

**Modeling the Effects of Climate Change, Nutrients, and Invasive  
Species on Lake Huron Food Webs**

By

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To the Kao's family  
Yanni, Mindy, and Michelle

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## **Abstract**

I used ecological models to investigate potential effects of climate change, variation in nutrients, and invasive species on food webs of Saginaw Bay and the main basin of Lake Huron. In Chapter 2, I used bioenergetics models to investigate climate change-induced effects of increased temperatures on the growth and consumption by three salmonines: Chinook salmon, lake trout, and steelhead. Results showed that future growth and consumption by these salmonines will increase substantially if prey availability is not limited but will decrease if prey availability remains at current levels. Of these three salmonines, results indicated that Chinook salmon required the greatest increase in prey consumption to maintain current growth under increased temperatures. In Chapter 3, I analyzed impacts of changing nutrients, and invasive dreissenids and alewives on the Saginaw Bay food web. I found that nutrient loads were positively correlated with biomass of most food web groups and that alewife biomass was negatively correlated with biomass of most fish and zooplankton groups. Modeled dreissenid impacts were most severe on lower trophic levels but were minor on fish groups relative to nutrient and alewife effects. Results suggest that the target level of nutrient reduction established in 1978 may not sustain current fishery harvests in Saginaw Bay, given food web changes caused by invasive dreissenids. In Chapter 4, I assessed effects of Chinook salmon, invasive dreissenids, and declines in nutrients on the collapse of alewives in the Lake Huron main basin. Results suggested that the collapse of alewives was caused by combined effects of relatively high Chinook salmon biomass, invasion of dreissenids, and decline in nutrients. Although the top-down control from Chinook salmon biomass decreased in years previous to the alewife collapse,



the bottom-up control increased as dreissenid mussels expanded and nutrient loads declined.

Under current conditions of low nutrient loads and high quagga mussel biomass, results showed that it is unlikely that alewives will recover. Overall, results indicate that given the current trend toward oligotrophication in Lake Huron and rising temperatures due to climate change, sustaining a desirable level of Chinook salmon population and catch is unlikely.

## **Chapter 1**

### **Overview**

#### **1.1 Research background**

The Laurentian Great Lakes form the largest freshwater ecosystems on Earth and contain about 20% of the planet's liquid surface freshwater. These ecosystems have provided important services including drinking water, hydropower, recreation, fisheries and a host of others to one-tenth of the population of the United States and one-quarter of the population of Canada (Beeton et al., 1999). Not surprisingly, the Great Lakes ecosystems have been since the 1900's seriously impacted by anthropogenic stressors including habitat degradation, overfishing, excess nutrient loads, and exotic species invasions (Beeton et al., 1999; Bunnell et al., 2014). In response, since the 1960s the United States and Canadian government agencies have implemented management programs aiming to restore native species and achieve ecosystems that provide valuable and sustainable services (Gaden et al., 2012).

The goal of this dissertation is to improve our understanding of food web dynamics in Lake Huron and by extension in the Great Lakes, which is required for improving management programs. The food web concept is not only a fundamental in ecology but also as an approach to understand changes in species composition of an ecosystem. Elton (1927) first addressed that the food web is a universal template of how species in an ecosystem are linked through feeding. Thus ecosystems, with different species composition and primary productivity can be compared in terms of food web properties such as length of the food chain, species connectance, and proportion of abundance of primary producers, herbivores, and secondary consumers. Further,

process knowledge accumulated from studies in one ecosystem can be applicable to another if the two ecosystems have similar food web properties (see reviews by Polis and Strong, 1996 and Petchey et al., 2006). As a result, changes in species composition can be predicted through understanding of food web dynamics in an ecosystem and similar ecosystems. However, food web dynamics in the Great Lakes are generally poorly understood. The knowledge gap is possibly because majority of past studies focused on single species assessments (e.g., Argyle, 1982; Eshenroder, 1992; Nalepa et al., 2007) or on particular compartments of food webs (e.g., Coble et al., 1990; Dobiesz et al., 2005; Madenjian et al., 2008). As these studies have provided insights into management issues and resulted in some success, research on food web dynamics in the Great Lakes has not been a priority until recently when ecosystems have undergone dramatic changes affecting local economies.

One powerful tool for understanding food web dynamics that can be used in the Great Lakes is ecological modeling (Jørgensen et al., 2012). Ecological models are mathematically formulated based on conservation of energy or mass and require integration of data that are collected at the ecosystem level as well as process knowledge accumulated from previous studies which can include those conducted outside the focal ecosystem. These models can be used to untangle effects of concurrent factors in large and complex ecosystems, where conducting manipulative experiments is probably impossible and statistical analyses have been limited by spatial and temporal scales of data. Furthermore, ecological models can be used to conduct timely evaluations of trade-offs among alternatives proposed by stakeholders (Redpath et al., 2013), which is required for successful ecosystem management.

To achieve the goal of improving the understanding food web dynamics in Lake Huron and the Great Lakes at large, I used ecological models to investigate food web changes in

Saginaw Bay and the Lake Huron main basin in response to effects of climate change, nutrients, and invasive species. Findings are important to Lake Huron ecosystem-based management.

Findings are also informative for lakes Michigan and Ontario that are similar to the main basin—deep and oligotrophic and for Green Bay, the Bay of Quinte, and Western Lake Erie among other embayments that are similar to Saginaw Bay—shallow and productive.

## **1.2 A brief ecological history of the Lake Huron ecosystem**

Historically in the offshore waters of Lake Huron, there were two predators, lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*), and a very diverse prey fish assemblage consisting of lake whitefish (*Coregonus clupeaformis*), lake herring (*Coregonus artedii*), six species of deepwater ciscoes (*Coregonus* spp.), and deepwater sculpin (*Myoxocephalus thompsoni*). In the nearshore waters, walleye (*Sander vitreus*) was the dominant predator and the prey fish assemblage mainly consisted of yellow perch (*Perca flavescens*) and emerald shiner (*Notropis atherinoides*).

In the early 20th century, sea lamprey (*Petromyzon marinus*) and alewives (*Alosa pseudoharengus*) reached the lake from the Atlantic Ocean through the Welland Canal that allowed them to bypass Niagara Falls (Ebener et al., 1995). Overfishing and mortality imposed by parasitic sea lamprey caused the collapse of lake trout and burbot around 1950 (Berst and Spangler, 1972; Smith, 1972). Later, fishing and sea lamprey pressure shifted to smaller species and caused severe declines of lake whitefish and lake herring and extinction of all deepwater ciscoes except for bloater (*Coregonus hoyi*), the smallest species. With the severe decline in overall fish abundance, planktivorous alewives became well established in the late 1950s (Miller, 1957) and caused major disruptions of the food web through predation on larvae of lake trout as

well as nearshore fish species like walleye, yellow perch, and emerald shiner (Madenjian et al., 2008).

Agencies started to control sea lamprey in the late 1950s mainly through application of chemical lampricides targeting sedentary larval stages in streams (Smith and Tibbles, 1980). To control alewives, agencies stocked hatchery-reared exotic salmonine predators including coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) starting from the late 1960s (Tody and Tanner, 1966). The introduction of salmonines, as expected, kept alewife abundance in check and resulted in profitable recreational fisheries (Thayer and Loftus, 2012).

Excessive nutrient loads that caused eutrophication became a major concern across the Great Lakes by the 1960s (Beeton, 1965). Although the Lake Huron main basin remained oligotrophic status even in the 1970s when nutrient loads peaked (Vollenweider et al., 1974), eutrophication caused problems such as harmful algal blooms in Saginaw Bay and coincided with extirpation of the benthic mayfly *Hexagenia limbata* nymphs (Bierman et al., 1984; Schaeffer et al., 2000). As the limiting nutrient in the Great Lakes was phosphorus, management agencies initiated phosphorus abatement programs in the 1970s and set limits on total phosphorus loads across the Great Lakes in the 1978 Great Lakes Water Quality Amendment (Dolan and Chapra, 2012). Since the 1980s, nutrient loads have continuously decreased in both Saginaw Bay and the main basin of Lake Huron (Dolan and Chapra, 2012).

Dreissenids (zebra and quagga mussels, *Dreissena polymorpha* and *D. bugensis*) and round goby (*Neogobius melanostomus*) invaded Lake Huron in the 1990s (Nalepa et al., 2007; Riley et al., 2008), transported via ballast water from ocean-going ships. Because dreissenids reached large population levels, they sequestered in their benthic habitats a substantial amount of primary production and constrained nutrients that would otherwise be available to phytoplankton

(Hecky et al., 2004; Higgins and Vander Zanden, 2010). Effects of zebra mussel are mostly confined to shallow areas and Saginaw Bay as populations are constrained by availability of hard substrates (Adlerstein et al., 2013; Nalepa et al., 2003), while quagga mussels are adapted to living on soft substrates and are more widely distributed in offshore areas (Nalepa et al., 2007). However, round gobies are able to feed on dreissenids, and, in turn, round gobies are available for consumption by higher trophic levels (Johnson et al., 2005; Pothoven and Madenjian, 2013).

Since the 1990s, there were decreases in prey fish biomass and in abundances of zooplankton (Barbiero et al., 2009) and benthic amphipod *Diporeia* spp. (Nalepa et al., 2007) with consequences on higher trophic levels. In 2003, the alewife population in Lake Huron collapsed (Riley et al., 2008). After the collapse, the biomass of Chinook salmon that mainly fed on alewives also decreased but native species stressed by alewives, such as lake trout, walleye, and emerald shiner, started to recover (Fielder et al., 2007; He et al., 2012; Schaeffer et al., 2008).

The physical environment of Lake Huron has also experienced several changes induced by global climate change since the 1980s. These changes included increases in water temperatures (Dobiesz and Lester, 2009), reduced ice-covered period and prolonged summer stratification period (Assel et al., 2003), and consequently higher annual evaporation rates and lower water levels (Hanrahan et al., 2010). Nevertheless, how Lake Huron food webs have responded to these changes is still unclear.

Throughout time in Lake Huron, there have been large time lags between unwanted changes in the food webs and management actions and later between these management actions and their positive ecosystem impacts. For example, sea lamprey control programs were initiated about 20 years after the sharp decline of lake trout abundance while lake trout rehabilitation through widespread natural reproduction, did not occur until about 40 years after initiation of sea

lamprey control (He et al., 2012). Further, most Lake Huron management objectives have not been revised since they were established. For example, Riley (2013) indicated that current fish-community objectives (DesJardine et al., 1995) may not be achievable given recent drastic changes in food web structures. Consequently, there is a need for a better understanding of food web dynamics to inform resource managers so they can take timely actions and adjust Lake Huron management objectives.

### **1.3 Modeling approach**

Among a wide range of available modeling approaches, I chose to use the Ecopath with Ecosim (EwE) modeling approach (Christensen and Walters, 2004) to investigate food web dynamics in Saginaw Bay and the main basin of Lake Huron. The EwE modeling approach provides a framework to model biomass flows among food web groups. It has two major components for analyzing biomass flows in a snapshot of the food web (Ecopath) and for simulating food web time dynamics under designed scenarios (Ecosim). There are several reasons that make this choice appropriate. First, within the EwE modeling approach, mathematically formulated based on the conservation of biomass, the rate of biomass change of a species or a species group is mainly controlled by the balance between predation loss and prey consumption. This is fitting as unwanted changes in the Lake Huron food webs were mostly driven by concurrent changes in predator–prey interactions. Second, the modeling approach was originally developed for evaluating impacts of fisheries in an ecosystem. Thus, the model is well suited to explore effects of fishery harvests on food web dynamics and effects of ecosystem changes on fisheries. Third, the modeling approach also has the flexibility to incorporate known ecological processes as driving forces of predator–prey interactions. Lastly, the modeling

approach and its open-source software (available at [www.ecopath.org](http://www.ecopath.org)) have been widely used, which provides confidence in model performance.

#### **1.4 Dissertation contents**

To achieve the goal of improving our understanding of food web dynamics in Lake Huron, I have three main research objectives. The first main objective is to investigate effects of increasing water temperatures induced by climate change on growth of main predators in the system. As organisms in the lake are all poikilothermic, increases in water temperatures would affect their growth, prey consumption, and thus predator–prey interactions. Results from this analysis inform how temperature increases should be incorporated when modeling food web dynamics in Saginaw Bay and the main basin of Lake Huron. To achieve this objective, in Chapter 2 I investigated effects of increases in water temperature on growth and consumption by salmonine top-predators Chinook salmon, lake trout, and steelhead (*O. mykiss*). I used bioenergetics models to simulate changes in these predator’s growth and consumption under model-projected water temperatures and prey availability scenarios. Results showed that growth and consumption will increase with increases in water temperatures if prey availability is not limited. This is because water temperatures in Lake Huron are generally lower than optimal temperatures for growth of selected species (Coutant, 1977). On the other hand growth will decrease if prey availability is limited because of increases in metabolic costs. Results also showed that temperature effects on growth and consumption by these salmonines are minor relative to effects of prey availability. Under scenarios where prey availability was limited, simulated growth of Chinook salmon decreased by as much as 10%, with increases in water temperatures, but simulated growth of lake trout and steelhead decreased considerably less, or



even did not decrease. Therefore, there was not a need to incorporate effects of increasing temperatures in the modeling of predator growth in Saginaw Bay and main basin food webs.

Chapter 2, as presented in the dissertation, is part of the research article accepted for publication in the journal *Environmental Biology of Fishes* entitled “Temperature effects induced by climate change on the growth and consumption by salmonines in Lakes Michigan and Huron” (Kao et al., in press).

The second main objective in this dissertation was to investigate effects of fluctuation in nutrients and of invasive alewives and dreissenids on the Saginaw Bay food web. I achieved this objective in Chapter 3 by implementing a model to represent the Saginaw Bay food web dynamics and simulating effects of these three factors on food web groups. Results showed that the Saginaw Bay food web was influenced more by nutrients and alewives than by dreissenids. Within a certain range, modeled effects of nutrients were positive on most groups in the food web due to increases in primary production. Modeled effects of alewives were negative on most fish and zooplankton groups due to predation and competition for food. Modeled effects of dreissenids were negative to most zooplankton groups but positive to most benthos groups due to shifting production from pelagic to benthic pathways, but were minor on fish groups. Most of fish species in Saginaw Bay are benthic feeders so further dreissenid shifting of production was not detrimental in the simulations. Results also suggest that a revision for the target nutrient loads established in 1978 is needed under current conditions of absence of alewives and reduced dreissenid biomass. Simulation results showed that the target level of nutrient loads cannot sustain current yellow perch and walleye fishery harvests in Saginaw Bay given food web changes caused by invasive species.

Chapter 3 as presented in the dissertation has been published in an article in the Journal of Great Lakes Research entitled “The relative impacts of nutrient loads and invasive species on a Great Lakes food web: An Ecopath with Ecosim analysis” (Kao et al., 2014).

The third main objective in this dissertation was to investigate effects of top-down and bottom-up controls on the collapse of alewives in Lake Huron during 2003. I achieved this objective in Chapter 4 by modeling the biomass flows and dynamics of the Lake Huron main basin food web. I simulated effects of variation of Chinook salmon biomass (as top-down controls) and of expansion of quagga mussels and decline in nutrients (as bottom-up controls) in the food web. Results from biomass flow analysis showed an increase in the relative importance of bottom-up controls as production decreased across all trophic levels in the food web. Major effects of increasing bottom-up controls were the decrease and depletion of non-dreissenid benthos production, which caused decreases in production of benthivorous pelagic prey species. Scenario simulations showed that top-down controls from Chinook salmon under 1984 to 2002 conditions were relatively constant but bottom-up controls from quagga mussels and nutrient loads increased jointly to unsustainable levels given Chinook salmon biomass. Hence, results showed that the collapse of alewives was caused by a combination of top-down and bottom-up effects. Results indicate that under current conditions of low nutrient loads and high quagga mussel biomass, it is unlikely for alewives to recover irrespective of Chinook biomass levels. These results also imply that restoring Chinook salmon recreational fisheries in Lake Huron is unrealistic.

### **1.5 Challenges encountered in modeling Lake Huron food webs**

Implementing the EwE approach to model dynamics of the Lake Huron food webs posed several challenges as the scope of modeling is much larger than most of those that have been published (available at [www.ecopath.org](http://www.ecopath.org)). The large scope resulted from the necessity to integrate in the models a large amount of data and literature information available for parameterization, and also because of detailed knowledge available about species interactions and ecosystem processes across the Great Lakes. Challenges encountered were met as the EwE approach is an interactive modeling process and allowed for refinement and deeper understanding of the systems while implementing the models.

The first challenge was integrating a large amount of available information and knowledge which requires high resolution of the food web structure in the model. For example, I aggregated zooplankton species into six groups rather than into one all-encompassing group because of available information on diets. Also, I assigned several fish species into age-stanza groups to represent known changes in predator–prey interactions with age. As a result, there are about 50 food web groups in the Saginaw Bay and the Lake Huron main basin EwE models while the majority of published EwE models have less than 30 groups.

Secondly, large number of food web groups, made parameterization and calibration of the Lake Huron EwE models extremely labor intensive and complex. To implement the EwE modeling analysis there are decisions to be made that require substantial knowledge about data sources and ecosystem characteristics and dynamics. Within the first modeling step, the target for parameterization is to balance the whole food web in an Ecopath model, such that production of every food web group is more than total predation and fishery losses. If the balance cannot be achieved by slightly adjusting input parameters based on the uncertainty associated with parameter estimates, this is an indication that there can be some systematic errors in parameter

estimation. In the main basin model, for example, available biomass estimates of all benthos groups were too low to achieve the balance. This prompted consideration that the biomass estimates were underestimated and further revision of estimation procedures indicated the need to adjust them by catchability of the sampling gear. Within the calibration procedure, the target is to be able to run the food web model and reproduce estimates close to those from observed data time series. If dynamics cannot be reproduced, this is an indication that some ecological processes might not be correctly incorporated in the model. For example, initially the Saginaw Bay model could not reproduce the food web dynamics, which prompted a review of how some main basin fish species such as alewives that were incorporated as a functional group in the model structure. Incorporating these species as group had not considered that those species use of Saginaw Bay as nursery area and that their dynamics is actually not driven by Saginaw Bay food web interactions but by main basin food web dynamics. Thus, these species needed to be incorporated in the model as forcing functions rather than as model groups. After exhaustive models refinements and achieving the targets of parameterization and calibration, the EwE models became very robust. This was an indication that the models successfully integrated available information and knowledge about the ecosystems following the law of conservation of mass and are reliable representations of the food webs in Saginaw Bay and the Lake Huron main basin within the time period considered in the analysis.

## **1.6 Syntheses of findings**

In this section, I synthesize findings from the three research dissertation chapters and suggest needs for future research to improving understanding food web dynamics and food web modeling in Lake Huron. In summary, results showed that: (1) the most important control on

food web dynamics in an oligotrophic lake as Lake Huron is nutrient loads; (2) that there is significant interdependence between food web dynamics of embayment areas and main basins; (3) that there might be conflicts between water quality and fishery management objectives; (4) that ongoing research is needed to understanding species consumption; and (5) that both top-down and bottom-up controls operate on aquatic food web dynamics and their strengths are interrelated. These conclusions should be informative for management of lakes Michigan and Ontario that are similar to the main basin and for Green Bay and the Bay of Quinte among other embayments that are similar to Saginaw Bay.

Results indicated that the most important control on food web dynamics in Lake Huron is nutrient loads. Results from Chapter 2 indicated that given that thermal habitats in cold and deep Lake Huron main basin to avoid high water temperatures near the surface will be available, effects of climate change on the growth of salmonines will depend on future prey availability. Further, food web modeling in Chapters 3 and 4 showed that nutrient loads were positively correlated to biomass of most food web groups across trophic levels, and that negative effects from dreissenids were stronger when nutrient loads were lower. In the main basin, there has been a general trend of reduction in biomass of phytoplankton (Reavie et al., 2014), zooplankton (Barbiero et al., 2009), benthos (Barbiero et al., 2011), and prey fish (Riley et al., 2012), and a shift in species composition of top predators from large-sized Chinook salmon dominance to median-sized lake trout (He et al., 2014) since around 2000. Results from the main basin food web model analyses in this dissertation suggest that these changes were mainly caused by decreases in nutrient loads.

Results from food web modeling also showed that there is interdependence between food web dynamics of Saginaw Bay and Lake Huron. The Saginaw food web model showed that

alewife biomass was an important control on the food web dynamics in the bay. On the other hand, the biomass of alewives, and other main basin species such as rainbow smelt that use the bay as nursery area, was not controlled by the food web dynamics in the bay but by the food web dynamics in the main basin. Ivan et al. (2014) showed that there has been a trend in increased abundance of nine resident fish species in the bay after the alewife collapse and decreases of only one species: spottail shiner, (*Notropis hudsonius*). Spottail shiner was one of the few groups positively correlated with increases in alewife biomass in the Saginaw Bay food web analyses. As nutrient loads have been relatively stable (Stow et al., 2014), dissertation model analyses suggest that these changes are the result of the collapse of alewives in the main basin. Another connection between the main basin and Saginaw Bay relates to decreases nutrient loads. Cha et al. (2011) showed that the proportion of nutrient loads that exported from Saginaw Bay to Lake Huron main basin decreased by 40%. This reduction can be in largely attributed to dreissenid consumption in Saginaw Bay. Hence the general decreasing trend in biomass across trophic levels in the main basin after 2000 is also associated with the food web dynamics in Saginaw Bay.

Dissertation results suggested that there is a need for revising nutrient load targets (Great Lakes Water Quality Protocol, 2012) and fish community objectives (DesJardine et al., 1995) in Lake Huron. Current target levels of nutrient loads in Saginaw Bay and Lake Huron were established 1978 for preventing cultural eutrophication. However the loads in Saginaw Bay were rarely below the target level while the loads in main basin were rarely above its (Dolan and Chapra, 2012). Hence, it is very hard to empirically access the effectiveness of these nutrient loads targets for preventing cultural eutrophication. Further, my analyses showed that current fish community objectives for harvests and the target of nutrient loads are in conflicts; i.e., the

target level of nutrient loads in Saginaw Bay is too low to maintain desirable fishery harvests in the bay while the target level in main basin is high enough to sustain an alewife population even with the invasion of dreissenid mussels and predation by Chinook salmon. My analyses also shows that fish community objectives are not achievable under persistent current nutrient load levels and high dreissenid biomass. Therefore, nutrient load targets and fish community objectives in Lake Huron should be simultaneously considered. My food web models can be used, in combination with water quality models (such as Bierman et al., 2005), to find levels of nutrient loads which are low enough to prevent eutrophication, allow to sustain an alewife population, and maintain desirable fishery harvests.

This food web modeling analysis indicates that ongoing research is needed to understanding prey consumption in Lake Huron. For example, after the collapse of alewives and sharp decreases in the biomass of rainbow smelt (Riley et al., 2012), consumption by lake whitefish might have become important in the Saginaw Bay food web dynamics. The biomass of lake whitefish in the main basin in recent years was large relative to other fish species (He et al., 2014) and the species uses Saginaw Bay as nursery area. Although catch rates in Saginaw Bay fish surveys conducted in early fall have been low (Fielder and Thomas, 2006), they probably underestimate biomass in the bay where fish are mostly found in early winter to spawn. However, there is little information about lake white fish consumption in Saginaw Bay and there is a need for studies on the species distribution and diets to fill that gap.

Modeling results in Chapter 3 and 4 showed that both top-down and bottom-up controls are important on Lake Huron food web dynamics, which are consistent with general patterns found for other ecosystems, but also offer further insight into their connectivity. Top-down (predation) and bottom-up (food) controls on food web dynamics is a topic often studied by

ecologists (Carpenter et al., 1985; Gripenberg and Roslin, 2007; Hunter and Price, 1992; Polis, 1999; Polis et al., 2000). Some studies have found extreme top-down controls (e.g., Menge, 2000) or bottom-up controls (e.g., White, 1978), but most studies show that both are important (e.g., Fretwell, 1987; Ives et al., 2003; Oksanen et al., 1981). Studies also show that top-down control is stronger in aquatic ecosystems than in terrestrial ecosystems (Borer et al., 2005; Gruner et al., 2008; Shurin et al., 2002) because they are characterized by stronger interactions among species and have trophically stratified food webs. Additionally, my analyses show that strong top-down controls can also occur when interactions are weak between species, and that strong interactions among species may not be required condition for strong top-down control. Results in Chapter 3 showed that a weak inter-species interaction consisting of a very small proportion of walleye larvae in the diet of alewives can ultimately control the food web dynamics in Saginaw Bay. In contrast, results in Chapter 4 showed that high consumptive demand on rainbow smelt from all predators had little control on rainbow smelt biomass. Lastly, my analyses further showed that top-down and bottom-up effects are interrelated. For example, increases in Chinook salmon biomass resulted in stronger top-down effects on alewife biomass when nutrient levels were low. Thus, investigating top-down and bottom-up effects separately may give incomplete understanding of a system and result in management oversights. The research in this dissertation shows that the food web analysis approach used is an ideal tool to investigate these interactions and can be used to explore management given alternative scenarios.

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## **Chapter 2**

### **Temperature effects induced by climate change on the growth and consumption by salmonines in Lake Huron**

#### **2.1 Abstract**

We used available bioenergetics models to investigate temperature effects induced by climate change on the growth and consumption by Chinook salmon *Oncorhynchus tshawytscha*, lake trout *Salvelinus namaycush*, and steelhead *O. mykiss* in Lake Huron. We updated model biological inputs to account for recent changes in the food webs and used temperature inputs in response to regional climate observed in the baseline period (1964–1993) and projected in the future period (2043–2070). Bioenergetics simulations were run across multiple age-classes and across all seasons in different scenarios of prey availability. Due to the increased capacity of prey consumption, future growth and consumption by these salmonines were predicted to increase substantially when prey availability was not limited. When prey consumption remained constant, future growth of these salmonines decreased in most cases but increased in some cases when the increase in metabolic cost could be compensated for by a decrease in waste (egestion and excretion) loss. Consumption was predicted to increase the most during spring and fall when prey energy densities are relatively high. Such seasonality benefits their future growth through increasing annual gross energy intake. Our results indicated that lake trout and steelhead would be better adapted to increases in temperature induced by climate than Chinook salmon. To maintain baseline growth, an increase of 10 % in baseline prey consumption

was required for Chinook salmon but considerably smaller or no increases in prey consumption were needed by lake trout and steelhead.

**Keywords:** climate change, temperature increase, bioenergetics model, salmonines, growth, prey consumption

## 2.2 Introduction

Following the global trend of changing climate, air temperatures in the Great Lakes region have increased by an average of 0.28 °C per decade since 1970 (NCDC 2013). The increased air temperature has resulted in several changes in aquatic habitats of the Great Lakes including increased water temperatures (McCormick and Fahnenstiel 1999; Dobiesz and Lester 2009), shortened ice-covered periods, and consequently prolonged summer stratification periods (Assel 2005). Based on current projections of global greenhouse gas emissions, air temperatures in the Great Lakes region will increase by 3–5 °C by the end of this century (Hayhoe et al. 2010). Hence further changes in aquatic habitats of the Great Lakes along observed trends are expected.

Climate change may affect the growth and consumption by fish in the Great Lakes directly through effects of warming water temperature on fish physiology and indirectly through effects of changes in aquatic environment on prey availability. Being poikilothermic organisms, fish may behaviorally thermoregulate by moving to preferred thermal habitats in which temperatures are closer to their optima for growth (Coutant 1987). In cold and deep parts of the Great Lakes, Magnuson et al. (1990) predicted that the availability of fish thermal habitats will increase in a warming climate. Correspondingly, the growth and consumption by fish in the Great Lakes may both increase in a warming climate if prey availability is not limited (Hill and

Magnuson 1990; Brandt et al. 2002). However, changes in aquatic environment induced by climate change may result in limited prey availability to fish in the Great Lakes (Magnuson et al. 1997; Kling et al. 2003). If prey consumption remains constant over time, the growth of fish in the Great Lakes may decrease with temperature increases because of the increase in metabolic rates (Hill and Magnuson 1990).

Among Great Lakes, salmonines (salmon and trout in the subfamily Salmoninae) are economically important as favorite targets in recreational fisheries in Lake Huron (Crawford 2001; Thayer and Loftus 2012). As salmonine populations are artificially maintained or supplemented by hatchery stocking, the potential for predator–prey imbalance in Lake Huron has long been a concern for researchers and resource managers (Brown et al. 1999). Such an imbalance could have occurred in Lake Huron where prey fish abundance decreased sharply after 2004 (Riley et al. 2008). Climate change may increase the potential of predator–prey imbalance because an increase in prey consumption is required for salmonine predators to offset the increase in metabolic costs in a warming water temperature regime.

In this study, we used bioenergetics models (Kitchell et al. 1977; Hanson et al. 1997) to investigate temperature effects induced by climate change on the growth and consumption by three salmonine species representing the bulk of recreational harvests in the Lake Huron main basin: Chinook salmon *Oncorhynchus tshawytscha*, lake trout *Salvelinus namaycush*, and steelhead *O. mykiss*. To our knowledge, only two studies used bioenergetics models to explore effects of climate change on growth and consumption by fish in the Great Lakes (Hill and Magnuson 1990; Brandt et al. 2002) but both studies were limited in scope and consequently applicability to fisheries management. These studies investigated climate change effects on annual growth and prey consumption by a species at a specific age and weight, but not cross



multiple ages. In addition, these researchers did not consider seasonal variation in diet composition, which has an important effect on attained growth and prey consumption by salmonines (Stewart 1980; Stewart et al. 1983).

We followed the scenario-simulation approach in Hill and Magnuson (1990) but made several major modifications in the method to generate more informative results for salmonine fisheries management in Lake Huron. Specifically, we (1) ran bioenergetics simulations across multiple age-classes and across all seasons, under scenarios of prey availability; (2) estimated prey consumption required to maintain baseline growth; and (3) assessed changes in growth, prey consumption, and seasonal and annual energy budgets under the projected temperature regime.

## 2.3 Methods

### 2.3.1 Bioenergetics models

The master equation of bioenergetics models used in this study (Rand et al. 1993; Stewart et al. 1983; Stewart and Ibarra 1991) represents the daily energy budget of a fish as:

$$C = P_{max} \times C_{max} = M + W + G \quad (2.1)$$

where  $C$  is the prey consumption in terms of the gross energy intake,  $P_{max}$  is the proportion of maximum consumption that is realized,  $C_{max}$  is the maximum (prey) consumption,  $M$  is the metabolic cost,  $W$  is the waste loss or the total of egestion and excretion, and  $G$  is the net energy for growth (including reproduction). Following the approach by Kitchell et al. (1977), consumption, metabolic cost, and waste loss were expressed as a series of species-specific functions of fish weight and temperature together with predetermined parameters, as detailed in

Appendix A. With required biological inputs, temperature inputs, and simulation parameters, fish growth and energy budget can be simulated using these bioenergetics models on a daily basis.

We coded and ran these bioenergetics models in R (version 2.8.1, R Develop Core Team 2008) instead of using the software package Fish Bioenergetics 3.0 (Hanson et al. 1997) for better computational efficiency. In addition, Madenjian et al. (2012) reported and corrected an error in algorithms for balancing daily fish energy budgets in Fish Bioenergetics 3.0. To ensure our R scripts are free from error, we validated outputs with outputs from the corrected Fish Bioenergetics 3.0 software package used in Madenjian et al. (2012).

### **2.3.2 Focal populations and biological inputs**

We focused our analysis on Chinook salmon, lake trout, and steelhead populations in the main basin of Lake Huron (Fig. 2.1). Following Eshenroder et al. (1995), we considered three lake trout populations: North, Central, and South Lake Huron..

Required biological inputs including growth (as initial and final weights of a bioenergetics simulation), reproduction, diet schedules, predator energy densities, and prey energy densities were selected to represent an average individual in each salmonine population. These inputs were updated to reflect changes resulting from invasive species and nutrient loads in the food web during the past 20 years (Vanderploeg et al. 2002; Riley et al. 2008; Dolan and Chapra 2012). Values and data sources of these inputs were detailed in Appendix B.

### **2.3.3 Temperature inputs**

Temperature inputs were calculated using spatially explicit temperature profiles in Lake Huron from B. Lofgren (National Oceanic and Atmospheric Administration-Great Lakes

Environmental Research Laboratory, unpublished) for the baseline period (1964–1993) and for the future period (2043–2070). These temperature profiles were outputs from a revised version of the Coupled Hydrosphere-Atmosphere Research Model (Lofgren 2004) based on climate conditions in the Great Lake region observed in the baseline period and projected under the global development scenario A2 (IPCC 2000), the “business as usual scenario”, in the future period. We selected the baseline period to represent a historical reference and the future period to represent the condition when climate change has made a substantial increase in the water temperature.

The temperature input in the bioenergetics model represents mean daily temperature experienced by the fish. Following the approach used by Stewart et al. (1983), the temperature experienced by the fish was set to the preferred temperature when it is available (Table 2.1). This approach was based on the assumption of behavioral thermoregulation so fish would move to a preferred thermal habitat when it became available so that their growth could be optimized. Based on obtained water temperature profiles in Lake Huron, these preferred temperatures were only available during part of summer when water temperature was highest near the surface and decrease with depth until 4 °C in both of the baseline and future periods. Therefore when water temperature in the surface layer is higher than the preferred temperature, we set temperature experienced by the fish to preferred temperature. When preferred water temperature was not available (spring, part of summer, fall, and winter), we use water temperature in the surface layer to approximate surrounding temperature of the fish because Lake Huron would be completely homothermous or homothermous to a great depth.

Specifically, we calculated temperature inputs (Fig. 2.2) using:

$$T(t) = \min [T_{pre}, T_{sur}(t)] \quad (2.2)$$

where  $T(t)$  is the temperature input at time  $t$ ,  $T_{pre}$  is the preferred temperature of the fish, and  $T_{sur}(t)$  is water temperature in the surface layer.  $T_{sur}(t)$  was calculated by averaging obtained water temperature profiles of surface cells (up to 1.5-m depth) in the geographical range of each salmonine population (Fig. 2.1). We did not allow daily temperature input  $T(t)$  to drop below 0.1 °C because these bioenergetics models would not generate reliable predictions of consumption and growth. Recent studies that investigated thermal habits of salmonines in the Great Lakes showed that the approximation of equation (2.2) is generally reliable and that salmonines did not seek the warmest temperature (about 4 °C) in the deep parts of the lakes during winter (Bergstedt et al. 2003; Stewart and Bowlby 2009; Bergstedt et al. 2012). Also, Bergstedt et al. (2012) showed that the lower limit of 0.1 °C for our temperature input was very close to the minimum temperature occupied by Lake Huron lake trout in February and March.

#### **2.3.4 Simulation parameters**

Required simulation parameters in the bioenergetics models include initial weight (g), simulation length (number of days), and one of the three parameters of  $P_{max}$ , final weight (g), or total prey consumed (g). Of these three parameters, one parameter is selected as a model input while the other two are generated as outputs from the bioenergetics simulation.

We ran bioenergetics simulations by age and population for each salmonine species. We set the initial weight as weight at a given age on the first day of simulation (Table 2.2) and ran bioenergetics simulations over the course of a year (365 days). Thus  $P_{max}$  and total prey consumption were on an annual basis and the final weight was the weight at the next older age on the first day of simulation. The bioenergetics modeling approach assumes that  $P_{max}$  remains constant during each year-long simulation. This is an assumption to which the bioenergetics

model estimates of consumption and growth appeared to be robust. Field evaluations of both the Chinook salmon bioenergetics model and the lake trout bioenergetics model indicated that model estimates of food consumption and growth were reliable (Brodeur et al. 1992; Madenjian et al. 2000). Further, results from laboratory evaluations of both Chinook salmon and lake trout models revealed little to no bias in model predictions of food consumption and growth (Madenjian et al. 2004, 2012, 2013).

We ran bioenergetics simulations across all age classes of the fish that reside in the lake (Table 2.2). For Chinook salmon, we ran simulations from age 0 (when they are stocked) to age 4 (when they leave to streams for spawning run) (Fenske and Shouder 1992; Hay 1992). For lake trout, we ran bioenergetics simulations from age 1 (when they are stocked) to a maximum age 10 as very few fish exceed this age (He et al. 2012). Steelhead are known to have different life history forms in the Great Lakes region (Rand et al. 1993), so we ran bioenergetics simulations for steelhead having the most common life history form, which enter the lake at lake age 0 as smolt and live for another four years.

### **2.3.5 Bioenergetics simulations**

We first ran bioenergetics simulations to construct the baseline, a historical reference, for assessing effects of climate change on the growth and consumption by salmonines in Lake Huron. Simulations were based on baseline growth inputs (Table 2.1) and temperature inputs (Fig. 2.2). For each salmonine population, we ran simulations over the course of year, age-specifically, and year-by-year throughout the 29-year baseline period. We averaged model-estimated  $P_{max}$  and consumption across years by age (baseline  $P_{max}$  and consumption) and used the averages to present different prey availabilities in the future scenarios.

We ran bioenergetics simulations under three future scenarios of prey availability. Under each scenario, we ran bioenergetics simulations over the course of year, population-specifically, age-specifically, and year-by-year throughout the 27-year future period. The first future scenario is a high consumption (HC) scenario, in which we used the baseline  $P_{max}$  of the fish to simulate growth and estimate consumption by age in the future period. As the  $C_{max}$  increases with temperature, consumption by the fish ( $P_{max} \times C_{max}$ ) would increase in this scenario. This scenario implies that future prey availability is not limited so that consumption by the fish can increase. The second scenario is constant consumption (CC) and third scenario in reduced consumption (RC). In the CC scenario, we used baseline consumption by the fish to simulate growth and estimate  $P_{max}$  by age in the future period. The RC scenario was the same as the CC scenario but input consumption was 90% of baseline consumption. These two scenarios imply that future prey availability will be limited so that consumption by the fish would be equal to or less than baseline consumption.

In addition to scenario simulations, we estimated prey consumption required for the fish to maintain baseline growth in the future period. To do so, we ran bioenergetics simulations using baseline growth inputs and future temperature inputs. We quantified the change in prey consumption by age, expressed as the percentage of baseline consumption.

To assess changes in growth and consumption by the fish under the future climate regime, we quantified changes in the following three measures by age in the three future scenarios: weight, prey consumption, and gross conversion efficiency (GCE). The GCE is a measure of the efficiency to convert ingested food into body weight and it was calculated as the percent change in fish weight relative to consumption in the simulation period. Changes in these three measures were expressed as the percentage of baseline value.

To assess changes in seasonal and annual energy budgets of the model fish under the projected future climate regime, we quantified changes in energy budgets in the HC and CC scenarios. We divided a year into four seasons based on the temperature experienced by the selected salmonines in baseline period: summer (when the lake was thermally stratified, June–October), fall (November and December), winter (when surface water temperature was lower than 4 °C, January–March), and spring (April and May). We quantified changes in quantities of prey consumption ( $C$ ), metabolic cost ( $M$ ), waste loss ( $W$ ), and net energy for growth ( $G$ ) in a relative manner, expressed as the percentage of baseline value; and quantified changes in proportions of  $M/C$ ,  $W/C$ , and  $G/C$  in an absolute manner, expressed as the difference from baseline value.

## **2.4 Results**

### **2.4.1 Temperature effects in general**

Our results showed the control of prey availability on responses in the growth and consumption by salmonines in Lake Huron to temperature effects induced by climate change. The growth of Chinook salmon, lake trout, and steelhead all increased substantially in the HC scenario where prey availability was not limited but generally decreased in the HC and RC scenarios where prey availability was limited (Fig. 2.3). Prey consumption of these salmonines also increased substantially in the HC scenario so that their gross conversion efficiencies (GCEs) generally increased or were maintained at baseline levels. In the CC and RC scenarios, the GCEs generally decreased.

Our results suggested that temperature effects on growth and prey consumption are stronger for Chinook salmon than for lake trout and steelhead, and also that effects are stronger

for older fish than for younger fish from the same population. Projected changes in growth and prey consumption under the future climate regime were similar in magnitudes among lake trout populations. We summarized results of our bioenergetics simulations by species in the following sections and reported model-estimated  $P_{max}$  in Appendix B.

#### **2.4.2 Effects on Chinook salmon**

The simulated growth of Chinook salmon increased substantially in the HC scenario, decreased in the RC scenario, and increased until age 1 but decreased thereafter in the CC scenario (Fig. 2.3). Mean weights at different ages increased by 32–60% in the HC scenario and decreased by 4–19% in the RC scenario (Fig. 2.4). In the CC scenario, mean weights increased by 4–7% at age 1 but decreased by 0–9% thereafter.

Mean consumption by Chinook salmon across age-classes in the HC scenario increased by 36–61% (Table 2.3). We estimated that a 10% increase in prey consumption is required for Chinook salmon to maintain baseline growth in the future period (Table 2.3).

Mean GCEs of Chinook salmon mostly increased before age 3 but decreased thereafter in the HC scenario and increased at age 0–1 but decreased thereafter in the CC and RC scenarios (Table 2.3). Changes in mean GCEs of Chinook salmon were less than 9% (increase or decrease) before age 3 but drastic decreases by at least 14% occurred thereafter in all future scenarios.

#### **2.4.3 Effects on lake trout**

The simulated growth of lake trout increased substantially in the HC scenario and decreased in the RC scenario but maintained at baseline levels in the CC scenario (Fig. 2.3). In the HC scenario, mean weights of lake trout at different ages increased by 27–69% among populations (Fig. 2.5). In the CC scenario, mean weights increased at ages before 5 and



decreased thereafter, ranging from an increase of 7% to a decrease of 2% among populations (Fig. 2.5). In the RC scenario, mean weights at different ages decreased by 6–14% among populations (Fig. 2.5).

Mean consumption by lake trout across age-classes in the HC scenario increased by 6–56% among populations (Table 2.4). We estimated that a small increase of 2% in prey consumption is enough for lake trout to maintain baseline growth in the future period (Table 2.4).

Mean GCEs of lake trout generally increased before age 3 by more than 3% in the three future scenarios (Table 2.4). At ages after 3, mean GCEs at different age-classes mostly increased by 10–20% in the HC scenario but mostly decreased by about 5% in the CC scenario and by 10% in the RC scenario (Table 2.4).

#### **2.4.4 Effects on steelhead**

The simulated growth of steelhead increased substantially in the HC scenario but decreased in the CC and RC scenarios (Fig. 2.3). Mean weights at different ages increased by 24–37% in the HC scenario, decreased by 0–6% in the CC scenario, and decreased by 11–17% in the RC scenario (Fig. 2.6).

Mean consumption by steelhead across age-classes increased by 26–41% in the HC scenario (Table 2.5). We estimated that an increase of 6% in prey consumption is required for steelhead to maintain baseline growth in the future period (Table 2.5).

Mean GCEs of steelhead increased in some age-classes but decreased in the others in the HC scenario but decreased across all age-classes in the CC and RC scenarios. Changes in mean GCE across age-classes ranged from a 16% increase to a 10% decrease in the HC scenario

(Table 2.5). Mean GCEs of steelhead across age classes decreased by 1–12% in the CC scenario and by 1–18% in the RC scenario.

#### **2.4.5 Effects on energy budgets**

Simulated energy budgets of the selected salmonines changed most during spring and fall in response to climate change. In the HC scenario, quantities of metabolic cost ( $M$ ), waste loss ( $W$ ), and net energy for growth ( $G$ ) all increased with the increase in prey consumption ( $C$ ) on an annual basis and in all four seasons (Table 2.6). The largest increases of these quantities occurred in spring and fall. In the CC scenario, prey consumption and metabolic cost decreased in summer but increased during the rest of the year while waste loss increased in spring but decreased during the rest of the year. As a result, net energy for growth increased substantially in spring. On an annual basis, the increase in metabolic cost was generally larger than the decrease in waste loss, resulting in a decrease in net energy for growth.

In both of the HC and CC scenarios, proportions of  $M/C$ ,  $W/C$ , and  $G/C$  of these salmonines changed little on an annual basis and in all seasons except spring (Table 2.6). Simulated proportions of  $M/C$  and  $W/C$  both decreased in spring and consequently the proportion of  $G/C$  increased substantially.

## **2.5 Discussion**

### **2.5.1 Processes underlying changes in growth and consumption**

Our simulations indicate that the increase in water temperatures induced by climate change will affect growth and consumption by salmonines in Lake Huron by increasing their capacity of prey consumption and by altering their energy budgets. These processes may be

controlled by behavioral thermoregulation and prey availability. Hence growth and consumption by these salmonines will be affected depending on future changes in the ecosystem under the future climate regime.

The projected increases in future water temperatures will increase the capacity of prey consumption for salmonines in Lake Huron and impart the potential for increased growth. Due to behavioral thermoregulation, temperatures experienced by these salmonines would never exceed their preferred temperatures under the projected future climate regime (Fig. 2.2) and in all cases the duration of optimal temperature conditions will actually increase. When temperature increases toward preferred temperature, maximum consumption by these salmonines increases with temperature more rapidly than the sum of metabolic cost and waste loss does. Hence changes in the growth and consumption by these salmonines under the future climate regime will depend on how much the increased maximum consumption rates can be realized, which, in turn, depends on prey availability. When prey availability was not limited, our simulations in the HC scenario showed that growth and consumption by these salmonines will always substantially increase under the future climate regime, and this part of our results was in complete agreement with results and implications from previous studies (Hill and Magnuson 1990; Magnuson et al. 1990; Brandt et al. 2002). If prey availability was limited, our simulations in the CC scenario showed that the growth of these salmonines will mostly, but not always, decrease under the future climate regime. This part of our results did not fully agree with results from Hill and Magnuson (1990), who concluded that the growth of a fish in the Great Lakes will always decrease without an increase in prey consumption that compensates for increased metabolic cost in the warming climate.

The disagreement between results from Hill and Magnuson (1990) and ours can be explained by examining the details of the energy budget. When prey consumption ( $C$ ) is constant over time, future growth ( $G$ ) of a fish will depend on changes in metabolic cost ( $M$ ) and waste loss ( $W$ ) as shown in the energy budget equation (2.1). With the increase in temperature, metabolic cost will surely increase but waste loss may decrease. The proportion of  $W/C$  of these salmonines is jointly controlled by the parameter  $P_{max}$  and temperature (Stewart et al. 1983). Within the range of model-estimated  $P_{max}$  among our simulation scenarios, the proportion of  $W/C$  would decrease with an increase in water temperature when lower than 5 °C and would change little with an increase in water temperature from 5 °C to the preferred temperature. Hence growth of fish will increase when prey consumption is limited if waste loss decreases more than the increase in metabolic cost under the projected future climate regime.

This study and the study by Hill and Magnuson (1990) both simulated growth of yearling lake trout under the same CC scenario but had opposite results: the simulated growth increased in this study but decreased in Hill and Magnuson (1990). This discrepancy results from a difference in winter water temperatures during baseline periods. Hill and Magnuson (1990) ran baseline simulations using Lake Erie temperatures, which were less frequently below 5 °C on an annual basis than those for Lake Huron. Consequently, projected future decreases in  $W/C$  for yearling lake trout in Lake Erie would be less pronounced than those in Lake Huron.

### **2.5.2 Seasonal effects**

Our results showed that temperature effects induced by climate change on the growth and consumption by salmonines vary by season. Due to behavioral thermoregulation, projected

surrounding temperatures increased most during spring and fall (Fig. 2.3). Thus simulated growth and consumption increased most in spring and fall under both the HC and CC scenarios.

Seasonality in prey consumption will benefit growth of salmonines through increasing the annual mean prey energy density in their diets. Mean prey energy densities in diets were primarily highest in fall and lowest in early summer because energy densities of the two most important prey fishes—alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*)—had similar seasonal cycles, which peaked in fall, gradually decreased through winter until the early summer minimum, and increased again until the fall peak (Dobiesz 2003). In addition, mean prey energy densities were the highest in spring for Chinook salmon and steelhead in Lake Huron because emerald shiner (*Notropis atherinoides*) that has high energy density (Madenjian et al. 2011) was important in their diets only at that time (Roseman et al. 2014).

The increases in prey consumption during spring and fall may lead to an increase in gross energy intake for these salmonines under the future climate regime, even when prey consumption, in terms of weight, remains constant over time. Our simulations in the CC scenario showed that gross energy intake could increase as much as 1% (as for lake-age-4 steelhead), which compensated for a 38% increase in metabolic cost.

### **2.5.3 Validity of behavioral thermoregulation**

The validity of our results from bioenergetics simulations especially depends on the validity of the behavioral thermoregulation assumption, which was used to model the temperature actually experienced by these salmonines in the projected future climate regime (Fig. 2.2). The assumption of behavioral thermoregulation depends on three components: (1) the existence of behavioral thermoregulation, (2) unchanged temperature preference, and (3)

occupation of the best available thermal habitat (where the temperature that is closest to the preferred temperature) under the future climate regime.

There is little doubt about the existence of behavioral thermoregulation of these salmonines as field evidence and bioenergetics model simulations both suggested current summer epilimnion temperatures in Lake Huron are too high for these salmonines to thrive. On an annual basis, many field studies (Spigarelli and Thommes 1979; Olson et al. 1988; Bergstedt et al. 2003; Stewart and Bowlby 2009; Bergstedt et al. 2012) have shown that temperatures experienced by adult salmonines in the Great Lakes all plateaued at different temperatures between 8 °C and 15 °C regardless of how high surface temperatures became. In addition, observed growth of these three salmonines could be accurately predicted by bioenergetics models when behavioral thermoregulation was assumed.

Preferred temperatures of these salmonines will probably change very little under the future climate regime. Two potential causes of changes in preferred temperatures are changes in prey distribution and changes in environmental conditions. As salmonines' prey also behaviorally thermoregulate, their distributions are also controlled by water temperature profiles (Wells 1968; Brandt et al. 1980). For example, Brandt et al. (2002) projected that the thermal habitat of adult alewives that prefer 13 °C in Lake Michigan will increase with climate change. Thus their density within the thermal habitat will decrease if the population size remains unchanged. In such case, lake trout that prefer 9 °C may be forced to stay in temperatures higher than 9 °C in order to meet their consumptive demand. In contrast, environmental factors that can force these salmonines out of their preferred thermal habitats, such as dissolved oxygen (Stefan et al. 2001) and light penetration (Magnuson et al. 1997), are unlikely to change with the water temperature. The main control on these environmental factors is nutrient loading, which is well

managed in Lake Huron (Dolan and Chapra 2012). Even if changes in preferred temperatures of these salmonines occur, preferred temperatures in the future climate regime will not be too much different from the ones used in this study because of physiological constraints of these salmonines and of their prey (Olson et al. 1988).

The most questionable component in the assumption of behavioral thermoregulation is the occupation of the best available thermal habitat. Field studies have shown salmonines in the Great Lakes did not always occupy the best available thermal habitat probably because of competition and the limitation of prey availability. In Lake Ontario, Stewart and Bowlby (2009) found that temperatures experienced by Chinook salmon were higher than those experienced by steelhead in June and July. Bergstedt et al. (2012) showed that temperatures experienced in Lake Huron by lake trout during May and June were lower in 2002–2005 than in 1998–2001 after the change in prey base (Riley et al. 2008). The study also showed that Lake Huron lake trout did not occupy the preferred thermal habitat of 9 °C until July, a month later than when it became available.

The studies by Stewart and Bowlby (2009) and Bergstedt et al. (2012) indicated modest departure from behavioral thermoregulation for part of the year. For example, the input temperature for Lake Huron lake trout was about 1 °C higher than the occupied temperature from field observations in May and June but was similar to those observed during other months (Bergstedt et al. 2012). With this difference, results from our bioenergetics simulations would slightly underestimate the consumption required to maintain the observed growth for Lake Huron lake trout in the Baseline, resulting in the slight underestimation of growth and consumption in the future scenarios.

In summary, the assumption of behavioral thermoregulation in this study is not perfect but is not far from reality. The absolute growth and consumption by these salmonines estimated in our bioenergetics simulations might be biased as discussed above. Nevertheless, the changes in growth and consumption by these salmonines between the base and the future periods projected in our bioenergetics simulations are robust to the validity of the assumption of behavioral thermoregulation.

#### **2.5.4 Message to fishery managers**

Our bioenergetics simulations showed how growth and consumption by salmonines in Lake Huron will change under the projected future climate regime for both high and low prey availability scenarios. However, future prey availability is unlikely to increase in Lake Huron because of the establishment of the quagga mussel (*Dreissena rostriformis bugensis*) population that has sequestered much of the primary production (Vanderploeg et al. 2002; Fahnenstiel et al. 2010) and the continued control of nutrient loads (Dolan and Chapra 2012). In addition, preferred temperatures of these salmonines will still occur in deeper parts of the lakes where prey availability may be lower in the future climate regime (Brandt et al. 2002). Thus, the projected changes in the growth and consumption by these salmonines in CC and RC scenarios, where prey availability is limited, are more likely to occur in the future. Based on bioenergetics simulations in these two scenarios, we predicted that (1) lake trout and steelhead will be better adapted to the projected future climate regime than Chinook salmon and (2) younger individuals will be less negatively affected by climate change than older individuals within the same salmonine population. In fact, simulated growth of age-0 and age-1 salmonines increased in many cases because of the warmer winter, during which the simulated growth was actually



negative under the baseline climate regime. However, older individuals will be more affected by climate change because of the allometric increase in metabolic cost with body weight. Lastly, we estimated a 10% increase in prey consumption would be sufficient for all of these salmonines to maintain current growth into the future climate regime.

