The Impact of a Large-Scale Climate Event on Antarctic Ecosystem Processes

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Extreme climate and weather events, such as a drought, hurricanes, or ice storms, can strongly imprint ecosystem processing and may alter ecosystem structure. Ecosystems in extreme environments are particularly vulnerable because of their adaptation to severe limitations in energy, water, or nutrients. The vulnerability can be expressed as a relatively long-lasting ecosystem response to a small or brief change in environmental conditions. Such an event occurred in Antarctica and affected two vastly different ecosystems: a marine-dominated coastal system and a terrestrial polar desert. Both sites experienced winds that warmed air temperatures above the 0°C threshold, resulting in extensive snow and ice melt and triggering a series of cascading effects through the ecosystems that are continuing to play out more than a decade later. This highlights the sensitivity of Antarctic ecosystems to warming events, which should occur more frequently in the future with global climate warming.

Keywords: climate change, coastal ecosystems, deserts, microbiology

Ecosystem structure and function are sensitive to climate change because it alters habitat suitability through changes in energy and the availability of water and nutrients (e.g., Elmendorf et al. 2014). Studies of ecosystem response to climate change have focused on temperate and tropical ecosystems, whereas Antarctic ecosystems have attracted much less attention (Priscu et al. 1998, Ducklow et al. 2007, Barrett et al. 2008, Younger et al. 2015). Given that only about 2% of the area on the continent is ice free, the paucity of data on terrestrial ecology is understandable. However, studies in these energy- and nutrient-limited environments with a paucity of biota yield important clues regarding physical versus biotic drivers in ecosystem structure, functioning, and resilience (Barret et al. 2008). Regarding the marine ecology of the Southern Ocean, growing pressure on Antarctic marine ecosystems from increased interest in marine resources accentuate the need to better understand ecosystem vulnerability. In the early 1990s, the National Science Foundation's Long Term Ecological Research Program (LTER) funded two long-term ecological research sites in Antarctica. The first of the two was the Palmer (PAL) LTER, a marine ecosystem within a highly productive continental shelf area west of the Antarctic Peninsula; the second was the McMurdo Dry Valleys (MCM) LTER, a microbial terrestrial ecosystem within a polar desert.

Both sites are highly responsive to small climatic perturbations because they are poised near the 0°C threshold between freezing and thawing. Small changes in weather or climate cross this threshold creating physical changes that trigger cascading ecological responses. A future of warmer, wetter conditions will have profound effects on biodiversity and biogeochemical cycling, and may leave the ecosystems more vulnerable to other drivers of environmental change, such as invasive species. Despite their obvious differences, the two sites have similarities, the most important of which is their icy environments. For PAL, the duration of the sea ice cover and for MCM lake ice thickness strongly influences the marine and lacustrine ecosystems, respectively (Ducklow et al. 2013, Obryk et al. 2016). Because sea-ice variability is driven by winds, temperature, and ocean circulation, it serves as the dominant integrated driver of marine ecosystem change. Most organisms' life cycles are synchronized with the annual changes in sea ice, so changes in ice-season duration can have profound effects on phenology and trophic interactions. For MCM, lake-ice thickness integrates the energy available from the air and solar radiation and controls under-ice light levels and photosynthesis. The energy balance also controls the production of glacial meltwater that feed the streams and lakes. This in turn
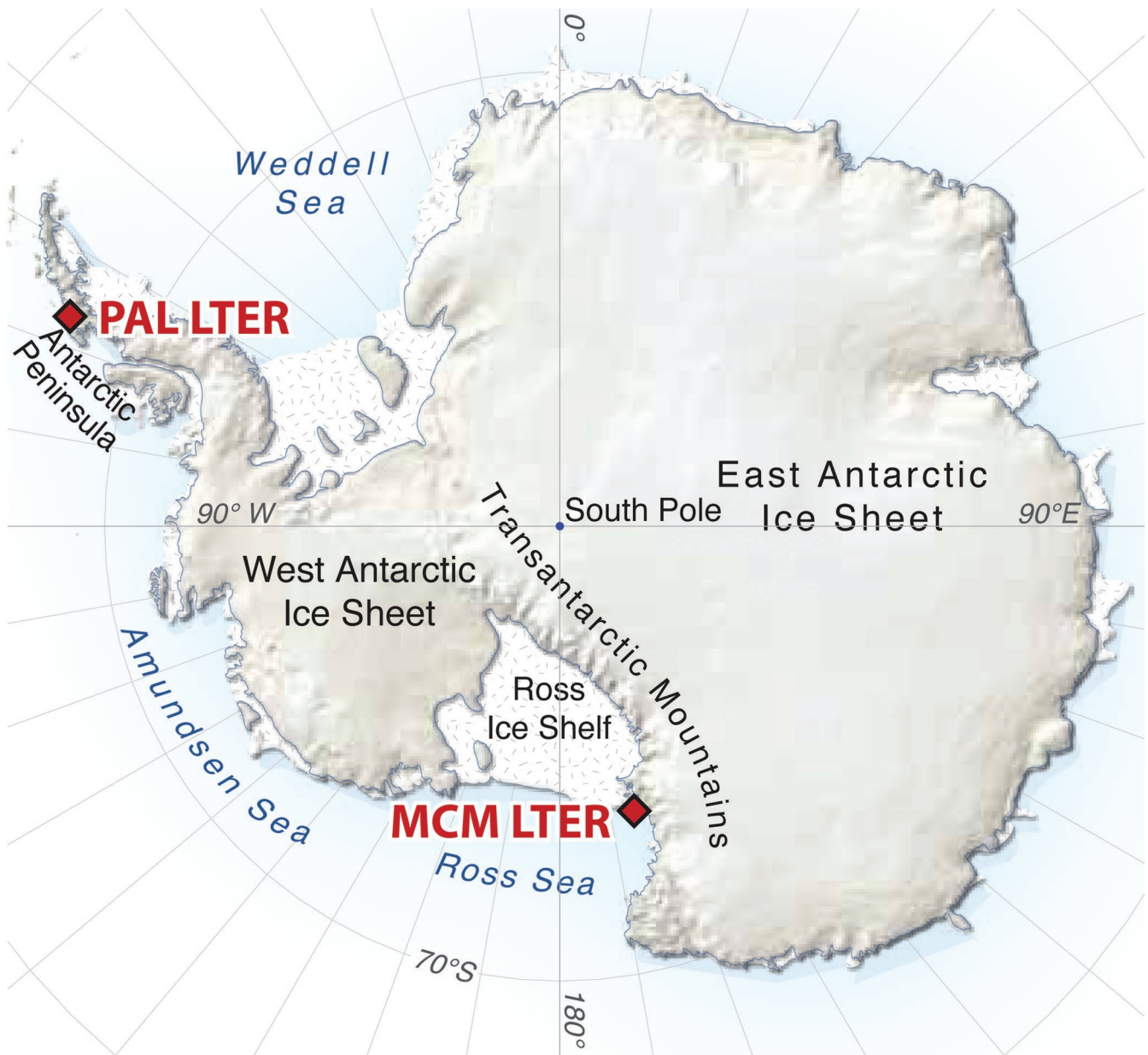
Figure 1. The location of the McMurdo Dry Valley (MCM) and the Palmer (PAL) long-term ecological research sites.

increases connectivity across the otherwise dry landscape. Both ecosystems respond to gradual changes in climate; however, extreme seasonal events can disturb these quasi-stable ecosystems, leaving an ecological legacy for a decade or more (Foreman et al. 2004, Fraser et al. 2013). Here, we focus on the climatic setting and ecological response of each site during a significant climatic event that affected both ecosystems during the austral summer of 2001–2002.

Study sites

The MCM is located in the largest ice-free area of the Antarctic continent (78°S, 162°E; figure 1) and hosts a landscape that

includes glaciers, perennially ice-covered lakes, seasonal melt-water streams, and arid soils (Fountain et al. 1998, Priscu 1998). Arid soils are the most extensive landform occupying 95% of glacier-free surface below 1000 meters (m; Burkins et al. 2001). No vascular plants or vertebrates inhabit the region, and food webs are dominated by bacteria, cyano-bacteria, fungi, yeasts, protozoa, and a few taxa of metazoan invertebrates (Freckman and Virginia 1997, Adams et al. 2006, Cary et al. 2010). The average annual air temperatures vary between –14.8 °C to –30.0 °C, depending on location, with winter (July–August) temperatures reaching –65° C and sum-mer (December–January) temperatures episodically warming

above freezing (Doran et al. 2002). The 65-year average annual air temperature, based on nearby (100 kilometers, km) Scott Base Station, is −19.9° C. Precipitation falls as snow with the greatest snowfall, 50 mm water equivalent, at the coastal margin of Taylor Valley and much less elsewhere (Fountain et al. 2010). Although snow is not an important source of water to the lakes (much of it sublimates before melting) it is an important moisture source for soils (Gooseff et al. 2003, Hagedorn et al. 2007, Langford et al. 2015). Glaciers mantle the valleys walls providing the primary source of meltwater to the streams, which convey water, solutes, sediment, and organic matter to the lakes (Fountain et al. 1998, McKnight et al. 1999). Meltwater is generated only when sufficient energy is available making the hydrology of the MDV energy rather than precipitation limited. Streams flow for up to 12 weeks in the austral summer providing a habitat for microbial mats abundant in streambeds stabilized by stone pavement (McKnight et al. 1999). Ice-covered lakes are the only perennial water environments in the MCM; they maintain biological activity year round, with food webs dominated by phytoplankton and bacteria (Laybourn-Parry 1997, Priscu et al. 1999, Bowman et al. 2016). Perennial ice cover suppresses turbulent mixing, and most lakes are permanently stratified because of strong vertical salinity gradients, with temperature gradients exerting little influence (Spiegel and Priscu 1998).

The PAL is a marine region extending from the coast to about 200 km offshore from Palmer Station on Anvers Island (64.771°S, 64.051°W), and southward about 700 km to Charcot Island (69.451°S, 75.151°W; Ducklow et al. 2007, 2013). The annual average air temperature at Faraday/Vernadsky Station (55 km south of Palmer Station) is −3.7°C with monthly average minimum winter temperatures reaching −24 °C and monthly average summer temperatures of about +7 °C. The extent, duration and seasonality of sea ice and inputs from glacial meltwater are strong influences on the ecological and biogeochemical processes in the coastal marine ecosystem. The ecosystem spans microbial organisms at the base of a food chain to penguins, seals and whales at the top. The annual melting of seasonal sea ice in austral spring provides ideal conditions for fostering large phytoplankton blooms that are typically dominated by large diatoms (Montes-Hugo et al. 2009). Antarctic krill, one of the most abundant metazoans on Earth, take advantage of these ice-edge blooms (Steinberg et al. 2015). Krill, in turn, are food for penguins, seals, and whales (Friedlaender et al. 2011, Saba et al. 2014). However, the annual ice season has decreased by more than 3 months since 1979 (Stammerjohn et al. 2012), inducing large changes in this marine ecosystem in terms of organismal composition, distribution, and trophic linkages (Ducklow et al. 2013).

One important climatic difference between the sites is the duration and intensity of solar radiation, because of a difference in latitude of about 10°. Although the high latitude of both sites ensures continuous sunlight during the austral summer, during the winter, total darkness engulfs MCM for almost 4 months, whereas PAL experiences twilight (figure 2). The ratio
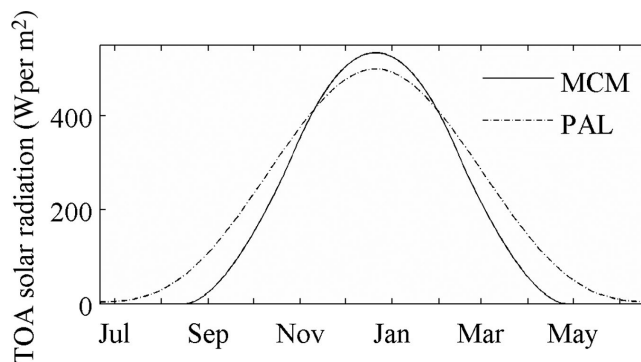

Figure 2. The theoretical top-of-atmosphere (TOA) daily averaged solar radiation in the McMurdo Dry Valleys (MCM) and Palmer Station (PAL). The annual cumulative solar radiation for MCM and PAL is 6.8×10^4 and 7.9×10^4 watts (W) per square meter (m^2), respectively.

of annually cumulative clear-sky solar radiation, MCM to PAL, is 0.85; PAL receives approximately 15% more solar energy.

