CHANGES IN DOUBLE-CRESTED CORMORANT (*PHALACROCORAX AURITUS*) REPRODUCTIVE SUCCESS AND CHICK BIOENERGETICS AFTER THE INVASION OF THE ROUND GOBY (*APPOLLONIA MELANOSTOMUS*)

Margaret A. Van Guilder

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Thesis Committee

_____ Committee Chair

_____ Faculty Member

_____ Faculty Member

_____ Faculty Member

Date: _____

_____ Dean
College of Graduate Studies

Date: _____

Committee:

Nancy Seefelt, Ph.D., Chair

Andrew Scott Mcnaught, Ph.D.

Thomas Gehring, Ph.D.

R. Gregory Corace III, Ph.D.

This thesis is dedicated to all those who helped me through this process, whether for offering advice or simply emotional support, as well as to the thousands of birds killed in the Beaver Archipelago in 2010.

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ABSTRACT

CHANGES IN DOUBLE-CRESTED CORMORANT (*PHALACROCORAX AURITUS*) REPRODUCTIVE SUCCESS AND CHICK BIOENERGETICS AFTER THE INVASION OF THE ROUND GOBY (*APPOLLONIA MELANOSTOMUS*)

by Margaret A. Van Guilder

Bioenergetics is the study of energy intake and expenditure of an organism. For birds, energy enters the body as food and from there is allocated to several functions such as growth and reproduction. More energy taken in allows for more energy to be allocated to body functions. The fish community in Lake Michigan has changed over the past ten years. Waterbirds nesting near the Beaver Archipelago, such as the Double-crested Cormorant, opportunistically consume these fish; therefore their diet reflects fish species abundance. Their diet has changed from primarily alewife (energetically rich) to primarily round goby (relatively energetically poor). This study was conducted to determine whether this change in diet would result in a change in reproductive output/success. Diet (regurgitate) and growth rate data were collected from Double-crested Cormorant chicks on the Beaver Archipelago islands of Whiskey and Hat in 2010 to (1) model the caloric density of round goby near the Beaver Archipelago, (2) model the bioenergetics of chick prey consumption in the Beaver Archipelago and (3) model the potential reproductive success of the Beaver Archipelago colonies in 2010. Findings were then compared to earlier research in the archipelago prior to the invasion of the round goby (i.e. 2000) to infer the impacts of this invasive species. Round goby was found to have a relatively low energy density compared to other dietary items. Double-crested Cormorant chicks were found to have consumed more fish per chick in 2010 than in 2000 of which round goby comprised the greatest proportion of the 2010 chick diet. The reproductive success of the Double-crested

Cormorant colonies in 2010 despite control efforts was estimated to be about 250 chicks. If no control had occurred on Hat Island, it is estimated that about half of the chicks would likely have fledged. This is lower than in 2000 (about 75% estimated to fledge) and could be attributed to poor diet or predation. The model presented here suggests that Double-crested Cormorants in the Beaver Archipelago consumed over 95% exotic invasive fish species in 2010 and could potentially act as a natural control for these invasive fishes.

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CHAPTER I

INTRODUCTION

The Beaver Archipelago of Northern Lake Michigan supports a diverse avifaunal community of which the Double-crested Cormorant is a member (*Phalacrocorax auritus*). The Double-crested Cormorant uses several of the islands within the archipelago as breeding sites (Seefelt and Gillingham, 2008). In the early 20th century, Double-crested Cormorants were not found to nest in the Beaver Archipelago, although there were established breeding colonies in the middle Canadian and mid-western region of the United States (Lewis, 1929).

By the 1910s, Double-crested Cormorants had become established in the Great Lakes basin (Ludwig et al. 1989). Due to perceived conflicts with fishermen and the presence of environmental pesticides (DDT), by the 1960s, cormorants were nearly extirpated as a breeding species in the Great Lakes (Ludwig et al. 1989; Hatch and Weseloh, 1999; Seefelt and Gillingham, 2004). After protection efforts were set in place and the elimination of DDT use, cormorant breeding populations began to increase again, reaching a peak in the Beaver Archipelago in the mid 1990s (Seefelt and Gillingham, 2004 and 2008). The number of breeding pairs had risen in the Great Lakes region from 149 in 1972 to at least 87,048 in the late 1990s (Ludwig, 1984; Wires and Cuthbert, 2009). In Lake Michigan alone, the number of active colonies rose from three in 1977 to 27 in 1997 (Cuthbert et al. 1997).

As of 1989, the cormorant breeding colonies found in Beaver Archipelago were among the largest three regions in terms of numbers of breeding birds in Lake Michigan increasing from 250 in 1984 to a high of 11,709 in 1997 (Ludwig et al. 1989). More recently, however, these numbers have declined to around 4000 pairs in 2010 (Seefelt, unpub. data). In 1997 the Beaver Archipelago islands supporting Double-crested Cormorant populations included Pismire,

Grape Spit, Timm's Spit, Whiskey, Hat and Gull (Cuthbert et al. 2003). Currently populations in the Beaver Archipelago are declining, with active colonies recently present on Hat, Gull, Pismire and Whiskey islands (Seefelt, unpub. data). Since 2007, the U.S. Department of Agriculture Wildlife Services (hereafter Wildlife Services) has been using lethal means to manage cormorant populations on many islands in the archipelago. These islands include those managed by the U.S. Fish and Wildlife Service, Seney National Wildlife Refuge (NWR) (i.e. islands of Michigan Islands NWR, including Gull, Hat, and Pismire). This refuge is then itself part of the larger National Wildlife Refuge System (Meretsky et al. 2006).

Life History

The Double-crested Cormorant is a fish-eating (piscivorous) waterbird common in North America (Hatch and Weseloh, 1999). Double-crested Cormorant life history begins when a breeding female lays a clutch eggs. Eggs are usually laid in mid-May to early June and incubated for 25 to 28 days (Lewis, 1929). The newly hatched chicks are altricial and therefore require much care from both parents (Hatch and Weseloh, 1999). However, the young chicks grow relatively quickly compared to other waterbirds reaching 90% of their maximum body mass by 33 days old. Fledging typically occurs at about six weeks of age (50 days), though some tree-dwelling young may not fledge until later (Hatch and Weseloh, 1999). Both parents actively feed the young by regurgitation. Chick diets change in consistency from liquid immediately after hatching to a mostly solid (whole fish) diet early in chick growth (three to five days) (Mendall, 1936). Once the young are able to fly (at about 7 weeks), they are, for the most part, able to feed and care for themselves (Hatch and Weseloh, 1999). By week 10, the young have

reached the juvenile stage and no longer rely on their parents for care of any kind (Hatch and Weseloh, 1999).

Among the leading causes of mortality of Double-crested Cormorant eggs and chicks are related to disturbance at breeding colonies that leave the young exposed to predation and the elements. In addition, disease, entanglement in fishing gear, and direct mortality due to humans (e.g. shooting) impact survivorship (Lewis, 1929; Hatch and Weseloh, 1999).

Changes in Cormorant Diet and Fish Populations

The predatory behavior of Double-crested Cormorants incorporates several components such as searching for prey, chase/capture, handling of the prey and ingestion (Holling, 1959). The action of these behaviors require much energy and, according to the theory of optimal foraging, organisms tend to forage in such a way that net energy intake is maximized per any given time unit (MacArthur and Pianka, 1966; Emlen, 1966). Ideally, Double-crested Cormorants will spend as little time as possible foraging for the most energetically valuable prey items. Optimal foraging often focuses on diet, patch choice, when to leave a patch and movement of the organism (Pyke, 1984). This study focuses primarily on the diet component of this theory, though also incorporates some patch choice.

Over the past 20 years, the diet of Double-crested Cormorants has changed substantially in response to the change in fish community structure. During the late 1980s, cormorants in Lakes Superior, Huron and Michigan consumed mostly alewife (*Alosa pseudoherengus*) and yellow perch (*Perca flavescens*) by biomass at ~57% and ~13% respectively, though these numbers varied by location (Hatch and Weseloh, 1999). Near the end of the breeding season (August), 100% of the diet was alewife (Ludwig et al. 1989). Between 2000 and 2001, Johnson

and McCullough (2007) determined that the diet of cormorants in eastern Lake Ontario by number of fish was 70-80% round goby (*Apollonia melanostoma*), followed by 17% alewife and 9% yellow perch on the Pigeon Island colony (Johnson and McCullough, 2007). This likely reflects the fish community at that time.

The fish community of Lake Michigan has changed substantially in the past 100 years. Near the beginning of the 20th century, the Lake Michigan fish profile was composed mainly of native fish species such as the yellow perch and lake trout (*Salvelinus namaycush*). However, since the introduction of non-native fish species such as the alewife (found in Lake Michigan in 1949) and the chinook salmon (*Oncorhynchus tshawytscha*), along with invasive species such as the round goby and sea lamprey (*Petromyzon marinus*), many populations of the native fish species have declined (Smith, 1970; Hatch and Weseloh, 1999; Bunnell et al. 2006).

Round goby is an invasive exotic fish, native to the Ponto-Caspian region of Europe and suspected of accessing the Great Lakes through ballast water transfer of trans-Atlantic freighters (Cooper et al. 2007). It is a small, benthic fish first documented in the Great Lakes Basin in 1990 (Jude et al. 1992; Hensler and Jude 2007). It has been observed in Lake Michigan since 1993 and captured by MI DNR since 1997, yet was not seen in the Beaver Archipelago until 2006 (Clapp et al. 2001; Galarowicz, unpub. data). Round goby has since become very abundant in the Great Lakes basin with densities as high as 130/m^2 and reaching a numeric density peak in Lake Michigan in 2008 (Chotkowski and Marsden 1999; Madenjian et al. 2010). The numeric density of round goby in Lake Michigan has been highly variable since 2003 however and in 2009 was approximately 84% lower than in 2008 (Madenjian et al. 2010). Round goby has been implicated in the decline of several fish species such as mottled sculpin (*Cottus bairdii*), logperch (*Percina caprodes*) and johnny darters (*Etheostoma nigrum*) (Dubs and Corkum, 1996;

French and Jude, 2001; Janssen and Jude, 2001; Lauer et al. 2004; Balshine et al. 2005). Goby prefer rocky substrates for spawning and feeding (fish eggs and small benthic invertebrates) making the Beaver Archipelago ideal habitat (Jude et al. 1995; Diggins et al. 2002). The current prevalence of round goby in Lake Michigan and more recently in the diet of Double-crested Cormorants of the Beaver Archipelago (2007) was a major impetus for this study (Seefelt, unpub. data).

Alewife, another invasive exotic fish has been prevalent in Lake Michigan after it was first observed in 1949 (Smith, 1970). During the 1960s, alewife populations had become so large that massive die-offs resulted in industrial blockages and beaches littered with carcasses (Brown, 1972). Since 1979, alewife populations have remained stable, though lower than in the 1960s due to top-down control measures implemented by the stocking of salmonines (Madenjian et al. 2002). Alewives have also been linked to the decline in several fish species, including deepwater sculpin (*Myoxocephalus thompsoni*), emerald shiner (*Notropis atherinoides*), cisco or lake herring (*Coregonus artedii*) and yellow perch, due to competition with these native fishes and consumption of native larval fish (Smith, 1970; Wells and McLain, 1970). Since the onset of alewife population control by the introduction of Salmonids, the species richness tended to increase in Lake Michigan until the late 1990s after which species richness tended to decline (Bunnell et al. 2006). This corresponds to a spike in alewife abundance around the same time period (Madenjian et al. 2010). In 2000 and 2001, alewife was a major diet component of Double-crested Cormorants and their chicks, resulting in a high reproductive output for these years, especially in 2001 (Seefelt and Gillingham, 2008). Since 2001, alewife has decreased in abundance across Lake Michigan, though this number increased from 2008 to 2009 (Madenjian et al. 2010). The historical prevalence of alewife in the Double-crested Cormorants diet as well

as their inadvertent reproductive benefits the since the 1990s makes the alewife a critical component to this study.

