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Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming?

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Summary. A central tenet of Antarctic ecology suggests that increases in Chinstrap Penguin (*Pygoscelis antarctica*) populations during the last four decades resulted from an increase in prey availability brought on by the decrease in baleen whale stocks. We question this tenet and present evidence to support the hypothesis that these increases are due to a gradual decrease in the frequency of cold years with extensive winter sea ice cover resulting from environmental warming. Supporting data were derived from one of the first, major multidisciplinary winter expedition to the Scotia and Weddell seas; recent satellite images of ocean ice cover; and the analysis of long-term surface temperature records and penguin demography. Our observations indicate there is a need to pay close attention to environmental data in the management of Southern Ocean resources given the complexity of relating biological changes to ecological perturbations.

Introduction

Populations of many krill-eating, Southern Ocean predators have exhibited significant changes during the last four decades. Notable among these, have been increases in the abundance of Chinstrap Penguins (*Pygoscelis antarctica*), which breed mainly on the Antarctic Peninsula and islands of the Scotia Sea (Watson 1975). At many colonies, numbers have increased 6–10% per annum (Laws 1985), and at some localities fivefold increases have occurred in the last 20 years (Rootes 1988). Chinstraps have also expanded their range southward along the western side of the Antarctic Peninsula (Parmelee and Parmelee 1987; Poncet and Poncet 1987) into areas historically dominated by the closely related adelie Penguin (*P. adeliae*; Fig. 1). A central tenet of Antarctic ecology explains these population changes in terms of a presumed increase in food availability that resulted from the decrease in baleen whale stocks due to commercial whaling (Sladen 1964; Emison 1968; Conroy 1975; Croxall and Kirkwood 1979; Croxall and Prince 1979; Croxall et al. 1984). This tenet is based on the fact that the dominant component in the summer diets of both Chinstraps and whales is the Antarctic krill (*Euphausia superba*). Although this tenet has been widely accepted, the possible mechanism by which a decrease in whales could have led to an increase in Chinstraps has not been questioned (cf. Horwood 1980). Indeed, the long-standing view has simply been that whaling led to a "krill surplus" that was used by krill-eating predators when competitive release altered the existing patterns of consumption (Laws 1985).

Although this whale reduction hypothesis has clearly been useful in guiding research on trophic interactions in the Southern Oceans, it is now apparent that increases in Chinstrap populations have not been mirrored by their sympatric, most closely related congener, the Adelie Penguin. Adelies share a significant portion of their range on the Antarctic peninsula and islands of the Scotia Arc with Chinstraps (Watson 1975). Alike in size and general appearance, both exhibit broad ecological similarities, not the least of which is a predominance of krill in their summer diets (Volkman et al. 1980; Trivelpiece et al. 1987, 1990; Trivelpiece and Trivelpiece 1990). Yet, when compared to Chinstraps, population increases in Adelies have not been as substantial, and at many sites appear to represent nothing more than recovery after human disturbance and exploitation (Poncet and Poncet 1987). Adelies, in fact, have declined noticeably at several localities on the Antarctic Peninsula, a change considered "unexplainable" by Poncet and Poncet (1987). This raises an interesting challenge to the whale reduction hypothesis: If the decrease of baleen whale stocks actually led to a krill surplus, why have populations of the ecologically similar Adelies residing in the same geographical areas shown such different responses?

Here we propose that the answer to this question does not rest with the idea of a krill surplus. Instead, we suggest

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that a long-term decrease in the frequency of cold years with extensive ice cover induced by environmental warming has changed the relative availability of critical Chinstrap and Adelie wintering habitats, thus altering patterns of recruitment and population growth. We base our hypothesis on recent information on the pelagic distribution of Chinstrap and Adelie penguins in the Weddell and Scotia seas during winter, long-term demographic data from nearby King George Island, recent, satellite images of ocean ice cover, and an analysis of long-term surface temperature records in the vicinity of the Antarctic Peninsula.

