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Southern Ocean Environmental Changes: Effects on Seabird, Seal and Whale Populations [and Discussion]

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Southern Ocean environmental changes: effects on seabird, seal and whale populations

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SUMMARY

The main changes in the distribution and abundance of marine top predators in the Antarctic in the last two centuries were caused by human over-exploitation. Hypotheses that increases in populations of krill-eating penguins and seals represent recovery from exploitation, accelerated by removal of krill-eating whales, are being re-evaluated in the light of correlations between population size and reproductive success of seabirds and seals and various features of the biological and physical environment. These correlations involve phocid and otariid seals, penguins and flying birds and sites ranging from the Antarctic continent to sub-Antarctic islands. Although the nature of, and balance between, physical and biological influences differ between sites, regions and different types of predator, processes (including potentially important links with the Southern Oscillation) involving sea-ice extent and distribution play a key role. Major uncertainties over the nature of the links between physical and biological processes and the responses of marine populations preclude any confident prediction of the potential effects of future environmental change. However, certain taxa, especially those of specialist ecology, extreme demography and restricted distribution (especially in high latitudes) are especially vulnerable to at least some of the likely environmental changes.

1. INTRODUCTION

The community of seabird, seal and whale top predators in the Antarctic marine system is probably the most abundant numerically and the most significant in terms of energy flux of any in the world. However, trying to use knowledge of past, recent and present population changes to assess the likely response of these predators to environmental change is difficult for several reasons.

First, the fossil record of these groups in Antarctica is very sparse and offers few clues to their history, especially in relation to the substantially different environments that have characterised the Antarctic since the initial appearance of penguins (early Eocene), whales (late Eocene) and seals (mid Miocene) (Fordyce 1989; Fordyce & Jones 1990). A considerable diversity of whales (both odontocetes and mysticetes) and penguins was extant in the late Oligocene, after a long period of cooling (to cool temperate conditions). This fauna apparently persisted through warming in the early Miocene but diversity decreased with the major cooling in late Miocene. Lobodontine seals radiated in the cool late Miocene, perhaps excluding otariid seals from higher latitudes (Fordyce 1989). Marine mammal and seabird faunas were probably broadly ecologically and taxonomically similar to present day ones by the Pliocene, indicating persistence in some form through subsequent glacial–interglacial cycles.

Second, almost all the documented population changes of seals, seabirds and whales relate to human exploitation causing changes of a magnitude far greater than any potentially cooccurring natural events (see below).

Third, quantitative data on population sizes and trends are virtually absent prior to the 1950s and very scarce before the mid-1970s. There are very few continuous datasets covering more than 15 years, a short time in relation to the suggested periodicity of significant fluctuations in the physical environment of Antarctica.

Fourth, we are dealing with highly mobile species (although seabirds and seals are constrained to some extent by the need to breed on land or ice) exploiting a remote marine environment whose biological and physical properties and interactions are poorly known at all spatial scales (Murphy *et al.* 1988). A crucial gap is understanding how the physical environment influences the distribution and abundance of the prey on which these predators depend.

Fifth, most seabirds, seals and whales have low reproductive and mortality rates and long generation times; responses to environmental change are therefore slow, hard to detect and difficult to interpret. Nevertheless, there is substantial variation in demo-

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Table 1. *Some demographic characteristics of Southern Ocean seals, seabirds and whales*

(Parentheses indicate only one species.)

species	age (years) at first breeding		adult survival (mean annual) (%)	breeding frequency (years)
	min.	mode		
penguins	(2)–3–6	3–8	80–90–(95)	(0.6)–1
albatrosses	6–8	9–12	90–95	0.5–1
petrels	3–7	5–9	90–95	(0.5)–1
seals	3	4–5	80–90	1
whales		5–8	?	0.5–(1)

graphy within and between the three major groups (table 1). Seals and albatrosses lie at opposite ends of the spectrum; in all but their deferral of sexual maturity, penguins cover the range of the other groups, showing significant interspecies variation. The significance of this demographic variation is that we should not necessarily expect different species to respond to environmental change at the same speed or in the same way.

Sixth, there is little detailed understanding of the mechanisms by which Southern Ocean top predator populations are regulated. Most species are unlikely to be limited by the availability of breeding sites. Populations are generally thought to be regulated ultimately by food supply (although the balance between summer and winter effects is much debated) and proximately by some combination of food supply, environmentally induced stochasticity and the interactions between these (Croxall & Rothery 1991; Testa *et al.* 1991).

