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# Comparing Decadal Census Trends and Yearly Variation in Abundance and Distribution of Breeding Double-crested Cormorants: Importance of Monitoring a Managed Species

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**Abstract.**—Binational colonial waterbird censuses were formally initiated in the Great Lakes in 1976, and have been repeated every eight to ten years. Although population estimates from these efforts are good trend indicators for some species, including Double-crested Cormorant (*Phalacrocorax auritus*), information is generally not available to examine population changes between census periods, especially at a local scale. The study examined short-term, annual population changes and distribution patterns of cormorants in the Beaver Archipelago of northern Lake Michigan between 2000 and 2007, and compared these data to decadal trends. Although no control efforts were underway between 2000 and 2006, an egg-oiling and culling program was initiated in 2007, after the completion of the decadal census. The peak number of breeders was documented in 1997, with lower population sizes between 2000 and 2006; however, in 2007, the population again approached peak numbers, suggesting that immigration from other regions occurred. Overall, yearly surveys determined that individual colonies showed great plasticity in breeding population size, with some colonies forming and others disappearing; some changes were due to environmental factors, while others indicate interactions with other species, human disturbance, and perhaps management activities in other areas of the Great Lakes. Yearly population estimates indicate that the long-term trends are probably captured with decadal colonial waterbird surveys, but the dynamic nature of cormorant populations is not. In addition, presence of yearly variation in the breeding population size of an “unmanaged” population emphasizes the importance of closely monitoring species that are managed aggressively. Received 17 September 2007, accepted 27 November 2009.

**Key words.**—Beaver Archipelago, colony disturbance, cormorant, decadal census, Lake Michigan, *Phalacrocorax auritus*, population controls, population monitoring.

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The distribution and abundance of colonial waterbirds in the Great Lakes has been documented by decadal surveys in 1976-77 (Scharf 1978), 1989-90 (Scharf and Shugart 1998), and 1997 (Cuthbert *et al.* 1997). Currently, the fourth decadal waterbird census is underway; Lakes Superior, Michigan and Erie, and the Detroit and Niagara Rivers were censused in 2007. The remaining Great Lakes and connecting waters were censused in 2008 and 2009. Because colonial waterbirds are a significant biological resource in the Great Lakes (Blokpoel and Scharf 1991), decadal surveys are of utmost importance in tracking the location and population trends of breeding colonial waterbirds, especially with the implementation of conservation efforts and management plans (Cuthbert *et al.* 1997). One trend that has been well-documented by the decadal censuses is the population growth of the Double-crested Cormorant (*Phalacrocorax auritus*; hereafter cormorant) in the Great Lakes (Cuthbert *et al.* 1997).

Formal nest count data for cormorants in Lake Michigan are available from the decadal censuses and additional surveys conducted in 1984 (Ludwig 1984) and between 2000 and 2007 (Seefelt 2005; this work). According to historical decadal counts, the number of cormorant colonies in the U.S. Great Lakes region grew from four in 1977 to 69 in 1997; in Lake Michigan, this was paralleled by an increase from three colonies in 1977 to 27 active colonies in 1997 (Cuthbert *et al.* 1997). In addition, cormorants have shown an overall population increase in the U.S. Great Lakes region, increasing from 171 pairs in 1977 to 48,931 pairs in 1997. This same trend is observed in Lake Michigan, where the number of breeding pairs increased from 75 in 1977 to 28,158 in 1997 (Cuthbert *et al.* 1997). From 1989 to 1990, Lake Michigan cormorants comprised approximately 43% (4743 pairs) of the overall population nesting in U.S. waters of the Great Lakes (11,099 pairs); by 1997, the Lake Michigan cormorant popu-

lation comprised >57% (28,158 pairs) of the breeding population in the U.S. waters of the Great Lakes (48,931 pairs; Cuthbert *et al.* 1997). The revival of cormorant populations has been no less pronounced in the Beaver Archipelago. In 1997, cormorants in the Beaver islands comprised almost 39% of nesting cormorant pairs within Michigan waters of the Great Lakes (Cuthbert *et al.* 1997; Ludwig and Summer 1997), and over 41% of the Lake Michigan breeding population (Cuthbert *et al.* 1997; Seefelt and Gillingham 2004a).

