University of Alberta

DOUBLE-CRESTED CORMORANT DIET ON BOREAL LAKES: IMPLICATIONS FOR FOOD WEB STRUCTURE AND FISHERIES MANAGEMENT

by

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of **Master of Science**

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta
Spring 2007

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Your file Votre référence
ISBN: 978-0-494-29955-5
Our file Notre référence
ISBN: 978-0-494-29955-5

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When one tugs at a single thing in nature, he finds it attached to the rest of the world.
– John Muir (1838-1914)

This thesis is dedicated, with love, to my parents.
To Dad - for encouraging me to undertake new challenges.
To Mom - for reminding me to have fun along the way.

Abstract

In lake ecosystems, knowledge of the direct and indirect effects of apex predators and piscivory is essential to managing fisheries and maintaining water quality. To determine if population increases of the double-crested cormorant (*Phalacrocorax auritus*) on boreal lakes are influencing food web structure and function via top-down effects, I used a combination of conventional diet and stable isotope analyses. Analysis of regurgitation samples collected from five colonies in the Lac La Biche area of north-central Alberta during 2003 and 2004 identified 13 different prey species in cormorant diets. The majority of fish consumed were small in size, less than 100 mm in length. Yellow perch was the most frequently captured species on all colonies and also comprised the largest proportion of biomass in regurgitation samples. Based on isotopic signatures and diet composition, birds nesting on small lakes were found to forage on the local nesting lake as well as on Lac La Biche; however, foraging appeared to be focused primarily on Lac La Biche. In large lakes, such as Lac La Biche, isotopic ratios of carbon and nitrogen yielded similar trophic levels for double-crested cormorants and predatory fish: walleye and northern pike.

Acknowledgements

Great thanks go to my supervisor, Cindy Paszkowski, for her guidance and support. Thanks also to my committee members Rolf Vinebrooke, Charles Wong and Chris Davis for their encouragement and insightful discussions. This research was made possible thanks to the generous financial support provided by the Alberta Conservation Association (ACA) Biodiversity Grant; North American Waterfowl Management Plan (NAWMP) Biodiversity Initiative; Canadian Circumpolar Institute C/BAR Grant; AB Sport, Recreation, Parks and Wildlife Foundation; the ACA Grant Eligible Fund; Alberta Sustainable Resource Development; and the University of Alberta.

I was fortunate to have a huge number of people who helped with field and laboratory work. I couldn't have done it without you. I am particularly indebted to my field assistant Jenice Bruinsma whose enthusiasm could make even the collection of bird puke fun. Thanks for all your hard work and patience and for learning to share my love of fish.

I would also like to extent great thanks to Alberta Sustainable Resource Development who provided in-kind support as well as field help and support throughout this project. I would especially like to thank Andrea McGregor, Chris Davis, Alicia Pruden, Nadine Marois, Dwayne Latty, and Jordan Walker. Thanks for all the good times in Lac La Biche.

Thanks to all the others who also helped in the field including Derek Bleakley, Josh Morrisey, Shuo Chan, and Selma Losic. For all the hours devoted to lab analysis I would like to thank Keith Jackson, Amy Darling, Wendy Markowski, Nicholas Wu, Emily Cliff, Serbhi Bansal, and Lindsey Wilson. Thanks for putting up with the smell of bird puke and partially digested fish. Thank you to Martina Hillbrand for generously volunteering your time for the benefit of the birds and the fishes.

I am very grateful to the many graduate students who provided a stimulating and fun environment in which to learn and grow. Thanks for providing many distractions and reminders that life does exist beyond my research. Thanks to the Paszkowski-Tonn Lab group for the discussions, the advice, and

the laughter – I will miss our Friday meetings.

Thanks to my family, Mom, Dad, and Monique, for your unfailing love and support. Thank you for always believing in me. Finally, thanks most of all to my husband, James, who provided unwavering support during meltdowns of all kinds (computer and emotional). Thanks for keeping me laughing during it all.

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Chapter 1

Introduction

1.1 The importance of apex predators in boreal lakes

Widespread changes are occurring in lake ecosystems across North America. Boreal regions are likely to be among the hardest hit by climatic changes and the cumulative effects of other anthropogenic stresses (Schindler, 1998*a*). Declines in fisheries and water quality have become an increasing concern in most large water bodies of the southern boreal zone (Schindler, 1998*b*). Native fish communities have been severely altered by overharvest, habitat degradation, pollution, and introduction of exotic species (Schindler, 2001). As a result of these intense pressures, the collapse of significant fisheries have been reported in many inland lakes (Post et al., 2002; Allan et al., 2005). These collapses have resulted in extinctions or substantial declines in piscivorous fish species such as lake trout (*Salvelius namaycush*), northern pike (*Esox lucius*), and walleye (*Sander vitreus*) (Post et al., 2002; Sullivan, 2003*a*). The loss of these large predators has important implications, not only for social and economic values (Sullivan, 2003*b*; Allan et al., 2005), but also to food web dynamics of these lakes (Pimm et al., 1991).

Predation in lake ecosystems is a major force that can act to structure biotic communities through direct or indirect effects (Kerfoot and Sih, 1987). Not only are specific prey populations affected by their predators, but other trophic levels of lakes may also be influenced through food web linkages. Apex predators have been known to shape the entire food web of lakes through top-down controls (Carpenter et al., 1985). These trophic cascades have been documented in a variety of ecosystems (Pace et al., 1999; Lathrop et al., 2002) and result in changes in abundance or biomass across more than one trophic link (Carpenter et al., 1985, 1987). The removal of a top predator in a lake system will often result in an explosion of populations of planktivorous fishes resulting in heavy predation on large herbivorous zooplankton (Kerfoot and Sih, 1987) and subsequent increases in algal productivity (Carpenter et al., 1987). Alternatively, effective management that increases populations of large predatory fish can accelerate improvements in water quality in some circumstances (Kitchell, 1992).

1.2 Studying food web structure

Food webs are used to describe interactions between organisms in a community (Pimm, 1982). Although aquatic food webs are incredibly complex, there are common patterns in food web structure that can be used to predict community dynamics (Pimm et al., 1991). Because of the inherent ecological complexity of food webs, a variety of tools are necessary to simplify these systems and characterize important biological processes which shape food web structure.

Food webs can be studied by observing directly the types of prey consumed by key organisms through analysis of stomach contents or regurgitation samples (Duffy and Jackson, 1986; Vander Zanden et al., 1997; Beaudoin et al., 1999). Direct diet analysis provides good taxonomic resolution to identify important prey resources consumed by predators, and thus can be used to assess predator-prey relationships. This method provides detailed quantitative results on prey consumption. Food web structure, and presumably diet, varies over time and space (Pimm et al., 1991); therefore, gathering stomach content data over sufficient time periods and localities can be logistically difficult. A large number of samples is required and subsequently a great deal of time must be spent analyzing these samples (Forero et al., 2004; Clarke et al., 2005). This method can become too time intensive to identify broad scale food web structure.

The analysis of naturally occurring isotopes, particularly carbon and nitrogen, can also be used as an efficient way to describe food webs and identify trends through time. Isotopic composition of an organism changes in predictable ways by the process of fractionation during elemental cycling in natural systems (Peterson and Fry, 1987). Stable isotope analysis offers many advantages over regurgitation or stomach content analyses because it reflects prey assimilation and can help identify important temporal and spatial variability in diet (Vander Zanden et al., 1997; Harvey and Kitchell, 2000; Vander Zanden and Vadeboncoeur, 2002).

Ratios of heavy to light isotope of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) from the tissue of various organisms can provide a variety of useful information in food web studies (Peterson and Fry, 1987; Fry, 1991). Carbon isotope ratios are usually conserved within a food chain (Vander Zanden and Rasmussen, 1999; Vander Zanden and Vadeboncoeur, 2002), therefore ratios in consumers can be used to differentiate between resources derived from different habitats or primary producers (Mizutani et al., 1990; Hobson et al., 1994; France, 1995; Vander Zanden and Rasmussen, 1999). Attached algae and detritus, located in littoral habitats, generally exhibit less ^{13}C fractionation than pelagic phytoplankton (France, 1995), therefore organisms deriving energy from the pelagic food web are typically more depleted in ^{13}C than organisms that feed in the littoral zone of a lake (Vander Zanden and Rasmussen, 1999; Post, 2002). In contrast, the heavy nitrogen isotope (^{15}N) of a consumer is enriched relative to its diet (Minagawa and Wada, 1984; Peterson and Fry, 1987). As organisms preferentially excrete the lighter nitrogen isotope, this will result in an increase in ^{15}N with increasing trophic level. Stable nitrogen isotope ratios can be used to estimate a discrete trophic position for each organisms based on a typical 3.4‰ enrichment per trophic level (Post, 2002). Calculating discrete trophic levels based on this enrichment can fail to take into consideration trophic omnivory that is often present in ecosystems. Alternatively, nitrogen ratios can be used as a continuous measure of trophic position which represents assimilated energy from different trophic pathways leading to an organism (Cabana and Rasmussen, 1996; Post, 2002).

There is inherent variation in carbon and nitrogen isotope values between primary consumers in different lakes because of differences in the isotope ratios of carbon and nitrogen available for uptake. Isotopic signatures of upper-level consumers can not be used for comparisons among lakes until they have been adjusted relative to an appropriate baseline. Use of long-lived primary consumers for baseline standardization enables quantitative estimates of trophic position for comparison across aquatic food webs (Vander Zanden et al., 1997; Post, 2002).

1.3 The Lac La Biche region

Lac La Biche (LLB) is a lake of important cultural and economic significance. It is the seventh largest lake in Alberta located in the Boreal Mixedwood Ecoregion of north-central Alberta (Mitchell and Prepas, 1990). The town of LLB (~2700 people), which originated as a Hudson's Bay trading post, is located on the southeast shore of the lake and the village of Plamondon (~300 people) is 3 km west of the lake. Approximately 30% of the land in the LLB catchment is used for agriculture (Neufeld, 2005). Shoreline development from cottages and lakefront homes is present on approximately two thirds of the lakeshore (Gammon, 2001).

Commercial fishing has been important in the area since the early 1900s (Mitchell and Prepas, 1990). Fish catch has been quite variable because of fluctuations in year class strength and population crashes due to overfishing and winterkill (Mitchell and Prepas, 1990). There are 13 fish species in the lake: walleye (*Sander vitreus*), yellow perch (*Perca flavescens*), Iowa darter (*Etheostoma exile*), ninespine stickleback (*Pungitius pungitius*), brook stickleback (*Culaea inconstans*), burbot (*Lota lota*), trout perch (*Percopsis omiscomaycus*), lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedi*), northern pike (*Esox lucius*), white sucker (*Catostomus commersoni*), longnose sucker (*Catostomus catostomus*), and spottail shiner (*Notropis hudsonius*). The fish community in the lake has changed dramatically over the years. Although walleye were once abundant in LLB, the population collapsed in the 1960s and despite extensive stocking efforts, numbers have not exhibited any substantial increase (Sullivan, 2003*a*). The lake fish community in recent years has come to be dominated by a high abundance of juvenile yellow perch and cisco (Chris Davis, provincial biologist, unpublished data).

LLB is recognized as an important bird area and the diversity and abundance of bird species is considered one of the most significant wildlife features in the area (Gammon, 2001). The lake supports a rich community of breeding colonial and non-colonial waterbirds, including western grebe (*Aechmophorus occidentalis*), California gull (*Larus californicus*), double-crested cormorant (*Phalacrocorax auritus*), great blue heron (*Ardea herodius*), American white pelican (*Pelecanus erythrorhynchos*), and Caspian tern (*Sterna caspia*) (Gammon, 2001). In 1925 the lake's islands were established as a bird sanctuary, and in 1952 a provincial park was created on Big Island (later named Sir Winston Churchill Park) (Mitchell and Prepas, 1990).

LLB is a large (234 km^2), shallow lake with a mean depth of 8.4 m. There are two main basins which are partly separated by a peninsula and two islands. The west basin is open and relatively deep (maximum depth 21.3 m), whereas the east basin of the lake has numerous islands and sand/gravel spits, which provide excellent nesting and loafing sites for a variety of aquatic bird species. This area of the lake also provides excellent spawning, rearing and adult habitat for the main sportfish species. The lake is hypereutrophic with mean total phosphorus levels of 117μg/L in the west basin and 108μg/L in the east basin (Mitchell and Prepas, 1990). Algal blooms occur annually during the summer months. Key concerns about the health of the lake ecosystem have included algal density, aquatic macrophyte growth, nutrient levels, and depletion of piscivorous fish populations (Mitchell and Prepas, 1990).

Increases in the number of double-crested cormorants in the region have generated concerns that these birds may be responsible for alterations in fish abundance and community structure in LLB. Cormorants in the region (which includes 82 lakes within a 50 km radial distance of LLB) have been observed foraging on 38 lakes and have been documented on nine nesting colonies (McGregor, 2004). A 2004 survey of double-crested cormorant colonies detected roughly 8000 nests on LLB and nearby lakes (McGregor, 2005). This number is up from approximately 7000 nests counted in 2003 (McGregor, 2004). Ninety five percent of these nests are found on four major colonies: High Island and Pelican Island (on LLB), Antoine Lake and Portage Lake. Since LLB is the largest lake in the area with abundant prey resources, it likely supports food not only for birds nesting on islands on LLB, but also from birds nesting on smaller surrounding lakes. Historical counts of cormorants in the area are limited but it is unlikely that these large numbers have occurred in the past (Hatch, 1995). Changes in cormorant numbers are likely a reflection of system-wide changes in lakes across North America with LLB being no exception (Hobson et al., 1989; Post et al., 2002; Sullivan, 2003*a*).

It is unlikely that cormorants contributed to the fisheries decline in LLB, but it is currently unknown whether the birds may impede a fisheries recovery effort. Public tolerance of the large numbers of birds is low and as a result of local political pressure, a cormorant management program was implemented in 2003 in the Lac La Biche region. This program was part of a strategy to control double-crested cormorant numbers and recover local fish populations (McGregor, 2004). This program has provided a valuable opportunity to collect information about an important aquatic predator with the potential to use this information to help guide future management initiatives.

1.4 Double-crested cormorant history and biology

The double-crested cormorant is one of six species of cormorant in North America and is the only North American cormorant species that inhabits inland bodies of fresh water (Hatch, 1995; Hatch and Wesoloh, 1999). Double-crested cormorant populations have fluctuated dramatically over the last century. Declines in the 1950s and 1960s were partly caused by organic contaminants leading to reduced productivity and eggshell thinning (Price and Weseloh, 1986; Weseloh and Ewins, 1994; Ludwig et al., 1995). Large scale anthropogenic destruction of eggs and cormorants in some regions was also thought to have contributed to the disappearance of many colonies in prairie Canada (Vermeer, 1969; Vermeer and Rankin, 1984). Due to concerns about low population numbers in many areas, cormorants were protected under federal law in the United States in 1972 when the birds were added to the Migratory Bird Treaty Act (Trapp et al., 1995); however, cormorants today remain unprotected by federal regulations in Canada (Keith, 1995).

Despite these historical causes of decline and persecution, widespread increases of cormorants have been observed across North America and Europe since the early 1980s (Hatch, 1995). Increases in cormorant numbers have been coupled with a rise in conflicts with commercial/recreational fisheries and aquaculture industries as cormorant species are often held responsible for declining fish catches (Carss, 1995; Wires et al., 2001; Rudstam et al., 2004). Cormorant population increases are likely a result of concomitant factors. Since restrictions on pesticide use in 1974, reproductive output has increased dramatically (Weseloh and Ewins, 1994). The widespread collapse of many sport fisheries across North America has provided an explosion of small-bodied fish species (Walters and Kitchell, 2001; Post et al., 2002). Cormorants may have benefited from these changes in fish species composition and additional prey resources (Hobson et al., 1989). In addition, the development of the aquaculture industry in the lower Mississippi River and along the Gulf Coast may provide food to enhance survival during the overwintering period (Weseloh and Ewins, 1994; Withers and Brooks, 2004).

Double-crested cormorants typically arrive in the LLB region in late April from their overwintering grounds in the southern United States between Texas and Florida (Dolbeer, 1991). Cormorants generally begin laying clutches of 3 to 4 eggs in early May (Brechtel, 1983). The young hatch after approximately 30 days and are ready to leave the nest to form creches when they are 3 to 4 weeks old (Hatch and Wesoloh, 1999). At 6 to 7 weeks, chicks will accompany adults on foraging bouts and at 10 weeks old they are completely independent.

Cormorants typically nest on islands in proximity to desirable foraging habitat. The majority of foraging is thought to occur at short distances from nesting colonies (< 3 km) (Custer and Bunck, 1992; Coleman et al., 2005), but heavy foraging pressure has also been found to range as widely as a 10 to 20 km radius from a colony (Neuman et al., 1997; Stapanian et al., 2002; Anderson et al., 2004) and maximum foraging distances up to 40 km have been recorded in some cases (Custer and Bunck, 1992). In general, cormorants require reliable food sources close to colonies (Duffy, 1995). Cormorants may commute farther if particularly attractive fishing grounds exist distant from appropriate nesting sites (Warke and Day, 1995; Anderson et al., 2004). There are energetic costs to foraging at greater distances (Neuman et al., 1997; Warke and Day, 1995); therefore, additional energy expenditures, through travel to more distant lakes, must be compensated by access to more easily captured, more abundant, or higher energy prey (Anderson et al., 2004).

Cormorants capture prey by pursuit diving and often forage in large groups that include other waterbird species (Hatch and Wesoloh, 1999). Foraging typically occurs in offshore habitat at water depths up to 10 m (Neuman et al., 1997; Custer and Bunck, 1992). Foraging behaviour of cormorants can be affected by the distribution of fishes in a lake, particularly schooling species, which are often identified as important components of the diet (Hobson et al., 1989; Anderson et al., 2004; Withers and Brooks, 2004). Time handling a prey item is much less than time spent searching for prey which suggests that cormorants will feed opportunistically on any prey encountered (Duffy, 1995).

The diet of double-crested cormorants at most locations is almost entirely fish; however, there is great spatial and temporal variability in species consumed between sites. More than 250 species of fish in salt and freshwater have been recorded in the diet. The most commonly consumed sizes of fish are less than 15 cm but prey sizes can range up to 40 cm (Hatch and Wesoloh, 1999). The majority of diet studies have found the prey of cormorants to be primarily small forage fishes with little commercial value (Robertson, 1974; Campo et al., 1993; Blackwell et al., 1995; Madenjian and Gabrey, 1995; Neuman et al., 1997; Wires et al., 2001; Withers and Brooks, 2004). In some lakes where sport fish are abundant, cormorants have been documented to increase mortality of certain age-classes of important species (VanDeValk et al., 2002; Lantry et al., 2002; Burnett et al., 2002; Rudstam et al., 2004). Since cormorant diet is so variable, prey consumption must be explored on a case specific basis.

Cormorant diet is most commonly studied using pellets, regurgitates, and gut content analyses (Duffy and Jackson, 1986; Carss, 1995; Seefelt and Gillingham, 2006). Several biases are associated with the use of pellets, including underestimating the length of fish consumed and the proportion of soft bodied fish species in the diet as well as overestimating the importance of invertebrates (Derby and Lovvorn, 1997; Seefelt and Gillingham, 2006). Although gut content analysis can provide an accurate assessment of prey importance, obtaining sufficient sample sizes of adult birds for gut content analysis is often not possible. Regurgitation analysis provides the most practical means of assessing cormorant diet (Seefelt and Gillingham, 2006) and a large number of samples can be obtained with minimal disturbance to the birds. With this method, variability during pre-chick and post-chick foraging periods is missed since regurgitation samples can only be obtained during the nesting period. Regurgitation samples represent material being fed to chicks at nests. These samples may differ from prey that the adults consume throughout the remainder of their time on the breeding grounds (Derby and Lovvorn, 1997; Neuman et al., 1997). Adult cormorants may bring larger (Carss, 1995; Hobson et al., 1989), or smaller (Duffy and Jackson, 1986) prey back to nestlings than prey they consume themselves. But despite these biases, regurgitation analysis is commonly used to assess diet of waterbirds (Duffy and Jackson, 1986) and has been found to be an accurate representation of adult consumption (Carss, 1995; Johnson et al., 2006; Seefelt and Gillingham, 2006).

1.5 Scope of the project

My work was conducted during the initial stages of the LLB cormorant management program. Prior to this program, there was little information on prey consumption by cormorants in the LLB ecosystem; however, political pressures often guide the human tendency to simply remove any predator that competes for valuable fisheries resources (Yodzis, 2001). The main objectives of my research were to provide a quantitative assessment of cormorant diet in the LLB region, which was previously unknown, and to characterize food web structure on cormorant nesting and feeding lakes.

Chapter 2 employs a conventional diet analysis using regurgitation samples to determine prey species and sizes in cormorant diet on the four main nesting colonies in the LLB region (Antoine Lake, Portage Lake, High Island (on LLB) and Pelican Island (on LLB)) during the 2003 and 2004 nesting seasons. In this chapter I also explore spatial (among colonies) and temporal (between years) variation in prey consumption.

In Chapter 3, I examine stable isotope ratios of carbon and nitrogen in macroinvertebrates, fishes, and cormorants to establish basic food web structure in LLB and three other local nesting lakes. By using stable isotopes to assess trophic position of cormorants compared to important fish species, such as walleye and northern pike, I will be able to clarify predator-prey dynamics and determine the place of cormorants in the trophic structure of these lakes.

I conclude the thesis with a general discussion on some implications of this research and my opinion on future directions for successful management of the

LLB system.

Information presented in this thesis can be used by resource managers to help develop a lake-management strategy that works towards restoring piscivorous fish populations as well as decreasing lake eutrophication, while maintaining a healthy, sustainable population of double-crested cormorants as an important part of aquatic ecosystems.

