University of Alberta

FISH HARVEST AND REPLACEMENT OF TOP PISCIVOROUS PREDATORS IN AQUATIC FOOD WEBS: IMPLICATIONS FOR RESTORATION AND FISHERIES MANAGEMENT

by

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in
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This thesis is dedicated to my husband, Darren and my mom, Denise, and to my friends in Fisheries Management who have supported me through seven long years of graduate school.

Abstract

The potential for walleye (*Sander vitreus*) restoration at Lac la Biche, Alberta, Canada is a social-ecological question that requires understanding of changes to ecosystem integrity and historical fidelity resulting from disturbance. This study explored variability in fisheries-induced disturbance across time, examined the effects of disturbance on ecosystem structure and functioning, characterized the system during different eras from pre-European settlement to the present, and assessed walleye restoration potential based on conceptual models describing the system response to disturbance.

An anthropological assessment of historical harvest was conducted (1800 to 1900) to estimate the magnitude of subsistence lake whitefish (*Coregonus clupeaformis*) harvest during rapid settlement of the Lac la Biche area. The results were compared to more recent harvest estimates (1900 to 2009) reflecting combined commercial, subsistence and recreational harvest, to describe the relative variability in the magnitude of fishing disturbances during the 200 years preceding the current restoration project.

Ecosystem models for 1800 and 1900 were used to examine how historical fisheries affected the structure, functioning, and resilience of the system, and to assess if targeting system conditions in 1900 would satisfy the restoration goal of a walleye-dominated ecosystem. Results suggest little change in ecosystem structure and function between 1800 and 1900, though the trend in the analyses is towards declining system maturity and resilience. Parameters and

state variables used as model inputs provide plausible values for guiding the restoration program.

Potential success of the walleye restoration program was addressed using a series of models representing four eras (1800, 1900, 1965, 2005) to test the for multiple ecosystem states, specifically a walleye-dominated equilibrium and a double-crested cormorant (*Phalacrocorax auritus*) dominated equilibrium. Identification of alternate stable attractors would influence the predictability of system recovery following a disturbance. Results from over 900 model simulations suggest both walleye and cormorant attractors existed in historical (1800, 1900) models but a single cormorant-dominated equilibrium is present in contemporary models (1965, 2005). Differential size-selective foraging of walleye and cormorants on yellow perch (*Perca flavescens*) provides a negative feedback stabilizing each state. Recovery of a walleye population seems possible but restoration of a walleye-dominated ecosystem was not predicted.

Acknowledgments

An ecosystem cannot be understood by studying only one species or component, and a thesis focused on historical reconstruction and ecosystem-level research cannot be completed by a single person. I have so many people to thank for their help and support in completing this thesis that I am not sure where to start.

I need to thank my supervisors Dr. A. Lee Foote and Dr. Michael Sullivan for accommodating the intensive work, school and life/travel schedule I set for myself and for waiting the seven years it took for me to complete my thesis because of it! I offer sincere thanks to my committee members, Dr. David Schindler, Dr. Rolf Vinebrooke, and Chris Davis for their continual support of me and my research and for answering all of my question regardless of how many times I asked them or how simple they might have seemed. I thank Dr. Scott Nielsen and Dr. Heather Proctor for their involvement on the examining committee for my candidacy exam, and I thank Dr. Don Pereira and Dr. Mark Poesch for being on the examining committee for my final thesis defense.

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indebted to the late Tom Maccagno, the local historian at Lac la Biche, for continually providing me with information and documents, often translated from French, pertaining to historical fisheries and fish use. Tom taught me that *friends* and *adversaries* are context dependent.

During my many years with the Department of Renewable Resources and in the Faculty of Agriculture, Life and Environmental Science I have been fortunate enough to make many valued friendships with fellow students and the academic and non-academic staff; some of these friendships might fade away with my school days while others will last forever. Both are very precious to me. Thank-you to Dr. Foote and my fellow lab mates and Dr. Naeth and the many 'Naethians' I have shared offices with over the years! Thanks to Dr. Nielsen and the students in the Nielsen/Schmiegelow lab, Dr. Hammond and Rick Pelletier and the students in the SIS lab, and Dr. John Spence and his bug-crazy students! By outlasting most of the students in these labs I have gained so many fantastic memories and I am very grateful for that! Long live FOP! I would also like to thank Drs. Paul Woodard, Peter Blenis, Glen Armstrong, Myles Dick, Derek McKenzie, David Chanasyk, Naomi Krogman, and Colleen Cassidy-St.Clair, John Acorn and Rick Pelletier for their encouragement and friendship.

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Chae, and Chris, Heather, Griffin and Parker Davis. Thank-you, thank-you, and thank-you again. I have no words.

To say that this thesis required the combined efforts of many people is an understatement. Without my friends and colleagues from the Fisheries Management Branch of Alberta Environment and Sustainable Resource Development in the Lac la Biche/Waterways area, I would not have learned half as much as I have, I would not have gotten nearly as much accomplished, and I certainly would not have had so much fun! Thanks so very much to everyone, especially Chris Davis, Alicia Pruden-Beniuk, Denyse Gullion, Alicia Morin, Daryl Watters, Eric Hegerat, Dwayne Latty, Aaron Foss, Jordan Walker, Kristen Forsberg, Sabrina Kratchmer, Sarah Bumstead, Heather Lovely, Paul MacMahon, Janet Boyd, and Nadine Marois. I feel so lucky to be part of such an amazing team and I am very grateful for each of you.

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Last but not least, I need to thank the most important people in my life – my dog Penny, my mom Denise, and my husband Darren. All of a sudden I am at a loss for words (hard to believe given the length of these acknowledgements!). It seems impossible for me to thank you for all that you have done for me. I have caused us all stress, lost sleep, and sometimes

loneliness but through it all we, our little 10-legged team, almost always stepped with the right set of legs at the right time, and we got to the end together. I could not have gotten to this point without your love and support. I hope in the end that we all learned something new, had some amazing and novel experiences, and are better off for it. Thank you for coming along with me through the good and the bad. I don't know what I would have done without you. I love you.

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Chapter 1 - Introduction

In 1999, Simon Levin made the profound statement: “Nature is not fragile…what is fragile are the ecosystem services on which humans depend.” When a system is no longer providing the ecosystem services expected of it, we turn to ecological restoration to help us get them back. Ecological restoration is defined as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (SER 2002 as stated in Higgs 2003). It can also be viewed as the desired product resulting from the act of restoration (Higgs 2003). In recent decades, ecological restoration has been attempted across a diverse range of landscapes. Arable fields are being restored to calcareous grasslands in Germany (Kiehl et al. 2006), shallow lakes in Europe and North America are being restored to a clear-water phase after eutrophication (Gulati and van Donk 2002, Jeppesen et al. 2007), and California’s giant sequoia (*Sequoiadendron giganteum*) groves are being restored following a century of fire exclusion (Stephenson 1999). The success of restoration attempts can be hindered by the complexity of systems. Effective restoration action requires understanding of the issues and processes operating both individually and collectively across spatial and temporal scales (Lindermayer et al. 2001).

Over most of the last 50 years the lake ecosystem at Lac la Biche, Alberta, Canada has supported an extremely low walleye (*Sander vitreus*) biomass due at least in part to human overharvest (R.L. & L. Environmental Services Ltd. 1992). In the last 25 years, there has been an exponential increase in the number of fish-eating double-crested cormorants (cormorant; *Phalacrocorax auritus*) foraging on the lake, and a noticeable decrease in the size but increase in the abundance of forage fish, namely yellow perch (perch; *Perca flavescens*). The result of these, among other recent changes to the lake ecosystem (for a brief review see Chapter 2), has been the development of a system which is unable to satisfy social demand for the provision of goods and services, predominately the opportunity to harvest walleye. In 2005, Alberta

Environment and Sustainable Resource Development introduced a long-term lake restoration project focused on walleye stocking and cormorant control as methods for recovering walleye dominance in the lake with the ancillary effect of improving the overall size structure of the fish community (Figure A-1). The social objective of this restoration was to “improve[ing] fishing opportunities for future generations” (Figure A-1). Though management initiatives are underway, the potential for restoration to a walleye-dominated ecosystem remains unclear.

The goals of the Lac la Biche fisheries restoration program are focused on achieving walleye restoration as a product. The performance standard is the return of a walleye population large enough to allow sustained, responsible harvest or, in other words, the recovery of the walleye population. My dissertation is focused on ecosystem restoration as a process that leads to a product; specifically, improving understanding of the processes and structure required to support the walleye and fish community biomass of historical times so we can attempt to recreate these conditions through restoration. There are two ecological concepts that emerge from this broad study of restoration theory and practice: the integrity of the resulting ecosystem, and its historical fidelity (Higgs 2003). A combined model of integrity and fidelity considers how closely the restored ecosystem resembles the historical conditions of the area and is based on three subsidiary principles: structural/compositional replication, functional success, and durability (Higgs 1997).

Ecosystem structure refers to the composition of the biotic community and the abiotic conditions in which it exists (Myster 2001, Cortina et al. 2006). Ecosystem function describes the processes that maintain the operation of the ecosystem in a specific state (Myster 2001). Intelligent and successful manipulation, management, or restoration requires a comprehensive understanding of structure and function to help ensure “ecological alignment” between the restored ecosystem and the historical reference (Higgs 2003). Durability is a key feature for evaluation of ecological restoration projects. To be durable, a restored ecosystem must achieve integrity and fidelity for a significant period of time that is appropriate to the focal system (Higgs 1997). In addition to durability, resilience can be used to judge success (Higgs 2003).

Ecosystem structure, function, and durability influence, and are influenced by, the disturbance regime under which they evolved. Ecological theory suggests the range of naturally occurring fluctuations experienced by a system influences its resilience (Holling 1973); thus, management regimes intended to increase system stability (i.e. fire suppression in terrestrial systems or maximum sustained yield of fish populations), are thought to decrease system resilience. Resilience is "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to retain essentially the same function, structure, identity, and feedbacks (Sheffer 2009). This implies that critical relationships can persist without the system 'flipping' into an alternate community configuration (Holling 1973).

There are three main conceptual models describing equilibrium dynamics of ecosystems that are generally applicable to disturbance and restoration ecology: continuum models, threshold models, and alternate stable state models (Hobbs and Suding 2009) (Figure 1-1). Continuum models predict a system response that is smooth, continuous, proportional to the size of the disturbance, and has a single ecosystem configuration (ecosystem state or attractor) (Odum 1969). Threshold models describe system dynamics in which a relatively small change to a controlling variable causes a large shift in ecosystem state (Hobbs and Suding 2009). Alternate stable state (ASS) models (Scheffer et al. 2001, Scheffer 2009) describe a specific type of threshold model in which a critical level of a controlling variable is surpassed, resulting in a change in system feedbacks that alters the trajectory of the systems development. When resilience is low, a disturbance is more likely to trigger an alternate stable state. In contrast to equilibrium models, stochastic models describe non-equilibrium dynamics with no consistent spatial or temporal patterns in system response to a disturbance (Hobbs and Suding 2009). Divergent, cyclic, and arrested trajectories that do not trend towards a stable system are common examples of stochastic dynamics (Hobbs and Suding 2009).

Alternate stable state theory suggests a single ecosystem can exist in more than one stable state with the shift between states being controlled by a sudden and difficult-to-reverse change in a controlling variable (Scheffer et al. 2001). When a threshold level of the controlling variable is surpassed the internal feedbacks controlling system structure and function may change (Walker and Myers 2004). The resulting change in the trajectory of system development usually leads to dominance of a less productive and generally less desired state (Folke et al. 2004). In such systems, management focused on affecting change in the factors or processes that caused the initial switch might be insufficient for ecological restoration because of a difference in the trajectories leading to and from an ASS (hysteresis) (Suding et al. 2004). In systems with hysteresis, more intensive effort might be required.

In this dissertation, I examined the potential for walleye restoration at Lac la Biche (the product) from a socio-ecological perspective concerned with understanding ecosystem integrity and historical fidelity (the process). When I began this process I had three general hypotheses that 1) the dominance of cormorants and lack of walleye at Lac la Biche could be explained by ASS theory and changing yellow perch size distribution and abundance acted as the feedback reinforcing each state, 2) life-history characteristics of the yellow perch population were controlled by foraging selection by the dominant piscivorous predator so that restoration of the walleye-dominated state could be achieved by increasing walleye biomass (stocking) and decreasing cormorant biomass (culling), and 3) restoration targets set to imitate system conditions in 1900 were not adequate for long-term sustainability of the walleye population. As I explored these hypotheses, I discovered that they could not be adequately addressed in the absence of a historical context. The next three chapters present the research required for understanding the process to achieve walleye restoration and for understanding walleye restoration potential for Lac la Biche.

Variability in disturbance across space and time is a vital attribute shaping ecological systems of the past and providing guidance and context for managing and restoring systems in the future (Landres et al. 1999). Changes in a fish population due to harvesting are a major class of disturbance impacting freshwater lakes (Holling 1973). In Chapter 2, I used anecdotal, qualitative and some quantitative reports of human population size and subsistence consumption of lake whitefish (*Coregonus clupeaformis*) to estimate annual fish harvest at Lac la Biche during the fur trade era (1800 to 1912). Using the lake whitefish harvest time series, I assessed the magnitude and potential influence of historical subsistence harvest estimates on contemporary commercial harvests (1913 to 2009). This work has been accepted by the Journal of Ecological Anthropology.

In Chapter 3, I used Ecopath with Ecosim (Pauly et al. 2000, Christensen et al. 2008) models to assess the biological and ecological impact of historical subsistence harvest on ecosystem structure and function between 1800 and 1900. I used the time series of fisheries harvests from Chapter 2 as the disturbance variable driving ecosystem dynamics during European settlement of the area. I compared ecosystem indices related to trophodynamics, thermodynamics, trophic flow analysis, and information theory (Christensen et al. 2008) to determine changes in structure and function resulting from the disturbance regime. State variables and parameters from models of 1800 and 1900 provided a range of variability for guiding restoration or other management goals, and for improving our understanding of the effects of disturbance on system structure, function, and resilience. Models developed in this chapter were also used in the assessment of alternate stable states in Chapter 4. This work is undergoing review by the North American Journal of Fisheries Management.

Restoration potential and approach requires an understanding of how a system is likely to respond to disturbances. Systems with more than one equilibrium state (attractor) require a different restoration approach than systems with a single attractor. In Chapter 4, I used forty Ecopath models representing Lac la Biche during four different time eras (1800, 1900, 1965, 2005) to assess the theoretical potential for alternate stable states defined by a walleye-dominated equilibrium and a cormorant-dominated equilibrium. I used Ecosim to test four hypotheses related to 1) the potential for ASSs given a large disturbance to walleye, yellow perch, or cormorant populations, 2) the size and type of disturbance required to trigger a catastrophic shift to an ASS, and 3) the potential for restoration of the historical walleye-dominated ecosystem, and 4) changes in the foraging relationship of walleye, cormorants, and perch in models with ASSs and models without. I also briefly discuss early trends in the ecosystem response to restoration efforts and how they compare to the outcomes of modeled scenarios.

Given that the mission of the Lac la Biche fisheries restoration program was to recover the walleye population by restoring the system, then the goal of this dissertation was to understand the system and to “demonstrate this understanding in an objective, unambiguous way” (Jordan et al. 1987:15). The complexity of ecological systems, including their feedbacks and interactions, ensures that studies of dynamic ecosystems will be full of uncertainty and incomplete knowledge. We can never know everything. But in attempting to discern what we can know from what we cannot we can follow the wisdom of the 18th century Italian philosopher Giovanni Battista Vico “…that verum et factum convertuntur: that is, the condition of being able to know anything truly, to understand it as opposed to merely perceiving it, is that the knower himself should have made it” (Collingwood 1994:64).

Figure 1-1. Three conceptual models illustrating ways in which an ecosystems equilibrium state can shift in response to changing conditions such as an increase in nutrient levels or heavy exploitation (adapted from Scheffer and Carpenter 2003). In the gradual continuum and threshold models only a single equilibrium point exists for a specific condition. In the alternate stable state model, up to three equilibra can exist at a given set of conditions.

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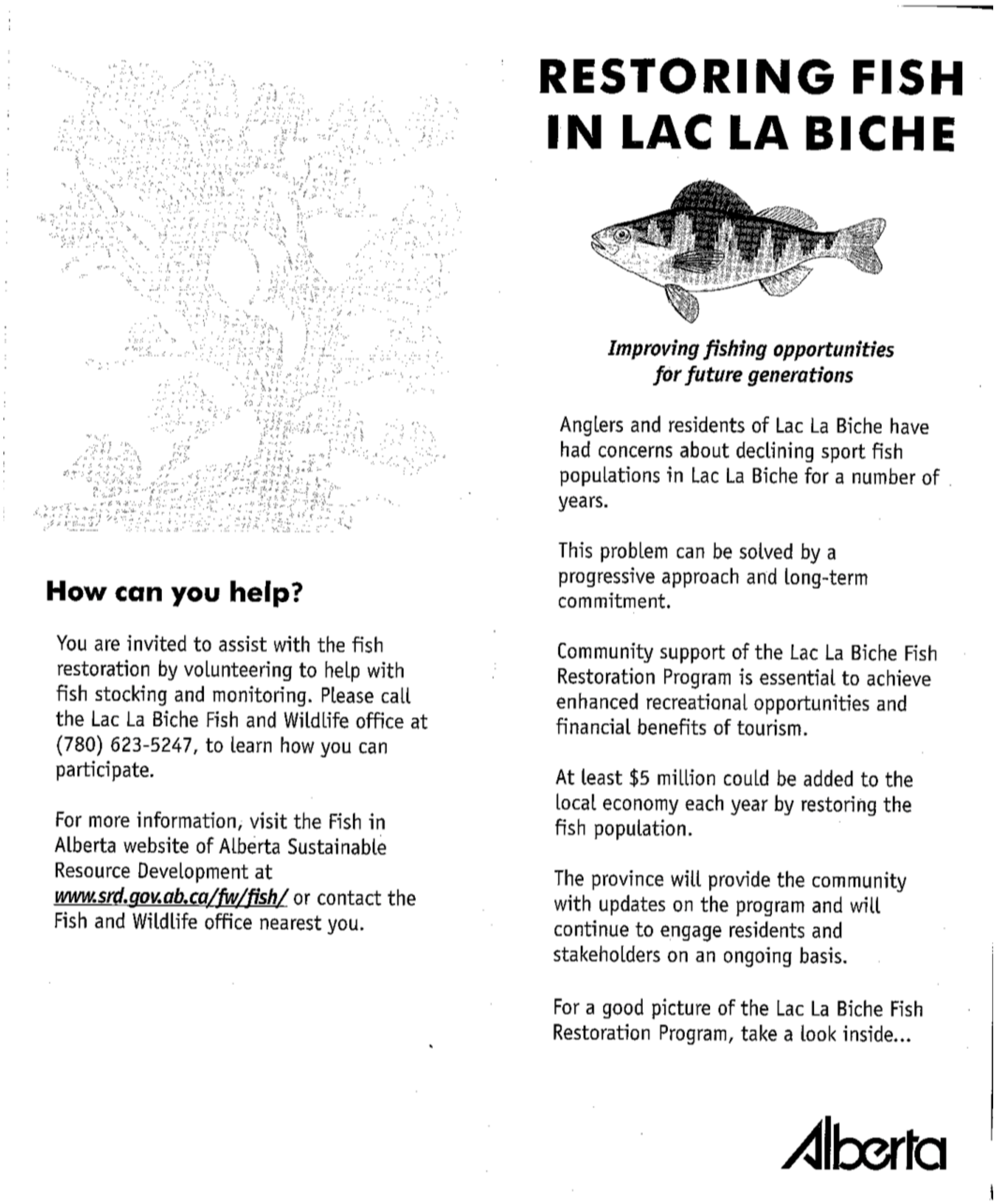
Appendix A -

Figure A-1. Alberta Environment and Sustainable Resource Development (2005) brochure describing the Lac la Biche Fishery Restoration Program and objectives.



How can you help?

You are invited to assist with the fish restoration by volunteering to help with fish stocking and monitoring. Please call the Lac La Biche Fish and Wildlife office at (780) 623-5247, to learn how you can participate.

For more information, visit the Fish in Alberta website of Alberta Sustainable Resource Development at <u>www.srd.gov.ab.ca/fw/fish/</u> or contact the Fish and Wildlife office nearest you.

RESTORING FISH IN LAC LA BICHE

Improving fishing opportunities for future generations

Anglers and residents of Lac La Biche have had concerns about declining sport fish populations in Lac La Biche for a number of years.

This problem can be solved by a progressive approach and long-term commitment.

Community support of the Lac La Biche Fish Restoration Program is essential to achieve enhanced recreational opportunities and financial benefits of tourism.

At least $5 million could be added to the local economy each year by restoring the fish population.

The province will provide the community with updates on the program and will continue to engage residents and stakeholders on an ongoing basis.

For a good picture of the Lac La Biche Fish Restoration Program, take a look inside...

Alberta

Overview○○○

Intense fishing over the years has led to the decline of the Lac La Biche fish population. Recovery has been prevented due to continued commercial and sport-fishing and, more recently, by thousands of fish-eating cormorants nesting in the area.

Currently, the lake has large numbers of very small perch and tullibee, modest numbers of whitefish, low numbers of pike, and very low numbers of walleye.

Biologists point out that cormorants have increased thanks to large numbers of very small "prey" fish (perch and tullibee). Numbers of prey fish increased because there were very few "predator" fish, such as walleye and pike, available to eat these prey.

Improving fish survival will require a number of management actions. This program will be reviewed on an annual basis.

Cormorant— a fish-eating bird that nests in abundance in the Lac La Biche area

○○○ The Lac La Biche Fish Restoration Program

Alberta's plan to restore fish populations in Lac La Biche involves these key management actions:

Cormorants

○ Continuing to reduce cormorant populations by oiling cormorant eggs to prevent hatching and persist with culling of birds.

Sportfishing

○ Reducing the sportfishing bag limit to one fish over 75 cm for pike and three for whitefish (all other sport fish limits remain unchanged).

Commercial fishing

○ Reducing commercial gill net fishing to one early summer fishery, with a quota of 30,000 kg for whitefish, tolerance limits of 500 kg for pike and 150 kg for walleye.

Fish stocking

○ Re-activating the provincial walleye stocking program in spring 2006 and stocking walleye into Lac La Biche.

Critical areas

○ Closing the Owl River, other tributaries and the lake outlet to fishing to protect critical spawning locations and restore damaged areas.

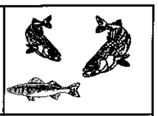
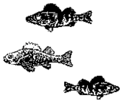
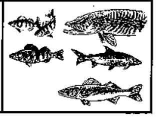
○ Closing the Owl River bay out to Birch and Currant islands to all net fishing.

Monitoring

○ Studying program progress, reporting on assessments and revising management actions as required.

WHERE WE'VE BEEN

History

1 Walleye Populations	Normal	
2 Perch Populations	Normal	
3 Average Size of Fish	Normal	
4 Numbers of Cormorants	Normal	
5 Fishing Impact	Sustainable	

About 100 years ago, walleye, pike, perch, tullibee and whitefish were abundant in Lac La Biche, with a healthy balance of populations.

As more settlers arrived, fishing for food and profit increased. By 1918, four large fish companies were harvesting up to 450,000 kg/year (1 million lbs.). By the 1920s, the fishery was in decline.

By the 1950s, tullibee had increased dramatically in response to the removal of key predators—walleye and pike.

By the mid-'60s, walleye populations had collapsed. Pike, whitefish and perch remained low. From 1980 to 2005, the local cormorants grew from a few hundred to over 8,000 nesting pairs due to high numbers of small fish.

2006

1 Walleye Populations	Very Few	
2 Perch Populations	Abundant and Small	
3 Average Size of Fish	Much Smaller	
4 Numbers of Cormorants	High	
5 Fishing Impact	Unsustainable	

Provincial fisheries staff completed meetings begun in 2005 with residents, stakeholder groups, county and municipal officials, and Métis and First Nations about the proposed Lac La Biche Fishery Restoration Program.

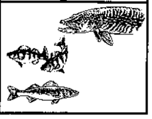
Based on the consultations, Alberta decided to take key steps to improve the fishery.

The focus on conservation includes aggressively restocking walleye and introducing fishing restrictions to protect the stocked fish and the existing pike population so they can reach adult size. Reduction of the cormorant population will improve the survival of small stocked walleye.

Annual reviews will determine when fishing opportunities can be increased.

WHERE WE'RE GOING

2010 - 2015

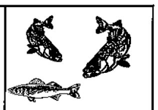
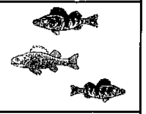
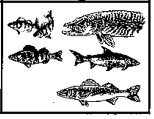
1 Walleye Populations	Recovering	
2 Perch Populations	Fewer and Larger	
3 Average Size of Fish	Growing	
4 Numbers of Cormorants	Dropping	
5 Fishing Impact	Reduced	

By 2010, the entire fishery will be improving. Walleye populations will be increasing. Fish of all species will be larger in size.

Pike, perch and whitefish populations will have recovered enough to provide increased harvest opportunities. Cormorant populations will have decreased substantially.

Besides producing first-rate fisheries for pike and perch, the program will improve other fisheries such as for lake whitefish. Healthy fish populations are part of a healthy lake and restoring populations will also help improve water quality.

2020 - 2025

1 Walleye Populations	Normal	
2 Perch Populations	Normal	
3 Average Size of Fish	Normal	
4 Numbers of Cormorants	Normal	
5 Fishing Impact	Sustainable	

By 2020 - 2025, a new generation of Albertans will be enjoying the Lac La Biche fishery. Management actions are expected to achieve a sustainable walleye harvest fishery. All fish species will have strong populations.

Recovered "predator" fish species such as walleye and pike will compete with cormorants by feeding on perch and tullibee. This competition will help keep cormorant populations low.

Chapter 2 - Of Fur and Fins: Quantifying Fur Trade Era Fish Harvest to Guide Contemporary Restoration Efforts at Lac la Biche, Alberta[1]

Summary

The history of fisheries exploitation in Canada has significant ties to the development and westward expansion of the fur trade. Understanding the scale and nature of this relationship is important when assessing the developmental or evolutionary history of a system. This study uses anecdotal reports of human population size and subsistence lake whitefish (*Coregonus clupeaformis*) consumption to estimate annual fish harvest at Lac la Biche, Alberta (54°52′N, 112°05′W) during the fur trade era and to assesses the magnitude of historical fish harvest and its potential influence on contemporary harvest potential. Historical (1800-1911) lake whitefish harvest is predicted to have increased approximately 10-fold, from 74,000 kg in 1800 to 811,000 kg in 1875, immediately preceding a lake whitefish population collapse in 1878. Following the initiation of commercial fishing, contemporary (1912 to 2009) harvest peaked at 424,000 kg, about one half the previous maximum of the subsistence fishery. The persistence of low contemporary harvest biomasses suggests a regime shift from a system of high- to low-lake whitefish harvestable biomass, possibly resulting from declining population resilience with increasing harvest pressure. Knowledge of historical fish harvest should minimize the impacts of the shifting baseline syndrome by elucidating the magnitude and impacts of

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[1] A version of this chapter has been accepted for publication by the Journal of Ecological Anthropology.

historical harvests on future harvest potential and can help guide the selection of restoration targets.

Introduction

Since humans first set foot in western North America almost 11,000 years ago (McCullough and Maccagno 1991:1), we have been changing the landscape and the fish and wildlife resources it supports. The earliest changes to both aquatic and terrestrial systems were the direct result of overharvest, but habitat alteration, pollution, and species introductions have all impacted systems from historical to contemporary times (Jackson et al. 2001). Since the westward expansion of the fur trade in the mid-1700s, the rate of change has increased and the implications of change have become more severe, resulting in the prevalence of highly modified or degraded ecosystems. These altered systems, when no longer able to satisfy the social demand for the provision of goods and services, often become candidates for restoration projects. Restoration projects offer ecologists and managers an opportunity to respond to past ecological degradation from anthropogenic disturbances, such as overharvest. To do so, however, managers require knowledge of the pre-disturbance conditions or the 'historical range of variability' of the targeted ecosystem, as well as knowledge of the magnitude and type of disturbance that influenced the development of the system (its 'evolutionary history') (Landres et al. 1999, Moore et al. 1999, Seastedt et al. 2008). Without this knowledge, managers, scientists and citizens are likely to assume that ecosystem conditions of the intermediate and distant past resembled those of their own remembered history and thus can be ignored – a classic characteristic of the shifting baseline syndrome (Pauly 1995, Humphries and Winemiller 2009 Papworth et al. 2009).

The objectives of this study were to: 1) estimate historical fish harvests and compare historical subsistence harvests to harvests resulting from the growth of a commercial fishing industry, 2) explain potential effects of historical fish harvests on future harvest potential, and 3) to place historical lake whitefish harvests within the context of current production. In this article, I aim to demonstrate that historical fish harvests, influenced by the westward advancement of the fur trade, resulted in overharvest of lake whitefish (*Coregonus clupeaformis*) at Lac la Biche, Alberta. To do this, I explore the role of fur trade era fish harvest in shaping the evolutionary history of a large inland lake and subsequently, and I place the magnitude and potential impact of historical harvests in context by comparing with contemporary harvest.

Lac la Biche and the development of the fur trade

Lac la Biche (54°52′N, 112°05′W) is a large (223 km^2), shallow (average depth 8.4 m, maximum depth 21.3 m), eutrophic lake located on the southern edge of the boreal forest in northeast Alberta, Canada (Figure 2-1). There are 13 species of fish in the lake of which the lake whitefish has the longest reported history of targeted harvest. This study site was chosen because of the recent (2005) development of a fisheries restoration program at the lake; however, the availability of historical data pertaining to the fur trade era, as well as archeological and anthropological reports on the evolutionary history of the land and its people, aided in model development.

Native settlement of the area around Lac la Biche began approximately 11,000 years ago, following the retreat of the Laurentide Ice Sheet (McCullough and Maccagno 1991:17). The original occupants of the area, thought to be the Beaver-Sarcee-Sekani and the Blackfoot Indians (McCullough 1982:56), were forest dwellers, seasonally transitioning between forest and parkland habitats in response to the availability of bison (*Bison bison bison*) herds (McCullough 1982:46,48). Occupancy of the area remained more or less constant until the mid-1700s when Cree middlemen from eastern Canada made their way to present-day Alberta.

The Cree were the frontiersmen of the fur trade. Equipped with firearms and superior equipment acquired through trading, they were able to expand rapidly through western Canada where they occupied the best fur trade sites by pushing the less advanced tribes into more marginal areas (McCullough

1982:39). The advancement of the Cree, and with them the fur trade, had important implications for the development of resource exploitation in the west. The presence of Cree settlements eventually attracted peddlers, freemen, and traders to the area. The two big trading companies of the time, the British-owned Hudson Bay Company (HBC) and the French-owned North West Company (NWC), were attracted to the lake because of its proximity to the Portage la Biche (Beaver River Route), which provided an important connection between the Athabasca and Churchill drainage basins. Between 1798 and 1799, three trading posts were built at Lac la Biche drawing many new people to the area. Even after the closure of the posts in 1802, the Portage la Biche maintained a steady flow of traders, 'vagabonds', and freemen through the country, many of whom took up permanent residence on the shores of the lake (McCullough and Maccagno 1991:83). By 1817, the NWC and the HBC were back operating in the area but in 1824, the Portage la Biche was abandoned by the HBC and with it came the closure of a permanent trading post in Lac la Biche. No post existed in the area until the 1850s when the La Biche Post was opened, remaining active in the area for over 50 years (Maccagno 1988:46).

Despite the lack of an active trading post for most of the early 1800s, a large population of Metis freemen and Native Americans settled on the shores of the lake. By 1840, this population had attracted the attention of missionaries and in 1852, Our Lady of Victories Roman Catholic Mission was officially founded on the southern shore of the lake. Between 1862 and 1899, the Sisters of Charity, also known as the Grey Nuns, operated a boarding school at the site of the mission which remained an active force in the area until its closure in 1963. The development of the mission and its boarding school attracted still more people to the area and the introduction of agriculture by the missionaries further stabilized the sedentary lifestyle initiated by the fur trade.

The changing lives of fishers

The reliance of the early occupants at Lac la Biche on fish resources has been debated, with McCullough (1982) suggesting that fishing was an integral part of the lives of forest dwelling tribes, and others reporting that fishing played a minor subsistence role with moose (*Alces alces*) hunting being the dominant preoccupation (Jenness 1932, Ridington 1968 as in McCullough 1982:58,60, Forbis 1970). Regardless, the reliance on both hunting and fishing to sustain early human populations is likely, with fish being an important subsistence resource during times of wildlife scarcity (Curtis 1970:19, Goddard 1916:216), and in the spring and fall when spawning species were abundant and easy to catch (McCullough 1982:64). In the winter, gillnets made from rawhide cord or willow root bark and hooks made from antlers were the main technologies for fish harvest, while bone-pointed spears, weirs and seines were used during the spawning season (Skinner 1912:27, Goddard 1916:216, Curtis 1970:20,62). Northern pike (*Esox lucius*) and lake whitefish were caught in the winter (Curtis 1970:19) and presumably consumed fresh. It can also be assumed that lake whitefish and cisco (*Coregonus artedi*) would have been harvested during the fall spawn while walleye (*Sander vitreus*), northern pike, white suckers (*Catostomus commersonii*) and longnose suckers (*Catostomus catostomus*) would have been consumed during the spring.

With the westward expansion of the Cree, the relationship between fishers and the resource experienced some subtle changes. The Cree generally fished for the same species and in the same ways as the Beaver-Sarcee-Sekani and Blackfoot Indians; however, the Cree had improved some of their fishing technologies through trade with the HBC (Skinner 1912:27), making them more efficient harvesters. Seasonal and long-term patterns of settlement and occupation by the Cree might also be different than previously experienced. For instance, in the Cree culture, women and children were left year round in large village settlements to fish while the men engaged in moose and beaver hunting activities (Thwaites 1959:227). In contrast, earlier tribes were presumably more nomadic, occupying lakes less frequently and more seasonally (Ridington 1968:39-42 as cited in McCullough 1982:58).

The arrival of the explorers and brigades of the fur trade, followed soon after by the Roman Catholic missionaries, solidified the change in the settlement pattern of the area that was initiated by the Cree; the populations had become centered around the lake (Champagne 1992:141) and the harvest pressure on the fisheries resource rapidly increased. Fish resources were important for satisfying subsistence needs of the trading posts. In fact, this relationship was so important that David Thompson wrote "…when a new trading House is built which is almost every year, every one is anxious to know the quality of the fish it contains for whatever it is they have no other for the winter." (Tyrrell 1916:111). Lac la Biche proved to be an excellent location for an inland post owing to the quality of its fisheries.

In 1798, during the first year of activity for the HBC post at Lac la Biche, David Thompson reported that net sets on Lac la Biche "…gave us fish of pike, White fish, Pickeral [walleye] and Carp [white suckers] for about one third of our support…" (Tyrell 1916:305). By 1819, lake whitefish was the main food of the HBC post (HBCA,PAM,B.115/e/1,fo.3d as referenced in McCullough and Maccagno 1991:101), and in 1864 William Traill wrote that "Fish is the staple article of the diet…" (McCullough and Maccagno 1991:132) at the fur trade post and he described how "…fish were eaten three times a day or as often as required" (Traill 1874 as referenced in McCullough and Maccagno 1991:135). Similarly, at the mission, fish were required to meet the subsistence needs of the Fathers, Brothers and nuns, as well as the orphans, boarders and students attending the mission school (Champagne 1992:32,51).

The fall fishery was critical for providing food to both the post and the mission. During this time, lake whitefish were harvested on their spawning grounds in large quantities by lighting the area with birch bark flambeau (torches) and spearing the fish (Moberly and Cameron 1929:86). These fish were either boiled fresh, dried, salted, split and smoked, frozen or in some way preserved for use over winter (Tyrell 1916:111, Traill 1874 as referenced in McCullough and Maccagno 1991:135). In the winter and through the summer, gill nets were set to supplement the fall spawn or to provide a source of fresh fish (Champagne 1992:51). Of all the available fish species, the lake whitefish was judged to be the most important food source due to its versatility in preparation, palatability when eaten plain, and the nutritional quality of its meat (Richardson 1836:195-196, Tyrell 1916:111).

Following the lake whitefish decline in 1878, the relationship between the fish and the fishers changed. Lake whitefish could no longer be relied upon to meet the subsistence needs of the people without an increase in harvest effort (Young 1882 as cited in McCullough and Maccagno 1991:150). In 1892, control of the fisheries began and in the fall of 1895, heavy restrictions were implemented and the first fishing permits given out (Champagne 1992:240,246). Despite these restrictions, the Department of Marine and Fisheries (1895:359) reported that the fisheries continued to fail and "…it has been found to be difficult to do anything towards protecting them." This conclusion was reached based on claims that despite fish being necessary for subsistence, the people of Lac la Biche made no preparations for the closed season such as drying fish, and all fish other than whitefish were wasted (Department of Marine and Fisheries 1895:359-360). In 1895, the Department of Marine and Fisheries (1896:191) commented that the fish populations at Lac la Biche were "…at a critical stage for [they] have been largely reduced in numbers." Despite this warning, by 1912, commercial fishing was introduced as an industry (Champagne 1992:282) and in 1915, the HBC shifted its business focus away from fur to fishermen (HBCA,PAM,D.FTR/3 as cited in McCullough and Maccagno 1991:185).

The development of the rail line and the inauguration of freight service in 1915 sped up the development of the commercial fishing industry and in 1916, the first fish plant was opened at Lac la Biche (Lac la Biche Heritage Society 1975:29). Rapid development of the export market prompted the building of four fish plants and by 1918, over 200 fishermen were harvesting and processing walleye, northern pike, cisco and lake whitefish (Lac la Biche Heritage Society 1975:29). However, two years later, "…the bloom was off the lake and many fish companies formerly based on Lac la Biche moved to Lake Athabasca" (Chipeniuk 1975:20). While the HBC was left responding to the downturn of the commercial fishing industry, rapid settlement of the area by Catholic and Orthodox families wishing to adhere to the custom of eating fish on Friday, drove a resurgence of the fishery (Lac la Biche Heritage Society 1975:31). Between 1928 and 1929, fish prices increased as a result of this demand and every storekeeper and farmer began peddling fish in response to the high prices (Lac la Biche Heritage Society 1975:31).

In 1930, the market switched again as mink ranching became popular in the area and the demand for cisco, the staple of the mink diet, increased (Champagne 1992:284). Nets set to capture cisco used smaller meshes to capture these smaller fish, and large biomasses of big yellow perch (*Perca flavescens*) and small walleye, lake whitefish and northern pike were also removed. Much of this by-catch would likely have been dumped back into the lake and almost certainly the vast majority of it would not have been reported. The small mesh nets (70 and 76 mm stretch measure) of the cisco fishery are thought to have had a large negative impact on the sustainability of the walleye population (Valastin and Sullivan 1997:6).

