Many animal populations are under stress and declining. For numerous marine bird species, only recent or sparse monitoring data are available, lacking the appropriate temporal perspective needed to consider natural, long-term population dynamics when developing conservation strategies. Here, we use a combination of established palaeoenvironmental approaches to examine the centennial-scale dynamics of the world’s largest colony (representing approx. 50% of the global population) of the declining and vulnerable Leach’s Storm-petrel (*Hydrobates leucorhous*). By reconstructing the last approximately 1700 years of the colony’s population trends, we corroborate recent surveys indicating rapid declines since the 1980s. More surprisingly, however, was that the colony size was smaller and has changed strikingly in the past, even prior to the introduction of human stressors. Our results challenge notions that very large colonies are generally stable in the absence of anthropogenic pressures and speak to an increasingly pressing need to better understand inter-colony movement and recruitment when inferring range- and species-wide trends. While the recently documented decline in storm-petrels clearly warrants conservation concern, we show that colony size was consistently much lower in the past and changed markedly in the absence of major anthropogenic activity. In response, we emphasize the need for enlarged protected area networks to maintain natural population cycles, coupled with continued research to identify the driver(s) of the current global seabird decline.

1. Introduction

Human activities have been linked to dramatic declines in animal populations due, in part, to habitat degradation, overexploitation, pollution, climate change, and facilitating the spread of invasive species [1]. To disentangle the natural range of population variability from relatively recent anthropogenically driven declines, long-term ecological and environmental studies are required. For example, long-term studies have been successfully applied in the restoration of natural wolf and moose populations on Isle Royale [2], understanding fish stock abundance in the face of changing climate [3], and declining Common Eider populations due to the growing availability of firearms and outboard motors in Greenland [4]. Unfortunately, despite general acceptance of the importance of long-term monitoring for conservation in the face of human influences, their presence in the research literature is declining [5].
Of the numerous declining animal populations, seabirds are particularly threatened and require long-term monitoring because of their ability to travel long distances across geographical and political boundaries, and thus experience varyingly effective and inconsistent management strategies. As a result, nearly half of seabird species are experiencing population declines [1,6]. This rate of loss threatens ecosystem structure and function as seabirds provide a variety of critical ecological services, including nutrient cycling, pest control, seed dispersal and pollination, among others [7]. Unfortunately, developing effective conservation strategies is often difficult without long-term data on population dynamics. To address emerging conservation issues due to recent declines, we examined the long-term population dynamics of the under-censused Leach’s Storm-petrel (Hydrobates leucorhous; Vieillot 1818; hereafter storm-petrel) using a landscape-scale palaeoenvironmental approach. The world’s largest colony (supporting 48–59% of the global population [8]) breeds on Baccalieu Island (48°08’ N, 52°48’ W), Newfoundland, a provincial ecological reserve established in 1995 to ‘preserve an internationally important seabird colony’ and ‘ensure viable, long-term populations’ [9].

The first population survey on Baccalieu, in 1984, estimated 3.36 million breeding storm-petrel pairs [10] but, alarmingly, when resurveyed in 2013, the colony had declined by approximately 40% to only 1.95 million pairs [11]. In response, and coupled with declines observed at several other colonies worldwide, the Leach’s Storm-petrel was uplisted to ‘Vulnerable’ [8], indicating the species is threatened with extinction. Suspected contributing causes of the decline are predominantly recent and anthropogenic, including contaminants [12,13], light pollution [14,15], and interactions with offshore infrastructure [16–18]. However, longer scale prey-based [19], predator-based [20], and marine ecosystem changes linked to climate perturbation in the North Atlantic [21] may also contribute.

