

Paleodietary changes by penguins and seals in association with Antarctic climate and sea ice extent

Tao Huang · Liguang Sun · Yuhong Wang · Steven D. Emslie

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Abstract Positioned near the top of the food web, the dietary composition of Antarctic penguins and seals can be an excellent indicator of the regional food web and thus the status of the marine ecosystem. The dietary composition of modern penguins and seals has been well investigated; a long-term time series of data on penguin and seal diets, however, are rare. Such data, especially any predating the initiation of human harvesting of fish, whales and seals in Antarctica, are crucial for understanding and predicting responses of regional marine food webs to natural climate changes. Here we review recent progress on research of paleodietary change in Antarctic penguins and seals, specifically the Adélie penguin (*Pygoscelis adeliae*) and Antarctic fur seal (*Arctocephalus gazella*). These studies indicate that the dietary changes of penguins correspond quite well with fluctuations in climate and sea ice extent during the Holocene. The depleted $\delta^{15}\text{N}$ ratios found in modern Adélie penguins support the “krill surplus hypothesis” in relation to historic human depletion of krill-eating fish, seals and whales.

Keywords *Pygoscelis adeliae* · *Arctocephalus gazella* · Dietary change · Stable isotope analysis · Krill surplus hypothesis

1 Introduction

Seabirds and marine mammals are very sensitive to changes in the environments in which they live and forage, and their diets are excellent indicators of regional food webs and thus the marine ecosystem [1]. For example, the diets of marine animals permit us to infer the availability of their prey species and the status of the marine environment that are difficult and costly to determine by shipboard survey. Therefore, the dietary study of marine animals is an important field in marine ecology and the effects of environmental changes.

Penguins and seals are upper trophic level predators in the Southern Ocean ecosystems and they are sensitive to changes in the marine environment. The annual formation and retreat of Antarctic sea ice is an important driver of marine ecological dynamics [2]. Penguins and seals are also very sensitive to sea ice conditions, and their diets are often affected by Antarctic climate and sea ice extent [3]. In addition, recent human exploitation of meso-predators, especially baleen whales, seals and fish in the Southern Ocean has affected the regional marine food web [4, 5]. Therefore, dietary studies of penguins and seals are multidisciplinary and require information from climate change, fluctuations in sea ice extent and history of human hunting and fisheries to fully assess their biological responses.

Though the diets of modern penguins and seals have been well studied, the time scale of these dietary data is usually too short to be useful for investigating the impact of climate change. Here, we review recent progress in dietary research in Adélie penguins (*Pygoscelis adeliae*) and Antarctic fur seals (*Arctocephalus gazella*) and focus on the paleodietary changes of these species and their responses to climate change and sea ice extent as well as human activities.

T. Huang · L. Sun (✉) · Y. Wang
Institute of Polar Environment, School of Earth and Space Sciences, University of Science and Technology of China, Hefei 230026, China
e-mail: slg@ustc.edu.cn

S. D. Emslie
Department of Biology and Marine Biology, University of North Carolina, Wilmington, NC 28403, USA

2 Methods and materials for dietary study

The primary conventional method for studying diets of top marine animals is to identify prey taxa from stomach contents [6], guano and excrement [7]. Dietary information also can be obtained from seabird-formed ornithogenic soils [8]. These traditional methods provide us with the prey items that are not completely digested. Biogeochemical methods are based on the analyses of stable C and N isotope ratios, fatty acids and DNA signatures on predator tissues, and they have been successfully used to infer an animal's average dietary composition [9–13]. A major advantage of these methods is that they are able to assess animal diets at different time scales, from days for blood plasma to weeks for feathers and hairs, and to months of collagen from bones [14]. Additionally, the common biases often associated with sampling stomach contents do not exist for these indirect biogeochemical methods. While the indirect approaches also have some limitations, such as that the stable isotope method could not provide the specific items in the diet.

Adequate study samples and materials are critical for paleodietary reconstructions. At present, there are primarily two types of material for past dietary reconstruction of penguins and seals in Antarctica. The first is the penguin-formed ornithogenic soils and seal-formed excrement soils in abandoned colonies, which contain organic remains such as bones, feathers, eggshell fragments, hairs, otoliths and squid beaks from the penguins/seals and their prey. This material, however, usually provides a discontinuous profile. The second is sediments containing excrement and prey remains deposited in lakes or ponds near penguin or seal colonies, or molt and haul out sites, with continuous accumulation of guano, excrement and organic remains on ice-free beaches and marine terraces [15]. The chronology of ornithogenic soils/sediments can be established by performing AMS¹⁴C dating on organic remains as old as about 50,000 years, and ²¹⁰Pb and ¹³⁷Cs dating on sediments no more than 200 years old. Identification of prey taxa from ornithogenic soils or stable isotope analyses on subfossil tissues thus provides a continuous or near-continuous record on the dietary composition of penguins and seals in the past and their responses to climate change, the marine environment and/or human activities.

3 Principles of stable isotope analysis for dietary reconstruction

Stable C and N isotope ratios can be used to trace prey sources because of the kinetic isotope effects in biological metabolic processes. Metabolic processes involve the breaking and/or synthesis of biochemical compounds, and

the molecules with lighter nitrogen-14 are preferentially utilized over the same molecules with the heavier nitrogen-15 [9, 10] in the processes. In marine food webs, the nitrogen isotope ratio (¹⁵N/¹⁴N, $\delta^{15}\text{N}$) shows an enrichment of $\sim 3\text{‰}$ – 5‰ from prey to predator [11]. The carbon isotope ratio (¹³C/¹²C, $\delta^{13}\text{C}$), however, does not show noticeable enrichment between each trophic level but changes remarkably between habitats such as inshore vs. offshore or benthic vs. pelagic [16]. Thus, the $\delta^{15}\text{N}$ value is used to indicate the trophic level of the predator, though not the specific items in the diets [11]; $\delta^{13}\text{C}$ of marine animals is usually employed to determine their foraging habitat and movement in space and time [16]. Stable C and N isotope ratios were used to determine ancient human diets in early research [17–19], and have been excellent tools for investigating marine ecology and environments during the past few decades [20–23].