**Table 2.1** Preferred temperatures ( $T_{pre}$ ) for salmonines in Lake Huron.

	$T_{pre}$ (°C)	Reference
Chinook salmon (age 0)	18	Stewart and Ibarra (1991)
Chinook salmon (age 1 and older)	13	Bergstedt <sup>a</sup> (unpublished)
Lake trout (age 1 and older)	9	Bergstedt et al. (2012)
Steelhead (lake age 0)	19	Rand et al. (1993)
Steelhead (lake age 1 and older)	15	Rand et al. (1993)

<sup>a</sup>R. Bergstedt, U.S. Geological Survey, Hammond Bay, Michigan, USA.

**Table 2.2** Baseline growth inputs used in bioenergetics simulations. Each value represents the initial weight (g) of the fish on the first day of simulation, the date (in parentheses) of which was based on data source as described in Appendix B. For age-4 Chinook salmon, we ended simulation on day 214 to represent that they leave the lake for spawning run and set the final weight to 7,136 g.

Age/ lake age	Chinook salmon (5/1)	Lake trout (6/1)			Steelhead (5/1)
		North	Central	South	
0	4.54				50
1	458	40	40	40	970
2	2,160	128	128	128	2,258
3	4,865	443	443	443	3,203
4	6,324	829	858	1,123	3,958
5		1,225	1,233	1,409	
6		1,729	1,689	1,785	
7		2,299	2,194	2,167	
8		2,756	2,603	2,595	
9		3,061	2,862	2,822	
10		3,400	3,147	3,056	

**Table 2.3** Model-estimated consumption and gross conversion efficiency (GCE) for Chinook salmon. Each value represents the mean of simulated values across 29 years in the baseline period or across 27 years in the future period. Corresponding standard errors were all less than 0.7 for consumption and all less than 0.4 for GCEs. HC: High consumption scenario; CC: Constant consumption scenario; RC: Reduced consumption scenario; MG: Prey consumption required to maintain baseline growth under the projected future climate regime.

Age	Consumption (kg)			GCE (%)			
	Baseline	HC	MG	Baseline	HC	CC	RC
0–1	1.7	2.3	1.6	26.6	28.7	28.6	28.4
1–2	8.1	11.7	8.4	21.1	19.3	19.8	20.0
2–3	17.3	26.1	18.1	15.7	16.3	14.7	14.3
3–4	19.7	29.9	21.3	7.4	6.3	6.2	6.3
4–4.6 <sup>a</sup>	15.6	21.7	17.2	5.2	1.7	4.1	4.1

<sup>a</sup> Simulation ends on day 214

**Table 2.4** Model-estimated consumption and gross conversion efficiency (GCE) for lake trout. Each value represents the mean of simulated values across 29 years in the baseline period or across 27 years in the future period. Corresponding standard errors were all less than 0.3 for consumption and all less than 0.2 for GCEs. HC: High consumption scenario; CC: Constant consumption scenario; RC: Reduced consumption scenario; MG: Prey consumption required to maintain baseline growth under the projected future climate regime.

Age	Consumption (kg)			GCE (%)			
	Baseline	HC	MG	Baseline	HC	CC	RC
<b>North Lake Huron</b>							
1–2	0.69	0.82	0.65	12.8	20.0	14.1	12.9
2–3	1.8	2.4	1.7	17.6	18.9	18.4	18.4
3–4	2.8	3.8	2.7	14.0	13.8	13.7	13.6
4–5	3.7	5.1	3.7	10.6	12.8	10.5	10.5
5–6	4.6	6.8	4.6	10.9	13.2	10.8	9.6
6–7	6.0	9.0	6.1	9.4	10.6	9.4	9.3
7–8	6.8	10.3	6.8	6.7	7.9	6.6	6.5
8–9	6.9	10.7	7.0	4.4	5.5	4.2	4.0
9–10	7.5	11.8	7.6	4.5	5.5	4.4	4.2
<b>Central Lake Huron</b>							
1–2	0.69	0.82	0.67	12.7	15.1	13.5	12.5
2–3	1.9	2.5	1.8	16.9	17.8	17.4	17.5
3–4	3.2	4.3	3.2	12.9	13.0	12.5	12.5
4–5	4.2	6.0	4.3	8.8	11.2	8.7	7.8
5–6	5.1	7.5	5.2	8.9	10.0	8.7	8.5
6–7	6.6	9.8	6.6	7.7	8.8	7.7	7.6
7–8	7.0	10.5	7.0	5.9	6.9	5.7	5.5
8–9	7.0	10.7	7.0	3.7	4.6	3.4	3.2
9–10	7.5	11.7	7.7	3.8	4.7	3.6	3.5
<b>South Lake Huron</b>							
1–2	0.63	0.73	0.60	13.9	16.6	15.1	13.9
2–3	1.6	2.1	1.6	19.5	20.2	19.5	19.4
3–4	4.0	5.1	3.9	17.1	16.9	17.4	17.6
4–5	3.6	4.6	3.6	8.0	9.1	7.3	7.0
5–6	4.4	5.9	4.4	8.6	11.1	8.3	7.5
6–7	5.2	7.1	5.2	7.4	8.2	7.2	6.6
7–8	6.1	8.4	6.2	7.0	7.9	6.9	6.9
8–9	6.0	8.3	6.1	3.8	4.6	3.6	3.5
9–10	6.3	8.9	6.4	3.7	4.4	3.5	3.4

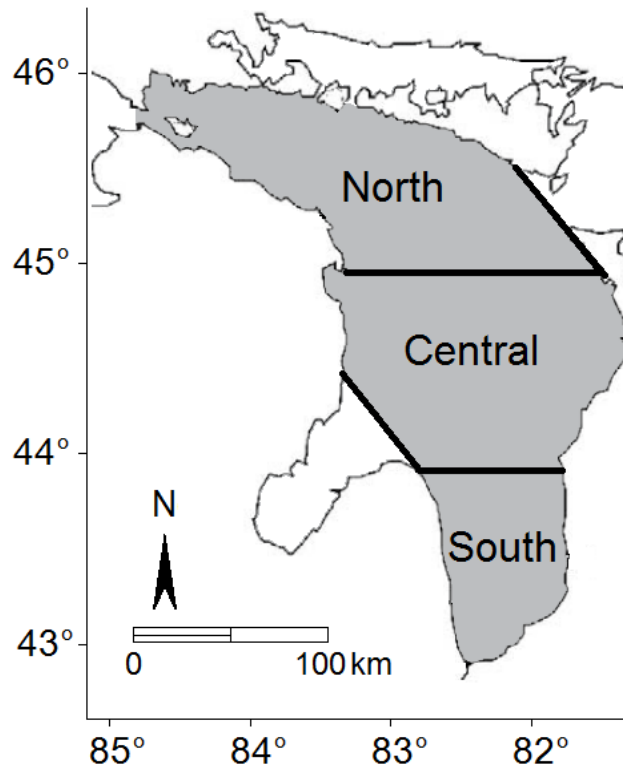
**Table 2.5** Model-estimated consumption and gross conversion efficiency (GCE) for steelhead. Each value represents the mean of simulated values across 29 years in the baseline period or across 27 years in the future period. Corresponding standard errors were all less than 0.5 for consumption and all less than 0.2 for GCEs. HC: High consumption scenario; CC: Constant consumption scenario; RC: Reduced consumption scenario; MG: Prey consumption required to maintain baseline growth under the projected future climate regime.

Lake age	Consumption (kg)			GCE (%)			
	Baseline	HC	MG	Baseline	HC	CC	RC
0–1	5.1	6.4	5.1	18.0	18.1	17.9	17.8
1–2	10.7	14.4	11.2	12.0	11.4	11.2	11.3
2–3	16.0	22.3	16.8	5.9	6.8	5.2	4.8
3–4	18.7	26.4	19.9	4.0	3.6	3.8	3.7

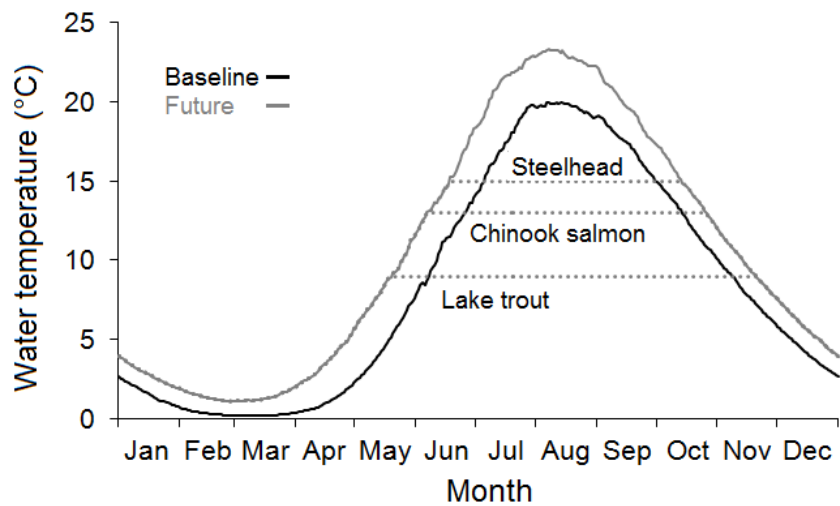
**Table 2.6** Simulated seasonal and annual changes in energy budgets for Chinook salmon, lake trout, and steelhead under the high consumption (HC) and constant consumption (CC) scenarios. The prey consumption ( $C$ ), in terms of gross energy intake, was partitioned into metabolic cost ( $M$ ), waste loss ( $W$ ), and growth ( $G$ ), and  $M/C$ ,  $W/C$ , and  $G/C$  were proportions of gross energy intake represented by metabolic cost, waste loss, and growth, respectively. For these proportions of consumption, the changes were similar in the HC and CC scenarios so results were pooled. Degrees of changes were divided into four levels based on the median of changes among ages and populations—substantial increase ( $\uparrow\uparrow$ ): increase over the baseline value by more than 0.10 for the proportions of  $M/C$ ,  $W/C$ , and  $G/C$  or by more than 40% for the quantities of  $C$ ,  $M$ ,  $W$ , and  $G$ ; increase ( $\uparrow$ ): increase over the baseline value by between 0.02 and 0.10 for the proportions or by between 5% and 40% for the quantities; little change ( $-$ ): change from the baseline by less than 0.02 for the proportions or by less than 5% for the quantities; and decrease ( $\downarrow$ ): decrease from the baseline value by between 0.02 and 0.10 for the proportions or by between 5% and 40% for the quantities.

	HC				CC				$M/C$	$W/C$	$G/C$
	$C$	$M$	$W$	$G$	$C$	$M$	$W$	$G$			
Spring	$\uparrow\uparrow$	$\uparrow$	$\uparrow$	$\uparrow\uparrow$	$\uparrow\uparrow$	$\uparrow\uparrow$	$\uparrow\uparrow$	$\uparrow\uparrow$	$\downarrow$	$\downarrow$	$\uparrow\uparrow$
Summer	$\downarrow$	$-$	$\downarrow$	$\downarrow$	$\uparrow$	$\uparrow$	$\uparrow$	$\uparrow$	$\uparrow$	$-$	$\downarrow$
Fall	$\uparrow$	$\uparrow$	$-$	$\uparrow$	$\uparrow\uparrow$	$\uparrow\uparrow$	$\uparrow\uparrow$	$\uparrow\uparrow$	$-$	$-$	$-$
Winter	$\uparrow$	$\uparrow$	$\downarrow$	$\uparrow^a$	$\uparrow\uparrow$	$\uparrow\uparrow$	$\uparrow$	$\uparrow^a$	$\downarrow$	$\downarrow$	$\uparrow$
Annual	$-$	$\uparrow$	$\downarrow$	$\downarrow$	$\uparrow$	$\uparrow\uparrow$	$\uparrow$	$\uparrow\uparrow$	$-$	$-$	$-$

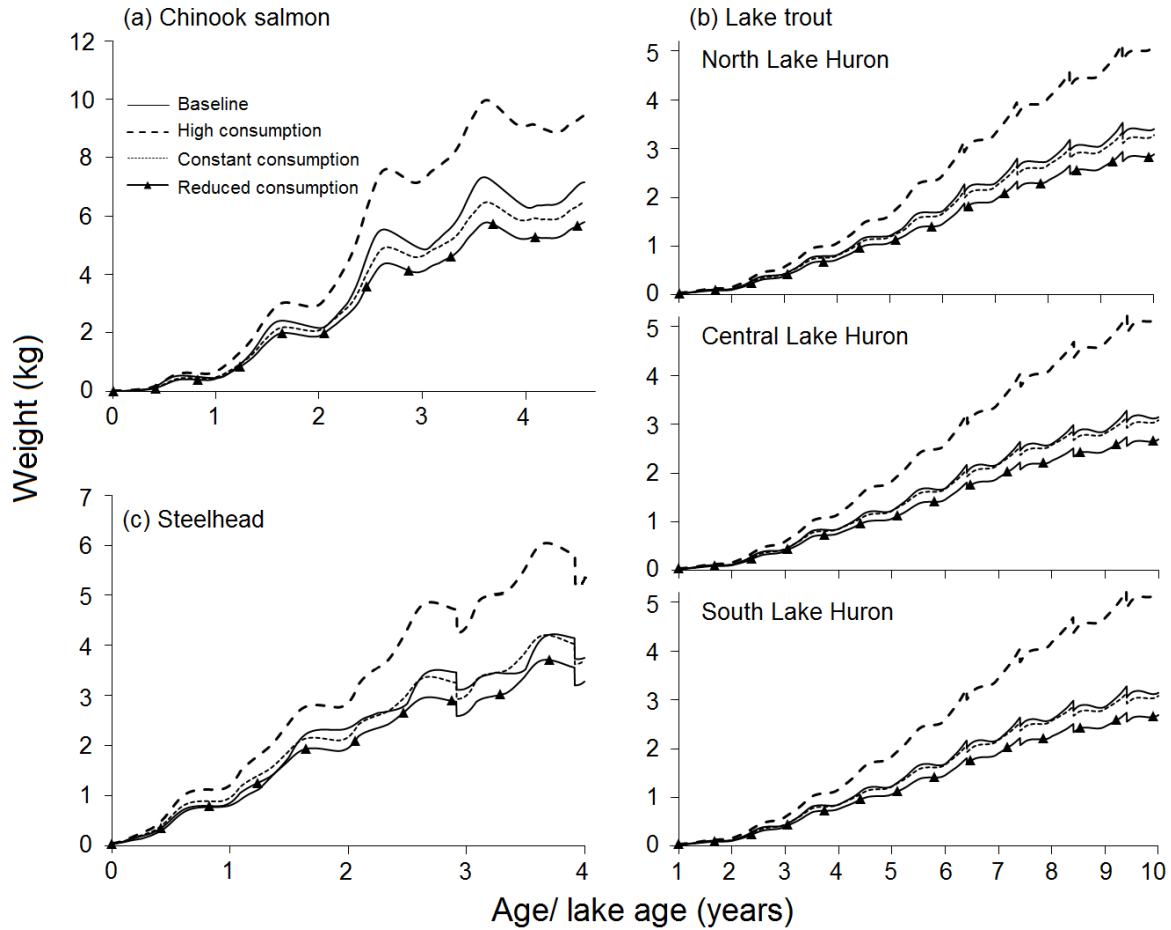
<sup>a</sup> In some simulations, this increase ( $\uparrow$ ) reflected a reduction in energy loss under the HC and CC scenarios compared with the baseline. Note that growth for these salmonines in the winter was predominately negative in the baseline period.



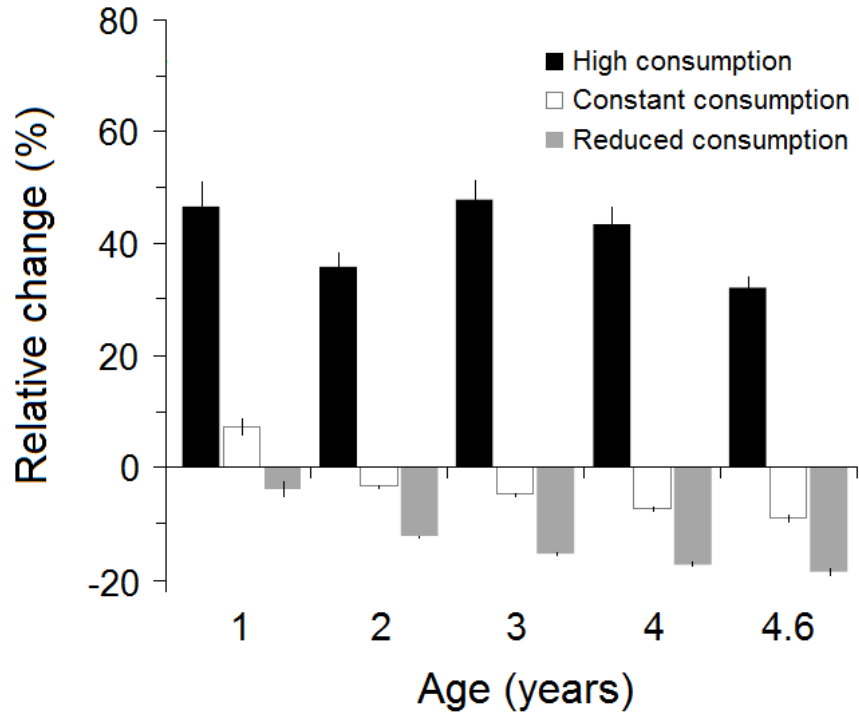
**Figure 2.1** Lake Huron main basin (shaded area). The Lake Huron main basin was divided into three lake regions using the 45 °N and 44 °N latitude lines, representing habitats of three lake trout populations.



**Figure 2.2** Mean water temperatures in Lake Huron projected by the Coupled Hydrosphere–Atmosphere Research Model for the baseline period (1964–1993) and for the future period (2043–2070). Horizontal lines represent preferred temperatures for selected salmonines at age 1 and older.

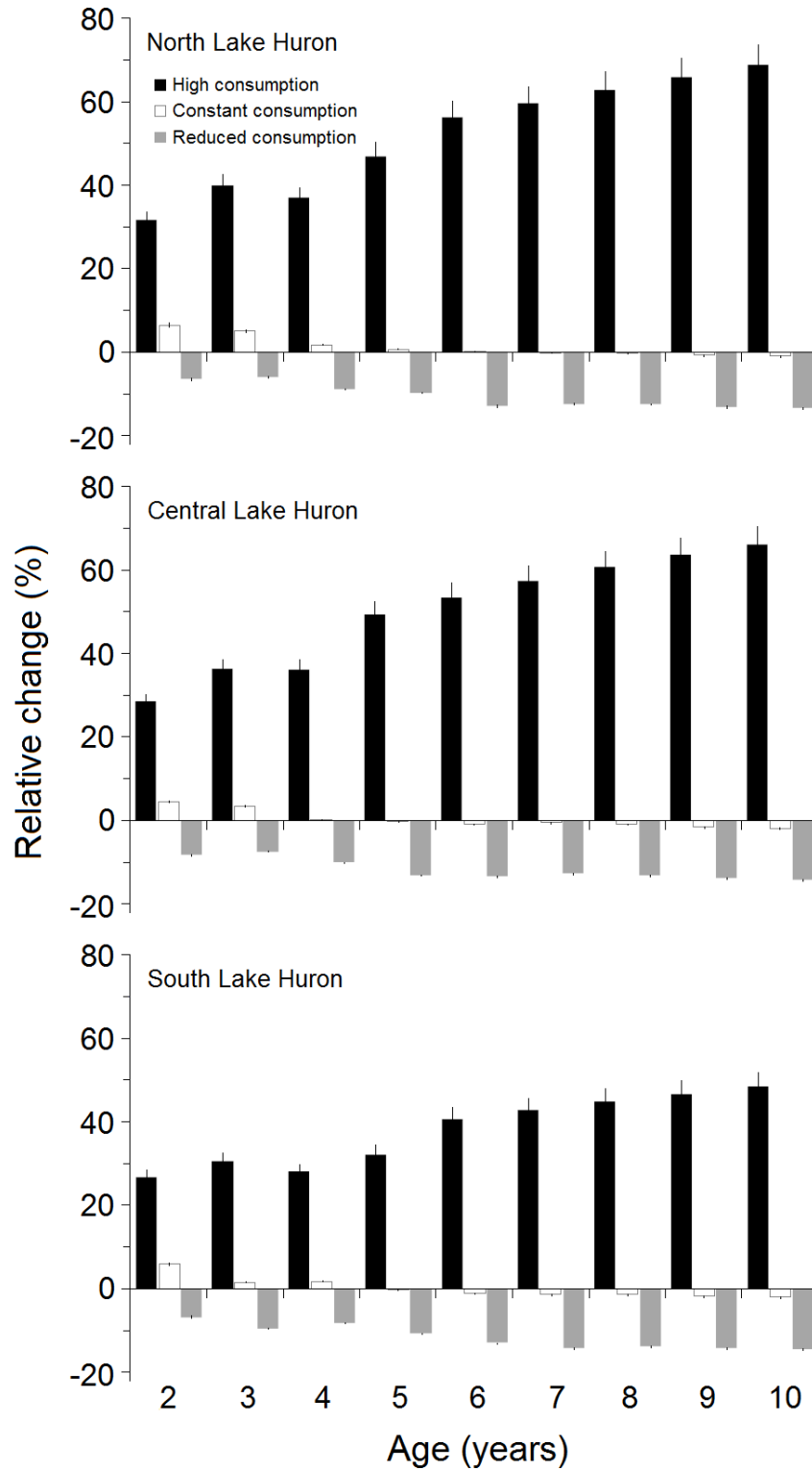


**Figure 2.3** Simulated growth trajectories of the selected salmonines in Lake Huron in the baseline and three future scenarios of prey availability. Each growth trajectory represents a 29-year average in the baseline period and a 27-year average in the future period. Relative to the baseline prey availability, future prey availability was assumed to increase in the high consumption scenario, to be limited in the constant consumption scenario, and to be reduced in the reduced consumption scenario.

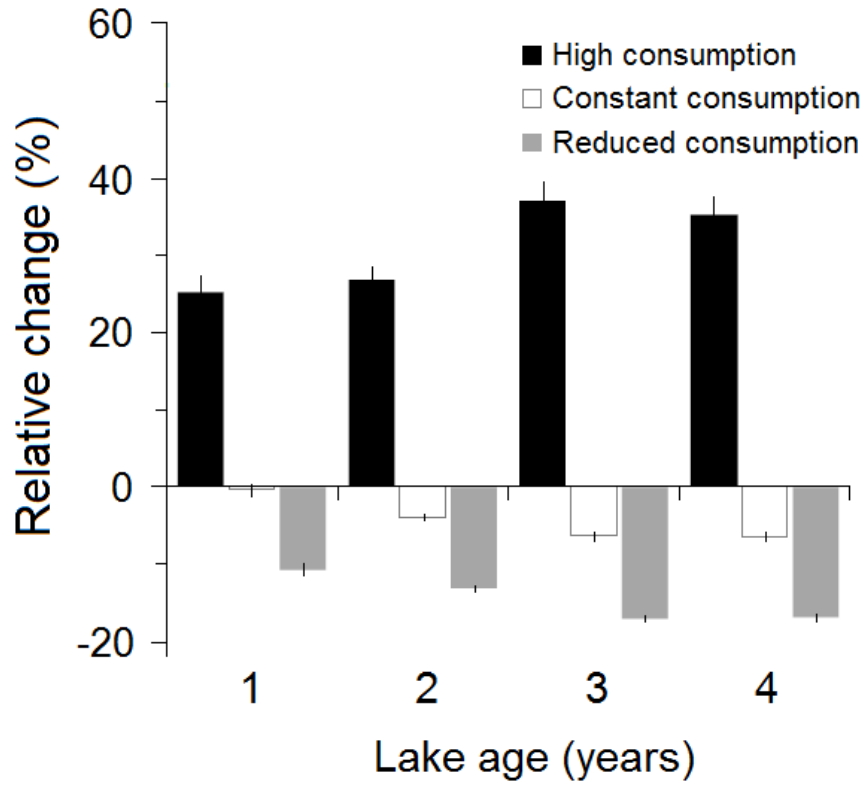


**Figure 2.4** Changes in model-estimated weights of Chinook salmon at different ages in the future scenarios. Each bar represents a mean change ( $\pm$  standard error) relative to the baseline weight at the same age across 27 years in the future period. Model-estimated weights at age 4.6 represent weights on simulation day 214 at age 4, when bioenergetics simulations ended to represent that Chinook salmon leave the lake for spawning.





**Figure 2.5** Changes in model-estimated weights of lake trout at different ages in the future scenarios. Each bar represents a mean change ( $\pm$  standard error) relative to the baseline weight at the same age across 27 years in the future period.



**Figure 2.6** Changes in model-estimated weights of steelhead at different ages in the future scenarios. Each bar represents a mean change ( $\pm$  standard error) relative to the baseline weight at the same age across 27 years in the future period.

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## **Chapter 3**

### **The relative impacts of nutrient loads and invasive species on the Saginaw Bay food web**

#### **3.1 Abstract**

Excessive nutrient loads and species invasions pose significant threats to productivity and function of Great Lakes aquatic ecosystems. We used an Ecopath and Ecosim model to analyze impacts of changes in phosphorus loads, and dreissenid mussel and alewife biomass on the Saginaw Bay food web, Lake Huron. We configured the food web model in Ecopath with pre-dreissenids (1990) data on organism biomass, production, consumption, and diet from federal and state agency surveys and other sources. We conducted 70-year simulations in Ecosim of single factors (nutrients, alewives, and dreissenids) and their combinations. Nutrients scenarios were run with high (1970s), average (current), and low (target) levels of total phosphorus loads; alewife scenarios were run with double the 1990–2003 average biomass, 1990–2003 average biomass, and alewife absence; dreissenid scenarios were run with the 1990–1996 average biomass, current (2009–2010) biomass, and dreissenid absence. Results indicated phosphorus loads were positively correlated with simulated biomass of most food web groups, and alewife biomass was negatively correlated with biomass of most fish groups and macrozooplankton. Dreissenid impacts were most severe on lower trophic levels but were relatively minor for fish groups compared with nutrient and alewife scenarios. Dreissenids had little effect on fish because chironomids, which feed on detritus and are the main component of fish diets, were not affected by dreissenids. Our results suggest that, under current conditions of absence of alewives

and reduced dreissenid biomass, the target nutrient loads established in 1978 would not sustain current fishery harvests in Saginaw Bay given food web changes caused by invasive species.

**Keywords:** Saginaw Bay, food web, invasive species, environmental stressors, management

### 3.2 Introduction

Eutrophication, habitat degradation and loss, and invasions of aquatic non-indigenous (invasive) species have profoundly affected structure and function of Great Lakes food webs and fisheries. In Saginaw Bay, Lake Huron, responses of the food web to these stressors have been well documented, and typify changes observed in many Great Lakes aquatic ecosystems (Beeton, 1984; Beeton et al., 1999; Fahnenstiel et al., 2010; Ludsin et al., 2001; Nalepa and Fahnenstiel, 1995; Vanderploeg et al., 2001, 2002). Excessive phosphorus loads have impacted productivity and species composition at all trophic levels in Saginaw Bay (Nalepa and Fahnenstiel, 1995). From the 1950s through the 1970s, Saginaw Bay experienced severe eutrophication which caused harmful algal blooms, water taste and odor problems, and coincided with extirpation of the benthic invertebrate mayfly *Hexagenia limbata* (Bierman et al., 1984; Schaeffer et al., 2000). In response to impairments, the 1970 Federal Clean Water Act mandated phosphorus abatement programs, and the 1978 Great Lakes Water Quality Amendment set limits on total phosphorus loads coming into the bay, and phosphorus and chlorophyll *a* concentrations in the water. With restrictions on point source loads, phosphorus concentrations decreased in the inner bay by up to 14% and anthropogenic impairments were at least partially alleviated by the early 1980s (Bierman et al., 1984). During 1980–2000, Saginaw Bay was subjected to fluctuating nutrient levels (Ludwig et al., 1993). High concentrations were associated with periodic peaks in river



discharges in 1985 and 1986. Discharges increased organic loadings from the Saginaw River and temporarily reversed the declining nutrient trends. Pollution-tolerant oligochaetes dominated the benthic community during the late 1980s (Nalepa et al., 2003). Since the 1990s, nutrient loads declined but have rarely gone below target levels set by management agencies (Stow et al., 2014).

Coincident with fluctuations in nutrient loads in Saginaw Bay were serial colonizations by invasive species that altered physical habitats and energy flow in the food web and affected fisheries. Historically, the bay produced the largest walleye (*Sander vitreus*) commercial fishery in the Great Lakes but it collapsed in 1944 likely because of habitat loss and degradation (Schneider and Leach, 1977). Alewives (*Alosa pseudoharengus*) that invaded Saginaw Bay around 1950 and non-indigenous rainbow smelt (*Osmerus mordax*) likely suppressed walleye recovery through predation on walleye larvae (Fielder et al., 2010; Schneider and Leach, 1977). The predation by alewife on fish larvae also likely caused recruitment failure in yellow perch (*Perca flavescens*) and emerald shiner (*Notropis atherinoides*) in Saginaw Bay (Brandt et al., 1987; Madenjian et al., 2008). By 1980, the fish community was nearly devoid of native predators. Intensive walleye stocking was implemented to restore walleye as the dominant predator (Fielder et al., 2000), and a major sport fishery developed in the bay, largely in response to walleye re-establishment, which accounted for about 90% of the harvest in Michigan waters of Lake Huron in the early 1990s (Rakoczy and Svoboda, 1997). Natural reproduction of walleye and emerald shiner increased dramatically after 2003 when alewife populations declined in Lake Huron's main basin (Fielder et al., 2007, 2010; Schaeffer et al., 2008). Walleye stocks are currently considered rehabilitated and stocking has ceased (Fielder et al., 2010), but recruitment of yellow perch remains low (Ivan et al., 2011).

Although other species subsequently invaded the Saginaw Bay ecosystem and disrupted food web function, including spiny water flea (*Bythotrephes cederstroemii*) in the 1980s (Vanderploeg et al., 1993), white perch (*Morone americana*) in the mid-1980s (Haas and Schaeffer, 1992), and round goby (*Neogobius melanostomus*) in 1999 (Fielder and Thomas, 2006), perhaps the most notable invasive species were dreissenid mussels (zebra mussel *Dreissena polymorpha* in 1991 (Nalepa et al., 1995), quagga mussel *D. bugensis* likely in 1999 (Thomas Nalepa, University of Michigan, personal communication). Comprehensive datasets documented the zebra mussel invasion and its impacts on water quality (Johengen et al., 2000), lower trophic levels (Adlerstein et al., 2013; Fahnenstiel et al., 1995a, 1995b; Nalepa et al., 1995, 1996, 2003), and fish (Adlerstein et al. 2007; Fielder et al., 2000; Fielder and Thomas, 2006). Zebra mussels rapidly colonized the bay and transformed ecosystem structure through intense filtration activity, increased water clarity, and shunting of energy from pelagic to benthic food webs (Fahnenstiel et al., 1995b; Johengen et al., 2000; Nalepa et al., 1996, 2003). The mussels immediately reduced abundance of phytoplankton (Adlerstein et al., 2013), selectively increased biomass of *Microcystis aeruginosa* that caused harmful blooms (Vanderploeg et al., 2001), and changed phytoplankton species composition (Fishman et al., 2009, 2010). Also, dreissenids appear to retain phosphorus in the inner Saginaw Bay, reducing nutrient transport to Lake Huron offshore areas which have subsequently become oligotrophic (Barbiero et al., 2012; Cha et al., 2013). After the dreissenid invasion, the Saginaw Bay fish community changed from a dominance of pelagic planktivores to dominance by benthivores (Fielder et al., 2000; Fielder and Thomas, 2006).

Changes in relative abundance of some taxa in Lake Huron and Saginaw Bay appear influenced by multiple factors. For example, catch rates of yellow perch in Saginaw Bay dropped

dramatically after 1989 as nutrient loads decreased and primary productivity declined from dreissenid filtration (Fielder et al., 2000). On the other hand, catch rates of forage fishes fluctuated considerably. The presence of zebra and quagga mussels facilitated successful establishment of round goby (Ricciardi, 2001), which caused an increase in benthivorous predator biomass as gobies became a substantial portion of predator diets (Roseman and Riley, 2009). In Lake Huron's main basin, invasion of dreissenids, along with increased predation by naturally reproduced Chinook salmon (*Oncorhynchus tshawytscha*) and declining nutrient loads, likely contributed to the decline of alewife in 2003 (Riley et al., 2008).

A modeling approach often is useful for disentangling effects of multiple factors on food web dynamics. Whereas statistical correlation analysis may be complicated by overlapping effects of multiple factors on individual year classes, a simulation model analysis can cleanly compare differences in factor impacts on populations over multiple generations. In this study, we summarize available information for the Saginaw Bay ecosystem and fisheries and evaluate the relative impacts of changes in nutrient loads and two invasive species groups, dreissenids and alewife, on the Saginaw Bay food web. To accomplish these goals we used the Ecopath with Ecosim (EwE) approach (Christensen and Walters, 2004). The EwE approach consists of a component for structuring biomass flows among food web groups (Ecopath) within a static temporal period, and a component for simulating food web time-dynamics under different scenarios (Ecosim). There has been increased interest in implementing EwE food web models for Great Lakes ecosystems, with several studies for Lake Superior (Cox and Kitchell, 2004; Kitchell et al., 2000), Lake Ontario (Blukacz-Richards and Koops, 2012; Hossain et al., 2012; Stewart and Sprules, 2011), Lakes Michigan and Huron (Langseth et al., 2012).

### **3.3 Methods**

#### **3.3.1 Study site**

Saginaw Bay is a large (2,770 km<sup>2</sup>, Johengen et al., 2000) embayment of Lake Huron representing 10% of total lake volume (Beeton et al., 1967). The bay primary production is among the highest in the Great Lakes region (Nalepa and Fahnenstiel, 1995). Nutrient inputs result from point and nonpoint sources of nitrogen, phosphorus, and chloride, due to intensive agricultural and extractive activities (Beeton, 1965). The bay receives flows from 28 fluvial systems, draining ~21,000 km<sup>2</sup> of southeast Michigan (Nalepa et al., 2003), with the Saginaw River constituting about 70% of the total inflow (Stow et al., 2014). Saginaw Bay can be divided into a shallow, inner region with mean depth of 5.1 m, and a deeper, outer region with mean depth of 13.7 m (Fig. 1) (Johengen et al., 2000). The inner bay is influenced by enriched runoff from the Saginaw River and the outer bay is influenced by nutrient-poor inflow from Lake Huron (Beeton and Saylor, 1995; Bierman and Dolan, 1981; Stoermer, 1978). Saginaw Bay has a rapidly changing circulation (Danek and Saylor, 1977) influenced by local winds and the circulation of Lake Huron frequently causing injections of lake water. Average flushing time reported by Beeton et al. (1967) is 186 days. Substrates range from cobble/rock to silt, where proportions of fine-grained material gradually increase along a depth gradient (Robbins, 1986; Wood, 1964). Substrate type is the main determinant of Saginaw Bay's benthic community composition (Adlerstein et al., 2013; Nalepa et al., 2003).

#### **3.3.2 The Ecopath with Ecosim (EwE) food web model**

To characterize and quantify the dynamics of the Saginaw Bay food web, and to evaluate the effects of nutrient loads and invasive species, we used the Ecopath with Ecosim (EwE) model

(Christensen and Walters, 2004). Derivations of Ecopath and Ecosim are detailed in Christensen and Pauly (1992) and Walters et al. (1997, 2000); software and documentation are available at <http://www.ecopath.org/>. We used the latest release of EwE version 6.3.

### 3.3.3 Mass balance modeling

Our Ecopath model represents the Saginaw Bay food web during the 1988–1990 period, prior to zebra mussel invasion. We configured 47 groups for the Ecopath model (Table 3.1). The Ecopath model was used to describe the biomass flows among groups in the food web:

$$B_i \times (P/B)_i \times EE_i = \sum_j B_j \times (Q/B)_j \times DC_{ij} + BA_i + Y_i + E_i \quad (3.1)$$

where  $B_i$  is the biomass for group  $i$ ,  $j$  represents all predators on group  $i$ , and  $(P/B)_i$  is the production/biomass ratio,  $EE_i$  is the ecotrophic efficiency which represents the proportion of production consumed by predators, used for biomass accumulation  $BA_i$ , or exported from the system through fishery harvest  $Y_i$  and net migration  $E_i$  (emigration minus immigration).  $B_j$  and  $(Q/B)_j$  represent the biomass and consumption/biomass ratio of predator  $j$ , and  $DC_{ij}$  the fraction of prey  $i$  in diet of predator  $j$ . Units are expressed in  $\text{g} \times \text{m}^{-2} \times \text{yr}^{-1}$  wet weight for flows ( $BA$ ,  $Y$ , and  $E$ ),  $\text{g}/\text{m}^2$  for biomass ( $B$ ),  $\text{yr}^{-1}$  for  $P/B$ , and  $\text{g} \times \text{g}^{-1} \times \text{yr}^{-1}$  for  $Q/B$ . Biomass, harvest and migration, and  $P/B$  and  $Q/B$  are annual averages (Table 3.2). We assumed  $BA_i$  to be zero in the Saginaw Bay Ecopath model because the food web was in a relatively steady-state condition from 1988 to 1990. We set  $E_i$  for fish groups in Ecopath to be zero although some move into the bay for part of the year. But emigration and immigration vary annually and are controlled outside of the modeled system by their population size in the Lake Huron main basin. Thus, in the Ecosim analysis we represented migration of those groups as described in the Dynamic Modeling section. Another required input to balance energy in Ecopath is the proportion of consumption

represented by unassimilated food (Christensen et al., 2005). We implemented and balanced the Saginaw Bay Ecopath model using 1990 data.

### **3.3.4 Food web structure, model inputs and data sources**

The configuration of the Ecopath model (Table 3.1) was informed by available information and data on community structure as described in Appendix C. We parameterized 7 fish species as having up to four age stanzas (e.g. ‘Walleye 2+’ stanza represents walleye that are age 2 and older) because of their trophic ontogeny and different vulnerability to the fisheries (Christensen and Walters, 2004). Among the groups, 42 were consumers (29 fish, five benthos, six zooplankton, one protozoa and one bacteria), three were producers (one macrophytes and two phytoplankton), and two were detritus groups (Fig. 3.2). We included a Pelagic detritus group to represent detrital materials that are available to bacteria, zooplankton, protozoa, and benthic filter feeders. We included a Settled detritus group to represent detrital materials available to benthic and fish deposit feeders (Fig. 3.2). We included two groups of invasive species that were absent before 1990: Dreissenids, combining zebra and quagga mussels, and Round goby. Zebra mussels invaded Saginaw Bay in 1991 (Nalepa et al., 2003) and round goby in 1999 (Fielder and Thomas, 2006). We assumed that quagga mussels invaded the bay in 1999 based on surveys in Lake Huron in 2000 and 2003 (Nalepa, 2007). It was necessary to include these groups in Ecopath to run dynamic simulations in Ecosim.

We estimated or obtained input parameters for each group in the Saginaw Bay Ecopath model including: biomass ( $B$ ), production to biomass ratio ( $P/B$ ) or total mortality rate ( $Z$ ) for stanza groups, consumption to biomass ratio ( $Q/B$ ), unassimilated food to consumption ratio ( $U/Q$ ), and fraction of prey in diet compositions ( $DC$ ). For harvested fish groups we also

estimated fishery yields ( $Y$ ). Estimation procedures and data sources of model inputs (Tables 2 and 3) were described in Appendix C. We estimated additional parameters required to link stanza groups (von Bertalanffy growth constant  $k$ , asymptotic weight  $w_{inf}$ , and weight at maturity  $w_m$ ) using fish length-at-age data from surveys and age at maturity data from literature (Table 3.4). We balanced the Ecopath model by modifying the diet compositions so that the model estimates for  $EE$  were  $< 1$  for all groups.

### 3.3.5 Dynamic modeling

We used the balanced 1990 Saginaw Bay Ecopath model as the initial condition for analyzing main temporal dynamics of the food web with Ecosim. We calibrated and fitted the model using biomass and fishery harvest data (Appendix C) and nutrient data for the 1990 to 2009 period (Stow et al., 2014). In the Ecosim model, biomass  $B$  of group  $i$  changes with time as:

$$dB_i / dt = G_i \times \sum_j Q_{ji} - \sum_j Q_{ij} - E_i - (MO_i + F_i) \times B_i \quad (3.3)$$

where  $G_i$  is the gross conversion efficiency and  $Q_{ji}$  is the consumption on group  $j$  by group  $i$ ,  $Q_{ij}$  is the predation rate by group  $j$  on group  $i$ ,  $E_i$  is the net migration rate,  $MO_i$  is the non-predatory natural mortality rate, and  $F_i$  is the fishing mortality rate. Consumption  $Q_{ij}$  was modeled based on foraging arena theory, in which prey biomass is divided into a predation-vulnerable fraction and non-vulnerable fraction (Christensen and Walters, 2004) using the equation:

$$Q_{ij} = \frac{p_{ij} \times v_{ij} \times B_i \times B_j \times f_1 \times S_{ij} \times M_{ij}}{v_{ij} \times (1 + f_2) + p_{ij} \times B_j \times f_3 \times S_{ij} \times M_{ij}} \quad (3.4)$$

where  $p_{ij}$  is the predation rate on prey group  $i$  by unit biomass of predator group  $j$  that can be adjusted by a forcing function  $S_{ij}$  and/or a mediation function  $M_{ij}$ ,  $v_{ij}$  is the vulnerability parameter, and  $f_1$ ,  $f_2$ , and  $f_3$  are functions representing effects of feeding time and handling time

on consumption (Christensen and Walters, 2004).

Primary production in Ecosim is modeled as a function of free nutrient concentration controlled by nutrient loads (Christensen and Walters, 2004) for primary producer group  $i$ :

$$P_i = B_i \times (P/B)_{max,i} \times \left( \frac{Nf}{Nf + K_i} \right) \times M_i \quad (3.5)$$

where  $(P/B)_{max,i}$  is the maximum production to biomass ratio,  $Nf$  is the proportion of free nutrients controlled by loads (of phosphorus in our model),  $K_i$  is a constant estimated by Ecosim, and  $M_i$  is another user defined-mediation function to model indirect effects on primary production.

### **3.3.6 Modeling consumption for invasive species in Ecosim: Forcing functions to modify vulnerabilities**

We applied forcing functions  $S_{ij}$  in equation (3.4) to simulate Dreissenids and Round goby invasions, similar to the mediating vulnerability approach in Langseth et al. (2012). The functions were to represent effects of Dreissenids and Round goby and suppress the group effects on their prey and predators until the year of invasion. The forcing function for Dreissenids as predator (Fig. 3.3a) was intended to model rapid and explosive increases in abundance of zebra mussels in 1991 and of quagga mussels in 1999, and return to equilibrium levels for both species. The other forcing functions represent a switch to turn on Dreissenids as prey (Fig. 3.3b), and Round goby as predator and prey (Fig. 3.3c, 3.3d).

### **3.3.7 Modeling groups of fish species that move into Saginaw Bay: Forcing functions for biomass**



We used biomass forcing functions to represent variable annual movements into Saginaw Bay of lake whitefish (*Coregonus clupeaformis*), rainbow smelt, and alewife (Fig. 3.4a–c). These groups use the bay as a nursery area and otherwise inhabit the main basin of Lake Huron. Their population abundance is not controlled by predator–prey dynamics in the bay and, thus, we forced biomass to be proportional to biomass in the main basin. We did not force the biomass of the Open lake group predators, as we wanted to evaluate their role on the food web. These are mostly adult Chinook salmon that also use the bay during part of the year,

### **3.3.8 Modeling indirect interactions: Mediation functions for selected groups**

We used four mediation functions to represent known or potential indirect interactions among food web groups. We used a function (Fig. 3.5a) to represent decline in consumption rates of zooplankton groups in the presence of high biomass of inedible blue green algae (Demott and Moxter, 1991; Gliwicz, 1990; Haney, 1987). We used a second function (Fig. 3.5b) to represent low efficiency in consumption of dreissenids by fish groups that cannot crack the shells (French, 1993; Magoulick and Lewis, 2002; Molloy et al., 1997). This function was needed to prevent unrealistically high proportions of dreissenids in fish diets, because in Ecosim consumption rate on a group is proportional to its biomass as in equation (3.5). We used a third function to represent dreissenid effect on oligochaetes (Fig. 3.5c). Dreissenids are filter feeders that accumulate material within clusters and sequester material from other areas and thus overall availability of detrital material affects detritivores in different ways depending on spatial overlap. Densities of dreissenids, amphipods and sphaeriids are highest in sandy areas, while oligochaetes and chironomids are mostly found in finer substrates (Nalepa et al., 2003). After the dreissenid invasion amphipod densities (where highest) increased as the group benefited from enhanced

detritus, sphaeriids and chironomids fluctuated with no trend, while oligochaetes decreased (Adlerstein et al., 2013; Nalepa et al., 2003). We used a fourth function (Fig. 3.5d) to represent effects of decreased density phytoplankton, protozoa, bacteria and pelagic detritus on light penetration. This was necessary as one of the most drastic effects of dreissenids in Saginaw Bay was high filtration rates of suspended particles resulting in increased water clarity (Fahnenstiel et al., 1995b) and enhanced macrophyte growth (Skubinna et al., 1995).

### 3.3.9 Ecosim parameterization and calibration

Although many parameters in Ecosim can be adjusted, we kept most parameters as default values and made two changes for modeling primary production. The first change was to represent the mesotrophic conditions of Saginaw Bay, and we set the “Base proportion of free nutrients” to 0.5 to represent the condition in the Ecopath year 1990 (Christensen et al. 2005). The second change was to represent higher growth responses of inedible phytoplankton to nutrients compared to edible phytoplankton and macrophytes (Downing et al., 2001). We set  $(P/B)_{max,i}$  in equation (3.5) to 1.6 times the Ecopath  $(P/B)_i$  value for Edible phytoplankton and Macrophytes, and 4.8 times the Ecopath  $(P/B)_i$  value for Inedible phytoplankton. We chose these  $P/B$  ratios to reproduce observed ratios of relative biomass of Inedible phytoplankton under high and low nutrient conditions (see *Nutrients* in the Simulation scenarios section).

To calibrate the model in Ecosim, we estimated vulnerability parameters in equation (3.4) by fitting model outputs to available biomass time series from 1990 to 2009. For each time series, we used a weighting factor  $Wf_i$ :

$$Wf_i = Cf_i / \left( n_i \times s_{\log(B_i)}^2 \right) \quad (3.6)$$

where  $Cf_i$  represents our level of confidence on the time series of group  $i$  based on knowledge about data sources,  $n_i$  is the number of data points, and  $s_{\log(B_i)}^2$  the variance of the log-transformed biomass.

### 3.3.10 Simulation scenarios

To investigate effects of nutrient loads and alewife and dreissenid biomass on the Saginaw Bay food web, we ran scenario simulations representing a range of observed conditions. The analysis was designed as a full factorial experiment with three factors: nutrients, alewives, and dreissenids, and three-levels of each factor (Table 3.5). We ran simulations under fishery mortality for harvested fish groups starting from 2009 levels, which corresponds to the last year of the calibration time series.

*Nutrients:* Values of total phosphorus loads that we used in Ecopath was 681 tons/year, the estimate for 1990. We ran nutrient scenarios in Ecosim under low (440 tons/year), average (767 tons/year), and high (2,059 t/year) levels. The low scenario represents target loads established by the 1978 Great Lakes Water Quality Agreement; average scenario represents mean 1990 to 2009 loads; and high scenario represents the historical high loads in 1974 (Bierman and Dolan, 1986). Loads in Saginaw Bay were about 1.4 times the Saginaw River load (Stow et al., 2014).

*Alewives:* We ran scenario simulations representing absence of alewives, and average and high alewife biomass. The average scenario represents our mean biomass estimates (Alewife 1+ =  $0.582 \text{ g/m}^2$  + Alewife 0 =  $0.295 \text{ g/m}^2$ ) in Saginaw Bay from 1990 to 2003 before the population collapsed, and the high biomass scenario is double that average.

*Dreissenids*: We ran simulations representing three levels of dreissenids (absence, low, high). Dreissenid biomass was set to 5.6 g/m<sup>2</sup> in the low scenario, representing current biomass in the bay. The low scenario corresponds to 20% of the high biomass scenario (28.0 g/m<sup>2</sup>), which was the mean dreissenid biomass for the 1991 to 1996 period from survey data as described in the Benthos groups section in Appendix C. The 20% estimate was from preliminary data analysis by Thomas Nalepa (University of Michigan, personal communication).

We conducted 70-year simulations for each scenario, a time frame at which stable conditions are expected. For each scenario, we summarized projected changes in biomass of each group as the ratio of mean equilibrium biomass during simulation years to initial Ecopath biomass (which corresponds to a scenario with no dreissenids, and close to average 1990–2009 nutrient loads and average 1990–2003 alewife biomass). To report simulation results we used linear models on the ratios of mean to initial Ecopath biomass and tested main factor effects (nutrients, alewives, and dreissenids) and interactions at the 95% confidence level. We used our model coefficients and took the approach used in Kitchell et al. (2000) to evaluate relevance of impacts as whether stressors caused at least a 25% change in group biomass from initial Ecopath biomass.

## **3.4 Results**

### **3.4.1 Model calibration**

After calibration, time series predictions of Ecosim modeled biomass for 30 groups were relatively well matched to the observed biomass time series (Fig. 3.6). The fits of predicted to observed biomass were better for fish groups, in particular for Walleye 2+ (Fig. 3.7) and for zooplankton groups, than for benthos and producer groups.

### **3.4.2 Responses of Saginaw Bay food web groups to scenarios of varying levels of nutrients, and dreissenids and alewife biomass**

#### ***Fish groups***

Results are reported for walleye and yellow perch, the two main harvested species in Saginaw Bay, and for gizzard shad (*Dorosoma cepedianum*), the native forage species with highest biomass. Results for the remaining fish groups are reported in Appendix D.

Biomass of Walleye groups positively responded to nutrients, negatively responded to alewives, but insignificantly increased in response to dreissenid scenarios (Table 3.6). Biomass of Walleye 0–0.5 increased about two-fold from low to high nutrient scenarios and decreased by about 30% from absence of alewife to high alewife scenarios (Fig. 3.8a). Biomass of Walleye 0.5–1 showed a stronger response to nutrient and alewife scenarios, and increased by about 3.5 times from low to high nutrient scenarios and decreased by about 75% from absence of alewife to high alewife scenarios (Fig. 3.8b). Patterns were further amplified for Walleye 1 and Walleye 2+ (Fig. 3.8c–d), to the extent that under low nutrient scenarios, biomass of Walleye 2+ was below the 1990 reference level in all simulations and declined to near zero in high alewife scenarios. In average and high nutrient scenarios, the biomass of Walleye 2+ decreased by about half from absence of alewife to high alewife scenarios.

Biomass responses of all Yellow perch groups to dreissenid scenarios were relatively modest, and only significant for Yellow perch age 3+, in comparison to the responses to nutrient and alewife scenarios (Table 3.6). Biomass of Yellow perch 0–0.5 and Yellow perch 0.5–1 collapsed at low nutrient and high alewife scenarios, increased by up to 2.3 times from average to high nutrient scenarios, and decreased by up to 70% from absence of alewife to high alewife

scenarios (Fig. 3.9a–b). For Yellow perch 1–2 and Yellow perch 3+ biomass trends were less straightforward (Fig. 3.9c–d). In low nutrient scenarios, their biomass decreased with increasing alewife levels to lower than the 1990 reference levels, but in average and high nutrient scenarios their biomass increased and stabilized at average alewife biomass. In average and high nutrient scenarios, Yellow perch 3+ increased with dreissenid biomass.

Biomass of Gizzard shad groups generally responded to nutrient and alewife scenarios and to a less extent to dreissenid scenarios (Table 3.6). Biomass of Gizzard shad 0 increased with increasing nutrient levels, decreased with alewife biomass but only at low nutrient levels, and did not respond significantly to dreissenids (Fig. 3.10a). Responses of Gizzard shad 1+ biomass to stressors were somewhat similar to those of Gizzard shad 0, except that responses to alewife scenarios were < 25% at all nutrient levels and responses to dreissenid biomass was positive although changes were also < 25% (Fig. 3.10b).