Methods

Our pelagic data are based on the results of one of the first, major multidisciplinary winter expeditions into the Scotia and Weddell Seas. This expedition, during the austral winter (June–August) of 1988, was part of the AMERIEZ (Antarctic Marine Ecosystem Research at the Ice Edge Zone) program, which has been described elsewhere (see Garrison and Siniff 1986; Ainley and Sullivan 1990). Using methods and techniques implemented during related work by Ainley et al. (1984) and Ainley (1985) in the Ross Sea, we employed strip censuses (300-m, width; 30-min duration whenever ship speeds exceeded 6 knots) to survey approximately 581 km^2 between 57°–62° south latitude and 36°–49° west longitude. This area encompassed habitats consisting of both open open water (54% of the censuses; N =130) and pack ice (46% of the censuses; N=110). During each census, the abundance and distribution of seabirds and marine mammals was recorded coincident with a detailed record of the physical environment. Diet samples were also taken from seabirds collected at selected sites.

Demographic data on Chinstrap and Adelie penguins are based on long-term ecological studies initiated at Admiralty Bay, King George Island (62° 10′ S, 58° 20′ W), Antarctica, in 1977 that have continued to the present. As shown in Fig. 1, this site is at the northern edge of the Adelie's range, within the southern portion of the Chinstrap's and encompasses the region where pack ice reaches its annual northern limit. It is also well within one of the most active historical whaling areas (Horwood 1980). For the sake of brevity, the protocols that have annually been implemented in conducting our research on these species will not be discussed, as these have already been detailed in numerous previous publications (see text and references cited in Trivelpiece and Trivelpiece 1990; Trivelpiece et al. 1990).

Surface temperature records for the Antarctic Peninsula during the last 50 years are based on published data available from the U.S. Department of Energy (Jones and Linbert 1987) for the four stations with the longest, most complete weather records. These are Faraday, Bellingshausen, Signy and Islas Orcadas (Fig. 1). Sea ice records are similarly based on published data available from the U.S. National Aeronautics and Space Administration (NASA; Comiso and Zwally 1989; Zwally et al. 1983). Other sources for these data are quoted within the text.

Results

Annual changes in breeding population size of Chinstrap and Adelie penguins at the Admiralty Bay study site on

