

Ecological responses of typical Antarctic marine organisms to climate change and anthropogenic impacts

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Received 20 February 2017; accepted 3 May 2017

Abstract To improve our understanding and ability to predict biological responses to global climate change, it is important to be able to distinguish the influences of natural forcing from anthropogenic impacts. In the ice-free areas of Antarctica, lake and terrestrial sediments that contain penguin guanos, seal excrement and other biological remains provide natural archives of ecological, geological and climatic information that range from hundreds to thousands of years old. Our review focuses on the paleoecology of typical Antarctic marine organisms (penguins, seals and Antarctic krill) and their responses to climate change and human activities over centennial and millennial timescales. Land-based seabirds and marine mammals play an important role in linking the marine and terrestrial ecosystems and act as bio-vectors, transporting large amounts of nutrients and contaminants from ocean to land.

Keywords penguins, seals, krill, climate change, anthropogenic impacts

Citation: Yang L J, Huang T, Xie Z Q, et al. Ecological responses of typical Antarctic marine organisms to climate change and anthropogenic impacts. *Adv Polar Sci*, 2017, 28 (2): 129-138, doi: 10.13679/j.advps.2017.2.00129

1 Introduction

The Antarctic regions have undergone rapid climate change in recent decades; in turn, large fluctuations in the population sizes of marine biota such as seabirds, seals and Antarctic krill have been observed (Croxall et al., 2002; Vaughan et al., 2003; Smetacek and Nicol, 2005). For example, the West Antarctic Peninsula (WAP) has experienced rapid regional warming associated with significant sea ice and krill stock reductions since the 1970s (Atkinson et al., 2004). Gentoo penguins (*Pygoscelis papua*) have expanded their range in the Antarctic Peninsula in response to recent warming trends, while Chinstrap (*P. antarctica*) and Adélie penguins (*P. adeliae*) have declined in many parts of the peninsula (Smith et al.,

1999; Peter et al., 2008; Trivelpiece et al., 2011). In the Ross Sea, Adélie penguins at Cape Bird showed an increasing trend in the 1980s, likely linked with changes in sea-ice extent and polynya size (Wilson et al., 2001; Ainley et al., 2005). These studies also indicated that ecological responses to the climatic and environmental changes varied both by species and by locations.

Population dynamics may be complicated by multiple influencing factors, which can be natural or anthropogenic. The population size of penguins is known to be affected by multiple factors such as temperature, sea ice extent, snow cover, winds and food availability (Fraser et al. 1992; Bricher et al., 2008; Ainley et al., 2010; Younger et al., 2016), while breeding performance of Gentoo penguins at a colony are negatively impacted by human disturbance, such as tourism (Cobley and Shears, 1999). Population changes in Antarctic seals over the last two centuries are linked to human interference (e.g., the activities of sealing and

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whaling industries) (Hodgson and Johnston, 1997; Yang et al., 2010), and natural influences seem to be related to sea-ice extent and atmospheric temperature (Sun et al., 2004; Hall et al., 2006). Changes in oceanic conditions associated with large-scale atmospheric forcing (e.g., the Southern Annular Mode) are also expected to have cascading effects on Antarctic marine ecosystems, from phytoplankton to krill and to upper trophic-level predators (Montes-Hugo et al., 2009; Trivelpiece et al., 2011; Saba et al., 2014).

To assess future climate and human impacts on the

Antarctic marine ecosystems, it is vital to reconstruct the ecological responses to past climate change, particularly those that pre-date the onset of human activities (Sun et al., 2013). We carried out eco-geology research in four typical Antarctic ice-free regions (King George Island, Vestfold Hills, Amanda Bay and Ross Island) (Figure 1), using lake and terrestrial sediments accumulated at penguin and seal colonies, and investigated the historical population dynamics of these marine organisms and their responses to climate change and anthropogenic impacts.

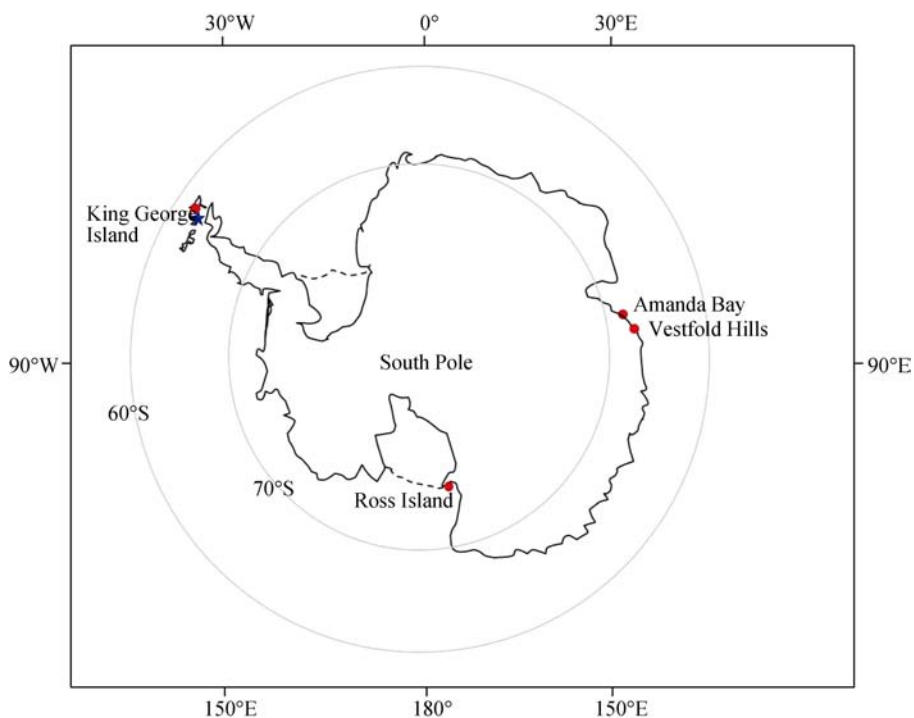


Figure 1 Typical Antarctic ice-free regions for paleoecology research on penguins (solid circles) and seals (star): King George Island, Ross Island, Vestfold Hills and Amanda Bay.

