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Climate Variability and Ecological Response of the Marine Ecosystem in the Western Antarctic Peninsula (WAP) Region

Raymond C. Smith
William R. Fraser
Sharon E. Stammerjohn

Introduction

The Antarctic Peninsula, a relatively long, narrow extension of the Antarctic continent, defines a strong climatic gradient between the cold, dry continental regime to its south and the warm, moist maritime regime to its north. The potential for these contrasting climate regimes to shift in dominance from season to season and year to year creates a highly variable environment that is sensitive to climate perturbation. Consequently, long-term studies in the western Antarctic Peninsula (WAP) region, which is the location of the Palmer LTER (figure 9.1), provide the opportunity to observe how climate-driven variability in the physical environment is related to changes in the marine ecosystem (Ross et al. 1996; Smith et al. 1996; Smith et al. 1999).

This is a sea ice–dominated ecosystem where the annual advance and retreat of the sea ice is a major physical determinant of spatial and temporal change in its structure and function, from total annual primary production to the breeding success and survival of seabirds. Mounting evidence suggests that the earth is experiencing a period of rapid climate change, and air temperature records from the last half century confirm a statistically significant warming trend within the WAP during the past half century (King 1994; King and Harangozo 1998; Marshall and King 1998; Ross et al. 1996; Sansom 1989; Smith et al. 1996; Stark 1994; van den Broeke 1998; Weatherly et al. 1991). Air temperature–sea ice linkages appear to be very strong in the WAP region (Jacka 1990; Jacka and Budd 1991; King 1994; Smith et al. 1996; Weatherly et al. 1991), and a statistically significant anticorrelation between air temperatures and sea ice extent has been observed for this region. Consistent with this strong coupling, sea ice extent in the WAP area has trended down

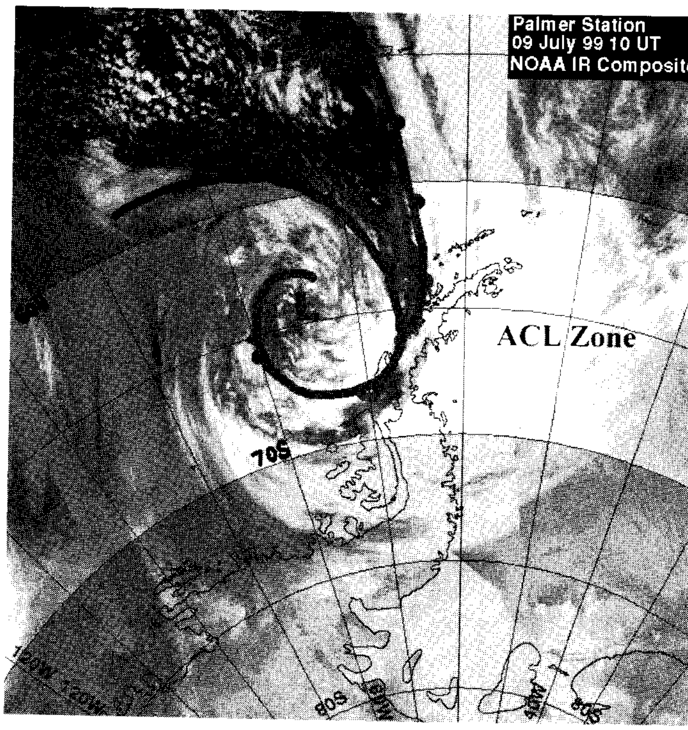

Figure 9.1 Satellite (NOAA infrared composite) image of the Antarctic Peninsula. A low-pressure system (with corresponding warm and cold fronts illustrated) is to the west of the peninsula. Palmer Station (64°41' S, 64°03' W), on Anvers Island is positioned roughly under the apex of the schematic outline of the frontal system. Also illustrated as an overlay on the image is the Antarctic Convergence Line (ACL), the mean position of the circumpolar low-pressure trough surrounding Antarctica. The ACL undergoes a semiannual cycle, whereby, on average, it is nearest the continent when the ice edge is near its extreme equatorward (spring) or poleward (autumn) position. The ACL, on average, is farther equatorward when the ice edge is at an intermediate position (winter, summer) (van Loon, 1967). The Palmer LTER regional sampling grid is along the western Antarctic Peninsula (WAP).

during this period of satellite observations, and the sea ice season has shortened. In addition, both air temperature and sea ice have been shown to be significantly correlated with the Southern Oscillation Index (SOI), which suggests possible linkages among sea ice, cyclonic activity, and global teleconnections.

Ecological responses to this climate variability are evident at all trophic levels, but are most clearly seen in a shift in the population size and distribution of penguin species with different affinities to sea ice. In the text that follows, we update both air temperature and sea ice records for the WAP to demonstrate their continued statistical significance and to place the related ecological and environmental observations into a long-term context that shows how the WAP region is responding to an increasing maritime, as opposed to continental, influence. We further show the correlation of these environmental variables to the Southern Oscillation Index (SOI), address issues of seasonal timing, and discuss the broad implications of these changes to the ecosystem.

