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FACTORS CONTROLLING THE DISTRIBUTION OF SEABIRDS: WINTER-SUMMER HETEROGENEITY IN THE DISTRIBUTION OF ADÉLIE PENGUIN POPULATIONS

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Recent and historical data on the distribution of Adélie Penguins in the western Antarctic Peninsula region were analyzed to examine and detect patterns and causes of heterogeneity, and to relate these to long-term population changes. Adélie Penguins are one of the dominant componensts of the region's seabird community in terms of biomass, but not in numerical abundance. Approximately 308,300 pairs breed in the region, 80% of which are found in five colony clusters. These colony clusters are associated with deep canyons and basins that intersect the continental shelf. Adélie Penguins confine foraging activities to regions over these deep features that are within 20-50 km from colony clusters. Winter distributions in the Weddell and Bellingshausen Seas exhibit similar spatial heterogeneity and also occur in association with anomalies in bottom topography. Available daylight in winter restricts available foraging time, an analog to summer conditions when similar restrictions occur due to the need to provision chicks. It is hypothesized that summer and winter heterogeneity in the distribution of Adélie Penguins is maintained by behavioral mechanisms, but is causally linked to the juxtaposition of suitable bottom topography, nesting habitat, pack ice and available daylight, features associated with high prey availability. Changes in the spatial and temporal juxtaposition of some of these features over ecological and geological time due to climate change are likely to drive changes in the populations of Adélie Penguins. Different regions of the Antarctic appear to be out of phase with each other from the standpoint of climate change for reasons that are not yet clear. As a result, trends in Adélie Penguin populations are not synchronized, but instead reflect region-specific changes in climate.

1. INTRODUCTION

The broad patterns of oceanic seabird distributions in the Antarctic have been known for more than five decades [*Bierman and Voous*, 1950], and as recently as the mid-1960s, the predominant view was that these distributions were controlled primarily by the abundance and availability of prey [*Voous*, 1965]. By the mid-1970s, however, studies in a number of marine systems began to suggest that most seabird species were actually constrained by specific physical features of the marine environment, including temperature and salinity, ocean depth, water transparency, depth of the mixed layer and wind regimes among others [e.g., *Abrams and Miller*, 1986 and references therein]. For the Southern Ocean, the presence or absence of sea ice was identified as a key feature influencing the distribution of seabirds and, indeed, the composition of the region's oceanic avian communities [*Cline et al.*, 1969; *Zink*, 1981; *Ainley and Jacobs*, 1981; *Ainley et al.*, 1984; *Abrams*, 1985]. From these studies, it became apparent that seabirds perceived discontinuities in the pelagic environment as habitat boundaries, which could, potentially, account for differences in their oceanic distributions unrelated to the direct availability of prey [concepts reviewed in *Fraser and Ainley*, 1986; hypotheses tested in *Ainley et al.*, 1992; 1993; 1994].

By the mid-1980s, with support from earlier research on ecological segregation in marine birds based on breeding habitat characteristics [*Cody*, 1974], the idea that seabird communities might be structured by diversity in their nesting and pelagic habitats had gained acceptance. The concept that seabird distributions reflected the juxtaposition of appropriate foraging and breeding habitats [*Ashmole*, 1971; *Diamond*, 1978; *Furness and Birkhead*, 1984; *Croxall and Prince*, 1980] thus provided a conceptual link to ideas developed two decades earlier for terrestrial bird communities [*MacArthur et al.*, 1966; *Cody*, 1974]. Still lacking, however, was an explanation for how seabirds integrate the juxtaposition of the two habitats as part of their life history strategies, which is ultimately necessary to account for their distributions from an ecological and evolutionary perspective. This issue arises because seabirds are not evenly distributed, even within the confines of their species-specific breeding and oceanic ranges, but the factors that drive this heterogeneity are not always apparent. Indeed, the issue is extremely complex, as it poten-

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TABLE 1. Breeding Status and Species Diversity of Seabirds Occurring in the Western Antarctic Peninsula Region.

Family	Species	
	Breeding	Non-breeding
Spheniscidae: Penguins	Emperor Penguin (*Aptenodytes forsteri*)	King Penguin (*A. patagonicus*)
	Macaroni Penguin (*Eudyptes chrysolophus*)	Rockhopper Penguin (*E. chrysocome*)
	Adélie Penguin (*Pygoscelis adeliae*)	
	Chinstrap Penguin (*P. antarctica*)	
	Gentoo Penguin (*P. papua*)	
Diomedeidae: Albatrosses		Wandering Albatross (*Diomedea exulans*)
		Black-browed Albatross (*D. melanophris*)
		Gray-headed Albatross (*D. chrysostoma*)
		Sooty Albatross (*Phoebetria fusca*)
		Light-mantled Sooty Albatross (*P. palperata*)
Procellariidae: Fulmars Prions Petrels	Southern Giant Petrel (*Macronectes giganteus*)	Northern Giant Petrel (*M. halli*)
	Antarctic Fulmar (*Fulmarus glacialoides*)	
	Cape Petrel (*Daption capense*)	Antarctic Petrel (*Thalassoica antarctica*)
	Snow Petrel (*Pagodroma nivea*)	Blue Petrel (*Halobaena caerulea*)
		White-chinned Petrel (*Procellaria aequinoctialis*)
		Antarctic Prion (*Pachyptila desolata*)
Oceanitidae: Storm Petrels	Wilson's Storm Petrel (*Oceanites oceanicus*)	Black-bellied Storm Petrel (*Fregetta tropica*)
Phalacrocoracidae: Cormorants	Blue-eyed Shag (*Phalacrocorax atriceps*)	
Chionididae: Sheathbills	Greater Sheathbill (*Chionis alba*)	
Stercorariidae: Skuas	South Polar Skua (*Catharacta maccormicki*)	
	Brown Skua (*C. lonnbergi*)	
Laridae:	Kelp Gull (*Larus dominicanus*)	
	Antarctic Tern (*Sterna vittata*)	Arctic Tern (*S. paradisaea*)

tially involves factors whose interactions span multiple spatial and temporal scales, and include the effects imposed by features as diverse as behavior [*Wittenberger and Hunt*, 1985] and environmental change [*Enfield*, 1992].

The objective of this chapter is to examine some of the factors associated with heterogeneity in the summer and winter distributions of Adélie Penguin (*Pygoscelis adeliae*) populations in the western Antarctic Peninsula region. This objective has three components. The first is to provide a background setting for the seabird research conducted under the LTER central hypothesis. The second is to examine the winter and summer distribution patterns of Adélie Penguin populations in the LTER region, and the third is to relate the findings of the second analysis to the broader ambit of this volume, namely, seabirds as one of the foundations for ecological research.

As mobile, long-lived upper-trophic level predators, seabirds integrate the effects of variability in aspects of the physical and biological environment over large spatial and temporal scales. The expression of this variability can, for example, be measured annually as changes in breeding success [*Croxall et al.*, 1988], or over the course of decades and centuries as changes in populations and community structure [*Fraser et al.*, 1992; *Emslie*, 1995]. The factors that affect seabird distributions at smaller scales can thus provide the basis for interpreting ecological processes related to populations and their distributions at larger scales. Understanding the relationships between scale-specific processes has long been recognized as one of the fundamental objectives of ecological research [*Levin*, 1992].