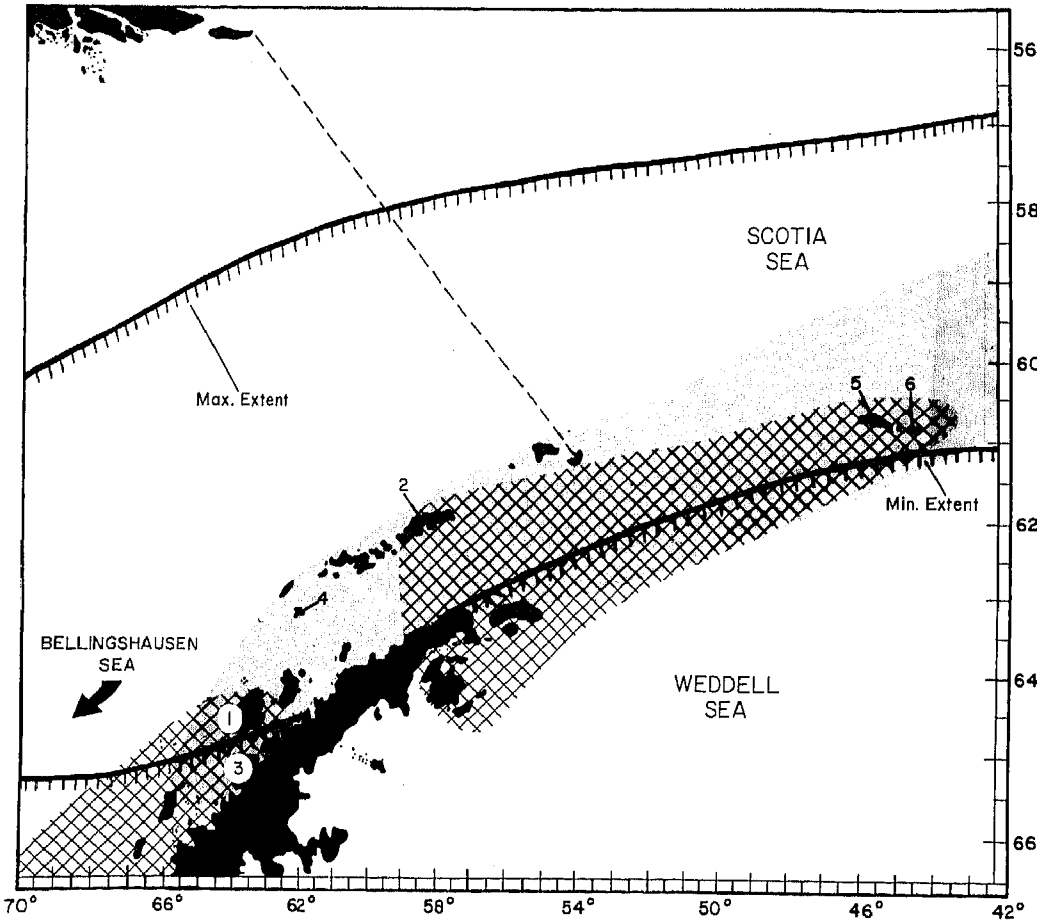

Fig. 1. The Antarctic Peninsula showing the ranges of Chinstrap (*light shading*) and Adelie penguins (*crosshatching*); the extremes of ice cover during September (when cover reaches maximum); study sites (Arthur Harbor, Anvers Island -- 1 and Admiralty Bay, King Geore Island -- 2); stations where complete weather records have been recorded since 1944 (Faraday -- 3, Bellingshausen -- 4, Singy -- 5, Islas Orcadas -- 6); and the (*dashed*) line along with the northward extent of the peak ice was compared in Fig. 4

King George Island are shown in Fig. 2. Large annual increases in Adelie numbers were coincident with large annual decreases in Chinstrap numbers. These changes were also related to the extent of winter and spring sea ice cover, with Chinstraps increasing when sea ice extent diminished and vise-versa. These data were until recently enigmatic because it has long been thought that both Adelie and Chinstrap penguins wintered on the same pack ice habitat that seasonally develops around Antarctica (Murphy 1936; Cline et al. 1969; Watson 1975), yet it was clear that each species was responding differently to similar winter sea ice conditions. The solution to this puzzle was obtained on the 1988 AMERIEZ winter cruise, where we found that Chinstraps and Adelies actually reside in completely different habitats (Fig. 3). As suspected, Adelies were indeed obligate inhabitants of the pack ice (cf. Ainley et al. 1983, 1984), comprising 99% of total avian biomass. Chinstraps, however, occurred almost exclusively in open water, where they exhibited a similar dominance of avian biomass (Fraser et al., in preparation; see Joiris, in press).

The trends apparent in Figs. 2 and 3 link annual variation in the size of Chinstrap and Adelie penguin breeding populations to sea ice extent and species-specific winter habitat preferences. Breeding population size is indicative of a number of factors, one of the most important being overwinter survival, which essentially provides a direct measure of how the year's potential breeders fared during the previous winter. Because of its potential impact on recruitment, overwinter survival can play a key role in driving long-term population change (Ricklefs 1973), which in view of the historical differences evident in the growth of Chinstrap and Adelie penguin populations, invites the following question: has the relative availability of these species' preferred wintering habitats (Fig. 3) been changing during the last four decades in a way that has favored Chinstraps but not Adelies?