Several conjectural explanations have been given to account for the population increases of cormorants in the Great Lakes. These include higher reproductive rates as the influence of organochlorine pollutants decreased and lower adult mortality after the cormorant was included on the list of protected species under the 1918 Migratory Bird Treaty Act in 1972 (Hatch and Weseloh 1999; USFWS 2003). Another factor is the increased food availability on breeding grounds due to changes in the fish community, including the introduction of non-native species (Hatch and Weseloh 1999). For example, Alewife (*Alosa pseudoharengus*) is a key species in Lake Michigan, and its population trends appear to be a driving force in fish community dynamics (Eck and Brown 1987; Bence *et al.* 2002; Madenjian *et al.* 2004); cormorant reproductive success may be intimately linked to Alewife population dynamics in some systems (Weseloh and Ewins 1994). Furthermore, the increase in aquaculture facilities on the wintering grounds may have enhanced over-wintering survivorship (Hatch and Weseloh 1999).

The Great Lakes decadal colonial water-bird censuses have been very successful in tracking the long-term population trends of cormorants. The purpose of this paper is to 1) examine the short-term, yearly population changes and distribution patterns of cormorants on a local scale in the Beaver Archipelago of northern Lake Michigan, and 2) compare these to decadal trends. In addition, this work examines yearly variations in cormorant clutch size and reproductive success, and provides some explanation for

the population fluctuations documented in the study area. With the exception of a total of 150 birds harvested in 2000 and 2001 for a diet study, and the onset of control measures in 2007 under the Public Resource Depredation Order (PRDO; USFWS 2003), this breeding population has not experienced the intense management conducted at many other locations within the Great Lakes basin. Control measures implemented in this area in 2007 included egg oiling (coating the eggs with vegetable oil to kill the embryos) and culling (killing birds with rifles and shotguns). The study provides context and explanation for the dynamic nature of unmanaged cormorant breeding populations, as well as insight for current and future management actions.

## METHODS

### Study Area

The Beaver Archipelago, located in Michigan waters of the colder, northern basin of Lake Michigan, consists of about ten main islands and numerous small islands (Fig. 1). The number of smaller islands depends on fluctuating lake levels. Gull Island (1.0 km<sup>2</sup>), Hat Island (0.05 km<sup>2</sup>), Pismire Island (0.02 km<sup>2</sup>), Hog Island (8.0 km<sup>2</sup>), Whiskey Island (0.4 km<sup>2</sup>) and an unnamed island (0.02 km<sup>2</sup>) southeast of Garden Island (hereafter SE Garden) have supported nesting colonies of cormorants between 1976 and the present. The Hog Island colonies have been located on two peninsulas, one on the west side of the island known as Grape Spit and the other on the east side of the island called Timms Spit. Gull Island has also supported two colonies, North and

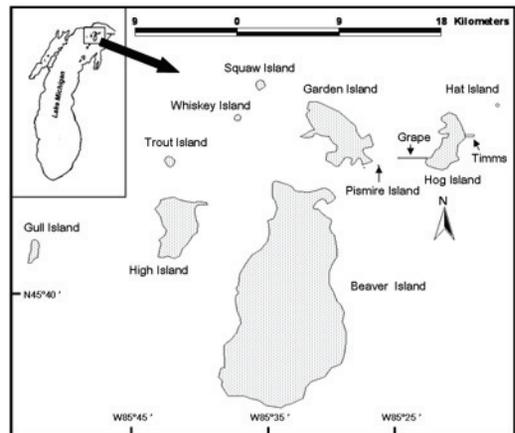


Figure 1. Beaver Archipelago northern Lake Michigan.

South, and is separated from the main island group by almost 18 km of open water west of Beaver Island.

#### Population Estimates

To estimate the breeding population of cormorants within the study area, complete ground counts were conducted, at minimum, once per year (2000 to 2007) at all active breeding colonies, with few exceptions (see below). Active colony sites were determined by aerial and boat surveys each spring. Because cormorants, as well as co-nesting species, can be very sensitive to human disturbance (Carney and Sydeman 1999), every effort was made to minimize disturbance to the colonies during visits.

