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Historical observations and paleoecological records reveal ecological transitions in the Antarctic Peninsula region

Raymond C. Smith, David Ainley, Karen Baker, Eugene Domack, Steve Emslie, Bill Fraser, James Kennett, Amy Leventer, Ellen Mosley-Thompson, Sharon Stammerjohn, and Maria Vernet

Mounting evidence suggests that the earth is experiencing a period of rapid climate change. Never before has it been so important to understand how environmental change influences the earth's biota and to distinguish anthropogenic change from natural variability. Long-term studies in the western Antarctic Peninsula (WAP) region provide the opportunity to observe how changes in the physical environment are related to changes in the marine ecosystem. Analyses of paleoclimate records (Mosley-Thompson 1992, Peel 1992, Domack et al. 1993, Thompson et al. 1994, Dai et al. 1995, Domack and McClennen 1996, Leventer et al. 1996) have shown that the WAP region has moved from a relatively cold regime between approximately 2700 BP and 100 BP, to a relatively warm regime during the current cen-

This century's rapid climate warming is occurring concurrently with a shift in the population size and distribution of penguin species

tury. Air temperature records from the last half-century show a dramatic warming trend, confirming the rapidity of change in the WAP area (Sansom 1989, Stark 1994, Rott et al. 1996, Smith et al. 1996). Significantly, polar ecosystem research over the last few decades (Fraser et al. 1992, Trivelpiece and Fraser 1996)

and paleoecological records for the past 500 years (Emslie 1995, Emslie et al. 1998) reveal ecological transitions that have occurred in response to this climate change.

In this article, we summarize the available data on climate variability and trends in the WAP region and discuss these data in the context of long-term climate variability during the last 8000 years of the Holocene. We then compare the available data on ecosystem change in the WAP region to the data on climate variability. Both historical and paleoenvironmental records indicate a climate gradient along the WAP that includes a dry, cold continental regime to the south and a wet, warm maritime regime to the north. The position of this climate gradient has shifted over time in response to the dominant climate regime, and it makes the WAP region a highly sensitive location for assessing ecological responses to climate variability. Our findings show that this century's rapid climate warming has occurred concurrently with a shift in the population size and distribution of penguin species.

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Climate change in the western Antarctic Peninsula

The marine environment of the WAP (Figure 1) includes an open-ocean area of shelf-slope waters, frontal regions, a highly variable seasonal sea ice zone, and both ice-free and glacier-covered islands and coastal areas. High variability and long-term change constitute the setting in which
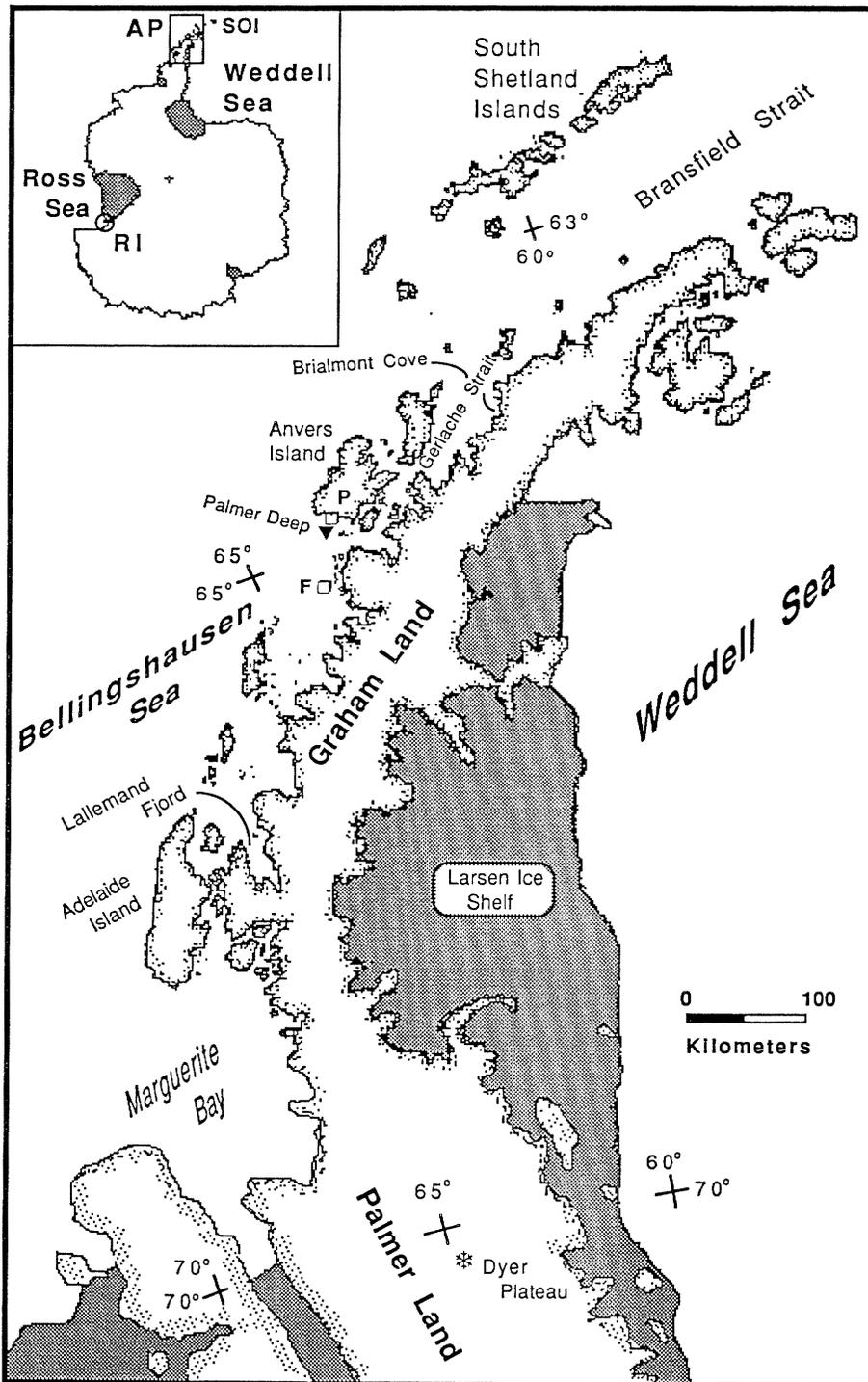
Figure 1. Antarctic Peninsula with the positions of geographic locations and features mentioned in the text. Dyer Plateau ice core drill site (70° 40' 16" S; 64° 52' 30" W; mean annual temperature –21 °C; altitude 2002 m), Palmer Station (P; southern coast of Anvers Island), Faraday Station (F) and the marine sediment core sites (Brialmont Cove, Palmer Deep, Lallemand Fjord) are indicated. The Palmer LTER regional sampling grid extends along the peninsula from Marguerite Bay to the South Shetland Islands (Smith et al. 1995). The insert of Antarctica shows the relative locations of Ross Island (RI), the Antarctic Peninsula (AP), and the South Orkney Islands (SOI).

records, and seabird distributions. All of these climate indicators consistently show a rapid warming trend in the WAP beginning early in the twentieth century. The WAP region is the area studied by the Palmer Long-Term Ecological Research (Palmer LTER) program (Smith et al. 1995), and a summary volume on ecological research for the area can be found in Ross et al. (1996).

