

Contents lists available at ScienceDirect

# Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

# Drivers of declines in common loon (*Gavia immer*) productivity in Ontario, Canada



# Kristin Bianchini<sup>a,b</sup>, Douglas C. Tozer<sup>a,\*</sup>, Robert Alvo<sup>c</sup>, Satyendra P. Bhavsar<sup>d</sup>, Mark L. Mallory<sup>b</sup>

<sup>a</sup> Long Point Waterfowl and Wetlands Research Program, Birds Canada, P.O. Box 160 (Courier: 115 Front Road), Port Rowan, Ontario NOE 1MO, Canada

<sup>b</sup> Biology Department, Acadia University, Wolfville, Nova Scotia B4P 2R6, Canada

<sup>c</sup> 45 Holland Ave., Unit 210, Ottawa, Ontario K1Y 4S3, Canada

<sup>d</sup> Ontario Ministry of the Environment, Conservation and Parks, Toronto, Ontario M9P 3V6, Canada

# HIGHLIGHTS

# GRAPHICAL ABSTRACT

- Common loon reproductive success declined in Ontario between 1981 and 2018.
- Declines were steeper on lakes with low pH, and that were farther west.
- Lake area, longitude, April temperature, pH, and Hg influenced loon productivity.
- Human disturbance and shoreline development did not affect loon chick numbers.

# ARTICLE INFO

Article history: Received 25 March 2020 Received in revised form 22 May 2020 Accepted 24 May 2020 Available online 30 May 2020

# Editor: Henner Hollert

Keywords: Acid rain Citizen science Common loon Fish abundance Mercury Reproductive success



# ABSTRACT

Common loons (*Gavia immer*) are top predators that depend on lake food webs to successfully fledge chicks. Common loon reproductive success is consequently recognized as an important indicator of aquatic ecosystem health. Existing evidence points to long-term declines in productivity in portions of the common loon range; however, the reason for these declines is not well understood. Our objectives were to define underlying baseline patterns of loon reproductive success in Ontario, Canada, and to identify drivers of temporal changes in loon productivity. We analyzed 38 years of reproductive data from over 1500 lakes using data from the Canadian Lakes Loon Survey, a citizen science loon monitoring program managed by Birds Canada that has run annually in Ontario since 1981. Overall, we estimated a declining trend in common loon reproductive success of -0.10 sixweek-old young per pair per year in Ontario between 1981 and 2018. We assessed the influence of 14 factors on loon reproductive success. We identified low pH and associated higher mercury as factors linked to loon productivity declines. We also demonstrated that lake area, longitude, and April temperatures can predict the number of six-week-old young per pair per year. We hypothesize that climate change-induced stress, acting through multiple interacting pathways involving mercury acidity, fish abundance, lake size, and geographic location, may account for declining loon productivity. These results will be important for focusing future research and conservation efforts to help understand and mitigate threats to common loon populations.

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The common loon (Gavia immer) is widely recognized in North

# 1. Introduction

\* Corresponding author. *E-mail address:* dtozer@birdscanada.org (D.C. Tozer).

America as a symbol of northern wilderness and as a useful indicator

of lake health (Evers et al., 2020). As a result, the common loon is the subject of several long-term monitoring programs, and its population dynamics in multiple locations are well characterized (Evers et al., 2020). Longitudinal datasets suggest that although loon populations are generally stable (Evers et al., 2020; Grear et al., 2009; Mitro et al., 2008), reproductive success has declined in Ontario, Canada (McNicol et al., 1995), and elsewhere within this species' range (e.g., McCarthy and Destefano, 2011; Tozer et al., 2013). It is possible that population declines could lag behind declines in reproductive success (reviewed in Tozer et al., 2013). Population declines can occur when reproductive rates fall below the estimated level required to offset adult and juvenile mortality (i.e., 0.48 young fledged per pair; Evers et al., 2020). Therefore, identifying the factors responsible for declines in reproductive success is important for understanding threats to common loon populations.

Acid rain and mercury are important threats to common loon productivity. Lower reproductive success on acidic lakes has been attributed to a combination of reduced food consumption and elevated mercury intake in loons (Merrill et al., 2005). Methylmercury is the more bioavailable form of mercury, and sulfate-reducing bacteria are thought to be the primary agents of mercury methylation in aquatic environments (Wiener et al., 2003). The sulfur oxides from acid rain increase the activity of sulfate-reducing bacteria and thereby enhance methylmercury production (Jeremiason et al., 2006). As a result, loon dietary mercury exposure is higher in more acidic lakes (Bodaly et al., 1993; Burgess and Hobson, 2006; Burgess and Meyer, 2008). Acidification negatively influences fish species richness and abundance (Howells et al., 1983; Schindler, 1988), resulting in a shortage of food for chicks and increased brood mortality (Alvo, 2009). Mercury exposure negatively affects loon parental care, foraging success, and chick development (Evers et al., 2008) and is therefore associated with lower chick production (Burgess and Meyer, 2008; Evers et al., 2008).

Due to patterns in the atmospheric transport and deposition of sulfur dioxide (Schindler, 1988), there is a longitudinal pattern in lake acidity across Canada, where acidity (Minns et al., 2008), and consequently mercury concentrations in lakes (Eckley and Hintelmann, 2006), fish (Depew et al., 2013a, 2013b), and loons (Evers et al., 1998), tend to increase from west to east. As a result, common loon reproductive success also decreases from west to east across Canada (Tozer et al., 2013).

Although acidifying sulfur dioxide emissions have declined in North America, and pH has increased in many degraded lakes (Jeffries et al., 2003; Jeziorski et al., 2008), biological recovery from acidification has been slow (reviewed by Keller et al., 2019). Moreover, recent evidence suggests that fish mercury concentrations are increasing in Ontario (Chen et al., 2018; Gandhi et al., 2014), and common loon blood mercury concentrations are positively correlated with fish mercury concentrations (Burgess and Meyer, 2008; Kenow et al., 2019; Scheuhammer et al., 2016). It is therefore likely that common loon mercury exposure is increasing, and it is possible that mercury, alongside the ongoing biological effects of acid rain, may be contributing to common loon productivity declines.

Human activities, such as shoreline development and watercraft use, have also been identified as threats to common loon reproductive success. Shoreline development can degrade loon nesting habitat, decrease the availability of nesting sites (Evers et al., 2020), and increase the density of egg and chick predators (McIntyre, 1988). Human recreational activities, including boating and waterskiing, can disrupt incubation, lower nest attentiveness, disturb foraging, and cause chick abandonment (Kelly, 1992; McIntyre, 1988). As well, boat collisions can be a significant source of loon mortality (Miconi et al., 2000). Many studies thus report a negative correlation between common loon productivity and watercraft use and shoreline development (e.g., Titus and Van Druff, 1981; Heimberger et al., 1983; Kelly, 1992), although others have found no relationship (Alvo, 1981; Badzinski and Timmermans, 2006; Buxton et al., 2019; McCarthy and Destefano, 2011).

