CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

LIFE HUNG BY A THREAD: ENDURANCE OF ANTARCTIC FAUNA IN GLACIAL PERIODS

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Abstract. Today, Antarctica exhibits some of the harshest environmental conditions for life on Earth. During the last glacial period, Antarctic terrestrial and marine life was challenged by even more extreme environmental conditions. During the present interglacial period, polar life in the Southern Ocean is sustained mainly by large-scale primary production. We argue that during the last glacial period, faunal populations in the Antarctic were limited to very few areas of local marine productivity (polynyas), because complete, multiannual sea-ice and ice shelf coverage shut down most of the Southern Ocean productivity within today's seasonal sea-ice zone. Both marine sediments containing significant numbers of planktonic and benthic foraminifera and fossil bird stomach oil deposits in the adjacent Antarctic hinterland provide indirect evidence for the existence of polynyas during the last glacial period. We advocate that the existence of productive oases in the form of polynyas during glacial periods was essential for the survival of marine and most higher-trophic terrestrial fauna. Reduced to such refuges, much of today's life in the high Antarctic realm might have hung by a thread during the last glacial period, because limited resources available to the food web restricted the abundance and productivity of both Antarctic terrestrial and marine life.

Key words: Antarctic; climate; ecology; ecosystem evolution; glaciology; physiology; polar.

LIFE IN THE COLD

Life in Earth's largest freezer, Antarctica, is energetically demanding, and sets limits at any hierarchical, organizational, and organismic level, ranging from molecules to everything that an organism does (Clarke 1983, Pörtner 2002). Cold adaptation is the basis of life in the cold, and many taxa with insufficient physiological capability for surviving there are known to have perished in the course of the evolutionary history of Antarctica (Aronson and Blake 2001, Thatje et al. 2005*a*), mainly during the process of Antarctic cooling, with the last major cooling step occurring at about 14 Ma ago (Clarke 1983, 1993, Zachos et al. 2001, Shevenell et al. 2004). Organisms had to evolve very sophisticated life history adaptations to survive the combined physiological and ecological constraints for prevailing in the cold environment. Additionally, they had to cope with the relatively short duration of food

supply during the season of productivity. Photosynthesis-based primary production is the basis for the abundance of most life seen in Antarctica today, but mainly depends on the exposure to sunlight, which is drastically reduced during the winter months. Recently, a chemotrophic ecosystem was discovered on the Antarctic shelf in a former sub-ice shelf setting (Domack et al. 2005), but its wider significance is as yet unclear. Within the seasonally sea-ice covered zone (SIZ) of the Southern Ocean, temporary to almost permanent sea-ice coverage with high interannual variability reduces the short season of photosynthesis-driven primary production (Arrigo et al. 1998). This poses a major challenge to both higher trophic level life that depends on terrestrial habitats, such as birds and seals, and marine animals, to synchronize their life cycles with the period of food availability (Clarke 1988, Jenouvrier et al. 2005*a*, *b*). Under-ice feeding on ice algae during Antarctic winter months is well known from the Antarctic krill (*Euphausia superba*), and primary production occurs both within and at the periphery of sea ice (e.g., Arrigo et al. 1998, Edwards et al. 1998). Nevertheless, the summer break-
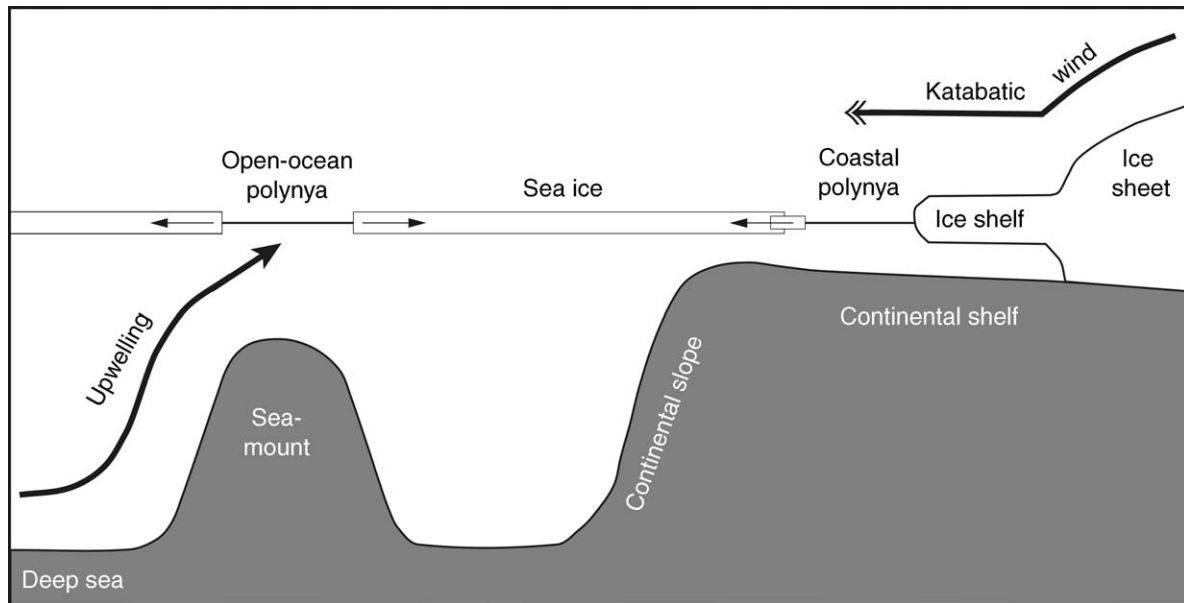
FIG. 1. Schematic illustration of the major mechanisms forming open-ocean and coastal polynyas in the modern Southern Ocean (redrawn after Martin [2001]).

