CONCEPTS & SYNTHESIS
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*Ecological Monographs*, 80(1), 2010, pp. 49–66

# Antarctic penguin response to habitat change as Earth's troposphere reaches 2°C above preindustrial levels

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*Abstract.* We assess the response of pack ice penguins, Emperor (*Aptenodytes forsteri*) and Adélie (*Pygoscelis adeliae*), to habitat variability and, then, by modeling habitat alterations, the qualitative changes to their populations, size and distribution, as Earth's average tropospheric temperature reaches 2°C above preindustrial levels (ca. 1860), the benchmark set by the European Union in efforts to reduce greenhouse gases. First, we assessed models used in the Intergovernmental Panel on Climate Change Fourth Assessment Report (AR4) on penguin performance duplicating existing conditions in the Southern Ocean. We chose four models appropriate for gauging changes to penguin habitat: GFDL-CM2.1, GFDL-CM2.0, MIROC3.2(hi-res), and MRI-CGCM2.3.2a. Second, we analyzed the composited model ENSEMBLE to estimate the point of 2°C warming (2025–2052) and the projected changes to sea ice coverage (extent, persistence, and concentration), sea ice thickness, wind speeds, precipitation, and air temperatures. Third, we considered studies of ancient colonies and sediment cores and some recent modeling, which indicate the (space/time) large/centennial-scale penguin response to habitat limits of all ice or no ice. Then we considered results of statistical modeling at the temporal interannual-decadal scale in regard to penguin response over a continuum of rather complex, meso- to large-scale habitat conditions, some of which have opposing and others interacting effects. The ENSEMBLE meso/decadal-scale output projects a marked narrowing of penguins' zoogeographic range at the 2°C point. Colonies north of 70° S are projected to decrease or disappear: ~50% of Emperor colonies (40% of breeding population) and ~75% of Adélie colonies (70% of breeding population), but limited growth might occur south of 73° S. Net change would result largely from positive responses to increase in polynya persistence at high latitudes, overcome by decreases in pack ice cover at lower latitudes and, particularly for Emperors, ice thickness. Adélie Penguins might colonize new breeding habitat where concentrated pack ice diverges and/or disintegrating ice shelves expose coastline. Limiting increase will be decreased persistence of pack ice north of the Antarctic Circle, as this species requires daylight in its wintering areas. Adélies would be affected negatively by increasing snowfall, predicted to increase in certain areas owing to intrusions of warm, moist marine air due to changes in the Polar Jet Stream.

*Key words: Adélie Penguin; Antarctica; climate change; climate modeling; Emperor Penguin; habitat optimum; sea ice; 2°C warming.*

## Introduction

In early 2007, the European Union formulated a $CO_2$ emissions goal under scenario Special Report on Emissions Scenarios (SRES) A1B (doubling of atmospheric $CO_2$ from 360 ppm and stabilizing at 720 ppm

Manuscript received 12 December 2008; revised 15 April 2009; accepted 5 May 2009. Corresponding Editor: S. R. Beissinger.

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after year 2100) in order to prevent Earth's mean air temperature from exceeding 2°C above preindustrial levels (i.e., levels preceding ~1860; Europa 2007, Parry et al. 2008). Using that goal, we herein synthesize existing data to gauge the predicted effects of change in the habitats of Antarctic penguins upon that tropospheric temperature being reached. By Antarctic penguins, we mean the two "ice obligate" species, Adélie (*Pygoscelis adeliae*) and Emperor (*Aptenodytes forsteri*), that associate closely with sea ice or sea-ice-influenced ocean. Penguins such as King (*A. patagonica*), Macaroni (*Eudyptes chrysolophus*), and Gentoo (*P. papua*) venture into ice-free areas south of the Antarctic Polar Front and may enter the outer reaches of the pack ice, but mainly they are sub-Antarctic in zoogeographic affinity, particularly their breeding ranges. The one exception to the latter is the Chinstrap Penguin (*P. antarctica*), which is restricted to waters south of the Antarctic Polar Front but nevertheless mostly avoids sea ice (Fraser et al. 1992, Ainley et al. 1994). Therefore, we concentrate attention on the two "true" Antarctic penguins.

Why consider Antarctic, pack ice penguins in this sort of exercise? Participation in the Antarctic Treaty requires countries to conduct bona fide research, and these two species, particularly the Adélie Penguin, occur in close proximity to research stations. Therefore, both species have been the subject of appreciable research with respect to habitat relationships and life-history patterns. It is highly possible that the Adélie Penguin is one of the best-known birds, and certainly seabirds, in the world (Ainley 2002). These penguins are large and easily viewed, having nowhere to hide or be cryptic or secretive, unlike many vertebrates elsewhere. Finally, though other habitat factors are importantly involved, both species are extremely sensitive to sea ice variation, and sea ice is one of the critical factors in both modulating and reacting to variation in Earth's climate. Thus, Antarctic sea ice, too, has been well researched, and therefore, these penguins illustrate well vertebrate species' interactions with habitat change.

Sea ice covers ~6% of the world ocean, about half in Antarctica (Gloersen et al. 1992), and plays an important role in the energy exchange between atmosphere and ocean. It is also extremely sensitive to climate, including both temperature (air and ocean) and wind patterns, and in the Southern Ocean has been and will continue to be dramatically affected by global climate change (Kwok and Comiso 2002, Parkinson 2002, Zwally et al. 2002, Russell et al. 2006*a*). Sea ice and other ocean characteristics have also, in this age of satellite imagery, become relatively easy to monitor with a high degree of spatial precision (Massom et al. 2006). The characteristics monitored include sea ice concentration, extent, and thickness, as well as wind patterns and air and ocean temperature, all of which, plus precipitation, have bearing on the well-being of Antarctic penguin populations.

In recent predictions of species' reactions to climate change, taking a large spatial-scale view is a common and necessary strategy (Pearson and Dawson 2003, Parmesan 2006). In these models, factors thought to confine a species to its current zoogeographic range are used to predict range shifts in accord with habitat change (e.g., species distribution models reviewed in Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith et al. 2006). For certain Antarctic fishes, for example, Cheung et al. (2008) predicted that some will go extinct with the loss of sea ice and rise in ocean temperature, largely because their habitat, as it shifts southward, will become increasingly confined by the presence of the Antarctic continent. In order to address the +2°C scenario, we consider penguins taking both this large/centennial–spatial/temporal-scale view as well as a meso/decadal-scale "habitat optimum" view (see Fraser and Trivelpiece 1996, Smith et al. 1999). In this way, with information obtained during the 30-year era of satellite-sensed weather and sea ice and concomitant penguin studies, we gain insights into the subtleties by which both penguin species will respond. We know, at least qualitatively, that within the interannual-decadal period the response will not be linear, neither spatially nor temporally, namely, that negative population growth switches to positive and then back to negative along a continuum of climate-induced habitat changes.

In part, our review complements that of Croxall et al. (2002), who identified some unresolved "paradoxes" in Antarctic penguins' response to climate change, specifically, recent increases in some areas but decreases in others. Obviously, these were paradoxical at that time because certain key data were lacking, a gap that we will fill in the current paper. Our effort also complements that of Thatje et al. (2008), who, on the basis of sediment cores and other biophysical data, assessed the effects of ice conditions during the Last Glacial Maximum on the Antarctic marine biota, including penguins. Temperatures were colder and there was much more sea ice, with a longer sea ice season then, at least at the spatially large scale; these are conditions quite contrary to what the future may hold for these birds, as will be discussed here.

In order to make the penguin population projections, it is necessary to (1) understand these two species' physical environment, namely sea ice conditions, air temperatures, winds, sea surface temperatures (SST), and precipitation, in the current Southern Ocean; (2) understand penguins' responses to spatiotemporal variations in ocean features, both at the large/centennial scale and the meso/decadal scale; (3) select climate models that appropriately simulate existing conditions; (4) run the climate models to project how penguin habitats will change: and, finally, (5) make qualitative projections of the manner in which penguins will respond based on the "habitat optimum" conceptual model.

Emperor Penguins currently breed in ~40 colonies (see Woehler 1993, Woehler and Croxall 1997; Fig. 1),

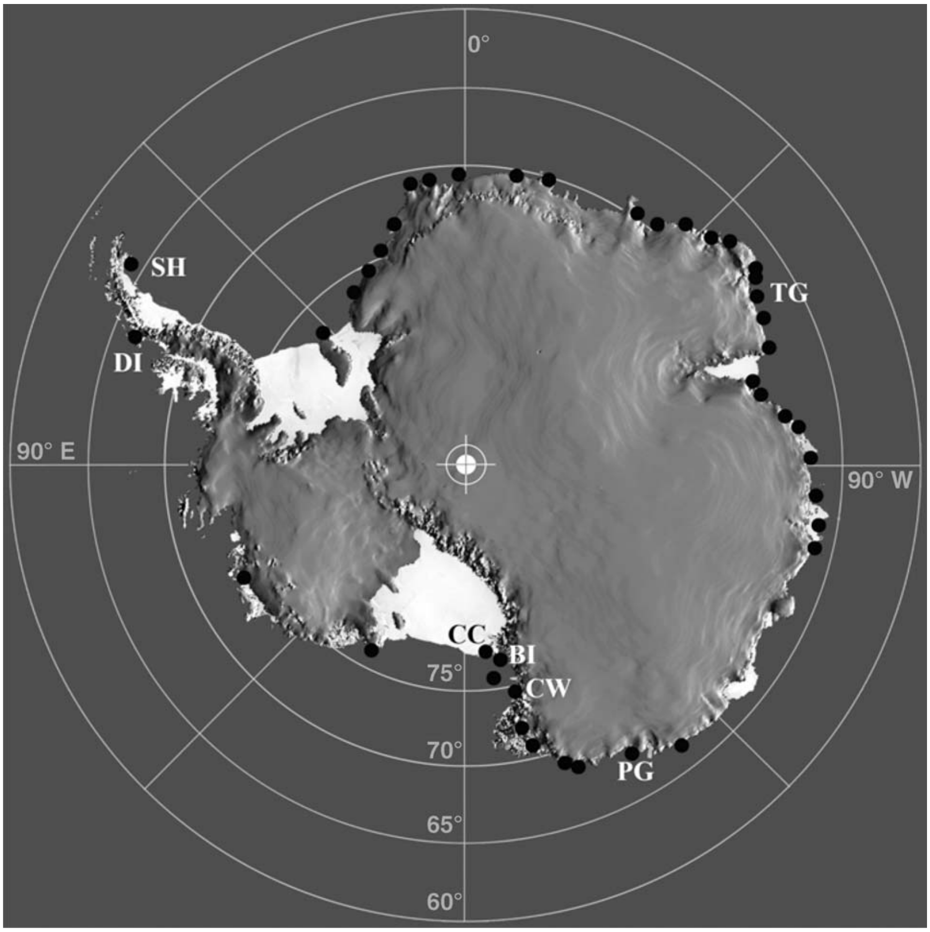


FIG. 1. The locations of known colonies of Emperor Penguins (*Aptenodytes forsteri*) on Antarctica (data from Woehler [1993] and Lea and Soper [2005]). Colonies discussed in this document are labeled: BI, Beaufort Island; CC, Cape Crozier; CW, Cape Washington; DI, Dion Islets; PG, Pointe Géologie; SH, Snow Hill; and TG, Taylor Glacier.

nine of which have been censused long enough that a statistically meaningful, decades-long time series exists with which to assess the species' response to habitat change. Likewise, Adélie Penguins currently breed in ~160 colonies (see Woehler 1993, Woehler and Croxall 1997, Ainley 2002; Fig. 2), eight of which have been investigated over the long term. These long-term studies will be our focus and from these records we will make qualitative projections, Antarctic-wide.

## METHODS

### *Sea ice definitions and concepts*

In this discussion, the following terms and especially their inter-relationships are important.

Sea ice is any layer on the ocean surface resulting from freezing. It can remain in place for months or years, locked in place by capes, islets, 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) is the distance from the coast to the outermost edge of the ice pack. The latter is defined as <15% cover as it is diffcult to distinguish ice from open water at lower ice concentrations using satellite imagery (Gloersen et al. 1992, Parkinson 2002, Zwally et al. 2002).

Sea ice concentration (SIC) is the percentage of a given area of ocean covered by ice. For example, with 80% cover there are only very narrow alleyways, or leads, among ice floes. The measure is very much (spatially) scale dependent. Sea ice concentration at the large scale, but not mesoscale, varies directly with SIE (Jacobs and Comiso 1989, Jacobs and Giulivi 1998, Stammerjohn et al. 2008).

Sea ice persistence or season is the length of time during the year, 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 is, in ice models, the fractional area of each grid cell covered by sea ice. This measure combines SIC, SIE, and sea ice persistence (and therefore time).

Ice thickness is the measure between the top and underside of ice. In windy areas, ice does not become

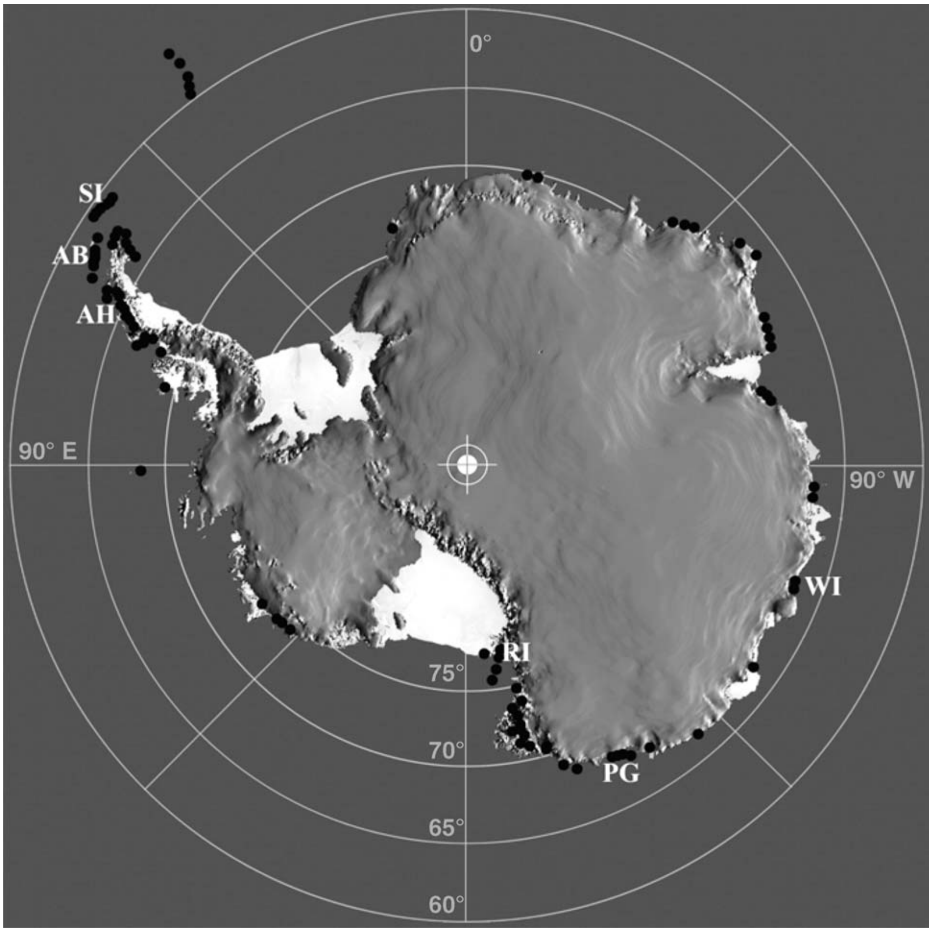


FIG. 2. The locations of known colonies of Adélie Penguins (*Pygoscelis adeliae*) on Antarctica (data from Woehler [1993]). In areas where colonies are densely concentrated, Antarctic Peninsula and eastern Ross Sea, not all are shown (see detailed maps in Woehler [1993] for those areas). Colonies discussed 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.

very thick (less than or approximately 1 m), as not long after formation it is blown northward to warmer waters where it thickens little, if at all (Jacobs and Comiso 1989). New ice then forms to start the freezing process again. Only during extended periods of calm and cold temperatures can fast ice thicken sufficiently (~2 m) that it no longer is susceptible to being blown loose by winds.