Against this background, this paper reviews: (i) the main historical changes in seabird, seal and whale populations, essentially the results and aftermath of human exploitation; (ii) current patterns of population change; (iii) evidence for direct and indirect interactions between population processes and elements of the biological and physical environments; (iv) implications of the foregoing in terms of future environmental change, including requirements for improved investigation of key relationships.

The main area under consideration here is Antarctica and its surrounding ocean north to the Antarctic Polar Front (referred to here as the Southern Ocean). Many details of the biology and ecology (particularly with respect to marine food webs) of the animals and environments considered are to be found in Laws (1984*a*), Siegfried *et al.* (1985), Croxall (1987*a*) and Kerry & Hempel (1990) and in references therein. Most of these sources focus on the major subsystem centred on Antarctic krill *Euphausia superba*. Especially away from the South Atlantic and Antarctic Peninsula regions, other food-web subsystems, especially involving squid and myctophids at lower latitudes and *Pleuragramma* and *Euphausia crystallorophias* at higher latitudes, are also important. Furthermore, there are significant changes in trophic relations between summer and winter, particularly in the extensive circum-Antarctic marginal ice zone, with diminished importance of krill and increased importance of other zooplankton, nekton and fish in winter (Ainley *et al.* 1986, 1991).

2. HISTORICAL AND CURRENT CHANGES IN POPULATIONS

Most exploitation of seals, seabirds and whales was centred on the sub-Antarctic islands. Antarctic and sub-Antarctic fur seals *Arctocephalus gazella* and *A. tropicalis* were exploited virtually to extinction in the 18th and 19th Centuries. Recovery of *A. gazella* started earlier (around 1940) and faster (17% per annum from 1958 to 1973) at South Georgia than elsewhere. This population is now increasing at around 10% per annum (Boyd 1992) and, despite substantial emigration to islands along the Antarctic Peninsula, South Georgia still holds more than 95% of the world population, with numbers probably well in excess of pre-exploitation levels (Bonner 1985). Sub-Antarctic fur seals increased through the 1970s at around 10% per annum but more recent data from the two main sites, at Gough and Amsterdam Islands, are lacking.

Southern elephant seals *Mirounga leonina* were very significantly reduced in numbers, mainly in the 19th Century. Sealing at Macquarie Island stopped in 1919; by the 1950s the population had recovered to a level (156000) judged to be 50% above the (rough) estimate of pre-exploitation stock (Hindell & Burton 1988). Subsequently there has been a steady decline, to a level (90000) around that of the pre-exploitation estimate (Hindell 1991), that mirrors declines at all other islands in the Indian Ocean (Skinner & Van Aarde 1983; Pascal 1986). At South Georgia sealing was strictly regulated after 1910 and stock size appears not to have changed since sealing ceased in 1964 (McCann & Rothery 1988). Other seal species were not or not significantly, exploited. Evidence for increasing crabeater seal *Lobodon carcinophagus* populations in the 1950s and 1970s (Laws 1984*b*) is equivocal (Bengtson & Laws 1985). Critical comparison of census data from 1968–69 and 1969–70 with 1983–84 suggests a reduction in seal density of 30–60% (after allowing for reductions in the 1968 estimate due to improved analytical techniques) (Erickson & Hanson 1990). Other seal populations have fluctuated significantly but without obvious or persistent trends (Croxall & Hiby 1983; Testa & Siniff 1987; Testa *et al.* 1990, 1991).

Whale harvesting involved consecutive over-exploitation of each species of Southern Ocean whale, reducing populations to 5–10% of pre-exploitation levels. The exception to this was the smallest species of baleen whale, the minke whale *Balaenoptera acutorostrata*, which was only exploited at the end of the whaling era. Its current population size is estimated to be about double that of initial levels (Gambell 1987).

