



Vertebrate records in polar sediments: Biological responses to past climate change and human activities [☆]



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ABSTRACT

Biological responses to climate and environmental changes in remote polar regions are of increasing interest in global change research. Terrestrial and marine polar ecosystems have suffered from impacts of both rapid climate change and intense human activities, and large fluctuations in the population sizes of seabirds, seals, and Antarctic krill have been observed in the past decades. To understand the mechanisms driving these regime shifts in polar ecosystems, it is important to first distinguish the influences of natural forcing from anthropogenic activities. Therefore, investigations of past changes of polar ecosystems prior to human contact are relevant for placing recent human-induced changes within a long-term historical context. Here we focus our review on the fossil, sub-fossil, archaeological, and biogeochemical remains of marine vertebrates in polar sediments. These remains include well-preserved tissues such as bones, hairs and feathers, and biogeochemical markers and other proxy indicators, including deposits of guano and excrement, which can accumulate in lake and terrestrial sediments over thousands of years. Analyses of these remains have provided insight into both natural and anthropogenic impacts on marine vertebrates over millennia and have helped identify the causal agents for these impacts. Furthermore, land-based seabirds and marine mammals have been shown to play an important role as bio-vectors in polar environments as they transport significant amounts of nutrients and anthropogenic contaminants between ocean and terrestrial ecosystems.

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1. Introduction

High latitude regions are currently experiencing pressure from both climate change and anthropogenic impacts, with some terrestrial and marine ecosystems having changed significantly in recent decades (e.g., Croxall, 1992; Smetacek and Nicol, 2005; Smol et al., 2005; Turner et al., 2006; Smol and Douglas, 2007; Trivelpiece et al., 2011; Murphy and Hoffmann, 2012). For example, Antarctic populations of

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pygoscelid penguins and Antarctic krill have declined dramatically in the Antarctic Peninsula, while remaining relatively stable or increasing in other regions (Woehler et al., 2001; Atkinson et al., 2004). Specifically, Gentoo penguins (*Pygoscelis papua*) have expanded their range in the Antarctic Peninsula in response to recent warming trends, while Chinstrap (*Pygoscelis antarctica*) and Adélie penguins (*Pygoscelis adeliae*) have declined in many parts of the peninsula (Smith et al., 1999; Ducklow et al., 2007; Trivelpiece et al., 2011). Both Arctic and Antarctic marine ecosystems have also been significantly modified by human hunting and fisheries in the past century (Laws, 1985; Everson, 2000; Douglas et al., 2004).

Unfortunately, it is often difficult to distinguish between natural and anthropogenic factors influencing vertebrate populations. In some studies reconstructions of past population changes have been explicitly related to known human impacts (historic sealing, whaling, and fisheries) over the past several centuries (Laws, 1985; Everson, 2000; Douglas et al., 2004). For instance, in Antarctic fur seals, the population changes over the last two centuries have been linked primarily to human exploitation of the marine environment (Hodgson and Johnston, 1997; Yang et al., 2010) while recent shifts in the breeding success of penguins have been linked to human visits to their breeding sites (Woehler et al., 1994; Copley and Shears, 1999). In other studies, changing abundances and distributions of penguins, other seabirds, and seals have been linked more closely to oceanographic (e.g., sea ice) and environmental changes (Croxall, 1992; Montes-Hugo et al., 2009) including the more recent (last 50 years) period of rapid climate warming (Smith et al., 1999; Ainley, 2002; Croxall et al., 2002).

To assess relative magnitudes of future climate and human impacts on polar ecosystems, it is important to understand the ecological responses to climate change in the past, particularly those that pre-date the onset of human activities. Paleocological approaches can be used to address this need. Here we summarize major findings from numerous investigations on how polar vertebrates have responded to climate changes and human activities over millennial and centennial time scales using a combination of morphological and biogeochemical markers found in sediments accumulated at seabird and seal colonies, and/or at molt and haul-out areas.

2. Morphological and biogeochemical evidence of vertebrates in polar sediments

Morphological evidence of past vertebrates includes sub-fossil and fossil bones, feathers, stomach oil, nests, eggshells (birds), hairs (seals) and even mummified whole remains. These tissues are frequently preserved quite well in cold, dry polar climates, thereby providing a natural archive of biological and biochemical information that can extend from hundreds to thousands of years old. Few regions in the world provide such archives for living species in the same area where they occur today. Recent advances in stable isotope analyses and ancient DNA provide further opportunities for understanding ecological responses to environmental change and anthropogenic impacts (Ritchie et al., 2004; Emslie and Patterson, 2007; Lorenzini et al., 2010; Huang et al., 2011a). Ornithogenic (bird-formed) soils in Antarctica are especially rich in both morphological remains of penguins and their prey, as well as biogeochemical signatures of their guano, providing insights into multiple levels of the food web. Many of these soils were formed by Adélie penguins, the most abundant penguin in Antarctica, and are commonly found on ice-free coastlines around the entire continent (Fig. 1).

