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Oceanographic mechanisms and penguin population increases during the Little Ice Age in the southern Ross Sea, Antarctica

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ABSTRACT

The Adélie penguin is a well-known indicator for climate and environmental changes. Exploring how large-scale climate variability affects penguin ecology in the past is essential for understanding the responses of Southern Ocean ecosystems to future global change. Using ornithogenic sediments at Cape Bird, Ross Island, Antarctica, we inferred relative population changes of Adélie penguins in the southern Ross Sea over the past 500 yr, and observed an increase in penguin populations during the Little Ice Age (LIA; 1500–1850 AD). We used cadmium content in ancient penguin guano as a proxy of ocean upwelling and identified a close linkage between penguin dynamics and atmospheric circulation and oceanic conditions. During the cold period of ∼1600–1825 AD, a deepened Amundsen Sea Low (ASL) led to stronger winds, intensified ocean upwelling, enlarged Ross Sea and McMurdo Sound polynyas, and thus higher food abundance and penguin populations. We propose a mechanism linking Antarctic marine ecology and atmospheric/oceanic dynamics which can help explain and predict responses of Antarctic high latitudes ecosystems to climate change.

1. Introduction

Understanding the mechanisms for Southern Ocean ecosystem responses to climate variability is challenging, and up to now there has been little research on the coupling of atmospheric circulation, ocean conditions, and Antarctic marine ecology over geologic time scale. The Ross Sea is the conjunction point of three different air masses from Victoria Land, the Ross Sea and the Ross Ice Shelf (Monaghan et al., 2005) and is highly sensitive to climate change. Climate in this region is mainly controlled by large-scale atmospheric circulation via changes in winds and temperature that further influence sea ice extent (Coggins and McDonald, 2015; Holland and Kwok, 2012; Hosking et al., 2013), and has been so over the last millennium, especially during the Little Ice Age (LIA; 1500–1850 AD). Records from Siple Dome ice cores show strengthened meridional atmospheric circulation since ∼1400 AD, coincident with the initiation of the LIA (Kreutz et al., 1997). Records from Talos Dome ice cores suggest a prolonged, cooler climate from the 16th to the beginning of the 19th centuries (Stenni et al., 2002). Marine sediments from McMurdo Sound exhibit higher open water diatom abundance, a more persistent Ross Sea polynya, and enhanced primary production in the southwestern Ross Sea from ∼1600–1875 AD (Leventer and Dunbar, 1988). All these data indicate that during the LIA, the Ross Sea experienced cooler and drier conditions, characterized by stronger katabatic winds, cooler sea surface temperatures, and larger polynyas than today (Bertler et al., 2011).

Changes in the oceanic conditions associated with large-scale atmospheric forcing are expected to have cascading effects on marine food webs, from phytoplankton to krill and to upper trophic level predators (Montes-Hugo et al., 2009; Saba et al., 2014; Trivelpiece et al., 2011). The Ross Sea currently supports over two million Adélie penguins (*Pygoscelis adeliae*) and this species is widely used as bio-indicator for climate and environmental changes (Ainley, 2002; Lynch and LaRue, 2014). The ecological history of Adélie penguins in the Ross Sea region, including occupation history (Emslie et al., 2003, 2007), population dynamics (Ainley et al., 2005; Wilson et al., 2001), and dietary changes (Ainley et al., 1998; Lorenzini et al., 2014; Polito et al., 2002) has been extensively examined. The population dynamics of penguins,

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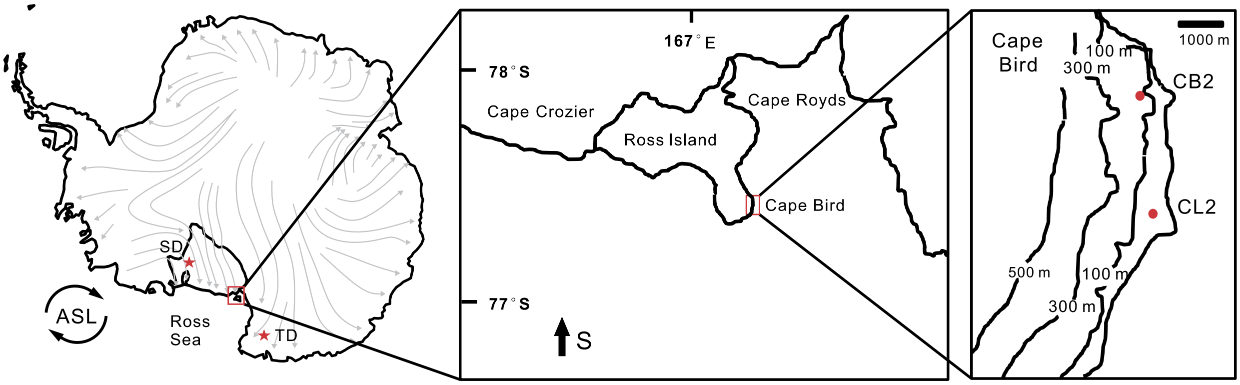