Local weather variation has also been linked to declines in loon reproductive success. Spring arrival on breeding lakes primarily depends on the timing of ice break up (Evers et al., 2020). Previous work in waterfowl suggests that late ice break up in the spring can lower annual productivity by delaying breeding (Mallory et al., 2003), and a similar relationship has been hypothesized for loons (Alvo, 1996). There is also evidence that early ice break up lowers loon productivity by permitting nonbreeders to appropriate territories before breeding pairs have returned (Piper et al., 2000). Temperature and precipitation can also affect the abundance and longevity of the black fly (Simulium annulus) that feeds on the blood of incubating loons. Cooler spring temperatures prolong the lives of biting adult female black flies (Davies, 1953), and cooler springs are thus associated with higher rates of nest abandonment and lower numbers of fledged loon chicks (Piper et al., 2018). Additionally, cool temperatures and heavy precipitation can increase the number and persistence of black fly hatching sites by intensifying spring runoff and by delaying when small streams dry up (Lamarre et al., 2018; Martinez-de la Puente et al., 2009). Lamarre et al. (2018) found that peregrine falcon (Falco peregrinus tundrius) nestling survival was reduced by up to 30% following a black fly outbreak caused by high spring snowfall. Extreme precipitation events and sudden drops in water levels due to drought can also flood or prevent access to nests, reducing productivity (Buxton et al., 2019; Windels et al., 2013). It is thus possible for spring and winter precipitation and spring temperatures to contribute to variation in common loon productivity.

There is increasing concern over how avian predators and competitors could affect common loon productivity. Bald eagle (Haliaeetus *leucocephalus*) and double-crested cormorant (*Phalacrocorax auritus*) abundance have grown rapidly since the 1970s (Dorr et al., 2020; North American Bird Conservation Initiative Canada, 2019). Bald eagles depredate loon eggs, chicks, and adults (McCarthy et al., 2010; Paruk et al., 1999; Piper et al., 2008), and in areas of high bald eagle abundance, eagles can be a significant source of nest failure and chick mortality (Cooley et al., 2019; Gutreuter et al., 2013). The possibility of doublecrested cormorants affecting common loon productivity has not been directly studied. However, there are concerns that double-crested cormorants harm local fish populations and that cormorant colonies damage nesting habitats for other breeding birds (reviewed by Dorr et al., 2020). Thus, the potential exists for expanding bald eagle and doublecrested cormorant populations to negatively influence loon productivity.

It is also important to consider the influence of lake size on common loon breeding. During the breeding season, loons prefer larger lakes (Evers et al., 2020), and there is a positive association between lake size and loon occupancy (Kuhn et al., 2011) and reproductive success (Tozer et al., 2013). There may be several advantages to breeding on larger lakes. Larger lakes tend to have higher total fish numbers than smaller lakes due to their greater volume (Alvo, 2009; Piper et al., 2012). Larger lakes also tend to be less acidic, as they typically have a higher acid buffering capacity than smaller lakes (Eilers et al., 1983). As well, larger lakes are typically deeper and cooler than smaller lakes (Bodaly et al., 1993). Higher water temperatures increase the activity of methylating bacteria (Wright and Hamilton, 1982). Therefore, given the combination of higher pH and lower water temperatures, larger lakes also tend to have lower methylmercury concentrations (Bodaly et al., 1993; Jeremiason et al., 2006). Furthermore, the availability of potential nesting habitats and the number of protected bays can be greater on larger lakes, which can help loons to avoid human disturbance (Caron and Robinson, 1994; Evers et al., 2020).

Clearly, several factors may directly or synergistically impair common loon reproductive success. However, the cause of long-term declines in loon productivity in portions of their range, particularly in Ontario, Canada, is not well understood. Ontario hosts over one third of the global breeding population of common loons (Evers, 2007; Wayland and McNicol, 1990); therefore, understanding why loon reproductive success has declined in Ontario is important for this species' conservation. Our first objective was to define underlying baseline patterns of loon reproductive success in Ontario as a function of lake location, lake size, and time (i.e., longitude, lake area, and year). We analyzed 38 years of loon reproductive data from 1577 Ontario lakes. These data were obtained from the Canadian Lakes Loon Survey (CLLS), a citizen science loon monitoring program managed by Birds Canada that has operated annually in Ontario since 1981 (McNicol et al., 1995; Tozer et al., 2013). Our second and primary objective was to explore support for various factors that might explain temporal trends in loon reproductive success in Ontario. Specifically, we investigated the relationship between common loon reproductive success, year, longitude, lake size, and 14 factors that have previously been shown or hypothesized to affect productivity: pH, fish abundance, mercury, human disturbance, shoreline development, bald eagle and double-crested cormorant occurrence, and seven factors indicative of spring temperatures and spring and winter precipitation.

# 2. Methods

# 2.1. Data collection and preparation

Our analysis considered the number of young that reached at least six weeks old per territorial loon pair per year as a measure of reproductive success (hereafter "six-week-old young per pair per year"). At six weeks of age, loon chicks are less vulnerable to predation, therefore the number of six-week-old young per pair per year is a reliable indicator of the number of young fledged (Evers, 2007). Data on loon reproductive success were obtained from the CLLS dataset. CLLS citizen scientists select a lake or a portion of a lake to survey a minimum of three times annually during the loon breeding season, although visits are typically made more often: on average 35.3 times (SD = 29.9, range 3–140) per breeding season (Tozer et al., 2013). Surveys are completed at least once in June (nesting period) to record the number of territorial pairs, in July (hatching period) to record the number of small/ downy young (<2/3 adult size), and in mid-to-late August (prefledging period) to record the number of six-week-old young (>2/3 adult size). Further details on the CLLS survey protocol can be found in the literature (Badzinski and Timmermans, 2006; Birds Canada, 2020; McNicol et al., 1995; Tozer et al., 2013; Wayland and McNicol, 1990). Only lakes where loon pairs were present were included in our calculation of the number of six-week-old young. We assumed that all six-week-old young present on the survey lakes were detected. Due to their large size, the aggressive and conspicuous territorial behaviours of adults, and their presence on a lake for most of the summer, common loons have very high detection probabilities in the breeding season (reviewed in Kuhn et al., 2011). As a result, monitoring data for breeding common loons are typically not adjusted for false absences (e.g., Badzinski and Timmermans, 2006; Kuhn et al., 2011; Cooley et al., 2019; McDuffie et al., 2019). Furthermore, detection rates were unlikely to have varied according to the covariates considered in our analysis (e.g., detectability of loons is unlikely to be different on a low or high pH lake). It is therefore unlikely that any possible differences in detectability influenced our results.

Shoreline development and boating activity data were also obtained from the CLLS dataset. From 1982 to 2004, volunteers estimated the percentage of shoreline development in the survey area and classified monthly watercraft use into eight categories: (1) no people, no boats; (2) people, no boats; (3) occasional use of boats/canoes without motors; (4) frequent use of boats/canoes without motors; (5) occasional use of boats with motors; (6) frequent use of boats with motors; (7) occasional water skiing and/or boat racing; and (8) frequent water skiing and/or boat racing. Similar to previous analyses of CLLS data in Ontario (Weeber, 1999), we found that boating activity was highly correlated among months in each lake. Therefore, following the methods of Weeber (1999), we selected watercraft use classifications for the month of August for analysis.

