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THE BREEDING BIOLOGY AND DISTRIBUTION OF ADÉLIE PENGUINS: ADAPTATIONS TO ENVIRONMENTAL VARIABILITY

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Adélie penguins are long-lived, highly philopatric seabirds that dominate the bird biomass of the Western Antarctic Peninsula region, and serve as focal animals for our Long-Term Ecological Research (LTER) study of the effects of environmental variability on animal populations in the Antarctic marine ecosystem. The major physical factors affecting the breeding success, distribution and demography of Adélie penguins in the Southern Ocean are variability in sea ice cover, ocean circulation patterns and terrestrial topography. We analyzed Adélie distributions in the Antarctic Peninsula region and concluded that Adélie penguins have discrete subpopulations in the northeastern and southwestern regions of the area. These subpopulations are separated by a 400 km gap in their respective distributions, but each is within several hundred kilometers of predictable pack ice areas in the Weddell and Bellingshausen Seas, respectively. We propose that these pack ice areas are the wintering grounds for each subpopulation, and that access to these pack ice areas, early in the season following courtship fasting, is the key to successful breeding in Adélies. We further analyzed the colony distributions within each subpopulation and found highly clumped distributions of Adélie penguins that were strongly correlated to physical factors such as bathymetry, currents and wind direction. We propose that these variables reduce the occurrence of pack ice in the vicinity of breeding colonies of Adélie penguin populations, thereby assuring access to open water in the early season. Finally, we examined the influence of the interaction of local topography and weather on the size, location and persistence of breeding groups within Adélie penguin colonies. Snow accumulation, melt water runoff and solar radiation all impact the microclimate of breeding colonies and influence the selection of nesting sites among Adélie penguins. The abandonment of breeding areas by Adélie penguins, following two to three years of failure at "poor" sites, suggests that changes in the population distribution of Adélie penguins may be very rapid in response to changing environmental conditions, such as increased snow deposition. Adaptations to environmental variability are seen in every aspect of the natural history of the Adélie penguin, from the distribution of subpopulations around Antarctica, to the sizes and distributions of colonies within regions, to the choice of breeding sites within colonies.

1. INTRODUCTION

The focus of our long-term seabird research has been a comparative study of the breeding biology, foraging ecology and demography of the Adélie penguin (*Pygoscelis adeliae*) populations breeding at Admiralty Bay, King George Island (62°10'S, 58°20'W) and Palmer Station, Anvers Island (64°46'S, 64°04'W; Figures 1*a*, *b*, *c*). These populations have exhibited fluctuations in abundance that have been related to changes in environmental conditions over a range of temporal scales: from annual variations in sea ice coverage [*Trivelpiece et al.*, 1987, 1990; Figure 2] to decadal trends related to global warming [*Fraser et al.*, 1992]. The goal of our research has been to improve our understanding of the mechanisms and processes whereby variability in the physical environment affects the prey (krill) and top predator (penguin) components of the Antarctic marine ecosystem.

Our current understanding of these interactions is largely based on our present knowledge of the effects of this variability on the reproductive ecology of several seabird species that dominate energy flow in this ecosystem [*Ainley et al.*, 1986, 1988; *Fraser and Ainley*, 1986; *Trivelpiece et al.*, 1987, 1990; *Croxall*, 1992; *Fraser et al.*, 1992; *Fraser and Trivelpiece*, submitted; *Trivelpiece and Trivelpiece*, submitted]. The links in the Antarctic food web between the primary producers, grazers and predators are short and may involve as few as three to four species [*Croxall et al.*, 1988; *Smith*, 1990]. The number of prey taxa in the Southern Ocean is limited [*Croxall and Prince*, 1980] and predators depend on a core group of prey species close to the base of the food chain [*Croxall and Prince*, 1980, 1987; *Trivelpiece et al.*, 1987, 1990; *Ainley et al.*, 1988; *Croxall et al.*, 1988]. Thus, the relatively simple food webs and the close coupling between these predator-prey interactions and the physical environment in which these interactions occur, present us with an ideal system in which to test hypotheses and model inter-