up of the winter sea ice causes a large-scale fertilization event that induces secondary production in the water column, which in turn fosters the pelagic and benthic food web (Brierley and Thomas 2002, Arrigo and van Dijken 2004, Hegseth and Von Quillfeldt 2004). In consequence, most life within the SIZ has become dependent on photosynthesis-driven primary productivity in open ocean conditions, which prevail during the ice-free spring and summer season, and in polynyas. Polynyas are large regions of open water, with length scales on the order of 100 km, that persist with intermittent openings and closings at the same locality for up to several months, and exhibit a high interannual variability in size (Martin 2001). Polynyas, which often appear in spring and precede the break-up of the winter sea-ice cover, locally prolong the period of primary production, and thus raise food availability to higher trophic levels.

MODERN SOUTHERN OCEAN POLYNYAS AND THEIR
SIGNIFICANCE FOR LIFE

Today, the Southern Ocean is characterized by many "coastal polynyas" (here we refer this term to all polynyas on the Antarctic continental shelf) and mainly two "open-ocean polynyas" (here we refer this term to all polynyas offshore from the shelf break) known from the Maud Rise and the Cosmonaut Sea (Comiso and Gordon 1987, Holland 2001, Martin 2001, Zwally et al. 2002, Arrigo and van Dijken 2003) (for locations see Fig. 2). Coastal polynyas are the result of southeasterly and very cold katabatic winds that sweep down the ice sheets, pushing the pack ice away from the coastline or the front of the floating fringes of the ice sheets, such as ice shelves or glacier tongues (Fig. 1; Martin 2001).

Coastal polynyas can only remove relatively small fractions of the pack-ice extent from early spring to late autumn. The oceanward driven sea-ice is then replaced by upwelling water, which immediately freezes when exposed to air with temperatures below the in situ freezing point, before the cycle starts again. Thus, a coastal polynya is typically a location where large amounts of sea ice are generated ("sea-ice factory"). At the sites of recurring coastal polynyas (e.g., in the Bellingshausen, Amundsen, and Ross Seas [Massom et al. 1998, Zwally et al. 2002, Arrigo and van Dijken 2003]), only a thin ice cover, compared to the thicker surrounding pack ice, forms during wintertime, which allows a much earlier spring melt and an earlier start in photosynthetic primary productivity that nourishes the entire food web in the high Antarctic.

Open-ocean polynyas are usually formed by geostrophic upwelling of warm, deep water at seamounts or similar types of submarine elevations (Fig. 1 [Comiso and Gordon 1987, Holland 2001, Martin 2001]) and can constitute areas of high productivity within sea-ice covered regions. A related type of open-ocean polynya results from eddies (i.e., circular currents of sea water moving independently from the direction of the main current), which transport relatively warm water close to the Antarctic continent when they cross the Polar Front (PF) and drift southward into the SIZ (Holland 2001). The life span of such eddies, however, is usually very short due to the low coriolis force at high latitudes, and thus only contributes temporarily and locally to any source of biological productivity.

The numerous polynyas found around Antarctica today are indeed important hot spots of primary productivity that favor the entire marine and higher
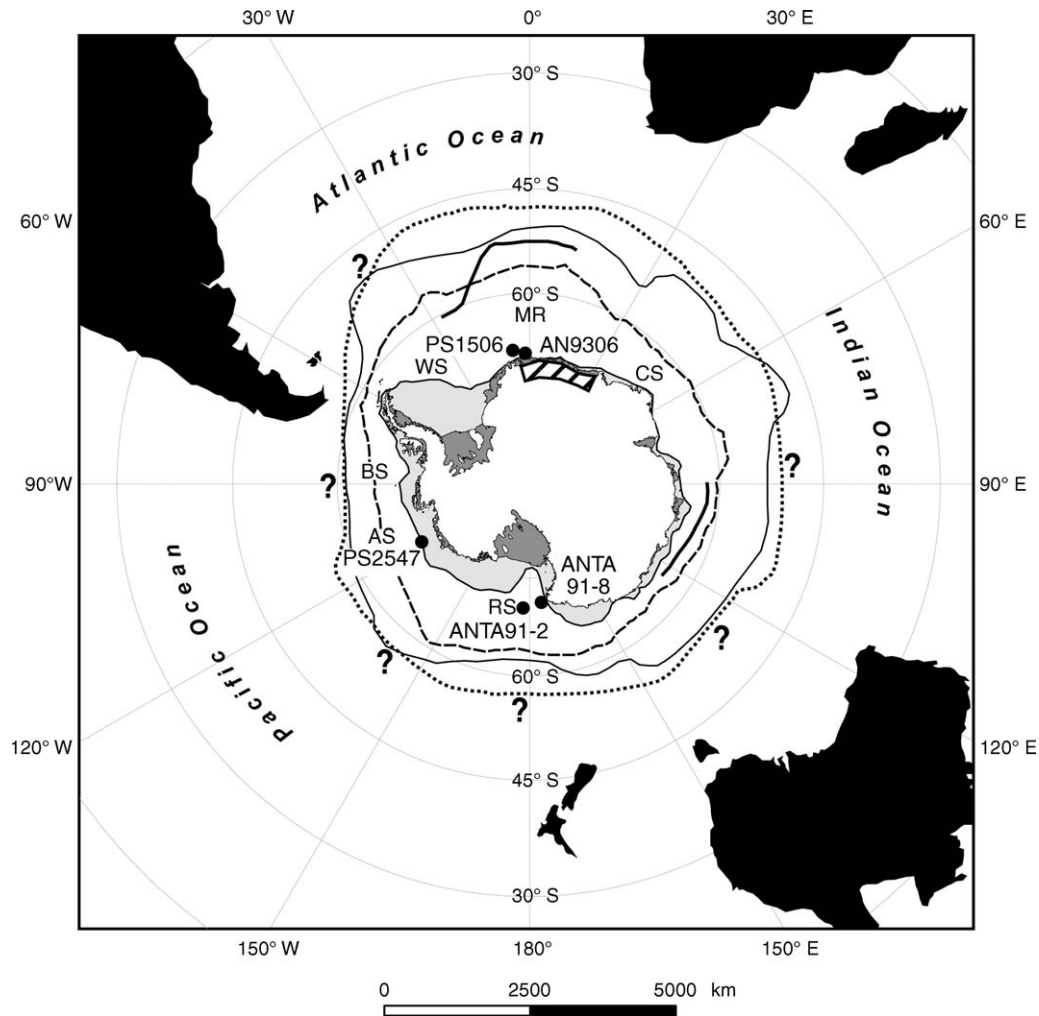
FIG. 2. Map of Antarctica and the surrounding Southern Ocean showing the locations of the modern Polar Front (thin black line), ice shelves (dark-gray shaded), and present summer (light-gray shaded) and winter (dashed line) sea-ice extent (taken from Gersonde et al. 2005). Reconstructed sea-ice extent during LGM (last glacial maximum) summer (bold black line) and LGM winter (dotted line) are also given (after Gersonde et al. 2005). The hatched area depicts Dronning Maud Land, where "mumiyo" was deposited during the last glacial period. Locations of sediment cores mentioned in the text are indicated by black dots (AN9306 indicates core site AN9306-SC1). Sites PS1388 and PS1389 are located very close to site PS1506 (Grobe et al. 1993) and are not shown. Key to abbreviations: MR, Maud Rise; CS, Cosmonaut Sea; RS, Ross Sea; AS, Amundsen Sea; BS, Bellingshausen Sea; WS, Weddell Sea.

