

PALMER LONG-TERM ECOLOGICAL RESEARCH ON THE ANTARCTIC
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Long-term studies in the western Antarctic Peninsula (WAP) region, which is the location of the Palmer LTER, provide the opportunity to observe how climate-driven variability in the physical environment is related to changes in the marine ecosystem. During the past 50 years the WAP region has experienced a statistically significant warming trend. Associated with this warming trend, during the last two decades, sea ice extent has trended down and the sea ice season has shortened. Ecosystem response to these trends is becoming evident at all trophic levels but is most clearly seen in a shift in population size and distribution of penguin species with different affinities to sea ice. Our results show that these trends in penguin populations are in accord with climate change predictions.

1. INTRODUCTION

The Palmer Long-Term Ecological Research (Palmer LTER) program seeks to understand the structure and function of the Antarctic marine ecosystem in the context of physical forcing (atmospheric, oceanic and sea ice) on seasonal to millennial time-scales (<http://www.icesc.ucsb.edu/lter/lter.html>). The western Antarctic Peninsula (WAP) region, the location of the Palmer LTER (Figure 1), is proving to be an exceptional area to study ecological response to climate variability (Smith *et al.*, 1995, 1999; Ross *et al.*, 1996). Mounting evidence (McCarthy *et al.*, 2001) suggests that the Earth is experiencing human-induced climate variability, and air temperatures from the last half-century confirm the rapidity of warming in the WAP area (Sansom, 1989; Weatherly *et al.*, 1991; King, 1994; Stark, 1994; Smith *et al.*, 1996; King and Harangozo, 1998; Marshall and King, 1998; van den Broeke, 1998a, 1998b; Smith and Stammerjohn, 2001). Consistent with this warming, the sea ice season

is shorter and the maritime system of the northern WAP is expanding southward and replacing the continental, polar system of the southern WAP. Ecosystem response to this latitudinal climate change is becoming increasingly evident at all trophic levels (Smith *et al.*, 1998; Smith and Stammerjohn, 2001; Quetin *et al.*, 1996). However, this change is most clearly seen in a shift in population size and distribution of penguin species with different affinities to sea ice (Fraser *et al.*, 1992; Fraser and Trivelpiece, 1996; Smith *et al.*, 1999, 2003). The Palmer LTER seeks to understand the full ecological response to and implications of this climate-related change in physical forcing that is presently occurring in the WAP region.

There is now widespread recognition of numerous natural and anthropogenic forced phenomena, such as El Niño-Southern Oscillation (ENSO), atmospheric ozone depletion, green-house gas accumulation, global deforestation, and global warming, that can potentially cause significant ecological change, but that require long-term studies to resolve (McCarthy *et al.*, 2001). The NSF-funded LTER program consists of a community of 24 ecological sites—referred to as the LTER Network (<http://lternet.edu>)—that study ecological systems with a long-term perspective. The LTER Network maintains a comprehensive set of core measurements made across individual sites and project-specific field experiments that test ecosystem-specific hypotheses to climate

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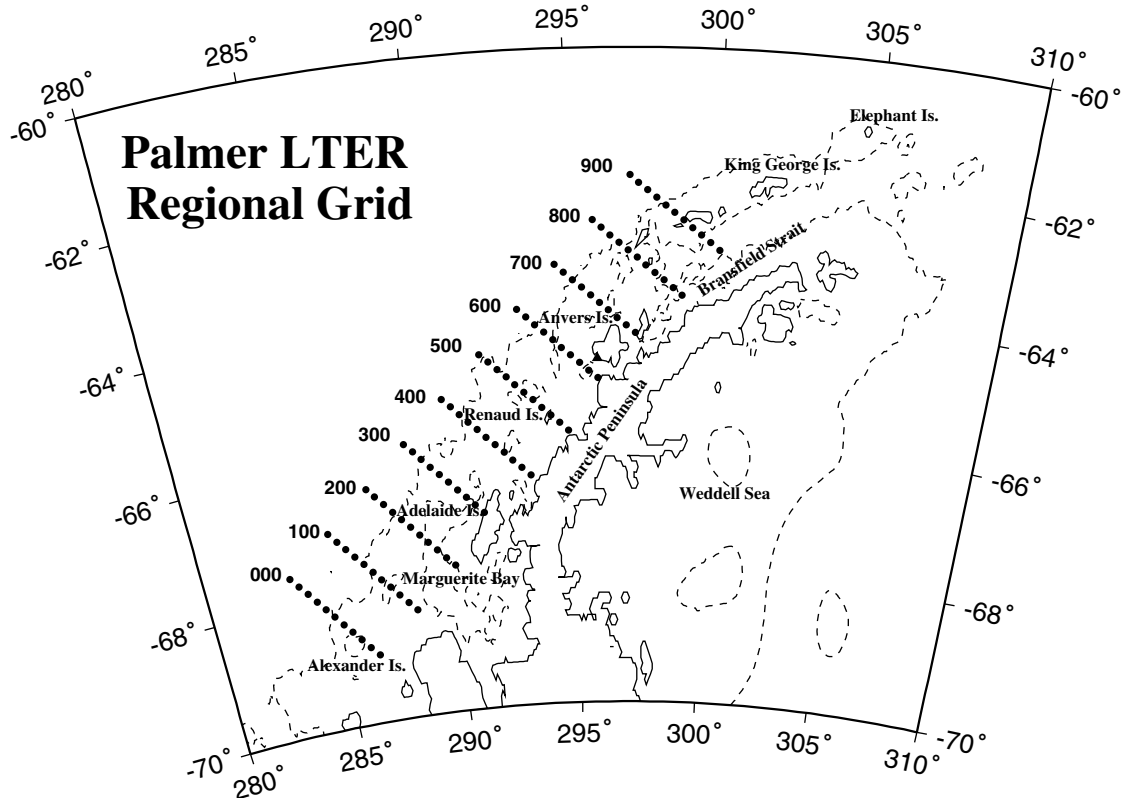


Fig. 1. Map of the western Antarctic Peninsula (WAP) region. The Palmer LTER sampling grid is denoted by the dots and each dot is a sampling station (perpendicular to the peninsula, the stations are 20 km apart, along the peninsula the sampling lines are 100 km apart). Palmer Station ($64^{\circ} 46' S$, $64^{\circ} 03' W$) is located on the southern end of Anvers Island and the Faraday/Vernadsky (formerly British, now Ukrainian) Station is roughly 30 nautical miles south of Palmer Station.

change (Callahan, 1984; Franklin *et al.*, 1990). Within this context of ecosystem variability on inter-annual, decadal and longer time scales the Palmer LTER conducts research on the Antarctic marine ecosystem. In the following section we review some Palmer LTER findings of relevance to the theme of Antarctic Peninsula climate variability on seasonal to multi-decadal time-scales. A summary is given in the last section.