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Chapter 2

Using Conventional Diet Analysis to Assess Prey Consumption by Double-crested Cormorants During the Nesting Season in Lac La Biche, Alberta

2.1 Introduction

Since the early 1980s cormorant numbers in North America and Europe have been on the rise (Hatch, 1995). Restrictions on pesticide use (Weseloh and Ewins, 1994), protection from human persecution (Vermeer, 1969; Vermeer and Rankin, 1984), and widespread anthropogenic changes to aquatic communities (Wires et al., 2001; Post et al., 2002) have all contributed to increases in cormorant abundance. These increases have been coupled with a rise in human/cormorant conflicts in areas where the birds are thought to be competing for valuable fish resources. Cormorants are opportunistic predators that feed primarily on fish (Weseloh and Ewins, 1994; Carss, 1995; Hatch and Wesoloh, 1999) and are often attracted to concentrated food sources (Duffy, 1995). Their diet has created conflicts with commercial/recreational fisheries and aquaculture industries as cormorant species are often held responsible for declining fish catches (Carss, 1995; Rudstam et al., 2004). However, the majority of diet studies have found the prey items of cormorants to be primarily forage fishes with little commercial value (Robertson, 1974; Campo et al., 1993; Blackwell et al., 1995; Madenjian and Gabrey, 1995; Neuman et al., 1997; Wires et al., 2001; Withers and Brooks, 2004).

Cormorants may have a greater effect on smaller inland lakes and reservoirs versus coastal and Laurentian Great Lakes areas where many other studies have taken place (Rudstam et al., 2004). In some freshwater lakes where sport fish are abundant cormorants have been documented to increase mortality of certain age-classes of important species (Burnett et al., 2002; Lantry et al., 2002; VanDeValk et al., 2002; Rudstam et al., 2004). Localized predation by cormorants during vulnerable periods for fishes, such as spawning or during stocking, may affect fish survival and recruitment (Simmonds et al., 2000; Jenson, 2001). Alternatively, there is potential for cormorants to benefit piscivorous fish populations through compensatory mechanisms (Engstrom, 2001; Walters and Kitchell, 2001). If cormorants decrease the numbers of forage fish, there would be less forage fish predation and competition which may allow predatory species to grow faster and survive through vulnerable juvenile life stages (Sullivan, 2003).

The important role of apex predators in lake systems has been well documented (Carpenter et al., 1985; McQueen et al., 1989). Cormorants are efficient predators of fish and, as a result, predation by large numbers of cormorants has the potential to alter fish communities (Rudstam et al., 2004). Increasing numbers of cormorants continue to be an issue for natural resource managers in many areas (Duffy, 1995; Wires and Cuthbert, 2006). Assessing the effects of cormorant predation for a specific system will require quantitative assessment of cormorant diet and foraging patterns, as well as detailed information on fish populations (Rudstam et al., 2004). Understanding these complex predator-prey interactions will be a critical challenge to predicting and assessing the effects of cormorant predation.

In the Lac La Biche (LLB) region of north-central Alberta, the double-crested cormorant (*Phalacrocorax auritus*) has been documented on nine nesting colonies (McGregor, 2004, 2005). A 2004 survey of double-crested cormorant colonies detected roughly 8000 nests on LLB and nearby lakes within a 50 km radial distance (McGregor, 2005). LLB is a large lake (234 km^2) and likely supports foraging from birds nesting on LLB as well as from birds nesting on smaller surrounding lakes (referred to as satellite colonies). As a result of local political pressure, a cormorant management program was implemented in 2003 in the LLB region as part of a long-term strategy to control double-crested cormorant numbers and restore lake fish communities (McGregor, 2004). Cormorant control has been erratic and has consisted of egg oiling in 2003 (McGregor, 2004) and 2005 and culling of adult birds by shooting in 2005 and 2006. The need for a cormorant control program and its effectiveness in increasing fish populations and restoring lake water quality are uncertain given that the impacts of cormorant predation on the lake ecosystem have not been well documented.

I used conventional diet analysis of regurgitation samples (Duffy and Jackson, 1986; Hobson et al., 1989; Neuman et al., 1997; Rudstam et al., 2004) to provide a detailed assessment of cormorant diet on four main nesting colonies in the LLB region (Antoine Lake, Portage Lake, High Island (on LLB) and Pelican Island (on LLB)) during the 2003 and 2004 nesting season. My main objectives were to (1) determine what prey species and prey sizes were present in double-crested cormorant diets, (2) describe spatial (among colonies) and temporal (between years) variation in prey consumption, and (3) investigate potential effects of cormorant predation on fish populations and the implications for management of the LLB system.

2.2 Methods

2.2.1 Description of study lakes

The LLB watershed is located in the Boreal Mixedwood Ecoregion of north-central Alberta, Canada. Approximately 30% of land in the LLB catchment is used for agriculture (Neufeld, 2005). The town of LLB (54.54N 112.00W) has approximately 2700 people and is situated on the southeast shore of the lake.

Table 2.1: Fish species present in double-crested cormorant nesting colony lakes in the LLB region of northern Alberta (Mitchell and Prepas, 1990)

Fish Species	LLB	Antoine	Portage
Walleye (*Sander vitreus*)	X	-	-
Yellow Perch (*Perca flavescens*)	X	-	-
Iowa darter (*Etheostoma exile*)	X	-	-
Ninespine Stickleback (*Pungitius pungitius*)	X	-	-
Brook Stickleback (*Culaea inconstans*)	X	X	X
Burbot (*Lota lota*)	X	-	-
Trout perch (*Percopsis omiscomaycus*)	X	-	-
Lake Whitefish (*Coregonus clupeaformis*)	X	-	-
Cisco (*Coregonus artedi*)	X	-	-
Northern Pike (*Esox lucius*)	X	-	-
White Sucker (*Catostomus commersoni*)	X	-	-
Longnose Sucker (*Catostomus catostomus*)	X	-	-
Fathead Minnow (*Pimephales promelas*)	-	X	X
Spottail Shiner (*Notropis hudsonius*)	X	-	-

In 1925 the lake islands were designated as a bird sanctuary, and in 1952 a provincial park was created on Big Island (later named Sir Winston Churchill Park).

Lac La Biche

LLB is a large (234 km^2), shallow lake with a mean depth of 8.4 m. There are two main basins which are partly separated by a peninsula and two islands. The west basin is open, and relatively deep (maximum depth 21.3 m) whereas the east basin of the lake has numerous islands and sand/gravel spits, which provide excellent nesting and loafing sites for a variety of aquatic bird species as well as valuable habitat for fish species in the lake. The lake is hypereutrophic with mean total phosphorus levels of 117μg/L in the west basin and 108μg/L in the east basin (Mitchell and Prepas, 1990). Algal blooms occur regularly during the summer and autumn months. Key concerns about the health of the lake ecosystem have included nutrient levels, algal density, aquatic macrophyte growth, and depletion of piscivorous fish populations, particularly walleye.

There are 13 fish species found in the lake (Table 2.1). Sport and commercial fishing on LLB have been important since the early 1900s. The fish community in the lake has changed dramatically over the years. For example, population crashes of cisco have been observed (Mitchell and Prepas, 1990). Although walleye were once abundant in LLB, the population collapsed in the 1970s and despite extensive stocking efforts, numbers have not exhibited any substantial increase since then (Sullivan, 2003). LLB also supports a rich community of breeding colonial and non-colonial waterbirds, including western grebe (*Aechmophorus occidentalis*), California gull (*Larus californicus*), double-crested cormorant, great blue heron (*Ardea herodius*), American white pelican (*Pelecanus erythrorhynchos*), and Caspian tern (*Sterna caspia*) (Gammon, 2001).

Double-crested cormorants are present in the LLB region from April until late October. There are two cormorant nesting colonies on LLB. The main colony is High Island (32 ha) located in a narrow passage between the two basins of the lake (Figure 2.1). The south side of the island is flat with minimal woody cover and extends into an open gravel bar. This portion of the island serves as nesting grounds for gulls and terns, as well as large numbers of double-crested cormorants. In 2003 approximately 2300 cormorant nests were counted on the island (McGregor, 2005). This number rose in 2004 to 3417 nests. The secondary colony is Pelican Island (1-2 ha) in the east basin of the lake. It supports a small cormorant colony on a low lying gravel spit that experiences fluctuations in water levels creating variation in the size of the colony. There were 284 and 119 nests in 2003 and 2004, respectively (McGregor, 2005).

Antoine Lake

Antoine Lake (4.5 km^2) is a small lake situated in an agricultural area located 9 km directly south of High Island on LLB (Figure 2.1). There is one deep area (maximum depth 8.5 m) situated on the east side of an island but the remainder of the lake is shallow. The lake contains brook stickleback and fathead minnow (Table 2.1). The island supports a colony of California gulls and double-crested cormorants. Surveys in 2003 and 2004 detected 2344 and 2339 cormorant nests respectively (McGregor, 2005).

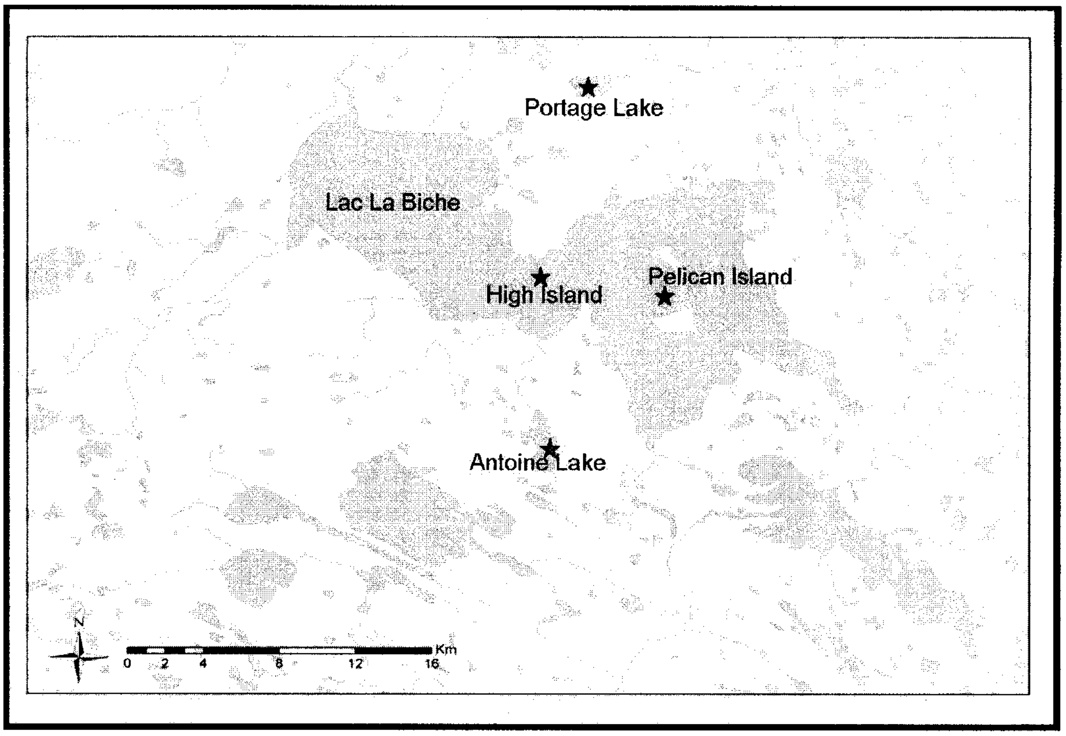

Figure 2.1: Locations of double-crested cormorant colonies in the Lac La Biche region. Colonies located on small lakes adjacent to Lac La Biche are referred to as satellite colonies

Portage Lake

Portage Lake (3 km^2) is approximately 10 kilometers north of High Island on LLB (Figure 2.1). The lake is uniformly shallow (maximum depth 2.7 m). Fish species present are brook stickleback and fathead minnow (Table 2.1). The lake contains an island with nesting populations of cormorants and American white pelicans. There were 1526 and 1842 cormorant nests counted in 2003 and 2004, respectively.

2.2.2 Collection of field samples

Diet data was gathered using regurgitation samples (boli) which can be easily collected and results in minimal disturbance to birds (Duffy and Jackson, 1986). Stomach regurgitates on the nesting colony are thought to represent the diet of adults and chicks alike during the breeding period (Warke and Day, 1995; Blackwell et al., 1995; Johnson et al., 2006). Samples were collected during the 2003 nesting season by Alberta Sustainable Resource Development (SRD) in conjunction with egg oiling effort during that year. During 2004 I collected samples in collaboration with additional Alberta SRD research in the area. Samples were collected at 2 week intervals (June - August) from High Island, Pelican Island, Antoine Lake, and Portage Lake as long as samples could be obtained on the colonies. To obtain samples, we flushed breeding cormorants from nesting colonies which resulted in spontaneous regurgitation of food items being delivered to chicks. Boli were selected from nest rims or immediately adjacent to a nest. Only moist, fresh looking boli were collected. Individual bolus samples were placed into plastic bags and stored on ice until they were transferred to a freezer for storage. A minimum of 5 crew members were present during island visits to ensure rapid collection of samples and to keep time on the colonies as short as possible ($<$ 30 min) to minimize disturbance to chicks (methods from McGregor, 2004).

2.2.3 Laboratory analysis

Fish in a bolus were counted and identified to species at the University of Alberta. Total length (from tip of snout to tip of tail) was recorded, provided the specimen was sufficiently intact to obtain an accurate length. All fish specimens were weighed and ageing structures (otoliths, fin rays, cleithrum, operculum, scales) were collected when possible.

2.2.4 Statistical analyses

Overall prey composition

I grouped prey species into five categories to minimize the effects of rare species on analyses. These categories were: (1) Coregonid species (cisco and lake whitefish); (2) Catostomus species (white sucker and longnose sucker); (3) Forage fishes (spottail shiner, fathead minnow, brook stickleback, ninespine stickleback, trout perch, and Iowa darter); (4) Piscivorous fishes (burbot, northern pike, and walleye); and (5) yellow perch. Yellow perch was recognized as a separate prey category because the species was so abundant in the diet.

To assess the importance of prey categories for different bird colonies, I calculated an *Index of Relative Importance* (IRI) to minimize the biases introduced by numerous but small items and rare but large items that could dominate a bolus (Duffy and Jackson, 1986). This index incorporated important characteristics of prey composition using three different metrics: relative biomass, relative numerical abundance, and frequency of occurrence. Prey categories that rank high in all three metrics are likely to be an important component of the diet (Duffy and Jackson, 1986; Blackwell et al., 1995). Biomass estimates were necessary because prey items in the diet varied greatly in size. Relative biomass (B) was expressed as the average contribution of a prey category to the total weight of each sample. This avoided the problem of small numerous prey items being assigned disproportionate importance (Duffy and Jackson, 1986). To avoid large, rare prey items becoming inflated in importance, numerical abundance (A) of prey category was also included. Numerical abundance is the percentage of prey items from one category out of all prey items in a bolus. Frequency of occurrence (F) is simply a presence/absence measure for each regurgitation sample for prey category encountered in the entire sample. The IRI is defined as $(A+B)\times F$.

Colony specific differences in key prey items

To assess temporal and spatial differences, I explored the relative contribution of prey categories with high IRI in cormorant diets. I used a 2-factor analysis of variance (ANOVA) to assess differences between nesting colonies and years. I used mean relative biomass within a bolus as a response which was arcsine transformed to ensure data followed a normal distribution (Sokal and Rohlf, 1995). Posthoc comparisons of differences between nesting colonies were conducted using Tukey comparisons. Bonferroni corrections were made to limit the overall error rate associated with conducting multiple tests (Sokal and Rohlf, 1995).

Prey size

I used a 2-factor ANOVA to assess whether prey size consumed by cormorants differed between colonies and between years. The sampling unit was mean prey length by individual bolus for all fish species combined. Analysis was conducted on log-transformed data to ensure normality and homogeneity of variances (Zar, 1999). Overall length of all prey items combined was analyzed to assess the size distribution of prey consumed during 2003 and 2004. Specifically, I used a Kolmogorov-Smirnov test to determine if there was a difference in the distribution of prey lengths between the 2 years (Zar, 1999). A Kolmogorov-Smirnov test was also used to specifically assess the size distribution of yellow perch consumed during 2003 and 2004 and to determine if there was a difference in the distribution of prey length between the 2 years.

2.3 Results

2.3.1 Overall prey composition

I analyzed a total of 340 boli from 2003 and 524 boli from 2004. These samples were comprised of 13,354 individual fish representing 13 different species (see Appendix A for complete species list and prey composition breakdown). Given the variety of prey items identified in the diet of cormorants nesting in LLB and satellite colonies, it is likely that many of these fish were captured on LLB. Satellite colonies clearly forage on lakes other than the nesting lake because Antoine and Portage Lakes do not have many of the fish species found in boli from these lakes (Table 2.1).

IRI ranged from 0 for piscivorous fish from Pelican Island in 2004 to 19032 for yellow perch for the same colony (Table 2.2). Based on IRI, yellow perch was the most important prey item in all colonies in both 2003 and 2004. Yellow perch ranged from 4 times (Portage Lake 2004) to 614 times (Pelican Island 2004) more important then the next most important prey category. The IRI for yellow perch was commonly 20 to 30 times higher than the prey category with the next highest IRI. Yellow perch made up 53.5% (Portage Lake 2004) to

Table 2.2: Summary of prey taxa identified in double-crested cormorant regurgitation samples collected from breeding colonies in the Lac La Biche region during the 2003 nesting period (Prey category ranked by IRI (Index of Relative Importance) = (A+B) x F, No. = number of individual fish, % Num = mean % numerical abundance per bolus, % Bio = mean % biomass per bolus, % Freq = mean % frequency of occurrence per bolus).

Colony/Year	**Prey Category**	**IRI**	**No.**	**% Num (A)**	**% Bio (B)**	**% Freq (F)**
Antoine Lake 2003 (105 Boli)	Yellow Perch	10829	1426	70.1	68.6	78.1
	Forage Fish	1287	396	17.0	16.0	39.0
	Coregonid sp.	239	13	8.1	9.9	13.3
	Piscivorous Fish	25	5	2.9	3.6	3.8
	Catostomus sp.	15	4	2.0	2.0	3.8
Portage Lake 2003 (163 Boli)	Yellow Perch	11468	3986	71.1	68.4	82.2
	Forage Fish	885	716	12.5	10.4	38.7
	Piscivorous Fish	237	21	9.2	10.2	12.3
	Coregonid sp.	157	24	6.2	8.8	10.4
	Catostomus sp.	15	12	1.0	2.2	6.1
Pelican Island 2003 (7 Boli)	Yellow Perch	14636	119	85.2	85.6	85.7
	Piscivorous Fish	408	1	14.3	14.3	14.3
	Forage Fish	10	1	0.5	0.1	14.3
High Island 2003 (65 Boli)	Yellow Perch	13589	1237	82.1	72.8	87.7
	Coregonid sp.	760	21	10.9	20.0	24.6
	Catostomus sp.	33	3	3.1	4.0	4.6
	Forage Fish	18	7	1.8	0.2	9.2
	Piscivorous Fish	16	3	2.1	3.0	3.1
Antoine Lake 2004 (139 Boli)	Yellow Perch	10016	1022	63.6	65.3	77.7
	Forage Fish	228	1050	25.2	19.9	5.0
	Piscivorous Fish	140	15	5.7	8.1	10.1
	Catostomus sp.	51	13	4.9	5.1	5.0
	Coregonid sp.	1	13	0.4	1.6	0.7
Portage Lake 2004 (99 Boli)	Yellow Perch	7417	446	53.5	56.1	67.7
	Forage Fish	1617	468	23.8	18.4	38.4
	Coregonid sp.	767	29	16.7	19.4	21.2
	Piscivorous Fish	28	4	3.4	3.6	4.0
	Catostomus sp.	21	4	2.6	2.6	4.0
Pelican Island 2004 (73 Boli)	Yellow Perch	19032	598	96.1	96.9	98.6
	Forage Fish	31	47	2.3	0.5	11.0
	Coregonid sp.	8	2	1.4	1.6	2.7
	Catostomus sp.	1	1	0.1	0.8	1.4
	Piscivorous Fish	0	1	0.1	0.1	1.4
High Island 2004 (213 Boli)	Yellow Perch	13680	1534	81.0	80.0	85.0
	Coregonid sp.	380	41	12.4	13.7	14.6
	Catostomus sp.	58	42	3.7	4.0	7.5
	Forage Fish	31	28	2.1	1.0	9.9
	Piscivorous Fish	3	3	0.8	1.2	1.4

96.1% (Pelican Island 2004) of the diet based on numerical abundance. Mean relative biomass of perch ranged from 56.1% (Portage Lake 2004) to 96.9% (Pelican Island 2004).

Interestingly, secondary prey items varied across colonies and between years. On satellite colonies, forage fish represented the second most important prey category. In 2004 forage fish represented 25.2% of prey items on Antoine Lake (IRI = 228) and 23.8% on Portage Lake (IRI = 1617). Numbers were lower for 2003 samples as forage fish made up 17.0% and 12.5% of prey number for Antoine Lake (IRI = 1287) and Portage Lake (IRI = 885) respectively. Approximately 10% to 20% of mean prey biomass consisted of forage fish in 2003 and 2004 on the satellite colonies. In contrast, coregonid species were the second most important prey category on High Island for both 2003 and 2004 (IRI = 760, 380). Coregonids were the third most important prey item, with an IRI of 767, on Portage Lake in 2004 and they represented a substantial component of the diet biomass (19.4%). Coregonid species were also high in mean relative biomass for High Island in 2003 (20.0%) and 2004 (13.7%). Most of the coregonid identified were cisco (Appendix A).

Because piscivorous fish were captured very infrequently on all colonies, they were omitted from more detailed analysis. For example, a large proportion of piscivorous fish biomass (14.3%) on Pelican Island in 2003 was simply an artifact of one large burbot identified from a small number of regurgitation samples. Catostomus species, which never represented more than 4% of the biomass, were rare across nesting colonies and were also omitted from further analysis.