Preservation of samples for stable isotope analyses is an important issue in paleodietary research. Diagenetic processes may change dietary signals in samples through time. For example, abnormally high $\delta^{15}\text{N}$ values were observed in penguin ornithogenic soils [24–26] and penguin and seal excrement sediments [27–30]. These very high values are due to substantial fractionation in the excrements from ammonia volatilization [24], during which ¹⁴N is emitted with ammonia and ¹⁵N is enriched in the remaining soils and sediments. Therefore the $\delta^{15}\text{N}$ value in ornithogenic soils or sediments is not a good proxy for dietary inference, though organic remains preserved in these soils are not affected by volatilization [31]. Although clear diagenetic alterations occur in outer margins of the eggshell carbonate following burial in ornithogenic soils, the inclusion of unaltered CO₃²⁻ from the original eggshell material allows for the fossil's use in isotopic reconstructions [32]. For samples that were less affected by the diagenetic process such as collagen of bone and keratinous feather and hair, their preservation status could be distinguished by comparing the C/N ratios between modern and ancient samples [33, 34].

Measurement of baseline values is another important issue in stable isotopic reconstruction of paleodietary change [27, 30]. For example, the change of predator's $\delta^{15}\text{N}$ values over time could be caused by either dietary change and/or variability of $\delta^{15}\text{N}$ values at lower trophic levels. Therefore, the measurement of baseline or lower trophic prey values is helpful for stable isotope dietary studies [35]. For a time series on isotope values of predators, it is best to conduct a comparison with the baseline over time. In the cases of absence for baseline values, we can study the change of the controlling factors that determine the baseline variability and infer whether or not it has contributed to fluctuations in paleodietary signals of the predators [27, 30].

4 Progress in dietary studies in penguins and seals

4.1 Modern diets of Adélie penguin and Antarctic fur seal

Dietary composition of modern penguins and seals provides a clue to their diets in the past. There have been numerous dietary studies of modern Adélie penguins and Antarctic fur seals in Antarctica and sub-Antarctica (Fig. 1). Adélie penguin diet has been investigated since the early 20th century [36]. Nearly a century of research from analyses of stomach contents and fecal samples of these seabirds indicate that Adélie penguins feed primarily on Antarctic krill (*Euphausia superba*) in the Antarctic Peninsula and Scotia Sea, ice krill (*E. crystallophias*) and Antarctic silverfish (*Pleuragramma antarcticum*) in the Ross Sea, and krill, fish and amphipods in coastal areas of East Antarctica [37] (see Table 2.1 in Ainley [37] and references therein). In addition, Adélie penguins foraging along or beyond the continental shelf break consume more *E. superba*, while penguins in coastal areas prey on a mixture of *E. superba*, *E. crystallophias*, and fish [38]. Stomach content and fecal analyses indicate that Antarctic fur seals primarily rely on Antarctic krill and fish, with a greater proportion of krill in high Antarctic areas and fish

in sub-Antarctica [39]. While Reid et al. [5] concluded that fur seals in Scotia Sea area used to eat a lot more fish before the industrial fishing.

There have been a growing number of stable isotope studies on the diet of modern penguins and seals in Antarctica. Ainley et al. [40] investigated temporal change in the diets of breeding Adélie penguins in the southwestern Ross Sea between 1994–2000 by using stable isotopes and stomach contents, and concluded that ice krill and silverfish are the main prey items of local Adélie penguins. Cheral [41] analyzed the stable carbon and nitrogen isotope values of Adélie penguins and their prey in Adélie Land, East Antarctica. Stable isotope ratios in amino acids and plasma are more accurate indicators for penguin's dietary compositions [42, 43]. By combining the analyses of stomach contents and stable isotopes in tissues, the inter-annual and species-specific differences in penguin diets can be tracked [40, 44]. For Antarctic fur seals in sub-Antarctic Crozet Islands, stable isotope values of their blood indicate that they are fish eater in this region [45].

4.2 Paleodiets of penguins and seals

The available time series of data for dietary research described above are relatively short from a few months to a