Storm-petrels are upper trophic level predators [22] that deposit acidic (pH = 5.86 ± 0.66 s.d.), nutrient-rich guano, and the only seabird that nests in high density in the catchments of ponds on Baccalieu Island (figure 1). Given this, we reasoned that high-resolution, dated sediment cores from a strategic selection of ponds draining the colony would record the long-term history of storm-petrel population change. The validity of the palaeolimnological methodology has been confirmed by numerous palaeo-reconstructions of seabird population dynamics (e.g. [4,23,24]). In our study, we build on previous palaeolimnological work by providing six independent proxies of the Leach’s Storm-petrel colony’s dynamics to help place recent declines in the context of potential long-term population drivers. We used a comparative palaeolimnological approach of four ponds on Baccalieu Island with varying degrees of current nesting storm-petrel influence, and a mainland reference pond where no storm-petrels or other seabirds nest. Mapping the most recent survey of nesting density onto the island’s watersheds (figure 1), we a priori classified Lumin, Brister, and Southern End ponds as high influence, and Gull Pond as moderate influence. This categorization is supported by a limnological gradient that indicates higher concentrations of nutrients (e.g. nitrogen, phosphorus) and storm-petrel-associated trace metals (e.g. cadmium, zinc) corresponding with higher nesting concentrations (electronic supplementary material, table S1). To measure temporal changes in storm-petrel influence, we employed a broad spectrum of proxy data, including: sedimentary δ13N:15N (expressed as δ15N), which has been used to reliably and quantifiably track past seabird inputs in a variety of palaeolimnological studies [4,25,26]; sub-fossil diatom (Class: Bacillariophyceae) assemblages, which are sensitive biocoindicators of water chemistry including pH and nutrients [27] linked to guano inputs; sub-fossil chironomid assemblages to assess past changes in deep-water oxygen concentrations linked to eutrophication [28]; geochemical data to identify which elements are introduced by storm-petrels using biogenic enrichment factors [23]; trends in sedimentary chlorophyll-a concentrations (including its main diagenetic products and isomers [29]) to track past shifts in overall pond primary production linked to storm-petrel guano fertilization; and fossil cholesterol to directly track the inputs of storm-petrels [4].

2. Material and methods

(a) Site description

Baccalieu Island, located 64 km north of St John’s, Newfoundland, Canada, currently supports the world’s largest known colony of Leach’s Storm-petrel, as well as smaller populations of seabirds nesting on the island’s peripheries, including Atlantic Puffin (Fratercula arctica), Common Murre (Uria aalge), Northern Gannet (Morus bassanus), Black-legged Kittiwake (Rissa tridactyla), and others [30]. Baccalieu Island and the surrounding area are classified as part of the Eastern Hyper-oceanic Barrens ecoregion, characterized by dwarfed krummholz balsam fir and spruce, grassy-hummocks, and fern habitats [10]. The underlying geology comprises red conglomerate, sandstone, and minor mudstone [31]. Notable history of Baccalieu Island is provided in electronic supplementary material, Methods S1.

Baccalieu Island has several small ponds (note that the term ‘pond’ in Newfoundland typically refers indiscriminately to all bodies of freshwater and does not refer to the absence of an aphotic zone). The four sampled ponds on Baccalieu were selected based on: (i) uniformity of size in order to minimize variation due to physical features and (ii) varying densities of nesting storm-petrels within the pond’s watershed.

The mainland reference pond was selected because it is the nearest pond to Baccalieu Island (approx. 4 km) with similar physical features (electronic supplementary material, table S2) to the studied storm-petrel-influenced ponds. As storm-petrels only nest on remote islands in order to avoid mammalian predation [32], it is highly unlikely that storm-petrels ever nested near this reference pond. Locally, this pond is named Gull Pond owing to the occasional presence of kittiwake and other gulls; however, for the purposes of this study, it is referred to as ‘Mainland Reference’.

(b) Relative storm-petrel inputs

To quantify the relative storm-petrel inputs into each pond, we measured the area of each watershed occupied by the current storm-petrel nesting grounds. Watersheds were delineated by contouring the island’s highest points (i.e. ridges and hills). The highly influenced ponds had the greatest number of nests within the watershed directly draining into the ponds (Lumin: 72% of the watershed inhabited with storm-petrel nests; Brister: 53%; Southern End: 24%). On Baccalieu Island, Gull Pond is in the same watershed near Southern End Pond, but does not have a significant nesting area draining directly into the pond, and therefore receives only moderate inputs (figure 1). The mainland reference pond is not known to have any nesting seabirds...
nearby and would therefore only be influenced by migratory aquatic bird stopovers, local kittiwake, and other gulls.

