Ecological changes on SG̲ang Gwaay over the last millennium: uncovering forest changes and avian activity with respect to human settlement and invasive species

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Abstract

Haida Gwaii (British Columbia) is an archipelago of immense cultural importance to the Haida people and ecological importance for breeding seabirds. In the past millennia, the islands were exposed to multiple stressors (e.g., Indigenous use of the land, European colonisation, invasive species introduction), thus its ecosystems are likely to have changed greatly; however, historical ecosystem trends are unknown and drivers of change difficult to unveil with contemporary field monitoring programs alone. Archeological and anthropological accounts provide short time-scale knowledge about past vegetation and seabird monitoring programs date back to the ~1980s. Thus, understanding long-term cycles of seabird population decline and increase is difficult with these short time-scale and punctual data. This thesis addresses the lack of knowledge regarding ecosystem changes over millennia using a multi-proxy paleoecological approach to reconstruct past ecosystems of SG̲ang Gwaay, Haida Gwaii and uncover vegetation and wildlife changes as they relate to anthropogenic activities at the former Haida settlement of Nintints (UNESCO world heritage site). With a dated sediment core (based on ^{210}Pb and ^{14}C), our results revealed vegetation and seabird changes occurring over ~1300 years. After the expansion of the Haida population at Ninstints c.a. 1235 CE, terrestrial vegetation declines, particularly with increased harvest of Western red cedar. This decline in vegetation is reflected by a decrease in plant sterols and stanols (sitosterol, stigmastanol), a decrease in lake-water TOC, C/N and δ^{13}C values. This decrease in terrestrial vegetation persists for ~800 years following human settlement expansion and is followed by an increase in chlorophyll *a*, increase in alagal sterols (campesterol, sitosterol/campesterol), increase pond microbial activity (shift in sitosterol/stigmastanol), and changes in diatom assemblages. Dominant diatom taxa post settlement expansion are indicative of increased lake-water turbulence, increased light availability, and a more acidic pH. Rhinoceros auklets (*Cerorhinca monocerata*) were present on SG̲ang Gwaay throughout the ~1300 year time period as demonstrated by sedDNA PCR, and ornithogenic proxies (trace-metals, δ^{15}N values). These proxies suggest a population decline after European contact and an additional significant period of decline when Keen's mice (*Peromyscus keeni*), a native predator, was consistently detected by PCR. Our results demonstrate that: (1) small-scale tree harvest had broader impacts for geochemical cycles and ecosystem primary productivity that can persist for centuries after initial impact; (2) centennial wildlife population declines might not be captured shorter term population trends inferred through monitoring over decades (e.g., surveys).

Co-Authorship

Chapter 2 was co-authored by Heather L. Major, Mark J. Hipfner, Kathryn E. Hargan. This chapter represents original work completed as part of my MSc thesis. This chapter is a review of the last two decades of invasive mammal management as it relates to Haida Gwaii's burrowing seabird species. The objectives of this chapter were to bring forward seabird population status in peer-review literature as much of the data is only available in governmental reports, and assess whether two decades of management were successful for burrowing seabird conservation. Heather contributed with original work from her PhD thesis and I conceived and wrote the majority of the manuscript. I would like to acknowledge the contribution of Dr. Ian Jones and Dr. Anthony Gaston in reviewing and providing ideas for this manuscript.

Chapter 3 was co-authored by Inmaculada Álvarez-Manzaneda, Evan Langille, Dilini Abeyrama, Carsten Meyer-Jacob, Neal Michelutti, Nadine Wilson, Mark J. Hipfner, Christopher Grooms, Theresa Burg, John P. Smol, and Kathryn E. Hargan. This chapter represents original work completed as part of my MSc thesis. I extracted six sediment cores from SG̲ang Gwaay (Haida Gwaii, B.C.) and used them to establish chronologies, process and analyse sediment samples for: sterols and stanols, sedDNA, stable isotopes, and trace-metals. Sedimentary chlorophyll *a* and diatoms were processed by Christopher Grooms and Inmaculada Álvarez-Manzaneda (with training from Neal Michelutti) respectively. Carsten Meyer-Jacob provided a total organic carbon reconstruction; Dilini Abeyrama and Theresa Burg led PCRs for invasive species; Evan Langille assisted with sterols and stanols; Nadine Wilson provided logistical and financial support; Mark J. Hipfner provided site coordination and ornithological expertise.

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Abbreviations

AMS – Accelerator mass spectrometry

B.C. – British Columbia

Bchron– B chronology

ca. – circa

CE – Common era

CFCS –constant flux constant sedimentation

Chl *a* – Chlorophyll *a*

C/N – Carbon to nitrogen ratio

CONISS – Constrained incremental sum of squares

COSEWIC– Committee on the Status of Endangered Wildlife in Canada

CRS –Constant rate of supply

CWS– Canadian Wildlife Service

DCM– Dichloromethane

DO–Dissolved oxygen

DOC–Dissolved organic carbon

DW– Dry weight

ddPCR–droplet digital polymerase chain reaction

ECCC– Environment and Climate Change Canada

sedDNA– Sedimentary DNA

e.g. – exempli gratia; meaning “for example”

GAM– Generalized additive model

GC-MS– Gas chromatography mass spectrometry

GIS – Geographic Information System

HCl – Hydrochloric acid

IUCN – International Union for Conservation of Nature

LIA–Little Ice Age

LOESS– Locally estimated scatterplot smoothing

OC– Organic carbon

OM–Organic matter

PCA– Principal component analysis

PCR–Polymerase chain reaction

qPCR– quantitative polymerase chain reaction

SST–Sea surface temperature or springtime surface temperature

TOC – Total organic carbon

UNESCO–United Nations Educational, Scientific and Cultural Organiztion

VNIRS – Visible-near infrared spectroscopy

VRS – Visible range spectroscopy

%C– percent carbon

%N– percent nitrogen

^{137}Cs – Cesium-137

^{14}C – Carbon-14

^{210}Pb – Lead-210

CHAPTER 1

Introduction and Literature Review

1.1 General Introduction

1.1.1 Contemporary change and long-term ecosystem changes

Canadian coastal ecosystems are facing rapidly changing conditions driven by climate change and anthropogenic disturbances (e.g., habitat destruction, pollution, invasive species) (Hutchings et al. 2020). Biodiversity in these coastal systems is changing rapidly and stewardship for diminishing populations can be improved (Gonzalez et al. 2016). However, in some instances multiple ecosystem stressors make it difficult to pin-point drivers of change and thereby establish management priorities. In addition to multiple drivers of ecosystem changes, our limited knowledge of the past prevents our modern-day understanding of what historical ecosystem trends might be, and thus our management plans might not target the right objectives to achieve restoration (Willis and Birks 2006). For instance seabirds can follow natural fluctuations in their population cycles that short-term monitoring efforts cannot capture, thus implementing management based on short-term observations can lead to erroneous conservation targets (Duda et al. 2020a). Similarly, short-term vegetation changes cannot be used to estimate forest resilience in the context of contemporary climate change (Morel and Nogué 2019). Humans engineered ecosystems for millennia, yet in many cases the impacts of ancient civilizations are unknown and therefore our present-day understanding of biodiversity does not acknowledge cumulative impacts prior to monitoring (Boivin et al. 2016).

The impacts of ancient civilizations on ecosystems can be difficult to unveil, but landscape changes are revealed in artifacts, historical records of human activities, and paleolimnological records. For example, in Jordan, human settlements in epipaleolithic increased vegetation around settlements, and sedentarization transported weeds to new places (Cordova 2007). A sediment core from California revealed vegetation changes from human ignited fires 3000 years ago and increased forest clearing after European contact (Cowart and Bryne 2013). Holocene charcoal records from the Mediterranean region reveal that some species (e.g., green oaks) thought to be resilient to burns on short-term time scales, do not exhibit the same resilience over decadal and centennial time scales (Colombaroli and Verschuren 2010). In other cases, the use of ecosystems beyond carrying capacity led to collapse. Palm tree forest clearings in Rapa Nui led to their extirpation in the 17-18th century, along with the disappearance of the forest middle-storey (Horrocks et al. 2015; Wozniak 2022). Paleoecological records reveal that short-term vegetation changes resulting from land use have broader implications for the carbon cycle, altering regional budgets (Kastowski, Hindered and Vecsei 2011; McGrowan et al. 2016). The carbon cycle is a complex process with influences from biotia (e.g., changes in primary productivity and vegetation), abiotic processes (e.g., geological and athmospheric exchanges and reactions) and human factors (e.g., combustion, land use changes and subsequent changes in weathering and erosion). Thus, understanding changes in the long-term carbon record can provide insight about human and naturally induced environmental change (Hillman, Abbott, and Yu 2018). Multi-proxy paleolimnological records such as lake-water total organic carbon (TOC), organic carbon, stable isotopes provide a window on to the past carbon record while other proxies such as sterols and stanols and chlorphyll *a* reveal sources of carbon to lakes (terrestrial, aquatic) and provide information about primary productivity. With this combination of provies we can understand ecosystem-level changes.

1.1.2 Haida Gwaii's ecosystems: contemporary and ancient civilization changes

Haida Gwaii is a remote archipelago of ~150 islands off the coast of British Columbia (B.C.) in the North Pacific (Moss 2008). The archipelago was first occupied by humans 13,000 years ago and remained isolated prior to European contact in the 18th century (Fedje and Mathewes 2005). Throughout time, the archipelago's ecosystem provided resources to the Kunghit Haida. However, after European contact the introduction of invasive species (e.g., rats, deer, raccoons, terrestrial and aquatic vegetation, invertebrates, fish) homogenized vegetation communities and caused the decline of seabirds and songbirds.This not only compromised the integrity of the ecosystems, but also threatened culturally important species (e.g., Western red cedar, yellow cedar) for the Haida (Sloan and Bartier 2004; Fedje and Mathewes 2005; Pojar 2008; Gaston 2010; chollet et al. 2015; Rodway, Campbell and Lemon 2019). Thus, invasive species are at the forefront of conservation concerns and management policies throughout the archipelago today (Sloan and Bartier 2004; Golumbia et al. 2008; Sjodin et al. 2020). Present-day anthropogenic activities were also identified as important threats to wildlife and vegetation composition on the archipelago and overall landscape alterations causing erosion and landslides (Pojar 2008). A striking example of logging activities' impact is the disappearance of old-growth forest, the breeding habitat of the marbled murrelet, a species on the IUCN red list (Bertram et al. 2015).

Although the impacts of present-day anthropogenic activities on Haida Gwaii's ecosystems are studied and targeted by management policies, historical impacts of humans on ecosystems are limited to invasive species research and little is known about how the Haida transformed the archipelago's ecosystems over millennia. Artifacts that are still standing today at former settlements in Haida Gwaii such as totem poles, and house foundations, are a testimony of the importance of the forest in Haida culture and civilization development (Turner 2020). Herein we are interested in uncovering the subtle and complex impacts of Haida land use on the carbon cycle of SG̲ang Gwaay (Haida Gwaii, B.C.) thus filling in the knowledge gap about historical ecosystem trends in Haida Gwaii .

1.1.3 Haida forest use and modern vegetation changes

Haida Gwaii formed after the last glaciation 10,000-13,000 years ago and during this last glacial episode, humans crossed to the archipelago through a narrow ice-free sheet bridging with Asia (Hayward 2012; Reimchem et al. 2005). The archipelago's coastline was occupied by humans and wildlife in the late Pleistocene as sea levels were rising (Reimchen, Bergstrom and Nosil 2005; Lacourse, Mathewes and Hebda 2007; Moss 2008). Settlements were occupied year round, although the Haida traveled to take seasonal advantage of marine and terrestrial resources. SG̲ang Gwaay ("Red Cod Island") was occupied by the Kunghit Haida since 360 CE making its Ninstints ("the one that is two") village site the southernmost, largest and longest occupied settlement (Acheson 1995). The village was occupied year round and population started expanding around ~1235 CE and today's archeological remains reveal 20 houses of an average floor area of 109.06±43.37 m^2 (Acheson 1995; Lacourse, Mathewes and Hebda 2007).

Western red cedar (*Thuja plicata*) was an essential resource for the Haida providing primary material for the cedar-plank houses, canoes, totem pole, clothing and other daily objects (e.g., ropes, baskets) (MacDonald 1983; Acheson 1995; Garibaldi and Turner 2004). Red cedars were harvested on land that belonged to the family needing the tree and although these harvest sites could be nearby the village sites, they were sometimes found on nearby islands. Thus, harvest was not always in proximity to villages (MacDonald 1983). The historical use of red cedar was tracked in the palynological record from SG̲ang Gwaay with a significant decrease in *T. plicata* pollen after ~950 CE (Lacourse, Mathewes and Hebda 2007). Despite this decrease in *T. plicata* pollen, western red cedars persisted in Haida Gwaii as the Haida harvested mature, large trees, and in some cases, if the entire tree was not needed, part of the bark was stripped from the tree. This practice can still be noted on some red cedars on SG̲ang Gwaay today (MacDonald 1983; Lacourse, Mathewes and Hebda 2007). Following European contact in the 18th century, activities at Ninstints diminished; the Haida population was highly affected by diseases and a smallpox epidemic ultimately led to the abandonment of the village in 1887-88 (Acheson 1995).

Lacourse, Mathewes and Hebda (2007) reported a pollen decline on SGang Gwaay related to the expansion of the former settlement at Ninstints in 1235 CE. The palynological record shows an increase in overall pollen post village abandonment; however, this brief increase is also followed by a decline persisting into modern times. A modern decrease in pollen on the island could be the result of black-tailed sitka deer (*Odocoileus hemionus sitkensis*) introduction in 1878 (Martin et al. 2010). Deer browsing homogenizes the forest understory and prevents the recruitment of red and yellow cedar (Stroh, Baltzinger and Martin 2008; Martin et al. 2010; Pojar 2008). Today, deer browsing combined with past harvest pressure prevent the regeneration of

Wester red cedar in old-growth forest (Stroh, Baltzinger and Martin 2008). On SG̲ang Gwaay a similar grazing pressure could be keeping Western Red cedar population low.

1.1.4 Haida Gwaii seabirds: current and historical threats

Haida Gwaii's isolation also contributed to a high number of endemic species being present on the island today. Perhaps one of the most important ecological roles of the archipelago is to provide habitat to 77 bird species and breeding grounds to 1.5 million birds, including 12 different seabird species, 9 of which are ground nesting-seabirds (Gaston and Masselink 1997; Golumbia 1999, Harfenist, Sloan and Bartier 2002; Gaston et al. 2008; Bellis et al. 2019). Haida Gwaii is the largest seabird breeding ground in B.C. and the most remote archipelago in the Pacific Northwest (Moss 2008).

A global decline in seabird populations has been observed since the 1950s (Paleczny et al. 2015) and surveying wildlife populations is costly and cannot be done often for remote areas, thus population baselines, or historical ecological knowledge, can be lacking. These limitations have been observed in Haida Gwaii, an ecosystem that changed in the last millennia, and for which historical ecological knowledge prior to the 20th century is missing. Researchers reported that permanent monitoring plots in Haida Gwaii did not detect broader seabird population declines recorded elsewhere in Haida Gwaii (Rodway and Lemon 2011).

Although the forest represents an important resource, marine life was equally dominant in Haida culture; salmon, herring, clams, and sea mammals were not only valuable food resources, but could also be traded post European contact (Fedje et al. 2005; Turner 2020). Zooarcheological records from Haida sites in Southeastern Alaska also demonstrate the use of seabirds (e.g., rhinoceros auklets, Cassin's auklets, tufted puffins, common murres) as a food resource through egg harvest and the consumption of adult birds and as cultural resources; skins provided material for clothing and bags, while beaks and feathers could be used for regalia and bones could be used for numerous purposes (Moss 2007). Although a detailed record of Haida use of seabird eggs on SG̱ang Gwaay is not available, the cultural harvest of eggs by Haida on the archipelago exists (Turner 2020).

1.1.5 Using paleoecology to complement modern-day conservation questions and historical ecosystem trends

Paleoecology — the ecology of the past — uses multidisciplinary tools, or proxies, to reconstruct vegetation changes and wildlife populations over geologic time thus overcoming the lack of long-term monitoring data and limitations of surveys. The concept of paleoecology first emerged when the British naturalist Edward Forbes described changes in benthic fauna occurring with shifts in barymethric zones and sediments, however the name "paleoecology" was truly established in the early 20th century with paleobotany studies (Wingard, Bernhardt and Wachnicka 2017).Starting in the 1970s through the 1990s, statistical, chronologic and biogeochemical methods emerged and allowed paleoecologists to model and interpret past environmental changes with statistical confidence and error. Today, ecological changes from the past are used to understand evolutionary processes and the connections between biotic and abiotic ecosystem processes (Watson et al. 2010; Wingard, Bernhardt and Wachnicka 2017). Thus, paleoecology fills in a knowledge gap about historical ecological trends.

Sediments at the bottom of water catchments, such as lakes and ponds, constitute a record of environmental and ecosystem change. A lake's catchment, through more or less constant sedimentation rates, captures biogeochemical signatures of humans, wildlife and plants, as well as changes from atmospheric deposition. It is therefore possible to track changes in these biogeochemical signatures to infer changes linked their biovectors (Duda et al. 2021). These environmental changes can be tracked through time with a well-established sediment core chronology, ranging from centuries to millennia, advanced by radioisotopic (^{14}C, ^{210}Pb, and ^{137}Cs) and other stratigraphic (e.g., pollen, tephra) methods (Burge et al. 2018) and, ultimately they help uncover ecological data over millennia.

Multi-proxy paleoecological studies are particularly relevant when trying to understand population dynamics of organisms that are difficult to survey because populations are dispersed, located in remote areas, or have several thousands of individuals (e.g., plants, wildlife in remote areas). For instance, a paleoecological study demonstrated that the population of northern common eiders (*Somateria mollissima*) in the Arctic declined in the 20th century after human settlement size increased in Greenland and increased firearm availability (Hargan et al. 2019). This decline of seaducks can be tracked in the sediment record with variations in stable-isotopes of nitrogen, sterol and stanols. Another multiproxy paleoecological study demonstrated that European settlements on Grand Colombier Island in the 19th century caused a disruption in the natural population cycles of Leach's storm-petrels (*Oceanodroma leucorhoa*). The study revealed that disturbances associated with human settlement (e.g., fishing activities, introduced species, habitat degradation) led the colony to be at only 16% of its carrying capacity today (Duda et al. 2020b). The paleoecological records of another storm-petrel colony on Baccalieu Island in the North Atlantic revealed that the population follows natural fluctuation cycles and that contemporary population levels, despite undergoing a decline cycle, were actually at its highest (Duda et al. 2020a).

Paleoecological records provide important, sought-out information about historical ecological trends, thresholds and resilience, climate change, biological invasions, and cultural landscapes (Burge, Edlund and Frisch 2017) at large temporal and demographic scales (i.e., several thousands of individuals) that could not be obtained in any experimental design. These ecological archives in sediments can help distinguish climate and anthropogenically driven changes in contemporary wildlife populations (Sun et al. 2013) and are a significant step forward in biological conservation, management, and restoration (Manzano et al. 2020). For instance, paleoecological records provide historical ecological information about forest vegetations and show how plant communities persist or disappear climatic patterns (Hunter et al. 1988; Lindblah et al. 2013). Such information can be used to prioritize the designation of conservation areas today.

In addition to providing long-term trends of population dynamics and pin-pointing causes of species declines and increases, paleolimnological techniques can be used to discriminate between factors of environmental change. For instance, paleolimnological techniques were used to untangle the sources of contamination of lakes. Stable isotope analysis demonstrated that salmon are biovectors that contribute to the contamination of lakes with the delivery of marine PCBs; however, two additional mechanisms contributing contaminants in lake sediments were also identified: atmosperhic deposition and scavenging (i.e., algal activity transfers contaminants from the water column to sediments) caused by increased aquatic production (Krummel et al. 2008; Stern et al. 2009; Blais, Rosen and Smol 2015; Korosi et al. 2017). In another instance, paleoecological techniques allowed differentiation between the impact of temperature changes, food availability, and insecticides on *Daphnia magna* populations. The study concluded that populations previsouly exposed to pesticides declined more significantly once exposed to warming conditions than populations only exposed to warming (Cambronero et al. 2018). Thus, paleolimnology can be used to differentiate between multiple stressors that cause environmental changes, and these studies are a unique opportunity to overcome the knowledge gap created by a lack of historical ecological data prior to the 20th century.

1.2 Thesis Objectives and outline

The objective of my thesis is to understand ecological changes on SG̲ang Gwaay over the last millennia and how they relate to anthropogenic activities at the former Haida settlement at Ninstints with a particular emphasis on complementing existing palynological, seabirds, and invasive species data. This multiproxy paleoecological analysis is within the scope, and funded by Park Canada's "The Living Landscapes of SG̲ang Gwaay: strengthening the land and people in a changing climate", a conservation and restoration project proposing archaeological surveys, maintaining Species at Risk habitat, forest understory maintenance and biosecurity management on SG̲ang Gwaay Island. Additionally, findings will inform Park Canada's "Llgaay gwii sdiihlda: Restoring Balance Project", a plan to mitigate impacts on plant communities caused by deer-browsing.

This thesis is composed of four chapters, including this first introduction chapter, a literature review chapter, a research chapter, and a general discussion and conclusion chapter. Chapter 2 is a review of the current status of burrowing seabirds in Haida Gwaii with respect to introduced mammalian predators and assesses the management measures implemented to conserve them since 1990. Haida Gwaii is a breeding ground to 1.5 million birds, including 9 species of burrowing seabirds (Gaston and Masselink 1997; Golumbia 1999; Rodway, Campbell and Lemon 2019). With the introduction of invasive mammalian predators post European contact at the end of the 18th century, seabird populations declined and some, such as the ancient murrelet, are now listed as a species of Special concern by COSEWIC following major predation events by rats (Harfenist, Sloan and Bartier 2002; Gaston et al. 2008). From the beginning of the surveys by the Canadian Wildlife Service in the 1980s to present, management plans were put in place to eradicate invasive species; however, it is still unclear if populations are recovering. With existing population data from governmental surveys and literature, first, I establish population status and then review the management measures that were implemented to achieve conservation and identify successes and failures of these programs. The discussion of this chapter ends with recommendations for future management based on programs and policies that were successful in other insular habitats affected by invasive species (e.g., New Zealand).

Chapter 3 examines past ecosystem changes on SG̲ang Gwaay using a combination of approaches including: (1) establishing an age-depth relationship in the core using lead and carbon radioisotopes to interpret changes for ~1300 years; (2) using sterols and stanols (campesterol, sitosterol, stigmastanol), stable isotopes ($\delta^{15}N$, $\delta^{13}C$, C/N), total organic carbon, diatoms, and chlorophyll-a, to track changes in terrestrial and aquatic vegetation on SG̲ang Gwaay as they relate to historical events at the former Ninstints village and previous pollen studies by Lacourse, Mathewes and Hebda (2007); (3) Using sedDNA, stable isotopes, and trace-metals to track the rhinoceros auklet population and assess the presence of native and introduced predators on the island, complementing seabird population trends reported by Rodway et al. (2011). In this research chapter, we are interested in two questions: (1) are there broader ecosystem changes, including island carbon cycling, linked to the decline in Western red cedar identified by Lacourse, Mathewes and Hebda (2007)? Particularly, we wanted to understand if small-scale tree harvesting by the Haida could drive long-term changes in the carbon cycle on the island and if there were any changes in aquatic primary production: (2) are there long-term changes in the population of the rhinoceros auklet colony that surrounds the pond? Although monitoring indicated that the population increased on SG̲ang Gwaay since 1985 (Rodway, Lemon and Kaiser 1988), only three data points are available and Rodway and Lemon (2011) identified shortfalls of permanent survey plots when interpreting broad scale population trends. Thus, we want to complement their observations by capturing long-term population dynamics. To thoroughly assess potential drivers of seabird population decline, we also assessed the presence of seabird predators (rats, mice) on SG̲ang Gwaay, a threat that ravaged seabird colonies elsewhere in Haida Gwaii in the last 20 years.

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CHAPTER 2

Invasive mammal management and burrowing seabird conservation in Haida Gwaii: is management successful?

2.1 Abstract

Invasive mammals have been present in Haida Gwaii for well over a century, causing decline of seabird populations in the archipelago. Rats and raccoons directly threaten burrowing seabirds through nest and individual predation, while deer indirectly affect seabirds by modifying their breeding habitat. Management measures undertaken since the 1990s address these threats and their success is mixed; while eradication is successful at times in certain places, (re)colonization from nearby source populations of invasives remains an issue. Here, we report the management history of invasive norway rats, black rats, raccoons, and sitka black-tailed deer in Haida Gwaii and establish current population status of ancient murrelet, rhinoceros auklet, Cassin's auklet, Leach's storm-petrel, fork-tailed storm-petrel, pigeon guillemot, and tufted puffin with respect to these invasive species. Rat and raccoon management prevented, so far, seabird populations from disappearing entirely, however we identified that monitoring bias leads to inconclusive population estimates, and population recovery to pre-eradication levels cannot be confirmed years later. Deer management in Haida Gwaii aims to restore native plant communities and does not target the restoration of seabird breeding habitat directly, yet deer are suspected to indirectly impact seabirds; links between seabird population changes caused by deer are yet to be studied in the archipelago. Finally, we recognize that breeding behavior (e.g ability

to relocate the nest site) and metapopulation dynamics (e.g., ability to move between colonies) play important roles in ensuring the persistence of seabird colonies facing invasions and should be accounted for when monitoring colonies post-eradication.

2.2 Introduction

Haida Gwaii is a remote archipelago of approximately 150 islands off the coast of British Columbia (B.C.) in the North Pacific (Moss 2008) offering habitat to 77 bird species and breeding grounds to 1.5 million birds, including 12 different seabird species, 9 of which are ground nesting-seabirds (Gaston and Masselink 1997; Golumbia 1999; Harfenist, Sloan and Bartier 2002; Gaston et al. 2008). Since European contact in ~1774 CE, invasive species have colonised many of Haida Gwaii's islands. Free of natural predators, these invaders cause population declines of seabirds. Burrowing seabirds are particularly vulnerable to invasive mammal predators; species such as the ancient murrelet (*Synthliboramphus antiquus*), are listed as a species of Special concern by COSEWIC following major population declines caused by invasive rat predation (Harfenist Sloan and Bartier 2002; Gaston et al. 2008).

Following evidence of major predation events by Norway rats (*Rattus norvegicus*) and raccoons (*Procyon loctor*) collected in the 1990s, the rapid collapse of the ancient murrelet colony on Langara Island, and the disappearance of breeding populations of Cassin's auklet (*Ptychorampus aleuticus*), rhinoceros auklet (*Cerorhinca monocerata*), Leach's storm-petrel (*Oceandroma leucorhoa*) and fork-tailed storm-petrel (*Oceandroma furcata*) management plans were implemented in Haida Gwaii to prevent the collapse of seabird populations on islands with large colonies (Hobson, Drever and Kaiser 1999; Kaiser et al. 1997). The 1995 management plans were a collective effort between provincial and federal agencies as well as local organizations and communities and eradication efforts targeted islands that supported 90% of the ancient murrelet, rhinoceros auklet, and storm-petrel populations and 70% of the Cassin's auklet population (Harfenist and MacDowell 2001). A second wave of management plans emerged in the 2000s through federal agencies (e.g., Parks Canada, Environment and Climate Change

Canada, hereafter ECCC). Implemented in 2011, SGin Xaana Sdiihltl'lxa: Night Birds Returning is a management plan that targeted islands ancient murrelet conservation through rat eradication on selected islands withtin Gwaii Haanas National Park. Implemented in 2017, Llgaay gwii sdiihlda in X̱aayda Kil, is a management plan aiming to restore the forest understory over-browsed by deer, indirectly protecting seabird breeding habitat. Implemented in 2018, Living Landscapes of SG̱ang Gwaay targets seabird conservation on only one island by culling deer, restoring habitat and preventing rats from invading the island (Parks Canada 2016; Parks Canada 2018) (Table 1.3). Two decades later, we are unifying survey data since the late 1980s, and eradication records to understand current population status of burrowing seabirds with respect to invasive mammals pre and post eradication. In this paper, we present a brief history of Haida Gwaii and an overview of native mammal predator invasions prior to identifying the invasive mammals that threaten burrowing seabirds as well as invasive mammals that could threaten seabirds in the near future. Finally we explore two questions about the management of these invaders with respect to the current status of six burrowing seabirds breeding in Haida Gwaii: 1) what is the current status of burrowing seabird species threatened by invasive mammals ?; 2) what have we learned since invasive species management began in Haida Gwaii in the 1990s?

2.2.1 History of Haida Gwaii

Approximately 15,000 years ago, the melting glaciers of the Hecate Strait led to a rise in sea levels and formed the modern landscape of Haida Gwaii (Fedje and Mathewes 2005; Hayward 2012; Blaise, Clague and Mathewes 2017). Archaeological evidence suggests that 10,000-13,000 years ago, shortly after the last glaciation, Haida Gwaii formed a narrow ice-free sheet that facilitated human settlement of the Americas from Asia (Reimchen et al. 2005;

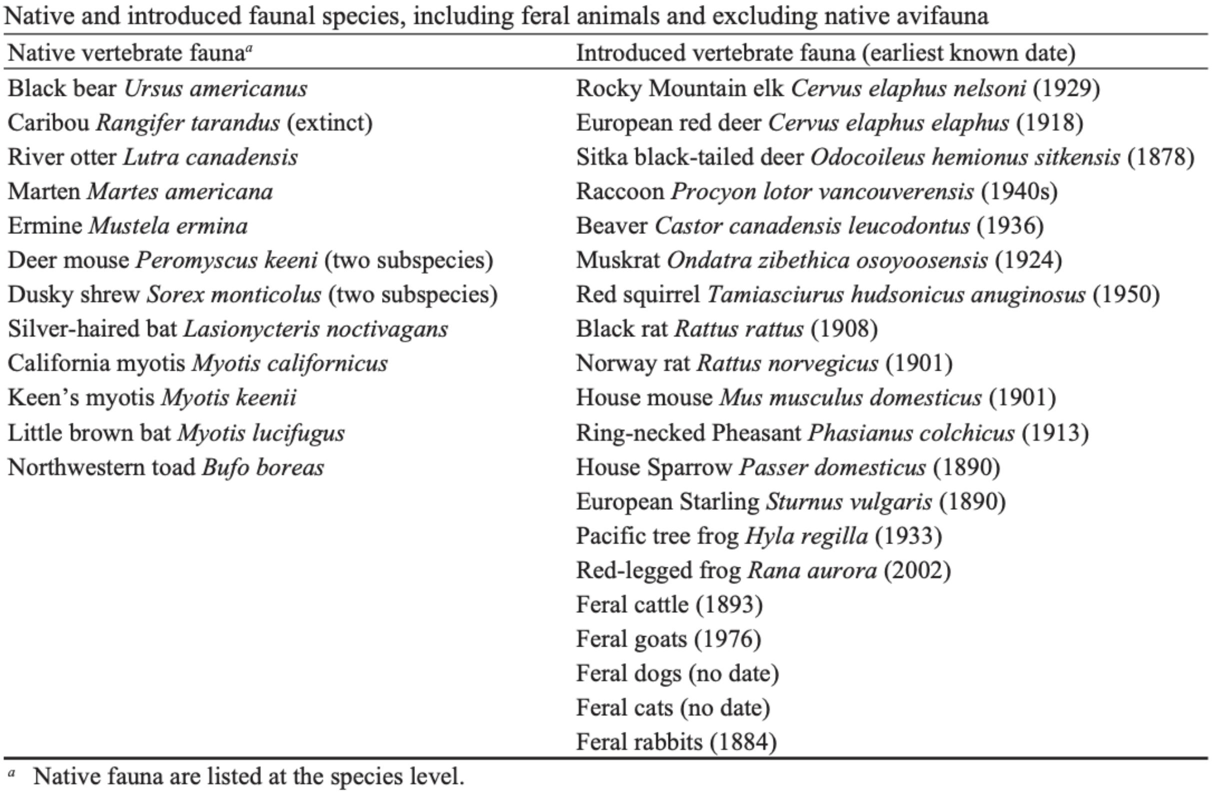
Hayward 2012). Oral history, artefacts found on sites of Haida settlements, as well as paleoecological records analysed by Lacourse, Mathewes and Fedje (2005) provide evidence that Haida Gwaii was populated by humans and wildlife in the late Pleistocene during sea level rise (Reimchen et al. 2005; Moss 2008). Several Haida settlements were established after the time of crossing; occupied sites were initially scattered throughout the coastline. The high endemism of mosses, flowering plants, beetles, fish, birds, and mammals of Haida Gwaii results from a divergence process; animals from the B.C. continental shelf provided source populations to Vancouver Island, Haida Gwaii, and Coastal B.C. during the post-glacial recolonization of the Holocene. Thus, speciation and sub-speciation resulted from adaptations to the unique ecosystem of Haida Gwaii (Reimchen et al. 2005)

DNA studies of Haida Gwaii's native mammals support the hypothesis that fauna on the islands descends from mainland lineages (Byun 1998). The now submerged Hecate Strait region connected Haida Gwaii to the main continental shelf during the last glacial period, and although hypotheses explored the idea of the archipelago isolating diverse communities from mainland throughout the last glaciation, geological evidence suggested that the ice cover on the islands was far too significant to allow such communities to persist throughout the glaciation. A more plausible explanation resides in mainland species finding refugia on the archipelago upon the melt throughout the Pleistocene. The high endemism of wildlife on the island developed throughout the Holocene from ecological adaptations to the dense rainforest (Byun, Koop and Reimchen 1997; Fedje and Mathewes 2005; Reimchen et al. 2005). Thus, some species from Canadian mainland such as deer mice and black bears are now endemic to Haida Gwaii.

There are eleven native mammal species, six of which are endemic to the islands: Haida Gwaii black bear (*Ursus americanus carlottae;* endemic), Dawson's caribou (*Rangifer tarandus*, extinct since 1908; endemic), river otter (*Lutra canadensis*), Marten (*Martes americana;* endemic), Ermine (*Mustela ermina;* endemic), Deer mouse (*Peromyscus keeni;* endemic), dusky shrew (*Sorex monticolus;* endemic), silver-haired bat (*Lasionycteris noctivagans*), California myotis (*Myotis californicus*), Keen's myotis (*Myotis keenii*), and little brown bat (*Myotis lucifugus*) (Gaston et al. 2008; Moss 2008). Furthermore, archaeological findings and paleoecological pollen studies demonstrate that humans and wildlife were present on the islands before western red cedar trees, western hemlock, and sitka spruce were part of the forest composition (Fedje and Mathewes 2005), thus humans and wildlife adapted as the vegetation of the islands changed from a tundra landscape to a forest.