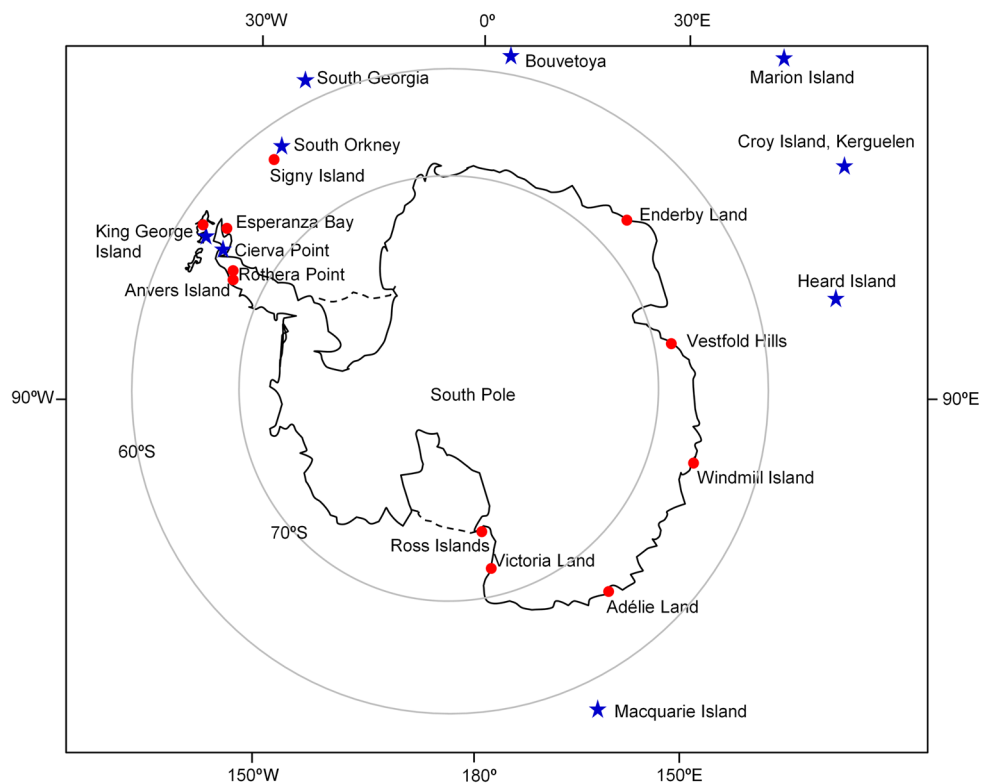


Fig. 1 (Color online) Primary sites of dietary studies on penguins (solid circles) and seals (stars) at islands and coastal areas of Antarctica and sub-Antarctica. Sites of paleodietary studies include King George Island, Anvers Island, Rothera Point, Ross Island, Victoria Land, the Windmill Islands and Vestfold Hills

few years in duration. Thus, the short time scale of these studies and lack of information on foraging habitat in some cases makes it difficult to interpret the data. For example, two studies on the diet of breeding Adélie penguins in the Vestfold Hills show contrasting results [46, 47]. The time series of dietary data collected on modern Adélie penguins is no more than 40 years [37, 40, 48]; therefore, any long-term data from sediments would be important complements to these modern studies.

From identification of prey taxa such as otoliths and squid beaks preserved in the ornithogenic soils, we can infer paleodietary composition and how it may have changed in Adélie penguins in the past. The results from Anvers Island, Antarctic Peninsula, indicate that the diet of Adélie penguins there consisted primarily of squid (*Psychroteuthis glacialis*), Antarctic silverfish (*Pleuragramma antarcticum*), and lanternfish (*Electrona antarctica*) over the past ~500 years, with a higher proportion of squid prior to the Little Ice Age (LIA) and more fish during the LIA though silverfish still are the most important prey [8]. Similar research in northern Marguerite Bay, Antarctic Peninsula, demonstrated that Adélie penguins there primarily preyed on silverfish and squid over the past ~6,000 years, with more silverfish during cold periods and more squid in warm periods [49]. Studies of ornithogenic soils in the Ross Sea region indicated that silverfish was the most abundant prey species of Adélie penguins in the past [50, 51]. In contrast with the results of Antarctic Peninsula, the inferred paleodietary composition of Adélie penguins in Ross Sea area consisted of less silverfish during cold time periods, and *vice versa*. For example, Polito et al. [50] found that silverfish had decreased in the diets of Adélie penguin at Ross Island over the past 600 years, perhaps in response to the onset of the LIA, and the proportion of silverfish in the diets of Adélie penguins in Victoria Land showed a peak from 4,000 to 2,000 years ago [51], a period of a warm climate optimum. These results are in accordance with the dietary change of modern Adélie penguins in the southwestern Ross Sea where they consume less silverfish during cold years with increasing sea ice extent that may block access to the area where the silverfish were prevalent [40, 52]. While due to the latitude gradient, the temperatures associated with “cold” in Marguerite Bay would be “warm” in the Ross Sea. The paleodietary data may also reflect the prey availability to penguins in Ross Sea affected by climate and sea ice. Prey remains recovered from ornithogenic soils in the Windmill Islands, East Antarctica, also indicated that silverfish was an important prey item for Adélie penguins in the past 9,000 years, but a gradual decrease in the remains of this species in increasingly older colonies may be due to the preservational problems [53].

Though ornithogenic soils contain direct prey remains of penguins, the inferred prey data in the past are scattered. In particular, all the prey remains from ornithogenic soils are non-krill components because krill could be easily and fully digested and lacks hard parts that typically preserve in these soils. To our knowledge, there is only one report on the paleodiet of seals [30], likely because old seal colonies and/or haul out sites are not well preserved in contrast to those of Adélie penguins.

Stable isotope analysis of tissues is an excellent tool for examining animal foraging habitats and diets [11, 14, 22]. This method allows assessment of the diets of ancient seabirds through their tissues preserved at specific sites [54]. Plentiful organic remains preserved in ornithogenic soils provide an opportunity to study the paleodiets of penguins by using stable isotope methodology. Emslie and Patterson [55] performed stable carbon and nitrogen isotope analyses on eggshell fragments of modern and ancient Adélie penguins in Antarctica and found an abrupt shift to lower trophic prey (i.e., krill) in penguin diets within the past ~200 years.

