

THE FATE OF ANTARCTIC PENGUINS WHEN EARTH'S TROPOSPHERIC TEMPERATURE REACHES 2°C ABOVE PRE-INDUSTRIAL LEVELS

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Abstract

We assessed how projected changes in the physical Southern Ocean will alter population trajectories of the two pack-ice penguins of the Antarctic, the Emperor (*Aptenodytes forsteri*) and Adélie (*Pygoscelis adeliae*). Using a subset of IPCC AR4 climate model output for emission scenario SRES A1B (doubling of CO₂ from 360 and stabilizing at 720 after 2100), we identify the time period at which global temperature will have increased by 2°C above pre-industrial levels. Using this benchmark, rather than an arbitrary year, allowed removal of some of the biases and uncertainties associated with the differing model sensitivities.

We, then, for the Antarctic, considered criteria and identified a subset of the “better” IPCC AR 4 climate model outputs. The “best” four — GFDL-CM2.1, GFDL-CM2.0, MIROC3.2(hires), and MRI-CGCM2.3.2a — were composited into an ENSEMBLE, which was then examined to look at conditions at the year of 2°C warming. Care was taken to evaluate the individual models that comprise the ENSEMBLE, as errors in different models tend to cancel one another often leading to an unjustified faith in the collective predictions. The ENSEMBLE output provided indicators of sea-ice coverage, wind speeds, and air temperatures for the Southern Ocean. These indicators of physical conditions were then used to assess the impacts of a 2°C global warming on penguins' habitat and ultimately their populations.

On the basis of the ENSEMBLE output, we concluded that 50% of Emperor colonies (40% of population) and 75% of Adélie colonies (70% of population) that currently exist at latitudes north of 70°S are in jeopardy of marked decline or disappearance, largely because of severe decreases in pack-ice coverage and, particularly for Emperors, ice thickness as well (especially in the eastern Ross and Weddell seas). Included are colonies on both sides of the northern Antarctic Peninsula and in East Antarctica. To

some degree, Adélie Penguins would be able to colonize areas where pack ice currently is too concentrated or where disintegrating ice shelves will be exposing coastline and providing new breeding habitat. However, this capacity will be importantly limited by the decreased persistence of pack ice in areas north of the Antarctic Circle, as this species seeks pack ice during winter where there is also daylight.

INTRODUCTION

The Emperor (*Aptenodytes forsteri*) and Adélie (*Pygoscelis adeliae*) penguin are the two 'true' Antarctic penguin species. They are sea ice 'obligates', their occurrence being largely confined to waters that are covered for a significant part of the year by sea ice. Where sea ice has disappeared, so have these species' colonies (Ainley 2002, Emslie 2001, Ducklow et al. 2007). Adélie Penguins breed in ~160 colonies around the continent (see Woehler 1993, Ainley 2002), but only 8 have been censused over a long enough time period to provide statistically meaningful time series, which extend decades, that can and have been used to assess the species' response to climate change. Likewise, the Emperor Penguin breeds in ~40 colonies (see Woehler 1993), but only at 4 have long time series of population size been accumulated. Therefore, these colonies at which long time series are available will be emphasized in this document.

Other penguins, such as King (*A. patagonica*), Macaroni (*Eudyptes chrysolophus*) and Gentoo (*P. papua*), do venture into ice-free areas south of the Polar Front and may enter the outer reaches of the pack, but mainly they are sub-Antarctic in their zoogeographic affinities. The one exception to the latter statement is the Chinstrap Penguin (*Pygoscelis antarctica*), which is restricted to waters lying south of the Polar Front but nevertheless mostly avoids sea ice (Fraser et al. 1992, Ainley et al. 1993).

Sea ice covers approximately 6% of the world's oceans (Gloersen et al. 1992) and plays an important role in the energy exchange between atmosphere and ocean. It is extremely sensitive to climate, including both temperature and wind patterns, and will continue to be dramatically affected by global climate change (Kwok & Comiso 2002, Zwally et al. 2002, Parkinson 2002, Russell et al. 2006a). It has also, in this age of satellite imagery, become relatively easy to monitor with a high degree of accuracy. Therefore, we have undertaken this project to assess how the two ice-obligate penguins will respond to changes in sea ice, as predicted by climate models.

To predict the future of penguin populations in the high-latitude Antarctic, it is necessary to understand how they have responded to past changes and then to predict how their physical environment – namely ice conditions, air temperatures, winds, sea surface temperatures (SST) and precipitation – will change in the future. The latter requires climate models that do well at capturing patterns evident at present in the Southern Ocean. Unfortunately, the climate models considered as part of the Intergovernmental Panel on Climate Change (IPCC 2007) Fourth Assessment Report (AR4) produce conflicting estimates of changes in the Southern Ocean, largely because the models differ substantially in their ability to simulate the strength and position of the Southern Hemisphere westerly winds, as well as other processes associated with the ocean component of the climate models (Russell et al. 2006b). A poor simulation of the Southern Hemisphere atmospheric jet greatly distorts the oceanic simulation because most of the vertical circulations in this region are wind-driven, and a poor simulation of the Southern Ocean for the present climate can be expected to distort aspects of the large-scale response to increased anthropogenic forcing. Sea ice is sensitive to both the atmosphere and the ocean, so changing the temperature or circulation patterns of either will lead to substantial changes in the sea ice upon which Antarctic penguins depend.

The Physical Setting

The Southern Ocean circulation is dominated by the Antarctic Circumpolar Current (ACC), the largest current in the world ocean. Due to the strength of westerly winds over the Southern Ocean, the Ekman drift in the surface layer is substantial. This northward drift of surface waters creates a divergence south of the Polar Front, which in turn creates vast areas of upwelling water (Peterson & Whitworth 1989). This upwelled water has a large effect on the high-latitude heat flux between the atmosphere and ocean. In addition to this heat effect, the amount of relatively fresh mode and intermediate waters exported north of the ACC in the shallow overturning circulation, the density gradient across the ACC, and the relative amount of salty deep water pulled near the surface from below the sill depth of the Drake Passage south of the ACC all affect a model's Southern Ocean and, therefore, will influence its response to anthropogenic forcing.

During the mid-1970s, the Southern Annular Mode (SAM) became positive and the Antarctic Ozone Hole (AOH) began to increase (Stammerjohn et al. 2008, Thompson & Solomon 2002). Both factors, working together have been causing changes in Southern Ocean climate. No longer does SAM oscillate between its negative and positive modes, as it did in previous centuries. Neither has the AOH abated, contributing to an increasing disparity of tropospheric and stratospheric temperatures, and in turn leading to increasing strength of the westerlies surrounding Antarctica (Russell et al. 2006a). In part related to the SAM positive mode, the southern jet stream has been moving south, as has the westerly belt of surface winds. In addition or perhaps a consequence, movement of a persistent low pressure system over the Amundsen Sea has resulted in greater offshore coastal winds in the Adélie Land to Ross Sea sector. The greater offshore winds in turn are leading to increasing sea-ice extent (SIE), increasing sea-ice season, increasing size and persistence of coastal polynyas, and decreasing sea-ice thickness (Zwally et al. 2002, Parkinson 2002, Russell et al. 2006a, Stammerjohn et al. 2008). The same weather system has resulted in the rising temperatures of the western Antarctic Peninsula, only in this case winds are blowing from the warm ocean lying to the north toward the continent. Related to the SAM, a bowing of the jet stream is bringing warming air from mid latitudes to the northern Antarctic Peninsula. As somewhat of an aside, these changes in the mid-late 1970s, amounting to a 'regime' shift, have had repercussions among a number of vertebrate and invertebrate populations mainly through the effect on ice (Ainley et al. 2005, Weimerskirch et al. 2003, Jenouvrier et al. 2005a, b). A lesser shift in population trajectory, around 1990, when the SAM ceased increasing (but didn't decrease), was also detected in some vertebrate populations (Ainley et al. 2005).

The above is what climate models need to be able to simulate in order to predict changes in the future. Studies using the IPCC AR4 coupled climate models generally create what is known as an *ensemble*: an individual variable from each of the various models is averaged to derive a robust consensus from the simulations. We will show that for sea ice, model errors tend to cancel, making the ensemble used in the IPCC analysis seem better than any of the individual components. Therefore, using a set of observational criteria, the pre-industrial control and 20th century runs, we winnowed the

available models on the basis of their Southern Hemisphere westerly winds and Antarctic Circumpolar currents. We then narrowed them further by comparing their results for sea ice and ocean frontal structure from the 20th century to the available observational record (from shipboard measurements and satellites). We then determined the year in which each model's globally averaged annual-mean temperature had risen by 2°C and used this benchmark to explore how the physical environment likely will change.

Sea Ice Definitions and Concepts

In this discussion, the following terms are important:

Sea ice is any layer of ice on the ocean surface resulting from the ocean freezing. This ice can either remain in place for long periods, as it is locked in place by geographic features such as capes or grounded icebergs, in which case it is called fast ice, or it can be broken into pieces, called floes, and is then called pack ice.

Sea-ice extent (SIE): the distance from the coast to the outermost edge of the ice pack. Usually the latter is defined as having ice <15% cover as satellite imagery has problems distinguishing ice from open water at lower concentrations (Gloersen et al. 1992, Parkinson 2002, Zwally et al. 2002).

Sea-ice concentration (SIC): the amount of water covered by ice, e.g. with 80% cover there are only very narrow leads among ice floes. The measure is very much scale dependent. SIC at the large scale varies directly with SIE (Jacobs & Comiso 1989, Jacobs & Giulivi 1998, Stammerjohn et al. 2008).

Sea-ice persistence, or season: the length of time, normally expressed in days or weeks, that sea ice is present in a given region (see Parkinson 2002, Stammerjohn et al. 2008).

Sea-ice coverage: in ice models, the fractional area of each grid cell covered by sea ice. This measure combines SIC, SIE and sea-ice persistence.

Ice thickness: measure of how thick an ice floe or extent of fast ice might be, from top to its underside. In windy areas, ice does not become very thick as not long after initial formation, winds have blown it northward to warmer waters where it thickens little, if at all (Jacobs & Comiso 1989). It is only during extended periods of calm and cold temperatures that fast ice thickens sufficiently that it no longer is susceptible to being blown loose by winds.

Polynya: an area within the region of ice cover that is ice free or persistently has significantly lower ice concentration than the surrounding pack. Much ice is created in coastal polynyas, and is then blown seaward (Barber & Massom 2007). One result is that with much offshore wind, SIE usually increases either through advection or Ekman transport (Hibler & Ackley 1983, Stammerjohn et al. 2008). Thus, SIE and polynya size, along with ice thickness, are all related.

CHOOSING CLIMATE MODELS

The Pre-industrial and Modern Simulations

Russell et al. (2006b) evaluated 18 of the coupled climate models by comparing the relationship between the pre-industrial westerly winds and the strength of the ACC, and we use this as our starting point. We compare the wind stress and ACC strength for the last 20 years of the 20th century run for each model (Figure 1). Several of the models are clustered close to the observations: these include the GFDL-CM2.1, GFDL-CM2.0, MIROC3.2(hires), MRI-CGCM2.3.2a, IAP-FGOALS1.0g, INM-CM3.0, and CCCMA3.1-T47 simulations, and as a first cut, these models seemed to be producing a Southern Ocean that is reasonable: they have winds and an ACC that is relatively close to the observations.

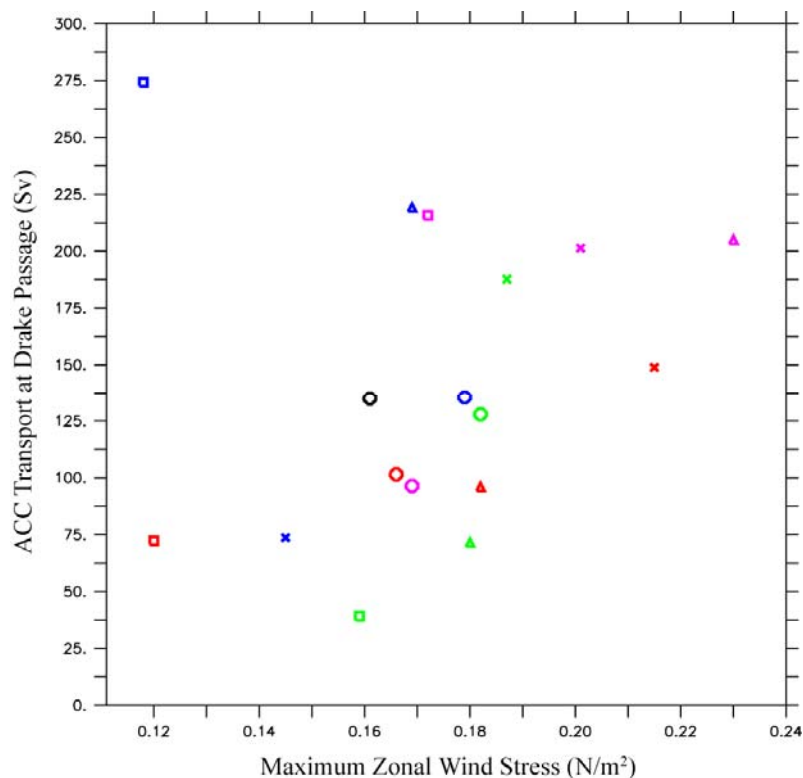


Figure 1: The maximum zonally-averaged annual-mean wind stress between 70°S and 30°S (N/m^2) plotted against the ACC transport at Drake Passage (69°W) for the 20th century. Observed (black circle), GFDL-CM2.1 (blue circle), GFDL-CM2.0 (red circle), CCCMA3.1-T47 (red triangle), CNRM-CM3 (red square), CSIRO-Mk3.5 (red cross), GISS-AOM (blue triangle), GISS-ER (blue square), IAP-FGOALS1.0g (blue cross), INM-CM3.0 (green triangle), IPSL-CM4 (green square), MIROC3.2 (hires) (green circle), MIROC3.2 (medres) (green cross), MRI-CGCM2.3.2a (purple circle), NCAR-CCSM-3.0 (purple triangle), UKMO-HadCM3 (purple square), and UKMO-HadGEM1 (purple cross). The 20th century annual mean for the model runs is defined as the average of all months between January 1981 and December 2000.

