of comparable size to ages 0-3 were young of year. Alewife in the diet of age 3+ burbot were assumed to be ages 1+. Other fish reported by Dobiesz (2003) were assumed to be age 0 lake whitefish, based on statements by Hensler et al. (2008) that burbot consumed lake whitefish eggs.

	Age 0-3	Age 3+
Age 0 lake whitefish	0.008	0.019
Age 0 alewife	0.297	0
Age 1+ alewife	0	0.334
Age 1+ rainbow smelt	0.259	0.449
Age 1+ bloater	0	0.039
Round Goby	0.0002	0.0001
Slimy sculpin	0.143	0.026
Deepwater sculpin	0.286	0.128
Ninespine stickleback	0.008	0.005
Dreissenids	0.0001	0.00005

Harvest

Burbot are not targeted in either commercial or recreational fisheries in Lake Huron, but are caught as bycatch in both the bloater and lake whitefish gill net fisheries. Commercial fishery bycatch data were used to calculate harvest of burbot in the bloater and lake whitefish gill net fisheries (Lloyd Mohr, OMNR, unpublished data). Values were average landings from 1985-2009 for all Canadian waters of Lake Huron, which includes the North Channel and Georgian Bay. Gill net mesh size is smaller in the bloater fishery than the lake whitefish fishery so I assigned bycatch in the bloater fishery to be age 0-3 burbot whereas bycatch in the lake whitefish fishery to be age 3+ burbot. Burbot were also captured in the lake whitefish trap net fishery, but bycatch was negligible and was excluded.

Bycatch$_{y=1985\text{-}2009,a=0\text{-}3,\text{bloater gill}}$ = 0.00014 g/m^2

Bycatch$_{y=1985\text{-}2009,a=3+,\text{lake whitefish gill}}$ = 0.00022 g/m^2

Time series

Ultimately, biomass time series for burbot were not included in the Ecosim fitting routine. A biomass time series for burbot from 1984-1998 was available from a Lake Huron consumption model based on bioenergetics (Bence and Dobiesz 2000), but was not considered suitable. The time series was based on limited relative abundance data and simply adjusted average recruitment to mimic an increase in burbot catch rates during the late 1980s. Another time series for most years from 1981-2007 from USGS bottom trawl surveys in Lake Huron was also available (Stephen Riley, USGS, personal communication). Biomass values in 1992, 1993, 1998, and 2000 were not used as part of the trawl-survey time-series because data were suspect due to surveys done earlier in the year, at slower speeds, or were incomplete (Stephen Riley, USGS, personal communication). The bottom-trawl surveys were not ideal indicators of burbot biomass either, and were initially included in Ecosim as a relative time series, so estimates in each year were divided by the estimate in 1981, and assumed to be for age 3+ burbot. Fits of burbot biomass wtihin Ecosim were consistently poor, so were ultimately not included in the fitting routine.

Alewife (*Alosa pseudoharengus*)

Age-structure

Alewife were divided into two age groups in the model: age 0 and age 1+. Age groups were chosen to reflect how surveys report alewife biomass; young of year for age 0, and yearling

and older for age 1+. Growth coefficients were calculated from index surveys performed by the OMNR (Adam Cottrill, OMNR, unpublished data). Limited age data was available prior to 1999 and so data from 1999-2008 were used in the calculations. He and Stewart (2001) reported that alewife K was 0.6935 in Lake Ontario.

$K = 0.625$

Biomass

Alewife biomass estimates were available from bottom-trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). Fishing-power corrected estimates on a main-basin wide basis from 1981 were used in the model.

$B_{1+} = 1.99$ g/m^2

P/B

Production to biomass ratios were calculated based on information from a bioenergetics study in Lake Michigan (Rand et al. 1995). A weighted average (weighted by biomass) was calculated for average daily estimates of total instantaneous mortality for ages 1-7 and multiplied by 365 days to achieve a yearly estimate. The same procedure was repeated for young of year values. Ratios for adults in Rand et al. (1995) were higher than other Lake Michigan bioenergetics studies which were both around 0.25 (Stewart and Binkowski 1983; Pothoven and Madenjian 2008).

$P/B_{1+} = 1.25$ yr^{-1}

$P/B_0 = 4.00$ yr^{-1}

Q/B

Consumption to biomass ratios were calculated based on total consumption and total biomass estimates from a bioenergetics study in Lake Michigan (Pothoven and Madenjian 2008). A similar process for calculating the ratios was used as for calculating ratios for *P/B*. The overall consumption across ages 1-6 was added and divided by the overall weight across ages 1-6 to get an average *Q/B* estimate for adult alewife. Values were taken for the time period after dreissenids invaded as identified by Pothoven and Madenjian (2008). Estimates of *Q/B* from Rand et al. (1995) were 35, but not used in order to achieve a higher gross conversion efficiency, and also because prey of alewife were unbalanced when such a high value was used.

$$Q/B_{1+} = 13.6 \text{ yr}^{-1}$$

Diet

Diet compositions were available from a bioenergetics models of Lake Michigan for the pre-dreissenid time period (Table 2; Pothoven and Madenjian 2008). Compositions within age groups over the course of the year were averaged to obtain an overall yearly estimate. Contributions of cladocerans and copepods were summed to obtain the overall zooplankton composition, and contributions of "other prey" were ignored. Yearling diets were assumed to reflect age 0 diets. Contributions of the invasive predatory zooplankton (*Bythotrephes*) were taken from the post-dreissenid time period and reduced by a $1/1000^{\text{th}}$ scaling factor during modeling. Other contributions were proportionally adjusted so that the total summed to one. Other diet studies were available however most were for Lake Michigan (Rand et al. 1995; Madenjian et al. 2006c).

	Age 0	Age 1+
Diporeia	0.116	0.308

Mysis	0.031	0.117
Predatory Zooplankton	0.00013	0.00005
Zooplankton	0.8525	0.575

Time series:

Biomass time series for age 0 and age 1+ alewife for most years from 1981-2007 were available from USGS bottom trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). The time series for age 1+ alewife biomass was used in Ecosim as a relative time series, so estimates in each year were divided by the estimate in 1981. Biomass values in 1992, 1993, 1998, and 2000 were not used because data were suspect. The time series for age 0 alewife was highly variable, and estimates of yearly production anomalies were sensitive to its use. Consequently, the time series for age 0 alewife biomass was not used in the fitting routine in Ecosim.

Biomass accumulation

Time series suggested a decreasing trend in age 1+ alewife biomass from 1981-1984. A biomass accumulation rate of -0.282 yr^{-1} was calculated by dividing the slope of the decrease by the initial biomass estimate in 1981.

Rainbow smelt (*Osmerus mordax*)

Age-structure

Rainbow smelt were divided into two age groups in the model: age 0 and age 1+. Age groups were chosen to reflect how surveys report rainbow smelt biomass; young of year for age 0, and yearling and older for age 1+. Growth coefficients could not be calculated from OMNR index surveys and thus weight-at-age data from a rainbow smelt bioenergetics model were used

to calculate K (Lantry and Stewart 1993). Values of K were within the range of values reported in He and Stewart (2001) for rainbow smelt in Lake Superior.

$K = 0.477$

Biomass

Rainbow smelt biomass estimates were available from bottom-trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). Fishing-power corrected estimates on a main-basin wide basis from 1981 were used in the model.

$B_{1+} = 2.46 \text{ g/m}^2$

P/B

Production to biomass ratios were calculated based on estimates provided in a Lake Huron bioenergetics model (Lantry and Stewart 1993). The age 0 P/B ratio was provided in Table 14, whereas the age 1+ P/B ratio was calculated as the weighted average of P/B ratios provided in Table 14, weighted by the biomass for each age (Table 13; Lantry and Stewart 1993).

$P/B_{1+} = 1.165 \text{ yr}^{-1}$

$P/B_0 = 2.64 \text{ yr}^{-1}$

Q/B

A consumption to biomass ratio was calculated based on estimates provided in a Lake Huron bioenergetics model (Lantry and Stewart 1993). The age 1+ Q/B ratio was calculated as the weighted average of Q/B ratios provided in Table 14, weighted by the biomass for each age

(Table 13; Lantry and Stewart 1993). Prey of rainbow smelt (particularly *Mysis*) were unbalanced, and so rainbow smelt Q/B was reduced to 5.5.

$$Q/B_{1+} = 6.69 \text{ yr}^{-1}$$

Diet

Diet contributions were calculated based on a bioenergetics model for each of the Great Lakes (Table 4; Lantry and Stewart 1993). A yearly weighted average, weighted by the number of days for samples within each age, was calculated across ages. For age 1+ diets, a simple average was taken of the overall age 1 and age 2+ diets. Contributions of fish for age 1+ diets were assumed to be half age 0 rainbow smelt, and one-fourth each of slimy sculpin and age 0 alewife. Contributions of dipterans were applied to benthic invertebrate. Contributions of invasive predatory zooplankter *Bythotrephes* were reduced by a $1/1000^{th}$ scaling factor, and the contributions of other prey items were reapportioned to other groups, proportional to the existing contributions of each group, so that total contributions summed to one. Age 0 rainbow smelt were unbalanced, and so contributions of all fish groups were reduced in the diet of age 1+ rainbow smelt. *Mysis* contributions were increased by 10%, 5% was applied to age 1+ rainbow smelt, and the remaining difference was applied to import diet components. Slimy sculpin was also unbalanced, even after reductions in the diet of age 1+ rainbow smelt. Consequently, contributions of slimy sculpin were removed from the diet of rainbow smelt all together.