Biogeochemical evidence of past vertebrates consists mainly of compounds associated with excrement accumulating in ice-free polar areas. For example, Antarctic pygoscelid penguins and Antarctic fur seals (*Arctocephalus gazella*) leave distinct excrement that is enriched for inorganic elements such as F, P, and Cu (Tatur and Keck, 1990) derived from their main prey, krill (*Euphausia* spp.), which themselves mainly feed on algae. Through biogeochemical cycling processes,

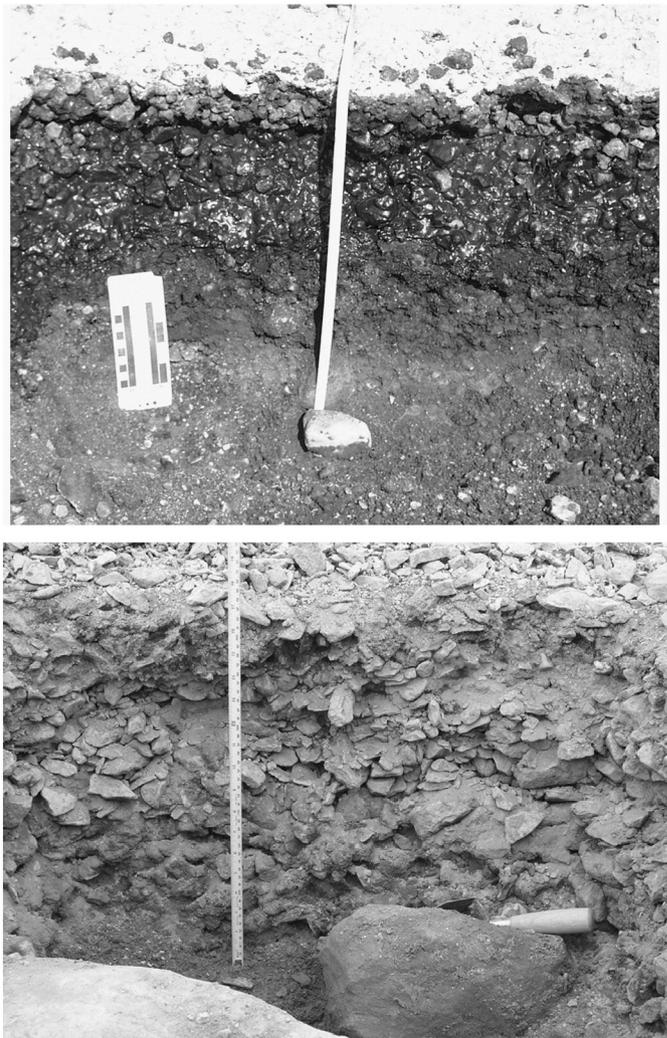


Fig. 1. Newly developing ornithogenic soils (top) at an active penguin colony at Cape Crozier, Ross Island, East Antarctica. The moist black sediments are still undergoing decay and are up to ~300 years old, while the lower dry sediments are ~500 years old. After abandonment, sediments dry and change to a reddish hue and are characterized by a lithology of mostly pebbles, plus bones, feather, and other organic remains. Fully developed ornithogenic soils at an abandoned colony (bottom) of Adélie penguins in the Windmill Islands, East Antarctica, dating to over 9200 BP. These sediments contain an archive of tissues of penguins and their prey, as well as biogeochemical markers from guano, that is unique in polar environments.

these marine-origin elements are transported into terrestrial and freshwater lacustrine sediments by penguins and seals via their guano. These penguin and seal-derived sediments contain unique biogeochemical markers that can be directly related to occupation history and the relative population size of colonies, evidence for dietary change, and indications of nutrient and contaminant transport from ocean to land.

In order to investigate the paleoecology of vertebrates in polar ice-free areas, it is desirable that the morphological and biogeochemical markers have accumulated either in high-resolution sediment sequences with reliable chronologies such as lake sediments (Sun et al., 2000a; Wagner and Melles, 2001), or in changing distributions over broad geographic ranges such as in seabird colonies or nesting sites (Emslie et al., 2007). The presence of vertebrate remains can provide information on the ecological, geological, and climate history of polar ice-free areas (Sun and Xie, 2001a), such as the onset of deglaciation (Huang et al., 2009a), relative sea level changes (Bentley et al., 2005), and climatic optima (Baroni and Orombelli, 1994; Emslie et al., 2007; Huang et al., 2009b). Seabird and marine mammal remains not only have provided important information on past distributions, but also

on the changing diets of these species, both living and extinct (Montevocchi and Hufthammer, 1990; Hobson and Montevocchi, 1991; Lefèvre et al., 1997; Polito et al., 2002; Causey et al., 2005; Moss et al., 2006; Emslie and Patterson, 2007; Lorenzini et al., 2010; Huang et al., 2011a). For example, Adélie penguins appear to have shifted their diet and prey size over millennia in the Ross Sea region (Lorenzini et al., 2009) and more recently to a largely krill-based diet in response to a krill surplus that resulted from extensive removal of baleen whales and krill-eating seals in the Southern Ocean over the past ~300 years (Emslie and Patterson, 2007). Additional tests for these hypotheses are ongoing.

