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THE WESTERN ANTARCTIC PENINSULA REGION: SUMMARY OF ENVIRONMENTAL AND ECOLOGICAL PROCESSES

The Palmer LTER Group[1]

Parts I to V of this volume provide overviews and syntheses of the many aspects and processes associated with the terrestrial and marine ecosystems in the western Antarctic Peninsula region. As such, they are a foundation that can be used as a basis for the Palmer Long-Term Ecological Research (LTER) program as well as a means for highlighting additional research opportunities and questions. This chapter is intended to briefly summarize the salient points in the previous chapters, indicate where linkages occur between systems and processes, and indicate how the Palmer LTER builds upon and extends the understanding of ecological processes in the region west of the Antarctic Peninsula.

1. INTRODUCTION

An objective and benefit of this volume is to gather in one place many of the historical data sets, published and unpublished, that exist for the region west of the Antarctic Peninsula. Thus, the chapters within this volume provide overviews and syntheses of the many aspects and processes associated with the terrestrial and marine ecosystems in the western Antarctic Peninsula region. As such, they are a foundation that can be used as a basis for the Palmer Long-Term Ecological Research (LTER) program as well as a means for highlighting additional research opportunities and questions. This collection allows the Palmer LTER to be seen within the context of the total ecosystem and to build on the efforts of past programs. Also, it provides a starting point for other programs to build upon the efforts of the Palmer LTER. Therefore, the objectives of this chapter are to briefly summarize the salient points in the previous chapters, indicate where linkages occur between systems and processes, and indicate how the Palmer LTER builds upon and extends the understanding of ecological processes in the region west of the Antarctic Peninsula. The reader should consult individual chapters for details and literature pertaining to particular subjects.

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Magnuson [1990] showed the insight that can be gained when events of the 'invisible present' are viewed against the background of long-term or sustained research. The availability of long-term historical data allows results from single years or single research efforts to be taken out of the 'invisible present' and placed into the appropriate temporal scale, thereby, providing insight into the long-term behavior of a natural system. The Palmer LTER program is situated in a climatically sensitive region with a sea ice regime that creates the opportunity for natural experiments on the effects of variation in sea ice extent. Thus, the Palmer LTER has the potential to detect effects of climate change and human disturbance on the Antarctic ecosystem over the background of natural variability.

The following section provides a summary of the characteristics of the physical environment and indicates how the physical system structures the ecological systems. This is followed by a discussion of the different components of the terrestrial and marine ecosystems. The fourth section describes the Palmer LTER and the linkages between the objectives of this program and what is known from historical data. The final section overviews national and international research programs that have taken place or are currently in progress or planned for the western Antarctic Peninsula region.

2. HABITAT STRUCTURE

2.1. *Paleoenvironmental Characteristics*

Ecological research implicitly recognizes that biological processes are only understood in terms of the physical regime in which they occur. The temporal scale of variation in physical processes ranges from days to decades to millenia. Similarly, spatial variations occur over scales that range from a molecular to global [*Murphy et al.*, 1988]. The net result of these temporal and spatial variations are reflected in seasonal, interannual, and long-term (geological or evolutionary) patterns in biological communities.

Structuring of the present day Antarctic system began about 40 million years ago as the Antarctic Continent separated from Gondwanaland. At about 20 million years before present, Drake Passage, the region between the tip of South America and the Antarctic Peninsula, opened which allowed formation of the Antarctic Circumpolar Current. This resulted in isolation of the waters around Antarctica from those in ocean basins to the north. The northern extent of the Antarctic waters is usually assumed to occur at the Polar Front, which extends throughout the water column, is circumpolar in nature, and is found near 60°S in Drake Passage. The Polar Front is a sharp boundary between Antarctic waters to the south and Subantarctic waters to the north, and as such it forms a hydrographic boundary as well as a biogeographic barrier.

The relatively short history of scientific exploration in the Antarctic [*El-Sayed*, this volume] provides a limited time record of variations in the physical factors that have structured the Antarctic ecosystem. The sediments, how-ever, provide a means of inferring changes in the physical and biological characteristics of the Antarctic system. The changes revealed by the sediment records range from large scale effects, such as movement in the historical location of the Polar Front [*Clarke*, this volume a], to localized changes in fjords along the western Antarctic Peninsula [*Domack and McClennen*, this volume]. Sedimentation rates obtained from sediment cores taken in the Palmer LTER region [*Domack and McClennen*, this volume] provide evidence for climate variations during the past several thousand years along the western Antarctic Peninsula. Sediment cores from north of Adelaide Island and near Gerlache Strait indicate that climate cooling began in this region several thousand years ago. The ice shelf in the southwest region started to advance about 400 years B.P., coincident with the onset of the Little Ice Age; whereas, it began to advance only 75 years B.P. in the northeast region [*Domack and McClennen*, this volume]. Moreover, the period prior to the glacial advance, i.e., about 2000 years B.P. was warmer, with lesser sea ice coverage and enhanced primary productivity.

The variations in the sediment records clearly indicate long term climatic changes in the western Antarctic Peninsula region and also show that this region is characterized by different climate zones. The southern portion of the Peninsula region is a typical polar climate, where sea ice has been a more permanent feature over time. At the latitude of the South Shetland Islands, the climate changes to subpolar maritime, where sea ice is less persistent. Anvers Island, where the Palmer LTER is based (Figure 1), is in the transition zone between the climate regimes. *Domack and McClennen* [this volume] suggest that this transition zone may be ideal for recording changes in productivity, and the flux of carbon to the sediments caused by subtle changes in sea ice cover produced by climate variations. These longer term changes reflected in the sediments provide a context for interpreting the shorter term records of increasing air temperature from the beginning of this century [*Smith et al.*, this volume a] and trends and cycles in sea ice extent from the late 1970s [*Stammerjohn and Smith*, this volume].

Fraser and Trivelpiece [this volume] suggest that winter habitats of the Adélie penguins are defined by a set of co-occuring features that include sea ice conditions, light regimes and bathymetry. Evidence of extinct penguin rookeries in the Palmer LTER area [*Fraser and Trivelpiece*, this volume] in fact suggests that habitat suitability has declined several times during the past several thousand years, forcing the penguins to abandon their rookeries [*Emslie*, 1995; *Tatur et al.*, in press]. Thus, both terrestrial and marine sediments provide paleoenvironmental indicators of seabird activity or of variation in biological functions that contribute to sedimentation, such as primary productivity and vertical carbon flux, over the past several thousand years.