(c) Seabird density map

A map of seabird densities on Baccalieu Island was developed prior to our palaeolimnological study using nest occupancy of the varying habitat types on the island. During May, June, and July 1984, storm-petrel and puffin habitats were described on Baccalieu Island as either grassy hummock, forest, or heath [10]. Each region of storm-petrel presence are derived using diatom-inferred constrained incremental sum of squares (CONISS). On the island map, the density of nesting storm-petrels is shown in varying shades of green, and the nesting locations of the next most abundant species, Atlantic Puffin, are shown in red. The density map is based on AMS radiocarbon dating. Here, dark green shading represents the larger, modern storm-petrel colony and lighter green represents the smaller, earlier colony. Regions of storm-petrel presence are derived using diatom-inferred constrained incremental sum of squares (CONISS). (Online version in colour.) CE: Common Era.

(d) Sediment coring and dating

Sediment cores were collected between 13 and 17 September 2017 from the deepest point of each pond (determined using a handheld depth sounder) using a high-resolution push corer [34] and

Figure 1. Representative diatom, δ¹⁵N, and ornithogenic metal profiles of the sediment cores from the four storm-petrel impacted ponds from Baccalieu Island, Newfoundland, Canada (red star on inset map) (a–d) and the mainland reference pond (e). On the island map, the density of nesting storm-petrels is shown in varying shades of green, and the nesting locations of the next most abundant species, Atlantic Puffin, are shown in red. The density map is based on a 1997 nesting concentration map by W.A. Montevecchi. Watersheds are delineated with a dashed line. In the sedimentary profiles, scale is shown in sediment depth, and chronologies are based on ²¹⁰Pb dates, highlighting the two surveying years, 1984 (3.36 million pairs) and 2013 (1.95 million pairs), and the last supported ²¹⁰Pb date. Italicized are extrapolated dates beyond supported ²¹⁰Pb and are therefore estimations that must be interpreted with caution. In Lunin Pond, our longest core, we include the calibrated dates of a smaller colony W.A. Montevecchi. Watersheds are delineated with a dashed line. In the sedimentary profiles, scale is shown in sediment depth, and chronologies are based on ²¹⁰Pb dates, of green, and the nesting locations of the next most abundant species, Atlantic Puffin, are shown in red. The density map is based on AMS radiocarbon dating. Here, dark green shading represents the larger, modern storm-petrel colony and lighter green represents the smaller, earlier colony. Regions of storm-petrel presence are derived using diatom-inferred constrained incremental sum of squares (CONISS). (Online version in colour.) CE: Common Era.
sectioned onsite at 0.5 cm intervals using a Glew extruder [35]. The age of the sediment cores was determined using 210Pb gamma spectrometry at the Paleontological Environmental Assessment and Research Laboratory (PEARL) at Queen’s University, Kingston, Ontario. Age models were generated with the constant rate of supply model [36], using the program ScienTissiME (Barry’s Bay, Ontario, Canada; see electronic supplementary material, figure S1). Accelerator mass spectrometry (AMS) radiocarbon dating of Lunin Pond was completed on small woody herbaceous stem fragments (no bark attached) from the 38–38.5 interval isolated by Paleotece Services in Ottawa, Canada. AMS dating was performed at the Keck Carbon Cycle AMS Laboratory at the University of California Irvine. The conventional 14C age of the sample was 1715 before present (BP) ± 20. Using the IntCal13 calibration curve [37], the calibrated age BP (95% confidence) of the sample was 1561–1634 (62.5%), 1649–1695 (32.4%). We extrapolated remaining dates using a smooth spline in the package CLAM v.2.3.2 [38] in R v.3.6.0 (electronic supplementary material, figure S2). For the shorter sediment records from Gull Pond, Brister Pond, Southern End Pond, and mainland reference, dates past the 210Pb profile were extrapolated using a second-order polynomial regression beyond the available 210Pb dates. This method provides a coarse date to estimate the age of the bottom of each sediment record and must be interpreted with caution.

(e) Ornithogenic proxies

All δ15N analyses were performed at the Jan Veizer Stable Isotope Lab at the University of Ottawa (Ottawa, Ontario, Canada), using standard techniques. Diatom preparation followed the methodology described in Battarbee et al. [39]. A minimum of 400 valves per sample were identified using Krammer & Lange-Bertalot [40] and Camburn & Charles [41].