Conflicts with Humans

Double-crested Cormorants, being opportunistic piscivores, are often blamed for the decline in populations of fish species of commercial and sport value. Although they can sometimes have an impact on fish populations, especially if they are foraging near desired fisheries or aquaculture facilities, a number of studies have indicated cormorants tend to have a small impact overall on Great Lakes fish populations and that impacts tend to be site-specific (Rudstam et al, 2004; Diana et al, 2006; Seefelt and Gillingham, 2008). For instance, Rudstam et al. (2004) determined that Double-crested Cormorants were primarily consuming yellow perch and walleye (*Sander vitreum*) stocks near a fishery in Lake Oneida from 1995 to 2000 though had a small overall impact on these populations. This lake, though much smaller than Lake Michigan, represents a system that has undergone a similar invasion of the exotic, invasive round goby and may therefore serve as an example for comparison. Diana et al. (2006) conducted a study in the Les Chaneaux islands in Lake Huron and determined that, while being a highly visible fish predator, Double-crested Cormorants have a very small impact overall on yellow perch (≤6.3%), which was measured to be less than one quarter of the annual fish mortality at any age class. In addition, Double-crested Cormorants have been shown to prey upon non-native fish species, particularly alewife (Hatch and Weseloh, 1999; Johnson et al. 2002; Seefelt and Gillingham, 2004, Seefelt and Gillingham, 2008) and more recently the round goby (Somers et al. 2003; Johnson et al. 2010).

Reasons for this change in diet composition could be due to the current prevalence of exotic species in the Great Lakes (Seefelt and Gillingham, 2004). Double-crested Cormorants feed in shallow waters where these fish are most often found and are therefore more likely to encounter the exotics (Lewis, 1929). Overall, the Double-crested Cormorant has rarely been shown to severely impact fisheries, even when they are eating large quantities of fish (i.e. during the breeding season) (Hatch and Weseloh; 1999). With such a diverse diet, the possibility of the Double-crested Cormorant having a negative impact on a single fish species is low (Craven and Lev, 1987). Some breeding colonies can consume, on average, 30 million individual fish annually, which is approximately 14 million kilograms of fish biomass; this usually only occurs locally, however, and is a small percentage of the overall mortality for these fish (Johnson et al. 2002).

Double-crested Cormorant Control Efforts

Since the initial Upper Great Lakes population began increasing in the 1970s, Double-crested Cormorant populations in the region have been under scrutiny due to the perceived impacts on sport fish populations. This has led to active control by Wildlife Services through permits issued by the U.S. Fish and Wildlife Service (USFWS) and regional states (Acord, 1995; Wires and Cuthbert, 2009). Cormorants are often seen as pests and a threat to natural resources such as unique habitats and fish species of sport and commercial value (Bédard et al. 1995). Large aggregations of Double-crested Cormorants may damage vegetation directly by using it as nesting material or indirectly through excrement introducing high levels of nitrogen into the area around colony sites (Bédard et al. 1995). Also of concern is the depredation of fish raised in

aquaculture facilities and possible crowding out of threatened or endangered co-nesting waterbirds (Blackwell et al. 2000; USDA APHIS WS, 2010).

Because of these concerns and related political pressure, the USFWS and the U.S. Department of Agriculture Wildlife Services have implemented management (i.e. control) practices to reduce Double-crested Cormorant population sizes and the number of colonies. These methods include shooting, coating the eggs in vegetable oil, harassment of nesting birds off colonies, and nest destruction. These methods can be effective, yet can also have unintended consequences. For instance, shooting directly kills adult birds, yet also inadvertently subjects young birds to the elements and starvation which may not be the intent of the control agency (Hatch and Weseloh, 1999). Egg oiling blocks the flow of oxygen into the egg, thus causing the developing chick to suffocate (Gross, 1951). This can be a highly effective means of control by significantly decreasing hatching success which subsequently reduces the amount of fish consumed in a breeding season (Johnson et al. 2000; Farquhar et al. 2001). This is a preferred method over the complete destruction of eggs because it discourages relaying due to continued incubation of oiled eggs (Pochop et al. 1998). Non-lethal controls (i.e. harassment) such as chasing birds from boats and using propane cannons promote fear, discourage predation of natural and commercial fish resources, and encourage breeding abandonment at colonies (Brian et al. 2010). Cormorants that have been repeatedly disturbed by humans or other animals at one colony location often move to less disturbed areas (Hatch and Weseloh, 1999). These controls are often successful if used for a limited time period, yet lethal controls may be implemented if birds become habituated to the harassment (Brian et al. 2010).

Bioenergetics

This study aims to investigate reproductive success and growth dynamics of Double-crested Cormorant chicks using a bioenergetics model based on allometric equations. Bioenergetics models are based on energy intake and expenditure, or "energy economics," of an organism (Nagy, 1989). For birds, energy enters the body as food and from there is allocated to several activities/functions. This relationship is shown in the following equation (Nagy, 1989):

$$I = M + G + R + F + U$$

where I is the caloric energy of the food consumed or ingested, M is the metabolism of the organism, G is the growth of the organism itself, R is the amount of energy allocated to reproduction in the form of gametes and biomass of the offspring, F is the amount of energy leaving the organism as undigested food or feces, and U represents the energy leaving the body as nitrogenous waste. The rate of intake of usable energy is often referred to as assimilation and can be described as either the sum of reproduction, metabolism and growth or as the amount of food intake minus energy voided as feces and nitrogenous waste (Nagy, 1989). Several studies have focused on using the rate of metabolism of an organism to determine percent assimilation and consequently amount of energy intake (Birt-Friesen et al. 1989; Nagy, 1989). Birt-Friesen et al. (1989) determined that the log metabolic rate of certain waterbirds (Northern Gannet) was strongly correlated to the log mass of the bird. Therefore, the mass of a bird could be used to determine metabolic energy expenditure in a bioenergetics model (Birt-Friesen et al. 1989).

Bioenergetics can also be applied to determine the overall amount of energy intake by a population. Madenjian and Gabrey (1995) used a daily energy expenditure (DEE) based on bird mass and an 80% assimilation efficiency to determine the amount of energy consumed in one day by several waterbird species. This energy intake was then divided by the mean energy density of the diet to determine the mass of food consumed. This value was then applied to the

population and breeding season (in days) to determine the biomass of fish consumed per population per breeding season (Madenjian and Gabrey, 1995). A similar method was used by Seefelt and Gillingham (2008) to determine the biomass of fish consumed by Double-crested Cormorant populations in the Beaver Archipelago. The model used was modified in the manner of Hebert and Morrison (2003) to determine the mass of each prey species consumed by the population over the breeding season. Though Hebert and Morrison (2003) used literature values to determine diet composition, Seefelt and Gillingham (2008) used regurgitate samples collected on the archipelago colonies. This study uses the methods of Seefelt and Gillingham (2008) to determine the overall mass of fish (by species) consumed by Double-crested Cormorant chicks in the Beaver Archipelago during the 2010 breeding season.

Project Objectives

Due to their perceived impact on fish populations, the Double-crested Cormorant has become the subject of multiple studies investigating their predation patterns. Many studies discuss the impact cormorants have on fish populations and their bioenergetic role (Craven and Lev, 1987; Glanville, 1992; Fielder, 2008; Seefelt and Gillingham, 2008). In a study conducted by Seefelt and Gillingham (2008) in the Beaver Archipelago in 2000 and 2001, the amount of prey consumed by the cormorant breeding colony was estimated using bioenergetics models. Findings showed that although cormorant chicks consumed less fish in year 2001 compared to 2000, they were assimilating the same amount of energy overall and adults produced more offspring in 2001 per breeding pair. One possible reason for this was that a higher proportion of alewives were found in the diets in 2001 and alewife has a higher caloric value than other fish in the diet (Seefelt and Gillingham, 2008). Round goby has an intermediate caloric density

compared to other forage fish of Lake Michigan (Ruetz et al, 2009) and therefore a larger quantity may need to be consumed to gain the same energy as a diet consisting of primarily alewife.

My study investigated hatching success, fledging success and overall growth dynamics of young Double-crested Cormorants in the Beaver Archipelago and related these productivity metrics to cormorant biomass consumption. The objectives of this study were to (1) model the caloric density of round goby near the Beaver Archipelago, (2) model the bioenergetics of chick prey consumption on the islands of Hat and Whiskey and (3) model the potential reproductive success of the Beaver Archipelago colonies in the summer of 2010 in light of confounding control efforts. Findings were then compared to earlier research in the archipelago prior to the invasion of the round goby (i.e. 2000) to infer the impacts of this invasive species. This research extends the bioenergetic models of Seefelt and Gillingham (2008) to determine the overall impact that cormorant reproductive success may have on a northern Lake Michigan ecosystem. Specifically, this study helps to further understand the influence breeding cormorant predation has on local fish populations in the Beaver Archipelago and how changes in the fish community are manifested through the bioenergetics of breeding cormorants.

CHAPTER II

MATERIALS AND METHODS

Study Site

Data were collected in the Beaver Archipelago of northern Lake Michigan (Charlevoix County) (Figure **1** 1). The archipelago is composed of 10 main islands and several satellite

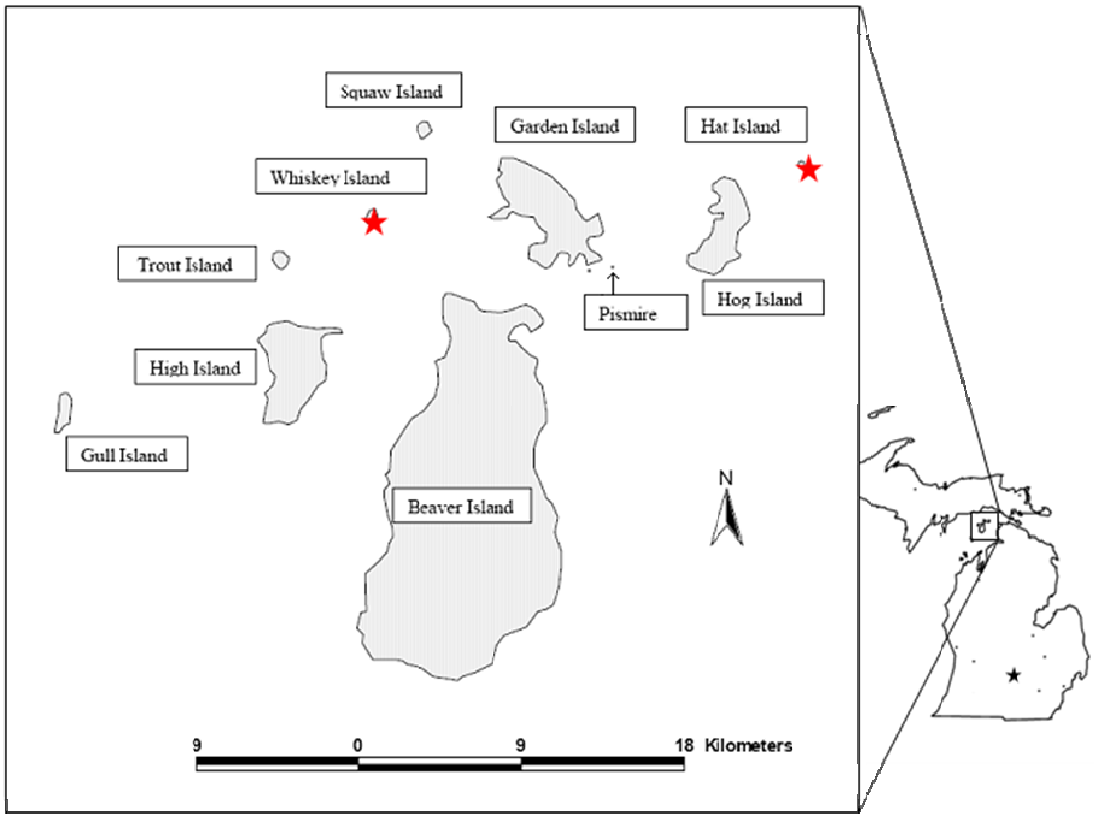

Figure 1. The Beaver Archipelago of Northern Lake Michigan. This study was conducted on Hat and Whiskey islands, denoted by the stars.

islands. It is characterized as a northern lakes and forests ecoregion (U.S. Environmental Protection Agency, 1999). For this study, data were gathered on Hat Island (0.5 km^2) and Whiskey Island (1.0 km^2). Because many aspects of these colonies differed, data from them

were analyzed individually and as a combined data set. The colony on Hat Island consisted of primarily ground nesting birds; while on Whiskey Island, there was a mix of ground nests and tree nests. Hat Island was chosen due to the consistent prevalence of cormorant colonies over the past 20 years. The study sites were accessed by boat during safe (no rain, waves less than 3 ft. etc.) weather conditions. Islands of interest were studied under the permit of Dr. Nancy Seefelt, my primary advisor. Data were collected in the summer of 2010 during the breeding season, which extended from early May to late July.