terrestrial fauna by extending the period of food availability during short summer seasons (Clarke 1988, Jenouvrier et al. 2005b). Variability of the time of formation and persistence and size of coastal polynyas can frequently explain the high variability in species abundance at higher trophic levels, such as in birds and mammals (Ainley et al. 2005, 2006; see also Olivier et al. 2005).

BENTHIC ORGANISMS AND ENVIRONMENTAL CONDITIONS IN ANTARCTICA DURING THE LAST GLACIAL PERIOD

During the last glacial period (in Antarctica ca. 70 to 10 ka) grounded ice masses occupied most of the Antarctic shelf (e.g., Anderson et al. 2002, Huybrechts 2002, Hodgson et al. 2003), whereas the remaining shelf

was covered with ice shelves (Domack et al. 1998, Shipp et al. 1999) or subject to heavy seafloor disturbance by intense iceberg scouring (Beaman and Harris 2003). In recent years, evidence was published that glaciers did not override some near-coastal terrestrial locations and lakes, mainly in East Antarctica, since ca. 30–40 ka (e.g., Gore et al. 2001, Takada et al. 2003), or even since the last peak warm time at ca. 125 ka (Hodgson et al. 2006). However, even at those locations, long-lived terrestrial snow cover, perennial lake ice, and low relative sea level prevented phototrophic biological activity throughout the last glacial period (Gore et al. 2001, Hodgson et al. 2006). Additionally, permanent and thick multiyear sea-ice coverage (Figs. 2 and 3) led to a shutdown of primary production in much of today's
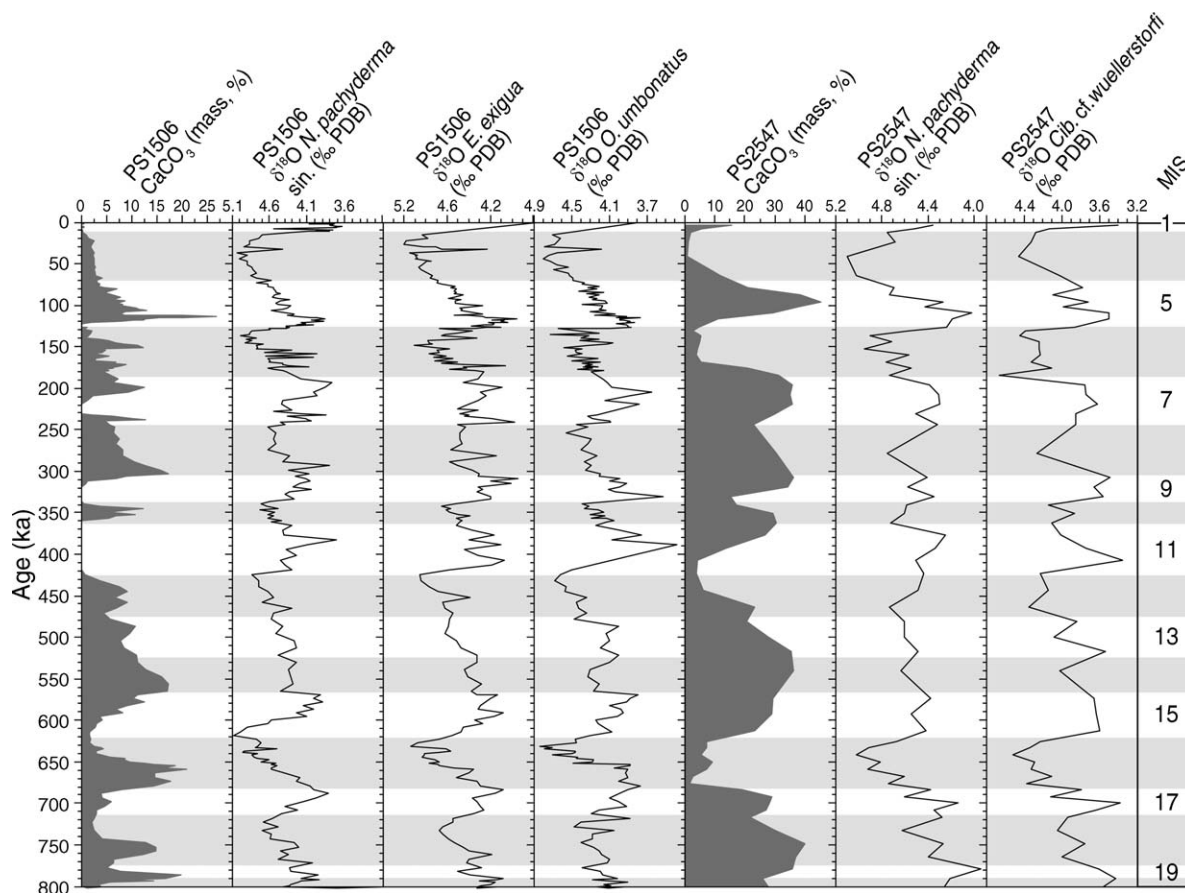
Fig. 3. CaCO$_3$ contents and δ^{18}O ratios (PDB = Pee Dee Belemnite standard) in planktonic (*Neogloboquadrina pachyderma* sinistral) and benthic (*Epistominella exigua*, *Oridorsalis umbonatus*, *Cibicides* cf. *wuellerstorfi*) foraminifera in cores PS1506 (Grobe et al. 1993, Mackensen et al. 1994) and PS2547 from the Amundsen Sea (Hillenbrand 2000, Hillenbrand et al. 2002). Open bars with numbers mark interglacial marine isotope stages (MIS), and gray bars mark glacial MIS (ages of MIS boundaries according to Lisiecki and Raymo [2005]).

