The cumulative effects of management on the population dynamics of the Double-crested Cormorant *Phalacrocorax auritus* in the Great Lakes

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Wildlife species have been subject to control efforts throughout human history due to real or alleged human–wildlife conflicts. The Double-crested Cormorant *Phalacrocorax auritus* in the interior of North America is no exception, with recent population growth leading to increased conflicts and consequently the development of many control programmes. These control programmes are usually conducted at local scales, often with little or no effort to assess their cumulative effects at the population level. We attempted the first comprehensive assessment of the cumulative effects of control at various spatio-temporal scales, focusing on 199 colonies of Double-crested Cormorant monitored during a 29-year period. Linear models were used to assess the relationship between colony-specific growth rates and a set of candidate factors using an information-theoretic approach. Colony-level density-dependent effects and local control efforts had the greatest influences on population growth. We detected a cumulative effect of management, whereby (i) the reduction in population growth rate was generally stronger when different control activities such as culling or egg oiling were combined, and (ii) past control operations tended to have a pervasive impact on growth rates, especially egg oiling and nest destruction, which negatively affected local recruitment. However, our results also suggest that catastrophic events and the culling of breeding adults that occurred at least 2 years previously could fuel subsequent recruitment or natural immigration from nearby colonies, for instance if the breeding success of remaining pairs was increased through a diminution of density-dependent regulatory processes. Density-dependence at the metapopulation level constituted a third source of regulation, as local growth rates were reduced with increasing number or proximity of active neighbouring colonies. We also found evidence that the culling of Double-crested Cormorants wintering in the southeastern USA could negatively impact the population growth of individual breeding colonies in the Great Lakes, although further research integrating models of migratory connectivity is needed to reach more definitive conclusions. Finally, despite previous studies emphasizing its importance, the net effect of management-induced dispersal appeared small at large spatial scales. We show that this can be explained in part by control strategies (e.g. spatially clustered operations). The continuation of Cormorant management efforts will provide an opportunity to refine the present assessment of the relative importance of density-dependence, breeding vs. non-breeding season management and dispersal, particularly if population models are coupled with monitoring programmes within an adaptive management framework.

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There is a long history of management efforts to mitigate human–wildlife conflicts across the world, involving diverse taxa ranging from commensal rodents to elephants, and including numerous bird species (Conover 2002). These control programmes are usually conducted at local scales, often with little or no effort to assess the cumulative effects of local control programmes at the population level. Given the numbers of organisms controlled through reproductive or lethal means and the controversy associated with many of these programmes, information on the cumulative impacts on populations is needed (Halpern *et al.* 2008).

The Double-crested Cormorant *Phalacrocorax auritus* is a native North American piscivorous waterbird. Reproductive failure caused by high levels of toxic contaminants in the environment led to virtual extirpation of Cormorants in the Great Lakes by the early 1970s (Weseloh *et al.* 1995). Environmental efforts coupled with protective regulations led to a dramatic recovery and expansion of the species across North America. The Great Lakes breeding population increased from approximately 135 breeding pairs in 1972 to 115 000 in 2000 (Weseloh *et al.* 1995, 2002). Other factors, such as exploitation of catfish during the recent expansion of aquaculture in the Cormorant's southeast wintering grounds, may have enhanced their overwinter survival (Glahn *et al.* 2000). At the same time, changes in Great Lakes fish communities may have increased the Cormorants' reproductive capacity during the breeding season (Weseloh *et al.* 1995).

The increase in Cormorant abundance has led to increased conflicts with people, due to real and perceived impacts to sportfish and aquaculture, competition with other colonial waterbirds and damage to vegetation (Taylor & Dorr 2003, OMNR 2006). To alleviate these conflicts, there has been a gradual increase in Cormorant population control efforts on both the breeding and the wintering grounds, a situation strongly reminiscent of Great Cormorant *Phalacrocorax carbo* control in Europe (Frederiksen *et al.* 2001).

Cormorant management operations are widespread in North America, and management policy varies by province (Canada) or state (USA). Cormorant management techniques may include harassment at roosting or breeding sites, culling of breeding or wintering Cormorants, egg oiling (to prevent hatching and re-laying), and nest destruction or removal. For instance, during 2009 in the USA (a fairly typical year: T. Doyle unpubl. data), 48 239 Cormorants were killed and 32 296 nests oiled or destroyed. However, few studies have addressed the consequences of Cormorant management and these have had a limited spatial scope (Bedard *et al.* 1995, Duerr *et al.* 2007, Dorr *et al.* 2012). While there currently is no stated population-level management strategy or goal, many programmes operating at regional or sub-population scales may cumulatively affect the population, warranting the need for a comprehensive assessment of the cumulative effects of management at various spatio-temporal scales.