2. TEMPERATURE AND SEA ICE

Paleoclimate records are consistent in showing that the WAP region has moved from a relatively cold regime between approximately 2700 BP and 100 BP to a relatively warm regime during the past century (Mosley-Thompson, 1992; Peel, 1992; Domack *et al.*, 1993; Thompson *et al.*, 1994; Dai *et al.*, 1995; Domack and McClennen, 1996; Leventer *et al.*, 1996; Smith *et al.*, 1999; and references in this volume). Instrument records, principally British Antarctic Survey (BAS) air temperature records for stations along the WAP, show a dramat-

ic warming trend during the past half century (Sansom, 1989; Weatherly *et al.*, 1991; King, 1994; Stark, 1994; Smith *et al.*, 1996; King and Harangozo, 1998; Marshall and King, 1998; van den Broeke, 1998a, 1998b; Smith and Stammerjohn, 2001). The warming trend in Faraday/Vernadsky air temperatures is strongest in mid-winter months and peaks in June at $0.11^{\circ} C y^{-1}$, representing a $6^{\circ} C$ increase in June temperatures over the 51 year record. Satellite observations of sea ice extent have been available for the past two decades and, during this period a statistically significant anti-correlation between air temperatures and sea ice extent has been observed for this region (Weatherly *et al.*, 1991; King, 1994; Smith *et al.*, 1996). During the period of satellite observations sea ice extent in the WAP has trended down and the sea ice season has shortened (Stammerjohn and Smith, 1996; Smith and Stammerjohn, 2001). These observations are summarized in Figures 2 and 3.

Figure 2a shows the Faraday/Vernadsky annual average air temperatures from 1951 to 2001 ($N=51$). Note, we no longer use the 'full' record ($N=57$) since the earli-

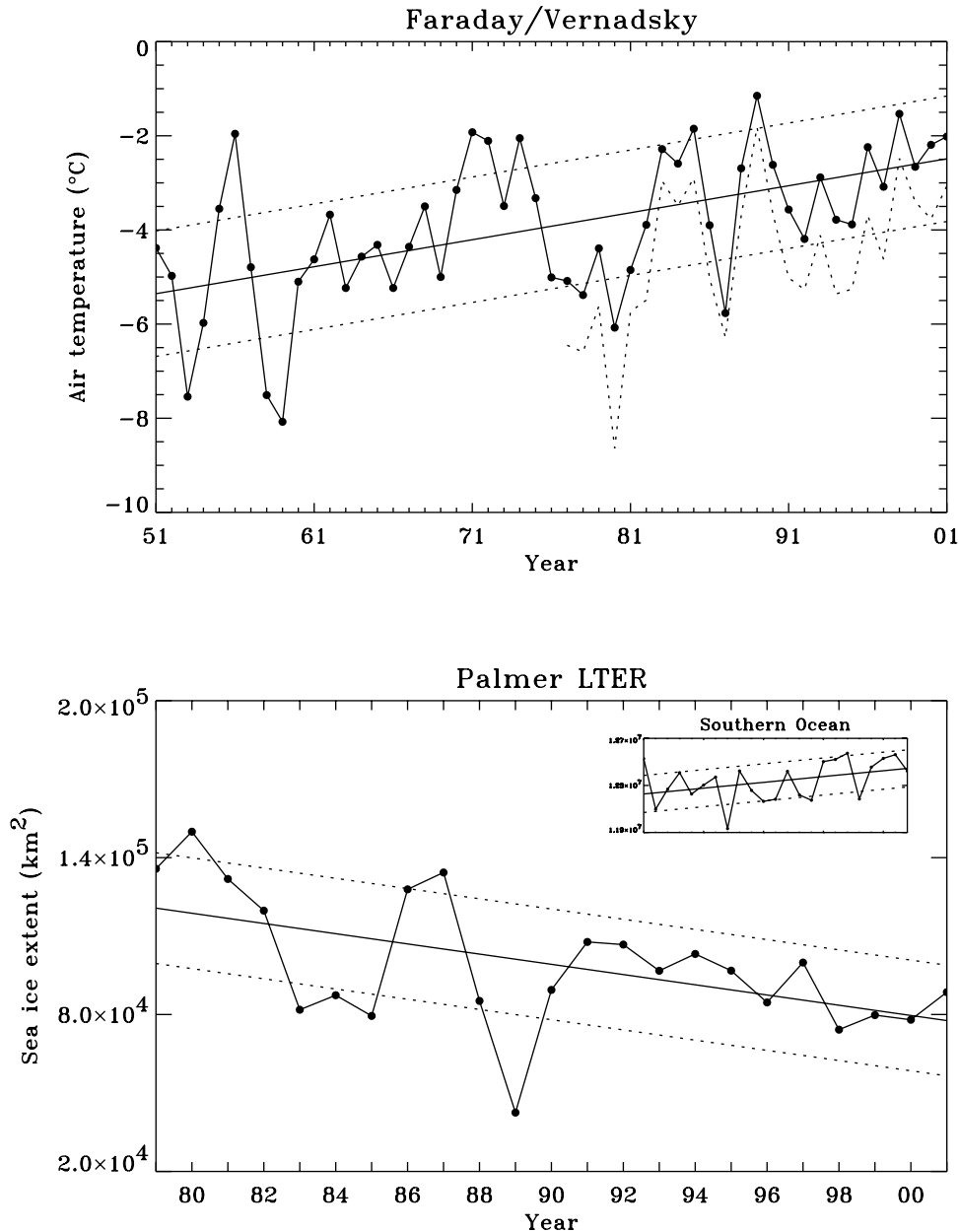


Fig. 2. (a) Faraday/Vernadsky ($65^{\circ} 15' S$, $64^{\circ} 15' W$) annual average air temperatures, 1951-2001 ($N=51$). The solid line is the least-squares regression line with a gradient of $0.057^{\circ} C a^{-1}$, and the dotted lines indicate ± 1 s.d. from this line. A linear regression model shows the warming trend over this period to be significant at greater than the 99% confidence level. (b) Mean annual sea ice extent for the Southern Ocean (insert) and the Palmer LTER region. See *Stammerjohn and Smith* (1997) for details on the satellite data used. Faraday/Vernadsky air temperature data provided by the British Antarctic Survey, and sea ice data provided by the National Snow and Ice Data Center.

