Double-crested Cormorant (*Phalacrocorax auritus*) chick bioenergetics following round goby (*Neogobius melanostomus*) invasion and implementation of cormorant population control

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A B S T R A C T

As the fish community changed in the Beaver Archipelago (northern Lake Michigan), so has the diet of breeding Double-crested Cormorants (*Phalacrocorax auritus*). In 2000, the energetically dense alewife (*Alosa pseudoharengus*) dominated the diet, but more recently, the relatively low quality round goby (*Neogobius melanostomus*) has become the most common prey item. Additionally, cormorant control measures have been underway in the archipelago. This study investigated decreases in cormorant chick numbers and changes in chick bioenergetics in response to this change in diet, as well as the influence of control efforts, and compared these results to an earlier study. Two colonies, one actively controlled the other only controlled following completion of this study, were investigated to determine changes in colony size throughout the breeding season, document chick diet, measure chick growth, and determine chick survivorship to fledging. The bioenergetics model estimated that in 2010, chicks consumed a greater biomass of prey to reach fledging due to the change in diet, but lower biomass overall due to fewer chicks in the system. Control efforts in combination with the change in diet reduced chick numbers. Overall, the impact of cormorant chicks on available fish biomass has declined in recent years due to control efforts. However, the birds have the potential to consume a greater biomass of round goby in the absence of control. The impact of cormorants on fisheries resources is complicated by the abundance and effects of non-native species.

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Introduction

The Double-crested Cormorant (*Phalacrocorax auritus*), or DCCO, is an opportunistic diving fish predator that often feeds in shallow waters near to shore (Lewis, 1929). Between the 1970s and early 2000s, the population of DCCOs inhabiting the interior of North America, including the Great Lakes, increased dramatically (Hatch and Weseloh, 1999; Ludwig, 1984; Ludwig and Summer, 1997). High densities of birds combined with their observed fish-eating behaviors have led to their implication in declines of both commercial and recreational fisheries throughout the Great Lakes region (Lantry et al., 1999; Ludwig et al., 1989; Neuman et al., 1997). Although they can sometimes have an impact on fish populations, a number of studies have indicated that cormorants tend to have a small impact on Great Lakes fish populations and that impacts tend to be site-specific (Diana et al., 2006; Rudstam et al., 2004; Seefelt and Gillingham, 2008). Regardless, the perceived conflicts have spurred

an active cormorant population control program by the U.S. Department of Agriculture—Wildlife Services (USDA-WS) through permits issued by the U.S. Fish and Wildlife Service (USFWS) and states (Wires and Cuthbert, 2006). Control methods include shooting birds, coating the eggs in vegetable oil (to kill embryos), harassment of nesting birds off colonies, and nest destruction. Although each method is successful at reducing cormorant numbers at a particular site, birds that have been repeatedly disturbed at one colony location often move to less disturbed areas (Hatch and Weseloh, 1999). The population of cormorants across Michigan waters of the Great Lakes has declined recently, partially due to the control program and perhaps due to changes in the forage base.

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 community was composed mainly of native fish species such as the yellow perch (*Perca flavescens*) and lake trout (*Salvelinus namaycush*). However, since the introduction of non-native fish species such as the alewife (*Alosa pseudoharengus*) and the chinook salmon (*Oncorhynchus tshawytscha*), along with invasive species such as the round goby (*Neogobius melanostomus*) and sea lamprey (*Petromyzon marinus*), many populations of native fish species have declined (Bunnell et al., 2006; Hatch and Weseloh, 1999; Smith, 1970). The round goby is a small, benthic fish first documented in the Great Lakes Basin in 1990 (Hensler and Jude, 2007; Jude et al., 1992). It has been

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observed in Lake Michigan since 1993 and captured by the Michigan Department of Natural Resources (MI DNR) since 1997, yet was not seen in the Beaver Archipelago until 2006 (Clapp et al., 2001, T. Galarowicz, Central Michigan University, pers. comm.). 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). Round goby has been implicated in the decline of several fish species such as mottled sculpin (*Cottus bairdii*), logperch (*Percina caprodes*) and johnny darter (*Etheostoma nigrum*) (Balshine et al., 2005; Dubs and Corkum, 1996; French and Jude, 2001; Janssen and Jude, 2001; Lauer et al., 2004). Goby prefer rocky substrates for spawning and feeding, making the Beaver Archipelago ideal habitat (Diggins et al., 2002; Jude et al., 1995).

The DCCO is an opportunistic fish-eating (piscivorous) waterbird common in North America (Hatch and Weseloh, 1999). Over the past 20 years, the diet of DCCOs 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 and yellow perch by biomass at ~57% and ~13% respectively, though these numbers varied by location and season (Hatch and Weseloh, 1999). 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, 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.

Due to perceived impact on fish populations, the DCCO has become the subject of multiple studies investigating their predation patterns. Many studies discuss the possible impact cormorants have on fish populations and their bioenergetic role (Craven and Lev, 1987; Fielder, 2008; Glanville, 1992; Seefelt and Gillingham, 2008). In a study conducted in the Beaver Archipelago in 2000 and 2001, the biomass of prey consumed by breeding cormorants was estimated using bioenergetics models (Seefelt and Gillingham, 2008). Findings indicate that cormorant chicks consumed less fish in year 2001 compared to 2000; adults were also able to produce more offspring in 2001 compared to 2000. One possible reason for this was that a higher proportion of alewives were found in the diets of cormorants in 2001, and alewife has a higher caloric value than other fish in the diet (Seefelt and Gillingham, 2008). Studies have indicated a link between energy density of an organism's diet and its growth and body composition. Decreased body mass as well as decreases in brown adipose tissue content was indicated in gerbils fed a high fiber (low calorie) diet compared to control gerbils fed a low fiber diet (Zhao and Wang, 2009). Additionally, diet shifts from *Daphnia pulex* to a varied diet by yellow perch (*Perca flavescens*) were accompanied by a decrease in fish growth (Mills and Forney, 1981). Round goby, which has recently become abundant in the archipelago, has an intermediate caloric density compared to other forage fish of Lake Michigan (Ruetz et al., 2009), such as alewife, and therefore a larger quantity may need to be consumed to gain the same energy as a diet consisting of primarily alewife.

This study aimed to investigate reasons for declines in cormorant chick numbers using field estimates and a bioenergetics model based on allometric equations at two colonies in the Beaver Archipelago in 2010. Findings are compared to earlier research in the archipelago completed in 2000 (Seefelt and Gillingham, 2008) prior to the invasion of the round goby and cormorant control efforts. This study documents how changes in fish community structure and the recent intensity of human disturbances are manifested in cormorant nesting success and prey consumption.

Materials and methods

Study site and data collection

Data were collected at cormorant colonies on Hat Island (0.5 km^2) and Whiskey Island (1.0 km^2), part of the Beaver Archipelago of

northern Lake Michigan (Charlevoix County) from May through late July 2010 (Fig. 1). The colony on Hat Island consisted of primarily ground nesting birds; on Whiskey Island, there was a mix of ground nests and tree nests. Hat Island was controlled extensively over the breeding season by USDA-WS. Control methods included shooting adult birds and coating eggs in vegetable oil. Whiskey Island was moderately controlled following data collection and methods included shooting of adult and newly fledged chicks. To be consistent for comparisons with Seefelt and Gillingham (2008), diet data from both colonies were combined. The study sites were accessed by boat periodically throughout the breeding season.

