Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s

DAVID G. AINLEY[1]*, ELIZABETH D. CLARKE[2], KEVIN ARRIGO[3], WILLIAM R. FRASER[4], AKIKO KATO[5], KERRY J. BARTON[6] and PETER R. WILSON[6]

[1]*H.T. Harvey and Associates, 3150 Almaden Expressway, Suite 145, San Jose, CA 95118, USA*
[2]*FRS Marine Laboratory, PO Box 101, 375 Victoria Road, Aberdeen AB11 9DB, UK*
[3]*Department of Geophysics, Stanford University, Stanford, CA 94305, USA*
[4]*Polar Oceans Research Group, PO Box 368, Sheridan, MT 59749, USA*
[5]*National Institute of Polar Research, Itabashi, Tokyo 173-8515, Japan*
[6]*Landcare Research New Zealand, Private Bag 6, Nelson, New Zealand*
*dainley@penguinscience.com

Abstract: Simultaneous, but contrary, decadal-scale changes in population trajectories of two penguin species in the western Pacific and Ross Sea sectors of the Southern Ocean, during the early/mid-1970s and again during 1988–89, correspond to changes in weather and sea ice patterns. These in turn are related to shifts in the semi-annual and Antarctic oscillations. Populations of the two ecologically dissimilar penguin species - Adélie *Pygoscelis adeliae* and emperor *Aptenodytes forsteri* - have been tallied annually since the 1950s making these the longest biological datasets for the Antarctic. Both species are obligates of sea ice and, therefore, allowing for the demographic lags inherent in the response of long-lived species to habitat or environmental variation, the proximate mechanisms responsible for the shifts involved changes in coastal wind strength and air and sea temperatures, which in turn affected the seasonal formation and decay of sea ice and polynyas. The latter probably affected such rates as the proportion of adults breeding and ultimately the reproductive output of populations in ways consistent with the two species' opposing sea ice needs. Corresponding patterns for the mid-1970s shift were reflected also in ice-obligate Weddell seal *Leptonychotes weddelli* populations and the structure of shallow-water sponge communities in the Ross Sea. The 1988–89 shift, by which time many more datasets had become available, was reflected among several ice-frequenting vertebrate species from all Southern Ocean sectors. Therefore, the patterns most clearly identified in the Pacific Sector were apparently spread throughout the high latitudes of the Southern Ocean.

Introduction

Decadal-scale shifts, with remarkable spatial and temporal coherency, have been identified in the climate and biota of the Atlantic and Pacific oceans. These climate shifts are related to the North Atlantic Oscillation (NAO) and Pacific Decadal Oscillation (PDO), which reflect long-term variation in atmospheric pressure systems and, in turn, wind regimes (Hurrell 1995, Hare & Mantua 2000, Mantua & Hare 2002). These changes then affect ocean processes related to productivity and food webs. On the basis of data series spanning several decades, and corresponding to the NAO- and PDO-mediated climatic shifts, changed population trends are apparent among all trophic levels of marine ecosystems in the North Pacific and North Atlantic oceans, including phytoplankton and zooplankton (McGowan *et al.* 1998, Planque & Taylor 1998), fish (O'Brien *et al.* 2000, Hare & Mantua 2000), and seabirds (Vandenbosch 2000, Ainley & Divoky 2001, Thompson & Ollason 2001).

Various climate proxies, such as tree rings or sediment layers, have identified ecosystem "regime shifts" (defined as step-like changes in the mean state of the system) related to the NAO and PDO over the past few hundred years (e.g. Mantua & Hare 2002). Such climate proxies, if ground-truthed, have been used to extend meteorological and ecological datasets. In the case of the PDO, two periodicities, one 15–25 years and the other 50–70 years, have become apparent. During the 20th century, negative ('cool') regimes existed approximately from 1890–1924, 1947–76, and 1989–91; while positive ('warm') regimes existed approximately from 1925–46, 1977–88, and 1992 until (at least) the late-1990s. The most intensively studied shift, as a result of the large quantity of physical and biological time series data available, is that of the mid-1970s. This was an especially dramatic shift when the two periodicities coincided, compared to one in the late 1980s when only one cycle was involved (Hare & Mantua 2000). Variation in the NAO often aligns with the PDO, but

sometimes not. The NAO was in its negative mode during 1952–73, 1976–80 and 1985–89 (Hurrell 1995). During most recent decades, coinciding nodes in both the PDO and NAO occurred in the mid-1970s (~1976–77) and late 1980s (~1988–89).

Due to the relatively short meteorological time series (and even shorter biological ones) available for the Southern Ocean, the region has hardly been part of the discussion of ecosystem regime shifts and even short-term climate periodicities have only recently been quantified. For instance, only during the last few years have relationships to El Niño–Southern Oscillation (ENSO) been recognized in the Antarctic (e.g. Simmonds & Jacka 1995, Peterson & White 1998, Bromwich *et al.* 2000, Yuan & Martinson 2000, Jacobs *et al.* 2002, Kwok & Comiso 2002), lagging ENSO analyses elsewhere in the world by decades (e.g. Rasmussen & Wallace 1983).

Despite the scant attention to the subject of short- and long-term ecosystem shifts in the Southern Ocean, decadal-scale shifts are apparent in at least two large-scale, atmospheric pressure-related systems in the region: the semi-annual oscillation (SAO) and the Antarctic Oscillation (AAO). Twice-annually, from March to June and from

September to December, the circumpolar trough of low pressure that encircles Antarctica expands and weakens, whilst it contracts and intensifies from June to September and December to March. This is the SAO. Sea ice, because it deflects sunlight thus inhibiting heat absorption by the ocean, appears to play an important role in SAO variability (Yuan & Martinson 2000). The position of the trough relative to the large-scale pack ice edge bears on the rate of pack ice expansion and retreat (Enomoto & Ohmura 1990, Watkins & Simmonds 1999). During the mid–late 1970s, the magnitude of the SAO had decreased, particularly during winter/spring, compared to the previous 20 years; this shift was related to a warming of the ocean at mid-latitudes (Hurrell & van Loon 1994, Meehl *et al.* 1998).

