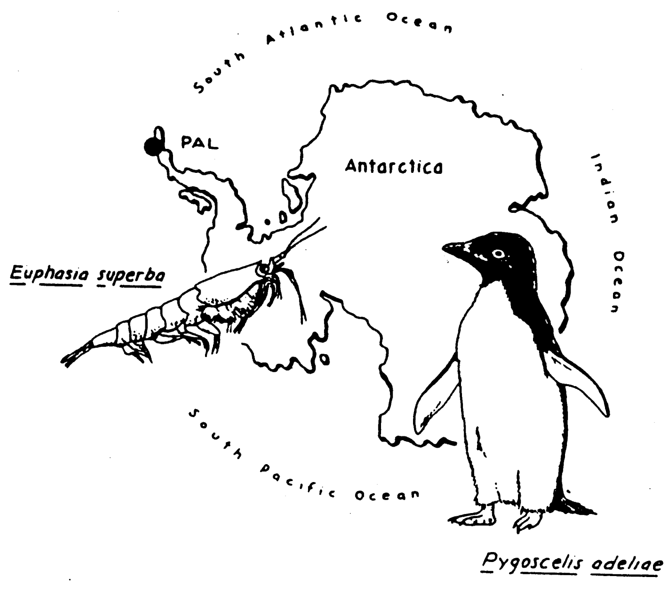
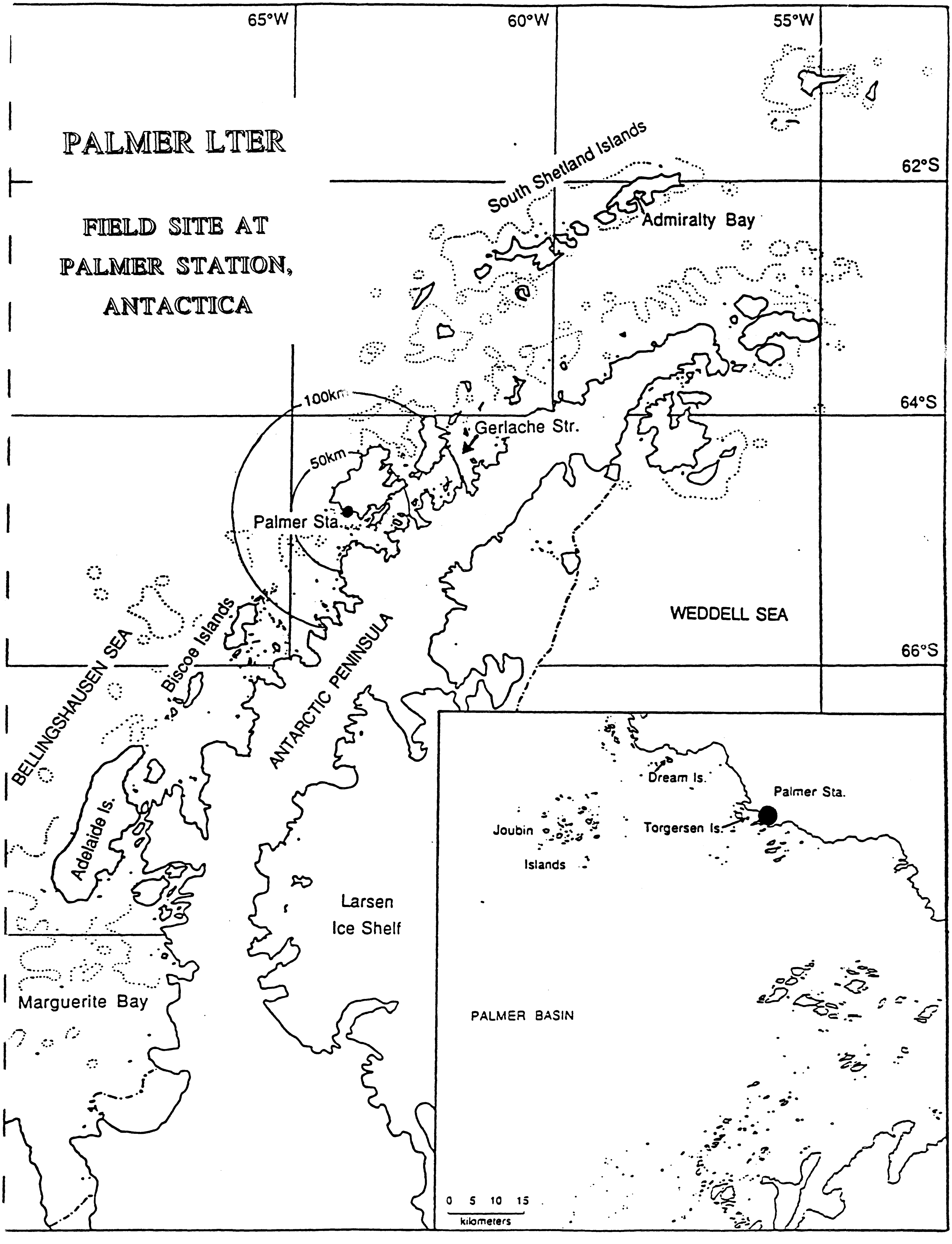
PALMER LTER

Briefing Book

Palmer Station Site Visit

February 1994




PALMER LTER
FIELD SITE AT
PALMER STATION,
ANTACTICA
65°W
60°W
55°W
62°S
64°S
66°S
South Shetland Islands
Admiralty Bay
Gerlache Str.
100km
50km
Palmer Sta.
WEDDELL SEA
BELLINGSHAUSEN SEA
Biscoe Islands
ANTARCTIC PENINSULA
Adelaide Is.
Larsen
Ice Shelf
Marguerite Bay
Dream Is.
Palmer Sta.
Joubin
Torgersen Is.
Islands
PALMER BASIN
0 5 10 15
kilometers

PALMER LTER
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I. Introduction

The annual advance and 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 and 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), and where microbial communities abound. Annual pack ice may also be the major physical determinant of temporal/spatial changes in the structure and function of polar biota (Ainley et al. 1986; Fraser and Ainley 1986; Smith and Vidal 1986; Smith and Nelson 1986; Walsh and McRoy 1986; Garrison et al. 1987; Ainley et al. 1988; Smith 1990). Thus, interannual cycles and/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, 1990).

A. Palmer Long-Term Ecological Research Project (LTER)

Research at the antarctic marine LTER site, Palmer Station and surrounding waters, focuses on the pelagic marine ecosystem and the ecological processes which link the extent of annual pack ice with the biological dynamics of different trophic levels.

The central hypothesis for all Palmer LTER research is that interannual variations in physical processes like the extent of pack ice and oceanic circulation affect all levels of the food web of the Southern Ocean.

Our general objectives are

(1) to document interannual variability in the development and extent of annual pack ice and in life-history parameters of primary producers and 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;

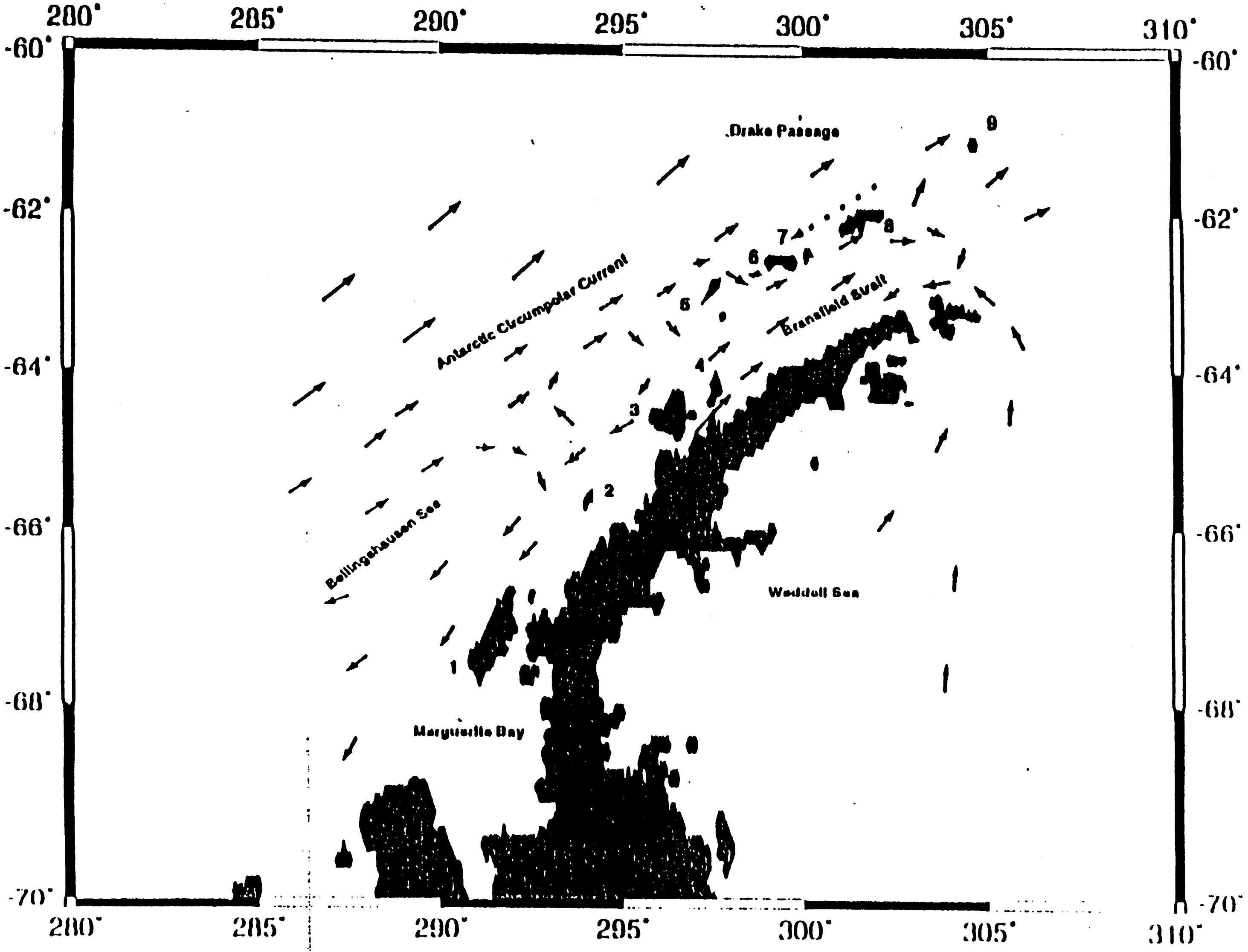


Figure 1. Schematic of the circulation in the upper 200-300 meters in the LTER study region. Circulation patterns were derived from the sources discussed in the text. The Polar Slope Current is indicated by the dotted arrow. The vectors with lighter shading in the eastern Bellingshausen Sea represent the possibility of a single cyclonic gyre in this region. Islands are identified as : 1, Adelaide: 2, Renaud; 3, Anvers; 4, Brabant; 5, Smith; 6, Snow; 7, Livingston; 8, King George; 9 Elephant. Gerlache Strait is between Anvers and Brabant Islands and the Antarctic Peninsula. Hofmann, E. E., C. M. Lascara, J. M. Klinck. 1992. Palmer LTER: Upper-ocean circulation in the LTER region from historical sources. Ant. J. U.S. 27(5):239-241.

(3) to construct models that link ecosystem processes to physical environmental variables, and that simulate the spatial/temporal relationships between representative populations; and

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

To achieve our objectives we require data from several spatial/temporal scales, including remote sensing, a field approach that includes both an annual monitoring program and a series of research cruises, and a modeling effort to provide linkages on multiple spatial and temporal scales between biological and environmental components of the ecosystem. Linkages between the models will be based on resource limitation, and will track the effects of interannual variation in the extent of pack ice cover on marine populations.

B. Ecosystem description: physical environment and food web

The amplitude and 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). The Palmer LTER study region surrounds Palmer Station (64°40'S, 64°03'W), on the southwest side of Anvers Island midway down the Antarctic Peninsula, and runs from the southern end of the Bransfield Strait to south of Marguerite Bay (Fig. 1). Observations spanning 15 years confirm that the maximum extent of ice cover in the Palmer LTER study area varies widely, ranging from near zero to halfway across Drake Passage (Quetin and Ross 1991; Stammerjohn 1993) (Fig. 2). This variation appears to be on a 6 to 8 year cycle, with colder winters and greater interannual variability in the 1970's (Zwally et al. 1983b; Smith et al. 1988; Stammerjohn 1993). The current regime is less well known, but there appears to be a SW setting flow offshore of Anvers Island, with the possibility of one or two cyclonic gyres (one near Anvers and Brabant Islands and one west of Adelaide Island) seaward of the SW setting flow (Stein 1988, 1991; Hofmann et al. 1992). The Antarctic Circumpolar Current flows NE on the outside of this gyre and forms the northern boundary

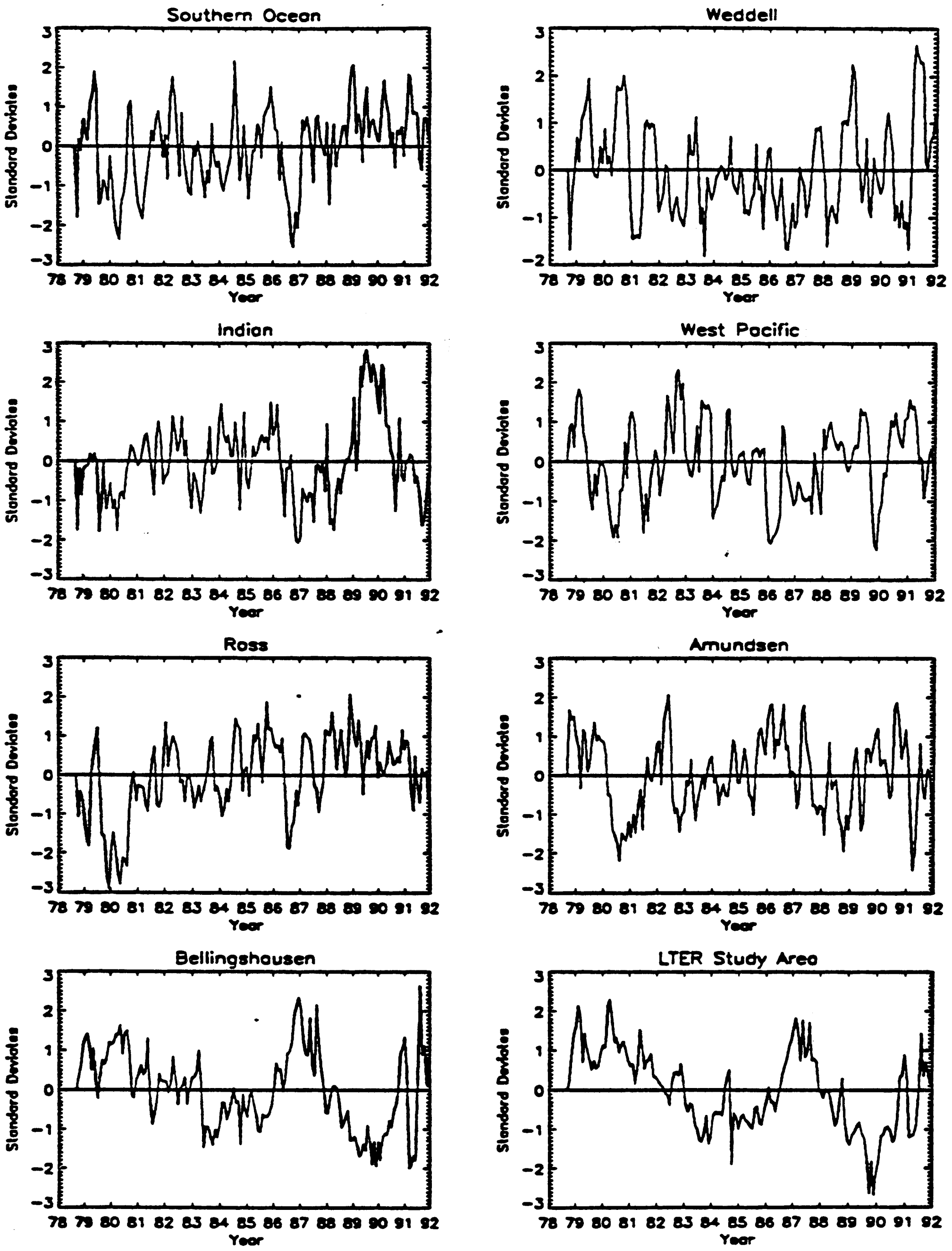


Figure 2. Standard deviates of the monthly anomalies for the Southern Ocean, Weddell, Indian, West Pacific, Ross, Amundsen, Bellingshausen and LTER regions. (Stammerjohn 1993)

of the study region. Our study area is thus well situated to take advantage of "natural experiments" to test our hypotheses on the local and regional implications of the interactions between physical structure (ice cover and currents) and biological populations.