Climate: The big picture over Antarctica

The global average annual temperature in the twentieth century has increased nearly +1°C and is predicted to continue to rise for decades (IPCC 2007). Effects of this change (i.e., temperature, moisture) manifest differently across the planet owing to differential temperature change and ecosystem sensitivity. On the Antarctic continent, warming is occurring faster than expected on the Antarctic Peninsula and surrounding region, extending as far south and west as Byrd Station in central West Antarctica (80°S, 120°W). This area has warmed five times faster than the global average (on the peninsula, +2.5°C since 1945, Montes-Hugo et al. 2009, McClintock et al. 2008; at Byrd Station, +2.4°C over 1958–2010, Bromwich et al. 2012). In contrast, air temperatures over the rest of the continent during the past half century have either shown little change (Turner et al. 2005) or are warming slowly (Steig et al. 2009).

Hemispheric-scale variations. The PAL and MCM sites are about 3800 km apart and exist in two very different climatic regimes. As we mentioned, MCM is part of East Antarctica, dominated by the continental climate of the Antarctic interior, where air temperature changes over the past half century are equivocal or slightly warming. PAL is a marine-dominated climate exhibiting rapid warming. These two sites are linked climatically through hemispheric patterns of air pressure. The primary mode of atmospheric variability at high southern latitudes is the Southern Annular Mode (SAM), which is a pressure oscillation between the high and midlatitudes of the Southern Hemisphere (Thompson and Wallace 2000). Atmospheric pressure is typically high over the Antarctic continent, low over the Southern Ocean (between approximately 60°S and 75°S) and high over midlatitudes. This pattern is responsible for the westerly winds over the Southern Ocean at approximately 60°S.
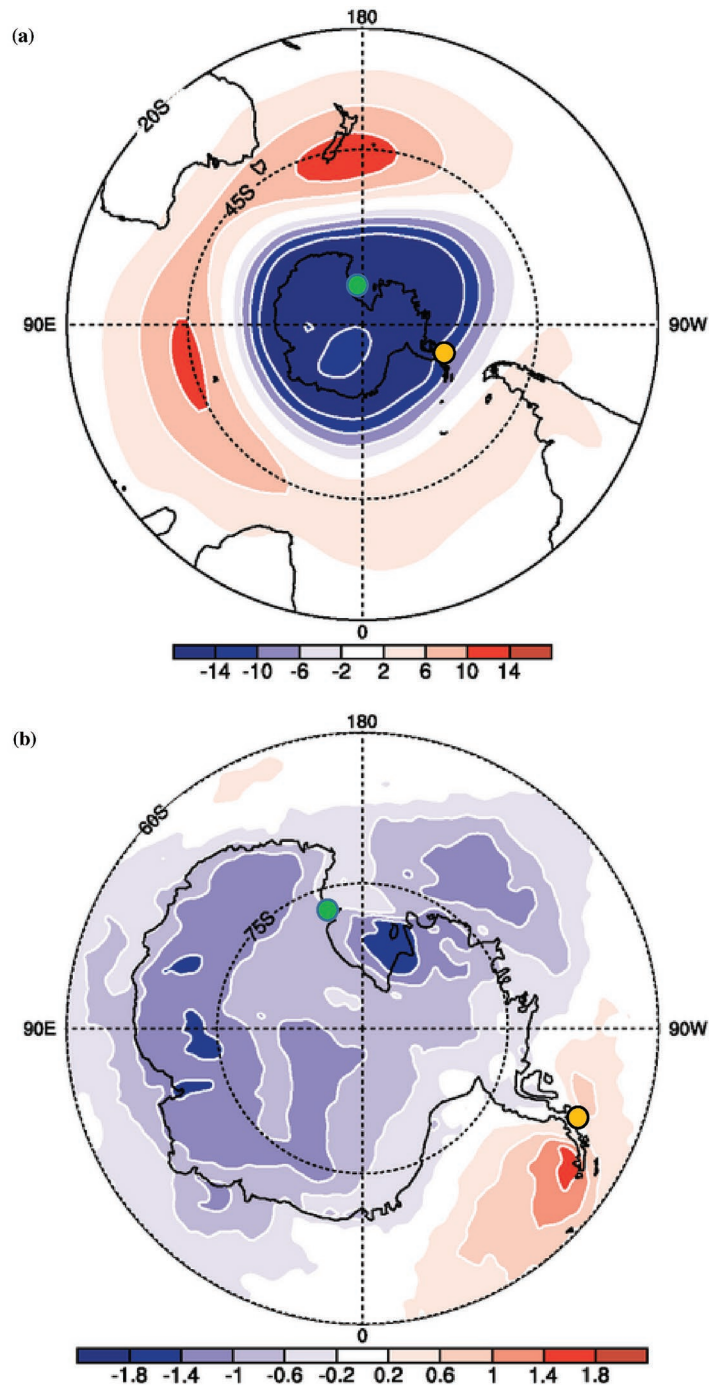
Figure 3. Atmospheric pressure and temperature patterns of the Southern Annular Mode (SAM) from 1982 to 2004, taken from Trenberth and colleagues (2007). The green dot is MCM, and the orange dot is PAL. (a) The positive SAM geopotential height pattern (hPa) as a regression based on the SAM index time series for seasonal anomalies at 850 hPa. Red denotes positive height anomalies (and correspondingly anomalously high surface pressure), and blue denotes negative height anomalies (and correspondingly anomalously low surface pressure). (b) Similarly, the positive SAM surface temperature pattern (degrees Celsius, °C) south of 60°S as a regression based on the SAM index time series. A positive SAM corresponds to anomalously warm surface temperatures in the peninsula area versus anomalously cool temperatures over the continent. Values exceeding about 0.4°C in magnitude are significant at the 1% significance level.

The SAM moves between positive and negative phases (figure 3). When the SAM is positive higher pressures blanket the midlatitudes and lower pressures cover high latitudes: the continent and surrounding ocean (figure 3a). Under these conditions, westerly winds over the Southern Ocean are intensified poleward. When the SAM is negative, conditions are reversed: Higher pressures occur over Antarctica, lower pressures occur over midlatitudes, and the westerly winds weaken.

The phase of the SAM has a major influence on surface temperatures across the Antarctic continent (figure 3b). When the SAM is positive, air temperatures on the Antarctic Peninsula (PAL) are warmer than usual, whereas temperatures over the Antarctic continent, including MCM, tend to be cooler than usual. The reverse is true for the negative SAM phase. A summary of the links between SAM and surface pressure and temperature across the continent—and at PAL and MCM specifically— is illustrated conceptually in figure 4.

The inverse relationship between SAM and surface pressure at PAL are clearly seen in figure 5. With a more positive SAM, surface pressure over the western Antarctic Peninsula (WAP) decreases (Lefebvre et al. 2004, Turner et al. 2009). This translates into an increase in northerly winds over the WAP, which brings warmer air from lower latitudes as well as drives the ice edge southward, leading to less sea ice, increased ocean heat loss, and the enhanced local warming of air temperatures. In contrast, the enhanced westerly winds during a more positive SAM favor cooler temperatures at MCM because of reduced advection of warmer air from midlatitudes. Another factor in the intensity of the WAP temperature response to the SAM is the phase of the El Nino Southern Oscillation (ENSO; figure 5). ENSO modulates the SAM–WAP pressure behavior such that an El Nino co-occurring with a negative SAM—or a La Nina with a positive SAM—can enhance the sea-level pressure (SLP) response, whereas an El Nino co-occurring with a positive SAM_or a La Nina with a negative SAM— can dampen the response (Stammerjohn et al. 2008). At MCM, there is no clear ENSO response or ENSO modulation of SAM.

Negative SAM Phase

Positive SAM Phase
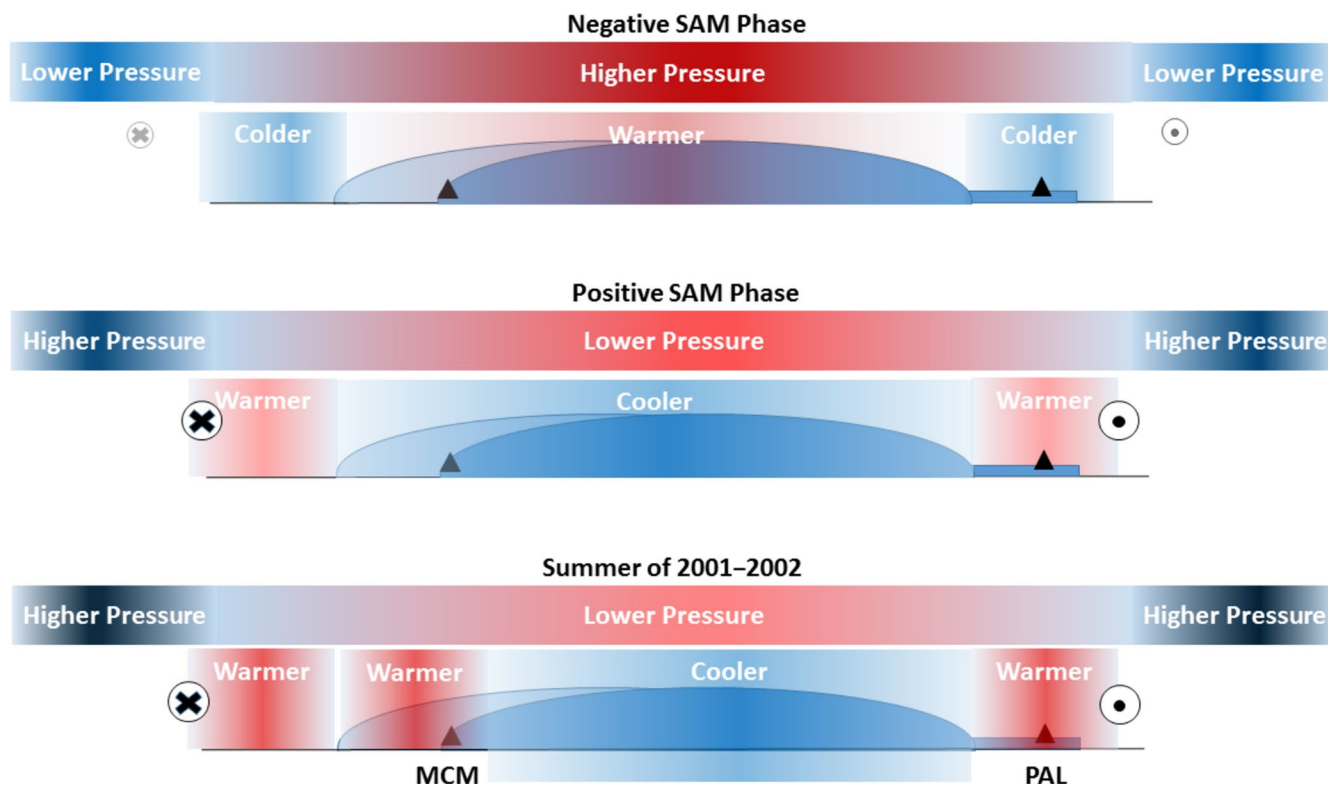
Summer of 2001–2002

Figure 4. A conceptual diagram of the negative and positive phases of the Southern Annular Mode over Antarctica and its effect on surface air temperatures and pressure. The circum-Antarctic wind flow direction and velocity are shown by the arrow out of the page (dot and circle) and the arrow into the page (x and circle). The larger bold markings indicate faster winds. The solid triangles represent the locations of MCM (left) and PAL (right). The double edge of the Antarctic continent on the left represents the geographical position of MCM within the Ross Sea away from the outer edge of Antarctica. The warmer air temperatures at MCM during the summer of 2001–2002 were due to local effects in response to hemispheric conditions.