Hazardous marine weather and the remote location of Haida Gwaii kept the islands free of Europeans until the 18th century. Westerly winds are frequent throughout the year and particularly high during winter, sea fog reduces visibility to 0.15 miles for 15% of the summer months, the shallow rocky shorelines make it difficult to approach islands by boat, and tides create difficult navigation conditions with currents attaining 3.5 knots, and tidal variations of 8 metres (Moss 2008). Current knowledge indicates no new fauna or flora colonised the archipelago prior to European contact in 1792 when three domestic pigs were unsuccessfully introduced to Magee Sound (Gaston et al. 2008). Many introductions followed 1792, some of which were unsuccessful (fox, mink) while others led to introduced species establishing self-sustaining populations in Haida Gwaii, most of which are recognized today as invasive species (Table 1.1).

Table 1.1. Table from Gaston (2008) providing an exhaustive list of introduced species in Haida Gwaii



Native and introduced faunal species, including feral animals and excluding native avifauna

Native vertebrate fauna[a]	Introduced vertebrate fauna (earliest known date)
Black bear *Ursus americanus*	Rocky Mountain elk *Cervus elaphus nelsoni* (1929)
Caribou *Rangifer tarandus* (extinct)	European red deer *Cervus elaphus elaphus* (1918)
River otter *Lutra canadensis*	Sitka black-tailed deer *Odocoileus hemionus sitkensis* (1878)
Marten *Martes americana*	Raccoon *Procyon lotor vancouverensis* (1940s)
Ermine *Mustela ermina*	Beaver *Castor canadensis leucodontus* (1936)
Deer mouse *Peromyscus keeni* (two subspecies)	Muskrat *Ondatra zibethica osoyoosensis* (1924)
Dusky shrew *Sorex monticolus* (two subspecies)	Red squirrel *Tamiasciurus hudsonicus anuginosus* (1950)
Silver-haired bat *Lasionycteris noctivagans*	Black rat *Rattus rattus* (1908)
California myotis *Myotis californicus*	Norway rat *Rattus norvegicus* (1901)
Keen's myotis *Myotis keenii*	House mouse *Mus musculus domesticus* (1901)
Little brown bat *Myotis lucifugus*	Ring-necked Pheasant *Phasianus colchicus* (1913)
Northwestern toad *Bufo boreas*	House Sparrow *Passer domesticus* (1890)
	European Starling *Sturnus vulgaris* (1890)
	Pacific tree frog *Hyla regilla* (1933)
	Red-legged frog *Rana aurora* (2002)
	Feral cattle (1893)
	Feral goats (1976)
	Feral dogs (no date)
	Feral cats (no date)
	Feral rabbits (1884)

[a] Native fauna are listed at the species level.

2.2.2 Haida Gwaii burrowing seabirds and invasive mammals

Burrowing seabirds that evolved in the absence of terrestrial predators are particularly vulnerable to introduced species due to their lack of morphological and behavioural defences against these predators (Harfenist and MacDowell 2001). This vulnerability varies from one seabird species to another depending on their breeding behaviour; the time spent on land to nest, lay eggs, incubate them and rear the hatchlings until fledging is a determinant factor when considering an individual bird's exposure to mammalian predators.

Following the initial seabird survey of the North Pacific in the late 1970s and beginning othe 1980s, the Canadian Wildlife Service established that invasive mammalian predators contribute to a decline in population levels of many seabirds nesting on Haida Gwaii (Kaiser et al.1997; Bellis et al. 2019). Invaders can (re)colonize new islands easily making management challenging, yet while oil spills, climate change, and other anthropogenic disturbances (e.g., gill net entanglements, habitat destruction) also pose threats to seabirds that breed in Haida Gwaii, priority management efforts have been allocated to invasive species control and eradication as invasive mammals directly cause seabird mortality and threaten the ecological integrity of the archipelago (Harfenist, Sloan and Bertier 2002; Gaston et al. 2008).

Invasive mammals disperse to the islands of the archipelago by swimming in the open waters from source populations to smaller islands, and by vessel (marine, air) travel. In a recent DNA study, Sjodin, Irvine and Russello (2020) uncovered two major rat introduction events in Haida Gwaii: a first introduction event of European origin occurred in the early 20th century in the South-central part of the archipelago, and a second introduction event from Vancouver occurred in the early 2000s in northern Haida Gwaii. These findings support past records of black rats (*Rattus rattus*) being introduced in 1901, and Norwegian rats (*Rattus norvegicus;* also commonly known as Brown rats) being introduced in 1908 (Golumbia 1999; Gaston et al. 2008) and demonstrate that despite its isolation, Haida Gwaii's biosecurity is threatened by human activities (e.g commercial and private marine and air traffic). Rats established source populations on large islands and disperse to smaller islands to prey on seabird eggs, chicks, and sometimes adults, causing population declines. The most notable example of seabird population decline caused by rats is Langara Island; with historical seabird population estimates of ~200 000 birds, following predation by rats, only ~20 000 birds remained in 1988 (Golumbia 1999). In 1995, 18 islands of the archipelago were known to be invaded by rats (Golumbia 1999).

Raccoons (*Procyon lotor*) introduced in the 1940s as "valuable furbearers", were the main cause of seabird population decline in Haida Gwaii in the 20th century (Gaston 1994;

Gaston et al. 2008; Golumbia 1999). Islands within a ~0.6 km radius of an established colony of raccoons are vulnerable to colonisation (Harfenist, Sloan and Bertier 2002); although raccoons can reach islands with crossing distances as great as 0.95 km (Hartman and Eastman 1999). The majority (~80%) of Haida Gwaii's seabird habitat can be reached by raccoons; however, Hartman and Eastman (1999) demonstrated that raccoons are more successful invaders on less isolated islands and larger islands as opposed to small barren rocky islands (Hartman and Eastman 1999). Seabirds at all life stages are vulnerable to predation; in a single season a handful of raccoons preyed on eggs, juveniles, and adults at a colony representing ~80% of the observed predation (Hartman and Eastman 1999).

Introduced house mice *(Mus musculus)* prey on seabird nests in Haida Gwaii (Kaiser et al. 1997), however this behavior is rarely observed and population decrease caused by house mice predation is not an issue based on population surveys since the 1980s (Rodway, Campbell and Lemon 2019). House mice are commensal and therefore limited to human dwellings (e.g., lighthouses, houses) and in general anthropogenic habitats. Furthermore, house mice dispersal in natural and semi-natural (e.g., agricultural) environments surrounding anthropogenic habitats is often unsuccessful in the presence of other predators (Pocock, Hauffe and Searle 2005) or readily accessible food sources (Wilson et al. 2018). For instance, rats and mice can compete for food resources and as such, native deer mice (*Peromyscus maniculatus*) and Keen's mice (*Peromyscus keeni*), could compete with introduced rats in Haida Gwaii. None the less, in the absence of other predators, house mice can pose a threat to seabirds and should be monitored; on Gough Island in the South Atlantic, house mice prey on Tristan albatross (*Diomedea dabbenena*) and Atlantic petrel (*Petrodroma incerta*) chicks (Cuthbert and Hilton 2004). The native mice are a greater threat to Haida Gwaii seabirds through egg predation (Gaston 1994). Generally, Keen's mice have a harder time preying on eggs larger than those of passerines, however predation of ancient murrelet and rhinoceros auklet eggs is an issue at some colonies in British Columbia. At Triangle Island, predation of rhinoceros auklet eggs caused the greatest egg loss at the colony in 1998 (Blight, Ryder and Bertram 1999). Keen's mice were more successful in rocky habitats where rock can assist in cracking the eggs (Blight, Ryder and Bertram 1999).

The effects of sitka black-tailed deer on seabird populations are indirect, and therefore their mechanisms are more difficult to unveil, yet studies state the need to investigate consequences further (Harfenist, Sloan and Bartier 2002; Gaston et al. 2008). In Haida Gwaii deer modify the forest understory (vegetation below 1.5 m) by browsing on shrubs: salal, huckleberry, salmonberry, young trees and vascular plants. Thus, plant diversity is reduced while spruce and red cedar recruitment is delayed (Gaston 1992; Stockton 2004; Vila, Guibald and Martin 2001). Ultimately, deer browsing homogenizes the shoreline and forest habitats of Haida Gwaii islands in cases where grazers were present for more than 5 decades (Martin et al. 2010). With reduced vegetation cover, seabirds are more exposed to avian predation. However, surveys showed that species (e.g., ancient murrelets, pigeon guillemot, tufted puffins) can successfully breed on islands free of vegetation (Vermeer and Lemon 1986). Other species, such as the rhinoceros auklet, are affected by introduced deer; burrows are damaged and soil erosion is increased in heavily browsed colony areas (Balbag and Hodum 2010). While it is known that deer decrease vegetation cover and affect seabird breeding habitat, responses from seabirds can vary and the mechanisms by which sitka black-tailed deer affect population levels is yet to be studied.

Predation of seabirds by larger endemic mammals (bears, ermine, marten, otters) can occur, but has not been identified as a factor of population decline since the surveys began

(Harfenist 2003; Gaston et al. 2008); however, notable events of colony destruction by bears have been observed (Harfenist, Sloan and Bartier 2002).

2.2.3 Management of invasive mammals

Since the first report on the status and conservation of marine and shoreline birds of Haida Gwaii (Vermeer and Morgan 1983), management measures have been undertaken to ensure the conservation of breeding seabird species threatened by invasive rats and raccoons, and to monitor priority species in British Columbia that could be affected by these invaders.

With twenty-eight seabird species occurring in Haida Gwaii (Rodway, Campbell and Lemon 2019), 12 are local breeders, and of these local breeders, 9 are ground-nesting 6 of which are known to be affected by invasive mammals. These species are: ancient murrelets, rhinoceros auklets, Cassin's auklets, Leach's storm-petrels, fork-tailed storm-petrels, and to a lesser extent tufted puffins, and pigeon guillemots. In most cases, population baseline data for these species dates back to the 1970s and 1980s with an official first census of "priority" species (e.g., ancient murrelets, rhinoceros auklets, Cassin's auklets, tufted puffins) in 1985 by CWS (Rodway, Lemon and Kaiser 1988). Management plans were first put in place in 1993 when funding became available to increase conservation efforts for seabird populations following the Nestucca oil spill. Since their implementation in the 90s, management plans have adopted methods similar to those adopted by New Zealand (e.g., baiting invasive rats with poison, culling deer). Mamagement as it relates to seabird conservation targeted the eradication of rats and raccoons. Recently, questions about deer-induced modification to seabird habitat have been raised in surveys and literature, however deer management is undertaken froma vegetation restoration perspective. Management plans are executed by federal agencies (e.g., ECCC/CWS, Parks Canada) with the help of local organizations (e.g., Laskeek Bay Conservation), and in consultation with the local government (e.g., The Council of the Haida Nation). The current dispersal of invasive species across the archipelago remains dynamic; while presence is certain in some locations, it is unknown in others, thus making management challenging (Figure 1.1).

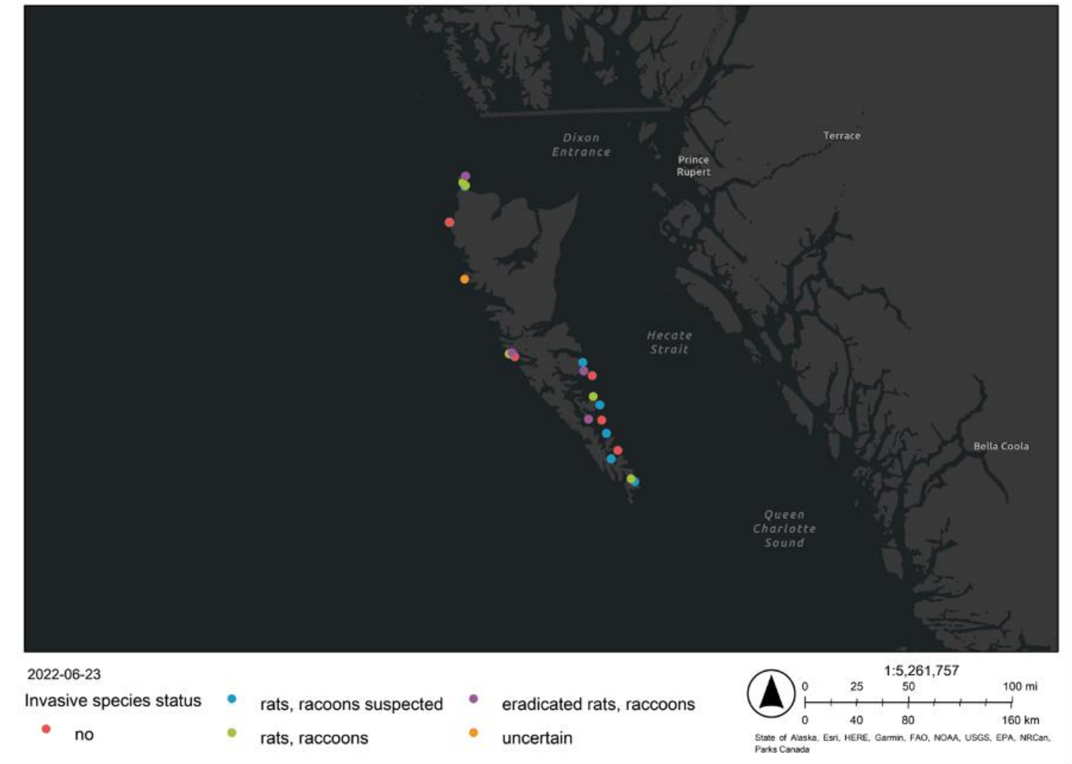


Figure 1.1 Map of seabird colonies and invasive species status

2.3 Haida Gwaii seabird breeding status and conservation measures with respect to invasive rats, raccoons, and deer (1990-2020)

Hereafter, we review the current status of these species and the conservation measures undertaken to protect them in the last three decades since population baselines became available for most species as of the late 1980s. Thus, for this review, the time period between ~1990 to

2020 is addressed. The identified seabird species in this review, ancient murrelets, rhinoceros auklets, Cassin’s auklets, Leach’s storm-petrels, fork-tailed storm-petrels, tufted puffins, and pigeon guillemots have different breeding behaviours and habitats (Table1.2). While some species relocated to smaller, rocky, isolated islands upon predation, other species do not exhibit this behaviour. Thus, the time spent on land, and the chosen habitat are determinant factors when assessing the threats occasioned by invasive mammalian predators and grazers. Table 1.3 summarises these breeding behaviours and presents an overview of the invaders that affect each species.

Table 1.3. Management plans in Gwaii Haanas.

Year started	**Plan**	**Species of concern**	**Management action**
2011	SGin Xaana Sdiihltl’lxa: Night Birds Returning	Seabirds nesting in Gwaii Haanas	Rat & raccoon eradication
2017	Llgaay gwii sdiihlda in X̱aayda Kil	Vegetation in the forest understory	Deer eradication
2018	Living Landscapes of SGang Gwaay	Seabirds nesting on SGang Gwaay	Deer eradication, rat monitoring

Table 1 .3 Burrowing seabirds of Haida Gwaii, their breeding behaviour, and the invasive species that affect them.

	Breeding habitat	**Clutch size, duration of incubation and provisioning**	**Identified invasive species of concern in Haida Gwaii**	**Literature**
Ancient murrelet	Burrows that are ~2 m long and are located in: soil, existing cavities near trees, and grass tussocks Burrows are located up to 450 m from the shore.	1-2 eggs are incubated for ~34.9 days. Chicks are precocial and depart to sea 0-4 days after hatching. There is no provisioning.	Norway rats Black rats Raccoons Remain to be assessed in Haida Gwaii: Black-tailed Sitka Deer	Breeding behaviour: (Sealy 1976) Invasive species: (Harfenist and Mac Dowell 2001; Gaston et al. 2008; COSEWIC 2013; Rodway, Campbell and Lemon 2019)
Rhinoceros auklet	Burrows are 1-5 m long and are located in soil, grass tussocks, and existing cavities near trees. Burrows are located ~200 m from the shore.	1 egg is incubated for ~45 days. Chicks depart 45-60 days after hatching. Night-time provisioning by adults lasts for that entire period.	Raccoons Norway rats* Black rats* Remain to be assessed in Haida Gwaii: Black-tailed Sitka Deer	Breeding behaviour (Bertram et al. 1991) Invasive species: (Harfenist and Mac Dowell 2001; Balbag and Hodum 2010; Rodway Campbell and Lemon 2019)

Cassin's auklet	Burrows are 0.7-1 m long and are located in soil, grass tussocks, existing cavities near trees, or natural cavities of rock crevices. Burrows are ~100 m from shore.	1 egg is incubated for ~38.7 days . Chicks depart 45-50 days after hatching.	Raccoons Norway Rats* Black Rats*	Breeding behaviour: (Vermeer et al. 1979 ; Ainley et al. 2020) Invasive species: (Harfenist and Mac Dowell 2001; Rodway Campbell and Lemon. 2019)
Leach's storm-petrel, fork-tailed storm-petrel	Burrows of Leach's Storm-petrels are ~45 cm long and located in soil of Sitka spruce forests or grasslands, and occasionally in rock crevices. Fork-tailed storm-petrels burrows tend to be found next to tree cavities in greater proportion than those of Leach's Storm-petrels. In Eastern Canada Leach's storm-petrels prefer heavily vegetated nest sites, and favoured ferns as opposed to areas showing signs of forestation.	Leach's storm-petrel: 1 egg is incubated for 37-50 days depending on location within the breeding range. Chicks depart the burrow ~63.3 days after hatching. Fork-tailed storm-petrel: 1 egg is incubated for 46-49 days. Chicks depart the burrow ~62 days after hatching.	Raccoons Norway Rats* Black Rats* Remain to be assessed in Haida Gwaii: Black-tailed Sitka Deer	Breeding behaviour: (Vermeer et al. 1988 ; d'Entremont et al. 2020 ; Pollet et al. 2020) Invasive species: (Harfenist and Mac Dowell 2001; Harfenist 2003; Campbell and Lemon 2019)

Pigeon guillemot	Closed crevices or cavities in rocks, tree roots, soil burrows if cavities are not available. Cavities are 79-93 cm deep.	2 eggs are incubated for 37.8 days. Chicks depart 36-38 days after hatching.	Raccoons	Breeding Behaviour: (Vermeer, Morgan and Smith 1993) Invasive species: (Vermeer, Morgan and Smith 1993; Rodway, Campbell and Lemon 2019)
Tufted puffin	Excavated crevices or burrows in vegetated areas	1 egg is incubated for ~45 days. Chicks depart ~43 days after hatching.	Rats	Breeding Behaviour: (Vermeer and Morgan 1983) Invasive species: (Harfenist and Mac Dowell 2001, Harfenist, Sloand and Bertram 2002; Gaston 2013; Rodway, Campbell and Lemon 2019)

*Predation by rats is assumed for rhinoceros auklets, however raccoons are identified as the main predator of rhinoceros auklet, Cassin's auklet, Leach's and Wilson's storm-petrel eggs, and cause for burrow damage.

2.3.1 Ancient murrelets

Current status. Ancient murrelets are listed as “Special Concern” under COSEWIC. Although information about population trends is available for certain islands, COSEWIC states that there are no reliable estimates of overall population size and trend for ancient murrelets in Canada and provides the following statistics: 25% of the population is found at colonies estimated to be increasing in size, 12% of the population is found at stable colonies, 34% of the population is found at colonies considered to be decreasing (COSEWIC 2013). Approximately half of the world’s population breeds in Haida Gwaii (Gaston 1994; Gaston et al. 2008), although there are estimates as high as 74% (Hartman and Eastman 1999), however the Haida Gwaii population decreased by ~50% between 1850 and 1990 (Harfenist 2003).

2.3.1.1 Management in the 1990s

Norway rats caused a 90% decline between 1986 and 1995 in the population of ancient murrelets nesting on Langara Island (COSEWIC 2013) by feeding on juvenile and adult ancient murrelets at their burrows (Drever and Harestad 1998). Additionally, raccoons and rats cause population decline on Helgesen, Saunders, Langara, Lyell, Kunghit, and Limestone islands, and a cause of abandonment at Lucy, Cox, Instructor, Boulder, Sea Pigeon, Skedans, Arichika, Bishof, Tar, and High islands (Gaston 1994). This predation behaviour was confirmed by examination of rat stomach contents, visual inspection of dead adult birds, presence of bones in active burrows, and stable isotopes analysis (Hobson, Drever and Kaiser 1999).

In 1988, the Langara Island Seabird Habitat Recovery Project was put in place to manage rats, but it was only in 1992 after the *Nestucca* oil spill that ECCC put in place a plan to eradicate rats on notable islands in British Columbia with significant seabird colonies (e.g., Langara, Cox, Lucy) (Taylor, Kaiser and Drever 2000; Gaston et al. 2008). Eradication followed a protocol developed in New Zealand; rats were baited with 50 ppm brodifacoum traps dispersed in such a way as each rat would have at least one trap within its home range (Taylor Kaiser and Drever 2000; Tompkins 2000). By 1995, all rats had been eradicated from Langara, Bischof, Cox, Lucy, and St. James islands. Using survey data before (1981-1993) and after rat eradication (1999-2004) on Langara Island, Regehr et al. (2007) showed that post eradication, the ancient murrelet population increased from approximately 13,000 to 24,000 breeding pairs and that the population dispersed on the island, yet density remained low. Contrary to these findings, Major (2011) used a different method to estimate population trends and could not conclude that ancient murrelet colonies on Langara spread over a larger area or increased in density, nor that the population was recovering. Following methods established by Major and Chubaty (2012), continuous and consistent survey data between 1981-2004, which were only available for one survey plot, was used to standardize survey data between years and reduce biases in data caused by different year-to-year survey efforts (i.e different survey frequency, intensity, and timing). Survey data for ancient murrelets on Langara was interpolated using density of burrows per square meter, and these results were used to compute the total area of the colony and the population size with the best supported generalized linear model (GLM). Using this model and the continuous survey data (only available for the site of McPherson Point for the period 1981-2004), Major (2011) demonstrated that the colony on Langara Island did not expand after rat eradication and that density increased post rat eradication while the colony area decreased, thus indicating that birds re-colonized some burrows post-rat eradication, but that the colony did not indicate recovery.

In the same study using best-supported GLM models to estimate population size, Major (2011) found that ancient murrelet populations were increasing at all at colonies monitored throughout Haida Gwaii between 1980-1997s, except those impacted by predators, however with all colony estimates combined, no evidence of regional population increase was found. These observations are indicative of metapopulation dynamics. This metapopulation model supports observations made by Gaston (2008); ancient murrelet population in Haida Gwaii increased at all colonies with the exception of sites impacted by predators, indicating metapopulation dynamics (i.e birds move between available sites and select the highest quality site to breed).

With the seabirds being absent from much of Langara Island over 20-30 years following eradication, questions were raised whether broader ecosystem changes induced by the presence of rats such as change in vegetative cover could affect the re-colonization of extant colony area by ancient murrelets. Major, Lemon and Hipfner (2012) surveyed 12 islands on Haida Gwaii, observing the relation between ancient murrelet breeding habitat and vegetation cover. The study concludes that ancient murrelets are flexible in choosing breeding habitat and that changes in vegetation cover induced by invasive mammals are unlikely to negatively affect re-colonization at Langara. This conforms to prior observations by Vermeer and Lemon (1986) regarding changes in ancient murrelet nest sites in the presence of Cassin's auklet. Finally, Major, Lemon and Hipfner (2012) note that re-colonization at Langara is likely to be successful with a stable and expanding source population at Frederick Island, thus supporting the idea that seabirds are more likely to re-colonize islands post eradication if there is a nearby source population on a "refugia" island (Buxton et al. 2013).

Following evidence collected in the early 1990s, in 1995, Parks Canada, Laskeek Bay Conservation, CWS, and BC's Ministry of the Environment, Lands, and Parks started controlling raccoon populations that spread to 86% of all islands in the archipelago. Islands included in this management plan were chosen based on the proportion of seabirds they supported and the likelihood to be invaded by raccoons (i.e. large islands near-shore were prioritised); the 37 chosen islands supported 90% of the ancient murrelet population (Harfenist and Mac Dowell 2001). In 1998, raccoons were eradicated from two of the islands, Helgesen and Limestone Island, that supported approximately 1,100 and 1,500 pairs of ancient murrelets. In the three years of operations to eradicate raccoons, monitoring proved to be an essential step to prevent recolonization as observed on Limestone Island in 2001, 2007 and 2009 (Gaston 2013). In 1988, less costly monitoring protocols, that included the help of local fishermen, were established.

2.3.1.2 Management in the 2000s

The Laskeek Bay Conservation Society monitored predation at the ancient murrelet colony on Limestone Island in various years using transects that represented 1.6 ha of the 12.6 ha of the colony area. In these transects they estimated that predators killed 70.6 murrelets/week in 2008, 20.4 murrelets/week in 2009, 2.7 murrelets/week in 2010 (Gaston 2013). Although no raccoons were observed, these predation estimates were obtained by inspecting the transect for bones and killed birds and cannot be associated with a particular predator, however many predators were present, including: bald eagles, river otters, peregrine falcons, common ravens.

In 2009, Parks Canada, the Council of the Haida Nation and Island Coastal Conservation debuted a conservation project titled "SG̲in X̲aana Sdiihltl'lx̲a: Night Birds Returning" aiming to eradicate rats from various islands with two initial phases of eradication efforts in 2011 and 2013 (Parks Canada Agency, Government of Canada 2018). Following these efforts, rats were eradicated from the Ramsay and Northern Juan Perez Sound International Bird Area (including

Murchison and Faraday islands), and Arichika and Bischof islands between 2011 and 2014 (Gill et al. 2014; Parks Canada Agency, Government of Canada 2018). Poisonous brodifacoum traps were dispersed to precise island locations by helicopter and invasive species presence was monitored using camera traps. A survey conducted on Ramsay Island in June 2012 using survey plots established in 1984 concluded that the average numbers of ancient murrelets burrows in the survey increased at a rate of 2% per year between 1984 and 2012 (Gaston 2013). Another survey conducted in 2011 using permanent plots established in 1984, indicated that the population of ancient murrelets on Ramsay, George and Rankine islands is constant or increasing (Rodway and Lemon 2011).

In 2019, under the Species at Risk Act, a Multi-species Action Plan for Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site was put in place (Parks Canada 2016). Within this Action Plan, the objective for the ancient murrelet population is to maintain population levels on rat-free islands and increase population levels on rat-invaded islands through continued eradication efforts deployed under "SG̲in X̲aana Sdiihltl'lx̲a: Night Birds Returning". This management plan includes a partnership with Environment and Climate Change Canada that provides updates on population levels and colony status, monitoring on ''key'' islands that have larger colonies (e..g, Rankine, George, Ramsay) for the early detection of rats and raccoons, as well as raising public awareness (e.g., mandatory public orientation in Gwaii Haanas, business licencing, engaging with the fishing industry and boaters). Establishing a baseline monitoring technique for the population is also a priority for management since some West coast colonies have not been surveyed since the 1980s (Parks Canada 2016). Finally, the Action Plan lists future measures that should be implemented including: early detection of invasive mammals using sniffer dogs, rat genetics analysis to examine movement patterns, removing rats from small islands (Kunga and Titul, Tanu, Huxley, Shuttle), remove rats from Kunghit Island if genetic analysis indicates a low re-invasion risk, facilitate seabird re-colonization using active restoration techniques (e.g., call-playback).

2.3.1.3 Other considerations for ancient murrelet conservation

In Haida Gwaii, ancient murrelets have been observed to breed exclusively in mature forests (Gaston 1992). Unchecked deer browsing is likely to have reduced the availability of suitable breeding habitat in Haida Gwaii over the last decades (Martin et al. 2010) and could impact ancient murrelet breeding habitat.

After observing population trends based on the survey of permanent monitoring plots in 2011, and contrasting these trends with other surveys outside of permanent plot boundaries within Haida Gwaii, it was concluded that the permanent monitoring plots were not effective in monitoring population trends. In fact, the permanent monitoring plots for ancient murrelets on Ramsay, George and Rankine islands were not representative of the major population decline because introduced rats and raccoons cause population declines on islands that are not regularly monitored such as Langara (Rodway and Lemon 2011). Furthermore, inconsistent monitoring efforts introduce biases in analyses of long-term population dynamics; when estimating population sizes, the same quadrats, number of transects, as well as survey frequency, intensity, and timing should be kept consistent in order to make accurate year-to-year comparisons (Major 2011).

Major (2016) monitored colony attendance of ancient murrelets in different environmental conditions (e.g., time light, weather) and found that colony attendance was different for breeding birds and non-breeding birds; breeding birds arrived at the colony earlier after sunset and were most influenced by light and weather conditions, whereas non-breeders arrived at the colony later in the night and were attending the colony later, irrespective of light and weather condition. These findings could have management implications as predator interactions could be different with breeding and non-breeding individuals.

2.3.2 Rhinoceros auklets

Current status. Rhinoceros auklets were listed as “Least Concern” by the IUCN in 2018 with a globally stable population (Government of Canada 2019a), but listed as a “species of interest” to monitor within the Pacific and Yukon sub-region as 70% of the global population breeds in Canada with approximately 40% of the population breeding in British Columbia. Systematic population monitoring was lacking prior to the 1970s and present trends cannot be interpreted with high reliability. Lucy, Pine, Triangle and SG̲ang Gwaay slands have been monitored by ECCC on a regular basis since 1984, and the population at SG̲ang Gwaay is increasing based on the number of burrows within survey areas, while it is stable at Lucy, Triangle and Pine islands (Rodway and Lemon 2011).

2.3.2.1 Population status with respect to invasive species, and invasive species management.

Following evidence collected in the 1990s, Parks Canada, Laskeek Bay Conservation, CWS, and B.C.’s Ministry of the Environment, Lands, and Parks started controlling raccoon populations on several islands. Islands included in this management plan were chosen based on the proportion of seabirds they supported with the chosen islands supporting 90% of the rhinoceros auklet population (Harfenist and Mac Dowell 2001, Gaston 2013). On these islands, populations of rhinoceros auklets had declined by 79%, and raccoon predation is identified as at least one major cause of the decline. On Helgesen Island a dozen of raccoons caused the loss of approximately 30% (10,000 breeding pairs) of the Haida Gwaii population. Furthermore, colony decline on Langara, Cox, Saunders, and Little Helgesen was attributed to invasive raccoons and rats in the 1990s (Harfenist 2003). A survey conducted in 2011 using permanent plots established in 1984, indicated that the populations of rhinoceros auklets on SG̲ang Gwaay are increasing; however, permanent monitoring plots for estimating population sizes did not detect population declines elsewhere in coastal British Columbia (e.g., Pine Island) (Rodway and Lemon 2011). Furthermore, rats and raccoons are absent on SG̲ang Gwaay and only 3 deer were present on the island as of 2021, therefore permanent monitoring plots on the island are not accounting for population declines caused by these predators (unpublished field observations Parks Canada 2021).

2.3.2.2 Other considerations for rhinoceros auklet conservation.

Keen's mice predation on rhinoceros auklet eggs at Triangle Island was the greatest cause of egg loss with 34% of eggs in one survey plot being lost (Blight, Ryder and Bertram 1999); however, this has not, historically, been identified as a cause of population decline in Haida Gwaii for rhinoceros auklets (ECCC 2021, personal communications). Keen's mice on Triangle Island are particularly large compared to other specimens in British Columbia and can therefore prey on larger eggs than elsewhere (Blight, Ryder and Bertram 1999). Stable isotopes analysis revealed that seabird eggs were a major part of Keen's mice diet throughout the breeding season on Triangle Island (Drever et al. 2000).

Black-tailed sitka deer (*Odocoileus columbianus*) were introduced to Haida Gwaii for the first time in the late 19th century, and again in the 20th century. The islands were, at the time of the first deer introduction, already populated with a native Dawson's caribou (*Rangifer tarandus dawsoni;* extinct in 1935) population (Rodway, Campbell and Lemon 2019). Thus, the archipelago's ecosystems were not unfamiliar with ungulates; however, caribou and deer have different diets and thus might impact ecosystems differently. Stable isotopes studies show that Dawson's caribou were likely foraging in intertidal habitat (Kubiak et al. 2021). Browsing by black-tailed changed Haida Gwaii's forests; plant-species diversity and density are negatively affected with most changes happening to vegetation in the browsing height (0-150 cm above ground), thus modifying the forest understory the most (Allombert, Stockton and Martin 2005). Shrubs disappeared from islands where deer have been present for more than 50 years; however, islands where deer have been present for less than 20 years also experience drastic reduction in vegetation cover in the forest understory, and have reduced tree recruitment (Vila, Guibald and Martin 2001; Allombert, Stockton and Martin 2005). Additionally, Black-tailed Sitka deer introduced to Protection Island (WA, USA) were found to cause damage in 85% of the rhinoceros auklet plots surveyed at the colony with 12.1% of burrows being damaged at the entrance, in the tunnel, or in the nest chamber (Balbag and Hodum 2010). Soil erosion induced by severe grazing is also a factor contributing to the decline of breeding habitat suitability (Pearson et al. 2009). Black-tailed Sitka deer introduced to rhinoceros auklet colonies in Haida Gwaii, such as the colony on SGang Gwaay, could cause similar damages to the burrows; however, the effect of deer on seabird nesting success remains to be addressed.

On Triangle Island, variation in rhinoceros auklet diet caused by marine bottom-up trophic effects negatively affect breeding success and caused declining population trends

(Borstad et al. 2011). A shift in springtime surface temperature (SST) caused a mismatch between phytoplankton blooms and emergence of sand lance larvae (*Ammodytes dubius*) thus inducing a decline in sand lance recruitment and reducing prey availability for rhinoceros auklets. Phytoplankton blooms in early April are strongly correlated with increased sand lance availability and in return sand lance availability is strongly correlated with fledgling success (Borstad et al. 2011). Chick fledging was less successful when sand lance represented a smaller part of the diet, and this was observed when phytoplankton blooms happened too late in the month of April (Borstad et al. 2011). Thus, in years when sand lance is less abundant, breeding success declines. With increased occurrence of climatic irregularities causing a mismatch between phytoplankton blooms and sand lance, it could be possible to observe a decline in the rhinoceros auklet population over a long-time scale (e.g., several year cycles).

2.3.3 Cassin’s auklets

Cassin’s auklet is listed as ‘Special Concern’ by COSEWIC (2014), a ‘Near threatened’ by IUCN (2018), a ‘Vulnerable’ species in Canada, and a ‘Priority’ species for the Pacific-Yukon subregion with 75-80% of the global population breeding in B.C. (Government of Canada 2019b). An estimated 279,000 breeding pairs of Cassin’s auklets breed in Haida Gwaii, representing about 80% of the global population (Rodway 1991; COSEWIC 2014).