Historical observations and modern instrumental records. Historical observations of physical features can indicate climate change from the recent Antarctic past. For example, fast ice—ice that forms seasonally and is attached to a shoreline—is easily observable from coastal research stations. Its duration at a given location typically reflects the annual advance and retreat of pack ice at that location. The British Antarctic Survey research station in the South Orkney Islands (Figure 1) has a 90-year time series of fast-ice duration in that area. Although fast-ice duration shows high interannual variability, an overall decreasing trend in duration is evident (Murphy et al. 1995) that is presumably related to regional warming.

Another physical feature for which historical observations are available is the extent of ice shelves—thick, floating or partially grounded ice sheets attached to the coast that typically rise 2–50 m or more above sea level. Ice shelves are nourished by annual snowfall and also, often, by land glaciers. Along the Antarctic Peninsula, ice shelves exist up to a climatic limit corresponding to the mean annual temperature isotherm

this polar marine ecosystem has evolved. Understanding the history of ecosystem development in response to environmental changes presents a considerable challenge, particularly because there are few time-series data of physical and biological change in the WAP region. Modern instrumental records that do exist span at most the last half of this century. Fortunately, paleoclimate records derived from Ant-

arctic ice sheet and marine sediment cores supplement and extend the limited historical observations and modern instrumental records. These records thus provide a critical context for understanding the most recent warming trend and the present-day biotic–environment relations.

We discuss climate indicators from four sources: historical observations and modern instrumental records, ice core records, marine sediment

of −8 °C (Vaughan and Doake 1996) and are therefore sensitive to atmospheric and oceanic warming. The more northern ice shelves in the WAP region have a history of recession over the past 50 years that has been related to increased air temperatures observed in the Antarctic Peninsula region (Doake 1982, Doake and Vaughan 1991, Vaughan and Doake 1996).

Comprehensive studies of land surface air temperature variations in the Southern Hemisphere over the past century indicate a long-term warming trend of approximately 0.5 °C (1881–1984; Jones et al. 1986) or 0.6 °C (1880–1985; Hansen and Lebedeff 1987). These trends are strongly correlated with the Southern Hemisphere marine temperature series of Folland et al. (1984). Jones (1990) combined climatological station data (Jones and Limbert 1987) and air temperature records for 26 overwinter expeditions in the Antarctic Peninsula and Ross Sea sectors of Antarctica to produce a time series of mean annual air temperatures from 1909 to 1987. Jones estimated annual air temperature values for each expedition site as anomalies from the reference period 1957–1975. Four of the five Antarctic regions studied by Jones exhibited linear warming trends of at least 2 °C over the last century. Jones concluded that Antarctica is now at least 1 °C warmer than it was at the beginning of the twentieth century.

Most instrument records for the Antarctic date from 1957, the International Geophysical Year. These records provide a relatively short time series compared to the instrumental records from more temperate regions of the world, which span more than 100 years. Both warming and cooling trends have been reported for some Antarctic continental regions (Rogers 1983, Taylor et al. 1990, Weatherly et al. 1991), but their statistical significance is unclear due to the brevity of records and high interannual variability. Instrument records from several coastal stations in the WAP region show statistically stronger warming trends, as well as an along-peninsula climate gradient (e.g., land surface air temperature; Schwerdtfeger 1970, Sansom 1989, King 1994, Harangozo et

Figure 2. Faraday Station annual average air temperatures, 1945–1997. The solid line is the least-squares regression line with a gradient of 0.050 °C/yr, and the dotted lines indicate ±1 standard deviation from this line. The linear regression model using the effective number of independent observations (n = 12.9) is sig-

nificant at the 94% confidence level (see Smith et al. 1996 for statistical details). Data are from the British Antarctic Survey (1998).
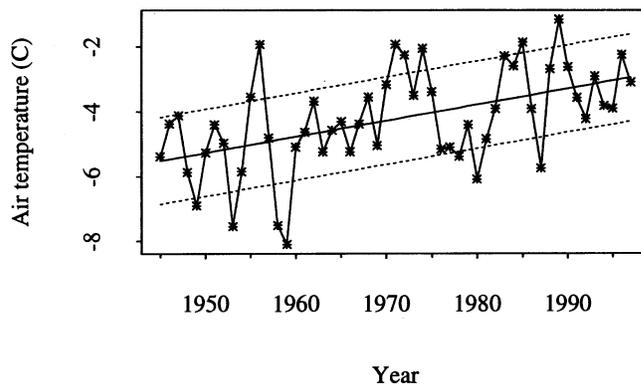
al. 1997). This north–south gradient of contrasting influences of marine versus continental climate regimes, with the potential for these contrasting regimes to shift in dominance, makes the WAP region unusually sensitive to climate change.

For example, several studies (King 1994, Stark 1994, Smith et al. 1996) have shown that midwinter land surface air temperature in the WAP region has warmed by 4–5 °C over the past 50 years, indicating that the maritime regime has been more dominant during this interval. The time series of annual average surface air temperature (British Antarctic Survey 1998), recorded at Faraday Station (Figure 1) from 1945 to 1997, shows this warming trend (Figure 2). The least-squares regression of the warming trend, which is significant at the 94% confidence level, is due in large part to the high frequency of warm years during the last three decades. Air temperatures at Faraday Station have been above average for 20 of the 27 years from 1970 to 1996.

We also analyzed each month of the Faraday air temperature time series separately. Breaking down the

Table 1. Monthly, seasonal, and annual trends in Faraday Station surface air temperature from March 1944 to March 1998.