2 Ecological history of penguins, seals and krill

Penguins, seals and krill are typical organisms in the Antarctic marine ecosystem, and are very sensitive to climatic and environmental changes. The depositional sediment sequences influenced by penguin guanos, seal excrement and biological relics can be directly related to occupation history and the relative population size of colonies (Sun et al., 2000; Sun and Xie, 2001; Huang et al., 2009). The sequences can provide a record of climate change over centennial and millennial timescales, such as the advance and retreat of the ice sheet, relative sea level changes and climatic optima (Bentley et al., 2005; Huang et al., 2009; Sun et al., 2013). Recent advances in stable isotopes also provide opportunities to study the paleodiet shifts of penguins and seals, and thus indicate the relative abundances of their prey, the Antarctic krill, in the

Southern Ocean (Polito et al., 2002; Emslie and Patterson, 2007; Huang et al., 2014).

2.1 Penguins

2.1.1 Penguin population dynamics and responses to climate change during the Holocene

The ornithogenic sediment from Lake Y2, a typical case for paleoecology of penguins using eco-geology methods, was collected at Ardley Island, King George Island. In this sediment profile, the values of Sr/Ba were greater than 1, indicating a typical marine sedimentary environment, but the B/Ga ratios were lower than 3.3, suggesting a typical freshwater lacustrine sedimentation environment (Sun et al., 2000). These seemingly contradictory results actually contributed to the lake sediments, with characteristic of triple properties including marine, lacustrine and biological depositions. The nine inorganic elements (Cu, Zn, Sr, Ba, Ca, P, S, Se and F) were strongly positively correlated with

each other, and identified as bio-element assemblages for penguin guano; the variations in their levels are associated with historical population changes (Sun et al., 2000). The ratios of $^{87}\text{Sr}/^{86}\text{Sr}$ in the acid-soluble fractions in the ornithogenic sediments show a similar pattern to the bio-elements (Figure 2). This isotopic method was much better at deducing the background interference, so it enabled more accurate identification of historical penguin

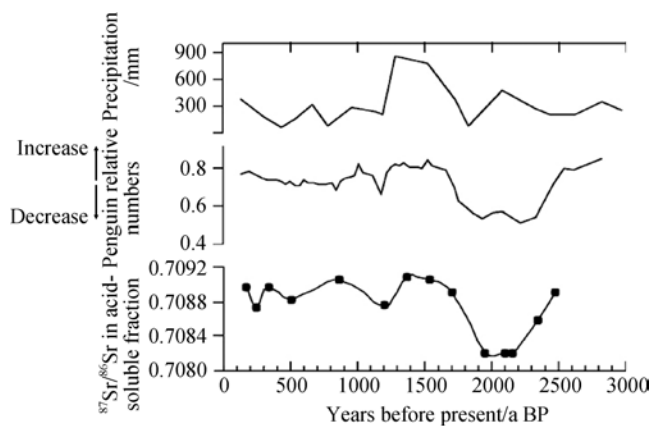


Figure 2 Changes in $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in the acid-soluble fraction of Y2 lake sediments (lower curve) and the inferred historical penguin populations (middle curve) on Ardley Island correlated well with local inferred precipitation (upper curve) (Sun et al., 2013).

population changes (Sun et al., 2005).

Radiocarbon dating of the Y2 sediment core indicates that penguins occupied Ardley Island as early as 3000 years before the present (BP), and that the population was at its lowest during a drier period between 2300 and 1800 BP (the neoglacial period). After that, the population increased and peaked between 1800 and 1400 BP, corresponding to a moister and presumably warmer climate (Figure 2). A marked decline in penguin populations between 450 and 200 BP was inferred from another ornithogenic sediment on the same island, corresponding to a cold climate anomaly during the Little Ice Age (LIA) (Liu et al., 2005). It suggested that penguin population dynamics were related to climate change, and that extremely high or low temperatures were unfavorable for penguin survival (Sun et al., 2000).

Huang et al. (2009) performed a similar elemental analysis and studied the occupation history and population dynamics of Adélie penguins during the Holocene in the Vestfold Hills, East Antarctica. 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. Compared with previous studies in the Antarctic Peninsula and Ross Sea regions, these data support a late Holocene ‘climatic/ penguin optimum’ in the circum-Antarctic regions (Figure 3).