	Age 0	Age 1+
Age 0 alewife	0	0.02
Age 0 rainbow smelt	0	0.05
Age 1+ rainbow smelt	0	0.05
Diporeia	0.065	0.2
Mysis	0.18	0.38
Benthic invertebrates	0.015	0.019
Predatory zooplankton	0.000006	0.000017

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Zooplankton	0.74	0.14
Import	0	0.141

Time series

　　Biomass time series for age 0 and age 1+ rainbow smelt for most years from 1981-2007 were available from USGS bottom trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). The time series for age 1+ rainbow smelt biomass was used in Ecosim as a relative time series, so estimates in each year were divided by the estimate in 1981. Biomass values in 1992, 1993, 1998, and 2000 were not used because data were suspect. The time series for age 0 rainbow smelt was highly variable, and estimates of yearly production anomalies were sensitive to its use. Consequently, the time series for age 0 rainbow smelt biomass was not used in the fitting routine in Ecosim.

Biomass accumulation

　　Time series suggested a decreasing trend in age 1+ rainbow smelt biomass from 1981-1997. A biomass accumulation rate of -0.044 yr^{-1} was calculated by dividing the slope of the decrease by the initial biomass estimate in 1981.

Bloater (*Coregonus hoyi*)

Age structure

　　Bloater were divided into two age groups in the model: age 0 and age 1+. Age groups were chosen to reflect how surveys report bloater biomass; young of year for age 0, and yearling and older for age 1+. Growth coefficients were calculated from OMNR index surveys (Adam Cottrill, OMNR, personal communication) covering ages 0-15 and years 1978-2008. Szalai et al.

(2003) modeled time varying values of K for Lake Michigan bloater, and found that the majority of yearly estimates were between 0.15 and 0.25.

$K = 0.185$

Biomass

Bloater biomass estimates were available from bottom-trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). Fishing-power corrected estimates on a main-basin wide basis from 1981 were used in the model.

$B_{1+} = 1.86$ g/m^2

P/B

Production to biomass ratios were calculated using data from a bioenergetics study in Lake Michigan (Table 5; Rand et al. 1995). A weighted average (weighted by biomass) was calculated for average daily estimates of total mortality for ages 1-6 and multiplied by 365 days to achieve a yearly estimate. The same procedure was repeated for young of year and larvae values, however only the second cohort of larvae was used. Ratios for adults in Rand et al. (1995) were similar to estimates in other Ecopath models. Estimates of P/B ranged from 0.5 for Lake Superior (Cox and Kitchell 2004) to 1.1 for Lake Michigan Ecopath models (Ann Krause, UT, personal communication).

$P/B_{1+} = 1.02$ yr^{-1}

$P/B_0 = 2.33$ yr^{-1}

Q/B

A consumption to biomass ratio was calculated using data from a bioenergetics study in Lake Michigan (Rand et al. 1995). Total lake wide consumption in Lake Michigan was 5037 kt/yr and bloater contributed 68% of that consumption, of which 77% was contributed by age 1+ bloater (Rand et al. 1995). Biomass estimates for bloater were calculated by summing the biomass of each age group in Table 5 of Rand et al. (1995). The overall Q/B ratio was then the ratio of total consumption to total biomass. The Q/B estimate from Rand et al. (1995) was within the range of estimates from other Ecopath models; 5.8 and 15.16 for Lake Superior Ecopath models (Cox and Kitchell 2004 and Kitchell et al. 2000, respectively) and 13.5 for a Lake Michigan Ecopath model (Ann Krause, UT, personal communication).

$$Q/B_{1+} = 8.6 \text{ yr}^{-1}$$

Diet

Dry weight diet percentages for adult bloater were available from a Lake Michigan study in the mid 1950s and early 1960s (Wells and Beeton 1963). Dry weights were converted to wet weights by multiplying by five for zooplankton (Cushing et al. 1958) and *Diporeia* (Johnson 1988), dividing by 0.15 for *Mysis* (Landrum et al. 1992), and multiplying by six for sphaerids (Jorgensen 1979, for standard benthos). Estimates were fairly comparable to estimates from a Lake Michigan bioenergetics model (Rand et al. 1995) and from Lake Michigan samples (TeWinkel and Fleischer 1999). Young of year diets were taken from a Lake Michigan study, and showed prey items were strictly zooplankton (Crowder and Crawford 1984). *Mysis* were unbalanced, so contributions of *Mysis* in the diet of age 1+ bloater were reduced to 35% and the difference added to zooplankton.

	Age 0	Age 1+
Diporeia	0	0.50

Mysis	0	0.35
Benthic invertebrates	0	0.01
Zooplankton	1.0	0.14

Harvest

Bloater are targeted by a commercial fishery in Lake Huron, and harvest is almost exclusively from Canadian waters. Lake wide data from 1981 were entered into the model (Baldwin et al. 2002).

$$\text{Landings}_{y=1981, a=1+} = 0.0054 \text{ g/m}^2$$

Time series

Biomass time series for age 0 and age 1+ bloater for most years from 1981-2007 were available from USGS bottom trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). The time series for age 1+ bloater biomass was used in Ecosim as a relative time series, so estimates in each year were divided by the estimate in 1981. Biomass values in 1992, 1993, 1998, and 2000 were not used because data were suspect. The time series for age 0 bloater was highly variable, and estimates of yearly production anomalies were sensitive to its use. Consequently, the time series for age 0 bloater biomass was not used in the fitting routine in Ecosim.

Time series of bloater harvest in Lake Huron were available from 1981-1999 (Baldwin et al. 2002) and from 2000-2008 (Lloyd Mohr, OMNR, personal communication). Harvest time series were not fit well in Ecosim even when bloater effort time series were used (Adam Cottrill, OMNR, unpublished data). I adjusted fishing effort for the bloater fishery to reflect assumed exploitation rates and to improve fits to harvest data. I divided harvest by biomass for available years to obtain a time series of estimated exploitation rates. For years where either harvest of

biomass were not available, I assumed values for fishing mortality based on linear interpolation between values before and after the years in question. I divided the time series of exploitation rates by the estimate in 1981 to obtain a relative time series, which was used as a proxy for fishing effort, and which resulted in improved Ecosim fits to bloater harvest.

Biomass accumulation

Time series suggested an increasing trend in age 1+ bloater biomass from 1981-1986. A biomass accumulation rate of 0.681 yr^{-1} was calculated by dividing the slope of the increase by the initial biomass estimate in 1981.

Round goby (*Neogobius melanostomus*)

Biomass

Round goby was modeled as an invasive species. Biomass estimates were available beginning in 1997 from bottom-trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). Cox and Kitchell (2004) recommended entering biomasses of invasive species from a year where biomass values were high and where diet data were available. Biomass estimates for all invasive species were high in 2002, so was used as the year from which Ecopath biomass estimates were based. Biomass in 2002 was divided by 1000 to reflect a scenario of low initial biomass. The 1/1000th scaling factor was used in order to cause biomass to be low enough initially so that predation by round gobies was minimal, but high enough so that diet contributions of round goby in the diets of its predators could be entered with sufficient significant digits.

$B = 0.000026$ g/m^2

P/B

The production to biomass ratio were calculated from a regression equation linking natural mortality (M) to maximum length in cm (L_∞), the von Bertalanffy growth coefficient (K), and water temperature (T) in degrees C (Pauly 1980). The equation was $M=L_\infty^{-0.28}K^{0.654}T^{0.463}$. Maximum length was assumed to be the average (11.8 cm) of the maximum reported lengths for males (12.4 cm) and females (11.2 cm) in the Detroit River (MacInnis and Corkum 2000). A von Bertalanffy growth coefficient of 0.4 was available from fishbase (www.fishbase.org) based on the study by MacInnis and Corkum (2000), and average yearly surface water temperature was calculated to be 12.2 based on data from NOAA temperature buoys 45003 and 45008 for 1981-2001 (http://www.ndbc.noaa.gov/maps/EastGL_hist.shtml).

$P/B = 0.88 \text{ yr}^{-1}$

Q/B

A consumption to biomass ratio was available from a Lake Erie/Lake St. Clair bioenergetics study (Table 2; Lee and Johnson 2005). Ratios were calculated for ages 0-3 and then averaged across ages for an overall Q/B estimate. No weighting by biomass was done.

$Q/B = 4.7 \text{ yr}^{-1}$

Diet

Diets of round gobies were available from a Lake Huron study (Schaeffer et al. 2005). Diet values were presented in average number of prey items at two depths for small and large round goby in 2001 and 2002 (Table 4; Schaeffer et al. 2005). Wet weight proportions were

calculated by multiplying each diet item by average dry weight values, and then by a dry weight to wet weight ratio. Average dry weight (g) values of $4x10^{-6}$ for cladocerans (Hawkins and Evans 1979); $1.11x10^{-5}$ for average adult copepods (Hawkins and Evans 1979); $7x10^{-5}$ for ostracoda, converted from shell to shell-free weights by dividing by 0.3 (Nalepa and Quigley 1980); 0.00099 for chironomidae, converted to dry weight from ash-free dry weight by dividing by 0.9 (Nalepa et al. 2002); 0.00056 for sphaeriidae, converted to dry weight from ash-free weight by multiplying by five (Nalepa et al. 2002); 0.193 for *D. bugensis* using the regression equation in Mills et al. (1999) with a shell length of 17.3 mm (Mills et al. 1999); $2.58x10^{-4}$ for *Bythotrephes* using the length (3.11 mm) from Barbiero and Tuchman (2004) with the regression equation from appendix 1 in Johannsson et al. (2000); and $2.6x10^{-3}$ for *Mysis* (Sell 1982). Dry weights were converted to wet weight by multiplying by five for cladocerans, copepods, and *Bythotrephes* (standard zooplankton value; Cushing et al. 1958); by six for ostracoda and sphaeriidae (standard zoobenthos; Jorgensen 1979); dividing by 0.142 for chironomidae (Smit et al. 1993), and dividing by 0.15 for *Mysis* (Landrum et al. 1992). Wet weights (g) were available for *Diporeia* (0.00787; Landrum 1988) and were calculated for *D. bugensis* using the regression from Mills et al. (1999).