2. BACKGROUND AND HISTORY

2.1. *Historical Perspectives*

The western Antarctic Peninsula region encompasses an area of 22,000 km^2 that extends from the tip of the Peninsula south to Alexander Island and west to the shelf break [*Hofmann et al.*, this volume]. Seventeen seabird species breed within this region and 14 occur as non-breeders [Table 1; *Watson*, 1975; *Parmelee*, 1992]. Despite its relative proximity to South America, data on the general distribution and abundance of the region's breeding and non-breeding seabirds are scarce prior to the late-1960s [references and review in *Poncet and Poncet*, 1987; *Parmelee*, 1992]. An interest in the region's penguin populations in the late 1970s, however, served as the catalyst for two comprehensive assessments of not only their abundance and breeding distribution, but those of several other species as well [*Croxall and Kirkwood*, 1979; *Poncet and Poncet*, 1987]. Marine surveys [*Erickson et al.*, 1972; *Kock and Reinsch*, 1978; *Zink*, 1981; *Stark and Wyrzykowski*, 1982] also determined the general patterns of regional seabird abundance and distribution, and provided the first quantitative evidence of potential links between these parameters and the presence or absence of sea ice. More localized surveys through the end of the decade that focused on coastal breeding species [*Poncet and Poncet*, 1985; *Parmelee and Parmelee*, 1987; *Shuford and Spear*, 1988] added further information on regional seabird distributions and abundance and culminated with a comprehensive record that is specific to the penguins [*Woehler*, 1993]. During this period, oceanic surveys remained scarce and limited in scope to the summer [*Wanless and Harris*, 1988; *Hunt et al.*, 1990]; winter data continue to be extremely rare [*Pietz and Strong*, 1986; *Fraser et al.*, 1989; *Whitehouse and Veit*, 1994] and critically needed for future assessments.

TABLE 2. Species Abundance and Biomass Relationships for the Seabird Community Within 6 km of Palmer Station, Anvers Island, Western Antarctic Peninsula. The Largest Adélie Penguin Colonies on Biscoe Point and Dream Island are not Included. Regional Abundance and Biomass Relationships for the Three Pygoscelid Penguins are Shown at the Bottom of the Table. Data for the Last Three Species are Adapted from *Woehler* [1993].

Species	Number of Breeding Pairs	Total Biomass (kg)
Adélie Penguin	13,303	117,066
South Polar Skua	736	1,840
Brown Skua	13	50
Blue-eyed Shag	687	2,885
Southern Giant Petrel	425	3,736
Kelp Gull	220	440
Antarctic Tern	85	24
Wilson's Storm Petrel	1,000	72
Greater Sheathbill	3	5
Adélie Penguin	308,348	2,713,462
Chinstrap Penguin	1,108,409	9,199,795
Gentoo Penguin	44,476	524,817

2.2. *Seabird Species Richness and Abundance*

The breeding status and species diversity of seabirds that occur in the western Antarctic Peninsula region are shown in Table 1. With the exception of the *Pygoscelid* penguins and the few species that breed close to long-term research sites (Table 2), the biology and population status of most of these species is generally better known for populations that occur outside rather than within the western Antarctic Peninsula region. *Hunt et al.* [1994] and *Croxall et al.* [1984] currently provide the only regional-scale reviews available on the oceanic occurrence of these species [also see *Ainley et al.*, 1994] and the status and distribution of breeding populations. Thirteen of the 14 species that do not breed in the region occur primarily during the summer, feeding at sea but breeding in areas beyond its northern boundary. Antarctic Petrels are the exception; this species breeds in areas beyond the regions' southern boundary, but feeds year-round in association with its ice-covered waters. The 16 species that breed in the region include both permanent and seasonal residents. *Parmelee* [1992] and *Ainley et al.* [1994 and references therein] review the occurrence of the more common members of this group in terms of their seasonal affinities to breeding and oceanic habitats. Although the latter study is based on Weddell Sea data, when combined with the work of *Hunt et al.* [1994], it provides the most comprehensive examination of the seasonal ecology of these species, including the factors associated with spatial and temporal changes in distribution, abundance and community structure.

Some general relationships between the abundance and biomass of the better known component members of the region's breeding seabirds and Adélie Penguins are shown in Table 2. Adélie Penguins have a circumpolar distribution and a minimum breeding population of 2.47 million pairs, of which 308,300 occur in the western Antarctic Peninsula region, where their range overlaps with Chinstrap (1.11 million pairs) and Gentoo (44,400 pairs) penguins [*Woehler,* 1993]. It is not known if these three species are the numerically dominant components of the region's breeding seabird community because no comparative population estimates are available for other abundant species such as Wilson's Storm Petrel. However, as is true of the Southern Ocean in general and suggested by Table 2, these penguins unquestionably represent the dominant component of the region's avian biomass. Along with Brown and South Polar Skuas, they also comprise one of the best studied seabird groups in the region [cf. *Parmelee,* 1992; *Trivelpiece and Fraser,* this volume], and the key reason why Adélie Penguins and South Polar Skuas were selected as LTER core species.

2.3. Seabird Research and the LTER Central Hypothesis

During the mid-1970s, the United States initiated two research programs focused on seabirds in the western Antarctic Peninsula region, one in the South Shetland Islands [*Trivelpiece and Volkman,* 1979] and the other in the Palmer Archipelago [*Parmelee et al.*, 1977]. These programs were still in existence at the inception of the LTER in 1990 and provided the LTER with well documented information on seabird breeding biology, foraging ecology and long-term regional population changes. Indeed, data based on these programs and an unrelated winter marine study in the Weddell Sea [*Ainley and Sullivan,* 1989] had already formulated and tested aspects of what later became the LTER central hypothesis [*Fraser et al.*, 1992]. This was accomplished through a challenge to the long-held view [cf. *Laws,* 1985] that increases in the regional abundance and distribution of some krill- (*Euphausia superba*) eating predators was due to a "krill surplus" that resulted from the post-1950s commercial exploitation and depletion of the great stocks of krill-eating baleen whales. *Fraser et al.* [1992] proposed instead that changes in these predator populations had a more reasonable ecological and evolutionary explanation in species-specific pelagic winter habitat preferences (pack ice vs. open water). These authors hypothesized that environmental warming during the last four decades led to a reduction in the frequency of cold years with extensive sea ice cover, conditions that ultimately favored species requiring open water rather than pack ice.

The implications inherent in this "ice reduction" hypothesis currently guide the analysis and interpretation of data related to the ecology and evolution of seabirds in the western Antarctic Peninsula region. The conceptual framework for these ideas rests on two key related hypotheses that directly address the issue of heterogeneity and habitat juxtaposition as discussed earlier in the text:

1. Sea ice mediates the outcome of many Southern Ocean trophic interactions, including, but not limited to the availability of krill and fish to predators.
2. Variability in the spatial and/or temporal presence of sea ice is causally linked to the long- and short-term occurrence patterns of penguin and other seabird populations.

As these hypotheses suggest, the ability to examine ecological patterns and their evolutionary implications relative to the conceptual framework from which they derive rests primarily on the coincident availability of data on other physical and biological components of the environment, of which sea ice and climate obviously play potentially critical roles. *Smith et al.* [this volume] and *Stammerjohn and Smith* [this volume] provide comprehensive reviews of climate and sea ice conditions in the region. Their analyses support the earlier work and conclusions by *Fraser et al.* [1992] regarding regional temperature trends, the periodicity with which maxima in sea ice coverage occur and the interactions between these two variables with respect to possible long-term change in patterns of sea ice coverage (see Sec. 3). The analysis and discussion that follows capitalizes on the availability of these new data, as well as those of *Hofmann et al.* [this volume] on regional water mass characteristics and bathymetry, to examine spacing heterogeneity in Adélie Penguin populations in the western Antarctic Peninsula region.