Local variations. The annual air temperatures at PAL and MCM are inversely related to each other through the SAM patterns, but both sites are warming. This suggests that both sites are climatically linked over the long term (decadal and longer), consistent with continental-wide observations (e.g., Steig et al. 2009). The record at Scott Base, the New Zealand station 5 km from McMurdo Station, shows annual temperatures have increased about 1°C (1958–2014). Over the same period, Faraday/Vernadsky warmed by about +3°C. The half century of warming at Scott Base is smaller than the variation of air temperature over any decade, whereas at Faraday/Vernadsky, the warming is equivalent to the decadal variation. These station-specific results are consistent with Turner and colleagues (2005) and Steig and colleagues (2009), suggesting that significant warming is occurring over the Antarctic Peninsula and parts of West Antarctica, whereas no statistically significant warming has occurred over East Antarctica.

On seasonal scales, trends in surface air temperature show no consistent pattern between sites (figures 6 and 7). The annual warming experienced at PAL is a result of warming during the winter, spring and fall seasons. At MCM, the winter season has been cooling slightly, whereas spring and autumn have been warming slightly. Summer, the most biologically productive period, shows no significant trends at either site and the correlation between sites is insignificant (figure 8).

Both sites, however, are highly sensitive to brief meteorological events (pulses) that can warm or cool the landscape across the melt or freeze threshold causing profound hydrological and ecological consequences. Although no significant correlations exist over annual to seasonal intervals, large-scale hemispheric patterns can create simultaneous pulse events that affect both sites dramatically. Pulses of energy in polar environments, although small by temperate latitude standards, can warm the environment above the melting threshold establishing important ecosystem legacies for decade(s) to come. We contend that the links between physical drivers and biological response can assume very different characteristics depending on the magnitude of the driver and climatic setting of the ecosystem. For example, a ±4°C episode at a mean temperature of +20°C or –20°C may stress an ecosystem but trigger little or no perturbation. However, a similar episode when the environment is stable near 0°C causes a nonlinear response in hydrology and may cause a large perturbation in the ecosystem.
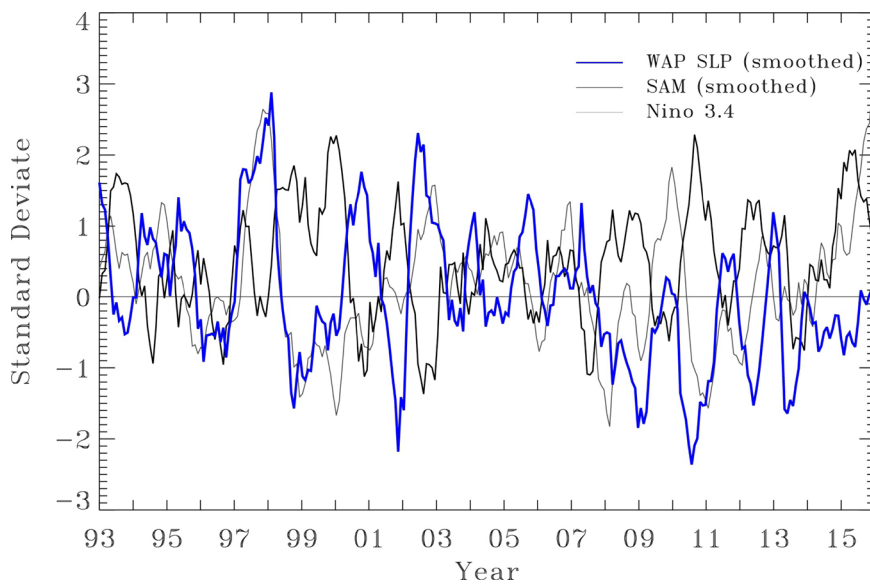
Figure 5. Monthly time series over 1993–2015 of the SAM index (dark gray; Marshall 2003), Niño 3.4 index (light gray; Cane et al. 1986), and sea-level pressure (SLP) extracted from the NCEP–NCAR reanalysis (blue; Kalnay et al. 1996) for the western Antarctic Peninsula region. The SAM and SLP were smoothed with a 7-month running mean filter. All time series are monthly anomalies normalized by the standard deviation.
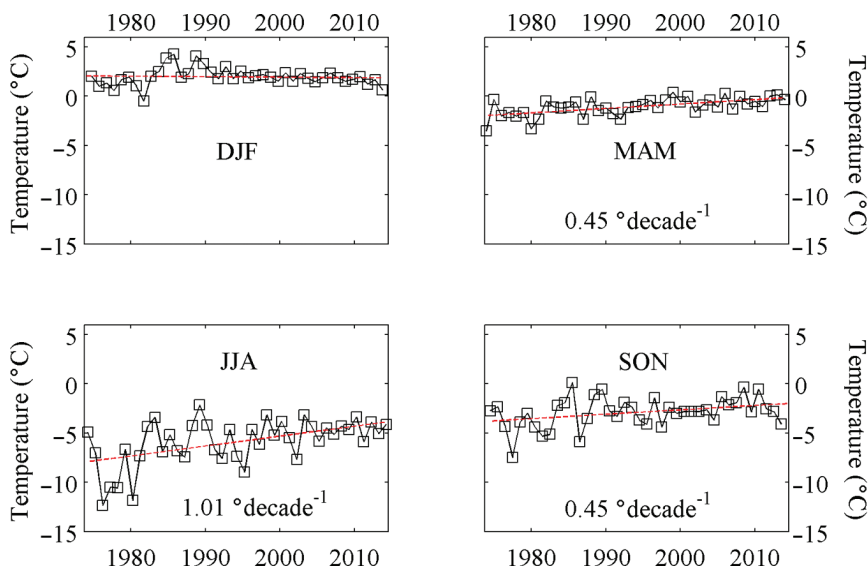

Figure 6. The seasonally averaged surface air temperature (1974–2014) at Palmer (Faraday/Vernadsky), with the trend (slope) over the period of measurements. DJF: December, January, and February. MAM: March, April, and May. JJA: June, July, and August. SON: September, October, and November. Only the statistically significant trends ($p < .05$) are shown.

The 2001–2002 climate event

An exceptional hemisphere-wide atmospheric circulation anomaly developed in September 2001 and persisted until February 2002 (Massom et al. 2006). A deep low-pressure anomaly developed over the Bellingshausen-Amundsen

seas with a very high-pressure anomaly over the South Atlantic (figure 9). The record of atmospheric pressure under the core of the high-pressure anomaly at South Georgia Island was four standard deviations above the 1971–2000 mean, revealing the unusual nature of this evident. In a sense, this anomalous pattern amplified the positive SAM conditions occurring at that time (figure 4) by decreasing pressure over the high latitudes, increasing the pressure over the midlatitudes, and increasing the north-westerly winds and air temperatures over the WAP. Air pressures over the interior Ross Sea and MCM were abnormally low. These hemispheric conditions provided the driver for the extreme conditions that were to follow at each site.

MCM. Before the summer of 2001–2002, the region experienced a cooling trend from 1986, the start of meteorological measurements, to 2000 (Doran et al. 2002a, 2002b). Lake levels decreased because of decreasing input from glacial melt and continual mass loss from sublimation. Lake ice thickened, decreasing light levels to the lake waters, which reduced phytoplankton productivity. Soil ecosystems contracted as populations decreased because of colder, drier soils (Doran et al. 2002b). One of the coldest summers on record was 2000–2001.

The following summer (2001–2002) started cooler than normal, but in mid-December, air temperatures warmed dramatically. A drainage wind from the high elevation Polar Plateau flowed into the valleys, warming adiabatically. This event was likely triggered by the deep and persistent low-pressure anomaly located over the Amundson and Ross seas (Doran et al. 2008, Speirs et al. 2010). Air temperatures increased up to almost +12°C and they remained elevated for several weeks (Doran et al. 2008). For comparison, the number of degree days above freezing in the previous summer (2000–2001) was 5.4, whereas during 2001–2002, it was 57. In a landscape largely devoid of surface water, the rapid melting of glacial ice that encircles the valley bottoms caused streams to flow at record discharge and raised lake levels, thereby regaining the water volume lost over the past decade (figure 10). The flood of water eroded
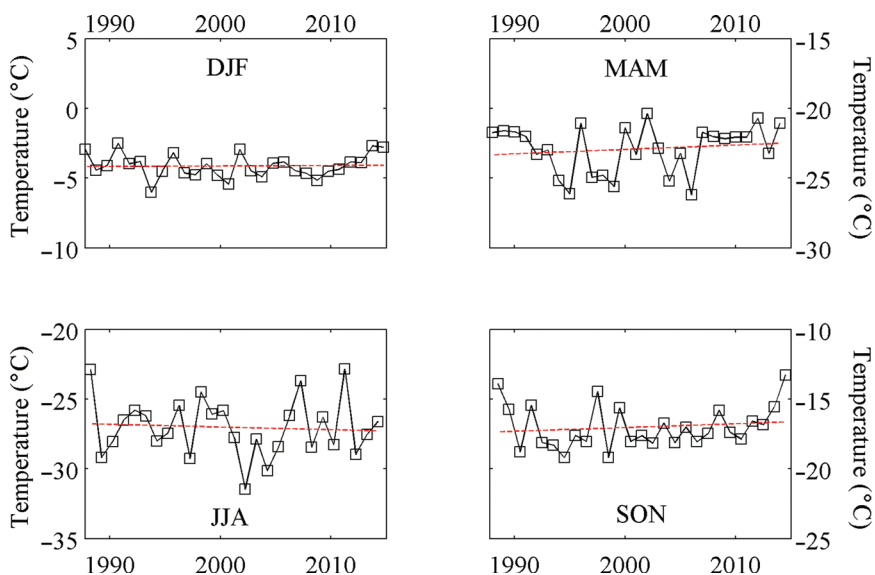
Figure 7. *The seasonally averaged surface air temperature (1987–2014) at McMurdo (Scott Base), with the trend (slope) over the period of measurements. Abbreviations as in figure 6. Note that for the temperature axis, the scale is constant, but the range changes. No significant trends ($p < .05$) were found.*
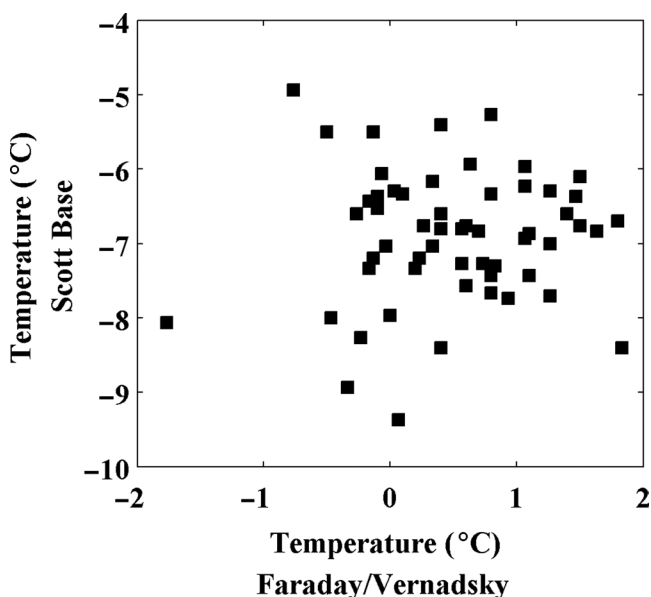

Figure 8. *The mean summer (DJF) air temperatures at Scott Base, McMurdo Sound, plotted against summer temperatures at Faraday/Vernadsky, Antarctic Peninsula.*

stream banks and the plume of sediment-rich stream water clouded the lakes.

