



Seasonal and annual patterns in density of double-crested cormorants in two coastal regions of Lake Huron

Mark S. Ridgway

Harkness Laboratory of Fisheries Research, Aquatic Research Section, Ontario Ministry of Natural Resources, Trent University, 2140 East Bank Drive, Peterborough, Ontario, Canada K9J 7B8

ARTICLE INFO

Article history:

Received 24 February 2009

Accepted 25 May 2010

Communicated by Stapanian/Hebert

Index words:

North Channel

Georgian Bay

Cormorant

Regime shift

Distance sampling

ABSTRACT

Aerial line transect distance sampling surveys of coastal areas in the North Channel and Georgian Bay, Lake Huron, were conducted to estimate density of double-crested cormorants (*Phalacrocorax auritus*). Surveys were approximately every two weeks through summer from 2000 to 2005. In each year, density of cormorants declined towards late summer indicating a large scale outward migration of cormorants from Lake Huron. The seasonal pattern of decline differed between the two regions based on a mixed model analysis. Seasonal patterns in apparent fledging patterns may reflect differences between the North Channel and Georgian Bay in nesting phenology, nesting synchrony or some combination of these factors. Density was generally higher in the North Channel relative to Georgian Bay seasonally and during the period 2000–2002 likely reflecting higher per unit area productivity in the North Channel. In the years 2003–2005, density was lower in both regions and similar compared to earlier years of the survey likely reflecting a regime shift that occurred in Lake Huron at that time. The effect of this change was greater in the North Channel than in Georgian Bay as indicated by a greater decline in cormorant density in the North Channel after 2002.

© 2010 Elsevier B.V. All rights reserved.

Introduction

The abundance of foraging waterbirds can be inferred from nest counts at colonies or based on sampling methods designed to estimate bird density away from colonies. In marine ecosystems, colony nest counts have been used to estimate prey consumed in large embayments (Bunce, 2001), the North Atlantic (Barrett et al., 2006), and even globally (Brooke, 2004). In the Laurentian Great Lakes, a similar approach incorporating colony nest counts for waterbirds, including double-crested cormorants (*Phalacrocorax auritus*), has been used to estimate prey consumption (Madenjian and Gabrey, 1995; Johnson et al., 2002; Seefelt and Gillingham, 2008). To track decadal changes in abundance, the Great Lakes Colonial Waterbird Survey (GLCWS) updates nest counts of colonial species as a population estimate for each lake in the Great Lakes (Weseloh et al., 2002). This survey provides relatively error-free estimates of adult colonial waterbird abundance.

Nest counts can serve as a basis for estimating density, and ultimately prey demand, if boundaries of aquatic ecosystems are sufficiently large to encompass movement of individuals. There are limitations with this approach. First, little or no information can be acquired on the spatial distribution of foraging waterbirds. Second, population estimates based on nest counts need to be extended beyond the nesting season to infer foraging densities at times after fledging. Since double-crested cormorants migrate south to wintering

areas at some point after the fledging period (Hatch and Weseloh, 1999), the timing of a decline in density is important at least in terms of adjusting downward numbers of cormorants remaining in any Great Lakes coastal ecosystem. Extrapolating densities from the nesting season to the entire foraging season is an important assumption in light of this seasonal behaviour. Third, assumptions about the proportion of non-nesting birds are necessary to account for their lack of detection in population estimates based on nest counts. This is especially important if trends in density do not coincide with trends in nest counts. These limitations are addressed by methods designed to detect waterbirds away from nesting colonies. In marine ecosystems, ship and aerial transect surveys have revealed heterogeneous distributions of waterbirds associated with coastal regions and upwelling zones (Ballance, 2007; Spear and Ainley, 2007).

There have been relatively few studies that incorporate sampling methods as part of surveys for estimating the distribution and abundance of waterbirds in the Laurentian Great Lakes. Two studies using ship-based strip transects (Tasker et al., 1984) found most double-crested cormorant detections close to shore (Stapanian and Bur, 2002; Langen et al., 2005), with approximately 80% of all detections in the western basin of Lake Erie occurring within 3 km of shore (Stapanian et al., 2002). Densities in the western basin of Lake Erie ranged from 2 to >100 cormorants/km² along shorelines away from nesting colonies (Stapanian and Bur, 2002; Stapanian and Waite, 2003). Offshore, density rarely exceeded 3 cormorants/km² (Stapanian and Waite, 2003). In the nearshore zone of the Les Cheneaux Islands, Lake Huron, aerial surveys ran parallel to shore, counted cormorants, and combined this count with ground-based estimates of

E-mail address: mark.ridgway@ontario.ca.

the proportion of birds leaving nesting colonies in the direction of the study area to estimate an index of cormorant use (Diana et al., 2006).

The purpose of this study is to summarize density estimates for double-crested cormorants in the North Channel and Georgian Bay using aerial line transect distance sampling for the years 2000–2005. During this time, dramatic change occurred in the Lake Huron food web including a return of fish assemblages in large embayments to a composition not observed for half a century (Fielder et al., 2007), resurgence of epilimnetic planktivores (Schaeffer et al., 2008), collapse of the demersal fish assemblage (Riley et al., 2008), and a shift in schooling planktivorous fish in coastal regions (Warner et al., 2009; Dunlop et al., 2010). Furthermore, non-predatory cladocerans are nearly extirpated and cyclopoid copepods have declined sharply (Barbiero et al., 2009). There has been a decline in the amphipod *Diporeia* and other benthic macroinvertebrates at depth in the main body of Lake Huron over the same time period as well (Nalepa et al., 2009). Collectively, many of these changes occurred in 2002–2004 with evidence of a sharp decline in primary productivity occurring in 2003 (Barbiero et al., 2009). Changes now taking place in Lake Huron may be unprecedented (Dobiesz et al., 2005), and likely qualify as a regime shift in an aquatic food web. Regime shift, a term used largely in marine ecology, is defined as “a persistent radical shift in typical levels of abundance or productivity of multiple important components of the [marine] biological community structure, occurring at multiple trophic levels and on a geographical scale at least regional in extent” (Bakun, 2004). Regime shifts can be driven by climatic and anthropogenic factors (Folke et al., 2004), and can be characterized as well by changes in the distribution of organisms at regional scales (Drinkwater, 2006). This description appears to characterize what is currently underway in Lake Huron.