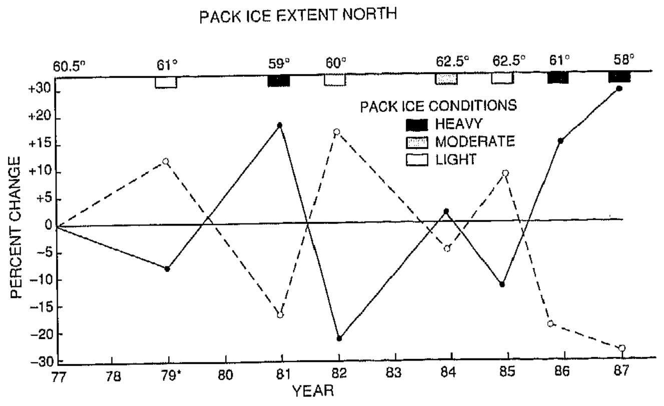

Fig. 2. Percent change in the number of Adelie (*closed circles*) and Chinstrap (*open circles*) breeding pairs on King George Island, Antarctica. The magnitude and direction (increasing or decreasing) is calculated relative to the preceding year's census. Whenever more than one year elapsed between censuses, the resultant change was divided by the number of years since the previous count to give an average percent annual change over the intervening period. Pack ice conditions are based on local ice cover during peak egg laying; the northern position of the ice edge in September, when it reaches its annual maximum, is shown on the top horizontal axis

As shown in Fig. 4, mean annual surface air temperatures have been increasing in the Antarctic Peninsula region since approximately 1950 (see also Everson 1977; Jacka et al. 1984, 1985; Allison and Keage 1986; Lewis-Smith and Bonner 1989; Lewis-Smith 1990). The long-term record on the impacts this warming trend has had on sea ice, however, is unfortunately incomplete because reliable satellite images are available only since 1973 and up-to-date summaries of the available images are lagging data accumulation. Nevertheless, coupling the post-1977 data on trends in surface air temperatures with those on

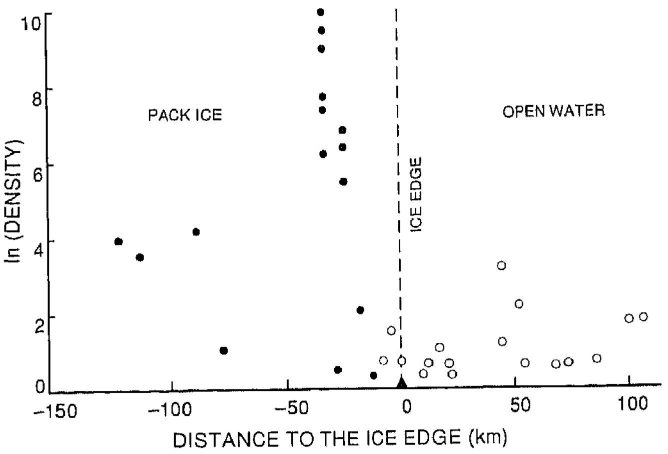

Fig. 3. Density and distribution of Adelie (*closed circles*) and Chinstrap (*open circles*) penguins relative to the ice edge in the Weddell Sea, Antarctica. Positive kilometers represent open water

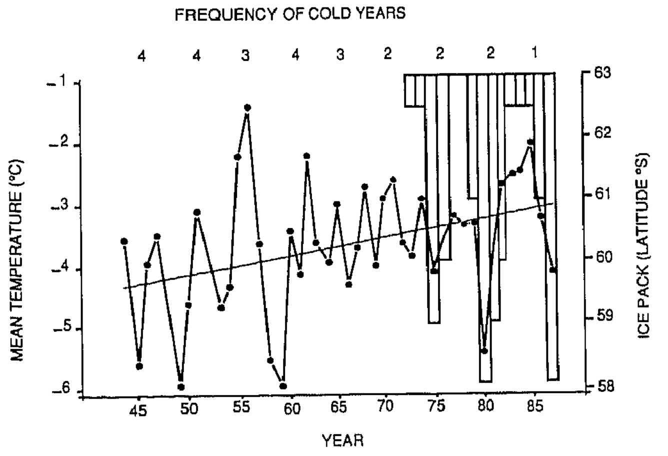

Fig. 4. Mean temperature at four stations (Farady, Bellingshausen, Signy and Islas Orcadas) in the Antarctic Peninsula region compared, for the 1973–87 period, to the latitude of northward extent of pack ice during September (indicated by bars). No satellite data for 1977 or 1978; 1987 extent from personal observation of DGA and WZT. Numbers at the top show the number of years per respective five-year period that mean temperature was less than or equal to -4.3 °C, the temperature during the 1973–87 period when pack ice reached northward to at least 60°.50'S. Formula for the regression line is: temperature $= -5.551 + 0.0278$ (yr), $F = 5.720$, $P = 0.021$. The relationship of ice extent to temperature is highly significant; Spearman rank correlation, $r = 0.886$, $t = 6.337$, $P < 0.001$