Sedimentary chlorophyll-a (which includes its isomers and its main diagenetic products, thus accounting for most diagenetic effects [29]) was measured every 0.5 cm using visible reflectance spectroscopy with a Model 6500 series Rapid Content Analyzer (FOSS NIRSystems Inc.). Results are provided in figure 2 and electronic supplementary material, figures S5–S9.

Elemental sediment and guano concentrations were measured by S.G.S. Canada Inc., Lakefield Ontario (certified by the Canadian Association for Laboratory Accreditation) using standard methodologies [42]. Biogenic enrichment factors (B) were used to determine which elements are enriched by storm-petrels as described in Brimble et al. [23]. This metric simply divides the concentration of an element in guano by the concentration of an element in the sediment of a reference pond. A B > 1 indicates that the concentration of the element is higher in the guano compared to the background geology and thus is more likely to be introduced via storm-petrel guano than lithology.

Chironomid samples were prepared following standard procedures from Walker [43]. A minimum of 50 individuals were counted per sample using standard identification manuals [44]. Sterols and stanols were completed at the University of Ottawa using methods outlined by Hargan et al. [4], with minor modifications. More detail for each of the palaeolimnological methods used in this study is available in electronic supplementary material, Methods S1.

Mean ornithogenic influence was developed by equally weighting all six measured proxies, including δ15N, % ornithogenic diatom sum, % Chironomus, geochemistry (Cd and Zn concentrations), sedimentary chlorophyll-a, and cholesterol. All proxies were standardized using a Z-score, and then arithmetically averaged to develop an overall trend.

(f) Storm-petrel guano

Leach’s Storm-petrels are frequently stranded on land every year in eastern Newfoundland, usually in September and October. The storm-petrels sampled in this study were found recently dead and collected by staff of Environment and Climate Change Canada (ECCC), or returned to ECCC by members of the public, under the authority of a Canadian Wildlife Service scientific salvage permit (SS2083).

To measure the acidity of storm-petrel faeces, guano was removed from three birds’ colons and lower intestines. Samples were measured in triplicate using a handheld Hannah pHEP meter in a consistent 1 : 10 sample to deionized water mass ratio, a method typical of highly organic substrates [45] as would be comparable to storm-petrel guano. Analysis of guano δ15N, elemental, and sterols and stanols concentrations were similarly determined from retrieved guano of recently deceased birds. However, in order to acquire sufficient mass for δ15N, the guano from nine birds was combined, and for elemental analysis, guano from 10 birds was combined.

3. Results

All six of our independent palaeolimnological proxies harmoniously tracked changes in the Baccalieu Island storm-petrel colony up to approximately 1700 years into the past. Sedimentary δ15N—used to quantitatively track higher trophic level seabird activity and inputs—was elevated in all of the storm-petrel-influenced ponds compared to the mainland reference. Storm-petrel guano inputs (δ15N = 14.2%,) caused an increase in all seabird-affected sediments beginning in the 1800s, prior to which δ15N was low, indicating low population densities (mean of measured samples in high-input ponds: 5.2‰ ± 0.9 s.d. to 7.9‰ ± 1.4 s.d.). Furthermore, in Lunin Pond (our longest temporal record), there is a secondary increase in δ15N to 7.7‰ at approximately 500 CE (figure 1a) and subsequent decline, suggesting an earlier seabird population on the island. Sedimentary δ15N in the mainland reference pond was directionless and markedly lower than all storm-petrel-influenced ponds, suggesting no seabird inputs (mean of measured samples: 2.1‰ ± 0.8 s.d.; figure 1c).

