Linking 19th century European settlement to the disruption of a seabird's natural population dynamics

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Recent estimates indicate that ~70% of the world's seabird populations have declined since the 1950s due to human activities. However, for almost all bird populations, there is insufficient long-term monitoring to understand baseline (i.e., preindustrial) conditions, which are required to distinguish natural versus anthropogenically driven changes. Here, we address this lack of long-term monitoring data with multiproxy paleolimnological approaches to examine the long-term population dynamics of a major colony of Leach's Storm-petrel (*Hydrobates leucorhous*) on Grand Colombier Island in the St. Pierre and Miquelon archipelago— an overseas French territory in the northwest Atlantic Ocean. By reconstructing the last ~5,800 y of storm-petrel dynamics, we demonstrate that this colony underwent substantial natural fluctuations until the start of the 19th century, when population cycles were disrupted, coinciding with the establishment and expansion of a European settlement. Our paleoenvironmental data, coupled with on-the-ground population surveys, indicate that the current colony is only ~16% of the potential carrying capacity, reinforcing concerning trends of globally declining seabird populations. As seabirds are sentinel species of marine ecosystem health, such declines provide a call to action for global conservation. In response, we emphasize the need for enlarged protected areas and the rehabilitation of disturbed islands to protect ecologically critical seabird populations. Furthermore, long-term data, such as those provided by paleoecological approaches, are required to better understand shifting baselines in conservation to truly recognize current rates of ecological loss.

paleolimnology | shifting baselines | population decline | conservation | islands

Seabirds are sensitive biological indicators of ocean ecosystem health, as changes in the marine environment and food webs are often manifested as fluctuations in their population numbers (1). Troublingly, Paleczny et al. (2) identified a ~70% decline in the world's monitored seabird populations since 1950 as a result of human interference and industrialization, signaling concern for the overall health of marine ecosystems. The authors also highlighted that only ~19% of the world's seabird populations are sufficiently monitored to make statistically supported inferences about population trends. Even with well-studied seabird populations, scientists have rarely, if ever, been able to document preindustrialization population numbers. A lack of systematic long-term surveying is common for most animal species (3) and results in data that are insufficient for developing reliable baselines needed to set effective conservation goals. This data vacuum is exacerbated by the disproportionate importance of long-term studies to inform biodiversity policy (4).

In response to the need for long-term data for effective management and realistic conservation goals, we demonstrate the capacity to use paleolimnological methods to reconstruct the historical population dynamics of a colony of vulnerable Leach's Storm-petrel (*Hydrobates leucorhous*; hereafter referred to as storm-petrels) over the past ~5,800 y on Grand Colombier Island in St. Pierre and Miquelon, France. Storm-petrels are globally distributed and inhabit both the Pacific and Atlantic Oceans in large numbers. At the start of the breeding season for Atlantic storm-petrels in March, birds migrate from tropical oceans between West Africa and Brazil to eastern Canada and form large colonies on remote islands that are generally inaccessible to

Significance

Globally, seabird populations are in decline. Without long-term monitoring, realistic conservation goals are difficult to establish. Here, we use lake sediment records to reconstruct the long-term dynamics of an important colony of Leach's Storm-petrels. We show that this seabird population underwent moderate natural population fluctuations until Europeans settled near the colony, after which seabird numbers were dramatically reduced. Our approach provides data concerning shifting baselines in conservation by demonstrating that the colony is only ~16% of the potential carrying capacity, and thus, reasonable conservation goals should be based on pre-industrialization population sizes. Likely, numerous other seabirds are also unknowingly in decline, highlighting the need for longer-term data and the immediate need to protect and rehabilitate the critical habitat.

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mammalian predators (5). Because of population declines in several major colonies, the Leach's Storm-petrel was uplisted to "Vulnerable" in 2016 in the International Union for Conservation of Nature's Red List (6). Despite substantial declines in many significant colonies (5), the prominent driver(s), whether anthropogenic (e.g., 7–9) or natural (e.g., 10–12), remains unclear.

Grand Colombier Island (46°49′20″ N, 56°9′55″ W) is located ~0.5 km north of St. Pierre Island within the Overseas Collectivity of St. Pierre and Miquelon, France, which is ~17 km southwest of mainland Newfoundland, Canada (Fig. 1). Grand Colombier is a small island (~0.54 km^2) but supports one of the world's largest colonies of Leach's Storm-petrels. The historic dominance of the seabirds on the island is attested to by a 1676 document of nautical instructions by Lt. Le Courcelle, who wrote that Grand Colombier was named so for the abundance of birds ("colombier" is a French term for a structure to house pigeons or doves) (13).

Ornithologists have only surveyed the storm-petrel colony on Grand Colombier Island four times, but each survey used different methodologies. The estimated colony size (as breeding pairs) was ~178,000 in the late 1980s (15), ~143,000 in 2004 (16), ~364,000 in 2008 (14), and ~146,000 in 2011 (17). Taken at face value, these surveys suggest that the storm-petrel population is stable and potentially experienced a boom in numbers in 2008, a stark contrast to the recent declines seen at all other major colonies in the Atlantic Basin (5, 6). However, the sampling effort and population estimation methods used by each survey differed, making direct comparisons between surveys problematic, and thus temporal trends remain unclear. If this colony is stable, Grand Colombier may have significance for sustaining the metapopulation of Leach's Storm-petrels and calls for research to understand the unique features of the island. In response, we reestimated the historical colony sizes from each of the four surveys using standardized techniques to clarify recent trends and then used multiproxy paleolimnological approaches to extend the monitoring window back in time to better understand the long-term colony trends before European colonization.