Each entire colony was censused using ground counts early in the breeding season (Hat Island on 22 May 2010 and Whiskey on 07 June 2010) and late in the breeding season (Hat Island on 09 July 2010 and Whiskey on 21 July 2010) to determine changes in colony size. In this study, the chick population was modeled based on the number of active nests (model based on nest decline from early to late counts) as well as average number of chicks per nest in the focal areas per day of collection. Chick population in the 2000 study was modeled by taking into account the maximum number of nests (early 8316) and number of successful nests (late 5433) counted during that field season as well as mean number of chicks per nest (mean clutch sizes: early 2.60; late 1.50) (Seefelt and Gillingham, 2008). In both cases, chick population sizes varied per day. During the early season, the chicks were just hatching and confined to their nests. During the late season count, chicks were able to leave the nest freely though trail cameras and identifying bands allowed an accurate match of chicks to nests. The differences in census dates reflect the different phenology of each colony. The cormorant colony on Hat Island has been established for decades and birds begin their nesting cycle earlier than at other colonies in the area, including on Whiskey Island, which is active some years but not others (Seefelt and Gillingham, 2004). Ground nests were counted and marked using colored popsicle sticks. These sticks were counted and bagged beforehand so that any remaining sticks could be counted and subtracted from the original number to provide a total nest count. Tree nests were counted using hand tallies. Nests were considered active if they were well maintained and/or contained eggs/chicks in the early count or chicks in the late count.

Extensive efforts were taken to minimize the effects of Ring-billed (*Larus delawarensis*) and Herring Gulls (*Larus argentatus*) on Hat Island, which supports populations of both these species. During data collection, only one focal area was evaluated at a time. The others were left alone (parents would return to their nests). Also, during collection, other researchers would protect the cormorant nests by scaring away gulls that attempted to prey upon the exposed eggs/chicks. Whiskey Island had a small number of Herring Gull nests near the focal areas and the few adults were easily rebuffed by the researchers.

To better document hatching events as well as fledging success, five focal areas on Hat Island (11 chicks banded) and two on Whiskey Island (18 chicks banded) were selected and monitored continuously by Moultrie® D-40 trail cameras with four gigabyte data cards. Cameras were set with a five minute delay between photo events and flash was turned off to avoid disturbing the birds after dark (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 based on availability due to cormorant control efforts (i.e. egg oiling and shooting of adults) by the USDA-WS that happened prior to and concurrently with this study. Areas that were lacking eggs post management or did not appear to be oiled (nests that were not marked with orange paint or that contained chicks), and consisted of at least twenty nests were selected. The number of chicks sampled in the focal areas varied over the course of sampling ranging from 14 chicks in the early count to 9 chicks in the late count. The Whiskey Island sites were chosen based on visibility of the nests due to the complex vegetation structure. This colony was not subjected to control
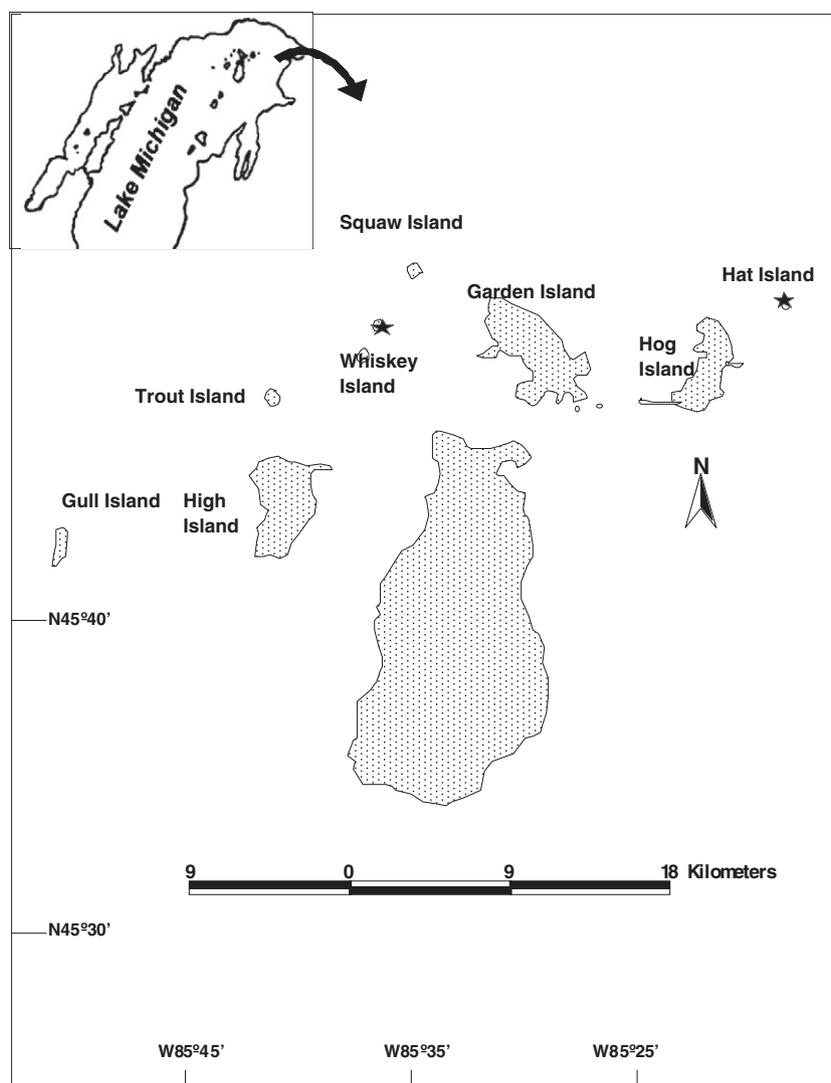
Fig. 1. The Beaver Archipelago of Northern Lake Michigan. This study was conducted on Hat and Whiskey islands, denoted by the stars.

efforts until young birds were fledging. Focal areas that had at least 10 nests located on the ground were selected. Focal area 1 on Whiskey Island was abandoned by the birds early in the season (prior to chick hatch), but focal area 2 was active the entire length of the study. The number of chicks sampled ranged from 3 chicks to 23 chicks. On both islands, each nest in the focal areas was marked with a numbered, brightly painted orange rock in order to easily keep track of the nests used. Focal area nest sites were also mapped by hand in order to keep track of individual nests and their contents, in case the rock markers were moved or soiled by birds.