We studied the impact of management on Cormorants in the Great Lakes region, part of the largest and most widespread (Interior) Cormorant breeding population, where conflict with people resulted in large-scale Cormorant control programmes (Wires & Cuthbert 2006). We first investigated management effects at various spatial scales. On a local scale, we were interested in how the different management techniques influenced Cormorant population growth rates. At a landscape scale, we addressed the effect of management in surrounding areas. Several studies have shown that local population dynamics may be strongly affected by natural dispersal processes in colonial waterbirds (Breton *et al.* 2006), and management can alter the rates of dispersal of birds from nearby colonies (Duerr *et al.* 2007). Finally, because many studies of migratory birds have suggested a link between conditions in the wintering range and adult survival or breeding success during the following season (Newton 2004), we also made an attempt to integrate the effect of culling operations in the wintering range on colony growth rates. On a temporal scale, we investigated the consequences of management history. In particular, delayed effects would be expected for techniques such as nest oiling because immatures do not generally recruit into

the breeding population before the age of 2 or 3 years (Blackwell *et al.* 2002). Specifically, our objectives were (i) to assess the expectation that population control at various spatio-temporal scales has cumulative effects on Cormorants, and (ii) to quantify the unique contribution of the different sources of population regulation. We aim to provide information on the relative importance of density-dependence, local control and control in neighbouring colonies or sites, as well as non-breeding season control, to better inform Cormorant management efforts in North America.

METHODS

Study area

The study area encompassed the Great Lakes of the USA and Canada, which represent approximately 52% of the total breeding pairs of Cormorants in the Interior Region (Wires & Cuthbert 2006). The Cormorant is also present in four other major breeding regions: Alaska, the Pacific Coast, Southeast US/Caribbean and the Northeast Atlantic Coast (Wires & Cuthbert 2006). The study area included the following areas (Fig. 1): the
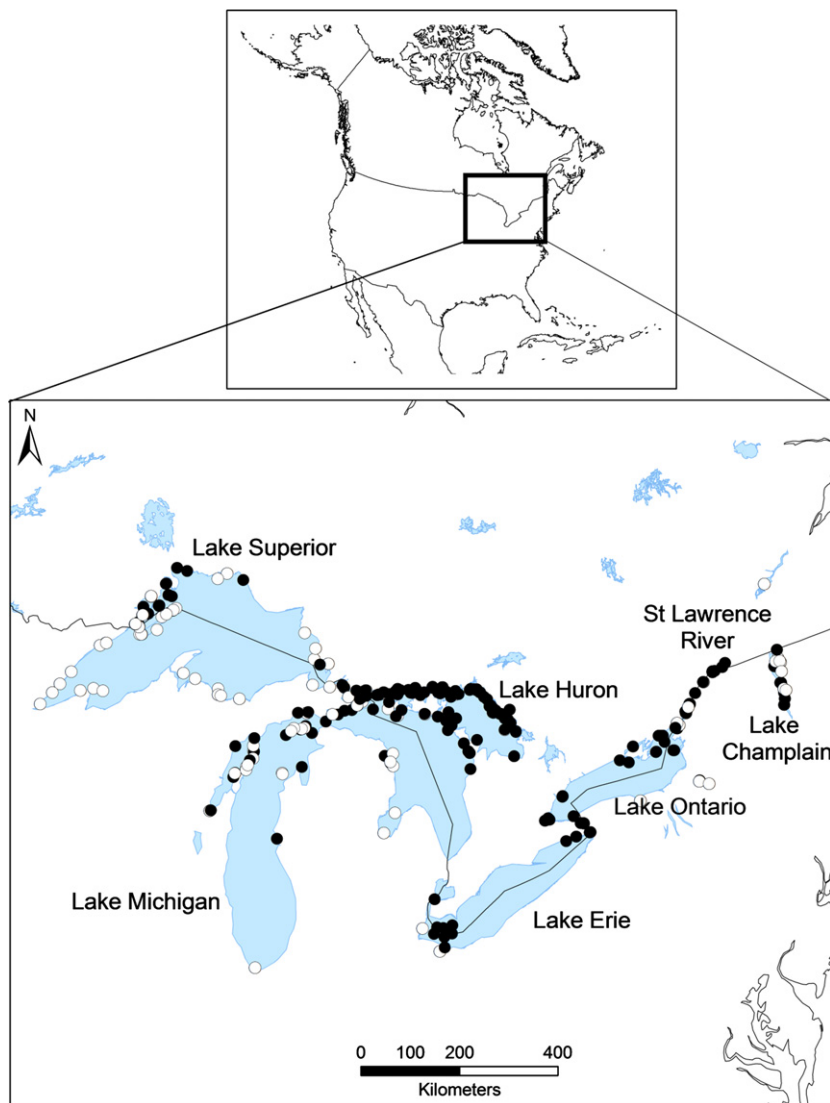

Figure 1. Study zone in the Great Lakes area. We used data from 308 colonies (open and black dots), and growth rates were obtained from 199 of them (black dots); many colonies are not visible due to overlap.