Current views of the antarctic marine food web with plankton-benthos coupling (Clark 1985) and energy flow through the microbial loop (Hewes et al. 1985) are certainly more complex than the simple and linear marine food chain from large phytoplankton cells to antarctic krill to larger predators first proposed (Tranter 1982). Nevertheless, the links in the food web between primary producers, grazers and larger predators (seabirds, seals and whales) are often short and 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 euphausids and fish residing close to the base of the food chain (Ainley et al. 1988; Croxall 1980, Croxall et al. 1988). This specialization and the dominance of a few predators allows us to represent major energy flow and interactions with a few species from each trophic level. For example, Adélie penguins comprise 60 to 70% of the entire antarctic avian biomass (Prevost 1981), and their diets are dominated by krill, i.e. 98% in the summer (Emison 1968; Volkman et al. 1980; Trivelpiece et al. 1987). Croxall et al. (1988) suggest that the apparent close coupling between trophic levels means that long-term studies of these predator-prey relationships and their environment will be critical to understanding variability in Southern Ocean ecosystems and generating a monitoring base for predicting the impact of man-induced perturbations on this ecosystem. The underlying assumption is that these apex predators sum and reflect environmental changes, whether cycles or trends, and are easier to monitor than the environmental changes themselves.

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, and ice algae. The physical barrier formed by pack ice between the atmosphere and 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 bottom water of higher salinity. 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 and summer months (El-Sayed 1971, 1978; Smith and Nelson 1986; Wilson et al. 1986; Smith 1987). Thus variation in the extent of the pack ice is a significant factor in estimating interannual variation in total primary production (Smith and Nelson 1986; Smith et al. 1988; Stammerjohn 1993).

The dynamics of ice-edge blooms are complex (Garrison et al. 1987). Independent studies of the sea-ice column have revealed the presence of a unique microbial community comprised largely of algae and bacteria (Palmisano and Sullivan 1983; Grossi et al. 1984; Garrison et al. 1986; Kottmeier et al. 1987) which may provide both a food supply for higher trophic levels as well as a seed stock for the initiation of ice-edge spring blooms when the sea ice retreats. Algal blooms appear to be restricted to the near surface waters of the marginal ice zone of Antarctica by the strong vertical stratification (El-Sayed 1978; Niebauer and Alexander 1985; Smith and Nelson 1985a, b, 1986; Wilson et al. 1986; Smith 1987). The center of the bloom proceeds southward with the receding ice edge and the seaward edge of the bloom is presumably diluted by deeper mixing processes. As such, the areal extent of any marginal ice-edge bloom is a passive tracer of the spatial balance between stratification processes induced by ice melting and the physical processes which promote vertical mixing (Wilson et al. 1986). This paradigm was supported by a three- season investigation of the ice-edge zone by AMERIEZ (Antarctic Marine Ecosystem Research at the Ice Edge Zone), and, as expected, the frontal zone of enhanced biological productivity exhibited seasonal variability and was highest in the spring (Nelson et al. 1989).

Open-water primary production in the Southern Ocean is thought to be limited by wind-induced turbulence and available light, not macro-nutrients (Hayes et al. 1984; Heywood and Whitaker 1984; Koike et al. 1986; Holm-Hansen et al. 1989; Karl et al. 1992). Although our basic assumption is that nutrients are non-limiting in antarctic waters, there are reports that inorganic nutrients are significantly depleted as ice-edge blooms develop (Smith and Nelson 1986; Perrin et al. 1987). Since nutrients are rapidly but not entirely depleted, the nutrient-status of these blooms is a debatable issue. On average, summer productivity is higher in nearshore coastal regions, in regions of upwelling, and at the ice edge than in the open ocean (El-Sayed 1985; Smith and Nelson 1986; Smith et al. 1988). Although low levels of primary production are detectable in winter (Kottmeier and Sullivan 1987), food availability for herbivores is intensely seasonal and spatially variable.

During the austral spring and summer, nearshore and highly productive blooms are either unialgal in composition or a mixture of phytoplankton species in which the relative dominance of small and large phytoplankton species changes over the season. 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 a (Chl a) biomass, shifting to < 30% in summer when phytoplankton abundance is greatest (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 and larval antarctic krill (*Euphausia superba*) are more efficient at ingesting larger phytoplankton cells than smaller flagellates (Quetin and Ross 1985), and the smaller phytoplankton components are most likely grazed by microzooplankton and invertebrate larvae (Siegfried et al. 1985).

Primary consumers. Unlike most other oceans where much of the primary production is grazed by copepods, antarctic krill, *Euphausia superba*, can be over 50% of the total zooplankton biomass in the epipelagic layer in the Southern Ocean (Hopkins 1985), and thus represent both an important grazer and 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 life-span of 6 to 8 years (Ettershank 1984; Siegel 1987), and 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 of swarms that vary in size from several individuals (Hamner 1984) to the rare "super swarm" over 12 km long (Macaulay et al. 1984). Although circumpolar in distribution, high concentrations of krill are found in only a few locations (Laws 1985), mostly within the area covered by the annual advance and retreat of sea ice - which suggests a close coupling between krill populations, ice dynamics and the associated ice-edge blooms.

Seasonal cycles of growth and reproduction in E. superba are marked and keyed to seasonal cycles of light and food in the environment (Quetin and Ross 1991). If herbivores are food-limited, as appears to be true for antarctic krill (Ross and Quetin 1986; Price et al. 1988; Quetin and Ross 1991), variability in phytoplankton biomass and production will cause variability in reproduction, growth and survival. Survival of the young-of-the-year during the first year is affected primarily by environmental conditions during two critical periods: (1) mid-summer when larvae first molt into the first feeding stage with its point-of-no-return of 10-14 d (Ross and Quetin 1989), and (2) the first winter, with a 6-mo period of low food availability coupled with the inability of larvae to starve for long periods (Ross and Quetin 1991). Although questions remain about the quantitative importance of ice algae, larvae and juveniles do feed on ice algae both winter and spring (Guzman 1983; Kottmeier and Sullivan 1987; Quetin and Ross 1991; Daly and Macaulay 1988; Marschall 1988).

Even though recruitment and reproductive success vary with environmental conditions, for animals with lifespans of more than several years, like krill and penguins, total biomass in an undisturbed population can be assumed to be constant, oscillating about a mean value

(Priddle et al. 1988). 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, the same temporal scale as natural cycles of variation in environmental conditions such as El Nino Southern Oscillations, ENSO's, (Priddle et al. 1988) and interannual variation in ice cover (Zwally et al. 1983a, b).

Pleuragramma antarcticum, the antarctic silverfish, has clupeid characteristics and ecology, and 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 and DeVries 1981;Volkman et al. 1980), including south polar skuas (Ainley et al. 1984; Pietz 1986, 1987). Although time and locations of spawning are not well known, spawning probably occurs during spring in the permanent pack ice zone near coastal waters of the antarctic continent, and larvae hatch in December (Kellermann 1986). Post-larval silverfish in their first year (Age Class 0 - AC0) and juveniles in their second year (AC1) remain in the surface layers of cold shelf water. However, older juveniles and sub-adult fish (AC2+ to AC11+, 6 to 20 cm) are commonly found in the same areas as krill, eating larval krill and other euphausiids (Hubold 1985; Williams 1985). Thus, changes in water mass distributions may alter fish distributions near seabird rookeries.

Larval abundance, growth and year class strength in silverfish appear to be related to the melting of the pack ice, and at least in the southern Weddell Sea are higher in warm years when the ice melts earlier (Hubold 1985, Hubold and Tomo 1989). Year class strength of antarctic silverfish should thus be the inverse of that of antarctic krill.

Secondary consumers. Adélie penguins (Pygoscelis adéliae) and south polar skuas (Catharacta maccormicki) represent the Palmer LTER secondary consumers. Adélie penguins are long-lived (Ainley et al. 1983), highly philopatric birds (Ainley et al. 1983; Trivelpiece et al. in preparation), that migrate annually to their natal rookeries to breed. Adélie penguins remain associated with these rookeries during the entire 4 to 5 month

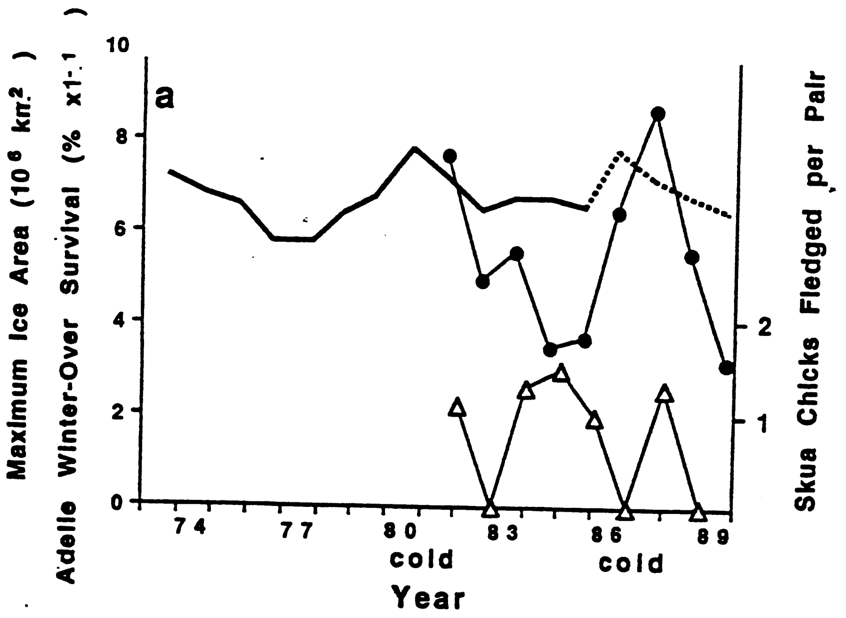


Figure 3a

Observed multiannual patterns in the Antarctic ecosystem. Observed patterns in maximum ice area in the Weddell Sea sector (20°E to 60°W) in September or October (Zwally et al. (1983) and Smith et al. (1988) solid line, personal observations in the waters west of the Antarctic Peninsula dashed line); winter-over survival of adult Adelie penguins (•) and number of chicks fledged per south polar skua pair (△) (Trivelpiece, unpubl data from Admiralty Bay)

pg 3a

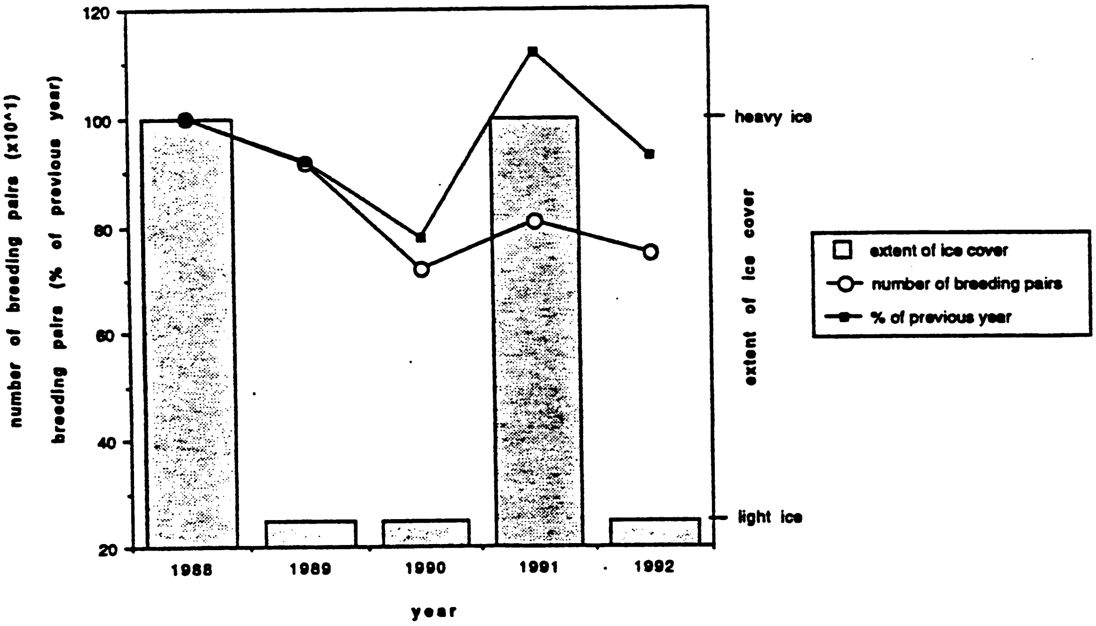


Figure 3b

Observed multi-annual patterns in the vicinity of Palmer Station: extent of ice cover (from personal observation); number of breeding pairs of Adelie Penguins at 21 colonies in the area; number of breeding pairs, expressed as a percentage of previous year's number.

summer reproductive season, October through February. However, they are dependent on pack ice for winter survival (Fraser et al. 1992; Trivelpiece et al. in preparation) and during critical stages in their reproductive cycle (Ainley et al. 1983; Trivelpiece et al. in press). Adélie penguins are shallow-diving, offshore foragers, with a maximum foraging range of about 50 km and depend primarily on krill for food during summer. In some years krill are scarce within the foraging area, which affects aspects of the reproductive biology of Adélie penguins.

Multiannual patterns in the physical environment, the temporal and spatial availability of the micronekton, and the breeding success of the large populations of seabirds dependent on these organisms have been described (El-Sayed 1988; Kellermann and Kock 1988; Rakusa-Suszczewski 1988; Stein 1988; Trivelpiece et al. 1990). For example, the long-term historical data on Adélie penguins collected from 1981 to 1989 at Admiralty Bay at the north end of the South Shetland Islands suggest that winter-over survival was higher (50-87%) during years of heavy ice than during years of light ice (<40%; Fig. 3a). At Palmer Station the number of breeding Adélie penguin pairs at 21 colonies monitored from 1988-1992 increased during summers following heavy ice years (1991) and decreased during summers following light ice years (1989, 1990, 1992; Fig. 3b).

The south polar skua feeds primarily on fish, with antarctic silverfish (primarily 10 to 13 cm long, of AC6+ to 8+) an important part of their diet for reproductive success (Young 1963; Ainley et al. 1984; Pietz 1986, 1987; Hubold and Tomo 1989). Upon arrival of the nesting pair at the rookery from their wintering areas, the male feeds the female with local food resources found 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.

We hypothesize that 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. 3a). Thus high recruitment in silverfish in a warm year will produce

Table 1: Selected results of microheterotrophic substrate uptake, turnover rates and mass fluxes for a variety of Southern Ocean habitats.

Location	Date	Substrate	Kinetic Parameters Tt[1] (d)	Vmax (ng l^{-1} hr^{-1})	Mass Flux[2] (ng l^{-1} hr^{-1})	Reference
Kerguelen Island	Dec	glucose	24	9.2	---[3]	Gillespie
(Sta. #16)	1970	glutamate	16	19	---	et al. (1976)
North of AC[4]	Jan	glutamate	37	35	---	Morita et al.
(Sta. #5)	1972					(1977)
South of AC	Jan	glutamate	33	56	---	Morita et al.
(Sta. #9)	1972					(1977)
Ross Ice Shelf	Jan	glutamate	13	63	---	Morita et al.
(Sta. #16)	1972					(1977)
Beneath the	Dec	glucose	20,800	---	---	Azam et al.
Ross Ice Shelf	1977	uridine	25,000	---	---	(1979)
(Sta. #J-9)		thymidine	6,250	---	---	
		ATP	5,000	---	---	
Scotia Sea	Feb-Mar	leucine	1	---	---	Azam et al.
	1981	glucose	4	---	---	(1981)
McMurdo Sound						
East Sector	Jan	leucine	5	---	---	Hodson et al.
(0-200 m)	1978	glucose	4.8	---	---	(1981)
		ATP	0.2-0.5	---	37-133	
West Sector	Jan	leucine	128	---	---	
(0-200 m)	1978	glucose	833	---	---	
		ATP	1-3	---	1.1-9.63	
Bransfield Strait	Nov-Dec	amino acids	2-83	---	50-600	Bolter and
	1980	glucose	4	---	200-1,000	Dawson (1982)
Drake Passage		glucose	4-20	---	---	Hanson et al.
(0-100 m)						(1983a)
Arthur Harbor	Feb	amino acids	8-58	---	---	Herwig et al.
	1986	glutamate	8-27	---	---	(1986)
Southern Drake	Feb	glutamate	3.5-11	---	13-225	Haberstroh et
Passage (0-200 m)	1987					al. (1987)
Gerlache Strait	Feb	glutamate	3-8	---	8-400	Haberstroh et
(0-200 m)	1987					al. (1987)
Weddell-Scotia Sea						
ice covered	Nov-Dec	amino acids	83	---	---	Sullivan et
waters	1983					al. (1990)
open waters	Nov-Dec	amino acids	13	---	---	
	1983					

[1] Tt = turnover time

[2] calculated from Tt estimate and direct measurement of ambient substrate concentration

[3] "---" indicates no data available

[4] AC = Antarctic Convergence

high prey availability for the south polar skuas eight years later i.e. high abundance of AC8+. 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 and major shifts in water masses (Sahrhage 1988).

In Adélie penguins, parental fitness is primarily a function of winter-over and spring conditions. The physiological condition of birds during spring determines their ability to fast during incubation of the eggs and to forage at sea. South polar skuas, on the other hand, are unable to store large amounts of fat, 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.