Fig. 1. Location of sampling sites of ornithogenic sediments (represented by red dots) at Cape Bird, Ross Island, as well as ice core sites (represented by red stars) in the Ross Sea, Antarctica. The grey arrows indicate katabatic wind flow (modified from Bertler, 2004). ASL: Amundsen Sea Low; CB2: this study; CL2: referring to Nie et al. (2015); SD: Siple Dome ice core, referring to Mayewski et al. (2004); TD: Talos Dome ice core, referring to Stenni et al. (2002). (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

seals and krill during the Holocene from studies in the Antarctic Peninsula and East Antarctica are tightly associated with climatic conditions (Huang et al., 2009, 2013; Sun et al., 2000, 2004, 2013) and likely so in the Ross Sea as well. For example, evidence suggests that Adélie penguin populations at Cape Bird, Ross Island, shifted locations of breeding sites there due to coastline variations and frequent storms under the colder climatic conditions of the LIA (Hu et al., 2013; Nie et al., 2015).

Here, we analyzed geochemical records in ornithogenic sediments from Cape Bird, Ross Island (Fig. 1), and used phosphorus (P) to reconstruct historic changes of Adélie penguin populations and cadmium (Cd) as a proxy for ocean upwelling intensity; stable nitrogen isotopes (δ^{15}N) in penguin feathers were used to infer penguin dietary changes for the past 500 yr. We also investigated the connection between atmospheric circulation, oceanic conditions and the impact of large-scale climate forcing on marine ecosystem along the southwestern Ross Sea.

2. Material and methods

2.1. Sampling site

The sediment core CB2 in this study was collected at Ross Island, southwestern Ross Sea, during the 2012 austral summer (Fig. 1). This 15-cm deep core was collected from a catchment on an elevated hillside at southern Cape Bird, with an active Adélie penguin colony nearby, indicating possibly high impact of penguin guano on the sediment. The profile was sectioned at 0.5 cm intervals, and a total of 30 subsamples were obtained and stored in a freezer at −20 °C prior to analysis. The CB2 profile contained numerous penguin feather fragments, but sample sizes per 0.5 cm section were small (fragments representing 3–5 individual feathers). Fragments were pooled into one sample per 0.5 cm section for δ^{15}N analysis.

2.2. Chronology

Two penguin feathers were selected from the CB2 profile (at depths of 9 cm and 15 cm) for AMS ^{14}C dating (Table 1). These two conventional radiocarbon dates were calibrated using the CALIB 7.0.2 computer program and the dataset of Marine13 (Reimer et al., 2013), and corrected using a $\Delta R = 750 \pm 50$ yr for the marine carbon reservoir effect in the Ross Sea region (Emslie et al., 2007). As a result, CB2 profile has a bottom age of ~1471–1695 AD (2σ range).

To obtain the chronology of the CB2 profile, the levels of bio-elements mercury (Hg) and phosphorus (P) were compared with those in another ornithogenic sediment profile (CL2) from the middle Cape Bird (Nie et al., 2015). The CL2 profile was taken from a small pond that is located on the fifth beach ridge above sea level with abandoned penguin colonies nearby. CB2 and CL2 are geographically close (~1 km apart), have similar ornithogenic influence on the two sediment cores from penguin guano, and thus the typical bio-elements Hg and P in the two cores are comparable. Based upon these comparisons, we established the age-depth model for CB2 by matching the two cores' bio-elemental characteristics (Fig. 2), with the bottom age calculated as ~1450 AD, consistent with the ^{14}C age (Table 1). Therefore, we established the complete and accurate chronology of CB2, which represents about 500 yr of deposition at the sampling site.

Table 1
^{14}C dates and calibrated ages for the CB2 profile.