The large pulse of melt water affected the physical nature of MCM for more than a decade, and we continue to see oscillations in parts of the ecosystem today. The surface of the lakes and glaciers melted, rapidly revealing sediment entrapped in the subsurface and reducing the albedo of the glaciers and lake ice covers (Jepsen et al. 2010). We suspect that the reduced albedo on the glaciers, resulting in elevated

absorption of solar radiation, increased glacial melt and streamflow compared with the pre-sediment exposure period (Hoffman et al. 2016). Streamflow became more variable and exhibited higher flows (discussed in more detail below). The legacy of the flood year is evident in the lake-level record (figure 10), which shows continuous level increase after the flood year in all lakes.

The flood event changed the clarity, chemistry, and biological activity of the lakes. The water clarity decreased dramatically because of a large influx of fine-grained sediment during the flood and the record at Lake Bonney is a good example (figure 11a). The lake required about 5 years for water clarity to return to pre-flood values because, like most lakes in the MCM, it has no outlet and the fine-grained, glacially derived, suspended sediment has a slow settling velocity. The flood also diluted the chloride concentrations of the near-surface waters, which over the past decade had been freeze-concentrating salts in the absence of sufficient freshwater replenishment (Barrett et al. 2008).

The near-surface waters of the lakes are either phosphate or nitrogen deficient and derive nutrients from upward diffusion across the chemocline and advection from inflowing streams (Priscu 1995). During the 2002 flood, the relative stream loading of dissolved inorganic nitrogen and soluble reactive phosphorus increased by a factor of eight, compared with that in the preceding 8 years (figure 12). The increased proportion of stream advected nitrogen and phosphorus during flood events, relative to that from upward diffusion, can drive the nutrient status of the lakes and associated primary productivity for years (Foreman et al. 2004).

Changes in water clarity (available sunlight) and nutrient availability affect chlorophyll concentrations. Integrated photic zone chlorophyll-*a* dropped almost threefold during the flood event, presumably caused by the turbid water reducing light and thereby phytoplankton primary production (figure 11b; Foreman et al. 2004). The subsequent rapid rise in chlorophyll concentrations and above-normal concentrations in the 5 years following the flood are likely the result of elevated advected nutrient loading during the flood.

Streamflow records are useful surrogates for differences in seasonally integrated surface energy balance. The streamflow record from the Lake Fryxell basin indicates a general decline in meltwater generation from 1990 to 2001 (figure 13). During this period, mean annual streamflow was 0.85×10^6 cubic meters (m^3; variance, 0.86×10^9 m^3). The highest annual flows on record occurred in the 2001–2002 flow season and the total streamflow exceeded 5×10^6 m^3. Although this was one of the warmer summers on record, it
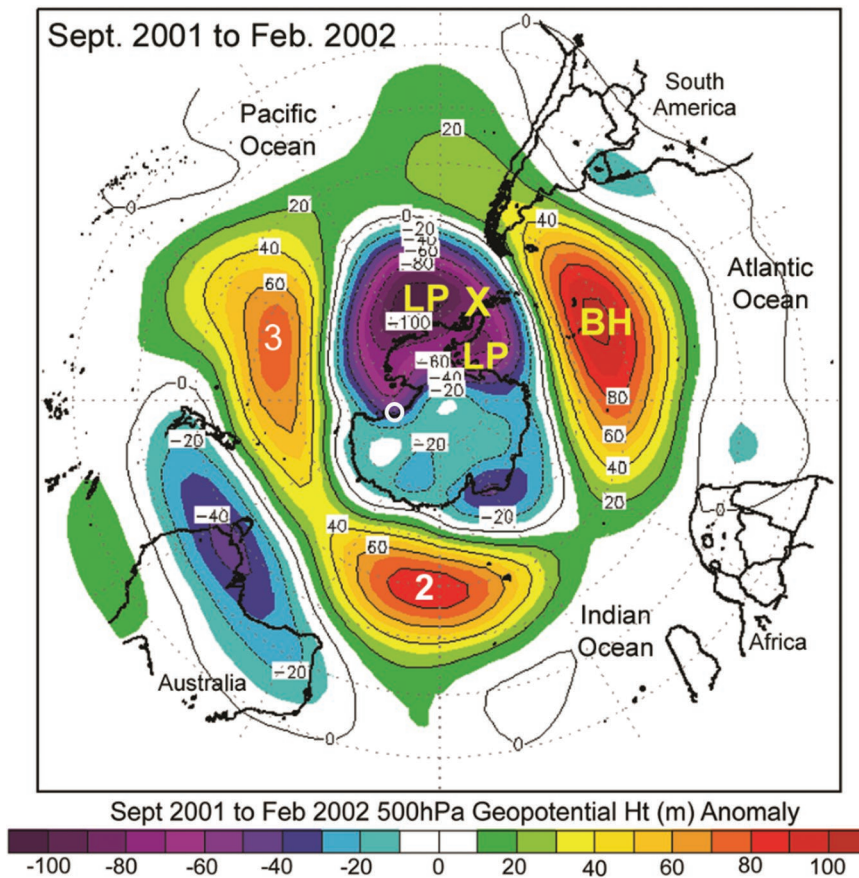
Figure 9. Monthly mean composite anomaly map of 500-hPa geopotential height centered over Antarctica for September 2001 to February 2002 relative to the mean calculated over September to February 1980–2001. BH and LP denote blocking high pressure and low-pressure anomalies, respectively. The X is close to Palmer Station, and the circle is McMurdo. Reproduced from the **Journal of Climate***, Massom et al. 2006 with permission from Robert Massom.*
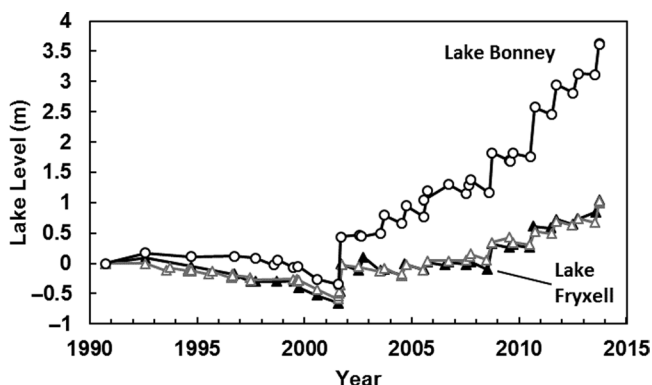

Figure 10. Lake level change since 1990 (datum) in Taylor Valley, Lake Bonney (open circles), Lake Hoare (gray open triangles), and Lake Fryxell (black closed triangles). Note the abrupt lake level rise of summer 2001–2002. Abbreviation: m, meters.

was not the warmest (figure 7), suggesting that solar radiation played a greater role in a more positive energy balance than in other years (Doran et al. 2008). Over the 10 years since 2001–2002, the mean annual discharge almost doubled

to 1.59×10^6 m^3 (variance, 1.28×10^9 m^3). This wetter and more variable condition is likely to have significant effects on the distribution of microbial mats in stream and associated diatom community diversity (Stanish et al. 2011), because both are sensitive to flow conditions and scour (Cullis et al. 2014). Stream algal biomass decreased in the decade prior to 2001–2002 and increased with the higher stream discharges in the decade after (Kohler et al. 2014). This finding is consistent with the cooling trend during the first decade when the ecosystem was contracting generally (Doran et al. 2002a) and then expanded with increased melt and streamflow.

The direct influence of the 2001–2002 flooding is less obvious in the soils because of the channeling of water in the streams. However, field experiments clearly show the effects of heat and moisture. The diversity and community structure of soil invertebrates are sensitive indicators of changing trends in the soil environment, especially temperature and moisture (Simmons et al. 2009, Ayres et al. 2010). Warming of Taylor Valley soils in a multiyear experiment decreased the population size of the dominant nematode *Scottnema lindsayae* by 42% (Simmons et al. 2009). Soil nematodes respond to sustained increases in soil moisture whether it was from melting snow patches (Ayres et al. 2010), the melting of buried ice (Nielsen et al. 2012), or the creation of local seeps (Ball and Virginia 2012, Smith TE et al. 2012). For the summer of 2001–2002, increased moisture shifted the nematode community structure in favor of species that are more limited by available soil moisture for several years (Barrett et al. 2008). A caveat regarding the interactive effects of moisture and salinity for determining the response for soil biota is important to mention. Water additions to saline soils may produce unfavorable osmotic conditions, but if salts are leached from the soil, then the habitat suitability for life can increase.

Changes in the soil thermal regime will alter the phenology and potential growth and reproduction of soil animals. *Scottnema lindsayae* becomes metabolically inactive when frozen or when soil gravimetric moisture drops below around 4% (Treonis et al. 2000). The response of soil invertebrates to climate change is difficult to predict, but both field experiments and field observations show that soil biota do respond to shifting soil climate and that these changes are probably coupled with processes such as carbon cycling and nutrient availability.

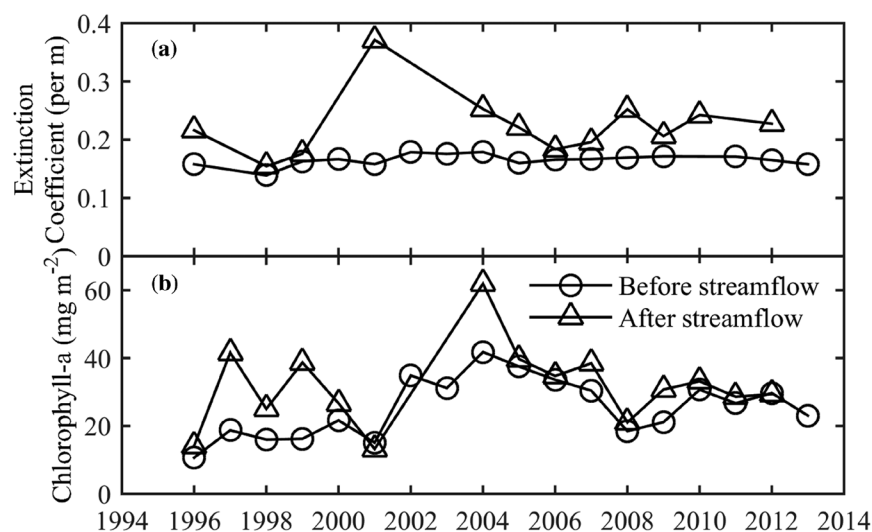**PAL.** The austral summer in the WAP is highly productive with the occurrence of large phytoplankton blooms

Figure 11. Water clarity and chlorophyll-a concentrations measured from near the bottom of the ice to the bottom of the trophogenic zone (5–20 meters [m]) in the west lobe of Lake Bonney. Measurements were made in the spring (October–November) before the onset of stream flow and again in mid–late summer (December–January) during the period when streams flow. (a) Water clarity represented by the average extinction coefficient of photosynthetically available radiation; higher extinction = less clarity. (b) Integrated chlorophyll-a concentration. The ice cover ranged from 3 m to 4 m thick over the period of measurement; the upper depth for all measurements was 5 m, approximately 1 m beneath the bottom of the ice. Abbreviation: m^2, square meters; mg, milligrams.

that support Antarctic krill and ultimately many marine top predators including penguins, whales, seals, fish, and flighted sea birds. This ecosystem is characterized by high interannual variability that is punctuated by strong positive anomalies of chlorophyll-*a* biomass and krill recruitment occurring every 4 to 6 years (figure 14; Fraser and Hofmann 2003, Smith RC et al. 2008, Saba et al. 2014, Steinberg et al. 2015). These cycles are a function of preceding winter and spring physical processes, which are driven by SAM and/or ENSO variability (Marshall et al. 2004, Stammerjohn et al. 2008, Venables et al. 2013, Saba et al. 2014). Factors that promote spring–summer *in situ* sea-ice melt also favor phytoplankton blooms. These factors include, on the basis of observations in Marguerite Bay and near Palmer Station, low winds in winter and a stable sea ice cover (typically a longer ice season), followed by conditions that enhance the stability of the water column: reduced spring–summer winds and a shallow, melt-enhanced ocean mixed layer (Venables et al. 2013, Saba et al. 2014). These conditions typically occur near Palmer Station during a negative SAM in winter and spring, when winds tend to be relatively weak but more southerly, bringing cold air from the continent (Saba et al. 2014). In contrast, during a positive SAM, strong, warm northwesterly winds dominate, decreasing the winter sea-ice cover and water-column stability (Saba et al. 2014).