While commercialization of the fishery was occurring, another new type of fishing pressure appeared – angling. Starting in 1935, Lac la Biche was marketed to tourists as a "sportsmen's paradise" and angling for walleye and northern pike was promoted (Johnson 1999:262-263). Local reports on fishing conditions between 1920 and 1975, summarized in Valastin and Sullivan (1997), frequently describe the abundance of the walleye, the ease of catching northern pike and the size of yellow perch, at the same time describing how these species were regularly wasted.

There was no market for walleye in the earliest years of the net fishery so they were dumped or "thrown out" (Valastin and Sullivan 1997:6,7) as by-catch.

During the spring spawn, northern pike were pulled from the creek with pitchforks and fed to the pigs while the children played with the large ones (Valastin and Sullivan 1997:8). Yellow perch were removed in huge quantities (113,000 kg to 318,000 kg) by the cisco fishery (Valastin and Sullivan 1997:12) and, though they were not wasted, this represents an important source of mortality. During the same period, harvests of lake whitefish were reported at only a fraction of the historical levels and the loss of "jumbo" individuals (3.2 kg to 3.6 kg) was described (Valastin and Sullivan 1997:13-14). Despite the apparent abundance of sport fish through the first half of the twentieth century, by 1970 walleye were extirpated and in the latter half of the century, both the northern pike and yellow perch fisheries had declined (Valastin and Sullivan 1997:22-23).

Since the mid-1990s both commercial and recreational harvest regulations have become more restrictive and subsistence harvest by First Nations, though not limited per se, has been minimal, likely due to significantly reduced catch rates. While a spring commercial fishery for lake whitefish still exists, there are only two active fishermen with a quota of 30,000 kg and fish are peddled locally with demand largely driving involvement in the fishery. Angling for northern pike (spring) and yellow perch (winter) dominate the recreational fishery while a large-scale, multi-year restoration program initiated in 2005 is focused on recovering the walleye population.

Quantification of historical lake whitefish harvest

To explore the hypothesis that historical subsistence fishing was capable of overharvesting the resource, it was necessary to quantify the magnitude of harvest. The settlement of the area around Lac la Biche through the 1800s, and the resulting changes inflicted on the abiotic and biotic resources of both the terrestrial and aquatic communities, can be attributed directly to the expansion of the fur trade and the development of the Roman Catholic mission. As the main forces influencing the population of the area through the 19th and early

20th centuries, the information recorded by these groups was valuable for estimating harvests. Reports of the number of fish harvested, approximate locations of harvests, harvest techniques, methods of fish preparation, daily rations or allotments for the men, women, children and dogs (from dog teams) associated with trading posts, as well as predicted subsistence needs of Metis and Native American families were all discussed in the journals of the fur trade posts, and especially in the narratives of David Thompson (Tyrrell 1916). Similar harvest information for the mission was regularly reported in the journals of the Oblate Fathers and has been translated and referenced in reports by Champagne (1992), Kulle (1993), Maccagno (1988), and McCullough and Maccagno (1991). In addition, general comments on the success of the fishery, utilization of the fish resources, management and environmental conditions were found in historical newspaper articles and reports from the Department of Indian Affairs.

To generate estimates of the total number of lake whitefish harvested during the historical period, including minimum and maximum estimates, I summarized all pieces of information that were available from the above mentioned sources into three categories: fur trade harvest, mission harvest, and subsistence harvest, which includes harvest by Metis, Native American, and other families not associated with the fur trade post or the mission. I estimated harvest separately for the fall/winter months (October 1 to May 10) and the spring/summer months (May 11 to September 30) because of differences in the nature of the harvest (Table 2-1). Seasonal harvests were added together to generate an annual harvest estimate. Since most harvest data were reported as the number of fish harvested, I estimated the total biomass removed by multiplying by 2.04 kg, the average weight of a lake whitefish harvested in 1819 by the trading post (HBCA,PAM,B.115/e/1,fo.3d, as cited in McCullough and Maccagno 1991:101). The expected harvests of each user group from 1800 to 1911 were combined to generate a time series of fish harvest data (Table 2-2).

Estimating subsistence harvest required information on the number of fish required to support a family as well as the number of families settled around and presumably relying on the lake. To generate a time series of the number of families in the area, I used references from fur trade and mission reports for the years between 1800 and 1869 (Tyrrell 1916, McCullough and Maccagno 1991; Champagne 1992), trading post census data from 1872 for the 1870s (Hardisty Papers, Glenbow-Alberta Institute, Calgary, as cited in McCullough and Maccagno 1991:136), field notes of the land surveyer P.R.A. Belanger for the late 1880s (Belanger 1889 as cited by McCullough and Maccagno 1991:163), and federal census data for the years 1901 and 1911 (Library and Archives Canada 1901,1911) (Figure 2-2). Estimates of the number of Mission residents and the number of school children, used in calculating summer fish consumption, were derived from Champagne (1992) (Figure 2-3).

Reductions in fish harvest after the decline of lake whitefish are justified, where necessary, through anecdotal reports describing declines in the supply of fish. For instance, McCullough and Maccagno (1991:141) describe how the failure of the fall fishery for lake whitefish in 1878 occurred in response to "…heavy fishing pressure brought on by increased population densities" and on December 9, 1882 the Edmonton Bulletin reported "…that the supply of fish is giving out." (McCullough and Maccagno 1991:150). In 1884, it was reported that the increasing scarcity of lake whitefish was the "…result of the taking of fish during their spawning season…" and that "If some steps [were] not taken to do away with this custom the result [would] be the extermination of the white fish…" (Dominion of Canada 1884:137). Similar reports documenting reductions in the fish supply occurred throughout the remainder of the 19th century (Champagne 1992:241,251; Department of Marine and Fisheries 1895; Dominion of Canada 1887:94) and were used to justify reduced harvest estimates during this period.

An initial harvest estimate of 77,000 kg (range 32,000 to 188,000 kg) for 1800 represents light harvest by nomadic peoples, specifically aboriginals and ‘freemen’ associated with the fur trade (Figure 2-4). Following the establishment of permanent trading posts in 1817, there was a slight increase but relative stability of the harvest. A rapid rise in fish harvest after 1855 reflects the development of the Oblate Mission and a large influx of people into the area. Rapid settlement resulted in estimated harvests of 824,000 kg (range 609,000 to 1,131,000 kg) in 1875 (Figure 2-4), shortly before the reported collapse of the lake whitefish population. Partial recovery was reported following the introduction of fishing regulations in the late-1800s, with harvests increasing to 725,000 kg (range 379,000 to 1,343,000 kg) in 1910 (Figure 2-4), just prior to the initiation of the commercial fishing industry.

The minimum estimate of 111,000 individual lake whitefish consumed in the winter (226,000 kg) and an average of 76,000 consumed in the summer (176,000 kg) by the entire settlement post-collapse (1878 to 1912), closely resembled the estimates reported in Belanger (1890:42) of 113,000 lake whitefish harvested during the fall spawning season of 1888, 108,000 harvested in the fall of 1887 and 500 to 1,000 fish harvested daily by the settlement during the summer. The similarity between this independent reporting of total fish harvest and the estimated fish harvest generated from this analysis, supports the reported time series data.

Potential maximum harvests of greater than one million kg (~45 kg • ha^{-1}) annually seem unrealistic given the predicted productivity of Alberta lakes for lake whitefish (5.62 kg • ha^{-1} • yr^{-1}) (Chris Davis, Alberta Sustainable Resource Development, Lac la Biche, Alberta, personal communication, 18 July 2011). However, a 2011 mark-recapture study on Pigeon Lake, Alberta, found lake whitefish densities of 75 adult fish • ha^{-1} (average fish weight = 1.77 kg) (J. Cooper and V. Buchwald, Alberta Sustainable Resource Development, Red Deer, Alberta, personal communication, 17 January 2011). If similar densities were possible for Lac la Biche, given the average reported weight of historically harvested lake whitefish at 2.04 kg, in the 1800s the lake would have had a standing biomass of 3.4 million kg (153 kg • ha^{-1}). Even at a conservative density of 50 lake whitefish • ha^{-1}, Lac la Biche might have supported 2.27 million kg (102 kg • ha^{-1}). Given that the anecdotal evidence tend to support such a large potential harvest, and current research suggests the biomass of lake whitefish required to support such high harvests is achievable for Alberta lakes, these estimates appear reasonable.

Given the feasibility of the historical harvest estimates, combined with the frequency and abundance of reports of significantly reduced lake whitefish populations after their decline in 1878, I would suggest that overharvest indeed occurred at Lac la Biche prior to the initiation of a formal commercial fishery. This overharvest was the result of increasing settlement associated with the westward expansion of the fur trade and the establishment of the Roman Catholic Mission.

Contemporary lake whitefish harvest (1912-2009)

To place historical lake whitefish harvest within the context of current production, I investigated the magnitude and dynamics of the contemporary harvest regime. Commercial harvesting of lake whitefish from Lac la Biche was first recognized in 1912. Prior to this time, harvests by the fur traders, missionaries, and local Native Americans, Metis, and freemen were considered subsistence fisheries since their main purpose was to provide rations for people and animals. Few data were available for the years prior to 1940 when provincial monitoring of the fishery began, so for the years between 1912 and 1947, mission-related harvest was calculated as the average of the harvest estimates of 1900 to 1911. I made the assumption that mission harvest was consistent during this period based on claims from 1927 that "…big budgets were avoided by relying on fish." (Champagne 1992:292) and that the children residing at the Mission were tired of eating fish (Champagne 1991: 292). The fishery was closed in 1948 in response to a major winterkill in 1946 and cisco die-off in 1947. From 1949 to the closure of the Mission in 1962, harvest was estimated at half of the 1947 harvest.

Between 1912 and 1927, subsistence harvest was conservatively estimated at 250,000 kg based on the comment in Chipeniuk (1975:21) that “All in all, the average yearly harvest of whitefish and pickeral would hardly have been less than 500,000 lb. [226,800 kg], and may well have reached 1,000,000 lb. [453,600 kg].”; the vast majority of these fish would have been lake whitefish because they were the target species of the fishery. When the subsistence estimate was combined with mission and commercial harvests, the total was close to the middle of the estimated range reported above. Between 1928 and 1947, I assumed that subsistence harvest was equivalent to reported commercial harvests based on reports of increased local consumption during this period (Lac la Biche Heritage Society 1975:31), and the claim that “for this market another kind of businessman began to tap the fish resources of the lake, the farmer who would fill his wagon box [with fish]…and then go peddling” (Lac la Biche Heritage Society 1975:31). No harvest was reported for 1948 due to a lake closure, and between 1949 and 1986, I gradually increased subsistence harvest from 1,000 kg to 25,000 kg to reflect increasing population size. Between 1987 and 2009, I gradually decreased harvest from 25,000 kg to 10,000 kg. I chose 1986 as the start of declining subsistence harvest to reflect a fairly significant decline in reported commercial harvest after this year, and an assumed decline in reliance on the fishery; however, no data are available to support this estimation.

No commercial harvest data were available for 1912 to 1922 so an estimate of 40,000 kg was used. This harvest value was chosen based on the first reported commercial harvest estimate of 42,900 kg in 1922. Commercial harvest data for 1922 to 1941 represent values published as part of the Fisheries Statistics of Canada (Dominion Bureau of Statistics for relevant years), and for the years between 1942 and 1946, I reported the average of the provincially-reported commercial harvest data (Scott 1976) and the Fisheries Statistics of Canada data. Lake whitefish data from 1947 to 2009 represent provincially documented commercial harvests (Scott 1976).

Contemporary lake whitefish harvests officially peaked in 1960 at 424,000 kg (Figure 2-5). Near the start of the fishery, however, the distinction between commercial and subsistence harvests was probably not discrete so early lake whitefish harvests could be considerably higher if local Metis, Cree and other Native Americans were either peddling locally or marketing the fish elsewhere. Regardless of the details, the rush to participate in the commercial fishery had a negative impact on the lake as evidenced in the comments by Chipeniuk (1975:20) that "By the 'twenties the bloom was off and many of the fish plants formerly based on Lac La Biche moved to Lake Athabasca." Indications of a decline in the quality of the lake whitefish fishery all occurred prior to the peak estimate for contemporary harvests in 1960, suggesting that the potential of the lake whitefish population had been impacted prior to the onset of commercial harvest.

Comparison of historical and contemporary lake whitefish harvest

To determine if historical overharvest was responsible for the observed trends in contemporary harvest required an understanding of the how the fishery evolved in response to changes in the human population over the last two centuries. To examine this relationship, I first combined the historical harvest times series' representing minimum, average, and maximum harvests with that of contemporary harvest, to examine the continuity of the data between the two periods (Figure 2-6). This combined harvest history for lake whitefish at Lac la Biche indicated that the average peak historical harvest in 1875 (811,000 kg) could have been as much as five times higher than the average of the contemporary harvest estimates (157,000 kg), whereas the minimum (609,000 kg) and maximum (1,131,000 kg) historical harvest estimates were more than four and seven times greater than the contemporary average, respectively. Based on this assessment, I chose to graph the time series combining the minimum historical fish harvest data estimates and average contemporary harvest, together with the human population data for the period between 1800 and 2009 (Figure 2-7). When lake whitefish harvest was assessed on a per capita basis, annual fish harvest increased from approximately 550 kg in the early 1800s to 1,000 kg in the 1870s. Following the lake whitefish collapse in 1878, annual harvest gradually decreased from 700 kg to 200 kg per person. In the 1940s, annual harvests decreased dramatically, fluctuating from less than 5 kg to 26 kg per person. From qualitative references describing the period after the lake whitefish collapse, it was assumed that total harvests decreased but fishing effort significantly increased to maintain subsistence harvest requirements given the reduced lake whitefish population size. It is also likely that the shortage of lake whitefish was compensated for by harvesting larger proportions of other species, especially northern pike, which was relied on by the mission in years when lake whitefish were not abundant (Champagne 1992:51). After the decline and during what was thought to be the recovery period for lake whitefish, historical harvests were still considerably higher than those reported during the period of commercial harvest and significant variability in harvest success was commonly reported.

That historical overharvest of lake whitefish caused a reduction in the harvest potential of contemporary fisheries can be inferred from the harvest trends; however, the paucity of anecdotal or quantitative data for the critical period between the lake whitefish collapse (1878) and the first data reports from the commercial fishery (1920) make it difficult to draw strong conclusions about the cause of the decreased harvest. With no estimates of lake whitefish abundance available for any point during the contemporary or historical periods, I was unable to determine if trends in biomass of fish harvested represent a reasonable proxy for the harvestable population size. While harvest trend data are generally the most widely available indicator of changes in fish population size, they are strongly influenced by the efforts of the fishers. Fisher effort is motivated by many factors not considered in this study including weather, fish price, market demand, alternate food sources, transportation, and fisheries quotas.

A plausible explanation for the observed contemporary harvest trend is that intense harvest through the mid- and late- 1800s decreased ecosystem resilience. This is supported both by the increased frequency of stochastic events negatively affecting the fishery, and by the increasing variability in reported harvest. Following the lake whitefish population decline there was a noticeable increase in anecdotal references to stochastic weather events (Dominion of Canada 1887:94, McCullough and Maccagno 1991:150), droughts (Dominion of Canada 1886:131, Champagne 1992:251) and summer/winter kills of fish (Chipeniuk 1975:22) which would have affected the survival or recruitment of the population (Dominion of Canada 1886:131). During the same time, there was evidence of increasing variability in fish harvest (Dominion of Canada 1887:94, Department of Marine and Fisheries 1895, 1896, Champagne 1992:240-241, 251). These types of fluctuations in state variables can be indicators of decreasing resilience (van Nes and Scheffer 2007). If perturbations caused by increasing harvest pressure decreased the resilience of the population, then a stochastic disturbance such as drought, could have caused such a regime shift to occur. If this shift resulted in the occurrence of a low-production lake whitefish system, this could explain why commercial harvests appear consistently low throughout the 20th century. Alternately, the apparent consistency of harvest might be the result of introduced harvest quotas (though they were poorly enforced) (Champagne 1992:240-241,251), underreporting of contemporary harvest (there are many reports that quotas were regularly exceeded) (Chipeniuk 1975:21), overestimation of historical subsistence harvest, or changes in harvest effort over time as the demand for lake whitefish changed (for examples see Lac la Biche Heritage Society 1975:30,31, McCullough and Maccagno 1991:185,189). Other biotic or abiotic changes to the lakes structure or functioning could also have decreased lake whitefish production, survival, or recruitment such as increasing water temperature (Viadero 2005), increasing predation on all sizes (Forney 1974), changes in prey availability (Adams et al. 1982), eutrophication (Powers et al. 2005), or loss of spawning habitat (Koenig et al. 2000).

Selection of restoration targets

The magnitude of historical fish removals suggests that restoration targets requiring large biomass recoveries might “seem unbelievable based on modern observations alone” (Jackson et al. 2001), but that extremely large biomasses could be supported by the ecosystem. Research that attempts to quantify historical removals counteracts the tendency towards the shifting baseline syndrome (Pauly 1995, Humphries and Winemiller 2009 Papworth et al. 2009) and helps prevent decision-makers from ‘settling’ on targets that are characteristic of highly degraded systems. Furthermore, the selection of restoration targets based on assumptions of historical system conditions can lead to ecosystem states that are unstable or have reduced resilience. When the resilience of a system has been significantly diminished through the accumulation of the impacts of disturbances, any further disturbance can cause a change in the trajectory of the system’s development (Walker and Meyers 2004) and usually results in the dominance of a less productive and generally less desired ecosystem state (Folke et al. 2004). This makes the selection of restoration targets very important. If a period of reduced resilience is chosen to represent a ‘natural’ ecosystem state, then the successfully restored system could be more susceptible to regime shifts resulting from future disturbances. For example, in the case of Lac la Biche, this analysis suggests that historical harvests resulting from the development of the fur trade were potentially significant and could have had an impact on realized harvests during the contemporary period. If restoration program targets were set to represent expected conditions based solely on the memories of current generations, then decreased resilience resulting from the previous period of intense harvest could be incorporated into the conditions of the restored ecosystem. In this way, the memory and legacy of the already shifted baseline conditions would be perpetuated.

Though this research illustrates the importance of considering the disturbance history of a system when establishing the time frame for setting restoration targets, the conclusions are not without debate. If resilient systems are adapted to the disturbance regime under which they developed (Sousa 1984, Nakamura 2000, Folke et al. 2004), then we must consider if it is even possible to achieve historical or 'natural' conditions given the changes to the disturbance regime over the last 250 years. The switch from stochastic, pulse disturbances such as droughts, to chronic, press disturbances such as eutrophication or climate change, can influence ecosystem resilience (Bengtsson et al. 2003, Waples et al. 2009) and restoration potential.

Conclusions

By assessing changes in historical (1800 to 1911) subsistence harvest demands I have demonstrated the strong likelihood that increasing settlement initiated by the westward expansion of the fur trade led to a decline in lake whitefish at Lac la Biche. By comparing harvest estimates for the historical and contemporary periods (1912 to 2009), I contend that historical harvest pressure may have had an impact on commercial harvest potential by decreasing the resilience of the lake whitefish population through changes in life history strategy and productivity, making them more susceptible to stochastic and other disturbances. Variable harvests, an increase in reports on the impacts of stochastic events on fish populations and a clear drop in the realized harvests support this conclusion. However, assessments of historical conditions can rely heavily on interpretation of how disparate pieces of historical information fit together into a comprehensive story. Interpretation error could conceivably account for some of the observed difference between historical and contemporary harvest, but it is not likely to account for a large proportion since minimum harvest estimates were used in the comparison of harvest between eras.

The conclusions drawn in this study represent the most complete and geographically targeted history for a large lake ecosystem that was found in an extensive literature review. Until better historical evaluations are assembled, these conclusions represent important guidelines for both fisheries management and for restoration projects. These evaluations highlight the significance of understanding the historical context in which fisheries issues developed and in doing so, help counteract for the effects of the shifting baseline syndrome when setting management goals.

Table 2-1 Summary of methodology for calculating annual historical (1800 to 1911) lake whitefish (*Coregonus clupeaformis*) harvest by season (winter or summer), time period, and harvester (subsistence, fur trade, Mission) for Lac la Biche, Alberta, Canada, including anecdotal references and assumptions underlying calculations.

Harvest Type	Years	Season	Calculation	Support	Source
Subsistence	1800-1877	Winter	# families x 2000 fish (min), 3000 fish (max), 2500 fish (avg)	"Every one kills fish for the winter (Traill 1874d). …"Most families have from 2 to 3 thousand [fish] according to the number of persons and dogs for all keep at least one train of dogs and as each dog must have a fish per day they require a good stock (Traill 1874d)."	McCullough and Maccagno 1991: 135
Subsistence	1878-1912	Winter	# families x 1000 fish (min), 2000 fish (max), 1500 fish (avg)	1892 - "The fisheries began to be controlled during this period. …The fisheries that fall were quite good, at least better than the previous year, but the numbers are much lower than those of twenty years before."	Champagne 1992: 240-241

Subsistence	1800-1912	Summer	# families x 5 fish/day (min), 10 fish/day (max), 7 fish/day (avg), x 142 days	Daily fish allotment assumed similar to fur trade post allotments. "The daily allowance of a Man is eight pounds of fish…" "The ordinary ration…at any of the Hudson Bay Company posts is either three large lake white fish, or three rabbits…per day per man." (McDougall 1902:110-111). "One whitefish was allowanced to each woman and a half to each child, if the fish were obtainable...Train dogs were fed two fish or four pounds of fresh meat daily."	Tyrrell 1916:112; McDougall 1902:110-111 as cited in Kulle 1993:66 Moberly and Cameron 1929:83
Fur Trade	1800-1801	Winter	1970 fish (min), 1970 fish x 2 (max), 1970 fish x 1.5 (avg)	Minimum estimate of 1970 lake whitefish based on the number of fish caught by Peter Fidlers crew from October 15, 1799 to May 10, 1800 (HBCA,PAM,B104/a/1,fo.36). Maximum estimate assumes equal harvest by Northwest Company (NWC) and Hudson Bay Company (HBC). Average harvest estimate is half way between minimum and maximum.	McCullough and Maccagno 1991:71
Fur Trade	1802-1817	Winter	0 fish (min), 1000 fish (max), 500 fish (avg)	Maximum and average harvests represent conservative harvest estimates for fur trade brigades moving through the area en route to other posts. "There appears to have been no permanent trading posts in the Lac la Biche region between 1800 and 1817...However, the transportation route through Portage La Biche remained in use by both companies on their brigades to the Athabasca country."	Kulle 1993:21

Fur Trade	1818-1820	Winter	11,000 fish (min), 15,000 fish (max), 13,000 fish (avg)	"The main food at Red Deers Lake House II was whitefish, and eleven thousand were laid up for the winter." Maximum and average estimates represent predictions of undocumented harvests by NWC and random fur brigades before merging of HBC and NWC in 1819.	McCullough and Maccagno 1991:101
Fur Trade	1821-1853	Winter	2000 fish (min), 3000 fish (max), 2500 fish (avg)	No fur trade post was active at this time; However, one trader and his family remained at the post during this time so harvest estimates represented as subsistence needs for a single family.	McCullough and Maccagno 1991:103, 109
Fur Trade	1853-1864	Winter	9000 fish (min), 10,000 fish (max), 9500 fish (avg)	"We had now to lay in the winter supply of whitefish for the women, children and dogs. Nine or ten thousand was considered a sufficient quantity."	Moberly and Cameron 1929:86
Fur Trade	1865-1877	Winter	10,000 fish (min), 15,000 fish (max), 12,500 fish (avg)	"Between 10,000 and 15,000 whitefish were required to support the Lac la Biche post through the winter…"	McCullough and Maccagno 1991:135

Fur Trade	1878-1911	Winter	2000 fish (min), 3000 fish (max), 2500 fish (avg)	No estimates available. Calculated as ~1/5 of the previous periods estimates based on reports from Lake St. Ann. "…Lake St. Ann's, which was famed for its whitefish, which they need to catch in large quantities. The Hudson Bay Company, from this lake, used to get from forty to fifty thousand fish each winter to feed their men and train dogs, but at present it is doubtful if eight thousand could be caught there. I only mention this as an example which will apply with equal force to Whitefish Lake, Lac la Biche, Saddle Lake, Pigeon Lake, Whale Lake, and others."	Dominion of Canada. Annual Report of the Department of Indian Affairs. 1884:137
Fur Trade	1800-1801	Summer	0	Included in winter harvest estimate	
Fur Trade	1802-1817	Summer	0 fish (min), 1000 fish (max), 500 fish (avg)	No fur trade post was active in the area. Maximum and average harvests represent conservative harvest estimates for fur trade brigades moving through the area en route to other posts.	Kulle 1993:21
Fur Trade	1818-1911	Summer	1/3 of winter harvest	No data were available for summer harvests during this period. Assume a conservative harvest represented as a proportion of the winter harvest.	
Mission	1800-1852	Winter	0	Not active	
Mission	1853-1854	Winter	200 fish (min), 1000 fish (max), 600 fish (avg)	Only a single Father residing at the Mission. Harvests represent 1/5 of harvest estimates from next time period with 5 to 7 residents.	Champagne 1992: 31

Mission	1854-1861	Winter	1000 fish (min), 5000 fish (max), 3000 fish (avg)	Minimum estimate from "The fall fishing has been good, with one thousand pieces from three visits to the nets." Maximum estimated based on an increase in number of Mission residents to ten during this period. Average is the middle of the minimum and maximum estimates.	Champagne 1992: 40
Mission	1862-1863	Winter	65 fish/day x 36 days fishing (min), 10,000 fish (max), 6000 fish (avg)	Minimum estimate from "…34 or 38 days in making the Fall Fishery as the fish was not in abundance, we had six nets in water in visiting the six nets we had not more than 50, 60, 80 etc.,..." Maximum estimate is double the minimum estimate to represent a doubling in the number of Mission residents at this time. Average estimate is assumed to be part way between the minimum and maximum.	Champagne 1992:51
Mission	1864-1877	Winter	9000 fish (min), 15,000 fish (max), 12,000 fish (avg)	Average estimate based on value from the period 1881-1884 during which the Mission achieved their needed supply of whitefish; This value was reduced to represent the smaller number of residents at the Mission during this time. Maximum estimate based on knowledge of the statement "Good fishing in the fall [of 1888] I took 14000" and the assumption that total winter harvest would be higher than this value.	Champagne 1992:229
Mission	1878-1880	Winter	9000 fish (min), 15,000 fish (max), 12,000 fish (avg)	"The fisheries were not very good… Of fifteen nets which had been set, they had caught only nine thousand fish, not enough for their needs." Maximum and average estimates assumed to be close to values from neighbouring periods.	Champagne 1992:174

Mission	1881-1884	Winter	10,000 fish (min), 15,000 fish (max), 12,500 fish (avg)	Average estimate based on the comment that the "...mission had achieved its needed supply", and the claims in the next two periods that harvests of 12,000 and 14,000 whitefish were large enough to supply the Mission.	Champagne 1992:178
Mission	1885-1911	Winter	12,000 fish (min), 15,000 fish (max), 13,500 fish (avg)	"The fisheries were good that fall, they got about twelve thousand white fish." Maximum estimate remains constant while average estimate is half way between between the minimum and maximum estimates.	Champagne 1992:219
Mission	1800-1852	Summer	0	Not active	
Mission	1853-1911	Summer	# of residents x 1 fish/day (min), 3 fish/day (max), 1.5 fish/day (avg) + # school children x 0.5 fish/day (min), 1.5 fish/day (max), 1 fish/day (avg) x 142 days	In the absence of summer harvest data, daily fish quotas were approximated from fur trade rations for men, women, and children.	Tyrrell 1916:112; McDougall 1902:110-111 as cited in Kulle 1993:66 Moberly and Cameron 1929:83

Table 2-2. Estimates of lake whitefish (*Coregonus clupeaformis*) harvest (kg x 10^3) by subsistence, fur trade post, and Roman Catholic mission harvesters in winter and summer seasons, including minimum, maximum, and average harvest estimates. The winter season was from October 1 to May 10, and the summer season was from May 11 to September 30.

	Subsistence - kg harvested (x10^3)					
		Winter			Summer	
Year	Min	Max	Avg	Min	Max	Avg
1800	20.4	122.4	51.0	7.2	57.9	20.3
1805	20.4	122.4	51.0	7.2	57.9	20.3
1810	20.4	122.4	51.0	7.2	57.9	20.3
1815	20.4	122.4	51.0	7.2	57.9	20.3
1820	20.4	122.4	51.0	7.2	57.9	20.3
1825	20.4	122.4	51.0	7.2	57.9	20.3
1830	28.6	153.0	76.5	10.1	72.4	30.4
1835	28.6	153.0	76.5	10.1	72.4	30.4
1840	40.8	183.6	102.0	14.5	86.9	40.6
1845	49.0	214.2	102.0	17.4	101.4	40.6
1850	49.0	214.2	102.0	17.4	101.4	40.6
1855	61.2	244.8	102.0	21.7	115.9	40.6
1860	81.6	336.6	204.0	29.0	159.3	81.1
1865	183.6	489.6	331.5	65.2	231.7	131.8
1870	326.4	673.2	459.0	115.9	318.6	182.5
1875	408.0	697.7	535.5	144.8	330.2	212.9
1880	204.0	469.2	324.4	144.8	333.1	214.9
1885	204.0	489.6	339.7	144.8	347.6	225.1
1890	204.0	530.4	355.0	144.8	376.6	235.2
1895	204.0	591.6	370.3	144.8	420.0	245.4
1900	204.0	632.4	385.6	144.8	449.0	255.5
1905	204.0	693.6	400.9	144.8	492.5	265.6
1910	204.0	754.8	416.2	144.8	535.9	275.8

Table 2.2. Continued.

	Fur Trade - kg harvested (x10^3)					
		Winter			Summer	
Year	Min	Max	Avg	Min	Max	Avg
1800	4.0	8.0	6.0	0.0	0.0	0.0
1805	0.0	2.0	1.0	0.0	2.0	1.0
1810	0.0	2.0	1.0	0.0	2.0	1.0
1815	0.0	2.0	1.0	0.0	2.0	1.0
1820	22.4	30.6	26.5	7.5	10.2	8.8
1825	4.1	6.1	5.1	1.4	2.0	1.7
1830	4.1	6.1	5.1	1.4	2.0	1.7
1835	4.1	6.1	5.1	1.4	2.0	1.7
1840	4.1	6.1	5.1	1.4	2.0	1.7
1845	4.1	6.1	5.1	1.4	2.0	1.7
1850	4.1	6.1	5.1	1.4	2.0	1.7
1855	18.4	20.4	19.4	6.1	6.8	6.5
1860	18.4	20.4	19.4	6.1	6.8	6.5
1865	20.4	30.6	25.5	6.8	10.2	8.5
1870	20.4	30.6	25.5	6.8	10.2	8.5
1875	20.4	30.6	25.5	6.8	10.2	8.5
1880	4.1	6.1	5.1	1.4	2.0	1.7
1885	4.1	6.1	5.1	1.4	2.0	1.7
1890	4.1	6.1	5.1	1.4	2.0	1.7
1895	4.1	6.1	5.1	1.4	2.0	1.7
1900	4.1	6.1	5.1	1.4	2.0	1.7
1905	4.1	6.1	5.1	1.4	2.0	1.7
1910	4.1	6.1	5.1	1.4	2.0	1.7

Table 2.2. Continued.

	Mission - kg harvested (x10^3)					
		Winter			Summer	
Year	Min	Max	Avg	Min	Max	Avg
1800	0.0	0.0	0.0	0.0	0.0	0.0
1805	0.0	0.0	0.0	0.0	0.0	0.0
1810	0.0	0.0	0.0	0.0	0.0	0.0
1815	0.0	0.0	0.0	0.0	0.0	0.0
1820	0.0	0.0	0.0	0.0	0.0	0.0
1825	0.0	0.0	0.0	0.0	0.0	0.0
1830	0.0	0.0	0.0	0.0	0.0	0.0
1835	0.0	0.0	0.0	0.0	0.0	0.0
1840	0.0	0.0	0.0	0.0	0.0	0.0
1845	0.0	0.0	0.0	0.0	0.0	0.0
1850	0.0	0.0	0.0	0.0	0.0	0.0
1855	2.0	10.2	6.1	1.4	4.3	2.2
1860	2.0	10.2	6.1	2.0	6.1	3.0
1865	18.4	30.6	24.5	7.0	20.9	11.9
1870	18.4	30.6	24.5	5.5	16.5	9.0
1875	18.4	30.6	24.5	10.7	32.2	17.2
1880	18.4	30.6	24.5	15.9	47.8	25.3
1885	24.5	30.6	27.5	9.8	29.5	15.6
1890	20.4	30.6	28.6	13.3	40.0	23.6
1895	20.4	30.6	28.6	15.5	46.5	25.8
1900	20.4	30.6	28.6	3.8	11.3	5.6
1905	20.4	30.6	28.6	2.6	7.8	3.9
1910	20.4	30.6	28.6	4.3	13.0	7.4

Figure 2-1. Map of Alberta showing the location of Lac la Biche relative to major cities. Subset map of the lake indicates the location of the Lac la Biche Mission and the Town of Lac la Biche.

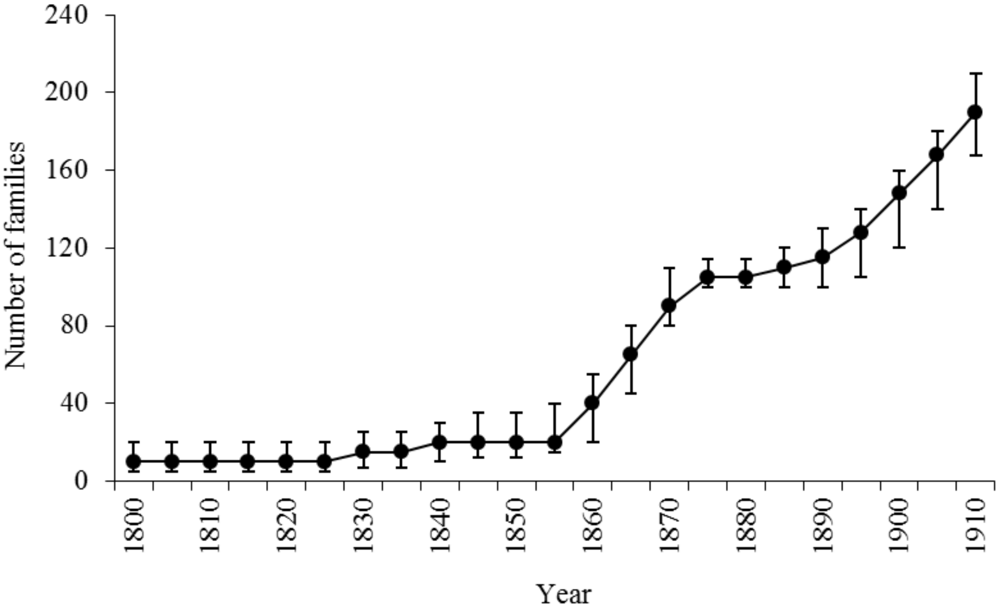

Figure 2-2. Number of families living in the Lac la Biche area for every fifth year between 1800 and 1910, including minimum and maximum estimates.

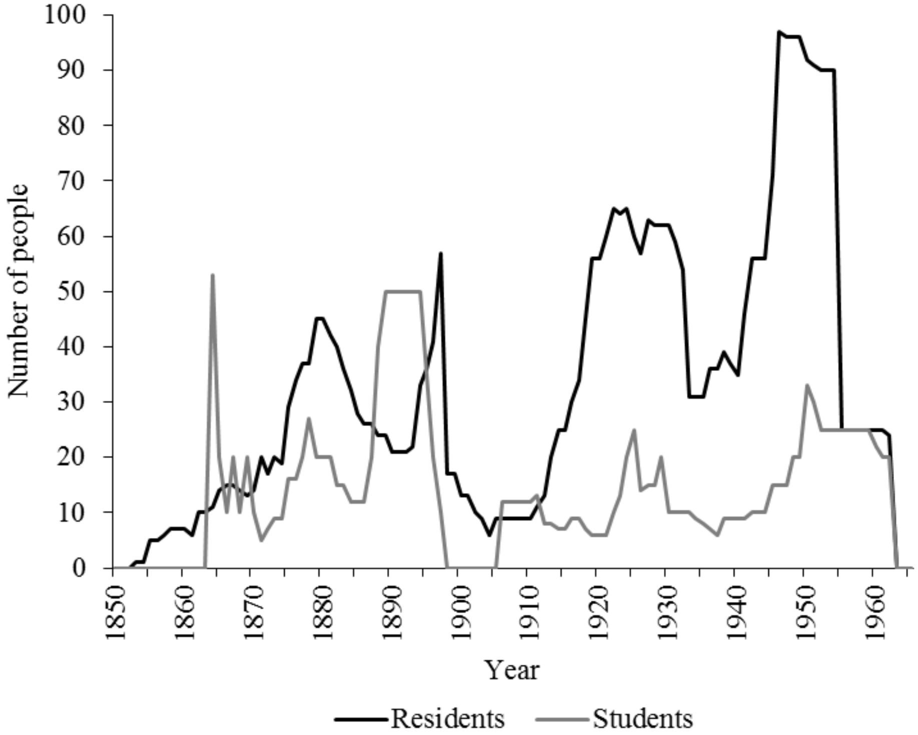

Figure 2-3. Number of residents (men, women, and boarders) and students residing at the Lac la Biche Mission from the arrival of the first priest in 1853 to the closing of the residential school in 1962.

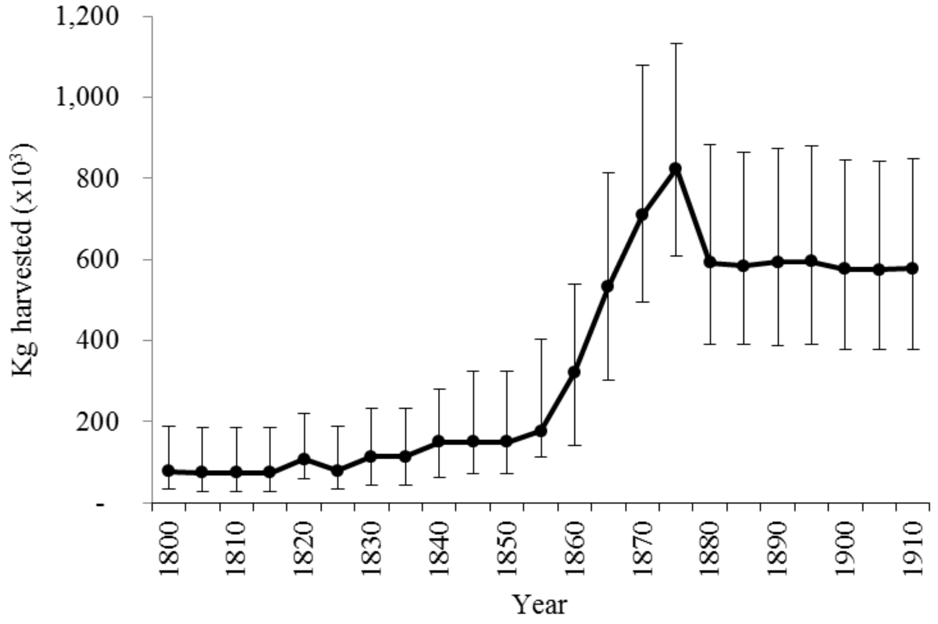

Figure 2-4. Estimated total lake whitefish (*Coregonus clupeaformis*) harvest (kg X 10^3) by the Lac la Biche settlement (subsistence, fur trade, and Mission harvest) for every fifth year between 1800 and 1911, including minimum and maximum estimates.

