The annual advance and retreat of pack ice may be the major physical determinant of spatial/temporal changes in the structure and function of Antarctic marine communities. Interannual cycles and/or trends in the annual extent of pack ice may also have significant effects on all levels of the food web, from total annual primary production to breeding success in seabirds. Historical records indicate that a 6 to 8 year cycle in the maximum extent of pack ice in the winter. During this decade winters were colder in 1980 and 1981, and again in 1986 and 1987. Winter-over survival in Adélie penguins varied on the same cycle, higher in winters with heavy pack ice. This LTER project proposes to define ecological processes linking the extent of annual pack ice with the biological dynamics of different trophic levels within Antarctic marine communities. The general focus is on interannual variability in representative populations from the Antarctic marine food web and on mechanistic linkages that control the observed variability in order to develop broader generalizations applicable to other large marine environments. To achieve our objectives we will require data from several spatial/temporal scales, including remote sensing, a field approach that includes an annual monitoring program, a series of process-oriented research cruises, and a modeling effort to provide linkages on multiple spatial and temporal scales between biological and environmental components of the ecosystem.

Our general approach capitalizes on easily accessible populations of seabirds that sample the marine environment during a prolonged breeding season near Palmer Station. We will monitor a suite of biological and environmental variables continuously on a small spatial scale (vicinity of Palmer Station) representing the seabird summer foraging area (30-100 km radius), but a long and recurrent temporal scale (annually, the entire breeding season). We will use satellite imagery to continuously monitor certain environmental parameters such as sea ice extent and thickness, sea surface temperature, and potentially color (fluorescence) on larger spatial scales and throughout the year. Research at Palmer Station and in the surrounding nearshore marine environment will focus on the seabirds (Adélie penguins, south polar skuas), the prey of the seabirds (Antarctic krill, Antarctic silverfish), primary production, and bio optical and hydrographic characteristics of the water column. We will monitor processes (reproduction, recruitment) and parameters (food availability) that are sensitive to environmental change and are important in the structure and function of the biota. We propose to extend the spatial scale of sampling of prey distribution, abundance, and physiological condition, primary production estimates, and water column characteristics during research cruises: a short annual summer cruise, and extended cruises during critical times between biological and interannual ice cycles. Observations and experiments during these cruises will validate the primary production and oceanic circulation models.

A set of five interfacing models will be developed. Each model simulates the processes occurring at one trophic level (biooptical model of primary production), within one of the representative species (krill population and swarm model, two seabird population dynamics models) or in the marine environment (regional oceanic-ice circulation). Each model will operate on individual spatial and temporal scales but will be linked or coupled to other models either through the effects of the physical environment or through resource limitation of one population by another. A concept
common to all the animal models is the effect of food limitation on parental fitness and thus reproductive output. Predictions suggest that the effects of global change (climate warming, ozone depletion and increased human pressure on resources) will be more pronounced in Antarctica than in mid latitudes. Results from this proposed LTER on the ice-dominated marine ecosystem will advance current and future efforts to predict the impact of interannual variability in pack ice extent on the vitality of the marine food chain, and to separate long term (decadal) systematic trends from large interannual variability in populations.

I. Introduction

The annual advance & retreat of pack ice, a characteristic feature of polar marine environments, affects about 50% of the Southern Ocean as well as vast areas of the Arctic Ocean & Bering Sea. In these polar environments, pack ice provides marine habitats that are clearly distinct from those of the open-water (Smith 1987, 1990; Murphy et al. 1988), & where microbial communities abound. Annual pack ice may also be the major physical determinant of temporal/spatial changes in the structure & function of polar biota (Ainley et al. 1986; Fraser & Ainley 1986; Smith & Vidal 1986; Smith & Nelson 1986; Walsh & McRoy 1986; Garrison et al. 1987; Ainley et al. 1988; Smith 1990). Thus, interannual cycles &/or trends in the annual extent of pack ice are likely to have significant effects on all levels of the food web, from total annual primary production (Smith et al. 1988) to breeding success in seabirds (Ainley et al. 1983; Trivelpiece et al. in press a,b).

A. Proposed Long-Term Ecological Research Project: LTER

This LTER project proposes to define ecological processes linking the extent of annual pack ice with the biological dynamics of different trophic levels within Antarctic marine communities. Results will advance current & future efforts to predict the impact of interannual variability in pack ice extent on the vitality of the marine food chain. Our approach recognizes that many processes operate simultaneously over a wide range of spatial & temporal scales to determine the success of individual populations & community structure. In particular we recognize that in contrast to terrestrial ecosystems, (1) marine ecosystems display dampened short-term variability & large amplitude variability at long time scales (Steele 1985; Bakun 1986), & (2) that interannual variability is greatest in physically-forced ecosystems (Barber & Smith 1981; Niebauer 1980).

We hypothesize that interannual variation in the extent of pack ice affects the vitality of ice edge phytoplankton, & associated krill & seabird populations.

Our general objectives are

1. to document interannual variability in the development & extent of annual pack ice & in life-history parameters of primary producers & populations of key species from different trophic levels in the Antarctic marine food web;

2. to quantify the processes that underlie natural variation in these representative populations;
3. to construct models that link ecosystem processes to physical environmental variables, & that simulate the spatial/temporal relationships between representative populations; &

4. to employ such models to predict & validate the impacts of altered periodicities in the annual extent of pack ice on ecosystem dynamics.

To achieve our objectives we will require data from several spatial/temporal scales, including remote sensing, a field approach that includes an annual monitoring program, a series of process oriented research cruises, & a modeling effort to provide linkages on multiple spatial & temporal scales between biological & environmental components of the ecosystem. Direct monitoring of biological & environmental parameters & selected experiments will be concentrated in the summer foraging area of dominant apex predators. Research cruises will extend the sampling & experimental area during critical periods. We will use a classical multispecies approach in modeling, a reasonable compromise between single species & ecosystems models which tend to aggregate species (Paine 1984). Models for the chosen representative species will be process oriented, & linkages between the models will be based on resource limitation. The linkages will track the effects of interannual variation in the extent of pack ice cover on marine populations.

B. Ecosystem & Site Description

Ecosystem description: physical environment & food web.

The amplitude & phase of interannual variability in the regional extent of pack ice is not the same in all sectors of the Southern Ocean (Zwally et al. 1983a). Our personal observations, spanning 15 years, confirm that the maximum extent of ice cover in our proposed study area, i.e. the region west of the Antarctic Peninsula & north of Marguerite Bay, varies widely, ranging from near zero to halfway across Drake Passage (Quetin & Ross in press). The variation in maximum extent of the ice pack appears to be on a 6 to 8 year cycle, with colder winters & greater interannual variability in the 1970's (Zwally et al. 1983b; Smith et al. 1988). West of the Antarctic Peninsula the periodicity of this variability appears best correlated to the Weddell Sea sector (between 20°E & 60°W). Our study area is thus well situated to take advantage of "natural experiments" to test our hypotheses on the local & regional implications of the interactions between physical structure (ice cover & currents) & biological populations.

Current views of the Antarctic marine food web are certainly more complex than the first proposed simple & linear marine food chain (Clarke 1985). Nevertheless, the links in the food web between primary producers, grazers & larger predators (seabirds, seals & whales) are often short & may involve fewer than three or four species (Smith 1990). The number of basic prey types available to predators is limited in the Southern Ocean (Croxall 1980). Predators tend to concentrate on a core group of species, especially some extremely abundant euphausiids & fish residing close to the base of the food chain (Ainley et al. 1988; Croxall 1980, Croxall et al 1988). Croxall et al. (1988) suggest that because of the apparent close coupling between trophic levels, long-term studies focusing on these predator-prey relationships & their environment will be critical to understanding variability in Southern Ocean ecosystems & generating a
monitoring base for predicting the impact of man-induced perturbations on this ecosystem. Dominant consumers serve as good indicators of ecosystem processes because they show the cumulative effect of changes in ecosystem dynamics. For example, Adélie penguin comprise 60 to 70% of the entire Antarctic avian biomass (Prevost 1981). Because their diets are dominated by krill (Emison 1968; Volkman et al. 1980; Trivelpiece et al. 1987), aspects of the reproductive biology of Adélie penguins have been proposed as sensitive indices of krill abundance & availability (Fraser et al. 1988). Reproductive biology of penguins, which feed over a 900 km² area, can be evaluated with greater precision than can the biomass & distribution of krill by classical oceanographic methods. Consumers can serve as indices of prey abundance & availability as long as mechanisms behind changes in prey levels are understood, i.e., changes in water mass distribution, variability in reproductive & recruitment success, & food availability during critical periods.

**Primary production.**

The base of the pelagic food web is the phytoplankton, primary producers responsible for the entry of inorganic carbon (CO₂, HCO₃⁻) into marine food chains. In the Southern Ocean, pack ice causes differences in primary production in open water communities, ice-edge blooms, & ice algae. The physical barrier formed by the pack ice between the atmosphere & polar seas dampens wind-forced turbulence in the water column in the winter. Melting pack ice at the ice edge during spring/summer creates a shallow, highly-stable, upper mixed layer over saltier bottom water. Coupled with increased incident radiation, these physical factors promote ice-edge blooms of phytoplankton throughout the austral spring that generally precede those seen in surrounding seas during summer months. Ice-edge phytoplankton blooms are believed to contribute significantly to the overall productivity of the Southern Ocean throughout the austral spring & summer months (cf. El Sayed 1971, 1978; Smith & Nelson 1986; Wilson et al. 1986; Smith 1987). Thus the variation in primary production predicted from variation in the extent of the pack ice is a significant factor in interannual variation in total primary production (Smith & Nelson 1986; Smith et al. 1988). Open-water primary production in the Southern Ocean is thought to be limited by wind-induced turbulence & available light, not nutrients (Hayes et al. 1984; Heywood & Whitaker 1984; Koike et al. 1986). Summer productivity is higher in nearshore coastal regions, in regions of upwelling, & at the ice edge than in the open ocean (El-Sayed 1985; Smith & Nelson 1986; Smith et al. 1988). Although low levels of primary production are detectable in winter (Kottmeier & Sullivan 1987), food availability for herbivores is intensely seasonal & spatially variable.

The dynamics of ice-edge blooms are complex. Each ice-edge bloom can become dominated by a few (but not necessarily the same) species of larger sized (>20 μm) diatoms seeded from the rich algal communities in nearby sea ice as the ice melts in the spring. Some of the released diatom species presumably grow rapidly & come to dominate algal communities in the surrounding nutrient-rich waters (Garrison et al. 1987). Algal blooms appear to be restricted to the near surface waters of the marginal ice zone of Antarctica by the strong vertical stratification (cf. El-Sayed 1978; Niebauer & Alexander 1985; Smith & Nelson 1985a,b, 1986; Wilson et al. 1986; Smith 1987). The center of the bloom proceeds southward with the receding ice edge & the seaward edge
of the bloom is presumably diluted by deeper mixing processes. As such, the areal extent of any marginal ice-edge blooms is a passive tracer of the spatial balance between stratification processes induced by ice melting & the physical processes which promote vertical mixing (Wilson et al. 1986).

During the austral spring & summer, nearshore & highly productive blooms are either unialgal in composition or a mixture of phytoplankton species in which the relative dominance of small & large phytoplankton species changes over the season. Perrin et al. (1987) indicate that prior to the spring bloom of large size diatoms in October to December, smaller (<20 μm) phytoplankton can account for more than 80% of water column chlorophyll (Chl) biomass. By summer, when phytoplankton abundances are greatest, smaller sized phytoplankton account for less than 30% of total Chl biomass in the water column. Presumably much of the change in the size distribution of plant biomass is due to the rapid increase in net phytoplankton during the spring & into the summer on top of a rather constant background of nanoplankton (Wilson et al. 1986; Perrin et al. 1987). The variability in dominant algal size class has direct implications for predictions of the impact of interannual variability in phytoplankton dynamics on the overall trophodynamic interactions in water column food webs. Adult & larval Antarctic krill (Euphausia superba) are more efficient at ingesting larger phytoplankton cells than smaller flagellates (Quetin & Ross 1985), & the smaller phytoplankton components are most likely grazed by microzooplankton & invertebrate larvae (cf. Siegfried et al. 1985).

Although our basic assumption is that nutrients are non-limiting in Antarctic waters (Hayes et al. 1984; Heywood & Whitaker 1984; Koike et al. 1986), there are reports that inorganic nutrients are significantly depleted as ice-edge blooms develop (Smith & Nelson 1986; Perrin et al. 1987). Since nutrients are rapidly, but not entirely depleted, the nutrient-status of these blooms is a debatable issue. However, changes in nutrient-status during a bloom & evidence of the impact of grazing by herbivorous zooplankton can be derived from the levels of degradation endproducts from either heterotrophic metabolism of phytoplankton or from cellular senescence (cf. Prezelin & Boczar 1986).

Primary consumers: Antarctic krill. If herbivores are foodlimited, variability in phytoplankton biomass & production will cause variability in reproduction, growth & survival. Growth & reproduction for Antarctic krill appear to be food-limited in most areas of the Southern Ocean (Ross & Quetin 1986; Price et al. 1988; Quetin & Ross in press). Unlike most other oceans where much of the primary production is grazed by copepods, this one species of euphausiid can be over 50% of the total zooplankton biomass in the epipelagic layer (Hopkins 1985), & thus represent about half the total animal matter available for larger carnivores to eat (Laws 1985).