3. PATTERNS OF HETEROGENEITY

3.1. Summer Breeding and Foraging Distributions

There are two north to south discontinuities or "gaps" in the breeding range of Adélie Penguins in the western Ant-

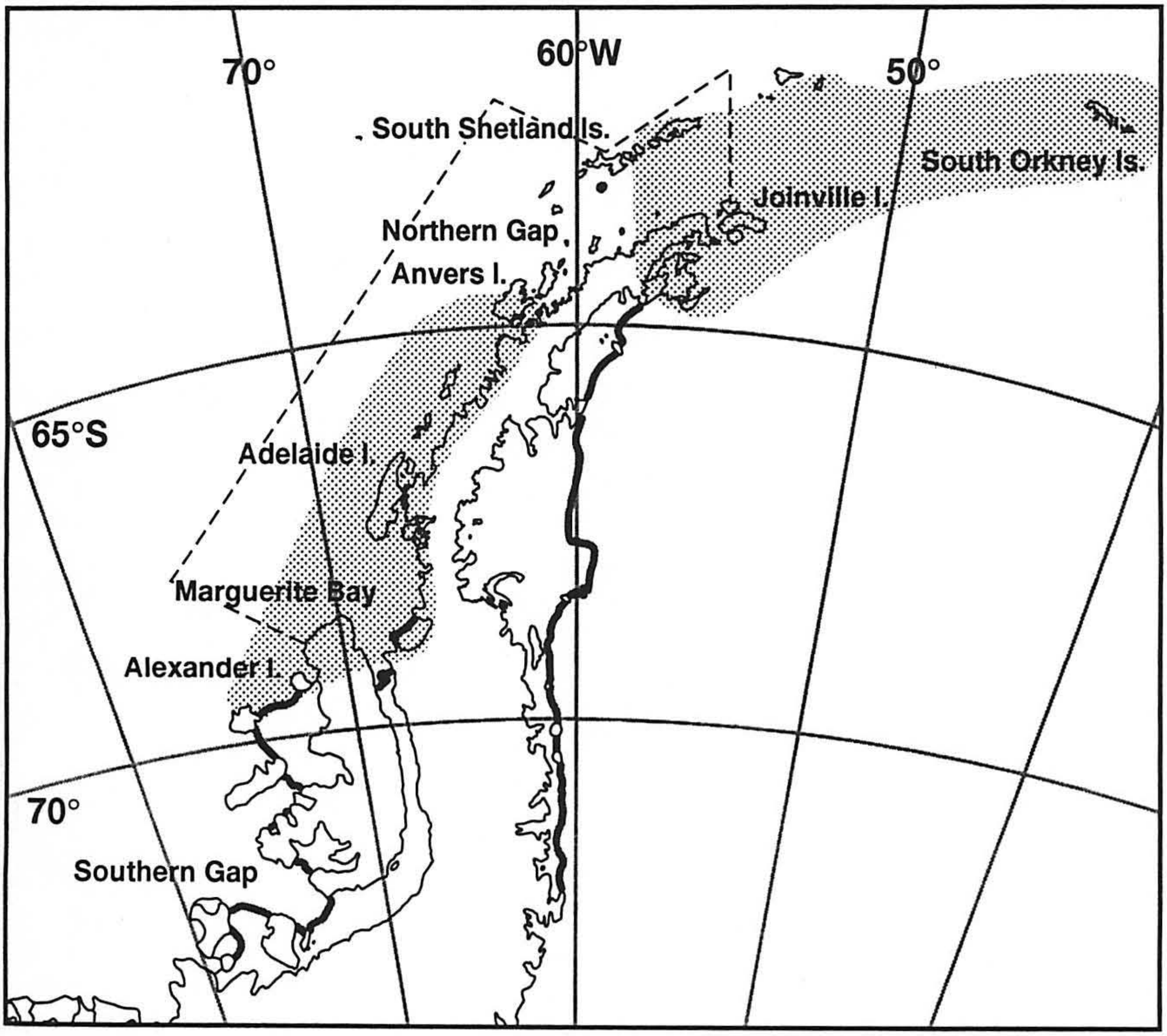

Fig. 1. The distribution of Adélie Penguins in the western Antarctic Peninsula region (shading). Dashed lines define the region's boundaries. Adapted from data in *Woehler* [1993].

arctic Peninsula region (Figure 1). A northern gap extends from the South Shetland Islands to the southern coast of Anvers Island. There are no known Adélie Penguin colonies in this well-surveyed area [*Poncet and Poncet,* 1987]. A southern gap extends from close to the south coast of Adelaide Island to the Ross Sea. The area here is not well surveyed, hence this southern gap may be due in part to undersampling. However, the region to at least Peter I Øy Island (68° 47'S, 90° 35'W) is known relatively well, and fewer than 150 breeding pairs of Adélie Penguins representing three separate colonies are known to occur in this vast area [*Woehler,* 1993].

Superimposed on this general distributional pattern is another, which is based on an analysis by *Ainley et al.* [in press] and is shown in Figure 2. Within their respective breeding ranges outside the northern and southern gaps, Adélie Penguins exhibit five population centers or clusters. Two of these are at the northern end of the western Antarctic Peninsula region, one on the South Shetland Islands and the other in the Joinville-Paulet Island area, which technically lies just outside the region's boundary. The three remaining clusters are to the south. The first of these is in the vicinity of Palmer Station on Anvers Island (30,355 pairs), the second in the vicinity of Armstrong Reef (19,300 pairs) and the third is associated with Red Rock Ridge, islands on the south shore of Adelaide Island