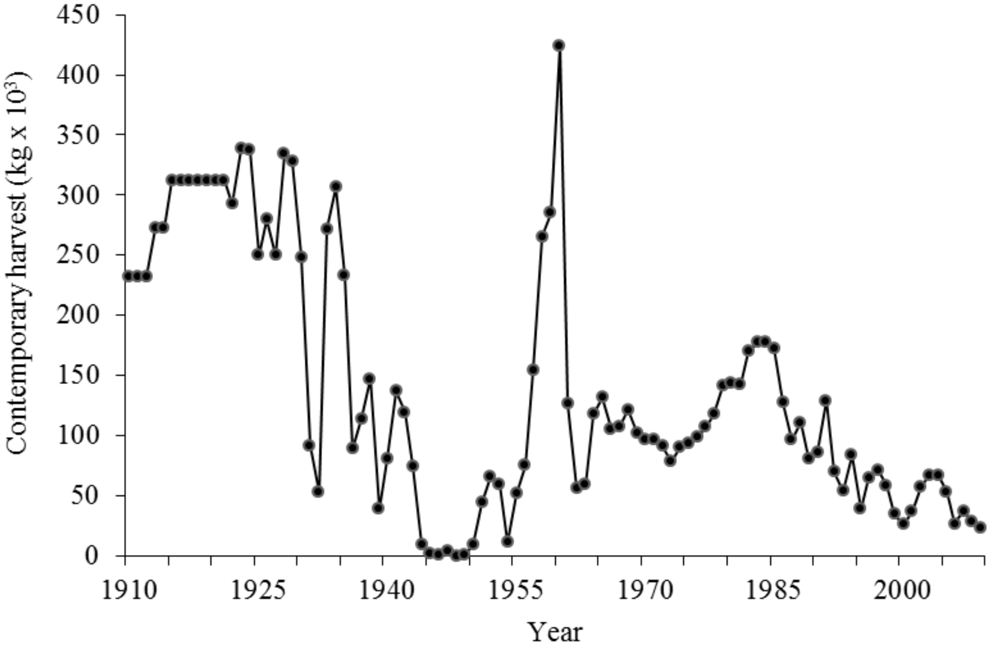

Figure 2-5. Estimated annual total (subsistence and commercial) lake whitefish (*Coregonus clupeaformis*) harvest (kg X 10^3) at Lac la Biche from 1910 to 2009. Points represent estimated subsistence harvest combined with documented commercial harvests (Dominion Bureau of Statistics for relevant years, Scott 1976).

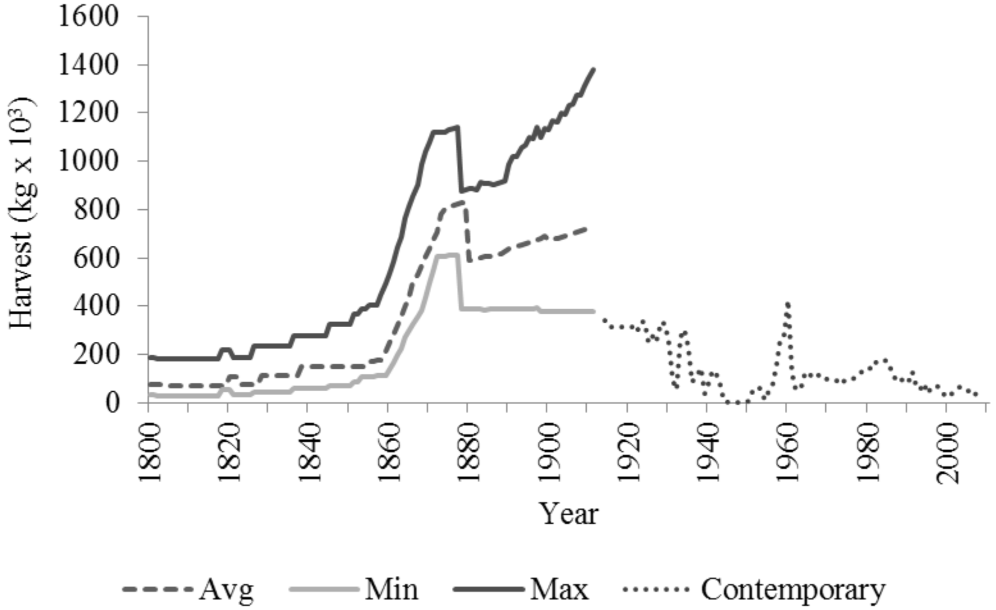

Figure 2-6. Minimum, average, and maximum historical (1800 to 1911) estimates for lake whitefish (*Coregonus clupeaformis*) harvest (kg X 10^3) relative to the contemporary (1912 to 2009) harvest representing estimates of subsistence harvest combined with recorded commercial harvest (Dominion Bureau of Statistics for relevant years, Scott 1976).

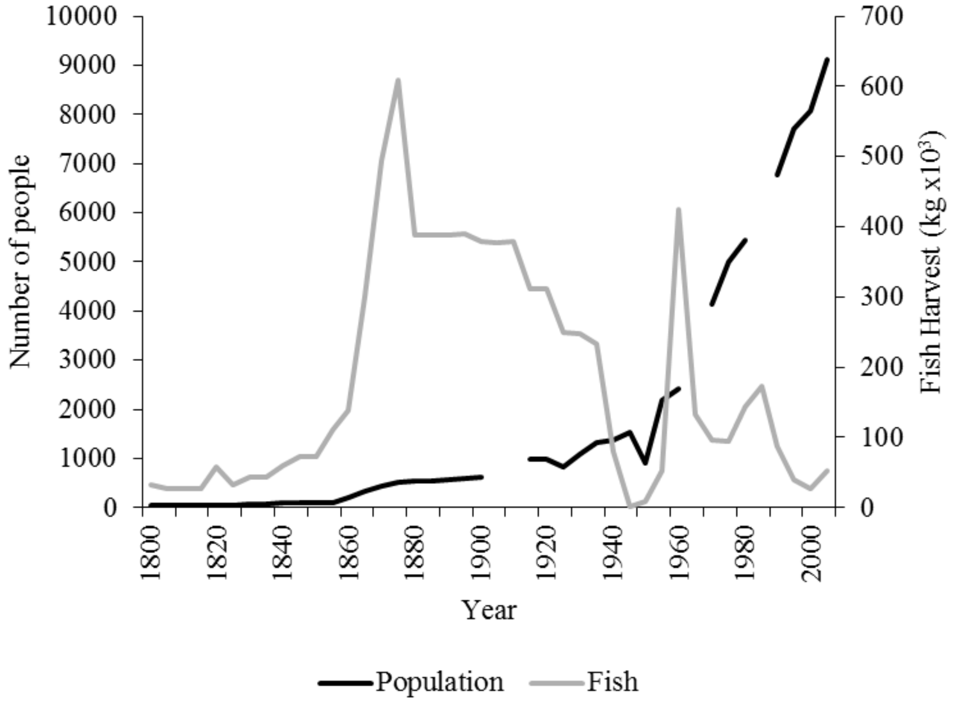

Figure 2-7. Times series of minimum estimates for lake whitefish (*Coregonus clupeaformis*) harvest (kg X 10^3) relative to the population of the Lac la Biche area from 1800 to 2009.

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Chapter 3 - Ecosystem modeling to provide an historical context for restoration and management goals for a large, boreal lake[2]

Summary

In 2005, the Fisheries Management Branch of Alberta Environment and Sustainable Resource Development (ESRD) initiated a fisheries restoration program at Lac la Biche, Alberta, Canada, focused on increasing both the abundance of walleye and average fish size. Alberta ESRD established a timeframe of 100 years ago, or approximately 1900, as a conceptual goal for restoration targets though little ecosystem information was available. Given that fisheries exploitation intensified in the 19th century, conditions existing in 1900 may not be suitable targets for meeting program objectives. This study assessed the effects of historical fish harvest on the structure and function of the Lac la Biche ecosystem, and described possible ecosystem conditions for 1800 and 1900. An Ecopath model for 1800 was used to characterize ecosystem structure, function, and maturity. Ecosim was used to force the 1800 model with historical fish harvest estimates under eight different trophic control scenarios. Parameters exported from each simulation were used to create eight Ecopath models for 1900. Changes in ecosystem structure, function and maturity were compared between 1800 and 1900 to assess potential effects of historical fish harvest. Model results suggest a high level of lake whitefish harvest and moderate to low walleye and northern pike harvests altered energy flows and community composition, but led to only marginal declines in ecosystem maturity. Based on

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[2] A version of this chapter has been submitted to the North American Journal of Fisheries Management and is currently under review.

these analyses, restoration goals targeting 1900 were considered appropriate for meeting the program objectives but trade-offs in potential fisheries yield and ecosystem resilience were identified for consideration.

Introduction

Ecological restoration projects often focus on attaining a ‘natural’ ecosystem with self-sustaining fish populations (Vander Zanden et al. 2003) by targeting conditions that existed before damaging or ecosystem altering harvests (Kitchell et al. 2000). Ensuring such “ecological alignment” between a restored ecosystem and its historical reference, however, requires a comprehensive understanding of structure and function for each system (Higgs 2003). Few quantitative data exist to describe historical ecosystems in this capacity (but see Pitcher 2001; Vander Zanden et al. 2003), especially for freshwater. As a result, the potential abundance of fish species and the productive capacity of ecosystems are being underestimated because there is no historical perspective for comparison (Jackson et al. 2001, Pandolfi et al. 2003, Rosenberg et al. 2005, McClenachan and Cooper 2008). In fact, studies in marine systems suggest that contemporary species abundances are a fraction of what they were 100 to 150 years ago (<1%) (Rogers-Bennett et al. 2002, Rosenberg et al. 2005). Given the lack of historical fish abundance estimates or harvest data it is difficult to establish baselines for assessing population declines and guiding restoration projects. In such cases, mass-balance modeling can be used to organize available information and assumptions to create hypotheses of energetically plausible historical ecosystems.

Ecopath with Ecosim is a valuable tool for modeling past ecosystems as a way of informing restoration choices (Pauly et al. 1998). Ecopath allows managers to re-create historical ecosystems using available local knowledge and data, while Ecosim can be used to assess how systems might have changed in response to historical harvests. Creation and use of these models can: 1) reveal important relationships to inform ecosystem restoration projects and ensure desired goods and services emerge and, 2) provide a plausible range of parameter estimates to guide restoration. Ecopath with Ecosim has been used successfully to model historical marine ecosystems (Pauly et al. 1998; Ainsworth et al. 2008) but no similar studies exist for freshwater systems.

In 2005, a large-scale restoration program began at Lac la Biche, Alberta, Canada with the objectives of recovering walleye and increasing the average fish size (Chris Davis, Alberta Environment and Sustainable Resource Development, personal communication). Alberta Environment and Sustainable Resource Development identified conditions of 100 years ago, approximately1900, as a qualitatively favourable baseline for lake restoration targets (Chapter 1) despite having little ecosystem information for this time. The suitability of this target era is worth investigating, given that increasing exploitation of fish resources throughout the 19th century resulted in an apparent lake whitefish "collapse" in 1878 (McCullough and Maccagno 1991:141) and the introduction of fisheries regulations by the 1890s (Champagne 1992:240,246). Managers should understand how fish harvest affected their systems during periods of rapid change so they can challenge conventional wisdom pertaining to characteristics of healthy, balanced ecosystems (Rosenberg et al. 2005). Estimating the range of variability in historical conditions is one way of informing conventional wisdom and preventing managers from setting restoration targets that "…grossly under-represent the productive potential of commercially important species" (Rosenberg et al. 2005). In this study, I used Ecopath with Ecosim as a tool for testing the suitability of 1900 as a timeframe for setting restoration program targets. I used a series of Ecopath models to: 1) describe characteristics of Lac la Biche during two periods in history (pre-European contact and pre-commercial fishing) and, 2) to assess changes in ecosystem structure and function from increasing fish harvest during European settlement.

Study Site

Lac la Biche is a large (223 km^2), shallow (average depth 8.4 m, maximum depth 21.3 m) eutrophic lake located on the southern edge of the boreal forest in northeast Alberta, Canada. There are 13 species of fish in the lake, of which the lake whitefish (*Coregonus clupeaformis*) has the longest recorded history of targeted harvest.

Aboriginal peoples entered the area roughly 11,000 years ago (McCullough and Maccagno 1991:1) and were alone on the landscape until fur traders arrived in the late 18th century. Permanent trading posts were built in the early 19th century attracting settlers to the area. In the mid-19th century, a Roman Catholic mission and boarding school was built on the lakeshore and subsistence harvest of lake whitefish increased dramatically with rapid settlement of the area. The fur trade post and the Mission each harvested 10,000 to 15,000 lake whitefish during the fall spawn (McCullough and Maccagno 1991:101) while individual families required 2,000 to 3,000 lake whitefish to feed themselves and their dog teams overwinter (Traill 1874 as cited in McCullough and Maccagno 1991:135). In the fall, lake whitefish were harvested by spearing them on the spawning grounds (Moberly and Cameron 1929:86) and gill nets were used during the winter and summer to provide fresh fish (Champagne 1992:51). By the late 1870s, increased harvests led to the decline of the lake whitefish population (McCullough and Maccagno 1991:141) and in the 1890s, the first fishery regulations were introduced (Champagne 1992:240,246).

In 1915, rail service allowed commercial fisheries to expand and by 1918, four fish plants supported over 200 fishermen harvesting lake whitefish, northern pike (*Esox lucius*), walleye (*Sander vitreus*), and cisco (*Coregonus artedi*) at Lac la Biche (Lac la Biche Heritage Society 1975:29). Following the closure of the fish plants by 1920, the fisheries of the area were highly variable, with fishing effort responding to price and demand for fish. In the 1930s, angling for walleye, northern pike (hereafter pike), and yellow perch (*Perca* *flavescens*) became popular (Johnson 1999:262-263) and a small mesh fishery (70 and 76 mm stretch measure) targeted cisco for the local mink farms (Champagne 1992:284). In the latter half of the century both the pike and yellow perch (hereafter perch) recreational fisheries declined and by 1970 walleye were extirpated (Valastin and Sullivan 1997:22-23).

Methods

Historical Reconstruction

I used the modeling software Ecopath with Ecosim (EwE) (model version 6.2.0.620) (Christensen et al. 2008, www.ecopath.org) as a tool for reconstructing energetically-balanced historical ecosystems and for assessing changes in the system in response to fish harvest. Ecopath uses a mass-balance approach for modeling each biological component of an ecosystem. Equilibrium conditions arising from this balance allow for the analysis of flows (energy or nutrients) between trophic levels, providing a means for estimating the relative importance of individual species, ecological guilds, or ecological processes (selective predation, targeted fisheries etc.) (Christensen et al. 2008). The complementary program, Ecosim, simulates changes over time to the steady state Ecopath model (Christensen et al. 2008).

Ecopath modeling is based on the parameterization of two master equations; one that describes the production term for each group, and a second that describes consumption associated with energy balance. Production for each modeled functional group in the ecosystem is described by the following basic equation:

Production = catches + predation mortality + biomass accumulation + net migration + other mortality (1)

The consumption equation used to ensure mass-balance can be expressed as:

Consumption = production + respiration + unassimilated food (2)

Model units were t/km^{-2} for biomasses and t·km^{-2}·year^{-1}(wet weight) for flows of organic matter where t represents a metric tonne.

Ecosim utilizes the output variables and input parameters from Ecopath for initial parameterization. Ecosim relies on a series of differential equations to describe changes in the biomass of modeled groups over time as a function of time varying biomass and harvest rates (Christensen et al. 2008).

Model Parameterization - 1800

The Lac la Biche ecosystem was modeled for 1800, prior to any major influences of fur trade and Mission harvest. Thirty-one functional groups were modeled including 17 groups of fish, four bird groups, four benthic invertebrate groups, four plankton groups, one submerged aquatic vegetation group, and one detritus group. Six fish species were modeled as multistanza groups for which the total biomass of the species was split into different life-history stanzas representing unique stages in their growth and development. (Christensen et al. 2008) (Table 3-1). For example, I divided fish species into multistanza groups based on diet similarity and expected mortality rates for different size classes. Biomass and consumption/biomass values were entered for the highest stanza (oldest fish group) only and values for the other stanzas were calculated by Ecopath using fish growth data. Few fisheries data for Lac la Biche exist until the late 1900s, so input parameters represent literature values from other systems, historical anecdotal references, unpublished data from the contemporary Lac la Biche ecosystem and other nearby systems, as well as estimates from biologists with knowledge of the lake. Main data sources and estimation methods can be found in Appendix B as Tables B-1 through B-3.

Density estimates for the largest size classes of walleye and pike represent catch-per-unit-effort values expected from a ‘healthy’ system (Sullivan 2003, C. Davis, ASRD, personal communication) converted to a density estimate. The density of large perch was estimated directly from Lac la Biche data for 2006 and 2007 (Milne 2007, Milne 2008), and lake whitefish density was derived from estimates of a similar lake system (Winefred Lake) with little or no exploitation (Fish and Wildlife Management Information System (FWMIS), Alberta Environment and Sustainable Resource Development, Edmonton, Alberta). A maximum density estimate for lake whitefish was derived from a recent population estimate on a high productivity lake whitefish lake in central Alberta (Pigeon Lake) (Cooper and Buchwald, ASRD, unpublished data). Sucker density was calculated relative to lake whitefish using catch ratios from Lac la Biche for 2003 to 2005, but a range was provided by published estimates (Kelso 1998). Burbot density was estimated from the literature (Davis 1997, Schramm et al. 2006). Density estimates were converted to biomass by multiplying by average fish weights for Lac la Biche from 2003 to 2005. An historical account of lake whitefish average weight (4.5 lbs or 2.0 kg) (HBCA, PAM, B.115/e/1,fo.3d) was decreased to 1500 g to account for smaller sized fish included in the model stanza and was used in calculating lake whitefish biomass. In estimating historical fish biomass, I assumed both predator population size (Rogers-Bennett et al. 2002, Rosenberg et al. 2005, Stevenson et al. 2007) and average fish weight (McClenachan 2009) would have been larger than observed in the contemporary system. Biomass of the stickleback and small fish groups was initially estimated by Ecopath given an ecotrophic efficiency of 0.97 for sticklebacks and 0.95 for small fish. I assumed high utilization of sticklebacks and small fish by predators, so I used large ecotrophic efficiencies to highlight their importance as prey. Similarly large values have been used for forage fish in other Ecopath models (Cox and Kitchell 2004, Lassalle et al. 2011).

Historical biomass estimates for cormorants and pelicans were unavailable so I assumed their populations would have been much smaller than in the contemporary system due to their recent exponential growth. Though Wires and Cuthbert (2006) suggest historical cormorant populations might actually have been quite large, the influence of cormorant and pelican consumption in the model, even when modeled at larger biomasses, was very small relative to total fish consumption suggesting the model was insensitive to the biomass assumption. Biomass estimates for piscivorous and non-piscivorous birds were calculated from surveys at Lac la Biche between 2003 and 2005 (C. Found, AESRD, unpublished data) and used directly in the historical model. Biomass of these groups was too small to have a large influence on model dynamics so I did not modify the values for use in the historical model.

Benthic invertebrate biomasses were derived from Lac la Biche estimates for 1965 and 1966 (Pinsent 1967) during a period of rapid cultural eutrophication (Schindler et al. 2008). I assumed a lower historical biomass for chironomids and dipterans based on the assumption of reduced detritus production prior to 1900. In contrast, I assumed larger historical biomasses of other invertebrate groups due to more submerged aquatic vegetation being present for food and habitat (Parsons and Matthews 1995) prior to increasing algal production with eutrophication (Bachelet et al. 2000), as well as reduced predation given a smaller population of invertivorous fish. Cyanobacteria and phytoplankton biomass was estimated from Lac la Biche data for 2003 and 2004 (D. Schindler, University of Alberta, unpublished data) and the historical biomass was assumed to be one-half of the contemporary value, based on the lake's historical classification as eutrophic combined with the large increase in plankton production throughout the 20th century (Schindler et al. 2008). Littoral and pelagic zooplankton and submerged aquatic vegetation were estimated by Ecopath.

Production/biomass (year^{-1}) (P/B) for most of the large fish groups was calculated as the annual mortality estimate from a catch-curve analysis using

Lac la Biche data for 2003 and 2005. Lake whitefish P/B was derived by calculating the natural mortality rate for a similar system (Touchwood Lake) then adding the fishing mortality estimate for Lac la Biche to estimate total mortality. No data were available for sticklebacks or small fish so literature values were used (Randall and Minns 2000, Jaegar 2006). Local data for 2003 to 2005 were used to calculate P/B for double-crested cormorants (*Phalocrocorax auritus*) and American white pelicans (*Pelecanus erythrorhynchos*) and values for all other groups were taken from literature (Table B-1).

Consumption/biomass (year^{-1}) (Q/B) values for fish were initially calculated according to Palomares and Pauly (1989, 1998 as referenced by Christensen et al. 2008). Calculated values were generally much larger than literature values and those used in other models, so I used published values to provide a range of estimates for model parameterization. Consumption/biomass for double-crested cormorants (hereafter cormorants) and American white pelicans (hereafter pelicans) was calculated from 2003 to 2005 field data; values for all other groups were taken from literature (Table B-1).

Seasonal field data for Lac la Biche were used as initial estimates of the historical diet compositions for fish and cormorants. For all other groups, diet was taken from literature (Table B-2 and B-3). Seasonal migrations by cormorant, pelican, piscivorous waterbird, and non-piscivorous waterbird groups were modeled using the 'diet import' approach (Christensen et al. 2008). The percentage of time spent outside of the model area was calculated for cormorants and pelicans based on a seasonal residence time of 115 days and the estimation that during the nesting season about 30% of cormorant diet and 40% of pelican diet came from sources other than Lac la Biche (A. McGregor, unpublished data). Total diet import for piscivorous and non-piscivorous waterbirds was estimated as 93% and 90% respectively. Due to a lack of information on waterbird season of residence, I assumed a greater proportion of their diet was imported relative to pelicans or cormorants because most foraging flocks observed on Lac la Biche during aerial surveys in 2005 to 2007 were present later in the summer season, were assumed not to be nesting on the lake, and were highly mobile. As a result, more of their diet was assumed to originate outside the system.

Lac la Biche was modeled as a closed system exhibiting steady state conditions with both biomass accumulation and net migration set to zero for all groups.

Model Parameterization - 1900

To model ecosystem characteristics in 1900, I used Ecosim to force the 1800 model with 110 years of estimated fisheries harvest trends under eight different assumptions for trophic control. The eight models for 1900 were generated using vulnerability and/or group info parameters reflecting different trophic control assumptions (Table 3-2). Vulnerability parameters describe the degree to which a large increase in predator biomass will affect the predation mortality of that predator on its prey (Christensen et al. 2008). A low vulnerability (close to 1.0) suggests little effect of a predator increase on its prey while a large vulnerability indicates a large effect. Top-down control was modeled by setting larger vulnerabilities for predators, bottom-up control by setting small values for low trophic level groups, and wasp-waist by setting lower values for invertebrate and zooplankton groups (Coll et al. 2006). Default vulnerabilities of 2.0 were maintained in tests of 'mixed control'. For most models the 'group info' inputs were left as default values to avoid further complicating the model with incorrect or biased assumptions.

For each of the eight model runs I used biomass and consumption/biomass outputs for 1900 as initial parameters for eight new models. Diet compositions from the 'best fit' model were exported and used in all models of 1900. Values estimating rate growth rate (von Bertalanffy, K) were reduced slightly between 1800 and 1900 in response to heavy harvest of these species (Heino and Godo 2002). Changes to K were guided by the growth function characteristics of local lakes with different densities and harvest pressures; the same values were used in all 1900 models. Model balance was achieved by making small changes in production/biomass values followed by changes in diet composition. Production/biomass was expected to respond to changes in size-selective mortality so it was reasonable to modify this value first following an intensification of the fishery. I avoided making changes to biomass and consumption/biomass values because they represented predictions resulting from the modeled ecosystem response to estimated fisheries harvests.

Estimation of historical fish harvest

Annual harvest estimates for lake whitefish were generated from a detailed analysis of anecdotal reports of fish harvest during the fur trade era (Chapter 2). Little information was available for estimating lake whitefish harvest post-decline (1878) so I assumed high annual harvest variability during lake whitefish recovery based on qualitative reports of variable fish availability and catch success by anglers, fur traders, and the Mission (Dominion of Canada 1887:94, Department of Marine and Fisheries 1895, 1896, Champagne 1992:240-241, 251). To accommodate uncertainty and variability in post-decline harvests, I randomly selected annual harvests for 1879 to 1910 from a range of pre-decline harvest estimates (1860 to 1875; 0.6 t/km-2 to 2.7 t/km-2). I chose 1860 to 1875 as appropriate for representing post-decline harvests because estimates from these years represent a harvest range that appeared able to support estimated annual subsistence needs of the fur traders and Mission.

Anecdotal accounts discuss, but rarely quantify, the harvest or consumption of fish species such as pike, walleye and white sucker (*Catostomus commersonii*). I generated annual harvest estimates for these species using catch proportions calculated from a fur trade post harvest summary from 1798 to 1799 (HBCA,PAM,B104/a/1.fo.36 as cited in McCullough and Maccagno 1991:71) (Table 3-3). I calculated harvests of pike, walleye, and white suckers relative to lake whitefish (Figure 3-1). Northern pike harvest proportion was decreased from 0.35 to 0.20 to prevent the loss of northern pike in the model. The reduction in harvest proportion is supported by reports of a much smaller proportion (0.083) of pike in fur trade post data from October 6-10, 1799 (Tyrell 1916). Walleye harvest proportion was similar between 1798 and 1799, and no white sucker harvest data were reported in 1799. Burbot (*Lota lota*) and yellow perch (*Perca flavescens*) were presumably harvested as bycatch but no catch records exist so they were modeled as a constant, low yield fishery. A low yield cormorant fishery was added to allow 'harvest' of cormorants as a form of population control.

Changes in structure and function

Changes in ecosystem structure, function, and maturity between 1800 and 1900 were assessed by comparing indices of trophodynamics, thermodynamics, trophic flow analysis, and information theory (i.e. ascendency (Ulanowicz 1986)) (Christensen et al. 2008). System components were aggregated into discrete trophic levels (TL) and a Lindeman spine (Lindeman 1942) was used to depict the average number of steps in the food web and to assess the efficiency of energy and material transfer among TLs. The transfer efficiency (TE) summarizes inefficiencies in the food web due to respiration, egestion, excretion, and natural mortality (Lindeman 1942) and was calculated by Ecopath as the ratio of the production of a TL relative to the preceding TL (Christensen and Pauly 1993). Total system throughput (TST) describes the overall size of the system calculated in terms of flows to production, consumption, respiration, imports and exports, and flows to detritus ($t \cdot km^{-2} \cdot year^{-1}$) (Shannon et al. 2003).

Total effect and total Mixed Trophic Impact were calculated from the mixed trophic impacts (MTI) analysis results in Ecopath. Total effect summarizes the overall effect of varying the biomass of each impacting group on the whole ecosystem, excluding the fishery. It was calculated as in Libralato et al. (2006) for each impacting group. Total mixed trophic impact is the sum of the positive and negative MTI values for each functional group (with the exception of the fisheries) resulting from a unit increase in the biomass of the impacting functional group, excluding the impact of a group on itself.

Ecological indicators describing community energetics, structure, cycling, and information flow were compared between model years and were used to assess ecosystem maturity and stability (Odum 1969; Christensen 1995; Pranovi et al. 2003). According to Odum (1969), total primary production/total biomass and net system production are expected to be lower in mature systems while total biomass/total throughput is thought to be higher in a mature system. Primary production/respiration is expected to approach unity with increasing maturity (Odum 1969; Christensen and Pauly 1993). The relative importance of detritus in the food chain is expected to increase in a mature system (Odum 1969), and an increase in detritus is generally associated with a decrease in primary productivity (Christensen and Pauly 1993). Ascendency is a metric proposed by Ulanowicz (1986) to describe ecosystem development based on both the extensive (flows) and intensive (organization) properties of the system; ascendency should increase in the absence of perturbations affecting growth and development. This measure captures attributes of both the structure and function of a “flow-storage model” (Whipple 1999). The development capacity describes the natural upper limit to ascendency (Baird and Ulanowicz 1993). Overhead describes a system’s ‘strength in reserve’ (Trites et al. 1999) and is related to system stability and the ability to respond to perturbations.

Results and Discussion

Characterization of the historical ecosystem – model balancing

Major changes in the diet of large piscivorous predators were required to balance the 1800 model. In balancing, I assumed that diets of large predatory fish would have included larger fish and more benthic invertebrates due to their availability relative to small fish. Increased consumption of larger, higher trophic level prey in historical systems has been documented for sea birds

(Norris et al. 2007) though no similar studies seem to exist for fish. Fish fry were added to the diet of planktivorous fish groups as a very small proportion of the total diet (<0.0001) to represent seasonal consumption that was difficult to detect (Schooley et al. 2008) but could have large impacts on fry survival and recruitment. Consumption/biomass (year^{-1}) (Q/B) for most fish groups was reduced below the minimum estimate by 20% to 60% to avoid unsupported increases to biomass of prey groups to satisfy predator consumption demands (Table 3-4). The required decreases are not unexpected given that most literature values represent contemporary systems and changes in both fish size and water temperature have likely occurred over the last 200 years. Historical fish populations are expected to have a larger proportion of big fish (Stevenson et al. 2007, McClenachan 2009) which eat relatively less than smaller fish (Pauly et al. 1990). A larger average fish size in 1800 would thus contribute to a lower Q/B. In addition, food consumption is known to increase with temperature (Pauly et al. 1990) suggesting that higher contemporary lake temperatures, or variability in lake temperatures between Lac la Biche and the literature sources (Europe and the Great Lakes), could have resulted in larger Q/B ratios than in cooler, historical systems. Fish size and water temperature can influence Q/B in opposite directions making predictions of overall change more difficult.

Production/biomass (year^{-1}) (P/B) was increased for small walleye (4.5X) and medium sized perch (2.5X) and decreased 30% for small perch (Table 3-4). These required changes can be explained by differences in stanza structure between Lac la Biche models and the reference systems. Changes in the age structure of fish can alter the P/B for a group or stanza (Banse and Mosher 1980). The changes in perch P/B reflect differences in how I defined the size and age of fish in each stanza compared to the reference model. For instance, Jaegar (2006) included only young-of-the-year perch in her smallest stanza (P/B = 3.8 to 7.15 /year), and yearling or older perch in her second stanza (P/B = 0.40 to 0.59 /year), whereas my smallest stanza included young-of-the-year and yearling perch up to 100 mm total length, and my largest stanza excluded perch larger than 200 mm total length. The inclusion of yearlings in the smallest perch stanza justified the decrease in P/B. The increase in the medium-sized perch P/B reflects the decision to model large perch as a separate stanza, leaving relatively smaller fish in the middle group. Differences in how the small walleye stanza was defined compared to the reference systems can also explain the increase in P/B for this group. The transition of biomass between the small- and medium-sized walleye stanzas at 51 mm total length occurs within a few months of hatching at Lac la Biche. As a result, the smallest stanza represents young fish which either die off or transition to the next stanza in much less time than the annual unit used to describe P/B (/year). To account for the short duration of young walleye in the smallest stanza a high P/B value was used to reflect a large total mortality (Z) (Allen 1971 as cited in Christensen et al. 2008). Large Z values can be necessary for freshwater species to deal with model accounting assumptions of continuous reproduction and monthly recruitment that do not accurately represent pulse reproduction strategies (C. Walters, pers. comm., February 23, 2010).

The biomass of most invertebrate groups, suckers, large burbot, and large perch was increased to achieve model balance (Table 3-4). Perch biomass was increased by 20 to 30 times the maximum estimate to accommodate modeled predation mortality. The large increase in perch biomass suggests assumptions for this group were flawed. The biomass of large perch was initially estimated from Lac la Biche hydroacoustics data for 2006 and 2007 (Milne 2007, Milne 2008). The density estimate of 5 fish/ha likely underestimated the true density since hydroacoustics cannot adequately survey the littoral zone (Beauchamp et al. 2009) where most large perch occur (Radabaugh 2006), and surveys were done at night when perch are least active (Radabaugh 2006). The average fish weight of 150 g was also probably an underestimate assuming that average fish size was larger 200 years ago. Biomass changes for other groups reflect uncertainty in historical conditions and generally reflect changes necessary to accommodate modeled predation mortality.

Each of the eight-1900 models was balanced using the same assumptions applied to the 1800 model; slight changes were made to P/B and diet compositions of cormorants, yellow perch, and cisco for balancing. .

Input parameters that resulted in balanced models for the historical ecosystem are included in Table 3-5. Between 1800 and 1900, the biomass of large lake whitefish (LKWH2) varied the most, declining from 11.00 t/km^{-2} to between 2.89 t/km^{-2} and 8.72 t/km^{-2} over the modeled period. The biomass of large walleye dropped from 3.68 t/km^{-2} in 1800, to an average of 2.49 t/km^{-2} by 1900 under the different trophic control assumptions. Large pike biomass declines were estimated to range between 28% and 57% from the 1800 biomass of 5.00 t/km^{-2}, and cormorant biomass in 1900 was two to three times greater than the 1800 biomass of 0.02 t/km^{-2}. Variability in all other parameters was greatest for fish and bird groups. Diet compositions used in the balanced 1800 and 1900 models can be found in Appendix B as Table B-1 and B-2. Knowledge of the parameter combinations and the range of values used in the balanced historical Ecopath models are useful for restoration because they can guide the creation of a “re-building plan based on the architecture of past ecosystems” (Pauly et al. 2008).

During model creation I found Ecopath was particularly sensitive to input parameters describing growth (von Bertalanffy K and ‘age in months’) of the multistanza fish groups. Additionally, Ecosim results varied substantially given different inputs for ‘vulnerabilities’ and ‘group info.’ The absence of a satisfactory tool for sensitivity analysis of model inputs was a weakness of the current software version. However, changing vulnerabilities to reflect different trophic control assumptions provided a strategic way to explore the range of variability in model results given the paucity of information describing historical ecosystem conditions.

In the absence of historical information, values used in initial model parameterization (1800 model) were a ‘best guess’ at representing historical conditions based on local knowledge and the ecological biases of the modeler(s).

For Lac la Biche, the 1800 model was strongly based on local expectations of historical biomasses for recreational and commercial fish species in a ‘pristine’ or ‘natural’ system. Other input parameters were modified to balance the model given the biomass assumptions. As a result, the 1800 model qualitatively, and perhaps inadvertently, reflects the expected endpoint of the restoration program. Forcing the 1800 model with harvest data under different trophic control assumptions generated a range of historical variability (Landres et al. 1999) that can guide restoration and the “… rebuilding of resources” (Pauly et al. 1998). Ecopath with Ecosim made it possible to test the suitability of the 1900 restoration target by allowing changes in ecosystem characteristics between 1800 and 1900 to be assessed, greatly improving knowledge of the relationships and processes that support the modeled system and those most impacted by fish harvest.

Change in structure and function

The relationship between ecological structure and function is complex. Flows of energy and matter or predator-prey interactions are controlled by the identity and diversity of the functional groups that define the system (Naeem et al. 1999) and modifications to these groups can alter ecosystem function. Changes in the flow of energy can also occur in response to changes in ecosystem structure following a disturbance (Levin 1980; Ulanowicz 1997). Ecopath ‘statistics’ and ‘network analysis’ tools provide the trophodynamic, thermodynamic, trophic flow, and information theory analyses necessary to evaluate changes in structure, function, and maturity.

Species abundance

Changes in species abundance reflect changes in overall ecosystem structure and are shown to affect system processes (Naeem et al. 1999). Modeling outputs suggest that by 1900, fishing activity reduced the biomass of demersal fish (14%) which generated an increase in both pelagic fish (18%) and bird (45%) groups (Figure 3-2). Negative changes in biomass were predicted for all size classes of walleye, adult pike and whitefish, sticklebacks, and pelagic zooplankton. Relative biomass of cormorants, pelicans, adult burbot and adult perch increased the most (Figure 3-3). The increase in adult burbot could be explained by the decline in northern pike predation mortality, and by an increase in their main prey, cisco. Similarly, the increase in large perch biomass was the direct result of decreased walleye predation as well as recruitment of intermediate sized perch to the largest size class. No clear relationships existed to explain the increase in cormorant biomass. I assumed, however, that declines in walleye and pike positively affected the survival of small and intermediate sized fish, increasing available prey for cormorants and resulting in increased growth and survival of the cormorant population. The relationship among piscivore predators, forage fish, and cormorants hints at contemporary fisheries issues regarding the ecosystem effects of cormorants resulting from the structural changes in the fish community.

Trophic structure

Changes in ecosystem function initiated by structural change can be expressed through species interactions, energy flow, productivity, and resilience (Zhou et al. 2010). Species interactions were described by Ecopath using trophodynamic concepts, specifically non-integer trophic levels and an index of omnivory. Non-integer trophic levels (TL) account for the diets of species that feed across TLs (Christian and Luczkovich 1999) and their value can change in space and time based on the encounter rate between predators and prey (Gascuel et al. 2011). The mean trophic level for all individuals of a species emerges as a result of the 'trophic functioning' of an ecosystem (Gascuel et al. 2011). The highest non-integer trophic levels (4.0 or higher) from Ecopath represented the dominant piscivorous predators, including cormorants, pelicans, large walleye, and large burbot (Table 3-6). Piscivorous birds (3.96) and all sizes of pike (3.92

to 3.94) occupied slightly lower TLs. Most other fish occupied TLs between 3.0 and 3.82, while invertebrate and zooplankton groups had TLs between 2.0 and 2.05, and primary producers and detritus had TLs of 1.0. Between 1800 and 1900 TL increased marginally for of all walleye, pike, and burbot groups, as well as non-piscivorous birds. Trophic level decreased for the two largest perch groups and for cormorants. Though the changes in TL are small they do reflect a change in species interactions of most predator groups and suggest a change in system functioning.