Data Collection

Data, including brood size, body mass (g) and prey capture/consumption, were collected to determine survivorship of offspring, growth rates, and overall bioenergetics of the Double-crested Cormorant chicks. The total number of nests per colony was counted twice over the sampling season (early: (Hat) 22 May 2010 and (Whiskey) 7 June 2010; late: (Hat) 9 July 2010 and (Whiskey) 21 July 2010) using small, decomposable color-coded sticks. The sticks were counted, marked and bagged beforehand. On each colony, one stick was dropped per nest and the remainder of sticks in the bag was subtracted from the original number. The difference corresponded to the number of nests counted. Colony counts for active nests were conducted at the beginning of the sampling period and near the end of the sampling period to model decline in colony nest numbers. Nests were considered active if they were well maintained and/or contained eggs/chicks in the early count or chicks in the late count.

Five focal areas on Hat Island and two on Whiskey Island were selected and each monitored by a Moultrie® D-40 trail camera with four gigabyte data cards in order to monitor both natural and human-caused disturbances, as well as predation. Cameras were set with a five

minute delay between events and flash was turned off to avoid disturbing the birds after dark. Therefore, nests were only monitored during daylight hours. Pictures were stamped with the date, time of day and focal area.

Focal areas on Hat Island were selected systematically due to major disturbance to the colony. Ongoing cormorant control efforts (i.e. egg oiling and shooting of adults) limited the area suitable for this study. Therefore, areas that were lacking eggs post disturbance or were not oiled and consisted of at least 20 nests were selected. Double-crested Cormorants can and often do re-lay in situations where their eggs are broken or preyed upon, most often occurring at times when the colony is disturbed (Hatch and Weseloh, 1999). Therefore, recently disturbed and empty nests were selected.

The Whiskey Island sites were also chosen systematically. However, the colony did not appear to be disturbed by humans on a regular basis during 2010. Focal areas that had at least 10 nests located on the ground were selected. Focal area 1a on Whiskey Island was abandoned early in the season (prior to chick hatch) and therefore the camera was moved to a second area (1b) to monitor several tree nests for disturbance, though further data was not collected from these nests due to their inaccessibility. A second ground focal area (2b) for collecting data was selected near area focal area 2 on Whiskey Island and monitored with camera 2.

For both islands, the cameras were mounted either on metal sign posts driven into the ground at each focal area, or attached to standing woody debris (i.e. snags). Each focal nest was marked with a numbered, brightly painted orange rock in order to easily keep track of the nests used. However, this proved an unreliable method as the birds often moved the rocks or soiled them so completely that nest identification was impossible. Nest sites were mapped by hand as a secondary method. Each Hat Island focal area consisted of 20 nests and each Whiskey Island

focal area consisted of 10 nests. Dense vegetation on Whiskey Island limited the range of the camera and therefore the number of nests to be monitored per site.

Brood sizes of each nest of the focal areas were counted at the beginning of each date of data collection for easy monitoring and to estimate the reproductive output of the entire colony. Throughout the sampling session, only a few nests produced chicks, even within the selected focal areas. Therefore, a more theoretical approach to data analysis was conducted (i.e. the number of chicks per colony as well as chick mass per day were estimated using models).

Chicks were captured by hand and weighed (g) once or twice a week for four weeks post-hatching. Mass was determined by placing the chick in a pillow case, weighing the pillow case and cormorant together, removing the chick and then reweighing the pillow case. The weight of the pillow case was then subtracted from the combined weight to determine the weight of the chick. The chicks were banded with numbered U.S. Fish and Wildlife bands and blue plastic colored bands with individualized white alpha-numeric codes when large enough to hold a band securely, and then immediately released. Since chicks hatch asynchronously, brood size and type (i.e. eggs, chicks, mixed) were determined for each focal area at each visit to the colonies.

Regurgitate samples were collected directly from the chicks at the focal nests using a gloved hand and placed in individual plastic Whirlpak® bags, distinctly labeled with the colony, nest and date. Samples were collected about once a week (per trip to the colony) so that chicks were continually supplied ample food items despite the removal of one regurgitate sample. The regurgitate samples were stored frozen. Prior to analysis, they were thawed and individual fish separated by hand. Fish species, mass (g) and length (mm), along with the number of fish per regurgitate sample were recorded. Contents that were overly digested or not identifiable were weighed and categorized as “fish parts” with an attempt to determine at least the number of fish

in the sample and the species. For regurgitate samples that contained fish parts too degraded to measure and weigh wholly, the total mass of the sample (minus any whole fish, which were weighed separately) was divided by the number of individual fish within the sample to determine an approximate mass for each individual fish in the sample. Regurgitate samples were labeled corresponding to their respective focal nests and, when possible, with the chick to which the regurgitate sample belonged. If pain or stress was suspected in any of the individual animals, that individual was exempt from measurements and sample collection.

Diet Analysis:

Data collected for this study were compared to data from 2000 (Seefelt and Gillingham, 2008) to determine any differences over time. Both years took into account all active colonies within the Beaver Archipelago excluding Gull Island due to its remoteness far west (almost 18km) from Beaver Island. The mass data of the chicks were averaged per day. Using the data collected, a bioenergetics model (updated from Seefelt and Gillingham, 2008) was developed and constructed in order to determine the ingestion of fish biomass by the chicks (described below). The parameters of this model include early and late season nest counts, focal area chick mortality rates, their food consumption and daily energy expenditure estimates among others. This model differs from that of Seefelt and Gillingham (2008) by focusing primarily on the chick bioenergetics.

The wet weight for each round goby found in the regurgitate samples was entered into the following equation to determine individual energy density in joules:

$$log_{10}(ED) = 3.57 + 0.10 * log_{10}(WW) \quad (1)$$

where ED = the energy density of the individual goby and WW = the goby wet weight (Reutz et al. 2009). The mean energy density was then determined for all round goby specimens. The energy density for the other dietary components was determined from the literature (Table 1). The mean energy density was then converted into kilocalories to be used in the bioenergetics model.

The proportion of each prey fish species in the diet was determined for Hat Island and Whiskey Island separately and for both islands combined. These values were then multiplied by their respective energy densities (Table 1) to determine the energetic proportion of each prey species in the diet. These values were subsequently summed to determine the average caloric density of the diet (ACD). The dietary proportion per regurgitate sample for each major prey species was compared between 2000 and 2010 by a Mann-Whitney U-test because samples contained many zeros and dietary proportion had anon-normal distribution.

Table 1. Energetic density in kcal/g of fish (by species) found in the Double-crested Cormorant chick diet in the Beaver Archipelago, 2010.

Prey Type	Energetic Density (kcal/g)
Alewife†	1.947
Round goby*	1.059
Brook stickleback†	1.493
Crayfish†	1.077
White sucker‡	0.884

* Calculated value, † Cummins and Wuycheck (1971), ‡ Bryan et al. (1996)

Bioenergetics Model

The number of nests in each focal area was determined in the field on each day of data collection. These numbers were plotted against the overall time period in days for data collection in a Microsoft Office Excel® spreadsheet to determine the rate of decline of focal area

nests (exponential decay). The following equation was used to determine the amount of decay per day:

$$M_f = M_i e^{rt} \quad (2)$$

where M_f is the late season nest count for the island, M_i is the early season nest count, r is the rate of decay determined from the focal areas and t is the time increment. Solving for t and dividing by the number of days of data collection established uniform decay increments. This time unit was then multiplied by the number day since the early nest count. This was plugged back into equation 2 as the new t to determine the number of active nests each day (new M_f). This procedure was repeated for each focal island and also for the total tree nests and total ground nests on Whiskey Island. Since Hat Island had undergone cormorant control (egg oiling and killing of adults), the rate of natural decline on Whiskey Island was also applied to the initial nest count on Hat Island to simulate natural patterns. This time increment was established by dividing the number of sampling sessions by the number of days of data collection. The number of nests per day was then multiplied by the mean number of chicks per active nests from the focal areas to determine the overall number of chicks.

A similar procedure was used to determine chick mass per day. The chick mean mass per sampling day was determined across focal areas per island. For Whiskey Island, these data were then plotted in Sigmaplot® Software producing a curve. The equation for this curve was determined then solved for each day of the data collection season resulting in an estimated mean chick mass per day. The same process was used for Hat Island. The equation produced was then solved for each day of collection. For chicks that had hatched prior to the beginning of data collection, a published growth rate (63 g/day; Hatch and Weseloh, 1999) was subtracted each day prior to initial measuring until reaching the mass range of newly hatched chicks. The

number of days prior to measurement was then subtracted from the first date of data collection to give a hatch date. This process was only applied to Hat Island where two weeks of inclement weather and an earlier than anticipated hatch prevented regular data collection.

The bioenergetic model presented here stems from that of Madenjian and Gabrey (1995); however it contains modifications similar to those of Seefelt and Gillingham (2008) and Hebert and Morrison (2003), and estimates prey consumption levels and energy demands of chicks. It is based on a series of allometric equations. These equations use a mean body mass per day to determine the daily energy expenditure of the nestlings (DEEN). Kendeigh et al. (1977) presented the following equation to determine DEEN:

$$\mathrm{DEEN} = 1.230\mathrm{W}^{0.7749} \tag{3}$$

where W = mean body mass for the chicks as determined above. DEEN was then divided by an assimilation efficiency of 0.80 (Furness, 1978) to determine the amount of energy assimilated by the chick. This number was then multiplied by the number of chicks in the colony as determined above for that day to determine the daily energy intake (DEIN) of the individual nestling birds. DEIN was then summed for all days of the sampling period. The DEIN was also divided by the ACD to determine the amount of food consumed per day (DFC) in kilograms. The summed DEIN was then multiplied by the proportion of each prey type in the diet to determine the DEIN per prey species (kcal). This was then divided by the energetic density of each prey type to determine the mass of each prey type consumed. These values were subsequently summed to determine the estimated amount (kg) of fish consumed during the sampling period (summarized in Figure 2).