Polynya is 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, latent-heat polynyas (heat generated from the processes of ocean water freezing) and is then blown seaward (Barber and Massom 2007).

With much offshore wind, SIE usually increases either through advection or Ekman transport (Hibler and Ackley 1983, Stammerjohn et al. 2008). Thus, SIE and polynya size, along with ice thickness, are all related. The importance of polynyas to SIC is spatially scale dependent. Most Antarctic polynyas are of the latent-heat type, though a few are of the sensible-heat type, developed by the upwelling of warm, circumpolar deep water along the continental slope (Jacobs and Comiso 1989, Jacobs and Giulivi 1998).

### *Characterizing the existing Southern Ocean as it relates to penguins*

The Southern Ocean circulation is dominated by the Antarctic Circumpolar Current (ACC), the world's largest current. 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 Antarctic Polar Front, which in turn creates vast areas of upwelling water (Peterson and Whitworth 1989). This upwelled water has a large effect on the high-latitude heat flux between the atmosphere and ocean (Russell et al. 2006*a*). Indeed, the northern extent of sea ice coincides in many regions with the southern boundary of the ACC (SBACC). In addition to this heat flux, 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 the Southern Ocean and, therefore, will influence its response to anthropogenic forcing. For further details on mode and intermediate waters, see McCartney (1977) and Piola and Gordon (1989).

Since the mid-1970s, the Southern Annular Mode (SAM) has exhibited a significant positive trend while the Antarctic ozone hole (AOH) has increased in size and seasonal persistence (Thompson and Solomon 2002, Stammerjohn et al. 2008). Global warming and the colder temperatures within the AOH due to ozone loss are contributing to an increasing disparity of tropospheric (warmer) and lower stratospheric (colder) temperatures. This increased temperature gradient has been contributing to changes in Southern Ocean climate through a poleward intensification of the surface expression of the westerly winds. In addition or perhaps as 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 of Antarctica. The greater offshore winds in turn are leading to increasing SIE, extending the sea ice season, increasing the size and persistence of coastal polynyas, and decreasing the sea ice thickness (Parkinson 2002, Zwally et al. 2002, Russell et al. 2006*a*, Stammerjohn et al. 2008). The same weather system has resulted in the rising temperatures over and on the western Antarctic Peninsula (Bellingshausen Sea), only in this case winds are blowing from the warm ocean in the north southward 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-to-late 1970s, amounting to a "regime" shift, have had repercussions among a number of vertebrate and invertebrate populations, in part through the effect on ice (Weimerskirch et al. 2003, Ainley et al. 2005, Jenouvrier et al. 2005*a*, *c*). 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, Jenouvrier et al. 2005*b*).

These climate patterns are what models must reproduce in order to be able to predict, with the least amount of uncertainty, future changes among habitat features in the Southern Ocean pertinent to penguins.

### *Choosing climate models that best simulate the current Southern Ocean*

Studies using the Intergovernmental Panel on Climate Change (IPCC 2007) Fourth Assessment Report (AR4) and coupled climate models referred to therein generally were used to create what is known as an "ensemble," in which individual variables from each of the models is averaged to derive a consensus. For the Southern Ocean, model errors in the IPCC ensemble tended to cancel one another, making the end result closer in its predictions to observations than any of the individual components (Lefebvre and Goosse 2008). Thus the result was not really a reliable "average" in which we could have confidence. Moreover, not all climate models have been equally reliable for all aspects of climate in all regions. Indeed, some models poorly simulate the current climate within the Southern Ocean (Perkins et al. 2007), and thus less confidence should be placed in them (Beaumont et al. 2008).

Therefore, using a set of observational criteria, a preindustrial control and 20th century runs (see Appendix), we winnowed the available 18 models on the basis of their ability to duplicate the strength and position of existing Southern Hemisphere westerly winds and the Antarctic Circumpolar Current. 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 spatial large-scale response to increased anthropogenic forcing (Russell et al. 2006*b*). So we deleted those models that poorly simulated the jet, ultimately to gain confidence in projections of future penguin habitat.

We then narrowed the model pool 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). This was necessary because sea ice is sensitive to both the atmosphere and the ocean (see Hibler and Ackley 1983), so changing the temperature or wind-generated circulation patterns of either will lead to substantial changes in the sea ice upon which Antarctic penguins depend. As noted above, these changes importantly, for penguins, affect sea ice concentration, extent, and thickness and include the persistence of all-important polynyas.

### *General habitat relationships of Antarctic penguins*

As detailed in the comparison by Ainley et al. (2005), Emperor and Adélie penguins are affected by sea ice both in similar and in 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 facility (see summary of natural history in Williams [1995]). Like other large birds, it also has an extended breeding season, of about nine months. An individual Emperor Penguin cannot 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. Therefore, the Emperor breeding season begins in the austral fall (March–April), as fast ice is forming and thickening, 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 (Williams 1995). Relative to the Emperor Penguin, the Adélie is exceedingly agile out of the water and can even scale very steep slopes. Small stones contained within the moraines of retreating, coastal glaciers provide material for these penguins to construct nests. The stones keep eggs and small chicks out of puddles and mud formed after snowfall during the summer breeding season and above most rivulets of water from melting glaciers (or rain in the northern Antarctic Peninsula region).

Critical to both the Adélie and Emperor penguin is the existence of polynyas, as they reduce the commuting time and energy expenditure between colony and food supply (Dewasmes et al. 1980). Lack of a nearby polynya slows travel, thus to disrupt coordination between mates going to and from the colony (see also Ancel et al. 1992, Kirkwood and Robertson 1997). Spatial analyses indicate close correlations between colony location and a polynya or post-polynya (Massom et al. 1998, Ainley 2002, Arrigo and van Dijken 2003).

In addition to locating colonies near polynyas, to cope with extensive, concentrated ice, 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 in part for extensive sea ice, male Emperor Penguins need to fast for four months from the time they arrive at the beginning of the breeding season and throughout the entire incubation period until their mates return from the sea at mid-winter. Adélies regularly fast for a period ranging from four to six weeks. This ability to mobilize fat is an adaptation that other penguin species lack and thus have difficulty coping with the early-season presence of persistent sea ice.

In the Appendix, with the above considerations in mind, we present our review of how Antarctic penguins have responded in time and space to habitat changes at both the large/centennial scale and then the meso/decadal scale.

## RESULTS

### *Penguin response to habitat change conducive to decadal-scale climate modeling: a summary*

As detailed in the Appendix, to move beyond the large/centennial-scale limits of 100% and 0% (or very low concentration) of sea ice, the "habitat optimum model" of population growth, as presented conceptually for the Adélie Penguin by Fraser and Trivelpiece (1996; see also Smith et al. 1999), is needed to understand these penguins' response to changes in sea ice and other factors at a scale that lends itself to our 2°C climate modeling. Their conceptual model treated SIC as a continuum over ecological time (decades), and they proposed that between the sea ice extremes, breeding populations increase or decrease as SIC reaches or moves away from an optimum condition. Little work thus far has been accomplished to quantitatively constrain conditions in the optimum. However, these conditions would differ for the two species, with Emperor Penguins being far more capable of dealing with high SIC than the Adélie, owing to the Emperor's greater capacity at fasting and also its longer breath-holding ability (thus to find food farther in from large ice-floe edges; Ainley 2002). During any given period of time, the sea ice conditions, which actually would include factors additional to SIC, may be generating different forcing on the breeding populations of these two species in the same area.

Given that polynyas figure very importantly in where these two penguin species establish colonies, the "habitat optimum" model is very sensitive to spatial scale. At the mesoscale (tens of kilometers), open water (a polynya) could exist adjacent to a colony (open water otherwise being anathema to these penguins), but otherwise sea ice must be present for these two species at the large scale (hundreds of kilometers). In that case, polynya size and persistence relative to surrounding ice becomes the important quantity (Massom et al. 1998, Ainley 2002, Arrigo and van Dijken 2003). As an example, and as pointed out by Emslie et al. (2007), the location known to be occupied the longest by Adélie penguins in the Ross Sea is a colony adjacent to the Terra Nova Bay polynya.

Another difference between the two species in regard to sea ice, and which figures into the optimum of the two species, is that Adélie Penguins winter in the pack ice, where the sea ice is sufficiently divergent and there is enough light to allow foraging. Therefore, unlike Emperor Penguins, who prepare for the next breeding cycle almost as the last one ends, Adélies spend about six months "wintering" (i.e., "hanging out").

In contrast, during fall, winter, and spring, Emperor Penguins are engaged in breeding at colonies along the coast and traveling to and from coastal polynyas to feed. After breeding, in early summer adult Emperors intensively forage in the pack ice or adjacent open water (where ice had recently been present), fatten, and then molt, also while positioned on coastal fast ice or very large ice floes. In East Antarctica, a region where very little pack ice remains in late summer (cf. Gloersen et al. 1992), pre-molt adults forage for one to two weeks in open waters (Wienecke and Robertson 1997, Wienecke et al. 2004, Zimmer et al. 2008), in stark contrast, for example, to Emperor Penguins of the more southerly Ross Sea (and presumably Amundsen and Weddell Seas), where extensive pack ice is well within reach for pre-molt foraging (Kooyman et al. 2000). Completing the molt, Emperors then again begin intensive foraging, to prepare for breeding, while making their way back toward breeding locations. Only fledgling Emperor Penguins venture far from the coastal sea ice, traveling in their first months, before they have acquired adult diving capacity, to the waters of the Antarctic Polar Front (Kooyman 2002).

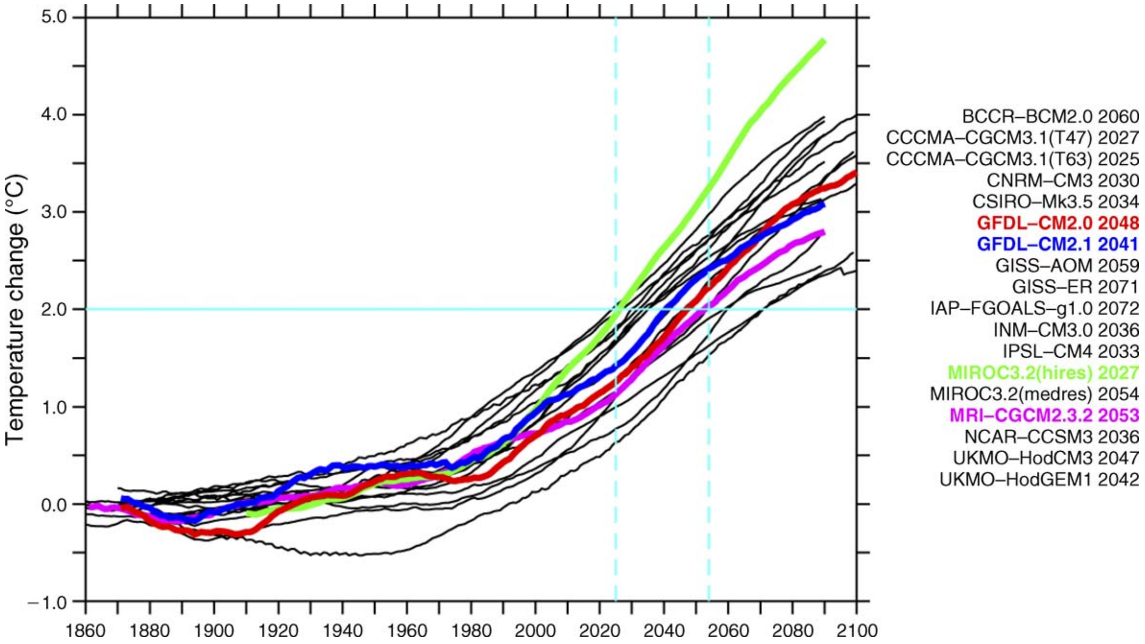


Fig. 3. The globally averaged annual mean air temperature anomaly for each model of the Intergovernmental Panel on Climate Change Fourth Assessment Report (AR4), with each run from the Special Report on Emissions Scenarios (SRES) A1B scenario. As in New (2005), a 21-year running mean filter has been applied to each time series, and the year of 2°C warming is the year in which the anomaly exceeds 2°C. The colored lines indicate models included in our ENSEMBLE model, and the black lines are the other models. The horizontal light-blue line indicates the 2°C threshold and the dashed, vertical light-blue lines bracket the times during which our chosen models exceed that threshold.

### *Species-specific mechanisms to successfully deal with rapidly changing habitats*

On the basis of the review presented in the Appendix, and comments above, the following qualities of penguin habitat are especially pertinent to our 2°C exercise.

The Emperor Penguin lives in an increasingly unstable world, where wind as well as air temperature are the factors critical to their well-being. Strong winds provide nearby open water, but also, along with rising temperatures (which actually facilitate thermoregulation; Jouventin 1974), they increase the instability of the fast ice on which this species forms colonies. Colonies can be very susceptible, therefore, to fast ice that does not remain in place for the full nine months needed, thus precluding colony formation in the first place or leading to total breeding failure once eggs or small chicks are present. The katabatic winds that decide the fate of this species are strongest during equinoctial periods (Parish and Cassano 2003), just the time that they are forming colonies (March–April). Given that this species breeds in winter at the coast, variation in SIE has no direct bearing on its well-being at the mesoscale level of habitat variability. Sea ice extent is a function of wind, so greater wind not only increases SIE but, much more importantly, also affects the positive and negative factors of sea ice and polynya formation, such as those related to ice thickness.

In the case of the Adélie Penguin, with respect to sea ice, between the extremes of too much ice or too little near the colony, presently, the optimum ice concentration is known to be broad but not yet constrained quantitatively, perhaps in the range of 20–80% ice cover (Lescroël et al. 2009). Unlike for the Emperor, SIE has direct bearing on this species during winter, as it spends that period at the large-scale pack ice edge where floes are divergent enough to allow easy access to the ocean. Increasing SIE to its extreme can carry this zone across the SBACC, where waters are less productive than those to the south; this affects overwinter survival, known in the case of juveniles (Wilson et al. 2001). Finally, warming temperatures and changing incursions of marine air affect the amount of snow fall. Heavy snow causes problems, as Adélie Penguins cannot find nesting stones or snow-free nesting habitat.

### *Selecting the year of 2°C temperature elevation*

Rather than choosing a calendar year at a somewhat random future time to examine the models, e.g., 2100, as noted in the *Introduction* we chose to compare them during their year of 2°C warming relative to the preindustrial control simulation (see New [2005] for the Arctic; Fig. 3). This functional definition, besides being pertinent to societal goals to alleviate anthropogenic warming, allowed us to take into account differences in the sensitivities of the various models while exploring the response or state of each 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 (the IPCC has defined the 20th century run to be the 140 years between 1860 and 2000 during which the evolving concentrations of radiatively active atmospheric gases are known and imposed) as the baseline. That is, if the 20th century run for model *X* started on 1 January 1850, then we averaged the 20 years of the control run from that point onward, 1 January 1850 to 31 December 1869, in this example. According to our ensemble, which we hereafter call ENSEMBLE, 2°C will be reached between 2025 and 2052 (Fig. 3).

Here we examine in detail changes to the physical environment projected for the 2°C benchmark. The subregions examined include the Antarctic Peninsula, Ross Sea, and eastern East Antarctica.

### *Projected changes at the 2°C benchmark*

As expected, a warmer global atmosphere leads to a warmer Southern Ocean and less sea ice around Antarctica. In general the ocean surface warms by >0.5°C, with greater increases downstream from Australia and in the Agulhas retroflection region off South Africa (Fig. 4). These are due to changes in 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 10–15% at 70° S and 5–10% at 60° S, where it is already sparse (Fig. 5). All models concur with respect to SST change; model predictions for sea ice changes are more variable, e.g., the GFDL-CM2.0 model shows an increase of coverage in the Weddell Sea while the GFDL-CM2.1 model indicates a decrease.