Additional variables for analysis were obtained from multiple data sources (Table A.1). Lake surface areas (in hectares) were obtained from the Gazetteer of Canada (Natural Resources Canada, 1997) or were calculated in QGIS (version 3.4.9-Madeira, QGIS Development Team, 2017), using Ontario waterbody shapefiles from Land Information Ontario's Ontario Hydro Network (2010). Lake pH measurements were obtained from Minns et al. (2008) or from the Broadscale Monitoring Program lake water quality data (Ontario Biodiversity Council, 2015). Annual measurements of pH were rarely conducted on each lake, and most lakes had only one pH measurement. Consequently, pH values were averaged across years for each lake, following the methods of Badzinski and Timmermans (2006) and Tozer et al. (2013). Although pH has improved on some lakes, recent studies suggest that pH changes over time are highly variable, and even in the highly affected areas (e.g., Sudbury, Ontario), where the biggest improvements might be expected, results for pH are mixed (Jeffries et al., 2003; Keller et al., 2007, 2019). More importantly, most evidence suggests that biological recovery is limited and has lagged behind any chemical recoveries (Jeffries et al., 2003; Keller et al., 2007, 2019). Therefore, averaging pH values across years likely gives a reasonable representation of how loons were and continue to be affected by lake acidity over this time period.

Fish abundance data (measured as catch-per-unit-effort of all species caught) were obtained from the Ontario Broad-scale Monitoring Program for Inland Lakes (Sandstrom et al., 2011). From 2008 to 2017, fish abundance was sampled once every five years, and data were reported in two, five-year cycles (Cycle 1: 2008-2012, Cycle 2: 2013-2017). On lakes with two cycles of data, we tested for differences in abundance between cycles using generalized linear mixed effects models (GLMMs) with Poisson distributions and log-link functions. Models included fish abundance as a response, cycle as a fixed effect, and lake identity as a random effect. We found no difference in fish abundance between Cycles 1 and 2 (cycle was eliminated from the best-approximating model). Therefore, fish abundance was averaged across years for each lake. Again, because the biological recovery of lakes from acid rain is slow (Jeffries et al., 2003; Keller et al., 2007, 2019), fish re-establishment is unlikely on acidified lakes lacking connections to other lakes with fish source populations (Keller et al., 2019). Therefore, averaging fish abundance across years likely also gives a reasonable representation of how loons have been and continue to be affected by acid rain-induced reductions in fish populations over the study period.

Monthly weather data were obtained from the climate point estimates of McKenney et al. (2013, 2011). For analyses, we included weather variables representative of spring temperatures (mean daily maximum temperatures in April, May, and June), spring precipitation (mean precipitation in April, May, and June), and winter precipitation (precipitation of the coldest quarter; correlated with mean precipitation in January and February,  $r^2 > 0.74$ ) for each lake in each year. Correlations were generally weak among these weather variables ( $r^2 < 0.50$ ), which reduced issues of collinearity.

Bald eagle and double-crested cormorant occurrence data were downloaded from eBird (Cornell Lab of Ornithology, 2019) using the auk package (Strimas-Mackey et al., 2018) in R version 3.6.1 (R Core Team, 2019). Data were filtered following the instructions in Strimas-Mackey et al. (2020) to only include complete checklists (i.e., checklists where all birds that an observer could detect and identify were reported). To reduce variations in detectability between checklists, data were also filtered to only include checklists where observations were made for <5 h, over <5 km, and by  $\leq$ 10 observers (Strimas-Mackey et al., 2020). For both species, only observations during the loon breeding period (May – Sept.) were included in analyses. The average breeding territory size of bald eagles is 2 km<sup>2</sup> (Buehler, 2020). Therefore, assuming circular territories, we drew 1.6 km buffers (i.e., the diameter of a 2 km<sup>2</sup> circle) around the perimeter of each lake in QGIS (version 3.4.9-Madeira; OGIS Development Team, 2017) using lake shapefiles from Land Information Ontario's Ontario Hydro Network (2010). We considered bald eagle observations within the 1.6 km-buffer of each lake to be associated with that lake. This yielded an average of 9.0 (SD =50.5) eBird checklists per year per lake (range = 1-1331) and 4.9 (SD = 5.2) years of eBird data per lake (range = 1-38 years). The average foraging range of double-crested cormorants is approximately 3 km (Dorr et al., 2020). We therefore considered observations of double-crested cormorants within a 3 km-buffer of each lake to be associated with that lake. These 3 km buffers yielded an average of 13.6 (SD = 88.5) eBird checklists per year per lake (range =1-2262) and 6.3 (SD = 5.9) years of eBird data per lake (range = 1-38 years). It should be noted that: 1) the individual density and territory sizes of both species are site-specific (Buehler, 2020; Dorr et al., 2020), and 2) eBird data can be geographically biased towards more populated areas (Sullivan et al., 2009). These data therefore represent estimates of each species' presence/absence on each lake during any year of the study. It should also be noted that CLLS citizen scientists collected bald eagle and double-crested cormorant occurrence data at each lake from 2005 onwards, but we used eBird data because it was available from 1981 onwards and yielded larger sample sizes for analysis.

Yellow perch (*Perca flavescens*) total mercury concentrations were obtained from the Ontario Ministry of Environment, Conservation and Parks (OMECP) Fish Contaminant Monitoring Program. We collected mercury data for yellow perch as this is the preferred prey of common loons (Barr, 1996), and previous work by Burgess and Hobson (2006) found positive correlations between total mercury concentrations in perch and adult and juvenile loons. Details on the methods for fish collection and tissue processing under the Fish Contaminant Monitoring Program protocol have been described previously (Bhavsar et al., 2010; Chen et al., 2018; Gandhi et al., 2014). Yellow perch mercury concentrations were measured in both skinless, boneless fillets and whole fish composites, and data were recorded at the secondary watershed level. Because loons consume whole fish, fillet concentrations were converted to whole body equivalents using the equation developed for yellow perch by Wyn et al. (2010),

$$Hg_w = 0.60 \times Hg_m$$

where  $Hg_w$  is the concentration of total mercury in the whole fish in  $\mu g/g$  (wet weight), and  $Hg_m$  is the concentration of total mercury in muscle in  $\mu g/g$  (wet weight). Fish mercury concentrations increase with fish size (Gewurtz et al., 2011). Therefore, to compare mercury concentrations in different locations, mercury levels were standardized at 12 cm, a standard length of yellow perch prey for common loons (Depew et al., 2013b). Power series regressions of fish mercury against size were constructed for every year and watershed combination using the equation,

$$\log(Y) = \log(a) + (b \times \log(X)),$$

where Y is fish mercury concentration in  $\mu g/g$  wet weight, X is fish length in centimeters, and *a* and *b* are regression coefficients (Gandhi et al., 2014). To avoid over-extrapolating standardized mercury concentrations, only fish lengths between 5 and 35 cm were included in the regression analysis (Chen et al., 2018; Gandhi et al., 2014). Additionally, any year-watershed combinations with less than three sampling events were excluded, and only sampling events resulting in positive associations between fish length and mercury were considered. In total, we constructed 49 power series regressions. Because measurements were not made annually, yellow perch mercury concentrations for each watershed were averaged by decade. A summary of the covariates considered in our analysis and the rationale for the inclusion of each covariate is given in Table 1.