Sub-fossil diatom composition—used to identify shifts in pondwater pH and nutrients linked to storm-petrel guano inputs—show concomitant changes with sediment δ15N, providing independent evidence of shifts in storm-petrel colony size (figure 1). In all storm-petrel-influenced ponds (figure 1a–d), acidic guano inputs drove increases in the acidobiont Asterionella ralfsii var. americana Körner (pH optimum = 5.18 [46]) from the 1800s to ca 1980, when its abundance peaked, only a few years before the survey of 3.36 million breeding pairs [10]. Our study also reveals a consistent decline in A. ralfsii var. americana since the 1980s, supporting the 2013 survey data that documented a declining petrel population. When storm-petrel density was lower, Aulacoseira taxa, which are associated with relatively nutrient-dilute and circumneutral waters [47], dominated the assemblages. In Lunin Pond, δ15N increased starting ca 270 CE in concert with the relative abundance of the acidophilic Fragilaria exigua Grunow in Cleve & Möller, a taxon with a higher pH optimum than A. ralfsii (pH optima = 6.0 [48], as Fragilaria virescens). The presence of F. exigua, as opposed to more acidobiontic taxa, as well as our other proxy data (see below), suggests a significantly smaller seabird colony resulting in less acidification of the landscape and water column. By contrast, the mainland reference pond is dominated by circumneutral Aulacoseira taxa throughout the sediment record (figure 1c). The synchronicity of the diatom, δ15N, and
following proxies in all ponds suggest that *A. ralfsii* var. *americana* and *F. exigua* are ornithogenic diatoms on Baccalieu Island, and dominate the assemblage when storm-petrel inputs increase. This provides a method to track the growth and decline of the Leach’s Storm-petrel colony, as opposed to simply the presence–absence.

Sub-fossil chironomid assemblages tracked changes in deep-water oxygen concentrations linked to storm-petrel inputs. With increasing storm-petrel numbers in the high-influence Lunin Pond, as tracked by sediment $\delta^{15}$N and ornithogenic diatoms, we record concomitant increases in *Chironomus* taxa. These species are tolerant to prolonged periods of deep-water anoxia and increased acidity [49], conditions that would be expected to amplify as storm-petrels fertilize the ponds with their acidic, nutrient-rich guano (figure 2a).

As an additional supporting proxy for past seabird occupation, we analysed sedimentary metal concentrations and developed biogenic enrichment factors [23] to identify which elements are introduced by storm-petrels (electronic supplementary material, Methods S1). We determined Cd

![Figure 2. Ornithogenic proxies measured in the Lunin Pond sediment core dating back to ca 270 CE. (a) Changes in $\delta^{15}$N, ornithogenic diatoms (sum of *Asterionella ralfsii* var. *americana* and *Fragilaria exigua*), low-oxygen indicating *Chironomus* spp., Cd/Al and Zn/Al concentrations, sedimentary chlorophyll-$a$, and cholesterol concentrations observed in Lunin Pond. Darker green shading represents the larger, modern storm-petrel colony and lighter green represents the smaller, earlier colony. Regions of storm-petrel presence are derived using diatom-inferred CONISS. (b) Measured ornithogenic proxies from Lunin Pond standardized using Z-score. The bolded black trend indicates the arithmetic mean of all measured proxies. The two available storm-petrel population surveys from 1984 (3.36 million pairs) to 2013 (1.95 million pairs) are indicated with a vertical dashed line. (Online version in colour.)

(1)
and Zn concentrations are enriched by guano, and in all storm-petrel-influenced ponds, metal concentrations closely track the seabird colony’s dynamics as determined by δ15N and diatom assemblages (figure 1). Meanwhile, Cd and Zn concentrations were low andunchanging in the mainland reference pond (figure 1c).

Sedimentary chlorophyll-α (which includes its isomers and its main diagenetic products [29]) concentrations—reflecting trends in whole-lake production—substantially increased coincident with the aforementioned proxy increases in the storm-petrel-influenced pond sediments, as would be expected from enhanced primary production from marine-derived nutrients (figure 2; electronic supplementary material figures S5–S9). By contrast, chlorophyll-α was low in the mainland storm-petrel-free pond.

As an additional direct measurement of seabird presence, we also analysed fossil sterols and stanols [4] from the high-input Lunin Pond (figure 2) and compared these data to the mainland reference pond (electronic supplementary material, figure S3). In Lunin Pond, there was a substantial increase in cholesterol (cholest-5-en-3β-ol), the dominant sterol in storm-petrel guano (97.8% ± 1.3% s.d. of 11 sterols and stanols measured; N = 4) since ca 1800 (figure 2a). In Lunin Pond’s earlier evidence of storm-petrel population peak ca 500 CE, there was no notable change in cholesterol concentration, suggesting a smaller storm-petrel colony that did not introduce significant amounts of cholesterol. Comparatively, cholesterol concentration was low andunchanging in the mainland reference pond (electronic supplementary material, figure S3).