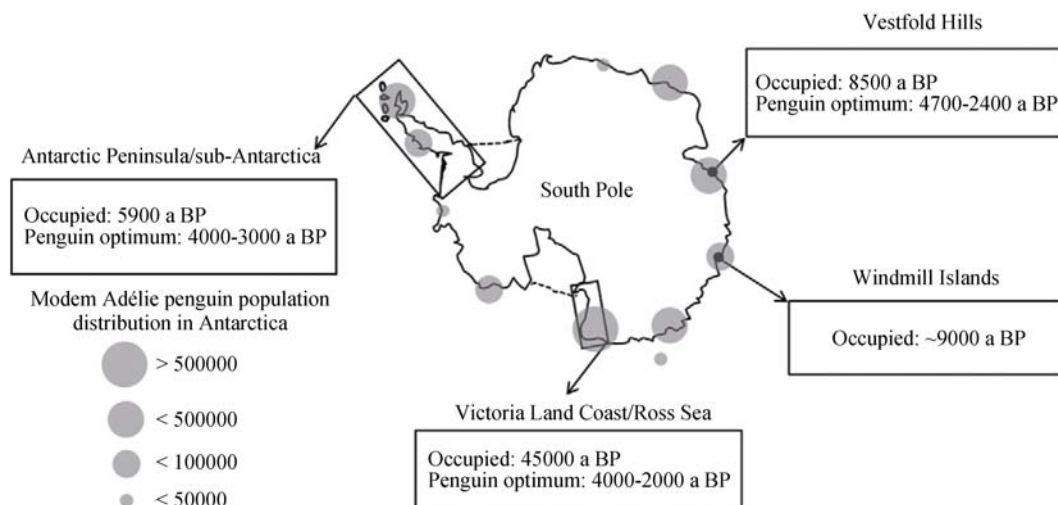


Figure 3 Adélie penguin occupation history and past population changes support a late Holocene ‘penguin optimum’ that may have been circum-Antarctic (Sun et al., 2013).

2.1.2 Penguin population records during the LIA in the Ross Sea, Antarctica

Using bio-elements and organic markers in the ornithogenic sediments, it has been possible to reconstruct historical changes in penguin populations and plant communities, and corresponding climatic and environmental changes in Antarctica (Wang et al., 2007; Huang et al., 2010). For example, cholesterol and cholestanol were used as indicators for penguins, and phytol was used as the

indicator for total vegetation. By analyzing organic markers in a sediment profile (MB6) collected at an active Adélie penguin colony at Cape Bird, Ross Island, Hu et al. (2013) reconstructed the history of Adélie penguin colonies over the past 700 years. The sum of cholesterol and cholestanol is significantly correlated with traditional proxies such as total organic carbon (TOC), total nitrogen (TN) and P, and was used as the indicator for penguin populations. The authors found this region transformed from a seal to a penguin habitat when the LIA (1500–1800 AD) began, and

then penguins became the dominant species. Penguin populations were at their highest during 1490–1670 AD, a cold period, which contrasts with results from other regions much farther north. Previous studies at low latitudes in Antarctica have indicated that penguin populations decreased when the climate became colder, and vice versa (Sun et al., 2000; Liu et al., 2005; Huang et al., 2011). This inconsistency suggested different responses to climate change by penguins at low latitudes and high latitudes in the Antarctica, even for the same species.

For a better understanding of penguin population dynamics in the Ross Sea, Nie et al. (2015) investigated four ornithogenic sediment profiles (MB6, MB4, MB1 and CL2) sampled from Cape Bird, Ross Island. They compared the historical penguin population change inferred from

bio-element assemblages over the past 1600 years. A clear succession of penguin population peaks was observed in different profiles at about 1400 AD, which suggested a high probability of penguin migration within this region (Figure 4). A sand layer lasting from 1400 to 1900 AD was found in profile MB4 and was deemed to be of marine derivation, which provided an insight into the cause of this migration event. Under the colder climatic conditions during the LIA in the Ross Sea region, isostatic subsidence with the movement of the shoreline inland, and frequent storm surges, were presumed to have caused the abandonment of the colonies in the coastal area of mid-Cape Bird (MB4 and CL2), and penguins moved northward (MB6) and to higher ground (MB1). This migration was an ecological response to global climate change and possible subsequent geological effects in Antarctica.