# 2.2. Data available for statistical analyses

Between 1981 and 2018, the CLLS dataset contained reproductive data for 1612 lakes. We excluded 29 lakes that did not meet an appropriate size criterion. Most lakes were under 155,000 ha, and we omitted six lakes that were over 384,000 ha from analyses as the entire surface of these large lakes was not surveyed. We also omitted 23 lakes that were < 5 ha, as loon breeding rarely occurs on lakes under this size in Ontario (Alvo, 2009; McNicol et al., 1995). We also omitted one lake near Hudson Bay and five near Lake Erie. As these were the only lakes

#### Table 1

Summary of the predictors considered in analyses of common loon reproductive success in Ontario, including each predictor's known or hypothesized effect on loon productivity, and the data available for each predictor.

Predictor	Known/hypothesized effect on loon productivity	Number of lakes with data	Years with data
Lake area (ha)	Loons prefer larger lakes for breeding (Kuhn et al., 2011), and productivity increases with lake area (Tozer et al. 2013)	1577	1981 – 2018 <sup>d</sup>
Longitude	Productivity decreases from west to east in Canada (Tozer et al., 2013)	1577	1981 – 2018 <sup>d</sup>
рН	Acidity negatively impacts productivity (Tozer et al., 2013)	1207	1981 – 2018 <sup>d</sup>
Fish abundance	Higher brood mortality on lakes with fewer fish (Alvo et al., 1988)	186	1981 -
Shoreline development (%)	Nesting habitat loss and degradation can lower productivity (Evers et al., 2020; Heimberger et al., 1983)	1284	1982-
Boating activity	Disruption of incubation and foraging can lower productivity (McIntyre, 1988)	1184	2004 1982– 2004
Weather variables <sup>a</sup>	Timing of ice break up (Piper et al., 2000) and black fly abundance and longevity (Piper et al., 2018) can impact	1549	2004 1981– 2015
Bald eagle occurrence	Bald eagles can depredate loon eggs, chicks, and adults (McCarthy et al., 2010; Paruk et al., 1999; Piper et al., 2008)	335	1981– 2018
DCCO <sup>b</sup> occurrence	DCCO are hypothesized to harm local fish populations and damage nesting habitats (Dorr et al., 2020)	393	1981-
Yellow perch Hg (µg/g wet weight)	Productivity decreases with increasing mercury exposure (Burgess and Meyer, 2008)	596 <sup>c</sup>	1981 – 2018 <sup>e</sup>

<sup>a</sup> Includes seven predictors: mean maximum temperatures in April, May, and June (°C); mean precipitation in April, May, and June (mm); and precipitation of the coldest quarter (mm).

<sup>b</sup> Double-crested cormorant.

<sup>c</sup> Values were recorded at the secondary watershed level (i.e., all lakes in the same watershed have the same values for yellow perch mercury).

<sup>d</sup> Predictor value is the same in all years.

<sup>e</sup> Predictor values were averaged by decade.



**Fig. 1.** Location of CLLS lakes used to investigate patterns in common loon reproductive success in Ontario between 1981 and 2018. Figure inset indicates the study area in North America represented on the map (a). Number of lakes (solid blue line) or common loon pairs (dashed gray line) surveyed per year (b) and the number of years that each lake was surveyed (c) by CLLS participants. In panel c, numbers above the bars indicate the value of each bar as a percentage of the total number of lakes surveyed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in the Northern Taiga and Lake Erie-Lake Ontario ecoregions, these six lakes were omitted as spatial outliers. This left a total of 1577 lakes with reproductive data (Fig. 1a). Lakes were located in the southern half of Ontario (<51.05° latitude). Most lakes in the CLLS (85%) were located in the Mixed Wood Shield ecoregion of Ontario, with a smaller number located in the Softwood Shield (7%) and Mixed Wood Plains (8%) ecoregions. An average of 373 (SD = 148) loon pairs and 212 (SD = 93) lakes were surveyed each year (Fig. 1b). Most lakes (77%) were surveyed for <10 years, and many lakes (49%) were surveyed in only one or two years (Fig. 1c). A summary of the data available for each predictor is given in Table 1.

# 2.3. Data analysis

Our analysis was conducted in three stages. In stage one, we addressed our first objective to define underlying baseline patterns of loon reproductive success as a function of longitude, lake area, and year. We examined support for 13 candidate models that included year, longitude, and/or lake area as fixed effects. Because our primary objective was to identify the factors contributing to the temporal trends in loon productivity, in all stages of the analysis only interactions with year were considered. In all models, the response variable was the number of young that were at least six weeks old per territorial loon pair per year (values were 0, 1, or 2).

Next, we addressed our second and primary objective to explore support for various factors that might explain any temporal trends in loon productivity. In the second stage of our analysis, we explored support for 13 factors shown or hypothesized to affect loon productivity in Ontario (mercury was tested in stage three, see below). Only 30 lakes had data for all 13 predictors. Given this data limitation, we conducted an exploratory analysis to minimize the number of co-variates included in the global model and, in doing so, maximize the number of lakes analyzed. Exploratory analyses separately tested each predictor (i.e., exploratory models contained only the predictor of interest plus year, longitude, and lake area) to identify which of the 13 factors influenced the number of six-week-old young per pair per year. Only factors found to affect the number of young in the exploratory analysis were included as predictors in the global model (see Appendix B for details).

Our exploratory analysis revealed relationships between loon productivity and six factors: pH, fish abundance, bald eagle presence, double-crested cormorant presence, mean maximum temperatures in April, and winter precipitation (see Results section for details). We included pH, mean maximum temperatures in April, winter precipitation, longitude, lake area, year, and the interactions of pH  $\times$  year and longitude  $\times$  year as fixed effects in the global model for stage two. Bald eagle and double-crested cormorant presence were not included in the global model because the positive relationship between bald eagle and double-crested cormorant presence and common loon reproductive success was likely driven by similarities in habitat quality for these three species, rather than by a direct effect on the number of six-week-old young per loon pair per year (McCarthy and Destefano,

#### Table 2

Model selection results for 13 candidate models explaining underlying baseline patterns in common loon reproductive success in 1577 Ontario lakes between 1981 and 2018. k = number of parameters,  $AIC_c = Akaike's$  information criterion corrected for small sample sizes,  $\Delta AIC_c =$  difference in  $AIC_c$  from the best approximating model, w = Akaike weight.