Paleolimnology is the study of the physical, chemical, and biological information stored in the sediments of lakes, ponds, and other water bodies (18). As sediments accumulate, they can provide a continuous historical record of changes in the surrounding ecosystem. Biovectors, such as storm-petrels, can substantially alter ecosystems by introducing high concentrations of nutrients, isotopes, and trace metals through waste products such as guano, eggshells, feathers, and carcasses. When these waste products run off into a water body, they alter the water chemistry and subsequently biotic assemblages, which are then archived in the sediments. By retrieving and dating a sediment core from a biovector-influenced pond and analyzing it for paleolimnological proxies, it is possible to reconstruct changes in various proxy data that can be used to reconstruct concentrations of avian waste products and thereby past population size. Several recent publications document the reliability of these methods (e.g., refs. 19 and 20), including at the world's largest breeding colony of Leach's Storm-petrels on Baccalieu Island, NL, Canada (21, 22). In our work, the sampling site "Grand Colombier Pond," or "GCP" (Fig. 1), was the only pond on the island. GCP is shallow ($Z_{max} = 0.6$ m) and small (1,600 m^2) and is surrounded by ferns, the preferred habitat of storm-petrels (22). To identify potential regional signals, such as climate, which may also affect our paleolimnological proxies, we collected three reference cores (St. Pierre Reference 1 to 3, or SPR1 to 3) from the nearby St. Pierre Island (Fig. 1). The reference ponds were selected based on proximity to Grand Colombier Island and similarity in physical and limnological features but, importantly, are not impacted by storm-petrels or other colonial seabirds (*SI Appendix*, Tables S1 and S2).

To reconstruct the seabird dynamics of Grand Colombier Island, we focused on five independent paleolimnological proxies that track the storm-petrel's potential to alter the surrounding terrestrial and aquatic environments via their acidic and nutrient-rich waste deposition (21, 22). We used the fractional deposition of stable nitrogen (δ^{15}N) and carbon (δ^{13}C) isotopes to track marine-derived nitrogen and changes in carbon source, respectively. Higher δ^{15}N values occur primarily because the heavier ^{15}N isotope is retained in tissues up the food web during amino acid synthesis, while the lighter ^{14}N is excreted during transamination and deamination (23). Storm-petrels occupy a high trophic position in the marine environment, and thus their wastes are elevated in δ^{15}N relative to terrestrial and freshwater sources (storm-petrel guano δ^{15}N = 14.2‰; 21). Similarly, colonial organisms such as seabirds indirectly enrich the environment near the colony with marine-derived carbon, increasing the abundance of C3 plants (e.g., mosses), lichens, and lake algae, and thus the ratio of ^{13}C to ^{12}C (24). We also used subfossil diatoms (class: Bacillariophyceae), which are a diverse group of siliceous algae that respond sensitively to an array of limnological parameters, including factors closely related to seabird waste deposition (e.g., acidity and nutrients; 18). By evaluating changes in diatom assemblage through time using dated sediment cores, it is possible to infer changes in population size. For example, with a larger colony size, we predict an increased relative abundance of eutrophic taxa. We also used the taxon-specific chitinous head capsules of chironomid (commonly known as
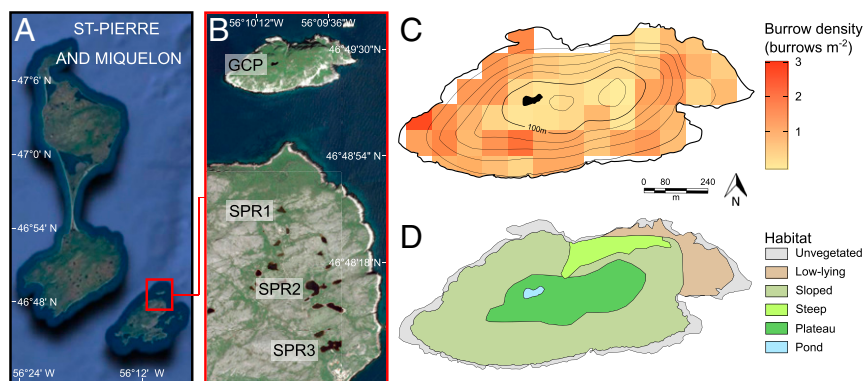

Fig. 1. Map of the study location, which (*A*) shows St. Pierre and Miquelon and highlights our study location and (*B*) indicates the four study ponds, GCP and SPR1 to 3. (*C*) Detection-corrected Leach's Storm-petrel burrow density on Grand Colombier based on the 2008 population survey by Lormée et al. (14). (*D*) Various habitat types on Grand Colombier Island.

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nonbiting midges) larvae, which are sensitive to limnological changes linked to seabird inputs, including oxygen concentration, pH, and trace metals (21, 25). In our study system with shallow and polymictic waters, changes in the chironomid assemblage likely reflect shifts toward taxa tolerant of high acidity and metal concentrations during periods of a larger colony (26). Finally, we used geochemical data to identify trace metal enrichment (27) linked specifically to storm-petrel inputs that have elevated trace metal concentrations from bioaccumulation (21). Since trace metals are generally in very low concentrations in reference lakes, their enrichment in sediments can act as a direct measure of seabird inputs. When combined, these proxies can provide a comprehensive overview of long-term trends in the seabird colony size (21). These long-term data can supplement sparse monitoring data, contextualize the timing and magnitude of recent trends, inform on potential drivers of decline, and be used to set reasonable conservation and wildlife-management goals without the confounding effects of the shifting baseline syndrome (i.e., changing reference conditions through time caused by the absence of historical information or context; 28).

Results

Both $\delta^{15}N$ and $\delta^{13}C$ measurements were elevated in the storm-petrel–impacted pond sediments relative to the reference ponds (Fig. 2). In the seabird-influenced GCP, $\delta^{15}N$ values significantly increased from 9.2‰ at the beginning of the pond's history ca. 5800 BP to a maximum of 15.5‰ ca. 4300 BP. From this point, $\delta^{15}N$ measurements stabilized ($\mu = 14.6‰$) until the recent decline to 12.7‰, starting ca. 280 BP (Fig. 2A). The ~4,000-y isotopic stability is likely associated with the saturation of ^{15}N in the local environment. $\delta^{15}N$ on Grand Colombier is primarily enriched via storm-petrel wastes and secondarily modified by peripheral variables such as ammonification and denitrification (29). Thus, once the pond's watershed became saturated with storm-petrel ^{15}N, it no longer tracked increases in the population. Once saturated, $\delta^{15}N$ values could only track significant declines in colony size, as recorded ca. 280 BP. In comparison, all three reference ponds consistently had much lower $\delta^{15}N$ values than GCP (2.7‰ to 8.0‰, $\mu = 5.9‰$; Fig. 2B).