Antarctic krill reach 50 to 60 mm in total length, have a lifespan of 6 to 8 years (Ettershank 1984; Siegel 1987), & can swim as well as small fish such as anchovy or sardines (Hamner et al. 1983). For most of their life krill occur in discrete schools or swarms that vary in size from several individuals (Hamner 1984) to the rare "super swarm" over 12 km long (Macaulay et al. 1984). Although krill are circumpolar in distribution, high concentrations are found in only a few locations (Laws 1985), mostly within the area covered by the annual advance & retreat of sea ice. This
distribution is suggestive of a close coupling between krill populations, ice dynamics & the associated ice-edge blooms. Krill can scrape algae off the bottom of sea ice (Hamner et al. 1983; Stretch et al. 1988), & adults have been found under the ice & feeding on ice algae in spring (Marschall 1988; O'Brien 1987). Thus both the ice algae & the ice-edge blooms may be significant food sources at certain times of year.

Seasonal cycles of growth & reproduction in E. superba are marked & keyed to seasonal cycles of light & food in the environment (Quetin & Ross in press). The timing & intensity of spawning & subsequent larval hatching fluctuates both between years & locations (Ross & Quetin 1986; Hosie et al. 1988; Sahrhage 1988). Because the point-of-no-return of the first feeding stage is only 10 to 14 days (Ross & Quetin 1989), the availability of food once the larvae reach the surface is critical, & not all calyptopis survive.

Unlike adult krill which have a suite of winter-over mechanisms that allow them to survive long periods of starvation (Quetin & Ross in press), larvae & juveniles cannot survive long periods of starvation (Elias MS thesis, submitted). This inability coupled with a 6-month period of low food availability in the winter suggests that food availability in the winter must be critical for survival of larvae & juveniles. Although questions remain about the quantitative importance of ice algae, larvae & juveniles do feed on ice algae both winter & spring (Guzman 1983; Kottmeier & Sullivan 1987; Quetin & Ross in press; Daly & Macaulay 1988; Marschall 1988).

Although recruitment & reproductive success vary with environmental conditions, for animals with lifespans of more than several years like krill & penguins, total biomass in an undisturbed population can be assumed to be constant, oscillating about a mean value (Priddle et al. 1988; Fraser et al. in press). Thus, fluctuations in the mesoscale abundance of Antarctic krill (Sahrhage 1988) are usually attributed to redistribution of krill by physical forces, not to intrinsic features of krill biology (Priddle et al. 1988). These mesoscale changes occur on the order of twice per decade, & are reflected in the breeding success of dependent predators (Priddle et al. 1988). These variations occur on the same temporal scale as natural cycles of variation in environmental conditions such as ENSO's (Priddle et al. 1988) & interannual variation in ice cover (Zwally et al. 1983a b).

Primary consumers: Antarctic silverfish. Pleuragramma Antarticum, the Antarctic silverfish, has clupeid characteristics & ecology, & is one of the most abundant fish in high-Antarctic marine environments (DeWitt 1970). As a consequence it is also an important prey item for many consumers (Eastman & DeVries 1981; DeWitt & Tyler 1960; Andriashev 1965; Emison 1968; Volkman et al. 1980), including south polar skuas (Ainley et al. 1984; Pietz 1986 1987). Variability in the distribution & density of these early life history stages is assumed to reflect seasonal & interannual variability in abiotic (transport by water masses & currents) & biotic conditions (food availability & predation) (Kellermann & Kock 1988). Time & locations of spawning are not well known, but spawning probably occurs during spring in the permanent pack ice zone near coastal waters of the Antarctic continent. Larvae hatch in December (Kellermann 1986). Post larval silverfish in their first year (Age Class 0 AC0) & juveniles in their second year (AC1) are most abundant in the surface layers of cold shelf water, i.e., in the same water masses as the spawning adults; older juveniles & sub-
adult fish (AC2+ to AC11+, 6 to 20 cm), however, have left the cold waters of the shelf to feed on copepods, larval krill & other euphausiids in the East Wind Drift (Hubold 1985; Williams 1985), & are often found in krill swarms (Rembiszewski et al. 1978; Sloszarczyk 1982). Thus the different life stages of this species are potential indicators of changes in water mass distributions which alter prey distributions near seabird rookeries. Larval abundance, growth & year class strength appear to be related to the melting of the pack ice, & at least in the southern Weddell Sea are higher in warm years when the ice melts earlier (Hubold 1985). Year class strength of Antarctic silverfish should thus be the inverse of that of Antarctic krill. The same correlation between year class strength & ice cover appears true for Alaskan pollock which feed on copepods in the Bering Sea. Higher abundances of copepods found in warm years mean the year class strength of Alaskan pollock is high (Smith & Vidal 1986; Walsh & McRoy 1986). And abundance & development of the copepods is completely controlled by the ice edge bloom (Smith & Vidal 1986).

**Secondary consumers.** Adélie penguins (Pygoscelis adeliae) & chinstrap penguins (P. Antarctica) are long-lived (Ainley et al. 1983), highly philopatric birds (Ainley et al. 1983; Trivelpiece et al. in press a), that migrate annually to their natal rookeries to breed. Adélies remain associated with these rookeries during the entire 4 to 5 month summer reproductive season, October through February. However, they are dependent on pack ice for winter survival (Fraser, pers comm; Trivelpiece et al. in press a) & during critical stages in their reproductive cycle (Ainley et al. 1983; Trivelpiece et al. in press a).

Both Adélie & chinstrap penguins are shallow-diving, offshore foragers, with a maximum foraging range of about 50 km for Adélies & 35 km for chinstraps. They are primary planktivores. Within the same nesting locality, both species eat adult krill of the same length (Fraser & Ainley 1989; Volkman et al. 1980, 1989). Although Adélie & chinstrap penguins depend on krill for food during summer, in some years krill are scarce within the foraging area & they must switch to prey such as the Antarctic silverfish, with a concomitant decrease in reproductive success.

The south polar skua (Catharacta maccormicki) feeds heavily on P. Antarctica (primarily AC8+, 10 to 13 cm) (Young 1963; Ainley et al. 1984; Pietz 1986, 1987; Hubold & Tomo 1989). The wintering area of the south polar skua is not known, but must be within the Southern Ocean (Ainley et al. 1984). Upon arrival of the nesting pair at the rookery, the male feeds the female using local food resources within their foraging range of 160 km (Ainley et al. 1984). Only with sufficient food at this time is the female able to lay eggs, unlike the penguins that arrive at the rookery ready to lay eggs.

Multiannual patterns in the physical environment, the temporal & spatial availability of the micronekton, & the breeding success of the large populations of seabirds dependent on these organisms have been described (El-Sayed 1988; Kellermann & Kock 1988; Rakusa-Suszczewski 1988; Stein 1988; Trivelpiece et al. in press c). At the north end of the South Shetland Island chain, the long-term data set on several seabird species at Admiralty Bay & the frequent Polish expeditions to the area allow us to examine the correlation of various population indices with interannual variability in sea-ice extent. Adélie winter-over survival was higher (50-87%) in years of heavy ice cover than in light years (< 40%) (Fig. 1a) over the nine years from 1981
to 1989. Reproductive success (the number of chicks fledged per pair) was relatively stable, but reproductive success is a complex measure, incorporating the success of experienced birds & novices. Novices are rarely successful at fledging chicks so in years with heavy pack ice when a greater percentage of novices attempt to breed, average reproductive success is depressed (Trivelpiece et al. in press a). Reproductive success of experienced birds, however, should be higher in years with heavy pack ice than in years of low ice cover.

Polish data suggest that krill are more abundant around the South Shetland Islands & in the northern Bransfield Strait after winters of heavy ice cover, & low after winters of low ice cover (Fig. 1b) (Rakusa-Suszczewski 1988). In the 1983-1984 season no krill were found in northern or southern Bransfield Strait, but krill were found in the Gerlache Strait all season long (Quetin & Ross unpubl data), suggesting a southward displacement of the center of the population.

The reproductive success of south polar skuas is linked to the extent of pack ice through the abundance of subadult (AC8+) Antarctic silverfish in the foraging area (Fig. 1a). Thus high recruitment in silverfish in a warm year will produce high prey availability for the south polar skuas eight years later i.e. high abundance of AC8+. Thus high reproductive success should occur the ninth summer after a warm winter. The one exception to this predicted trend was during the 83-84 summer which was also noted for the lack of krill in the Bransfield Strait region & major shifts in water masses (Sahrhage 1988).

In Adélie penguins, parental fitness is primarily a function of winter-over & spring conditions. The physiological condition of birds during spring determines their ability to fast during incubation of the eggs & to forage at sea. South polar skuas, on the other hand are unable to store large amounts of fat because they must fly, so they depend on prey availability during spring. If prey availability is low, they will not attempt to breed. In south polar skuas, breeding success (number of chicks per pair) is more variable than in Adélies, perhaps because the ability to breed depends on prey availability during a short period of time. Geographical location & description

The proposed LTER region surrounds Palmer Station, on the southwest side of Anvers Island midway down the Antarctic Peninsula (Fig. 2). Within a 9-km radius of Palmer Station are two exposed, prominent points, & groups of islands that extend to the edge of the Bismarck Strait to the SE. Palmer Basin, 22 km SW of Palmer Station, is the only deep basin in the area. The maximum depth is 1280 m, & the basin is connected to the open ocean on the west side of Anvers Island, & to the southern end of Gerlache Strait by Bismarck Strait to the NE. Both channels are about 450 m deep.

Adélie penguins dominate the seabird assemblage, but the islands & points of land in the area also support chinstrap penguins & south polar skuas. About 12,000 Adélie pair are distributed among five main island rookeries within 2 miles of the station (Ainley et al. in press). The Palmer Station Adélies winter in the pack ice of the Bellingshausen Sea near to Palmer (Parmelee et al. 1978). Dream Island, 9 km NW, has colonies of both Adélie & chinstrap penguins. About 600 pairs of south polar skuas reside on about a dozen islands in the vicinity. The seabirds depend on resources in the adjacent deep-water foraging area. Seabird populations are large enough
to provide adequate sample sizes for all aspects of this LTER study, yet small enough to ensure that we can cover the area completely, a critical mix when demographic data are of importance in testing population hypotheses & interactive models.

Water circulation in the Bransfield Strait & outside the South Shetland Islands is reasonably well known (Clowes 1934; Gordon & Nowlin 1978) & has been successfully modeled (Capella 1989). Less is known about mesoscale circulation around Palmer Station, but there appears to be a SW setting flow (East Wind Drift), beginning around Anvers Island, that feeds into a cyclonic eddy west of Adelaide Island & seaward of the SW setting flow (Stein 1988). The Antarctic Circumpolar Current flows NE on the outside of this gyre.

C. Conceptual Model & General Approach

Conceptual model.

Our central hypothesis states that many significant biological processes in the Antarctic marine environment are strongly affected by physical factors, particularly the annual advance & retreat of pack ice & variations in ocean currents. Our conceptual model of the interaction between these physical processes & the components of the ecosystem is based on our present knowledge of interannual variability in the extent of pack ice & in the reproductive success of the species that dominate energy flow (Fig. 3). Timing & maximum extent of pack ice (sea ice) & the strength of various currents (oceanic circulation) are forced to a great extent by large scale atmospheric processes (meteorology) (Sahrhage 1988). Since type & abundance of species found in identifiable water masses are different, a decrease or increase in the strength of the current can change the type & abundance of prey in the foraging area of penguins & south polar skuas. Oceanic circulation, meteorology (wind speed, mixing), sea ice & incident radiation, but not nutrients, also affect the timing & extent of primary production (phytoplankton). Each of the apex predators is dependent on the presence of one of the two prey species for reproductive success. And recruitment success in our two prey species is linked directly to the presence or absence of ice. One of the species, Antarctic krill, is the major component in both the summer & winter diet of Adélie penguins, & is positively affected by the presence of ice. The Antarctic silverfish, the preferred food item for south polar skuas & the alternate prey for Adélie penguins, is linked in a complex manner to pack ice extent.

General approach.

Our general approach capitalizes on populations of seabirds that are easily accessible near Palmer Station during a prolonged breeding season & that sample the marine environment. We will monitor a suite of critical biological & environmental variables continuously on a small spatial scale (Palmer Station & environs) representing the seabird summer foraging area (30-100 km radius) (Fig. 2), but a long & recurrent temporal scale (every year, the entire penguin breeding season). We will use satellite imagery to continuously monitor certain environmental parameters such as sea ice extent & thickness, sea surface temperature, & potentially color (fluorescence) on larger spatial scales throughout the year. Automatic weather stations at several selected positions in the region will continuously monitor atmospheric pressure, wind speed & direction, air temperature etc., also on larger spatial scales.
Research at Palmer Station & in the surrounding nearshore marine environment will focus on the seabirds, the prey of the seabirds, primary production & hydrographic characteristics of the water column during the entire austral spring/summer. We will capitalize on the fact that penguins & south polar skuas are effective environmental monitoring devices of the abundance of the two prey items, krill & silverfish, within our study area. We will monitor processes (reproduction, recruitment) & parameters (food availability) that are sensitive to environmental change & are important in the structure & function of the communities.