Of sub-Antarctic penguins, king penguins *Aptenodytes patagonicus* were exploited for oil (and food) during the sealing era of the 18th and 19th Centuries. Subsequently king penguins have increased very substantially at all breeding sites (Rounsevell & Copson 1982; Gales & Pemberton 1988; Jouventin & Weimerskirch 1990). At South Georgia the rate of increase in the early 1980s (12% per annum) was substantially faster than in the previous 60 years (Croxall *et al.* 1988). Evidence for exploitation of the smaller crested penguins *Eudyptes* spp. is equivocal. Data on their population changes are anecdotal but may indicate increases, at least at South Georgia in the 1960s (Croxall *et al.* 1988). In the late 1970s macaroni penguins *Eudyptes chrysolophus* at South Georgia decreased by almost 50% over five years but have remained stable subsequently (J. P. Croxall, unpublished data). Truly Antarctic penguins were not exploited. All adequately documented populations of Adelie and chinstrap penguins *Pygoscelis adeliae* and *P. antarctica* in the Antarctic Peninsula region increased between the late 1940s (the date of the first quantitative records) and the mid 1970s (Croxall & Kirkwood 1979; Croxall *et al* 1981; Poncet & Poncet 1985, 1987). In the last decade or so these Adelie and chinstrap populations have fluctuated without any clear overall trend (Trivelpiece *et al.* 1990, Fraser *et al.* 1992, J. P. Croxall, unpublished data). Antarctic continent populations of Adelies appear to have been more stable (albeit based on very few data). Population declines in the late 1960s in the Ross Sea were followed by substantial increases from 1982 onwards (Taylor *et al.* 1990; Wilson 1990). Populations in Adelie Land increased between 1960 and 1985 (Jouventin & Weimerskirch 1991) and monitored colonies at Prydz Bay, east Antarctica also increased between 1982 and 1988 (Whitehead *et al.* 1990). Few population data exist for emperor penguins *Aptenodytes forsteri*; the colony in Adelie Land, stable from 1962 to 1976, declined by 50% in the next decade (Jouventin & Weimerskirch 1990) but other colonies have remained broadly stable (Woehler 1992).

Long-term regular population data for petrels (none of which were directly exploited by man) are very limited. Both species of giant petrel have decreased in the 1980s at Ile de la Possession (Iles Crozet) and southern *Macronectes giganteus* (but not northern *M. halli*) giant petrels at Bird Island (South Georgia) (Croxall *et al.* 1984; Jouventin & Weimerskirch 1991). Southern giant petrels have also decreased at all other breeding sites (except Anvers Island) where reliable data exist (Croxall *et al.* 1984; Croxall 1987*b*) but many, if not most, of these are close to manned stations and giant petrels (and the southern species in particular) are very susceptible to disturbance. Many other petrel species have decreased on sub-Antarctic islands which have introduced predators (such as cats, rats, pigs) (Croxall 1987*b*; Jouventin & Weimerskirch 1991). These situations will not be discussed further here. In Adelie Land, Antarctic fulmar *Fulmarus glacioloides* and snow petrel *Pagodroma nivea* populations have fluctuated considerably between 1964 and 1988, the former maintaining status, the latter increasing somewhat (Jouventin & Viot 1985; Jouventin & Weimerskirch 1991). Exploitation of albatrosses (mainly eggs for food) virtually stopped in the 1950s (Croxall *et al.* 1984) and effects of this today will be minimal. Wandering albatrosses *Dionedea exulans* have decreased substantially over the last 20 years at all breeding sites (Croxall 1979; Weimerskirch & Jouventin 1987; Croxall *et al.* 1990). The main cause of this is incidental mortality associated with commercial fishing operations, mainly outside the Southern Ocean. This is now well documented and will not be discussed here further. Black-browed albatrosses *Diomedea melanophris* decreased at Kerguelen from 1962 to 1982 (Jouventin & Weimerskirch 1991) and at Bird Island from 1978 to 1981 but thereafter remained broadly stable (P. A. Prince, unpublished data). Grey-headed albatrosses *D. chrysostoma* at Bird Island have shown a fluctuating decline over the past 10 years (P. A. Prince, unpublished data).