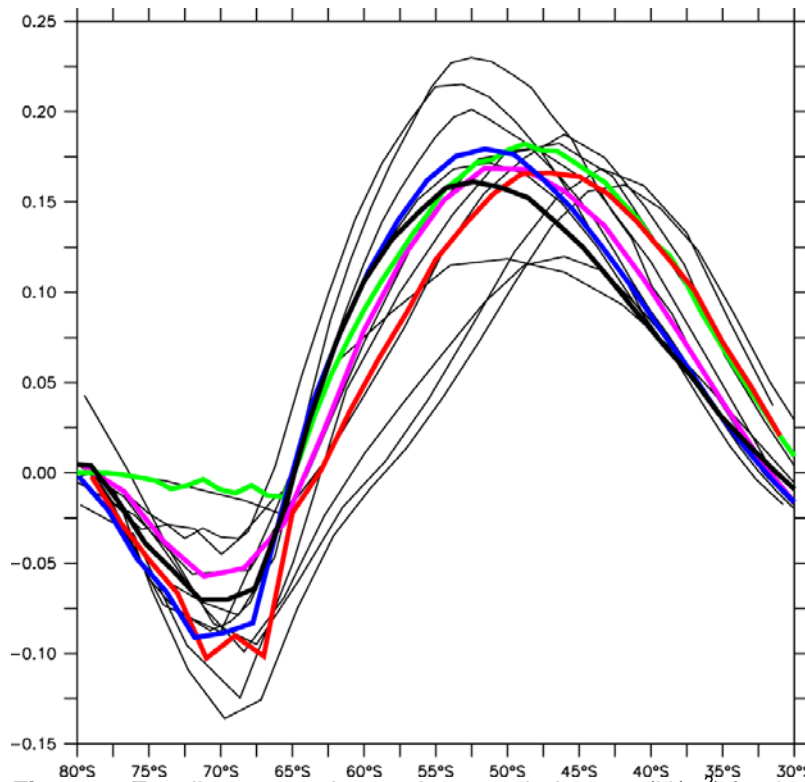
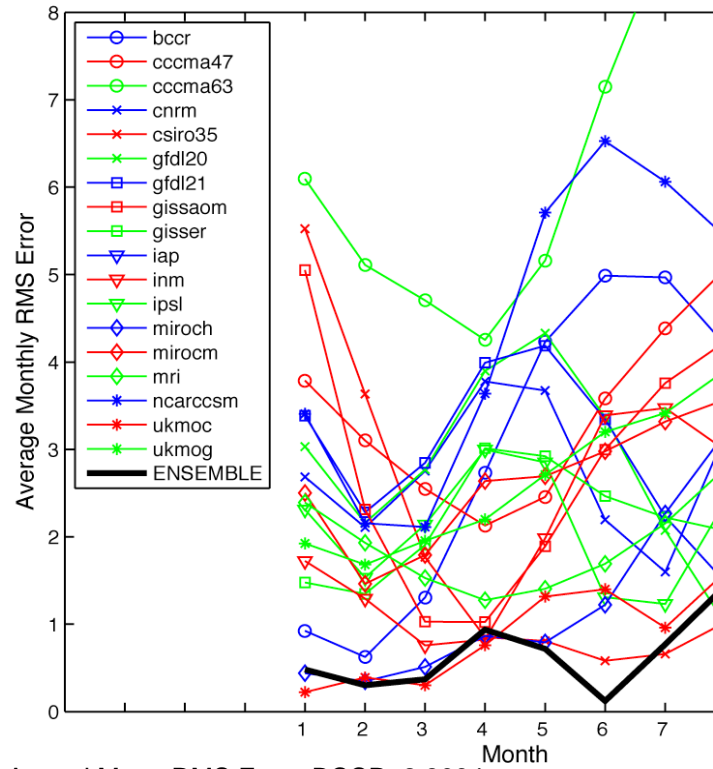
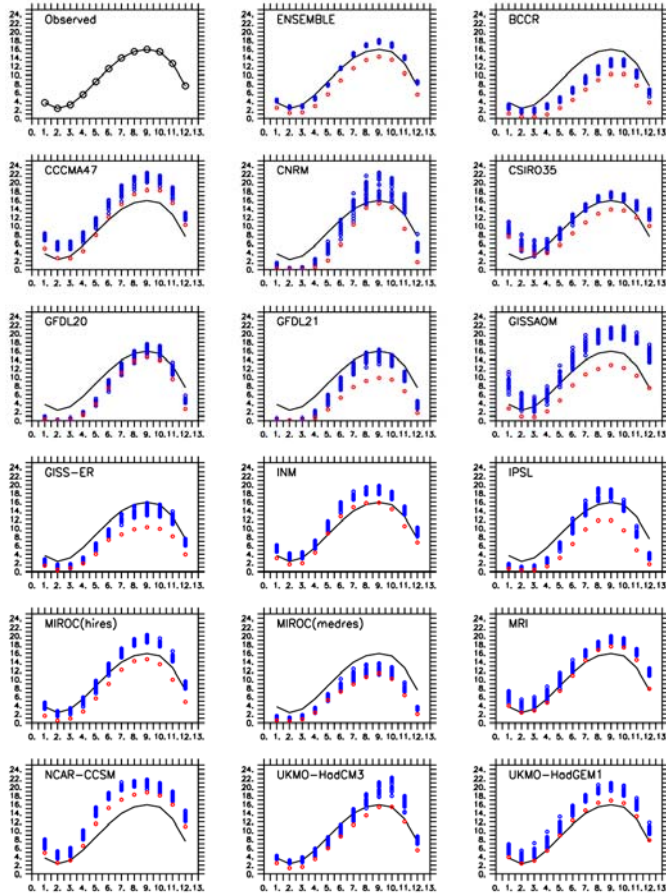


Figure 2: Zonally-averaged annual mean wind stress (N/m^2) for the 20th century. Observed long-term mean from NCEP (thick black), GFDL-CM2.1 (blue), GFDL-CM2.0 (red), MIROC3.2 (hires) (green), and MRI-CGCM2.3.2a (purple). Models included in the original analysis but omitted from our ENSEMBLE are indicated with thin black lines and include: CCCMA3.1-T47, CNRM-CM3, CSIRO-Mk3.5, GISS-AOM, GISS-ER, INM-CM3.0, IPSL-CM4, MIROC3.2 (medres), UKMO-HadCM3, and UKMO-HadGEM1. The 20th century annual mean for the model runs is defined as the average of all months between January 1981 and December 2000.

Figure 2 shows the zonally-averaged annual-mean wind stress from the models for the last 20 years of the 20th century. As Russell et al. (2006b) noted, most of the models have a maximum wind stress equatorward of the observations, some by more than 10° latitude. The models singled-out in Figure 1 all have a relatively accurate wind profile: neither too weak nor too strong and a maximum within 6° latitude of the observed. [As we eventually eliminated the CCCMA47, IAP, and INM models from our ENSEMBLE, their wind stress curves are not separated out from the rest of the pack.]



B) Annual Mean RMS Error: BCCR 2.8094; CCCMA47 4.0274; CNRM 2.8718; CSIRO35 2.0707; GFDL20 2.3797; GFDL21 2.8040; GISSAOM 3.7827; GISSER 1.8940;

INM 2.0082; IPSL 2.3100; MIROCH 1.6376; MIROC M 3.1794; MRI 2.4868; NCARCCSM 4.6182; UKMOC 1.6758; UKMOG 2.9309; **ENSEMBLE 0.8963**

Figure 3a) The interannual variability for each month of the total Antarctic sea-ice coverage for the pre-industrial control (blue) and at the year of 2°C warming; and b) the mean RMS error for each month for the total area of Antarctic sea ice for the 20 years of the pre-industrial control experiment, relative to the modern observations. The thick black line is the RMS error of the 16-member ensemble. The table indicates the annual mean of the monthly RMS error for each model.

As the next part of our winnowing process, we examined the seasonal cycle of sea ice around Antarctica (Figure 3a). Most of the models had a reasonable range of total ice area, between 0 and 20 million km². The modern observations still have sea ice around Antarctica in February (month of the yearly minimum), but some of the models have no sea ice at all for one or more months of the year. We chose to use a root-mean-squared error calculation so problems with too little ice in the austral summer would not be weighted as strongly as a significant error in winter. One of the models, IAP, which has nearly perpetual ice cover out to almost 40°S, was excluded from further consideration. Figure 3b is a clear example of why care must be taken when looking at ensembles of different models. The RMS error in June for the collection of models is significantly lower than that for any individual model!

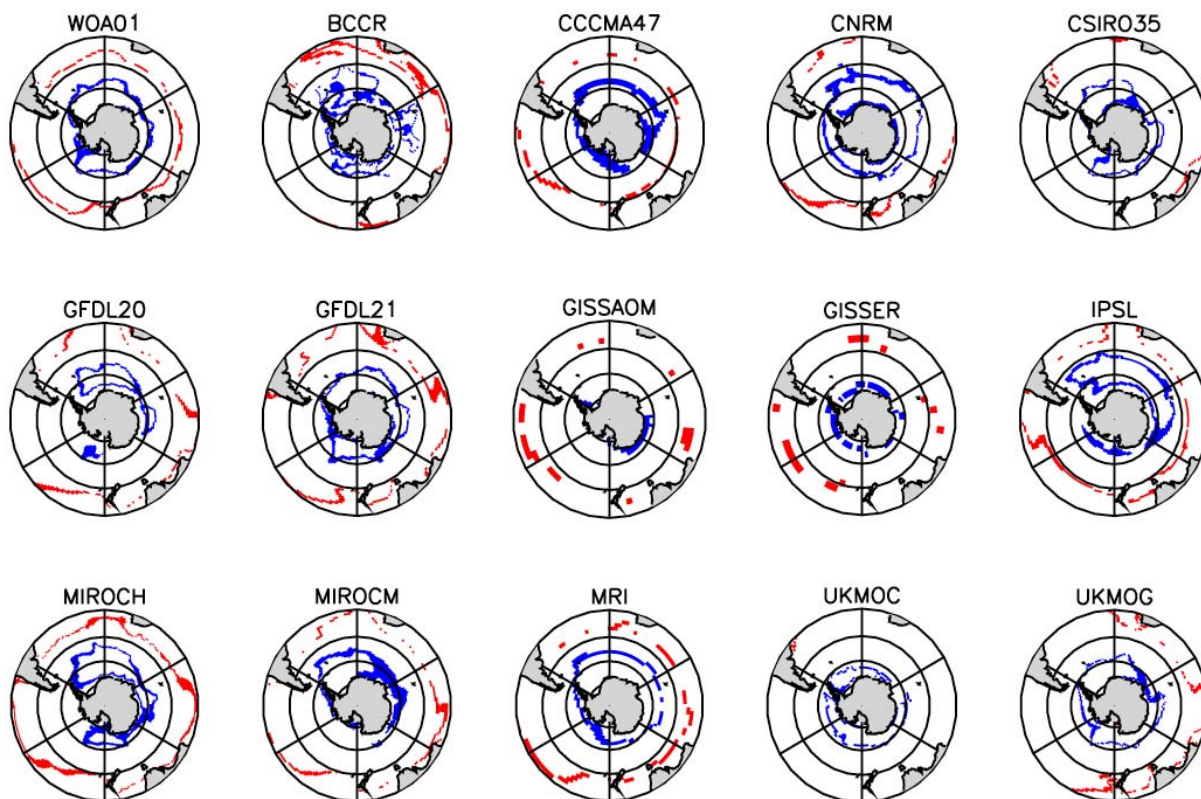


Figure 4: The ACC is demarcated by the subtropical front to the north and by the southern boundary close to the continent. The definitions for these boundaries are taken from Orsi et al. (1995)

We chose to further winnow the models by comparing their simulations of the boundaries of the ACC to the observational record. Orsi et al. (1995) defined the northern boundary of the ACC as the subtropical front (the location of salinities between 34.9 and 35.0 at 100 m) and defined the southern boundary as the surface transition from Upper Circumpolar Deep Water to the denser Lower Circumpolar Deep Water (the location of the $27.6 \sigma_\theta$ isopycnal at 200 m). Of the models not eliminated in the first pass or due to serious flaws in the sea-ice simulations (GFDL-CM2.1, GFDL-CM2.0, MIROC3.2(hires), MRI-CGCM2.3.2a, INM-CM3.0, and CCCMA3.1-T47), the CCCMA47 simulation was eliminated due to its extremely poor frontal structure. There were no ocean data for the INM model for the 20th century run, so although it seemed to be a reasonable simulation, we felt we could not include it in our ENSEMBLE either. Therefore, as a result of the above winnowing, the ENSEMBLE that we used in this analysis is composed of the GFDL-CM2.1, GFDL-CM2.0, MIROC3.2(hires), and MRI-CGCM2.3.2a models.