In GCP sediments, the $\delta^{13}C$ profile had similar trends to $\delta^{15}N$ (Fig. 2A). $\delta^{13}C$ measurements significantly decreased from −26.5‰ at the beginning of the GCP's history ca. 5800 BP to −28.1‰ ca. 5180 BP. Afterward, $\delta^{13}C$ stabilized ($\mu = -27.7‰$) until a significant increase at ca. 140 BP to −26.4‰. Despite the broad range of $\delta^{13}C$ and significant shifts in the reference ponds ($\delta^{13}C = -29.4‰$ to −21.6‰, $\mu = -25.4‰$), none correspond with $\delta^{15}N$ trends or other proxies (see below).

We used the first principal response curve (PrC) to summarize the main directions of change in our biological assemblage data. In GCP, the PrC explained 64% of the diatom assemblage variation (Fig. 2A). From the beginning of the sediment record ca. 5800 BP until ca. 3500 BP, the diatom assemblage was dominated (in terms of relative abundance) by *Aulacoseira crassipunctata* Krammer and *Aulacoseira perglabra* (Østrup) Haworth. Following this period, we observed a shift in dominance to taxa that thrive in more acidic and eutrophic conditions, such as *Pinnularia maior* (Kützing) Rabenhorst and *Neidium sacoense* Reimer, which would be expected with a larger storm-petrel colony. The assemblage then briefly shifted back to *A. crassipunctata* and *A. perglabra* by ca. 1800 BP and back again to *P. maior* and *N. sacoense* ca. 1350 BP, indicative of fluctuation in colony size. Finally, we observed sequential shifts in diatom assemblages suggestive of decreasing acidity and nutrient concentrations as would be expected from a diminishing colony size from ca. 170 BP until the present, from 1) *P. maior* and *N. sacoense* to 2) *A. crassipunctata* and *A. perglabra* to 3) *A. distans* (Ehrenberg) Simonsen and *Achnanthes acares* Hohn & Hellerman. The modern dominance of *A. distans* and *A. acares* suggest

low dissolved carbon and total nitrogen, as has been observed in northern ponds (30). Interestingly, we also observed *Fragilaria exigua* Grunow from ca. 5790 until −35 BP, which was a dominant taxon also recorded during periods of storm-petrel presence in sediment records of Baccalieu Island, a similar island inhabited by storm-petrels (21).

For the reference ponds SPR1 to 3, the PrC summarized 65%, 23%, and 32% of the variation in the diatom assemblage, respectively (Fig. 2B). In SPR2 and SPR3, the diatom assemblages were unchanging and dominated by a variety of low-nutrient indicators, such as *Aulacoseira*, *Eunotia*, *Brachysira*, and *Frustulia*. Interestingly, in SPR1, we observed a significant shift from taxa indicative of higher nutrients, such as *Aulacoseira* and *Fragilaria exigua*, to taxa indicative of lower nutrients, including *Tabellaria flocculosa* (Roth) Kützing (str. III *sensu* Koppen), *Semiorbis hemicyclus* (Ehrenberg) Patrick, and *Brachysira brebissonii* Ross occurring ca. 1360 BP. We associate this change with a local habitat shift (i.e., pond-specific) and not with an ecosystem-scale shift because the other nearby reference ponds were unchanged.

In GCP, the chironomid PrC represented 62% of the assemblage variation (Fig. 2A). From ca. 5660 BP, GCP was dominated by *Microtendipes* spp. Starting ca. 4600 BP, we observed an increase in *Chironomus* spp., taxa indicative of acidic and hypoxic conditions, which were also dominant during peaks in seabird colony size in geographically and morphologically similar ponds on Baccalieu Island (21) and therefore considered representative of high seabird inputs and thus population dynamics. Similar to the shifts observed in the diatom assemblages, we identified a significant decline in the PrC starting ca. 2350 BP that was predominantly driven by a decline in the relative abundance of *Chironomus* spp., followed by a secondary increase in this genus beginning ca. 1250 BP. During this inflection in the PrC, *Glyptotendipes* spp. were dominant. Afterward, *Chironomus* spp. were again dominant until ca. 190 BP, when the community shifted to dominance by *Microtendipes* spp., the taxa dominant at the beginning of the pond's record. When contrasted with the reference ponds, there were only sufficient chironomid head capsules to make ecological inferences in SPR1 (Fig. 2B). Low chironomid counts as observed in SPR2 and SPR3 have been described in similarly unproductive systems that limit chironomid abundances, such as in Newfoundland (26) and the High Arctic (31). In SPR1, the chironomid PrC explained 62% of the assemblage variation. In this reference pond, we observed a single significant shift from *Dicrotendipes* spp. and Tanytarsini dominance to *Psectrocladius* spp. ca. 950 BP. The shift in chironomid assemblage corroborates a pond-specific change as suggested by diatoms.