The abundance of nesting DCCO increased exponentially in the North Channel and Georgian Bay in the past 25 years, peaked in 2001, and subsequently reached a carrying capacity (Ridgway et al., 2006). Regime shifts in the Lake Huron food web could very well affect the distribution and abundance of cormorants throughout their foraging area on Lake Huron.

The density of double-crested cormorants was summarized for the North Channel and Georgian Bay for the purpose of: 1) estimating annual and seasonal patterns of density using aerial line transect surveys over large spatial areas without reliance on nest counts; 2) determining whether the 2001 peak in nest counts (numbers of adults) corresponds to a peak in density away from nest colonies detected by aerial surveys, and 3) determining whether a regime shift detected in Lake Huron registers in density of cormorants and assessing the magnitude of possible change in density from before to after the regime shift.

Methods

Study area

Georgian Bay and the North Channel are two large ecosystems of Lake Huron with different limnological and productivity characteristics. Coasts of both ecosystems include extensive exposed shorelines of Precambrian Shield bedrock as well as dolomite limestone and numerous island archipelago systems (Sly and Munawar, 1988). Compared to the North Channel, Georgian Bay has a longer flushing time, lower river volume input from surrounding landscapes and more extensive depositional areas (Bennett, 1988; Thomas, 1988; Weiler, 1988). Sediments in the North Channel are similar in composition to non-depositional areas of Georgian Bay reflecting the scale of water movements in characterizing the North Channel (Thomas, 1988). Both ecosystems are considered oligotrophic with a high flushing rate (<2 years) in the North Channel effectively lowering the effects of higher phosphorus loadings compared to Georgian Bay (Weiler, 1988). Slope and intercept differences in plankton size spectra point to greater

particle abundance and greater trophic transfer efficiency in the North Channel relative to Georgian Bay (Sprules et al., 1988). Amphipod (*Diporeia*) abundance was greater in the North Channel than in Georgian Bay at most depths especially in the deep profundal (Nalepa et al., 2007). Collectively, these features suggest that densities of organisms at higher trophic levels could be greater in the North Channel than Georgian Bay.

Aerial survey

Aerial surveys were distributed among seven sample frames in Georgian Bay and the North Channel (Fig. 1). Sample frames were each 20 km × 20 km and positioned in 2000 to encompass approximately 1000–2000 nests per frame. Nesting colonies occur widely along both coasts and in areas within and beyond this aerial survey. Nesting colonies are mapped in Weseloh et al. (2002).

In each frame, 10 flight lines were mapped perpendicular to shore with each line partitioned into eight 2.5 km sections that served as the line length for distance sampling transects. Only line sections passing over water (including shoreline) were included in the sampling effort available for observation so some line lengths were less than 2.5 km. Total length of the survey was 1043 km with 438 km in Georgian Bay and 605 km in the North Channel. Aerial surveys occurred approximately every two weeks beginning in early summer and continuing until late summer (see Appendix A). Early years of the study included six flights with four and five flights occurring in 2004 and 2005, respectively (Appendix A).

Aerial surveys were conducted at 100 m altitude in a float plane flown at 167 km/h (indicated airspeed) which is approximately 50 m/s ground speed. Flight paths were maintained on course with the use of computer-based GPS tracking system registering the path of the plane on a mapped flight line. Two observers conducted the survey with one on each side of the plane. Observers sighted cormorants perpendicular to the plane through distance bands marked by cable on the wing struts that were positioned with the use of a clinometer and according to formulas in Buckland et al. (2001). Illustrations and examples of distance sampling band widths are provided in Buckland et al. (2001). Distance bands began from the edge of the pontoons (= 0 m) outward to 200 and 520 m in 2000–2002; 0, 200, 520 and 1000 m in 2003; and 0, 50, 150, 300, 500, and 1000 m in 2004–2005. In the early years of the study, cormorant abundance was higher and it was initially felt that observers could better manage fewer bands.

Observers recorded cormorant detections on portable tape recorders that were later transcribed. Detections of cormorant(s) were classified as being on the water, flying or loafing on land. Cormorants detected on land were adjacent to the lake shore standing on ground and not in tree roots. Most islands in Georgian Bay and the North Channel are treeless. An estimate of group size was made for each detection as well as allocating each detection to a distance band. An estimate of detection probability using double-observer methods was incorporated in data analysis for all years ($g(0) = 0.724$; $se = 0.059$; Bachler and Liechti, 2007; Ridgway, in press). Detection functions were estimated for each behavioural category (water, flying or land) for both the North Channel and Georgian Bay separately. Density estimation via distance sampling was done using DISTANCE 3.5 (Thomas et al., 1998). Group size vs. distance band regression (size bias regression) was used to compensate for bias stemming from detection of larger groups of cormorants further from the plane than smaller groups. Conventional distance sampling was done because density estimates were post-stratified by behavioural category and then summed for a final estimate.

The assessment of seasonal and annual patterns in cormorant density was conducted in a series of steps. First, cormorant density estimates from the aerial survey were summarized by date of flight and year for Georgian Bay and the North Channel. Ninety percent (90%) confidence limits were chosen because of the scale of the ecosystem monitored in this study.

