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Productivity of an iconic waterbird, the Common Loon, is decreasing across the southern portion of its breeding range

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Abstract

The Common Loon (*Gavia immer*) is an iconic waterbird of the northern wilderness and an indicator of the health of aquatic ecosystems. We conducted a benchmark comparison of productivity rates and long-term trends in productivity (6-week-old young raised per territorial pair) from 45 591 breeding events across 12 different study populations throughout the southern portion of species' breeding range in North America. While all regions showed long-term mean productivity rates at or above the threshold considered necessary for population stability (0.48 chicks fledged per territorial pair), we found significant declines in productivity (ranging from −0.17% to −2.8% per year) in seven regions, nonsignificant but downward trends in four others, and a nonsignificant increase in one region (Maine). Although productivity is only one of three demographic parameters that dictate the stability of a population, long-term decreases in productivity could signal looming population declines in Ontario, the Prairie, and Atlantic provinces, New York, Massachusetts, and New Hampshire. We suggest that a variety of region-specific anthropomorphic and natural factors, in addition to increased rainfall secondary to climate change are at fault for such declines. Identifying causes of productivity decline might lead to successful efforts to mitigate contributing factors, thus stabilizing or increasing loon populations.

Key words: breeding population, population status, range-wide, fledgling, *Gavia immer*

Introduction

Global, regional, and local species losses due to human impacts have devastated native biodiversity and show no sign of abating (Sala et al. 2000; Ceballos et al. 2017; Rosenberg et al. 2019; Habibullah et al. 2022). Therefore, it is crucial to determine regional and large-scale population trends to inform species-level conservation and management (Horns et al. 2018). Across the globe, conservation efforts have primarily focused on rare or range-restricted species that face imminent extinction (Gaston 2008; Inger et al. 2015). Small declines in abundant species can be difficult to detect, but can result in substantial loss of biomass (Ellison et al. 2005) and disrupt trophic interactions (Ellison 2019) and ecosystem dynamics (Gregory et al. 2007; Van Dyck et al. 2009; Elliot et al. 2024).

Fifty-two percent of North American waterbirds among five families (Gaviidae, Laridae, Ardeidae, Rallidae, and Podicipedidae) are in decline, according to a recent analysis (Rosenberg et al. 2019). Much of the decline has been associated with habitat loss (Donnelly et al. 2020), disease (Kenow et al. 2018), environmental pollutants (Lagos et al. 2008; Travis et al. 2020), and climate change (Haig et al. 2019). Waterbirds depend on the ecological integrity of aquatic environments and act as indicators of the quality and integrity of these habitats (Amat and Green 2009). Since waterbirds can be sentinels for the health of aquatic systems, it is critical to monitor population trends of keystone waterbird species to understand their rates of decline (Kushlan 1993; Amat and Green 2009; Mansfield et al. 2024). Unfortunately, few waterbird species have been monitored across large spatial scales; how-

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ever, studies have documented region-specific trends in abundance and productivity, and provided some understanding of population decline for specific species. Long-term studies that monitor widespread waterbird species, and the regions associated with declines, across a longitudinal and latitudinal gradient are essential to identify effective conservation and management approaches for recovery across a species' range.

The Common Loon (*Gavia immer*; hereafter "loon") is a cultural icon and apex predator of northern ecosystems (Evers 2007). Loons are widely recognized as important bioindicators of aquatic ecosystem health in North America (McNicol et al. 1995; Evers et al. 1998; Evers 2006; Yang et al. 2020; Bianchini et al. 2021*a*). As top predators in freshwater food webs, loons are exposed to high levels of bioaccumulating environmental pollutants, like mercury (Meyer et al. 1998; Evers et al. 2003, 2008). They are also indicators of disruptions to food webs (i.e., lower fish abundance; Bianchini et al. 2020).

Although loons are widespread in North America, long-term monitoring programs in portions of their range have documented declines in breeding productivity (Tozer et al. 2013; Bianchini et al. 2020) and abundance (Piper et al. 2020; Saunders et al. 2021) over the past two decades. Productivity, the number of young produced per territorial pair, is one of several factors that determine whether an adult population of animals is increasing, stable, or declining. Adult survival and juvenile survival/recruitment are of even greater importance to population dynamics in species with slow life-histories like loons, but production of young provides a vital indication of a population's ability to both maintain itself over time and recover from declines (e.g., Rees and Crawley 1989; Drummond et al. 2019). Further, declines in productivity across portions of the U.S. and Canada as determined by studies that monitored breeding and nonbreeding individuals (Grear et al. 2009; Tozer et al. 2013; Saunders et al. 2021) may be reflective of substantial regional declines in resource availability and juvenile recruitment for loons overall.

Despite a wealth of studies on loon breeding ecology across the species' range, the regional focus of most studies has made it challenging to obtain a clear overall picture of North American loon productivity. Productivity of loons across southern Canada decreased by 14% between 1992 and 2010 and was predicted to lead to overall population declines by 2016 with productivity levels below the demographic source-sink threshold (Tozer et al. 2013). Achieving a broader understanding of productivity, and the factors influencing it, across the breeding range, might enable us to recognize where population declines are occurring or are likely to occur.

In the absence of a single range-wide analysis, long-term declines in productivity have been ascribed to numerous factors, including changes in land use resulting in reduced nesting habitat and increased human recreational disturbance (Saunders et al. 2021), variation in lake ice-off dates (Bianchini et al. 2021*b*), lake acidity (Bianchini et al. 2020, 2021*a*), increased precipitation (Saunders et al. 2021; Piper et al. 2024), increased temperature (Tozer et al. 2013), high environmental mercury loads (Evers et al. 1998, 2008; Burgess and Meyer 2008; Schoch et al. 2020), and increased predation by Bald Eagles (*Haliaeetus leucocephalus*; Paruk et al. 1999; McCarthy et al. 2010; Adirondack Center for Loon Conservation unpub. data). The most detailed analysis of loon population decline, which took place between 1993 and 2019 in the state of Wisconsin, demonstrated that chick mass and fledging success fell by 11% and 26%, respectively, and survival of nonbreeding adults plummeted by over 50% (Piper et al. 2020). In this study system, heavy rainfall and the subsequent reductions in water clarity was associated with reduced chick body mass as it may inhibit foraging and increase mortality (Piper et al. 2024).