Cd and Zn, two metals associated with storm-petrel inputs (*SI Appendix, Supplementary Methods*; 21), were elevated in the storm-petrel–impacted GCP sediments compared to the reference ponds (Fig. 2). To minimize the influence of terrestrial metal inputs from erosion, we normalized our data against Al. From the beginning of the record ca. 5800 BP, Cd/Al and Zn/Al were slightly enriched compared to the reference ponds (Fig. 2). Both Cd/Al and Zn/Al began an increase in concentration ca. 3800 BP and reached a peak ca. 2250 BP. In this period, Cd/Al increased ~170% and Zn/Al increased ~380%. Following this period, Cd/Al and Zn/Al significantly declined by ~70% and ~75%, respectively, to a trough ca. 1690 BP. Next, up until ca. 650 BP, there was an ~430% increase in Cd/Al and an ~480% increase in Zn/Al. At ca. 100 BP, the metal concentrations then rapidly declined, having reduced back to concentrations near the origin of the pond and approaching concentrations of the reference ponds. In contrast, all three reference ponds had metal concentrations near or below the detection limits for Cd (0.05 μg g^{-1}) and Zn (5.0 μg g^{-1}) and directionless throughout the available records up to 4900 BP (Fig. 2B).
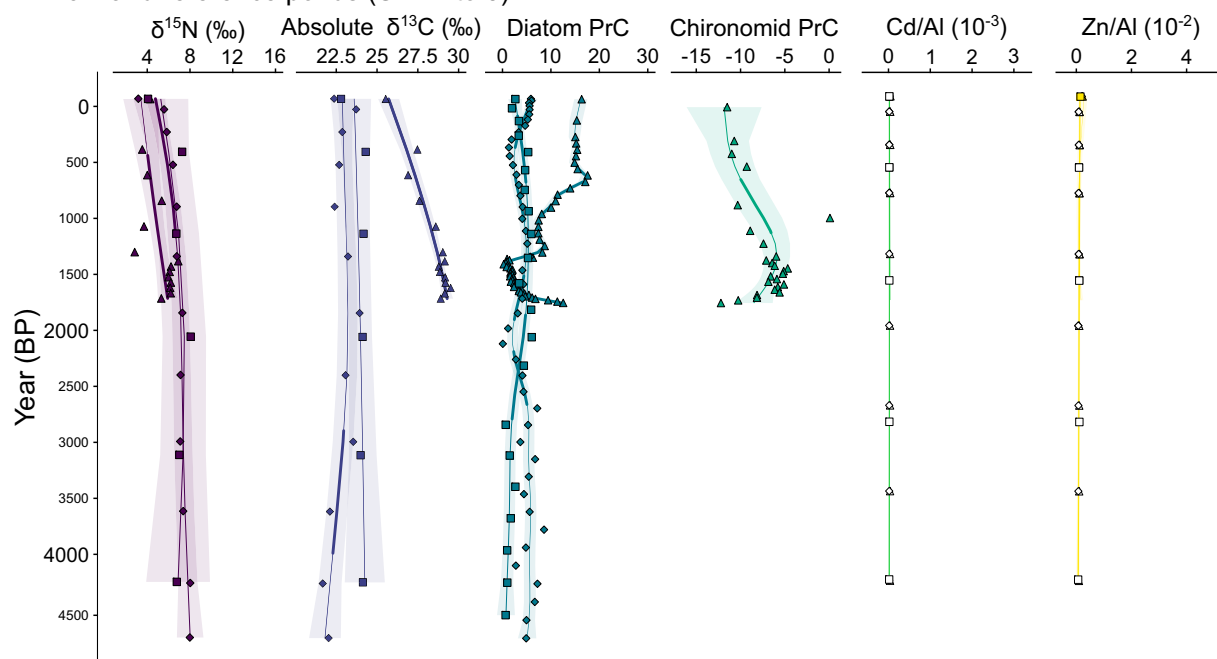
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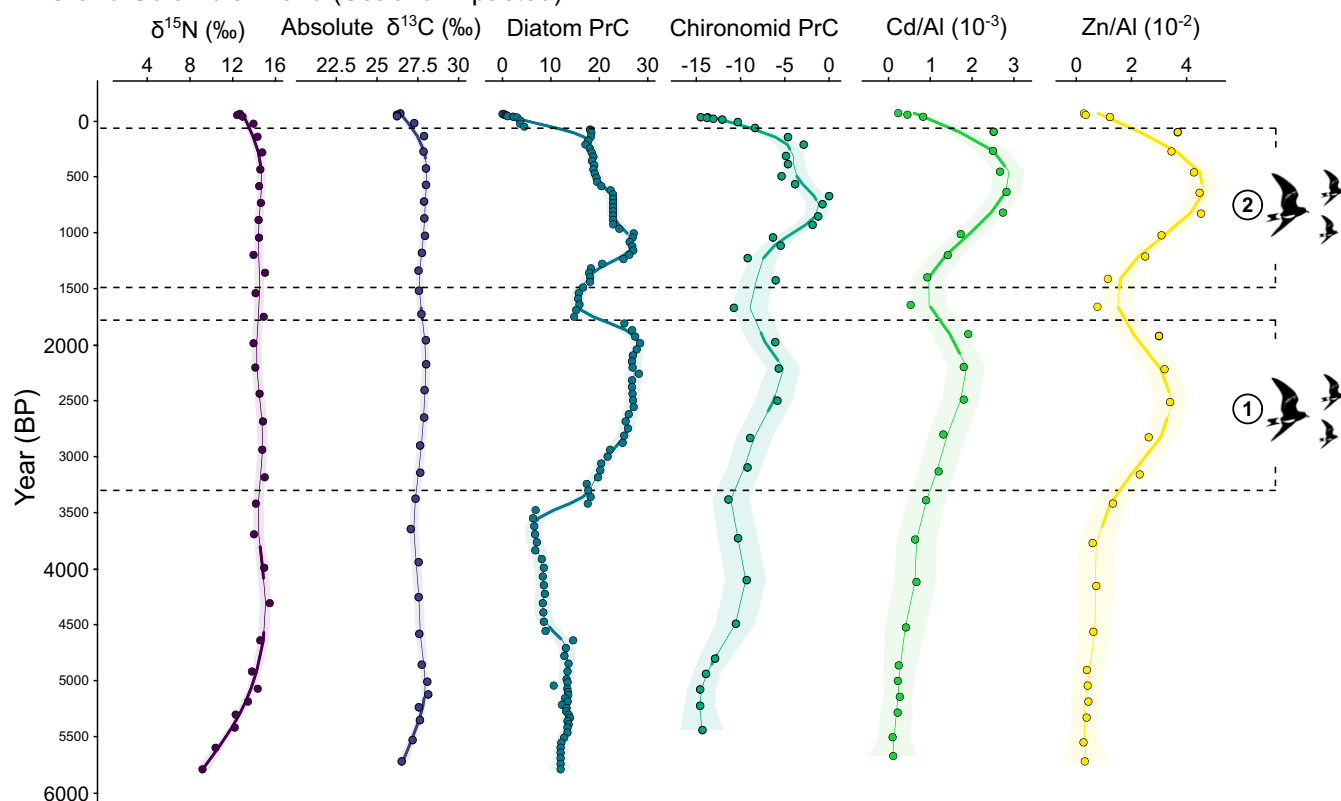
Fig. 2. All measured paleolimnological proxies in the seabird-impacted GCP (*A*) and the mainland reference ponds (*B*) (SPR1 to 3), shown on equal scales. The areas enclosed with dashed lines and storm-petrel icons indicate the two periods of a large Leach's Storm-petrel colony size. $\delta^{13}C$ is normalized to account for the Suess effect. Diatom and chironomid data are summarized as PrC. The trends of each proxy are fitted with GAMs, with significant periods of change shown with bold lines. The shaded bands are 95% CIs. In *B*, SPR1 is represented with triangles, SPR2 with diamonds, and SPR3 with squares. Chironomid concentrations were below the minimum threshold for interpretation in SPR2 and SPR3 and therefore omitted from the figure. For Cd/Al and Zn/Al concentrations, intervals that were below the detection limit are expressed in white.