St. Lawrence River, Lakes Superior, Michigan, Huron (including Georgian Bay, North Channel and the St. Marys River), Erie (including the Detroit and Niagara Rivers and Lake St. Clair), Ontario (including Oneida Lake) and Champlain, the last-named being connected with Lake Ontario by dispersal (Duerr *et al.* 2007). Further information on the study population (changes of population size, distribution of colonies, etc.) is given elsewhere (Weseloh *et al.* 1995, 2002, Ridgway *et al.* 2006).

Data collection

We compiled all available colony-specific nest counts (the number of apparently occupied nests, containing eggs or empty) and management operations (the number of nests oiled, nests destroyed and Cormorants culled) for the Great Lakes area from 1977 to 2009 (see Acknowledgements for data sources). We obtained data for 362 colonies, of which we discarded 49 because exact geographical coordinates were not available, and five because of uncertainties regarding management data. Culling also occurred at 27 sites beyond breeding colonies (e.g. loafing sites), of which eight were discarded because exact coordinates were not available. Colonies were not necessarily surveyed each year, especially early during the study period. In contrast, some colonies were visited several times in a single breeding season. In this case, we used the largest nest count available, as well as the maximum numbers of nests oiled and destroyed in a single management session.

Response variable

For each colony i with nest count N in year t, the colony growth rate between year t and $t + 1$ was calculated as

$$GR(i,t) = \frac{N(i, t+1) - N(i,t)}{\max(N(i, t+1), N(i,t))} \quad (1)$$

This index was preferred to the classical $\lambda = N(i,t+1)/N(i,t)$ because (i) a series of simulations showed that both indices were monotonically related (not shown) and Spearman's rank correlation coefficient between λ and GR in our data set was 1.0, and (ii) λ, which is designed to quantify endogenous population growth, does not accommodate colony initiation well (it returns infinity).

Colony initiations are of primary importance in metapopulation dynamics in general and our analyses in particular, as they may be the consequence of density-dependent processes or management activities in nearby colonies. Our index (GR) has the preferable property of being symmetrical as regards colony initiation ($N(i,t) = 0$, $N(i, t + 1) > 0$: $GR = +1$, upper bound) and collapse ($N(i,t) > 0$, $N(i,t + 1) = 0$: $GR = -1$, lower bound). However this index requires knowledge of both $N(i,t)$ and $N(i,t + 1)$ and therefore is suitable only for description purposes and not as a tool for predicting abundance. Hence, by using the GR index a population growth rate could be calculated if two conditions were met: the colony was surveyed in two consecutive years, and the nest count was non-zero in at least one of them.

Explanatory factors

Explanatory factors were grouped into six distinct classes (Supporting Information Appendix S1).

Unexplained spatial variation (SV)
A different intercept was allowed for each colony to account for spatial variation not explained by other factors in the model.

Density-dependent effects (DD)
Three variables were computed: the initial nest count ni ($= N(i,t)$), the nest count in the previous year nip ($N(i,t−1)$) and the previous growth rate grp ($= GR(i,t−1)$). When the latter two variables were not available, we used the closest available previous nest count or growth rate (e.g. $N(i,t−2)$, $GR(i,t−2)$).

Seasonal effect of management (WM)
A variable called W_cul was created to account for the management of Cormorants outside the breeding season. Our aim was to calculate the total number of Cormorants culled in the 12 southeastern (SE) US states that form its main wintering range between the years t and $t + 1$ (October–April). The wintering area (as inferred from Hatch & Weseloh 1999) comprised a rectangle roughly delimited by Florida, Texas, Oklahoma and North Carolina. Because the month of take was not readily available, we estimated W_cul as the average number of birds culled during the years t and $t + 1$: $W\_cul = (N\_cul(t + 1) + N\_cul(t))/2$. This estimate is reasonable if the vast majority of

Cormorants in these 12 SE US states were culled during the winter period and better if the effort is equivalent for October–December and January–April, which we regard as likely.

Local effect of management (LM)

Four variables measured the intensity of management at the focal colony. *L_oil*, the proportion of nests oiled, was calculated as the maximum number of nests oiled in a single management operation divided by the nest count. *L_nd*, the proportion of nests destroyed, was calculated as the maximum number of nests destroyed divided by the nest count. Untreated nests were either empty or not accessed (e.g. in trees). *L_cul*, the proportion of culled Cormorants, was calculated as the total number of Cormorants culled at the colony during the breeding season divided by two times the nest count. To avoid a few overly large values (e.g. when culling occurred in a year with no breeding, *L_cul* would be infinity), we set *L_cul* to 2 whenever *L_cul* > 2. Culled Cormorants were generally adults, but sometimes chicks may have been included even if not explicitly acknowledged.