SIZ (Hillenbrand and Cortese 2006 and references therein). Benthic fauna observed under the modern McMurdo and Amery ice shelves for a distance of up to 100 km from open water is probably mainly nourished by lateral advection of food particles (Dayton and Oliver 1977, Bruchhausen et al. 1979, Lipss et al. 1979, Riddle et al. 2007). The recorded filter-feeding communities are likely to depend on organic material (plankton) originating from open-marine settings beyond the ice-shelf front (Dayton and Oliver 1977, Riddle et al. 2007). It has also been shown that advection through tide cracks can support substantial under-ice fish populations (Knox et al. 1996).

Today, assemblages of sea-ice algae occur in brine channels of interannual sea ice (e.g., Thomas et al. 1998), which is penetrated by lower spectral sunlight, but biological productivity both within and below sea ice is up to several orders of magnitude lower than at the sea-ice edge or in open-water settings (e.g., Boyd et al. 1995, Savidge et al. 1995, Smith et al. 1996, Arrigo et al. 1998, Edwards et al. 1998). The biological production of sea-ice algae in today's SIZ during glacial periods is probably negligible, because of thicker and compressed multiannual sea ice (e.g., Hillenbrand and Cortese 2006 and references therein) and the likely coverage of the permanent sea ice with snow. Furthermore, without the summer breakup of sea ice, release events of substantial diatom and bacteria biomass into the glacial Southern Ocean were unlikely, although under-ice grazing might have been possible for some taxa. Consequently, both pelagic and benthic marine life had to cope with the shutdown of primary production that must have severely affected the entire marine and terrestrial food web. Furthermore, most of the benthic organisms inhabiting today's Antarctic shelf and slope, and especially sessile filter-feeding communities, were erased when grounded ice masses advanced to the shelf break and the slope was subject to recurrent mass wasting events and turbidity current flows (i.e., sediment-laden currents of water, which move rapidly downslope and often erode the seabed) (Thatje et al. 2005b). Marine and terrestrial geological data (Anderson et al. 2002, Wagner

et al. 2004) and modelling approaches (Huybrechts 2002) indicate a diachronous (i.e., time transgressive) advance and retreat of grounded ice masses around Antarctica and across the shelf during the last glacial period. If the maximum extent of grounded ice happened diachronously as well, this might have led to shallow-water shelters for seafloor communities on the continental shelf. However, most life in such shelters should have starved to death because of the coverage with permanent sea ice or floating ice shelves. Reconstructions of sea-ice limits during the last glacial maximum (LGM, ca. 19.5–16 ka [Gersonde et al. 2005]) suggest that the distance between open water and shelf sites, which may have been covered with floating ice only, exceeded 250 km even during the summer months (Fig. 2). Thus food supply to these sites via lateral advection should have been insignificant. Nevertheless, modern sub-ice shelf habitats, e.g., in the Ross Sea, to some extent might resemble glacial shelter conditions. Today's sub-ice shelf benthic communities are characterized by very low species abundances, e.g., of filter feeders that can live on the finest food particles provided by lateral oceanic advection (Dayton and Oliver 1977). Here, we address the question of how marine benthic animals and secondary consumers that use terrestrial habitats for breeding or mating (such as birds and seals) survived the scarcity of food during the last glacial period.

