CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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

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. 2006a). 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.

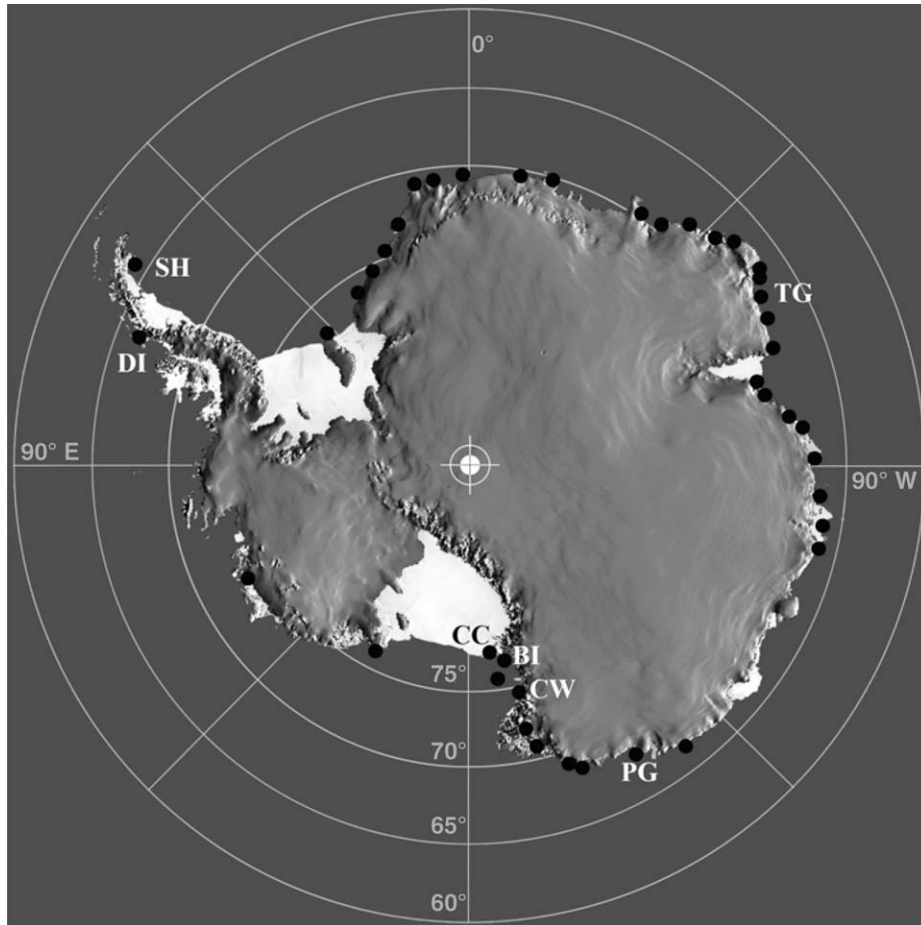Emperor Penguins currently breed in ~40 colonies (see Woehler 1993, Woehler and Croxall 1997; Fig. 1),

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.

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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
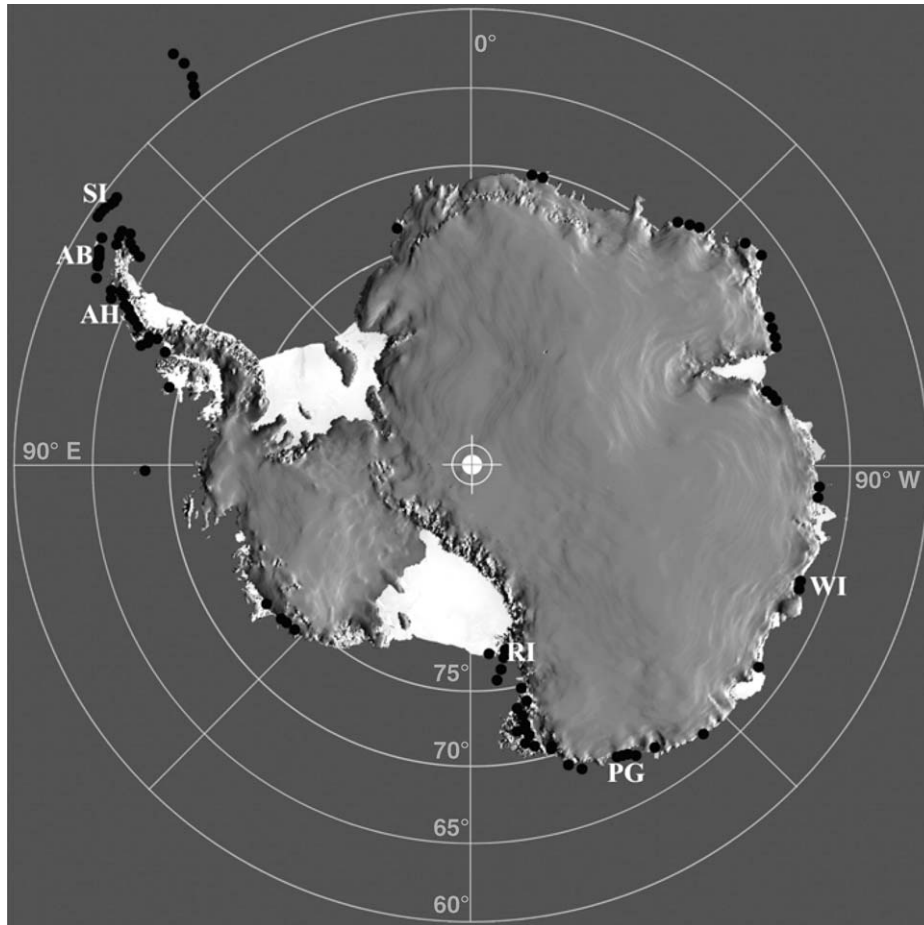
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FIG. 2. The locations of known colonies of Adélie Penguins (*Pygoscelis adeliae*) on Antarctica (data from Woehler [1993]). In areas where colonies are densely concentrated, Antarctic Peninsula and eastern Ross Sea, not all are shown (see detailed 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. 2006a). 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. 2006a, 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. 2005a, 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. 2005b).