### ***Benthos groups***

Biomass of Dreissenids increased with nutrients but was not affected by alewife biomass (Table 3.6). Biomass of Amphipods and Chironomids responded similarly to stressors: both did not respond to alewife biomass, but increased with increasing dreissenid biomass and increased with nutrients in high dreissenid scenarios (Fig. 3.11a–b). Sphaeriids biomass responded positively to increases in nutrients and alewife biomass (< 25% change), but did not change with increasing dreissenid biomass scenarios (Fig. 3.11c). Oligochaetes biomass was highest in average nutrient scenarios, showed no response to increasing alewife biomass, and strongly decreased at high dreissenid scenarios (Fig. 3.11d).

### ***Zooplankton groups***

Except Nauplii and Rotifers, biomass of all zooplankton groups increased with increasing nutrient loads and decreased with increasing levels of alewives (Table 3.6, Fig. 3.12a–d). Nauplii biomass responded positively to increases in nutrient levels but changes were < 25%, and did not respond to alewife scenarios (Fig. 3.12e). Rotifers biomass increased with both nutrient loads and alewife biomass (Fig. 3.12f). Responses to dreissenid scenarios varied among zooplankton groups: Predatory cladocerans and Cladocerans showed no response (Fig 3.12a–b) while the other groups negatively responded (Fig 3.12c–f). However, changes in Nauplii biomass were < 25% in response to dreissenid scenarios.

### ***Protozoa, Bacteria, and producer groups***

Biomass of Protozoa and Bacteria both positively responded to nutrients and significantly increased with increasing alewife biomass but with < 25% change (Table 3.6). Biomass of Protozoa was negatively affected by dreissenids (Fig 3.13a). Biomass of Bacteria significantly decreased with increasing dreissenid biomass but changes were < 25% (Fig 3.13b).

Biomass of Inedible phytoplankton and Edible phytoplankton responded positively to increases in nutrient loads, did not respond to dreissenid scenarios, and had variable responses to alewife scenarios (Table 3.6). While Edible phytoplankton responded positively (< 25% change) to alewife scenarios, Inedible phytoplankton was not affected. Inedible phytoplankton biomass more than doubled from low to average nutrients scenarios and further increased by a factor of five under high nutrient scenarios (Fig. 3.13c). Responses of Edible phytoplankton to nutrients were more moderate than Inedible phytoplankton (Fig. 3.13d).

Biomass of Macrophytes did not respond to dreissenids, but responded negatively to nutrients and also to increases in alewife biomass but change was < 25% (Table 3.6). Biomass of Macrophytes had strong and nonlinear responses to nutrients with minor increase at average levels and strong decrease at high levels (Fig. 3.13e).

### ***Detritus groups***

Biomass of Pelagic detritus and Settled detritus both increased with increasing nutrients levels but did not respond to alewife scenarios (Table 3.6). Biomass of Pelagic detritus showed little response to increases in dreissenid biomass but biomass of Settled detritus increased with increasing levels of dreissenids (Table 3.6). There was some increase in biomass of Pelagic detritus within alewife scenarios at low nutrient level and an overall decrease at high dreissenid level (Fig. 3.14a). Biomass of Settled detritus was higher in average and high nutrient scenarios than in low nutrient scenarios (Fig. 3.14b).

## **3.5 Discussion**

### **3.5.1 Overview and synthesis of model results**

Our results indicate that the Saginaw Bay food web was influenced more by nutrients and alewives than by dreissenids. Most groups across trophic levels responded positively to increasing nutrient scenarios, and few groups of fish and zooplankton responded negatively to increasing alewife scenarios. Responses to increasing dreissenids were relatively modest, although benthivorous fish groups increased greatly and several zooplankton groups decreased.

Most food web groups in our analysis were positively affected by simulated nutrient increases through enhanced productivity. Among the five food web groups that responded



negatively to nutrients, Open lake predators and Spottail shiner were impacted by nutrient-induced increases of Walleye 2+ through competition and predation. Freshwater drum and Round goby in high dreissenid scenarios were negatively affected by competitors such as yellow perch which were enhanced in high nutrient scenarios. Finally, Macrophytes were negatively affected by shading from nutrient-enhanced increases in plankton and pelagic detritus.

Evidence for nutrient influences on lake ecosystems through empirical correlations is extensive. Positive relationships between phosphorous concentrations and phytoplankton biomass (chlorophyll *a*) have been often reported (Cha et al., 2013; Stow et al., 2014; Vollenweider, 1976; Vollenweider et al., 1974). Nalepa et al. (2007) reported positive relationships between nutrients and benthos biomass in Great Lakes ecosystems. Ludsin et al. (2001) reported biomass declines of Lake Erie benthos, phytoplankton and zooplankton as nutrients declined. There are reports of positive relationships between nutrients and chlorophyll *a*, zooplankton biomass, and fish production (Downing et al., 1990; Egertson and Downing, 2004; Hanson and Peters, 1984; Oglesby, 1977; Plante and Downing, 1993). Pace et al. (1999) found that nutrients have greater influence on upper trophic levels in absence of top predators. Our analysis supports the above literature by considering interactions between nutrient loading and other stressors.

Increased alewife biomass scenarios had predominantly negative impacts for Saginaw Bay food web groups through predation and indirect effects, and few groups benefited from alewife as prey. Except for Rotifers, zooplankton groups declined as alewife biomass increased because of alewife predation. Biomass of several fish groups declined because of alewife predation on larvae and competition for zooplankton prey (all age stanzas of Walleye, White perch, and Other prey fishes, Yellow perch, Emerald shiner, and Gizzard shad groups depending

on nutrient scenarios). Macrophytes were negatively affected by increased alewife biomass because of lower light conditions owing to lowered grazing pressure from macrozooplankton. Biomass of a few groups increased in response to increased alewife biomass. Among fish groups, the Open lake predator that occupy the bay as adults benefited from alewife as prey because they did not experience alewife-imposed larval mortality, while the Spottail shiner and Nearshore predator groups benefited by reduced predation and competition from adult Walleye and Yellow perch groups, owing to alewife predation on their young-of-the-year (YOY) stanzas. Under high nutrient scenarios, Yellow perch 1–2 and 3+ and Emerald shiner 0.5+ also benefited from increased alewife biomass as they could compensate for higher larval mortality through rapid growth and biomass increase after attaining a size (age stanza) at which they can escape predation. Lower food web groups that increased with alewife biomass, i.e. Rotifers, Protozoa, Bacteria, and Edible phytoplankton, responded to reduced predation from lower macrozooplankton biomass. Sphaeriids benefited from reduced competition for microzooplankton with macrozooplankton.

Alewife impacts on Great Lakes food webs have been well documented. Negative effects from alewives on fish have been related to competition for food and near shore spawning habitat (Smith, 1970), and larval and egg predation. Madenjian et al. (2008) found that greatest alewife negative impacts were through predation on larvae of lake trout (*Salvelinus namaycush*), yellow perch, walleye, rainbow smelt, and emerald shiner eggs and fry, with lesser impacts through early mortality syndrome on coho salmon (*Oncorhynchus kisutch*) and lake trout. In shallow habitats like Saginaw Bay, larvae of many fishes have been reported as prey of adult alewives, including walleye (Brooking et al., 1998), yellow perch (Brandt et al., 1987), and centrarchid fishes (Kohler and Ney, 1980). Positive effects of alewives as forage fish for salmonines have

been reported by Bence et al. (2008) and Thayer and Loftus (2012), among others. This exotic species, originally considered a nuisance, has become a valuable resource after Chinook salmon, introduced as their biological control, became a favorite target of recreational fisheries (Tody and Tanner, 1966).

In our food web analysis, simulated dreissenid increases had positive effects on most groups and directed energy from pelagic to benthic pathways. Benthivorous fish benefited from increased biomass of dreissenids as prey and from dreissenid-induced increases in biomass of benthos groups. Nearshore predator and Open lake predator groups benefited from increased dreissenid biomass because of overall increases in prey fish biomass. The only fish groups negatively affected were Emerald shiner groups because of their unique reliance on zooplankton. Most zooplankton groups and to a lesser extent Protozoa were negatively affected by predation and competition for food. Edible phytoplankton did not show declining trends in our simulations because dreissenids also caused declines in zooplankton groups, which are more efficient filter feeders than dreissenids (as derived from McNaught et al. (1980) and Fanslow et al. (1995)). Among benthos groups, only Oligochaetes negatively responded to dreissenid-induced reduction of detrital material.

As observed for other Great Lakes ecosystems, our results show dreissenid-mediated shifts in production from pelagic to benthic pathways with variable consequences. The benthic pathway was important in the Saginaw Bay food web before dreissenid invasions. According to the 1990 Ecopath model, about 50% of primary production entered the detrital pathway and 45% of non-predatory zooplankton and benthos group diets originated from detritus. Thus, further dreissenid shifting of energy was not detrimental to fish. Our results are consistent with a meta-analysis on effects of dreissenids on ecosystems across North America and Eurasia, which

highlighted dreissenids' ability to shift energy flows (Higgins and Vander Zanden, 2010). Similar impacts of dreissenid-induced shunt to benthic pathways have been described for Great Lakes ecosystems by Hecky et al. (2004) and Vanderploeg et al. (2002). In oligotrophic lake ecosystems with predominant pelagic pathways, such as the main basins of Lakes Ontario, Michigan, and Huron, stronger dreissenid impacts were documented on the lower food webs than we found in our Saginaw Bay analysis (Barbiero et al., 2009; Fahnenstiel et al., 2010; Haynes et al., 2005; Nalepa et al., 2006, 2007; Stewart et al., 2010; Vanderploeg et al., 2010, 2012). These results suggest that dreissenid effects on lake food webs will depend on nutrients and energy pathways.

### **3.5.2 Model–data comparisons**

Projections in our simulations can help interpret long-term effects of nutrients, alewife and dreissenids on the Saginaw Bay food web. Correlations between nutrients, dreissenids and benthos trends have been observed between 1950 and 1996 (Nalepa et al., 2003). Nutrients and biomass of oligochaetes and chironomids increased from the mid-1950s to the early 1970s, equivalent to our results of response to nutrient increases from low to average scenarios. From the 1970s to late 1980s, nutrients decreased and benthos biomass remained stable. Nalepa et al. (2003) argued that stability of benthos biomass was unexpected, particularly for oligochaetes, given decreases in Great Lakes ecosystems after phosphorus abatement programs. Our results suggest that nutrient decreases were not enough to affect benthos. After 1990, nutrient loads were stable, and when dreissenids peaked in abundance, oligochaetes decreased temporarily, chironomids fluctuated with no trend, and amphipods (except *Diporeia* spp.) increased. Our

results indicate that dreissenid effects on benthos occur only at high dreissenid biomass and also that nutrient effects would be stronger (positive and negative) at high dreissenid biomass.

Our results also help explain drivers of walleye and yellow perch abundance trends observed since the 1970s (Adlerstein et al., 2007; Fielder and Thomas, 2006; Ivan et al., 2011). From 1980 to 2003, abundance of age 2 and older walleye decreased and younger walleye ages fluctuated with no trend, while after 2003, when alewife population collapsed, abundance of all ages increased. The walleye decline has been related to habitat degradation and overfishing, low prey abundance, and alewife and rainbow smelt predation (Fielder, 2002; Schneider and Leach, 1977). Our results showed that trends of all Walleye stanzas were driven by alewife predation and decreases in nutrients, and that the strong walleye recovery was possible after the alewife population collapsed and also under average nutrient conditions. Notably, our results showed that even in absence of alewives, declines in nutrients from high to low scenarios would cause a 60% reduction in Walleye 2+ biomass. Yellow perch abundance showed fluctuating trends since the 1970s. Reproductive success of yellow perch also has been related to changes in alewife biomass, and declining perch trends from 1980s to 2008 were attributed partially to increase in walleye predation (Fielder and Thomas, 2006; Roswell, 2011). Our simulations indicated that biomass of YOY yellow perch and walleye would increase with alewife decreases. Thus, although predation mortality of YOY yellow perch decreased with alewife collapse, increased adult walleye biomass allowed them to control older yellow perch stanzas.

### **3.5.3 Model–model comparisons**

Despite differences in ecosystem productivity and food web structure, effects of invasive species on predators and recovery of native fish species reported by other EwE investigations

were generally similar to those we found in Saginaw Bay but occurred through diverse mechanisms. Kitchell et al. (2000) used an Ecosim model to investigate dreissenid effects on the Lake Superior food web. The authors found that dreissenids-induced decline in native *Diporeia* spp. would negatively affect sculpins and other benthivores, which would cause increases in biomass of *Mysis diluviana* and its exotic predators, rainbow smelt and salmonines. In Saginaw Bay, benthos is dominated by chironomids that were not affected by dreissenids. Thus, in contrast to Kitchell et al.'s (2000) results, our analysis of Saginaw Bay showed that effects of dreissenids were positive for benthivores through increased prey.

Further analysis of Lake Superior by Cox and Kitchell (2004) showed that declines in rainbow smelt (playing a similar role to alewives in Saginaw Bay) caused by lake trout predation would allow recovery of native lake herring (*Coregonus artedii*). In our analysis, alewife declines also permitted recovery of native prey.

Dreissenid enhancement of salmonines was reported in Lake Ontario by Stewart and Sprules (2011) using an Ecopath analysis. This is similar to our Saginaw Bay results where Open lake (salmonine) predators were enhanced by dreissenid-induced increase in benthivorous fish groups. Also in both analyses, dreissenids limited nutrient transfer from nearshore to offshore areas. Thus, although dreissenids can reduce nutrient transfer and shunt energy to the benthos, predators such as Chinook salmon that feed as juveniles on benthic prey and zooplankton in nearshore areas can redirect energy to offshore pelagic systems.

Also for Lake Ontario, Hossain et al. (2012) used Ecopath to analyze how eutrophication and dreissenids have affected the Hamilton Harbour food web. The authors argued that although nutrient loading reductions achieved since 1992 were sufficient to bring the system to the present state, further reduction alone would not result in predator biomass increases. This result agrees

with our finding that increases in walleye biomass in Saginaw Bay could only be achieved after reduction of alewives.

Finally and also for Lake Ontario, Blukacz-Richards and Koops (2012) used Ecopath to evaluate Bay of Quinte improvements of beneficial use impairments (BUIs) through bottom-up controls. Results were not consistent with our findings and showed that phytoplankton reduction caused biomass increases in most fish groups except for Walleye, whereas in Saginaw Bay we found a positive effect of nutrients (which increased phytoplankton) for fish groups except Spottail shiner. Nevertheless, dreissenid biomass in the Bay of Quinte was about 8 times higher than our high dreissenid scenario, which precludes further elaboration and comparison.

#### **3.5.4 Potential model biases**

There are potential biases associated with our EwE analysis of multiple-stressor impacts on the Saginaw Bay food web. First and foremost, our approach to simulating dreissenid effects probably resulted in understating their impacts. It was not possible to run a high dreissenid scenario at the biomass we estimated for the 1992 historical peak as the model crashed over the simulation period, indicating that level is not sustainable. We then reduced biomass to the 1991 to 1996 average, which is about 35% of the peak. Thus, our results would not capture short term responses to peak biomass or their consequences for the food web.

Our analysis does not capture annual changes in species composition within Saginaw Bay lower food web groups. Phytoplankton composition changed as dreissenid filtration increased water clarity and caused a shift from light-intolerant to light-tolerant species (Adlerstein et al., 2013; Fishman et al., 2009, 2010). Zooplankton composition changed after alewife collapsed: among cladocerans, abundance of *Bosmina longirostris* decreased and *Daphnia galeata*

increased; among cyclopoids, *Cyclops* spp. decreased while other species increased; and among predatory cladocerans, *Bythotrephes cederstroemii* increased and *Leptodora kindti* remained stable (Pothoven et al., 2013). This should not have significant consequences for our results as  $P/B$  and  $Q/B$  ratios of lower food web groups remain relatively constant regardless of species composition (Shuter and Ing, 1997; Straile, 1997).

Seasonal dynamics are not captured by the EwE modeling approach parameterized to represent an annual average. Seasonal variation is characteristic of Saginaw Bay phytoplankton abundance (Stoermer and Theriot, 1985) and zooplankton grazing (McNaught et al., 1980), as in other Great Lakes ecosystems where the EwE approach has been applied. However, impacts are likely minimal of ignoring seasonality in lower trophic level dynamics because input parameters were estimated with data collected throughout the growing season.

We included two detritus groups in our model although EwE is not designed to handle flow among detritus pools. The inability of EwE to model this flow is a known flaw of the software. We configured a Pelagic detritus group and a Settled detritus group to represent materials available to filter and deposit feeders, but in our model the unused production of Pelagic detritus will not flow into Settled detritus and unused Settled detritus will not accumulate. Underestimating Settled detritus in the Saginaw Bay food web should have minimal effects on our results given that model outputs show that Settled detritus is not limiting production of detritivores in the system.

There are possible shortcomings in our analysis derived from characteristics of available biomass input data for lower food web groups. Limitations on data from these levels are typical for ecosystems worldwide and continue to limit food web modeling (van Oevelen et al., 2010). For groups such as Sphaeriids, lack of contrast within the short time series affected our ability to



model their dynamics in simulations. Limitations on phytoplankton inputs relate to suspected biomass bias (Fishman et al., 2009). We expect that moderate bias in phytoplankton biomass would not affect vulnerability parameters estimation and overall fit in our analysis because producer biomass is controlled by nutrient loads and consumption by zooplankton and benthos.

Finally, physical habitat information or spatial complexity of the Saginaw Bay ecosystem was not fully incorporated in the food web model. For example, effects of currents and temperature are largely ignored. Nevertheless, we incorporated understanding of spatial and temporal dynamics into our biomass estimates and into concepts of prey vulnerability, which alleviates spatial effects that could influence our results.

### **3.5.5 Management implications**

Our model results have implications for achieving nutrient loading targets at the possible expense of maintaining biomass of key sport fishes. Bottom-up regulation of nutrients remains a management strategy to mitigate beneficial use impairments (BUIs) of the Saginaw Bay ecosystem (Michigan Department of Environmental Quality, 2012). Based on our results, in particular given the presence of dreissenids, it is necessary to consider that target nutrient loads might be underestimated. Although high nutrient levels in our simulation scenarios caused high biomass of inedible (blue green) phytoplankton, which would cause undesirable conditions known to produce bad odor and taste of drinking water, low target nutrients in several scenarios resulted in severe reductions of some model groups at different food web levels. In particular, most fish groups responded with lower biomass to decreases in nutrient levels, and at low nutrient levels dreissenids had a more negative effect. Therefore, managers may want to reconsider reductions in nutrient loadings for Saginaw Bay given that target levels of phosphorus

loads would likely result in lower biomass of walleye and yellow perch, and that dreissenid impacts would be most harmful at low nutrient load scenarios. Our model may be used to explore tradeoffs between desirable levels of nutrient loads and fisheries biomass.

**Table 3.1** Saginaw Bay food web groups in the Ecopath with Ecosim model.

Group (stanza age)	Scientific name or main taxa in the group
<b>Fish Groups</b>	
Open lake predators	<i>Oncorhynchus tshawytscha</i> and <i>Salvelinus namaycush</i>
Nearshore predators	<i>Esox lucius</i> and <i>Micropterus dolomieu</i>
Walleye (0–0.5, 0.5–1, 1, 2+)	<i>Sander vitreus</i>
Yellow perch (0–0.5, 0.5–1, 1–2, 3+)	<i>Perca flavescens</i>
Freshwater drum	<i>Aplodinotus grunniens</i>
Common carp	<i>Cyprinus carpio</i>
Lake whitefish	<i>Coregonus clupeaformis</i>
Channel catfish	<i>Ictalurus punctatus</i>
White sucker	<i>Catostomus commersonii</i>
White perch (0, 1+)	<i>Morone americana</i>
Rainbow smelt (0, 1+)	<i>Osmerus mordax</i>
Alewife (0, 1+)	<i>Alosa pseudoharengus</i>
Gizzard shad (0, 1+)	<i>Dorosoma cepedianum</i>
Emerald shiner (0–0.5, 0.5–1)	<i>Notropis atherinoides</i>
Spottail shiner	<i>Notropis hudsonius</i>
Trout perch	<i>Percopsis omiscomaycus</i>
Round goby	<i>Neogobius melanostomus</i>
Other prey fishes	<i>Carpiodes cyprinus</i> , <i>Ictiobus</i> spp. and <i>Lepomis</i> spp.
<b>Benthos Groups</b>	
Dreissenids	<i>Dreissena polymorpha</i> and <i>D. bugensis</i>
Amphipods	<i>Gammarus</i> spp. and <i>Diporeia</i> spp.
Sphaeriids	<i>Pisidium</i> spp.
Chironomids	Chironomidae larvae and pupae stages
Oligochaetes	Naididae and tubificidae
<b>Zooplankton Groups</b>	
Predatory Cladocerans	<i>Leptodora kindti</i> and <i>Bythotrephes cederstroemii</i>
Cladocerans	Non-predatory <i>Bosmina longirostris</i> and <i>Daphnia</i> spp.
Cyclopoids	<i>Diacyclops bicuspidatus</i> , <i>Tropocyclops prasinus mexicanus</i> after nauplius stage
Calanoids	<i>Leptodiaptomus</i> spp. after nauplius stage
Nauplii	Copepods at nauplius stage
Rotifers	<i>Keratella</i> spp., <i>Synchaeta</i> spp., and <i>Ploesoma</i> spp.
<b>Micro-organism Groups</b>	
Protozoa	Heterotrophic chrysophytes, cryptomonads, dinoflagellates, flagellates, and ciliates
Bacteria	Pelagic bacteria
<b>Producer Groups</b>	
Inedible phytoplankton	Cyanophytes
Edible phytoplankton	Bacillariophytes, chlorophytes and autotrophic genera of chrysophytes, cryptomonads, dinoflagellates, and flagellates
Macrophytes	Benthic vascular plants
<b>Detritus Groups</b>	
Pelagic detritus	Dissolved and suspended organic matter in the water column
Settled detritus	Organic matter settled to the bottom

**Table 3.2** Input parameters in the 1990 Saginaw Bay Ecopath model. Parameters estimated by the model are in bold. *P/B* is production to biomass ratio for groups with only one stanza, *Z* is total mortality rate for multi-stanza groups, *Q/B* is consumption to biomass ratio, and *U/Q* is proportion of unassimilated food in consumption. Trophic level is estimated by Ecopath based on diet composition. Harvest is the total yield of commercial and recreational fisheries per unit area.

Group	Trophic level	Biomass (g/m <sup>2</sup> )	<i>P/B</i> or <i>Z</i> (1/yr)	<i>Q/B</i> (1/yr)	<i>U/Q</i>	Ecotrophic efficiency	Harvest (g×100 <sup>-1</sup> ×m <sup>-2</sup> )
Open lake predator	<b>4.2</b>	0.20	0.7	5.2	0.23	<b>0.19</b>	2.7
Nearshore predator	<b>4.0</b>	0.10	0.4	3.1	0.17	<b>0.08</b>	0.3
Walleye 0–0.5	<b>3.1</b>	<b>0.01</b>	4.6	<b>14.2</b>	0.24	<b>0.81</b>	–
Walleye 0.5–1	<b>4.0</b>	<b>0.04</b>	1.9	<b>6.5</b>	0.18	<b>0.08</b>	–
Walleye 1	<b>3.9</b>	<b>0.19</b>	0.3	<b>3.7</b>	0.18	<b>0.01</b>	–
Walleye 2+	<b>3.9</b>	1.93	0.4	2.3	0.18	<b>0.06</b>	2.9
Yellow perch 0–0.5	<b>3.1</b>	<b>0.03</b>	5.5	<b>43.0</b>	0.30	<b>0.86</b>	–
Yellow perch 0.5–1	<b>3.1</b>	<b>0.09</b>	2.7	<b>18.7</b>	0.30	<b>0.45</b>	–
Yellow perch 1–2	<b>3.2</b>	0.71	1.0	8.5	0.21	<b>0.33</b>	–
Yellow perch 3+	<b>3.3</b>	<b>0.29</b>	1.6	<b>5.5</b>	0.21	<b>0.40</b>	4.2
Freshwater drum	<b>3.3</b>	0.33	0.7	3.9	0.24	<b>0.13</b>	1.0
Common carp	<b>2.4</b>	1.01	0.3	6.3	0.34	<b>0.37</b>	7.9
Lake whitefish	<b>3.1</b>	0.39	0.7	9.1	0.33	<b>0.39</b>	7.6
Channel catfish	<b>3.1</b>	0.51	0.5	5.2	0.24	<b>0.65</b>	14.7
White sucker	<b>3.1</b>	2.30	0.6	4.5	0.34	<b>0.03</b>	2.4
White perch 0	<b>3.1</b>	1.51	4.6	22.0	0.24	<b>0.06</b>	–
White perch 1+	<b>3.2</b>	<b>1.53</b>	2.3	<b>8.5</b>	0.24	<b>0.02</b>	0.7
Rainbow smelt 0	<b>3.1</b>	0.07	5.5	<b>18.8</b>	0.24	<b>0.74</b>	–
Rainbow smelt 1+	<b>3.3</b>	<b>0.11</b>	1.2	6.2	0.24	<b>0.76</b>	< 0.1
Alewife 0	<b>3.1</b>	0.30	5.0	<b>47.9</b>	0.24	<b>0.49</b>	–
Alewife 1+	<b>3.2</b>	<b>0.56</b>	1.0	17.6	0.24	<b>0.88</b>	–
Gizzard shad 0	<b>2.8</b>	0.99	4.6	<b>29.8</b>	0.34	<b>0.56</b>	–
Gizzard shad 1+	<b>2.3</b>	<b>1.05</b>	1.9	12.0	0.34	<b>0.27</b>	–
Emerald shiner 0–0.5	<b>3.1</b>	<b>0.04</b>	4.6	<b>35.0</b>	0.46	<b>0.89</b>	–
Emerald shiner 0.5+	<b>3.1</b>	0.33	2.4	13.3	0.46	<b>0.71</b>	–
Spottail shiner	<b>2.8</b>	0.59	1.7	18.2	0.46	<b>0.82</b>	–
Trout perch	<b>3.1</b>	0.26	1.2	8.1	0.34	<b>0.61</b>	–
Round goby	<b>3.1</b>	0.25	2.4	15.7	0.24	<b>0.64</b>	–
Other prey fishes	<b>3.1</b>	1.00	1.0	7.8	0.21	<b>0.37</b>	–
Dreissenids	<b>2.1</b>	0.40	2.1	15.2	0.66	<b>0.46</b>	–
Amphipods	<b>2.0</b>	0.36	6.2	20.7	0.50	<b>0.46</b>	–
Sphaeriids	<b>2.1</b>	0.27	1.4	24.6	0.50	<b>0.10</b>	–
Chironomids	<b>2.1</b>	24.93	14.4	41.2	0.50	<b>0.31</b>	–
Oligochaetes	<b>2.0</b>	14.60	6.4	19.7	0.50	<b>0.71</b>	–
Predatory cladocerans	<b>3.2</b>	0.01	11.0	43.9	0.40	<b>0.42</b>	–
Cladocerans	<b>2.1</b>	4.74	27.0	108.1	0.40	<b>0.47</b>	–
Cyclopoids	<b>2.2</b>	0.67	15.7	62.9	0.40	<b>0.53</b>	–
Calanoids	<b>2.1</b>	1.03	10.6	42.3	0.40	<b>0.43</b>	–
Nauplii	<b>2.1</b>	0.18	31.4	125.7	0.40	<b>0.31</b>	–
Rotifers	<b>2.2</b>	5.12	38.2	152.7	0.50	<b>0.24</b>	–
Protozoa	<b>2.3</b>	1.19	150	500	0.40	<b>0.72</b>	–
Bacteria	<b>2.0</b>	2.01	110	440	0.40	<b>0.86</b>	–
Inedible phytoplankton	<b>1.0</b>	0.53	310	–	–	<b>0.58</b>	–
Edible phytoplankton	<b>1.0</b>	9.11	245	–	–	<b>0.75</b>	–
Macrophytes	<b>1.0</b>	60	10	–	–	< <b>0.01</b>	–
Pelagic detritus	<b>1.0</b>	140	–	–	–	<b>0.37</b>	–
Settled detritus	<b>1.0</b>	120	–	–	–	<b>0.79</b>	–

**Table 3.3** Diet inputs (%) for groups in the Saginaw Bay Ecopath model and reference sources.

No. Prey	Predator																					
	1 <sup>a</sup>	2 <sup>b</sup>	3 <sup>c</sup>	4 <sup>c</sup>	5 <sup>c</sup>	6 <sup>c</sup>	7 <sup>c</sup>	8 <sup>c</sup>	9 <sup>c</sup>	10 <sup>c</sup>	11 <sup>d</sup>	12 <sup>be</sup>	13 <sup>f</sup>	14 <sup>d</sup>	15 <sup>g</sup>	16 <sup>h</sup>	17 <sup>i</sup>	18 <sup>j</sup>	19 <sup>j</sup>	20 <sup>k</sup>	21 <sup>k</sup>	
1 Open lake predator																						
2 Nearshore predator																						
3 Walleye 0–0.5 (×10)		1.8							0.1	0.4												3.3
4 Walleye 0.5–1		0.3			0.1	0.1																
5 Walleye 1		0.2																				
6 Walleye 2+		3.0																				
7 Yellow perch 0–0.5		0.7			0.3	0.2			0.2	0.5	0.3											1.0
8 Yellow perch 0.5–1		1.1		1.5	1.6	0.3			0.2	0.7	0.4			0.5			0.3					
9 Yellow perch 1–2	6.1	3.1			4.5	2.5					1.2											
10 Yellow perch 3+	4.0	2.0			3.0	1.7																
11 Freshwater drum		0.9									0.4			0.4								
12 Common carp		1.2									0.5			0.5								
13 Lake whitefish	2.3	1.2																				
14 Channel catfish		1.0																				
15 White sucker		6.1																				
16 White perch 0		6.0		2.9	3.0	1.7			0.5	1.4	2.4						1.5					
17 White perch 1+		3.0			1.5	0.8					1.2											
18 Rainbow smelt 0	3.3	1.7		8.0	2.4	1.4			0.4	1.1	0.7			0.7			0.4		3.3			
19 Rainbow smelt 1+	3.3	0.5		2.6	0.8	0.5					0.2			0.2			0.1					
20 Alewife 0	12.8	6.4		31.0	9.5	5.4			1.5	4.4	2.6											
21 Alewife 1+	13.8	2.3			3.4	6.5					0.9											
22 Gizzard shad 0		19.8		28.5	29.1	16.5			4.5	13.4	7.9			8.5			5.1					
23 Gizzard shad 1+		8.7			12.8	7.2								3.7								
24 E. shiner 0–0.5		0.8		2.4	1.2	0.2			0.2	0.6									1.6		1.1	
25 E. shiner 0.5+	6.7	3.4		4.9	10.0	5.6			0.8	2.3	1.4								6.6			
26 Spottail shiner		4.3		6.2	12.7	7.2			1.0	2.9	1.7			1.9			1.1		8.5			
27 Trout perch	2.7	1.4		2.0	0.7	0.4			0.3	0.9	0.5		1.7	0.6			0.1					
28 Round goby	5.2	7.8		3.8	1.3	0.7			0.6	1.8	1.0		3.3	1.1			0.2					
29 Other prey fishes		13.0		6.3	2.1	1.2					1.7			1.9			1.1					
30 Dreissenids								0.1	0.1	0.1	3.5	0.1	3.9	0.1	0.2		0.1					
31 Amphipods (×10)			2.5				1.2	3.7	3.9	3.4	92.2	1.9	104.0	2.5	4.4	3.4	2.9	0.2	1.0	0.2	1.1	
32 Sphaeriids (×10)							0.6	0.7	0.6	0.5	0.3	0.6	0.4	0.7		0.5						
33 Chironomids			39.5				19.7	59.1	63.0	55.1	49.4	29.9	56.0	39.4	70.9	55.3	47.2	4.0	15.8	4.0	17.8	
34 Oligochaetes			10.3				5.1	15.4	16.4	14.3	12.9	7.8	14.6	10.2	18.4	14.4	12.3	1.0	4.1	1.0	4.6	
35 Pred. cladocerans (×10)			0.4				0.7	0.2	0.1			0.0	0.1	0.1	0.1	0.3	0.3	0.8	0.6	0.8	0.7	
36 Cladocerans			36.6				54.9	18.3	8.0			1.8	8.9	13.3	8.9	21.9	23.9	69.5	47.8	69.5	59.7	
37 Cyclopoids			3.0				4.5	1.5	1.3			0.1	0.4	0.5	0.4	1.8	3.9	5.7	7.8	5.7	9.8	
38 Calanoids			3.1				4.7	1.6	0.7			0.1	0.4	0.6	0.4	1.9	2.1	6.0	4.1	6.0	5.1	
39 Nauplii (×10)			16.5				24.8	8.3	0.4			0.0	0.2	0.3	0.2	9.9	1.1	31.4	2.2	31.4	2.7	
40 Rotifers			5.6				8.4	2.8				0.1	0.3	0.5	0.3	3.4		10.6		10.6		
41 Protozoa																						
42 Bacteria																						
43 Inedible phyt.																						
44 Edible phyt.														10.0								
45 Macrophytes														10.0								
46 Pelagic detritus																						
47 Settled detritus													40.0		15.0							

**Table 3.3 Continued.**

No. Prey	Predator																					
	22 <sup>d</sup>	23 <sup>d</sup>	24 <sup>l</sup>	25 <sup>l</sup>	26 <sup>dl</sup>	27 <sup>d</sup>	28 <sup>m</sup>	29 <sup>b</sup>	30 <sup>n</sup>	31 <sup>o</sup>	32 <sup>o</sup>	33 <sup>o</sup>	34 <sup>o</sup>	35 <sup>o</sup>	36 <sup>p</sup>	37 <sup>o</sup>	38 <sup>o</sup>	39 <sup>o</sup>	40 <sup>o</sup>	41 <sup>o</sup>	42 <sup>o</sup>	
1	Open lake predator																					
2	Nearshore predator																					
3	Walleye 0–0.5 (×10)																					
4	Walleye 0.5–1																					
5	Walleye 1																					
6	Walleye 2+																					
7	Yellow perch 0–0.5																					
8	Yellow perch 0.5–1																					
9	Yellow perch 1–2																					
10	Yellow perch 3+																					
11	Freshwater drum																					
12	Common carp																					
13	Lake whitefish																					
14	Channel catfish																					
15	White sucker																					
16	White perch 0																					
17	White perch 1+																					
18	Rainbow smelt 0																					
19	Rainbow smelt 1+																					
20	Alewife 0																					
21	Alewife 1+																					
22	Gizzard shad 0																					
23	Gizzard shad 1+																					
24	E. shiner 0–0.5																					
25	E. shiner 0.5+																					
26	Spottail shiner																					
27	Trout perch																					
28	Round goby																					
29	Other prey fishes																					
30	Dreissenids																					
31	Amphipods (×10)																					
32	Sphaeriids (×10)																					
33	Chironomids																					
34	Oligochaetes																					
35	Pred. cladocerans (×10)																					
36	Cladocerans																					
37	Cyclopoids																					
38	Calanoids																					
39	Nauplii (×10)																					
40	Rotifers																					
41	Protozoa																					
42	Bacteria																					
43	Inedible phyt.																					
44	Edible phyt.																					
45	Macrophytes																					
46	Pelagic detritus																					
47	Settled detritus																					

<sup>a</sup> Dobiesz (2003); <sup>b</sup> Froese and Pauly (2013); <sup>c</sup> Hass and Schaeffer (1992); <sup>d</sup> Price (1963); <sup>e</sup> Garcia-Berthou (2001) and King and Hunt (1967); <sup>f</sup> Pothoven and Nalepa (2006); <sup>g</sup> Tremblay and Magnan (1991); <sup>h</sup> Prout et al. (1990); <sup>i</sup> Parrish and Margraf (1990); <sup>j</sup> Price (1963) and Pothoven et al. (2009); <sup>k</sup> Pothoven and Madenjian (2008); <sup>l</sup> Hartman et al. (1992) and Pothoven et al. (2009); <sup>m</sup> Taraborelli et al. (2010); <sup>n</sup> MacIsaac et al. (1991); <sup>o</sup> Leidy and Ploskey (1980), Balcer et al. (1984), Wetzel (2001) and Thorp and Covich (2010); <sup>p</sup> Balcer et al. (1984) and Vanderploeg et al. (1993).

**Table 3.4** Parameters used to link multi-stanza groups in the Ecopath model:  $k$  is the growth constant in the von Bertalanffy growth model and  $w_m/w_{inf}$  is the ratio of weight at maturity to asymptotic weight.

Group	$k$ (1/yr)	$w_m/w_{inf}$
Walleye	0.53	0.28
Yellow Perch	0.33	0.17
Freshwater drum	0.19	0.20
White perch	0.42	0.28
Rainbow smelt	0.59	0.33
Alewife	0.77	0.32
Gizzard shad	0.61	0.35
Emerald shiner	0.87	0.13

**Table 3.5** Scenarios in Saginaw Bay food web model simulations.

Factor	Level	Code
Nutrient	Low (target phosphorus loads)	N0
	Average (1990–2009 average phosphorus loads)	N1
	High (1974 phosphorus loads)	N2
Alewife	Absence	A0
	Average (1990–2003 average biomass)	A1
	High ( $2.0 \times$ 1990–2003 average biomass)	A2
Dreissenid	Absence	D0
	Low ( $0.2 \times$ 1991–1996 average biomass)	D1
	High (1991–1996 average biomass)	D2

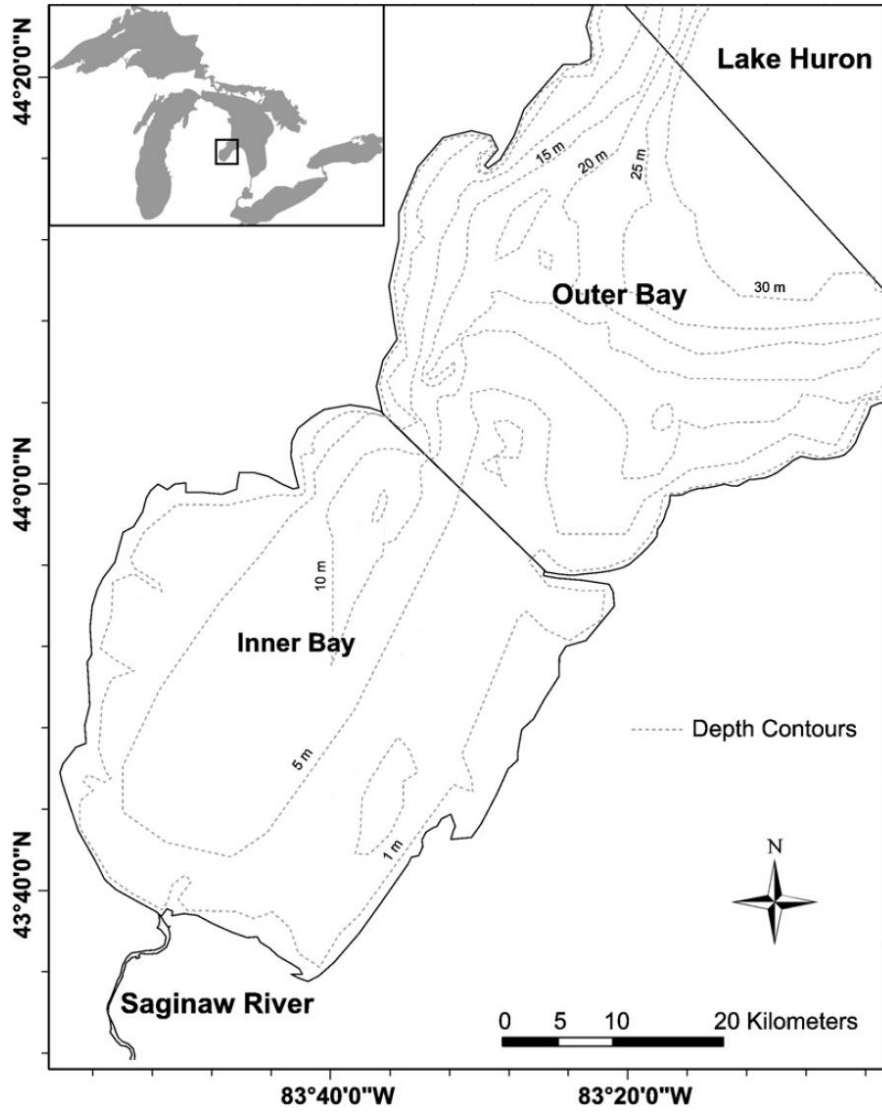
**Table 3.6** Summary of Ecosim results based on linear models indicating overall effects of nutrient and invasive species scenarios on biomass of Saginaw Bay food web groups. Positive or negative indicates that the effect is significant at the 95% confidence level and change is > 25% in relative biomass among simulation scenarios; No effect+ indicates that the trend is significant and positive but change is < 25%; No effect- indicates that the trend is significant and negative but change is < 25%; and No effect indicates that the trend is not significant.

	Scenario			Interaction
	Nutrient	Alewife	Dreissenid	
Open lake predator	Negative	Positive	Positive	
Nearshore predator	No effect+	No effect+	Positive	
Walleye 0–0.5	Positive	Negative	No effect	
Walleye 0.5–1	Positive	Negative	No effect	
Walleye 1	Positive	Negative	No effect	
Walleye 2+	Positive	Negative	No effect	
Yellow perch 0–0.5	Positive	Negative	No effect	
Yellow perch 0.5–1	Positive	Negative	No effect	
Yellow perch 1–2	Positive	Interaction	No effect	Negative: Alewife/Low nutrient Positive: Alewife/Ave. & high nutrient
Yellow perch 3+	Positive	Interaction	Interaction	Negative: Alewife/Low nutrient Positive: Alewife/Ave. & high nutrient Positive: Dreissenid/Ave. & high nutrient
Freshwater drum	Interaction	No effect	Positive	Negative: Nutrient/High dreissenid
Common carp	Interaction	No effect	Positive	Positive: Nutrient/High dreissenid
Channel catfish	No effect+	No effect	Positive	
White sucker	Interaction	No effect	Positive	Positive: Nutrient/High dreissenid
White perch 0	Positive	Negative	No effect	
White perch 1+	Positive	Negative	No effect	
Gizzard shad 0	Positive	Interaction	No effect	Negative: Alewife/Low nutrient
Gizzard shad 1	Positive	No effect –	No effect+	
Emerald shiner 0–0.5	Positive	Negative	Negative	
Emerald shiner 0.5+	Positive	Interaction	Negative	Positive: Alewife/High nutrient Negative: Alewife/Low & average nutrient
Spottail shiner	Negative	Positive	No effect+	
Trout perch	No effect+	No effect	No effect	
Round goby	Interaction	No effect	Positive	Negative: Nutrient/High dreissenid
Other prey fishes	No effect+	No effect–	No effect+	
Dreissenids	Positive	No effect	—	
Amphipods	Interaction	No effect	Positive	Positive: Nutrient/High dreissenid
Sphaeriids	Positive	No effect+	No effect	
Chironomids	Interaction	No effect	Positive	Positive: Nutrient/High dreissenid
Oligochaetes	Interaction	No effect	Negative	Positive: Nutrient/Absence & low dreissenid Negative: Nutrient/High dreissenid

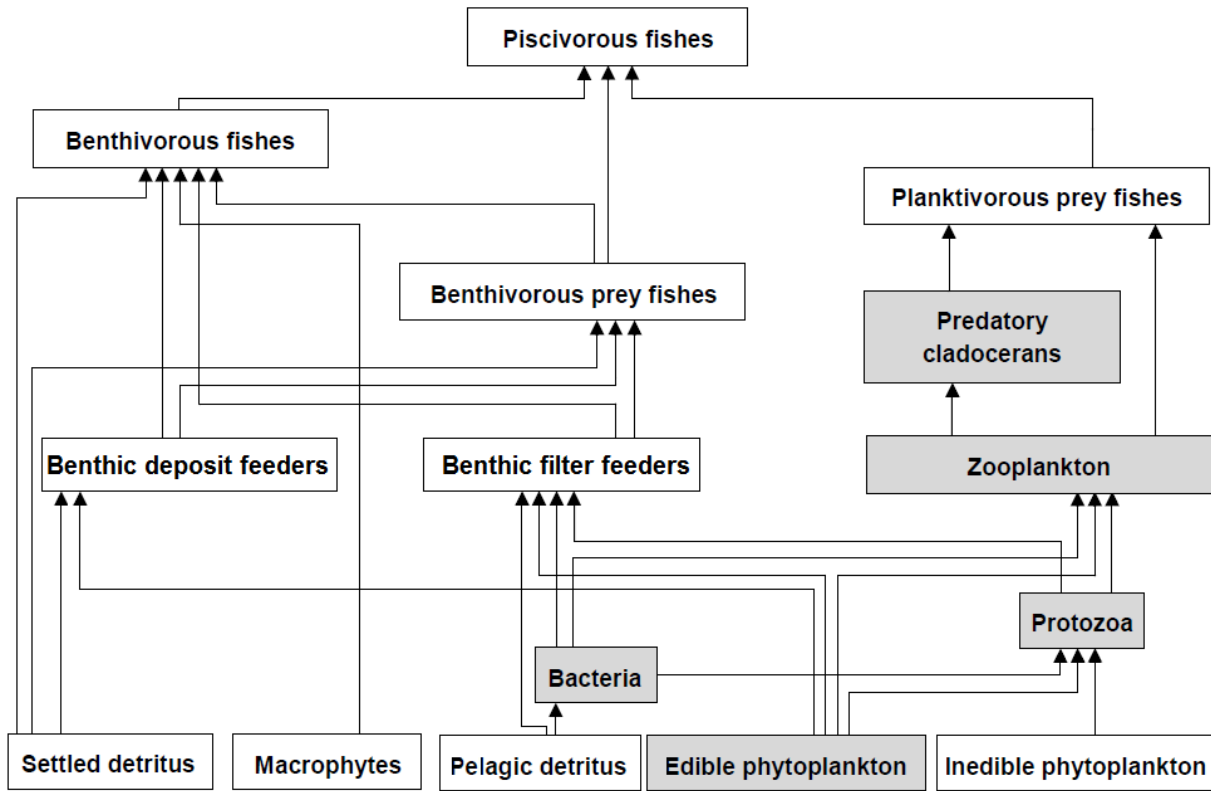


**Table 3.6** *Continued.*

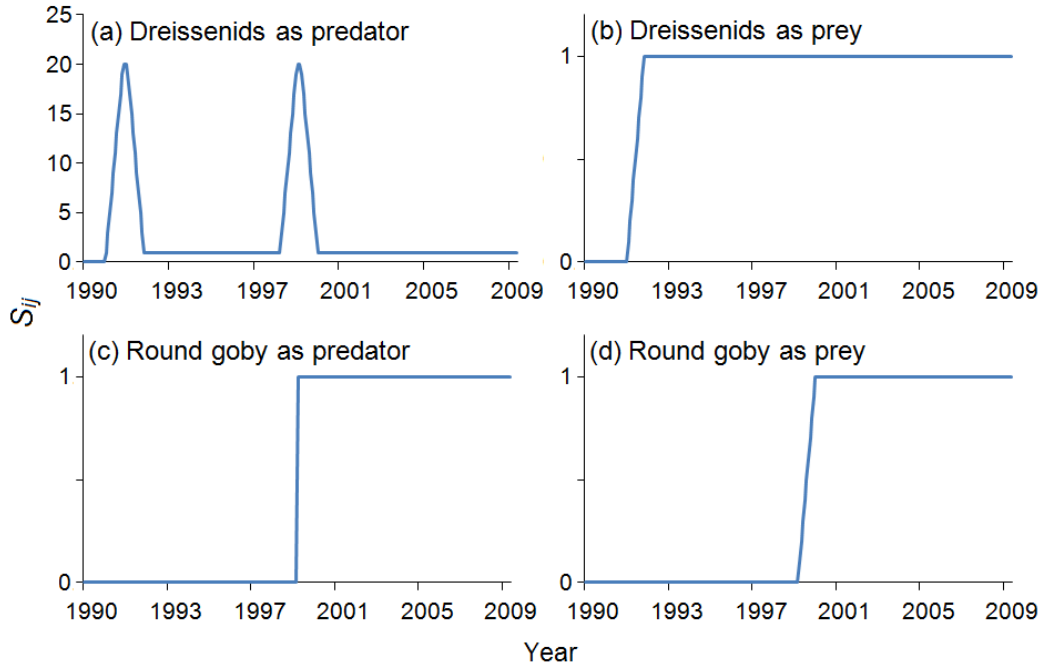
	Scenario			Interaction
	Nutrient	Alewife	Dreissenid	
Predatory cladocerans	Positive	Negative	No effect	
Cladocerans	Positive	Negative	No effect	
Cyclopoids	Positive	Negative	Negative	
Calanoids	Positive	No effect–	Negative	
Nauplii	No effect+	No effect	No effect–	
Rotifers	Positive	Positive	Negative	
Protozoa	Positive	No effect+	No effect–	
Bacteria	Positive	No effect+	Negative	
Inedible phytoplankton	Positive	No effect	No effect	
Edible phytoplankton	Positive	No effect+	No effect	
Macrophytes	Negative	No effect–	No effect	
Pelagic detritus	Positive	No effect	No effect	
Settled detritus	Interaction	No effect	Positive	Positive: Nutrient/High dreissenid



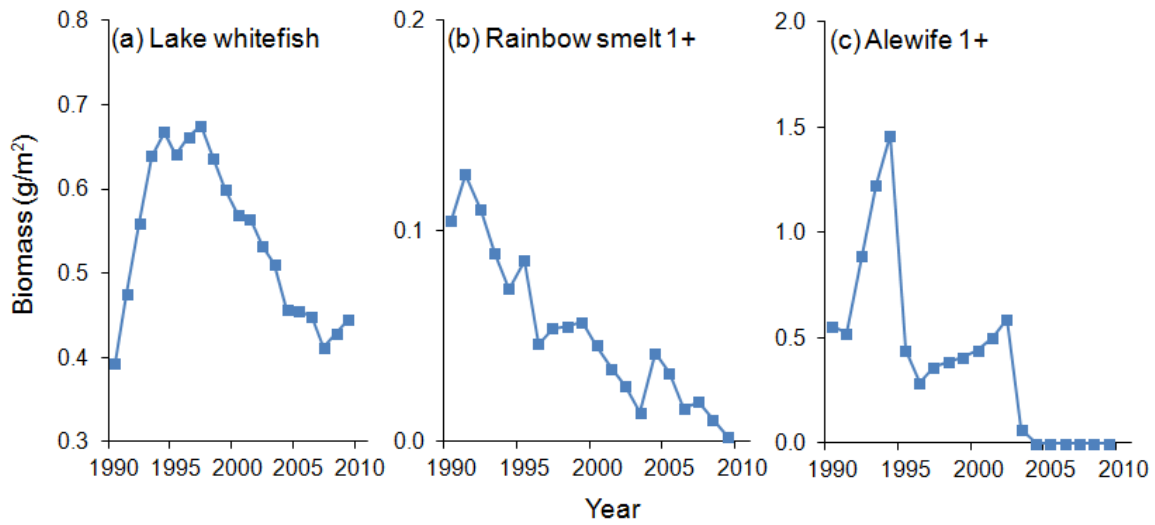
**Figure 3.1** Map of the Saginaw Bay study area.



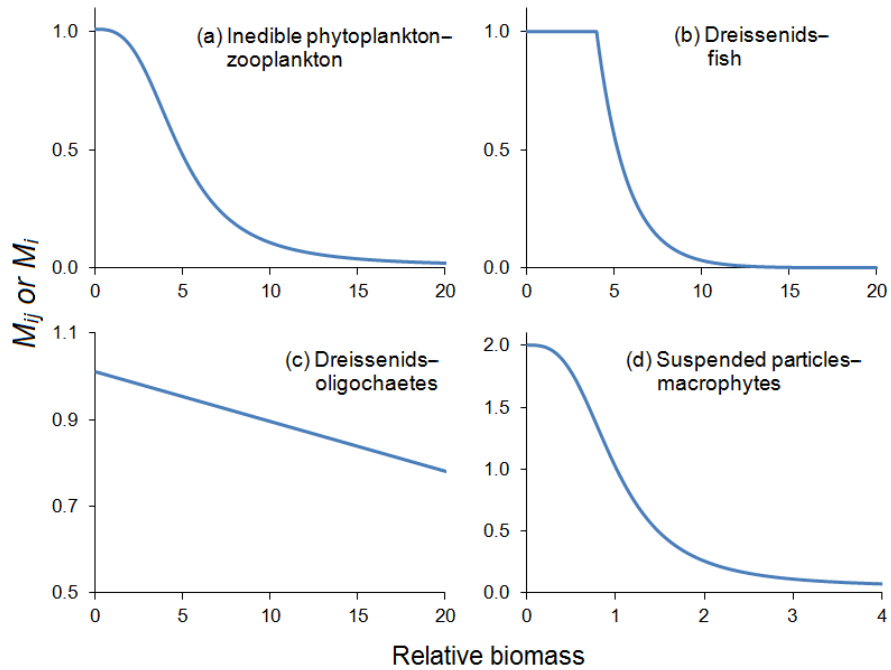
**Figure 3.2** Simplified Saginaw Bay food web with aggregated groups based on similar trophic preference. Arrows indicate energy flow. Vertical position reflects trophic levels. Shaded boxes represent groups that generate detrital material suspended or dissolved in the water column; other groups contribute to detritus that settles to the bottom. Piscivorous fishes include Open lake predators, Nearshore predators, and Walleye 0.5–1, 1, and 2+. Benthivorous fishes include Freshwater drum, Common carp, Lake whitefish, Channel catfish, and White sucker. Benthivorous prey fishes include Yellow perch 0.5–1, 1–2 and 3+, White perch 1+, Gizzard shad 1+, Spottail shiner, Trout perch, Round goby, and Other prey fishes. Planktivorous prey fishes include Walleye 0–0.5, Yellow perch 0–0.5, White perch 0, Gizzard shad 0, Alewife, Rainbow Smelt, and Emerald shiner. Zooplankton (non-predatory) includes Calanoids, Cladocerans, Cyclopoids, Rotifers, and Nauplii. Benthic deposit feeders include Chironomids, Amphipods, and Oligochaetes. Benthic filter feeders include Dreissenids and Sphaeriids. More detailed group information is given in Table 1.