Sample	Depth (cm)	Material	Conventional ^{14}C age (BP)	Calibrated age (AD)
CB2-18	9	Feather	1065 ± 36	/
CB2-30	15	Feather	1463 ± 38	1471~1695 (2σ)

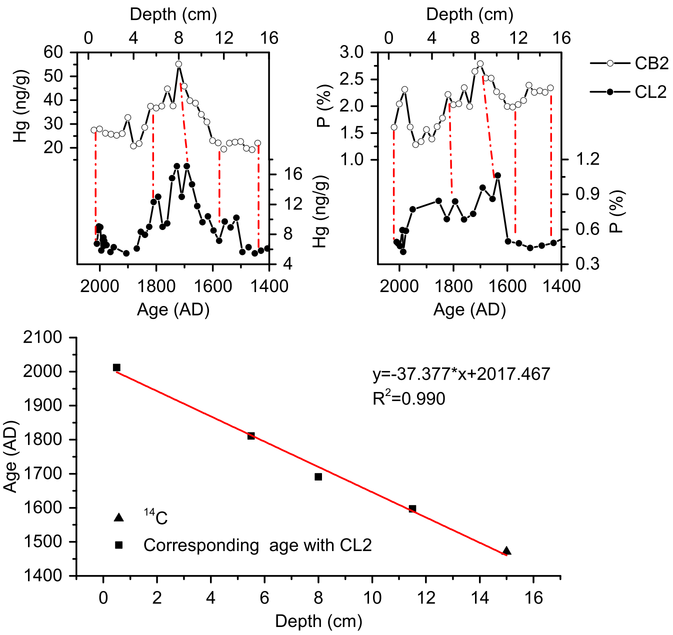

Fig. 2. Chronology of the profile CB2. Upper panel: comparison of mercury (Hg) and phosphorus (P) concentrations in profile CB2 and CL2, respectively; bottom panel: age-depth model for profile CB2, with a linear fitting.

2.3. Geochemical analysis

All subsamples in CB2 were air-dried and homogenized by grinding after careful removal of larger rock fragments and penguin remains (bone fragments, feathers and eggshells). The final powdered samples were passed through a 74 µm mesh sieve.

For Cd and P analysis, 0.25 g air-dried subsamples were precisely weighed and digested with multi-acids (HNO_3–HCl–HF–$HClO_4$) in Teflon tubes by electric heating; their concentrations were measured by Inductively Coupled Plasma-Optical Emission Spectroscopy (ICP-OES, Perkin Elmer 2100 DV). For Hg analysis, 0.1 g air-dried subsamples were precisely weighed and digested with H_2O_2–HNO_3–Fe^{3+} oxidant in colorimeter tubes by electric heating and then determined by Atomic Fluorescence Spectrometry (AFS-930, Titan Instruments Co., Ltd.). Measurements were conducted at constant solution volume on both ICP-OES and AFS. Reagent blanks and standard reference materials were included in every batch of samples for quality control, with a relative standard deviation less than 0.5%.

Penguin feather remains for stable nitrogen isotope analysis were cleaned with Millipore water and 2:1 chloroform:methanol solution, and then dried in an oven at 40 °C. The cleaned samples were cut into small pieces and weighed in a tin capsule. Stable nitrogen isotope ratios in penguin feathers were determined using an isotope ratio mass spectrometer at the G.G. Hatch Isotope Laboratories, Earth Sciences, University of Ottawa, with a precision ≤ 0.2‰. Isotope ratios ($^{15}N/^{14}N$) in samples are expressed in δ notation, and defined as follows:

$$\delta^{15}\mathrm{N}(‰) = (\mathrm{R_{sample}}/\mathrm{R_{standard}} - 1) \times 1000$$

where R_{sample} is isotope ratio of the sample, and $R_{standard}$ of the air.

3. Results

Cd levels in the CB2 profile ranged from 2.22 to 5.31 µg/g, with a mean value of 3.54 ± 0.87 µg/g, much higher than Cd content in the bedrock (Liu et al., 2013), and thus indicating that the Cd in the sediments is sourced primarily from penguin guano. We calibrated Cd levels in ornithogenic sediments to Cd content in penguin guano ($[Cd]_p$) using the methods of Sun and Xie (2001). $[Cd]_p$ ranged from 4.48 to 10.10 µg/g, with a mean value of 6.94 ± 1.60 µg/g. $[Cd]_p$ is relatively high between ~1450 and ~1600 AD, then begins to rise and reaches a peak value at ~1700 AD, followed by a decline to a low and stable level after ~1825 AD. To eliminate the effect of penguin guano content on Cd levels, we also calculated the Cd/P ratio in the sediments and found it to be consistent with $[Cd]_p$ (Fig. 3c).