Beginning with the first census data, the clutch/brood size of each focal area nest was recorded. Focal areas were visited weekly (weather permitting) to monitor changes, document chick hatching and chick mass, and to change data cards in the cameras. Focal area chicks were captured by hand and weighed (g). As chicks tend to hatch asynchronously in each nest and do not leave the nest when young, it was usually easy to identify individual chicks in each focal nest during each visit. Images taken by the cameras also aided in identifying individual chicks in each nest. When the chicks attained appropriate size (approximately 900 g), they were banded with standard metal bands and blue plastic colored bands with individualized white alpha-numeric codes (N.E. Seefelt, permit #23467). These plastic bands allowed chicks to be identified at a distance and in photos (to aid in estimating survivorship). These birds were subsequently weighed

on additional visits until close to fledging. Many chicks that were initially measured died before banding size (sibling competition, predation, exposure, etc.). A total of 29 focal area chicks were banded with measurements taken. All were documented and their ecology followed though several died (bands discovered) or disappeared from camera records and their bands not found (assumed fledged). For those that died, their data were collected until the collection day before they expired. If pain or stress was suspected in any of the individual animals, that individual was exempted from measurements and sample collection.

Regurgitated food samples were collected directly from focal area chicks using a gloved hand and placed in individual plastic Whirlpak® bags. Each bag was labeled with the colony name, focal nest number, chick identity and date. Chicks regurgitated as the investigators approached the nests. The regurgitate was therefore found in the immediate vicinity of the offending chick. Chicks did not typically regurgitate fully digested samples as one might see in stomach content analyses. In this study area, Seefelt and Gillingham (2006) documented percent biomass of prey species determined from regurgitates equaled that determined from stomach samples. Regurgitate samples contained mostly whole fish (some fish had partially digested tails or heads). Adult regurgitate was recognizably larger and found away from the nests. As the model is based on average caloric density (ACD) of the chick diet determined through allometric equations, it was not necessary to determine individual bolus mass per chick mass. Samples were collected about

once a week (weather permitting) so that chicks were continually supplied ample food items despite the removal of one sample.

The regurgitate samples were stored frozen until analysis. Samples were thawed and separated by hand. Each prey item was identified to species when possible. In addition, all identified prey items, including partially digested prey missing tail fins, were individually weighed. Complete fish were measured to the nearest 0.5 mm. These measurement methods were consistent with Seefelt and Gillingham (2008) for regurgitated food items.

Model construction

The bioenergetic model used follows a procedure outlined by Madenjian and Gabrey (1995) and modified to include individual prey species by Hebert and Morrison (2003) and chick prey consumption (Seefelt and Gillingham, 2008). As in the Seefelt and Gillingham (2008) model, in this study the models were developed using a spreadsheet (Microsoft Office Excel®). The model uses allometric equations dependent on body mass to determine model input parameters such as daily energy expenditure (DEE) and average caloric density (ACD) of chick diet using prey energy density values (Tables 1 and 2) for cormorant chicks as they grow from hatching to fledging. By dividing DEE by ACD, daily food consumption (DFC) can be determined for each chick; these values can be summed and extrapolated to the entire colony to determine total prey consumption by chicks over the entire breeding season. These equations have successfully been used in the past (Birt-Friesen et al., 1989; Hebert and Morrison, 2003; Madenjian and Gabrey, 1995; Seefelt and Gillingham, 2008). Details of the equations used can be found in Appendix 1 of Madenjian and Gabrey (1995), and also detailed in Seefelt (2005) and Van Guilder (2011). As with previous models, hatch date was modeled synchronously to simplify calculations. Major departures in this model from Seefelt and Gillingham (2008) are that nest success rate was modeled based on two estimates (as opposed to three), focal area nest chick mass was measured in the field throughout the study to incorporate this value into the model (as opposed to literature values) and round goby energy density was calculated specifically for the study area (see below). In addition, the model differs from Seefelt and Gillingham (2008) in that only the pre-fledging time period is examined. As with earlier models, the major parameters of this model include nest counts, chick mortality rates, prey type, and prey consumption.

To determine the nest success rate for the colony, 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). Eq. (1) was used to determine the amount of decay per day:

$$M_f = M_i e^{rt} \tag{1}$$

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

Prey type	Energy density (kcal/g)
Alewife[a]	1.947
Round goby[b]	1.059
Brook stickleback[a]	1.493
Crayfish[a]	1.077
White sucker[c]	0.884

[a] Cummins and Wuycheck (1971).
[b] Calculated value.
[c] Bryan et al. (1996).

Table 2
Life history characteristic input parameters used to model prey consumption by Double-crested Cormorant chicks in the Beaver Archipelago in (a) 2010 and (b) 2000 (see text for details regarding timing of early and late nest counts).

a.

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)
Focal area chick mortality rate	$y = 332e^{-0.037x}$	$y = 3721e^{-0.014x}$
Study duration (days)	32 (20 Jun–21 July)	33 (29 May–30 Jun)
Chick growth rate	$y = 41.69 + (2331.83)/(1 + (x/28.50)^{-297})$	$y = 951.00 + 62.07x + 0.75x^2$
Mean mass at hatch	40.54	34.00[a]
DEE (kcal)	$DEEN = 1.230\ W^{0.7749}$	$DEEN = 1.230\ W^{0.7749}$
Assimilation efficiency (%)	80[b]	80
Average caloric density (cal)	1330.70	1225.47

b.

Characteristic	2000[c]
Number of nests (seasonal high)	8316
Clutch size—early season	2.6
Clutch Size—mid season	1.5
Number of incubation days	28
Hatch rate (% of eggs laid)	62
Fledge (days)	50
Hatch-year mortality (% year)	42
Mass at hatch (g)	34
Growth increment (g/day)	40

All other inputs were measured in the field or calculated by the authors.
[a] Hatch and Weseloh (1999).
[b] Furness (1978).
[c] Seefelt and Gillingham (2008).

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 (Carson, 2001). 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 of days since the early nest count. This value was then used in Eq. (1) as the new t to determine the number of active nests each day (new M_f). This procedure was repeated for each entire colony and also for the total tree nests and total ground nests on Whiskey Island as tree nests persisted more so on this 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 for comparison to observed values. 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 on any given day.

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 and were plotted in Sigmaplot Software producing a curve that best fit the data collected. The equation for this curve was determined, resulting in an estimated mean chick mass per day. Measured and calculated chick masses from both colonies were calculated separately and then combined to produce individual modeled growth curves and to determine change in chick mass per day. These curves were then compared to the curve used in Seefelt and Gillingham (2008).

To determine the specific energy density of round goby in the study area, the wet weight for each round goby found in the regurgitate

samples was entered into Eq. (2) to determine individual energy density in joules:

$$\log_{10}(ED) = 3.57 + 0.10^* \log_{10}(WW) \qquad (2)$$

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

Data collected for this study were compared to data from 2000 (Seefelt and Gillingham, 2008) to determine any differences in chick DEE, ACD, DFC and biomass/prey types consumed by chicks between the study periods. The dietary proportion per regurgitate sample for each major prey species was compared between 2000 and 2010 by a Mann–Whitney U-test.

An individual parameter perturbation method was used to conduct sensitivity analysis for the model (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 DCCO chicks. 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.

Results

Diet analysis

The regurgitate samples (n = 61) contained 236 individual whole fish. The diet of cormorant chicks included five species: round goby, alewife, brook stickleback (*Culaea inconstans*), white sucker (*Catostomous commensonii*) and crayfish (*Orconectes* spp.). By biomass at both locations, round goby (67%) constituted the majority of the chick diet and alewife (29%) was the second most abundant prey. Brook stickleback was found in the diet only on Hat Island (<0.1%). White sucker and crayfish were only found in the diet on Whiskey Island, 4% and <0.1%, respectively (Table 3). The regurgitate samples contained 180 round goby. The mean energy density of round goby in the Beaver Archipelago was calculated as 4430.6 J/g (SD: 511.5 J/g; range: 3178.5 J/g–5656.8 J/g) or 1.059 kcal/g (Table 1).