The exceptional 2001–2002 spring–summer season did not follow the normal seasonal pattern and it had a profound impact on sea ice and biota in the PAL study region, with both positive and negative ecological consequences. Typically, low-pressure systems move through the WAP on a quasi-weekly basis (King and Turner 1997), but in the spring of 2001–2002, storm activity was persistent and intense, bringing much greater snowfall than normal. During the 6-month period from September 2001 to February 2002 (figure 9), warm, moist northwesterly winds blew across the WAP at speeds greater than the PAL time series average (more than 10 m per second; Massom et al. 2006). This resulted in a rapid ice-edge retreat in early spring that compacted the marginal ice zone southeastward against the peninsula (figure 15), greatly reducing the areal extent of sea ice while dramatically increasing its thickness (Massom et al. 2006). It was this compaction and thickening of sea ice that was so unusual, which also resulted in sea ice persisting through summer.

The anomalous climate–sea ice conditions triggered equally anomalous ecological responses that encompassed all levels of the food web (Bowman et al. 2016, Obryk et al. 2016). Despite persistent high winds and reduced sea ice extent, phytoplankton productivity and biomass were anomalously positive (figure 14; Massom et al. 2006, Saba et al. 2014). Large phytoplankton blooms occurred both within and offshore of the compacted marginal ice zone (Massom et al. 2006). Waters near Palmer Station exhibited the highest summer depth-integrated (50 m) primary productivity (8000 milligrams per square meter per day) and one of the highest depth-integrated chlorophyll-*a* accumulations (200 milligrams per square meter) recorded since the start of PAL (figure 14; Saba et al. 2014). Although pigment data were not available for this season, accumulations of this magnitude are typically indicative of diatom dominance. In addition to seasonal sampling near Palmer Station, PAL also conducts a research cruise along the WAP every January since 1993. On the basis of those region-wide observations, chlorophyll-*a* trends in Marguerite Bay in the southern WAP are similar to those farther north near Palmer Station. In January 2002, however, chlorophyll concentrations at the inshore cruise grid stations in the center of Marguerite Bay and in the Marguerite Trough were the highest or second highest compared with those in other years recorded in the PAL time series. These extensive blooms were likely a function of mixed layer freshening that resulted from increased snowfall and warm air melting the compacted sea ice (Massom et al. 2006, Saba et al. 2014). In addition, the intense winds caused ice floes to collide and pulverize, releasing microalgae from
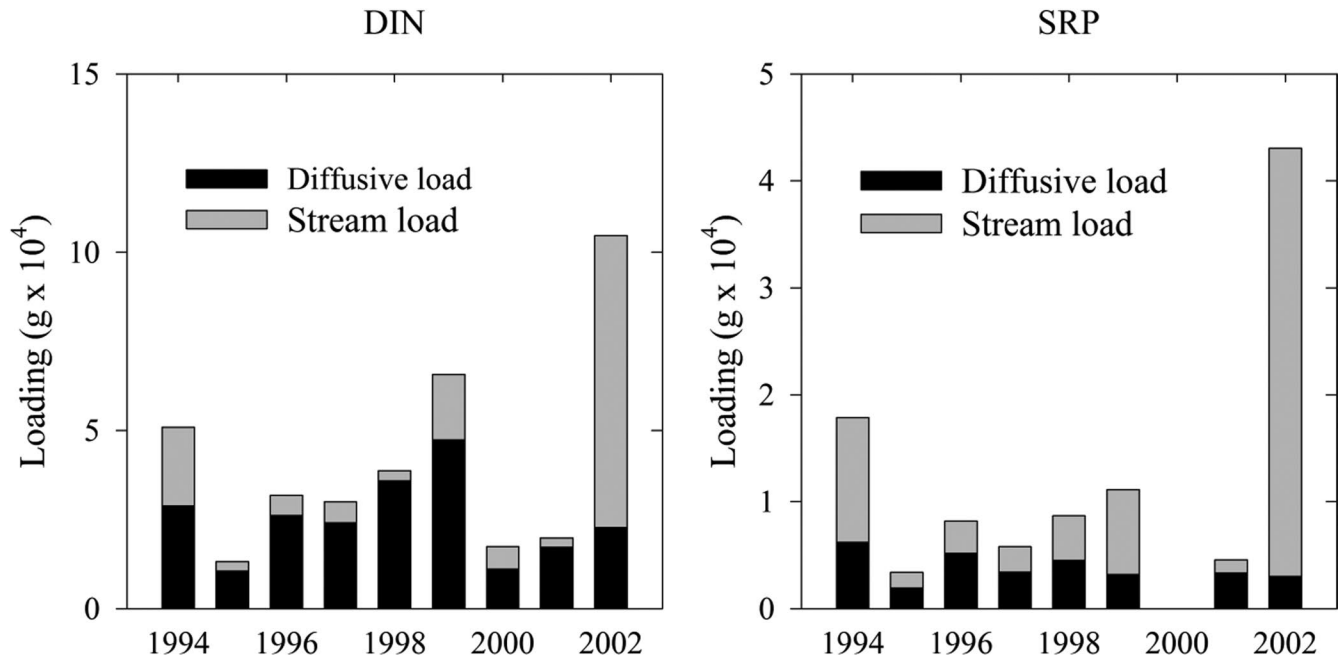
Figure 12. Nutrient loadings for Lake Fryxell from upward diffusion across the chemocline and advective stream loading flow. Abbreviations: DIN, dissolved inorganic nitrogen (nitrate-N + nitrite-N + ammonium-N); g, grams; SRP, soluble reactive phosphorus.
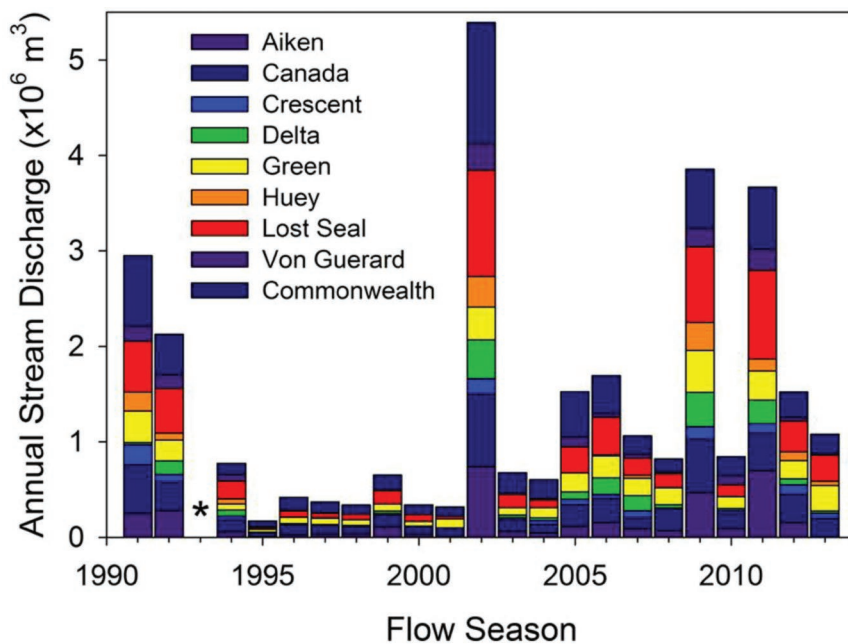

Figure 13. Annual streamflow volumes observed at stream gauges in the Lake Fryxell basin. The flow season is indicated by the following year that occurs during the flow season (i.e., the 1997–1998 flow season is labeled as 1998); * indicates no data. Over the instrumental record, episodic equipment problems interrupted data collection, and in these cases, we used flow season correlations to adjacent streams to estimate discharge records (all correlations $R^2 > .70$). Abbreviation: m^3, cubic meters.

the sea ice, and the reduced sea ice extent increased the area of open water to sunlight (Massom et al. 2006).

By January 2002, several zooplankton species showed positive abundance anomalies along the western Antarctic Peninsula (Steinberg et al. 2015). Abundances of krill species *Euphausia superba* and *E. crystallorophias* were higher than the PAL time series average, probably because sea ice and productivity were concentrated inshore (Massom et al. 2006), where these species tend to dominate (Steinberg et al. 2015). Offshore, in the ice-free slope region, species that prefer lower sea ice conditions were also more abundant, including krill species *Thysanoessa macrura*, salps (*Salpa thompsoni*), pteropods (*Limacina helicina*), chaetognaths, and polychaete worms (Steinberg et al. 2015). The positive chlorophyll-*a* anomaly in 2001–2002 corresponded to a statistically significant krill recruitment event (evidenced in Adélie penguin diet samples) that resulted in the start of a new krill cohort the following 2002–2003 season (figure 14; Saba et al. 2014).
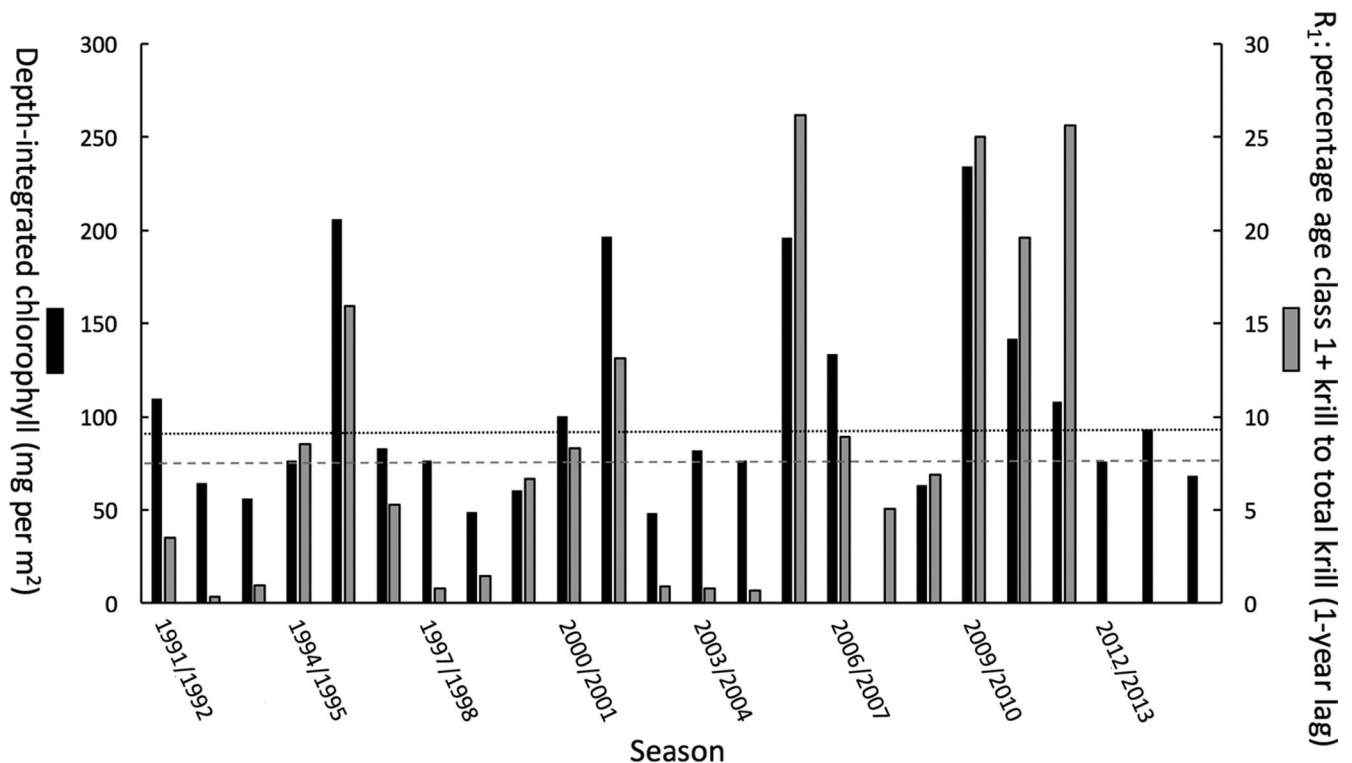
*Figure 14. The interannual variability of Palmer Station chlorophyll-*a *(black bars) and Antarctic krill (*Euphausia superba*) recruitment (gray bars) for the PAL-LTER time series, 1991–2015. Chlorophyll-*a *was depth integrated (0 m–50 m) for each profile, and data were pooled from two sampling stations near Palmer Station and averaged for each summer season (December–January–February). The average depth-integrated summer chlorophyll-*a *was 104 milligrams per square meter (black dotted line). Krill recruitment of age class 1+, or R1, is defined as the percent contribution of krill less than 30 millimeters to the total number of krill in Adélie penguin diets near Palmer Station during each January, with a 1-year time lag following the previous summer chlorophyll-*a*. The average R1 was 8.8% (gray dashed line). (See Saba et al. 2014 for detailed methods.) Abbreviations: m², square meters; mg, milligrams.*