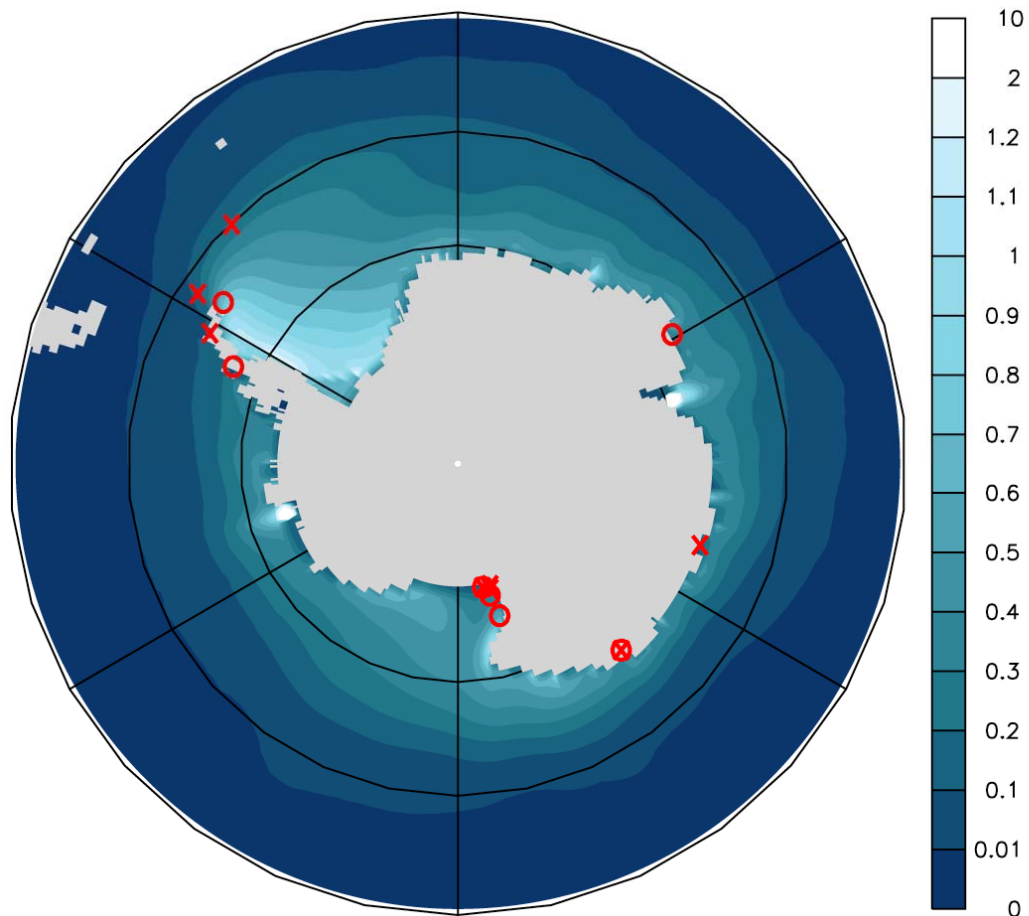


Figure 5: Modeled annual mean sea-ice thickness for our ENSEMBLE during the satellite era (1982-2007; compare to Timmermann et al. 2005). The red X's indicate the locations of Adélie Penguin colonies having a long time series of population trends, the red open O's indicate analogous Emperor Penguin colonies, and closed O's are sites where both species have been studied a long time.

As a check on the reasonableness of our choices, we now compare the simulated annual mean ice thickness from our collection to the observational record. The models do a reasonable job of simulating the observed annual mean sea-ice thickness. The thickest ice is in the western Weddell Sea along the eastern shore of the Antarctic Peninsula and in the eastern Ross Sea. The central Ross Sea has less ice cover in both the data and the models than does the area near Ross Island (location of the largest coastal polynya in the Antarctic).

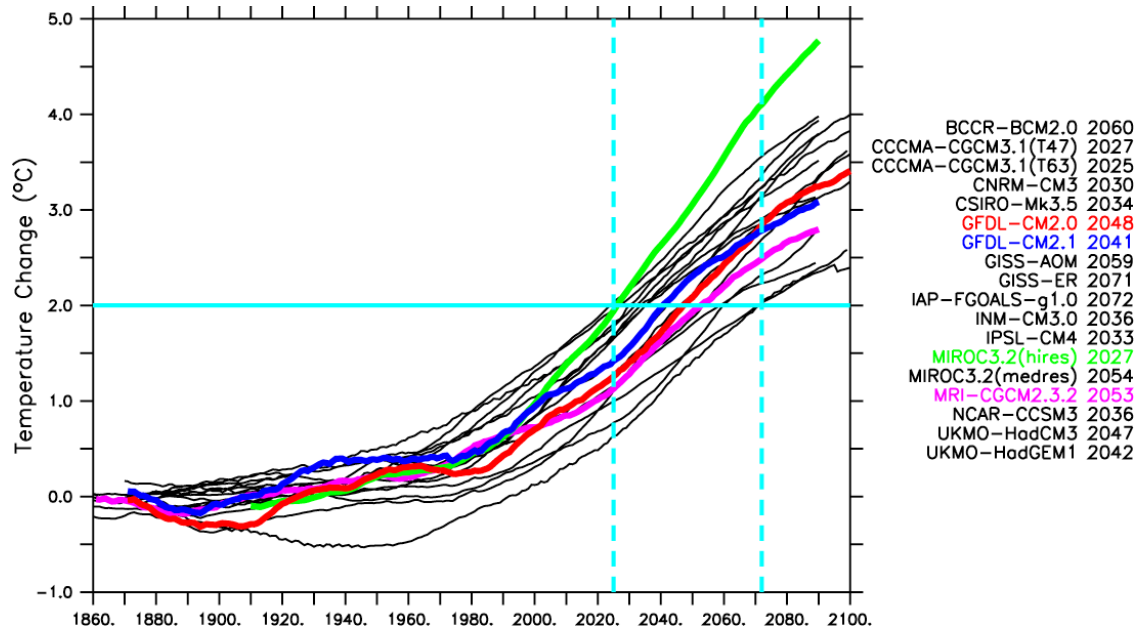
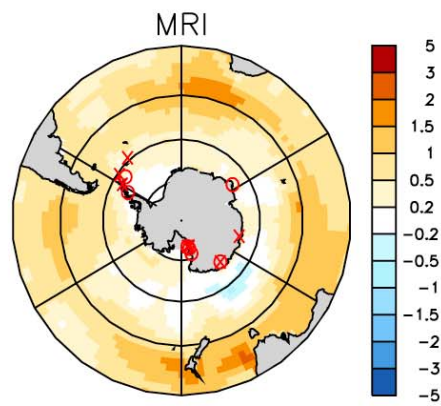
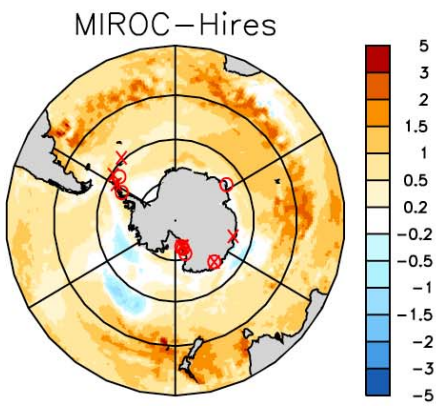
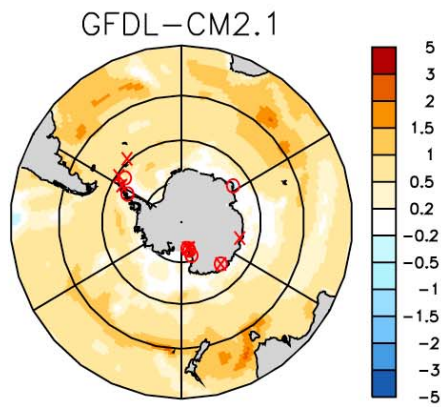
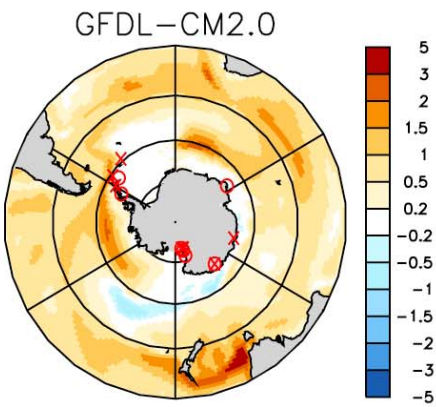
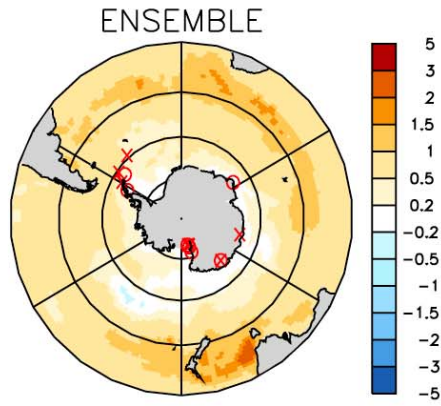
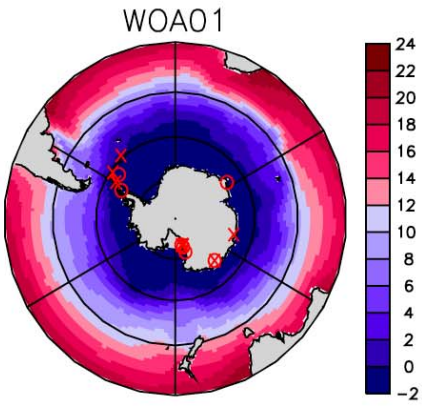


Figure 6: The globally-averaged annual-mean air temperature anomaly for each model. As in the Mark New report (2005), a 21-year running mean filter has been applied to each time series and the year of 2°C warming is the year in which the anomaly exceeds 2°C. All runs are from the SresA1B scenario. The colored lines are the models included in our ensemble and the black lines are the other models. The solid light blue line indicates the 2°C threshold and the dashed, vertical light blue lines bracket the times during which our chosen models exceed this threshold.

RESULTS

The Year of 2°C Warming and Conditions in the Southern Ocean

Rather than picking a calendar year in the future to examine the models, we chose to compare them during their year of 2°C warming (as was done by New (2005)), which is defined for the purposes of this study as the year in which the globally averaged, annual mean surface temperature has risen 2°C above the pre-industrial control simulation. This functional definition allowed us to take into account differences in the sensitivities of the various models while exploring their response at a common juncture. We used the first 20 years of the control simulation after the point at which it diverged from the 20th century simulation as the baseline. That is, if the 20th century run for model X started on 1 Jan 1850, then we averaged the 20 years of the control run from that point onward, 1 Jan 1850 to 31 Dec 1869, in this example.