For a predator, variance of the non-integer TLs of its prey species is reported as the omnivory index (OI) (Christensen and Pauly 1993). The majority of species contributing to TL II (benthic invertebrates and zooplankton) and TL III (small perch, cisco, lake whitefish, suckers, sticklebacks and other small fishes) had the lowest OI values (< 0.05) indicating that they are trophic specialists (Table 3-6). Specialization declines with increasing TL due to limitations in the availability of prey species to meet the consumption needs of higher level predators (Lindeman 1942). Model results suggest less specialization or greater omnivory of intermediate and higher level piscivorous predators (walleye, pike, perch, burbot) at Lac la Biche (OI = 0.1 to 0.5). Considerably larger OI values for piscivorous birds, especially pelicans (0.9) and cormorants (1.4), indicate they are trophic generalists capable of benefitting from prey across a range of TLs. Such high omnivory can be a benefit in volatile systems by stabilizing system responses to perturbations (McCann 2000). The decline in the OI for cormorants and most fish groups between model years could suggest reduced system stability due to increased diet specialization. Though apparently small, modeled changes in TL and OI suggest historical harvests altered the trophic functioning of the ecosystem.

Mixed trophic impacts

Changes in the relative abundance, age distribution, and sex ratios of species through harvest or other selective mortality can greatly affect some species interactions and others not at all, resulting in variable effects on overall system function. Total effect, which measures the relative effect of changing the biomass of one functional group on the whole ecosystem, indicated that low trophic level species had the largest overall effect on other modeled groups (Figure 3-4). Specifically, the chironomid and dipteran, and phytoplankton groups had the largest total effect (0.85 to 0.95) on the system. The smallest effects were attributed to young-of-the-year walleye and both piscivorous and non-piscivorous bird groups (< 0.005). There were notable increases in the effect of small fish, adult perch, pelicans, and cormorants between model years while large declines were observed for sticklebacks, small perch, and adult lake whitefish, pike, and walleye.

The estimation of each functional group as having a positive or negative contribution on the total effect is useful in determining the influence of bottom-up and top-down control of the system (Libralato et al. 2006). Total mixed trophic impact (tMTI) indicated that an increase in the biomass of lower trophic levels groups (primary producers, some plankton, invertebrate, and forage fish groups) had an overall positive effect on other modeled groups (Figure 3-5). In contrast, an increase in the biomass of predator groups had a negative effect on other groups. The large positive tMTI for detritus and submerged aquatic vegetation in both model years (1.9 to 2.0) suggested bottom-up control of these groups. That fisheries harvests did not produce any major change in the tMTI values for the producer groups supports this conclusion. Top-down control was strongest for large pike (-1.5). Large harvests of pike and walleye led to a decline in their tMTI by 1900, suggesting a reduction in their top-down influence and a change in their functional ecosystem role. All other groups represented a mixture of bottom-up and top-down control. An increase in the top-down influence of large yellow perch, cormorants, and pelicans in 1900 suggests an increase in their structuring role following reductions in adult pike and walleye. Identification of the groups with the largest potential effect on the whole system is useful in guiding management actions during restoration and in identifying overlooked groups with important ecosystem roles.

Energy flow

Patterns of energy flow are a critical determinant of the form, function, and diversity of life (Odum 1968). Ecological succession sensu Odum (1968) involves a fundamental change in patterns of energy flow. Though what constitutes a fundamental change is not specifically defined, energy flow at Lac la Biche was altered as a result of historical harvest, suggesting a change in system function between 1800 and 1900. Flows have been summarized by Ecopath and are represented as a Lindeman's spine (Lindeman 1942) with primary production and detritus depicted separately (Figure 3-6). In both 1800 and 1900, the majority of the flows through the system (measured as total system throughput (TST) (%)) occurred at trophic levels (TL) I and II, becoming less significant at the higher TLs. The average transfer efficiency (TE) for the eight-1900 models was consistently higher in 1900 with the magnitude of the difference increasing with TL (4% to 88%). Transfer efficiency was greatest between TLs III and IV in both model years highlighting the importance of predator-prey interactions between piscivorous predators (medium and large walleye and pike, large burbot, cormorants, pelicans and piscivorous birds) and their main prey (small and medium perch, cisco, and lake whitefish). The increase in TE at the upper TLs indicates an increase either in consumption or production used to support the fishery (Pranovi et al. 2003), and improved flow of energy to high level predators (Brando et al. 2004). Between 1800 and 1900, TE and TST increased at higher TLs suggesting production and thus potential yields for pike and walleye may have been improved following heavy harvests of lake whitefish. If this is the case, then a management decision that would focus restoration efforts on achieving high walleye biomass for recreational harvest represents a trade-off in commercial lake whitefish harvest potential.

Ecosystem maturity

Community energetics, structure, cycling, and information flow indices are commonly used to assess changes in an ecosystems maturity and stability over time and among similar systems (Brando et al. 2004, Freire et al. 2008). Average ecosystem indices suggest a marginal decline in maturity of the modeled system by the early part of the 20th century; however, the wide range in values for 1900 implies no difference between model eras. Average values for total system throughput, consumption, respiratory flow, flows to detritus, and total system biomass were lower in 1900 suggesting a decline in system maturity (Table 3-7). Total primary production/total biomass was lower (1.3%) in 1800, consistent with the accumulation of biomass in mature systems (Christensen 1995). Net system production, primary production/respiration, and total net primary production were higher in 1900 further supporting a decline in maturity. Total biomass/total throughput did not change between years indicating biomass supported per unit energy flow was not affected by historical harvests. Most of the network flow indices were larger (0.04% to 3.9%) in 1800, consistent with higher system maturity. Finn's cycling index (FCI) and throughput cycled were higher in 1800 suggesting a more mature system (Odum 1969) that was better able to maintain its structure and function through stabilizing feedbacks (Brando et al. 2004). Ascendency was larger in 1800 indicating a more mature system while lower overhead suggested a less stable system. Though there was little change (< 1%) in the average value of most of the summary statistics beteween1800 and 1900, the balance of measures suggests a possible trend towards declining system maturity that could be indicative of a slight decline in ecosystem resilience. If this trend was allowed to persist, it could lead to system collapse and a regime shift in extreme cases (Scheffer and Carpenter 2003).

Conclusions

Ecopath with Ecosim was a useful tool for testing assumptions regarding the character of historical lake ecosystems and the effects of harvest. Achieving mass-balance in Ecopath is an iterative process that challenges our preconceptions and can lead to increased understanding of both ecosystem and single-species population dynamics. Using this tool, I produced a range of plausible parameter values for use in the creation of alternative ecosystem models to guide and monitor restoration success. If restoration efforts can successfully reestablish any of the parameter combinations from the balanced models of 1800 or 1900, then the restoration program objectives of increasing walleye abundance and fish size should be realized.

From these findings, I would suggest the period immediately preceding the onset of rapid human settlement and development (1900) represents an acceptable period for setting restoration targets. Few major changes to structure, function, or maturity between eras suggests that the modeled system is sufficiently resilient to support estimated historical harvest levels. Thus, targeting ecosystem conditions resembling 1900 would provide a reasonable compromise between allowing harvest of top predators to satisfy social demand while maintaining the general integrity of the system. Characteristics of the balanced models for 1800 and 1900 suggest historical fishing could have initiated changes in the structure and function of the Lac la Biche ecosystem, capable of marginally decreasing system maturity and resilience. That being said, by choosing an earlier ecosystem on which to model restoration programs, or by identifying the trade-offs in system potential that could result from choosing more recent targets, managers help minimize the potential for the shifting baseline syndrome (Pauly 1995) by emphasizing the legacy of historical harvests on ecosystem structure and function.

In addition to identifying the potential effects of historical harvests on ecosystems, this research provides one of the only reviews to estimate and assess the compatibility of a plausible range of ecosystem parameters and state variables for an energetically-balanced large lake ecosystem in North America. This type of historical modeling provides valuable insight to managers and policy makers by providing them with a “regional-historical viewpoint”

(Ricklefs 1987) from which to approach restoration projects, and by fostering relationships between science and management.

Table 3-1. Description of groups used in the Ecopath models for Lac la Biche, 1800 and 1900. TL refers to fish total length.

Model Group	Description
WALL1	Walleyes (*Sander vitreus*) up to 50 mm TL
WALL2	Walleyes from 51 to 350 mm TL
WALL3	Walleyes 351 mm TL and larger
NRPK1	Northern pike (*Esox lucius*) up to 350 mm TL
NRPK2	Northern pike 351 mm TL and larger
YLPR1	Yellow perch (*Perca flavescens*) up to 100 mm TL
YPLR2	Yellow perch from 101 to 200 mm TL
YLPR3	Yellow perch 201 mm TL and larger
CISC1	Cisco (*Coregonus artedii*) up to 140 mm TL
CISC2	Cisco 141 mm TL and larger
LKWH1	Lake whitefish (*Coregonus clupeaformis*) up to 260 mm TL
LKWH2	Lake whitefish 261 mm TL and larger
BURB1	Burbot (*Lota lota*) up to 350 mm TL
BURB2	Burbot 351 mm TL and larger
Suckers	White sucker (*Catostomus commersonii*) and longnose sucker (*Catostomus catostomus*), all sizes. Mostly white sucker.
Stickle.	Ninespine stickleback (*Pungitius pungitius*) and brook stickleback (*Culaea inconstans*). Mostly ninespine stickleback.
Small Fish	Spottail shiners (*Notropis hudsonius*), trout-perch (*Percopsis omiscomaycus*), and Iowa darters (*Etheostoma exile*). Mostly spottail shiners.
DCCO	Double-crested cormorant (*Phalacrocorax auritus*)
AWPE	American white pelican (*Pelecanus erythrorhynchus*)
Pisc. Birds	Piscivorous waterbirds
Non-P. Birds	Non-piscivorous waterbirds
Chiro. & Dip.	Chironomids and Dipterans
Amphi.	Amphipods
Mollusc & Gastro.	Molluscs and gastropods
Inverts.	All other aquatic invertebrates
Litt. Zoopl.	Littoral zooplankton
Pel. Zoopl.	Pelagic zooplankton
Cyano.	Cyanobacteria
Phyto.	Phytoplankton
SAV	Submerged aquatic vegetation including: macrophytes, periphytes, and epiphytes

Table 3-2. Vulnerability parameters and ‘group info’ used in the eight Ecosim runs of the 1800 model used to generate models for 1900. Vulnerability parameters describe the degree to which a large increase in predator biomass will affect the predation mortality of that predator on its prey (Christensen et al. 2008). A low vulnerability (close to 1.0) suggests little effect of a predator increase on its prey while a larger vulnerability indicates a larger effect. See Table 1 for a description of model group acronyms.

Scenario	Description	Vulnerabilities	Group Info
1	Top-down/ Bottom-up - Inverts	**3.0** - predators (WALL3, NRPK2, YLPR3, BURB2, DCCO, AWPE) **1.5** - invertebrates and plankton (Chiro&Dip., Amphi., Molluscs & Gastro., Inverts., Litt. Zoopl., Pel. Zoopl.) **2.0** - all other groups	Default
2	Top-down/ Bottom-up - Zoopl.	**3.0** - predators (WALL3, NRPK2, YLPR3, BURB2, DCCO, AWPE) **1.5** - plankton (Litt. Zoopl., Pel. Zoopl.) **2.0** - all other groups	Default
3	Bottom-up - Zoopl.	**1.5** - plankton (Litt. Zoopl., Pel. Zoopl.) **2.0** - all other groups	Default
4	Top-down	**3.0** - predators (WALL3, NRPK2, YLPR3, BURB2, DCCO, AWPE) **2.0** - all other groups	Default
5	Wasp-waist	**1.5** - invertebrates and plankton (Chiro&Dip., Amphi., Molluscs & Gastro., Inverts., Litt. Zoopl., Pel. Zoopl.) **2.0** - all other groups	Default
6	Mixed	**2.0** - all groups (Ecosim default)	Default
7	Fitted 1	**1.0** - WALL1, NRPK1, YLPR1, CISC1, LKWH1, BURB1 **1.5** - YLPR2, Chiro. & Dip., Amphi., Mollusc & Gastro., Inverts., Litt. Zoopl., Pel. Zoopl., Cyano, Phyto. **2.0** - YLPR3, CISC2, Suckers, Stickle., Pisc. Birds, Non-P. Birds **2.5** - WALL2, NRPK2, LKWH2, BURB2 **3.0** - WALL3, DCCO, AWPE	Default
8	Fitted 2	Same as 'Fitted 1'	Best Fit

Table 3-3. Harvest proportions for lake whitefish (*Coregonus clupeaformis*) (LKWH), walleye (*Sander vitreus*) (WALL), northern pike (*Esox lucius*) (NRPK), and white suckers (*Catostomus commersonii*) (WHSC) calculated from a Lac la Biche fur trade post harvest summary from 1798 to 1799 (HBCA,PAM,B104/a/1.fo.36 as cited in McCullough and Maccagno 1991:71).

	LKWH	WALL	NRPK	WHSC
Count	2126	190	749	229
Propn of LKWH	1	0.089	0.352	0.108

Table 3-4. Values represent a multiplier indicating the magnitude of changes to Ecopath input parameters required for model balance when values were outside the range of values compiled from a variety of sources (see Appendix B Tables B-1 and B-2 for input data ranges and references). Values larger than 1.0 indicate model inputs that were increased beyond the largest value in the range and values less than 1.0 indicates numbers reduced below the smallest value. See Table 3-1 for a description of model group acronyms.

Group Name	B (t/km^2)		P/B ($year^{-1}$)		Q/B ($year^{-1}$)	
	1800	1900	1800	1900	1800	1900
WALL1			4.3	4.5		
WALL3					0.4	0.4
NRPK2	0.9				0.6	0.7
YLPR1			0.7	0.7		
YPLR2			2.4	2.0		
YLPR3	21.3	30.4			0.7	0.7
CISC2					0.6	0.5
LKWH2					0.8	0.9
BURB2		1.3			0.8	0.7
Suckers	2.5	3.1			0.6	0.6
Stickle.				1.1		
Small Fish					1.4	1.4
Pisc. Birds	0.7	0.6				
Non-P. Birds						
Chiro. & Dip.	0.6	0.6				
Amphi.	4.0	4.2				
Mollusc & Gastro.	1.6	1.8				
Inverts.	2.0	2.0				

Table 3-5. Input parameters for the balanced 1800 model and the average and range of parameters used in the eight-1900 models. B (t/km^{-2}) is biomass, P/B (year^{-1}) is the production/biomass ratio, Q/B (year^{-1}) is the consumption/biomass ratio. See Table 3-1 for a description of model group acronyms.

Group Name	B (t/km^2)			P/B (year^{-1})			Q/B (year^{-1})		
	1800	1900	1900 Range	1800	1900	1900 Range	1800	1900	1900 Range
WALL1	0.00	0.00		10.50	10.89	10.25-11.60	74.01	74.36	73.42-76.55
WALL2	0.11	0.10	0.09-0.12	0.74	0.76	0.70-0.81	5.41	5.44	5.31-5.56
WALL3	3.68	2.49	1.96-3.11	0.17	0.20	0.20-0.21	1.50	1.58	1.57-1.62
NRPK1	0.04	0.04	0.03-0.04	1.35	1.31	1.25-1.50	7.34	8.15	7.79-9.04
NRPK2	5.00	3.33	2.15-3.61	0.16	0.23	0.23-0.25	1.40	1.63	1.59-1.80
YLPR1	1.01	1.08	1.00-1.12	2.60	2.83	2.80-3.00	11.67	11.91	11.79-12.05
YPLR2	2.77	3.16	2.96-3.45	0.96	0.81	0.75-0.84	4.56	4.43	4.34-4.49
YLPR3	1.60	2.28	1.99-2.54	0.49	0.50	0.45-0.55	2.84	2.82	2.79-2.83
CISC1	0.49	0.58	0.54-0.64	1.89	1.89	1.80-2.00	11.46	10.75	8.14-11.39
CISC2	6.50	8.07	6.83-9.13	0.53	0.52	0.50-0.52	3.69	3.44	2.58-3.63

Table 3.5. Continued

Group Name	B (t/km^2)			P/B (year^{-1})			Q/B (year^{-1})		
	1800	1900	1900 Range	1800	1900	1900 Range	1800	1900	1900 Range
LKWH1	1.71	1.48	1.21-1.89	1.30	1.27	1.15-1.45	5.91	6.16	5.37-6.59
LKWH2	11.00	7.11	2.89-8.72	0.35	0.38	0.28-0.60	2.35	2.56	2.35-2.66
BURB1	0.16	0.22	0.19-0.28	0.85	0.79	0.70-0.85	5.25	5.02	4.63-5.36
BURB2	0.65	1.15	0.86-1.53	0.31	0.29	0.25-0.35	1.95	1.86	1.81-1.92
Suckers	6.50	7.86	7.67-8.43	0.30	0.30		2.26	2.18	2.14-2.19
Stickle.	1.14	0.88	0.71-1.07	2.75	3.03	3.00-3.20	9.53	9.81	9.61-9.96
Small Fish	0.93	0.93	0.77-1.08	1.71	1.75	1.71-2.00	8.66	8.69	8.60-8.73
DCCO	0.02	0.05	0.04-0.07	0.52	0.52		72.90	72.64	72.50-72.82
AWPE	0.01	0.01		0.20	0.20		110.00	110.40	110.30-110.50
Pisc. Birds	0.004	0.004		0.25	0.25		58.00	57.80	57.62-58.00
Non-P. Birds	0.01	0.01		0.25	0.25		58.00	57.94	57.82-58.10

Table 3.5. Continued

Group Name	B (t/km^2)			P/B (year^{-1})			Q/B (year^{-1})		
	1800	1900	1900 Range	1800	1900	1900 Range	1800	1900	1900 Range
Chiro. & Dip.	25.00	24.72	24.60-24.85	13.10	13.10		62.40	62.56	62.34-62.85
Amphi.	4.00	4.12	3.65-4.43	5.70	5.70		30.20	29.96	29.05-30.78
Mollusc & Gastro.	4.00	4.38	4.19-4.60	3.80	3.80		24.40	23.96	23.42-24.29
Inverts.	4.00	3.96	3.90-4.06	5.35	5.35		31.80	31.82	31.57-32.01
Litt. Zoopl.	0.37	0.35	0.32-0.38	35.00	35.38	35.00-37.00	120.00	124.00	120.40-127.30
Pel. Zoopl.	0.16	0.12	0.08-0.14	35.00	40.50	40.00-42.00	120.00	146.71	129.90-163.60
Cyano.	2.18	2.18	2.18-2.19	131.50	131.50				
Phyto.	3.18	3.22	3.17-3.33	131.50	131.50				
SAV	115.12	114.90	114.10-115.60	20.00	20.00				
Detritus	0.50	0.50		0.50	0.50				

Table 3-6. Output parameters for the balanced 1800 model and the average outputs from the eight-1900 models. The non-integer trophic level (TL) describes the average trophic position of each functional group (Baird and Ulanowicz 1993). The omnivory index (OI) describes the variance of non-integer TLs of the prey of each predator (Christensen and Pauly 1993) and provides an index of trophic specialization. See Table 3-1 for a description of model group acronyms.

Group Name	TL		OI	
	1800	1900	1800	1900
WALL1	3.56	3.57	0.25	0.25
WALL2	3.80	3.82	0.21	0.20
WALL3	4.00	4.02	0.11	0.10
NRPK1	3.93	3.94	0.10	0.10
NRPK2	3.92	3.94	0.13	0.13
YLPR1	3.01	3.01	0.00	0.00
YPLR2	3.17	3.15	0.13	0.12
YLPR3	3.43	3.40	0.25	0.25
CISC1	3.00	3.00	0.00	0.00
CISC2	3.01	3.01	0.00	0.00
LKWH1	3.01	3.01	0.00	0.00
LKWH2	3.02	3.02	0.00	0.00
BURB1	3.60	3.57	0.23	0.23
BURB2	4.04	4.05	0.02	0.02
Suckers	2.99	2.99	0.01	0.01
Stickle.	3.01	3.01	0.00	0.00
Small Fish	3.02	3.02	0.00	0.00

Table 3.6. Continued.

Group Name	TL		OI	
	1800	1900	1800	1900
DCCO	4.25	4.23	1.43	1.41
AWPE	4.20	4.20	0.89	0.89
Pisc. Birds	3.96	3.96	0.54	0.54
Non-P. Birds	2.80	2.81	0.28	0.29
Chiro. & Dip.	2.00	2.00	0.00	0.00
Amphi.	2.05	2.05	0.05	0.05
Mollusc & Gastro.	2.00	2.00	0.00	0.00
Inverts.	2.02	2.02	0.02	0.02
Litt. Zoopl.	2.00	2.00	0.00	0.00
Pel. Zoopl.	2.01	2.01	0.01	0.01
Cyano.	1.00	1.00	0.00	0.00
Phyto.	1.00	1.00	0.00	0.00
SAV	1.00	1.00	0.00	0.00
Detritus	1.00	1.00	0.21	0.21

Table 3-7. Ecological indicators describing community energetics, structure, cycling, and information flow parameters for Lac la Biche in 1800 and the average of values for the eight models of 1900. Bold text highlights values indicating higher system maturity.

	Units	1800	1900	1900 Range
Statistics and flows				
Sum of all consumption	$t\cdot km^{-2}\cdot yr^{-1}$	**2115**	2108	2,085-2,117
Sum of all exports	$t\cdot km^{-2}\cdot yr^{-1}$	1748	1754	1,730-1,783
Sum of all respiratory flows	$t\cdot km^{-2}\cdot yr^{-1}$	**1262**	1260	1,241-1,266
Sum of all flows into detritus	$t\cdot km^{-2}\cdot yr^{-1}$	**3197**	3191	3,169-3,221
Total system throughput	$t\cdot km^{-2}\cdot yr^{-1}$	**8322**	8313	8,270-8,369
Sum of all production	$t\cdot km^{-2}\cdot yr^{-1}$	3437	3436	3,416-3,461
Calculated total net primary production	$t\cdot km^{-2}\cdot yr^{-1}$	**3007**	3009	2,985-3,039
Total primary production/total respiration		**2.38**	2.39	2.371-2.423
Net system production	$t\cdot km^{-2}\cdot yr^{-1}$	**1745**	1749	1,726-1,778
Total primary production/total biomass		**14.94**	15.14	14.961-15.496
Total biomass/total throughput		0.024	0.024	0.0234-0.0242
Total biomass (excluding detritus)	t/km^2	**201.33**	198.80	194.1-200.4

Table 3.7. Continued.

	Units	1800	1900	1900 Range
Total catches	$t \cdot km^{-2} \cdot yr^{-1}$	0.222	2.20	2.196-2.196
Mean trophic level of the catch		3.27	3.23	3.230-3.233
Primary production required to sustain the fishery	%	1.35	10.93	10.25-12.45
Network Flow Indices				
Throughput cycled (Excluding detritus)	$t \cdot km^{-2} \cdot yr^{-1}$	**0.830**	0.798	0.76-0.82
Predatory cycling index (excluding detritus)	%	0.040	0.040	0.04
Throughput cycled (Including detritus)	$t \cdot km^{-2} \cdot yr^{-1}$	**780.06**	767.64	758.96-779.25
Finn's cycling index (including detritus)	%	**9.37**	9.24	9.07-9.39
Finn's mean path length		**2.77**	2.76	2.749-2.796
Connectance Index		0.242	0.242	0.24
System Omnivory index		0.129	0.134	0.133-0.135
Information Indices				
Ascendency (Total)	Flowbits	**9945**	9929	9,839-9,999
Overhead (Total)	Flowbits	19,356	19,448	19,261-19,524
Capacity (Total)	Flowbits	29,301	29,376	29,100-29,494

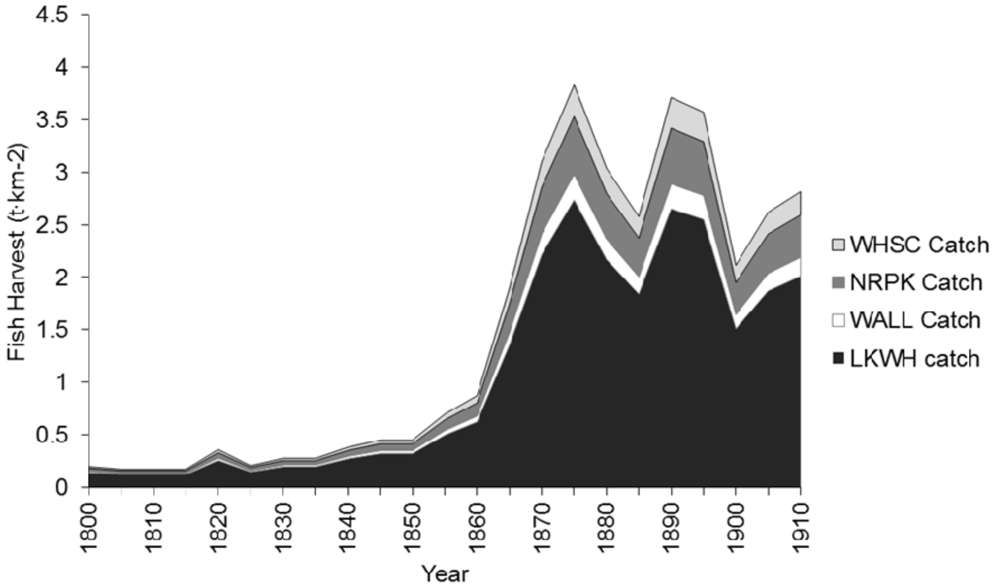

Figure 3-1. Time series of estimated harvest of lake whitefish (*Coregonus clupeaformis*; LKWH), walleye (*Sander vitreus*; WALL), northern pike (*Esox lucius*; NRPK), and white sucker (*Catostomus commersonii*; WHSC) used in Ecosim to challenge the balanced conditions of the 1800 model for Lac la Biche and to generate starting conditions for the 1900 model. Lake whitefish harvest estimates were supported by anecdotal reports of fur traders and Oblate missionaries. Harvest estimates of other species were estimated as a proportion of LKWH harvest derived from historical estimates of relative harvest proportions. Harvest proportions were 9% for WALL, 11% for WHSC, and 20% for NRPK.

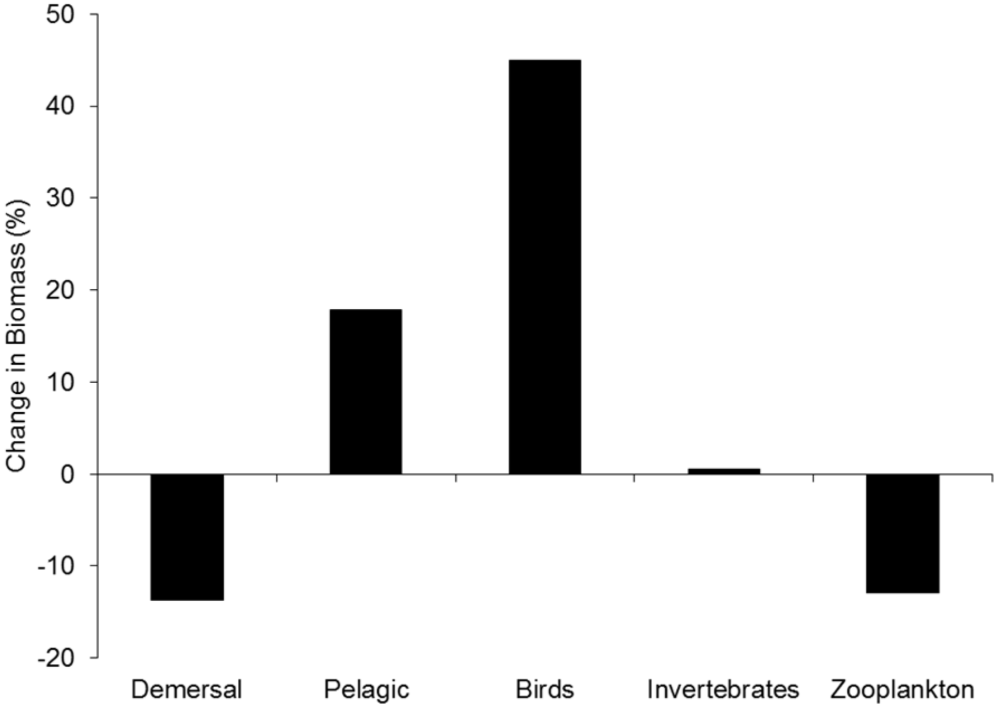

Figure 3-2. Percent change in the combined absolute biomass (t·km^{-2}·year^{-1}) between 1800 and 1900 (average of eight-1900 models) of all functional groups included in the Lac la Biche models, presented as ecological groupings. Demersal and pelagic refer to fish groupings.

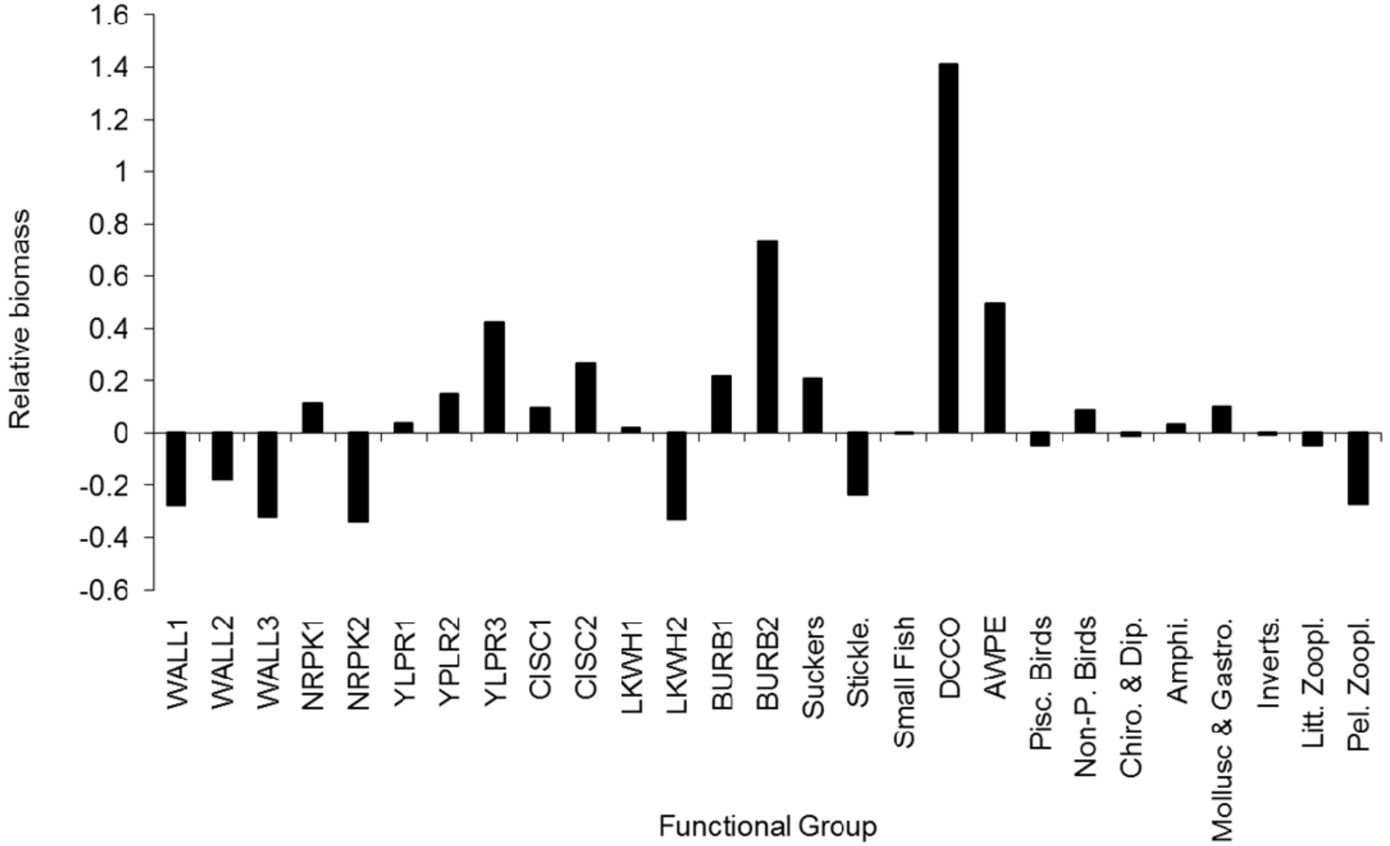

Figure 3-3. Change in the relative biomass (excluding primary producer and detritus groups) between 1800 and 1900 (average of eight-1900 models) of all functional groups included in the Lac la Biche models. See Table 3.1 for a description of model group acronyms.

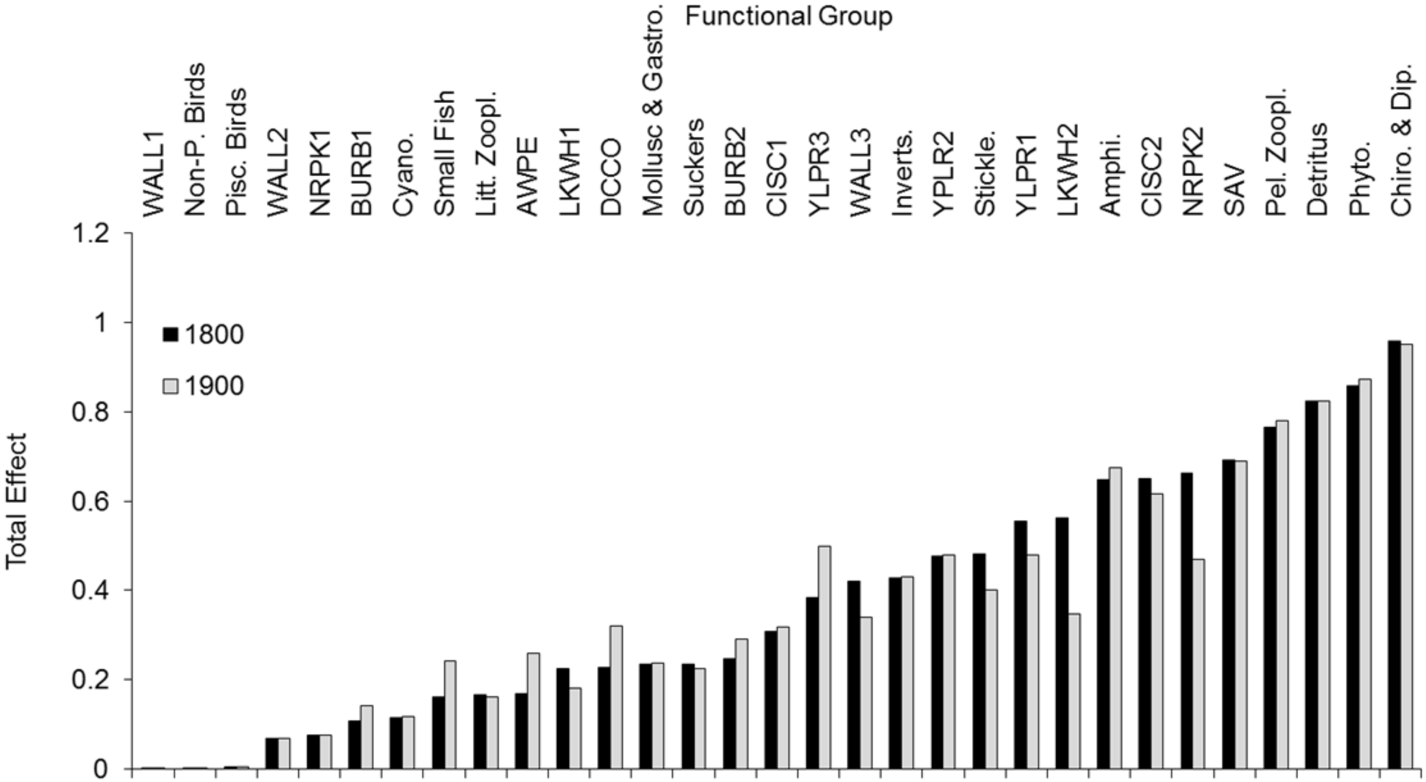

Figure 3-4. Total predicted effect of each functional group in the Lac la Biche model on all other modeled groups. Total Effect is represented as the change in the biomass of all groups as a result of a unit change in the biomass of the functional groups separated by model year. See Table 3.1 for a description of model group acronyms.

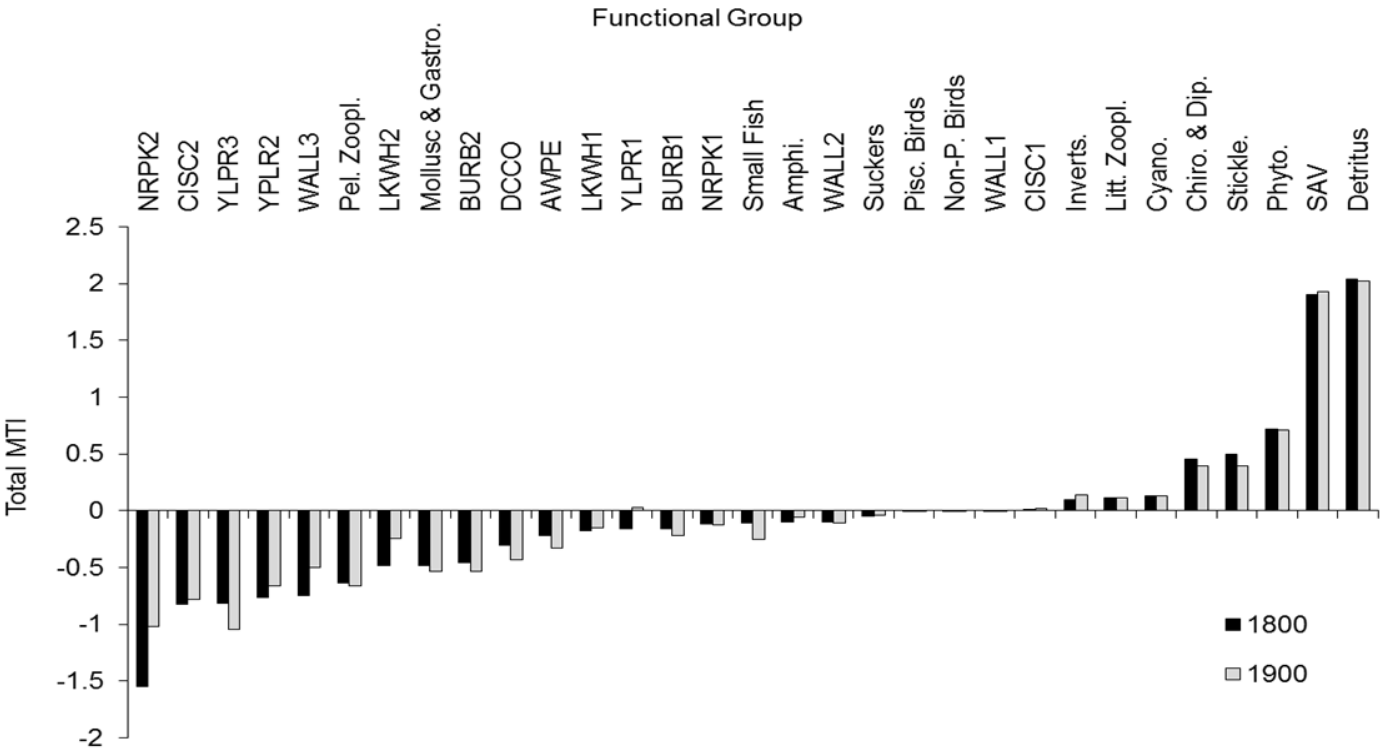

Figure 3-5. Total mixed trophic impact (tMTI) of each functional group on all other groups in the 1800 and 1900 models for Lac la Biche. Mixed trophic impacts (MTI) analysis highlights the direct and indirect effects of trophic interactions resulting from a hypothetical increase in one unit biomass of a single groups on all other groups (Ulanowicz and Puccia 1990). Total MTI is calculated as the sum of the positive and negative MTI values for each functional group, excluding the impact of a group on itself. Negative values for tMTI suggest a top-down influence of the functional groups within the system while positive values suggest a bottom-up influence. See Table 3.1 for a description of model group acronyms.