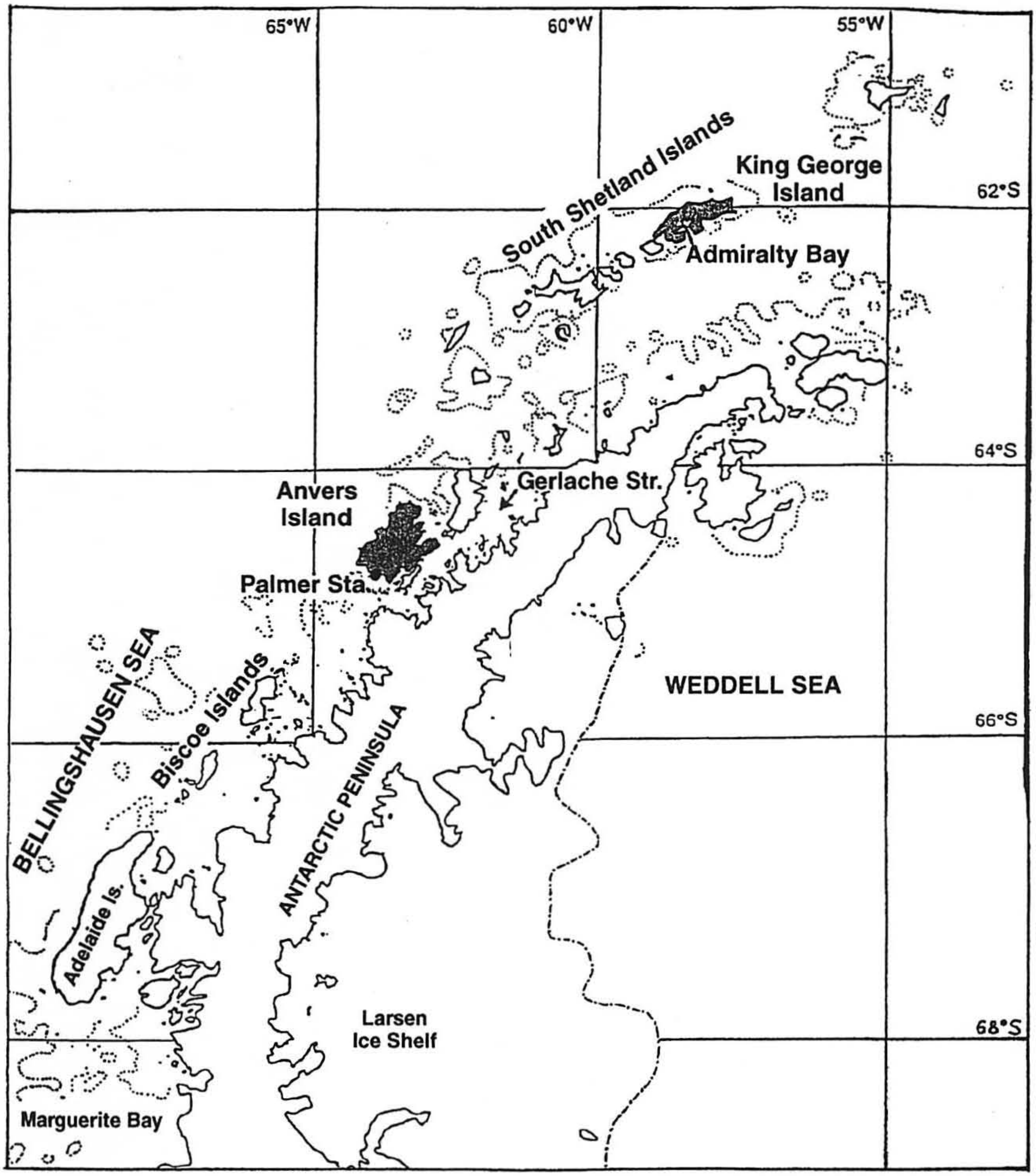

Fig. 1*a*. The Western Antarctic Peninsula region of the LTER study with the location of the two land-based penguin colonies at Palmer Station, Anvers Island and Admiralty Bay, King George Island.

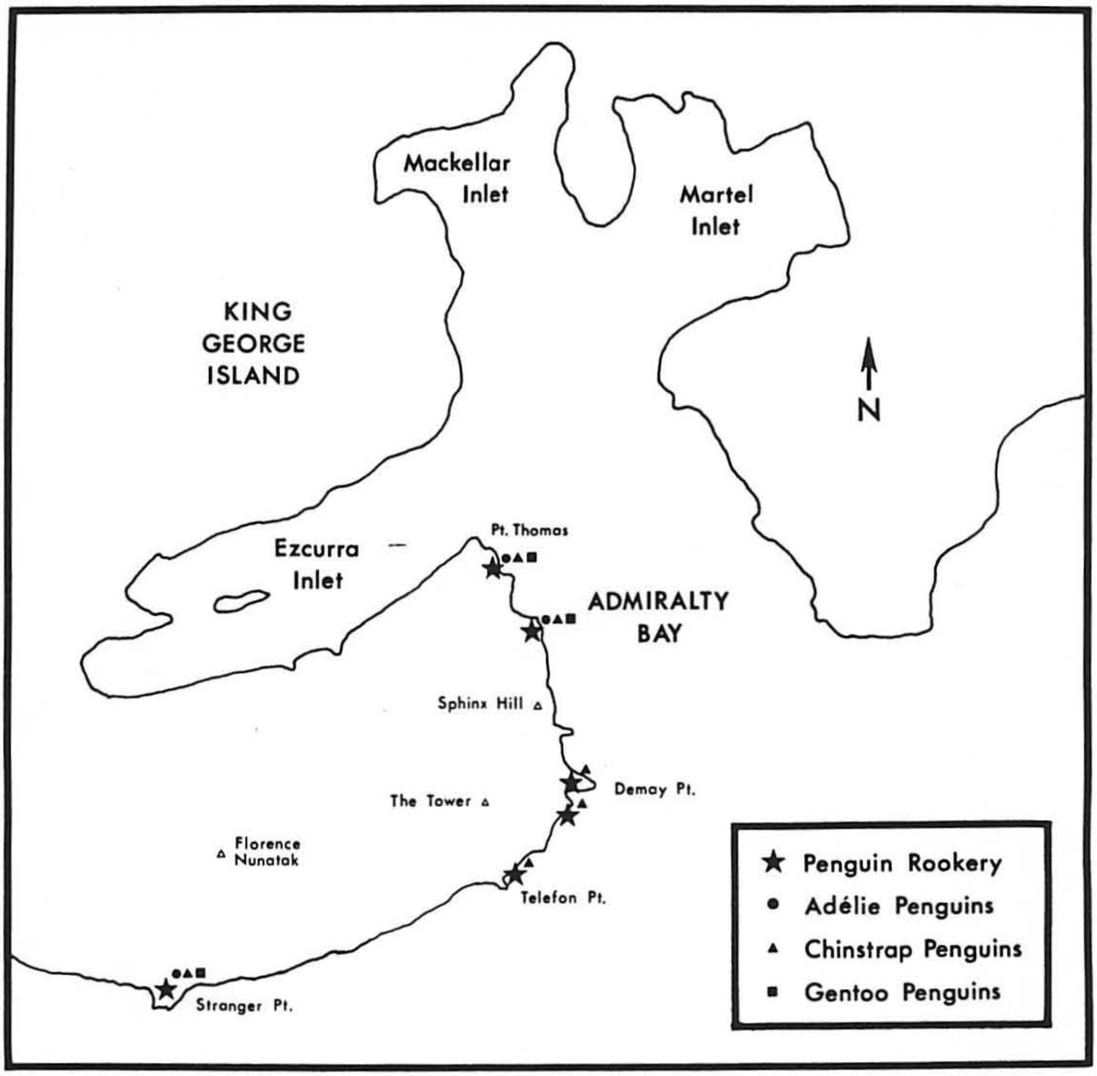

Fig. 1*b*. The distribution and species composition of the Admiralty Bay penguin colonies.

actions on the effects of environmental variability on biological processes and populations.

2. SEABIRD RESEARCH AND THE LTER HYPOTHESES

A central tenet of our LTER study is that interannual variations in the physical environment significantly affect the structure and function of Antarctic marine communities. The major physical factors impacting the Western Antarctic Peninsula marine ecosystem are reviewed elsewhere in this volume and include: variability in the annual timing and extent of sea ice cover (Part II, Chapter 3) and regional differences in oceanic currents and water mass distributions (Part II, Chapter 2). These, in turn, are forced by large scale atmospheric processes (Part II, Chapter 4). Variability in these physical parameters affects the timing and extent of primary production (Part IV, Chapter 2) which significantly affects the fecundity, survival and distribution of prey and predator populations.