Another source of variation in the pressure gradient between mid-latitudes (40°S) and high latitudes (65°S), including measured interannual and decadal variation, has recently been identified as the Antarctic Oscillation (AAO; Gong & Wang 1999, Fyfe *et al.* 1999), or Southern Annular Mode (Lefebvre *et al.* 2004). The normalized zonal mean sea level pressure difference has been called the Antarctic Oscillation Index (AAOI). The AAOI varied but was low during the 1960s and into the 1970s, but in the early–mid 1970s it began to increase (Fig. 1; cf. Hurrell & van Loon 1994, Meehl *et al.* 1998, Gong & Wang 1999). A sharp drop occurred during 1989–92, after which the index returned to a high, variable level but without further significant overall increase. At the same time the overall trend in the Southern Oscillation Index (SOI) was in the opposite direction. Moreover, the SOI shifted from positive to negative around the same time as the AAOI shifted from negative to positive during the 1970s, and it also showed the same fall in 1989–92 (cf. Jacobs & Giulivi 1998). A positive AAO leads to stronger westerly winds and increased Ekman transport of sea ice north (i.e. increased large-scale sea ice extent) in the Pacific sector of the Southern Ocean (Liu *et al.* 2004).

Most recently, attention has been directed towards the Antarctic Dipole, which is a seesawing of surface air temperature, sea ice extent and sea level pressure between the Pacific and Atlantic sectors of the Southern Ocean (Yuan & Martinson 2001, Liu *et al.* 2002, 2004). Like the AAO, the ADP is closely correlated with the SOI, as expressed in sea ice extent in the two sectors. However, there has yet to be a decadal-scale analysis of ADP variability and an ADP index has not yet been derived. Therefore, herein we will confine our attention to the AAO for which a long time series is available.

We present data to elaborate on the above-mentioned late-1980s shift in the AAOI for the sea ice zone in the Pacific sector of the Southern Ocean, and we propose that a shift occurred as well during the mid-1970s, before the age of remote sensing of sea ice began. These shifts affected sea ice characteristics (Liu *et al.* 2004) and, we propose, are expressed by changes in population trajectories of sea ice
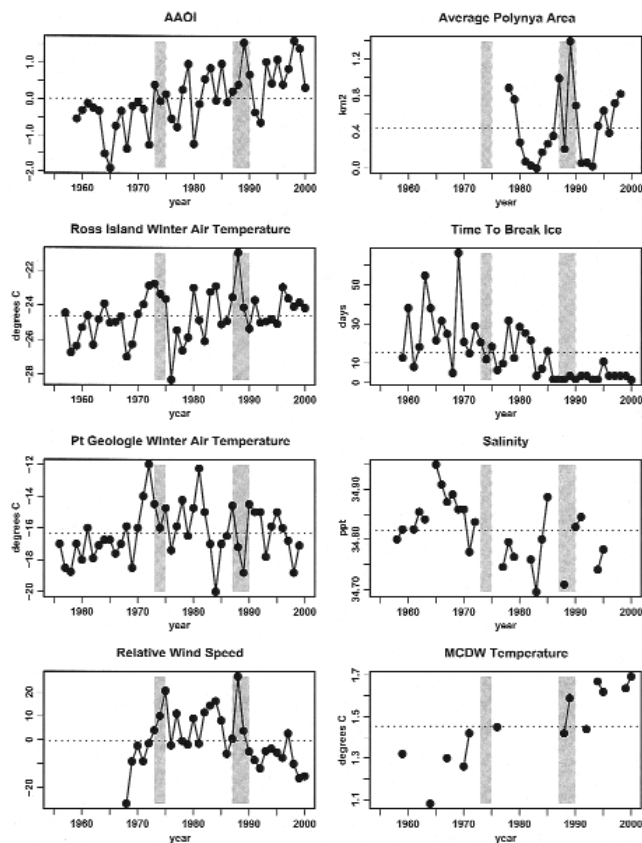

Fig. 1. Indices of the Antarctic Oscillation (AAO) and trends in meteorological and sea ice variables used in this analysis; see Table I for explanation of variables. The grey bars indicate periods of changed trajectory in the environmental variables.
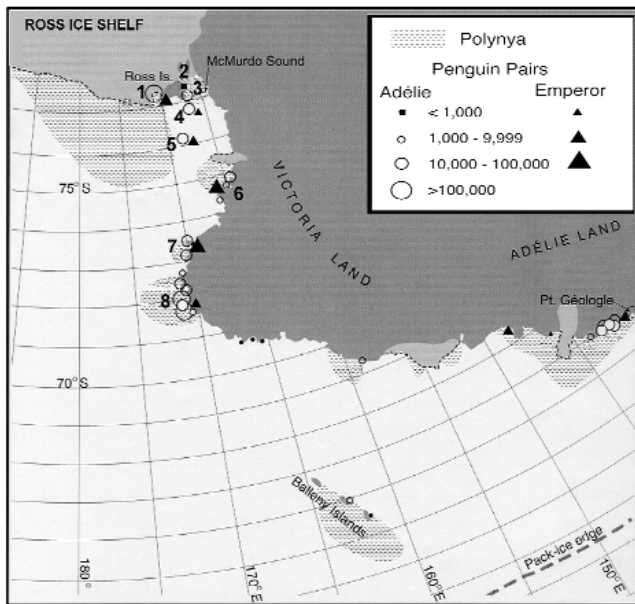
Fig. 2. The Victoria Land and Terre Adélie (Pacific) sector of Antarctica showing locations of penguin colonies and polynyas discussed herein. Sources of data for penguin colonies: Woehler (1993); and for polynyas: Jacobs (1992), Jacobs & Comiso (1989), Martin *et al.* (1992), and Massom *et al.* (1998). Victoria Land colonies indicated by numbers: 1 = Cape Crozier, 2 = Cape Royds, 3 = Cape Bird, 4 = Beaufort Island, 5 = Franklin Island, 6 = Terra Nova Bay colonies, 7 = colonies in vicinity of Coulman Island, 8 = colonies in vicinity of Cape Adare.

obligate vertebrate species. In other words, the penguin responses may be a proxy for changes in sea ice, applicable to the pre-satellite era. We compare records beginning in the 1950s of annual counts of breeding Adélie penguins *Pygoscelis adeliae* and the ecologically dissimilar emperor penguin *Aptenodytes forsteri* at sites in the Pacific Sector of Antarctica (Fig. 2). Our comparison of recent segments of the penguin data to climatic, meteorological and sea ice data (only available since 1979), indicates a tie to decadal shifts in the AAO. We speculate on possible links between changed climate, regional weather and the responding penguin populations. Using some of the same datasets that we explore here, Reid & Croxall (2001), Croxall *et al.* (2002) and Weimerskirch *et al.* (2003) have hypothesized that a 'regime shift' occurred about 1989 in both the Scotia Sea and the sub-Antarctic Indian Ocean, respectively. Noting a correspondence to shifts in air temperatures, and assuming that these are a proxy for a cascade of ecosystem changes, these authors speculated that changes in the food web were directly responsible for the changed population trajectories. These possibilities will be discussed later in this paper.