er data is now deemed less reliable. The solid line represents the least-squares regression line. After accounting for serial correlation present in this 51 year record (for method, see *Smith et al.*, 1996), the trend is statistically significant at a $>99\%$ confidence level. The dotted line

indicates the ± 1 standard deviation (s.d.) from the regression line and has been used as a designator for defining “high” (above one s.d.) or “low” (below one s.d.) temperature years. The record from Rothera station (further south on the WAP) shows a strong temporal

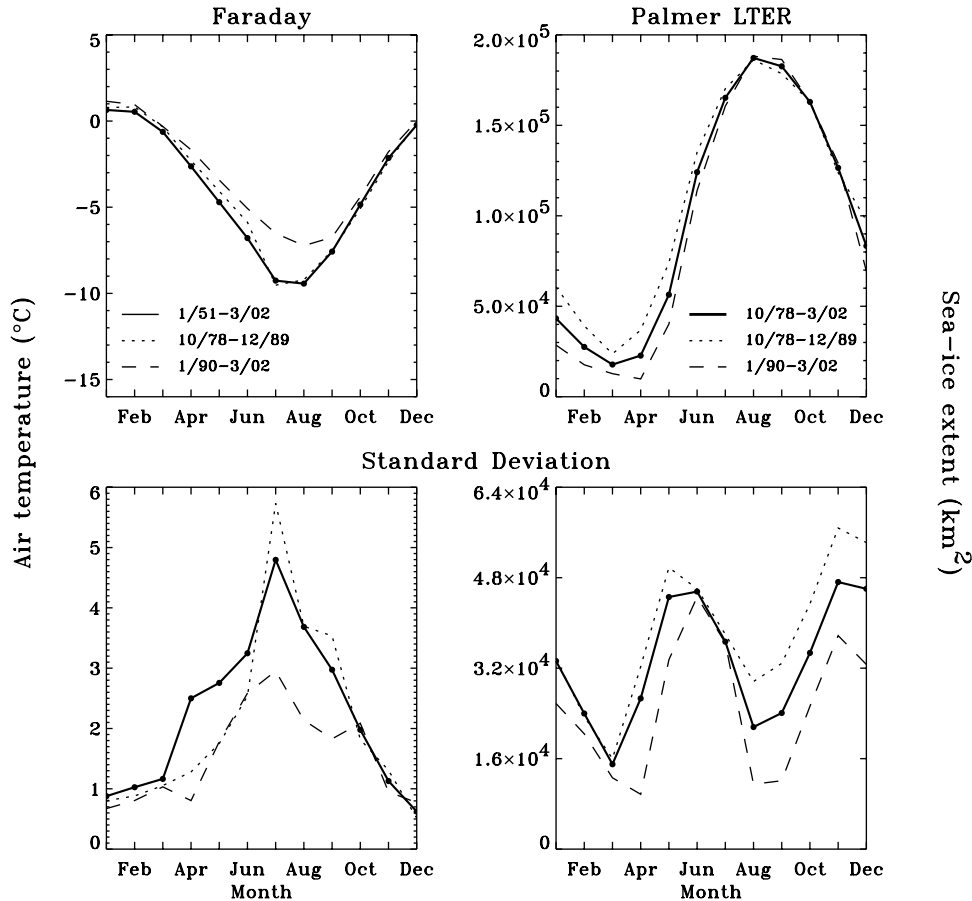


Fig. 3. Annual curves of monthly mean (a) Faraday/Vernadsky air temperature and (b) Palmer LTER sea-ice extent, shown for three different periods: the full record (bold line with solid dots) that includes 1/51-3/02 for (a) and 10/78-3/02 for (b); the period covering the first half of the sea-ice record (dotted line) that includes 10/78-12/89; and the period covering the second half of the sea-ice record (dashed line) that includes 1/90-3/02. Standard deviations of the monthly mean (c) Faraday/Vernadsky air temperature and (d) Palmer LTER sea-ice extent, shown for the same three periods. Faraday/Vernadsky air temperature data provided by the British Antarctic Survey, and sea ice data provided by the National Snow and Ice Data Center.

coherence (*King, 1994; Smith et al., 1996*) with the mean annual temperatures averaging a few degrees cooler than Faraday/Vernadsky but displaying similar trends. This evidence suggests that there is a north/south temperature gradient along the WAP and that observed trends are coherent throughout the region.

Associated with the increasing trend in annual WAP air temperature is a decreasing trend in annual sea ice extent (Figure 2b) from 1979 to 2001 for the Palmer LTER region (see *Stammerjohn and Smith (1996)* for details on the satellite data used). The satellite sea-ice record is too short and the variability too high for the decreasing trend to be statistically robust, however the strong anticorrelation between WAP air temperature and sea-ice poses the possibility that sea-ice extent has been decreasing over

the last 50 years in association with the increase in WAP air temperature. Seasonal analysis also shows that the decreasing sea-ice trend is due mostly to decreasing sea ice during spring, summer, and fall, in conjunction with the observed decrease in the length of the sea-ice covered period (*Smith and Stammerjohn, 2001*). In contrast to the decreasing trend in WAP sea-ice extent, the inset in Figure 2b shows that sea-ice extent for the whole Southern Ocean is trending upward. *Thompson and Solomon (2002)* provide an interpretation of recent Southern Hemisphere climate change leading to the observed spatial variability.

The seasonal variability of air temperature and sea ice change during the past two decades is illustrated in Figure 3 (see *Smith and Stammerjohn, 2001* for meth-

ods). Figures 3a and 3b show monthly mean air temperature and sea-ice extent for the following periods: the full instrument record (solid line for air temperature, 1/51-3/02, and sea-ice, 10/78-3/02); roughly the 1980s, i.e., the first half of the sea-ice record (dotted line for 10/78-12/89); and roughly the 1990s, i.e., the second half of the sea-ice record (dashed line for 1/90-3/02). Figures 3c and 3d show the standard deviations of monthly mean surface air temperatures and sea ice for the same periods plotted in Figures 3a and 3b, respectively.