The incubation period in cormorants is typically between 25 and 28 days (Hatch and Weseloh 1999). Cormorants in the Beaver Archipelago may hatch as early as the first week of June, with most chicks hatching by mid-June. Chicks fledge by seven weeks, though they may not reach independence until week ten (Hatch and Weseloh 1999); in the Beaver Archipelago, most chicks fledge at the end of July or early August. A few birds may fledge as early as mid-July in the study area. To best determine population size and how this changed over the breeding season, each colony site was visited three times during 2000 and 2001. Dates for each year roughly correspond to time periods when reproductive attempts are at their seasonal high in the archipelago, with egg laying and incubation being the predominant activities (late May through early June), when most pairs are actively brooding and rearing young (mid-June through mid-July), and when chicks are beginning to fledge and nests that remain are those that are successful (late July). Nests were considered successful if they were well-maintained and/or occupied by large chicks (or large chicks were in close proximity to the nests) in July. Survey methods followed those of Cuthbert *et al.* (1997), where nests, eggs and chicks were hand-tallied for each colony. Nest counts from the first count at each colony were used to estimate the total number of breeding pairs. By counting eggs and chicks, as well as the number of active nests as the breeding season progressed, reproductive success was also estimated (see analysis below).

In other years (2002 to 2007), the number of colony visits varied by year and colony location (Table 1). Regardless, each ground count was a complete census and used hand-tallies and/or colored popsicle sticks to mark/count nests (unless otherwise noted), following the same methodology as above. When colonies were visited only once per season, the census was timed to occur at the breeding population peak based on observations at the Pismire Island colony. In 2004, however, Gull and Hat Island breeding cormorant estimates were obtained from high-resolution digital photos. To verify the validity of the counts from these digital photos, ground counts of Pismire Island were compared to counts obtained from an aerial photo of the Pismire colony. In addition, the 2003 Gull Island census was a partial ground count completed by Seney National Wildlife Refuge personnel.

#### Analysis

Breeding cormorant population numbers for the Beaver Archipelago were tabulated for each year (2000 to 2007). In addition, breeding cormorant population estimates for 2000 and 2001 were tallied to describe changes in the number of breeding cormorants at each of the colonies as the breeding season progressed. By comparing early nest and egg counts with mid-season nest, egg and chick counts at each colony, mean clutch sizes for early and mid-season birds were calculated. These estimates were used to calculate mean clutch size for all colonies combined for each season (early and mid-season) for each of the years (2000 and 2001). The South Gull Island colony nest counts were not used to determine mean clutch size for any season or year because many nests were in trees and their contents were not countable. Mean clutch size data were then analyzed using a single-factor analysis of variance (ANOVA; Microsoft Excel®). Because differences were detected, pairwise *t*-tests were performed to compare early and mid-season clutch sizes for each year. In addition, between-year comparisons for early and mid-season mean clutch sizes were also analyzed using *t*-tests (Microsoft Excel®). A Bonferroni correction was used to re-set appropriate significance levels for these *t*-tests ( $\alpha = 0.008$ ), to avoid making spurious positives.

**Table 1. Number of Double-crested Cormorant nest counts by year and colony in the Beaver Archipelago, northern Lake Michigan, 2000 to 2007. All counts were complete ground counts, except where noted. Zero values indicate no cormorants nested; all colony sites were visited each year to determine presence of breeding birds.**

Colony	Number of cormorant nest counts							
	2000	2001	2002	2003	2004	2005	2006	2007
Grape Spit	3	3	1	0	0	0	0	0
Gull Island	3	3	1	1 <sup>a</sup>	1 <sup>b</sup>	1	2	1
Hat Island	3	3	1	1	1 <sup>b</sup>	1	2	1
Pismire Island	3	3	3	3	2	3	2	1
SE Garden Island	0	0	1	1	2	2	2	0
Timms Spit	3	3	0	0	0	0	0	0
Whiskey Island	0	0	0	0	2	0	0	0

<sup>a</sup>Partial ground count by Seney National Wildlife Refuge personnel.

<sup>b</sup>No actual ground count; count from high-resolution digital photographs.