Methods

Datasets

Long time series of penguin population estimates are

available from the western Pacific sector of the Southern Ocean. Numbers of breeding Adélie penguins at Ross Island colonies (vicinity 77°34'S, 166°11'E; Fig. 2) were estimated from ground counts each year during the 1960–70s but thereafter using aerial photographs taken about 5 December. Data were available from 1960–2000, 1965–2000 and 1962–2000, respectively, for colonies at capes Royds, Bird and Crozier. Census data for all but the most recent years have been published elsewhere (Taylor & Wilson 1990, Wilson *et al.* 2001). Census data based on ground counts for the emperor penguins at Pointe Géologie (Terre Adélie: 66°42'S, 140°15'E), in the western Pacific sector (Fig. 2), were available from 1956–99.

Elsewhere the time series of penguin population size are much shorter in duration and begin more recently. Adélie penguin numbers on several islands in Lützow–Holm Bay, eastern Indian Ocean Sector (69°S, 39°E) (Syowa) have been monitored since 1981. However, at one very small colony in the Lützow–Holm Bay dataset, Ongulkalven, data are available since the early 1960s (Kato *et al.* 2002). Data from Signy Island, eastern side of the Pacific Sector (61°S, 55°W, Drake Passage), are available since 1979 (Croxall *et al.* 2002), and data from Arthur Harbour, Anvers Island (64°S, 64°W), are available from 1975–98 (Fraser & Patterson 1997).

The following climate, meteorological, and sea ice data were obtained from sources given in Table I: Antarctic oscillation index (AAOI); average winter air temperature (April–November) and relative wind strength at Scott Base, Ross Island; average winter air temperature (April–November) at Pointe Géologie; average salinity between 450 and 550 m deep over the southern continental shelf of the Ross Sea; Circumpolar Deep Water (MCDW) temperatures in the Ross Gyre, immediately north of the Ross Sea continental shelf; northward extent and number of days to break the ice channel in McMurdo Sound; and average size (15 November–1 December) of the Ross Sea polynya adjacent to the Ross Island penguin colonies

Data analysis

Colony size and polynya size were modelled using cubic smoothing splines. Normal errors were assumed. The models were fitted in the statistical environment R (R Development Core Team 2004), using the mgcv package (Wood 2001), which uses generalized cross-validation (GCV) to objectively select the amount of smoothing required for each term (Wood 2000). Approximate confidence bands and approximate p-values (conditional on the smoothing parameters) for each of the terms are provided (Wood 2000).

Trends in colony size and polynya size were modelled using year as a covariate. To explain the changes in colony size and polynya size by corresponding changes in environmental variables, we modelled the size of each

Table I. Sources and details of environmental data.

Data	Source	Details
AAOI	Gong & Wang (1999), NOAA National Weather Service, Center for Climate Prediction	Annual indices for 1959–97 were obtained from Gong & Wang (1999). These were extrapolated to 2000 in the following way. A second annual time series was obtained by averaging monthly values produced by NOAA for 1979–2003. The Gong & Wang values were regressed against the NOAA values for the years 1979–97, and the resulting regression line was used in conjunction with the NOAA indices for 1998–2000 to extend the Gong & Wang indices to the year 2000.
Air temperature at Pointe Géologie, Adélie Land	Barbraud & Weimerskirch (2001)	Monthly temperatures averaged over April–November (winter) and December–March (spring).
Air temperature at Scott Base, Ross Island	NIWA*	Monthly temperatures averaged over April–November (winter) and December–March (spring).
Relative wind strength at Scott Base, Ross Island	NIWA*	Two time series available: mean daily speed and highest gust. The latter covered gaps in the former. Average daily wind speed for August–October and the average daily highest gust for August–October were calculated and standardized by expressing each as percent difference from the long-term mean. "Relative wind speed" then estimated as the average of the two indices.
Temperatures between 190 and 440 m depth of T_{max} in the Ross Gyre	Jacobs *et al.* (2002)	Just north of the Ross Sea shelf
Average salinity between 450 and 550 m deep, south-western Ross Sea	Jacobs & Giulivi (1998)	west of 180°
Fast ice extent and thickness in McMurdo Sound	US Coast Guard	1 January is the date on which icebreakers begin to break a channel to McMurdo Station. The effort, as a proxy for ice thickness after 1978, is not comparable to preceeding years when less powerful icebreakers were used.
Ross Sea Polynya: average size from 15–30 November1995	NASA	Estimated by averaging passive microwave data measuring the amount of open water (ice concentration < 100%) every two days. The area investigated, immediately north of the Ross Ice Shelf, was bounded by 70–79°S, 162–205°E for 1979–99. Sensors on NASA satellites were as follows: SMMR 1979 to June 1987, SMMI-F08 June 1987–December1991, SMMI-F11 December 1991–April, and SMMI-F13 April 1995–2001.

*NIWA = National Institute for Water and Atmospheric Research, New Zealand

colony as a sum of smooth functions of the environmental variables, i.e. an additive model. We allowed the following covariates to be included in the models (variable names as used in the tables are in parentheses): Antarctic Oscillation Index (AAOI), air temperature April–November on Ross Island for Adélie penguins or Pointe Géologie for emperor penguins (winter), relative wind speed August–October on Ross Island (wind; as described above) and number of days to break the ice channel in McMurdo Sound (ice). Northward extent of the McMurdo Sound fast ice was also tested as a covariate but did not perform as well as the number of days to break the ice channel, and so was discarded. We did not use salinity or MCDW temperature as covariates since they had a large proportion of missing values. Since the time series for polynya size was short, it was not used as a covariate in the models for colony size.