Finally, various events that have a potential impact, including one-time or temporally limited events and some events that were not systematically recorded, were accounted for by the variable *L_div* (hereafter referred to as 'catastrophic' events). These events include harassment, illegal culling or nest destruction, predation and flooding of the colony. *L_div* takes a relative rank value of 1 when any such event was reported, 0.5 for suspicions only (e.g. vandalism), and 0 otherwise.

Spatial effect of management (SM)

To evaluate the intensity of management in areas surrounding each focal colony i, we used a method from autologistic models (Guillaumet *et al.* 2008), in which each neighbouring area j is assigned a weight according to its distance from the focal colony. For instance, *S_cul* was calculated as:

$$S\_cul(i,t) = \left(\sum_{j=1}^{n} w_{ij} \cdot n\_cul(j,t) \right) / \sum_{j=1}^{n} w_{ij} \qquad (2)$$

where n is the number of neighbours, *n_cul* is the number of Cormorants culled and w_{ij} the weight assigned to this neighbour. In our main analysis, w_{ij} was calculated as the inverse of the geographical distance between i and j:

$$w_{ij} = 1/(dist_{ij} + 1) \qquad (3)$$

We did the same for the remaining management variables (*S_oil*, *S_nd* and *S_div*). However, we also explored the consequence of using different weighting schemes, corresponding to alternative dispersal kernels (Supporting Information Appendix S2).

Inter-colony competition (IC)

Three variables were calculated for the year t: *GR_n* is the average growth rate of neighbours, calculated by combining Equations 2 and 3 but replacing *n_cul(j,t)* by *GR(j,t)*, *dmin* is the geographical distance of the focal colony to the nearest active neighbouring colony (a colony is regarded as active from the year of first observed breeding onwards), and *nb_n* is the number of active neighbouring colonies within the foraging perimeter of the focal colony. As an estimate of the foraging *radius*, we used the formula established by Ridgway *et al.* (2006) for cormorants and shags, where $radius(i,t) = 1.31 + 0.87 \cdot \sqrt{N(i,t)}/2$.

Effect of management history

Each growth rate *GR(i,t)* was tentatively explained by the management operations at the local and broader spatial scales that occurred during the years $t+1$, t, $t-1$ and $t-2$. For instance, at the local scale, the proportion of nests oiled in year t and in year $t-2$ corresponds to the variables *L_oil_0* and *L_oil_m2*, respectively. At the spatial scale, *S_nd_m1* is the average number of nests destroyed in surrounding colonies at $t-1$ (see Appendix S1 for a description of all variables).

Statistical analyses

Our final dataset consisted of 1581 growth rates obtained from 199 colonies, over 29 years (i.e. an average of 7.94 per colony, sd = 6.17), and a set of 40 explanatory factors. We excluded from analyses colonies that had either no growth rate at all (< two successive nests counts) or a single growth rate (because we could not compute *grp*). However, the nest counts and management data from the 109 excluded colonies and data from 19 additional culling sites were used to compute the explanatory factors concerning inter-colony competition and spatial management classes (see above). All quantitative variables were standardized (mean = 0, sd = 1) prior to analyses.

Model selection

Our aim was to investigate the statistical support and unique contribution of the different classes of explanatory factors. Mixed and state-space Bayesian hierarchical models were used in preliminary analyses to model the relationship between the response and explanatory variables. As they yielded similar results to linear models (not shown), we only present the latter for simplicity. We did not consider possible interactions between factors in this analysis because the large number of potential factors would have necessitated a considerable number of degrees of freedom, while within- and between-class model selection (see below) would have required the comparison of too many models. As a consequence, our estimates of management effects are restricted to additive effects.

We identified within each class the best set of predictors using the Akaike information criterion (AIC), hereafter called within-class model selection. The combination yielding the lowest AIC value was retained for subsequent analyses. For the two management classes *LM* and *SM*, the number of variables (16) would require comparing > 65 000 models. To avoid this, a two-step approach was implemented. First, a principal component analysis (PCA) was performed on the initial set of variables (one independent PCA for each class) and we retained only independent axes explaining a higher amount of variation than initial variables (i.e. eigenvalue > 1). This corresponded to five predictors for each class (PC1–PC5). Next, these five predictors were subjected to within-class model selection; while the best model included all five predictors for local management, only PC1 and PC5 were retained for spatial management.

We then built all 31 possible models with five classes of factors (*DD*, *WM*, *LM*, *SM*, *IC*). The sixth class, *SV* was always included, so *SV* alone constituted the 32nd model investigated. The models were ranked by rescaling the AIC values relative to the model with the lowest AIC. We then calculated the Akaike weights (Burnham & Anderson 2001).

The unique contribution of each class of factors was estimated by the coefficient of determination (R^2) difference between a model that incorporated that class and a model that did not. Classes of factors were added sequentially, starting with the class that yielded the largest reduction in AIC.