In addition to the discontinuous ornithogenic soils, excrement and the included organic remains found in sediments deposited in lakes or ponds near penguin or seal colonies have been used as another important source for studying past changes in these species in Antarctica [56–59]. These sediments and their organic remains are ideal for documenting dietary changes of penguins and seals in the past [27, 30]. Huang et al. [30] studied dietary changes of Antarctic fur seals along the West Antarctic Peninsula during the 20th century by analyzing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of archival hairs in seal excrement sediments. The increasing $\delta^{15}\text{N}$ values of seal hairs in the past century indicated a declining proportion of krill in their diets in agreement with the observed decreasing krill populations for the past 30 years. On a longer time scale, the diets of Adélie penguins in the Vestfold Hills varied significantly during the past 8,000 years, as indicated by stable nitrogen isotope values of bones and feathers handpicked from ornithogenic sediments [27]. The depleted stable nitrogen isotope ratios of Adélie penguins during 8,500–7,600 a BP (before present) and 6,300–5,700 a BP indicated more krill in the penguin's diets, while the enriched ratios during 7,500–6,300 a BP and 4,800–2,200 a BP showed that penguins consumed higher trophic prey, primarily fish [27].

4.3 Paleodietary fluctuations in penguins and seals in association with climate change and sea ice extent

As one of the most spectacular seasonal changes on earth, the annual formation and retreat of Antarctic sea ice is an important driver of climate, the marine physical

environment and its ecological dynamics; sea ice is also impacted by both long-term climate change and short-term fluctuations in the marine environment (i.e., El Niño Southern Oscillation events) [2, 60–62]. Antarctic krill is a cold-water planktonic species and it is very sensitive to climate change. The Antarctic krill-centered food web and thus the marine ecosystem also are sensitive to the changes of Antarctic sea ice extent. It is reported that both krill recruitment and its abundance are positively correlated with sea ice conditions in the preceding winter, with good recruitment and high abundance in extensive sea-ice years and poor recruitment and low density with reduced regional sea-ice formation [63, 64] (Fig. 2). Krill abundance also has been linked with sea temperature and the latitudinal extent of cool water [65]. Antarctic krill density, from scientific net sampling, has declined since the 1970s in the southwest Atlantic sector [64], accompanied by regional increasing sea surface temperature [66] and declining sea ice extent [67] during the same period. Winter sea ice cover is also a critical habitat for the spawning of silverfish [68] that is another important prey for penguins and seals.

As a keystone species of Southern Ocean food webs, krill forms an important linkage between the physical marine environment and its top predators. Sea ice affects penguin and seal foraging behavior through its influence on krill availability and abundance. Studies in the southwestern Ross Sea showed that sea ice extent and presence of baleen whales affected prey availability to Adélie penguins and thus their diets [40, 52, 69]. Dietary compositions of Adélie penguins and Antarctic fur seals could be an indicator of krill availability and abundance in foraging areas [70]. The long-term time series of data from archived seal hairs at Fildes Peninsula, King George Island, showed decreasing $\delta^{15}\text{N}$ values in Antarctic fur seals over the past century. This trend suggests a declining proportion of krill in their diet and thus a decrease in relative krill abundance [30]. By comparing the regional sea surface temperature and sea ice extent in the past century (Fig. 3a), Huang et al. [30] proposed that the change of $\delta^{15}\text{N}$ values in seals at Fildes Peninsula is likely due to the regional warming of the ocean with a concomitant decline in sea ice. The dietary change, reconstructed from nitrogen isotopes, in Adélie penguins in the Vestfold Hills showed strong correspondence with episodes of regional climate and sea ice changes over the past ~ 8000 years (Fig. 3b): depleted $\delta^{15}\text{N}$ ratios were recorded in penguin tissues dating to cold intervals with extensive sea ice, while enriched $\delta^{15}\text{N}$ ratios were in tissues dating to warm periods [27].

As discussed above, dietary changes in Adélie penguins and Antarctic fur seals are tightly linked with climate and sea ice extent, and thus the paleodietary changes in penguins and seals reflect sea ice conditions in the past, especially when comparing distinctly different climatic

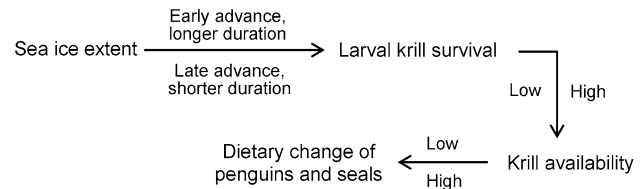


Fig. 2 Sketch-process chart of Sea ice extent that affects krill population dynamics [63] and thus the dietary change of penguins and seals