P concentration in CB2 ranged from 1.28 to 2.79%, with a mean value of 2.06 ± 0.39%, much higher than the background concentration at Cape Bird (Liu et al., 2013). P reached maximum values in the levels dated to ~1600–1825 AD, but decreased in the pre-1600 AD levels, and declined to minimum after ~1825 AD.

The $\delta^{15}N$ values in penguin feathers from CB2 ranged from 9.01 to 13.33‰, a 4.32‰ difference. These values were relatively high in levels dated pre-1600 AD, decreased afterwards, and reached the most depleted level at ~1720 AD; then $\delta^{15}N$ values began to rise and remained at a relatively high level since ~1825 AD, with occasional dips in the 1920s and 1970s.

4. Discussion

4.1. Changes in penguin populations and prey selection for the past 500 yr recorded in CB2

P is a well-known bio-element in penguin ornithogenic sediments in the Antarctic Peninsula, Vestfold Hills and Ross Sea regions (Huang et al., 2009; Nie et al., 2015; Roberts et al., 2017; Sun et al., 2000), and has been used successfully in the reconstruction of past penguin population changes (Hu et al., 2013; Huang et al., 2011). Adélie penguin populations as inferred from P (Fig. 3a) at southern Cape Bird declined slightly from ~1450 to ~1600 AD, began to rise afterward and reached their highest level in ~1700 AD, then declined with fluctuations to the lowest levels through ~1900 AD. For the past 100 yr, Adélie penguin populations experienced a sharp rise and drop. Monitoring data have shown that Adélie penguins at Cape Bird had an increasing trend in the 1970s, likely linked with changes in sea-ice extent and polynya size, but also with variation in competition with minke whales (Ainley et al., 2005; Wilson et al., 2001). Our study suggests that the penguin populations increased in the 1960s as well, consistent with their research.

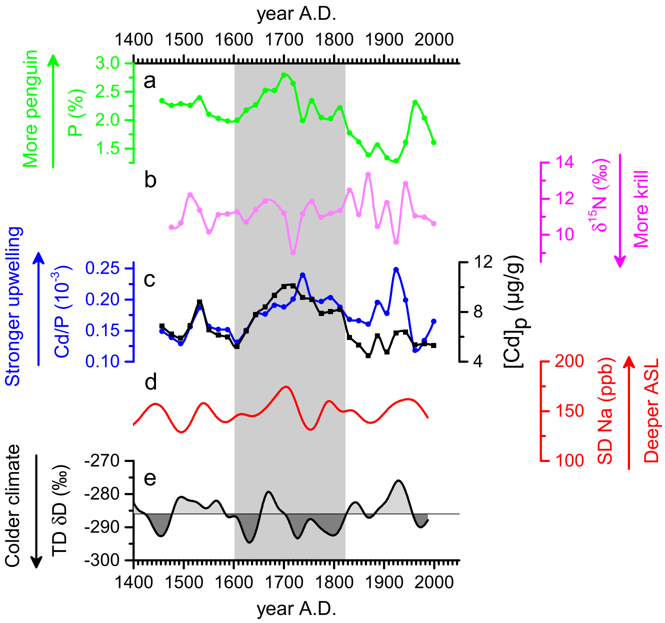

Fig. 3. Proxy indices of ocean ecological processes and climate records for the past 500 yr. (a) Adélie penguin population change at Cape Bird indicated by P concentrations in profile CB2. (b) Krill abundance indicated by stable nitrogen isotopes. (c) Ocean upwelling indicated by $[Cd]_p$ and Cd/P ratio. (d) Past ASL intensity indicated by Na concentration in Siple Dome ice core (25-yr running mean) (Mayewski et al., 2004). (e) Climate changes from the δD record in Talos Dome ice core (20-yr running mean) (Stenni et al., 2002), light grey represent warmer climate and dark grey represent colder climate. Original data of Na and δD are downloaded from the website: http://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/ice-core. The shaded areas stand for the cold climate period (~1600–1825 AD).