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. 2006b). 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).
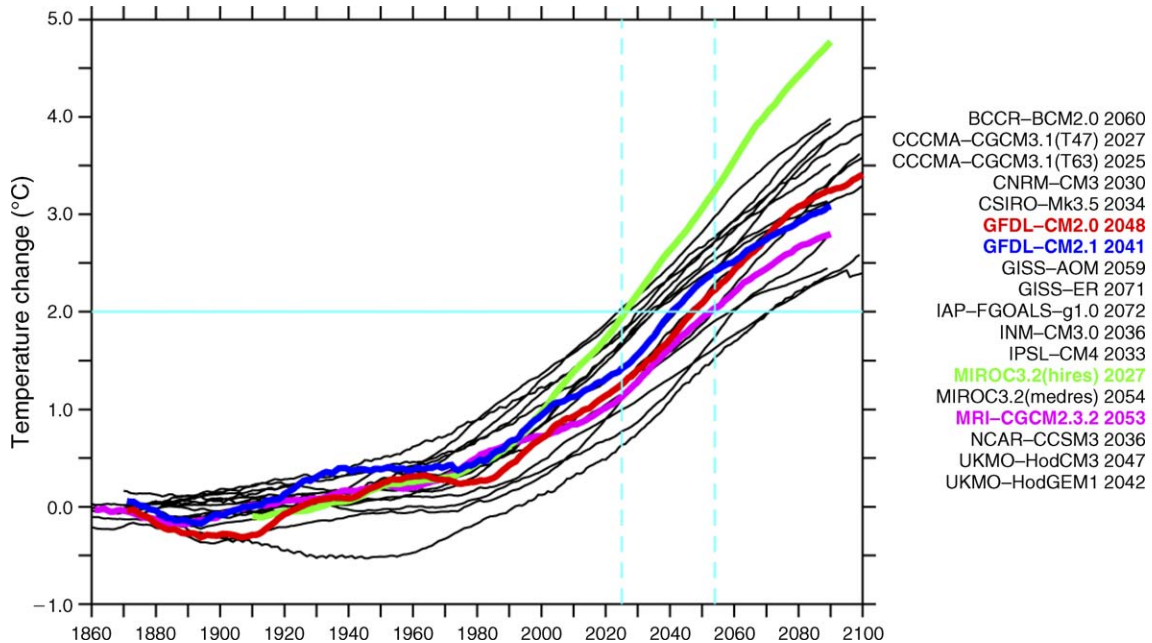
FIG. 3. The globally averaged annual mean air temperature anomaly for each model of the Intergovernmental Panel on Climate Change Fourth Assessment Report (AR4), with each run from the Special Report on Emissions Scenarios (SRES) A1B scenario. As in New (2005), a 21-year running mean filter has been 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
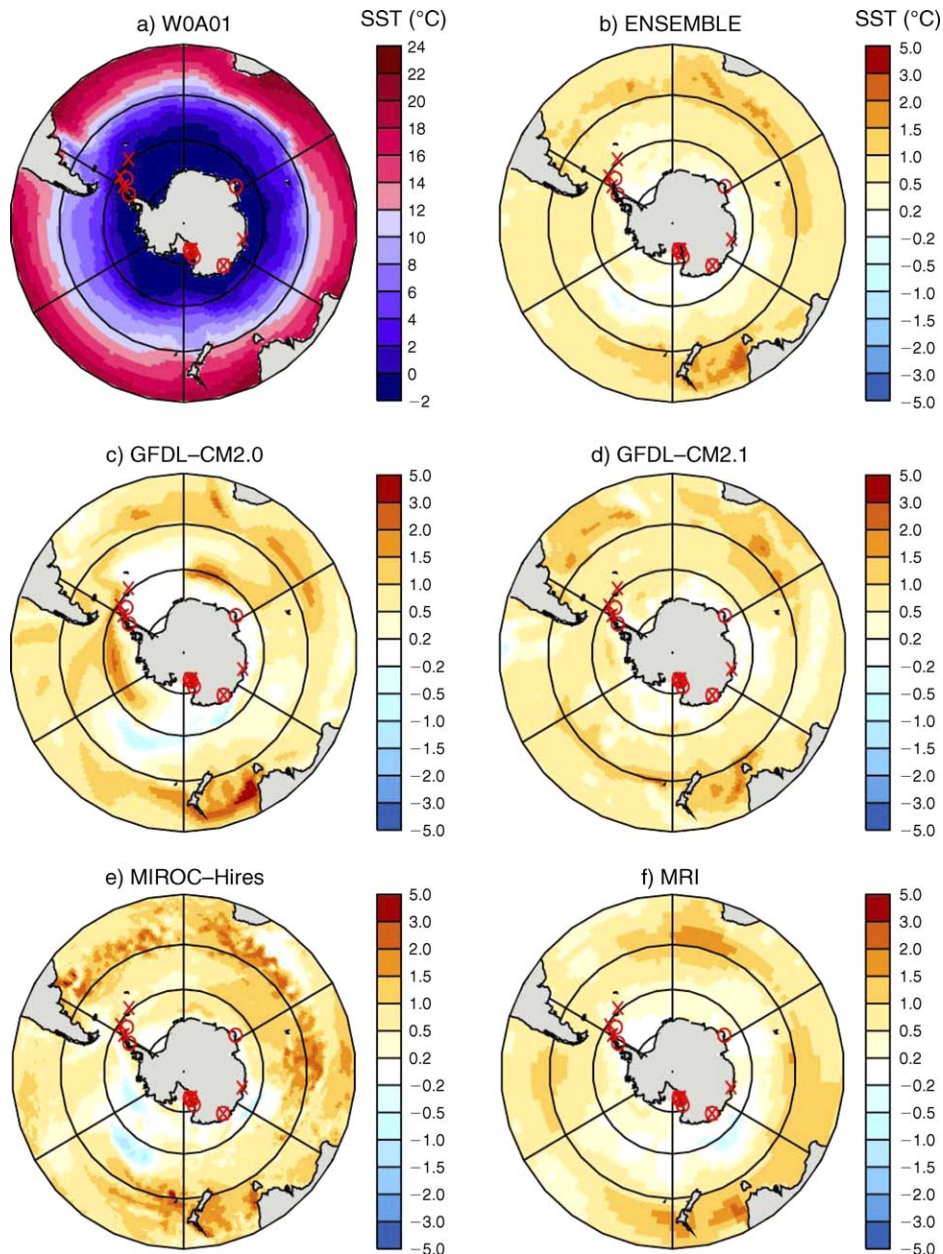
Fig. 4. Sea surface temperatures (SST; °C, 0–100 m average): (a) World Ocean Atlas, observed annual mean (Conkright et al. 2002); (b) ENSEMBLE model, change by the year of 2°C warming relative to the modern era (1981–2000 average); and (c–f) results from each of the four models comprising it. Latitude 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. 2005a, 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.
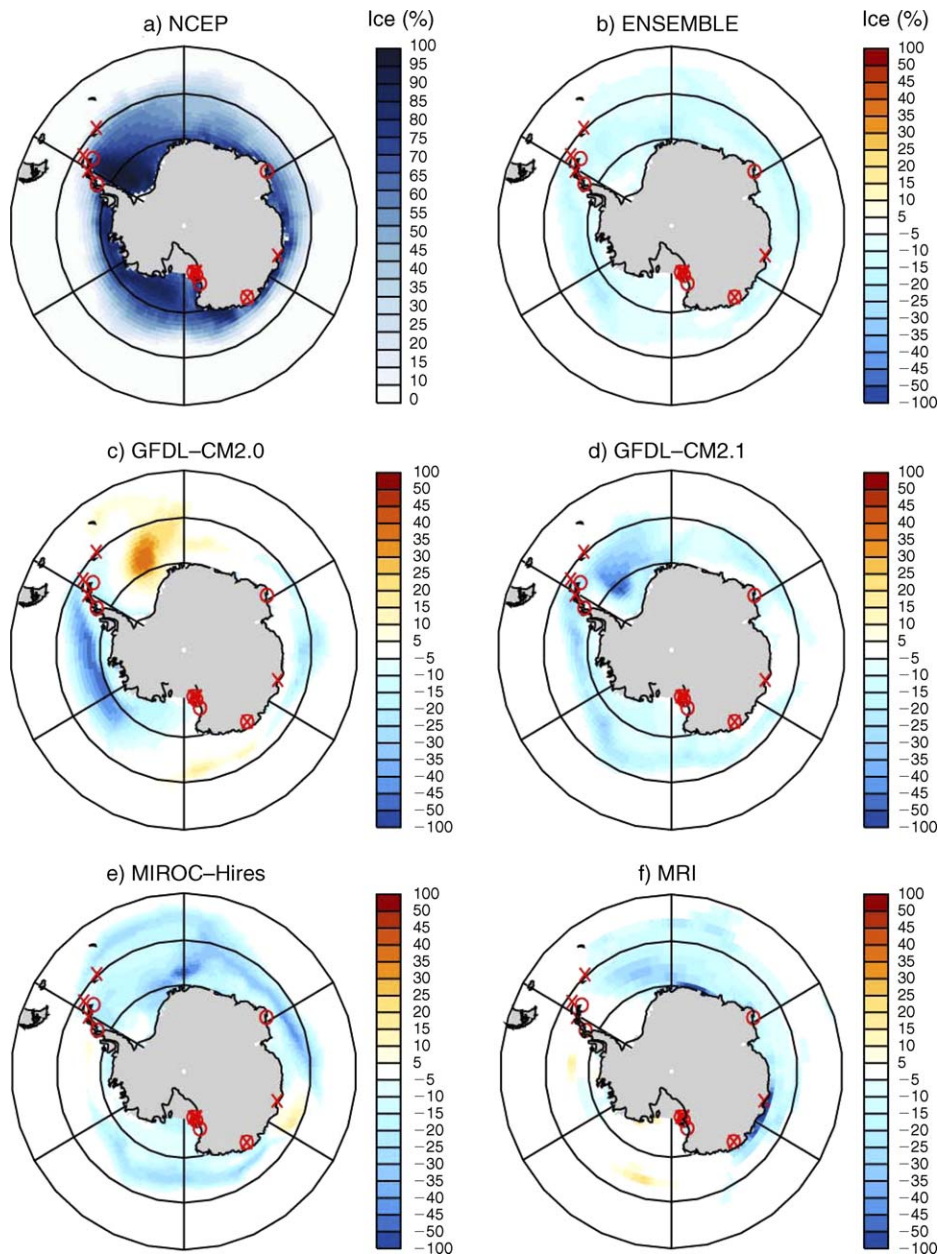
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FIG. 5. Sea ice coverage (%): (a) National Center for Environmental Prediction (NCEP), observed annual mean (Conkright et al. 2002); (b) ENSEMBLE model, change by the year of 2°C warming relative to the modern era (1981–2000 average); and (c–f) results 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-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
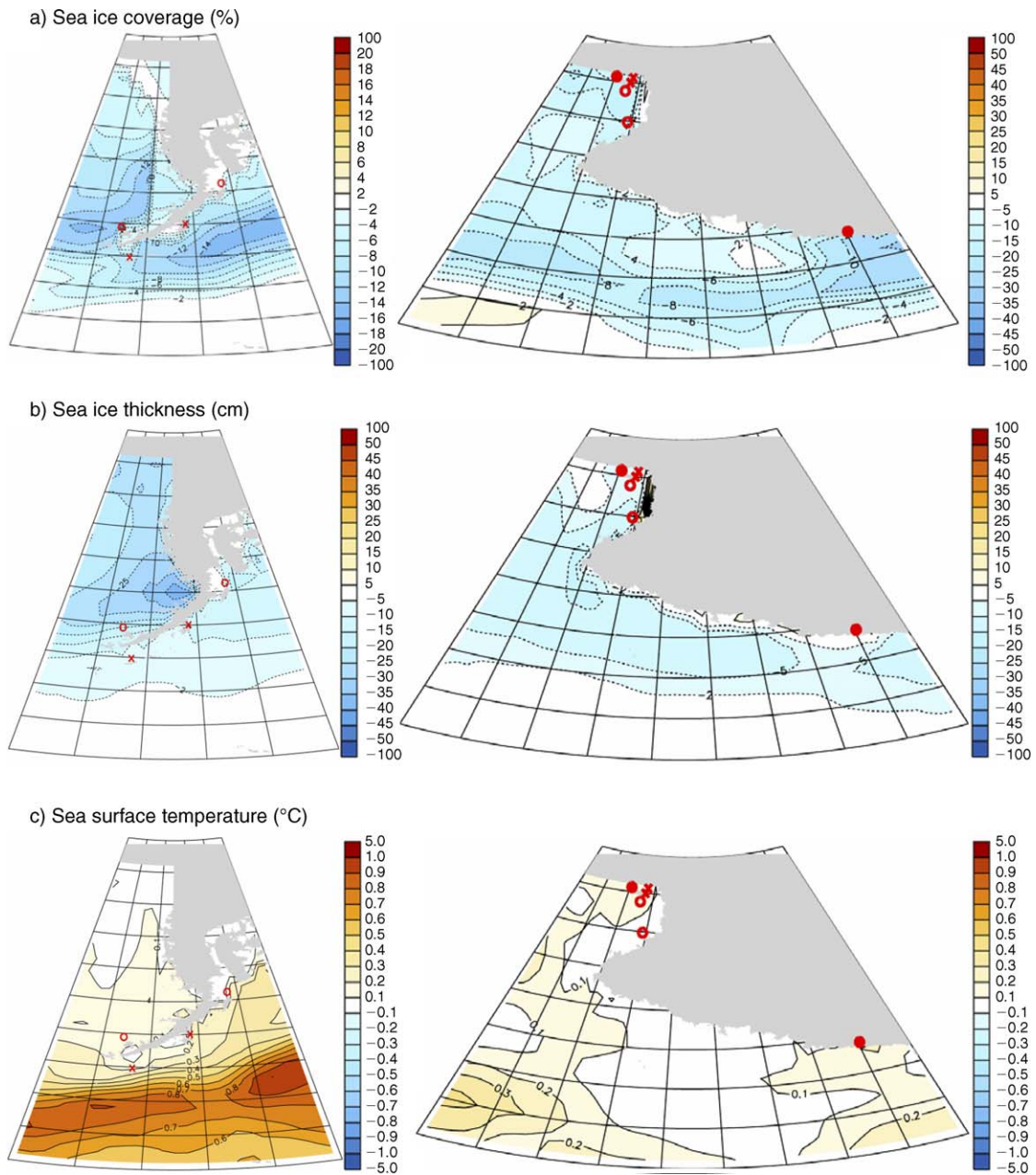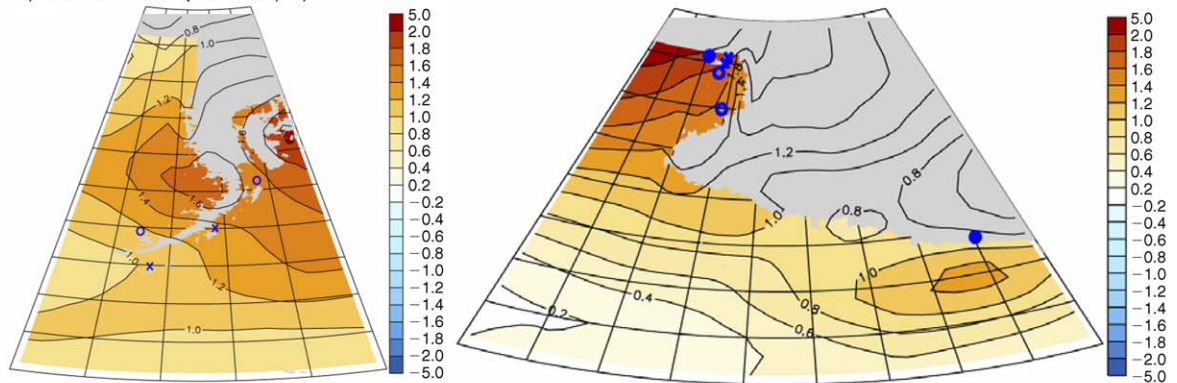
a) Sea ice coverage (%)