3. Antarctic vertebrate records

Paleoecologists have been studying the paleohistory of penguins in Antarctica since the early 1960s. This area of research has focused on locating and excavating abandoned penguin colonies, where ornithogenic soils (at nesting sites) and sediments (in catchments by the colonies) have accumulated over hundreds to thousands of years. Studies of these sediments and the morphological and geochemical evidence they contain have advanced considerably since they were first described by Syroechkovskij (1959) and there is a large body of information that has been published on their formation and geochemistry (e.g. Ugolini, 1972; Speir and Cowling, 1984; Tatur, 1989). Moreover, radiocarbon dating of the organic remains recovered within them provides the necessary temporal context (Harrington and McKellar, 1958; Campbell and Claridge, 1966; Stonehouse, 1970). The ages of these sediments now extend into the Pleistocene in the Ross Sea (Baroni and Orombelli, 1994; Emslie et al., 2003, 2007). Beginning in the early 1990s, investigations further demonstrated the value of penguins as bioindicators of past marine conditions (Baroni and Orombelli, 1994; Emslie, 1995; Emslie et al., 1998; Ainley, 2002; Emslie et al., 2003) and advanced to include analysis of penguin tissues to assess diet from stable isotopes, mercury availability, and microevolution from ancient DNA (Lambert et al., 2002; Ritchie et al., 2004; Shepherd et al., 2005; Emslie and Patterson, 2007; Emslie et al., 2007; Lorenzini et al., 2009, 2010; Brasso et al., 2012). These studies thus indicate when and where penguins nested, what geobiological conditions must have existed in the past for this occupation to occur, and how they responded to environmental changes.

One finding is that the occupation history of pygoscelid penguins in the Antarctic Peninsula and adjacent northern islands appears to be relatively young (Emslie, 2001). Radiocarbon dating on penguin guano deposited in lake sediment cores indicates that penguins occupied Ardley Island and King George Island as early as 3000 years before present (BP);

Sun et al., 2000a). The results suggest that the penguin population size was linked to climate change (Fig. 2). Specifically, the population began to decline after 3000 BP and was lowest during a drier period between 2300 and 1800 BP. After that, the population increased and peaked between 1800 and 1400 BP, corresponding to a moister, and presumably warmer climate. At Byers Peninsula, Livingston Island, Gentoo penguins have been present only for the last thousand years (Emslie et al., 2011) and at Anvers Island only for the past ~50 years (Emslie et al., 1998; Smith et al., 1999). Further south in Marguerite Bay numerous radiocarbon dates on subfossil penguin remains attest to a longer occupation history there, with penguins colonizing Lagoon Island around 5990 BP following local deglaciation, and with peak populations occurring at 4000–3000 BP during a climatic optimum (Emslie and McDaniel, 2002).

The data on the penguin occupation history in East Antarctica are concentrated in the Vestfold Hills, Windmill Islands, and the Ross Sea regions. In the Windmill Islands, Adélie penguins were present as early as 9000 BP, immediately after deglaciation of this region (Emslie and Woehler, 2005). Further studies at the Vestfold Hills indicated that Adélie penguin populations reached their highest levels between ~4700 and 2400 BP during the warmer mid-Holocene, and then declined significantly in response to the onset of local neoglaciation (Huang et al., 2009b). Compared with previous studies in the Antarctic Peninsula and Ross Sea regions, these data support a late Holocene penguin optimum that may have been circum-Antarctic (Fig. 3).

Biogeochemical markers of marine vertebrates recovered from lake sediment cores include chemical species associated with penguin guano and seal excrement that can be used to detect the relative abundances of past populations. At Great Wall Station, King George Island, Sun et al. (2000a) collected a 67.5 cm long sediment core from a freshwater lake Y2 on Ardley Island. In this sediment core, the P_2O_5 content was very high at 5–15%, as was the Sr concentration at 600–800 $\mu\text{g/g}$. The levels of nine inorganic elements (i.e., Sr, F, S, Se, P, Cu, Zn, Ca and Ba), were strongly positively correlated with each other (see fig. 1 in Sun et al., 2000a). The Sr/Ba ratios were >1 , indicating a typical marine sedimentary environment, but the B/Ga ratios were <3.3 , suggesting a typical freshwater lacustrine environment (Sun et al., 2000b, Fig. 4). These seemingly contradictory results actually provide a logical sequence of deposition after further in-depth analyses under a larger frame of interacting natural systems. When the influence of penguin guano, rich in P_2O_5 and many other of these bio-elements from a nearby colony was considered, it explained the variation in the sedimentary layers with changes in penguin populations through time (Fig. 4).

Sun et al. (2004) performed a similar elemental analysis and counted seal hair numbers in a terrestrial sediment sequence in an area of Fildes Peninsula, King George Island, occupied by seals. This study showed that changing concentrations of S, Se, F, Zn, Hg and P_2O_5 could be used as inorganic geochemical proxies for seal populations in this region. Employing a combination of different lines of evidence including seal hair numbers, bio-element concentrations, total organic carbon, total nitrogen, and $\delta^{15}\text{N}$ and $^{87}\text{Sr}/^{86}\text{Sr}$ in the acid-soluble sediment fractions, these authors estimated historical seal populations at King George Island for the past ~1500 years. These data indicated that seal populations had exhibited dramatic fluctuations with two peaks during 750–500 BP and 1400–1100 BP and two valleys during 1100–750 and 500–200 BP, all prior to direct human interference (Fig. 5). These natural fluctuations appeared to be linked to climate-related factors such as sea ice coverage and atmospheric temperature.