2.2. *Physical Structuring of the Marine Ecosystem*

The chapters on hydrography and circulation [*Hofmann et al.*, this volume] and sea ice cover [*Stammerjohn and Smith*, this volume] clearly illustrate that the marine habitat of the west Antarctic Peninsula region has unique properties and that it is an area with strong seasonal and interannual variability. The deepness of the continental shelf in this region results in a water mass structure over the shelf that is essentially oceanic below 100-150 m. This brings a relatively warm, salty water mass, Circumpolar Deep Water (CDW), onto the shelf, which then extends across the shelf to nearshore regions. The presence of CDW at the base of the mixed layer provides a heat source, which *Hofmann et al.* [this volume] show is sufficient to melt ice, thereby potentially making the western Antarctic Peninsula a region of ice melt rather than ice formation. *Stammerjohn and Smith* [this volume] also suggest that the presence of this water may result in thinner ice and the formation of more polynyas.

Within the Palmer LTER region, timing of the advance and retreat of the annual sea ice is variable [*Stammerjohn and Smith*, this volume]. The mean annual ice cycle with its long period of ice retreat (~7 months) followed in the late fall and winter by a short period of ice advance (~5 months) is in contrast to other regions around the Southern Ocean where the advance is longer than the retreat. Evidence from satellite data from 1978 to 1994 suggests that there is a repeating cycle in the Palmer LTER area, with several high ice years followed by several low ice years [see also *Fraser et al.*, 1992 and *Fraser and Trivelpiece*, this volume]. *Stammerjohn and Smith* [this volume] also demonstrate a negative correlation between sea ice extent in the Palmer

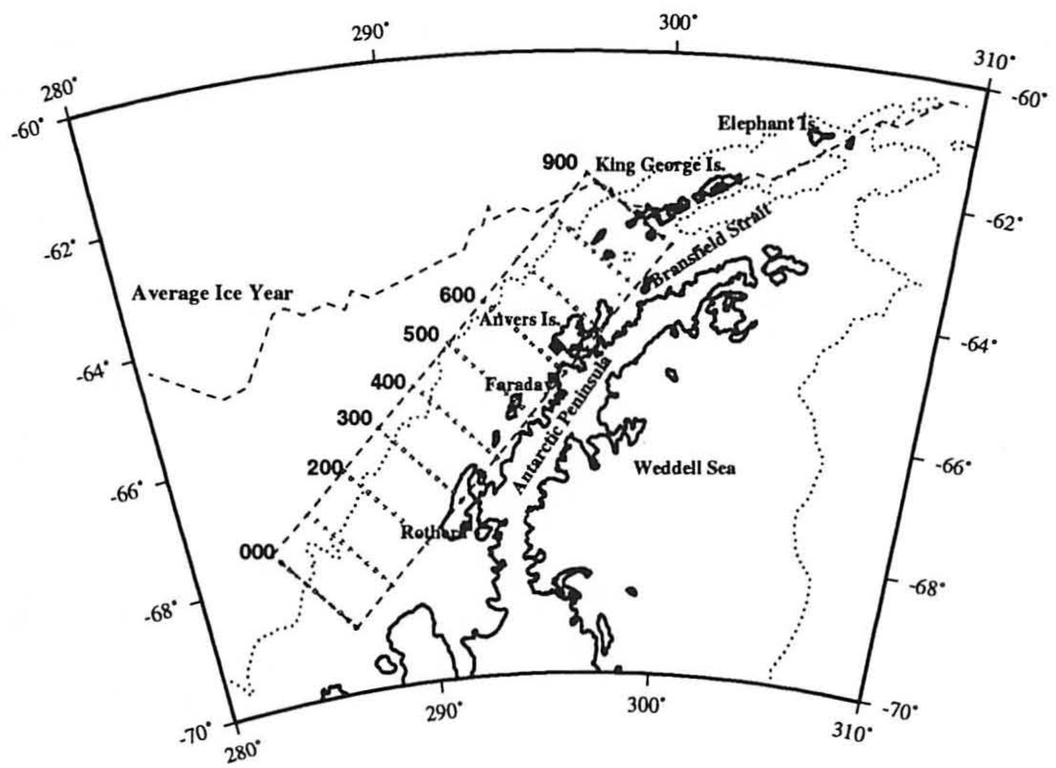

Fig. 1. The Palmer LTER region (900 × 200 km dashed rectangle) is located west of the Antarctic Peninsula, Antarctica. Points within the rectangle show the location of the cardinal sampling stations. Palmer Station (solid diamond) is on the southwest side of Anvers Island. The locations (solid squares) of the British Antarctic Survey stations, Faraday and Rothera, are noted. The 1000 m isobath (dotted line) and sea ice extent (dashed line) for September 1993, which was an average sea ice year, are shown.

LTER and the Southern Oscillation Index (SOI). The potential linkages between climate processes along the west Antarctic Peninsula with those in the Pacific Ocean are supported by correlations between air temperature, sea ice extent, and lead/lag relationships described in *Smith et al.* [this volume a], which also support earlier observations made by *Fraser et al.* [1992]. Additionally, the structure of the ecosystem or recruitment in individual species may be correlated with SOI and thus large scale oceanographic processes. For example, years in which salp abundances are high tend to be El Niño years [*Ross et al.*, this volume], and the strength of seal cohorts may be indirectly linked to the SIO through its interaction with pack ice variability [*Costa and Crocker*, this volume].

3. OVERVIEW OF TERRESTRIAL AND MARINE ECOSYSTEMS

The theme of alongshore and offshore gradients in space was common in chapters discussing patterns of distribution and abundance of the biota from all biomes. The various assemblages are often classified into zones, provinces, or climatic regions, and these categories are then associated with gradients in physical factors, whether climate [*Smith et al.*, this volume a], bathymetry, hydrography [*Hofmann et al.*, this volume] or sea ice [*Stammerjohn and Smith*, this volume]. There are linkages between the biomes and across these gradients, however, and common physical factors that impact structure and function. Moreover, the terrestrial and freshwater habitats do not exist in isolation, but rather are coupled to the marine pelagic ecosystem in several ways. For example, nutrients dispersed from the colonies of many breeding seabirds or from ocean spray enrich the soil and enhance the development of the nearby terrestrial and freshwater biota [*Smith*, this volume]. This section summarizes many of the important features of the terrestrial and marine ecosystems.

3.1. Terrestrial and Freshwater

The northeast to southwest gradient in climate along the Antarctic Peninsula described above results in a gradient in species diversity associated with the terrestrial ecosystem. Species diversity declines from north to south, with the maritime climate of the western Antarctic Peninsula allowing greater species diversity within the terrestrial and freshwater assemblages than is found in the rest of the Antarctic [*Smith*, this volume]. Indeed this is the only region of Antarctica with flowering plants. The region from about the latitude of southern Anvers Island to just south of Adelaide Island has been termed the botanically richest region of Antarctica. However, despite this richness and complexity, the little terrestrial biological research that has been done is mostly of a qualitative nature, and the taxonomy of many groups remains untreated [*Smith*, this volume]. Climatically sensitive flora, such as mosses and liverworts dominate the macroscopic vegetation, and a there is a range of trophically simple terrestrial communities that could be used for experimentation. Thus, this region seems ideally suited for studying the effects of climate change (warming, ultraviolet (UV-B) radiation) on species and community assemblages. In fact, *Smith* [this volume] speculates that the documented introduction of new species may be related to the long-term increase in temperature in the western Antarctic region.