Here, we undertook a collaborative, range-wide assessment of loon productivity and considered its importance as a driver of regional population viability. Our objectives were to (1) compare loon productivity from various study regions across North America; (2) investigate temporal trends in loon productivity across the range; and (3) propose hypotheses to explain range-wide declines in productivity for loons.

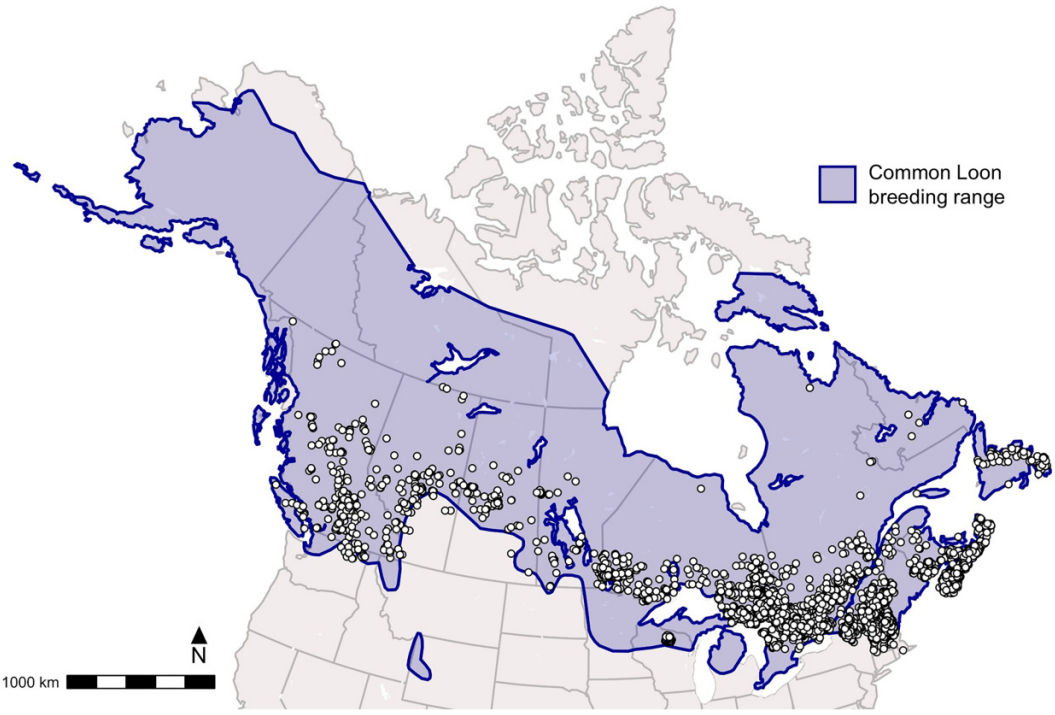
Methods

Study species

The Common Loon is a piscivorous migrant that breeds on freshwater lakes throughout most of Canada and the northern U.S. (Paruk 2021; Paruk et al. 2021). Loons begin to establish breeding territories at 4–6 years of age (Evers et al. 2008; Piper et al. 2015), and some individuals survive beyond 30 years (Piper et al. 2017; Evers pers. comm.) with one continuing female at least 39 years of age (Bird Banding Laboratory 2025). Once established, adults show strong site fidelity to breeding territories (Evers 2001; Paruk et al. 2021). Females usually lay two eggs (Timmermans et al. 2004), which the nesting pair incubates for about 28 days. Hatching is asynchronous (Paruk et al. 2021) and within hours of hatching, chicks can swim and ride on their parents' backs. Parents provision offspring for 11 weeks or more, but reduce feedings from 6 weeks until independence (Barr 1996).

For long-term loon monitoring projects, productivity is often estimated by the number of 6-week-old chicks (Tozer et al. 2013; Piper et al. 2024; hereafter "fledglings") because (1) reliable data are not available beyond this age for most populations; and (2) the number of young that reach this age are considered to be a good representation of the number of chicks that will eventually reach adulthood (survivorship; Evers 2007). However, it is important to note that 6-week-old chicks may still be at risk to higher rates of mortality in regions where there is high intraspecific competition and predation risk. For loon monitoring programs, observers verified if a chick was at least 6 weeks old by comparing the size of the chick relative to an adjacent adult. If the chick is at least 2/3 the length of the adult then it is deemed to be at least 6 weeks old (Tozer et al. 2013), even if it is still in brown downy plumage. Chicks more than 7 weeks old have some juvenile feathering and are completely in juvenile plumage by 9 weeks of age.

Fig. 1. Map of the Common Loon breeding range (blue) and the 3421 surveyed lakes (white dots) throughout the twelve regions that monitored loons for this study. This map was created using R version 4.0 (R Core Team 2020) and assembled from the following data sources: Common Loon breeding range (USGS Relative Abundance Shapefiles for Geographic Analyses; Sauer et al. 2017) and surveyed lake coordinates (data sources listed in Data Collection section). The base map used was from the 2021 Census Boundary Files, courtesy of Statistics Canada (https://open.canada.ca/data/en/dataset/ef70dc3b-1069-4037-9bce-61f47e628a1d). Major lakes included in the map were from Natural Earth 1:50m Physical Vectors (https://www.naturalearthdata.com/downloads/50 m-physical-vectors/).



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Data collection

We obtained data on loon breeding events (n = 45 591) from nine Canadian provinces and seven U.S. states throughout the southern portion of the Common Loon's breeding range (Fig. 1, Table 1). We combined some provinces and states for analysis, resulting in 12 loon regions and 5 loon conservation units as identified by Larison et al. (2021). These data were obtained from nonprofit, government, and academic monitoring projects on loons from across the species' range in North America. Projects or organizations that contributed data to the analysis were the Canadian Lakes Loon Survey delivered by Birds Canada, The Loon Project (Chapman University), Maine Audubon, Maine Department of Inland Fisheries and Wildlife, Massachusetts Division of Fisheries and Wildlife ("MassWildlife"), Massachusetts Department of Conservation and Recreation, Biodiversity Research Institute, Loon Preservation Committee, Vermont Center for Ecostudies, and Adirondack Center for Loon Conservation (Table 1). Data analyzed in this study encompassed 49 years of loon productivity on 3421 lakes from 12 regions: British Columbia (1992–2019), the Prairie provinces (Alberta, Saskatchewan, and Manitoba all with data between 1992 and 2019), Ontario (1981–2019), Quebec (1992–2019), the Atlantic provinces (New Brunswick (1992–2018), Nova Scotia (1992–2019), Newfoundland and Labrador (1992–2019)), Maine (1987–2023), New Hampshire (1975–2023), Massachusetts (1984–2022), Vermont (1988–2023), New York (2004–2023), Wisconsin (1993–2022), and Washington (1995–2023). Owing to limited sample sizes (<500 observations over 20 years), Alberta, Manitoba, and Saskatchewan were combined into one region (Prairie provinces) and Newfoundland and Labrador, Nova Scotia, and New Brunswick were combined as the Atlantic provinces (Table 1). It is important to note that the loon territories monitored and used in this analysis only represent a small portion of the populations in each of the regions (with exception of New Hampshire, Vermont, and Massachusetts) and may not fully reflect population trends across each region. Due to temporal variation in what lakes were accessible across years, some lakes were not visited every year of the study period. However, there were no obvious biases in the unsampled lakes. For example, in any particular year the lakes that were not sampled were not all small lakes or ones in a particular region. The missed lakes were mainly random selections of sampled lakes within given regions. While our analysis examined productivity data from 12 different loon regions (Table 1), we later discuss our results in the context of five conservation units differentiated via geography and genetic relatedness according to Larison et al. (2021).