The proportion of successful nests was determined by comparing the number of active nests at the beginning of the breeding season with the number of active nests remaining in July for each colony in each year. These proportions were then analyzed using a *t*-test (Microsoft Excel®). In addition, total reproductive output (total number of fledged chicks) for breeding cormorants in 2000 and 2001 was estimated each year by multiplying the mean clutch size by the number of active nests remaining at the end of each breeding season. Because data at Pismire were collected in the same manner from 2002 to 2005, this colony was used to determine within- and between-year trends. In addition, in 2006, the number of successful nests was estimated based on the number of fledglings observed at the site. Pismire colony was abandoned in 2007 due to control measures.

## RESULTS

The number of breeding cormorants in the Beaver Archipelago has fluctuated over the past 30 years (Table 2). From 1984 to 1997, the breeding population increased from 250 to 11,709 breeding pairs, over a 46-fold increase. However, between 1997 and 2000, the population declined by 13.5%, and between 2000 and 2001, the population size decreased by another 4.1%. Between 2001 and 2002, the number of cormorant pairs attempting to breed declined by another 31.4%; however, the actual number of successful breeders in 2002 was much lower (see below). The number of breeding pairs increased in 2003 to 9,554+ pairs, but because only a partial nest count is available

from Gull Island in 2003, the actual magnitude of this increase remains uncertain. However, in 2004, the number of breeding pairs again declined, only to rebound in 2005 and 2006. By 2007, the number of breeding cormorants approached the population peak recorded in 1997.

The number of active breeding pairs tended to decline as the season progressed in the Beaver Archipelago (Fig. 2). In 2000, the largest number of nests was counted at the onset of the breeding season during the early count season (late May to early June) at each of the colonies, including Pismire, Grape, Hat and Gull (North and South, collectively). However, in 2001, this was the case at Gull Island colonies only. Grape Island numbers remained approximately the same, and at Pismire, there was a modest increase of 28 nests. At Hat Island, this increase was more pronounced (340 nests; Fig. 2). Regardless of these differences, by the late count date (late July) in each year, the number of active breeders declined at all colonies. In 2000, the final number of active nests was 6,652, a decrease of 34.3% from the early nest count. In 2001, the final number of active nests was 7,642, a decrease of 21.3% from the early nest count.

Mean clutch size also varied between the early and mid-breeding seasons, and from year to year in 2000 and 2001 (Fig. 3a). Single-factor ANOVA indicated a significant

**Table 2. Number of Double-crested Cormorant nests in the Beaver Archipelago, northern Lake Michigan, 2000 to 2007, by colony.**

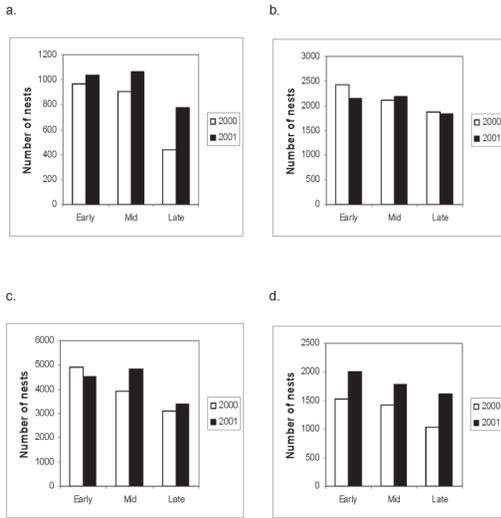
	Grape	Gull	Hat	Pismire	SE Garden	Timms	Whiskey	Total
1984 <sup>a</sup>	0	139	54	57	0	0	0	250
1989 <sup>b</sup>	291	260	294	35	0	0	0	880
1997 <sup>c</sup>	3,509	1,887	4,617	383	0	753	560	11,709
2000	2,431	1,532	4,917	987	0	277	0	10,144
2001	2,146	2,013	4,511	1,035	0	0	0	9,705
2002	1,339	957	3,659	615	87	0	0	6,657
2003	0	435 <sup>d</sup>	7,341	1,164	614	0	0	9,554
2004	0	1,274	3,515	725	798	0	95	6,407
2005	0	2,332	5,289	838	44	0	0	8,503
2006	0	2,464	5,776	512	148	0	0	8,900
2007	0	2,821	7,942	660	0	0	0	11,423

<sup>a</sup>Nest count data from Ludwig (1984).

<sup>b</sup>Nest count data from Scharf and Shugart (1998).