Looking more regionally at sea ice changes, it will decrease in coverage everywhere but more so around the Antarctic Peninsula (Fig. 6a). Changes near Ross Island would be noticeable but less and may not be ecologically meaningful to either species as this region would still be mostly (>80%) ice-covered in the annual mean. The more equatorward locations, Admiralty Bay, Arthur Harbor (Antarctic Peninsula), and Pointe Géologie (and other colonies in East Antarctica), all north of 70° S, would experience the most pronounced decreases in ice; in the Antarctic Peninsula region (east and west sides) there may be no sea ice north of 65° S. Ice thickness changes (Fig. 6b) would be moderate near all colonies, although ice thickness is already thin throughout East Antarctica. One possible exception is the western Ross Sea, e.g., Cape Washington (165° E, 75° S) and neighboring colonies, where average ice thickness will have decreased by as much as 10 cm. Substantial thinning will also occur on the downwind (eastern) side of the Antarctic Peninsula; other Emperor Penguin colonies occur here (see Woehler 1993). Changes to SST (defined in this study as the 0–100 m average; Fig. 6c) will be small poleward of 65° S, being <0.2°C near the coast where penguin colonies currently exist.

Increasing westerly winds (positive increases in the zonal mean stress) will clearly occur over the circumpolar channel (Fig. 7a). 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 Southern Hemisphere westerly winds. Near Ross Island, the westerly flow will decrease, owing to shifts in the jet stream. Air temperatures (Fig. 7b) will warm 1–2°C over all locations, with the largest changes, again, near Ross Island. However, Ross Island mean annual temperature currently is ~10°C colder than the coast of East Antarctica (see Ainley et al. 2005).

Note that Ross Island is on the eastern boundary between East Antarctica, where temperatures have been decreasing in recent decades, and West Antarctica, where temperatures have been increasing (Kwok and Comiso 2002); thus it is in an especially unstable climate location. The warming there would be consistent with less cold air advection (decreased wind) from the continent. As the current annual temperature averages approximately −24°C, the effect of changing temperature on sea ice formation should be minimal, though ice thickness would be importantly affected (decrease). This climatic change, however, would also affect precipitation (Fig. 7c): a possible increase of >10 cm per year of snow, again consistent with both the warming (warm air holds more water) and the weakening winds (more marine air). In fact, our ENSEMBLE predicts a 25–30% increase in precipitation over Ross Island by the year of 2°C warming.

The model's spatial resolution is too coarse to simulate the peri-Antarctic polynyas accurately. As an approximation, though, we have plotted the total ice cover within the western Ross Sea under the assumption that a decrease in coverage is actually an increase in the area of the Ross Sea polynya (Fig. 8) and not necessarily a reduction in SIE. In fact, the ENSEMBLE shows little change in ice coverage up to the late 20th century, which is a pattern consistent with measured growth in SIE in that region at the same time that the large and coastal Ross Sea Polynya has also become more prevalent (see Parkinson 2002, Zwally et al. 2002). 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 adversely affected by higher air temperatures and the concomitant increased snowfall, both of which are predicted by the ENSEMBLE for this region. (See discussion of snowfall in Ducklow et al. [2007] for Antarctic Peninsula and Bricher et al. [2008] for East Antarctica.)

## DISCUSSION

Our results indicate that limiting carbon emissions so that Earth's atmosphere does not exceed +2°C warming above preindustrial levels, while important, will still have major implications for some enigmatic species. By the time that the 2°C level is reached, major changes to

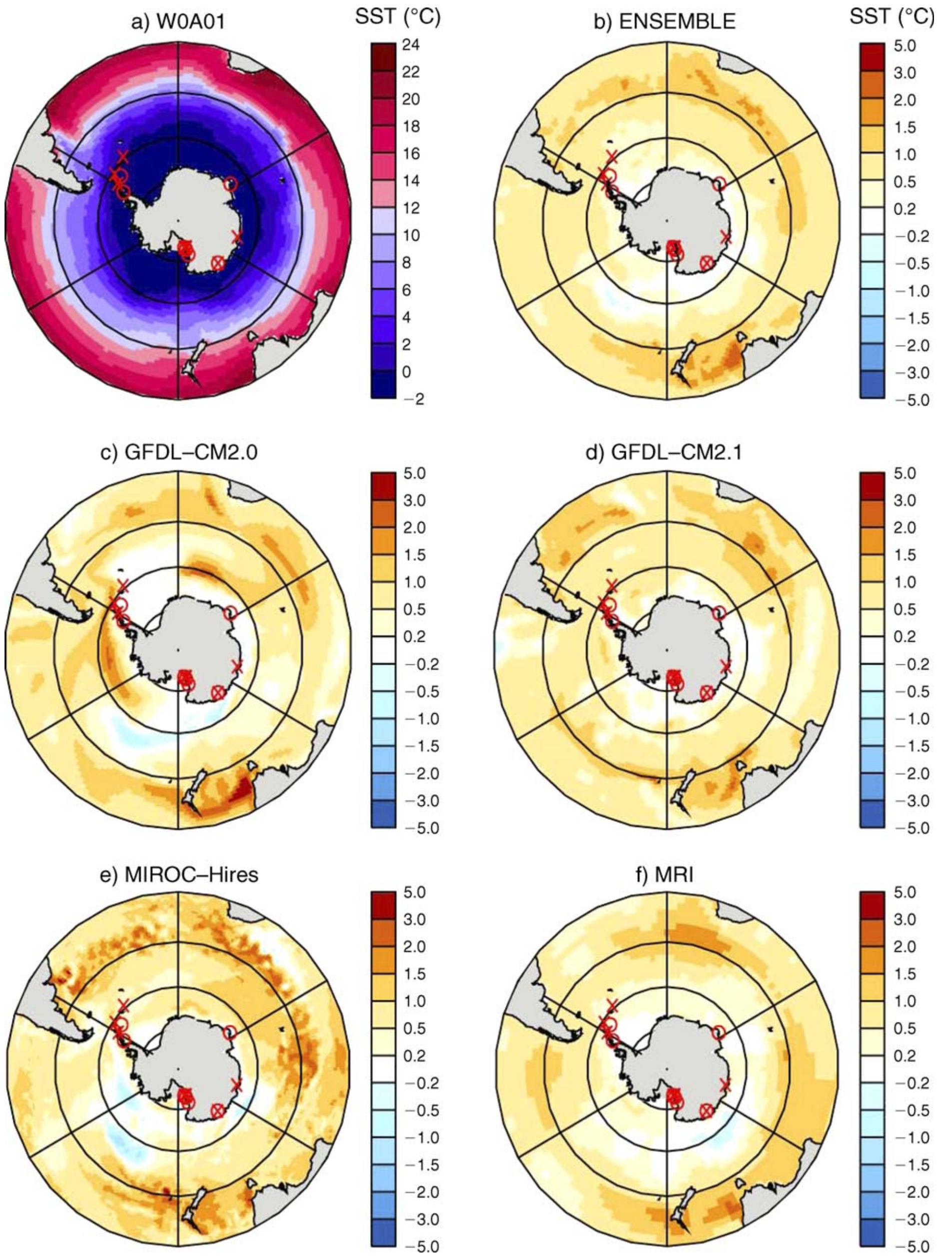


FIG. 4. Sea surface temperatures (SST; °C, 0–100 m average): (a) World Ocean Atlas, observed annual mean (Conkright et al. 2002); (b) ENSEMBLE model, change by the year of 2°C warming relative to the modern era (1981–2000 average); and (c–f) results from each of the four models comprising it. Latitude lines are 75°, 60°, and 45° S; red circles denote Emperor Penguin colonies, and red X's denote Adélie Penguin colonies (see Figs. 1 and 2).

Antarctic penguins' habitat will have occurred in several ways. We have also shown (in the Appendix) that climate effects on penguin vital rates (proportion of adults breeding, age at first breeding, age-specific survival and productivity, emigration), at the meso/decadal spatiotemporal scale are complex, involving different aspects of climate in different seasons. Some processes are contrary to one another in terms of penguins' needs, e.g., stronger winds produce larger polynyas but thinner ice, and others interact, e.g., warmer temperatures loosen the sea ice but bring more snow. Moreover, these factors eventually affect populations through different demographic processes, i.e., changes in adult survival, breeding incidence, chick survival, etc. (Jenouvrier et al. 2005*a*, *b*, Lescroël et al. 2009).

Indeed, the penguins' response to climate variation with respect to the habitat optimum is far more complex than mere responses to reduction in SIE or increasing temperature, the factors pertinent to a large-scale view.

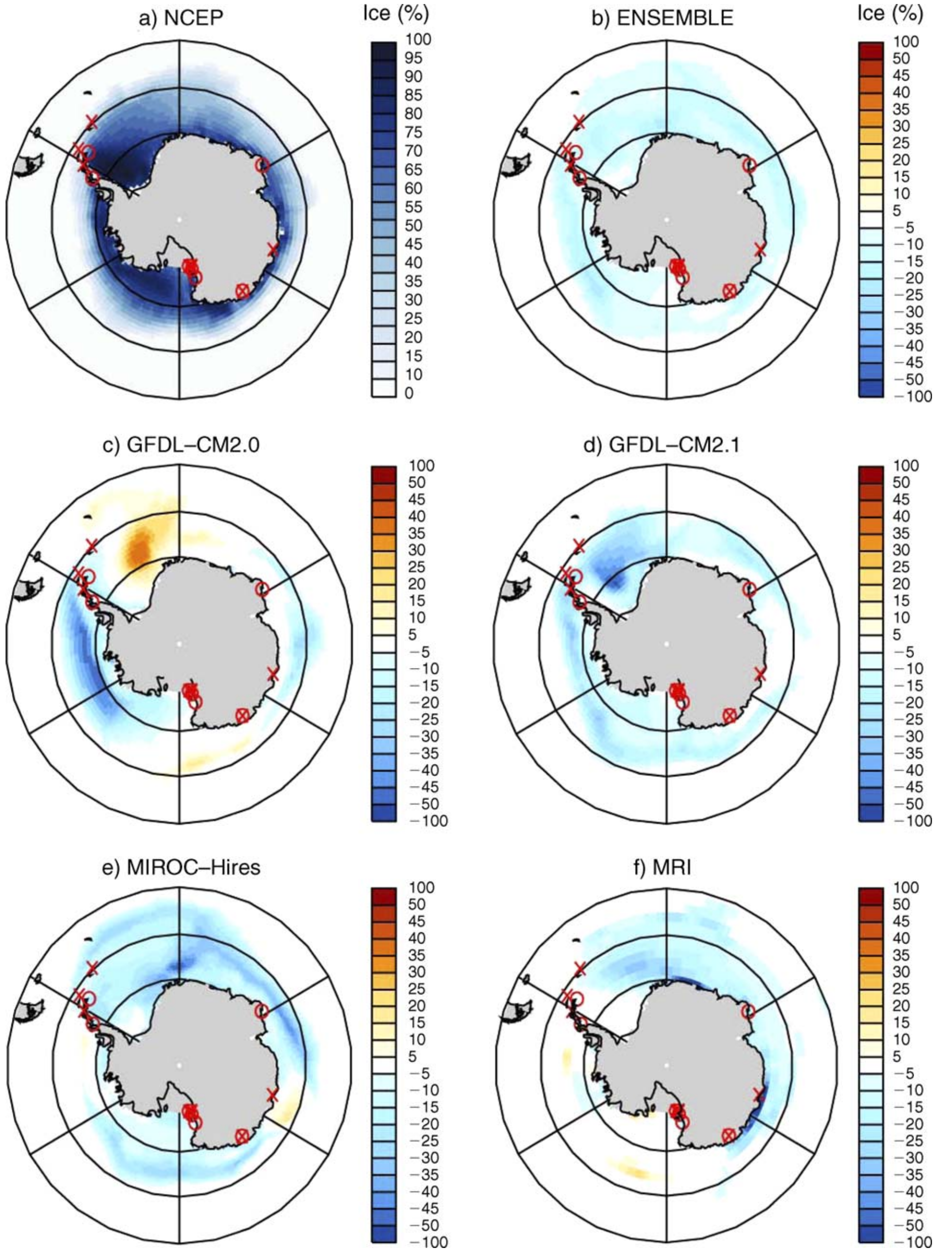
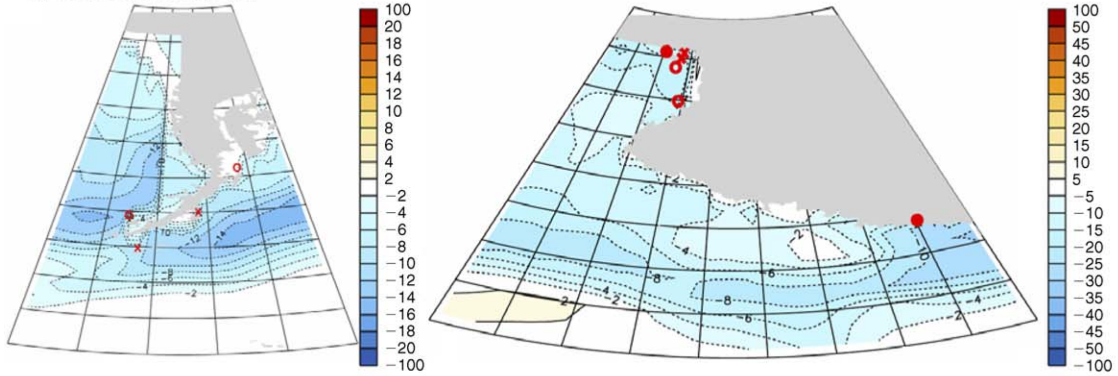


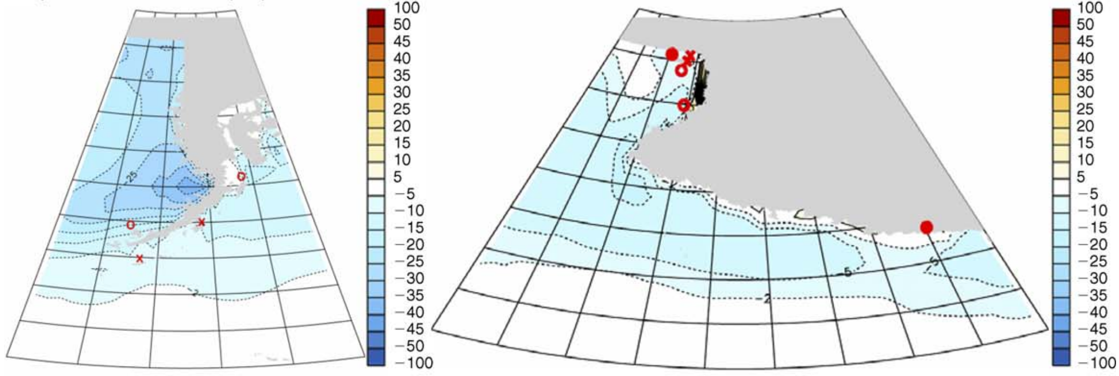
FIG. 5. Sea ice coverage (%): (a) National Center for Environmental Prediction (NCEP), observed annual mean (Conkright et al. 2002); (b) ENSEMBLE model, change by the year of 2°C warming relative to the modern era (1981–2000 average); and (c–f) results from each of the four models comprising it. Latitude lines are 75°, 60°, and 45° S; red circles denote Emperor Penguin colonies, and red X's denote Adélie Penguin colonies (see Figs. 1 and 2).