Bioenergetics model

A total of 3721 active nests were counted on Hat Island during the early nest count, however only ten were still active during the second nest count due to control efforts. On Whiskey Island, a total of 332 nests (184 on the ground and 148 in the trees) were counted (737 chicks modeled) during the early nest count. During the late nest count, the colony had declined to 107 nests (95 in trees and 12 on the ground) or a modeled 221 chicks (Fig. 2a). A model estimate of chicks per nest for the late colony count on Hat Island was <0.01 chicks/nest, while on Whiskey Island this was 2.07 chicks/nest. Chick numbers on Hat Island declined in the focal areas from 22 birds to 9 birds (Fig. 2b).

Based on population calculations and field data, an estimated 238 (32% of the estimated maximum number of chicks hatched) chicks survived to fledging on Whiskey Island. By the end of sampling, an estimated total of 19 (41% of maximum number of chicks hatched) chicks survived to fledging on Hat Island despite control efforts. Assuming no control had taken place, an estimated 3702 (51% of maximum) chicks could have survived to fledging on Hat Island.

Table 3
The proportions of prey species by biomass found in the Double-crested Cormorant diet in 2000 and 2010.

Species	Proportion			
	2000[a]	2010		
		Whiskey	Hat	Total
Alewife (*Alosa pseudoharengus*)	0.54	0.32	0.19	0.29
Round goby (*Neogobius melanostomus*)	0.00	0.66	0.81	0.67
Brook stickleback (*Culaea inconstans*)	0.01	0.00	<0.01	< 0.01
Crayfish (*Orconectes* spp.)	0.24	<0.01	0.00	<0.01
White sucker (*Catostomus commersonii*)	0.11	0.05	0.00	0.04
Sculpin (*Cottus* spp.)	0.06	0.00	0.00	0.00
Other[b]	0.04	0.00	0.00	0.00
Total	1.00	1.00	1.00	1.00

[a] Seefelt and Gillingham (2008).
[b] *Pungitius pungitius*, *Etheostoma nigrum*, *Percopsis osmiscomaycus*.

The chick masses measured in the field from Hat and Whiskey islands combined produced a sigmoidal shaped growth curve (Fig. 3). The growth curve used in 2000 was linear. The minimum mass measured was 30.00 g (Whiskey Island) and the maximum mass measured by the focal area chicks was 2175.00 g (Hat Island). 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. Over week one the chicks exhibited relatively slow growth at 34.64 g/day. Over weeks 2–3.5 chicks exhibited increased growth at 64.26 g/day. Growth slowed again relative to body size during the final week prior to asymptote to 41.95 g/day.

The modeled daily food consumption in 2010 ranged from 18.06 g per day to 387.79 g per day with a total amount of food consumed per chick until fledging of 7.32 kg, which is higher than in 2000 (5.11 kg). At any given mass, the model indicates that chicks were consuming more food in 2010 than in 2000 (Fig. 4). This difference in food consumption ranged from 2.36 g to 93.60 g more in 2010 than in 2000 at 40.00 g and 1849.00 g chick mass, respectively. In 2000 chicks consumed between 18.00 g of food at 40.00 g mass and 333.00 g of food
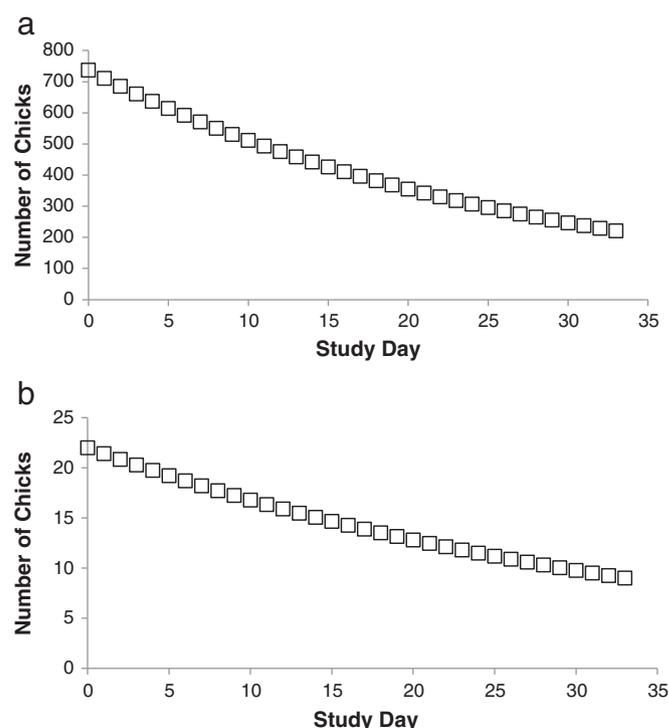

Fig. 2. Modeled number of Double-crested Cormorant chicks per study day based on nest decline on a) Whiskey Island; b) Hat Island.
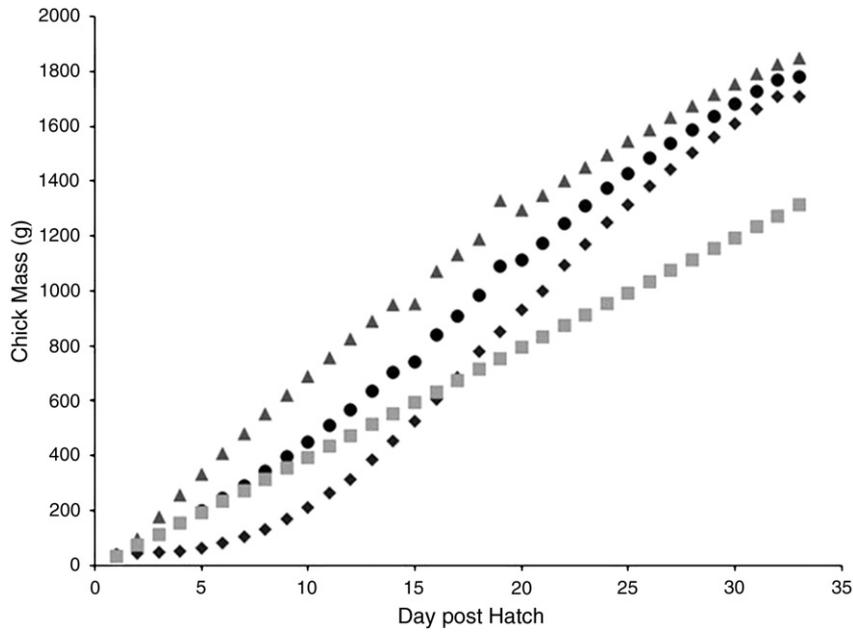
Fig. 3. Mean modeled mass of Double-crested Cormorant chicks per sampling day during the 2010 field season on Hat Island (triangles), Whiskey Island (diamonds), averaged between Hat and Whiskey Islands (circles), and for the 2000 Beaver Archipelago population (squares; Seefelt and Gillingham, 2008).

at 1849.00 g mass, whereas in 2010 chicks consumed 20.36 g of food at 40.00 g mass and 426.62 g of food at 1849.00 g mass based on model outputs.