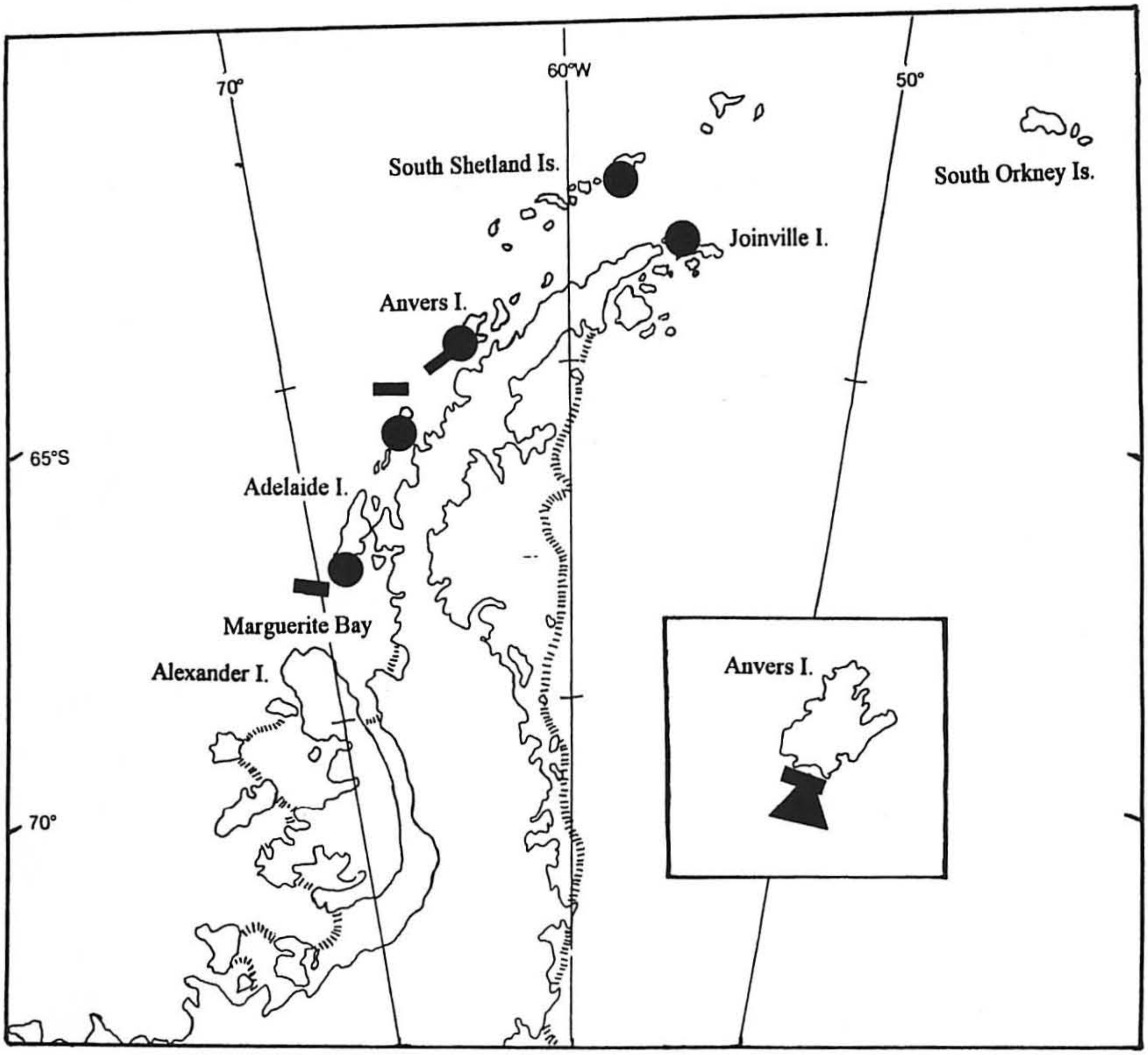

Fig. 2. Population clusters (circles) and foraging areas (rectangles) of Adélie Penguins in the western Antarctic Peninsula region. The Anvers Island inset shows foraging distributions in January 1993 (rectangle) and 1995 (triangle). Cluster locations are adapted from *Ainley et al.* [in press], and the maps are adapted from *Woehler* [1993]. Foraging distributions are based on unpublished data; survey methods are referenced in *Fraser et al.* [1992].

(41,700 pairs). Together, these three clusters encompass approximately 77% of the 119,264 pairs of Adélie Penguins estimated to be breeding between Anvers and Alexander Islands [*Woehler*, 1993]. More remarkable, at least as an illustrative point regarding the degree of heterogeneity in the distribution of the breeding population, is that cluster "diameter" (longest distance between the inclusive colonies) among the three southern locations is nowhere greater than 30 km for any one cluster [analysis based on population data in *Woehler*, 1993]. Roughly scaled relative to the straight-line distance between Anvers and Alexander Islands (600 km), this spacing pattern suggests that most of the population of Adélie Penguins actually occupies a nearly inconsequential amount of shoreline breeding habitat.

The summer foraging distributions of Adélie Penguins in the area between Anvers and Alexander Islands (i.e., the LTER pelagic sampling region) are shown in Figure 2. These distributions correspond with areas of high penguin abundance, which not surprisingly are closely associated with the clusters identified by *Ainley et al.* [in press]. The actual dynamics of change in foraging distributions, how-

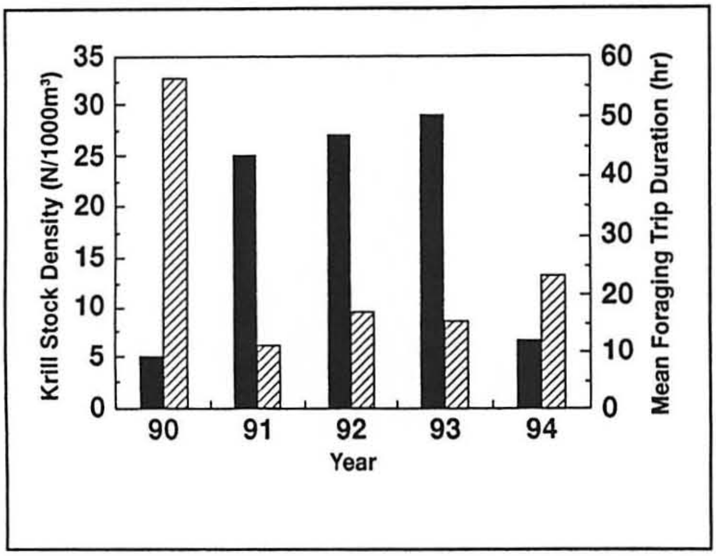

Fig. 3. Relationships between krill stock density (dark bars) and the duration of Adélie Penguin foraging trip duration (light bars). Good krill recruitment occurred during the 1990 winter. The effects, an increase in krill stock density and a decrease in foraging trip duration, are seen in 1991. Krill recruitment was poor during the 1993 winter, a year of minimal winter ice (see Fig. 7), resulting in diminished stocks in 1994 and an increase in foraging trip duration. Data are adapted from *Fraser and Trivelpiece* [in press] and *Siegel and Loeb* [in press]. Krill stock estimates for 1994 provided by V. Loeb (pers. comm).

ever, are only well known for the area around Anvers Island where more intensive sampling has been conducted [*Smith*, in press]. Here, based on summer shipboard surveys, few penguins have been observed at distances much greater than 90 km from the colonies during the last three seasons (1993 to 1995). Actual locations where foraging birds are concentrated, however, show interannual patterns in which distance from the colony may vary as much as 300%, with minimum and upper limits of approximately 15-20 km and 50-60 km, respectively (Figure 2).

There is a large body of literature that discusses the possible causes of variability in penguin foraging ranges, and the implications to ecological, physiological and energetic processes [reviews in *Croxall and Lishman*, 1987; *Culik*, 1993, 1994; *Williams*, 1995]. A recent analysis [*Fraser and Trivelpiece*, in press] suggests that in the LTER sampling region the primary factors associated with variability in foraging range are changes in krill (*Euphausia superba)* availability, the primary prey of Adélie Penguins during the breeding season. Changes in krill availability are induced by changes in krill abundance that result from year-specific variability in sea ice coverage and its effects on krill recruitment [*Fraser and Trivelpiece*, in press; *Siegel and Loeb*, in press].

The implications of this analysis to LTER-related research on Adelie Penguins are only now being ascertained. A direct and extremely important effect of variability in krill recruitment, for example, is that it significantly alters the duration of Adelie Penguin foraging trips, or the time it takes adults to find prey and provision chicks (Figure 3). This parameter, which is measured with instruments that are externally attached to penguins, is regarded as a key indicator of krill availability to these predators, and therefore critically important to the interpretation of short- and long-term data being gathered by ecosystem monitoring programs [*CCAMLR*, 1992]. A crucial gap in our knowledge about ecosystem processes is understanding how the physical environment influences the abundance and distribution of prey on which predators depend [*Croxall*, 1992]. The analysis by *Fraser and Trivelpiece* [in press] links annual variability in sea ice coverage to corresponding variability in krill recruitment and abundance, and the effects of these on foraging ranges and foraging trip durations. This analysis provides the basis for future investigations into the causal mechanisms that link physical and biological processes that may affect apex predators at several spatial and temporal scales.

