

# Density-dependent growth of double-crested cormorant colonies on Lake Huron

Mark S. Ridgway, J. Bruce Pollard, and D.V. Chip Weseloh

**Abstract:** By analyzing 20+ years of data, we found that the nesting colonies of double-crested cormorants (*Phalacrocorax auritus* (Lesson, 1831)) in the North Channel and Georgian Bay of Lake Huron exhibit density-dependent population regulation. This conclusion is based on four lines of evidence. First, a time series of nest counts at specific colonies (1979–2001) showed density-dependent growth based on randomization tests of the time series. Second, the per capita rate of change in colony size declined with increasing colony size over a 10-year period. Third, a Ricker model of aggregate nest counts showed that population growth of nesting double-crested cormorants stabilized in recent years (through 2003), with  $K$ , the carrying capacity parameter, being 11 445 nests in the North Channel and 10 815 nests in Georgian Bay. Fourth, a colony area index showed near complete coverage of coastal areas by adult nesters coinciding with overall declines in population growth. High rates of population increase of double-crested cormorants on Lake Huron have largely come to an end, but changes in fish abundance may result in changes in carrying capacity.

**Résumé :** À l'étude de 20+ années de données, nous trouvons qu'il y a dans les colonies de nidification des cormorans à aigrettes (*Phalacrocorax auritus* (Lesson, 1831)) du chenal Nord et de la baie Géorgienne du lac Huron un contrôle de population dépendant de la densité. Cette conclusion se base sur quatre séries de preuves. D'abord, une série chronologique de dénombrements de nids dans des colonies spécifiques (1979–2001) indique une croissance dépendante de la densité d'après des tests de randomisation de la série chronologique. En deuxième lieu, le taux de changement par individu de la taille de la colonie est fonction inverse de la taille de la colonie sur une période de dix ans. Troisièmement, un modèle de Ricker des dénombrements combinés de nids montre que la croissance de population des cormorans à aigrettes s'est stabilisée au cours des dernières années (jusqu'en 2003 inclusivement) avec un  $K$ , le paramètre du stock limite, égal à 11 445 nids dans le chenal Nord et de 10 815 nids dans la baie Géorgienne. Finalement, un indice de surface des colonies indique une couverture quasi complète des régions côtières par les nidificateurs adultes qui coïncide avec des déclin généraux dans la croissance démographique. Les forts taux de croissance démographique des cormorans à aigrettes ont généralement pris fin au lac Huron, mais les changements dans l'abondance des poissons pourraient provoquer des changements du stock limite.

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## Introduction

Local prey depletion around nesting colonies of waterbirds is believed to be an important mechanism limiting numbers of nesting adults (Ashmole 1963; Birkhead and Furness 1985; Furness and Monaghan 1987; Croxall and Rothery 1991). A "halo effect" generated by local prey depletion near the colony results in birds from larger colonies foraging farther than adults in small colonies (Ashmole

1963). Direct evidence supporting Ashmole's hypothesis is rare, but one study showed declines in prey fish abundance as a function of distance from a nesting colony of double-crested cormorants (*Phalacrocorax auritus* (Lesson, 1831)) (Birt et al. 1987).

Evidence of density-dependent growth of waterbird nesting colonies is limited because a full examination requires data on population trends as well as colony-specific measures of variables such as adult foraging behaviour and chick growth and survival or other vital rates. An analysis of colony growth in northern gannets (*Morus bassanus* (L., 1758)) found density-dependent growth of nest numbers at the population level and a positive correlation between colony size and adult foraging-trip duration at the individual level (Lewis et al. 2001). Two possible mechanisms based on competitive interference among adult foragers were proposed to account for density-dependent colony growth without a concomitant depletion of local fish abundance (Lewis et al. 2001). First, a reduction in fish vulnerability through escape and disruption caused by foraging birds leads adults to forage over a wider area at greater cost with increasing colony size. Second, the geometry of central-place foraging and similar requirements for prey consumption per individual, independent of colony size, leads adults to integrate foraging success at greater cost over a wider area with increasing colony size.

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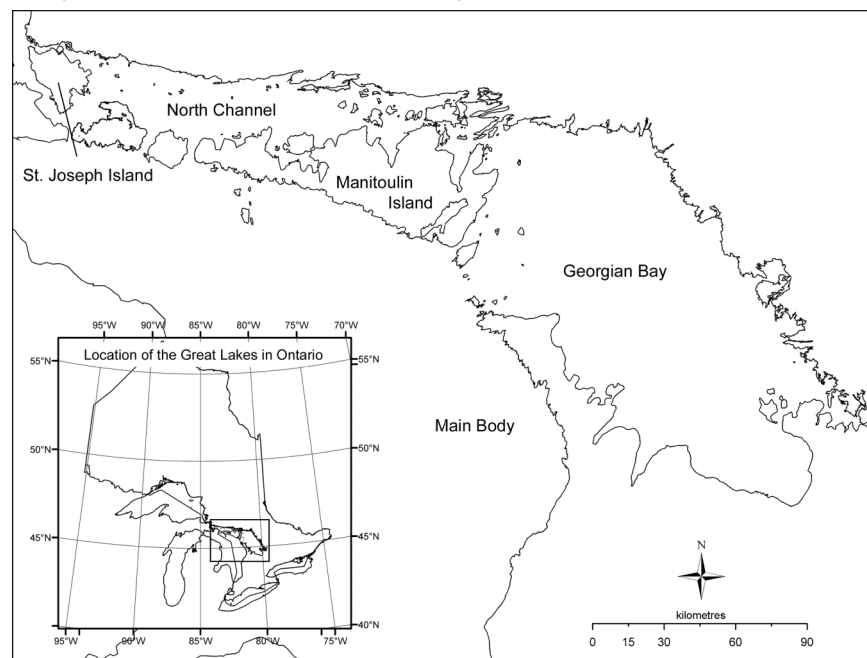
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**Fig. 1.** Map of Ontario showing the location of Lake Huron. The enlargement shows the locations of the North Channel and Georgian Bay.



The regulation of numbers of breeding double-crested cormorants is relevant to the ongoing debate concerning the role of this species in the aquatic ecosystems of the Laurentian Great Lakes. Here, rapid increases in numbers of double-crested cormorants over the past 25 years have provoked debate about their role in reductions of nearshore fish through consumption (Burnett et al. 2002; Johnson et al. 2002; Stapanian et al. 2002), a debate that is reflected in other locations with other species of cormorants demonstrating similar capacities for population growth and density-dependent regulation (Fredericksen et al. 2001; Bregnballe et al. 2003). The population expansion contributed as well to a wider call for viewing waterbird ecology within a broader ecosystem context for the Great Lakes in general (Hebert and Sprules 2002) and for research into population regulation of double-crested cormorants specifically (Erwin 1995).