Climate and Ecological Data

Surface Air Temperature

The British Antarctic Survey (BAS) has a long and distinguished history of scientific research in Antarctica, and their meteorological observations at Faraday/Vernadsky Station have been especially useful to WAP research because of their length (5+ decades), consistency, and quality control. In this chapter, we update and augment earlier studies (Smith et al., 1996) with data from the 1990s. Figure 9.2 shows the Faraday/Vernadsky annual average air temperatures from 1945 to 2000 (N = 56). The solid line is the least-squares regression line, which shows a statistically significant warming trend over the last 56 years. The dotted lines indicate the ± 1 standard deviation (s.d.) from the regression line and has been used as a designator for defining "high" (above 1 s.d.) or "low" (below 1 s.d.) temperature years.

After accounting for serial correlation present in this 56-year record (for method, see Smith et al., 1996), we found the trend to be statistically significant at a >99% confidence level. These annual results are further supported by a monthly and seasonal analysis (see table 1 in Smith et al., 1996) showing that the warming trend in Faraday/Vernadsky air temperatures is strongest during the midwinter months and peaks in June at 0.11°C/year. This represents about a 6°C increase in June temperatures over the 56-year record. Spring and summer trends, however, are not as pronounced. The record from Rothera (further south on the WAP) shows a strong temporal coherence (King 1994; Smith et al., 1996) to Faraday/Vernadsky, displaying similar trends but with mean annual temperatures that average a few degrees cooler. This evidence suggests there is a north-south temperature gradient along the WAP and that observed trends are coherent throughout the region.

The annual progression of temperatures and the amount of variability associated with those temperatures have also changed over the last half century. Figure 9.2 shows that the last two decades (1980s and 1990s) were warmer than the previous several decades. The seasonal variability associated with this change is illustrated in figure 9.3a, where we have plotted the annual curves of monthly mean air temperature for Faraday/Vernadsky for the following periods: the full instrument record, 3/44 to 12/99 (solid); the period 1/78–12/89 (hereafter called the 1980s, dotted); and the period 1/90–12/99 (the 1990s, dashed). The curves in figure 9.3a also illustrate that the largest temperature changes have occurred in winter (Jun–Aug), in contrast to less change in spring and early summer (Sept–Dec).

Figure 9.3c shows the standard deviations of the monthly mean surface air temperatures shown in figure 9.3a. Several observations in air temperature variability are apparent. First, there is significantly higher variation from May through September during all periods. Second, during the summer, when ice-free conditions are increasingly typical and maritime conditions prevail, there is relatively lower vari-

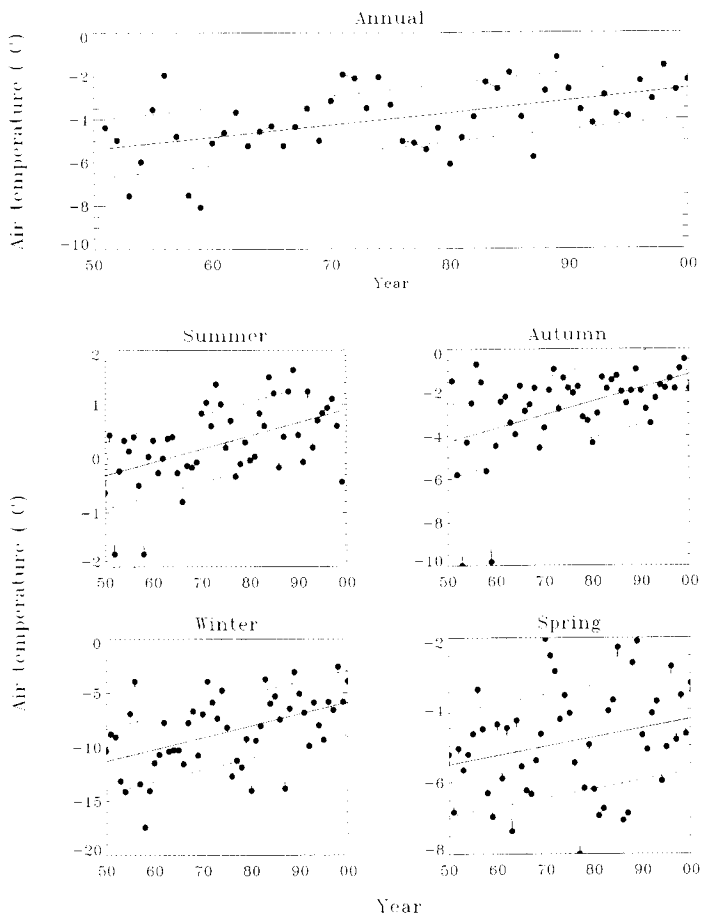

Figure 9.2 Faraday/Vernadsky (65° 15' S, 64° 15' W) annual average air temperatures from 1945 to 2000 (N=56). The solid line is the least-squares regression line with a gradient of 0.052°C/year, and the dotted lines indicate ± 1 standard deviation from this line. A linear regression model shows the warming trend over this period to be significant at greater than the 99% confidence level. The shorter-period Rothera (67° 34' S, 68° 08' W) annual temperature is plotted as a dotted line. Temperature data for Faraday/Vernadsky and Rothera kindly supplied by the British Antarctic Survey.