Microbial loop. Heterotrophic bacteria and other microorganisms are ubiquitous in the marine environment, regardless of latitude, water depth or distance from continental land masses. Antarctic marine habitats are no exception, and bacteria are an important component of the indigenous microbial assemblage (McLean 1918; Darling and Siple 1941; cf Sieburth 1965, and Bunt 1971). During the past several years, in situ investigations designed to gain a general appreciation for the existence and metabolic activities of the microheterotrophic component of the food web have created a more coherent picture of microbial processes and rates. Substantial regional/temporal variability exists in bacterial biomass, substrate uptake rates, productivity and specific growth rates for microbial assemblages from a variety of habitats within the Southern Ocean (Tables 1 and 2). However, the numbers fall within the ranges measured in temperate and tropical marine ecosystems, indicating that antarctic bacterial assemblages are not unique (Table 2). The extremely wide ranges observed, even within seasons and over short distances, suggest that there may be strong local controls on bacterial rate processes.

The relatively long turnover times of one to several weeks of organic substrates found in a majority of Southern Ocean habitats argue for either slow uptake rates, large ambient

Table 2: Selected results on the abundance, productivity and growth rates for bacterioplankton assemblages in a variety of Southern Ocean habitats.

Location	Date	Cell numbers[1] (ml^{-1})	Biomass (mg C m^{-3})	Production[2] (mg C m^{-3} d^{-1})	u (d^{-1})	Reference
Sodruzhestvo Sea	Dec 1982-Jan 1983	2-8 x 10^5	6-40	0.05-3[3]	---	Samyshev (1986)
Pacific-Indian Ocean Sector	Dec 1983-Feb 1984	~2 x 10^5	---	0.07-0.8	~0.1	Kogure et al. (1986)
Scotia Sea	Feb-Mar 1981	2-5 x 10^5	---	---	0.17-0.35	Azam et al. (1981)
McMurdo Sound	Dec 1978	2-10 x 10^5	---	0.01-1.7	---	Fuhrman and Azam (1980)
Prydz Bay	Mar-Apr 1984	2.1-3.3 x10^5	3.9-5.6	0.1-0.6	0.03	Painting et al. (1985)
Atlantic Sector	Jan-Feb 1981	0.6-6 x 10^5	1.9-19	0.5-2.6[3]	0.02-0.16	Samyshev et al. (1987)
Ross Sea	Nov-Dec 1982	0.02-0.3 x 10^6	0.6-4.7	0.005-0.1	0.002-0.05	Kottmeier et al. (1987)
Drake Passage	Sept-Oct 1980	0.1-0.5 x 10^6	0.8-4.2	2.6-17.1	0.9-2.1	Hanson et al. (1983b)
Bransfield Strait	Sept	---	---	0.1-0.6	---	Kottmeier and Sullivan (1987)
Weddell Sea	Nov-Dec 1983					
	open water	0.06-0.3 x 10^6	0.2-17.3	0.001-9	0.002-1.2	Sullivan et al. (1990)
	ice-edge	0.01-0.2 x 10^6	0.2-5.1	0.002-2.4	0.004-0.9	
	Mar 1986					
	open water	0.01-0.6 x 10^6	0.3-15.2	0.05-6.7	0.04-1.8	Cota et al. (1990)
	ice-edge	0.03-0.4 x 10^6	0.5-8.6	0.002-1.0	0.007-1.1	

[1] cell numbers measured by epifluorescence microscopy

[2] production measured by ^{3}H-Tdr incorporation, unless otherwise noted

[3] measured by dark ^{14}C-CO$_2$ uptake (Romanenko 1964)

pools or both. Without direct estimates of the ambient pools, however, turnover times may be overestimated by the common radiotracer techniques which add 14C or 3H to the ambient pool. Direct measurements of either the total dissolved organic carbon (DOC) or specific constituents range from 0.5 to 12 mg C l-1 (El-Sayed and Taguchi 1981; Dawson et al. 1985; Zdanowski 1985; Bolter and Dawson 1982). However, there appears to be no direct correlation between DOM pools and microheterotrophic activity (Morita et al. 1977; Bolter and Dawson 1982; Bird and Karl 1991), which argues that either we may not be able to distinguish between the total and 'microbiologically available' pools (King and Klug 1982; Karl 1986) or that a temporal uncoupling exists between organic matter production by phototrophs and consumption by heterotrophs.

The relative importance of the 'microbial' loop (heterotrophic bacteria, protozoans, and viruses) and the linear food chain associated with net phytoplankton production and macrozooplankton grazers to biogeochemical cycling and food chain dynamics varies widely within different marine ecosystems. In most systems, microbial loop activity is positively correlated with phytoplankton production and the release of DOM, and is higher under certain environmental conditions (Bird and Kalff 1984; Cole et al. 1988).

However, because the coastal waters of the Southern Ocean are routinely characterized by (1) saturating concentrations of macronutrients, (2) phytoplankton blooms dominated by large-sized diatoms that cannot be consumed by protozoans, (3) secondary production dominated by herbivorous macrozooplanktonic and micronektonic grazers, and (4) bacterial respiration limited by temperature, the microbial loop in the Southern Ocean may play a lesser role in nutrient cycling and secondary production than in other oceans. Low bacterial activity is currently hypothesized to be either substrate or temperature limited in these waters (Karl 1993). The increasing body of knowledge on growth dynamics of bacterioplankton and microzooplankton in antarctic pelagic waters will help in evaluating the role of the microbial loop in the Southern Ocean.

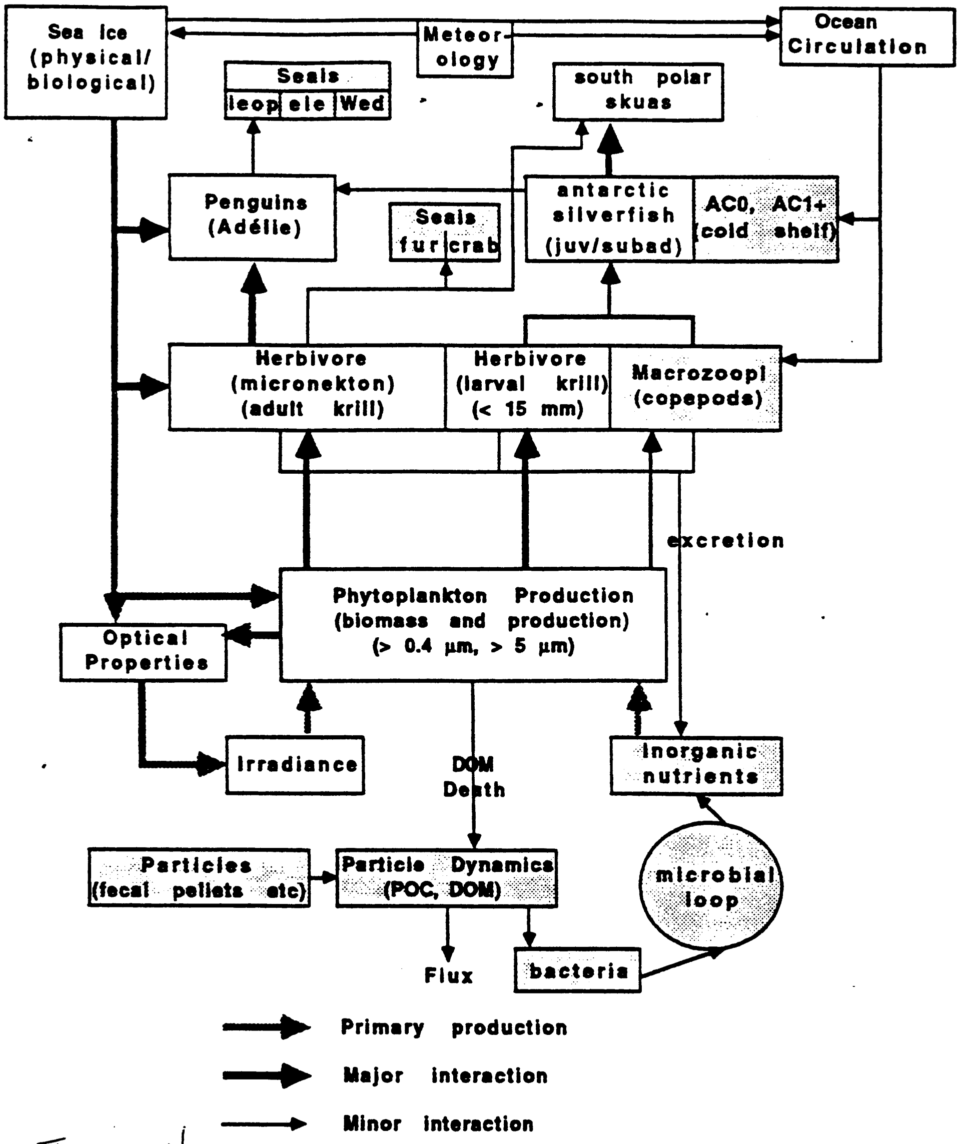


Figure 4

Conceptual diagram of the ecosystem (food web and environmental factors) investigated by the Palmer LTER. Open boxes indicate components with both processes and parameters measured. Shaded boxes indicate components with parameters only measured.

C. Conceptual Model and General Approach

Our central hypothesis states that many significant biological processes in the antarctic marine environment are strongly affected by physical factors, particularly the annual advance and retreat of pack ice and variations in ocean currents. Our conceptual model (Fig. 4) of the interaction between these physical processes and the components of the ecosystem is based on our present knowledge of interannual variability in the extent of pack ice and in the reproductive success of the species that dominate energy flow (Fig. 3). Timing and maximum extent of pack ice (**sea ice**) and the strength of various currents (**oceanic circulation**) are forced to a great extent by large scale atmospheric processes (**meteorology**) (Sahrhage 1988). Since type and abundance of species found in identifiable water masses are different, a decrease or increase in the strength of the current can change the type and abundance of prey in the foraging area of penguins and south polar skuas. Oceanic circulation, meteorology (wind speed, mixing), sea ice and incident radiation, but not nutrients, also affect the timing and 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 predator/prey pair, **antarctic krill and Adélie penguins**, is positively affected by the presence of ice, whereas the other, **antarctic silverfish and south polar skuas**, are negatively affected by pack ice extent in a complex manner. At present bacteria are the most significant members of the **microbial loop** in our conceptual model because bacteria recycle nutrients in the upper layers. Within this conceptual model we also include parameters, such as nutrient concentrations and bacterial numbers, that are of interest but that we do not believe control ecosystem functioning.

General approach

To achieve our objectives we must use data from a long-term program of comprehensive measurements for several spatial/temporal scales. The program includes

Table 3. Research cruises for the Palmer LTER with number of transects. Transects are not necessarily complete, from weather, ice, or time.

Year	Spring	Summer	Fall	Winter
1991-1992	91Nov 2.5 weeks 3 transects			
1992-1993		93Jan 1 Jan - 7 Feb 5 transects	93Mar 25 Mar - 15 May 10 transects	93Aug 23 Aug - 29 Sept 5 transects
1993-1994		94Jan (scheduled) 1 Jan - 7 Feb 3 or 4 transects		

Table

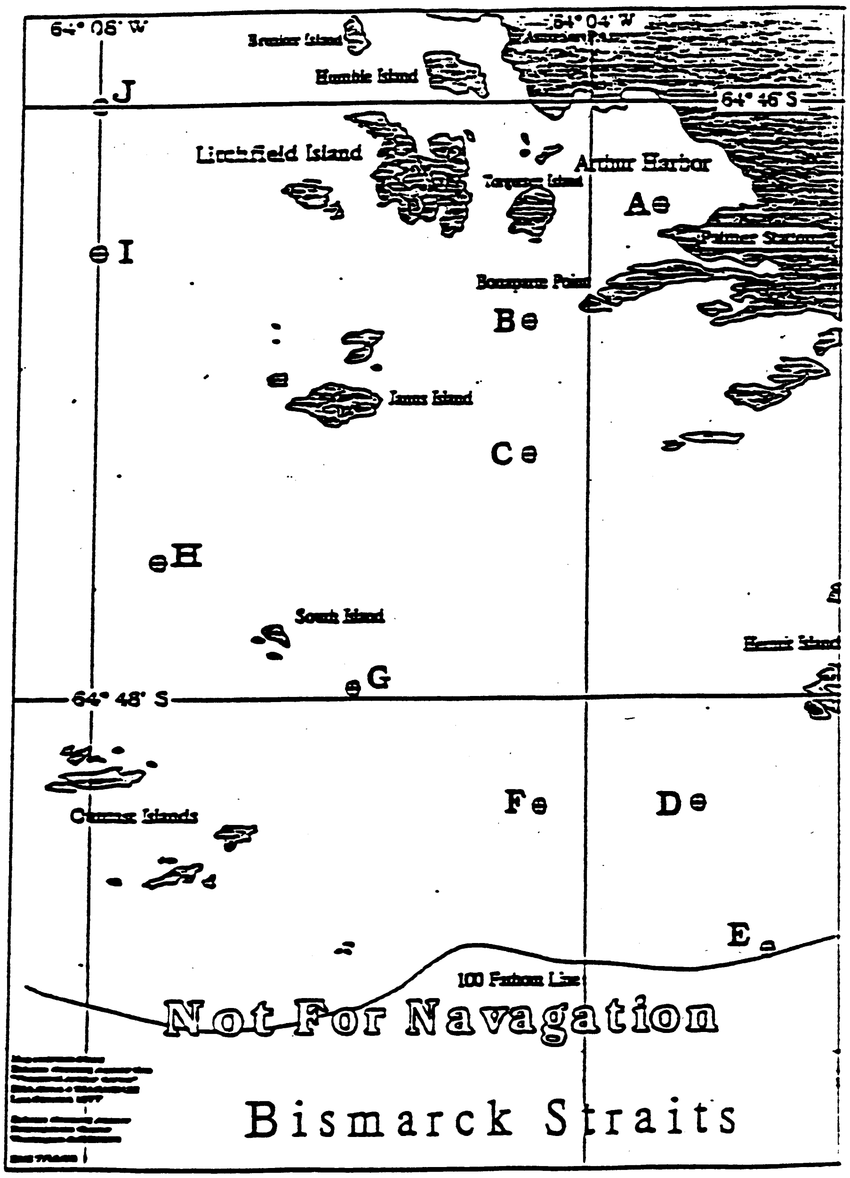


Figure 5

measurements from remote sensing, a field approach that includes an annual monitoring program, a series of process-oriented research cruises (Table 3), and a modeling effort to provide linkages on multiple spatial and temporal scales between biological and environmental components of the ecosystem.

The annual nearshore monitoring program occurs throughout the austral spring and summer (mid-October to mid-March) within the 2 nmi (3 km) boating limit for Palmer Station when small boat operations are possible. Research in the nearshore marine environment surrounding Palmer Station focuses on hydrographic and optical characterisitics of the water column, phytoplankton populations, primary production, the prey of the seabirds, and the seabirds. During this 5-mo period, seabird colonies are monitored regularly and two transects within the Palmer grid (stations A-E and F-J, Fig. 5) are sampled either weekly or biweekly. We monitor processes (reproduction, recruitment) and parameters (food availability) that are sensitive to environmental change and are important in the structure and function of the communities.

Satellite imagery is used to provide important data for several environmental parameters on regional spatial scales and roughly daily temporal scales. These satellite data include information on: meteorology, sea ice, surface and cloud reflectance and incident surface irradiance, aerosol climatology and water vapor, ozone concentrations and corresponding surface UV flux, sea surface temperature and ocean color for the estimation of phytoplankton biomass and production.