We only included productivity data from populations where loon pairs were either individually marked for long-term study (i.e., at least 10 years of individual monitoring) or

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Table 1. A summary of the datasets from loon monitoring groups used in this study, including years of study, sample size, the number of lakes monitored, and a description of the scope and affiliation of the contributors of the data.

Loon region	Province or State	Conservation unit	Year range	Number of breeding attempts	Number of monitored lakes	Mean and range of the number of pairs monitored per year	Affiliated organization	Monitoring program description
British Columbia	British Columbia	Pacific Northwest	1992–2023	1714	238	55 (10–87)	Canadian Lakes Loon Survey (Birds Canada)	Long-term program delivered by Birds Canada. Participants survey the lake of their choice, visiting it at least three times during the breeding season.
Prairies	Alberta	Central Canada	1992–2023	986	112	31 (8–49)	Canadian Lakes Loon Survey (Birds Canada)	Long-term program delivered by Birds Canada. Participants survey the lake of their choice, visiting it at least three times during the breeding season.
Prairies	Saskatchewan	Central Canada	1992–2023	1759	65	55 (9–110)	Canadian Lakes Loon Survey (Birds Canada)	Long-term program delivered by Birds Canada. Participants survey the lake of their choice, visiting it at least three times during the breeding season.
Prairies	Manitoba	Central Canada	1992–2023	484	57	15 (3–39)	Canadian Lakes Loon Survey (Birds Canada)	Long-term program delivered by Birds Canada. Participants survey the lake of their choice, visiting it at least three times during the breeding season.
Ontario	Ontario	Eastern Canada	1981–2023	16 682	1408	388 (83–668)	Canadian Lakes Loon Survey (Birds Canada)	Long-term program delivered by Birds Canada. Participants survey the lake of their choice, visiting it at least three times during the breeding season.
Quebec	Quebec	Eastern Canada	1991–2023	2529	348	79 (53–135)	Canadian Lakes Loon Survey (Birds Canada)	Long-term program delivered by Birds Canada. Participants survey the lake of their choice, visiting it at least three times during the breeding season.
Atlantic	New Brunswick	New England	1992–2023	270	58	9 (1–38)	Canadian Lakes Loon Survey (Birds Canada)	Long-term program delivered by Birds Canada. Participants survey the lake of their choice, visiting it at least three times during the breeding season.
Atlantic	Nova Scotia	New England	1992–2023	893	273	28 (6–183)	Canadian Lakes Loon Survey (Birds Canada)	Long-term program delivered by Birds Canada. Participants survey the lake of their choice, visiting it at least three times during the breeding season.
Atlantic	Newfoundland and Labrador	New England	1992–2023	197	67	6 (1–33)	Canadian Lakes Loon Survey (Birds Canada)	Long-term program delivered by Birds Canada. Participants survey the lake of their choice, visiting it at least three times during the breeding season.
Maine	Maine	New England	1987–2023	2085	43	56 (9–94)	Biodiversity Research Institute, Maine Audubon	Long-term research program using ongoing state-run monitoring programs and volunteer efforts to survey Maine lakes

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Table 1. (*concluded*).

Loon region	Province or State	Conservation unit	Year range	Number of breeding attempts	Number of monitored lakes	Mean and range of the number of pairs monitored per year	Affiliated organization	Monitoring program description
Massachusetts	Massachusetts	New England	1984–2023	1058	60	27 (8–53)	Massachusetts Department of Conservation and Recreation, Massachusetts Division of Fisheries and Wildlife, Biodiversity Research Institute	Long-term program through state government to monitor loon populations on a subset of lakes and reservoirs
New Hampshire	New Hampshire	New England	1975–2023	9862	241	201 (62–345)	Loon Preservation Committee	Long-term conservation program to track New Hampshire's statewide loon population and improve loon survival and breeding success.
Vermont	Vermont	New England	1988–2023	2404	285	67 (14–138)	Vermont Center for Ecostudies	Long-term monitoring and management program done through Vermont Center for Ecostudies, which engages and trains volunteers to track loon breeding success.
New York	New York	New England	2004–2023	2208	122	110 (82–140)	Adirondack Center for Loon Conservation	Long-term reproductive success, survival, and population monitoring study, conservation, and education initiative in New York's Adirondack Park.
Wisconsin	Wisconsin	Midwest	1993–2022	2177	157	73 (9–109)	Chapman University	University-led long-term monitoring across Wisconsin lakes to monitoring loon breeding success and population dynamics
Washington	Washington	Pacific Northwest	1995–2023	283	21	10 (4–17)	Biodiversity Research Institute	Long-term research program using comprehensive field scientist surveys in northeastern Washington

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where lakes occupied by loons were consistently monitored for at least 10 years. We defined pairs as territorial adults with a mate, a nest, and/or young, and only included pairs that were monitored at least once after territory settlement, once during incubation, and once to verify fledging success. In addition, each of the studies from which we accepted data included measures of the number of territorial loon pairs present on a given lake and the productivity of a given pair (i.e., the number of fledglings).