ability in air temperatures. Third, the high midwinter (July) variation during the 1980s is caused by greater extremes between warm and cold winters. These changes in the annual progression of temperature and the amount of variability associated with those temperatures suggests a climate shift, in which continental influences are giving way to increasing maritime influences along the WAP. Smith and Stammerjohn (2001) have detailed why these observations are consistent with the characteristics of a maritime environment in which temperatures are moderated by the open ocean.

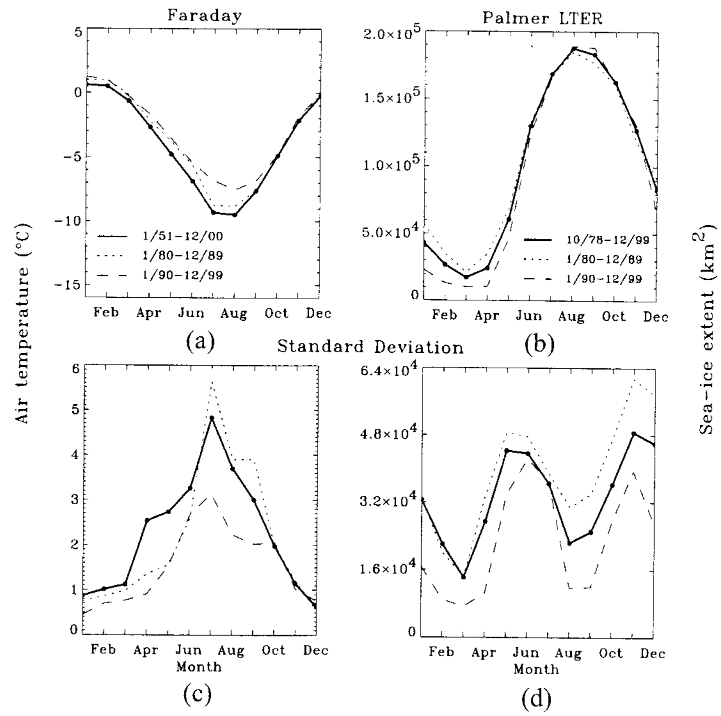

Figure 9.3 (a) Annual curves of monthly mean surface air temperatures for Faraday/Vernadsky for the total period of the instrument record (3/44–12/99, bold line with solid dots), the decade of the 1980s (1/80–12/89, dotted line), and the decade of the 1990s (1/90–12/99, dashed line). (b) Annual curves of monthly mean sea ice extent for the Palmer LTER region for the full period of satellite passive microwave data (10/78–12/99, bold line with solid dots), the decade of the 1980s (10/80–12/89, dotted line), and the decade of the 1990s (1/90–12/99, dashed line). Sea ice data supplied by the National Snow and Ice Data Center. (c) Standard deviations of the monthly mean surface air temperatures for the same periods shown in part (a). (d) Standard deviations of the monthly mean sea ice extent for the periods shown in part (b).

Although the mechanistic processes linked to these WAP temperature trends are still being debated, the role of the mean position of the circumpolar atmospheric low-pressure trough (i.e., the Atmospheric Convergence Line (ACL), figure. 9.1) bears close inspection as a possible causal mechanism. The Antarctic Peninsula is the only area in Antarctica where the ACL crosses land. The seasonal cycle displayed in temperature, pressure, wind, and precipitation (Schwerdtfeger 1984; van Loon 1967) is linked to both increased cyclonic activity and a southward shift of approximately 10° of latitude of the ACL during spring and autumn. The relative position of the ACL influences not only the semiannual cycle of climate variables but also the timing and distribution of sea ice. Van Loon suggested that this seasonal temperature cycle is associated with enhanced meridional flow from middle to high latitudes during winter.

Indeed, more recent work by Meehl (1991) confirms that transient eddy heat flux likely contributes to this seasonal cycle in the Antarctic coastal zone. King and coworkers (King 1994; King and Harangozo 1998; Marshall and King 1998) also show a strong correlation between surface air temperature and meridional sea-level pressure indexes calculated for the WAP area. Their results demonstrate that increased boundary-layer winds, flowing from the northwest sector toward the WAP, are associated with increased cyclonic activity and warm air advection from lower latitudes. The increase in surface temperatures associated with the increase in northerly winds consequently produces an environment with more maritime (warm and moist) characteristics, as opposed to the continental environment (cold and dry) that would result from the effects of southerly winds and colder temperatures. Stammerjohn et al. (2003) have discussed in detail the responses of sea ice and drift dynamics to synoptic forcing in the WAP region and suggested that, with longer term shifts in the mean position of the ACL, these synoptic-scale systems may provide a mechanism for longer term climate variability.