4. Discussion

Using a weight-of-evidence approach, and corroborated by generalized additive modelling (electronic supplementary material, figure S4), we conclude that the earlier population peak ca 500 CE revealed by Lunin Pond data (our only sediment record of sufficient length to reach this earlier time period) represented a smaller colony of seabirds compared to the recent 3.36 million pair population in 1984 (figure 2b).

This inference is supported by smaller peaks in δ15N, Cd, and Zn concentrations, sedimentary chlorophyll-α, cholesterol concentration, and the dominance in the acidophilic Fragilaria exigua instead of acidobiontic Asterionella americana var. ralfsii (figure 2a). As storm-petrels are the only Northwest Atlantic seabird that nests inland in large concentrations for long periods (four and six months) [32], the earlier peak can be confidently attributed to a storm-petrel colony.

Our results provide a new perspective on the population dynamics of Leach’s Storm-petrels and other long-lived and migratory seabirds generally expected to have relatively stable population sizes when environmental conditions are suitable and anthropogenic influences are limited. First, we corroborate the recent declines inferred from the 1984 and 2013 population surveys [11]. Importantly, the hitherto unknown period of rapid colony size growth (early colony: approx. 200 years from trough to peak; modern colony: approx. 400 years) sheds light on the dynamic nature of large seabird colonies. Population drivers of Leach’s Storm-petrel are still poorly understood [11], and diagnosing specific drivers at a time when a range of potential factors trending in similar directions (e.g. artificial night-lighting, increasing pollution, ocean warming, and overfishing [50]) remains challenging.

Our results suggest that on Baccalieu Island, conditions were favourable for colony growth until the 1980s. Awareness of this hitherto unknown population growth period will help to contextualize current declines and should be used in future studies of storm-petrel population trends.

The dynamic nature of these large colonies, as indicated by our results from Baccalieu Island, indicate a pressing need to understand the population’s intrinsic long-term inter-colonial recruitment, movement, response to climate variation, and range-wide patterns in population trajectories.

5. Conclusion

The six independent proxies we used to track past storm-petrel populations indicate that the world’s current largest
storm-petrel colony has experienced declines since approximately 1980, corroborating census data (figure 2b). Importantly, however, our palaeoenvironmental data suggest that the Baccalieu colony size in the 1980s was at its highest level in nearly two millennia. If that first survey had been conducted instead, for example, in the 1960s, the current population might be considered stable compared to 2013, masking the alarmingly rapid rate of the current decline. Conversely, had the first survey been conducted in the early 1800s, the colony would appear to be increasing—a cautionary result urging for the reassessment of other short-scale population trends, and emphasizing the need for long-term retrospective monitoring made available with developing palaeoenvironmental approaches. Strikingly, the current storm-petrel colony was increasing until the 1980s, during a time of intensifying fishing and ocean activity in Newfoundland, while the earlier, smaller colony peak ca 500 CE occurred in the absence of modern anthropogenic impacts. These rapid population changes highlight the dynamic nature of very large aggregations of the storm-petrel, and likely other mobile species, and speak to considering habitat protection as ecological networks encompassing not only land, while the earlier, smaller colony peak ca 500 CE occurred in the absence of modern anthropogenic impacts. These rapid population changes highlight the dynamic nature of very large aggregations of the storm-petrel, and likely other mobile species, and speak to considering habitat protection as ecological networks encompassing not only current, but also future colony sites. We show that remarkable population changes have occurred naturally in the past, but recognizing the current global decline of storm-petrels [50], as well as the majority of seabirds [1,6], we emphasize the need to continue research to identify the driver(s) of current declines and conservation action to mitigate negative effects.

Data accessibility. Data associated with this manuscript are available in the electronic supplementary material.

Authors’ contributions. M.P.D., G.J.R., and J.P.S. designed the study. M.P.D. and C.G. completed fieldwork. M.P.D. measured guano pH and completed diatom and sedimentary chlorophyll-a analyses. W.A.M. completed the seabird nesting density survey of Baccalieu Island and M.P.D. digitized the map. I.E.K. and J.M.B. carried out isotopic analysis. D.C.E. and J.K. completed steroid and stanol analysis. J.E.L. completed the chironomid analysis. All authors contributed to writing and editing the manuscript.

Competing interests. The authors have no conflicts of interest to declare.

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