MARINE GEOLOGICAL INDICATIONS FOR POLYNYAS DURING THE LAST GLACIAL PERIOD

Based on the finding that bottom waters in the world ocean were saltier during the LGM, Paillard and Parrenin (2004) postulated that coastal polynyas were widespread on the Antarctic shelf at the beginning of the last glacial period. According to their hypothesis, intensive sea-ice formation in these polynyas caused brine rejection (i.e., the release of highly saline water caused by sea-ice formation), and these salty water masses filled the deep ocean basins, leading to stratification and thus locking up CO_2 in the deep oceans. The authors suggested that sea-ice formation in polynyas was drastically reduced when grounded ice masses covered the Antarctic shelf completely at the end of the glacial period, which resulted in weakening of the stratification in the global deep oceans and in CO_2-release into the shallow oceans and subsequently into the atmosphere, triggering global deglaciation. This hypothesis, however, is in conflict with the observations of a diachronous advance and retreat of grounded ice masses across the shelf around Antarctica during the last glacial period (references in Thatje et al. 2005b). Mackensen et al. (1996) pointed out that disregarding the overall change in the formation of Antarctic bottom-water (AABW) during the last glacial period (increase, decrease, or no change in AABW production compared to the present interglacial situation), the contribution of saline water formed in polynyas was of the same

magnitude as at present or even larger. Brine rejection probably took place within the glacial-age SIZ (Mackensen et al. 2001). These conclusions, however, are only indirect measures for the existence of polynyas during the last glacial period.

Sea-ice diatom data for the LGM are not available for the whole circum-Antarctic region because of the problem of opal dissolution and terrigenous dilution close to the Antarctic continent (Fig. 2; Gersonde et al. 2005). Two sediment cores (ANTA91-2 and ANTA91-8) recovered from the continental rise in the western Ross Sea off Cape Adare (Fig. 2) bear an interval enriched in planktonic and benthic foraminifera, which was deposited during the LGM as indicated by radiocarbon dating (Brambati et al. 2002). The high biogenic content in this interval suggests significant biological productivity in the surface waters of the western Ross Sea during the LGM. However, an alternative chronology for one of the cores (ANTA91-8), which was inferred from thorium radioisotope ($^{230}Th_{ex}$) measurements, indicates that the foraminifera-bearing interval may span not only the LGM, but also the previous relatively cool interglacial period (Marine Isotope Stage 3, ca. 57–39 ka) (Ceccaroni et al. 1998). Moreover, proxies for biological productivity (accumulation rates of biogenic opal, organic carbon, biogenic barium) analyzed on the foraminifera-bearing interval show that during the corresponding time period export production was almost negligible (Ceccaroni et al. 1998). Even if there was significant biological production in the western Ross Sea during the LGM, the necessary open-ocean conditions might have been a consequence of a relatively southern limit of the LGM summer sea-ice coverage in that area rather than a consequence of polynyas. This is suggested by the LGM summer sea-ice limit farther to the west, which was located relatively close to the shelf break (Fig. 2) (Gersonde et al. 2005).

Continuous deposition of calcareous planktonic and benthic foraminifera throughout the last 800 kyr is evident from site PS2547 located at 72° S in the Amundsen Sea (Fig. 2). The down-core oxygen isotopic composition of a planktonic foraminifera species (*Neogloboquadrina pachyderma* sinistral) and a benthic foraminifera species (*Cibicides* cf. *wuellerstorfi*) exhibits fluctuations typical for the late Quaternary glacial–interglacial cycles (Hillenbrand 2000, Hillenbrand et al. 2002), and therefore documents that the foraminifera in the glacial-age sediments lived during glacial periods and were not reworked from older interglacial sediments (Fig. 3). At site PS2547 the calcite content reflects the concentration of calcareous foraminifera, but shows no consistent glacial–interglacial pattern (Fig. 3). This may be explained by nonsystematic shifts in the depth of the calcite compensation depth (CCD; i.e., the water depth below which the rate of supply of calcite equals the rate of dissolution, such that no calcite is preserved) from an interglacial period to a glacial period and between glacials and interglacials, respectively, in response to

variations in productivity and the related flux of organic matter to the seafloor. Because site PS2547 is located near the summit of a seamount, the location is likely to have triggered upwelling of relatively warm Circumpolar Deep Water (CDW), which may have formed a seasonal open-ocean polynya above the seamount during glacial periods. However, we cannot exclude the possibility that the summer sea-ice limit during the LGM was located south of 72° S in the Amundsen Sea, because the reconstruction of the LGM summer sea-ice extent in the Pacific sector of the Southern Ocean is still incomplete (Fig. 2; Gersonde et al. 2005).

In the eastern Atlantic sector of the Southern Ocean, sea-ice diatoms suggest that the summer sea-ice limit during the LGM was located at ~53°–60° S (Fig. 2; Gersonde et al. 2005). However, sediment cores located farther to the south, on the continental margin in the southeastern Weddell Sea (PS1388, PS1389, PS1506, AN9306-SC1; Fig. 2), bear continuously calcareous planktonic and benthic foraminifera throughout the late Quaternary glacial and interglacial periods (Fig. 3 [Mackensen et al. 1989, 1994, Grobe and Mackensen 1992, Forsberg et al. 2003]). Furthermore, in these cores oxygen isotopic variations of the planktonic foraminifera species N. pachyderma sinistral and of the two benthic species Epistominella exigua and Oridorsalis umbonatus document that foraminifera lived during the glacial periods (Fig. 3). The calcite content at site PS1506 reveals that during the last 800 ka, calcareous foraminifera were abundant during moderate interglacial and glacial periods and less abundant or nearly absent during peak warm times. Grobe and Mackensen (1992) and Grobe et al. (1993) attributed this pattern to systematic CCD shifts throughout a glacial–interglacial cycle caused by changes in biological production. During glacial periods the benthic foraminifera assemblages reported from the cores off Dronning Maud Land (DML) are dominated by the opportunistic phyto-detritus feeding species E. exigua (Mackensen et al. 1989, 1994). According to the authors, the dominance of E. exigua may indicate the presence of large polynyas with at least seasonally significant primary production. It is noteworthy that all core sites are located on a regional terrace on the continental slope (Mackensen et al. 1989, 1994), which is likely to favor upwelling of deep water and thus formation of open-ocean polynyas. We conclude that during the last glacial period, large open-ocean polynyas beyond the shelf edge existed in the Weddell Sea and likely around major parts of the Antarctic continent.