Our approach to investigating the linkages between and mechanisms underlying trophic structure in the Antarctic ecosystem has been to focus on representative species that dominate the energy transfer from primary production to apex predators in the Southern Ocean. We selected two predators, the Adélie penguin and the south polar skua (*Catharacta maccormicki*), as subjects for this ecosystem research, as they are abundant and are dependent on different prey types, krill (*Euphausia superba*) and fish, respectively. Environmental variability affects the breeding biology and population dynamics of these predators over different tem-

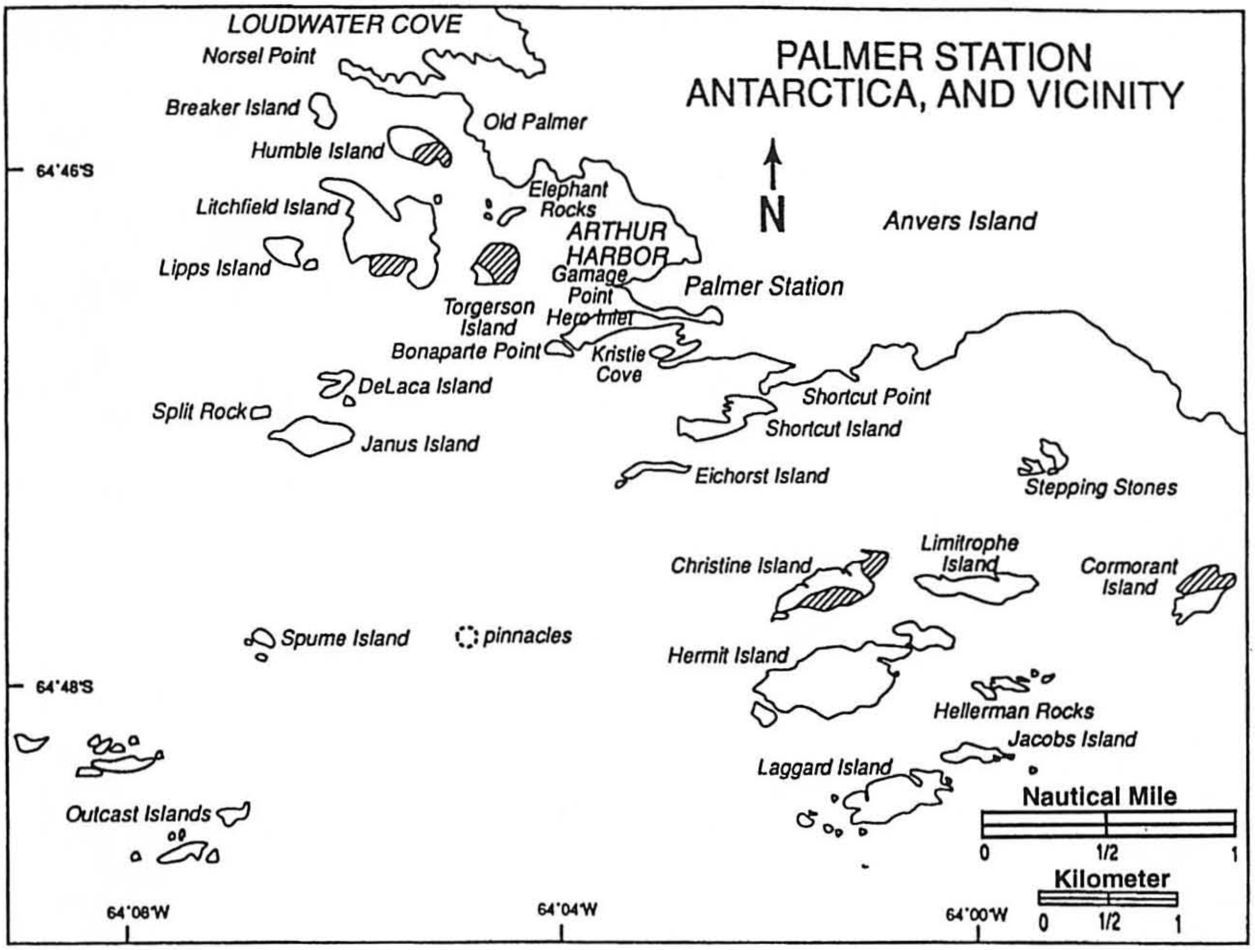

Fig. 1*c*. The distribution of Adélie penguin colonies (shaded areas) in the vicinity of Palmer Station.

poral and spatial scales and has significant impacts at the individual and population levels.

Here, we will review the breeding ecology of the Adélie penguin to examine the direct effects of environmental variability on this species' life history patterns and distribution of its breeding population. The Adélie penguin is one of three species of the *Pygoscelis* penguins, which account for approximately 90% of the Western Antarctic Peninsula region's bird biomass [*Watson*, 1975; *Everson*, 1977; *Prevost*, 1978; *Woehler*, 1993]. Adélie penguins are a migratory species that winter in the pack ice surrounding Antarctica [*Fraser et al.*, 1992] and have a circumpolar breeding distribution between 60° and 77°S latitude (Figure 3). Adélie penguins are ideal subjects for this research as they return to breed in their natal colonies, begin breeding as early as three years of age and may survive up to 20 years [*Sladen and LeResche*, 1970; *Ainley et al.*, 1983]. Hence, they afford us the opportunity to study the impacts of environmental variability on selected individuals over many breeding seasons and to follow discrete populations through time.

3. PHYSICAL FACTORS

The physical factors that directly affect Adélie penguin populations in the Southern Ocean fall into three habitat categories; those related to the terrestrial, ice and ocean environments. A summary of the features and variables associated with these habitats is presented in Table 1. It is not our aim to address all aspects of every variable, rather, we will focus on selected examples that we feel significantly impact the life history strategies of the Adélie penguin. As background, we will briefly review key aspects of these habitats that are of importance to our later discussions; detailed accounts of the marine physical features are reviewed more fully elsewhere in this volume.

3.1. Terrestrial Habitat

Penguins are among the most exclusively marine of all seabirds, yet, like all birds, they must come ashore to lay eggs and rear their young. The topography and geology of ice free land in Antarctica impacts the breeding biology of penguins via the interactions between topography and weather. Access to the breeding areas, exposure of the breeding colonies to prevailing winds, slope of the site, snow accumulation and suitable substrate for nest building are all parameters that are impacted by variability in the physical environment. These factors affect the timing of migration, the availability of snow-free nesting areas and subsequent snow accumulation and water runoff on the colonies [*Reid*, 1964; *Yeates*, 1968, 1975; *Ainley and LeResche*, 1973; *Spurr*, 1975; *Volkman and Trivelpiece*, 1981; *Ainley et al.*, 1983; *Trivelpiece et al.*, 1987; *Fraser and Patterson*, in press]. These features, in concert with varying productivity in the adjacent marine environment, impact the annual reproductive success of the penguins and determine the distribution and size of penguin populations in the Peninsula region and likely elsewhere in the Southern Ocean.