These two factors were used, appropriately, by Cheung et al. (2008) to construct species-specific, large/centennial-scale "climate envelopes" for Antarctic fish. They then compared species' responses to climate model outputs much farther into the future than the 2°C benchmark used here. In the case of fish, they are known to be directly and sensitively affected by changes in ocean temperature, but this is not the case for warm-blooded birds. If we were modeling, as did Cheung et al. (2008), penguins' response to the large/centennial–spatiotemporal-scale presence or absence of sea ice, climate envelope models would be practical and would, or should, support the actual findings of Emslie (2001) and Emslie et al. (2003, 2007; see Appendix). Owing to the complexity of the penguins' relationships to their respective habitat optimums and the complexity of the manner in which climate affects sea ice in the Southern Ocean, however, we are not yet in a position in which a suitable habitat optimum model could be constructed in a form sufficiently sophisticated for any Antarctic

a) Sea ice coverage (%)



b) Sea ice thickness (cm)



c) Sea surface temperature (°C)

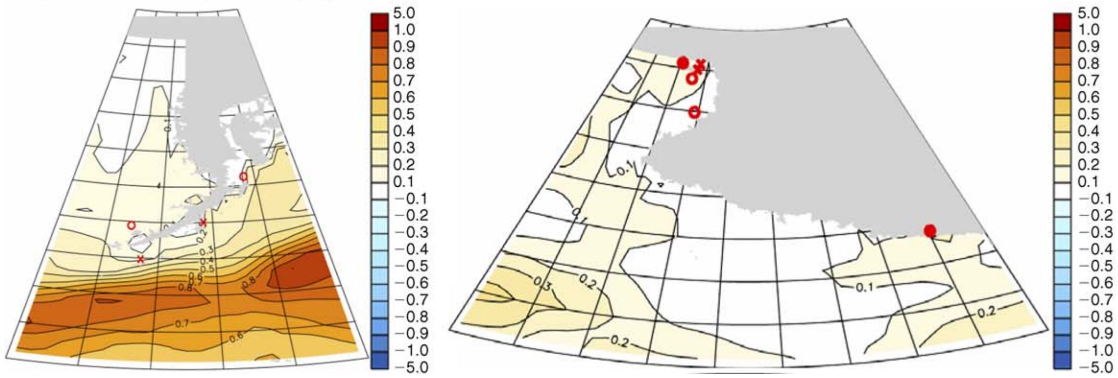
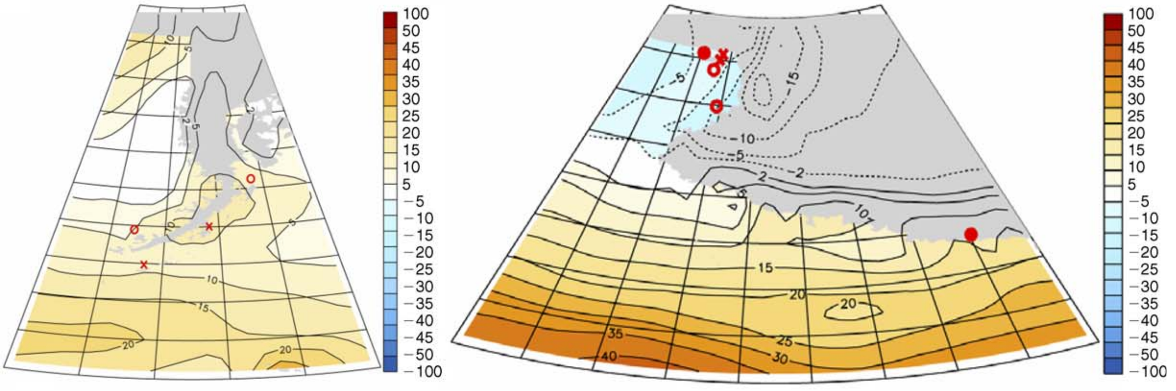


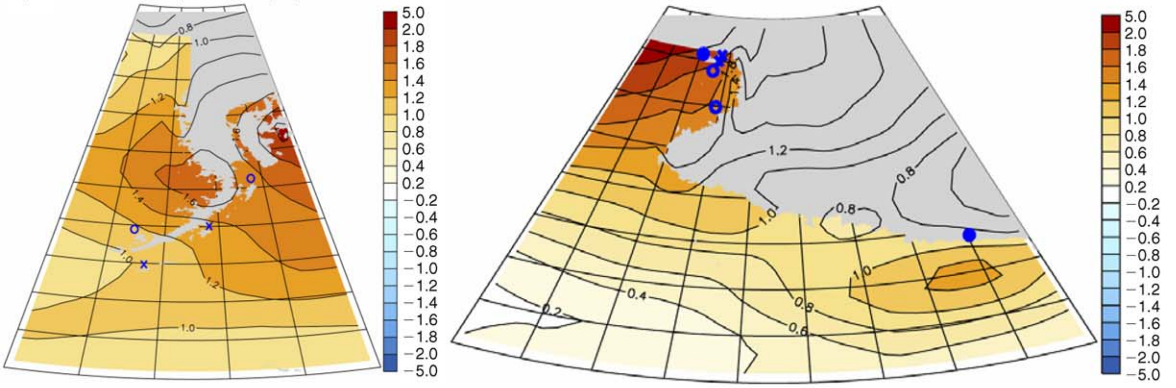
Fig. 6. ENSEMBLE model: simulated change in annual mean (a) sea ice coverage, (b) sea ice thickness, and (c) sea surface temperature (°C, 0–100 m average). Left panels show results for the Antarctic Peninsula, from 80° S at the top to 55° S at the bottom, with grid lines every 2.5°, and from 50° W on the left to 75° W on the right, with grid lines every 5°. Scientifically important penguin colonies (long time series) are indicated in red: Adélie colonies (X), Emperor colonies (open circles), and sites having both species (solid circles). Colonies are (from left to right): Admiralty Bay, Arthur Harbor (Adélie), and Dion Islets (Emperor). Right panels show results for 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° E on the left to 135° E on the right, with grid lines every 5°. Important penguin colonies are indicated (symbols as in left panels). Colonies are (clockwise around Ross Island): Cape Crozier (both Adélie and Emperor), Cape Royds, Cape Bird, and Beaufort Island (both Adélie and Emperor); Cape Washington (Emperor) is north of Ross Island, and Pointe Géologie (both Adélie and Emperor) is to the right. See Figs. 1 and 2 for a larger-scale view and labeling of colonies.

penguin species. This is demonstrated by Lescroël et al. (2009), who found that what was thought to be challenging SIC (80%) for Adélie Penguins may, in fact, have been merely approaching the upper limit. On the other hand, at least with this synthesis, we know the variables on which to focus, and species distribution models should be the next step to quantitatively project the penguin responses to climate change.

a) Zonal wind stress ($10^{-3}$ N/m²)



b) Surface air temperature (°C)



c) Precipitation (cm)

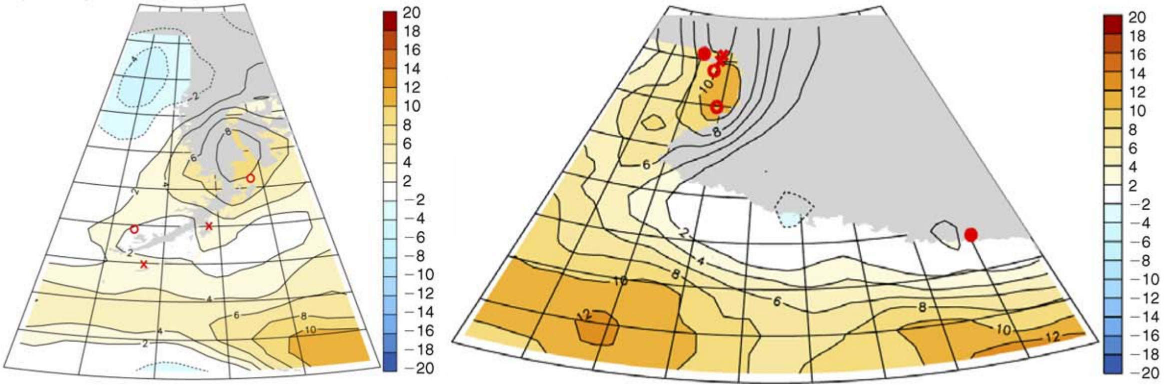


Fig. 7. ENSEMBLE model: simulated change in annual mean (a) zonal wind stress (note that due to the orientation of the figure a positive change means a greater stress directed toward the left/east of the figure); (b) surface air temperature; and (c) precipitation. Penguin colonies and the area shown in each panel are as in Fig. 6 (see also Figs. 1 and 2).

In using the habitat optimum concept, a further approach would be to include the demographic processes, i.e., estimate the impact of the range of variation in several habitat features on vital rates, to ultimately include those relationships in a demographic model (see the approach developed by Jenouvrier et al. [2009]). Once sea ice coverage is resolved spatiotemporally into its components of sea ice concentration, extent, and thickness, with attention to polynya size and persistence, i.e., length of sea ice season, those models could be applied to quantitatively project the penguin population responses to small increments of future ocean habitat change. At only one site (Adélie Penguins, Ross Island) are these data currently being collected, but it will be a few years before they are available in a sufficiently long time series for a more complex analysis.

In the meantime, and from here onward, we complete the process begun above in which, armed with knowledge of the manner in which penguins have responded to climate change in the past (see Appendix), we make

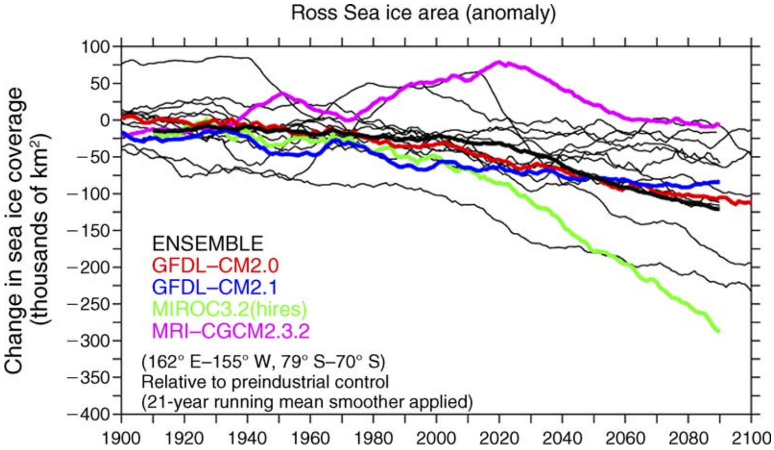


FIG. 8. Change in annual mean sea ice coverage over the Ross Sea relative to the preindustrial annual mean for the ENSEMBLE model (thick black line) and for each model of the Intergovernmental Panel on Climate Change Fourth Assessment Report (AR4). The colored lines indicate models included in our ENSEMBLE model, and the black lines are the other models.

broad projections for the future on the basis of our ENSEMBLE climate prediction in a world reaching temperatures 2°C above preindustrial levels. We do not aim to give quantitative results, as would be the case of the yet-to-be-developed population models, but rather we present qualitative projections. The latter we feel will validly indicate at least the areas where climate effects will be obvious and the types of population trends to be expected.

The significant lessening of SIC and thickness as projected by the ENSEMBLE at latitudes north of 70° S should have negative effects on most colonies by 2025–2052. Approximately 50% of Emperor Penguin colonies, representing almost 40% of the total world population (Figs. 1 and 9), and ~75% of colonies and ~70% of numbers of Adélie Penguins (Figs. 2 and 10) currently exist north of 70° S. The extreme northern colonies, i.e., north of 67–68° S, should disappear, which includes that at Pointe Géologie. On the basis of our results, including sea ice thickness in a modeling approach such as the one used by Jenouvrier et al. (2009) would likely indicate marked population decline among Emperor Penguins at Pointe Géologie in the next few decades.

The trends of disappearing colonies in conjunction with decreasing sea ice coverage currently seen along the west coast of the Antarctic Peninsula, therefore, would broaden in geographic extent. If they do not disappear or begin to decrease, at least in the case of Adélie Penguins, colonies should at least cease any increasing trends evident in recent decades. This would be so particularly for Adélie Penguins in the Antarctic Peninsula region (west coast and northeast coast) and in East Antarctica as well. Most vulnerable would be colonies at the tip of the Antarctic Peninsula, especially the Emperor Penguin colony on the east side at Snow Hill Island (64°28′ S, 57°12′ W), which is a popular destination for tourists (see Todd et al. 2004). Colonies of Adélie Penguins in the Ross Sea region, however, where 38% of the population currently nests, should experience few negative effects.

Further increase in coastal polynyas, which is predicted, may not help these penguins beyond what benefits they have experienced thus far from this change. Moreover, the factors that bring increased polynyas also bring decreased sea ice thickness, a direct problem for Emperor Penguins. As noted above, increases among larger colonies appear already to be slowing (e.g., leveling of growth trajectories; see Appendix: Figs. A9 and A10). Moreover, because coastal (latent heat) polynyas are the result of the channeling of continental (katabatic) winds at specific locations, owing to local topography (mountain valleys, etc.; Parish and Cassano 2003), there should not be many new polynyas appearing where they currently do not exist. That should be true unless the coastal physiography of glacial ridges and valleys dramatically changes with the recession of ice shelves and glaciers. Therefore, in spite of projected increased winds in the Southern Ocean, we cannot expect them to facilitate penguin colonization along sections of coast where polynyas, and penguins, do not currently exist.

Consistent with the record during the early Holocene (Emslie et al. 2003, Thatje et al. 2008), it is highly likely that Adélie Penguins would colonize new areas as various ice shelves collapse in northern latitudes, thus exposing new coastline, and as sea ice in areas where it currently is highly concentrated in southern latitudes, e.g., along the eastern side of the Antarctic Peninsula and in the southern Bellingshausen and Amundsen Seas, becomes more divergent. Indeed, we may soon see the conditions that existed during the mid-Holocene "Penguin Optimum," when ice diverged enough that Adélie Penguins will reoccupy colonies, now ice bound, along the southern Victoria Land coast (Baroni and Orombelli 1994). Overall, then, there may well be less net loss of

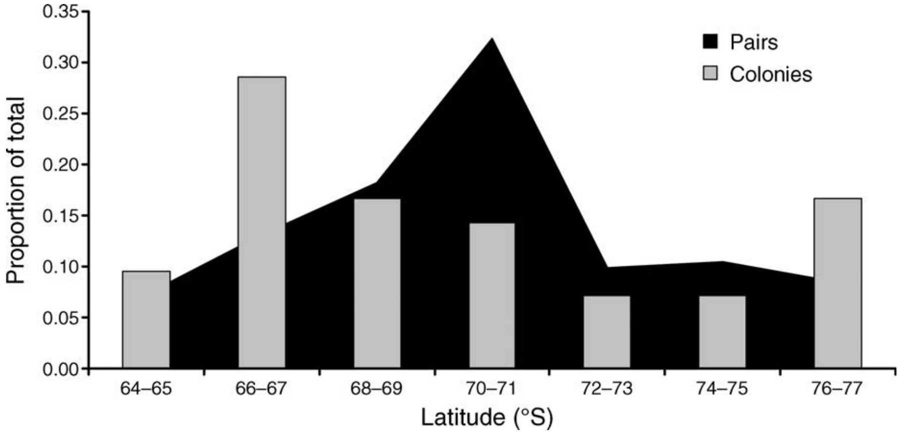


FIG. 9. Proportions of the total number of current Emperor Penguin colonies ($n = 42$) and breeding pairs (248 000) by latitude (data from Woehler [1993] and Woehler and Croxall [1997]).

Adélie Penguin populations at least initially (losses in some regions, gains in others).

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 around the Antarctic, including the inner reaches of the Ross Sea, where a disproportionate number of Emperor Penguins nest (26% of world population). In part this decrease is related to increased winter air temperatures and winds and the continued increase in coastal polynyas also resulting from thinning sea ice. Thus, finding stable, long-lasting fast ice for breeding may be difficult even at appreciably higher latitudes. The incidence of premature blow-out of ice on which the penguins are nesting should increase in frequency, with a concomitant decrease in breeding success. Whether or not colonies become founded on land, as is the case at Taylor Glacier (see Appendix), remains to be seen, but this may not be a common event. Fast ice, or even coastline, along which ice rafting ridges have not formed, as pack ice is pushed by the wind against the fast ice edge or shore, is rare and would be required for the less-than-nimble Emperor Penguin.

Working against the founding of colonies at higher latitudes would be the decrease of ice coverage in pack ice areas where Adélie Penguins currently winter. As noted by Fraser and Trivelpiece (1996) and investigated intensively by G. Ballard et al. (*unpublished manuscript*), this species winters only in pack ice areas where there is sufficient light (including twilight) 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 adverse effects on the annual migration and wintering survival of this species.

