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Dynamics of Antarctic penguin populations in relation to inter-annual variability in sea ice distribution

Abstract To investigate the role of sea ice cover on penguin populations we used principal component analysis to compare population variables of Adélie (*Pygoscelis adeliae*) and chinstrap (*Pygoscelis antarctica*) penguins breeding on Signy Island, South Orkney Islands with local (from direct observations) and regional (from remote sensing data) sea ice variables. Throughout the study period, the Adélie penguin population size remained stable, whereas that of chinstrap penguins decreased slightly. For neither species were there significant relationships between population size and breeding success, except for an apparent inverse density-dependent relationship between the number of Adélie breeding pairs and the number of eggs hatching. For both species, no general relationship was found between either population size or breeding success and the local sea ice conditions. However, the regional sea ice extent at a particular time prior to the start of the breeding season was related to the number of birds that arrived to breed. For both species, this period occurred before the sea ice reached its maximum extent and was slightly earlier for Adélie than for chinstrap penguins. These results suggest that sea ice conditions outside the breeding season may play an important role in penguin population processes.

Introduction

The nature and causes of variability in the Southern Ocean marine ecosystem have been much studied. In respect of top predators, most attention has been given to the role of food supply, particularly in relation to the commercial harvesting and the consequential affects on the ecosystem following the removal of baleen whales; that is the so called "krill surplus" (Sladen 1964;

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Croxall and Kirkwood 1979; Laws 1985). Recently, however, more attention has been directed towards the role of physical factors (Croxall et al. 1988; Priddle et al. 1988; Testa et al. 1991; Fraser et al. 1992; Murphy et al. 1995), resulting primarily from an interest in environmental changes that may be associated with "global warming" (see review in Croxall 1992). In relation to the regulation of population processes among top predators, the physical factor attracting most attention has been the distribution and extent of sea ice.

It is well established that the prolonged presence of sea ice close to penguin breeding sites may delay the start of breeding, reduce clutch size, or reduce breeding success (Ainley et al. 1983; Lishman 1985a, 1985b; Croxall et al. 1988). Recently, however, Fraser et al. (1992), working with Adélie (*Pygoscelis adeliae*) and chinstrap (*Pygoscelis antarctica*) penguins at Admiralty Bay, King George Island, South Shetland Islands, suggested that sea ice conditions prior to the breeding season could also influence the size of breeding populations. Based on evidence in Ainley et al. (1994) and Joiris (1991), Fraser et al. (1992) indicated that, in winter, Adélie penguins were obligate inhabitants of the pack ice whereas chinstraps were almost exclusively birds of the open water. Furthermore, Fraser et al. (1992) suggested that sea ice conditions had opposite effects on the two species, possibly by influencing over-winter survival. Thus, in years of extensive or persistent sea ice, breeding populations of Adélies increased whereas those of chinstraps decreased. In addition, Fraser et al. (1992) proposed that the current trend of increasing surface air temperature in the Antarctic Peninsula region was associated with a reduction in the frequency of cold years with extensive sea ice cover and that this had favoured population increases in chinstrap but not in Adélie penguins. They also suggested that this could explain many of the changes in penguin populations in recent decades.

The model proposed by Fraser et al. (1992) has major implications for understanding pygoscelid penguin

population dynamics and for assessing their current
and future population trends, not only within the Ant-
arctic Peninsula region, but also in other areas of the
Antarctic. However, the data set used by Fraser et al.
(1992), though spanning 11 years, had just 8 years of
data with only 4 that were consecutive; furthermore,
the years without data were treated by averaging over
the missing period. The magnitude of population
changes reported by Fraser et al. (1992) was much
larger than could be accounted for by changes in over-
winter survival; changes in recruitment and deferred
breeding and possibly changes in emigration and immi-
gration between colonies must also be involved (see
Croxall and Rothery (1995) for gentoo penguin *Pygo-
scelis papua*). Furthermore, the classification of sea ice
conditions used by Fraser et al. (1992) was imprecise,
depending upon a single value for the maximum ice-
edge position and a subjective classification of the local
sea ice conditions.

Therefore, we sought to investigate further the rela-
tionships between penguin population processes and
sea ice by using longer series of continuous penguin
data together with objective criteria for sea ice condi-
tions. In this paper, we report the analysis of data on
breeding population size and productivity of Adélie
and chinstrap penguins collected at Signy Island, South
Orkney Islands (1979–1992), in conjunction with data
on local sea ice conditions (1947–1992) and data on
regional sea ice extent derived from satellite imagery
(1973–1988).

Our main questions were:
1. Is there evidence of any trend in either the sea ice
duration or extent at Signy Island and/or in the pen-
guin population size or breeding success at Signy
Island?
2. Are there correlations between penguin population
size and/or reproductive performance and the time of
arrival and breakout (as well as duration) of local sea
ice or the maximum extent of the regional sea ice?