3. CORRELATIONS WITH CHANGES IN BIOLOGICAL AND PHYSICAL ENVIRONMENTAL PROCESSES

It is almost axiomatic that changes in population processes of top predators reflect the direct, indirect and interlinked influences of biological and physical environmental variables. Most of the relevant predator data available for examination are annual population counts (usually of breeding animals); for some sites we also have data on reproductive performance (e.g. proportion of offspring reared to independence, duration of parental foraging trips, offspring mass at independence, etc.). These two kinds of variables are likely to respond to and reflect interactions with the environment in difference ways and on different timescales. Thus breeding success reflects events with a relatively short time span, usually 2–4 months (penguins, fur seals, most albatrosses). Other indices of reproductive performance may operate over even shorter periods (days–weeks). Changes in breeding performance should therefore relate, at least in the proximate sense, to relatively current or recent phenomena. However because parental age, experience and intrinsic individual quality can significantly effect breeding performance (e.g. Croxall *et al.* 1992), changes in population structure can also influence breeding success. In contrast, population size reflects survival of breeding animals since the previous year (modified by the extent to which surviving previous breeders do not breed), combined with the recruitment rate, which is itself a reflection of breeding success several years previously coupled with post-independence juvenile survival. (For most species under consideration emigration–immigration rates or philopatry are probably reasonably consistent from year to year, this is most true for albatrosses, least true for fulmarine petrels and possibly also fur seals.) Thus changes in population size will reflect the sum of various factors which may operate more or less independently and react on different timescales.

After the era of direct human exploitation, most of the detectable changes in top predator populations were increases (table 2). Explanation of these changes tended to focus on the proposition that the huge amount (*ca.* 150 million tonnes; Laws 1977*a*,*b*, 1985)

Table 2. *General population trends in some Antarctic top predators*

species	exploited	main food	change	
			recent	current
minke whale	Y	krill	increase	increase
other baleen whales	YYY	krill	stable?	stable?
crabeater seal	N	krill	increase?	decrease?
Weddell seal	N	fish	stable	stable
elephant seal	YY	squid, fish	?	decrease
Antarctic fur seal	YYY	krill	increase	increase
sub-Antarctic fur seal	YYY	mixed	increase	increase
emperor penguin	N	fish	stable	stable or decrease
king penguin	YY	fish	increase	increase
Adelie penguin	N	krill	increase	stable or increase
chinstrap penguin	N	krill	increase	stable or increase
macaroni penguin	N	krill	increase	decrease?
black-browed albatross	N	krill	stable?	stable or decrease
grey-headed albatross	N	squid	stable?	decrease
wandering albatross	N	squid	decrease	decrease
southern giant petrel	N	various	decrease	decrease
fulmarine petrels	N	krill, fish	increase?	stable

of krill once consumed annually by the baleen whales removed from the Southern Ocean system would have been redistributed throughout this system with other top predators being especial beneficiaries. Thus increases in the 1950s and 1960s in the krill-eating Adelie and chinstrap penguins and putative increases in krill-eating crabeater seals were regarded as directly attributable to the increased availability of krill; the very high rates of increase in the krill-eating Antarctic fur seals were attributed to recovery from exploitation accelerated by enhanced krill availability (e.g. Sladen 1964; Croxall & Prince 1979; Laws 1985). This hypothesis (the so-called 'krill surplus') rapidly became the widely accepted explanation for most, if not all, increases in seabird and seal (and minke whale) population. However, it had always been recognized that the 'krill surplus' concept would mainly apply to the areas of major whaling (i.e. especially the South Atlantic sector) and that many areas around the Antarctic continent (and perhaps especially the Ross Sea), where predators depended as much, if not more, on euphausiids other than *E. superba* and where whale and seal populations had historically been relatively small, could easily show different population trends. Nevertheless, there are some compelling reasons for taking the krill surplus hypothesis seriously, even though it cannot be critically evaluated because of the almost total lack of relevant data from the appropriate period. First, the removal of baleen whales was probably the most significant short-term perturbation the Southern Ocean ecosystem had ever sustained. Second, complex systems once perturbed are highly unlikely to return to previous equilibria (May *et al.* 1979). Third, krill, with its vast population but patchy distribution might be just the type of resource to sustain long term increases in its predators until they become limited by some combination of density-dependent processes or the difficulties of consistently locating adequate krill concentrations, particularly at times of year when the distribution of predators or prey might be constrained (e.g. by breeding, distribution of ice, etc.). Fourth, recovery rates and reproductive performance of species in areas of high krill abundance are faster or better than elsewhere.

Even increases in populations of species which do not themselves eat krill (e.g. king penguins, blue-eyed shags (Shaw 1984), Antarctic skuas (Hemmings 1984)) could conceivably relate to greater availability of krill to the species which these predators do eat (fish, squid). Indeed many fish and squid are known to eat krill (Targett 1981; Nemoto *et al.* 1988), although its importance to their diets may be exaggerated by the location of studies and the fact that many species were sampled in association with krill swarms (Rodhouse *et al.* 1992).