We did not have environmental variables available at the locations of the colonies in the Indian Ocean (Syowa, Ongulkalven) or far eastern Pacific sector (Signy, Arthur Harbour), and the values for Ross Island were used as proxies. We, therefore, would not expect the models for these time series to fit as well as for the Ross Island and

Pointe Géologie time series.

Model selection for the models including environmental variables was guided by Wood (2001), using backward selection from the initial models described below. Candidate terms for removal were those whose confidence bands included zero everywhere. If more than one term was a candidate, the one having the largest p-value was chosen. If the GCV score reduced substantially when this term was removed, it was removed permanently from the model. The process was repeated until no further terms could be removed. Because of the complexity of the models and hence the large number of parameters (degrees of freedom) relative to the sample size for each colony, the total number of parameters in the initial model was constrained in the following way. For colonies with sample size > 20 annual estimates, the initial model included smooths with a maximum of 4 degrees of freedom (df) through each of the covariates: AAOI, wind, winter and ice. For colonies with sample size < 20, a maximum of 3 df was allowed in each smooth.
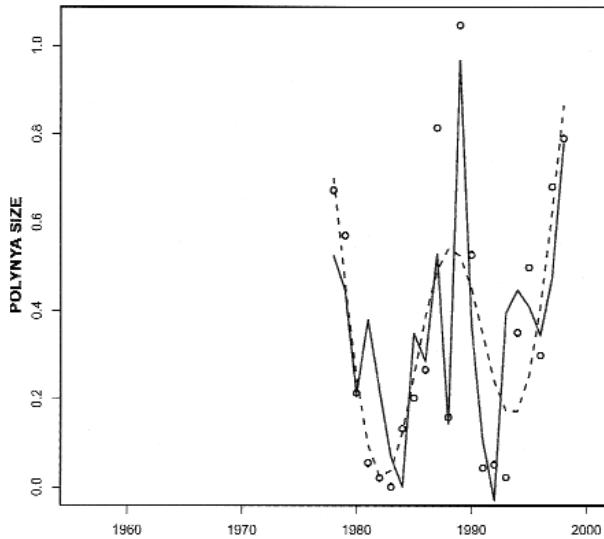
Fig. 3. Change in the average area of the Ross Sea Polynya, 15 November–1 December 1978-99 (km² x 10⁵), compared to size as modelled on the basis of AAOI and wind speed (solid line), and the trend through time, modelled as a smooth function of year (dotted line).

Results

Changes in weather and ocean conditions

Where data are available, most of these time series (AAOI, air temperature and wind speed) show low values in the 1960s, which then increase noticeably in the early-mid 1970s, followed by a sharp fall in 1976, with a subsequent rise in the late 1970s. This first 'node' (*c*. 1973–75) represents the first time that

   i) the AAOI exceeded zero (0),

   ii) Ross Island winter temperature warmed to -23,

   iii) Pointe Géologie winter temperature warmed to -14,

   iv) relative wind speed reach 10.

Subsequently, the pattern differed among sites, with AAOI, Ross Island winter air temperature and relative wind speed continuing to rise until the 1990s, whilst Pointe Géologie winter air temperature decreased suddenly in the early 1980s. However, all show a sudden change between 1987–90, the second 'node' in the time series. The sudden changes between 1973–75 and 1987–90, which coincide with NAO and PDO nodes, have been highlighted with grey bars in Fig. 1. Time series for other environmental covariates are shorter or sparser, but where data are available they are consistent with the sudden changes in AAOI, air temperature and wind speed. In particular, polynya area changed suddenly between 1987 and 1990 (data not available for early 1970s; Fig. 3). MCDW temperature showed a gradual increase over 1960–2000 in accordance with increasing AAOI, whilst salinity showed a corresponding decrease. The time series for ice-thickness (icebreaking effort) is internally comparable over 1960–78 and 1979–2000, but cannot be used to identify longer-term trends. However, ice-thickness (and hence icebreaking effort) generally decreased with increasing temperature and wind speed as we would expect (i.e. thinner ice: Jacobs & Comiso 1989, Parkinson 2002, Liu *et al.* 2004). Changes in polynya size were well explained by other environmental covariates (Fig. 3, Table II), with R^2 = 58%. AAOI and relative wind speed were selected in the model, with polynya size generally increasing with increasing AAOI, whilst it is largest at average wind speed and decreases as

Table II. The models fitted to the penguin population size data. Column contents are as follows: (1) colony modelled, (2–5) characteristics of the model fitted to the population size data – where a symbol indicates that the covariate was included in the model, + indicates a function that generally increased with increasing covariate values, - a function that generally decreased with increasing covariate values, and = indicates a function whose overall effect was neither increasing nor decreasing, or else was small compared to those of other covariates, (6) sample size of data , (7) total number of parameters in the model, (8) adjusted R^2 for the fitted model, and (9) adjusted R^2 for a model with a smooth through year with the same number of parameters as the fitted model. Adjusted R^2 were calculated in the usual way:· where y_i represents the *i*th observation, the fitted value for the *i*th observation, and *n* and *p* are as above.

Colony	Ice	Wind	Winter	AAOI	*n*	*p*	R^2_e	R^2_y
Polynya size		=		+	21	7.7	58	48
W Pacific/Ross Sea Sector								
Emperor	+	-		-	31	6.6	52	88
Pointe Géologie								
Adélie								
Cape Royds	-			+	31	3.8	52	77
Cape Bird	-	+			33	3.8	32	67
Cape Crozier	=				16	2.7	14	52
Indian Ocean Sector								
Adélie								
Ongulkalven	=	-	+		26	6.8	37	44
Lützow-Holm		-	+	+	17	4.9	61	46
E Pacific Sector								
Adélie								
Signy Island	-	+		=	21	6	58	35
Arthur Harbour	+	-		-	17	4.8	62	62

wind speed moves away from its average.