2.3.2 Colony specific differences in key prey items

Diet composition varied between the four nesting colonies (Figure 2.2). In order to characterize important differences in prey composition, I selected three key prey categories for detailed analysis: yellow perch, forage fish and coregonid species, which ranked consistently high in the index of relative importance (Table 2.2). Diet descriptors based on biomass can lead to an overestimate of

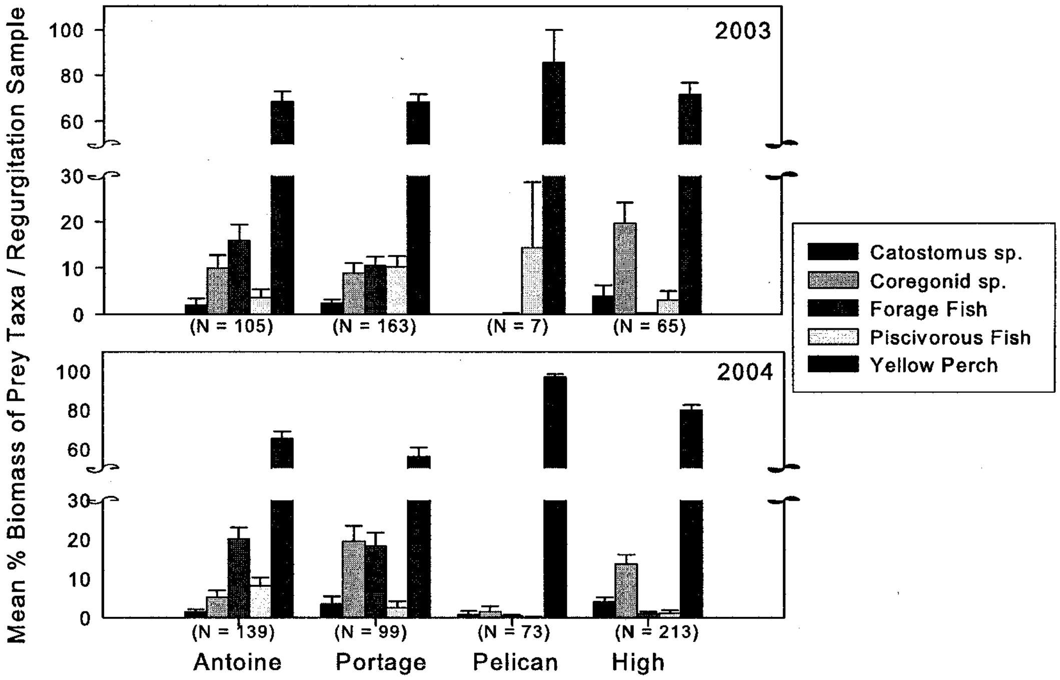

Figure 2.2: Prey composition based on biomass of regurgitation samples collected from double-crested cormorant nesting colonies on Lac La Biche and satellite colonies in northern Alberta during the 2003 and 2004 nesting seasons.(Error bars represent standard error)

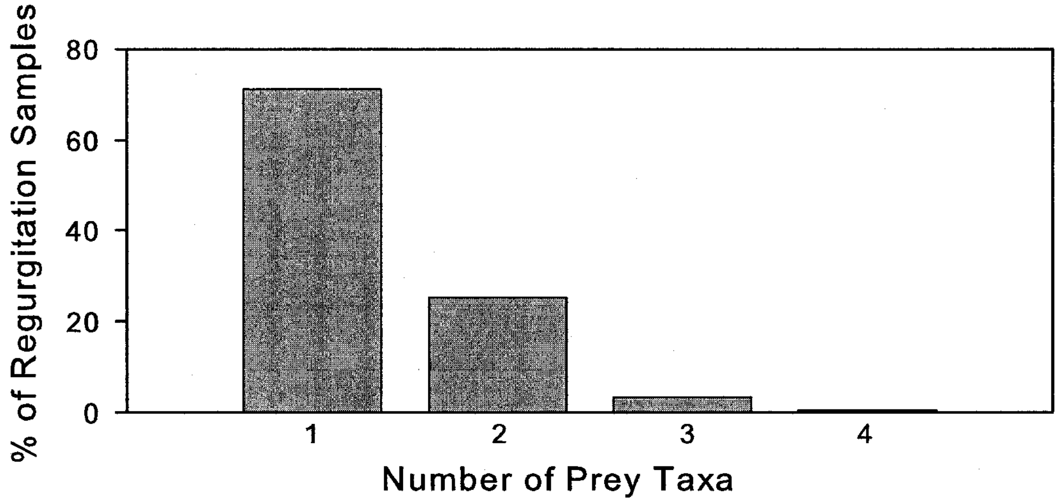

Figure 2.3: Number of prey taxa identified in regurgitation samples collected from four double-crested cormorant colonies in the Lac La Biche area during the 2003 and 2004 nesting seasons (N = 864 regurgitation samples)

the large prey items that are present very infrequently in diet samples (Duffy and Jackson, 1986). However, this information is important when calculating the biomass of fish being removed from a lake by cormorants and thus for modelling flow of energy and material in the ecosystem. Biases can exist for biomass estimates based on boli because regurgitation samples are collected at varying stages of digestion (Duffy and Jackson, 1986). However, it is likely that all prey items in a single bolus were captured at roughly the same time and therefore should be at similar stages of digestion. Using the relative proportion of biomass represented by a single prey category within a bolus will avoid this problem of differential digestibility among different samples. There may also be differential digestibility among prey species (Brugger, 1993). Soft bodied whitefish species often appeared more digested in boli compared to other prey taxa. This problem could not be avoided in the analysis because it was not possible to correct for differential digestibility among species. Most boli samples (71.3%) contained only one prey category within an individual sample (Figure 2.3), therefore the bias associated with differential digestibility is likely quite small.

Two-factor ANOVAs were conducted on the three most important prey categories, and therefore, the significant p-value was adjusted according to the Bonferroni correction ($0.05/3 = 0.017$). Relative biomass of yellow perch was significantly different among nesting colonies ($F_{3,855} = 9.732$, $p < 0.001$) but did not differ significantly between years ($F_{1,855} = 0.021$, $p = 0.884$). The interaction between colony and year was not significant ($F_{3,855} = 2.230$, $p = 0.083$). Yellow perch accounted for significantly more prey biomass in samples collected from colonies located on LLB compared to samples from the two satellite colonies (Figure 2.4). This significant difference is driven by percent biomass of yellow perch in 2004, which was approximately 20% greater on LLB colonies compared to satellite colonies (Table 2.2). In 2003, the relative biomass for LLB colonies was only slightly higher than for satellite colonies (Table 2.2).

The contribution of forage fish to diets was consistent between years ($F_{1,855}$

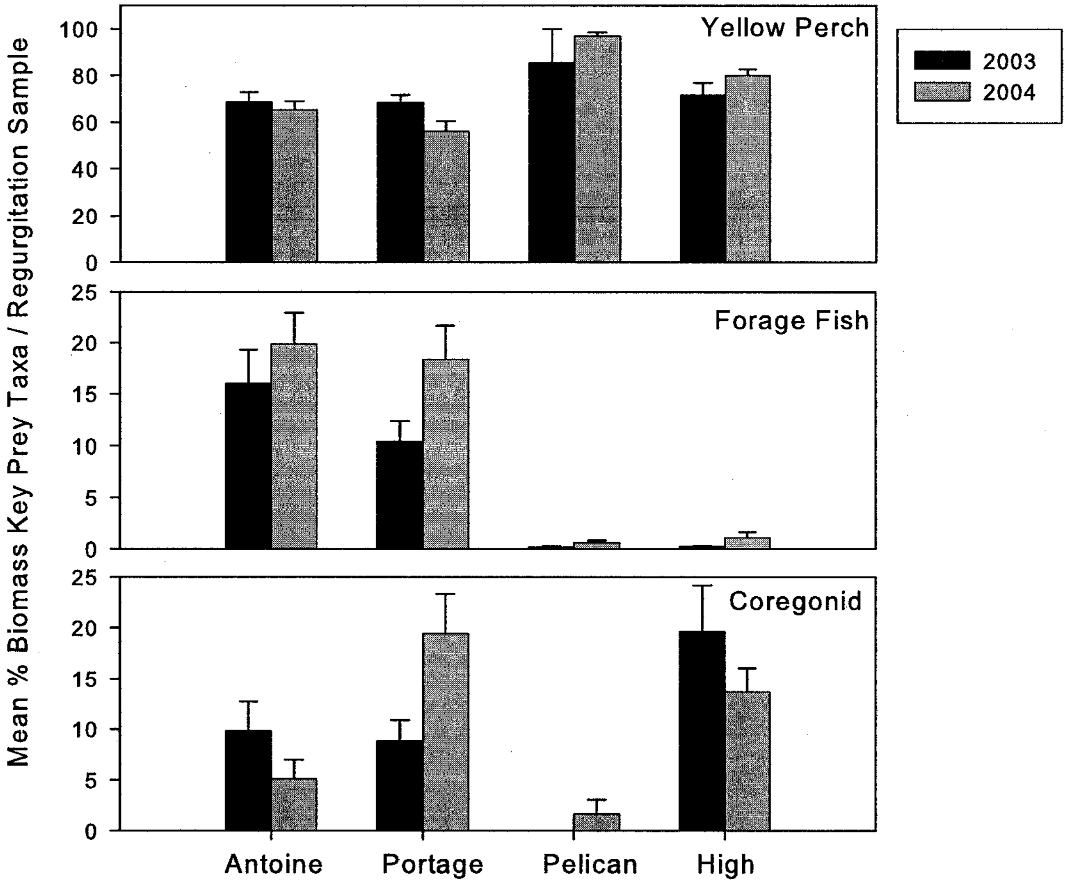

Figure 2.4: Mean biomass (within an individual bolus) of prey categories collected from nesting colonies of double-crested cormorants on Lac La Biche (Pelican and High) and satellite colonies (Antoine and Portage) during the 2003 and 2004 nesting season. (Error bars represent standard error)

= 1.171, p = 0.280) and there was no significant interaction between colony and year ($F_{3,855}$ = 0.813, p = 0.487). There was, however, highly significant differences among colonies ($F_{3,855}$ = 18.987, $p < 0.001$). There was a significantly greater contribution of forage fish biomass to cormorant diets on satellite colonies compared to colonies from Lac La Biche during both 2003 and 2004 (Figure 2.4).

Biomass of coregonid species was also significantly different between colonies ($F_{3,855}$ = 4.366, p = 0.005) but did not differ significantly between years ($F_{1,855}$ = 0.072, p = 0.787). A significant interaction was detected for relative biomass of coregonid species ($F_{3,855}$ = 3.417, p = 0.017). Between 2003 and 2004, there was an increase in coregonid species consumed by birds from Portage Lake while during this same period there was a decrease in coregonid species in the diet of birds from High Island (Figure 2.4). In 2003, mean coregonid biomass from High Island was at least twice as great as the relative biomass from other colonies (Figure 2.4). In 2004, there was a greater proportion of coregonids identified from Portage Lake and High Island compared to the diet from Antoine Lake and Pelican Island (Figure 2.4).

2.3.3 Prey size

Mean prey length differed among colonies ($F_{3,759}$ = 12.013, $p < 0.001$) as well as between the two years ($F_{1,759}$ = 60.816, $p < 0.001$) of sample collection, but the interaction was not significant ($F_{3,759}$ = 1.143, p = 0.331). A single factor ANOVA was then conducted using Tukey tests to assess pair-wise comparisons between colonies in each of the years. A significance value of p = 0.025 was used based on the Bonferroni correction (0.05/2 = 0.025). In 2003, High Island (mean = 85.3 mm) had a significantly larger mean prey length (by 31%) within a bolus sample than Antoine Lake (mean = 65.3 mm) ($F_{3,272}$ = 3.220, p = 0.023; Figure 2.5). Portage Lake (mean = 73.8 mm) did not differ significantly from either Antoine Lake, High Island, or Pelican Island (mean = 62.6 mm) nesting colonies in this year (Figure 2.5). In 2004, bolus samples from High Island (mean = 106.7 mm), Pelican Island (mean = 94.8 mm), and Portage

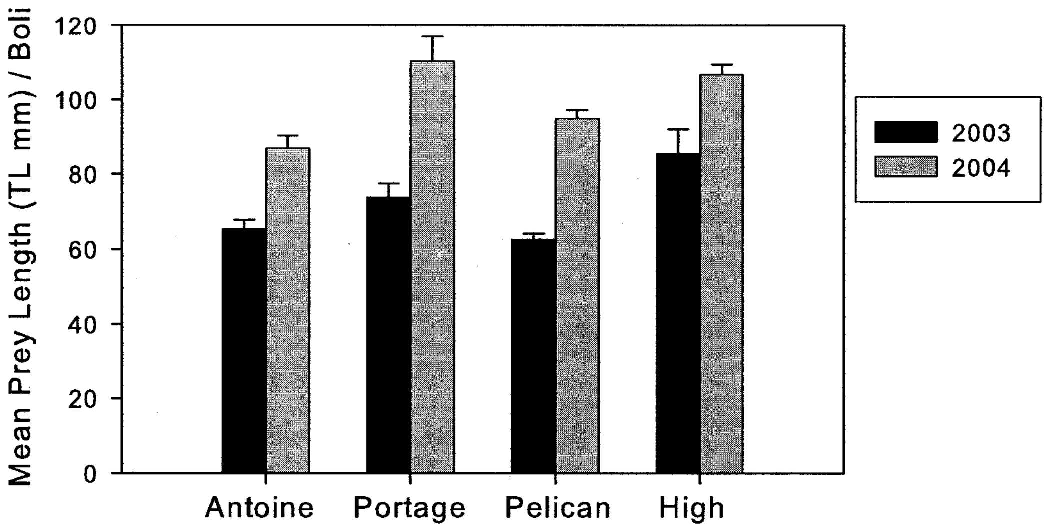

Figure 2.5: Mean total length of prey items in regurgitation samples collected from double-crested cormorant nesting colonies during the nesting season (May-Aug 2003 and 2004) (Error bars represent standard error)

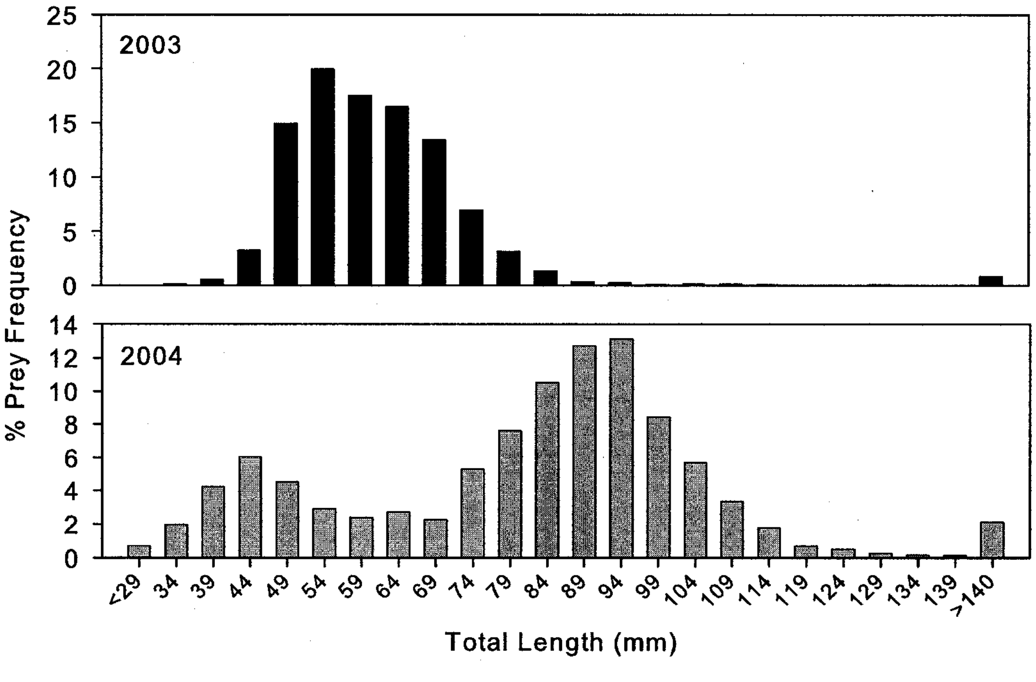

Figure 2.6: Size distribution of all prey items consumed by double-crested cormorants during the nesting season in the Lac La Biche area (n = 5780 individual fish in 2003; n = 4592 individual fish in 2004)

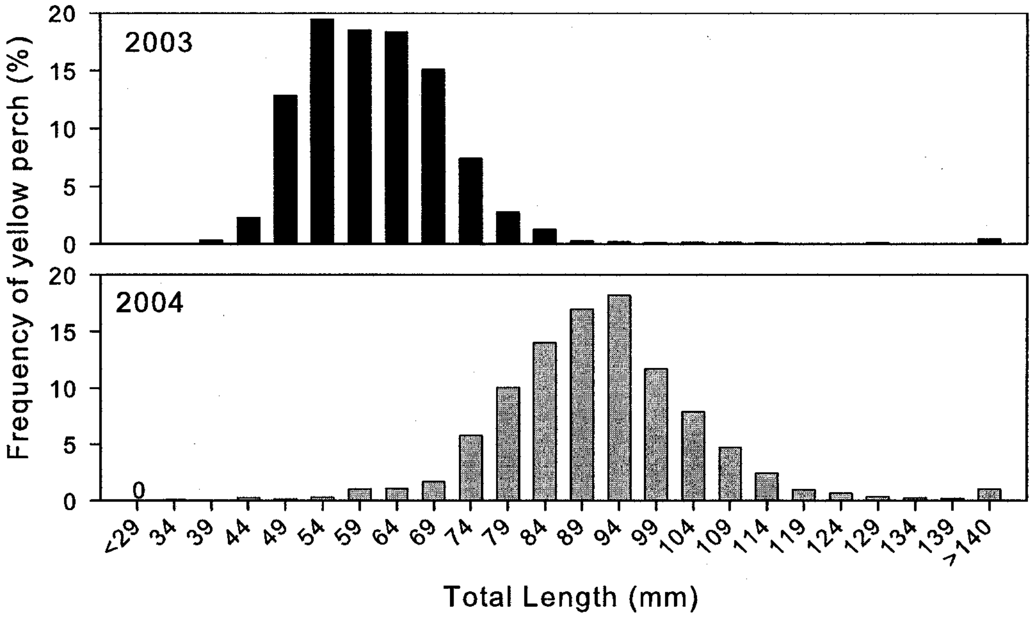

Figure 2.7: Size distribution of yellow perch identified in regurgitation samples collected from nesting colonies of double-crested cormorants in the Lac La Biche area (n = 4987 individual fish in 2003, n = 2917 individual fish in 2004)

Lake (mean = 110.3 mm) had significantly higher mean prey lengths (from 9 to 27% greater) than bolus samples collected from Antoine Lake (mean = 86.9 mm) ($F_{3,487} = 13.025$, $p < 0.001$).

Lengths of individual fish identified in the diet were quite variable, ranging in size from 19 to 337 mm. A Kolmogorov-Smirnov test showed that the structure of length-frequency distributions differed between the years ($Z = 30.663$, $p < 0.001$). In 2004, the prey captured exhibited a bimodal distribution and most prey items were less than 110 mm (94.4%; Figure 2.6). In 2003, most of the prey captured were less than 75 mm (93.4%).

The change in distribution of prey sizes between 2003 and 2004 appears to be driven by large numbers of perch of different sizes in each year. A Kolmogorov-Smirnov test identified significant interannual differences in the size distribution of yellow perch consumed ($Z = 37.29$, $p < 0.001$). The mean total length was lower in 2003 (mean = 59.6 mm) than in 2004 (mean = 89.3 mm; Figure 2.7). There was also a significant difference in the size

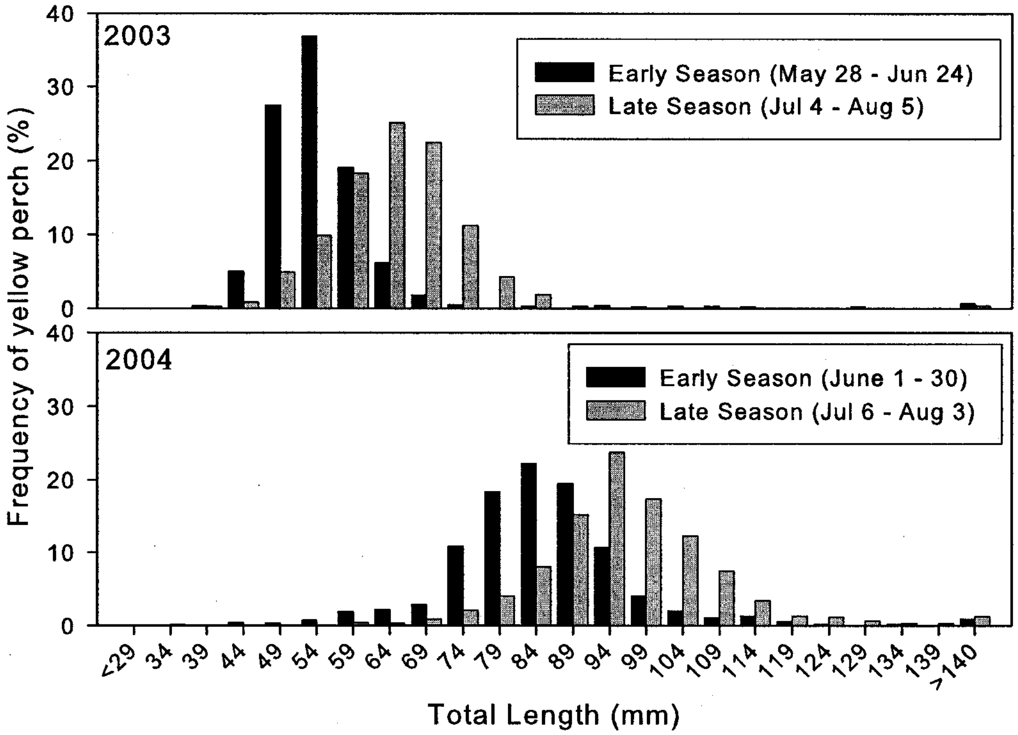

Figure 2.8: Temporal shifts in size distribution of yellow perch identified in regurgitation samples collected from nesting colonies of double-crested cormorants in the Lac La Biche area (Early 2003, n = 1763; Late 2003, n = 3224; Early 2004, n = 1356; Late 2004, n = 1845)

distribution of yellow perch consumed early and late in the season within a year (Kolmogorov-Smirnov test, 2003, $Z = 19.346$, $p < 0.001$; 2004, $Z = 13.7$, $p < 0.001$). Growth of perch throughout the season was observed through increases in mean length of perch within cormorant boli. Mean length increased from 53.5 mm in early season (May 28 - Jun 24) samples to 63.0 mm in late season (Jul 4 - Aug 5) samples in 2003, and increased from 82.6 mm to 94.0 mm from early (Jun 1 - Jun 30) to late (Jul 6 - Aug 3) season samples in 2004 (Figure 2.8).