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.
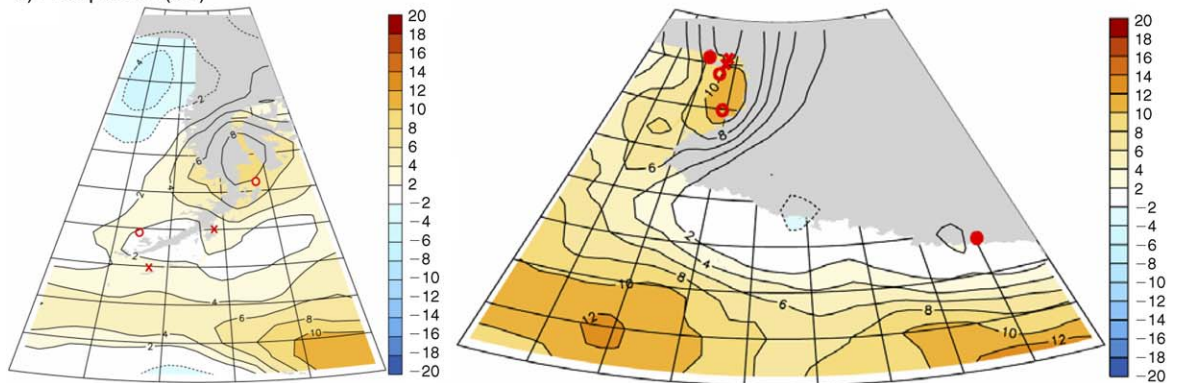
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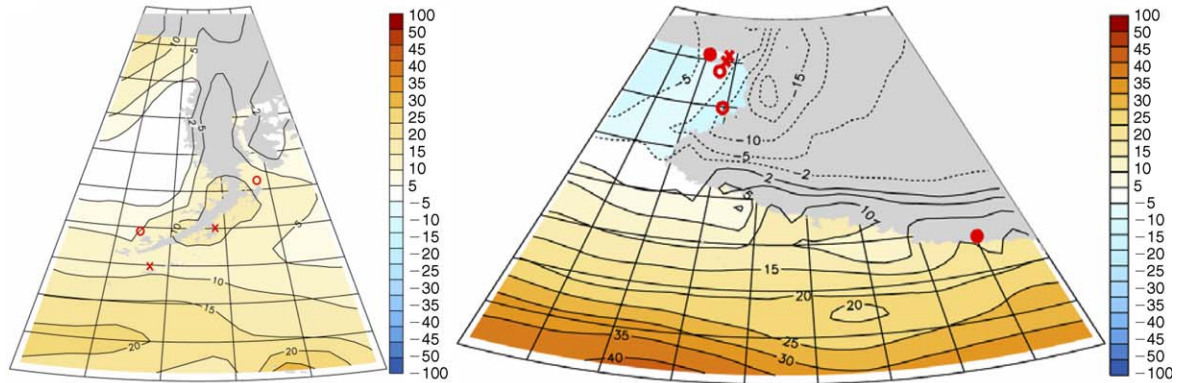
FIG. 7. ENSEMBLE model: simulated change in annual mean (a) zonal wind stress (note that due to the orientation of the figure a positive change means a greater stress directed toward the left/east of the figure); (b) surface air temperature; and (c) precipitation. Penguin colonies and the area shown 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
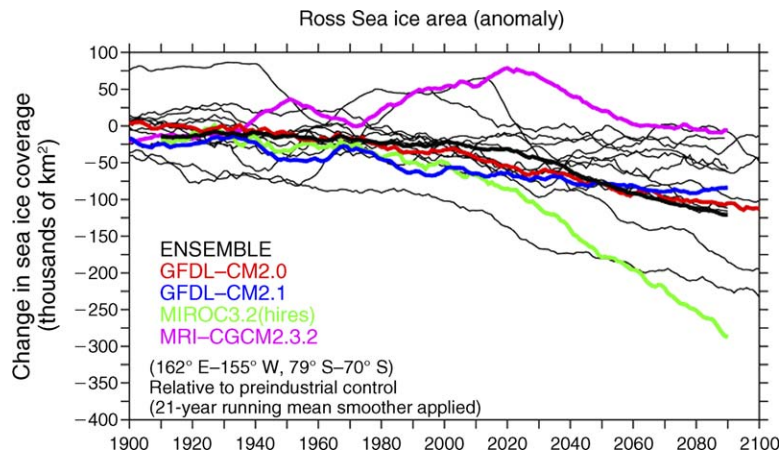
Fig. 8. Change in annual mean sea ice coverage over the Ross Sea relative to the preindustrial annual mean for the ENSEMBLE model (thick black line) and for each model of the Intergovernmental Panel on Climate Change Fourth Assessment Report (AR4). The colored lines indicate models included in our ENSEMBLE 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
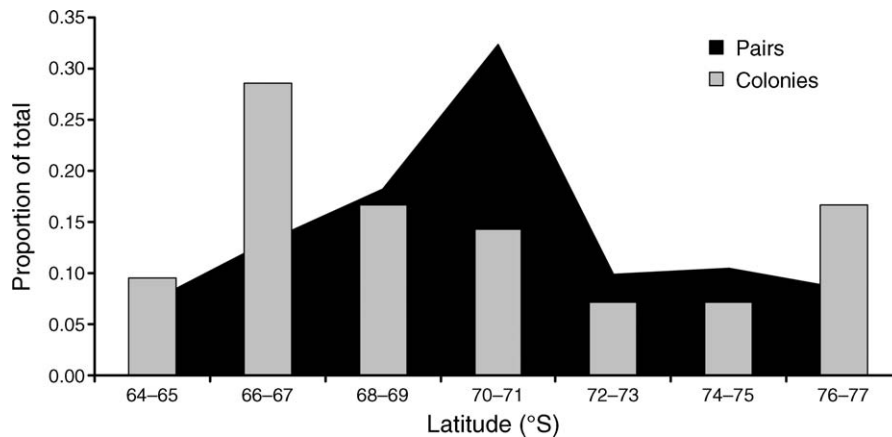
FIG. 9. Proportions of the total number of current Emperor Penguin colonies ($n = 42$) and breeding pairs (248 000) by latitude (data from Woehler [1993] and Woehler and Croxall [1997]).