All analyses were performed with ʀ version 2.7.2 R Development Core Team (2008).

RESULTS

The best model contained variables from all classes except spatial management and explained nearly a third of total variance in colony growth rates (Table 1 & 2). The residuals were not normally distributed (Shapiro–Wilk test, W = 0.982, $P < 0.001$) because of two heavy tails in the growth rate data. Non-normality should not influence the results because of our large sample size (Sharma & Ali 1996). Indeed, exploratory analyses using either a generalized linear mixed model, coding the growth rate as positive or negative, or a regression based on the Skew-*t* distribution, which allows the skewness and heavy tails of distributions to be modelled (Azzalini & Genton 2008), yielded similar results (not shown).

The most important class appeared to be density-dependence, which explained 7.9% of the variance in growth rates (Table 2). Two variables in this class were retained in the within-class variable selection (previous growth rate and nest count), and both have strongly negative estimates (Table 3), as expected under a scenario of population regulation caused by natural density-dependent factors.

The next most important class was local management, explaining 5.5% of the variance. The first principal component (PC1) had the strongest influence, explaining 3.3% of the variance by itself

Table 1. Information-theoretic statistics. Ranking of best-approximating models (of 31 models in the candidate set), incorporating effects of five classes of factors (the sixth class, SV, was always included); only the four models with Akaike weight $w_i \geq 0.001$ are shown.

SV	DD	IC	LM	SM	WM	np	AIC	Δ_i	w_i
√	√	√	√		√	211	4321.22	0.00	0.601
√	√	√	√	√	√	213	4322.66	1.44	0.292
√	√	√	√	√		212	4325.97	4.75	0.056
√	√	√	√			210	4326.13	4.91	0.052

SV, unexplained spatial variation; DD, density-dependent effects; IC, inter-colony competition; LM, effect of local management; SM, effect of broader-scale management (i.e. neighbouring colonies or sites); WM, seasonal effects of (winter) management; *np* is the number of parameters fitted and Δ_i is AIC_i-min(AIC) (see text for details). A √ signifies that the variable (class of factors) was included in the model; otherwise, blank.

Table 2. Contribution of classes of factors to goodness-of-fit. Unique contribution (*diff*, %) of each class of the best model (see Table 1) to R^2; w_i are Akaike weights; see text for details and Table 1 for the description of classes.

Model	w_i	Classes of factors	R^2	*diff*
	0.00	SV	0.142	
	0.00	SV + DD	0.222	+ 7.9
	0.00	SV + DD + LM	0.276	+ 5.5
	0.052	SV + DD + LM + IC	0.307	+ 3.1
Best model	0.601	SV + DD + LM + IC + WM	0.310	+ 0.3
2nd best model	0.292	SV + DD + LM + IC + WM + SM	0.311	+ 0.1

(Table 4; see also Table 3). Since the loadings of all 16 individual variables were positive (Table 4), PC1 could be seen as a measure of management intensity, and revealed a strong cumulative impact of management (any type of management action occurring at any time yielding an additional reduction of the growth rate). PC2 and PC3, although retained in the within-class variable selection, turned out to be non-significant once factors from other classes are factored in, and only explained an additional 0.3% of variance. The difference (~1.9%) was due to PC4 and PC5. PC4 was positively related to 'catastrophic' events, except those that occurred 2 years before (*L_div_m*2; see Table 4), and negatively related to growth rates (Table 3). Hence, most recent 'catastrophic' events appeared to have a regulation effect beyond the 'average' effect described by PC1. PC5 was positively related to prior culling and 'catastrophic' events that occurred 2 years before (*L_cul_m*2 and *L_div_m*2), which had strong positive loadings on PC5 (Table 4), whereas PC5 itself was positively related to growth rates (Table 3). Hence, positive values for these two variables contributed negatively to growth rates via PC1 and positively via PC5. We performed simulations based on the best fitting model to predict the net effect of these two variables. This was achieved by (i) creating pseudo datasets with new values for management variables (for instance, all values of *L_div_m*2 were increased by one); (ii) re-estimating corresponding (pseudo) PC1–PC5 values using principal axes; and (iii) comparing pseudo growth rates calculated using coefficients of the best fitting model with actual growth rates. We found that increasing the value of *L_cul_m*2 and *L_div_m*2 yielded a net increase in colony growth rates independently of the values given to other management variables (not shown). In other words, the cumulative effect of management, apparently valid for the remaining 14 variables, was not valid for prior culling and 'catastrophic' events (at *t*−2), which tended to favour positive current growth rates.