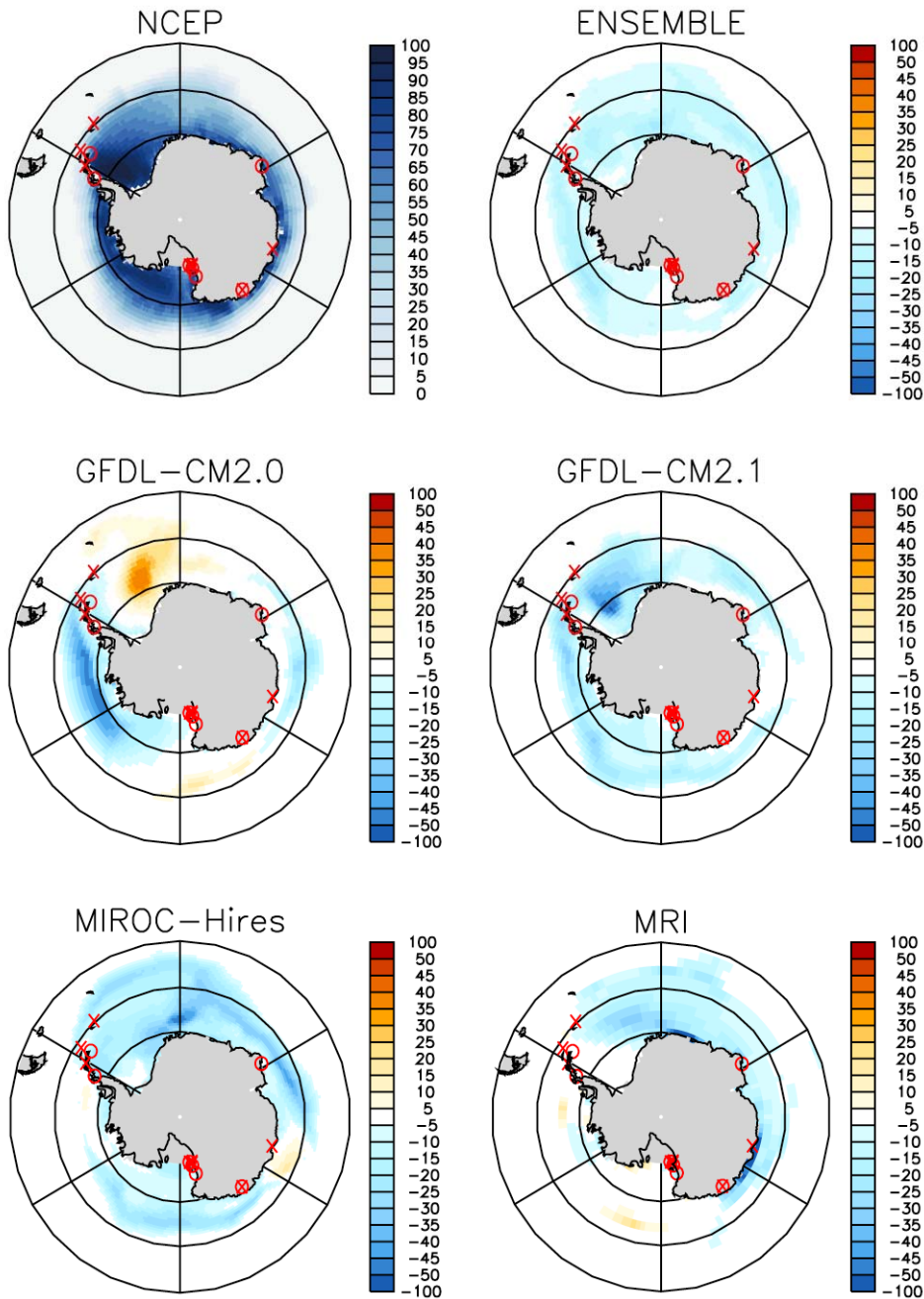


Figure 7: Top, a) Observed annual mean SSTs ($^{\circ}\text{C}$, 0-100 m average) from the World Ocean Atlas (WOA01, Conkwright et al. 2002) and the change in SST from the four models and the ENSEMBLE at the year of 2°C warming relative to the modern era (1981-2000 average). Bottom, b) Observed annual mean sea-ice coverage (%) from the National Center for Environmental Prediction reanalysis (NCEP; Reynolds et al. 2002) and the change in sea-ice coverage from the four models and the ENSEMBLE at the year of 2°C warming relative to the pre-industrial control. Red circles denote Emperor Penguin colonies, and red x's denote Adélie Penguin colonies (see Figure 5).

As expected, a warmer atmosphere leads to a warmer Southern Ocean and less sea ice around Antarctica (Figure 7). In general the ocean surface warms by $> 0.5^{\circ}$ with greater increases downstream from Australia and in the Agulhas retroflection region.

These are due to changes in the circulation: a faster ACC entrains more water at its northern edge increasing the advection of warm subtropical waters in all three ocean basins. The simulated annual mean sea-ice coverage decreases by 5-10% at 60°S and by 10-15% at 70°S. The four models agree with each other with respect to changes in the SST. There is more variability between the models with respect to projected changes in the sea ice; the GFDL-CM2.0 model shows an increase of sea-ice coverage in the Weddell Sea while the GFDL-CM2.1 model indicates a decrease.

HOW PENGUINS HAVE RESPONDED TO CLIMATE CHANGE IN THE PAST

Penguins' Relationship to Sea Ice

As detailed by Ainley et al. (2005), Emperor and Adélie penguins are affected by sea ice in both similar and different ways, depending on circumstances. The former raises its young on fast ice, usually annual fast ice, it being too large, bulky, and clumsy to climb over high jumbles of rocks or broken sea ice with any facility. Like other large birds, it also has an extended breeding season, in its case about 9 months. Unlike its close relative, the King Penguin (*A. patagonica*), an individual Emperor can not extend its breeding season longer than one year, because finding fast ice with a low freeboard that remains in place longer than a year would be difficult (to be successful a King Penguin requires a season >12 months long, and can breed no more than once every two years). Therefore, the Emperor breeding season begins in austral fall (April), once fast ice has formed and thickened, and continues through to the following mid-summer (December). In contrast, Adélie Penguins do not nest on the sea ice but rather nest on ice- and snow-free terrain, other than vertical cliffs, that are within a few hours walk of open water, polynyas or persistent ice cracks. Relative to the Emperor Penguin, the Adélie is exceedingly agile out of the water, and can even scale relatively steep cliffs. Small nest stones contained within the moraines of retreating, coastal glaciers provide material for these penguins to construct nesting platforms. The stones keep eggs and small chicks out of puddles and mud formed after snowfall during the season, and above most rivulets of water from melting glaciers (or rain in the northern Antarctic Peninsula region).

In the case of both species, there can be too much sea ice. Useful in understanding their response to sea ice is the "habitat optimum model" of population growth relative to SIC presented by Fraser & Trivelpiece (1996) for the Adélie Penguin. This model treats SIC as a continuum over ecological time (decades to centuries) and proposes that too much sea ice is as detrimental as too little sea ice, in both cases resulting in negative population growth. Thus, implied, is that penguin populations increase as SIC reaches an optimum condition between these two extremes. The 'optimum' for the two species differs, with Emperor Penguins being far more capable of dealing with fast ice (high SIC) than the Adélie.

If the Adélie Penguin is faced with a walk of more than a couple of kilometers on a regular basis, its colonies will disappear (Ainley 2002, Emslie et al. 2003); in contrast, many Emperor colonies are located many kilometers from open water. In the case of the Adélie, its response to too much ice is well chronicled. It disappeared along the coast of Victoria Land, leaving remains at extinct colonies, when extensive fast ice

returned after a brief, mid-Holocene warm period (Emslie et al. 2003, 2007). Because Emperors nest on annual sea ice, they've left no remains to chronicle their history at geologic time scales. To cope with extensive, concentrated ice (which slows the travel of mates going to/from the colony), to some degree both species are capable of quickly accumulating and then slowly using huge amounts of body fat on which to live while fasting, awaiting the return of their mates. To compensate for extensive sea ice, male Emperor Penguins need to fast for 4 months from the time the birds arrive at the colonies and throughout the entire incubation period until their mates return from the sea. Adélie's regularly fast for 4-6 weeks. This ability to mobilize fat is an adaptation that other penguin species lack and thus have difficulty coping with sea ice. As another 'adaptation' to extensive or concentrated sea ice, both species are attracted to sections of the coast adjacent to polynyas, where most of their foraging takes place (Ancel et al. 1992, Massom et al. 1998, Kirkwood & Robertson 1997, Ainley 2002, Arrigo & van Dijken 2003). Swimming is energetically more efficient than walking and, therefore, access to polynyas reduces the metabolic cost of obtaining food. The largest colonies tend to be closest to the polynyas or to areas where the sea ice becomes divergent by the time chicks need to be fed.

Another difference between the two species in regard to sea ice is that the Adélie Penguin winters at the large-scale pack ice edge, where ice is sufficiently divergent and there is enough light to forage effectively. However, before winter, it seeks areas where pack ice still remains in order to molt while staying on a large ice floe for 3-4 weeks (again, fasting). In contrast, Emperor Penguins are engaged in breeding at colonies along the coast and traveling to and from polynyas to feed during winter. After breeding, adult Emperors forage in the pack ice or in open waters where ice had recently been present, fatten, and then molt, also while positioned on coastal fast ice or very large ice floes. Instead of staying in the pack ice for months like Adélie's, the Emperors begin to move back toward breeding locations in February, after molting. Only fledgling Emperor Penguins, and to some extent pre-molt adults, venture far from the sea ice, traveling in their first months — before they've acquired adult diving capacity — to the waters of the Antarctic Polar Front (Kooyman 2002); the pre-molt adults from the Auster and Taylor Glacier colonies forage for 1-2 weeks in open waters north of the ice (Wienecke et al. 2004).

It is their diving capabilities, as well as their capacity to accumulate fat quickly and then live off it for long periods, that allow the Adélie and Emperor penguins to exploit the pack ice habitat. If sea ice disappears, then open-water species, such as Gentoo Penguin, move in (e.g. Ducklow et al. 2007). These other species, including the Chinstrap, can out-compete Adélie Penguins for nesting space (Trivelpiece et al. 1987, Volkman & Trivelpiece 1981). It is likely that its close congener, the King Penguin, can easily displace the Emperor Penguin. After all, the King's capacity for an extended breeding season allows it to exist in areas where food availability is much diminished compared to the current high Antarctic. The Emperor requires abundant food to accomplish a much shortened breeding season compared to the King. Therefore, the King Penguin can exploit many more potential habitats.

Emperor Penguin Response to Climate Change

There have been three investigations in which the demography and population dynamics of the Emperor Penguin have been related to ice characteristics (Barbraud & Weimerskirch 2001, Ainley et al. 2005, Jenouvrier et al. 2005a). All dealt with the data derived from studies at Pointe Géologie (66° 40'S, 140° 01'E), which is one of the most northerly located of all colonies of this species (Figure 8).

The findings of these studies were as follows:

- Barbraud & Weimerskirch (2001) found that survival, particularly of males, decreased when SST north of the pack ice was higher and SIE was reduced. Their data also showed a marked, 50% decrease in colony size during the mid-1970s, owing to a short period of low adult survival, and one from which the colony has yet to recover. They noted that after this decrease, breeding success became far more variable than before, due especially to an increasing frequency of years in which the fast ice has blown out prematurely (zero reproductive success).
- Ainley et al. (2005), using the same data set but several different covariates and a different analysis, found that population change was related directly to SIE and inversely to wind strength and the index to the Southern Annular Mode. They noted that average breeding success was much lower after the mid-1970s.
- Jenouvrier et al. (2005a) showed that population size is positively related to SIC and SIE during autumn, and to the Southern Oscillation Index (SOI). They showed that annual survival and breeding success contributed equally to explain population variation, and that male survival was lower than that of females. Further, they showed that adult survival varied inversely with air temperature during summer and winter; and that male survival was positively related to SIC.

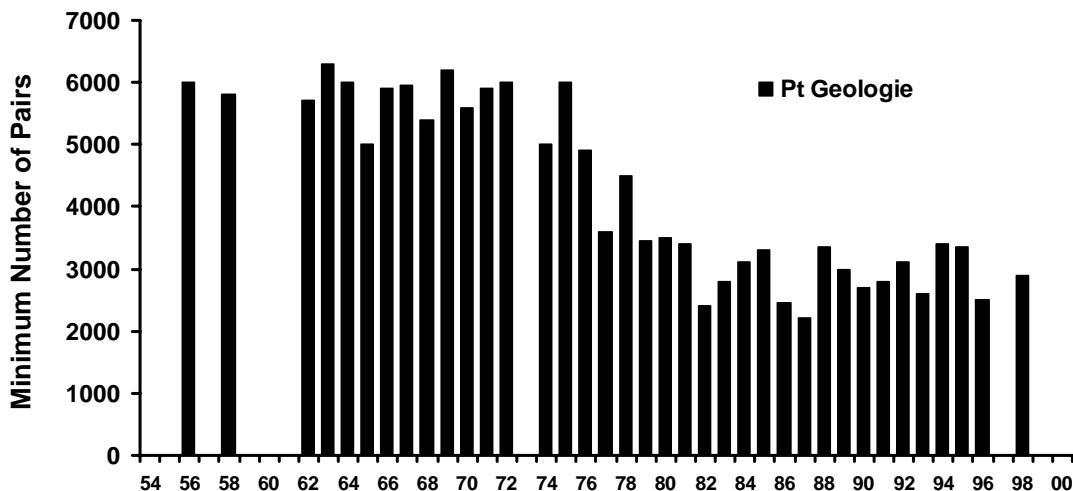


Figure 8: Number of adult Emperor Penguins at Pointe Géologie (data from Barbraud & Weimerskirch (2001)).