Years	Months	Gradient (°C/yr)	Standard error (°C/yr)	F-test (%)[a]	N[a]
1945–1998	January	0.0234	0.0064	99.9	54.0
1945–1998	February	0.0305	0.0084	99.9	54.0
1944–1998	March	0.0243	0.0094	98.7	55.0
1944–1997	April	0.0520	0.0210	98.3	54.0
1944–1997	May	0.0787	0.0220	90.2	12.9
1944–1997	June	0.0965	0.0256	100.0	54.0
1944–1997	July	0.0735	0.0387	93.7	54.0
1944–1997	August	0.0911	0.0296	99.7	54.0
1944–1997	September	0.0583	0.0253	97.5	54.0
1944–1997	October	0.0191	0.0168	73.9	54.0
1944–1997	November	0.0300	0.0111	99.1	54.0
1944–1997	December	0.0118	0.0052	97.3	54.0
1945–1998	Summer[b]	0.0269	0.0070	100.0	54.0
1944–1997	Autumn	0.0758	0.0192	91.0	11.4
1944–1997	Winter	0.0823	0.0296	83.0	14.1
1944–1997	Spring	0.0298	0.0097	84.9	12.8
1945–1997	Annual	0.0495	0.0121	94.0	12.9

[a]The significance of the linear regression analysis, as estimated by the F-test, and the number of observations (N) used to calculate the F-test are reported in the last two columns. Using the approach outlined in Smith et al. (1996), if the linear regression displayed autocorrelation in the error terms, then the degrees of freedom were penalized by determining the effective number of independent observations. Those regressions that were affected have a reduced number.
[b]The seasons were defined as follows: summer (January–March), autumn (April–June), winter (July–August), and spring (September–December).
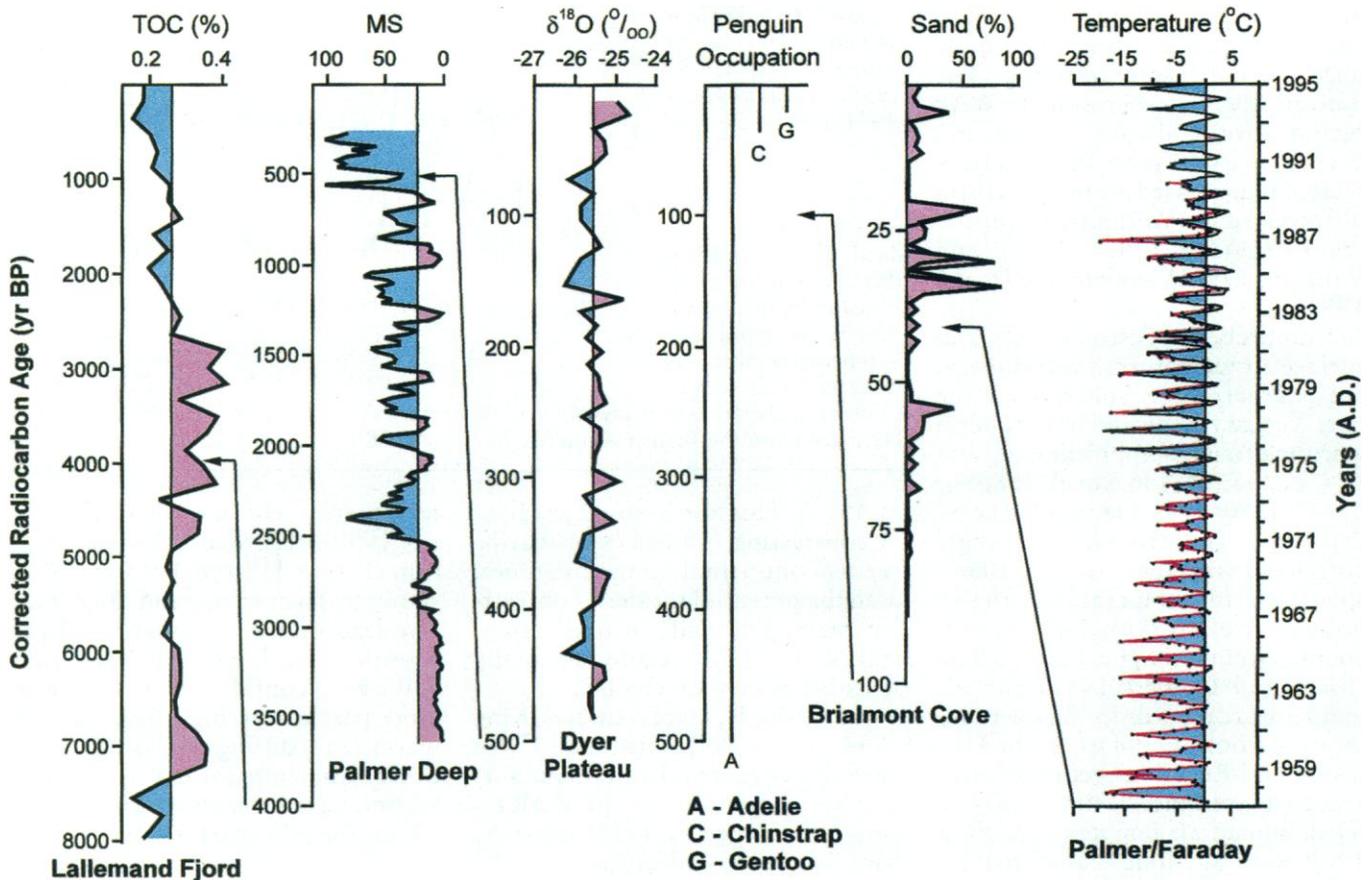
Figure 3. Comparison of paleoenvironmental records from the Antarctic Peninsula region with different temporal resolutions and duration. The blue and pink shading represent cool and warm periods, respectively. From left to right, resolution of the record increases and its duration decreases. The Lallemand Fjord record (Shevenell et al. 1996) represents the last 8000 radiocarbon years and is based on percentage of total organic carbon (TOC %) in marine sediments. The onset of Neoglacial cooling is evident around 2500 BP, and the carbon minimum at approximately 400 BP corresponds to the onset of the Little Ice Age. The straight vertical line is arbitrary and does not represent mean value. The marine sediment record (MS) from Palmer Deep (Leventer et al. 1996) illustrates magnetic susceptibility as a paleoproductivity proxy for the last 3700 years. The correspondence with the Lallemand Fjord record is evident, as are high-frequency (approximately 200-year) oscillations in productivity. The MS record is terminated at approximately 270 BP due to incomplete core recovery. The straight vertical line is arbitrary and does not represent mean value. The ice core record for the last 480 years from Dyer Plateau (Thompson et al. 1994) demonstrates reconstructed temperature based on oxygen isotope analyses ($\delta^{18}O$). The record ends around 1989, when the core was collected. The last two decades (1970s–1980s) are among the warmest in the 480 years of the record. The straight vertical line is at mean value. Penguin occupation history for the vicinity of Palmer Station shows that Adélie penguins (A) have been present for the last 500 years; chinstrap (C) and gentoo (G) penguins arrived more recently. Data on Adélie history are from abandoned rookeries and radiocarbon chronology. Data on chinstrap and gentoo penguins are from historical records (Parmelee 1992). The glacial meltwater record from marine sediments in Brialmont Cove for the last 100 years is based on ^{210}Pb age determinations (Domack and McClennen 1996). Peaks in sand abundance represent "warm" melt events in a glacier-proximal setting. Meteorological records of monthly mean temperature for Palmer and Faraday stations (after Domack 1996) show a recent increase in both winter and summer mean temperatures since the 1960s. The straight vertical line is at 0 °C.

seasonal time series in this way helps to eliminate autocorrelation in the error terms and shows whether the warming trend is more prevalent in any one season. Table 1 shows the trend detected for each month's time series (as well as seasonal and annual trends for comparison), the standard error, and the significance of the linear regression analysis as estimated by the F-test. The F-test shows that 9 of the 12 monthly regressions are

significant at confidence levels greater than 95%. The warming trend in Faraday air temperatures is strongest in midwinter months and peaks in June at 0.097 °C/yr, representing a 5.0 °C increase in June temperatures over the 54-year period. It is important to note that the midwinter amplification of the warming trend can affect the extent, thickness, and concentration of the seasonal sea ice cover, as well as the

marine ecology associated with sea ice.

