



Multicentury perspective assessing the sustainability of the historical harvest of seaducks

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Where available, census data on seabirds often do not extend beyond a few years or decades, challenging our ability to identify drivers of population change and to develop conservation policies. Here, we reconstruct long-term population dynamics of northern common eiders (*Somateria mollissima borealis*). We analyzed sterols together with stable nitrogen isotopes in dated pond sediment cores to show that eiders underwent broadscale population declines over the 20th century at Canadian subarctic breeding sites. Likely, a rapidly growing Greenland population, combined with relocation of Inuit to larger Arctic communities and associated increases in the availability of firearms and motors during the early to mid-20th century, generated more efficient hunting practices, which in turn reduced the number of adult eiders breeding at Canadian nesting islands. Our paleolimnological approach highlights that current and local monitoring windows for many sensitive seabird species may be inadequate for making key conservation decisions.

biomarkers | paleolimnology | Arctic | seabirds | conservation

The factors that shape population dynamics of wildlife often act over time periods well beyond the scope of retrospective analyses of available field information such as population surveys (1). This is particularly true in remote locations like the Canadian Arctic and West Greenland where standardized bird surveys only began in the 1950s and even then occurred rarely with incomplete spatial coverage (2). These remote Arctic locations are also experiencing extensive change, and there is a need for information to assess whether contemporary estimates of species abundance and patterns of fluctuation are disconcerting, or within the realm of natural variation (3).

New biomarker techniques applied to dated lake sediment cores have unlocked the opportunity to examine long-term population trends among colonial nesting seabirds and seaducks. Lipophilic biomarkers identified from bird feces (sterols and stanols), along with more traditional geochemical biomarkers such as stable nitrogen isotopes ($\delta^{15}\text{N}$) preserved in pond sediments, allow for a multiproxy reconstruction of population changes from sedimentary records over decades to centuries (4, 5). This is because nutrient flow from bird guano and related deposition is dynamic and reflects the number of birds present or absent as nesting populations change over time (4, 6). Sterols and stanols, found in varying concentrations and combinations in the feces of animals (7), are emerging as important proxies to directly track animal inputs to lake sediments over decadal-scale and century-scale time periods (1, 8). For example, the ratio of cholesterol (cholest-5-en- β -ol) to cholesterol and sitosterol (β -sitosterol), a common phyto-sterol, demonstrated significant enrichment of cholesterol in pond sediments closest to a nesting colony of northern fulmars (*Fulmarus glacialis*) in the High Arctic and was significantly correlated with ornithogenic $\delta^{15}\text{N}$ enrichment of sediment (9). This “seabird sterol index” provides a direct measure of seabird presence and, when measured in sediment cores, can be used to infer population

trends through time. Furthermore, this proxy can be corroborated with stable nitrogen isotopes, an already established tool in assessing seabird-derived nitrogen release to coastal environments, both spatially and temporally (1, 4).

Here, we apply biomarker methods available to paleolimnologists to assess long-term population trends of northern common eiders (*Somateria mollissima borealis*) at nesting colonies in the eastern Canadian Arctic. We examine changes in $\delta^{15}\text{N}$, as well as sterols and stanols, in dated sediment records from ponds on nesting islands, as an index to reconstruct colony occupancy of eiders through centuries. In contrast to other studies, which have often focused on one colony location (5, 9), we present data from many island colonies distributed across a large geographic range in Hudson Strait, Nunavut—the core of the Arctic eider breeding range (10). At these same island colonies, there is significant $\delta^{15}\text{N}$ enrichment in moss and soil samples compared with non-colony islands and mainland reference sites (11), indicating that nutrients originate from a trophically elevated source.

The northern common eider is a long-lived seaduck with a circumpolar distribution including Arctic Canada and Greenland (10). Between 60 and 80% of the eiders breeding in Arctic Canada are estimated to migrate to southwest Greenland to

Significance

The paucity of monitoring data for seabird populations at suitable temporal and spatial scales challenges the development of realistic and effective conservation policies. We employ newly developed paleoenvironmental techniques at 10 key subarctic seaduck colonies to reconstruct broadscale population changes at decadal timescales through the 20th century. We show that harvesting practices in southwestern Greenland and northeastern Canada were unsustainable, timed with the advent of widespread use of shotguns and outboard motors for hunting across the North. Our historical population reconstructions, corroborated with two independent proxies (sterols and stable nitrogen isotopes), reaffirms that hunting restrictions were necessary to prevent the collapse of this subspecies.