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),
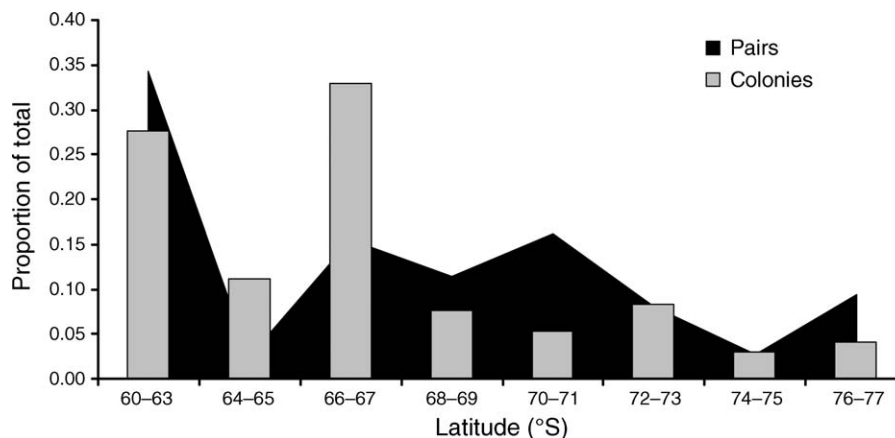