Finally, considering factors other than sea ice, an increase in snowfall has a major negative effect on Adélie Penguin breeding in the Antarctic Peninsula region (Fraser and Patterson 1997, Massom et al. 2006),

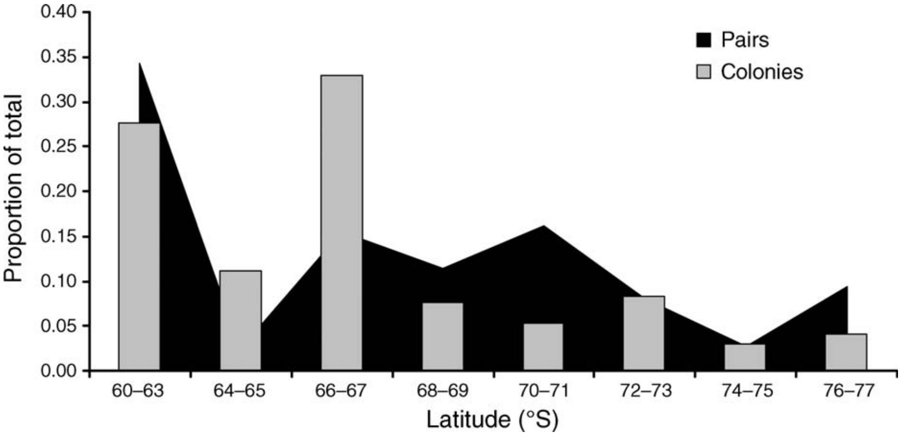


FIG. 10. Proportions of the total number of the current Adélie Penguin colonies ($n = 170$) and of breeding pairs (3 million) by latitude (data from Woehler [1993] and Woehler and Croxall [1997]).

as well as East Antarctica (Bricher et al. 2008). In the latter area, snowfall has been increasing as temperatures warm near the coast, consistent with the model, and in fact, as well, rain was recorded for the first time in 2001–2002 (E. Woehler, *personal observation*). When the penguins of the Antarctic Peninsula have arrived in spring during recent years, they have not been able to find their former nests nor stones needed to build them. All have been buried in snow. By the time the snow melts, Gentoo and Chinstrap Penguins have arrived, and these two species easily displace Adélies from nesting areas (Volkman and Trivelpiece 1981, Lishman 1985, Trivelpiece et al. 1987). The Gentoo and Chinstrap are currently absent in East Antarctica, except for a small Chinstrap colony of unknown age on the Balleny Islands (66°55′ S, 163°20′ E; Woehler 1993). In the Ross Sea region, where the greatest change in snowfall is projected, current Adélie colonies have far more terrain available than they currently occupy (Ainley et al. 2004). Thus, even with a large increase in snowfall, plenty of nesting space should remain. However, we predict an increased probability of events such as those occurring in 2001 and 2007, when hundreds of incubated adults were buried by deep snowdrifts, thus causing extensive mortality and/or loss of eggs/chicks (D. G. Ainley, *personal observation*). The penguins would have to shift to more exposed locations. Otherwise, conditions that favor low-latitude penguin species (temperate temperatures, ice-free) will not be materializing for the Ross Sea anytime within the +2°C warming scenario. The same cannot be said of the coast of East Antarctica, which lies between the zoogeographic center of the Chinstrap range (Scotia Sea) and the Balleny Islands.

### *Final thoughts*

We have had little to say about how climate change might have direct effects on the food web and ultimately the populations of Antarctic penguin species (see also Siniff et al. [2008] for similar points made in regard to Antarctic pack ice seals). In regard to our analyses here, as noted by Croxall et al. (2002), the food web topic is far too complex with insufficient data presently available and involves perhaps decreases in certain prey (e.g., Antarctic silverfish [*Pleuragramma antarctica*] and Antarctic krill [*Euphausia superba*] and related species; Emslie and McDaniel 2002, Atkinson et al. 2004, Ducklow et al. 2007, Cheung et al. 2008) and increases in others, particularly in coastal, continental shelf areas, especially with larger, more persistent polynyas (favoring, e.g., crystal krill [*E. crystallorophias*], and therefore their main predator, silverfish; La Mesa et al. 2004, Deibel and Daly 2007).

In addition, the very much perturbed food web of the Southern Ocean is undergoing adjustment as some species recover and others decrease due to industrial fishing, sealing, and whaling (see Ballance et al. 2006, Emslie and Patterson 2007, Ainley and Blight 2008). Thus, how to tease climate-related changes from that state of affairs is a challenge (a concept suggested briefly by Croxall et al. [2002]). Recent modeling has shown that the sensitivity of marine food webs to climate change increases markedly as food webs are simplified by overfishing (Österblom et al. 2007, Watermeyer et al. 2008), a predicament that certainly would apply to much of the Southern Ocean. As an example of how complex the question of climate vs. fishing/whaling effects on the food web can be, specific to our study areas, is evident for the ocean off Adélie Land. There, various authors have hypothesized reductions in food for Emperor Penguins and other avian species (e.g., Barbraud and Weimerskirch 2001, 2006), while the Adélie Penguin seems to be doing well, as our review has indicated. In addition, the humpback whale (*Megaptera novaeangliae*) population, certainly a species that would eat the same prey as the Emperor (and Adélie), has been increasing at a phenomenal 9.6% per annum over the past few decades (Branch 2006) and now is so abundant there that Japan wants to renew whaling on that species. Off the west coast of the Antarctic Peninsula, on the other hand, these whales are increasing more slowly, while most penguin populations decrease (cf. Branch 2006, Ducklow et al. 2007, Hinke et al. 2007). Finally, Ainley et al. (2007) proposed that the growth of Ross Sea and Adélie Land Adélie Penguin colonies was positively affected by greater polynya persistence, a growth that possibly was facilitated by the coincident dynamics of whale removal and recovery. To be fair it should be noted that different species might respond differently to ecosystem change, depending on their respective life history strategy (Jenouvrier et al. 2005*a*, Forcada et al. 2006, 2008). Using an intraspecific example pertinent to our study, Emperor Penguin males, compared to females, are more sensitive to food web change (Jenouvrier et al. 2005*a*) because they incur a greater energy cost during the breeding season. A higher proportion of females in the population, following a higher mortality of males, may reduce population fecundity to ultimately affect population growth (S. Jenouvrier, H. Caswell, C. Barbraud, and H. Weimerskirch, *unpublished manuscript*). Of course, the humpback whales mentioned above arrive at their feeding grounds in great energy debt as well, which, in the absence of direct food web sampling, further increases the apparent complexity of this ecosystem. Nevertheless, on the basis of changes in the physical habitat alone and the penguin life cycle, it appears from our analysis that by the time Earth's troposphere reaches +2°C above preindustrial levels, we can expect major reductions and alterations in the abundance and distribution of pack ice penguins regardless of climate impacts on the food web.

As noted above, 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 sea ice habitat of the Southern Ocean, unlike other penguin species. If sea ice disappears, then open-water species, such as Gentoo and

Macaroni Penguins, move in (e.g., Ducklow et al. 2007). These other species, including the Chinstrap, as noted, can outcompete Adélie Penguins for nesting space. It is likely that its close congener, the King Penguin, would easily displace the Emperor Penguin, owing to the King's year-long residency at colony sites (Williams 1995). Moreover, the King's capacity for an extended breeding season is the result of existing where food availability is much diminished compared to, currently, the high Antarctic. The Emperor requires abundant, energy-rich food (more, larger fish) to accomplish a much-shortened breeding season compared to the King. Therefore, it would seem likely that the King Penguin can exploit many more potential breeding and oceanic habitats than can the more specialized Emperor Penguin and therefore should fair relatively well (but that is relative: see Le Bohec et al. 2008).

In summary, changes to distribution and abundance of pack ice, as well as sub-Antarctic penguins, can be expected to reflect habitat alteration as a result of changing climatic regimes. At the least, the zoogeographic range of the pack ice penguins, especially the Emperor, will become severely compacted southward, thus increasing susceptibility to the effects of warming in excess of 2°C. We encourage researchers over the next few decades to collect demographic data to understand better the mechanisms of population change in the face of profound changes to their habitat due to climate change and overexploitation of biotic resources, thus ultimately to model penguins' response at the meso/decadal scale using the habitat optimum approach.

## ACKNOWLEDGMENTS

This project was funded by the World Wildlife Fund and the National Science Foundation, NSF grant OPP-0440643 (D. G. Ainley), and a Marie-Curie Fellowship to S. Jenouvrier. For providing logistical and financial support in acquiring long-term penguin data, we thank the U.S. Antarctic Research Program and NSF for Ross Sea Emperor Penguin and Palmer Station Adélie Penguin data; NZ Foundation for Research, Science and Technology, Antarctica New Zealand, and Nga Pae o te Maramatanga for Ross Sea Adélie Penguin data; French Polar Institute (IPEV) and Terres Australes et Antarctique Francaise (project 109, H. Weimerskirch leader) for Pointe Géologie data; and the national programs of the United Kingdom and Australia for acquiring other data. We thank C. Barbraud, L. Blight, B. Wienecke, and two anonymous reviewers for comments on the manuscript and I. Gaffney for executing some of the figures.

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## APPENDIX

The derivation of a model ensemble useful for predicting changes in penguin habitat (*Ecological Archives* M080-001-A1).

*Ecological Archives* M080-001-A1

## David Ainley, Joellen Russell, Stephanie Jenouvrier, Eric Woehler, Philip O'B. Lyver, William R. Fraser, and Gerald L. Kooyman. 2010. Antarctic penguin response to habitat change as Earth's troposphere reaches 2°C above preindustrial levels. *Ecological Monographs* 80:49–66.

Appendix A. The derivation of a model ensemble useful for predicting changes in penguin habitat.

Russell et al. (2006*b*) evaluated 18 of the coupled IPCC 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 compared the wind stress and ACC strength for the last 20 years of the 20th century for each model run (Fig. A1). Several of the models 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 reasonably true: they have winds and an ACC that is relatively close to the observations.

As Russell et al. (2006*b*) noted, most climate models have a maximum wind stress equator-ward of the observations, some by more than 10° latitude. The models singled-out in Fig. A2 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 from the remainder.]

Continuing the winnowing process, we examined the seasonal cycle of sea ice around Antarctica (Fig. A3a). Most of the models had a reasonable range of total ice area, between 0 and 20 million km$^2$. In modern observations, sea ice still exists around Antarctica in February (month of the yearly minimum), but some models had no sea ice at all for one or more months of the year. We chose to use a root-mean-squared error calculation so that 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. Fig. A3b provides a clear view 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!

The next step in the winnowing of models involved comparing their simulations of the boundaries of the ACC to the observational record (Fig. A4). 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 ppt at 100 m) and defined the Southern Boundary of the ACC as the surface transition from Upper Circumpolar Deep Water to the denser Lower Circumpolar Deep Water (the location of the 27.6 ppt isopcynal 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 steps in winnowing, our ENSEMBLE was composed of the GFDL-CM2.1, GFDL-CM2.0, MIROC3.2(hires), and MRI-CGCM2.3.2a models.

As a final check on the appropriateness of our model choices, we then compared the simulated annual mean ice thickness from our collection to the observational record (Fig. A5). In fact, the models chosen did a reasonable job of simulating that variable. The thickest ice is in the western Weddell Sea along the eastern shore of the Antarctic Peninsula and in the eastern Ross Sea. The southwestern Ross Sea has less ice cover in both the data and the models owing to the Ross Sea Polynya, the largest coastal polynya in the Antarctic.

## PENGUINS’ RESPONSE TO HABITAT VARIABILITY: A REVIEW

### *A view at the large-/centennial- to millennial- spatio-/temporal-scales*

In the case of both species, at the large spatial and temporal scales, there can be too much sea ice. It almost goes without saying that if the coast is comprised of a glacier or an ice shelf, without a polynya and without any persistent fast ice also being present in the case of the Emperor, neither species will be found nesting. Using 14C -datable remains found in extinct and existing Adélie Penguin colonies, well documented for the last 45,000 years, i.e. the last glaciation and inter-glacial periods on either side, is the colonization of the coast as ice shelves retreated to expose nesting habitat or, conversely, extinction of colonies as ice sheets and shelves advanced (Emslie et al. 2007).

Because Emperors nest on annual sea (fast) ice, they have left no remains to chronicle their breeding history at geologic (millennial) time scales. Therefore, we have no idea about how this species faired during glacial periods. With the Ross and Weddell seas covered by glacial ice sheets, and glacial ice extending farther out than now in general, obviously Emperors could only nest at low latitudes. During these periods, penguins would likely have experienced an ocean significantly reduced in primary productivity owing to persistent and concentrated sea ice; any local foodwebs, as well as Emperor Penguins, would be restricted to where ever polynyas occurred adjacent to ice shelves (Thatje et al. 2008). As these authors note, overall conditions were more severe than currently, with some data indicating more but others indicating fewer polynyas.

Currently, Emperor Penguins at the two largest colonies, Coulman Island and Cape Washington in the Ross Sea (Woehler 1993), experience a 20-30 km walk over fast ice to reach a flaw lead at the fast ice edge, with the looser pack ice there being part of the marginal ice zone of the Ross Sea Polynya (see Marshall and Turner 1997). Emperor Penguins at other colonies require walks of up to 100 km (Kirkwood and Robertson 1997). Massom et al. (2009) showed that variation in the distance between 10 and 70 km can have inverse effects on breeding success at Pointe Géologie.

In the case of Adélie Penguins, if faced with a commute of more than a couple of kilometers during the chick-provisioning portion of the annual cycle (when chicks need to be fed almost daily), its colonies will disappear. This is well documented along the Victoria Land coast, where extensive fast ice that is about 20 km wide precludes Adélie Penguins from nesting (Ainley 2002, Emslie et al. 2003). However, when the fast ice disappeared during a brief, mid-Holocene warm period, the penguins colonized this area but then deserted it when the fast ice returned. Recent, short-term 'natural experiments' support this: 1) unusually compacted pack ice off colonies on the west coast of the Antarctic Peninsula during one spring (owing to anomalously persistent on shore winds) resulted in the temporary skipping of breeding and thus a one-year dramatic decrease in nesting numbers (Massom et al. 2006); and 2) in a scenario still unfolding, unusually concentrated sea ice in the Southwest Ross Sea for several years (owing to blockage by immense, grounded ice bergs; Arrigo et al. 2002) is resulting in substantial but different rates of population decrease and emigration among four widely-spread colonies whose demography is being studied simultaneously (Ainley, Ballard, Dugger, Lyver, unpublished data; but see Shepherd et al. 2005). Before the latter scenario began to unfold, Adélie Penguins were beginning to re-colonize an area (Cape Barne) that required a 2-3 km walk over fast ice during the incubation period, but which was fast ice free during the chick period (Ainley, pers. obs.)

The other extreme, that of no sea ice at all, has also been investigated at the geologic time scale, again using datable Adélie Penguin remains in conjunction with sediment cores to indicate the presence/absence of ice (cf. Smith et al. 1999, Emslie 2001). Adélie Penguins colonized the northwestern coast of the Antarctic Peninsula when sea ice extended increasingly northward with the Little Ice Age. In recent decades, as the sea ice cover has receded (Stammerjohn et al. 2008), Adélie Penguins have been disappearing and ice-avoiding penguin species have been replacing them (Ducklow et al. 2007, Hinke et al. 2007). The advance of the latter species is unprecedented in the existing, 600 yr sub-fossil record (Emslie et al. 1998).

This scenario can be inferred for Emperor Penguins from the modeling of Jenouvrier et al. (2009a). Using IPCC model output for the generalized sea-ice coverage and extending to the 22nd century, the colony at Pointe Géologie was projected to decrease from 2600 pairs at present to 400 pairs as sea ice disappears. In a scenario similar to that of Cheung et al. (2008) for Antarctic fish, the authors note that if the model is extended farther in time, there is no sea ice and no Emperor Penguins. This scenario, in fact, is apparent in real time at Dion Islets (67° 52'S, 68° 43'W). The colony disappeared in accord with the dramatic decrease in sea ice along the west coast of the Antarctic Peninsula (cf. Ainley et al. 2005, Ducklow et al. 2007). Sea ice has yet to retreat significantly from the colder east coast of the Peninsula and, thus, Emperor colonies there are currently doing fine, even a few latitude degrees farther north than Dion Islets (Fig. 1).

### *A view at the meso-/decadal- spatio-temporal scales*

*Emperor Penguin response to habitat change.* – Three investigations have discussed the demography and population dynamics of the Emperor Penguin with respect to variability in ice and other habitat characteristics at the meso-/decadal- spatio-temporal scale (Barbraud and Weimerskirch 2001, Ainley et al. 2005, Jenouvrier et al. 2005*a*). 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 (Figs. 2, EA6).

The findings of these studies were as follows:

- Barbraud and Weimerskirch (2001) found that survival, decreased when SST north of the pack ice was higher and SIE was reduced (see also Jenouvrier et al. 2005a: male correlation to SIE even more sensitive than females). Their data also showed a marked, 50% decrease in colony size during a few years in the mid-1970s and one from which the colony has not yet recovered. They showed that the population crash coincided with a period of low adult survival and that after the population crash, breeding success became far more variable than before, due especially to an increasing frequency of years in which the fast ice blew out prematurely and along with it eggs and chicks (zero reproductive success).