Fixed effects	k	AIC <sub>c</sub>	$\Delta \text{AIC}_{\text{c}}$	w
Longitude + area <sup>a</sup> + year + longitude $\times$ year	8	29,936.0	0.0	0.549
Longitude + area + year	7	29,938.8	2.8	0.133
Area + year	6	29,939.4	3.4	0.098
Longitude + area + year + longitude $\times$ year +	8	29,940.2	4.3	0.065
area $ imes$ year				
Longitude + area + year + area $\times$ year	8	29,940.2	4.3	0.065
Area $+$ year $+$ area $\times$ year	7	29,940.9	4.9	0.047
Longitude + area	6	29,942.2	6.2	0.025
Area	5	29,942.9	6.9	0.018
Longitude + year + longitude $\times$ year	7	29,949.9	13.9	< 0.001
Year	5	29,953.1	17.1	< 0.001
Longitude × year	6	29,953.6	17.6	< 0.001
Intercept only (null)	4	29,956.6	20.6	< 0.001
Longitude	5	29,957.1	21.1	< 0.001

<sup>a</sup> Lake area was log<sub>10</sub> transformed.

# Table 3

Descriptive statistics, interquartile range (IQR), parameter estimates ( $\beta$ ), and 85% confidence limits (85% CL) for covariates in the best supported model explaining underlying baseline patterns in common loon reproductive success in 1577 Ontario lakes between 1981 and 2018. Covariates were standardized prior to model fitting.

Parameter	Median	Min	Max	IQR	β	85% CL (lower, upper)
Year	2000	1981	2018	16	-0.10	-0.14, -0.06
Lake area <sup>a</sup>	458	5	155,400	1295	0.07	0.05, 0.10
Longitude	-79.0	-95.1	-75.7	3.1	0.03	0.01, 0.06
Longitude $\times$ year	-	-	-	-	0.03	0.01, 0.05
Intercept	-	-	-	-	-0.46	-0.51, -0.41

<sup>a</sup> Lake area was log<sub>10</sub> transformed for analyses. Back-transformed values (in ha) are given for descriptive statistics and the IQR for ease of interpretation.

2011). There was a moderate positive correlation between fish abundance and pH ( $R^2 = 0.47$ ). To eliminate issues of collinearity, and because only a small number of lakes had data for fish abundance (n = 186), we omitted fish abundance from our second model set. Ultimately, stage two of the analysis included 1196 lakes with data from 1981 to 2015. We considered the global model, all possible combinations of the six factors and two interaction terms, and an intercept-only model, for a total of 104 candidate models.

Finally, in stage three of our analysis, mercury was added as a predictor to assess whether it improved the overall fit of the best approximating model from stage two (i.e., we tested whether the inclusion of mercury increased the amount of variation in loon productivity explained by the best fitting model from stage two). We took this approach given that mercury concentrations were averaged by decade and were measured at the watershed level, rather than in individual lakes.

Data were analyzed using generalized linear mixed effects models (GLMMs) with log-link functions and Poisson distributions, which was suitable given the count structure of the response variable (Zuur et al., 2009). Longitude was in decimal degrees (e.g.,  $-80.35^{\circ}$ ), lake area and fish abundance were log<sub>10</sub> transformed, boating activity was

encoded as an ordered factor, and bald eagle and double-crested cormorant occurrence were encoded as factors (0 = absent, 1 = present). For all predictors, annual measurements were used in analyses (i.e., variables were allowed to vary temporally), except for pH and fish abundance (which were averaged across years) and fish mercury (which was averaged by decade). Year was encoded as a continuous variable to assess temporal trends. All continuous predictors were standardized to have a mean of zero and a standard deviation of one. We tested for collinearity among predictors in all global models using the ols\_vif\_tol function in the olsrr package (Hebbali, 2020). All models (except the models for mercury) included a random intercept for lake identity, as 47% of the lakes surveyed had loon reproductive success data for more than one breeding pair per year. Models to assess the effects of mercury included a random intercept for lake identity nested within watershed. For all models, inclusion of a temporal autocorrelation structure (ar1) by year improved the model fit, as determined by lower AIC<sub>c</sub> scores (Burnham and Anderson, 2002).

All analyses were performed in R version 3.6.1 (R Core Team, 2019). GLMMs were run in the glmmTMB package (Brooks et al., 2017). Lower AlC<sub>c</sub> scores were used for model selection, and we considered all models within  $\Delta$ AlC<sub>c</sub> < 2 to be of equivalent model fit (Burnham and Anderson, 2002). We considered variables to have influenced loon reproductive success when 85% confidence intervals of the parameter estimate did not overlap zero (Arnold, 2010). Model selection was completed using the bbmle package (Bolker and R Development Core Team, 2017). All plotting was performed using the packages ggplot2 (Wickham, 2016) and cowplot (Wilke, 2019). Maps were generated using packages ggmap (Kahle and Wickam, 2013) and RgoogleMaps (Loecher and Ropkins, 2015).

# 3. Results



**Fig. 2.** Reproductive success of common loons as a function of year (a), lake area (log transformed), b), longitude (c), and longitude and year (d). Lines indicate model-based predictions  $\pm$  a 95% confidence interval. In panel d, lines were split into east (solid blue line) and west (dashed gray line) at a longitude of  $-79^{\circ}$ , the median longitude of the CLLS lakes. Horizontal dashed lines indicate the minimum estimated number of fledged young per pair (0.48) required to support a stable common loon breeding population (Evers et al., 2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In the first stage of the analysis, we examined underlying baseline patterns in loon productivity in Ontario. Longitude, lake area, year, and longitude  $\times$  year were retained in the best model explaining

#### Table 4

Model selection results for 104 candidate models investigating the factors that affect temporal trends in common loon reproductive success in 1196 Ontario lakes between 1981 and 2015. k = number of parameters, AIC<sub>c</sub> = Akaike's information criterion corrected for small sample sizes,  $\Delta$ AIC<sub>c</sub> = difference in AIC<sub>c</sub> from the best approximating model, w = Akaike weight, AT = mean maximum temperature in April, WP = winter precipitation. Only models with  $w \ge 0.010$  are shown.

Fixed effects	k	AIC <sub>c</sub>	$\Delta AIC_{c}$	w
Longitude + area <sup>a</sup> + year + pH + AT + longitude $\times$ year + pH $\times$ year	11	25,039.4	0.0	0.339
Longitude + area + year + pH + AT + WP + longitude $\times$ year + pH $\times$ year	12	25,040.0	0.6	0.245
Longitude + area + year + pH + AT + longitude $\times$ year	10	25,040.5	1.1	0.192
Longitude + area + year + pH + AT + WP + longitude $\times$ year	11	25,041.0	1.6	0.149
Area + year + pH + AT + pH $\times$ year	9	25,045.7	6.4	0.014
$Longitude + area + year + pH + longitude \times year + pH \times year$	10	25,046.4	7.0	0.010

<sup>a</sup> Lake area was log<sub>10</sub> transformed.

variation in reproductive success (Akaike weight [w] = 0.55), and there was little support for any of the other models ( $\Delta AIC_c > 2.0$ , w < 0.15; Table 2). Confidence limits around parameter estimates for all factors in the best supported model did not include zero (Table 3). We confirmed that the number of six-week-old young per pair per year decreased between 1981 and 2018 in Ontario (Fig. 2a). The number of six-week-old young per pair per year also increased with lake area (Fig. 2b) and increased from west to east (Fig. 2c). As well, the interaction of longitude  $\times$  year suggested that the temporal decrease in chick production was steeper in western than in eastern Ontario (Fig. 2d).