3.2. Winter Distributions

The large-scale, winter distribution of Adélie Penguins in the western Antarctic Peninsula region remains largely unknown, a situation true for the species in all parts of its range. Areas where high numbers of wintering Adélie Penguins have been observed, however, are shown in Figure 4, which is based on Weddell Sea surveys made in June-July 1988 [*Fraser et al.*, 1992] and in the Bellingshausen Sea in August 1993 [*Fraser*, unpubl. data]. The winter dis-

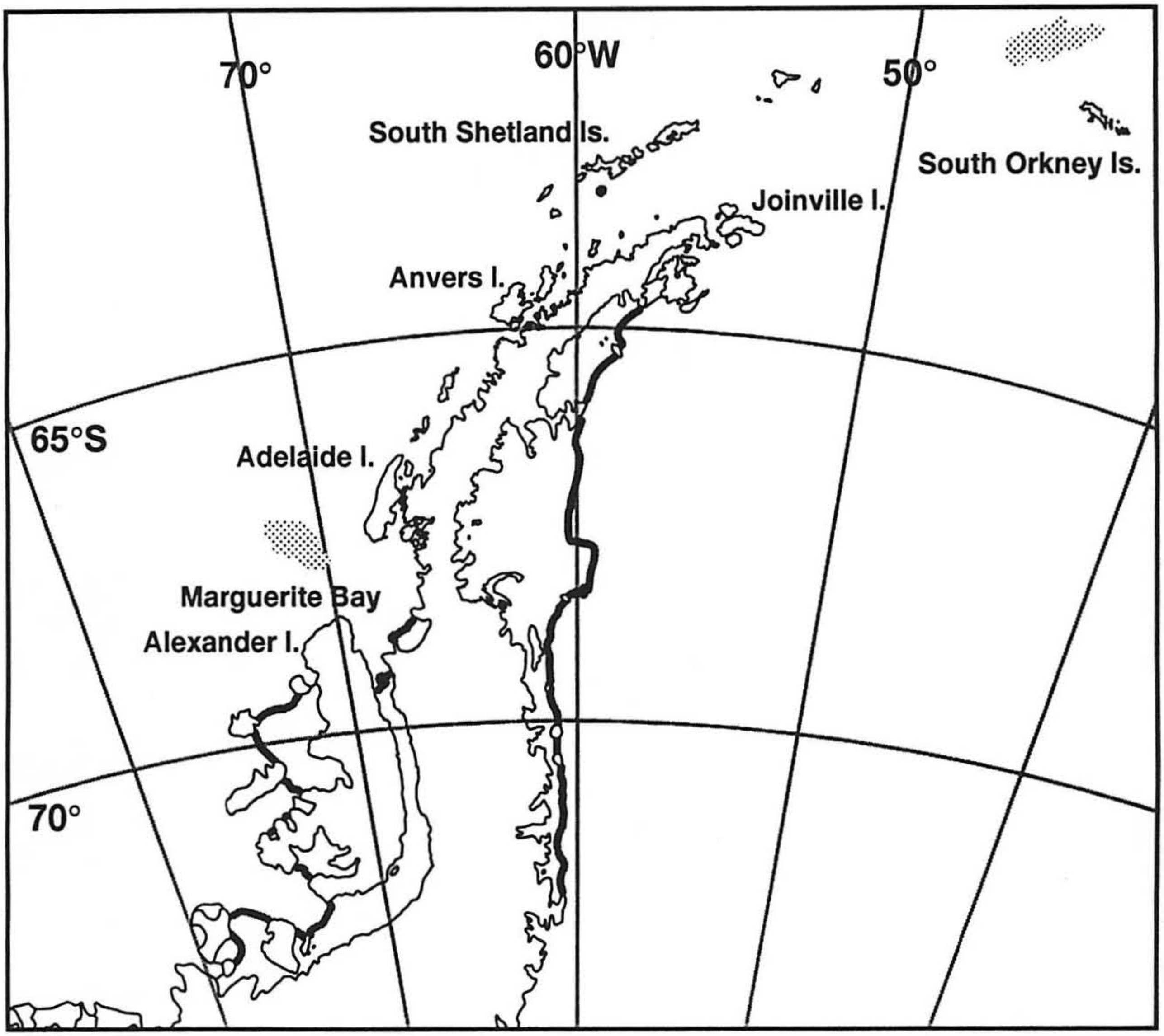

Fig. 4. The known winter distribution of Adélie Penguins in the western Antarctic Peninsula region (shading). The Bellingshausen Sea distributions are based on unpublished data; the Weddell Sea distributions are based on Fraser *et al.*, [1992]. Maps are adapted from Woehler [1993].

tribution of Adélie Penguins is extremely patchy and the species exhibits a strong affinity to pack ice, with the highest densities occurring in the pack ice interior (Figure 5). This pack ice region reflects two habitat qualities that appear to be important: stability and predictable access to open water for foraging.

The reason why these features may be important is shown in Figure 6. Adélie Penguins time their foraging in winter to coincide with available daylight, but need a platform on which to haul out at night. The pack ice interior (e.g., > 150 km from the ice edge) is typically stable but highly consolidated, offering limited access to open water. Conversely, areas near the ice edge offer access to open wate but the available ice is unstable due to the combined effects of age (new ice), wind and swell [see *Ainley et al.*, 1993]. In contrast to either habitat, the pack ice regions in which Adélie Penguins are abundant consist of 80-90% ice cover [*Ainley et al.,* 1992; 1994], with frozen pans of older ice that typically hold large floes in place near leads with exposed open water.

It is not known if this habitat manifests oceanographic conditions that makes certain regions more attractive to prey than others. However, in addition to the similarities in sea ice habitats, the other common feature associated with high or increasing numbers of Adélie penguins in both the Weddell and Bellingshausen Seas is a complex bottom bathymetry. In the Weddell Sea, this feature included shelf and slope regions west, north and east of the South Orkney Islands [see *Daly and Macaulay*, 1991]; in the Bellingshausen Sea, it included canyons and deep holes that intersect the continental shelf south of Adelaide Island [see Fig. 1*a* in *Hofmann et al.*, this volume; also *Trivelpiece and Fraser*, this volume]. In summer, similar bathymetric features are associated with high prey and predator concentrations [*Ainley et al.*, 1984], but high prey densities have not always been documented in these regions during winter [*Daly and Macaulay*, 1991]. Accurate assessment of the prey field under pack ice, however, is a difficult task, hence the possibility that these bathymetric features are associated with higher winter prey concentrations cannot be dismissed.

4. SYNTHESIS AND DISCUSSION

4.1. The Significance of Life History Strategies

Barring the effects of human disturbance, the distribution and persistence of any seabird population over time ultimately reflects the coincident availability of suitable nesting and foraging habitats. Spatial and temporal variability in the availability of these factors influence life history strategies, which represent species-specific evolutionary responses to minimize the negative effects of environmental variability on reproduction [*Ricklefs*, 1973]. The distribution of Adélie Penguin colonies in the western Antarctic Peninsula region is characterized by extreme heterogeneity. This heterogeneity encompasses several spatial and temporal scales that reflect the collective expression of individuals (summer-winter foraging distributions and colony clusters) and of populations (regional gaps). What do these spacing patterns suggest about Adélie Penguin life history strategies and the selection pressures that affect the observed heterogeneity?