Only lakes where loon pairs were present were included in our calculation of the number of fledglings. We assumed that all fledglings present on the survey lakes were detected. Due to their large size, the aggressive and conspicuous territorial behaviours of adults, and their constant presence on lakes throughout an entire summer when breeding, adult loons have high detection probabilities (reviewed in Kuhn et al. 2011). For example, the Wisconsin data in this study is collected on a weekly basis where every territorial pair is checked, thus chick detectability is placed at 100%. Furthermore, the number of loon chicks hatched in Washington is known with detectability of greater than 95% (D. Poleschook personal communication, 2025). As a result of the high detection rates in loon regions, monitoring data for breeding 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 populations considered in our analysis (e.g., detectability of loons is unlikely to be different on a lake in New Hampshire versus Ontario). It is therefore unlikely that any possible differences in detectability substantially influenced our results. Even though loon monitoring programs may have high detection rates, it is important to highlight that imperfect detections can inevitably lead to some underestimates of productivity.

Statistical analysis

We compared annual indices (i.e., annual estimates of mean productivity) and trends generated from all 12 loon regions following the approach of Walker and Taylor (2017, 2020) and Bianchini and Tozer (2023). For each loon region, we fit generalized linear mixed models (GLMMs) relating year (categorical predictor variable) to productivity (i.e., the number of fledglings; response variable) for a total of 12 models, one for each region. We included productivity as a count of either 0, 1, 2, or 3 fledglings. We gave productivity a value of zero for any year where a loon pair was observed at least once on a given lake and where eggs and/or chicks were recorded, but no 6-week-old chicks were observed. Due to slight variations in loon monitoring protocols and the temporal and spatial resolution of the data, we were unable to incorporate all data into a single model to assess an overall trend across the range. Furthermore, for the New York dataset, if pairs had surviving chicks as of the last check and the chicks were not at least 6 weeks old, they were still included in the analysis as having a productivity value of zero (347 of 2208 breeding attempts in NY (15.7%) or 0.74% of all 46 401 breeding attempts in this study). We recognize that this may bias the results towards nesting pairs that hatched earlier in the season and underestimate productivity given that some younger chicks (<6 weeks old) would survive to fledging age.

For most loon regions, GLMMs were fit using a Poisson distribution since our response variable was count data, but as data from New York and Massachusetts were overdispersed, models for these regions were fit using negative binomial GLMMs (Zuur et al. 2009). All models included a fixed effect for year to produce annual indices of productivity for each year, which could then be used to compare annual indices across the loon populations when nonlinear temporal trends occurred (Walker and Taylor 2017). All models also included a random intercept for lake identity to account for repeated visits to a single lake over the course of multiple decades and the spatial groupings of loon surveys.

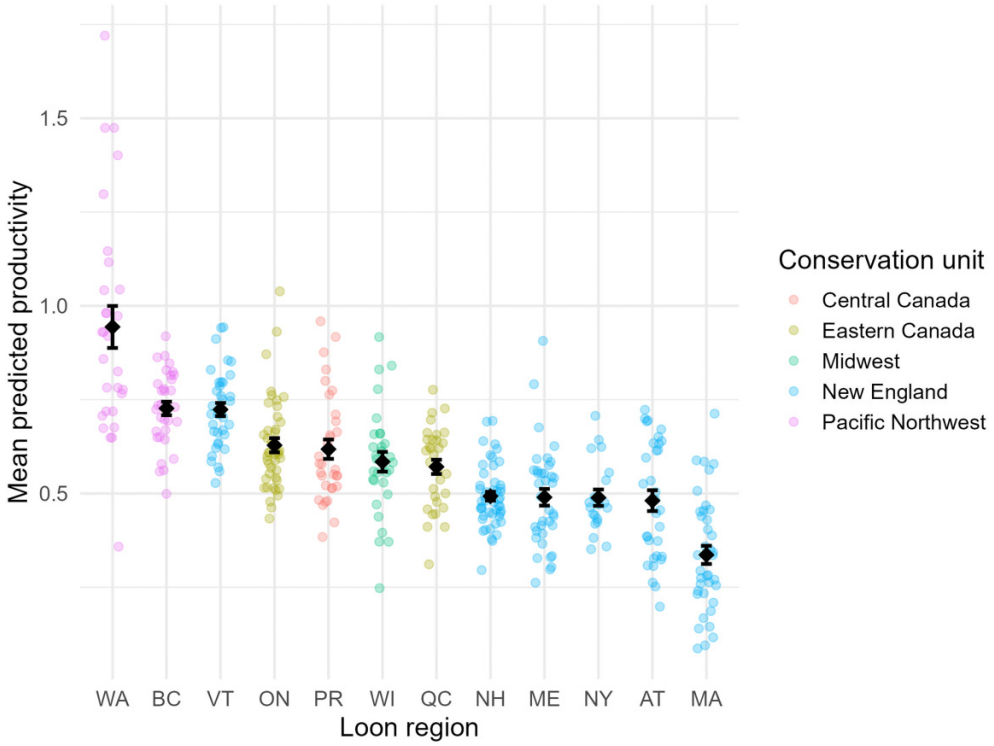
To determine variation in productivity across years for loons, we calculated annual indices of productivity (i.e., the number of fledglings) by calculating predicted values for each year. We computed predicted values from the above GLMMs using the *ggeffects* package (Lüdecke 2018; R Core Team 2020). Annual indices for each region were only calculated for years with productivity data from at least four or more lakes or pairs.

For each loon region, we calculated temporal trends in productivity by fitting linear models (LMs) relating annual productivity indices to year. These LMs included annual indices generated from the above GLMMs as the response variable and year as a fixed effect, with annual sample sizes as weights (Pasek et al. 2020). Year was included as a continuous variable to assess temporal trends, and was weighted by sample size to reflect greater uncertainty in years with fewer observations. We used a Shapiro–Wilk normality test to confirm that the predicted annual indices of productivity met the linear model's assumption of normality. We used annual indices to calculate temporal trends rather than raw data because changes in monitoring effort over time, particularly an increase in survey coverage (i.e., the number of lakes monitored each year) over time, could produce trends that were disproportionately influenced by more recent years (Walker and Taylor 2020; Bianchini and Tozer 2023). We generated lines of best fit through annual indices using the *predict* function in the *stats* package (R Core Team 2020). Finally, trends in productivity were calculated as the geometric mean rate of change between predicted values from the line of best fit for the first and last year (these years varied for each loon region). This value was expressed as an annual percent change as described in eq. 4 of Smith et al. (2014) :

$$\%\,\text{change per year} = 100 * \left[\left(\frac{\text{Line of best fit prediction}_{\text{endYear}}}{\text{Line of best fit prediction}_{\text{startYear}}} \right)^{\frac{1}{\text{endYear}-\text{startYear}}} - 1 \right]$$