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overwinter (12, 13) (Fig. 1A). Reports suggest that there were once millions of eiders in the Greenland–Canada region (14), but numbers were substantially reduced by the late 20th century (15–17). Eider breeding colonies are remote, often difficult to access, and can have high interannual variation in occupancy, so only sparse nest count records exist. To supplement these records, we employed a comprehensive spatial paleolimnological study of one colony in the Canadian High Arctic, “Tern Island” (Fig. 1A), with no local hunting; three nesting islands in Digges Sound, Hudson Strait southwest of the community of Ivujivik (~370 people) with low-to-moderate local hunting pressure; and six nesting islands southeast of the community of Cape Dorset in Hudson Strait (~1,450 people) with high local hunting pressure (Fig. 1B). These islands do not support large numbers of other bird species because they are flat, and most marine birds nest on cliffs, whereas eiders are the predominant ground-nesting marine bird in the Canadian Arctic. Tern Island (75°49' N, 96°20') is distinguished from the other islands due to its remote location in the High Arctic and inaccessibility by sea canoe. At this site, a unique set of circumstances has led to the segregation of Arctic tern (*Sterna paradisaea*) and eider colonies into separate drainage basins of two ponds (~1 km apart), which have distinct water chemistry and sediment geochemistry reflecting the seabird nesting in its catchment (18). For example, the Tern Pond sediment record has $\delta^{15}\text{N}$ values that are ~5% greater than in the

Eider Pond sediment record, which may be due to the higher trophic level of Arctic terns relative to common eiders (18).

Overall, across all study islands, eiders use freshwater ponds to drink during summertime incubation (10), and a positive relationship exists between breeding success and distance to the nearest pond (19, 20). Thus, islands supporting ponds are attractive breeding sites, and nesting eiders are observed concentrated around an island's main pond such that vegetation coverage and soil depth are greatest around an island's pond and decrease with increasing distance from pond margins (11). Once female eiders reach these breeding grounds (displaying high philopatry) and commence incubation, they remain on the nest 99.8% of the time (21), losing ~45% of their body mass over ~24 d (22). Waste products released from the nesting colonies become archived in pond sediments, which serve as historical records of seaduck densities on the island (1, 23).

Results

Sediment Chronologies for Dated Cores. Profiles of the ^{210}Pb activity trends for sediment cores CD135, CD044, and CD056 followed a classic exponential decline with increasing depth, with highest initial ^{210}Pb activity levels measured in CD044 (~1,000 Bq/kg) (SI Appendix, Fig. S1). Several of the sediment cores (CD045, CD114) showed greater fluctuation in initial ^{210}Pb activity levels with some plateaus in the first few centimeters (DS003, DS012), but all of the cores still exhibited a clear ^{210}Pb decay (SI Appendix, Fig. S1). The shallow nature of some of our ponds, coupled with bird activity, may have contributed to some modest sediment mixing. Some deeper ponds, namely CD045, CD056, and CD054, have distinct peaks in the artificial radionuclide ^{137}Cs , which align well with ~1960 (peak of atmospheric nuclear weapons testing), as inferred by Constant Rate of Supply (CRS) models based on ^{210}Pb activity (SI Appendix, Fig. S1). However, vertical transport of ^{137}Cs seems to have occurred to some extent in most cores. This process is known to occur at some sites due to net downward and upward molecular diffusion and adsorption, recycling of sedimentary ^{137}Cs in the water column, and delayed input from the watershed (24).

Extrapolation of the resulting ^{210}Pb chronologies to the base of the sediment cores indicates that the Cape Dorset sediment records capture longer time periods, ~160 to ~400 y, compared with the Digges Sound cores that extend back ~120 to ~210 y before present (B.P.). Although our equations used to extend the dates beyond the limit of ^{210}Pb dating had strong goodness-of-fit (SI Appendix, Table S3), these may result in overestimations of sedimentation rates (25). Here, we use extrapolated dates to provide a best estimate of the time period encompassed by the sediment cores and provide a complete history for eider abundance on all islands. However, we acknowledge that dates extrapolated beyond ~1850 should be cautiously interpreted.

Stable Nitrogen Isotopes in Guano and Sediments. The mean $\delta^{15}\text{N}$ of fresh (i.e., not weathered) common eider guano collected from eastern Hudson Strait was 10.1‰ ($n = 11$) (11, 26), corresponding to the mean $\delta^{15}\text{N}$ in many of our sediment records. A comparison of our study sites with published sediment records of $\delta^{15}\text{N}$ from coastal sites along Hudson Strait with no bird colonies within the pond catchment demonstrates that the $\delta^{15}\text{N}$ of eider ponds is enriched by a mean of ~3.6–7.3% and shows greater variability over the last several hundred years (SI Appendix, Fig. S2). The closest sediment cores collected on Digges Island (~40 km north of Digges Sound eider islands) (27) receiving no seabird inputs (between 900 and 1,900 km from a seabird colony and ~200 meters above sea level) have average $\delta^{15}\text{N}$ values (across ~27 sedimentary core intervals) of $4.2 \pm 0.09\text{‰}$ (DI04) and $6.0 \pm 0.08\text{‰}$ (DI05) (27). Two other coastal reference ponds on southern Baffin Island near Kimmirut (~250 km east of CD135, Fig. 1B) also have low and stable $\delta^{15}\text{N}$, $2.2 \pm 0.3\text{‰}$ for