The annual nearshore monitoring within the Palmer grid is linked to the mesoscale Peninsula grid during both an annual time-series cruise in mid-summer (January) and less frequent process research cruises. Within the Peninsula grid sampling stations are spaced at 20 km intervals along transects spaced every 100 km along the peninsula (Fig. 6) (Waters and Smith 1992). One of the objectives of both types of cruises is to confirm that monitoring of critical environmental parameters on the scale of the Palmer grid will allow modeling of regional processes. We are particularly interested during the annual cruise to

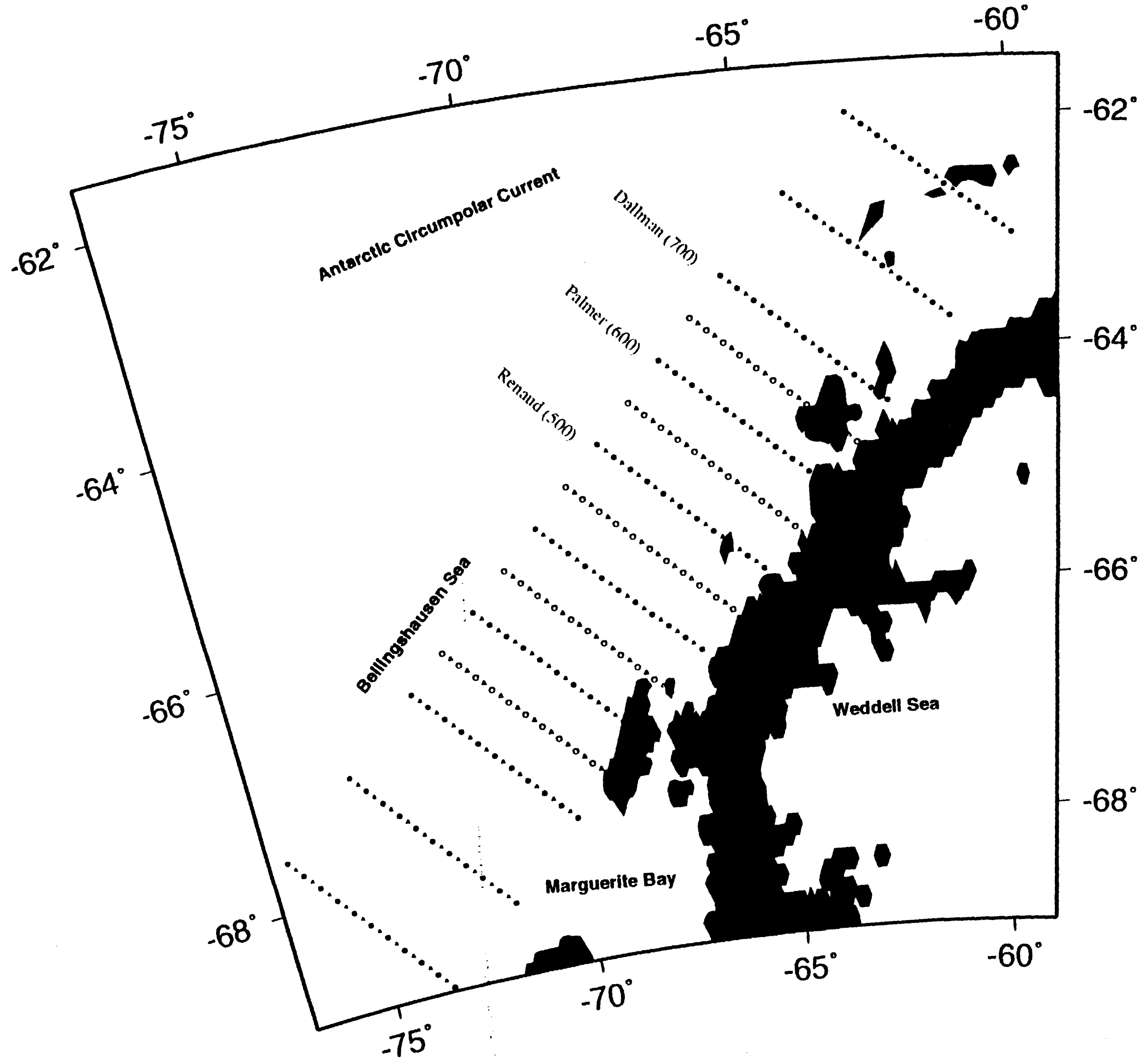


Figure 6. The Palmer LTER grid stations. Primary transect lines have solid symbols, secondary transect lines open symbols. Circles are primary stations spaced 20 km apart. Triangles are located midway between the primary stations.

learn how well our continuous measurements of the nearshore marine environment represent Palmer Basin and the 30 to 160 km foraging area of the seabirds. The cruise also serves as a time-series cruise to assess interannual variation over the middle of the Peninsula grid in zooplankton populations, water column properties, primary production estimates, and hydrographic and optical measurements.

Specific objectives of the process research cruises include mesoscale observations of the distribution and abundance of the two prey species, seabird distribution and ecology, and the density field and surface circulation. The first of two pairs of cruises, in fall and late winter of 1993, represent a year when winter ice formed late (mid-August) and quickly. We plan to schedule a second pair around a winter of early and high ice extent during the next funding cycle of the Palmer LTER.

II. Description of Research

A. Remote sensing and environmental optics (Ray Smith, University of California at Santa Barbara)

Remote Sensing and Environmental Optics Satellite sensors provide a means of obtaining synoptic information on regional and global scales and over long time periods. Multiplatform sampling strategies utilizing contemporaneous buoy, zodiac, research ship, aircraft and satellite sensors are essential to cover the range of space/time scales of physical and biological processes relevant to the Palmer LTER (Smith et al. 1987). Available, or potentially available, satellite data include visible and infrared imagery, passive and active microwave as well as spectrometer data. A key component of the Palmer LTER effort is the development and testing of models linking sea ice dynamics, ocean circulation, primary production, population energetics of krill and population characteristics of avian predators. Satellite data and algorithms are an important element in this modeling effort.

The spatial and temporal variability of Southern Ocean sea ice coverage is a major physical determinant of the ecology of the Palmer LTER. Low resolution (25km) sea ice

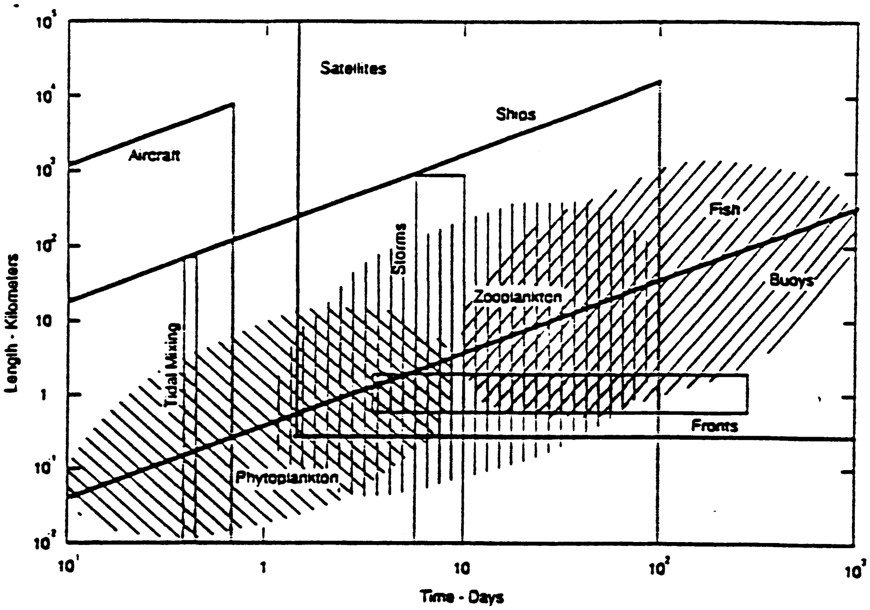


Figure 7. Space/time domain for various oceanic phenomena and limits of coverage for various platforms. Stippled areas indicate space/time scales for selected physical forcings. Hatched areas show the excursion-generation times of some biological components, and the solid lines indicate the space/time coverage for buoys, ships, aircraft, and satellites. Adapted from Steele (1978) and Esaias (1981). (Smith et al, Applied Optics, 1984)

coverage for the whole Southern Ocean is available from passive microwave satellite data since the mid-70's and has been analyzed from the Palmer LTER perspective by Stammerjohn (1993). These data provide more than a decade of consistent information on the extent and timing of sea ice coverage in the LTER area, are expected to be available into the forseeable future, and are valuable for a number of purposes. First, these data provide the "large scale" extent of pack ice. We are currently working to develop objective and quantitative "indices" of sea ice extent, coverage, and duration for the LTER area. Second, these data provide an important input for a model of phytoplankton productivity based upon a receding ice edge (Smith and Nelson 1985; Smith et al. 1988). Stammerjohn (1993) provides an example of such a model for the LTER area. Third, relatively low resolution passive microwave data provide a basis for investigating ice coverage on smaller spatial scales by means of both visible/infrared imagery and active microwave sensors. Our ability to link the large scale LTER grid to the Palmer area (small scale) grid is an important problem and an effort is underway to tie high resolution (1 km) estimates of ice coverage to the large scale, low resolution passive microwave estimates. Our objective is to make this linkage so that we have an objective and quantitative methodology to describe the space/time variability of sea ice on scales from the whole Southern Ocean to Palmer-specific ice indices related to krill distributions and avian predator rookeries.

Weather (temperature, precipitation, calm or storm, clear or cloudy) is a major short term (days) physical forcing factor influencing the ecology of the Palmer LTER. Average or long-term (months to years) weather patterns may be related to sea ice distributions and ocean circulation. Weather is also a pervasive element of all antarctic research logistics. Imagery from visible and infrared (IR) polar-orbiting satellites has been interpreted to provide current conditions and medium range forcast weather analyses which are immediately valuable for logistical planning and longer range for retrospective analyses of weather influences. In particular, these images are a vital tool for monitoring storms or signs of storm development in the Southern Ocean and evaluating their impact. These visible/infrared data are available from the TeraScan system at Palmer (Bob Whritner, Antarctic Research Center/Scripps Institute of Oceanography) and from Bruce Sinkula (Antarctic Meteorology Center, Univ. of Wisconsin). Our intent is to utilize past satellite weather records for the purpose of investigating correlations with sea ice, ocean circulation and other possible relevant LTER variables. When clear, the IR data also can be analyzed to provide areal sea surface temperature (SST) information.

Incident solar radiation at the ocean surface is of fundamental importance to climate, ocean and ice dynamics and the biosphere. A number of research groups (eg. Gautier et al. 1980; Bishop and Rossow 1991) have developed methods for utilizing visible and infrared satellite data for the quantitative estimation of incident solar irradiance. The distribution of clouds and their brightness is an important component of these models, and such data are available from the TeraScan system operated since 1989 at Palmer Station by Bob Whritner. These data are currently being analyzed for the purpose of developing a cloud climatology specifically for the Palmer LTER area. In addition, these data can also be used for the estimation of photosynthetic available radiation (PAR, Frouin et al. 1989), which is a key parameter in various models used for the estimation of phytoplankton production (Platt 1986; Bidigare et al. 1987; Morel and Berthon 1989; Smith et al. 1989; Balch et al. 1989). Bidigare, Prezelin and Smith (1991) provide a review of bio-optical models with specific consideration of past and future ocean color satellite sensors. Sullivan et al. (1993) have provided an estimate of the distribution of phytoplankton blooms in the Southern Ocean using Coastal Zone Color Scanner (CZCS) imagery. It is anticipated that the Palmer TeraScan system will provide near real time access to ocean color imagery after the launch of the SeaWiFS sensor scheduled for July 1994. These data will be utilized to estimate pigment biomass (chlorophyll concentrations) and to drive bio-optical models of phytoplankton productivity. In addition, the irradiance data are available for climate, ocean heat budget and ice thermodynamics modeling.

Optical signals provide the proxy parameters for important biological constitutents in bio-optical models. Our environmental optics sampling strategy is geared toward determining the energy available for photosynthesis and optically characterizing the water for accurate bio-optical modeling. In addition, under NASA funding (to RCS), we are developing SeaWiFS inwater and atmospheric algorithms and providing "optical surface validation" for the Antarctic region. Our in-situ work provides both the small scale observations for local modeling and the data necessary to optimally utilize ocean color satellite imagery.

The antarctic ozone hole and the consequent increase in ultraviolet radiation has been shown to impact natural phytoplankton communities. The Total Ozone Mapping Spectrometer (TOMS, now available from NASA Goddard Space Flight Center from the Russian Meteor satellite) provides global coverage of column ozone concentration. These data, in concert with visible data to estimate solar irradiance, may be used to estimate areal distributions of incident UVB. Our aim is to develop and test a model, using a UVB bio-optical model as input, to estimate the areal impact of the antarctic ozone hole on phytoplankton in the Southern Ocean. Further, the TOMS data permit an important correction to be made in the SeaWiFS atmospheric algorithm. In short, TOMS data available from NASA/GSFC are a very useful component of our modeling.

Marine environments, with plant populations that can double and/or be advected from one location to another in days, have a stronger day-to-day variability than the distributions and production of biomass on land. As a consequence, remote sensing plays an especially important role by filling a critical gap in the space/time sampling domain of marine environments (Smith et al. 1987). Also, logistical difficulties associated with antarctic research argue for the use of satellite sampling. Our objective is to utilize these satellite data to link both across space/time scales and the various component models of the LTER.

B. Microbial processes and carbon flux. (David Karl, University of Hawaii)

Microbial processes. Research during the Antarctic Marine Ecosystem Research at the Ice Edge Zone (AMERIEZ) has helped establish the various temporal and spatial scales on which microbial processes vary. During three research cruises to the marginal ice-edge zone of the Weddell Sea in austral spring, autumn and winter, microbial assemblages seaward of the ice-edge influence, within the ice-melt region and beneath the pack ice were sampled and compared. The enhanced levels of phytoplankton biomass and production at the ice-edge margin, especially in spring, were expressed at both higher trophic levels of the food web (Ainley et al. 1986; Fraser and Ainley 1986) and within various components of the detrital-based microbial loop. Bacterioplankton showed large scale spatial heterogeneity in austral spring (Sullivan et al. 1990). However, bacteria were a relatively small percentage of the available standing stock of particulate matter during the initial period of the spring bloom at the ice-edge margin. During spring positive correlations were observed between time-and-space coupled autotrophic and heterotrophic processes, and bacterioplankton production averaged about 11% of the contemporaneous rate of primary production.

In autumn 1986, the ice-edge was close to its seasonal extreme, and heterotrophic microbial assemblages showed biomass and activity maxima that were generally coherent with those measured for the photoautotrophic assemblage, with higher values in the open water regions of the ice-edge margin (Cota et al. 1990). Minimal values for biomass, productivity and growth rate were recorded under the pack ice or at depth in the water column. In contrast to spring, however, depth-integrated bacterial production often exceeded rates of primary production. Clearly a microheterotrophic succession followed the spring/summer bloom. However, information on the sources of carbon and energy required for this net heterotrophic ecosystem metabolism are not available, so interpretation of these events is uncertain.

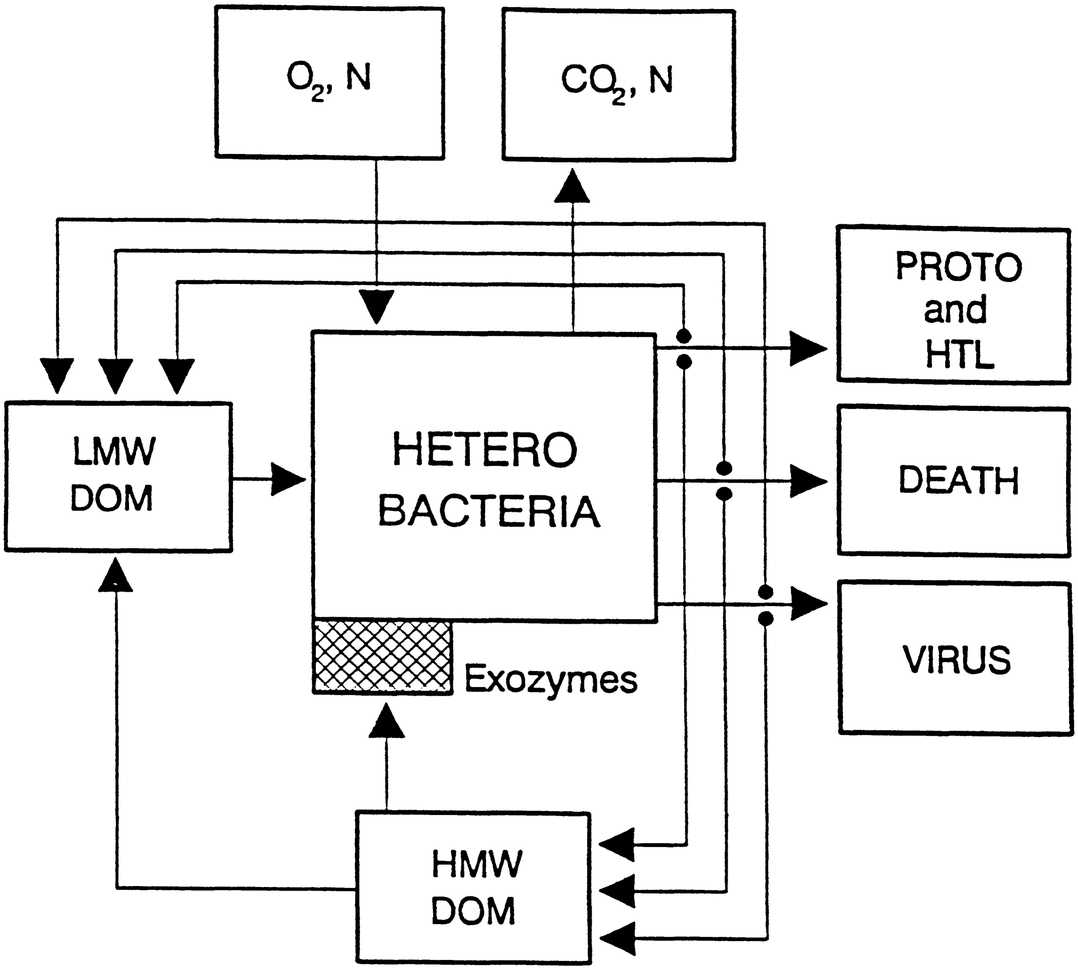


Figure 8. Schematic representation of the role of heterotrophic bacteria (HETERO BACTERIA) in Southern Ocean microbial loop based, in part, on Billen and Fontigny (1987). In this ecosystem model, bacteria rely upon the availability of "utilizable" low and high molecular weight dissolved organic matter (LMW DOM and HMW DOM) for their carbon and energy demands. The molecular composition of these available carbon pools determines the production rate, growth yield and end-product formation. In the absence of available substrate, bacteria exhibit a characteristic starvation-survival response (Morita 1982). HMW DOM, which cannot be used directly, is made available by the action of attached (periplasmic) or cell-free exoenzymatic activities or by chemical hydrolysis (e.g., polysaccharides + H_2O --> monosaccharides). During metabolism, heterotrophic bacteria consume oxygen (O_2) and produce carbon dioxide (CO_2). The stoichiometry of O_2/CO_2 dynamics is again determined by the DOM pool composition. Dissolved nutrients (N), including N, P, S and a variety of trace elements, are also required for balanced growth. Depending upon the molecular composition of the substrates utilized, N may also be regenerated. Bacterial biomass is removed by the combined effects of grazing by protozoans (PROTO) and higher trophic levels (HTL), death and autolysis (DEATH) and viral infection (VIRUS), all of which return some carbon and energy to both the LMW and HMW DOM pools (FROM: Karl 1993).