Materials and methods

Sea-ice data

Two data sets describing sea ice conditions were used. The first
covers the local sea ice conditions at Factory Cove, Signy Island
where data are available for the period 1947–1992, apart from
a short gap in the mid-1950s. Factory Cove is situated approxim-
ately 2.5 km from Pageant Point, 2.5 km from Clowes Bay and
4.5 km from North Point, the sites of the various penguin study
colonies (Fig. 1). The data set records the date on which fast ice first
forms in Factory Cove, as well as the data on which the final
breakout occurs (Murphy et al. 1995); however, these dates may
span ice-free periods in the cove when the fast ice blows out during
a winter gale. For this data set, the date of formation is defined as the
date on which the sea ice can first support the weight of a person.
This is a somewhat subjective assessment, but is essential as the fast
ice forms slowly. In contrast, the date of breakout is always precise.
This is because the fast ice does not melt in Factory Cove, but
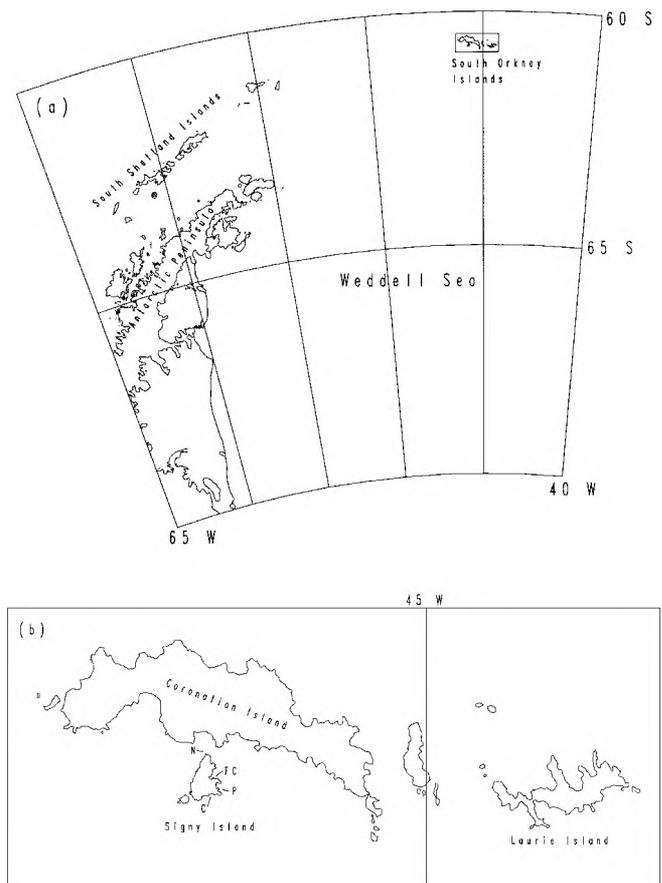
Fig. 1a, b Map showing **a** the location of the South Orkney Islands
and the South Shetland Islands, and **b** the South Orkney Islands
with Signy Island and the locations of Factory Cove (*FC*), North
Point (*N*), Pageant Point (*P*) and Clowes Bay (*C*). Adélie colonies
1, 2, 3 and 4 are at North Point, colony 41 is at Pageant Point;
chinstrap colonies 79, 80 and 81 are at Pageant Point, colony 47 is in
Clowes Bay

normally blows out during a spring gale. As a consequence, the end
date is always on a date equal to, or after, the date that the regional
sea ice edge has retreated south past the South Orkney Island group.

The second data set describes the cricumpolar sea ice extent
(Knight 1984) and contains the mean weekly location of the sea ice
edge at 1° longitudinal intervals for the period 1973–1988. These
data were prepared by the US Navy/National Oceanic and Atmo-
spheric Administration (NOAA) Joint Polar Ice Center and con-
verted into a digital format prescribed by the World Meteorological
Organization. The data are a blend of shore station reports, ship
reports, aerial reconnaissance and satellite imagery, with the latter
accounting for 90–98% of data points (Knight 1984).

Penguin data

The South Orkney Islands have large populations of Adélie and
chinstrap penguins, totalling approximately 250,000 and 600,000
breeding pairs, respectively (Croxall and Kirkwood 1979; Poncet
and Poncet 1985). Signy Island is one of the important sites in the
island group with about 37,000 breeding pairs of Adélie penguins
and 80,000 of chinstraps. Population changes in the region and at
Signy Island have been described by Croxall and Kirkwood (1979),
Croxall and Prince (1979), Croxall et al. (1981, 1988) and Poncet and

Poncet (1985). Data on penguin breeding population size and productivity collected annually at selected Adélie and chinstrap colonies on Signy Island from 1979 to 1992 were used in our study. In our analysis, data from a particular breeding season are represented by the date of the year in which fledging occurred, e.g. data from the 1978/1979 season are represented at 1979. For each species, the number of breeding pairs was counted immediately laying ceased and immediately hatching finished and the number of chicks was counted just before fledging started. Counts were the average of those made by two or more observers. Where the census date differed from the standard census date, the count of breeding pairs and the count of eggs hatching were corrected for losses prior to the census date, either using data on a small colony subject to detailed study in the same season or by using the average values from the study of Lishman (1985a). The colonies used in the present analysis are those for which the most complete data are available and cover the full range of colony sizes monitored at Signy Island (excluding some very small, newly founded, chinstrap penguin colonies).

Data analysis

The sea ice data and the penguin census data provide time series which, though covering different intervals, include substantial periods of overlap. The conventional method for comparing such independent time series is either to use cross-correlation, having applied a linear moving average filter, or to fit an auto-regressive integrated moving average (ARIMA) model (Chatfield 1992). However, for the present study these methods are inappropriate, largely due to problems associated with the relatively short time span covered by the penguin series. As a result, we present the results of a set of principal component analyses (Gauch 1989) based on the covariance matrix of the penguin colony data and the sea ice data, following normalisation of both data sets between 0 and 100.