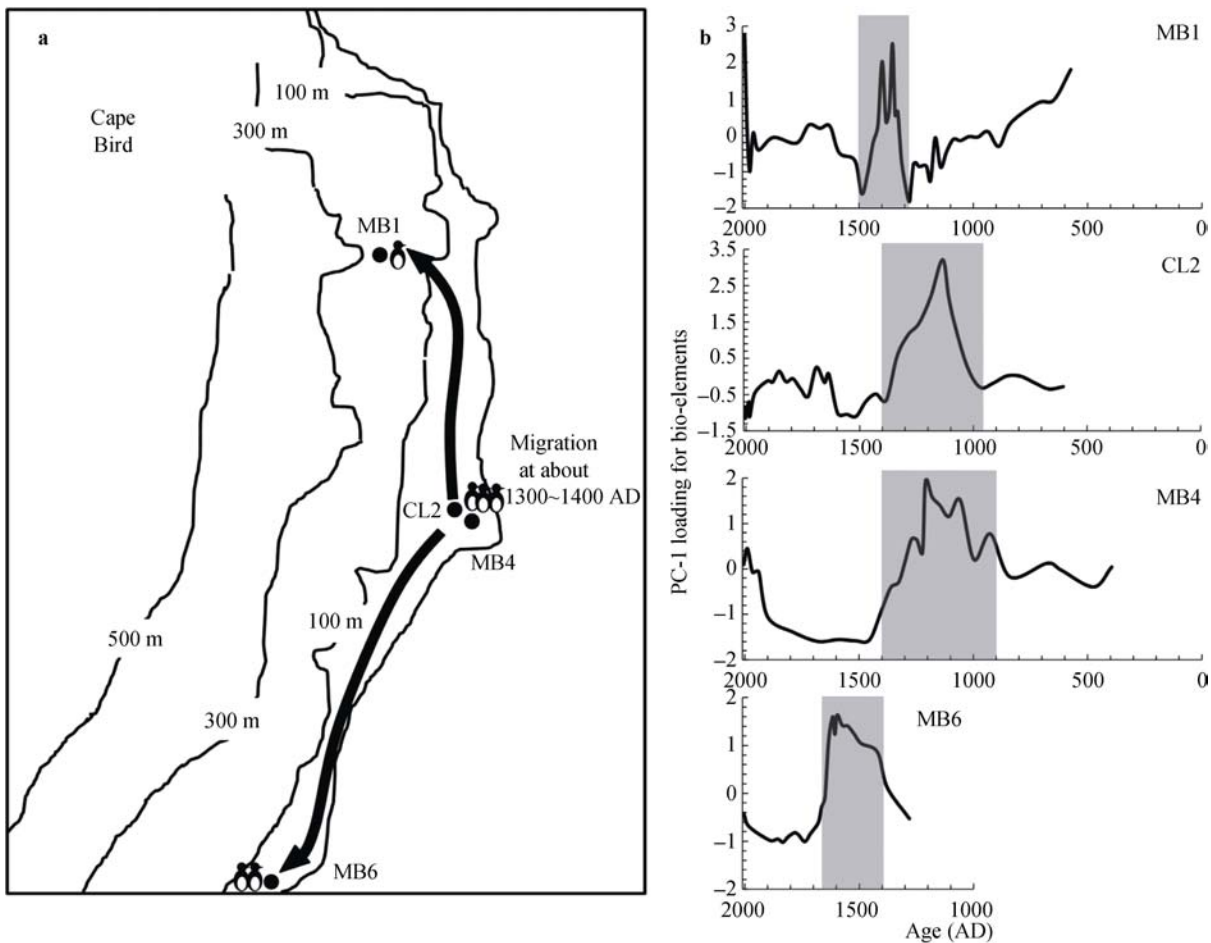


Figure 4 Penguin population change inferred from four ornithogenic sediment profiles from Cape Bird and a possible migration route during 1300–1400 AD (Nie et al., 2015). **a**, Penguin migrated from the coastal area of mid-Cape Bird (as indicated at MB4 and CL2) northward (as indicated at MB6) and to higher ground (as indicated at MB1); **b**, Penguin population inferred from four profiles, clear succession of population peaks were observed at about 1300–1400 AD.

2.1.3 Emperor penguin populations during the LIA at Amanda Bay, East Antarctica

Emperor penguins (*Aptenodytes forsteri*) are known to be

extremely sensitive to changes in climate and sea ice dynamics. Demographic models and IPCC climate projections estimated that at least two-thirds of emperor penguin colonies will have declined dramatically by more

than one-half at the end of this century if sea ice extent continues to decrease (Jenouvrier et al., 2014). Unlike Adélie penguins, they have been less studied for their paleoecology, because they breed on the fast sea ice and therefore there is a lack of archives on land. Using genetic methods, Younger et al. (2015) showed that sea ice extent might have forced emperor penguins into refugia during the last glacial maximum. During the field investigation at Amanda Bay, East Antarctica, Huang et al. (2016) obtained an emperor penguin ornithogenic sediment profile (PI). By using the bio-elements (P, Se, Hg, Zn and

Cd) in sediments and stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) in feather remains, relative population size and dietary change in emperor penguins were inferred. High penguin populations occurred with depleted $\delta^{15}\text{N}$ during the LIA (1540–1866 AD) (Figure 5), indicating that emperor penguins consumed less ^{15}N -enriched fish. This could be because of the cold climate related impacts on penguin's prey availability, and potential interspecific competition. Further analysis of modern, fossil and sub-fossil samples of emperor penguins in other Antarctic regions should be performed in the future.