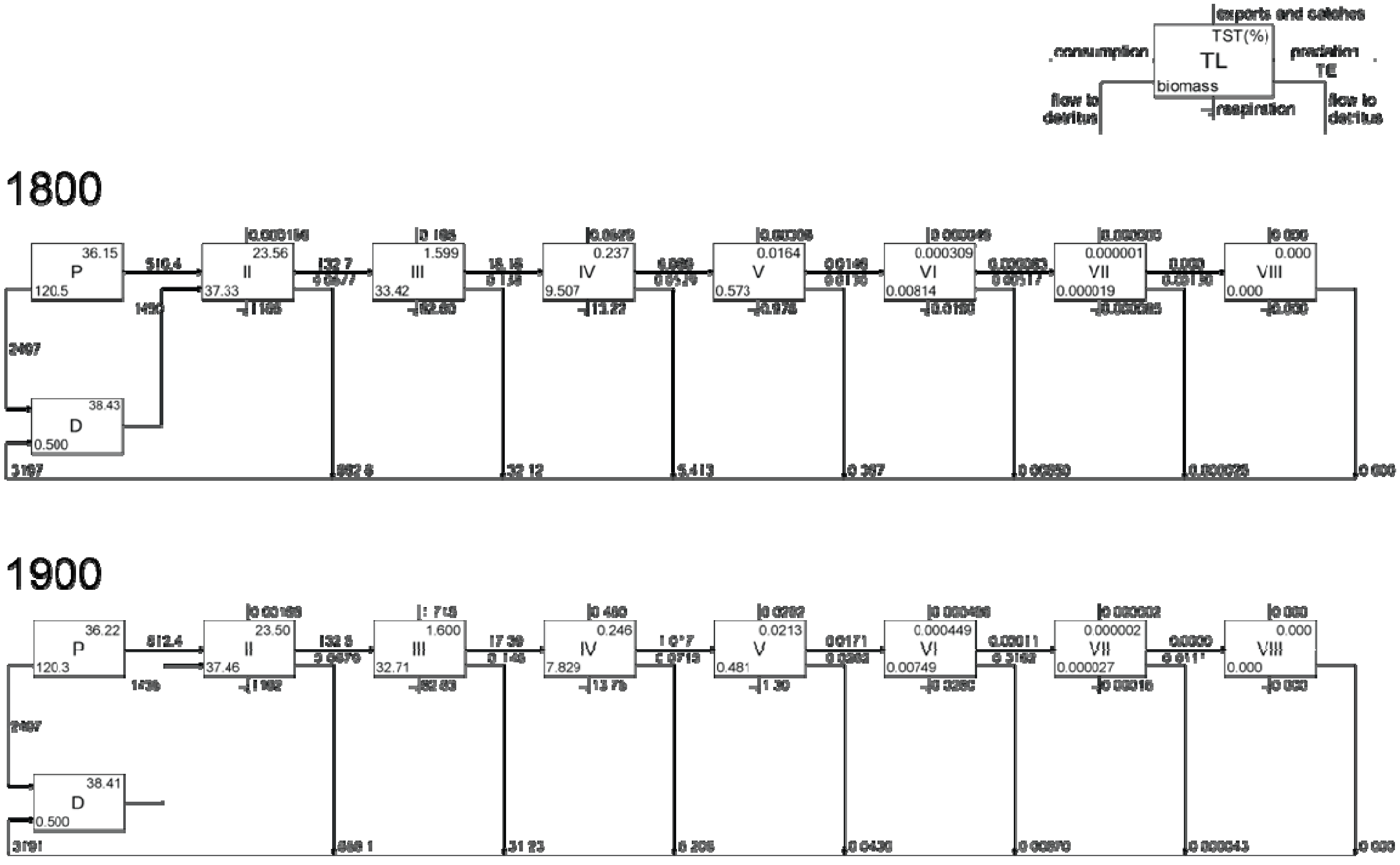
exports and catches
TST(%)
TL
consumption
predation
TE
biomass
flow to detritus
respiration
flow to detritus
1800
P
36.15
120.5
510.4
II
23.56
37.33
III
1.599
33.42
IV
0.237
9.507
V
0.0164
0.573
VI
0.000309
0.00814
VII
0.000001
0.000019
VIII
0.000
0.000
2497
D
38.43
0.500
3197
32.12
5.413
1900
P
36.22
120.3
812.4
II
23.50
37.46
III
1.600
32.71
IV
0.246
7.829
V
0.0213
0.481
VI
0.000449
0.00749
VII
0.000002
0.000027
VIII
0.000
0.000
D
38.41
0.500
31.23
0.000

Figure 3-6. Ecosystem flow diagram for Lac la Biche in 1800 and 1900. Functional groups are organized by integer trophic level and represented as a Lindeman spine (Lindeman 1942). Primary production (P) and detritus (D) are depicted separately but both are associated with trophic level 1.0.

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Appendix B -

Table B-1. Summary of biomass, production/biomass (P/B), and consumption/biomass (Q/B) values used in the initial model parameterization for Lac la Biche, including references for the source data and notes describing the logic and steps involved in model calculations.

Functional Group	Original Value	Source	Notes
WALL1			
P/B	1.47-2.42 $year^{-1}$	Jaegar 2006	
WALL2			
P/B	0.47-0.8 $year^{-1}$	Jaegar 2006	
WALL3			
Biomass	3.685 t/km^2		Based on an estimated Catch-per-unit-effort (CPUE) of 25-30 walleyes per unit of sampling gear (C. Davis, ASRD, Personal communication). Walleye density was estimated with the following equation CPUE = 1.5667*(density)+3.6576 (J. Walker, ASRD, unpublished data). Average fish weight used to calculate biomass was 2191 g (from field samples in 2003, 2005-2007) (FWMIS database).

P/B	0.17-0.48 year^{-1}	Randall and Minns 2000; Jaegar 2006; www.fishbase.org.	0.17 refers to the average conditional natural mortality for walleyes in Alberta lakes (Michael G. Sullivan, ASRD, unpublished data).
Q/B	3.64-8.32 year^{-1}	Jaegar 2006; Empirical equation 17 from Christensen et al. 2008.	
NRPK1			
P/B			No data were available for this parameter.
NRPK2			
Biomass	5.85 t/km^2		Based on an estimated Catch-per-unit-effort (CPUE) of six northern pike per unit of sampling gear (C. Davis, ASRD, Personal communication). Density was estimated with the following equation CPUE = 0.3438*(density)+1.3773 (Davis, ASRD, unpublished data). Average fish weight used to calculate biomass was 4500 g (assumed that historic weights would have been 8-10 lbs).
P/B	0.15-0.27 year^{-1}	Randall and Minns 2000; Jaegar 2006; www.fishbase.org.	Annual mortality estimate from catch-curve analysis done with FAST 2.0 software (Slipke and Maceina 2001) using Lac la Biche data for 2003 and 2005 (FWMIS database).
Q/B	2.48-8.40 year^{-1}	Raat 1990; Helkinheimo and Korhonen 1996; Jaegar 2006; Empirical equation 17 from Christensen et al. 2008.	

YLPR1			
P/B	3.80-6.14 year^{-1}	Jaegar 2006	
YPLR2			
P/B	0.4 year^{-1}	Jaegar 2006	
YLPR3			
Biomass	0.075 t/km^2		Estimated density of 5 yellow perch/ha based on hydroacoustics assessments of Lac la Biche in 2006, 2007 (Milne 2007, Milne 2008) and a local average fish weight of 150 g for large yellow perch in 2009 (FWMIS database).
P/B	0.40-0.50 year^{-1}	Randall and Minns 2000; Jaegar 2006; www.fishbase.org.	Annual mortality estimate from catch-curve analysis done with FAST 2.0 software (Slipke and Maceina 2001) using Lac la Biche data for 2003 and 2005 (FWMIS database).
Q/B	3.80-9.23 year^{-1}	Bajer et al. 2003; Jaegar 2006; Empirical equation 17 from Christensen et al. 2008.	
CISC1			
P/B			No data were available for this parameter.
CISC2			
Biomass			No data were available for this parameter.
P/B	0.35-1.71 year^{-1}	Randall and Minns 2000; Jaegar 2006; www.fishbase.org.	Annual mortality estimate from catch-curve analysis done with FAST 2.0 software (Slipke and Maceina 2001) using Lac la Biche data for 2003 and 2005 (FWMIS database).

Q/B	6.42-12.84 year^{-1}	Jaegar 2006; Empirical equation 17 from Christensen et al. 2008	
LKWH1			
P/B			No data were available for this parameter.
LKWH2			
Biomass	9.0- 15.3 t/km^2		Lowest density calculated from 2007 Winefred Lake FWIN CPUE for LKWH >260 mm TL (FWMIS database). Density was estimated using the mean Winefred Lake CPUE of 3.24 and the regression equation Density = CPUE/0.1216 generated from 2006, 2007 hydroacoustics data for Lac la Biche. Winefred Lake was chosen as the model for Lac la Biche because it is representative of a lake with only low pressure aboriginal harvest for lake whitefish (C. Davis, ASRD, personal communication). The upper estimate reflects the estimated biomass given an adult density of 75 fish/ha[1] as observed for Pigeon Lake (Cooper and Buchwald, ASRD, unpublished data). An average weight of 1500 g used in biomass calculations represents the average weight of lake whitefish historically harvested (HBCA,PAM,B.115/e/1,fo.3d as cited in McCullough and Maccagno 1991), reduced slightly to accomodate the smaller fish sizes included in this mulstistanza group.

P/B	0.20-0.458 year^{-1}	Randall and Minns 2000; Jaegar 2006; www.fishbase.org.	Annual mortality estimate from catch-curve analysis done with FAST 2.0 software (Slipke and Maceina 2001) using Touchwood Lake commercial fishing data from 2003, 2004 for age 6 to 13 year fish (FWMIS database). To estimate P/B for Lac la Biche, the harvest mortality was calculated and subtracted from the total mortality estimate to get an estimate of natural mortality according to the equation Z=F+M. Commercial fishing mortality for Lac la Biche was calculated for 2003, 2005 (FWMIS database) and added to natural mortality to estimate Z.
Q/B	2.80-9.16 year^{-1}	Cox and Kitchell 2004; Madenjian et al. 2008; Empirical equation from Christensen et al. 2008	
BURB1			
P/B			No data were available for this parameter.
BURB2			
Biomass	0.03-0.885 t/km^2	Davis 1997; Schram et al. 2006	An average burbot weight of 2500 g was used in biomass calculations. This values represents the average all individuals captured during fieldwork in 2005 and by the commercial fishery in 2006.

P/B	0.17-0.43 year^{-1}	Randall and Minns 2000; Jaegar 2006; Schram et al. 2006; www.fishbase.org	
Q/B	2.5-6.72 year^{-1}	Paakkonen and Marjomaki 2000; Cox and Kitchell 2004; Jaegar 2006; Empirical equation from Christensen et al. 2008.	
Suckers			
Biomass	2.15-2.56 t/km^2	Kelso 1988	An initial density estimate of 25 white suckers/ha[1] was calculated from the ratio of the average lake whitefish CPUE to white sucker CPUE from 2003 and 2005 index netting results (FWMIS database). The ratio was multiplied by the density estimate for LKWH2 to generate a density for suckers. An average sucker weight of 1025 g was calculated for Lac la Biche using data from 2005 (FWMIS database).
P/B	0.17-0.38 year^{-1}	Kelso 1988; Randall and Minns 2000; Jaegar 2006; www.fishbase.org	
Q/B	3.65-7.73 year^{-1}	Jaegar 2006; Empirical equation 17 from Christensen et al. 2008	

Stickle.			
Biomass			Estimated by Ecopath
P/B	0.37-2.73 year^{-1}	Randall and Minns 2000; Jaegar 2006; www.fishbase.org	The value of 0.37 year^{-1} reported by Jaegar (2006) for Oneida Lake and was used to represent “all minnow-like fish” including darters, log-perch, and sculpins.
Q/B	3.74-13.12 year^{-1}	Jaegar 2006; Empirical equation 17 from Christensen et al. 2008	The value of 3.74 year^{-1} reported by Jaegar (2006) for Oneida Lake and was used to represent “all minnow-like fish” including darters, log-perch, and sculpins.
Small Fish			
Biomass			Estimated by Ecopath
P/B	0.37-1.89 year^{-1}	Randall and Minns 2000; Jaegar 2006	A value of 1.71 year^{-1} reported by Jaegar (2006) represents emerald shiners and golden shiners in Oneida Lake and the Bay of Quinte, while a value of 1.35 year^{-1} was reported for trout perch.
Q/B	3.74-6.33 year^{-1}	Cox and Kitchell 2004; Jaegar 2006	An average value of 6.38 year^{-1} reported by Jaegar (2006) represents emerald shiners and golden shiners in Oneida Lake and the Bay of Quinte, while an average value of 5.56 year^{-1} was reported for trout perch.

DCCO			
Biomass	0.021 t/km^2	A. McGregor, ASRD, unpublished data	Calculated using an assumption of 500 nests in the pre-european contact period and the ratio of breeding:non-breeding adults/nests calculated for Lac la Biche in 2005. Average adult bird weight was 2015 g and average young-of the-year weight was 1623 g. Cormorant biomass was entered as the combined biomass of adult and young-of-the-year birds.
P/B	0.52-0.78 year^{-1}	Jaegar 2006; A. McGregor, ASRD, unpublished data	Calculated as the total weight of all fledglings divided by the total weight of all nesting and non-nesting adults birds for 2003-2005.
Q/B	72.90-85.80 years^{-1}	Jaegar 2006; A. McGregor, ASRD, unpublished data	Calculated by dividing the total consumption (kg/yr) of adult birds by the total biomass of adult birds (kg). The total consumption by adult birds was calculated by multiplying the average adult bird weight by the lower range of the estimate of adult daily consumption (20-25% of body weight per day (Dunn, 1975)) and multiplying this daily consumption rate by 365 days.
AWPE			
Biomass	0.005 t/km^2	A. McGregor, ASRD, unpublished data	Calculated using an assumption of 100 nests in the pre-european contact period and the ratio of breeding:non-breeding adults/nests calculated for Lac la Biche in 2005. Average adult bird weight was 4519 g and average young-of the-year weight was 3378 g. Pelican biomass was entered as the combined biomass of adult and young-of-the-year birds.

P/B	0.2 year^{-1}	A. McGregor, ASRD, unpublished data	Calculated as the total weight of all fledglings (assumed fledgling weight of 3.5 kg) divided by the total weight of all breeding birds. This values does not include the weight of non-breeding adult birds as no estimate of this number was available.
Q/B	110 year^{-1}	A. McGregor, ASRD, unpublished data	Calculated by dividing the total consumption (kg/yr) of adult birds by the total biomass of adult birds (kg). The total consumption by adult birds was calculated by multiplying the average adult bird weight by the middle of the range of estimates of adult daily consumption (20-40% of body weight per day (Hall 1925)) and multiplying this daily consumption rate by 365 days.
Pisc. Birds			
Biomass	0.006 t/km^2	C. Found, ASRD, unpublished data	Biomass was estimated by multiplying the average number of each taxa observed during waterbird surveys in 2003 and 2005 by the average bird weight for that taxa then summing the weights for all species.
P/B	0.25 year^{-1}	Moreau et al. 1993	
Q/B	58 year^{-1}	Moreau et al. 1993	

Non-P. Birds			
Biomass	0.014 t/km^2	C. Found, ASRD, unpublished data	Biomass was estimated by multiplying the average number of each taxa observed during waterbird surveys in 2003 and 2005 by the average bird weight for that taxa then summing the weights for all species.
P/B	0.25 year^{-1}	Moreau et al. 1993	
Q/B	58 year^{-1}	Moreau et al. 1993	
Chiro. & Dip.			
Biomass	44.24 t/km^2	Pinsent 1967	Calculated as the proportion of chironomids present in benthic samples from Lac la Biche in 1965 and 1966, relative to the total average biomass (t/km^2, wet wt.).
P/B	4.97-18.5 year^{-1}	Graham and Burns 1983; Jorgensen et al. 1991; Jaegar 2006	
Q/B	62.4-69.3 year^{-1}	Jaegar 2006	
Amphi.			
Biomass	0.99 t/km^2	Pinsent 1967	Calculated as the proportion of amphipods present in benthic samples from Lac la Biche in 1965 and 1966, relative to the total average biomass (t/km^2, wet wt.).

P/B	2.14-8.76 $year^{-1}$	Jorgensen et al. 1991; Mistri and Ross 1999; Jaegar 2006	Average values from Jorgensen et al. (1991) were given as a range from 0.008-0.043 day^{-1}. An average estimate of 0.024 day^{-1} was multiplied by 365 days to get 8.76 $year^{-1}$. Additional estimates for *Gammarus pulex* and *Hyallela azteca* are included.
Q/B	30.2 $year^{-1}$	Jaegar 2006	
Mollusc & Gastro.			
Biomass	2.48 t/km^2	Pinsent 1967	Calculated as the proportion of pelecypoda present in benthic samples from Lac la Biche in 1965 and 1966, relative to the total average biomass (t/km^2, wet wt.).
P/B	0.2-5.8 $year^{-1}$	Picken 1979; Jorgensen et al. 1991; Hall et al. 2001; Jaegar 2006	Average values from Jorgensen et al. (1991) were given as a range from 0.005-0.02 day^{-1}. An average estimate of 0.013 day^{-1} was multiplied by 365 days to get 0.3 $year^{-1}$. Additional estimates for *Sphaerium corneum* and *Psidium casertanum* (shell-free) are also included.
Q/B	24.4 $year^{-1}$	Jaegar 2006	
Inverts.			
Biomass	1.99 t/km^2	Pinsent 1967	Calculated as the proportion of other invertebrates present in benthic samples from Lac la Biche in 1965 and 1966, relative to the total average biomass (t/km^2, wet wt.).

P/B	2.2-5.6 year^{-1}	Jaegar 2006	Values range from 2.2 year^{-1} for leeches to 5.6 year^{-1} for 'other insects'.
Q/B	31.8-36.10 year^{-1}	Jaegar 2006	
Litt. Zoopl.			
Biomass			Estimated by Ecopath
P/B	20-55 year^{-1}	Jorgensen et al. 1991; Cox and Kitchell 2004; Angelini and Agostinho 2005; Jaegar 2006	Range includes estimates for both eutrophic and mesotrophic waterbodies
Q/B	82-250 year^{-1}	Cox and Kitchell 2004; Angelini and Agostinho 2005; Jaegar 2006	
Pel. Zoopl.			
Biomass			Estimated by Ecopath
P/B	20-55 year^{-1}	Jorgensen et al. 1991; Cox and Kitchell 2004; Angelini and Agostinho 2005; Jaegar 2006	Range includes estimates for both eutrophic and mesotrophic waterbodies
Q/B	82-250 year^{-1}	Cox and Kitchell 2004; Angelini and Agostinho 2005; Jaegar 2006	

Cyano.			
Biomass	2.18 t/km^2		Entered as one-half of the biomass estimated for Lac la Biche using 2003 and 2004 data (D.W. Schindler, University of Alberta, unpublished data).
P/B	87-176 year^{-1}	Jaegar 2006	
Phyto.			
Biomass	3.179 t/km2		Entered as one-half of the biomass estimated for Lac la Biche using 2003 and 2004 data (D.W. Schindler, University of Alberta, unpublished data).
P/B	87-250 year^{-1}	Angelini and Agostinho 2005; Jaegar 2006	
SAV			
Biomass			Estimated by Ecopath
P/B	8.8-120	Cox and Kitchell 2004; Angelini and Agostinho 2005; Jaegar 2006; Fetahi and Mengistou 2007	Includes representative values for epiphytes, macrophytes and periphytes

Table B-2. Range of diet proportions (by biomass) from field data and literature values for each functional group in the model.

Prey/Predator	WALL1	WALL2	WALL3	NRPK1	NRPK2
WALL1					
WALL2					0.000-0.041
WALL3					
NRPK1					0.000-0.033
NRPK2					
YLPR1	Present	0.035-0.489	0.000-0.038	0.000-0.294	0.001-0.003
YPLR2		0.000-0.673	0.000-0.707		0.000-0.048
YLPR3		0.000-0.034	0.000-0.186		0.000-0.072
CISC1		0.000-0.040	0.000-0.174		0.000-0.036
CISC2			0.000-0.516		0.548-0.719
LKWH1		0.000-0.088	0.000-0.645	0.000-0.706	0.024-0.138
LKWH2					0.000-0.020
BURB1			0.000-0.273		0.000-0.148
BURB2					0.000-0.033
Suckers					0.004-0.093
Stickle.	Present	0.139-0.511	0.000-0.038	0.000-0.488	0.000-0.005
Small Fish	Present	0.000-0.006	0.000-0.082		0.000-0.006
DCCO					
AWPE					
Pisc. Birds					
Non-P. Birds					0.000-0.003
Chiro. & Dip.	Present	0.000-0.443	0.000-0.001		
Amphi.	Present		0.000-0.000		0.000-0.000
Mollusc & Gastro.					0.000-0.001
Inverts.	Present		0.000-0.001	0.000-0.071	
Zoopl.	Present				
Cyano.					
Phyto.					
SAV					
Detritus					
Import					

Table B-2. Continued.

Prey/Predator	YLPR1	YPLR2	YLPR3	CISC1	CISC2
WALL1					
WALL2					
WALL3					
NRPK1					
NRPK2					
YLPR1		0.000-0.055	0.043-0.123		
YPLR2			0.051-0.236		
YLPR3					
CISC1		0.000-0.162	0.000-0.364		
CISC2					
LKWH1					
LKWH2					
BURB1					
BURB2					
Suckers					
Stickle.		0.000-0.250	0.026-0.659		
Small Fish			0.000-0.064		
DCCO					
AWPE					
Pisc. Birds					
Non-P. Birds					
Chiro. & Dip.	0.063-0.699	0.438-0.936	0.018-0.616	0.000-0.975	0.376-0.539
Amphi.	0.000-0.072	0.000-0.312	0.003-0.014	0.000-0.009	0.001-0.199
Mollusc & Gastro.		0.000-0.002	0.000-0.002		
Inverts.	0.000-0.299	0.000-0.065	0.005-0.063		0.000-0.063
Zoopl.	0.016-0.901	0.000-0.124		0.016-1.00	0.199-0.623
Cyano.					
Phyto.					
SAV					
Detritus					
Import					

Table B-2. Continued.

Prey/Predator	LKWH1	LKWH2	BURB1	BURB2	Suckers
WALL1					
WALL2					
WALL3					
NRPK1					
NRPK2					
YLPR1			0.000-0.294	0.008-0.022	
YPLR2			0.000-0.392	0.000-0.036	
YLPR3				0.000-0.056	
CISC1				0.040-0.635	
CISC2				0.000-0.618	
LKWH1				0.042-0.182	
LKWH2					
BURB1				0.000-0.031	
BURB2					
Suckers				0.000-0.144	
Stickle.		0.000-0.000	0.101-0.451	0.023-0.161	
Small Fish				0.000-0.000	
DCCO					
AWPE					
Pisc. Birds					
Non-P. Birds					
Chiro. & Dip.	0.242-0.839	0.212-0.898	0.000-0.203	0.000-0.000	0.9963
Amphi.	0.000-0.024	0.006-0.429	0.000-0.479	0.000-0.001	
Mollusc & Gastro.	0.005-0.019	0.096-0.351	0.009-0.019	0.000-0.000	0.0004
Inverts.	0.000-0.732	0.000-0.047	0.000-0.051	0.000-0.000	0.0022
Zoopl.	0.000-0.156				0.0011
Cyano.					
Phyto.					
SAV					
Detritus					
Import					

Table B-2. Continued.

Prey/Predator	Stickle.	Small Fish	DCCO	AWPE	Pisc. Birds
WALL1					
WALL2			0.000-0.045	0.000-0.220	
WALL3					
NRPK1			0.031-0.056	0.000-0.01	
NRPK2					
YLPR1			0.024-0.547	0.000-0.244	0.061-0.105
YPLR2			0.007-0.580	0.000-0.244	0.061-0.105
YLPR3			0.003-0.245	0.000-0.244	
CISC1			0.000-0.220	0.000-0.070	
CISC2			0.200-0.333	0.000-0.070	
LKWH1			0.000-0.014	0.1	
LKWH2			0.000-0.009	0.1	
BURB1			0.002-0.049	0.010-0.044	
BURB2			0.000-0.002	0.010-0.044	
Suckers			0.011-0.126	0.020-0.410	
Stickle.			0.006-0.111	0.073-0.961	0.165-0.285
Small Fish			0.009-0.040	0.000-0.585	0.165-0.285
DCCO					
AWPE					
Pisc. Birds					
Non-P. Birds					
Chiro. & Dip.	0.000-0.503	0.000-1.00			
Amphi.	0.000-0.067	0.000-1.00			
Mollusc & Gastro.					
Inverts.	0.000-0.387	0.000-0.006			0.050-0.410
Zoopl.	0.043-1.00	0.000-0.023			
Cyano.					
Phyto.					
SAV					0.000-0.040
Detritus					
Import			0.000-0.027		

Table B-2. Continued.

Prey/Predator	Non-P. Birds	Chiro. & Dip.	Amphi.	Mollusc & Gastro.
WALL1				
WALL2				
WALL3				
NRPK1				
NRPK2				
YLPR1	0.000-0.013			
YPLR2				
YLPR3				
CISC1				
CISC2				
LKWH1				
LKWH2				
BURB1				
BURB2				
Suckers				
Stickle.	0.000-0.018			
Small Fish	0.000-0.018			
DCCO				
AWPE				
Pisc. Birds				
Non-P. Birds				
Chiro. & Dip.	0.02-0.664		0.000-0.072	
Amphi.	0.009-0.950			
Mollusc & Gastro.	0.030-0.285			
Inverts.	0.010-0.686		0.000-0.072	
Zoopl.	0.036-0.570	0.000-0.000	0.000-0.775	
Cyano.				0.000-?
Phyto.		0.043-0.642	0.000-0.286	0.000-?
SAV	0.023-0.855	0.000-0.400	0.036-0.287	0.5-1.0
Detritus		0.100-0.900	0.225-0.800	0.000-0.50
Import		0.050-0.800		

Table B-2. Continued.

Prey/Predator	Inverts.	Zoopl.
WALL1		
WALL2		
WALL3		
NRPK1		
NRPK2		
YLPR1		
YPLR2		
YLPR3		
CISC1		
CISC2		
LKWH1		
LKWH2		
BURB1		
BURB2		
Suckers		
Stickle.		
Small Fish		
DCCO		
AWPE		
Pisc. Birds		
Non-P. Birds		
Chiro. & Dip.		
Amphi.		
Mollusc & Gastro.		
Inverts.	0.000-0.100	
Zoopl.	0.000-0.950	0.000-0.175
Cyano.		
Phyto.	0.000-0.150	0.825-1.000
SAV	0.039-0.980	
Detritus	0.011-0.800	
Import		

Table B-3. References and notes pertaining to the range of diet composition values used to inform model parameterization for each functional group.

Functional Group	Source
WALL1	Mathias and Li 1982; Meerbeek et al. 2002
DCCO	Earle 2007; Marois and Hegerat, ASRD, unpublished data
AWPE	Hall 1925; Findholt and Anderson 1995; Somers 2006
Pisc. Birds	Storer and Nuechterlein 1992; Mallory and Metz 1999; Stout and Nuechterlein 1999; Titman 1999; Evers et al. 2010
Non-P. Birds	Gauthier 1993; Austin and Miller 1995; Eadie et al. 1995; Johnson 1995; Dubowy 1996; Brown and Fredrickson 1997; Leschack et al. 1997; Austin et al. 1998; Hohman and Eberhardt 1998; Cullen et al. 1999; Mowbray 1999; Eadie et al. 2000; Brisbin et al. 2002; Brua 2002; Drilling et al. 2002; Mowbray 2002; Rohwer et al. 2002; Woodwin and Michot 2002
Chiro. & Dip.	Mackey 1979; Ward and Williams 1986; Pennak 1989; Voshell 2002; Henriques-Oliveira et al. 2003; Tarkowska-Kukuryk and Mieczan 2008
Amphi.	Pennak 1989; MacNeil 1997; Summers et al. 1997; Kay 1999; Voshell 2002
Mollusc & Gastro.	Pennak 1989; Kay 1999; Voshell 2002; Lance et al. 2006
Inverts.	Cummins 1973; Pennak 1989; Kay 1999; Voshell 2002
Zoopl.	Pennak 1989; Kay 1999

*Diets of all other fish groups available for 2005 to 2008 from McGregor, ASRD, unpublished data.

Table B-4. Diet matrix used in the 1800 model for Lac la Biche showing balanced diet compositions (by biomass) for all functional groups. The names down the left side refer to the functional group of the prey. Numbers across the top refer to the predator group, identified by the numbers down the left edge of the table.

	Prey \ predator	1	2	3	4	5	6	7	8
1	WALL1			<0.0001			<0.0001		
2	WALL2				0.005	0.005			
3	WALL3								
4	NRPK1			0.0007		0.004			
5	NRPK2								
6	YLPR1	0.311	0.25	0.155	0.2	0.017	<0.0001	0.05	0.1
7	YPLR2		0.21	0.35	0.15	0.02			0.02
8	YLPR3		0.009	0.055		0.03			
9	CISC1		0.015	0.0275	0.2	0.05			0.01
10	CISC2			0.0042	0.005	0.4			
11	LKWH1		0.023	0.104	0.2	0.12			0.001
12	LKWH2					0.05			
13	BURB1			0.0038		0.01			
14	BURB2					0.005			
15	Suckers			0.0034	0.1	0.137			
16	Stickle.	0.244	0.25	0.11		0.012		0.075	0.2
17	Small Fish		0.003	0.1	0.035	0.02		0.028	0.09
18	DCCO								
19	AWPE								
20	Pisc. Birds								
21	Non-P. Birds								
22	Chiro. & Dip.	0.375	0.24	0.06	0.0005		0.6	0.5	0.47
23	Amphi.	0.03		0.0004			0.06	0.17	0.005
24	Mollusc & Gastro.	0.01						0.012	0.001
25	Inverts.	0.02		0.026	0.1	0.12	0.27	0.16	0.098
26	Litt. Zoopl.	0.005			0.004		0.06	0.005	0.005
27	Pel. Zoopl.	0.005			0.0005		0.01		
28	Cyano.								
29	Phyto.								
30	SAV								
31	Detritus								
32	Import								

Table B-4. Continued.

	Prey \ predator	9	10	11	12	13	14	15	16
1	WALL1	<0.0001	<0.0001						
2	WALL2						0.001		
3	WALL3								
4	NRPK1						0.001		
5	NRPK2								
6	YLPR1	<0.0001	<0.0001			0.23	0.01		
7	YPLR2						0.03		
8	YLPR3						0.05		
9	CISC1	<0.0001	<0.0001				0.22		
10	CISC2						0.3		
11	LKWH1	<0.0001	<0.0001				0.1		
12	LKWH2						0.05		
13	BURB1	<0.0001	<0.0001				0.009		
14	BURB2						0.001		
15	Suckers						0.17		
16	Stickle.					0.35	0.034		
17	Small Fish						0.02		
18	DCCO								
19	AWPE								
20	Pisc. Birds								
21	Non-P. Birds								
22	Chiro. & Dip.	0.688	0.539	0.6	0.45	0.005	0.0007	0.98	0.503
23	Amphi.	0.01	0.199	0.042	0.34	0.35	0.002		0.067
24	Mollusc & Gastro.	0.001		0.03	0.2	0.01	0.0007	0.001	
25	Inverts.	0.001	0.063	0.278	0.01	0.054	0.0006	0.005	0.3
26	Litt. Zoopl.	0.1	0.05	0.04					0.1
27	Pel. Zoopl.	0.2	0.149	0.01		0.001		0.004	0.03
28	Cyano.								
29	Phyto.								
30	SAV								
31	Detritus							0.01	
32	Import								

Table B-4. Continued.

	Prey \ predator	17	18	19	20	21	22	23	24
1	WALL1	<0.0001							
2	WALL2		0.022	0.006					
3	WALL3								
4	NRPK1		0.002	0.013		<0.0001			
5	NRPK2								
6	YLPR1		0.017	0.008	0.018	0.0005			
7	YPLR2		0.025	0.004	0.0002				
8	YLPR3		0.055	0.001					
9	CISC1		0.002	0.001					
10	CISC2		0.054	0.001					
11	LKWH1		0.001						
12	LKWH2								
13	BURB1		0.011	0.006					
14	BURB2								
15	Suckers		0.028	0.051					
16	Stickle.		0.001	0.001	0.025	0.0006			
17	Small Fish		0.004	0.015	0.025	0.0006			
18	DCCO								
19	AWPE								
20	Pisc. Birds								
21	Non-P. Birds								
22	Chiro. & Dip.	0.6				0.02			
23	Amphi.	0.36				0.02			
24	Mollusc & Gastro.					0.015			
25	Inverts.	0.01			0.0016	0.02			
26	Litt. Zoopl.	0.02				0.0006		0.05	
27	Pel. Zoopl.	0.01							
28	Cyano.								0.0001
29	Phyto.					0.0007	0.1	0.181	0.15
30	SAV				0.0012	0.023	0.05	0.287	0.7
31	Detritus						0.85	0.482	0.15
32	Import		0.778	0.893	0.929	0.899			

Table B-4. Continued.

	Prey \ predator	25	26	27
1	WALL1			
2	WALL2			
3	WALL3			
4	NRPK1			
5	NRPK2			
6	YLPR1			
7	YPLR2			
8	YLPR3			
9	CISC1			
10	CISC2			
11	LKWH1			
12	LKWH2			
13	BURB1			
14	BURB2			
15	Suckers			
16	Stickle.			
17	Small Fish			
18	DCCO			
19	AWPE			
20	Pisc. Birds			
21	Non-P. Birds			
22	Chiro. & Dip.			
23	Amphi.			
24	Mollusc & Gastro.	0.005		
25	Inverts.	0.005		
26	Litt. Zoopl.	0.01		
27	Pel. Zoopl.			0.01
28	Cyano.			0.15
29	Phyto.		0.25	0.84
30	SAV	0.65	0.55	
31	Detritus	0.33	0.2	
32	Import			

Table B-5. Diet matrix showing the value, or range in values, used in the eight-1900 models for Lac la Biche showing diet compositions (by biomass) for all functional groups. The names down the left side refer to the functional group of the prey. Numbers across the top refer to the predator group, identified by the numbers down the left edge of the table.

	Prey \ predator	1	2	3	4	5	6
1	WALL1			<0.0001		<0.0001	<0.0001
2	WALL2				0.005	0.004	
3	WALL3						
4	NRPK1			0.0006		0.003	
5	NRPK2						
6	YLPR1	0.357	0.270	0.159	0.228	0.019	<0.0001
7	YPLR2		0.240	0.381	0.176	0.024	
8	YLPR3		0.014	0.078		0.047	
9	CISC1		0.015	0.027	0.219	0.053	
10	CISC2			0.005	0.005	0.400-0.441	
11	LKWH1		0.018	0.08	0.141	0.097-0.139	
12	LKWH2					0.019	
13	BURB1			0.0038		0.011	
14	BURB2					0.005	
15	Suckers			0.003	0.093	0.131	
16	Stickle.	0.205	0.214	0.091		0.011	
17	Small Fish		0.003	0.094	0.035	0.02	
18	DCCO						
19	AWPE						
20	Pisc. Birds						
21	Non-P. Birds						
22	Chiro. & Dip.	0.364	0.226	0.054	0.0005		0.6
23	Amphi.	0.034		0.0004			0.069
24	Mollusc & Gastro.	0.011					
25	Inverts.	0.019		0.023	0.093	0.114	0.262
26	Litt. Zoopl.	0.005			0.004		0.059
27	Pel. Zoopl.	0.005			0.0005		0.01
28	Cyano.						
29	Phyto.						
30	SAV						
31	Detritus						
32	Import						

Table B-5. Continued.

	Prey \ predator	7	8	9	10	11
1	WALL1			<0.0001	<0.0001	
2	WALL2					
3	WALL3					
4	NRPK1					
5	NRPK2					
6	YLPR1	0.056-0.064	0.114-0.148	<0.0001	<0.0001	
7	YPLR2		0.024-0.034			
8	YLPR3					
9	CISC1		0.011	<0.0001	<0.0001	
10	CISC2					
11	LKWH1		0.0008	<0.0001	<0.0001	
12	LKWH2					
13	BURB1			<0.0001	<0.0001	
14	BURB2					
15	Suckers					
16	Stickle.	0.035-0.067	0.100-0.181			
17	Small Fish	0.02-0.028	0.073-0.093			
18	DCCO					
19	AWPE					
20	Pisc. Birds					
21	Non-P. Birds					
22	Chiro. & Dip.	0.490-0.530	0.469-0.529	0.694-0.767	0.529-0.682	0.599
23	Amphi.	0.188	0.0057	0.012	0.160-0.223	0.05
24	Mollusc & Gastro.	0.013	0.0011	0.001		0.035
25	Inverts.	0.153	0.0951	0.001	0.06	0.268
26	Litt. Zoopl.	0.0048	0.0049	0.090-0.099	0.040-0.048	0.039
27	Pel. Zoopl.			0.120-0.193	0.050-0.140	0.009
28	Cyano.					
29	Phyto.					
30	SAV					
31	Detritus					
32	Import					

Table B-5. Continued.