The $\delta^{15}N$ values in biological tissues have been extensively used to infer dietary and foraging behavior of seabirds (Emslie and Patterson, 2007; Huang et al., 2013; Lorenzini et al., 2014) and are enriched ~3–5‰ for every increase in trophic level through the marine food chains (Cherel, 2008). Using $\delta^{15}N$ values in ancient Adélie penguin tissues as a proxy, Huang et al. (2013) inferred relative krill abundance in penguin diet at the Vestfold Hills during the Holocene, with more krill consumed in cold periods based on lower $\delta^{15}N$ values at those times. Here, $\delta^{15}N$ values of Adélie penguin feathers in the CB2 profile have an amplitude of 4.32‰, indicating a significant change in Adélie penguin dietary composition. Modern Adélie penguins in the Ross Sea feed primarily on ice krill (*Euphausia crystallorophias*) and silverfish (*Pleuragramma antarctica*) (Ainley et al., 1998). Adélie penguins breeding at Cape Bird would be molting, and growing new feathers, along the shelf break of the eastern Ross Sea, where penguin diet would be Antarctic krill (Ainley et al., 1984; Ballard et al., 2012). It is impossible to tell if the feathers sorted from the CB2 profile were from adult penguins (grown during molt at the shelf break) or from chicks at Cape Bird, so we could not distinguish krill species in this study. Although δ^{15}N values between ∼1600 and ∼1825 AD are not depleted as a whole (indicating a mixture of krill and silverfish in penguin diet), a large dip in value occurred at ∼1720 AD (Fig. 3b), suggesting a relatively high amount of krill in penguin diet at that time. After ∼1825 AD, δ^{15}N values became more enriched, but fluctuated widely, indicating penguin diet was dominated by silverfish or krill at specific intervals, probably in response to variations in oceanographic conditions. Currently, silverfish is more important in the diet of Adélie penguins in the southern Ross Sea, possibly due to increased removal by fisheries of Antarctic toothfish that also prey on silverfish, leaving a surplus of this prey that benefits penguins (Ainley et al., 2017; LaRue et al., 2013; Lyver et al., 2014). Alternatively, a decline in sea ice at Anvers Island, Antarctic Peninsula, has been correlated with disappearance of silverfish in Adélie penguin diet there (Sailley et al., 2013; Schofield et al., 2010). It is apparent, then, that there are many complex interactions that determine major prey consumption by Adélie penguins, including oceanographic variations due to climate, sea ice extent, polynya size and primary productivity, and trophic cascades.

Over the past 500 yr at Cape Bird, Adélie penguin populations increased during the cold period (∼1600–1825 AD; Fig. 3e), which is inconsistent with the general pattern in other studies, for example, penguin populations increased when climate became warmer, and vice versa (Emslie et al., 2007; Huang et al., 2009; Sun et al., 2000). Due to different geographical effects or oceanic conditions, though, there may have been different responses by penguins to climate change in the late Holocene. Here, we focus on the linkage between penguin ecology and atmospheric/oceanic conditions, i.e., winds, ocean upwelling, and polynya size.

4.2. Upwelling in the Ross Sea continental shelf and its association with the Amundsen Sea Low (ASL)

The Circumpolar Deep Water (CDW), a relatively warm and nutrient-rich water mass that originates from the Antarctic Circumpolar Current (ACC) (Orsi et al., 1995), can be found near the continental shelf around most of the Antarctica. In the Ross Sea, CDW mixed with the shelf waters to form Modified Circumpolar Deep Water (MCDW), and crosses the shelf break at specific locations primarily determined by the bathymetry, but eventually floods much of the shelf (Dinniman et al., 2011). In their model, the simulated dye concentration (representing CDW) around Ross Island increased over time; in the model of 620 days, some of the dye advected underneath the Ross Ice Shelf, primarily entering near Ross Island. In addition, CDW from off the continental shelf could carry nutrients (e.g., Fe) into the surface waters around Ross Island (McGillicuddy et al., 2015; M.S. Dinniman, personal communication). Along the western half of Ross Ice Shelf, a layer of MCDW extends to Ross Island, and the extent and frequency of MCDW intrusions may contribute to explain the historic abundance and distribution of larger toothfish near McMurdo Sound (Ashford et al., 2017).