Once diets were converted to total wet weights, a weighted average (weighted by number of samples) of each prey item across size, depth, and year was calculated. Total weights were summed, and the proportion of each prey item to the total weight was calculated. Percent contributions of cladocera and copepoda were low and were not included in the overall diet. ostracoda, chironomidae, and sphaeriidae were combined into the benthic invertebrate category. Contributions of the invasive groups dreissenids and *Bythotrephes* (predatory zooplankton) were

reduced by $1/1000^{th}$ scaling factor, and contributions of other groups were rescaled so that total contributions summed to one.

Diporeia	0.358
Mysis	0.134
Benthic invertebrates	0.507
Dreissenids	0.000928
Predatory Zooplankton	5.00×10^{-6}

Harvest

Artificial harvest of invasive species was used as a way to cause invasive species to increase at the time of their invasion. The level of harvest was based on the instantaneous rate of population increase (r) from observed biomass time series data estimated by $B_t = B_0 e^{rt}$, where B_0 was the first biomass estimate in the time series, which was for 1997, and B_t was the biomass estimate t years after 1997. The rate was calculated based on minimizing the sum of squared deviations for the first five data points in the biomass time series and was 1.09. Harvest was set so that fishing mortality on round goby was 1.09. To offset the added fishing mortality rate, the initial P/B ratio was increased by an amount equivalent to the level of fishing mortality. Increasing P/B ratios ensured that estimates for $M0$ were taken only from trophic interactions with other species, and that when fishing mortality was removed, Ecosim estimates of P/B ratios would be appropriate.

Landings $= 2.834 \times 10^{-5}$ g/m^2

Time series

Biomass time series for round goby from 1997-2007 were available from USGS bottom trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). Biomass values

in 1998 and 2000 were not used because data were suspect. The time series for round goby

biomass was used in Ecosim as an absolute time series because the fit in Ecosim to an absolute

time series was less sensitive to initial biomass values than was a relative time series, which was

important when comparing ways to model species invasion (Chapter 3). Biomass time series

were used to determine the year in which invasion was assumed to occur, which was 1997, the

first year of positive capture in the trawl. However, observations of round goby in the St. Clair

River, from where it was assumed to have originally entered the Great Lakes, occurred in 1990

(Jude et al. 1992).

Slimy sculpin (*Cottus cognatus*)

Biomass

Slimy sculpin biomass estimates were available from bottom-trawl surveys in Lake

Huron (Stephen Riley, USGS, personal communication). Fishing-power corrected estimates on a

main-basin wide basis from 1981 were used in the model. Slimy sculpin were unbalanced and

therefore biomass was increased by five fold to achieve mass balance. The value reflected below

is the unbalanced value.

$B = 0.00167$ g/m^2

P/B

The production to biomass ratio from the Lake Superior Ecopath model was used in the

model (Kitchell et al. 2000). Slimy sculpin were unbalanced in the model and their gross

conversion efficiency was low, around 0.07, so the *P/B* ratio provided below was increased to

1.5. Estimates from other Ecopath models were 1.12 from the Lake Michigan Ecopath model

(Ann Krause, UT, personal communication) and 1.0 from the Lake Ontario Ecopath model (Halfon et al. 1996).

$P/B = 0.86$ yr^{-1}

Q/B

The consumption to biomass from the Lake Superior Ecopath model was used in the model (Kitchell et al. 2000). Other estimates were available from the Lake Ontario Ecopath model (4.74; Halfon et al. 1996), and another Lake Superior Ecopath model (4.2; Cox and Kitchell 2004). Lowering the Q/B ratio to these values could also have achieved higher gross conversion efficiencies, however it was not done because doing so would not have improved mass balance for the species, like changing the P/B ratio did.

$Q/B = 12$ yr^{-1}

Diet

Dry weight diet contributions were available from a Lake Michigan study from 2000-2001 (Hondorp et al. 2005). Diets were reported for slimy sculpin captured in both deep and shallow waters at three locations during three sampling periods. A weighted average (weighted across the number of samples) was calculated across sampling location, month, and year. Assuming a weight of 100 g, the dry weight diet proportions were converted to wet weights and then divided by the overall wet weight to generate wet weight diet proportions. Dry weight was converted to wet weight by dividing by 0.2 for *Diporeia* (combination of 0.269 (Landrum 1988) and 0.15-0.2 (Johnson 1988)); dividing by 0.15 for *Mysis* (Landrum et al. 1992); multiplying by six for fish eggs (standard zoobenthos; Jorgensen 1979); and dividing by 0.142 for "other prey",

which was assumed to be chironomids and was included in the model as benthic invertebrates (Smit et al. 1993). Contributions of fish eggs were assumed to be of bloater and deepwater sculpin, based on comments by Hondorp et al. (2005), and were evenly divided into the lowest age group for each species.

Age 0 bloater were unbalanced in the model. To achieve balance, contributions of fish eggs (bloater and deepwater sculpin) in slimy sculpin diets were removed and diets reapportioned to *Diporeia* (5%) and *Mysis* (8%). Other diet studies for slimy sculpin were available but were from Lake Ontario and were based on prey number rather than weight (Owens and Dittman 2003, Walsh et al. 2008), or from Lake Michigan in the 1960s (Wells 1980).

Diporeia	0.68
Mysis	0.23
Benthic invertebrates	0.09

Time series

Biomass time series for slimy sculpin for most years from 1981-2007 were available from USGS bottom trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). Biomass values in 1992, 1993, 1998, and 2000 were not used because data were suspect. The time series for slimy sculpin biomass was used in Ecosim as a relative time series, so estimates in each year were divided by the estimate in 1981.

Biomass accumulation

Time series suggested a decreasing trend in slimy sculpin biomass from 1981-1986. A biomass accumulation rate of -0.0905 yr^{-1} was calculated by dividing the slope of the decrease by the initial biomass estimate in 1981.

Deepwater sculpin (*Myoxocephalus thompsoni*)

Biomass

     Deepwater sculpin biomass estimates were available from bottom-trawl surveys done in

Lake Huron (Stephen Riley, USGS, personal communication). Fishing-power corrected

estimates on a main-basin wide basis from 1981 were used in the model.

$B = 0.218$ g/m2

P/B

     The production to biomass ratio from the Lake Superior Ecopath model was used in the

model (Kitchell et al. 2000). Deepwater sculpin had low gross conversion efficiency, around

0.06, so the *P/B* ratio provided below was increased to 0.9 and more similarly reflected the value

from the unpublished Lake Michigan model (0.92; Ann Krause, UT, personal communication).

$P/B = 0.6$ yr^{-1}

Q/B

     The consumption to biomass from the Lake Superior Ecopath model was used in the

model (Kitchell et al. 2000). Other estimates were available from another Lake Superior Ecopath

model (2.5; Cox and Kitchell 2004), or from the Lake Michigan Ecopath model (10.5; Ann

Krause, UT, personal communication). Lowering the *Q/B* ratio to these values could also have

achieved higher gross conversion efficiencies.

$Q/B = 10$ yr^{-1}

Diet

Dry weight diet contributions were available from a Lake Michigan study from 2000-2001 (Hondorp et al. 2005). Diets were reported for deepwater sculpin captured in both deep and shallow waters at three locations during three sampling periods. A weighted average (weighted across the number of samples) was calculated across sampling location, month, and year. Assuming a weight of 100 g, the dry weight diet proportions were converted to wet weights and then divided by the overall wet weight to generate wet weight diet proportions. Dry weight was converted to wet weight by dividing by 0.2 for *Diporeia* (combination of 0.269 (Landrum 1988) and 0.15-0.2 (Johnson 1988)); dividing by 0.15 for *Mysis* (Landrum et al. 1992); multiplying by six for fish eggs (standard zoobenthos; Jorgensen 1979); and dividing by 0.142 for "other prey", which was assumed to be chironomids and was included in the model as benthic invertebrates (Smit et al. 1993). Contributions of fish eggs were assumed to be of bloater and deepwater sculpin, based on comments by Hondorp et al. (2005), and were evenly divided into the lowest age group for each species.

Age 0 bloater were unbalanced in the model. To achieve balance, contributions of age 0 bloater in deepwater sculpin diets were lowered to 2% with the difference added to benthic invertebrates. Iterations in achieving balance revealed that *Mysis* were consumed in large quantity by deepwater sculpin, and so contributions of *Mysis* were lowered by 10% and the difference was added to *Diporeia*. Other diet studies for deepwater sculpin were available but were from Lake Ontario and were based on prey number rather than weight (Owens and Dittman 2003), or from Lake Michigan in the mid 1960s (Wells 1980).