sea ice extent, and extrapolating on the longer-term temperature record, suggest a mechanism by which these increases in Chinstrap populations could have been mediated. Since 1973, sea ice has been minimal along the western edge of the Antarctic Peninsula during years when surface air temperatures averaged at four stations (Fig. 1) have been warmer than −4.3 °C (Fig. 4). This is a pattern consistent with thermodynamic models of sea ice formation and cover in the Antarctic Peninsula/Weddell Sea region (Hibler 1984; Parkinson and Bindschadler 1984; Hibler and Ackley 1987; Husby et al. 1989). The key to the longer term extrapolation, however, is not whether temperatures and sea ice have shown a perfectly coupled response, but whether the frequency of cold/warm years, and thus extensive/reduced ice years, has changed sufficiently and over a long enough period of time to influence resident penguin populations. As shown in Fig. 4, the frequency of cold years has in fact changed during the last 45 years from an average of 4 out of 5 during mid-century to an average of only 1 or 2 out of five during the last 20 years. If our hypothesis is correct, this pattern suggests that the number of years with minimal ice has indeed increased during the last four decades, providing more than ample time for populations of the ice-avoiding Chinstraps to show a positive response.

Discussion

The key factor guiding the argument in favor of the whale reduction hypothesis is the similarity in the diets of penguins and whales. As Croxall et al. (1985) have recently indicated, however, competition between krill-eating predators cannot be assumed (nor denied) without question on the basis of diet alone. Implicit in the whale reduction hypothesis is the idea that before stocks were depleted, krill consumption by whales had to either limit penguin breeding success during summer, or somehow reduce overwinter survival (Croxall et al. 1985), these being the foci wherein seabird populations are regulated (Lack 1954; Ricklefs 1973; Birkhead and Furness 1985). Thus, although diet similarity is important, it is only one of several factors related to the more complex problem of foraging niche overlap, and the remaining critical question of whether krill availability to penguins was ever limited by whales.

There are several lines of evidence that indicate that overlap in the foraging niches of penguins and whales was actually less significant than that suggested by the whale reduction hypothesis. First, a recent model by Murphy et al. (1988) predicts that the benefits of a reduction in baleen whales would have been most directly conferred to predators of similar size and behaviour, namely, other whales. For similar reasons, other models suggest that intraspecific competition for food among seabirds is far more important in limiting population size than is interspecific competition (Furness and Birkhead 1984; Birt et al. 1987; Croxall et al. 1985, 1988). On a theoretical basis, therefore, it is not clear how whale trophic "function" in the system could have greatly affected penguins. In support of these models, population estimates of krill-eating minke whales (*Balaenoptera acutorostrata*), whose relatively small size made them less attractive to whalers, indicate a two-fold increase from pre-whaling days (Laws 1985). Equally important is that minkes, unlike other baleen whales, winter in the marginal ice zone (Ribic et al. 1991), and thus exhibit complete seasonal overlap with penguins. Despite this whale's winter presence and increased numbers, Chinstrap populations have also increased.

Second, it has been hypothesized that congeneric, sympatric Antarctic penguins, like other seabirds, adjust breeding phenology to reduce interspecific diet competition (Cody 1973; Croxall and Prince 1980; Lishman 1985). This hypothesis has been questioned in other studies (Bedard 1976; Trivelpiece et al. 1987; Ainley and Boekelheide 1990), and we are no longer convinced it applies to Antarctic penguins. The exploited baleen whales were only seasonally present in the Antarctic from about November to May (Brown and Lockyer 1984; Laws 1985), meaning that assumed competition with penguins occurred primarily during their summer breeding season. In the past 40 years, however, no changes in penguin breeding phenology have been recorded, which might have been expected (cf. Ashmole 1963; Birt et al. 1987) if more krill did in fact become available due to reduced competition from whales. This suggests that other variables may be more important determinants of breeding phenology in Antarctic penguins (see below).