Visual inspection of Figure 2a shows that the last two decades (1980s and 1990s) were warmer than the previous several decades. Figure 3a shows that the largest temperature changes between the 1980s and 1990s have occurred in winter (June-August) in contrast to relatively less change in late spring and summer (November-March). Figure 3c illustrates that in general (i.e., for the entire time period) there is significantly less variation in air temperatures during summer, when sea ice-free conditions and maritime conditions prevail, as compared to late fall and winter (May through September), when both sea-ice conditions and polar continental influences are highly variable. However, the winter variability in the 1990s is less than that for the 1980s, indicating that warmer air temperatures in winter are becoming more the norm.

The seasonal variability of sea ice (Fig. 3b) is inversely related to the seasonal cycle of air temperature (Fig. 3a) except that the summer sea ice extent minimum lags the summer air temperature maximum by two to three months. Most noteworthy, however, is that the 1990s winter warming and increased variability (shown in air temperature) is not associated with a seasonal anticorrelated response in sea-ice extent. There is no clear decrease in winter sea-ice extent between the 1980s and 1990s, but instead there has been a detectable decrease in summer-early fall (January to May) sea-ice extent. Figure 3d illustrates that in general there is increased variability during periods of sea-ice advance (May-July) and retreat (October-January). However, as seen for air temperature, variability has decreased from the 1980s to the 1990s indicating that later sea-ice advances and earlier sea-ice retreats are also becoming more the norm.

The overall timing and magnitude of the annual cycle of sea ice advance and retreat is influenced not only by long-term trends but also by El Niño-Southern Oscillation (ENSO) time scales of variability. Air temperature and sea ice extent for various regions of the Southern Ocean show some correlation with the Southern Oscillation Index (SOI, determined by the standardized sea-level pressure difference between Tahiti and Darwin, Australia). Several authors have suggested

(Carleton, 1988; Mo and White, 1985; van Loon and Shea, 1985; van Loon and Shea, 1987; Smith et al., 1996; White and Peterson, 1996; White et al., 1998) that these relationships support the idea of linkages between sea ice, cyclonic activity and global teleconnections. Recently, strong statistical associations between ENSO variability and Southern Ocean climate have been demonstrated (Yuan and Martinson, 2000, 2001; Kwok and Comiso, 2002). Martinson and co-workers, studying opposing anomalies in surface air and sea surface temperatures, sea-level pressure and sea ice extent between the southeastern Pacific and southwestern Atlantic sectors, describe the Antarctic Dipole (ADP) as an out-of-phase relationship which is coherent with ENSO variability. Recent work (Liu et al., 2003) also discuss possible teleconnection mechanisms whereby the variability in the ADP is associated with ENSO-related variability in the regional mean meridional atmospheric circulation. Since the ENSO time scale of variability is second only to seasonal variability in driving worldwide weather patterns, an understanding of these teleconnected spatial patterns of variability are essential to an understanding of climate variability, sea ice forcing and ecological response within the WAP. Also, Thompson and Solomon (2002) have presented evidence that trends in the Southern Hemisphere annular mode, a large-scale pattern of variability characterized by fluctuations in the strength of the circumpolar vortex, have contributed to the observed warming over the WAP.

While the mechanistic processes that link WAP temperature and sea ice trends continue to be researched, the role of the mean position of the atmospheric circumpolar low-pressure trough (CPT) continues to be viewed as a possible linking mechanism. The Antarctic Peninsula is the only area in the Southern Ocean where the CPT 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 CPT during spring and autumn. The relative position of the CPT influences not only the semiannual cycle of atmospheric variables but also the timing and distribution of sea ice and other oceanographic variables. Van Loon suggested that this seasonal temperature cycle is associated with enhanced meridional flow from middle to high latitudes during spring/fall. 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 co-workers (King, 1994; King and Harangozo, 1998; Marshall and King, 1998) also show a

strong correlation between surface air temperature and meridional sea-level pressure indices 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 due to the effects of southerly winds and colder temperatures. *Stammerjohn et al.* (2003) discuss in detail the response of sea ice extent and drift dynamics to synoptic forcing in the WAP region and present a conceptual model of ice-SAO-ENSO linkages that may explain both seasonal and long-term variability. They suggest such a conceptual model may provide a linkage between synoptic-scale systems and a mechanism for long-term climate variability. Regardless of the mechanisms, both the modern instrument record and the paleohistory of the WAP suggest competitive interactions between two distinct latitudinal climatic zones—maritime to the north and continental to the south. The observed statistically significant warming trend over the past century is modulated by tropical-polar teleconnections with ENSO-like variability and the mechanisms behind these changes is an area of active and future research.

3. PHYTOPLANKTON AND SEA BIRDS

The physical forcing of the WAP marine ecosystem is undergoing change in conjunction with the seasonal variability and trends in air temperature and sea-ice as discussed above. As noted, these observations are indicative of a climate change where continental influences (cold and dry) are giving way to increasing maritime influences (warm and moist) along the WAP latitudinal climate gradient. The Palmer Station area in particular, located approximately two thirds of the way up the peninsula on the south edge of Anvers Island, has been within the region of increased maritime influence for at least the last several decades.

Ecological response to this environmental change can be manifest, or not, dependent upon circumstances. For example, key species sensitive to changes in sea-ice can amplify this change by causing a cascading response within the entire ecosystem (*Smith et al.*, 2003). One notable amplification mechanism occurs because the temperature threshold for an ice-to-water phase change may create a pronounced non-linear ecosystem response

to what is a relatively small temperature shift (*Welch et al.*, 2003). From the perspective of a sea ice-dominated ecosystem, the later advance and earlier retreat of sea ice in the 1990s (as compared with the 1980s) translates into a shorter sea ice season (the average period for sea ice coverage at Palmer Station) by roughly two weeks. A shift to a more oceanic marine ecosystem reduces the seasonality and geographical extent of the sea ice habitat and consequently will influence all trophic levels of the WAP sea ice dominated marine ecosystem.