Inter-colony competition constituted the third largest source of regulation, explaining 3.1% of the variance. Local growth rates tended to be reduced as a function of the number and distance of active neighbouring colonies (Table 3). Management in the wintering grounds also appeared to have a negative impact (Table 3), although models excluding winter management received a non-negligible

Table 3. Regression coefficients ('estimate') of the best model, which incorporates effects of five classes of factors but excludes the 'spatial management' class; note that coefficients for *colony* (class SV) are not shown. se, standard error. For the local management (LM) class, the five factors PC1–PC5 were derived from a within-class principal component analysis based on 16 original variables; positive or negative loading of original variables is given in the 'definition' column (e.g. '+ culling' indicates that culling variables are positively related to PC3; see Table 4 for details); for PC5, 'recent' refers to management during year *t* + 1 and 'prior' refers to management during year *t*−2. See text, Table 1 and Appendix S1 for additional information, including definition of classes and detailed definition of factors.

Factors	Definition	Class	Estimate	se	*t*-value	*P*-value
grp	Previous growth rate	DD	−0.25	0.03	−9.92	< 0.001
ni	Nest count	DD	−0.23	0.04	−5.28	< 0.001
PC1	Management intensity	LM	−0.22	0.04	−6.18	< 0.001
PC2	+ Nest destruction	LM	0.02	0.04	0.51	0.61
PC3	+ Culling + 'Catastrophic' events	LM	−0.01	0.03	−0.37	0.71
PC4	− Culling + 'Catastrophic' events	LM	−0.12	0.03	−3.66	< 0.001
PC5	− Recent culling and 'catastrophic' + Prior culling and 'catastrophic'	LM	0.09	0.03	3.42	< 0.001
nb_n	No. of active neighbouring colonies	IC	−0.20	0.05	−4.38	< 0.001
dmin	Distance to the nearest active neighbour colony	IC	0.09	0.03	3.07	0.002
GR_n	Growth rate of neighbour colonies	IC	0.04	0.03	1.65	0.10
W_cul	No. of Cormorants culled in winter	WM	−0.09	0.04	−2.45	0.014

Table 4. Loading of local management variables subjected to a principal component analysis; also called variable coordinates (here normed to the square root of the eigenvalues).

	PC1	PC2	PC3	PC4	PC5
L_oil_1	0.409	−0.513	−0.308	0.115	0.129
L_oil_0	0.476	−0.639	−0.322	0.177	0.099
L_oil_m1	0.497	−0.632	−0.261	0.189	0.038
L_oil_m2	0.393	−0.487	−0.165	0.161	−0.008
L_nd_1	0.453	0.551	−0.322	0.012	−0.032
L_nd_0	0.467	0.626	−0.384	0.120	0.082
L_nd_m1	0.468	0.583	−0.363	0.174	0.069
L_nd_m2	0.418	0.409	−0.317	−0.033	0.110
L_cul_1	0.584	−0.054	0.186	−0.410	−0.368
L_cul_0	0.551	−0.024	0.294	−0.517	−0.067
L_cul_m1	0.333	−0.063	0.069	−0.464	−0.442
L_cul_m2	0.421	−0.007	0.404	−0.377	0.332
L_div_1	0.237	0.088	0.344	0.544	−0.454
L_div_0	0.360	0.106	0.616	0.517	−0.115
L_div_m1	0.355	0.096	0.622	0.348	0.104
L_div_m2	0.239	0.040	0.479	−0.079	0.643

PC1 alone explained 3.33% of the variance in growth rates, which corresponds to 61% of the variance explained by local management variables; PC2 explained 0.22% (4%), PC3 explained 0.05% (1%), PC4 explained 1.33% (24%), and PC5 explained 0.53% (10%).

statistical support (sum of Akaike weights > 0.10, Table 1), and winter management only explained 0.3% of the variance (Table 2). Although spatial management was excluded from the best model, it was included in the second best model with an Akaike weight of 0.29 (Table 1). The fact that it explained only 0.1% of the variance (Table 2), and that neither of the two spatial management variables (PC1 and PC5) were significant once other factors were introduced (both $P > 0.23$, not shown), suggests that the net effect of spatial management was, at most, weak.

DISCUSSION

We investigated the factors involved in the dynamics (regulation) of the Double-crested Cormorant over the entire Great Lakes ecosystem over almost three decades. Natural density-dependence at local (i.e. colony) and meta population scales and active control operations at the local scale appeared to be the main source of regulation in colony-specific growth rates.

The impact of colony-specific control programmes can be immediate, as when management affects survival of breeders, or delayed, as when it affects local recruitment through past egg oiling or nest destruction (PC1 in Table 3, see also variable loadings in Table 4). Most importantly, there appears to be a strong cumulative effect of management, wherein: (i) the reduction in growth rate is generally stronger when different management activities such as culling or egg oiling are combined, as suggested by variable loadings on PC1 (Table 4) and confirmed by simulations based on the best fitting model (not shown); and (ii) past management operations have a pervasive negative impact on growth rates, with the notable exceptions of culling and 'catastrophic' events 2 years before. Unlike egg oiling or nest destruction, some 'catastrophic' events such as partial colony flooding or the introduction of a terrestrial predator, as well as past culling of breeding adults, could actually favour subsequent recruitment or natural immigration from nearby colonies, for instance if the breeding success of remaining pairs is increased through a diminution of density-dependent regulatory processes (Henaux et al. 2007).