Ice core records. Carefully extracted ice cores provide annual- to decadal-scale paleoenvironmental records that can supplement and extend historical observations and modern instrumental records. Ice core records contain proxy histories of atmospheric conditions, including temperature, chemistry, dust content, and

volcanic emissions. These paleoenvironmental histories are inferred from the particulates, chemical species, and gases preserved in ice sheets and ice caps (Mosley-Thompson 1992, Peel 1992). In addition, the history of net snow accumulation may be reconstructed by identifying individual annual layers or known time-stratigraphic horizons.

The $\delta^{18}O$ isotopic record extracted from an ice core on the Dyer Plateau (Figure 1) provides a 480-year paleoclimate history of the Antarctic Peninsula region (Figure 3; Thompson et al. 1994, Dai et al. 1995). The $\delta^{18}O$ composition of ice reflects a combination of four factors: the air temperature at which condensation occurs, atmospheric processes occurring along the trajectory of the air mass from the source of evaporation to the site of condensation, local conditions during the transformation of the snow to ice, and the surface elevation and latitude of the deposition site (for reviews, see Dansgaard et al. 1973, Bradley 1985). The Dyer Plateau record indicates an increase in net snow accumulation since the beginning of the twentieth century and a distinct warming trend beginning in the 1940s.

Ideally, the $\delta^{18}O$ signal should be calibrated against in situ observations, but doing so has proven difficult due to the short occupation of the Dyer Plateau drilling site. However, the $\delta^{18}O$ history from the Dyer Plateau cores has been shown to be consistent with available temperature observations recorded at various Antarctic Peninsula stations over the last 50 years (Thompson et al. 1994). The 480-year Dyer Plateau $\delta^{18}O$ history (Figure 3) shows almost no consistent pattern except for a marked cooling around 150 BP, followed by nearly a century of below-normal temperatures and, subsequently, by an abrupt warming in the last half-century. Warming, as indicated by less negative $\delta^{18}O$, began in the 1930s and has continued to the present, with the last two decades being among the three warmest in the 480-year history of the plateau.

Marine sediment records. Marine sediment cores have been used to reconstruct past climate and associated productivity changes in the WAP region for the last 8000 years (Domack et al. 1993). The long-term history of the WAP has been marked by pulses of warm and cool episodes accompanied by changes in the extent and duration of regional ice cover (Domack and McClennen 1996, Leventer et al. 1996). These marine sediment records not only are crucial for characterizing the long-term natural variability in the WAP region but also provide a context for this century's warming trend, as documented in historical observations, modern instrumental records, and ice cores.

The marine sediment cores from fjords and bays along 450 km of the WAP (Figure 1) contain a paleoclimate record that varies in temporal resolution, composition, and nature of paleoenvironmental proxy. In the southern region of the WAP (Lallemand Fjord), low temperatures, perennial sea ice, and low glacial meltwater give rise to slow (1–2 mm/yr) rates of ice-rafted terrigenous sedimentation (i.e., sedimentation derived from rock debris that is carried by sea ice, icebergs, or ice shelves and is released to the water column as ice melts, overturns, or fractures). In the midpeninsula region (Palmer Deep), the pronounced seasonality of sea ice yields higher (3–4 mm/year) rates of biogenous (i.e., produced by living organisms) and ice-rafted terrigenous sedimentation. In the northern region of the WAP (Brialmont Cove), the long melt season gives rise to high (5–10 cm/year) rates of ice-rafted terrigenous sedimentation. The variability in sedimentation content and rate along the WAP reflects the regional climate gradient and can therefore be used to infer the environmental context of deposition.

Sedimentation rates determine the amount of time that is represented in a given length of core: the slower the sedimentation rate, the longer the record. The slow sedimentation rate in the Lallemand Fjord core yields a deposition record extending back at least 8000 years in only 5 meters of core. For the Lallemand Fjord core, the most effective paleoenvironmental proxy so far discovered is total organic carbon, which reflects the record of primary production.

Total organic carbon levels have been found to be elevated during minimal sea ice conditions and depleted during persistent sea ice conditions (Shevenell et al. 1996). Thus, changes in total organic carbon levels are inferred to reflect oscillations between warm and cold episodes. Within the time frame captured by the Lallemand Fjord core (Figure 3), it is easiest to resolve millennial-scale variations in climate, such as the middle Holocene warm episodes (5000–2500 BP), the Neoglacial cooling, beginning at approximately 2500 BP, and the Little Ice Age, from approximately 500 to 100 BP.

At the location of the Palmer Deep core (Figure 1), biogenous sedimentation is enhanced primarily by favorable sea ice conditions and a more open ocean location. The name Palmer Deep refers to the 1440 m deep basin at this location that is surrounded by shallower ridges (200–500 m deep) of the continental shelf. The Palmer Deep basin appears to be a natural sediment trap, because the pelagic and hemipelagic sediments collected from the center of this basin are free of the stratigraphic "noise" caused by sediment gravity flows (e.g., slumps and debris flows). For the Palmer Deep core, magnetic susceptibility is the paleoenvironmental proxy for productivity; low and high magnetic susceptibility are inferred to reflect intervals of high and low productivity, respectively (Leventer et al. 1996).

The 9 m long Palmer Deep core shows bicentury oscillations of primary productivity and ice rafting over the last 3700 years (Figure 3). Comparison of the Lallemand Fjord and Palmer Deep records clearly demonstrates a similar record of events for the last 3700 years, although at different temporal resolutions. The relatively high temporal resolution of the Palmer Deep record also displays both short-term cycles (200–300 years) and longer-term events (approximately 2500-year cycles). Both the long- and short-term cycles are thought to be related to global climatic fluctuations (Leventer et al. 1996).

Oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotopic records have proven to be highly effective proxies of paleotemperature change during the Ho-

locene, especially in the interval after the retreat of glaciers following 6000 BP. Oxygen and carbon isotopic records have been extracted from benthic foraminifera (e.g., *Bulimina aculeata*) found in Palmer Deep cores. Benthic foraminiferal $\delta^{18}O$ oscillations range between approximately 0.25 and 0.5 parts per thousand, which suggests oscillations in bottomwater temperature of approximately 1–2 °C during the late Holocene (i.e., the last 3700 years). The inferred paleotemperatures of waters in these deep basins indicate that there have been distinct climate shifts, some occurring over periods as brief as a few decades.

Bottom waters in the Palmer Deep are derived largely from upwelled circumpolar deep water (CDW), the amounts of which may have fluctuated through time (Ishman 1990). CDW constitutes the water mass with the greatest volume in the Southern Ocean (Sievers and Nowlin 1984, Carmack 1990). It is marked by a temperature maximum at intermediate depths and periodically floods the bottom waters of the WAP region, where the continental shelf is relatively deep. Thus, the temperature oscillations of Palmer Deep bottom water during the last several thousand years may reflect the changing influence of CDW in the shelf-slope waters of the WAP.

Because CDW is a relatively warm water mass, it may provide a heat source to surface waters, especially during periods of greater CDW upwelling. Consequently, the increased sea surface temperatures would result in decreased sea ice extent. This hypothesis is supported by the changes in the carbon isotopic ($\delta^{13}C$) record, which indicate that warmer intervals of the climate record are generally associated with lower $\delta^{13}C$ values. Lower $\delta^{13}C$ values are indicative of higher nutrient concentrations in bottom water, which is expected with stronger influence of nutrient-rich CDW in the Palmer Deep. Such a correlation is consistent with lower sea ice extent and higher primary productivity (Leventer et al. 1996).

In the northern region of the WAP, where air temperatures are often above freezing, glacial meltwater, which is typically laden with high amounts of terrigenous material, contributes significantly to marine sedimentation (Domack and Williams 1990, Domack and Ishman 1993). The high terrigenous sedimentation rates caused by glacial meltwater dilutes the biogenous sedimentary components, making it difficult to extract good chronologies from cores collected in such places as Brialmont Cove (Domack and McClennen 1996). However, in two cores that had intact sediment–water interfaces, meltwater events were recognizable based on the abundance of sand and other terrigenous deposits. These sand layers were found only in the uppermost meter of the cores (Domack and McClennen 1996). Domack (1990) suggests that these sand layers resulted from changes in sedimentary processes as a result of recent warming in the region. The latest chronology for these cores (Figure 3) shows that the inferred meltwater events began approximately 60 years ago, with a noticeable abundance in sand approximately 25–35 years ago. This observed depositional change in the sedimentary process and inferred climate change are consistent with historical records of increasing mean monthly surface air temperatures.

Seabird distributions. Seabirds are relatively long lived (15–70 years) upper–trophic level predators that appear to integrate environmental variability over large spatial (thousands of square kilometers) and temporal (years to decades) scales (Ainley and Boekelheide 1990, Furness and Greenwood 1993). Seabirds are also relatively wide ranging because they depend on the patchy distribution of their prey and respond to changes in their physical environment (e.g., sea ice; Fraser et al. 1992). Consequently, changes in their abundance and distribution provide an indication of ecosystem and environmental change. For example, in the WAP region and elsewhere in Antarctica, information from both paleoecological (Baroni and Orombelli 1991, 1994, Denton et al. 1991, Emslie 1995) and modern census (Taylor et al. 1990, Fraser et al. 1992) studies suggest that penguin distributions are undergoing a fundamental reorganization due to climatic factors that influence their long-term recruitment.

Adélie penguins (*Pygoscelis adeliae*) and their sympatric, closely related congener, chinstrap penguins (*Pygoscelis antarctica*) are estimated to make up more that 80% of the avian biomass of the Southern Ocean (Woehler 1997). Accordingly, international efforts are underway to monitor changes in the abundance of these species through various national and international programs (e.g., Scientific Committee on Antarctic Research; SCAR 1987). Interannual changes in breeding population size is a standard protocol to assess population status (CCAMLR 1992). The most recent 20-year trends in Adélie and chinstrap breeding populations on islands near Palmer Station (Figure 4) are believed to be representative of broad trends in the WAP region as a whole (Fraser and Patterson 1997).

In the WAP region, Adélie breeding populations have been stable or declining slowly, whereas chinstrap breeding populations have increased several hundred percent (Fraser et al. 1992). In contrast, the number of Adélie breeding penguins in the Ross Sea area increased rapidly during the 1980s and has since remained relatively stable. The Adélie penguin is an obligate associate of winter pack ice (Ribic and Ainley 1988, Ainley et al. 1994), whereas the chinstrap penguin occurs almost exclusively in open water (Ainley et al. 1994). It has been suggested that the change in the distribution of breeding populations in recent years is a result of changes in the environment, especially the reduction in sea ice–related habitats resulting from warming trends in WAP air temperatures (Fraser et al. 1992).

Abandoned penguin rookeries in Antarctica, which are marked by the presence of nest stones, preserved guano, and chick remains, can provide considerable information on past population changes and migration of Adélie and chinstrap penguins (Baroni and Orombelli 1991, 1994, Zale 1994, Emslie 1995, Emslie et al. 1998). Analysis of bones and other organic remains preserved in the sediments provide information about the penguin species that inhabited a site, the time they inhabited the site, and their diet. These data can be compared to other paleoclimate

records to determine if the changes observed in the penguin populations are indicative of climate change.

Six abandoned rookeries, all found to have been previously inhabited by Adélie penguins, were excavated in the near vicinity of Palmer Station in March 1997 (Figure 1; Emslie et al. 1998). Radiocarbon dates of penguin bones and squid beaks recovered from the sediments indicate that these rookeries were occupied from 644 BP to the present (mean corrected date; see Emslie et al. 1998). The absence of chinstrap or gentoo penguin (*Pygoscelis papua*) bones in the surveys of the abandoned rookeries suggests that either these two species are relatively recent arrivals to the Palmer area or that their remains have not yet been located. The first hypothesis seems most likely, because the chinstrap and gentoo penguins currently inhabiting the Palmer region are near the southern boundary of their breeding ranges, and the present colonies are believed to have been established in the last 20–50 years (Parmelee 1992). Thus, records from excavated abandoned rookeries in the Palmer region (Figure 3) show that Adélie penguins have been permanent occupants for at least the past 600 years, whereas the recent population expansions by chinstrap and gentoo penguins southward along the WAP appear to be correlated with regional warming during the past 50 years (Fraser et al. 1992).