The Palmer LTER is accumulating evidence that links the timing and magnitude of sea ice advance and retreat to the seasonal progression and life history patterns of phytoplankton, krill and sea birds (*Fraser et al.*, 1992; *Quetin et al.*, 1996; *Fraser and Trivelpiece*, 1996; *Smith et al.*, 1998, 1999, 2002; *Fraser and Hofmann*, 2003; *Quetin and Ross*, 2001; *Vernet et al.*, personal communication) as well as key biogeochemical processes (*Karl et al.*, 1996; *Carrillo and Karl*, 1999). Marine ecosystems are tightly coupled to physical forcing so we can anticipate that, as the temperature and sea ice trends described above continue, there will be changes in the abundance and distribution of key species in response to climate variability. In the following, we focus on indicators at the base (primary productivity) and at the top (seabird abundance) of the food web, respectively.

Within the context of climate variability, ecological response, and the interpretation of paleoclimatic records, it is important to recognize that the interannual variability in primary productivity in the WAP area is relatively large. Figure 4 (updated from *Smith et al.*, 2001) shows the annual primary production ($\text{gC m}^{-2} \text{yr}^{-1}$) determined near Palmer Station for each growing season from 1991/92 to 2001/02 using three different methods as described in the figure legend. The comparison shows that there is good agreement between the three methods (making use of surface and satellite observations as well as results from modeled primary productivity). There is also wide spatial variability as can be seen in Plate 1 which shows the Chl-a concentration (mg chl-a m^{-3}) averaged within the euphotic zone of the Palmer LTER grid for each January cruise from 1993 to 2002. The surface observations shown in Plate 1, and corresponding ocean color satellite (*Smith et al.*, 2001) data (not shown), illustrate both the seasonal and interannual variability as well as the spatial variability of phytoplankton production in the WAP region. Mechanisms underlying this observed variability within the WAP region have been previously discussed (*Smith et al.*, 1996, 2001) and include factors that can control growth rates (temperature, light, and nutrients) and/or by those that control the

Annual Primary Production at Palmer

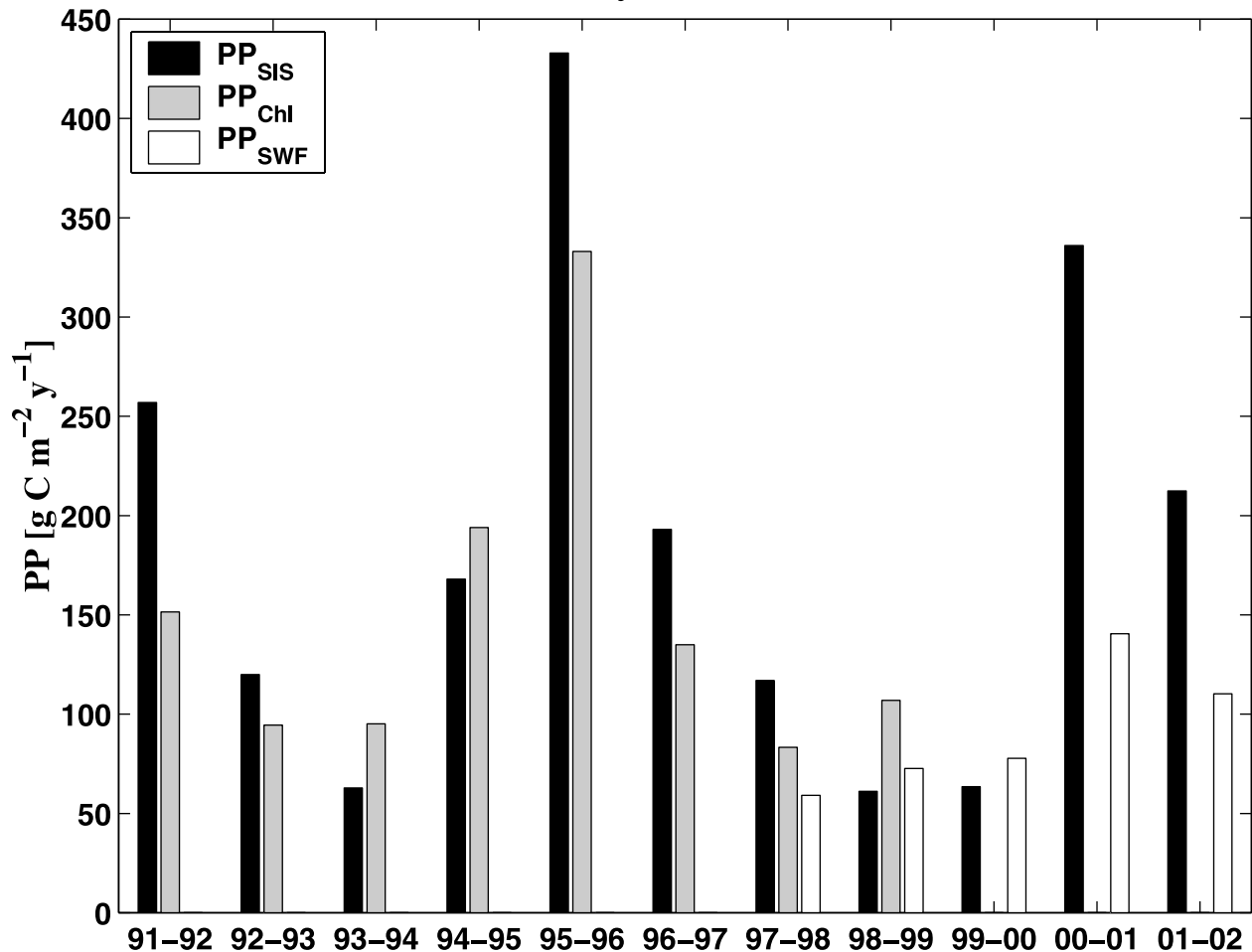


Fig. 4. Annual primary production ($\text{gC m}^{-2} \text{yr}^{-1}$) determined near Palmer Station for each growing season from 1991/92 to 2000/02. First, annual estimates have been made from integrated near-weekly surface sampling over the growing season from November to March (152 days) at Palmer Station (PP_{SIS}). Second, annual production estimated based on Palmer Station chl-a measurements using our production model and integrated over the same growing season (PP_{CHL}). Third, estimates from modeled primary production based on average monthly chl-a retrieved from SeaWiFS ocean color data (for the years since the satellite has been in orbit) (PP_{SWF}).

accumulation rate of cells in the euphotic zone and hence population growth (grazing, water column stability, and sinking). This high variability at the base of the food chain influences organisms at all trophic levels.