Weathered soils uninfluenced by penguin and seal excrement also contained trace amounts of the bio-elements discussed above. It was therefore necessary to test whether the natural fluctuations of these background element concentrations could affect the reconstructed historical penguin and seal populations. Stable isotopic geochemistry can be a powerful method to separate the elemental proxies used as biological indicators, from the low concentrations and small natural fluctuations of these bio-elements in weathered soils. Using this technique,

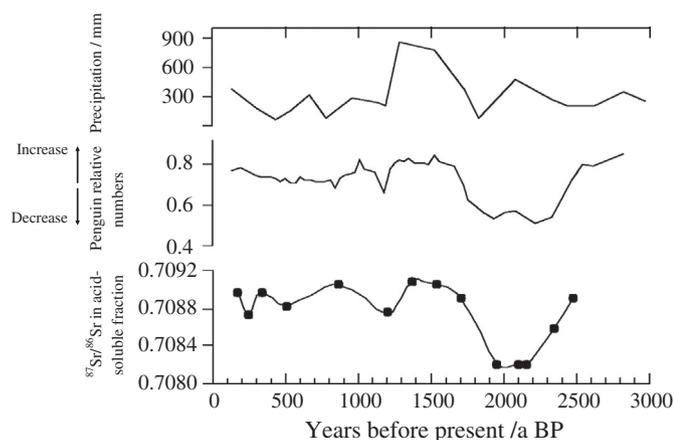


Fig. 2. Changes of $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in the acid-soluble fraction of Y2 lake sediments (lower curve) (Sun et al., 2005a) and the inferred historical penguin populations (middle curve) on Ardley Island (Sun et al., 2000a) correlated well with local inferred precipitation (upper curve; Zhao, 1991).

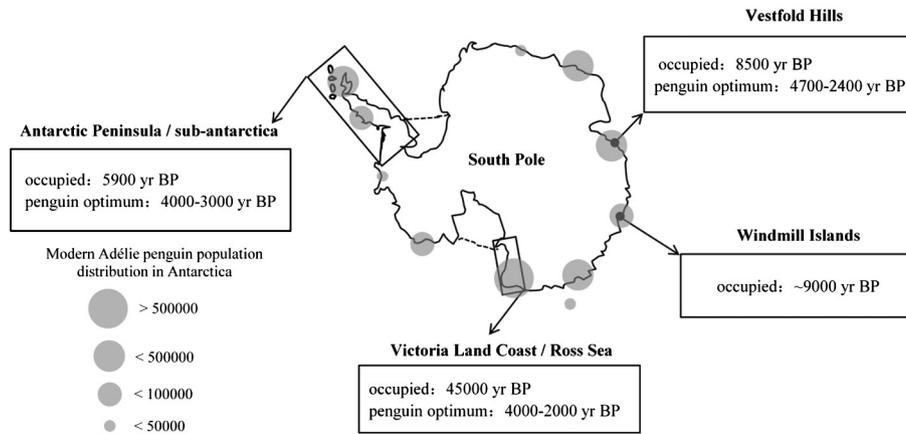


Fig. 3. Adélie penguin occupation history and past population changes support a late Holocene penguin optimum that may have been circum-Antarctic (redrawn from Huang et al., 2009b).

Sun and his colleagues found that ratios of $^{87}\text{Sr}/^{86}\text{Sr}$ in the acid-soluble fractions and the $\delta^{15}\text{N}$ values enabled more accurate identification of sediments responding to historical penguin and seal population changes (Sun et al., 2005a; Liu et al., 2006). This combination of organic geochemical methods and isotopic values has been successfully used to study palaeoecological changes in penguins on King George Island and in the Vestfold Hills (Wang et al., 2007; Huang et al., 2010).

Variability in marine ecosystems can affect a predator's foraging behavior. Combining morphological and biogeochemical methods can also be used to identify changes in the diet of marine vertebrates linked to natural and anthropogenic impacts. Krill (*Euphausia superba* and *Euphausia crystallophias*) are key prey species in the Southern Ocean supporting large numbers of fish, seabirds, seals and whales (Marr, 1962; Hofmann and Murphy, 2004; Nicol, 2006). While modern krill populations have been estimated directly by ship surveys (Atkinson et al., 2004), the historical krill density in the Southern Ocean is unknown. Antarctic fur seals feed preferentially on krill (Murphy et al., 2007) and variations in $\delta^{15}\text{N}$ in seal tissues reflect changes in the proportion of krill in the seal's diet and thus krill availability in the foraging area. Low $\delta^{15}\text{N}$ values indicate a greater reliance on krill, while high $\delta^{15}\text{N}$ values indicate a diet based more on fish. Recently Huang et al. (2011a) performed stable isotope analyses on Antarctic fur seal hairs deposited in sediments and reconstructed variations in trophic feeding patterns from which changes in the relative abundances of krill in the fur seal diet could be inferred. Their results of increasing $\delta^{15}\text{N}$ values in hair over the past century indicated a greater reliance on fish in seal diet and were directly correlated with reduced krill stocks since the 1970s. Recent regional warming was likely a major factor in the declining krill abundance (Huang et al., 2011a).

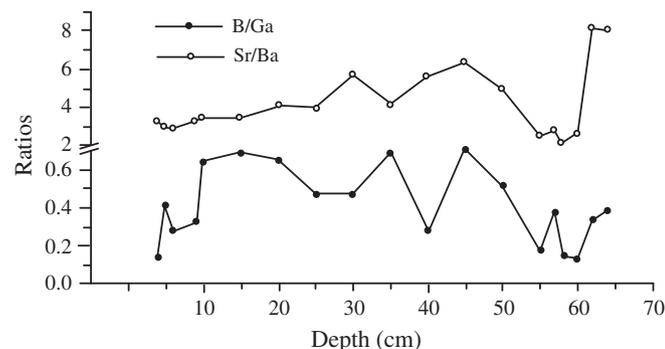


Fig. 4. Ratios of Sr/Ba and B/Ga in the Y2 core of Ardley Island (Sun et al., 2000b) showing that the sediments have both marine and lacustrine original materials.