Subsequent investigation of correlates of population change has mainly used short to medium-term (5–15 years) datasets to examine changes at more restricted temporal and spatial scales. Croxall *et al.* (1988) contrasted the relative importance of biological and physical influences on the population processes of birds and seals at South Georgia (54°S) and the South Orkney Islands (61°S). At South Georgia the reproductive performance of the krill-eating species monitored (gentoo penguin *Pygoscelis papua*, marconi penguin, Antarctic fur seal, black-browed albatross) was significantly depressed in years of very reduced availability of krill. In contrast, squid and fish-eating species (grey-headed and wandering albatrosses) were essentially unaffected. For the former group of species there were often associated changes in breeding population size, usually in the succeeding season (and primarily due to adult mortality), sometimes in the same season (when mainly due to failure to breed by previous-breeding surviving adults). Croxall *et al.* (1988) also noted that the two years (1984, 1987) of major unavailability of krill to predators (and commercial fisheries) each occurred one year after a major El Nino Southern Oscillation (ENSO) event. However in 1990–1991 there were major reductions in reproductive performance in all krill-eating species, apparently unassociated with any ENSO event. The magnitude and persistence of these reductions in krill availability cannot be explained by variations in krill demography and must involve large-scale distribution changes brought about by ocean–atmosphere processes (Priddle *et al.* 1988). Alteration in the hydrographic structure of surface waters, resulting from prolonged periods of southward air flow (such as existed in the winter of 1983 and was associated with southward displacement of warm surface water and pack ice in the Weddell Sea) is such a process. In the South Georgia predator data the direct effects of physical influences were also detectable. In particular, early and persistent ice and snow in some years contributed to low breeding population size and poor reproductive performance respectively for black-browed and grey-headed albatrosses. However, these and other effects were generally less important than those thought to relate directly to changes in prey availability.

At Signy Island, South Orkney Islands, however, the only demonstrable influence on breeding performance of both Adelie and chinstrap penguins (and especially the latter) was the persistence of ice cover, which significantly depressed breeding performance and influenced most aspects of breeding chronology and phenology. Apart from the suggestion that chinstrap breeding populations were lower in years of late ice break-out, there were no obvious correlations with breeding population size, other than a tendency for populations to decrease 3–4 years later, presumably due to reduced recruitment. There was no evidence (but also very few data) of changes in food supply relating to changes in ice cover.

There is much additional evidence of the important influence of climate and of ice cover and break-out date on predator populations at high latitudes (e.g. Ainley & LeResche 1973; Ainley *et al.* 1983; Lishman 1985; Jouventin & Weimerskirch 1990, 1991). Thus breeding population size of Antarctic fulmars is apparently correlated with the extent of snow cover in spring (Jouventin & Weimerskirch 1991) and snow cover also correlates with decreased breeding success in Antarctic fulmars and snow petrels (Jouventin & Weimerskirch 1991; Chastel *et al.* 1992). For penguins, extensive sea ice increases the time and energy used in reaching the breeding colony, whether early in the season (to start breeding) or later when feeding chicks. In the emperor penguin, adult survival can also be affected, especially of the males which undertake a 75 day incubation fast (Jouventin & Weimerskirch 1991). Conversely, if sea ice breaks up before chicks can survive independently at sea, widespread breeding failure will result. The decline in emperor penguin populations at Adelie Land since 1976 has been attributed to decreasing breeding success (accentuated by almost complete failure in 1972) and increased adult mortality (Jouventin & Weimerskirch 1991), thought to relate to more general changes in ice conditions. Relations between ice conditions and emperor penguin breeding success and survival are clearly complicated and need further elucidation.

In Adelie Land, the 1976–77 season was one of very low reproductive success, followed by high mortality of adults, for emperor and Adelie penguins, snow petrels and Antarctic fulmars. For snow petrels a similar situation prevailed in 1983–84 and Chastel *et al.* (1992) suggest that these events may be linked in some way to the ENSOs of 1976 and 1983. However no general relationship between sea-ice conditions and snow petrel demography could be demonstrated. This may reflect that snow petrels are virtually obligate pagophiles, resident in the pack and marginal ice zone and therefore may benefit in years of greater ice cover; except perhaps in extreme years which may reduce the extent of polynyas and other features associated with snow petrel feeding behaviour. Both snow petrels and emperor penguins (and Adelie penguins) are closely dependent on the ice zone all year round and therefore particularly sensitive to any long-term changes in conditions in this zone.