Principal component analysis (PCA) has previously been used to examine time series of data. For example, relationships between sea ice extent in different sectors of the Antarctic and over different temporal scales have been examined by Lemke et al. (1980), whilst temporal effects within the global temperature record have also been examined by Elsner and Tsonis (1991) and Ghil and Vautard (1991). More recently, Murphy et al. (1995) have also used principal component analysis to examine temporal relationships in sea ice data, relating their sea ice series to the El Niño Southern Oscillation Index.

To investigate annual variability in penguin breeding success in relation to the sea ice record, we have adjusted each normalised time series by lagging each value in year n to years $n + 1$, $n + 2$, $n + 3$ and $n + 4$. Given the cyclical signals evident in the Factory Cove sea ice data set over recent years (Murphy et al. 1995), a limit of four lags was considered sufficient. Thus, in our analyses each PCA was carried out by calculating the eigenvectors from the covariance matrix, which included the first four lags of each time series. In their analysis, Ghil and Vautard (1991) differentiate the eigenvectors from the principal components, which they describe as the loadings involved in the expansion of each lagged copy; we follow this same definition.

Results

Signy Island sea ice duration

Variability in the arrival, duration and breakout of sea ice at Signy Island over the period 1947–1992 (Fig. 2a,b,c) showed no significant long-term trend, although cyclical fluctuations were evident (Murphy et al. 1995). The duration of sea ice cover in Factory Cove was strongly correlated with the date of ice breakout and negatively correlated with the date of ice formation (Murphy et al. 1995). Thus, years of long ice duration were the result of two factors: an early ice start date, and more importantly for penguins, a late ice breakout. Conversely, in years of short sea ice duration there was a late ice start date and an early ice breakout. This pattern was evident for the period for which penguin breeding data were available, 1979–1992.

The ice breakout date is important for penguins as they require unimpeded access between their breeding colonies and their feeding grounds particularly during the chick-rearing period. The mean date of ice breakout at Signy Island is in late October (mean of day 294) and is after the time that Adélie penguins arrive (mean of day 275; range 264–281) (Lishman 1985a), but before the time that they usually lay their eggs (mean of day 300; range 295–305) and before the time that chinstrap penguins arrive (mean of day 304; range 289–315). Exceptionally, however, as in 1980/1981 (Lishman
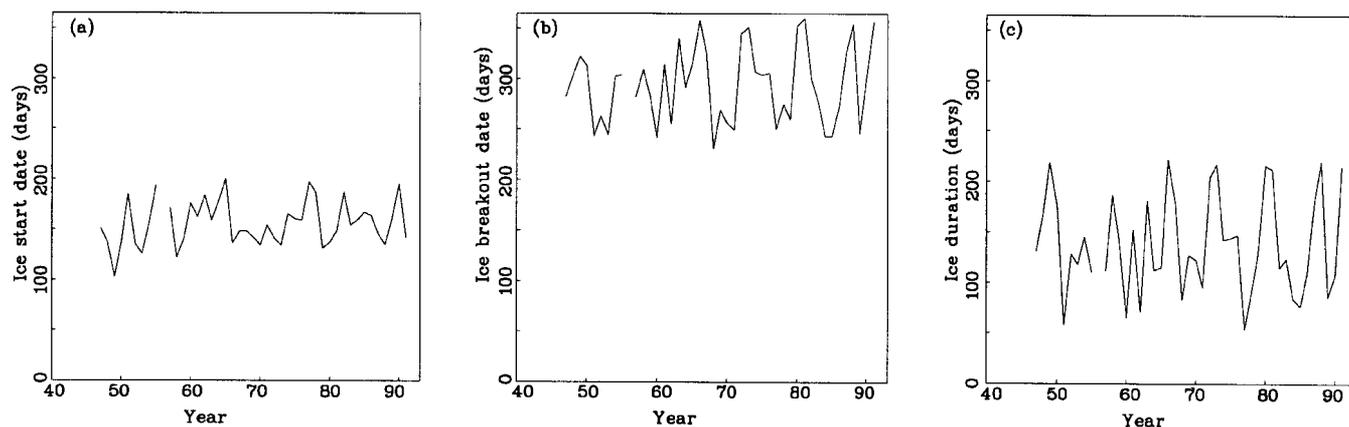
Fig. 2a–c Sea ice data for Factory Cove, Signy Island, 1947–1992 a ice start date, b ice breakout date, and c sea ice duration. Units are julian days

1985a), sea ice can remain locally until early February, coinciding with the normal date of fledging for Adélie chicks (mean of day 37; range 35–46) and mid-way through the rearing period of chinstrap chicks, which fledge later (mean of day 60; range 56–61) (Lishman 1985a). In contrast the date of ice arrival is in early June (mean of day 156) and is well after the end (March/April) of the penguin breeding and moulting season.