Total colony size was reestimated with data from population surveys in 2004, 2008, and 2011 using a consistent geographic information system approach to estimate the island size, surface area of each habitat type (Fig. 1D), and seabird occupancy per habitat. The reestimation yielded similar population sizes with overlapping confidence intervals across the three surveys, indicating no apparent trend, as follows: ~173,000 breeding pairs in 2004, ~253,000 in 2008, and ~200,000 in 2011 (Table 1). There were insufficient data to provide a meaningful reestimation of the 1980s survey (*SI Appendix, Supplementary Methods*). We estimate that Grand Colombier Island likely has a potential carrying capacity of ~1.29 million pairs of Leach's Storm-petrels, which indicates that the current colony size is only ~16% of Grand Colombier's potential carrying capacity. This estimate is based on the occupied burrow densities from Baccalieu Island, which supports similar habitats as Grand Colombier, in the 1980s when the population was peaking (21). Moreover, the potential of Grand Colombier to support significantly more seabirds is visually evident by the low burrow density across the island (Fig. 1C).

Discussion

By combining our five independent paleolimnological proxies and using a weight-of-evidence approach, we reconstructed the last ~5,800 y of Leach's Storm-petrel colony dynamics on Grand Colombier Island, St. Pierre and Miquelon (Fig. 3A). In the storm-petrel–impacted GCP, all proxies recorded coherent temporal shifts consistent with variable waste inputs from a colony displaying large population fluctuations, which together provide a holistic reconstruction of the storm-petrel population dynamics (Fig. 3A). We are confident that we are tracking changes in the storm-petrel population (as opposed to other seabirds), as they are the only Northwest Atlantic seabird that nests inland around ponds for long periods (5), our recorded changes in diatom assemblages reflect the nutrient-rich and acidic composition of storm-petrel guano, and changes in species-specific trace metal concentrations (i.e., Cd and Zn) have been established in prior work with this species (21). Furthermore, in the nearby reference ponds SPR1 to 3, although we observed significant shifts in some proxies, none of these changes are consistent among reference sites nor with shifts in the GCP record to suggest influence from extrinsic regional signals, such as climate (Fig. 2B). Together, our paleoecological data provide insights concerning the long-term population changes of this vulnerable seabird.

We observed evidence of the limnological influence of the storm-petrel colony since GCP's inception ca. 5800 BP, as exemplified by elevated trace metal and isotope concentrations and the presence of eutrophic diatom assemblages compared to the reference ponds (Fig. 2). Furthermore, similar to what was described at the storm-petrel colony on Baccalieu Island (21), we observed distinct periods of growth and decline in the colony size before modern human influences. On Grand Colombier, the first peak in the colony lasted ~1,530 y, from ca. 3300 BP to ca. 1770 BP, and reached a maximum ca. 2550 BP (Fig. 3). After 250 y, the second increase in colony size began and lasted ~1,420 y. The second rise in the storm-petrel colony peak occurred from ca. 1480 BP to 60 BP and peaked ca. 670 BP. Following the second colony peak, the population experienced a relatively subtle decline until the beginning of the 19th century. Coinciding with the rapid recolonization and permanent establishment of St. Pierre by the French in 1816 CE, the storm-petrel colony on Grand Colombier experienced a rapid and precipitous decline (Fig. 3). Importantly, our paleolimnological data indicate that the colony has not recently stabilized, nor has it begun to recover to predisturbance numbers.

Our paleolimnological observations differed from the limited survey data, which suggested population stability from the 1980s to 2011 (Table 1), although differing survey methods made temporal comparisons problematic. In an attempt to address some of these inconsistencies, we reanalyzed the 2004, 2008, and 2011 estimates using comparable methods. Although there is still a 46% increase from 173,000 pairs to 253,000 breeding pairs (reestimated population) from 2004 to 2008, the differences are not as large as the original estimate (155% increase from 143,000 to 364,000 breeding pairs). Three years later, the reestimated 2011 survey indicated a return to a similar population size (200,000 breeding pairs) as 2004 (Table 1). The available short-term surveying data suggests that the colony is currently stable in size, but when placed into the long-term context made available with our paleolimnological data, they indicate that the current colony is stunted at only ~16% of its potential carrying capacity and is currently similar to only that of the beginning of the paleolimnological record ~5,800 y ago (Fig. 3A).

Human impacts on the storm-petrel population are primarily a result of indirect perturbation of the island ecosystem and surrounding waters as opposed to direct harvest of the birds. Based on Lt. Le Courcelle's 1676 CE nautical documents, burrowing birds on Grand Colombier were called "carcaillou" (roughly translating to "quail," likely referring to storm-petrels) and were "worth nothing to eat" (13). Otherwise, oily seabirds such as storm-petrels were occasionally collected and used as candles (32; as "stormy petrels"). However, European arrival to St. Pierre and Miquelon may have had many deleterious impacts on the island's ecology, as has been described in similar ecosystems, including introduced species (33) and increased fishing and marine impacts (34, 35). Documents describe anecdotal evidence that "big rats that infest the island have a heyday among the hatching eggs and nesting birds. The rats are said to have arrived on the island from a sinking ship many years ago" (36). However, there is currently only evidence of meadow vole (*Microtus pennsylvanicus*) on Grand Colombier (14), which are not considered a major threat to storm-petrels.