3.2. Benthic Habitat and Communities

Benthic processes in Antarctic waters have been studied far less than benthic population distributions. The three chapters on benthic distributions and processes [*Clarke*, this volume a,b,c] provide overviews of what is known of the patterns of distribution in marine benthic communities in the Antarctic, the processes (including ice-related processes) that control these patterns, and the ecological processes involved in the development of characteristic reproduction and recruitment patterns in the benthos, including egg and larval strategies, and episodic and uneven recruitment.

The benthic habitat within the Palmer LTER region ranges from abyssal plains to the intertidal, and from soft siliceous sediments in the deepest waters to rocky pools scoured by ice, with glacial marine sediments forming a wide halo around the continent [*Clarke*, this volume a]. The lack of rivers and the presence of extensive ice shelves, which prevent large scale transport of ice rafted materials in the Antarctic, means that terrigenous input to sediments is lower than in the Arctic. As a result, the typically diverse intertidal mudflat habitat is absent in the Antarctic.

The Palmer LTER region is characterized by deep continental shelves, [Figure 1*a* in *Hofmann et al.*, this volume], with even deeper inner shelf depressions that were produced by the passage of glaciers and ice shelves. These deep shelves are likely to be relatively free of iceberg scour, and suffer less physical and biological disturbance (e.g., from bottom feeding whales) than continental shelves in the Arctic [*Clarke*, this volume a]. In contrast, the ecology of the shallow neashore marine system does show significant impact from ice bergs and scouring by brash ice. One of the most striking effects is the near absence of intertidal biota.

On the large scale, the benthic fauna are divided into the High Antarctic Region (permanently ice-covered), and the Antarctic Region (seasonal ice-coverage, and usually ice free) [*Clarke*, this volume c], and both regions occur within the Palmer LTER. Fine scale patterns show a high degree of heterogeneity, and a vertical zonation in shallow near-shore waters similar to that which occurs world wide. Much of the research on vertical zonation shows that sea ice is one of the most important physical forces impacting the vertical distribution and community dynamics of Antarctic marine benthos [*Clarke*, this volume c].

The Polar Front appears to provide the same biogeographical barrier for benthic biota as for epipelagic biota. As with many Antarctic pelagic species, most benthic species distributions are circumpolar, as there do not appear to be any major long-term barriers to dispersal. One key biogeographic feature is the high degree of endemism, from 50-90%. Generally the benthic fauna are a diverse community, but gradients exist within that generalization. On the western side of the Antarctic Peninsula, there is a latitudinal decrease in species richness in macroalgae going from the northeast to the southwest, i.e., from Elephant Island to Marguerite Bay (68°S). Such a decline may reflect changes in physical constraints or the difference in evolutionary history along the region [*Clarke*, this volume b]. *Clarke* [this volume c] emphasizes that the Antarctic and Arctic have different evolutionary histories, with the older Antarctic having a much greater species richness than the Arctic, and illustrates the usefulness of applying historical processes in attempting to understand present day patterns.

3.3. Pelagic

Four chapters, which range from phytoplankton and microzooplankton community composition and distribution [*Garrison and Mathot*, this volume; *Karl et al.*, this volume] to the dynamics of primary and bacterial production [*Bidigare et al.*, this volume; *Smith et al.*, this volume b], treat different aspects of the pelagic microbial community. These chapters present considerable evidence at several levels within the food web that shows that the structure and efficiency of the food web in the pelagic region varies over space (coastal to oceanic) and time (summer phytoplankton blooms of large cells to smaller flagellates to mid-winter starvation conditions).

The base of the pelagic food web is composed of a complex microbial 'network' of viruses, bacteria, and autotrophic and heterotrophic nano- and microplanktonic organisms that occur in both the water column and sea ice [*Bidigare et al.*, this volume; *Garrison and Mathot*, this volume]. Although few studies have been conducted of the microbial communities west of the Antarctic Peninsula, *Garrison and Mathot* [this volume] emphasize that the role of the microbial loop may be an essential one in oceanic waters in Antarctic pelagic ecosystems. Pigment studies west of the Antarctic Peninsula [*Bidigare et al.*, this volume], as well as studies in the Ross, Weddell and Scotia Seas [*Smith and Sakshaug*, 1990] support the generality, that oceanic algal assemblages are most often dominated by autotrophic nano- or picoplankton producers which are grazed by nano- and microheterotrophs. The implications of these results for recycling of nutrients and sedimentation rates as a result of grazing activity within the oceanic food web are multiple, and are partially explored in *Karl et al.* [this volume].

Garrison and Mathot [this volume] also describe the microbial communities inhabiting sea ice, including bottom-layer, surface and interior assemblages. These assemblages contain the same structural components as water column microbial communities. The sea ice communities contain some species that are endemic to that habitat, and others that also belong to the assemblage in the water column [*Garrison and Mathot*, this volume]. The links between the sea ice and pelagic communities may be both as a seed population when the ice melts in the spring, and by harvesting of particulates in the water column by ice crystals rising to form frazil ice that will include this biological material in the fall and winter [*Garrison and Mathot*, this volume]. Processes controlling these populations are not well known, partly due to logistical problems and partly due to need to develop new methods for assessing *in situ* productivity and grazing within the ice itself.

The role of the microbial network may not be equally important at all times and in all places. For example, in a time series done at Signy Island, larger diatoms and colonial forms showed the classical short summer bloom, with nanoflagellates showing an extended bloom with significant concentrations in winter [*Clarke*, this volume b]. On a larger spatial scale, patterns in phytoplankton distribution based on both historical [*Smith et al.*, this volume b] and new data [*Bidigare et al.*, this volume] show a marked decrease in phytoplankton biomass with distance from the coast. This decrease in phytoplankton accumulation, both in chlorophyll a concentration and cell number abundance, is correlated with a decrease in cell size. Large (>20 μm) cells and chain-forming species are associated with coastal phytoplankton. Small and solitary species (<20 μm) are more abundant offshore, seawards from the shelf break [*Bidigare et al.*, this volume].