3.2. Sea Ice

Sea ice cover on the Southern Ocean undergoes a strong seasonal cycle of growth and decline from a summer minimum in February of 4 million km^2 to a winter maximum in September of 20 million km^2 [*Zwally et al.*, 1983]. Satellite records from 1973 onwards indicate that winter pack ice reaches its maximum coverage in the Western Peninsula region of the Southern Ocean at six to eight year intervals, and that the year-to-year variations in ice cover are greater in extent in the Western Antarctic Peninsula area than in any other region of Antarctica. Within our LTER region, year-to-year variations in winter ice cover tend to be large in the northeastern Peninsula area in the vicinity of the Admiralty Bay study site, and fairly consistent in the southwestern Peninsula region adjacent to the Anvers Island study site. Further annual pack ice cycles in this region are characterized by a five month period of ice advance followed by a seven-month period of ice retreat. This is the opposite of the more common annual cycle of ice advance-retreat in other regions of the Southern Ocean [*Stammerjohn*, 1993; *Stammerjohn and Smith*, this volume]. Although the physical factors underlying these differences in the annual advance-retreat cycle of the pack ice are unknown, they may have important biological impacts on the food web in this area. The comparatively rapid advance of pack ice in fall may accelerate and enhance the establishment of the diatom community associated with the pack ice in winter, while the slower retreat of spring pack ice may affect the timing and productivity of the spring bloom associated with the melting of this ice. Whatever the mechanism, it is clear that annual and interannual variability in the timing and extent of pack ice coverage impacts all levels of the Antarctic marine food web, from primary production to breeding success in predators [*Ainley et al.*, 1986, 1988; *Trivelpiece et al.*, 1987, 1990; *Croxall et al.*, 1988; *Fraser et al.*, 1992; *Eicken*, 1992].

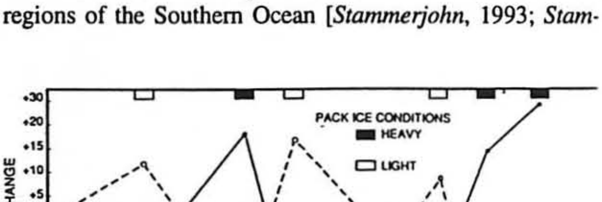

Fig. 2. Changes in numbers of breeding Adélie (solid circles) and chinstrap (open circles) penguins at Admiralty Bay, following winters of heavy versus light pack ice cover. Adapted from *Trivelpiece et al.* [1990].

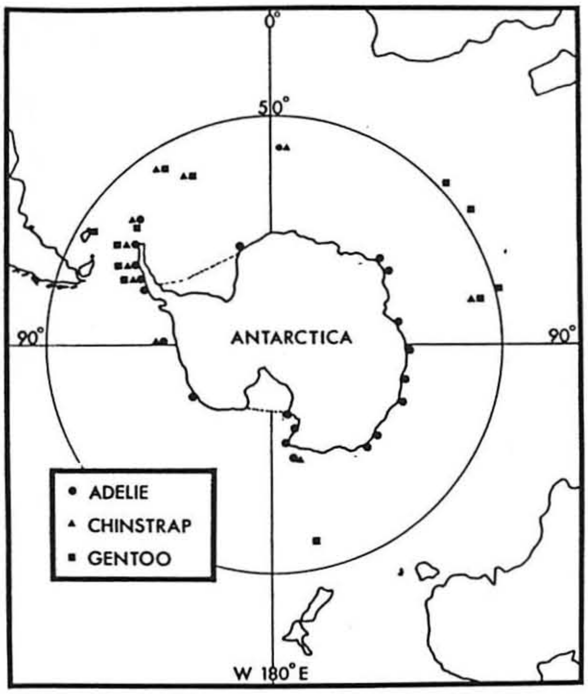

Fig. 3. The circumpolar distribution of Pygoscelid penguins. Adapted from *Trivelpiece et al.* [1987].

3.3. *Ocean Circulation*

Our LTER study site encompasses most of the Western Antarctic Peninsula, extending from the tip of the Peninsula to Marguerite Bay, including the coastal waters adjacent to the Peninsula and the offshore continental shelf waters. The continental shelf waters in the Antarctic Peninsula region are characterized by a cold (-1.0° to -1.8°C), shallow (< 200 m) surface mixed layer that overlies a region of warm, salty Circumpolar Deep Water (CDW), extending to the bottom [*Capella et al.*, 1992; *Hofmann et al.*, this volume]. Within

TABLE 1. Habitat variables affecting penguin distribution and breeding biology.

HABITAT	FEATURES	VARIABLES	IMPACTS
Ocean	Global circulation	Water mass	Affects prey distribution & flux
	Regional circulation	Temperature, Salinity, Density	Affects biomass of prey in area, penguin population size & distribution
	Fronts & Eddies	Nutrient concentration	Affects prey distribution & penguin foraging behavior
	Topographic interactions	Current velocity	Affects ice & impacts access to breeding areas in early spring
Ice	Interannual variability	Ice area–global/regional	Affects overwinter survival of penguins, biomass & recruitment of prey
	Seasonal cycle	Ice edge position	Affects penguin foraging & prey availability
	Regional	Ice dynamics, Marginal Ice Zone	Refuge for prey & winter habitat for Adélie penguins
	Local	Polynya & leads Type/thickness	Affects penguin distribution via access to colonies
Terrestrial	Topography aspect	Snow cover, Water runoff	Affects nest site availability & breeding success
	Geology	Breeding site suitability -slope -wind direction -substrate -solar radiation	Affects recruitment to breeding groups in colonies, the timing of breeding events & breeding success

this region are two subregions: Bransfield Strait, which covers the northeast one-third and an extensive shelf-slope area that covers the remaining two-thirds of the region. The Adélie penguin population at Admiralty Bay is located within the former and the Anvers Island population within the latter of these two subregions (Figure 1*a*). Each subregion is distinguished by regional differences in bathymetry, water mass distributions and circulation patterns, which in turn influence their respective penguin populations.

4. ENVIRONMENTAL VARIABILITY–REPRODUCTIVE EFFECTS

4.1. *Colony Access–Sea Ice Effects*

The effects of environmental variability on the breeding success of Adélie penguins have been described in detail by *Stonehouse* [1963], *Yeates* [1968, 1975], *Ainley and LeResche* [1973], *Spurr* [1975] and *Whitehead et al.* [1990].