Age 0 bloater	0.02
Deepwater sculpin	0.057
Diporeia	0.423
Mysis	0.453
Benthic invertebrates	0.047

Time series

Biomass time series for deepwater sculpin for most years from 1981-2007 were available from USGS bottom trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). Biomass values in 1992, 1993, 1998, and 2000 were not used because data were suspect. The time series for deepwater sculpin biomass was used in Ecosim as a relative time series, so estimates in each year were divided by the estimate in 1981.

Biomass accumulation

Time series suggested a decreasing trend in slimy sculpin biomass from 1981-1986. A biomass accumulation rate of -0.0696 yr^{-1} was calculated by dividing the slope of the decrease by the initial biomass estimate in 1981.

Ninespine stickleback (*Pungitius pungitius*)

Biomass

Ninespine stickleback biomass estimates were available from bottom-trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). Biomass estimates were available after 1994, however abundance estimates were available in 1981. Biomass in 1981 was calculated by dividing the abundance in 1981 by the ratio of abundance to biomass in 1994.

$B = 0.0072$ g/m^2

P/B

Production to biomass estimates were calculated from a regression equation linking natural mortality (M) to maximum length in cm (L_∞), the von Bertalanffy growth coefficient (K),

and water temperature (T) in degrees C (Pauly 1980). The equation was $M=L_\infty{}^{-0.28}K^{0.654}T^{0.463}$. Maximum length was assumed to be 7.6 cm (www.fishbase.org), the von Bertalanffy growth coefficient was assumed to be 1.6 (www.fishbase.org), and average yearly surface water temperature was calculated to be 12.2 based on data from NOAA temperature buoys 45003 and 45008 for 1981-2001 (http://www.ndbc.noaa.gov/maps/EastGL_hist.shtml).

$P/B = 2.45 \text{ yr}^{-1}$

Q/B

Consumption to biomass estimates for ninespine stickleback were difficult to find. The species has not been often used in past Ecopath models. Consequently, the same Q/B ratio of slimy sculpin was assumed for ninespine stickleback based on assumed similarities between the species.

$Q/B = 12 \text{ yr}^{-1}$

Diet

Diet proportions based on volume for ninespine stickleback greater than 50 mm in length were available from a Lake Superior study performed in 1968-1969 (Table 18; Griswold and Smith 1973). I assumed percent volume appropriately estimated percent wet weight, so no adjustments were made. I took a weighted average (weight by number of stomachs with food) of diet compositions across all months. I ignored unidentified contributions and contributions from nemotoda, and reapportioned remaining contributions to sum to one. I assumed that coregonine eggs were from bloater, and assigned them as age 0 bloater in the model. I also assigned other benthos and chironomidae to benthic invertebrates, and copepoda and cladocera to zooplankton.

Age 0 bloater were unbalanced and so their contributions were removed and reapportioned to other groups, proportional to the existing contributions of each group, so that total contributions summed to one.

Age 0 bloater	0.02
Diporeia	0.64
Mysis	0.215
Benthic Invertebrates	0.025
Zooplankton	0.100

Time series

Biomass time series for ninespine stickleback for most years from 1994-2007 were available from USGS bottom trawl surveys in Lake Huron (Stephen Riley, USGS, personal communication). Biomass values in 1998 and 2000 were not used because data were suspect. The time series for ninespine stickleback biomass was used in Ecosim as a relative time series, , so estimates in each year were divided by the initial Ecopath biomass value.

Diporeia (*Diporeia spp.*)

Biomass

Biomass estimates of *Diporeia* were available from Lake Huron surveys done in the 1970s and late 1990s. Dobiesz et al. (2005) provided a summary of numerical estimates for *Diporeia* stratified by depth for 1970-1972, 1997, and 1998. I averaged numerical estimates across depths using depth-proportions of Lake Huron, and calculated overall biomass by converting numerical estimates to biomass estimates based on individual wet weights from Landrum (1988) of 0.0058 g for waters shallower than 50 m and 0.00787 g for waters deeper than 50 m. Depth proportions of Lake Huron were 0.252 for water shallower than 30 m, 0.155 for waters between 30 and 50 m, 0.306 for waters between 50 and 90 m, and 0.287 for waters

deeper than 90 m (Ed Roseman, USGS, personal communications). Biomass estimates for 1972 and 1997 were both 26.8 g/m^2, and therefore an assumed value of 26 g/m^2 was used in Ecopath. Estimates for the 1970s studies were also available from Nalepa et al. (2007) but had different numerical values and therefore produced different biomass estimates. Estimates from Dobeisz et al. (2005) were used for *Diporeia* because values in 1972 were more similar to values in 1997 than the estimates for 1972 and 2000 in Nalepa et al. (2007).

$B = 26$ g/m^2

P/B

Production to biomass ratios were available from studies done in Lake Huron from 1980-1982 (Table 2; Johnson 1988). The average *P/B* ratio across years was calculated, and used in the model. Estimates for other studies or models varied from 1.9 for another Lake Huron study (Guiger and Barton 2002), approximately 2.0 for the Lake Superior (Kitchell et al. 2000) and Lake Ontario (Halfon et al. 1996) Ecopath models, and 3.0 for the Lake Michigan Ecopath model (Ann Krause, UT, personal communication). Gross conversion efficiencies were fairly low originally, so the *P/B* ratio was increased during model balancing from the value below to 2.0.

$P/B = 1.43$ yr^{-1}

Q/B

The consumption to biomass ratio from the Lake Superior Ecopath model was used (Kitchell et al. 2000). Estimates from other models were 17.6 for the Lake Ontario Ecopath model (Halfon et al. 1996), and 22 for the Lake Michigan Ecopath model (Ann Krause, UT,

personal communication). Gross conversion efficiencies were fairly low originally, so the *Q/B* ratio was decreased during model balancing from the original value below to 15.

$$Q/B = 25 \text{ yr}^{-1}$$

Diet

Diet proportions were available from a Lake Michigan study (Evans et al. 1990). Evans et al. (1990) found that nearly 99% of contents consisted of silt and other sediment, with remains of diatoms and phytoplankton being the few biological remains. Therefore, *Diporeia* were assumed to consume 99% detritus, with the remaining 1% assigned to phytoplankton. A Lake Huron study supports the claim that *Diporeia* will consume diatoms when available (Guiger and Barton 2002) and thus the percentage of phytoplankton, which includes diatoms, may be greater.

Phytoplankton	0.01
Detritus	0.99

Time series

Biomass time series for *Diporeia* from 1997-2006 were calculated from numerical estimates from Environmental Protection Agency (EPA) sampling in Lake Huron (Ric Barbiero, EPA, unpublished data). The same procedure for calculating wet weight biomass estimates for the initial Ecopath input was repeated for each year in the time series. Another time series of biomass estimates was available for Lake Huron (French et al. 2009) but was not used because it only included years 2001-2007.

Biomass accumulation

Diporeia were the prey of round goby, an invasive species. Round goby were included in Ecopath despite not being present in Lake Huron in 1981. To offset the predation caused by round goby in Ecopath, negative biomass accumulation was added to *Diporeia*. The value of the biomass accumulation was -4.37×10^{-5} g/m^2/yr, which was equal to the value of consumption by round goby on *Diporeia*.

Mysis (*Mysis diluviana*)

Biomass

Biomass estimates were available from a review of previously published Great Lakes studies (Sell 1982). Dry weight biomass in Lake Huron study in 1971 (originally by Carpenter et al. 1974) was estimated at 0.53 g/m2 (Table 2; Sell 1982). I converted dry weight to wet weight using a conversion factor 0.15 (Landrum et al. 1992).

$B = 3.53$ g/m^2

P/B

Production to biomass estimates were available from Lake Huron and other Great lakes studies (Sell 1982). *Mysis P/B* was increased during balancing from the original value below to 3.0 to achieve mass balance. Other studies had *P/B* ratios of 2.0 (Kitchell et al. 2000), 2.3 (Cox and Kitchell 2004), 2.13 (Ann Krause, UT, personal communication), and 3.1 (Halfon et al. 1996).

$P/B = 2.8$ yr^{-1}

Q/B

Consumption to biomass data was not available from published studies and therefore the estimate from the Lake Superior Ecopath model was used (Kitchell et al. 2000). Ratios from other Ecopath models for *Q/B* were 41.16 (Halfon et al. 1996) and 21.3 (Ann Krause, UT, personal communication). Substantial changes were made to *Mysis Q/B* during balancing, and the final model reflects a value lower (12) than the original value below.

$Q/B = 25 \text{ yr}^{-1}$

Diet

Diet contributions for *Mysis* were available from a 1995 study in Lake Ontario (Table 3; Johannsson et al. 2001). *Keratella*, *Kellicotia*, *Notholca*, *Tricocera*, and amphipods were not included because their diet proportions were low. Dry weights of individual prey items and number of prey items consumed per mysid during the daytime were averaged across sampling months to obtain yearly estimates. Two sampling gears were used during nighttime sampling, so a weighted average across sampling gears of the number of prey items per mysid was used. Following the assumption of Johannsson et al. (2001), nighttime estimates for prey numbers were weighted 10% for benthic sampling gears, and 90% for pelagic sampling gears. Once yearly average prey dry weights and daytime and nighttime prey numbers were calculated, the total diet dry weight and percentages of each diet item were calculated.