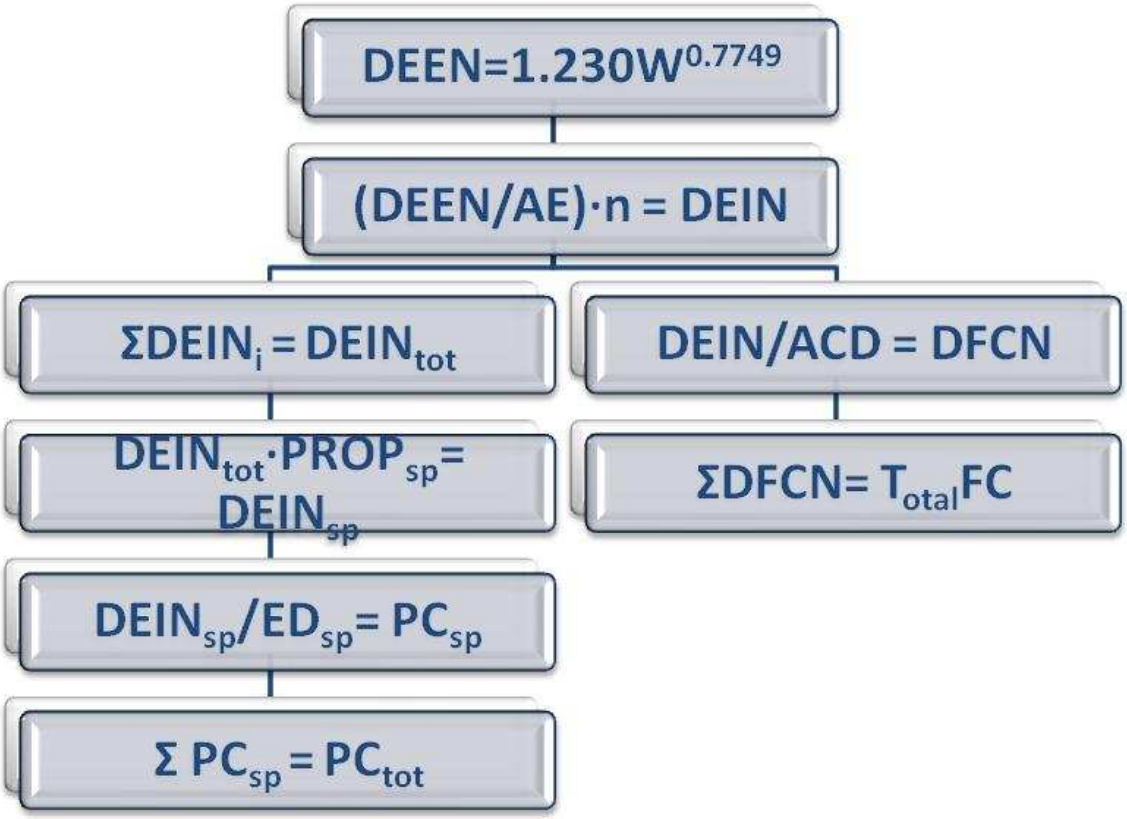

Figure 2. Flow diagram including allometric equations used to determine the bioenergetics and prey consumption of DOUBLE-CRESTED CORMORANT chicks in this study. DEEN=daily energy expenditure of nestlings; W= mean mass of chicks; DEIN =daily energy intake of nestlings (i=per day; tot=total over sampling season; sp=per species); AE=assimilation efficiency (0.80; Furness, 1978); n=number of chicks/day/colony; ACD = average caloric density of the diet; DFCN = daily food consumption of nestlings; PROP= energetic proportion of diet components; PC=Prey Consumed; ED = energy density of diet components.

The mean chick mass assuming simultaneous hatching was then averaged for both islands and the mean chick abundance was summed for both islands. These data were then applied to the above bioenergetics model assuming simultaneous hatching on May 29 (day 0) and asymptotic growth on July 1 (day 33). A 33 day period was chosen because it corresponded to the longest time period of actual data collection for a single colony in 2010. Additionally, the

dietary data from 2010 was entered into the 2000 model to determine the amount of food (kg) consumed given similar chick numbers and growth data as in 2000. The change in chick mass from each previous day (assuming simultaneous hatching) was calculated from the overall mean masses. From these values, the mean increase per week and overall was determined. The amount of food consumed at the mean mass per each sampling day was compared between 2000 and 2010.

An individual parameter perturbation method was used to conduct sensitivity analysis for the model above (Madenjian and Gabrey, 1995). This process helped to determine which model parameters were most important in determining daily energy intake and prey consumption of the Double-crested Cormorant chicks investigated in this study. Ten model inputs were subjected to a 10% increase or decrease perturbation for a total of 20 simulations. During each simulation, the parameter being examined was increased or decreased 10% while all other parameters remained at their original values. The simulation outputs were then compared to the original model output. A percent difference was then determined.

CHAPTER III

RESULTS

Colony counts for active nests were conducted at the beginning and near the end of the sampling period to model nest number decline (see Table 2 for nest counts). On Whiskey Island, 184 nests were constructed on the ground and 148 nests were constructed in the trees at the initial colony count. Most of the ground nests on Whiskey and Hat Islands were unsuccessful.

Table 2. Early (Hat: 22 May 2010; Whiskey: 7 June 2010) and late (Hat: 9 July 2010; Whiskey: 21 July 2010) nest counts for Whiskey and Hat Island colonies sampled in the Beaver Archipelago during 2010.

Colony	**Nests**	
	Early	**Late**
Hat Island	3721	10
Whiskey Island	332	107

Diet Analysis

The regurgitate samples (n=61) collected over 29 days contained 236 individual whole fish, 180 of which were round goby. The mean energetic density of round goby in the Beaver Archipelago was 4430.6 J/g (SD: 511.5 J/g; Range: 3178.5 J/g - 5656.8 J/g) or 1.059 kcal/g and exhibited a normal distribution (Figure 3). The mean mass for individual round goby (accounting for partially digested fish) found in the archipelago chicks' diet was 7.76 g (n=242, SD: 9.26, Range: 0.21-66.94 g). The mean length of fish in the diet was 82.55 mm (n=236, SD: 29.45, Range: 20-188 mm) with 92% of the fish less than 125 mm. A similar trend was seen in the alewife and round goby in the diet (Figures 4, 5 and 6).

The diet of the Double-crested Cormorant chicks on both colonies consisted of five species: round goby, alewife, brook stickleback (*Culaea inconstans*), white sucker (*Catostomus*

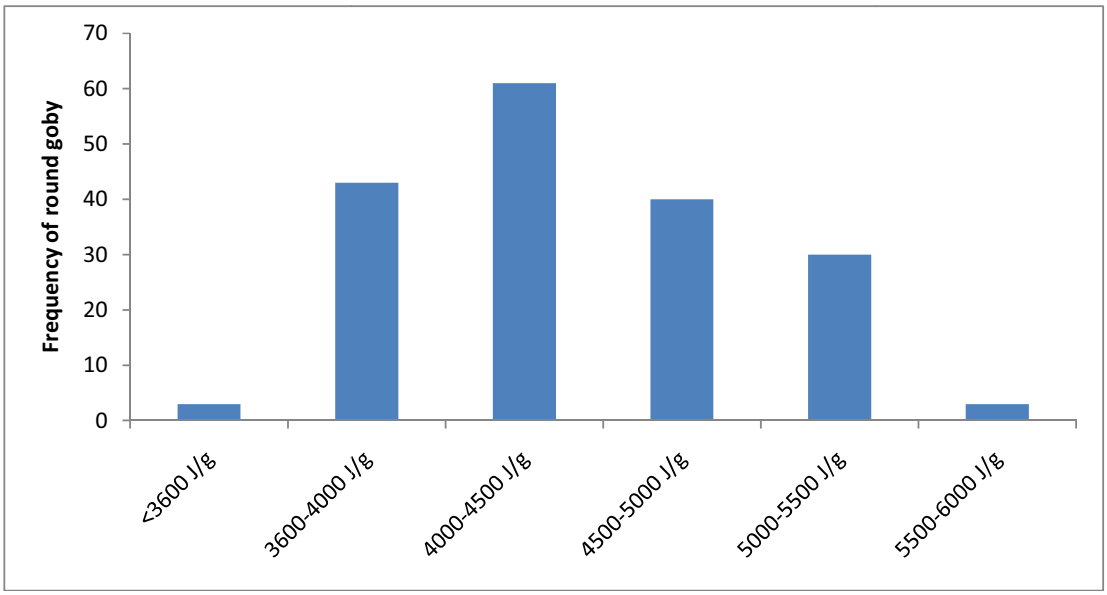

Figure 3. Frequency distribution of round goby energy densities, based on fish wet weight, found in the diet of chick Double-crested Cormorants in the Beaver Archipelago, 2010 (n=180, based on 60 regurgitate samples).

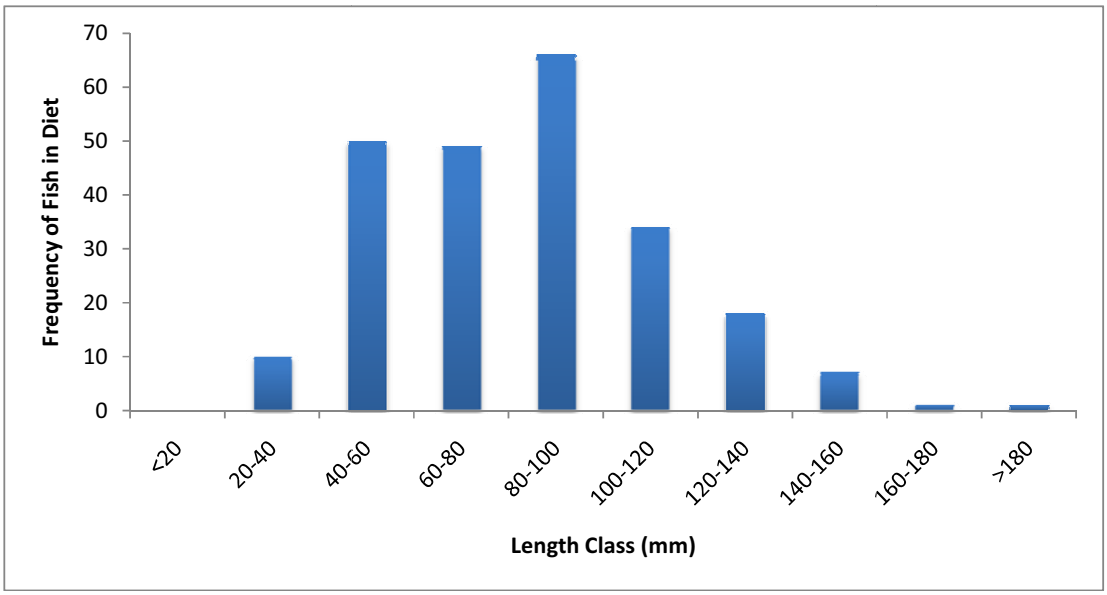

Figure 4. Length frequency distribution of all fish found in the diet of Double-crested Cormorants in the Beaver Archipelago, 2010 (n=236, based on 61 regurgitate samples).

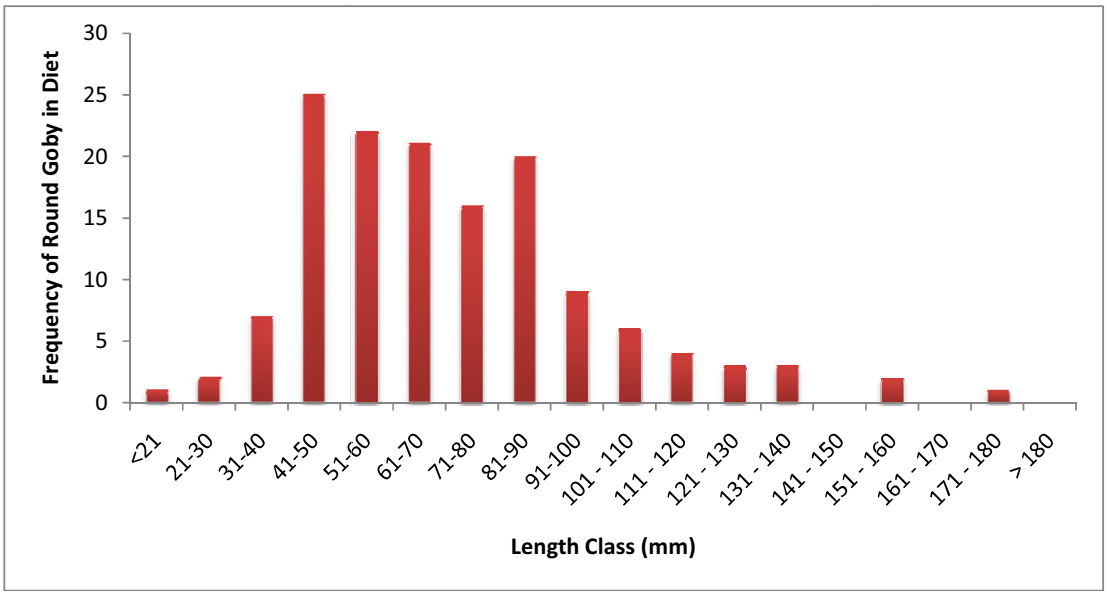

Figure 5. Length frequency distribution of round goby found in the diet of Double-crested Cormorants in the Beaver Archipelago, 2010 (n=142, based on 61 regurgitate samples).