Penguins are some of the longest studied species in the PAL and include Adélie (*Pygoscelis adeliae*), gentoo (*P. papua*) and chinstrap (*P. antarctica*). Their contrasting demographics responses to the 2001–2002 event provided important insights into key mechanistic processes that determine the winners and losers among top predator populations in this rapidly warming environment. Significant changes in the abundance of this predator guild have occurred in the PAL region during the last four decades. Adélie penguins have decreased by 85%, whereas chinstrap and gentoo penguins have increased by approximately 3700% and approximately 22,700%, respectively (figure 16). Key demographic metrics that are important determinants of population growth rates of these species (cf. Ainley 2002) are shown in table 1. In contrast to chinstrap and gentoo penguins, whose breeding populations exhibited minimal losses (3% and 17%, respectively) when compared with those in the previous season, Adélie penguin breeding numbers decreased by 40%. Chick production (chicks crèched per breeding pair) was even more depressed, falling between seasons by 55%, whereas in chinstrap and gentoo penguins, this important metric decreased only marginally by 6% and 13%, respectively. For Adélie penguins, another

important metric exhibiting a significant change between seasons was chick fledging weight, which decreased by 8%, and represents the lowest fledging weight ever recorded in our multidecadal time series (Chapman et al. 2011, Cimino et al. 2014). Unfortunately, comparable data are not available for gentoo and chinstrap penguins. Indeed, 2001–2002 stands as the worst breeding season for Adélie penguins in the 40-year records available for this species.

The 2001–2002 summer season illustrates at least one of many confounding issues of penguin ecology. Like most Southern Ocean predators, the diets of these penguins' species are heavily dependent on Antarctic krill *Euphausia superba* and its abundance can increase rapidly between seasons following successful recruitment events. Such events can have equally positive impacts on many aspects of penguin breeding and foraging ecology (Fraser and Hofmann 2003). Unsurprisingly, causal explanations regarding population growth rates in these penguin species have emphasized changes in krill abundance and availability (e.g., Trivelpiece et al. 2011). Although this tenet has long been questioned (Fraser et al. 1992), support for more robust explanations remains elusive (Trathan et al. 2012). The summer of 2001–2002 proved to be an extremely
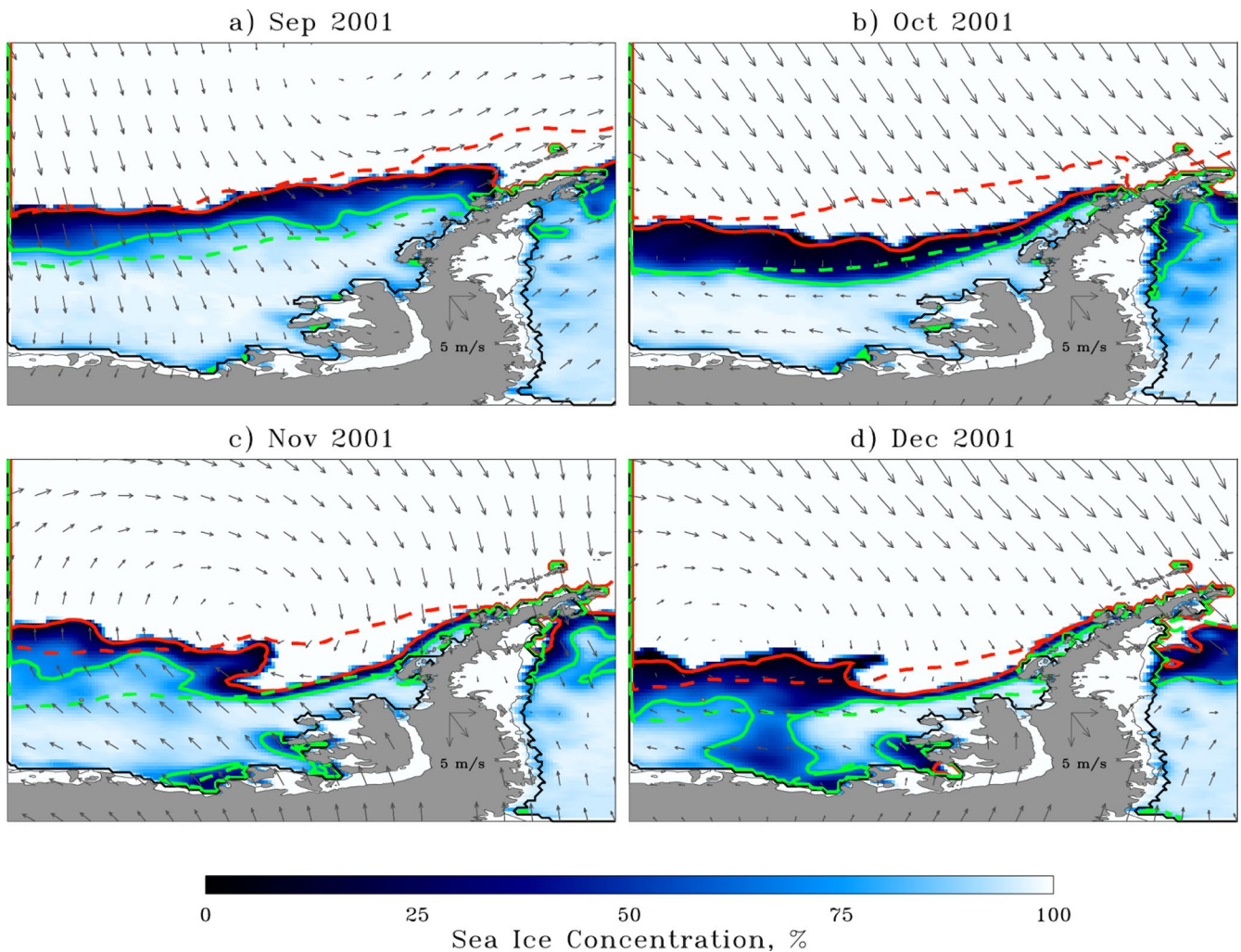
Figure 15. Maps of monthly sea-ice concentration (in blue-white) and wind anomalies (gray vectors) for September 2001 to December 2002. Sea-ice concentration is denoted by the color bar at bottom, with 100% open ocean seaward of the ice edge indicated in white. The continental landmass is in gray, and the ice shelves adjacent to land are in white. The magnitude of the wind speed anomaly is shown by the vector legend. The red and green solid contours indicate the locations of the 15% and 75% ice concentration isopleths, whereas the red and green dotted contours indicate the long-term mean (1978–2013) locations of the 15% and 75% isopleths. The satellite-observed sea-ice concentrations are from the Goddard Space Flight Center (GSFC) Bootstrap Scanning Multi-Channel Microwave Radiometer-Special Sensor Microwave/Imager (SMMR-SSM/I) Version 2 time series (Comiso 2010). The wind anomalies were computed using NCEP-NCAR reanalysis (Kalnay et al. 1996) monthly mean 10-m winds, with anomalies derived from 1978–2013 means.

successful krill recruitment season (Saba et al. 2014), but the demographic responses by the penguins were not only inconsistent between species but indeed either trended completely away from expectations (cf. Fraser and Hofmann 2003) or were basically unchanged relative to the previous season (figure 16; table 1). Despite having similar diets, it is this variability in demographic signatures over annual to decadal scales within and between these species throughout the WAP that brings into question the assumed nearly singular role that krill may have in penguin ecology.