For each dataset, we calculated confidence intervals (CI) for trends in productivity with bootstrapped models using the *boot* package (Davison and Hinkley 1997; Canty and Ripley 2021). To classify the strength of the trends, we separated patterns based on the productivity (%) gained or lost per year. We classified trends as steep decline (−2.5% to −1.5% per year), medium decline (−1.5% to −1.0% per year), weak de-

Fig. 2. Mean model-predicted values of Common Loon productivity (i.e., number of 6-week-old fledglings) of each year (dots) for Prairie (PR) provinces (Alberta, Manitoba, and Saskatchewan combined), Atlantic (AT) provinces (New Brunswick, Newfoundland and Labrador, and Nova Scotia combined), British Columbia (BC), Ontario (ON), Quebec (QC), Maine (ME), New York (NY), New Hampshire (NH), Vermont (VT), Massachusetts (MA), Wisconsin (WI), and Washington (WA). Diamonds and error bars indicate mean and standard error of the model-predicted annual values in productivity. All data are color-coded according to the Common Loon conservation units defined by Larison et al. (2021).



cline (−1.0% to −0.5% per year), weak decline or near stable (−0.5% to 0.0%), and stable or weak increase (0.0% to 0.5%).

We carried out all statistical analyses using R version 4.0 (R Core Team 2020). GLMMs were run using the *glmmTMB* package (Brooks et al. 2017). LMs were run using the *lm* function in the *stats* package. Plots of annual indices were generated using the packages *ggplot2* (Wickham 2016) and *cowplot* (Wilke 2020). We processed spatial data and prepared maps using the sf (Pebesma 2018; Pebesma and Bivand 2023), rmapshaper (Teucher and Russel 2023), ggspatial (Dunnington 2023), and ggplot2 (Wickham 2016) packages in R.

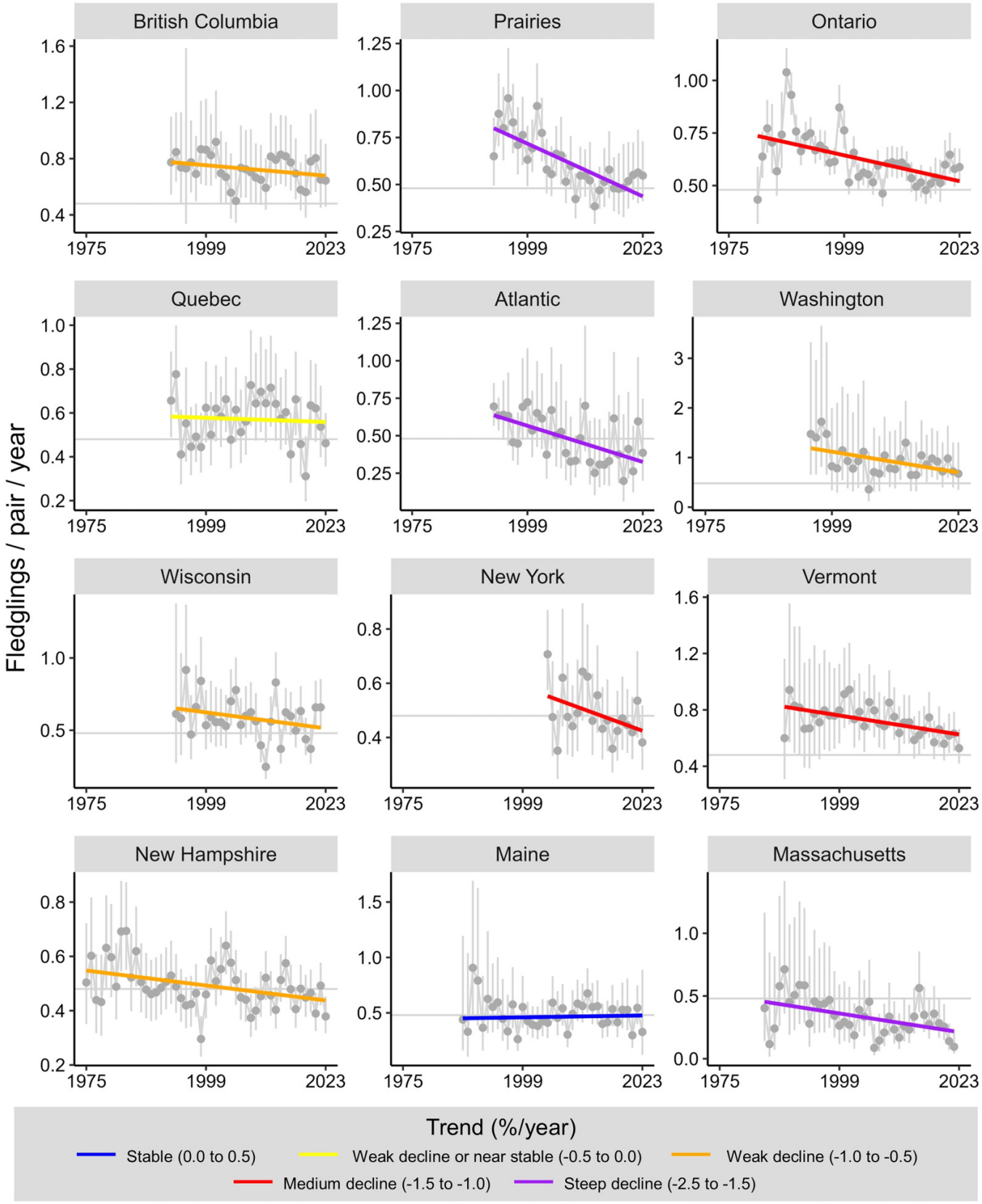
Results

We found substantial regional variation in loon productivity across the conservation units as described by Larison et al. (2021). Our results indicate that trends in annual indices of loon productivity varied substantially among loon regions. Overall mean model-predicted number of fledglings per territorial pair per year in all regions ranged from 0.16 to 0.94 (Fig. 2). All regions exhibited substantial temporal variation in productivity throughout the study duration with the overarching pattern that loon productivity has experienced long-term declines in nearly all regions except Maine (Figs. 3 and 4).