Ecological responses to climate change

Investigations of the impact of possible global warming and climate change on entire ecosystems are becoming increasingly important for understanding interactions among the atmosphere, ocean, and biosphere and for testing models depicting these interactions. Long-term studies in the WAP provide the rare opportunity to integrate time-series data related to the physical environment, biology, and paleoecology of the Antarctic marine ecosystem. These data reveal that ecological responses have occurred over the past 500 years in association with well-documented climate changes in the WAP region.

The complex trophic relationships

Figure 4. Twenty-year trends in chinstrap and Adélie penguin populations at Arthur Harbor (Palmer Station). Open symbols, chinstrap penguins; solid symbols, Adélie penguins; crosses, Adélie penguins at Cape Royds, which is located on Ross Island in the Ross Sea (see insert in Figure 1; Taylor and Wilson 1990, Taylor et al. 1990, Blackburn et al. 1991; data augmented by Peter R. Wilson, Landcare Research, New Zealand Ltd., personal communication). In the WAP region, the two species have exhibited opposite trends, with chinstrap penguins increasing over 500% since the mid-1970s and Adélie penguins decreasing by nearly 25%. Trends in Adélie penguin populations at Cape Royds in the Ross Sea show an increase through the late 1980s, with roughly stable populations thereafter. Adélie data are given as percentage of 1975 counts, whereas chinstrap data are given as percentage of 1977 counts because there were no recorded chinstrap breeding pairs in the Palmer area in 1975.
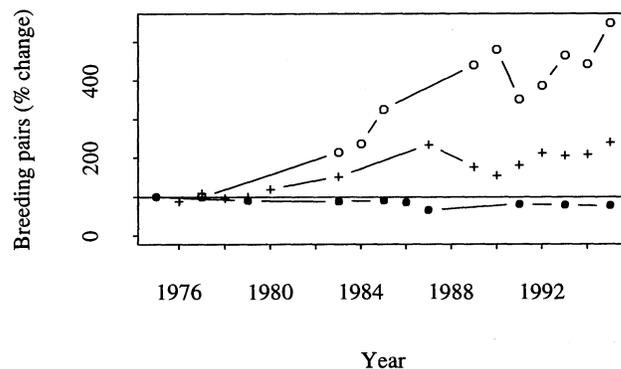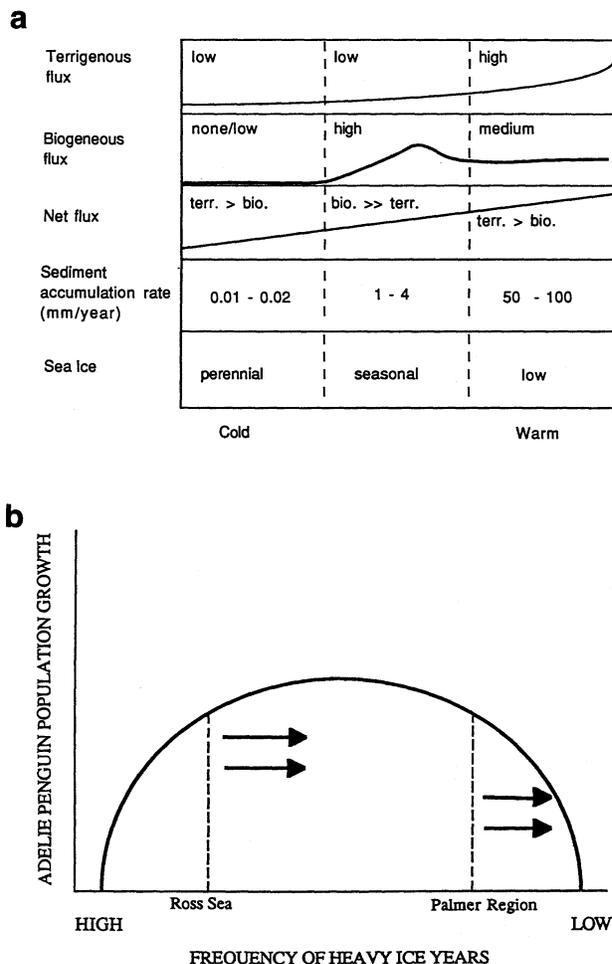
in Antarctica are often short and involve relatively few species (e.g., Ainley and DeMaster 1990, Smith et al. 1995). Krill, a major herbivore that transfers energy within the Antarctic marine ecosystem, is closely coupled to sea ice during various periods of its annual life cycle (Ross and Quetin 1986, 1991, Quetin and Ross 1991, Loeb et al. 1997); it is expected to be an important link between phytoplankton and penguins, although that link is not yet fully understood. How krill populations change with climate is therefore an important question when considering their influence on penguin populations.

The current dearth of long-term data makes it difficult to address this question or many others concerning linkages in the Antarctic marine ecosystem. We have focused instead on the ecosystem components for which we do have long-term data and have developed two conceptual models relating Antarctic biota and environment. For cold and warm climate scenarios, the first model depicts changes in phytoplankton production, whereas the second model depicts changes in seabird populations. In the second model, seabirds are used as a surrogate for change in the upper trophic levels (although it is important to note that we are unable to disentangle the effects of changes in bird populations that are directly

tied to environmental changes from those that are mediated by trophic interactions—that is, predator–prey dynamics). Over time, more long-term data on the Antarctic marine ecosystem should become available to test and modify our conceptual models and to create new ones that more fully describe the processes involved in ecosystem response to climate change.

Conceptual model of biogenic flux optimum. A simplified diagram (Figure 5a) illustrates idealized relationships between the sedimentary record and overlying biological production and terrigenous influx. This model represents the modern continuum from polar to subpolar conditions along a south-to-north gradient roughly parallel to the WAP. Over long time scales, as recorded in paleoclimate records, this system will migrate north or south in response to climate change. At the cold end of this climate gradient, perennial sea ice is present in surface waters. Under these conditions, the contribution of sedimentation from melting ice, which is often embedded with rock debris, is low. Thick, multi-year sea ice also reduces light penetration, resulting in little to no biological production in either sea ice or surface waters. The net result is low accumulation rates of biogenous and terrigenous sediments (approximately

Figure 5. Ecological responses to climate change. (a) Conceptual model indicating the relationship between the sedimentary record and overlying biological production. The hypothesized trends in fluxes and sedimentation rates in relation to differing sea ice conditions (representing cool, moderate, and warm climate conditions) are based on analyses of the WAP sediment cores as summarized in this article. (b) Conceptual model indicating the direction of Adélie penguin population changes in the Ross Sea and Palmer Station regions in relation to global warming and a decline in the frequency of heavy ice years. At Ross Sea, Adélie populations will continue to rise until reaching the optimum and will then decline. Populations at Palmer Station will continue to decline to extirpation.

a

Terrigenous flux	low	low	high
Biogeneous flux	none/low	high	medium
Net flux	terr. > bio.	bio. >> terr.	terr. > bio.
Sediment accumulation rate (mm/year)	0.01 - 0.02	1 - 4	50 - 100
Sea Ice	perennial	seasonal	low

Cold   Warm

b

ADÉLIE PENGUIN POPULATION GROWTH

Ross Sea   Palmer Region

HIGH   LOW

FREQUENCY OF HEAVY ICE YEARS

0.01–0.02 mm/yr; Domack et al. 1995, Shevenell 1996, Shevenell et al. 1996).