	Prey \ predator	12	13	14	15	16	17
1	WALL1						<0.0001
2	WALL2			0.001			
3	WALL3						
4	NRPK1			0.001			
5	NRPK2						
6	YLPR1		0.255	0.011			
7	YPLR2			0.035			
8	YLPR3			0.077			
9	CISC1			0.2			
10	CISC2			0.325			
11	LKWH1			0.108			
12	LKWH2			0.018			
13	BURB1			0.01			
14	BURB2			0.001			
15	Suckers			0.159			
16	Stickle.		0.29	0.03			
17	Small Fish			0.02			
18	DCCO						
19	AWPE						
20	Pisc. Birds						
21	Non-P. Birds						
22	Chiro. & Dip.	0.425	0.005	0.0005	0.98	0.504	0.564
23	Amphi.	0.357	0.389	0.002		0.079	0.4
24	Mollusc & Gastro.	0.209	0.011	0.0005	0.0012		
25	Inverts.	0.009	0.049	0.0005	0.0048	0.29	0.009
26	Litt. Zoopl.					0.098	0.018
27	Pel. Zoopl.		0.001		0.0038	0.029	0.009
28	Cyano.						
29	Phyto.						
30	SAV						
31	Detritus				0.01		
32	Import						

Table B-5. Continued.

	Prey \ predator	18	19	20	21	22
1	WALL1					
2	WALL2	0.007-0.019	0.005-0.006			
3	WALL3					
4	NRPK1	0.0016	0.013		<0.0001	
5	NRPK2					
6	YLPR1	0.016	0.009	0.02	0.0006	
7	YPLR2	0.025-0.037	0.005-0.006	0.0002		
8	YLPR3	0.052-0.072	0.001			
9	CISC1	0.002-0.015	0.001			
10	CISC2	0.05	0.001			
11	LKWH1	0.0007				
12	LKWH2					
13	BURB1	0.008-0.010	0.006			
14	BURB2					
15	Suckers	0.022-0.032	0.049			
16	Stickle.	0.0007	0.001	0.022	0.0005	
17	Small Fish	0.0033	0.015	0.025	0.0006	
18	DCCO					
19	AWPE					
20	Pisc. Birds					
21	Non-P. Birds					
22	Chiro. & Dip.				0.019	
23	Amphi.				0.022	
24	Mollusc & Gastro.				0.016	
25	Inverts.			0.002	0.019	
26	Litt. Zoopl.				0.0006	
27	Pel. Zoopl.					
28	Cyano.					
29	Phyto.				0.0007	0.1
30	SAV			0.001	0.022	0.05
31	Detritus					0.85
32	Import	0.778	0.893	0.929	0.899	

Table B-5. Continued.

	Prey \ predator	23	24	25	26	27
1	WALL1					
2	WALL2					
3	WALL3					
4	NRPK1					
5	NRPK2					
6	YLPR1					
7	YPLR2					
8	YLPR3					
9	CISC1					
10	CISC2					
11	LKWH1					
12	LKWH2					
13	BURB1					
14	BURB2					
15	Suckers					
16	Stickle.					
17	Small Fish					
18	DCCO					
19	AWPE					
20	Pisc. Birds					
21	Non-P. Birds					
22	Chiro. & Dip.					
23	Amphi.					
24	Mollusc & Gastro.			0.005		
25	Inverts.			0.005		
26	Litt. Zoopl.	0.05		0.01		
27	Pel. Zoopl.					0.01
28	Cyano.		0.0001			0.15
29	Phyto.	0.181	0.15		0.25	0.84
30	SAV	0.287	0.7	0.65	0.55	
31	Detritus	0.482	0.15	0.33	0.2	
32	Import					

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Chapter 4 - Using ecosystem models for a large lake ecosystem to examine dynamic relationships between walleye, cormorants, and yellow perch.

Summary

Increased population sizes of double-crested cormorants (*Phalacrocorax auritus*) and small-bodied yellow perch (*Perca flavescens*) have occurred at Lac la Biche, Alberta, Canada since fisheries collapsed the walleye (*Sander vitreus*) population. A walleye restoration program was introduced in 2005 but uncertainty around the ecosystem's response (global stability or alternate stable state) to management masks the interpretability of program success. This study used forty variations of Ecopath with Ecosim models representing ecosystem conditions over 200 years to test the potential for multiple attractors in a large lake ecosystem. Results suggest that alternate stable states, defined by walleye-dominated and cormorant-dominated equilibriums, existed in historical models (1800, 1900) while contemporary models (1965, 2005) had a single cormorant-dominated attractor. ASSs were triggered by smaller perturbations in 1900 than in 1800, and model responses were more intense in 1900, suggesting a decline in system resilience between model periods. Total prey biomass consumed by walleye was up to four times greater than the biomass consumed by cormorants in historical models, but dropped to 10% of cormorant consumption in 2005 models. Differential size-selection pressures of cormorants and walleye on yellow perch provide a strong feedback that stabilizes each state. These results provide important theoretical support for alternate stable states as well as practical insights for restoration of large lake ecosystems affected by human-induced overharvest of top-level fish predators.

Introduction

Over most of the last 50 years the lake ecosystem of Lac la Biche, Alberta, Canada has existed in a state of extremely low walleye (*Sander vitreus*) biomas resulting from centuries of human overharvest. In the last 25 years, there has been an exponential (McGregor, *unpublished*) increase in the number of fish-eating birds, dominated by double-crested cormorants (cormorant; *Phalacrocorax auritus*), and a noticeable change in the size and abundance of forage fish, namely yellow perch (perch; *Perca flavescens*). The result of these, among other recent changes to the lake ecosystem (for a brief review see Schindler et al. 2008), has been the development of a system which is unable to satisfy social demands for harvestable-sized walleye as well as other goods and services. In 2002, local concerns were recognized through the posing of the Fisheries (Alberta) Amendment Act, a private members bill outlining the need for active management of piscivorous water birds and fish populations (Province of Alberta, Statutes of Alberta, 2002, Chapter 14). In 2005, Alberta Environment and Sustainable Resource Development responded to these concerns by introducing a long-term lake restoration project focused on commercial and recreational fishery reductions, walleye stocking, and cormorant control as suitable methods for recovering walleye in the lake and for improving the overall size structure of the fish community. Though management initiatives are underway, the potential for restoration to a walleye-dominated equilibrium remains unclear.

Restoration potential and approach require an understanding of how a system is likely to respond to a disturbance. There are three main conceptual models describing equilibrium dynamics of ecosystems that are generally applicable to disturbance and restoration ecology: continuum models (global stability), threshold models, and alternate stable states models (Hobbs and Suding 2009). Continuum models predict a system response that is smooth, continuous, proportional to the size of the disturbance, and has a single ecosystem configuration (ecosystem state or attractor) (Odum 1969). Threshold models describe system dynamics in which a relatively small change to a controlling variable causes a large shift in ecosystem state (Hobbs and Suding 2009). Alternate stable state (ASS) models (Scheffer et al. 2001, Scheffer 2009) describe a specific type of threshold model in which a critical level of a controlling variable is surpassed, resulting in a change in system feedbacks that alters the trajectory of the system's development. When resilience is low, a disturbance is more likely to trigger an alternate stable state.

A system exhibiting global stability is expected to recover to its pre-disturbance state along a predictable successional pathway that is steady, directional, and driven by strong stabilizing feedback mechanisms (Odum 1969). In such cases, restoration should proceed unassisted though management interventions can be used to initiate, assist, or speed up succession (Hobbs and Suding 2009). Restoring a system following a threshold shift can be far more challenging, especially given ASS dynamics. A characteristic of ASSs is that the trajectory leading to an alternate attractor is generally different from that required for recovery of the target state, a concept known as hysteresis (Suding et al. 2004). In such systems, management focused on affecting change in the factors or processes that caused the initial switch might be insufficient to achieve recovery, might not address the real problem, or more intensive effort might be required.

Ecosystems are complicated and the interactions of their components make their response to disturbance hard to predict. It is important, however, that we try to understand how a system responds to disturbance because there is risk in making assumptions. Active management of continuum dynamics can waste both time and resources, while a hands-off approach will be unsuccessful in restoring an ASS (Hobbs and Suding 2009). Thus, accurately characterizing ecosystem dynamics has important implications for restoration projects.

In this study, I focus on describing the dynamic relationships between walleye, perch, and cormorants at Lac la Biche to improve our understanding of the long-term restoration potential for walleye. I hypothesize that the historical walleye-dominated equilibrium and the contemporary cormorant-dominated equilibrium represent alternate attractors and that the transition between states is controlled by the dynamics of the yellow perch population. Specifically, I used a series of ecosystem models representing historical, contemporary and transitional ecosystem conditions to answer the following research questions:

1) Does Lac la Biche exhibit alternate stable states defined by the relative influence of walleye, yellow perch and cormorants?

2) What size and type of disturbance is required to trigger alternate stable state dynamics?

3) Can we restore the walleye-dominated equilibrium by stocking walleye and controlling cormorants?

4) Is there any difference in the relationships between walleye, perch, and cormorants in models with alternate stable states and models without?

Similar recent increases in cormorant populations in North America and Europe have been closely linked to changes in fish communities, specifically fewer large predators and increased forage fish (Johnson et al. 2002), making results of this research widely applicable.

Methods

Modeling Approach

The Lac la Biche ecosystem was modeled using Ecopath with Ecosim software (EwE) version 6.2.0.620 (Pauly et al. 2000, Christensen et al. 2008). The Ecopath model uses a series of linear equations to balance the energy gains and losses for each biological component of an ecosystem over a defined time period (usually one year). The equilibrium condition arising from this balance allows for the estimation of initial, static flows (energy or nutrients) between trophic levels, and it provides a means for estimating the relative importance of individual species/ecological guilds, or ecological processes (selective predation, targeted fisheries etc.) (Christensen et al. 2008). The master equation for production by each functional group can be expressed as:

Production = catches + predation mortality + biomass accumulation + net migration + other mortality (1)

This equation is more commonly expressed using the following parameters: biomass (B) ($t \cdot km^{-2}$), production/biomass (P/B) ($year^{-1}$), consumption/biomass (Q/B) ($year^{-1}$), and ecotrophic efficiency (EE) (the proportion of production that is utilized by the system for predation or export) (Christensen et al. 2008). If one of the four basic parameters (B, P/B, Q/B, EE) is not entered, Ecopath can estimate that parameter given the input of the following secondary parameters: fisheries catches (Y), net migration (M), biomass accumulation (BA), food assimilation (A), or diet composition (DC). Mass balance is achieved when the consumption by each functional group is balanced by the sum of their production, respiration, and estimates of unassimilated food. Model units were t/km^{-2} for biomasses and $t \cdot km^{-2}.year^{-1}$ (wet weight) for flows of organic matter, where t refers to a metric tonne.

The complementary dynamic model, Ecosim (Walters et al. 1997), uses a combination of differential equations for predicting changes in flow rates as functions of prey and predator abundances for each trophic link. Species that show strong trophic ontogeny in feeding and/or size-selective harvesting and vulnerability to predation, are modeled using monthly difference equations to predict changes in age and size structure (Walters et al. 2009). For a detailed description of the EwE software package see Christensen et al. (2008).

Model development

Forty Ecopath models were used to capture variability in ecosystem scenarios over the study period and to explore how different ecosystem configurations affected the system response to a disturbance. Models differed from one another in biomass, production/biomass, consumption/biomass, and diet composition, across ranges estimated using limited historical information. Walleye-dominated states were represented by twenty models of the "historical" ecosystem representing the years 1800 and 1900. Models from 1800 (n=10) depicted possible conditions prior to European settlement when the walleye population was assumed to be only lightly disturbed. Parameters for 1800 were compiled from scientific literature, historical sources, anecdotal and anthropological studies, expert opinion, and data from similar systems (Chapter 3). Models of 1900 (n=10) describe a range of ecosystem conditions expected after 100 years of subsistence harvest by the local aboriginal community, the fur trade post, and the Roman Catholic Mission, but prior to the development of a formal commercial fishing industry. To estimate values for 1900 I used Ecosim to subject a balanced 1800 model to a time series of 112 years of fisheries catch estimates and exported the biomass and diet composition predictions for use in the 1900 models (Chapters 2 and 3). Exports from the temporal simulation were used in the initial parameterization of the 1900 models, but to achieve mass-balance the remaining model parameters were altered within the range of values compiled for the 1800 models. A description of the modeled groups and the range of parameter values represented by the models are included in Appendix C (Tables C-1 to C-5). For a detailed description and justification of data sources and methodologies used in historical model development see Chapter 3.

Contemporary ecosystem variability was captured in twenty models representing two different system states: a cormorant-dominated state (2005) (n=12) and a transition state where both cormorants and walleye were present at extremely small biomasses (1965) (n=8). The transition models were parameterized following the same process used for the 1900 models. A balanced Ecopath model for 1900 was tuned to trends in biomass (t/km^{-2}) and fisheries catch ($t \cdot km^{-2} \cdot yr^{-1}$) estimates for the years between 1900 and 2009. Predictions of biomass and diet composition for 1960, 1965, and 1970 were exported from Ecosim and used to guide the initial parameterization of the transition model.

Where parameter changes were needed to achieve mass-balance, they were bounded (where possible) by the range of values used in other contemporary models (2005). Input parameters for the cormorant-dominated models (2005) are mainly from unpublished field data from Lac la Biche collected between 2003 and 2005, as well as estimates from biologists with knowledge of the lake. Where local data were not available, the model was parameterized using either data or literature values from other systems. Main data sources and estimation methods for the 2005 models are described in Appendix D. A description of the modeled groups and the range of parameter values represented by the contemporary models are included in Appendix C (Tables C-1 to C-5).

Hypothesis evaluation with Ecosim

Ecosim was used for assessing the possible existence of ASSs at Lac la Biche, and for describing the relationship between the size and nature of a disturbance and the intensity of the ASS response. Fishing represents a common disturbance directly influencing fish biomass in aquatic systems. Fishing disturbances were modeled by changing the Ecopath base fishing effort in each Ecosim scenario. All Ecosim scenarios were run following the same general procedure. First, I allowed the model to run for 15 years to ensure rate balance (no rapid change in biomasses) for the baseline state. At year 15, I changed the fishing effort for a single functional group (eg. cormorants or adult walleye) for a period of five years to cause a short duration disturbance in the system. After five years the fishing effort was returned to baseline. The model was run for an additional 80 years to see if the groups returned to baseline (continuum dynamics – global stability), showed cycling of the functional groups that was centered around baseline, or moved to an alternate state with no indication of a return to baseline (ASS – multiple attractors) (Figure 4-1). Continuum dynamics and cycling were both reported as a negative ASS result.

Assumptions about trophic control, i.e. top-down versus bottom-up control of predation rates, impact system dynamics by altering the interactions between predators and prey (Cury et al. 2000, Shannon et al. 2000). Trophic control is modeled in Ecosim through 'vulnerabilities' which describe the effect of an increase in the biomass of a predator on the predation mortality of its prey (Christensen et al. 2008). All scenarios were run using conservative vulnerabilities (v = 1.0 to 3.0) (Table 4-1) because large values are known to cause instability in models (Araujo et al. 2006, Christensen et al. 2008) and I wanted to be confident that an ASS response was triggered by the disturbance and not by model instability. A similar process was used by Feng et al. (2006) in an assessment of ASSs across a sample of 26 published Ecopath models.

Assessment of ASSs

In total, 640 theoretical scenarios were run to assess the existence of ASS under different assumptions of ecosystem conditions, disturbance levels, and trophic control. An outline of the scenarios can be found in Table 4-2, research question 1. For each scenario, fishing effort was increased to 10X the Ecopath baseline for walleye, cormorants, and yellow perch, and also to 100X for yellow perch. The presence (positive response) or absence (return to baseline or cycling around baseline) of an ASS was reported. For each era (1800, 1900, 1965, 2005) and each trophic control type, the number of models with at least one positive response was counted to give a frequency of occurrence of ASSs. The identity of the disturbance was not considered in this analysis so if one or all four disturbances caused a positive ASS response in a model it was treated as a single positive response.

ASS triggers – size and identity

Models exhibiting ASSs in the baseline assessment (10X effort increase for walleye or cormorants, 10X or 100X increase for yellow perch) were further tested to determine the smallest biomass disturbance required to trigger a transition. On the set of models testing positive for ASSs, I ran an additional 90 scenarios that focused on decreasing disturbance sizes (2X , 5X). Model scenarios are summarized in Table 4-2, research question 2. Disturbances smaller than 10X were not tested on perch because even at a 10X increase in fishing effort there was generally no model response in perch biomass. Dual (sequential) 5X walleye/5X cormorant (and the reverse) disturbances were included to test how the order of a disturbance influenced the ability to shift a system between alternate attractors. All scenarios assumed top-down/bottom-up control because: a) a positive reaction was most likely under top-down or top-down/bottom-up control; b) there was no difference in model response between this and the top-down control; and c) McQueen (1986) concluded that lakes were generally structured by top-down/bottom-up control.

For models that did not exhibit ASSs in the baseline assessment, additional scenarios were run to determine if a stronger disturbance was required to trigger a switch between states. I ran an additional 100 scenarios representing increased ‘fishing effort’ and biomass additions through stocking (Table 4-2, research question 2). Stocking was modeled through a biomass multiplier on small walleye. Hatchery stocking was included as a disturbance to ‘shock’ the walleye biomass in a meaningful way since the adult walleye biomass was too low to initiate an ecosystem response to increased fishing effort. A multiplier of 3000X was chosen based on the relationship between the baseline biomass of small walleye and the estimated biomass of walleye stocked as fry at Lac la Biche.

For each scenario the intensity of the model response was coded based on the largest positive or negative change in the relative biomass of the functional groups at year 100 of the model run. Model responses were coded as: 0 = no ASS response; 1 = weak response (< 0.2X); 2 = moderate response (0.2X to 0.5X); 3 = strong response (> 2.0X). An index of the reaction intensity (IRI) was calculated by multiplying the response code (1 to 3) and the frequency of each response by model year and disturbance type.

Restoration potential for the walleye-dominated equilibrium

Walleye restoration at Lac la Biche has been underway since 2005. Management has been operating under the assumption that ASSs exist and that a walleye-dominated equilibrium can be restored given a large enough disturbance to the system. Walleye stocking and cormorant control are the main management tools currently being used to trigger ASSs. Reductions in recreational pike (*Esox lucius*) harvest and commercial harvest of lake whitefish (*Coregonus clupeaformis*) were also used as restoration tools though they are not explicitly modeled in this study. The efficacy of walleye stocking and cormorant control as management tools for restoration was assessed using the 2005 models (n=12) and a set of 'alternate models' that incorporated walleye stocking both directly and indirectly in a variety of ways. The alternate models are described as follows:

1. Modification of a 2005 model to include stocked walleye as a separate multistanza group (age structured population) in the balanced model. The walleye stocking disturbance (3000X biomass multiplier on walleye fry) was applied to the stocked walleye group.
2. Modification of a 2005 model to increase the Ecopath base (initial) walleye biomass to 1900 levels (~2.5 t/km^{-2}) to see if the system was capable of supporting a larger walleye population with no changes to other functional group parameters.
3. Modification of an Ecopath base model for 2005 to make both walleye and cormorant biomasses equivalent to a 1:1 prey consumption ratio.
4. Creation of a new Ecopath model (2011) using data from Lac la Biche representing conditions in 2011 in which walleye stocked between 2006 and 2011 were incorporated directly into the population of 'wild' walleye.

Scenarios tested on each alternate model are summarized in Table 4-2, research question 3.

Relationship between walleye, perch, and cormorants in ASSs

The resilience of an equilibrium state depends on reinforcement by stabilizing feedbacks and the extent to which the abiotic and biotic components have been changed (Briske et al. 2008). I assessed the change over time in the relative influence of walleye, perch and cormorants in the system in terms of their foraging impact. Foraging impact incorporates changes in the biomass of the biotic community with changes in the distribution of predation pressure. Selection pressure from foraging can alter feedback mechanisms by influencing recruitment, growth, and mortality rates. For each set of models representing a different era (1800, 1900, 1965, 2005) with and without ASSs, I averaged the biomass and consumption/biomass values for the three walleye groups, three perch groups, and one cormorant group. I multiplied the average biomass (t/km^{-2}) for each group by its average consumption/biomass ($year^{-1}$) to calculate the total consumption ($t \cdot km^{-2} \cdot yr^{-1}$) by group. The three walleye estimates were summed to get a single consumption estimate for walleye and likewise for perch. Ratios of foraging intensity were calculated relative to cormorant consumption to elucidate changes in the ratios between systems with and without ASSs for guiding restoration.

Recent ecosystem trends in response to predator manipulation

Empirical data describing the ecosystem response to restoration efforts were assessed to determine if early trends in the perch, walleye, or cormorant populations resemble those of the simulation model outputs. Relative trends in perch and walleye population size were assessed in terms of catch-per-unit-effort (CPUE; $fish \bullet 100m^{-2} \bullet 24h^{-1}$) calculated from index netting data collected by Alberta Environment and Sustainable Resource Development (AESRD) each September from 2005 to 2011 (Data provided by: Fish & Wildlife Management Information System (FWMIS). Alberta Sustainable Resource Development. Edmonton, AB. Accessed on April 2, 2012). Catch-per-unit-effort ($fish \bullet 100m^{-2} \bullet 24h^{-1}$) data were bootstrapped 10,000 times and the median and 95%

confidence intervals were plotted. Trends in cormorant abundance were assessed from annual nest count data over the same period (2005 to 2011) (McGregor 2012).

Change in the size structure of the fish population was assessed to determine if average size was increasing in response to management efforts. Data on fish size were provided by AESRD from the same fall index netting data used to calculate annual CPUE. As an index of the size structure of the population, total CPUE was calculated by mesh size (stretched meshes – 12, 19, 25, 38, 51, 63, 76, 102, 127, and 152 mm) for all fish captured by year between 2005 and 2011. Individual mesh CPUEs were grouped to represent small (those captured in the 12 and 19 mm meshes), medium (25, 38, 51, and 63 mm), and large (76, 102, 127, and 152 mm) size classes of fish. Catch-per-unit-effort (fish•100m^{-2}•24h^{-1}) data for each size class were bootstrapped 10,000 times and the median and 95% confidence intervals were plotted. I assessed changes in the general size structure of the fish community by comparing regression lines for each size class of fish. Fish of all species were used in this analysis to address the restoration program objective of increasing the overall size structure of the fish community. To assess the influence of perch population dynamics on the trend in CPUE, I plotted the median CPUE (perch•100m^{-2}•24h^{-1}) and error bars for 95% confidence intervals over time.

Results

Assessment of ASSs

In total, I found that ASSs occurred in 70% to 80% of the historical models (1800, 1900) but in none of the contemporary models (1965, 2005) (Table 4-3). Assumptions of top-down and top-down/bottom-up control gave the largest number of positive results (1800 – 70%, 1900 – 80%). I also observed alternate state responses under bottom-up control in 20% of the 1800 models and 30% of the 1900 models. Trophic control assumptions did not influence the occurrence of ASSs in the contemporary models so further analysis of the nature of ASSs was restricted to the two historical models (1800, 1900).

ASS triggers – size and identity

Larger perturbations (10X walleye and cormorant, 100X perch) were equally likely to trigger a positive ASS response in 1800 as in 1900 (Table 4-4). In 1800, there was an increase in the number of positive responses between 2X and 5X perturbations for walleye (100%) and cormorants (75%), and between 10X and 100X for perch (250%). Between 1800 and 1900, the number of scenarios exhibiting an ASS response increased most (relative to the 1800 response frequency) for disturbances targeting walleye and for the smallest perturbation (2X - 133%, 5X – 33%, 10X – 14% increase). I observed a similar trend with increases in cormorant and perch fishing effort. In 1800, a walleye disturbance preceding a cormorant disturbance was more likely (80%) to trigger a switch between equilibrium states while in 1900, disturbing cormorants first caused a larger number of switches (75%),

Response intensity increased between model years, especially for walleye perturbations (Table 4-4). For a given year, response intensity increased with perturbation size across all disturbance types, especially between a 2X and 5X fishing effort increase for walleye (120%) and cormorants (170%). In general, small perturbations (2X) caused more intense ASS responses in 1900 than in 1800 regardless of the nature of the trigger. Disturbances targeting walleye caused the most intense ASS reactions in general but the largest overall impact was for a 10X increase in cormorant effort. Disturbances to yellow perch triggered less intense ASS responses than either walleye or cormorants.

None of the contemporary models tested positive for ASSs even when the perturbation size was dramatically increased. Low amplitude cycling around the baseline was evident in 25% of models under top-down, mixed, and wasp-waist trophic control, and 17% of bottom-up models. Cycling was generally triggered by yellow perch perturbations though larger cormorant perturbations

(10X or higher) triggered cycling in mixed control models. In all other cases, the models exhibited a single equilibrium dominated by cormorants.

Restoration potential for walleye-dominated equilibrium

Among the 86 model scenarios representing the current ecosystem (2005 – 15 models, 2011 – 1 model) there were two apparently positive ASS responses. In alternate model 4, the 50X and 100X cormorant perturbations eliminated cormorants from the system resulting in a persistently high walleye biomass producing the appearance of an ASS.

Cycling was not observed in any of the four alternate models using conservative vulnerability values. Tests using higher vulnerabilities (5.0, 10.0) triggered cycling in alternate models 2 and 3 under all perturbations, and in alternate model 1 when cormorant effort was increased.

Contemporary models (2005, 2011) responded to the addition of stocked walleye with a spike in the relative biomass of each walleye age stanza. For adult walleye, the spike in relative biomass ranged from 2X to 300X and was sustained for 15 to 20 years, before returning to the low baseline biomass. Large spikes in walleye biomass had little perceptible impact on other modeled groups.

Relationship between walleye, perch, and cormorants in ASSs

In general, I found that total consumption of prey by walleye decreased with time while the total consumption by cormorants increased in all years except 1965 (Table 4-5). Relative to total consumption by cormorants, consumption by walleye was up to four times higher in the historical models but one to two orders of magnitude lower in the contemporary models. Total consumption by yellow perch generally increased between model years (with the exception of ‘no ASS’ models for 1800) though relative consumption was highest in 1965 when both cormorant and walleye total consumption was low.

Recent ecosystem trends in response to predator manipulation

Between 2005 and 2011, the nesting cormorant population declined 73% in response to management efforts (Figure 4-2). During the same period the walleye catch-per-unit-effort (CPUE; walleye•100m^{-2}•24h^{-1}) increased over 300% from stocking. Yellow perch CPUE did not show a consistent trend, though CPUE in the last year of survey (2011) was more than 500% above the 2005 level. Perch catch rate peaked in 2009 (292 perch•100m^{-2}•24h^{-1}), declined by two-thirds in 2010 (98 perch•100m^{-2}•24h^{-1}), but increased again in 2011 (181 perch•100m^{-2}•24h^{-1}). Large variability in perch CPUE between 2009 and 2011 was likely the result of very large year-classes.

The distribution of the total CPUE between small, medium, and large-sized fish for each study year suggests a weakly increasing trend in the CPUE for small fish (slope = 35.20, p = 0.10), no trend for medium-sized forage fish (slope = 0.5737, p = 0.92) and a consistent increase in the catch of fish in the largest meshes (slope = 1.287, p = 0.092) (Figure 4-3). On average, yellow perch accounted for the largest proportion of the total CPUE for small fish (x = 0.73, range = 0.58 to 0.92), declining with increasing size class (medium fish: x = 0.40, range = 0.14 to 0.81; large fish: x = 0.02, range = 0.01 to 0.04). The slope of the regression line for small perch was smaller than the line for all fish (slope = 27.1, p = 0.14), larger for medium perch (slope = 1.911, p = 0.76), and smaller for large perch (slope = 0.02637, p = 0.57) (Figure 4-4). Between 2008 and 2009 the dominant species in the large size class shifted from white suckers (*Catostomus commersonii*) to walleye.

Discussion

By employing a series of ecosystem models over a period of intense ecosystem change, I was able to show that alternate stable states, defined by walleye-dominated and cormorant-dominated equilibriums, existed in historical models while contemporary models had a single attractor. I was also able to show that in 1900, ASSs were triggered by smaller perturbations than in 1800 and that the intensity of the modeled response was stronger in 1900. Disturbances impacting walleye and cormorant populations were more likely to trigger a positive reaction than disturbances to yellow perch. These results provide important theoretical and practical insights for restoration of Lac la Biche and other large lake ecosystems.

Shifts between alternate attractors result from the combination of the magnitude of a perturbation and the resilience of the ecosystem (Folke et al. 2010). When resilience is reduced by human actions, it becomes increasingly likely that a smaller perturbation will trigger an ASS (Folke et al. 2010). Evidence from model scenarios of 1800 and 1900 suggests a decline in system resilience which is supported by historical accounts from the area (See Chapters 2 and 3). For example, overharvest during European settlement of Lac la Biche caused the reported decline of lake whitefish by the late-1870s (McCullough and Maccagno 1991:141). Reports of variability in the availability of lake whitefish (Champagne 1992:240-241, 251) and the frequency of drought conditions (Dominion of Canada 1886:131, Champagne 1992:251) and stochastic weather events (Dominion of Canada 1887:94, McCullough and Maccagno 1991:150) were increasingly common towards the end of the century. In addition to lake whitefish harvest, historical harvest of northern pike, walleye, suckers (*Catostomus spp*.), and burbot (*Lota lota*) also occurred (Tyrell 1916:305, HBCA,PAM,B.115/e/1,fo.3d as referenced in McCullough and Maccagno 1991:71) with potential impacts on ecosystem resilience.

The failure of walleye stocking, cormorant control, or increased perch fishing to result in ASSs in any of the contemporary models may be explained in several ways: a) model parameters did not accurately reflect reality or change over time in the same way as the real system; b) stocked walleye were not appropriately incorporated into the predator-prey dynamics of the systems; c) perturbations were not large enough to trigger a positive response due to high system resilience; d) ASSs existed but required different ‘triggers’ that I did not test; or e) the current system has a single attractor. If any of the first four options is true, then a combined research and management approach should focus on fine-tuning parameter estimates, finding a better way to incorporate stocked fish, and identifying appropriate triggers to improve understanding of the restoration trajectory (Hobbs and Suding 2009). If, however, one of the historical attractors has been lost due to changing ecosystem conditions, current management will not be able to restore the walleye-dominated state of historical times given current management actions because the potential for that state does exist given current conditions.

Identifying the success of the restoration program at Lac la Biche depends on the temporal scale of assessment. If management results (walleye stocking and cormorant control) are judged annually or over the short-term (decades), then from the perspective of an angler or a fisheries manager, the walleye population can be 'restored' in virtually all scenarios. The increasing trend in walleye catch-per-unit-effort over seven years of index netting supports the results of contemporary model scenarios suggesting that walleye recovery is indeed underway. What remains to be seen, however, is whether the model predictions that the adult walleye biomass originating from stocking will only be sustained for 15 to 20 years before returning to the baseline Ecopath biomass, does indeed occur. Thus, from a long-term perspective, restoration of the walleye-dominated state will not occur given current management actions because the walleye-dominated state does not exist. The loss of an attractor could have occurred if critical parameters or environmental conditions changed and altered the stability landscape of the system (Beisner et al. 2003, Petraitis and Dudgeon 2004, Scheffer 2009). At Lac la Biche, changes to ecosystem conditions through the 20th century were numerous. Fish populations were heavily harvested, walleye were extirpated, major fish kills occurred in 1946 and 1965, the watershed was cleared for agriculture, treated sewage discharge into the lake began, and settlement around the lake increased (Champagne 1992: 319, Schindler et al. 2008). Any one of these activities could have altered important ecosystem parameters thereby changing the system potential for ASSs.

Petraitis and Dudgeon (2004) suggest that an alternate state is stable when "at least one of the species in the alternative community…become[s] common enough in biomass, individual size, and/or density…to establish the positive feedbacks needed to maintain the assemblage". Evaluation of the ratios of total consumption for cormorants, perch, and walleye supports the hypothesis that the alternate attractors in modeled scenarios were stabilized through the differential predator-prey interactions of cormorants and walleye with their main prey source, yellow perch. The mechanisms underlying the ASS transition have been assumed from field observations and an understanding of local biology and ecology. In 2005, the cormorant biomass was large enough that by dominating walleye and perch in terms of total consumption, cormorants were able to establish a strong stabilizing feedback within the population of a key prey source, yellow perch. Preferential foraging on moderate-sized individuals (10 cm to 20 cm) encouraged a life history strategy in perch promoting slow growth and early reproduction (Law 1979). The result was an abundance of small planktivorous individuals capable of hindering walleye recruitment through predation on and competition with their young – a classic example of a cultivation-depensation effect (Walters and Kitchell 2001). Increased production of yellow perch resulting from cultural eutrophication of the lake (Egertson and Downing 2004) further benefitted cormorants and increased system resilience at a state that was incompatible with walleye dominance. In contrast, in the walleye-dominated state of the historical models, foraging selection pressure of walleye exceeded that of cormorants suggesting that walleye historically had more potential to influence the structure of the prey community. Selective predation on small perch by walleye encouraged faster growth and later reproduction at larger sizes. Selection due to cannibalism by large yellow perch (Tarby 1974, Persson et al. 2004) was in the same direction as adult walleye predation. Total consumption by yellow perch was higher than walleye, but their combined foraging impact favored the same life-history trend in perch and strengthened the foraging efficacy of walleye. Despite these assumed feedbacks, the combined selection pressure from foraging of walleye and large perch in the historical models is much less than the impact of cormorant consumption in models of 2005, which might explain the lower resilience of the historical models.

Differential foraging selection pressure of cormorants and walleye was expected to affect the life history strategy of yellow perch, encouraging small perch under cormorant dominance and larger perch under walleye dominance. As a result, I expected a shift towards larger perch (and a general increase in body size within the whole fish community) as cormorants declined and walleye biomass increased. Catch-per-unit-effort (CPUE; fish•$100m^{-2}$•$24h^{-1}$) results from index netting at Lac la Biche suggest that the smallest forage fish (predominately perch) have increased since 2005, medium-sized fish have remained fairly constant with shifting dominance between perch and cisco, and large fish have increased reflecting the growth of the stocked walleye. These early trends can be explained in a few ways: 1) gear selectivity in the smallest meshes of the gill nets combined with annual variability in the growth rates of small fish led to variability in the CPUE index that does not represent actual population trends, 2) annual declines in medium-sized fish released small fish from predation and competition resulting in high but cyclic juvenile survival and recruitment, 3) prey consumption by walleye was not large enough to influence the structure of the forage community, or 4) the dynamics of the smallest size classes of yellow perch (< 100 cm total length) in the contemporary system were not controlled by walleye so a large population of small perch existed despite an increased walleye population. Variability in the field observations for forage fish CPUE and the short time frame for field assessments make it difficult to ascertain what is actually happening at the ecosystem level so the originally predicted patterns may still emerge. As these results represent the earliest years of the restoration program, more time is required for assessing modeling results and the loss of a walleye-dominated state.

Using models to illustrate ASSs has been widely criticized (Dudgeon et al. 2010) but also promoted as an important tool for increasing our understanding about sensitive species and systems at reduced financial cost and low risk (Hobbs and Suding 2009). Ecopath with Ecosim proved useful for exploring concepts important to determining the restoration potential for a walleye-dominated equilibrium at Lac la Biche. The consistency of the perturbation responses across models in each time period improved confidence in the results of this research. However, weaknesses were identified that could impact the outcome of scenarios run on contemporary models. The difficulty in incorporating stocked fish biomass into the model was highlighted as a weakness that may influence our understanding of the practical potential for walleye restoration. The failure to produce a walleye-dominated state in any of the base 2005 models or the four alternate models, however, supports the theoretical conclusion that the potential for a walleye-dominated ecosystem resembling historical conditions has been lost. Though field data show a clear increase in the walleye population and decline in the cormorant population, variability in forage fish trends complicates any assessment of a change in the selection pressure structuring the yellow perch population.

Given the results of this study, I would suggest that restoration of the historical walleye-dominated equilibrium is not likely but the current management strategy, including continued intervention in the form of walleye stocking and cormorant control, provides opportunity for a recovery of the walleye population under a different set of ecosystem conditions than historically existed. Continued monitoring of system dynamics is important for the adaptive management cycle, improved modeling, and to provide indicators of long-term system dynamics (Hobbs and Suding 2009). While the timeframe for assessing the conclusions of this study is long (minimum of 15-20 years), continuity of the research is critically important for assessing the value of the modeling process and building the link between theoretical and empirical knowledge of alternate stable states.

Table 4-1. Ecosim vulnerability settings set to describe the impact of an increase in the biomass of a predator on the mortality of its prey (Christensen et al. 2008) under each of four trophic control assumptions. TD – top-down, TD-BU – top-down/bottom-up, BU – bottom-up, WW – wasp-waist. See Table C-1 for a list of the functional groups described in this table.

Trophic control	Vulnerability value		
	1.0	2.0	3.0
TD		Default	WALL3, YLPR3, DCCO
TD-BU	Litt. Zoopl., Pel. Zoopl.	Default	WALL3, YLPR3, DCCO
BU	Litt. Zoopl., Pel. Zoopl.	Default	
WW	Chiro.&Dip., Amphi., Molluscs&Gasto., Inverts., Litt. Zoopl., Pelagic Zoopl.	Default	YLPR1, YLPR2, Stickle., Small Fish

Table 4-2. Overview of the number of model scenarios run for each of the first three research questions. Year refers to the era of models on which the scenarios were run (All – 1800, 1900, 1965, 2005). TD-BU describes the top-down/bottom-up trophic control assumption (All – top-down, top-down/bottom-up, bottom-up, wasp-waist). Table values report the number of models on which a perturbation scenario was assessed for each for each research question. Perturbation intensity (2X, 5X, 10X etc.) describes the magnitude of the fishing effort (relative to the Ecopath baseline) or stocking increase applied to each group (walleye (*Sander vitreus*), cormorant (*Phalocrocorax auritus*), yellow perch (*Perca flavescens*)) or combination of groups (dual: WALL (walleye)/DCCO (cormorant)). The 'Dual' disturbances tested the model response to an ordered perturbation to walleye then cormorants (and the reverse) in the same model run.

			Walleye						Cormorant					Yellow Perch				Dual		Total Runs
Research Question	Year	Trophic Control	2X	5X	10X	50X	100X	3000X Stocking	2X	5X	10X	50X	100X	10X	100X	500X	1000X	5X WALL 5X DCCO	5X DCCO 5X WALL	N
1	All	All			160						160			160	160					640
2	1800, 1900	TD-BU	15	15					15	15								15	15	90
	1965, 2005	TD-BU						20				20	20			20	20			100
3	2005	TD-BU						12				12	12							36
	Alt. 1	TD-BU	1	1	1	1	1	1	1	1	1	1	1					1	1	13
	Alt. 2,3	TD-BU	2	2	2	2	2		2	2	2	2	2					2	2	24
	Alt. 4	TD-BU	1	1	1	1	1	1	1	1	1	1	1					1	1	13

Table 4-3. Number of models that exhibited an alternate stable state response to at least one of four perturbations under each of four different trophic control scenarios (TD = top-down, TD-BU = top-down/bottom-up, BU = bottom-up, WW = wasp-waist).