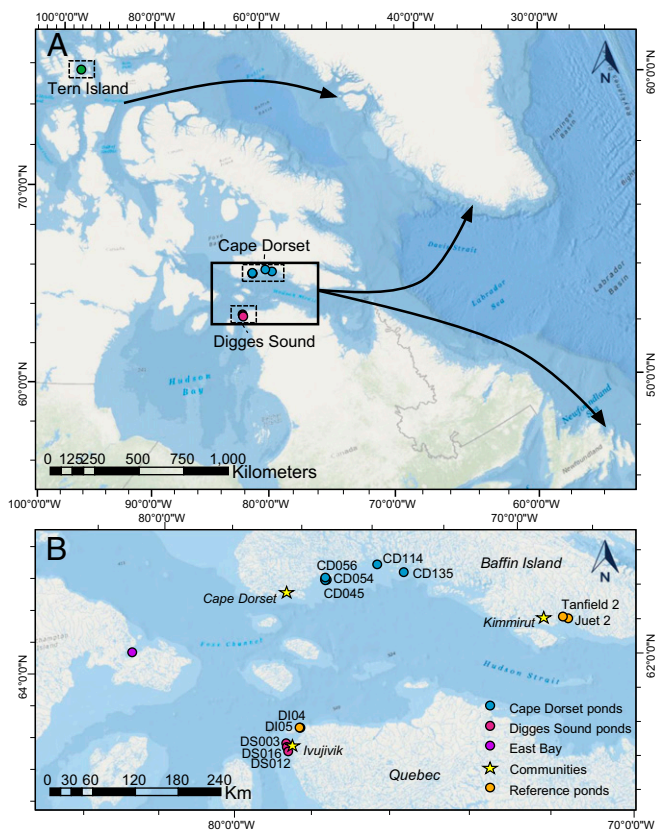


Fig. 1. Subarctic common eider nesting sampling islands and autumn migratory routes. (A) Tern Island [unofficial name, 75°50' N, 96°20' W; core published in Michelutti et al. (18)] in the High Arctic and the main study region in Hudson Strait highlighted within a box. Solid arrows identify the general northern common eider autumn migration routes to West Greenland and the coast of Newfoundland in winter (11, 12). (B) Study islands with common eider nesting colonies in Digges Sound southwest of Ivujivik (islands starting with “DS”) and islands southwest of Baffin Island, Hudson Strait near Cape Dorset (islands starting with “CD”).

Juet-2 and $3.8 \pm 0.2\text{‰}$ for Tanfield-2 (28). For these four reference ponds, the $\delta^{15}\text{N}$ was highly stable over hundreds of years and demonstrated no similar directional change between cores (*SI Appendix, Fig. S2*). Eider ponds exhibited more variable $\delta^{15}\text{N}$ profiles than nonbird ponds (average SDs = 0.88 and 0.35, respectively) (Fig. 2 and *SI Appendix, Fig. S2*), demonstrating that $\delta^{15}\text{N}$ values varied little in the absence of common eiders. Hence, we attribute the higher $\delta^{15}\text{N}$ values in our study pond sediments to an influx of ^{15}N -enriched eider guano, reflecting an eider's primary diet of marine bivalves.

Temporal Trends in $\delta^{15}\text{N}$. Eider pond sediment profiles showed enriched $\delta^{15}\text{N}$ values (relative to Hudson Strait sediment cores with no marine bird colonies within their catchments) (27, 28) from the base of the cores to the present, indicating that the eiders have nested on the islands for the time represented by the sedimentary records, ranging between ~ 115 and ~ 400 y B.P. (Fig. 2 and *SI Appendix, Fig. S1*). The two longest records (CD135, CD054) show a continuous gradual decline in $\delta^{15}\text{N}$ from ~ 1620 to the present (-3.2 and -6.2‰ , respectively), whereas the historical sedimentary $\delta^{15}\text{N}$ for three islands (CD044, CD045, CD056) peaks at the turn of 20th century until ~ 1930 and then declines to the present (-3.8 , -2.1 , and -2.8‰ , respectively) (Fig. 2). CD114 sedimentary $\delta^{15}\text{N}$ peaks at ~ 1900 and then declines $\sim 1\text{‰}$ to 1916, where it stabilizes for the rest of the sediment core. Fluctuations in $\delta^{15}\text{N}$ in the sedimentary records from Digges Sound, with lower local hunting pressure, are less variable than the islands supporting

larger eider colonies and greater local hunting pressure near Cape Dorset (Fig. 2). DS003 shows stable $\delta^{15}\text{N}$ from ~ 1800 to the present ($7.8 \pm 0.26\text{‰}$, greatest change -0.86‰), and the $\delta^{15}\text{N}$ of DS012 gradually increases from the base of the record at 1900–2015 ($8.8 \pm 0.43\text{‰}$). From ~ 1950 –2000, the $\delta^{15}\text{N}$ for DS016 is on average 1‰ lower than from ~ 1870 to 1926. The core from Tern Island in the High Arctic (18) recorded a relatively complacent profile of $\delta^{15}\text{N}$ over the past ~ 200 y, $5.4 \pm 0.63\text{‰}$ (Fig. 2).