<sup>c</sup>Nest count data from Cuthbert *et al.* (1997).

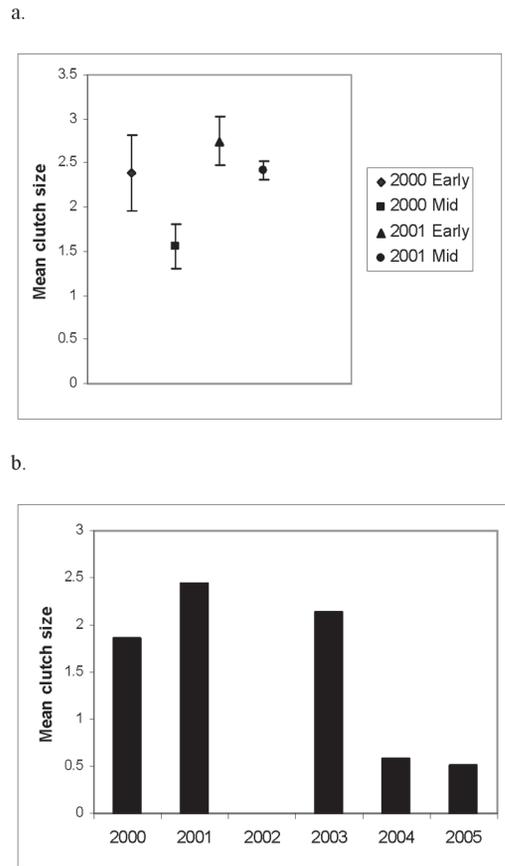
<sup>d</sup>Partial ground count completed by Seney National Wildlife Refuge personnel.



**Figure 2.** Number of active Double-crested Cormorant nests counted during the early, mid-, and late breeding season in 2000 and 2001, for a) Pismire, b) Grape, c) Hat, and d) Gull Island colonies.

difference among mean clutch sizes, both within each year and between years ( $F_3 = 11.18755$ ,  $P = 0.000861$ ). Pairwise  $t$ -tests indicated that only the mid-season clutch size between-year comparison was significant ( $P = 0.00279$ ). The Pismire colony illustrates the variability in mean clutch size during the mid-season period among years (Fig. 3b). In 2000, the mean clutch size was 1.86, which increased to 2.45 young per pair in 2001. Mean clutch size was not available for 2002 because few eggs and no chicks were produced. In 2003, mean clutch size was 2.13; in 2004, mean clutch size decreased to 0.56, and in 2005 declined to 0.51.

The mean number of successful breeders increased from 2000 to 2001 (Fig. 4a). This increase, as examined by a  $t$ -test, was not significant ( $P = 0.056781$ ). Year-to-year variability in the number of successful breeders is apparent at the Pismire colony (Fig. 4b). Only an estimated 45% of the initial breeders at Pismire were successful in 2000. The estimate increased in 2001 to 75%. No breeders were successful in 2002. However, in 2003 an estimated 69% of the pairs were successful, followed by a decline to 50% in 2004. In 2005, an estimated 53% nested successfully on Pismire Island. Very few birds (<25 pairs)



**Figure 3.** a) Mean clutch size (with standard error) for all Double-crested Cormorant colonies during the early and mid-breeding season in 2000 and 2001. Mid-season clutch sizes in 2000 and 2001 were significantly different from each other ( $P = 0.00279$ ). b) Mean clutch size in the mid-breeding season for Pismire Island, 2000 to 2005.

nested successfully on Pismire in 2006, and no birds were successful in 2007.

The estimated number of chicks produced in the Beaver Archipelago increased by 174% between 2000 and 2001, from 9,659 to 16,786 chicks (Fig. 5a). Year-to-year variability in chick production is illustrated by the Pismire colony (Fig. 5b). In 2000, an estimated 811 chicks were produced; this increased to 1,901 chicks in 2001, but no chicks were produced in 2002. An estimated 1,720 chicks were produced in 2003. In 2004, chick production declined to 209 chicks and increased slightly to 225 chicks in 2005. Chick production at Pismire declined dramatically in 2006 (<25 chicks), and no chicks were produced in 2007.