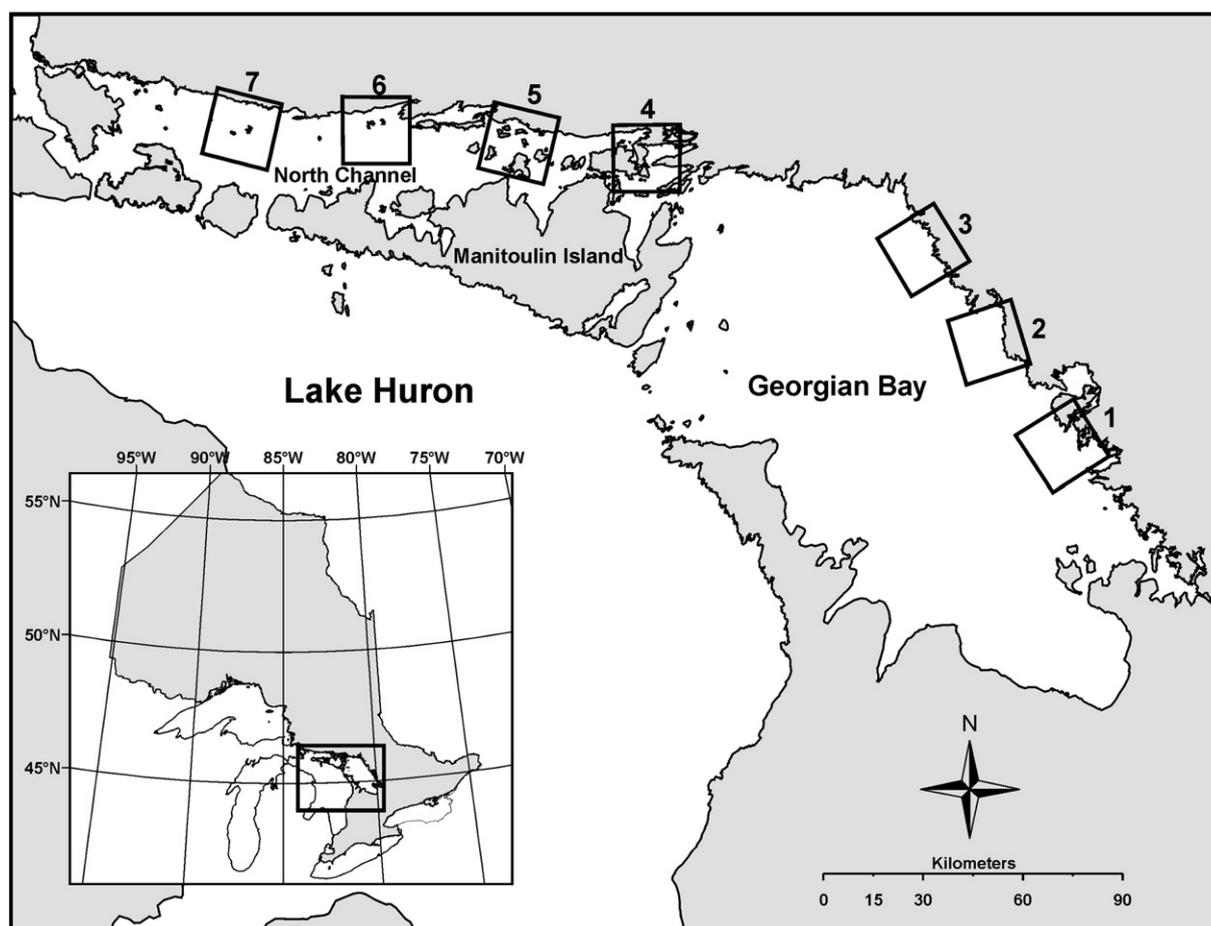


Fig. 1. Map of Lake Huron showing the seven sample frames in Georgian Bay (1–3) and the North Channel (4–7). Inset shows study area within the Laurentian Great Lakes.

Second, fixed and mixed model ANOVAs were conducted to evaluate annual and seasonal variation in cormorant density from frame-level density estimates. Recent general summaries of mixed/multilevel models in ecology are provided by Wagner et al. (2006) and Bolker et al. (2008), including variance components of random effects (percent of variance in response variable due to variation in random effects), restricted maximum likelihood as a method of parameter estimation (REML, used in this study), and increased standard errors of fixed effects stemming from variation due to random effects (minimizes Type 1 errors relative to considering all factors as fixed).

Initially, a single factor ANOVA was conducted comparing oiled and un-oiled frames over the study period to assess the possible effect of egg oiling on summer density of cormorants. No significant effect of oiling was found ($F_{1,222} = 0.399$; $p = 0.53$), so oiling was excluded from further analyses of cormorant density.

Model selection procedures (Akaike Information Criterion corrected for sample size, AICc; Burnham and Anderson, 1998) were used to assess whether 2003 or 2004 best represented the appropriate demarcation of the effects of any regime shift on cormorant density. A mixed model ANOVA was used with main fixed effects of Region (Georgian Bay or the North Channel) and Year (2000–2005), and random effect Region nested within ($Regime_i$) where i is 2003 or 2004. $Regime_i$ designated years preceding the year in question as one factor and the year in question and all following years as a second factor. Since the timing of a regime shift is not a factor an investigator can control it is designated as a random effect. The variance estimation and precision package (VEPAC) of Statistica (StatSoft, Inc., 2009) was used in all ANOVA analyses utilizing the REML method (Bolker et al., 2008).

A mixed model ANOVA was used to assess variation due to year effects and season effects (flights within a summer) for the North Channel and Georgian Bay (based on Type III sum of squares). Least square means from the mixed models were used to assess two interaction factors, $Region \times Season$ and $Region \times Year$. For examining the $Region \times Season$ interaction, fixed effects were Region, Season, and their interaction term. Random effects included Year, $Year \times Region$, $Year \times Season$, and Frame nested within Year. For examining the $Region \times Year$ interaction, fixed effects were Region, Year and their interaction term. Random effects were Season, $Season \times Region$, $Season \times Year$, and Frame nested within Year. The purpose of the second ANOVA for examining the $Region \times Year$ effect was to provide comparable standard errors (i.e., larger than using fixed effects) to the first mixed model ANOVA through designation of Season as a random effect for the least squares means comparison. Only REML derived output is reported here from the first mixed model ANOVA where Year is a random effect along with interaction terms including Year. Fisher's least significant difference test (LSD test) and pairwise comparisons within regions (provided F statistic was significant) were used to determine if there were significant differences among Seasons or Years.

Least square means in the $Region \times Season$ analysis were used to examine seasonal decline in cormorants that occurs prior to late fall each year. The loss of cormorants as registered by seasonal declines in density was used to estimate instantaneous rates of decline for the North Channel and Georgian Bay. Instantaneous rates of decline were calculated as $\log_e(\hat{D}_2/\hat{D}_1)/t$ where \hat{D}_2 and \hat{D}_1 are density estimates from the last flight (taken as Sept 1) and the peak in density regardless of time period, respectively. The number of days, t , between \hat{D}_2 and \hat{D}_1 will vary depending on region-specific peaks in density relative to the density at the end of the summer. The loss of cormorants will incorporate

Table 1
Density (number/km²) of double-crested cormorants in the North Channel. Peak density in bold.