With climate change, the advance and retreat of annual sea ice controls the composition and volume of material settling to the sea floor. Although terrigenous input increases with increased meltwater, the impact of warming on the biological system is even more significant. High primary production is often associated with the marginal ice zone because melting sea ice (which is fresher than sea water) stabilizes the upper water column (Hart 1934, Smith and Nelson 1985, Mitchell and Holm-Hansen 1991). Under these conditions, biogenous material dominates the particle flux and overall sediment accumulation rates range from 1 to 4 mm/yr (Domack et al. 1993, Domack and McClennen 1996, Leventer et al. 1996). This situation currently applies to the area just south of Anvers Island, which may be an optimum location for the detection of subtle changes in sea ice extent and its influence on phytoplankton production and flux of carbon to the sediment (Domack and McClennen 1996). In the WAP region, Anvers Island is also hypothesized to be the northern boundary for the distribution of Adélie penguins (Fraser and Trivelpiece 1996) and roughly the southern boundary for chinstrap penguins (Fraser et al. 1992).

At the warm end of this climate gradient, the region experiences longer ice-free periods. Without sea ice melt to stratify the upper water column, the open-water system undergoes increased wind mixing, resulting in lower annual average primary production and organic flux to the sea floor. However, due to the relatively warm conditions, glacial meltwater input of terrigenous material is high, leading to sediment accumulation rates of up to 10 cm/year (Domack 1990, Domack and McClennen 1996).

Leventer et al. (1996) provide a schematic model to illustrate how changes in water column stratification can lead to contrasting phytoplankton bloom conditions that result in different sediment records. Their model, which provides testable hypotheses linking sea ice, upper–water column stratification, primary productivity, and vertical flux to the sea floor, indicates that of all the factors that may influence primary productivity in Antarctic waters, variability of sea ice coverage is among the most important. Because the ecological impact of sea ice is a complex space–time matrix of biology and physical forcing, sea ice indexes have been developed to give a common context with which to link variability in sea ice coverage to variability in the marine ecosystem (Smith et al. 1998).

Several workers (Sansom 1989, Weatherly et al. 1991, King 1994, Smith et al. 1996) have found that the anticorrelation between surface air temperature and sea ice extent is much stronger in the WAP region than elsewhere in the Antarctic. In the WAP region, the statistically significant increase in surface air temperature is associated with an observed decrease in sea ice, particularly summer sea ice, as recorded by passive microwave satellite data over the last two decades (Stammerjohn and Smith 1997). The decrease in sea ice coverage is in contrast to an observed increase in sea ice coverage for the Antarctic as a whole (Cavalieri et al. 1997, Stammerjohn and Smith 1997). For the WAP region, if the observed anticorrelation between air temperature and sea ice is assumed to have held for the full 53-year period for which air temperature data are available (1945–1997), then there would have been a southward shift of 100–200 km in seasonal sea ice coverage along the WAP. Consequently, modern instrumental and satellite records are consistent with the sediment records in suggesting a warming trend with a southward shift in seasonal sea ice extent. Because primary productivity is strongly influenced by the presence or absence of sea ice, the southward shift in sea ice extent is accompanied by a southward shift in the dominance of biotic over abiotic sedimentation (Figure 5a).

Conceptual model of Adélie penguin population growth and sea ice. Adélie

penguins are obligate inhabitants of pack ice, whereas their congeners, the chinstrap penguins, occur almost exclusively in ice-free waters from the Antarctic to the sub-Antarctic. These two species have a similar breeding cycle of courtship, egg laying, incubation, brooding, and fledging, but the Adélie's breeding cycle begins one month earlier than the chinstrap's. Adélie penguins begin laying eggs in early to mid-November; after 50–55 days, the young birds fledge and depart for the sea. Chinstrap penguins lay eggs in late November to early December, with fledging and departure of young birds in late February to mid-March. The timing associated with this relatively fixed breeding chronology, in association with interannual variability in sea ice cover and in the life histories of primary and secondary producers, provides the ecological context that determines breeding success.

Figure 5b illustrates a conceptual model for seabird population growth in Antarctica using Adélie penguins as an example. This model shows that population growth is highest during conditions of moderate sea ice coverage (i.e., between extremes of excessive and insufficient sea ice coverage; Fraser and Trivelpiece 1996). Adélie penguins are true Antarctic penguins—that is, they live within or near the pack ice zone year-round. They show strong fidelity to both a winter sea ice habitat and to their natal rookery, to which they return in the spring for breeding. Breeding colonies are established in coastal areas, the topography of which permits the penguins to build pebble nests in places where neither snow nor meltwater accumulates (Wilson et al. 1990). Consequently, colony location and long-term survival are associated with several sea ice–mediated factors (Baroni and Orombelli 1994), including relatively ice-free coastal areas in late spring, the availability of suitable nesting sites (i.e., that are free of snow or meltwater), and sufficient prey within the foraging range of these sites. The abundance of prey is linked in turn to environmental conditions controlling primary production, in particular to the presence or absence of sea ice, as discussed above.

Our conceptual model integrates these environmental conditions and is roughly analogous to the intermediate disturbance model (Connell 1978), which hypothesizes an optimum condition intermediate between extremes of disturbance. Not all of the mechanisms that control these environmental conditions are fully understood. However, it is known that regions of heavy and persistent sea ice cover—or, conversely, of no sea ice cover—provide unsatisfactory conditions for breeding Adélie penguins. Over the past 20 years, the frequency of heavy sea ice years in the WAP region has been decreasing (Figure 2) in conjunction with decreasing Adélie populations (Figure 4). By contrast, Adélie populations in the Ross Sea (Figure 4) have been increasing (Taylor et al. 1990). At Cape Royds in the Ross Sea region (Figure 1), where the southernmost colony of Adélie penguins is located, the recent warming trend and consequent decreasing sea ice is postulated to have improved the nesting success of these colonies and to have increased food availability for them (Taylor et al. 1990).