4. Arctic vertebrate records

In the Arctic, studies of deep deposits of ornithogenic soils and sediments are lacking, but there is a long-term record of vertebrates preserved in lake and pond sediments as well as other natural deposits and the archaeological record. For example, Wagner and Melles (2001) were able to reconstruct a 7500-year history of seabird colonization in East Greenland from a lake sediment core. This core contained biogeochemical evidence for the presence or absence of seabirds as the lake acted as a catchment for organic remains when the colony was active. The periods prior to 7500 BP, and from 1000 to 500 and after ~100 BP, indicated an absence of seabird colonies that was attributed to unsuitable environmental conditions. Similarly, Yuan et al. (2010) applied both geochemical and stable isotope analyses to a sediment core from a paleo-notch deposit on Svalbard to estimate the presence of seabirds on this island since ~9400 BP, or after deglaciation. Their study provided the first Holocene evidence for seabirds on this island.

Seabird and marine mammal remains from archaeological middens in the Arctic and sub-Arctic also have provided important information on past distributions and diets of these species, both living and extinct (Montevicchi and Hufthammer, 1990; Hobson and Montevicchi, 1991; Lefèvre et al., 1997; Causey et al., 2005; Moss et al., 2006). For example, Causey et al. (2005) used zooarchaeological evidence of food remains from three early Aleut middens to compare the relative abundance of seabirds that were hunted from ~3500 to 650 BP. The Aleuts were efficient hunters of marine vertebrates and invertebrates so deposition of these remains provides a reliable index of changes in the relative abundance of these species over time. Based on this information, Causey et al. (2005) identified periods of warming and cooling in the past with relative abundance of nearshore (cormorants, parakeet auklets) versus pelagic foraging seabirds (murre, kittiwakes) in the deposits. Moss et al. (2006) extracted ancient DNA from bones of three pinniped species from archaeological sites in Alaska, Vancouver Island, and Oregon in an attempt to track the origins of these animals to existing populations in the Pribilof Islands. While they were unable to determine strong geographic associations from the genetic data, their study was one of the first to successfully extract ancient DNA from these pinnipeds. Thus, we expect sediment records in both polar regions to continue providing considerable information biogeography and on natural forcing and anthropogenic impacts on marine vertebrates.

5. Bio-transfer of natural materials and anthropogenic contaminants from sea to land in polar regions

Many mobile marine animals (including mammals, seabirds, fish, and sea turtles) can transport materials through their movements and thus play an important role in the biogeochemical cycling of elements.

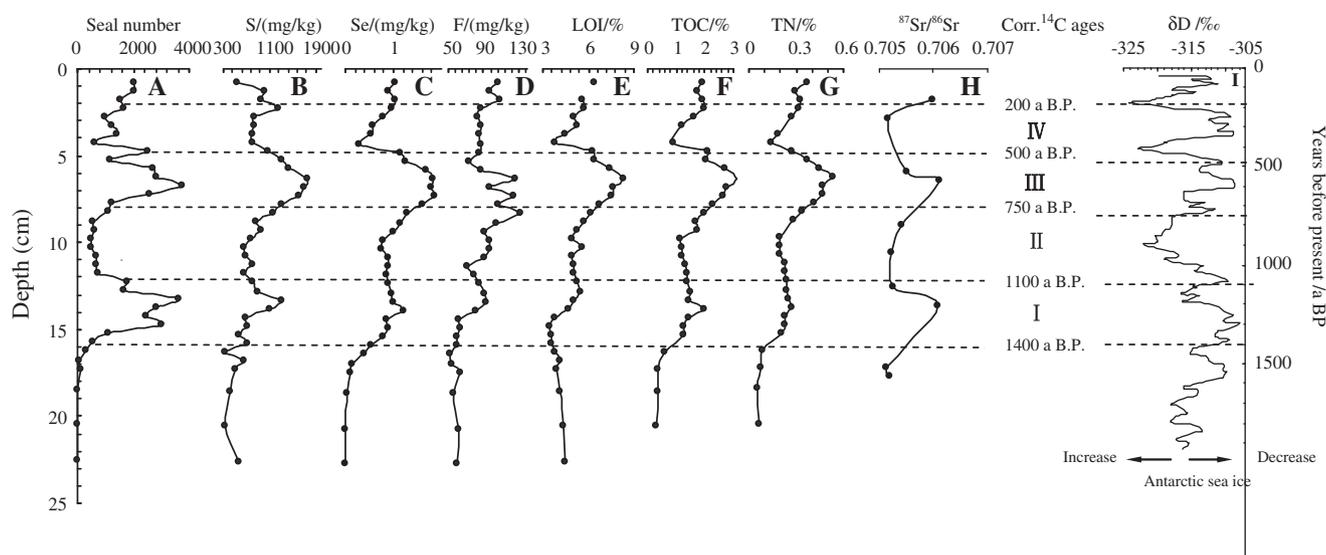


Fig. 5. Seal population changes over the past 1500 years (redrawn from Sun et al., 2004) correlated well with the variability of past sea ice cover reconstructed from ice cores (Steig et al., 1998), where the peaks in the seal populations correspond to less sea ice cover, and vice versa.