Sterols in Eider Guano. Eider guano samples ($n = 3$) were composed of 95% cholesterol ($55.3 \pm 9.0 \mu\text{g/g}$ dry weight), 0.27% sitosterol ($0.29 \pm 0.04 \mu\text{g/g}$ d.w.), 2.28% coprostanol ($1.74 \pm 0.92 \mu\text{g/g}$ d.w.), and 1.44% epicoprostanol ($1.04 \pm 0.53 \mu\text{g/g}$ d.w.) of the total sterol concentrations, corroborating sterol analysis of guano from other seabirds (e.g., ref. 9). Thus, we conclude that the amount of cholesterol entering the ponds relative to the plant sterol, sitosterol, is a good proxy for tracking eider presence and abundance over time, as shown for other bird colonies (1, 9). These low-lying off-shore Arctic islands are free of cliff-nesting seabirds and large animals (e.g., Arctic fox, caribou) that would deposit cholesterol directly into the pond or its catchment, although polar bears (*Ursus maritimus*) occasionally visit the islands to consume eggs (29).

Temporal Trends in the Seabird Sterol Index. Sedimentary sterols indicated declining eider numbers on subarctic Hudson Strait islands, tracked using the seabird sterol ratio (Fig. 3). Declining trends in sedimentary $\delta^{15}\text{N}$ values concurrent with declining seabird sterol ratios further corroborate our interpretation of declining eider numbers at these locations. Like $\delta^{15}\text{N}$, the seabird ratio on islands CD135 and CD054 records the largest decline over time (-0.62 and -0.45 , respectively), and CD044, CD056, and CD114 demonstrate moderate declines from maximum ratios in the late 1800s to minimum ratios in the mid-20th century (-0.31 , -0.33 , and -0.25 , respectively). The seabird ratio for CD045 suggests increasing bird presence ($+0.25$) with a small difference in mean seabird ratio from the 1800s (~ 0.38) to the mid-1900s (~ 0.43). Ponds on islands in Digges Sound demonstrate smaller declines in the seabird ratio through the mid-20th century than on seabird islands near Cape Dorset with higher local hunting pressure. Similar to its stable $\delta^{15}\text{N}$ record, the sterol seabird ratio from island DS003 also falls outside the regional trend for this proxy, showing an overall increase through time ($+0.29$) with a small decline from 1960 to 1999 (Fig. 3). The DS016 ratio dipped from a ratio of ~ 0.60 to 0.35 in 1949 and then increased back to ~ 0.60 in the late 1980s. The seabird sterol ratio at Tern Island increased from 0.23 at the base of the record (~ 1830) to 0.73 in 2000, with a short increase and decline again of ~ 0.20 during the late 19th century. Sediment cores from ponds with historically high local hunting pressure on eiders, like those near Cape Dorset, have the greatest fluctuations in our sedimentary proxies over time, demonstrating significant correlations between the seabird sterol index and $\delta^{15}\text{N}$ values (*SI Appendix, Table S4*).

Discussion

The $\delta^{15}\text{N}$ and seabird sterol index track a general long-term decline in eider inputs and hence local populations in the early 20th century across the Hudson Strait colonies. Not surprisingly, some cores tracked stronger seabird enrichment patterns than others, and a few showed some divergence in $\delta^{15}\text{N}$ and sterol proxies of seabird influence (*SI Appendix, Table S4*).

An eider population decline in the early 20th century may be explained by two significant anthropogenic stressors that were pronounced near Cape Dorset at this time. First, relocation of nomadic Inuit to create large communities like Cape Dorset (30) greatly increased harvest pressure (of adults and feather down) on some local eider colonies (e.g., CD054, CD044, CD056, CD045) and may have caused eiders to move to new islands (31). However, for the broad region, juxtaposing known sales and distribution of