2.4 Discussion

2.4.1 Prey composition

Prey categories that ranked high on the IRI on all colonies included yellow perch, forage fish species (cyprinids and sticklebacks), and coregonid species (Table 2.2). Because of the variety of prey items identified in regurgitation samples from all colonies, it is clear that cormorants from the satellite colonies must be foraging on sites other than the local nesting lake.

Yellow perch are commonly found in northern lakes and have often been identified as an important prey source to double-crested cormorants in other studies (Engstrom, 2001; Burnett et al., 2002; VanDeValk et al., 2002; Rudstam et al., 2004). For example, in Lake Winnipegosis, Manitoba, Canada, yellow perch made up 63.8% of the diet by number and 27.6% of the diet by weight (Hobson et al., 1989). Consumption of yellow perch in Oneida Lake, New York, USA, represented from 33.5% to 64.8% of the total number of fish captured in the diet of double-crested cormorants over a 6-year period (Rudstam et al., 2004).

Yellow perch tend to occur in large schools in relatively shallow habitats and appear to be highly susceptible to cormorant predation. Based on fish gill netting data collected by Alberta Sustainable Resource Development (Chris Davis, provincial biologist, unpublished data), the catch per unit effort (CPUE) for yellow perch in LLB was well above values for other prey categories (Figure 2.9). This high abundance of yellow perch in LLB is clearly reflected in the diet of cormorants (Figure 2.4). Cormorant predation may, therefore, have implications for the structure of fish communities. Perch have high reproductive potential and are effective at competing for food resources (Scott and Crossman, 1979). This can lead to perch outcompeting other valued fish in the absence of cormorant predation. Piscivorous fish have a greater age at maturity and can often be replaced by these highly fecund, short-lived species (Scott and Crossman, 1979). Perhaps cormorant predation on yellow perch is preventing the population from expanding even further and outcompeting small

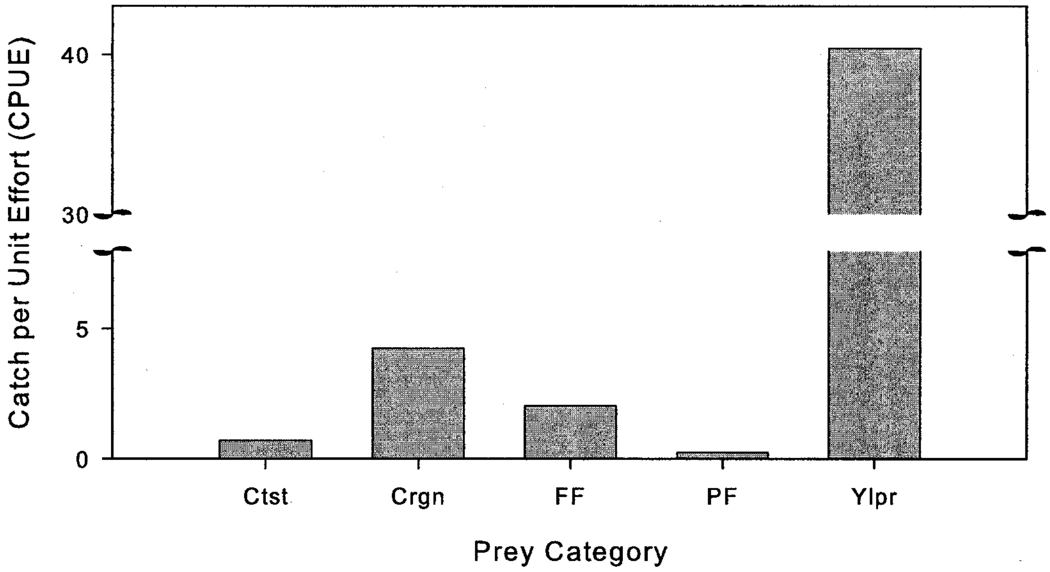

Figure 2.9: Catch per unit effort of fish captured in gill net sets conducted by Alberta Sustainable Resource Development during Fall 2004 at random locations in Lac La Biche (Ctst=Catostomus species; Crgn=Coregonid species; FF=Forage Fish; PF=Piscivorous Fish; Ylpr=yellow perch)

walleye.

Using chick regurgitants, pellets, and stomach content analyses, cormorant consumption of walleye in Oneida Lake ranged from 1.6% to 16.5% by number over 6 years of sample collection (Rudstam et al., 2004). This is much higher than the proportion of walleye taken from LLB; for example, only a single walleye was identified in a boli sample collected from Antoine Lake in 2003 and 4 walleye were found from the same colony in 2004 (Appendix A). Also contrary to the diet composition in LLB, Hobson et al. (1989) found white sucker to be an important part of the diet by weight (46.4%). Walleye and suckers are likely not present in large enough abundance in LLB (Figure 2.9) to be present in large numbers in cormorant diet. Although fish species other than perch were present in the diet, it is clear that yellow perch was by far the most important prey item in the diet on all colonies.

2.4.2 Spatial variation

Differences in cormorant prey consumption in space and time will ultimately determine the degree to which cormorants affect a particular lake system (Neuman et al., 1997). In this study, cormorants from different nesting locations exhibited varying diets in terms of prey composition (Figure 2.2). Birds from satellite colonies ate more forage fish compared to birds nesting on LLB (Figure 2.4). Coregonids made up a larger proportion of the diet of birds nesting on High Island and Portage Lake colonies (Figure 2.4). Consistent with other studies, the location of cormorant breeding colonies affected the type of food found in bolus samples (Neuman et al., 1997; Coleman et al., 2005). These differences may be related to the proximity of a nesting colony to local prey populations (Neuman et al., 1997) or to individual foraging preferences (Coleman et al., 2005).

Since cormorants will consume prey based on availability, I believe the major differences in prey composition can be attributed to the location of the nesting colonies. Fish populations will vary with lake habitat structure (Benson and Magnuson, 1992) and cormorants will typically exploit the nearest appropriate food source (Duffy, 1995; Warke and Day, 1995; Neuman et al., 1997; Collis et al., 2002). Cormorants have been found to forage in both pelagic and littoral habitats (Duffy, 1995) and up to great distances from the nesting colony (Custer and Bunck, 1992; Anderson et al., 2004). The maximum foraging distance from a nesting colony is thought to be approximately 40 km (Custer and Bunck, 1992); this is well beyond distances that cormorants likely travelled in the LLB region where major colonies are all within 10 km of High Island. Given the larger proportion of forage fish species present in the diet of birds from satellite colonies, it is likely that many of these small fish were captured on the local lake. Since the fish community on Antoine and Portage Lakes is quite simple (Table 2.1), the diverse prey items appearing in the diet must originate from other lakes. It is likely that the majority of the diet items that could not come from the nesting lake were derived from LLB. During aerial surveys conducted by Alberta Sustainable Resource Development, cormorants were documented to forage on 32 lakes in the region (McGregor, 2005). The proportion of cormorants foraging on LLB was estimated to range from 26% to 80% of the total birds observed during a flight (McGregor, 2005).

Because LLB is a large and heterogeneous lake, the structure of fish communities differs between the two basins. The west basin of the lake is deeper and more open than the east basin, which is shallower and contains many small islands and gravel bars. Lake whitefish and cisco are schooling fishes that inhabit the pelagic areas of lakes (Scott and Crossman, 1979). These fish will often move into deeper water as the lake temperature rises during the summer (Scott and Crossman, 1979). Consequently, the west basin provides more suitable habitat for coregonid populations. Since birds from the High Island colony had a significantly greater proportion of coregonids in the diet, it is likely that they foraged to a greater extent in the west basin of the lake. This may also help explain the high numbers of coregonid species found in the diet of birds from Portage Lake in 2004. Perhaps these birds were also foraging heavily in this west basin or on other nearby lakes (such as Heart Lake) with coregonid populations.

2.4.3 Temporal variation

Diet composition differed between the two years studied (Figure 2.2). However, in both years yellow perch was identified as the most important prey item. Annual diet differences may be caused by fluctuations in fish populations between years but also could have been affected by human activities. In 2003, 75% of eggs on nesting colonies from Antoine Lake, Portage Lake, and Pelican Island were oiled (McGregor, 2004). Oiling the eggs may have altered the nesting phenology in that year. Cormorants will continue to incubate eggs that have been oiled (Christens et al., 1995; Wires et al., 2001); however, birds may re-nest later in the season when the eggs do not hatch. This shift toward a longer nesting period resulted in greater numbers of samples collected later in the summer (see Appendix A for sample dates). Such a shift should have resulted in an increase in mean fish size in 2003, as fish would be captured later in the year when they had additional time for growth. In fact, the differences in size between years was actually the opposite; mean prey length was greater in 2004 (mean = 80mm) than in 2003 (mean = 60mm) (Figure 2.5).

Greater mean fish size in 2004 (80.1 mm) compared to 2003 (59.6 mm) appears instead to have been driven primarily by the consumption of larger yellow perch in 2004 (Figure 2.7). The abundance of smaller perch in 2003 was probably due to lower growth rates this year compared to 2004. Yellow perch growth rates can vary between years due to temperature (Power and van den Heuvel, 1999), population densities (Wilberg et al., 2005; Pierce et al., 2006), and lake productivity (Paukert and Willis, 2001). Annual variation in fish size was also found in cormorant diet in Lake Ontario (Johnson et al., 2006) and was thought to be related, in part, to different rates of fish growth between the years.

Based on Alberta SRD netting data the abundant yellow perch were thought to be primarily age-1+ (Chris Davis personal communication). This was confirmed for perch consumed in 2004 through ageing of opercula extracted from perch in boli (Earle, unpublished data). Yellow perch consumed by cormorants in other studies were also captured as juveniles (Burnett et al., 2002; Rudstam et al., 2004; Johnson et al., 2006). Age-0 perch are not likely to be as common in the diet because they tend to move immediately after hatch to deeper pelagic areas of lakes to avoid predation (Bystrom et al., 2003; Harvey and Brown, 2004). The size distribution of yellow perch identified in cormorant diet throughout the nesting season (Figure 2.8) clearly reflects the growth of perch that would be expected during this time period. This confirms a generalist foraging strategy for cormorants in which prey items consumed reflect primarily the abundance of prey available in foraging areas rather than the targeting of a preferred size of prey.

Distribution of prey size exhibited a unimodal distribution in 2003 and a bimodal distribution in 2004 (Figure 2.6). The mean length of Age-1+ yellow perch in 2003 was approximately 60 mm and was thus similar to the sizes of other forage based fishes. In 2004, yearling yellow perch were closer to 90 mm, which is larger than the remainder of forage species. The bimodal distribution observed in 2004 seems to be driven by differences in sizes of two dominant prey items: yellow perch and forage fishes.

Numbers of cormorants on Lake Ontario were found to be closely tied to alewife (*Alosa pseudoharengus*) abundance in the lake (Weseloh et al., 1995); there were more breeding cormorants during years of high alewife abundance. If cormorants are simply eating what is most available in the lake, their diet may provide some indication of fluctuations in populations of small fish species in the system (Blackwell et al., 1995; Neuman et al., 1997). Hobson et al. (1989) suggest that increases in cormorants have been caused by increases in abundance of forage fish which in Lake Winnipegosis was caused by excessive commercial exploitation of large piscivorous fishes. This may also be the case in LLB.

In this study, I was unable to define separate time periods in the annual cormorant breeding cycle due to asynchronous hatch dates (Weseloh and Ewins, 1994) and major temporal differences in individual colony nesting patterns. The timing of sample collection, for logistical reasons, thus did not systematically span different stages of the nesting season. Also, I did not analyze prey consumption outside of the nesting period. There are likely differences in prey consumption outside of the nesting season which could not be assessed using regurgitation samples from the nesting colonies. Regurgitation samples represent material being fed to chicks and may differ from prey that adults consume throughout the remainder of their time on breeding lakes (Derby and Lovvorn, 1997; Neuman et al., 1997). Adult cormorants may bring larger (Hobson et al., 1989; Carss, 1995) or smaller (Duffy and Jackson, 1986) prey back to nestlings than prey they consume themselves. Further exploration of prey consumed during spring and fall periods will be necessary to provide a complete temporal assessment of cormorant prey consumption and their impacts on fish populations.

2.4.4 Potential impacts to fish communities

Analysis of cormorant diet on the major nesting colonies in the LLB region indicates that predatory fish make up a very small component of the diet (Figure 2.2). Numbers of predatory fish are extremely low in LLB (Figure 2.9), therefore, it is not surprising for these fish to be captured infrequently by cormorants. Although predatory fish do not make up a large part of the cormorant diet, given the large numbers of birds foraging on the lake, cormorant predation may still contribute to a significant biomass of predatory fish being removed from the lake. Quantitative data on cormorant diet is being used by Alberta SRD to estimate biomass of fish being removed from the lake (Chris Davis, pers comm). The large numbers of fish being removed may not be sustainable for predatory species such as walleye and pike that have already suffered massive population declines. It is also possible that cormorants pose an indirect threat to walleye preventing the reestablishment of healthy populations. For example, there may be competition between cormorants and walleye (Madenjian and Gabrey, 1995) if prey fish populations are reduced to a limiting resource for piscivores (Anderson et al., 2004). This is currently an unlikely factor because yellow perch remain abundant in the lake and predatory fish populations in LLB are nearly absent (Figure 2.9).

Alternatively, cormorants may benefit piscivorous fish by altering competitive interactions among fish species (Engstrom, 2001). Decreased abundance of yellow perch created by cormorant predation may result in reduced competition between this species and young walleye (Simmonds et al., 2000; Walters and Kitchell, 2001). Top fish predators are often vulnerable to predation by intermediate predators at early life stages (Rudstam et al., 2004). If depensatory dynamics exist in LLB then recovery of walleye populations may be difficult to achieve since walleye abundance has already been so severely reduced (Myers et al., 1995). The effects of low adult numbers may be exaggerated by increased forage fish abundance causing a decrease in juvenile walleye survival (Walters and Kitchell, 2001).

Cormorants may affect age structure and population dynamics of prey species (Rudstam et al., 2004). The rate of consumption of different age classes of yellow perch, which make up such a large component of the diet, may be important to understanding cormorant impacts on fish communities (Burnett et al., 2002). The implication of losses of large numbers of juvenile perch needs to be explored in greater detail. Consumption of subadult yellow perch by cormorants nesting in Oneida Lake was predicted to reduce future angler harvest of yellow perch (VanDeValk et al., 2002). Cormorant predation on yellow perch in LLB may present similar threats to the perch population in the lake.

To assess the impacts of cormorants on the fish communities in LLB, diet composition, cormorant population size and seasonal consumption of prey from LLB need to be considered (Carss, 1995; Weseloh et al., 2002). Information on predators in lake systems becomes less valuable if the prey populations are ignored (Suter, 1995; Rudstam et al., 2004). Biomass of fish consumed by the birds will need to be compared to available biomass of fish in the lake (Madenjian and Gabrey, 1995; VanDeValk et al., 2002).

2.5 Conclusions

I found the main prey item of the double-crested cormorant diet to be small bodied fishes (mostly <100 mm), particularly juvenile yellow perch. Satellite colonies located on small lakes near LLB had a greater abundance of other small bodied fish species (cyprinids and sticklebacks) in their diet. LLB appeared to be the main source of prey for birds nesting on and off the lake. Cormorants appear to be opportunistically consuming fish species and size classes based on availability. Limited data on prey populations in the lake makes comprehensive assessment of cormorant impacts difficult.

Conflicts between cormorants and humans on LLB and elsewhere will likely be complex to solve (Duffy, 1995; Nisbet, 1995). Understanding the ecology of cormorants will allow the development of effective management solutions to perceived problems. The implementation of every management action should be evaluated with much care to avoid unintended consequences. The challenge to managers is to construct effective management programs that balance scientific assessment of ecosystem implications along with service to sociological and economic interests.

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Chapter 3

The Role of Double-crested Cormorants (*Phalacrocorax auritus*) in the Aquatic Food Webs of Nesting and Feeding Lakes in Boreal Alberta Based on Stable Isotope Analysis

3.1 Introduction

The structure of lake food webs, as represented by trophic levels or food chain length (Vander Zanden and Rasmussen, 1999), can have important implications for the dynamics of aquatic communities. Lake food web structure can affect species diversity, community stability, contaminant levels in biota, and biogeochemical fluxes (Cabana and Rasmussen, 1994; Vander Zanden and Rasmussen, 1999). The importance of piscivorous fish in regulating lake productivity through top-down controls has long been recognized (Carpenter et al., 1985). Consequently, stocking of piscivorous fish has been used as a lake management tool to rehabilitate highly eutrophic lakes (Carpenter et al., 1987; Hansson et al., 1998; Lathrop et al., 2002). Predation by piscivorous birds is often overlooked (Steinmetz et al., 2003) even though fish-eating birds can occupy similar trophic positions to predatory fish (Hobson et al., 1994), and predation by piscivorous birds can affect food webs and, consequently, lake ecosystems.

Cormorants are known to be opportunistic predators on fish and have the potential to alter fish communities in lakes (Rudstam et al., 2004). They are frequently held responsible for declining fish populations in areas of North America and Europe (Carss, 1995; Rudstam et al., 2004); however, the role of cormorants in the food webs of nesting and feeding lakes is often poorly understood. Quantitative assessments of food web structure of lakes that serve as cormorant feeding sites can help identify feeding patterns (Pimm et al., 1991) and assess the impacts of cormorants on lake systems. Stable isotope analysis can illuminate trophic structure and feeding relationships in lake ecosystems (Peterson and Fry, 1987). This method offers many advantages over conventional diet analysis (samples from regurgitation or stomach contents) because isotopic analysis reflects prey assimilation and can help identify important temporal and spatial variability in diets (Vander Zanden et al., 1997; Harvey and Kitchell, 2000; Vander Zanden and Vadeboncoeur, 2002).

Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ from the tissue of various organisms can be used as an effective method to determine food web structure (Peterson and Fry, 1987; Fry, 1991). Carbon isotope ratios are usually conserved within the food chain (Vander Zanden and Rasmussen, 1999), therefore ratios in consumers can be used to differentiate between resources derived from different habitats or primary producers (Mizutani et al., 1990; Hobson et al., 1994; France, 1995; Vander Zanden and Rasmussen, 1999). Pelagic organisms are typically more depleted in ^{13}C than organisms that feed in the littoral zone of a lake (Vander Zanden and Rasmussen, 1999; Post, 2002). Carbon signatures should help determine which lakes, and more specifically, in what areas of a lake (littoral or pelagic) organisms forage. In contrast, the heavy nitrogen isotope (^{15}N) increases with trophic level and is used as a continuous measure of trophic position (Cabana and Rasmussen, 1996; Post et al., 2000; Swanson et al., 2003). Nitrogen signatures provide an indication of prey sources to a consumer. If cormorants, for example, are feeding on large piscivorous fishes, then there will be an enrichment in the nitrogen signature of cormorant tissue compared to piscivorous fishes, whereas if cormorants are foraging on similar prey items to large piscivorous fish then they should occupy a similar trophic level and display comparable nitrogen signatures.

Increases in numbers of double-crested cormorant (*Phalacrocorax auritus*) in northeastern Alberta, Canada, has generated concern that these birds may be responsible for alterations in fish abundance and community structure in Lac La Biche (LLB), a large eutrophic lake. In 2004, approximately 8000 nests were counted on 9 nesting colonies located within a 50 km radius of the lake (McGregor, 2005). As cormorant populations have increased there has been a concomitant decrease in walleye (*Sander vitreus*) abundance in LLB and an increase in the numbers of small yellow perch (*Perca flavescens*) (Chris Davis, unpublished data). Concurrent with alterations in fish abundance and community structure, there have also been increases in measures of lake eutrophication, through increasing phosphorus levels and frequency of blue-green algal blooms in LLB. The decline of walleye populations and their continued low abundance in LLB prompted the implementation of this study in collaboration with Alberta SRD in 2003 to explore the contribution of cormorants to the decline of walleye. It is possible that cormorants contributed significantly to walleye declines through predation or, alternatively, cormorants may have simply replaced walleye as the new top predator in LLB creating an altered trophic structure which has lead to changes in ecosystem processes.

The objective of my study is to examine stable isotope ratios of carbon and nitrogen in macroinvertebrates, fishes, and cormorants to establish basic food web structure in LLB and other local cormorant nesting lakes. I compare trophic position of cormorants to fish species in nesting and feeding lakes. Cormorants typically feed on schooling fishes, concentrating on species that are present in greatest abundance near nesting colonies (Duffy, 1995; Warke and Day, 1995; Neuman et al., 1997; Collis et al., 2002), and therefore, I expect cormorants in the LLB region to occupy a similar trophic position to piscivorous fish which prey primarily on abundant forage fish species. I use both cormorant muscle tissue and eggs laid on the nesting colonies to evaluate cormorant food web position. I also compare stable isotope signatures of cormorants and potential prey organisms among lakes supporting breeding colonies to determine which lakes in the region are the principal foraging sites of cormorants from various colonies. Dietary patterns inferred from stable isotope analysis are compared to conventional diet analysis based on regurgitation samples to assess the utility of these two methods and to further clarify predator-prey relationships.

3.2 Methods

3.2.1 Description of study lakes

The study centered on four lakes in northeastern Alberta: LLB, Beaver Lake, Antoine Lake, and Portage Lake. All lakes have islands with nesting populations of double-crested cormorants but provide contrasting conditions as foraging sites for cormorants. These lakes are all eutrophic but vary in area, composition of fish communities, and numbers of nesting cormorants (Table 3.1, 3.2). Antoine and Portage Lakes are both small in area and contain a simple fish community of small-bodied fishes (Table 3.2). Fish populations in Antoine and Portage Lakes are not capable of sustaining the large numbers of cormorants that nest on these lakes, and therefore, foraging on other lakes must occur. Cormorant nesting colonies on Antoine and Portage Lakes (both approximately 10 km from High Island on LLB) are thought to forage primarily on LLB. For a lake of its size, LLB is quite shallow with a mean depth of 8.4 m. There are two cormorant colonies on LLB: High Island, a large colony in the west basin of the lake; and Pelican Island, a smaller colony in the lake's east basin. LLB has a diverse fish community with piscivores, pelagic fishes, and littoral fishes (Table 3.2). The town of Lac La Biche (approximately 2700 people) is located on the southeast basin of the lake.