Year	Late June–early July	Mid July	Late July–early Aug	Mid Aug	Late Aug	Early Sept
2000:						
Mean	6.05	8.27	8.53	6.18	5.57	4.58
90% CI	(3.99–9.18)	(5.19–13.18)	(5.82–12.53)	(4.20–9.09)	(3.77–8.22)	(3.33–6.30)
2001:						
Mean	6.96	7.65	9.10	10.92	8.66	3.65
90% CI	(4.51–10.73)	(5.03–11.61)	(6.02–13.74)	(7.31–16.30)	(5.49–13.64)	(2.73–4.88)
2002:						
Mean	8.20	13.25	12.56	11.17	9.04	8.51
90% CI	(6.00–11.22)	(9.18–19.11)	(8.24–19.15)	(7.91–15.77)	(5.99–13.64)	(6.43–11.28)
2003:						
Mean	2.08	3.71	4.97	7.65	5.15	1.31
90% CI	(1.36–3.19)	(2.04–6.76)	(2.22–11.15)	(5.06–11.57)	(2.85–9.31)	(0.64–2.70)
2004:						
Mean	NA	1.46	2.60	2.15	1.18	NA
90% CI		(1.04–2.05)	(1.79–3.79)	(1.41–3.30)	(0.61–2.30)	
2005 ^a :						
Mean	3.44	NA	2.64	1.63	1.64	NA
90% CI	(2.36–5.03)		(1.70–4.08)	(1.12–2.37)	(1.06–2.54)	

NA, not available meaning no flights during this time period.

^a First flights of 2005 took place from June 14 to 17 with an estimated density of 1.57 cormorants/km² (90% CI, 1.06–2.35).

losses due to mortality as well as emigration from the Lake Huron coast. Instantaneous loss rates provide a way of reducing population estimates using nest counts from the spring on a daily or weekly basis over the course of a summer prior to their complete departure in the fall.

Results

Based on the aerial surveys, there was a seasonal decline in density of double-crested cormorants in each year of the aerial survey in both the North Channel (Table 1) and Georgian Bay (Table 2). Density estimates at the end of each survey were approximately half or less of the earlier peak densities. The peak density for each year varied with some years peaking in late July–early August and other years peaking before or after this time period. The highest densities for both coastal regions occurred in 2002 with 13.25 cormorants/km² in the North Channel (mid July; Table 1) and 9.63 cormorants/km² in Georgian Bay (early July; Table 2).

Generally, the density of cormorants in 2000–02 was higher in the North Channel than in Georgian Bay for any aerial survey with the exception of early July 2002 in Georgian Bay (Tables 1 and 2). In 2003–05, density clearly declined in the North Channel to levels not observed in the previous time period (2000–02) for most aerial surveys. A similar

pattern occurred in Georgian Bay with density declining in 2004–05 relative to early years of the survey. However, during these years, density in Georgian Bay returned to levels observed previously for this coastal region (2000–01 vs. 2004–05; Table 2). Density of cormorants in 2004–05 was similar for the North Channel and Georgian Bay. This observation represents a departure from the earlier pattern of more cormorants per km² in the North Channel relative to the Georgian Bay. The net effect is a clear decline in density of cormorants in the last 2 years of the survey relative to the peak years of density.

The distribution of cormorants reflected a strong nearshore orientation of free-ranging birds. For the North Channel and Georgian Bay combined, the proportion of cormorants detected on the water or flying (ie., active birds) was greater within 2.5 km of the coast than away from the coast (>2.5 km; Fig. 2). For most of the aerial surveys, approximately 70–80% of active birds were detected near the coast (Fig. 2). For years with September aerial surveys, the proportion of active cormorants detected within 2.5 km of the coast declined relative earlier surveys reflecting a clear tendency to locate birds on the water away from the coast. This was particularly evident in frames 6 and 7 located in the western half of the North Channel.

Most cormorants were detected loafing on shoreline habitat (land; Fig. 3). The pattern of percent cormorants on land was similar for both

Table 2
Density (number/km²) of double-crested cormorants in Georgian Bay. Peak density in bold.

Year	Late June–early July	Mid July	Late July–early Aug	Mid Aug	Late Aug	Early Sept
2000:						
Mean	4.33	2.42	4.53	2.74	2.47	0.93
90% CI	(2.58–7.28)	(1.55–3.77)	(2.79–7.34)	(1.97–3.80)	(1.66–3.65)	(0.60–1.45)
2001:						
Mean	3.80	4.85	4.80	2.14	2.64	2.31
90% CI	(2.45–5.91)	(3.13–7.50)	(3.50–6.56)	(1.55–2.96)	(1.78–3.91)	(1.51–3.54)
2002:						
Mean	9.63	8.32	6.35	6.34	5.07	2.32
90% CI	(6.60–14.05)	(5.41–12.80)	(4.60–8.78)	(4.60–8.75)	(3.74–6.89)	(1.65–3.27)
2003:						
Mean	5.92	5.51	3.48	4.25	2.32	3.86
90% CI	(3.760–9.32)	(3.72–8.17)	(2.42–5.00)	(2.81–6.45)	(1.61–3.34)	(2.73–5.46)
2004:						
Mean	NA	2.06	2.33	2.72	1.58	NA
90% CI		(1.39–3.06)	(1.72–3.16)	(1.82–4.08)	(1.02–2.43)	
2005 ^a :						
Mean	1.87	NA	3.81	1.94	2.03	NA
90% CI	(1.33–2.63)		(2.58–5.63)	(1.26–3.00)	(1.45–2.84)	

NA, not available meaning no flights during this time period.

^a First flights of 2005 took place from June 14 to 17 with an estimated density of 1.65 cormorants/km² (90% CI, 1.12–2.43).

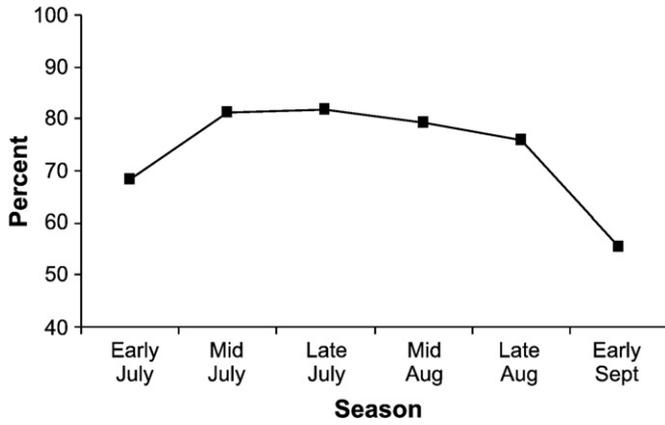


Fig. 2. Mean percent of active cormorants within 2.5 km of the coast in Georgian Bay and the North Channel combined for six years (2000–2005). Active cormorants were birds detected flying and on the water. Cormorants detected loafing on land were not included. Seasonal intervals represent flight periods.

coastal regions until August. For the North Channel and Georgian Bay, the peak in the percent of cormorants on land was mid August and late August, respectively. In late summer, the pattern diverged between the two coasts with a relatively stronger decline in the North Channel where cormorants were detected on the water more frequently than in early summer aerial surveys. In Georgian Bay, this decline did not occur until September (Fig. 3).