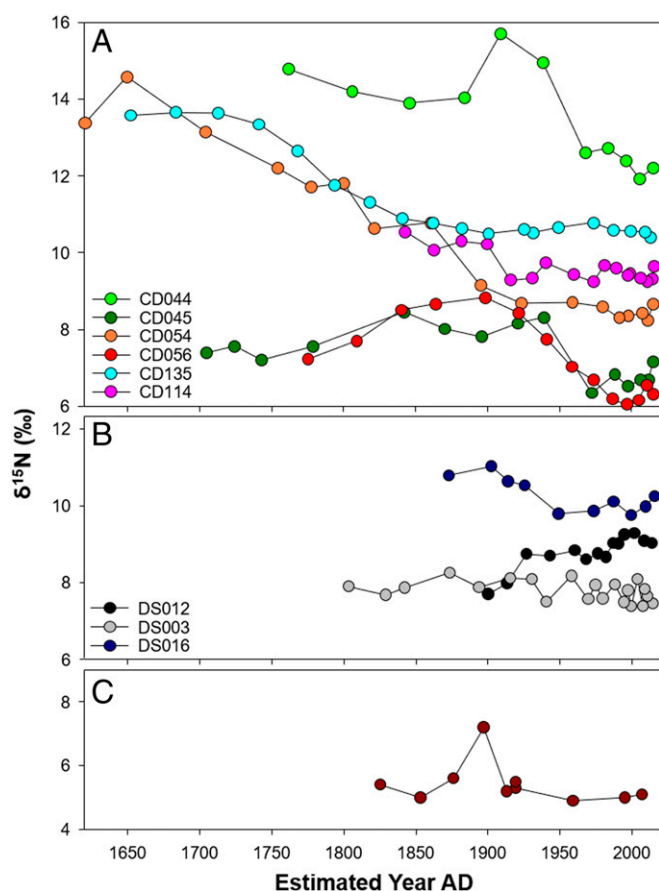


Fig. 2. Historical sedimentary stable nitrogen isotope ratios at individual eider nesting islands. Changes in sedimentary $\delta^{15}\text{N}$ profiles for common eider breeding colony islands located at (A) Cape Dorset (CD), southwest of Baffin Island in Hudson Strait; (B) Ivujivik, Digges Sound (DS), Hudson Strait; and (C) Tern Island near Bathurst Island in the High Arctic.

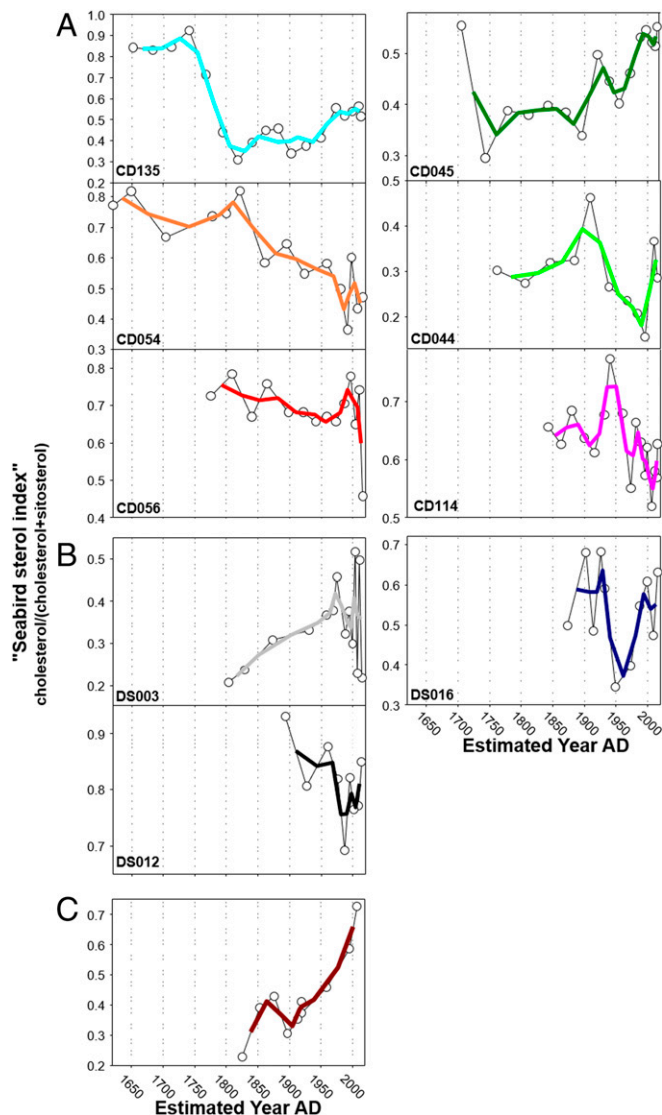


Fig. 3. Historical sterol seabird index across eider nesting islands. This index infers seabird presence and inputs to a pond over time, calculated as cholesterol/(cholesterol + sitosterol), with higher ratios suggesting a greater seaduck influence on an island. The thick, darker lines represent a 2-y moving average, and the colors correspond to the same sediment cores graphed in Fig. 2. Each panel represents an island with a common eider breeding colony which are located: (A) off the southwestern coast of Baffin Island in Hudson Strait near the community of Cape Dorset (CD); (B) Digges Sound (DS), Hudson Strait southwest of the community of Ivujivik; and (C) Tern Island near Bathurst Island in the High Arctic.