As a top predator, seabirds in particular are a common bio-vector and transfer material and energy between ocean and land, and therefore can have significant influence on the productivity, biodiversity and population structure of terrestrial ecosystems (Sánchez-Piñero and Polis, 2000; Ellis et al., 2006; Michelutti et al., 2009a). A clear example of nutrient and contaminant biotransfer was recorded near a colony of 10,000 breeding pairs of northern fulmars (*Fulmarus glacialis*) nesting on cliffs above a series of coastal ponds at Cape Vera on Devon Island, in the Canadian High Arctic (Blais et al., 2005). Pond waters below the seabird colony were dramatically enriched in total phosphorus, total nitrogen, and dissolved organic carbon compared to reference ponds located on the same coastline but further away from the seabird colony (Keatley et al., 2007). The effects of seabird fertilization on the distribution of diatoms (Keatley et al., 2009, 2011) and invertebrates (Michelutti et al., 2011; Stewart et al., 2013) were also investigated. Likewise, pond sediments directly below the fulmar colony contained 10-, 25-, and 60-fold higher hexachlorobenzene, total mercury, and DDT concentrations (Blais et al., 2005), indicating that seabird guano was enriching these contaminants in ponds near the colonies, and elevated ratios of the metabolite DDE relative to the parent DDT isoforms supported the hypothesis that the biotransported contaminants had been processed in the marine food web prior to deposition in pond sediments.

Pond sediments at the Cape Vera site were further examined in vertical profile by extracting cores and radiometrically dating them with ^{210}Pb , ^{137}Cs , and ^{226}Ra . Profiles of chironomid head capsule densities, inferred chlorophyll *a*, $\delta^{15}\text{N}$, and PCB concentrations revealed increases in ornithogenic inputs over the past 50 years (Michelutti et al., 2009b). Ornithogenic elements were also identified, having elevated concentrations in guano and low relative concentrations in background pond sediments, including P, As, Cd, K, and Zn, with several reaching concentrations in ornithogenic sediments that exceeded federal guidelines for protecting aquatic life (Brimble et al., 2009). These studies revealed a major biotransport pathway for contaminants and nutrients at this site, with evidence that ornithogenic contaminants were also transferred to the coastal terrestrial food web (Choy et al., 2010a,b). Moreover, understanding these biotransport processes in living species is vital in demonstrating how biogeochemical markers can be interpreted from ancient sediments.

In Antarctica, land-based penguins (*P. adeliae*, *P. antarctica* and *P. papua*) and seals (*Mirounga leonina* and *A. gazella*) transport large amounts of nutrients (carbon, nitrogen, and phosphorus) and contaminants from ocean to land environments in the form of guano, excrement

and dead tissues (Tatur and Myrcha, 1984; Sun et al., 2005b; Roosens et al., 2007; Xie and Sun, 2008; Yin et al., 2008; Huang et al., 2011b; Brasso et al., 2012; Nie et al., 2012). For example, the annual mass of phosphorus transferred by penguins from ocean to land was estimated as high as 1.5×10^4 – 2.0×10^4 ton (Tatur and Myrcha, 1984). In the Arctic and northern high latitudes, seabirds act as important bio-vectors for transporting contaminants. As a result of biomagnification and/or bioaccumulation through the marine food web, large amounts of metals (such as Hg, Cu, Zn, As, Cd and etc.) and persistent organic pollutants (POPs) are transferred by seabirds from ocean to terrestrial ecosystems (Blais et al., 2005, 2007; Foster et al., 2011), much more than those transported by atmospheric circulation and ocean currents.

Different species have distinct transport efficiencies due to different living habitats (foraging area, foraging behavior, and diets); seabirds occupy a higher trophic level and have higher efficiency of transferring metal than lower trophic level species. For example, Michelutti et al. (2010) compared the sedimentary concentrations of metals, along with a paleolimnological assessment of nitrogen isotopes, diatoms, and chironomids from two nearby ponds on a small ~3 km long island near Cornwallis Island (Nunavut, High Arctic Canada). One pond was within the catchment of a large colony of nesting Arctic terns (*Sterna paradisaea*), while the second lake drained a large congregation of nesting common eider ducks (*Somateria mollissima*). The diets of these two birds are very different, with terns feeding mainly on small fish (and so are high on the trophic food web), while the main diet of eider ducks are benthic mollusks. Sediments from the tern-affected pond recorded the highest levels of $\delta^{15}\text{N}$, which reflected their higher trophic position, as well as the greatest concentrations of metals that are known to bioaccumulate in marine ecosystems such as Hg and Cd. In contrast, the sediments of the eider duck pond contained higher levels of elements associated with benthic feeders (e.g., Pb, Al and Mn). These data indicate that population size alone is not the best indicator of contaminant transport by seabirds, and that species and foraging patterns must also be considered.

Comparable work has also been completed in the European Arctic. For example, a clear case of biotransported contaminants in an Arctic setting was shown on the southern margins of Bjørnøya (Bear Island), Norway, where more than a million seabirds arrive annually in summer (Evenset et al., 2007). In one instance, elevated persistent organic pollutants and $\delta^{15}\text{N}$ were observed in sediments and biota of Lake Ellasjøen, which receives large numbers of seabirds along its coastlines (Evenset et al., 2004, 2007). A detailed lake budget indicated that

seabird guano could account for approximately 80% of the PCB and DDT inventory of this lake, with concentrations in sediment and biota that were over 10 times higher than a nearby lake that does not receive seabirds (Evenset et al., 2007). These studies demonstrated some of the most pronounced examples on record of biotransported pollutants by seabirds.