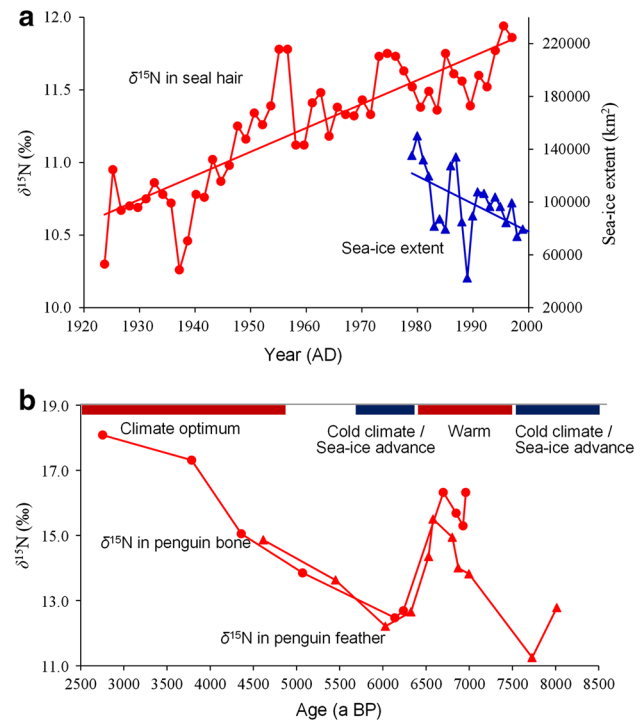


Fig. 3 Paleodietary change of Antarctic penguins and seals and their relationship with climate change and sea ice extent (redraw according to references [27, 30]). **a** ~80-year record of $\delta^{15}\text{N}$ values of Antarctic fur seal hair (solid circle) in the Fildes Peninsula [30] and the observed annual average sea ice extent (triangle) for the Palmer region from 1979 to 2004 [67]; **b** an ~8000-year record of $\delta^{15}\text{N}$ values of Adélie penguin bone (solid circle) and feather (triangle) in Vestfold Hills [27] with reconstructed changes of climate and sea ice extent [71]

periods. There is a debate about the sea ice conditions around the Scott Coast, Victoria Land, between 2,000–1,100 a BP. Studies [72, 73] by Emslie and his co-workers found that after the penguin optimum between 4,000–2,000 a BP, this coastline was abandoned by breeding Adélie penguins and remains unoccupied today, probably due to extensive sea-ice coverage that blocked access to the ice-free coastline beginning at 2,000 a BP and persists to this day. Hall et al. [74], however, argue that a warm period occurred at ~2,300–1,100 a BP as evidenced

by abundant elephant seal remains (hair, bone) found in sediments along the Victoria Land Coast. They proposed that this “seal optimum” was due to warming that reduced coastal sea ice and allowed more seals to haul out and breed, and that sea-ice reduction was unfavorable for Adélie penguin populations. However, penguins respond quickly to changing sea ice conditions in the Ross Sea today, occupying coastline formerly blocked by ice [37], and appear to have done so in the past as well (i.e., the penguin “optimum” at 4,000–2,000 a BP on the Scott Coast). If this coast had been accessible to seals (and thus penguins) until 1,100 a BP, as proposed by Hall et al. [74], then penguin occupation should have persisted until that time, but it ended by 2,000 a BP when all colonies were abandoned. Moreover, no *bona fide* evidence of past seal breeding has been recovered (i.e., bones of pups) and the hairs and adult bones that have been found could have resulted from animals occasionally visiting this region on annual molt migrations. Investigation of paleodietary changes in penguins during this period could provide further evidence for climate and sea ice conditions at that time.

4.4 Historic human impacts on Southern Ocean ecosystems reflected in penguin paleodietary records

Historic human exploitation in Antarctica has modified the Southern Ocean ecosystems significantly [4, 75]. For example at South George Island and the South Shetland

Islands, Antarctic fur seals were hunted to near extinction from the late 18th to early 20th centuries [76, 77]. With the ban of hunting in the Southern Ocean in the 1960s, Antarctic fur seal populations recovered rapidly throughout this region in the past several decades [56, 78–80]. In the 20th century, whaling increased significantly in the Southern Ocean and 90 %–95 % of baleen whale (*Mysticeti*) populations were killed by mid-century [81]. During the late 1970s to early 1980s, hundreds of thousands of tonnes of krill-dependant finfish were depleted from many parts of the Southern Ocean, especially Scotia Sea by intensive industrial fishing [82, 83]. The severe depletion of these krill-eating predators was believed to have resulted in a large amount of unconsumed krill, thus forming the basis for the “krill surplus hypothesis” (KSH) in Southern Ocean ecosystems [4, 84]. If true, it should be recorded in the paleodietary changes of Adélie penguins.

Emslie and Patterson [55] provided the first direct evidence in support of the KSH with stable carbon and nitrogen isotope analyses of Adélie penguin eggshell fragments from modern and ancient colonies. Their results showed an abrupt shift in penguin diet within the past ~200 years to lower trophic krill [55] (Fig. 4), in accordance with the human removal of krill-eating seals, whales and fish in the Southern Ocean. Further stable isotope analysis on modern and ancient Gentoo penguin eggshells from the Antarctic Peninsula indicated additional, but weak support for the KSH, though this species feeds proportionally more on fish today and probably did so in the past [31]. Additional evidence for KSH has been reported by