Changes in penguin populations

Breeding numbers of Adélie penguins declined rapidly at Cape Royds during the early 1960s, owing in part to human disturbance, which was stopped by 1963 (Thomson 1977); numbers then quickly recovered to pre-disturbance levels (Fig. 4). Otherwise, numbers at both Royds and Bird were stable to the early 1970s, and then, with some occasional plateaus, began to increase to reach a peak in 1987, followed by a sharp decline between 1987 and 1990, coinciding with sudden changes in environmental variables, as noted above. After this, the Royds population recovered to levels seen in the later 1980s, whereas the Bird population has remained at early 1980s levels. Where data are available, the population trajectory at the very large Cape Crozier is very similar to that at Cape Bird but less
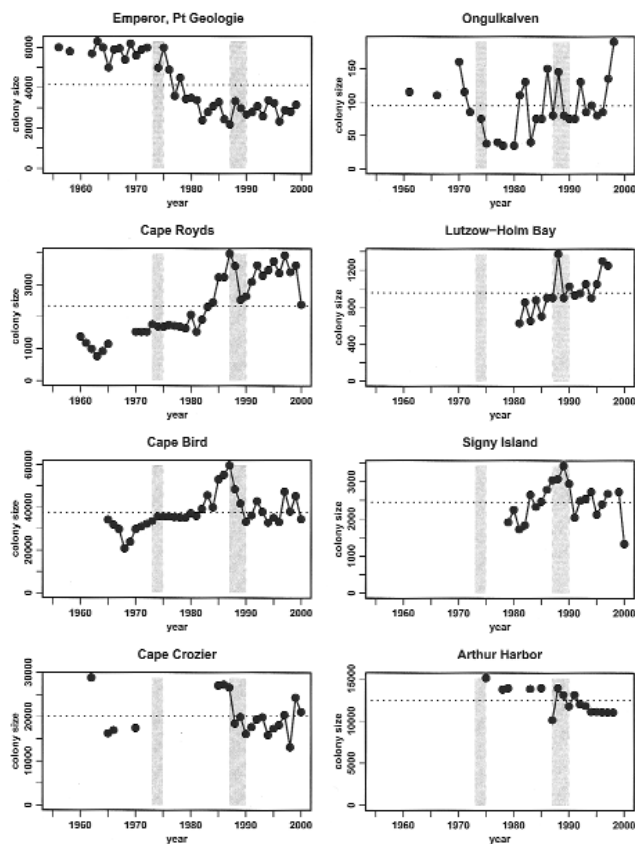
extreme. In this Ross Island metapopulation, the degree of change has been inverse to colony size: during the period of increase (to late 1980s), the small Royds colony quadrupled in size, medium-sized Bird increased by 50%, and the large Crozier colony increased by only ~30%.

Changes in Adélie penguin populations at other locations in the Southern Ocean showed a similar pattern (Fig. 4). As on Ross Island, penguin numbers at Signy Island increased to reach a peak in the late 1980s, followed by a steep decline and subsequent slower and more variable growth. The Ongulkalven data are very variable, no doubt related to the very small size of the colony, but indicate a decline through the 1970s, followed by a slight increase in the early 1980s with a levelling thereafter (Kato *et al.* 2002; Fig. 4). Only at Arthur Harbour off the north-west coast of the Antarctic Peninsula (eastern Pacific Sector) - the only other long-term penguin dataset available - have trends been clearly different. There, Adélie penguin numbers have declined since the 1970s (Fraser & Patterson 1997; Fig. 4).

In contrast, the population trajectory of the emperor penguin at Pointe Géologie, just to the west of the Ross Sea
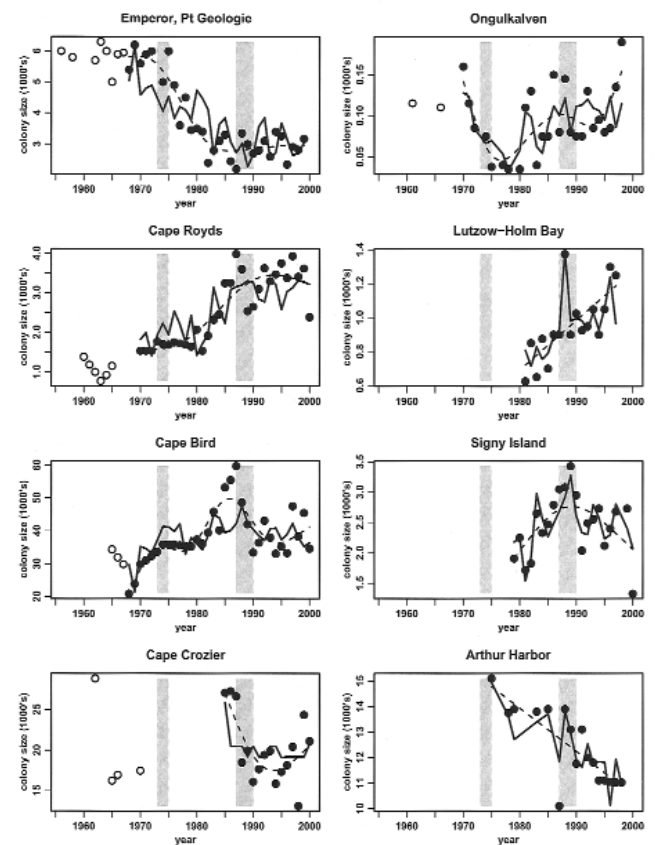

Fig. 4. Annual breeding population size for several penguin colonies in the Antarctic. The colonies are: Pointe Géologie (emperor); the three Ross Island Adélie colonies; and Adélie colonies at Ongulkalven and all colonies in Lützow-Holm Bay (Syowa; *c*. 69°S, 39°E), Indian Ocean Sector (data courtesy Japanese Antarctic Program); Signy Island, Pacific/Atlantic Sector (Drake Passage: 61°S, 55°W; from Croxall *et al.* 2002); and at Arthur Harbour, Anvers Island (Pacific Sector, but west coast Antarctic Peninsula: 64°S, 64°W; from Fraser & Patterson 1997).

Fig. 5. Penguin breeding population size for the same colonies as Fig. 4. The full line represents the trend obtained by fitting colony size to smooth functions of environmental variables. The dashed line represents the trend obtained by fitting colony size to a smooth function of year. The open circles indicate the points excluded from the analysis due to missing environmental data.

(Fig. 2), is roughly opposite that of the Adélie penguins (except those of the western Antarctic Peninsula). Numbers of breeding emperor penguins were relatively constant through the 1950s and 1960s. Then in the mid 1970s, coinciding with the sudden change in environmental variables, the emperor numbers began to decline. The decline continued until the early 1980s, after which numbers remained stable at the lower level (Fig. 4).