6. Responses of marine vertebrates to anthropogenic impacts

Early human exploitation of the polar oceans has caused significant changes in some regional marine and terrestrial ecosystems, and a record of this history can be extracted from natural biogeological archives in addition to written records. Archaeological and paleolimnological data from Arctic lake sediments show that the frequent whaling activity by Thule Inuit from AD 1200–1600 markedly changed Arctic pond water quality and ecology (Douglas et al., 2004; Hadley et al., 2010a, b). In the Antarctic seal hair numbers and chemical proxies in the sediments impacted by seal excrement indicate that seal populations declined to near extinction in the past two centuries due to human hunting (Fig. 6; Hodgson and Johnston, 1997; Yang et al., 2010). The rapid recovery of seal populations in these regions results from the ban on sealing and whaling since the 1960s (Yang et al., 2010), and a surplus of their food source, Antarctic krill, is associated with the very slow recovery in whale populations (Fig. 6).

Paleoecological methods can also track atmospheric pollutants, from the early processing and smelting activities of ancient Egyptian civilizations and the Chinese Dawenkou culture to the present day. It is estimated that, since the time of ancient Rome around 2500 BP, humans have released hundreds of thousands of tons of mercury (Hg) into the atmosphere—more than enough to influence natural Hg concentrations in seawater, the atmosphere and the earth's surface (Mellor, 1952). Pollutants such as Pb and Hg are usually dispersed in the open system of atmospheric and water cycles and can be enriched by biomagnification in marine food chains, transported, and eventually deposited in excrement in sediments thus providing an archive of human impacts through time. Sun et al. (2006) observed marked fluctuations of Hg concentrations in seal hairs over the past ~2000 years extracted from a lake-sediment core on King George Island. These variations were closely linked with historical records of gold and silver mining around the world, which involved the use of the Hg-amalgamation process (Sun et al., 2006, Fig. 7). Increased lead concentrations in penguin guano in the past ~200 years show that contaminants from the industrial revolution have been transported to the Southern Ocean food webs (Sun and Xie, 2001b). Both of these studies show that the influence of human civilization on the Antarctic did not begin with the direct human presence on this continent and show how paleoecological methods can track long term pollutant inventories arising from anthropogenic sources (Fig. 7).

Finally, Brasso et al. (2012) investigated Hg levels in three species of *Pygoscelis* penguins in the Antarctic Peninsula by analyzing modern egg

membranes. Among four regions, including the South Orkney and South Shetland Islands, and the eastern and western peninsula, they found relatively low and homogenous concentrations of Hg indicating uniform atmospheric deposition. One species, Chinstrap penguin (*P. antarctica*) had significantly higher Hg levels in its membranes though $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analysis indicated no differences in diet with Gentoo or Adélie penguins. However, it is likely that Chinstrap penguins are exposed to greater Hg levels via a diet based more on mesopelagic fish, which are isotopically similar to other fish consumed by Gentoo and Adélie penguins, where bioaccumulation is greater (Brasso et al., 2012). Ongoing studies of penguin feathers and egg membrane from ornithogenic sediments that are hundreds to thousands of years old also have detectable levels of Hg and may provide additional information on natural versus anthropogenic variations in Hg availability in the Antarctic.

7. Conclusions

This review summarizes the state of knowledge on the paleoecology of marine vertebrates in polar regions. It is by no means an exhaustive review, but one meant to illustrate how natural versus anthropogenic impacts can be distinguished when well-preserved records are available. Polar regions also offer excellent opportunities to investigate past ecological responses by marine vertebrates to climate change or human perturbations that include depleted stocks of krill, fish, seals, and whales and increased contaminants. The major points of this review are:

1. The accumulated profiles of biogeochemical markers, fossil and sub-fossil remains within well-dated sediments provide excellent archives for assessing changes in some seabird and marine mammal populations in polar regions. Few regions of the world provide such long-term records for living species that can be used to address hypotheses on ecological responses to natural versus anthropogenic impacts.
2. Populations of penguins and seals changed markedly during the past few thousands of years in the absence of human interference.
3. Land-based seabirds and marine mammals play an important role as bio-vectors of nutrients and contaminants and provide key linkages between marine and terrestrial ecosystems. Study of active systems provides a means to interpret similar bio-markers preserved in polar sediments.
4. The historical information on long-range pollution by human civilizations over the past several thousand years is preserved in Antarctic seal hairs and in sediments influenced by penguin excrement.
5. Using sedimentary profiles and other deposits to reconstruct past vertebrate populations and their effects on ecosystems is a relatively new and developing field of study and there are many unique and compelling research opportunities in this area.