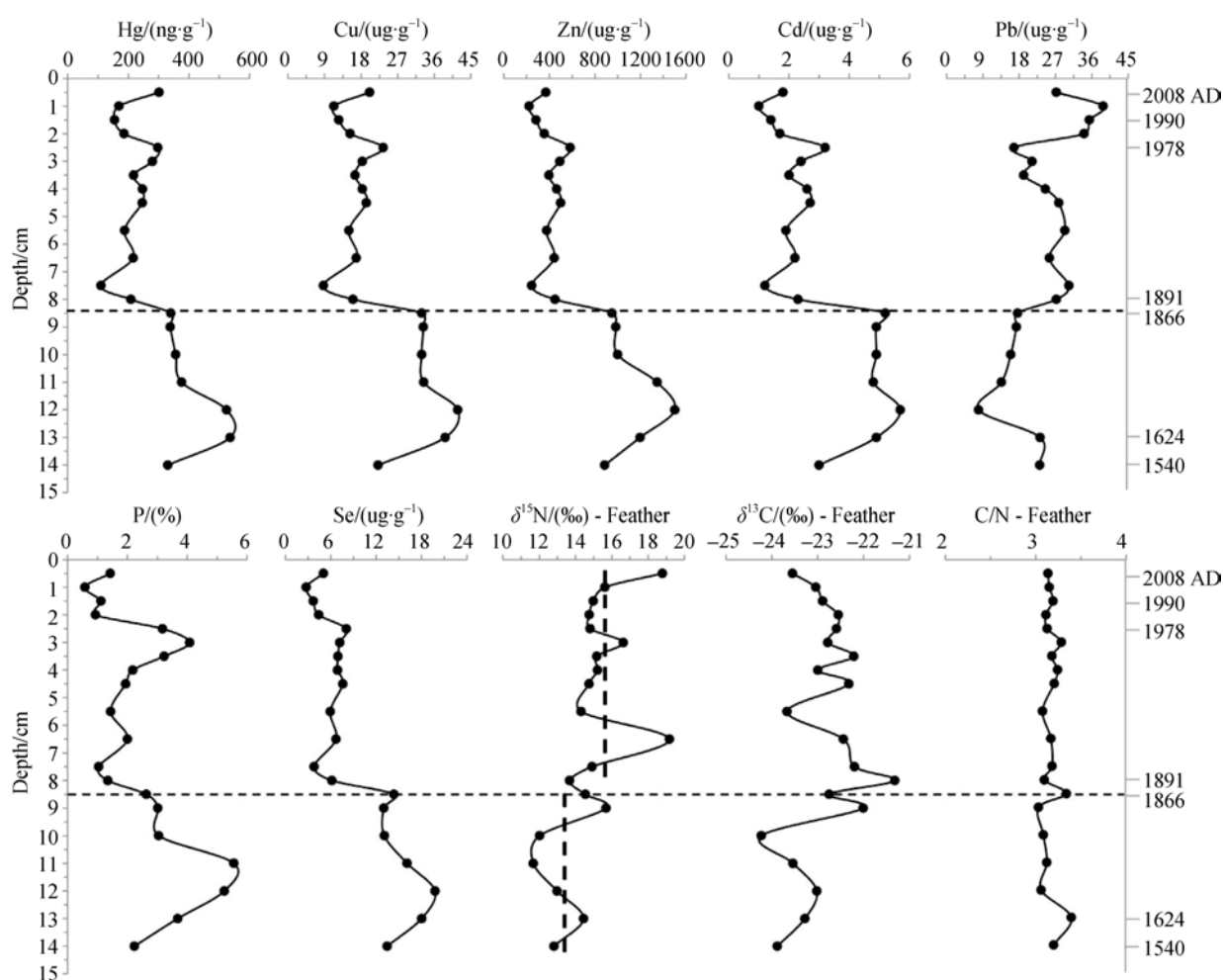


Figure 5 Vertical profiles of bio-elements and Pb in sediments, and of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and C/N in penguin feathers from PI core (redrawn from Huang et al. (2016)). The black dashed lines in the $\delta^{15}\text{N}$ profile indicate the mean value between different periods.

2.2 Seals

Currently, there is relatively less information on the paleoecology of Antarctic seals. According to seal hair numbers in lake sediment from Signy Island, Antarctic Peninsula, Antarctic fur seals have been active on Signy Island for at least 6500 years (Hodgson et al., 1997). In the Ross Sea region, southern elephant seals occupied Inexpressible Island about 6000 years ago, and a large

numbers of seal hairs dating from 2300–1100 BP suggested that climate conditions at that time were warmer than at present, with declined sea-ice extent (Hall et al., 2006). The latest research suggests that seals migrated from the McCurray Islands to this region ~8000 years ago, and left around 1000 years ago as sea ice concentrations increased (de Bruyn, 2009).

Sun et al. (2004) reconstructed historical seal populations using a terrestrial sediment sequence (HF4)

adjacent to seal colonies in an area of Fildes Peninsula, King George Island. The elements including Se, F, S, P_2O_5 and Zn (which are closely related to seal hair numbers, TN, and TOC), are identified as the characteristic bio-elemental assemblage for the seal excrement sediments. Employing a combination of these inorganic proxies with $\delta^{15}N$ and $^{87}Sr/^{86}Sr$ in the acid-soluble sediment fractions, the authors estimated historical seal populations at King George Island for the past ~1500 years (Figure 6). The results showed that, prior to direct human interference in the Southern Ocean

ecosystem, seal populations had exhibited dramatic fluctuations. These appeared to be linked to climate variations, sea ice coverage and seal foraging behavior, although seal populations declined to near extinction at Fildes Peninsula over the past 200 years, due to human hunting (Hodgson et al., 1997; Yang et al., 2010). A rapid recovery in seal populations occurred in these regions following the prohibition on sealing and whaling in the 1960s; and a surplus in their food source, Antarctic krill, is associated with the very slow recovery in whale populations.