FIG. 10. Proportions of the total number of the current Adélie Penguin colonies ($n = 170$) and of breeding pairs (3 million) by latitude (data from Woehler [1993] and Woehler and Croxall [1997]).

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. 2005a, 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. 2005a) 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.

Literature Cited

Ainley, D. G. 2002. The Adélie Penguin: bellwether of climate change. Columbia University Press, New York, New York, USA.

Ainley, D. G., and L. K. Blight. 2008. Ecological repercussions of historical fish extraction from the Southern Ocean. Fish and Fisheries 9:1–26.

Ainley, D. G., E. D. Clarke, K. Arrigo, W. R. Fraser, A. Kato, K. J. Barton, and P. R. Wilson. 2005. Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. Antarctic Science 17:171–182.

Ainley, D. G., C. A. Ribic, G. Ballard, S. Heath, I. Gaffney, B. J. Karl, K. R. Barton, P. R. Wilson, and S. Webb. 2004. Geographic structure of Adélie Penguin populations: size,

overlap and use of adjacent colony-specific foraging areas. Ecological Monographs 74:159–178.

Ainley, D. G., C. A. Ribic, and W. R. Fraser. 1994. Ecological structure among migrant and resident seabirds of the Scotia–Weddell Confluence region. Journal of Animal Ecology 63:347–364.

Ainley, D. G., et al. 2007. Paradigm lost, or, is top-down forcing no longer significant in the Antarctic Marine Ecosystem? Antarctic Science 19:283–290.

Ancel, A., G. L. Kooyman, P. J. Ponganis, J.-P. Gender, J. Lignon, X. Mestre, N. Huin, P. H. Thorson, P. Robisson, and Y. Le Maho. 1992. Foraging behavior of Emperor Penguins as a resource detector in winter and summer. Nature 360:336–339.

Arrigo, K. R., and G. L. van Dijken. 2003. Phytoplankton dynamics within 37 Antarctic coastal polynya systems. Journal of Geophysical Research 108:3271.

Atkinson, A., V. Siegel, E. Pakhomov, and P. Rothery. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432:100–103.

Ballance, L., R. L. Pitman, R. P. Hewitt, D. B. Siniff, W. Z. Trivelpiece, P. J. Clapham, and R. L. Brownell, Jr. 2006. The removal of large whales from the Southern Ocean: Evidence for long-term ecosystem effects? Pages 215–230 in J. A. Estes, D. P. Demaster, D. F. Doak, T. E. Williams, and R. L. Brownell, Jr., editors. Whales, whaling and ocean ecosystems. University of California Press, Berkeley, California, USA.

Barber, D. G., and R. A. Massom. 2007. The role of sea ice in Arctic and Antarctic polynyas. Pages 1–54 in W. O. Smith and D. G. Barber, editors. Polynyas: windows to the world. Elsevier, London, UK.

Barbraud, C., and H. Weimerskirch. 2001. Emperor penguins and climate change. Nature 411:183–186.

Barbraud, C., and H. Weimerskirch. 2006. Antarctic birds breed later in response to climate change. Proceedings of the National Academy of Sciences USA 103:6248–6251.

Baroni, C., and G. Orombelli. 1994. Abandoned penguin colonies as Holocene paleoclimatic indicators in Antarctica. Geology 22:23–26.

Beaumont, L. J., L. Hughes, and A. J. Pitman. 2008. Why is the choice of future climate scenarios for species distribution modelling important? Ecology Letters 11:1135–1146.

Branch, T. A. 2006. Humpback abundance south of 60°S from three completed sets of IDCR/SOWER circumpolar surveys. Paper SC/A06/HW6. International Whaling Commission, Cambridge, UK.

Bricher, P. K., A. Lucieer, and E. J. Woehler. 2008. Population trends of Adélie penguin (Pygoscelis adeliae) breeding colonies: a spatial analysis of the effects of snow accumulation and human activities. Polar Biology. [doi: 10.1007/s00300-008-0479-z]

Cheung, W. W. L., V. W. Y. Lam, and D. Pauly. 2008. Modelling present and climate-shifted distribution of marine fishes and invertebrates. Fisheries Centre Research Report 16(3). University of British Columbia, Vancouver, British Columbia, Canada.

Conkright, M. E., R. A. Locarnini, H. E. Garcia, T. D. O'Brien, T. P. Boyer, C. Stephens, and J. I. Antonov. 2002. World ocean atlas 2001: objective analyses, data statistics, and figures. CD-ROM. National Oceanographic Data Center, Silver Spring, Maryland, USA.

Croxall, J. P., P. N. Trathan, and E. J. Murphy. 2002. Environmental change and Antarctic seabird populations. Science 297:1510–1514.

Deibel, D., and K. L. Daly. 2007. Zooplankton processes in Arctic and Antarctic polynyas. Pages 271–322 in W. O. Smith, Jr. and D. G. Barber, editors. Polynyas: windows to the world. Elsevier, London, UK.

Dewasmes, G., Y. Le Maho, A. Cornet, and R. Groscolas. 1980. Resting metabolic rate and cost of locomotion in long-

Concepts & Synthesis

term fasting Emperor Penguins. Journal of Applied Physiology 49:888–896.

Ducklow, H. W., K. Baker, D. G. Martinson, L. B. Quetin, R. M. Ross, R. C. Smith, S. E. Stammerjohn, M. Vernet, and W. R. Fraser. 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. Philosophical Transactions of the Royal Society B 362:67–94.

Elith, J. et al. 2006. Novel methods improve prediction of species distributions from occurrence data. Ecography 29: 129–151.

Emslie, S. D. 2001. Radiocarbon dates from abandoned penguin colonies in the Antarctic Peninsula region. Antarctic Science 13:289–295.

Emslie, S. D., P. A. Berkman, D. G. Ainley, L. Coats, and M. Polito. 2003. Late-Holocene initiation of ice-free ecosystems in the southern Ross Sea, Antarctica. Marine Ecology Progress Series 262:19–25.

Emslie, S. D., L. Coats, and K. Licht. 2007. A 45,000 yr record of Adélie penguins and climate change in the Ross Sea, Antarctica. Geology 35:61–64.

Emslie, S. D., and J. D. McDaniel. 2002. Adélie penguin diet and climate change during the middle to late Holocene in northern Marguerite Bay, Antarctic Peninsula. Polar Biology 25:222–229.