2.3.3.1 Population status with respect to invasive species, and invasive species management.

Colonies on Helgesen have declined due to predation by raccoons, and other colonies on Saunders, Langara, Cox, and St. James islands have been abandoned based on evidence collected in the 1990s (Harfenist 2003). Following evidence collected in the 1990s, several governmental agencies and Laskeek Bay Conservation started controlling raccoon populations on several islands. Islands included in this management plan were chosen based on the proportion of seabirds they supported; the chosen islands supported 70% of the Cassin's auklet population and birds at colonies on these islands were heavily preyed upon by raccoons (e.g., Helgesen Island a dozen of raccoons caused a decline of 95% of Cassin's auklets) (Harfenist and Mac Dowell 2001).

A survey conducted in 2011 using permanent plots established in 1984, indicated that the populations of Cassin's auklets on Ramsay, Rankine, and East Cooper islands are decreasing significantly (Rodway and Lemon 2011). In 2019, under the Species at Risk Act, a Multi-species Action Plan for Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site was put in place (Parks Canada 2016). Within this Action Plan, the objective for the Cassin's auklet population is to maintain population levels on rat-free islands and increase population levels on rat-invaded islands through continued eradication efforts deployed under "SG̲in X̲aana Sdiihltl'lx̲a: Night Birds Returning". Rankine, East Copper, Ramsay and SG̲ang Gwaay islands have been identified as key monitoring places (Parks Canada 2016). Other identified measures under the Action Plan are identical to measures implemented for ancient murrelets.

2.3.3.2 Other considerations for Cassin's auklet conservation.

Acoustic recorders demonstrated that Cassin's auklets were less affected by rat presence than other seabird species (e.g., ancient murrelets, fork-tailed storm-petrels); relative abundance and vocal activity of Cassin's auklets was not negatively correlated with rat presence (Halpin

2014). Pollution and other contaminants have been identified as a major threat for Cassin's auklets. As they depart breeding grounds, Cassin's auklets are particularly vulnerable to oil spills South of Haida Gwaii, in proximity to Triangle islands where boat traffic is high (COSEWIC 2014). Approximately 32% of the birds that died in the 1988 *Nestucca* oil spill were Cassin's auklets. Accoridng to the Environmental Impact Assessment process, new projects in port Vancouver have been identified as risk factors for seabirds as they will lead to an increased traffic of oil tankers in B.C.'s waters. Climate change is an additional threat with ocean acidification, and warming waters, causing a "mismatch" between birds and prey thus affecting survival of Cassin's auklets (COSEWIC 2014).

2.3.4 Leach's storm-petrels and fork-tailed storm petrels

While the fork-tailed storm-petrel is listed as a species of "Least concern" by the IUCN (2018) and an "Apparently secure" species in Canada, the Leach's storm-petrel is listed as "Vulnerable" by the IUCN (2018) (Government of Canada 2019c), an "Apparently secure" species in Canada, and a "Priority" species in several sub-regions in Atlantic Canada, Quebec and the Pacific-Yukon (Government of Canada 2019d). In Haida Gwaii, fork-tailed storm-petrels and Leach's storm-petrels have been observed breeding on the west coast of Graham Island, Petrel Island, and Hippa Island. The breeding season is approximately six months for fork-tailed storm-petrels and five months for Leach's storm-petrels (Vermeer, Devito and Rankin 1988). In 1983 it had been estimated that 10,666 pairs of Leach's storm-petrels and 9,396 pairs of fork-tailed storm-petrels were breeding on Petrel Island. The most recent estimate for these two species breeding in Haida Gwaii is 53,000 pairs of fork-tailed storm-petrels and 103,000 pairs of Leach's storm-Petrels (Harfenist and Mac Dowell 2001). Estimates of storm-petrel populations are interpreted with caution as surveys in Haida Gwaii do not always distinguish between the two species. Furthermore, storm-petrels nest in presence of other birds, oftentimes Leach's storm-petrels, and elsewhere have been observed to use burrows of other species (i.e. inter and intra-specific competition (Rodway, Campbell and Lemon 2019) , making it more difficult to distinguish their burrows and estimate their population size based on burrow density alone (Rodway, Campbell and Lemon 2019).

2.3.4.1 Population status with respect to invasive species, and invasive species management.

Rats destroyed colonies of fork-tailed storm-petrels on Langara and Cox islands, and in Haida Gwaii an additional 13 colonies of storm-petrels have been abandoned (reasons are not explained) (Harfenist and MacDowell 2001; Harfenist 2003). Prior to rat invasion on Langara Island, deer mice were present, however as of 1946, mice were considered as absent from the island with rats being the dominant predator (Harfenist and Mac Dowell 2001; Gaston et al. 2008). Following evidence collected in the 1990s, Parks Canada, Laskeek Bay Conservation, CWS, and B.C.'s Ministry of the Environment, Lands, and Parks started controlling raccoon populations on several islands. Islands included in this management plan were chosen based on the proportion of seabirds they supported; the chosen islands supported 70% of the storm-petrel population (species were not distinguished) (Harfenist and MacDowell 2001).

Evidence of raccoon predation on storm-petrels was observed on Instructor and Little Helgesen islands in the 1990s. At the time it was noted that the persistence of storm-petrels on these raccoon infested islands contrasted with the disappearance of alcids (Cassin's auklet, ancient murrelets and rhinoceros auklets) in 1986 following raccoon predation, suggesting that storm-petrels might be more resistant to raccoon invasions than burrowing alcids (Gaston and Masselink 1997). On East Limestone Island the storm-petrel activity increased since racoon eradication (Harfenist and Mac Dowell 2001; Gaston 2013).

Luxmore and Rogers islands support a larger colony of storm-petrels; however, predation by native river otters is a cause of population decline in the 1990s (Vermeer et al. 1988; Gaston and Masselink 1997). In 1993, 30 fork-tailed storm-petrels and 60 Leach's storm-petrels were found to be victims of predation by river otters. Notable events of storm-petrel colony destruction by bears were observed on Queen, Ogilvie and McKenzie islands in the 1960s (Harfenist and Mac Dowell 2001; Harfenist, Sloan and Bartier 2002; Gaston 2013).

2.3.4.2 Other considerations for Leach's and fork-tailed storm-petrel conservation

Storm-petrel populations appear to persist on raccoon-invaded islands while alcid populations disappear (Gaston and Masselink 1997), and overall adult survival in B.C. is higher than in the Atlantic population due to a reduced exposure to oil-exploitation facilities (Rennie et al. 2020). However, both species remain threatened by invasive mammals. Acoustic recorders demonstrated that fork-tailed and Leach's storm-petrels were negatively affected by rat presence with relative abundance and vocal activity negatively correlating with rat presence (Halpin 2014). Additionally, in contrast with larger alcid species, storm-petrels lay eggs small enough to be predated by native mice species (e.g., Keen's mice), and are therefore still vulnerable to native rodent predation. Finally, the breeding habitat of storm-petrels in Haida Gwaii consists of salal, grassy patches and forested areas (Rodway, Lemon and Kaiser 1988), and the species is therefore likely to be affected by deer browsing. Although studies about breeding habitat do not exist in Haida Gwaii, adult survival of storm-petrels in the Western Atlantic was observed to be higher at colonies where vegetation cover was dense (i.e. dense ferns, or vegetated forest understory) as opposed to habitats that lacked vegetation cover in the forest understory. A survival study following 571 breeding individuals between 2016 and 2021 at a colony where predators are managed shows decreased adult survival in forested habitat and particularly forests with a reduced understory (Gutowsky et al. 2023). Transect surveys found 52% of carcasses in forest habitat with a reduced cover as opposed to fern and shoreline habitat (10% and 12.5% respectively). Researchers note that a possible explanation for increased avian predation in forested areas is the ability of avian predators to take advantage of tree cover to remain undetected. This was an issue at colonies where management aimed to reduce avian predation to increase storm-petrel survival; avian predators were difficult to find (Gutowsky et al. 2023).

2.3.5 Tufted puffin

Current status. Tufted puffins are listed as a species of 'Least Concern' by the IUCN in 2018 (Government of Canada 2019e), designated as an 'imperiled' species by Wild Species Canada and a 'priority' species within the Pacific and Yukon sub-region due to changes in prey availability and predation by introduced mammals. ECCC monitors the species in the southern part of its Canadian breeding range with fixed plots on the Triangle Island where 60% of the Canadian population is located. In Haida Gwaii breeding for ~560 pairs (0.5% of the global population) is confirmed on 14 islands of the Southern West and at the Southern tip of the archipelago, although more than 1000 individuals can be observed in Haida Gwaii's waters during non-breeding months (Harfenist, Sloan and Bartier 2002).

2.3.5.1 Population status with respect to invasive species, and invasive species management

Tufted puffins were once present on Langara Island, but abandoned the breeding site due to predation by rats (Harfenist and Mac Dowell 2001; Harfenist, Sloan and Bartier 2002; Gaston et al. 2008). Upon rat invasion on St. James Kunghit, Langara, Lyell, and Murchison islands, colonies of Cassin's and rhinoceros auklets, and storm-petrels disappeared, while colonies of tufted puffins and pigeon guillemot relocated to cliff tops or offshore rocks (Bailey and Kaiser 1993). The extent to which rats affected the colonies of tufted puffins on St. James and Kunghit islands is unknown.

2.3.5.2 Other considerations for tufted puffin conservation

Tufted puffins breed on open cliffs and are more present at their nest as opposed to storm-petrels, rhinoceros auklets, Cassin's auklet, and ancient murrelets that are present at nest sites during the night (Bailey and Kaiser 1993). This behavior led tufted puffins to relocate colonies on small remote, bare and rocky islands that are harder to access for rats and raccoons, as otherwise adults are unable to attend their nest in the presence of predators. Thus, by avoiding predation and relocating their colony, tufted puffin populations are able to persist instead of experiencing major declines such as the ones observed for other burrowing-birds in Haida Gwaii; burrowing species such as ancient murrelets are away from the nest the majority of the time, thus adults avoiding predation, however eggs and hatchlings are left unattended in the presence of predators.

2.3.6 Pigeon guillemot

Pigeon guillemot is listed as a species of 'Least Concern' in the 2018 IUCN assessment, an 'Apparently secure' species in Canada and is a 'Priority' species in the Pacific-Yukon sub-region with conservation concerns arising from oil spills and predation by introduced mammals (Government of Canada 2019f). In Haida Gwaii, pigeon guillemot population estimates are still unreliable due to a lack of systematic survey data, except in the Skidegate Inlet (Rodway, Campbell and Lemon 2019).

2.3.6.1 Population status with respect to invasive species, and invasive species management.

Haida Gwaii population estimates for pigeon guillemot are extremely approximate with 4722 birds estimated to breed in the archipelago (Rodway, Campbell and Lemon 2016). Although predation by introduced mammals is suspected, there are few studies quantifying the impact. Upon rat infestation on Langara Island, pigeon guillemot relocated to rocky, steep habitat (Bailey and Kaiser 1993). Raccoons have been identified as invasive predators of eggs and individuals on Ferry Island and smaller unidentified islands of Haida Gwaii (Vermeer, Morgan and Smith 1993).

2.3.6.2 Other considerations for Pigeon Guillemot conservation

The Laskeek Bay Conservation Society gathered annual chick number and nest-departure date data on East Limestone Island in the past decades to inform lacking population baselines in Haida Gwaii (Gaston 2013). With respect to predation by invasive mammals, pigeon guillemot can relocate to islands where they can avoid predation and their population numbers seem stable.

2.4 Conclusions and considerations for management in Haida Gwaii

2.4.1 Lack of consistent monitoring & the need of a continuous effort to monitor and eradicate invaders

Management efforts have extensively been deployed to conserve ancient murrelets and Cassin’s auklets. With Haida Gwaii population baselines missing for species like rhinoceros auklet, pigeon guillemot, tufted puffin, Leach’s storm-petrel, and fork-tailed storm-petrel, it is difficult to determine if sufficient conservation efforts are deployed to limit the impact of invasive mammals on these species. The last spatially extensive census of birds in Haida Gwaii dates back to 1984 and 1993, and while regular monitoring for species of interest exists, population trends from survey plots can be misleading (Rodway and Lemon 2011). Current population status cannot be reliably interpreted with data from permanent monitoring plots alone as demonstrated by Major (2016). Some species (e.g., ancient murrelets) attend different colonies when an island becomes invaded by a predator. Such movement within the metapopulation highlights the importance to monitor colonies outside of regular survey plots to estimate population trends at local scale. This behavior is also observed for tufted puffin and pigeon guillemot that avoid predation by relocating to rocky cliffs that cannot be reached by invasive rats and raccoons.

Management of invasive rats, raccoons and deer is still being deployed today in Haida Gwaii. Invasive mammals can recolonize islands and therefore monitoring and management efforts need to be continuous. Norway rats were detected on Murchison and Faraday islands in 2017 after eradication in the phase 1 and 2 of the conservation project “SG̱in X̱aana Sdiihltl’lx̱a: Night Birds Returning”, and in 2018 6-12 rats colonised Gandll K’in Gwaay yaay (Hotspring Island), and Aataana Gwaay yaay. Thus, in their 2018 management plan, Parks Canada maintained the objective to control rat, raccoon, and deer populations as they still represent a threat to ground-nesting seabirds that breed in the archipelago (Parks Canada Agency, Government of Canada 2018). In 2019, Norway rats were detected on Tar Island, Agglomerate, and Ramsay islands.

Modern DNA techniques help reveal mechanisms of invader dispersal between islands and therefore show how species can re(invade) islands despite eradication efforts. Unsuccessful eradication on Faraday and Murchison islands is caused by recolonization; using DNA from 606 rats captured between 2008-2018, Sjodin (2019) identified Lyell Island as the source population for all recolonization events on the Faraday and Murchison islands (Sjodin 2019). Considering source populations is an important factor in prioritizing new islands to manage and DNA sampling proved to be an efficient way to uncover source populations (Sjodin, Irvine and Russello 2020). Despite management efforts being deployed to small islands where seabirds breed, management on larger islands such as Lyell and Kunghit seem to be an unavoidable step for permanent eradication of invasive rats. Although management of larger islands, and in some cases populated by humans, presents new challenges (e.g., covering a larger area, increased financial burden, access to private land for ground-baiting, access to infrastructure, development of social engagement programs), eradication is possible. In 2019 rodents were eradicated from The Lord Howe Island in the Tasman Sea, an island inhabited by 350 people, using a combination of aerial and ground bait dispersal (Harper, Pahor and Birch 2020). Carr et al. (2021) highlight that beyond eradication efforts, islands should be restored; restoring ecosystems damaged by invaders post-eradication could increase the number of seabirds re(colonizing) the island by as much as 32 times (~4306 pairs without vegetation restoration vs. ~319 762 pairs with vegetation restoration).

Another consideration for successful eradication is the invader's ecology. To maximise trapping efforts, invaders should be baited at times when their populations are lower (e.g., a decline in population caused by food scarcity) (Gill et al. 2014). This was implemented during eradication efforts on Farday and Murchison islands. Rat trapping on Langara Island demonstrated that rats are less likely to get trapped when ancient murrelets were present at the colony as opposed to when the colony was vacant (0-0.7 captures/100 nights of snap trapping with ancient murrelets present versus 9.9-14.0 captures/100 nights of snap trapping in the vacant colony) (Drever 2004). This concludes that trapping efforts should be maximised before and after the breeding season of ancient murrelets. A similar observation was made for the effective control of raccoons on Helgesen island. Animals were easier to kill when seabirds were absent from the colony as raccoons were easily found foraging in the intertidal zone, as opposed to being in the dense forest (Harfenist and Mac Dowell 2001). Thus, eradication efforts should be focused on near shore islands at times when seabirds are absent from the colony (Drever 2004) and when predator ecology is favourable.

Furthermore, it is important to reevaluate management measures to reduce costs, and target audiences that are directly impacting the success of invasive species introduction. In 2016, Parks Canada and B.C. Parks requested a report about best management practices for biosecurity in important bird areas of Haida Gwaii (Gill et al. 2016). Coastal Island Conservation reviewed management practices and reported that efforts to eradicate and prevent rats from (re)colonising Haida Gwaii islands should be deployed in parallel to raising awareness of target audiences contributing to the spread of invasive species (e.g., fishermen, tourists). Coastal Conservation emphasised the importance of communicating negative impacts of invasive alien species to broad audiences that involuntarily spread of these species such as boaters, fishermen, and tourists by distributing infographics in target media and venues. Furthermore, the need to develop a vessel screening protocol, and better enforcement of food and waste management were also stressed as important measures for bird area biosecurity. For instance, such measures would be particularly relevant in maintaining Langara Island's ancient murrelet colony rat free as the only touristic attraction located on the island is a fishing lodge. They suggested reducing management costs (monitoring, having trained staff to eradicate species and survey bird colonies, etc.) by designating one entity such as Parks Canada or a non-government organisation that would be responsible for implementing the biosecurity plan in all bird areas and that would pool resources from all local organisations. Similar management measures (e.g., increasing social awareness, collaborating with local communities) are identified as essential steps for large-scale eradications in other countries where invasive species destroyed ecosystems. The last decades of eradication efforts in New Zealand bring forward that "scaling up" of eradication is not sufficient to rid the island of pests by 2050; coordination between local communities and governmental agencies implementing eradication is necessary, especially in scenarios where pests are found within communities and on private land (Peltzer et al. 2019). The last decades of invasive species management in Haida Gwaii have focused efforts in Gwaii Haanas National park as well as wildlife reserves, however to prevent re-colonization of islands by invaders, extending efforts beyond these places should be considered.

2.4.2 Post-eradication efforts to increase colony attendance

Major et al. (2011) established that post rat eradication in 1997, although ancient murrelet colony size increased at McPherson point on Langara Island, the trends at that site were not indicative of definitive colony recovery pot-eradication. Rat eradication stopped further local decline of ancient murrelets on Langara Island, however additional factors of colony success (e.g., variations in SST, gill net entanglement, fishing activities) might still prevent recovery (Bertram 1995). Kappes and Jones (2014) identified passive recovery (i.e. letting the birds re-colonize the island post-eradication without further management) as a poor method to ensure ecosystem restoration post eradication. Seabird colonies are unlikely to fully recover passively on islands where ecosystems were modified by invaders, especially if no source-populations exist within a 25 km radius (Buxton et al. 2014). Active restoration techniques such as call playback, the use of mirrors, were successful in 83% of restoration projects involving Procellariidae, but far less successful with Phalacrocoracidae (Kappes and Jones 2014) suggesting that such techniques are species-dependent. Under the 2019 Multi-species Action Plan for Gwaii Haanas (developed under the Species at Risk Act) active-restoration techniques were listed as a measure to be used to increase ancient murrelet recovery. Considering meta-population dynamics observed for the species within the archipelago, these active restoration techniques should also be used on islands outside of Gwaii Haanas National Park to ensure recovery.

2.4.3 Considering deer in seabird management plans

Although management of sitka black-tailed deer in Haida Gwaii receives attention due to these grazers modifying plant communities (e.g., the "“Llgaay gwii sdiihlda: Restoring Balance” is an active plan since 2017 to eradicate deer in Gwaii Haanas in order to restore the forest undercover and bring back traditional plants) and causing a decrease in songbird populations by as much as 55-70% (Allombert, Stockton and Martin 2005; Veitch et al. 2019), the impacts of deer on seabird breeding habitat are not assessed thoroughly or quantified. Deer browsing reduced vegetation cover in the forest understory thereby changing the seabird breeding habitat in Haida Gwaii, especially on shorelines where vegetation cover is reduced faster than in the interior forest (Martin et al. 2010). If burrows were once concealed by shrubs and vascular plants it is no longer the case; islands where deer have been present for 20 years and more have reduced shoreline vegetation, whereas islands where deer have been present for 50 years have simplified (vegetation is less diverse, and cover is reduced in the understory) vegetation on both shorelines and in the interior forest (Martin et al. 2010). Once burrows are exposed, seabirds experience increased predation by avian predators (e.g., crows, ravens, gulls) (Martin, Allombert and Gaston 2008). The effects of grazing by sitka black-tailed deer on seabird colony success is yet to be quantified (Harfenist, Sloan and Bertram 2002). Increased avian predation in habitats that severely browsed by ungulates occurs in other contexts; soay sheep (*Ovius aries*), an invasive grazer at Hirta Island, decreased brush cover on the island reducing protection for Leach's storm-petrels from avian predators (Jones 2013). Seabirds (e.g., ancient murrelets, storm-petrels) that breed exclusively in mature forests or prefer vegetated areas (Vermeer and Lemon 1986; Rodway, Lemon and Kaiser 1988; Gaston 1992) are most likely to be concerned by these vegetation changes. For instance, Vermeer and Lemon (1986) note that only 3 ancient murrelet burrows were located in rock crevices and Gaston (1992) confirms that in Haida Gwaii, ancient murrelets will only breed in mature forests. Thus, this species could be particularly vulnerable to deer browsing. Other seabird species in Haida Gwaii (e.g., tufted puffins, pigeon guillemot) can successfully breed on islands free of vegetation and relocated their colonies when affected by rat and raccoon predation. Thus, deer pose a different level of indirect threat to burrowing seabirds of Haida Gwaii that remains to be quantified.

Elsewhere, deer cause direct damage to seabird burrows: 12% of rhinoceros auklet burrows at a colony in Washington were damaged by deer (Pearson et al. 2009). Additionally, grazing by cattle and rabbits is a serious threat for seabirds breeding along B.C. coastlines, such as the pink-footed Shearwater according to COSEWIC; grazers caused structural damage at 48% of the burrows in some instances, and the colony occupancy was at ~20% before grazer eradication (COSEWIC 2016).

Another justification to consider deer in seabird management plans can be found in the bait competition between sitka black-tailed deer and rats. During the pre-implementation of rat eradication programs on Faraday and Murchison islands, bait competition between deer and rats reduced eradication success; rodenticide uptake was reduced for rats, and uptake of rodenticide by deer increased the risk of secondary poisoning for native scavengers (e.g., ravens, crows, black bears, bald eagles, gulls) (Gill et al. 2014). Deer culls were implemented prior to rodenticide deployment and deer populations were reduced, but not eradicated. Deer management remains a major consideration in the successful management of rats in Haida Gwaii.

Invasive mammals altered Haida Gwaii burrowing seabirds since their introductions in the last centuries, whether it is by directly preying upon individuals and eggs, by damaging their burrows, or by altering the nesting habitat. As these species continue to be present in Haida Gwaii, broader ecosystem changes (e.g., nutrient cycle disruption, environmental physical alterations through herbivory) are likely to occur (Simberloff 2014). For instance, by preying on seabirds, rats disrupted the nutrient flow on New Zealand islands. A seabird decline led to changes in egg shell, guano and dead bird inputs that contribute, in nutrients, to below-ground communities (e.g., microbial communities).

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CHAPTER 3

Ecological changes on SG̲ang Gwaay over the last millennium: tracking long-term forest changes and avian activity with respect to human settlement and invasive species

3.1 Abstract

Large-scale anthropogenic disturbances of forest ecosystems can be dramatic, causing immediate vegetation loss. Comparatively, long-term small scale ecosystem changes are difficult to track, yet they can still have long-term implications for community composition and geological processes. We used a paleolimnological approach combining sterol and stanol lipids, stable carbon (C) isotopes, inferred lake-water total organic carbon (TOC), diatoms, and chlorophyll *a* to assess terrestrial and aquatic changes on SG̲ang Gwaay (Haida Gwaii, B.C.). We interpret these changes as they relate to European contact, and historical events at the former Ninstints village (UNESCO heritage site), with the objective of unveiling long-term trends in C allocations in insular ecosystems. In doing so, we use paleoecological tools to help uncover anthropogenic impacts on long-term C cycling. Stable isotopes, sitosterol, and campesterol indicate that historically the C in the pond was predominantly from terrestrial plants (allochotonous). After ~1588 CE, C is autochthonously-derived with an increase of aquatic primary productivity and changes in lake trophic status. TOC declines from 22 to 15 mg L^{-1} after ~1250 CE until present, $\delta^{13}C$ values decline until present, and C/N declines from 37.5 to ~23. Pond primary production changes in ~1388 CE with a peak in chlorophyll *a* and a shift in diatom assemblages, which likely tracks a pH increase and change in light availability within the pond, as a benthic/tychoplanktonic diatom species becomes dominant. The decline of sitosterol and the increase of campesterol in lake sediments indicate the beginning of a shift in phytosterol origin in the pond starting ~1250 CE and a complete transition to autochotonous C sources after ~1625 CE when sitosterol/campesterol falls below a ratio of 6.6. Our results demonstrate that small-scale sustainable tree harvesting has a significant impact on island C allocations, aquatic primary production, and lake trophic status. PCR indicates that rhinoceros auklets and Keen's mice were present on SG̲ang Gwaay throughout the ~1300 year time period. A first decline in ornithogenic trace-metals occurs in ~1526 CE and a second decline in ~1790 CE. δ^{15}N values decline starting ~1385 CE until present. With ~70% of rhinoceros auklets breeding in Canada, these results are informative for the conservation status of the species.

3.2 Introduction

3.2.1 Insular ecosystems: sentinels to understanding ecological change

Multiple environmental stressors make it difficult to build effective management policies for the conservation of ecosystems and wildlife populations. For example, the baseline abundance of a population can be misinterpreted or even unknown and the mechanisms of population decline are hard to uncover, especially in situations when species are difficult to survey and sites are heavily degraded (Freud and Willis 2008; Desroches et al. 2013; Gonzalez et al. 2016). Although the concept of ecological "baselines" is debated as no past ecosystem state should necessarily provide a template for restoration (Alagona, Sandlos, and Wiersma 2012), there is value in uncovering historical eocosystem trends to understand how environmental change affects living organisms and has shaped the modern ecosystem in which we base our research. An even greater difficulty lies in assessing ecological changes at broad time scales and large geographic extents such as changes in carbon (C) cycling, affected by landscape changes (Schimel 1995) and changes in wildlife populations that follow long-term population cycles (Duda et al. 2020c).

Islands are more sensitive to change with many insular ecosystems rapidly collapsing following the introduction of invasive species, anthropogenic activities, or climatic events (Reaser et al. 2007; Paxton et al. 2016; Bergstrom, et al. 2021). Limited resources and a diminished biological pool preventing genetic rescue are factors contributing to the fragility of insular ecosystems. Islands can be sentinels of ecological changes at larger scales helping to identify mechanisms of collapse as insular ecosystems respond to environmental changes more rapidly (Bergstrom et al. 2021). Rapa Nui provides an example of ecosystem collapse caused by the coupling of climate and ancient civilization's use of the land. Polynesian clearing and use of the forest led to palm tree extirpation in the 17-18th centuries and the disappearance of shrubs, herbaceous plants, and grasses (Horrocks et al. 2015, Wozniak 2022). Palynological studies also reveal that expansion and regression of the palm tree forest was sensitive to natural climatic patterns which was exacerbated due to a tipping-point by human driven land-use change. However, our knowledge regarding how ancient civilizations affected insular ecosystems remains limited.

Globally seabirds have declined since the 1950s (Paleczny et al. 2015) with biological invasions being one of the largest causes of decline (Dias et al. 2019). Islands are hotspots of biological invasions across taxonomic groups (Dawson et al. 2017). Establishing management of invasions on islands to restore habitat and eradicate invasive predators is a tangible way to help mitigate the decline of pan-global organisms such as seabirds threatened by anthropogenic disturbances across legal boundaries and governing bodies (e.g., gill-net entanglements, pollution, fishery collapse) (Paleczny et al. 2015).

3.2.2 Tracking the C cycle over long time scales

Current models used by the Intergovernmental Panel on Climate Change (IPCC) cannot reliably predict changes in organic C at fine-scales (i.e., nationwide to private land scale); however, Smith et al. (2012) argue that a better understanding of C soil dynamics, storage, and primary productivity is needed to gain accuracy at small geographic scales. Furthermore, land-use history is often unknown making it difficult to establish a baseline and therefore use predictive models of C stocks (Smith et al. 2012). Vegetation turnover disturbance and biome shifts contribute to the uncertainty of ecosystem models predicting the future terrestrial C cycle (Ahlström et al. 2015). Thus, understanding past vegetation changes over long time scales with respect to stressors helps uncover long-term C dynamics and can provide insight about how to adapt modern management.

Managed forests, as opposed to unmanaged ones, have a reduced C pool; trees are younger and most C is allocated to above-ground growth (leaves, trunk), as opposed to stored in roots, thus depleting the soil C (Noormets et al. 2015). The extent of C loss is dictated by the time and intensity of harvesting, as well as the replacement rate of harvested trees (Arneth et al. 2017). Thus, land use, as well as species ecology, plays an important role in C cycling with intensive tree removal depleting C pools by eroding soils and preventing vegetation replacement (Arneth et al. 2017).

3.2.4 Tracking seabirds over long term time scales

The behavioural ecology of seabirds often forces monitoring to happen during the breeding season when birds are on land; monitoring efforts can be costly and often requires the travel to remote locations. Thus, monitoring efforts are often constrained by these factors and cannot be consistent. Furthermore, burrowing seabirds can be especially laborious to survey; methods of assessing occupancy include: examination of burrow characteristics, response to audio vocalization playback, removing birds from burrows, using cameras, however these methods have varying degrees of certainty (Lavers, Hutton and Bond 2019). While longer term data is available for some populations, no population data is available prior to the mid 20th century for any seabird species (Sun et al. 2013; Paleczny et al. 2015; Duda et al. 2020a), thus understanding long-term population dynamics pinpointing causes of decline and establishing targets for conservation can be challenging.

3.2.5 Paleoecology: a multi-proxy approach to a multi-stressor question

Paleolimnological records can be used to understand past vegetation and landscape changes as they relate to human civilizations. For example, pollen analysis and $\delta^{15}N$ values were used to track agriculture commensalism that dictated the present-day landscape of the Western Liaohe River Basin, Mongolia (Li et al. 2006), and $\delta^{13}C$ values were used to track eutrophication from Iroquois horticultural activities between ~400-1200 CE (Crawford Lake, Canada) that altered diatom assemblages more significantly than subsequent agriculture in the ~1800s (Ekdahl et al. 2004). Holocene paleolimnological records also show that land use change can have the greatest immediate impact on the C cycle; increased erosion through vegetation removal leads to higher sedimentation rates with lower C content (minerogenic inwash) (McGowan et al. 2016).

Research demonstrates how historical human cultures can alter C cycling, although most studies are centered on agricultural practices and mainland civilizations. For instance, in Scandinavia, long-term lake-water TOC declines between 1450-1600 CE were associated with the expansion of summer forest grazing and farming, thus proving that the impact on TOC resulting from use of forest resources by early civilizations has been underestimated (Meyer-Jacob et al. 2015).

Changes in wildlife populations can also be tracked using a multi-proxy paleoecological approach. For example, the sediment biogeochemical signatures of Adélie penguins yielded historical population trend data and provided insight about food webs and contaminant dispersal (Sun et al. 2013) and a multi-proxy analysis revealed the decline of a storm-petrel population on Colombier Island post European contact in the 19th century (Duda et al. 2020a). Ecological archives in sediments can help distinguish climate and anthropogenically driven changes in contemporary seabird populations (Sun et al. 2013; Duda et al. 2020a) and are a significant step forward in biological conservation and management.

Palynological changes on SG̲ang Gwaay (Haida Gwaii, British Columbia) over the last millennia showed a decline in Western red cedar (*Thuja plicata*). Here, we assess the long-term ecosystem impacts of relatively sustainable tree harvest on SG̲ang Gwaay over the last millennium augmenting past vegetation changes first reported by Lacourse, Mathewes and Hebda (2007) and seabird population trends complementing ongoing monitoring efforts reported by Rodway and Lemon (2011).

3.2.6 Haida Gwaii: a millennium of land-use changes from the Kunghit Haida to European contact and UNESCO status

Haida Gwaii is a remote archipelago of ~ 150 islands off the coast of British Columbia in the North Pacific (Moss 2008). Archaeological evidence suggests that 10,000-13,000 years ago, shortly after the last glaciation, Haida Gwaii formed a narrow ice-free sheet that facilitated human settlement of the Americas from Asia (Reimchen et al. 2005; Hayward 2012). Oral history and artifacts found on sites of Haida settlements, as well as paleoecological records, provide evidence that Haida Gwaii was populated by humans and wildlife in the late Pleistocene during sea level rise (Lacourse, Mathewes and Fedje 2005; Reimchen et al. 2005; Moss 2008). Several Haida settlements were established after the time of crossing; occupied sites were initially scattered throughout the coastline. SG̲ang Gwaay ("Red Cod Island") was occupied by the Kunghit Haida since 360 CE making its Ninstints ("the one that is two") village site the southernmost, largest and longest occupied settlement (Acheson 1995). The village was occupied year-round and population started expanding around ~1235 CE and today's archeological remains reveal 20 houses of an average floor area of 109.06±43.37 m^2 (Acheson 1995, Lacourse, Mathewes and Hebda 2007)

Western red cedar (*Thuja plicata*) was an essential cultural resource for the Haida (Garibaldi and Turner 2004). The construction of a house in Haida settlements involved the harvest of large trees on a site recognized as belonging to the family of the chief, or a site to which he could buy harvest privilege from another family. Thus, harvest sites could be on nearby islands and taking down a tree could involve to forty men in 5-6 people canoes and skidding with cedar ropes to bring the chosen trees to the house site (MacDonald 1983). These dwellings were less used during the summer as people dispersed throughout the islands using cedar canoes to take advantage of seasonal marine and land resources, however the village site was occupied year-round (Acheson 1995, Moss 2008). Large red cedars were also used to carve totem poles which were erected at the entrance of the house. Some of these poles can still be seen today at Ninstints (MacDonald 1983; Acheson 1995; Moss 2008). The historical use of red cedar can be tracked in the palynological record of SG̲ang Gwaay with a significant decrease in *T. plicata* pollen after ~950 CE (Lacourse, Mathewes and Hebda 2007). Other species were used for firewood, and some plots on the island might have been burned to favour growth of fruit-bearing brush (Lacourse, Mathewes and Hebda 2007). Despite this decrease in pollen implying a decline of the red cedar population on the island, western red cedars persisted in Haida Gwaii as sustainable harvest of mature, large trees was targeted by the Haida. In cases when only the bark of the tree was needed, the Haida stripped part of the tree from its bark. This practice can still be noted on some red cedars on SG̲ang Gwaay today (MacDonald 1983; Lacourse, Mathewes and Hebda 2007). Today, although its use has diminished, western red cedar is still of immense cultural importance for the Haida and contributes to the peoples' approach to using the land sustainably and advocating for the development of conservation areas to preserve the remaining trees (Garibaldi and Turner 2008; Zahn, 2018).

European contact in the late 18th century (~1741-1774) brought many changes to the archipelago: new fauna and flora species were brought to the islands and diseases (e.g., smallpox, scrofula) impacted settlements across Haida Gwaii. The population of SG̲ang Gwaay declined to 308 people in 1836-1841 (Acheson 1995); however, the smallpox epidemic of 1887-1888 CE led to evacuation of Ninstints leaving the island without any inhabitants as most people relocated to larger settlements (e.g., Massett, Daajing Giids) (Acheson 1995, Lacourse, Mathewes and Hebda 2007). The former village became a UNESCO World Heritage Site in 1981.