Regional sea ice extent

Fluctuations in the position of the ice-edge along longitude 46°W (Signy Island lies at approximately 60°43'S, 45°C38'W) showed no discernable trend with time (Fig. 3a,b). Murphy et al. (1995) have shown that recent regional anomalies in the maximum sea ice extent field process around the Antarctic Continent with a periodicity of approximately 7 years and that these correspond to a pronounced 7- to 8-year cycle in the fast-ice duration at Signy Island. Thus, despite the short extent of the regional statellite data (17 years), the data set shows strong correlations with the Signy Island sea ice data (Murphy et al. 1995). This suggests that there were no major local anomalies at Signy Island and that the Signy Island time series reflects the larger-scale ice dynamics of the southern Scotia Sea.

Penguin breeding population size

For both Adélie and chinstrap penguins, there was considerable inter-annual variation in the number of pairs breeding at each colony, as well as in the total number of breeding pairs summed over all colonies combined (Fig. 4a,b). During the study period, no significant long-term trend was evident in the size of either the separate Adélie colonies or of the overall population. For the chinstraps, however, a small but significant decline ($P < 0.05$) was apparent in the size of the overall population.

Due to the decline in the chinstrap population, all subsequent analyses for the species were carried out twice, using either population counts that were adjusted, or that were unadjusted, for the trend. No material differences were found between the two sets of results; only the results based on the unadjusted data are presented here.

For Adélie penguins, a PCA was carried out based on the normalised and lagged counts of the breeding pairs at the five colonies. The first 2 eigenvectors from the analysis accounted for 69% of the included variation and a plot of the principal components (Fig. 5a) showed that 4 of the colonies (colonies 1, 2, 3 and 4) were similar in their pattern of variability, whereas the other colony (colony 41) was different. The colonies that were alike had similar principal component loadings with the various time lags also having comparable loadings. The relative difference in the loadings for the individual lags (1, 2, 3 and 4 years) suggests that each colony varied in a similar manner. The dissimilar colony (colony 41) is situated at Pageant Point at the south-east end of Signy Island, whereas the other colonies are all situated at North Point, some 7 km distant at the northern end of the island. These results suggest that local factors, either earlier in the year or possibly at the time that the birds first arrived in the colony area, may influence the numbers that breed.

A similar PCA carried out for the four separate chinstrap colonies generated eigenvectors where the first two accounted for 61% of the included variation. The four chinstrap colonies (Fig. 5b) had similar principal component loadings, with the various lags also having comparable loadings. The relative difference in the loadings for the separate lags (1, 2, 3 and 4 years) also suggests that each chinstrap colony varied in a similar manner. Colony 47, situated in Clowes Bay, is some 1.5 km distant from the other colonies (colonies 79, 80, 81) at Pageant Point, yet is still showed