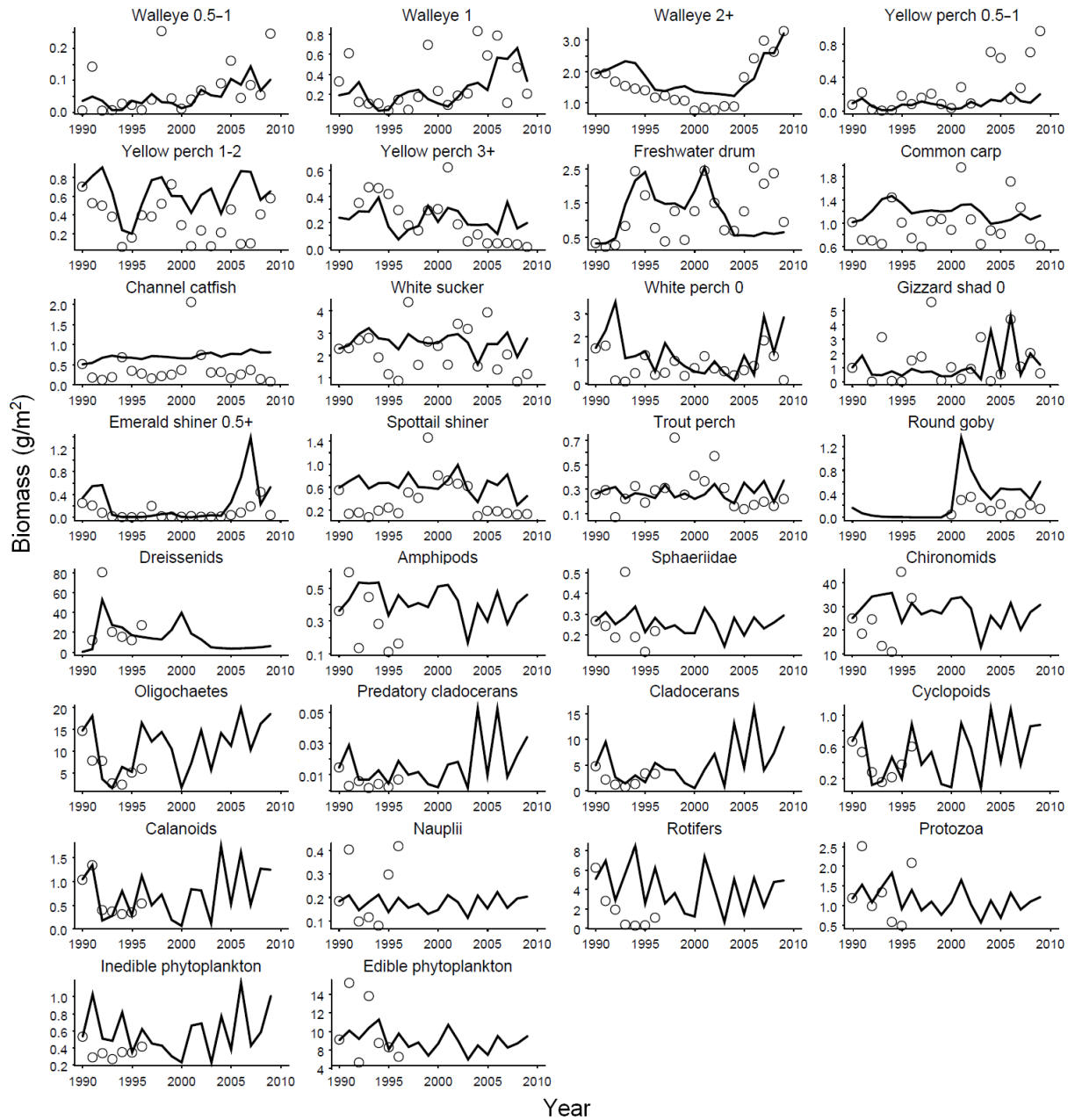
**Figure 3.3** Forcing functions,  $S_{ij}$  in equation (3.4), used to model Dreissenids and Round goby groups that invaded Saginaw Bay after the 1990 Ecopath year.



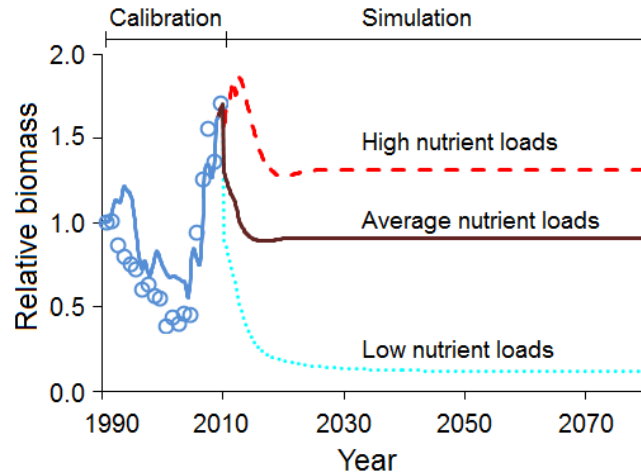
**Figure 3.4** Forcing functions used to model biomass of fish groups that move into Saginaw Bay for part of the year: Lake whitefish, Rainbow smelt 1+, and Alewife 1+. The dynamics of the groups are determined by the main basin dynamics.



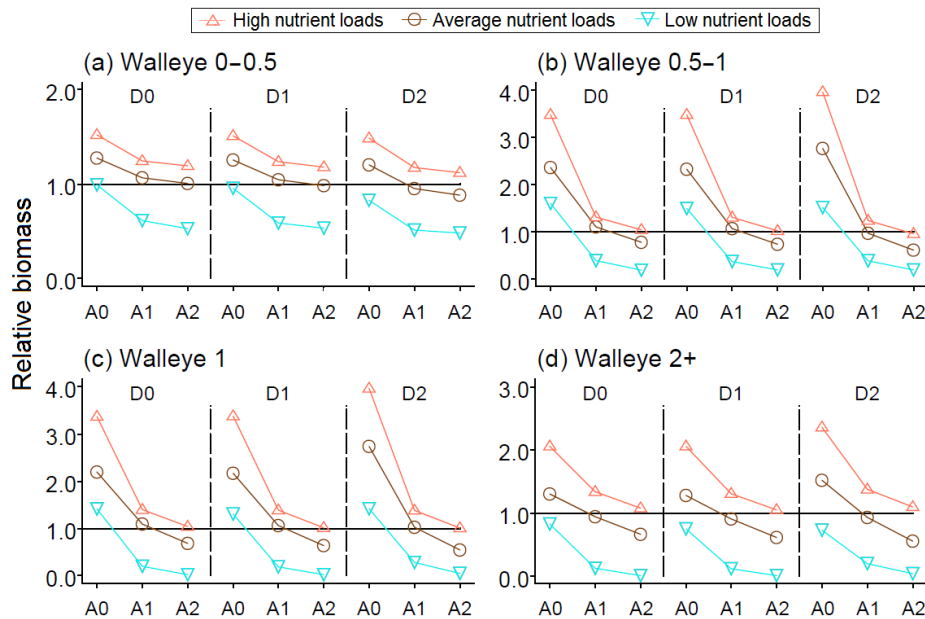
**Figure 3.5** Mediation functions,  $M_{ij}$  in equation (3.4) or  $M_i$  in equation (3.5), used to model interactions among selected groups representing the: (a) effects of blue green algae on consumption by zooplankton groups; (b) low predation efficiency of some fishes preying on dreissenids; (c) remote reduction on availability of detrital material for oligochaetes by dreissenids; and (d) enhanced growth of macrophytes by increased water clarity caused by dreissenid filtration. X-axis represents the biomass of affecting group(s) projected by Ecosim relative to the Ecopath biomass value.



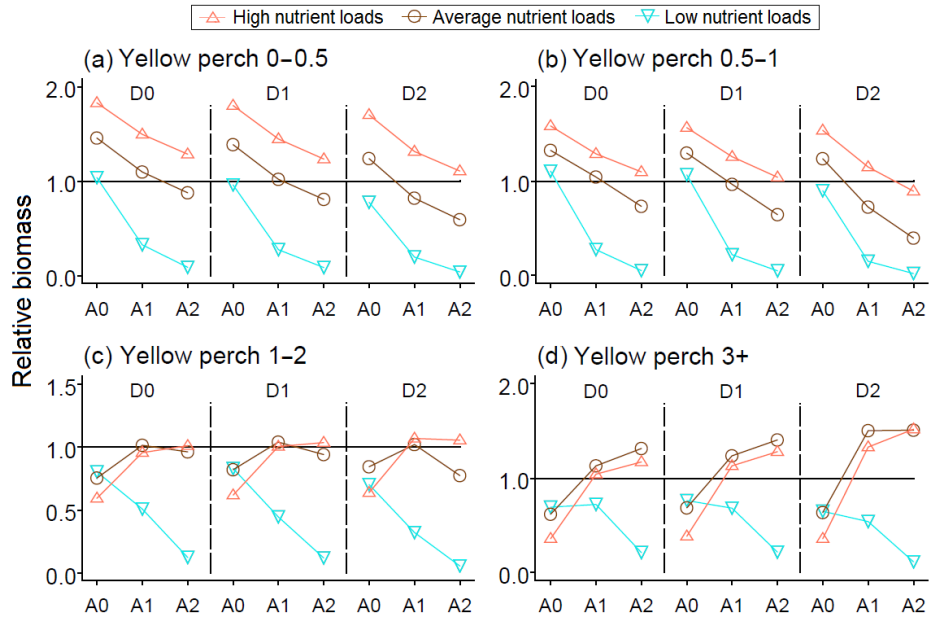
**Figure 3.6** Results of calibration of the Saginaw Bay food web model for all groups with biomass time series included in Ecosim.



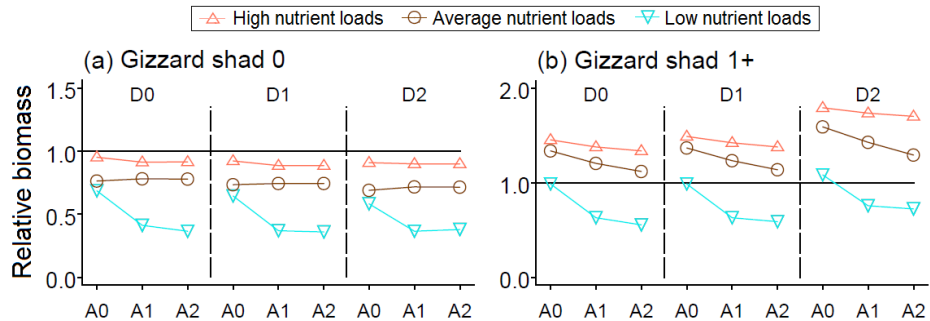
**Figure 3.7** Walleye age 2+ results of calibration and results of 70-year simulation runs under three nutrient scenarios, and average alewife and low dreissenid biomass scenarios. The line from 1990 to 2009 represents the model fitted biomass and lines after 2009 represent the simulated biomass under the simulation scenarios. Circles indicate the input time series for calibration. The average alewife and low dreissenid biomass scenarios correspond to A1 and D1 scenarios in Fig. 8 and Fig. 9 where 30-year biomass average after reaching equilibrium is represented.



**Figure 3.8** Results of simulation scenarios for walleye groups. Symbols represent a 30-year biomass average after reaching equilibrium. A0–A2: absence, average, and high alewife scenarios; and D0–D2: absence, average, and high dreissenid scenarios.

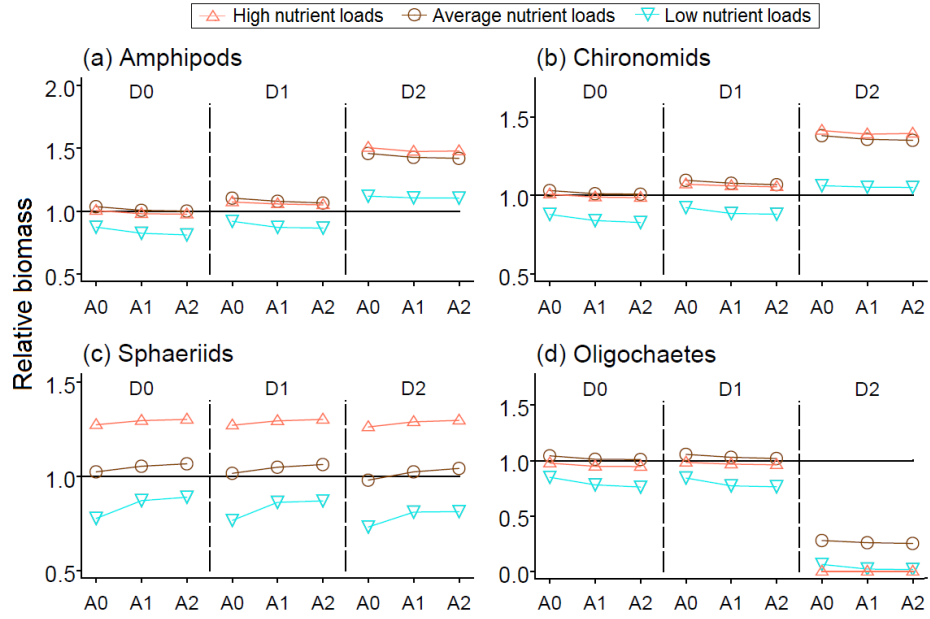


**Figure 3.9** Results of simulation scenarios for yellow perch groups. Symbols represent a 30-year biomass average after reaching equilibrium. A0–A2: absence, average, and high alewife scenarios; and D0–D2: absence, average, and high dreissenid scenarios.

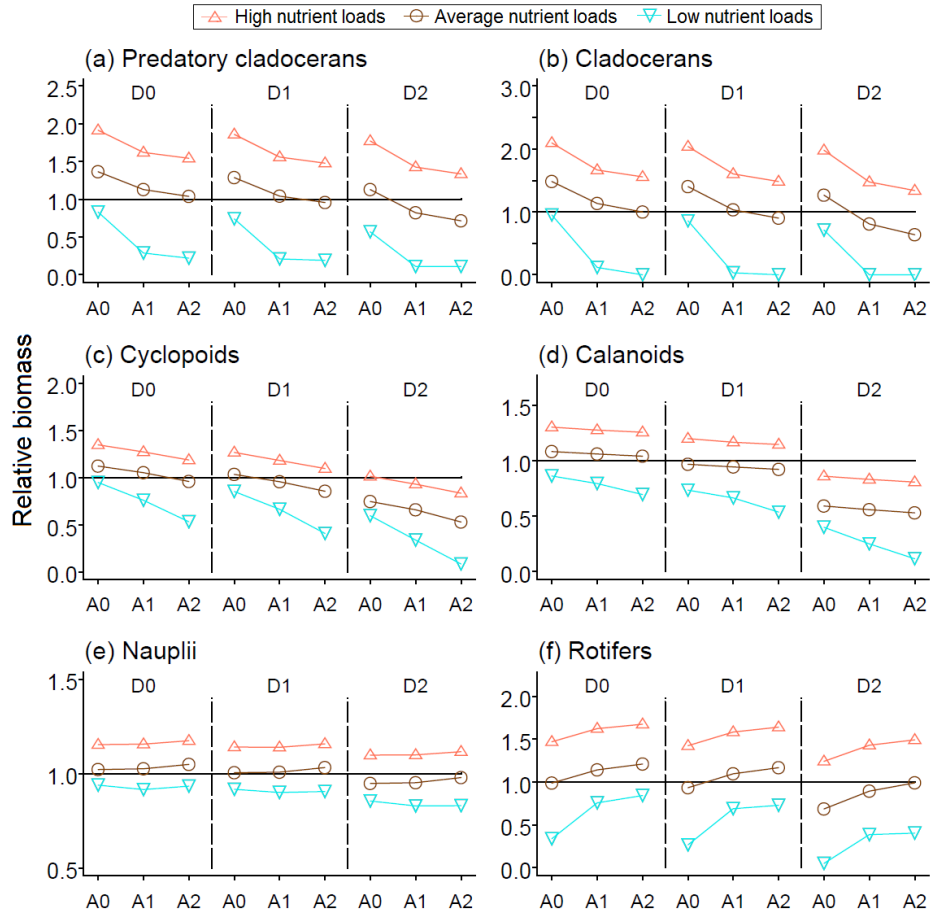


**Figure 3.10** Results of simulation scenarios for gizzard shad groups. Symbols represent a 30-year biomass average after reaching equilibrium. A0–A2: absence, average, and high alewife scenarios; and D0–D2: absence, average, and high dreissenid scenarios.

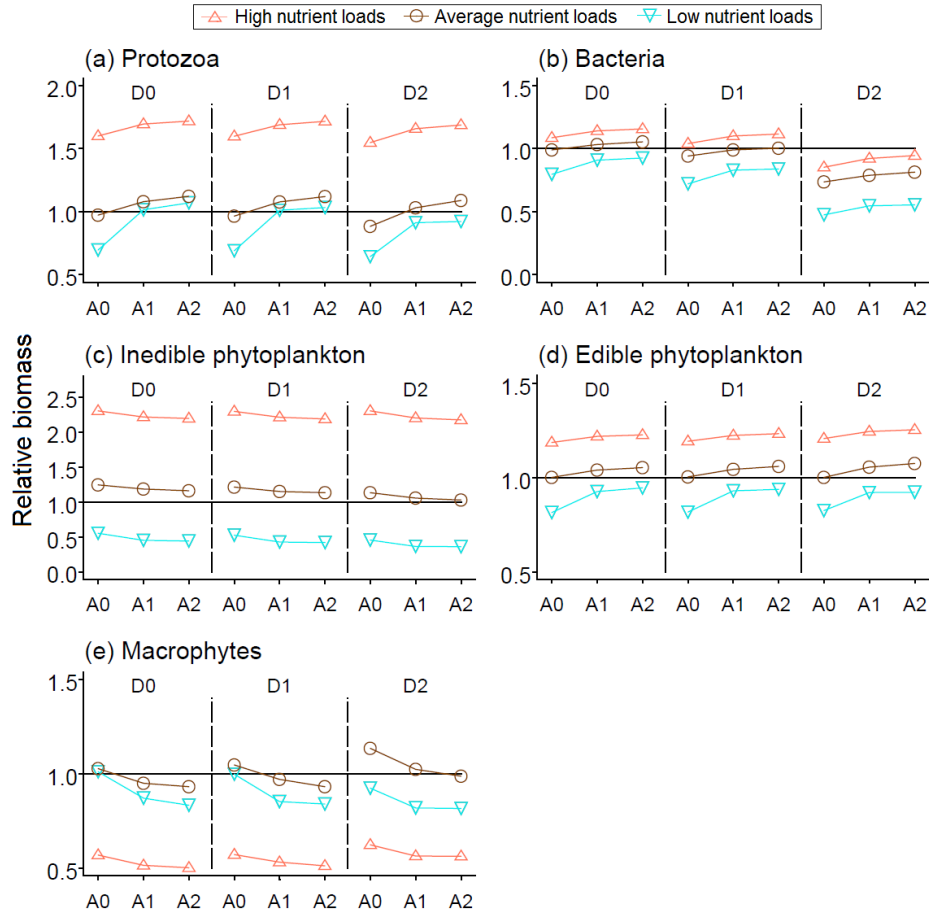




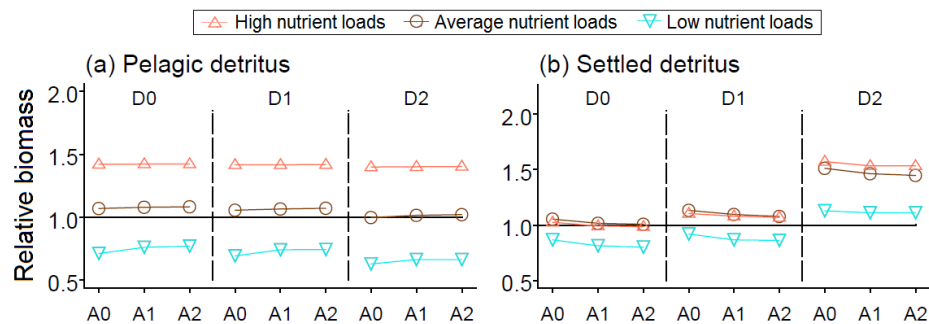
**Figure 3.11** Results of simulation scenarios for benthos groups. Symbols represent a 30-year biomass average after reaching equilibrium. A0–A2: absence, average, and high alewife scenarios; and D0–D2: absence, average, and high dreissenid scenarios.



**Figure 3.12** Results of simulation scenarios for zooplankton groups. Symbols represent a 30-year biomass average after reaching equilibrium. A0–A2: absence, average, and high alewife scenarios; and D0–D2: absence, average, and high dreissenid scenarios.



**Figure 3.13** Results of simulation scenarios for protozoa, bacteria, and producer groups. Symbols represent a 30-year biomass average after reaching equilibrium. A0–A2: absence, average, and high alewife scenarios; and D0–D2: absence, average, and high dreissenid scenarios.



**Figure 3.14** Results of simulation scenarios for detritus groups. Symbols represent a 30-year biomass average after reaching equilibrium. A0–A2: absence, average, and high alewife scenarios; and D0–D2: absence, average, and high dreissenid scenarios.

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## Chapter 4

### Food web assessment of top-down and bottom-up effects on the collapse of alewives in Lake Huron

#### 4.1 Abstract

We used an Ecopath with Ecosim modeling approach to assess effects of top-down control from Chinook salmon (*Oncorhynchus tshawytscha*) and bottom-up control from quagga mussels (*Dreissena rostriformis*) and nutrient loads on the 2003 collapse of alewife (*Alosa pseudoharengus*), a pelagic prey fish, in Lake Huron. We parameterized two Ecopath models to characterize changes in trophic interactions among food web groups between 1984, the earliest year with sufficient data to implement the model, and in 2002, the year before alewives collapsed. Then we built an Ecosim model to simulate food web time-dynamics under scenarios of different levels of top-down and bottom-up control. Results from Ecopath biomass flow analysis showed an increase in the relative importance of bottom-up effects as production across all trophic levels decreased. Major impacts of bottom-up effects were the decrease and depletion of non-dreissenid benthos production, which caused decrease in production of pelagic prey species that feed on them. Our Ecosim scenario simulations showed that top-down effects from Chinook salmon under 1984 to 2002 conditions were relatively constant but bottom-up effects from quagga mussel and nutrient loads increased jointly to unsustainable levels given the coinciding Chinook salmon biomass. Hence, the collapse of alewives was caused by a combination of top-down and bottom-up controls. Under current conditions of low nutrient loads and high quagga mussel

biomass, our results showed it is unlikely for alewives to recover irrespective of the levels of Chinook biomass. These results imply that restoring Chinook salmon recreational fisheries in Lake Huron is unrealistic.

**Keywords:** alewife, Chinook salmon, quagga mussel, nutrient loads, Lake Huron, food web

## **4.2 Introduction**

Freshwater ecosystems have been severely impacted by anthropogenic stressors such as habitat degradation, overexploitation, and exotic species invasion (Pauly et al., 2002; Smith, 2003; Strayer, 2010). Consequently, many freshwater ecosystems have permanently lost their productivity, species richness, and ability to provide ecosystem services that are adequate to meet social needs (Dudgeon et al., 2006; Strayer and Dudgeon, 2010). In response to increasing human demands on freshwater ecosystems, resource managers worldwide have taken actions to conserve biodiversity and maintain sustainability of ecosystems (Carpenter et al., 2009; Goldman et al., 2008; Vorosmarty et al., 2010).

Food web models are powerful tools to inform ecosystem management (Jørgensen et al., 2012). The models require integration of process knowledge and data collected in the focal ecosystem, and can be used to untangle effects among concurrent factors in complex ecosystems where conducting manipulation experiments is not feasible and statistical analyses may be limited by temporal lags between effects and responses. Further, adjusting ecosystem management objectives requires ecologists to provide timely evaluations for trade-offs among alternatives proposed by stakeholders (Redpath et al., 2013), which may not be achievable without using ecological models (Jørgensen et al., 2012).

In this study, we used a food web modeling approach to assess effects of top-down (i.e., predation-driven) and bottom-up (i.e., resource-driven) control on the collapse of alewives (*Alosa pseudoharengus*) in Lake Huron which occurred during 2003 (Riley et al., 2008). Lake Huron (Fig. 4.1) has been continuously impacted by anthropogenic stressors since the late 18th century and by management activities since the 1960s (Beeton et al., 1999; Gaden et al., 2012; Heck, 2014). The alewife, an invasive planktivorous prey fish, reached a nuisance level of abundance around 1960 (Ebener et al., 1995) and drew public attention after their decaying bodies fouled beaches during several massive winter die-off events (Smith, 1970).

To control alewives, the United States and Canadian government agencies stocked hatchery-reared exotic salmonine predators including coho salmon (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) starting from the late 1960s (Tody and Tanner, 1966). The introduction of salmonines, as expected, reduced alewife abundances and resulted in profitable recreational fisheries (Thayer and Loftus, 2012). However, the perceived role of alewife was changed from a nuisance species to a valuable resource as it became the most important prey of the new favorite target in the recreational fisheries—Chinook salmon (Dobiesz, 2003).

In addition to top-down control from Chinook salmon, alewives in Lake Huron were impacted by bottom-up effects from invasive dreissenids (zebra and quagga mussels, *Dreissena polymorpha* and *D. bugensis*) and from reductions in nutrient loads. Soon after the introduction of quagga mussels in the late 1990s, dreissenid populations increased greatly (Nalepa et al., 2007) and sequestered a large amount of nutrients otherwise available to phytoplankton (Hecky et al., 2004; Higgins and Vander Zanden, 2010). At the same time, phosphorus abatement programs initiated in the 1970s to reverse cultural eutrophication conditions have continuously reduced nutrient loads in Lake Huron (Dolan and Chapra, 2012).



The collapse of alewives in Lake Huron posed an important challenge to resource managers not only because recreational harvests of Chinook salmon dropped sharply and have remained low since 2005 (Su and He, 2013), but also because conflicts among management objectives emerged after changes in the ecosystem and demands on ecosystem services. For example, the level of nutrient loads required to sustain the alewife population and profitable Chinook salmon fisheries after invasions of dreissenid mussels may be high enough to cause localized eutrophication. Further, alewives negatively impacted reproductive success of native fishery species including lake trout (*Salvelinus namaycush*), walleye (*Sander vitreus*), and yellow perch (*Perca flavescens*) through predation on larvae (Madenjian et al., 2008). A large alewife population that benefits Chinook salmon fisheries results in decreases in native fishery species. These conflicts are all likely to expand when they are linked to power relations among stakeholders and values rooted in social and cultural history (Raik et al., 2008).

We used the Ecopath with Ecosim (EwE) ecological modeling approach (Christensen and Walters, 2004) to assess the role of top-down effects from Chinook salmon and bottom-up effects from quagga mussels and nutrient loads on the collapse of the alewife population in Lake Huron. The EwE approach consists of a component for understanding trophic interactions among food web groups (Ecopath) and a component for simulating food web time-dynamics under designed scenarios and ecosystem forcings (Ecosim). We used available information to configure Lake Huron EwE models and implement the models to (1) characterize trophic interactions among food web groups between 1984, a historical reference year when data on all trophic levels were first available, and 2002, the year before alewives collapsed, and to (2) simulate food web time-dynamics under scenarios of different levels of Chinook salmon and quagga mussel biomass, and nutrient loads.

## **4.3 Methods**

### **4.3.1 Study area**

Lake Huron, the second largest among the Great Lakes, is comprised of four distinct sub-basins: the North Channel, Georgian Bay, Saginaw Bay, and the main basin (Fig. 4.1). We modeled the food web in the main basin, which is a deep and oligotrophic water body with an area of  $3.78 \times 10^4 \text{ km}^2$  (63% of the lake surface area), a mean depth of 73 m, and a maximum depth of 229 m (Beeton and Saylor, 1995). The major water inflow to the main basin is from Lake Superior via St. Mary's River (Beeton and Saylor, 1995) but the most important nutrient input is the outflow of Saginaw Bay (Dolan and Chapra, 2012). The main basin is connected to Lake Michigan via the Straits of Mackinac and outflows to Lake St. Clair via the St. Clair River. The border between Canada and the United States is in the middle of the main basin, with the province of Ontario on the east and State of Michigan on the west.

### **4.3.2 The Ecopath with Ecosim food web model**

The Ecopath with Ecosim (EwE) modeling approach was developed based on the conservation of biomass (Polovina, 1984). Derivations of the model were detailed in Christensen and Pauly (1992) for Ecopath and in Walters et al. (1997) and in Walters et al. (2000) for Ecosim. We used the software EwE version 6.3 (available at <http://www.ecopath.org/>).

### **4.3.3 Lake Huron Ecopath models**

We parameterized two Ecopath models to represent the Lake Huron food web in 1984 and 2002. Available biomass data suggested that the food webs in the periods of 1981–1986 and

1998–2002 were in relatively steady-state conditions, which is the assumption in the Ecopath biomass flow analysis (Christensen and Pauly, 1992).

In the Ecopath modeling approach, biomass flows among food web groups are represented as a system of linear equations in the form:

$$B_i \times (P/B)_i \times EE_i = \sum_j B_j \times (Q/B)_j \times DC_{ij} + BA_i + Y_i + E_i \quad (4.1)$$

where  $B_i$  is the biomass ( $\text{g}/\text{m}^2$  in wet weight) of group  $i$ ,  $(P/B)_i$  is the annual average production to biomass ratio,  $EE_i$  is the ecotrophic efficiency,  $B_j$  and  $(Q/B)_j$  are the biomass and average annual consumption to biomass ratio of group  $j$  that has a proportion of  $DC_{ij}$  of group  $i$  in diet,  $BA_i$  is the biomass accumulation,  $Y_i$  is the fishery yields, and  $E_i$  is net migration (emigration – immigration). The parameter  $EE_i$  represents the proportion of production of group  $i$  that is lost to predation or exported through fishing and migration. Units for parameters  $BA$ ,  $Y$ , and  $E$  were  $\text{g} \times \text{m}^{-2} \times \text{yr}^{-1}$ .

The second equation in Ecopath model represents energy balance for each consumer group  $i$  as:

$$(P/Q)_i + (R/Q)_i + (U/Q)_i = 1 \quad (4.2)$$

where  $(P/Q)_i$ ,  $(R/Q)_i$ , and  $(U/Q)_i$  are proportions of consumption represented by production, respiration, and unassimilated food, respectively. The energy balance of producer groups was ensured at parameterization as their production equals net primary production (Christensen et al., 2005).

#### 4.3.4 Food web configuration, model inputs, and data sources

We configured 52 groups in the 1984 Ecopath model and 55 groups in the 2002 model (Tables 4.1 and 4.2) based on available information and data on community structure described

in Appendix E. The additional groups into the 2002 model represented species that invaded Lake Huron in the 1990s: zebra mussel, quagga mussel, and round goby (*Neogobius melanostomus*). To represent trophic ontogeny and selectivity to fishery, we parameterized 10 out of the 15 fish taxa as multi-stanza groups (Christensen et al., 2005) with up to four age stanzas. For example, “Lake trout 5+” stands for lake trout that are age 5 and older, which is the only stanza vulnerable to the fishery. The food web groups in the models can be categorized into eight components based on their functional traits (Table 4.1, Fig. 4.2): Predators (17 groups), Lake whitefish (3 groups), Pelagic prey fishes (6 groups), Benthic prey fishes (10 groups), Zooplankton (6 groups), Benthos (7 groups), Microplankton (including 4 groups of phytoplankton, protozoa, and pelagic bacteria), and Detritus (2 groups).

Other input parameters were required for the two Ecopath models. These parameters included biomass ( $B$ ), production to biomass ratio ( $P/B$ ) for groups with only one stanza, or total mortality rate ( $Z$ ) for multi-stanza groups, consumption to biomass ratio ( $Q/B$ ), proportion of unassimilated food in consumption ( $U/Q$ ), diet composition ( $DC$ ), and fishery yields ( $Y$ ). We set biomass accumulation ( $BA$ ) for all groups to zero as the food web was in a relatively steady-state condition in both 1984 and 2002. We also set net migration ( $E$ ) to zero because the software cannot model migration for multi-stanza groups. Nevertheless, we followed different procedures to represent the temporary presence of five taxa (double-crested cormorants, sea lamprey, Chinook salmon, other salmonines, and walleye) in the Lake Huron main basin. For Double-crested cormorants, Sea lamprey, and Walleye, input parameters were based on estimates representing the predator–prey interactions in the main basin. For example, the  $Q/B$  of Double-crested cormorants was based on consumption estimates during the breeding season only when they feed in the main basin (Ridgway and Fielder, 2012). For the oldest stanza group of Chinook

salmon and other salmonines (5+) that migrate into streams during spawning runs and die, we set their diets as 100% “Import” and detritus fates as 100% “Export” so that consumption and detritus generation would not affect model biomass balance (Christensen et al., 2005). We detail estimation procedures and data sources of these input parameters (Tables 4.2–4.4) in Appendix E. In the 1984 and 2002 Ecopath models, inputs for parameters  $P/B$  and  $Q/B$  were the same for most groups (Table 4.2), but inputs for diet composition were moderately different because of changes in food web structure (Tables 4.3 and 4.4).

For fish taxa parameterized as multi-stanza groups, additional parameters are required to model recruitment. The von Bertalanffy growth constant ( $k$ ) and the ratio of weight at maturity to asymptotic weight ( $w_m/w_{inf}$ ) are needed to model fish growth and maturity, respectively. Further, inputs of biomass and  $Q/B$  are required only for the leading-stanza groups as Ecopath estimates these parameters for the other stanza groups (see Appendix F of the detail). Following the assumption in Ecopath that weight is proportional to cubic length (Christensen et al., 2005), we estimated the two parameters using length-at-age or weight-at-age data from surveys and age at maturity information from literature (Table 4.5).

The ecotrophic efficiency ( $EE$ ) and respiration to consumption ratio ( $R/Q$ ) were estimated by Ecopath through solving a set of linear equations (4.1) and (4.2) (Christensen et al., 2005). We slightly modified inputs of biomass and diet composition to ensure that the biomass balance was achieved ( $EE < 1$ ) for all groups. We also ensured that the energy balance was achieved ( $R/Q > 0$ ) at parameterization.

#### **4.3.5 Biomass flow analysis**

We first summarized changes in the production, biomass, and ecological size of the whole Lake Huron food web between 1984 and 2002. We used the total system throughput ( $TST$ ) as the measure of ecological size of a food web based on Finn (1976).  $TST$  is calculated as:

$$TST = Q_T + R_T + FD_T + Ex_T \quad (4.3)$$

where  $Q_T$  is the total consumption,  $R_T$  is the total respiration,  $FD_T$  is the total flow into detritus, and  $Ex_T$  is the total export of the whole food web. Finn (1976) also suggested that the proportion of each component ( $Q_T$ ,  $Ex_T$ ,  $R_T$ , and  $FD_T$ ) in  $TST$  can be used to characterize the biomass flow structure in a food web. The Ecopath tool “Statistics” automatically calculates total production, total biomass, and  $TST$  once the food web model is parameterized (Christensen et al., 2005).

Note that biomass of detritus groups is excluded in the calculation of total food web biomass. As detritus is non-living organic matter, the biomass of a detritus group stands for a parameter in the Ecopath model, not a real biomass in an ecological context (Christensen et al., 2005).

To characterize trophic interactions of the whole Lake Huron food web in 1984 and 2002, we reported production, biomass, and ecotrophic efficiencies by trophic level for trophic levels I–IV. Change in production by trophic level is also an indicator of the change in relative importance of top-down and bottom-up effects in the whole food web. If the relative importance of top-down effects increases, the trophic cascade theory (Carpenter et al., 1985) suggests that production changes will vary among trophic levels in an alternating manner, with increases in production from trophic levels IV and II, and decreases in production from trophic levels III and I. If the relative importance of bottom-up effects increases, production should decrease across all trophic levels (Vanderploeg et al., 2002).

We calculated biomass by trophic level using outputs from the routine “Trophic level decomposition” in the Ecopath tool “Network analysis”, in which the biomass of each group is

apportioned into discrete trophic levels based on diet composition input (Christensen et al., 2005).

We calculated the production ( $P$ ) and ecotrophic efficiency ( $EE$ ) by trophic level  $l$  ( $l = \text{I, II, III, and IV}$ ) as:

$$P_l = \sum_i [B_{i,l} \times (P/B)_i] \quad (4.4)$$

$$EE_l = \sum_i [B_{i,l} \times (P/B)_i \times EE_i] / \sum_i [B_{i,l} \times (P/B)_i] \quad (4.5)$$

where  $B_{i,l}$  is the biomass of a non-detritus group  $i$  that is apportioned into trophic level  $l$  based outputs of the routine “Trophic level decomposition”.

To further characterize trophic interactions in the Lake Huron food web in 1984 and 2002, we summarized production, biomass, ecotrophic efficiency, and allocation of production by functional component. We also quantified changes in production, biomass, and ecotrophic efficiency and identified major changes in allocation of production for each functional component between these two years.

#### 4.3.6 Lake Huron Ecosim dynamic modeling

We used Ecosim to simulate time-dynamics of the Lake Huron food web under scenarios of different levels of Chinook salmon and quagga mussel biomass, and nutrient levels. The master equation in Ecosim is the derivative form of the Ecopath master equation (4.1), which represents how biomass  $B$  of group  $i$  changes with time as:

$$dB_i/dt = G_i \sum_j Q_{ji} - \sum_j Q_{ij} - E_i - (M0_i + F_i) \times B_i \quad (4.6)$$

where  $G_i$  is the dimensionless gross conversion efficiency,  $Q_{ji}$  is the consumption on group  $j$  by group  $i$ ,  $Q_{ij}$  is the predation by group  $j$  on group  $i$ ,  $E_i$  is the net migration rate,  $M0_i$  is the non-predatory natural mortality rate, and  $F_i$  is the fishing mortality rate.

The consumption ( $Q_{ij}$ ) in Ecosim is modeled based on the foraging arena theory (Walters

et al., 1997) as:

$$Q_{ij} = \frac{p'_{ij} \times v_{ij} \times B_i \times B_j \times f_1}{v_{ij} \times (1 + f_2) + p'_{ij} \times B_j \times f_3} \quad (4.7)$$

$$p'_{ij} = p_{ij} \times S_{ij} \times M_{ij} \quad (4.8)$$

where  $p_{ij}$  is the predation rate on prey group  $i$  by unit biomass of predator group  $j$  that can be adjusted by a forcing function  $S_{ij}$  and a mediation function  $M_{ij}$ ,  $v_{ij}$  is the vulnerability parameter, and  $f_1, f_2$ , and  $f_3$  are functions representing effects of feeding time and handling time on consumption (Christensen and Walters, 2004).

We used the 1984 Lake Huron Ecopath model as the initial condition of the Ecosim model, with slight modifications related to the inclusion of the invasive groups Round goby, Zebra mussel, and Quagga mussel so that they could be incorporated in the simulations. We set low biomass for Round goby ( $0.25 \text{ g/m}^2$ ) and for Zebra mussel and Quagga mussel ( $0.60 \text{ g/m}^2$ ), and used the values for parameters  $P/B$ ,  $Q/B$ , and  $U/Q$  as in the 2002 Ecopath model (Table 4.2). Correspondingly, we modified the diet composition input (Table 4.6) as described in Appendix E. We set biomass inputs for obtaining ecotrophic efficiencies of about 0.50 for Round goby and about 0.15 for Zebra mussel and Quagga mussel. These ecotrophic efficiencies were based on outputs of the 2002 Ecopath model and literature information on temporal changes in feeding preferences among groups in response to invasive species, as described in Appendix E. For example, the feeding preference of double-crested cormorants shifted from pelagic alewives and rainbow smelt to benthic round goby (Johnson et al., 2010), while Lake whitefish 3+ feeding preference shifted from soft-bodied benthos *Diporeia* spp. to zebra and quagga mussels (Pothoven and Nalepa, 2006) and round goby (Pothoven and Madenjian, 2013).



#### **4.3.7 Modeling effects of species invasions: Forcing functions to modify predation rates**

To represent species invasions in the Ecosim model, we used the approach of modifying predation rates described in Kao et al. (2014). We used forcing functions  $S_{ij}$  in equation (4.8) to represent that predator–prey interactions between an invasive group (Zebra mussel, Quagga mussel, and Round goby) and other groups would not occur until the year of invasion. Hence, the shape of these forcing functions (Fig. 4.3a–f) represents a switch to turn on predator–prey interactions at the year of invasion. In addition, the shape of the forcing function for Zebra mussel as predator (Fig. 4.3b) was to model the initial proliferation followed by the population gradual decrease (Nalepa et al., 2003). The shape of the forcing function for Quagga mussel as predator (Fig. 4.3c) was to represent a constant population expansion until the end of the model calibration period (1984–2006).

We used a forcing function to model the change in the consumption to biomass ratio ( $Q/B$  in Table 4.2) of Lake whitefish 3+ after the invasion of zebra and quagga mussels (Fig. 4.3g). Lake whitefish 3+ was the only group known to have changed  $Q/B$  after incorporating invasive groups Zebra mussel and Quagga mussel into their diet (Madenjian et al., 2008).

#### **4.3.8 Modeling indirect effects: Mediation functions**

We used three mediation functions to represent observed indirect effects among food web groups. We used a function (Fig. 4.4a) to represent low efficiency in consumption of Zebra mussel and Quagga mussel by fish groups that ingest mussels including shells (French, 1993). We used this function to prevent unrealistically high proportions of zebra and quagga mussels in fish diets as in Ecosim the consumption rate on a group is proportional to its biomass, as shown in equation (4.7). We assumed the same digestion efficiency on zebra and quagga mussels. The

second function (Fig. 4.4b) was to represent decreases in the consumption by zooplankton groups when the biomass of Inedible phytoplankton (cyanophytes) is high, as observed by McNaught et al. (1980). The third function (Fig. 4.4c) was to represent the decrease in consumption by Cladocerans and Cyclopoids with the increase in biomass of Predatory cladocerans. These groups inhabit colder and deeper portions of the water column to avoid predation risks from the predatory cladoceran *Bythotrephes cederstroemii* (Pangle et al., 2007).

#### **4.3.9 Modeling groups that cross system boundaries: Biomass forcing time series**

In dynamics simulations, we used biomass forcing time series for Double-crested cormorants, Sea lamprey, and Walleye groups (Fig 4.5) because their abundances are not controlled by predator–prey interactions in the main basin. Double-crested cormorants are able to feed outside the main basin when prey availability is low (Ridgway and Fielder, 2012). Sea lamprey abundance is controlled by application of chemical lampricides in streams (Sullivan et al., 2013), and walleye population is controlled by recruitment and food web dynamics in Saginaw Bay (Fielder and Bence, 2014). Biomass forcing time series of these groups were based on available estimates as described in Appendix E.

#### **4.3.10 Modeling fish stocking as immigration**

We represented hatchery stockings of Chinook salmon 0–0.5, Lake trout 0–0.5, Lake trout 0.5–1, and Other salmonines 0 in the Ecosim model as immigration. The Ecopath with Ecosim software can only model either stocking or natural recruitment of a group but cannot incorporate both (Christensen et al., 2005). By modeling stocking as immigration, the stocked biomass time series is added to natural recruitment biomass in simulations. To our knowledge,

only one study has used this approach to represent stocking in an Ecopath model (Fayram et al., 2006). We had to modify the source code of the EwE software because it did not have a routine to input immigration time series in Ecosim. Coding and testing of this modification was done with the assistance of Jason Breck (Department of Computer Sciences, University of Wisconsin–Madison) and Jeroen Steenbeek (Ecopath Research and Development Consortium Technical Committee, Vancouver).

To correctly model stocking as immigration for fish groups, we also needed to modify the Ecosim parameter “Maximum consumption to biomass ratio” or  $(Q/B)_{max,i}$ . The  $(Q/B)_{max,i}$  has a default value of 1,000 times the Ecopath  $(Q/B)_i$ , which allows predator consumption to increase with the ratio of vulnerable prey biomass to predator biomass but without the limit of handling time (Christensen et al., 2005). This default parameter value generally has no effect on Ecosim simulations because the estimation of predator consumption is controlled by the vulnerability parameter, as shown in equation (4.7). However, the default parameterization is problematic here for stocked fish groups because of the large interannual variation in stocked biomass during the calibration period from 1984 to 2006 (FWS/GLFC, 2010). In Ecosim, biomass of all stanza groups of one stocked fish taxa respond simultaneously to the change in stocked biomass. When there is a large decrease in stocked biomass, the model-estimated consumption can be unrealistically high because it inversely relates to predator biomass as shown in equation (4.7). To represent limits on consumption associated with time required to handle prey, we set the  $(Q/B)_{max,i}$  to 1.3 times the Ecopath  $(Q/B)_i$  for Chinook salmon, 1.5 times for Lake trout, and 2.0 for Other salmonines, based on literature information on consumption rates (as described in Appendix E).

#### 4.3.11 Modeling primary production as a function of nutrient loads

The primary production ( $P$ ) of producer group  $i$  in Ecosim is represented as a function of free nutrients concentration:

$$P_i = B_i \times (P/B)_{max,i} \times Nf / (Nf + K_i) \quad (4.9)$$

where  $(P/B)_{max,i}$  is the maximum production to biomass ratio,  $Nf$  is the concentration of free nutrients that is calculated in Ecosim based on nutrient loads time series, and  $K_i$  is a constant estimated by Ecosim (Christensen et al., 2005).

Two parameters “Base proportion of free nutrients” and  $(P/B)_{max,i}$  are required to implement equation (4.9) that links nutrient loads to primary production (Christensen et al., 2005). The “Base proportion of free nutrients” parameter is used to link the initial  $Nf$  to the initial nutrient loads so that  $Nf$  can be calculated by Ecosim in the simulation based on nutrient loads time series. We set the  $Nf$  value to 0.35 to represent oligotrophic conditions (Christensen et al., 2005). We used the  $(P/B)_{max,i}$  parameter to represent higher growth responses of inedible phytoplankton to nutrients compared to edible phytoplankton (Downing et al., 2001). We set  $(P/B)_{max,i}$  to 1.6 times the Ecopath  $(P/B)_i$  value for Edible phytoplankton and 4.8 times for Inedible phytoplankton. These values were taken from a Saginaw Bay 1990 Ecopath model (Kao et al., 2014). We used these values because biomass ratios of inedible to edible phytoplankton were similar in Saginaw Bay and the main basin under similar levels of nutrient loads. This was the case under relatively low nutrient loads levels in 1990 in Saginaw Bay and in 1984 in the main basin, and under high nutrient loads in the 1970s. In Saginaw Bay in 1990, the biomass ratio of inedible to edible phytoplankton (0.058) was about the same as the ratio in Lake Huron in 1984 (0.055). Nutrient loads in Saginaw Bay in 1990 and in the main basin in 1984 were also at the same level (Dolan and Chapra, 2012; Stow et al., 2014). Biomass ratios of inedible to

edible phytoplankton were both about 0.25 in Saginaw Bay (Bierman and Dolan, 1986) and the main basin (Munawar and Munawar, 1982) under similar high nutrient loads of the 1970s.

#### **4.3.12 Ecosim calibration**

To calibrate the Lake Huron Ecosim model, we estimated vulnerability parameters by fitting simulated biomass to available biomass time series in the period from 1984 to 2006. Except parameters indicated above, we set all Ecosim parameters to model default values in the calibration.

#### **4.3.13 Simulation scenarios**

To assess top-down and bottom-up effects on the collapse of alewives in Lake Huron, we conducted simulations under scenarios that represented historically observed levels of Chinook salmon biomass, quagga mussel biomass, and nutrient loads. We designed this analysis as a factorial experiment. For the factor Chinook salmon, we used 21 levels of Chinook salmon 1–4 biomass ranging from 0.00 g/m<sup>2</sup> to 0.20 g/m<sup>2</sup>. The upper end represents the peak biomass that occurred in the 1980s. Biomass of the other Chinook salmon stanza groups was estimated by Ecopath. For the factor quagga mussel, we used five levels of Quagga mussel biomass ranging from 0 g/m<sup>2</sup> to 80 g/m<sup>2</sup>. The upper end represents the biomass that occurred in 2007, a year after the end of calibration period. For the factor nutrients, we used three historical levels of total phosphorus loads: 2,575 ton/year (corresponding to an average input concentration of 15.0 µg/l), 1,803 ton/year (10.5 µg/l), and 1,526 ton/year (8.9 µg/l). The high level represents the average loads between 1984 and 1997, the median level represents the average between 1998 and 2002, and the low level represents the average between 2002 and 2006.

We ran simulations under scenarios representing effects of each factor (Chinook salmon, quagga mussel, and nutrients) and their combinations, and summarized changes in simulated Alewife 1+ biomass. In scenarios representing effects of one factor, we kept the other two factors unchanged at reference levels, which were 0 g/m<sup>2</sup> for Chinook salmon, 0 g/m<sup>2</sup> for quagga mussel, and 2,575 ton/year (the high level) for nutrients. Similarly, in scenarios representing combined effects of two factors, we kept the last factor unchanged at the reference level.

We set simulations to a 40-year period within which the food web was expected to reach an equilibrium condition. In simulations, we used 2006 stocking biomass levels of Lake trout 0.5–1 and Other salmonines 0, and 2006 fishing mortality rates for groups subjected to fishery harvests (Table 4.2); 2006 corresponded to the last year of calibration period. We did not model the stocking of Chinook salmon 0–0.5 in simulations because the biomass was estimated by Ecopath and fixed in each scenario, which means that the stocked biomass are different in order to maintain different Chinook salmon biomass in scenarios. We considered alewives as collapsed when the equilibrium biomass fell below 0.01 g/m<sup>2</sup>.

## **4.4 Results**

### **4.4.1 Ecopath biomass flow analysis: Changes at the food web level**

Results from Ecopath biomass flow analysis showed that there were decreases in productivity and ecological size of the whole Lake Huron food web between 1984 and 2002, but an increase in standing biomass. The total production and total system throughput (*TST*) decreased by 25% and 22% while the total biomass increased by 14% (Table 4.7). Changes in proportions of *TST* represented by different components showed increases in efficiencies of utilizing primary production and recycling detrital material, as proportions of total flow into

detritus and total export both decreased while proportions of total consumption and total respiration increased.

Results of production, biomass, and ecotrophic efficiencies (*EE*) by trophic level in the Ecopath Lake Huron food web models (Table 4.8) showed an increase in the relative importance of bottom-up effects between 1984 and 2002. The production decreased across all trophic levels, by 23%, 9%, 17%, and 27% from trophic level IV to trophic level I, respectively. Changes in biomass and *EE* indicated trophic levels II and III sequestered higher proportions of total production in 2002 than in 1984. The biomass decreased by 30% and 18% in trophic levels IV and I but increased by 13% and 23% in trophic levels III and II, respectively. *EE* decreased by 23% and 15% in trophic levels IV and III but increased by 3% and 15% in trophic levels II and I.

#### **4.4.2 Ecopath biomass flow analysis: Changes at the functional component level**

Results from Ecopath biomass flow analysis showed that production of all functional components decreased in the Lake Huron food web between 1984 and 2002 except for Lake whitefish and Benthic prey fishes (Table 4.9). In both years, most biomass flow passed through the pelagic pathway from Microplankton to Zooplankton and Pelagic prey fishes to Predators. However, there was an increase in the proportion of biomass flow passing through the benthic pathway from Detritus to Benthos and Benthic prey fishes to Lake whitefish.