The North Channel and Georgian Bay regions of Lake Huron have experienced exponential increases in the abundance of nesting double-crested cormorants, with nest numbers increasing from approximately 200 in 5 colonies in 1979 to 22 997 in 70 colonies in 2003. We hypothesized that the population of double-crested cormorants in this ecosystem exhibits density-dependent regulation after 20+ years of growth. A full examination of this hypothesis would include information on colony-specific vital rates and population trajectories. Unfortunately, no colony-specific data exist that enable us to identify mechanisms regulating nest numbers at any colony on Lake Huron. In the absence of such information, nest counts of cormorant colonies must serve as baseline data for determining whether or not cormorants are now in a period of density-dependent regulation at the population level (Weseloh et al. 1995, 2002). Four predictions stem from our hypothesis of density-dependent regulation. First, a randomization test of nest numbers in colonies should reveal evidence for density-dependent growth of colonies (Pollard et al. 1987; Lewis et al. 2001). Second, the

intrinsic rate of increase for colonies should be inversely related to colony size (Turchin 1999, 2003). Third, a phase plot of population data ought to reveal a clockwise trajectory when the population is at carrying capacity and provide a significant fit to a population growth model incorporating a carrying capacity parameter (Turchin 2003). Fourth, if food limitation is the main mechanism in population regulation, complete or extensive spatial coverage of available foraging habitat associated with nesting colonies ought to occur when a population reaches carrying capacity, unless a lack of suitable colony sites is limiting geographical range. We assess an alternative hypothesis of colony growth to determine whether differences in perimeter growth of small (relatively rapid perimeter growth as a function of colony size) and large colonies (relatively slow perimeter growth as a function of colony size) can account for the observed growth in Lake Huron colony sizes (Moss et al. 2002).

## Methods

### Study area

The North Channel and Georgian Bay represent a substantial part of the Lake Huron ecosystem (Fig. 1). The North Channel has a maximum length of 150 km, a surface area of 3950 km<sup>2</sup>, and a mean depth of 22 m (Sly and Munawar 1988). Georgian Bay has a maximum length of 215 km, a surface area of 15 111 km<sup>2</sup>, and a mean depth of 44 m (Sly and Munawar 1988). The boundaries of the North Channel are defined as the eastern end of Manitoulin Island in the east and St. Joseph Island in the west (Fig. 1). Georgian Bay is the area from the eastern end of Manitoulin Island, around the coast, and up to the tip of the Bruce Peninsula (Fig. 1).

The nesting colonies of double-crested cormorants are located along much of the coast of Lake Huron. Most nests are located on the ground in Lake Huron colonies, with a

small proportion located in shrubs and small trees (Weseloh et al. 2002). All nest counts were conducted in mid to late June each year, when nest initiation was complete. We used data from the appendix of Weseloh et al. (2002; their Figs. 3 and 4) to provide colony location data for the years 1990, 1993–1994, 1997, and 2000. Nesting colonies in Georgian Bay, the North Channel, and Canadian waters of Lake Huron (main body) were counted in 2003 at the locations in Weseloh et al.'s (2002) appendix as well as new locations. In all surveys, apparently occupied nests were counted. Census data for the early and late 1990s are regarded as complete because the surveys were conducted as part of the Cooperative Canadian–US Great Lakes Colonial Waterbird Census. The 2003 surveys had the same timing and coverage as previous surveys and were conducted by some of the same field biologists as the earlier waterbird censuses. Three additional colonies were located in Georgian Bay in 2003 that were apparently not present during earlier surveys. The 1997 census data in Weseloh et al.'s (2002) appendix occasionally indicate that nesting may have occurred (?) or that a nesting colony was present but not censused (+). Based on this assessment, we assumed that a colony was present in those locations in 1997 and determined the average rate of annual increase for colonies that were visited between 1994 and 2000 to infer nest counts at those locations.

Four approaches were used to assess the presence of density dependence in the growth of double-crested cormorant nesting colonies. First, thirteen colonies in the North Channel and Georgian Bay provided a time series of nest counts spanning 10 to 23 years over the period 1979–2001. On occasion, some annual nest counts were missing for some colonies. In these cases, the per capita rate of population growth was calculated from observed data that bracketed the missing count, and an estimated nest count was then used in the analysis. The time series for each colony was examined for density-dependent growth using a distribution-free randomization test (Pollard et al. 1987). The slope  $b$  of the relationship  $\log_e N_{t+1}$  versus  $\log_e N_t$ , where  $N_t$  is the nest count in year  $t$ , for each time series was compared with slope estimates derived from 10 000 random permutations of each time series (Pollard et al. 1987; Lewis et al. 2001). Estimated slopes were then compared with the distribution of slopes from the randomization process to determine significance. Density dependence in time series of population estimates has been demonstrated for a wide range of organisms using this and other analytical methods (Brook and Bradshaw 2006).

Second, the nest count data from all nesting colonies present in the North Channel and Georgian Bay in 1990 and 2000 were used to determine whether the per capita rate of population change declined with increasing colony size. The per capita rate of population change,  $r$  ( $\log_e(N_{t+1}/N_t)$ ), is a fundamental feature of regulation (Turchin 1999, 2003). The ability to accurately detect rates of change as a function of population size is largely a function of the length of the time series of observed abundance (Hassell et al. 1989; Wolda and Dennis 1993) and the magnitude of sampling error in the population estimate at any one time (Shenk et al. 1998). Since movement among nesting colonies is a possibility, the success of this approach depends on extensive coverage of most or all colonies in an

aquatic ecosystem. This approach was used successfully in two long-term studies of colonial waterbirds with broad regional assessments of the size of nesting colonies at a 10-year interval (Coulson 1983; Lewis et al. 2001). The per capita growth rate was assessed only for colonies with nest counts in both 1990 and 2000 ( $= 43$  colonies) (Weseloh et al. 2002). The per capita rate of change ( $\log_e(N_{2000}/N_{1990})$ ) was compared with the initial colony size ( $\log_e N_{1990}$ ).

Third, a Ricker population growth model (a derivation of the continuous logistic growth model; Turchin 2003) for the time series of nest counts for the North Channel and Georgian Bay was used to describe the change in population increase and to determine the carrying capacity in the North Channel and Georgian Bay. The general form of the Ricker model was used:

$$N_{t+1} = N_t \exp r_0(1 - N_t/K)$$

where  $K$  is the carrying capacity and  $r_0$  is the realized per capita growth rate of the population in the absence of density-dependent factors, typically observed in the earliest stages of population growth. In the Ricker model, the characteristic return time to equilibrium,  $K$ , is  $\gamma = 1/r$  (May 1976). The data on aggregate nest counts from the early 1980s onward were used as a measure of adult population size in the North Channel and Georgian Bay. Nest counts from the 1980s (see Fig. 2) and nest counts from the whole-lake survey years (1990, 1994, 1997, 2000, and 2003) represented the known population of adult nesting double-crested cormorants in those years. Nest counts were done for a subset of nesting colonies for the years between whole-lake surveys (1991–1993 and 2001–2002). The intrinsic rate of increase was calculated for this subset and applied to nest counts from years with whole-lake surveys to project the population between these years. For the periods 1995–1996 and 1998–1999, very few nesting colonies were counted, so nest counts for these periods are absent.