The findings of these three analyses are compatible with one another and *together* they show how this species has responded and will be affected by further climate change, especially as it affects sea ice and polynyas. The most difficult covariate to deal with is SST (as perceived by satellite) north of the sea ice (Barbraud & Weimerskirch 2001). Many factors can alter SST. Certainly, elevated SST could directly contribute to reduced SIE (melting at its outer edge). However, as will be discussed below, reduced wind also causes SIE to decrease, but at the same time would also lead to greater stratification of surface waters, leading in turn to higher SSTs owing to heat absorption from solar insolation. Finally, the upwelling of Circumpolar Deep Water, which is warm, can be involved as well and, in fact, this is the factor that likely would be most important to the penguins and their food web.

Ainley et al. (2005) found that the Pointe Géologie Emperor colony increased with less positive SAM, and decreased with higher wind and thinner ice. The latter two results may seem contradictory, except when considered in light of Jenouvrier et al.'s (2005a) results that both breeding success and adult survival equally affect population growth variation. As noted by Ainley et al. (2005), greater wind at Pointe Géologie is likely responsible for thinner and more unstable ice (see Jacobs & Comiso 1989), and hence greater chance of premature blow-out (cf Barbraud & Weimerskirch 2001). On the other hand, greater wind (as long as it is not too strong) would lead to a persistently open polynya, more easy access to food, and thus an increase to survival and breeding success. The fact that Jenouvrier et al. (2005a) found higher survival with lower air temperatures would be consistent with effects of katabatic winds (which are cold) on maintaining the adjacent coastal polynya and ice formation (see Barber & Massom 2007). More work obviously is needed to better relate Pointe Géologie Emperor population growth to local, polynya favorable vs unfavorable winds, ice thickness, and ice stability.

Another aspect awaiting more conclusive work is the cause of mortality associated with the initial, steep decrease in the Emperor population during the mid-1970s. If anything is clear, it is the unusual nature of this event, it having never been nor since observed among any other vertebrates anywhere in the Antarctic, i.e. a short-term massive mortality of adults, quite like for instance that observed during intense El Niño in upwelling regions of eastern boundary currents and which similarly affect most populations of upper trophic level vertebrates (e.g., Murphy 1925, 1936, 1981). Barbraud & Weimerskirch (2001) and Jenouvrier et al. (2005a) argued that changes in the ocean food web caused mass starvation, in a way similar to seabirds, mammals and fish in Peru during El Niño, with several non-exclusive factors leading to this result. As noted below, this event or its lack of recovery appears to have been restricted to Emperor Penguins at Pointe Géologie and not Emperor Penguins nor other vertebrate populations in East Antarctica or elsewhere. Considering the unusual nature of the event, Ainley et al. (2007) proposed that at least contributing to that rapid population decrease might be increased, short-term predation of Emperor Penguins by local pods of killer whales (*Orcinus orca*), whose foraging patterns might have been disrupted by an intense slaughter of their usual prey, Antarctic minke whales (*Balaenoptera*

bonaerensis), that occurred in the area at the same time. Starving penguins would be even easier prey and the fact that this mortality event occurred with decreased SIE argues also for a reduced polynya (both SIE and polynyas decrease with weaker winds) and thus increased foraging (energetic) costs for the penguins. Therefore, it will be awhile before, if ever, the explanation for the mass mortality at Pointe Géologie is explained.

The Emperor Penguin population in Terre Adélie has not been able to recover since the mid-1970s regime shift, a pattern similar to that exhibited by other seabirds that, elsewhere, suffer a catastrophic mortality unrelated but occurring after an ocean regime shift. For example, in new regimes, the capacity to breed successfully became reduced, e.g. penguins in the Galapagos (*Spheniscus mendiculus*) and Common Murres (*Uria aalge*) in the California Current (Ainley & Divoky 2001) and, therefore, these populations could not easily recover from an intense El Niño and/or a large oil spill, respectively.

Changes in Emperor Penguin breeding success after the mid-1970s regime shift have been reported by Barbraud & Weimerskirch (2001; see also Ainley et al. 2005). Results from a population model demonstrated that those changes in post-regime shift breeding limit population recovery (Jenouvrier et al., ms). Many factors likely responsible for reduced breeding success are prolonged blizzards (and deepening cold temperatures), which increase chick mortality (Jouventin 1974); and premature ice break-out, which contributes to fledging failure (Budd 1962; see also Barbraud & Weimerskirch 2001). In fact, the latter authors noted an increased frequency of premature break-out after the mid-1970s. Sea-ice characteristics (e.g. SIC, SIE, but especially of fast ice) may also cause longer foraging trips between the colony and the nearest open water site and higher energetic costs, which ultimately reduce breeding success (Wienecke & Robertson 1997). Finally, with lower breeding success, potential recruits among subadults resulting from previous years' breeding may have been discouraged from recruiting into the Pointe Géologie colony (see Danchin et al. 1997, 1998). That is, in years when the colony was blown out to sea, upon returning to the colony late in the breeding period (as young seabirds do), they found no adults nor chicks and, therefore, would likely go elsewhere.

The Taylor Glacier colony (67° 28'S, 60° 53'E), also in East Antarctica, is one of only two, so far known, that exist on land. [The other, at Dion Island (67° 52'S, 68° 43'W), has decreased severely as well, but it is in an area where sea ice is completely disappearing (Ainley et al. 2005; more below).] Therefore, the Taylor Glacier colony would not be affected directly either by ice thickness nor stability of fast ice for breeding. This colony during the past 20 years has remained at about the same size as it was during the 1950s and 1960s (cf Horne 1983, SCAR 2003; B Wienecke, pers. comm.). Thus, either it never saw a decrease or, unlike, Pointe Géologie, it has recovered. If the latter scenario is a possibility, the fact that it is fairly close to other colonies, in contrast to the relative isolation of Pointe Géologie (see Map 2 in Woehler 1993), then this might encourage the recruitment of returning subadults and emigrants.

Also indirectly contributing to this discussion on the effects of ice stability and its characteristics on Emperor Penguin population growth is the record in the southern Ross Sea: at Cape Crozier (Ross Island) and Beaufort Island (Kooyman et al. 2007; Figure 9). At Cape Crozier, the colony is situated at the front of the Ross Ice Shelf where it squeezes by Ross Island in its constant northward growth, and becomes very fractured in the process. As a result of the fractures, this corner also breaks back after several years of growth (calving lots of small icebergs). When the front is well south of its maximum position (2-3 km), the colony is exposed to rafting sea ice, and huge pressure ridges, and also vulnerable to early ice break-out. Breeding success is low. The penguins have difficulty climbing over the ice ridges, 10s of meters high. This was especially the case from the late 1960s through the 1980s. Then, as the Shelf front progressively moved forward, without breaking off, it provided a 'bay' between Shelf and shore, as its growth caused it to veer offshore from the island as well. With a persistent, fast-ice covered bay providing reliable, stable and protected habitat year after year, the colony experienced rapid growth in the 1990s. Indeed, breeding success was high and the colony grew. The bay was destroyed when crashing large icebergs broke back the ice front in 2001, and the colony decreased. At Beaufort Island, the colony exhibited its largest size when several icebergs grounded on other parts of the submerged caldera and offered protected, stable fast ice on which to breed successfully. The colony is located between grounded icebergs and the north shore of the island.

The severe decrease in the small Dion Island colony, located on the northwestern Antarctic Peninsula (Ainley et al. 2005), likely is attributable to the large-scale disappearance of sea ice in that region (sea ice chronicled by Stammerjohn et al. 2008). The decrease is consistent with that of Adélie Penguins in that area for the same reasons (Ducklow et al. 2007). Both are sea-ice obligate species, with similar 'habitat optimum' responses to the disappearance of sea ice (see above).

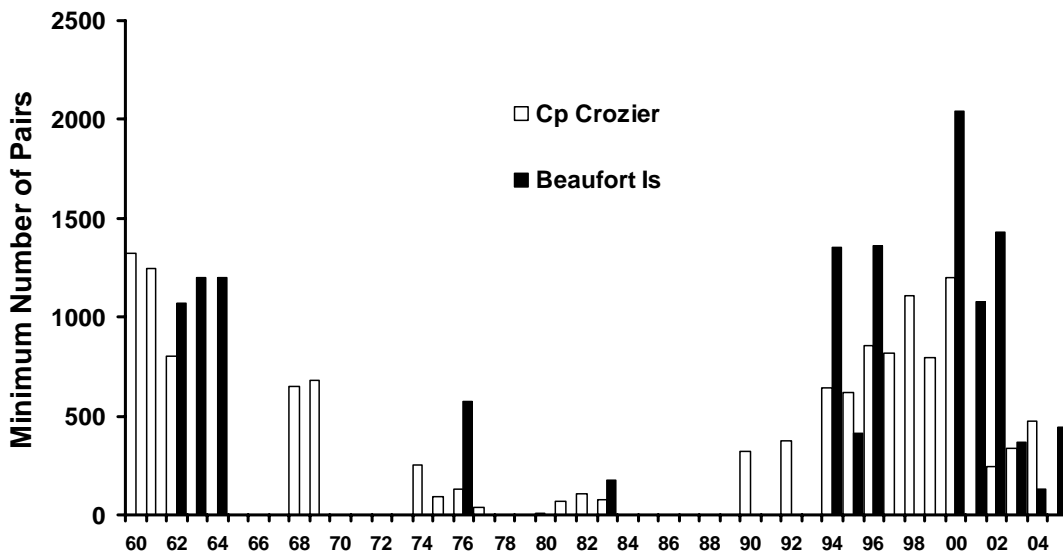


Figure 9: Numbers of adult Emperor Penguins at two colonies in the southern Ross Sea; estimates are from chick counts and thus are a minimum (from Kooyman et al. 2007).

Adélie Penguin Response to Climate Change

Adélie Penguins do not nest on sea ice, and thus understanding population trends are far less complex, in some regards, than for Emperor Penguins.

A number of studies have related population trends of the Adélie to sea-ice variability (Fraser et al. 1992, Trathan et al. 1996; Wilson et al. 2001; Jenouvrier et al. 2006). Three studies conducted in the Antarctic Peninsula region confirm one side of the bell-shaped curve of the Fraser-Trivelpiece model (see explanation above; Figure 10), showing that colonies of this species decrease as sea ice disappears. Long-term studies at Arthur Harbor (Ducklow et al. 2007), Admiralty Bay (Hinke et al. 2007), and Signy Island (Forcada et al. 2006) described fluctuating penguin numbers around a mean until the late 1980s, when all then began to decrease in accord with decreasing sea-ice season and persistence (cf Parkinson 2002, Stammerjohn et al. 2008). Otherwise, the population response confirms the sub-fossil record showing that Adélie Penguin colonies are founded when sea ice becomes more persistent and become extinct when it disappears (Emslie 2002).

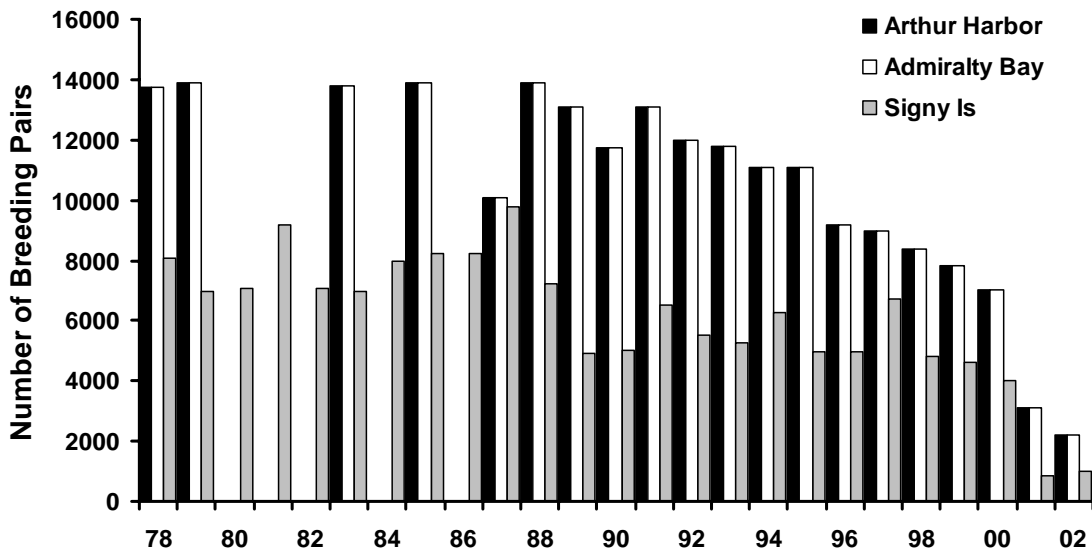


Figure 10: Population trajectories of Adélie Penguin colonies along the north and northwest coast of the Antarctic Peninsula: Arthur Harbor (Ducklow et al. 2007), Admiralty Bay (Hinke et al. 2007), and Signy Island (Forcada et al. 2006).