Response of penguins to environmental variability

The models of colony size with environmental covariates, on the whole, performed well at explaining the changes in colony size using few parameters, with R^2 of more than 50% for 5 out of 8 colonies (Table II, Fig. 5). Among the remaining three colonies, the high peak in the late 1980s at Cape Bird proved difficult to model, whilst the peak at Cape Crozier was modelled at the cost of fitting the subsequent plateau. Ongulkalven, being a small colony, was unusually variable, and the environmental models usually performed almost as well as the models with year as a covariate. The models with a smooth through year picked up the overall trend, whereas the models with environmental covariates picked up much of the short-term variation in colony size (Fig. 5). The models for the colonies outside the Ross Sea performed surprisingly well given the fact that the Ross Sea environmental variables were geographically remote. Ice thickness [using days to break ice (ice) as a proxy] and relative wind speed were selected in 6 out of 8 models (Table II), whilst AAOI and winter air temperature were selected in 5 and 3 of the models, respectively. Model terms rarely used more than 2 df, and covariates were often linear, making the models relatively simple, with relatively few parameters compared with the number of data points.

Thus the environmental variables, in particular wind speed and ice thickness, explained much of the changes in colony size. In particular, we successfully modelled the trends through the 1980s, and the models reflect the sharp drop in the late 1980s in all relevant penguin colonies. Inspection of the functions fitted in the models showed that, in general, colony size decreased with increasing ice thickness and increased with increasing AAOI and winter temperature, apart from Arthur Harbour and emperor penguins at Pointe Géologie. The latter increased with increasing ice thickness and decreased with increasing winter temperature and AAOI. The functions fitted to relative wind speed were more variable and had no general patterns.

Discussion

Effects of changed weather and sea ice on penguins

General considerations, *both species*. The key to understanding the mirror-image population changes exhibited by the populations of the Adélie and the emperor

penguin in the Pacific Sector is the requirement of locked fast ice and nearby polynyas by the emperor (Prévost 1961, Kirkwood & Robertson 1997, Massom *et al.* 1998) as opposed to the persistent but divergent pack ice (remaining from polynyas earlier in the year) by the Adélie (Ainley 2002, Arrigo & van Dijken 2003). In areas where sea ice has disappeared for most of the year, e.g. the west coast of the northern Antarctic Peninsula at the northern edge of the species' range, the (ice-obligate) Adélie penguin has been disappearing as well (see above, Figs 4 & 5). No significant fast ice occurs on the north-west coast and, thus, neither does the emperor penguin. Farther south on the west coast (much warmer than the east coast), a population of emperor penguins at Dion Island has declined from about 250 pairs in the 1960s to 10 pairs in 2001 (WRF, unpublished data; cf. Woehler 1993).

Wilson *et al.* (2001) found that annual population change at Royds and Bird (which had the longest time series), within the era of satellite imagery (post 1978), was significantly correlated inversely with sea ice extent during winter. As there was a 5-year lag to the response (again, average age of Adélie penguin recruitment; Ainley *et al.* 1983), variation in subadult survival was deemed to be the immediate causative factor. In other words, changes in the breeding population due to adult mortality or restriction of access to the colony would be evident immediately (e.g. similar to the post-1988 drop discussed above), but changes due to subadult mortality would not be evident until recruitment into the breeding population some years later (discussed more fully below). While 30% of variation in population change was explained by winter sea ice extent, understanding of the Adélie penguins' population trajectory, obviously, was incomplete.

Taylor & Wilson (1990) correlated changes in Adélie penguin populations to warming on Ross Island. Similarly, Barbraud & Weimerskirch (2001; see also Weimerskirch *et al.* 2003) correlated changes in emperor penguin populations at Pointe Géologie to warming. Barbraud & Weimerskirch (2001: their fig. 1) ascribed the change in emperor population size to reduced survival of adults (especially males) during a several-year period (mid-1970s) when sea surface temperatures (north of the sea ice zone), explaining 87% of the survival variation, were warmer and ice-edge distance (i.e. distance from the colony to northern edge of the large-scale ice pack) was reduced. However, the low population persisted after ice-edge distance and temperature returned to former levels (sea ice data available only since 1973). The lower population after the mid-1970s was temporally consistent with greater interannual variability in egg hatching, which in turn (and in reverse to adult survival) was correlated with more extensive winter sea ice (Barbraud & Weimerskirch 2001). However, Barbraud & Weimerskirch noted that the proximate cause of reduced hatching success was an increase in the frequency at which fast ice, on which the emperor penguins nest, blew

out prematurely and/or severe blizzards occurred. Considering all these factors, the continued low population of emperor penguins has not been fully explained.

Processes involved in sea ice and polynya formation have an immediate impact on the population processes of Adélie and emperor penguins. The larger size of the Ross Sea Polynya during spring (September–October), with subsequent more rapid decay of pack ice, would allow easier access to colonies by Adélie penguins in the southern Ross Sea, where pack ice concentration (percent cover) is normally very high (cf. Gloersen *et al.* 1992). The penguins' southern migration from the northern (outer) edges of the ice pack occurs during September–October (Ainley 2002). More extensive and persistent polynyas would also aid ocean access by emperor penguins (Kirkwood & Robertson 1997, Massom *et al.* 1998). For both species, easier access increases the proportion of the population that attempts to breed (particularly young breeders), as noted above, as well as increasing the proportion of pairs that nest successfully. Both factors would lead to an increase in the size of the breeding population, although the second factor would have a lagged effect (Stonehouse 1967, Ainley & LeResche 1973, Wilson *et al.* 2001, Ainley 2002).

The decline in Adélie penguin numbers at Arthur Harbour is clearly related to the loss of sea ice and increased snowfall (Fraser *et al.* 1992, Fraser & Patterson 1997). Both of these factors are related to higher air temperature in that region (Jacobs & Comiso 1993, 1997, Smith *et al.* 1999, Comiso 2000). Because of the importance of these factors to populations of the western Antarctic Peninsula, as opposed to the polynya-related factors important at higher latitudes (see below), we will not discuss the Arthur Harbour populations further.

The pattern of change in the Pointe Géologie Adélie penguin population loosely mirrors the Ross Island pattern (Weimerskirch *et al.* 2003), but disturbance from station activities has had confounding effects (Micol & Jouventin 2001). Similarly, the Ross Island pattern is exhibited as well by the Whitney Point, Wilkes Land, Adélie penguin population, but the censuses are somewhat sporadic in the early years and numbers, too, have been affected by station activities (Woehler *et al.* 1994, 2001). Thus, we did not include further analysis of these datasets here.

