Adélie penguins colonization history and paleodiet trends document Holocene environmental changes in Victoria Land (Antarctica)

C. Baroni,[1] S. Lorenzini,[1] M. C. Salvatore,[2] and S. Olmastroni[3]

[1]Dipartimento di Scienze della Terra, Università di Pisa, Via S. Maria 53, 56126 Pisa, ITALY (baroni@dst.unipi.it, lorenzini@dst.unipi.it)
[2]Dip. Scienze della Terra, Università di Roma "La Sapienza", P.le A. Moro, 5, 00185 Roma, ITALY (mariacristina.salvatore@uniroma1.it)
[3]Dipartimento di Scienze Ambientali "G. Sarfatti", Università di Siena, Via P. A. Mattioli 4, 53100 Siena, ITALY (olmastroni@unisi.it)

Summary The identification of several abandoned penguin colonies on Victoria Land coastal areas and more than 200 radiocarbon dates provide a ≈7200-yr spanning Adélie penguin history (> 8000 yr BP considering calibrated dates). These data also supply information about Holocene environmental changes, especially regarding sea-ice extension. Between 5000 and 2500 years BP, Adélie Penguin colonies were more numerous than at present and those presently occupied were more extended (*penguin optimum*). Between 2300 and 1100 penguin population dramatically decreased in southern Scott Coast and in Terra Nova Bay; sea-ice extension and persistence were reduced due to warmer-than present condition in the Ross Sea. Paleodietary studies also contribute to better define the Holocene environmental picture. Due to ecological competition, variation of fish exploitation respect to krill in Adélie penguin diet seems to reflect sea-ice extension and persistence.

Citation: Baroni, C., S. Lorenzini, M. C. Salvatore, and S. Olmastroni (2007), Adélie Penguins colonization history and paleodiet trends document Holocene environmental changes in Victoria Land (Antarctica), in Antarctica: A Keystone in a Changing World – Online Proceedings of the 10th ISAES X, edited by A. K. Cooper and C. R. Raymond et al., USGS Open-File Report 2007-1047, Extended Abstract 108, 4 p.

Introduction

Never inhabited by humans before a hundred years ago, Antarctica can be regarded as the continent of penguin settling. Apart from Emperors and other few exceptions, penguins breed on ice-free areas around Antarctica. With an estimated population of more than 5 million individuals, Adélie penguins (*Pygoscelis adeliae*) are the most widely distributed penguin species on the Antarctic continent (Ainley, 2002). They are considered the most resistant to extreme conditions and occupy the southernmost colony in the world, at Cape Royds in the Ross Sea (77° 30' S). Furthermore, due to their well-known strong environmental sensitivity, they currently represent one of the best-studied species, with particular regard to the comprehension of current global changes (Forcada et al., 2006; Ainley et al, 2005; Croxall et al., 2002). The main ecological factors that regulate and also limit the distribution of Adélie penguins around Antarctica are: 1) ice-free coastal terrains, 2) sea ice extension & persistence, 3) open water close to the colony for access to the sea, 4) availability of food (krill, small fishes and squids), 5) relative absence of predators. Although Adélie Penguins show strong natal return, local and global environmental changes force them to migrate elsewhere (and eventually to abandon their colony) as demonstrated by DNA analysis (Shepherd et al., 2005).

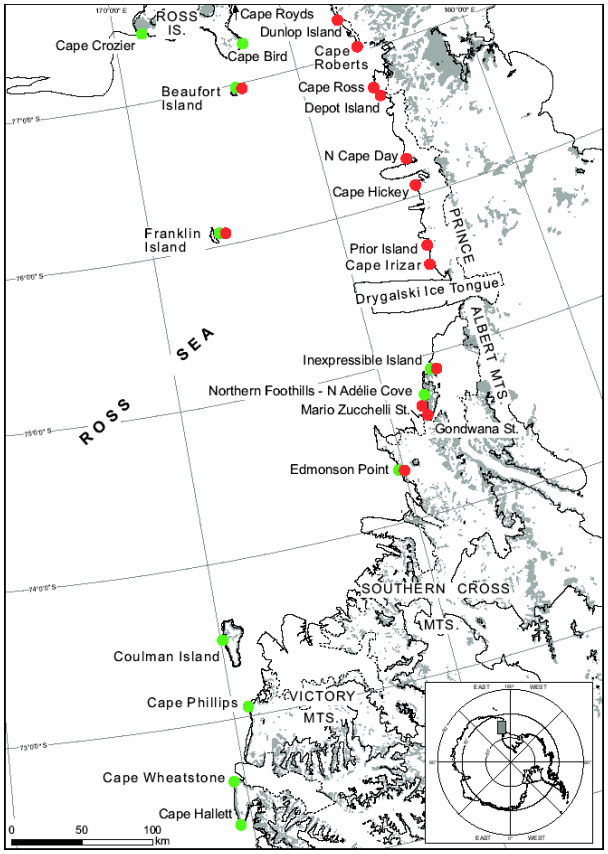

Figure 1. Distribution of present (green circles) and abandoned (red circles) Adélie penguin colonies along the Victoria Land coast.