In East Antarctica and the Ross Sea, the situation has been more complex, because there the pattern for some colonies has been steady growth while for large colonies there has been a subsequent leveling off in numbers (e.g., Cape Bird, Cape Crozier; Figure 11). The leveling occurred at about the same time that colonies in the Antarctic Peninsula region began to decrease (late 1980s). Smaller colonies at Cape Royds,

Pointe Géologie and the Windmill Islands (Whitney Point) continued to grow (Figure 12). Thus, besides the response to ice conditions at a broader scale some sort of density dependence must be involved in these responses to physical conditions.

Three studies have related the demography and population dynamics of the Adélie Penguin to ice characteristics in the Ross Sea-East Antarctica sector (Wilson et al. 2001, Jenouvrier et al. 2005c, Ainley et al. 2005). The findings of these studies were as follows:

- Wilson et al. (2001) found that for colonies on Ross Island, greater SIE during winter reduced colony growth five years later (Figure 11). These authors surmised that extensive ice moved the penguins' wintering area north of the southern boundary of the Antarctic Circumpolar Current. As a result subadults, in particular, had more difficulty in coping with reduced food availability in those waters. The fact that the response did not show up until 5 years later is related to the average age of recruitment, ~5 years (Ainley 2002).
- Jenouvrier et al. (2005c) found similar results for the colony at Pointe Géologie (Figure 12): population size increased 6 years after a year of reduced SIE (and SIC). As with Wilson et al. (2001), these authors also found a relation to the SOI, the wind patterns associated with which affect SIE and SIC (Stammerjohn et al. 2008).
- Ainley et al. (2005), investigating trends at several colonies in East Antarctica and the Ross Sea, found that, in general, colony size decreased with increasing ice thickness and increased with increasing SAM and winter air temperature.

As with the Emperor Penguin, these results are not incompatible with one another and *together* tell the story of how Adélie Penguins have been responding to climate and sea-ice variation in areas where there is still plenty of sea ice (everywhere but the west coast of the Antarctic Peninsula). These results complete the 'habitat optimum model' showing growth in Adélie Penguin colonies as SIC, in the form of growing polynyas, lessens (see explanation of the model above). When SAM entered its positive mode and the AOH began to grow in the mid-1970s, circumpolar and katabatic winds began to increase in strength, leading to larger, more persistent coastal polynyas and, thus, lower SIC and thinner sea ice itself in coastal areas (see Parkinson 2002, Russell et al. 2006a, Stammerjohn et al. 2008). Larger, more persistent polynyas reduce the foraging energetic costs of the penguins. The importance of polynyas is particularly evident by the somewhat counter results of a growing sea-ice season and SIE in the Ross Sea sector (Zwally et al. 2002, Parkinson 2002, Stammerjohn et al. 2008), while at the same time growing coastal polynyas have also occurred.

These results also may show that once a colony reaches a certain size that further growth in polynya persistence or size is not beneficial, and that other factors come into play. These factors are likely 'biological' in nature stemming from density dependent relationships to the availability of food (Ballance et al. 2008). Ainley et al. (2007)

hypothesized that the intense slaughter of minke whales (thousands), a food competitor of Adélie Penguins, in the ocean between Adélie Land and the Ross Sea sector may be one factor involved. Timing of the slaughter overlapped the period of growth for all colonies (late 1970s to mid-1980s), and upon severe reduction of the whale take growth in large penguin colonies ceased.

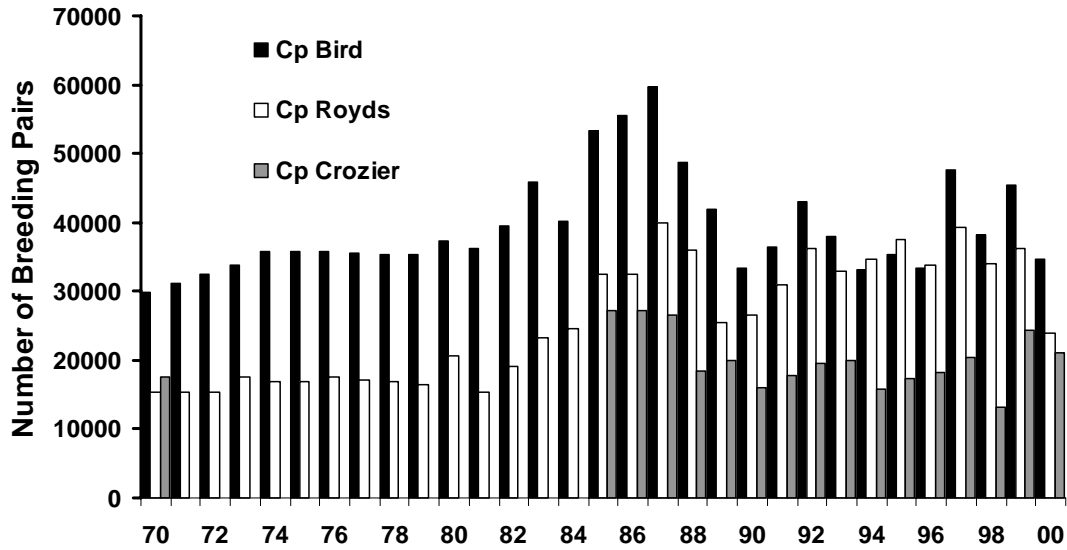


Figure 11: Population trajectories of Adélie Penguins at colonies in the Ross Sea (Bird, Royds, Crozier). Data are from Wilson et al. (2001).

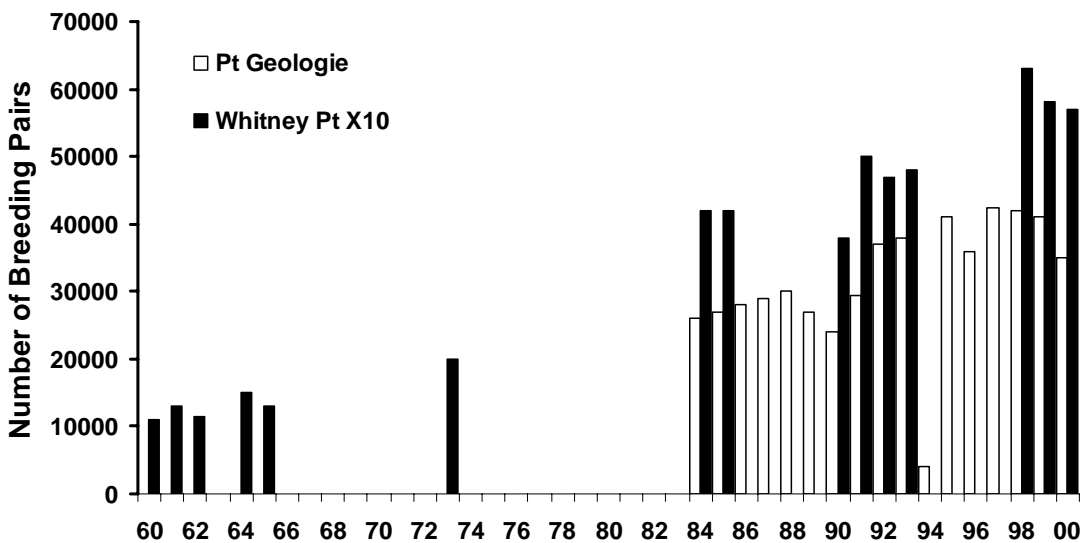


Figure 12: Population trajectories of Adélie Penguins at colonies in East Antarctica. Data for Whitney Point are from Woehler et al. (2001), and for Pointe Géologie from Jenouvrier et al. (2005c).

THE SOUTHERN OCEAN AT 2°C: POTENTIAL EFFECTS ON PENGUIN POPULATIONS

We now examine in detail projected changes to the physical environment at the time Earth's average temperature reaches 2°C above pre-industrial levels. We include ice area and thickness, SST, air temperature, winds and precipitation, in specific regions where well-studied penguin populations currently exist. The regions examined include the Antarctic Peninsula, Ross Sea, and eastern East Antarctica.

Sea-ice coverage will have decreased everywhere (Figure 13a), but more so near Ross Island than around the Antarctic Peninsula. Changes in coverage near Ross Island may not be particularly significant as this region would still be mostly (>80%) covered in the annual mean. The more equatorward locations, Admiralty Bay, Arthur Harbor and Pointe Géologie, would show the most pronounced decreases in ice. Ice thickness changes (Figure 13b) would be moderate near all colonies, with the possible exception of Cape Washington (165°E, 75°S; the largest Emperor Penguin colony at present), where ice thickness (this colony is located on fast ice) will have decreased by as much as 10 cm. Note the substantial thinning will have occurred as well on the downwind (eastern) side of the Peninsula; other Emperor Penguin colonies occur here, also on fast ice (see Woehler 1993). Changes to SST (Figure 13c) will be small poleward of 65°S, being <0.2°C near the coast where penguin colonies currently exist.

The ramping up of westerly winds (positive increases in the zonal mean stress) will clearly occur over the circumpolar channel (Figure 14a). As was noted by Yin (2005), all of the IPCC AR4 coupled climate models show a poleward shift in the main axis, as well as a strengthening of the westerly winds in the Southern Hemisphere. Near Ross Island, the westerly flow will decrease in strength. Air temperatures (Figure 14b) will be 1°-2°C warmer (in the annual mean) over all locations with the largest changes, again, near Ross Island. The warming there would be consistent with less cold air advection (decreased wind) from the continent. As the current annual average temperature is around -20°C, the effect on sea ice formation should be minimal, though ice thickness would be affected. This climatic change, however, would also be seen in the amount of precipitation: a possible increase of >10 cm per year over the western Ross Sea, again consistent with both the warming (warm air holds more water) and the weakening winds (more marine air). In fact, the model ensemble predicts a 25-30% increase in the precipitation over Ross Island by the year of 2°C warming.

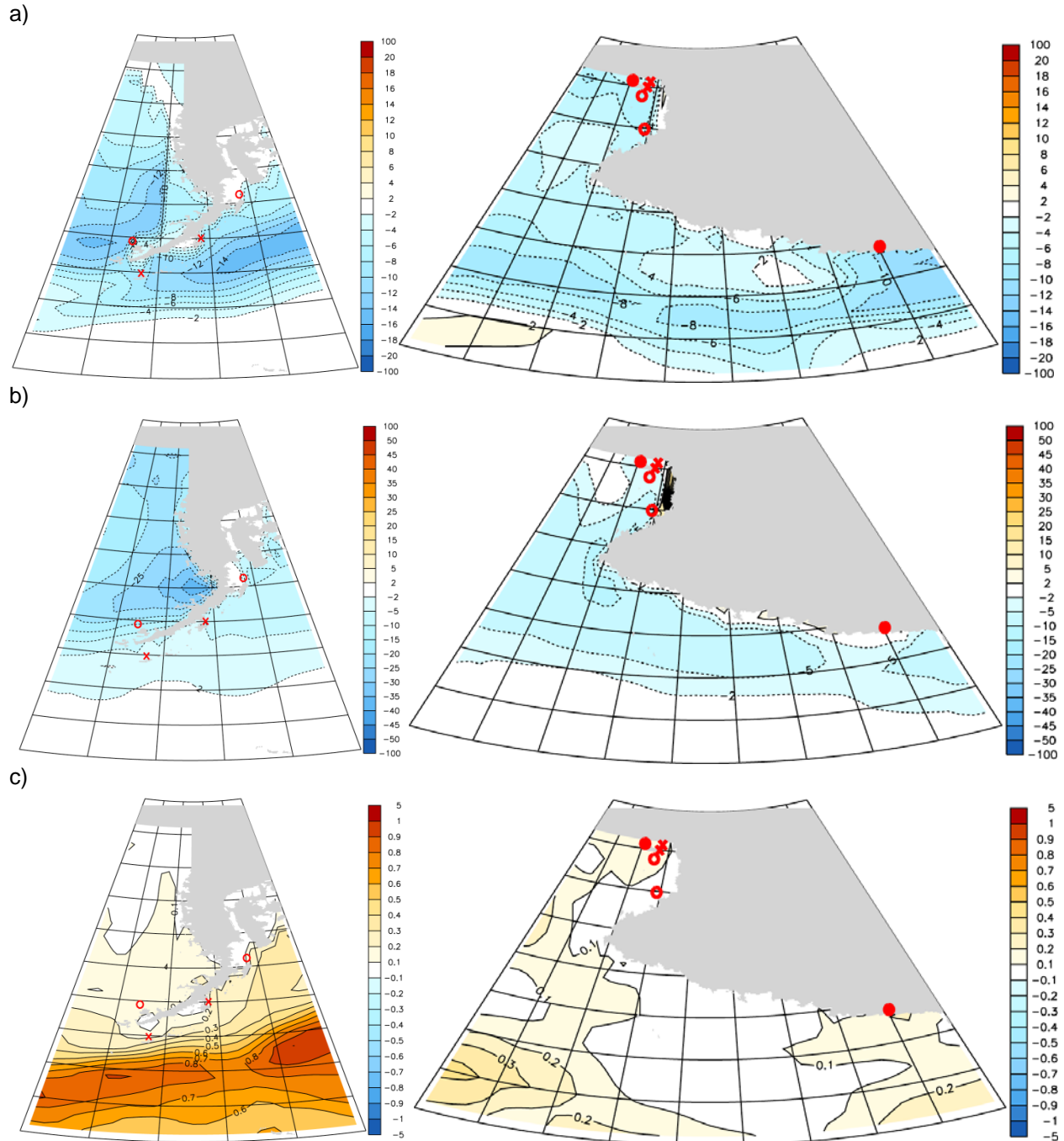


Figure 13: Simulated change for the ENSEMBLE in the a) annual mean sea-ice coverage; b) annual mean sea-ice thickness (cm); and c) annual mean SST ($^{\circ}\text{C}$, 0-100 m average). The panels on the left are the Antarctic Peninsula, from 80°S at the top to 55°S at the bottom with grid lines every 2.5° , and from 50°W on the left to 75°W on the right with grid lines every 5° . The scientifically important penguin colonies (long time series) are indicated in red: Adélie colonies with an X, Emperor colonies with an open O, and sites having both species present with a closed O. From left to right they are Admiralty Bay, Arthur Harbor (Adélie), and Dion Island (Emperor). The panels on the right are the Ross Sea and eastern East Antarctica, from 80°S at the top to 60°S at the bottom with grid lines every 2.5° , and from 180° on the left to 135°E on the right with grid lines every 5° . The important penguin colonies indicated are (symbols as above): clockwise around Ross Island — Cape Crozier (both Adélie and Emperor), Cape Royds, Cape

Bird, and Beaufort Island; Beaufort Island and Cape Washington (Emperor) north of Ross island, and Pointe Géologie (both Adélie and Emperor) is to the right.