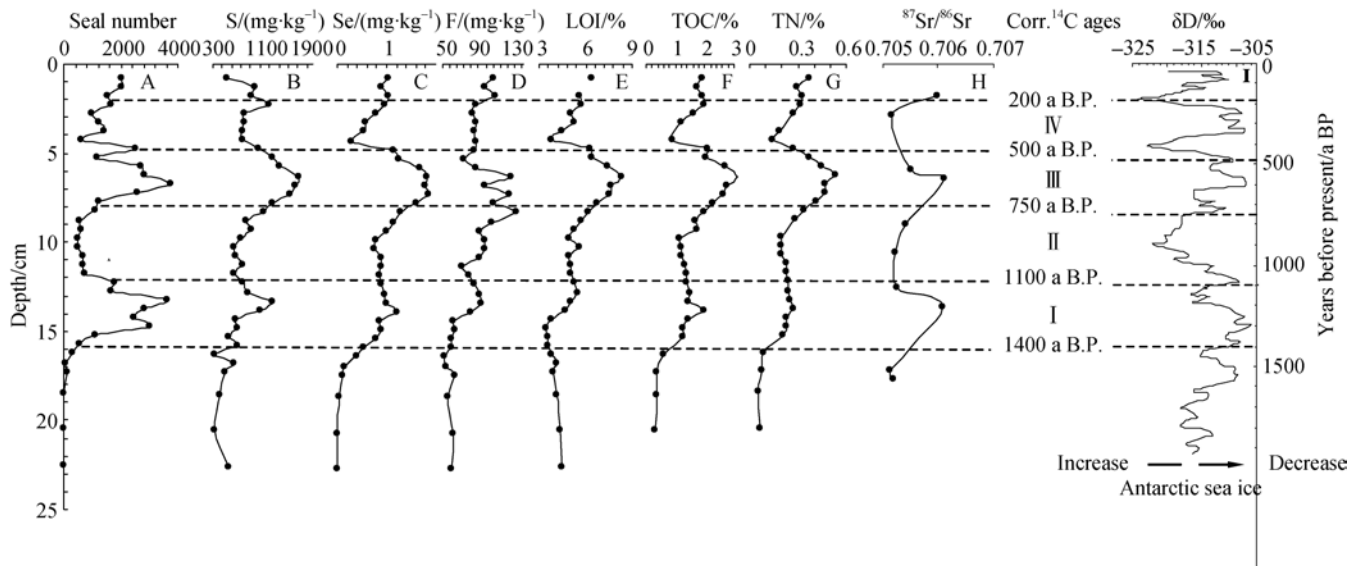


Figure 6 Seal population changes over the past 1500 years correlated well with the variability in past sea ice cover reconstructed from ice cores (Sun et al., 2013), where the peaks in the seal populations correspond to less sea ice cover, and vice versa.

2.3 Krill

Antarctic krill (*Euphausia superba*) is a predominant species in the Southern Ocean and supports a large number of upper trophic-level predators, and it is also a major fishery resource (Everson, 2001; Hofmann and Murphy, 2004). To a large extent, the krill abundance and distribution pattern determines the fate of the Antarctic marine ecosystem, and knowledge of long-term krill population dynamics is essential for understanding and predicting the responses of krill to natural climate change (Nicol, 2006). Past relative krill abundance is difficult to obtain, but can be inferred from the paleodiets of krill predators such as Antarctic fur seal and Adélie penguins (Reid et al., 1999; Huang et al., 2014).

Huang et al. (2011) inferred relative krill abundance along the WAP over the 20th century from the dietary change in Antarctic fur seal, using stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes of seal hairs deposited in excrement sediment. The increasing $\delta^{15}N$ values in seal hairs for the past century indicated a declining proportion of krill in seal diets, and were directly correlated with reduced krill stocks since the 1970s, accompanied by recent regional warming and declined sea ice extent during the same period (Figure 7a).

Huang et al. (2013) studied the diets of Adélie penguins in the Vestfold Hills over a longer period, and inferred relative krill abundance during the Holocene, as indicated by $\delta^{15}N$ values of ancient penguin bones and feathers extracted from ornithogenic sediments. The authors found that variations in krill abundance during the Holocene were in accord with episodes of regional climate and sea ice changes, showing greater krill abundance in cold periods with extensive sea ice (Figure 7b). An abrupt shift in penguin $\delta^{15}N$ values between modern and ancient samples was observed, with more depleted $\delta^{15}N$ ratios in modern penguin samples. This indicates a greater proportion of krill in their diet, which supports the 'krill surplus hypothesis' in modern times resulting from the recent hunting of krill-eating seals and whales by humans (Emslie and Patterson, 2007).

3 Historical records of human civilizations

Since the time of ancient Rome around 2500 BP, humans have released pollutants such as mercury (Hg) and lead (Pb) into the atmosphere, from early processing and smelting activities (Mellor, 1957). Hg is a globally transported pollutant that can be dispersed in the remote Antarctic regions through atmospheric deposition and ocean currents,