Based on the model and incorporating the results from the control measures on Hat Island, the DCCO chicks consumed a total of 2289.36 kg of prey (Hat: 129.13 kg, Whiskey: 2160.23 kg) in 2010. On both Hat Island and Whiskey Island in 2010, most of the fish consumed were round goby (1688.8 kg), followed by alewife (444.5 kg; Table 4). In 2000 when there were no cormorant control measures, DCCO chicks consumed 114,367.25 kg of prey. Assuming no control on Hat Island in 2010, the chicks had the potential to consume 27,349.52 kg of prey over the sampling period with 25,189.29 kg on Hat Island alone, including 23,927.84 kg of round goby.

The results of sensitivity analysis suggest that the 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 5). 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. These results are consistent with earlier models (Birt-Friesen et al., 1989; Hebert and Morrison, 2003; Madenjian and Gabrey, 1995; Seefelt and Gillingham, 2008).

Discussion

Due to active control measures on Hat Island, the number of cormorant nests in the Beaver Archipelago declined dramatically during the 2010 breeding season. Cormorant chick numbers in the study area were low and few chicks survived to fledging compared to pre-control seasons. The cormorant population used in the 2000 model was much
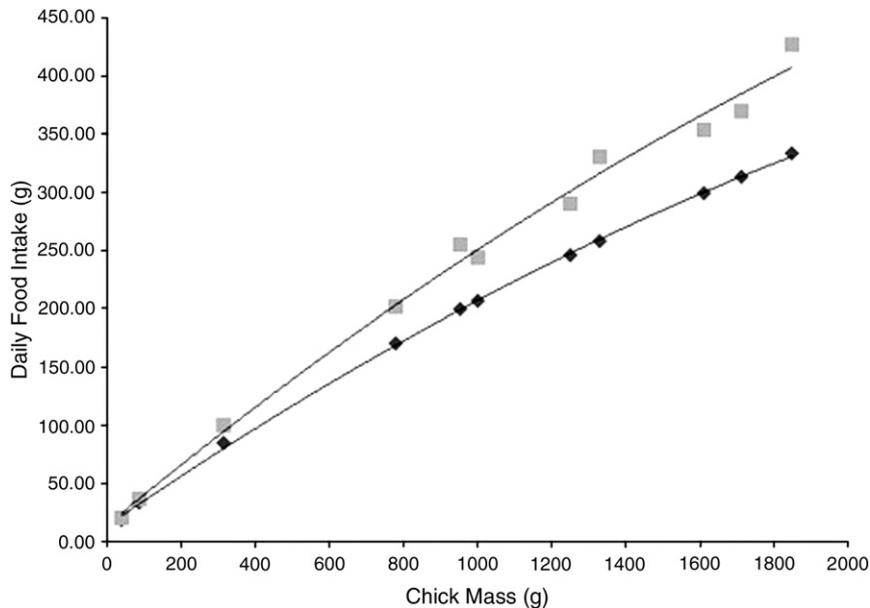

Fig. 4. Daily modeled food consumption in grams for nestling Double-crested Cormorants at a given mean mass (n = 11) in the Beaver Archipelago in 2000 (diamonds) and 2010 (squares).

Table 4
Biomass (kg) of fish species consumed on Whiskey and Hat islands separately, combined and compared to data from 2000.

With no control				
	Whiskey	Hat	Total	2000[a]
Alewife	428.69	2796.40	3225.08	48,879.70
Round goby	1568.64	22,359.20	23,927.84	0
Brook stickleback	0.00	33.69	33.69	679.74
Crayfish	10.48	0.00	10.48	38,309.24
White sucker	152.43	0.00	152.43	21,377.01
Other	0	0	0	5121.57
Total	2160.24	25,189.29	27,349.52	114,367.25

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
Total	2160.24	129.13	2289.36

[a] Seefelt and Gillingham (2008).

larger than the cormorant population in 2010 (over 16,600 vs. ~9600). Additionally, the 2000 model of population size included a post-fledging period which was not included in 2010. The 2000 model assumes a linear mass increase of 40 g/day, which extends the sampling period to 49 days. This study takes into account actual mass data from hatching to near fledging mass, which takes about 30–33 days only (Hatch and Weseloh, 1999). Adjusting for a similar date range of sampling produces a much different prey consumption value (~60,000 kg of prey) though chick masses on these dates are not consistent between years. In addition, because the diet was composed primarily of round goby, a relatively poor (low caloric density) prey item, chicks consumed more food between hatching and fledging compared to 2000 when alewife (high energy density) made up the majority of the diet. Furthermore, at any given mass, cormorant chicks in 2010 needed to consume substantially more food per day compared to chicks in 2000. In general, because there were few chicks produced in the archipelago, there was substantially less prey biomass consumed by cormorant chicks in 2010 compared to 2000. However, in the absence of control, there is potential that cormorant chicks could consume a large number of round goby in the Beaver Archipelago. Additionally, increased food consumption by chicks in 2010 may have led to increased competition among siblings, resulting in lower chick numbers. This may have been exacerbated by the fact that chicks tended to hatch asynchronously giving older chicks a competitive size advantage. Prey, on the whole, was likely not a limiting factor in the Beaver Archipelago in 2010. Though Ashmole's halo (Birt et al., 1987) was not measured, round goby density, the primary food source during 2010 did not appear to decrease. Individual fish were observed throughout the season around colony sites. Moreover, Tucker (2011) indicates that cormorants in the Beaver Archipelago in 2010 were foraging in locations away from the

Table 5
Sensitivity analysis results for change in input parameters on daily energy intake of Double-crested Cormorant chicks as determined by bioenergetics models.

Model output	Input perturbation error	
	+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 (chicks/day)	0.00	0.00
Study duration (days)	+12.69	−13.41
Chick growth rate (g/day)	+8.39	−7.22
Mass at hatch (g)	+0.06	−0.06
Assimilation efficiency (%)	−9.10	+11.11
Energy density of prey (kcal/g)	−9.10	+11.11

colonies, further reducing the competition in areas near the colonies. The low number of chicks and adult birds supported by the archipelago in 2010 as well as the high round goby densities in Lake Michigan that year (8.55 kt) suggest that competition for goby likely did not have an impact on adult or chick survival.

The dramatic nest decline in the Beaver Archipelago in 2010 was mostly due to control of DCCO population on Hat Island. Cormorant management began prior to data collection, limiting parts of this study. On 17 and 18 May 2010, all nests with eggs (4231 nests) were oiled and 215 adult birds were killed on Hat Island (USDA-WS, 2010). Oiling was repeated on 6 June (1864 nests) and an additional 213 adult birds were killed. On 1 July, oiling was again repeated (1419 nests) (USDA-WS, 2010). Control efforts successfully decreased the number of chicks on Hat Island from an estimated potential of 8045 to only about 19 and caused colony abandonment by 05 July 2010 (Tucker, 2011; Van Guilder, 2011). On Whiskey Island, the abandonment of ground nests was likely influenced by the presence of avian predators, including eagles and possibly owls (Van Guilder, 2011). An additional cause of natural decline could be the failed breeding attempts of younger birds (Hatch and Weseloh, 1999).