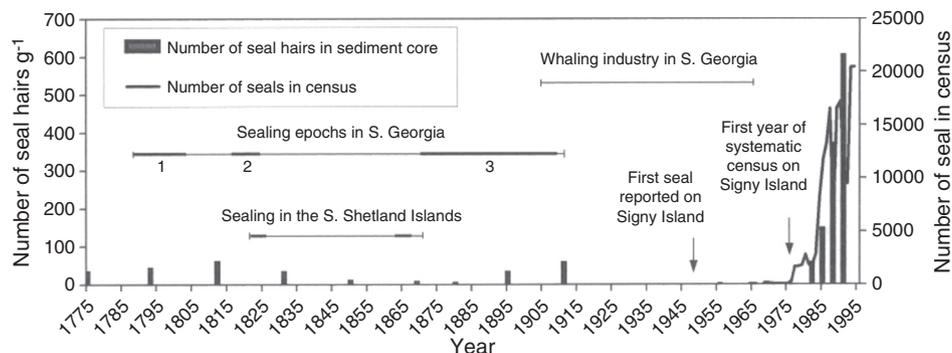


Fig. 6. Histogram showing the number of Antarctic fur seal hairs in the upper 10 cm (AD 1775 to the present) of a short sediment core from Sombre Lake, Signy Island and line graph giving seal census data from 1977. Horizontal bars indicate periods when the sealing industry was active in the nearby South Shetland Islands and South Georgia, and when the whaling industry was active at South Georgia. Bold sections correspond to periods of peak harvest (based on Hodgson and Johnston, 1997).

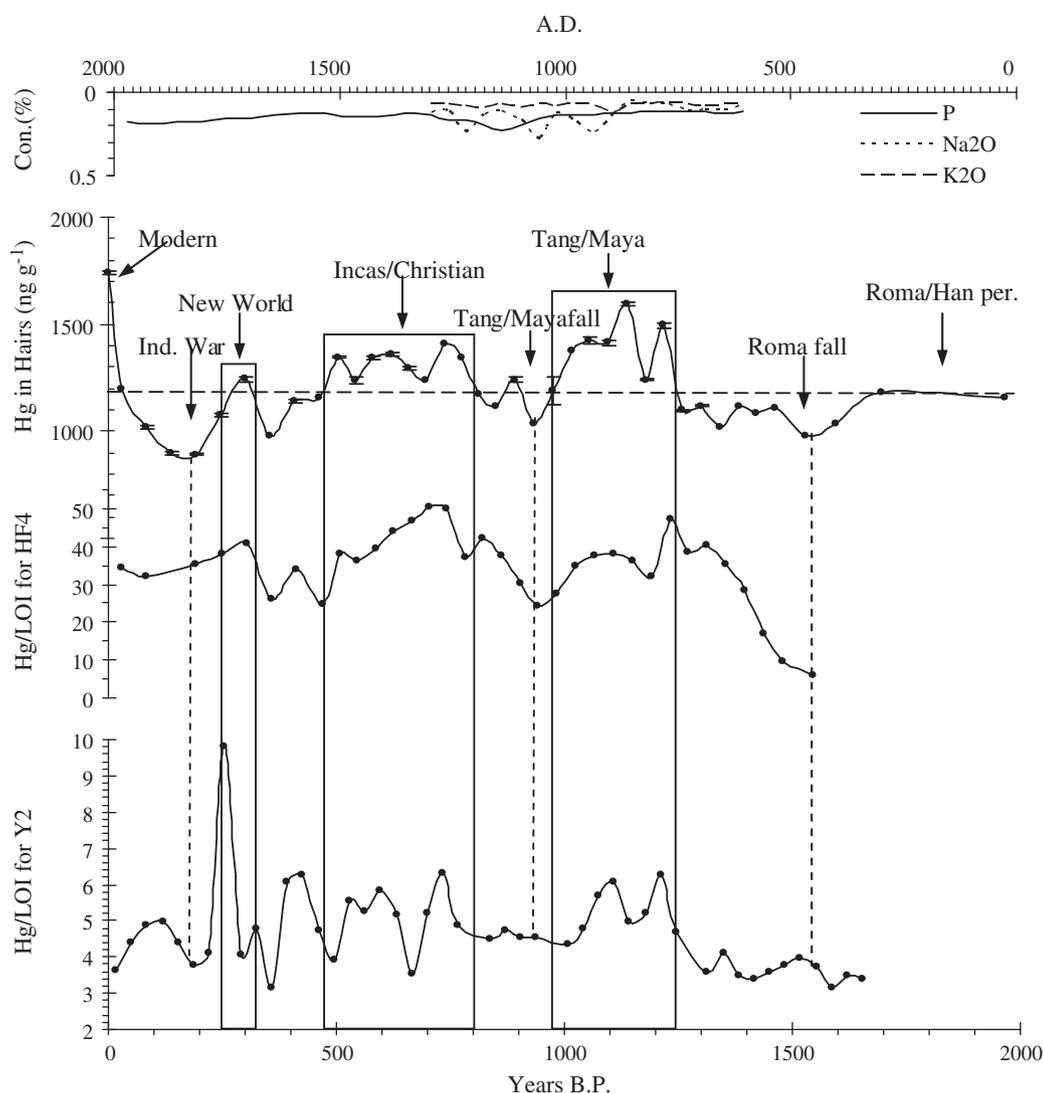


Fig. 7. Changes of mercury concentration in seal hairs over the past 2000 years show striking associations with ancient civilizations, where concentrations of essential elements K_2O (— —), Na_2O (...) and P (—) in the seal hairs and the calibrated Hg concentration in the sediments of HF4 and Y2 are indicated. The calibration was performed to remove the effect of excrement content on the Hg concentration (Sun et al., 2006).

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