Third, the affinities for pack ice and ice edge/open water habitats shown by Adelie and Chinstrap penguins, respectively, also characterize the winter habitat preferences of some krill-eating marine mammals, notably Crabeater (*Lobodon carcinophagus*) and Southern Fur (*Arctocephalus gazella*) seals (Fraser et al. 1989; Ribic et al., 1991). Based on diet characteristics alone, these mammals are not only the most direct, potential competitors for krill with penguins (Croxall et al. 1985; Croxall and Pilcher 1984), but according to recent models, may in fact have been in a trophically superior position to "replace" baleen whales in the system due to their size and behaviour (Murphy et al. 1988). Nevertheless, as in Adelies, the most recent censuses suggest that the pack ice dependent Crabeaters are now exhibiting declining populations, particularly in the Weddell Sea (Erickson and Hanson 1990). The ice-avoiding Fur Seals, however, like Chinstraps, are experiencing significant population growth. Indeed, at South Georgia, Fur Seal populations are now thought to exceed pre-exploitation levels (Bonner 1985; Laws 1985; Croxall et al. 1988). Noteworthy in this regard, is that other Southern Ocean predators not considered to be krill consumers, but which like Fur Seals tend to avoid sea ice, are also exhibiting population increases and/or range expansions (Fraser, in preparation). These include Southern Elephant Seals (*Mirounga leonina*) at the southern extremes of their range, Blue-eyed Shags (*Phalacrocorax atricepts*), and South Polar Skuas (*Catharacta maccormicki*), species that have increased 200–600% since the early 1970's (unpublished data from long-term censuses in the vicinity of Palmer Station, Fig. 1; see Brownell and Ainley 1976; Heimark and Heimark 1988). This may explain population changes in many other Southern Ocean predators as well (see Croxall and Prince 1979; Croxall et al. 1988).

Fourth, Gentoo Penguins (*Pygoscelis papua*) also share a significant portion of their range on the Antarctic Peninsula with Chinstraps and Adelies, and in fact occur in mixed-species colonies with these penguins at several localities (Poncet and Poncet 1987). Similar to Chinstraps and Adelies in size and in many aspects of their ecology and behaviour, Gentoos also have summer diets composed largely of krill (Volkman et al. 1980; Trivelpiece et al. 1987). Unlike either species, however, Gentoos are not migratory; that is, they tend to winter in-shore, often in sheltered bays and open channels close to their breeding sites (Fraser et al. 1989, unpublished data based on winter surveys between Anvers and King George Islands; Trivelpiece et al. 1990). Notably, this most sedentary of the three pygoscelid penguins has throughout its range also shown the least evidence of long-term population change (Croxall and Prince 1979; Poncet and Poncet 1987). This again implicates habitat differentiation rather than diet as a key variable driving population change in krill-eating predators.

These new prespectives on the influence sea ice has on these penguins have resolved several other problematic patterns related to their distribution and behaviour. First, the previously unexplained 400 km "gap" between Anvers and King George islands, devoid of breeding Adelies but full of Chinstraps (Fig. 1; cf. Watson 1975; Poncet and Poncet 1987), intimates that two Adelie populations inhabit the Peninsula, one residing from Anvers Island south that relies on the ice of the Bellingshausen Sea, and another residing from King George Island north and east that relies on the ice of the Weddell Sea. We hypothesize that this gap exists because it represents an area too distant from either the Bellingshausen or Weddell sea ice to allow successful nest relief after egg laying by Adelies needing to return to the pack ice after fasting early in the season (Trivelpiece et al., in preparation). This supports the long-held view that to breed successfully, Adelies, but not Chinstraps, must establish colonies at some minimum distance from major, predictable ice concentrations (Ainley et al. 1983; Ainley et al. 1984; Trivelpiece et al. 1987).