Although density-dependence at the local scale appeared to explain a higher fraction of the variance than local management operations (Table 2), we acknowledge that our analyses did not allow an accurate measurement of the contribution of density-dependence. For instance, part of the variance ascribed here to density-dependent effects may actually correspond to unaccounted count errors (Green 2008). Our objective was to partial out density-dependent effects, in order to estimate better the impact of management. Control operations in the USA and Canada are a relatively recent occurrence and are likely to have coincided with the period when the colonies were reaching carrying capacity (OMNR 2006, Ridgway et al. 2006 see also Fig. 2). This could have caused some statistical confusion between density-dependent and management effects. However, management variables contributed a significant amount of variance even after density-dependence was accounted for. For instance, the Akaike weight of the model including all classes except local management (on the breeding grounds) was null ($w_i = 2.9 \times 10^{-14}$, $\Delta AIC = 61.3$; not shown), suggesting that the regulation impact of management is not a statistical artefact.

A third source of regulation corresponds to density-dependence at the metapopulation rather than colony level (what we called inter-colony competition). In agreement with results published for different seabird species (e.g. Ballance et al. 2009
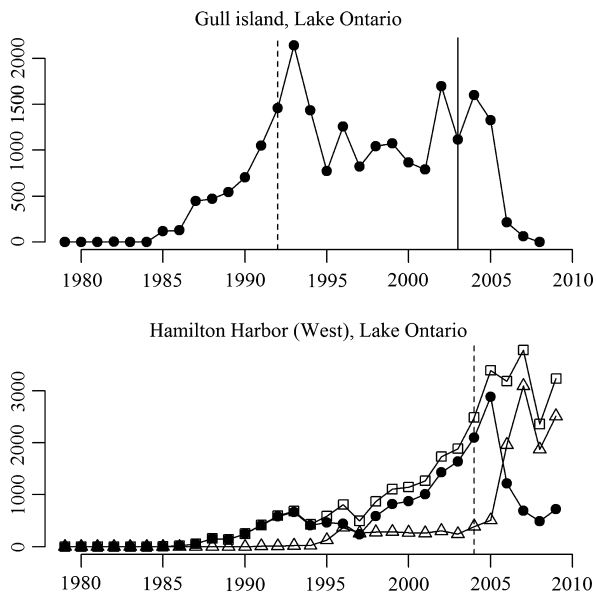
Figure 2. Example of individual colony dynamics and regulation factors. Nest count (*y*-axis) is represented over time (*x*-axis). Upper part: Gull Island, Lake Ontario (central basin): egg oiling (90–100%) was performed from 2003 (solid vertical line) to 2006; management impact is visible on the second and third year of management; note that part of the decrease may be due to density-dependent effects; the dashed vertical line shows very similar dynamics (1992–1995) that is not due to management (no management activities were reported); rather, it could be due to the colony overshooting, and then fluctuating around its carrying capacity. Lower part: Hamilton Harbor, Lake Ontario (western basin): the filled circles curve shows the dynamics of the colony at Pier 27, the open squares curve shows the cumulative number of nests in the harbour (all colonies pooled), and the open triangles curves is all colonies pooled minus Pier 27. Again, the 2004–2007 dynamics at Pier 27 is not due to management and appears to be due to emigration to neighbouring colonies in 2006–2007.

and references therein), we found that growth rates of Cormorant colonies tended to be reduced when the number of conspecific colonies increased in surrounding areas. Our data did not allow the investigation of the mechanisms involved, but disturbance and density-dependent depletion of prey around breeding colonies (Ashmole's hypothesis; Ashmole 1963) have been identified as important factors in other studies (e.g. Lewis *et al.* 2001).

Proximity of active nearby colonies could also facilitate natural emigration (not induced by population control), as dispersal tends to be distance-dependent in Great Cormorants and other birds (Henaux *et al.* 2007). Colony saturation, habitat destruction by Cormorants themselves (Boutin *et al.* 2011) and new breeding substrates provide incentives for dispersal (see also Henaux *et al.*

2007). For instance, the largest colony in Hamilton Harbor, Ontario, for two decades (1985–2005) lost three-quarters of its breeding Cormorants in just 2 years (2006–2007). The majority of missing Cormorants apparently relocated to nearby islands, of which three were constructed to provide nesting habitat for colonial nesting waterbirds in 1996 (Fig. 2). However, natural emigration–immigration alone seems unable to explain the negative association between local growth rates and proximity of nearby colonies, as one would predict a balance between colonies that gain immigrants and colonies losing emigrants.