Our observations show that this high variability is characteristic of several biogeochemical provinces (coastal shelf zone, seasonal sea ice zone, permanently open ocean zone, polar front zone) within the larger WAP region (Treguer and Jacques, 1992; Smith *et al.*, 1998). Given this high variability, detecting trends in primary productivity is problematic and emphasizes the need for long-term records to properly resolve mechanisms that may permit predictive estimates of this vari-

ability. In spite of this variability, results from nearly a decade of both in situ and satellite observations show links between sea ice variability and primary production as well as some persistent spatial patterns (Smith *et al.*, 1998, 2001; Dierssen *et al.*, 2000). The challenge now is to understand how the combined influence of a long-term warming trend and ENSO-related variability is modifying the WAP ecosystem.

While a positive correlation between primary production and sea ice has been observed and is consistent with the Palmer LTER's original hypothesis, we find that the seasonal timing of sea ice advance and retreat and other factors, including the recently observed increase in gla-

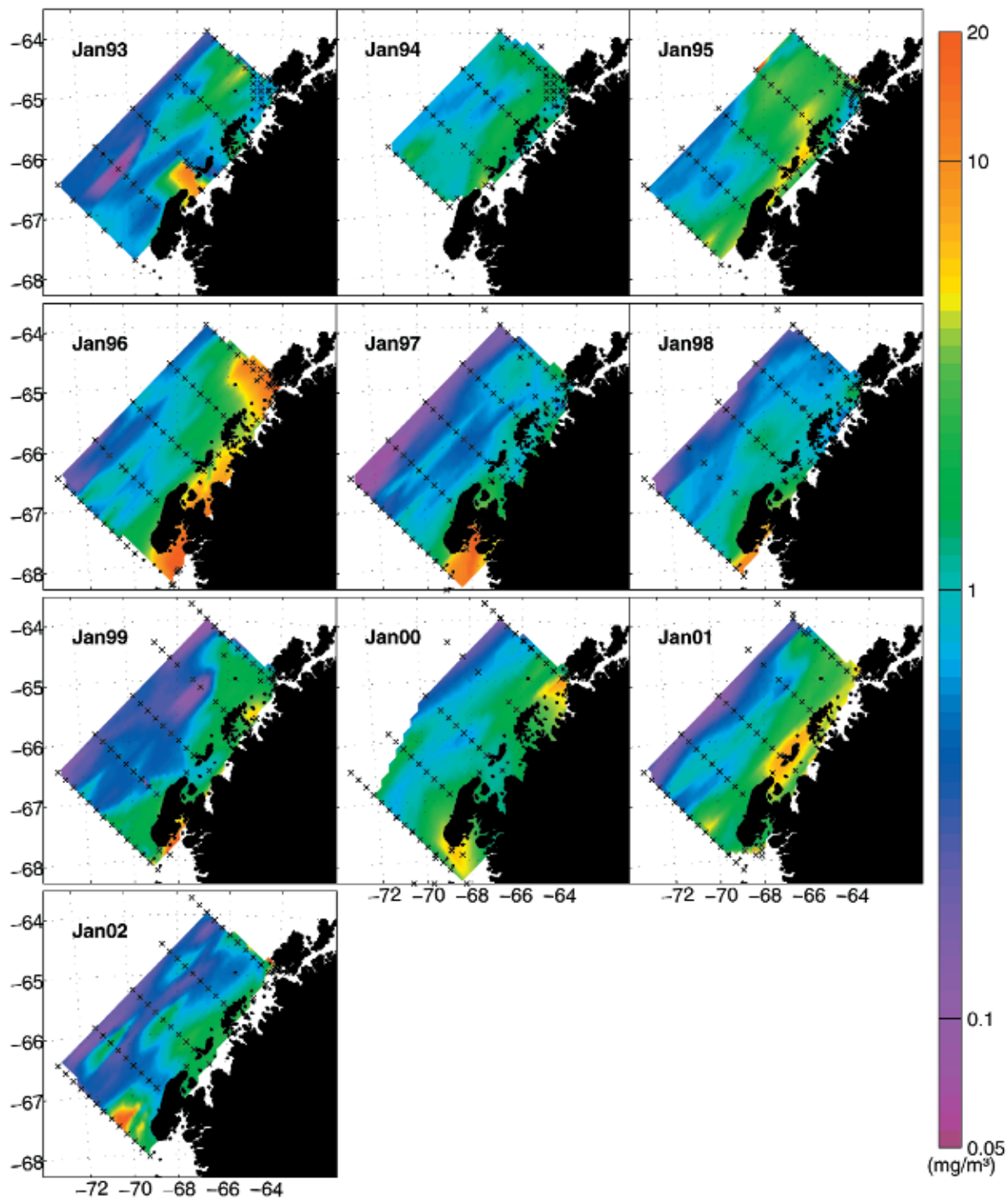


Plate 1. Chl-a concentration (mg chl-a m⁻³) averaged within the euphotic zone (roughly to the 1% light level) in the Palmer LTER grid for each January cruise from 1993 to 2002.

cial melt water input, are also important. Through several lines of evidence collected in conjunction with the Palmer LTER, *Dierssen et al.* (2002) have postulated that the freshening and warming of coastal surface waters over summer months are influenced not solely by sea ice melt, as suggested by the literature, but also by an influx of glacial melt water. Dierssen and co-workers suggest that glacial melt water in turn can significantly influence both the marine ecosystem and sea ice dynamics. They find that a stabilizing surface lens (top 50 meters of the water column) of low salinity melt water persists in recent years well past the late spring period that is influenced by sea ice-melt. This low salinity surface lens can extend up to 100 km from the coast and is associated with higher levels of primary productivity.

Currently the influence of glacial melt water on the WAP ecosystem is being subjected to more rigorous analysis. However, this example demonstrates the conflicting influences of a warming trend on primary production. The earlier departure of sea-ice would mean an earlier occurrence of a stabilizing fresh water lens (caused by sea-ice melt) that by late spring could be destroyed by wind-mixing caused by storms. However, the earlier departure of sea-ice also is associated with warmer summers and increased glacial-melt run-off, providing another fresh water source that could maintain or reestablish a stabilizing fresh water lens. Dierssen and co-workers also note that glacial melt-water may provide a replenishment of macro (and micro) nutrients in the later summer and early fall when the nutrient pool may be diminished from earlier blooms. Finally, a shallow fresh water lens will freeze more easily the following fall, thus possibly influencing the timing and location of sea ice advance in the WAP region. Understanding the mechanisms behind these conflicting influences is an important goal toward understanding the high temporal and spatial variability of primary productivity and the overall ecological response to the observed climate variability.