Chick/egg mortality due to gull predation was not measured in this study. Both Ring-billed and Herring Gulls are known chick and egg predators of DCCOs. However the efforts taken to minimize the effects of these birds were very successful. Additionally, the control efforts on Hat Island were effective enough to supply an adequate amount of nonviable egg prey to the gulls without encouraging them to steal from the adult cormorants and risk injury. On Whiskey Island, in addition to the efforts listed above, the cormorants tended to build their nests in vegetation which naturally discouraged gull predation. Because of the efforts taken, gull predation likely did not have an impact on the results of this study. Other predators, such as bald eagles (*Haliaeetus leucocephalus*), were observed preying on cormorants in the focal areas during 2010. This may have had an impact on population size. However, it is more likely to have lead to desertion of the colony which was already declining due to management actions. As cormorants breed in groups, at least in part for protection from predators, predation by eagles would likely have scattered the few breeding pairs remaining after implementation of control.

Between 2000 and 2010, the diet of cormorant chicks in the study area changed from a high energy diet of primarily alewife to a low energy diet of primarily round goby. This change is reflected by the changes in DFCN (Nestling Daily Food Consumption) and total food consumption estimated by the bioenergetics models for each year. Weseloh and Ewins (1994) suggest that alewife consumption may be linked to DCCO reproductive success, and this is supported in the Beaver Archipelago by model outputs and cormorant nesting success in 2000 and 2001 (Seefelt and Gillingham, 2008). The high energy density of alewife combined with their tendency to school (Schultz, 2004) may make them easier to catch and energetically worth the effort. Alewife, as a key species in Lake Michigan, appear to be a driving force in fish community dynamics (Eck and Brown, 1987; Madenjian et al., 2004) and was abundant in the system in 2000 (Madenjian et al., 2004). Alewife abundance (adult: ~300/ha; YOY: ~750/ha) spiked in 2000. Lake-wide biomass for Lake Michigan was estimated at ~25 kt in 2000. Also, there was an abundance of attractively sized alewife as prey in the early part of the decade, presumably because of large hatch numbers in 1997–1998 and favorable conditions for alewife survival (Madenjian et al., 2004). By 2010, alewife abundance had declined and lake-wide biomass for Lake Michigan was estimated at 6.41 kt (Bunnell et al., 2009; Madenjian et al., 2005). More recently, Lake Michigan-wide bottom trawl data indicated in 2010, round goby comprised the highest biomass (8.55 kt), followed by bloater (*Coregonus hoyi*, 7.79 kt) and alewife (6.4 kt) (Bunnell et al., 2011). Fish abundance may vary by location as well as by year/season, but diet data suggest that round goby was abundant in the archipelago in 2010 and that alewife had declined. Cormorants, being opportunistic

predators, have reflected this change in prey species abundance in their diets.

Overall, the model produced results consistent and comparable with earlier works (Birt-Friesen et al., 1989; Hebert and Morrison, 2003; Madenjian and Gabrey, 1995; Seefelt and Gillingham, 2008). One departure from earlier models was that chicks exhibited a sigmoidal growth rate pattern in 2010; in earlier works, growth was assumed linear (Seefelt and Gillingham, 2008). This linear growth is based on a standard growth increment/day though this may not be representative of actual growth curves. Other studies, based specifically on cormorant chick growth, indicate that cormorant chicks exhibit a sigmoidal growth curve which was incorporated into this study (Dunn, 1975, 1976; Léger and McNeil, 1987). For this work, chick masses were measured directly in the field to produce the grow rate and results are similar to those reported by Dunn (1975, 1976) and Léger and McNeil (1987). The slow growth during the early stages of development modeled in this study may be due to an energy poor food source (round goby), the allocation of energy to thermoregulation, or potentially due to nest density and competition for prey, particularly on Whiskey Island. Since Hat Island produced few chicks, those that were produced likely did not have to compete for resources and were able to grow more quickly than in 2000. Whiskey Island nests were much more densely clustered. This may have led to competition for prey near the Whiskey Island colony and potentially fewer chicks raised to fledging though Tucker (2011) indicates that cormorants were foraging away from the colonies in 2010, again suggesting that competition was likely not the cause for decreased population size. The slow growth near fledging may be due to the allocation of energy for the production of flight feathers and increased mobility. It is unclear as to whether the differences found in this study are indicative of a dietary change or if growth rates can vary in this species for other reasons, including abiotic factors.

A dietary shift from alewife to round goby by cormorants in the Beaver Archipelago may have several implications. Round goby population densities can become large fairly quickly (MacInnis and Corkum, 2000) and its current prevalence in the Great Lakes makes it a potentially important forage fish for predators such as cormorants. Female gobies can spawn up to five times per season and the males guard the nests leading to an increased hatch rate of the eggs (MacInnis and Corkum, 2000). As round goby populations continue to increase and spread, cormorants and other piscivorous waterbirds may help contribute to the natural control of these invasive fish populations. Furthermore, as round goby, a relatively poor food source, becomes increasingly important in the diet, it will require that overall fish consumption by cormorants increases because chicks will need more food in order to reach similar historical weights. Alternatively, if the adults do not catch enough fish to sustain historical growth rates of their offspring, it is likely that overall chick development time will increase or reproductive success will decrease. It is unlikely that adults will seek out other forage fish species to supplement the chick diet as cormorants are opportunistic hunters (Hatch and Weseloh, 1999; Lewis, 1929). They simply feed on what is available. Additionally, the female breeders may need to consume more food to produce typical clutch sizes. In essence, a diet rich in round goby may help to "naturally" control DCCO populations by reducing the number of chicks that can be successfully fledged per pair (Seefelt and Gillingham, 2008).

Conclusions

Bioenergetic models are valuable tools in estimating the potential impacts that waterbirds have on fishery resources. They also allow for temporal comparisons as fish communities change and management tools are used. This study provides insight on how these factors may influence the reproductive success of cormorants in the Beaver Archipelago. The round goby, being less energy dense, in combination with

control efforts, contributed to lower survivorship of chicks at fledging. Because DCCOs are highly visible opportunistic fish eaters, they have been implicated in the decline of fish populations of sport and commercial value. This has led to conflicts with fishermen in a region that supports an economically important fishery as well as pressure to control the growing DCCO population. However, a large DCCO population could help remove large quantities of round goby (fish egg predators) in a given region if gobies are most abundant. Competition for round goby could also increase the energy demands of adult DCCOs potentially leading to lower survivorship of offspring if the parents cannot meet the energy demands of the chicks. Round goby energy density along with potential piscivorous competitors such as fish (i.e. burbot (*Lota lota*), walleye (*Sander vitreus*), smallmouth bass (*Micropterus dolomieu*), and northern pike (*Esox lucius*; Madenjian et al., 2011; Reyjol et al., 2010; Weber et al., 2011)) and other waterbirds (i.e. Red-breasted Merganser (*Mergus serrator*) Bur et al., 2008) could allow for less invasive control of DCCO populations. This natural control could reduce the inadvertent negative impacts of cormorant management on co-nesting threatened or endangered species of the area (i.e. Common terns (*Sterna hirundo*), Caspian terns (*Hydroprogne caspia*) and Black-crowned Night-herons (*Nycticorax nycticorax*)). Although all models have limitations, it is likely that this work is representative of the 2010 field season and comparable to previous investigations. The impacts of the round goby as well as management on cormorants are apparent. Because an adaptive approach is imperative for sound management of natural resources, studies like this should help to inform such decisions. Cormorants are an important component of the Great Lakes ecosystem and their role is complicated by the current abundance of non-native forage species.