These authors, working at Continental colonies in the Ross Sea and Prydz Bay regions, concurred that annual variation in Adélie penguin breeding success is largely due to the timing of sea ice breakout. When ice covers the sea adjacent to colonies during the breeding season, Adélie penguins must walk from wintering areas to their colonies, then later, again must walk from the colony to the feeding grounds. Travel over ice is much slower and more energetically expensive than swimming, and these added costs decrease reproductive success by reducing the fat stores available to sustain the birds during the three to five week fasting period following their arrival at the colony. Egg losses due to failure to complete the long fasts of the incubation period are the single most important factor reducing breeding success in Adélie penguins [*Davis*, 1982; *Ainley et al.*, 1983; *Trivelpiece and Trivelpiece*, 1990].

The presence of ice adjacent to breeding colonies affects breeding success by delaying arrival at the colony [*Penney*, 1968; *Spurr*, 1975]; increasing durations of nest reliefs during incubation, resulting in desertion of eggs [*Yeates*, 1968], reducing egg masses and increasing proportions of single egg clutches [*Ainley and LeResche*, 1973; *Spurr*, 1975] and reducing food load sizes brought to chicks [*Emison*, 1968]. During four seasons at Cape Royds, *Yeates* [1968] reported breeding success rates between 50% and 68% in three years when sea ice breakout occurred between early and mid-December; however, success fell to only 26% in a fourth season when sea ice breakout was delayed until late January. *Ainley and LeResche* [1973] and *Spurr* [1975] reported low reproductive success among Adélie penguins at Capes Crozier and Bird, respectively, during years of high and persistent sea ice cover, and increased success during subsequent years of low sea ice cover. *Ainley and LeResche* [1973] also reported more young birds attempted to breed in years when sea ice breakout occurred before January. Similarly, *Whitehead et al.* [1990] reported Adélie penguin breeding success at Prydz Bay, East Antarctica, varied between 0.69 and 1.33 chicks fledged per pair over seven seasons between 1981 and 1987. Reproductive success was greatest in years when fast-ice breakout occurred before the end of December, and was lowest when pack ice cover persisted into January within the foraging range of penguins feeding chicks.

4.2. *Colony Location–Microclimate Effects*

The microclimate of an area has a strong influence on the size of the Adélie colonies and on the placement of breeding groups within the colonies [*Stonehouse*, 1963]. Wind speed, wind direction, and snow deposition are important factors affecting breeding success in Adélie penguins [*Moczydlowski*, 1986, 1989; *Fraser and Patterson*, in press]. The existence of an extensive snow-free land area is likely a major reason why Adélie penguins have so successfully colonized Cape Crozier compared to nearby Cape Royds. The exposed Cape Crozier colony has an Adélie penguin population of approximately 150,000 breeding pairs [*Emison*, 1968; *Taylor et al.*, 1990], while nearby Cape Royds, protected from southerly winds by high mountains, has only 3-4,000 breeding pairs [*Taylor et al.*, 1990], even though much additional nesting habitat is available later in the season [*Stonehouse*, 1963].

Several inactive Adélie penguin colonies in the vicinity of Cape Royds were noted by *Spellerberg* [1970], who suggested their abandonment was likely the result of changing patterns of polynya formation and sea ice break-out in McMurdo Sound. Alternatively, *Yeates* [1971] suggested that the colonies could have been decimated by severe drifting, which may have affected recruitment patterns of young birds to the colonies. Counts made in colonies during the reoccupation phase [*Sladen*, 1958] of the Adélie cycle at Cape Royds indicated that new pairs selected nest sites in breeding groups in which chicks were already present. The presence of chicks in these areas would indicate to young, inexperienced birds that at least minimal conditions were met to assure successful breeding in that area. A majority of the penguins engaging in these late season pairings are young, prebreeding birds, and the experience they gain during this period has been shown to influence their subsequent choice of a breeding site [*Ainley et al.*, 1983].

The Adélie penguin population on Litchfield Island, near Palmer Station, has experienced a significant decrease since 1975. This decline has been related to the effects of local topography and wind direction on changes in the patterns of snow accumulation in the vicinity [*Fraser and Patterson*, in press]. The predominant wind direction during storms at Palmer Station is from the northeast [*Smith et al.*, this volume] and snow accumulates on the southwestern side of ridges. The Adélie penguin colony on Litchfield Island is located in the lee of the island's highest peak and is subject to large snow deposits. Further analysis of five colonies in the immediate vicinity of Palmer Station (i.e., within a two mile radius) revealed that 18 of the 21 breeding groups that have recently been abandoned are located to the southwest of prominent topographical features, and are thus in the snow shadow of the prevailing winds of the region (Figure 4).

Fraser et al. [1992] suggested that a warming trend in the Antarctic Peninsula region over the last 40 years has resulted in a decrease in the number of years with extensive ice cover, a pattern confirmed by recent analyses of sea ice and weather data [*Stammerjohn*, 1993; *Stammerjohn and Smith*, this volume; *Smith et al.*, this volume]. Sea ice blocks the exchange of water vapor with the atmosphere and colder winters would therefore have been correlated with diminished snow fall [*Barry*, 1982; *Foster*, 1989]. The recent increase in the frequency of winters with open water has resulted in an increase in the mean annual snowfall in the area, and the effect of this has been a loss of breeding habitat at sites downwind from prominent topographical

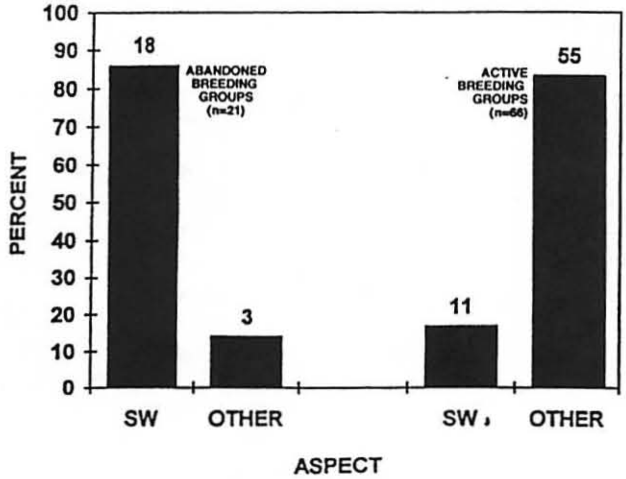

Fig. 4. The relationship between the location of breeding groups in the Palmer Station vicinity and the active versus abandoned status of these groups. Penguin nesting sites with a southwest (SW) aspect are in the lee of topographical features and accumulate snow during storms. Adapted from *Fraser and Patterson* [1995].

features. The disappearance of breeding groups can be fairly rapid, requiring only a couple of seasons of breeding failure to cause abandonment [*Yeates,* 1975; *Fraser and Patterson,* in press]. This argues that annual recruitment to breeding areas is a major factor in the persistence of colonies through time, and that very short-term changes in the environment can result in rapid shifts of the populations in an area.