The Ricker growth model is an appropriate choice given the trends in nest counts for the set of colonies with long time series of nest counts and the slower population growth in recent years. Estimates of per capita population growth at low population sizes,  $r_0$ , are difficult to acquire because data on population size are rarely available during a founding event. The cormorant nest count data for Lake Huron are an exception to this situation. We used the realized per capita rate of growth from the first three nest counts (founding colony count is year 1) for colonies initiated in the 1980s to empirically estimate  $r_0$  for the North Channel ( $N = 14$  colonies; median  $r_0 = 0.4855$ ), Georgian Bay ( $N = 14$  colonies; median  $r_0 = 0.5567$ ), and both regions combined (median  $r_0 = 0.5276$ ). The carrying capacity parameter,  $K$ , was estimated using nonlinear least squares procedures from the data on nest counts ( $N_t, N_{t+1}$ ).

Fourth, a perimeter rule was used as a colony area index to define the possible extent of foraging around each colony based on the recent analysis of foraging behaviour of northern gannets (Lewis et al. 2001). In the gannet study, the square root of colony size ( $\sqrt{N}$ , where  $N$  is the number of nests) was positive and significantly correlated with observed foraging-trip duration and total distance. The mean



total travel distance will be proportional to  $\sqrt{N}$  for central-place foragers encountering randomly distributed fish schools around a nesting colony (Box 1 in Lewis et al. 2001). In our study, half of the total travel distance was taken as the foraging perimeter for each colony, assuming birds fly straight out from the colony ( $\sqrt{N}/2$  represents the maximum travel distance away from the colony on a foraging trip). For a colony of 1000 nests, a radius of 15.8 km would define the perimeter around the colony for foraging breeders. Nesting colonies in the North Channel and Georgian Bay can be relatively close together, so the foraging perimeters of large colonies can completely cover the foraging perimeters of neighbouring small colonies. In these situations, the nest count of the smaller colony was incorporated into the nest count of the larger colony for the purpose of calculating an index of outer foraging perimeter for a particular location.

We examined published accounts of foraging movements of different species of cormorants and shags (Phalacrocoracidae) to determine whether foraging distances during the nesting period were positively correlated with colony size. The 99th percentile of foraging distances was determined following a reconstruction of published distributions of the data (e.g., Wanless et al. 1991; Custer and Bunck 1992; Coleman et al. 2005) or by multiplying the standard deviation of foraging distances by 3 (e.g., Pearson 1968; Quintana 2001; Stapanian et al. 2002; Sapoznikow and Quintana 2003). Based on this information, there was a positive relationship between the upper limits of foraging range and the perimeter rule of  $\sqrt{N}/2$  (Spearman rank correlation,  $r_s = 0.76$ ;  $N = 13$ ;  $p < 0.01$ ) with a slope close to 1 ( $\hat{b} = 0.87$ ;  $SE = 0.27$ ), although more data are required to refine this estimate (maximum foraging distance =  $1.31 + 0.87(\sqrt{N}/2)$ ;  $R^2 = 0.49$ ;  $p < 0.01$ ).

We did not constrain foraging distances between colonies to be equidistant between a pair of sites. The foraging perimeters were mapped around colonies assuming foraging birds were evenly distributed over foraging areas. Colonial waterbirds typically forage in specific locations relative to the nesting colony and neighbouring colonies (Cairns 1989; Sapoznikow and Quintana 2003); however, we do not have data on colony-specific foraging locations in Lake Huron. In Lake Erie, cormorants forage around the nesting colony rather than in a specific location(s) (Stapanian et al. 2002).

We assumed that most foraging by double-crested cormorants occurred at depths  $\leq 20$  m, although we recognize that some foraging attempts likely exceed this limit. Our decision was based on two considerations. First, published accounts of diving depths in this species indicate that most birds are diving in water less than 20 m deep (Hatch and Weseloh 1999). Observed water depths at foraging locations include 1–9 m (Custer and Bunck 1992), 1.5–7.9 m (Cooper 1986), 2–7 m (Lewis 1929, cited in Custer and Bunck 1992), and less than 9 m (Mendall 1936, cited in Custer and Bunck 1992). Stapanian et al. (2002) described foraging flocks of double-crested cormorants in the western basin of Lake Erie diving more frequently in water less than or equal to 8 m deep. Approximately 63% of all foraging flocks ( $N = 156$ ) in the western basin of Lake Erie were foraging in water 6–10 m deep (Stapanian et al. 2002). Coleman et al.

(2005) found that foraging double-crested cormorants selected foraging depths  $\leq 5$  m in a shallow lake ecosystem where all depths were within their foraging range. Finally, a linear regression analysis of abiotic factors influencing colony size of double-crested cormorants found that the area of aquatic habitat 11–20 m in depth within 4 km of the colony was consistently an important explanatory variable in accounting for colony size (Johnson and Krohn 2002).

For each colony area index associated with a nesting colony, the area ( $\text{km}^2$ ) of water  $\leq 20$  m deep was determined based on digital bathymetric data available for the North Channel and Georgian Bay. The density of nests was based on the nest count for a given colony divided by the area of water  $\leq 20$  m deep from the colony area index. All colony area index mapping was done using ArcView<sup>®</sup> 3.1 (ESRI Inc., Redlands, California).

Second, we calculated the aerobic capacity of double-crested cormorants to assess possible foraging depths given observed rates of descent in cormorants (approximately  $1 \text{ m}\cdot\text{s}^{-1}$ ; Wanless et al. 1993). The aerobic capacity of double-crested cormorants was determined using a recent equation for field metabolic rate ( $\text{FMR} = 16.69m^{0.651}$ , where FMR is field metabolic rate ( $\text{kJ}\cdot\text{day}^{-1}$ ) and  $m$  is mass (grams), Ellis and Gabrielsen 2002). This equation has recently been used to determine worldwide levels of food consumption by seabirds (Brooke 2004). The combustible energy provided by a litre of oxygen ( $19.3 \text{ kJ}\cdot\text{L}^{-1}$ ; Boyd and Croxall 1996) and reported oxygen capacity were used to estimate the consumption of oxygen per day (litres per day; field metabolic rate divided by energy per litre of oxygen). This volume consumed per day was converted to millilitres per minute and divided by the mean mass of double-crested cormorants (2 kg) to arrive at an estimate of  $45.16 \text{ mL O}_2\cdot\text{min}^{-1}\cdot\text{kg}^{-1}$ . Dividing this estimate by the overall oxygen capacity of blood ( $46 \text{ mL O}_2\cdot\text{kg}^{-1}$ ; Boyd and Croxall 1996) provided an estimate of 60 s of aerobic dive time for double-crested cormorants. To remain within aerobic limits during diving, a double-crested cormorant foraging at a depth of 20 m will require approximately 40 s of travel time (descent and ascent) and will have approximately 20 s at the foraging depth.

An alternative explanation for the rapid growth of small colonies relative to large colonies is the difference in the accrual of nests at the perimeter of colonies as a function of colony size (Moss et al. 2002). This is particularly relevant for colonies that are disc-shaped or that have limited available nesting habitat (i.e., cliffs). Colony growth can be “size-dependent” because the accrual of nests at the colony perimeter is more rapid for small colonies than for large colonies. A full examination of this model requires detailed mapping of colony development through time (Moss et al. 2002); however, data of this kind were lacking in this study. As an alternative, we followed the procedure of Moss et al. (2002) and plotted the growth rate of colonies from 1990 to 2000 as a function of the inverse of the square root of the nest count ( $1/\sqrt{N}$ ). The slope of this relationship is equal to  $3.54k$ ,  $k$  being a constant of proportionality and  $3.54k$  representing the proportional change in the expanding perimeters of colonies (see Moss et al. 2002). The observed population growth of colonies from 1990 to 2000 was compared with the colony growth, based on the perimeter  $k$  of the size-dependent

**Table 1.** (A) Total nest and colony counts of double-crested cormorants (*Phalacrocorax auritus*) in the North Channel and Georgian Bay, Lake Huron (data for 1990–2000 from Weseloh et al. 2002) and (B) annual rate of change in total nest count and total colony count during four time periods, 1990–2003.