- Ainley et al. (2005), using the same data set but several different covariates and a different analysis, found that the population increased with less positive SAM, and decreased with greater wind, SIE and thinner ice. They also noted that average breeding success was much lower after the mid-1970s, corresponding to the time when SAM switched from negative to positive.

- Jenouvrier et al. (2005*a*) showed that population size is positively related to SIC and SIE during autumn, and to the Southern Oscillation Index (SOI). Adult survival varied inversely with air temperature during summer and winter months for both genders, and was positively related to SIC for males.Using population models, they showed that annual survival and breeding success contributed equally to explain population variation.

The basic findings of these analyses in regard to how Emperor Penguins have responded to *past* but relatively recent sea-ice variability are compatible with one another and *together* they show how this species responds to habitat change. The most difficult covariate to deal with is SST (as perceived by satellite) north of the sea ice (see Barbraud and Weimerskirch 2001), as many factors can alter SST with likely different ecological consequences. Certainly, elevated SST could directly reduce SIE (melting at its outer edge) as in the case of the coincidence of the pack ice edge with SBACC (see above). The warmer ocean extends to depth. However, as will be discussed in climate model projections, reduced wind also causes SIE to decrease, but at the same time reduced wind would also lead to greater stratification of surface waters. The latter would lead to higher SSTs, owing to heat absorption from solar insolation, in the thin, surface layer sampled by satellites. Underlying waters would remain cool. Finally, the upwelling of Circumpolar Deep Water, which is warmer than Antarctic Surface Water, can also be involved and, in fact, this is the factor that would be most important to the penguins on the basis of our climate modeling. In fact, sensible heat polynyas are the result of this upwelling.

The findings of Ainley et al. (2005) that the Pointe Géologie Emperor colony increased with less positive SAM (see also Massom et al. 2009), and decreased with higher wind and thinner ice may seem contradictory to the findings of Jenouvrier et al. (2005a) that population increases with greater SIE. However, as noted by Ainley et al. (2005), greater wind at Pointe Géologie leads not just to greater SIE (pack ice), but also to thinner and more unstable fast ice (see Jacobs and Comiso 1989), and hence greater chance of premature fast-ice blow-out. 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. (2005*a*) found higher adult survival with lower air temperatures is consistent with effects of the hurricane force katabatic winds (which consist of cold air draining off the Antarctic plateau towards the coast) on maintaining the adjacent coastal polynya, ice formation and greater SIE (see Barber and Massom 2007). The katabatic winds of the Adélie Land coast reduce air temperature or at least they did during the negative SAM (Wendler et al. 1997). The fact that male emperor penguin survival decreases when SIE decreases during winter is consistent with less wind that would also reduce or negate the development of the Mertz Glacier Polynya, thus increasing the time and energy needed for the emaciated males to reach open water and food (see Massom et al. 2009). Obviously, more work is needed to understand the effect of local, polynya-favorable vs -unfavorable winds, polynya size, ice thickness, and ice stability in regard to the Pointe Géologie Emperor colony's growth through direct effects on vital rates.

The Emperor Penguin population at Pointe Géologie, as noted by all authors, has not been able to recover from a major decrease in the mid-1970s (see especially Jenouvrier et al. 2009 b). This is similar to the pattern exhibited by seabirds elsewhere that have suffered a catastrophic adult mortality unrelated but occurring after a regime shift. It is well known that for long-lived species, such as the Emperor Penguin (and many other seabirds), adult survival is a key driver in population trends, but that breeding success also contributes (e.g., Jenouvrier et al. 2005*a*). Indeed, it has been shown that in certain states of climate oscillations, the capacity of a population to recover appears to be limited by breeding success. For example, the capacity to breed successfully became reduced in new regimes for the endemic Galapagos penguins (*Spheniscus mendiculus*) in the Peru Current and Common Murres (*Uria aalge*) in the California Current (Ainley and Divoky 2001) and, therefore, these populations could not easily recover from single-event mortalities: an intense El Niño and/or a large oil spill, respectively.

The factors likely responsible for reduced breeding success of the Emperor Penguins during more recent years are prolonged katabatic blizzards (and deepening low temperatures), which increase chick mortality (Jouventin 1974); and especially in recent years premature ice break-out, which causes total loss of eggs, or chicks, depending on timing (Budd 1962; see also Barbraud and Weimerskirch 2001). Finally, with dramatically lower breeding success, and especially total breeding failure, subadults resulting from previous years' breeding likely would be discouraged from recruiting into the Pointe Géologie colony, especially if the extent of recruitment is affected by a performance-based assessment of a colony's vitality, as has been shown in other seabird species (e.g. Danchin et al. 1997, 1998). That is, in years when the colony was blown out to sea, upon arriving later in the breeding period (as young seabirds do), these potential recruits would find neither adults nor chicks present and, therefore, may look elsewhere for a more viable colony.

The Taylor Glacier Emperor Penguin 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 Islets, has decreased by > 90% since the 1940s, but it is in an area where sea ice is completely disappearing (Ainley et al. 2005; see main text).] Therefore, the Taylor Glacier colony would not be directly affected either by sea-ice thickness or stability of fast ice for breeding. This colony during the past 20 years has remained at about the same size that it was during the 1950s and 1960s (cf. Horne 1983, SCAR 2002; B. Wienecke, pers. comm.); there was a hiatus in censusing during the 1970s. 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 Fig. 1), then this might further encourage the recruitment of returning subadults and emigrants. On the other hand, by no means is Pointe Géologie completely isolated (Fig. 1).

Also indirectly contributing to this discussion is the record in the western Ross Sea: Emperor Penguin colonies at Cape Crozier (Ross Island) and Beaufort Island (Kooyman et al. 2007; Fig. A7). The extent of variability in fast ice stability is quite instructive, although the cause is not thinning sea ice and katabatic winds. At Cape Crozier, the colony is situated at the north face of the Ross Ice Shelf where it squeezes by Ross Island in its constant northward growth, and becomes fractured in the process. As a result, this corner breaks back after several years of growth, calving lots of small icebergs and bergy bits. When the Shelf front has retreated well back from of its maximum position (2-3 km), the colony is vulnerable to rafting sea ice, insurmountable pressure ridges 10s of meters high, and early sea-ice break-out as no features lock it in place. In these conditions, breeding success has been low and the colony has remained small or decreased further. 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 slightly 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, owing at the least to high breeding success. The bay was destroyed when crashing large icebergs broke back the ice front in 2001, and the colony decreased severely in size.

At nearby Beaufort Island, the fast ice on which the colony exists is locked in place by icebergs that ground on other parts of the submerged caldera (of which Beaufort Island is part) and offer protection, and stable fast ice on which to breed successfully. The colony's growth pattern has been similar to that at nearby Cape Crozier; whether the two adjacent colonies may be part of a metapopulation, with the well-being of one contributing directly to the other through emigration/immigration, is not presently known.

The growth and variability of other Ross Sea colonies were investigated by Barber-Meyer et al. (2008), but with a record beginning only in 1983. As with the Kooyman et al. (2007) study, these authors analyzed chick counts, which act as a crude proxy of actual colony size because the number of chicks is a function of adult population size, proportion of adults breeding (i.e., effort), and breeding success. Nevertheless, they do indicate trends in relative colony size as indicated in the studies at Pointe Géologie. As with Barbraud and Weimerskirch (2001) and Jenouvrier et al. (2005*a*), Barber-Meyer et al. (2008) for some colonies found the same growth relationships with SIE (positive) and SST (negative). They found a relationship to SAM similar to that described by Ainley et al. (2005) and Massom et al. (2009), and concluded, consistent with the story that emerges from the various other studies of this species, mesoscale rather than large-scale sea-ice patterns are the most important.

*Adélie Penguin response to habitat change.*– Several studies have related population trends of Adélie Penguins to sea-ice variability at a spatio-temporal meso-/decadal-scale consistent with the habitat optimum model (Fraser et al. 1992, Trathan et al. 1996; Wilson et al. 2001; Jenouvrier et al. 2005*c*). Three studies conducted in the Antarctic Peninsula region confirm one side of the bell-shaped curve of the Fraser-Trivelpiece model (see explanation above; Fig. A8), 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 early to late 1970s, when all then began to decrease in accord with decreasing sea-ice season/persistence and extent (cf. Parkinson 2002). According to Stammerjohn et al. (2008), in 1979 the sea ice season off the western Antarctic Peninsula was 365 d long, but by the early years of the 21st century it was at most 270 days including some years when it was zero. In their study area of 182 x 105 $km^2$ (Ducklow et al. 2007), maximum ice decreased an order of magnitude from it being almost entirely covered to one-third covered, at most. All this time Adélie Penguin numbers decreased.

In East Antarctica and the Ross Sea, the situation has been more complex, because there the pattern for some colonies has been steady growth over decades, while for large colonies there has been a subsequent leveling of numbers (e.g., Cape Bird, Cape Crozier; Fig. A9). 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 (Fig. A10). Thus, besides the response to ice conditions at a broader scale some sort of regional-scale 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 sea-ice characteristics in the Ross Sea-East Antarctica sector. The findings of these studies were as follows:

- Wilson et al. (2001) found that for colonies on Ross Island, greater SIE during the winter months reduced colony growth five years later (Fig. A9). These authors surmised that when extensive ice moved the penguins' wintering area north of the southern boundary of the Antarctic Circumpolar Current subadults, in particular, had more difficulty in coping with reduced food availability in those waters and/or were subjected to higher predation. Waters north of the SBACC are depleted in prey compared to those to the south (Tynan 1998, Nicol et al. 2000). The fact that the response did not show up until five years later is related to the average age of recruitment, ~5 years (Ainley 2002).

- Jenouvrier et al. (2005*c*) found similar results for the colony at Pointe Géologie (Fig. A10): population size increased six 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 (i.e., everywhere surrounding the Antarctic continent except the west coast of the Antarctic Peninsula). These results complete the "habitat optimum model" showing growth in colonies as local SIC, in the form of growing polynyas, lessens.

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. 2006*a*, Stammerjohn et al. 2008). The importance of polynyas, as well as the spatial scale at which they are assessed, is particularly evident by the somewhat counter results of a growing, large-scale sea-ice season and SIE in the Ross Sea sector (Zwally et al. 2002, Parkinson 2002, Stammerjohn et al. 2008), but nevertheless, at the same time, growing coastal polynyas at the regional scale.

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 among the number of penguins foraging at any one time and the availability of food within their foraging range (Ballance et al. 2009).

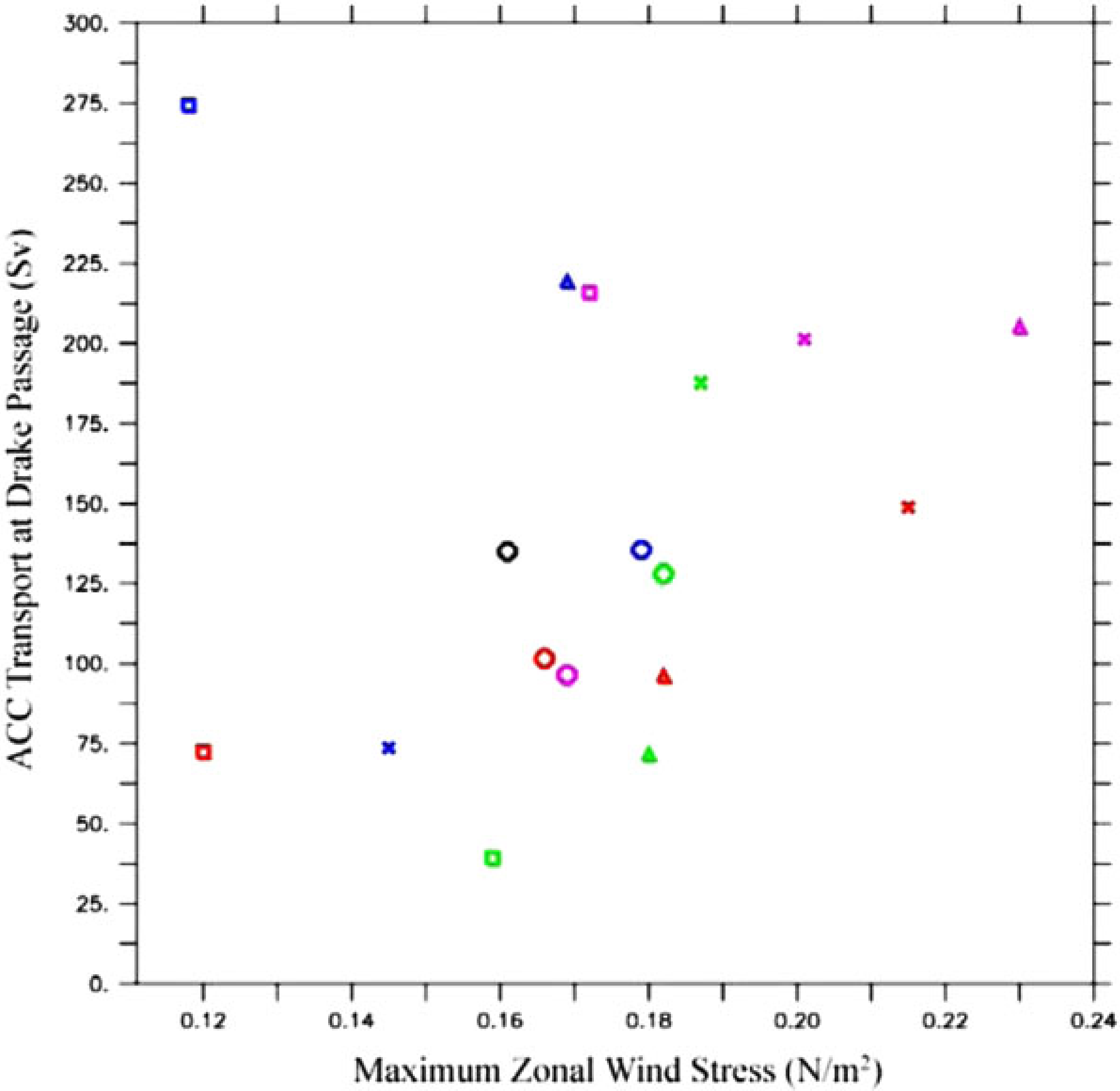


FIG. A1. The maximum zonally-averaged annual-mean wind stress between 70°S and 30°S (N/$m^2$) plotted against the ACC transport at Drake Passage (69°W) for the 20th century. Observed (black circle), GFDL-CM2.1 (blue circle), GFDL-CM2.0 (red circle), CCCMA3.1-T47 (red triangle), CNRM-CM3 (red square), 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.