Adélie penguins. Annual growth or decline of Adélie penguin populations on Ross Island indeed appear to be sensitive to the size (and rate of seasonal growth) of the Ross Sea Polynya. The relationship, however, is complex owing to varying lags in demographic processes and seasonal population dynamics that can contribute to population change and which are not yet fully understood (see also Thompson & Ollason (2001) for a discussion of a similar problem in addressing responses to changing climate in another seabird, the northern fulmar *Fulmarus glacialis*). Ultimately, a simulation model of demography

for the penguin will be required, and data collection is underway. In any case, we believe that much of the remaining 70% variation in annual population change (re: the sea ice extent model presented by Wilson *et al.* 2001 and mentioned above) will be explained by the polynya relationship, as is apparent in our analyses here.

In the context of the information presented above, our interpretation of the trajectories of the Ross Island colonies is as follows. The populations were declining during the 1960s mostly due to concentrated and persistent sea ice. Adding support to this idea is the analysis of Curran *et al.* (2003) who concluded that sea ice extent has been declining in East Antarctica since the 1950s, with perhaps a plateau in the signal during the 1960s followed by additional decline. The increased winds and increasing air temperature that began in the early–mid 1970s, as reported here, resulted in enough dissipation of spring sea ice that the proportion of potential Adélie penguin breeders increased after a demographically-related lag (hence only a slight rise in populations in 1973). Continued warming and stronger winds (larger polynya), with a greater proportion of adults breeding (and doing so successfully) led to more rapid population increase (1980 and thereafter), coinciding with a generally positive AAOI. Populations increased through 1987, after which a crash occurred in 1988 and 1989. This crash occurred during an unusually strong positive excursion of the AAO. Obviously, weather and sea ice would have been affected, but what immediate factors were involved remains to be determined. It appears that high mortality occurred rather than reduced breeding propensity, because penguin numbers did not rebound immediately. Rather, they began to recover at the same rate of growth evident before the crash. After 1988–89, the smaller Ross Sea colonies grew rapidly but the large ones (Crozier) did not; changes in emigration direction may have been involved (Ainley, Ballard *et al.* unpublished data). During this post-1988–89 period, ocean temperature continued to warm, although winds and air temperature diminished. Therefore, seasonal sea ice persistence likely was affected (see also Parkinson 2002, Zwally *et al.* 2002).

Emperor penguins. Thinner sea (fast) ice during winter or more rapidly decaying ice in spring, both the result of stronger winds (and higher temperatures), would be especially critical to this species. In fact, although Barbraud & Weimerskirch (2001) found a negative correlation between hatching success and winter sea ice extent (distance from the coast to outer edge of pack ice), breeding emperor penguins do not occur at the outer edge of the pack during that part of the year. Rather, as noted above, they occur in breeding colonies on fast ice near the continent and depend on adjacent loose pack or polynyas for feeding (Kirkwood & Robertson 1997, Massom *et al.* 1998). Barbraud & Weimerskirch could find no relationship between breeding success (result of egg hatching and

subsequent chick survival to fledging) and sea ice or sea surface temperature, surmising that unknown factors confounded the importance of variation in hatching success. However, annual reproductive success during 1952–73 averaged 64.5 ± (s.e.) 5.1% ($n = 15$ years), and only once did it dip to the unusual low of < 30% (data from Barbraud & Weimerskirch 2001, fig. 1). That average compares with a much lower success of 49.2 ± 4.7% ($n = 24$), with as many as six years at < 30% during 1974–97 ($z = 2.094$, $P = 0.036$). In fact, Barbraud & Weimerskirch noted that especially low reproductive success in the later period resulted from premature fast ice breakout and/or blizzards. This latter observation is consistent with thinner ice, as noted above, and is also consistent with the presumed stronger winds during the period of low emperor penguin populations, i.e. the late 1970s–90s. Earlier, presumably, winds were weaker, which would encourage less extensive pack ice but more reliable fast ice. Thicker fast ice would be less likely to blow out prematurely.

As somewhat of an aside, readers may wonder if the status of the small, but long-studied emperor penguin colony at the edge of the Ross Ice Shelf and the Ross Sea Polynya has any bearing on this discussion. It does not. That colony has grown from a few hundred pair in the 1960s to a minimum 1201 pair by 2000 (DGA unpublished data). This growth is directly related to the increased protection offered by the growing, western portion of the Ross Ice Shelf (Keys *et al.* 1998, DGA, personal observation). It is now far better protected. Thus, the colony has been increasing for reasons not directly related to climatic effects on sea ice.

Factors that change the mortality rate of adult emperor penguins at Pointe Géologie are more difficult to understand with the data at hand. Hurrel & van Loon (1994) noted that the SAO shift in the mid-1970s delayed by one month the period of peak springtime winds. Both female and male emperor penguins fast during the entire pre-laying and laying periods (a month), and the male continues to fast during incubation (an additional 1.5 month). Upon being relieved of nesting duties, each member of the pair requires ready access to open water and food in order to quickly regain body condition. Stronger winds and persistent polynyas would facilitate satisfying these needs, and having fasted considerably longer, quick access to food would be even more critical to the male (see also Kirkwood & Robertson 1997). In fact, Barbraud & Weimerskirch (2001) found higher survival with more extensive pack ice, the condition induced by stronger winds, which also lead to polynya development. The period of low adult survival noted by these authors occurred only during a short time span, 1976–80. This pulse of high mortality (highest for males) apparently lowered the population, which, in subsequent years owing to reduced breeding success (above), was unable to recover. As noted, populations of penguins are particularly sensitive to changes in adult mortality (Barbraud & Weimerskirch 2001, Wilson *et al.* 2001), but dramatically lower fecundity can contribute, too,

Table III. A summary of trends in various physical and biological aspects of the Southern Ocean, 1950–97.