Our Adélie penguin population growth model provides a hypothesis explaining the different high–trophic level responses to climate change in these regions. Optimum sea ice conditions for Adélie penguins no longer exist in the WAP region and populations continue to decline, whereas in the Ross Sea region optimum sea ice and habitat conditions have not yet occurred and populations are increasing. The paleoecology records also support this hypothesis. In the Ross Sea region, there is evidence that Adélie populations were larger during 4200–2800 BP (Baroni and Orombelli 1994)—a period that, according to an ice core from Dome C, a coring site on the east Antarctic plateau (74.7° S, 124.2° E), was a warm phase (Lorius et al. 1979). Paleoecology evidence suggests that in the WAP region, Adélie populations have occupied sites in the area of Palmer Station since at least the coldest period of the Little Ice Age, whereas chinstrap populations expanded during warm phases of the Little Ice Age (Figure 3; Emslie 1995, Emslie et al. 1998). Our conceptual model predicts that, with present-day warming, Adélie populations in the Ross Sea will reach a peak and then begin to decline. In the WAP region, Adélie populations will continue to decline and the locus of their distribution will be forced farther south along the peninsula, whereas chinstrap populations will continue to increase.

Mechanisms of climate change

The mechanisms responsible for the cycles and trends observed in the modern instrumental and paleoclimate records are poorly known. Large-scale atmospheric processes, perhaps driven by global mechanisms (Stuiver and Brazuinas 1993) and acting on the unique geographic features of the WAP, could provide the overall forcing. The Antarctic Peninsula is the only area in Antarctica where the mean position of the circumpolar atmospheric low-pressure trough (i.e., the Atmospheric Convergence Line [ACL]) crosses land. The seasonal cycle displayed in temperature, pressure, wind, and precipitation (van Loon 1967, Schwerdtfeger 1984) is linked to both increased cyclonic activity and a southward shift of approximately 10° of latitude of the ACL during spring and autumn. The ice edge is near its extreme equatorward (spring) or poleward (autumn) positions when the mean position of the ACL is nearest the Antarctic continent; conversely, the ACL is, on average, farthest equatorward when the sea ice edge is at an intermediate position (van Loon 1967). Therefore, the relative position of the ACL will influence not only the semiannual cycle of temperature, pressure, wind, and precipitation, but also sea ice distribution. The effect of increasing or decreasing sea ice extent could lead to additional feedbacks. For example, greater storminess has been associated with regions of higher temperatures and lower sea ice extent (Ackley and Keliher 1976). Consequently, large-scale atmospheric processes that influence the intensity of the westerlies (i.e., the belt of west to east winds between 30° and 60° latitude) and the mean position of the ACL (van Loon 1967, Schwerdtfeger 1984, Enomoto and Ohmura 1990, Harangozo 1994, Smith et al. 1996) may be the atmospheric mechanisms

influencing sea ice extent.

Alternatively, or in concert, the oceans may play a critical role in the distribution of sea ice (Broecker 1990, 1997, Stuiver and Brazuinas 1993) by changing thermohaline circulation and thereby influencing both the production of oceanic deep water and the strength and distribution of CDW. As already noted, CDW is the water mass with the largest volume in the Southern Ocean (Sievers and Nowlin 1984, Carmack 1990) and is found along the margin and over the shelf of the WAP at depths greater than a few hundred meters (Domack et al. 1992, Hofmann et al. 1996, Jacobs et al. 1996). Jacobs and Comiso (1993, 1997) suggest that greater upwelling of CDW could reduce sea ice thickness and coverage. Consequently, seasonal heating of the increased amount of exposed open water would lead to later sea ice formation in autumn (Jacobs and Comiso 1989). Because this relatively warm water mass is sufficient to melt sea ice (Hofmann et al. 1996), a change in the intensity or distribution of CDW, driven by either local or global events, can potentially determine the timing and spatial extent of sea ice in the WAP region.

Future challenges

All of the modern and paleoclimate records are consistent in showing a rapid warming trend in the WAP region during this century. This trend is evident in spite of large interannual variability associated with shorter term fluctuations in climate (e.g., El Niño–Southern Oscillation). Before this century's warming trend, the marine sediment record indicates a cooler climate, roughly coincident with the Little Ice Age (beginning approximately 500 BP), which was preceded in turn by a warmer period beginning approximately 2700 BP (Björck et al. 1991, Domack and McClennen 1996). In addition, cyclical fluctuations in organic matter preservation on 200–300-year time scales in the mid-WAP region (around Anvers Island) resulted from cycles in primary productivity (Domack et al. 1993, Leventer et al. 1996). Evidence for such cycles has not been found in cores at more northern or southern locations along the WAP,

and these workers have suggested that in the mid-WAP region, slight changes in sea ice extent might amplify the influence of climate variability on primary production and, subsequently, on higher trophic levels. Consequently, the climatic gradient along the WAP is a valuable scale for assessing ecological responses to climate variability.

Contrasts in habitat preference (sea ice–obligate Adélie penguins and sea ice–intolerant chinstrap penguins) provide a gauge for assessing ecological change along the WAP. Before the warming in the twentieth century, the previous several centuries appear to have been cooler, with greater and more persistent sea ice coverage in the mid-WAP region providing Adélie penguins with a more suitable habitat than at present. Conversely, the increased sea ice in the eighteenth and nineteenth centuries along the WAP provided a generally less suitable habitat for chinstrap penguins. Warming within the twentieth century has reversed these habitat conditions, and Adélie populations are declining whereas chinstrap populations are increasing. These results are consistent with both modern penguin censuses and paleoecology records excavated from penguin rookeries.

These results, although consistent with one another, leave several important issues unresolved. One key question is whether the recent warming is part of a natural cycle. Leventer et al. (1996) hypothesized that the increased productivity during the 200–300-year productivity cycles in the WAP was due to warmer atmospheric and sea surface temperatures and to a corresponding reduction in sea ice. However, these mechanisms remain unproven. A shift in the ACL to the south will bring increased storminess, warmer air from the northwest, and less sea ice (Ackley and Keliher 1976), but the global and regional mechanisms influencing the position of the ACL are not fully understood. Similarly, an increase of CDW onto the WAP shelf will lead to enhanced heat flux to the surface, less sea ice, and correspondingly warmer temperatures, but the mechanisms controlling CDW upwelling are also not fully understood.

Primary productivity, as suggested

by the conceptual models shown in Figures 5a and 5b, is linked to the marginal ice zone, but there are other controls on primary production not considered in this article. Also, the trophic linkages and their association with sea ice are not fully understood. Sea ice clearly influences primary production and habitat suitability for Adélie and chinstrap penguins, but the direct and indirect mechanisms underlying our conceptual models need to be refined with future research. One ideal location for that future research appears to be the WAP region, whose climate gradient provides the opportunity to investigate ecosystem response to climate change. In particular, the 200–300-year cycles seen in the paleoclimate records of the WAP challenge us to understand these fundamental processes if we hope to distinguish, both now and in the future, natural from anthropogenic causes of climate change.

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