Beaver Lake is a modestly sized lake with a similar fish assemblage to LLB. Contrary to LLB, Beaver Lake has a healthy walleye population. A small cormorant colony is located on one of the small islands in the southeast basin.

Table 3.1: Characteristics of study lakes (TP=Total Phosphorus; Number of cormorant nests counted during 2006 nesting season).

Lake	TPμg/L	Area (km^2)	Max depth (m)	Number of cormorant nests
LLB	113	234	21.3	3417(High Is.) 119 (Pelican Is.)
Beaver	33	33	15.2	46
Antoine	191	4.5	8.5	2339
Portage	121	3	2.7	1842

Table 3.2: Fish species present in double-crested cormorant nesting colony lakes in the Lac La Biche region of northern Alberta

Fish Species	LLB	Beaver	Antoine	Portage
Walleye (*Sander vitreus*)	X	X	-	-
Yellow Perch (*Perca flavescens*)	X	X	-	-
Iowa darter (*Etheostoma exile*)	X	X	-	-
Ninespine Stickleback (*Pungitius pungitius*)	X	-	-	-
Brook Stickleback (*Culaea inconstans*)	X	X	X	X
Burbot (*Lota lota*)	X	X	-	-
Trout perch (*Percopsis omiscomaycus*)	X	-	-	-
Lake Whitefish (*Coregonus clupeaformis*)	X	X	-	-
Cisco (*Coregonus artedi*)	X	-	-	-
Northern Pike (*Esox lucius*)	X	X	-	-
White Sucker (*Catostomus commersoni*)	X	X	-	-
Longnose Sucker (*Catostomus catostomus*)	X	-	-	-
Fathead Minnow (*Pimephales promelas*)	-	-	X	X
Spottail Shiner (*Notropis hudsonius*)	X	X	-	-

Beaver Lake provides a contrast to the highly altered conditions of LLB and the simple fish communities of Portage and Antoine Lakes. Fish populations in Beaver Lake would provide sufficient resources for nesting cormorants.

3.2.2 Field sampling

Invertebrates were collected from littoral and pelagic zones of each lake. Benthic invertebrates were sampled with an Eckman grab. Macroinvertebrates were picked from sediments and rinsed with distilled water. I collected invertebrates from the littoral zone by using a dip net to gather individuals from disturbed sediment and vegetation. After collection, live invertebrates were sorted taxonomically to family or class and held in water for 24 hours to allow them to void their guts. Chilled samples were transferred to whirl-packs and kept frozen at -20°C.

Long lived primary consumers were selected to establish a lake-specific baseline to enable comparisons of stable isotope signatures among lakes (Vander Zanden and Rasmussen, 1999). Large long-lived primary consumers are more suitable for establishing a stable isotope baseline for a food web than are primary producers because consumers require less frequent sampling and integrate temporal variability in primary production (Vander Zanden et al., 1997). Clams (Class Pelecypoda) were obtained from LLB and Beaver Lake to represent the isotope signature of the pelagic food webs (Vander Zanden et al., 1997; Vander Zanden and Rasmussen, 1999; Lake et al., 2001; Post, 2002). Unionid clams (Unionidae) were collected from Beaver Lake by dip netting and snorkeling. Fingernail clams (Sphaeriidae) were collected from LLB via Eckman grab sampling. Snails (Class Gastropoda) were used to represent the base of the littoral food web (Lake et al., 2001; Post, 2002). Because Antoine and Portage are shallow and had no clams, the littoral baseline was used to represent the entire lake food web.

Fish from each lake were sampled at various locations using gill nets, beach seines, and minnow traps. Multi-mesh gill nets were set for a maximum of 3 hours in both littoral and pelagic habitat at varying depths. Minnow traps were unbaited and usually set overnight in littoral areas. A minimum of three individuals were targeted for each species, sampling location, and time period.

Sampling of birds, fishes, and invertebrates occurred in LLB, Beaver Lake, Antoine Lake, and Portage Lake during four time periods in 2004 in May, June, July and September. Supplemental samples were also collected from Antoine and Portage Lakes during June 2005 to fill in gaps in sampling from the previous year. I collected cormorant chick carcasses opportunistically from the nesting islands. Several adult birds were obtained as accidental by-catch from local commercial fishermen as well as from a culling program implemented by Alberta SRD. Tissues of bird eggs are derived from the diet of the laying female (Hobson, 1995) and therefore provide another source of material to assess trophic relations via isotopic signatures. Fresh cormorant eggs were collected randomly from nests near the beginning of the breeding season from colonies on Pelican Island, Antoine Lake, and Portage Lake. Egg freshness was determined by the appearance of newly deposited calcium carbonate residue around the shell. Later in the season, fresh eggs from re-nests were also obtained. Eggs were wrapped in aluminum foil and stored on ice until transferred to a freezer.

In collaboration with the Alberta SRD research program, I collected regurgitation samples during the 2004 nesting season at 2 week intervals (June - August) from cormorant colonies on LLB, Beaver, Antoine, and Portage Lakes. To obtain the samples, we flushed breeding cormorants from nesting colonies which resulted in spontaneous regurgitation of food items being held to deliver to chicks on the nesting colonies. Regurgitation samples were selected from nest rims or immediately adjacent to nests.

3.2.3 Sample preparation and processing

Organisms were thawed, measured and weighed prior to preparation for isotope analysis. Lipids were not removed because this can affect trophic level estimates and result in poorer resolution of dietary relationships (Pinnegar and Polunin, 1999). Snails and clams were removed from their shells. A part of the foot muscle was dissected out of each large Unionid clam. The entire organism was used for all other invertebrates. Dorsal muscle tissue was extracted from fish collected from each lake and from selected fresh regurgitation samples. I used white muscle tissue because it exhibits less variability in stable isotope signatures than other vertebrate tissues (Pinnegar and Polunin, 1999). I extracted pectoralis muscle tissue from nestling and adult cormorants to provide an isotopic signature for cormorants on the five nesting colonies. Pectoralis muscle from cormorants provided an appropriate tissue comparison to dorsal muscle tissue of fish due to comparable fractionation rates of this type of tissue across vertebrate groups (Hobson and Clark, 1992*a*). Samples of albumen were extracted from partially thawed cormorant eggs. Lipids tend to be more depleted in ^{13}C than other tissues (Hobson, 1995), and therefore, albumen (which contains low lipid concentrations) rather than egg yolk was used.

I placed extracted tissues in a freeze dryer at -20°C for 48 hours and then ground these into a fine powder with a mortar and pestle. Homogenized samples of 1.0 ± 0.1 mg were weighed into 6 x 4 mm tin capsules and sent to the Department of Soil Science at the University of Saskatoon and the Biogeochemical Analytical Laboratory at the University of Alberta for analysis of carbon and nitrogen isotopes. A Robo prep elemental analyzer (MWG Biotech Ag., D85560 Ebersberg, Germany) interfaced with a Europa 2020 continuous flow isotope ratio mass spectrometer (CFIRMS; PDZ Europe, Northwich Cheshire, UK) at the University of Saskatoon assessed carbon and nitrogen ratios. At the University of Alberta, analysis was performed on an IsoPrime continuous flow isotope ratio mass spectrometer (GV Instruments, Manchester, UK) connected to a EuroEA 3028-HT elemental analyzer (Eurovector, Milan, IT). Stable isotope results are expressed as parts per thousand (‰ or per mil) delta values (δ^{15}N and δ^{13}C) which are measures of the ratio of heavy to light isotopes in a sample (Peterson and Fry 1987). δ^{13}C and δ^{15}N are presented as relative difference between the ratios of the sample and an international standard:

$$\delta X = [(Rsample/Rstandard) - 1] \times 1000, \tag{3.1}$$

where X = ^{13}C or ^{15}N, and R = ^{15}N/^{14}N or ^{13}C/^{12}C. The standard reference materials are carbon in PeeDee belemnite and atmospheric nitrogen gas (Peterson and Fry 1987). Calibration of 30 samples between the two laboratories indicated no significant difference between analysis results (See Appendix B for lab results).

3.2.4 Isotopic baseline adjustment

Since the δ^{15}N at the base of the food web varied significantly between lakes, absolute values of δ^{15}N from organisms in different food webs could not be compared. Instead, I calculated an adjusted δ^{15}N value to represent a continuous measure of trophic position for each consumer using a baseline correction to enable comparison of trophic position among lakes. For LLB and Beaver Lake, I used a modified version of the two-end member mixing model proposed by Post (2002). Adjusted δ^{15}N for these lakes was calculated as follows:

$$Adjusted\delta^{15}N = \delta^{15}N_{consumer} - [\alpha(\delta^{15}N_{littoralbase}) + (1-\alpha)(\delta^{15}N_{pelagicbase})]. \tag{3.2}$$

δ^{15}N$_{consumer}$ is the unadjusted nitrogen value obtained from the tissue of a consumer. The littoral baseline (δ^{15}N$_{littoralbase}$) was represented by snails. Clams served as the baseline (δ^{15}N$_{pelagicbase}$) for pelagic areas of the lake. The carbon signature can be used to indicate the extent to which a diet is derived from littoral versus pelagic organisms. By using equation 3.3, carbon signatures of the two sources were used to estimate α, which represents the proportion of prey resources the consumer derived from the base of the littoral food web:

$$\alpha = (\delta^{13}C_{consumer} - \delta^{13}C_{littoralbase})/(\delta^{13}C_{littoralbase} - \delta^{13}C_{pelagicbase}). \tag{3.3}$$

This model ensured no more than 100% reliance on either pelagic or littoral sources (Vander Zanden and Vadeboncoeur, 2002). If δ^{13}C of the consumer fell outside the δ^{13}C littoral to pelagic baseline range, the α was set at either 1 or 0. Estimates of trophic position have not been found to be sensitive to assumptions about trophic fractionation of δ^{13}C (Post, 2002; Vander Zanden and Vadeboncoeur, 2002), and therefore, no trophic enrichment in δ^{13}C was assumed in this model.

The adjusted δ^{15}N values for cormorant chicks from Antoine and Portage Lakes were calculated using a modified version of the above two-source mixing model. In addition to prey derived from littoral and pelagic foraging on LLB, a third source of prey was supplied by fish captured on the nesting lake. These small, shallow lakes were assumed to offer only littoral foraging. The mixing model was modified using the following equation:

$$Adjusted\delta^{15}N = \delta^{15}N_{chick} - [\beta(\delta^{15}N_{LLB}) + (1-\beta)(\delta^{15}N_{nestinglake})]. \tag{3.4}$$

The proportion of prey from LLB (β) compared to prey from the nesting lake was estimated from regurgitation samples from colonies on these lakes. Stickleback biomass in the diet of birds from colonies on Antoine and Portage Lakes were assumed to be derived entirely from these lakes. The proportion of stickleback biomass comprised approximately 5% of the diet biomass for Antoine Lake and 2% of the diet biomass on Portage Lake (Table 3.4). The value for $\delta^{15}\mathrm{N}_{LLB}$ in equation 3.4 was calculated using the two-source mixing model described as:

$$\delta^{15}N_{LLB} = [\alpha(\delta^{15}N_{littoralbase} + (1-\alpha)\delta^{15}N_{pelagicbase}]. \qquad (3.5)$$

The remainder of the Antoine and Portage Lake food webs were based on a model used by Cabana and Rasmussen (1996). Since there is no clear distinction between littoral and pelagic zones in these lakes, only a baseline correction for the littoral zone was used (Beaudoin et al., 2001; Vander Zanden and Vadeboncoeur, 2002). Lake-specific baseline δ^{15}N values from snails ($\delta^{15}\mathrm{N}_{littoralbase}$) were subtracted from consumer δ^{15}N values in the lake using the following equation:

$$Adjusted\delta^{15}N = \delta^{15}N_{consumer} - \delta^{15}N_{littoralbase}. \qquad (3.6)$$

3.3 Data analyses

Time periods for all prey categories were pooled to ensure sufficient sample sizes for analysis. Macroinvertebrates were grouped to class or order. When a range of sizes were available for individual fish species they were grouped into size classes (Table 3.3) because of ontogenetic diet shifts that can occur with increasing body sizes (Scott and Crossman, 1979). Fish species were separated into size categories based on expected size at sexual maturity (Scott and Crossman, 1979) (Table 3.3).

Food web structure was compared using common macroinvertebrate groups, fishes and nesting cormorants from LLB, Beaver Lake, Antoine Lake, and Portage Lake. Maximum trophic position for these lakes was calculated using the species with the highest mean adjusted δ^{15}N (Post et al., 2000). The

Table 3.3: Codes and size ranges (mm) of fish species processed for stable isotope analysis from four boreal lake food webs

Code	Species	LLB	Beaver	Antoine	Portage
BS	Brook Stickleback	43 - 58	32 - 56	48 - 57	47 - 68
BSB	Brook Stickleback - boli	36 - 64	-	42 - 54	-
BU	Burbot - immature	56 - 60	-	-	-
CS1	Cisco - immature	77 - 80	-	-	-
CS2	Cisco - adult	232 - 310	-	-	-
FM	Fathead Minnow	-	-	57 - 60	57 - 64
IW	Iowa Darter	22 - 56	32 - 48	-	-
LK	Lake Whitefish	185 - 457	471 - 508	-	-
NS	Ninespine Stickleback	47 - 56	-	-	-
NP1	Northern Pike - immature	-	85 - 145	-	-
NP2	Northern Pike - adult	480 - 680	320 - 584	-	-
SP	Spottail Shiner	27 - 87	26 - 56	-	-
WA1	Walleye - immature	305 - 322	197 - 322	-	-
WA2	Walleye - adult	490 - 571	432 - 471	-	-
WS1	White Sucker - immature	38 - 163	-	-	-
WS2	White Sucker - adult	205 - 575	-	-	-
YPB	Yellow perch - boli	-	-	81 - 89	
YP1	Yellow perch - YOY	32 - 59	41 - 47	-	-
YP2	Yellow Perch - immature	84 - 123	-	-	-
YP3	Yellow Perch - adult	131 - 241	129 - 298	-	-

species occupying this position as well as the values were compared among the four nesting lakes.

Mean δ^{13}C and δ^{15}N values for cormorants were grouped into adults from LLB and chicks from each nesting colony. Mean values of adjusted δ^{15}N were compared with ANOVAs to detect differences between cormorants and predatory fishes in LLB and Beaver Lake. ANOVAs were used to compare nitrogen isotopic signatures of cormorant chick muscle tissue and eggs laid on the nesting colonies. Posthoc comparisons for all ANOVAs were conducted using Tukey comparisons. To determine in which lakes cormorants were foraging, isotopic signatures of fish from cormorant regurgitation samples were compared, using t-tests, to fish taken directly from satellite colony lakes and from LLB.

3.4 Results

3.4.1 Baseline isotope variability

Baseline δ^{15}N values for snails (ANOVA, $F_{3,48} = 28.693$, $p < 0.001$) and clams (ANOVA, $F_{1,37} = 104.60$, $p < 0.001$) differed significantly among lakes. Mean δ^{15}N values of snails were lowest in LLB (mean = 3.7‰) and highest in Portage Lake (mean = 10.5‰, Figure 3.1). The pelagic baseline from clams in LLB was also lower in δ^{15}N (mean = 6.0‰) when compared to nitrogen baseline signatures of clams from Beaver Lake (mean = 8.9‰). Mean baseline δ^{13}C values were significantly different among lakes for both snails (ANOVA, $F_{3,48} = 51.561$, $p < 0.001$) and clams (ANOVA, $F_{1,37} = 65.975$, $p < 0.001$). Carbon was most depleted for snails in LLB (mean = -25‰) and least depleted for Portage Lake (mean = -17.4 ‰) (Figure 3.1). Clams in LLB were lower in δ^{13}C (-26.4‰) compared to Beaver Lake (-24.2‰). Given the variability in isotope baseline values, these results demonstrate the importance of implementing baseline corrections when comparing food web structure across sites. I created simplified food webs for each lake using the appropriate baseline adjustments for δ^{15}N.

3.4.2 Food web structure

Stable carbon signatures indicated that there was a differentiation between species that fed in the pelagic and littoral zones in LLB. However, the variation in δ^{13}C was small and only ranged 3.6‰. Invertebrate groups including odonates and chironomids were similarly depleted in δ^{13}C to sphaeriidae clams indicating a shift towards occupying the pelagic area of the lake (Figure 3.2A). As a result, certain fishes such as small yellow perch and cisco which rely more heavily on pelagic invertebrates were also depleted in δ^{13}C (Figure 3.2A). The remainder of the LLB food web appears strongly linked to the littoral areas of the lake. Carbon signatures for other invertebrate groups including adult coleoptera, trichoptera, amphipoda, and hirudinea were less depleted in δ^{13}C compared to pelagic invertebrates (Figure 3.2A). These organisms provided

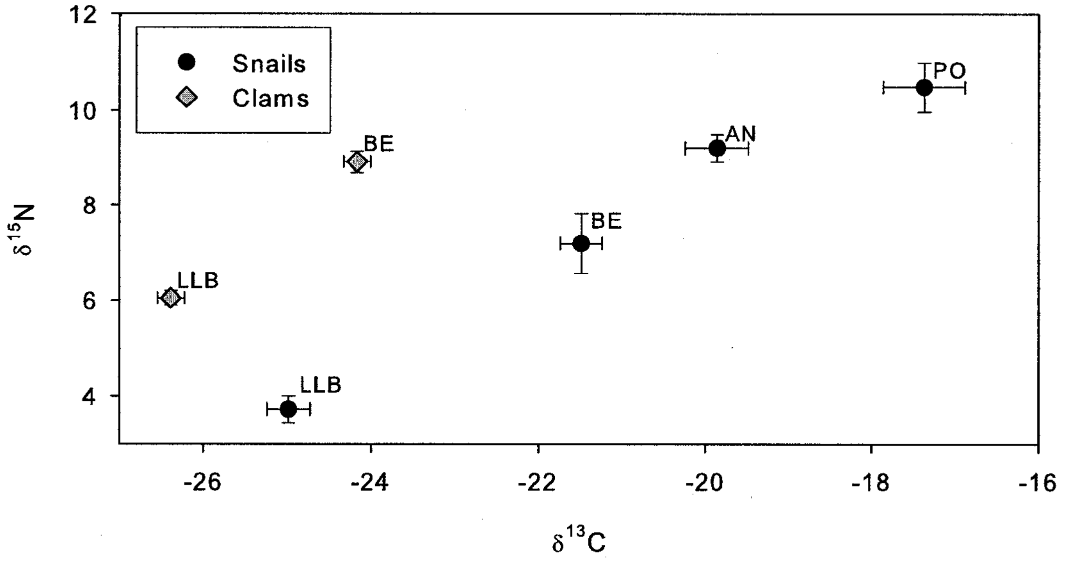

Figure 3.1: Comparison of lake-specific stable isotope baseline values from four lakes in the Lac La Biche region of northern Alberta. Samples were collected from May - September 2004 and June 2005. Snails were used to establish the littoral baseline and clams the pelagic baseline. (LLB = Lac La Biche, BE = Beaver Lake, AN = Antoine Lake, PO = Portage Lake, Mean values reported, Error bars = SE, n = 3-34)

carbon sources to fish species foraging in littoral habitats. Based on similarities in stable carbon signatures, prey items for cormorant adults and chicks alike may include, yellow perch, cisco, suckers, brook stickleback, ninespine stickleback, and spottail shiner.

In Beaver Lake, unionid clams were the only pelagic invertebrate sampled. The carbon signature for clams in Beaver Lake was not as depleted in $\delta^{13}C$ as the carbon signature for clams in LLB. Young-of-year yellow perch, lake whitefish and spottail shiner (fishes known to rely on pelagic sources) had similar carbon signatures to clams from Beaver Lake. Amphipods, trichopterans, and hirudineans appeared more clearly linked to a littoral carbon source compared to most fish species collected in Beaver Lake (Figure 3.2B). Gastropods were an appropriate baseline to represent littoral primary production for littoral foraging fish species including Iowa darter, large yellow perch, northern pike, brook stickleback, and walleye. Cormorant chicks from the nesting colony on Beaver Lake had an isotopic signature similar to organisms collected from the

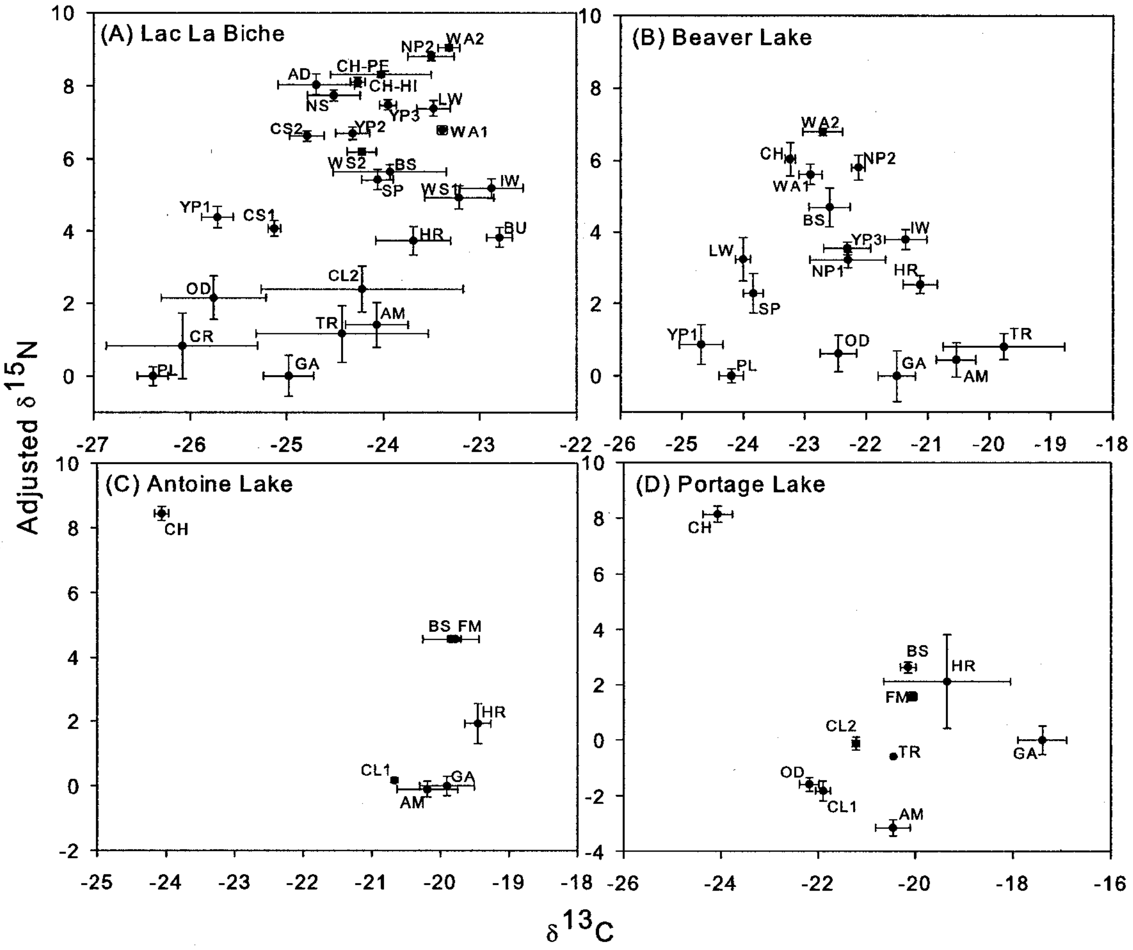

Figure 3.2: Food webs based on stable isotope analysis for four boreal lakes supporting double-crested cormorant colonies (AD=double-crested cormorant adult, AM=amphipoda, CH=double-crested cormorant chick, CH-HI=chicks from High Island, CH-PE=chicks from Pelican Island, CR=chironomid, CL1=coleoptera larvae, CL2=coleoptera adult, GA=gastropoda, HR=hirudinea, OD=odonata, PL=pelecypoda, TR=trichoptera, BS=brook stickleback, BU=burbot, CS1=cisco (immature), CS2=cisco (adult), FM=fathead minnow, IW=iowa darter, LK=lake whitefish, NS=ninespine stickleback, NP1=northern pike (immature), NP2=northern pike (adult), SP=spottail shiner, WA1=walleye (immature), WA2=walleye (adult), YP1=yellow perch (yoy), YP2=yellow perch (age 1-2), YP3=yellow perch (age 3+), Mean values reported, Error bars = SE, n = 1 - 34)

Beaver Lake food web. The carbon signature for these chicks was situated between littoral and pelagic baselines, thus, prey items could be derived from either area of the lake and could include lake whitefish, spottail shiner, small northern pike, yellow perch, small walleye, and brook stickleback.