The current conceptual model for the role of heterotrophic bacteria in the Southern Ocean microbial loop distinguishes between high and low molecular weight organic substrates for microheterotrophic populations, the "HSB" model of Billen and Fontigny (1987) (Fig. 8). This conceptual model as incorporated into an "ecophysiological" model of phytoplankton and bacterioplankton growth (Lancelot et al. 1989) has proven useful for determining microbial rate processes and control mechanisms. One interesting and unexpected result of a study in Prydz Bay based on this model and that focused on several distinct habitats - the open sea, the divergence frontal region, and the marginal ice zone - was the relationship discovered between phytoplankton and bacterioplankton. The phytoplankton and bacterioplankton biomasses were not positively correlated, contrary to what is often observed (Bird and Kalff 1984; Cole et al. 1988). Billen and Becquevort (1991) hypothesized that these results could be due to a lagged response in the growth of bacterioplankton following the spring phytoplankton bloom caused by the composition of the dissolved organic matter (DOM) pools, and not to a differential temperature inhibition as suggested by Pomeroy and Deibel (1986). There are several alternative hypotheses that may be formulated to explain these results:

H1: The decoupling of the phytoplankton and bacterioplankton biomasses is due to the composition of the DOM pools. During the initiation of the bloom, predominantly high molecular weight DOM is produced by the phytoplankton requiring hydrolysis by exozymes (extracellular enzymes) before the carbon and energy is available for bacterial growth. This effect would cause about a 1 mo temporal separation between the phytoplankton and bacterial biomass and activity peaks.

H2: The decoupling of the phytoplankton and bacterioplankton biomasses is due to delayed production of extracellular carbon by the phytoplankton population and temporally coupled utilization by microheterotrophs.

H3: The decoupling of the phytoplankton and bacterioplankton biomasses is due to delayed growth of micro- and macrozooplankton populations, relative to the

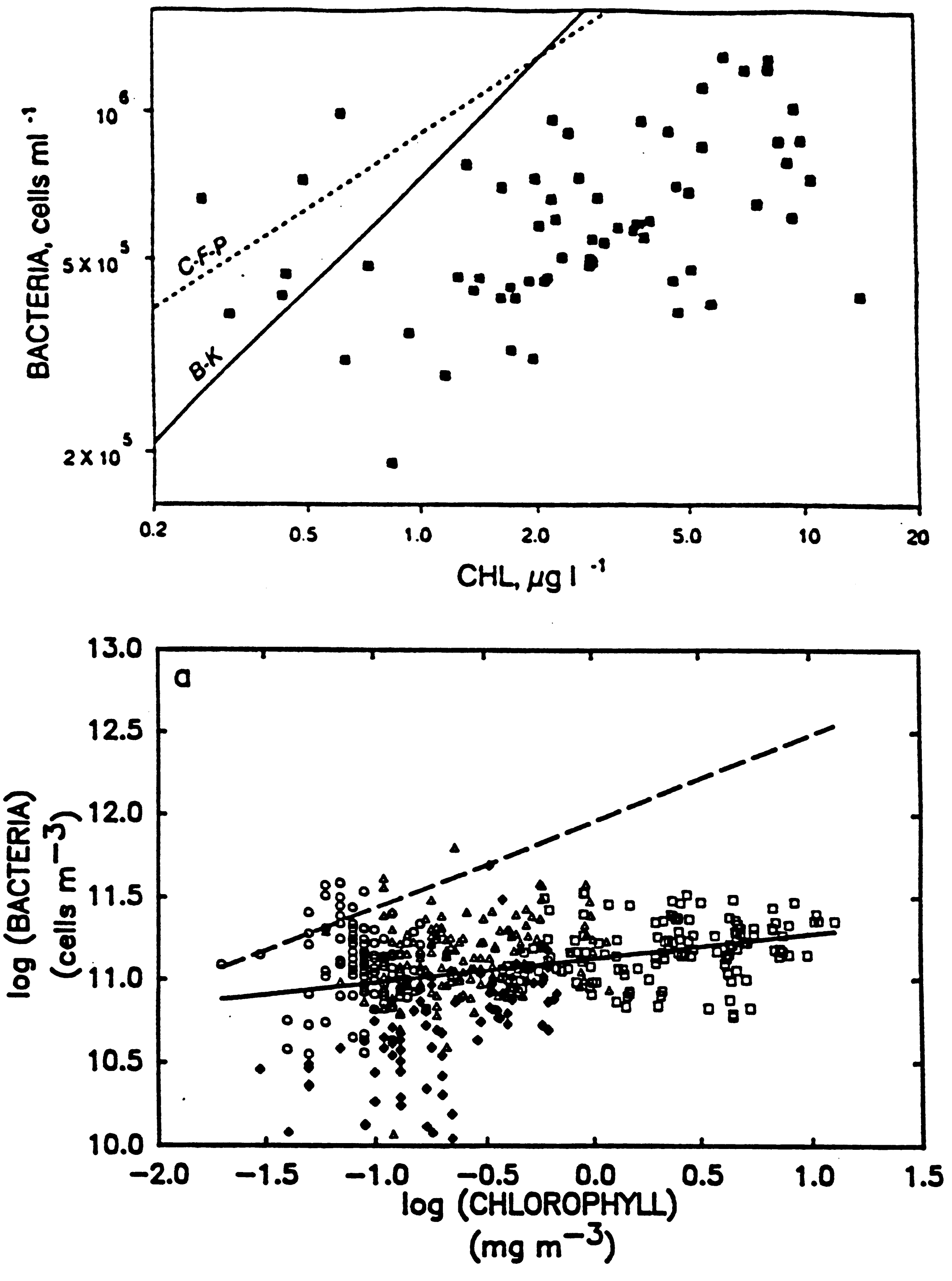


Figure 9: Relationships between bacterial cell numbers and chl *a* concentrations for two antarctic data sets. *Top* (FROM: Karl et al. 1991a): RACER program (1986-87) Drake Passage, Bransfield Strait and Gerlache Strait regions. The two lines indicate predictions based on the empirical relationships for a variety of previously studied aquatic environments and summarized in Bird and Kalff (1984; solid line) and Cole et al. (1988; dotted line). *Bottom* (FROM: Cota et al. 1990): $\log_{10}$ transformed data on bacterial cells versus chl *a* concentrations from the AMERIEZ ice edge program showing the regression line of best fit (solid) versus the predicted empirical relationship of Cole et al. (dashed).

initiation of the spring bloom, followed by a period of intense feeding and a rapid response of microheterotrophs to the organic substrates generated during the grazing processes.

The surprising results of Billen and colleagues have clearly focused attention on several important parameters of carbon and energy flow through plankton assemblages, namely: the importance of direct and indirect production of dissolved organic matter by phytoplankton populations, the importance of characterizing the molecular composition of the total dissolved organic carbon (DOC) pool and the importance of temporal lags and successional stages in Southern Ocean ecosystems.

Similar comparisons between bacterial cell numbers and chlorophyll (chl) a concentrations for the AMERIEZ, in the Weddell Sea, and RACER programs, west of the Antarctic Peninsula in the north of Anvers Island but in the northern part of the Palmer LTER Peninsula grid, also revealed empirical relationships (Fig. 9) that were different from previous analyses of similar data from a variety of marine and freshwater ecosystems (Cota et al. 1990; Karl et al. 1991a). The RACER database showed a deficiency in bacterial cells at chl a concentrations >2.5 µg Chl a l-1 of up to an order of magnitude (Fig. 9). At the present time we do not know whether this is a fundamental difference between non-polar and polar habitats, or whether the eutrophic coastal regions of the Antarctic Peninsula are unique in this regard.

As part of the Palmer LTER microbial loop research, we are investigating standing stocks, production rates and possible control mechanisms. Standing stock estimates are derived from a combination of lipopolysaccharide (LPS) concentrations, bacterial enumeration by dual-laser flow cytometry, and closure calculations of microbial biomass from particulate organic carbon (POC), ATP, Chl a, and LPS measurements using inverse modelling techniques. Production rate investigations include determination of dissolved organic carbon (DOC), estimates of microheterotrophic activity from amino acid (leucine) incorporation, exoenzyme activities (beta-glucosidase and leucine aminopeptidase), the stoichiometry of oxygen/carbon dioxide dynamics, bacterial starvation assays, and the effects of temperature on growth processes. In addition, experiments on the effects of addition of organic substrates on bacterial growth will help elucidate whether the observed bacterial/algal decoupling is due to resource limitation. Bacterial biomass is removed by the combined effects of grazing by protozoans and higher trophic levels, death and autolysis, and viral infection.

Carbon flux and the Southern Ocean biological pump. The oceans act as a regulator of atmospheric carbon dioxide (CO2) and thus occupy a central role in the debate over the effects of increasing levels of greenhouse gases. Both physical and biological processes control the rate of removal of atmospheric CO2. First, the exchange can be rapid, and is influenced by ocean circulation and oceanic biological activity (Sarmiento and Toggweiler 1984; Siegenthaler and Wenk 1984; Karl et al. 1991b). Second, biological processes in the surface ocean produce particulate carbon that sinks into the deep ocean where it is either remineralized en route to the seabed or buried in deep-sea sediments (Brewer 1983). Consequently, the ocean's interior is continuously enriched with a variety of bioelements (e.g., C, N, P, Si) resulting from surface ocean production, particulte matter flux and dissolution/remineralization - a series of processes that has been termed the "biological pump" (Moore and Bolin 1987). Variation in the rate and efficiency of the biological pump is thought to be controlled by inorganic nutrient inputs from outside the euphotic zone.

Recent box models of the ocean-atmosphere system have demonstrated the potential importance of the Southern ocean in the regulation of atmospheric CO2 (Ennever and McElroy 1985), so the rate and efficiency of the biological pump in the Southern Ocean is a topic of great importance in the study of oceanic carbon cycles. However, the factors controlling the biological pump in polar environments appear to be different from those in other oceanic regions, and the biological pump in polar regions appears to be functioning at less than full capacity (Knox and McElroy 1984). Most of the Southern Ocean is characterized by high surface nutrient concentrations, but low rates of primary production

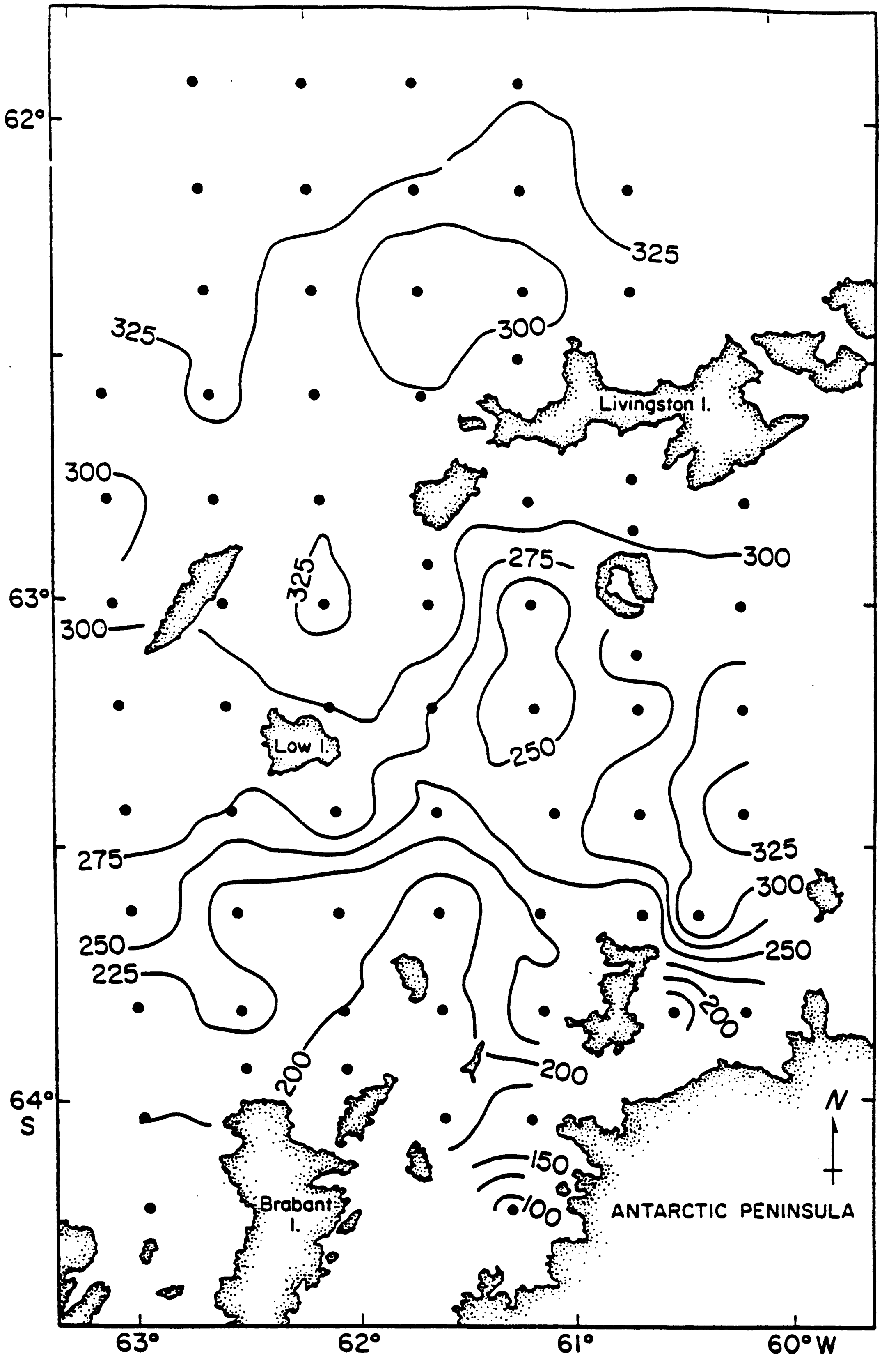


Figure 10: Regional distribution of pCO_2 in the Research on Antarctic Coastal Ecosystem Rates (RACER) study area which includes the southern portion of Drake Passage, central Bransfield Strait and the northern portion of Gerlache Strait. The offshore-to-onshore decrease of pCO_2 coincided with the occurrence of a large bloom of phytoplankton (FROM: Karl et al. 1991b).

and export production (Holm-Hansen et al. 1977; Honjo 1990). If all the surface nutrients in the Southern Ocean were used by the phytoplankton, the biological pump activity could transfer significant amounts of atmospheric CO2 to the ocean's interior. Instead it appears as if the excess inorganic nutrients are ultimately removed during the formation of Antarctic Deep and Antarctic Intermediate water masses. A resolution of this Southern ocean biological pump enigma is a topic of great importance in the study of oceanic carbon cycles.

Some recent studies are relevant to the activity of the biological pump in the Southern Ocean. Studies of pCO2 fluctuations during the spring bloom of antarctic coastal ecosystems during RACER in a region in the northern part of the LTER Peninsula grid revealed a substantial decrease in the surface water pCO2 (surface water concentrations <100 μatm compared to atmospheric concentrations of about 325 μatm) (Fig. 10). The air-to-sea flux of carbon during the height of the spring bloom was estimated to be about 10 mmol C m-2 d-1 (Karl et al. 1991b). The large pCO2 gradients during the spring bloom may be enhanced by a large flux of carbon to the atmosphere by air-breathing birds and mammals, the dominant predators in the spring bloom food web of antarctic coastal waters. This flux has been described as a 'leak' in the biological carbon pump for the Southern Ocean (Huntley et al. 1991), and because the oxygen used by the predators is derived from the atmosphere rather than from the ocean, this leak should result in an uncoupling of the anticipated dissolved seawater O2:CO2 relationships and may also affect quantitative C:N and C:P stoichiometries (Sambrotto et al. 1993).

Another important component of the biological pump, the export of particulate organic matter from the surface waters, also referred to as "export production", can be measured with sediment traps positioned near the base of the euphotic zone (Eppley 1989). Particle flux measurements in antarctic coastal waters and at the ice-edge boundary have revealed a tremendous seasonality and interannual variability (Fig. 4), which is likely related to variations in the ice-edge blooms.