Fig. 3a, b Sea ice data along 46°W (Signy Island), 1973–1988 **a** monthly maximum extent, and **b** monthly extent showing long-term maximum, minimum, median and quartiles
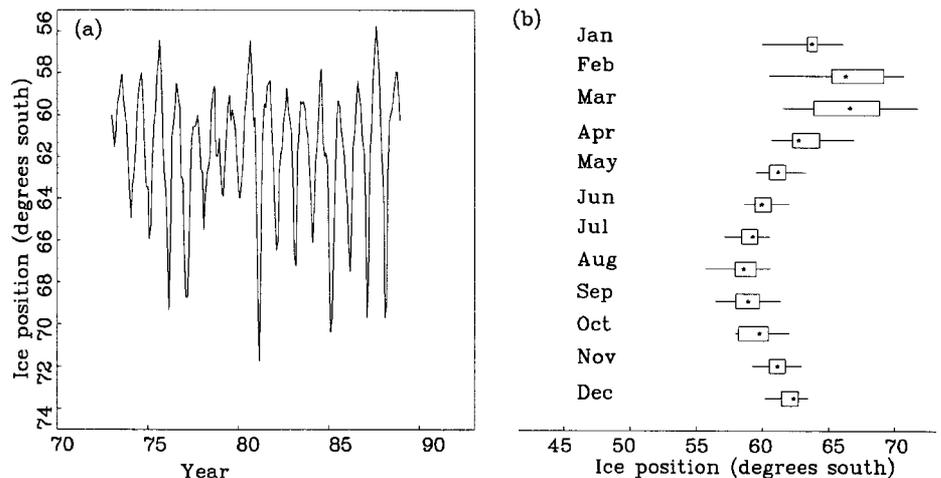
Fig. 4a–f For Adélie and chinstrap penguin combined populations at Signy Island 1979–1992 **a, b** number of breeding pairs, **c, d** number of eggs hatching per pair, and **e, f** number of young fledging per pair
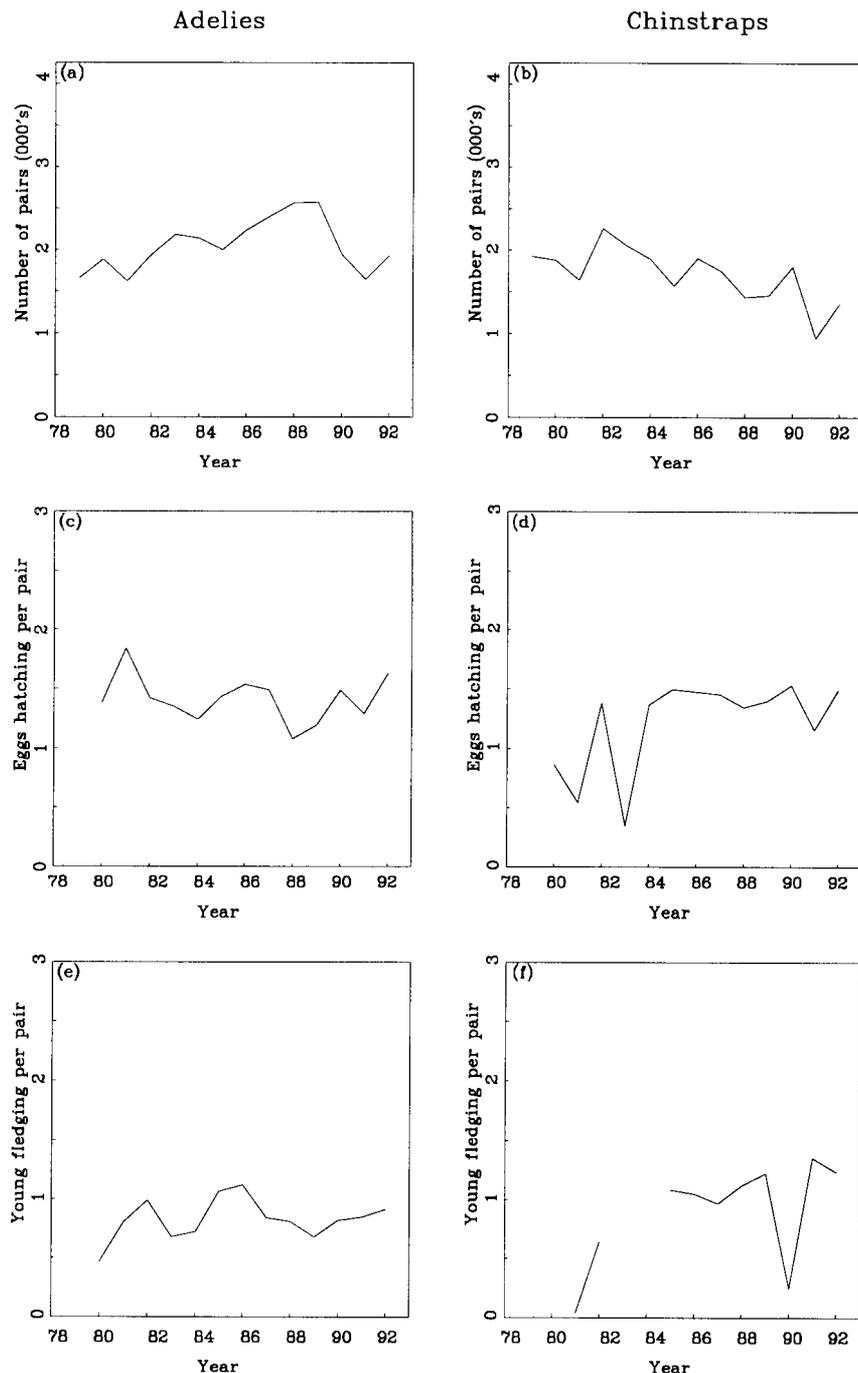
the same inter-annual pattern in the loadings for the separate lags.

The PCAs suggest that the inter-annual variability in colony size was different for the two penguin species, but generally similar for the colonies of the same species. For subsequent analyses involving the number of breeding pairs, all colonies of each species (except for Adélie colony 41) were grouped into a single larger population. If Adélie colony 41 was included the results were comparable, though slightly less clear.

Penguin breeding success

At the different Adélie and chinstrap colonies, hatching success and fledging success showed considerable inter-annual variability; however, no significant long-term trends were apparent when expressed as counts per breeding pair. For both species, the overall population counts summed from the combined colonies also showed similar patterns of variability (Fig. 4c–f), but again no significant trends were apparent. Compared

Fig. 5a, b First 2 components
from the PCA including the
separate **a** Adélie colonies
(1, 2, 3, 4 and 41), and **b** chinstrap
colonies (47, 79, 80 and 81):
Signy Island 1979–1992. Lag 0 is
indicated by the *colony number*
with other lags indicated by
+ *1*, + *2*, + *3* and + *4*
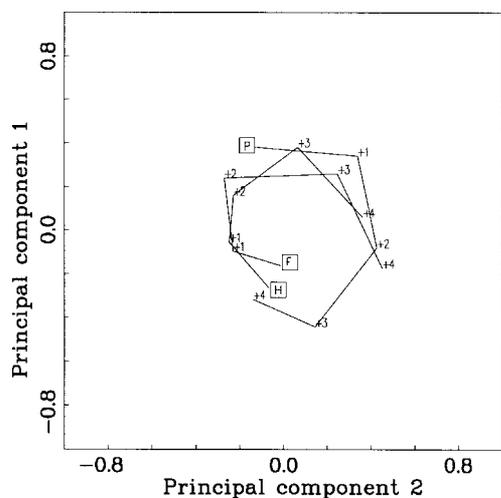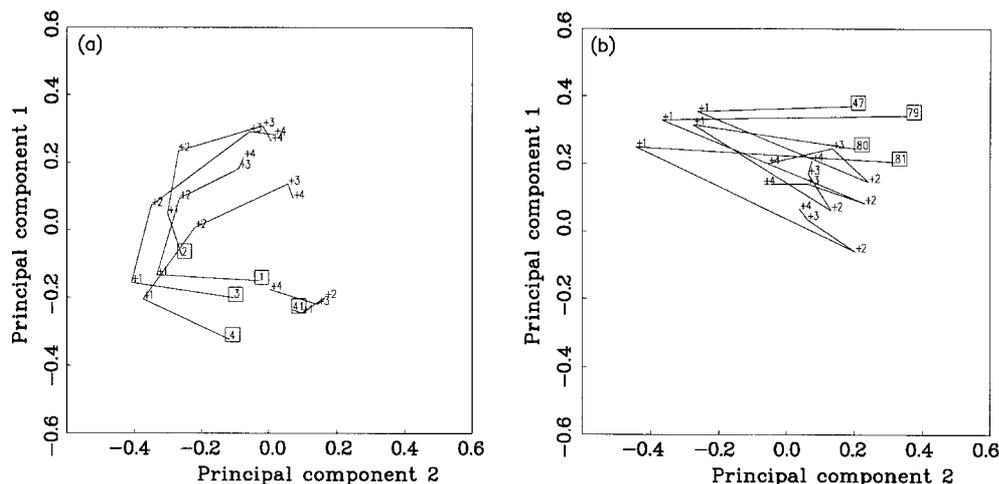
Fig. 6 First 2 components from the PCA including the number of
pairs of Adélie penguins (*P*), the number of eggs hatching per pair
(*H*) and the number of young fledging per pair (*F*): Signy Island
1979–1992. Lags are indicated by + *1*, + *2*, + *3* and + *4*