Year	N	TD	TD-BU	BU	WW
1800	10	7	7	2	0
1900	10	8	8	3	0
1965	8	0	0	0	0
2005	12	0	0	0	0

Table 4-4. Model responses to different combinations of perturbation type and intensity. The # ASS refers to the number of models that exhibited an alternate stable state (ASS) reaction in response to each type and intensity of perturbation. The IRI is the index of reaction intensity that refers to the size of the system response to each type and intensity of perturbation, measured as the change in relative biomass of the model groups that were most impacted. The IRI was calculated as the magnitude of the response (0=no response to 3=strong response) multiplied by the frequency of each type of response. (WALL = walleye (*Sander vitreus*), DCCO = cormorant (*Phalocrocorax auritus*), YLPR = yellow perch (*Perca flavescens*)). The 'Dual' disturbances tested the model response to an ordered perturbation to walleye then cormorants (and the reverse) in the same model run.

			Walleye			Cormorant			Yellow Perch		Dual	
Reaction	Year	N	2X	5X	10X	2X	5X	10X	10X	100X	5X WALL 5X DCCO	5X DCCO 5X WALL
# ASS	1800	10	3	6	7	4	7	7	2	7	5	1
	1900	10	7	8	8	5	7	7	3	7	1	4
IRI	1800	10	5	11	15	6	16	18	4	12	9	2
	1900	10	13	18	18	9	15	19	6	14	1	8

Table 4-5. Average total consumption ($t \cdot km^{-2} \cdot yr^{-1}$) of cormorants (DCCO; *Phalacrocorax auritus*), yellow perch (YLPR; *Perca flavescens*), and walleye (WALL; *Sander vitreus*) by year for models exhibiting alternate stable states (ASS) and models that did not (No ASS). The ratio represents total yellow perch and walleye consumption relative to one unit of cormorant consumption.

			Total Consumption ($t \cdot km^{-2} \cdot yr^{-1}$)			
Reaction	Year	N	DCCO	YLPR	WALL	Ratio
ASS	1800	7	1.5	25.4	6.1	1 : 17 : 4
	1900	8	4.4	30.9	5.1	1 : 7 : 1
No ASS	1800	3	1.5	83.6	8.8	1 : 56 : 6
	1900	2	2.9	51.7	8.8	1 : 18 : 3
	1965	8	0.5	53.6	0.07	1 : 107 : 0.1
	2005	12	22.4	159.8	0.2	1 : 7 : 0.009

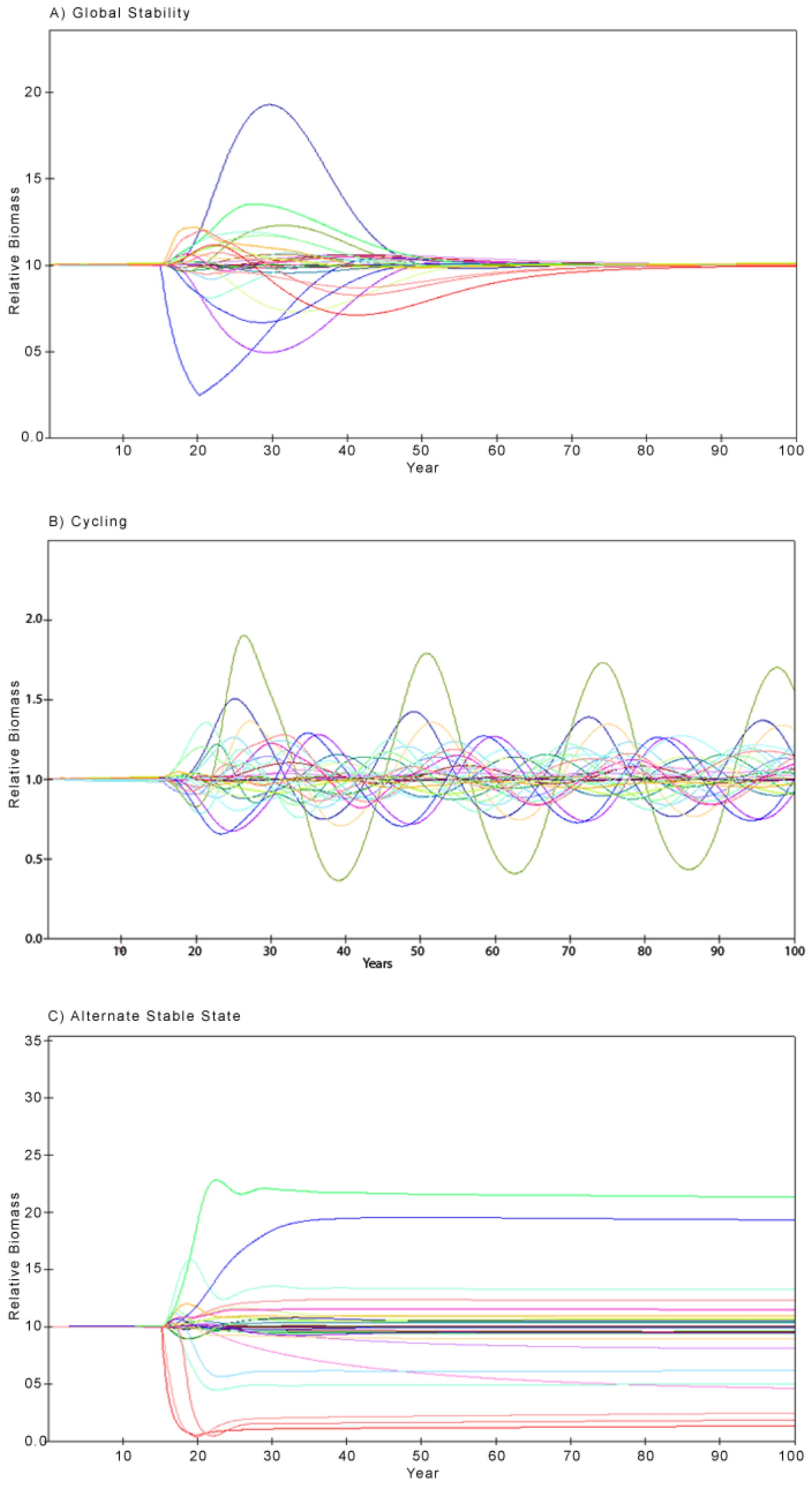
A) Global Stability
Relative Biomass
20
15
10
05
0.0
10
20
30
40
50
60
70
80
90
100
Year
B) Cycling
Relative Biomass
2.0
1.5
1.0
0.5
0.0
10
20
30
40
50
60
70
80
90
100
Years
C) Alternate Stable State
Relative Biomass
35
30
25
20
15
10
05
0.0
10
20
30
40
50
60
70
80
90
100
Year

Figure 4-1. Possible Ecosim responses to perturbations modeled as an increase in the fishing effort of a single functional group between years 15 and 20, followed by a return to baseline for 15 years then a removal of all fishing effort between years 35 and 40. Possible model responses were a) global stability: model groups smoothly returned to the baseline following a perturbation; b) cycling: model dynamics are cyclic around baseline conditions; and c) alternate stable states: system attains a different stable equilibrium state. Each line represents the relative biomass of a functional group in the model.

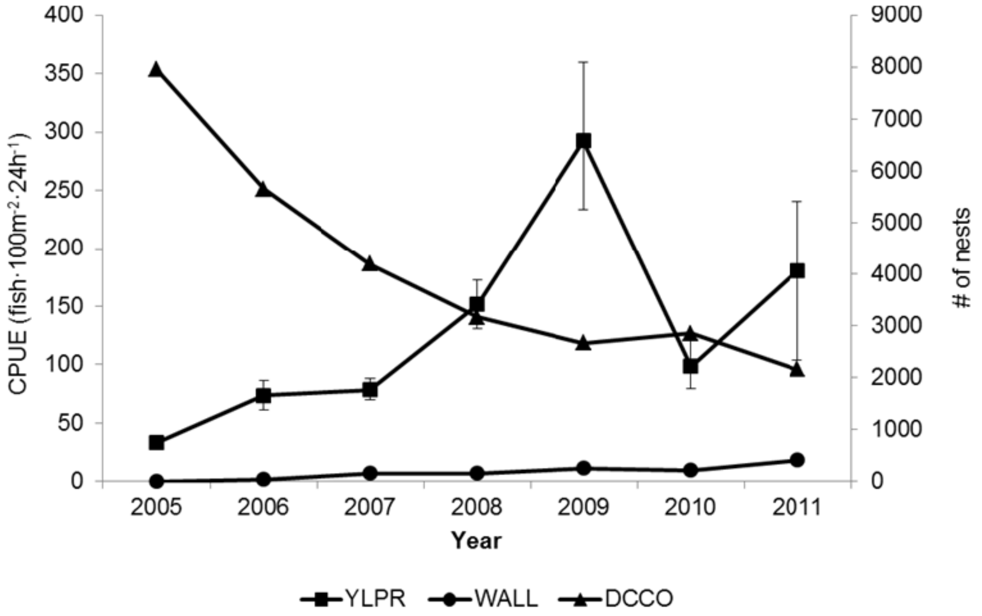

Figure 4-2. Comparison of walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) catch-per-unit-effort (CPUE; fish•100m^{-2}•24h^{-1}) from fall index netting (Data provided by: Fish & Wildlife Management Information System (FWMIS), Alberta Sustainable Resource Development, Edmonton, AB.), and double-crested cormorant (*Phalocrocorax auritus*) nest counts for each year of the Lac la Biche fishery restoration program between 2005 and 2011. Error bars show 95% confidence intervals on the median of the CPUE data bootstrapped 10,000 times.

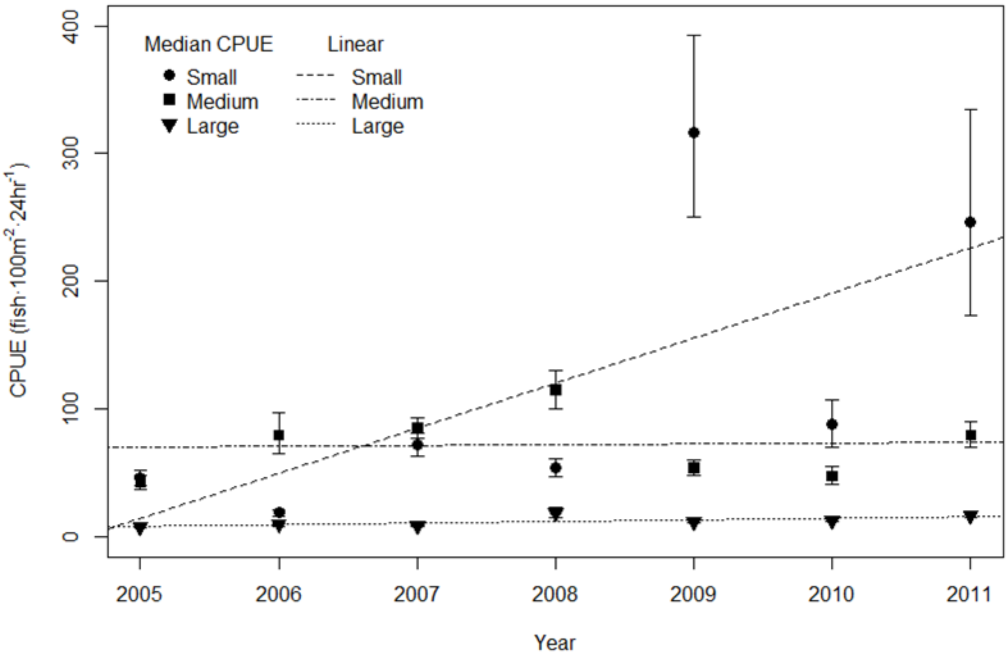

Figure 4-3. Series of regressions illustrating changes in the catch-per-unit-effort (CPUE; fish•100m^{-2}•24h^{-1}) of small fish (caught in 12 mm and 19 mm stretched mesh gill nets), medium fish (25, 38, 51, 63 mm meshes), and large fish (76, 102, 127, 152 mm meshes) captured during fall index netting at Lac la Biche, Alberta, Canada between 2005 and 2011. Error bars show 95% confidence intervals on the median of the CPUE data bootstrapped 10,000 times. The slope and p-values for each line are – Small: slope = 35.20, p = 0.10, Medium: slope = 0.5737, p = 0.92, Large: slope = 1.287, p = 0.09. Data provided by: Fish & Wildlife Management Information System (FWMIS), Alberta Sustainable Resource Development, Edmonton, AB.

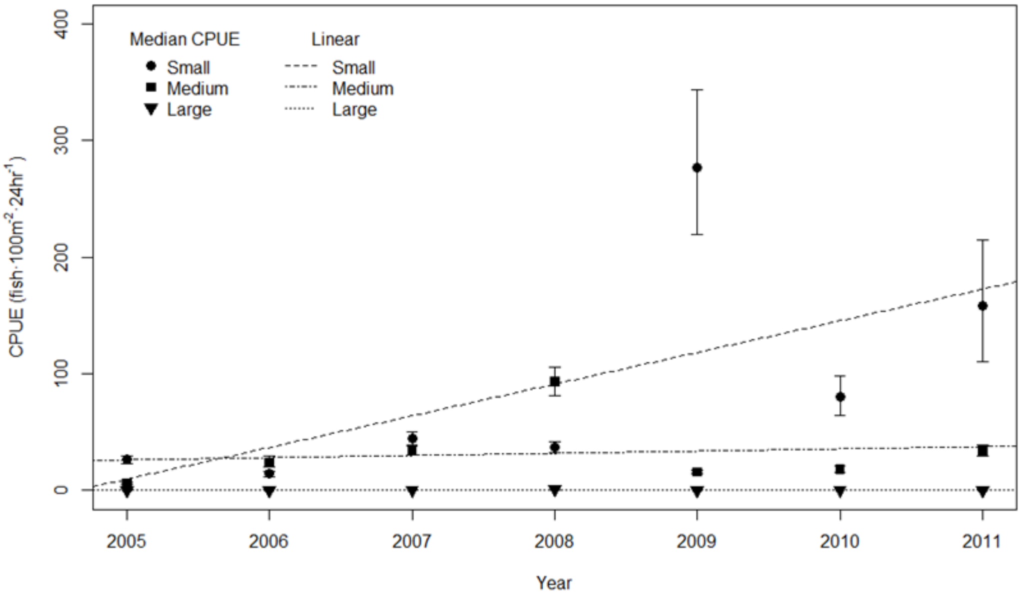

Figure 4-4. Series of regressions illustrating changes in the catch-per-unit-effort (CPUE; fish•100m^{-2}•24h^{-1}) of small yellow perch (*Perca flavescens*) (caught in 12 mm and 19 mm stretched mesh gill nets), medium perch (25, 38, 51, 63 mm meshes), and large perch (76, 102, 127, 152 mm meshes) captured during fall index netting at Lac la Biche, Alberta, Canada between 2005 and 2011. Error bars show 95% confidence intervals on the median of the CPUE data bootstrapped 10,000 times. The slope and p-values for each line are – Small: slope = 27.10, p = 0.14, Medium: slope = 1.911, p = 0.76, Large: slope = 0.02637, p = 0.57. Data provided by: Fish & Wildlife Management Information System (FWMIS), Alberta Sustainable Resource Development, Edmonton, AB.

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Appendix C -

Table C-1. Description of functional groups used in Ecopath models for Lac la Biche.

Functional Group	Description
WALL1	Walleyes (*Sander vitreus*) up to 50 mm total length (TL)
WALL2	Walleyes from 51 to 350 mm TL
WALL3	Walleyes 351 mm TL and larger
NRPK1	Northern pike (*Esox lucius*) up to 350 mm TL
NRPK2	Northern pike 351 mm TL and larger
YLPR1	Yellow perch (*Perca flavescens*) up to 100 mm TL
YPLR2	Yellow perch from 101 to 200 mm TL
YLPR3	Yellow perch 201 mm TL and larger
CISC1	Cisco (*Coregonus artedii*) up to 140 mm TL
CISC2	Cisco 141 mm TL and larger
LKWH1	Lake whitefish (*Coregonus clupeaformis*) up to 260 mm TL
LKWH2	Lake whitefish 261 mm TL and larger
BURB1	Burbot (*Lota lota*) up to 350 mm TL
BURB2	Burbot 351 mm TL and larger
Suckers	White sucker (*Catostomus commersonii*) and longnose sucker (*Catostomus catostomus*), all sizes. Mostly white sucker.
Stickle.	Ninespine stickleback (*Pungitius pungitius*) and brook stickleback (*Culaea inconstans*). Mostly ninespine stickleback.
Small Fish	Spottail shiners (*Notropis hudsonius*), trout-perch (*Percopsis omiscomaycus*), and Iowa darters (*Etheostoma exile*). Mostly spottail shiners.
DCCO	Double-crested Cormorant (*Phalacrocorax auritus*)
AWPE	American white pelican (*Pelecanus erythrorhynchus*)
Pisc. Birds	Piscivorous waterbirds
Non-P. Birds	Non-piscivorous waterbirds
Chiro. & Dip.	Chironomids and Dipterans
Amphi.	Amphipods
Mollusc & Gastro.	Molluscs and gastropods
Inverts.	All other aquatic invertebrates
Litt. Zoopl.	Littoral zooplankton
Pel. Zoopl.	Pelagic zooplankton
Cyano.	Cyanobacteria
Phyto.	Phytoplankton
SAV	Submerged aquatic vegetation including: macrophytes, periphytes, and epiphytes

Table C-2. Range of biomass (t·km^{-2}) values used in the balanced Ecopath models for each of the four modeled eras (1800, 1900, 1965, 2005).

	Biomass (t·km^{-2})			
Functional Group	1800	1900	1965	2005
WALL1 stocked			0.000-0.000	0
WALL2 stocked			0.019-0.019	0.002
WALL3 stocked			0.169-0.169	0.001
WALL1	0.000-0.000	0.000-0.0002	0.000-0.000	0.000-0.003
WALL2	0.099-0.247	0.101-0.801	0.001-0.015	0.000-0.048
WALL3	2.25-3.76	2.24-3.77	0.006-0.061	0.000-0.210
NRPK1	0.030-0.057	0.024-0.089	0.011-0.079	0.013-0.102
NRPK2	1.90-5.01	1.42-8.70	0.623-2.66	0.910-2.00
YLPR1	0.793-4.48	0.764-4.66	0.993-2.37	0.495-10.4
YLPR2	0.382-2.87	0.533-3.94	0.963-5.97	0.539-20.0
YLPR3	1.10-7.60	0.900-8.60	0.451-5.43	0.096-10.5
CISC1	0.38-1.67	0.331-2.29	0.254-0.765	0.656-9.37
CISC2	3.50-10.5	4.04-18.00	1.50-6.00	4.63-10.6
LKWH1	0.654-2.06	0.301-2.55	0.124-2.22	0.113-0.469
LKWH2	6.50-13.8	2.53-12.6	0.900-5.41	0.841-1.10
BURB1	0.122-0.431	0.140-0.853	0.087-0.265	0.178-0.620
BURB2	0.650-2.43	0.726-3.00	0.307-0.948	0.368-0.762
Suckers	2.50-6.50	2.01-6.58	3.50-8.20	1.10-3.50
Stickle.	0.801-2.90	0.865-5.20	0.329-1.27	1.00-3.13
Small Fishes	0.325-2.15	0.322-2.65	0.069-1.00	0.102-1.08
DCCO	0.210-0.210	0.210-0.073	0.006-0.009	0.290-0.309
AWPE	0.005-0.005	0.005-0.006	0.006-0.009	0.006-0.040
Pisc. Birds	0.004-0.006	0.004-0.006	0.003-0.003	0.008-0.008
Non-Pisc. Birds	0.010-0.014	0.010-0.014	0.011-0.011	0.019-0.019
Chiro. & Dip.	5.19-25.00	5.00-25.0	7.13-24.9	3.96-40.4
Amphi.	0.906-4.00	0.901-4.20	0.774-4.99	1.60-8.96
Molluscs & Gastro.	1.19-4.00	1.21-4.22	0.768-4.08	0.553-46.6
Other Inverts	0.973-4.00	0.978-4.35	0.580-3.85	1.23-32.9
Litt. Zoopl.	0.357-1.40	0.349-0.358	0.380-0.392	0.374-0.374
Pel. Zoopl.	0.154-5.00	0.139-5.00	0.259-3.85	0.120-7.51
Cyanobacteria	2.18-4.36	2.18-4.36	2.16-4.48	4.48-8.72
Phytoplankton	3.18-6.36	3.18-6.38	3.15-5.24	5.92-12.0
Macrophytes	0.311-115	0.312-115	0.266-115	0.128-115
Detritus	0.500-0.500	0.005-0.500	0.005-0.600	0.005-10.0

Table C-3. Range of production/biomass (year^{-1}) values used in the balanced Ecopath models for each of the four modeled eras (1800, 1900, 1965, 2005).

	Production/Biomass (year^{-1})			
Functional Group	1800	1900	1965	2005
WALL1 stocked			5.5	6.00
WALL2 stocked			0.6	2.40
WALL3 stocked			0.25	0.40
WALL1	4.90-11.20	2.80-13.00	5.00-11.00	6.00-16.00
WALL2	0.73-0.95	0.60-0.90	0.60-0.90	0.65-2.00
WALL3	0.17-0.25	0.20-0.31	0.25-0.45	0.25-0.72
NRPK1	1.25-1.40	0.65-1.33	0.65-1.40	0.65-2.80
NRPK2	0.15-0.27	0.21-0.27	0.27-0.40	0.25-0.40
YLPR1	2.60-5.25	2.60-5.00	2.30-3.25	1.70-8.00
YLPR2	0.96-2.00	0.82-1.92	0.77-2.19	1.25-2.83
YLPR3	0.45-0.60	0.46-0.60	0.42-0.65	0.40-1.31
CISC1	1.89-2.30	1.40-2.40	1.60-2.75	1.60-3.35
CISC2	0.53-0.60	0.50-0.65	0.65-0.90	0.62-1.50
LKWH1	0.90-2.00	0.90-2.00	1.50-2.00	1.30-2.00
LKWH2	0.30-0.46	0.30-0.68	0.30-0.60	0.40-0.53
BURB1	0.65-1.00	0.83-0.94	0.8-1.50	0.75-1.75
BURB2	0.29-0.31	0.29-0.31	0.30-0.40	0.26-0.43
Suckers	0.30-0.38	0.30-0.41	0.30-0.41	0.30-0.85
Stickle.	2.75-3.00	2.75-3.00	3.00-3.20	1.90-3.15
Small Fishes	1.71	1.71-2.00	1.85-2.00	1.60-2.50
DCCO	0.52	0.45-0.56	0.52	0.52
AWPE	0.2	0.19-0.20	0.19-0.20	0.19-0.20
Pisc. Birds	0.25	0.25	0.25	0.25
Non-Pisc. Birds	0.25	0.25	0.25	0.25
Chiro. & Dip.	13.1	13.1	13.1	13.10-18.00
Amphi.	5.7	5.70-6.60	5.70-6.60	5.70-8.76
Molluscs & Gastro.	3.8	3.00-3.80	3.00-3.80	3.00-6.11
Other Inverts	5.35	4.63-5.35	4.63-5.35	4.63-7.35
Litt. Zoopl.	35	35.00-37.00	35	35.00
Pel. Zoopl.	35	32.00-44.00	32.00-40.00	32.00
Cyanobacteria	131.5	131.5	131.50-200.0	131.50-200.00
Phytoplankton	131.5	131.50-176.00	176.00-200.00	131.50-200.01
Macrophytes	8.80-20.0	8.80-20.00	8.80-20.00	8.80-20.00

Table C-4. Range of consumption/biomass (year^{-1}) values used in the balanced Ecopath models for each of the four modeled eras (1800, 1900, 1965, 2005).

	Consumption/Biomass (year^{-1})			
Functional Group	1800	1900	1965	2005
WALL1 stocked			49.45	45.34
WALL2 stocked			4.26	6.39
WALL3 stocked			1.85	1.85
WALL1	73.43-88.20	48.16-87.98	45.03-70.14	103.38
WALL2	5.40-6.57	4.26-6.54	3.35-4.26	11.38
WALL3	1.50-1.95	1.50-1.95	1.50-1.85	1.50-3.64
NRPK1	7.20-8.94	6.27-8.94	5.44-6.49	3.87-12.51
NRPK2	1.40-1.95	1.40-1.95	1.40-1.90	1.40-3.00
YLPR1	11.67-16.70	11.73-18.72	11.00-19.54	9.01-52.34
YLPR2	4.56-6.75	4.45-6.68	4.38-8.16	3.86-14.20
YLPR3	2.74-3.57	2.84-3.57	2.84-3.50	1.46-5.00
CISC1	11.15-12.97	10.44-14.41	10.19-11.97	9.25-18.79
CISC2	3.65-3.69	3.65-4.00	3.60-4.00	3.69-6.42
LKWH1	5.41-11.60	5.16-12.13	5.43-12.13	5.71-10.80
LKWH2	2.35-2.85	2.35-3.00	2.35-3.00	2.35-3.00
BURB1	4.24-6.34	4.02-6.14	4.02-6.30	3.65-11.27
BURB2	1.90-2.22	1.90-2.22	1.95-2.00	1.95-3.30
Suckers	2.25-2.26	2.25-3.80	2.26-3.80	2.26-3.80
Stickle.	9.53-11.28	9.53-14.00	10.50-14.0	6.30-14.00
Small Fishes	6.42-8.66	6.42-10.00	8.66-10.00	6.38-10.00
DCCO	72.9	72.9	72.9	72.9
AWPE	110	110	110	110
Pisc. Birds	58	58	58	58
Non-Pisc. Birds	58	58	58	58
Chiro. & Dip.	62.4	62.4	62.4	62.40-65.85
Amphi.	30.2	30.2	30.2	27.20-30.20
Molluscs & Gastro.	24.4	24.4	24.4	21.40-24.40
Other Inverts	31.8	31.8	31.8	24.00-31.80
Litt. Zoopl.	120	120	120	120
Pel. Zoopl.	120	120.00-150.00	120	113.00-176.00

Table C-5. Range in fishery catches (t·km^{-2}·yr^{-1}) used in the balanced Ecopath models for each of the four modeled eras (1800, 1900, 1965, 2005).

	Fisheries Catches (X 10^{-2}) (t·km^{-2}·yr^{-1})			
Functional Group	1800	1900	1965	2005
WALL3	0.86-5.90	5.56-16.99	0.045 -5.56	0.0013-0.43
NRPK2	1.42-38.00	12.00-32.50	5.75-30.31	4.58-5.54
YLPR3	0.40-0.73	0.67-1.10	0.67-134.47	0.15-1.60
CISC2	0.25-0.40	0.27-1.60	0.51-300.00	0.21-12.72
LKWH2	14.20-163.80	73.37-165.00	40.00-183.50	23.29-28.03
BURB2	0.50-4.88	2.01-5.42	2.010-26.68	0.048-4.50
Suckers	1.37-7.00	2.60-28.50	2.26-11.85	0.36-3.74
DCCO	<<0.1-0.1	0.010-0.37	<<0.10-0.10	0.010-0.10

Appendix D - Description of functional group parameters for the 2005 Ecopath models including data sources, references, and calculation and analysis methods.

Fish

Lac La Biche is home to 13 fish taxa which are represented in the model as 18 functional groups. Six species (walleye, northern pike, burbot, yellow perch, lake whitefish, and cisco) were represented as multistanza groups chosen to reflect observed cutpoints in the size-selective harvest of each species by cormorants and other predators. The multistanza groups for walleye and perch also represented changes in life-history strategy as well as dominant size classes within the system.

All other fish taxa were combined into three groups including sticklebacks (nine-spine stickleback and brook stickleback), suckers (white sucker and long-nose sucker), and other small fishes (Iowa darter, spottail shiner, and trout perch). In each case the taxa were grouped based on the availability of data and assumed similarities in their functional ecosystem role. Model parameters in each case reflect values for the dominant species within the grouping, specifically, nine-spine stickleback, white sucker, and spottail shiner.

Walleye (WALL)

Walleye is one of the most important species in the Lac La Biche ecosystem and the species on which the restoration efforts of this project are focused. As such, walleye was represented by three multistanza groups corresponding to size classes with different life stages and predation pressures. The group WALL1 represents individuals with a total length (TL) of less than or equal to 50 mm, roughly corresponding with the size at which they transition from invertebrate to fish prey. WALL2 represents piscivorous fish of the size generally consumed by cormorants; these fish are between 51 and 350 mm (TL).The final group, WALL3, represents the largest piscivorous walleye in the system with a minimum total length of 351 mm. These large walleye are generally beyond the range of cormorant consumption and are the target of fish harvest efforts.

Biomass

Walleye biomass was estimated using the average weight of walleye sampled during netting activities at Lac La Biche in the fall of 2003 and 2005 to 2007 (weight = 2.19 kg). Three independent estimates for the density of walleye form the range of variation in biomass considered for the model. One estimate was derived from a regression of density and the catch-per-unit-effort for walleye in the 2003 (CPUE = 1.27 walleye$\cdot$100 $m^{-2}\cdot ha^{-1}$) fall walleye index netting using the formula CPUE = 1.5667*(density) + 3.6576 (Walker 2004). As a second estimate, the density of walleye was derived from a population estimate conducted in 2002 (0.12 walleyes/ha) (Davis 2002) and applied to Lac

La Biche for 2003. A third estimate of 1500 walleye was suggested by the area fisheries biologist based on personal experience and the assumption that calculated estimates were too high (C. Davis, personal communication). Ecopath was allowed to estimate the biomass of the WALL1 and WALL2 stanza.

Production:Biomass (P/B)

As an estimate of P/B (year^{-1}) the total mortality (Z) was calculated independently for each of the multistanza groups. For WALL3 an estimate of the total conditional mortality for Alberta walleyes (Sullivan, unpublished data) was combined with an estimate of fishing mortality for Lac La Biche walleyes in 2003/2004 for a total mortality estimate of 0.30 year^{-1}. Similar estimates of 0.30 year^{-1} (Koops et al. 2006), and 0.38 year^{-1} (Jaegar 2006) were reported for the Bay of Quinte and Oneida Lake, which are similar systems to Lac La Biche. A total mortality estimate of 0.32 year^{-1} represents the average for similar systems reported at Fishbase.org (http://www.fishbase.org). Estimates of total mortality for WALL1 and WALL2 were derived from the average of values reported for Oneida Lake and the Bay of Quinte (Jaegar 2006).

Consumption:Biomass (Q/B)

A consumption/biomass of 8.32 year^{-1}was estimated for WALL3 using Equation 22 from the Ecopath Users Manual (2009) and based on the work of Palomares and Pauly (1989, 1998). This value was much higher than the average of the values (3.80 year^{-1}) reported by Jaegar (2006) for Oneida Lake (3.96 year^{-}

^{1}) and the Bay of Quinte (3.64 year^{-1}) and was used only as an upper limit during model balancing. Q/B estimates for the WALL1 and WALL2 multistanza groups were generated by Ecopath.

Diet Composition

Walleye diet samples were collected seasonally (winter, spring, summer, fall) during 2005 and 2006 from a combination of sources. Due to a small number of walleye samples and a lack of seasonal samples, data from all years and seasons were pooled. Diet composition by biomass was determined for the WALL3 multistanza group. No individuals from the WALL1 groups, and few individuals from the WALL2 group were represented in the 2005 and 2006 samples so data from the fall of 2007 were used in model parameterization (McGregor, unpublished data).

Ecotrophic Efficiency (EE)

The EE for each walleye multistanza group was estimated by Ecopath.

Northern Pike (NRPK)

Northern pike are an important predator fish and an important sportfish in Lac La Biche; however, limited local data were available for use in the model. Pike were split into two multistanza groups (NRPK1 - <350 mm TL; NRPK2 – 350+ mm TL) based on the predation pressure and the maximum size consumed by cormorants.

Biomass

The average weight of pike >350 mm (TL) was calculated from individuals sampled during the fall walleye index netting (FWIN) (weight = 2.28 kg). The initial pike density was estimated from a regression of density and catch-per-unit-effort (CPUE) (CPUE = 0.3461*(density) – 0.0504; $R^2 = 0.9095$) created using data from Garner Lake (Wilcox 2005) and McGuffin Lake (McGregor 2010). CPUE from the 8-panel net (2003 = 2.81 pike·100 m^{-2}·ha^{-1}, 2005 = 2.29) was used in the regression and the average density from the two survey years was used in the model.

Production:Biomass (P/B)

As an estimate of P/B $year^{-1}$the total mortality (Z) was calculated independently for each of the multistanza groups. For NRPK2 the Z value (Z = 0.23 $year^{-1}$) was the average of mortality estimates from the survivorship curve for LLB pike from 2003 to 2005 (Z = 0.27 $year^{-1}$), and the mean of the estimates for each year (2003 = 0.24 $year^{-1}$; 2005 = 0.13 $year^{-1}$) generated through catch-curve analysis in FAST 2.1 (Slipke and Maceina 2001). Estimates of Z available from Fishbase (www.Fishbase.org) (Z = 0.15 $year^{-1}$) and published data for Oneida Lake (Z = 0.20 $year^{-1}$) and the Bay of Quinte (Z 0.24 $year^{-1}$) (Jaegar 2006) were used to guide changes to mortality required to balance the model. The initial estimate for NRPK1 was derived from the value for NRPK2 and expectations for mortality of small pike, combined with knowledge of the higher turnover rate of smaller fish.

Consumption:Biomass (Q/B)

Q/B was entered as the average of the estimates for Oneida Lake (3.40 year^{-1}) and the Bay of Quinte (3.24 year^{-1}) (Jaegar 2006). Additional consumption/biomass values were used to define the range of reasonable estimates including a value of 2.48 year^{-1} for NRPK2 derived from Equation 22 from the Ecopath with Ecosim Users Manual (Christensen et al. 2008) and based on the work of Palomares and Pauly (1989, 1998). Values of 4.30 year^{-1} (Heikinheimo and Korhonen 1996) and 8.40 year^{-1} (Raat 1990) were also reported in the literature. Q/B for NRPK1 was estimated by the program.

Diet composition

Pike diet samples were collected seasonally (winter, spring, summer, fall) during 2005 and 2006 from a combination of sources (McGregor, unpublished data). Due to small seasonal sample sizes, data from all years and seasons were pooled. Diet composition by biomass was determined for the both the NRPK1 and NRPK2 groups.

Ecotrophic Efficiency (EE)

Reasonable estimates were available for required input parameters thus Ecopath was allowed to estimate the value for EE.

Yellow Perch (YLPR)

Yellow perch are one of the most important prey species in the Lac La Biche system and are thought to be a key player both influencing, and responding to changes in ecosystem structure and function. To adequately reflect perch dynamics and to highlight the significance of different size classes as prey to cormorant and fish predators, three multistanza groups were developed. YLPR1 represents planktivorous and insectivorous fish with a total length of less than 98 mm. These fish represent a significant prey resource for walleyes. YLPR2 represents fish transitioning from an insectivorous to a piscivorous diet. Fish in this group are between 98 mm and 200 mm (TL) and represent one of the main prey species for cormorants. YLPR3 covers predominately piscivorous perch with a minimum total length of 201 mm and represents the size removed by recreational and commercial fishing efforts.

Biomass

Average weights for each size class represented the mean of individual weights of fish captured during the 2005 Lac La Biche FWIN (YLPR1 = 3.45 g, YLPR2 = 10.46 g, YLPR3 = 82.91 g). The population density for YLPR3 was approximated from a regression of yellow perch catch-per-unit effort and density (CPUE = 0.008*(density) + 1.9182; $R^2 = 0.8625$) (McGregor, *unpublished data*) and the average of the 2003 (CPUE = 30.52 perch·100 m^{-2}·ha^{-1}) and 2005 (CPUE = 4.56 perch·100 m^{-2}·ha^{-1}) 8-panel catch rates. For comparison, and to provide a range of potential perch biomass values, a regression equation was created using LLB hydroacoustics (Milne 2007, Milne 2008) and FWIN data from 2006 and 2007 (CPUE = 0.4179*(density) + 0.8919, $R^2 = 0.9831$).

Biomass estimates for YLPR1 and YLPR2 were generated by Ecopath. To validate the estimate for YLPR2, the population density was calculated using the regression equation CPUE = 0.003 *(density) + 0.6401 ($R^2 = 0.9809$) and the average of the 2003 (CPUE = 91.71 perch·100 m^{-2}·ha^{-1}) and 2005 (CPUE = 1.06 perch·100 m^{-2}·ha^{-1}) 8-panel catch rates. As for YLPR3, a similar regression based on population estimates from hydroacoustics (Milne 2007, Milne 2008) (CPUE = 0.0546 *(density) + 0.1712, $R^2 = 0.989$) was used to provide a range of possible values. Reasonable density estimates for YLPR1 could not be generated using the available sampling techniques, so Ecopath biomass estimates were used.

Production:Biomass (P/B)

For YLPR3, P/B $year^{-1}$was calculated as the average of the Z values derived from a catch curve analyses of 2003 (Z = 0.466 $year^{-1}$) and 2005 (Z = 0.496 $year^{-1}$) FWIN data for LLB, and the value generated from an analysis of the survivorship curve for perch between 2003 and 2005 (Z = 0.46 $year^{-1}$). Additional estimates available for Oneida Lake (Z = 0.40 $year^{-1}$) and the Bay of Quinte (Z = 0.55 $year^{-1}$) (Jaegar 2006) and from www.fishbase.org (Z = 0.42 $year^{-1}$) were used to define the range of potential values. The value for YLPR2 was not available and was assumed to be similar to YLPR3, while 4.97 year^{-1} was used for YLPR1 and was the average of the estimates for Oneida Lake (Z = 6.14 year^{-1}) and the Bay of Quinte (Z = 3.80 year^{-1}) (Jaegar 2006).

Consumption:Biomass (Q/B)

The Q/B year^{-1} value for YLPR3 was derived from the average of values reported by Jaegar (2006) for Oneida Lake (3.80 year^{-1}) and the Bay of Quinte (4.10 year^{-1}). A much higher estimate of 9.23 year^{-1}was calculated using Equation 22 from the Ecopath Users Manual (Christensen et al. 2008) and based on the work of Palomares and Pauly (1989, 1998). Another estimate of 4.82 year^{-1}was calculated following the procedure outlined in Bajer et al. (2003). These values were used to guide the range of potential values during the model balancing process. Values for YLPR2 and YLPR1 were generated by Ecopath.

Diet Composition

Yellow perch diet samples were collected seasonally (winter, spring, summer, fall) during 2005 and 2006 from a combination of sources (McGregor, unpublished data). Due to small seasonal sample sizes, data from all years and seasons were pooled. Diet composition by biomass was determined for all multistanza groups.

Ecotrophic Efficiency (EE)

The ecotrophic efficiency for each of the perch multistanza groups was generated by Ecopath during the model balancing routine.

Burbot (BURB)

Few local data were available to describe the burbot population in LLB; However, burbot are significant fish predators at all sizes, and are an important prey source at smaller sizes. Burbot were represented as two multistanza groups with BURB1 incorporating fish with a maximum total length of 350 mm, and BURB2 being a minimum size of 351 mm (TL).