The distribution and type of grazers are tightly coupled with phytoplankton such that large macrozooplankton (i.e., Antarctic krill, *Euphausia superba*) are more abundant nearer shore [*Ross et al.*, this volume] and microzooplankton (i.e., heteroflagellates, ciliates and tintinnids) dominate in open waters [*Garrison and Mathot*, this volume]. The large phytoplankton cells contribute a larger proportion to carbon than do small cells [*Bidigare et al.*, this volume] which might contribute, together with size, to their increased value as food for macrozooplankton. However, feeding efficiency and food availability also play a role in determining the value of a particular food source.

Karl et al. [this volume] integrate information on selected topics within the field of Antarctic microbial ecology. In contrast with temperate aquatic ecosystems, the bacterial biomass in coastal waters west of the Antarctic Peninsula was < 1-2% of the phytoplankton standing stock, and it did not appear to be coupled with phytoplankton biomass. These results suggest a fundamental difference in the autotrophic-heterotrophic relationships in the Antarctic within the microbial loop than in marine habitats elsewhere. One aspect of nitrogen cycling that involves multiple trophic levels and clearly deserves more attention is grazing by small organisms, subsequent remineralization of nitrogen, and the relation to bloom intensity.

Export production and mesopelagic microbial processes are relevant not only to questions of control of primary production, but to the link of the pelagic ecosystem to benthic habitats. Of particular relevance to these questions is the discussion of *Karl et al.* [this volume] on the concept of new production, particle formation and removal, and sediment trap-derived particle flux. The measured particle fluxes show considerable temporal and spatial variability, and the export flux in Antarctic coastal waters is reported to be 2 or 3 orders of magnitude larger than those in open ocean waters [*Karl et al.*, this volume]. Considerable interannual variability has also been observed in particle flux in Antarctic coastal waters. Whether the sinking particulate matter is cells of the primary producers themselves, or fecal pellets from grazers, has important implications for the nature of the food web, and for biogeochemical cycling [*Karl et al.*, this volume].

Grazers in the Southern Ocean range in size from the microzooplanktonic heterotrophic flagellates and ciliates [*Garrison and Mathot*, this volume] to mesozooplankton like copepods and macrozooplankton like euphausiids and salps [*Ross et al.*, this volume]. The themes of onshore/offshore gradients and the influence of the physical environment on the structure and function of the assemblages of the macrozooplankton are continued in *Quetin et al.* [this volume] and *Ross et al.* [this volume]. Zooplanktonic provinces (assemblages) also correspond to oceanic and continental shelf regions (neritic), with an intervening transition zone. The smaller species (mesozooplankton) and those thought to depend on small phytoplankton cells, such as salps, are more abundant in oceanic provinces; whereas, those with higher ingestion efficiencies on larger cells are more abundant over the continental shelf and slope. Interannual and seasonal variability in zooplankton assemblages are illustrated by the contrast between the Palmer LTER and the United States Antarctic Marine Living Resources (AMLR) study region at the northern tip of the Antarctic Peninsula. Differences in timing and abundance of macrozooplanktonic assemblages in these areas may result from hydrographic changes and latitudinal differences in life cycle succession.

One important characteristic of Antarctic krill, *Euphausia superba*, is its strong tendency to form aggregations. This heterogeneous distribution impacts the ecology of both the phytoplankton upon which krill graze, and the foraging ecology of the vertebrate predators that depend on krill as their food [*Fraser and Trivelpiece*, this volume; *Fraser and Trivelpiece*, in press]. *Ross et al.* [this volume] describe seasonal and interannual differences in the patterns in the distribution, size, and degree of clustering of krill aggregations west of the Antarctic Peninsula. The presence of large aggregations in winter in regions of broken pack ice or open water was a particularly critical observation for the understanding of winter strategies in this abundant species.

Quetin et al. [this volume] discuss specific factors affecting the patterns of distribution and abundance of meso- and macrozooplankton. The relationship between life cycle strategies of the meso- and macrozooplankton and the timing of peaks of abundance are explored, with particular attention to whether reproduction is fueled by stored reserves or food availability during the reproductive season. Two aspects of population survival, patterns seen in winter-over strategies for pelagic crustaceans and interannual variation in recruitment, are reviewed, with particular attention to Antarctic krill. The impact of sea ice on distributions is evaluated, by examining differences in the degree of association of larval and adult *E. superba* with ice in the winter, and the concept of 'risk balancing' applied to this species as an example.

3.4. Epi- and Mesopelagic Habitat

Kellermann [this volume] gives a comprehensive review of midwater fish assemblages west of the Antarctic Peninsula, what is known of their life history patterns, and places these within the context of sea ice and oceanic circulation distributions. Myctophids (vertical migrators inhabiting the midwater) and demersal or benthopelagic Nototheniids are important members of the midwater fish assemblage. The myctophids are a cold-intolerant group, appear to prefer depth ranges that correspond to CDW, and migrate into the surface waters to feed on calanoid copepods and euphausiids. Most of the Nototheniids are tolerant of cold water, and many enter the water column to feed on Antarctic krill [*Kellermann*, this volume]. Thus, the midwater fish community is linked to the pelagic waters through their feeding, and to the benthos through active vertical transport of material from the surface to the midwater and subsequent fecal pellet flux.

Kellermann [this volume] also suggests that sea ice is the principal factor affecting fish life history strategies, recruitment variability, and assemblage structure. For example, hatching times are predictable, but year-to-year variability in pack-ice retreat affects feeding conditions at hatching. *Kellermann* [this volume] hypothesizes that the interplay between the timing of pack ice retreat and the onset of the phytoplankton and zooplankton blooms dictates the success or not of successful feeding and/or yolk absorption by Notothenioid fish larvae. However, it remains to be determined whether differences in yolk absorption rate or other factors are responsible for the observed large interannual variability in fish recruitment [*Kellermann*, this volume].

3.5. Vertebrate Predators

Three chapters focus on the apex predators in the waters west of the Antarctic Peninsula. Two focus on habitat use and reproductive ecology in the Adélie penguin and emphasize the strong ties between these animals and the timing and extent of sea ice coverage [*Fraser and Trivelpiece*, this volume; *Trivelpiece and Fraser*, this volume]. The third chapter considers marine mammals [*Costa and Crocker*, this volume] and also identifies the presence or absence of sea ice as a key feature that influences the distribution and community structure of these animals. Seabirds and marine mammals also apparently rely on oceanographic or bathymetric features to detect habitat boundaries or regions in which their prey aggregate [*Fraser and Trivelpiece*, this volume; *Costa and Crocker*, this volume]. Many of the apex predators depend entirely or in large part on Antarctic krill, which requires that the demand for this food source be apportioned across a space-time-prey size-foraging range continuum [*Costa and Crocker*, this volume].

Although sixteen breeding seabird species and fourteen non-breeding species occur in the western Antarctic Peninsula region, the biology and population status is less well known within this area than elsewhere [*Fraser and Trivelpiece*, this volume]. The three species of pygoscelid penguins (Adélie, Chinstrap and Gentoo penguins) clearly are the dominant component of the region's avian biomass. These penguins and two species of skua, brown and South Polar skuas, are the most studied seabird groups in the region.