Trend estimates across all loon regions in the New England conservation unit (including the U.S. and Canada according to Larison et al. 2021), though variable, showed a consistent long-term decline in productivity, except for Maine, which appeared stable (Fig. 3), and several other states where the range in productivity trends or the CI bounded zero. For the Atlantic provinces of Canada, we found significant evidence for a steep declining productivity trend of −2.39% per year (−3.45, −1.33; lower CI, upper CI), which amounted to an estimated total productivity loss of 74% between 1992 and 2023 (Table 2; Fig. 3). In New York, we found weak evidence to suggest a moderate, long-term declining trend in productivity of −1.35% per year (−2.83, 0.11; Table 2; Fig. 3) that occurred between 2004 and 2023, resulting in about a 25% decline in the last two decades. In New Hampshire, we found significant evidence for a declining productivity trend of −0.43% per year (−0.70, −0.16; Table 2; Fig. 3), which amounted to an estimated total productivity loss of about 21% between 1975 and 2023. We found significant evidence for a steep decline in productivity in Massachusetts, which lost −1.66% per year (−2.56, 0.76; Table 2; Fig. 3), leading to a loss in productivity of about 64% between 1984 and 2023 (although the breeding population has increased in the past 2-3 decades). In Vermont, we found significant evidence for a moderate decline in productivity of −1.07% per year (−1.44, −0.70; Table 2; Fig. 3), resulting in a decline of about

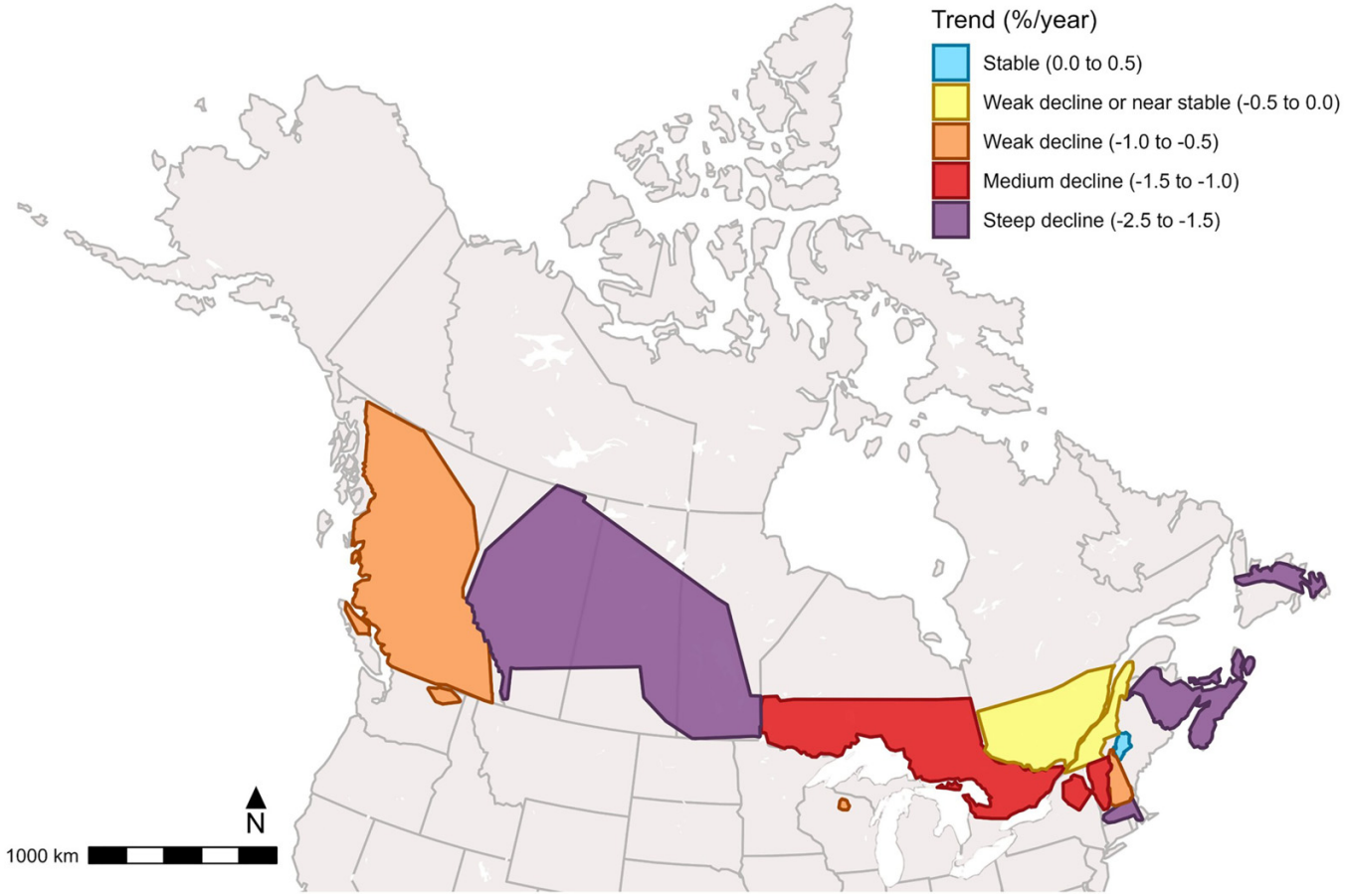
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Fig. 3. Plots of the predicted annual indices of loon productivity for Prairie provinces (Alberta, Manitoba, and Saskatchewan combined), Atlantic provinces (New Brunswick, Newfoundland and Labrador, and Nova Scotia combined), British Columbia, Ontario, Quebec, Maine, New York, New Hampshire, Vermont, Massachusetts, Wisconsin, and Washington. The points represent model-predicted means and the bars represent 95% confidence intervals. The colored line represents the predicted linear fit as predicted by models using data from various loon monitoring programs. The horizontal gray line on each panel indicates 0.48 fledglings per territorial pair per year, which is the predicted productivity rate required to maintain a stable loon population (Evers et al. 2008).