Not all important prey items could be quantified based on standard gut content analysis and therefore additional prey items were considered. Johannsson et al. (2001) found that attributing 50% of the diet dry weight in May to diatoms would reconcile stable isotope analysis signatures with standard gut content analysis, and that attributing small percentages of the September diet dry wet to *Diporeia* and phytoplankton would reconcile observations that *Mysis*

consume these groups with poor isotope signatures for including them. Consequently, I added

50% of the diet dry weight in May to diatoms, and 5% each of the diet dry weight in September

to *Diporeia* and algae, and recalculated the overall diet percentages. For inputting the diet

percentages into Ecopath, I combined *Limnocalanus*, calanoids, cyclopoids, *Bosmina*,

Eubosmina, and *Daphnia* into the zooplankton group, and diatoms and algae into the

phytoplankton group. To convert diet dry weight to diet wet weights, I divided dry weights by

0.2 for zooplankton (Cushing et al. 1958), and for *Diporeia* (combination of 0.269 from

Landrum 1988 and 0.15-0.2 from Johnson 1988), and divided by 0.08 for phytoplankton

(Cushing et al. 1958).

   Adjustments were made to *Mysis* diets during balancing based on assumed diet values of

Mysis in the Lake Michigan Ecopath model (Ann Krause, UT, personal communication).

Contributions of zooplankton were reduced to 50%, with the differences added between

Diporeia, phytoplankton, and detritus.

Diporeia	0.08
Zooplankton	0.50
Phytoplankton	0.30
Detritus	0.12

Biomass accumulation

   Mysis were the prey of round goby, an invasive species. Round goby were included in

Ecopath despite not being present in Lake Huron in 1981. To offset the predation caused by

round goby in Ecopath, negative biomass accumulation was added to *Mysis*. The value of the

biomass accumulation was -1.64×10^{-5} g/m^2/yr, which was equal to the value of consumption by

round goby on *Mysis*.

Benthic invertebrates

Biomass

Benthic invertebrates represented a combination of oligochaete, sphaeriid, and chironomid groups. Biomass estimates of benthic invertebrates were available from Lake Huron surveys done in the 1970s and late 1990s. Nalepa et al. (2007) provided a summary of numerical estimates stratified by depth for 1970-1972, 2000, and 2003. I averaged numerical estimates across depths using depth-proportions of Lake Huron, and calculated overall biomass by converted numerical estimates to biomass estimates based on average individual ash-free dry weights, and ash-free dry weights to wet weight ratios.

Depth proportions of Lake Huron were 0.252 for water shallower than 30 m, 0.155 for waters between 30 and 50 m, 0.306 for waters between 50 and 90 m, and 0.287 for waters deeper than 90 m (Ed Roseman, USGS, personal communications). Ash-free dry weights per individual were calculated from average number and ash-free dry weights in 1987-1996 from a Saginaw Bay study (Table 5 and 6; Nalepa et al. 2002). An ash-free dry weight to wet weight ratio of 0.182 for oligochaete (Smit et al. 1993), 0.129 for chironomid (Smit et al. 1993), and 0.033 for sphaeriid groups were used to determine the overall wet weight for each group. The sphaeriid ratio was the product of an ash-free dry weight to dry weight ratio of 0.2 (Johnson and Brinkhurst 1971) and a dry weight to wet weight ratio of 0.167 for standard benthos (Jorgensen 1979). The biomass of all three groups was summed to generate a single estimate for benthic invertebrates. Estimates for the 1970s studies were also available from Dobiesz et al. (2005) but had different numerical values and therefore produced different biomass estimates.

$B = 3.17$ g/m^2

P/B

Production to biomass ratios of benthic invertebrate groups were available from a Lake Ontario study (Table 5; Johnson and Brinkhurst 1971). A weighted average (weighted by biomass in 1972 (Nalepa et al. 2007)) *P/B* ratio across oligochaeta, sphaeriidae, and chironomidae was calculated. Johnson and Brinkhurst (1971) calculated *P/B* ratios for two time periods, and thus the average *P/B* for each group across the two time periods was used. Production to biomass ratios for other benthic invertebrates groups were available for Lake Erie and ranged from 2.0 – 4.2 (Johannsson et al. 2000).

P/B = 2.36 yr^{-1}

Q/B

Consumption to biomass ratios of benthic invertebrate groups were available from the Lake Michigan Ecopath model (Ann Krause, UT, personal communication). A weighted average (weighted by biomass in 1972 (Nalepa et al. 2007)) *Q/B* ratio across oligochaeta, sphaeriidae, and chironomidae was calculated. Consumption to biomass ratios for other benthic invertebrates groups were available for Oneida lake and the Bay of Quinte, Lake Ontario (Jaeger 2006). Estimates from Jaeger (2006) were higher, and likely reflected the more productive systems studied.

Q/B = 8.14 yr^{-1}

Diet

Diet proportions were available from the Lake Michigan Ecopath model (Ann Krause, UT, personal communication). Chironomidae and oligochaeta were grouped into one group and

consumed 5% chironomidae and oligochaeta, and 95% detritus. Sphaeriidae consumed 100% detritus. Thus benthic invertebrates were assumed to have 5% of their diet from benthic invertebrates, and the remaining 95% from detritus.

Benthic invertebrates   0.05
Detritus   0.95

Time series

Biomass time series for benthic invertebrate groups from 2001-2007 were calculated from numerical estimates from a Lake Huron study (Figure 2 in French et al. (2009); data provided by Jeff Schaeffer, USGS, personal communication). Multiple measurements were made within each depth strata, so measurements at each location were averaged to achieve a yearly estimate at each depth. The same procedure for calculating biomass for the initial Ecopath model was repeated for each year in the time series, with one slight difference. Only depths shallower than 90 m were sampled, so lake-depth proportions for 0-90 m were rescaled so the sum would be one. The estimates from French et al. (2009) for benthic invertebrates were comparable to those for 2000 and 2003 from Nalepa et al. (2007). The time series for benthic invertebrate biomass was used in Ecosim as a relative time series, relative to the initial biomass input.

Biomass accumulation

Benthic invertebrates were the prey of round goby, an invasive species. Round goby were included in Ecopath despite not being present in Lake Huron in 1981. To offset the predation caused by round goby in Ecopath, negative biomass accumulation was added to benthic invertebrates. The value of the biomass accumulation was -6.195×10^{-5} $g/m^2/yr$, which was equal to the value of consumption by round goby on benthic invertebrates.

Dreissenid mussels

Biomass

Driessenids was modeled as an invasive species. Dreissenids represented a combination of zebra mussels (*Dreissena polymorpha*) and quagga mussels (*D. bugensis*). Although the groups have different depth ranges, occupy different substrates, and have expanded within the lake at different times (Vanderploeg et al. 2002), data inputs for both, but particularly quaggas are limited, and thus the groups were combined. Biomass estimates beginning in 2001 were calculated as the product of numerical estimates from a Lake Huron survey (Figure 2 in French et al. 2009 but data provided by Jeff Schaeffer, USGS, personal communication) and average weights from other surveys performed in the Great Lakes. Cox and Kitchell (2004) recommended entering biomasses of invasive species from a year where biomass values were high and where diet data were available. Biomass estimates for all invasive species were high in 2002, so was used as the year from which Ecopath biomass estimates were based. Biomass in 2002 was divided by 1000 to reflect a scenario of low initial biomass. The 1/1000th scaling factor was used in order to cause biomass to be low enough initially so that predation by dreissenids was minimal, but high enough so that diet contributions of dreissenids in the diets of its predators could be entered with sufficient significant digits.

Numerical estimates of dreissenids were reported for multiple ports and stratified into 27 m, 46 m, and 73 m depth classes (French et al. 2009). Estimates were averaged across ports, and then averaged across depths using depth-proportions for Lake Huron of 0.252 for waters shallower than 30 m, 0.155 for waters between 30 and 50 m, and 0.306 for waters between 50 and 90 m (Ed Roseman, USGS, personal communication). Sampling was not performed at

depths greater than 90 m so the average numerical estimates were calculated with lake-depth proportions for 0-90 m rescaled so the sum would be one.

Once a yearly average across ports and depths was calculated, numerical estimates were converted to wet weight biomass estimates. An average shelled wet-weight per individual of 0.195 for *D. polymorpha* and 0.447 for *D. bugensis* was assumed from length-weight relationships for a Lake Ontario study (equations 1-4; Mills et al. 1999) using lengths for both species from Olcott and Thirty Mile Point in Table 2 of Mills et al. (1999). Shelled weights were converted to shell-free wet-weight using conversions from a Lake Erie study (Johannsson et al. 2001) of 0.56 for *D. polymorpha* and 0.58 for *D. bugensis*.

$B = 0.098$ g/m^2

P/B

Production to biomass ratios were available from a Lake Ontario and Lake Erie study (Table 1; Chase and Bailey 1999). Production to biomass ratios where no components (either Ps, Pg, or Pr in Table 1 of Chase and Bailey, 1999) were negative were used for each year and depth from the Port Dalhousie samples (Chase and Bailey 1999). If any components were negative, I calculated *P/B* myself by summing over the positive production components only, and dividing by biomass. I calculated an overall estimated by taking a simple average over all years and depths using my adjusted values when necessary. Reported *P/B* ratios were not calculated by simply dividing the presented total production value by the biomass estimate in Table 1 of Chase and Bailey (1999) and so my method is not the same done by Chase and Bailey (1999). Nonetheless, the overall estimate was within the range, although near the lower end, of values

presented in Table 4 of Chase and Bailey (1999). Values for another Lake Ontario study, although for a more productive inlet within Lake Ontario, was 1.35 (Jaeger 2006).