More than 30% of the world Adélie penguin population occurs on Victoria Land (VL) coastal areas at the western margin of the Ross Sea, one of the southernmost marine ecosystem on Earth (Ainley, 2002) (Fig. 1). Present penguin colonies rest on Holocene raised beaches and marine terraces but they also expand on debris cones and slopes, piedmont rock glaciers, ice-cored and depositional moraines. In places, penguins can climb to nest on surrounding rocky hills up to some hundreds meters above the sea level, from several hundreds meters to some kilometers inland. The colony extension varies as a function of penguin population. Every year, penguin parents arrange pebbles selected with their beak to build the nest. Several hundreds to some hundred thousands of pebbly patches

cover the colonized areas. In a long-term occupied colony, penguin guano is seeped through the permeable pebbly nests and accumulates at their base and in the vicinity to form ornithogenic soils. The older the colony the thicker the accumulation of pebbles and guano is (Ugolini, 1972). Furthermore, the high mortality produces penguin carcasses resting between nests and at the colony margins. A single enduring occupation of a colony drops a thick layer of superposed nests, penguin remains, and guano.

Abandoned penguin nesting sites occur in the vicinity or on the outskirts of several currently occupied colonies, testifying the endurance of favourable conditions for penguin life and settlement and variations in penguin population. Furthermore, abandoned penguin nesting sites found in areas where the Adélies do not nest at present have been recognized as relict colonies (Baroni and Orombelli, 2004). The cold and dry Antarctic environment preserves in ornithogenic soils penguin carcasses and other remains (bone, skin, feathers, guano and eggshells) that supplied the best-preserved ancient DNA yet discovered (Lambert et al., 2002). Moreover, relict colonies and organic soils retain valuable archives of the history of penguin colonization in Antarctica. If we consider Adélie Penguin colonies «bellwether» of recent climate changes (Ainley, 2002), data obtained from relict colonies and abandoned nesting sites in still occupied colonies reflect penguin ecological responses to episodes of past environmental and climatic changes.

The high concentration and the well-preserved organic remains supplied relevant radiocarbon dates for reconstructing the deglaciation phases that followed the Last Glacial Maximum and Holocene environmental changes in VL: almost two hundreds of ^{14}C dates were obtained from penguin guano and bones collected in several relict penguin colonies and abandoned nesting sites along the VL coast. Previous published studies have just reported a series of superimposed dates that document, for this region, a > 7000-yr spanning radiocarbon Adélie penguin history (Baroni, 1994; Baroni and Orombelli, 1994; Baroni and Hall, 2004; Hall et al., 2004; Hall et al., 2006; Emslie et al. 2007). The excellent preservation of prey items remains in ornithogenic soils can also give considerable information on Adélie penguin paleodiet, on their foraging strategies and, consequently, on the paleoecology and paleoclimatology of the Antarctic ecosystem. In the Ross Sea region, krill, fish, and squid are the major components of Adélie penguin diets, mixed in different proportions depending on seasonal availability in relation to climate and marine conditions, especially to sea-ice extension and persistence. Penguins may have altered the relative abundance of prey taxa not only in reacting to climate changes but also as ecological responses to feeding competition with other predators (Ainley et al., 2006). Here we present an updated Adélie Penguin colonization history of the VL coast and new results on paleodiet studies based on the analysis of more than one hundred guano samples (C-14 dated) collected from several abandoned penguin colonies along the VL.

Materials and methods

Aerial photographs analysis, several field surveys, and detailed geomorphologic analysis of key sites have been conducted along the VL coast. The accurate field survey of ice-free areas allowed us to discover tens of relict Adélie penguin colonies from Cape Adare to Ross Island (Baroni, 1994; Baroni and Orombelli, 1991, 1994; Baroni and Hall, 2004; Hall et al., 2004). They are common landscape features along the VL coast. Well-sorted pebbles selected by penguins for building their nests characterize abandoned nesting sites: after the abandonment of nests, pebbles are concentrated at the surface by wind deflation and prevent the erosion of the lower guano. Pebbly patches hide and protect the lower organic soil formed by bird ejecta and remains.