In a 7-year study at Prydz Bay (68°S), Whitehead *et al.* (1990) showed synchrony in patterns of chick production in Antarctic fulmars. Antarctic petrels (*Thalassoica antarctica*) and Adelie penguins. Production was greatest in years with early ice break-out and lowest when pack ice cover persisted within the foraging range of birds during chick-rearing. In the years of highest and lowest productivity, the abundance of the main prey species (*Euphausia crystallorophias*) was correspondingly high and low. Congruent data on reproductive success exist for other sites in some years, indicating that effects were consistent over quite large areas. This was particularly so in 1985–86 which was also a poor year in Adelie Land (some 1000 km east), supporting suggestions that widespread climatic anomalies may be involved.

Various population processes in ice-breeding seals show marked fluctuations. Notable are the strong cohorts apparent 4–5 year intervals in the age structure of crabeater seals in the Antarctic Peninsula (Bengtson & Laws 1985), the appearance at Macquarie Island of large numbers of leopard seals *Hydrurga leptonyx* every 4–5 years (Rounsevell 1988) and the 4–6 year fluctuations in reproductive rate in Weddell seals *Leptonychotes weddellii* at McMurdo (Testa & Siniff 1987). Testa *et al.* (1991) examined these fluctuations in relation to the operational Southern Oscillation Index (SOI), a measure of the strength of ENSO events. They found that all seal datasets showed evidence of cyclicity with an approximate 5 year periodicity. Weddell seals were generally in phase with the SOI (despite a recent shift in cycle periodicity), whereas leopard seals were in phase in the 1960s but have subsequently followed the SOI by one-quarter cycle (i.e. just over 1 year). Links between SOI and crabeater seals were more complex: as expected when using a seal 'index' which integrates juvenile and adult survival. The nature and frequency of any population cycle (given the few examples of biological cycles that have either stood the test of time or proved useful in identifying proximate and/or ultimate factors controlling them) may be less significant than the indication that population processes in ice-breeding seals may be profoundly affected by ocean–atmosphere processes operating on at least region-wide scales. Indeed, given their apparent frequency, such density-independent events may contribute significantly to the regulation of top predator populations (Croxall & Rothery 1991; Testa *et al.* 1991).

In all discussions of the effects of physical factors, especially ice, on top predators it is implicit that there may be very different, even opposite, effects on species characteristically or obligately associated with ice (pagophilic) and on species lacking this association. On the basis of Adelie and chinstrap penguins belonging, respectively, to the former and latter group of species, Fraser *et al.* (1992) suggested that the apparently inverse population fluctuations detected at the South Shetland Islands (62°S, 58°W) relate directly to the extent of ice cover, that the increases in chinstrap populations reflect the decreasing frequency of cold years with extensive ice cover and that environmental warming, rather than any involvement of reallocation of krill following whale removal, is responsible for these and other changes in Antarctic penguin populations.

Leaving aside the extensive evidence for increases in both Adelie and chinstrap populations throughout the Antarctic Peninsula (including the South Shetland Islands) up to at least the late 1970s, and the fact that Adelies are increasing in the Ross Sea, in parallel with increases in local temperature, there are numerous problems inherent in Fraser *et al.*'s (1991) data. These include population counts being available for only 7 of 10 consecutive years, the chinstrap data coming from a very small, potentially atypical, colony, and the apparent assumption that population changes solely reflect annual changes in adult survival. Furthermore, analysis of a similar but longer (15 years) and unbroken dataset from the nearby South Orkney Islands (61°S, 46°W) provides limited support for their hypotheses. Although classification of ice cover is similar at the two sites, interannual changes in breeding populations of the two penguins species at the South Orkney Islands are more often in the same, rather than opposite, directions and there is no simple relationship between degree of ice cover and population change (J. P. Croxall, unpublished data). In addition, ice data for the South Orkney Islands reveal no long-term trends since 1947, either in cover or break-out date (Murphy *et al.* 1992). Both South Shetland and South Orkney Islands datasets agree in showing interannual population fluctuations much greater than can be accounted for by annual changes in adult survival. Variation in some combination of recruitment, emigration and immigration rates and in deferred breeding is necessary to explain the interannual changes. These variables operate in different ways, especially on different temporal scales and it is unrealistic to expect population change alone to give good correlations with local ice conditions. This conclusion does not deny the importance of physical factors, especially ice, in influencing penguin populations, nor that Adelies and chinstraps are affected by ice to different degrees. However, it is certainly premature to relate short-term biological datasets to selected long-term physical datasets and to interpret the results as indicating that physical environmental changes are and have been the main influence regulating populations of Antarctic penguins, without more detailed data and critical analysis.