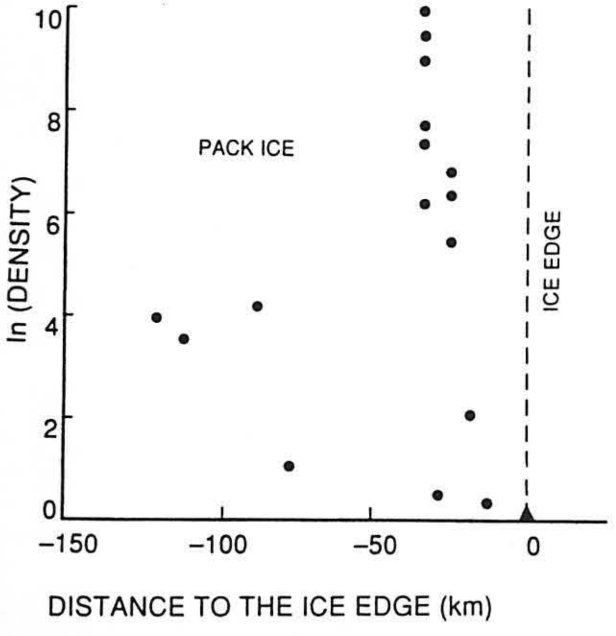

Fig. 5. Density and distribution of Adélie Penguins relative to the ice edge in the Weddell Sea. Data adapted from *Fraser et al.* [1992].

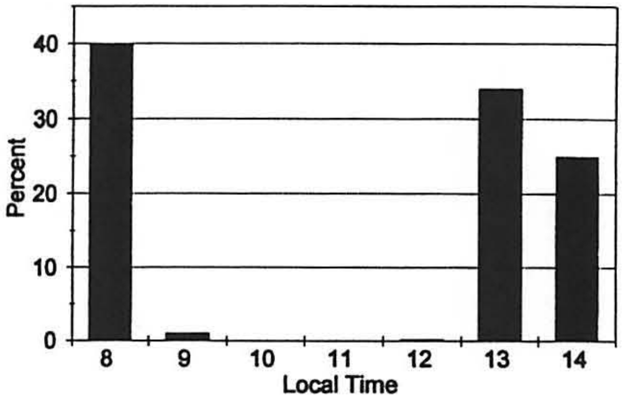

Fig. 6. Relationship between local time and the number of Adélie Penguins hauled out on sea ice during June-July 1988 in the Weddell Sea. The patterns reflect sightings of 37,393 Adélie Penguins. The decrease evident at 14:00 hr does not indicate a return to foraging, but rather poor visibility as birds became covered with drifting snow. Data based on unpublished information obtained during the study described by *Fraser et al.* [1992]. Adequate light to conduct censuses was available from approximately 07:30 to 14:30 depending on cloud cover.

The point was made earlier that the factors that affect seabird distributions at smaller scales can provide the basis for interpreting ecological processes related to populations and their distributions at larger scales (see Sec. 1). The discussion that follows builds on this approach and concludes by addressing the longer-term issue of population change over ecological time (decades to centuries).

4.2. Short-Term Perspectives: Factors Affecting Summer-Winter Distributions

4.2.1. Physical features and prey availability. The summer and winter distributions of Adélie Penguins have three features in common. The first is the actual degree of heterogeneity exhibited by the spacing patterns of the respective populations. Of the 308,300 pairs of Adélie Penguins estimated to be breeding in the western Antarctic Peninsula region [*Woehler*, 1993], nearly 80% are associated with the five colony clusters shown in Figure 2 and identified by *Ainley et al.* [in press]. Similarly, of the 39,500 Adélie Penguins censused during winter transects in the Weddell and Bellingshausen Seas (Figure 4), 89% occurred in only 16% of the transects containing the species (N = 25). These transects also exhibited high spatial coherence, encompassing comparatively small regions (75-100 km) relative to the total area surveyed in each oceanic basin.

The second feature is that each of the respective populations is constrained in terms of available foraging time. In the case of winter populations, this constraint is imposed by available daylight (Figure 6); for summer populations, it is the need to return to shore to provision chicks. The third feature is implied by the second, but has only been quantified for summer populations. Based on data from breeding birds on Anvers Island (Figure 2), foraging is highly localized, with distances from the colonies rarely exceeding 90 km and averaging 20-50 km. The winter pattern may not be much different. In the 4-5 hours of available foraging time in mid-winter (Figure 6), an Adélie Penguin swimming at average speeds [*Culik*, 1993, 1994] would maximally cover a straight-line distance of 35-40 km assuming it did not stop to forage. This assumption is obviously unrealistic, suggesting that penguins may actually forage much closer to their winter haul-out sites than the 35-40 km suggested by the above calculation.

These winter-summer comparisons suggest that one of the more important factors controlling the breeding and oceanic distribution of Adélie Penguins is access to proximal oceanic areas of high productivity. Although Adélie Penguins can cover long (>2,500 km) distances when migrating between summer and winter habitats [L. Davis, pers. comm.], their size and inability to fly limit the spatial scales of interaction with the marine environment when constrained by factors such as breeding and parental duties, or limited winter daylight. Given these restrictions, selecting breeding and wintering habitats that are closely associated with regions where prey availability is less variable presents a reasonable alternative strategy.

A preliminary test of this hypothesis by *Trivelpiece and Fraser* [this volume] supports its basic premises. Their results show that the five colony clusters (Figure 2) identified by *Ainley et al.* [in press] are associated with deep submarine canyons and basins that intersect the western Antarctic Peninsula shelf [also see *Hofmann et al.*, this volume]. Moreover, in the better sampled region below Anvers Island, three of the foraging areas associated with these colony clusters (Figure 2) actually overlay these submarine features, suggesting good spatial coherence in the juxtaposition of foraging and breeding habitats. Conclusions regarding winter distributions must necessarily remain tentative because of undersampling. However, the correspondence between anomalous bathymetry and high numbers of penguins (Sec. 3.3) in two different oceanic basins (Figure 4) is consistent with theoretical expectations given the constraints imposed on foraging time by limited daylight.

4.2.2. Behavioral considerations. In their analysis of the factors affecting the breeding distribution of Adélie Penguins on the Antarctic Peninsula, *Ainley et al.* [in press, 1995] reviewed the importance of behavioral factors as mechanisms for maintaining the geographic structure (i.e., colony spacing relative to size) of the population, but did not consider the effects of bathymetry as a cause for the structure. Their view, that natal philopatry (chicks return as adults to breed in the colonies where they hatched) and breeding site fidelity (adults select the same breeding site each season), may be important mechanisms by which the structure of these populations is maintained, is particularly relevant to the above stated hypothesis.

Although coloniality may serve a number of functions in seabird ecology [reviewed in *Wittenberger and Hunt*, 1985], natal philopatry and breeding site fidelity in particular assure that individuals return to specific areas to reproduce. The fact that these behaviors are so highly developed in Adélie Penguins [*Ainley et al.*, 1983] agrees with the idea that needing to return to areas in which the prey base has proven to be dependable over ecological time (i.e., prey availability is, on average, less variable at the spatial and temporal scales required to establish and maintain populations) is indeed a critical component of the species' life history strategy. This is a more defensible argument for explaining the maintenance of geographic structure in summer breeding populations, but the ecological scenario proposed here also suggests a possible winter role. Behaviors that assure that individuals return to "traditional" wintering areas would appear to be equally valuable from an evolutionary perspective, given the constraints imposed on foraging by available daylight (Figure 6) and the need for specific pack ice habitats (Sec. 3.3; Figure 5).