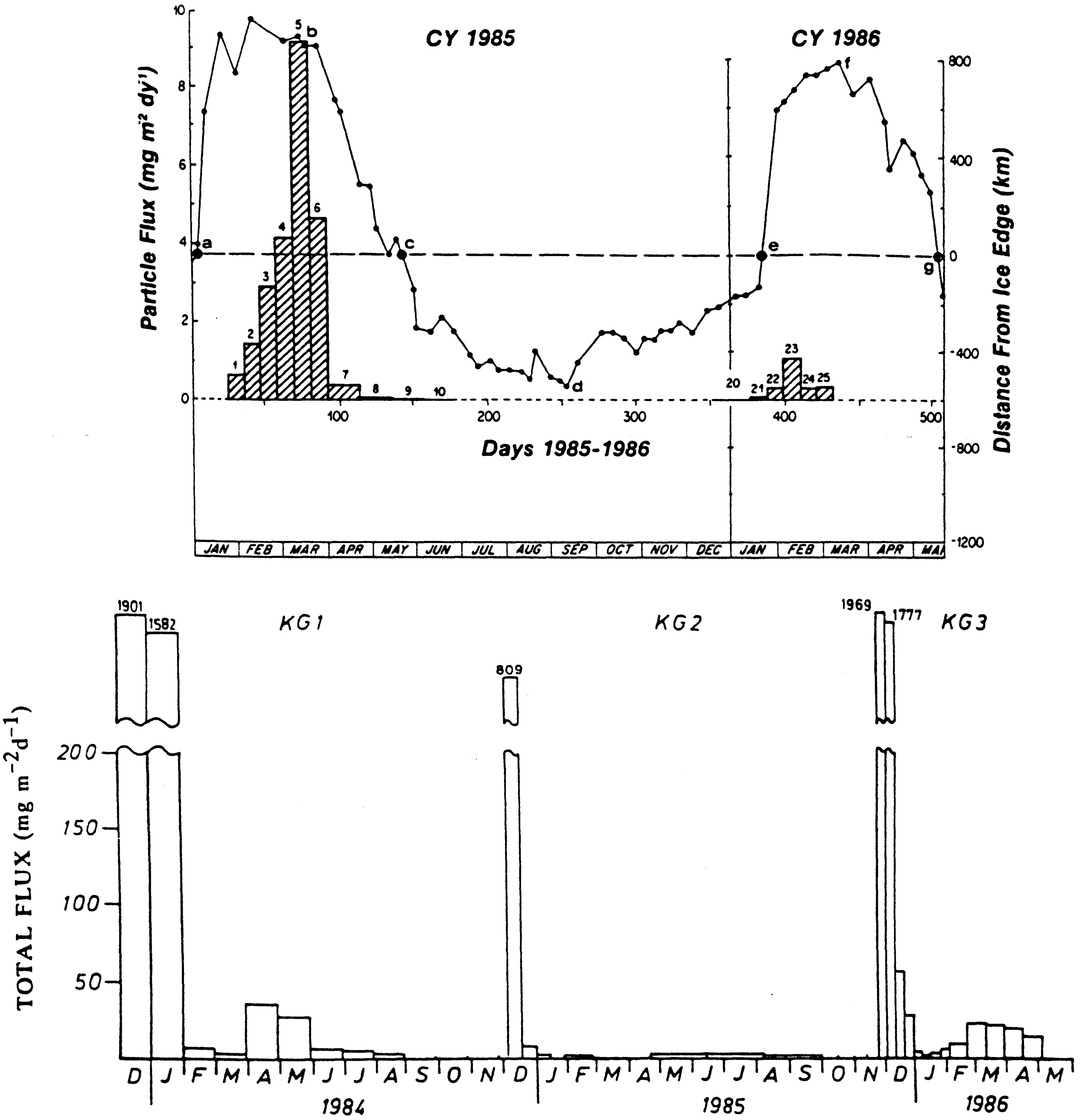


Figure 11. Seasonal variability in the downward flux of particulate matter at two antarctic time-series stations. *Top*: Total flux for each period (bar graph, shadowed) at the north-central Weddell Sea station during 1985 and 1986. Superimposed is the closest distance from the approximate ice edge to the sediment trap site 3 weeks before, during, and after the experiment, based on weekly Antarctic Ice Charts (NPOC) compiled from the NOAA polar orbiter, NASA Nimbus-7 Scanning Multichannel Microwave Radiometer (SMMR), GEOSAT altimeter, and visual data using NOPC ice coverage scales. (a) Ice-edge passage over the trap site during the 1985 regression. (b) The maximum opening of ice lasted about 60 days. The ice edge rapidly moved northward after early April 1985. (c) Ice edge passage over the trap site during the 1985 transgression. (d) 1985 maximum ice extension. The ice edge was 550 km north of the trap site. (e) Ice edge passage over the trap site during the 1986 regression. (f) Maximum ice opening during 1986. (g) Ice edge passage over the trap site during the 1986 transgression (FROM: Fischer et al. 1988 and Honjo 1990). *Bottom*: 30-month record of particle flux from the Bransfield Strait showing the intense annual and interannual variability observed in this region (FROM: Wefer 1989).

Fig 11

On Palmer LTER research cruises several measurements relevant to carbon flux and questions concerning the biological pump in the Southern Ocean are measured. Gases (oxygen, total dissolved inorganic carbon and alkalinity) are measured at the same stations as all other parameters for estimates of air-to-sea carbon flux. In addition three sediment traps have been moored in Palmer Basin about a points two/thirds of the way seaward of the bottom of the 600.* transect and at a points the retreating ice edge should pass in the spring after winters of high ice cover. These traps were first deployed in November of 1992, and recovered in April 1993 after the end of the 1992-1993 season's high production. The three traps were redeployed in April 1993 and will be retrieved and redeployed during the January 1994 LTER cruise. The cups on the sediment traps are programmed to rotate at periods varying from 4 days during the anticipated periods of high production to up to 4 weeks during the winter when production and thus "export production" is expected to be low.

C. Phytoplankton Productivity and Community Dynamics (Barbara Prézelin, University of California at Santa Barbara)

Given the evidence that led to the central LTER hypothesis that interannual variation in the extent of the pack ice is a major determinant of interannual variation in primary production (sect. IB), three general working hypotheses were proposed which provided the initial framework for developing a preliminary field strategy of data collection and hypothesis testing.

H1: Neritic phytoplankton dynamics reflect spatial/temporal changes in the distribution and nature of frontal boundaries between antarctic oceanic water masses and 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 and ice edge blooms and sea ice algae. Total primary production may therefore vary with the extent of the pack ice during the previous winter and spring as the spatial and temporal extent of the ice-edge phytoplankton blooms should be greater in years with greater ice pack coverage.

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

Background and Initial Conceptual Approach. This primary productivity research team had little or no prior Antarctic research experience at the time the Palmer LTER proposal was written. Solicitation for our participation was based largely upon our prior laboratory and field studies of potential mechanisms controlling the photoadaptive physiology and rates of primary productivity of in situ phytoplankton communities in diverse and highly variable waters of temperate and subtropical oceans (Prézelin et al. 1987, 1991; Smith et al. 1987, 1989; Prézelin and Glover 1991; Bidigare et al. 1992; Prézelin 1992). These regulation studies combined intensive field monitoring and experimental studies to define and/or model the mechanisms underlying the time/space variability in phytoplankton distribution, community structure, photosynthetic physiology and rates of whole cell carbon fixation. Results emphasized the light-dependent and, to a lesser extent, the nutrient-dependent and cell cycle-dependent nature of phytoplankton productivity. Studies (*Fronts '85*, *Watercolors '88*) done in collaboration with Ray Smith (UCSB) and Bob Bidigare (University of Hawaii) led to a bio-optical model of primary productivity that accurately predicted directly measured instantaneous, daily, and daily integrated rates of carbon fixation in diverse coastal waters (Prézelin et al. 1987; Smith et al. 1987, 1989; Bidigare et al. 1992). We proposed that a similar combination of bio-optical monitoring, experimental, and modeling approaches could be applied to a mechanistic study of primary productivity in the Southern Ocean, with the caveat that there were unusual properties of antarctic phytoplankton ecosystems that would have to be considered.

First, Tilzer and co-workers (1985) had shown that the photosynthetic capacity (P_{max}) and maximum quantum efficiency of photosynthesis were much lower in natural antarctic phytoplankton compared to nonpolar phytoplankton (Jacques 1983; Hoepffner 1984;

S-016 (Prézelin) DATA COVERAGE

database id	# of PI curves	hplc	NO3	NO2	NH3	PO4	Si	chn
91nov	**250**	**422**	**324**	**269**	**287**	**324**		*239*
9192pal	**640**	**953**	**404**	omit	lost	**404**	**404**	*741*
93jan	**158**	**832**	**858**	omit	**800**	**853**	**852**	MSI
93mar	**215**	**893**	**DK**	omit	??	**DK**	**DK**	MSI
9293pal	**491**	**623**	**268**	omit	**268**	**268**	**268**	MSI
93aug	**160**	**369**	MSI	omit	MSI	MSI	MSI	MSI
total	1914	4092						

Table 4. Boldface items have been uploaded and are largely in their final format. **DK**, represents measurements made by Dave Karl's group during those particular cruises. *Italicized items*, were measured on the LTER grids but analyses of samples was provided by non-LTER funding sources within Dr. Prezelin's lab. MSI, indicate data bases that are either being presently analyzed in the Marine Science Institute analytical lab at UCSB or where databases are not yet ready for uploading into the LTER database within CRSEO.

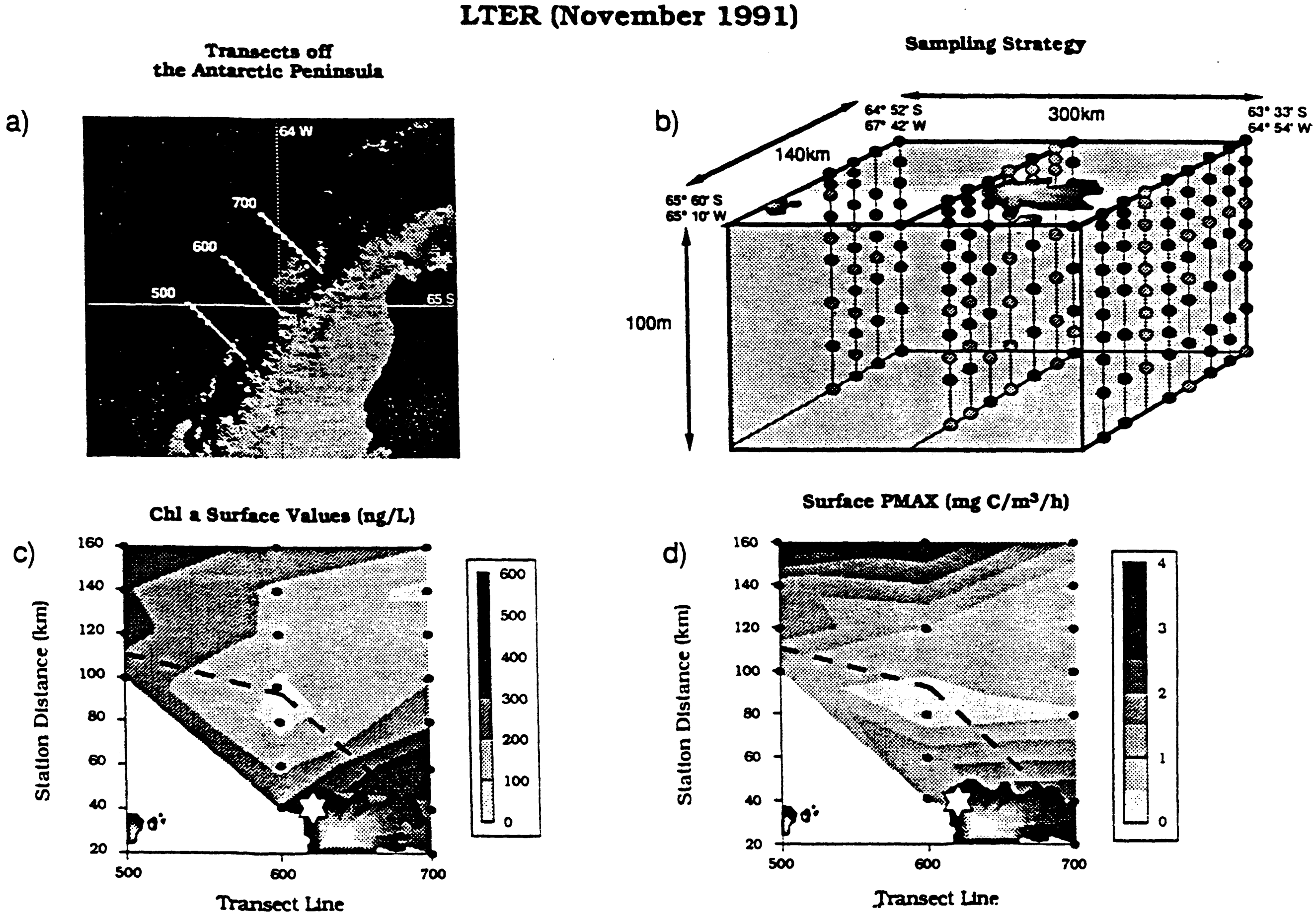


Figure 12 LTER grid, November 1991 (*A*) location of three transects west of the Palmer Peninsula; (*B*) vertical distribution of chemical (all *circles*; includes pigmentation and inorganic nutrients) and productivity (*black circles* only) discrete samples collected with the BOPS II (Smith et al. 1992); (*C* and *D*) surface contour plot of distribution of volumetric chlorophyll *a* and P_{max}, respectively, with station locations (shown as *black circles*), the edge of the MIZ (*dashed line*) and the location of Palmer Station (*star*).

Wilson et al. 1986). They suggested that inefficient low-light photosynthesis was due to temperature-controlled processes, i. e. possible alterations in the fluidity of photosynthetic membranes which in turn disrupted the functional arrangement of photosynthetic components. Thus photochemistry could become temperature rather than light-limited. Such observations left us wondering how generalized temperature hypersensitivity might be in antarctic phytoplankton communities and to what degree small and/or sudden temperature changes (ie. associated with the freezing and thawing of sea ice) might induce large changes in primary productivity. It seemed important to test assumptions about temperature-independent and purely bio-optical regulation of quantum yield which would affect the abilities of a bio-optical model to predict accurately in situ rates of carbon fixation over a range of time and space scales. Preliminary Q10 experiments in the first year indicated photosynthesis-irradiance (PI) relationships were hypersensitive to small changes in environmental temperature; however, the patterns were inconsistent for samples collected at different times and places. Reality was that such experimental studies could not be supported past the first field season as limited resources were refocused on maintaining a redefined core data base of inorganic nutrient, cell composition and production measurements (Table 4, Fig. 12).

Second, Antarctic literature suggested some groups of polar phytoplankton might be capable of relatively high rates of light-independent carbon fixation via *b*-carboxylation reactions which could supplement photosynthetic carbon fixation by as much as 30% (Mortrain-Bertrand 1988). Should *b*-carboxylation occur, it might contribute to an overwintering strategy for antarctic phytoplankton and, if undetected, would lead to overestimates of the apparent quantum efficiency of photosynthesis and to an underestimate of the rates of primary production predicted solely on the basis of a bio-optical model. Hundreds of spring and summertime determinations, based upon measurements of carbon fixation in the light in the presence of a photosynthetic inhibitor DCMU, indicated *b*-carboxylation rarely exceeded 5-10% of the total carbon fixed in the absence of a