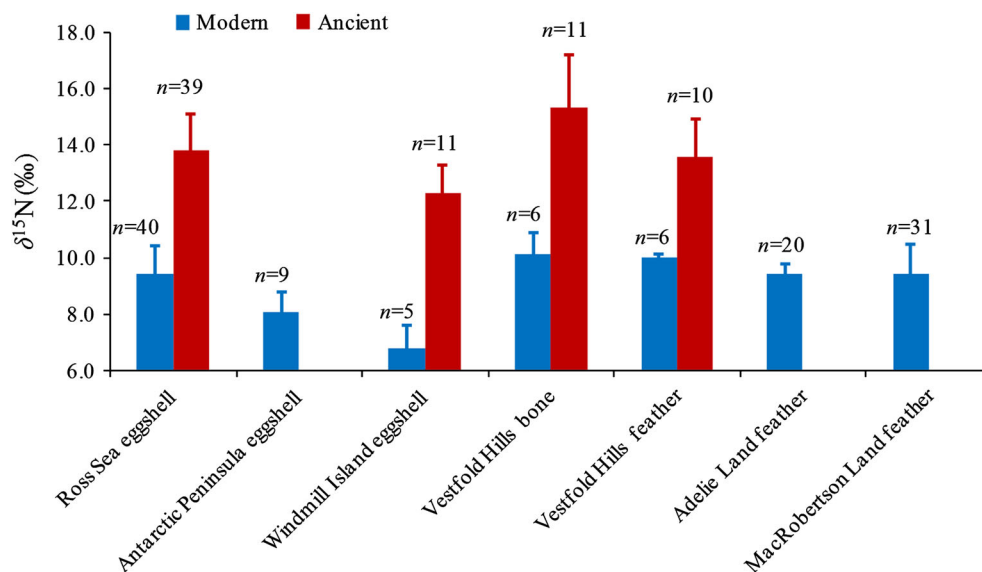


Fig. 4 $\delta^{15}\text{N}$ values (mean \pm std) of modern and ancient (older than 500 years) Adélie penguins in Antarctica. These data compiled by Emslie and Patterson [55] for the Ross Sea, Windmill Islands, and Antarctic Peninsula, Huang et al. [27] for Vestfold Hills, Jaeger et al. [85] for Adélie Land and Tierney et al. [86] for MacRobertson Land

Huang et al. [27] in $\delta^{15}\text{N}$ in modern to 8,000-year-old Adélie penguin bones and feathers extracted from ornithogenic sediments at the Vestfold Hills. They also documented an abrupt shift in penguin $\delta^{15}\text{N}$ values between modern and ancient samples (Fig. 4), with more depleted $\delta^{15}\text{N}$ ratios in modern penguin samples, indicating a greater proportion of krill in their diet. Exactly when the KSH impacted penguin diets in the different regions and how it varied for specific species, additional investigations are required. In addition, Ainley et al. [87] showed that the methanesulfonic acid (MSA) signature in ice cores also changed in accord with the KSH.

5 Conclusions

We have reviewed the evidence that the diet of penguins and seals is tightly linked with their foraging habits, climate change, sea ice extent and prey depletion. Stable isotope analyses provide an excellent complement to traditional approaches for dietary studies (i.e., stomach lavage), and this method has developed rapidly for both dietary and paleodietary reconstructions in marine species. However, the issues of sample preservation, baseline trophic measurements and differences in isotopic fractionation among tissues should be considered carefully in stable isotopic analyses. As the methods continue to improve, stable isotope analysis could become an even more powerful tool for tracing paleodietary changes of Antarctic animals and their responses to natural climate, sea ice extent and human activities. The KSH has been supported with paleodietary changes in penguins; additional studies in other locations are needed, especially for documenting variation in the timing and extent of the krill surplus in different regions of the Southern Ocean.

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References

- Furness RW, Camphuysen CJ (1997) Seabirds as monitors of the marine environment. *ICES J Mar Sci* 54:726–737
- Nicol S, Worby A, Leaper R (2008) Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. *Mar Freshwater Res* 59:361–382
- Reid K, Croxall JP (2001) Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proc R Soc B* 268:377–384
- Laws RM (1977) Seals and whales of the Southern Ocean. *Phil Trans R Soc B* 279:81–96
- Reid K, Davis D, Staniland IJ (2006) Spatial and temporal variability in the fish diet of Antarctic fur seal (*Arctocephalus gazella*) in the Atlantic sector of the Southern Ocean. *Can J Zool* 84:1025–1037
- Wilson RP (1984) An improved stomach pump for penguins and other seabirds. *J Field Ornithol* 55:109–112
- Reid K (1995) The diet of Antarctic fur seals (*Arctocephalus gazella* Peters 1875) during winter at South Georgia. *Antarct Sci* 7:241–249
- Emslie SD, Fraser W, Smith RC et al (1998) Abandoned penguin colonies and environmental change in the Palmer Station area, Anvers Island, Antarctic Peninsula. *Antarct Sci* 10:257–268
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786–798
- Iverson SJ, Arnould JPY, Boyd IL (1997) Milk fatty acid signatures indicate both major and minor shifts in the diet of lactating Antarctic fur seals. *Can J Zool* 75:188–197
- Deagle BE, Chiaradia A, McInnes J et al (2010) Pyrosequencing faecal DNA to determine diet of little penguins: is what goes in what comes out? *Conserv Genet* 11:2039–2048
- Bearhop S, Furness RW, Hilton GM et al (2003) A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. *Funct Ecol* 17:270–275
- Sun LG, Emslie SD, Huang T et al (2013) Vertebrate records in polar sediments: biological responses to past climate change and human activities. *Earth Sci Rev* 126:147–155
- Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar Ecol Progr Ser* 329:281–287
- Ambrose SH (1986) Stable carbon and nitrogen isotope analysis of human and animal diet in Africa. *J Hum Evol* 15:707–731
- Hu YW, Shang H, Tong HW et al (2009) Stable isotope dietary analysis of the Tianyuan 1 early modern human. *Proc Natl Acad Sci USA* 106:10971–10974
- Si Y, Lü EG, Li X et al (2013) Exploration of human diets and populations from the Yanghai Tombs, Xinjiang. *Chin Sci Bull (Chinese Ver)* 58:1422–1429 (in Chinese)
- Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnol Oceanogr* 33:1182–1190
- Cai DL, Li HY, Tang QS et al (2005) The foundation of successive trophic chart for food webs in the ecosystem of the Yellow and East China Seas: the result from carbon and nitrogen stable isotope techniques. *Sci China Ser C Life Sci* 35:123–130
- Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. *Mar Mammal Sci* 26:509–572
- Ramos R, Gonzalez-Solis J (2012) Trace me if you can: the use of intrinsic biogeochemical markers in marine top predators. *Front Ecol Environ* 10:258–266
- Mizutani H, Kabaya Y, Wada E (1985) Ammonia volatilization and penguin rookery high $^{15}\text{N}/^{14}\text{N}$ ratio in Antarctica. *Geochem J* 19:323–327
- Mizutani H, Hasegawa H, Wada E (1986) High nitrogen isotope ratio for soils of seabird rookeries. *Biogeochemistry* 2:221–247
- Lorenzini S, Baroni C, Fallick AE et al (2010) Stable isotopes reveal Holocene changes in the diet of Adélie penguins in Northern Victoria Land (Ross Sea, Antarctica). *Oecologia* 164:911–919