Solar radiation and water runoff are additional factors that affect breeding success and site selection in Adélie penguins. Most colonies of Adélie penguins along the Antarctic coast are located on north-facing hillsides [*Yeates,* 1975; *Aoyanagi,* 1979; *Ainley and DeMaster,* 1980]. In the Adélie penguin colonies in Admiralty Bay, nest sites received an especially large amount of solar radiation due to the pronounced clustering of their breeding areas on northern slopes. In addition, measurements of albedo in the area indicated that the highest amounts of solar radiation were absorbed by the terrain associated with the breeding areas of Adélie penguins [*Moczydlowski,* 1986]. Similarly, all Adélie penguin nesting locations in Admiralty Bay are characterized as being located on well-drained slopes, ridges and moraines with porous substrates and good water runoff [*Moczydlowski,* 19-89].

5. ENVIRONMENTAL VARIABILITY–POPULATION SIZE AND DISTRIBUTION EFFECTS

Stonehouse [1967] suggested that the distribution of Adélie penguin colonies, in the southernmost regions of their range, reflects primarily the presence of anomalous areas that are characterized by persistent open water in spring adjacent to ice-free land. These polynya areas occur because of locally strong currents, such as at Cape Royds [*Taylor,* 1962; *Stonehouse,* 1967], and/or strong winds, such as at Cape Crozier [*Ainley et al.,* 1983]. Strong winds and currents might be expected to play an important role in determining early season access to Continental Adélie penguin colonies due to the colder climate and consequently greater seasonal persistence of pack ice in this region. However, our evaluation of the distribution of Adélie penguins in the Peninsula region suggests that variability in physical factors, such as oceanic currents, bathymetry, wind and pack ice, are equally important in determining the distributions of the penguin colonies there.

5.1. *Distribution of Adélie Penguin Colonies in the Bellingshausen Sea*

The Adélie penguin population in the Bellingshausen Sea region of the Peninsula consists of approximately 125,000 breeding pairs in 40 colonies between southern Anvers Island and Marguerite Bay [*Poncet and Poncet,* 1987; *Woehler,* 1993; Figure 5]. Although these colonies are distributed throughout the 500 km long Peninsula and offshore island groups of this area of the Bellingshausen Sea, 90,000 pairs (72%) breed within 25 km of Anvers Island or Marguerite Bay. The bathymetry of this region is characterized

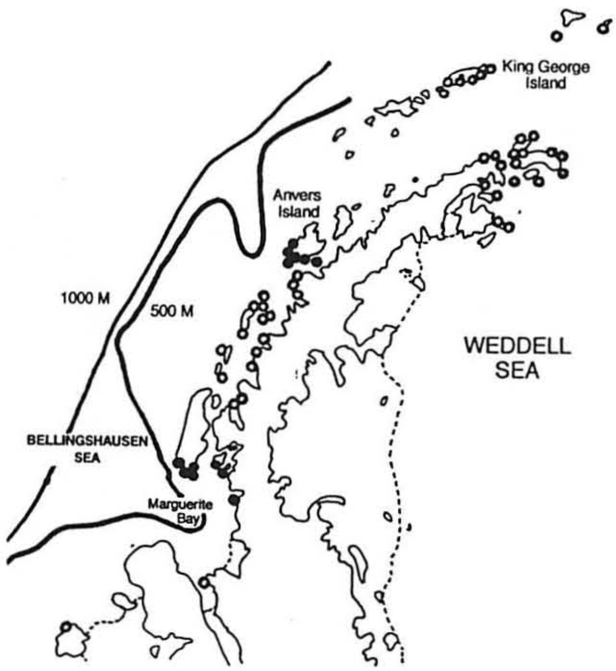

Fig. 5. The distribution of Adélie penguin colonies and the bathymetry (500 m and 1000 m isobaths) in the Bellingshausen Sea region. Adélie penguin colonies adjacent to the offshore canyons (solid circles) hold 72% of all breeding pairs in the region. Other Adélie penguin colonies (open circles) contain the remaining 28% of the region's Adélie penguin population.

by a shallow, 200-400 m deep, extensive shelf-slope area 140-200 km wide, bisected by two deep canyons. Both canyons are between 500 and 700 m deep; the northern canyon cuts across the shelf adjacent to Anvers Island, while the southern canyon extends into Marguerite Bay [*Hofmann et al.*, this volume; Figure 1*a*]. The juxtaposition of the canyons and the clumped distribution of Adélie penguin populations suggests an underlying cause-effect link between them.

Upwelling and eddies associated with the canyons may serve to enhance nutrient input and productivity of the associated water column in the vicinity and provide a predictable and easily accessible food base for prey and predators alike. However, there is little evidence to suggest that food supply is limiting for Adélie penguins during the breeding season, and a recent analysis of the factors affecting Adélie penguin populations in the Peninsula region concluded that prey availability cannot explain the sizes and/or distributions of colonies in this region [*Ainley, et al.*, in press]. Alternatively, we suggest that a link between the canyons and the Adélie penguin distributions is found in the interactions among the canyons, the warm Circumpolar Deep Water (CDW) off the shelf break and its effect on sea ice cover in these locales.

The most prominent water mass of the Western Antarctic Peninsula region is the CDW, characterized by a temperature maximum of >1°C and a salinity of 34.8 psu [*Hofmann et al.*, this volume]. This water mass is found at the shelf break at a depth of 400 to 700 m. In this region, CDW can flood onshore via the deep canyon cuts that traverse the shelf at Anvers Island and Marguerite Bay and may be a factor in reducing sea ice cover in these areas. *Klinck and Smith* [1994] calculated the vertical diffusion of heat into the surface layer of these shelf waters to be 90 W m^{-2} and suggested that this heat flux could not be accounted for without an import of heat from offshore. Thus, they reasoned that there must be a general onshore flow of warm CDW, and we suggest that the canyons provide a physical conduit that concentrates this flow in the Anvers Island and Marguerite Bay areas. We suggest that the clumped distributions of the Adélie penguin populations at colonies in the Anvers Island and Marguerite Bay areas reflect the species' preference for breeding sites that, over long periods of time and varying temperature/sea ice conditions, have predictable, early season polynyas that result from the upwelling of warm CDW in these areas.