firearms (Fig. 4) against our eider population proxies suggests that eider colonies were much reduced in the periods immediately following the introduction of guns and their widespread use to hunt eiders wintering in West Greenland in the early to mid-20th century. Historically, a large factor in adult survival of eiders in North America and elsewhere has been hunting pressure by humans (14). Although comprehensive population records are sparse, there is a common consensus (based on winter counts in Greenland) that the northern common eider population suffered a major decline in the mid- to late-20th century due to overharvest (17). During eider down collection from 1822 to 1831, surveys estimated a minimum of 110,000 nests in West Greenland; however, by the late 20th century, local nesting numbers had been reduced to ~15,000 (17). The veracity of these declining numbers is further corroborated by archival records of bird-skin carpets and clothes, suggesting that

the annual harvest at the turn of the 19th century was estimated to be a minimum of 150,000 eiders (15, 32). Our paleolimnological records support the conclusion that eiders in the Canadian subarctic experienced a major population decline in the mid-20th century due to unsustainable overharvest by humans in West Greenland (14), and perhaps locally in Arctic Canada as well. Additionally, traditional knowledge suggests that there is no evidence of disease such as avian cholera contributing to these declines through the 20th century (33).

Overall, we propose a scenario where, in the early 1800s, Greenlanders likely resided closer to eider colonies, exploiting the abundance of resources at these islands (e.g., down, eggs, meat, and pelts). Over time, as breeding eider numbers dwindled, Greenlanders reportedly transitioned from hunting local breeding eiders to harvesting eiders that winter there, most of which originated from Arctic Canada by the mid-20th century. Concomitant with this transition was the increased availability of firearms, as measured from sales and trades in West Greenland from 1860 to 1955, as well as motorized boats (34, 35) (Fig. 4) and refrigeration technology. We suggest that technical advancements of hunting practices, a rapidly growing population of hunters in southwest Greenland (Fig. 4), and the development of a commercial harvest enabled the harvest of substantially more eiders during winter.

At a local scale, the precipitous drop in inferred eider numbers since the ~1950s at four sites ~40 km east of Cape Dorset (CD054, CD044, CD056, CD045) was concurrent with relocation of Inuit to the new community of Cape Dorset. We suspect that eider colonies experienced the same fate as those in Greenland—intense local harvest pressure for eider down and adult meat—contributing to population declines at these sites (32), in addition to the broader regional pressure on these eiders due to harvest at their wintering sites in Greenland and Atlantic Canada. More recent survey data suggest that colonies are increasing with a relaxation of local pressure (29).

In contrast, the eider nesting colony on isolated Tern Island (High Arctic Canada) demonstrates stable $\delta^{15}\text{N}$ over the past ~200 y (Fig. 2C) and a trend in the seabird ratio far different from Hudson Strait eider colonies (Fig. 3C). These results suggest that the local population at Tern Island rapidly increased through the 20th century (with a small dip between ~1900 and 1915). Given the more northerly and isolated location of this island relative to colonies in Hudson Strait (+11°N), eiders from Tern Island may winter in more northern open-water areas in West Greenland (e.g., north of Nuuk) to reduce their migration distance (12) (Fig. 14). At these northern locations, away from the main human settlement of Nuuk, there has historically been less hunting pressure (12). In addition, there has been no hunting pressure on the eider colony on Tern Island during the summer because of its remoteness from Inuit communities that

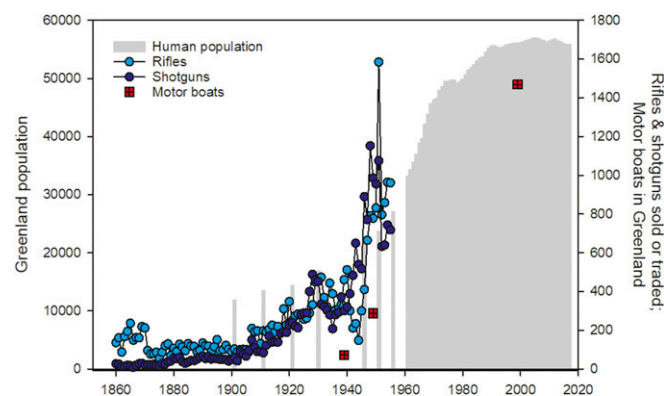


Fig. 4. Greenland population (1901, 1911, 1921, 1930, 1946, 1951, 1956, 1961–2017), shotguns and rifles traded or sold in West Greenland (1860–1955) (34), and three annual records for outboard motor sales in Greenland (1939, 1949, 1999) (35).

were only established in the 1950s (30). With evidence that eiders display philopatry to wintering locations (36), eiders that consistently overwintered in a refuge with low hunting pressure may have escaped island population declines in the 20th century.

Sediment cores from islands CD135 and CD054 record proxies that indicate substantial declines in local nesting eider population before an increase in 20th-century hunting pressure. These declines, which commenced during the 1600s, do not match known harvest records, and may represent the influence of heavier sea ice (iced-over feeding areas, easier access to mammalian predators) following a period of reduced ice cover during the Little Ice Age (37, 38).