4.3. Long-Term Perspectives: Population Change Over Ecological Time

Although behavior may be the mechanism that maintains spacing patterns in Adélie Penguin populations [*Ainley et al.*, in press], this study suggests that the source of these patterns is causally linked to the juxtaposition of nesting habitat, pack ice, suitable bathymetry and a minimal daylight period. Implied is that the spatial and temporal relationships between these factors determine the distribution of the species at the population level, and that changes in these relationships will produce corresponding responses, either negative or positive, in populations and, ultimately, their distributions. The dynamics of some of these relationships are addressed in this concluding section by examining the regional-scale breeding distribution of Adélie Penguins relative to the features that might be in-

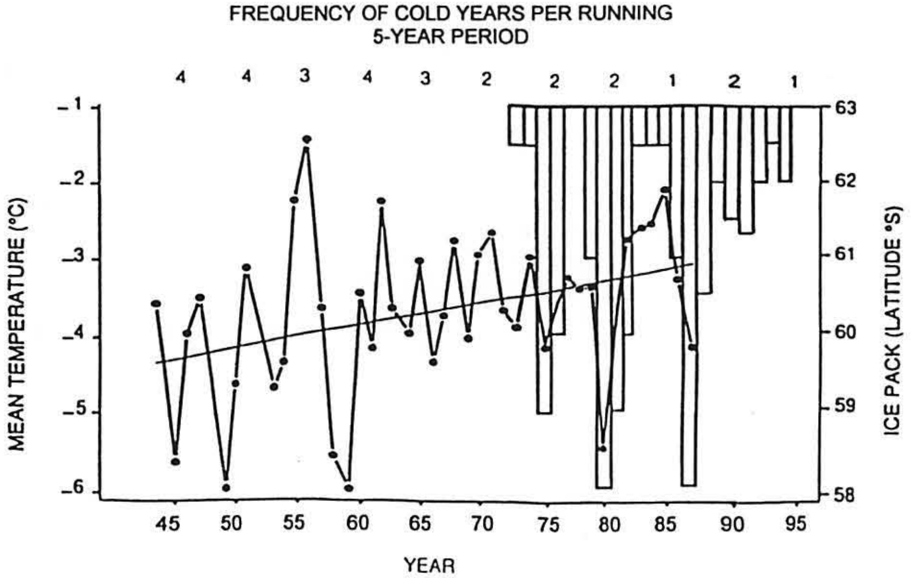

Fig. 7. Variability in sea ice extent in the western Antarctic Peninsula region, 1973-1994. No satellite data are available for 1977 and 1978. Numbers at the top show the number of years per respective running five-year period that mean air temperature was less than or equal to -4.3°C, the temperature during the 1973-1987 period when sea ice extent reached north to at least 60°50'S. The formula for the regression line is: temperature = -5.551 + 0.0278(yr), F = 5.720, P = 0.021. The relationship between sea ice extent and air temperature is highly significant; Spearman rank correlation, r = 0.886, t = 6.337, P < 0.001. The figure is adapted from *Fraser et al.* [1992]; sea ice extent data for the years 1988-1994 were provided by *Stammerjohn and Smith* [this volume].

volved in forcing population changes at time scales of decades and centuries.

4.3.1. The role of sea ice. As shown in Figure 1, the breeding distribution of Adélie Penguins in the western Antarctic Peninsula exhibits two clear discontinuities. Neither bottom topography nor nesting habitat can explain these gaps. Bottom topography exhibits similar deep features adjacent to land margins in both gaps [*Hofmann et al.*, this volume; J. Klinck, pers. comm.], and there is an apparent excess of potential nesting habitat both within and outside the gap boundaries [*Poncet and Poncet*, 1987; *Ainley et al.*, in press; *Fraser and Patterson*, in press]. The primary feature distinguishing these gaps is the seasonal availability and persistence of sea ice. The northern gap is within a region of highly variable sea ice coverage (Figure 7; see also *Stammerjohn and Smith*, this volume]. Here, maxima in sea ice extent occur at 5 to 7 year intervals, with intervening years of minimal sea ice cover. South of Adelaide Island (the northern border of the southern gap) sea ice becomes progressively less seasonal [*Stammerjohn and Smith*, this volume], eventually forming a permanent feature of the marine habitat in the region of the southern Bellingshausen and Amundsen Seas [*Jacobs and Comiso*, 1993].

Thus, the breeding distribution of Adélie Penguins in the western Antarctic Peninsula region suggests that the pattern is causally linked to variability in the spatial and/or temporal presence of sea ice. Sea ice appears to determine a "habitat optimum" with boundaries defined by the equally restrictive effects of excessive and insufficient variability in its seasonal persistence. Some of the factors that might structure this habitat optimum have only recently become apparent. Suitable nesting and feeding habitats are obviously involved (Sec. 4.2), but critically important is that the juxtaposition of sea ice (in space and time) accommodate the temporal requirements of Adélie Penguin breeding chronology.

Extensive, unbroken sea ice, for example, directly impacts early-season return to nesting areas and the timing of subsequent breeding season events. These conditions have been shown to delay breeding and negatively impact most aspects of the reproductive effort [*Ainley and LeResche*, 1973; *Ainley et al.*, 1983; *Croxall*, 1992]. Although this might imply that less ice is optimal, that option is countered by another, equally important factor, the requirement that females replenish energy stores after fasting and egg-laying. This also involves a critical time component because they must return to their incubating, fasting mates before the male's own energy stores are drawn down to the level where nest abandonment occurs, which is a significant source of egg mortality [*Ainley et al.*, 1983; *Trivelpiece and Trivelpiece*, 1990]. Ice edges provide one of the only predictable sources of prey in the spring [*Daly and Macaulay*, 1991], and it has been suggested that these are the areas to which forging females return after the first incubation shift [*Trivelpiece and Trivelpiece*, 1990]. This may explain why the species must establish colonies at some minimum distance from major, predictable ice concentrations [*Ainley et al.*, 1983], and agrees with the hypothesis advanced above (Sec. 4.2) that close access to oceanic areas of high productivity are key to the species' life history strategy.

Implied but not directly stated, is that the spatial and temporal juxtaposition of sea ice mediates the potential availability of nesting habitat to Adélie Penguins on a regional scale. This is exemplified by the northern gap with its sharp southern boundary on Anvers Island (Figure 1). This region is devoid of breeding Adélie Penguins but full of the closely related, but ice-intolerant Chinstrap Penguins [*Poncet and Poncet*, 1987*; Fraser et al.*, 1992; *Trivelpiece and Fraser*, this volume], and neither the lack of nesting habitat nor deep features adjacent to land margins (i.e., foraging habitat) are the limiting factors (see above). *Trivelpiece and Fraser* [this volume] have hypothesized that this gap exists because it represents an area too distant from the pack ice of either the Weddell or Bellingshausen Seas to allow female Adélie Penguins to feed and return to their mates in time to prevent nest desertion. The presence of this gap intimates that two Adélie Penguin populations inhabit the western Antarctic Peninsula region, one on the north that depends on the ice of the Weddell Sea and one another to the south that depends on ice of the Bellingshausen Sea [*Fraser et al.*, 1992].

4.3.2. The effects of climate change**.** The concept of an ice-mediated habitat optimum is instructive for a number of reasons, not the least of which is that it provides the conceptual framework for an hypothesis on how climate change might affect populations and, ultimately, their distributions over several space and time scales. For example, although there is general agreement that the effects of climate warming on sea ice conditions is the most likely cause for changes in Adélie Penguin populations during the last few decades [*Taylor and Wilson*, 1990; *Blackburn et al.*, 1991; *Fraser et al.*, 1992], there is less agreement on the causal mechanisms and linkages involved [*Croxall*, 1992]. Especially problematic is that despite parallel increases in temperature, some regional populations have increased [Ross Sea, *Taylor and Wilson*, 19-90] while others have decreased or remained stable [Antarctic Peninsula, *Trivelpiece et al.*, 1990; *Fraser and Pat-terson*, in press].