Since Shen et al. (1987) used Cd as a tracer of historical upwelling in corals, it has been widely applied as a proxy of ocean upwelling (Reuer et al., 2003). Cd is an important nutrient in the Southern Ocean water column and shows similar vertical distribution with phosphate (Boyle et al., 1976). In ocean surface water, Cd is depleted by biological activities, while in the CDW Cd is enriched by organic matter decomposition and re-mineralization (Abouchami et al., 2011). Hence, Cd in surface water is mainly replenished by upwelling of Cd-rich CDW, absorbed by phytoplankton, and ultimately enriched in marine top predators such as Adélie penguins. Penguin ornithogenic sediments from Ross Island, Vestfold Hills, and Amanda Bay contain high Cd concentrations (Huang et al., 2011, 2016; Liu et al., 2013). Similar results have been reported in penguin tissues from the Antarctic Peninsula and Ross Sea region; Cd concentration in fresh penguin guano is as high as 5.3 μg/g, probably caused by convective upwelling of Cd-rich deep waters (Ancora et al., 2002; Espejo et al., 2014; Metcheva et al., 2011).

It is complicated when considering the exact source of the Cd in the ornithogenic soils. Adélie penguins breeding at Cape Bird would have incorporated Cd in their tissues in late summer, when feeding and molting along the shelf break in the eastern Ross Sea. When these adult penguins return to Cape Bird the following breeding season, they fast at their nests through the first incubation cycle, but not for the entire breeding season (Ainley et al., 1983; Vleck and Vleck, 2002). So, we suggest that Cd in the ornithogenic sediments (mainly from penguin guano, both adults and chicks) is mainly derived from the feeding zones around Ross Island and thus impacted by the upwelling occurring along the shelf break. However, we cannot exclude the possibility that some of the Cd was assimilated by penguins when feeding in the eastern Ross Sea. The lack of any noticeable positive correlation between $[\mathrm{Cd}]_p$ and δ^{15}N in the CB2 profile (Fig. 3b, 3c) suggests that the trophic level of penguins is unlikely the determining factor for high $[\mathrm{Cd}]_p$ levels. Therefore, we conclude that $[\mathrm{Cd}]_p$ could be used as the tracer of CDW upwelling and a reliable proxy for the nutrient condition of ocean surface water in the Ross Sea.

Model studies have highlighted the importance of winds in the CDW upwelling process (Dinniman et al., 2011; Klinck and Dinniman, 2010; Thoma et al., 2008). In addition, the western Ross Sea is known to be a site of vigorous vertical mixing due to strong katabatic winds (Parish et al., 2006). The Amundsen Sea Low (ASL) is the climatological area of low pressure located in the South Pacific sector of the Southern Ocean, and it strongly influences the wind field over the West Antarctic region (Coggins and McDonald, 2015; Hosking et al., 2013; Turner et al., 2013). Kreutz et al. (2000) reported that Na concentration in the Siple Dome (SD) ice core provides an indication of past ASL variability; a deeper ASL transports more sea salt aerosol to the ice core site. They also reported a deepened ASL during the LIA. $[\mathrm{Cd}]_p$ in the CB2 profile exhibited a strong correlation with Na in SD the ice core, especially during the period from ∼1600 to ∼1825 AD (Fig. 3c, 3d). We suggest that the ASL is indeed the dominant factor in wind strength over the Ross Sea region, and thus in the development of CDW inflow onto the continental shelf.

Transport of CDW/MCDW onto Antarctic continental shelves has important effects in physical and biological processes. For example, the Ross Sea polynya, although it is a latent-heat polynya formed by katabatic winds, maintains open water where convective upwelling of warm CDW emerge at the surface (Reddy et al., 2007). MCDW is thought to supply a significant amount of micronutrient iron to the euphotic zone of the Ross Sea and thus stimulates primary productivity (Hiscock, 2004; Peloquin and Smith, 2007). In addition, CDW intrusions on the Ross Sea shelf are apparently linked to the location and reproduction of Antarctic krill (Sala et al., 2002), which are also found in canyons along the shelf break (i.e., outer 1/3 of Ross Sea shelf waters). These krill are fed upon by various predators, including penguins, and a large decline in this keystone species could cause a trophic cascade within the marine food web (Ainley et al., 2006). Therefore, changes in the atmospheric forcing would likely generate substantial changes in the wind pattern and oceanographic and ecological impacts in the Ross Sea.