The two chapters that focus on the ecology of the Adélie penguin relate present day distributions and breeding ecology of these birds to environmental conditions over both the recent past and evolutionary time periods. *Trivelpiece and Fraser* [this volume] analyze the adaptations to environmental variability seen in every aspect of the natural history of the Adélie penguin. For example, offshore topography, which potentially affects food supply, and weather, which affects access to nesting sites, impact the annual reproductive success and ultimately recruitment to the Adélie penguin population. The gaps in the breeding range of Adélie penguin populations in the western Antarctic Peninsula region [*Trivelpiece and Fraser*, this volume; *Fraser and Trivelpiece*, this volume], and the limited number of population clusters are assumed to have developed over ecological time, and to be a result of Adélie penguins occurring in a habitat optimum.

The single most important factor affecting annual variation in Adélie penguin breeding success is the timing of sea ice breakout, and its influence on successful completion of the long fasts during the incubation period. Because disappearance of breeding groups can be fairly rapid, *Trivelpiece and Fraser* [this volume] suggest that very short term changes in the environment can result in rapid shifts of the populations in an area. Population changes in penguin colonies in the

Peninsula region that have been continuously abandoned and reoccupied over the past several thousand years have been correlated with changes in sea ice conditions and sea levels [*Emslie*, 1995; *Tatur et al.*, in press]. The limited number of population clusters between Anvers and Adelaide Islands, in fact, may be a result of the proximity of those sites to inner shelf depressions, the presence of CDW that floods the shelf through these depressions, and its effect on sea ice cover and ultimately the timing of ice breakout [*Trivelpiece and Fraser*, this volume].

Costa and Crocker [this volume] discuss life history and reproductive characteristics of several pinneped species found in the Antarctic, and relate these to the need for presence of fast or pack ice for breeding. Four of the six species of pinnepeds in the Southern Ocean, the crabeater, leopard, Ross and Weddell seals, require pack ice for some or all of their life history [*Costa and Crocker*, this volume]. The reproductive rates for three of these seals, the crabeater, leopard and Weddell seals, show a 4 to 5 year cycle between strong cohorts, which has some coherence with the SOI [*Costa and Crocker*, this volume]. Such correlations suggest that large scale oceanographic processes may be an important factor regulating the populations of ice-breeding seals.

4. PALMER LTER

4.1. Basis for the Palmer LTER Central Hypothesis

Sea ice provides a range of habitats for many components of the Antarctic ecosystem, from a surface and lattice for large microbial communities [*Garrison and Mathot*, this volume] to haul out platforms for penguins [*Fraser and Trivelpiece*, this volume] to breeding habitats for seals [*Costa and Crocker*, this volume]. Sea ice cover also directly impacts estimates of total annual primary production through the ice edge blooms that often follow the retreating ice edge [*Smith et al.*, this volume b], and the reproductive cycles of many of the meso- and macrozooplankton as mediated by variability in primary production [*Quetin et al.*, this volume]. The melting ice edge in spring creates a gradient of phytoplankton, bacterial biomass and production, that results in grazing gradients that may be different for small and large grazers. Sea ice also affects food availability in the benthic habitat in subtle ways [*Clarke*, this volume a], through the connection between latitude, sea ice timing, primary production, and total carbon flux to the bottom as a food source.

Sea ice is an integral part of the life history of larger organisms such as Antarctic krill [*Quetin et al.*, this volume], penguins [*Fraser and Trivelpiece*, this volume; *Trivelpiece and Fraser*, this volume] and seals [*Costa and Crocker*, this volume]. Thus, variability in the extent of sea ice cover leads to variations in recruitment success and hence contributes to changes in population structure over seasonal, interannual and evolutionary time scales [*Fraser and Trivelpiece*, this volume; *Fraser and Trivelpiece*, in press; *Quetin et al.*, this volume].

4.2. Brief Description of the Palmer LTER

The western Antarctic Peninsula region is characterized by a diversity of interlocking marine and terrestrial biomes. Within this large system the Palmer LTER study region (Figure 1) encompasses the coastal and continental shelf zone and the seasonal sea ice zone, which is characterized by the annual advance and retreat of sea ice. The Palmer LTER focuses on the pelagic marine ecosystem, including the seabirds that forage within it, and takes as its central premise that the annual advance and retreat of sea ice is a major physical factor determining variability in the structure and function of this ecosystem [*Smith et al.*, 1995]. Given this central premise, the LTER research program is designed to provide measurements of the physical environment and ecosystem components that are directly affected by sea ice and those, perhaps not so strongly affected by sea ice, but can still provide information on sea ice effects. The aspect of the LTER that makes it unique is a focus on two seabird species, the Adélie penguin and the South Polar skua. These two species dominant the avian biomass and depend on Antarctic krill and fish, repectively as their primary food source.

The Palmer LTER sampling program combines seasonal time-series data from a fine-scale nearshore grid (within 3.7 km of Palmer station), with data from research cruises conducted over some or all of the large-scale Peninsula grid (Figure 1). An annual oceanographic cruise in January, which is timed to coincide with a critical period for Adélie penguin chick fledging success, provides large scale sampling over the Peninsula grid, and small scale intensive sampling within the Adélie penguin foraging area. Because the annual cruise occupies the same region, it provides measurements that can be used as a basis for understanding interannual variations in biological recruitment and production as well as for ecosystem synthesis studies.

4.3. Climate and Long-Term Studies in the Western Antarctic Peninsula Region

The Palmer LTER region may be viewed as a transitional area along the latitudinal gradient of the Antarctic Peninsula. As a consequence, it is well placed to address the central Palmer LTER hypothesis that the annual advance and retreat of the seasonal sea ice impacts all trophic levels. The Palmer LTER area is the only area that shows long-term persistence in monthly anomalous ice coverage, which produces consecutive high ice years followed by consecutive low ice years [*Fraser et al.*, 1992; *Stammerjohn and Smith*, this volume]. Regions to the north and east do not show this persistence. This cyclic variation in sea ice cover provides an opportunity for natural experiments on the effects of differences in sea ice extent and timing on different components of the Antarctic marine ecosystem. The Palmer LTER area is also characterized by a large marginal ice zone, open pack ice areas, and numerous leads and polynyas, which allow for studies of shorter term phenomena.