5.2. *Distribution of Adélie Colonies in the Scotia Arc*

The Adélie penguin population of the upper Peninsula region (including the South Shetland and South Orkney Islands groups), consists of approximately 500,000 breeding pairs [*Woehler*, 1993]. The distribution of the colonies on King George Island, site of our Admiralty Bay study, is indicative of the patterns seen in the population as a whole; all 56,000 breeding pairs of Adélie penguins are confined to colonies on the southern (Bransfield Strait) side of the Island [*Jablonski*, 1984; Figure 6]. However, marine sampling [*Siegel and Loeb*, in press] and fisheries catches [Report WG-EMM, 1995], suggest that the biomass of krill is significantly greater on the northern (Drake Passage) side of the South Shetland Islands, where 95% of the more than 300,000 chinstrap penguins (*P. antarctica*) breed [*Jablonski*, 1984]. *Lishman* [1985] suggested that the separation in breeding habitat between Adélie and chinstrap penguins, as well as the three to four week separation in their breeding cycles were adaptations to reduce competition between these two closely related species. However, *Trivelpiece et al.* [1987] suggested that these differences were the result of adaptations by each species to differing environmental conditions at the centers of their respective geographical ranges. Adélie penguins have evolved a strategy that allows them to breed successfully in the short, four month summers of Continental Antarctica. A key to their success is their ability to fast for prolonged periods, thereby allowing them to begin breeding in early spring. However, this strategy requires that colony sites are easily accessible in the spring, as energetically costly travel over ice may severely deplete energy stores needed for breeding.

Both the Drake Passage and Bransfield Strait sides of the South Shetland Islands have strong, alongshore currents that move in a northeasterly direction [*Capella*, 1992]. However, the predominant wind direction in this region is westerly, with winds strong and persistent, especially in the spring and fall [*Smith et al.*, this volume]. These winds push pack ice up against the northwestern shores of the South Shetland Islands, while clearing the bays and shores on the southeastern side of the islands. We suggest that the Adélie penguin distribution is confined to the leeward (Bransfield Strait) side of the South Shetland Islands due to the differences in accessibility afforded them by this wind-pack ice interaction, a problem that the later breeding chinstraps do not face.

5.3. *Adélie Distribution–Pack Ice Interactions*

Research cruises in the Weddell and Bellingshausen Seas have confirmed that Adélie penguins are confined to the pack ice habitat during winter [*Fraser et al.*, 1992; LTER August Cruise,1993; pers. obs.; Figure 7]. Adélie penguins migrate from their pack ice wintering grounds to their breeding colonies in the Antarctic Peninsula region between late September and mid-October. The peak of egg laying among Adélie penguins in the Admiralty Bay region is late October, approximately two and four weeks earlier than their sympatrically breeding congeners, the chinstrap and gentoo (*P. papua*) penguins, respectively. We hypothesize that the reason Adélie penguins are able to begin breeding at such early dates, a critical factor in an environment of short summer seasons, is their reliance on prey associated with the pack ice community, as a food resource after clutch completion.

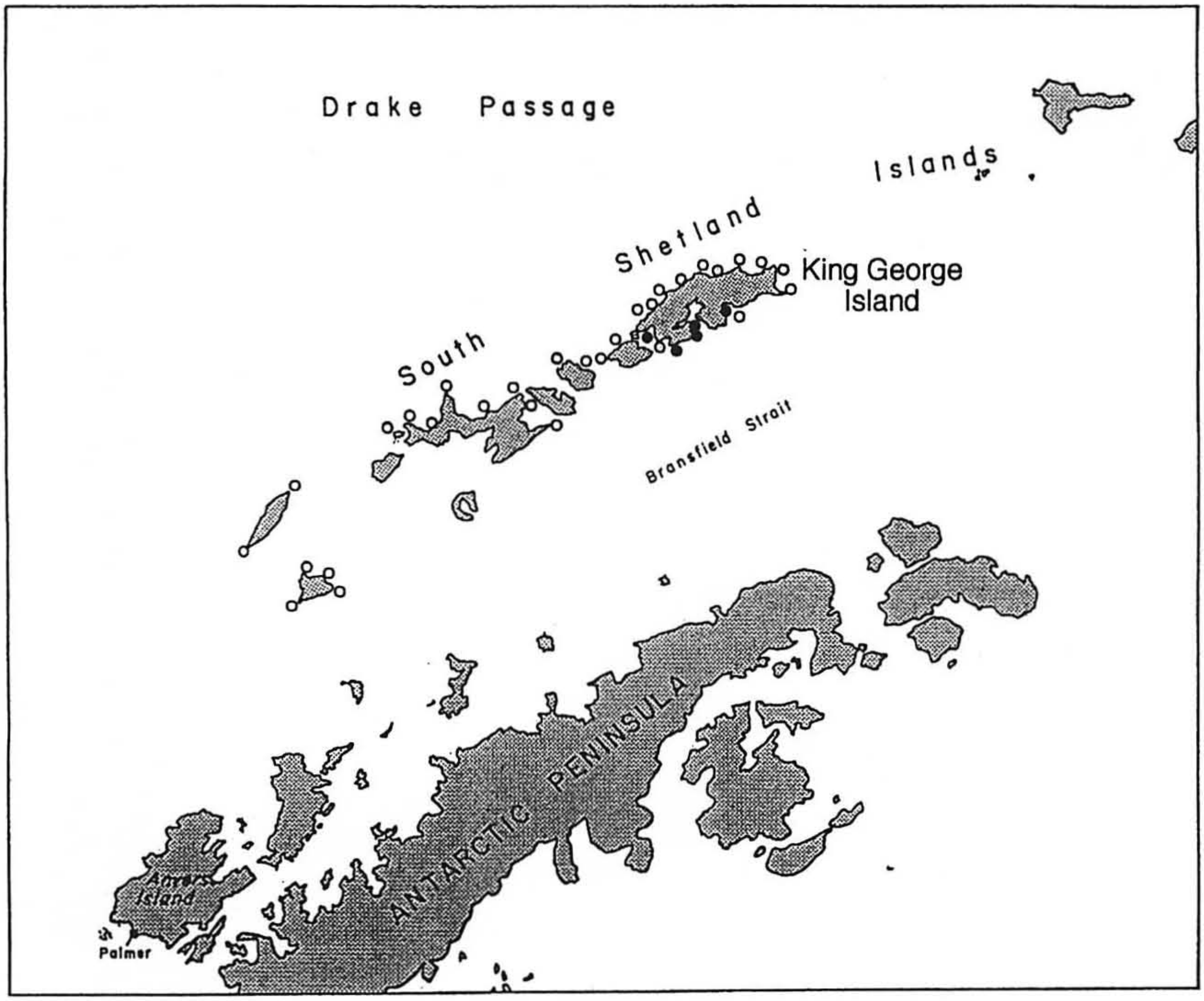

Fig. 6. The segregation of Adélie (solid circles) and chinstrap (open circles) penguin colonies in the South Shetland Islands. All Adélie penguin colonies are found on the "ice free", Bransfield Strait side of King George Island, while most large chinstrap penguin colonies (>5,000 pairs) are found on the outer, Drake Passage side of the islands.