to the overall average, chinstrap penguins showed very
poor reproductive performance in a number of years,
whereas in others performance was relatively consis-
tent. This is evident for the different chinstrap colonies
as well as for the overall population.

For the Adélie penguins, a PCA was carried out
based on the number of breeding pairs, the number of
eggs hatching per pair and the number of chicks fledg-
ing per pair. The first two eigenvectors accounted for
56% of the variation and a plot of the principal compo-
nents (Fig. 6) showed that the number of eggs hatching
per pair and the number of chicks fledging per pair
varied in a similar manner, whereas the number of
breeding pairs varied in a different way. The number of
eggs hatching per pair and the number of chicks fledg-
ing per pair had similar component loadings, with
the various lags also having comparable loadings. The

relative difference in the component loadings for
the individual lags (1, 2, 3 and 4 years) suggests that
both hatching and fledging success varied in a similar
manner. As the breeding data are expressed on a per
pair basis, the relationship is not simply a reflection
of the population size. Thus, the linear regression
(y = 66.6 − 0.465x) based on the unlagged number of
breeding pairs and the unlagged number of eggs hatch-
ing per pair has a negative slope ($F_{1,11} = 5.56$;
$P < 0.05$), whereas the linear regression (y = 20.7 +
0.580x) based on the number of eggs hatching and
the number of chicks fledging has a positive slope
($F_{1,11} = 5.09$; $P < 0.05$). This inverse relationship
between population size and hatching (but not fledging)
success was the only significant interaction between
population size and breeding success for Adélie
penguins.

Due to gaps in the chinstrap penguin breeding data,
it was not practical to carry out a PCA that included
fledging counts; however, a PCA was carried out based
on the number of breeding pairs and the number of
eggs hatching per pair. The first two eigenvectors from
this analysis accounted for 64% of the variation; how-
ever, based upon the principal component loadings, the
number of breeding pairs and the number hatching per
pair did not vary in a related way. The relative differ-
ence in the component loadings for the separate lags
(1, 2, 3 and 4 years) also suggests that there was no
similarity.

Interactions between penguin breeding population and performance and Signy Island sea ice duration

The Signy Island data on sea ice, though reflecting the
larger-scale sea ice dynamics of the southern Scotica
Sea (Murphy et al. 1995), can be used to test whether
local sea ice affects either the breeding numbers or the
breeding success of Adélie and chinstrap penguins. In
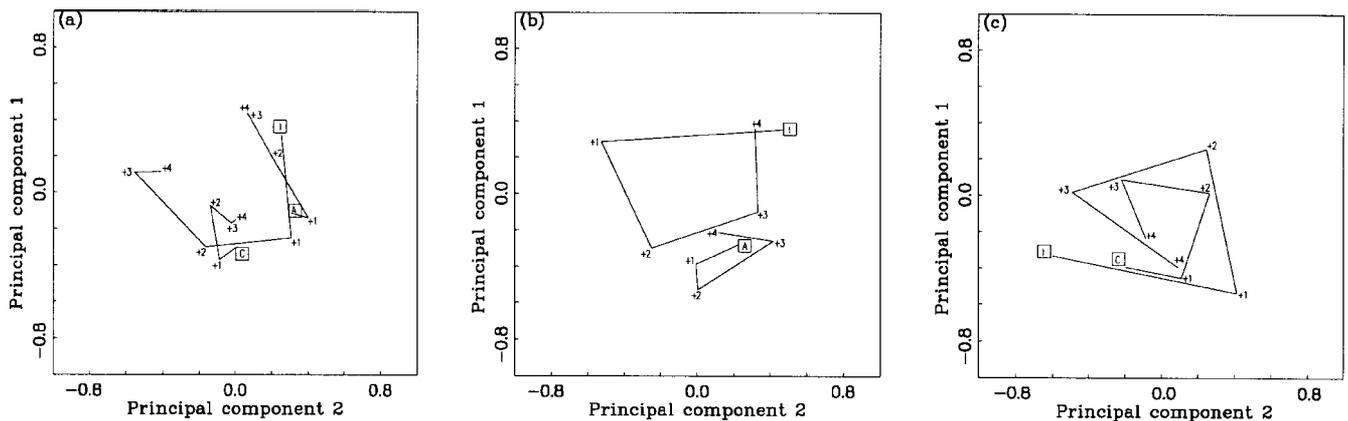
Fig. 7a–c First 2 components from the PCA including **a** local sea ice duration (*I*), number of breeding Adélie pairs (*A*) and number of breeding chinstrap pairs (*C*), **b** regional sea ice extent (*I*) and number of breeding Adélie pairs (*A*), and **c** regional sea ice extent (*I*) and number of breeding chinstrap pairs (*C*) : Signy Island 1979–1992. Lags are indicated by + *1*, + *2*, + *3* and + *4*