Declines in density began in 2003 and continued into 2004 in both the North Channel and Georgian Bay. Based on the criterion of minimizing AIC, the mixed model using the nested random effect Region (Regime₂₀₀₃) was superior ($\Delta AIC = 10.37$) to an alternative incorporating Region (Regime₂₀₀₄) (Table 3). From the mixed models, the variance component in density of cormorants accounted for by the random effect was higher for Region (Regime₂₀₀₃) than Region (Regime₂₀₀₄) at 28.1% and 13.1%, respectively (Table 3). A consistent pattern in significance of fixed and random effects was found using the ANOVA method for mixed models. In the model with the random effect Region (Regime₂₀₀₃), Region was not significant ($F_{1,216} = 1.03$; $p = 0.496$) while Year ($F_{4,216} = 9.70$; $p < 0.0001$) and Region (Regime₂₀₀₃) ($F_{1,216} = 18.51$; $p < 0.0001$) were significant. In the model with the random effect Region (Regime₂₀₀₄), Region was not significant ($F_{1,216} = 1.11$; $p = 0.483$) while Year ($F_{4,216} = 11.99$; $p < 0.0001$) and Region (Regime₂₀₀₄) ($F_{1,216} = 7.12$; $p = 0.008$) were significant.

A mixed model ANOVA with fixed effects (Region + Season + Region × Season) and random effects (Year + Year × Region + Year ×

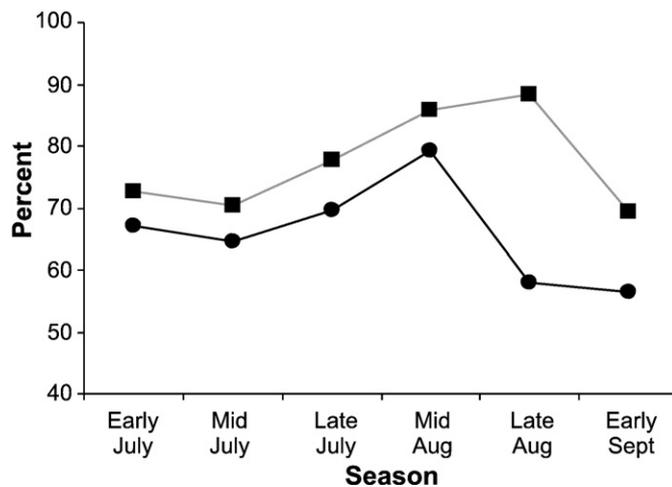


Fig. 3. Mean percent of cormorants detected on land for Georgian Bay and the North Channel. Grey line represents Georgian Bay and black line represents the North Channel. Seasonal intervals represent flight periods.

Table 3

Model selection examining year of regime change on density of double-crested cormorants based on a mixed model ANOVA including Region effects nested within Regime, period. Random effects were Region (Regime_i), k is the number of parameters in the model. Variance component of the dependent variable Density represented by the random effect Region (Regime_i) is a percentage of total variance from the mixed models.

Model	k	AICc	% Variance component, Region (Regime _i)
Region + Year + Region (Regime ₂₀₀₃)	13	526.91	28.1%
Region + Year + Region (Regime ₂₀₀₄)	13	537.28	13.1%

Season + Frame (Year)) was used to summarize variation in cormorant density among summer seasons. The fixed factor Region was not significant ($F_{(1,5)} = 3.742$; $p = 0.111$) but both Season ($F_{(5,21)} = 3.921$; $p = 0.0115$) and its interaction with Region (Region × Season, $F_{(5,151)} = 3.794$; $p = 0.0029$; Fig. 4) were significant. The variance components of cormorant density with respect to random effects showed that Year and Frames within Year (i.e., Frame (Year)) combined for 40.4% of variation in density (Table 4). Interaction terms between Year and Region or Season accounted for less variation in cormorant density (Table 4).

Least square means of density in the Region × Season interaction were plotted using 90% CI that incorporate random effects from the mixed model (Fig. 4). Density estimates from mid July to mid August are significantly higher in the North Channel than in Georgian Bay over the same period (Fisher's LSD test; $p < 0.027$ for all pairwise comparisons). For late summer periods (late August to early September), the density of cormorants in both the North Channel and Georgian Bay was similar and significantly lower when compared to early and mid July surveys (Fisher LSD test; $p < 0.01$ for all pairwise comparisons).

However, the pattern leading to the late summer drop in density differs between the North Channel and Georgian Bay (Fig. 4). Georgian Bay showed a summer long decline in density from the first survey flights to the last. In contrast, in the North Channel the decline in density of cormorants occurs only after late July (Fig. 4) following a period of increase in density that occurred largely through the month of July.

Instantaneous rates of decline for the summer season were calculated for the North Channel and Georgian Bay based on when the peak in density occurred (Fig. 4). The highest density for Georgian Bay occurred in early July (4.79 cormorants/km²; Fig. 4), and this was taken as the peak for that region until early September (1.17 cormorants/km²). The summer long decline in density for Georgian Bay occurred over a two month period (early July to early September = 62 days). For

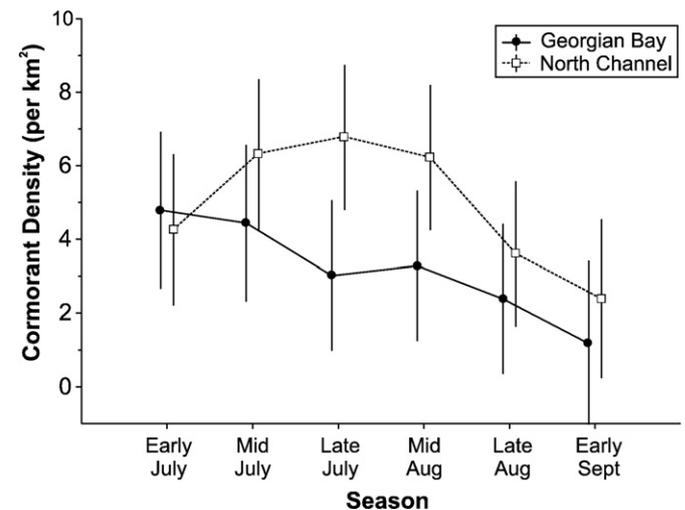


Fig. 4. Least square means of cormorant density (per km²) for flights from early July to early September based on mixed model ANOVA with Year, Year × Region, Year × Season and Frame (Year) as random effects.