	Up to ~1973	1973–88	~1989–97
AAOI	negative	first positive 1973, then mostly positive and increasing 1978 onwards	highest positive 1989, then steep decline; return to mostly positive with no long-term increase
Winds, Ross Sea	weakest	strongest, especially Aug–Oct	moderate
Air temperatures, winter			
Ross Island	cold	warmest	warm
Pointe Géologie	cold	warmest	warm
salinity, Ross Sea	high	low	low
temperature, MCDW in Ross Gyre	low	warmer	warmest
fast ice, McMurdo Sound	extensive, thick	declining in thickness	thin
Adélie penguin populations			
Ross Island	low/declining	since 1960s, initial increase 1973; sustained growth late 1970s onwards	crash 1989, then variable growth
Lützow-Holm Bay		growing (record begins 1980)	crash 1989, then variable growth
Signy Is		growing (record begins 1979)	crash 1990, then variable growth
Emperor penguin populations,			
Pointe Géologie	abundant, stable	decline begins 1975 (to 1978) then low	low, stable
Weddell seal population, McMurdo Sound	high	decline begins early 1970s (to mid-1970s), then low	low, stable
Sponge communities, McMurdo Sound			
Homaxinella and predators	rare	dominant	no data
Minke whale populations,			
Antarctic wide	high	lower	
Antarctic krill,			
Drake Passage:		abundance index positive	abundance index negative

to population change (or lack thereof). A similar pattern is implicated among diving (high energy demanding) seabirds in the mid-latitude North and South Pacific (including penguins on the Galápagos Islands): populations crashed as a result of high adult mortality during El Niño 1982–83 and then failed to recover in the new, less productive ocean (warm PDO) regime that existed 1976 to the late 1990s (Ainley & Divoky 2001). The higher mortality of adult emperor penguins during 1976–80 was correlated to (but was it caused by?) higher sea surface temperature (see below for how food webs could have been affected).

Broader implications

The population trajectories of penguin populations in the sea ice zone of the Southern Ocean, as presented above, if used as a proxy, have identified corresponding shifts in the regimes of climate indices, weather, and sea ice during the early–mid 1970s and the late 1980s (Table III). A somewhat analogous correspondence in physical and biological patterns was identified for the North Atlantic (Aebischer *et al.* 1990) prior to the time when the now much researched NAO was first recognized by biologists. We hypothesize that had there been Southern Ocean datasets from lowest trophic levels, the organisms of which respond to climate shifts at a population level much more immediately than do long-lived, top trophic species (see e.g. Batchelder *et al.* 2002, Peterson & Schwing 2003), then organismic responses to the mid-1970s and late 1980s regime shifts proposed herein would have been even clearer.

Shorter-term datasets (Table III) indicate that biological shifts proposed for the Pacific sector were more widespread than what has been discussed thus far.

For instance, a marked reduction in the circumpolar population of the Antarctic minke whale *Balaenoptera bonaerensis*, a pack ice species (Naito 1982, Ribic *et al.* 1991), has become apparent during the 1990s (1991–97 circumpolar surveys) compared to surveys in 1978–83 and 1984–90 (Branch & Butterworth 2001). Among the most plausible explanations offered by these authors were

1) that the whales had undergone a change in distribution within the sea ice zone (where whale boats do not go), or

2) that the 2–3 week delay in the latest surveys may have missed the peak of whale abundance.

If the pack ice has become more divergent in the new warm regime, as we suggest, then both explanations would apply: the whales have 'escaped' detection by moving farther into a more divergent pack ice where, like whale-catcher boats, whale-survey vessels do not venture.

Before the mid-1970s compared to the 1960s, a certain sponge *Homaxinella balfourensis* and its predators were rare in waters < 30 m deep in McMurdo Sound (Dayton 1989). Any attempt by this sponge to colonize shallower depths was thwarted by the formation of anchor ice, which crystallized around colonists and by increasing their buoyancy, ripped them out and floated them upward in the water column. After the mid-1970s, anchor ice formation became irregular and the *Homaxinella* communities began to appear. The colder air temperature and longer residence time of sea ice in the Ross Sea before the mid-1970s, as proposed herein, would lead to a downward cooling of surface waters. In response, ice would form to deeper depths and encourage crystallization around objects, such as sponges, that begin to grow too high in the water column (see Hunt *et al.* 2003). Dayton (1989), in fact, proposed that composition of sponge communities indicated a decadal shift in ocean conditions during the mid-1970s.

Coinciding with the more extensive or thicker ice in McMurdo Sound before the mid-1970s was a larger population of Weddell seals *Leptonychotes weddellii* (Cameron 2001). These seals, like emperor penguins, depend on fast ice in order to successfully produce young. Like the emperor penguins, Weddell seals dive deep for prey and, actually, diets of these two predators are very similar. A decline in seal numbers occurred from at least 1973 to 1978. In part this may have been due to harvesting of seals to feed sled dogs. The latter activity, however, ended in the early 1980s but the population has not shown signs of recovering. The population trajectory, thus, is very similar to that of the emperor penguins at Pointe Géologie.

In the Scotia Sea (South Georgia), Atlantic Sector of the Southern Ocean, population data for Antarctic fur seal *Arctocephalus gazella* and gentoo penguin *Pygoscelis papua*, archived from the early 1980s, indicate increases to 1988–89 followed by a decrease; data for black-browed albatross *Thalassarche melanophrys* and macaroni penguins *Eudyptes chrysolophus* show a shift in trajectory in 1985. Reid & Croxall (2001; see also Croxall *et al.* 2002) ascribed these changes to the availability of Antarctic krill *Euphausia superba*, the population of which at South Georgia is believed to be advected upstream from sea ice covered regions to the south. They noted that the krill abundance index of Siegel *et al.* (1998) for the Drake Passage area was positive to 1985 and consistently negative from 1988 onward to 1996. Similarly, Weimerskirch *et al.* (2003) also hypothesized that a 1988–89 shift in population trajectories of various Antarctic and sub-Antarctic seabirds and pinnipeds in the Indian Ocean sector involved changes in the food web.

Whether or not changes in the food web have been involved in the changes discussed herein, especially for the Pacific/Ross Sea sector, is subject to an even higher level of conjecture than what we have presented thus far. For example, it is possible that variation in the infusion of warmer Modified Circumpolar Deep Water (MCDW) onto the continental shelf or its upwelling at continental margins (Jacobs & Giulivi 1998, Jacobs *et al.* 2002) affect the

natural history patterns of the top predators' prey (cf. Reid & Croxall 2001). Although we have not addressed the issue exhaustively, we would feel more comfortable with changes in food web structure as an explanation of the results presented herein if the changes in MCDW salinity and temperature, as indicators of water-column processes, had contributed to the penguin population models. As it was, changes in sea ice and polynyas alone accounted for the trends.

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