To verify that this area is representative of the entire region we propose to extend the spatial scale of sampling of prey distribution, abundance, & physiological condition, water column properties, primary production estimates, & hydrographic measurements during two types of research cruise. (1) Short cruises (10 day) will be scheduled for the same time frame every year (midsummer) to survey the foraging area of the seabirds. Observations & experiments during this cruise will document how well our continuous measurements of the nearshore marine environment represent Palmer Basin & the foraging area of the seabirds. (2) Extended research cruises (6-8 weeks) at critical times in biological cycles are planned to confirm that local monitoring of critical environmental parameters will allow modeling of regional processes. The specific objectives of the research cruises include mesoscale observations of: the distribution & abundance of the two prey species, seabird distribution & ecology, & the density field & surface circulation. Observations & experiments during these cruises will also validate the primary production & oceanic circulation models. The first of these pairs of cruises are planned for the fall & spring of years representing the extremes of pack ice cover.

D. Modeling & Synthesis

Models of oceanic circulation-ice, primary production, population energetics & swarm behavior of Antarctic krill, & population models of avian predators will play several vital roles in achieving our objectives.

1. Sampling design & exploration: to guide the design of the cruise track during the research cruises in the fall & spring to ensure that data collection is on the appropriate spatial/temporal scales.

2. Synthesis: to integrate our knowledge of the effects of abiotic & biotic factors on the structure & function of the populations of interest.

3. Comparison: to allow us to compare the processes operating in this large marine ecosystem to processes occurring in other large marine ecosystems & in other LTER ecosystems.

4. Extrapolation: to develop predictions of the effects of man-induced disturbances that can used as indices of change.

We will develop a set of five interfacing models (Table 1). Each model simulates the processes occurring at one trophic level (primary production), within one of the representative species (Antarctic krill, Adélie penguins, south polar skuas) or in the marine environment (regional oceanic-ice circulation). Although we will not develop a full population model for Antarctic silverfish, an empirical model based on the
correlation between interannual variability in observed abundances, growth rates & physiological condition of the early life history stages & monitored environmental parameters will be developed. This model will be coupled with the oceanic circulation model to predict the availability & abundance of the year classes used as prey by south polar skuas. Each model will operate on individual spatial & temporal scales, but will be linked or coupled to other models in several ways. One coupling is through the effects of the physical environment (ice-edge dynamics, oceanic circulation) on the various populations, such as variability in the timing & areal extent of melting ice that affects production in ice edge blooms or large scale interannual variability in oceanic circulation patterns that affect the distribution of prey items within the foraging range of the seabird nesting areas. The other type of coupling is through resource limitation of one population by another, such as the availability of the right sized phytoplankton as food for krill at the right time & in adequate amounts. A concept common to all the animal models is the effect of food limitation on parental fitness & thus reproductive output.

Models play a critical role in achieving the general objectives of both this LTER for the Antarctic ecosystem & the goals set out for the LTER program. Comparability of results of research addressing common topics, such as the pattern & control of primary production, & spatial & temporal distribution of populations representing trophic structure, is best done through models. It is also through models that include our understanding of control mechanisms that we can discern similarities & differences in the sensitivity of different ecosystems to variability in physical structure or to major disturbances, whether man-induced or natural.

Predictions suggest that the effects of global change (climate warming, ozone depletion, & increased human pressure on resources) will be more pronounced in Antarctica than in mid-latitudes & thus detection of these changes above the ever present background of high natural variability will be easier in Antarctica (Manabe & Stouffer 1979). The terrestrial & marine ecosystems in Antarctica are distinct & very different. Exchange of organic matter/nutrients appears to only flow one way from the marine to the terrestrial. Seabirds supply land-based plants with vital nutrients, but terrestrial organisms are not a source of either nutrients or food for marine organisms (Anon. 1989b). Because terrestrial organisms only occupy 2.4% of the land mass of Antarctica are found only in low population densities (Weller et al. 1987), do not appear to significantly impact the dominant marine ecosystem, we have chosen to base our proposed LTER for Antarctica solely on the marine ecosystem.

Monitoring the ecological effects of changes in sea-ice extent & thickness & studying the processes underlying these effects, as recommended by the International Geosphere-Biosphere Programme (IGBP) (Anon., 1989a), will enable us to predict the impacts of climate change on Antarctic biota. Our conceptual model predicts that populations at all levels in the food web may be significantly impacted by changes in the extent of sea ice & in oceanic circulation caused by global warming. In fact some changes may have already occurred. Although many attribute the increase in populations of some consumers of krill in Antarctica to competitive release (Laws 1985), an alternative hypothesis is that the increase in some predators is due to increasingly warmer winters (Fraser et al. in press). An additional concern is the seasonal thinning
of the ozone layer over Antarctica which leads to increases in UVB radiation. Phytoplankton within ice-edge blooms may be particularly susceptible because the stable water column confines them to the surface layer. Decreases in this component of primary production may impact the whole ecosystem if the availability of this source of phytoplankton is as critical as we hypothesize.

Separation of long-term (decadal) systematic trends from large interannual variability in populations will require long-term monitoring programs. Because populations differ in their response times to environmental change, & in their sensitivity to the same factor, monitoring several levels in the food web will optimize our ability to separate trends from cycles. Phytoplankton populations have shorter response times than consumers which integrate changes over several seasons. Using this logic, CCAMLR has chosen to monitor the consumers of krill rather than the krill themselves in an effort to detect long-term trends in krill biomass from commercial fishing. Separation of natural cycles of variability from man-induced trends is especially difficult for long-lived creatures such as krill & seabirds. For example, interannual variation in numbers of breeding Adélie penguins at Admiralty Bay is large (> 20 % between some years), but the population was stable over the 10-year period (Trivelpiece et al. in press a,c).

II. Models of Environment & Populations

A. Coupled Circulation-Ice & Krill Models

A series of mathematical models developed for the South Shetland Islands-Bransfield Strait region form the basis for the circulation-ice & krill modeling studies proposed for this LTER. These modeling studies had two principal objectives: (1) to understand the relationship between physical processes & the distribution of gravid females, eggs & early larvae of E. superba, & (2) to simulate & understand the dynamical mechanisms that produce the circulation in this region. Three models were constructed & implemented: a regional circulation model; a time & temperature-dependent model that simulated the descent-ascent behavior of the krill egg & larva; & a Lagrangian particle tracing model, which is a combination of the two previous models (Capella 1989) (see Results of Prior NSF Support, Hofmann, Ross & Quetin, for more detail). These models provided mechanisms to synthesize & integrate the diverse & numerous observations (laboratory & field) on krill & hydrographic conditions in the South Shetland Islands-Bransfield Strait region. The successful completion of these modeling studies illustrates that models can be used to investigate processes that influence & control the distribution of Antarctic krill. Further, the results of these and other modeling studies (e.g., Wroblewski 1977; Walsh et al., 1988; Hofmann 1988), demonstrate the usefulness of this approach for bringing together the results of multidisciplinary programs.

Oceanic Circulation Model. The time-dependent, three-dimensional, primitive equation circulation model developed by Semtner (1974) was successfully adapted by Capella (1989; 1990) to simulate the circulation in the region around the South Shetland Islands Bransfield Strait. The simulated circulation distributions (Fig. 1, 2 in Results of Prior NSF Support) show seasonal variability in the upper 150 m that occurs in response to changes in the wind stress field. A southward flowing coastal-current
along the eastern side of the Antarctic Peninsula is a seasonal feature that only appears in summer months when the wind stress is reduced.

**Time & Temperature-Dependent Model.** The time & temperature dependent model simulates the effect of temperature on controlling the depth to which krill eggs sink & the rate at which krill larvae ascend. Temperature affects the rate at which eggs develop (Ross et al., 1988), which in turn determines the rate at which eggs sink (Quetin & Ross 1984a). Temperature also affects larval development time (Ross et al., 1988) & the rate at which the larvae swim (Ross et al., 1985). The primary result of the time & temperature-dependent simulations is that when the krill egg encounters warm water at depth (Circumpolar Deep Water) it hatches at a shallow depth. The larva then reaches the surface sooner & therefore has longer to find food before its carbon reserves are depleted. Observations on the distribution of schools of gravid krill (Quetin & Ross 1984b) show these populations in areas where warm Circumpolar Deep Water is found at depth. While speculative, the implication of these results is that the primary spawning grounds of Antarctic krill may have evolved to coincide with areas in which warm water is found at depth. By releasing eggs in such regions the probability of survival of the juvenile is enhanced.

**Lagrangian Model.** The Lagrangian particle tracing model combines the two models described above to simulate the trajectories of krill eggs & larvae in the region of the Bransfield Strait & South Shetland Islands. Lagrangian trajectories show that most of the horizontal transport of the egg-larva particle takes place after the larva has reached the surface (Fig. 4). Trajectories of the egg-larva particles released to the north of the South Shetland Islands & east of Livingston Island are to the west. Eggs released in the zone of northward flow, north of Snow Island, are advected into Drake Passage. The region of the Bransfield Strait & the South Shetland Islands receives krill larvae from both the Bellingshausen Sea to the west & the Weddell Sea to the east. Lagrangian experiments show that: (1) eggs released north of the South Shetland Islands complete their development faster than eggs released in Bransfield Strait or east of the Antarctic Peninsula, (2) surface flow is the primary factor influencing egg-larva trajectories, & (3) timing of krill spawning has a significant effect on the eventual position of feeding larvae because of seasonal changes in the current regime.

**Proposed Modeling Studies**

Circulation-Ice Model. To address the objectives of this LTER, it will be necessary to accurately model the temporal & spatial patterns of the circulation & the sea-ice cover in the study region. The general circulation model of Semtner (1974, 1986), will be used to simulate the circulation in the study region. Given our previous experience with this circulation model (Capella 1989, 1990), the extension of this model to include the region of interest for the LTER will not involve a major effort. The major effort will be directed towards including a sea ice model, & its associated thermodynamic forcing at the sea-ice boundary, in the regional circulation model. Several ice models are available for coupling to the circulation model. Among these, the model described in Semtner (1976a) has been applied to the Arctic ice-ocean environment (Semtner 1976b & 1987) & to the Antarctic Ocean (Ypersele 1986). Adequate coupling between this ice model & Semtner's ocean circulation model has therefore been demonstrated. However, a new generation of ice models (Hakkinen
which includes more sophisticated dynamics & thermodynamics will be evaluated before a final decision is made as to which ice model will be used. We are also aware of the ice processes & ice models described in Hibler (1979), Hibler & Bryan (1987), Pollard et al. (1983), Roed & O'Brien (1983) & Steele et al. (1989). These studies will be included in our evaluation of the most appropriate ice model for this research.

Models of the spatial & temporal distribution of sea ice are strongly dependent on the spatial scale of the model domain because of the parameterization of subgrid-scale mechanical & thermodynamical processes. The trend in ice-ocean modeling has shifted from basin scale models (Semtner 1976a; Parkinson & Washington 1979) to regional scale models with at least mesoscale resolution (Hakkinen 1986 & 1987a; Ikeda 1988 & 1989; McPhee et al., 1987; Overland & Pease 1988). Selection of the ice model will be the first task in the proposed work; selection criteria need to balance model complexity versus computational efficiency. It is inappropriate to choose a particular ice model at this point until we have tested the various models, & determined which ice model best meets the objectives of the LTER.

After selection of an ice model appropriate for our objectives & region of interest, the major effort will be to integrate the ice & the ocean circulation models & to test the final coupled model against historical ice cover data. Before any kind of prognostic capability is attained careful evaluation of the circulation-ice model will be necessary. It is anticipated that the circulation-ice model will make use of the computing facilities at NCAR. The circulation model is already running on the computers at NCAR & some of the ice models (e.g., Ypersele 1986) are also designed to use the computing facilities at NCAR.

Implementation & verification of the circulation-ice model requires several data sets: bottom topography, wind stress, hydrographic distributions, sea ice distributions & current meter measurements. The previously mentioned DBDB5 Worldwide Gridded Bathymetry data set will provide the bottom topography for the circulation model. Wind stress measurements will come either from the Hellerman & Rosenstein (1983) wind data set or a new global wind stress data set (Trenberth et al. 1989) which has improved estimates of the wind stress in the Southern Ocean. Additional measurements of wind direction & speed & atmospheric conditions (air temperature, atmospheric pressure, humidity, & vertical changes in air temperature) will be obtained from several automatic meteorological stations (ARGOS) that are maintained by NSF at five locations in the Antarctic Peninsula, most on the east side of the peninsula. These data are published each year by the Department of Meteorology at the University of Wisconsin. As part of the LTER, two or three additional automatic meteorological sampling stations will be deployed in the Palmer Basin region to improve our knowledge of regional meteorology.

Hydrographic distributions can be obtained from the Southern Ocean data set described in Gordon & Baker (1982). These observations will be supplemented with CTD & XBT observations obtained during the LTER field studies. Our previous modeling studies demonstrated that temperature distributions are adequate for verifying the results of the circulation model. Additional hydrographic observations are available from the BIOMASS program (FIBEX & SIBEX surveys). Similarly, current meter
measurements are available from moorings deployed north of the South Shetland Islands during the International Southern Ocean Studies program. Although the latter two data sets are east of the region of interest for the LTER, the circulation-ice model will include this area. Therefore, these data will be used as a check for the simulated velocity distributions.