Table 4

Variance components of random effects in a mixed model ANOVA with cormorant density as the dependent variable. Fixed effects were Region, Season and their interaction.

Random effect	% Variance components of cormorant density
Year	26.3
Frame(Year)	14.1
Year × Region	11.0
Year × Season	10.2
Error	38.5

the North Channel, peak density was in late July (6.77 cormorants/km²; Fig. 4) until early September (2.38 cormorants/km²). The decline in the North Channel occurred over a one month period (late July to early September = 31 days). The per capita daily rate of change in Georgian Bay was -0.023 compared to the North Channel per capita daily rate of change of -0.034 .

An ANOVA with fixed effects (Region + Year + Region × Year) and random effects (Season + Season × Region + Year × Season + Frame (Year)) was used to summarize variation in cormorant density among years. The interaction of Region × Year was significant ($F_{(5,151)} = 2.514$; $p = 0.0323$) as a fixed effect. Least square means of the Region × Year interaction stemming from the mixed model were plotted and incorporated 90% CI based on random effects (Fig. 5). Cormorant densities in 2002 stand out relative to other years. In Georgian Bay, 2002 density was significantly higher than other years with the exception of 2003 (Fisher's LSD test; all $p < 0.05$). In the North Channel, density for 2002 was significantly higher than other years with the exception of 2001 (Fisher's LSD test; all $p < 0.02$). From 2003 to 2005, no differences in density were present within or between the North Channel and Georgian Bay.

The mean decline in cormorant density in the North Channel after 2002 registered as 6–8 cormorants · km⁻² (Fisher LSD test; Δ mean density = 5.91 cormorants · km⁻² (90% CI; 3.61–8.21) in 2003; Δ mean density = 8.19 cormorants · km⁻² (90% CI; 5.74–10.64) in 2004). By 2004–2005, the decline in Georgian Bay registered as approximately 4 cormorants · km⁻² (Fisher LSD test; Δ mean density = 4.11 cormorants · km⁻² (90% CI; 1.37–6.84) in 2004; Δ mean density = 4.02 cormorants · km⁻² (90% CI; 1.29–6.75) in 2005).

Discussion

The density of double-crested cormorants was variable among years and seasons and between the North Channel and Georgian Bay

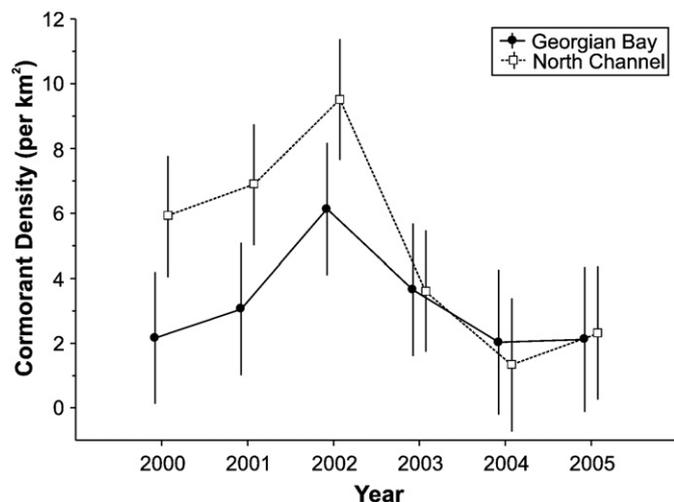


Fig. 5. Least square means of cormorant density (per km²) for years 2000–2005 based on mixed model ANOVA with Season, Season*Region, Season*Year and Frame(Year) as random effects.

over the course of this study. Based on confidence intervals from the aerial surveys, density ranged from a low of approximately 1 cormorant · km⁻² to a high of 19 cormorants · km⁻². Double-crested cormorant density was higher in the early years of the aerial survey, prior to 2003, and has since declined. Since most active cormorants (flying or on water) were detected within 2.5 km of the coast any food web changes that may have contributed to this shift in abundance may have occurred within the nearshore zone of Lake Huron. Aerial (this study) and ship-based visual sampling both demonstrate the strong coastal orientation of this species in the Great Lakes (Stapanian and Bur, 2002; Langen et al., 2005).

Generally, there was a seasonal decline in density of double-crested cormorants in the North Channel and Georgian Bay each year of the aerial survey. The timing of the peak in density varied from year-to-year in the aerial surveys (Tables 1 and 2). When variation in density was analyzed using a mixed model approach the seasonal pattern of decline in density, as shown by least squares means, differed between the North Channel and Georgian Bay over the summer season. In Georgian Bay the decline progressed from early July surveys through to early September. In contrast, the North Channel pattern began with an increase in density through July followed by a sharper drop in density over August. The late summer decline detected in the North Channel is similar in timing to late summer declines detected in the Les Cheneaux Islands (Diana et al., 2006). When per capita rates of decline were compared, the daily loss rate for Georgian Bay was lower because it extended over a longer time period than in the North Channel.

The seasonal patterns revealed in this study point to possible differences in phenology of nesting cormorants between the North Channel and Georgian Bay. The timing of fledging may occur sooner in the summer period in Georgian Bay whereas the peak in the North Channel may reflect fledging in late July. It would require a significant difference between the two regions in seasonal factors such as warming rate, aquatic productivity or access to fish for phenology to be the sole explanation of seasonal density patterns. There does not seem to be a sufficient latitudinal gradient between the North Channel and Georgian Bay to account for a difference of at least a month in the timing of fledging based on abiotic factors (Hatch and Weseloh, 1999).

Differences between the two regions in productivity may be important in explaining the mixed model results. Ecosystem productivity is higher in the North Channel than Georgian Bay (Sprules et al., 1988), and watershed influences are higher in the North Channel as well (Bennett, 1988; Thomas, 1988; Weiler, 1988). Higher densities recorded in the North Channel during fledging may reflect these differences between the two regions. Given these patterns, differences in nesting synchrony between regions may account for the seasonal patterns with Georgian Bay reflecting less synchrony in the timing of fledging than the North Channel. The steady decline in cormorant density in Georgian Bay over summer may therefore indicate a wider range in fledging dates in addition to a possibly earlier nest initiation period relative to the North Channel. Whatever the precise cause, differences between the two regions in summer abundance patterns reflect differences in density and the fledging process.