4.3. Effects of large-scale atmospheric forcing on oceanic conditions and marine ecosystems in the Ross Sea

Bertler et al. (2011) summarized the atmospheric and oceanic conditions during the past millennium across Antarctica. Here,

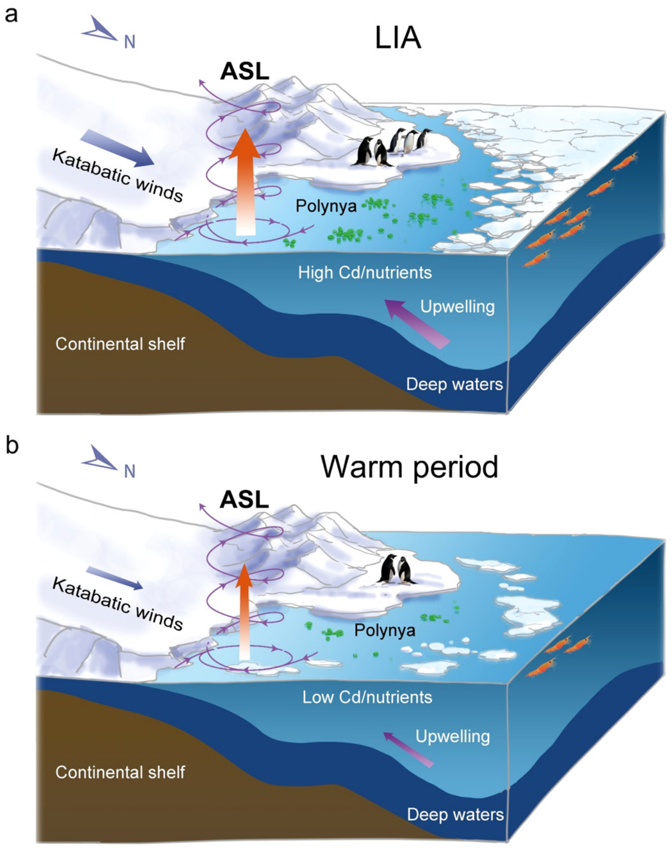

Fig. 4. Effects of large-scale atmospheric forcing on oceanic conditions and marine ecological processes in the Ross Sea. (a) LIA (∼1600–1825 AD). (b) Warm period (since ∼1825 AD). Data for the past ASL intensity by Kreutz et al. (1997, 2000) and Mayewski et al. (2004); data for the katabatic winds by Bertler et al. (2011) and Rhodes et al. (2012); data for polynya size by Leventer and Dunbar (1988); data for ocean upwelling, primary productivity (green ovals), prey abundance and penguin population by this paper. The land where penguins are located is Ross Island. It is probably westerlies that induce MCDW upwelling, while katabatic winds would contribute to vertical mixing. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

based on records of historical Adélie penguin populations and dietary changes in the Ross Sea region, we propose a synthetic perspective for the linkage between these marine ecological processes and the atmospheric/oceanic dynamics (Fig. 4). Changes in the atmospheric circulation would induce substantial changes in wind strength and thus oceanographic conditions (i.e., MCDW formation, nutrient input and polynya size). Ultimately, these atmospheric and marine environmental changes would affect the marine primary productivity, krill and silverfish abundance and the open-water access that penguins need for foraging.

In polar regions, cooler temperatures coincide with more intense atmospheric circulation, and vice versa (Mayewski et al., 2009). In West Antarctica, the LIA was characterized by intensive atmospheric circulation with a deepening of the ASL (Kreutz et al., 1997). Ice core records from Mt. Erebus Saddle, Ross Island, demonstrated that cooler temperatures promoted stronger katabatic winds over the Ross Ice Shelf, resulting in an enlarged Ross Sea polynya between ∼1600 and ∼1850 AD (Rhodes et al., 2012) and increased diatom abundance in McMurdo Sound (Leventer and Dunbar, 1988). The Ross Sea polynya (with the McMurdo Sound polynya, although it being very small), is the most productive area in the Southern Ocean and favorable to Adélie penguins (Ainley, 2002). Higher primary productivity occurs within the polynyas, which increases in size with stronger katabatic winds (Rhodes et al., 2012). Moreover, increased westerlies during the LIA associated with a deeper ASL (Bertler et al., 2011) likely intensified the Ross Gyre, and in turn induced more MCDW intrusions (and hence nutrient input) onto the continental shelf (Dinniman et al., 2011). Therefore, we propose that cooler climatic conditions occurred from ∼1600–1825 AD in the Ross Sea region, while the deeper ASL led to stronger winds, and thus enlarged the Ross Sea and McMurdo Sound polynyas, providing penguins with more open-water access for food and perhaps shorter foraging trips. Marine primary production also increased with enhanced MCDW upwelling and polynya size, leading to higher food abundance and larger penguin populations on Ross Island.