Several historical data sets exist for sea ice location & sea ice cover in the Antarctic. Monthly sea ice location on a 1 by 1 latitude-longitude grid are available (Esbensen & Kushnir 1981) as are global monthly sea surface temperature & sea-ice pack limits (Alexander & Mobley 1976). Also available are global monthly sea-ice concentration fields in the Southern Hemisphere on a 1 by 1 latitude-longitude grid (Zwally et al. 1983a). These historical distributions will be used to verify the predicted sea ice cover obtained from the circulation-ice model. The real-time observations of sea-ice cover & sea surface temperature from remote sensing will provide additional data that can be used for verification of the ice distributions obtained with the circulation-ice model. All of the above referenced historical data sets have been obtained & are currently available on the computer system at Old Dominion University. These data sets are also available on the computer system at NCAR.

The simulated circulation & ice distributions obtained from the coupled circulation-ice model will be used as input to the krill & ice-algae biological model components. The temperature, salinity, & velocity fields will be used in the models of the development & advection of krill life stages; the spatial & temporal distribution of sea ice is required for ascertaining the availability of ice cover & ice algae.

**Krill models.** Our previous modeling studies included the processes that affect the development & distribution of the egg & early larval stages of the Antarctic krill. To address the objectives of this LTER, these models will be extended to include the later life stages of the Antarctic krill with a focus on winter-over survival in the first winter & reproductive capacity of adults, & distribution of the various life stages under different environmental conditions. This will require inclusion of processes that influence the development & growth of these life stages. Because the older krill stages are good swimmers & form schools or swarms, we will also model the processes that contribute to swarming behavior. Below are given brief descriptions of these models. However, as with the circulation-ice model, it is inappropriate to choose a particular model at this point. Model development will be an iterative process that will be guided by the observations & theory development throughout the period of the LTER.

**i) Krill Population Model** The krill population model will be designed to simulate the effects of food (& food limitation) & temperature on development & growth of the older life stages (Calyptopis 3 to adult). Formulations for the processes included in the model (e.g., ingestion, respiration, growth, reproduction) will be based upon laboratory & field measurements already collected by Quetin & Ross. The initial version of the population model will consist of a system of ordinary differential equations. Models that simulate swimming in older krill life stages will also be developed based on past & on-going research by Quetin & Ross. The results of the population & swimming models will be combined in an energetics model, similar to the time & temperature-dependent model, to estimate carbon requirements & carbon use for the older krill life stages.
ii) School Model An important aspect of the modeling component of the LTER will be the development of a model(s) to describe the swarming behavior of Antarctic krill. The swarm model will be based upon observations of the distribution, size & volume of krill swarms from echo sounder traces such as have been collected during several of the past eight years (Fig. 5). Our first efforts will be focused on using these data to obtain estimates of parameters used to describe krill swarms. Such parameters consist of estimates of the characteristic length & size of swarms, the number of swarms in a given area, & the average separation distance between swarms. These analyses will be done using techniques similar to those used by Weber et al. (1986) & Morin et al. (1989) to estimate krill spatial distribution patterns, & associated statistics, from acoustic measurements. The results of this analysis will provide statistical descriptions of the observed distribution patterns of krill swarms. Observational data to be used in the analysis will come from existing data sets (cf. Fig. 5) & from measurements made during the LTER.

Concurrent with the analysis of the swarm data, will be a parallel effort directed at constructing a model that will simulate krill swarm formation & provide predictions of krill swarm distribution. Verification of the swarm model will be provided by the statistical descriptions of swarm distributions obtained from the above data analysis. Attempts at constructing such swarm models have started (Levin et al. 1989) & the results of these initial models indicate that purely physical models of turbulent redistribution are not sufficient to explain krill distributions at small scales. Levin et al. (1989) concluded that future attempts at constructing krill models of krill swarms will need to incorporate spatially variable growth rates of krill, krill loss rates due to predators, & density-dependent attraction of krill to account for small scale aggregations. The first of these two quantities will be provided by the krill population model & by the observations of krill predator foraging that will be obtained during the LTER. The latter quantity can possibly be obtained from laboratory observations & theoretical considerations of small-scale biodiffusion (e.g., Okubo 1980). The development of the model of krill swarms will build upon the work currently being done in this area by Drs. Simon Levin, Akira Okubo, both of whom have agreed to participate in this LTER, & by Dr. T. Powell who has agreed to act as a consultant (Levin et al., 1989).

B. Bio-Optical Model of Primary Production

We will develop a regional bio-optical model of primary production for the area of the LTER that meshes models of ice-edge dynamics with respect to phytoplankton biomass & production, & bio optical models of both phytoplankton biomass & production. The model will generate spatial/temporal estimates of phytoplankton biomass & productivity for the entire LTER region during the study period. We will verify & fine-tune the model by comparing results to systematic field observations: spot measurements all spring & summer, measurements from a larger spatial area (Palmer Basin) during 10-day cruises every year in mid-summer, & regional coverage during 6-week research cruises in the fall & spring of two of the six years. Although coverage of open water at high latitudes is sparse & often obscured by cloud cover, ocean color sensors (SeaWiFS) will provide some useful information with respect to spatial/temporal variability of phytoplankton biomass & productivity.
The primary productivity model has several components: a model of production for the marginal ice zone which provides a temporal estimate of ice-related production for the entire Southern Ocean; high-latitude ocean color algorithms for use with the next generation ocean color satellite sensors for the regional estimation of pigment biomass & primary productivity; & local & mesoscale bio-optical estimates of pigment biomass & primary productivity. One objective of this research will be to appropriately link the resolution of these productivity models to circulation models & the higher trophic level models at spatial/temporal scales best suited to the objectives of the LTER.

Identification of an atmospheric model for the estimation of incident solar PAR (photosynthetically available radiation) to use as input to the in-water bio-optical model is currently underway. Smith & Baker (under research currently funded by NSF-DPP) are evaluating various atmospheric models presently used for mid-latitudes (Baker et al. 1990, 1982; Green et al. 1988; Frouin et al. 1989; Frederick & Lubin 1988) for both atmospheric & in-water computations at high latitudes. We expect that the low-sun, long atmospheric path length & persistent cloud cover conditions of the Antarctic will require revision of these models. It is possible, by use of an atmospheric model, to use satellite data to estimate cloud cover. The atmospheric models will be used to extrapolate over time & space the limited surface measurements of irradiance obtained in the field so as to provide meso to regional scale irradiance input to the bio-optical productivity model.

The bio-optical model predicts rates of light-dependent carbon fixation from field measurements of water-column optical properties & phytoplankton absorption properties combined with verifiable assumptions regarding photosynthetic quantum yield (Smith et al 1990). Variants of the bio-optical model are already within 30% of accurately estimating instantaneous, diurnal & daily integrated productivity rates from profiles of bio-optical properties in coastal waters (Smith et al. 1987, 1989). On-going research funded by NSF-DPP ["Ozone Dimunition, UVB, & Phytoplankton Biology in Antarctic Waters" (Smith, Prezelin,, Bidigare, Karentz, MacIntyre)] will result in the extension of the bio-optical model to the low temperature & possibly ultraviolet radiation impacted waters of the Southern Ocean. It will be tested during an upcoming cruise in austral spring of 1990.

**C. Seabird Population Models**

We will construct models of the population dynamics of the seabirds, with two submodels :(1) reproductive effort to describe the mechanisms by which interannual variability in the environment influence population dynamics of populations, & (2) energetics of adults & chicks to provide the interface between oceanic circulation-ice-weather & the population dynamic model.

Models for Adélie penguins will be constructed with data on the demographics & reproductive effort of the Palmer population as far as is possible, because information on prey availability & the hydrographic regime will be most complete at Palmer Station. However, in the initial phases of model-development, we will use results of research on the Admiralty Bay populations of Adélie penguins when we have insufficient information regarding the Palmer population. The model will be based on principles that should hold true for both the Palmer Station & Admiralty Bay
populations, & will be further tested & verified by applying it to the Admiralty Bay Adélie population. In constructing the south polar skua model we will use information from Admiralty Bay & Cape Crozier populations, because at present our demographic & reproductive information on the south polar skuas at Palmer at present is less complete than it is for the Adélie penguins. However, within a relatively few years the Palmer skua population will provide a rich source of relevant data with simultaneous measures of prey availability & hydrographic regimes.

Population dynamics. A population dynamics model will be constructed for each species (Adélie penguin & south polar skua); the two models will be of similar form & structure, but will differ with respect to parameters. These models allow: (1) density-dependence; (2) stochastic variation, & (3) environmental influence. Age-specific survival & age-specific fecundity are two elements of the model that can change, either randomly or forced by environmental factors. These models of the population dynamics of the seabirds will be used for multiple objectives. 1) Predict seabird numbers through time to establish baseline levels of seabird population size & age structure. These numbers can then be extrapolated, after making assumptions regarding the action or absence of environmental influences & compared with observed numbers. This comparison will allow us to evaluate the impact of putative environmental factors. 2) Predict the degree of stochastic (or chaotic) variation in population size & age structure to allow us to distinguish between natural environmentally-induced variation & anthropogenic influences. 3) Evaluate the relative sensitivity of seabird population dynamics and measured parameters to various factors. Factors of potential importance include: (i) Density dependence, (ii) Intrannual variation in food-resources, and (iii) Mean level of food resources. 4) Refine field observation techniques to maximize resolution (e.g. change sampling numbers or intervals to optimize our ability to detect significant differences).

Seabird reproductive effort model. We assume that through natural selection, seabird behavior has evolved to maximize Darwinian fitness (Lack 1954). We will have all the demographic ingredients to estimate fitness. Differences in parental behavior which can be viewed as reproductive effort will impact fitness in several ways. Greater effort, such as greater expenditure of energy & time in foraging, can result in both gains & losses. The gain is greater reproductive success over that time period, ultimately expressed as number of recruits. However, the gain may be balanced by a loss in future reproductive success. Breeding may cause lower adult survival to the next breeding opportunity or poorer parental condition even if the adult survives (Nur 1988a). Previous research suggests that seabird reproductive effort varies with age, experience, time of breeding, food availability etc. (Nur 1987), & will be sensitive to environmental variation as prey availability. Parental condition is another possible factor.

The submodel for seabird reproductive effort provides a technique to evaluate the demographic impact of a change in reproductive effort. It addresses the question of parental condition, how it is influenced by weather variables & food resource, & how parental condition affects adult survival & ultimately reproductive success. Reproductive effort links parental condition & reproductive success. For example, deterioration of the environment does not inevitably lead to decreased adult survival,
if the birds simultaneously refrain from breeding (Ainley et al., 1990) or abandon the breeding effort or base later investment in offspring on levels of early offspring mortality. Conversely, melioration of the environment does not inevitably lead to improved average reproductive success if novice breeders attempt to breed only in these "good" years. Reproductive success in novice breeders is low compared to experienced breeders. The submodel for reproductive effort is a model based on the physiology & behavior of the birds, & the mechanisms that underlie variability in reproductive effort & success, not just demographic characteristics of the population.

The submodel of reproductive effort will be primarily an optimality model, that can be confirmed with a population-genetic simulation, & will be validated during the LTER. The time scale of this model varies from daily to seasonal, i.e., from daily foraging behavior to decisions about breeding chronology or whether to attempt to breed at all. This model will be validated with direct observations of interannual variability in such parameters as foraging effort & breeding chronology & success under variable but known environmental conditions. The submodel addresses events on a temporal scale of days to weeks, & thus complements the population model which is based on a seasonal or annual time scale.

We can use this submodel in several ways. First, we can compare the change in reproductive effort (parental investment) caused by an increase in a single factor such as breeding-independent mortality of adults or the cost of breeding & rearing young (Nur 1988b) or by a change in offspring survival probabilities. We can also consider & evaluate the outcome of changes in the environment that alter two or more factors, with positive effects on one or more factors & negative on the other. For example, if the probability of offspring survival increases but that of parental survival probability decreases, or if parental survival varies during the season. We are thus linking reproductive effort to the physiological condition of the parents & of the young, not just environmental conditions. Second, we can make specific, quantitative predictions about parental behavior & reproductive effort with varying age & environmental factors. Change in the level of reproductive effort has important implications for subsequent survival & condition of adults as well as for chick development & survival. Third, the model will provide the link between changes in foraging effort and the distribution & abundance of the prey items, Antarctic krill & silverfish. In years with greater reproductive effort in a colony, there will be greater predation pressure on prey items.

In summary the submodel provides an important interface between seabird demography (population model) & more proximal levels of ecological processes. Demographic parameters will not simply & conveniently reflect environmental perturbation. However, the reproductive behavior of individuals is predicted to be a sensitive index of environmental variability.

III. Remote Sensing

A. Objectives

Satellite sensors provide data on geographical & temporal scales that otherwise would not be available. Several satellite derived products which will provide complementary spatial/temporal coverage of important parameters in this ecosystem study include: sea-ice extent & thickness; pigment biomass & primary productivity;
hydrographic characteristics of near surface layers of the ocean. A key objective of our remote sensing component will be to create a climatology of the Southern Ocean of the annual advance & retreat of sea-ice & the related spatial/temporal variability of pigment biomass & phytoplankton productivity. Satellite estimates of these parameters will permit extrapolation of local observations in space & time with relatively high accuracy, provide a global context in which to embed smaller scale observations & permit full scale modeling of the Southern Ocean.