The production and biomass of the pelagic functional components decreased from 1984 to 2002. Production of fish predators decreased by about 30% (Table 4.9), resulting from a large change in the composition of food web groups in this functional component (Table 4.2). Most importantly, the production of Chinook salmon decreased by 52% but production of Lake trout and Walleye increased by 35% and 60%, respectively. The production and biomass of Pelagic

prey fishes decreased by about 60%, mainly because of a 78% decrease in the production of Rainbow smelt 1+. The production and biomass of Zooplankton decreased by about 5% as there were only minor changes in production (< 11% increase or decrease) of Cladocerans, Cyclopoids, and Calanoids groups that made up about 80% of overall Zooplankton production. The production and biomass of Microplankton decreased by 27% and 22%, as production and biomass decreased by 12–58% among all groups in this functional component.

Production and biomass of benthic functional components increased from 1984 to 2002. The production and biomass of Lake whitefish increased by 152% and 105% respectively, and production and biomass of Benthic prey fishes increased by 18% and 8% (Table 4.9). The increase in production of Benthic prey fishes resulted from the contribution of the invasive group Round goby, which was more productive than most of the other groups in this functional component (Table 4.2). The production of Benthos decreased by 14%, this despite a 76% increase in biomass, following the large additional biomass from Zebra mussel and Quagga mussel. This decrease in production was because biomass of more productive Amphipods and Oligochaetes was replaced by biomass of less productive Zebra mussels and Quagga mussels. Detritus production and biomass decreased by 27% and 17% respectively. Most production of Detritus was from unassimilated food and unconsumed production of Microplankton and Zooplankton. The decrease in Detritus production mainly resulted from a 45% decrease in the detritus production from Microplankton.

There was no general trend in *EE* between 1984 and 2002 among functional components (Table 4.9) as changes in *EE* depended on relative changes in the production of the functional component to the consumptive demands on the functional component. Among the pelagic functional components, the *EE* of Predators increased by 66% (Table 4.9) mainly because of a



114% increase (from 10%) in the proportion of production exported through fishery harvests (Fig. 4.6). The *EE* of Pelagic prey fishes decreased by 16% because of a 46% decrease (from 38%) in the proportion of production consumed within the functional component. The proportion of Pelagic prey fishes production consumed by Predators actually increased by 46% (from 8%). The *EE* of Zooplankton decreased by 18% mainly because of changes in predation by Pelagic prey fishes and Zooplankton. The proportion of Zooplankton production consumed by Pelagic prey fishes decreased by 43% (from 27%) while the proportion consumed by Zooplankton increased by 58% (from 8%). The *EE* of Microplankton increased by 15% mainly because of a 27% increase (from 51%) in the proportion consumed by Zooplankton (Table 4.2).

Among the benthic functional components, the *EE* of Lake whitefish decreased by 39% (Table 4.9) mainly because a 30% decrease (from 14%) in the proportion of production exported through fishery harvests (Fig. 4.6). The *EE* of Benthic prey fishes increased by more than 300% because of increases in consumptive demands of all functional components that fed on this functional component. The *EE* of Benthos decreased slightly by 3%. However, there were a 48% decrease (from 38%) in the proportion of Benthos production consumed by Pelagic prey fishes and a 185% increase (from 6%) in the proportion consumed by Lake whitefish. The *EE* of Detritus increased by 6% mainly because of a 21% increase (from 38%) in the proportion of production consumed by Microplankton.

#### **4.4.3 Ecosim Calibration**

After calibration, the time series of simulated biomass generally tracked the observed time series of 27 groups (Fig. 4.7). Among fish groups, comparisons between observed and simulated time series were better for predator and pelagic prey fish groups such as Chinook

salmon 1–4 and Alewife 1+ than for benthic prey fish groups such as Yellow perch 1–2 and Slimy sculpin. For groups in lower trophic levels (i.e. zooplankton, benthos, and phytoplankton groups), observed versus simulated comparisons were not as good as for fish groups. Trends of simulated and observed biomass time series were very consistent across all groups, but the simulated time series did not have the large inter-annual variations common to observed biomass time series.

#### **4.4.4 Ecosim scenario simulations: The factorial experiment on Alewife 1+ biomass**

The biomass of Alewife 1+ reached equilibrium within 20 simulation years under all scenarios that represented effects of individual factors (Chinook salmon, quagga mussel, and nutrients) and their combinations (Fig. 4.8). In single factor simulations, biomass of Alewife 1+ decreased with increases in Chinook salmon and quagga mussel biomass but increased with increases in nutrient loads (Fig. 4.9a). The equilibrium Alewife 1+ biomass decreased by 34% under Chinook salmon scenarios and by 28% under quagga mussel scenarios but increased by 174% under nutrient loads scenarios. In two-factor simulations, Alewife 1+ biomass fell below  $0.01 \text{ g/m}^2$  (i.e., collapsed) at low level of nutrient loads in combination with Chinook salmon or with quagga mussel threshold levels, i.e., when Chinook salmon 1–4 biomass was greater than  $0.07 \text{ g/m}^2$  or when Quagga mussel biomass was greater than  $60 \text{ g/m}^2$  (Fig. 4.9b). Combined Chinook salmon and quagga mussel effects did not cause Alewife 1+ to fall below  $0.01 \text{ g/m}^2$  without the reduction in nutrient loads. The equilibrium biomass of Alewife 1+ decreased by as much as 61% under combined Chinook salmon and quagga mussel effects. Three-factor scenario simulations showed that Alewife 1+ biomass fell below  $0.01 \text{ g/m}^2$  at the median level of nutrient loads when Chinook salmon 1–4 biomass was greater than  $0.05 \text{ g/m}^2$  and Quagga mussel

biomass was greater than 40 g/m<sup>2</sup>. At low level of nutrient loads, simulated biomass of Alewife 1+ fell below 0.01 g/m<sup>2</sup> when biomass of Chinook salmon 1–4 was greater than 0.03 g/m<sup>2</sup> and Quagga mussel biomass was greater than 20 g/m<sup>2</sup>.

## **4.5 Discussion**

### **4.5.1 Overview and synthesis**

Although the production and biomass of alewives changed little between 1984 and 2002 in Lake Huron, an increase in the relative importance of bottom-up effects was a sign of their potential collapse in 2003. This is indicated by the biomass flow analysis which suggested that a shift occurred from the pelagic pathway to the benthic pathway in the food web between these years. The initial shift in biomass flow was clearly associated with the invasion of benthic dreissenid mussels. Although the decrease in primary production resulting from nutrient load reduction and dreissenid invasion caused little decrease in zooplankton production, about half of the production of non-dreissenid benthos, on which most fish species feed, was replaced by dreissenid production. As a result, in 2002 almost all of non-dreissenid benthos production (94%) and only about a quarter (26%) of dreissenid mussel production was consumed. The limited availability of non-dreissenid benthos likely caused decreases in production for pelagic prey fishes, in particular rainbow smelt (about 80%), and its predators. Although a sharp decrease in alewife biomass had not occurred in 2002, results from biomass flow analyses implied that consumptive demand by predators on alewives would increase with the sharp decrease in rainbow smelt biomass.

Ecosim simulation scenarios shed further light on the relative importance of top-down (Chinook salmon) and bottom-up (quagga mussel and nutrient) effects that could have caused the

collapse of alewives in Lake Huron. The simulated alewife biomass collapsed under a scenario representing conditions observed in 2003–2004 of median levels of Chinook salmon ( $0.07 \text{ g/m}^2$ ) and quagga mussel ( $40 \text{ g/m}^2$ ), and low level of nutrients. Therefore, although alewives were still abundant in 2002, our scenario simulations showed that their population would collapse soon after if conditions of 2003–2004 persisted. Ecosystem conditions reported after 2004 correspond to scenarios of low nutrient loads (Dolan and Chapra, 2012) and high quagga mussel biomass (Thomas Nalepa, University of Michigan, unpublished data). Under such conditions, simulation results show that bottom-up effects from reduced nutrients and quagga mussel filtration are strong enough to keep alewives from recovery even in scenarios where Chinook salmon are absent.

Simulation results suggest that there was an upper limit to Chinook salmon predation on alewives in Lake Huron, and that this limit was expanded with increases in bottom-up control caused by dreissenid consumption and reduction in nutrients. An upper limit of Chinook salmon predation on alewives probably results from limited spatial overlap determined by temperature preference. In the Lake Huron main basin, Chinook salmon are generally found in areas where temperatures are close to  $13 \text{ }^\circ\text{C}$  (Bergstedt, USGS Hammond Bay Biological Station, Millersburg, Michigan, unpublished), but alewives are distributed in areas within a wider temperature range as they are found throughout the water column from nearshore to depth of over 110 m (Adlerstein et al., 2007). Therefore, large part of alewife biomass in the main basin was probably not vulnerable to Chinook salmon predation until bottom-up control increased.

Increases in Chinook salmon predation on alewives associated with bottom-up control possibly resulted from changes in the biomass proportion of available pelagic prey to Chinook salmon's diet. Alewives and rainbow smelt are the two most important prey for Chinook salmon,

and simulated biomass of rainbow smelt decreased more under scenarios of quagga mussel or nutrient effects than alewife biomass (Fig. 4.9 and 4.10). Therefore, given increases in bottom-up control that caused decreases in alternative prey, Chinook salmon were forced to explore a wider area beyond their temperature preference increasing the proportion of alewife biomass that was vulnerable to predation.

Many studies have empirically linked Chinook salmon predation (He et al., 2014), dreissenid invasion (Nalepa et al., 2007), or reduction in nutrients (Barbiero et al., 2012), to the collapse of alewives in Lake Huron, while our analyses showed a possible causality that integrates findings from these studies. The combined results from biomass flow analysis and scenario simulations suggest that the collapse of alewives in Lake Huron can be described in chronological order as: (1) an increase in top-down control from increased Chinook salmon predation, followed by (2) an increase in bottom-up control from reduction in production caused by decreases in nutrients and increases in dreissenids, which caused (3) a decrease in biomass of non-dreissenid benthos, and (4) a decrease in biomass of rainbow smelt, (5) an increase in the proportion of alewife in Chinook salmon's diet and thus predation mortality, finally resulting in the collapse of alewife population.

#### **4.5.2 Potential model biases**

There are several potential biases associated with Ecopath input parameter estimates that may affect our model results. There are consequences from the data quality even when we integrated the best available information for the Lake Huron ecosystem. Among these data issues are biomass estimates for food web groups that were not always representative of annual averages and their full distribution ranges (see Appendix E for data sources). For example, prey

fish biomass can be underestimated as sampling is conducted with surveys during fall after most predation mortality on prey fish has taken place (He et al., 2014) and also surveys only cover areas at depths between 9–110 m. On the other hand estimates for zooplankton might be overestimated as they were from surveys conducted between 50–140 m and biomass in deeper areas of the lake might be higher than the lakewide average. This is because in those areas zooplankton is less vulnerable to the predation by pelagic prey fishes, which are most abundant in areas < 80 m in depth (Adlerstein et al., 2007). Therefore extrapolating lakewide zooplankton biomass from survey data may overestimate the annual average biomass while extrapolating lakewide prey fish biomass from fall survey data may under estimate the annual average biomass. Consequently, consumption by pelagic prey fish on zooplankton in both 1984 and 2002 Ecopath models might be underestimated. However, the consumption underestimation should have minimal effects on our general results of biomass flow analyses and scenario simulations, as the Ecopath models showed that zooplankton production would have not been a limiting factor for production of pelagic prey fishes in 1984 or 2002.

Another data issue associated with biomass model inputs is estimating absolute biomass from survey indices. The main difficulty is generated for fish groups by the absence of estimates of survey gear catchability for most species. Also, available data are in different units across trophic levels, such as carbon weight for phytoplankton, dry weight for zooplankton, ash-free dry weight for benthos, and wet weight for fish, which need to be converted into wet weight. The assumptions we made for conversion factors and gear catchabilities (see Appendix E for assumptions) were reasonable as we could balance both Ecopath models and obtain generally good fits in Ecosim calibration for most groups. However, better estimates for gear catchabilities and biomass conversion factors are needed for improving food web modeling in the Great Lakes.

Other potential bias in our analysis is overestimation of consumption by quagga mussels in the simulations and inconsistent results from Ecosim modeling of bloater biomass time series. As the quagga mussel population was expanding during the calibration period, the population was dominated by young individuals (Nalepa, unpublished) and consumption to biomass ratio is higher than that of older individuals. Therefore, the Ecosim-modeled consumption represented consumption of a population dominated by young individuals and an equilibrium population probably has a higher proportion of older age classes. For bloaters, changes in the biomass time series estimated from survey data were much larger than those projected in our model (Fig. 4.7). Although it is possible that bloater indices are not representative of population abundance, poor fit is probably because bloater recruitment is not controlled by predator–prey interactions but by intra-specific factors as proposed by Bunnell et al. (2006) and Collingsworth et al. (2014). We do not expect the lack of fit to affect our results because bloaters did not constitute a significant prey of food web groups in our models, and given that biomass of bloaters in 1984, initial year for Ecosim, was relatively low.

#### **4.5.3 Implications for top-down and bottom-up effects in Lake Huron**

Our results inform understanding of food web dynamics under top-down and bottom-up controls in Lake Huron, which should not be affected by the potential biases listed above. These findings are also informative to dynamics in Lake Michigan and Lake Ontario where food web structures, anthropogenic stressors, and management activities are similar to those in Lake Huron before the collapse of alewives (Adkinson and Morrison, 2012; Bunnell, 2012).

An important implication from our findings is that top-down effects of salmonine predation on pelagic prey fishes would have reached an upper limit since the mid 1980s. This is

suggested by simulation results that showed an upper limit of Chinook salmon effects on alewives. As discussed above, this upper limit indicates a depletion of vulnerable prey fish biomass. Since most salmonines in the Great Lakes prefer to inhabit the pelagic zone where temperatures ranged from 9 to 15 °C (Coutant, 1977), top-down effects would not increase with increases in salmonine biomass until the vulnerable prey fish biomass in the pelagic zone is depleted. In Lake Michigan, Lake Huron, and Lake Ontario, salmonine biomass has been at high levels since the mid-1980s and thus top-down control imposed on pelagic prey fishes has probably been very strong but constant.

The general notion that top-down control of salmon predation on pelagic prey fishes has an upper limit is supported by relatively constant estimated lake wide consumption by salmonines despite changes in species composition and biomass of both prey fishes and salmonines. This was observed in Lake Michigan between 1982 and 1988 (Stewart and Ibarra, 1991), in Lake Huron between 1988 and 2004 (He et al., 2014), and in Ontario between 1987 and 1994 (Rand and Stewart, 1998). This upper limit concept in Lake Huron also is supported by reports of significant negative relationships between estimates of salmonine predation and indices of prey fish recruitment if using data collected in the 1970s. During that period, salmonine biomass increased from very low to high levels. On the other hand, no significant relationships between salmonine and prey biomass is observed when data collected after 1980 are included (Bunnell et al., 2014; Collingsworth et al., 2014; Madenjian et al., 2005; O'Brien et al., 2014; O'Gorman et al., 2004).

Model results suggest that in benthos responds to bottom-up effects earlier than zooplankton. For Lake Huron, our biomass flow analysis showed zooplankton production decreased much less than non-dreissenid benthos between 1984 and 2002. With increases in



bottom-up effects in this period, our results showed that zooplankton could maintain production and biomass by consuming a higher proportion of primary production and secondary production from bacteria that recycled organic matter into the pelagic pathway. Consequently, the availability of detritus that settled on the bottom of the lake decreased more than the decrease in primary production. Empirical data indicate that patterns in decreasing biomass of zooplankton biomass were not clear until the 2000s in Lake Huron as well as in Lake Michigan and Lake Ontario (Bunnell et al., 2014; Dobiesz et al., 2005; Madenjian et al., 2002), but decreasing biomass of non-dreissenid benthos has been observed since the 1970s (Mills et al., 2003; Nalepa et al., 2007; Nalepa et al., 2009). Although Mills et al. (2003) reported decreases in zooplankton biomass in two Lake Ontario stations from 1980 to 1995 the same trend was not seen in lakewide survey data (Bunnell et al., 2014).

Model simulations indicated that dreissenid mussels impacted the ecosystem mainly through nutrient sequestration but it is unlikely that they out-competed zooplankton for resources causing decreases in biomass after 2002. The biomass flow analysis showed that zooplankton consumption of phytoplankton was 13 times higher than that of dreissenid mussels in Lake Huron in 2002. This ratio estimate is in line with a previous study in Lake Erie (Zhang et al., 2011). On the other hand, effects of nutrient sequestration by dreissenid mussels in Lake Huron main basin might be insignificant compared to their impact of sequestration in nearshore areas. Our simulations showed that bottom-up effects from nutrient reduction were stronger than effects from increases in quagga mussel biomass but this does not consider that mussels were partially responsible for this reduction. Cha et al. (2011) showed that the proportion of nutrient loads from Saginaw Bay to Lake Huron main basin decreased by 40% after the invasion of dreissenid

mussels. As a result, part of bottom-up effects attributed to nutrients in our simulations should also be attributed to dreissenid mussels.

#### **4.5.4 Result implications for predicting alewife population trends in Lake Michigan and Lake Ontario**

Our results have implications for management in Lake Michigan and Lake Ontario. Sustaining a prey base for predators that are target of valuable fisheries has been a concern for resource managers ever since the collapse of alewives in Lake Huron. The main difference among these three lakes is that Lake Huron is oligotrophic and nutrient loads have been much lower than those in Lakes Michigan and Ontario. The biomass of Chinook salmon and quagga mussel in these two lakes (Rogers et al., 2014; Stewart and Sprules, 2011), as well as nutrient loads (Dolan and Chapra, 2012), were above the upper limits in our simulation scenario, and thus we cannot directly use our results to make predictions. However, we expect that the process of alewife collapse would be the same among these lakes. Based on observed changes in Lake Michigan and Lake Ontario (Table 4.10), it is reasonable to expect that alewives will collapse in both lakes if consecutive years of low nutrient loads are in the horizon. Currently in these two lakes, the biomass flow to Chinook salmon is through a simple pelagic pathway: phytoplankton → zooplankton → alewives → Chinook salmon. When nutrients become limited, both top-down and bottom-up effects on alewives will become very strong and will most certainly result in population collapse in these systems.

#### **4.5.5 More on management implications**

Our model results show that there are conflicts to achieving management objectives that have been established independently. In Lake Michigan, Lake Huron, and Lake Ontario, management has attempted to control alewife abundance, reversing cultural eutrophication and later, and after quagga mussel invasion, maintaining Chinook salmon recreational fisheries. In all lakes, controlling alewife abundance—the main objective of introducing Chinook salmon—has been achieved. The objective of reversing cultural eutrophication through nutrient reduction has also been achieved. In fact, “cultural oligotrophication” is more of a management concern now in the Great Lakes (Evans et al., 2011). Maintaining Chinook populations at desirable levels is probably impractical under such conditions. In Lake Huron, the alewife population has even collapsed and our model results also suggest that they are unlikely to recover. The collapse drove the decline in the salmon population, and would have not happened, based on our model if nutrient levels would have been higher, and in the absence of quagga mussels. Thus, it may not be possible to maintain the Chinook salmon recreational fisheries at current or historic levels observed in the 1990s and 2000s while achieving the other objectives under current expansion of the quagga mussel populations.

**Table 4.1** Functional components and food web groups in the Lake Huron Ecopath models.

Functional component	Group (stanza age)	Scientific name or main taxa in the group
Predators	Double-crested cormorant	<i>Phalacrocorax auritus</i>
	Sea lamprey	<i>Petromyzon marinus</i>
	Chinook salmon (0–0.5, 0.5–1, 1–4, 5+)	<i>Oncorhynchus tshawytscha</i>
	Lake trout (0–0.5, 0.5–1, 1–4, 5+)	<i>Salvelinus namaycush</i>
	Other salmonines (0, 1–4, 5+)	<i>Oncorhynchus mykiss</i> and <i>O. kisutch</i>
	Burbot (0–0.5, 0.5–1, 1+)	<i>Lota lota</i>
	Walleye	<i>Sander vitreus</i>
Lake whitefish	Lake whitefish (0, 1–2, 3+)	<i>Coregonus clupeaformis</i>
Pelagic prey fishes	Alewife (0, 1+)	<i>Alosa pseudoharengus</i>
	Rainbow smelt (0, 1+)	<i>Osmerus mordax</i>
	Bloater (0, 1+)	<i>Coregonus hoyi</i>
Benthic prey fishes	Yellow perch (0–0.5, 0.5–1, 1–2, 3+)	<i>Perca flavescens</i>
	Deepwater sculpin (0–0.5, 0.5+)	<i>Myoxocephalus thompsonii</i>
	Slimy sculpin	<i>Cottus cognatus</i>
	Ninespine stickleback	<i>Pungitius pungitius</i>
	Other prey fishes	<i>Percopsis omiscomaycus</i> and <i>Catostomus commersonii</i>
Zooplankton	Round goby	<i>Neogobius melanostomus</i>
	Predatory cladocerans	<i>Bythotrephes cederstroemii</i> and <i>Leptodora kindti</i>
	Cladocerans	<i>Daphnia</i> spp. and <i>Bosmina longirostris</i>
	Cyclopoids	<i>Diacyclops bicuspidatus</i> and <i>Tropocyclops prasinus mexicanus</i> after nauplius stage
	Calanoids	<i>Leptodiaptomus</i> spp. and <i>Limnocalanus macrurus</i> after nauplius stage
	Nauplii	Copepods at nauplius stage
	Rotifers	<i>Kellicottia</i> spp., <i>Keratella</i> spp., and <i>Ploesoma</i> spp.
Benthos	Mysis	<i>Mysis diluviana</i>
	Amphipods	<i>Diporeia</i> spp.
	Chironomids	Chironomidae larvae and pupae stages
	Oligochaetes	Tubificidae
	Sphaeriids	<i>Pisidium</i> spp.
	Zebra mussel	<i>Dreissena polymorpha</i>
	Quagga mussel	<i>Dreissena bugensis</i>
Microplankton	Protozoa	Heterotrophic chrysophytes, cryptomonads, dinoflagellates, flagellates, and ciliates
	Bacteria	Pelagic bacteria
	Inedible phytoplankton	Cyanophytes
	Edible phytoplankton	Bacillariophytes, chlorophytes and autotrophic genera of chrysophytes, cryptomonads, dinoflagellate and flagellates
Detritus	Pelagic detritus	Dissolved and suspended organic matter
	Settled detritus	Organic matter settled to the bottom

**Table 4.2** Parameters in the 1984 and 2002 Lake Huron Ecopath models. Parameters estimated by Ecopath are in bold. Parameters that are identical in both Ecopath models are not shown for the 2002 model. *P/B*: the production to biomass ratio for groups with only one stanza; *Z*: the total mortality rate for multi-stanza groups; *Q/B*: the consumption to biomass ratio; *Y*: fishery yields; *U/Q*: the proportion of unassimilated food in consumption.

No.	Group	Biomass (g/m <sup>2</sup> )		<i>P/B</i> or <i>Z</i> (/yr)		<i>Q/B</i> (/yr)		<i>Y</i> (×10 <sup>-2</sup> g/m <sup>2</sup> )		Ecotrophic efficiency		<i>U/Q</i> 84
		84	02	84	02	84	02	84	02	84	02	
<b>Predators</b>												
1	Double-crested cormorant	1.1×10 <sup>-5</sup>	2.2×10 <sup>-3</sup>	0.2		50		–	–	<b>0.00</b>	<b>0.00</b>	0.20
2	Sea lamprey	4.6×10 <sup>-4</sup>	4.3×10 <sup>-4</sup>	1.2		130		–	–	<b>0.00</b>	<b>0.00</b>	0.96
3	Chinook salmon 0–0.5	<b>5.5×10<sup>-4</sup></b>	<b>6.7×10<sup>-4</sup></b>	1.1	2.5	<b>26.0</b>	<b>25.8</b>	–	–	<b>0.04</b>	<b>0.04</b>	0.27
4	Chinook salmon 0.5–1	<b>5.4×10<sup>-3</sup></b>	<b>4.5×10<sup>-3</sup></b>	0.75	1.4	<b>12.6</b>	<b>12.2</b>	–	–	<b>0.04</b>	<b>0.04</b>	0.27
5	Chinook salmon 1–4	0.19	0.09	0.53	0.74	5.2		1.29	2.34	<b>0.28</b>	<b>0.56</b>	0.23
6	Chinook salmon 5+	<b>0.01</b>	<b>4.3×10<sup>-3</sup></b>	3.0		<b>3.9</b>	<b>3.7</b>	–	–	<b>0.00</b>	<b>0.00</b>	0.23
7	Lake trout 0–0.5	<b>7.6×10<sup>-5</sup></b>	<b>5.7×10<sup>-5</sup></b>	5.0		<b>37.5</b>	<b>39.7</b>	–	–	<b>0.82</b>	<b>0.81</b>	0.27
8	Lake trout 0.5–1	<b>3.7×10<sup>-4</sup></b>	<b>2.8×10<sup>-4</sup></b>	1.7		<b>15.8</b>	<b>16.7</b>	–	–	<b>0.04</b>	<b>0.04</b>	0.27
9	Lake trout 1–4	<b>0.04</b>	<b>0.03</b>	0.30	0.29	<b>4.4</b>	<b>4.7</b>	–	–	<b>0.14</b>	<b>0.18</b>	0.23
10	Lake trout 5+	0.05	0.07	0.52	0.35	2.7		0.55	0.64	<b>0.43</b>	<b>0.48</b>	0.23
11	Other salmonines 0	<b>4.3×10<sup>-4</sup></b>	<b>2.6×10<sup>-4</sup></b>	1.4		<b>20.0</b>		–	–	<b>0.04</b>	<b>0.04</b>	0.27
12	Other salmonines 1–4	0.02	9.1×10 <sup>-3</sup>	0.45		6.9		0.11	0.20	<b>0.24</b>	<b>0.61</b>	0.23
13	Other salmonines 5+	<b>1.4×10<sup>-3</sup></b>	<b>8.3×10<sup>-4</sup></b>	3.0		<b>5.2</b>		–	–	<b>0.00</b>	<b>0.00</b>	0.23
14	Burbot 0–0.5	<b>2.2×10<sup>-4</sup></b>	<b>1.5×10<sup>-4</sup></b>	5.0		<b>23.4</b>		–	–	<b>0.71</b>	<b>0.81</b>	0.24
15	Burbot 0.5–1	<b>9.7×10<sup>-4</sup></b>	<b>6.7×10<sup>-4</sup></b>	1.7		<b>10.1</b>		–	–	<b>0.04</b>	<b>0.04</b>	0.24
16	Burbot 1+	0.04	0.03	0.63		3.4		–	–	<b>0.41</b>	<b>0.55</b>	0.24
17	Walleye	0.01	0.02	0.43		2.3		0.37	0.20	<b>0.67</b>	<b>0.23</b>	0.18
<b>Lake whitefish</b>												
18	Lake whitefish 0	<b>7.2×10<sup>-3</sup></b>	<b>0.02</b>	2.5		<b>34.5</b>	<b>44.4</b>	–	–	<b>0.04</b>	<b>0.04</b>	0.34
19	Lake whitefish 1–2	<b>0.11</b>	<b>0.27</b>	0.50		<b>11.7</b>	<b>14.5</b>	–	–	<b>0.04</b>	<b>0.05</b>	0.33
20	Lake whitefish 3+	0.46	0.90	0.51	0.67	6.1	7.5	4.31	7.59	<b>0.27</b>	<b>0.16</b>	0.33
<b>Pelagic prey fishes</b>												
21	Alewife 0	<b>0.53</b>	<b>0.52</b>	5.1		<b>43.7</b>		–	–	<b>0.50</b>	<b>0.42</b>	0.24
22	Alewife 1+	1.02	1.01	1.2		14.6		–	–	<b>0.31</b>	<b>0.31</b>	0.24
23	Rainbow smelt 0	<b>1.89</b>	<b>0.42</b>	4.3		<b>20.6</b>		–	–	<b>0.88</b>	<b>0.80</b>	0.24
24	Rainbow smelt 1+	4.96	1.11	1.3		7.3		< 0.01	< 0.01	<b>0.09</b>	<b>0.13</b>	0.24
25	Bloater 0	<b>0.02</b>	<b>0.01</b>	2.5		<b>28.9</b>	<b>32.1</b>	–	–	<b>0.80</b>	<b>0.53</b>	0.33
26	Bloater 1+	0.48	0.47	0.83	0.63	8.4		1.24	0.07	<b>0.11</b>	<b>0.08</b>	0.33
<b>Benthic prey fishes</b>												
27	Yellow perch 0–0.5	<b>7.8×10<sup>-3</sup></b>	<b>6.5×10<sup>-3</sup></b>	5.5		<b>74.9</b>		–	–	<b>0.41</b>	<b>0.56</b>	0.30
28	Yellow perch 0.5–1	<b>0.03</b>	<b>0.02</b>	2.7		<b>32.2</b>		–	–	<b>0.18</b>	<b>0.32</b>	0.30
29	Yellow perch 1–2	0.18	0.15	1.2		14.4		–	–	<b>0.01</b>	<b>0.06</b>	0.21
30	Yellow perch 3+	<b>0.08</b>	<b>0.07</b>	1.4		<b>8.7</b>		0.63	0.34	<b>0.06</b>	<b>0.05</b>	0.21
31	Deepwater sculpin 0–0.5	<b>0.01</b>	<b>7.6×10<sup>-3</sup></b>	5.0		<b>24.5</b>		–	–	<b>0.43</b>	<b>0.43</b>	0.34
32	Deepwater sculpin 0.5+	1.45	1.08	1.1		3.7		–	–	<b>0.03</b>	<b>0.04</b>	0.34
33	Slimy sculpin	0.06	0.12	1.3		4.0		–	–	<b>0.31</b>	<b>0.39</b>	0.34
34	Ninespine stickleback	0.03	0.11	1.9		10.7		–	–	<b>0.12</b>	<b>0.47</b>	0.34
35	Other prey fishes	0.10	0.27	1.4		6.2		–	–	<b>0.08</b>	<b>0.18</b>	0.34
36	Round goby	–	0.24	–	1.8	–	7.9	–	–	–	<b>0.87</b>	0.24

**Table 4.2** *Continued.*

No	Group	Biomass (g/m <sup>2</sup> )		<i>P/B</i> or <i>Z</i> (/yr)		<i>Q/B</i> (/yr)		<i>Y</i> (g/100/m <sup>2</sup> )		Ecotrophic efficiency		<i>U/Q</i>
		84	02	84	02	84	02	84	02	84	02	84
<b>Zooplankton</b>												
37	Predatory cladocerans	0.15	0.37	8.3		30.6		–	–	<b>0.86</b>	<b>0.29</b>	0.38
38	Cladocerans	8.68	9.63	14.9		59.5		–	–	<b>0.29</b>	<b>0.36</b>	0.40
39	Cyclopoids	4.26	4.65	8.7		34.6		–	–	<b>0.44</b>	<b>0.18</b>	0.40
40	Calanoids	13.96	12.65	5.8		23.3		–	–	<b>0.39</b>	<b>0.19</b>	0.40
41	Nauplii	3.58	1.82	19.3		77.0		–	–	<b>0.43</b>	<b>0.37</b>	0.40
42	Rotifers	0.40	0.53	21.0		84.0		–	–	<b>0.65</b>	<b>0.61</b>	0.50
<b>Benthos</b>												
43	Zebra mussel	–	6.56	–	1.03	–	4.9	–	–	–	<b>0.27</b>	0.65
44	Quagga mussel	–	30.48	–	0.51	–	1.8	–	–	–	<b>0.26</b>	0.65
45	Mysis	0.59	0.34	2.8		22.4		–	–	<b>0.66</b>	<b>0.99</b>	0.30
46	Amphipods	20.12	6.19	2.0		10.5		–	–	<b>0.65</b>	<b>0.97</b>	0.50
47	Chironomids	0.97	2.03	3.1		17.2		–	–	<b>0.71</b>	<b>0.97</b>	0.50
48	Oligochaetes	4.94	2.69	1.8		9.0		–	–	<b>0.64</b>	<b>0.92</b>	0.50
49	Sphaeriids	1.25	0.73	1.4		18.7		–	–	<b>0.21</b>	<b>0.31</b>	0.50
<b>Microplankton</b>												
50	Protozoa	1.92	1.23	102		340		–	–	<b>0.77</b>	<b>0.88</b>	0.40
51	Bacteria	1.65	1.06	125	172	463	638	–	–	<b>0.86</b>	<b>0.99</b>	0.40
52	Inedible phytoplankton	0.56	0.24	411	410	–	–	–	–	<b>0.36</b>	<b>0.32</b>	–
53	Edible phytoplankton	10.22	8.64	182	165	–	–	–	–	<b>0.84</b>	<b>0.95</b>	–
<b>Detritus</b>												
54	Pelagic detritus	150	125	–	–	–	–	–	–	<b>0.60</b>	<b>0.66</b>	–
55	Settled detritus	13	11	–	–	–	–	–	–	<b>0.06</b>	<b>0.08</b>	–

**Table 4.3** Diet composition inputs (%) in the 1984 Lake Huron Ecopath model.

No. Prey	Predator																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 Double-crested cormorant																		
2 Sea lamprey																		
3 Chinook salmon 0–0.5 ( $\times 10^3$ )					1.6				1.1	1.3		0.8						1.8
4 Chinook salmon 0.5–1 ( $\times 10^3$ )					10.8				7.1	8.7		5.3						11.8
5 Chinook salmon 1–4		25.3																
6 Chinook salmon 5+																		
7 Lake trout 0–0.5 ( $\times 10^3$ )					1.0				0.7	0.8		0.5						1.1
8 Lake trout 0.5–1 ( $\times 10^3$ )					1.7				1.1	1.4		0.8						1.8
9 Lake trout 1–4		2.8																
10 Lake trout 5+		11.1																
11 Other salmonines 0 ( $\times 10^3$ )				0.4	1.6				1.1	1.3		0.8						1.8
12 Other salmonines 1–4		0.9																
13 Other salmonines 5+																		
14 Burbot 0–0.5 ( $\times 10^3$ )					3.0				1.9	2.4	0.5	1.5						3.2
15 Burbot 0.5–1 ( $\times 10^3$ )				1.2	4.4				2.9	3.6		2.2						4.8
16 Burbot 1+		17.9																
17 Walleye		0.2																
18 Lake whitefish 0 ( $\times 10^2$ )				1.3	4.8				3.2	3.9	1.8	2.4			0.5	2.1	5.2	
19 Lake whitefish 1–2 ( $\times 10^2$ )					14.4				9.5	11.7	2.7	7.1			3.1	25.6	15.7	
20 Lake whitefish 3+		35.7																
21 Alewife 0	12.0			19.5	7.2				9.5	5.8	5.3	7.1			0.8	6.4	7.8	
22 Alewife 1+	25.6			1.8	32.9				8.7	10.6	1.2	6.5			0.7	5.8	7.2	
23 Rainbow smelt 0	5.6			59.1	21.7			4.9	28.6	17.6	16.1	21.5			2.3	19.3	23.7	
24 Rainbow smelt 1+	11.2			18.8	34.5				45.5	55.9	6.4	34.2			3.7	30.6	37.6	
25 Bloater 0 ( $\times 10$ )				1.8	1.6				1.1	1.3	0.6	1.6			0.2	1.5		
26 Bloater 1+		6.4		0.3	2.1				0.7	0.9	0.4	1.1			0.2	1.9		
27 Yellow perch 0–0.5 ( $\times 10$ )					1.1				0.8	0.9	0.4	1.1				0.5		
28 Yellow perch 0.5–1 ( $\times 10$ )	32			0.5	1.9				1.2	1.5	0.7	1.8			0.2	0.8	4.0	
29 Yellow perch 1–2 ( $\times 10$ )	72								3.8	4.7	1.1	2.9			0.6	2.6	12.6	
30 Yellow perch 3+ ( $\times 10$ )										2.5		1.5					6.6	
31 Deepwater sculpin 0–0.5 ( $\times 10$ )				0.4				0.3	0.9	1.1								
32 Deepwater sculpin 0.5+									5.8	7.1					1.9	19.4		
33 Slimy sculpin ( $\times 10$ )	32			0.5	1.8			0.4	1.2	3.0	0.7	1.8			0.8	3.2	2.0	
34 Ninespine stickleback ( $\times 10$ )	120			0.8	2.8				0.9	1.1	0.5	1.4			0.6	2.5	1.5	
35 Other prey fishes ( $\times 10$ )				1.0	3.6				2.3	2.9	1.3	3.5			0.4	1.6	7.7	
36 Round goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
37 Predatory cladocerans ( $\times 10$ )			0.8				1.5	0.9			0.3	0.9		2.3				4.4
38 Cladocerans			1.5				3.0	2.0			1.5	1.1		4.5				20.4
39 Cyclopoids			2.2				4.3	1.9			0.8	0.7		6.5				11.0
40 Calanoids			4.7				9.3	4.3			1.5	1.5		14.0				19.5
41 Nauplii			14.8				29.7	1.5			1.9	0.7		44.5				26.0
42 Rotifers			1.8				3.5	0.2			0.2			5.3				2.7
43 Zebra mussel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
44 Quagga mussel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45 Mysis			0.6				0.4	0.9			0.5	0.2		0.2	1.0	0.2		0.2
46 Amphipods			21.9				14.6	59.2			18.7	7.0		7.3	62.7	11.8		5.8
47 Chironomids			17.7				11.8	5.4			15.1	5.7		5.9	5.7	0.4		4.7
48 Oligochaetes			34.7				23.2	16.3			29.6	11.1		11.6	17.3	2.1		9.3
49 Sphaeriids								3.2							3.4	0.5		
50 Protozoa																		
51 Bacteria																		
52 Inedible phytoplankton																		
53 Edible phytoplankton																		
54 Pelagic detritus																		
55 Settled detritus																		
56 Import		20				100							100					20

**Table 4.3 Continued.**

No. Prey	Predator																		
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
1 Double-crested cormorant																			-
2 Sea lamprey																			-
3 Chinook salmon 0-0.5 ( $\times 10^3$ )																			-
4 Chinook salmon 0.5-1 ( $\times 10^3$ )																			-
5 Chinook salmon 1-4																			-
6 Chinook salmon 5+																			-
7 Lake trout 0-0.5 ( $\times 10^3$ )				2.0															-
8 Lake trout 0.5-1 ( $\times 10^3$ )																			-
9 Lake trout 1-4																			-
10 Lake trout 5+																			-
11 Other salmonines 0 ( $\times 10^3$ )																			-
12 Other salmonines 1-4																			-
13 Other salmonines 5+																			-
14 Burbot 0-0.5 ( $\times 10^3$ )				5.0															-
15 Burbot 0.5-1 ( $\times 10^3$ )																			-
16 Burbot 1+																			-
17 Walleye																			-
18 Lake whitefish 0 ( $\times 10^2$ )																			-
19 Lake whitefish 1-2 ( $\times 10^2$ )																			-
20 Lake whitefish 3+																			-
21 Alewife 0						2.8					4.8	9.6							-
22 Alewife 1+																			-
23 Rainbow smelt 0		2.0				17.0					14.5	29.0							-
24 Rainbow smelt 1+																			-
25 Bloater 0 ( $\times 10$ )						1.3													-
26 Bloater 1+																			-
27 Yellow perch 0-0.5 ( $\times 10$ )				0.7							1.5	3.1							-
28 Yellow perch 0.5-1 ( $\times 10$ )											2.5	4.9							-
29 Yellow perch 1-2 ( $\times 10$ )																			-
30 Yellow perch 3+ ( $\times 10$ )																			-
31 Deepwater sculpin 0-0.5 ( $\times 10$ )				0.8		0.3													-
32 Deepwater sculpin 0.5+																			-
33 Slimy sculpin ( $\times 10$ )		0.1				0.4					1.2	2.4							-
34 Ninespine stickleback ( $\times 10$ )		0.3									0.5	0.9							-
35 Other prey fishes ( $\times 10$ )		0.2									1.2	2.4							-
36 Round goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
37 Predatory cladocerans ( $\times 10$ )	9.2	1.8	5.5	18.4	5.0	11.5	5.5	4.6	2.3	2.2	2.3		3.0	0.3	0.8	11.5	4.6		-
38 Cladocerans	10.6	2.1	25.5	21.1	22.9	13.2	25.5	5.3	4.5	5.0	2.6		6.0	1.3	3.8	13.2	5.3		-
39 Cyclopoids	6.9	1.4	13.7	13.8	12.3	8.7	13.7	3.5	6.5	4.7	1.7		8.6	0.7	2.1	8.7	3.5		-
40 Calanoids	14.8	3.0	24.4	29.6	22.0	18.5	24.4	7.4	14.0	10.8	3.7		18.7	1.2	3.7	18.5	7.4		-
41 Nauplii	6.7	1.3	32.5	13.5	29.2	8.4	32.5	3.4	44.5	3.9	1.7		59.3	1.6	4.9	8.4	3.4		-
42 Rotifers			3.4		3.0		3.4		5.3	0.5			7.1	0.2	0.5				-
43 Zebra mussel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
44 Quagga mussel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45 Mysis	0.7	1.0		1.4	0.1	0.4		5.6	0.2	0.6	0.6	0.5		6.7	1.0	0.6	0.9		-
46 Amphipods	41.8	62.7		16.7	7.2	24.5		65.9	7.3	21.9	19.6	16.8		78.3	67.1	40.8	55.7		-
47 Chironomids	3.8	5.7		0.4	0.7	0.9		1.6	5.9	17.7	15.9	13.6		1.9	2.4	1.4	5.1		-
48 Oligochaetes	11.5	17.3		1.4	2.0	4.3		5.7	11.6	34.7	31.1	26.7		6.7	11.7	7.1	15.3		-
49 Sphaeriids	2.2	3.4						1.2			2.8	2.4		1.4	2.8		3.0		-
50 Protozoa																			-
51 Bacteria																			-
52 Inedible phytoplankton																			-
53 Edible phytoplankton																			-
54 Pelagic detritus																			-
55 Settled detritus																			-
56 Import																			-



**Table 4.3 Continued.**

No. Prey	Predator														
	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
1 Double-crested cormorant							-	-							
2 Sea lamprey							-	-							
3 Chinook salmon 0-0.5 ( $\times 10^3$ )							-	-							
4 Chinook salmon 0.5-1 ( $\times 10^3$ )							-	-							
5 Chinook salmon 1-4							-	-							
6 Chinook salmon 5+							-	-							
7 Lake trout 0-0.5 ( $\times 10^3$ )							-	-							
8 Lake trout 0.5-1 ( $\times 10^3$ )							-	-							
9 Lake trout 1-4							-	-							
10 Lake trout 5+							-	-							
11 Other salmonines 0 ( $\times 10^3$ )							-	-							
12 Other salmonines 1-4							-	-							
13 Other salmonines 5+							-	-							
14 Burbot 0-0.5 ( $\times 10^3$ )							-	-							
15 Burbot 0.5-1 ( $\times 10^3$ )							-	-							
16 Burbot 1+							-	-							
17 Walleye							-	-							
18 Lake whitefish 0 ( $\times 10^2$ )							-	-							
19 Lake whitefish 1-2 ( $\times 10^2$ )							-	-							
20 Lake whitefish 3+							-	-							
21 Alewife 0							-	-							
22 Alewife 1+							-	-							
23 Rainbow smelt 0							-	-							
24 Rainbow smelt 1+							-	-							
25 Bloater 0 ( $\times 10$ )							-	-							
26 Bloater 1+							-	-							
27 Yellow perch 0-0.5 ( $\times 10$ )							-	-							
28 Yellow perch 0.5-1 ( $\times 10$ )							-	-							
29 Yellow perch 1-2 ( $\times 10$ )							-	-							
30 Yellow perch 3+ ( $\times 10$ )							-	-							
31 Deepwater sculpin 0-0.5 ( $\times 10$ )							-	-							
32 Deepwater sculpin 0.5+							-	-							
33 Slimy sculpin ( $\times 10$ )							-	-							
34 Ninespine stickleback ( $\times 10$ )							-	-							
35 Other prey fishes ( $\times 10$ )							-	-							
36 Round goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
37 Predatory cladocerans ( $\times 10$ )							-	-							
38 Cladocerans	91.6		3.6	0.5			-	-	20.1						
39 Cyclopoids	1.6		1.0	0.1			-	-	3.4						
40 Calanoids	1.4		2.3	0.3			-	-	3.0						
41 Nauplii	4.9		1.9	0.3			-	-	2.1						
42 Rotifers	0.6		0.9	0.03		5.0	-	-	1.3						
43 Zebra mussel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
44 Quagga mussel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45 Mysis							-	-	0.2						
46 Amphipods							-	-	9.4			0.2			
47 Chironomids							-	-			1.5	0.3			
48 Oligochaetes							-	-	0.4		0.5	0.5			
49 Sphaeriids							-	-							
50 Protozoa		8.7	8.3	3.1	2.8	2.6	-	-		0.9			6.0	10.9	
51 Bacteria		9.1	10.8	9.5	9.7	9.2	-	-		0.9			6.3	7.6	
52 Inedible phytoplankton							-	-						12.7	
53 Edible phytoplankton		82.2	71.1	86.1	87.5	83.2	-	-	25.0	8.2			57.0	68.8	
54 Pelagic detritus							-	-	13.5	90			30.7		100
55 Settled detritus							-	-	21.5		98	99			
56 Import							-	-							

**Table 4.4** Diet composition inputs (%) in the 2002 Lake Huron Ecopath model.

No. Prey	Predator																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 Double-crested cormorant																		
2 Sea lamprey																		
3 Chinook salmon 0–0.5 ( $\times 10^3$ )					7.7				6.6	7.1		4.5						10.1
4 Chinook salmon 0.5–1 ( $\times 10^3$ )					28.8				24.8	26.4		16.9						37.6
5 Chinook salmon 1–4		25.3																
6 Chinook salmon 5+																		
7 Lake trout 0–0.5 ( $\times 10^3$ )					1.3				1.1	1.2		0.8						1.7
8 Lake trout 0.5–1 ( $\times 10^3$ )					2.2				1.9	2.0		1.3						2.8
9 Lake trout 1–4		2.8																
10 Lake trout 5+		11.1																
11 Other salmonines 0 ( $\times 10^3$ )				0.7	1.7				1.4	1.5		1.0						2.2
12 Other salmonines 1–4		0.9																
13 Other salmonines 5+																		
14 Burbot 0–0.5 ( $\times 10^3$ )					3.5				3.0	3.2	0.8	2.1						4.6
15 Burbot 0.5–1 ( $\times 10^3$ )				2.1	5.3				4.5	4.8		3.1						
16 Burbot 1+		17.9																
17 Walleye		0.2																
18 Lake whitefish 0 ( $\times 10$ )				0.7	1.8				1.6	1.7	0.9	1.1				0.2	1.5	
19 Lake whitefish 1–2 ( $\times 10$ )					6.1				5.3	5.6	1.4	3.6				1.2	20.3	
20 Lake whitefish 3+		35.7																
21 Alewife 0		8.8		48.0	12.2				21.0	11.2	11.5	14.3				1.2	10.1	15.9
22 Alewife 1+		19.2		4.4	55.7				19.2	20.5	2.6	13.1				1.1	9.3	14.6
23 Rainbow smelt 0		4.0		32.9	8.3			3.7	14.4	7.7	7.9	9.8				0.8	6.9	10.9
24 Rainbow smelt 1+		8.8		10.4	13.3				22.8	24.4	3.1	15.6				1.3	11.0	17.3
25 Bloater 0 ( $\times 10$ )				2.4	1.5				1.3	1.4	0.7	1.8				0.2	1.3	
26 Bloater 1+		6.4		0.5	2.7				1.2	1.2	0.6	1.6				0.3	2.2	
27 Yellow perch 0–0.5 ( $\times 10$ )					1.6				1.4	1.5	0.8	1.9					1.4	
28 Yellow perch 0.5–1 ( $\times 10$ )		24		1.1	2.7				2.3	2.5	1.3	3.1				0.3	2.2	7.0
29 Yellow perch 1–2 ( $\times 10$ )		56							7.2	7.7	2.0	4.9				0.8	6.9	21.8
30 Yellow perch 3+ ( $\times 10$ )										4.0		2.6						11.4
31 Deepwater sculpin 0–0.5 ( $\times 10$ )				0.7				0.8	1.5	1.6								
32 Deepwater sculpin 0.5+									9.6	10.3						2.2	18.6	
33 Slimy sculpin ( $\times 10$ )		24		2.7	6.8			3.1	5.9	12.6	3.2	8.0				2.7	22.7	8.9
34 Ninespine stickleback ( $\times 10$ )		96		7.6	19.4				8.3	8.9	4.6	11.4				3.8	32.2	12.7
35 Other prey fishes ( $\times 10$ )				6.9	17.5				15.1	16.1	8.3	20.6				1.7	14.5	45.8
36 Round goby		19.2		1.6	2.0			0.9	6.9	18.3	1.9	11.7				2.0	16.6	10.4
37 Predatory cladocerans ( $\times 10$ )			1.1				2.1	1.5			0.4	1.3						5.9
38 Cladocerans			3.7				7.4	5.3			3.1	2.2			11.1			41.7
39 Cyclopoids			1.8				3.6	0.5			0.4	0.4			5.5			5.1
40 Calanoids			3.8				7.5	2.4			0.8	0.8			11.3			10.6
41 Nauplii			12.9				25.9	1.2			1.4	0.5			38.8			18.2
42 Rotifers			2.7				5.4	0.4			0.3				8.0			3.8
43 Zebra mussel								1.5								1.6	0.02	
44 Quagga mussel								3.4								3.5	0.6	
45 Mysis			0.3				0.2	1.4			0.2	0.1			0.1	1.5	0.5	0.1
46 Amphipods			0.6				0.4	18.9			0.5	0.2			0.2	20.0	8.8	0.2
47 Chironomids			59.6				39.7	39.4			50.8	19.1			19.9	41.7	0.9	15.9
48 Oligochaetes			14.5				9.7	18.1			12.4	4.7			4.8	19.1	3.7	3.9
49 Sphaeriids								2.4								2.5	0.4	
50 Protozoa																		
51 Bacteria																		
52 Inedible phytoplankton																		
53 Edible phytoplankton																		
54 Pelagic detritus																		
55 Settled detritus																		
56 Import		20				100							100					20

**Table 4.4 Continued.**

No. Prey	Predator																		
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
1 Double-crested cormorant																			
2 Sea lamprey																			
3 Chinook salmon 0–0.5 ( $\times 10^3$ )																			
4 Chinook salmon 0.5–1 ( $\times 10^3$ )																			
5 Chinook salmon 1–4																			
6 Chinook salmon 5+																			
7 Lake trout 0–0.5 ( $\times 10^3$ )					1.5														
8 Lake trout 0.5–1 ( $\times 10^3$ )																			
9 Lake trout 1–4																			
10 Lake trout 5+																			
11 Other salmonines 0 ( $\times 10^3$ )																			
12 Other salmonines 1–4																			
13 Other salmonines 5+																			
14 Burbot 0–0.5 ( $\times 10^3$ )					4.0														
15 Burbot 0.5–1 ( $\times 10^3$ )																			
16 Burbot 1+																			
17 Walleye																			
18 Lake whitefish 0 ( $\times 10$ )																			
19 Lake whitefish 1–2 ( $\times 10$ )																			
20 Lake whitefish 3+																			
21 Alewife 0							8.0					8.9	17.8						
22 Alewife 1+																			
23 Rainbow smelt 0			3.8			10.9						6.1	12.2						
24 Rainbow smelt 1+																			
25 Bloater 0 ( $\times 10$ )							2.0												
26 Bloater 1+																			
27 Yellow perch 0–0.5 ( $\times 10$ )					0.7							2.4	4.8						
28 Yellow perch 0.5–1 ( $\times 10$ )												3.9	7.8						
29 Yellow perch 1–2 ( $\times 10$ )																			
30 Yellow perch 3+ ( $\times 10$ )																			
31 Deepwater sculpin 0–0.5 ( $\times 10$ )				0.8		0.6													
32 Deepwater sculpin 0.5+																			
33 Slimy sculpin ( $\times 10$ )			1.5			2.2						5.0	10.0						
34 Ninespine stickleback ( $\times 10$ )			8.8									3.5	7.1						
35 Other prey fishes ( $\times 10$ )			4.0									6.4	12.8						
36 Round goby			1.8			0.7						2.9	5.8						
37 Predatory cladocerans ( $\times 10$ )	12.7	2.5	7.4	25.3	6.7	15.8	7.4	6.3	3.2	3.8	3.2		4.2	0.4	1.1	15.8	6.3	0.7	
38 Cladocerans	22.2	4.4	52.1	44.4	46.9	27.8	52.1	11.1	11.1	13.3	5.6		14.8	2.6	7.8	27.8	11.1	5.2	
39 Cyclopoids	3.6	0.7	6.4	7.1	5.8	4.5	6.4	1.8	5.5	1.3	0.9		7.3	0.3	1.0	4.5	1.8	0.6	
40 Calanoids	8.1	1.6	13.3	16.1	12.0	10.1	13.3	4.0	11.3	6.0	2.0		15.1	0.7	2.0	10.1	4.0	1.3	
41 Nauplii	4.9	1.0	22.8	9.7	20.5	6.1	22.8	2.4	38.8	3.0	1.2		51.7	1.1	3.4	6.1	2.4	2.3	
42 Rotifers			4.7		4.3		4.7		8.0	1.0			10.7	0.2	0.7			0.5	
43 Zebra mussel	10.8	15.3										1.5	1.3		0.1		1.4	16.2	
44 Quagga mussel	23.7	33.5						1.0				2.4	2.1		1.2	3.6	3.2	35.5	
45 Mysis	0.5	0.6		1.3	0.2	1.1		5.2	0.1	0.3	0.2	0.2		6.2	3.0	1.9	1.3	0.7	
46 Amphipods	6.0	8.5		15.7	2.4	18.9		61.0	0.2	0.6	0.5	0.5		72.5	49.7	31.4	17.8	9.0	
47 Chironomids	12.6	17.8		0.7	5.1	2.0		2.7	19.9	59.6	50.8	43.6		3.2	5.3	3.3	37.1	18.8	
48 Oligochaetes	5.8	8.2		2.3	2.3	8.0		9.0	4.8	14.5	12.4	10.6		10.7	21.2	13.4	17.0	8.6	
49 Sphaeriids	0.8	1.1						1.0				2.1	1.8		1.2	2.2		2.3	1.1
50 Protozoa																			
51 Bacteria																			
52 Inedible phytoplankton																			
53 Edible phytoplankton																			
54 Pelagic detritus																			
55 Settled detritus																			
56 Import																			

**Table 4.4 Continued.**

No. Prey	Predator														
	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
1 Double-crested cormorant															
2 Sea lamprey															
3 Chinook salmon 0–0.5 ( $\times 10^3$ )															
4 Chinook salmon 0.5–1 ( $\times 10^3$ )															
5 Chinook salmon 1–4															
6 Chinook salmon 5+															
7 Lake trout 0–0.5 ( $\times 10^3$ )															
8 Lake trout 0.5–1 ( $\times 10^3$ )															
9 Lake trout 1–4															
10 Lake trout 5+															
11 Other salmonines 0 ( $\times 10^3$ )															
12 Other salmonines 1–4															
13 Other salmonines 5+															
14 Burbot 0–0.5 ( $\times 10^3$ )															
15 Burbot 0.5–1 ( $\times 10^3$ )															
16 Burbot 1+															
17 Walleye															
18 Lake whitefish 0 ( $\times 10$ )															
19 Lake whitefish 1–2 ( $\times 10$ )															
20 Lake whitefish 3+															
21 Alewife 0															
22 Alewife 1+															
23 Rainbow smelt 0															
24 Rainbow smelt 1+															
25 Bloater 0 ( $\times 10$ )															
26 Bloater 1+															
27 Yellow perch 0–0.5 ( $\times 10$ )															
28 Yellow perch 0.5–1 ( $\times 10$ )															
29 Yellow perch 1–2 ( $\times 10$ )															
30 Yellow perch 3+ ( $\times 10$ )															
31 Deepwater sculpin 0–0.5 ( $\times 10$ )															
32 Deepwater sculpin 0.5+															
33 Slimy sculpin ( $\times 10$ )															
34 Ninespine stickleback ( $\times 10$ )															
35 Other prey fishes ( $\times 10$ )															
36 Round goby															
37 Predatory cladocerans ( $\times 10$ )															
38 Cladocerans	94.9		5.0	0.7			2.42	0.81	22.3						
39 Cyclopoids	1.4		1.4	0.2			0.03	0.01	3.3						
40 Calanoids	0.7		2.6	0.4			0.06	0.02	1.6						
41 Nauplii	2.3		1.21	0.2			0.30	0.10	1.1						
42 Rotifers	0.7		1.5	0.1		5.0	0.19	0.06	1.7						
43 Zebra mussel															
44 Quagga mussel															
45 Mysis									0.4						
46 Amphipods									8.9			0.2			
47 Chironomids												1.0	0.3		
48 Oligochaetes									0.7			1.0	0.5		
49 Sphaeriids															
50 Protozoa		7.3	6.7	2.6	2.3	2.2	4.5	6.2		0.7			4.6	9.7	
51 Bacteria		10.5	12.0	10.8	11.0	10.5	6.4	8.9		1.0			6.6	9.3	
52 Inedible phytoplankton														7.5	
53 Edible phytoplankton		82.3	69.6	85.1	86.7	82.3	50.6	34.9	31.6	8.2			52.2	73.4	
54 Pelagic detritus							35.5	49.0	11.1	90.0			36.6		100
55 Settled detritus									17.3			98	99		
56 Import															

**Table 4.5** Parameters used to link multi-stanza groups in the 1984 and the 2002 Lake Huron Ecopath models.  $k$  is the growth constant in the von Bertalanffy growth model and  $w_m/w_{inf}$  is the ratio of weight at maturity to asymptotic weight.