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Fig. 4. Map of trends in annual indices of Common Loon productivity generated from boot-strapped predicted values of linear models for Prairie provinces (Alberta, Manitoba, and Saskatchewan combined), Atlantic provinces (New Brunswick, Newfoundland and Labrador, and Nova Scotia combined), British Columbia, Ontario, Quebec, Maine, New York, New Hampshire, Vermont, Massachusetts, Wisconsin, and Washington. Trend values are categorized as steep declines (−2.5% to −1.5% per year), medium decline (−1.5% to −1.0% per year), weak decline (−1.0% to −0.5% per year), weak decline or near stable (−0.5% to 0.0% per year), and stable or increasing (0.0% to 0.5% per year). This map was created using R version 4.0 (R Core Team 2020) and assembled using surveyed lake coordinates (data sources listed in the Data Collection section) and analytical trend results. The base map used for this figure is from the 2021 Census Boundary files, courtesy of Statistics Canada (https://open.canada.ca/data/en/dataset/ef70dc3b-1069-4037-9bce-61f47e628a1d). Major lakes included in the map were from Natural Earth 1:50m Physical Vectors (https://www.naturalearthdata.com/downloads/50 m-physical-vectors/).



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37% over the past 35 years. There was little evidence to suggest a decline in productivity in Maine, but trends suggested that productivity in Maine had remained stable over the past 35 years (increase of 0.17% per year; −0.76, 1.12; Table 2; Fig. 3).

In the Eastern Canada conservation unit, moderate declines occurred in Ontario, while loon productivity in Quebec appeared near stable. In Ontario, significant evidence indicated that productivity had moderately declined by approximately −1.08% (−1.54, −0.63; Table 2) per year between 1981 and 2023. This would result in an estimated 45% decline in productivity over this time period. Trends in productivity for loons in Quebec indicated weak evidence for an apparent decline of −0.14% per year (−0.88, 0.56; Table 2; Fig. 3), which was almost stable.

Despite rates of decline, regions in the Pacific Northwest demonstrated the highest productivity indices across the study period (Fig. 2). In British Columbia, weak evidence suggested an apparent decline in productivity of −0.46% per year (−0.95, 0.02; Table 1; Fig. 3), which amounted to an estimated total productivity loss of 14% between 1992 and 2023. In the west, weak evidence also indicated that Washington has experienced a declining productivity trend of −0.94% per year (−1.60, −0.27; Table 2; Fig. 3) resulting in a loss of productivity of about 26% between 1995 and 2023.

Some of the steepest declines in loon productivity in North America occurred in Central Canada within the Prairie provinces. In the Prairies, we found significant evidence for a steep decline in productivity of −2.09% per year (−2.87, −1.38; Table 2; Fig. 3), resulting in a decline in productivity of approximately 65% between 1992 and 2023.

In the Midwest conservation unit (Larison et al. 2021), rates of productivity bounded zero as well, indicating that despite a weak decline, productivity of these populations appeared

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Table 2. Model results from linear models that fitted annual indices of loon productivity over time.

Region of loon breeding range	Estimate and standard error (lower 95% confidence interval, upper 95% confidence interval)	*F* value	*p* value
British Columbia	−0.003 ± 0.002 (−0.007, 0.0007)	2.84	0.10
Prairie provinces	−0.01 ± 0.001 (−0.01, −0.008)	38.85	<0.007
Atlantic provinces	−0.01 ± 0.002 (−0.01, −0.006)	29.43	<0.007
Quebec	−0.0009 ± 0.001 (−0.004, 0.003)	0.20	0.65
Ontario	−0.006 ± 0.001 (−0.009, −0.004)	24.86	<0.001
New York	−0.006 ± 0.003 (−0.01, 0.0003)	3.99	0.06
Vermont	−0.008 ± 0.001 (−0.01, −0.005)	31.86	<0.002
Maine	0.0007 ± 0.02 (−0.003, 0.005)	0.13	0.71
New Hampshire	−0.002 ± 0.0007 (−0.003, −0.0005)	7.29	0.009
Washington	−0.01 ± 0.005 (−0.02, 0.00)	4.13	0.05
Wisconsin	−0.004 ± 0.03 (−0.01, 0.002)	1.80	0.19
Massachusetts	−0.006 ± 0.01 (−0.01, −0.002)	10.82	0.002

Note: Results include beta estimates ± standard error (SE), *f* statistics (*F* value), and the *p* value to determine significance of the line of best fit. Note that the percentage change per year reported in the text are bootstrapped estimates based on these models using eq. 4 in Smith et al. (2014).

generally stable. In Wisconsin, we estimated a declining productivity trend of −0.65% per year (0.13, −1.44; Table 2; Fig. 3), but there was weak evidence to support that this decline was significant between 1993 and 2022 (~18% decline over 30 years).

Discussion

Evers et al. (2008) calculated 0.48 chicks fledged per territorial pair (CF/TP) as an estimate of productivity that would lead to a stable adult population, presuming an adult annual survival rate of 92%, a juvenile survival rate (i.e., survival to approximately 6 weeks old) of 41%, and a mean age at first breeding of 6 years. These demographic values were reasonable based on data collected in the early 2000s in New England and Wisconsin (Mitro et al. 2008; Piper et al. 2012). If we presume that these values still hold for loon populations across the range, while accounting for regional changes in chick survival rates due to predation and other factors, then most have equaled or exceeded the 0.48 CF/TP threshold for stability during the past few decades (Fig. 2). Thus, a cursory view might lead one to conclude that loon populations are generally either stable or likely to increase in the future.

There are three potential factors that temper this conclusion and warrant further discussion. First, we report here that productivity is declining across the monitored portions of the loon breeding range. For many of the regions, up until the early 2000s, productivity of loons was stable or increasing, potentially, in part, due to recovery from overhunting and indirect effects of air pollution on lake health. However, large variations in productivity declines have continued since the 2000s, likely due to various regional threats. Continued declines in chick production will soon push several populations below the 0.48 CF/TP threshold (Fig. 3). Those regions most clearly at risk appear to be New York, New Hampshire, the Atlantic provinces, Massachusetts, Ontario, and the Prairie provinces (Fig. 3). Second, a recent finding indicates that juvenile survival has abruptly plunged in one closely–watched population. In Wisconsin, systematic reobservation of loons marked as chicks indicates that the juvenile survival rate has fallen there from 41% in 2000 to an estimated 12.7% by 2019, which is a likely cause of the recent decrease in the adult population there (Piper et al. 2020). If similar sharp declines in juvenile survival occurred elsewhere, then 0.48 CF/TP is too low a rate of productivity to maintain a stable population. Third, a decline in productivity also may indicate a loss of phenotypic quality in the adult loon population. In Wisconsin, deterioration of breeding conditions has resulted not only in a lower rate of chick production but in a decline in body condition among chicks that fledge. Lower body condition among fledged chicks, in turn, has resulted in lower survival and chick production by those individuals once they reach adulthood (a "silver spoon effect"; see Piper et al. 2025). Thus, lower productivity is likely to have other ramifications, causing a decline in additional demographic parameters.