To understand the ecological impacts of apparently sustainable tree harvest on islands, we used a high resolution paleoecological record from SG̲ang Gwaay to track long-term vegetation changes on the island over ~1300 years and compare vegetation changes to historical events (e.g., European contact, changes in Haida use of the land, population expansion at Ninstints, and village abandonment). Establishing an age-depth relationship for the core using ^{210}Pb and ^{14}C radioisotopes, we interpreted changes in vegetation along with elemental chemistry and stable isotopes (δ^{15}N, δ^{13}C, C/N), inferred lake-water total organic carbon (TOC), diatom assemblage changes, and trends in chlorophyll *a*, as well as tracking the settlement at Ninstints using human-produced fecal coprostanol. Changes in vegetation were tracked using plant phytosterols, campesterol and sitosterol, as well as stigmastanol, the microbially-reduced version of sitosterol. Individual sterols and stanols and ratios informed on changes in terrestrial and aquatic vegetation and pond microbial activity. Additionally, as the pond is in proximity to a rhinoceros auklet (*Cerorhinca monocerata*) colony, a seabird of cultural importance to the Haida, we aimed to track long-term changes in the seabird population, assessing the impact of harvesting and invasive species with ornithogenically-enriched trace-metals, sterols and stanols, stable isotopes, and sedDNA. This multi-proxy approach provides several independent measures of vegetation dynamics, seabird and invasive species population abundances over time at SG̲ang Gwaay, B.C.

3.3 Materials and Methods

3.3.1 Study area

The study pond is located on SGang Gwaay (52°05’29.5’’N, 131°212’43.9’’W; google maps 52.091532, -131.212205) and at its easternmost edge, the pond is ~24 m from the ocean. SGang Gwaay is within Gwaii Haanas National Park, B.C., in the Haida Gwaii archipelago and the pond is in proximity (~800 m) to Ninstints, an extant village established 1590±160 BP (~360 CE) and occupied for ~1550 years by the Kunghit Haida (Fig. 3.1). Ninstints was the largest and longest occupied Haida village within the archipelago (Acheson 1995). Haida settlements were occupied year-round and were composed of cedar-plank houses accommodating several members of a lineage group. The climate in this region is a mild and temperate with annual temperature variations of ~20 degrees Celcius. The pond is surrounded by a forest composed of Western hemlock (*Tsuga heterophylla*), sitka spruce (*Picea sitchensis*) and Western red cedar (*Thuja plicata*) forest with a moss-rich understory. The immediate area surrounding the southwest and northwest side of the pond is marsh-like with grass tussocks and sedges. On the east, the pond is adjacent to a rock shelf dropping into the ocean. Lacourse, Mathewes and Hebda (2007) identified a significant decline in Cupressaceae pollen on SGang Gwaay linked to the harvest of large cedar trees by the Haida. We collected two sediment cores from the deepest part of the pond.

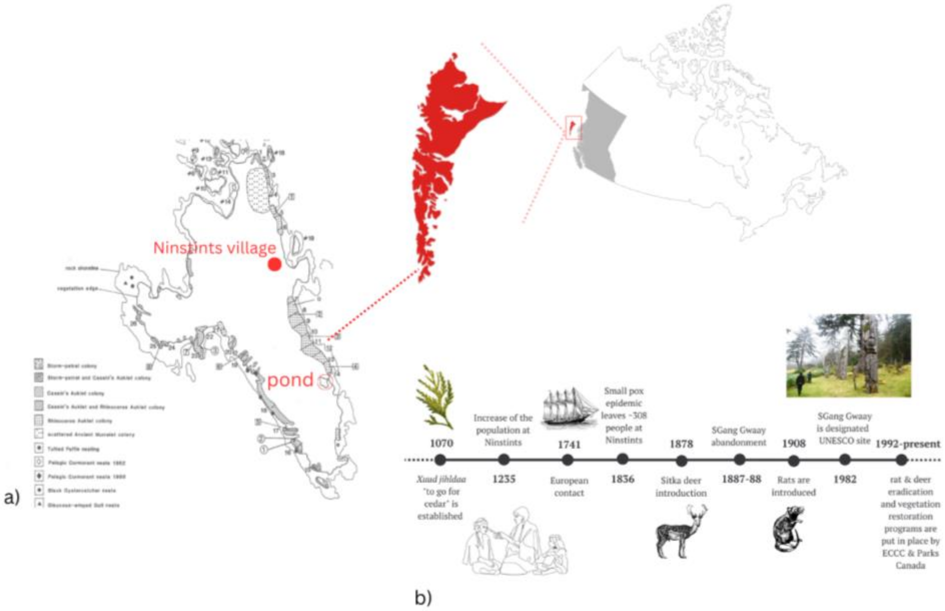

Figure 3.1. (a) SG̲ang Gwaay Island and a timeline of historical events. (b) The Haida settlement at Ninstints village, surrounding seabird colonies, and the SG̲ang Gwaay pond where sediment samples were collected in July 2021.

Previous to our study, a 106 cm long sediment core, dating back to 1750±120 cal BP, was extracted from the SG̲ang Gwaay pond in 1984 (Hebda and Mathewes 1986). Pollen and macrofossil analyses revealed vegetation changes on the island within the timeline established by the radiocarbon dating, and indicated that the vegetation changed very little for ~1800 years; *Picea sitchensis* and *Tsuga heterophylla* dominated the forest, while the understory was dominated by *Alnus crispa* and Polypodiaceae ferns (Lacourse, Mathewes and Hebda 2007). A notable finding, however, was the decline of *Thuja plicata* at ca. 1000 BP, or ~500 years following the establishment of the Haida village. This decline was explained by the selective harvest of *T. plicata* by the Haida for the construction of monumental poles, houses, canoes, clothing, mats, baskets, and cordage. Soil samples were also analysed for pollen and showed an expansion of the Haida settlement ~600 BP through the decrease in *Picea* pollen, possibly indicating a removal of trees as the village site expanded (Lacourse, Mathewes and Hebda 2007).

The pond is also surrounded by a colony of rhinoceros auklets (and in proximity to a Cassin's auklet colony breeding on the opposite shore of the island, ~400 m away; Fig. 3.1). Following European contact, invasive species (e.g., Norway rats (*Rattus Norvegicus*) and Black rats (*Rattus rattus*), Sitka black-tailed deer (*Odocoileus hemionus sitkensis*)) were introduced to the islands, changing ecosystem dynamics at seabird breeding colonies in Haida Gwaii (Rodway, Campbell and Lemon 2019). The rhinoceros auklet colony is a permanent monitoring plot established in the 1980s by Environment and Climate Change Canada (ECCC), and therefore data is available for the last four decades. Starting in 1995, rat eradication programs and deer reduction programs were deployed within Gwaii Haanas to restore vegetation and prevent further predation of seabirds by rats during the breeding season (Rodway, Campbell and Lemon 2019). Recently vegetation restoration programs were deployed to mitigate the impacts caused by deer browsing on the forest understory under Park Canada's "Llgaay gwii sdiihlda: Restoring Balance Project".

3.3.2 Core collection

In collaboration with Parks Canada, we extracted two complete sediment cores (core 1 at 128 cm long, and Core 2 at 123 cm long) from SG̲ang Gwaay in July 2021. Each complete core sequence was composed of three smaller cores of ~50 cm with an overlap of 15 cm between cores. Thus, a total of six ~50 cm cores were extracted from the pond to obtain two complete sediment records of ~100 cm. The pond is shallow and has a maximum depth of 78 cm, and the top, watery segment of each core was extracted with a push-corer adapted to shallow lakes (Glew and Smol 2016) and the two bottom segments were extracted with a Russian peat corer with a barrel length of 50 cm and diameter of 6 cm. Core 2 was used for most analysis, although some sedDNA and trace-metals were sampled from Core 1, as discussed below.

The cores extracted with a push-corer were sectioned in 0.5 cm increments on-site using a Glew extruder (Glew 1988). Sub-sampling for sedDNA was done in the field. The remoteness of the sampling location prevented sectioning and subsampling to occur in a clean, sterile environment. In such cases when subsampling in clean, sterile environments (e.g., dedicated laboratory room) is not possible and/or it is logistically impossible to freeze a continuous sediment core to subsample later, subsampling in the field should be prioritized (Brasell et al. 2021). Thus, we prioritized subsampling DNA in the field and freezing samples as quickly as possible to maintain DNA intergrity and prevent biological activity (e.g., microbial activity) from affecting subsequent DNA analysis. The subsampling method was similar to the one described by Lejzerowicz et al. (2013): sedDNA was subsampled from the center of 0.5 cm core increments as they were sectioned. To prevent contamination, sedDNA samples were collected using sterile microbial loops and sealed in sterile 15 mL centrifuge tubes. Sediment samples were refrigerated, and sedDNA sub-samples were frozen the day of collection. The cores extracted with a Russian peat corer were transferred to aluminum foil and sectioned in 0.5 cm increments off site using a sterile knife, cleaned with alcohol between each sample. Sub-sampling for sedDNA from the center of the 0.5 cm core increments occurred at that stage to prevent sample contamination. Sediment samples were kept frozen at -80°C prior to being freeze dried for 48 h for stable isotopes, lipids, radiocarbon and ^{210}Pb dating, chlorophyll *a*, trace metals, and diatom analysis. sedDNA samples were kept frozen at -80°C prior to isolations for PCR.

3.3.3 Surface water sample collection

Pond water was collected on August 8th, 2022 in 1.0 L Nalgene bottles and refrigerated until processing. Samples were filtered and sent to the National Laboratory for Environmental Testing (NLET, Burlington, ON) to be analyzed for nutrients, major ions, and trace metals using their standard procedures (Environment Canada Manual of Analytical Methods 1994a, 1994b).

3.3.4 Faecal sample collection

Faecal samples from Sitka black-tailed deer were collected on SG̲ang Gwaay in July 2021 and kept frozen. Rhinoceros auklet and Cassin's auklet cloacal swabs for DNA analysis were collected on Pine and Triangle Island under banding permit SC-BC-2021-10667 F in 2021, and additional faecal samples of rhinoceros auklets from Triangle Island were collected directly on aluminum foil for stable isotopes, metals, and lipids analyses under scientific permit SC-BC-2022-0015-01 in 2022.

3.3.5 Chlorophyll a and lake-water TOC

Trends in the sedimentary concentrations of chl *a,* a proxy for pond primary production and trophic status, were measured at PEARL following methods outlined by Michelutti et al. (2010). This method also measures all the isomers of chlorophyll *a* as well as its main diagenetic products (Michelutti et al. 2010; Michelutti and Smol 2016). Freeze-dried sediments were sub-sampled every centimeter in each core and placed in scintillation vials to be measured with visible range spectroscopy (VRS) using a model 6500 Rapid Content Analyser (FOSS NIRsystems Inc.). Chlorophyll *a* concentrations were calculated using an improved model, namely a log-transformed regression of the equation from Michelutti et al. (2010). Inferred chl *a* values were used to establish periods of change in the pond primary production, and align overlapping cores based on trend similarities. Past total organic carbon (TOC) concentrations in the pond water were reconstructed using methods similar to chlorophyll *a* and include dissolved organic carbon (DOC). The complete visible near-infrared (VNIR) spectra between 400-2500 nm were recorded using a 6500 Rapid Content Analyser (FOSS NIRsystems Inc.). The diffuse reflectance (R) of light in the VNIR regions was transformed to apparent absorbance (A) with the equation A=log(1/R). Fuinally Orthogonal Partial Least Squares regression modelling was used to establish the calibration model between the VNIR spectra and TOC concentration in the surface water. The methods are outlined in Meyer-Jacob et al. (2017).

3.3.6 Diatoms

Diatoms were analyzed from 0.1 g of freeze-dried sediment subsampled at every 0.5 cm interval of Core 2. The 0.1 g of freeze-dried sediment was digested using a 1:1 molecular weight ratio of sulfuric and nitric acid and heated at 80°C for 2 h. After that, the resultant slurry was neutralized by consecutively rinsing with deionized water. Once a neutral pH was reached, aliquots of the slurry were pipetted onto coverslips which were mounted onto slides using Naphrax®.

At least 400 diatom valves were counted and identified for each sediment interval using sample preparation techniques summarized in Rühland and Smol (2002). Diatoms were identified to the lowest taxonomic level using a Leica DMRB microscope under oil immersion at 1000× magnification, mainly following the taxonomy of Krammer and Lange-Bertalot (1986–1991), and Antoniades et al. (2008). Diatom count data were transformed to relative abundances and a stratigraphy was prepared in Tilia software (ver. 2.6.1, E. C. Grimm, Illinois State Museum Research and Collections Center, Springfield, IL, USA).

3.3.7 Establishing core chronologies

Chronologies were established for both cores (Core 1 and Core 2) using radioisotopes ^{14}C, ^{210}Pb and additional ^{208}Pb/^{206}Pb, ^{206}Pb/^{207}Pb ratios were used for core 1 to generate reliable chronologies. For both cores, sediments from the top of the push core (Core 1: n = 7, Core 2: n = 8) were dated through ^{210}Pb analysis using gamma spectrometry at Queen's University Paleoecological Environmental Assessment and Research Lab (PEARL) following methods described by Appleby (2001). Ages for each sample were generated with the Constant Flux Constant Sedimentation (CFCS) model as the samples failed the assumptions of the more frequently used Constant Rate of Supply (CRS) model. The R package "serac" (Bruel 2020) was used to visualize the CFCS model for each core and generate chronologies for intermediate samples that were not dated with radiometric techniques.

Older samples (>~150 years) of the core ($n = 6$) were dated with radiocarbon analysis. Macrofossils of well-preserved pine needles (*Picea sitchensis*), Sitka alder cones (*Alnus viridis*), and wood fragments were used as available in samples to determine ^{14}C ages with accelerator mass spectrometry in samples older than ~150 where ^{210}Pb activity was low. Analysis was performed at the University of Ottawa André E. Lalonde Accelerator Mass Spectrometry (AMS) Laboratory with macrofossil samples (pine needles, tree bark, pinecones; images available in Appendix I Fig.S-1). Age-depth modeling was performed in R using results from ^{210}Pb analysis and ^{14}C analysis. Radiocarbon dates were calibrated to calendar years using the 'IntCal20' calibration curve. A compound Poisson-Gamma model (Haslett and Parnell 2008) was used to calculate the continuous chronology of Core 2 with the function ‘Bchronology’ in the R package ‘Bchron’ v 4.7.6 (Haslett and Parnell 2008) with the ^{14}C and ^{210}Pb dates and dates identified by $^{206}Pb/^{207}Pb$ and $^{208}Pb/^{206}Pb$ when available. This package was selected as opposed to other available packages that model age-depth relationships as it takes into consideration age inversions.

3.3.8 %C, %N, and Stable isotopes

Samples were weighed out in 7x7 mm tins and an initial analysis was carried out at MUN’s TERRA. For organic carbon (OC) analysis, a set of samples were pre-treated with HCl following methods outlined in Komada, Anderson and Dorfmeier (2008) to determine $\%C_{org}$ and $\delta^{13}C_{org}$. The standards used to calibrate the instrument for ^{13}C isotope analysis were CaCO3 ($\delta^{13}C$ = -40.12±0.09‰) and D-fructose $\delta^{13}C$ = 71.03±0.78‰). IAEA-N-2 ($\delta^{15}N$ = 20.32± 0.12 ‰) and USGS 25 ($\delta^{15}N$ = -30.25 ± 0.21 ‰) were used to calibrate the instrument for ^{15}N. Acetanilide was used to prepare a %C and %N calibration curve for elemental analysis. Values of $\delta^{15}N$, $\delta^{13}C$ and $\delta^{13}C_{org}$ were reported in parts per thousand (‰). The ratio ^{13}C is measured with $R = {}^{13}C/{}^{12}C$ for each sample and compared to the R value of a standard specific to the element of interest, thus the $\delta^{13}C$ is given by $[(R_{sample}/R_{standard})-1] \times 1000$. Nitrogen ratios are calculated with similar formulas.

Additional stable isotope analysis ($\delta^{15}N$, $\delta^{13}C$) was carried out at the Ján Veizer Stable Isotope Laboratory at the University of Ottawa where an elemental analyzer (Isotope Cube, Elementar, Germany) coupled with an isotope ratio mass spectrometer (Delta Advantage, Thermo, Germany) was used to determine isotopic ratios and carry out elemental analysis. Internal standards used are: (in ‰ for $\delta^{15}N$, $\delta^{13}C$) are C-51 Nicotiamide (0.07,-22.95), C-52 mix of ammonium sulphate + sucrose (16.58,-11.94), C-54 caffeine (-16.61,-34.46), blind std C-55: glutamic acid (-3.98, -28.53). Values are reported in delta notation d, the units are per mil (‰) and defined as d = ((Rx-Rstd))/Rstd)*1000 where R is the ratio of the abundance of the heavy to the light isotope, x denotes sample and std is an abbreviation for standard. $\delta^{15}N$ is reported as ‰ vs. AIR and normalized to internal standards calibrated to international standards IAEA-N1(+0.4‰), IAEA-N2(+20.3‰), USGS-40(-4.52‰) and USGS-41(47.57‰).

Changes in C/N ratios were analyzed alongside changes in chlorophyll *a* and compared with pollen changes identified by Lacourse, Mathewes and Hebda (2007) to differentiate the origins (terrestrial, lacustrine) of carbon in the pond sediments.

3.3.9 Geochemistry

Freeze dried and ground sediment samples of the surface of Core 1 were sub-sampled at 3 cm intervals and analysed for elemental concentrations at SGS Inc. (Lakefield, Ontario). Due to high water content of the sediments, there was not enough sediment remaining in Core 2 for metal analysis. Total metal(loid) concentrations were analysed using Inductively Coupled Plasma Mass Spectrometry (ICP-MS). Concentrations were reported in $\mu g\ g^{-1}$ and values below detection limits (0.07 $\mu g\ g^{-1}$) were replaced with MDL/√2 (Hornung and Reed 1990). A total of thirty-four metal(loids) were analyzed. SG̲ang Gwaay is located on the upper triassic Karmutsen formation composed of basalts and therefore the concentration metals were normalised to titanium to account for weathering (Hornung and Reed 1990; Dostal et al. 2010).

Herein we were interested in lead isotopes to supplement depth-date models. Changes in lead isotope ratios ($^{206}Pb/^{207}Pb$ and $^{208}Pb/^{206}Pb$) are indicative of the phasing out of leaded gasoline in Canada as of 1974 and were used to confirm chronologies in the top part of the core (Bagur and Widory 2020).

An additional trace-metal analysis was carried out for fecal samples of Rhinoceros auklets from colonies in B.C. (Pine Island, Triangle Island) as, to our knowledge, there is no available data for this bird species and enrichment factors at Western-Pacific colonies. To meet minimum weight for analysis, samples from 14 different birds were used in two different samples ($n = 2$) for trace-metal analysis. Results were compared with data from three previous studies reporting on metals bioenriched by rhinoceros auklets and other Charadriiformes. Shoji et al. (2018) previously identified mercury (Hg), and cobalt (Co) as bioenriched at Rhinoceros auklet colonies in Japan, and De La Peña-Lastra et al. (2022) identified cadmium (Cd) and lead (Pb) as the main metals excreted by Charadriiformes. Additionally, Grant et al. (2022) identified arsenic, Cd, and Pb at higher concentrations in Charadriiform faecal samples compared to other seabird species.

3.3.10 Lipids

Sedimentary sterols and stanols were determined using methods adapted from Hargan et al. (2019). Our analysis targeted sterols and stanols that are proxies for vegetation, seabirds, mammals (e.g., deer), and humans. Sitosterol, stigmastanol, and campesterol can be used to discriminate between vegetal inputs of marine or terrestrial origin in water catchments (Volkman 1986; Meyers and Ishiwatari 1993). Specifically, the ratio of sitosterol/campesterol can be used to distinguish between higher plants and microalgae inputs (Carreira et al. 2002; Zhang et al. 2018). Other relevant ratios include sitosterol/stigmastanol, a ratio that informs on hydrogenation and sitosterol/cholesterol, a ratio used to track sewage input and phytoplankton productivity in instances where anthropogenic runoff is unlikely to be the main source of cholesterol (Zhang et al. 2018; Mudge et al. 1999). Seabird inputs were tracked using cholesterol (cholest-5-en-3β-ol), a sterol present in cell membranes of vertebrates, and its microbially-reduced product, cholestanol (5α-cholestan-3β-ol); plants were tracked with sitosterol (β-sitosterol) and its microbially reduced from stigmastanol (5α-stigmastan-3β-ol), campesterol; coprostanol tracked human inputs to the pond. Cholesterol is present in vertebrate tissue and feces. This sterol and its microbially reduced product, cholestanol, are used to track inputs from seabirds to ponds (Duda et al. 2020b). Herein we used the expanded "seabird index" (cholesterol+cholestanol/cholesterol+cholestanol+sitosterol+stigmastanol) described by Hargan et al. (2018), to estimate enrichment from seabirds surrounding the pond and to distinguish the seabird sterol inputs from higher plant inputs. This is a modified version of the seabird index (cholesterol+/cholestanol+sitosterol) described by Cheng et al. (2016). Similarly, the ratio of coprostanol to its microbially reduced product, cholestanol (coprostanol/cholesterol; the human index), is used to indicate human presence (Vane et al. 2010; Briles et al. 2019). All sterols and stanols targeted by GC-MS analysis and their retention time are presented in Appendix I Table S-1.

One hundred milligrams of copper (Cu; Fisher) were added to ashed scintillation vials and sonicated for 10 minutes with 10 mL of dichloromethane (DCM). The DCM was discarded after the first sonication and this step was repeated twice more. The Cu was air dried, and to each vial, 100 mg of freeze-dried material was added. Sediment was subsampled every 4 cm (*n* = 28) in Core 2 and faecal material from several individual deer, and rhinoceros auklets were combined to obtain the target weight to add to each vial. Each sample was spiked with 100 µL of 50 ppm (3α)-Allopregnanolone. Information about the purity of standards used is presented in

Appendix I Table S-2. Method blanks containing only copper were spiked with 50 ppm 9 standard mix. Samples were evaporated dry and refrigerated for 12 h at 4°C. To extract lipids from samples, 10 mL of 10% Ethyl acetate and 90% Dichloromethane (DCM high-grade Optima ® brand) was added to each vial and samples were sonicated for 10 minutes. The solvent mixture was pipetted into 50 mL centrifuge tubes and this step was repeated twice more. Samples were centrifuged at 3000 rpm for 20 minutes and then transferred to solvent washed Turbovap tubes and evaporated to 2 mL under a gentle nitrogen stream. The remaining sample was transferred to a SPE column with 1.0 g of Si (Millipore), which was prior pre-conditioned with 6 mL of DCM. The Turbovap tube was rinsed with 0.3 mL DCM which was transferred to the columns, and samples were then eluted with a total of 40 mL DCM. All DCM was removed from the columns under vacuum pressure. The samples were transferred to solvent-washed Turbovap tubes and evaporated to 1 mL under a gentle nitrogen stream. The 1 mL samples were transferred to GC vials and evaporated to dryness under a gentle nitrogen stream. At this step, 100 µL of internal standard, 50 ppm (3α)-Allopregnanolone, was also evaporated dry. Once dry, 100 µL of 99% N,O-bis(trimethylsilyl)trifluoroacetamide) + 1% trimethylchlorosilane was added and samples were vortexed and then heated at 70°C for 2 h. Samples were cooled for 15 minutes and 890 µL of Toluene (high-grade Optima ® brand) and 10 µL of 250 ppm p-terphenyl-d_{14} (brand) were added to each sample. Samples were vortexed and analysed on the GC-MS.

Lipid analyses were carried out using an Agilent Technologies 6890 GC (G1530A) coupled to an Agilent Technologies 5973A MSD (G1098A) using an HP5MS-UI column from Agilent Technologies (19091S-433-UI; 30 m x 250 µm x 0.25 µm). Helium was the carrier gas at a constant flow of 1 mL min^{-1}, resulting in a pressure of 10.5 PSI. Injections were performed using an Agilent Technologies 7683 series injector in triplicate for each sample, with a 1.0 µL injection volume. Injections were made using a pulsed spitless mode with the injector heater set at 280°C, and injection pulse pressure of 16.26 PSI for 1.0 min. The oven was maintained at 100°C for 1 minute, followed by a ramp of 12°C/min to 265°C, followed by a ramp of 0.5°C to 275°C then 20°C/min to 320°C and held for 2 minutes. The total runtime was 39.00 min. The MSD was operated in selected ion monitoring (SIM) mode with a collision energy of -70 eV, the transfer line was heated to 280°C and details of the parameters can be found in the appendix. All quantifier ions were monitored with a dwell time of 100 ms while the qualifiers were measured for 40 ms. The low mass filtering setting was used (+/- 0.7-0.9 m/z). Lipid values are reported in mg L-1 and µg g-1 of dry weight sediment and were corrected to the internal standard, (3α)-Allopregnanolone added to each sample when applicable. All sterols and stanols were corrected to organic carbon by multiplying with the organic carbon content of each sample and values are available in Appendix II Fig. S-13. Sterol and stanol values are reported in µg $(gOC)^{-1}$.

3.3.11 sedDNA and PCR

sedDNA samples were isolated using a *Qiagen DNeasy PowerSoil Pro Kit.* A metagenomics analysis was carried out at the University of Lethbridge where primers were designed, and samples were amplified using Polymerase Chain Reaction (PCR). A series of sequences were downloaded from GenBank for each group of species: rodents (Keen's mice, house mice) ungulates (Sitka deer, Dawson's caribou), and seabird (rhinoceros auklet, Cassin's auklet) to design PCR primers. For each group sequences from any species found on Haida Gwaii or nearby were included. A set of semi-nested PCR primers were developed for each group targeting either conserved areas (common primers) or divergent areas (species-specific primers). The common set of primers amplify multiple species in the group (e.g., common rodent primers for black rat, Norway rat, and Keen's mouse) while the species-specific ones would only amplify DNA from that species. For all PCRs we used positive controls (Norway rat, black rat, common mouse, Cassin's auklet, rhinoceros auklet, black-tailed Sitka deer, and Dawson's caribou).

The first round of PCR was done using common pairs of primers (family specific). sedDNA was amplified in 25 µl reactions. with GoTaq® Flexi buffer, 1.5 mM MgCl2, 0.1 mM dNTP, 0.4 µM forward and reverse primers and 0.1 unit of GoTaq® Flexi DNA polymerase. Amplification consisted of one cycle of 120 s at 94°C, 45 s at 46°C, 60 s at 72°C; 37 cycles of 30 s at 94°C, 45 s at 46°C, 60 s at 72°C and one final cycle of 300 s at 72°C.

PCR products from the first round of PCR were diluted 1:50 in water. A second round of PCR was done using species-specific primers and using the same PCR conditions as in the first round of PCR with the exception of the forward primer (Appendix I Table S-3). To reduce non-specific binding, deliberate mismatches were introduced. PCR products from the second round were visualized on a 3% agarose gel stained with ethidium bromide. For a subset of samples from each of the species-specific primer pairs, PCR products were sent to Génome Québec, McGill University for sequencing. DNA sequences were edited in MEGA 5.2 and a blast search was done to identify similar sequences. PCR results were plotted in R with the packages 'ggplot2' v 3.3.5 and 'stats' v.4.1.2.

3.3.12 Data visualization and statistical analyses

The relationship of chl *a* versus depth was interpreted with break-point analysis in R with the package "segmented" (Muggeo 2008). Changes in diatom assemblages were established by cluster analysis using constrained incremental sum of squares (CONISS) and the number of important zones were determined with a broken-stick model in R with the packages “ggplot2” (Whickam 2016), and “tidypaleo” (Dunnington et al. 2022). A principal component analysis (PCA) was carried out to summarize changes in diatom assemblages over time by using the package “ellipse” (Murdoch 2022)

Trends for stable nitrogen and carbon isotopes, TOC, and trace metals were fitted using a generalized additive model (GAM) using the R package ‘mgcv’ v.1.8-41, ‘gratia’ v.0.7.3, and ‘ggplot2’ v 3.3.5. This model was used to identify significant change (periods when the derivative of the GAM is not 0). Model outputs provided estimated values for core depths that were not analyzed. To standardize all proxies, Z-scores ($Z = (x-\mu)/\sigma$) for all proxies were averaged and plotted to see overall trends in the core. Changes in the seabird colony were inferred with $\delta^{15}N$ values, sterol and stanol ratios, and bioenriched seabird metal(loid)s. Changes in vegetation were identified using $\delta^{13}C$, C/N, inferred lake-water TOC, chl *a,* and sterols and stanols. Sterols and stanols data were modeled using a local regression curve (LOESS). Data was verified for outliers using both Z scores and interquartile range in R using “stats” v 4.1.2. Values above Q3-1.5 IQR and below Q1-1.5 IQR were considered outliers.

3.4 RESULTS

3.4.1 Water samples

The pond water is dark and has high dissolved organic carbon (DOC) of 65.4 mg L^{-1} whereas particulate organic carbon was at 1.1 mg L^{-1}. The pH was 5.2, and specific conductivity was 220 µS cm^{-2}. The major cation in the pond was sodium and the major anion was chloride with concentrations of 36.2 mg L^{-1} and 57.7 mg L^{-1}, respectively (Appendix II Table S-4). Total dissolved nitrogen is below detection limits, and total phosphorus was high at 0.0704 mg L^{-1}.

3.4.2 Faecal samples (trace-metals and isotopic analysis)

Isotopic analyses of faecal samples from rhinoceros auklets (*n = 3*) have an average value of -21.6‰ for $\delta^{13}C$, 14.1‰ for $\delta^{15}N$, 24.7 %N and a C/N ratio of 1.6 C/N (individual stable isotope samples results are available in Appendix II Table S-5). The concentration of Co in faecal samples was the highest of the metals previously identified to be bioenriched by rhinoceros auklets and Charadriiformes (De La Peña-Lastra et al. 2022) with 0.055 µg g^{-1}, Cd was present in samples at 0.47 µg g^{-1}, Pb was detected at 0.39 µg g^{-1}, and Hg was detected at 0.30 µg g^{-1}. Ca, P, K, Na, and Fe (*n* = 2) were also detected with 24,000 µg g^{-1}, 14,000 µg g^{-1}, 11,000 µg g^{-1}, 1800 µg g^{-1}, and 4600 µg g^{-1} respectively. A table for trace-metal analysis of the fecal samples is available in Appendix II Table S-6.

3.4.3 Core chronology and sedimentation rate

^{210}Pb activities in Core 2 are low (SG surface activity (0-0.5 cm) with surface activities of 154.8 Bq kg^{-1}; Appendix II Table S-8). The chronology for the top part of the core (~150 years) was modeled using the R package "serac" (Bruel and Sabatier 2020) with excess ^{210}Pb. The samples failed the assumptions of the constant rate of supply (CRS) model in which the main assumption is a constant flux of excess ^{210}Pb to the water catchment as decay was observed with an increase in depth; however, at 4 cm a fluctuation in the activity was observed. The chronology for the top part of the core was established with the constant flux constant sedimentation (CFCS) model (Appendix II Table S-8). Artificially produced ^{137}Cs and ^{241}Am molecules are used to pin-point chronologies in recent sediment samples. The deposition of these isotopes reached a maximum in ~1963 with nuclear testing. In Core 2, ^{137}Cs and ^{241}Am activity increases between centimeters 0-4 in the core (Fig. 3.2b), indicating that ~1963 occurs within that period (Vane et al. 2010).

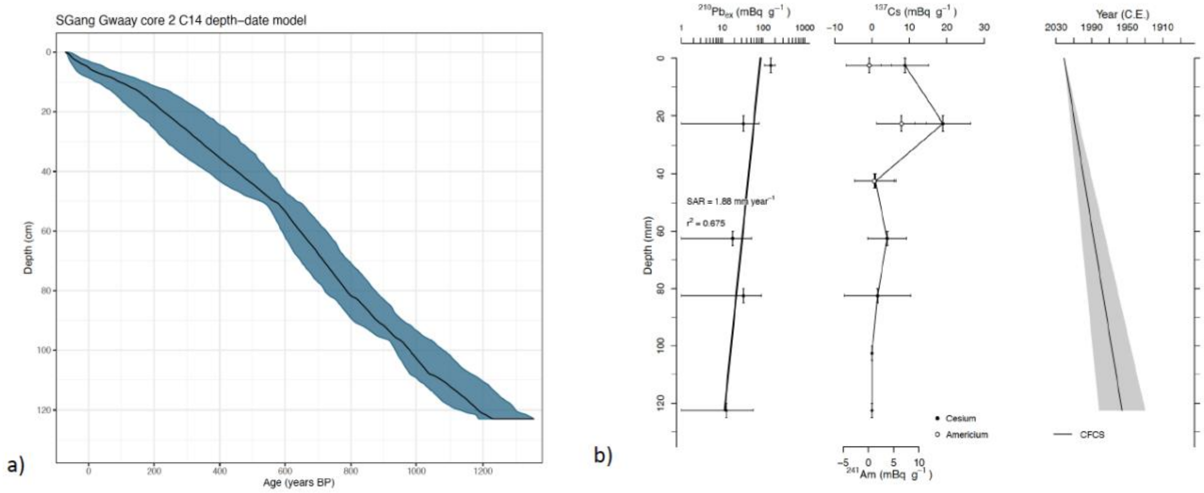

Figure 3.2. a) Age-depth model generated in R with Bchron (v. 4.7.6) for Core 2 with 95% confidence intervals displayed in dark blue. ^{14}C ages found in appendix VI Table 2 and were calibrated with InterCal20; **b)** ^{210}Pb, ^{137}Cs, ^{241}Am decay profiles and ^{210}Pb age-depth CFCS model for Core 2.