Annual patterns in density were also different with the North Channel having higher densities of cormorants from 2000 to 2002 when compared to Georgian Bay. Mixed model results show a clear peak in density for both regions in 2002 followed by a sharp decline in density in subsequent years. Model selection procedures confirmed that 2003 represented the year that best demarcated a period of high cormorant density (2000–02) from a period of low density (2003–05). Cormorant densities are similar between the two regions after the regime shift in 2003 indicating that declines in cormorant density in the North Channel were greater on a per unit area basis than in Georgian Bay.

The peak in nest counts for both regions occurred in 2001 (Ridgway et al., 2006). Results from this study clearly show the peak in cormorant

density for both regions was 2002 indicating a one year lag between the two measures of abundance. The lag may be accounted for in a number of ways. First, it suggests that a proportion of the high densities detected in 2002 were sub-adult birds. Higher densities in 2002 may stem from increased juvenile production arising in 2001. Second, since some food web changes in Lake Huron were underway by 2002 (Fielder et al., 2007; Dunlop et al., 2010), higher densities may stem from a lack of nesting success due to food web change and therefore greater movement, possibly along with greater numbers, accounting for consistent high densities detected in 2002.

Alewife (*Alosa pseudoharengus*) is now largely absent from the North Channel and Georgian Bay (Warner et al., 2009; Dunlop et al., 2010) and has been a major diet item for cormorants in the Great Lakes (Seefelt and Gillingham, 2008). The loss of alewife in the North Channel and Georgian Bay was detected through a decline in daytime benthic fish schools in inshore areas after 2001 with a decline of over 50% in the number of benthic schools occurring between 2001 and 2002 (Dunlop et al., 2010; their Figs. 3 and 4). Cormorant density did not decline until after 2002. The decline in cormorant density after 2002 in the North Channel and Georgian Bay is likely due to the loss of alewife that appeared to precede the drop in cormorant numbers by approximately one year.

The timing of the decline in density of double-crested cormorants corresponds to a time period with sharp changes in fish abundance including declines of alewife (Fielder et al., 2007; Warner et al., 2009; Dunlop et al., 2010), shifts in fish school location and abundance (Dunlop et al., 2010), increases in walleye year-class production (Fielder et al., 2007), a decade-long decline in the demersal fish assemblage including a sharp drop in species occurrence beginning in 2003 (Riley et al., 2008), increases in emerald shiner abundance in the epilimnion (Schaeffer et al., 2008), as well as major declines in zooplankton groups (Barbiero et al., 2009) and native benthic macroinvertebrates (Nalepa et al., 2009). Since this pattern of change also includes an apparent decline in primary productivity in 2003 (Barbiero et al., 2009), the suite of indicators, including double-crested cormorant density (as a measure of carrying capacity), points to a regime shift in Lake Huron with broad effects on the structure of the food web. Collectively, changes in the Lake Huron food web may signal one of the most profound and rapid regime shifts to have been detected in the Laurentian Great Lakes.

Acknowledgments

Numerous observers collected data for this study including Naomi Barrett (2000–02), Karen Rayner (2000–02), Mel Alkins (2003), Rebecca Klady (2003), Debbie Jenkins (2004), Laura Warren (2004–05), Jenn Todd (2002–04), Mike Dowdall (2005), and Nadean Schryer (2005). Gary Pitre (2000–04) and Kevin Denston (2005) piloted the flights. I thank them all for their tremendous efforts... and iron stomachs.

Appendix A. Flight dates for aerial survey of the North Channel and Georgian Bay

	2000	2001	2002	2003	2004	2005 ^a
Flight 1	July 4–7	June 25–26	July 2–5	July 2–7	NA ^b	July 6–8
Flight 2	July 17–20	July 9–12	July 15–18	July 8–10	July 6–13	NA
Flight 3	Aug 1–4	July 23–26	July 29–Aug 2	July 22–24	July 26–29	July 25–27
Flight 4	Aug 14–17	Aug 7–13	Aug 12–15	Aug 11–14	Aug 11–16	Aug 15–17
Flight 5	Aug 26–30	Aug 21–23	Aug 26–29	Aug 25–28	Aug 23–30	Aug 29–31
Flight 6	Sept 13–15	Sept 4–7	Sept 5–8	Sept 8–9	NA	NA

^aFirst flight of 2005 was on June 14–17 but was outside of flight times of previous years and not included in the analysis.

^bNA: not available.