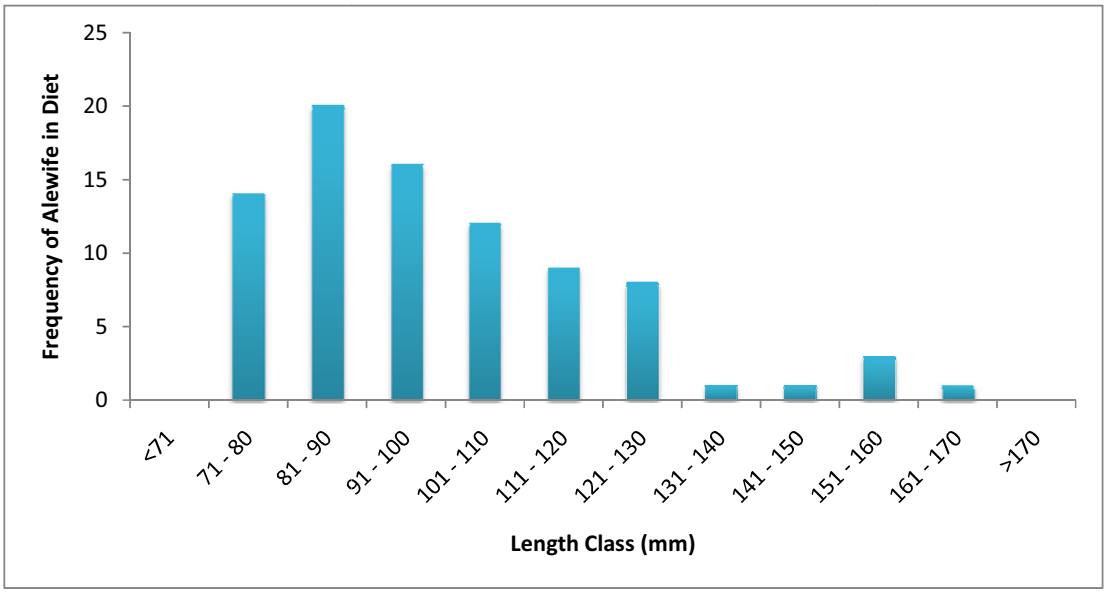

Figure 6. Length frequency distribution of alewife found in the diet of Double-crested Cormorants in the Beaver Archipelago, 2010 (n=85, based on 61 regurgitate samples).

commersonii) and crayfish (*Orconectes* spp.). The proportion of each species in the diet per colony and overall was also determined (Table 3). In 2000 the major fish species in the diet was

Table 3. Proportion of prey biomass by fish species in the Double-crested Cormorant nestling diet in the Beaver Archipelago, 2010 (n=61 regurgitate samples).

Species	Whiskey	Hat	Total
Alewife	0.32	0.19	0.29
Round goby	0.66	0.81	0.67
Brook stickleback	0.00	<0.01	<0.01
Crayfish	<0.01	0.00	<0.01
White sucker	0.05	0.00	0.04

alewife (54.4%; Seefelt and Gillingham, 2008). In 2010 this proportion dropped to 28.9%; whereas round goby, conspicuous because of its absence in 2000, comprised 66.7% of the chick diet. The remaining dietary components made up only 4.4% of the chick diet and declined in dietary abundance by an average 88% (n=3, SD: 12.28) from 2000. The median proportion of alewife in 2000 and 2010 were 0.2919 and 0.0000 respectively. The distributions of the two groups were significantly different (U=4501.5, p<0.0002). Round goby, being new to the diet in 2010, was not found in 2000, and therefore no comparisons were made. The average caloric density varied per colony and overall (Whiskey Island: 1330.70 cal/g, Hat Island: 1225.48 cal/g, Total: 1308.46 cal/g).

Bioenergetics Model

Mean mass of focal area chicks increased over the 3 sampling periods for Hat Island and 8 sampling periods for Whiskey Island (Appendix A). The mean modeled mass of Double-crested Cormorant chicks on Whiskey Island produced a sigmoidal growth curve (Figure 7Figure

). The modeled growth equation for Hat Island produced a steady increase to an asymptote (Figure 8).

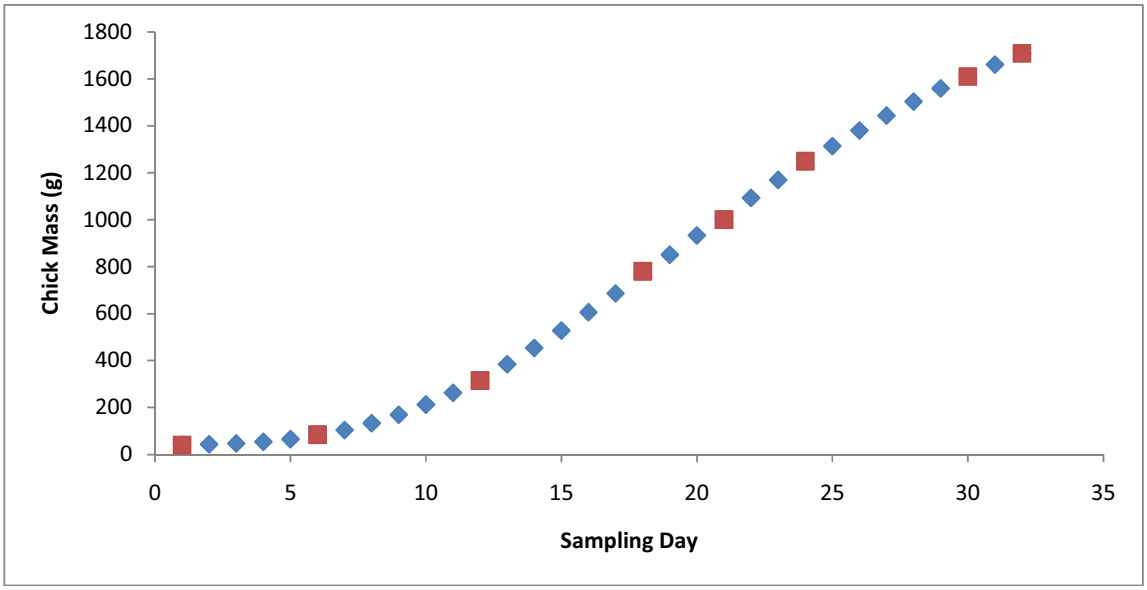

Figure 7. Mean modeled mass of Double-crested Cormorant chicks per sampling day on Whiskey Island during 2010 season. Red squares indicate measured values (n=8); blue diamonds indicate modeled values.

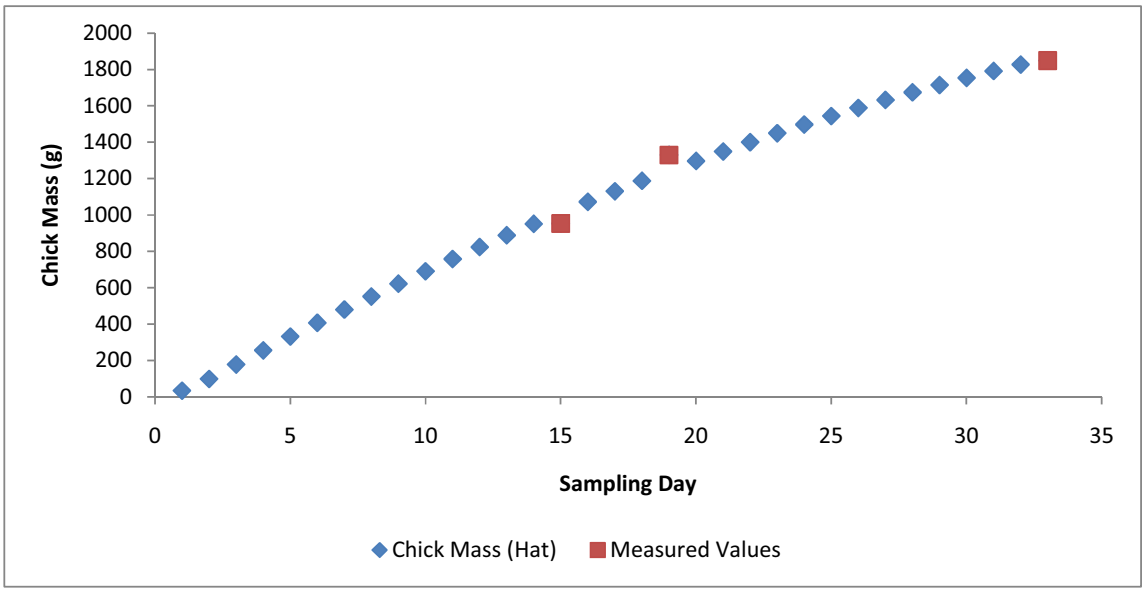

Figure 8. Mean modeled mass of Double-crested Cormorant chicks per sampling day on Hat Island during 2010 season. Red squares indicate measured values (n=3); blue diamonds indicate modeled values.

When averaged for both islands, the mean chick mass assuming simultaneous hatching produced a somewhat sigmoidal shaped curve (Figure 9). The Whiskey Island colony hatch date (20 June)

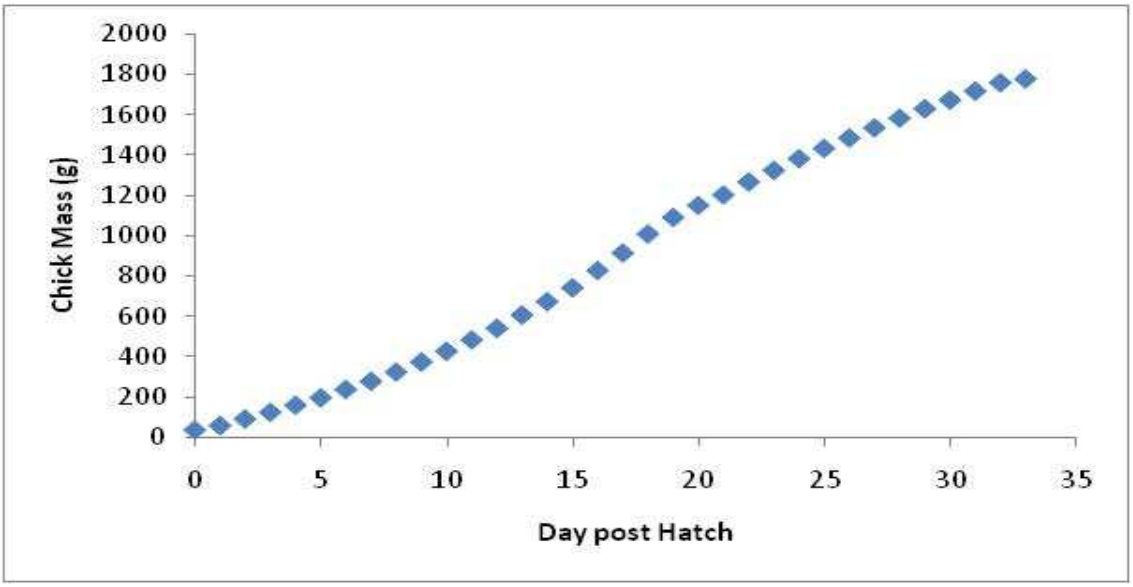

Figure 9. Mean modeled mass of Double-crested Cormorant chicks per sampling day averaged between Hat and Whiskey Islands during 2010 season. Blue diamonds indicate modeled values.

was much later than on Hat Island (~29 May). The maximum mass measured by the focal area chicks was 2,175.00 g (Hat). The minimum mass measured was 30.00 g (Whiskey). Sample size increased near the beginning of the sampling season as new chicks hatched and tended to decline near the end of sampling. The mean number of chicks per active focal nest on Hat Island was 1.96 (SD: 1.01; Min: 1.00; Max: 4.00; n=28), the mean on Whiskey Island was 2.22 (SD: 0.89; Min: 1.00; Max: 4.00; n=50), and the combined mean was 2.13 (SD: 0.94; Min: 1.00; Max: 4.00; n=78).