Different attributes of an eider's diet, catchment processes, and autochthonous pond dynamics may contribute to a change in the delivery and taphonomy of our sedimentary record of stable nitrogen isotopes and sterols. Overall, the mean $\delta^{15}\text{N}$ of common eider guano collected from eastern Hudson Strait (10.1‰) (11) corresponds to the mean $\delta^{15}\text{N}$ in the majority of our sediment records. However, slightly lower $\delta^{15}\text{N}$ values occur in CD045 and CD056, which may reflect the relatively larger catchments surrounding these ponds leading to a possible dilution of the $\delta^{15}\text{N}$ from their eider colonies. In comparison, sedimentary $\delta^{15}\text{N}$ values were elevated relative to eider guano across a few ponds (e.g., CD044 and CD135 values approach $\sim 15\%$). These spatial fluctuations in sedimentary $\delta^{15}\text{N}$ may also reflect a variation in eider diet obtained along migration routes, which was measured in blood isotopic composition of individual eiders sampled during the prebreeding period at East Bay, mean $\delta^{15}\text{N}$ of 12.4‰, with minimum and maximum values of 10.6 and 14.3‰, respectively (13). However, these elevated sedimentary $\delta^{15}\text{N}$ values may also indicate catchment volatilization of ammonia in guano (39) and possibly denitrification occurring within the ponds. The lighter ^{14}N isotope volatilizes faster than the heavier ^{15}N isotope following N release by organic decomposition, leading to higher proportions of ^{15}N in residual guano than in bird tissues (39). Given that organic sediment proxies may be diagenetically modified, we compare $\delta^{15}\text{N}$ and sterols in a multiproxy comparison with corroborating inferences of declining eider populations through the 20th century.

A changing food source for common eiders may contribute to a shifting sedimentary $\delta^{15}\text{N}$ and seabird sterol ratio through time. However, for this to explain the $\delta^{15}\text{N}$ trends across Hudson Strait islands, eiders would have had to consume food higher in trophic position, potentially resulting in guano with greater $\delta^{15}\text{N}$ entering ponds early in the sediment records. Across several northern locations (e.g., ref. 40), including the long-term field station in northern Hudson Bay, close to our sampling islands, blue mussels (*Mytilus edulis*; $\delta^{15}\text{N} \sim 8.5\%$) are the dominant prey of eiders (41). In Hudson Bay eiders, other bivalves have also been noted in their diet including *Serpipes* spp. ($\delta^{15}\text{N} \sim 10\text{--}11\%$), as well as amphipods (*Gammarus* spp., $\delta^{15}\text{N} \sim 8.5\%$) and gastropods (*Acmea testudinalis*, $\delta^{15}\text{N} \sim 10.5\%$) (41). Between these prey items, a switch from a dominance of *Serpipes* spp. and/or gastropods to blue mussels could have resulted in a decline in ^{15}N concentration within guano. However, there is no documentation of a long-term, rather than seasonal, switch of this kind occurring for eiders. Sea ice is known to affect foraging conditions and prey selection by eiders (42), with late ice breakup leading to eiders consuming greater amphipods as they cannot access deeper mussel-rich beds (41). Nonetheless, amphipods have similar $\delta^{15}\text{N}$ signatures to blue mussels, so this dietary shift should not result in a change in the $\delta^{15}\text{N}$ of eider guano.

Concurrently, it is unlikely that a changing prey source would affect the cholesterol content of eider guano. At the Tern Island eider colony where there has been less or no hunting pressure, the $\delta^{15}\text{N}$ profile is complacent through time, suggesting no changing food source for these eiders. In addition to eiders, cholesterol has been identified as the dominant sterol found in the stomach bile and guano of other avian secondary consumers,

including northern fulmar (9), cattle egret (*Bubulcus ibis*) and heron (43), and gulls (when anthropogenic food sources are not present) (1, 44). The dominance of cholesterol in the guano of these birds reflects a balance between dietary intake, metabolic production of sterols, and the biota resident in the digestive tract (7, 45). It is true that herbaceous birds have a greater sitosterol concentration in their guano as seen for livestock ducks (45). However, even birds that have a cholesterol-free diet will excrete some cholesterol in their feces, which is biosynthesized by the intestinal wall and then secreted into the intestinal lumen and either reabsorbed or excreted in the feces (45). Seaducks consume a diet high in cholesterol content [the lipid content of mussels is composed of $\sim 50\%$ cholesterol and less than 4% sitosterol (46)], as well as undergo metabolic production of cholesterol yielding high cholesterol abundances in their feces. Therefore, previous publications that have utilized the sterol ratio (1, 9) have established the main premises for its use such that it works best in an environment where birds are the dominant animal within a pond's catchment, where cholesterol is the dominant and abundant sterol found in a bird's guano, and where terrestrial plant sources of sitosterol are likely to be smaller due to less vegetation in the lake's catchment. These three conditions are clearly met for our study sites and study species.