References

Balshine, S., Verma, A., Chant, V., Theysmeyer, T., 2005. Competitive interactions between round gobies and logperch. J. Great Lakes Res. 31, 68–77.
Birt, V.L., Birt, T.P., Goulet, D., Cairnse, D.K., Montevecchi, W.A., 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Mar. Ecol. 40, 205–208.

Birt-Friesen, V.L., Montevecchi, W.A., Cairns, D.K., Macko, S.A., 1989. Activity-specific metabolic rates of free-living northern gannets and other seabirds. Ecology 70 (2), 357–367.

Bryan, S.D., Soupir, C.A., Duffy, W.G., Freiburger, C.E., 1996. Caloric densities of three predatory fishes and their prey in Lake Oahe South Dakota. J. Freshwater Ecol. 11, 153–161.

Bunnell, D.B., Madenjian, C.P., Claramunt, R.M., 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (Alosa pseudoharengus). Can. J. Fish. Aquat. Sci. 63 (11), 2434–2446.

Bunnell, J.D., Madenjian, C.P., Holuszko, T.J., Desorcie, D.B., Adams, J.V., 2009. Status and trends of prey fish populations in Lake Michigan, 2008. A Report to the Great Lakes Fishery Commission. Lake Michigan Committee, Ypsilanti, MI (March 26, 2009).

Bunnell, D.B., Madenjian, C.P., Holuszko, J.D., Desorcie, T.J., Adams, J.V., 2011. Status and trends of prey fish populations in Lake Michigan, 2010. A Report to the Great Lakes Fishery Commission. Lake Michigan Committee, Ypsilanti, MI (March 22, 2011).

Bur, M.T., Stapanian, M.A., Bernhardt, G., Turner, M.W., 2008. Fall diets of red-breasted Merganser (Mergus serrator) and walleye (Sander vitreus) in Sandusky Bay and adjacent waters of Western Lake Erie. Am. Midl. Nat. 159 (1), 147–161.

Carson, Simon, 2001. The exponential function. Phys. Rev. 10 (4), 13.

Chotkowski, M.A., Marsden, J.E., 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. J. Great Lakes Res. 25, 26–35.

Clapp, D.F., Schneeberger, P.J., Jude, D.J., Madison, G., Pistis, C., 2001. Monitoring round goby (Neogobius melanostomus) population expansion in eastern and northern Lake Michigan. J. Great Lakes Res. 27, 335–341.

Craven, S.R., Lev, E., 1987. Double-crested Cormorants in the Apostle Islands, Wisconsin, USA: population trends, food habits, and fishery depredations. Colon. Waterbird. 10 (1), 64–71.

Cummins, K.W., Wuycheck, J.C., 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Theor. Angew. Limno. 18, 1–51.

Diana, J.S., Maruca, S., Low, B., 2006. Do increasing cormorant populations threaten sportfishes in the great lakes? A case study in Lake Huron. J. Great Lakes Res. 32 (2), 306–320.

Diggins, T.P., Kaur, J., Chakraborti, R.K., DePinto, J.V., 2002. Diet choice by the exotic round goby (Neogobius melanostomus) as influenced by prey motility and environmental complexity. J. Great Lakes Res. 28 (3), 411–420.

Dubs, D.O.L., Corkum, L.D., 1996. Behavioral interactions between round gobies (Neogobius melanostomus) and mottled sculpin (Cottus baridi). J. Great Lakes Res. 22, 838–844.

Dunn, E.H., 1975. Growth, body components and energy content of nestling Double-crested Cormorants. Condor 77 (4), 431–438.

Dunn, E.H., 1976. Development of endothermy and existence energy expenditure of nestling Double-crested Cormorants. Condor 78 (3), 350–356.

Eck, G.W., Brown, E.H., 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of the alewife (Alosa pseudoharengus). Can. J. Fish. Aquat. Sci. 44, 53–60.

Fielder, D.G., 2008. Examination of factors contributing to the decline of the yellow perch population and fishery in Les Cheneaux Islands, Lake Huron, with emphasis on the role of Double-crested Cormorants. J. Great Lakes Res. 35, 506–523.

French III, J.R.P., Jude, D.J., 2001. Diets and diet overlap of nonindigenous gobies and small benthic fishes co-inhabiting the St. Clair River, Michigan. J. Great Lakes Res 27, 300–311.

Furness, R.W., 1978. Energy requirements of seabird communities: a bioenergetics model. J. Anim. Ecol. 47, 39–53.

Glanville, E.V., 1992. Cooperative fishing by Double-crested Cormorants Phalacrocorax auritus. Can. Field Nat. 106 (4), 522–523.

Hatch, J.J., Weseloh, D.V., 1999. Double-crested Cormorant. The birds of North America. In: Poole, Gill (Eds.), Life Histories for the 21st Century: Cornell Lab. Ornithol. Acad. Nat. Sci., 441.

Hebert, C.E., Morrison, H.A., 2003. Consumption of fish and other prey items by Lake Erie waterbirds. J. Great Lakes Res 29, 213–227.

Hensler, S.R., Jude, D.J., 2007. Diel vertical migration of round goby larvae in the Great Lakes. J. Great Lakes Res. 33 (2), 295–302.

Janssen, J., Jude, D.J., 2001. Recruitment failure of mottled sculpin Cottus bairdi in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby Neogobius melanostomus. J. Great Lakes Res. 27, 319–328.

Johnson, J.H., McCullough, R.D., 2007. Diet composition and fish consumption of Double-crested Cormorants from the Pigeon and Snake Island Colonies of Eastern Lake Ontario in 2007. NYSDEC Special Report.

Jude, D.G., Reider, R.H., Smith, G.R., 1992. Establishment of Gobiidae in the Great Lakes basin. Can. J. Fish. Aquat. Sci. 49, 416–421.

Jude, D.J., Janssen, J., Crawford, G., 1995. Ecology, Distribution, and Impact of the Newly Introduced Round and Tubenose Gobies on the Biota of the St. Clair and Detroit Rivers in the Lake Huron Ecosystem: Ecology, Fisheries and Management (Ecovis. World Mg. Ser). In: Munawar, M., Edsall, T., Leach, J. (Eds.), SPB Academic Publishing, Amsterdam, Netherlands, pp. 447–460.