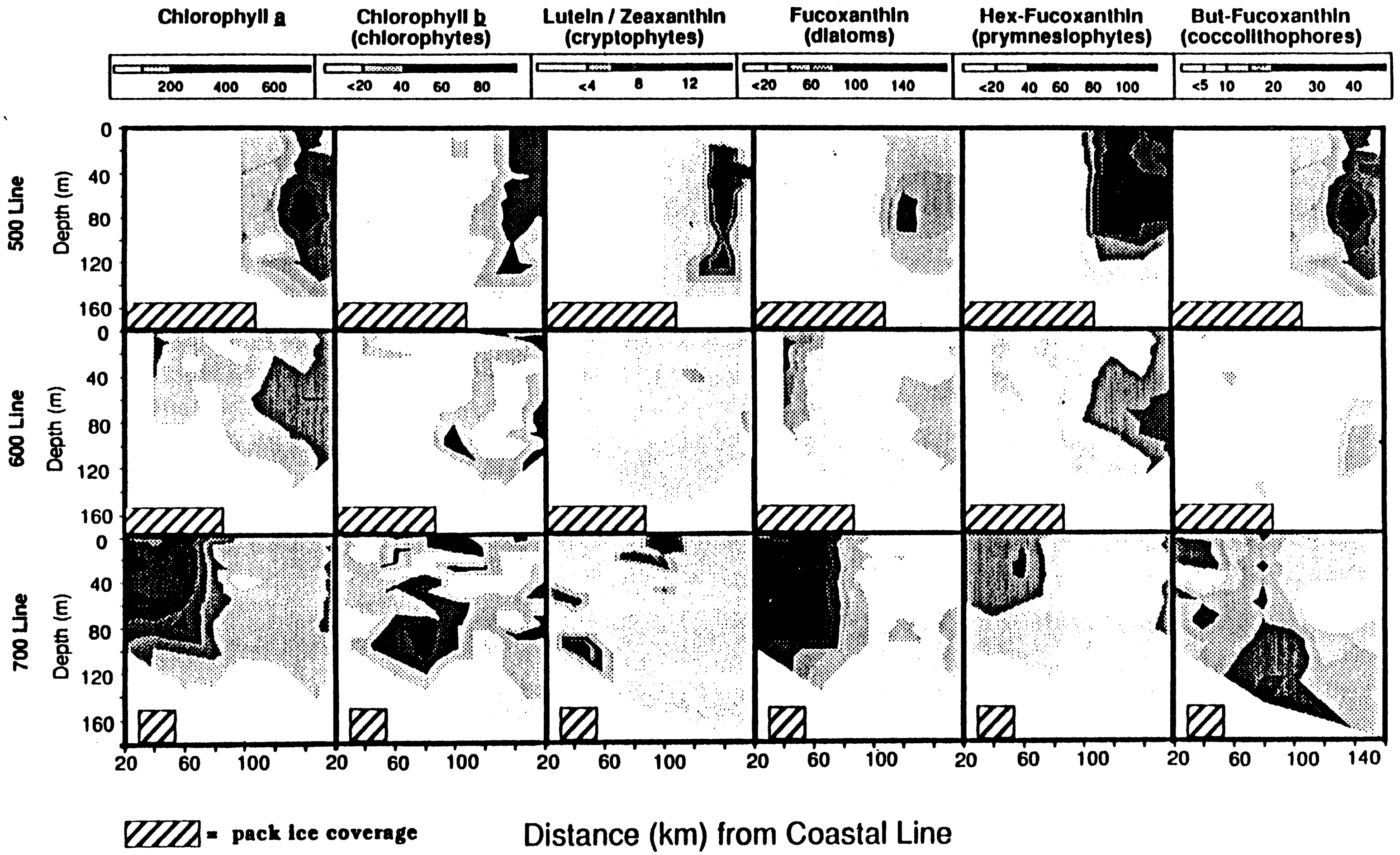


Figure 13. HPLC pigment distributions along the 500, 600, and 700 LTER gridlines during November 1991. Concentrations are expressed in ng/L. Using pigments as chemotaxonomic markers to identify various phytoplankon groups (in parentheses), data collected from during this cruise illustrates the mesoscale variations in community sturcture within the sampling grid. For example, on the 500 line, prymnesiophytes (hex-fucoxanthin) such as *Phaeocystis* spp. dominated the mixed phytoplankton communities 20km beyond the marginal ice zone (MIZ) while diatoms (fucoxanthin) and other groups were sparce. In contrast, the inshore shallow waters of Dallmann Bay (700 line) showed diatoms to be the major contributor to the high biomass (Chlorophyll a) giving way to other groups (chlorophytes, coccolithophores and prymnesiophytes) in deeper offshore waters.

photosynthetic inhibitor. Several measurements were made in a separate study (*Icecolors '90*) which indicated that spring time communities along the MIZ excreted little if any of the organic carbon formed by photosynthesis (Prézelin, unpubl. observation). The phytoplankton appeared to be surviving and growing largely as obligate photoautotrophs.

Third, it is widely recognized that significant and often repeatable variations in phytoplankton biology are often induced and commonly observed on time scales less than a day, i.e. diel or diurnal periodicities (Prézelin 1992). Given that diurnal patterns vary significantly with taxonmic group, cell cycles, physiological state, environmental time keepers (i.e. photoperiod, temperature), and the rate of change of many enviromental variables (ie. irradiance, ammonia or nitrate pulses), it is of considerable importance to assess and define linkages between the daily variability in phytoplankton growth and productivity and their possible driving forces. A number of studies have shown that attempts to predict in situ rates of primary productivity would err significantly if the daytime variations in photosynthesis were not taken into account (Fee 1975; Harding et al. 1982; Brown and Field 1985; Prézelin et al. 1987a and 1989b; Smith et al. 1987, 1989; Prézelin and Glover 1991; Prézelin 1992) and attempts were made to include this variability. For instance, the pattern of daytime periodicity may change dramatically with rapid changes in photoperiod, with one study (Rivkin and Putt 1987) suggesting the timing of peak P_{max} for antarctic phytoplankton shifts from ca local noon to ca local midnight as the natural photoperiod lengthened from a few hours to continuous illumination. While the resulting impact on sampling strategies and productivity estimates is obvious, the universality of such seasonally-dependent changes in production patterns is unknown. We made a concerted effort to get some preliminary indication of the magnitude and seasonal variation in photosynthetic periodicity in the first field season. To date, time and personnel constraints have precluded detailed analyses of this portion of the database. Also, limited resources and shifting priorities have reduced the number of diurnal measurements significantly. At present diurnal measurements are made sparsely through the season and

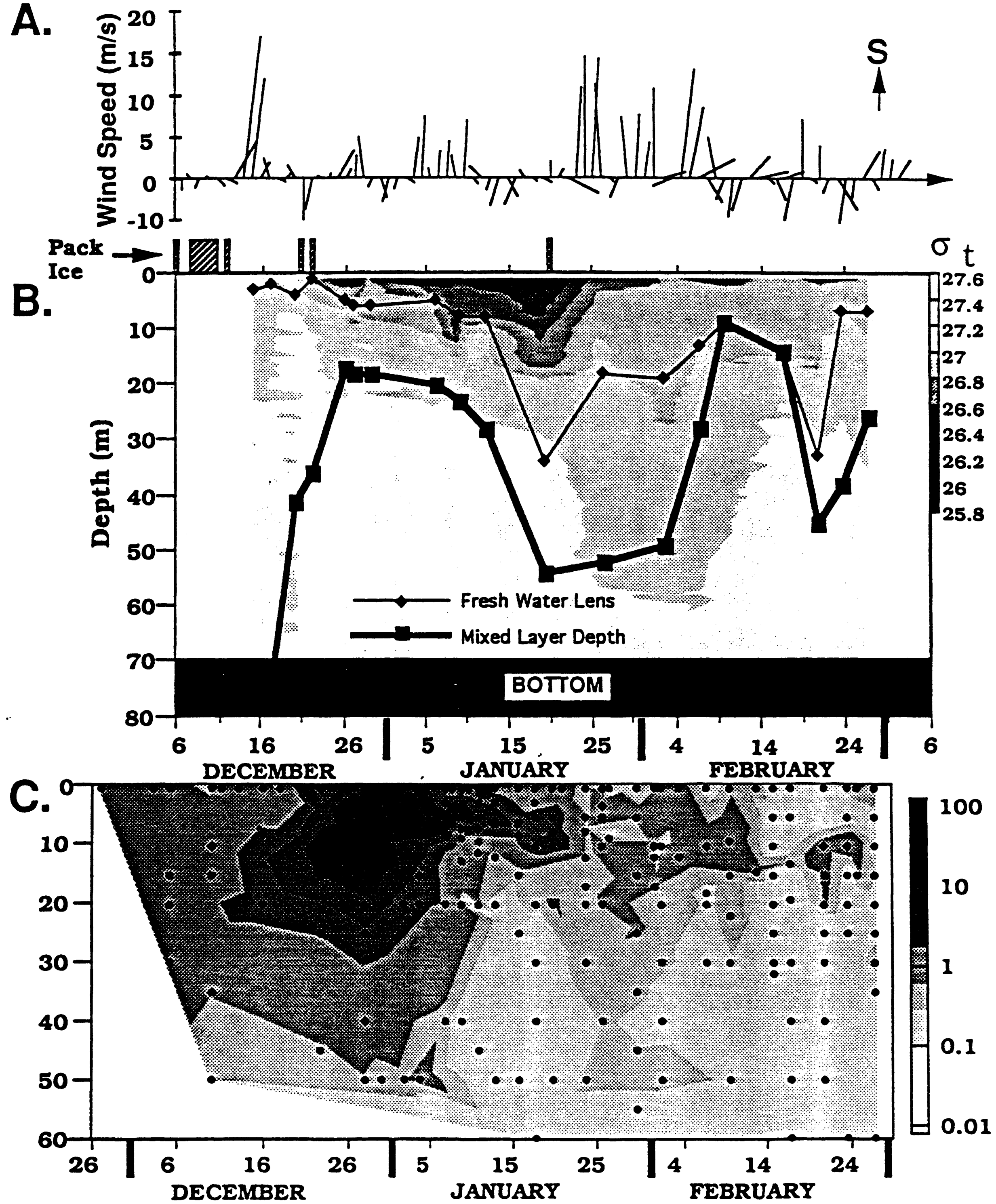


Figure 14. A) Average daily wind speed at Palmer Station from December 6, 1991 to March 3, 1992. Vectors are the direction of the wind. B) Calculated upper mixed layer superimposed on contour plot of sigma-t from Station B over the same time period. Presence of pack ice also included. C) Contour plot of the log distribution of Chlorophyll a from Station B with depth. Concentrations in µg/L. Sampling points illustrated by filled squares.

will be used only to time-correct productivity measurements made at different times of day (Prézelin et al. 1987; Smith et al. 1987). In the context of the longer term goals of the LTER, which will focus on interannual comparisons of seasonal patterns of primary productivity, a complete understanding of the seasonal regulation of patterns of daytime periodicity in primary production will be required eventually in order to assure the predictive accuracy of bio-optically modeled datasets which rely on satellite (i.e. SeaWifs) measurements made at a fixed time of day over a season.

Lastly, the potentially harmful effects of ultraviolet radiation on primary productivity needs extra consideration in the Southern Ocean where the UVB dosage is artificially increased each spring due to the photolysis of atmospheric ozone by polluting aerosols (CFCs). The study of "UV Radiation, Ozone Depletion and Phytoplankton Biology" has been addressed in the recent *Icecolors '90 and '93* studies of Smith and Prézelin and are outside the scope of the Palmer LTER. (see section VII, C).

Initial Strategy. 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 proposed to 1) monitor the spring to fall temporal/spatial variability in the abundance, size-distribution, composition and productivity of the phytoplankton communities within nearshore waters; 2) use traditional radiolabel measures of productivity to calibrate a bio-optical model; 3) bio-optically monitor as continuously as possible the spring to fall *in situ* temporal/spatial variability in hydrography, light availability and utilization, and primary productivity; 4) employ bio-optical data to model phytoplankton production in the region around the study site as a function of space and time; 5) extend the spatial scale of the measurements and model during cruises in the fall and spring of two years, one with heavy and one with light ice cover; and 6) verify and refine the model with data from # 1-4. These studies would be accompanied by an extensive array of experiments to test the validity, define the limitations, and determine acceptable modifications for a bio-optical

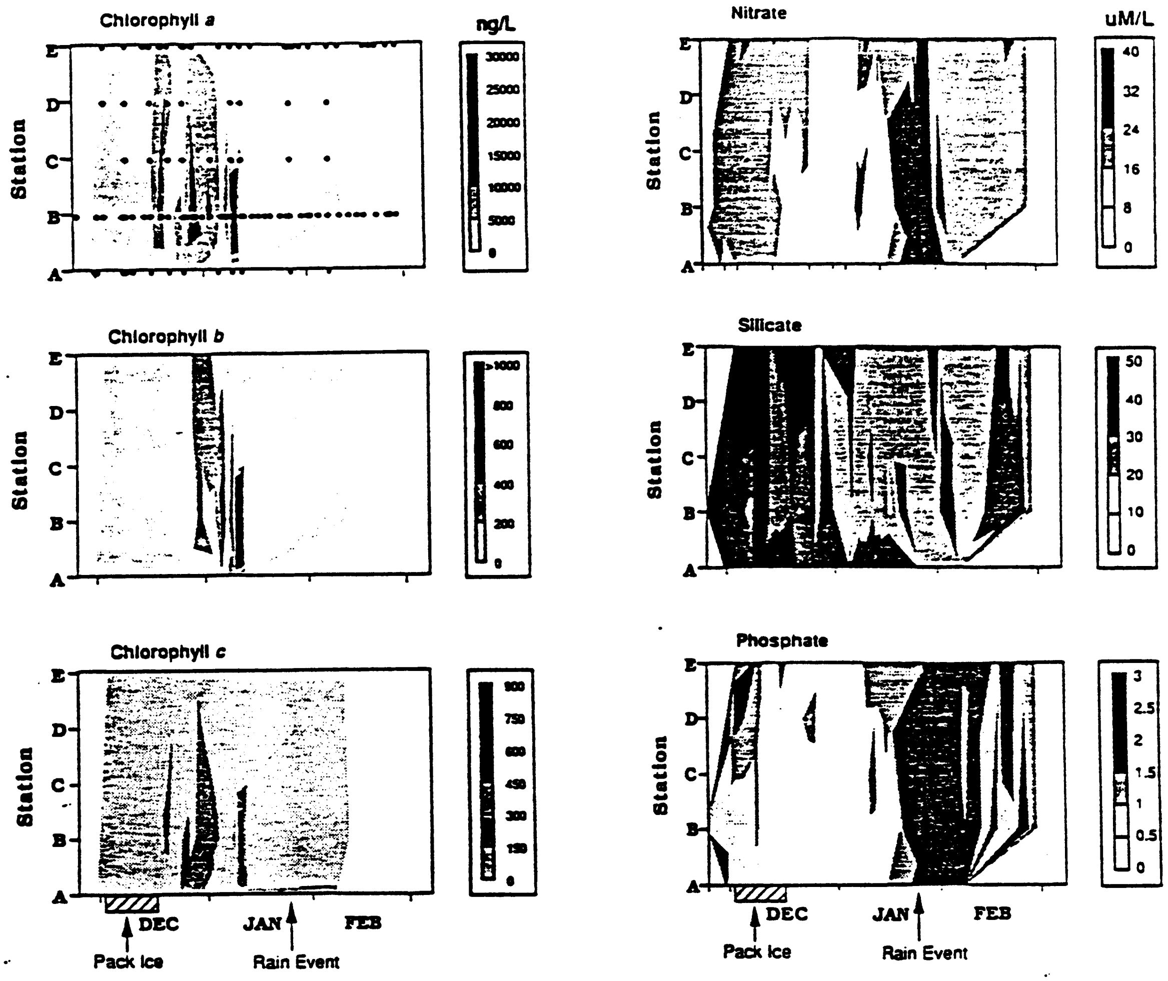


Figure 15. Contour plots of the spatial and temporal variability in pigment and inorganic nutrient distribution along the transect line between December 1991 and March 1992. Only surface data is reported.

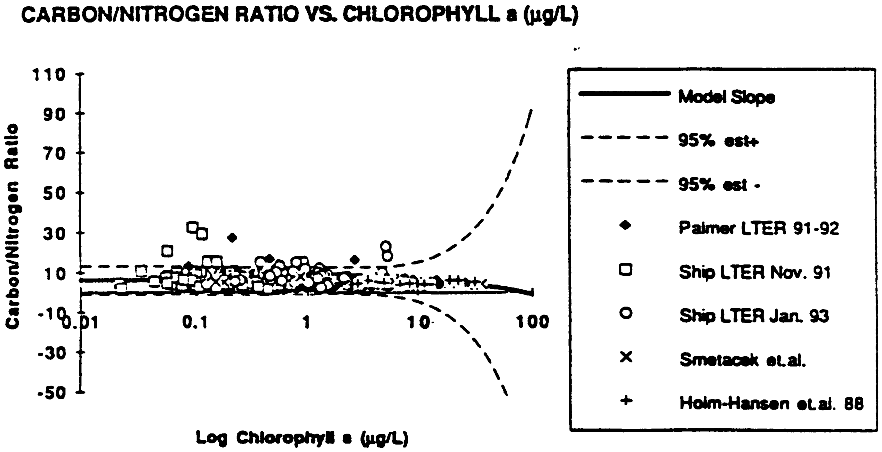


Figure 16. Plot of the particulate carbon:nitrogen ratio as a function of chlorophyll a concentration for all samples collected on two LTER cruises, one inshore Palmer grid field season, and published data. Despite the three orders of magnitude in biomass, the C:N ratio in phytoplankton is consistent.

model to predict accurately the rates of Antarctic primary productivity over a wide range of time and space scales.

Temporal/Spatial Variability. Table 4 summarizes the present LTER productivity database collected and analyzed during the last 3 field seasons. Like other Antarctic researchers (El-Sayed 1971, 1978; Tilzer et al. 1985; Smith and Nelson 1986; von Bodungen 1986; Wilson et al. 1986; Perrin et al. 1987; Smith 1987), we can show that nearshore phytoplankton biomass, size distribution, species composition and rates of carbon fixation showed significant regional variations throughout the austral spring and summer in the Antarctic (Figs. 12-15) that is unrelated to the nutritional status of the cell (Fig. 16). Our time and space coverage represents the most extensively and highly resolved assemblage of quantitative data on phytoplankton seasonal succession, photophysiology, and primary productivity collected to date in the Southern Ocean. Furthermore, this data can be linked to several hydrographic and optical properties of the water column for further studies of both bio-optical models of primary production and circulation/water column stratification based models of primary production (see sect. IIF).

The ability to predict patterns of phytoplankton distribution and in situ productivity for different regions of the LTER grid are presently problematic for at least two reasons. First, the present correlative databases are sufficient to document the co-occurrence of physical, biological and chemical events, but are not sufficiently experimental to test apparent mechanistic linkages that underly long term ecolological modeling.