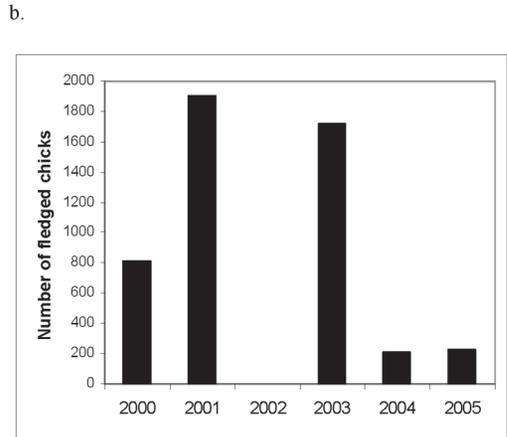
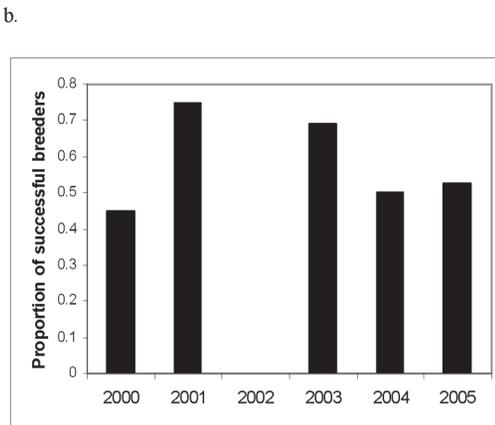
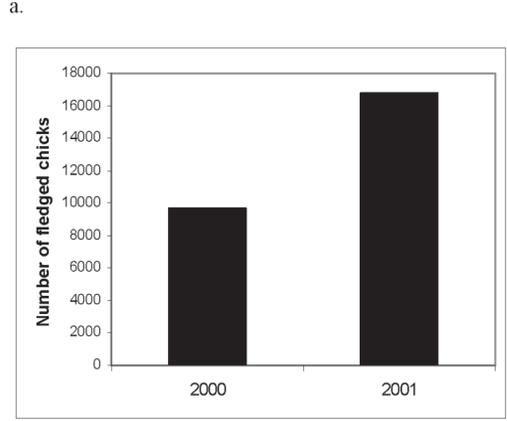
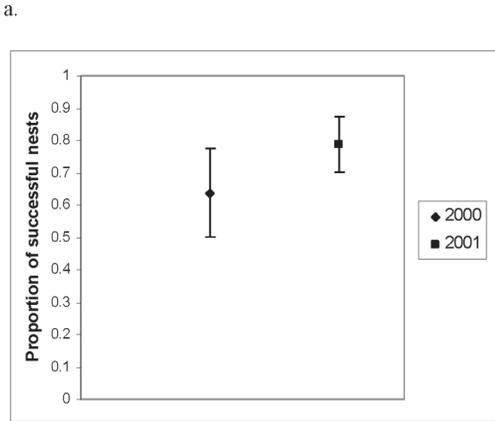


Figure 4. a) Mean proportion of successful Double-crested Cormorant breeding pairs (with standard errors) based on early- and late-season ground counts for all colonies during the 2000 and 2001 breeding seasons. b) Proportion of successful breeding pairs based on early- and late-season ground counts for Pismire Island, 2000 to 2005.

Figure 5. a) Estimated number of fledged Double-crested Cormorant chicks produced by pairs breeding at all colonies during the 2000 and 2001 breeding seasons. b) Estimated number of fledged chicks produced by pairs breeding on Pismire Island, 2000 to 2005.

DISCUSSION

In the past, colonial waterbird censuses have been conducted in the U.S. waters of the Great Lakes every eight to twelve years (Scharf 1978; Scharf and Shugart 1998; Cuthbert *et al.* 1997). A recent cormorant management plan (USFWS 2003) recommended that population monitoring be continued at regular intervals at the breeding colonies. In this study, breeding cormorants were monitored during each reproductive season beginning in 2000 and ending in 2007 (the decadal census) to better document year-to-year variability in breeding

population size and distribution within the Beaver Archipelago. In addition, the within-season trends documented here emphasize the importance in timing cormorant census efforts with peak nesting (later incubation and the onset of hatching) when estimating breeding population size (Ewins *et al.* 1995).