Sea Ice

Also shown in figure 9.3 are the mean annual cycles of sea ice extent (figure 9.3b) and the standard deviations of the monthly means (figure 9.3d). Means for the full period of the passive microwave satellite record (1978–1999, solid) and for the 1980s (dotted) and the 1990s (dashed) are included. Methods we used when working with passive microwave satellite data are described in Stammerjohn and Smith (1996) and Smith et al. (1998). Several observations can be made with respect to figure 9.3. First, the winter seasonal cycle of air temperature (figure 9.3a) is inversely related to the winter seasonal cycle of sea ice extent (figure 9.3b), but the summer sea ice extent minimum lags the summer air temperature maximum by 2 to 3 months. Second, summer (Jan–Mar) and fall (Apr–May) sea ice extent in the 1990s is below that for the 1980s. Third, spring (Sept–Dec) also follows this pattern, with the 1990s showing less sea ice on average than the 1980s. Fourth, the earlier retreat and later advance of sea ice in the 1990s (as compared with the 1980s) translates into a shorter sea ice season by roughly two weeks. The variance also changed (figure 9.3d); the 1980s, when contrasted to the 1990s, have a higher variance because of the seasonal persistence of anomalies during April to September.

Within the period of satellite multichannel microwave records (1978 to present), anomalies in WAP air temperature and sea ice extent (King 1994; Smith et al. 1996; Weatherly et al. 1991) have been shown to be significantly anticorrelated. Figure 9.4a shows monthly standard deviates of Faraday/Vernadsky air temperature versus Palmer LTER sea ice extent smoothed with a 5-month running average. Standard deviates are the normalized anomalies determined by dividing the anomaly (for the month and year in question) by the standard deviation of the anomaly (for the month in question). However complex the mechanisms linking air temperature and sea ice trends are, these data show that since 1978 these two parameters behave almost as mirror images within the WAP. During the 1980s, when anomalies in sea ice extent showed strong persistence, so did air temperature, but during the 1990s this persistence gave way to greater month-to-month variability in both parameters.

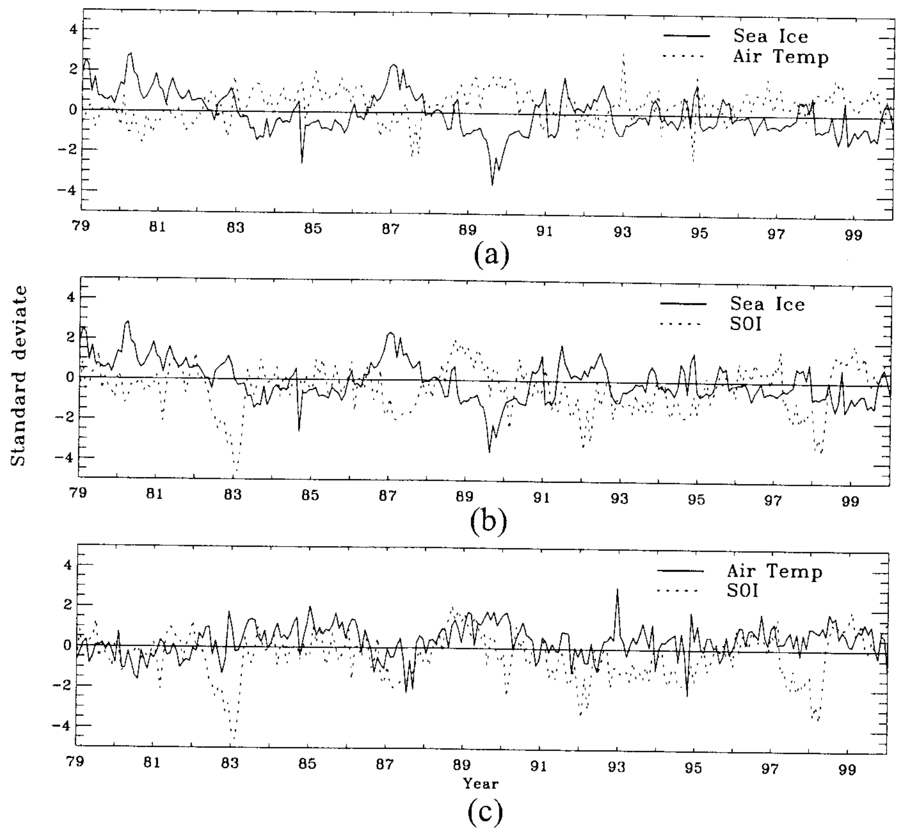

Figure 9.4 Monthly standard deviates (smoothed by a 5-month running mean) from January 1979 to December 1999. (a) Faraday/Vernadsky air temperature (dotted line) and Palmer LTER sea ice extent (solid line). (b) Palmer LTER sea ice extent (solid line) and Southern Oscillation Index (dotted). (c) Faraday/Vernadsky air temperature (solid line) and Southern Oscillation Index (dotted). The SOI data were obtained digitally (http://www.cpc.ncep.noaa.gov/data/indices/soi) from the Climate Prediction Center (Department of Commerce, NOAA).