The food webs of Antoine and Portage Lakes were less depleted in δ^{13}C than the food webs from LLB and Beaver Lake (Figure 3.2). Antoine and Portage Lakes were functionally composed entirely of littoral habitat, thus, amphipods, gastropods, coleopterans, odonates, trichopterans, and hirudineans provided an anchor for carbon sources for fathead minnow, and brook stickleback present in these food webs (Figure 3.2C, D). Cormorant chicks from satellite colonies were depleted in δ^{13}C compared to the remainder of the food web and were enriched in δ^{15}N compared with the top of the local food web (represented by fathead minnow and brook stickleback) by 3.8‰ and 5.5‰ for Antoine Lake and Portage Lake, respectively.

A general pattern of trophic enrichment was evident in all the food webs. Macroinvertebrates and forage fishes had lower adjusted δ^{15}N values than cormorants, walleye, and northern pike which are known to prey on fish species from lower trophic levels. Ordering the organisms from LLB and Beaver Lake food webs into a trophic ladder (Hobson et al., 1994) based on adjusted δ^{15}N demonstrates a gradual enrichment in stable nitrogen signatures (Figure 3.3). Consumers in these two lakes seem to feed along a continuum of trophic levels rather than occupying discrete trophic positions along a food chain.

Maximum trophic position (MTP) in each system is represented by the largest adjusted δ^{15}N. This value can also be used to quantify food chain length (FCL) (Vander Zanden et al., 1999; Post et al., 2000). In LLB, walleye occupied the MTP, and the FCL was 9.0‰ (Figure 3.2A). The MTP for Beaver Lake was also occupied by walleye however FCL was considerably shorter (6.8‰; Figure 3.2B). Excluding cormorants from the food web of Antoine and Portage Lakes, the MTP was occupied by brook stickleback (Figure 3.2C,D). If double-crested cormorants were excluded, the FCL of Antoine Lake (4.6‰) and Portage Lake (2.6‰) was much shorter than LLB and Beaver Lake be-

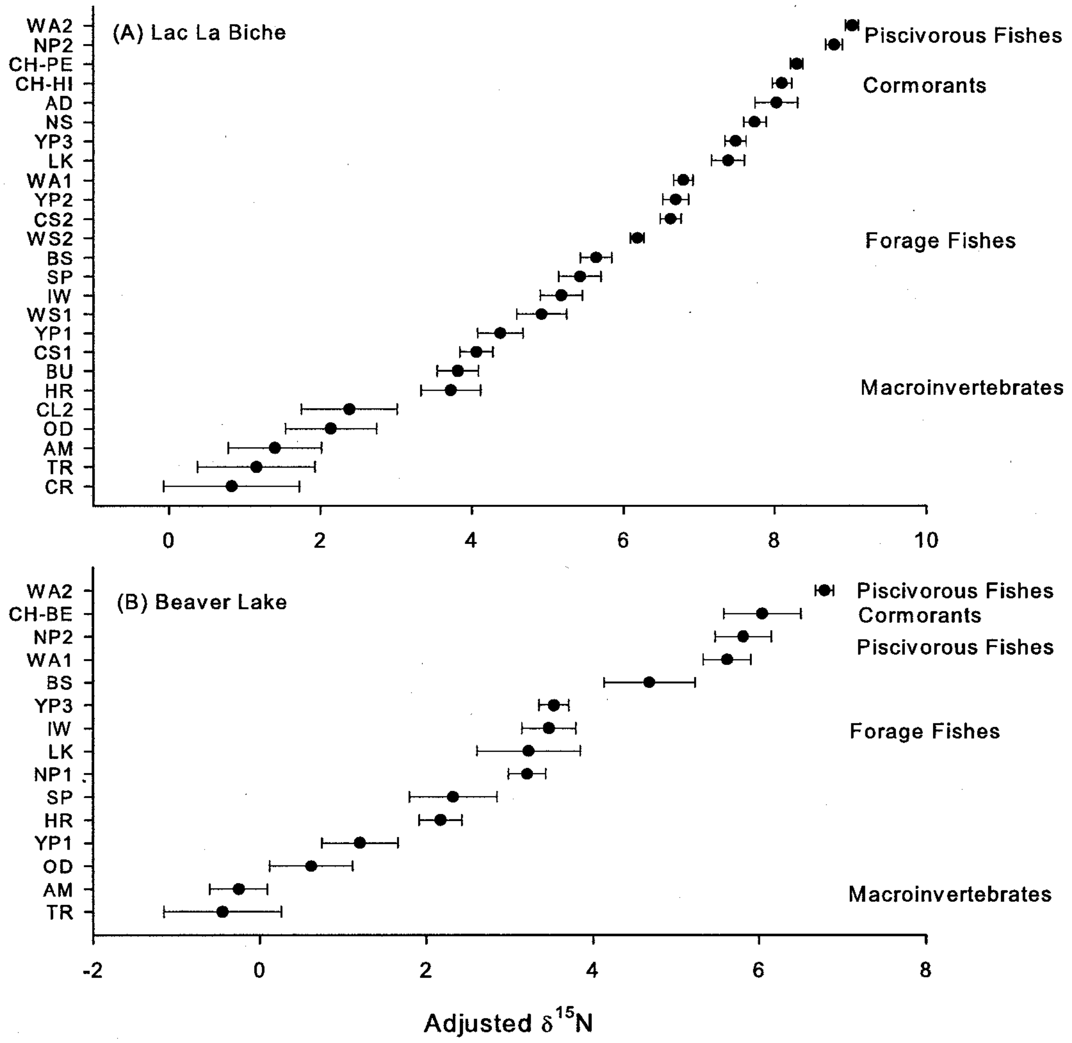

Figure 3.3: Baseline adjusted stable-nitrogen isotope concentrations in various components of Lac La Biche and Beaver Lake food webs. (Mean values reported, Error bars represent standard error, n = 1-19, Species codes according to Table 3.3.)

cause these lakes lacked piscivorous fishes (Table 3.2). Cormorant chicks from Antoine and Portage Lakes clearly ate prey items from sources other than nesting lakes (Figure 3.2, Table 3.4). If cormorants are included in Antoine Lake and Portage Lake food webs, they represent the MTP for these lakes and FCL's are increased for both Antoine Lake (8.4‰; Figure 3.2C) and Portage Lake (8.1‰)(Figure 3.2D).

3.4.3 Trophic relationships

Comparisons of mean adjusted δ^{15}N for cormorants and piscivorous fish suggest that cormorants feed at a similar trophic level to both northern pike and walleye within a lake. There was no significant difference in adjusted δ^{15}N values between cormorant adults or chicks (from nesting colonies on LLB and satellite colony lakes) and piscivorous fishes from LLB (walleye and northern pike) (ANOVA, $F_{6,35} = 2.046$, $p = 0.085$, Figure 3.4). Within Beaver Lake, the mean adjusted δ^{15}N for cormorant chicks, walleye and northern pike were also not significantly different (ANOVA, $F_{2,8} = 2.003$, $p = 0.197$). However, both cormorants and piscivorous fish from Beaver Lake were at a significantly lower trophic level than the same predators from LLB (ANOVA, $F_{9,43} = 13.087$, $p < 0.001$).

Cormorants nesting on Antoine and Portage Lakes have similar isotopic signatures to cormorants nesting on LLB (Figure 3.5) suggesting that these birds are foraging primarily on LLB. Because of the simple fish community and short food webs on Antoine and Portage Lakes (Table 3.2), the high trophic level of cormorants nesting on these lakes must necessarily come from fish species from other lakes. Analysis of yellow perch (YPB) taken directly from regurgitation samples of Antoine Lake cormorants yielded similar isotopic signatures, in both carbon and nitrogen, to yellow perch (YP2) of similar sizes from LLB (t-test, δ^{13}C, $t = .469$, df $= 16$, $p = 0.646$; δ^{15}N, $t = 2.76$, df $= 16$, $p = 0.786$; Figure 3.5) which confirms the expectation that LLB is the main foraging lake. However, brook stickleback (BSB) collected from Antoine Lake regurgitation samples had similar isotopic values to brook stickleback

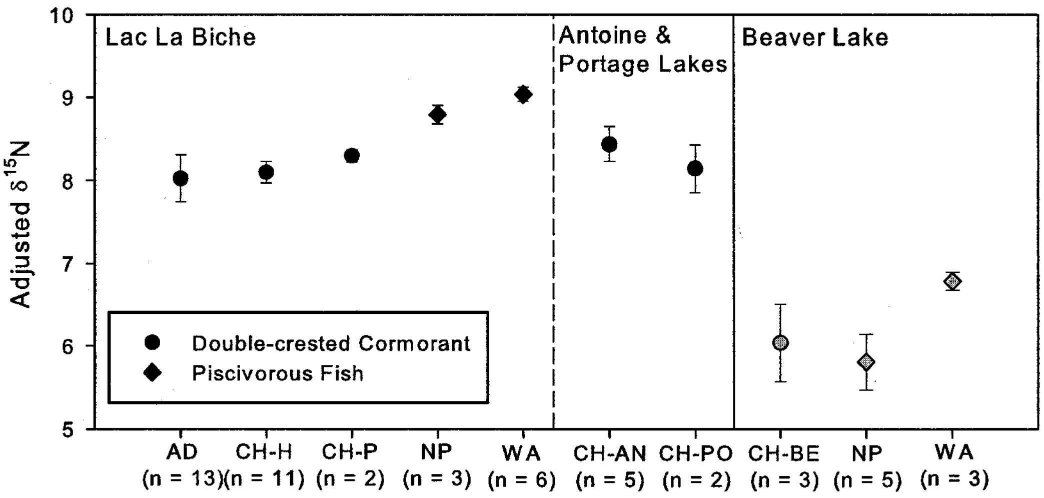

Figure 3.4: Comparison of baseline adjusted stable-nitrogen signatures of double-crested cormorants and piscivorous fish from Lac La Biche and Beaver Lake (AD = double-crested cormorant adult, CH-H = cormorant chick from High Island, CH-P = cormorant chick from Pelican island, CH-AN = cormorant chick from Antoine Lake, CH-PO = cormorant chick from Portage Lake, CH-BE = cormorant chick from Beaver Lake, NP = northern pike, WA = walleye, n = number of individuals, Mean values reported, Error bars represent standard error.)

(BS) from Antoine Lake (t-test, δ^{13}C, t = -0.469, df = 4, p = 0.664; δ^{15}N, t = -1.286, df = 4, p = 0.268; Figure 3.5) indicating that not all foraging takes place on LLB and that cormorants do feed to some extent on the satellite lakes.

Unadjusted isotopic values were used to allow comparisons among different tissue types from cormorants from a single colony. Stable isotopic ratios for cormorant chick muscle tissue were significantly lower than isotopic values for eggs laid on the colonies for both δ^{13}C (ANOVA, $F_{6,26} = 3.887$, $p = 0.007$) and δ^{15}N (ANOVA, $F_{6,26} = 20.301$, $p < 0.001$, Figure 3.6). The isotopic signatures of cormorant muscle tissue reflects similar signatures to the dorsal muscle tissue of piscivorous fishes such as walleye and northern pike in LLB (Figure 3.6). The eggs reflected more variability, particularly in δ^{13}C, compared to isotopic values observed for muscle tissues.

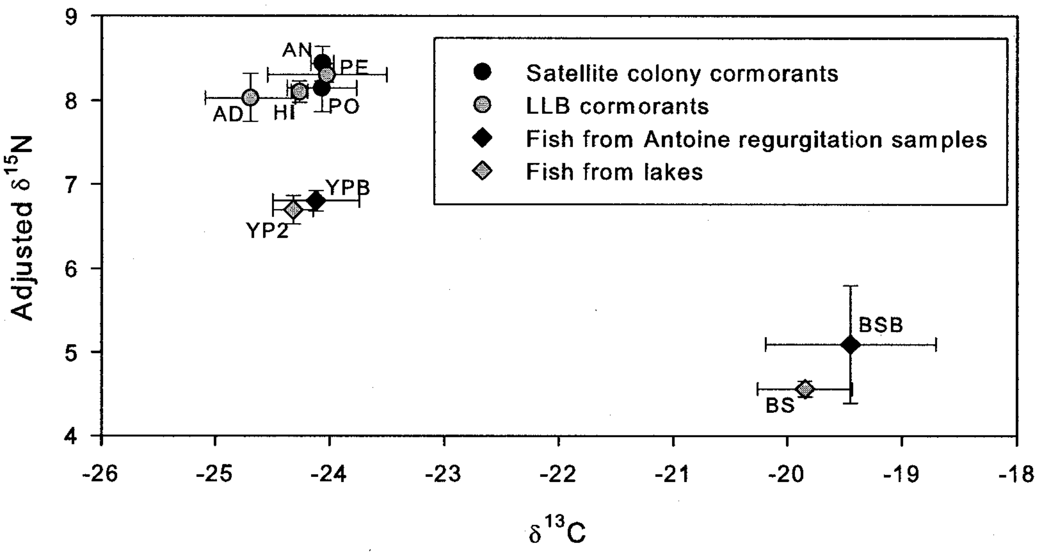

Figure 3.5: Comparison of stable isotope signatures from double-crested cormorants nesting on Lac La Biche versus satellite colonies. (AD = cormorant adult, HI = chick from High Island (LLB), PE = chick from Pelican Island (LLB), AN = chick from Antoine Lake, PO = chick from Portage Lake, YPB = yellow perch from Antoine Lake regurgitation samples, YP1 = small yellow perch from LLB, BSB = brook stickleback from Antoine Lake regurgitation samples, BS = brook stickleback from Antoine Lake, Mean values reported, Error bars represent standard error, Species codes according to Table 3.3.)

3.4.4 Prey composition of cormorants using conventional diet analysis

Medium-sized yellow perch comprised the largest proportion of biomass (64.3%) in regurgitation samples from cormorants nesting on LLB (High Island) (Table 3.4). Coregonid species (e.g. lake whitefish and cisco) also made up a substantial part of diet biomass (22.6%). Cormorants nesting on Antoine and Portage Lakes also displayed a large proportion of medium-sized yellow perch in regurgitation samples based on biomass (Table 3.4). Composition of regurgitation samples provides further confirmation that these cormorants were likely foraging on LLB. There was a large proportion of biomass composed of coregonid species (38.6%) in samples from the Portage Lake cormorant colony which may also have originated in LLB. Regurgitation samples from Beaver Lake chicks were also comprised mostly of yellow perch (86.5%; Table 3.4). The next largest contributing prey category after perch was walleye (13.1%).

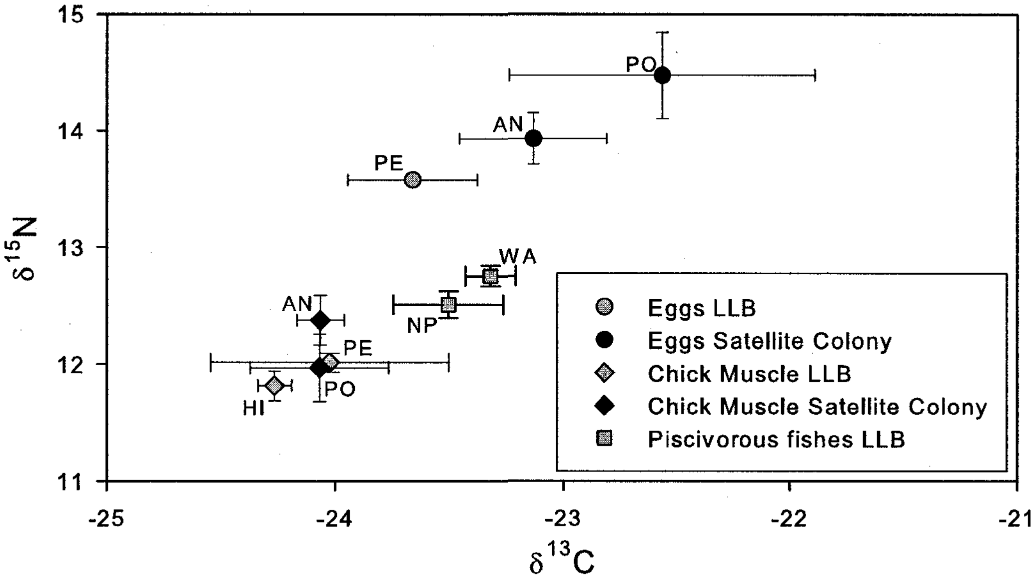

Figure 3.6: Comparison of stable isotope signatures of double-crested cormorant chick and piscivorous fish muscle tissue to egg albumen from nesting colonies. (AD = cormorant adult, HI = chick from High Island (LLB), PE = chick from Pelican Island (LLB), AN = chick from Antoine Lake, PO = chick from Portage Lake, WA = walleye, NP = northern pike, Mean values reported, Error bars represent standard error.)

Table 3.4: Percent biomass of prey identified in regurgitation samples collected from double-crested cormorant colonies during 2004 nesting season (n = number of individual fish identified, Species codes according to Table 3.3.)

Colony	n	WA	YP1	YP2	YP3	BS/NS	CS/LW	NP	WS	SP	Other
LLB	1648	0.0	0.1	64.3	4.7	0.0	22.6	1.3	4.5	0.3	2.2
Beaver	42	13.1	0.1	47.2	39.2	0.0	0.0	0.0	0.0	0.4	0.0
Antoine	2113	3.4	0.4	55.7	8.1	4.4	7.3	11.3	3.3	6.0	0.0
Portage	951	0.0	0.5	32.3	7.6	1.8	38.6	2.4	4.0	8.0	4.8

Since there were a limited number of samples collected on Beaver Lake, this large biomass arises from a single fish and it is unknown how truly representative our samples were of the entire diet.

Stable isotope analysis for mobile predators, such as cormorants, should be coupled with focused analyses of regurgitation samples to confirm isotopic results. Through regurgitation analysis yellow perch were identified as the most important prey item in cormorant diets from all nesting colonies in the LLB area. This taxa specific information could not be obtained through stable isotope analysis alone.

3.5 Discussion

Using stable isotopes to assess trophic position of cormorants, I determined that cormorants foraging in the LLB area occupied a similar trophic position to other top-level aquatic predators, such as walleye and northern pike. Cormorants nesting on small satellite lakes foraged on multiple lake systems and likely derived the majority of prey resources from LLB. With accurate quantification of baseline signatures, it is possible to make comparisons across the variety of cormorant foraging lakes.

3.5.1 Baseline isotope variability

Comparisons among lakes in this study demonstrate the importance of making the appropriate correction for variability in source of primary productivity ($\delta^{13}C$) as well as trophic enrichment ($\delta^{15}N$). It is important to develop a baseline model that places each organism of interest into the appropriate ecosystem context. The four lakes included in this study had large variation in baseline $\delta^{13}C$ (-26 to -17‰) and $\delta^{15}N$ (4 to 11‰) isotope signatures among lakes (Figure 3.1). In other studies, $\delta^{15}N$ values for baseline organisms have been found to vary over a range of -2 to 9‰ (Post, 2002). Baseline variability, particularly enrichment of $\delta^{15}N$, has been linked to nitrogen transformation (Vander Zanden and Rasmussen, 1999), nutrient inputs (Lake et al., 2001), and human densities (Cabana and Rasmussen, 1996). LLB has the highest human populations in proximity to the lake but had the lowest $\delta^{15}N$; therefore, other factors must be contributing to high nitrogen enrichment in the other lakes. Housing communities along the Beaver Lake shoreline may also influence nutrient inputs to the lake. Runoff from abundant agricultural land use may contribute to nitrogen enrichment in the selected lakes. Nutrient input from colonial birds may also contribute to high $\delta^{15}N$ in Antoine and Portage Lakes given the large numbers of nests and small surface area of these lakes (Kameda et al., 2006). Alternatively, differences in nitrogen-cycle dynamics (Hart and Lovvorn, 2002), for instance, increases in denitrification and ammonification which are accompanied by increased nitrogen isotope fractionation (Vander Zanden and Rasmussen, 1999) may cause inherent differences in the δ^{15}N of these shallow lakes with their extended littoral zones.