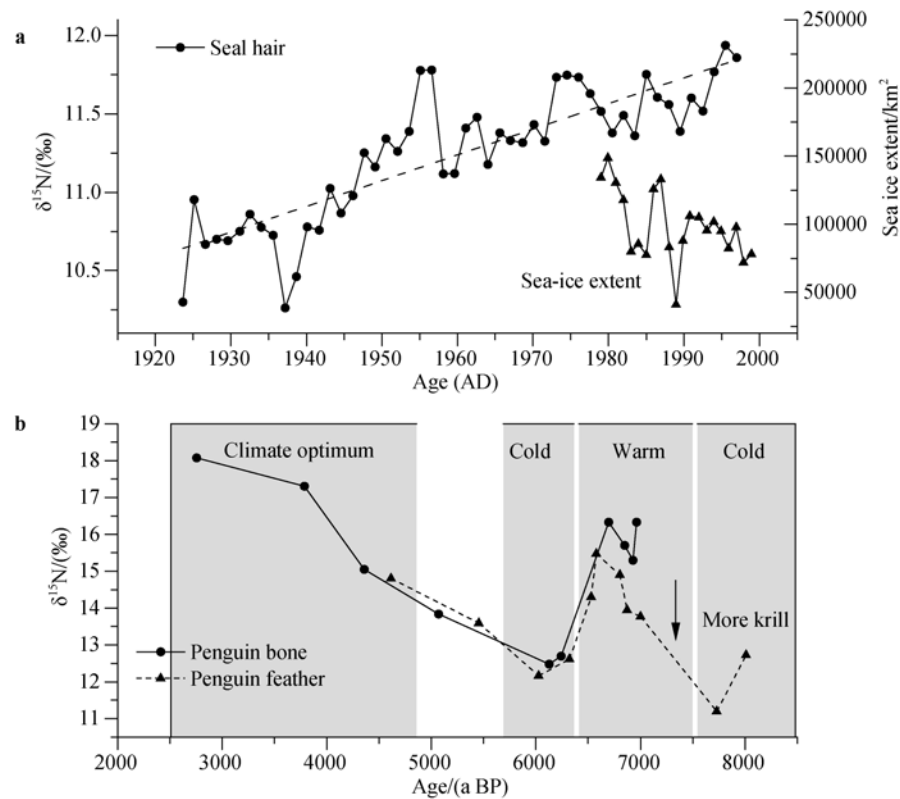


Figure 7 Paleodietary change of Antarctic penguins and seals and their relationship with climate change and sea ice extent (redrawn from Huang et al. (2014)). **a**, ~80-year record of $\delta^{15}\text{N}$ values in Antarctic fur seal hair (solid circle) in the Fildes Peninsula and the observed annual average sea ice extent (triangle) for the Palmer region from 1979 to 2004 ; **b**, ~8000-year record of $\delta^{15}\text{N}$ values of Adélie penguin bone (solid circle) and feather (triangle) in Vestfold Hills with reconstructed changes in climate and sea ice extent.

and enriched by biomagnification effects in seabirds and marine mammals (Bargagli et al., 1998; Fitzgerald et al., 1998), which provide an ideal archive for exploring ancient human civilizations. Sun et al. (2006) observed marked fluctuations in Hg concentrations over the past ~2000 years in seal hairs 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, showing severe Hg pollution in this period (Figure 8). Recent industrial development has intensified not only global mercury pollution, but also the lead content in penguin guano, seal hairs and weathering sediments, which have increased sharply in the past ~200 years (Sun and Xie, 2001; Yin et al., 2006). These studies show that the influence of human civilization on the Antarctica did not begin with the direct human presence on this continent, and enable us to explore the lost civilizations.

4 Bio-transfer of nutrients and contaminants from sea to land in Antarctica

In Antarctica, seabirds and marine mammals forage in marine habitats or tidal zones and breed on land, acting as

bio-vectors and transporting large amounts of nutrients (C, N and P) and contaminants from marine to terrestrial ecosystems (Sánchez-Piñero and Polis, 2000; Blais et al., 2005; Ellis et al., 2006). Qin et al. (2014) estimated that the annual mass of P transferred by penguins from ocean to land in three important penguin colonies at Ardley Island, the Vestfold Hills and Ross Island, could be up to 12349, 167036 and 97841 kg, respectively. The concentration of phosphine (PH₃) in the atmosphere has been monitored in the Milo Peninsula for the first time, and the maximum concentration of PH₃ appeared in a penguin colony (Zhu et al., 2016). It was concluded that penguin activity significantly increased soil phosphine formation and P contribution, thus playing an important role in the P cycle in terrestrial ecosystems of maritime Antarctica (Zhu et al., 2014).

As a result of biomagnification and/or bioaccumulation through the marine food web, large amounts of heavy metals (such as Hg, Cu, Zn, As and Cd) are also transferred by seabirds from the ocean to terrestrial ecosystems (Blais et al., 2005). Xie et al. (2008) analyzed an 1800-year record of As concentrations in lake sediments affected by penguin droppings, and found it to be about double that of the background sediments where penguins were absent. Nie et al. (2012) observed high Hg content in guano and a positive correlation between Hg and a guano bio-element (such as P)