As expected from the relationships discussed previously, but in contrast to the Southern Ocean as a whole, the annual mean sea ice extent has trended down in the WAP region (figures 9.5). Here the mean annual sea ice extent for the WAP region (a) and the Southern Ocean (inset) are presented along with mean seasonal data for summer (b), autumn (c), winter (d), and spring (e). The annual trend is due mostly to the decreasing trend in summer sea ice, which was also inferred from figure 9.3. Given the relatively short satellite record and high interannual variability, these trends are not statistically significant. However, the trends are suggestive, and less summer sea ice is consistent with increased maritime influence in the WAP region as noted previously. During the 1980s over half the annual means are greater than ± 1 s.d. from the regression line, in contrast to the 1990s when all the annual means

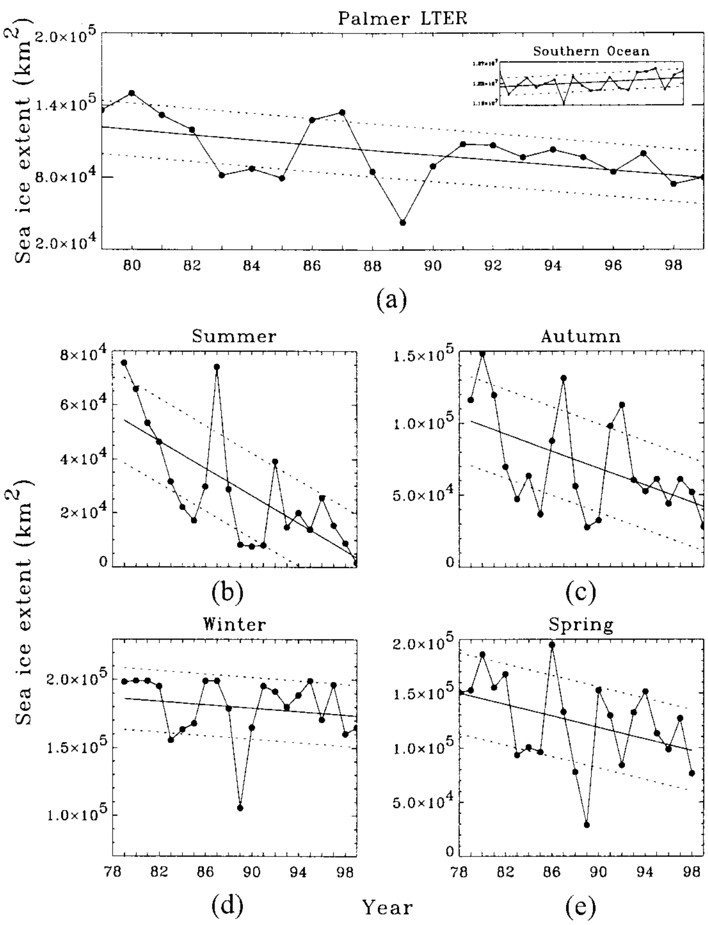

Figure 9.5 Mean annual sea ice extent for the Southern Ocean (insert) and the Palmer LTER region (a). See Stammerjohn and Smith (1996) for details on the satellite data used. Mean annual sea ice extent for the Palmer LTER region for summer (b), autumn (c), winter (d), and spring (e) are shown to illustrate that the annual trend in the Palmer LTER region is due mostly to the decreasing sea ice trend during summer.

are within ± 1 s.d. Also, during the earlier decade the periods of anomalously high (1979–1981 and 1986–1987) and low (1983–1985 and 1988–1990) sea ice extents stand out clearly. We expect the ecosystem to respond to these anomalies.

Links to the Southern Oscillation Index

Monthly standard deviates of Palmer LTER sea ice extent and Faraday/Vernadsky air temperature versus the Southern Oscillation Index (SOI) (which is determined by the standardized sea level pressure difference between Tahiti and Darwin, Australia) are shown in figures 9.4b and c, respectively. Figure 9.4b shows an anticorrelation between Palmer LTER sea ice extent and SOI. As expected based on the relationship shown in figure 9.4a, figure 9.4c shows a correlation between Faraday/Vernadsky air temperature and SOI. Smith and coworkers (1996) have discussed this relationship previously and we include an updated figure here to show that the relationships continue to hold throughout the 1990s. These relationships support the idea of possible linkages among sea ice, cyclonic activity and global teleconnections (Carleton 1988; Mo and White 1985; van Loon and Shea 1985; van Loon and Shea 1987; White and Peterson 1996; White et al. 1998; Yuan and Martinson 2000). In particular, the semiannual oscillation (SAO, the twice-yearly contraction and expansion of the atmospheric low-pressure trough around Antarctica) is an important component of the Southern Hemisphere climate regime and has been shown to be linked to variability in air temperature and cyclonic activity in the WAP and elsewhere in the Antarctic (Meehl 1991; van den Broeke 2000; van Loon 1967).