PALAEOBIOLOGICAL EVIDENCE FOR GLACIAL POLYNYAS

Radiocarbon ages of subfossil stomach oil deposits ("mumiyo") from breeding colonies of Snow Petrels (Pagodroma nivea) and Antarctic Petrels (Thalassoica antarctica) in DML (Fig. 2) give evidence that some colonies existed at least from 36 ka to the late Holocene (Hiller et al. 1988, 1995, Wand and Hermichen 2005).

The breeding success of P. nivea is negatively correlated with sea-ice extent (Barbraud et al. 2000, Olivier et al. 2005). This implies that a few polynyas must have existed in the southeastern Weddell Sea during the last glacial period, because the distance between subfossil breeding sites in DML and the northern summer sea-ice limit was >2000 km (Fig. 2; Gersonde et al. 2005), and the maximum foraging range of adults is known not to exceed 440 km from the breeding site in Snow Petrels, due to their energetic thresholds (Goldsworthy and Thomson 2000). The finding of mumiyo deposits of glacial age in DML agrees with the evidence for continuous biological productivity at site PS1506 and nearby core locations (~300 km away from the mumiyo sites in DML) throughout the last glacial period, which provides strong evidence for the presence of open-ocean polynyas offshore from the shelf break.

The glacial East Antarctic Ice Sheet (EAIS) in DML must have thinned before 36 ka and may have exposed increased numbers of nunataks, which could be colonized by Snow and Antarctic Petrels since that time. A relatively early ice sheet thinning in DML during the last glacial period is consistent with the early retreat of grounded ice from the shelf in the southeastern Weddell Sea around 25 ka reported by Elverhøi (1981) and Anderson et al. (2002). Early deglaciation of this part of the EAIS provides a useful tool for testing the reliability of glaciological models simulating the EAIS during the last glacial period. We consider that after ca. 25 ka coastal polynyas may have existed on the shelf off DML. This scenario of a diachronous retreat of grounded ice from the shelf around Antarctica supports the hypothesis by Thatje et al. (2005b) that some marine benthic taxa with adapted life cycles may have survived glacial periods by moving from one continental shelf shelter to another.

THE IMPLICATIONS OF POLYNYAS FOR THE MARINE FOOD WEB DURING THE LAST GLACIAL PERIOD

Effects on the pelagic food web

The multiannual sea-ice coverage during the last glacial period caused a broadscale shutdown of primary production in the southern part of the Southern Ocean (Fig. 2). This should have affected the pelagic food web and hampered any secondary productivity. Moreover, multiannual sea ice and likely snow cover should not have allowed for much under-ice algal growth as it is found in today's annual sea ice. These conclusions are in accordance with findings that biological productivity in the southern part of the Southern Ocean during the last glacial period was insignificant (Hillenbrand and Cortese 2006 and references therein). Within the oceanic regions covered by multiannual sea ice, most of the primary productivity driving the pelagic food web could only have taken place in open-ocean polynyas (Arrigo and van Dijken 2003), but given their likely scarcity they could have enabled benthic life only very locally. Furthermore, due to the isolated geographic location

of open-ocean polynyas during the last glacial period, it is unlikely that these polynyas served as biogeographic "stepping stones" sustaining migratory pelagic taxa, including whales, seals, and penguins.

Effects on the benthos

During the last glacial period, seafloor communities encountered unfavorable environmental conditions on the continental shelf and slope of Antarctica. The shallow-water fauna was displaced from the continental shelf by the circum-Antarctic advance of the grounded ice, and mass wasting and turbidity currents severely affected survival of fauna on the continental slope around Antarctica (Huybrechts 2002, Thatje et al. 2005b). For most benthic taxa, survival was possible in the circum-Antarctic deep sea, but given the shutdown of primary productivity under multiannual sea ice, communities should have suffered from starvation. Today, low abundances and patchiness of filter feeders (sponges, actinarians, and bivalves) found underneath the multiannual sea-ice cover of the Ross Sea illustrate the effects of low food supply on benthic systems (Dayton and Oliver 1977). Studies of seafloor communities under today's ice shelves have shown that they largely depend on lateral advection of food particles, which can nourish low abundances of seafloor organisms up to 100 km away from the ice edge (Dayton and Oliver 1977, Riddle et al. 2007). At locations where advection processes can be ruled out, benthos and fish were only recorded under ice thinner than 5 m or under 5–20 m thick ice that is criss-crossed by crevasses. The occurrence of fauna at such sites was attributed to local under-ice primary production (Littlepage and Pearse 1962, Lipps et al. 1979, Cromer et al. 2005, Riddle et al. 2007).