After identifying abandoned colonies, we established test pits (generally 1-2 m^2). Cleaning the entire surface from the top, we excavated layer-by-layer the organic soils and reached the underlying bedrock or undisturbed marine/glacial sediments. The thickness of ornithogenic soils ranges from some centimeters to some decimeters. The areal extension of organic layers is functions of the size, the age of the establishment, and the persistence of the colony. Through the accurate stratigraphic excavation of penguin settlements, we identified multi-occupational phases of the colonies (eventually separated by mineral layers such as sand and gravel of colluvial or periglacial origin, aeolian deposits, etc.). With this approach, we could identify and already separate during field work different individual remains even within the same layer. We could also prevent contamination from the top, mixing between materials from different levels, and enable identification wedges of sediment reworked by periglacial processes (Baroni, 1994). This careful stratigraphic field work allowed sorting of several well-preserved penguin bones and eggshell fragments as well as penguin guano samples at distinct layers. For preventing the complete destruction of the relict colonies, which must be regarded as a unique record of the heritage of penguin settling, we collected soil samples weighting (as a mean) only some hundreds grams. All soil and sediment samples have been washed in laboratory and sieved (mesh sizes ranging from 2 mm to 63 μm). Matrix from each mesh has been dried and subsequently sorted under a low-power (5-10x) stereomicroscope. Organic material preserved in the sediments, including penguin bones, feathers, eggshell fragments but also fish bones (*vertebrae*), scales and otoliths (hard parts of prey remains deposited by penguins during the nesting periods) has been recovered. Picked fish otoliths have been identified using the anatomic-comparative tables, proposed by Williams and McEldowney (1990) for Antarctic fish taxa.

Datable penguin organic remains recovered from ornithogenic soils are used to reconstruct a radiocarbon chronology of penguin occupations. Radiocarbon dates are based on penguin guano, bones, and eggshells (Baroni,

1994; Baroni and Orombelli, 1994; Lambert et al., 2002; Polito et al., 2002; Baroni and Hall, 2004; Hall et al., 2004; Hall et al., 2006; Emslie et al., 2007). Due to the upwelling of old water in the Southern Ocean, these dates must be corrected for a 1300-yr marine-carbon reservoir effects, which is, at present, the best estimate and conventional value used for the Ross Sea region, based on dates of pre-bomb organism of known age (Berkman and Forman, 1996). Although the calibration of the dates would be preferable, this approach allowed us to compare the date coming from penguin remains with sets of dates supplied by other organisms (i.e. elephant seals; Hall et al., 2006) and with other proxy data, such as ice-core data sets (Lorius et al, 1985; Petit et al., 1990).

Results

Considered together with other datable organic materials, penguin remains provided data for reconstructing the retreat of glaciers in coastal areas after the last Glacial Maximum and the Holocene curve of the coastal emersion of VL coast (Baroni and Orombelli, 1991; Baroni and Hall, 2004; Hall et al. 2004). The final unloading of ice from the Terra Nova Bay took place shortly before 7000 ^{14}C yr BP (Baroni and Hall, 2004). Deglaciation and southward retreat of the Ross Sea ice sheet grounding line occurred only ≈600 years earlier at Terra Nova Bay than it did farther south along the Scott Coast where the grounded ice recession occurred about 6600 ^{14}C years BP.

Datable Adélie penguin organic remains also permit the reconstruction of the colonization history of this species. A 7200-yr spanning chronology (> 8000 yr BP considering calibrated dates) documents the duration and continuity of penguin presence in VL as well as Holocene fluctuations in their population (Baroni and Orombelli, 1994; Lambert et al., 2002; Polito et al., 2002).

Food remains recovered from all investigated sites have confirmed that fish, especially Antarctic silverfish, has been an important component in Adélie penguin paleodiet. Fish bones and otoliths are the most diffused (if not exclusive) remains preserved in ornithogenic soils. Any other dietary remains (e.g. cephalopod chitonous beaks) are recovered in guano samples, although Polito et al. (2002) identified several squid beaks in organic sediments at Ross Island. Taxonomic identification of fish otoliths indicate that the non-euphausid prey of penguin consisted primarily of *Pleuragramma antarcticum* Boulenger, 1902 (88% of total number of otoliths) and, in decreasing order of importance, of *Trematomus bernacchii* Boulenger, 1902 (1,1%) and *Trematomus scottii* Boulenger, 1907 (0,13%); a number of otoliths is identified only as *Trematomus* sp. (0.3%) and *Pagothenia* sp. Nichols & Lamonte, 1936 (1.4%) or remain taxonomic unknown.

Several guano samples do not contain prey items remains, probably reflecting a krill-based paleodiet, since krill is not preservable in the soils. The spatial and temporal distribution of these samples has been compared to that of the productive ones for highlighting trends eventually related to episodes of climate change or to other ecological factors. While samples older then 4500 yr BP show a relative equivalent consumption of fish and krill, between ≈4500 and ≈2300 yr BP the penguin exploitation of fish items seems to increase respect to krill (Fig. 2).