Taxa	$k$ (/yr)	$w_m/w_{inf}$	Data source
Chinook salmon	0.45	0.46	He et al. (2014)
Lake trout	0.18	0.29	He et al. (2014)
Other salmonines	0.41	0.42	Swank (2005)
Burbot	0.34	0.40	Dobiesz (2003)
Lake whitefish (1984)	0.21	0.18	Pothoven and Madenjian (2008)
Lake whitefish (2002)	0.15	0.10	Pothoven and Madenjian (2008)
Yellow perch	0.26	0.16	Mohr (OMNR, Owen Sound, Ontario, Canada, unpublished); Diana and Salz (1990)
Alewife	0.55	0.30	Pothoven and Madenjian (2008)
Rainbow smelt	0.50	0.25	Lantry and Stewart (1993)
Bloater	0.29	0.19	Schaeffer (2004)
Deepwater sculpin	0.16	0.18	Selgeby (1988)

**Table 4.6** Diet composition inputs (%) in the modified 1984 Lake Huron Ecopath model that was used as initial conditions in Ecosim simulations.

No. Prey	Predator																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
1 Double-crested cormorant																			
2 Sea lamprey																			
3 Chinook salmon 0–0.5 ( $\times 10^3$ )					1.6				1.0	1.2		0.7						1.7	
4 Chinook salmon 0.5–1 ( $\times 10^3$ )					10.7				6.9	8.0		4.9						11.1	
5 Chinook salmon 1–4		25.2																	
6 Chinook salmon 5+																			
7 Lake trout 0–0.5 ( $\times 10^3$ )					1.0				0.7	0.8		0.5						1.0	
8 Lake trout 0.5–1 ( $\times 10^3$ )					1.7				1.1	1.2		0.8						1.7	
9 Lake trout 1–4		2.8																	
10 Lake trout 5+		11.1																	
11 Other salmonines 0 ( $\times 10^3$ )				0.4	1.6				1.0	1.2		0.7						1.7	
12 Other salmonines 1–4		0.9																	
13 Other salmonines 5+																			
14 Burbot 0–0.5 ( $\times 10^3$ )					2.9				1.9	2.2	0.5	1.3						3.0	
15 Burbot 0.5–1 ( $\times 10^3$ )				1.2	4.4				2.8	3.3		2.0							
16 Burbot 1+		17.9																	
17 Walleye		0.2																	
18 Lake whitefish 0 ( $\times 10$ )				0.1	0.5				0.3	0.4	0.2	0.2			0.05	0.4			
19 Lake whitefish 1–2 ( $\times 10$ )					1.4				0.9	1.1	0.3	0.7			0.3	4.7			
20 Lake whitefish 3+		35.7																	
21 Alewife 0	11.7			19.4	7.1				9.2	5.3	5.17	6.6			0.7	5.8	7.4		
22 Alewife 1+	25			1.8	32.5				8.4	9.7	1.2	6.0			0.63	5.3	6.7		
23 Rainbow smelt 0	5.5			58.7	21.5			4.7	27.7	16.0	15.6	19.9			2.1	17.6	22.3		
24 Rainbow smelt 1+	11			18.7	34.1				44.1	50.9	6.2	31.6			3.3	27.9	35.4		
25 Bloater 0 ( $\times 10$ )				1.8	1.6				1.0	1.2	0.6	1.5			0.2	1.3			
26 Bloater 1+		6.4		0.3	2.1				0.7	0.8	0.4	1.0			0.2	1.7			
27 Yellow perch 0–0.5 ( $\times 10$ )					1.1				0.7	0.8	0.4	1.0				0.9			
28 Yellow perch 0.5–1 ( $\times 10$ )	31			0.5	1.8				1.2	1.4	0.7	1.7			0.2	1.5	3.8		
29 Yellow perch 1–2 ( $\times 10$ )	70								3.7	4.3	1.0	2.6			0.6	4.7	11.9		
30 Yellow perch 3+ ( $\times 10$ )										2.2		1.4					6.2		
31 Deepwater sculpin 0–0.5 ( $\times 10$ )				0.4				0.3	0.9	1.0									
32 Deepwater sculpin 0.5+									5.6	6.5					1.7	14.2			
33 Slimy sculpin ( $\times 10$ )	31			0.5	1.8			0.4	1.2	2.7	0.7	1.7			0.7	5.9	1.9		
34 Ninespine stickleback ( $\times 10$ )	117			0.8	2.8				0.9	1.0	0.5	1.3			0.5	4.6	1.4		
35 Other prey fishes ( $\times 10$ )				1.0	3.5				2.3	2.6	1.3	3.2			0.3	2.9	7.3		
36 Round goby	1.9			0.7	1.2			0.3	3.1	8.9	0.9	5.5			1.2	9.8	4.9		
37 Predatory cladocerans ( $\times 10$ )			0.8				1.5	0.9			0.3	0.9		2.3				4.4	
38 Cladocerans			1.5				3.0	2.0			1.5	1.1		4.5				20.4	
39 Cyclopoids			2.2				4.3	1.9			0.8	0.7		6.5				11.0	
40 Calanoids			4.7				9.3	4.3			1.5	1.5		14.0				19.5	
41 Nauplii			14.8				29.7	1.5			1.9	0.7		44.5				26.0	
42 Rotifers			1.8				3.5	0.2			0.2			5.3				2.7	
43 Zebra mussel									0.1						0.1	0.00			
44 Quagga mussel									0.1						0.1	0.00			
45 Mysis			0.6				0.4	0.9			0.5	0.2		0.2	1.0	0.2		0.2	
46 Amphipods			21.9				14.6	59.1			18.7	7.0		7.3	62.6	11.8		5.8	
47 Chironomids			17.7				11.8	5.4			15.1	5.7		5.9	5.7	0.4		4.7	
48 Oligochaetes			34.7				23.2	16.3			29.6	11.1		11.6	17.2	2.1		9.3	
49 Sphaeriids									3.2						3.4	0.5			
50 Protozoa																			
51 Bacteria																			
52 Inedible phytoplankton																			
53 Edible phytoplankton																			
54 Pelagic detritus																			
55 Settled detritus																			
56 Import		20				100							100					20	

**Table 4.6 Continued.**

No. Prey	Predator																		
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
1 Double-crested cormorant																			
2 Sea lamprey																			
3 Chinook salmon 0–0.5 ( $\times 10^3$ )																			
4 Chinook salmon 0.5–1 ( $\times 10^3$ )																			
5 Chinook salmon 1–4																			
6 Chinook salmon 5+																			
7 Lake trout 0–0.5 ( $\times 10^3$ )				2.0															
8 Lake trout 0.5–1 ( $\times 10^3$ )																			
9 Lake trout 1–4																			
10 Lake trout 5+																			
11 Other salmonines 0 ( $\times 10^3$ )																			
12 Other salmonines 1–4																			
13 Other salmonines 5+																			
14 Burbot 0–0.5 ( $\times 10^3$ )				5.0															
15 Burbot 0.5–1 ( $\times 10^3$ )																			
16 Burbot 1+																			
17 Walleye																			
18 Lake whitefish 0 ( $\times 10$ )																			
19 Lake whitefish 1–2 ( $\times 10$ )																			
20 Lake whitefish 3+																			
21 Alewife 0						2.8					4.4	8.9							
22 Alewife 1+																			
23 Rainbow smelt 0		6.2				16.8					13.4	26.9							
24 Rainbow smelt 1+																			
25 Bloater 0 ( $\times 10$ )						1.3													
26 Bloater 1+																			
27 Yellow perch 0–0.5 ( $\times 10$ )				0.7							1.4	2.8							
28 Yellow perch 0.5–1 ( $\times 10$ )											2.3	4.6							
29 Yellow perch 1–2 ( $\times 10$ )																			
30 Yellow perch 3+ ( $\times 10$ )																			
31 Deepwater sculpin 0–0.5 ( $\times 10$ )				0.8		0.3													
32 Deepwater sculpin 0.5+																			
33 Slimy sculpin ( $\times 10$ )		0.3				0.4					1.1	2.3							
34 Ninespine stickleback ( $\times 10$ )		0.8									0.4	0.9							
35 Other prey fishes ( $\times 10$ )		0.5									1.1	2.2							
36 Round goby		0.7				0.2					1.5	3.0							
37 Predatory cladocerans ( $\times 10$ )	9.2	1.8	5.5	18.4	5.0	11.5	5.5	4.6	2.3	2.2	2.3		3.00	0.28	0.83	11.5	4.6	0.6	
38 Cladocerans	10.6	2.1	25.5	21.1	22.9	13.2	25.5	5.3	4.5	5.0	2.6		6.05	1.27	3.82	13.2	5.3	2.5	
39 Cyclopoids	6.9	1.4	13.7	13.8	12.3	8.7	13.7	3.5	6.5	4.7	1.7		8.6	0.7	2.1	8.7	3.5	1.4	
40 Calanoids	14.8	3.0	24.4	29.6	22.0	18.5	24.4	7.4	14.0	10.8	3.7		18.7	1.2	3.7	18.5	7.4	2.4	
41 Nauplii	6.7	1.3	32.5	13.5	29.2	8.4	32.5	3.4	44.5	3.9	1.7		59.3	1.6	4.9	8.4	3.4	3.2	
42 Rotifers			3.4		3.0		3.4		5.3	0.5			7.1	0.2	0.5			0.3	
43 Zebra mussel	0.8	1.1									0.4	0.3			0.00		0.1	1.2	
44 Quagga mussel	0.4	0.5						0.01			0.1	0.1		0.02	0.02		0.1	0.6	
45 Mysis	0.6	0.9		1.4	0.1	0.4		5.6	0.2	0.6	0.6	0.5		6.6	1.0	0.6	0.9	1.0	
46 Amphipods	41.0	58.0		16.7	7.2	24.5		65.9	7.3	21.9	19.5	16.7		78.3	67.1	40.8	55.6	61.4	
47 Chironomids	3.7	5.3		0.4	0.7	0.9		1.6	5.9	17.7	15.8	13.5		1.9	2.4	1.4	5.1	5.6	
48 Oligochaetes	11.3	16.0		1.4	2.0	4.3		5.7	11.6	34.7	30.9	26.5		6.7	11.7	7.1	15.3	16.9	
49 Sphaeriids	2.2	3.1						1.2			2.8	2.4		1.4	2.8		3.0	3.3	
50 Protozoa																			
51 Bacteria																			
52 Inedible phytoplankton																			
53 Edible phytoplankton																			
54 Pelagic detritus																			
55 Settled detritus																			
56 Import																			

**Table 4.6 Continued.**

No. Prey	Predator														
	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
1 Double-crested cormorant															
2 Sea lamprey															
3 Chinook salmon 0–0.5 ( $\times 10^3$ )															
4 Chinook salmon 0.5–1 ( $\times 10^3$ )															
5 Chinook salmon 1–4															
6 Chinook salmon 5+															
7 Lake trout 0–0.5 ( $\times 10^3$ )															
8 Lake trout 0.5–1 ( $\times 10^3$ )															
9 Lake trout 1–4															
10 Lake trout 5+															
11 Other salmonines 0 ( $\times 10^3$ )															
12 Other salmonines 1–4															
13 Other salmonines 5+															
14 Burbot 0–0.5 ( $\times 10^3$ )															
15 Burbot 0.5–1 ( $\times 10^3$ )															
16 Burbot 1+															
17 Walleye															
18 Lake whitefish 0 ( $\times 10$ )															
19 Lake whitefish 1–2 ( $\times 10$ )															
20 Lake whitefish 3+															
21 Alewife 0															
22 Alewife 1+															
23 Rainbow smelt 0															
24 Rainbow smelt 1+															
25 Bloater 0 ( $\times 10$ )															
26 Bloater 1+															
27 Yellow perch 0–0.5 ( $\times 10$ )															
28 Yellow perch 0.5–1 ( $\times 10$ )															
29 Yellow perch 1–2 ( $\times 10$ )															
30 Yellow perch 3+ ( $\times 10$ )															
31 Deepwater sculpin 0–0.5 ( $\times 10$ )															
32 Deepwater sculpin 0.5+															
33 Slimy sculpin ( $\times 10$ )															
34 Ninespine stickleback ( $\times 10$ )															
35 Other prey fishes ( $\times 10$ )															
36 Round goby															
37 Predatory cladocerans ( $\times 10$ )															
38 Cladocerans	92.3		3.6	0.5			2.18	0.73	20.1						
39 Cyclopoids	1.4		1.0	0.1			0.03	0.01	3.4						
40 Calanoids	0.8		2.3	0.3			0.07	0.02	3.0						
41 Nauplii	4.9		1.93	0.3			0.58	0.19	2.1						
42 Rotifers	0.6		0.9	0.03		5.0	0.14	0.05	1.3						
43 Zebra mussel															
44 Quagga mussel															
45 Mysis									0.2						
46 Amphipods									9.4			0.2			
47 Chironomids												1.0	0.3		
48 Oligochaetes									0.4			1.0	0.5		
49 Sphaeriids															
50 Protozoa		8.7	8.3	3.1	2.8	2.6	5.8	8.3		0.9			6.0	10.9	
51 Bacteria		9.1	10.8	9.5	9.7	9.2	6.1	8.7		0.9			6.3	7.6	
52 Inedible phytoplankton														12.7	
53 Edible phytoplankton		82.2	71.1	86.1	87.5	83.2	55.3	39.5	35.5	8.2			57.0	68.8	
54 Pelagic detritus							29.7	42.4	9.6	90			30.7		100
55 Settled detritus									14.9			98	99		
56 Import															



**Table 4.7** Ecopath outputs for total production, total biomass, and total system throughput (*TST*) of the whole Lake Huron food web in 1984 and 2002.

	1984	2002
Total production ( $\text{g}\times\text{m}^{-2}\times\text{yr}^{-1}$ )	2,894	2,195
Total biomass ( $\text{g}/\text{m}^2$ )	85	97
Total system throughput ( $\text{g}\times\text{m}^{-2}\times\text{yr}^{-1}$ )	7,676	6,025
Total consumption (% <i>TST</i> )	41%	44%
Total exports (% <i>TST</i> )	13%	11%
Total respiration (% <i>TST</i> )	19%	21%
Total flows into detritus (% <i>TST</i> )	27%	24%

**Table 4.8** Calculated production, percent biomass, and ecotrophic efficiency by trophic level in the Lake Huron food web in 1984 and 2002. Values were based on outputs of the routine “Trophic level decomposition” in the Ecopath tool “Network analysis”.

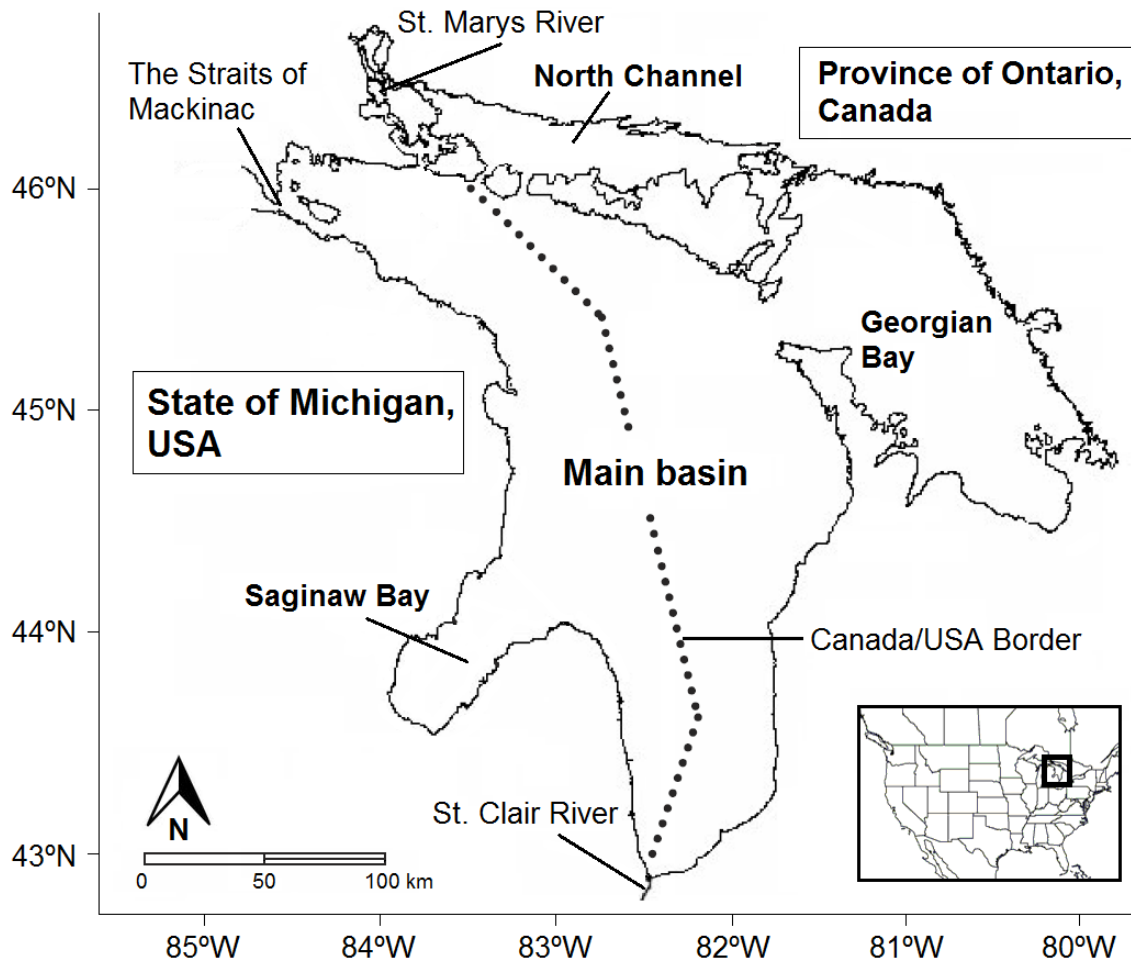
Trophic level	Production ( $\text{g}\times\text{m}^{-2}\times\text{yr}^{-1}$ )		Biomass ( $\text{g}/\text{m}^2$ )		Ecotrophic efficiency	
	1984	2002	1984	2002	1984	2002
IV	6.4	5.0	2.6	1.8	0.41	0.32
III	88.4	80.2	15.0	16.9	0.47	0.40
II	710	587	56.3	69.1	0.63	0.65
I	2,089	1,523	10.8	8.9	0.79	0.91

**Table 4.9** Summary of Ecopath outputs for production, biomass, and ecotrophic efficiencies by functional component in the Lake Huron food web in 1984 and 2002.

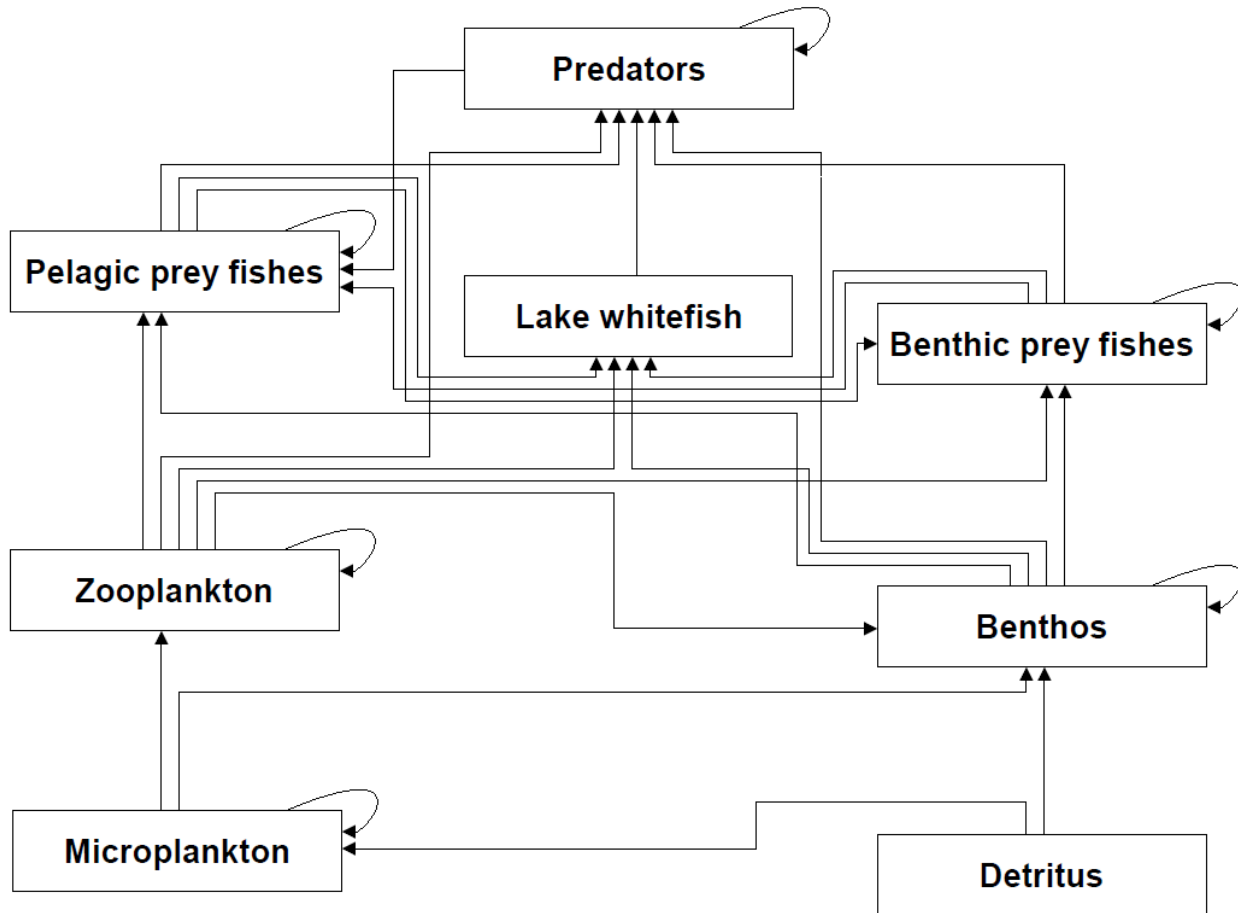
Functional component	Production ( $\text{g}\times\text{m}^{-2}\times\text{yr}^{-1}$ )		Biomass ( $\text{g}/\text{m}^2$ )		Ecotrophic efficiency	
	1984	2002	1984	2002	1984	2002
<b>Pelagic pathway</b>						
Predators	0.24	0.16	0.38	0.27	0.25	0.42
Pelagic prey fishes	18.9	7.5	8.9	3.5	0.51	0.43
Zooplankton	326	306	31	30	0.37	0.30
Microplankton	2,491	1,830	14	11	0.79	0.91
<b>Benthic pathway</b>						
Lake whitefish	0.31	0.78	0.58	1.18	0.22	0.13
Benthic prey fishes	2.4	2.8	1.9	2.1	0.06	0.26
Benthos	55	48	28	49	0.64	0.62
Detritus	2,032	1,478	163	136	0.50	0.57

**Table 4.10** References for changes associated with the collapse of alewives in Lake Huron that have been observed in Lake Michigan and Lake Ontario.

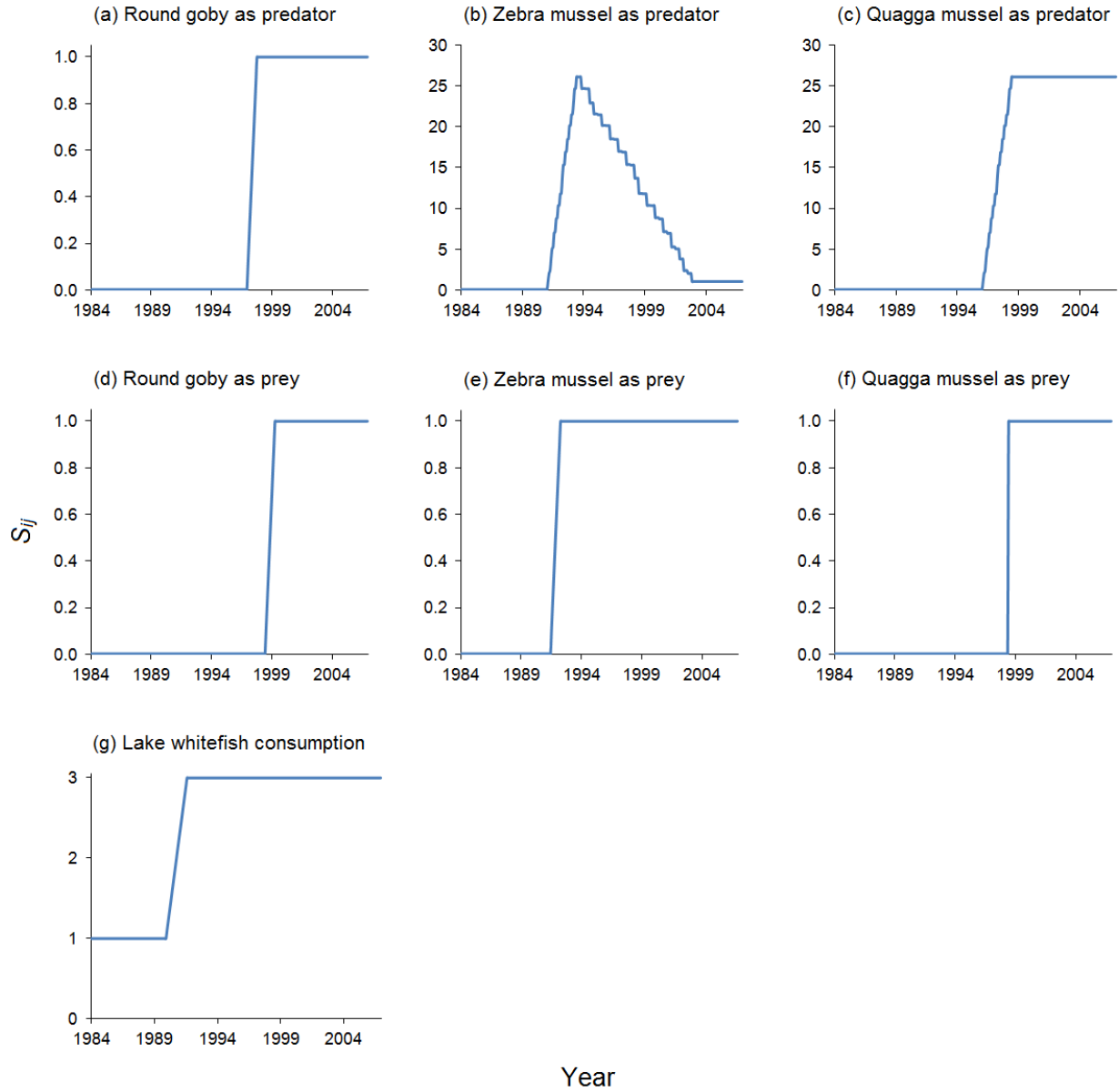
Change	Lake Michigan	Lake Ontario
Increases in Chinook salmon	Claramunt et al. (2013)	Connerton et al. (2014)
Decreases in nutrients	Dolan and Chapra (2012)	Dolan and Chapra (2012)
Increases in dreissenids	Nalepa et al. (2009)	Wilson et al. (2006)
Decreases in non-dreissenid benthos	Barbiero et al. (2011)	Barbiero et al. (2011)
Decreases in rainbow smelt	Rogers et al. (2014)	Weidel and Connerton (2012)
Increases in the proportion of alewife in Chinook salmon's diet	Jacobs et al. (2013)	Stewart and Sprules (2011)



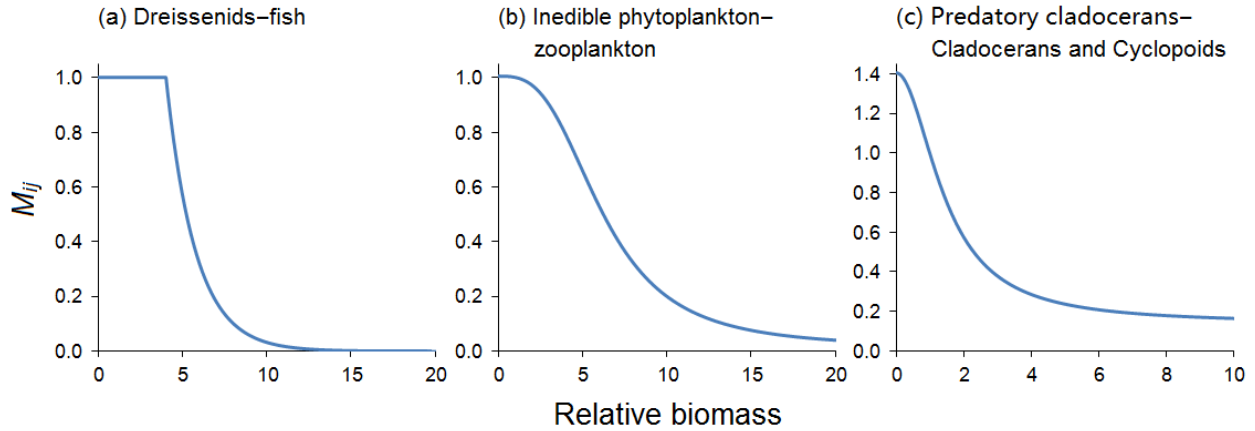
**Figure 4.1** Lake Huron and its four sub-basins.



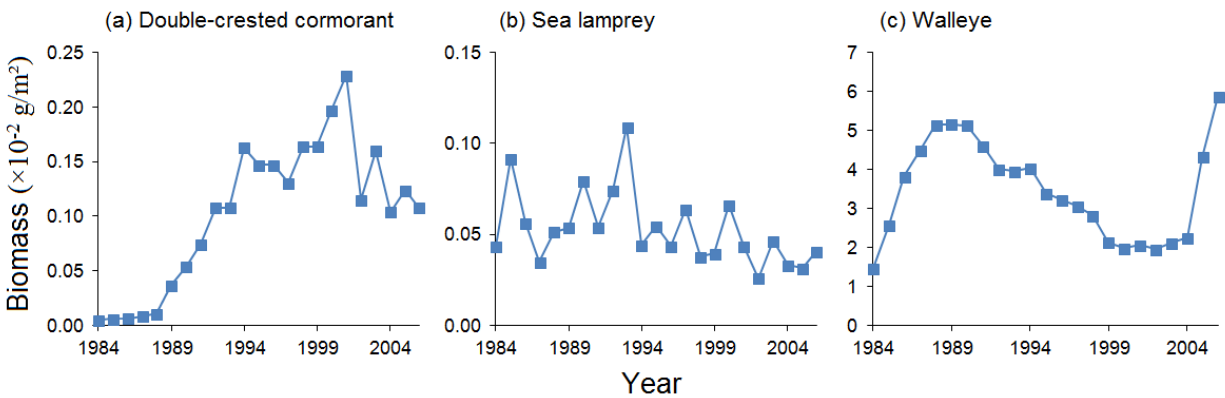
**Figure 4.2** The structure of Lake Huron food web model. Arrows indicate biomass flows among functional components as defined in Table 4.1. The vertical position of each box approximates the functional component's trophic level.



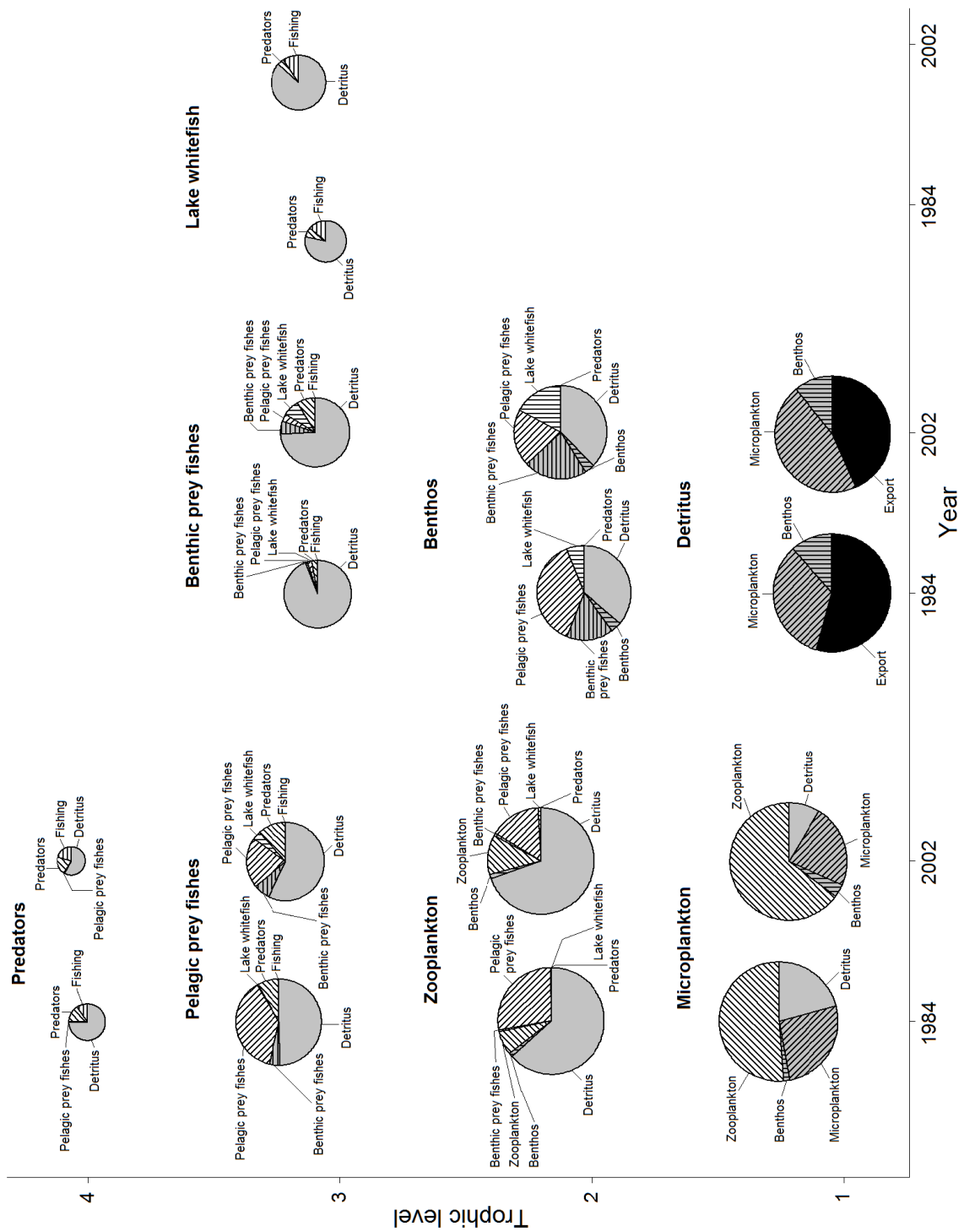
**Figure 4.3** Forcing functions ( $S_{ij}$  in equation 4.8) used to model three groups—Round goby, Zebra mussel, and Quagga mussel—that invaded Lake Huron after 1984 and the change in the consumption to biomass ratio of Lake whitefish 3+.



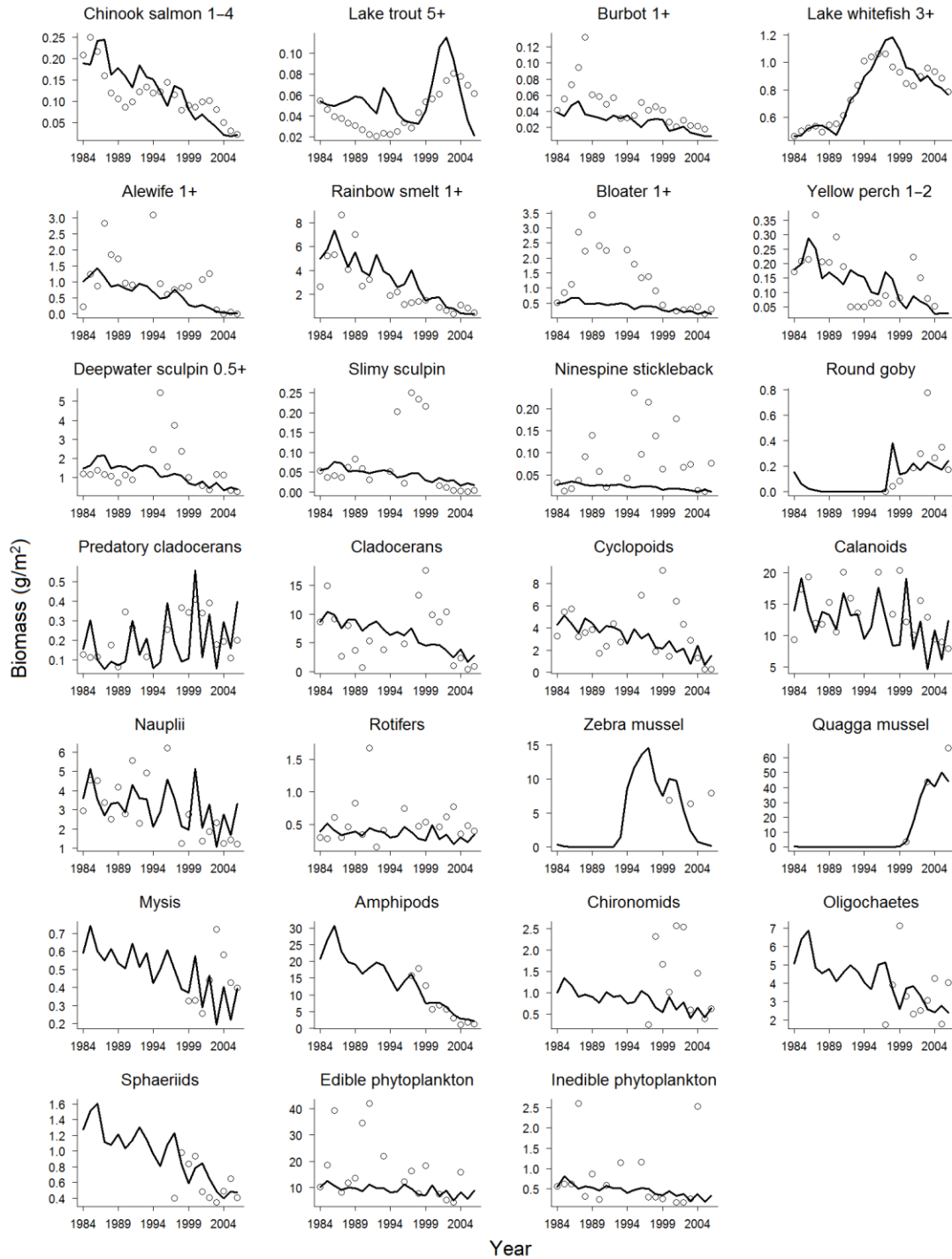
**Figure 4.4** Mediation functions ( $M_{ij}$  in equation 4.8) used to represent interactions among selected groups including: (a) low predation efficiency on zebra and quagga mussels (dreissenids) for some fish taxa; (b) effects of blue green algae on consumption by zooplankton; (c) reduction in consumption by cladocerans and cyclopoids with the presence of predatory *Bythotrephes longimanus*. The relative biomass on X-axis is the biomass of affecting group(s) modeled in Ecosim relative to the Ecopath biomass.



**Figure 4.5** Biomass forcing time series used to model Double-crested cormorants, Sea lamprey, and Walleye groups in Ecosim. Population abundances of these groups are not controlled by predator-prey interactions in the Lake Huron main basin.

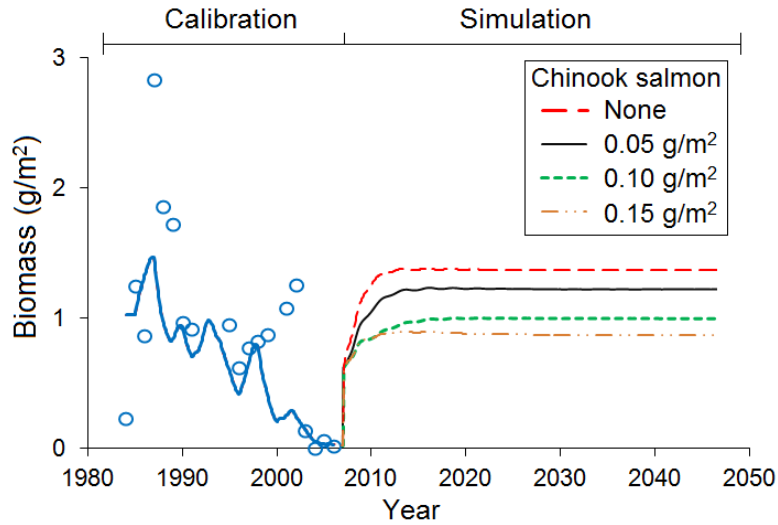


**Figure 4.6** Summary of Ecopath outputs for the trophic level and allocation of production for each functional component in the Lake Huron food web in 1984 and 2002. The bubble size is proportional to log-transformed production.

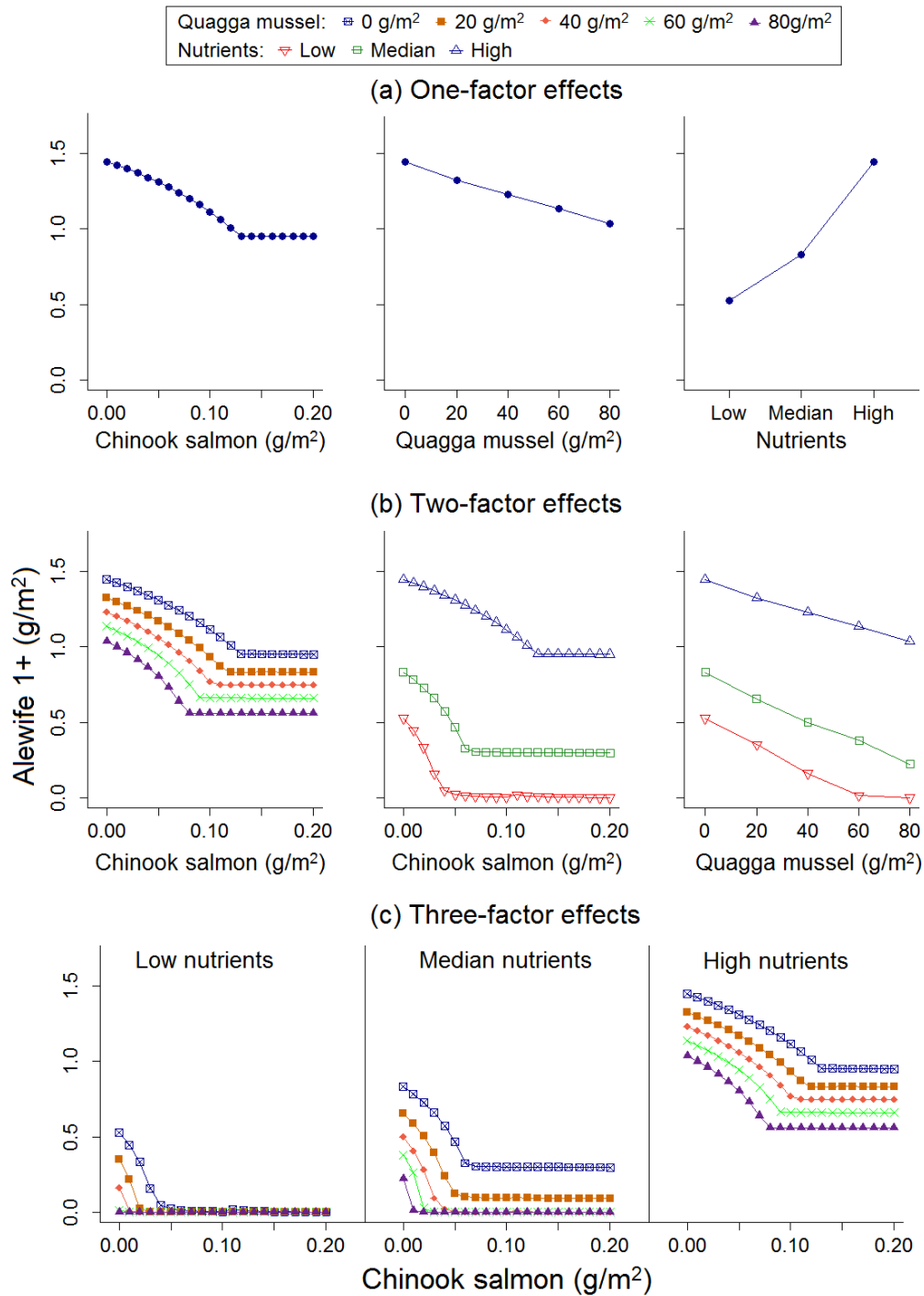


**Figure 4.7** Calibration results of the Lake Huron Ecosim model for groups with available biomass time series. The line represents the best-fit biomass and circles are observed biomass time series in the calibration period from 1984 to 2006.

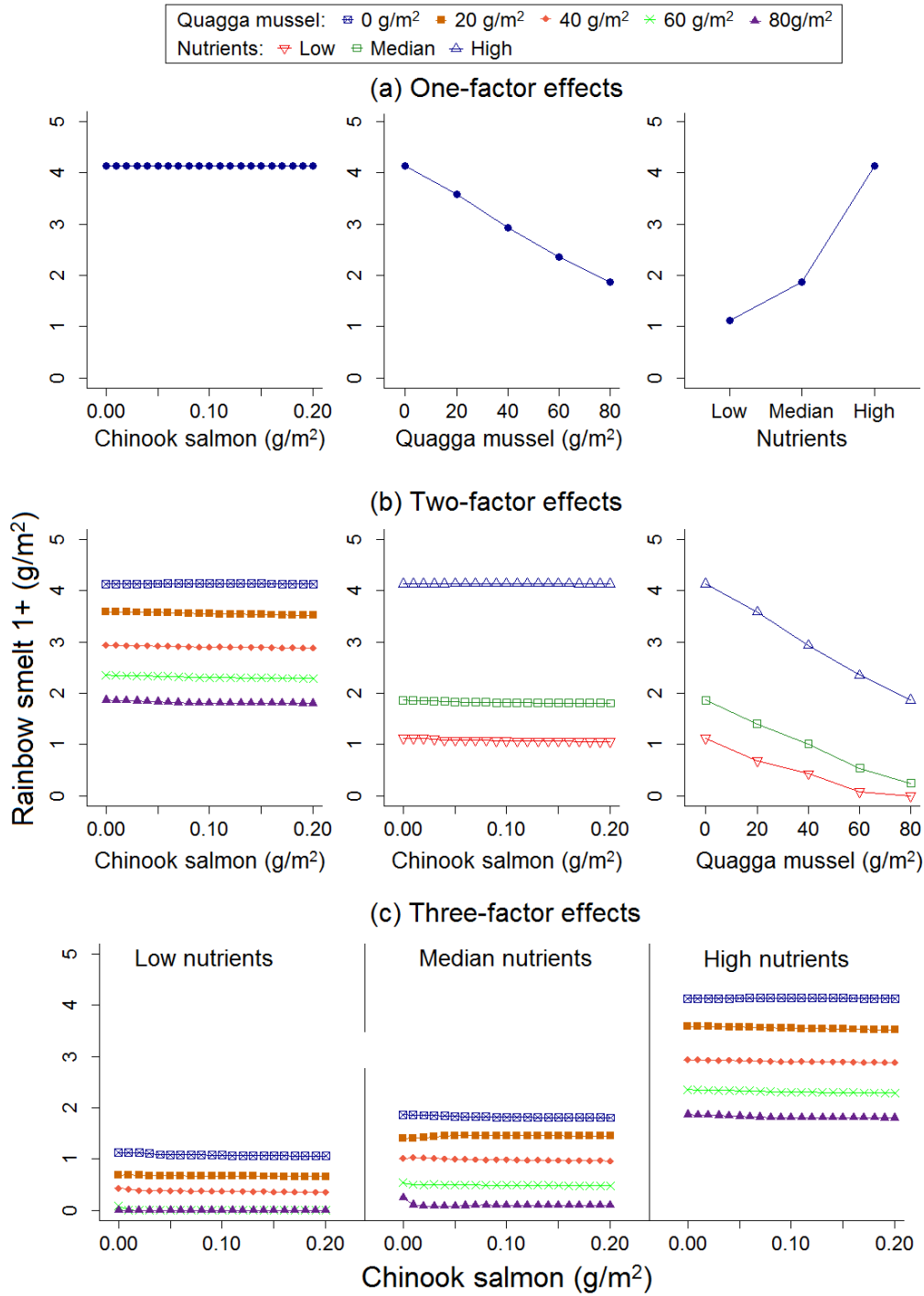




**Figure 4.8** Calibration and part of simulation results for Alewife 1+ biomass from Ecosim. The line from 1984 to 2006 represents the best-fit biomass and circles are observed biomass time series. Lines after 2007 represent 40-year simulations under scenarios of four different levels of Chinook salmon 1–4 biomass, a low level of Quagga mussel biomass of 20 g/m<sup>2</sup>, and a high level of nutrient loads. The 20-year biomass average after reaching equilibrium in each scenario corresponds to a point of the same scenario in Fig. 4.9.