On Whiskey Island, the mean number of chicks lost per day based on modeled data was 16.11 (n=31; SD: 5.30, Range: 8.84-26.44). By 21 July 2010, an estimated 238 (32% of the estimated maximum number of chicks) chicks survived to fledging. The modeled total number of chicks per total number of nests for the late colony count on Whiskey Island in 2010 was 2.07. Due to the considerable amount of control, it was difficult to determine the actual number of chicks lost per day on Hat Island. Modeled numbers suggest a mean loss of 88.77 chicks/day assuming no control (n=33; SD; 12.14; Range: 70.13-110.35) and about one bird every 2.60 days in the uncontrolled focal areas on Hat (mean=0.39 chick/day; n=33; SD: 0.10; Range: 0.25-0.57). By 21 July 2010, an estimated 19 (41% of maximum) chicks survived to fledging on Hat Island despite control efforts. If no control had taken place, an estimated 3,702 (51% of maximum) chicks could have survived to 21 July 2010. The modeled total number of chicks per total number of nests for the late colony count on Hat Island in 2010 was <0.01. If no control had taken place this value would have risen to 1.32. The mean chick abundance when summed for both islands produced a steady decline (Figure 10)

Pictures from the trail cameras on both Whiskey and Hat Islands reveal the presence of and potentially significant predation of chicks by Bald Eagles (*Haliaeetus leucocephalus*) (Appendix B). Black-crowned Night Herons (*Nycticorax nycticorax*) were captured on camera on Whiskey Island perching in and near trees containing active Double-crested Cormorant nests (Appendix B). Bald Eagles were also captured on camera on Hat Island, though this was near the end of the sampling period (Appendix B).

The modeled DFC on Whiskey Island ranged from 20.36 g to 369.61 g and on Hat Island from 19.29 g to 421.46 g per day over the course of the sampling period (Figure 11). According

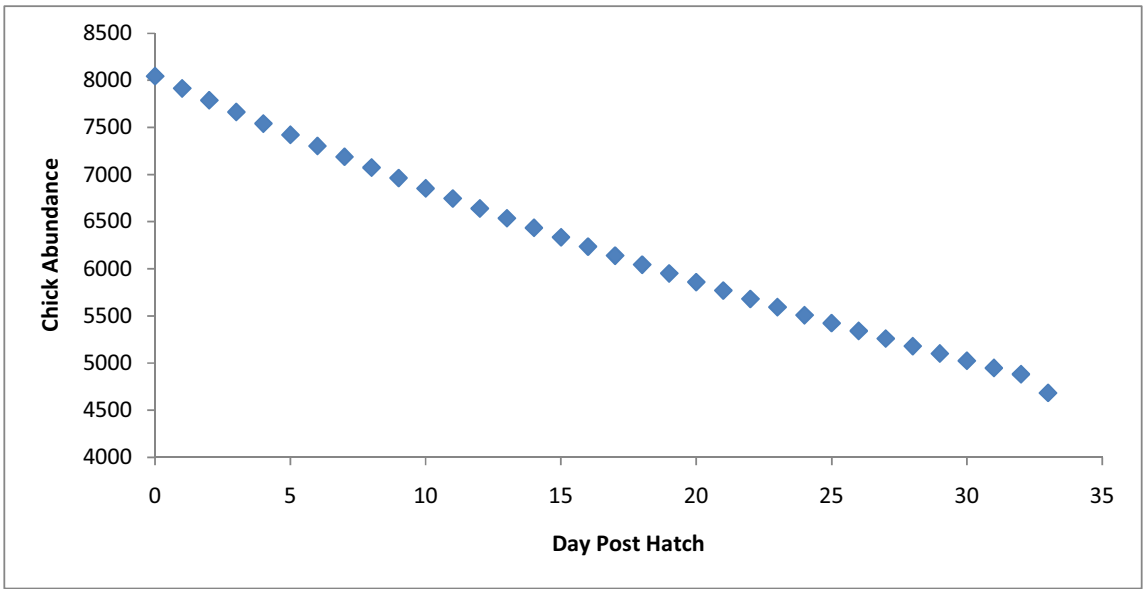

Figure 10. Modeled mean Double-crested Cormorant chick abundance (Whiskey Island + Hat Island) per sampling day during 2010 season. Blue diamonds indicate modeled values.

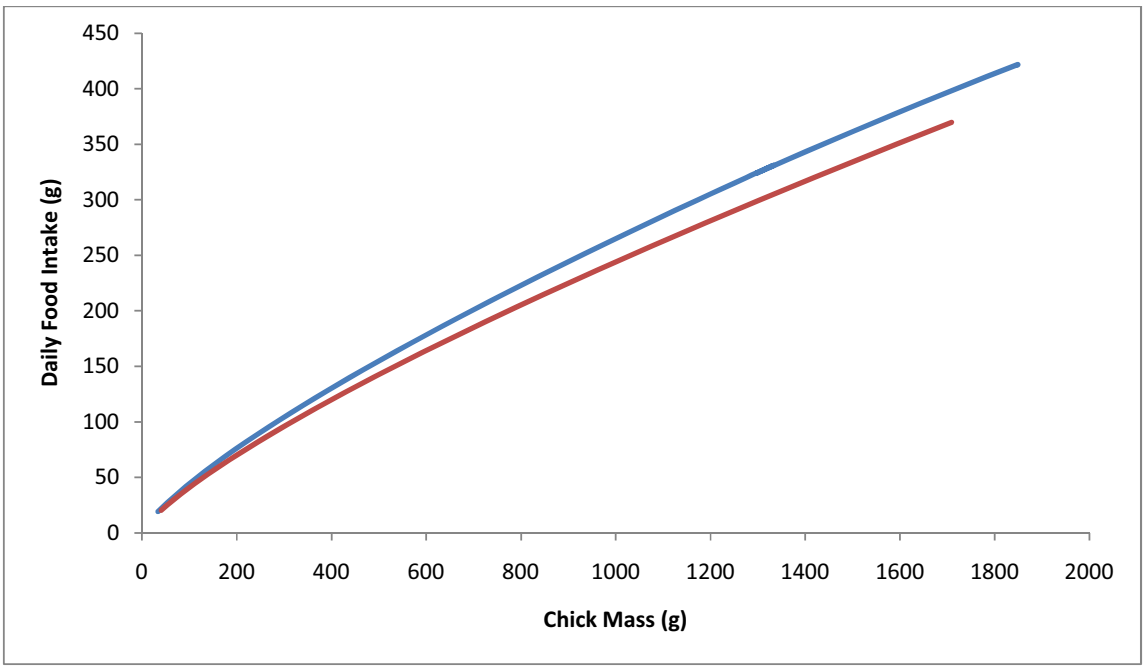

Figure 2. Daily modeled food consumption in grams for nestling Double-crested Cormorants at a given mean mass in the Beaver Archipelago, 2010. Blue=Hat; Red=Whiskey.

to the model, the total amount of food consumed per chick over the course of sampling was 9.28 kg on Hat and 5.74 kg on Whiskey. When combining the data from both islands, the amount of food consumed ranged from 18.06 g to 387.79 g with a total amount of food consumed per chick of 7.32 kg. The amount of food consumed per chick over similar time periods was higher in 2010 (7.32 kg) than in 2000 (5.11 kg).

Based on the above model (incorporating the results from the control measures on Hat Island) the Double-crested Cormorant chicks consumed (Whiskey and Hat Islands combined) a total of 2,289.36 kg of prey (Hat: 129.13 kg, Whiskey: 2,160.23 kg). Assuming no control on Hat Island, the Beaver Archipelago birds had the potential to consume 27,349.52 kg of prey over the sampling period (Hat: 25,189.29kg). Using nest count and chick mass data from 2000 in the model developed for 2010, the chicks consumed 89,024.36 kg of prey over the corresponding 33 day period. On both Hat Island and Whiskey Island in 2010, most of the fish consumed were round goby, followed by alewife (Table 4).

Based on the 2000 model of Seefelt and Gillingham (2008) but substituting in the 2010 dietary data (i.e. proportions of prey consumed), chicks would have consumed 21% more fish given a 2010 diet (144,767.22 kg) than a 2000 diet (114,367.25 kg). The amount of alewife in the diet would have been 47% lower, brook stickleback would have been 94% lower, crayfish consumption would have been 98% lower, and white sucker would have been 63% lower (Table 5).

According to the model, at any given mass chicks were consuming more food in 2010 than in 2000 (Table 6). This difference ranged from 2.36 g of food at 40.00 g chick mass and

Table 4. Biomass (kg) of prey consumed (by species) by nestling Double-crested Cormorants in the Beaver Archipelago, 2010 taking into consideration control efforts and assuming no control.

With No Control			
	Whiskey	**Hat**	**Total**
Alewife	428.69	2796.40	3225.08
Round goby	1568.64	22359.20	23927.84
Brook stickleback	0.00	33.69	33.69
Crayfish	10.48	0.00	10.48
White sucker	152.43	0.00	152.43
With Control			
	Whiskey	**Hat**	**Total**
Alewife	428.69	14.34	443.02
Round goby	1568.64	114.62	1683.26
Brook stickleback	0.00	0.17	0.17
Crayfish	10.48	0.00	10.48
White sucker	152.43	0.00	152.43

Table 5. Modeled biomass of prey consumed (in kg) by species in 2000 and modeled potential prey biomass consumed by species given chick growth rates and numbers from 2000 and dietary data from 2010.

Prey Type	**2000**	**2010**
Alewife	48,879.70	25,935.94
Round goby	0.00	110,279.95
Brook stickleback	679.74	42.71
Crayfish	38,309.24	547.25
White sucker	21,377.01	7,961.36
Total	114,367.25	144,767.22

93.60 g of food at 1849.00 g chick mass. In 2000 chicks consumed between 18.00 g food at 40.00 g mass and 333.00 g food at 1849.00 g mass, whereas in 2010 chicks consumed 20.36 g of food at 40.00 g mass and 426.62 g food at 1849.00 g mass based on model outputs.

The mean change in chick mass over the course of sampling, assuming simultaneous hatch, was 52.87 g/day (n=33; SD: 17.60; Range: 18.53-94.16). This mean changed by week, however (Week 1: 34.64, 2: 56.48, 3: 75.77, 4: 54.49, 5: 41.95). Over week one the chicks

Table 6. Modeled amount of food consumed (g) for the mean Double-crested Cormorant chick mass at each sampling session (n=11) in 2010 in the Beaver Archipelago. The amount of prey consumed in 2000 for each corresponding chick mass and the difference between the two years is also listed for comparison.