The penguin population change at Cape Bird might be linked with the penguin emigration due to isostatic subsidence and inland-ward movement of the shoreline when the LIA began (Hu et al., 2013; Nie et al., 2015). This, however, is unlikely because first, the shoreline change event occurred at ∼1300–1400 AD, 300 yr earlier than the observed penguin population change. Second, penguin migration tends to occur in a short time period (Hu et al., 2013). Thus, we suggest that Adélie penguin population changes in the Ross Sea during ∼1600–1825 AD were mainly caused by atmospheric-mediated changes in the wind strength and the aspects of the oceanic conditions.

When the climate warmed after ∼1825 AD, a reverse process might occur: katabatic winds and thus polynya size declined, nutrients in the surface ocean were depleted, primary productivity was reduced, and prey abundance and Adélie penguin populations decreased at Cape Bird (Fig. 4b). This observation is consistent with the association between the recent warming and the declines in sea ice, phytoplankton biomass, krill abundance and Adélie penguin populations in the West Antarctic Peninsula region (Montes-Hugo et al., 2009; Saba et al., 2014; Trivelpiece et al., 2011). Even though climate warming during the 20th century provides a definite end to LIA cooling, atmospheric circulation might still be in the LIA-mode (Kreutz et al., 1997), and there are no convincing observations that the ASL had weakened since ∼1825 AD. However, ice core records in the Ross Sea show clear evidence of decreasing katabatic winds and polynya size during this warm period (Bertler et al., 2011; Rhodes et al., 2012). This inconsistency with our model (Fig. 4b) may be explained by a location shift of the ASL. Location of the ASL is attracting increasing attention by researchers (Hosking et al., 2013). Ross Sea winds are more sensitive to the location of the ASL than to its depth, and the summer response to the ASL is very different from the winter one (Coggins and McDonald, 2015). There is a well-defined seasonal cycle in the average location of the ASL: remaining west of the Antarctic Peninsula in austral summer and moving westward to the Ross Sea by winter (Turner et al., 2013). Therefore, the ASL might have shifted eastward after ∼1825 AD, thereby reducing its influence on Ross Sea winds and the size of the polynyas. In addition, dramatic variations in δ^{15}N values in CB2 and inferred penguin diets in the warm period possibly reflected an unstable marine environment, stressed both from natural forcing and human impacts (see below), that reduced the role of atmospheric forcing and increased the uncertainties of our model.

In the modern industrial period, biological systems in the Ross Sea are also modified by anthropogenic impacts (e.g., global warming, the ozone hole, and industrial fishing). The Ross Sea is the ocean basin least affected by anthropogenic impacts on Earth, but the intensive extraction of Blue whales by the 1920s severely depleted their populations there, and there are signs of only very slow recovery (Ainley, 2009). Hence, the transient high krill abundance during the 1920s is likely due to the removal of krill-eating whales. Since the 1970s, the Southern Annular Mode (SAM) entered its positive phase induced by the Antarctic ozone depletion and greenhouse gas increases (Marshall, 2003). The ASL also has deepened (Turner et al., 2009), which strengthens the southerly winds over the Ross Sea, resulting in the northward advection of sea ice and an enlarged Ross Sea polynya (Drucker et al., 2011), thus increasing primary production and krill abundance.

5. Conclusions

Increases in greenhouse gases and the Antarctic ozone hole have impacted the Southern Hemisphere atmospheric circulation in recent decades (Fogt and Zbacnik, 2014; Shindell, 2004; Turner et al., 2009). In this study, we have proposed geochemical proxies to infer historical wind strength, polynya size, food availability and penguin population changes at Ross Island for the past 500 yr and their interconnections. We propose that changes in the atmospheric forcing exerted a series of impacts on the oceanic conditions and thus marine ecological processes during the LIA, and that the Antarctic marine food webs are strongly linked with atmospheric/oceanic dynamics. We present this synthetic model to help explain the complexity of responses of Southern Ocean ecosystems to large-scale climate variability. Future changes in atmospheric circulation will likely have profound impacts on oceanic conditions and marine ecological processes in the Ross Sea and other Antarctic regions. The recent increase in sea ice in the Ross Sea is in contrast to the ongoing and rapid declines observed in the West Antarctic Peninsula that are linked to increased strength of relatively warm northerly winds (Lefebvre et al., 2004). Antarctic sectors tend to have different regional climate regimes based on aspects of wind, sea ice, and bathymetry and often generate different (and even opposite) ecological responses. Thus, our model can be tested and modified as additional data are gathered from these regions.

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