There is no guarantee that a given class of satellite sensor will be in orbit for the duration of the LTER. Our intent is to make use of historical satellite data for retrospective modeling purposes & to use relevant satellite data which may be available in the future. Satellite sensors of value in this effort include: passive microwave observations for sea ice extent & thickness; ocean color observations for pigment biomass, phytoplankton productivity & cloud cover; ultraviolet backscatter observations for total atmospheric ozone concentrations; infrared (IR) observations for sea surface temperature & cloud cover; & microwave scatterometers for surface wind stress & altimeters for geostrophic currents should these latter instruments become available for coverage in the Southern Ocean.

B. Satellite Observations & Sources of Data

Zwally & co-workers (e.g. 1983b) have shown that sea ice concentrations can be reliably derived from passive microwave observations. They have used data from the Electrically Scanning Microwave Radiometer (ESMR on the Nimbus 5) & the Scanning Multifrequency Microwave Radiometer (SMMR on the Nimbus 7) to provide climatologies of yearly sea ice extent & concentration. These data are available from Goddard Space Flight Center & our intent is to use these data to monitor the spatial & temporal advance & retreat of sea ice as a component of this LTER.

Smith & co-workers (1986, 1988) have estimated the interannual variations in primary productivity of the marginal ice zone by combining field data with remote sensing data on ice position & concentrations. We have adapted this conceptual model of phytoplankton bloom dynamics in the marginal ice zone & intend to utilize surface & passive microwave observations for creating a monthly estimation of phytoplankton concentrations in this area of the Southern Ocean. This ice-edge algal bloom model, with spatial resolution of about 1! by 1! (100 km by 100 km) will complement finer scale observations.

Gordon & Morel (1983) have reviewed the use of ocean color for the estimation of pigment biomass & Smith et al. (1984) reviewed the use of these data for regional & global estimation of biomass & productivity. In spite of the high percentage of cloud cover over the Southern Ocean, there is an historical data set from the Coastal Zone Color Scanner (CZCS) available for retrospective modeling of pigment biomass. We propose to investigate this data set for Southern Ocean biomass estimations in anticipation of the next generation ocean color scanner (SeaWiFS) scheduled for launch in the early 1990's. When the SeaWiFS data become available they will provide sporadic (i.e., when there is no cloud cover) regional coverage of pigment biomass estimation on a spatial scale of a few square kms for comparison with other
complementary satellite & surface observations. When SeaWiFS is in orbit these data will be available from NASA & we are prepared to process & analyze these data.

In addition to their primary purpose, both visible & IR satellite sensors provide a relatively high resolution (few square kms) measure of cloud cover. Since primary productivity in the Southern Ocean is light limited, & cloud cover along with solar elevation are major environmental factors influencing solar irradiance variability at the ocean surface, these cloud cover data (along with an appropriate atmospheric model) can provide a first order estimation of energy available at the surface for photosynthesis. As a consequence, an estimation of the upper limit to primary productivity can be made (eg. Smith & Baker 1978) on regional to global scales by modeling light limited productivity.

The Total Ozone Mapping Spectrometer (TOMS) & the Solar Backscatter UltraViolet (SBUV) instruments have been used since the late 1970's to map ozone concentrations over the earth. Our intent is to utilize these data for at least two purposes: to map ozone concentrations & thus, by means of an appropriate atmospheric model, the UVB:UVA:PAR incident at the ocean surface; & as an input parameter to the ocean color atmospheric algorithm (Morel 1988). It has been hypothesized that increased UBV incident at the ocean surface, caused by reduced stratospheric ozone concentrations (the "ozone hole"), may adversely influence phytoplankton production in the southern ocean. Under separate funding (DPP/NSF) we (Smith, Prezelin, Bidigare, Karentz, MacIntyre) will be doing field work in the Antarctic during the austral spring of 1990 to test this hypothesis. Because of the low solar elevations & consequent long atmospheric path lengths in Antarctic regions the atmospheric algorithms necessary for accurate retrieval of pigment biomass from ocean color satellite sensors require correction for variable ozone concentrations. As a consequence the TOMS ozone concentrations are valuable ancilliary data for SeaWiFS derived products & will be so used.

Advanced Very High Resolution Radiometer (AVHRR) data are now routinely being captured & processed in real time at both Palmer & McMurdo. These data, while limited to cloud-free areas for sea surface temperature determinations, are known to reveal ocean surface features & so provide complementary information to surface observations. Also, as mentioned above, these data may be used with an appropriate cloud model to estimate surface irradiance for input to bio-optical productivity models. Both scatterometer data for surface wind stress & altimeter data for geostrophic currents would provide valuable input to the circulation models but we are unsure of the possibility of future satellite coverage of high latitude regions.

C. Data Base Management of Satellite & Ancilliary Data

We anticipate making use of NASA browse systems to access & obtain the satellite data required for this LTER. Data storage capabilities are improving so rapidly that it is premature to become committed to specific hardware. Our computer capabilities & storage capabilities at CRSEO (Center for Remote Sensing at University of California at Santa Barbara) are in general compatible with those at NASA & we expect to maintain this capability throughout the duration of the LTER.

IV. Seabird Component
A. Working Hypotheses.

Four hypotheses guide the research on the effects of pack ice on apex predators (Adélie penguins & south polar skuas) within the proposed LTER area. The hypotheses are in two sets, each similar for the two species. The two chosen species hold different positions in the food webs: one is principally a planktivore, the other a piscivore.

H1. Winter-over survival & physiological condition of adult Adélie penguins upon their return to the natal rookery to breed is a function of winter & early spring food availability in the pack ice & on the location of winter pack ice habitat relative to the rookeries (extent of winter pack ice). Adult winter-over survival, physiological condition, & the percent of young birds that attempt to breed will be higher when pack ice extent is greater during winter.

H2. Breeding success of Adélie penguins, barring the effects of spring snow conditions & catastrophic summer storms, is linked to the extent of sea ice through its effects on spring & summer food availability. During cold summers krill availability will be higher, so breeding success in Adélie penguins will be higher. Foraging trips will be shorter, the number of chicks fledged per adult greater, & fledging weights heavier during cold summers than during warm summers.

H3. Physiological condition of south polar skuas, the piscivore, during the pre-egg stage of reproduction is a function of food availability. Territory occupancy will be earlier & more constant, & the onset of reproduction will be earlier when prey are easily available.

H4. Breeding success of the south polar skua will exhibit different cycles than those of Adélies. Recruitment in their primary prey, the Antarctic silverfish (P. antarcticum), is affected negatively by heavy pack ice during the spring of cold years. Since south polar skuas primarily eat subadult fish, breeding success will be a function of ice conditions eight to ten years previous.

B. Objectives.

During several cycles of the perceived six to eight year cycle of maximum pack ice cover in the Antarctic winter we will: (1) characterize the effect of winter & early spring conditions on winter-over survival, nutritional history, & spring breeding condition of known age Adélie penguins from the rookeries surrounding Palmer Station & the interaction of these parameters with key environmental variables; (2) characterize the breeding chronology & success of these Adélies during the incubation & chick rearing periods in the spring & summer as related to measures of critical behavior patterns, prey availability & environmental parameters; (3) document the variability in winter-over survival & age of recruitment of known-age south polar skuas from the Palmer Station area; (4) document the breeding chronology & reproductive effort of this population of skuas & the breeding success of the same population as functions of spring & summer prey availability respectively; & (5) calibrate the above parameters to marine habitat use by Adélie penguins & south polar skuas during proposed cruises in the summer (annual) & in the spring & fall (heavy & light ice years).

C. Motivation.
The ultimate density-dependent factor regulating seabird populations appears to be food supply during the leanest season of the year. If there is little seasonality to the food supply, food availability during the breeding season when seabirds are restricted to island nesting grounds is liable to be the critical factor (Ashmole 1963; Furness & Birkhead 1984). At other times of year the birds can forage over greater distances &/or migrate to more favorable areas. In highly seasonal environments, the nonbreeding or winter season will be the major time of mortality (Lack 1954, 1966; Ainley & Bockelheide 1990). In seabird populations studied to date (kittiwakes Coulson 1959, Coulson & White 1958, Wooler & Coulson 1977; yellow-eyed penguins Richdale 1957; emperor penguins Mougin & Van Beveren 1979; Adélie penguins Ainley et al. 1983; cormorants Bockelheide & Ainley 1989), population stability appears to be maintained by deferred breeding & higher mortality in prebreeders than in adults. The cost of breeding, as measured by annual survival & intermittent breeding, is also much greater for young birds than for older birds (kittiwakes Wooler & Coulson 1977; Adélie penguins Ainley et al. in press). Ainley & DeMaster (1980) argued that breeding should be delayed until penguins acquire the feeding proficiency & social skills necessary for pairing & successfully rearing young in order to make the risks of predation profitable.

Recruitment is the key parameter driving directional change in any breeding population (see Murphy 1936; Garrison & Siniff 1986) & is defined by reproductive success & cohort survival. For penguins, reproductive success & cohort survival depend on food availability & predation pressure (Ainley & DeMaster 1980; Ainley et al. 1983; Croxall 1984).

The first working hypothesis addresses the effect of winter conditions on various aspects of Adélie penguins' pre& postbreeding ecology. We believe that the correlation between winter-over survival and extent of pack ice (cf. Fig. 1a) is a function of energetics, mediated through the abundance & availability of prey in the pack ice, & by the migratory distances that penguins must travel from their winter pack-ice habitat to their summer breeding rookeries. If winter-over survival indicates nutritional conditions before & during the return to the rookeries, then physiological condition of adults in the spring, feather growth over the late fall and winter (ptilochronology), & some basic demographic parameters including cohort survival, recruitment & age-specific reproductive attempt/success will vary with annual sea ice extent, exhibiting positive responses during years of heavy ice cover & visa-versa. The rate at which the breeding population grows (arrivals/day) should also provide an index of the degree of dispersion of birds before they begin their movements to rookeries in spring.

Adult Adélies in better physiological condition, as measured by body mass and possibly percent lipid in the blood, will be better able to withstand the long fasts required to successfully fledge chicks. Ptilochronology may also be a useful tool for testing our hypothesis on winter nutritional conditions for Adélie penguins. Striations on the rachis of feathers represent daily growth increments during molt, & since feather growth rates are influenced by food supply in birds (Grubb 1989), variability in the growth of feathers may serve as an index of annual variations in prey availability. This technique would be particularly advantageous for studies of Adélie penguins as they appear to
migrate to their wintering areas in the pack ice to "fatten up" for the molt. Thus, ptilochronology may provide a valuable means of measuring interannual variations in resource levels in the winter habitat which is difficult to sample directly on an annual basis. In addition, young Adélies (2 to 5-year olds), making their first visit to their natal rookeries in any austral summer, may carry with them in their feather striations a measure of the previous fall's pack ice resources. Similar arguments can be lodged for the south polar skua (H3), though the wintering grounds of adults are unknown.

The second & fourth hypotheses concern the effect of summer conditions on breeding success in Adélie penguins & south polar skuas. Breeding success refers to a suite of parameters that include: the chronology of egg laying, number & size of eggs laid, number of chicks hatched & number fledged, & causes of reproductive failure. These parameters are affected by environmental conditions at different times throughout the summer season. Some are sensitive to short-term variations in resource levels &/or physical conditions, & others sum the effects of longer-term environmental changes. As a result of their dependence on oceanic prey & the variables that determine access to those prey, many aspects of the behavior & biology of seabirds can be explained in terms of their foraging ecology (Lack 1966; Ainley & Bockelheide 1990). For instance, the rate that adult penguins deliver food to their chicks is determined by the distance of the food from the rookery, its abundance & availability.

What is not clear, but is in fact critically important to the primary hypotheses developed in this proposal, are the spatial & temporal scales over which sea ice impacts prey abundance &/or availability & thus seabird reproduction, survival & recruitment. Changes in prey availability can result from short-term phenomena, such as high wind conditions (unpubl. data), or from longer-term phenomena either directly (prey survival & recruitment) or indirectly (prey distribution) mediated by sea ice (see Prey Component).

For both seabird species selected for this project, each feeding at a different trophic level, food availability most directly affects the amount of time individuals take to find food. Given our logistic constraints we can measure this by foraging trip duration (Trivelpiece et al., 1986, 1987, in press c; Pietz 1987) and indirectly by other means. We will determine foraging trip duration both during the incubation period & during chick rearing. We will use telemetry and time-lapse video recording to monitor the comings and goings of adults. When food availability is high, parents are able to capture food in shorter periods, then rest ashore for the remainder of the feeding interval (Trivelpiece et al. 1986, 1987). Diet composition is also an indication of the availability of the primary prey species of the seabird involved. The size of krill in the diet varies both within & among years (Trivelpiece et al. 1987, unpubl. data; Jablonski 1984) & between sites in the same season (Fraser et al. 1988).

The body masses of chicks at fledging & other periods are functions of food availability during the summer, the experience of the parents & the timing of reproduction. Chick weight is therefore a measure of parental foraging success during summer. Chick weight at fledging among cohorts (Trivelpiece et al. 1987; Ainley & Boekelheide 1990) shows significant interannual variation.