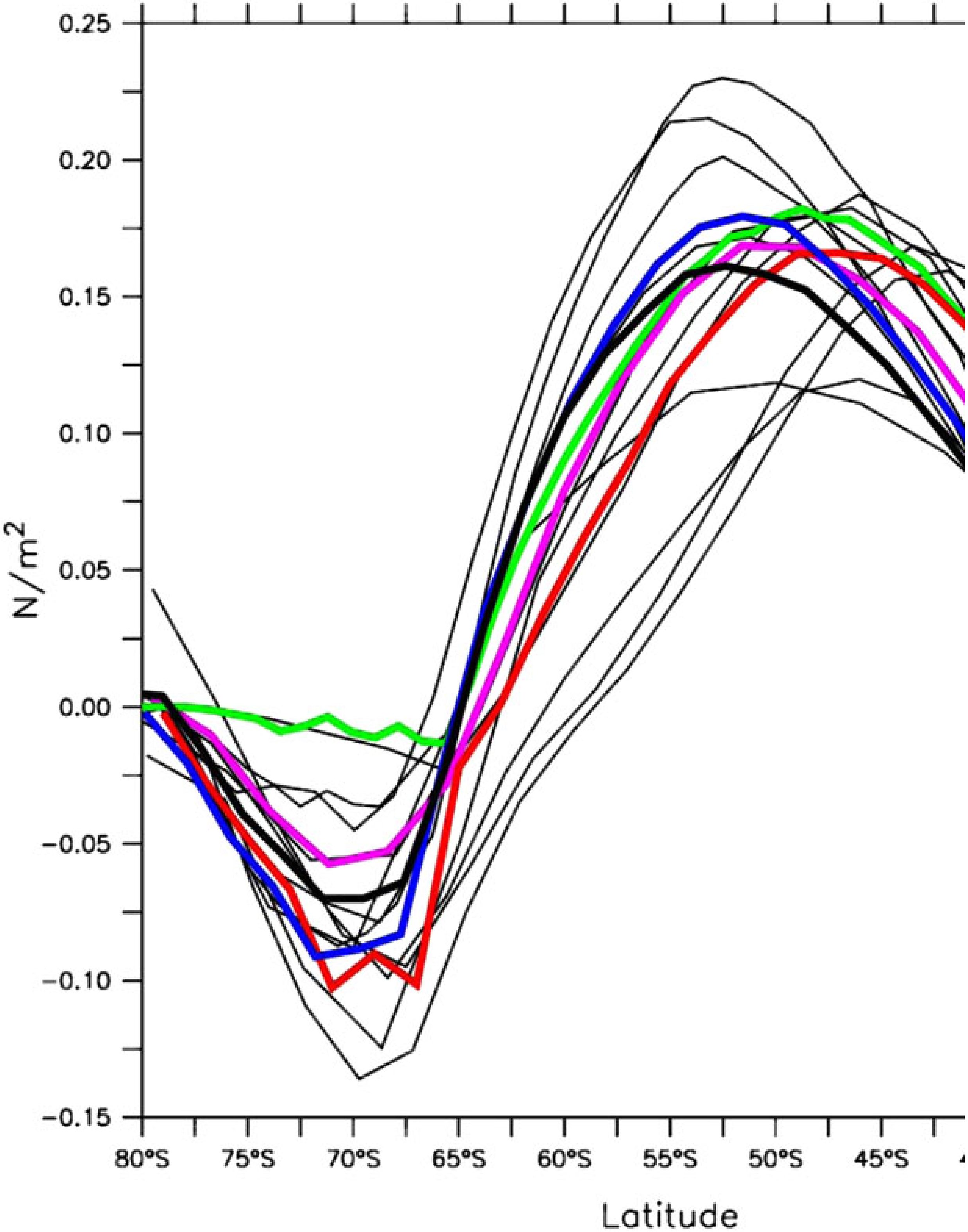
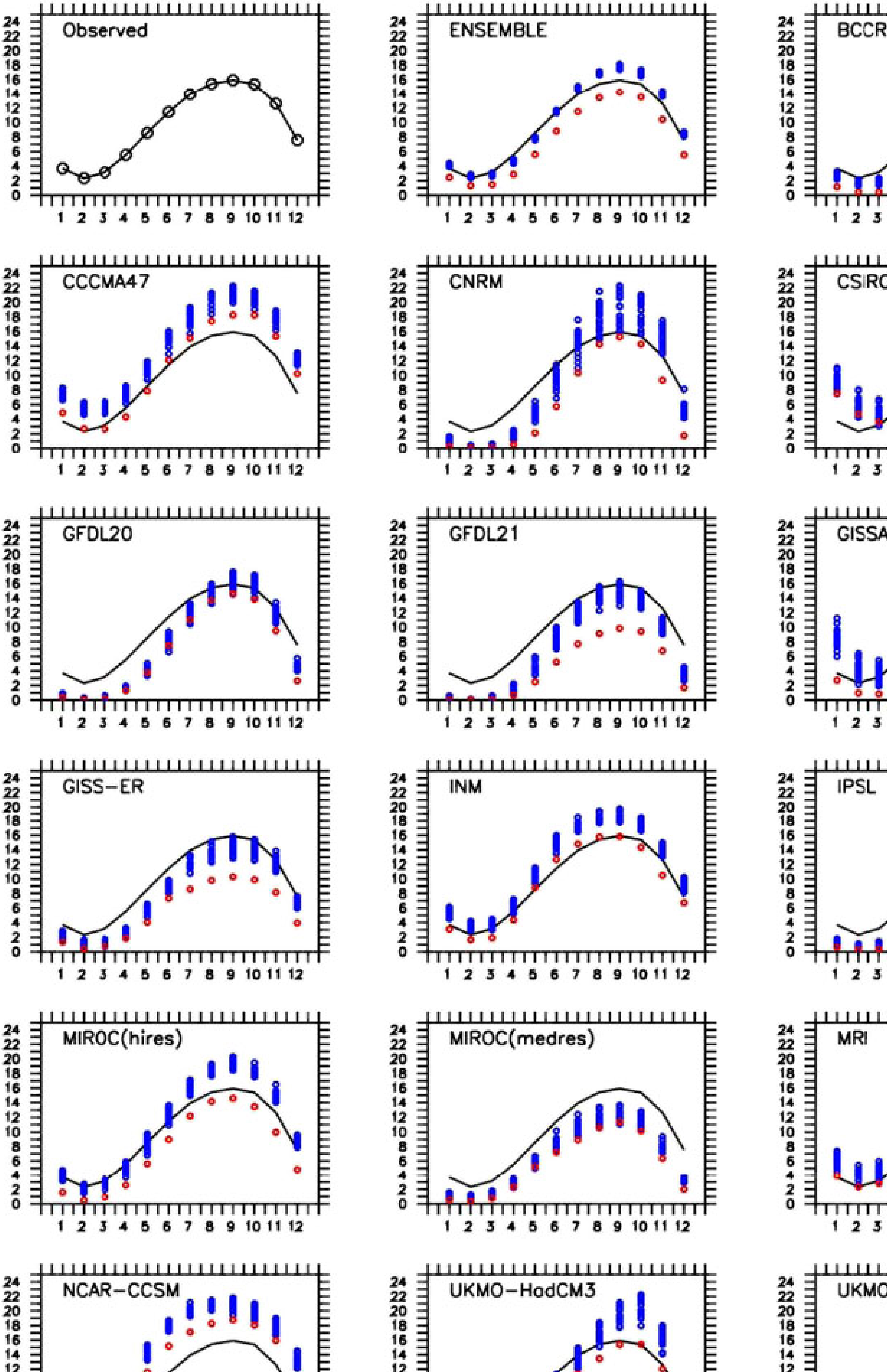

0.25
0.20
0.15
0.10
0.05
0.00
−0.05
−0.10
−0.15
N/m$^2$
80°S
75°S
70°S
65°S
60°S
55°S
50°S
45°S
Latitude

FIG. A2. Zonally-averaged annual mean wind stress (N/m$^2$) for the 20th century. The 20th century annual mean for the model runs is defined as the average of all months between January 1981 and December 2000; wind stress is defined as positive toward the east, so when winds blow from east to west as they do near the Antarctic coast (polar easterlies), the wind stress is negative. Observed long-term mean from National Center for Environmental Prediction (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 eventually 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.


Observed
ENSEMBLE
BCCR
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CNRM
CSIRO
GFDL20
GFDL21
GISSA
GISS-ER
INM
IPSL
MIROC(hires)
MIROC(medres)
MRI
NCAR-CCSM
UKMO-HadCM3
UKMO
0 2 4 6 8 10 12 14 16 18 20 22 24
1 2 3 4 5 6 7 8 9 10 11 12

Fig. A3a. 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 (red).

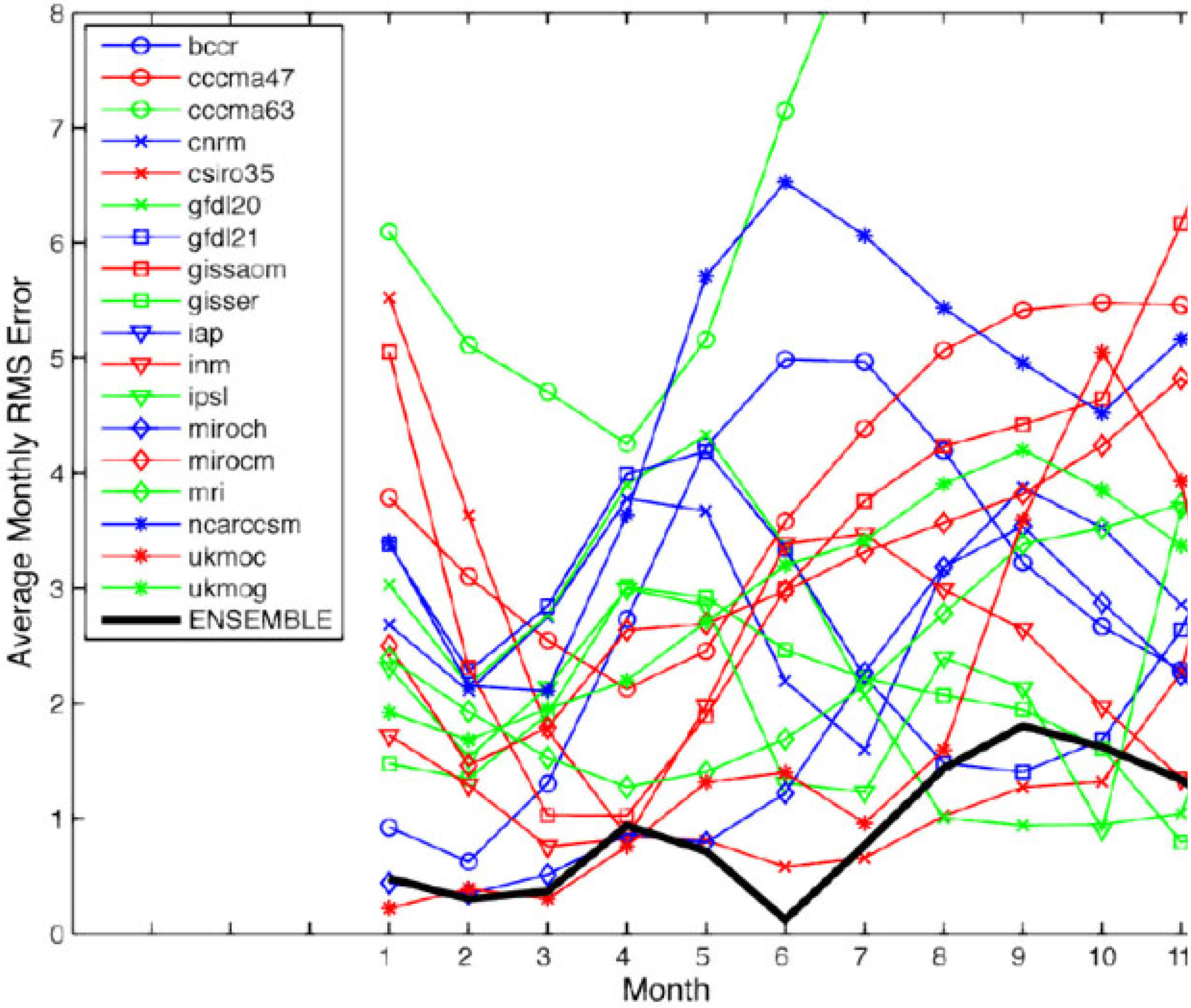

Fig. A3b. the mean RMS error for each month for the total area of Antarctic sea ice for the 20 years of the pre-industrial control experiment, relative to the modern observations. SIC coverage is the percent of grid cells having ice, as function also of time (season) in units of $10^6$ $km^2$.The thick 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.

FIG. A4. The ACC in each of the models considered. It is demarcated by the subtropical front to the north (red) and by the southern boundary close to the continent (blue); boundary definitions taken from Orsi et al. (1995). WOA01 refers to the existing ocean, taken from the World Ocean Atlas (Conkwright et al. 2002); latitude lines are 75°, 60° and 45° S.

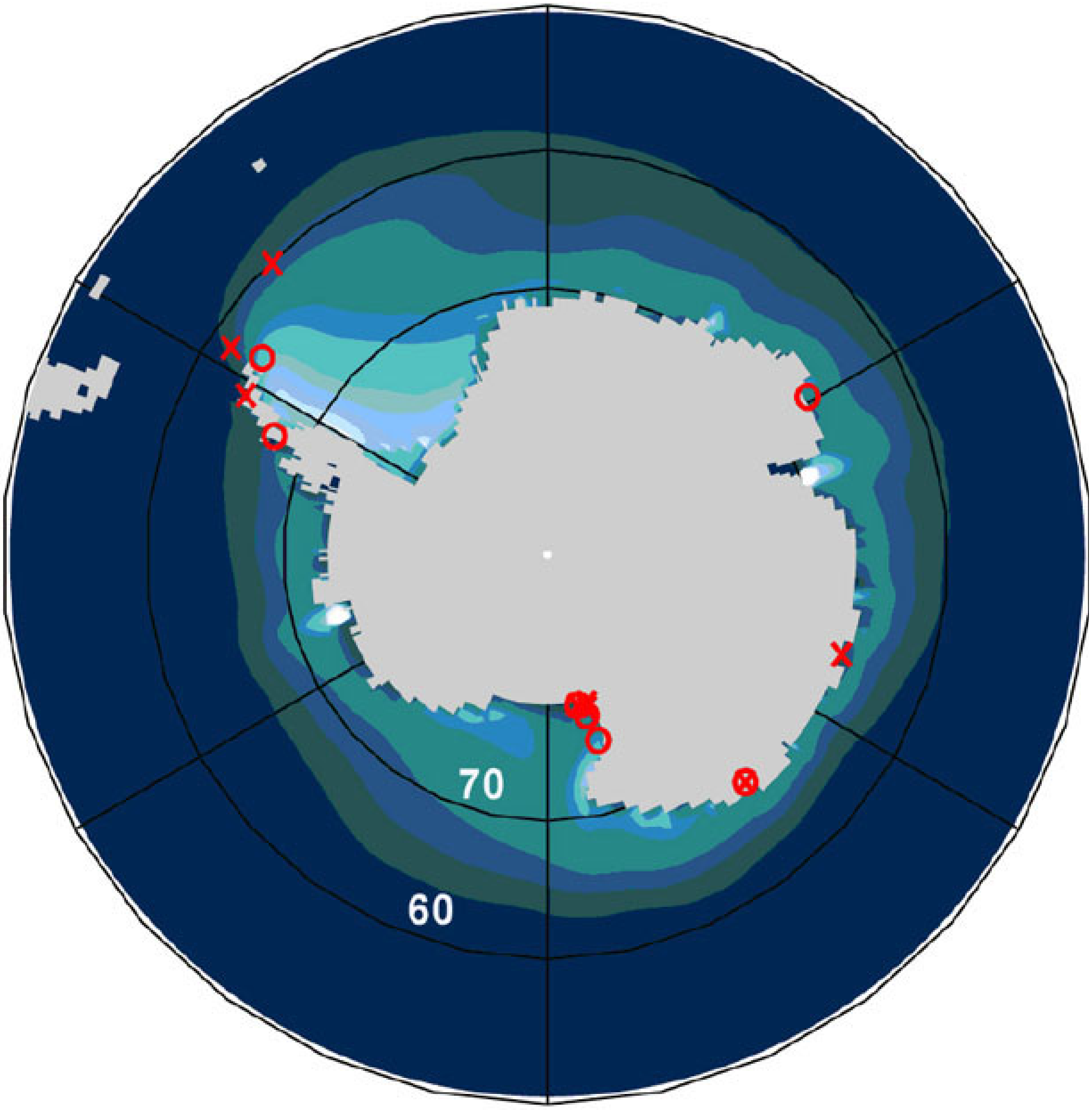

FIG. A5. ENSEMBLE: annual mean sea-ice thickness (m) during the satellite era (1982-2007; compare to Timmermann et al. 2004). Also shown are colonies of Adélie Penguin (X), Emperor Penguin (open O), and locations where both occur, and which are mentioned in the text (see text Figs. 1, 2).