The timing of changes in our paleolimnological data implicates European colonization of the St. Pierre archipelago as the prominent driver of the decline in the seabird population. There is archeological evidence of continuous occupation by various Paleo-Inuit and other Indigenous Peoples starting ca. 5000 BP, although there is little to suggest permanent settlements (37). Our proxy data do not indicate any notable changes in the storm-petrel population that can be attributed to these early occupations of the region. Our paleolimnological data do, however,

Table 1. Original and reestimated Leach's Storm-petrel colony sizes on Grand Colombier Island, St. Pierre and Miquelon

Survey year	Original population (breeding pairs)	Reestimated population (breeding pairs)	95% CI
1980s	177,750 (14)	N/A	N/A
2004	142,783 (15)	173,481	128,744–227,126
2008	363,787 (16)	253,254	224,056–280,676
2011	146,213 (17)	199,935	171,709–228,572

There was insufficient data to meaningfully reestimate the 1980s survey. N/A, not applicable.
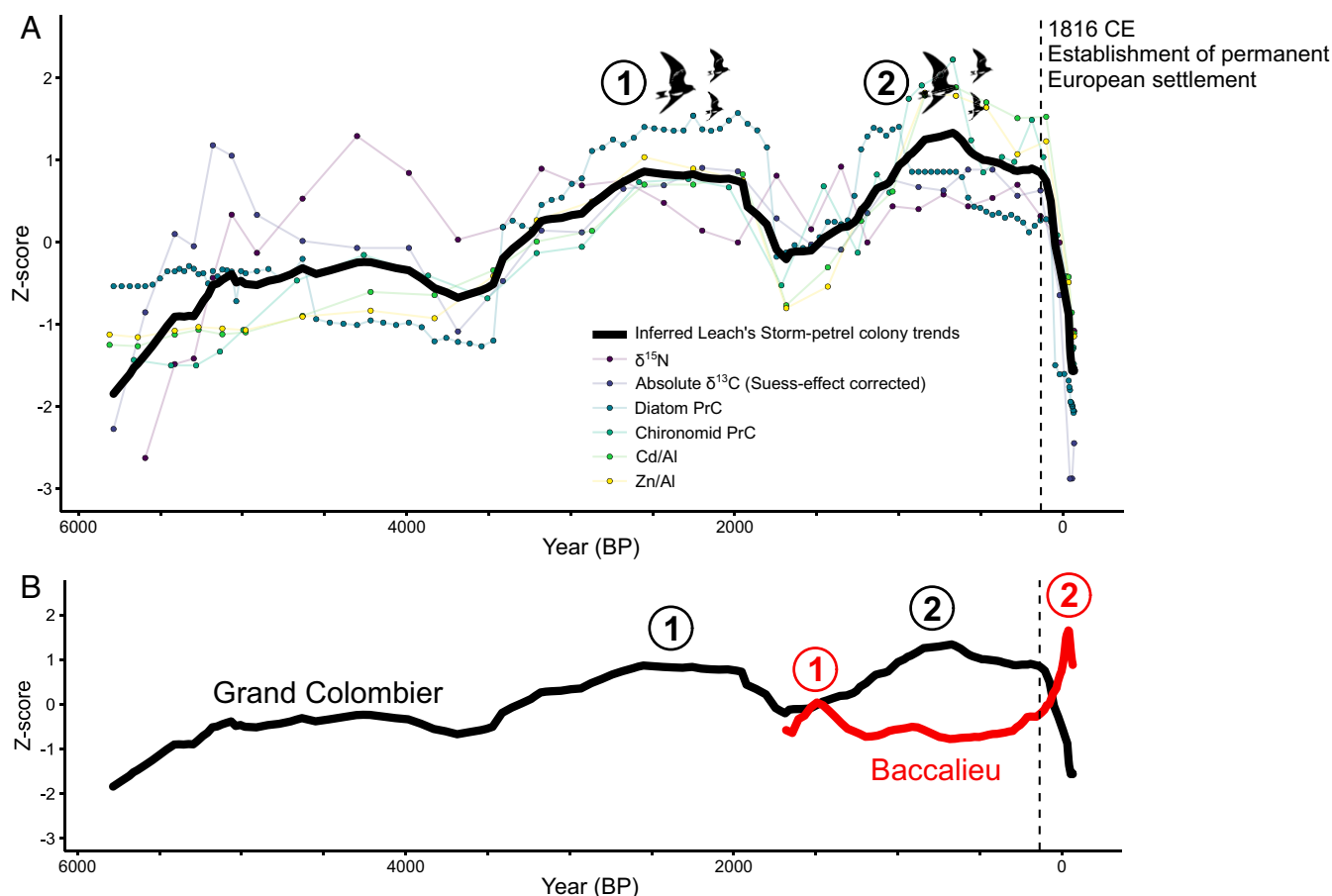
Fig. 3. Long-term population trends of the Leach's Storm-petrel colony. (*A*) Overall trends in the Grand Colombier Island Leach's Storm-petrel population as determined by the mean of all paleolimnological proxies on Grand Colombier Island. Note the rapid decline in population concurrent with the European population expansion in the St. Pierre and Miquelon archipelago beginning in 1816 CE. (*B*) Trends of Grand Colombier Island contrasted to ~1,700 y of population trends on Baccalieu Island, as detailed in Duda et al. (21). The distinct peaks in the storm-petrel colony size are identified numerically.

show that the storm-petrel colony peaked before European arrival and experienced a rapid decline in population after a permanent human settlement was established. From 1520 to 1816 CE, the human population varied greatly, from seasonal fishers to 200 permanent settlers described as "wretched souls" in the 17th century (38) to a short peak of 2,000 permanent settlers until 1778, when the town was razed by the English (13). When resettled in 1816 CE by 150 families (38), St. Pierre experienced a steady increase in population to the current size of ~6,000 individuals, mainly sustained by ocean-based activity, including fishing, shipping, and tourism. Many documented cases and reviews link seabird population disruptions to human settlement (e.g., refs. 39 and 40). Together with the amplifying effects of climate warming and pollution, these disruptions threaten overall ecosystem health and require management attention (41). Furthermore, the Baccalieu Island colony, which is also in the Atlantic Basin but does not have a large nearby settlement like Grand Colombier, grew in size during this same period of human expansion (Fig. 3*B*), further supporting our conclusion that proximity to human impacts (rather than regional environmental changes) had deleterious effects on the seabird colony on Grand Colombier. Given the numerous documented impacts of human settlement on seabird populations, the synchronous timing of the decline in the storm-petrel population with an increase in the human population, and the lack of confounding evidence from our reference sites or the more remote Baccalieu Island, we propose that there is a strong link between the decline in storm-

petrel numbers and the permanent European settlement in 1816 CE.

Extinctions of seabirds as a direct response to the arrival of human explorers and/or settlers are well documented. For two flightless species (Great Auk [*Pinguinus impennis*] in the North Atlantic and Spectacled Cormorant [*Phalacrocorax perspicillatus*] in the North Pacific), human interference and overhunting led to extinction (42, 43). These dramatic effects are not exclusive to flightless species: several seabirds that were behaviorally similar to storm-petrels were also driven to extinction as Europeans explored the Atlantic (e.g., Saint Helena Petrel [*Pseudobulweria rupinarum*] and Lava Shearwater [*Puffinus olsoni*]; 44).