We also found evidence that the culling of Cormorants wintering in SE USA could negatively impact the population growth of individual breeding colonies in the Great Lakes. This suggests that population control during both seasons may contribute to population reductions on the breeding grounds (Newton 2004, Stromborg *et al.* 2012). However, this conclusion is not very robust (see Results), and clearly future research, possibly incorporating theoretic modelling, will be required to understand better the relative contribution of winter management to population control on breeding grounds.

Contrary to our expectations, management in surrounding colonies did not have an important effect on local population dynamics. This result is at odds with the finding of Duerr *et al.* (2007) of a 3–20% breeding dispersal from a managed to an unmanaged colony in Lake Champlain. Our inability to find a relationship with spatial management may be due to a combination of several factors. First, our study had a reduced statistical power: Duerr *et al.* (2007) used mark–recapture data while we used time-series abundance data; for instance, management-induced movements from a small to a large colony may go undetected. We note, however, that we were able to detect another type of spatial effect (inter-colony competition, see above).

Secondly, there was a tendency for the spatial clustering of managed colonies (Supporting Information Appendix S3), which should reduce the impact of management-induced dispersal, as departing Cormorants from one managed colony may be compensated for by the ones coming from nearby managed colonies.

Thirdly, there was a tendency for management operations to simultaneously include culling and oiling (e.g. Spearman's rank correlation between

L_cul_1 and L_oil_1, $\rho = 0.34$, $n = 1581$, $P < 0.001$) which may reduce the impact of management-induced dispersal, because potentially departing birds are culled.

Fourthly, the weighting function (Equation 3) was not based on prior knowledge of the dispersal kernel. However, additional analyses suggested that our conclusions do not rely on the actual weighting scheme (Appendix S2). Although management-induced dispersal certainly does occur (Duerr et al. 2007), our data suggest that its net effect at large spatial scales may be small, partly because of the current management strategies.

Goodness-of-fit indices suggest that we could explain nearly a third of the total variance in growth rates ($R^2 = 0.31$, Table 2). As our set of explanatory factors was not designed to explain positive growth rates (e.g. during initial phases of colony growth), which can be expected to account for roughly half of the total variance, the best model probably explains altogether between one-third and two-thirds of the variance corresponding to population regulation. Several non-mutually exclusive explanations may account for the difference.

First, our data are intrinsically noisy despite our best efforts at standardization. In particular, nest counts are generally obtained on a single date that may vary between years, and the number of nests may vary widely within the breeding season (Ewins et al. 1995). In addition, data were not always collected or reported in a consistent fashion, an unavoidable consequence of the long period of time and large number of persons involved. For instance, nest removal was sometimes performed before the nest count was achieved (e.g. OMNR 2008, p. 34) without this critical information being acknowledged in the reports. In future, we advocate that managers systematically count nests before they initiate management activities. Unreported management operations constitute another source of noise. In Canada, private landowners are not required by law to report their operations (P. Hubert pers. comm.).

Secondly, some factors that were not explicitly accounted for may influence regulation of Cormorant populations, such as predation, diseases (Kuiken 1999), adverse climatic conditions (Ridgway et al. 2006) and food abundance (Ridgway et al. 2012). Reproductive success of Cormorants in the Great Lakes region is suggested to be dependent on large forage fish populations, notably Alewife

Alosa pseudoharengus (Weseloh et al. 1995). Consequently, colony dynamics may have been affected by a decline in Alewife abundance in at least some Great Lakes regions (e.g. Breton et al. 2008).

The probable continuation of Cormorant management efforts will provide a unique opportunity to refine the present assessments of the relative importance of density-dependence, breeding vs. non-breeding season management and dispersal hypotheses. Better data standardization and gathering of new important covariates will certainly contribute, and spatially explicit metapopulation models accounting for migratory connectivity (such as that presented in Guillaumet et al. 2012) incorporating feedback from monitoring programmes within a coordinated adaptive management framework (e.g. Lyons et al. 2008) could also provide an important step towards that goal. Importantly, population models may need to be parameterized according to the phase of development of local individual colonies and overall regional breeding numbers, because the surplus of potential recruits (and thereby the impact of control operations) is likely to change between the phase of population expansion, the first years after stagnation and further beyond stagnation. In other words, it is important to acknowledge that although in this paper we were interested in large-scale 'average' cumulative effects, the relative importance of regulation factors may actually vary sequentially in time at a smaller spatial scale. Further estimating the relative impacts of different types of control operations (e.g. nest destruction vs. egg oiling), and prior vs. current control operations may constitute additional challenges. Carefully designed experimental (rather than statistical) approaches could provide invaluable information in this respect, and could also be used to test for the existence of non-additive cumulative management impacts (Halpern et al. 2008).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Summary of explanatory variables.

Appendix S2. Optimization of the spatial management variables.

Appendix S3. Spatial clustering of managed and unmanaged colonies.