Next, we conducted exploratory analyses to select factors that influence loon productivity for inclusion in our second model set (see Appendix B for details). Exploratory analyses revealed a positive relationship between the number of six-week-old young per pair per year and pH, fish abundance, mean maximum temperatures in April, and bald eagle presence, and a negative relationship between the number of six-week-old young per pair per year and winter precipitation. Interaction effects suggested that the temporal decrease in reproductive success was steeper on lakes with lower pH, lower fish abundance, and without the presence of double-crested cormorants. Exploratory analyses also showed that shoreline development and boating activity did not influence loon productivity.

In the second stage of our analysis, we assessed support for the factors found to affect the number of six-week-old young per pair per year in the exploratory analysis. Longitude, year, lake area, pH, April temperatures, longitude × year, and pH × year were retained in the best ranked model (w = 0.34). Three other models also received support and included winter precipitation and different combinations of the interaction covariates (Table 4). Other models received little support ( $\Delta AIC_c > 6.0, w < 0.02$ ). Confidence limits around parameter estimates for all factors except winter precipitation and longitude did not overlap zero (Table 5). There was a positive relationship between pH and the number of six-week-old young per pair per year, such that fewer

#### Table 5

Descriptive statistics, interquartile range (IQR), parameter estimates ( $\beta$ ), and 85% confidence limits (85% CL) for covariates in the best supported model investigating the factors that affect temporal trends in common loon reproductive success in 1196 Ontario lakes between 1981 and 2015. Covariates were standardized prior to model fitting.<sup>a</sup>

Parameter	Median	Min	Max	IQR	β	85% CL (lower, upper)
Year	1997	1981	2015	14	-0.12	-0.16, -0.08
Longitude	-78.9	-95.1	-75.9	2.9	0.03	-0.001, 0.06
Lake area <sup>b</sup>	513	5	155,400	1592	0.07	0.04, 0.10
рН	7.2	4.3	9.5	1.2	0.08	0.05, 0.11
April temperature	10.3	2.9	17.2	3.1	0.07	0.04, 0.10
Longitude $\times$ year	-	-	-	-	0.05	0.03, 0.07
$pH \times year$	-	-	-	-	0.02	0.004, 0.04
Intercept	-	-	-	-	-0.44	-0.49, -0.39

<sup>a</sup> Precipitation of the coldest quarter was not retained in the best supported; its  $\beta$  (and associated 85% confidence limits) in the global model were: -0.02 (-0.05, 0.01).

<sup>b</sup> Lake area was log<sub>10</sub> transformed for analyses. Back-transformed values (in ha) are given for descriptive statistics and the IQR for ease of interpretation.

young were produced on more acidic lakes (Fig. 3a). The interaction of  $pH \times year$  suggested that the temporal decrease in reproductive success was steeper on lakes with lower pH (Fig. 3b). We also found that the number of six-week-old young per pair per year increased with warmer April temperatures (Fig. 4).

Finally, in the third stage of the analysis, we added yellow perch mercury concentrations as a predictor to the best supported model from stage two of our analysis to assess whether it helped to explain more variation in loon reproductive success (i.e., improved the model fit). A total of 500 lakes from 1981 to 2015 had data for all five predictors. The inclusion of yellow perch mercury concentrations improved the model fit ( $-1.0 \text{ AIC}_c$  compared to the model without mercury), but all models received support ( $\Delta \text{AIC}_c < 2.0$ ; Table 6). The 85% confidence limit around the parameter estimate for mercury did not include zero (-0.08, -0.005), and showed that the number of six-week-old



**Fig. 3.** Common loon reproductive success was lower (a) and temporal declines were steeper (b) on more acidic lakes. Lines indicate model-based predictions  $\pm$  a 95% confidence interval. In panel b, lines were split into high pH (solid blue line) and low pH (dashed gray line) lakes at a pH of 6, as loon productivity can be negatively affected at pH ≤ 6 (Alvo, 2009). Horizontal dashed lines indicate the minimum estimated number of fledged young per pair (0.48) required to support a stable common loon breeding population (Evers et al., 2020). pH values were averaged across years for each lake. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4.** Common loon reproductive success increased with April temperatures. Line indicates model-based predictions  $\pm$  a 95% confidence interval. Horizontal dashed line indicates the minimum estimated number of fledged young per pair (0.48) required to support a stable common loon breeding population (Evers et al., 2020). Weather data were for individual lakes in each year.

young per pair per year decreased with increasing yellow perch mercury concentrations ( $\beta = -0.04$ ; Fig. 5).

# 4. Discussion

Data from citizen science monitoring demonstrated a consistent downward trend in common loon reproductive success in Ontario between 1981 and 2018. Loon populations in Ontario are generally thought to be stable; however, estimates of breeding loon numbers are speculative in Canada (Evers et al., 2020). An estimated threshold reproductive rate of 0.48 young fledged per pair per year is required to maintain a stable common loon breeding population (Evers et al., 2020), and our estimates of loon productivity suggest that declines in the number of breeders may already be underway on some lakes in Ontario, provided there are no nearby source populations to compensate for losses. Our results suggest that declines below 0.48 six-week-old young per pair have already occurred on lakes west of  $-79^{\circ}$  longitude and on lakes below pH 6.0. It is therefore possible that low productivity has affected the number of common loon breeding pairs on some lakes. Tozer et al. (2013) predicted that common loon reproductive success would drop below the threshold reproductive rate in eastern Canada between 2003 and 2126, and found that productivity dropped below 0.48 young per pair per year in Canada on pH 6.0 lakes around 2001 (1995–2009), which is similar to our results for Ontario. Breeding common loon numbers have declined substantially across much of its southern range, and loons have been extirpated from many U.S. states (Evers et al., 2020). This trend is expected to continue, as the common loon range is predicted to shift northward due to climate change, with a 56% loss in the loon's current breeding range by 2080 (National Audubon Society, 2015). These projected losses, however, may be offset

#### Table 6

Model selection results for 3 candidate models investigating the influence of yellow perch mercury concentrations (Hg) on common loon reproductive success in 500 Ontario lakes between 1981 and 2015. k = number of parameters,  $AIC_c = Akaike's$  information criterion corrected for small sample sizes,  $\Delta AIC_c =$  difference in  $AIC_c$  from the best approximating model, w = Akaike weight, AT = mean maximum temperature in April.