Before the arrival of Europeans, Grand Colombier Island experienced at least two peaks in storm-petrel colony size ca. 2550 BP and 670 BP (Fig. 3*A*). When combined with the asynchronous fluctuations in colony size described on Baccalieu Island (Fig. 3*B*), the peaks and subsequent declines in colony size were possibly driven by the Leach's Storm-petrels' propensity for intercolonial recruitment and movement (5, 10, 45). Because storm-petrels are small seabirds that are vulnerable to predation (5, 45, 46) and climatic perturbations, long-term persistence likely requires intercolonial movement and recruitment to maintain population size. The differing timing of peaks in the storm-petrel colonies on Grand Colombier and Baccalieu Island (Fig. 3*B*) suggests that either local factors (e.g., predators, habitat availability, and competition) and/or regional climatic factors were the primary drivers of the long-term population dynamics.

For example, the arrival of a predator can diminish the number of breeding adults and kill vulnerable chicks and eggs and may force the movement of prebreeding immature storm-petrels to build their burrows on different, predator-free islands (45). Similarly, regional oceanographic shifts may also play a role in the reciprocal trends between colonies (47). Baccalieu Island is at the northern edge of the species' distribution (5) and is strongly influenced by the cold Labrador Current and seasonal spring pack ice (48). Periods of cooling may make the northeast coast of Newfoundland unsuitable for large numbers of storm-petrels, potentially shifting their distribution south to suitable islands mediated by the warmth of the Gulf Stream, like Grand Colombier. Regardless of the cause(s) of the large shifts in storm-petrel colony size, our data, combined with global declines at other major colonies (5), indicate that recent perturbations have overridden natural drivers of population change and have led to the notably more rapid rates of decline than experienced over the last ~5,800 y.

Our results stress the importance of long-term data in evidence-based conservation policy and ecosystem management. The added population context provided by long-term paleoecological data provides a partial solution to the shifting baseline syndrome (changing reference conditions through time caused by the absence of historical information or context; 28) and allows for better management goals in conservation. As exemplified with the Leach's Storm-petrel population on Grand Colombier, the available survey data since the 1980s (although limited) indicated that the population was stable and did not require immediate management. However, our added long-term context shows that the modern population of this globally significant colony is now only ~16% of the pre-European potential carrying capacity of 1.29 million breeding pairs. Despite the general acceptance of the importance of long-term data among ecologists, studies are limited by the need for continual economic support and restrictive pressures on obtaining immediate results (49). As such, novel approaches to reconstructing long-term population and biodiversity data, such as those provided by paleolimnological approaches, should be embraced to provide effective conservation research to policymakers in collaboration with scientists using whole-genome sequencing (50, 51) and any available traditional ecological knowledge (52). To reverse the regional population declines of Leach's Storm-petrels in the Atlantic Basin (5), immediate actions are required to minimize human impacts on ecologically sensitive islands, such as restoring deteriorated islands affected by introduced species and habitat degradation, improving policies for continued monitoring and protection, and local community engagement (40).

Conclusions

Our paleoecological data show that the associated impacts of European colonization and expansion on St. Pierre Island disrupted the natural population fluctuation of storm-petrels on the nearby Grand Colombier Island. The current storm-petrel population is only ~16% of the potential carrying capacity that was likely supported ~740 y ago. Because of the general lack of long-term data, numerous other species may also have experienced declines in numbers. Given that seabirds are sentinel species indicative of marine ecosystem health (1), the rapid decline in this globally significant storm-petrel population on Grand Colombier may be regarded as a "canary in the coal mine" for Atlantic Ocean health. The storm-petrel declines and global diminishment of seabird populations (2) signal the need to expand island protection and to restore islands devastated by introduced species and habitat degradation.

Materials and Methods

Mapping. The maps presented in Fig. 1 were created using satellite imagery available using Google Earth with the R package ggmap v.3.0.0 (53). The

satellite image used for Fig. 1*B* was taken on August 2, 2019. Fig. 1*C* was created with ggplot2 (54) using burrow density corrected by detection probability from the 2008 population survey (14).

Sediment Collection and Chronologies. Sediment cores were collected between August 26 and 28, 2018. The cores for the three reference sites (SPR1 to 3) and the top portion of GCP were collected using standard techniques, namely, a high-resolution push corer, and sectioned on site. To retrieve the entire history of GCP, we used a Jowsey (55) corer to collect sediments at depths beyond the capability of the push corer. To create a "master core" (total length = 128 cm), the two cores were aligned using a combination of visual markers (e.g., changes in sediment color and grain size), coherent changes in high-resolution visible reflectance spectroscopy–inferred sedimentary chlorophyll a, and diatom assemblages. The sediments of GCP were composed of gyttja with a large proportion of organic material. In contrast, the reference cores were composed of much finer silts and did not have notable organic material. The bottom of our sediment core was a dense clay plug associated with the pond's formation, indicating that we collected the entire available paleolimnological history of GCP.

The age of the sediment cores was determined using a combination of ^{210}Pb gamma spectrometry and accelerator mass spectrometry ^{14}C dating. ^{210}Pb age models were generated with the constant rate of supply model (56) (*SI Appendix*, Figs. S1, S3, S5, and S7). We used classical non-Bayesian modeling to extrapolate dates for the reference cores using one or two carbon dates per core (*SI Appendix*, Figs. S4, S6, and S8) and flexible Bayesian modeling to extrapolate the remaining dates in GCP using four carbon dates (*SI Appendix*, Fig. S2). For all models, our ^{14}C dates were calibrated using the IntCal13 calibration curve (57). All ^{14}C ages are presented as years BP, for which 1950 CE is 0 BP. More detail is provided in *SI Appendix, Supplementary Methods*.