The factors controlling phytoplankton composition in the waters west of the Antarctic Peninsula, in addition to phytoplankton primary production, are related to water column stability, mainly driven by melt water, and expected to be affected by decreases in sea ice and/or increases in glacier melt water (*Dierssen et al.*, 2002). These changes, in turn, are expected to affect abundance and distribution of the main grazer, *Euphausia superba*. Phytoplankton assemblages in the WAP have varying proportions of diatoms, cryptomonads, prymnesiophytes, prasinophytes, chrysophytes, dinoflagellates and unknown flagellates (< 5 micrometers in diameter)

(*Garibotti et al.*, 2003). *Moline et al.* (2000) have proposed that glacier melt water is instrumental in promoting cryptomonad growth in the area near Anvers Island while *Walsh et al.* (2001) proposed krill grazing as the mechanism which shifts the system from diatom- to cryptomonad-dominated communities, a conclusion supported by *Garibotti et al.* (personal communication) based on krill grazing on phytoplankton total biomass. Furthermore, *Prezelin et al.* (2000) have proposed that upwelling promotes diatom growth, and identify the area around Anvers Island and in particular the area offshore of Renaud Island as regions where upwelling should sustain diatom growth. These authors suggested that the lower than expected diatom concentration in the water column during sampling was due to the time of sampling being too early in development of the seasonal phytoplankton succession. An alternative hypothesis would be that krill grazing in this region of high krill biomass control bloom dynamics and keeps the standing stock of diatoms low, as seen in other areas such as the North Pacific. However, the ten-fold interannual variability in krill biomass, in part due to episodic recruitment (*Quetin and Ross* 2002), means that krill are not always in high enough abundance to affect either bloom dynamics (*Ross et al.* 1998) or phytoplankton composition. If the various phytoplankton assemblies vary in space and time in response to climatic change, krill distributions may shift to match regions of optimal foraging. Alternatively, if krill remain in specific regions, and the phytoplankton assemblies shifts to one of lower than optimum food quality, the overall productivity of the krill population may decrease (*R. Ross and L. Quetin*, personal communication).

Garibotti and co-workers (personal communication) have also documented considerable variability in phytoplankton community composition, cell abundance and biomass alongshore in the inner shelf regions of the WAP. This variability is attributed not only to the selective removal of diatoms by krill but also appears to display different stages of seasonal succession as a consequence of the north to south retreat of sea ice. Thus, for phytoplankton within the WAP region, we can expect climate variability to influence changes not only in primary production but also on phytoplankton composition due to direct effects of ice and water-column physics or as consequence of direct and indirect effects of grazer's and their distribution and efficiency in controlling phytoplankton. Processes controlling the spatial and temporal patterns and variability of phytoplankton abundance (Plate 1) within the WAP region continue to be an active area of research by the Palmer LTER.

The ecosystem modifications most clearly manifest in the context of the WAP warming trend are the changes in upper level predator populations (Fraser *et al.*, 1992; Fraser and Patterson, 1997; Smith *et al.*, 1999, 2001; Fraser and Hofmann, 2003). Figure 5 shows the changes in Adelie and chinstrap penguin populations near Palmer Station during the past two decades and in gentoo penguins populations since founder colonies became established in the area during the early 1990s. Fraser and co-workers (Fraser *et al.*, 1992) hypothesized that a decrease in the number of cold years with heavy winter sea ice due to climate warming produced habitat conditions more suitable for the ice-intolerant (chinstrap and gentoo) penguins, as opposed to the ice-dependent (Adelie) penguins. The trends shown in Figures 2, 3 and 5 are consistent with this hypothesis.

Furthermore, the causal mechanisms suggested by this hypothesis have been implicated as key factors affecting penguin demography over a range of spatial and temporal scales in both paleoecological and demographic studies (Taylor *et al.*, 1990; Baroni and Orbelli, 1991, 1994; Denton *et al.*, 1999; Emslie, 1995; Emslie *et al.*, 1998; Fraser and Patterson, 1997; Smith *et al.*, 1999, 2002; Emslie, this volume). Indeed, Emslie and co-workers (1998) have shown 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 Adelie penguin remains. This pattern stands in sharp contrast to trends evident 250 km north of the Palmer area where the relative dominance of Adelie and chinstrap penguins has changed cyclically in response to multi-century cooling and warming periods (Emslie, 1995, this volume). That chinstrap and gentoo penguins have invaded the Palmer Station region would seem to affirm the unusual nature of this 20th century WAP warming event.

Indicator species are invaluable for assessing ecological change. The founder colonies of chinstraps and gentoo species have increased dramatically while conversely Adelie penguins have decreased substantially in roughly just 25 years (Figure 5). Penguins integrate the influence of climate change across relatively wide spatial and temporal ranges, and the shifts in abundance and distribution of these species are consistent with expected habitat shifts based on the observed physical changes outlined above. In addition, Fraser and Hofmann (Fraser and Hofmann, 2003), who analyzed changes in the diets of Adelie penguins that span nearly a 30 year record, show there is a direct, causal relationship between variability in sea-ice cover, krill recruitment, krill abundance and predator foraging ecology. They suggest that the

variability inferred from the penguin diets might be related to changes in physical forcing associated with the Antarctic Circumpolar Wave (ACW) (White and Peterson, 1996). The periodicity of the ACW has been attributed to an ENSO-related teleconnection (e.g., Gloersen and White, 2001) and ENSO-related teleconnections with the WAP area have been suggested by others as discussed above.