**Figure 4.9** Simulated Alewife 1+ biomass under all scenarios of Chinook salmon 1–4 biomass, Quagga mussel biomass, and nutrient loads. The analysis was designed as a factorial experiment with three factors: Chinook salmon, quagga mussel, and nutrients. Each point represents a 20-year biomass average after reaching equilibrium under a scenario representing effects of one factor or a combination of two or three factors.



**Figure 4.10** Simulated Rainbow smelt 1+ biomass under all scenarios of Chinook salmon 1–4 biomass, Quagga mussel biomass, and nutrient loads. The analysis was designed as a factorial experiment with three factors: Chinook salmon, quagga mussel, and nutrients. Each point represents a 20-year biomass average after reaching equilibrium under a scenario representing effects of one factor or a combination of two or three factors.

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## Appendix A

### Salmonine bioenergetics models

Functions and parameters (Table A.1) in bioenergetics models used in Chapter 2 were briefly summarized here. Detail derivation for these bioenergetics models can be obtained in Stewart and Ibarra (1991) for the Chinook salmon model, in Stewart et al. (1983) for the lake trout model, and in Rand et al. (1993) for the steelhead model.

As described in Chapter 2, the master equation in the bioenergetics model represents the energy budget of a fish as:

$$C = P_{max} \times C_{max} = M + W + G \quad (\text{A.1})$$

where  $C$  is the consumption in terms of the gross energy intake of the fish,  $P_{max}$  is the proportion of maximum consumption that is realized,  $C_{max}$  is the maximum consumption,  $M$  is the metabolic cost,  $W$  is the waste loss, and  $G$  is the net energy for growth (including reproduction). Terms in equation (A.1) are in the unit of daily specific rate ( $\text{J} \times \text{g}^{-1} \times \text{day}^{-1}$ ). Each of consumption, metabolic cost, and waste loss in equation (A.1) has a submodel, expressed as a series of functions of fish weight and temperature together with species-specific parameters.

#### A.1 Consumption submodel

The consumption submodel of lake trout is expressed as:

$$C = P_{max} \times C_{max} = P_{max} \times CA \times B^{CB} \times \exp(CQ \times T) \times ED_{prey} \quad (\text{A.2})$$

where  $B$  is the wet weight of the fish (g),  $T$  is the temperature experienced by the fish ( $^{\circ}\text{C}$ ),  $ED_{prey}$  is the mean prey energy density in diet (J/g), and  $CA$ ,  $CB$ , and  $CQ$  are species-specific parameters.  $ED_{prey}$  is calculated based on model inputs of the diet schedule and prey energy densities.

Consumption submodels of Chinook salmon and steelhead are both expressed as:

$$C = P_{max} \times C_{max} = P_{max} \times CA \times B^{CB} \times K_A \times K_B \times ED_{prey} \quad (\text{A.3})$$

in which

$$K_A = CK1 \times L1 / [1 + CK1 \times (L1 - 1)] \quad (\text{A.4})$$

$$L1 = \exp[G1 \times (T - CQ)] \quad (\text{A.4a})$$

$$G1 = \ln[0.98 \times (1 - CK1) / (0.02 \times CK1)] / (CTO - CQ) \quad (\text{A.4b})$$

$$K_B = CK4 \times L2 / [1 + CK4 \times (L2 - 1)] \quad (\text{A.5})$$

$$L2 = \exp[G2 \times (CTL - T)] \quad (\text{A.5a})$$

$$G2 = \ln[0.98 \times (1 - CK4) / (0.02 \times CK4)] / (CTL - CTM) \quad (\text{A.5b})$$

where  $CTO$ ,  $CTM$ ,  $CTL$ ,  $CK1$ , and  $CK4$  are species-specific parameters.

## A.2 Metabolic cost submodel

Metabolic cost submodels of these three salmonines are all expressed as:

$$M = R + S = RA \times B^{RB} \times e^{RQ \times T} \times e^{(RTO \times VEL)} \times 13,560 + SDA \times (C - F) \times ED_{prey} \quad (\text{A.6})$$

in which

$$\begin{cases} VEL = RK1 \times W^{RK4} & \text{when } T > RTL \\ VEL = ACT \times W^{RK4} \times e^{BACT \times T} & \text{when } T \leq RTL \end{cases} \quad (\text{A.7})$$

where  $R$  is the specific respiration rate ( $J \times g^{-1} \times day^{-1}$ ),  $S$  is the specific dynamic action ( $J \times g^{-1} \times day^{-1}$ ),  $F$  is the specific egestion rate ( $J \times g^{-1} \times day^{-1}$ ), 13,560 is an oxy-calorific coefficient for carnivorous fish ( $J/gO_2$ ) from Elliott and Davison (1975), and  $RA$ ,  $RB$ ,  $RQ$ ,  $RTO$ ,  $RTL$ ,  $RK1$ ,  $RK4$ ,  $ACT$ ,  $BACT$ , and  $SDA$  are species-specific parameters.

### A.3 Waste loss submodel

Waste loss submodels of these three salmonines are all expressed as:

$$W = F + U = PF \times C + UA \times T^{UB} \times e^{UG \times P_{max}} \times C \times (1 - PF) \quad (A.8)$$

in which

$$PF = (FA \times T^{FB} \times e^{FG \times P_{max}} - 0.1) / 0.9 \times (1 - PFF) + PFF \quad (A.9)$$

where  $U$  is the specific excretion rate ( $J \times g^{-1} \times day^{-1}$ ),  $PFF$  is the mean indigestible proportion of prey in diet, and  $FA$ ,  $FB$ ,  $FG$ ,  $UA$ ,  $UB$ , and  $UG$  are species-specific parameters.  $PFF$  is calculated based on model the input of diet schedule, an indigestible proportion of 0.033 for fish prey, and an indigestible proportion of 0.1 for non-fish prey (Stewart et al. 1983).

### A.4 Predator energy density

The predator energy density ( $ED_{pred}$ ) in the bioenergetics model is the energy density of the fish. In this study, energy densities of these salmonines were modeled as linear functions of weight:

$$ED_{pred} = \begin{cases} \alpha_1 + \beta_1 \times B & \text{when } B \leq B_c \\ \alpha_2 + \beta_2 \times B & \text{when } B > B_c \end{cases} \quad (A.10)$$

where  $ED_{pred}$  is the predator energy density ( $J/g$ ),  $\alpha_1$  and  $\beta_1$  are the intercept and slope of the linear function when the weight is less than or equal to the weight threshold  $B_c$  (g) and  $\alpha_2$  and  $\beta_2$

are the intercept and slope when the weight is larger than the weight threshold. Parameters  $\alpha_1$ ,  $\beta_1$ ,  $\alpha_2$ ,  $\beta_2$  and  $B_c$  were obtained from literature or estimated them using available data (Table A.2). As did Rand et al. (1993), we used the same parameters of Chinook salmon for steelhead.

### A.5 Modeling fish weight

Based on the law of conservation of energy, the energy content of the fish at the beginning of day  $t + 1$  is the sum of the energy content of the fish at the beginning of day  $t$  and the net energy gain on day  $t$ . This relationship can be expressed as:

$$B(t+1) \times ED_{pred}(t+1) = B(t) \times ED_{pred}(t) + G(t) \times B(t) \quad (\text{A.11})$$

where  $G(t)$  is the specific growth rate on day  $t$  ( $\text{J} \times \text{g}^{-1} \times \text{day}^{-1}$ ) and is calculated based on equation (A.1) as:

$$G(t) = P_{max} \times C_{max}(t) - M(t) - W(t) \quad (\text{A.12})$$

Substituting  $ED_{pred}(t+1)$  with a linear function of  $B(t+1)$  in equation (A.11),  $B(t+1)$  can be solved using the quadratic formula:

$$B(t+1) = \frac{-\alpha(t+1) + \sqrt{\alpha^2(t+1) + 4 \times \beta(t+1) \times [B(t) \times ED_{pred}(t) + G(t) \times B(t)]}}{2\beta(t+1)} \quad (\text{A.13})$$

where  $\alpha(t+1)$  and  $\beta(t+1)$  are the intercept and slope of the linear function used to model predator energy density based on predator weight on day  $t+1$ , as in equation (A.10). Finally the daily weight of fish can be modeled using equation (A.13) with a known initial weight, required model inputs, and specified simulation parameters.

**Table A.1** Values of species-specific parameters in salmonines bioenergetics models.

Submodel	Parameter	Chinook salmon	Lake trout	Steelhead
Consumption	CA	0.303	0.0589	0.628
	CB	-0.275	-0.307	-0.3
	CQ	5	0.1225	5
	CTO	15		20
	CTM	18		20
	CTL	24		24
	CK1	0.36		0.33
	CK4	0.01		0.2
Metabolic cost	RA	0.00264	0.00463	0.00264
	RB	-0.217	-0.295	-0.217
	RQ	0.06818	0.059	0.06818
	RTO	0.0234	0.0232	0.0234
	RTM	0	0	0
	RTL	25	11	25
	RK1	1	1	1
	RK4	0.13	0.05	0.13
	ACT	9.7	11.7	9.7
	BACT	0.0405	0.0405	0.0405
Waste loss	SDA	0.172	0.172	0.172
	FA	0.212	0.212	0.212
	FB	-0.222	-0.222	-0.222
	FG	0.631	0.631	0.631
	UA	0.0314	0.0314	0.0314
	UB	0.58	0.58	0.58
	UG	-0.299	-0.299	-0.299

**Table A.2** Parameters in the linear function used to model predator energy densities, equation (A.10). Predator energy densities are expressed in J/g.  $\alpha_1$  and  $\beta_1$  are the intercept and slope of the linear function when predator weight is less than or equal to the weight threshold ( $W_c$ ) and  $\alpha_2$  and  $\beta_2$  are the intercept and slope of the linear function when predator weight is larger than the weight threshold.

Parameter	Chinook salmon	Lake trout		
		North	Central	South
$\alpha_1$	4,566	5,302	5,787	6,148
$\beta_1$	0.877	2.285	2.431	1.784
$W_c$ (g)	2,994	1,355	1,074	1,649
$\alpha_2$	7,182	8,400	8,400	9,090
$\beta_2$	0	0	0	0

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## **Appendix B**

### **Biological inputs and baseline $P_{max}$ for bioenergetics simulations**

Herein (1) values and data sources of biological inputs and (2) baseline values of the simulation parameter  $P_{max}$ , the proportion of maximum consumption that is realized, were documented for bioenergetics simulations in Chapter 2. These biological inputs were selected to represent an average individual in each of Chinook salmon (*Oncorhynchus tshawytscha*), lake trout (*Salvelinus namaycush*), and steelhead (*O. mykiss*) in Lake Huron.

#### **B.1 Growth and reproduction**

Growth inputs (Table 2.1) of the bioenergetics model are initial and final weights of the fish in a simulation run. As our bioenergetics simulations were run age-specifically, the initial weight was set to the weight at one age and the final weight was set to the weight at the next older age on the first day of simulation.

For Chinook salmon, the first simulation day was set to May 1st representing the median date of stocking age-0 Chinook salmon. Growth inputs were taken from Dobiesz (2003). We ended bioenergetics simulations for age-4 Chinook salmon on simulation day 214 when they leave the lake for spawning run, as did Stewart and Ibarra (1991).

For lake trout, the first simulation day was set to June 1st representing the median date of stocking lake trout yearling. The weight of age-1 lake trout was set to 40 g, the mean weight of yearling stocked in Lake Huron in June between 2004 and 2008 (USFWS and GLFC 2010). For

age-4 and older lake trout in three Lake Huron populations, we obtained growth inputs from J. He (Michigan Department of Natural Resources, Alpena, Michigan, USA, personal communication), who estimated these values using gill net survey data collected between 2004 and 2008. Owing to the low catch rate in gill net survey, we assumed weights of age-2 and age-3 lake trout in three Lake Huron populations to be the same as those of Lake Michigan lake trout off Sturgeon Bay (Madenjian et al. 1998).

Although steelhead are known to have different life history forms in the Great Lakes region (Rand et al. 1993), we focused on steelhead with the most common life history form in this study. Steelhead in the life history form live 1–2 years in the stream before entering the lake and then live in the lake for four years (Rand et al. 1993). The first simulation day was set to May 1st representing the date when steelhead smolts enter the lake. Growth inputs for lake-age-1 and older steelhead were estimated using data collected by Swank (2005). The weight of lake-age-0 steelhead was set to 50 g (Rand et al. 1993).

## **B.2 Reproduction**

Reproduction in the bioenergetics model is represented as an average loss in weight due to spawning at the beginning of a pre-defined simulation day. We did not model the reproduction of Chinook salmon as they are semelparous. For lake trout, we set spawning to occur on simulation day 150 and result in a loss of 6.8% in weight starting from age 6 (Dobiesz 2003). For steelhead, we set spawning to occur on simulation day 336 and result in a loss 10% in weight starting from lake age 3 (Rand et al. 1993).

### **B.3 Diet schedule**

The diet schedule and prey energy densities were used to calculate the mean prey energy density in diet ( $ED_{prey}$ ) in the bioenergetics model. It describes changes in diet composition (on a wet-weight basis) of the fish over time in the simulation. We tabulated diet schedules for Chinook salmon, lake trout, and steelhead in Tables B.1–B.3.

Diet schedules of age-1 and older Chinook salmon and steelhead were built using data collected in Lake Huron (Roseman et al., 2014). For age-0 Chinook salmon, we kept proportions of non-fish categories in diet the same as those in Stewart and Ibarra (1991), and the proportion distribution across the fish categories was set equal to the proportion distribution across the fish categories for age-1 Chinook salmon diet composition in the same season. For lake-age-0 steelhead, we kept proportions of non-fish categories to be the same as those in Rand et al. (1993), and proportion distribution across the fish categories was set equal to the proportion distribution across the fish categories for age-1 steelhead diet composition in the same season.

For lake trout populations, we built diet schedules using data from He et al. (2014).

### **B.4 Prey energy density**

We used ten prey categories in diet schedules of these salmonines including two non-fish categories: benthic invertebrates and zooplankton; and eight fish categories: alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), bloater (*Coregonus hoyi*), emerald shiner (*Notropis atherinoides*), round goby (*Neogobius melanostomus*), sculpin (*Cottus* spp.), stickleback (*Pungitius* spp.), and other fish. Energy densities were input as constant over an annual cycle (Table B.4) except for alewife and rainbow smelt when seasonal energy density data were available (Dobiesz 2003) as shown in Fig. B.1.

Energy densities of prey categories benthic invertebrates, zooplankton, emerald shiner, round goby, sculpin, and stickleback were not specific to a salmonine population. The energy density of benthic invertebrates was approximated as the mean energy density of amphipods *Diporeia* spp. (Madenjian et al. 2006a), opossum shrimp *Mysis diluviana* (Madenjian et al. 2006a), and chironomids (Cummins and Wuycheck 1971). The energy density of zooplankton was approximated as the mean energy density of cladocerans (Cummins and Wuycheck 1971). Energy densities of emerald shiner, round goby, sculpin, and stickleback were obtained from previous studies (Dobiesz 2003; Hondorp et al. 2005; Madenjian et al. 2011).

Energy densities for prey categories bloater and other fish were specific to a salmonine population. The mean length of bloater was 196 mm in lake trout's diet (Madenjian et al. 1998) and was 100 mm in Chinook salmon's and steelhead's diets (Roseman et al., 2014). Empirical relationships between energy density and dry weight to wet weight ratio for bloater were developed by Dobiesz (2003). To estimate dry weight to wet weight ratio for bloater with a known length, we used the empirical relationship between wet weight and length developed from data collected by Bunnell et al. (2006) and the empirical relationship between dry weight and wet weight in Rudstam et al. (1994). As did Madenjian et al. (1998) for Lake Michigan lake trout, we approximated the energy density of "other fish" as the mean energy density of the most common items in this category. The most common items in "other fish" were small yellow perch (*Perca flavescens*), small gizzard shad (*Dorosoma cepedianum*), and age-0 lake trout for lake trout populations (He et al., 2014). The energy density of small yellow perch was obtained from Diana and Salz (1990). The energy density of small gizzard shad was approximated by the energy density of small alewife (Madenjian et al. 2006b).

## **B.5 Values of the simulation parameter $P_{max}$**

We summarized model-estimated values of the simulation parameter  $P_{max}$  in applicable scenarios in Table B.5.

**Table B.1** The diet schedule of Chinook salmon. Values represent percent diet composition on a wet-weight basis.

Age	Simulation days		Prey category							
	Start	End	Benthic invertebrates	Zoo-plankton	Emerald shiner	Alewife	Rainbow smelt	Stickle-back	Bloater	Round goby
0	1	61	96	1	1		2			
	62	123	48	2		3	39	5	1	2
	124	335	13	4			71	1	3	8
	336	365			88		12			
1-3	1	61			10		12	10	60	8
	62	123				5	78	11	2	4
	124	335					85	1	4	10
	336	365			88		12			
4	1	61			10		12	10	60	8
	62	123				5	78	11	2	4
	124	214					85	1	4	10

**Table B.2a** The diet schedule of North Lake Huron lake trout. Values represent percent diet composition on a wet-weight basis.

Age	Simulation days		Prey category							
	Start	End	Benthic invertebrates	Alewife	Rainbow smelt	Sculpin	Stickle-back	Bloater	Round goby	Other fish
1	1	184	68	4	17	10	1			
	185	365	39	14	26	20	1			
2	1	184	39	8	32	20	1			
	185	365	13	17	35	25	4		5	1
3	1	184	13	10	42	25	4		5	1
	185	365		15	41	5	8		30	1
4-5	1	184		14	42	5	8		30	1
	185	365		15	41	5	8		30	1
6	1	184		14	42	5	8		30	1
	185	365		9	31	4	6	3	45	2
7	1	184		14	26	4	6	3	45	2
	185	365		8	33	3	3	3	47	3
8-9	1	184		20	21	3	3	3	47	3
	185	365		8	33	3	3	3	47	3

**Table B.2b** The diet schedule of Central Lake Huron lake trout. Values represent percent diet composition on a wet-weight basis.

Age	Simulation days		Prey category							
	Start	End	Benthic invertebrates	Alewife	Rainbow smelt	Sculpin	Stickle-back	Bloater	Round goby	Other fish
1	1	184	68	4	17	10	1			
	185	365	39	14	26	20	1			
2	1	184	39	8	32	20	1			
	185	365	13	16	30	24	1		13	3
3	1	184	13	7	38	24	1		13	4
	185	365		7	20	1	2		68	2
4-5	1	184			27	1	2		68	2
	185	365		7	20	1	2		68	2
6	1	184			27	1	2		68	2
	185	365		6	20	2	2	3	64	3
7	1	184		12	14	2	2	3	64	3
	185	365		5	23	5		3	62	2
8-9	1	184		17	11	5		3	62	2
	185	365		5	23	5		3	62	2

**Table B.2c** The diet schedule of South Lake Huron lake trout. Values represent percent diet composition on a wet-weight basis.

Age	Simulation days		Prey category							
	Start	End	Benthic invertebrates	Alewife	Rainbow smelt	Sculpin	Stickle-back	Bloater	Round goby	Other fish
1	1	184	68	4	17	10	1			
	185	365	6	22	50	18	2		2	
2	1	184	6	7	65	18	2		2	
	185	365		19	55	1			24	1
3-4	1	184		5	69	1			24	1
	185	365		19	55	1			24	1
5	1	184		5	69	1			24	1
	185	365		17	58	1			22	2
6	1	184		4	71	1			22	2
	185	365		13	51	1		2	31	2
7	1	184		4	60	1		2	31	2
	185	365		12	50			2	32	4
8-9	1	184		4	58			2	32	4
	185	365		12	50			2	32	4

**Table B.3** The diet schedule of steelhead. Values represent percent diet composition on a wet-weight basis.

Lake age	Simulation days		Prey category							
	Start	End	Benthic invertebrates	Zoo-plankton	Emerald shiner	Alewife	Rainbow smelt	Stickle-back	Bloater	Round goby
0	1	31	83	5	6					6
	32	61	83	5			3			9
	62	123	57	5			9			28
	124	335	31	7		4	18	4	1	36
	336	365	31	7	31					31
1-3	1	31			50					50
	32	123				1	24			74
	124	335				6	28	6	2	57
	336	365			50					50

**Table B.4** Prey energy densities that were input as constant over an annual cycle.

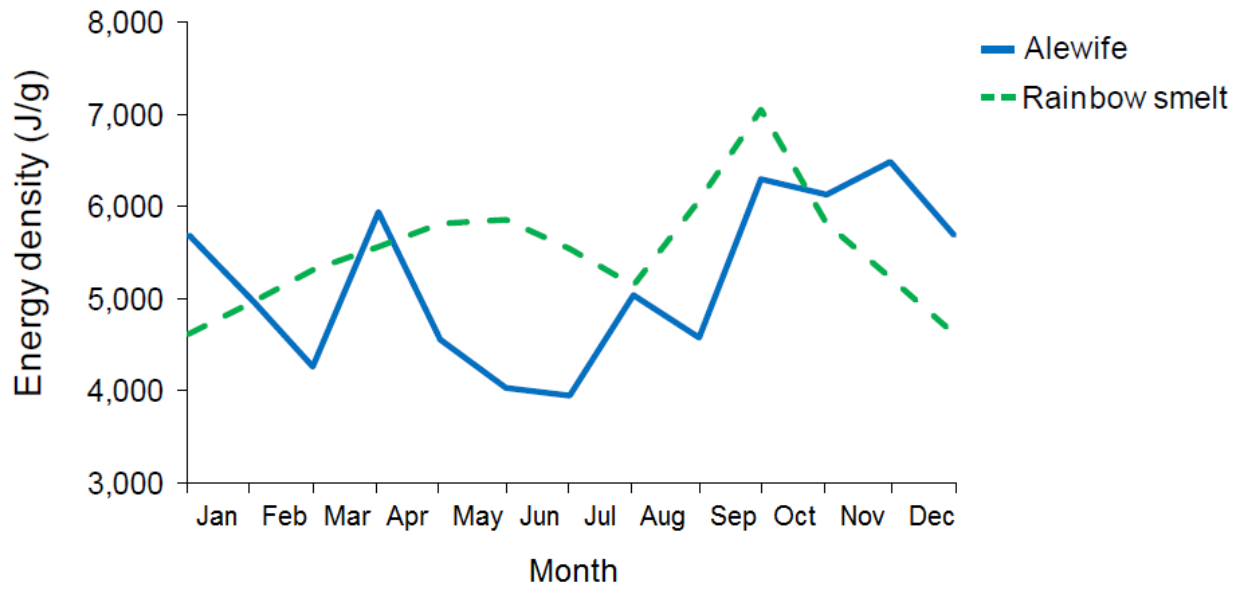
Prey category	Energy density (J/g)	Note
Benthic invertebrates	3,431	
Zooplankton	2,194	
Emerald shiner	7,330	
Round goby	3,621	
Sculpin	5,000	
Stickleback	5,194	
Bloater	6,762	Used in Chinook salmon simulations
	4,435	Used in lake trout and steelhead simulations
Other fish	4,785	Used in lake trout simulations



**Table B.5** Fitted values of the simulation parameter  $P_{max}$ , the proportion of maximum consumption that is realized, under applicable scenarios. Each value represents an average across 29 years in the baseline or across 27 years in the future scenarios. Standard errors of these averages were all less than 0.006.

Age/ lake age	Chinook salmon	Lake trout			Steelhead
		North	Central	South	
<b>Baseline scenario</b>					
0-1	0.81				0.66
1-2	0.76	0.70	0.70	0.67	0.52
2-3	0.79	0.80	0.81	0.69	0.52
3-4	0.62	0.68	0.76	0.83	0.50
4-5	0.51 <sup>a</sup>	0.66	0.74	0.53	
5-6		0.65	0.70	0.56	
6-7		0.67	0.74	0.56	
7-8		0.65	0.68	0.59	
8-9		0.60	0.62	0.52	
9-10		0.61	0.63	0.52	
<b>Constant consumption scenario</b>					
0-1	0.74				0.61
1-2	0.66	0.65	0.65	0.62	0.47
2-3	0.71	0.72	0.74	0.63	0.47
3-4	0.57	0.62	0.69	0.77	0.46
4-5	0.49 <sup>a</sup>	0.60	0.67	0.49	
5-6		0.59	0.64	0.52	
6-7		0.62	0.68	0.53	
7-8		0.60	0.62	0.55	
8-9		0.55	0.57	0.49	
9-10		0.56	0.58	0.49	
<b>Reduced consumption scenario</b>					
0-1	0.72				0.58
1-2	0.64	0.62	0.62	0.59	0.45
2-3	0.69	0.70	0.72	0.62	0.46
3-4	0.56	0.60	0.67	0.75	0.45
4-5	0.48 <sup>a</sup>	0.59	0.66	0.48	
5-6		0.58	0.63	0.50	
6-7		0.61	0.67	0.52	
7-8		0.59	0.61	0.54	
8-9		0.55	0.56	0.49	
9-10		0.55	0.57	0.49	

<sup>a</sup> The simulation ends on day 214. Refer to the Methods section in the main text for the detail.



**Figure B.1** Seasonal energy density cycles for alewife and rainbow smelt in Lake Huron.

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## Appendix C

### Parameterization of the Saginaw Bay food web model

This appendix provides data sources and procedures for estimating input parameters for groups in the Saginaw Bay food web model including: biomass ( $B$ ), production to biomass ratio ( $P/B$ ) or total mortality rate ( $Z$ ), fishery yields ( $Y$ ), consumption to biomass ratio ( $Q/B$ ), proportion of unassimilated food in consumption ( $U/Q$ ), and fraction of diet composition ( $DC$ ).

#### C.1 Fish groups

Biomass inputs in the model for most fish groups were estimated using 1990–2009 data from annual bottom trawl surveys from Michigan Department of Natural Resources (MDNR) (Adlerstein et al., 2007; Fielder et al., 2000; Fielder and Thomas, 2006). We used generalized additive models (GAMs) (Hastie and Tibshirani, 1990) to estimate catch per unit effort ( $CPUE$ ) as mean numbers caught per 10-minute tow by 1 m depth intervals weighted by the Saginaw Bay bathymetry (Assel, 2005). The  $CPUE$  was then converted to biomass using:

$$B = CPUE \times W \times C^{-1} \times Vf^{-1} \times 3,442^{-1} \quad (C.1)$$

where  $W$  is the average fish weight in the catch (g),  $C$  is the gear catchability,  $Vf$  is a vertical adjustment factor, and 3,442 in  $m^2$  is the area swept by the bottom trawl tow (Haas and Schaeffer, 1992). Parameter values used to estimate fish group biomass of small and large species are in Table C.1. The average fish weight  $W$  was calculated from fish length, estimated from survey length frequencies, and using appropriate length–weight relationships (Fielder and Thomas, 2006; Johnson et al., 2005; Schneider et al., 2000). Catchability estimates  $C$  for walleye were from

Irwin et al. (2008) and ranged from 0.07 to 0.32 depending on length, and were also applied for large fish groups such as channel catfish and common carp. A catchability estimate for yellow perch of 0.42 was from Haas and Schaeffer (1992), and was also applied for groups consisting of small size species, such as emerald shiner and trout perch, and for juvenile stanzas of other fish groups. We further corrected catchability estimates for these groups by a vertical adjustment factor  $V_f$  which relates density distribution in the water column of the group compared to that of yellow perch (Haas and Schaeffer, 1992). For example, we calculated a vertical adjustment factor of 0.64 for emerald shiner reflecting that 64% of the population overlaps with yellow perch in the water column.

Biomass inputs for other fish groups were estimated following different procedures dependent on available data. For walleye age-2 and older (Walleye 2+), biomass in Saginaw Bay was calculated from total abundance estimates generated by a catch-at-age population model (Fielder and Bence, 2014) and converted to biomass using length-at-age data from MDNR surveys and a weight-length regression developed by Fielder et al. (2000). To obtain biomass inputs for the model, the total biomass was then divided by  $2.77 \times 10^9 \text{ m}^2$ , the area of Saginaw Bay (Johengen et al., 2000). Biomass values of Open Lake Predators, Nearshore Predators, and Other Prey fish groups, species that were not well sampled in MDNR surveys, were estimated from fishery harvest rates (Zhenming Su, MDNR, unpublished data). Lake whitefish also is not well sampled by MDNR surveys, and is a species that constitutes an important commercial fishery in Saginaw Bay (Baldwin et al., 2009). To estimate biomass for this group, we assumed that total biomass in Saginaw Bay is 10% of that in the Lake Huron main basin, based on the 1986 to 1995 ratios of commercial harvests in these two areas. The main basin biomass was obtained from available estimates from a catch-at-age population model (Modeling

Subcommittee, 2011). Round goby is an invasive species that was not present in Saginaw Bay in 1990 but an initial biomass was necessary in Ecopath for the group to be included in the time dynamic simulation in Ecosim. We used an initial biomass of 0.25 (g/m<sup>2</sup>) based to obtain an ecotrophic efficiency estimate of about 0.50 as known for round goby in Lake Erie (Johnson et al., 2005).

Production to biomass ratio ( $P/B$ ), or total mortality rates ( $Z$ ) of fish groups with multiple age/stage stanzas, were mostly obtained from literature and also estimated from length frequency distribution data (Pauly, 1983) from MDNR surveys (Table C.2). For first stanza groups (Walleye 0–0.5, White perch 0, Gizzard shad 0 and Emerald shiner 0–0.5) for which neither literature information nor length data were available, we used a total mortality rate similar to YOY yellow perch (Irwin et al., 2009). For common carp,  $P/B$  was estimated assuming its natural mortality rate was similar to that of channel catfish (Haak, 1987).

Fishery yield inputs were estimated using data from commercial yields (Baldwin et al., 2009) and recreational catch from MDNR (Su and He, 2013). We converted catch to biomass using median catch weights. Fishing mortality for all groups subjected to fisheries was estimated as fishery yield divided by the Ecopath biomass (Christensen et al., 2005).

Consumption to biomass ratios ( $Q/B$ ) for leading stanzas of yellow perch and walleye were derived from consumption estimates available for Saginaw Bay (Haas and Schaeffer, 1992). For other leading stanza fish groups, we estimated  $Q/B$  values from information in other areas in the Great Lakes region or from an empirical equation (Palomares and Pauly, 1998) (Table C.2). Implementing the empirical equation requires input values for asymptotic weight, mean habitat temperature, aspect ratio of height to surface area of the caudal fin, and type of food consumed. Asymptotic weights were from Michigan State Record Fish available at the MDNR web site

([www.michigan.gov/dnr](http://www.michigan.gov/dnr)) or FishBase (Froese and Pauly, 2012). Mean habitat temperature of Saginaw Bay was assumed to be 17°C based on mean temperature during the growing season from April to November reported by Johengen et al. (2005). Caudal fin aspect ratios were measured from photographs available at the MDNR web site or FishBase. Food types were based on diet compositions as reported in Table 3.4. Proportions of unassimilated food in consumption ( $U/Q$ ) for fish groups were obtained from Hanson et al. (1997). When the estimate for a group was not available, the value for a group with similar size and diet was used.

Diet composition inputs ( $DC$ ) for fish groups were estimated from literature using stomach content data for species in Saginaw Bay or in similar ecosystems (Table 3.4). However, available information on diets often had lower resolution for prey than groups defined in our model. For example, fish prey data were reported for species not desegregated by age, and zooplankton prey were not desegregated into finer groups. In such cases, we allocated diet proportion to prey groups based on feeding preferences reported in the literature. We defined preference categories as highly-preferred fish, preferred fish, non-preferred fish, preferred benthos, non-preferred benthos, preferred zooplankton, non-preferred zooplankton, and excluded from diet. Next, we used size of prey and predator and prey body shape, and predator-prey spatial overlap to assign prey groups into these categories. For example, large prey fish with spiny dorsal fins which are hard to ingest were non-preferred for all fish predators; and inner bay chironomids were non-preferred benthos prey of outer bay lake whitefish because of little spatial overlap. Finally, the diet proportion of each preference category was allocated to every prey group within the category in proportion to the production of the prey group (Villy Christensen, Fisheries Centre of the University of British Columbia, personal communication). The original diet matrix was slightly modified in Ecopath until mass-balance was achieved.



## C.2 Benthos groups

Biomass of benthos groups was estimated using data collected from 1990 to 1996 in Saginaw Bay monitoring surveys conducted by the National Oceanic and Atmospheric Administration Great Lakes Environmental Research Laboratory (NOAA-GLERL) (Adlerstein et al., 2013; Nalepa et al., 2002). Benthos samples in soft and sandy sediments were collected using Ponar grabs, and dreissenids on hard substrates were sampled by scuba divers. Estimates of benthic organism densities and ash-free dry weights (*AFDW*) in  $\text{g}/\text{m}^2$  were available by taxa. To convert *AFDW* to biomass for each benthos group in Saginaw Bay, we first calculated a mean *AFDW* weighted by the area of the inner and outer bay and substrate type. We estimated substrate type proportions for Saginaw Bay from a geographic information system-based substrate composition map of Saginaw Bay (<http://ifrgis.snre.umich.edu/projects/GLGIS>) developed from data reported by Robbins (1986) and Wood (1958). Substrate composition estimates are: 9% hard, 66% sand, and 25% mud/silt for the inner bay; 1% hard, 97% sand, and 2% silt for the outer bay. These estimates differ from estimates provided by Nalepa et al. (2003) which were based only on map from Robbins (1986). We then used:

$$B = AFDW \times C^{-1} \times Cf \quad (\text{C.2})$$

where  $C$  is the catchability (efficiency) of the gear used to sample the benthos and  $Cf$  is a conversion factor for *AFDW* to wet weight.  $C$  for scuba diving was assumed to be 1. Catchability of the Ponar grab, on the other hand, depends on vertical distribution of organisms in the sediments and their relative size or weight (Flannagan, 1970). We used efficiency (catchability) estimates evaluated from nearshore Lake Michigan samples of 0.67, 0.77, and 0.48 for Amphipods, Sphaeriids, and Oligochaetes, respectively (Nalepa et al., 1988). The estimate of 0.07 reported for Chironomids in Lake Michigan was considered too low for Saginaw Bay

samples that consisted of much larger individuals, so we used the Amphipod estimate of 0.67 which is in line with Flannagan (1970), the only other study of the Ponar grab efficiency for Chironomids. The  $C_f$  for each benthos group was calculated as the median  $AFDW$  to wet weight conversion factors among similar species in freshwater ecosystems using data reported by Brey et al. (2010). For Dreissenids, a group not present in Saginaw Bay in 1990, an initial biomass was necessary in Ecopath to include the group in the time dynamic simulation in Ecosim. We estimated a biomass of  $0.40 \text{ (g/m}^2\text{)}$  for dreissenids based on obtaining an ecotrophic efficiency of 0.40; which corresponds to a non-predatory mortality rate of 1.26/year, estimated from daily non-predatory mortality rates of zebra mussels observed in the Hudson River from June to August (Boles and Lipcius, 1997).

$P/B$  values of benthos groups were assumed to be similar to those reported for Bay of Quinte, Lake Ontario (Johnson and Brinkhurst, 1971), except for Dreissenids for which a  $P/B$  of 2.1/year was estimated using the neural network model from Brey (2012). To implement the model we used a median shell length of 10 mm observed in 1991–1992 (Nalepa et al., 1995), a 5.1 m average depth in the inner bay, and an average temperature during the growing season of  $17^\circ\text{C}$ .

To estimate  $Q/B$  for benthos groups we used:

$$Q/B = \frac{P/B}{P/A \times (1 - U/Q)} \quad (\text{C.3})$$

where values for the  $U/Q$ , and  $P/A$  (production to assimilation) ratios were from literature or estimated using information available from literature. We estimated a  $U/Q$  of 0.50 for Oligochaetes, Amphipods, Sphaeriids, and Chironomids, which is the median  $U/Q$  among benthic herbivore-detritivores summarized from different sources by Leidy and Ploskey (1980). For Dreissenids, we estimated a  $U/Q$  of 0.66 assuming that about 23% of filtered organic

particles are egested as pseudo feces (Madenjian, 1995), and that 55% of ingested food items are turned into fecal material. The 55% and a  $P/A$  of 0.40 for Dreissenids were estimated from relationships developed by McMahon (1996) based on zebra mussel size and water temperature, and implemented using Saginaw Bay population structure reported by Nalepa et al. (1995), and a mean Saginaw Bay temperature during the growing season of 17°C. For other benthos groups, we used  $P/A$  values reported by Johnson and Brinkhurst (1971) of 0.60, 0.10, 0.68, and 0.65, for Amphipods, Sphaeriids, Oligochaetes, and Chironomids, respectively.

Diet composition ( $DC$ ) inputs for benthos groups were based on diet information from literature, indicating that all groups feed mainly on some type of detritus (Table 3.4). Our model incorporates two detritus groups: ‘Settled detritus’ and ‘Pelagic detritus’, and links were set to represent that Amphipods, Chironomids, and Oligochaetes are deposit feeders and consume Settled detritus, and that Dreissenids and Sphaeriids are filter feeders and consume Pelagic detritus.

### **C.3 Zooplankton groups and Protozoa**

Biomass values of zooplankton groups were estimated using data from the 1990–1996 NOAA-GLERL survey of Saginaw Bay (Adlerstein et al., 2013; Nalepa et al., 2002).

Zooplankton samples were collected using vertical net tows from 1 m above the bottom to surface with conical plankton nets with a 63  $\mu\text{m}$  mesh (Bridgeman et al., 1995). Biomass in dry weight ( $DW$ ,  $\text{g}/\text{m}^2$ ) was available by taxa identified up to the species level. We estimated mean  $DW$  for all taxa weighted by area of each bay region (inner and outer), and converted to biomass using:

$$B = DW \times C^{-1} \times Cf \tag{C.4}$$

The gear catchability ( $C$ ) of a vertical tow net was assumed to be one. A conversion factor from dry weight to wet weight ( $C_f$ ) of 10 was used for all zooplankton taxa (Hanson et al., 1997; Doohan, 1973) except for a factor of 25 used for *Asplanchna* spp (Dumont et al., 1975). The biomass of the Protozoa group, including heterotrophic genera of chrysophytes, cryptomonads, dinoflagellates, and flagellates, was estimated using data from the 1990–1996 NOAA-GLERL survey of Saginaw Bay (Fahnenstiel et al., 1995). Data on ciliates were not available and biomass was assumed to be twice of heterotrophic flagellates biomass based on structure of planktonic food webs across the Great Lakes (Fahnenstiel et al., 1998). Samples were collected by Niskin bottles at a vertical depth of 1 to 5 m below the water surface at stations in the inner and outer Saginaw Bay. Data consisted of cell counts by taxa identified to species level when possible, except for flagellates which were aggregated. We estimated mean weight biomass based on cell densities and known cell volume, weighted by the area of the inner and outer Saginaw Bay, and assuming that the density of cells is similar to that of water ( $1 \text{ g/cm}^3$ ).

$P/B$ ,  $Q/B$ , and  $U/Q$  values for zooplankton groups and Protozoa were obtained from literature or estimated using empirical relationships and available information. We used gross conversion efficiencies ( $P/Q$ ) of 0.25 and 0.30 to relate  $Q/B$  and  $P/B$  for zooplankton groups and for Protozoa, respectively (Straile, 1997).  $P/B$  values for Rotifers, Cladocerans, Cyclopoids, and Calanoids were estimated using group specific empirical relationships (Shuter and Ing, 1997), where  $P/B$  is a function of mean temperature during the growing season ( $17^\circ\text{C}$ ) and the mean duration of the growing season (244 days, April to November).  $Q/B$  estimates for Nauplii and Predatory cladocerans were obtained by McNaught et al. (1980) and Vanderploeg et al. (1993), respectively. For Protozoa,  $P/B$  was estimated from Taylor and Johannsson (1991) and Carrick et

al. (1992). We used a  $U/Q$  value of 0.50 for Rotifers and 0.40 for all other zooplankton groups (Leidy and Ploskey, 1980) and Protozoa (Sleigh, 1989).

Diet composition input values for zooplankton groups and Protozoa were obtained from literature (Table 3.4). The diet composition of each zooplankton group represented an average diet of major species in the group. The diet of nauplii and copepodite stages was apportioned into Edible phytoplankton, Bacteria and Protozoa proportional to their productions. Protozoa diets were apportioned into the Inedible phytoplankton, Edible phytoplankton, Bacteria and Protozoa groups (Sigee et al., 1999).

#### **C.4 Primary producers and Bacteria**

The biomass of phytoplankton was estimated using data collected using data from the 1990–1996 NOAA-GLERL survey of Saginaw Bay (Fahnenstiel et al., 1995). Samples were collected and processed as described for Protozoa. We aggregated bacillariophytes, chlorophytes and autotrophic genera of chrysophytes, cryptomonads, and dinoflagellates into an Edible phytoplankton group. We placed cyanophytes into the Inedible phytoplankton group. We estimated mean biovolume for phytoplankton groups based on cell densities and known species cell volume, weighted by the area of the inner and outer Saginaw Bay, and converted biovolume to wet weight biomass by assuming that the density of algal cells is similar to that of water ( $1 \text{ g/cm}^3$ ). For calibration we used a time series of densities as indices of relative biomass because of suspected classification issues in the source data for diatoms for years after 1991 that could not be resolved (Eugene Stoermer, University of Michigan, personal communication). Data on biomass of bacteria and macrophytes were not available for Saginaw Bay. To estimate the biomass of Bacteria we applied carbon biomass ratios of planktonic bacteria to phytoplankton

(0.75 in spring and 0.50 in summer) known for planktonic food webs across the Great Lakes (Fahnenstiel et al., 1998). Carbon-to-wet-weight ratios were 0.07 for Edible phytoplankton (Eugene Stoermer, University of Michigan personal communication), 0.10 for Inedible phytoplankton (Sicko-Goad et al., 1984), and 0.25 for Bacteria (as observed in Sandusky Bay in Lake Erie; Hwang and Heath, 1997). Biomass in the habitat area for benthic macrophytes was calculated by dividing the production of phytoplankton by a  $P/B$  of 10 /year using the approach proposed by Reyes-Marchant et al. (1993) which assumes that production of macrophytes and phytoplankton are the same. Suitable habitat for macrophytes corresponds to depth < 2 m which is 25% of the Saginaw Bay area (Skubinna et al., 1995).

$P/B$  values for phytoplankton groups were estimated from primary production rates taken from literature (Fahnenstiel et al., 1995). We used Fahnenstiel et al.'s (1995) estimate of average primary production ( $PP$ ) during the 1990 Saginaw Bay growing season. To apportion  $PP$  to phytoplankton groups we assumed that 35% of the summer  $PP$  was from Inedible phytoplankton (Fahnenstiel and Carrick, 1992).  $P/B$ ,  $Q/B$ ,  $U/Q$ , and  $DC$  for Bacteria were obtained from literature or estimated using empirical relationships. We used gross conversion efficiencies of 0.25 to relate  $Q/B$  and  $P/B$  (del Giorgio and Cole, 1998). Production was estimated from the 1990 average  $PP$  during the growing season in Saginaw Bay (Fahnenstiel et al., 1995) and using an empirical relationship between  $PP$  and bacterial production (Cole et al., 1988). To convert bacterial production to wet weight production, we used a carbon-to-wet-weight ratio of 0.25 (Hwang and Heath, 1997). The  $U/Q$  of Bacteria was assumed similar to that of Protozoa (Stewart and Sprules, 2011). Bacteria  $DC$  was linked to the Pelagic detritus group only.

## **C.5 Detritus groups**

Biomass of detritus groups were estimated using literature information. The carbon biomass of Pelagic detritus was estimated as the total of particulate organic carbon (POC) and dissolved organic carbon (DOC) per unit area (Johengen et al., 2000). The carbon biomass of Settled detritus was estimated as the product of sedimentation rates ( $405\text{--}780\text{ g/m}^2$ ) in Saginaw Bay (Kemp and Harper, 1977; Robbins, 1986) and the organic carbon content (1–5%) in surface sediments (Robbins, 1986). To obtain biomass input values of detritus groups, we divided carbon biomass by a carbon-to-wet-weight ratio of 0.25 (Hwang and Heath, 1997), assuming that carbon content in detrital material is similar to that of bacteria.

**Table C.1** Values used to estimate biomass inputs ( $B$ ) in the Saginaw Bay Ecopath model for fish groups using equation (C.1).  $CPUE$  is mean catch in numbers per 10-minute tow effort and weighted by bay bathymetry,  $W$  is average fish weight,  $C$  is gear catchability, and  $V_f$  is a vertical distribution adjustment factor.

Group	$CPUE$	$W$ (g)	$C$	$V_f$
<b>Small fish</b>				
Yellow perch 1–2	34.2	29.8	0.42	1.00
White perch 0	522.2	4.1	0.42	0.97
Rainbow smelt 0	67.8	1.5	0.42	1.00
Alewife 0	98.5	2.9	0.42	0.66
Gizzard shad 0	103.8	13.3	0.42	0.96
Emerald shiner 0.5+	86.1	3.5	0.42	0.64
Spottail shiner	151.3	5.6	0.42	1.00
Trout perch	58.6	6.4	0.42	1.00
<b>Large fish</b>				
Freshwater drum	7.3	49.7	0.32	1.00
Common carp	2.3	318.8	0.21	1.00
Channel catfish	2.0	180.4	0.20	1.00
White sucker	3.7	389.6	0.18	1.00



**Table C.2** Sources for input parameters  $P/B$  or  $Z$  and  $Q/B$  for fish groups in the Saginaw Bay Ecopath model.

Group	$P/B$ or $Z$ (/year)	$Q/B$ (/year)
Open lake predator	Brenden et al. (2012); He et al. (2012)	Dobiesz (2003)
Nearshore predator	Kaemingk et al. (2012)	Converted from $P/B$ using the $P/Q$ of Open lake predator (0.13)
Walleye 0–0.5	Assumed similar to Yellow perch	Ecopath estimated
Walleye 0.5–1	Fielder (2002)	Ecopath estimated
Walleye 1	Fielder and Bence (2014)	Ecopath estimated
Walleye 2+	Fielder and Bence (2014)	Haas and Schaeffer (1992)
Yellow perch 0–0.5	Irwin et al. (2009)	Ecopath estimated
Yellow perch 0.5–1	Irwin et al. (2009)	Ecopath estimated
Yellow perch 1–2	Haas and Schaeffer (1992)	Haas and Schaeffer (1992)
Yellow perch 3+	Estimated in this study	Ecopath estimated
Freshwater drum	Bur (1984)	Palomares and Pauly (1998)
Common carp	Estimated in this study	Palomares and Pauly (1998)
Lake whitefish	Johnson et al. (1995)	Pothoven and Madenjian (2008)
Channel catfish	Haak (1987)	Palomares and Pauly (1998)
White sucker	Estimated in this study	Palomares and Pauly (1998)
White perch 0	Assumed similar to Yellow perch	Parrish and Margraf (1990)
White perch 1+	Estimated in this study	Ecopath estimated
Rainbow smelt 0	Lantry and Stewart (2000)	Ecopath estimated
Rainbow smelt 1+	Lantry and Stewart (2000)	Lantry and Stewart (1993)
Alewife 0	Hewett and Stewart (1989)	Ecopath estimated
Alewife 1+	Hewett and Stewart (1989)	Hewett and Stewart (1989)
Gizzard shad 0	Assumed similar to Yellow perch	Ecopath estimated
Gizzard shad 1+	Estimated in this study	Palomares and Pauly (1998)
Emerald shiner 0–0.5	Assumed similar to Yellow perch	Borgmann and Ralph (1985)
Emerald shiner 0.5+	Estimated in this study	Ecopath estimated
Spottail shiner	Estimated in this study	Palomares and Pauly (1998)
Trout perch	House and Wells (1973)	Palomares and Pauly (1998)
Round goby	Taraborelli et al. (2010)	Taraborelli et al. (2010)
Other prey fishes	Madenjian et al. (2011)	Palomares and Pauly (1998)

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## **Appendix D**

### **Supplementary results for fish groups from Saginaw Bay food web model**

Biomass responses of White perch groups were positive to nutrient, negative to alewife, and not significant to dreissenid scenarios (Table 3.6). White perch biomass patterns were similar to those of Yellow perch 0–0.5 and 0.5–1 except that biomass of White perch 0 (Fig. D.1a) and White perch 1+ (Fig. D.1b) collapsed at low nutrient scenarios. Also, White perch biomass changed more than Yellow perch biomass. For example, biomass of White perch age 0 and age 1+ increased two-fold from the average to high nutrient scenarios, and decreased by about half from the alewife absence to high alewife scenarios.

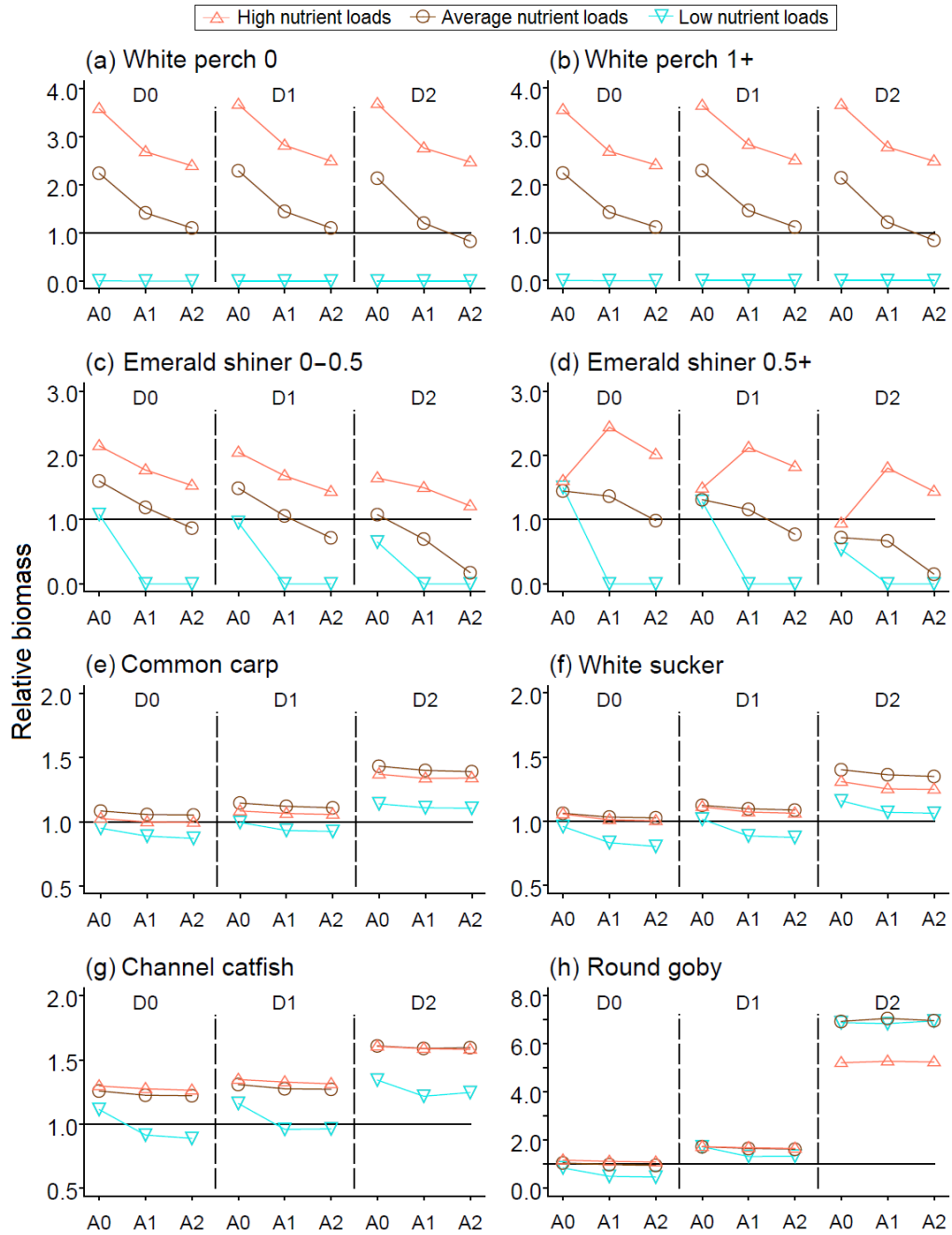
Biomass responses of Emerald shiner were positive to nutrient, negative to alewife except in high nutrient scenarios and negative to dreissenid scenarios (Table 3.6). Patterns also were similar to those for Yellow perch 0–0.5 and 0.5–1, but dreissenid effects were more noticeable for Emerald shiner, and in low nutrient scenarios. Emerald shiner biomass could only be sustained in absence of alewives (Fig. D.1c, D.1d). Biomass of Emerald shiner 0.5+ had a stronger response to nutrient scenarios than did Emerald shiner 0–0.5, and in high nutrient scenarios Emerald shiner 0.5+ biomass increased to a peak at intermediate alewife levels.