Biomass

Weight for BURB2 represents the average of the measurements of individuals captured during the 2005 FWIN and netted by commercial fishermen in the spring of 2006 (2500 g). Due to the limitations of the gear used for sampling, small burbot were not caught and an average weight was not available for BURB1. Local estimates of burbot density were not available so published values were used to describe the potential range of densities. A preliminary estimate of 2.3 burbot/ha (Davis, 1997) was considered reasonable and was applied to the model. The range of burbot densities reported by Schram et al. (2006) for Lake Superior (0.12 butbot/ha to 3.54 burbot/ha) was used to guide changes required to balance the model.

Production:Biomass (P/B)

Due to a lack of local data, the total mortality (Z) was parameterized with literature values from other areas. The initial model input of 0.26 year^{-1} came from a model of Oneida Lake (Jaegar 2006); values used in model balancing ranged from 0.17 year^{-1} (www.fishbase.org) to 0.40 year^{-1} (Cox and Kitchell 2004) and 0.43 year^{-1} both for Lake Superior (Schram et al. 2006). Estimates for the smaller BURB1 group were not available from literature or local sources so values for NRPK1 were used to approximate BURB1 total mortality based on similar diet and behaviour of the two species.

Consumption:Biomass (Q/B)

An initial Q/B value of 3.52 year^{-1} for BURB2 was the estimate for Oneida Lake used by Jaegar (2006). The range of reasonable values was bounded by 2.54 year^{-1} (Rudstam et al. 1995, Cox and Kitchell 2004) on the low end, and 6.72 year^{-1} on the upper end (calculated using equation 22 from the Ecopath Users Manual (Christensen et al. 2008) and based on the work of Palomares and Pauly (1989, 1998).

Diet Composition

The diet of burbot was assessed from samples collected during dedicated sampling events in the spring, summer, and fall of 2005, and all four seasons in 2006 (McGregor, unpublished data). Due to small seasonal sample sizes, data from all years and seasons were pooled.

Ecotrophic efficiency (EE)

The EE for each burbot group was estimated by Ecopath.

Lake Whitefish (LKWH)

Lake whitefish are an important fish species in Lac La Biche, with a history of commercial harvest dating back to the early 20th century. Smaller whitefish are regularly consumed by cormorants as well as large fish predators such as pike, walleye, and burbot. To allow for a distinction between human removal through harvest and their removal as bird and fish prey, whitefish were modeled as a multistanza group. LKWH1 represents prey sized fish with a total length of 260 mm and less, and LKWH2 represents the larger individuals (261+ mm TL) which are harvested primarily by commercial and domestic fisheries.

Biomass

The average weight of fish in each multistanza group (LKWH1 = 77.6 g; LKWH2 = 773.0 g) was calculated for Lac La Biche from the 2005 FWIN data. To calculate population density for each multistanza group, hydroacoustics data from Lac La Biche (2006 and 2007) (Milne 2007, Milne 2008) and Wabamun Lake (2007) were combined with catch-per-unit-effort data to generate a regression with the formula CPUE = 0.1216*(density) ($R^2 = 0.986$) (McGregor, unpublished data). This regression was used to generate an average whitefish density (11 fish·ha^{-1}) from 2003 and 2005 FWIN catch rates (2003 = 1.30 whitefish·100 m^{-2}·ha^{-1}; 2005 = 1.33 whitefish·100 m^{-2}·ha^{-1}).

The density of LKWH1 was estimated by Ecopath. To validate the estimate, population density was calculated using the regression equation CPUE = 0.0235 *density ($R^2 = 0.8521$) and the average of the 2003 (CPUE = 2.77 whitefish·100 m^{-2}·ha^{-1}) and 2005 (CPUE = 2.42 whitefish·100 m^{-2}·ha^{-1}) 8-panel catch rates.

Production:Biomass (P/B)

Three methods were used to generate total mortality estimates for LKWH2; the initial estimate (Z = 0.35 $year^{-1}$) used in the model was calculated by combining an estimate of natural mortality retrieved from www.fishbase.org (Z = 0.20 $year^{-1}$) with the average of the fishing mortality calculated from commercial harvest statistics for Lac La Biche for 2003 (F = 0.17 $year^{-1}$) and 2005 (F = 0.13 $year^{-1}$). To validate this estimate and to generate a range of possible values, a second calculation used commercial fisheries data from Touchwood Lake to generate von Bertalanffy growth parameters (L_∞, K, and t_0). These parameter values were combined with individual fish length data from the 2003 Lac La Biche FWIN, and the inverse von Bertalanffy equation (Age = t_0 – (1/K)*(LN(1-TL)/ L_∞)) was used to generate ages for each fish. From the calculated age distribution a Z-value of 0.30 $year^{-1}$was estimated for all whitefish. A third calculation generated a total mortality of 0.26 $year^{-1}$ from the distribution of total lengths (Beverton and Holt 1957) discussed in the Ecopath Users Manual (Christensen et al. 2008). For comparison, a Z-value of 0.18 $year^{-1}$ was reported for whitefish in Lake Superior (Cox and Kitchell 2004). The total mortality for LKWH1 was estimated through knowledge of the level of predation on smaller whitefish and through comparison with other species.

Consumption:Biomass (Q/B)

The Q/B value of 2.80 year^{-1} used to parameterize the model was calculated using the method reported in Madenjian and O'Conner (2006) and is identical to the value reported by Cox and Kitchell (2004) for Lake Superior. Few other estimates were available for defining the range of potential values; However, a value of 9.16 year^{-1} was calculated using equation 22 from the Ecopath Users Manual (Christensen et al. 2008) and based on the work of Palomares and Pauly (1989, 1998).

Diet Composition

Whitefish diet samples were collected seasonally (winter, spring, summer, fall) during 2005 and 2006 from a combination of sources (McGregor, unpublished data). Due to small seasonal sample sizes, data from all years and seasons were pooled.

Ecotrophic efficiency (EE)

The EE for each whitefish group was estimated by Ecopath.

Cisco (CISC)

Cisco, along with yellow perch, represents the largest biomass of forage fish in the lake. As an important prey fish for both cormorants and piscivorous predators, and as a predator of insects, plankton, and fish fry, they can significantly influence the structure of the ecosystem. Cisco are represented in the model as a multistanza group composed of CISC1 ($\leq$ 140 mm TL) and CISC2 (141+ mm TL). These groups were chosen based on the size preference of the dominant predator species; specifically, CISC2 are a key food resource for cormorants, large burbot, and pike.

Biomass

The average weight of an individual in each of the multistanza groups was calculated from fish data collected during the 2005 FWIN. The population density for CISC2 was estimated from a regression of fish density and catch-per-unit-effort generated from hydroacoustics data (Milne 2007, Milne 2008) and FWIN data for Lac La Biche for 2006 and 2007. FWIN catch rates for 2003 and 2005 (2003 = 43.29 cisco·100 $m^{-2}\cdot ha^{-1}$; 2005 = 22.16 cisco·100 $m^{-2}\cdot ha^{-1}$) were subbed into the regression equation CPUE = 0.1011*(density) + 0.1966 (R^2 = 0.9794) to generate density estimates for each year. An average density of 322 fish·ha^{-1} was used in the initial biomass calculation. The biomass of CISC1 was generated by Ecopath.

Production:Biomass (P/B)

A total mortality of 0.60 year^{-1} for CISC2 was used to parameterize the model. To generate this value a catch curve analysis was conducted in FAST 2.0 (Slipke and Maceina 2001) using FWIN data from both 2003 (0.803 year^{-1}) and 2005 (0.651 year^{-1}) and the average was calculated. This value was compared with the estimate of 0.47 year^{-1} derived from an analysis of the survivorship curve for LLB cisco from 2003 to 2005, and the average of the estimates was used. Estimates of 1.71 year^{-1} from Oneida Lake (Jaegar 2006) and 0.35 year^{-1} (www.fishbase.org) were used to define the range of probable values during the model balancing procedure. The total mortality of CISC1 could not be calculated with available data so the estimate of 1.71 year^{-1} from Oneida Lake was used as a preliminary input value.

Consumption:Biomass (Q/B)

The Q/B estimate of 6.42 year^{-1} from Oneida Lake (Jaegar 2006) was used as the initial value for CISC2 in the model. The range of reasonable estimates could not be defined due to a lack of published values; However, an alternate Q/B of 12.84 year^{-1} was calculated using equation 22 from the Ecopath Users Manual (Christensen et al. 2008) and based on the work of Palomares and Pauly (1989, 1998).

Diet composition

Cisco diet samples were collected seasonally (winter, spring, summer, fall) during 2005 and 2006 from a combination of sources (McGregor, unpublished data). Due to small seasonal sample sizes, data from all years and seasons were pooled.

Ecotrophic efficiency (EE)

The EE for each cisco group was estimated by Ecopath.

Suckers

Both the longnose sucker and the white sucker exist in Lac La Biche; however, the longnose sucker occurs at low densities and makes up only a small part of the overall biomass of the sucker group. As a result, data used to parameterize the model were generally specific to the white sucker. Suckers were represented as a single group due to a lack of available local data on any size class, and because they are not generally harvested by humans.

Biomass

The average weight of suckers in Lac La Biche (1025 g) was calculated from data collected during the 2005 FWIN and likely overestimates the true biomass as the fishing gear selects for larger individuals. Despite having counts of suckers captured in the FWIN gear, a population density estimate was not available due to the lack of a defined relationship between FWIN catch rate and sucker density. An initial estimate of 25 suckers·ha^{-1} was calculated from the average ratio of LKWH catch-per-unit-effort to sucker catch-per-unit-effort in the 2003 and 2005 FWIN. The ratio was then multiplied by the density estimate for LKWH2 to generate a density for suckers. Few published estimates were available for comparison though Kelso (1988) reported a sucker density of 21 suckers·ha^{-1} for Turkey Lake.

Production:Biomass (P/B)

The P/B value of 0.35 year^{-1} used in model parameterization represents the average of the values for Oneida Lake (0.32 year^{-1}) and the Bay of Quinte (0.38 year^{-1}) as reported by Jaegar (2006). Alternate values used to guide model balancing were 0.21 year^{-1} from www.fishbase.org, and 0.17 year^{-1} reported by Kelso (1988) for the Turkey Lake watershed.

Consumption:Biomass (Q/B)

Consumption/biomass was entered as the average of the values reported by Jaegar (2006) for Oneida Lake (3.65 year^{-1}) and the Bay of Qinte (3.80 year^{-1}). An alternate value of 7.73 year^{-1} was calculated using equation 22 from the Ecopath Users Manual (Christensen et al. 2008) and based on the work of Palomares and Pauly (1989, 1998).

Diet composition

Sucker diet samples were collected seasonally (winter, spring, summer, fall) during 2005 and 2006 from a combination of sources (McGregor, unpublished data). Due to small seasonal sample sizes, data from all years and seasons were pooled. Contents in the majority of stomachs were unrecognizable so the final composition was based on locally collected data but was modified using published diet reports.

Ecotrophic efficiency (EE)

The EE for suckers was estimated by Ecopath.

Sticklebacks

The stickleback group consists of brook sticklebacks (BRST) and nine-spine sticklebacks (NNST); However, due to the predominance of NNST in the diet of both fish and bird species, and the frequency of observation of NNST relative to BRST during survey events, the model was parameterized with NNST data. Sticklebacks were included as a distinct group in the model, rather than being incorporated into the 'Other small fishes' group, because they represent an important transitional food source for small walleye, pike and burbot, as well as large perch.

Biomass

The weight used in the estimate of stickleback biomass was 1.0 $g \cdot fish^{-1}$. This value was derived from individuals sampled as prey during the stomach contents analysis of Lac La Biche fish (McGregor, *unpublished data*) and represents a best estimate. Few alternate measurements of stickleback weight were available because they are rarely captured by sampling gear. No density estimate was available for sticklebacks in Lac La Biche, so the initial density used in the model was calculated from the ratio of the count of NNST to spottail shiners (SPSH) found in the diet of cormorants, multiplied by the density estimate for SPSH. The predicted density of 10,692 sticklebacks·ha^{-1} could not be verified because no published values were found in the literature.

Production:Biomass (P/B)

Initial model parameterization used 0.37 year^{-1} for the P/B of sticklebacks. This number was reported by Jaegar (2006) for Oneida Lake and was used to represent "all minnow-like fish" including darters, log-perch, and sculpins. This became the initial estimate because parameterization of the model incorporated Oneida Lake data as the default for many other species. An alternate estimate of 2.10 year^{-1}was reported at www.fishbase.org and provided the only other value available to guide the model balancing procedure.

Consumption:Biomass (Q/B)

A consumption/biomass value of 3.74 year^{-1} was reported by Jaegar (2006) for "minnow-like fishes" and was used as the initial estimate in the model. The only other estimate was 13.12 year^{-1} calculated using equation 22 from the Ecopath Users Manual (Christensen et al. 2008) and based on the work of Palomares and Pauly (1989, 1998). This value was not considered a reasonable estimate and was not used in during model balancing.

Diet composition

Stickleback diet samples were collected seasonally (winter, spring, summer, fall) during 2005 and 2006 from a combination of sources (McGregor, unpublished data). Due to small seasonal sample sizes, data from all years and seasons were pooled.

Ecotrophic efficiency (EE)

The EE of sticklebacks was estimated by Ecopath.

Other small fishes

The functional group called ‘Other small fishes’ consists of spottail shiners (SPSH), trout perch (TRPR), and Iowa darters (IWDR). Parameterization was based primarily on the characteristics of SPSH because most data were available for this species and it is assumed that they make up the majority of the biomass for this group. Spottail shiners are also the most important prey species described by this group.

Biomass

A weight of 3.49 g was used for SPSH based on the average weight of individuals in the 2005 FWIN. To calculate population density, hydroacoustics data from Lac La Biche (2006 & 2007) (Milne 2007, Milne 2008) were combined with catch-per-unit-effort data to generate a regression with the formula CPUE = 0.0172*(density) + 0.3481 ($R^2 = 0.9089$) (McGregor, *unpublished data*). This regression was used to generate an average spottail shiner density (235 fish·ha^{-1}) from 2003 and 2005 FWIN catch rates (2003 = 0.15 spottails·100 m^{-2}·ha^{-1}; 2005 = 8.64 spottails·100 m^{-2}·ha^{-1}). The biomass of this group was reported for spottail shiners only; trout perch and Iowa darters were not expected to significantly contribute to overall biomass and it was assumed that their contribution was captured within the range of biomass estimates calculated for SPSH.

Production:Biomass (P/B)

An initial P/B value of 1.71 year^{-1} was used to parameterize the model. This value was reported by Jaegar (2006) for emerald shiners and golden shiners in Oneida Lake and the Bay of Quinte. To provide a range of estimates for use in model balancing, a P/B value for trout perch (1.35 year^{-1}) was used (Jaegar 2006).

Consumption:Biomass (Q/B)

The initial Q/B value of 6.38 year^{-1} used to parameterize the model represents the average of the values for emerald shiners and golden shiners in models of Oneida Lake (6.42 year^{-1}) and the Bay of Quinte (6.33 year^{-1}) (Jaegar 2006). To guide changes to the production/biomass value during model balancing, the average (5.56 year^{-1}) of the values for trout perch in Oneida (5.71 year^{-1}) and the Bay of Quinte (5.40 year^{-1}) was used. No other estimates were available.

Diet composition

Spottail shiner diet samples were collected seasonally (winter, spring, summer, fall) during 2005 and 2006 from a combination of sources (McGregor, unpublished data). Due to small seasonal sample sizes, data from all years and seasons were pooled. Few diet data were available for trout perch and no local diet was collected for Iowa darters.

Ecotrophic efficiency (EE)

The EE of this group was estimated by Ecopath.

Birds

Lac La Biche is an important foraging, roosting, and breeding site for a large number of bird species. Many of these species rely on the lake's biomass to provide some part of their daily or seasonal energy requirements. To avoid introducing unnecessary model complexity, bird species represented in the model were restricted to those that either nest or regularly forage on the lake in large numbers, or for which there was a management concern.

Double-crested Cormorant (DCCO)

Biomass

Population estimates for DCCO for the 2003 to 2005 came from McGregor (2009). Biomass estimates were calculated based on an estimated average of 15,000 young-of-the-year birds present each year with an average weight of 1.6 kg/bird. Adult bird biomass was estimated at 22,131 nesting and non-nesting birds with an average weight of 2.015 kg/bird. Cormorant biomass was entered as the combined biomass of adult and young-of-the-year birds.

Production:Biomass (P/B)

The P/B ratio was calculated as the total weight of all fledglings (fledgling weight estimated to be 5% less than adult weight or 1.85 kg (Leger and McNeil 1987, Dunn 1975a)) divided by the total weight of all nesting and non-nesting adult birds.

Consumption:Biomass (Q/B)

The Q/B ratio was calculated by dividing the total consumption (kg/yr) of adult birds by the total biomass of adult birds (kg). Total consumption by adult birds was calculated by multiplying the average adult bird weight by the lower range of the estimate of adult daily consumption (20-25% of body weight per day (Dunn, 1975b)) and multiplying this daily consumption rate by 365 days. Consumption by young-of-the year birds was calculated following the same procedure. Both Q/B estimates were the same.

Diet Composition

Cormorant diet samples in the form of boli were collected from all major colonies on and around Lac La Biche since 2003 by staff of Alberta

Environment and Sustainable Resource Development (ESRD). Diet composition data were made available by ESRD staff (Marois and Hegerat, unpublished data) and were used to assess diet proportions by biomass. Diet items found in the boli representing species not found in LLB were lumped as 'import'. To account for the fact that cormorants season of residence in the LLB area is only 115 days on average (McGregor, unpublished data), and of the time spent in LLB only about 70% of the foraging occurs on the lake itself (McGregor, unpublished data), the diet proportions were scaled to reflect a 'diet import' proportion of 0.78.

American White Pelican (AWPE)

Biomass

Pelican population size was estimated by averaging the sum of the number of pelicans nesting on the Portage Lake colony and the number of chicks fledged, annually between 2003 and 2005 (McGregor 2009). Biomass calculations were based on a young-of-the-year population estimate of 439 individuals with an average weight of 3.37 kg, and an adult breeding population of 1,619 individuals with an average weight of 4.50 kg. Pelican biomass was estimated as the sum of adult and young-of-the-year biomass.

Production:Biomass (P/B)

The P/B ratio was calculated as the total weight of all fledglings (assumed fledgling weight of 3.5 kg) divided by the total weight of all breeding birds. This value does not include the weight of non-breeding adult birds as no estimate of this number was available. Due to the omission of non-nesting birds the P/B ratio may be an overestimate.

Consumption:Biomass (Q/B)

The Q/B ratio was calculated by dividing the total consumption (kg/yr) of adult birds by the total biomass of adult birds (kg). The total consumption by adult birds was calculated by multiplying the average adult bird weight by the middle of the range of estimates of adult daily consumption (20-40% of body weight per day (Hall 1925)) and multiplying this daily consumption rate by 365 days. Consumption/biomass for young-of-the-year birds was assumed to be the same as for adult birds.

Diet Composition

Pelican diet composition was derived from a combination of literature reports (Somers 2006; Findholt and Anderson 2005) and observations made locally by ERSD staff while working on the Portage Lake breeding colony (McGregor, unpublished data). Pelican season of residence was assumed to be similar to the cormorants (115 days), with only 40% of their local foraging activity occurring at LLB (McGregor, unpublished data). To address these assumption diet proportions were scaled to reflect a diet ‘import’ proportion of 0.89.

Piscivorous Waterbirds / Non-piscivorous Waterbirds

The piscivorous bird group consists of five taxa (common loon, common merganser, red-breasted merganser, red-necked grebe, western grebe) observed foraging on LLB during summer waterfowl surveys conducted by Christine Found, Wildlife Biologist with ESRD (unpublished data). The non-piscivorous waterbird group consists of 18 taxa: American coot, American wigeon, Barrow's goldeneye, blue-winged teal, bufflehead, canvasback, common goldeneye, eared grebe, gadwall, green-winged teal, lesser scaup, mallard northern pintail, northern shoveller, redhead, ring-necked duck, ruddy duck, white-winged scoter.

Biomass

The biomass of each waterbird group was estimated by multiplying the average number of individuals in each taxa observed in 2003 and 2005 by their average bird weight and then summing of the weights for all species.

Production:Biomass (P/B)

Information for the calculation of local P/B estimates was not available so a literature value of 0.25 year^{-1} (Moreau et al. 1993) was applied to both functional groups.

Consumption:Biomass (Q/B)

Information for the calculation of local Q/B estimates was not available so a literature value of 0.58 year^{-1} (Moreau et al. 1993) was applied to both functional groups.

Diet Composition

Diet information was gathered for all 18 non-piscivorous (Gauthier 1993, Austin and Miller 1995, Eadie et al. 199,; Johnson 1995, Dubowy 1996, Brown and Fredrickson 1997, Leschack et al. 1997, Austin et al. 1998, Hohman and Eberhardt 1998, Cullen et al. 1999, Mowbray 1999, Eadie et al. 2000, Brisbin et al. 2002, Brua 2002, Drilling et al. 2002, Mowbray 2002, Rohwer et al. 2002, Woodwin and Michot 2002) and five piscivorous taxa (Storer and Nuechterlein 1992, Mallory and Metz 1999, Stout and Nuechterlein 1999, Titman 1999, Evers et al. 2010) from individual species accounts published in the Birds of North America series. The average diet for each group was calculated by partitioning diet composition based on the relative proportion of species within each group. I assumed 90% of the diet of all waterbirds was imported due to seasonal migration or local foraging on lakes other than LLB.

Invertebrates

The choice of invertebrate groups was based on the level of detail provided by diet composition data of bird and fish species, as well as the lack of local invertebrate biomass, production, or consumption data for use in model parameterization. The ‘chironomid and dipteran’ group was chosen because it represents a significant prey for all size classes of perch as well as a number of the other fish species. The ‘amphipod’ group (predominantly *Hyalella azteca*) and the ‘molluscs and gastropods’ group (predominantly *Psidium spp.*) were highlighted because of their importance in the diet of lake whitefish and cisco. ‘Other invertebrates’ reflects the invertebrates found in the diet of northern pike and many of the other fish groups. These groups also reflect commonly observed invertebrates that are easy for non-entomologists to identify.

Chironomids and dipterans

Biomass

Chironomid and dipteran biomass was parameterized in two ways. For some models, Ecopath was allowed to estimate the biomass required to meet the predation demands of higher trophic levels under the constraints of the ecotrophic efficiency. Biomass was estimated because there was no source of information for estimating even relative values with any certainty under current model conditions. Alternately, a biomass estimate of 40 t/km^2 was calculated for LLB from 1964 and 1965 data (Pinsent 1967). Informal benthic assessment in 2010 and 2011 suggest estimates of 40 t/km^2 are not unreasonable (McGregor, *unpublished data*).

Production:Biomass (P/B)

The initial P/B value of 13.80 year^{-1} represents the average of the estimates used in the Oneida Lake (13.10 year^{-1}) and Bay of Quinte models (14.50 year^{-1}) (Jaegar 2006). This value falls within the range (4.97 year^{-1} to 18.5 year^{-1}) reported for other systems (Graham and Burns 1983, Mann 1971 as cited in Jorgensen et al. 1991). An extreme P/B estimate of 202 year^{-1} was reported for a riverine snag system (Benke 1998) suggesting that values can be much higher than those commonly reported in the literature.

Consumption:Biomass (Q/B)

The initial Q/B ratio of 65.85 year^{-1} is the average of the estimates reported in Jaegar (2006) for Oneida Lake (62.40 year^{-1}) and the Bay of Quinte (69.30 year^{-1}).

Diet

Local diet composition data for chironomids and dipterans were not available. Diet was estimated from diet compositions reported by Kay (1999) and diet descriptions from Thorp and Covich (2001) and Voshell (2007).

Ecotrophic Efficiency (EE)

Ecotrophic efficiency was estimated to be between 0.6 and 0.9. These values were in line with research from two forested streams that reported predators consumed 72 to 92% of all secondary production in the streams resulting in high losses of the invertebrate population due to predation (Hall et al. 2001). The EE was assumed to be highest for this invertebrate group because of the significance of this group in the diet of fish species.

Amphipods

Biomass

Amphipod biomass was parameterized in two ways. In some models, Ecopath was used to estimate this parameter using the ecotrophic efficiency value provided. For the other models, an approximate biomass estimate of 2 t/km^2 was derived from LLB data collected by Pinsent (1967) for 1964 and 1965.

Production:Biomass (P/B)

A value of 5.70 year^{-1} as reported by Jaegar (2006) for the Oneida Lake and Bay of Quinte models and was used to as the initial P/B estimate for amphipods in LLB. This value falls well within the range (4.2 year^{-1} to 8.76 year^{-1}) reported for other systems (Waters 1977, Greze 1973 as cited in Jorgensen et al. 1991, Mann 1971 as cited in Jorgensen et al. 1991).

Consumption:Biomass (Q/B)

The Q/B value of 30.20 year^{-1} used in the initial parameterization of the model is the value used in both the Bay of Quinte and Oneida Lake ecosystem models (Jaeger 2006).

Diet

Local diet composition data for amphipods were not available. Diet was estimated from diet composition values reported by Kay (1999) and diet descriptions from Thorp and Covich (2001) and Voshell (2007).

Ecotrophic Efficiency (EE)

As for the chironomids and dipterans, the EE for this group was estimated to be between 0.6 and 0.9. Total loss of amphipods as a direct result of predation is assumed to be moderately less than that of the other invertebrate groups so the EE assumed for this group was lower.

Molluscs and Gastropods

Biomass

Mollusc and gastropod biomass was parameterized in two ways. In some models, biomass was estimated by Ecopath so that the predation needs of higher trophic levels were met for the given ecotrophic efficiency value. For the other models, an approximate biomass estimate of 4 t/km^2 was derived from LLB data collected by Pinsent (1967) for 1964 and 1965.

Production:Biomass (P/B)

The P/B value (3.80 year^{-1}) used in the initial model parameterization represents the value used for clams in the Bay of Quinte and Oneida Lake ecosystem models (Jaeger 2006). Clams were used as the estimate for this group because the majority of items found in fish diets were small clams, though gastropods were also identified. This value was higher than the range of estimates (0.2 year^{-1} to 3.5 year^{-1}) reported for other systems (Picken 1979).

Consumption:Biomass (Q/B)

The initial Q/B estimate of 24.40 year^{-1} was reported by Jaeger (2006) for the Bay of Quinte and Oneida Lake ecosystem models. No other estimates were available.

Diet

Diet composition was derived from estimates reported by Kay (1999) as well as background information gleaned from a variety of other sources (Voshell 2007, Lance et al. 2006, Thorp and Covich 2001, Clifford 1991).

Ecotrophic Efficiency (EE)

Ecotrophic efficiency was estimated to be between 0.6 and 0.9. Compared to the other invertebrate groups, the EE of molluscs and gastropods was assumed to be low to moderate as predation was likely a less significant portion of the total mortality.

Other invertebrates

This group is an amalgamation of all remaining genera that were observed as prey items in fish stomachs. Leeches were the dominant contributor to the overall biomass of the group though the aquatic larvae of terrestrial invertebrates (primarily odonates, corixids, trichopterans, and ephemeropterans) were also major contributors.

Biomass

Invertebrate biomass was parameterized in two ways. In some models, Ecopath was allowed to estimate the biomass required to meet the predation and ‘other mortality’ constraints imposed by the ecotrophic efficiency applied to this group. For the other models, an approximate biomass estimate of 2 t/km^2 was derived from LLB data collected by Pinsent (1967) for 1964 and 1965.

Production:Biomass (P/B)

The initial P/B estimate of 4.63 year^{-1} was the average of the Oneida Lake (5.35 year^{-1}) and Bay of Quinte (3.90 year^{-1}) estimates for leeches and insects used in Jaeger (2006).

Consumption:Biomass (Q/B)

The initial Q/B estimate of 33.95 year^{-1} represents the average of the values used in ecosystem models of Oneida Lake (31.80 year^{-1}) and Bay of Quinte (36.10 year^{-1}) (Jaeger 2006).

Diet

Initial diet estimates were derived from the compositional diet data reported by Kay (1999), modified to reflect the diet as reported by Voshell 2007, Thorp and Covich 2001, and Clifford 1991.

Ecotrophic Efficiency (EE)

The EE for this group was expected to be lower than or similar to the estimate applied to ‘molluscs & gastropods’ but still within the range of 0.6 year^{-1} to 0.9 year^{-1}. The low EE was assumed because of the breadth of species amalgamated into this group.

Plankton

Plankton was split into four groups for use in the model, specifically pelagic zooplankton, littoral zooplankton, phytoplankton, and cyanobacteria. Species within each group were aggregated because the diet compositions for the fish and invertebrate species preying on plankton could not be accurately assessed at any finer scale. Pelagic and littoral zooplankton was separated to reflect differential predation based on habitat separation. Phytoplankton and cyanobacteria were treated as separate functional groups because of the significant difference in their use as a prey source.

Pelagic and Littoral Zooplankton

Biomass

Pelagic zooplankton density and biomass data from LLB for 2003 and 2004 were provided by the laboratory of D.W. Schindler at the University of Alberta (*unpublished data*). Biomass data for 23 zooplankton species, six genera, and eleven copepod life stages were used for this analysis. Biomass data for all species, genera, and life stages were amalgamated and a total biomass (ug/L; dry weight) was calculated for each survey month. Dry weight biomass was converted to wet weight (ug/L; WW)) by assuming a water content for zooplankton of 95% (Rolf Vinebrooke, *personal communication*, 26 July 2009). Monthly estimates were converted from ug/L (WW) to g/m^3, and then to g/m^2 by multiplying by the average lake depth (m). To obtain an average seasonal biomass estimate, data were generated for those months during which no sampling occurred (January, March, November, December) by inferring an average biomass from neighbouring months. January biomass was assumed to be the same as February, March was calculated as the mid-point between February and April, November was assumed to be one-half the biomass of October, and December was one half of the combined biomass for October and November.

Littoral zooplankton biomass and the ratio of littoral/pelagic zooplankton biomass was provided by Catherine McGavigan (School of Environmental Sciences, University of Ulster, Personal communication, 5 June 2011). Average littoral biomass (cladoceran and copepoda) was 451 ug C/L and pelagic zooplankton was 15 ug C/L.

Production:Biomass (P/B)

The initial P/B estimate for zooplankton (32 year^{-1}) is the average of the copepod P/B reported for the Bay of Quinte and Oneida Lake ecosystem models (BQ-QL CMP Workgroup as cited by Jaeger 2006). This values falls within the 22 to 55 year^{-1} range reported for zooplankton in a variety of other mesotrophic to eutrophic systems (BQ-QL CMP Workgroup as cited by Jaeger 2006, Angelini and Agostinho 2005, Cox and Kitchell 2004, Waters 1977).

Consumption:Biomass (Q/B)

The initial zooplankton Q/B estimate of 120 year^{-1} (Cox and Kitchell 2004) falls within the range (82 year^{-1} to 250 year^{-1}) reported for zooplankton in Oneida Lake, the Bay of Quinte, and a variety of other systems (BQ-QL CMP Workgroup as cited by Jaeger 2006, Angelini and Agostinho 2005).

Diet

Locally collected diet data were not available so an average diet composition was derived from a variety of sources (Thorp and Covich 2001, Kay 1999, Pennak 1989).

Phytoplankton and Cyanobacteria

Biomass

Phytoplankton and cyanobacteria density and biomass data from LLB for 2003 and 2004 were provided by the laboratory of D.W. Schindler at the University of Alberta (Schindler, unpublished data). A total of 218 identifiable species found during the two survey years were amalgamated into six groups including: cyanobacteria, chlorophytes, chrysophytes, diatoms, dryptophytes, and dinoflagellates. Monthly biomass (mg/m^3) data were available for May through October; biomasses for November through February were calculated as a decreasing proportion of the previous month's value. March and April biomasses were increased to achieve the values reported from May field sampling. The monthly biomass of all phytoplankton, with the exception of cyanobacteria, was averaged to provide an annual phytoplankton biomass in mg/m^3. This number was converted to g/m^2 by multiplying by average lake depth. Identical calculations were performed to estimate the biomass of cyanobacteria.

Production:Biomass (P/B)

The P/B estimate initially used to parameterize the model (131.5 $year^{-1}$) is the average of the values used by Jaeger (2006) and Koops et al. (2006) for Oneida Lake and the Bay of Quinte. This falls within the range of values reported from other systems (Fetahi and Mengistou 2007, Angelini and Aghostinho 2005, Cox and Kitchell 2004).

Submerged Aquatic Vegetation (SAV)

The SAV group represents macrophytes, as well as epiphytes and periphytes. These groups were combined to control uncertainty because data were not available for any of the groups.

Biomass

No data were available for estimating SAV biomass for LLB. Ecopath was allowed to generate the biomass required to satisfy the constraints imposed by the P/B and EE values provided.

Production:Biomass (P/B)

A P/B value of 8.80 year^{-1} (Jaeger 2006) was used to maintain consistency with the main source of parameter estimates for other species. This value is low compared to the estimate of 35 year^{-1} reported by Angelini and Agostinho (2005) for the Upper Parana River floodplain.

Ecotrophic Efficiency (EE)

The initial EE of 0.11 is as reported by Angelini and Agostinho (2005) for the Upper Parana River floodplain.

Appendix D - Literature Citations

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Chapter 5 - General discussion and synthesis.

According to Leonard Duhl, “Ecology may be defined as that inter-intra confrontation of biological, social and historical factors…” (Anderson 1996 as cited in Keller and Golley 2000). Throughout my dissertation I have discussed ecosystem restoration as a social and ecological process (Jackson 1995) that requires an understanding of both the disturbance history of an ecosystem (Landres et al. 1999, Moore et al. 1999), and the ecosystem response to disturbance. Ecosystems are dynamic and their development is inseparable from the formal and informal management practices of the past. How people used ecosystem goods and services (clean water, power, navigation, food, recreation) historically altered the system in ways that affected their structure, function, and resilience and predisposed them to further change (Seastedt et al. 2008). The combined impact of anthropogenic disturbances (i.e. eutrophication and fisheries harvests) is a degraded ecosystem “…characterized by unpredictability and surprise in [its] capacity to generate ecosystem services” (Folke et al. 2004). Whether a degraded ecosystem exhibits a gradual phase shift, an alternate stable state (ASS), or non-equilibrium stochastic dynamics in response to a disturbance influences the approach and response to restoration (Hobbs and Suding 2009).

My research on the restoration potential of walleye within a large lake ecosystem currently dominated by cormorant foraging selection contributes to our understanding of how disturbance, system structure and function, and resilience influence the existence of alternate stable states. My dissertation combined the theoretical and practical components of ecological restoration to address a fisheries management issue by 1) estimating harvest disturbance from pre-European contact to the present time (Chapter 2 [McGregor in review]), 2) creating a plausible representation of the state variable and parameter combinations that might have existed historically and modeling the response of these variables and parameters to historic fisheries harvest (Chapter 3 [McGregor in review]), 3) exploring how the ecosystem response to a disturbance changes over time as variable and parameter combinations change

(Chapter 4), and questioning/providing guidance on the restoration potential and management approach most likely to achieve the recovery of the walleye population (Chapter 4). This type of research is not possible using a traditional, empirical approach in isolation because we lack data from historic periods, system complexity at the ecosystem level is too large, and the temporal scale for observing ecosystem change is too long for a single research study. Using ecosystem models parameterized with the best quantitative and empirical data available, I overcame many of these challenges and helped discovery and learning to proceed. To derive the full benefit from my research, however, it is important that empirical study of the Lac la Biche ecosystem continues into the future so that model predictions can be validated or refuted and our understanding of how the system operates can be improved. Additional research to assess the role of eutrophication in historic system dynamics and future restoration potential would also enhance understanding of the ecosystem.

In the introduction to my dissertation I posed three general hypotheses that 1) the Lac la Biche ecosystem exhibits ASSs defined by walleye and cormorant dominated equilibriums and that the transition between these states is controlled by the size structure and biomass of the yellow perch population, 2) restoration to a walleye-dominated state can be achieved through walleye stocking and cormorant control, and 3) restoration targets set to imitate system conditions in 1900 are not adequate for long-term sustainability of the walleye population. These hypotheses can be tested by combining the outcomes of Chapters 3 and 4. The third hypothesis in its original form was rejected; changes to ecosystem variables and parameters resulting from historical fisheries harvests were smaller than expected suggesting that restoration goals targeting the year 1900 are appropriate for meeting the program objectives. However, trade-offs in potential fisheries yield and ecosystem resilience were identified for consideration (Chapter 3). The first hypothesis was supported and the second hypothesis was partially rejected by the outcomes of the simulation experiments in Chapter 4. Results suggest hypothesized ASSs existed in the historical ecosystem (1800, 1900) but that a single equilibrium attractor exists in the contemporary ecosystem (1965, 2005). The loss of the walleye attractor was likely due to anthropogenic changes in the abiotic and biotic conditions of the system throughout the 20th century. The stability of each equilibrium state was determined by the differential foraging selection of the dominant predator (walleye or cormorants) on their main prey species, yellow perch. From these results I concluded that the walleye-dominated state of the historic ecosystem cannot be restored because it no longer exists in the system's potential. However, enhanced understanding of the interactions and feedbacks in the system resulting from the combined research of all chapters suggests fisheries managers can imitate desirable conditions of the historic ecosystem (Jordan et al. 1990), namely recovery of the walleye population to near historic biomasses, through walleye stocking and cormorant control. The parameters and variables representing ecosystem conditions in 1800 and 1900 (Chapter 2) provide valuable targets for guiding this process.

Restoration has become a 'hot topic' in fisheries management in recent years and this dissertation provides an important and unique approach to understanding restoration potential from both a theoretical and practical perspective. Specifically assessing the alternate stable state relationship between walleye, double-crested cormorants, and yellow perch has wide-ranging value in North America (Johnson et al. 2002, Hebert and Morrison 2003, Fenech et al. 2004, Rudstam et al. 2004, Dorr et al. 2012), Europe (Frederiksen et al. 2001, Behrens et al. 2008, Russell et al. 2008), and some countries in Asia (Kameda et al. 2003 as cited in Russell et al. 2008, Tsuboi and Ashizawa 2012) where the interactions between cormorants (or other birds) and fish populations has demanded management action. The commonality of issues (decrease in fish predators, increase in forage fish, explosion of cormorants) between these spatially disparate areas suggests the results of my research can and should inform the understanding and thinking of ecologists and managers. I recognize that these results are not prescriptive and will not be generally applicable across systems. This is expected because ecology is "…a science of case studies" (Keller and Gulley 2000). However, the restoration process described by this dissertation is valuable to the fields of ecology and wildlife management because it offers "…an ecological technique, the comprehensive form of medicine, a science and art of healing at the community and ecosystem level" (Keller and Gulley 2000). As the human population grows and the need and desire for restoration develops and changes, this prescription of discovery and verification, understanding and creation will become ever more important.

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