During the last glacial period some oceanic regions located close to the Antarctic continent should have been nourished by pelago-benthic organic fluxes resulting from production in open-ocean polynyas. These polynyas might thus have played an important role in locally maintaining the chronically starved deep-sea communities in glacial Antarctica. Glacial food limitation to seafloor communities might indeed explain why many species inhabiting the seafloor today can survive long periods of starvation, and why many filter feeders, such as sponges and gorgonian fan corals, have evolved feeding mechanisms to prey upon very fine-grained food particles (Gili and Coma 1998).

Effects on Southern Ocean top predators

Although the southern elephant seal (*Mirounga leonina*) is mainly an open-ocean species in the Southern Ocean, with today's major breeding sites being on subantarctic islands, its biogeography and life history patterns, such as foraging distances and breeding/mating sites, are closely related to cold-water masses and food availability within the SIZ of the Southern Ocean. Consequently, the species is known to be affected by

changes in sea ice extent (Testa et al. 1991, Bornemann et al. 2000, Carlini et al. 2005, McMahon and Burton 2005). Today, tracking data show that elephant seals do forage in the SIZ, and travel large distances, >1000 km, from their breeding to their feeding sites (Bornemann et al. 2000, McMahon and Burton 2005).

Historically, southern elephant seals have occurred far beyond their present predominantly subantarctic and Antarctic distribution range, with evidently common breeding stocks at Juan Fernández Islands (Chile) and the coast of northwestern Tasmania, and a migratory behavior and moulting grounds reaching subtropical latitudes under cold-water influence, such as the Humboldt Current (Lewis et al. 2006). The species was near to extinction following hunting in the 19th century, which continued until 1964 at South Georgia. Southern elephant seals exhibited a comeback in numbers since the protection of the species, but without regaining their former geographic distribution range (McMahon et al. 2003, Lewis et al. 2006). However, with respect to the exploitation history of elephant seals and considering present distribution patterns, major breeding and mating sites of the species seem to have existed mainly at Península Valdés (Argentina), South Georgia, and the northern tip of the Antarctic Peninsula (Lewis et al. 2006). The loss of principal mating and breeding sites along the Antarctic Peninsula and feeding grounds in Antarctica during glacial periods should have forced the species to migrate to lower latitudes. This explains the historically wide latitudinal distribution of southern elephant seals, although the present-day concentration of major parts of the population around Antarctica, following some recovery from over-exploitation, proves that modern environmental conditions of the Southern Ocean are particularly suitable for elephant seal populations. One such important environmental factor may be the Southern Ocean's richness in food availability, e.g., of squid and nothothenioid fish that form a major source of prey to elephant seals (Carlini et al. 2005). Considering that the recolonization of major breeding sites of this species along the northernmost islands off the Antarctic Peninsula only took place a few decades ago (McMahon et al. 2003, Lewis et al. 2006), the example of elephant seals underlines the importance of ice-free terrestrial habitats in Antarctica. Given that most subantarctic islands were surrounded by sea ice for most of the year during the last glacial period (Fig. 2), the breeding sites of elephant seals were probably displaced far to the north, e.g., to South America. Even if elephant seals are capable of traveling long distances to their feeding sites, this displacement should have limited the species' access to the food-rich SIZ during the last glacial period.

Ainley et al. (2006) studied stable isotope variations of $\delta^{13}C$ in mumiyo lipids of *P. nivea* from East Antarctica and in the plankton-derived organic matter of marine sediments recovered from the East Antarctic continental margin. The authors concluded that throughout the last

10 000 years, changes in δ^{13}C values reflect a shift in foraging of petrels from ^{13}C-enriched neritic prey during warm phases to normally ^{13}C-depleted pelagic prey during cold phases. The record was interpreted as a move to foraging at distal productive pack-ice edges during cooler periods, a pattern that could well be applicable for the harsher sea-ice conditions that many birds and seals encountered in the last glacial period.

Considering the shutdown of primary production within vast areas of multiannual sea ice around Antarctica during the last glacial period, feeding grounds for crabeater seals (*Lobodon carcinophagus*) and Weddell seals (*Leptonychotes weddellii*), as well as summer feeding grounds for many whale species, were restricted to the seasonally sea-ice-free regions (Fig. 2). Many of the subantarctic islands, which theoretically might have provided terrestrial breeding and moulting grounds for warm-blooded life during the last glacial period, were glaciated and/or located in the region with multiannual sea-ice coverage (Fig. 2), and could not serve as refuges for displaced seal (in particular elephant seal) and penguin populations (Hall 2004).

Where did all the penguins go?

During the last glacial period, Antarctic penguins lost their terrestrial, ice-free nesting sites as well as their traditional Southern Ocean feeding grounds (Fig. 2; Ainley 2002). The global sea level dropped by ~120 m during the LGM, but it is very unlikely that this sea-level fall generated new terrestrial habitats directly around Antarctica, because of the over-deepening of the Antarctic shelf, with an average water depth of ~400 m today. Shallow banks, as they are known from the Ross Sea (water depth is between 200 and 300 m), were overridden by grounded ice during the last glacial period (e.g., Shipp et al. 1999). Additionally, the Antarctic ice sheet had thickened during the LGM and therefore depressed the continent isostatically, so that the average water depth of the Antarctic shelf during the LGM was probably deeper than 280 m. This is confirmed by the numerous occurrences of raised beaches along the present Antarctic coast, which date back to the time of post-LGM ice retreat and have raised by isostatic uplift in response to ice sheet thinning (e.g., Conway et al. 1999, Takada et al. 2003, Bentley et al. 2005). Consequently, penguins had to move to subantarctic regions in order to breed successfully (Ainley 2002), which should have implied competition with modern subantarctic penguin species occupying very similar ecological niches (Kooyman 2002). Due to the sea-level drop during the last glacial period, ideal alternative breeding grounds for Antarctic penguins might have been the Patagonian shelf, which unfortunately remains submerged today and is thus difficult to sample for radiocarbon dating of potential LGM penguin colonies.