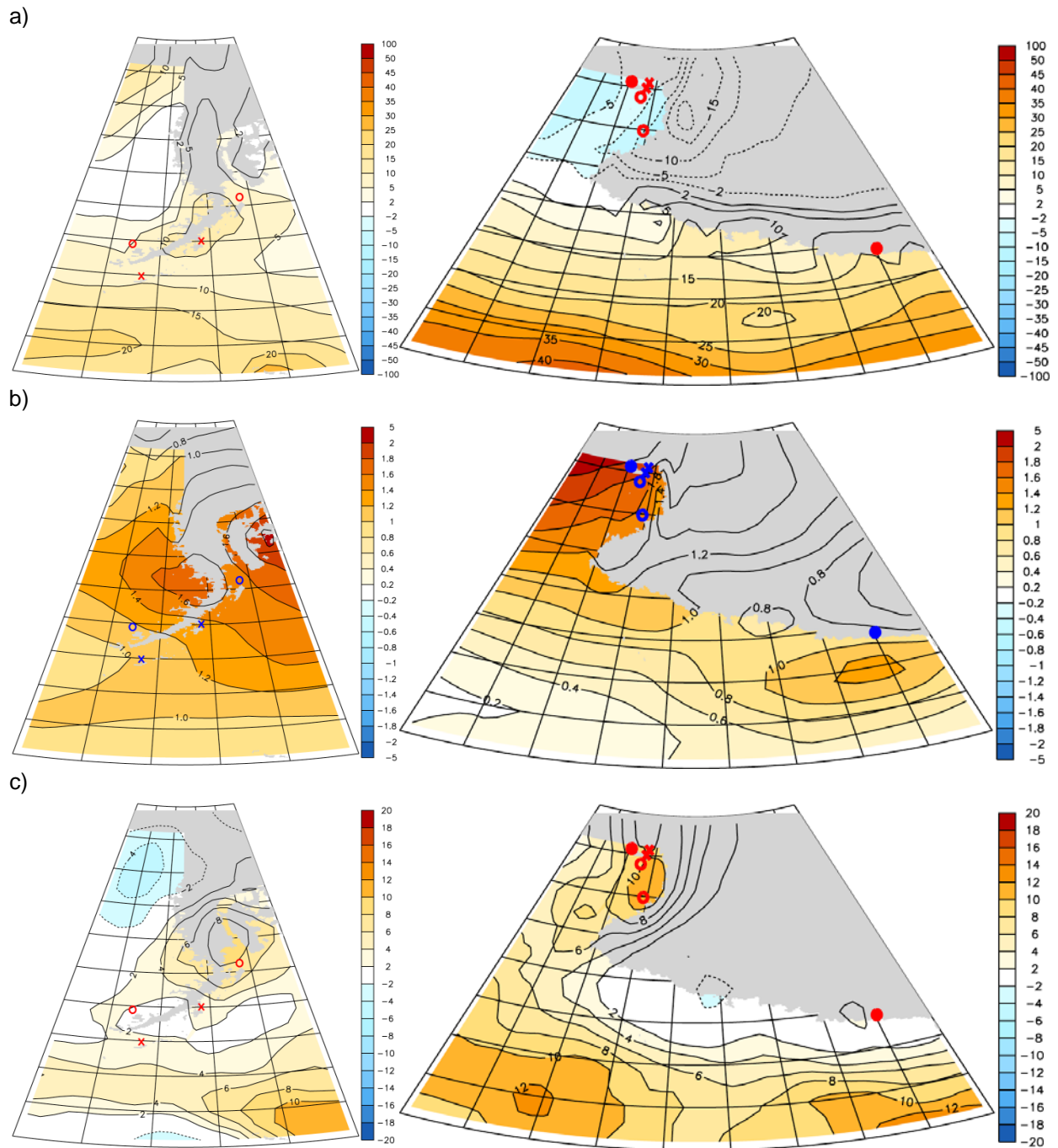


Figure 14: Simulated change for our ENSEMBLE in the a) annual mean zonal wind stress (10^{-3} N/m^2 , note that due to the orientation of the figure a positive change means a greater stress directed toward the *left/east* of the figure); b) annual mean surface air temperature ($^{\circ}\text{C}$); and c) annual mean precipitation (cm). Penguin colonies and the area shown in each panel are as in Figure 13.

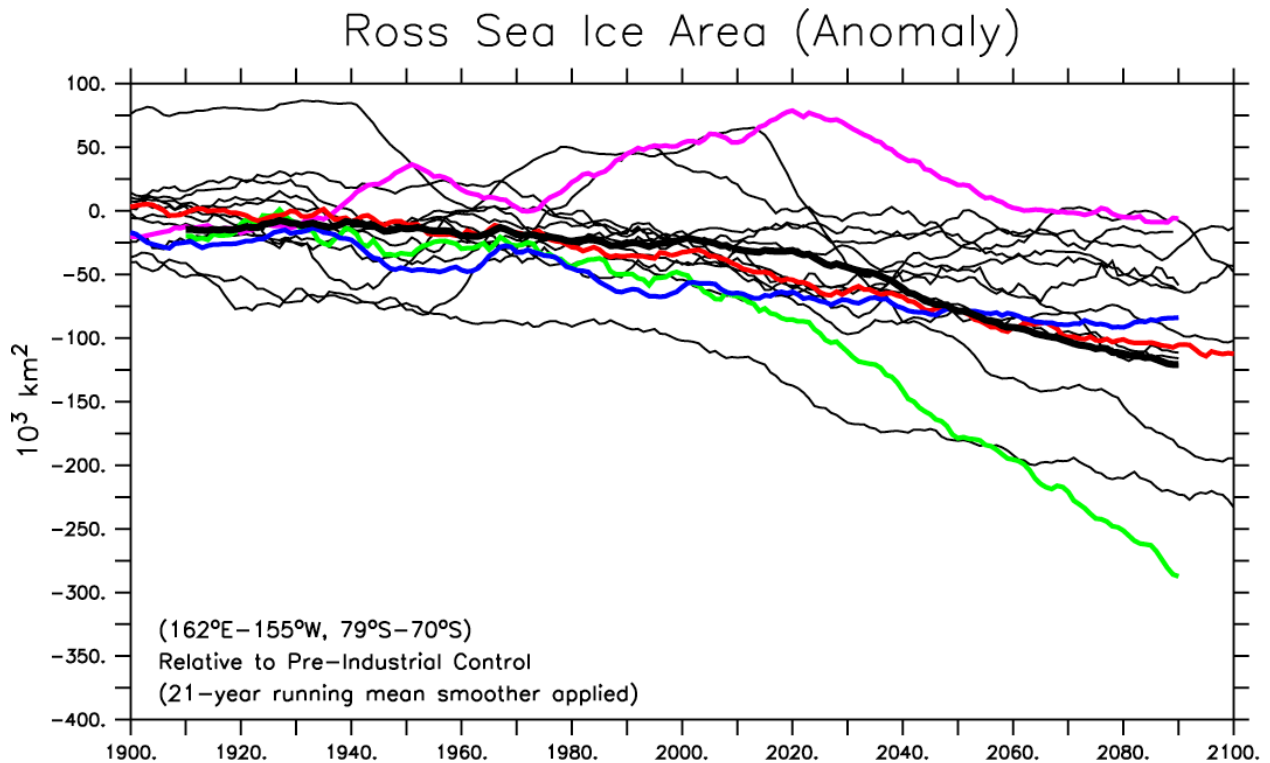


Figure 15: Change in annual average sea-ice coverage over the Ross Sea relative to the pre-industrial annual mean. ENSEMBLE (thick black), GFDL-CM2.1 (blue), GFDL-CM2.0 (red), MIROC3.2(hires) (green), MRI-CGCM2.3.2a (purple), the other models are indicated with thin black lines.

The model resolution is not fine enough to simulate polynyas accurately, but as a coarse approximation, we have plotted the total ice cover within the western Ross Sea under the assumption that a decrease in area is actually an increase in the area of the Ross Sea Polynya (Figure 15). Ainley et al. (2005) showed, for the period 1970-2001, that a positive correlation exists between the area of the polynya and the penguin populations adjacent to it. However, they also noted that Adélie populations are affected negatively by warmer air temperatures and increased snowfall, both of which are predicted by the ENSEMBLE (see also Ducklow et al. 2007 for Antarctic Peninsula, Bricker et al. 2008, for East Antarctica).

FUTURE PROSPECTS FOR ICE-OBLIGATE PENGUINS

Existing north of 70° S, currently, are approximately 50% of Emperor Penguin colonies, representing almost 40% of the total world population (Figure 16); and about 75% of colonies and about 70% of numbers of Adélie Penguins (Figures 17-19). The significant lessening of sea ice projected at these latitudes by 2025-2070, should have negative effects on these colonies, although the degree of decrease can not be accurately estimated. The trends of decreasing sea ice and colonies currently seen along the west coast of the Antarctic Peninsula (see Ducklow et al. 2007), thus, would broaden in geographic extent. If they do not disappear, at least in the case of Adélie Penguins,

colonies should at least cease any increasing trends evident in recent years. This would be so particularly for penguins in the Antarctic Peninsula region (west coast and northeast coast) and East Antarctica. Most vulnerable would be colonies at the tip of the Antarctic Peninsula, east side, including the very popular tourist destination, the Emperor colony at Snow Hill Island ($64^{\circ} 28'S$, $57^{\circ} 12'W$; see Todd et al. 2004). The fact that coastal polynyas likely will increase further in persistence may not help these penguins beyond what benefits they've experienced thus far from this change. As noted above, increases among larger colonies appear already to be slowing. Moreover, because coastal (latent heat) polynyas are dependent on the channeling of continental (katabatic) winds at specific locations, owing to local topography (mountain valleys etc; Massom et al. 1998, Barber & Massom 2007), there should not be many new polynyas appearing where they currently do not exist, thus, to facilitate penguin colonization along sections of coast where polynyas, and penguins, do not currently exist.

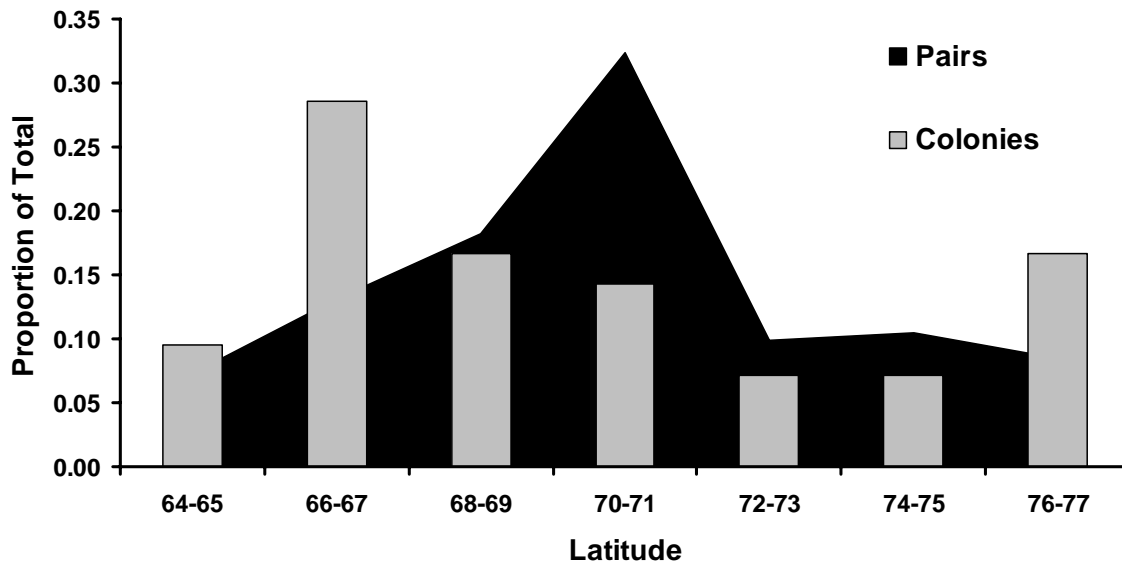


Figure 16: A summary of the location of current colonies ($n = 42$) and numbers (348,440 breeding pairs) of Emperor Penguins, by latitude (data from Woehler 1993, with a few additions).