Fixed effects	k	AIC <sub>c</sub>	$\Delta \text{AIC}_{\text{c}}$	w
Longitude + area <sup>a</sup> + year + pH + AT + Hg + longitude × year + pH × year	13	12,968.9	0.0	0.490
$\begin{array}{l} \text{Longitude} + \text{area} + \text{year} + \text{pH} + \text{AT} + \text{longitude} \\ \times \text{year} + \text{pH} \times \text{year} \end{array}$	12	12,969.9	1.0	0.300
$\begin{array}{l} \text{Longitude} + \text{area} + \text{year} + \text{pH} + \text{AT} + \\ \text{Hg} + \text{longitude} \times \text{year} + \text{pH} \times \text{year} + \\ \text{Hg} \times \text{year} \end{array}$	14	12,970.6	1.7	0.210

<sup>a</sup> Lake area was log<sub>10</sub> transformed.



**Fig. 5.** Common loon reproductive success decreased with increasing mercury concentrations in yellow perch. Line indicates model-averaged prediction  $\pm$  a 95% confidence interval. Horizontal dashed line indicates the minimum estimated number of fledged young per pair (0.48) required to support a stable common loon breeding population (Evers et al., 2020). Mercury concentrations for each watershed were averaged by decade.

by restoration and conservation efforts, which are increasing numbers of breeding loons in some U.S. states (e.g., New Hampshire and Vermont; Evers et al., 2020).

Acid rain has been identified as one of the most important stressors to common loon reproductive success (Alvo, 2009; Burgess and Meyer, 2008; Evers et al., 2008; Piper et al., 2012; Tozer et al., 2013). We found that lake acidity was associated with declines in loon reproductive success in 1196 Ontario lakes, and exploratory analyses and analyses of fish mercury concentrations at the watershed level suggest that low fish abundance or mercury may be proximate drivers for pH-associated declines. Our results suggest that loon reproductive success was below the positive growth rate threshold of 0.48 young per pair for lakes with pH ~ 4.5, and data suggest that declines below this growth rate threshold occurred in the mid-2000s on many lakes with pH < 6.0. This is consistent with the results of Alvo (2009), who observed no fledging success below pH 4.4 and high brood mortalities on lakes with pH 4.4-5.8 (especially on small lakes). The results for fish abundance and mercury also agree with the findings of previous studies showing that common loon reproductive success is lower on lakes with fewer fish (Alvo, 2009; Alvo et al., 1988) and higher fish mercury concentrations (Burgess and Meyer, 2008; Evers et al., 2008). Similar to previous studies (e.g., Alvo et al., 1988; Alvo, 2009; Piper et al., 2012; Tozer et al., 2013), we also found that the number of six-week-old young per pair per year was lower on smaller lakes, which are typically more acidic, have fewer fish, and have higher methylmercury concentrations (Bodaly et al., 1993; Eilers et al., 1983; Matuszek and Beggs, 1988).

Common loon reproductive success appears to continue to be negatively affected by lake acidity in Ontario. Despite reductions in acidifying emissions, limited biological recovery has occurred on many lakes (Jeffries et al., 2003; Keller et al., 2019). Lake acidification is often associated with other changes in lake chemistry, like calcium declines (Jeziorski et al., 2008), which can slow biological recovery (Keller et al., 2019). As well, fish re-establishment is unlikely on lakes lacking connections to other lakes with fish source populations (Keller et al., 2019). Recent evidence suggests that climate change may be limiting the recovery of lakes from acid rain (Jeffries et al., 2003; Keller et al., 2019). Climate change models predict an increase in the frequency and severity of hot summer temperatures and droughts (Hayhoe et al., 2007; IPCC, 2008). Warmer summer temperatures are expected to inhibit the re-establishment of cool- and cold-water fish species in lakes affected by acid rain (Keller et al., 2019), and droughts can promote the release of sulfur from watershed wetlands and exposed littoral sediments into lakes, resulting in further lake acidification (Arnott et al., 2001; Dillon et al., 1997; Jeffries et al., 2003).

There is a clear relationship between elevated loon mercury exposure and reduced productivity in loons (Burgess and Meyer, 2008; Evers et al., 2008), and increases in fish mercury concentrations since the 1990s have also been linked to changes in local weather and global climate drivers (Chen et al., 2018). Regional water level oscillations are intensifying with climate change (Benateau et al., 2019), and rising water levels create conditions that promote mercury methylation (Watras et al., 2020). As a result, mercury concentrations in lakes, fish, and common loons increase as water levels increase (Watras et al., 2020). Indeed, mercury concentrations in loons fluctuate in phase with long-term regional water level fluctuations. Therefore, episodic increases in common loon mercury concentrations are expected to occur more frequently in the future with climate change, despite declines in mercury deposition (Watras et al., 2020), and this may contribute to further reductions in common loon reproductive success.

We found that the number of six-week-old young per pair per year was higher in southeastern Ontario relative to northwestern Ontario (note the distribution of CLLS lakes in Ontario, where more eastern lakes are also farther south; Fig. 1a). This is contrary to earlier findings by Tozer et al. (2013), who found that loon reproductive success decreased from west to east across Canada. Acidifying emissions are predominantly carried eastward and northeastward by prevailing winds (Schindler, 1988). Therefore, lake acidity (Minns et al., 2008) and mercury concentrations in lakes (Eckley and Hintelmann, 2006), fish (Depew et al., 2013a, 2013b), and loons (Evers et al., 1998), tend to increase from west to east across Canada. Southeastern Ontario, however, is an exception to this trend. Soils in southeastern Ontario have a high buffering capacity, and the eutrophication that results from high agricultural and urban land use in this area has the potential to limit mercury bioaccumulation in aquatic food webs (reviewed in Depew et al., 2013b; Wayland and McNicol, 1990). Therefore, despite receiving elevated mercury and sulfate deposition, risks to common loon breeding pairs in southeastern Ontario are low (Depew et al., 2013b). Moreover, there is a concentration of acidic lakes (<pH 6.0) near Sudbury, Ontario, located in the western portion of our study area (46.4917°, -80.9930°; Keller et al., 2004), which is an important point source of acidifying emissions (Keller et al., 2019). There is thus a complex interplay of factors that could be contributing to the observed relationship between the number of six-week-old young per pair per year and longitude in Ontario, including the effects of local geochemistry and geographic scale.

Our analyses of local weather variation showed that loon productivity was lower in years with cool April temperatures, and exploratory analyses suggested that lower loon productivity may also be associated with high winter precipitation. Colder temperatures delay ice break up (Sharma et al., 2013), and thus these results could suggest that late ice break up negatively influences common loon reproductive success. There is a negative correlation between the timing of ice break up and breeding in many waterfowl species (e.g., Mallory et al., 2003; Mehlum, 2012), where late ice break up can delay egg laying, leaving chicks an insufficient amount of time for development before migration (reviewed in Mehlum, 2012). Common loons, however, do not appear to be time constrained during breeding and often wait 4 to 6 weeks after arrival on breeding territories to reproduce (Evers, 2007). Moreover, previous studies have either observed no correlation between the timing of ice break up and common loon reproductive success (Gutreuter et al., 2013) or have found a positive relationship between ice break up and loon productivity with higher production in years with later break up (Piper et al., 2012).