Macrofossils of well-preserved pine needles (*Picea sitchensis*), Sitka alder cones (*Alnus viridis*), and wood fragments were used to determine ^{14}C ages with accelerator mass spectrometry in samples older than ~150 years where ^{210}Pb activity was low. Multiple possible ^{14}C age inversions occurred in Core 1 at depths of 75 cm, 106 cm, and 128 cm indicating possible mixing within core 1. The age-depth relationship is available in Appendix II (Fig. S-2; S-3; S-4; Table S-8). The error of the ages in Bchron increases towards the bottom of Core 1 where these inversions are observed, however dates in the top part of Core 1 and Core 2 are consistent and allow sample comparison between cores. Based on these observations, we decided to carry out multi-proxy analysis on Core 2 and the top part (0-43 cm) of Core 1 when sediment was limited in Core 2. In Core 2 a single age inversion was observed between samples SG 82-

82.5 cm dating at 895 cal BP and SG 91-91.5 cm dating at 579 cal BP. Ages from the CFCS model and ^{14}C ages (cal BP) were used to generate an age-depth model for Core 2 using Bchron v. 4.7.6 (Parnell et al. 2021), a compound Poisson-Gamma model with a modified Markov chain Monte Carlo fitting algorithm. Model outputs provide mean, maximum and minimum ages for each depth of the cores with a 95% confidence interval (Haslett and Parnell 2008) (Fig. 3.2a). The mean date for the top of the core based on the Bchron model is -67.831cal BP (maximum age -60 BP and minimum age -71 BP) and the bottom of the core dates to 1260.736 cal BP (maximum age 1363 BP and minimum age 1184 BP). A table with dates for every 0.5 cm interval of the core is available in the Appendix II Table S-9. Dates for historical events on SGang Gwaay were sources from other studies and have errors as following: decreased *Cupressacea* pollen c.a. 1000 BP; 950 CE (Lacourse, Hebda and Mathewes 2007) (maximum age 1086 BP, minimum age 936 BP); expansion of the village ~715 BP; 1235 CE (Acheson 1998; Lacourse, Hebda and Matthewes 2007) (maximum age 1136 BP, minimum age 1178 BP) ; small pox epidemic of 114 BP; 1836 CE (maximum age 173 BP, minimum age 65 BP).

Sedimentation rates for Core 2 were determined using Bchron with 0.25, 0.5 and 0.75 percentiles. Model outputs for the 50th percentile are used as sedimentation rates and are provided in years/cm. Compared to other age-depth models available, Bchron overestimates variations in sedimentation rates (Trachel and Telford 2017), therefore the results presented in Appendix II Fig. S-5 are interpreted with caution. Due to chronology inconsistencies in the bottom parts of core 1 (core 1.2 and 1.3), Core 2 was used for analysis and all results below, except trace-metals and sedDNA which except for samples from the top part of Core 1, are from Core 2 (Appendix I Fig. S-2).

3.4.4 Chlorophyll a

VRS inferred chl *a* is low and stable throughout most of the core (123-27 cm), with values fluctuating between 0.01 and 0.02 mg g^{-1} D.W. until 27 cm when it increases significantly to ~0.1 mg g^{-1} D.W. at the top part of the core (0-27 cm). Break-point analysis with the R package "segmented" indicates a breaking point in the chl *a* with an increase in chl *a* between 27 cm and the surface of the core (Fig 3.3 a); Appendix II Fig. S-6).

3.4.5 Diatoms

From the bottom of the core until ca. 1388 CE (45 cm), the diatom assemblage is diverse. *Stauroforma exiguiformis* and *Eunotia incisa* dominate with relative abundances between 40-60%, with *Platessa hustedtii* and *Staurosira construens* var. *venter* present in relative abundances between ~20-40% and other species present in low relative abundances around ~5% (Fig. 3.3).

After ca. 1388 CE, *Stauroforma exiguiformis* is no longer encountered in the diatom counts, whereas early core diatoms with relative abundances of ~5% or less, such as *Neidium sacoense, Pinnularia viridis, Tabellaria flocculosa,* and *E. intermedia*, experience a peak (Fig. 3.3).

Towards the surface of the core, starting ca. 1588 CE (27 cm) until the top of the core, *Aulacoseira crassipunctata,* becomes highly abundant with relative abundance between 80-100% and *E. incisa* persists with a relative abundance of ~20% (Fig. 3.3). Other species disappear or are present in very low (~5%) abundances. Changes in diatom assemblages relate to changes in chl *a*; a shift in dominant species occurs at the same depth in the core as the increase in chl *a*. CONISS and the broken-stick model identified 3 significant groups (Appendix II Fig. S-7).

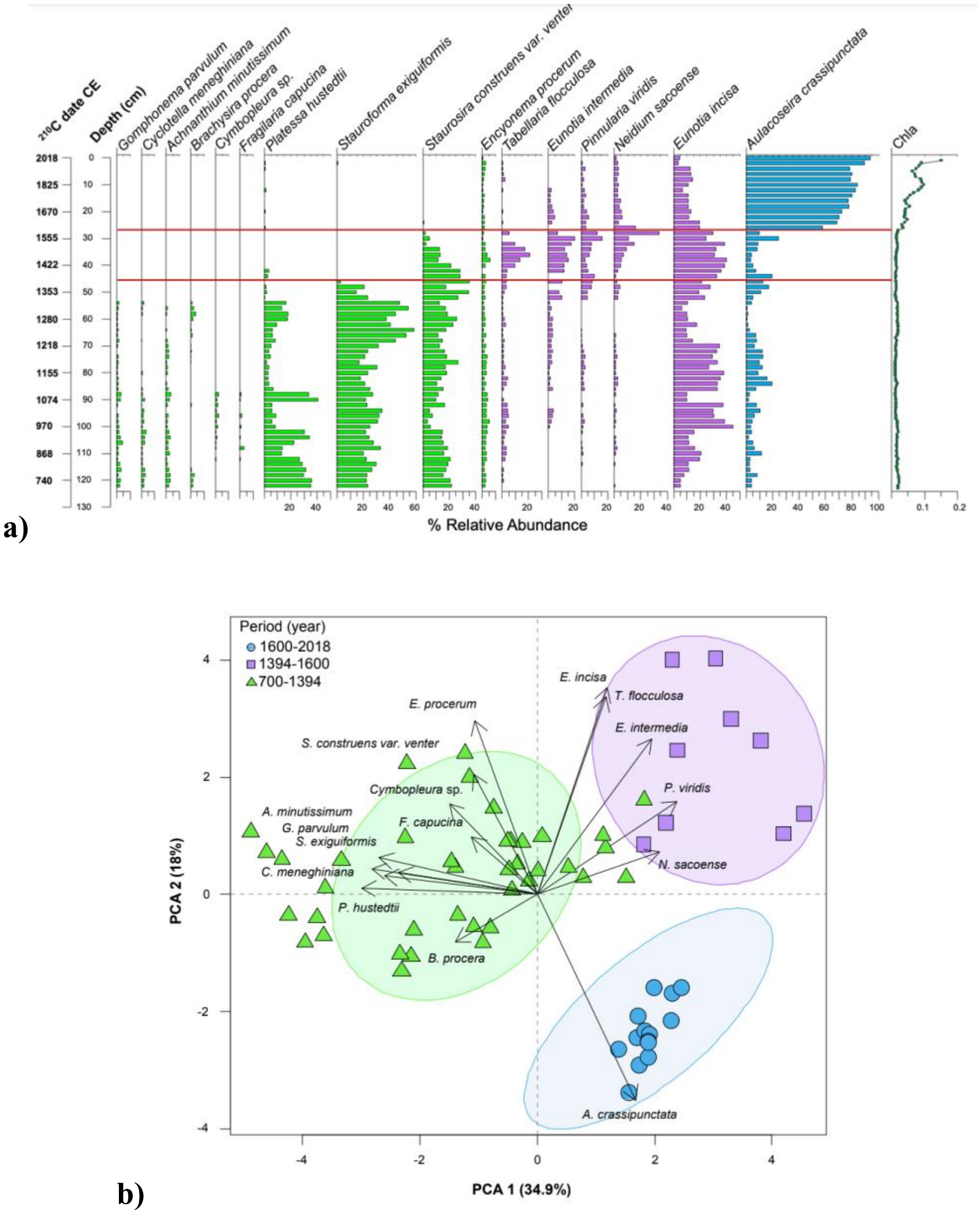

Figure 3.3. a) Diatom assemblages (>5% relative abundance) plotted as percent relative abundance and sedimentary chlorophyll a (mg/g dry weight) trends in the SGang Gwaay core. Red lines identify the two first significant changes in diatom assemblages determined using constrained sum of squares (CONISS) and broken stick analysis. **b)** Principal component analysis depth scores for axis 1 and 2 (PCA 1 and PCA 2) with diatom species time periods of the sediment core (based on CONISS and red line breaks in the stratigraphy) highlighted with 3 colours

3.4.6 %C, $\delta^{13}C$, %N, C/N and lake-water TOC

$\delta^{13}C$ values can be used to differentiate between marine and terrestrial plant sources (including freshwater algae) of carbon with marine derived $\delta^{13}C$ values ranging between -20 and -22‰ and terrestrial derived $\delta^{13}C$ values averaging -27‰ (Meyers 1997). The SG̲ang Gwaay $\delta^{13}C$ values range between -29.8 and -27.6‰ and these values, once corrected for the Suess effect, range from -28.5 to -26.7‰ (Appendix II Fig. S-8); however, $\delta^{13}C$ values cannot be used to distinguish the origin of the plants any further. C/N ratios can be used to further differentiate between marine and lacustrine algae as well as C3 and C4 land plants. While lower C/N ratios, ranging between 4 and 10, are indicative of cellulose-deprived aquatic plants, ratios above 20 are typical of the cellulose rich vascular land plants. The SG̲ang Gwaay sediment C/N atomic ratios are high, ranging between 23.4 and 40.1, and therefore typical of C3 land plants, although some inputs are also derived from lacustrine algae as demonstrated by some of the lower $\delta^{13}C$ values after ca. 1588 CE (Meyers and Ishiwatari 1993). C/N trends vary throughout the record (Fig. 3.4). First, there is an increase in C/N between ca 689-1230 CE (from ~30 to 40). This period of increase is followed by a sharp C/N decline from 40 to ~30 between ca. 1230-1268 CE, and another increase from between ca. 1268-1388 CE. Finally, the C/N declines starting at ca. 1388 CE cm from 37.5 to ~23.

The %OC values range between 17.7 and 47.7% and follow a decrease similar to those of C/N, and $\delta^{13}C$ values (Appendix II Fig. S-8). Pond water TOC follows a similar trend and declines from 22 mg L^{-1} to 15 mg L^{-1} after ca. 1250 CE until present, except for a small significant period of increase between ca. 1850-1925 CE. The decrease in these proxies (%OC, TOC, C/N, $\delta^{13}C$) at the top of the core (0-27 cm) contrasts with the increase in chl *a* occurring at the same time. Given the dominance of land plants in the $\delta^{13}C$ and %OC signatures, it is unlikely that these proxies track primary production in the pond. Furthermore, during periods of high productivity, preferential uptake of ^{12}C by aquatic plants leads to an increase in $\delta^{13}C$ (Leng and Marshall 2004), which is not the case in the SG̲ang Gwaay pond, indicating that the main source of carbon in the pond is unlikely to be aquatic.

Inferred lake-water TOC declines starting ca. 1250 CE and keeps declining until 1850 CE when it inclines until 0 cm (Fig. 3.4). As discussed by Meyer-Jacob et al. (2017), the absolute TOC inference must be interpreted with caution, but the approach captures overall trends in lake-water TOC. Modern-day DOC concentration in the pond is very high (65.4 mg L^{-1}) and outside of the calibration range of the model; however, the overall trend remains informative. Lake-water TOC, C/N, and $\delta^{13}C$ data were fitted with GAMs and show significant periods of decline starting ca. 1250 until the present day (Fig. 3.4).

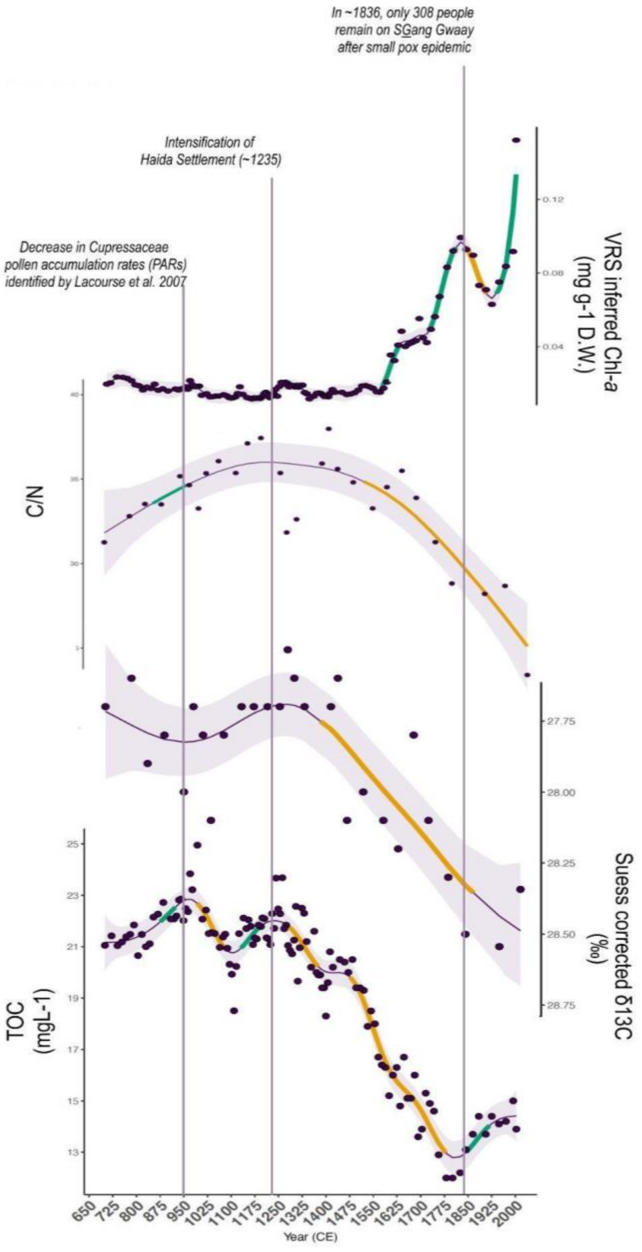

Figure 3.4. Proxies related to vegetation and organic matter changes in the SGang Gwaay pond. Data are fitted with a general additive model (GAM) and periods of significant decrease are depicted in orange while periods of significant increase are depicted in green. For coherence in data presentation, the y- axis of the Suess-corrected $\delta^{13}C$ values is reversed. Known major historical events on the island are identified with vertical grey lines. The shaded areas represent 95% confidence intervals.

The δ^{15}N values are overall low, ranging from 3.1‰ to 4.6‰ (Fig. 3.7). Although sources of nitrogen to lake sediments can be more difficult to pinpoint (Meyers 1997), those observed in the SG̲ang Gwaay samples are not as high as values reported in paleolimnological studies of many seabird-impacted ponds (e.g., Xu et al. 2011; Duda et al. 2020a; Duda et al. 2020c). The δ^{15}N values are more similar to the isotopic signature of land plants (Peterson and Howart 1987; Meyers 1997).

3.4.7 Geochemistry

Z-scores of ornithogenic trace metal concentrations in the SG̲ang Gwaay pond samples were calculated to compare trends across metals. Concentrations are reported in Appendix II Fig. S-9. While Hg and Pb were identified as bioenriched by Charadriiformes, these metals are highly mobile and easily influenced by organic matter concentrations and changes in aquatic ecosystems (Hart 1982). With the high DOC in the pond, and the increase of chl *a* after ca. 1550 CE, we interpret these results with caution. Ornithogenic metals decrease starting ca. 1790 CE around the time of European contact. Mercury standardized to titanium (Hg/Ti) decreases and remains constant after ca.1645 CE (Appendix II Fig. S-9) around ~ 0.00034-0.00088. Lead standardized to titanium (Pb/Ti) increases between 1647-1825 CE from ~0.0021 to 0.0034 before decreasing to 0.003 in ca. 2021 CE (Appendix II Fig. S-10). A first decrease is observed for these ornithogenic metals between ~1420-1645 CE, followed by an increase after ca. 1645 CE until ca. 1825 CE before declining continuously until the surface at 2020 CE.

3.4.8 Lipids

Plant lipids. Sterols and their microbially reduced versions, stanols, are important biomarkers that can be used to distinguish the sources, aquatic or terrestrial, of C and N stable isotopes signature in lacustrine sediments (Volkman 1986; Meyers and Ishiwatari 1993). Multiple sterols and stanols were identified in the sediment samples from SG̲ang Gwaay; however, plant-derived sterols and stanols 24-methylcholesta-5-en-3β-ol (campesterol), 24-ethylcholest-5-en-3β-ol (sitosterol), and 24-methylcholestan-22-en-3β-ol (stigmastanol) are predominant throughout the core while animal biomarkers cholest-5en-3β-ol (cholesterol), 5α-cholestan-3β-ol (cholestanol), 5β-cholestan-3β-ol (coprostanol) are present in lower concentrations. Due to significant changes in OC trends, all sterol and stanol values were corrected to OC and are reported in $\mu g(gOC)^{-1}$.

In the SG̲ang Gwaay samples, sitosterol ranges between 5.6-23.4 $\mu g(gOC)^{-1}$, stigmastanol ranges between 7.9-33.6 $\mu g(gOC)^{-1}$, and campesterol ranges between 0.1-22.1 $\mu g(gOC)^{-1}$. Sitosterol, campesterol, and stigmastanol follow a similar increasing trend from ~725 until ~1100 CE followed by a decline until ~1235 CE.

To further distinguish phytosterol sources between higher and microalgae, a ratio of sitosterol/campesterol can be used with values below ~6.6 indicating that phytosterols are likely derived from diatoms as opposed to land plants (Zhang et al. 2018). In the SG̲ang Gwaay samples, the sitosterol/campesterol ranges between 10.2 and 0.28 with the ratio following a decline starting ca.1325 CE indicating that plant inputs in the pond shift from higher plants to microalgae (Fig. 3.5). The ratio drops below 6.6 at ca.1625 CE completing the shift in phytosterol sources to the pond from higher land plants to microalgae. These changes in sitosterol/campesterol ratio follow the decoupling in sitosterol to campesterol trends in the pond starting ca. 1235 CE when campesterol remains stable as sitosterol declines (Fig. 3.5). Additionally, the ratio of sitosterol/cholesterol informs on phytoplankton productivity with a lower value of sitosterol/cholesterol indicating eutrophic-favouring alagae/more eutrophic state and a higher value an oligotrophic state (Zhang et al. 2018). The ratio of sitosterol/cholesterol ranges between ~19-15 (more oligotrophic) from 750 until ca.1235 CE when it starts declining to ~8 (more eutrophic) before increasing again at ca. 1700 to reach ~12 in recent times (Appendix II Fig. S-14).

Stigmastanol is a reduced and much more stable version of sitosterol obtained through hydrogenation, a microbial process (Gaskell and Eglinton 1975). Sedimentary analysis of sitosterol, campesterol and stigmasterol can be used to track total plant inputs, from higher and lower plants, in lacustrine environments over time with the ratio of sitosterol/stigmastanol also provides information about microbially induced redox of sitosterol (Stevenson et al. 2020). Lower ratios of sitosterol/stigmastanol indicate higher hydrogenation. In the SG̲ang Gwaay samples, hydrogenation increases starting at ca. 1325 until ca.1700 (Fig. 3.6).

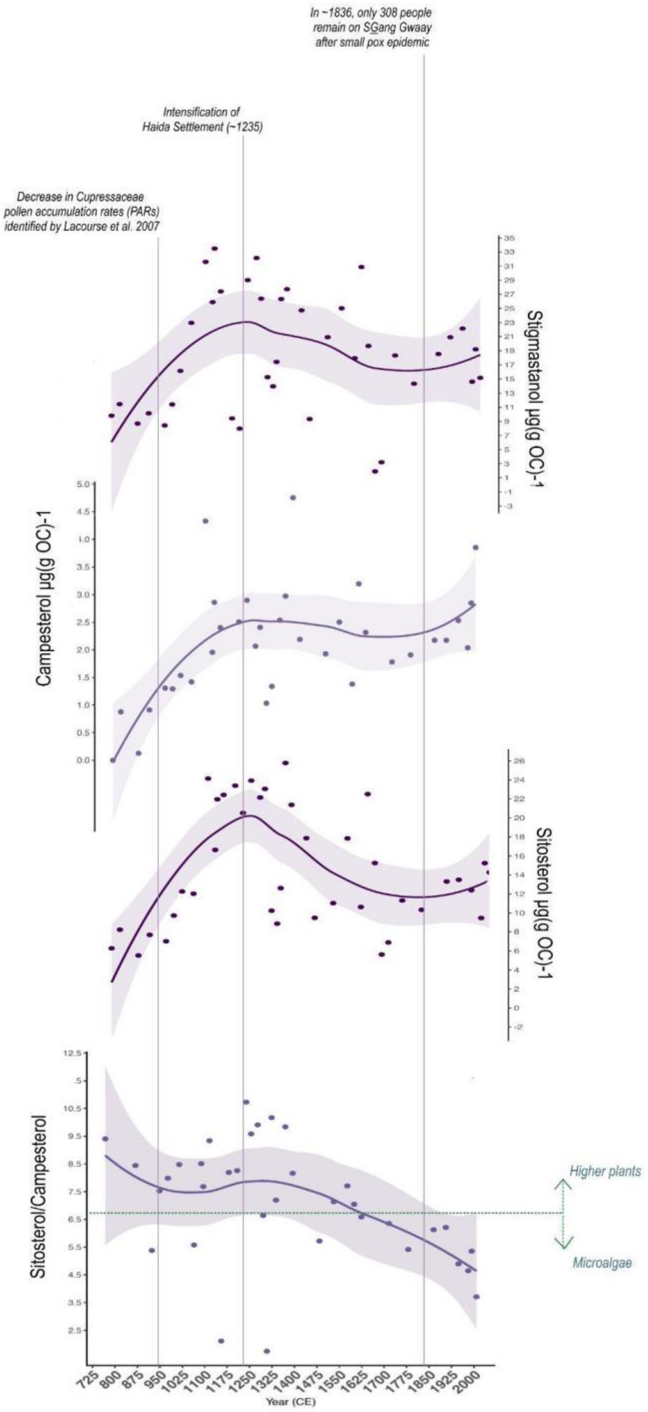

Figure 3.5. Plants lipid profiles in the SG̲ang Gwaay core. Vertical lines mark notable events on SG̲ang Gwaay and the horizontal line marks a sitosterol/campesterol ratio of ~6.6, a threshold at which plant lipids shift from higher plants to microalgae (Zhang et al. 2018).

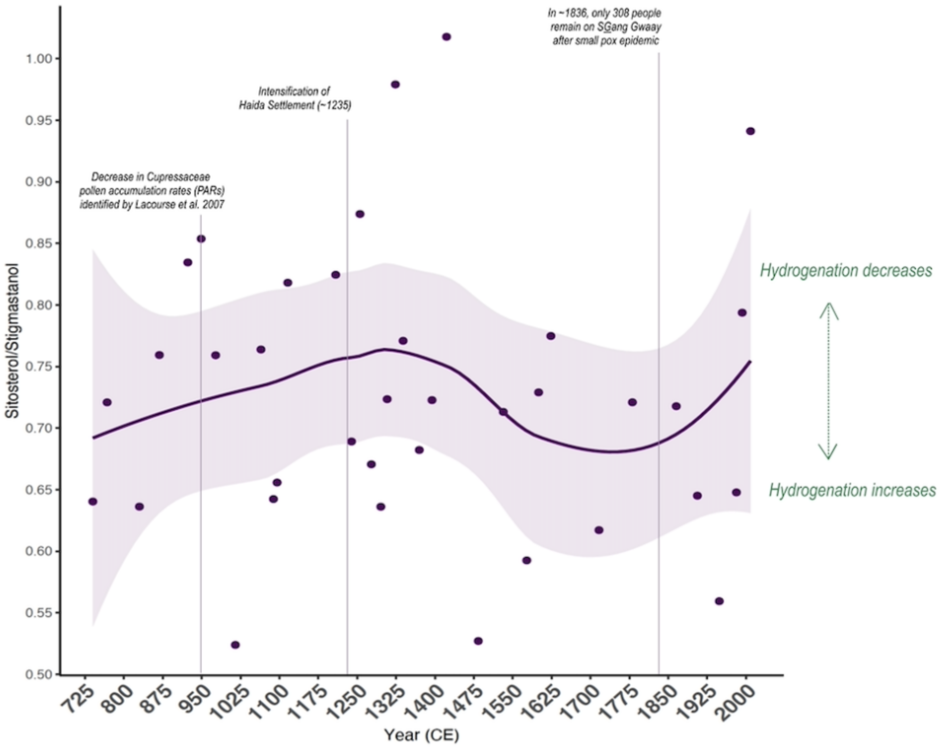

Figure 3.6. Hydrogentation as observed by changes in Sitosterol/Stigmastanol ratio in the SGang Gwaay samples. Smaller values on the y-axis indicate an increase in hydrogenation while higher values indicate less hydrogenation. This change in hydrogenation is represented by the green arrows.

Human and seabird lipids. Corprostanol has been used to track sewage inputs in aquatic environments with coprostanol/cholesterol values above 0.2 indicating human faecal contamination (Vane et al. 2010). These markers are present in human feces, but cholesterol is also common in seabird guano and coprostanol can also be found in trace amounts (Cheng et al. 2016). Sediment samples from the SGang Gwaay pond have coprostanol concentrations between 1.8-8.4 µg(gOC)$^{-1}$ and cholesterol concentrations between 0.3-3.4 µg(gOC)$^{-1}$ (Appendix I Fig. S-9), while to uncorrected concentration of these lipids in sediment samples is between 0.27-1.77 µg g^{-1} D.W and 0.04-0.83 µg g^{-1} D.W . In the seabird samples (*n* = 3) from SGang Gwaay, cholesterol concentrations average 5026 µg g^{-1} D.W., and coprostanol concentrations average 6.2

μg g^{-1} D.W. These sterols represent 99.3% and 0.1% of the faecal sample respectively, with the remaining of the sample containing 0.2% ergosterol 0.2% campesterol, 0.1% sitosterol, and 0.1% stigmastanol. Epicoprostanol is an important biomarker for humans and cholestanol is a biomarker for both humans and seabirds (Cheng et al. 2016; Schroeter et al. 2020), however they were not detected consistently in all samples, and further analysis was not possible.

The coprostanol/cholesterol ratio in the pond was modeled with a LOESS and values range between 3-6, well above 0.2, the threshold for human fecal contamination and 10, the value typically found in raw sewage (Vane et al. 2010). The human index LOESS curve peaks at 6.0 at ca. 700 CE before declining to 3.7 at ca. 1050 CE and peaking again at 4.7 at ca.1040 CE. After this last peak, the human index declines to 3 at ca. 2000 CE (Appendix II Fig. S-15). We aimed to use the expanded seabird index ratio (cholesterol+cholestanol/cholesterol+cholestanol+sitosterol+stigmastanol) to track seabird inputs in ponds with significant plant-derived lipid signals (Hargan et al. 2018), however, the expanded seabird index could not be used, nor could the seabird index described by Cheng et al. (2016). The low values of the cholesterol relative to plant sterols and stanols, and the failure to detect cholestanol consistently throughout the core prevent the calculation of the seabird index and indicate that the seabird sterols and stanols signals are dampened by plant signals and cannot be interpreted reliably.

3.4.9 sedDNA and PCR

sedDNA concentrations in the SG̲ang Gwaay core sample were low (average of 10 ng μL^{-1}) and short sequence (~100 bp) species-specific primers were designed to maximise PCR amplification of the targeted species. Despite our efforts to distinguish between Rhinoceros auklets that populate the area immediately adjacent to the pond and Cassin's auklets that burrow ~500 m away from the pond, we were unable to distinguish the two seabird species. DNA sequencing of PCR results did not allow discrimination between the two species; the Cassin's auklet primer amplified rhinoceros auklet sequences.

PCR results indicate that rhinoceros auklets were present on SG̲ang Gwaay since at least ca. 700 CE (Fig. 3.7). There are two distinct periods when no seabird sedDNA was amplified with PCR: ca.1736-1710 and earlier at ca. 1088-1074 CE. Norway rats, Black rats, and Sitka deer are not detected. Keen's mouse DNA was detected on SG̲ang Gwaay starting ca. 700 CE until ca. 1935. There are two time periods when Keen's mouse DNA was consistently detected on the island between ca. 768-1020 CE and ca. 1199-1249 CE. PCR results indicate that DNA was more often detected between ca. 700-1249 CE. Following ca. 1249 CE until modern times the rodent's DNA is detected in a scattered and less consistent pattern. Dawson's caribou went extinct in Haida Gwaii in the early 20th century. The sedDNA record detects this ungulate at 4 instances: ca. 1048, ca. 1069, ca. 1526 and ca. 1618 CE.

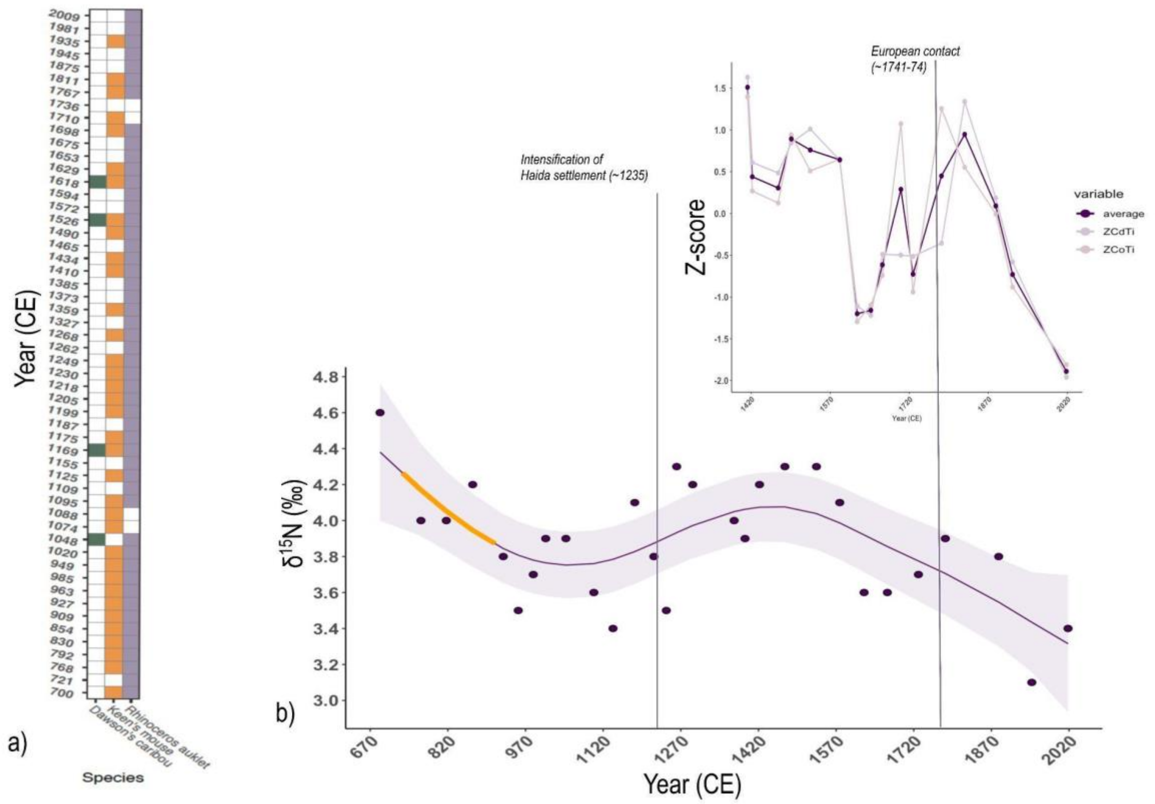

Figure 3.7. Ornithogenic proxies a) sedDNA PCR matrix with coloured squares indicating a presence of species-specific sedDNA in samples b) LOESS fitted expanded seabird index, GAM fitted $\delta^{15}N$ and two ornithogenic trace-metals bioenriched by rhinoceros auklets, Co, Cd standardized to Ti and their Z-score. The shaded areas represent 95% confidence intervals.

3.5 Discussion

Lacourse, Mathewes and Hebda (2007) suggested that the selective harvest of Western red cedars and forest clearing to expand Ninstints at ca.1235 CE caused impacts on the island's ecosystem beyond the time of occupancy. Their study concluded that red cedars were harvested at an apparently sustainable rate. Red cedars have a lifespan over 1000 years and archeological remains at Ninstints (i.e. totem poles, houses) document that selective harvest focused on large mature trees therefore allowing recruitment and red cedars to persist until present day. Our paleolimnological record of stable isotopes, sterols and stanols, diatom assemblages, and primary production indicators from the pond on S<u>G</u>ang Gwaay support that, although the tree harvest prevented the collapse of Western red cedar on the island, there were substantial underlying ecosystem-scale changes on the island that are reflected in the long-term carbon pool.

3.5.1 Changes in island vegetation and carbon sources to the pond

Organic carbon in lake sediments is a mix of allochtonous and autochthonous sources (Stevenson et al. 2021). Allochtonous sources are carbon inputs from terrestrial matter (e.g., soil erosion, leaves, bark) and autochthonous sources are carbon inputs from within lake producers (e.g., algae, microorganisms). While it is difficult to assess with accuracy the proportion of OM that is autochtonously vs. allochthonously derived in lakes, stable isotope can be used to identify sources of carbon and their fate (Doi 2009; Guo 2020). Suess-corrected $\delta^{13}C$ values from the S<u>G</u>ang Gwaay lake sediments indicate that C in the pond sediments originates mostly from land plants with some from freshwater algae after the $\delta^{13}C$ decline from -27.8 to -26.8‰ starting ca.1588 CE until present (0-27 cm; Appendix II Fig. S-8). The $\delta^{13}C$ isotopic signature of C3 and C4 land plants is preserved when the OC from the plant is transferred to soil and sediments, although the proportion of C4 plants is less accurately depicted in the sedimentary $\delta^{13}C$ (Dawson et al. 2002; Wynn and Bird 2007). Thus, it is possible to distinguish between C3 and C4 plant-derived OM in sediments through $\delta^{13}C$ signatures. The overall C/N ratios are typical of C3 land plants. C/N trends vary throughout the record (Figure 4). First, there is an increase in C/N between ca 689-1230 CE (from ~30 to 40) marking enhanced terrestrial plants contribution to the high $\delta^{13}C$ signature during that time. Stable isotopes indicate that a majority of the C in the pond is from land plants from ca. 689-1235 CE. However, after ca.1235 CE, the origin of C to the pond sediments changes.

A sharp decline from 40 to ~30 C/N occurs between ca. 1230-1268 CE, following by a brief increase from between ca. 1268-1388 CE. Finally, the C/N declines starting at ca. 1388 CE until c.a 2021 from 37.5 to ~23. This decrease can be associated with a decline in terrestrial vegetation caused by selective tree harvest. With a village expansion after c.a. 1235 (Lacourse Hebda and Mathewes 2007), vegetation cover around the pond is likely to have decreased with more harvest of red cedar to build houses, canoes, and objects (e.g., ropes, clothing, etc.) (Acheson 1995).