order to look for interactions, a number of PCAs were carried out to examine the relationship between the penguin breeding data and the date of arrival, duration and breakout of sea ice at Signy Island.

There was no evidence of any general relationship between either penguin breeding population or performance and the local sea ice conditions at Signy Island. Thus, the PCA based on the overall counts of Adélie and chinstrap breeding pairs and the Signy Island sea ice duration (Fig. 7a) indicated that there was no consistent pattern of variation. The relative difference in the principal component loadings for the separate lags (1, 2, 3 and 4 years) suggests that variability in the number of breeding pairs did not reflect variability in the local sea ice conditions.

The absence of general relationships suggests that local sea ice duration at Signy Island was unlikely to be the major factor controlling the variability in the number of breeding pairs, or the breeding success of either penguin species. In extreme years, however, sea ice conditions at Signy Island can have a major influence on the number of birds arriving to breed and/or on breeding success, especially of chinstrap penguins (Lishman 1985a; Croxall et al. 1988).

Interactions between penguin numbers and the regional sea ice extent

The location and extent of sea ice may affect food availability and/or foraging ability during the breeding season (see Lishman 1985a). Sea ice distribution may also be important at other times of the year and may determine where birds forage (Fraser et al. 1992) and therefore how well they feed. As a result, sea ice may

affect the number of adult birds that survive or that attain breeding condition and arrive at the colony to mate (Spurr 1975). Therefore, we used the weekly regional sea ice data to look for interactions at broader scales and at other times of the year. We conducted a number of PCAs to examine the variability in the penguin census data and the weekly sea ice extent along 46°W for the months prior to the September to April breeding season.

The weekly sea ice extent during individual months and during consecutive groups of months was examined to determine whether particular periods influenced the variability in the number of breeding pairs. In these analyses, the mean sea ice position was derived from the mean of the weekly ice-edge positions for those months included. For both Adélie and chinstrap penguins, a period was found where the variance explained in the PCA was maximised and where this figure decreased if the period was moved either earlier or later in the year.

For the PCAs based on the number of Adélie penguin breeding pairs and the regional sea ice extent, the late autumn/early winter months (June and July) maximised the variance explained. In this analysis the first two eigenvectors accounted for 70% of the included variation. The relative differences in the component loadings for the individual lags (1, 2, 3 and 4 years) suggest that the number of breeding pairs and the sea ice extent varied in a similar manner (Fig. 7b); however, the actual loadings on the first component were generally much higher for the sea ice than for the number of breeding pairs. A linear regression (y = 64.0 − 0.223x) based on the unlagged number of breeding pairs of Adélies and the unlagged sea ice extent data was not significant ($F_{1,9} = 0.35$; $P > 0.05$), but also suggested that there may be an inverse relationship between the number of breeding pairs and the maximum sea ice extent in early winter.

For the PCAs based on the number of chinstrap penguin breeding pairs and the regional sea ice extent, the early winter months (July and August) maximised the variance explained. The first two eigenvectors accounted for 68% of the included variation. The

component loadings for the number of breeding pairs were similar to the loadings for the sea ice extent and the relative differences in the loadings for the individual lags (1, 2, 3 and 4 years) suggest that the number of pairs and the sea ice extent varied in a similar manner (Fig. 7; c). This relationship was opposite to that suggested for the Adélies; it was also much more clear. A linear regression (y = 34.5 + 0.52x) based on the unlagged number of breeding pairs of chinstraps and the unlagged sea ice extent data ($F_{1,9} = 7.64$; $P < 0.025$) indicated that there was an apparent increase in breeding numbers following years when the maximum sea ice extent in early winter was further south than average.

Discussion

Sea ice duration and extent

At Signy Island there is little evidence for any trend with time (Murphy et al. 1995), either locally in terms of sea ice duration (Fig. 2a, b, c) or regionally in terms of sea ice extent (Fig. 3a, b). In contrast, Jacobs and Comiso (1993) reported a relationship between reduced sea ice cover and increasing surface air temperatures west of the Antarctic Peninsula. Recent warming trends, however, have not been constant throughout the Antarctic (Jacka et al. 1984), so the absence of a clear trend in the Signy Island sea ice duration or in the regional sea ice extent may not be surprising.