Differences in breeding patterns, foraging patterns & preferred prey in Adélie penguins & south polar skuas are important in addressing our central hypothesis on the
effects of interannual variability in the maximum extent of pack ice cover in the winter. Breeding success shows much larger interannual variations in the south polar skua than the Adélie, & is closely correlated with the presence or absence of P. antarcticum in the diet at both Admiralty Bay & Palmer Station (Trivelpiece et al. in press b). South polar skuas form extremely stable pairs through time, & rarely change either mates or territories (Ainley et al. 1990). Thus variations in reproductive parameters are probably not affected by age & experience, but are significantly affected by prey availability. Age of recruitment & arrival dates of these migratory seabirds on their breeding grounds are predicted to be indices of local food resources, & correlated with gross physiological condition among the individuals of the population. The time spent on the breeding territory between the arrival of the pair & the initiation of the clutch appears also to be a function of local prey availability. South polar skuas exhibit a breeding pattern that is particularly sensitive to springtime food availability. Because courtship feeding determines whether a female will breed, many parameters reflect prey availability in the local marine environment: foraging trip duration, timing of egg laying, percent of the breeding population that breeds annually, & percent of breeders laying one versus two-egg clutches. In years of low food availability, many skua pairs in the peninsula region do not lay eggs, while in other years all pairs lay normal two-egg clutches (Trivelpiece & Volkman 1982; Neilson 1983; Pietz 1984; Trivelpiece et al. in press a).

Marine habitat usage of penguins and skuas changes as a function of ice conditions and prey availability (Ainley et al. 1984, Fraser & Ainley 1986, Ainley and Boekelheide 1990). Predator dispersion increases as food becomes less available. In turn, many of the parameters reviewed above are assumed to alter accordingly, although the opportunity to directly measure the relationship has been rare. Supporting information exists for pelicans (Pelecanus occidentalis) in southern California (Anderson et al. 1982) and seabirds at the Farallon Islands (Ainley & Boekelheide 1990, unpubl). In the absence of breeding data a wealth of information exists on the distribution of seabirds at sea in polar regions as affected by oceanographic influences (reviewed in Smith 1990).

D. Methods

Most of the methods (Table 2) have been in use at several study sites in the Antarctic Peninsula region since about 1977. Many are currently standard international protocols to study & monitor the biology of penguins at various locations in Antarctica (CCAMLR Secretariat 1988). All procedures will be conducted on Torgersen Island unless otherwise stated. Torgersen is the only rookery where access during October-November is guaranteed either via zodiac or skiing over the sea ice.

Wintering of Adélies. Interannual trends in breeding population size will be determined by selecting colonies consisting of 100300 nesting pairs in each of the 6 rookeries at Palmer for annual censuses one week following peak egg laying (late November). Spring body condition will be measured by weighing a sample (25/d) of birds as they arrive for the first time on the beach. We will explore the use of automatic scales to increase the sample size. Several colonies will be censused every 2-3 days to use annual growth rate of the breeding population as another index of local conditions. If the population is dispersed due to low food availability, growth rate should be lower.
To characterize variation in cohort survival, age-specific mortality, annual recruitment & the reproductive success of young breeders, 1000 Adélie chicks will be banded annually at Humble Island. In subsequent years, the rookery will be searched frequently, the same number of man-hours per year, for returnees. Upon sighting a previously banded bird, its location & status (alone or paired) will be recorded. If breeding, the pair's breeding success will be followed throughout the summer. Annual banding of Adélies has been ongoing since the 1987-1988 cohort.

Relative nutritional conditions after breeding, in the fall, will be determined from growth rates of the central tail feather & compared to actual pelagic prey distribution & abundance estimates during the cruises. Because significant numbers of Adélies molt near their breeding sites at Palmer Station, the central tail feather can be pulled just before the birds depart after breeding, & it will grow again while they forage in pelagic regions near their wintering grounds. We will take an annual subsample of feathers from 30 birds, band them, recapture surviving birds when they return the following year, & again pull this feather for laboratory analysis.

Breeding success in Adélie penguins. Each year, all pairs in portions of three breeding colonies (the reproductive sample) will be followed to provide annual, independent samples of breeding success to control for the confounding effects produced by first-time breeders (banded birds). Photographs taken of the colony will be used to identify nests.

Pairs in the reproductive sample will also be used to measure breeding chronology & success. Breeding success (clutch size, egg & chick weights & the number of chicks hatched & fledged per breeding pair) will be determined for the entire reproductive sample by regular checks of each nest site throughout the breeding season.

Sex-specific foraging time at sea will be determined by visiting nests of banded birds regularly to note which sex (determined earlier by morphometric measurements & behavior) is on the nest. After the chicks hatch, foraging trip duration will be measured with telemetry equipment & automatic data loggers. Small 10-15 g transmitters will be fastened with epoxy to the back feathers of a subsample (15 birds) on Humble Island & monitored continuously (presence/absence data) through the chick creche stage. PRBO is currently funded by the National Marine Fisheries Service to use this technique on penguins at Palmer Station.

During the chick period, we will capture & pump the stomachs of 5-10 adult penguins per week for diet analysis & to provide fish otoliths and fresh krill samples to the Prey Component of this proposal (water off-loading technique; Wilson 1984). Birds will be taken as they arrive on the beaches, but before they feed their chicks.

Chick weights are an indication of parental foraging success in the summer. Both chicks from two-chick broods from 30 pairs in the reproductive sample will be weighed on the day the oldest chick is 21 days old. At fledging, large numbers of fledged chicks will be weighed annually by automatic scales as they pass through a gate on their way to the beach prior to their fledging exodus to provide a precise estimate of nutritional condition of a cohort. These data are expected to provide information on the relationship between chick weight, cohort survival & eventual recruitment as breeding adults.
Reproduction & recruitment in south polar skuas. To determine winter-over survival of adult skuas, annual censuses of banded birds will be conducted. Many skua pairs (n = 200) in the Palmer area are banded. In addition, to examine variation in cohort survival & age of recruitment, approximately 500-700 chicks will be banded annually. As with penguins, young birds will recruit only in years when food is abundant.

Breeding chronology & success will be determined from periodic nest checks through the hatching period of an independent subsample (50 pairs) from among the banded pairs. Survival of chicks in this subsample will be followed through fledging for per pair reproductive success. Data will include dates of arrival, clutch initiation/completion, hatching & fledging success, & mortality. The relative occurrence of 1 & 2-egg clutches and percent of the population breeding will also be observed. The nutritional status of this chick population will be determined by measuring growth parameters (mass & culmen, tarsus & primary feather length) at 10 & 20 days of age. Foraging effort will be estimated through the use of time-lapse video recording of territory attendance by breeding adults. Annual population growth rate will be determined by daily census of birds on Bonaparte Point which is accessible from Palmer Station.

Habitat use. To more accurately define the spatial & temporal scales over which apex predators & lower trophic levels interact, we will quantify the occurrence patterns of birds relative to the pack ice & prey availability on both the short annual & longer fall & spring research cruises. These data will also help calibrate some of the reproductive parameters discussed above. In other words, if prey are not available, we should find predators dispersed or absent from waters near Palmer. We will census birds on a grid of cruise tracks within the study area at the same time as the spatial distribution & abundance of prey under different ice conditions is determined. Bird censusing will also help to direct sampling of lower trophic levels, as the foraging birds indicate, in part, the opportune localities to sample micronekton. Procedures will be similar to those described in Ainley et al. (1984).

V. Prey Component

A. Working Hypotheses.

Several hypotheses guide our approach to the study of the effects of interannual differences in the extent of pack ice on Antarctic krill, E. superba & the Antarctic silverfish, P. Antarticum, the major prey items of our apex predators, the Adlie penguin & the south polar skua.

H1: In winters with a greater extent in pack ice cover, larval & juvenile krill (young-of-the-year) in waters west of the Antarctic Peninsula will be in better physiological condition, have higher growth & development rates, & higher winter-over survival than in winters of low ice cover.

H2: In years with greater food availability, reproductive output of adult krill within the summer foraging area of the penguins will be higher. Abundance & duration of food availability will be greater after winters with a greater extent in pack ice cover than after winters of low ice cover.

H3: Interannual variation in krill abundance within the penguin foraging area near rookeries is primarily related to changes in the distribution of water masses
dominated by krill, not to variations in recruitment to the krill population. Water mass distributions, the extent of pack ice cover in winter, & meteorological conditions will follow the same cycle.

**H4:** In winters & springs with a greater extent of pack ice cover, recruitment in Antarctic silverfish will be lower than after winters with low ice cover. Interannual variation in abundance of the size fish eaten by the south polar skuas within the summer foraging area will be related to variation in recruitment 8 to 10 years previous, & to the distribution of water masses.

**B. Objectives.**

During several annual cycles within the perceived six to eight year cycle of maximum pack ice cover in the Antarctic winter we propose (1) to characterize the parameters governing recruitment of young Antarctic krill into the adult population; (2) to characterize the variation in availability, distribution, physiological condition & reproductive output of krill within the summer foraging range of penguins; (3) to document the availability, distribution & physiological condition of juvenile & sub-adult P. Antarcticum; (4) to extend the spatial scale of our observations & experiments during an annual 10-day cruise & four 6-week long cruises in both the fall & spring of two years.

**C. Motivation.**

Annual & geographical variations in recruitment & estimated population densities of pelagic organisms are a function of both survival of the larvae & reproductive output of the adults. Interannual differences in population densities generated by annual variations in recruitment will be less (1) in longer-lived organisms, (2) in situations where recruitment failures are infrequent & do not occur in series, & (3) when mortality in the adult population is low (Priddle et al. 1988). We believe that (1) & (3) are true for Antarctic krill, but that recruitment failures may occur several years in a row during any one 6 to 8 year cycle.

Survival of larvae. Adult krill survive the 6 month period of low food availability in the austral winter with a combination of lowered metabolic rates & use of stored lipid (Quetin & Ross 1989), but larval & juvenile krill spawned in the summer have not accumulated the lipid reserves necessary to survive the austral winter without eating (Elias, M.S. thesis submitted). Their winter-over survival thus depends on finding a source of food other than open water phytoplankton. The logical source of food is the ice algae, whether in the sea ice or in the water column after winter storms have broken up the ice & released the phytoplankton. However, larvae & juveniles cannot swim well enough to migrate long distances horizontally in search of the ice edge & associated ice algae. Although primary production is low in the winter, the areal extent of this food source is greater in years of heavy pack ice cover. Thus winter-over survival should be greater & the physiological condition of the larvae better in these years. Recruitment into the adult population in the third summer of life will primarily depend on survival & condition during & after this first critical winter & to a lesser degree on environmental conditions affecting growth & survival of this cohort the following summer & winter. In years with no or little ice cover, recruitment may fail entirely. Given a cycle of maximum ice cover which alternates several winters of heavy ice cover with several
winters of low ice cover, recruitment may fail for several consecutive years, decreasing the adult population by a factor of eight (Priddle et al. 1988). This level of change in biomass is probably not detectable with current techniques. However, the length frequency distribution of krill will indicate both recruitment success, & movement of different size classes inshore & offshore within a year. Two years after a failure in recruitment, the average size will increase, & two years after a successful year, the large cohort of 25-35 mm krill will cause the average size to decrease (Priddle et al. 1988).

Physiological condition (condition factor, percent lipid, & growth rates) of the larvae & juveniles of a particular cohort in the fall & following spring is an index of the ability to survive & contribute to the adult population. Condition factors of larvae collected on two winter cruises, one with heavy ice cover (1987) & one with light ice cover (1989) support our prediction that physiological condition will be higher in winters of heavy ice cover & thus greater availability of ice algae for food than in winters of low ice cover (Quetin & Ross unpubl. data) Condition factor was also related to growth as was found for some marine copepods (Durbin & Durbin 1978, 1981). Ongoing laboratory research (Quetin & Ross DPP 88) will quantify the relationship between condition factor, nutritional history, & starvation tolerance.

Reproductive output. The general pattern of spawning in waters west of the Antarctic Peninsula is a rapid increase from zero in early to late December to a longer period of higher spawning frequencies, then a sharp decrease in late February/early March (Ross & Quetin 1986). Spawning frequency varies not only within the season, but also among schools in the same region. We also know that the initiation of spawning is delayed at lower latitudes (Makarov 1976), & possibly after winters of heavy ice cover (unpubl data). However, early spawning does not necessarily mean a prolonged spawning period (Sahrhage 1988). Inter-school variability in the spawning frequency is of the same magnitude within years as between years in the waters north of the South Shetland Islands & in the Bransfield Strait, suggesting that the major variables affecting reproductive output are the length of the spawning season & the percent of the population spawning, not interannual differences in the spawning frequency.

Calculations of the costs of egg production predict that females produce eggs at the rates observed in the waters surrounding the South Shetland Islands only when relatively high concentrations of phytoplankton are available (~ 1-5 g chl a l⁻¹) (Ross & Quetin 1986). Such concentrations are not common in oceanic areas, but do occur in the bays around the Antarctic Peninsula (Bienati et al. 1977) & in ice edge blooms (Smith & Nelson 1986). If ice edge blooms provide a source of food essential to fuel a long reproductive season, then temporal & spatial availability of food will be greater, & physiological condition (condition factor & percent lipid) of the female before the beginning of the spawning season will be greater in years of heavy winter ice cover. Egg production, in turn, will be related to physiological condition, as shown for some marine copepods (Durbin et al. 1983).