27. Huang T, Sun LG, Long NY et al (2013) Penguin tissue as a proxy for relative krill abundance in East Antarctica during the Holocene. *Sci Rep* 3:2807
28. Huang T, Sun LG, Wang YH et al (2014) Transport of nutrients and contaminants from ocean to island by emperor penguins from Amanda Bay, East Antarctic. *Sci Total Environ* 468–469:578–583
29. Liu XD, Sun LG, Yin XB et al (2004) Paleocological implications of the nitrogen isotope signatures in the sediments amended by Antarctic seal excrements. *Prog Nat Sci* 14:786–792
30. Huang T, Sun LG, Stark J et al (2011) Relative changes in krill abundance inferred from Antarctic Fur Seal. *PLoS One* 6:e27331
31. Emslie SD, Polito MJ, Patterson WP (2013) Stable isotope analysis of ancient and modern gentoo penguin egg membrane and the krill surplus hypothesis in Antarctica. *Antarct Sci* 25:213–218
32. Cavallerano EJ (2005) Temporal diagenetic alternations in Adélie penguin eggshells throughout the late Holocene of Antarctica. M.Sc. Thesis, University of North Carolina Wilmington
33. DeNiro MJ (1985) Post-mortem preservation and alternation of *in vivo* bone collagen isotope ratios in relation to palaeodietary reconstruction. *Nature* 317:806–809
34. Price TD, Blitz J, Burton JH (1992) Diagenesis in prehistoric bone: problems and solutions. *J Archaeol Sci* 19:513–530
35. Polito MJ, Reiss CS, Trivelpiece WZ et al (2013) Stable isotopes identify an ontogenetic niche expansion in Antarctic krill (*Euphausia superba*) from the South Shetland Islands, Antarctica. *Mar Biol* 160:1311–1323
36. Wilson EA (1907) Aves in British National Antarctic Expedition Report 1901–1904. *Nat Hist* 2:1–121
37. Ainley DG (2002) The Adélie penguin: bellwether of climate change. Columbia University Press, New York
38. Endo Y, Asari H, Watanuki Y et al (2002) Biological characteristics of euphausiids preyed upon by Adélie penguins in relation to sea-ice conditions in Lützow-Holm Bay, Antarctica. *Polar Biol* 25:730–738
39. Casaux R, Baroni A, Carlini A (1998) The diet of the Antarctic fur seal *Arctocephalus gazella* at Harmony Point, Nelson Island, South Shetland Islands. *Polar Biol* 20:424–428
40. Ainley DG, Ballard G, Barton KJ et al (2003) Spatial and temporal variation of diet within a presumed metapopulation of Adélie Penguins. *Condor* 105:95–106
41. Chérel Y (2008) Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica. *Mar Biol* 154:813–821
42. Lorrain A, Graham B, Menard F et al (2009) Nitrogen and carbon isotope values of individual amino acids: a tool to study foraging ecology of penguins in the Southern Ocean. *Mar Ecol Prog Ser* 391:293–306
43. Beaulieu M, Ropert-Coudert Y, Le Maho Y et al (2010) Foraging in an oxidative environment: relationship between delta C-13 values and oxidative status in Adélie penguins. *Proc R Soc B* 277:1087–1092
44. Polito MJ, Trivelpiece WZ, Karnovsky NJ et al (2011) Integrating stomach content and stable isotope analyses to quantify the diets of pygoscelid penguins. *PLoS One* 6:e26642
45. Chérel Y, Hobson KA, Guinet C et al (2007) Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *J Anim Ecol* 76:826–836
46. Green K, Johnstone G (1988) Changes in the diet of Adélie penguins breeding in East Antarctica. *Aust Wildlife Res* 15:103–110
47. Puddicombe RA, Johnstone GW (1988) The breeding season diet of Adélie penguins at the Vestfold Hills, East Antarctica. *Hydrobiologia* 165:239–253
48. Fraser WR, Hofmann EE (2003) A predator's perspective on causal links between climate change, physical forcing and ecosystem. *Mar Ecol Prog Ser* 265:1–15
49. Emslie SD, McDaniel JD (2002) Adélie penguin diet and climate change during the middle to late Holocene in northern Marguerite Bay, Antarctic Peninsula. *Polar Biol* 25:222–229
50. Polito M, Emslie SD, Walker W (2002) A 1000-year record of Adélie penguin diets in the southern Ross Sea. *Antarct Sci* 14:327–332
51. Lorenzini S, Olmastroni S, Pezzo F et al (2009) Holocene Adélie penguin diet in Victoria Land, Antarctica. *Polar Biol* 32:1077–1086
52. Ainley DG, Wilson PR, Barton KJ et al (1998) Diet and foraging effort of Adélie penguins in relation to pack-ice conditions in the southern Ross Sea. *Polar Biol* 20:311–319
53. Emslie SD, Woehler EJ (2005) A 9000-year record of Adélie penguin occupation and diet in the Windmill Islands, East Antarctica. *Antarct Sci* 17:57–66
54. Ainley DG, Hobson KA, Crosta X et al (2006) Holocene variation in the Antarctic coastal food web: linking delta D and delta C-13 in snow petrel diet and marine sediments. *Mar Ecol Prog Ser* 306:31–40
55. Emslie SD, Patterson WP (2007) Abrupt recent shift in delta C-13 and delta N-15 values in Adélie penguin eggshell in Antarctica. *Proc Natl Acad Sci USA* 104:11666–11669
56. Hodgson DA, Johnston NM (1997) Inferring seal populations from lake sediments. *Nature* 387:30–31
57. Sun LG, Xie ZQ, Zhao JL (2000) Palaeoecology—a 3,000-year record of penguin populations. *Nature* 407:858
58. Sun LG, Liu XD, Yin XB et al (2004) A 1500-year record of Antarctic seal populations in response to climate change. *Polar Biol* 27:495–501
59. Liu XD, Nie YG, Sun LG et al (2013) Eco-environmental implications of elemental and carbon isotope distributions in ornithogenic sediments from the Ross Sea region Antarctica. *Geochim Cosmochim Acta* 117:99–114
60. Arrigo KR, Worthen D, Schnell A et al (1998) Primary production in Southern Ocean waters. *J Geophys Res* 103:15587–15600
61. Parkinson CL (2004) Southern Ocean sea ice and its wider linkages: insights revealed from models and observations. *Antarct Sci* 16:387–400
62. Arrigo KR (2013) Sea ice ecosystems. *Annu Rev Mar Sci* 6:13.1–13.29
63. Loeb V, Siegel V, HolmHansen O et al (1997) Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387:897–900
64. Atkinson A, Siegel V, Pakhomov E et al (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–103
65. Nicol S, Pauly T, Bindoff NL et al (2000) Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. *Nature* 406:504–507
66. Gille ST (2002) Warming of the Southern Ocean since the 1950s. *Science* 295:1275–1277
67. Ducklow HW, Baker K, Martinson DG et al (2007) Marine pelagic ecosystems: the West Antarctic Peninsula. *Phil Trans R Soc B* 362:67–94
68. Schofield O, Ducklow HW, Martinson DG et al (2010) How do polar marine ecosystems respond to rapid climate change? *Science* 328:1520–1523
69. Ainley DG, Ballard G, Dugger KM (2006) Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea, Antarctica. *Ecology* 87:2080–2093
70. Agnew DJ (1997) Review—the CCAMLR Ecosystem Monitoring Programme. *Antarct Sci* 9:235–242
71. Denis D, Crosta X, Schmidt S et al (2009) Holocene productivity changes off Adélie Land (East Antarctica). *Paleoceanography* 24:PA3207