Emslie, S. D., and W. P. Patterson. 2007. Abrupt recent shift in δ^{13}C and δ^{15}N values in Adélie penguin eggshell in Antarctica. Proceedings of the National Academy of Sciences USA 104:11666–11669.

Europa. 2007. Limiting global climate change to 2 degrees Celsius. European Union Affairs Memo 07/16. Europa, Brussels, Belgium. ⟨http://europa.eu/rapid/pressReleasesAction. do?reference=MEMO/07/16⟩

Forcada, J., P. N. Trathan, and E. J. Murphy. 2008. Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. Global Change Biology 14:2473–2488.

Forcada, J., P. N. Trathan, K. Reid, E. J. Murphy, and J. P. Croxall. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. Global Change Biology 12:411–423.

Fraser, W. R., and D. L. Patterson. 1997. Human disturbance and long-term changes in Adélie penguin populations: a natural experiment at Palmer Station, Antarctica. Pages 445–452 in B. Battaglia, J. Valencia, and D. W. H. Walton, editors. Antarctic communities: species, structure and survival. Cambridge University Press, Cambridge, UK.

Fraser, W. R., and W. Z. Trivelpiece. 1996. Factors controlling the distribution of seabirds: winter–summer heterogeneity in the distribution of Adélie penguin populations. Antarctic Research Series 70:257–272.

Fraser, W. R., W. Z. Trivelpiece, D. G. Ainley, and S. G. Trivelpiece. 1992. Increases in Antarctic penguin populations: Reduced competition with whales or a loss of sea ice due to environmental warming? Polar Biology 11:525–531.

Gloersen, P., W. J. Campbell, D. J. Cavalieri, J. C. Comiso, C. L. Parkinson, and H. J. Zwally. 1992. Arctic and Antarctic sea ice, 1978–1987: satellite passive-microwave observations and analysis. NASA SP-511. National Aeronautics and Space Administration, Washington, D.C., USA.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecological Letters 8:993–1009.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.

Hibler, W. D., III, and S. F. Ackley. 1983. Numerical simulation of the Weddell Sea pack ice. Journal of Geophysical Research 88:2873–2887.

Hinke, J. T., K. Salwicka, S. G. Trivelpiece, G. M. Watters, and W. Z. Trivelpiece. 2007. Divergent responses of Pygoscelis

penguins reveal a common environmental driver. Oecologia 153:845–855.

IPCC. 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Jacobs, S. S., and J. C. Comiso. 1989. Sea ice and oceanic processes on the Ross Sea continental shelf. Journal of Geophysical Research 94:18195–18211.

Jacobs, S. S., and C. F. Giulivi. 1998. Interannual ocean and sea ice variability in the Ross Sea. Antarctic Research Series 75:135–150.

Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2005a. Long-term contrasted responses to climate of two Antarctic seabird species. Ecology 86:2889–2903.

Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2005b. Sea ice affects the population dynamics of Adélie penguins in Terre Adélie. Polar Biology. [doi: 10.1007/s00300-005-0073-6]

Jenouvrier, S., H. Caswell, C. Barbraud, M. Holland, J. Stœve, and H. Weimerskirch. 2009. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. Proceedings of the National Academy of Sciences USA 106:1844–1847.

Jenouvrier, S., H. Weimerskirch, C. Barbraud, Y.-H. Park, and B. Cazelles. 2005c. Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked to climate. Proceedings of the Royal Society B 272:887–895.

Jouventin, P. 1974. Mortality parameters in Emperor Penguins Aptenodytes forsteri. Pages 434–446 in B. Stonehouse, editor. The biology of penguins. Macmillan, London, UK.

Kirkwood, R., and G. Robertson. 1997. The foraging of female emperor penguins during winter. Ecological Monographs 67: 155–176.

Kooyman, G. L. 2002. Evolutionary and ecological aspects of some Antarctic and sub-Antarctic penguin distributions. Oecologia 130:485–495.

Kooyman, G. L., E. C. Hunke, S. F. Ackley, R. P. van Dam, and G. Robertson. 2000. Moult of the emperor penguin: travel, location, and habitat selection. Marine Ecology Progress Series 204:269–277.

Kwok, R., and J. C. Comiso. 2002. Southern Ocean climate and sea ice anomalies associated with the Southern Oscillation. Journal of Climate 15:487–501.

La Mesa, M., J. T. Eastman, and M. Vacchi. 2004. The role of notothenioid fish in the foodweb of the Ross Sea shelf waters: a review. Polar Biology 27:321–338.

Lea, M.-A., and T. Soper. 2005. Discovery of the first Emperor Penguin Aptenodytes forsteri colony in Marie Byrd Land, Antarctica. Marine Ornithology 33:59–60.

Le Bohec, C., J. M. Durant, M. Gauthier-Clerc, N. C. Stenseth, Y.-H. Park, R. Pradel, D. Grémillet, J.-P. Gendner, and Y. Le Maho. 2008. King penguin population threatened by Southern Ocean warming. Proceedings of the National Academy of Sciences USA 105:2493–2497.

Lefebvre, W., and H. Goosse. 2008. Analysis of the projected regional sea-ice changes in the Southern Ocean during the twenty-first century. Climate Dynamics 30:59–76.

Lescroël, A., K. M. Dugger, G. Ballard, and D. G. Ainley. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. Journal of Animal Ecology 78:798–806.

Lishman, G. S. 1985. The comparative breeding biology of Adelie and Chinstrap penguin Pygoscelis adeliae and P. antarctica at Signy Island, South Orkney Islands. Ibis 127: 84–99.

Massom, R. A., P. T. Harris, K. J. Michael, and M. J. Potter. 1998. The distribution and formative processes of latent-heat polynyas in East Antarctica. Annals of Glaciology 27:420–426.

Massom, R. A. et al. 2006. Extreme anomalous atmospheric circulation in the West Antarctic Peninsula region in Austral

spring and summer 2001/02, and its profound impact on sea ice and biota. Journal of Climate 19:3544–3571.