The annual progression of surface air temperatures shown along the Peninsula [*Smith et al.*, this volume a] also shows the contrasting influences of climate throughout the region, from maritime Antarctic in the northern part of the grid to continental climate regimes in the southern area. For many habitats, the central Palmer LTER region is a transition zone, where influence of climate change may have the most pronounced effect on the structure of ecological communities. In fact, the most significant warming trends for air temperature are found in the western Antarctic Peninsula region, with increases of 3 to 5°C in mid-winter temperatures over the past 50 years [*Smith et al.*, this volume a]. The strong linkages between air temperature, sea ice, and the Antarctic marine ecosystem make the Palmer LTER region an ideal natural laboratory in which to study long term trends and cycles, and to detect perturbations in these cycles due to global warming, increases in UV-B radiation, variation in sea ice cover and timing, and the ecological processes affected by these variations. Although the Palmer LTER is focused on the marine pelagic ecosystem, the richness of terrestrial and benthic habitats within the area creates multiple opportunities for additional investigations.

4.4. Site Integrity

One requirement for a long-term ecological research site is the ability to guarantee that the site will remain undisturbed by uncontrolled human influences. This requirement is of concern for the west Antarctic Peninsula region which has seen the development of several shore-based scientific research stations and a growing tourism industry. *Naveen* [this volume] reviews the potential adverse effects of human disturbance on the Antarctic environment and discusses The Protocol on Environmental Protection to the Antarctic Treaty, signed in 1991, which designates Antarctica as a natural reserve, and sets forth requirements for all activities in Antarctica. Some areas (Antarctic Specially Protected Areas, ASPAs) are closed to visitors, while others (Antarctic Specially Managed Areas, ASMAs) accommodate tourists subject to restrictions. The Antarctic Site Inventory project, initiated as a pilot study in 1994 by the United States National Science Foundation, is designed to determine if periodic site inventories of biological and physical features in areas commonly visited by tourists would provide a way to monitor potential environmental impacts on the environment [*Naveen*, this volume]. Within the Palmer LTER area, visitors are not permitted to land on most islands with nesting seabirds during the breeding season.

One measure of disturbance is to determine how far from pristine an environment has come. *Kennicutt and McDonald* [this volume] summarize and discuss inventories of contaminants, contaminant sources, transport and depositional processes, and potential biological impacts in the western Antarctic Peninsula region. Although there is evidence that organisms have been exposed to contaminants, most events are local (100s of meters) and are confined to regions of human activity. Fossil fuel spills from ship traffic pose the greatest risk of future contamination, although the nature and volume of the potential spills would indicate that long-term damage would be minimized [*Kennicutt and McDonald*, this volume]. Overall, *Kennicutt and McDonald* [this volume] conclude that the west Antarctic Peninsula is still relatively pristine.

Agnew and Nicol [this volume] review the history of the exploitation of the living resources (seals, birds, whales, fish and krill) of the Antarctic and Subantarctic, with specific reference to CCAMLR (Convention for the Conservation of Antarctic Marine Living Resources) subarea 48.1 which includes the Antarctic Peninsula region. The Palmer LTER region is at the southern and western extent of subarea 48.1. Commercial fisheries for krill and fish occur in subarea 48.1, although fish catches are low. The majority of the fishing effort, for krill in particular, is concentrated along the edge of the continental shelf between Livingston Island and Elephant Island, north of the Palmer LTER region. Although the primary fishing grounds are north of the Palmer LTER region, fishing is still a consideration since the size of the stock fished is likely dependent upon input from upstream sources in the Palmer LTER region and the Bellingshausen Sea [*Agnew and Nicol*, this volume].

Although the total number of metric tons removed by commercial fisheries in the Antarctic Peninsula region is small, there is concern that the fishery will provide additional competition for predators, especially those that depend on krill. Hence, harvesting marine living resources in the Antarctic is regulated by a number of international conventions which are administered by commissions, in particular CCAMLR. In particular, CEMP (CCAMLR Environmental Monitoring Program) monitors indices of predator breeding success, such as penguin foraging trip duration [*Fraser and Trivelpiece*, this volume], chick food ration, and fur seal pup growth at a number of sites in the Peninsula region, including Palmer Station. These changes are then related to changes in prey availability, in order to determine whether or not the changes are the result of natural fluctuations or commercial harvesting [*Agnew and Nicol*, this volume].

5. PALMER LTER AND OTHER ECOLOGICAL PROGRAMS IN THE WESTERN ANTARCTIC PENINSULA AREA

Scientific exploration in the Antarctic Peninsula region started in the early 1800s [*El-Sayed*, this volume] and these early studies provided a basis for many of the more recent scientific programs in this region. The emphasis in this sec-

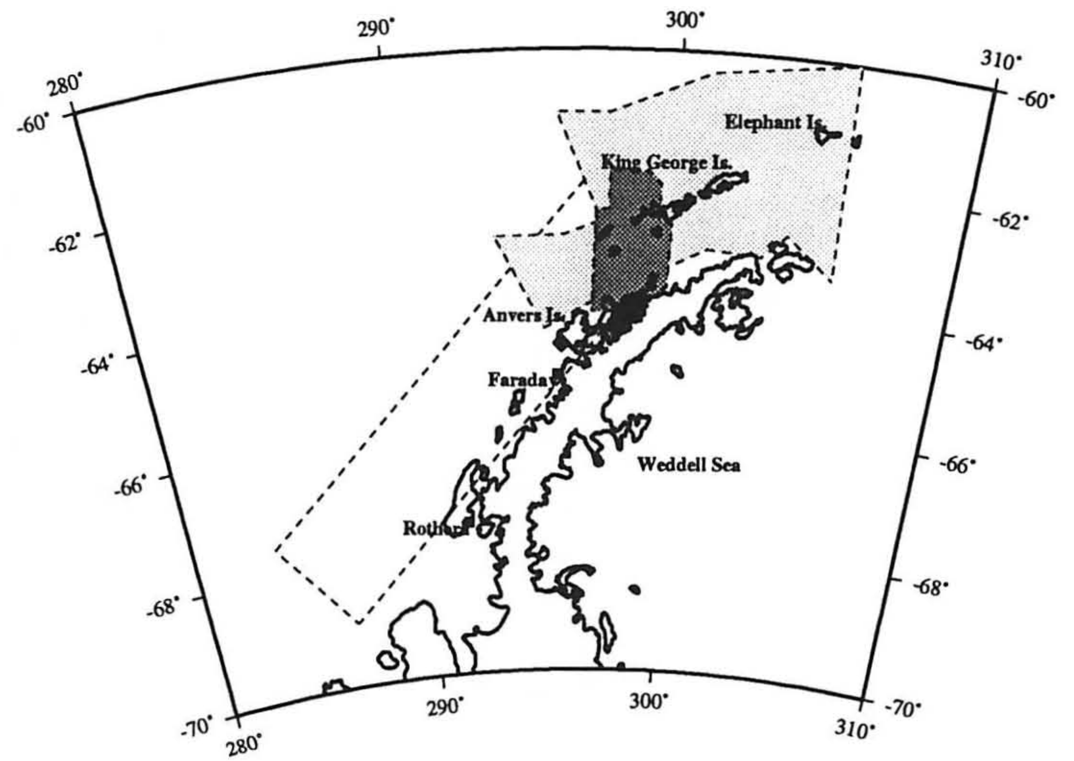

Fig. 2. The region sampled during BIOMASS (light shading) included the northern portion of the LTER sampling region (dashed rectangle) and extended north and eastward as far as Elephant Island. The region sampled during the first RACER (dark shading) field season included part of the northern portion of the LTER sampling grid. Sampling during the two subsequent RACER field seasons (darkest shading) included inshore portions of the LTER sampling grid.