72. Emslie SD, Berkman PA, Ainley DG et al (2003) Late-Holocene initiation of ice-free ecosystems in the southern Ross Sea, Antarctica. *Mar Ecol Progr Ser* 262:19–25
73. Emslie SD, Coats L, Licht K (2007) A 45,000 yr record of Adélie penguins and climate change in the Ross Sea, Antarctica. *Geology* 35:61–64
74. Hall BL, Hoelzel AR, Baroni C et al (2006) Holocene elephant seal distribution implies warmer-than-present climate in the Ross Sea. *Proc Natl Acad Sci USA* 103:10213–10217
75. Everson E (2000) Krill: biology, ecology and fisheries. Blackwell Science, London
76. Smith RIL, Simpson HW (1987) Early nineteenth century sealers' refuges on Livingston Island, South Shetland Islands. *Br Antarct Surv Bull* 74:49–72
77. Boyd IL (1993) Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarct Sci* 5:17–24
78. Jabour J (2008) Successful conservation-then what? The de-listing of *Arctocephalus* fur seal species in Antarctica. *J Int Wildl Law Pol* 11:1–29
79. Yang QC, Sun LG, Kong DM et al (2010) Variation of Antarctic seal population in response to human activities in 20th century. *Chin Sci Bull* 55:1084–1087
80. Huang J, Sun L, Wang X et al (2011) Ecosystem evolution of seal colony and the influencing factors in the 20th century on Fildes Peninsula, West Antarctica. *J Environ Sci* 23:1431–1436
81. Croxall JP, Callaghan T, Cervellati R et al (1992) Southern Ocean environmental changes: effects on seabird, seal and whale populations. *Phil Trans R Soc B* 338:319–328
82. Ainley DG, Blight LK (2009) Ecological repercussions of historical fish extraction from the Southern Ocean. *Fish Fish* 10:13–38
83. Marschoff ER, Barrera-Oro ER, Alescio NS et al (2012) Slow recovery of previously depleted demersal fish at the South Shetland Islands, 1983–2010. *Fish Res* 125:206–213
84. Sladen WJL (1964) The distribution of the Adélie and chinstrap penguins. *Biologie Antarctique*. Hermann, Paris, pp 359–365
85. Jaeger A, Cherel Y (2011) Isotopic investigation of contemporary and historic changes in penguin trophic niches and carrying capacity of the Southern Indian Ocean. *PLoS One* 6:e16484
86. Tierney M, Emmerson L, Hindell M (2009) Temporal variation in Adélie penguin diet at Bechervaise Island, east Antarctica and its relationship to reproductive performance. *Mar Biol* 156:1633–1645
87. Ainley D, Ballard G, Blight LK et al (2010) Impacts of cetaceans on the structure of Southern Ocean food webs. *Mar Mamm Sci* 26:482–498