(A) Total nest and colony counts.				
Year	Number of nests		Number of colonies	
	Georgian Bay	North Channel	Georgian Bay	North Channel
1990	3985	4310	22	16
1994	9854	7281	28	18
1997	8217	8494	34	31
2000	12821	12441	38	35
2003	11470	11527	37	33
(B) Annual rate of change.				
Period	Per capita rate of change		Per colony rate of change	
	Georgian Bay nests	North Channel nests	Georgian Bay colonies	North Channel colonies
1990–1994	0.226	0.131	0.060	0.029
1994–1997	–0.061	0.051	0.065	0.181
1997–2000	0.148	0.127	0.037	0.040
2000–2003	–0.037	–0.025	–0.009	–0.019

**Note:** Annual rate of change is  $\log_e(N_{t+\Delta}/N_t)/\Delta$ , where  $N_t$  is the count in year  $t$ .

model of colony growth, to determine whether the size-dependent projection of colony size in 2000 matched the observed colony size in 2000. Failure of the size-dependent model of colony growth to match the observed nest counts, especially if the observed counts are higher than the model estimate, points to colony growth being set by additional factors other than the simple expansion of colonies' perimeters.

Finally, an experimental egg oiling project was initiated in the central region of Georgian Bay and the eastern end of the North Channel in 2002. Egg oiling does not result in an immediate reduction of the number of nests but can affect nest counts slowly over a period of years (Bédard et al. 1995). However, egg oiling could potentially influence whether breeders with oiled eggs return to or abandon the colony in the subsequent year. We did not expect this activity to affect total nest counts at the large scale of this study given the complete coverage of the Lake Huron coast in the nest count surveys.

## Results

### Nest counts

The total count of nests for the North Channel and Georgian Bay colonies points to a recent decline in breeding double-crested cormorants on Lake Huron for the first time since the period of rapid increase over 20 years ago (Table 1). The apparent decline in nest numbers in 1997 was in part due to an incomplete survey of the region (Appendix 1 in Weseloh et al. 2002) but also due to relatively fewer nests in colonies that were counted. The realized per capita rate of population change based on these data,  $r_t$  ( $= \log_e(N_{t+\Delta}/N_t)/\Delta$ ), reveals a sharp increase in growth through the 1990s, with the exception of Georgian Bay in the 1994–1997 period, and a recent negative rate of change in both total nest count and the number of colonies in 2003 (Table 1). Growth in the number of colonies was

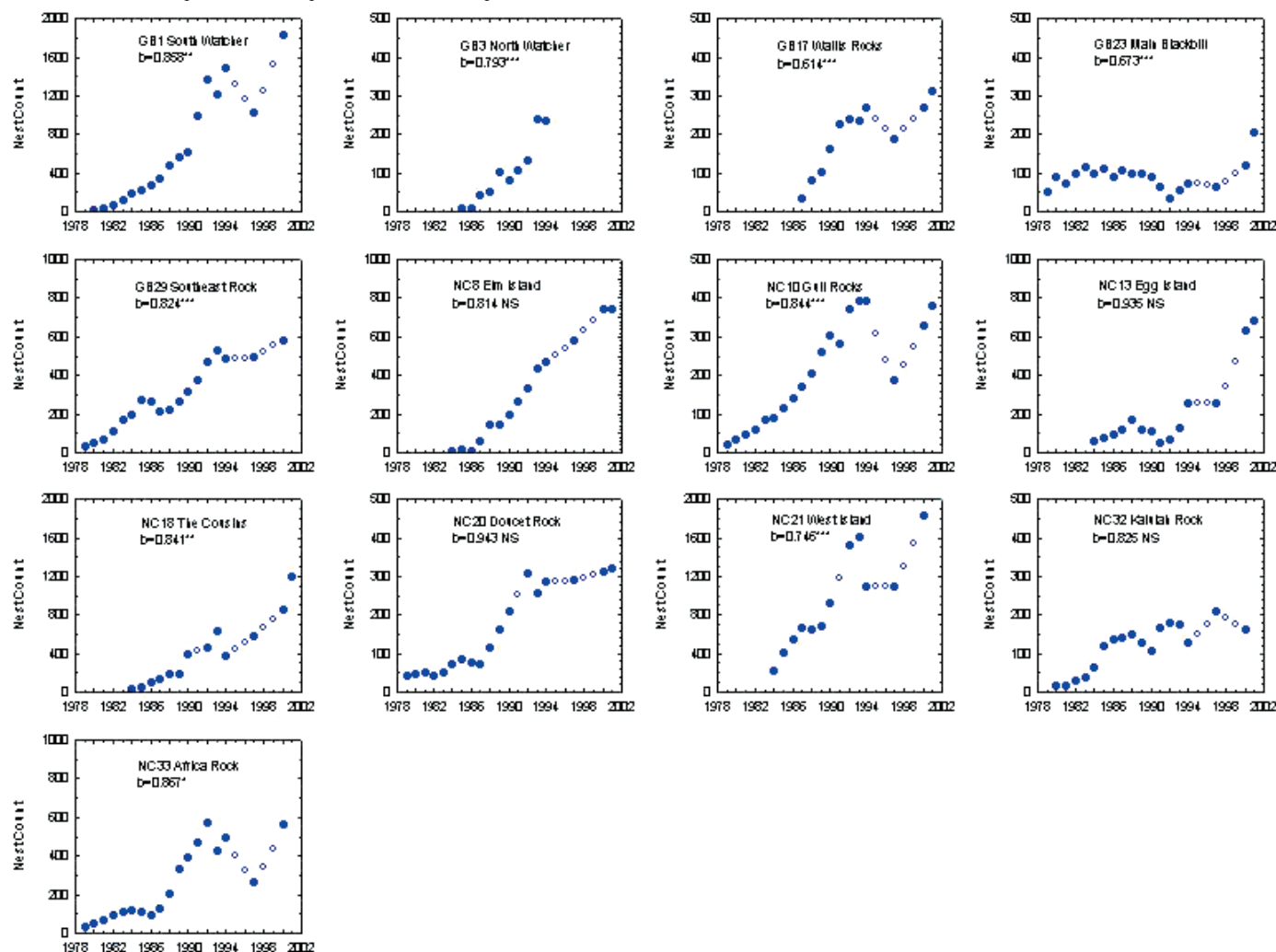
highest in the mid-1990s, had slowed by 2000, and was negative by 2003 (Table 1B). The rate of increase in the number of nests between 1990 and 2000 was 11.7% per year in Georgian Bay and 10.6% per year in the North Channel.