4. SUMMARY

There is increasing evidence of the ecological impacts on natural systems of recent climate change (Walther *et al.*, 2002; Parmesan and Yohe, 2003; Root *et al.*, 2003). This evidence shows climate change is influencing a broad range of organisms in environments from the tropics to the poles. In the Climate Change 2001 report McCarthy *et al.* (2001) discuss the implications of climate change and describe two contrasting paradigms for the way ecosystems will respond to global change: ecosystem movement and ecosystem modification. The former is a gross simplification that assumes ecosystems will migrate relatively intact to a new location that is a closer analogue to their current climate and environment. Basic ecological knowledge suggests that this paradigm, while valuable for testing simple hypotheses, is unlikely to actually occur. The modification paradigm (Kennedy, 2002) assumes that, as climate and other environmental factors change with a consequent shifting of the co-evolved synchrony of the food web, there will be a change in the abundance, distribution and dominance of key species. As the length of the sea ice season shortens (Figure 3) the seasonal timing of this sea ice dominated marine ecosystem can be expected to shift with corresponding changes in ecologically important events and life histories of key species (Smith *et al.*, 1995, Figure 4). Our results show that trends in penguin populations are in accord with climate change predictions.

The above data show that Adelies have declined in abundance in the Palmer Station area and suggest that the locus of their distributions will be forced further 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, including 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 volume). The Palmer LTER PI's have argued (Ducklow *et al.* personal communication) that these observations for upper level predators presage evidence

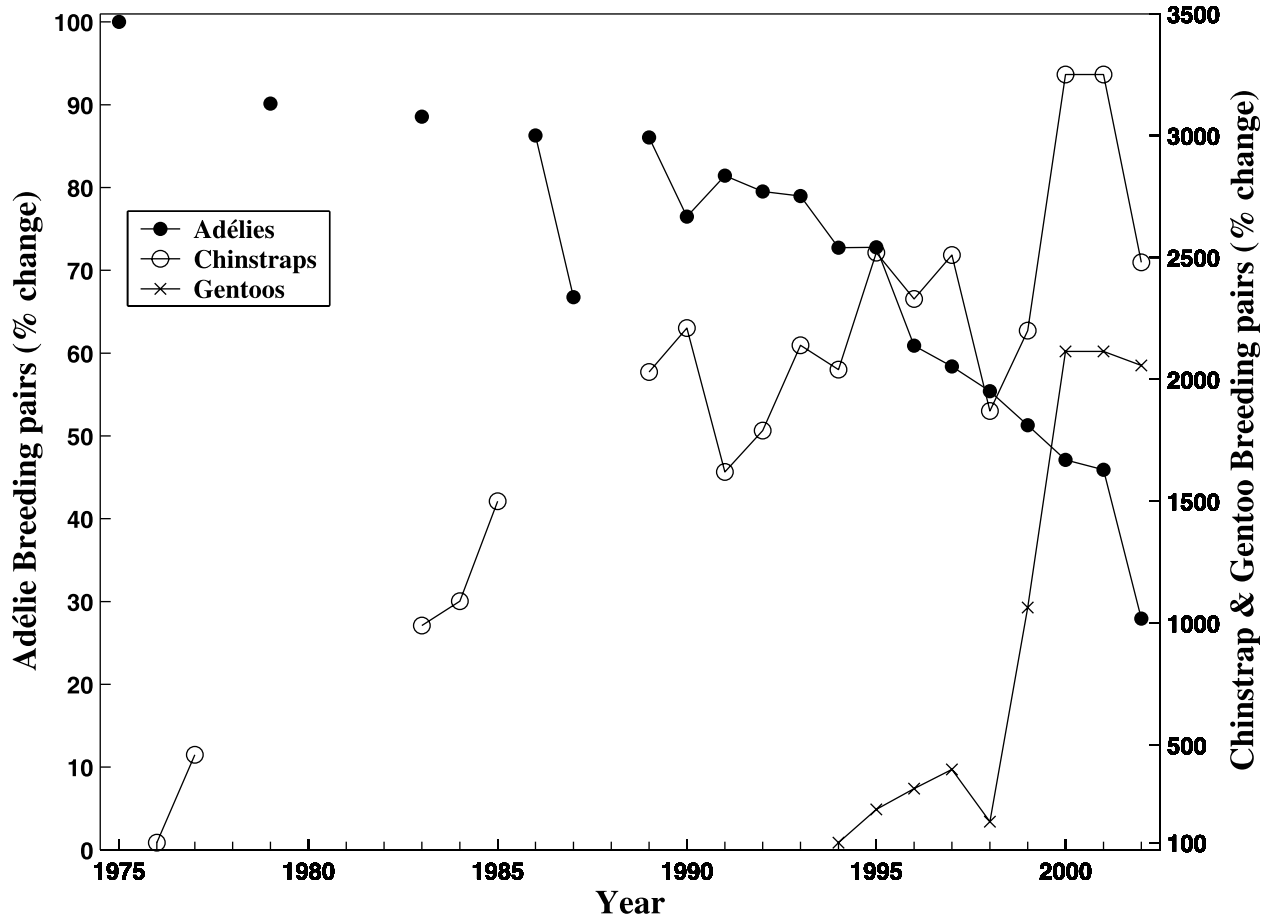


Fig. 5. Twenty six year trends in Adélie and chinstrap penguin populations at Arthur Harbor (Palmer Station) and for gentoo penguins since founder colonies became established in the early 1990's. Solid dots, Adélie penguins normalized to 100% in 1975 when the record began. The Adélie population of breeding pairs was 15,202 in 1975 and has declined to 7,161 in 2000. Chinstrap (open circles) and gentoo (plus signs) penguins are normalized to 100% in 1976 and 1994, respectively, when the founding colonies began. Chinstrap population of breeding pairs in 1976 was 10 and this founding population increased to 325 breeding pairs in 2000 while the gentoo population was 14 breeding pairs in 1994 and increased to 296 breeding pairs in 2000.

for ecosystem migration at lower trophic levels. A critical issue here is that the timing of change at different trophic and/or taxonomic groups may not be synchronous thus giving rise to profound ecological consequences. Future Palmer LTER studies are aimed at understanding these ecological consequences within the context of a changing environment.

The space/time variability in pigment biomass and primary production, discussed above, show that longer term observations will be needed to determine statistically significant trends. On the other hand, the interannual and ENSO-related variability in physical forcing and sea ice coverage provide an opportunity to “conduct” natural experiments by monitoring parameters and processes

during and after seasons/years of different physical forcing and sea ice coverage. A challenge is to understand how the combined influence of a long-term warming trend and ENSO-related variability is modifying the WAP ecosystem. Future Palmer LTER studies include studies to understand the mechanisms underlying these trends and the consequent spatial and temporal patterns in phytoplankton productivity. Climate variability along the Antarctic Peninsula offers a unique opportunity to study these changes within this Antarctic marine ecosystem.

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