Chick Mass (g)	Grams Consumed/Chick		Difference (g)
	2000	2010	
40	18.00	20.36	2.36
85	33.00	35.97	2.97
315	84.50	99.70	15.20
780	170.50	201.33	30.83
953	199.00	255.30	56.30
1000	206.50	244.09	37.59
1250	245.50	289.99	44.49
1330	258.00	330.51	72.51
1610	299.00	352.94	53.94
1710	313.00	369.60	56.60
1849	333.00	426.62	93.62

exhibited relatively slow growth at 34.64 g/day. Over weeks 2-3.5 chicks exhibited increased growth per day compared to the literature (63 g/day; Hatch and Weseloh, 1999) at 64.26 g/day. Growth slowed again relative to body size during the final week prior to asymptote to 41.95 g/day (Figure 12).

The results of sensitivity analysis suggest that the parameters (Table 7) of duration of the study period, the mean number of chicks/active nest, assimilation efficiency and the energy density of the prey (kcal/g) had the greatest impact on model output (Table 8). Chick mortality rate and mass at hatching had almost no impact on the output of the model. All other inputs had relatively low impacts on model output.

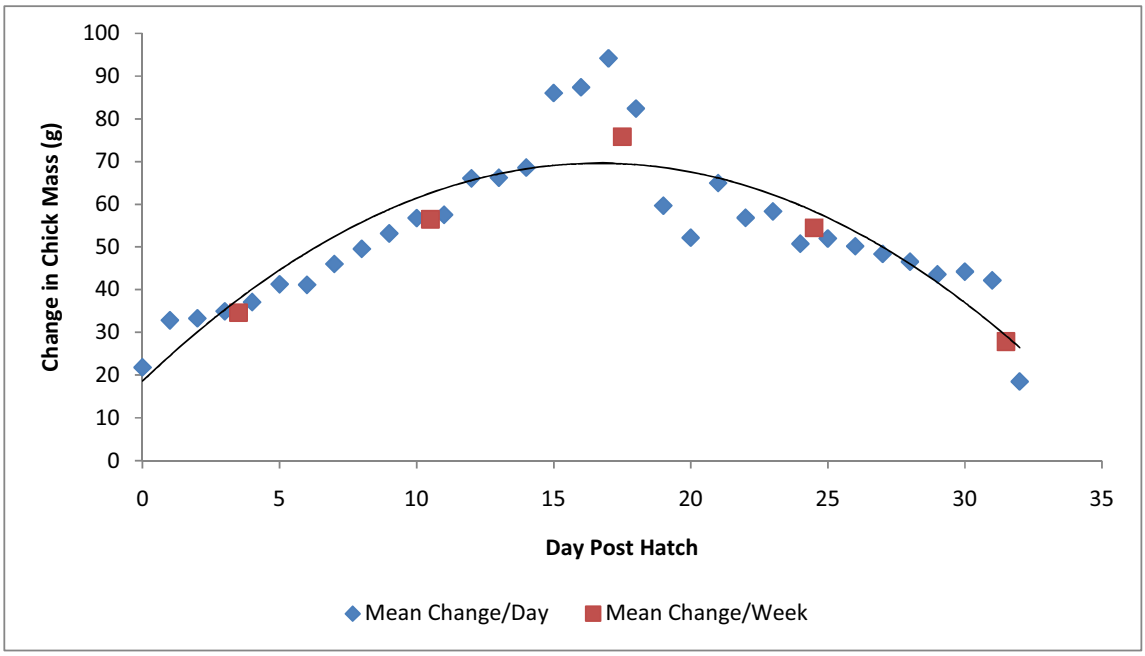

Figure 3. Change in Beaver Archipelago chick mass per day and per week over the course of sampling in the 2010 breeding season.

Table7. Life history characteristic input parameters used to model prey consumption by Double-crested Cormorant chicks in the Beaver Archipelago, 2010 (early: (Hat) 22 May 2010 and (Whiskey) 7 June 2010; late: (Hat) 9 July 2010 and (Whiskey) 21 July 2010).

Characteristic	Whiskey Island	Hat Island
Nest Count (Early)	332	3721
Nest Count (Late)	107	10
# chicks/active nest (mean)	2.22 (Range: 1-4)	1.96 (Range: 1-4)
FA Chick Mortality Rate	$y=332e^{-0.037x}$	$y=3721e^{-0.014x}$
Study Duration (days)	32 (20 Jun-21July)	33 (29 May-30 Jun)
Chick Growth Rate	$y = 41.69 + \frac{2331.83}{1 + \left(\frac{x}{23.50}\right)^{-2.97}}$	$y = 951.00 + 62.07x + 0.75x^2$
Mass at Hatch	40.54	34.00*

*Hatch and Weseloh, 1999
All other inputs were measured in the field or calculated by the authors

Table 1. Sensitivity analysis results for change in input parameters on daily energy intake of Double-crested Cormorant chicks as determined by bioenergetics models.

	Input Perturbation Error	
Model Output	**+ 10%**	**– 10%**
Nest Count (Early)	+3.58	-3.75
Nest Count (Late)	+6.26	-6.43
# chicks/active nest (mean)	+10.00	-10.00
FA Chick Mortality Rate	0.00	0.00
Study Duration (days)	+12.69	-13.41
Chick Growth Rate	+8.39	-7.22
Mass at Hatch	+0.06	-0.06
Assimilation Efficiency	-9.10	+11.11
Energy Density of Prey (kcal/g)	-9.10	+11.11

CHAPTER IV

DISCUSSION

The number of active nests in the Beaver Archipelago in 2010 declined dramatically from 4,053 at the early count to only 117 at the late count. This decline was mostly due to control practices on Hat Island in 2010. The caloric density of round goby in the Beaver Archipelago Double-crested Cormorant chick diet was found to be 1.059 kcal/g. Round goby was the primary diet component in 2010 followed by alewife. Chicks on Whiskey Island were found to exhibit sigmoidal growth whereas on Hat Island, chicks exhibited steady growth to an asymptote. Moreover, at any given mass, individual chicks were consuming more prey biomass in 2010 than in 2000. This resulted in more prey being consumed total in 2000. However, if chick numbers had remained that same between 2000 and 2010, more prey would have been consumed in 2010, based on the change in diet. Control also resulted in low reproductive success in 2010. This low reproductive success was also likely impacted by predation late in the season and possibly the lower energy density of the chick diet.

The dramatic nest decline in the Beaver Archipelago in 2010 was mostly due to control of Double-crested Cormorant populations on Hat Island. Egg oiling and shooting adult and fledged birds created much disturbance leading many breeding birds to abandon their nests. Nest abandonment was also likely influenced by the presence of predatory birds such as the bald eagle. Abandoned nests were quickly disassembled by nesting birds and the materials reused in active nests.

The mean energy density of round goby found in the Beaver Archipelago in 2010 was found to be 1.059 kcal/g and is similar to the energetic density found in the Muskegon Lake watershed, which empties into Lake Michigan just south of Muskegon, Michigan (4,411 J/gWW;

Reutz et al. 2009). Round goby has a lower energy density than alewife, the primary dietary component in 2000. This value was relatively low compared to other dietary components.

The diet of the Double-crested Cormorant chicks was different in 2010 compared to 2000. New to the diet in 2010 was round goby, a recent invader to Lake Michigan (Clapp et al. 2001), the Great Lakes Basin (Jude et al. 1992) and the Beaver Archipelago, whereas spottail shiner (*Notropis hudsonius*) and johnny darter, though present in the 2000 diet, were lacking in 2010. Since it was first observed in the Beaver Archipelago Double-crested Cormorant diet in 2007 (Seefelt, unpub. data), round goby has become the primary dietary component. The length of fish in the Beaver Archipelago Double-crested Cormorant diet tended to lie between 40.0 and 120.0 mm with over 90% of the fish less than 125 mm. This is consistent with other sources (Campo et al. 1993; Neuman et al. 1997).

Some published data and previous bioenergetics studies suggest that Double-crested Cormorant chicks exhibit a linear increase in growth (Madenjian and Gabrey, 1995; Hatch and Weseloh, 1999; Seefelt and Gillingham, 2008). The results of this study are similar to Léger and McNeil (1987) and Dunn (1975 and 1976) and suggest that chicks exhibit a more sigmoidal shaped growth curve with the highest rate of growth occurring after the first week of age, yet before week five. As chicks near their adult mass, the increase in mass/day begins to decline (Lewis, 1929; Léger and McNeil, 1987). The slow growth during the early stages of development modeled in this study may be due to low energy density of the fish pieces given, the allocation of energy to thermoregulation, or it could be simply a product of sampling. Similarly, the slow growth near fledging is likely due to the allocation of energy resources to the production of flight feathers rather than to growth.

The modeled DFCN was higher in 2010 than in 2000, as was the modeled amount of food consumed over the sampling period (7.55 kg and 5.11 kg respectively). This could be due to decreased energy density of the nestling diet leading to an increased dietary need to raise the mass of a single nestling bird. In other words, with a lower overall dietary energy density in 2010, model outputs suggest that more food needed to be consumed over the same amount of time to reach similar growth goals (i.e. fledging). This increased need led to an increase in food consumption of chicks overall if chick numbers had remained the same between 2000 and 2010. However, since Hat Island was extensively controlled in 2010, there were fewer chicks produced and subsequently much less prey biomass consumed overall. If no control had occurred and chick numbers had remained the same from 2000 to 2010, more prey would have been consumed overall due to the lower energy density of the 2010 diet.

In 2010, according to the model, chicks consumed 1,688.81 kg of round goby taking into account control efforts on Hat, and could have consumed 23,920.29 kg if no control had taken place. With a mean goby mass of 7.76 g, an estimated 217,704 and 3,083,563 fish were or would have been consumed, respectively, in 2010 by the Hat and Whiskey Island breeding colonies during the sampling period. Round goby population densities can become large fairly quickly (MacInnis and Corkum, 2000). Females can spawn up to five times per season and the males guard the nests leading to an increased hatch rate of the eggs (~95%; MacInnis and Corkum, 2000). This study, among others (Somers et al. 2003; Johnson et al. 2010), has shown that round goby are currently important dietary components of Double-Crested Cormorants. As round goby populations continue to increase and spread, picivorous waterbirds such as the Double-crested Cormorant may help contribute to the natural control of these invasive fish populations. Alternatively, since round goby have such a low energetic density, their

consumption may help to control Double-crested Cormorant populations by reducing the number of chicks that can be successfully fledged per pair (Seefelt and Gillingham 2008).

Weseloh and Ewins (1994) suggest that alewife consumption may be intimately linked to Double-crested Cormorant reproductive success. Their energy density is high (Cummins and Wuycheck, 1971) and they tend to school (Schultz, 2004) making them easier to catch and energetically worth the effort. In 2000, alewife comprised the highest proportion, by mass, in the Beaver Archipelago cormorant diet (Seefelt and Gillingham, 2008). In 2010, round goby made up the highest proportion while alewife had declined considerably. Lake Michigan-wide bottom trawl data indicate that in 2009, alewife was more abundant in Lake Michigan than round goby (Madenjian et al, 2010). In 2010, however this trend had reversed. Round goby comprised the highest biomass (8.55 kt) though had the highest variability, followed by bloater (*Coregonus hoyi*, 7.79) and alewife (6.41) (Bunnell et al. 2011). This data could vary by location as well as by year/season, and may indicate why round goby was so abundant in the Double-crested Cormorant nestling diet in 2010 while alewife had declined.

According to a telemetry study concurrently conducted with this study in 2010, Double-crested Cormorants were shown to be foraging closer to the shoreline (i.e. shallower depths) than earlier in the decade (Tucker, 2011). This change in foraging location could correspond to the increase in the benthic round goby in the diet. Because the 2010 diet of the nestling Double-crested Cormorants contained fewer energy-dense alewives and a high proportion of moderately energy-dense round goby, chicks of any given mass needed to consume more grams of fish in 2010 to attain a similar increase in mass as in 2000 according to the model. Similarly, model data suggest that if chick abundance and growth were equal between 2000 and 2010, there would be an increase in overall prey consumption by over 20% based solely on 2010 dietary changes.