Species competition, limited food sources, and competition for nesting sites should have challenged Antarctic penguins during the last glacial period, and it is unlikely that populations of penguins as large as those found today existed during that time. The Emperor Penguin (*Aptenodytes forsteri*) is the only Antarctic penguin that should have been able to maintain breeding colonies in Antarctica during the last glacial period. Because Emperor Penguins incubate their egg on their feet and cover it with an abdominal fold of skin to protect it from the cold of the ice (Lemaho 1977), it is the only penguin species that does not require ice-free breeding grounds in Antarctica. Due to the lack of coastal polynyas in the last glacial period, we postulate that most Emperor Penguins had to move breeding colonies farther north within energetic migration thresholds of the sea-ice edge during the last glacial period. Because Emperor Penguins do mainly forage in coastal polynyas today (Kirkwood and Robertson 1997, Massom et al. 1998), their geographic displacement to the outer pack-ice edge would have required a change in foraging behavior in this species.

Nevertheless, Emperor Penguins might indeed have been favored by environmental conditions during the last glacial period. Because of their ecology they should have out-competed other species; a fact that is still evident today; they are the only penguin species next to the Adélie Penguin that is able to thrive and successfully breed in high Antarctic conditions of the Weddell and Ross Seas (Lemaho 1977, Ainley 2002). If open ocean polynyas were permanent sites of productivity in the last glacial period, Emperor Penguins might have shared the fate of Snow and Antarctic Petrels, being the only warm-blooded species that maintained permanent breeding populations in the high Antarctic (Hiller et al. 1988, 1995, Steele and Hiller 1997). The unique DNA structure found in Ross Sea Adélie Penguins today (Ainley 2002 and references therein) was interpreted to indicate the survival of an isolated Ross Sea Adélie population during the last glacial period. Cape Adare, which may not have been glaciated during the last glacial period, was suggested as the possible site of a colony for this population. An open-ocean polynya offshore from Cape Adare could have formed the basis for nourishing such an isolated population within the multiannual sea-ice belt around Antarctica during the LGM. However, Emslie et al. (2007) did not find any evidence for the persistence of penguin colonies in the Ross Sea between 27 ka and 13 ka, and showed that the penguin colonization at Cape Adare did not start until ca. 2.2 ka. The analysis of ancient DNA in Adélie Penguins points to a Pleistocene origin and Holocene expansion of two distinct Adélie Penguin lineages in Antarctica (Ritchie et al. 2004). Given the low haplotype diversity within the Antarctic Adélie Penguins (Lambert et al. 2002), one could indeed suggest that a few glacial refuge populations that radiated during interglacial periods might explain the low haplotype diversity pattern in this species, a hypothesis that will require much closer investigation.

CONCEPTS & SYNTHESIS

CONCLUSIONS

1) There is evidence from the marine-geological and scarce terrestrial fossil record in Antarctica ("mumiyo") that polynyas existed during the last glacial period and that most high-Antarctic life both on land and in the sea depended on such local "hot spots" of primary production around Antarctica.

2) We provide evidence that open-ocean polynyas occurred during the last glacial period (e.g., in the southeastern Weddell Sea off Dronning Maud Land), whereas the coastal polynyas that typically drive the high Antarctic trophic web today did not exist because of ice coverage of the Antarctic continental shelf.

3) During the last glacial period, open-ocean polynyas might have been survival "hot spots" for shelf-inhabiting communities, which were displaced from the continental shelf to the continental slope and the deep sea by the advancing grounded ice and associated mass wasting processes on the continental slope.

4) The scenario of diachronous ice advance and retreat across the Antarctic shelf during the last glacial period supports the hypothesis that some marine benthic organisms with adaptive life cycles could have survived by moving from one shelf shelter to another, with polynyas playing an important role for these shelters.

5) The drastic reduction of primary production during glacial periods by thick and multiannual sea ice affecting large areas of the Southern Ocean is likely to have fostered the evolution of feeding mechanisms and life forms able to live from the very fine-grained food particles available. This factor might have been the evolutionary key to the flourishing of filter and suspension feeders typical of today's continental shelf and slope seafloor communities of Antarctica.

6) We suggest that most large marine top predators, such as whales and seals, were displaced from their interglacial feeding and breeding grounds.

7) During glacial periods Emperor Penguins had to move with the expanding sea-ice belt, whereas all other penguin species must have been displaced from Antarctica due to the complete loss of nesting grounds.

8) Fossil mumiyo records (e.g., in DML) indicate that Snow Petrels (*Pagodroma nivea*) and Antarctic Petrels (*Thalassoica antarctica*) were the only warm-blooded species that maintained small breeding colonies in glacial Antarctica, limited to only a few ice-free locations within physiologically feasible range of open-ocean polynyas. Today's occurrence of Snow Petrels in small breeding colonies scattered around Antarctica may still reflect this survival strategy of a species that challenges extremes like no other.

9) Due to the scarcity of fossil records in Antarctica, it remains unclear whether species became extinct as a consequence of selective conditions during the last glacial period. Future molecular studies, however, should allow unravelling of genetic diversity (i.e., haplotype diversity) at the population level, which might point to population sizes that survived the last glacial period.

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