Pygoscelid Penguins, Upper Trophic Level Predators

High variability and long-term change constitute the setting in which this polar marine ecosystem has evolved. Solar radiation, atmospheric and oceanic circulation, and air temperature and sea ice cover are the physical forcing mechanisms that drive variability in biological processes at all trophic levels. The extreme seasonality of these forcing mechanisms in conjunction with the seasonal timing of ecologically important events in the life histories of key species from each trophic level provides a conceptual model for understanding WAP trophic interactions (Smith et al. 1995, figure 4). Figure 9.6 presents annual time lines of selected physical and biological components in the WAP region with emphasis on the variability of sea ice and the life histories of three sympatric, congeneric penguins, the Adélie (*Pygoscelis adeliae*), chinstrap (*P. antarctica*), and gentoo (*P. papua*). Adélie penguins are obligate inhabitants of the winter pack ice, whereas chinstraps and gentoos are almost exclusively associated with ice-free Antarctic and sub-Antarctic waters (Fraser et al. 1992). These three species are closely related and have a similar breeding cycle of courtship, egg laying, incubation, brooding, and fledging. However, as illustrated in figure 9.6, the Adélie breeding cycle begins roughly 3 weeks earlier than that of the other two species. The timing associated with these relatively fixed breeding chronologies, 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 penguin breeding success and recruitment.

The basis for understanding the possible causal factors associated with WAP penguin population trends originated with the hypothesis that a decrease in the number of cold years with heavy winter sea ice because of climate warming produced habitat conditions more suitable for the ice-intolerant, as opposed to the ice-dependent, species (Fraser et al. 1992). Figure 9.7 shows the changes in Adélie and chinstrap penguin populations near Palmer Station during the past two decades, and for gentoo penguins since founder colonies became established in the area during the early 1990s. These trends clearly support this ice reduction hypothesis. Chinstrap and gentoo penguins, the more ice-intolerant species, have increased,

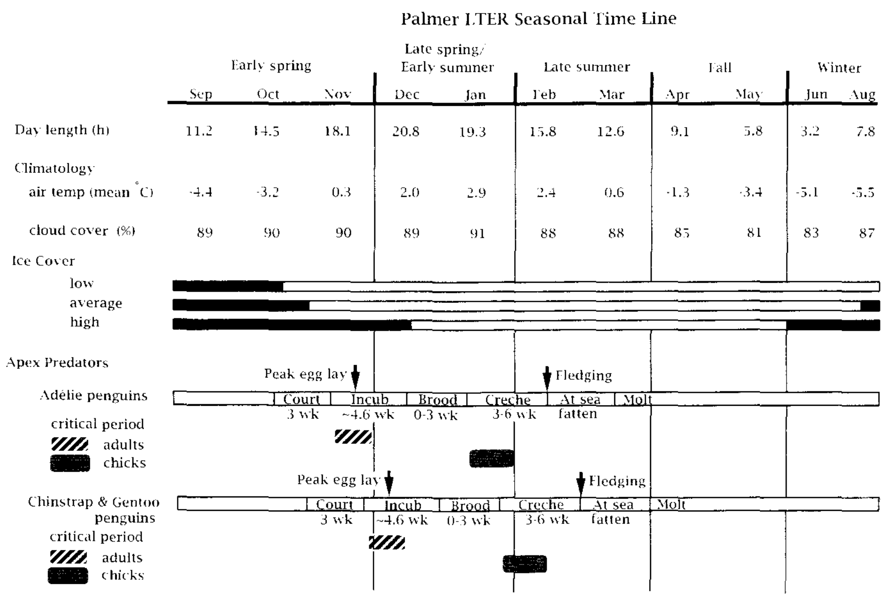

Figure 9.6 Annual time lines of selected physical and biological components in the WAP region: day length (h), mean monthly air temperature (°C), cloud cover (%), ice cover variability, Adélie penguins, Chinstrap and Gentoo penguins (include peak egg lay, critical periods for adults and chicks, incubation, brood, creech, fledging, molt periods). This schematically illustrates how the variability in sea ice cover relates to the relatively fixed breeding chronology of selected upper level predators.

whereas the ice-dependent Adélie penguins have decreased. Moreover, the causal mechanisms suggested by this hypothesis have now been implicated as key factors affecting penguin demography at a range of spatial and temporal scales in both paleoecological and demographic studies (Baroni and Orombelli 1991; Baroni and Orombelli 1994; Denton et al. 1991; Emslie 1995; Emslie et al. 1998; Fraser and Patterson 1997; Smith et al. 1999; Taylor et al. 1990). The emerging evidence is that penguin distributions are undergoing a fundamental reorganization in the WAP and other regions of Antarctica (see Fraser and Trivelpiece 1996) as the result of climatic factors that appear to influence long-term recruitment.