Although representative of the southern Scotia Sea, the strong correlation at Signy Island between the local sea ice duration and the regional sea ice extent (Murphy et al. 1995) may not be typical of the conditions at King George Island, South Shetland Islands, where the study colonies of Fraser et al. (1992) are located. Thus, the characteristics of sea ice around Signy Island could be very different from those close to the South Shetland Islands where the influence of the Bellingshausen Sea and the topography of the Bransfield Strait will be important.

Penguin populations and productivity

The dynamics of the Adélie and chinstrap penguin populations at the study colonies on Signy Island are broadly in accord with other recent data sets recorded from the Antarctic Peninsula region (see review in SC-CAMLR 1992). These data sets (SC-CAMLR 1992) show little evidence of systematic directional change in populations of Adélies or chinstraps since the 1980s, but suggest small decreases in chinstrap numbers at some localities. Nevertheless, the overall general stability of Adélie and chinstrap penguin populations since the late 1970s does not affect the conclusion that, for all

adequately documented populations of both species in the Antarctic Peninsula region, breeding populations increased between the 1940s (the date of the first quantitative records) and the mid-1970s (Croxall and Kirkwood 1979; Croxall et al. 1981; Poncet and Poncet 1985, 1987). Where adequate data exist, chinstraps undoubtedly increased faster than Adélies.

The Signy Island data on Adélie and chinstrap penguin breeding productivity show no trend, whether expressed as hatching, chick rearing or overall breeding success. The inverse density-dependent relationship between population size and hatching success in Adélie penguins may reflect a tendency for more pairs to fail when conditions ashore are particularly crowded near the beginning of the breeding season. Beyond this, there is no suggestion of any systematic relationship between breeding population size and breeding success for either species. Thus, when conditions favour a large breeding population, they do not necessarily favour a high level of breeding success. This is not surprising given that the breeding population size reflects conditions over a wide area and during an extended period, whereas breeding success primarily reflects food availability relatively close to the breeding colony during a 6-week period in the summer.

Interactions between sea ice and penguins

The evidence from Signy Island suggests that at the population level, there is no systematic relationship between penguin breeding success and local sea ice duration (Fig. 7a) or between breeding success and regional sea ice extent. However, the number of breeding pairs of both penguin species does appear to be related to the regional sea ice conditions during a period outside the breeding season, with the number of breeding pairs varying in a manner related to the maximal sea ice extent (Fig. 7b, c). Therefore, it is possible that the condition of the regional sea ice in the areas where penguins forage after one breeding season ends and before the next starts, is of major importance for over-winter survival, or for regaining breeding condition. Our results suggest that late autumn/early winter is a critical time for Adélie penguins (Fig. 7b) that finish breeding and moulting in February/March, whereas early winter may be more critical for chinstraps (Fig. 7c), which do not complete their moult until April. This relationship, however, is much stronger for chinstrap than for Adélie penguins.

Our results indicate some of the potential complexities in the relationships between penguins and sea ice and help develop the simple model suggested by Fraser et al. (1992).

The fact that relationships are complex is not surprising given that the number of breeding pairs in any single year is the result of changes in annual adult survival combined with juvenile survival over several

years. Furthermore, survival rates are the result of a complex mixture of factors (e.g. age, status or condition), all of which are likely to be modified by the biological (e.g. food availability) and/or physical (e.g. sea ice) environment. As such, it is unlikely that penguin population size would show any simple relationship to sea ice conditions or that penguin population dynamics, or inter-specific differences in population dynamics, would simply reflect a trend in sea ice conditions. Although a simple relationship may be unlikely, the physical environment, in particular that relating to sea ice, could have a significant effect upon penguin population dynamics. However, in order to fully understand any complex relationship, additional data will be required.

There is increasing evidence (Plötz et al. 1991; Joiris 1991; Ainley et al. 1993, 1994) to suggest that in winter Adélie penguins are primarily birds of the pack ice whereas chinstraps are to be found in the marginal sea ice zone or in open water. Therefore, if the two species winter in separate habitats, it is logical to expect a different response to the properties of sea ice. Thus, the response of penguins to seasonal sea ice extent may reflect the structure and dynamics of sea ice and its associated biological communities, especially those that provide food for penguins. However, at present we have only very limited data on the diet of Adélie and chinstrap penguins outside the breeding season, although there are indications (Ainley et al. 1992) that fish may play a more important role in winter than they do in summer, when Antarctic krill (*Euphausia superba*) are the main food source (Lishman 1985b; Trivelpiece et al. 1987). Furthermore, data on the geographic distribution of the main prey species of penguins, as well as data on the degree of association between these prey and the seasonal sea ice regime are entirely inadequate to assess the nature of predator-prey interactions, let alone suggest how these may vary in relation to the distribution and extent of sea ice in different years. For example, there still remains considerable uncertainty regarding the dependence of krill upon winter sea ice, both in terms of feeding and distribution. Hence, at present we are almost entirely ignorant of what features of the winter biological and physical environment are of key importance in determining the distribution, density, condition or future breeding status of penguins.

Trying to unravel the seasonal interactions (and their balance) between the physical and the biological environment of penguins and their demographic processes will be a major challenge. In addressing this a number of things are certain to be required: detailed long-term study of penguin population dynamics, accurate data on the distribution, extent (and characteristics) of sea ice throughout the annual cycle of advance and retreat, and in situ studies of penguin-prey-environment interactions in the pack-ice zone, complemented by remote sensing studies of the locations of penguins and their prey within this environment.

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