$P/B = 0.315 \text{ yr}^{-1}$

Q/B

A consumption to biomass estimates from a productive inlet of Lake Ontario for *D. polymorpha* was used in the model for dreissenids (Jaeger 2006). The Lake Michigan model used higher estimates (38; Ann Krause, UT, personal communication), but were not used because initial attempts to balance, albeit with high dreissenid biomass, proved challenging when *Q/B* ratios were high. Furthermore, the larger *Q/B* value resulted in very small gross conversion efficiencies for dreissenids, and so was not used.

$Q/B = 8.6 \text{ yr}^{-1}$

Diet

Diet proportions were available from the Lake Michigan Ecopath model (Ann Krause, UT, personal communication). Contributions of benthic bacteria in the Lake Michigan Ecopath model were assumed to be detritus for the Lake Huron Ecopath model. Initial attempts at balancing with high dreissenid biomass caused large imbalances for phytoplankton. Consequently, the contribution of phytoplankton was reduced, and the difference was added to detritus. Moreover, *D. bugensis* has began occupying deeper waters where I thought contributions of phytoplankton would be lower than originally used, particularly at time when the lake is stratified.

Phytoplankton	0.2
Detritus	0.8

Harvest

Artificial harvest of invasive species was used as a way to cause invasive species to increase at the time of their invasion. The level of harvest was based on the instantaneous rate of population increase (r) from observed biomass time series data estimated by $B_t=B_0e^{rt}$, where B_0 was the first biomass estimate in the time series, which was for 2000, and B_t was the biomass estimate t years after 2000. The rate was calculated based on minimizing the sum of squared deviations for the first three data points in the biomass time series and was 1.07. Harvest was set so that fishing mortality on dreissenids was 1.07. To offset the added fishing mortality rate, the initial P/B ratio was increased by an amount equivalent to the level of fishing mortality. Increasing P/B ratios ensured that estimates for $M0$ were taken only from trophic interactions with other species, and that when fishing mortality was removed, Ecosim estimates of P/B ratios would be appropriate.

Landings = 0.1049 g/m^2

Time series

Biomass time series for dreissenid groups were calculated from numerical estimates from two Lake Huron surveys done in 2000 and 2003 (Table 5; Nalepa et al. 2007) and in 2001-2007 (Figure 2 in French et al. 2009; data provided by Jeff Schaeffer, USGS, personal communication). The same procedure for calculating biomass for the initial Ecopath model was repeated for each year in the time series, with one slight difference. Nalepa et al. (2007) presented results for depths greater than 90m, so depth proportions for waters deeper than 90 m (0.287) was used in the calculates for 2000. The biomass estimate in 2000 (Nalepa et al. 2007)

was added to the 2001-2007 time series (French et al. 2009) for fitting because biomass estimates

for 2003 were similar between Nalepa et al. (2007) and French et al. (2009). The time series for

dreissenid biomass was used in Ecosim as an absolute time series because the fit in Ecosim to an

absolute time series was less sensitive to initial biomass values than was a relative time series,

which was important when comparing ways to model species invasion (Chapter 3).

Biomass time series were used to determine the year in which invasion was assumed to

occur, which was 1997, the first year of positive capture for round gobies. The first year of

positive capture for dreissenids was not used because dreissenids are key prey items of round

goby, and affected fits to gobies if not present in the model at high enough biomass prior to

round goby invasion. Although we assumed dreissenid invasion occurred in 1997, dreissenids

had spread throughout the Great Lakes by 1990 (Vanderploeg et al. 2002).

Predatory zooplankton (*Bythotrephes longimanus*)

Biomass

Predatory zooplankton was modeled as an invasive species. Predatory zooplankton was

assumed to reflect predominantly *Bythotrephes*, although other predatory zooplankton are

present in Lake Huron, namely *Cercopagis pengoi*, and *Leptodora sp.* (Barbiero et al. 2001).

Biomass estimates were available beginning in 1998 from Environmental Protection Agency

surveys at depths of the shallower of 100m or 2m from the bottom (Ric Barbiero, EPA, personal

communication). The EPA reports both *Leptodora* sp. and *Bythotrephes* as predatory

zooplankton, however the latter dominated the samples, and so were assumed to represent the

entirety of predatory zooplankton in the lake. Biomass was calculated as the product of

volumetric dry-weight biomass (Ric Barbiero, EPA, personal communication), dry weight to wet

weight ratio of 0.2 (Cushing et al. 1958), and an average depth of 89 m (Table 1; Barbiero et al. 2009). Greater details on the sampling can be found in Barbiero et al. (2001), Barbiero and Tuchman (2004), and Barbiero et al. (2009).

Cox and Kitchell (2004) recommended entering biomasses of invasive species from a year where biomass values were high and where diet data were available. Biomass estimates for all invasive species were high in 2002, so was used as the year from which Ecopath biomass estimates were based. Biomass in 2002 was divided by 1000 to reflect a scenario of low initial biomass. The 1/1000th scaling factor was used in order to cause biomass to be low enough initially so that predation by round gobies was minimal, but high enough so that diet contributions of round goby in the diets of its predators could be entered with sufficient significant digits.

$B = 0.385$ g/m^2

P/B

A production to biomass ratio for *Bythotrephes* was calculated from a Lake Ontario study (equations 1 and 2; Johannsson et al. 2001). The two equations related dry weight to daily *P/B* based on temperature. Average dry weight was calculated following the length-weight regression in the appendix of Johannsson et al. (2000), with an average length of 3.11 mm (Barbiero and Tuchman 2004). Average yearly surface water temperature data was used to determine that the number of days where water temperature was greater than 10 degrees C based on NOAA temperature buoys 45003 and 45008 for 1981-2001 occurred from July to October, or 123 days (http://www.ndbc.noaa.gov/maps/EastGL_hist.shtml). Once daily *P/B* ratios were calculated, they were summed to obtain an overall yearly estimate. During balancing, predatory zooplankton

were unbalanced, and therefore the original *P/B* ratio below was increased to 25 (Ora Johannsson, DFO, personal communication).

$P/B = 10 \text{ yr}^{-1}$

Q/B

Consumption to biomass was calculated by assuming a gross food conversion efficiency value of 25% (Ora Johannsson, DFO, personal communication). Straile (1997) found that mean and median gross food conversion efficiencies for zooplankton were between 20-30%. Consumption to biomass was therefore the product of *P/B* and GCE. Values for *Q/B* of *Bythotrephes* in the Lake Michigan Ecopath model was 86 (Ann Krause, UT, personal communication).

$Q/B = 40 \text{ yr}^{-1}$

Diet

Diet contributions for *Bythotrephes* from a Lake Huron study revealed that *Bythotrephes* prey exclusively on zooplankton (Vanderploeg et al. 1993).

 Zooplankton   1

Harvest

Artificial harvest of invasive species was used as a way to cause invasive species to increase at the time of their invasion. The level of harvest was based on the instantaneous rate of population increase (*r*) from observed biomass time series data estimated by $B_t = B_0 e^{rt}$, where B_0 was the first biomass estimate in the time series and B_t was the biomass estimate *t* years the year

for B_0. Observed biomass estimates for predatory zooplankton started at high values, so the

increase in biomass over the course of the invasion could not be measured. Consequently, I

estimated r by setting B_0 to be the initial Ecopath biomass estimate with the 1/1000th scaling

factor, and minimized the sum of square deviation of $B_{t=1998}$ with the first data point in the

observed biomass time series, which was in 1998. The year of B_0 was 1984, the year when

Bythotrephes were first observed in Lake Huron (Lehman and Caceres 1993). Harvest was set so

that fishing mortality on predatory zooplankton was 0.46. To offset the added fishing mortality

rate, the initial *P/B* ratio was increased by an amount equivalent to the level of fishing mortality.

Increasing *P/B* ratios ensured that estimates for *M0* were taken only from trophic interactions

with other species, and that when fishing mortality was removed, Ecosim estimates of *P/B* ratios

would be appropriate.

$$\text{Landings} = 1.68 \times 10^{-4} \text{ g/m}^2$$

Time series

Biomass time series for *Bythotrephes* from 1998-2006 were calculated from dry weight

volumetric biomass estimates for EPA sampling in Lake Huron (Ric Barbiero, EPA, personal

communication). Wet-weight areal biomass estimates were calculated using the same procedure

as for estimating the initial biomass value, except that no 1/1000 scaling factor was used.

Biomass for 1999 was a full order of magnitude higher than for other years, which seemed

questionable. I therefore did not include 1999 estimates in the time series inputted into the

model. The time series for *Bythotrephes* biomass was used in Ecosim as an absolute time series

because the fit in Ecosim to an absolute time series was less sensitive to initial biomass values

than was a relative time series, which was important when comparing ways to model species

invasion (Chapter 3). Biomass time series were used to determine the year in which invasion was assumed to occur, which was 1998, the first year of positive capture. Although we assumed *Bythotrephes* invasion occurred in 1998, *Bythotrephes* was first observed in Lake Huron in 1984 (Lehman and Caceres 1993).