3.5.2 Food web structure

Overall, the lake food webs, as constructed by stable isotope analysis, were trophically similar to other lakes in the boreal region (Beaudoin et al., 2001; Paszkowski et al., 2004). Although stable carbon isotopic signatures did not appear to exhibit as wide a range in values within a lake compared to other studies. Beaudoin et al. (2001) observed a range in δ^{13}C from approximately -30‰ to -15‰ and Paszkowski et al. (2004) reported a similarly wide range of δ^{13}C values from roughly -27‰ to -14‰. I documented the widest range of carbon isotopic signatures in Beaver Lake which still only spanned approximately 5‰ in δ^{13}C (-19.8‰ to -24.7‰). LLB exhibited a carbon isotopic range from -21.8‰ to -26.4‰. Pelagic foraging species could be identified by depleted δ^{13}C relative to littoral species. Nitrogen isotopes were enriched in consumers relative to expected prey items (Figure 3.3). Discrete levels of trophic feeding were not observed but instead adjusted δ^{15}N values were used to represent a continuous measure of trophic level (Figure 3.3).

Mean enrichment between trophic levels has been determined to be approximately 3.4‰ (Post, 2002); however, this level of enrichment was not observed in the study lakes. Enrichment in δ^{15}N of cormorants compared to possible prey items ranged from 0.4 to 4.0‰ in LLB and 0.4 to 4.8‰ in Beaver Lake. Compared to yellow perch, known to be an abundant item in the diet (Table 3.4), trophic enrichment was approximately 1.5 and 2.5‰ for LLB and Beaver Lake, respectively. Lower levels of trophic enrichment suggests that trophic omnivory is present in these lakes. Trophic omnivory, when individual predators consume prey across multiple trophic levels, is common in boreal lakes due to low species diversity and large fluctuations in population densities from year to year (Beaudoin et al., 2001). This can have important implications for ecosystem resistance to changes as top-down regulation of prey populations can weaken if predator diets are diversified (Vander Zanden and Vadeboncoeur, 2002; Vadeboncoeur et al., 2005). For example, cormorants may simply be able to switch between prey resources as the abundance of various fish populations change over time.

Extirpations of species or additions of new species can be reflected in food chain length (FCL) (Vander Zanden et al., 1999; Lake et al., 2001). Cormorants do not provide a prey source for other strictly aquatic organisms in the lake, thus cormorant predation could lengthen the food chain through the addition of a new apical trophic level. Instead, cormorant predation is not likely to have increased FCL since cormorants are simply exploiting a feeding niche created by decreased numbers of piscivorous fish and increased numbers of smaller bodied prey fish. Cormorants were found to occupy a similar trophic position to predatory fish (Figure 3.4).

FCL in LLB was longer than Beaver Lake (Figure 3.2A,B). FCL has been found to be closely related to fish species richness, lake area, and productivity (Vander Zanden et al., 1999; Post et al., 2000); therefore, a longer food chain length in LLB is not unexpected due to it's greater species richness, much larger surface area, and high productivity. FCL is positively correlated to concentrations of persistent contaminants (Cabana and Rasmussen, 1994). This could lead to increased contaminant levels in fish derived for human consumption from the sport and commercial fishery in the lake.

3.5.3 Trophic relationships

Cormorants from LLB, Antoine Lake, and Portage Lake occupy a similar trophic position to piscivorous fishes in LLB (Figure 3.4). Isotopic signatures from chicks from Beaver Lake are similar to piscivorous fishes in that lake, not LLB (Figure 3.4). This indicates that birds nesting on Beaver Lake are also foraging on Beaver Lake and not traveling 15 km to feed on LLB. Cormorants are opportunistic foragers that typically consume fish species that are most abundant (Blackwell et al., 1995; Weseloh et al., 1995; Neuman et al., 1997). Trophic similarities between LLB and Beaver Lake were observed even though Beaver Lake supported larger populations of piscivorous fish than LLB which could potentially yield an elevated trophic position for cormorants in Beaver Lake. It is possible that cormorants are still preying on walleye or northern pike present in Beaver Lake but predation may occur at smaller size classes of predatory fishes with lower δ^{15}N values and cormorant trophic position would therefore not be elevated. Walleye are known to exhibit ontogenetic shifts in diet from invertebrates to fish as size increases (Scott and Crossman, 1979). Analysis of young-of-year and yearling predatory fishes, which would be appropriate sizes for cormorants, was not done because these fish were not captured during netting efforts in the lakes. Still, it is unlikely that these fishes make up a substantial part of the diet, despite the healthy populations in Beaver Lake, because they will still be much less abundant than forage fishes in either lake.

Trophic similarity based on stable isotope analysis does not directly translate into strong similarities in diet since the stable nitrogen signature provides an average trophic position based on all prey items combined (Hobson et al., 1994; Forero et al., 2004). Cormorants are known to consume a wide variety of prey species (Blackwell et al., 1995; Neuman et al., 1997; Wires et al., 2001; Rudstam et al., 2004; Withers and Brooks, 2004), which could affect the interpretation of isotopic signatures. Although similar isotopic values does not necessarily identify identical diets, it does suggest that cormorants and piscivorous fishes occupy a similar and important place at the top of the food chain. Additional information (such as stomach analysis of cormorants and fish) is essential to further interpretation of these isotopic results (Hobson et al., 1994).

Although it is possible for some breeding migratory birds to import nutrients from overwintering areas (Hobson et al., 1997), there is no evidence that cormorants do so. Based on studies of double-crested cormorants from the Great Lakes, cormorants did not transfer nutrients from overwintering to breeding locations (Hobson et al., 1997). Material for egg formation is thus likely obtained from lakes within the breeding area. Stable isotope analysis of eggs from red-necked grebes have proven suitable to assess trophic relationships of this species on boreal lakes (Paszkowski et al., 2004). However, the use of eggs in the LLB food web may provide misleading results since the eggs are considerably enriched in both δ^{13}C and δ^{15}N compared to muscle tissue taken from chicks from the same colonies (Figure 3.6). Comparisons with the remainder of the food web, particularly piscivorous fishes, using only eggs misrepresents trophic relationships by suggesting cormorants are more trophically elevated than piscivorous fishes. The differences in δ^{13}C and δ^{15}N between eggs and muscle tissue could also be representative of changes in cormorant diet subsequent to egg laying. The signature of Antoine Lake and Portage Lake eggs may reflect preferred use of the nesting lakes for foraging during the egg-laying period since these lake food webs were also enriched in δ^{13}C and δ^{15}N compared to LLB. However, eggs collected from Pelican Island on LLB were also shifted compared to chick muscle tissue. Differences observed in isotopic signatures of eggs versus muscle could also result if female cormorants were consuming large, spawning yellow perch early in spring. Alternatively, the change in isotopic signature may simply reflect differences in isotopic fractionation in different tissue types (Hobson and Clark, 1992*b*; Pinnegar and Polunin, 1999). Although eggs may offer a more desirable tissue type for isotopic analysis to avoid destroying adult birds, or if chick carcasses are not available, comparisons among food web organisms using different tissue types should be made with caution.

3.5.4 Comparison of stable isotope and conventional diet analyses

Both stable isotope analysis and conventional diet analysis provided clear evidence that cormorants in the LLB region prey exclusively on fish. Stable isotope analysis demonstrated that cormorants have similar trophic position to piscivorous fish in the lake but provided limited information on proportional contribution of prey species to the diet. Analysis of regurgitation samples indicated that the majority of cormorant diet during the nesting period was comprised of yellow perch (Table 3.4). Stable isotope analyses were consistent with this conclusion but regurgitation analysis provided a taxonomic resolution that was not attainable with isotope analysis (see also Vander Zanden et al. (1997); Beaudoin et al. (1999)). Without direct analysis of regurgitation samples, I could not have identified yellow perch as the most important prey item to cormorants. Similar isotopic signatures were found for a number of prey items in LLB including yellow perch, white suckers, cisco, spottail shiner, and brook stickleback, and the relative importance of each of these items would have been difficult to assess.

Analysis of food webs through regurgitation analysis provided detailed quantitative results on prey consumption; however, this method can have biases and offer logistical challenges given the large numbers of samples required to address spatial and temporal diet variability (Vander Zanden and Rasmussen, 1999; Forero et al., 2004; Clarke et al., 2005). Most conventional diet analysis for birds looks at diet during the breeding season (Hobson et al., 1994) and consequently provides a limited temporal assessment. The diet of cormorants changes seasonally (Neuman et al., 1997) and gathering regurgitation data over longer time periods can be problematic due to limited availability of samples outside of the nesting season (Pinnegar and Polunin, 1999; Vander Zanden and Vadeboncoeur, 2002). Stable isotope analysis provides an efficient way to estimate trophic position and identify trends through time (Hobson et al., 1994), but is most effective when done in combination with conventional diet analyses (Clarke et al., 2005).

3.5.5 Lake management implications

The double-crested cormorant occupies an important position in the food chain in some boreal lakes since predators have the potential to alter ecosystem function through top-down controls (Carpenter et al., 1985). Trophic cascades have been documented in a variety of ecosystems (Pace et al., 1999; Lathrop et al.,

2002) and result in changes in abundance or biomass across more than one trophic link (Carpenter et al., 1985, 1987). The removal of a top predator in the system will often result in an explosion of planktivorous fishes and subsequent increases in algal productivity (Carpenter et al., 1985). Reductions in the numbers of cormorants may release predation on forage fishes leading to further explosions of planktivores and consequently undesirable effects on water clarity in LLB. In contrast, increases in abundance of walleye and northern pike have been documented to reduce planktivore density to produce a noticeable increase in water clarity (Lathrop et al., 2002); however, no such documented effect has been observed from cormorant predation.

The presence of multiple predators, or a single species of predator with a broad diet, could dampen the effects of a potential trophic cascade (Post et al., 2000a; Finke and Denno, 2005; Vadeboncoeur et al., 2005). Thus, large numbers of cormorants may not exert the same kind of influence in controlling planktivores as predation pressure exerted by walleye and pike since cormorants may be less specialized in their diets than these other piscivores. New predators to aquatic systems can adversely affect interactions within native fish populations (Vander Zanden et al., 1999). Although cormorants are not new to the area, present population numbers are thought to be larger than historical values estimated for the region (Hatch, 1995).

Predicting the effects of biomanipulation of these lakes, such as culling cormorants or re-stocking walleye in the lake, is clearly not straightforward. The effects of such actions should be carefully evaluated and monitored at an appropriate temporal scale. Lepak et al. (2006) used stable isotopes to identify a response in the lake food web to the removal of an introduced apex predator. Stable isotope analysis in LLB could also be used to detect changes following perturbations. However, there may be time delays in trophic-level interactions (Persson et al., 1992) and long term monitoring will likely be necessary after any manipulation. Although biomanipulation may provide a valuable tool in lake management, success in restoring ecosystem function and increasing water clarity will ultimately require a reduction in nutrient inputs to the lake (Schindler, 1977).

An ecosystem-level approach will be critical for providing an understanding of lake-wide trophic level dynamics. Management actions directed towards a single species is too narrow a focus to bring about any substantial changes to the lake system. Prior to management actions on cormorants, it will be necessary to also obtain information on lake fish populations so that the impacts of cormorant predation and subsequent changes to fish communities and water quality can be assessed. If a change in the current ecosystem state of LLB is desired it will be necessary to understand what actions can cause an ecosystem shift and what characteristics will be used to quantify a successful shift. Anthropogenic disturbances to LLB are not likely to disappear, therefore managers will need to consider how future perturbations such as recreational fishing pressure, continued commercial harvest, agricultural land use, lake shore development, and climate change will affect the food web structure of LLB and other boreal lakes.

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Chapter 4

General Discussion

Prior to the cormorant management program initiated in 2003 there was very little information about cormorant diet in the Lac La Biche (LLB) region. My thesis represents a scientific contribution towards developing a better understanding of local prey consumption by cormorants. The efforts of local government biologists continue to generate useful information on cormorants and fish to help place some of my data in a broader context and ultimately to assess implications of this research for fisheries and wildlife management.

Using regurgitation samples (boli) from nesting colonies I found the main prey item of the double-crested cormorant diet to be small bodied fishes (mostly $<$ 100 mm). Yellow perch was identified as particularly important since this species represented the majority of the diet using diet metrics of percent biomass, percent numerical abundance, and percent frequency of occurrence. This heavy predation on yellow perch is likely a reflection of high perch abundance in LLB which appeared to be the main source of prey for birds nesting both on and off the lake. With accurate quantification of baseline signatures, it was possible to make stable isotope comparisons across a variety of aquatic systems (Vander Zanden and Rasmussen, 1999; Post, 2002). Cormorants foraging in the LLB region occupied a similar trophic position to other aquatic predators such as walleye and northern pike in large lakes.

The information gathered in this study is an initial step to understanding the role of cormorants in LLB. There will be substantially more research required to be able to assess the impact of cormorant predation on fish populations and ultimately predict cormorant influence in structuring this system.

4.1 Gaps in current knowledge

The inability to assess adequately the impacts of cormorant predation on the LLB fishery, through direct and indirect effects, is due primarily to the lack of detailed information on fish populations themselves (Nisbet, 1995). Biomass estimates of fish species being removed from local lakes by cormorants will ultimately need to be compared to available biomass in the lakes (Madenjian and Gabrey, 1995; VanDeValk et al., 2002). Quantitative information on numerical abundance of prey species and sizes, as well as knowledge of density dependent growth, predator avoidance strategies, and compensatory responses, will be critical to understanding the implications of cormorant predation on the LLB ecosystem (Wires et al., 2001; Rudstam et al., 2004). Simply documenting fish consumption by cormorants will not readily translate into potential impacts of these birds on the LLB fish community.

There are temporal biases of prey species and sizes captured associated with changes in fish behaviour throughout the season (Neuman et al., 1997). This will affect prey vulnerability to predation and thus alter cormorant diet composition. Temporal limitations of regurgitation sampling prevents the analysis of seasonal differences in prey exploitation. Prey consumption outside of the nesting season is mostly unknown. There may be shifts to different prey species or sizes in the spring prior to egg laying or in the fall before migration to overwintering areas. Cormorant diet will also exhibit short term and long term temporal shifts which reflect changes in the abundance of prey species (Blackwell et al., 1995; Neuman et al., 1997). Continued monitoring will be needed to encompass sufficient temporal range to document changes in cormorant diet with natural and human-induced fluctuations in fish populations.

With a migratory species such as the double-crested cormorant, it is difficult to simply manage populations on a local scale since factors affecting populations in overwintering areas are largely unknown (Erwin, 1995). A large-scale banding and marking program would provide a clearer picture of migration pathways and overwintering habitats. This type of program would be also be useful to document movement between nesting colonies on the breeding grounds, which is currently unknown.

4.2 Cormorant population control

Management policies regarding cormorant populations vary across Canada and the United States. Cormorants are managed under provincial jurisdiction in Canada (Keith, 1995). While a national management plan for cormorants does not exist, government control of cormorant populations has been implemented in a number of provinces (Keith, 1995).

Destruction of eggs and nestlings have commonly been used to control populations, but have had limited success because cormorants will typically renest later in the season (Wires et al., 2001). Egg oiling, which uses white mineral oil to suffocate the embryo by preventing gas exchange through the shell (Christens et al., 1995), has proven to be more effective at reducing renesting. Because double-crested cormorant egg laying is not synchronous among females, if egg oiling is to be successful at controlling populations, then multiple egg oilings throughout the season are required (Wires et al., 2001). Shooting adult cormorants is thought to be more effective at reducing cormorant populations than destroying eggs, nestling, or fledglings (Wires et al., 2001). The cost effectiveness of these strategies need to be evaluated against potential economic gains from reduced cormorant numbers.

Cormorants subject to an intensive control program on nesting grounds in LLB will also be facing pressures at overwintering sites and the unpredictable spread of diseases (Nisbet, 1995). Double-crested cormorant numbers have been severely reduced in the past by anthropogenic impacts (Weseloh et al., 1995) and given the species' sensitivity to disturbance, it is possible to severely reduce populations again (Ellison and Cleary, 1978; Duffy, 1995). Caution should be used during proposed control programs. It would be wise to establish targets of a desirable cormorant population size that balances sociological tolerance and biological sustainability with pressures to prevent fish losses to cormorant predation.

4.3 Impacts to other colonial nesters

The diversity and abundance of bird species is considered one of the most significant wildlife features in LLB (Gammon, 2001). The lake supports a rich community of breeding colonial and non-colonial waterbirds that could be affected by the increases in cormorant numbers, as well as by management actions to reduce these numbers.

Cormorants are found on nesting sites with other colonial waterbirds including gulls, terns, pelicans, and herons. Large numbers of cormorants could affect these other colonial waterbirds through physical displacement or by alteration of the vegetation used for nests (Wires et al., 2001; Weseloh et al., 2002). If nesting sites are a limiting factor then a reduction in cormorant numbers may reduce this competition with other bird species. However, there is also a risk that cormorants nesting on colonies where management actions are implemented may simply be displaced to colonies not subject to management. Emigration from nesting colonies has been documented for double-crested cormorants (Anderson et al., 2004) and could occur due to increased human disturbance. If only certain colonies are subject to controls there is a concern that birds from disturbed colonies will move to other colonies. High Island, the main cormorant colony on LLB, has been designated a protected area (Mitchell and Prepas, 1990) and therefore access to the colony has been more limited and cormorant controls have been focused on other nearby colonies, primarily Antoine and Portage Lakes. Colonies of Caspian terns, great blue herons, and various gull species that nest on High Island could be displaced if cormorants were found to migrate to this colony from other disturbed sites.

Threats to other waterbirds that inhabit the same nesting areas would also be present during any direct killing of adult cormorants. Negative impacts to the American White Pelican and Caspian Tern, which are considered "sensitive" in Alberta, are a concern. Pelicans and terns could be killed during shooting of cormorants and repeated disturbance to nesting colonies could reduce reproductive output.

4.4 Fish stocking

Attempts to restore the walleye population of LLB through stocking will need to be carefully evaluated. Stocking of walleye fry or small fingerlings may simply result in additional prey for cormorants. Modeling of the effects of cormorants on a walleye stocking program in the Great Lakes was predicted only to increase the number of cormorants and not the number of walleye (Jenson, 2001). Cormorants in the LLB region were found to prey opportunistically on small fish ($<$ 100 mm). If a large number of walleye fry are released into LLB, then it is likely that predation pressures from cormorants and juvenile yellow perch would severely impact survival. Walleye are approximately 100 mm long after their first year (Scott and Crossman, 1979), therefore stocking programs will need to ensure that stocked walleye are large enough to avoid substantial predation.

In the Lake Mendota biomanipulation program, 20 million walleye fry stocked each spring for 3 years were found to have negligible survival rates (Lathrop et al., 2002). Stocking efforts in Lake Mendota only succeeded with intensive stocking of fingerlings of walleye (2.7×10^6) and pike (1.7×10^5) during a 13 year period (1987-99) (Lathrop et al., 2002). With this massive stocking effort and very restrictive fishing regulations, a moderate increase in piscivore densities was observed. The increase in piscivore density also contributed to improvements in water clarity in this formerly eutrophic lake. A stocking program to restore LLB piscivorous fishes will likely require massive amounts of resources and long term effort in order to bring about a substantial change in piscivorous fish densities. To improve survival of stocked walleye, efforts should be focused on introducing the largest-sized fish possible. This could be costly in the short term but may lead to a more successful piscivore recovery.

4.5 Summary of food web impacts

There are conflicting views on the forces driving trophic interactions in lakes. Bottom-up theory suggests that biomass at each trophic level is controlled by energy sources at the bottom of the food web (McQueen et al., 1986). In contrast, the top-down view argues that higher-level consumers regulate plankton communities and primary productivity (Carpenter et al., 1985; Northcote, 1987). In reality, most lakes will be influenced by a combination of predation (top-down) and resource availability (bottom-up) (McQueen et al., 1989). The relative importance of bottom-up and top-down forces can be altered by productivity level of a lake (McQueen et al., 1986). In eutrophic lakes, such as LLB, top-down effects are predicted to be strong at the top of the food web and to dampen as they cascade down (McQueen et al., 1986, 1989). Reductions in the numbers of cormorants in the LLB region may lead to an increase in numbers of planktivorous fishes in LLB due to a decrease in direct predation on these fishes if cormorants are not replaced in the food web by piscivorous fishes. Top-down controls will likely be weaker on planktivore and zooplankton interactions and have even less impact on zooplankton and phytoplankton interactions. A decrease in cormorant numbers through management actions, therefore, is not likely to result in a corresponding increase in phytoplankton biomass and a decrease in water clarity. Successfully restoring full ecosystem function in LLB, with healthy fish populations and good water quality, will require more than biomanipulation of cormorants and fish. Bottom-up strategies that reduce nutrient inputs to the lake must also play a role.

4.6 Management considerations

Managing cormorants in an attempt to restore the LLB fishery still does not remedy the circumstances leading to the original collapse. Systems such as LLB that have been subjected to decades of overexploitation will likely require a substantial effort in order to restore fish stocks. Anthropogenic disturbances to LLB are not likely to disappear, therefore managers will need to consider how future perturbations such as angler fishing pressure, continued commercial harvest of whitefish, agricultural land use, lake shore development, and climate change will affect the food web structure of LLB and other boreal lakes.

The process of adaptive management will facilitate rapid learning about how this large complex system works (Walters and Holling, 1990). This will require steps that involve initial research programs followed by management, and subsequent monitoring. The research component should be combined with extensive public outreach so that the public understands the reasons for management actions and the management can be designed based on societal needs and values. Most problems and solutions involve altering human attitudes (Duffy, 1995).