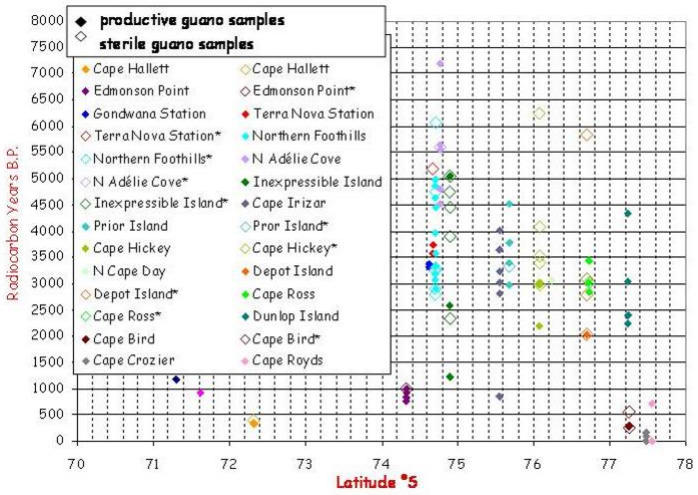

Figure 2. Spatial and temporal distribution of productive and sterile guano samples.

Discussion and conclusion

Although coastal deglaciation was completely accomplished about 7000 yr BP, radiocarbon dates from abandoned penguin colonies scattered on VL coast (from the northernmost site at Cape Adare to the southernmost sites at Ross Island) testify that Adélie penguins occupied colonies in the Terra Nova Bay region since 7200 yr BP (> 8000 yr BP considering calibrated dates): from then on, Adélie penguins colonized several coastal sites in VL (unoccupied during the Last Glacial Maximum).

Geomorphologic and stratigraphic data and ^{14}C dates so far obtained attest that, during the Holocene, penguin population varied according to changing environmental condition. Several colonies have been occupied continuously for a long period of time, indicating local endurance of favourable condition

for penguin breeding. In the Terra Nova Bay area, the still-active colony of Inexpressible Island was continuously occupied since at least 6000 yr BP. Other sites, such as Northern Foothills and Prior Island, recorded millennial continuous penguin occupation, but these sites are not currently colonized. Between ≈4500 and ≈2500 yr BP, a significant spreading of Adélie penguin colonies is documented, as testified by a great amount of radiocarbon dates and relict colonies. This period, indicated as "*penguin optimum*" by Baroni and Orombelli (1994), represents a time of major

diffusion of penguins in the southern VL. During this interval, about fifteen colonies existed from Wood Bay to Cape Ross, where only three still-occupied colonies survive at present. Abrupt environmental changes caused the end of the "*penguin optimum*", inducing a drastic abandonment of several colonies, never reoccupied since that time. In fact, between 2300 and 1100 penguin population dramatically decreased in southern Scott Coast and in Terra Nova Bay. Sea-ice extension and persistence were reduced due to warmer-than present condition in the Ross Sea as documented by the contemporary settling of elephant seals breading sites (Hall et al. 2006). The diffusion of elephant seal colonies in the Ross Embayment indicates sub-Antarctic climatic/environmental condition that persisted in this region up to ca 500 yr ago (Hall et al., 2006).

Radiocarbon dates from relict colonies also support 8000-yr spanning dietary record. Among the identified fish taxa, *Pleuragramma antarcticum* represents the most eaten prey all over the investigated time period. This is in agreement with present-day key-role played by this fish species in Adélie penguin non-krill diet composition. However, our data indicate a statistically significant distribution of silverfish remains in ornithogenic sediments. As suggest by Ainley et al. (1998), a possible explanation for variation in dietary prey remains is that Adélie penguins compensate for low krill and less sea-ice extent years by targeting different prey species, such as *Pleuragramma antarcticum*.

We also exploited radiocarbon chronology for analysing temporal and spatial distribution of productive (containing fish remains) and not-productive (sterile, interpreted as krill prevalent diet composition) guano samples. Superposition of productive and not-productive layers can be interpreted as potential penguin dietary shifts with respect to environmental/climatic changes or to other ecological factors. The first phases of penguin colonization are characterized by equal exploitation of krill and fish. Guano layers dated to the end of the *penguin optimum* show a relative increase of productive samples. This evidence can be interpreted as penguin ecological responses to an increase of fish availability.

Demonstrated potentially interesting for paleoenvironmental studies, further investigation on abandoned penguin colonies can certainly provide new relevant data on Holocene environmental evolution of VL. Coupled with paleodiet analysis, this research can also help to define patterns in penguin dietary shifts and penguins biological response to episodes of climate change or to other ecological limiting factors.

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