This is likely attributed to an increase in a relatively energy poor dietary item (round goby) and a decrease in an energy dense prey item (alewife).

The current prevalence, ideal prey size and continued spread of round goby increases the probability that it will become prey to forage fish consumers such as Double-crested Cormorants. As round goby population densities increase in the archipelago, it is likely its dietary proportion will also increase. This may lead to an increase in overall fish consumption as adult cormorants will have to feed their chicks more food in order to reach similar historical weights. Alternatively, if the adults cannot catch enough fish to sustain historical growth of their offspring, it is likely that overall chick development time will increase or reproductive success will decrease as it will become harder for the parents to successfully care for more chicks. Additionally, the adult Double-crested Cormorants may need to consume more food to simply produce the same amount of eggs as with an energetically dense diet. It is unlikely that Double-crested Cormorants will seek out other forage fish species to supplement the chick diet as cormorants are opportunistic hunters (Lewis, 1929; Hatch and Weseloh, 1999). They simply feed on what is available. Since round goby had the highest dietary proportion, it is likely that this was the most abundant fish in the Beaver Archipelago Double-crested Cormorants' foraging locations in 2010.

Double-crested Cormorants search for available prey and attempt to spend as little time as possible consuming the most energetically favorable prey items (Emlen, 1966). One of the facets of optimal foraging theory states that predator foraging behavior has evolved over the species existence into this particular method of expending as little time and energy possible searching for beneficial prey items in order to survive and produce offspring (Pyke at el. 1977). Prior to the invasion of the round goby, this foraging strategy was very beneficial, as alewife, the

primary dietary item at the time, was energetically dense and provided enough energy to produce many offspring (Seefelt and Gillingham, 2008). Round goby is relatively energetically poor. They also tend to live in shallow rocky substrates near shorelines (Jude et al. 1995). A concurrent study conducted in the Beaver Archipelago investigated foraging locations of Double-crested Cormorants to determine if these locations had changed since the invasion of the round goby. This study suggests that Double-crested Cormorants are foraging significantly closer to shorelines than prior to round goby invasion (Tucker, 2011). This would tend to favor the Double-crested Cormorants foraging strategy as it takes little time and it costs very little energy to simply travel right off the edge of the colony, eat as many fish as possible and quickly return to the nest. However, this could be detrimental, as round goby are so energy poor. This low energy intake could lower the fitness of the Double-crested Cormorant and eventually drive the evolution of alternate foraging strategies. This type of change, according to optimal foraging theory, is developed over many generations though natural selection (MacArthur and Pianka, 1966). Since the invasion of round goby there has simply not been enough evolutionary time to compensate for this dietary change. As round goby persists in the Double-crested Cormorant diet, the ability to produce many offspring may decrease and the population may decline. Other confounding factors (control, stochastic events) may then possibly lead to an extirpation event on these colonies.

Under natural conditions, at least half of the Double-crested Cormorant eggs in a clutch typically hatch, and up to 95% of young per clutch will survive to fledging (Hatch and Weseloh, 1999). The reproductive success of Hat and Whiskey Islands, combined, without control efforts was estimated to be 3,940 (52% of those estimated to hatch) chicks raised to fledging or near maximum body mass by 21 July 2010. Despite control, an estimated 247 (32% of hatch) chicks

would have reached fledging or near adult body mass by 21 July 2010. Chicks generally fledge at 50 days old and reach 90% of their adult mass by 33 days old (Hatch and Weseloh, 1999). In 2000, 76% of chicks estimated to hatch were estimated to have fledged. This 25% decrease in reproductive success could be attributed to the energetically poor diet exhibited in 2010 or potentially to increased predation. By 21 July 2010 all the chicks on Hat Island had likely fledged and most of the chicks on Whiskey would have at least reached more than 90% of their maximum body mass. Double-crested Cormorants are thought to exhibit high natal colony-site fidelity and usually do not breed until two years of age (Lewis, 1929; Hatch and Weseloh, 1999). Since the recruitment was so low in 2010 due to control, the 2012 population of breeding birds in this area is also likely to be lower.

Over the course of data collection, several Bald Eagles were observed by the authors at the study sites. On one instance, six eagles were observed on Hat Island alone. Picture data indicates that the eagles were actively preying upon the cormorant chicks on Whiskey Island (Appendix B). The author directly observed several chicks that had been torn apart within and around the focal areas (Appendix B). Eagles were also captured on camera in the focal areas on Hat Island (Appendix B). Bald Eagles are known to attack Double-crested Cormorants, especially large chicks, and their arrival tends to cause panic among the adults, which can also be captured as prey (Hatch and Weseloh, 1999). Following the extensive control efforts and eagle invasion of the island, the remaining adult cormorants abandoned Hat Island during the rest of the 2010 breeding season. Black-crowned Night Herons were captured on camera near the tree nests on Whiskey (Appendix B). Black-crowned Night Herons are known to nest near Double-crested Cormorant colonies (Weseloh, 2005), have been recorded to feed on nestlings of other waterbird species (Kushlan and Hancock, 2005) and could potentially feed on young cormorants.

They are also known to feed on carrion and could feed on chick regurgitate (Kushlan, 1978). These predatory birds are likely an additional cause of natural decline in the colonies studied here in 2010. Other causes of natural decline, such as abandonment of entire clutches, could be due to the breeding attempts of younger birds (Hatch and Weseloh, 1999). Abandonment by younger breeders has been suggested by some to be an adaptation to avoid starvation (Hatch and Weseloh, 1999).

Impacts of Control

Much of this study is theoretical due to the efforts of the US Department of Agriculture Animal and Plant Health Inspection Service Wildlife Services (USDA APHIS WS) to control Double-crested Cormorant populations. Because cormorants are fish eating birds and their population has increased over the past 20 years, concern for sport and forage fish populations (among other concerns) has led to successful control of one of the colonies in this study. Lethal management caused a major decline in cormorant populations on Hat Island which, during this study, was controlled extensively undergoing a regimen of egg oiling and shooting of both adult and newly fledged birds. Much of this control occurred just prior to data collection, limiting the scope of this study. All 4,231 nests with eggs (5,233 nests total) were treated with vegetable oil over 17 May and 18 May, 2010 (USDA/APHIS/WS, 2010). Also on 17 May, 215 adult birds were killed. Oiling was repeated on 6 June (1,864 nests) as well as the killing of another 213 adult birds. By this time, the total number of active nests had declined to 2,968. On 1 July, oiling was again repeated (1,419 nests) and was witnessed by the author. Active nest numbers had declined to 1,877 (USDA/APHIS/WS, 2010). The egg oiling successfully decreased the number of chicks from an estimated potential of 8,045 to only about 19. Though egg oiling did not occur

on Whiskey Island and killing birds did not occur during the study period, reports from the bird banding laboratory confirm that several of the focal chicks from that island were shot during continued control following this study.

The control on Hat Island delayed the cormorants from successfully renesting and producing offspring, leading to site abandonment by most birds prior to July. The remaining cormorants were finally subjected to predation by Bald Eagles leading them to abandon the colony completely by early July. Aerial surveys report that the adult cormorants did not return to Hat in 2010, but several were recorded loafing on the neighboring island of Shoe for several weeks afterward (USDA/APHIS/WS, 2010).

The results of this study are based on a model. Therefore, it may not fully reflect the actual Hat and Whiskey Island systems in 2010. Also, this study was not comprehensive. Focal areas were used to represent the entire colony. In addition, accurate egg and chick counts for the tree nests on Whiskey Island were not feasible for this study. Therefore total chick numbers may have been skewed for Whiskey Island. The results compiled may not actually reflect what occurred on these islands, though it is likely to be representative. Furthermore, this study does not take into account the prey community composition in and around the Beaver Archipelago in 2010. This may help to elucidate why the diet had shifted. Data were also not collected as frequently as would be ideal. If the data collection were more consistent and frequent, it may more accurately represent the natural system in 2010.

Conclusion

Double-crested Cormorant chicks in the Beaver Archipelago colonies on Hat and Whiskey Islands consumed more fish per chick (total and at any given chick mass) than in 2000.

Round goby, which was found to have a lower energy density than the primary 2000 dietary component, comprised the greatest proportion (by biomass and number) of the diet of cormorant chicks in 2010. This low energy density likely contributed to the increased amount of prey consumed in 2010 than in 2000.

The reproductive success (i.e. chicks raised to fledging) of the 2010 Whiskey Island and Hat Island Double-crested Cormorant colonies despite control efforts was estimated to be about 250 chicks. Since Double-crested Cormorants are believed to return to the colony at which they were hatched, it is likely that the population of breeding birds in the Beaver Archipelago may be lower in the coming years. If no control had occurred on Hat Island, it is estimated that about half of the chicks would likely have fledged. This is lower than in 2000 (about 75% estimated to fledge) and could be attributed to diet or predation.

This model suggests that Double-crested Cormorants in the Beaver Archipelago consumed over 95% round goby and alewife in 2010 and could potentially act as a natural control for these invasive fishes. Lethal control of the Double-crested Cormorant colonies, however decreases the amount of fish, overall (and subsequently the amount of exotic fish), that are being consumed. Alewife and round goby have both been implicated in the decline of several native fish species. Therefore, natural populations of fish-eating birds, at least while these exotic fish are prevalent, may help to increase the populations of native forage fish and those of commercial and sport value.

APPENDICES

Appendix A

Mean mass (g) of focal area chicks by colony during each of 11 sampling sessions of 2010 in the Beaver Archipelago.

Date	Colony	N	Mean	SD	Min	Max
13-June	Hat	8	953.1	241.3	675.0	1310.0
17-June	Hat	10	1330.0	247.4	950.0	1650.0
1-July	Hat	9	1848.9	247.6	1525.0	2175.0
20-June	Whiskey	3	40.540	0.874	39.560	41.240
25-June	Whiskey	21	84.52	39.71	30.00	175.00
1-July	Whiskey	23	315.0	145.3	90.0	575.0
7-July	Whiskey	19	780.2	293.7	190.0	1160.0
10-July	Whiskey	14	1000.4	231.4	460.0	1365.0
13-July	Whiskey	9	1249.4	259.5	900.0	1650.0
19-July	Whiskey	7	1610.0	196.3	1235.0	1785.0
21-July	Whiskey	4	1709.0	299.0	1275.0	1950.0

Appendix B

Photographs taken from trail cameras exhibiting signs of possible predation on Double-crested Cormorant nests in the Beaver Archipelago during the 2010 breeding season.

Immature Bald Eagle captured on camera on Whiskey Island. Note blood on bill and the focal area Double-crested Cormorant nest in the back ground. This picture was taken 8 June 2010 on Whiskey Island in Focal Area 1a. Focal Area 1a was abandoned, possibly due to disturbance by predators such as this eagle.

Likely the same Immature Bald Eagle as above among the Double-crested Cormorant nests 12 minutes later on Whiskey Island in Focal Area 1a.

Immature Bald Eagle within the Double-crested Cormorant colony on Whiskey Island. The adult Cormorant in this picture is actively protecting its young. This picture was taken 11 July 2010 on Whiskey Island in Focal Area 2.

Immature Bald Eagle, likely the same individual from above, pulling a Double-crested Cormorant chick from its nest (the same nest as from the previous picture) on Whiskey Island (Focal Area 2). Part of the chick's leg and also the band were recovered.

Remains of a dismembered Double-crested Cormorant chick. This picture was taken 9 July 2010 on Whiskey Island in Focal Area 2b.

Three Bald Eagles (one immature, two mature) within Focal Area 5 on Hat Island. The eagles were documented spending approximately one hour in the colony on 5 July 2010 and about 30-45 minutes in the same area on 6 July 2010.

Black-crowned Night Heron perching within the trees of the Double-crested Cormorant colony on Whiskey Island, Focal Area 1b.

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