Although the earlier, more periodic population counts are invaluable in documenting the recovery of these birds across the Great Lakes, there does appear to be enough yearly variation to warrant monitoring non-managed cormorant populations more frequently when population controls are underway elsewhere (even nearby) in

the Great Lakes. For example, the influx of birds into the Beaver Archipelago in 2007 may be due primarily to disturbance and colony abandonment by nesting birds at sites elsewhere in northern Lake Michigan. With onset of egg oiling at two of the three colonies and the killing of birds at or near all colonies in the Beaver Archipelago in 2007, it is difficult to predict further population trends. Possibly, the local population will decline as birds emigrate to other regions, but it is also possible that birds will move either to other historical colony locations within the archipelago or to new sites where suitable habitat is available. Although the decadal census (1997 and 2007) reported a decline in breeding birds in the region, if the census had taken place at an eight-year interval, the magnitude of the decline would have appeared much greater. Cormorant breeding populations in the archipelago are dynamic; it is important to closely monitor this migratory species, currently under intense management, not only to better understand cormorant biology, but also to measure the outcomes of management practices.

As a reflection of change in population size, the number of breeding birds at specific colony sites has fluctuated in the Beaver Archipelago from year to year. In other areas, such colony dynamics have been attributed to changes in suitable habitat, often due to species interactions, predation, and/or human disturbance (Kury and Gochfeld 1975; Ellison and Cleary 1978; Verbeek 1982; Gotmark 1992; Cairns *et al.* 1998; Carney and Sydeman 1999; Skagen *et al.* 2001; Seefelt and Gillingham 2004b). In addition, changes in water level have impacted the breeding habitats of a wide variety of birds, including Piping Plovers (*Charadrius melodus*; North 1986), Caspian Terns (*Hydroprogne caspia*, formerly *Sterna caspia*; Cuthbert 1988) and Dalmatian Pelicans (*Pelecanus crispus*; Pyrovesti 1997). All of these factors are probably at play within the Beaver Archipelago. Lower than average lake levels have been recorded in the Lake Michigan-Huron basin over the past several years, with the highest rate in lake level re-

duction occurring between 1998 and 2000, and the lowest water levels documented in 2003 (NOAA 2003). The trend appears to be continuing. Such changes in lake level affect, at minimum, the shape and size of shoreline habitat and the type/abundance of vegetation. Such changes in the number of available nest sites may, in part, regulate colonial waterbird populations (Croxall 1987). Although cormorants in the Great Lakes may not be limited by the number of available nest sites (Hatch and Weseloh 1999), trends in colony location and size in the Beaver Archipelago may be partially due to changes in availability of desirable nesting locations (Seefelt and Gillingham 2004b). In addition, in the North Channel of Lake Huron, Ridgeway *et al.* (2006) reported that cormorants exhibit density-dependent population growth; whether such regulation has occurred in the Beaver Archipelago remains uncertain.

Not only has the breeding population fluctuated over the past several years in the study area, but the reproductive success of these birds has also been variable. In 2002, reproductive failure (except for two nests) at the Grape Spit colony can be attributed, in part, to mammalian predators crossing from Hog Island proper due to low water levels. In high water years, the spit actually becomes two islands, Grape Islands East and West (Seefelt and Gillingham 2004b). The abandonment of the Whiskey Island colony in 2005 also appears to be related to the arrival of a Coyote (*Canis latrans*) on the island (N. Seefelt, unpubl. data). The major trends across the study area probably also reflect year-to-year climatic differences and changes in prey availability. Changes in prey availability could be due to colder summer water (and air) temperatures, as well as unrelated fluctuations in prey population sizes based on their life history traits. For example, during the 2002 field season, air and water temperatures remained unseasonably low through early July (NOAA NDBC 2007). Possibly in response, cormorants at Pismire, SE Garden and Gull North colonies, as well as the depredated Grape Spit colony, abandoned nesting at-

tempts. Chick production declined at Hat and South Gull colonies compared to other years. Ring-billed Gulls (*Larus delawarensis*), Herring Gulls (*L. argentatus*) and Caspian Terns showed similar trends (Seefelt and Gillingham 2004b). In 2004, water and air temperatures were again lower than average (NOAA NDBC 2007), and reduced reproductive output was documented at Pismire. Although many factors could be influencing variability in nesting success and the number of fledged chicks, it is apparent that weather patterns and lake water temperatures do impact cormorant colonies by influencing their prey base in the study area. This warrants further investigation.