McCartney, M. S. 1977. Subantarctic mode water. Pages 103–119 *in* M. Angel, editor. A voyage of discovery: George Deacon 70th anniversary volume. Elsevier, New York, New York, USA.

New, M. G. 2005. Arctic climate change with a 2°C global warming. Pages 1–15 *in* L. D. Rosentrater, editor. Evidence and implications of dangerous climate change in the Arctic. World Wildlife Fund, Oslo, Norway.

Österblom, H., S. Hansson, U. Larsson, O. Hjerne, F. Wulff, R. Elmgren, and C. Folke. 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. Ecosystems 10:877–889.

Parish, T. R., and J. J. Cassano. 2003. The role of katabatic winds on the Antarctic surface wind regime. Monthly Weather Review 131:317–333.

Parkinson, C. L. 2002. Trends in the length of the Southern Ocean sea ice season, 1979–99. Annals of Glaciology 34:435–440.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Parry, M., J. Palutikof, C. Hanson, and J. Lowem. 2008. Squaring up to reality. Nature Reports 2:68–70.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Perkins, S., A. Pitman, N. Holbrook, and J. McAveney. 2007. Evaluation of the AR4 climate models—simulated daily maximum temperature, minimum temperature and precipitation over Australia using probability density functions. Journal of Climate 20:4356–4376.

Peterson, R. G., and T. Whitworth III. 1989. The subantarctic and polar fronts in relation to deep water masses through the southwestern Atlantic. Journal of Geophysical Research 94:10817–10838.

Piola, A. R., and A. L. Gordon. 1989. Intermediate waters in the southwest South Atlantic. Deep Sea Research, Part A 36:1–16.

Russell, J. L., K. W. Dixon, A. Gnanadesikan, R. J. Stouffer, and J. R. Toggweiler. 2006*a*. The Southern Hemisphere westerlies in a warming world: propping open the door to the deep ocean. Journal of Climate 19:6382–6390.

Russell, J. L., R. J. Stouffer, and K. W. Dixon. 2006*b*. Intercomparison of the southern ocean circulations in IPCC coupled model control simulations. Journal of Climate 19:4560–4575.

Siniff, D. B., R. A. Garrott, J. J. Rotella, W. R. Fraser, and D. G. Ainley. 2008. Projecting the effects of environmental change on Antarctic seals. Antarctic Science 20:425–435.

Smith, R. C., E. Domack, S. Emslie, W. R. Fraser, D. G. Ainley, K. Baker, J. Kennett, A. Leventer, E. Mosley-Thompson, S. Stammerjohn, and M. Vernet. 1999. Marine ecosystem sensitivity to historical climate change: Antarctic Peninsula. BioScience 49:393–404.

Stammerjohn, S. E., D. G. Martinson, R. C. Smith, X. Yuan, and D. Rind. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability. Journal of Geophysical Research 113:C03S90.

Thatje, S., C.-D. Hillenbrand, A. Mackensen, and R. Larter. 2008. Life hung by a thread: endurance of Antarctic fauna in glacial periods. Ecology 89:682–692.

Thompson, D. W. J., and S. Solomon. 2002. Interpretation of recent Southern Hemisphere climate change. Science 296:895–899.

Todd, F. S., S. Adie, and J. F. Splettstoesser. 2004. First ground visit to the Emperor Penguin *Aptenodytes forsteri* colony at Snow Hill Island, Weddell Sea, Antarctica. Marine Ornithology 32:193–194.

Trivelpiece, W. Z., S. G. Trivelpiece, and N. K. Volkman. 1987. Ecological segregation of Adelie, Gentoo, and Chinstrap penguins at King George Island, Antarctica. Ecology 68:351–361.

Volkman, N. K., and W. Z. Trivelpiece. 1981. Nest-site selection among Adélie, Chinstrap and Gentoo Penguins in mixed species rookeries. Wilson Bulletin 93:243–248.

Watermeyer, K. E., L. J. Shannon, J.-P. Roux, and C. L. Griffiths. 2008. Changes in the trophic structure of the northern Benguela before and after the onset of industrial fishing. African Journal of Marine Science 30:351–382, 383–403.

Weimerskirch, H., P. Inchausti, C. Guinet, and C. Barbraud. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. Antarctic Science 15:249–256.

Wienecke, B., R. Kirkwood, and G. Robertson. 2004. Pre-moult foraging trips and moult locations of Emperor penguins at the Mawson Coast. Polar Biology 27:83–91.

Wienecke, B. C., and G. Robertson. 1997. Foraging space of emperor penguins *Aptenodytes forsteri* in Antarctic shelf waters in winter. Marine Ecology Progress Series 159:249–263.

Williams, T. D. 1995. The penguins. Oxford University Press, Oxford, UK.

Wilson, P. R., D. G. Ainley, N. Nur, S. S. Jacobs, K. J. Barton, G. Ballard, and J. C. Comiso. 2001. Adélie penguin population change in the Pacific sector of Antarctica: relation to sea ice extent and the Antarctic Circumpolar Current. Marine Ecology Progress Series 213:301–309.

Woehler, E. J. 1993. The distribution and abundance of Antarctic and Subantarctic penguins. Scientific Committee for Antarctic Research, Cambridge, UK.

Woehler, E. J., and J. P. Croxall. 1997. The status and trends of Antarctic and sub-Antarctic seabirds. Marine Ornithology 25:43–66.

Yin, J. H. 2005. A consistent poleward shift of the storm tracks in simulations of 21st century climate. Geophysical Research Letters 32:L18701.

Zimmer, I., R. P. Wilson, C. Gilbert, M. Beaulieu, A. Ancel, and J. Plötz. 2008. Foraging movements of emperor penguins at Pointe Géologie, Antarctica. Polar Biology 31:229–243.

Zwally, H. J., J. C. Comiso, C. L. Parkinson, D. J. Cavalieri, and P. Gloersen. 2002. Variability of Antarctic sea ice 1979–1998. Journal of Geophysical Research 107. [doi: 10.1029/2000JC000733]

APPENDIX

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

CONCEPTS & SYNTHESIS