Zooplankton

Biomass

      Zooplankton represented a combination of calanoid, cyclopoid, rotifer, and non-predatory caldoceran zooplankton groups. Biomass estimates were available from a study done by the EPA in Lake Huron in 1984 (Makarewicz 1988). Summary data were provided on a volumetric dry weight estimate of 0.0273 g/m^3, however the depth with which to convert to areal estimates was unknown because sampling was done at depths both reaching near the bottom and at depths down to 20m. An areal estimate of 1.15 g/m^2 dry weight was calculated based on the data from Makarewicz (1988) that accounted for the depth of each sampling location (Yu-Chun Kao, University of Michigan, personal communication). Dry weight estimates were converted to wet weight estimates using a ratio of 0.2 (Cushing et al. 1958). Another study done in 1971 in Lake Huron estimated zooplankton biomass to be 0.051 g/m^3 dry weight (Watson and Carpenter 1974).

$B = 5.76$ g/m^2

P/B

      Production to biomass ratios were calculated following the assumptions made by Johannsson et al. (2000) for all subgroups in the zooplankton group. Production to biomass ratios

were calculated based on assumed temperature-dependent relationships. Ratios for non-predatory cladocerans were calculated on a daily basis, and were 0.162 when water temperature < 10 C, and 0.042 when water temperatures > 10 C (Johannsson et al. 2000). Average yearly surface-water temperature data was used to determine that the number of days where water temperature was greater than 10 degrees C based on NOAA temperature buoys 45003 and 45008 for 1981-2001 was 123 days from July to October (http://www.ndbc.noaa.gov/maps/EastGL_hist.shtml). Ratios for rotifers, chclopoids, and calanoids were calculated on an annual basis and equaled $\log_{10}(P/B) = A + 0.0293*T$, where T is the annual temperature over the year, and A = 1.33 for rotifers, 0.975 for cyclopoids, and 0.692 for calanoids (equation 7; Shuter and Ing 1997). The annual temperature was assumed to be 12.2, based on NOAA temperature buoys 45003 and 45008 for 1981-2001 (http://www.ndbc.noaa.gov/maps/EastGL_hist.shtml). Therefore, the annual *P/B* estimate was 30 for non-predatory cladocerans, 11 for calanoids, 20 for cyclopoids, and 50 for rotifers. An overall weighted average *P/B* for zooplankton was calculated, weighted by biomass estimates for the subgroups in 2000 (Ric Barbiero, EPA, personal communication).

Production to biomass estimates were available from other Ecopath models. Cox and Kitchell (2004) used a value of 25, while Kitchell et al. (2000) used a value of 12.9 for Lake Superior Ecopath models. Estimate from the Lake Ontario Ecopath model were lower (7; Halfon et al. 1996), but estimates from the Lake Michigan Ecopath model ranged from 5-42 depending on the subgroup (Ann Krause, UT (UT), personal communication).

$P/B = 21.1$ yr^{-1}

Q/B

Consumption to biomass was calculated by assuming a gross food conversion efficiency value of 25% (Ora Johannsson, DFO, personal communication). Straile (1997) found that mean and median gross food conversion efficiencies for zooplankton were between 20-30%. Consumption to biomass was therefore the product of *P/B* and GCE.

Values for *Q/B* of zooplankton in other Ecopath models ranged widely. Cox and Kitchell (2004) used a value of 120, while Kitchell et al. (2000) use a value of 365 for Lake Superior Ecopath models. Estimates from the Lake Ontario model were even lower at 102.8 (Halfon et al. 1996), but estimates from the Lake Michigan model ranged from 86-200 depending on the subgroup (Ann Krause, UT, personal communication).

$Q/B = 105.2 \text{ yr}^{-1}$

Diet

Diet composition for zooplankton was available from a Lake Michigan Ecopath model (Ann Krause, UT, personal communication). All prey items of non-predatory groups were phytoplankton subgroups.

 Phytoplankton   1

Time series

Biomass time series for *Bythotrephes* from 1998-2006 were calculated from dry weight volumetric biomass estimates for EPA sampling in Lake Huron (Ric Barbiero, EPA, personal communication). The time series for zooplankton biomass was used in Ecosim as a relative time series, relative to the dry weight volumetric biomass estimate from Makarewicz (1988) for 1984. I used the estimate from Makarewicz (1988) instead of the initial Ecopath biomass estimate because the estimates from Watson and Carpenter (1974), Makarewicz (1988), and the biomass

time series were in the same units, so no conversion to wet weight areal biomass was necessary. In contrast, the initial Ecopath biomass estimate was specifically calculated in units better suited for Ecopath, and therefore I felt was less comparable. Furthermore, the initial Ecopath biomass estimate was about half as large as the converted estimate from Makarewicz (1988), even though the data used in the calculations were the same. I wanted to maintain the similarity between the dry weight estimates from past studies and the time series, without introducing differences caused by applying a different method for converting to areal wet weight biomass for the initial Ecopath estimate.

Biomass estimates from zooplankton surveys have been performed by the EPA in Lake Huron for most years since 1983. Surveys from 1983-1996 sampled down to 20 m depths, and therefore did not capture zooplankton occupying deeper layers of the water column. Since 1997, sampling has been done to depths of the minimum of 100 m or 2 m from the bottom. Due to the discrepancies in sampling procedures, I could not obtain biomass estimates prior to 1998. Details of the sampling procedures are available from Barbiero et al. (2001), Barbiero and Tuchman (2004), and Barbiero et al. (2009).

Biomass accumulation

Zooplankton were the prey of predatory zooplankton, an invasive species. Predatory zooplankton were included in Ecopath despite not being present in Lake Huron in 1981. To offset the predation caused by predatory zooplankton in Ecopath, negative biomass accumulation was added to zooplankton. The value of the biomass accumulation was -0.0373 $g/m^2/yr$, which was equal to the value of consumption by predatory zooplankton on zooplankton.

Phytoplankton

Biomass

     Phytoplankton represented a combination of all major photosynthetic planktonic groups, including diatoms. Biomass estimates were available in 1983 for a Lake Huron study (Makarewicz and Bertram 1991). Volumetric biomass was estimated to be 0.37 g/m^3 and was converted to an areal estimate by multiplying by the sampling depth, 20 m (Makarewicz and Bertram 1991). The sampling depth roughly corresponded to the depth of the summer epilimnion (between 14-17 m; Barbiero and Tuchman 2001), below which biomass of phytoplankton was assumed to be zero. I assumed that biomass estimates were wet weight biomass values because biomass was converted from biovolume using an assumed specific gravity of 1.0 (Makarewicz and Bertram 1991).

$B = 7.4$ g/m^2

P/B

     Production to biomass ratios were available from the Lake Michigan Ecopath model for subspecies of phytoplankton groups (Ann Krause, UT, personal communication). An overall weighted average *P/B* for phytoplankton was calculated, weighted by biomass estimates for the subgroups from sampling done in Lake Huron in 2000 (data from Barbiero and Tuchman 2001 provided by Ric Barbiero, EPA, personal communication). Biomass estimates were averaged across north and south basins, and across summer and spring sampling periods, and were converted from volumetric biovolume estimates to areal biomass estimates by assuming a specific gravity of one and depth of 20 m. Production to biomass ratios for phytoplankton in

other Ecopath models ranged from 442 in Kitchell et al. (2000) to 125 in Cox and Kitchell (2004) for Lake Superior Ecopath models.

$P/B = 278 \text{ yr}^{-1}$

Q/B

Phytoplankton are primary producers and therefore no Q/B information was needed.

Diet

Phytoplankton are primary producers and therefore no diet information was needed.

Time series

Phytoplankton time series were not used in the fitting routine because of the paucity of available estimates. Estimates for 1983-1985 were presented in Makarewicz and Betram (1991), and estimates for 1999 and 2000 were presented in Barbiero and Tuchman (2001).

Biomass accumulation

Phytoplankton were the prey of dreissenids, an invasive species. Dreissenids were included in Ecopath despite not being present in Lake Huron in 1981. To offset the predation caused by dreissenids in Ecopath, negative biomass accumulation was added to phytoplankton. The value of the biomass accumulation was -0.1686 $\text{g/m}^2/\text{yr}$ which was equal to the value of consumption by dreissenids on phytoplankton.

Detritus

Biomass

Detrital biomass was calculated using a regression equation relating primary production and euphotic depth to biomass (equation A5; Pauly et al. 1993). The equation was $\log_{10}(D) = -2.41 + 0.954 \log_{10}(PP) + 0.863 \log_{10}(E)$, where D was detrital biomass in grams of carbon per area (gC/m^2), PP was the primary production in gC/m^2, and E was euphotic depth in m, which was assumed to be 26 m (Fahnenstiel et al. 2000). Primary production of phytoplankton was calculated as the product of biomass and P/B and was converted to g of carbon from wet weight by dividing by 42 (Cushing et al. 1958). Detrital biomass was converted from g of carbon to wet weight by first converting g of carbon to dry weight by multiplying by 2.22 (Jorgensen 1979) and then converting dry weight to wet weight by multiplying by the conversion factor for phytoplankton (12.5; Cushing et al. 1958).

$B = 73.56$ g/m^2

Ratio of unassimilated to consumed food

Ecopath uses the ratio of unassimilated to consumed food to calculate the amount of usable food that goes towards growth of a predator as well as the amount of detritus available in the system. The possible values range from 0-1. The default ratio is 0.2 (Christensen et al. 2005), but it is recommended to increase this value for messy eaters.