tion is primarily on the more recent oceanographic programs and their relevance to the Palmer LTER. The existence of terrestrial research programs, undertaken by British and Argentine scientists, within the Palmer LTER region are a distinct addition to ongoing ecological research [*Smith*, this volume], as are the series of automatic weather stations funded through the United States National Science Foundation [*Bromwich and Stearns*, 1993; *Smith et al.*, this volume a].

5.1. Past Programs

Over the past 15 years several multi-year studies have taken place within the Palmer LTER region (Figures 2 and 3). While differing in both detail and geographical scope, these programs focused on understanding trophic linkages in the Antarctic marine environment. As a result, there is a rich data base for some components of the Antarctic marine system that can form the foundation for multidisciplinary programs such as the Palmer LTER.

5.1.1. Biological Investigations of Marine Antarctic Systems and Stocks. The Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) program was an international research effort conducted in the Antarctic Peninsula region between 1980 and 1985 [*El-Sayed*, 1994]. The principal objective of BIOMASS was to gain a better understanding of the structure and dynamic functioning of the Antarctic marine ecosystem as a basis for the future management of potential living resources. One of the four BIOMASS study sites overlapped the northern sector of the Palmer LTER Peninsula grid (Figure 2). Observations from this cruise, as well as the other BIOMASS cruises, provide a rich historical data base for the Palmer LTER.

5.1.2. Research on Antarctic Coastal Ecosystem Rates. The Research on Antarctic Coastal Ecosystem Rates (RACER) program, which took place in the mid 1980s, was designed to test several hypotheses on physical-biological interactions and their control on several aspects of the marine ecosystem in coastal waters west of the Antarctic Peninsula [*Huntley et al.*, 1991]. The region included in the RACER field studies overlapped portions of the northern part of the Palmer LTER sampling region (Figure 2). The results from RACER show that mixed layer depth is the primary factor controlling phytoplankton blooms, and that high growth rates of larval Antarctic krill are associated with coastal productive areas. The presence of coastal currents,

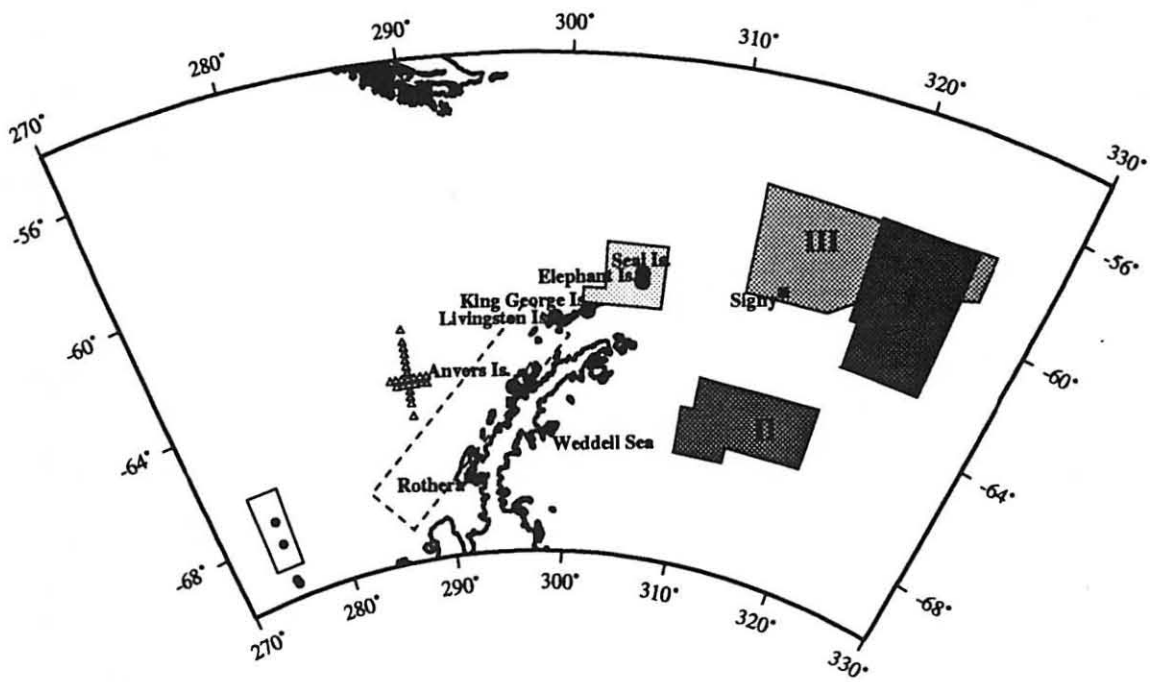

Fig. 3. The CEMP sampling locations (filled dots) are located on King George Island, Anvers Island, Livingston Island, Seal Island, and Elephant Island. The AMLR sampling region (light shading) is centered around Seal Island, but extends westward to Elephant Island. The regions sampled during the AMERIEZ cruises are shown by the shaded areas labeled I, II, and III. The region sampled during ICECOLORS-90 (triangles) was just west of the LTER sampling region (dashed rectangle). The BOFS ice edge study region and sampling locations are shown by the rectangle and filled circles to the southwest of the LTER sampling region.

such as the Bransfield Current, may be of importance in redistributing biogenic material from the coastal productive areas towards open ocean and can explain in part the persistent onshore-offshore gradient in chlorophyll a observed along the western coast of the Antarctic Peninsula.

5.1.3. Antarctic Marine Ecosystem Research on Ice Edge Zones. The Antarctic Marine Ecosystem Research on Ice Edge Zones (AMERIEZ) program took place in the 1980s and was directed at understanding the mechanisms that result in enhanced productivity at all trophic levels within the marginal ice zone, and at understanding the ice edge an ecological interface between the open ocean and pack ice [*Smith and Garrison*, 1990]. Moreover, the sampling in AMERIEZ was sufficient to provide seasonal information for addressing these research issues. As a result of the AMERIEZ studies, the mechanisms that are responsible for the enhancement of phytoplankton biomass at the ice edge, and the two-fold nature of that enhanced productivity (ice communities and ice-edge phytoplankton blooms) became well known. The influence of the pack ice on deep-water pelagic organisms and their predators made it clear that the ice edge is an important ecological interface. Although the AMERIEZ study region was different from the LTER study region (Figure 3), the results from this program are still relevant to many of the studies being done as part of the Palmer LTER.