Both sexes, females first, have lengthy (11 to 14 day) first trips to sea following a prolonged, three week courtship fast. We suggest that this first long trip is necessary to allow each member of the pair time to return to the pack ice environment to feed—this being the only habitat with predictable and plentiful prey in the early spring period.

We hypothesize that there are two distinct Adélie penguin populations inhabiting the Antarctic Peninsula region. One is distributed from Anvers Island southward and winters in the Bellingshausen Sea pack ice; the second occurs from King George Island eastward and winters in the Weddell Sea pack ice (Figure 8). We suggest that the reason there are no Adélie penguins breeding between King George and Anvers Islands (approximately a 400 km gap), while over one million chinstrap penguins breed there, is because this gap represents a middle "no man's land", that is, on average, too far from either the Weddell or Bellingshausen Sea pack ice areas to allow pairs to successfully complete their first incubation shifts. Given the Adélie penguin's affinity for its natal colony [*Ainley et al.*, 1983], we further suggest that these areas may represent genetically isolated populations which may have distinctive demographic characters adapted to regional environmental conditions.

6. BIOGEOGRAPHY OF PENGUIN POPULATIONS

The distribution and biomass of penguin populations in the Antarctic Peninsula region have changed dramatically over the past 50 years, with evidence suggesting that there has been an overall increase in chinstrap penguins, with a concomitant decrease in Adélie penguins [*Croxall and Kirkwood*, 1979; *Woehler*, 1993]. Earlier authors suggested that the increase in chinstrap penguins was related to an increased abundance of their food (krill) brought about by the demise of the world's baleen whale stocks in the region [*Sladen*, 1964; *Conroy*, 1975; *Croxall and Prince*, 1979; *Laws*, 1985]. However, *Fraser et al.* [1992] challenged this hypothesis and argued instead that the population changes were related to decreasing winter pack ice cover in the area. Increased temperatures were correlated with a reduction in the frequency of winter pack ice which in turn negatively affected the pack ice wintering Adélie penguins while benefiting the pelagic wintering chinstrap penguins.

If, as suggested here, penguins are sensitive to environmental fluctuations, then penguin colonies must have been abandoned and reoccupied throughout the past hundreds to millions of years. *Emslie* [in press] and *Tatur et al.* [in press] have reported excavating penguin colonies in the Peninsula region that have been continuously abandoned and reoccupied over the last several thousand years, and have correlated these population changes to changes in sea ice conditions and sea levels. The impact of sea ice on the distribution of the Adélie penguin population in the Peninsula region may have been especially important as recently as the Little Ice Age (16th to 18th centuries), when global cooling may have significantly affected the access of Adélie and chinstrap penguins to their breeding areas.

Given that Adélie penguins are extremely faithful to their breeding colonies, the current concentrations of this species near areas of warm, upwelled CDW in the Bellingshausen Sea region, may reflect the greater stability of these sites over evolutionary time; as access to breeding sites during colder periods would have favored individuals breeding in

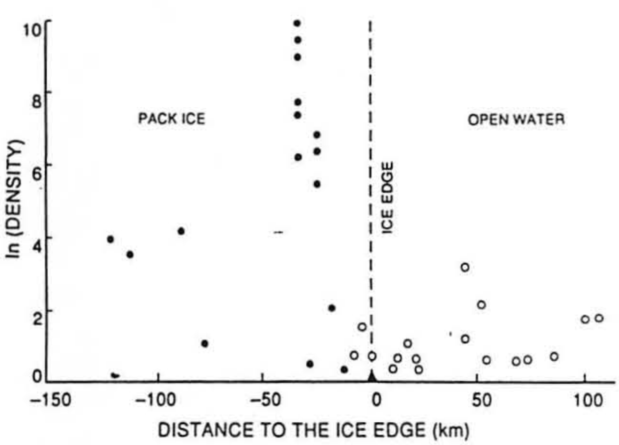

Fig. 7. The winter distribution of Adélie (solid circles) and chinstrap (open circles) penguins in the Weddell Sea. Adélie penguins are found associated with the winter pack ice habitat, while chinstrap penguins are found in the open pelagic areas to the north of the pack ice. Adapted from *Fraser et al.* [1992].

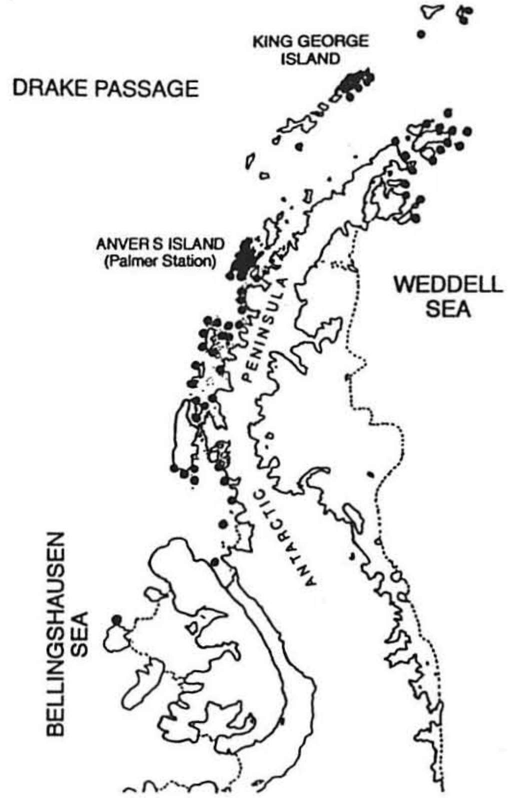

Fig. 8. The distribution of the Adélie penguin population in the Antarctic Peninsula region. There are two spatially distinct populations in the region; one is distributed from Anvers Island southward and winters in the Bellingshausen Sea pack ice, the second is distributed from King George Island eastward and winters in the Weddell Sea pack ice.

the vicinity of polynyas. Likewise, the "gap" in the distribution of Adélie penguins in the Peninsula region may be a temporary artifact of the current, warm environmental temperatures. This break in the species distribution may have closed during earlier, colder periods; an hypothesis that could be tested by fossil excavations at abandoned colonies in the gap and genetic analyses of the current subpopulations. Such data would provide important information on changes in penguin populations in the past and would provide insights into the potential consequences of continued global warming in the future.

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