However, assuming that some variability in the spatial and temporal availability of sea ice is the optimal condition (Figure 1), it is not unreasonable to imagine that climate warming could simultaneously force an increase or decrease in populations. This would depend on what factors are initially limiting the population relative to the optimum. Where sea ice has been a more permanent feature of the marine environment, as in the Ross Sea [*Jacobs and Comiso*, 1989], climate warming may be forcing habitat conditions towards the optimum. In this region, Adélie Penguin population increases are attributed to improving spatial and temporal access to nesting and foraging habitats due to earlier break-up of the sea ice and the formation of polynyas close to land margins [*Taylor and Wilson*, 1990; *Taylor et al.*, 1990]. Where sea ice is a more variable feature of the marine environment, as in the western Antarctic Peninsula region [Figure 7; see also *Stammerjohn and Smith*, this volume], climate warming may be forcing habitat conditions away from the optimum. Here, population decreases may be linked to increasing variability in prey availability during the reproductive cycle and diminishing access to nest sites due to increasing winter precipitation [*Fraser and Patterson*, in press; *Fraser and Trivelpiece*, in press].

How winter habitat suitability might factor into this conceptual framework has been discussed by *Fraser et al.* [1992]. Summer breeding success and overwinter survival are the foci through which seabird populations are regulated [*Lack*, 1954; *Rickleffs*, 1973; *Birkhead and Furness*, 1985]. In Adélie Penguins, the relationships between the foci may be amplified; winter foraging conditions not only affect survival, but fat stores accumulated during the winter ultimately determine the fasting capabilities of breeders during the early courtship and egg-laying period in spring [*Chappell et al.*, 1993]. As suggested by this analysis, Adélie Penguin winter habitats are narrowly defined by the coincidence of very specific sea ice conditions (Figure 5), light regimes (Figure 6) and bathymetry (Sec. 3.3). Changes in winter sea ice extent due to climate warming could thus have far greater effects on long-term Adélie Penguin population dynamics than if only factors related to summer breeding success were affected. Research focused on the winter ecology of the species is critically needed.

4.3.3. Changes in biogeography**.** The long-term history of climate change in the western Antarctic Peninsula region is characterized by pulses of warm and cool periods, which marine sediments suggest were accompanied by coincident changes in the extent and duration of regional ice cover [*Domack et al.*, 1993]. In the Anvers Island (Figure 2) area, for example, the Little Ice Age (mid-1500s to the 1850s) sediment record suggests that sea ice was much more of a permanent, as opposed to a seasonal, feature of the marine environment about 330 years ago, the peak of the Little Ice Age [*Domack et al.*, this volume]. Expression of this feature may have included permanent fast ice and/or ice that broke out late in the season. Since then, long-term regional ice cover characteristics (permanent vs. seasonal) have probably reversed one or more times. The dates for expression of the "modern" record (the last shift from more permanent to more seasonal ice) cannot be estimated with precision. Based on coupled air temperature and sea ice extent relationships (Figure 6), however [see also *Smith et al.*, this volume], sea ice was a less variable feature of the region's marine environment during mid-century and earlier. The pattern of high variability in sea ice coverage that is observed today began between 1965 and 1970 (Figure 7), a period during which global-scale changes in climate took an abrupt shift towards warmer temperatures [*Kerr*, 1994; *Miller et al.*, 1994].

Using Figure 1 as a template for long-term change in the biogeography of Adélie Penguins, it is not unreasonable to imagine that longer-term cooling trends would have the effect of forcing the habitat optimum northward, while warming trends would have the opposite effect. Two lines of evidence support this hypothesis. The first is the presence of extinct colonies. In the Anvers Island area, for example, the surface area covered by these colonies suggests that an additional 10,000-15,000 pairs of Adélie Penguins nested within 10 km of the largest colony in the cluster identified by *Ainley et al.* [in press] at some time in the past [unpublished data based on *Fraser and Patterson*, in press]. The time periods associated with this "penguin/habitat optimum" are unknown, but the presence of extinct colonies implies that habitat conditions have clearly deteriorated for Adélie Penguins in this area during the recent past and is continuing at present in accordance with predictions on how climate change might affect the species [*Fraser et al.*, 1992; *Fraser and Patterson*, in press, 1995].

The second line of evidence is indirect and preliminary, based on the fossil record of habitat occupation by the closely related, but ice-intolerant Chinstrap Penguin [see *Trivelpiece and Fraser*, this volume]. *Emslie* [1995] has shown that during the Little Ice Age, this species may have occupied rookeries only during warming periods, in effect the concurring situation of what would be predicted based on a deteriorating habitat optimum for Adélie Penguins [*Fraser et al.*, 1992]. The northern gap in the distribution of Adélie Penguins (Figure 1) thus may be of relatively recent origin, reflecting a general southward retreat of the species' habitat optimum since the last significant cooling period approximately 300 years ago.

The factors involved in these longer-term changes in populations and biogeography are unquestionably linked to coupled atmospheric and oceanic forcing, and their direct or indirect effects on habitat availability and food web processes. *Hofmann et al.* [this volume] discuss the implications that the presence of relatively warm Circumpolar Deep Water has to the formation of regional winter sea ice, and *Fraser et al.* [1992] and *Smith et al.* [this volume] show a clear link between ambient air temperatures and winter sea ice extent. Although the scope and nature of the mechanisms involved remain obscure, the dynamic interactions between these variables shape the spatial and temporal characteristics of the habitat optimum for Adélie Penguins. To the extent that sea ice may be viewed as the "ultimate product" of these interactions, and its presence or absence as the foundation for ecosystem-level changes in the region, then understanding what forces its development and persistence over space and time is critically necessary. The biogeographic patterns herein discussed suggest interactions between these variables that are punctuated by thresholds in which the relative effects of oceanic forcing factors are mediated by climate warming or cooling. Stated differently, whether or not Circumpolar Deep Water actually moderates sea ice formation in winter depends on the air temperature. Given the similarities in the general terrestrial and oceanic features that determine Adélie Penguin habitats throughout their range, this model may account for the different population trends currently seen in higher and lower latitude oceanic basins.

5. SUMMARY AND PROSPECTUS

This review has drawn on the results of many disciplines to develop the conceptual framework for a model on how interactions between oceanic and atmospheric processes might affect, either directly or indirectly, the population dynamics and biogeography of Adélie Penguins. A key assumption of the model is that Adélie Penguins occur in a "habitat optimum" in which boundaries are determined by the juxtaposition of suitable bottom topography, nesting habitat, sea ice and available daylight. This assumption is based on recent data on the factors associated with summer and winter heterogeneity in the distribution of Adélie Penguins in the western Antarctic Peninsula region. In this model, changes in the habitat optimum result, first, in changes in Adélie Penguin populations, and, ultimately, in their biogeography. It is hypothesized that changes in the habitat optimum are forced primarily by variability in the seasonal development and persistence of sea ice. This variability may be ultimately mediated by climate warming or cooling and their effects on the influence that Circumpolar Deep Water has on regional heat budgets.

Long-term demographic data of Antarctic seabirds, and Adélie Penguins in particular, are presently emerging as important tools for monitoring the effects of climate change and human activity on the marine environment. Interpretation of these data will obviously depend on how well we understand the interactions between the physical and biological components of this environment, and how these interactions affect short- and long-term population change. A cruical present gap in our data concerns the winter ecology of Adélie Penguins. Although instruments can help determine where this species winters, they will not resolve the more pressing need to understand their foraging ecology and habitat preferences. Without this information, winter effects on population change will necessarily remain obscure, and potentially diminish our ability to interpret and model demographic data. The development of dedicated, multidisciplinary programs more strongly focused on apex predator research in the Antarctic marine environment would unquestionably prove immediately valuable in resolving these and related ecosystem questions.

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