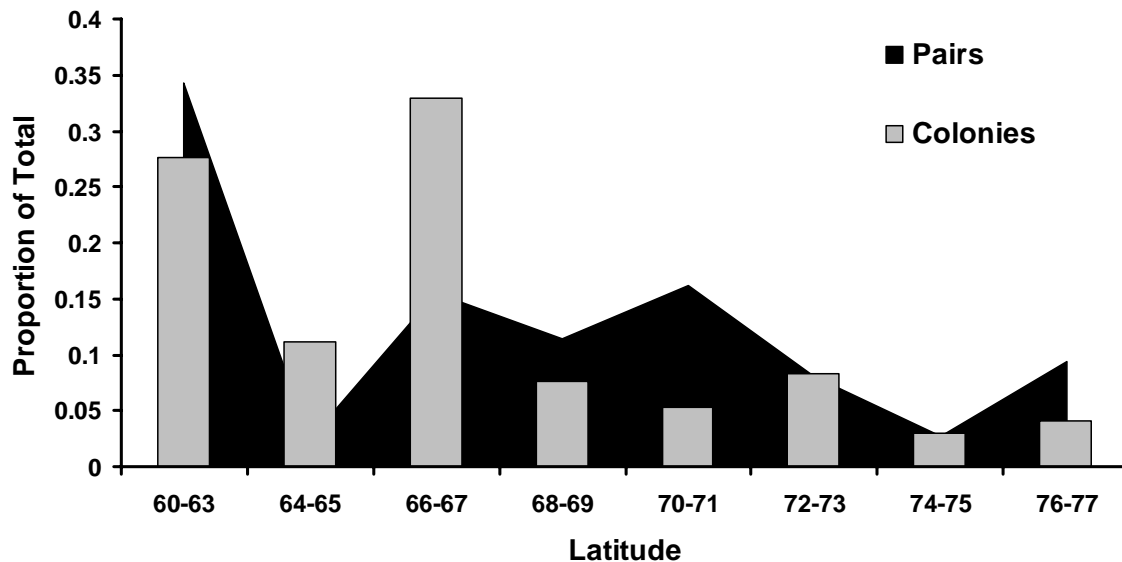


Figure 17. A summary of the location of current colonies (n = 170) and numbers (3,026,813 breeding pairs) of Adélie Penguins, by latitude (data from Woehler 1993).

It is highly likely that Adélie Penguins would colonize new areas as various ice shelves collapse exposing new coast line and as sea ice in areas where it currently is highly concentrated, e.g. along the eastern side of the Antarctic Peninsula and in the southern Bellingshausen and Amundsen seas, becomes more divergent. Overall, then, there may well be less net loss of their populations than at first appears. In contrast, Emperor Penguins may be far more challenged to find new nesting areas. This is because of the predicted decrease in ice thickness in many areas, including within the inner reaches of the Ross Sea. In part this decrease is related to increased winter air temperatures and the continued increase in coastal polynyas, also resulting from thinning sea ice. Thus, finding stable, long lasting fast ice may be difficult even at appreciably higher latitudes. Whether or not colonies become founded on land, as is the case at Taylor Glacier, remains to be seen, but likely would not be a common event.

Working against the founding of colonies at higher latitudes would be the decline of ice coverage in pack ice areas where Adélie Penguins currently winter. As noted by Fraser & Trivelpiece (1996), and investigated intensively by Toniolo et al. (ms), this species winters only in pack ice areas where it is light for at least a few hours per 24-hr period. Where ice no longer reaches beyond the Antarctic Circle (66.5°S), wintering by Adélie Penguins would be limited. It may be that SIE does not change much but its winter persistence at its maximal extent does, as is currently the case in the Antarctic Peninsula region (Stammerjohn et al. 2008). This would still have negative effects on the migration and wintering of this species.

The increase in snowfall has had a major negative effect on Adélie Penguins in the Antarctic Peninsula region (Fraser & Patterson 1997). When the penguins have arrived in spring during recent years, they've not been able to find their former nests nor snow-

free terrain to find the stones needed to build nests. By the time the snow melts, Gentoo and Chinstrap Penguins have arrived. The latter two species easily displace Adélie from nesting areas (Volkman & Trivelpiece 1981, Lishman 1985). Recent, changing snow fall has also altered the breeding colonies of penguins in East Antarctica (Bricker et al. 2008). In the Ross Sea region, where the greatest change in snow fall is projected, current colonies have far more terrain available than they currently occupy (Ainley et al. 2004). Thus, other than events where hundreds of incubating adults are buried by deep drifts as occurred in 2001 and 2007, plenty of nesting space should remain and general conditions that favor low-latitude penguin species will not be materializing anytime within the 2°C scenario.

We have had nothing to say about how climate change might affect the food web, and ultimately the populations of these species. In regard to our analysis here, that topic is far too complex with insufficient data and involves perhaps decreases in certain prey (e.g., Antarctic silverfish *Pleuragramma antarctica* and Antarctic krill *Euphausia superba* and dependent species; Emslie & McDaniel 2002, Atkinson et al. 2004) and increases in others particularly in coastal, continental shelf areas (e.g., *E. crystallorophias*). Regardless, it appears that by the time Earth's troposphere reaches 2°C above pre-industrial levels, on the basis of changes in the physical habitat alone, we can expect major reductions and alterations in the abundance and distribution of pack-ice penguins.

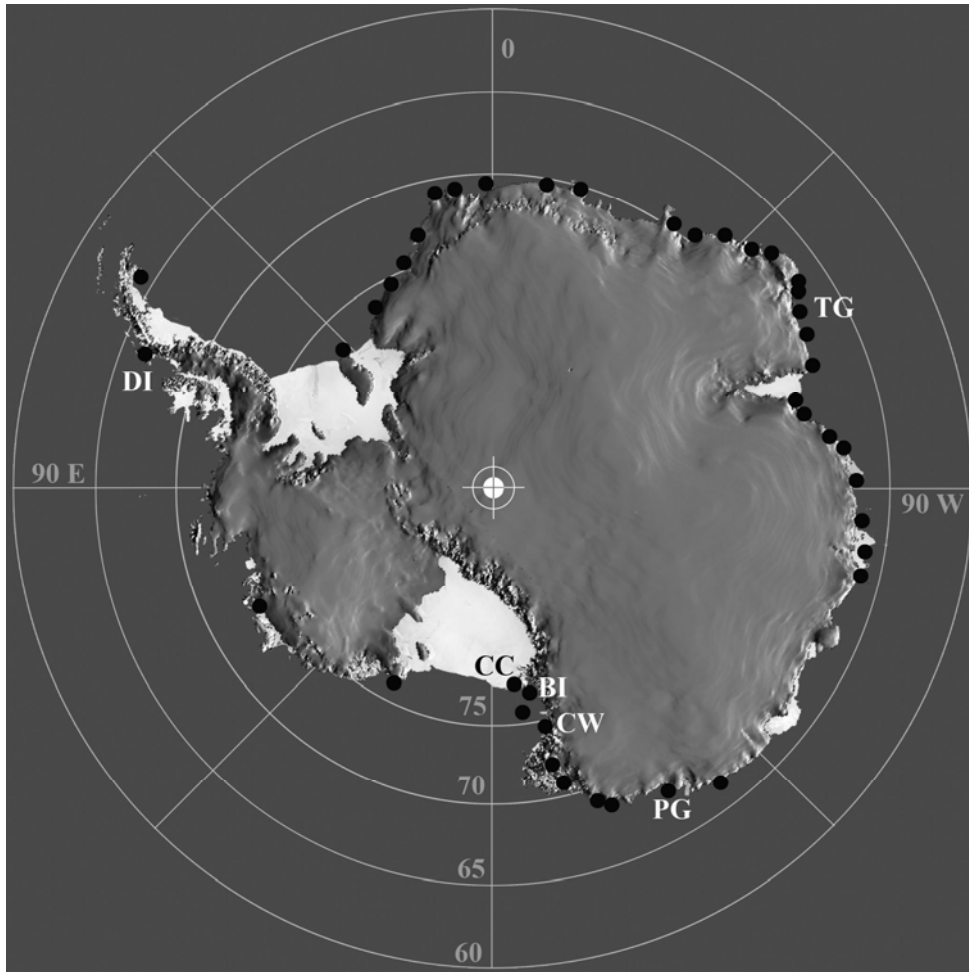


Figure 18: The location of known colonies of Emperor Penguins (data from Woehler 1993, Lea & Soper 2005). Colonies discussed specifically in this document are labeled: BI, Beaufort Island; CC, Cape Crozier; CW, Cape Washington; DI, Dion Island; PG, Pointe Géologie; and TG, Taylor Glacier.

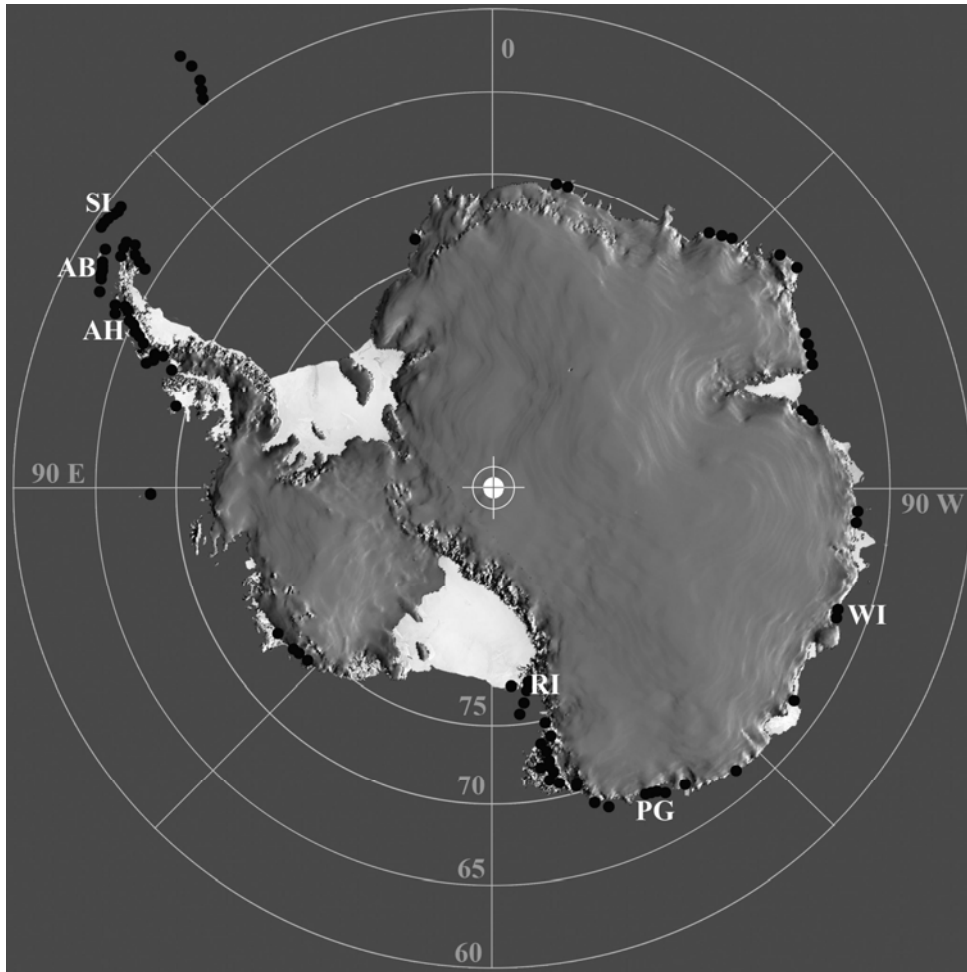


Figure 19: The locations of known colonies of Adélie Penguins (data from Woehler 1993). In areas where colonies are densely concentrated — Antarctic Peninsula and eastern Ross Sea — not all are shown (see detail maps in Woehler 1993 for those areas). Colonies discussed in this document are labeled: AB, Admiralty Bay; AH, Arthur Harbor; PG, Pointe Géologie; RI, Ross Island (capes Crozier, Royds and Bird); SI, Signy Island; and WI, Windmill Islands.

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