We found significant density-dependent growth in all five Georgian Bay colonies examined and in four of eight North Channel colonies (Fig. 2). The annual nest count in some years for some colonies was based on the estimated per capita growth rate between observed nest counts. For six data sets, a complete time series of nest counts was available to test for density dependence. Again, significant density-dependent colony growth was found in three of these colonies (GB2, South Watcher,  $\hat{b} = 0.873$ ,  $N = 15$ ,  $p < 0.01$ ; GB29, Southeast Rock,  $\hat{b} = 0.814$ ,  $N = 17$ ,  $p < 0.01$ ; NC10, Gull Rocks,  $\hat{b} = 0.879$ ,  $N = 16$ ,  $p < 0.01$ ). Three of the six time series did not reveal density-dependent population growth (NC8, Elm Island; NC32, Kalulah Rock; NC33, Africa Rock).

Forty-three double-crested cormorant colonies were present in 1990 and 2000 in the Canadian waters of Lake Huron. The realized per capita rate of growth for these colonies over a 10-year period declined with increasing colony size (Fig. 3; slope =  $-0.551$ ,  $df = 41$ ,  $p < 0.001$ ). Thirty-six colonies (84% of total) showed an increase in the number of nesting pairs (positive per capita rate of change), while seven colonies (16%) registered a loss of nesting pairs (negative per capita rate of change) over the time period.

Similarly, from 2000 to 2003, the realized per capita growth rate also showed density-dependent growth for 70 colonies (Fig. 4). Twenty-seven colonies in 2003 were in decline (38%). Splitting the colonies present in 2000 into two groups above and below the overall median colony size (median = 240 nests) shows that a relatively small proportion of colonies (5 of 27; 18.5%) below the median nest count represented colonies in decline. Colonies above the

**Fig. 2.** Time series of nest counts in 13 colonies of double-crested cormorants, *Phalacrocorax auritus*, in the North Channel (NC) and Georgian Bay (GB). The number associated with each colony (e.g., GB1) is based on colony identification in Appendix 1 of Weseloh et al. (2002). Solid circles are observed nest counts. Open circles are estimates of nest counts based on per capita rates of growth or decline from observed nest counts that bracket the time period without nest counts. Note scale differences in the y-axis. Significance is based on a randomization test: \*,  $p < 0.05$ ; \*\*,  $p < 0.02$ ; and \*\*\*,  $p < 0.01$ .



overall median nest count represented a larger percentage of the colonies in decline (22 of 27; 81.5%). The experimental egg oiling initiated in 2002 at some locations did not have a clear effect on colony size in 2003. Eight of the 15 colonies oiled in 2002 showed a negative per capita rate of change, while the remainder registered a positive per capita rate of change.

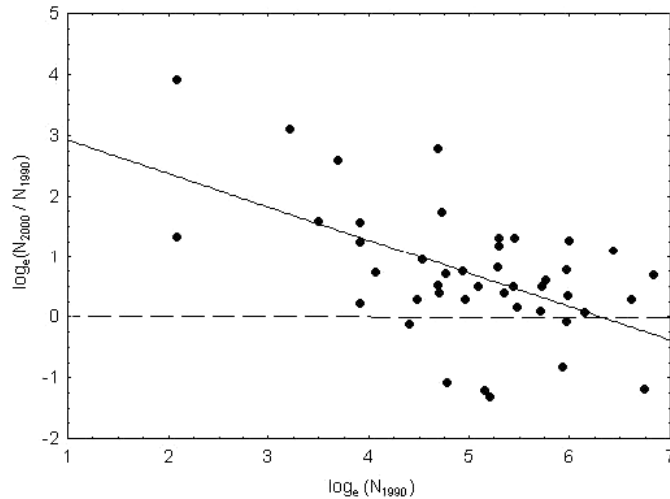
To address the effect of the size-dependent hypothesis on colony growth, the growth rate of the cormorant colonies over the 1990–2000 period was regressed upon the inverse of the square root of colony size (Moss et al. 2002). The slope of this relationship was 1.198 (the slope under the size-dependent hypothesis is equivalent to  $3.54k$ , and the parameter  $k$  was 0.338). We applied this growth rate to the observed colony sizes in the 1990 survey and compared the projected mean colony size under size dependency with the observed count in 2000. The mean observed colony size in 2000 was 477 nests (95% CI 332–621), while the projected mean colony size under size-dependent growth was 328 nests (95% CI 234–422). The difference between observed

and projected nest counts is significant ( $t = 2.473$ ;  $df = 42$ ;  $p = 0.0175$ ). The approach indicates that density-dependent colony growth cannot be fully accounted for by the size-dependent growth hypothesis alone, especially since observed colony sizes were generally greater than projected colony sizes.

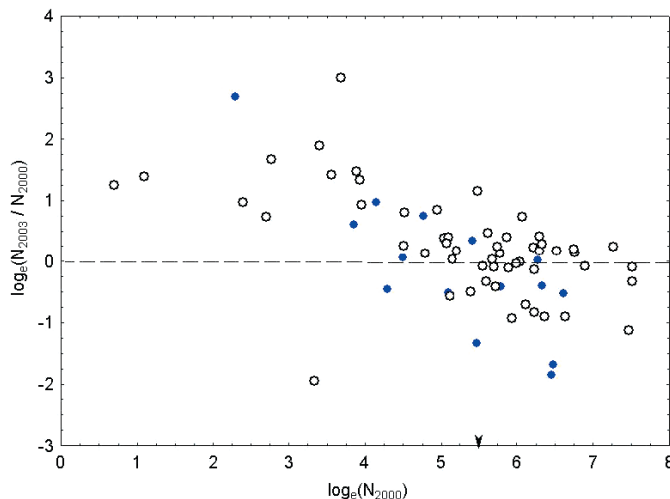
### Population growth

There was a good fit of the population growth model to the nest count data for the North Channel ( $R^2 = 0.887$ ; Fig. 5) and Georgian Bay ( $R^2 = 0.901$ ; Fig. 6). Both regions show clear evidence of reaching a population carrying capacity. The carrying capacity parameter,  $K$ , was estimated as 10815 nests for Georgian Bay (95% CI 8533 – 13067 nests) and 11445 nests for the North Channel (95% CI 8433 – 14456 nests). Although  $K$  is quite similar between the two regions, total water area and water area  $\leq 20$  m deep are less in the North Channel than in Georgian Bay, indicating that the carrying capacity per unit area is higher in the North Channel than in Georgian Bay. Both regions

**Fig. 3.** The realized per capita rate of change,  $r$ , from 1990 to 2000 for double-crested cormorant colonies in the Canadian waters of Lake Huron as a function of colony size in 1990. The linear estimate is  $y = 3.47 - 0.55x$ .



**Fig. 4.** The realized per capita rate of change,  $r$ , from 2000 to 2003 for double-crested cormorant colonies in Canadian waters of Lake Huron as a function of colony size in 2000. Closed circles are colonies that received oiling in 2002 and open circles are colonies that did not receive oiling. The arrow on the x-axis is the median colony size in 2000 for Lake Huron.