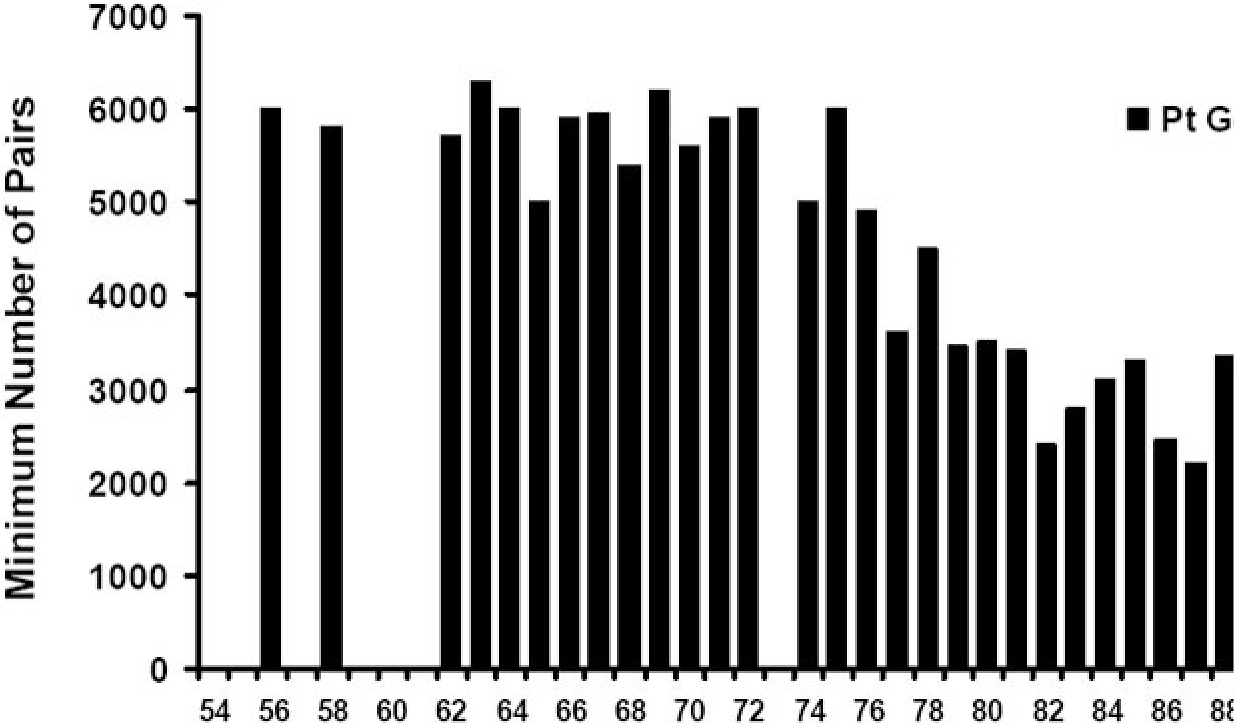

FIG. A6. Minimum numbers of breeding pairs of Emperor Penguins at Pointe Géologie, 1956–1998 (data from Barbraud and Weimerskirch (2001)).

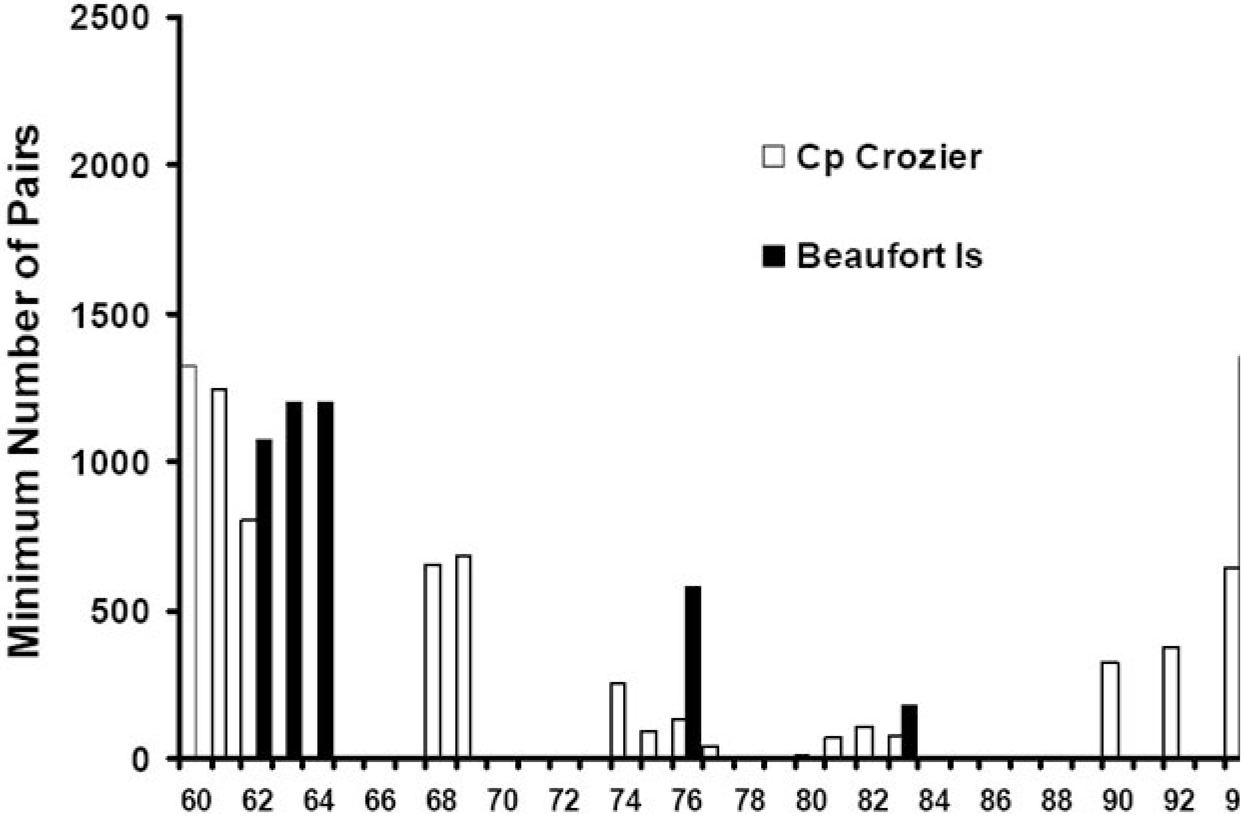

FIG. A7. Numbers of breeding pairs of Emperor Penguins at two colonies in the southern Ross Sea, 1960–2005 - numbers are from chick counts and, therefore, constitute a minimum estimate of breeding population size (from Kooyman et al. 2007).

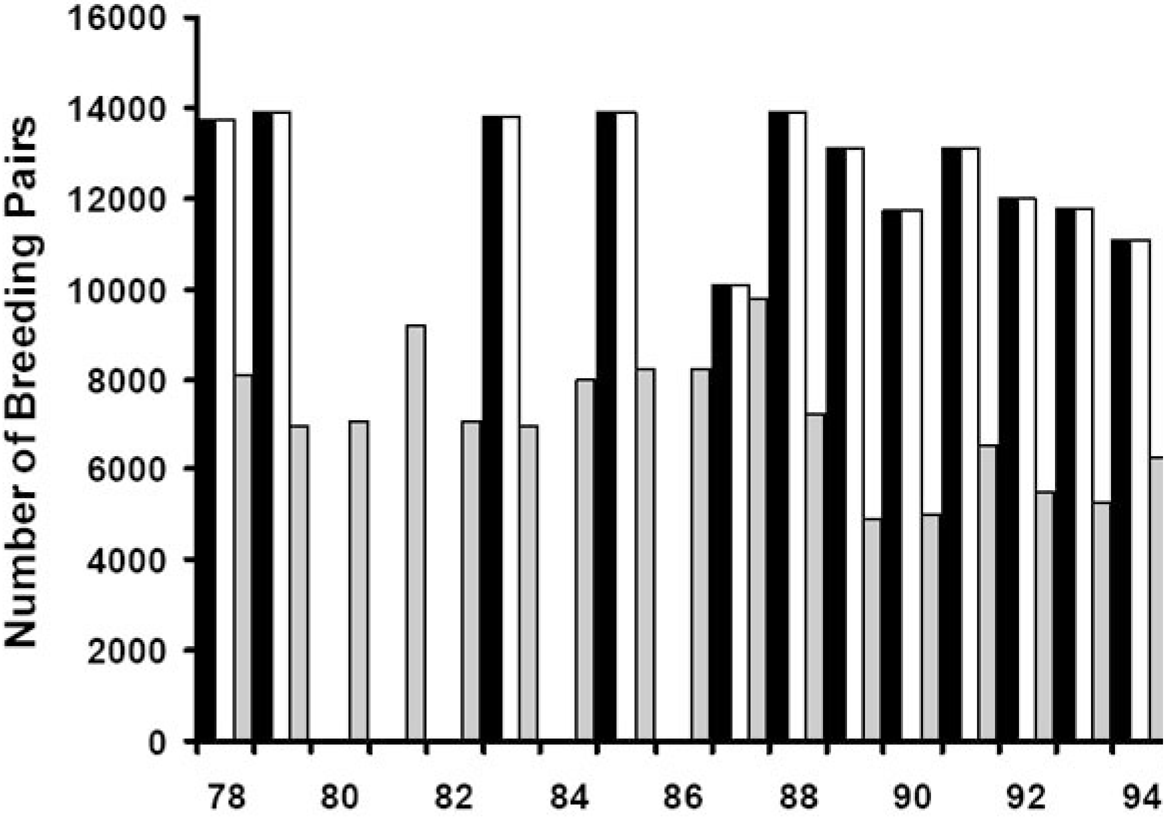

FIG. A8. Numbers of breeding pairs of Adélie Penguin at three colonies along the north and northwest coast of the Antarctic Peninsula: Arthur Harbor (Ducklow et al. 2007), Admiralty Bay (Hinke et al. 2007), and Signy Island (Forcada et al. 2006).

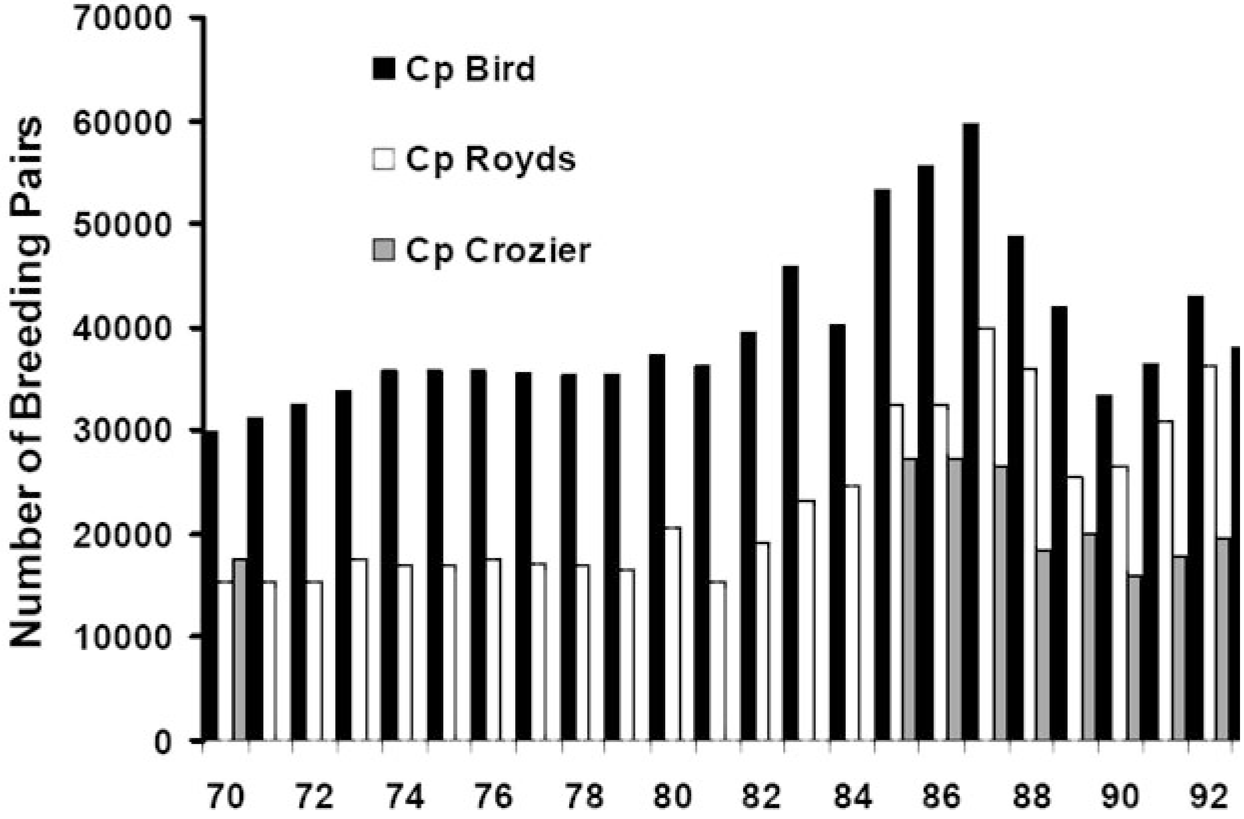

FIG. A9. Numbers of breeding pairs of Adélie Penguins at three colonies in the Ross Sea (Cape Bird, Cape Royds, Cape Crozier East), 1970–2000. Data are from Wilson et al. (2001).

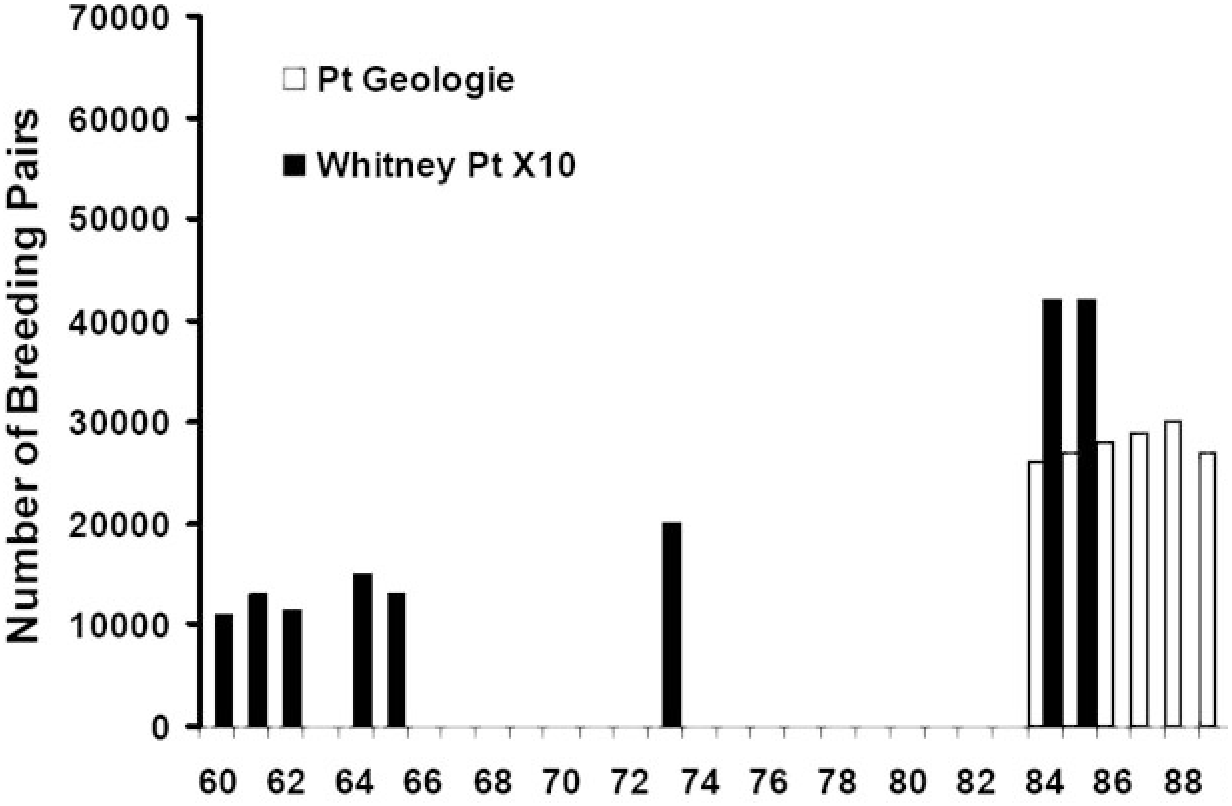

FIG. A10. Numbers of breeding pairs of Adélie Penguins at two colonies in East Antarctica, 1960–2000. Data for Whitney Point are from Woehler et al. (2001), and for Pointe Géologie from Jenouvrier et al. (2005*c*). Those from Whitney Point were multiplied by 10 in order that the trend would show up next to the Pointe Géologie data.

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