At Pismire Island, the number of successful breeders and the number of fledged chicks declined markedly between 2003 and 2004, and remained low through 2006. In 2007, the lack of successful breeding was due to colony abandonment following egg oiling and culling at the site. The decline could be due to a wide variety of factors, including human disturbance, lake levels and local food availability. Human disturbance has increased at Pismire, primarily due to harassment of these birds, both intentional and unintentional. This colony is well known and is in close proximity (approximately three kilometers) to the only human population center in the archipelago, the town of St. James and its harbor. Remote camera work (N. Seefelt, unpubl. data) shows periodic disturbances in which all birds flush from their nests, often several times per day, beginning in 2003. Field observations from an on-colony blind and from monitoring camps on nearby islands indicate that birds often take flight due to pleasure craft traffic passing close to the colony. Similar evidence was gathered at the SE Garden colony, which is approximately 1.5 km to the west of Pismire Island. In addition, between 2003 and 2004, the number of Herring and Ring-billed Gulls nesting on Pismire Island began to increase, after the abandonment of Grape Spit. Between 2000 and 2002, only a few Herring Gulls were observed nesting at this site. Although 2007 census data (N. Seefelt, unpubl. data) indi-

cated that the number of Herring Gulls was at historical levels as compared to the 1989-90 decadal census (Scharf and Shugart 1998), Ring-billed Gulls were not reported to breed on Pismire when this earlier census was completed. The decline in cormorant reproductive success at Pismire is likely due to the synergism of many factors including human disturbance, interaction with gulls, and ecological factors, including but not limited to, exposure on this bare island of cobble and sand.

Croxall (1987) stated that food shortages are another important factor that can regulate seabird populations, both in terms of abundance and distribution. Lower availability of suitable prey could have contributed to reproductive failure at some colonies and a decline in the number of successful breeding birds in 2002 and 2004. In some systems, a decline in nearby food sources can be attributed to the birds themselves (Ashmole's Halo; Birt *et al.* 1987). However, during these years, large numbers of adult Alewife may not have returned to shallow waters during the prime cormorant breeding season due to lower water temperatures. Although Alewife biomass in Lake Michigan remained relatively stable between the early 1980s and 2003 (Bence *et al.* 2002; Madenjian *et al.* 2004), the local availability of these fish may have fluctuated in the system. In addition, warm spring temperatures in 1998 led to moderately high levels of age-3 Alewives in 2001. In fact, this year class dominated survey catches in 2001 (Madenjian *et al.* 2004). The large number of Alewife in the diet of cormorants in 2001 as compared to 2000 (Seefelt 2005) could be in response to the increased availability of Alewife of a preferred size. Actual relative availability of prey in the Beaver Archipelago is not known, and there is no direct evidence that cormorants in the Beaver Archipelago were influenced by a food shortage during 2000 or 2001; birds did shift their diet, possibly based on food availability, within the study area (Seefelt 2005). In addition, Ludwig *et al.* (1989) compared yearly Alewife trawling estimates to cormorant diet data in the upper Great Lakes and found that bird diet

shifted based on the availability of Alewife; this supports suggestions that cormorant reproductive success may be linked to Alewife availability (Weseloh and Ewins 1994).

Overall, the size and distribution of cormorant breeding colonies in the Beaver Archipelago show considerable yearly variation. A multitude of factors influence these birds, including human disturbance, population management, food availability, interaction with other species and climatic factors. Yearly population estimates indicate that although the long-term trends are probably captured with decadal colonial waterbird surveys, these censuses provide only a snapshot of actual population dynamics. Yearly variation in breeding population size, distribution, and reproductive output of an "unmanaged" population, embedded in a region with intensive cormorant control, demonstrates the importance of closely monitoring species that are aggressively managed. This monitoring should include yearly censusing, as well as documenting reproductive output, in order to better understand population dynamics and the impacts of management. The Beaver Archipelago cormorants exemplify the concept that the number of breeding cormorants at any location within the Great Lakes basin will fluctuate due to local factors, but also in response to actions and conditions elsewhere in the region.

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