The strong and persistent northwesterly flow of mild and moist air across the WAP in 2001–2002 (figure 15) also produced a record high snowfall (more than 5.5 mm per day) that encompassed much of the critical spring and early summer breeding period of these penguins (Massom et al. 2006). As evidenced by the partial recovery of breeding adults in 2002–2003 (figure 16), the 40% decrease in Adélie penguin breeding pairs during 2001–2002 was due in part to deferred breeding during this anomalous snowfall rather than mortality. The flooding of nests due to snowmelt—leading to parental abandonment, the drowning of large numbers of eggs and chicks, and enhanced energetic costs due to the wetting of surviving chicks—has now been linked unequivocally to the dismal reproductive performance of Adélie penguins during this season (Massom et al. 2006, Chapman et al. 2011, Cimino et al. 2014).
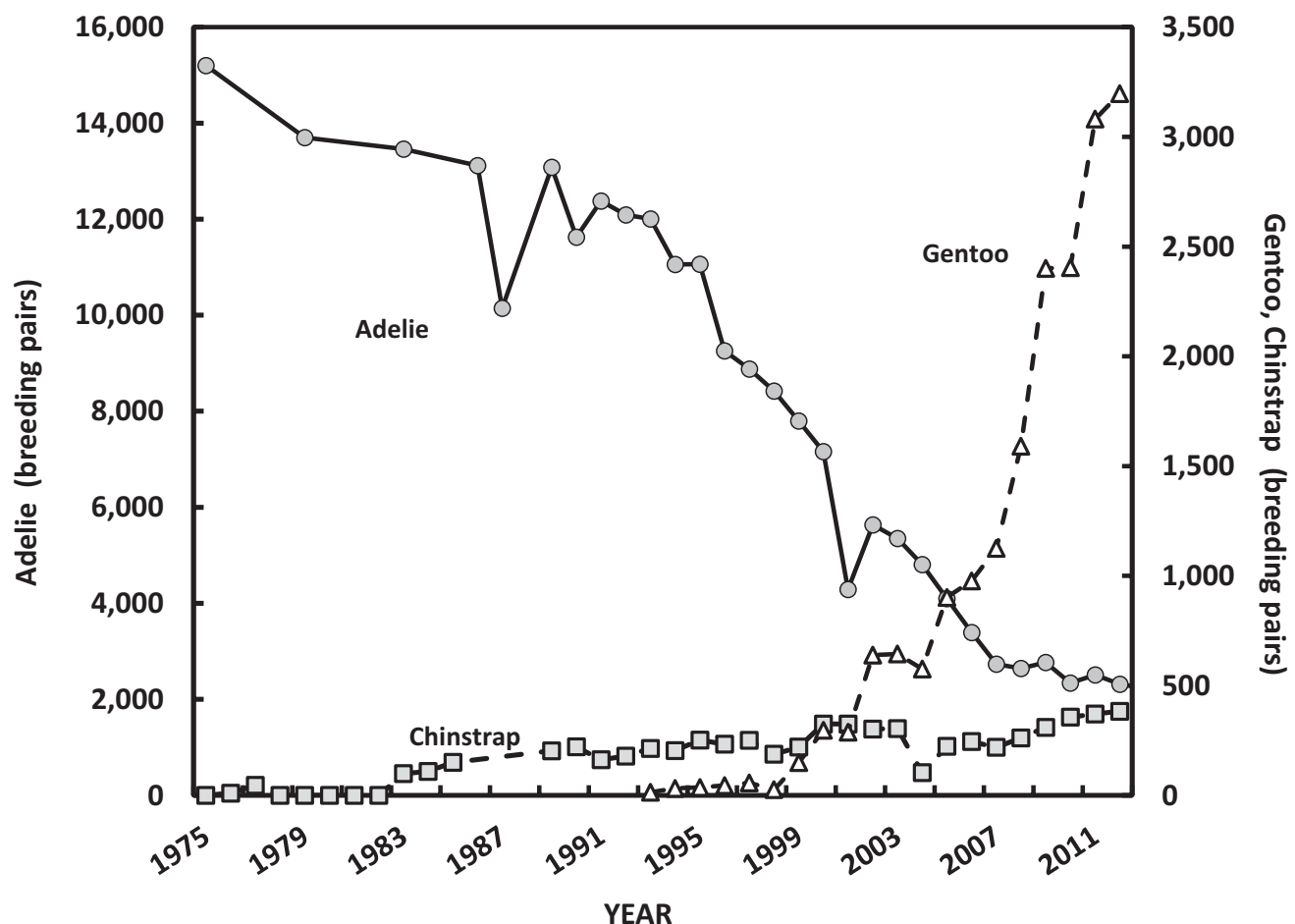
Figure 16. Decadal changes in the number of Adélie, chinstrap, and gentoo breeding pairs at selected PAL study sites.

These observations and analyses by Fraser and colleagues (2013) show that variability in the demography of these species is regulated at least in part by interactions between breeding habitat geomorphology (colony position relative to elevation, slope and aspect) and spatiotemporal patterns of snow deposition during winter and spring storm events. A critical difference in the breeding chronology of these three penguin species is that chinstrap and gentoo penguins may breed up to 3 weeks later than Adélies, a life-history trait that seems to allow these species to effectively avoid the flooding events that invariably follow early spring storms. Indeed, a noted pattern supporting this observation is that the increases in chinstrap and gentoo populations in our region (figure 16) do not occupy new breeding colonies but instead reoccupy colonies abandoned by Adélie penguins. Increased snow deposition in this rapidly warming marine ecosystem may therefore be favoring some life-history strategies over others and at least in part may be driving the structural changes in the composition of seabird communities now evident in the region (Fraser et al. 2013).

Although the effects of the 2001–2002 season clearly continue to affect the MCM Dry Valleys, they have not persisted in the WAP. There is some evidence of a cascading effect in

Adélie penguins (population decreased at about 5.89% per year from 2002 to 2012, compared with only 2.26% per year from 1987 to 2000); however, no overall changes in chlorophyll-*a* or Antarctic krill have occurred in the PAL region since 2001–2002 (Saba et al. 2014, Steinberg et al. 2015). Instead, abundance peaks such as those seen in 2001–2002 have continued to occur every 4–6 years, and even more frequently for krill in the last 5 years (figure 14; Saba et al. 2014). These cyclic phenomena, which are tightly coupled to water-column processes (Venables et al. 2013, Saba et al. 2014), may make some marine ecosystem variables more resilient to extreme events while still being vulnerable to longer-term climate change (e.g., Montes-Hugo et al. 2009).

There were other years when persistent positive SAM and blocking high conditions simultaneously occurred (e.g., 1999–2000; Massom et al. 2006), but the impact on winds and sea ice was quite different. The difference between these other years and 2001–2002 season appears to be related to the interaction between SAM and ENSO. During the 2001–2002 season, SAM was positive and ENSO was relatively neutral, whereas during the 1999–2000 season, SAM was positive concurrently with La Niña conditions. In general, conditions along the western Antarctic Peninsula are similar during a

Table 1. Changes in key demographic metrics between 2000–2001 and 2001–2002 for three penguin species.

Penguin Species	Breeding pairs		Reproductive success		Fledging weights	
	2000–2001	2001–2002	2000–2001	2001–2002	2000–2001	2001–2002
Adélie	7171	4288	1.47	0.66 (1.15)	3068	2836 (3057)
Chinstrap	307	254	1.45	1.37 (1.30)	No Data	No Data
Gentoo	296	288	1.57	1.37 (1.37)	No Data	No Data

Note: Reproductive success is measured as chick crèche per breeding pair, and fledging weights are given in grams. The numbers in parentheses compare these data with long-term averages for Adélie (1991 per 12), chinstrap (1991 per 12), and gentoo (1993 per 12) penguins.

La Niña as they are during positive SAM conditions, with an increase in storm frequency and a decrease in sea ice cover (Yuan 2004, Stammerjohn et al. 2008). However and in contrast to 2001–2002, the winds were more northerly and less northwesterly, leading to less compaction of sea ice against the peninsula (and more southward advection of sea ice out of the PAL region), such that by January 2000 there was little to no sea ice in the PAL area. The lack of a compacted marginal ice zone going into summer is the main reason for the low biological productivity observed during 1999–2000. Near Palmer Station, chlorophyll-*a* biomass and primary productivity were 68% and 87% lower, respectively, during the 1999–2000 season compared with that observed in 2001–2002. Both summer mixed layer depth (SMLD) and the permanent pycnocline (the depth of the temperature minimum [T_{min}] in the remnant nutrient-rich Winter Water layer underlying the surface waters) in this region were deeper during 1999–2000 compared with those during 2001–2002 (SMLD: 11.5 m versus 8.6 m; T_{min}: 35 m versus 15 m). Furthermore, both the SMLD and depth of T_{min} in 1999–2000 were deeper than the PAL time series average, whereas they were shallower than average during the 2001–2002 season because of the presence of the compacted marginal ice zone and the enhanced melt of snow and sea ice. A shallower SMLD and depth of T_{min} are correlated with higher primary productivity and chlorophyll biomass, likely because of increased potential for the injection of macro- and micronutrients in the upper mixed layer. Steinberg and colleagues (2015) also reported lower-than-average primary productivity, chlorophyll-*a* biomass, and abundances of several major zooplankton species (*Euphausia superba*, *Thysanoessa macrura*, and *Salpa thompsoni*) over the entire PAL sampling grid during the 1999–2000 season.

Conclusions

Ecosystem processes in both terrestrial and marine environments are often influenced by discrete climate events, traditionally described as *pulses* (Berkelmans et al. 2004; Schwinning et al. 2004). Such events can be extreme in terms of magnitude (e.g., intense precipitation, ice melt) but may or may not have substantial impacts on the ecosystem. In fact, such temporal climate variability is a characteristic property that contributes to both the structure—in terms of community composition—and functioning, such as its biogeochemistry and production. However, discrete climate

events occurring near a physio-ecological threshold can have a disproportional influence over ecosystems relative to the temporal scales over which they occur (Pennington and Collins 2007, Diaz and Rosenberg 2008). These effects can vary spatially over time and can influence ecosystem heterogeneity at many scales. We find these principles to apply to our study sites in Antarctica.

The two LTER sites in Antarctica are distinct, and each responds to its own mesoscale climatic influences. Periodically, these two disparate sites are linked by a continental-wide atmospheric pattern that pulses each site more or less simultaneously. Although the process of pulsing at each site is quite different—low pressure draws föhn winds at MCM, whereas low pressure over PAL means enhanced storminess and increased northerly winds—both sites were exposed to unusually warm winds. Although such ephemeral teleconnections certainly exist elsewhere, the importance and effect in polar regions can be dramatic for three reasons. First, the summer climate is close to the freeze or thaw threshold, and small changes in available energy (air temperature, solar radiation) create a highly nonlinear response in precipitation and hydrology between the dry, frozen state and the wet, thawed state. Ecosystems dependent on or threatened by one state or the other respond accordingly in a dramatic manner. Second, the space for terrestrial habitat in Antarctica is quite limited, conferring an island-type geography with little or no space for refuge or migration for highly adapted species in response to rapid environmental change. Consequently, a pulse event can severely alter—if not eliminate—an otherwise thriving ecosystem. Finally, episodic pulse events in nutrient-poor, energy-limited environments have long legacy effects that perturb the environment and limit recovery.

Acknowledgments

References cited

Adams BJ, et al. 2006. Diversity and distribution of Victoria Land biota. Soil Biology and Biochemistry 38: 3003–3018.

Ainley D. 2002. The Adélie Penguin: Bellwether of Climate Change. Columbia University Press.

Ayres E A, Nkem JN, Wall DH, Adams BJ, Barrett JE, Simmons BL, Virginia RA, Fountain AG. 2010. Experimentally increased snow accumulation alters soil moisture and animal community structure in a polar desert. Polar Biology 33: 897–907.

Ball BA, Virginia RA. 2012. Meltwater seep patches increase heterogeneity of soil geochemistry and therefore habitat suitability. Geoderma 189–190: 652–660.

Barrett JE, Virginia RA, Wall DH, Doran PT, Fountain AG, Welch KA, Lyons WB. 2008. Persistent effects of a discrete warming event on a polar desert ecosystem. Global Change Biology 14: 2249–2261.

Berkelmans R, De'ath G, Kininmonth S, Skirving WJ. 2004. A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: Spatial correlation, patterns, and predictions. Coral Reefs 23: 74–83.

Bowman JS, Vick-Majors TJ, Morgan-Kiss R, Takacs-Vesbach C, Ducklow HW, Priscu JC. 2016. Microbial community dynamics in two polar extremes: The lakes of the McMurdo Dry Valleys and the West Antarctic Peninsula marine ecosystem. BioScience 66: 829–847.

Burkins MB, Virginia RA, Wall DH. 2001. Organic carbon cycling in Taylor Valley, Antarctica: Quantifying soil reservoirs and soil respiration. Global Change Biology 7: 113–125.

Cane MA, Zebiak SE, Dolan SC. 1986. Experimental forecasts of El Nino. Nature 322: 827–832.

Cary SC, McDonald IR, Barrett JE, Cowan DA. 2010. On the rocks: The microbiology of Antarctic cold desert soils. Nature Reviews Microbiology 8: 129–138.

Chapman, EW, Hofmann, EE, Patterson, DL, Ribic, CA, Fraser, WR. 2011. Marine and terrestrial factors affecting Adélie penguin Pygoscelis adeliae chick growth and recruitment off the western Antarctic Peninsula. Marine Ecology Progress Series 436: 273–289.

Cimino MA, Fraser WR, Patterson-Fraser DL, Saba V, Oliver MJ. 2014. Large-scale climate and local weather drive interannual variability in Adélie penguin chick fledging mass. Marine Ecology Progress Series 51: 3253–3368.

Comiso JC. 2010. Polar Oceans from Space. Springer.

Cullis JDS, Stanish LF, McKnight DM. 2014. Diel flow pulses drive particulate organic matter transport from microbial mats in a glacial meltwater stream in the McMurdo Dry Valleys. Water Resources Research 50: 86–97.

Diaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems. Science 321: 926–929.

Doran PT, McKay CP, Clow GD, Dana GL, Fountain AG, Nylen T, Lyons WB. 2002a. Climate observations from the McMurdo Dry Valleys, Antarctica, 1986–2000. Journal of Geophysical Research: Atmospheres 107: 1–12.

Doran PT, et al. 2002b. Antarctic climate cooling and terrestrial ecosystem response. Nature 415: 517–520.

Doran PT, McKay CP, Fountain AG, Nylen T, McKnight DM, Jaros C, Barrett JE. 2008. Hydrologic response to extreme warm and cold summers in the McMurdo Dry Valleys, East Antarctica. Antarctic Science 20: 499–509.

Ducklow HW, Baker KS, Martinson DG, Quetin LB, Ross RM, Smith RC, Stammerjohn SE, Vernet M, Fraser W. 2007. Marine pelagic ecosystems: The West Antarctic Peninsula. Philosophical Transactions of the Royal Society B 362: 67–94.

Ducklow H, et al. 2013. West Antarctic Peninsula: An ice-dependent coastal marine ecosystem in transition. Oceanography 26: 190–203.

Elmendorf SC, et al. 2014. Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. Proceedings of the National Academy of Sciences 112: 448–452.

Foreman CM, Wolf CF, Priscu JC. 2004. Impact of episodic warming events. Aquatic Geochemistry 10: 239–268.

Fountain AG, Dana GL, Lewis KJ, Vaughn BH, McKnight DM. 1998. Glaciers of the McMurdo Dry Valleys, southern Victoria Land, Antarctica. Pages 65–75 in Priscu JC, ed. Ecosystem dynamics in a polar desert: The McMurdo Dry Valleys, Antarctica. Antarctic Research Series, vol. 72. American Geophysical Union.

Fountain AG, Nylen TH, Monaghan A, Basagic HJ, Bromwich D. 2010. Snow in the McMurdo Dry Valleys, Antarctica. International Journal of Climatology 30: 633–642.

Fraser WR, Hofmann EE. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. Marine Ecology Progress Series 265: 1–15.

Fraser WR, Trivelpiece WZ, Ainley DG, Trivelpiece SG. 1992. Increases in Antarctic penguin populations: Reduced competition with whales or a loss of sea ice due to global warming? Polar Biology 11: 525–531.

Fraser WR, Patterson-Fraser DL, Ribic CA, Schofield O, Ducklow H. 2013. A nonmarine source of variability in Adélie penguin demography. Oceanography 26: 207–209.

Freckman DW, Virginia RA. 1997. Low-diversity Antarctic soil nematode communities: Distribution and response to disturbance. Ecology 78: 363–369.

Friedlaender AS, Johnston DW, Fraser WR, Burns J, Patrick NH, Costa DP. 2011. Ecological niche modeling of sympatric krill predators around Marguerite Bay, Western Antarctic Peninsula. Deep-Sea Research Part II: Topical Studies in Oceanography 58: 1729–1740.

Gooseff MN, McKnight DM, Runkel RL, Vaughn BH. 2003. Determining long time-scale hyporheic zone flow paths in Antarctic streams. Hydrological Processes 17: 1691–1710.

Hagedorn B, Sletten RS, Hallet B. 2007. Sublimation and ice condensation in hyperarid soils: Modeling results using field data from Victoria Valley, Antarctica. Journal of Geophysical Research 112 (art. F03017). doi:10.1029/2006JF000580

Hoffman MJ, Fountain AG, Liston GE. 2016. Distributed modeling of ablation (1996–2011) and climate sensitivity on the glaciers of Taylor Valley, Antarctica. Journal of Glaciology 62: 215–229.

Jepsen SM, Adams EE, Priscu JC. 2010. Sediment melt dynamics in permanent Antarctic lake ice. Arctic, Antarctic, and Alpine Research 42: 57–66.

Kalnay E, et al. 1996. The NCEP/NCAR 40-year reanalysis project. Bulletin of the American Meteorological Society 77: 437–471.

King JC, Turner J. 1997. Antarctic Meteorology and Climatology. Cambridge University Press.

Kohler TJ, Stanish LF, Crisp SW, Koch JC, Liptzin D, Baeseman JL, McKnight DM. 2014. Life in the Main Channel: Long-term hydrologic control of microbial mat abundance in McMurdo Dry Valley Streams, Antarctica. Ecosystems 18: 310–327.

Langford ZL, Gooseff MN, Lampkin DJ. 2015. Spatiotemporal dynamics of wetted soils across a polar desert landscape. Antarctic Science 27: 197–209.

Laybourn-Parry J, James MR, McKnight DM, Priscu J, Spaulding SA, Shiel R. 1997. The microbial plankton of Lake Fryxell, southern Victoria Land, Antarctica, during the summers of 1992 and 1994. Polar Biology 17: 54–61.

Lefebvre W, Goosse H, Timmermann R, Fichefet T. 2004. Influence of the Southern Annular Mode on the sea ice–ocean system. Journal of Geophysical Research 109 (art. C09005). doi:10.1029/2004JC002403

Marshall GJ. 2003. Trends in the Southern Annular Mode from observations and reanalyses. Journal of Climate 16: 4134–4143.

Marshall GJ, Stott PA, Turner J, Connolley WM, King JC, Lachlan-Cope TA. 2004. Causes of exceptional atmospheric circulation changes in the Southern Hemisphere. Geophysical Research Letters 31: 2437–2440.

Massom RA, et al. 2006. Extreme anomalous atmospheric circulation in the West Antarctic Peninsula Region in Austral Spring and Summer 2001/02, and its profound impact on sea ice and biota. Journal of Climate 19: 3544–3571.

McClintock J, Ducklow H, Fraser W. 2008. Ecological responses to climate change on the Antarctic Peninsula. American Scientist 96: 302–310.

McKnight DM, Niyogi DK, Alger AS, Bomblies A, Conovitz PA, Tate CM. 1999. Dry valley streams in Antarctica: Ecosystems waiting for water. BioScience 49: 985–995.

Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE, Schofield O. 2009. Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. Science 323: 1470–1473.

Nielsen UN, Wall DH, Adams BJ, Virginia RA, Wall BA, Gooseff MN, McKnight D. 2012. The ecology of pulse events: Insights from an extreme event in a polar desert ecosystem. Ecosphere 3: 1–15.

Obryk MK, Doran PT, Friedlaender AS, Gooseff M, Priscu JC, Stammerjohn SE, Steinberg SE, Ducklow HW. 2016. Responses of Antarctic marine and freshwater ecosystems to changing ice conditions. BioScience 66: 864–879.

Pennington DD, Collins SL. 2007. Response of an aridland ecosystem to interannual climate variability and prolonged drought. Landscape Ecology 22: 897–910.

Priscu JC. 1995. Phytoplankton nutrient deficiency in lakes of the McMurdo Dry Valleys, Antarctica. Freshwater Biology 34: 215–227.

Priscu JC, Fritsen CH, Adams EE, Giovannoni SJ, Paerl HW, McKay CP, Doran PT, Gordon DA, Lanoil BD, Pinckney JL. 1998. Perennial Antarctic lake ice: An oasis for life in a polar desert. Science 280: 2095–2098.

Saba GK, et al. 2014. Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. Nature Communications 5 (art. 4318). doi:10.1038/ncomms5318

Schwinning S, Sala OE, Loik ME, Ehleringer JR. 2004. Thresholds, memory, and seasonality: Understanding pulse dynamics in arid/semi-arid ecosystems. Oecologia 141: 191–193.

Simmons BL, Wall DH, Adams BJ, Ayres E, Barrett JE, Virginia RA. 2009. Long-term experimental warming reduces soil nematode populations in the McMurdo Dry Valleys, Antarctica. Soil Biology and Biochemistry 41: 2052–2060.

Smith RC, Martinson DG, Stammerjohn SE, Iannuzzi RA, Ireson K. 2008. Bellingshausen and western Antarctic Peninsula region: Pigment biomass and sea-ice spatial/temporal distributions and interannual variability. Deep-Sea Research Part II: Topical Studies in Oceanography 55: 1949–1963.

Smith TE, Wall DH, Hogg ID, Nielsen UN, Virginia RA. 2012. Thawing permafrost alters nematode populations and soil habitat characteristics in an Antarctic polar desert ecosystem. Pedobiologia 55: 75–81.

Speirs JC, Steinhoff DF, McGowan HA, Bromwich DH, Monaghan AJ. 2010. Foehn winds in the McMurdo Dry Valleys, Antarctica: The origin of extreme warming events. Journal of Climate 23: 3577–3598.

Stammerjohn SE, Martinson DG, Smith RC, Yuan X, Rind D. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niñö–Southern Oscillation and Southern Annular Mode variability. Journal of Geophysical Research 113 (art. C03S90). doi:10.1029/2007JC004269

Stammerjohn S, Massom R, Rind D, Martinson D. 2012. Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. Geophysical Research Letters 39 (art. L06501). doi:10.1029/2012GL050874

Stanish LF, Nemergut DR, McKnight DM. 2011. Hydrologic processes influence diatom community composition in dry valley streams. Journal of the North American Benthological Society 30: 1057–1073.

Steig EJ, Schneider DP, Rutherford SD, Mann ME, Comiso JC and Shindell DT. 2009. Warming of the Antarctic ice-sheet surface since the 1957 International Geophysical Year. Nature 457: 459–462. doi:10.1038/nature07669

Steinberg DK, et al. 2015. Long-term (1993–2013) changes in macrozooplankton off the Western Antarctic Peninsula. Deep Sea Research Part I: Oceanographic Research Papers 101: 54–70.

Thompson DWJ, Wallace JM. 2000. Annular modes in the extratropical circulation, part I: Month-to-month variability. Journal of Climate 13: 1000–1016.

Trathan PN, Forcada J, Murphy EJ. 2012. Environmental forcing and Southern Ocean marine predator populations: Effects of climate change and variability. Pages 335–353 in Rogers A, Johnston N, Clarke A, Murphy EJ, eds. Antarctic Ecosystems: An Extreme Environment in a Changing World. Blackwell.

Trenberth KE, et al. 2007. Observations: Surface and atmospheric climate change. In Solomon S, Qin D, Manning M, Chen Z, Marquis M. Averyt KB, Tignor M, Miller HL, eds. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press. (8 August 2016; *www.ipcc.ch/publications_and_data/ar4/wg1/en/ch3.html*)

Treonis AM, Wall DH, Virginia RA. 2000. The use of anhydrobiosis by soil nematodes in the Antarctic Dry Valleys. Functional Ecology 14: 460–467.

Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proceedings of the National Academy of Sciences 108: 7625–7628.

Turner J, Colwell SR, Marshall GJ, Lachlan-Cope TA, Carleton AM, Jones PD, Lagun V, Reid PA, Iagovkina S. 2005. Antarctic climate change during the last 50 years. International Journal of Climatology 25: 279–294.

Turner J, Comiso JC, Marshall G, Lachlan-Cope TA, Bracegirdle T, Maksym T, Meredith MP, Wang Z, Orr A. 2009. Non-annular atmospheric circulation change induced by stratospheric ozone depletion and its role in the recent increase of Antarctic sea ice extent. Geophysical Research Letters 36 (art. L08502). doi:10.1029/2009GL037524.

Venables HJ, Clarke A, Meredith MP. 2013. Wintertime controls on summer stratification and productivity at the western Antarctic Peninsula. Limnology and Oceanography 58: 1035–1047.

Younger JL, Emmerson LM, Miller KJ. 2015. The influence of historical climate changes on Southern Ocean marine predator populations: A comparative analysis. Global Change Biology 22: 474–493.

Yuan X. 2004. ENSO-related impacts on Antarctic sea ice: A synthesis of phenomenon and mechanisms. Antarctic Science 16: 415–425.

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