A particularly interesting feature of Murphy *et al.*'s 1992 data on sea-ice extent is the existence of a sub-decadal (about 7–8 years) cycle in local sea-ice cover since 1966 and the suggestion that this is part of a circumpolar precession in sea-ice anomalies around the Antarctic continent. Fluctuations of similar periodicity were reported independently for the South Orkney and South Shetland Island area by Pozdeeva *et al.* (1990). P. P. Fedulov (unpublished data) was able to link the latter data to variations in the catch-per-unit-effort (CPUE) of the fisheries for krill around South Georgia; these variations in CPUE also correlate significantly with various indices of reproductive performance of the krill-eating predators at South Georgia (J. P. Croxall & P. P. Fedulov, unpublished data).

So far in this section we have mentioned most of the species for which there is evidence of significant population change and suggested some environmental influences that may be associated with these. Explaining the pattern of change in elephant seal populations is particularly difficult because of the apparent stability of the South Georgia stock and the concurrent recent persistent decline in Indian Ocean populations. Hindell (1991) noted that none of the previous hypotheses, including effects of commercial overfishing, is adequate and suggested that the Indian Ocean populations may be declining following 'overshoot' after post-exploitation recovery. A similar tentative explanation has been advanced to account for the possible recent decline in crabeter seals (Erickson & Hanson 1990). If these hypotheses are correct, one would predict a similar phenomenon occurring in the Antarctic fur seal population at South Georgia before too long. It is also interesting that the quadrupling of this fur seal population in the last decade has coincided with marked reductions in some local breeding populations of macaroni penguins and black-browed albatrosses, whose main prey is also krill. However, we have no suitable data to evaluate past or existing interspecies competition. For future interpretations a crucial requirement is estimates of local and regional krill stocks and of interseasonal and interannual variations in these.

4. IMPLICATIONS

The previous sections have provided numerous examples of changes in abundance or reproductive performance of seabirds and seal populations that correlate with previous or simultaneous changes in characteristics of the biological and physical environment. Comparative data for whales, in contrast, are almost non-existent, although apparently cyclical variations in abundance were reported by whalers (Priddle *et al.* 1988).

It is important to reiterate that each type of environmental change can have both direct and indirect effects on top predators. Biological changes (even in UV-B radiation) are likely to have their main effects through modifications to food web processes. Even physical changes, while exerting important direct influences (e.g. via more or less clement weather), are likely to have most influence through indirect effects acting on the nature and extent of breeding habitat, or on feeding habitat (e.g. via presence or absence of polynya), or on distribution and abundance of food supplies. In the last case the effect will probably be greatest for prey biota seasonally or permanently associated with ice-covered areas. In all cases the responses of predators are likely to differ widely, depending on the extent to which they are themselves pagophilic or pagophobic or depend on prey which have these characteristics.

For example, ice-breeding seals may be directly effected by the extent of suitable breeding habitat (including with respect to access to water for feeding and mating) and by relationships between local prey (e.g. krill) abundance and availability and the nature and extent of ice. Fur seals, however, are largely unaffected directly by ice. Indirectly and later they are affected by the influence of ice on prey populations which may originate in seasonally ice-covered habitat and migrate or be transported to fur seal breeding areas. In addition, both types of seal may be influenced directly and indirectly by other features of the ocean–atmosphere processes which gave rise to the changes in ice characteristics (e.g. by changes in water circulation patterns).