Prey availability. The third & fourth hypotheses address the cause(s) of variations in the local distribution of adult Antarctic krill & of sub-adult P. antarcticum. Changes in oceanic circulation patterns & the pack ice seasonal cycle are linked through large scale variations in atmospheric circulation (Sahrhage 1988), & may
affect the location of water masses & their representative prey items on a scale of 10 m to several hundred kilometers. Thus changes in mesoscale distributions & abundances of E. superba & P. antarcticum may be linked to the ice cycle through changes in oceanic circulation patterns &/or the direct effect of the pack ice on survival & behavior of the prey.

The causes of seasonal & interannual variations in the size & number of aggregations of krill are poorly understood, yet the distribution & size of schools may play an important role in population dynamics of krill (Okubo pers. comm.), & in prey availability for the seabird predators. Purely physical models of turbulent redistribution cannot explain observed krill distribution patterns at small scales (Levin et al. 1989). Possible mechanisms include food gathering (Antezana & Ray 1983), active horizontal migration (Kanda et al. 1982; Siegel 1988), enhancements due to local eddies (Everson 1984; Rakusa-Suszewski 1988), or spatially variable growth & predation rates & density-dependent effects (Levin et al. 1989). Therefore, local krill availability will result from the interaction between variation in recruitment, water mass distribution caused by large scale changes in atmospheric circulation, & seasonal & interannual changes in school size & distribution.

The same factors affect availability of P. antarcticum. Both Adélie penguins & south polar skuas eat P. antarcticum with a mean otolith size corresponding to AC8+ (Ainley et al. 1984; Hubold & Tomo 1989), so we will focus on patterns of variability in distribution & abundance, & physiological condition of fish during their prolonged juvenile & early subadult phase, when they are found in the same water masses as Antarctic krill. Since growth of fish of AC2+ & older is restricted to summer months, the otolith rings record the effect of environmental conditions during past seasons (Hubold & Tomo 1989). Otolith analysis will identify years of lower growth, & thus poor recruitment. Such patterns will facilitate our ability to establish relationships between recruitment success, growth rates & prey availability for the south polar skuas & environmental factors such as timing of the ice retreat.

D. Methods

Our overall approach (Table 3) will be to monitor physiological condition & spawning characteristics of both adult & larval krill collected within the foraging range of the penguins throughout the spring & summer of all years. Larval physiological condition consists of a suite of parameters: condition factor (5g carbon &/or dry weight per length3), percent lipid, & growth & development rates. For adults, only condition factor & percent lipid can be monitored continuously. If, as has been shown for fish, poor condition factors, low growth & poor recruitment are significantly correlated, then physiological condition of larvae will be an index of recruitment. Larvae & juveniles of Antarctic krill will be collected from a day boat with a ring net (500 5m mesh). Adélie & chinstrap penguins will be our samplers of the local adult krill population (within ~ 50 km) during the late spring & summer every year. Chick rearing begins 3 weeks earlier in Adélie than in chinstrap penguins, so we will use both species as "samplers" to extend our yearly collecting season from mid December until mid-March. We will also collect & analyze the otoliths of silverfish eaten by penguins & of dead silverfish found near skua nests throughout the spring & summer of all years. When food is abundant these leavings are common (Ainley & Fraser, pers.
Quantitative estimates of distribution & abundance of larval krill & silverfish, & adult krill schools throughout the foraging range of the seabirds will be made yearly during the same time period each summer on a 10-day cruise. In addition, longer research cruises will be scheduled for the fall & spring of two years to extend the spatial scale of these quantitative & physiological measurements. On these longer cruises, we will also collect samples for determination of physiological condition of adult & larval krill & of silverfish, & spawning characteristics of adult krill.

Wintering-over of larval krill. Winter-over survival of the year's cohort will be quantified & related to physiological condition during two of the six years. Estimates are complicated by the problems common to sampling any oceanic population of zooplankton, & by the occurrence of larvae & juveniles under the ice. One of the functions of the present & proposed models of oceanic circulation and ice in the research area is to assist in the design of a sampling effort to assess winter-over survival of larvae & juveniles in years of heavy & light ice cover. We will use the models to predict where larvae sampled in the fall should be found in the spring, & include those areas in our total survey area. Transects within the survey area will be a combination of searching with the side-scan sonar (88 kHz), which is particularly useful in locating schools of late furcilia larvae & juvenile krill, & standard stations. Because krill inhabit both water column & under-ice habitats we will use a mixture of techniques to estimate population numbers. Although not ideal, we believe that the signal to noise ratio in this instance will allow us to evaluate the success of recruitment. During the fall & spring cruises larval & juvenile krill will be collected with paired 1-m bongo nets (500 5m mesh) equipped with flow meters & towed obliquely from 0 to 300 m. Animals from one cod-end will be used for abundance estimates, stage & length analysis, & from the other cod-end for physiological condition. If ice exists, divers will quantify the distribution both of the numbers of larvae & juveniles & of the available ice algae found under first year ice, & sample the larvae & juveniles for physiological condition. Techniques for quantifying young krill & the ice algae available to them to eat are presently being tested by Quetin & Ross (DPP88). Mortality during the winter will be estimated from the difference between total numbers in the different stages in the survey area fall & spring, & known developmental times under winter conditions (unpubl data).

Reproductive potential. We will determine the sex & maturity stage, & physiological condition of a subsample (100) of adults from stomach contents of breeding Adélie & chinstrap penguins throughout the summer. Maturity stage includes the external appearance of the animal & the number of size classes of oocytes in a "squash" of the ovary (classification being developed by J. Cuzin-Roudy in conjunction with Ross, Quetin & Amsler). Krill are multiple spawners (Quetin & Ross 1983), & can simultaneously carry oocytes of three different size classes, i.e., three distinct broods that will be released at different times (Cuzin-Roudy 1987). Before the spawning season begins, all females should have all three size classes of oocyte. When one or more size classes of oocyte is missing, the spawning season has begun. At the end of the spawning season, ovaries from all females will contain only the germ layer & oogonia, but no oocytes. The percent of the population of mature adults reproducing, & their physiological condition are indices of the reproductive potential of the local population. Simultaneous measurements of the timing & concentration of food available
(phytoplankton biomass) & of the extent of the pack ice cover in the winter will allow us to test our hypothesis on the reproductive potential of adult krill. During the midsummer cruise, we will conduct experiments to determine spawning frequency & egg production rates of any spawning females, in addition to the standard measurements. Summer cruises to extend the spatial scale of our knowledge of the timing & magnitude of reproduction will be delayed until later in the LTER.

Relative local prey abundance. Several methods, each with its own intrinsic errors, have been used to estimate krill abundance. Although the results from nets & acoustic surveys on the same ship & at the same time differ greatly, both methods are equally valid (Everson 1988). The discrepancy prevents us from accurately estimating absolute abundance of krill populations. However, within the restricted summer foraging area of the penguins we can use a predator derived index to estimate relative local prey abundance & relate that abundance to measurements of penguin population dynamics. We propose to derive a predator "CPUE" based on the composition of the penguin stomachs & the foraging duration (Seabird Component), or time to fill that stomach, during the late spring & summer. The predator "CPUE" for krill is the percent krill in the stomach times total stomach weight divided by the foraging duration, & is a valuable index of seasonal & interannual variation in local krill abundance. A predator "CPUE" for P. Antarticum can also be calculated from the number of otoliths found in the penguin stomachs. Both this "CPUE" & the foraging trip duration of the south polar skuas (Seabird Component) are indices of prey availability for the south polar skua.

During research cruises we will survey the region for both adult krill & juvenile & subadult P. Antarticum to compare our predator "CPUE"s from the rookeries to larger spatial scales, & evaluate the extent to which this index characterizes the region. The number, size & distribution of krill schools will be determined acoustically along transects both within & outside the foraging area, ranging south to the assumed winter-over grounds of the Adélie penguins. These data are necessary for the model of krill schools (cf. Fig. 5). A random selection of schools will be sampled for length-frequency & maturity stage analysis, physiological condition, & instantaneous growth rate. Instantaneous growth rates (Quetin & Ross in press) are the best possible summation of environmental quality & production rates & can be related to our measures of food availability & temperature.

We will survey the same region for juvenile & sub-adult P. a ntarcticum with a 2-m square trawl designed to maintain the mouth opening perpendicular to the direction of travel & reduce bridle interference, thus minimizing avoidance. Our goals are to quantify the distribution & availability of silverfish to the south polar skuas, & determine interannual variability in the physiological condition of the juveniles & sub-adults. Condition factor & percent lipid are estimates of the more recent nutritional history of the fish, whereas standard otolith analysis (cf. Hubold & Tomo 1989) will yield the relative growth rates of the fish during the last 8 years or so. The otoliths thus represent a record of the past nutritional history. The oceanic circulation-ice model & the empirical model of the population dynamics of P. a ntarcticum will be linked to predict prey availability for south polar skuas in their summer foraging range.

VI. Phytoplankton Biomass & Primary Production
A. Working Hypotheses.

Our working hypotheses have been guided by the observation that in the Antarctic, nearshore phytoplankton biomass, size distribution & species composition show significant regional variations throughout the austral spring & summer (cf. Tilzer et al. 1985; von Bodungen 1986; Perrin et al. 1987). These hypotheses are also supported by recent work on phytoplankton dynamics by other Antarctic researchers (cf. El-Sayed 1971, 1978; Smith & Nelson 1986; Tilzer et al. 1985; von Bodungen 1986; Wilson et al. 1986; Smith 1987).

**H1:** Neritic phytoplankton dynamics reflect spatial/temporal changes in the distribution & nature of frontal boundaries between Antarctic oceanic water masses & nearshore currents, as well as episodic ice-edge phytoplankton blooms that occur sequentially over the short growing season.

**H2:** The components of Antarctic primary production include contributions from open water phytoplankton & ice edge blooms & sea ice algae. Total primary production may therefore vary with the extent of the pack ice during the previous winter & spring as the spatial & temporal extent of the ice-edge phytoplankton blooms should be greater in years with greater ice pack coverage.

**H3:** The size composition & abundance of phytoplankton biomass change with the season. During the blooms, larger sized phytoplankton will dominate the community.

B. Objectives.

Over the 6 year period, which should include years with significant variability in the extent of maximum pack ice cover in the Antarctic winter, we propose (1) to document the fluctuations of harvestable plant biomass in the water column by monitoring the spring to fall temporal/spatial variability in the abundance, size-distribution, composition & vitality of the phytoplankton communities within nearshore Antarctic waters; (2) to use traditional radiolabel measures of primary productivity to calibrate a bio-optical model of primary production; (3) to bio-optically monitor as continuously as possible the spring to fall in situ temporal/spatial variability in hydrography, light availability & utilization, & primary productivity; (4) to employ bio-optical data to model phytoplankton production in the region around the study site as a function of space & time; (5) to extend the spatial scale of the measurements & model during research cruises in the fall & spring of two years, one with heavy & one with light ice cover; & (6) to verify & refine the model with data from # 1-4.

C. Motivation.

Our bio-optical approach to primary production has several advantages. First, the bio-optical approach will provide a more continuous measure of short-term fluctuations in carbon fixation rates than traditional radiolabel measures of productivity. Radiolabel (14C) determinations of primary production will be routinely used for calibration & verification of the model. Second, since standard hydrographic parameters (temperature, conductivity, depth) will be measured at the same time as the water-column optical properties & phytoplankton absorption properties, we will be able to identify spatial/temporal changes in the distribution & nature of water masses. And third, our approach provides continuous measures of in-water optical & hydrographic properties,
many of which will be needed to define & quantify linkages between oscillations in
the physical field & incoming radiation & water column productivity.

There are several aspects of differences in the photobiology &/or metabolic
physiology of Antarctic phytoplankton that may affect our model of primary production
based on water-column optical properties that will be considered during an upcoming
cruise to the Weddell Sea in the austral spring of 1990 to define "Ozone Dimunition,
UVB, & Phytoplankton Biology in Antarctic Waters" (Smith, Prezelin, BBidigare,
Karentz, MacIntyre). The following issues will be addressed in depth to refine the bio-
optical model of primary production to represent the extreme conditions of the Southern
Ocean & ice-edge phytoplankton blooms. Results from these studies will provide an
improved understanding of phytoplankton dynamics of ice edge blooms prior to the
proposed LTER, thereby advancing monitoring approaches to be used at the LTER site.

First, Tilzer & co-workers (1985) have shown that the photosynthetic capacity
& maximum quantum yield of photosynthesis are lower, on average, in natural
also suggest that this diminished lowlight photosynthesis may be caused by temperature-
controlled rate-limited processes that become dominant in otherwise light-limited
situations. Therefore assumptions about photosynthetic quantum yield in the model of
primary productivity will be verified. Second, Antarctic phytoplankton are capable of
relatively high rates of light-independent carbon fixation via B-carboxylation reactions
(Mortrain-Bertrand 1988) which supplement photosynthetically available radiation
(PAR)dependent photosynthetic carbon fixation & affect total primary productivity.
Third, photosynthetic activity in Antarctic phytoplankton communities shows changing
diel patterns with daylength & irradiance (Rivkin & Putt 1987; Putt et al. 1988).