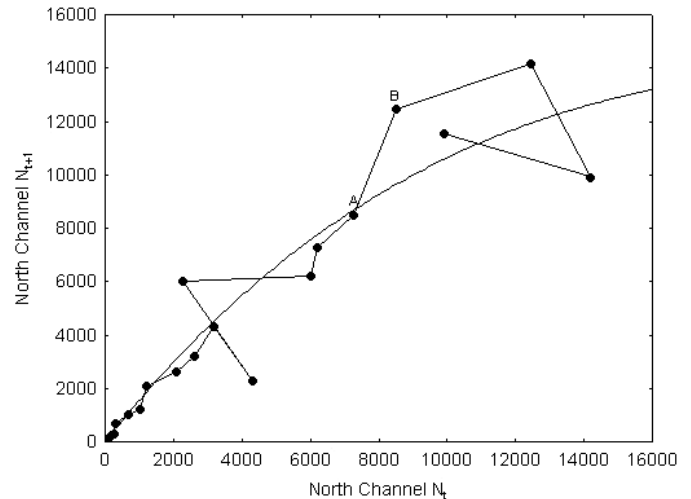


show movement of the population of nesting adults above and below the fitted line as the population trajectory reaches a carrying capacity, followed by a clockwise trajectory at carrying capacity.

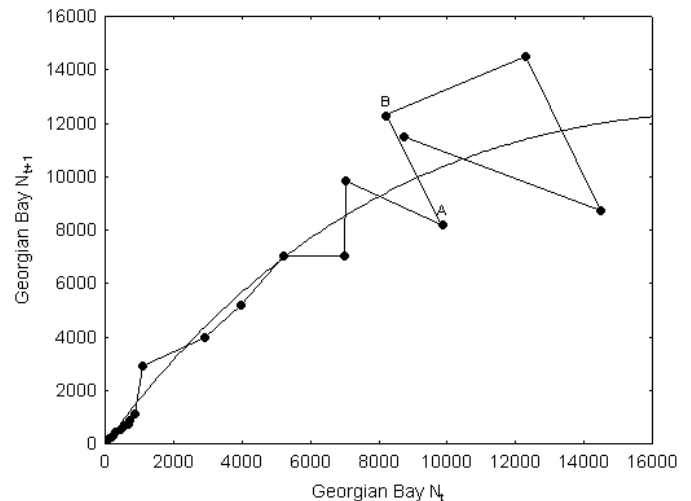
### Colony area index

The population increase and spatial expansion of nesting double-crested cormorants in the North Channel and Georgian Bay can be shown using the colony area index (Fig. 7). In 1990, the number of nesting birds was sparsely distributed throughout the North Channel and Georgian Bay (Fig. 7). From 1990 until 2003, the area covered by the cormorant colony area index increased to eventually cover most of the coastal zone of the North Channel and Georgian Bay.

**Fig. 5.** Phase plot of population growth for the aggregate nest count of double-crested cormorants (1979–2003) in the North Channel, Lake Huron. The periods of multiple-year intervals are indicated by A (1994–1997) and B (1997–2000).



**Fig. 6.** Phase plot of population growth for the aggregate nest count of double-crested cormorants (1979–2003) in Georgian Bay, Lake Huron. The periods of multiple-year intervals are indicated by A (1994–1997) and B (1997–2000).

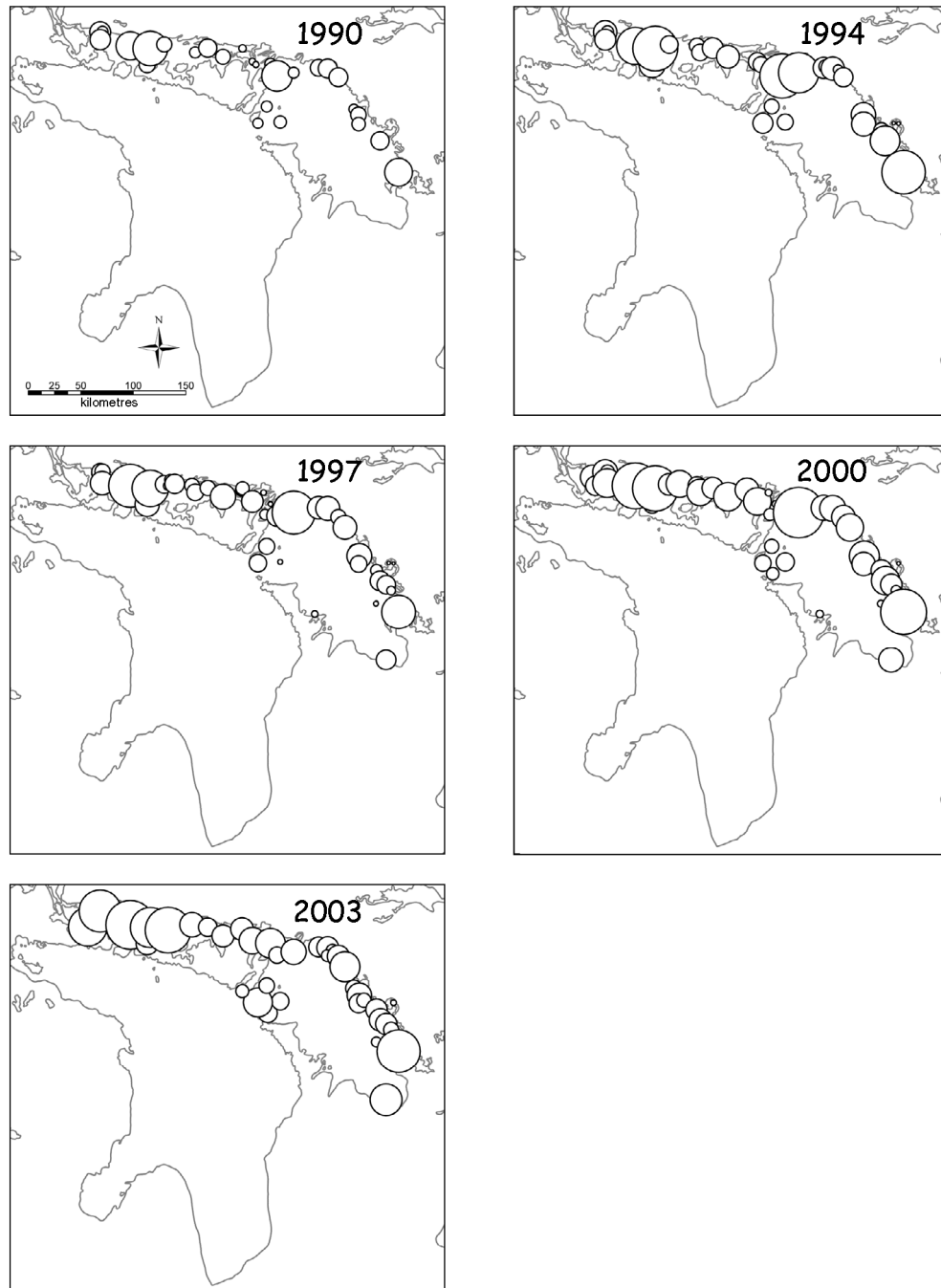


As the population of nesting double-crested cormorants increased, the percent coverage of the lake surface  $\leq 20$  m deep by colony area indexes increased from approximately 35% in 1990 to 70%–80% in 2003 (Fig. 8).