Discussion and Summary

Several comments can be made with respect to the air temperature and sea ice data. First, to place the more recent observations within the context of the past half century, it is important to recall that the decade of the 1990s is the warmest for the entire period of the instrument record (figure 9.2). Second, the strong inverse relationship between air temperature and sea ice extent continues to be clearly evident. Further, in contrast to earlier periods, departures from the mean during the decade

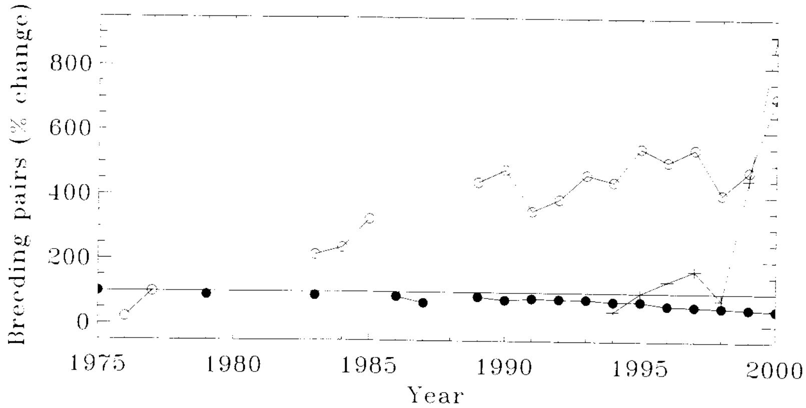

Figure 9.7 Twenty-five-year trends in Adélie and chinstrap penguin populations at Arthur Harbor (Palmer Station) and for gentoo penguins since founder colonies became established in the early 1990s. Adélie penguins (solid dots) are normalized to 100% in 1975 when the record began. Chinstrap (open circles) and gentoo (plus signs) penguins are normalized to 100% in 1977 and 1995, respectively, one year after founding colonies were established.

of the 1990s are relatively low. Third, the trends in the WAP area are such that there are fewer high sea ice years, and the seasonal progression of sea ice, although highly variable from year-to-year, is such that the average ice-free period is roughly 2 weeks longer than it was 5 decades ago. Fourth, climate warming in the Antarctic Peninsula has, in some areas, raised the mean annual temperature above the suggested climate limit (−5°C) for ice shelf stability, leading to the complete disintegration of some shelves (Skvarca et al. 1999; Vaughan and Doake 1996). The removal of large areas of this ice-related habitat illustrates the role that temperature plays in the phase transition between ice and water, which has important consequences for this marine ecosystem.

King and Harangozo (1998) have discussed the trends in climate change in the WAP and identified two possible factors as causes for the interannual variability in the temperature record: changes in atmosphere-ice-ocean interactions, and variability in maritime versus continental control on climate. The increased maritime influence during recent decades is relatively clear from the data, whereas the mechanisms underlying atmosphere-ice-ocean interactions and the causative factors involved remain to be elucidated. The variability of the Antarctic Convergence Line (ACL, figure 9.1), both semiannual and long-term, with its corresponding influence on climatic conditions in the WAP, appears to play a significant role at temporal scales that range from synoptic to long-term. We can thus hypothesize that maritime conditions are likely to become the prevailing climatic regime in the WAP region, and this, in turn, will force a restructuring of the marine ecosystem from a more polar to a more maritime state.

Climate variability along the peninsula holds the potential to cascade through the ecosystem through a variety of mechanisms. Recent work (Dierssen et al. 2002) has shown the potential influence of glacial meltwater, as distinct from the usual meltwater from sea ice, on the hydrography of the WAP ecosystem. Glacial meltwater freshens and warms coastal surface waters, leading to enhanced water column stability and increased primary productivity. The influence of glacial meltwater on the space-time variability of the system is currently under investigation, but the potential of this mechanism to act as a catalyst influencing both the magnitude and timing of primary production and to cascade this influence to higher trophic levels is clear. Further, the amount of meltwater may have important secondary effects on the ecosystem by influencing the timing of sea ice formation the following fall.

The life histories of various polar marine species are synchronized with the seasonality of the sea ice (Ross et al. 1996; Smith et al. 1995). For example, Ackley and Sullivan (1994) have proposed a conceptual model of the seasonal cycle of sea ice with the following characteristics: (1) autumn formation entrains phytoplankton as a seed population within the sea ice matrix; (2) entrained sea ice communities grow and develop during winter as the sea ice evolves; and (3) sea ice decay in the spring releases a potential bloom inoculum of particulate organic matter into the water column. Palmer LTER multiyear observations on phytoplankton biomass and production variability support this hypothesis because several factors controlling abundance and distribution of phytoplankton biomass, often dominated by diatom blooms, have been shown to be modulated by sea ice (Smith et al. 1998; Smith and Stammerjohn 2001). Further up the food web, the Antarctic krill (*Euphausia superba* Dana), a major herbivore responsible for the transfer of energy within the ecosystem, has a life history that is closely coupled to sea ice (Quetin et al. 1996). It has been hypothesized that the wintertime survival of larval krill depends on sea ice to provide a habitat and an algal food source. Further, recent evidence supports the hypothesis that maximum krill growth rates are only possible during diatom blooms and that year-class success in Antarctic krill is limited by both food quantity and quality (Ross et al. 2000). This suggests strong linkages among sea ice, phytoplankton, and krill. Continued significant warming will reduce the dominance of sea ice in the WAP ecosystem with subsequent changes and/or shifts in primary and secondary production.