References

- Bachler, E., Liechti, F., 2007. On the importance of $g(0)$ for estimating bird population densities with standard distance-sampling: implications from a telemetry study and a literature review. *Ibis* 149, 693–700.
- Bakun, A., 2004. In: Robinson, A.R., Brink, K. (Eds.), Chapter 25. Regime Shifts. : The Sea, vol. 13. Harvard University Press, Cambridge, MA, pp. 971–1018.
- Ballance, L.T., 2007. Understanding seabirds at sea: why and how? *Mar. Ornithol.* 35, 127–135.
- Barbiero, R.P., Balcer, M., Rockwell, D.C., Tuchman, M.L., 2009. Recent shifts in the crustacean zooplankton community of Lake Huron. *Can. J. Fish. Aquat. Sci.* 66, 818–828.
- Barrett, R.T., Chapdelaine, G., Anker-Nilssen, T., Mosbech, A., Montevecchi, W.A., Reid, J. B., Veit, R.R., 2006. Seabird numbers and prey consumption in the North Atlantic. *ICES J. Mar. Sci.* 63, 1145–1158.
- Bennett, E.B., 1988. On the physical limnology of Georgian Bay. *Hydrobiol* 163, 21–34.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2008. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127–135.
- Brooke, M.deL., 2004. The food consumption of the world's seabirds. *Proc. R. Soc. Lond. B (Suppl)* 271, S246–S248.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford.
- Bunce, A., 2001. Prey consumption of Australasian gannets (*Morus serrator*) breeding in Port Phillip Bay, southeast Australia, and potential overlap with commercial fisheries. *ICES J. Mar. Sci.* 58, 904–915.
- Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: a Practical Information-Theoretic Approach. Springer, New York.
- Diana, J.S., Maruca, S., Low, B., 2006. Do increasing cormorant populations threaten sportfishes in the Great Lakes? A case study in Lake Huron. *J. Great Lakes Res.* 32, 306–320.
- Dobiesz, N.E., McLeish, D.A., Eshenroder, R.L., Bence, J.R., Mohr, L.C., Ebener, M.P., Nalepa, T.F., Woltd, A.P., Johnson, J.E., Argyle, R.L., Makarewicz, J.C., 2005. Ecology of the Lake Huron fish community, 1970–1999. *Can. J. Fish. Aquat. Sci.* 62, 1432–1451.
- Drinkwater, K.F., 2006. The regime shift of the 1920s and 1930s in the North Atlantic. *Prog. Oceanogr.* 68, 134–151.
- Dunlop, E.S., Milne, S.W., and Ridgway, M.S., 2010. Temporal trends in the numbers and characteristics of Lake Huron fish schools between 2000 and 2004. *J. Great Lakes Res.* 36, 74–85.
- Fielder, D.G., Schaeffer, J.S., Thomas, M.V., 2007. Environmental and ecological conditions surrounding the production of large year classes of walleye (*Sander vitreus*) in Saginaw Bay, Lake Huron. *J. Great Lakes Res.* 33, 118–132.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Underson, L., Holling, C.S., 2004. Regime shifts, resilience and biodiversity in ecosystem management. *Ann. Rev. Ecol. Syst.* 35, 557–581.
- Hatch, J.J., Weseloh, D.V., 1999. Double-crested cormorant (*Phalacrocorax auritus*). In: Polle, A., Gill, F. (Eds.), *The Birds of North America*, No. 441. The birds of North America, Inc, Philadelphia, PA.
- Johnson, J.H., Ross, R.M., McCullough, R.D., 2002. Little Galloo Island, Lake Ontario: a review of nine years of double-crested cormorant diet and fish consumption information. *J. Great Lakes Res.* 28, 182–192.
- Langen, T.A., Twiss, M.R., Bullerjahn, G.S., Wilhelm, S.W., 2005. Pelagic bird survey on Lake Ontario following Hurricane Isabel, September 2003: observations and remarks on methodology. *J. Great Lakes Res.* 31, 219–226.
- Madenjian, C.P., Gabrey, S.W., 1995. Waterbird predation on fish in western Lake Erie: a bioenergetics model application. *Condor* 97, 141–153.
- Nalepa, T.F., Pothoven, S.A., Fanslow, D.L., 2009. Recent changes in benthic macroinvertebrate populations and impact on diet of lake whitefish (*Coregonus clupeaformis*). *Aquat. Ecosyst. Health Manage.* 12, 1–10.
- Nalepa, T.F., Fanslow, D.L., Pothoven, S.A., Foley, A.J., Lang, G.A., 2007. Long-term trends in benthic macroinvertebrate populations in Lake Huron over the past four decades. *J. Great Lakes Res.* 33, 421–436.
- Ridgway, M.S., 2010. Line transect distance sampling in aerial surveys for double-crested cormorants in coastal regions of Lake Huron. *J. Great Lakes Res.* 36, 403–410.
- Ridgway, M.S., Pollard, J.B., Weseloh, D.V., 2006. Density-dependent growth of double-crested cormorant colonies on Lake Huron. *Can. J. Zool.* 84, 1409–1420.

- Riley, S.C., Roseman, E.F., Nichols, S.J., O'Brien, T.P., Kiley, C.S., Schaeffer, J.S., 2008. Deepwater demersal fish community collapse in Lake Huron. *Trans. Am. Fish. Soc.* 137, 1879–1890.
- Schaeffer, J.S., Warner, D.M., O'Brien, T.P., 2008. Resurgence of emerald shiners *Notropis atherinoides* in Lake Huron's main basin. *J. Great Lakes Res.* 34, 395–403.
- Seefelt, N.E., Gillingham, J.C., 2008. Bioenergetics and prey consumption of breeding double-crested cormorants in the Beaver Archipelago, northern Lake Michigan. *J. Great Lakes Res.* 34, 122–133.
- Sly, P.G., Munawar, M., 1988. Great Lake Manitoulin: Georgian Bay and the North Channel. *Hydrobiol* 163, 1–19.
- Spear, L.B., Ainley, D.G., 2007. Storm-petrels of the eastern Pacific Ocean: species assembly and diversity along marine habitat gradients. *Ornithol. Monogr.* No. 62.
- Sprules, W.G., Munawar, M., Jin, E.H., 1988. Plankton community structure and size spectra in the Georgian Bay and North Channel ecosystems. *Hydrobiol* 163, 135–140.
- Stapanian, M.A., Bur, M.T., 2002. Overlap in offshore habitat use by double-crested cormorants and boaters in western Lake Erie. *J. Great Lakes Res.* 28, 172–181.
- Stapanian, M.A., Waite, T.A., 2003. Species density of waterbirds in offshore habitats in Lake Erie. *J. Field Ornith.* 74, 381–393.
- Stapanian, M.A., Bur, M.T., Tyson, J.T., Seamans, T.W., Blackwell, B.F., 2002. Foraging locations of double-crested cormorants on western Lake Erie: site characteristics and spatial associations with prey fish densities. *J. Great Lakes Res.* 28, 155–171.
- StatSoft, Inc., 2009. STATISTICA (data analysis software system), version 9.0. www.statsoft.com2009.
- Tasker, M.L., Jones, P.H., Dixon, T., Blake, B.F., 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* 101, 567–577.
- Thomas, L., Laake, J.L., Derry, J.F., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Strindberg, S., Hedley, S.L., Burt, M.L., Marques, F., Pollard, J.H., Fewster, R.M., 1998. Distance 3.5. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. <http://www.ruwpa.st-and.ac.uk/distance>1998.
- Thomas, R.L., 1988. Distribution and composition of surficial sediments of Georgian Bay and the North Channel. *Hydrobiol* 163, 35–45.
- Wagner, T., Hayes, D.B., Bremigan, M.T., 2006. Accounting for multilevel data structures in fisheries data using mixed models. *Fisheries* 31, 180–187.
- Warner, D.M., Schaeffer, J.S., O'Brien, T.P., 2009. The Lake Huron pelagic fish community: persistent spatial pattern along biomass and species composition gradients. *Can. J. Fish. Aquat. Sci.* 66, 1199–1215.
- Weiler, R.R., 1988. Chemical limnology of Georgian Bay and the North Channel between 1974 and 1980. *Hydrobiol* 163, 77–83.
- Weseloh, D.V., Pekarik, C., Havelka, T., Barrett, G., Reid, J., 2002. Population trends and colony locations of double-crested cormorants in the Canadian Great Lakes and immediately adjacent areas, 1990–2000: a manager's guide. *J. Great Lakes Res.* 28, 125–144.