Given the potential complexity of these interactions we can be confident that: (i) the nature and effects of and balance between physical and biological environmental change will be different in different regions of the Antarctic. An obvious distinction exists between continental and sub-Antarctic regions; other areas with distinct local characteristics are the Antarctic Peninsula and the Ross Sea. Generally, physical factors will be more important directly – but only possibly so indirectly – in higher rather than in lower latitudes. The Antarctic Peninsula, bridging these latitudes, will be a particularly complex area; (ii) different species will show different responses. A major distinction is likely between pagophilic and pagophobic species. The former are likely to be particularly sensitive to environmental change. However it is impossible at present to answer even apparently simple questions like whether a greater extent of ice has, overall, a beneficial effect on pagophilic species or not. This is chiefly because we do not know, for instance, if more ice means more prey or less prey. Also, the extent and nature of species' dependence on seasonally and permanently ice-covered habitat is very poorly known, even where highly pagophilic species are concerned; (iii) the response of any one species to environmental change will differ according to the season of the year (summer versus winter, breeding versus non-breeding) and the stage of the breeding cycle. Only for a very few species do we have adequate knowledge of population dynamics to predict the most sensitive aspect to particular types and magnitude of changes (see Croxall & Rothery 1991). For no species do we have a clear understanding of how populations are regulated or even what is the balance of density-dependent and density-independent factors in these regulatory processes.

Consequently our predictions of the effects of environmental change on top predator populations are restricted to very imprecise generalisations. In terms of sensitivity to the most likely environmental changes, species particularly at risk will be: (i) residents; (ii) pagophiles; (iii) those of restricted distribution (with the possible exception of recent colonists); and (iv) those with low reproductive rates and long generation times. It should not be overlooked, however, that certainly in the sub-Antarctic, by far the most significant agents (in terms of influencing top predators) of change in the short term are commercial fisheries at sea and introduced non-native predators (cats, rats, etc) on land.

Leaving these problems aside, the most crucial gap for our ability to predict likely consequences of environmental change for top predators is the absence of data on the effects of physical environmental change on prey populations, particularly those associated with seasonally ice-covered habitats. Concurrent with research on this theme, scientists working on top predators need to obtain and analyse data on survival and recruitment rates (and on intermittent breeding) in relation to relevant characteristics of ice or oceanography and to estimates of local and regional availability of the main prey species. For both topics it is obviously essential to investigate the nature of interactions between ENSO and local and regional sea-ice cycles; in short to understand the key ocean–atmosphere processes which are likely to have particularly significant effects on the dynamics of Antarctic marine food webs.

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Discussion

T. Callaghan (*Institute of Terrestrial Ecology, Merlewood Research Station, Cumbria, U.K.*). Cyclicity in population size and events also occurs in Arctic animals and plants, although we do not understand what triggers this. Could a breakdown in cyclicity be one of the first signs of an impact of climate change?

J-P. Croxall. In the Southern Ocean the evidence for regular cycles of defined frequency, rather than periodic strong fluctuations of irregular frequency, still remains to be confirmed. Even with strong regular cycles, detecting a gradual change in amplitude or frequency is very difficult; in the Antarctic we are probably more likely to see first trends in reproductive performance or population size in areas near the periphery of species' range.

R. Cervellati (*Italian Antarctic Project, Italy*). The correlation Dr Croxall has between the rate of change of Chinstrap and Adelie penguin populations is impressive. But, perhaps there are large observation errors; and, in addition, the area of observation was rather limited. Could he comment on that?

J. P. Croxall. In fact, my contention was that the proposed inverse correlation between changes in Adelie and Chinstrap penguin populations – based on data from King George Island, South Shetland Islands – is not a strong one, based on more extensive data from Signy Island, South Orkney Islands. The population counts are, however, in both cases accurate to at least ± 10%.

D. W. H. Walton (*British Antarctic Survey, Cambridge, U.K.*). Bearing in mind what is already known about the biology of fur seals would Dr Croxall like to extrapolate present population trends and suggest when the fur seal population might reach its maximum?

J. P. Croxall. The fur seal population at Bird Island (the centre of the population recovery and explosion) has been fairly stabe for the latter part of the last decade. However, away from the northwest end of South Georgia, populations are still increasing rapidly and colonizing new areas. Problems in making any prediction, especially about the total South Georgia population, are: (i) there is ample breeding space at South Georgia to accommodate the current 10% rate of increase for several decades to come; (ii) the primary food resource, Antarctic krill, could, in most years, sustain a much larger fur seal population, provided animals can locate krill swarms within 100 km of their breeding site; and (iii) events in the non-breeding season, when fur seals are pelagic, may be just as important for population regulation but almost no data are available for this period.

At Bird Island we may now be seeing some signs which could indicate the start of density-dependent population regulation (e.g. reduced pup growth rates even in 'good' krill years); I would guess, therefore, that maximum breeding population size for Antarctic fur seals at South Georgia could be reached within the next decade or so.