While the widespread drop in productivity is clearly a worrisome sign for loons, the case in New England illustrates that we must not equate a mere decline in productivity with a fall in the adult loon population. Vermont productivity is in decline at present, but chick production (together with juvenile and adult survival) there remains sufficiently high (roughly 0.6 CF/TP, E.W. Hanson, C.C. Rimmer, and J. Gobeille (unpublished report, 2000); Fig. 2)) so that Vermont's loon population has increased sharply in recent decades. Similar comparisons can be made for populations of adult loons in Massachusetts (40% increase in pairs from 2014 to 2024) and New Hampshire (19% increase in pairs from 2014 to 2024) where despite declines in productivity, there have been increases in the number of adult pairs. Increasing loon populations despite productivity declines could be due to various regional factors. In New Hampshire, for example, the growth in the loon population may be linked to increased adult survival due

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to legislation restricting the sale and use of lead fishing tackle (Grade et al. 2018), outreach to educate the public about lead tackle and other sources of anthropogenic mortality (Toomey and Domroese 2013), and increased rescues of sick or injured loons (Buxton et al. 2020). Even though there is no direct evidence to support that the growth of the adult loon population in New Hampshire is due to fishing tackle regulations, population models developed by Grade et al. (2018) demonstrated that lead tackle-related mortality reduced the population growth rate by 1.4%, thus inferring there would be an increase in the adult population if lead tackle was not used. The differences seen in rates of productivity and adult loon densities could also be an artifact of regional intraspecific competition due to decreased available breeding habitat or other resources (Piironen et al. 2025).

Understanding possible mechanisms driving the broad decline in productivity is challenging, given geographic variation in climate, habitat, and extent and nature of anthropogenic threats. Various factors have been proposed to explain declines in loon productivity within regions. These include loss of nesting habitat due to increased shoreline development (Hammond et al. 2012; Spilman et al. 2014), disturbance during nesting (McCarthy and Destefano 2011), increased egg and chick predation by raccoons (*Procyon lotor*), Bald Eagles (McCarthy et al. 2010; Cooley et al. 2019), and other predators, anthropogenic, and climate change-related water level fluctuations that flood nests or make them inaccessible (DeSorbo et al. 2007; Windels et al. 2013; Schoch et al. 2024), nest abandonment due to black flies (*Simulium annulus*; Piper et al. 2018), changes in water clarity (Piper et al. 2024), lead poisoning (Grade et al. 2018), methylmercury contamination (Schoch et al. 2014; Bianchini et al. 2021*a*), and increased lake acidity (Bianchini et al. 2020). While these mechanisms might explain declines in loon productivity on a local scale, no single threat would appear to explain the broad-scale declines in productivity across the loon breeding range that we report here.

The multitude of threats to breeding success throughout the range suggests a first hypothesis for the widespread productivity decline. In addition to predation, perhaps multiple anthropogenic factors related to increased human development, activity, impacts on habitat, or chemical contaminants, acting cumulatively or synergistically, have resulted in the overall decline in productivity in loons across their breeding range. These impacts, which may overlap in some cases, but differ in other cases from one region to another, are linked only by being caused by humans. Density dependent compensatory declines in productivity might be expected in some recovering loon populations (e.g., Piironen et al. 2025) and could be an additional, natural, confounding factor.

Our second hypothesis is more narrowly focused. It presumes that increased rainfall owing to climate change is responsible for the decline in productivity. Precipitation could decrease loon breeding success in three ways. First, increased frequency and severity of storm events, predicted by climate models (Hettiarachchi et al. 2018; Martel et al. 2021) might reduce productivity through increases in nest flooding, nest abandonment (DeSorbo et al. 2007; Windels et al. 2013; Buxton et al. 2020; Schoch et al. 2024), or mortality of newly-hatched chicks (George pers. comm.). Second, increased precipitation has two longer-term negative ecological impacts on loon reproduction. Populations of black flies, which attack incubating adult loons and can cause widespread nest abandonment (Piper et al. 2018), are known to surge following years of high precipitation (Franke et al. 2016; Lamarre et al. 2018). Third, increased precipitation washes organic material (e.g., dissolved organic matter) and anthropogenic sources of phosphates and nitrates into lakes, reducing water clarity directly or by supporting phytoplankton growth (Lisi and Hein 2019). A decline in water clarity has been shown to reduce loon chick mass, presumably through reduced foraging efficiency by adults and causing a reduction in chick provisioning (Piper et al. 2024).

In this study, we demonstrate that productivity is decreasing across most of the monitored portions of the Common Loon's breeding range. Despite the ubiquitous nature of loons, a range-wide study such as this one would not be possible without volunteer science programs designed to collect data related to loon productivity and engage the public with real world conservation issues (Toomey and Domroese 2013; De Sherbinin et al. 2021). While we demonstrated that historical productivity levels were sufficient to maintain stable adult populations, we concluded that the ongoing decline in productivity observed in this study suggests that current levels of productivity may no longer be sufficient to sustain population stability or prevent further steep declines (Piper et al. 2020). We recommend that future research prioritizes identifying the effects of likely environmental threats to productivity that may occur on broad scales. Using a similar approach to Piper et al. (2024), we first recommend that future studies examine the effects of water clarity on loon productivity across the entire breeding range, which is possible given that it is one of few environmental covariates that could be collected and standardized across North America. Secondly, low productivity might signal a drop in habitat quality that reduces the ability of chicks to survive and breed as adults (a negative "silver spoon effect") and lead to population decline. Thus, we also recommend further studies prioritize examining individual-level effects of environmental threats such as rainfall, lake acidity, shoreline development, or pollutants on individual chick and adult condition across the breeding range to better understand the effects of habitat quality on breeding performance and long-term fitness. Lastly, given that lead poisoning appears to be a major cause of mortality in parts of the loon's breeding range, we recommend that future research questions focus on improving the understanding of the effects of toxic lead fishing tackle on loons and the subsequent impacts on population growth rates. Such studies could focus on determining intraspecific variation in lead poisoning across loon conservation units and the spatial extent of lead contamination on loon territories. By identifying the mechanisms explaining broad declines in loon productivity, efforts can be made to mitigate them, thus stabilizing or increasing loon populations.

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Data availability
Data for this study can be found on FigShare at the following http://doi.org/:10.6084/m9.figshare.30375541.

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The authors declare there are no competing interests.

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