For higher trophic predators such as penguins, variability in sea ice concentrations can affect foraging ecology directly through its effects on krill recruitment and abundance (Fraser and Hofmann 2003) or indirectly through habitat changes that mediate the availability of krill (Fraser et al. 1992; Fraser and Trivelpiece 1996; Fraser and Patterson 1997). A conceptual model that is roughly analogous to the intermediate disturbance model (Connell 1978) was proposed by Fraser and Trivelpiece (1996) and Smith et al. (1999) to account for the direction of change in Adélie penguin populations in the Ross Sea and WAP regions in relation to climate warming and a decline in the frequency of heavy sea ice years. Penguin breeding colonies are located on coastal sites that offer an optimal combination of foraging and nesting habitats. Such sites, we are now beginning to understand, are associated with environmental conditions that ensure some level of predictability in the availability of prey at ecological time scales, here associated with the presence or absence of sea ice via its controlling effects on primary and secondary production.

Although the mechanisms that control these conditions are not fully understood, significant progress has recently been made in understanding cause and effect between some of the basic linkages circumscribed by weather, ice, primary and secondary production, and predator population responses. This has provided a better perspective on the magnitude of the changes induced by the current warming trend and on the linearity or nonlinearity of the associated processes. A most interesting observation based on the paleoecological record is that the presence of chinstrap and gentoo penguins in the Palmer Station area is unprecedented in the 600-year fossil record, which is entirely dominated by Adélie penguin remains (Emslie et al. 1998). This pattern stands in sharp contrast to trends evident 250 km north of the Palmer area, where the relative dominance of Adélie and chinstrap penguins has changed cyclically in response to multicentury cooling and warming periods (Emslie 1995). That chinstrap and gentoo penguins have invaded the Palmer region thus seems to affirm the unusual nature of this twentieth-century WAP warming event. However, that founder colonies of these species have increased so dramatically—and, conversely, that Adélie penguins have decreased so substantially—in roughly 25 years (figure 9.7) strongly suggests that causal processes are more linear than nonlinear, involve fewer potentially diffusive links, and may impinge directly on key aspects of the life history of penguins and/or their prey.

Evidence supporting this perspective stems from recent studies by Fraser and Hofmann (2003), who analyzed changes over a period of 30 years in the diets of Adélie penguins. Their results show that there is a direct, causal relationship between variability in ice cover and krill recruitment, krill abundance, and predator foraging ecology. Of particular relevance is the observation that time lags between sea ice formation and changes in the responses of Adélies foraging on krill are short, less than 12 months during some years, and can simultaneously affect parameters such as chick fledgling weight that have longer term consequences to recruitment (Salihoglu et al. 2001). Moreover, there is some evidence that the coupling strength between these interactions shows a strong 4–5 year periodicity. This periodicity is consistent with the periodicity of the Antarctic Circumpolar Wave (ACW) (White and Peterson 1996) and is coherent with the development of cold temperatures and heavy ice years in the WAP. Possible teleconnections between the ACW and the SOI were previously discussed.

Several studies (Fraser and Hofmann 2003; Smith et al. 1996; White et al. 1998; Yuan and Martinson 2000) strongly suggest that ENSO-type events govern key biophysical interactions in the WAP that affect all trophic levels, but the unprecedented characteristics of the current warming trend make it difficult to envisage an "end scenario" to these climate-induced ecosystem changes. In light of present sea ice trends, however, it is not inconceivable that Adélie penguins will continue to decline in the Palmer Station area and that the locus of their distribution will be forced farther south along the WAP, while chinstrap and gentoo penguins emerge as the dominant top predators. The fossil record already supports such a scenario at more northern sites along the WAP, where there is also evidence that squid and fish replaced krill as the dominant component in penguin diets as the climate warmed (Emslie 1995; Emslie et al. 1998). This would imply that, at least within the confines of some spatial and temporal scales, climate-induced ecological effects were complete (defined as one food web replacing another) before new climate events restored the marine ecosystem to its previous state. This scenario thus argues in favor of cyclical as opposed to absolute changes in WAP ecosystems in response to climate change. The fault with this argument, of course, is that previous changes in climate were in all probability unrelated to anthropogenic forcing.

Acknowledgment This work was supported by NSF Office of Polar Programs grants OPP-9632763 (RCS and WRF) and OPP-9505596 (WRF). This is Palmer LTER contribution # 214.

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CLIMATE VARIABILITY AND ECOSYSTEM RESPONSE AT LONG-TERM ECOLOGICAL RESEARCH SITES

Edited by

David Greenland

Douglas G. Goodin

Raymond C. Smith

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2003