Climate and precipitation patterns also influence $\delta^{13}C$ and $\delta^{15}N$ signatures in soil OM where wetter conditions are associated with decreased $\delta^{13}C$ and $\delta^{15}N$ values (Hammerlund et al. 2003; Ma et al. 2012; Tahmasebi et al. 2017). Little Ice Age (LIA) in Western Canada spans between ca. 1300-1900 CE and is associated with temperature anomalies and changes in precipitation patterns. Tree-ring reconstructions show that temperature anomalies were fluctuating both above and below average in the June-July period by ~2 degrees Celcius while annual temperatures remained below average (Pitman and Smith 2012; Malcomb and Wiles 2013) and relatively stable for Vancouver Island expect a notable increase in precipitation between c.a. 1560-1760 CE (Zhang and Hebda 2005). Increased precipitation could contribute to decreased $\delta^{13}C$ and $\delta^{15}N$ values in soil OM; however, the increase in chl *a* and the decrease of C/N following the LIA sugget that the decline in Suess-corrected $\delta^{13}C$ values we observe in our samples cannot be explained with climatic variations in the LIA alone. Lake-water TOC undergoes a decline during this period suggesting a reduction in allochotonous-derived C to the pond. Thus, we maintain that the selective harvest of western red cedar is at the root of $\delta^{13}C$ and C/N decline in the pond.Vegetation decline is further supported by visual inspection of the core samples containing less plant macrofossils at the top of the core. These observations match those of Lacourse, Mathewes and Hebda (2007) marking a decrease in total macrofossils starting at ca.600 BP (1350 CE). Changes in plant sterols and stanols are indicative of decline in terrestrial vegetation and an increase in aquatic vegetation, further supporting that changes in stable isotopes are not driven by climate variations in the LIA alone.

Sitosterol is a precursor for cellulose synthesis in higher plants (i.e. pteridophytes, gymnosperms, angiosperms), and is present in almost all land plants alongside campesterol, a molecule playing a role in plant development as a precursor to brassinosteroids (Volkman 1986; Seo et al. 1988; Hartmann 2003; Otto and Simpson 2006). Microalgae, such as diatoms, also contain these two phytosterols (Nishimura and Koyama 1976; Gladu et al. 1991) but have a lower occurrence of sitosterol (Volkman 1986). From ca. 725 CE until ~1100 CE sitosterol, campesterol, and stigmastanol follow a similar increasing trend followed by a decline until ca.1235 CE when the Haida settlement at Ninstints intensifies. This suggests that plant phytosterols likely have a common source. However, after ca. 1235 CE, campesterol remains stable in the pond while sitosterol and stigmastanol decrease, suggesting a decoupling of these two phytosterols. While sitosterol and campesterol inputs to the pond is mainly allochotonous prior to ca.1235 CE, after this date, sitosterol and stigmastanol still originate mostly from terrestrial plants, while campesterol originates mostly from an autochotonous source: algae, or diatoms. The decline of sitosterol/cholesterol starting ca.1235 CE provides further evidence of a shift from higher plants to microalgae lipid inputs and increased primary production in the pond.

A decline in lake-water TOC begins c.a 1250 CE, around the time of village expansion, and persists until c.a 1850 CE after which it increases. Stable isotopes ($\delta^{13}C$, C/N) undergo a decrease that persists beyond the time of village vacancy c.a 1887-88 after the small pox epidemic that led Haida to evacuate to mainland Haida Gwaii. This is not surprising; forests have large C stores and can exhibit large effects with lagged impacts and take a long recovery time to replenish stocks after climatic or anthropogenic disturbances (Frank et al. 2015; Williams et al. 2016).

The human index marks an increase in the Haida population between ca. 1100-1425 CE. This time frame corresponds to interpretation of intensified tree harvest on the island. Although no exact date is known for the time when the village was at its largest, Acheson (1995) estimates that population increased after ca. 1235 CE, as village sites and cultural artifacts increased after that period. Thus, it is possible that a population maximum is reached ~200 years later. If population maximum was paralleled with increase tree harvesting on the island, this could explain the increase in sedimentation rates c.a. 1490 as soil erosion would be higher with increased land-use changes (McGowan et al. 2015). Population decline between the 15th and 18th centuries, coinciding with European contact, is hard to explain as pre-contact records are limited and do not account for factors of population decline such as epidemics and conflict. Following the 18th century, population decline relates to historical events: armed conflict with Europeans, smallpox and scrofula epidemics, and ultimately the village abandonment in the 19th century (Acheson 1995). We interpret the human index with caution for two reasons. First, during periods when plant sterols and stanols dominate the signal, the signal of other lipids present in lower concentrations can be hampered. Second, the Haida may well have had designated latrine sites, and depending on where they might have been on the island, it is possible that drainage of human sewage to the pond was limited or delayed and that the signal in the pond might be offset. The initial peak in the Human index can be a true peak in population or a delayed peak in population. As White et al. (2018) observed in their reconstruction of the Cahokia population, changes at population scale can take longer to be reflected at watershed levels.

3.5.2 The rise of aquatic production and changes in environmental parameters

Selective tree harvest on SG̲ang Gwaay, and particularly in proximity to the pond through the removal of large Western red cedars contributed to decreased allochtonous delivery of C to the pond and the increase of autochthonously-derived C in sediments. Additionally, this selective harvest contributing to decreasing vegetation cover altered the pond physical environment or changed aquatic habitat within the pond (i.e., light penetration, physical mixing with wind). Complementing evidence of the increase in autochtonously-derived C in the lake, our data shows an increase in primary production and increase in autotrophic/mixotrophic production that is likely caused by increased light exposure driven by a decline in TOC Vegetation cover directly affects the lake trophic status; above and below a certain TOC threshold in shallow lakes, autotrophs and heterotrophs are light limited (McGowan et al. 2018). With forest thinning around the pond, less terrestrial material is deposited in the pond, therefore leading to a decrease in TOC. Chl *a* is a biomarker of autotrophs (Vadeboncoeur et al. 2006; McGowan et al. 2018) and its increase c.a 1550 CE marks a significant change in lake dynamics as vegetation cover decreases alongside TOC. McGowan et al. (2018) note that autotrophs are limited by ultraviolet light exposure in shallow lakes, where depth cannot offer reduced light penetration. In the same study, lakes without vegetation cover had a lower concentration of chl *a* whereas lakes with Boreal forest cover had more autorophic and mixotrophic taxa and increased chl *a*. Hydrogenation (sitosterol/stigmastanol), a ratio indicative of microbial activity, increases starting at ca. 1325 until ca. 1700 further indicating changes in trophic status. Our findings support those of McGowan et al. (2018) indicating that algae and bacteria have an optimal range of TOC and light exposure, however as we did not calculate carbon accumulation rates in this study, our comments about carbon sinks and sources remain hypothetical. Trophic levels determine whether lakes are a C source or sink with autotrophic lakes being a sink (Tranvik et al. 2009). Particularly, small eutrophic lakes have a large annual rate of C burial (Tranvik et al. 2009), and this remains true for shallow lakes (Sun et al. 2020; Downing et al. 2003).

Here we interpret chl *a* increases occurring due to increased light penetration to the pond from reduced tree shading and reduced TOC, likely corresponding to clearer waters. However, climate change around the globe, including North America, is leading to increased primary production in many lakes and autochthonously-sourced C (Rühland, Paterson and Smol 2008; Häder, Villafane and Helbling 2014). Increasing temperatures supports warmer waters, enhanced thermal stratification, and longer growing seasons. Additionally, increased precipitation causes enhanced delivery of nutrients to water catchments, thus stimulating primary productivity in lakes (Soares et al. 2022; McGowan et al. 2015). Climatic conditions were reported to be relatively stable throughout the Holocene based on tree-ring models from nearby Vancouver Island (Zhang and Hebda 2005). Precipitation increased during the LIA ca. 1560 CE. Thus, it is possible to think that the chl *a* increase we observed starting ca. 1550 CE is caused by primary productivity resulting from increased nutrient delivery to the pond. There is an increase in sedimentation rates c.a. 1490 CE which may contribute to increased nutrient delivery to the pond. In Sweden, post-medieval distrubances caused an increase in autochotonous-derived OM in lakes (Anderson, Renberg and Segerstrom 1995) and fertilization can increase productivity in shallow lakes by stimulating phytoplanktonic activity (Vandeboncoeur et al. 2003). To our knowledge, no agricultural activities were undertaken on SG̲ang Gwaay as the Haida historically relied on marine food resources with a lower portion of land-plants being harvested (Crone and Mehrkens 2013). Thus, it is unlikely that a chl *a* increase is caused by agricultural fertilization on

SG̲ang Gwaay; however, land-use erosion could have increased nutrient delivery to the lake, stimulating autochtonous production.

Furthermore, although warming in the mid-1800s is associated with an increase in lake primary production globally (REF), it is unlikely that this is the case on SG̲ang Gwaay. Firstly, the increase of chl *a* occurs at the same time as *Aulacoseira crassipunctata* dominance starting 1588 CE, well before global warming trends start in the mid-1800s. Secondly, *Aulacoseira* species experienced a global decline after warming toward the end of the 20th century as it is not favoured in warming conditions, which tend to reduce wind mixing in lakes and ponds (Rühland, Paterson and Smol 2008). Highly silicified, *Aulacoseira* require high mixing in order to be suspended in the water column, thus periods of warming when the water column is more stable do not favour these species (Rühland, Paterson and Smol 2008).

The decrease in the lake-water TOC trend starts in ca. 1250 CE and the diatom community changes with a decline in relative abundance of the two most dominant species, *S.exiguiformis* and *P.hustedtii* from 30-60 to 0; however, it is not until ca. 1550 and ca. 1588 CE that chl *a* increases, and changes in diatom assemblages start happening respectively. The dominant species at the bottom of the core are non-motile and can be found in brackish, acidic water, and are oligotrophic (Cameron et al. 1998; Freitas et al. 2021) with less abundant species being semi-motile (Morales and Spauldig 2013; Rondón and Aragón 2018; Tibby et al. 2019). After ca. 1388 CE, *Stauroforma exiguiformis* is no longer encountered, whereas early core diatoms with relative abundances of ~5% or less, such as *Neidium sacoense, Pinnularia viridis, Tabellaria flocculosa,* and *E. intermedia*, experience a peak (Fig. 3). These species are characterized by moderate motility (DeColibus 2013; Burge, Edlund and Frisch 2017).

In northern lakes, light conditions are a main driver of primary production and high TOC concentrations in lake water are associated with increased light extinction (Seekell et al. 2015). Here, we propose that a decrease in lake-water TOC, associated with decline of vegetation cover surrounding the pond, would favour light penetration (assuming a correlation between TOC and lake water colour). Thinning of the forest surrounding the pond would favour physical mixing. Increasing light penetration would support higher autochthonous primary production and greater wind mixing supports the increasing dominance of a tychplanktonic *Aulacoseira* diatom taxa. Typically these diatoms of this genus are more heavily silicified and required turbulence to respend valves from the benthos into the photic zone. Such occurences were observed in lakes when the surrounding forest was clearcut; fossil records showed increased wind stress, deep water column mixing, and less anoxia (Scully et al. 2000).

Changes in lake-water TOC relate to changes in carbon cycling between terrestrial and aquatic ecosystems and, in return, TOC concentrations dictate changes in aquatic productivity by changing environmental parameters (pH, water clarity) (Seekell et al. 2015). SG̲ang Gwaay diatom assemblages reflect changes in environmental conditions in the pond: the dominant species at the bottom of the core are non-motile and found in brackish, acidic water with less abundant species being semi-motile (Morales 2013; Rondón and Aragón 2018; Tibby et al. 2019). The dominance of *Aulacoseira crassipunctata* indicates that light penetration likely started increasing, and pH became more acidic after ca.1388 CE and by ca.1588 CE was optimal for *A. crassipunctata* to have a relative abundance of 80-100%, while circumneutral water species, such as *S.exiguiformis* disappeared (Van Dam, Mertens and Sinkeldam 1994). *E. incisa* dominate pre-acidification assemblages (Battarbee et al. 1997). Water colour is strongly correlated to TOC (Ouyang et al. 2006). Present day DOC is very high (65.4 mg L^{-1}) and the corer could not be viewed in the water after ~30 cm depth, also indicating that the pond is dark. Before ca. 1250 CE, lake-water TOC values fluctuate, but are generally higher (~21 mg L^{-1}) before they decline to ~15 mg L^{-1} at ca. 1850 CE. Furthermore, there is a small significant period of increase in TOC between ca. 1850-1925 CE. During that time both chl *a* and relative abundance of *A. crassipunctata* decrease, further supporting this relationship.

Aulacoseira crassipunctata has often been misidentified with *Aulacoseira canadensis* and knowledge with respect to this species is still limited, especially with respect to its distribution in Western North America (Bahls et al. 2009). The genus *Aulacoseira* is reported in a variety of environmental conditions ranging from nutrient depleted to eutrophied lakes (Pedraza Garzon and Saros 2022; Duda et al. in press). The relative abundance of other species of the genus *Aulacoseira* has been shown to be limited by light, and in light-depleted conditions, nutrient availability stimulated growth (Pedraza Garzon and Saros 2022).

Nevertheless, it is known that *A. crassipunctata* is typically open-water species requiring turbulence and is indicative of a pH of 5–6 and has been found in systems stained with humic acids (Bahls et al., 2009), conditions similar to our sampling site. Although no pH optimum is known for this species, its optimum is estimated to be between a pH of 5-6. (Bahls et al. 2009). Our observations from SG̱ang Gwaay indicate that a pH of 5.5 likely favours this species, given its dominance in the assemblage. Earlier diatom assemblages in the pond suggest less acidic conditions than those recorded in the present (pH of 5.5 vs. ~6). The dominance of *A. crassipunctata* indicates changes in pond light penetration and these changes are supported by an increase in chlorophyll *a*. It is likely that prior to ca. 1588 CE, light penetration, physical mixing of the lake-water and the less acidic pH limited *A. crassipunctata.*

3.5.3 Seabird and mammal trends

Haida Gwaii offers a breeding ground to ~70% of the global population of rhinoceros auklets, and therefore seabird status with respect to invasive mammals is closely monitored on the islands. Norway rats, black rats, and Sitka deer have not been detected in our sedDNA analyses. The absence of rats aligns with Park Canada’s monitoring program for rodents on SG̱ang Gwaay, and historical accounts of rat dispersal in Haida Gwaii (Golumbia 1999). However, the absence of Sitka deer DNA in our samples does not align with the current situation on SG̱ang Gwaay, as deer were observed and present on the island at the time when the core was collected. The low detection rate of these two ungulates might be linked with their ecology. Sitka deer disperse within Haida Gwaii by swimming between islands and caribou elsewhere also disperse in this manner (Miller 1995; Webber et al. 2021). Both species are therefore not always present on SG̱ang Gwaay, but rather visit when browsing resources are lacking elsewhere. Furthermore, caribou are cryptic species (Pond et al. 2016) and were hunted by the Haida (MacDonald 1983), making it unlikely for them to forage on SG̱ang Gwaay very often during the time of Haida occupation. The paleoecological records from SG̱ang Gwaay demonstrate that it is difficult to capture the sedDNA of species that live in low density and disperse, therefore this technique cannot detect invasive species such as Sitka deer well. Keen’s mouse DNA was detected on SG̱ang Gwaay starting ca. 700 CE until ca. 1935 with two time periods when sedDNA was consistently detected: ca. 768-1020 CE and ca. 1199-1249 CE. From ca. 1249 CE until modern times, the rodent’s DNA is detected in a scattered and less consistent pattern. This decrease in Keen’s mouse DNA detection after 1020 CE and the increase in δ^{15}N values following 1120 CE following indicate a possible link between egg predation and rhinoceros auklet population increase. Keen’s mouse is a small rodent that can predate seabird eggs as large as rhinoceros auklet and Cassin’s auklet, especially when birds neglect their nest (Blight, Ryder and Bertram 1999; Drever and Blight 2000). Thus, it is possible that after ca. 1020 CE birds were released from egg predation leading to an increase in population on SGang Gwaay. It is unlikely that Haida harvest of rhinoceros auklet eggs and birds caused population decline as indicated by the increase in $\delta^{15}N$ values at ca. 1235 CE when the settlement intensification was observed, and its subsequent decline starting at ca. 1385 CE.

Seabird trends, as indicated by $\delta^{15}N$ values and ornithogenic metal concentrations, suggest a decline in the rhinoceros auklet population following European contact until the present. Eight Rhinoceros auklet monitoring plots (together capturing 1-3% of the colony) on SGang Gwaay suggest that the population increased between 1980-2012 CE (Rodway and Lemon 2011); however, authors of this study indicate that permanent monitoring plots failed to detect broader population declines and not all plots were surveyed consistently in that time period. For instance, no data are available between ~1980 and 2004 CE and all 8 plots were never surveyed in a given year with 6-7 plots being surveyed instead. Furthermore, plots were subjectively established in areas of high density, thus with these two factors combined, permanent monitoring plots might fail to detect colony decline in a given survey year. Trace-metals can bind with dissolved organic matter with the following binding order Hg > Cu > Pb > Zn ~ Cd (Hart 1982), however standardization of the trace-metals to TOC did not show any changes in trace-metal trends over time (Appendix II Fig. S-12). Based on these observations, we estimate that the decline in ornithogenic metals after 1775 CE is a true decline, and not a trend resulting from DOM binding.

Cations such as Ca^{2+} and Mg^{2+} interfere in trace-metal absorption; they are present in the pond at high concentrations and compete with trace-metals for binding sites (Hart 1982;

Penttinen, Kostamo and Kukkonen 2009). Inland lakes and bogs (Mayer Lake, Tow Hill and Drizzle Lake) in Haida Gwaii typically have Ca^{2+} concentrations between 0 and 2 mg L^{-1}, Mg^{2+} concentrations between 0.9-1.4 mg L^{-1}, Na^{+} concentrations between 6.5-12.0 mg L^{-1}, conductivities of ~50-90 µS cm^{-1}, and have a pH between ~4.25-4.75 (Howie and Meervald 2013). The SG̲ang Gwaay pond has a higher concentration of Ca^{2+} ions, conductivity, and pH compared to these catchments in Haida Gwaii. The proximity of the SG̲ang Gwaay pond to the ocean, compared to the other sites for which water chemistry is available in Haida Gwaii, explains the much higher concentrations of Na^{+} and Cl^{-} ions. Cation binding with organic matter in the pond is an additional mechanism that would prevent ornithogenic trace-metal absorption in the SG̲ang Gwaay pond after 1775 CE.

We acknowledge that negative PCR results cannot be interpreted as an absence of species at those times. However, sedDNA samples are not well preserved in acidic, humid and warm (instead of frozen) conditions. Although we froze sedDNA samples upon collection, the DNA preservation in the sediment (i.e., environmental conditions) was not optimal. Thus, it is possible that some samples have DNA fragments of insufficient quality or quantity to be amplified through PCR leading to false negative results. This is a frequent observation in sedDNA studies (Beng and Corlett 2020).

3.6 Conclusions

Using a multiproxy analysis, we reconstructed environmental change on SG̲ang Gwaay since the establishment of the island's main pond, and interpreted these results with respect to anthropogenic activities at Ninstints, European contact, and invasive species management. We found that tree harvesting by the Haida altered the C cycle on SG̲ang Gwaay during the ~1300 year period captured by the core. The decrease in vegetation resulted in a change of C stock allocations; terrestrial matter delivery to the pond decreased as trees were harvested in great numbers after ca.1235 CE. With less C delivery to soil ecosystems and the pond, environmental conditions (i.e., light penetration, pH) were favourable for an increase in aquatic primary production. Following a reduction in lake-water TOC, microbial activity increased, followed by an increase in chl *a* and changes in diatom assemblages. Our data demonstrates that insular habitats are highly sensitive to landscape alterations. C allocations on SG̲ang Gwaay changed after increased tree harvesting and geochemical cycle alterations have impacts at ecosystem level that persist well beyond initial disturbance ~800 years ago. Small-scale tree harvest changes the source of lacustrine C pools: lake-water TOC declines and stable isotopes indicate a shift from allochotonous to autochotonous C-sources. These changes impacted pond primary production positively and lake trophic status became more autotrophic/mixotrophic, as opposed to heterotrophic.

Rhinoceros auklets and Keen's mice were present on SG̲ang Gwaay throughout the ~1300 year time period covered by our sediment analysis, and ornithogenic proxies suggest a population decline after European contact. Rodway and Lemon (2011) estimated that the rhinoceros auklet colony at SG̲ang Gwaay increased since monitoring efforts began in the 1980s, however, our data suggests that the population is currently undergoing a long-term decline that started in 1385 CE. Data from permanent monitoring plots and ornithogenic proxies suggest that population census over short time scales might not capture broader cycles of population declines that occur over longer time scales. The $\delta^{15}N$ values start to decline ca. 1385 CE and continue until present, and a significant period of decline is associated with constant Keen's mice presence on the island indicating possible predation pressure. Our data shows that the early detection of invasive mammals that forage opportunistically and disperse easily (e.g., ungulates) can be a challenge.

Small-scale tree harvest likely decreased the above ground C pool on SG̲ang Gwaay after 1250 CE and although harvest stopped after the abandonment of Ninstints in the 19th century, it is possible that vegetation recruitment is hampered by deer browsing in modern times, however more research is needed to understand the impact of browsing. Management of invasive species could benefit vegetation restoration and an increase in aboveground C stocks after anthropogenic disturbance.

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CHAPTER 4

General discussion and conclusion

4.1 Summary and general discussion

Modern day ecosystem and wildlife management can benefit from long-term ecological data. Environmental stressors trigger ecosystem changes at long temporal scales that cannot be revealed through experimental designs alone. Paleoecology opens a window onto past ecosystems and unveils changes in processes that follow declining or increasing trends through time (e.g., geochemical cycles, wildlife population cycles). This can provide information about what stressors triggered these changes in the past allowing us to better estimate how ecosystems will respond to similar stressors in the future (Larina et al. 2010; Duda et al. 2022). The current epoch, the Anthropocene, is defined by anthropogenic forcing on the Earth's systems (e.g., CO_2 perturbation, increased greenhouse gases) that are recorded in the geological timescale (Lewis and Maslin 2015; Zalasiewicz et al. 2017); however, ecosystem scale changes of the anthropocene are also transforming ecosystem communities through the direct removal of wildlife and vegetation and the dispersal of biota to new geographical extents (Thomas 2020). Long before the mid 20th century and the beginning of the anthropocene (Lewis and Maslin 2015), humans started modifying ecosystems. However, the environmental consequences of ancient human civilizations remain relatively unknown although historical ecological data is valuable for conservation objectives today. Understanding what triggered ecosystem changes in the past provides valuable information with respect to species composition, vegetation changes and natural disturbances (Burney and Burney 2007; Lindblah et al. 2013).

The objective of this thesis was to unveil ecosystem changes on SG̱ang Gwaay (Haida Gwaii, B.C.) and inform current management plans within Park Canada's "The Living Landscapes of SG̱ang Gwaay: strengthening the land and people in a changing climate", a conservation and restoration project proposing archaeological surveys, maintaining Species at Risk habitat, forest understory maintenance and biosecurity management on SG̱ang Gwaay. Based on the findings of this project, vegetation restoration for the island could be re-assessed to increase Western red cedar populations to pre-expansion levels. Management plans and past research on SG̱ang Gwaay pointed out two areas of interest with respect to ecosystem changes: (1) changes in island vegetation caused by a decline in Western red cedar identified by Lacourse, Mathewes and Hebda 2007, and deer-browsing; (2) changes in the rhinoceros auklet colony size as identified by Rodway and Lemon (2011).

Chapter 2 is a review of management plans addressing the conservation of Haida Gwaii's burrowing seabirds (ancient murrelets, rhinoceros auklets, Cassin's auklet, Leach's storm-petrel, fork-tailed storm-petrel, tufted puffin, pigeon guillemot) with respect to invasive mammals (e.g., rats, deer, raccoon) since management was first implemented after the 1993 Nestucca oil spill. The objective of this chapter was to identify successes and shortfalls in the policies that aim to conserve these seabirds in Haida Gwaii based on Canadian Wildlife Survey (CWS) survey data and literature. Population trends and invasive species dispersal studies showed that although invasive species are managed in Haida Gwaii, shortfalls prevent seabird colonies from recovering completely. The lack of consistent monitoring and the continuous dispersal of invasive species either through natural dispersal (e.g., swimming) or human assisted dispersal (e.g., fishing boats, tourism) from source populations allows invaders to affect seabird colonies before they can be detected. Furthermore, on islands where invasive rats or raccoons were eradicated, colony recovery is not certain yet as demonstrated by Major (2011). Inconsistent monitoring efforts introduce biases in analyses of long-term population dynamics; when estimating population sizes, the same quadrats, number of transects, as well as survey frequency, intensity, and timing should be kept consistent in order to make accurate year-to-year comparisons (Major 2011). Deer-browsing and its effects on seabird habitat are not addressed in seabird management plans in Haida Gwaii, however, studies show increased avian predation in habitats severely browsed by ungulates (e.g., soay sheep (*Ovius aries*) browsing on Hirta Island (Jones 2013)). In Haida Gwaii, ancient murrelets and storm-petrels breed exclusively in mature forests or prefer vegetated areas (Vermeer and Lemon 1986; Rodway, Lemon and Kaiser 1988; Gaston 1992) and are most likely to be concerned by these vegetation changes compared to other species (e.g., tufted puffins, pigeon guillemot) that can successfully breed on islands free of vegetation. On islands heavily affected by deer-browsing, vegetation restoration could benefit seabirds by increasing breeding habitat. These shortfalls demonstrate that invasive species management with respect to burrowing seabird conservation can be improved in Haida Gwaii and that seabird monitoring can benefit from supplemental long-term data to assess population trends with greater certainty.

Based on findings from chapter 2, as well as shortfalls in monitoring plots identified by Rodway and Lemon (2011), we wanted to use alternative techniques to classical survey methods to uncover long-term population dynamics of a seabird colony from a permanent monitoring plot on SG̲ang Gwaay (Haida Gwaii). Additionally, we wanted to expand on findings of vegetation decrease on the same island identified by Lacourse, Mathewes and Hebda (2007). Thus, in **chapter 3**, building-on survey data presented in Rodway and Lemon (2011) and palynological data from Lacourse, Mathewes and Hebda (2007), we use paleolimnological techniques to uncover long-term ecosystem changes on SG̲ang Gwaay over the last 1300 years since the establishment of the pond on the island. We interpreted vegetation changes and seabird population trends with respect to anthropogenic activities at Ninstints, European contact, and invasive species management.

Our results clearly show that small-scale tree harvesting by the Haida altered the C allocations on the island over the ~1300 year period captured by the core, especially after intensification of the settlement at Ninstints c.a 1235 CE. Terrestrial matter delivery to the pond decreased (reduced lake-water TOC) as tree harvest increased after ca.1235 CE. This changed pond C allocations from allochtonous to autochtonous. With less C delivery to the pond, environmental conditions (i.e., light penetration, pH) were favourable for an increase in aquatic primary production. This is supported by increased microbial activity, followed by an increase in chl *a,* and a move towards a diatom assemblage dominated by one tychoplanktic species. Lake trophic status becomes more autotrophic/mixotrophic, as opposed to heterotrophic as the lake becomes more eutrophic. Our data demonstrate that insular habitats are highly sensitive to landscape alterations such as selective tree harvest and that ecosystem-broad impacts persist well beyond initial disturbance ~800 years ago.

Rodway and Lemon (2011) estimate that the rhinoceros auklet colony on SG̲ang Gwaay increased since surveys began in the 1980s; however, our data suggests that the population is currently undergoing a broader population-level decline as demonstrated by declines in $\delta^{15}N$ values starting ca. 1385 CE. Additionally, a large period of inferred seabird decline is associated with constant Keen's mice presence, based on PCR results, on the island indicating possible increased predation pressure. Although we were successful in detecting Keen's mice with sedDNA PCR from paleolimnological records, we were unable to detect sitka deer on SG̲ang

Gwaay despite their presence being confirmed on the island at the time of sampling in July 2021 (~2-3 individuals). Our data clearly demonstrate that long-term centennial population cycles can be omitted by short-term (decadal) survey data and that the early detection of invasive mammals that forage opportunistically and disperse easily (e.g., ungulates) can be a challenge.

4.2 Limitations

4.2.1 Limitations: Haida Gwaii burrowing seabird management with respect to invasive mammal predators

The review of management measures undertaken to conserve burrowing seabirds in Haida Gwaii between 1990-2020 identified some management shortfalls and measures that could improve conservation efforts (e.g., eradication of invasives at source populations, consistent survey of seabird colonies); however, this review has a limited perspective on the scalability of these measures. The social implications of eradication measures are not discussed in this review; however, socio-political considerations play a key role in the success of invasive species management (Crowley et al. 2017). The social and economic cost of invasive species in Haida Gwaii is not discussed, although we address the impact of invasive species on seabird populations our perspective is centered in Western science.

Eradication measures deployed at large scales in Haida Gwaii (e.g., eradication on Moresby and Graham Island) will affect people as poisoned baits will likely be deployed on private property. Beyond this consideration, eradication with poisoned baits exposes other native species to poison, such as raprtors and corvids, as the birds prey and scavange on species targeted by eradication (Howald et al. 1999; Veltman and Westbrooke 2001). These undesired effects of eradication should be addressed with the local community as corvids and raptors are culturally important species for the Haida. In New Zealand, where such large-scale eradication measures were deployed, public support for eradication decreased after lack of social engagement, concerns over impacts, and distrust (Black et al. 2021).

4.2.2 Limitations: Paleoecological reconstruction of SG̱ang Gwaay ecosystems

The sediment core we collected from the SG̱ang Gwaay pond complemented the palynological findings from a previous study. Our findings show that pollen declines on SG̱ang Gwaay identified by Lacourse Hebda and Mathewes (2007) caused by the selective harvest of Western red cedar caused changes in C allocations on SGang Gwaay. This is supported with historical trends in biogeochemical indicators (e.g., TOC, δ^{13}C, C/N, terrestrial and aquatic vegetation strerols and stanols, chl *a* , diatom assemblages). Additionally, we uncovered the historical trends in the human settlement at Ninstints, and rhinoceros auklets nesting on the island. Thus, our paleoecological study has a broad scope and successfully fills a knowledge gap about the historical ecological trends on SG̱ang Gwaay with respect to many componenets (i.e., aquatic and terrestrial vegetation, wildlife, humans, aquatic primary productivity), however this knowledge has some limitations that should be acknowledged and warrant future research.

Historical ecological trends captured by our sediment cores cannot be extrapolated to island scale and are limited to the pond catchment on SG̱ang Gwaay) and its immediate surrounding area. This limitation is well noted by additional studies on SG̱ang Gwaay with soil cores sampled closer to the village site (Hebda et al. 2005) that captured changes in island vegetation, particularly a selective harvest of Sitka spruce, that were not reflected in the sediment core used for the palynological study by Lacourse Hebda and Mathewes (2007). Aditionally, changes in diatom assemblages in one ecosystem cannot necessarily be extrapolated to other similar ecosystems (Anderson et al. 2018). Thus, the interpretation of our results, although informative, should be used with caution in subsequent studies of lacustrine environments with similar conditions in Haida Gwaii and cannot be extrapolated to sites with similar human history. Although our study demonstrates that C allocations changed following selective tree harvest, these results are limited to the pond and cannot be interpreted as changes in the soil ecosytems at island scale. Furthermore, our interpretation of carbon sources and sinks remains hypothetical at best, as carbon accumulation rates were not incorporated in this study. Therefore, although we identify a change in lake trophic status that can be linked with a transition of the pond from a source to a sink of C, we cannot draw further conclusions without additional proxies.

Additional limitations related to seabird historical trends arise. The sampling method used to extract the bottom part of the core prevented geochemistry analysis in the time sequence of ~689-1400 CE, thus ornithogenic trace-metal results are limited to the period between ~1400-2021 CE. The sterols ans stanols analysis was not successful as we were unable to consistently detect cholestanol and the $\delta^{15}N$ values are low indicating a low signal from the rhinoceros auklet colony despite its proximity to the pond. Additional seabird proxies would be helpful in overcoming the limitation of a lipid and nitrogen isotope signal hampered by vegetation and support trends observed in ornithogenic trace-metals.

4.3 Future research

4.3.1 Diatom ecology and pH

This thesis provided evidence that small-scale tree harvesting can alter ecosystems, and particularly lacustrine ecosystems. However, our understanding of how environmental parameters in the pond on SGang Gwaay changed remains limited. For instance, we were unable to depict the full picture of pH changes throughout the 1300 year period captured by the core beyond commenting on the fact that acidification likely occurred. This limitation could be overcome with more knowledge about the ecology of diatom species, such as *Aulacoseira crassipunctata,* that were clearly limited by environmental parameters prior to 1588 CE. This could be achieved by sampling more lakes in Haida Gwaii and taking pH, lake-water light penetration, and DOC measures to survey the environmental gradients favouring *A. crassipunctata*. This additional information about optima can be used to reconstruct past lake-water pH (Birks et al. 1990) and would be valuable in understanding broader ecosystem processes caused by alterations to terrestrial vegetation communities.

4.3.2 Paleoecology and sedDNA techniques– quantifying wildlife with qPCR and ddPCR

Chapter 2 and 3 demonstrated the need for the early detection of invasive species in Haida Gwaii and better monitoring techniques for seabirds over short and long time scales. In chapter 3 we explored the possibility of detecting invasive species in paleolimnological records with sedDNA PCR. Although we were successful in detecting Keen's mouse, a small native predator of seabirds, we were unable to detect sitka deer, although 2-3 individuals were present on the island at the time of sampling. This limitation highlights the difficulty in detecting low-abundance species that distribute easily (i.e., foraging on various islands, as opposed to being established in one location) with PCR. Additionally, DNA concentrations in our samples were low (Nanodrop value between 0.9-95.9 µg/g, mean 9.4 µg/g) and the lake-water is acidic (pH

5.2), therefore it is likely that PCR absence in some samples was due to DNA degradation (Seymour et al. 2018) as opposed to true absence. This limitation, alongside different sedimentation rates for different core depths, and sediment types are all factors contributing to DNA preservation–and detection in PCR (Savichtcheva et al. 2011; Domaizon et al. 2017). Quantitative PCR (qPCR) and digital droplet PCR (ddPCR) can offer further insight on the abundance of DNA within a sample, and both techniques can be used to correlate with field related biomass, density and occupancy for aquatic vertebrates (Pilliod et al. 2013; Doi et al. 2015; Di Muri et al. 2020; Xin et al 2022). In mesocosm experiments ddPCR offered the strongest correlations, compared with qPCR, to measure the DNA of fish in water and had more accurate results for biomass and abundance estimates (Doi et al. 2015).

4.3.3 16s metabarcoding

Microbes respond to environmental changes (e.g., nutrient availability, trace-metal contamination, changes in organic matter) rapidly and can therefore be an interesting proxy for environmental change. Shifts in lake-water microbial communities provide additional information about changes in the primary productivity of lakes (Pearman et al. 2022). Microbial metabarcoding, or 16s sequencing, offers approximations of microbial community changes over time in lacustrine environments (Pearman et al. 2022). Pairing 16s with a multi-proxy paleolimnological analysis, Tse et al. (2018) found synchronicity between changes in microbial communities and changes in diatom assemblages, sterols and stanols, nutrients, and pigments. Understanding changes in the microbial community for the SG̱ang Gwaay pond could provide additional information about lake-water environmental parameters over time that favoured certain microorganisms over others (e.g., nutrient availability, anoxia conditions, etc.).