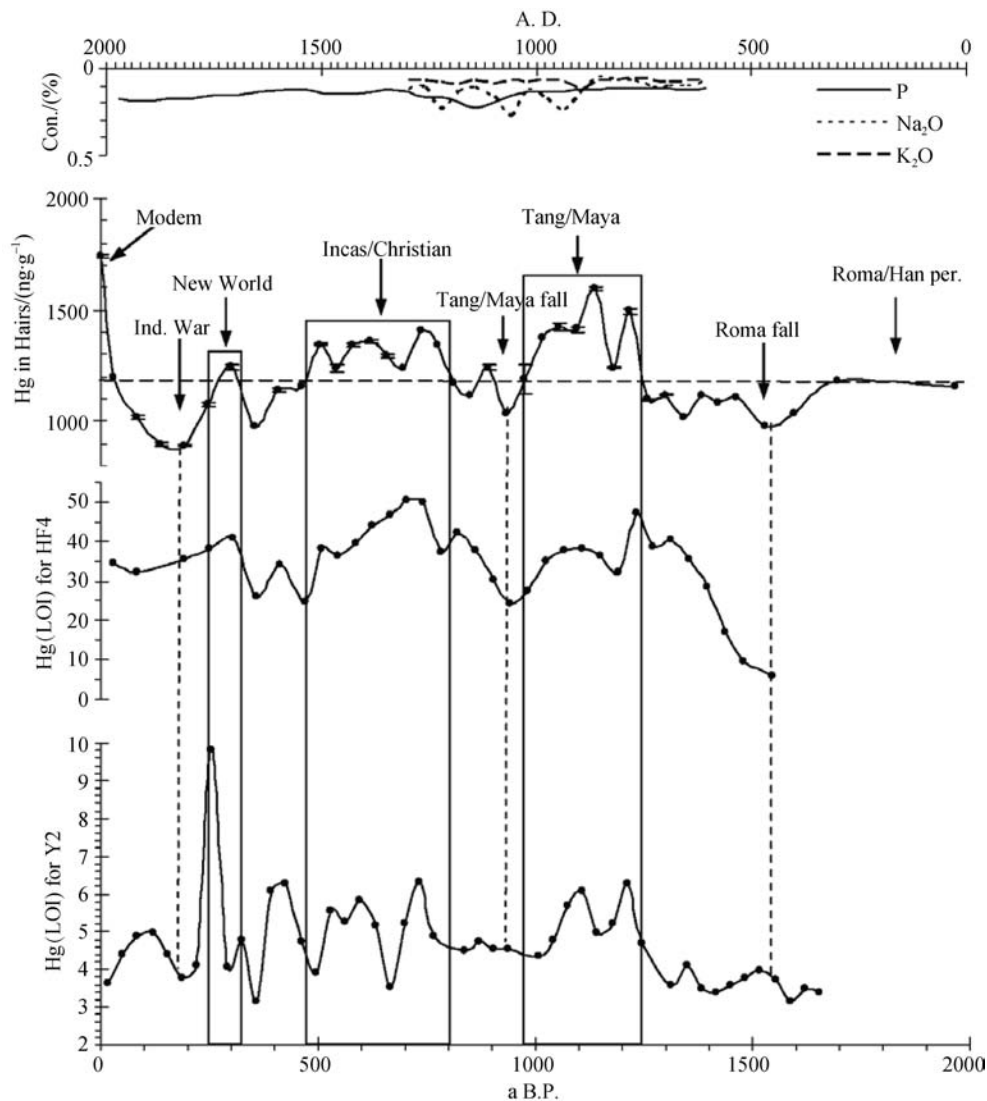


Figure 8 Changes in Hg concentration in seal hairs over the past 2000 years show striking associations with ancient civilizations, where concentrations of essential elements K_2O (--), Na_2O (...) and P (—) in the seal hairs and the calibrated Hg concentration in the sediments of HF4 and Y2 are indicated (Sun et al., 2006). The calibration was performed to remove the effect of excrement content on the Hg concentration.

in the ornithogenic sediment profiles. This suggests that Hg was strongly influenced by guano input and that sedimentary Hg may be an effective trophic-level indicator from seals to penguins. Zheng et al. (2015) explored the use of Hg stable isotope compositions in historical and modern biological deposits as a new approach for discerning Hg sources and tracing MeHg cycling in the ocean and bioaccumulation in marine biota. They suggested that penguin and seal feces were the dominant sources of Hg in the sediments at different time periods. Huang et al. (2014) indicated that, because of its high trophic level and transfer efficiency, the emperor penguin can transport a large amount of nutrients and contaminants from ocean to land even with a relatively small population. Its roles in the biogeochemical cycle between the oceanic and terrestrial environment should not be ignored.

5 Conclusions

This review summarizes recent progress in the paleoecology of typical marine organisms and corresponding responses to climate change and anthropogenic impacts in Antarctica. The major points are:

- (1) Historical penguin and seal populations have experienced dramatic fluctuations over the past several thousands of years, showing responses to the episodes of warm and cold climate. Penguin population dynamics during the LIA in the Ross Sea were also related to migrations, an ecological response to global climate change and possible subsequent geological effects in Antarctica.
- (2) The dietary changes in penguins and inferred relative krill abundance were corresponded quite well with

changes in climate and sea ice extent during the Holocene. The depleted ^{15}N ratios found in modern Adélie penguins support the ‘krill surplus hypothesis’ in relation to historic human depletion of krill-eating fish, seals and whales.

(3) Historical information about human civilizations over the past several thousands of years is well preserved in Antarctic seal hairs and in ornithogenic sediments, and these biological archives offer a novel approach for exploring past civilizations.

(4) Land-based seabirds and marine mammals act as bio-vectors that transport large amounts of nutrients and contaminants from marine to terrestrial ecosystems.

Acknowledgments The authors are grateful to the Chinese Arctic and Antarctic Administration (CAA) for logistical support in the fieldwork. This study was funded by the Chinese Polar Environment Comprehensive Investigation and Assessment Program (Grant nos. CHINARE2017-02-01, 2017-04-04, 2017-04-01). Sample information and data were issued by the Resource-sharing Platform of Polar Samples (<http://birds.chinare.org.cn>) maintained by the Polar Research Institute of China (PRIC) and the Chinese National Arctic & Antarctic Data Center. Samples were provided by the Polar Sediment Repository of PRIC.

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