D. Methods.

We will use HPLC separation techniques to monitor changes in algal size &
dominance, as well as levels of degradative endproducts, in discrete algal size fractions.
We choose to use 0.4 5m cutoff filters for determination of whole-water biomass &
productivity, & 5.0 5m cut off filters to separate out larger components most likely
to be efficiently grazed by adult krill (Quetin & Ross 1985). The difference (0.4 5 5m)
biomass would represent the size fraction grazed by smaller heterotrophs.

Day boats will be used to deploy simple strings of instruments in the area to
monitor the day-to-day variability in the in situ vertical profile of phytoplankton
community dynamics & in the bio-optical & hydrographic properties of the water
column in the near-shore waters throughout the spring & summer. The same protocols
will be followed onboard a larger research vessel capable of surveying all of Palmer
Basin during the midsummer cruise each year. Light weight spar buoys equipped with
Biological-Optical Monitoring Systems (BOMS) & incubation racks will be deployed at
three depths: surface, 50% incident irradiance (Io) & 10% Io about twice a week
during the spring & summer. Deployment will be at midday for about 2 hours. Buoy
deployment will be preceded & followed by a vertical profile to characterize the bio-
optical properties (BOMS), & hydrographic characteristics (Seabird CTD) of the water
column, & to provide biological samples for laboratory analysis & in situ or
deckboard incubation. Samples for size-fractionated HPLC analysis will be taken each
time, & incubations for radiolabeled determinations of primary productivity done periodically. With this approach we optimize our chances for near-continuous measurement of in situ bio-optical properties, productivity measurements, & concurrent discrete sampling for laboratory determination of size-fractioned biomass distribution & radiolabel carbon uptake rates.

BOMS (Booth & Smith 1988) provides measurements of downwelled spectral irradiance, upwelled radiance (which includes in situ fluorescence), temperature & depth. BOMS will provide continuous (every 4 min) data on temperature & a number of discrete wavebands in the visible spectrum. Downwelling wavebands are centered at 410, 441, 488, 520 & 560 nm; upwelling wavebands are identical with the exception that the 560 nm detector is replaced with a passive Chl a fluorescence detector at 683 nm.

Incubations for radiolabeled determinations of primary productivity will involve incubating 10 samples at each depth: (a) 4 light-exposed samples containing 14C-bicarbonate will be used to measure in situ rates of autotrophy in different microbial size fractions, (b) 3 light-exposed samples containing 14C-bicarbonate will have DCMU added, & (c) 3 samples will provide data on the degree & nature of changes in community structure during incubation. From these measurements & measurements of PAR from the BOMS, we can calculate Chl-specific photosynthetic performance & in situ quantum yield photosynthesis. Deckboard or on station incubations will be used when ice coverage or working conditions interfere with deployment of the spar buoys.

During the 6-week fall & spring cruises, vertical & horizontal profiling of hydrographic, optical & chemical properties in a grid around the Palmer study site & extending south toward Adelaide Island will be conducted. At each working location, one in situ BOMS will be deployed for the longest icefree period possible. At the same time, a vertical profiling UVspectroradiometer will be deployed via a winch line. It will remain in the water column all day, if possible, while routinely profiling the upper 30 m & transmitting optical & hydrographic data back to shipboard computers. Intensive vertical profiling of bio-optical parameters via a separate instrument package (BOPSII) will provide rapid, concurrent measurements of conductivity, temperature, PAR, downwelling & upwelling spectral irradiance, upwelling spectral radiance, transmittance, & in vivo Chl fluorescence intensity. After viewing the physical & biological vertical structure of the water column during the BOPSII downcast, a 10-bottle GoFlo rosette sampler interfaced with BOPSII will be used to obtain water samples on the upcast. Depending upon the biological/chemical analyses to be carried out, 4 to 8 depths will be sampled during discrete casts & will include the surface, the middle & the base of the mixed layer, as well as samples below the mixed layer but still within the euphotic zone. Depending upon need, water samples will be: 1) analyzed to assess the present bio-optical state of phytoplankton communities; & 2) apportioned into incubation bottles for in situ &/or deckboard analyses of primary productivity.

Similar spatial & temporal quantification for sea-ice communities is technically beyond the scope of the initial stages of the present proposal, but will be addressed as remote optical procedures & measures of the extent & activity of ice-embedded phytoplankton communities develop in the future.
VII. Organization & Management

The University of California at Santa Barbara is the lead institution for this LTER, with the Marine Science Institute serving as the coordinating center (see Fig. 6 for management plan). The staff of the Marine Science Institute will prepare & distribute the annual report & data base catalog. The seabird group (W. Fraser, W. Trivelpiece, D. Ainley & N. Nur) is located at Point Reyes Bird Observatory, a non-profit institution oriented toward long-term ecosystem research. Modelers of oceanic circulation-ice & of krill populations reside at several institutions (E. Hofmann, Department of Oceanography, Old Dominion University; S. Levin, Center for Environmental Research, Cornell University; A. Okubo, Marine Sciences Research Center, State University of New York, Stony Brook) & are unified through E. Hofmann (Fig. 6). J. Klinck (Old Dominion University) & T. Powell (UC Davis) have agreed to consult on these models.

R. Ross & L. Quetin will be the project co-managers, coordinating the research cruises and field research, networking databases & facilitating integration of research components into hierarchies of ecosystem analyses. Co-project managers appear to be the best idea, leaving one manager stateside while the other is often onsite during the prolonged Antarctic field season. They have collaborated on polar research projects in the LTER region since 1981-1982. They will be the individuals primarily responsible for communication & coordination with other LTER study sites.

The site manager (W. Fraser) will coordinate the four research projects while at Palmer Station, & be responsible for holding weekly meetings during the austral spring & summer to ensure that data collection & facilities' use are going as planned, & that opportunities to exchange information are not missed. Regular (bi-weekly) communication from Palmer to PIs at their home institutions will be possible via telemail.

The UCSB PIs (R. Ross, L. Quetin, B. Prezelin, R. Smith), one representative from PRBO (Fraser or Trivelpiece depending on availability), & E. Hofmann will form an executive committee responsible for decision-making. Project direction will be set by the Executive Committee. The Executive Committee will meet formally twice a year. Since changes in project direction may be made during the season on site or at the end of the season after some analysis of the data, we believe that a few, long meetings will be more beneficial than frequent, brief meetings. Regular meetings during the austral spring & summer are impossible because of the far-distant field site, but portions of the executive committee &/or their representatives will be in the field together for months at a time. This proximity will allow for frequent interaction at the site. More formal progress reports will be clustered over telemail at quarterly intervals. Six internationally renowned scientists have agreed to serve on our Steering Committee & are listed below. They represent disciplines & areas of expertise that are important to the LTER. Two members are participants in other marine LTER projects, thereby facilitating our communication with other LTER researchers.

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Oceanic circulation Dr. Ray Dueser Dept. of Environmental Sciences University of Virginia Charlottesville, VA 22903
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Virginia Coastal Reserve LTER, director Dr. George Hunt Department of Ecology & Population Biology University of California Irvine, California 92717
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Seabird ecology Dr. Tom Fisher Horn Point Environmental Laboratory University of Maryland Cambridge, Maryland
Phone: 301-228-8200 Omnet: T.Fisher
Chesapeake Bay LTER, nutrients Dr. Marlon Lewis Department of Oceanography Dalhousie University Halifax, Nova Scotia Canada
Omnet: M.Lewis
Remote sensing, microturbulence (on leave at NASA, Goddard)

The Steering Committee will be kept informed of research progress on a bi-annual basis, & will meet with the PIs at an annual meeting at UCSB. Prior to this meeting they will receive the cluster of annual progress reports that will be compiled into the annual report. The formal annual meeting will follow the working group meeting of PIs in mid-summer where the season's results will be synthesized & plans for the following season finalized. The Steering Committee will review our progress, & also contribute advice. The first meeting will be scheduled for summer of 1991, prior to the onset of field work.

The integration of LTER research activities into Palmer Station logistics & facilities will be through the Program Manager of Polar Biology & Medicine in the Division of Polar Programs. The limitations & restrictions imposed on the research program by official policy & the regulations of the Antarctic Treaty will not interfere with our research goals. The Palmer Station area was recently proposed as an Antarctic Protected Area (APA) under the auspices of the Antarctic Treaty. Response to the proposal by other nations, thus far, has been favorable. Recognition as an APA will provide for different levels of use for designated sites in order to protect ongoing research from the effects of man. The biological basis for this proposal has been established (Quetin & Ross 1989). This protection would insure the long-term integrity of the entire area. Presently, the area is controlled through specific permits for collection & use of plants & animals, & for use of sites as designated within the Antarctic Treaty. One island with large penguin rookeries is a Specially Protected Area under the Antarctic Treaty & several others are being considered as Sites of Scientific Interest (SSSI), with access for scientific purposes only. The Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) has proposed that Palmer be included in its network of sites where certain penguin parameters should be measured annually (to monitor krill availability). The one disadvantage to such firm guarantees of site integrity is that permission to manipulate seabird populations to simulate disturbances will not be likely. With long-term data sets, however, we will be in a position to respond
opportunistically to unavoidable man-induced disturbances & assess the effects of such disturbances. The direct impact of the oil spill from the recent grounding of the Bahia Paraiso (January 1989) on the area was limited to within a few kilometers of the wreck & to a several week period (Kennicutt II et al. in prep.). Investigations into the longer-term effects of the spill are continuing, & Fraser & Ainley are studying the effects on birds.

This LTER does not answer all questions about the physical & biological processes operating in the Antarctic marine ecosystem. The existence of this long-term data base will provide the opportunity for others to propose research to address hypotheses that would benefit from our long-term data base, & to propose research that will verify or disprove some of our implicit or explicit assumptions. For these reasons we believe that site promotion is an important management responsibility. Site promotion will come from our annual report sent to the Steering Committee & a limited list of interested Antarctic researchers, from speaking engagements by the PIs, & from participation in scientific meetings. The annual report will contain not only an initial synthesis of our results, but also the catalog of data bases with Level I information which we hope will encourage the submission of complimentary proposals by other scientists.

VIII. Data Management

Five broad long-term data bases will be generated during the proposed LTER (Fig. 6). Our data management plan is based on the expertise of the three subgroups within the LTER who have successfully linked multi-disciplinary data sets in the past (Hofmann, Ross & Quetin; Smith & Prezelin in Fronts 85 & Watercolors 88; Ainley & Fraser in AMERIEZ). Our data management system has four functions: (1) to establish essential cross-links between individual data bases; (2) to establish quality assurance protocols; (3) to document the data bases & generate routine reports on the status of the data base; (4) to archive the data in protected yet accessible form. The first two functions are critical to the success of on-going research; & the second two are important for coordinated transitions during personnel changes & for the secondary use of the data for complimentary research outside the LTER.

Specific quality assurance protocols (range checking, routine graphics & statistics, inspection & calibration of remote & laboratory instruments, etc.) & format requirements for data entry will be developed by the Executive Committee before the first field season with information received from all PIs. The PI(s) of origin will take responsibility for data entry into a format(s) compatible with the needs of the entire LTER, & conduct their own quality checks. Data will be on-line in their own institutions so that any errors can be corrected in place, & not propagated through a central data base. Documentation of data will be at two levels (Michener et al. 1987). Level I contains information about the project or experiment which is available to interested individuals & will be in the annual report. Level II documentation contains detailed information about the conditions under which the data was generated & information about the accessibility of the data (contact point, restrictions, form). Immediately after the summer season or after a cruise, each PI will submit a written report to the Executive Committee giving Level I documentation on the data gathered. Level II documentation will follow with the raw numbers after quality checks have been completed.
Multiple copies of the data sets will be maintained on at least two separate systems by the PIs. The actual media will depend on the quantity of the data. We anticipate that each PI will create a series of files that can be off-loaded to other systems through computer networks such as INTERNET or BITNET or through 90 megabyte storage disks for exchange within this LTER. Level II documentation with the raw data for each year &/or cruise will be stored on 90 megabyte storage disks. Archival storage of raw data will be on an optical disk (350 gigabytes). During our first meeting we will discuss the details of how to network the data sets, how to collect & handle the numbers, & data entry specifications. We will also agree upon the time frames in which the different data sets will become available. Data on optical disks & supporting documents will be archived at UCSB.

IX. Schedule of Activities

Major activities during the proposed 6 years will be in three phases: (1) initiation, modeling, design of shipboard research transects/grids; (2) monitoring physical & biological parameters at Palmer Station & on short cruises; & (3) four 6-week research cruises, in the fall & spring of both 1993 & 1996. During the initial period of 6 to 9 months, we will acquire & build the necessary equipment & recruit students. We will install automatic meteorological stations at selected points prior to October 1991. We will also hold a meeting of the Executive Committee & all additional PIs & collaborators to complete the data management scheme, & to discuss protocols & logistics, in the spring of 1991. We will begin construction & testing of the various models with historical data sets, & use these models to refine our approach to the routine sampling & monitoring to be carried out during the first field season (Oct 1991 to Mar 1992). We will begin planning the first research cruise after one full year of monitoring activities & have scheduled this cruise at the end of the routine field season of 1992-1993. If necessary, we will modify our cruise plans for the next spring (1993) after receiving the first cruise reports. The monitoring, experimental & modeling activities will be presented at meetings & submitted as manuscripts after the first complete field season, but extension of our results to greater spatial scales will be delayed until shortly after the first cruise.