Food web theory provides a warning in the use of biomanipulation as it may be difficult to predict the response of the rest of the system (Pimm et al., 1991). I believe a successful management plan will involve specific targeted objectives and a broad ecosystem scale vision. Of the utmost importance in any successful management strategy is the desire to obtain an interdisciplinary collaboration including groups of scientists, resource managers, stakeholders, and concerned citizens. An isolated single species approach that fails to consider both biotic and abiotic components of a system, as well as social and economic considerations, will struggle to make any substantial changes in the current state of LLB.

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Appendix A

Conventional Diet Analysis

Table A.1: Summary of prey taxa identified in double-crested cormorant regurgitation samples collected from breeding colonies in the Lac La Biche region during the 2003 nesting period (N = number of individual fish, TL = mean total length (measured from tip of snout to tip of tail), % Num. = mean % total numerical abundance, % Bio. = mean % total biomass, % Freq. = mean % frequency of occurrence. Mean boli values ranged from 0 to 100%.)

Fish Species	**N**	**TL (mm)**	**Range TL (mm)**	**% Num.**	**% Bio.**	**% Freq.**
Antoine Lake 2003 (105 Boli)						
Yellow Perch	1425	59	40 - 154	77.3	71.0	78.1
Ninespine Stickleback	152	48	34 - 61	8.2	1.7	15.2
Brook Stickleback	111	45	28 - 57	6.0	1.9	10.5
Fathead Minnow	107	60	42 -74	5.8	3.1	8.6
Spottail Shiner	25	68	56 - 86	1.4	0.9	10.5
Coregonid Sp.	10	-	-	0.5	8.9	9.5
Cisco	4	-	-	0.2	4.6	3.8
White Sucker	4	-	-	0.2	1.9	3.8
Burbot	2	-	-	0.1	2.7	1.9
Northern Pike	2	-	-	0.1	1.3	1.0
Walleye	1	-	-	0.1	2.1	1.0
Total	1843	57	28 - 154	100.0	100.0	
Portage Lake 2003 (163 Boli)						
Yellow Perch	3986	59	28 - 175	83.8	59.7	82.2
Ninespine Stickleback	306	49	35 - 61	6.4	1.7	22.1
Brook Stickleback	237	50	34 - 60	5.0	1.6	4.3
Spottail Shiner	171	73	32 - 99	3.6	3.5	23.3
Coregonid Sp.	15	239	201 - 269	0.3	9.7	7.4
Northern Pike	14	222	61 - 304	0.3	11.0	8.0
White Sucker	11	183	180 - 185	0.2	2.6	6.1
Cisco	9	-	-	0.2	6.2	3.1
Burbot	7	182	182	0.1	4.0	4.3
Iowa Darter	2	46	46	0.0	0.0	1.2
Total	4758	59	28 - 304	100.0	100.0	
Pelican Island 2003 (7 Boli)						
Yellow Perch	119	62	46 - 79	98.3	57.8	85.7
Burbot	1	-	-	0.8	42.2	14.3
Ninespine Stickleback	1	44	44	0.8	0.1	14.3
Total	121	62	44 - 79	100.0	100.0	
High Island 2003 (66 Boli)						
Yellow Perch	1237	61	31 - 210	97.3	61.4	87.7
Coregonid Sp.	11	-	-	0.9	12.5	10.8
Cisco	10	234	188 - 292	0.8	19.3	13.8
Spottail Shiner	4	69	65 - 74	0.3	0.2	4.6
Burbot	3	173	146 - 190	0.2	1.9	3.1
Ninespine Stickleback	3	56	52 - 59	0.2	0.0	4.6
White Sucker	3	183	180 - 185	0.2	4.8	4.6
Total	1271	63	31 - 292	100.0	100.0	

Table A.2: Summary of prey taxa identified in double-crested cormorant regurgitation samples collected from breeding colonies in the Lac La Biche region during the 2004 nesting period (Column headings same as for Figure A.1.)

Fish Species	**N**	**TL (mm)**	**Range TL (mm)**	**% Num.**	**% Bio.**	**% Freq.**
Antoine Lake 2004 (143 Boli)						
Yellow Perch	1022	84	47 - 180	48.4	64.2	77.7
Brook Stickleback	543	41	19 - 55	25.7	3.4	12.9
Spottail Shiner	351	58	26 - 104	16.6	6.0	31.7
Ninespine Stickleback	117	42	29 - 60	5.5	0.8	3.6
Stickleback sp.	39	41	29 - 58	1.8	0.2	1.4
White Sucker	13	95	68 - 185	0.6	3.3	5.0
Northern Pike	11	238	184 - 295	0.5	11.3	7.2
Coregonid Sp.	11	145	145	0.5	4.8	5.0
Walleye	4	218	191 - 233	0.2	3.4	2.9
Cisco	2	-	-	0.1	2.5	0.7
Total	2113	67	19 - 295	100.0	100.0	
Portage Lake 2004 (99 Boli)						
Yellow Perch	446	85	40 - 177	46.9	40.3	67.7
Spottail Shiner	263	63	27 - 98	27.7	8.0	35.4
Brook Stickleback	165	43	34 - 51	17.4	1.4	2.0
Ninespine Stickleback	40	54	45 - 67	4.2	0.4	4.0
Cisco	17	216	160 - 270	1.8	22.8	13.1
Coregonid Sp.	11	225	163 - 295	1.2	14.4	10.1
White Sucker	4	175	152 - 197	0.4	4.0	4.0
Burbot	2	205	205	0.2	4.8	2.0
Northern Pike	2	285	285	0.2	2.4	2.0
Lake Whitefish	1	0	-	0.1	1.4	1.0
Total	951	77	27 - 295	100.0	100.0	
Pelican Island 2004 (76 Boli)						
Yellow Perch	598	89	37 - 185	92.1	93.8	98.6
Brook Stickleback	36	35	25 - 60	5.5	0.2	1.4
Spottail Shiner	8	66	54 - 78	1.2	0.3	8.2
Stickleback sp.	3	-	-	0.5	0.1	1.4
Cisco	2	191	178 - 203	0.3	2.4	2.7
White Sucker	1	220	220	0.2	2.6	1.4
Northern Pike	1	-	-	0.2	0.6	1.4
Total	649	86	25 - 220	100.0	100.0	
High Island 2004 (215 Boli)						
Yellow Perch	1534	94	30 - 208	93.1	69.1	85.0
White Sucker	42	102	65 - 253	2.5	4.5	7.5
Spottail Shiner	23	64	36 - 92	1.4	0.3	8.5
Cisco	21	218	140 - 279	1.3	14.7	8.5
Coregonid Sp.	18	225	210 - 239	1.1	6.4	6.1
Trout Perch	3	93	84 - 98	0.2	0.1	0.9
Burbot	2	256	175 - 337	0.1	2.1	0.9
Lake Whitefish	2	180	180	0.1	1.5	0.9
Northern Pike	1	333	333	0.1	1.3	0.5
Stickleback sp.	1	50	50	0.1	0.0	0.5
Brook Stickleback	1	46	46	0.1	0.0	0.5
Total	1648	95	30 - 337	100.0	100.0	

Table A.3: Dates of regurgitation sample collection during 2003 and 2004 nesting periods.

Colony	Date (2003)	# Boli	Date (2004)	# Boli
Antoine	28-May-03	11	1-Jun-04	19
	12-Jun-03	13	9-Jun-04	33
	17-Jun-03	18	29-Jun-04	58
	24-Jun-03	36	12-Jul-04	27
	8-Jul-03	11	4-Aug-04	6
	22-Jul-03	22		
Portage	6-Jun-03	31	2-Jun-04	39
	20-Jun-03	24	30-Jun-04	30
	4-Jul-03	34	9-Jul-04	19
	17-Jul-03	31	3-Aug-04	11
	20-Jul-03	2		
	31-Jul-03	45		
	15-Aug-03	5		
Pelican	6-Jun-03	1	29-Jun-04	26
	20-Jun-03	1	12-Jul-04	50
	17-Jul-03	5		
High	22-Jul-03	42	21-Jun-04	31
	5-Aug-03	21	6-Jul-04	83
	15-Aug-03	1	19-Jul-04	101

Appendix B

Stable Isotope Analysis

Table B.1: Mean stable carbon and nitrogen isotope signatures of organisms collected from Lac La Biche during May - September 2004 (No. = number of individuals. δ^{15}N values are unadjusted for baseline correction. See Table 3.3 for fish lengths and codes.)

Lac La Biche					
Organism	**No.**	**δ^{13}C**	**(Range)**	**δ^{15}N**	**(Range)**
Invertebrates					
Amphipoda	12	-24.1	(-26.1 to -16.2)	5.3	(1.5 to 7.6)
Chironomid	6	-26.1	(-28.1 to -23.9)	5.7	(4.6 to 6.9)
Dytiscid Beetle	4	-24.2	(-26.2 to -21.4)	6.8	(6.2 to 7.6)
Gastropoda	34	-25.0	(-29.4 to -22.4)	3.7	(-1.6 to 6.3)
Hirudinea	19	-23.7	(-25.9 to -22.0)	7.8	(5.3 to 10.6)
Odonata	9	-25.8	(-29.5 to -23.8)	6.9	(5.6 to 8.0)
Pelecypoda	28	-26.4	(-27.7 to -23.9)	6.0	(4.6 to 8.1)
Trichoptera	9	-24.4	(-26.8 to -18.3)	5.8	(2.8 to 8.5)
Fishes					
Brook Stickleback	10	-23.9	(-27.1 to -22.2)	9.8	(8.7 to 10.9)
Burbot (immature)	3	-22.8	(-23.1 to -22.6)	7.5	(7.1 to 8.0)
Cisco (immature)	3	-25.1	(-25.2 to -25.0)	8.0	(7.6 to 8.5)
Cisco (adult)	11	-24.8	(-25.7 to -23.3)	10.5	(9.9 to 11.1)
Iowa Darter	14	-22.9	(-24.6 to -20.9)	8.9	(7.1 to 11.2)
Lake Whitefish	5	-23.5	(-24.1 to -23.0)	11.1	(10.7 to 11.9)
Ninespine Stickleback	4	-24.5	(-25.0 to -23.9)	11.5	(11.1 to 11.8)
Northern Pike (adult)	3	-23.5	(-23.8 to 23.0)	12.5	(12.3 to 12.7)
Spottail Shiner	14	-24.1	(-24.9 to -22.8)	9.1	(7.4 to 10.3)
Walleye (immature)	2	-23.4	(-23.4 to -23.3)	10.5	(10.4 to 10.6)
Walleye (adult)	6	-23.3	(-23.7 to -23.1)	12.7	(12.5 to 13.0)
White Sucker (immature)	5	-22.8	(-24.4 to -22.0)	8.4	(7.7 to 10.2)
White Sucker (adult)	10	-24.1	(-24.7 to -23.6)	9.7	(9.6 to 10.3)
Yellow Perch (yoy)	12	-25.7	(-26.9 to -25.2)	9.2	(7.8 to 10.8)
Yellow Perch (immature)	15	-24.3	(-25.5 to -23.0)	10.5	(9.6 to 11.2)
Yellow Perch (adult)	9	-24.0	(-24.5 to -23.7)	11.2	(10.3 to 11.7)
Yellow Perch (from boli)	3	-23.7	(-24.4 to -22.5)	10.9	(10.5 to 11.2)
Cormorants					
Cormorant Adult	13	-24.7	(-26.8 to -22.3)	12.4	(11.4 to 13.6)
High Island Chick	11	-24.3	(-24.6 to -23.8)	11.8	(11.1 to 12.5)
Pelican Island Chick	2	-24.0	(-24.5 to -23.5)	12.0	(11.9 to 12.1)
Pelican Island Egg	2	-23.7	(-24.0 to -23.4)	13.6	(13.5 to 13.6)

Table B.2: Mean stable carbon and nitrogen isotope signatures of organisms collected from Beaver Lake during May - September 2004 (No. = number of individuals. δ^{15}N values are unadjusted for baseline correction. See Table 3.3 for fish lengths and codes.)

Beaver Lake					
Organism	**No.**	δ^{13}C	**(Range)**	δ^{15}N	**(Range)**
Invertebrates					
Amphipoda	12	-20.5	(-22.5 to -18.8)	7.0	(5.3 to 8.9)
Chironomid	5	-24.6	(-26.0 to -22.6)	5.1	(4.3 to 5.7)
Gastropoda	12	-21.5	(-22.6 to -19.8)	7.2	(4.1 to 10.0)
Hirudinea	9	-21.1	(-22.5 to -20.1)	9.5	(7.9 to 10.4)
Odonata	5	-22.5	(-23.4 to -21.6)	8.4	(7.2 to 10.6)
Pelecypoda	11	-24.2	(-25.2 to -23.4)	8.9	(7.7 to 10.0)
Trichoptera	6	-19.8	(-22.6 to -16.7)	6.9	(4.8 to 9.4)
Fishes					
Brook Stickleback	9	-21.1	(-23.8 to -21.4)	13.0	(10.1 to 14.3)
Iowa Darter	9	-21.4	(-23.0 to -20.2)	10.9	(8.9 to 12.2)
Lake Whitefish	2	-24.0	(-24.1 to -23.9)	12.1	(11.5 to 12.6)
Northern Pike (immature)	3	-22.3	(-23.5 to -21.5)	10.9	(10.1 to 11.6)
Northern Pike (adult)	5	-22.1	(-22.5 to -21.8)	13.4	(12.6 to 14.2)
Spottail Shiner	9	-23.8	(-24.6 to -23.1)	11.0	(8.4 to 12.3)
Walleye (immature)	3	-23.0	(-23.3 to -22.6)	13.8	(13.4 to 14.4)
Walleye (adult)	4	-22.7	(-23.1 to -22.1)	14.4	(14.2 to 15.1)
Yellow Perch (yoy)	3	-24.7	(-25.4 to -24.2)	10.1	(9.5 to 11.0)
Yellow Perch (adult)	5	-22.3	(-23.3 to -21.2)	11.3	(10.5 to 12.2)
Cormorants					
Beaver Lake Chick	3	-23.2	(-23.4 to -23.1)	14.4	(13.3 to 15.0)

Table B.3: Mean stable carbon and nitrogen isotope signatures of organisms collected from Antoine Lake during June 2005 (No. = number of individuals. δ^{15}N values are unadjusted for baseline correction. See Table 3.3 for fish lengths and codes.)

Antoine Lake					
Organism	**No.**	**δ^{13}C**	**(Range)**	**δ^{15}N**	**(Range)**
Invertebrates					
Amphipoda	3	-20.2	(-20.8 to -19.3)	9.1	(8.7 to 9.5)
Chironomid	1	-24.2		8.5	
Dytiscid Beetle	1	-24.6		8.5	
Dytiscid larva	2	-20.7	(-20.7 to -20.7)	9.4	(9.3 to 9.5)
Gastropoda	3	-19.9	(-20.3 to -19.1)	9.2	(8.7 to 9.7)
Hirudinea	3	-19.5	(-19.8 to -19.1)	11.1	(10.5 to 12.4)
Fishes					
Brook Stickleback	3	-19.8	(-20.6 to -19.2)	13.8	(13.7 to 14.0)
Brook Stickleback (from boli)	3	-19.4	(-20.9 to -18.7)	14.3	(13.7 to 15.1)
Fathead Minnow	3	-19.8	(-19.9 to -19.6)	13.8	(13.7 to 13.9)
Yellow Perch (from boli)	3	-24.1	(-24.7 to -23.4)	10.5	(10.3 to 10.7)
Cormorants					
Antoine Lake Chick	5	-24.1	(-24.3 to -23.8)	12.4	(11.8 to 13.1)
Antoine Lake Egg	6	-23.1	(-24.0 to -22.0)	13.9	(13.3 to 14.8)

Table B.4: Mean stable carbon and nitrogen isotope signatures of organisms collected from Portage Lake during June 2005 (No. = number of individuals. δ^{15}N values are unadjusted for baseline correction. * = samples collected May 2004. See Table 3.3 for fish lengths and codes.)

Portage Lake					
Organism	**No.**	**δ^{13}C**	**(Range)**	**δ^{15}N**	**(Range)**
Invertebrates					
Amphipoda	6	-20.5	(-21.9 to -19.6)	7.3	(6.5 to 8.3)
Dytiscid Beetle	2	-21.2	(-21.3 to -21.1)	10.4	(10.1 to 10.6)
Dytiscid larva	3	-21.9	(-22.1 to -21.6)	8.7	(8.1 to 9.3)
Gastropoda	3	-17.4	(-18.3 to -16.7)	10.5	(9.6 to 11.4)
Hirudinea	3	-19.4	(-21.6 to -17.1)	12.6	(9.3 to 15.0)
Odonata	4	-22.2	(-22.5 to -21.6)	8.9	(8.3 to 9.4)
Trichoptera	1	-20.5		9.9	
Fishes					
Brook Stickleback	5	-20.2	(-20.6 to -19.7)	13.1	(12.7 to 13.6)
Fathead Minnow*(2004)	3	-19.9	(-20.0 to -19.8)	11.8	(11.6 to 11.9)
Fathead Minnow	3	-20.2	(-20.4 to -19.9)	12.3	(12.1 to 12.7)
Cormorants					
Portage Lake Chick	2	-24.1	(-24.4 to -23.8)	12.0	(11.7 to 12.3)
Portage Lake Egg	5	-22.6	(-24.4 to -20.9)	14.5	(13.6 to 15.5)

Table B.5: Dates of isotope sample collection for fish and invertebrates in Lac La Biche during 2004 field work.

Lac La Biche					
Organism	May 27 - Jun 6	Jun 25 - Jun 29	Jul 28 - Aug 1	Sept 26 - Sept 28	Total
Invertebrates					
Amphipoda	3	3	3	3	12
Chironomid	-	3	-	3	6
Dytiscid Beetle	1	1	2	-	4
Gastropoda	8	12	6	8	34
Hirudinea	5	4	1	3	13
Odonata	4	5	-	-	9
Pelecypoda	4	6	9	9	28
Trichoptera	3	-	-	6	9
Fishes					
Brook Stickleback	1	3	2	3	9
Burbot (immature)	-	-	3	-	3
Cisco (immature)	-	-	-	3	3
Cisco (adult)	2	3	3	3	11
Iowa Darter	3	3	5	3	14
Lake Whitefish	-	-	5	-	5
Ninespine Stickleback	1	3	-	-	4
Northern Pike (adult)	-	-	3	-	3
Spottail Shiner	5	3	3	3	14
Walleye (immature)	-	-	-	2	2
Walleye (adult)	1	-	4	1	6
White Sucker (juvenile)	1	2	5	-	8
White Sucker (adult)	-	4	3	-	7
Yellow Perch (yoy)	-	1	3	8	12
Yellow Perch (immature)	3	6	6	-	15
Yellow Perch (adult)	4	3	2	-	9

Table B.6: Dates of isotope sample collection for fish and invertebrates in Beaver Lake during 2004 field work.

Beaver Lake					
Organism	May 16 - May 31	Jun 27 - Jun 29	Jul 23 - Jul 26	Sept 27	Total
Invertebrates					
Amphipoda	3	3	3	3	12
Chironomid	-	-	3	2	5
Gastropoda	3	3	3	3	12
Hirudinea	-	3	3	3	9
Pelecypoda	3	2	3	3	11
Trichoptera	-	3	-	3	6
Fishes					
Brook Stickleback	1	-	2	3	6
Iowa Darter	-	3	3	3	9
Lake Whitefish	2	-	-	-	2
Northern Pike (immature)	-	-	2	1	3
Northern Pike (adult)	1	1	3	-	5
Spottail Shiner	3	3	3	-	9
Walleye (immature)	-	-	3	1	4
Walleye (adult)	3	-	-	-	3
Yellow Perch (yoy)	-	-	3	-	3
Yellow Perch (adult)	2	3	-	-	5

Table B.7: Dates of cormorant carcass collection 2004 field sampling.

Organism	Jun 1 - Jun 8	Jun 21 - Jun 30	Jul 6 - Jul 12	Jul 15 - Jul 19	Oct 1	Total
Cormorant Adult (LLB)	1	-	-	2	10	13
High Island Chick	-	5	4	2	-	11
Pelican Island Chick	-	1	1	-	-	2
Antoine Lake Chick	-	3	2	-	-	5
Portage Lake Chick	-	-	2	-	-	2
Pelican Island Egg	2	-	-	-	-	2
Antoine Lake Egg	3	3	-	-	-	6
Portage Lake Egg	2	2	-	-	-	4

Table B.8: Comparison of stable isotope results conducted at the University of Alberta Biogeochemical Analytical Laboratory and the Department of Soil Sciences at the University of Saskatoon. (Results from the two labs were not significantly different, t-test, δ^{13}C, t = .938, p = 0.352; δ^{15}N, t = -.348, p = 0.729).

Sample ID	δ^{13}C U of A	δ^{13}C U of S	δ^{15}N U of A	δ^{15}N U of S
A1	-24.17	-24.30	11.25	11.76
A2	-24.83	-24.94	12.40	12.85
A3	-23.80	-23.81	11.72	12.17
A4	-24.58	-24.67	12.60	13.12
A5	-22.37	-22.51	10.06	10.46
A6	-24.30	-24.37	10.80	11.22
A7	-25.42	-27.13	10.51	11.10
A8	-25.88	-26.41	5.86	5.80
A9	-22.90	-24.07	4.56	3.50
A10	-23.77	-23.90	5.14	5.13
B1	-24.20	-24.84	5.05	4.70
B2	-24.55	-25.24	9.36	9.68
B3	-26.03	-26.71	4.84	4.91
B4	-23.67	-23.84	7.89	7.99
B5	-26.30	-26.18	6.13	6.61
B6	-22.06	-22.53	4.62	4.89
B7	-22.17	-22.56	4.00	4.10
B8	-22.36	-22.64	13.18	13.84
B9	-23.09	-23.38	12.99	13.63
B10	-20.66	-20.93	14.34	14.98
C1	-23.47	-23.74	10.30	10.63
C2	-25.86	-26.77	12.46	12.93
C3	-22.74	-22.77	11.93	12.38
C4	-23.86	-24.28	11.38	11.86
C5	-23.27	-23.49	7.97	8.22
C6	-24.39	-24.66	9.51	9.75
C7	-21.39	-21.52	9.85	10.09
C8	-25.09	-25.19	8.23	8.54
C9	-22.50	-22.77	11.56	11.98
C10	-22.69	-23.01	12.01	12.37