4.3.4 Expanding the sterol and stanol analysis to uncover more changes in vegetation and diatom assemblages

The sterols and stanols targeted in our analysis allowed us to track changes in C3 land plants and the rise of aquatic primary productivity. Precisely, sitosterol/campesterol was used to track inputs from terrestrial plants vs. algae, the hydrogenation ratio (sitosterol/stigmastanol) was used to track microbial activity in the pond, and the sitosterol/cholesterol, was used to track sewage input and phytoplankton productivity (Mudge et al. 1999; Carreira et al. 2002; Zhang et al. 2018). However, targeting some additional sterols and stanols could benefit our analysis with respect to changes in vegetation and diatom assemblages. For instance, diatom species can be tracked with fucosterol (Gladu et al. 1991), resinous plants can be tracked with α-amyrin, plants with bark tissue can be tracked with β-amyrin (Chávez-Lara et al. 2019). Changes in α/β amyrins can be particularly interesting when trying to understand changes caused by tree harvest or grazing in terrestrial plant communities. For instance, selective tree harvest or tree recruitment hampered by ungulate grazing could be captured with a decline in β-amyrin. Although diverse sterol and stanol ratios exist to track grazing in the context of pastoral activities, these ratios cannot reliably be associated with grazing events when grazer abundance is low (i.e., not in the context of pastoralism, but rather of introduced species present in lower abundance) (Davies et al. 2022). Thus, tracking diverse plant groups with their respective biomarkers and relating changes in these biomarkers in paleolimnological records with historical records of grazing and sedDNA records could help uncover vegetation changes caused by browsing, even at low abundance as is the case with deer browsing on SG̲ang Gwaay.

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APPENDIX I: CHAPTER 3 METHODS

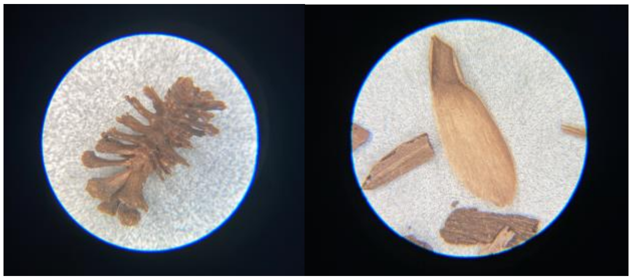


Figure S-1. a) Macrofossils used for ^{14}C analysis and to establish core chronologies

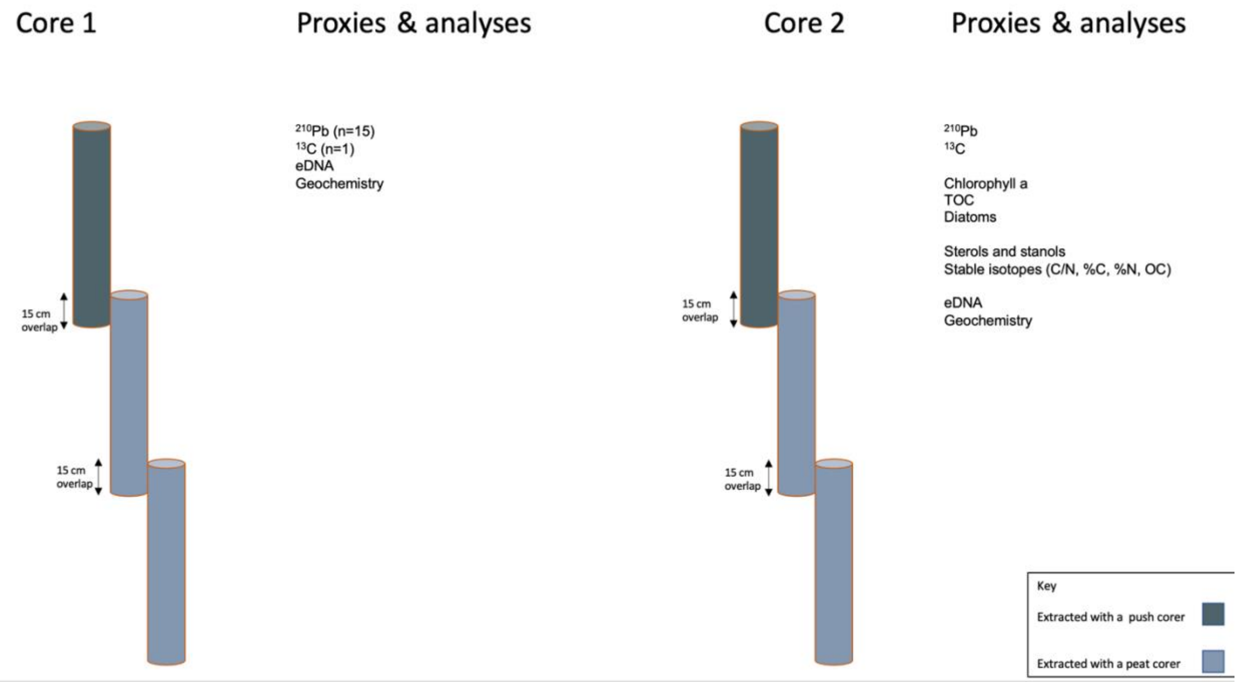
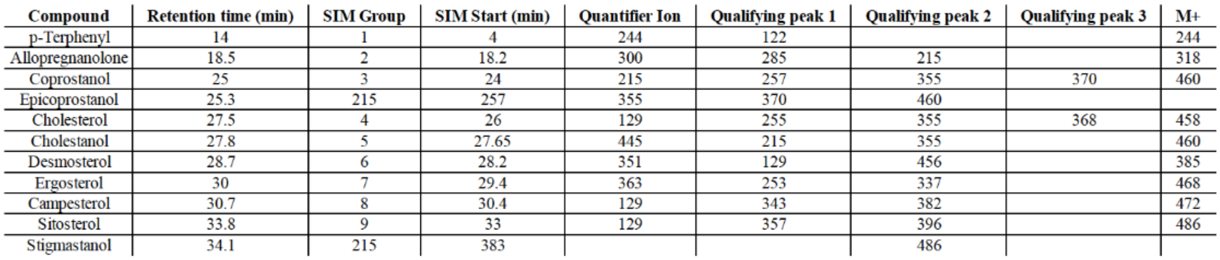


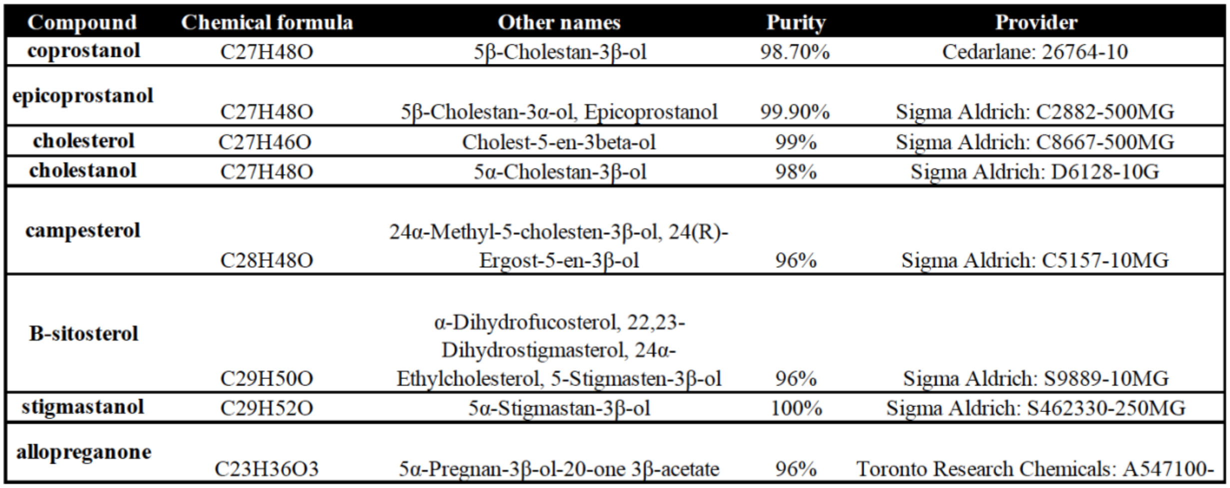
Figure S-1 b) Multi-proxy analysis breakdown in Core 1 and Core 2

Table S-1. Compounds targeted by GC-MS analysis, their retention time and qualifying peaks



Compound	Retention time (min)	SIM Group	SIM Start (min)	Quantifier Ion	Qualifying peak 1	Qualifying peak 2	Qualifying peak 3	M+
p-Terphenyl	14	1	4	244	122			244
Allopregnanolone	18.5	2	18.2	300	285	215		318
Coprostanol	25	3	24	215	257	355	370	460
Epicoprostanol	25.3	215	257	355	370	460		
Cholesterol	27.5	4	26	129	255	355	368	458
Cholestanol	27.8	5	27.65	445	215	355		460
Desmosterol	28.7	6	28.2	351	129	456		385
Ergosterol	30	7	29.4	363	253	337		468
Campesterol	30.7	8	30.4	129	343	382		472
Sitosterol	33.8	9	33	129	357	396		486
Stigmastanol	34.1	215	383			486		

Table S-2. Purity of standards used for sterols and stanols analysis



Compound	Chemical formula	Other names	Purity	Provider
coprostanol	C27H48O	5β-Cholestan-3β-ol	98.70%	Cedarlane: 26764-10
epicoprostanol	C27H48O	5β-Cholestan-3α-ol, Epicoprostanol	99.90%	Sigma Aldrich: C2882-500MG
cholesterol	C27H46O	Cholest-5-en-3beta-ol	99%	Sigma Aldrich: C8667-500MG
cholestanol	C27H48O	5α-Cholestan-3β-ol	98%	Sigma Aldrich: D6128-10G
campesterol	C28H48O	24α-Methyl-5-cholesten-3β-ol, 24(R)-Ergost-5-en-3β-ol	96%	Sigma Aldrich: C5157-10MG
B-sitosterol	C29H50O	α-Dihydrofucosterol, 22,23-Dihydrostigmasterol, 24α-Ethylcholesterol, 5-Stigmasten-3β-ol	96%	Sigma Aldrich: S9889-10MG
stigmastanol	C29H52O	5α-Stigmastan-3β-ol	100%	Sigma Aldrich: S462330-250MG
allopreganone	C23H36O3	5α-Pregnan-3β-ol-20-one 3β-acetate	96%	Toronto Research Chemicals: A547100-

Table S-3. Primers used to amplify sedDNA. Lower case letters in the primers indicate where a deliberate mismatch was introduced to reduce non-specific binding.

Family/Species	Primer name	Primer sequence	size
Rodent (common)	cytb rodent common F124	GATCCYTWCTTGGAGTMTGCC	~195 bp
	cytb rodent common R297	ATYTGCYTATTCCTCCATGTAG	
Deer (common)	deer cytb common F97	TTTGGCTCTCTACTAGGAATCTG	~240 bp
	deer cytb common R313	TTTCTAGGAAGGTGTATGATCC	
Bird (common)	BirdF1	TTCTCCAACCACAAAGACATTGGCAC	~211 bp
	alcid CO1 R299	CGAAGCCGCCAATTATGA	
Black rat[1]	black rat cytb F182	ATACACTACACATCCGACACTT	~139 bp
Norway rat[1]	Norway rat cytb F172	TCCTAGCAATACACTACACGTCT	~145 bp
Keen's mouse[1]	Keen's mouse cytb F180	ATACACTACACATCAGACACAACT	~120 bp
Caribou[2]	caribou cytb F180	AACAGCATTCTCCTCTGTTACT	~155 bp
Sitka[2]	Sitka and black-tailed cytb F124	ATTCTACAAATTCTTACCCGC	~200 bp
Rhinoceros auklet[3]	RHAU CO1 F152	GGCACTGCCCTCAGGTTG	~148 bp
Cassin's auklet[3]	CAAU CO1 F132	GCGCATGAGCCGGTATAGTC	~211 bp

(1) Used with cytb common rodent R297; (2) used with cytb common deer R313; (3) used with COI alcid R299; (4) primer from Sorenson 1999.

APPENDIX II: CHAPTER 3 RESULTS

Table S-4. Major ions and nutrients in water samples of the SGang Gwaay pond

Matrix	Concentration (mg/L)	Detection limit (mg/L)
Calcium	2.66	0.01
Fluoride	0.02	0.01
Chloride	57.7	0.01
Magnesium	4.45	0.01
Sodium	36.2	0.01
Sulfate	5.15	0.01
Potassium	1.94	0.01
Silica	10.7	0.01
Total Phosphorus	0.0704	0.0005
Particulate organic Carbon	1.1	0.003
Particulate organic Nitrogen	0.117	0.001
Ammonia as N	0.099	0.005
Dissolved organic Carbon	65.4	1
Nitrate/Nitrite as N	0.026	0.005
Nitrite as N	0.056	0.001
Total dissolved Nitrogen	<0.015	0.015
Total Kjeldahl dissolved Nitrogen	1.37	0.14
Soluble reactive Phosphorus	0.0308	0.0002
Total dissolved Phosphorus	0.0641	0.0005
Dissolved inorganic Carbon	1.4	0.2
Chlorophyll	2.9	0.1
Corrected Chlorophyll	1.2	0.1

Table S-5. Isotopic analyses of rhinoceros auklet faecal samples (n = 3)

Sample	$\delta^{13}C$	$\delta^{15}N$	%N	C/N
RHAU 1	-21.6	16	25	1.7
RHAU 2	-21.6	11.8	22.4	1.74
RHAU 3	-21.7	14.4	26.8	1.3
Average	-21.6	14.1	24.7	1.58

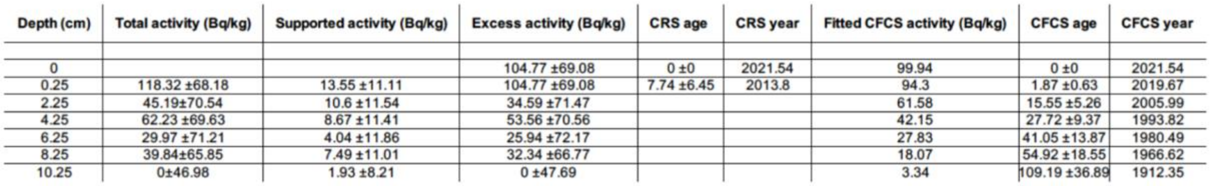
Table S-6. Trace-metal analyses of rhinoceros auklet faecal samples (n = 2)

Trace-metal	Concentration (ug/g)
Mercury	0.30
Silver	< 1
Arsenic	4.0
Aluminum	150
Barium	1.4
Beryllium	< 0.02
Bismuth	< 0.09
Calcium	24000
Cadmium	0.47
Cobalt	0.055
Chromium	< 0.5
Copper	32
Iron	1800
Potassium	11000
Lithium	< 2
Magnesium	2300
Manganese	20
Molybdenum	0.46
Sodium	4600
Nickel	0.25
Phosphorus	14000
Antimony	< 6
Selenium	5.1
Tin	< 2
Strontium	88
Titanium	9.1
Thallium	0.024
Uranium	0.029
Vanadium	< 1
Yttrium	0.046
Zinc	210
Lead	0.39
Lead	0.39
Lead	0.39

Core 1 ^{210}Pb activity. Radiometric profile shows that ^{210}Pb activity in samples of Core 1 from the SGang Gwaay pond are low (surface activity in SG 0-0.5 cm begins at 154.1 Bq/kg;

(Appendix II Table S-7 and Fig. S-2). The chronology for the top part of the core (~150 years) was modeled in the R package "serac" (Bruel 2020) using excess ^{210}Pb. Geochemistry analysis was used to supplement ages for the top part of Core 1. In Canada, isotopic ratios of ^{208}Pb/ ^{206}Pb and ^{206}Pb/^{207}Pb from anthropogenic sources range from ^{208}Pb/ ^{206}Pb < 1.17 and ^{206}Pb/^{207}Pb < 1.16 (Preciado 2007). In the SG̲ang Gwaay core, isotopic ratios of ^{208}Pb/ ^{206}Pb and ^{206}Pb/^{207}Pb are low indicating low anthropogenic input to the pond. Trends in ratios change at 7 cm in the core (Appendix II Fig. S-3). This change in ratios corresponds with the phasing out of leaded gasoline in Canada starting 1974 CE (Bagur and Widory 2020). Artificially produced ^{137}Cs and ^{241}Am molecules are used to pin-point chronologies in recent sediment samples. In Core 1, ^{241}Am activity is undetected and ^{137}Cs activity does not peak within the top of the core (Appendix II Table S-7 and Fig. S-2), therefore it is difficult to assign ages related to historic nuclear events within the top part of the core.

Table S-7. ^{210}Pb activity and chronologies for the top part of Core 1 (~150 years) based on the CRS and CFCS models



Depth (cm)	Total activity (Bq/kg)	Supported activity (Bq/kg)	Excess activity (Bq/kg)	CRS age	CRS year	Fitted CFCS activity (Bq/kg)	CFCS age	CFCS year
0			104.77 ±69.08	0 ±0	2021.54	99.94	0 ±0	2021.54
0.25	118.32 ±68.18	13.55 ±11.11	104.77 ±69.08	7.74 ±6.45	2013.8	94.3	1.87 ±0.63	2019.67
2.25	45.19±70.54	10.6 ±11.54	34.59 ±71.47			61.58	15.55 ±5.26	2005.99
4.25	62.23 ±69.63	8.67 ±11.41	53.56 ±70.56			42.15	27.72 ±9.37	1993.82
6.25	29.97 ±71.21	4.04 ±11.86	25.94 ±72.17			27.83	41.05 ±13.87	1980.49
8.25	39.84±65.85	7.49 ±11.01	32.34 ±66.77			18.07	54.92 ±18.55	1966.62
10.25	0±46.98	1.93 ±8.21	0 ±47.69			3.34	109.19 ±36.89	1912.35

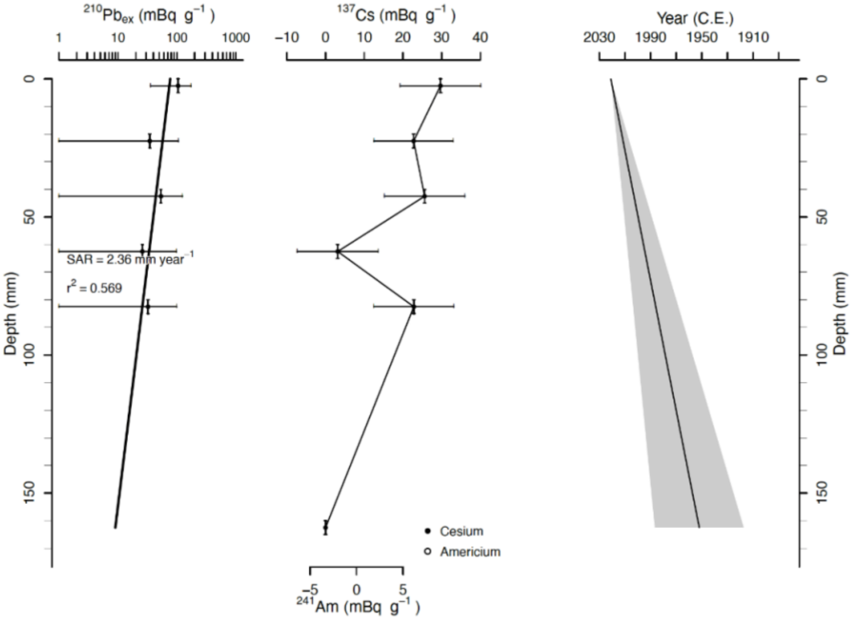
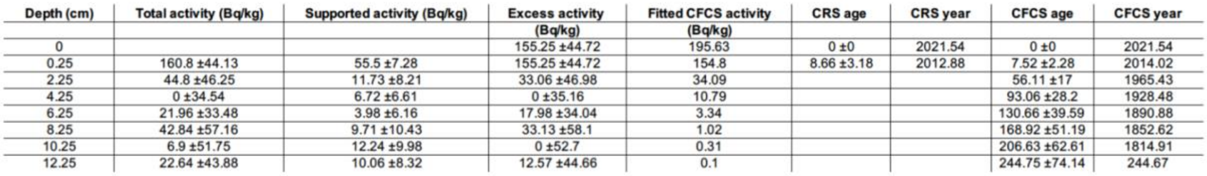


Figure S-2. ^{210}Pb, ^{137}Cs, ^{241}Am decay profiles and ^{210}Pb age-depth CFCS model for Core 1

Table S-8. ^{210}Pb activity and chronologies for the top part of Core 2 (~150 years) based on the CRS and CFCS models



Depth (cm)	Total activity (Bq/kg)	Supported activity (Bq/kg)	Excess activity (Bq/kg)	Fitted CFCS activity (Bq/kg)	CRS age	CRS year	CFCS age	CFCS year
0			155.25 ±44.72	195.63	0 ±0	2021.54	0 ±0	2021.54
0.25	160.8 ±44.13	55.5 ±7.28	155.25 ±44.72	154.8	8.66 ±3.18	2012.88	7.52 ±2.28	2014.02
2.25	44.8 ±46.25	11.73 ±8.21	33.06 ±46.98	34.09			56.11 ±17	1965.43
4.25	0 ±34.54	6.72 ±6.61	0 ±35.16	10.79			93.06 ±28.2	1928.48
6.25	21.96 ±33.48	3.98 ±6.16	17.98 ±34.04	3.34			130.66 ±39.59	1890.88
8.25	42.84 ±57.16	9.71 ±10.43	33.13 ±58.1	1.02			168.92 ±51.19	1852.62
10.25	6.9 ±51.75	12.24 ±9.98	0 ±52.7	0.31			206.63 ±62.61	1814.91
12.25	22.64 ±43.88	10.06 ±8.32	12.57 ±44.66	0.1			244.75 ±74.14	244.67

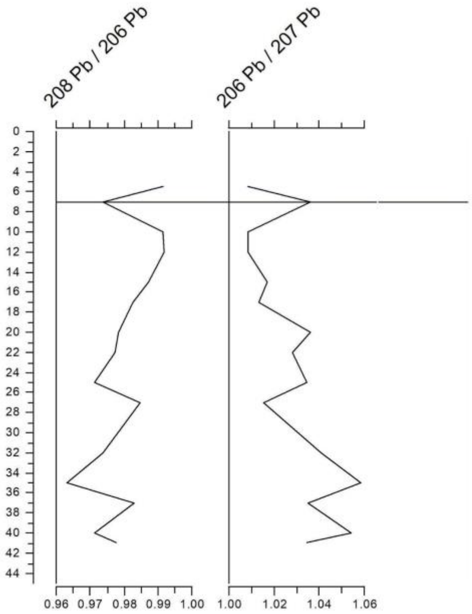


Figure S-3. Isotopic ratios in samples from the SG̲ang Gwaay Core 1. The line at depth=7cm indicates the inversion in activity trends caused by the ban of leaded gasoline in Canada starting 1974.

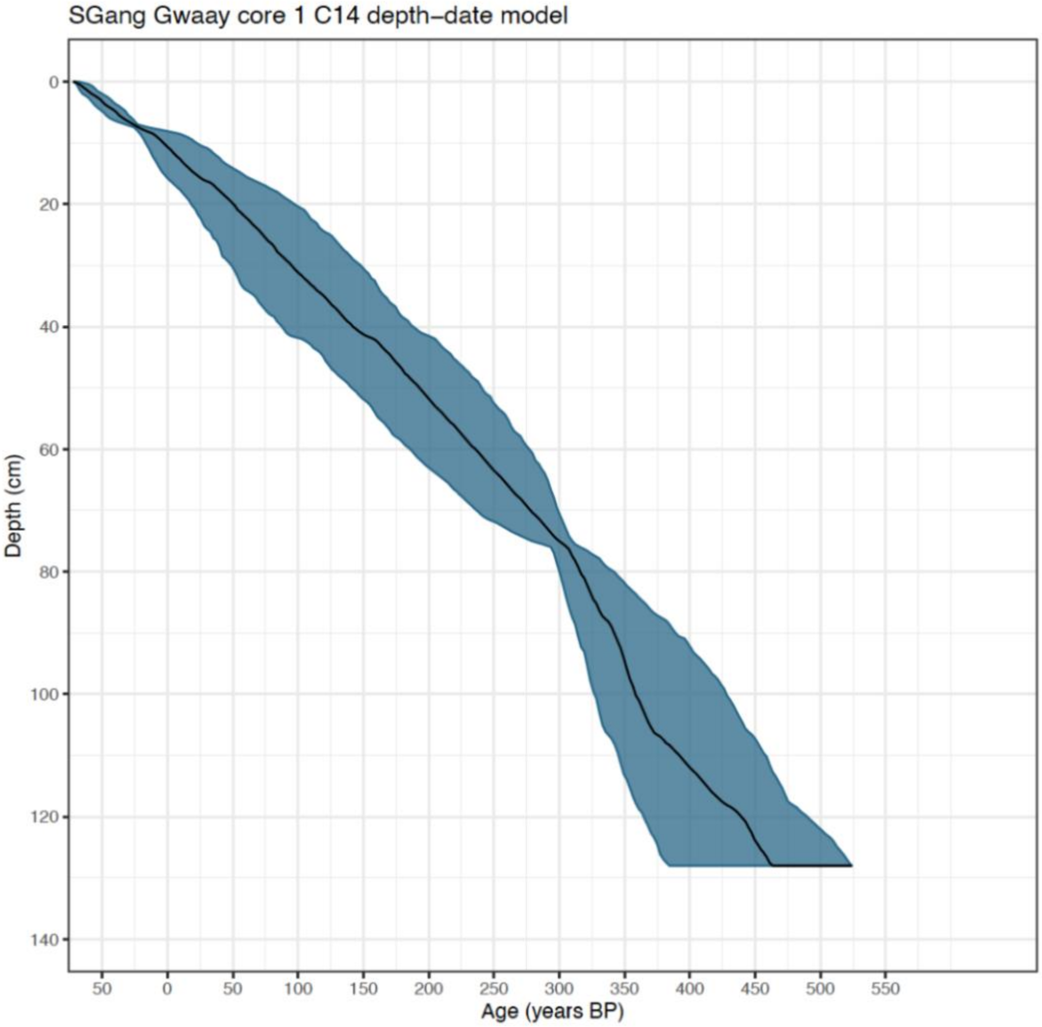
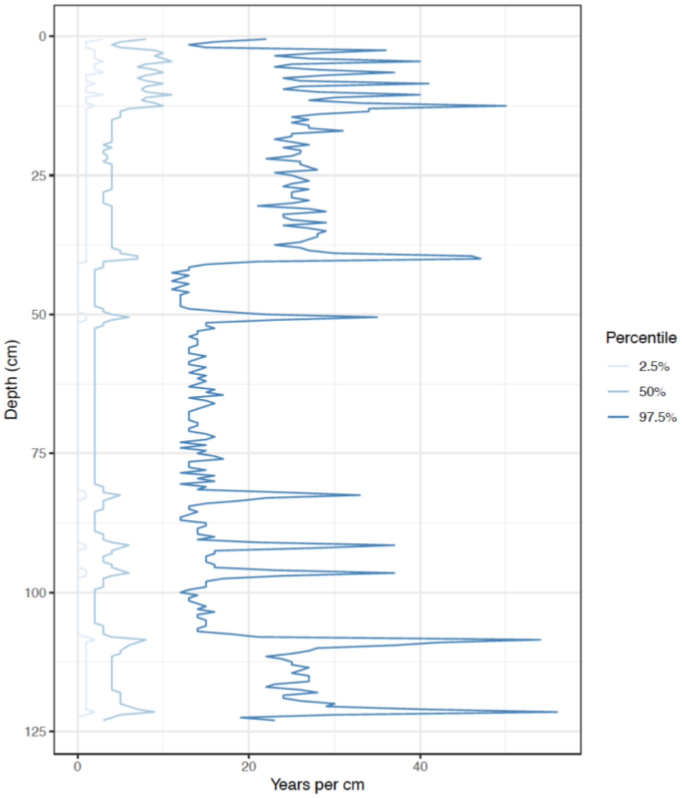


Figure S-4. Depth-date model for Core 1 with 95% confidence intervals



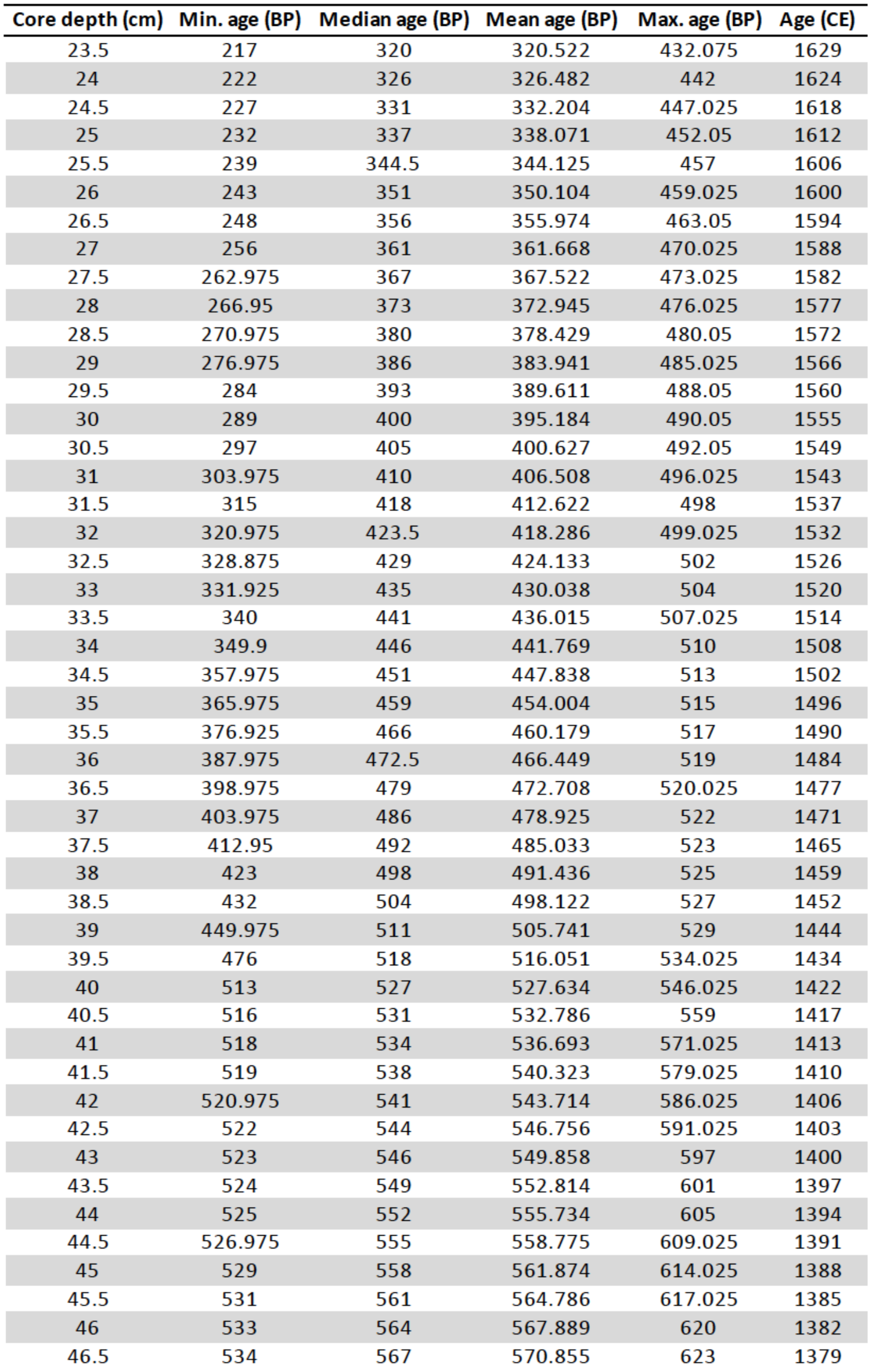
S-5. Sedimentation rate for Core 2 based on Bchron age-depth model

APPENDIX II (continued)

Table S-9. Ages estimated with Bchron for Core 2 table 2 ⅙

Core depth (cm)	Min. age (BP)	Median age (BP)	Mean age (BP)	Max. age (BP)	Age (CE)
0	-71	-69	-67.831	-60	2018
0.5	-65	-60	-58.763	-44	2009
1	-63	-55	-53.124	-35	2003
1.5	-61	-49	-48.173	-28.975	1998
2	-59	-44	-42.614	-19	1993
2.5	-53	-32	-31.42	-3.975	1981
3	-43	-22	-19.826	10	1970
3.5	-38	-11	-9.588	23	1960
4	-33	1	1.649	40	1948
4.5	-20.025	15	15.19	53.025	1935
5	-13	24	24.751	63.025	1925
5.5	-7.025	33	33.626	73	1916
6	-1	44	43.846	87	1906
6.5	12	56	56.388	103	1894
7	25	65	66.143	112.025	1884
7.5	32.975	75	75.022	122	1875
8	37.975	84	84.57	134.025	1865
8.5	49	97	97.118	148	1853
9	57.975	106	106.778	160.025	1843
9.5	65	114	115.519	173	1834
10	71.975	124	125.44	187.025	1825
10.5	81.95	136.5	138.692	200.05	1811
11	88	147	149	218	1801
11.5	95.95	156	158.233	233.025	1792
12	102	167	169.248	248	1781
12.5	111.95	180.5	183.364	270.025	1767
13	119.975	189	192.639	286	1757
13.5	128	196	200.509	302	1749
14	132	203	207.557	311.025	1742
14.5	136.975	209.5	214.388	325.075	1736
15	143.975	215.5	220.948	333.05	1729
15.5	147	221	227.29	340	1723
16	151	227.5	233.672	345	1716
16.5	154	234	239.558	348.025	1710
17	157.975	241	245.874	355.125	1704
17.5	162.95	248	251.732	362.075	1698
18	165	254	257.668	371	1692
18.5	171	260	263.453	376.025	1687
19	174.975	266	269.081	378.05	1681
19.5	178	271	274.931	382.025	1675
20	183	278	280.536	388	1669
20.5	188	284	286.352	394.025	1664
21	194	290	291.957	401	1658
21.5	197.975	296	297.463	403.025	1653
22	204	302	302.934	408.075	1647
22.5	209.975	308	308.773	415.025	1641
23	212	314	314.598	426.05	1635