Expressing the number of nests in a colony as a density (nests/km<sup>2</sup> of surface water  $\leq 20$  m deep within each colony area index; Table 2) provides an interesting contrast with the observed changes in numbers and distribution of nesting cormorants. The density of breeding adults at the level of the colony area index (breeding adults = nest count  $\times$  2) remains relatively constant at approximately 3–4 nests/km<sup>2</sup> throughout the period of whole-lake surveys, when colony formation was not complete (i.e., 1990), as well as when the population as a whole had reached a carrying capacity (2000–2003).



**Fig. 7.** Map series showing coverage of the North Channel and Georgian Bay by the colony area index,  $\sqrt{N}/2$ . The size of each circle reflects the nest count per colony ( $N$ ). Some small colonies adjacent to a large colony were included in the large-colony estimate.



## Discussion

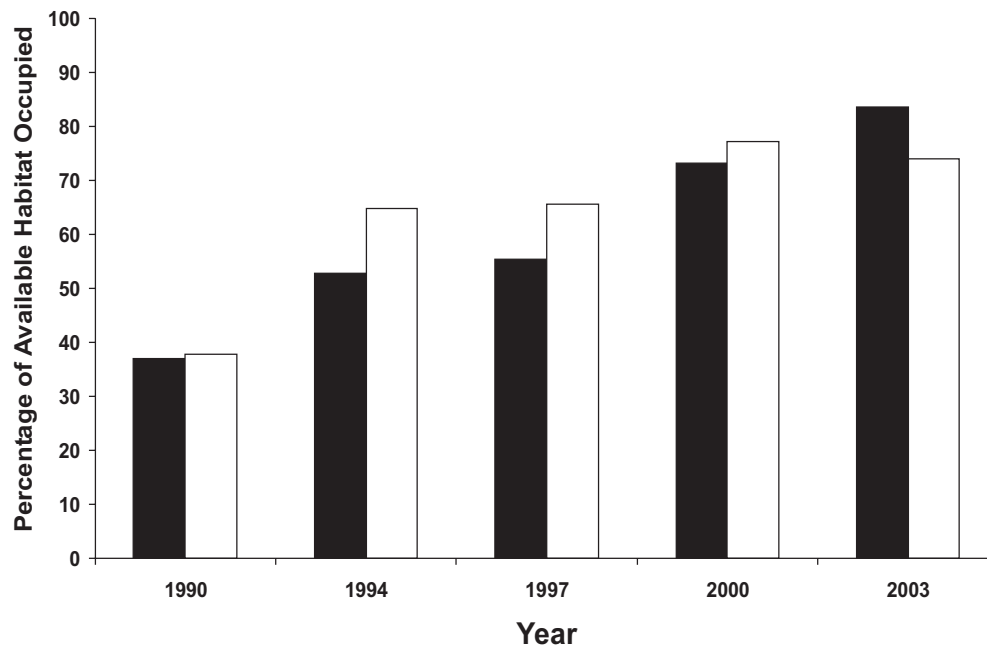
The period of sharp increases in the number of nesting double-crested cormorants has come to an end on Lake Huron after 20+ years of population expansion. We found evidence for density-dependent population regulation. First, a time series of nest counts at specific colonies reveals density-dependent growth in the number of nesters in most colonies. Second, the per capita rate of increase from 1990 to 2000 was higher in small nesting colonies than in large nesting colonies. In the most recent period, 2000–2003, larger nesting colonies (i.e., those above the median colony

size) represented a greater proportion of declining colonies than smaller nesting colonies. Experimental oiling did not result in negative growth at all oiled colonies in the first year subsequent to oiling. Third, phase plots of the aggregated counts of double-crested cormorants in the North Channel and Georgian Bay follow a Ricker population growth model, with a clockwise turn occurring in recent years in both regions. Fourth, the spatial coverage of the North Channel and Georgian Bay is extensive by 2000–2003, as indicated by the colony area index, coinciding with the initial clockwise turn in the phase plots.

Changes in the nesting population of double-crested cor-



**Fig. 8.** Percent coverage of foraging habitat ( $\leq 20$  m water depth contour) by the foraging area index perimeters in the North Channel (black bars) and Georgian Bay (open bars).



**Table 2.** Mean number of nests (per square kilometre of surface water  $\leq 20$  m deep) in the Georgian Bay and North Channel areas of Lake Huron based on whole-lake surveys of nesting colonies (1990–2003).

Year	Georgian Bay			North Channel		
	N	Mean	95% CI	N	Mean	95% CI
1990	13	2.70	1.88, 3.52	15	3.19	2.61, 3.77
1994	18	3.30	2.17, 4.43	13	3.70	2.62, 4.78
1997	20	3.32	2.45, 4.19	24	3.25	2.62, 3.88
2000	20	3.89	2.81, 4.97	24	3.26	2.72, 3.80
2003	23	3.54	2.72, 4.36	13	3.96	2.98, 4.94

**Note:** Estimates are based on the area of circular colony area indexes ( $N$  = number of colony area indexes); 95% confidence intervals are reported for each year.

morants found in this study followed a pattern observed in recent years in other locations with other species of cormorants (Bregnballe et al. 2003). Total nest counts increased sharply in the early to mid-1990s; after this period, a decrease in the realized per capita growth rate resulted in much lower rates of population change. In recent years there have been declines in the number of nesters reflected as decreases in total nest counts and colony numbers over large geographic areas. Bregnballe et al. (2003) described this change as a transition from growth to saturation at the population level. Others, using the logistic growth model, have shown that cormorants can reach a carrying capacity on lakes during winter (Suter 1995). In Europe, population growth of great cormorants (*Phalacrocorax carbo* (L., 1758)) is density dependent following an initial phase of population expansion (Frederiksen et al. 2001).

The mechanism(s) of density-dependent population regulation in cormorants in the Laurentian Great Lakes has not been examined. There is little published data on colony-specific parameters such as reproductive success, survival,

chick growth, and production or adult foraging behaviour in this region to resolve this question. Research on other species of cormorants and colonial waterbirds may be relevant here. Bregnballe (1996) and Frederiksen and Bregnballe (2000a, 2000b) found indications of density-dependent changes in chick production, adult survival, colony fidelity, natal philopatry, and prospecting by subadults in a Danish colony of great cormorants. Reductions in food availability at high population abundance were regarded as the mechanism behind these changes. Alvo et al. (2002) documented increases in numbers of double-crested cormorants at inland locations adjacent to Lake Huron and speculated that prospecting by cormorants may have been driven by intraspecific competition. Dispersal of great cormorants from breeding colonies to new breeding locations increases with declines in mean brood size (Hénaux et al. 2006). Since mean brood size declines with colony size in great cormorants (Bregnballe 1996), food shortages thought to be behind declines in colony productivity may be driving cormorant dispersal and prospecting behaviour (Schjorring et al. 1999, 2000; Frederiksen and Bregnballe 2001). Lewis et al. (2001) found that foraging-trip duration in northern gannets increased with colony size and that colony growth declined as colonies became larger. Reductions in prey fish availability because of disturbance by foraging gannets or the need to integrate foraging success over wider areas as a function of colony size, and not simply lower food biomass associated with larger colonies, could account for these changes. In Audouin's gull (*Larus audouinii* Payraudau, 1826), the probability of whether or not a nesting colony was in decline was solely a function of whether the colony was increasing or decreasing in the previous year, with a higher probability of decline associated with declines in previous years (Martinez-Abraín et al. 2003). Reproductive success, island habitat features, historical patterns of occupancy, or interspecific effects did not appear to affect colony dynamics in Audouin's gulls.