Lantry, B.F., Eckert, T.H., Schneider, C.P., 1999. The relationship between the abundance of smallmouth bass and Double-crested Cormorants in the Eastern Basin of Lake Ontario. Final Report: To Assess the Impact of Double-crested Cormorants Predation on the Smallmouth Bass and Other Fishers of the Eastern Basin of Lake Ontario. NYSDEC Special Report, February, 1999, pp. 1–10 (Section 12).

Lauer, T.E., Allen, P.J., McComish, T.S., 2004. Changes in mottled sculpin and johnny darter trawl catches after the appearance of round gobies in the Indiana waters of Lake Michigan. T. Am. Fish. Soc. 133, 185–189.

Léger, C., McNeil, R., 1987. Brood size and chick position as factors influencing feeding frequency, growth, and survival of nestling Double-crested Cormorants Phalacrocorax auritus. Can. Field Nat. 101 (3), 351–361.

Lewis, H.F., 1929. The Natural History of the Double Crested Cormorant (Phalacrocorax auritus auritus (Lesson)). Ru-Mi-Lou Books, Ottawa, Canada.

Ludwig, J.P., 1984. Decline, resurgence and population dynamics of Michigan and Great Lakes Double-crested Cormorants. Jack Pine Warbler. 62 (4), 91–102.

Ludwig, J.P., Summer, C.L., 1997. Population status and diet of cormorants in Les Cheneaux Islands area. History, Status, and Trends in Populations of Yellow Perch and Double-crested Cormorants in Les Cheneaux Islands, Michigan.

Ludwig, J.P., Hull, N., Ludwig, M.E., Auman, H.J., 1989. Food habits and feeding ecology of nesting Double-crested Cormorants in the Upper Great Lakes, 1986–1989. Jack Pine Warbler. 67 (4), 115–126.

MacInnis, A.J., Corkum, L.D., 2000. Fecundity and reproductive season of the round goby Neogobius melanostomus in the upper Detroit River. T. Am. Fish. Soc. 129 (1), 136–144.

Madenjian, C.P., Gabrey, S.W., 1995. Waterbird predation of fish in western Lake Erie; a bioenergetics model application. Condor 97, 141–153.

Madenjian, C.P., Desorcie, T.J., Holuszko, J.D., 2004. Status and trends of prey populations in Lake Michigan, 2003. Report, Great Lakes Fishery Commission. Lake Michigan Committee Meeting, Ypsilanti, Michigan.

Madenjian, C.P., Bunnell, J.D., Desorcie, D.B., Holuszko, T.J., Adams, J.V., 2005. Status and trends of prey fish populations in Lake Michigan, 2004. A report to the Great Lakes Fishery Commission. Lake Michigan Committee, Ypsilanti, MI (March 22, 2005).

Madenjian, C.P., Bunnell, D.B., Holuszko, J.D., Desorcie, T.J., Adams, J.V., et al., 2010. Status and trends of prey fish populations in Lake Michigan, 2009. A Report to the Great Lakes Fishery Commission. Lake Michigan Committee, Windsor, ON (March 23, 2010).

Madenjian, C.P., Stapanian, M.A., Witzel, L.D., Einhouse, D.W., Pothoven, S.A., Whitford, H.L., 2011. Evidence for predatory control of the invasive round goby. Biol. Invasions. 13, 987–1002.

Mills, E.L., Forney, J.L., 1981. Energetics, food consumption, and growth of young yellow perch in Oneida Lake New York. Trans. Am. Fish. Soc. 110 (4), 479–488.

Neuman, J., Pearle, D.L., Black, R., Ewins, P.J., Weseloh, D.V., Pike, M., Karwowski, K., 1997. Spatial and temporal variation in the diet of Double-crested Cormorant (Phalacrocorax auritus) breeding on the lower Great Lakes in the early 1990s. Can. J. Fish. Aquat. Sci. 54, 1569–1584.

Reyjol, Y., Brodeur, P., Mailhot, Y., Mingelbier, M., Dumont, P., 2010. Do native predators feed on non-native prey? The case of round goby in a fluvial piscivorous fish assemblage. J. Great Lakes Res. 36, 618–624.

Rudstam, L.G., VanDeValk, A.J., Adams, C.M., Coleman, J.T.H., Forney, J.L., Richmond, M.E., 2004. Cormorant predation and population dynamics of walleye and yellow perch in Oneida Lake. Ecol. Appl. 14, 149–163.

Ruetz III, C.R., Strouse, D.L., Pothoven, S.A., 2009. Energy density of introduced round goby compared with four native fishes in a Lake Michigan Tributary. T. Am. Fish. Soc. 138 (4), 938–947.

Schultz, K., 2004. Ken Schultz's Field Guide to Saltwater Fish. John Wiley and Sons, Inc., Hoboken, New Jersey.

Seefelt, N.E., 2005. Foraging ecology, bioenergetics and predatory impact of breeding Double-crested Cormorants (Phalacrocorax auritus) in the Beaver Archipelago, northern Lake Michigan. Doctoral Dissertation, Michigan State University, East Lansing.

Seefelt, N.E., Gillingham, J.C., 2004. The Double-crested Cormorant in Lake Michigan: a review of population trends, ecology and current management. The State of Lake Michigan: Ecology, Health and Management: Ecovis. World Mg. Ser.

Seefelt, N.E., Gillingham, J.C., 2006. A comparison of three methods to investigate the diet of breeding Double-crested Cormorants (Phalacrocorax auritus) in the Beaver Archipelago, northern Lake Michigan. Hydrobiologia 567, 57–67.

Seefelt, N.E., Gillingham, J.C., 2008. Bioenergetics and prey consumption of breeding Double-crested Cormorants in the Beaver Archipelago Northern Lake Michigan. J. Great Lakes Res. 34, 122–133.

Smith, S.H., 1970. Species interactions of the alewife in the Great Lakes. T. Am. Fish. Soc. 99, 754–765.

Tucker, T., 2011. Changing movements of Double-crested Cormorants in the Beaver Archipelago, northern Lake Michigan. M.S. Thesis. Central Michigan University.

USDA-WS, 2010. Beaver Archipelago, Lake Michigan 2010 DCCO Management Activity Report.

Van Guilder, M.A., 2011. Changes in Double-crested Cormorant (Phalacrocorax auritus) reproductive success and chick bioenergetics after the invasion of the round goby (Apollonia melanostomus). M.S. Thesis. Central Michigan University.

Weber, M.J., Dettmers, J.M., Wahl, D.H., Czesney, S.J., 2011. Size preferences and behaviors of native yellow perch foraging on invasive round gobies. J. Great Lakes Res. 37 (3), 584–587.

Weseloh, D.V.C., Ewins, P.J., 1994. Characteristics of a rapidly increasing colony of Double-crested Cormorants (Phalacrocorax auritus) in Lake Ontario: population size reproductive parameters and band recoveries. J. Great Lakes Res. 20, 443–456.

Wires, L.R., Cuthbert, F.J., 2006. Historic populations of the Double-crested Cormorant (Phalacrocorax auritus): implications for conservation and management in the 21st century. Waterbirds 29 (1), 9–37.

Zhao, Z.J., Wang, D.H., 2009. Plasticity in the physiological energetics of Mongolian gerbils is associated with diet quality. Physiol. Biochem. Zool. 82 (5), 504–515.