I increased values for ratios of unassimilated to consumed food to 0.4 for dreissenids, zooplankton, and predatory zooplankton groups, and to 0.9 for sea lamprey. Values for zooplankton groups were based on recommendations by Christensen et al. (2005). The value for dreissenids was based on the large amount of pseudofeces they produce. Lastly, the value for sea lamprey was assumed to be high because sea lampreys ingest a small fraction of the overall

weight of their prey; if predation results in death of the prey, the majority of the prey's mass becomes detritus.

Feeding time adjustment rates

Ecosim uses a ratio, ranging from 0 to 1, to determine the extent to which a predator will adjust its feeding time in order to maintain a steady Q/B ratio (Christensen et al. 2005). A feeding time adjustment rate of 0 corresponds to constant feeding time (Christensen et al. 2005). Natural mortality rates are proportional to adjustments in feeding time, and therefore when feeding time changes (i.e. feeding time adjustment rates are greater than zero), other mortality rate ($M0$) in Ecopath will vary as well (Walters and Juanes 1993; Christensen and Walters 2004). The default value for feeding time adjustment rates for all groups is 0.5. I set feeding time adjustment rates to 0 for all groups except the youngest age for each age-structured group, which were kept at default values (V. Christensen, University of British Columbia, personal communication). The youngest age-stanza for Chinook salmon and steelhead did not contribute to the model because these groups were stocked at older ages, in which case the feeding time adjustment rates for the second youngest age-stanzas (the ages at which stocking occurred) were kept at default values.

CHAPTER 5

Conclusions

The overall objective of my research was to assess the effects of alternative harvest policies for the commercial lake whitefish fishery in Lake Huron on biomass and harvest of lake trout and lake whitefish while specifically accounting for the potential effects of changes in the food web. I compiled data from published and non-published sources to construct a food-web model of Lake Huron using the Ecopath with Ecosim (EwE) software for the year 1981 (appendix 2B, 4B). Time series of biomass data for 17 species were used to estimate model parameters so that the model was able to reproduce observed biomass dynamics from 1981 to 2008 (appendix 4B). Harvest policies were simulated into the future and alternative assumptions in model parameters and in the understanding of the Lake Huron food-web were considered (Chapter 4).

My analysis revealed that lake trout and lake whitefish were directly affected by changes in harvest policies. Policies where lake trout bycatch rates were adjusted performed better at balancing tradeoffs between lake trout biomass and lake whitefish harvest than policies where fishing rate was adjusted (Figure 4.3). My analysis also revealed that when model parameters were estimated within Ecosim, indirect interactions between lake trout and lake whitefish were minimal (Figures 4.4 and 4.6). Limited indirect interactions suggests that based on biological interactions alone, greater lake trout biomass would not negatively affect lake whitefish populations. Even with the addition of a small component of direct predation by lake trout on lake whitefish, and competition between the two species on a common prey item, indirect interactions between the two species were minimal (Figure 4.4).

Including alternative assumptions in model parameters in my analysis revealed important processes, and therefore was an important component of my research. Alternative assumptions in vulnerability parameters influenced my Ecosim modeling results. Not only did vulnerabilities

increase the extent to which changes in data inputs during balancing in Ecopath affect Ecosim results (Chapter 2), they also influenced the strength of indirect interactions between lake whitefish and lake trout (Figures 4.4 and 4.6). When vulnerabilities of prey to lake whitefish were increased, indirect interactions caused lake trout to be less sensitive to changes in fishing mortality (Figure 4.6). Changes in vulnerability of prey to lake trout had little effect on lake whitefish. Previous research suggested that vulnerabilities were important parameters (Christensen and Walters 2004; Ahrens et al. 2012), and my results point to a similar conclusion.

Despite being important parameters, vulnerabilities are difficult to estimate. Within the Lake Huron model, the choice of vulnerability for lake whitefish mattered. Vulnerabilities are often described in terms of bottom-up or top-down control, and thus it is important to consider whether lake whitefish exert top-down control (high vulnerabilities) or are controlled by bottom-up processes (low vulnerabilities). Initial estimates of vulnerability parameters suggest that lake whitefish are control by bottom-up processes. However, when lake whitefish were set to exhibit greater top-down control, fits to observed biomass time series were no worse than when Ecosim estimated lake whitefish vulnerabilities itself. Consequently, the existing time series data, when applied to my model, provided little evidence for the type of control of lake whitefish. If managers believe that the type of control for lake whitefish is more top-down, then trophic interactions with lake whitefish would affect lake trout responses to fishing. If managers believe that the type of control for lake whitefish is driven more by bottom-up control, then trophic interactions between lake whitefish and lake trout can be ignored.

Alternative assumptions about values for future primary production were also important. Productivity affects the magnitude of expected biomass and harvest for lake whitefish and lake trout more than the range of harvest rates considered (Figure 4.5). Under high productivity, lake

trout harvest exhibited signs of overfishing, suggesting that changes in productivity influence lake trout in more ways than simply affecting the magnitude of biomass and harvest. The future state of Lake Huron remains uncertain. Many species in Lake Huron have shown recent declines in abundance (Figure 4.1), which drove model-estimated production anomalies (Figure 4.2). If productivity remains low, then expectations for yields of lake whitefish and biomass of lake trout should be substantially lower than if primary productivity increases in the future.

Two questions arose during construction of the EwE model which were addressed in ways that I hope will benefit the EwE community. The first question was how to adjust data inputs in Ecopath so that mass-balance was achieved, and whether adjustments affected Ecosim results (Chapter 2). I addressed this question by balancing the model in two distinct, yet realistic, ways. I compared the two balancing approaches by developing three metrics to determine the difference in biomass between modeled groups caused by balancing and by system perturbations. I found that balancing influenced Ecosim less than did the choice of vulnerability, but had a greater relative influence when system perturbations were small (Figure 2.3, Table 2.5). Given the large changes in Lake Huron from 1981 to 2008, I concluded that the process of balancing had small effects on the results of my Ecosim model.

After balancing was accomplished, the second question was how to include invasive species in my model. I compared four methods for modeling species invasion and found all were able to simulate the process of invasion while still obtaining reasonable fits to non-invasive groups (Chapter 3). Species invasions have been modeled in EwE models before (Cox and Kitchell 2004; Espinosa-Romero et al. 2011; Pine et al. 2007) but methods for doing so have not been compared prior to my analysis. I presented advantages and disadvantages for all four

methods, in hopes that doing so will allow future modelers to make their own choices on which method best meets their objectives.

Constructing my food-web model also provided an opportunity to compare biomass dynamics for many species in a single analysis, and therefore was beneficial for understanding patterns in Lake Huron. It was very apparent that biomass for many species in Lake Huron has declined (Figure 4.1). Most previous research on Lake Huron fisheries has generally focused on only one or two trophic levels; my analysis in EwE provided an opportunity to look at patterns across trophic levels, and assess mechanisms for why the patterns occurred. The decline in biomass was explained in my Ecosim model by a declining trend in primary productivity. Allowing deviations in primary production is not required in the model, and thus future work could be done to assess whether trophic interactions such as increases in invasive species biomass could explain the biomass declines in other groups when changes in primary productivity are constrained to be absent or minimal.

I encountered challenges during my research that I was not able to fully address, thus here I present them as possible directions for future EwE modelers to consider. Perhaps most importantly would be ways in which to more accurately assess the values of vulnerabilities. Tagging studies and acoustic arrays can be used to assess exchanges rates between locations, which with assumptions about the vulnerable status of prey within locations, could be used to inform estimates of vulnerabilities (Ahrens et al. 2012). Ahrens et al. (2012) present additional ways that can be used to estimate vulnerability parameters, including direct monitoring of prey mortality and predator biomass. The Ecosim model could also be used to compare future predictions about modeled values (e.g. about mortality rates) when low and high vulnerabilities

are used. Experiments could then be developed to test the predictions *in situ*, and inform which values of vulnerabilities are most probable.

A secondary improvement would be to analyze the performance of the fitting procedure used to estimate vulnerability parameters. I achieved a slightly greater sum of squared residual values when vulnerabilities for all groups were fit than when vulnerabilities of lake whitefish were set and those of other groups were estimated. Improved sum of squared residuals suggest difficulty of the fitting procedure in obtaining a global minimum. Given that vulnerabilities are influenced by the fitting procedure, improved performance of the fitting routine could result in less uncertainty of estimated vulnerability values.

Additional improvements include how Ecosim links stocked species and their wild counterparts. I considered methods for linking stocked and wild lake trout, however chose instead to keep them separate primarily because the methods for linking stocked and wild groups are ad-hoc. I would recommend the development of an addition to the software that allows wild lake-trout egg-production to be an explicit function of population biomass for both wild and stocked adults groups. Currently, egg production of a species is calculated based on the fecundity of mature individuals for that species. Modeling stocking more explicitly would allow for wild recruitment to be affected by abundance of stocked and wild components of a species.

Overall, Ecopath with Ecosim was a useful approach to assess the direct and indirect effects of harvest policies on the commercial lake whitefish fishery in Lake Huron. Modeling is an ongoing process, and the development of EwE models is no exception. The results within this dissertation should not be used to set policy, primarily because I viewed my analysis, and EwE models in general, as exploratory tools. Rather, the results within this dissertation should be used to inform policy, particularly the development and use of single-species models. Overall, it is my

hope that the findings in this dissertation will be used as stepping stones for improved

understanding of the Lake Huron food web and better management of commercial fisheries

within the food web.

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