There was a reduction in population growth from 1994 to 1997 in our data set (Table 1). Colony-specific trends showed a sharp decline in nest counts in 1997 for 4 of 13 colonies (Fig. 1). The decline in nesting adults at this scale can be due to large-scale emigration or a reduction in recruitment to the nesting population. Since no large-scale increase in inland nesting colonies was detected in Ontario at that time, the observed nest declines in 1994–1997 likely reflect a decline in recruitment. The strongest candidate explanation is the effect of the Mount Pinatubo eruption in 1992, which sharply decreased water temperatures in the Laurentian Great Lakes and disrupted year-class production in nearshore fish species (Casselman 2002). If this ecosystem disruption affected offspring production in cormorants in 1992, then the decline in nests in 1994–1997 would reflect a lag response in adult recruitment.

Competition for nest sites is a possible regulatory mechanism but one that seems unlikely in our study region of Lake Huron, where thousands of islands define the North Channel and Georgian Bay. Intra-colony differences in nest-site quality could play a role in chick production, but we have no data to resolve this question. We found that the growth of double-crested cormorant colonies in Lake Huron is not well defined by the size-dependent hypothesis (Moss et al. 2002). Two small rock islands in the North Channel that might be expected to have colony growth based on habitat size did not show density-dependent growth (Fig. 2; NC32, Kalulah Rock; NC33, Africa Rock). Although our analysis does not eliminate size-dependent growth as a possible mechanism for explaining colony growth relative to density-dependent processes, we found that cormorant colonies were generally larger than predicted by the size-dependent hypothesis, indicating that other aspects of their ecology are setting upper limits on colony size.

The North Channel is shallower, has a shorter flushing time (approximately 2 years for the North Channel and 8.5 years for Georgian Bay), has greater phosphorous loadings, and has greater seasonal depletion of nutrients than Georgian Bay (Weiler 1988). Benthic biomass is generally higher in the North Channel than in Georgian Bay and the benthic community composition of the North Channel is more like that of Lake Superior (Barton and Griffiths 1984; Auer and Kahn 2004). Fish density in the North Channel is potentially higher because of the more river-like environment, and higher nutrient loadings can support more fish per unit area (Minns 1995). Considering these differences, and similar estimates of  $K$  in both regions (North Channel, 11 445 nests; Georgian Bay, 10 815 nests), the population of double-crested cormorants along the coast of the North Channel is likely at a higher density than that along the coast of Georgian Bay.

Some population characteristics found in this study are similar to estimates from published research on cormorants with more detailed time series of abundance and productivity. The strength of density regulation at  $K$ ,  $\gamma$ , for the nesting population of cormorants in our study (2.06 for the North Channel, 1.80 for Georgian Bay) is similar to  $\gamma$  for the great cormorant (2.10) and greater than that for the European shag, *Phalacrocorax aristotelis* (L., 1761) (0.36) (Saether and Engen 2002). Saether and Engen (2002) found the parameter  $\gamma$  to be positively correlated with environmen-

tal variance for nesting populations of birds. As well, the apparent annual survival of adult great cormorants from the long-term study in Denmark ranged from 0.74 to 0.95 (Fredriksen and Bregnballe 2000a). An annual survival estimate of 0.85 was employed in a population model of Lake Ontario double-crested cormorants (Blackwell et al. 2002). Assuming these estimates cover the range of survival for adult double-crested cormorants on Lake Huron, interpolating from the negative relationship found by Saether and Engen (2002) between adult survival and  $r_0$  leads to a close match between our empirical estimates of  $r_0$  employed in the Ricker model and expected values of  $r_0$  from their regression model.

Circular indexes describing foraging radii have been used to estimate trophic transfer patterns in other waterbirds (e.g., Furness 1978). An assumption of equal distance between colonies has been used to argue for foraging competition as a mechanism controlling colony size (Furness and Birkhead 1984) or determining the relative availability of foraging areas between adjacent colonies (Cairns 1989). Detailed information on colony-specific foraging locations is not available for colonies on Lake Huron. We assumed the potential foraging radii of nesting adults increased as a function of colony size, which seemed reasonable given the positive correlation between maximum foraging distance in cormorants and shags and  $\sqrt{N}/2$ , where  $N$  is the number of nests in a colony (see also Lewis et al. 2001). The colony area index should be viewed as a general index of spatial coverage for a given colony size. In other cormorant species, foraging locations appear to be colony-specific with relatively little overlap over large scales (Quintana 2001; Sapoznikow and Quintana 2003). In this study, maximum coverage of the coast of Lake Huron based on the colony area index coincided with the period when phase plots showed a clockwise turn characteristic of a population at carrying capacity.

An important question at this point is whether density dependence during the breeding season operates at the colony and (or) local level during the nesting period or more globally at the level of coastal regions. Recent theoretical work on colony formation shows that a combination of local density-dependent processes (i.e., nest site limitation) and strong nest-site fidelity results in slow development of new colonies because of limited adult movement, with colony sizes achieving a rather narrow size distribution (Matthiopoulos et al. 2005). In contrast, under global density-dependent processes (i.e., food limitation), strong nest-site fidelity results in increased variability in colony sizes, the aggregate count of breeding birds shows a rapid increase to an overall carrying capacity, and the persistence and size of individual colonies are generally a result of competition for limiting resources and the timing of initial colony formation (Matthiopoulos et al. 2005). In both cases, apparently suitable colony sites remain unoccupied largely because of limited movement in the case of local density dependence and because of stochastic timing and competition in the case of global density dependence. Colonies on Lake Huron are present on a small percentage of available islands along the coast, suggesting that one or both processes outlined by Matthiopoulos et al. (2005) are operating in this system. Results from this study point to the large scale (i.e., global in the context of Lake Huron) as the scale at

which population regulation operates in the North Channel and Georgian Bay. Colony-specific trajectories of nest numbers revealed density dependence in some cases, but not all (Fig. 2). Lake Huron colonies varied widely in size (e.g., see y-axes in Fig. 2; Fig. 7), with the aggregate population trend (Figs. 5 and 6) reflecting none of the local variation in nest numbers at the colony level or any transient behaviour (see Fig. 3 in Matthiopoulos et al. 2005). Foraging movements in a number of cormorant species are extensive (e.g., Stapanian et al. 2002), as is prospecting for nest sites among colonies (Schjorring et al. 1999). This may be a general phenomenon in colonial waterbirds, as food limitation is widely seen as limiting the growth of populations (Ashmole 1963; Birkhead and Furness 1985; Furness and Monaghan 1987; Croxall and Rothery 1991), and is likely the case for double-crested cormorant colonies on Lake Huron. A broader ecosystem context includes the recognition that piscivorous birds can have strong top-down effects in aquatic food webs (Steinmetz et al. 2003; Rudstam et al. 2004).

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