5.1.4. Biogeochemical Ocean Flux Study. The Biogeochemical Ocean Flux Study (BOFS), which was undertaken by British scientists in October to December 1992, was designed to study biogeochemical fluxes in the marginal ice zone (MIZ) of the Bellingshausen Sea (Figure 3) [*Turner and Owens*, 1995]. Many of the MIZ processes studied as part of BOFS, such as the microbial communities growing in or on sea ice, are of direct relevance to the Palmer LTER. The results from BOFS challenged the prevailing idea that the highest levels of primary productivity would be found in the MIZ and present the alternative hypothesis of enhanced productivity associated with fronts.

5.1.5. ICECOLORS. The ICECOLORS-90 cruise was carried out in October of 1990 in order to assess the effects of ozone-related increases in ultraviolet radiation on phytoplankton in Antarctic waters. The work took place in the MIZ of the Bellingshausen Sea in an area west of Palmer Station at 72°W (Figure 3) that is representative of an open ocean system swept by seasonal sea ice. Because of evidence for an extreme thinning of the ozone layer over Antarctica, the research objective was to obtain data used to test the hypothesis that marine life in Antarctic waters is impacted by ozone diminution. The MIZ, where meltwater often stabilizes near surface water and supports phytoplankton growth, was chosen as a location to investigate the impact of enhanced UV-B on phytoplankton. Within the MIZ a 6 to 12% reduction in primary production was found to be associated with ozone depletion [*Smith et al,* 1992]. Within the MIZ, intensive sampling transects were run both perpendicular and parallel to the ice edge in the area of maximum pigment biomass associated with the MIZ during a six-week cruise period. Further work, emphasizing coastal bloom situations was carried out during October 1993 when work was done in the vicinity of Palmer Station and in Dallmann Bay, which is north of Anvers Island.

5.2. Current and Future Programs Within the Palmer LTER Grid

5.2.1. Antarctic Marine Living Resources. The United States AMLR program is based at the northern tip of the Antarctic Peninsula (Figure 3), in the vicinity of Elephant Island and was initiated in the mid 1980s. The objective of this long-term study is to describe the functional relationships between krill, their predators, and key environmental variables. Of particular interest are the two hypotheses about krill predators, and their response to changes in the availability of their food, and the environmental effects on the distribution of krill. In addition to the oceanographic work around Elephant and Seal Islands, and the field camp at Seal Island, research on the ecology of Adélie penguins is conducted at Palmer Station each year. The AMLR study provides a complementary data set for comparison with the Palmer LTER data sets.

5.2.2. Global Ocean Ecosystems Dynamics. The United States and International Global Ocean Ecosystems Dynamics (GLOBEC) programs have identified the Southern Ocean as a research site. It was recognized that the unique characteristics of the Antarctic marine food web make the Southern Ocean an ideal environment in which to test many of the GLOBEC core hypotheses that consider the effects of variability in the physical environment on population dynamics. Additionally, Southern Ocean GLOBEC is focused on understanding overwintering strategies of key zooplankton species, including Antarctic krill, and top predators. To date, three GLOBEC-sponsored workshops have taken place to define the science questions [*GLOBEC*, 1991; *GLOBEC*, 1993] and an implementation strategy [*GLOBEC*, 1995] for a Southern Ocean GLOBEC program. The Southern Ocean GLOBEC program will consist of modeling studies and field studies that will occur in the Antarctic Peninsula region, the eastern Weddell Sea, and the Indian Ocean sector. Modeling studies have already been initiated and it is anticipated that field studies will begin no later than 1997. It is anticipated that a Southern Ocean GLOBEC program in the Antarctic Peninsula region would complement the research ongoing as part of the Palmer LTER.

5.2.3. British Antarctic Survey Program. Research on the nearshore marine ecosystem has been ongoing at the British Antarctic Survey (BAS) shore-based station at Signy Island from 1962 until its closure in 1995. A new program will start at Rothera Station (Figure 1) in the 1996/97 season, which is planned to be a long-term program (at least ten years) of oceanographic monitoring, together with a series of individual autecological studies or process studies. The oceanographic monitoring will provide year-round data on seawater temperature, chlorophyll standing crop (size fractionated) and macro-nutrient concentration. These data will be taken weekly from a single station in the mixed layer and combined with a CTD/fluorometer/PAR cast to determine water column structure. This time series will provide a valuable high temporal resolution seasonal data set against which to compare the more detailed spatial coverage of the Palmer LTER cruises, and the high temporal resolution time series conducted at Palmer Station within the nearshore grid.

Oceanographic monitoring at Rothera will probably also include regular sampling of the pelagic microbial community, and monthly measures of vertical flux. Rothera is currently equipped with an AVHRR (Advanced Very High Resolution Radiometer) receiver and downloading of SeaWiFS (Sea Wide-Field-of-Viewing Sensor) data is planned, once these data become available. It is also intended to fly ocean color sensors from BAS DHC-6 (twin otter) aircraft fitted for remote sensing to provide detailed spatial coverage of Marguerite Bay and the adjacent Palmer LTER area.

5.2.4. Ecology of the Antarctic Sea-Ice Zone. The program at Rothera will also provide input for the Scientific Committee on Antarctic Research (SCAR) Ecology of the Antarctic Sea-Ice Zone (EASIZ) program and the International Land-Ocean Interactions in the Coastal Zone (LOICZ) project. EASIZ is an integrated program of biological and oceanographic work in the nearshore and coastal region of Antarctica. It explicitly links the nearshore to the coastal marine ecosystem and also explicitly links the pelagic and benthic marine ecosystems. The program was developed at a series of international workshops sponsored by SCAR (Trondheim, May 1990; Bremerhaven, September 1991; Cambridge, September 1992; Bremerhaven, September 1993; and Padova, May 1994). The overall aim of the EASIZ initiative is to determine the role of the Antarctic sea-ice zone in Antarctic marine systems, and in the control of global biogeochemical and energy exchanges. Specifically, the goal is to improve understanding of the structure and dynamics of the Antarctic coastal and shelf marine ecosystem, the most complex and productive in Antarctica, and likely the most sensitive to global environmental change. Particular attention will be paid to those features that make this ice-dominated ecosystem so distinctive, and to understanding seasonal, interannual and long-term changes. The program started in 1995 and will run for ten years. It is intended to provide an integrated scientific framework for marine biology undertaken in the coastal ecosystem of Antarctica.

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