Alternatively, the relationship between cool April temperatures and reproductive success may be related to the effect of spring temperature on black fly abundance and longevity. Cooler temperatures prevent small streams from drying up, which increases the abundance of black fly hatching sites and the duration of blackly emergence (Berenger and Parola, 2017; Hiltner and Hershey, 1992; Martinez-de la Puente et al., 2009). Cooler spring temperatures also increase the longevity of biting female black flies (Davies, 1953), although black flies are more active and numerous on avian nests when temperatures are warmer (Martinez-de la Puente et al., 2009; Piper et al., 2018). In Wisconsin,

common loon nest abandonment was higher when April and May temperatures were cooler (Piper et al., 2018). Curiously, black fly season runs from May to late June in Ontario (Bennett, 1960), yet we saw no association between May and June temperatures and the number of sixweek-old young per pair per year. Further research would be useful to better assess black fly harassment and loon productivity in Ontario.

Exploratory analyses showed that the number of six-week-old young per pair per year was higher on lakes where bald eagles were present and revealed shallower temporal declines in the number of six-week-old young per pair per year on lakes where double-crested cormorants were present. Bald eagles, double-crested cormorants, and common loons are all piscivorous species that share similar breeding habitat requirements, with all three species preferring large lakes with high fish abundance (Buehler, 2020; Dorr et al., 2020; Evers et al., 2020). The presence of eagles and cormorants may therefore serve as an index of habitat quality for breeding loons. Similarly, McCarthy and Destefano (2011) found that common loons were more likely to select nest sites near bald eagle nests. However, these authors also saw a decrease in the number of common loon chicks hatched as bald eagle nest density increased, and therefore the positive relationship between loon reproductive success and eagle presence observed here may not hold in areas of high bald eagle abundance (Cooley et al., 2019; Gutreuter et al., 2013). Although there is concern that double-crested cormorants deplete local fish populations and damage shoreline habitats (Dorr et al., 2020), our results suggest that cormorants do not negatively influence loon reproductive success. Thus, eagles and cormorants are not major factors contributing to the decline in common loon chick productivity in Ontario.

Despite the documented negative effects of human disturbance on common loon productivity (Heimberger et al., 1983; Kelly, 1992; Titus and Van Druff, 1981), we found no relationship between levels of shoreline development, boating activity, and the number of six-week-old young per pair per year, consistent with some previous studies (Badzinski and Timmermans, 2006; Buxton et al., 2019; Caron and Robinson, 1994; McCarthy and Destefano, 2011). Loons may become habituated to human presence (McIntyre, 1988), but alternately they can also avoid human disturbance by selecting nest sites away from areas with shoreline development and high boating activity, thereby limiting the effect of disturbance on breeding success (Alvo, 1981; Caron and Robinson, 1994; McCarthy and Destefano, 2011). Avoiding human disturbance appears to be easier on larger lakes. Larger lakes can offer loons more potential nesting habitat and more protected bays for nesting and nurseries than smaller lakes (Caron and Robinson, 1994; Evers et al., 2020). Indeed, although most Ontario CLLS lakes had high watercraft use (73% of lakes with boating activity  $\geq$ 6; i.e., frequent use of boats with motors), we found that boating activity tended to be higher on larger lakes, a relationship that has been observed previously elsewhere (Caron and Robinson, 1994). However, we also found that common loon reproductive success was higher on larger lakes compared to smaller lakes. Therefore, although boating activity was higher, these larger lakes may have afforded loons more opportunities to avoid watercraft disturbance. One caveat to these results is that the majority of lakes in the Ontario CLLS dataset had relatively undeveloped shorelines (52% of lakes with  $\leq$ 30% shoreline development). This may have limited our ability to detect differences in reproductive success among lakes with varying degrees of shoreline development (Badzinski and Timmermans, 2006). Nonetheless, our results suggest that human disturbance and shoreline development are not major factors contributing to declining reproductive success of common loons in Ontario.

We defined underlying baseline patterns of common loon reproductive success in Ontario. We also assessed how a diverse suite of 14 different factors affect loon reproductive success and evaluated whether these factors influence temporal trends in loon productivity. This study is, to our knowledge, the most comprehensive analysis on this topic to date. However, it is possible that other additional factors help explain these observed trends. For example, ingested lead (e.g., fishing sinkers), organic pollutants, oil spills, botulism, and emaciation syndrome can either directly lower loon productivity or can lower loon reproductive success by negatively affecting adult body condition (Evers et al., 2020). Despite these additional potential influences, our results provide broad regional evidence for generating hypotheses for future consideration.

# 5. Conclusions

We identified low pH as an important factor linked to common loon productivity declines over the last 40 years in Ontario, and we demonstrated that lake area, longitude, and April temperatures can predict the number of six-week-old young per pair per year. We also provided further evidence that shoreline development and human disturbance have little influence on chick productivity, and suggested that bald eagles and double-crested cormorants are relatively unimportant factors. We suggest that investigations into how these factors are influenced by climate change are a key area for additional research. Documented long-term climate-driven increases in mercury contamination in fish in Ontario (Chen et al., 2018) has presumably increased mercury concentrations in loons (Burgess and Meyer, 2008; Scheuhammer et al., 2016), and mercury contamination is known to reduce loon productivity (Burgess and Meyer, 2008; Evers et al., 2008). Therefore, we further hypothesize that climate change may exacerbate historic acid rain and mercury contamination issues. We predict that our results and working hypothesis will help direct future research and conservation efforts to mitigate threats to common loon reproductive success.

Supplementary data to this article can be found online at https://doi. org/10.1016/j.scitotenv.2020.139724.

## **CRediT authorship contribution statement**

Kristin Bianchini: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Visualization. Douglas C. Tozer: Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition. Robert Alvo: Writing - review & editing, Supervision. Satyendra P. Bhavsar: Data curation, Writing - review & editing. Mark L. Mallory: Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition12.

# Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

The authors thank the thousands of CLLS volunteers who collected the common loon reproductive data reported in this paper. We also thank Kathy Jones for coordinating and promoting the CLLS in Ontario and across southern Canada, and Tracy Barber for processing data. We are grateful to all of the researchers who generously shared their data: additional pH data were provided by Ken Minns, Cindy Chu provided the fish abundance data, and Dan McKenney and Pia Papadopol provided the local weather variables. We thank members of the Long Point Waterfowl and Wetlands Research Program scientific advisory committee for comments that improved the paper. Support for the CLLS has been provided by the Biodiversity Institute, Environment and Climate Change Canada, Environmental Partners Fund, James L. Ballie Memorial Fund, John and Pat McCutcheon Charitable Foundation, Kenneth M. Molson Foundation, North American Loon Fund, Northern Reflections, Ontario Federation of Anglers and Hunters, Ontario Wildlife Foundation, Shell Environmental Fund, TD Friends of the Environment Foundation, The Millennium Fund, The Peacock Foundation, The Ontario Trillium Foundation, The Wildlife Toxicology Fund, Volkswagen, and CLLS participant and Birds Canada supporter donations. This work was supported by Mitacs through the Mitacs Accelerate Postdoctoral Scholarship, Birds Canada through the Long Point Waterfowl and Wetlands Research Program, Acadia University, SC Johnson, and The Bluff's Hunting Club.

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