Paleolimnological Proxies. Samples and standards were analyzed for stable isotope ratios of nitrogen and carbon with an elemental analyzer (Isotope Cube, Elementar) and an isotope ratio mass spectrometer interface (Delta Advantage, Thermo). All isotope analyses were performed at the Ján Veizer Stable Isotope Laboratory at the University of Ottawa (Ottawa, ON, Canada). Our data were reported in parts per thousand against atmospheric N_2 for nitrogen and PeeDee belemnite for carbon. To make accurate interpretations of recent trends in δ^{13}C, we normalized our data to pre-1840 levels of δ^{13}C using methods presented in Schelske and Hodell (58) to account for the Suess effect (i.e., decreasing δ^{13}C because of human industrialization). Also, δ^{13}C is traditionally presented as a negative ratio, and therefore a more negative δ^{13}C ratio equates to increased allochthonous and C3-plant inputs, as would be expected with high densities of burrowing seabirds. However, for clarity when combined with our other proxies, we present absolute values of δ^{13}C concentrations in figures.

Diatom preparation followed standard procedures described by Battarbee et al. (59). Approximately 0.3 g of dry sediment was digested using a 1:1 molecular weight ratio of sulfuric and nitric acid and heated at 80 °C for 2 h. The resultant slurry was then repeatedly rinsed with deionized water until a pH of 7 was reached. The aliquots of the slurries were pipetted onto coverslips, dried using a slide warmer, and mounted to slides with Naphrax. At least 400 diatom valves were identified to species per sample. The expanded diatom counts of common taxa are available in *SI Appendix*, Figs. S9–S12.

Chironomid head capsules were isolated using the standard techniques described in Walker (60). Briefly, a subsample of 0.1 to 4.9 g dry weight was heated at 80 °C for 30 min in 80 mL 5% KOH to deflocculate the sediments and digest excess organic matter in the sample. Next, each sample was passed through a 100-μm sieve, washed with deionized water, and preserved with 95% ethanol. Chironomids were picked from a grooved Perspex (Bogorov) sorter. We counted head capsules with a full mentum as one and capsules with half a mentum as half. Head capsules with less than half a mentum were omitted. Head capsules were placed on a glass coverslip with their ventral sides facing upward and mounted on a microscope slide using Entellan. As recommended by Quinlan and Smol (25), at least 50 chironomid head capsules were identified from each interval to the genus level to make ecologically meaningful interpretations. The head capsule concentrations for SPR2 and SPR3 were very low (<50 head capsules), and therefore chironomid analyses were omitted for these sites. Full chironomid counts are available in *SI Appendix*, Figs. S13–S16.

The sedimentary metal concentrations were analyzed at Queen's University Analytical Services Unit in Kingston, ON, Canada, using inductively coupled plasma mass spectrometry. A full list of the 28 measured metals, with detection limits, is provided in *SI Appendix, Supplementary Methods*. The metal concentrations were normalized against Al to minimize the

influence of minerogenic and granulometric effects (61). As in previous work (21), we determined that Cd and Zn were the primary metals introduced by storm-petrels using biogenic enrichment factors (i.e., a higher metal concentration in guano than reference sediments; 27) (*SI Appendix, Supplementary Methods*) and thus were the focus of our interpretations. For several intervals in the reference cores (SPR1 to 3), Cd and Zn concentrations were below the detection limit. In such cases, we approximated the metal concentration using detection limit/$\sqrt{(2)}$, as suggested by Hornung and Reed (62).

Statistical Analyses. Given the complex nature of our diatom and chironomid community data, we used PrC to summarize compositional change. For our PrC analysis, we followed the procedures described in Simpson and Birks (63) using the R package analogue v.0.17-4 (64). The species abundances were first square-root transformed to stabilize variance, and we used principal component analysis (PCA) axis-1 scores as the starting point for curve fitting. To confirm that the PrC tracked changes in the seabird population size, we also examined the autecology of the dominant taxa to support the curve.

We used generalized additive models (GAMs) and methods suggested in Simpson (65) to account for heteroscedasticity in our data. Periods of statistically significant change were determined using periods of the nonzero rate of change in the GAM first derivative (65). The statistical analyses were carried out using the R packages mgcv v.1.8-31 (66) and gratia v.0.3.1 (67) and plotted with ggplot2 v.3.3.0 (53).

We used an arithmetic mean of all proxies when standardized using a Z-score (or standard score) to estimate the storm-petrel colony's trends. As the relationships between paleolimnological proxies and seabird populations are nonlinear, it is impossible to assign accurate population numbers to our trends. Instead, our trends should be used to add context to current and historical population dynamics. We identified periods of notable storm-petrel colony size change when there were notable fluctuations in the overall trend. The peaks and troughs described in the population size were identified using local maxima and minima in the Z-score colony estimate.

Population Survey Reestimation. The original methods of each population survey are described in detail in *SI Appendix, Supplementary Methods*. In our revised estimates, we focused on standardizing the approach to classify the habitat and estimate the area occupied by Leach's Storm-petrels and on estimating uncertainty from as many sources as possible. We also acknowledge that the distributions of occupied burrow densities within habitats tend to show a right skew, and therefore the Delta method may not fully capture the true shape of the underlying distributions. In general, we followed the approach in Wilhelm et al. (68), in which the number of occupied burrows in each plot is estimated from the data, and randomization procedures are used to propagate uncertainty through to the final estimates of colony size. We only reestimated surveys from 2004, 2008, and 2011 because there was sufficient data for a meaningful population estimate. The 1980s

survey was exploratory and did not sufficiently survey the various habitats to be used in a reestimation.

Potential Carrying Capacity. We estimated the potential carrying capacity of Leach's Storm-petrels on Grand Colombier Island to determine the portion of available habitat on the island that is currently occupied. To do so, we used the maximum occupied burrow density (OD) observed on Baccalieu Island during its peak storm-petrel abundance in the mid-1980s (21, 68). We focused on the two habitat types present on both Baccalieu and Grand Colombier Island, namely, fern (3.594 ± 1.021 SE) to represent sloped habitats and soft ground heath (0.513 ± 0.140 SE) to represent the central plateau and low-lying areas. We then multiplied OD with the island surface area calculated in this study to obtain a potential carrying capacity of 1,216,000 pairs in the sloped habitat and 69,000 pairs in the plateau and low-lying areas, for a total maximum of 1,285,000 breeding pairs on Grand Colombier Island. We acknowledge that this estimate assumes that the habitat of Grand Colombier has not changed over the measured time frame despite the known impacts of storm-petrels on vegetation communities (22).

Data Availability. All study data are included in the article and supporting information.

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