Biomass of Common carp and White sucker increased with dreissenid biomass and with nutrient loads in the high dreissenid scenario but did not respond to alewife scenarios (Table 3.6). Highest biomass of these two groups was in average rather than in high nutrient scenarios (Fig. D.1e, D.1f). Response of Channel catfish was similar to Common carp but the effect of nutrients



was significant, although the change in biomass from low to high nutrient scenarios was < 25% (Fig. D.1g). Biomass of Round goby, similar to Common carp and White sucker, did not to respond to changes in alewife biomass, increased with increasing dreissenid biomass and only responded, but negatively, to nutrients in high dreissenid scenarios (Table 3.6). At high dreissenid biomass levels, Round goby biomass was higher at low and average nutrient loads than at high loads (Fig. D.1h). Responses of Freshwater drum biomass to nutrient, alewife, and dreissenid scenarios were similar to those of Round goby, but with a stronger positive response of Freshwater drum to dreissenid scenarios (Fig. D.1i).

Biomass of Spottail shiner responded to nutrient and alewife scenarios, and to dreissenid scenarios but with < 25% change (Table 3.6). Spottail shiner was one of the few groups that responded negatively to nutrients while biomass increased with increasing alewife and dreissenid scenarios (Fig. D.1j). Biomass responses of Open lake predators to nutrient, dreissenid and alewife scenarios were similar to Spottail shiner (Fig. D.1k), but the increase with dreissenid scenarios was > 25% (Table 3.6). Biomass of Nearshore predators also responded positively to nutrients, alewives and dreissenids, but only dreissenid effects were > 25% (Table 3.6, Fig. D.1l). Biomass of Other prey fishes responded positively to nutrients and dreissenids, and negatively to alewives, but all effects caused less than 25% change (Table 3.6, Fig. D.1m). Trout perch responded positively only to nutrients although with < 25% changes (Fig. D.1n).



**Figure D.1** Supplementary results of simulation scenarios for fish groups. Symbols represent the 30-year biomass average after reaching equilibrium. A0–A2: absence, average, and high alewife scenarios; and D0–D2: absence, average, and high dreissenid scenarios.

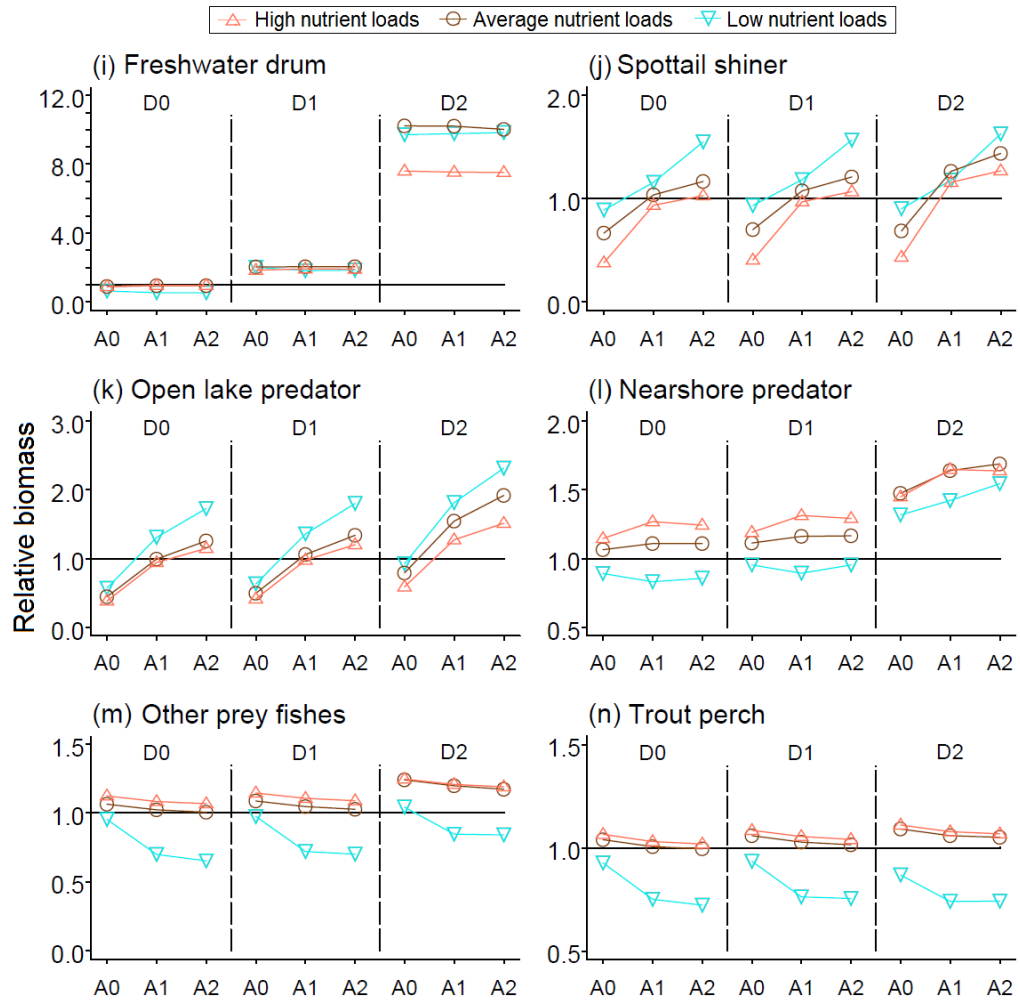


Figure D.1 Continued.

## **Appendix E**

### **Parameterization of the Lake Huron Ecopath with Ecosim models**

This appendix summarizes data sources and procedures to estimate input parameters in the 1984 and 2002 Lake Huron Ecopath models including biomass ( $B$ ), production to biomass ratio ( $P/B$ ) or total mortality rate ( $Z$ ), consumption to biomass ratio ( $Q/B$ ), proportion of unassimilated food in consumption ( $U/Q$ ), diet composition ( $DC$ ), and fishery yields ( $Y$ ). The appendix also includes details on the time series of biomass and fishery yield used to calibrate the Lake Huron Ecosim model.

Biomass inputs in Ecopath were calculated for 10 leading-stanza and 26 single-stanza groups in the models and fishery yield inputs were calculated for the eight groups that were harvested by commercial and recreational fisheries (Table 4.2). Biomass inputs were calculated as total biomass estimates (g) for the Lake Huron main basin divided by the basin area  $3.78 \times 10^{10}$  m<sup>2</sup>. Biomass time series were generated from 1984 to 2006 for most groups and from 1997 to 2006 for the Mysis and all benthos groups. Available information was insufficient to generate biomass time series for six groups: Other salmonines 1–4, Other prey fishes, Protozoa, Bacteria, Pelagic detritus, and Settled detritus. Fishery yield inputs and time series from 1984 to 2006 were calculated as total annual harvests (g/yr) from commercial and recreational fisheries in the Lake Huron main basin divided by the basin area. Other details on input estimation follow.

#### **E.1 Double-crested cormorants**

Total biomass of Double-crested cormorants was calculated based on average numbers of chicks per nest and average weights of chicks and adults from Ridgway and Fielder (2012), estimates of nest numbers from Ridgway and Fielder (2012) and Weseloh et al. (1995, 2002), and the assumption that there were two adults per nest.

Other input parameters were obtained from literature. The  $P/B$  was from Seamans et al. (2012),  $Q/B$  from Ridgway (2010), and  $U/Q$  from Ridgway (2010). The  $DC$  was based on Diana et al. (2006) and Ridgway and Fielder (2012).

## E.2 Sea lamprey

Total biomass of parasitic-phase Sea lamprey inhabiting Lake Huron was calculated based on estimates of spawning adult numbers that returned to Lake Huron tributaries (Sullivan et al., 2013). Adult abundance in Lake Huron was back calculated by assuming a 75% survival from the parasitic to spawning phases (Jones et al., 2009). It was also assumed that 80% of parasitic sea lamprey in Lake Huron actively feed in the main basin while the remaining 20% mostly feed in the North Channel and Georgian Bay (Mullett et al., 2003; Walter and Treble, 2012). A mean weight of 96 g (Bergstedt and Swink, 1995) was used to convert total abundance estimates to total biomass.

Sea lamprey  $P/B$  was estimated = 1.2/yr based on a bioenergetics study for sea lamprey in Lake Huron (Madenjian et al. 2003). The same study estimated a  $Q/B$  of 6.0/yr and a  $U/Q$  of 0.18. However, bioenergetics represents blood consumption by sea lamprey but not the host mortality associated with consumption. Thus, the  $Q/B$  and  $U/Q$  would underestimate sea lamprey imposed mortality in the EwE modeling approach. Accordingly,  $Q/B$  of Sea Lamprey was estimated using:

$$(Q/B)_{Sea\ lamprey} = \left( \sum_{i=1}^8 B_i \times Z_{i, Sea\ lamprey} \right) / B_{Sea\ lamprey} \quad (E.1)$$

where  $B_i$  is the biomass of group  $i$  of the eight host groups and  $Z_{i, \text{Sea lamprey}}$  is the sea lamprey imposed mortality rate (Table E.1). Sea lamprey imposed mortality rates were estimated based on Eshenroder and Koonce (1984) as:

$$Z_{i, \text{Sea lamprey}} = LW_i \times (1 - LS_i) / LS_i \quad (\text{E.2})$$

where  $LW_i$  is the average number of sea lamprey wounds per individual on the host group  $i$  and  $LS_i$  is the probability of surviving one lamprey attack.  $LW_i$  and  $LS_i$  of the eight host groups were obtained from literature (Table E.1). Following estimation of  $(Q/B)_{\text{Sea lamprey}}$ , the  $U/Q$  and  $DC$  of Sea lamprey were calculated as:

$$(U/Q)_{\text{Sea lamprey}} = 1 - [(P/B)_{\text{Sea lamprey}} + (R/B)_{\text{Sea lamprey}}] / (Q/B)_{\text{Sea lamprey}} \quad (\text{E.3})$$

$$DC_{i, \text{Sea lamprey}} = B_i / B_{\text{Sea lamprey}} \times Z_{i, \text{Sea lamprey}} / (Q/B)_{\text{Sea lamprey}} \quad (\text{E.4})$$

where the respiration to biomass ratio  $(R/B)_{\text{sea lamprey}}$  of 3.7/yr was from Madenjian et al. (2003).

### E.3 Other fish groups

#### *Biomass of piscivores and lake whitefish*

Except for walleye, piscivorous fish species and lake whitefish were parameterized as multi-stanza groups (Table 4.1). For these groups, the leading-stanza were Chinook salmon 1–4, Lake trout 5+, Other salmonines 1–4 (mainly steelhead and coho salmon at ages 1–4), Burbot 1+, and Lake whitefish 3+. Total biomass estimates for these groups were obtained from literature or estimated using survey and recreational catch data.

Biomass inputs of Chinook salmon 1–4 and Lake trout 5+ were based on total biomass estimates from statistical catch-at-age (SCAA) models (He et al., 2014). Estimates for Chinook salmon were from an updated model developed by Brenden et al. (2012) and for lake trout estimates were from a model developed by Sitar (1996).

As estimates were not available for the Other salmonines 1–4 stanza, inputs for the 1984 and 2002 Ecopath models were calculated based on recreational harvest rates (Johnson and Gonder, 2013; Su and He, 2013). It was assumed that the biomass of Other salmonines 1–4 was 10% of the biomass of Chinook salmon 1–4, the same as the relationship between harvest rates (in weight per angler hour) of all species in Other salmonines group and Chinook salmon during 1986–1990 and 1998–2002.

Biomass inputs of Burbot 1+ were based on catch rates in fishery independent gillnet surveys conducted by Ontario Ministry of Natural Resources (OMNR) (Adlerstein et al., 2007; Stapanian et al., 2008). A generalized additive model (GAM) (Hastie and Tibshirani, 1990) was used to estimate mean catch per unit effort (CPUE) as numbers caught per 1-km of gillnet by depth (Table E.2). Annual mean CPUE in the main basin was calculated as GAM estimates weighted by the main basin bathymetry from a map in Assel (2005). A factor of  $6 \times 10^8$  (g/CPUE) was used to convert annual mean CPUE to total biomass. This factor is the ratio of average burbot age 1 and older biomass in 1984–1998 ( $2.1 \times 10^9$  g) from a burbot population model Dobiesz et al. (2005) to the average gillnet CPUE (3.6 fish/km) in the same period.

Biomass inputs of Walleye were based on abundance estimates for the Lake Huron population from a SCAA model (Fielder and Bence, 2014). Walleye in Lake Huron are distributed in the southern main basin including Saginaw Bay, and it was assumed that walleye abundance in the main basin corresponded to 50% of this population (Fielder et al., 2010). Estimates of walleye abundance were converted to total biomass using weight-at-age data from commercial harvests in southern main basin (Lee, 2013).

Biomass inputs of Lake whitefish 3+ were based on total biomass estimates from SCAA models (Ebener et al., 2005; He et al., 2014). Estimates are for total biomass of six populations in

the Lake Huron main basin and Saginaw Bay, which are distributed across 14 management units. One of these populations is distributed across three of these management units (WFH-06, WFH-07, and WFH-08) including Saginaw Bay so that only 75% area of these units is in the main basin. Total biomass of this population was calculated by assuming a uniform spatial distribution.

### *Biomass of prey fish*

Prey fish species were parameterized as multi-stanza groups for alewife, rainbow smelt, bloater, yellow perch, and deepwater sculpin, and single-stanza groups for ninespine stickleback, slimy sculpin, round goby, and species aggregated into the Other prey fishes group (Table 4.1). Among the multi-stanza groups, the leading-stanza were Alewife 1+, Rainbow smelt 1+, Bloater 1+, Yellow perch 1–2, and Deepwater sculpin 0.5+. The Round goby invaded Lake Huron after 1997 so was not parameterized in the 1984 Ecopath model. Total biomass estimates of prey fish groups were (1) obtained from Riley et al. (2012), which were based on bottom trawl survey data collected by the United States Geological Survey Great Lakes Science Center (USGS-GLSC); or (2) estimated from the original USGS data (Adlerstein et al., 2007).

Total biomass estimates from Riley et al. (2012) were directly used for Alewife 1+, Rainbow smelt 1+, Bloater 1+, and Ninespine stickleback. Total biomass estimates for slimy sculpin, deepwater sculpin, and round goby needed adjustment. Estimates from Riley et al. (2012) are for age-2 and older fish, as indicated by length frequency data. To expand the estimates to include biomass of younger ages, the species biomass was multiplied by factors of 2.4, 2.0, and 2.9, respectively. These factors are based on age-specific mortality rates and weights of the three species from Selgeby (1988) and Taraborelli et al. (2010). Total biomass estimates of Yellow



perch 1–2 and Other prey fishes were not reported and were estimated using USGS data following the same procedures as in Riley et al. (2012).

Total biomass estimates needed further adjustment to account for limited spatial coverage of USGS surveys and for gear catchability. The USGS surveys covered areas with depth up to 110 m, which made it necessary to extrapolate biomass estimates for several groups that are distributed beyond this range. Further, biomass had to be adjusted for gear catchability as the USGS surveys used 12-m and 21-m (headrope) trawls at different periods. Reported estimates are standardized to the 21-m trawl (Adams et al., 2009). Because catchability estimates from literature are only available for the 12-m trawl, available total biomass estimates were standardized to the 12-m trawl ( $TB$ ) using conversion factors in Adams et al. (2009). Then the  $TB$  of prey fish group  $i$  was expanded as:

$$B_i = TB_i \times Af_i^{-1} \times q_i^{-1} \quad (E.5)$$

where  $Af_i$  is an area expansion factor to account for the depth distribution and  $q_i$  is the catchability of the 12-m trawl.

The  $Af$  was determined based on information of the bathymetric distribution of the group from GAM analyses in Adlerstein et al. (2007). A value of 0.85 was used for Deepwater sculpin 0.5+ and Alewife 1+ as they are distributed in areas > 110 m. A value of 1.00 was used for all other groups as they are distributed in areas < 110 m.

Estimates of  $q$  were obtained from literature for selected species and ages. The catchability of alewives was available for age-0 fish (0.10) and age-3 and older fish (0.30) from Tsehaye et al. (2014) and an intermediate value of 0.15 was used for Alewife 1+. The catchability of age-3 and older alewives was used for Bloater 1+ because of similar length and distribution in the water column (Argyle, 1992). A catchability of 0.12 for Rainbow smelt 1+

was taken from Tsehaye et al. (2014) and a value of 0.42 for Yellow perch 1–2 was taken from Haas and Schaeffer (1992). The catchability of Yellow perch 1–2 was used for Ninespine stickleback, Round goby, and Other prey fishes as they are all demersal species. Catchabilities for Slimy sculpin and Deepwater sculpin 0.5+ were estimated as the ratio of day to night biomass estimates from bottom trawl surveys conducted by Yule et al. (2008). Based on the assumption that the catchability of the night bottom trawl is one, a catchability of 0.20 was calculated for Slimy sculpin and of 0.72 for Deepwater sculpin.

### *Production*

Estimates for  $P/B$  (or  $Z$  of multi-stanza groups) were mostly obtained from literature (Table E.3). For some prey fish groups, total mortality rates were estimated using Pauly's (1983) method based on length frequency data. Because neither literature information nor length frequency data were available, total mortality rates of Burbot 0–0.5, Burbot 0.5–1, Lake whitefish 0, Lake whitefish 1–2, and Deepwater sculpin 0–0.5 were assumed similar to those of groups with similar body shapes and spatial distributions (Table E.3). A total mortality rate of 3.0/yr was used for Chinook salmon 5+ and Other salmonines 5+ groups; these two groups migrate into streams and do not inhabit the main basin during the spawning run and die after spawning. This value was selected so that most biomass in these two groups would be eliminated in the model before they reach age 6.

### *Consumption and assimilation*

Estimates for  $Q/B$  were mostly obtained from literature (Table E.3). For the Stickleback and Other prey fishes groups,  $Q/B$  was estimated using an empirical equation for carnivorous fishes from Palomares and Pauly (1998). Inputs required to implement this equation are

asymptotic weight, aspect ratio of height to surface area of the caudal fin, and mean habitat temperature. Asymptotic weights were obtained from FishBase (Froese and Pauly, 2013) and caudal fin aspect ratios were measured from photographs in FishBase. The mean habitat temperature of 12 °C was based on Bai et al. (2013).

Estimates of  $U/Q$  were obtained from Hanson et al. (1997) and Lee and Johnson (2005). When the estimate for a group was not available, the estimate for a group with similar size and diet was used.

### *Diet composition*

Diet composition inputs ( $DC$ ) were estimated using available stomach content data from Lake Huron studies or similar ecosystems (Table E.4). However, available information often had lower resolution for prey than groups defined in our model. For example, fish prey data were reported for species but not desegregated by age, and zooplankton prey were not desegregated into finer groups. In such cases, we allocated diet proportion to prey groups based on feeding preferences reported in the literature. We defined preference categories as i) highly preferred fish, ii) preferred fish, iii) non-preferred fish, iv) preferred zooplankton, v) non-preferred zooplankton, vi) *Mysis*, vii) preferred benthos, viii) non-preferred benthos, and ix) excluded from diet. Next, we used prey size, prey body shape, and predator-prey spatial overlap to assign prey groups into these categories for each predator groups. For example, large yellow perch with spiny dorsal fins which are hard to ingest were non-preferred fish for all fish predators. Finally, the diet proportion of each preference category was allocated to every prey group within the category in proportion to production of the prey group (Villy Christensen, Fisheries Centre of the University of British Columbia, personal communication).

### *Fishery yields*

Fishery yield inputs were calculated for eight groups that were harvested by commercial and recreational fisheries in US and Canadian waters: Chinook salmon 1–4, Lake trout 5+, Other salmonines 1–4, Walleye, Lake whitefish 3+, Yellow perch 3+, Rainbow smelt 1+, and Bloater 1+. Total annual harvest (g/yr) for each group from commercial fisheries was obtained from Baldwin et al. (2009). Total annual harvest (g/yr) for Chinook salmon 1–4, Lake trout 5+, Other salmonines 1–4, Walleye, and Yellow perch 3+ from recreational fisheries was calculated based on estimates of US recreational catch (number/yr) (Su and Clapp, 2013; Su and He, 2013), average fish weight (g) in the recreational fishery (Rakoczy and Rogers, 1990), and the assumption that recreational harvest in Canada is 10% of that in the US (Mohr and Ebener, 2005). Estimates of recreational catch were not available for 1984 and 1985 and the 1986–1990 averages were used.

### **E.4 Zooplankton**

Biomass inputs of zooplankton groups including Predatory cladocerans, Cladocerans, Cyclopoids, Calanoids, Nauplii, and Rotifers were based on total biomass estimates derived from survey data collected by the US Environmental Protection Agency's Great Lakes National Program Office (EPA-GLNPO) (Barbiero et al., 2001). Zooplankton were sampled starting from 1983 and using shallow (vertical) tows taken from a depth of 20 m with a 64  $\mu\text{m}$  mesh net. After 1998, sampling also included deep (vertical) tows taken from a depth of 100 m with a larger mesh of 153  $\mu\text{m}$ . Data from both shallow- and deep-tow samples were used to estimate total biomass. Data were available as dry weight by volume ( $\text{g}/\text{m}^3$ ) by taxa. Data were converted to areal unit ( $\text{g}/\text{m}^2$ ) by integrating biomass through the water column (m). GAMs were used to

estimate mean biomass of zooplankton groups ( $\text{g/m}^2$ ) by depth and to standardize estimates to deep tow samples (Table E.2). Total biomass (g) was extrapolated from GAM estimates to the main basin area using bathymetric data from a map in Assel (2005). Dry weight was converted to wet weight by multiplying by a factor of 25 for *Asplanchna* spp. (Dumont et al., 1975) and a factor of 10 for all other zooplankton taxa (Doohan, 1973; Hanson et al., 1997).

$P/B$ ,  $Q/B$ , and  $U/Q$  were obtained from literature or estimated using empirical equations. For Predatory cladocerans, the  $P/B$  and  $Q/B$  were from Bunnell et al. (2011) and  $U/Q$  was from Yurista and Schulz (1995). For the other groups, a production to consumption ratio ( $P/Q$ ) of 0.25 was used for the conversion between  $P/B$  and  $Q/B$  (Straile, 1997) and  $U/Q$  was from Leidy and Ploskey (1980).  $P/B$  of Cladocerans, Cyclopoids, Calanoids, and Rotifers was estimated using empirical equations from Shuter and Ing (1997), which linked  $P/B$  to the mean temperature in the growing season ( $12\text{ }^\circ\text{C}$ ) and the length of the growing season (220 days, from April to November). The  $Q/B$  of the Nauplii was from McNaught et al. (1980).

Diet composition inputs ( $DC$ ) were calculated as the average diet of major species in each zooplankton group and based on information from literature (Table E.5). Diets of the Nauplii group and copepods (cyclopoids and calanoids) at copepodite stages were apportioned into Edible phytoplankton, Bacteria, and Protozoa proportional to their productions.

## **E.5 Mysis**

Because data were not available between 1972 and 1997, the biomass input in the 1984 Ecopath model was based on 1971 density data (Carpenter et al., 1974). It was assumed that biomass remained stable during these years as nutrient loads did not change significantly (Dolan and Chapra, 2012). Density data ( $\text{number/m}^2$ ) available by 25-m depth interval were converted to

biomass ( $\text{g/m}^2$ ) using mean weight (g) in EPA-GLNPO surveys (Barbiero et al., 2001). The total biomass (g) was calculated as the sum of the 25-m interval biomass multiplied by the interval area ( $\text{m}^2$ ) based on a bathymetry map in Assel (2005).

The biomass input in the 2002 Ecopath model was derived from data collected by EPA-GLNPO zooplankton surveys in deep-tow samples (Barbiero et al., 2001). Data were available as dry weight per volume ( $\text{g/m}^3$ ) and were converted to areal unit ( $\text{g/m}^2$ ) by multiplying by the station depth (m). A GAM was used to estimate mean biomass ( $\text{g/m}^2$ ) by depth (Table E.2). Total biomass (g) was extrapolated from GAM estimates to the main basin area using bathymetric data from a map in Assel (2005). Dry weight was converted to wet weight by multiplying by a factor of 5 (Mida, 2010).

Other input parameters were obtained from literature. The  $P/B$  was from Sell (1982), and  $Q/B$  and  $U/Q$  were obtained from Rudstam (1989). Diet composition inputs were based on literature listed in Table E.5, which indicated the *Mysis* opportunistically feed on zooplankton, phytoplankton, and detritus.

## **E.6 Benthos**

### *Biomass*

Biomass inputs of benthos groups Amphipods, Chironomids, Oligochaetes, and Sphaeriids were from surveys that collected density data ( $\text{number/m}^2$ ) from soft substrate samples using Ponar grab. Biomass inputs in the 1984 Ecopath model were based on data collected by the University of Michigan's Great Lakes Research Division in 1972 (Nalepa et al., 2007). It was assumed that biomass remained unchanged between 1972 and 1984 as nutrient loads changed little during this period (Dolan and Chapra, 2012). Biomass inputs starting in 1997

were based on density data collected by EPA-GLNPO surveys (Barbiero et al., 2011). Biomass ( $\text{g}/\text{m}^2$ ) was calculated using mean ash-free dry weights (AFDW) in Lake Michigan and ratios of wet weight to AFDW from literature (Table E.6). Biomass estimates were adjusted to account for Ponar grab efficiency (Table E.6). GAMs were used to estimate mean biomass ( $\text{g}/\text{m}^2$ ) by depth on soft substrate areas (Table E.2). Total biomass (g) on soft substrate areas was extrapolated from GAM estimates using maps of bathymetry (Assel, 2005) and substrate (Thomas et al., 1973). On bedrock, the biomass of these benthos groups was assumed to be zero.

Biomass inputs of the Zebra mussel and Quagga mussel in the 2002 Ecopath model were calculated based on density data ( $\text{number}/\text{m}^2$ ) in Nalepa et al. (2007) and unpublished density data provided by T. Nalepa (University of Michigan). These groups invaded Lake Huron after 1990 so they were not parameterized in the 1984 Ecopath model. Data were from surveys that collected samples on soft substrates stations deeper than 18 m using Ponar grabs in 2000, 2003, and 2007. Following procedures stated above, densities were converted to biomass ( $\text{g}/\text{m}^2$ ) with adjustments for ponar efficiencies (Table E.6). GAMs were used to estimate mean biomass ( $\text{g}/\text{m}^2$ ) by depth on soft substrate areas  $> 18$  m (Table E.2). Total biomass (g) was extrapolated from GAM estimates using maps of bathymetry (Assel, 2005) and substrate (Thomas et al., 1973). For Zebra mussel, the mean biomass ( $\text{g}/\text{m}^2$ )  $< 18$  m was assumed to be the same as in Saginaw Bay in 1993–1996 when biomass was relatively stable (Nalepa et al., 2002). The biomass on hard substrate (bedrock) sampled in Saginaw Bay by SCUBA divers was estimated to be 5.5 times that on soft substrates in 1990–1996 (Nalepa et al., 2002). For Quagga mussel, the mean biomass ( $\text{g}/\text{m}^2$ )  $< 18$  m was assumed to be the same as the mean biomass in 18–30 m (T. Nalepa, personal communication) and the biomass on hard substrate was assumed to be 8.4 times that on soft

substrates based on a Lake Erie study (Patterson et al., 2005). For year 2002, when surveys were not conducted, total biomass was calculated through linear interpolations.

*Production to biomass ratio*

$P/B$  of Amphipods, Chironomids, Oligochaetes, and Sphaeriids was based on estimates in Lake Ontario obtained from Johnson and Brinkhurst (1971).  $P/B$  of Zebra mussel and Quagga mussel was estimated using a neural network model for herbivore molluscs from Brey (2012), which links  $P/B$  to the weight, habitat depth, and growing season temperature (Table E.7).

*Consumption and assimilation*

$Q/B$  of a benthos group  $i$  was estimated as:

$$(Q/B)_i = (P/B)_i \times (P/A)_i^{-1} \times [1 - (U/Q)_i]^{-1} \quad (E.6)$$

where  $P/A$  is the production to assimilation ratio.  $P/A$  obtained from Johnson and Brinkhurst (1971) of 0.38, 0.36, 0.40, and 0.15 were used for Amphipods, Chironomids, Oligochaetes, and Sphaeriids, respectively. The median  $U/Q$  of 0.50 for benthic herbivore-detritivores from Leidy and Ploskey (1980) was used for these groups. Values of  $P/A$  were 0.60 for Zebra mussel and 0.80 for Quagga mussel based on Baldwin et al. (2002). These values for  $P/A$  represent dreissenid mussels with shell length of 11–13 mm, at habitat temperature of 5–15 °C, and consuming low-quantity but high-quality food. A  $U/Q$  of 0.65 was used for both dreissenid groups based on the assumption that 25% of filtered particles were not ingested but egested as pseudofeces (Madenjian, 1995) and 53% of the ingested particles were not assimilated (McMahon, 1996).



### *Diet composition*

Diet composition inputs for benthos groups were based on information from literature (Table E.5), which indicated that benthos groups can be divided into deposit feeders and filter feeders. Chironomids and Oligochaetes are deposit feeders and their diets were almost exclusively linked to Settled detritus. Amphipods, Sphaeriids, Zebra mussel, and Quagga mussel are filter feeders and their diets were linked to Pelagic detritus, Edible phytoplankton, Protozoa, and Bacteria.

## **E.7 Phytoplankton, bacteria, and protozoa**

### *Biomass*

Biomass inputs for Phytoplankton and Protozoa groups were based on data collected in EPA-GLNPO surveys (Barbiero and Tuchman, 2001a), in which ciliates and bacteria were not sampled. Estimates for phytoplankton biomass ( $\text{g}/\text{m}^3$ ) by taxa (including diatoms, chlorophytes, cyanophytes, chrysophytes, cryptophytes, and dinoflagellates) were obtained from Balcer et al. (2008). Biomass estimates were converted to total biomass (g) by multiplying by the volume of the euphotic zone  $1.06 \times 10^{12} \text{ m}^3$  (Fahnenstiel et al., 1998). It was assumed that the volume of the euphotic zone did not change in the period of 1984–2006 based on observed Secchi depth data in Lake Huron main basin (Dobiesz and Lester, 2009). Diatoms, chlorophytes, and autotrophic chrysophytes, cryptophytes, and dinoflagellates were aggregated into the Edible phytoplankton group. Cyanophytes constituted the Inedible phytoplankton group. Heterotrophic genera of chrysophytes, cryptomonads, dinoflagellates and ciliates constituted the Protozoa group. Biomass for ciliates and Bacteria was estimated based on information on the Lake Huron planktonic food web structure described by Fahnenstiel et al. (1998): the biomass of ciliates was

2.1 times that of heterotrophic flagellates, and the biomass and of bacteria was 2.6 times that biomass.

### *Phytoplankton production*

The *P/B* of phytoplankton groups were estimated using estimates of net primary production (*NPP*). The 1984 *NPP* was calculated using Vollenweider et al.'s (1974) empirical equation:

$$NPP = NPP_{max} \times \left[ \frac{10 \times TPL^{0.6}}{9 + 10 \times TPL^{0.6}} \right] \quad (E.7)$$

where *NPP* is in  $\text{gC} \times \text{m}^{-2} \times \text{yr}^{-1}$ , *NPP*<sub>max</sub> is the maximum primary production, and *TPL* is the total phosphorus load in  $\text{g P} \times \text{m}^{-2} \times \text{yr}^{-1}$ . The original *NPP*<sub>max</sub> estimate of 420 ( $\text{gC} \times \text{m}^{-2} \times \text{yr}^{-1}$ ) in Vollenweider et al. (1974) based on bottle incubation experiments led to an underestimation of *NPP* (Verduin, 1960; Welch, 1968). Hence the *NPP*<sub>max</sub> was modified to 790 ( $\text{gC} \times \text{m}^{-2} \times \text{yr}^{-1}$ ) based on the 2002 *NPP* estimate provided by D. Warner (USGS-GLSC, unpublished) and a *TPL* estimate from Dolan and Chapra (2012). Warner's *NPP* estimate was derived from satellite images between March and November in 2002.

To partition primary production among phytoplankton groups, 30% of *NPP* was assumed to be from Inedible phytoplankton (Fahnenstiel and Carrick, 1992). *NPP* estimates were converted to wet weight production by multiplying by a factor of 10 for Inedible phytoplankton (Sicko-Goad et al., 1984) and of 14 for Edible phytoplankton (Eugene Stoermer, University of Michigan, personal communication).

### *Other input parameters for Bacteria and Protozoa*

The  $P/B$  of Bacteria was estimated using an empirical relationship that links bacterial production to net primary production in carbon units (Cole et al., 1988). The carbon production was converted to wet weight production by multiplying by a factor of 2.9 (Hwang and Heath, 1997). A  $P/Q$  of 0.30 was used to relate  $Q/B$  to  $P/B$  following Carrick et al. (1992). The  $U/Q$  was assumed similar to that of Protozoa (Stewart and Sprules, 2011). The  $DC$  was linked to the Pelagic detritus only (Wetzel, 2001).

The  $P/B$  of Protozoa was obtained from Carrick et al. (1992). A  $P/Q$  of 0.30 was used to relate  $Q/B$  to  $P/B$  (Straile, 1997) and the  $U/Q$  was obtained from Sleigh (1989). The  $DC$  was apportioned into Protozoa, Bacteria, Inedible phytoplankton, and Edible phytoplankton based on Sigee et al. (1999).

## E.8 Detritus biomass

Biomass of Pelagic detritus was estimated based on the empirical relationship from Christensen and Pauly (1993):

$$\log(B_{\text{Pelagic detritus}}) = -2.41 + 0.954 \times \log(NPP) + 0.863 \times \log(D) \quad (\text{E.8})$$

where  $B_{\text{Pelagic detritus}}$  is the biomass in  $\text{gC}/\text{m}^2$  and  $D$  is the euphotic depth (m), which was set to 28 m based on Fahnenstiel et al. (1998). The carbon biomass was converted to wet weight by multiplying by a factor of 2.9 (Hwang and Heath, 1997). It was assumed that the carbon content of pelagic detritus is similar to that of bacteria.

The biomass of Settled detritus was estimated as the total of organic matter settling to the lake bottom in a year, assuming that settled organic matter will be no longer available to consumers one year after settlement. The biomass was estimated as the product of annual sedimentation  $1.02 \times 10^{13}$  g (Kemp and Harper, 1977), the organic carbon content in the surface

sediments of 1.6 % (Thomas et al., 1973), and a wet weight to carbon ratio of 2.9 (Hwang and Heath, 1997). Data for organic carbon content in Lake Huron sediment were very limited.

**Table E.1** Average number of sea lamprey wounds ( $LW$ ) per host and probability of surviving a lamprey attack ( $LS$ ) used to estimate sea lamprey mortality rates ( $Z_{Sea\ lamprey}$ ).  $LW$  were obtained from Prichard and Bence (2013) for lake trout groups and from Ebener (1995) for the other groups.

Host group	$LW$	$LS$	$Z_{Sea\ lamprey}$	Reference for $LS$
Burbot 1+	15	0.37	0.255	Swink (2003)
Chinook salmon 1–4	15	0.66	0.077	Assumed similar to Lake trout 5+
Lake trout 1–4	4	0.45	0.049	Swink (2003)
Lake trout 5+	23	0.66	0.118	Madenjian et al. (2008a)
Other salmonines 1–4	5	0.60	0.033	Swink (2003)
Walleye 2+	1.3	0.66	0.007	Assumed similar to Lake trout 5+
Lake whitefish 3+	1.5	0.25	0.045	Swink (2003)
Bloater 1+	0.2	0.20	0.008	Swink (2003)

**Table E.2** Generalized additive models (GAMs) used to estimate biomass inputs for the Burbot 1+, Mysis, zooplankton, and benthos groups. Data were from surveys. GAMs were fitted with a Gamma probability distribution and a log link. A smoothing spline  $s(\cdot)$  with four degrees of freedom was used to model depth. The other two predictors were entered as factors: (Year) represent the years modeled and (Tow) account for the tow type (shallow and deep tow) in zooplankton surveys.

	Dependent variable ( $\mu$ )	Model	Years modeled
Burbot 1+	CPUE (catch/km-gillnet)	$\log(\mu) \sim (Year) + s(Depth)$	1984–2005
Zooplankton	Biomass (g/m <sup>2</sup> )	$\log(\mu) \sim (Year) + (Tow) + s(Depth)$	1984–2006
Mysis	Biomass (g/m <sup>2</sup> )	$\log(\mu) \sim (Year) + s(Depth)$	1998–2006
Benthos	Biomass (g/m <sup>2</sup> )	$\log(\mu) \sim (Year) + s(Depth)$	1997–2006

**Table E.3** Sources of information for production to biomass ratio ( $P/B$ ) or total mortality rate ( $Z$ ) and consumption to biomass ratio ( $Q/B$ ) for fish groups in Lake Huron Ecopath models

Group	$P/B$ or $Z$ (/yr)	$Q/B$ (/yr)
Sea lamprey	Madenjian et al. (2003)	This study
Chinook salmon 0–0.5	He et al. (2014)	Ecopath estimated
Chinook salmon 0.5–1	He et al. (2014)	Ecopath estimated
Chinook salmon 1–4	He et al. (2014)	Dobiesz et al. (2005)
Chinook salmon 5+	This study	Ecopath estimated
Lake trout 0–0.5	Ferreri et al. (1995)	Ecopath estimated
Lake trout 0.5–1	He et al. (2014)	Ecopath estimated
Lake trout 1–4	He et al. (2014)	Ecopath estimated
Lake trout 5+	He et al. (2014)	Dobiesz et al. (2005)
Other salmonines 0	Rand et al. (1993); Swank (2005)	Ecopath estimated
Other salmonines 1–4	Rand et al. (1993); Swank (2005)	Rand et al. (1993)
Other salmonines 5+	This study	Ecopath estimated
Burbot 0–0.5	Assumed similar to Lake trout 0–0.5	Ecopath estimated
Burbot 0.5–1	Assumed similar to Lake trout 0.5–1	Ecopath estimated
Burbot 1+	Dobiesz (2003)	Dobiesz et al. (2005)
Walleye	Fielder (unpublished)	Dobiesz et al. (2005)
Lake whitefish 0	Assumed similar to Bloater 0–1	Ecopath estimated
Lake whitefish 1–2	Assumed similar to Bloater 1+	Ecopath estimated
Lake whitefish 3+	He et al. (2014)	Madenjian et al. (2010); Pothoven and Madenjian (2008)
Yellow perch 0–0.5	Irwin et al. (2009)	Ecopath estimated
Yellow perch 0.5–1	Irwin et al. (2009)	Ecopath estimated
Yellow perch 1–2	This study	Haas and Schaeffer (1992)
Yellow perch 3+	This study	Ecopath estimated
Alewife 0	Hewett and Stewart (1989)	Ecopath estimated
Alewife 1+	This study	Hewett and Stewart (1989); Pothoven and Madenjian (2008)
Rainbow smelt 0	Lantry and Stewart (1993)	Ecopath estimated
Rainbow smelt 1+	This study	Lantry and Stewart (1993)
Bloater 0	Rand et al. (1995)	Ecopath estimated
Bloater 1+	This study	Rand et al. (1995)
Deepwater sculpin 0–0.5	Assumed similar to Lake trout 0–0.5	Ecopath estimated
Deepwater sculpin 0.5+	Selgeby (1988)	Mychek-Londer and Bunnell (2013)
Slimy sculpin	Selgeby (1988)	Mychek-Londer and Bunnell (2013)
Stickleback	This study	Palomares and Pauly (1998)
Other prey fishes	House and Wells (1973)	Palomares and Pauly (1998)
Round goby	Taraborelli et al. (2010)	Taraborelli et al. (2010)

**Table E.4** Sources of stomach content data used to estimate diet composition inputs (*DC*) for fish groups in Lake Huron Ecopath models. *DC* were assumed similar for 1984 and 2002 models.

Group	Data source
Sea lamprey	Ebener (1995); Prichard and Bence (2013)
Chinook salmon 0–0.5	Stewart and Ibarra (1991)
Chinook salmon 0.5–1	Stewart and Ibarra (1991)
Chinook salmon 1–4	Dobiesz (2003); Johnson et al. (1995)
Lake trout 0–0.5	Roseman et al. (2009); Swedberg and Peck (1984)
Lake trout 0.5–1	Hudson et al. (1995); Roseman et al. (2009)
Lake trout 1–4	Dobiesz (2003); Johnson et al. (1995); He et al. (2014)
Lake trout 5+	Dobiesz (2003); Johnson et al. (1995); He et al. (2014)
Other salmonines 0	Johnson et al. (1995); Rand et al. (1993)
Other salmonines 1–4	Johnson et al. (1995); Rand et al. (1993)
Burbot 0–0.5	Ghan and Sprules (1993)
Burbot 0.5–1	Ryder and Pesendorfer (1992)
Burbot 1–3	Dobiesz (2003); Hensler et al. (2008); Schaeffer and Woldt (2005)
Walleye	Dobiesz (2003); Haas and Schaeffer (1992); Krueger et al. (1995)
Lake whitefish 0	Pothoven and Nalepa (2006); Claramunt et al. (2010)
Lake whitefish 1–2	Pothoven and Nalepa (2006)
Lake whitefish 3+	Pothoven and Nalepa (2006); Pothoven and Madenjian (2013)
Yellow perch 0–0.5	Siefert (1972)
Yellow perch 0.5–1	Haas and Schaeffer (1992)
Yellow perch 1–2	Haas and Schaeffer (1992); Truemper et al. (2006)
Yellow perch 3+	Haas and Schaeffer (1992); Truemper et al. (2006)
Alewife 0	Mills et al. (1995); Price (1963); Rand et al. (1995)
Alewife 1+	Madenjian et al. (2008b); Pothoven and Madenjian (2008)
Rainbow smelt 0	Lantry and Stewart (1993); Mills et al. (1995); Siefert (1972)
Rainbow smelt 1+	Lantry and Stewart (1993); Stedman and Argyle (1985)
Bloater 0	Crowder and Crawford (1984); Warren and Lehman (1988)
Bloater 1+	Crowder and Crawford (1984); Hondorp et al. (2005)
Deepwater sculpin 0–0.5	Hondorp et al. (2011); Mychek-Londer et al. (2013)
Deepwater sculpin 0.5+	Hondorp et al. (2011); Mychek-Londer et al. (2013)
Slimy sculpin	Hondorp et al. (2011); Mychek-Londer et al. (2013)
Stickleback	Cameron et al. (1973)
Other prey fishes	Blouzdis et al. (2013); Price (1963)
Round goby	Schaeffer et al. (2005); Taraborelli et al. (2010)

**Table E.5** Sources of diet composition information used to calculate composition inputs (*DC*) for lower trophic level groups in Lake Huron Ecopath models.

Group	Data source
Predatory cladocerans	Lehman and Branstrator (1995); Vanderploeg et al. (1993)
Cladocerans	Balcer et al. (1984); Lair (1991)
Cyclopoids	Balcer et al. (1984)
Calanoids	Balcer et al. (1984)
Nauplii	McNaught et al. (1980)
Rotifers	Leidy and Ploskey (1980); Thorp and Covich (2010)
Mysis	Branstrator et al. (2000); Grossnickle (1982); Johannsson et al. (2001)
Zebra mussel	MacIsaac et al. (1991); Thorp and Covich (2010)
Quagga mussel	MacIsaac et al. (1991); Thorp and Covich (2010)
Amphipods	Sierszen et al. (2006); Thorp and Covich (2010)
Chironomids	Thorp and Covich (2010)
Oligochaetes	Thorp and Covich (2010)
Sphaeriids	Thorp and Covich (2010)
Protozoa	Sleigh (1989)
Bacteria	Wetzel (2001)



**Table E.6** Values and data sources of the mean ash-free dry weight (mean AFDW), the ratio of wet weight to ash-free dry weight (WW:AFDW), and Ponar efficiency used to convert benthos density (number/m<sup>2</sup>) or benthos biomass in ash-free dry weight (g/m<sup>2</sup>) to benthos biomass in wet-weight (g/m<sup>2</sup>).

Group	Parameter	Value	Reference
Amphipods	Mean AFDW (mg)	0.72	Nalepa and Quigley (1983)
	WW:AFDW	6.31	Brey et al. (2010)
	Ponar efficiency	0.74	Nalepa et al. (1988)
Chironomids	Mean AFDW (mg)	0.07	Nalepa and Quigley (1983)
	WW:AFDW	9.18	Brey et al. (2010)
	Ponar efficiency	0.10	Nalepa et al. (1988)
Oligochaetes	Mean AFDW (mg)	0.13	Nalepa and Quigley (1983)
	WW:AFDW	15.26	Brey et al. (2010)
	Ponar efficiency	0.54	Nalepa et al. (1988)
Sphaeriids	Mean AFDW (mg)	0.25	Nalepa and Quigley (1983)
	WW:AFDW	11.35	Brey et al. (2010)
	Ponar efficiency	0.91	Nalepa et al. (1988)
Zebra mussel	Mean AFDW (mg)	4.68	Nalepa et al. (unpublished)
	WW:AFDW	28.06	Nalepa et al. (2010)
	Ponar efficiency	0.91	Assumed to be the same as Sphaeriids
Quagga mussel	Mean AFDW (mg)	3.44	T. Nalepa (unpublished)
	WW:AFDW	20.48	Nalepa et al. (2010)
	Ponar efficiency	0.91	Assumed to be the same as Sphaeriids

**Table E.7** Inputs for implementing the artificial neural network model from Brey (2012) to estimate *P/B* of Zebra mussel and Quagga mussel. Weights (J) were calculated from mean ash-free dry weights of zebra and quagga mussels (Table E.6) and a conversion factor of 47.8 joule per mg ash-free dry weight (Madenjian et al., 2006). Habitat depth is based on survey data (Nalepa et al., 2002; Nalepa et al., 2007). Growing season temperature is from Bai et al. (2013).

	Zebra mussel	Quagga mussel
Weight (J)	224	164
Habitat depth (m)	10	40
Growing season temperature (°C)	15	6

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## Appendix F

### The estimation of biomass and consumption to biomass ratio for non-leading stanza fish groups in the Ecopath model

Herein I provided mathematical details for estimating biomass ( $B$ ) and consumption to biomass ratio ( $Q/B$ ) of non-leading stanza groups for fish taxa parameterized as multi-stanza groups in the Ecopath software based on information from Christensen et al. (2005) and Walters et al. (2000). This estimation is based on inputs of the leading stanza group, total mortality rate ( $Z$ ) of all stanza groups, and the von Bertalanffy growth parameter  $k$  of the fish taxa.

The biomass  $B$  of a non-leading stanza fish group  $i$  is estimated based on the relationship:

$$B_i/B_l = \sum_{\tau=\tau_{min,i}}^{\tau=\tau_{max,i}} [N(\tau) \times w(\tau)] / \sum_{\tau=\tau_{min,l}}^{\tau=\tau_{max,l}} [N(\tau) \times w(\tau)] \quad (F.1)$$

where  $B_l$  is the biomass input of the leading stanza group  $l$ ,  $N(\tau)$  is the number of fish at age  $\tau$ ,  $w(\tau)$  is the mean weight,  $\tau_{min,i}$  and  $\tau_{max,i}$  are the minimum and maximum ages of the non-leading stanza, and  $\tau_{min,l}$  and  $\tau_{max,l}$  are the minimum and maximum ages of the leading stanza.  $N(\tau)$  is modeled as:

$$dN(\tau)/d\tau = -Z(\tau) \times N(\tau) + (BA/B) \times N(\tau) \quad (F.2)$$

where  $Z(\tau)$  is the total mortality rate at age  $\tau$  and  $BA/B$  is the population growth rate of the fish taxa, which is assumed to be constant. By solving equation (F.2),  $N(\tau)$  can be expressed as:

$$N(\tau) = N(0) \times \exp \left[ -\sum_{m=0}^{m=\tau} Z(m) + \tau \times (BA/B) \right] \quad (F.3)$$

where  $N(0)$  is the number of fish at age 0 and  $m$  is an index of summation. The mean weight  $w(\tau)$  is assumed to be proportional to cubic length. Based on the von Bertalanffy growth model,  $w(\tau)$  can be expressed as:

$$w(\tau) \propto (1 - e^{-k \times \tau})^3 \quad (\text{F.4})$$

Substituting equations (F.3) and (F.4) into equation (F.1), the biomass of a non-leading stanza fish group can be estimated as:

$$B_i = B_l \times \frac{\sum_{\tau=\tau_{min,i}}^{\tau_{max,i}} \exp\left[-\sum_{m=0}^{m=\tau} Z(m) + \tau \times (BA/B)\right] \times (1 - e^{-k \times \tau})^3}{\sum_{\tau=\tau_{min,l}}^{\tau_{max,l}} \exp\left[-\sum_{m=0}^{m=\tau} Z(m) + \tau \times (BA/B)\right] \times (1 - e^{-k \times \tau})^3} \quad (\text{F.5})$$

Generally,  $BA/B$  is assumed to be 0 to represent that the food web is in steady-state conditions. In such cases, equation (F.5) can be simplified as:

$$B_i = B_l \times \frac{\sum_{\tau=\tau_{min,i}}^{\tau_{max,i}} \exp\left[-\sum_{m=0}^{m=\tau} Z(m)\right] \times (1 - e^{-k \times \tau})^3}{\sum_{\tau=\tau_{min,l}}^{\tau_{max,l}} \exp\left[-\sum_{m=0}^{m=\tau} Z(m)\right] \times (1 - e^{-k \times \tau})^3} \quad (\text{F.6})$$

The consumption to biomass ratio  $Q/B$  of a non-leading stanza fish group  $i$  is estimated based on the  $Q/B$  input of its leading stanza group  $l$  and the relationship:

$$\frac{(Q/B)_i}{(Q/B)_l} = \frac{\sum_{\tau=\tau_{min,i}}^{\tau_{max,i}} Q(\tau)}{\sum_{\tau=\tau_{min,l}}^{\tau_{max,l}} Q(\tau)} \times \frac{\sum_{\tau=\tau_{min,l}}^{\tau_{max,l}} [N(\tau) \times w(\tau)]}{\sum_{\tau=\tau_{min,i}}^{\tau_{max,i}} [N(\tau) \times w(\tau)]} \quad (\text{F.7})$$

where  $Q(\tau)$  is the total consumption at age  $\tau$ .  $Q(\tau)$  is assumed to be proportional to the 2/3 power of weight. Based on equation (F.4),  $Q(\tau)$  can be expressed as:

$$Q(\tau) \propto [w(\tau)]^{2/3} \propto (1 - e^{-k \times \tau})^2 \quad (\text{F.8})$$

Thus the  $Q/B$  of a non-leading stanza fish group can be estimated as:

$$\left(\frac{Q}{B}\right)_i = \left(\frac{Q}{B}\right)_l \times \frac{\sum_{\tau=\tau_{min,j}}^{\tau=\tau_{max,i}} (1-e^{-k \times \tau})^2}{\sum_{\tau=\tau_{min,l}}^{\tau=\tau_{max,j}} (1-e^{-k \times \tau})^2} \times \frac{\sum_{\tau=\tau_{min,l}}^{\tau=\tau_{max,j}} \exp\left[-\sum_{m=0}^{m=\tau} Z(m) + \tau \times (BA/B)\right] \times (1-e^{-k \times \tau})^3}{\sum_{\tau=\tau_{min,i}}^{\tau=\tau_{max,j}} \exp\left[-\sum_{m=0}^{m=\tau} Z(m) + \tau \times (BA/B)\right] \times (1-e^{-k \times \tau})^3}$$

(F.9)

When  $BA/B$  is assumed to be 0, equation (F.9) can be simplified as:

$$\left(\frac{Q}{B}\right)_i = \left(\frac{Q}{B}\right)_l \times \frac{\sum_{\tau=\tau_{min,j}}^{\tau=\tau_{max,i}} (1-e^{-k \times \tau})^2}{\sum_{\tau=\tau_{min,l}}^{\tau=\tau_{max,j}} (1-e^{-k \times \tau})^2} \times \frac{\sum_{\tau=\tau_{min,l}}^{\tau=\tau_{max,j}} \exp\left[-\sum_{m=0}^{m=\tau} Z(m)\right] \times (1-e^{-k \times \tau})^3}{\sum_{\tau=\tau_{min,i}}^{\tau=\tau_{max,j}} \exp\left[-\sum_{m=0}^{m=\tau} Z(m)\right] \times (1-e^{-k \times \tau})^3}$$

(F.10)

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