We use a multiproxy approach and compare sterols with $\delta^{15}\text{N}$ to show that independent proxies corroborate the concurrent declines in eider populations in these locations. The $\delta^{15}\text{N}$ and specific sterols, such as cholesterol, are typically not otherwise correlated to each other except when both track seabird inputs (*SI Appendix, Table S4*). As discussed, each proxy has different processes that contribute to its production in guano and eventual incorporation in pond sediments; however, when used in tandem, similar trends between the two proxies corroborate a single changing source to these isolated ponds over time.

From the 2000s onward, the seabird ratio at several eider nesting sites, including CD044, DS012, and DS016, suggests a recovery of eider nesting populations to pre-20th century levels (Fig. 3). Given that eiders are long-lived and faithful to both their overwintering and breeding sites (10, 36), our findings suggest that new harvest regulations instituted since 2002 may be having the desired positive effect on eider populations and that this recovery is registered in guano deposition and related pond sediments. Since hunting regulations were instated in 2002 (17), including a reduced length of the hunting season from October 1st to May 31st in Southwest Greenland (wintering area) and from August 16th to May 31st north of the wintering area to October 15th to February 15th, the western Greenland breeding population has increased by 12% per year (47), reaching close to 100,000 breeding pairs (17). Despite these promising results, we suggest that this trend in sedimentary proxies be re-examined in a decade.

Conclusions

Our sediment core data indicate that harvesting practices through the 20th century in West Greenland and northern Canada had deleterious impacts on eiders nesting on remote offshore islands in the Canadian Arctic. With eider populations now possibly an order of magnitude lower than historical levels, these results continue to emphasize the need for late-20th century hunting restrictions. Our multicentury perspectives indicate that the current monitoring window for many sensitive seabird species may be inadequate for making key conservation decisions and reinforce the value of reconstructing long-term seabird dynamics to better understand drivers that contribute to population instability and possibly collapse.

Materials and Methods

Sediment Collection, Chronologies, and Stable Nitrogen Isotopic Analyses. Sediment cores were collected in 2014 and 2015 from nine ponds on eider nesting islands in western Hudson Strait of the Canadian subarctic (*SI Appendix, Table S1*) and extruded into 0.5-cm sections in the field (Fig. 1 and *SI Appendix, Supplementary Methods*). To establish a core chronology, freeze-dried

sediments were analyzed for radioisotopes (^{210}Pb , ^{214}Pb , ^{137}Cs) at Queen's University (Kingston, ON, Canada) using an Ortec High Purity Germanium Gamma Spectrometer (Oak Ridge) (SI Appendix, Fig. S1). All sediment chronologies were calculated using the CRS model (48). The Tern Island pond core chronology was previously published (18) and calculated using a Constant Initial Concentration model. Second-order polynomial equations were fitted through the CRS dates to infer dates beyond the range of ^{210}Pb activity (SI Appendix, Table S3).

Samples and standards were analyzed for $\delta^{15}\text{N}$ with an elemental analyzer (Isotope Cube; Elementar) interfaced to an isotope ratio mass spectrometer (Delta Advantage; Thermo). Amounts needed for the isotopic analyses were based on the results of the %N elemental analysis. All analyses were performed at the G. G. Hatch Stable Isotope Lab at the University of Ottawa (Ottawa, ON, Canada). Our $\delta^{15}\text{N}$ data were reported using delta (δ) notation and expressed in parts per thousand (‰), where $\delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$, where R_{sample} is the ratio of $^{15}\text{N}/^{14}\text{N}$ in the sample and R_{standard} is the isotopic ratio of N_2 in air. Analytical precision of standards was $\pm 0.2\%$, well below the intra- and interpond variation in $\delta^{15}\text{N}$. Nitrogen isotopes were corrected to internal standards calibrated to International standards IAEA-N1 (0.4%), IAEA-N2 (20.3%), USGS-40 (-4.52%), and USGS-41 (47.57%).

Sterol/Stanol Analyses and Seabird Ratios. Cholesterol and sitosterol were extracted from freeze-dried sediments and eider guano. Analytical methods

for analyzing sterols and stanols in sediments and guano were performed at the University of Ottawa using methods based on Cheng et al. (9) and detailed in SI Appendix, Supplementary Methods, along with detection limits (SI Appendix, Table S2) and quality assurance/quality control measures.

A seabird ratio established by Cheng et al. (9)—cholesterol/(cholesterol + sitosterol) (where cholesterol is the dominant sterol in eider guano, and sitosterol is the dominant phytosterol in plant tissues)—was calculated as an independent, complementary means to $\delta^{15}\text{N}$ for tracking common eider fecal inputs to lake sediments over time.

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