Ages estimated with Bchron for Core 2 table 2 2/6



Core depth (cm)	Min. age (BP)	Median age (BP)	Mean age (BP)	Max. age (BP)	Age (CE)
23.5	217	320	320.522	432.075	1629
24	222	326	326.482	442	1624
24.5	227	331	332.204	447.025	1618
25	232	337	338.071	452.05	1612
25.5	239	344.5	344.125	457	1606
26	243	351	350.104	459.025	1600
26.5	248	356	355.974	463.05	1594
27	256	361	361.668	470.025	1588
27.5	262.975	367	367.522	473.025	1582
28	266.95	373	372.945	476.025	1577
28.5	270.975	380	378.429	480.05	1572
29	276.975	386	383.941	485.025	1566
29.5	284	393	389.611	488.05	1560
30	289	400	395.184	490.05	1555
30.5	297	405	400.627	492.05	1549
31	303.975	410	406.508	496.025	1543
31.5	315	418	412.622	498	1537
32	320.975	423.5	418.286	499.025	1532
32.5	328.875	429	424.133	502	1526
33	331.925	435	430.038	504	1520
33.5	340	441	436.015	507.025	1514
34	349.9	446	441.769	510	1508
34.5	357.975	451	447.838	513	1502
35	365.975	459	454.004	515	1496
35.5	376.925	466	460.179	517	1490
36	387.975	472.5	466.449	519	1484
36.5	398.975	479	472.708	520.025	1477
37	403.975	486	478.925	522	1471
37.5	412.95	492	485.033	523	1465
38	423	498	491.436	525	1459
38.5	432	504	498.122	527	1452
39	449.975	511	505.741	529	1444
39.5	476	518	516.051	534.025	1434
40	513	527	527.634	546.025	1422
40.5	516	531	532.786	559	1417
41	518	534	536.693	571.025	1413
41.5	519	538	540.323	579.025	1410
42	520.975	541	543.714	586.025	1406
42.5	522	544	546.756	591.025	1403
43	523	546	549.858	597	1400
43.5	524	549	552.814	601	1397
44	525	552	555.734	605	1394
44.5	526.975	555	558.775	609.025	1391
45	529	558	561.874	614.025	1388
45.5	531	561	564.786	617.025	1385
46	533	564	567.889	620	1382
46.5	534	567	570.855	623	1379

Ages estimated with Bchron for Core 2 table 2 3/6

Core depth (cm)	Min. age (BP)	Median age (BP)	Mean age (BP)	Max. age (BP)	Age (CE)
47	535.975	570	573.956	627	1376
47.5	538	573	577.108	631	1373
48	540.975	576	580.33	634	1370
48.5	543	580	583.724	637	1366
49	545.975	583	587.315	640.05	1363
49.5	548.975	587	591.432	646.025	1359
50	553	592.5	597.105	653.025	1353
50.5	558	602	605.82	664	1344
51	562	608	611.481	672.05	1339
51.5	564	613	615.674	678.025	1334
52	566	617	619.383	682	1331
52.5	568	621	622.879	685	1327
53	569	624	626.275	689	1324
53.5	570.975	628	629.627	694	1320
54	572	632	632.899	702	1317
54.5	574.975	635	636.079	706.05	1314
55	575.975	638	639.161	710.075	1311
55.5	577.975	642	642.172	716.025	1308
56	579	645	645.212	724	1305
56.5	581	647.5	648.251	725.05	1302
57	584	651	651.257	730	1299
57.5	585	655	654.438	732.025	1296
58	588.975	658	657.49	737	1293
58.5	590	661	660.535	739.025	1289
59	592	665	663.633	743	1286
59.5	594	668	666.676	745.025	1283
60	596	670.5	669.675	748.025	1280
60.5	597	672.5	672.702	751.025	1277
61	598	676	675.923	753.025	1274
61.5	599.975	679	679.03	757	1271
62	601.975	682	682.174	762.025	1268
62.5	604.975	685	685.21	766.025	1265
63	606	688	688.204	770.025	1262
63.5	609.95	691	691.447	774.025	1259
64	611.975	694	694.677	778.025	1255
64.5	613	697	697.971	784.025	1252
65	616.925	700	701.172	786	1249
65.5	620.975	704	704.456	794	1246
66	623	708	707.763	798	1242
66.5	626	711.5	710.976	800.05	1239
67	629	714.5	714.066	803	1236
67.5	634.95	717	717.004	805.025	1233
68	636.975	720	719.94	807	1230
68.5	638.975	722	723.046	810	1227
69	641	725	726.203	814	1224
69.5	644.95	727	729.252	815.05	1221

Ages estimated with Bchron for Core 2 table 2 4/6

Core depth (cm)	Min. age (BP)	Median age (BP)	Mean age (BP)	Max. age (BP)	Age (CE)
70	646.975	731	732.265	819	1218
70.5	651.975	734	735.213	821	1215
71	653.975	737	738.314	824.025	1212
71.5	657.975	739.5	741.46	826	1209
72	661.975	743	744.666	828.025	1205
72.5	664.975	747	747.708	831.025	1202
73	666.975	749	750.643	836.05	1199
73.5	671	753	753.61	840.025	1196
74	673	757	756.496	845	1194
74.5	675	760	759.496	847.025	1191
75	678.975	763	762.578	849.025	1187
75.5	681.975	765.5	765.906	851.025	1184
76	684.975	768	769.131	855.025	1181
76.5	689	771	772.01	857	1178
77	692	773.5	775.134	861.075	1175
77.5	694	776	778.185	867	1172
78	701.95	778.5	781.372	869	1169
78.5	705.975	782	784.499	870	1166
79	709.975	785	787.957	872	1162
79.5	712.975	788	791.341	875.025	1159
80	716.975	792	794.759	877.025	1155
80.5	722.95	794	798.009	879.025	1152
81	725.975	798	801.673	883	1148
81.5	729	803	805.551	885.025	1144
82	733.975	809	810.971	891	1139
82.5	742	818	819.407	899	1131
83	747	824	825.057	905	1125
83.5	750.975	829.5	829.846	909.025	1120
84	755	833	833.885	911.025	1116
84.5	757	837	837.452	915	1113
85	761	841	841.078	919	1109
85.5	764	844	844.622	921.025	1105
86	768.975	848	847.995	924.025	1102
86.5	769	852	851.265	927.05	1099
87	772.95	855	854.52	930.025	1095
87.5	776.975	860	858.05	934	1092
88	779.975	863	861.556	936	1088
88.5	784.95	867	865.049	939	1085
89	788	871	868.59	942	1081
89.5	791	874	872.392	945.05	1078
90	793.975	878	876.314	951.025	1074
90.5	795.975	882	880.382	954.075	1070
91	799	887	885.613	960	1064
91.5	807	898	895.042	966	1055
92	816	905	901.927	972	1048
92.5	823.975	909	907.027	976	1043
93	830.975	914	911.674	979	1038

Ages estimated with Bchron for Core 2 table 2 ⅚

Core depth (cm)	Min. age (BP)	Median age (BP)	Mean age (BP)	Max. age (BP)	Age (CE)
93.5	833.975	917	916.222	982	1034
94	838.975	921	920.745	990	1029
94.5	846	926	925.243	991.075	1025
95	851	930	929.859	996.05	1020
95.5	854	934	934.966	1001	1015
96	865	940	941.35	1010.025	1009
96.5	878.9	949	950.604	1021.025	999
97	884.975	955.5	956.664	1025.05	993
97.5	890	960	961.275	1031	989
98	903.925	964	965.418	1036	985
98.5	907.95	968	969.339	1043.025	981
99	910.975	972	973.055	1051.05	977
99.5	916.925	976	976.507	1054.025	973
100	919	979	979.923	1059	970
100.5	921.975	983	983.374	1061.15	967
101	923.975	986	986.887	1069.025	963
101.5	925	990	990.309	1072.05	960
102	928	994	993.867	1077	956
102.5	931.925	997	997.499	1081	953
103	935.95	1001	1001.02	1086.05	949
103.5	939	1005	1004.66	1094.025	945
104	941.975	1009	1008.256	1096.025	942
104.5	946	1012.5	1011.85	1097.025	938
105	949.975	1015	1015.425	1100.025	935
105.5	952	1019	1018.991	1103.025	931
106	954	1023	1022.874	1109.025	927
106.5	958.975	1026	1026.672	1111.025	923
107	963.975	1030	1030.674	1113.025	919
107.5	968.975	1035	1035.222	1116.075	915
108	970.975	1040	1040.973	1120.025	909
108.5	985.925	1051	1053.87	1156.1	896
109	994	1060	1064.77	1168	885
109.5	999	1067	1073.657	1176.025	876
110	1003.975	1074	1081.553	1188.025	868
110.5	1010.975	1081	1088.895	1195.025	861
111	1016.975	1089	1095.816	1202	854
111.5	1021	1095	1102.073	1211.025	848
112	1026.975	1101	1108.074	1218.075	842
112.5	1032	1106	1114.02	1228.025	836
113	1035	1113	1120.058	1232.05	830
113.5	1040.95	1120.5	1126.254	1239.025	824
114	1046	1126	1132.665	1245	817
114.5	1050.975	1131	1138.929	1249.05	811
115	1059	1138	1145.188	1255	805
115.5	1064.975	1146	1151.434	1259	799
116	1067	1151	1157.599	1263.025	792
116.5	1074	1157	1163.565	1267.025	786

Ages estimated with Bchron for Core 2 table 2 6/6

Core depth (cm)	Min. age (BP)	Median age (BP)	Mean age (BP)	Max. age (BP)	Age (CE)
117	1075	1163	1169.594	1272.025	780
117.5	1085.975	1169	1175.68	1277	774
118	1093	1174	1182.336	1281	768
118.5	1100.95	1179	1188.864	1284.025	761
119	1107.975	1183	1195.63	1291	754
119.5	1117.975	1187	1202.481	1296.025	748
120	1124	1192	1209.971	1303	740
120.5	1133	1197	1218.132	1310.05	732
121	1154.975	1204	1228.828	1320	721
121.5	1179.975	1217.5	1242.651	1336	707
122	1181.975	1230	1249.986	1345	700
122.5	1183	1239	1255.504	1354	694
123	1184	1250	1260.736	1363.025	689

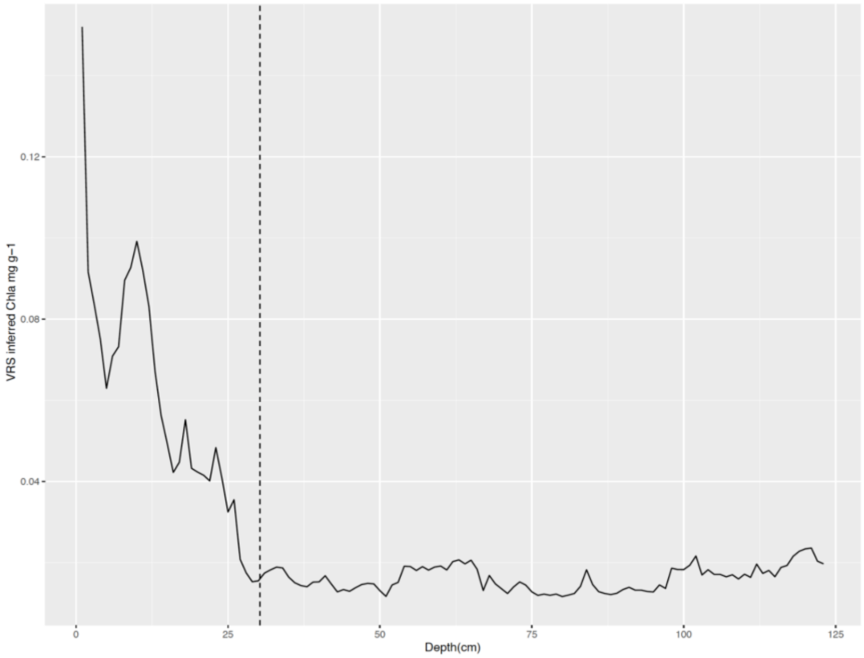


Figure S-6. VRS inferred Chlorophyll-*a* vs. depth in the SGang Gwaay core with the dashed line indicating a significant break-point.

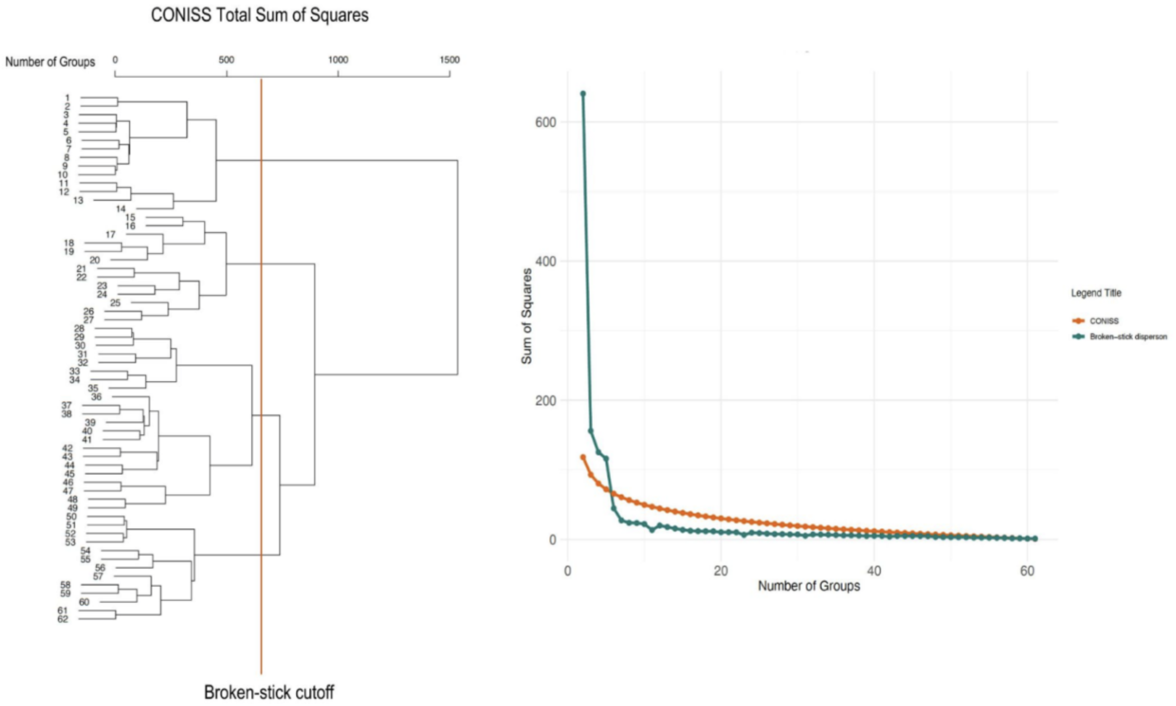


Figure S-7. CONISS Total Sum of Squares and Broken-stick model

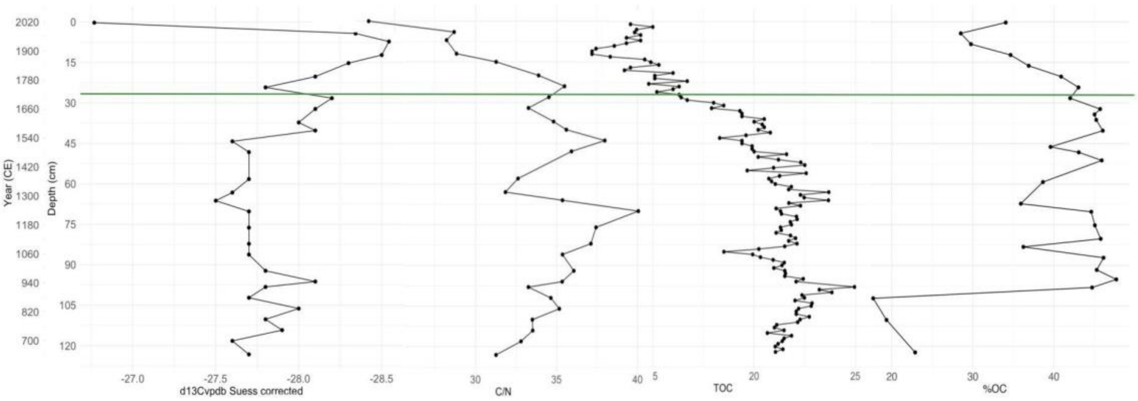


Figure S-8. Proxies related to vegetation and organic matter changes in the SG̲ang Gwaay pond.

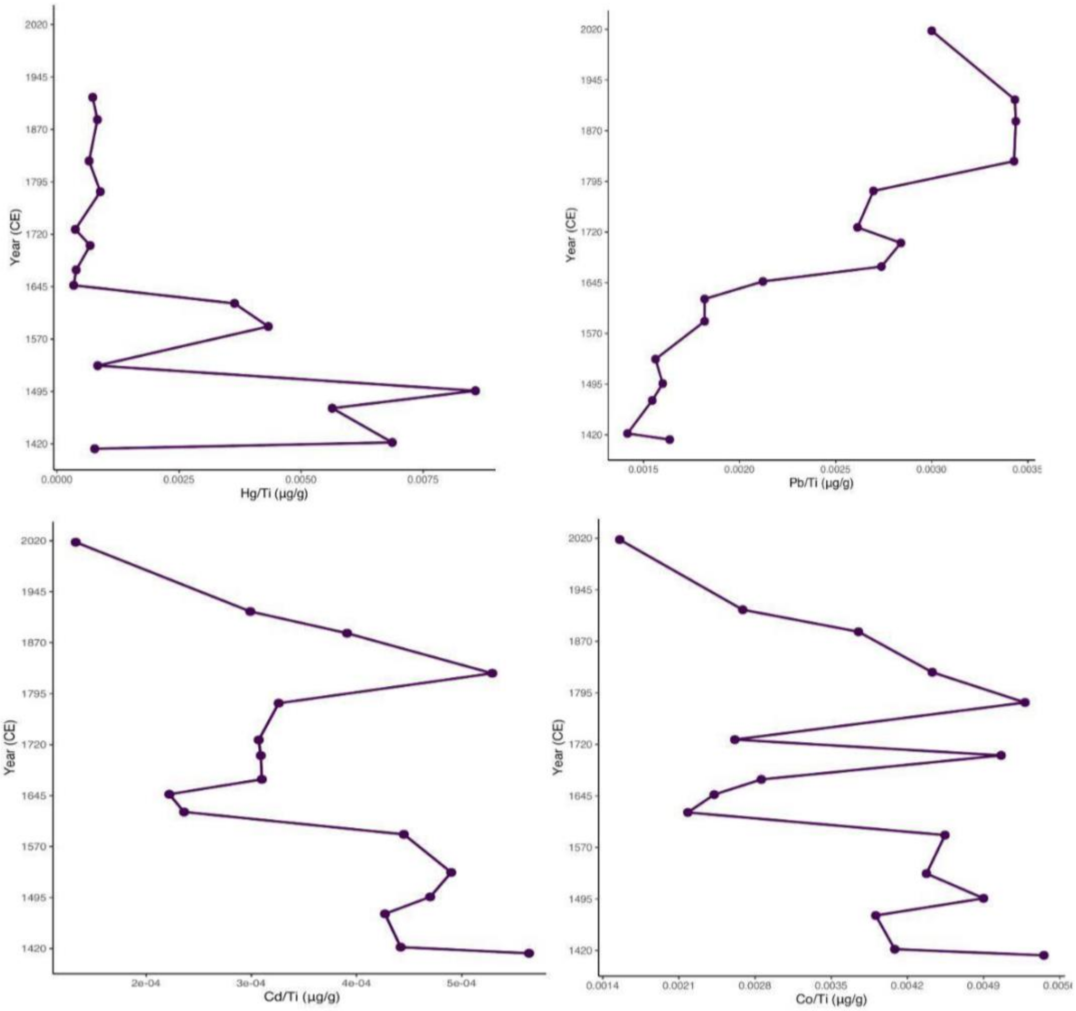


Figure S-9. Ornithogenic trace metals

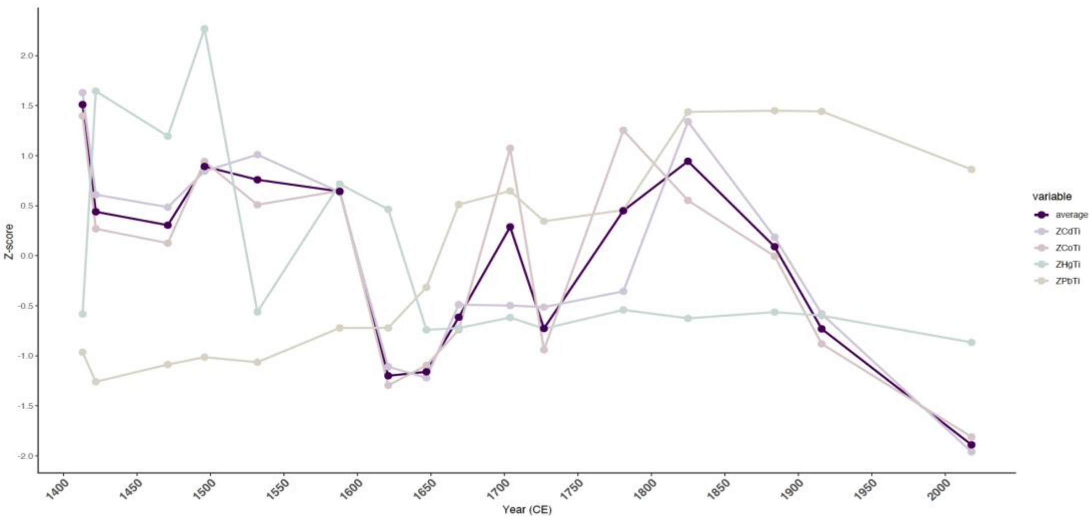


Figure S-10. Z-score of ornithogenic trace-metals standardized to Ti and their z-score arithmetic average

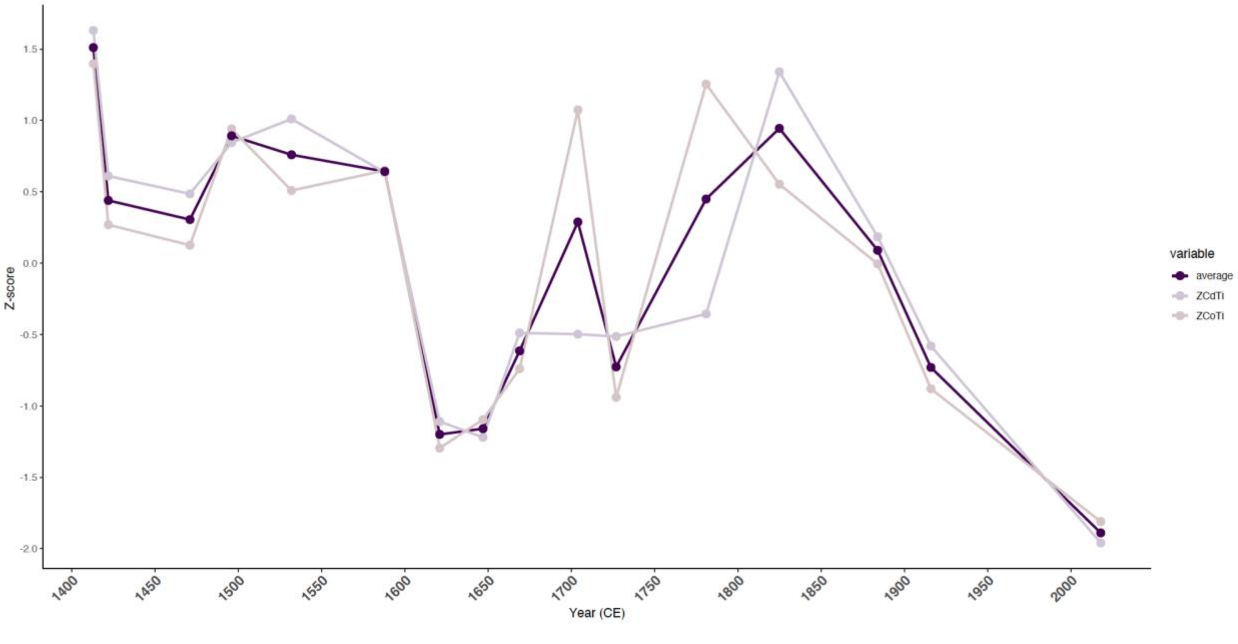


Figure S-11. Z-score of ornithogenic trace-metals without metals influence by atmospheric deposition and OM (i.e Pb, Hg) and their z-score arithmetic average

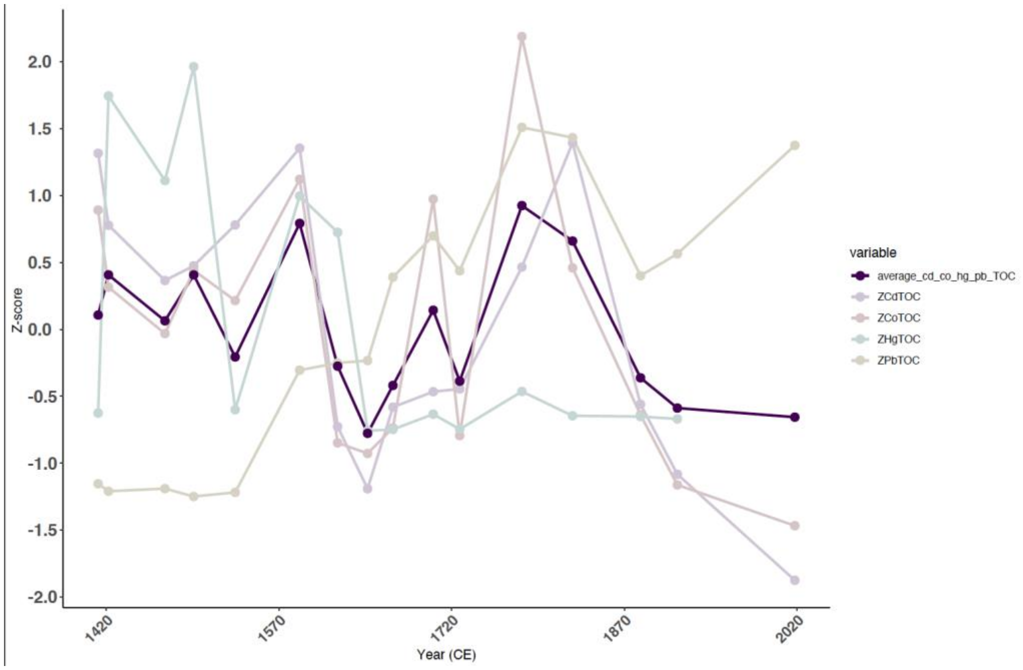


Figure S-12. Z-score of ornithogenic trace-metals standardized to TOC and their z-score arithmetic average

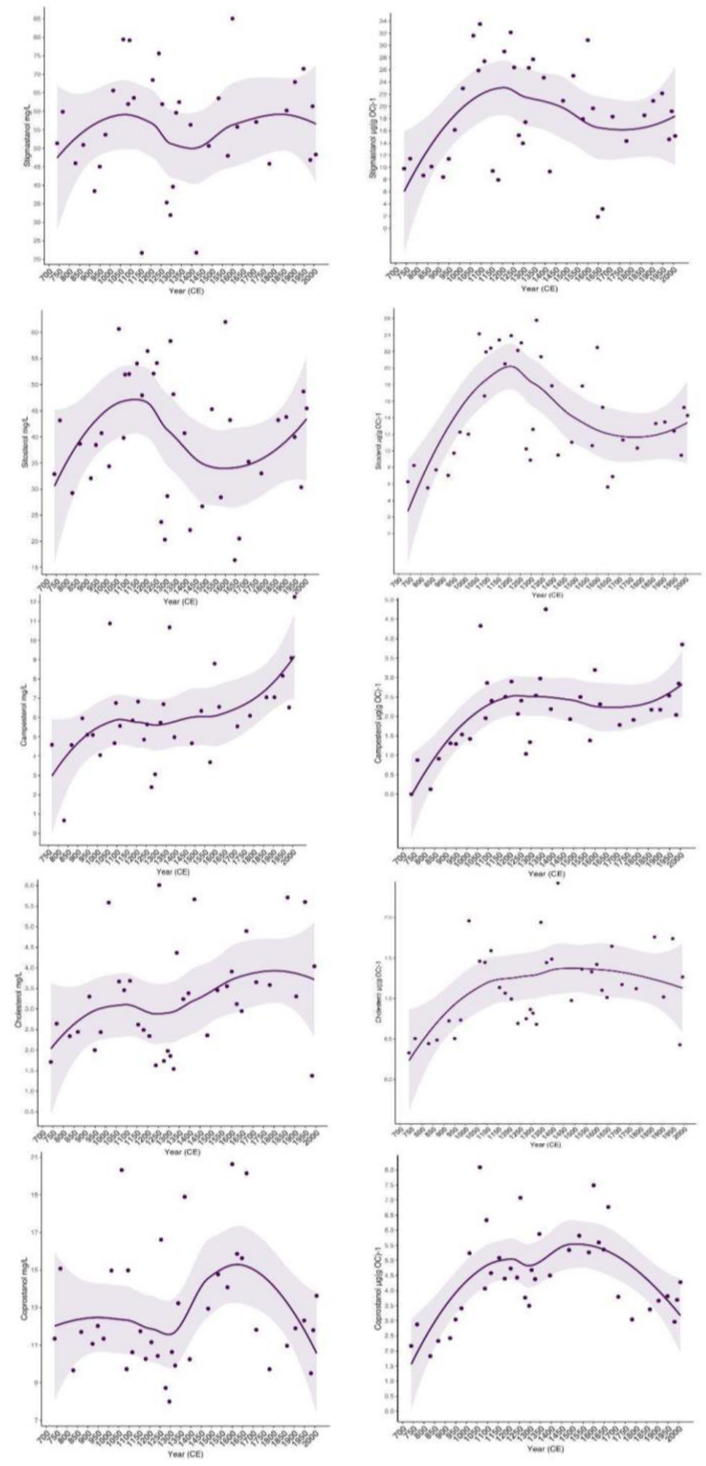


Figure S-13. Sterols and stanols analyzed in the SG̲ang Gwaay core fitted with a LOESS for values corrected to organic carbon and uncorrected values.

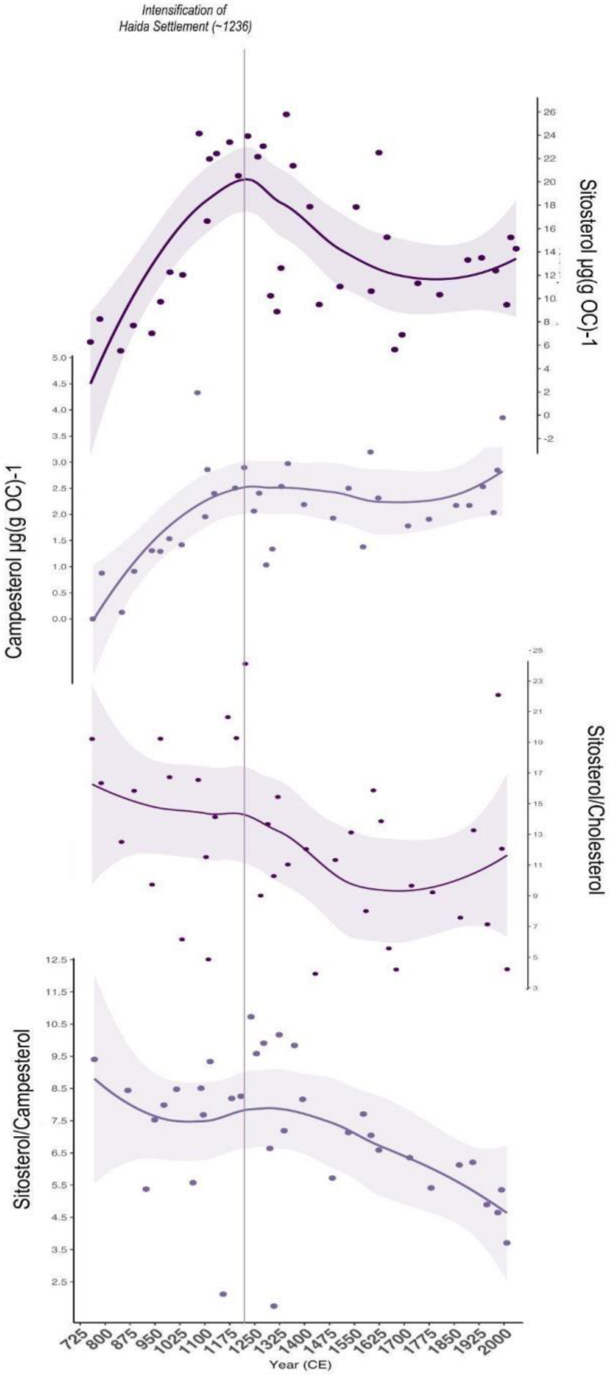


Figure S-14. Lipid profiles and ratios demonstrating a shift in sources of lipid inputs to the pond from higher plants to microalgae

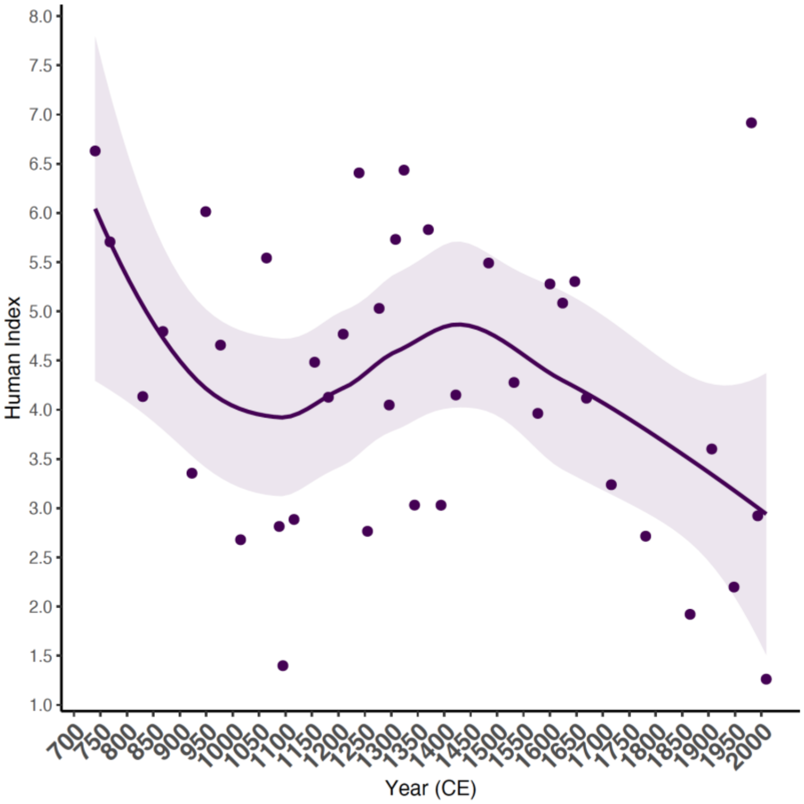


Figure S-15. GAM of the human index (coprostanol/cholesterol)