Second, late breeding by Chinstraps (2–3 weeks later than Adelies) may be viewed as an ice-avoidance adaptation that allows for the break-up of winter ice in the spring and the performance of breeding duties later in the summer when sea ice retreats to its annual minimum. Early breeding by Adelies, on the other hand, may prolong access to winter pack ice close to their colonies (Trivelpiece et al. 1987, in preparation). By breeding early, Adelies may also be able to avoid breeding duties during minimal summer pack ice conditions (Ainley et al. 1983, 1984). Variation in the breeding phenology of these penguins may thus represent species-specific strategies related more to optimizing the use of critical habitats than, as proposed by Lishman (1985), reducing interspecific competition for krill.

Third, Volkman et al. (1980) and Trivelpiece et al. (1990, unpublished data) have shown that trends in the breeding success of Chinstrap and Adelie penguins, which also include the number of young birds that attempt to breed for the first time, tend to follow prevailing winter and spring sea ice conditions. Generally, Chinstraps do well and Adelies do poorly during years of minimal sea ice, while the opposite is true during years when sea ice is heavier. Due to the long fasts associated with breeding (cf. Trivelpiece and Trivelpiece 1990), reproductive success in these penguins is largely dependent on fat reserves accumulated in late winter and early spring before egg laying commences. This suggests that annual variation in the reproductive success of these penguins is in large part driven by pack ice mediated changes in the marine habitat, and its effects on foraging success and pre-breeding physiological condition.

And finally, throughout their shared ranges, decreases in Adelie populations have not mirrored the increases in Chinstrap populations (Poncet and Poncet 1987). This pattern seems enigmatic in view of our hypothesis because it suggests that increases in the availability of Chinstrap habitat have occurred without equal and coincident decreases in the availability of Adelie habitat. We believe, however, that this scenario may actually be correct. In the Southern Oceans, Adelie colonies tend to be located near oceanic basins where sea ice persist throughout the year. In the vicinity of the Antarctic Peninsula, where the ranges of Chinstraps and Adelies overlap, these basins include the Weddell and Bellingshausen seas. Common to both, is that sea ice can form in the more extreme southern latitudes and be transported north by gyres. We therefore suspect that these physical processes have buffered the more local effects of habitat loss in northern latitudes, thus slowing the rate of decrease in Adelie populations. The greatest changes in Adelie populations have occurred not at the core of their breeding range, but rather at its periphery (Poncet and Poncet 1987; Jouventin and Weimerskirch 1990), a pattern consistent with all predictions on how climate change might affect biodiversity and populations (Wilson 1988).

Our hypothesis accounts for a number of seemingly anomalous changes in the populations and occurrence patterns of Southern Ocean predators without invoking the questionable trophic interactions implicit in the whale reduction hypothesis. However, given the lack of empirical data on the pelagic ecology of virtually all these predators, we feel it may be premature to dismiss all aspects of the whale reduction hypothesis. What might seem more prudent in the absence of these critical data, therefore, is to realize that sea ice may ultimately mediate the outcome of many Southern Ocean trophic interactions, including, but not limited to, the availability of krill. Indeed, if there is merit in the whale reduction hypothesis, we suggest that Chinstrap and other ice avoiding predators could not have taken advantage of the krill surplus without an increase in the frequency of years with minimal winter ice.

The implication inherent in this conclusion is that research that advocates a direct causal link between krill availability and changes in predator populations may be based on assumptions that do not fully consider the potential complexity of Antarctic trophic interactions. Because the effects of climate change on trophic interactions are predicted to be amplified at high latitudes (Bolin et al. 1986), this could seriously compromise the interpretation of data being gathered as part of long-term monitoring programmes to detect ecosystem changes resulting from increased direct human activity such as whaling or krill fishing. Particularly at risk in this regard, may be the current effort to monitor the effects of a krill fishery by using upper trophic level predators as indicators. The rationale behind this effort rests on the notion that krill predator populations directly mirror the availability of their prey in the environment. Although there is some value in this approach, Croxall et al. (1979, 1985, 1988) and others have already demonstrated how environmental variability, and sea ice in particular, may confound interpretation of the data in the analysis of long-term trends. This suggests that the usefulness of these monitoring programmes, at least from a management perspective, will necessarily remain limited unless provisions are made to incorporate basic research on the effects of sea ice and other environmental variables on Southern Ocean trophic interactions.

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