Second, correlative analyses and casual observation indicate that the priority of determinant factors controlling primary production likely changes through seasons and that frequent episodic events do occur of sufficient magnitude to quickly alter phytoplankton dynamics within distinct areas of the LTER grid. There are times when the phytoplankton biomass at a given location can change by orders of magnitude with the horizontal advection of sea ice laden with ice algae. We have documented such events occurring within a few hours near Palmer Station, which last for a few to several days and then suddenly are blown away. At other times in the same season at the same location, the horizontal advection or local formation of sea ice is essentially void of ice algae and thus contributes little to local productivity while having a profound effect on the optical and hydrographic characteristics of the previously ice-free water column (Fig. 15). Episodic disruption of phytoplankton dynamics in the water column appears to be the norm for Antarctic ecosystems and provides intriguing challenges for future ecosystem studies.

D. Secondary production. (Robin Ross and Langdon Quetin, University of California at Santa Barbara)

Several hypotheses guide our approach to the study of the effects of interannual differences in the extent of pack ice on two species chosen to represent secondary production. The two hypotheses concerning recruitment in antarctic krill and its population dynamics, the survival of the larvae (H1) and recruitment potential or population reproductive output (H2), are based on the concept that food availability at critical times is linked to either winter or spring ice dynamics. Two hypotheses address mechanisms underlying the interannual variability in distribution of prey species within the summer foraging ranges of the dependent apex predators, krill and Adélie penguins (H3) and antarctic silverfish and south polar skuas (H4).

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

H2: In years with greater food availability, reproductive output of adult krill will be greater. Abundance and duration of food availability within the mesoscale LTER grid 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, and meteorological conditions will follow the same cycle.

H4: In winters and 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, and to the distribution of water masses.

Annual and geographical variations in recruitment in antarctic krill may be due either to variations in reproductive output (spawning success) and/or survival of the larvae during critical periods during the early life history (Ross and Quetin 1991). Summers of high reproductive output are predicted to follow winters of high ice extent and presumably more extensive ice edge blooms. Winter-over survival of larvae would be higher after a winter of high ice cover with the ice biota providing good winter grazing. Together the two predictions suggest that if several winters of heavy ice cover alternate with several of low ice cover (Stammerjohn 1993), recruitment may fail in at least two consecutive years. Changes in adult biomass from such a failure will not be detectable with current techniques (Priddle et al. 1988). However, differences in recruitment will be seen in length frequency distributions of subadult and adult krill from the annual cruises. Two years after a failure in recruitment, a higher average size will result from a lack of krill in their third summer (25-35 mm), and two years after a successful year, the average size will decrease with the addition of large numbers of small krill (Priddle et al. 1988).

Survival of larvae. Physiological condition (condition factor as a measure of robustness or carbon per length cubed (volume), percent lipid as a measure of stored reserves, and instantaneous growth rates as an index of nutrition during the intermolt period (2-4 weeks)) of larvae during a winter with extensive ice cover was higher than during one with low ice cover (Ross and Quetin 1991), evidence for the idea that larvae must find a source of food other than open water phytoplankton or starve during their first winter (Elias 1990). One commonly suggested alternate source of food is ice algae. In years with no or late ice cover and thus low winter food availability, recruitment may fail entirely even if reproductive output was high. Physiological condition of larvae and juveniles collected each austral spring is an annual index of a year class's ability to survive the winter. The quantitative relationship between physiological condition and imminent starvation is currently being explored under a separate grant to Quetin and Ross.

In addition to the annual index, during the first pair of pre- and post-winter cruises (1993) winter-over survival of the year's cohort will be quantified and related to physiological condition. A second pair of cruises in the next funding cycle would repeat the study under different winter conditions. Quantification of the distribution of larval and juvenile krill and ice algae under first year ice is done by divers who also collect krill for physiological condition. Mortality during the first winter will be estimated from total numbers and stage composition in the survey area fall and spring, and known developmental times under winter conditions (Elias 1990).

Reproductive output. Inter-school variability in the spawning frequency during the 3+ months summer reproductive season (Ross and Quetin 1986) is of the same magnitude within years as between years, suggesting that the major variables affecting reproductive output are length of the spawning season and percent of the population spawning, not interannual differences in the spawning frequency. Krill need relatively high food concentrations to reproduce (Ross and Quetin 1986), thus temporal and spatial availability of food, particularly ice edge blooms in austral spring, may be an important determinant of both the length of the spawning season, and the percent of the population spawning (Quetin, Ross and Clarke 1993). Over the past decade we have seen large interannual variability in the percent of the population of mature adults reproducing that are consistent with observed interannual differences in reproductive output (Brinton et al. 1987; Amsler, Quetin, Ross and Cuzin-Roudy in preparation), although not solely with winter ice extent.

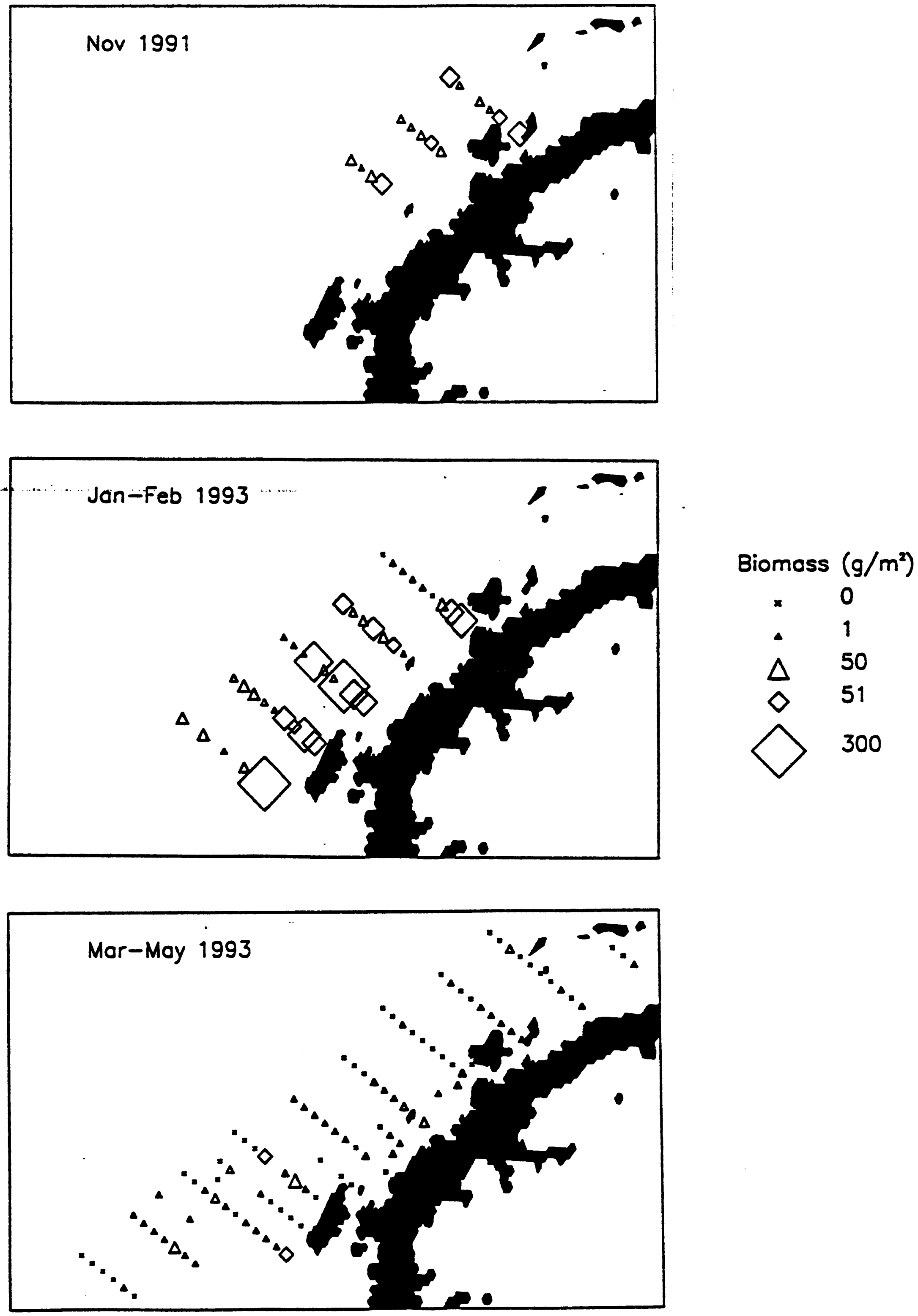


Figure 17. Biomass values of *Euphausia superba* in the Palmer LTER grid area from three different seasons. Values were obtained with a BioSonics acoustic package with a 120 kHz transducer.

Annual estimates of the percent of the population in the 'resting' stage (Cuzin-Roudy and Amsler 1991) during the LTER summer cruise, timing and concentration of food available, and the extent of pack ice cover in the winter will allow us to investigate this hypothesized linkage.

Prey availability. The third and fourth hypotheses address the cause(s) of variations in the distribution of adult antarctic krill and of sub-adult silverfish within the summer foraging range of their respective predators. Changes in mesoscale distributions and abundances of krill and silverfish may be linked to the ice cycle in a complex manner through changes in oceanic circulations linked to atmospheric changes (Sahrhage 1988) and/or the direct effect of pack ice on survival and/or behavior of the prey.

The causes of seasonal and interannual variations in the size and number of aggregations of krill are poorly understood, yet the distribution and size of schools may play an important role in population dynamics of krill (Okubo pers. comm.), and 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), but models of biological diffusion in a variable environment such as those of Davis et al (1991) may provide better simulations. Therefore, local krill availability will result from the interaction between variation in recruitment, water mass distribution caused by large scale changes in atmospheric circulation, and seasonal and interannual changes in school size and distribution.

Bioacoustics (BioSonics, 120 kHz transducer) are being used to quantitatively map the spatial and temporal distribution of antarctic krill, both during research cruises and from the zodiac throughout the spring and summer. Seasonally, biomass values over the peninsula grid change a great deal, and were higher in summer than in either fall or spring (Fig. 17). However, the pattern of distribution and biomass of krill schools does hold constant over shorter periods, as evidenced by a repeat set of transects in January 1993 (Lascara et al. in press). Length frequency distributions of krill also varied seasonally. Larger and reproductively mature individuals were found further offshore than subadults and immatures in both spring and summer, but not in austral fall. During the first summer cruise (Jan.-Feb. 1993), reproducing krill were found primarily at offshore stations in the southern reaches of the Peninsula grid (300.* and 200.* transects, refer to Fig. 6) which coincidentally is covered by ice each winter (Stammerjohn 1993). Reproductive success in krill may be greater and less variable in areas covered by ice every winter then in areas where ice cover is more variable.

Although similar climatic and recruitment factors may affect fish distributions, historical records of pelagic fish, especially antarctic silverfish, in the Palmer LTER region are sparse. For silverfish, densities are not high and not all length classes have been found in the region (Kellerman 1986; Hubold and Tomo 1989; Reisenbichler 1994). Initial objectives for the net collections and for otoliths from guano samples from south polar skuas were (1) to document interannual variation in distribution and abundance of pelagic fish with a midwater trawl throughout the grid and particularly in shelf waters where adult silverfish were thought to occur, (2) to measure physiological condition and age distribution of subadult silverfish populations, i.e., those eaten by the south polar skuas, and (3) to investigate whether interannual variability in growth rates from otolith analysis of either larval or adult fish would allow us to test whether recruitment in silverfish followed the pattern predicted by the hypothesis, i.e. that recruitment is higher (as implied by higher growth rates for fish in their first year (AC1+)) after years of low winter ice extent. Our present and proposed future approach reflects the current state of our knowledge and an evaluation of various possible techniques.

Initially fish in January/February 1993 were sampled at all possible stations, onshore and offshore, on transects 600.*, 500.*, 400.* and 300.* Since in other regions subadult silverfish had been found with krill schools offshore in the East Wind Drift (Hubold 1985) and the shelf stations inside the Biscoe Islands had been suggested as a possible spawning ground for silverfish populations west of the Antarctic Peninsula (Fig. 18). However,

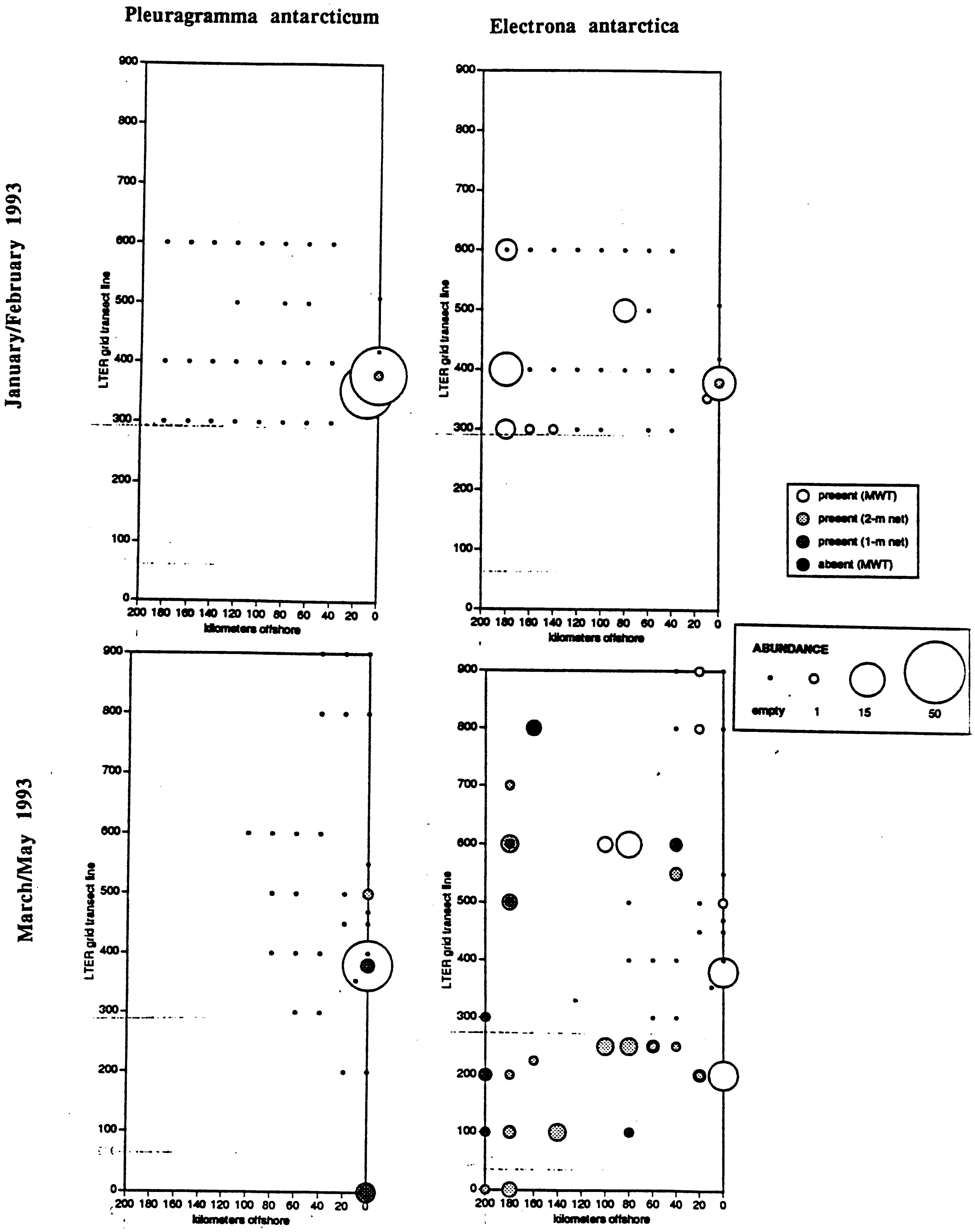


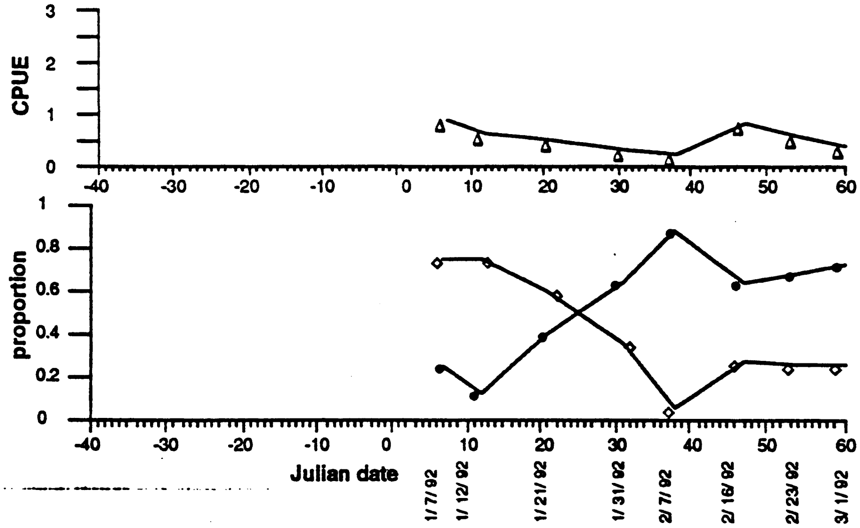
Figure 18. Abundance of post-larval Pleuragramma antarcticum and Electrona antarctica captured in trawls within the LTER study region during the January/February and March/May 1993 cruises. (MWT= midwater trawl).

silverfish were only found in shelf waters near the Antarctic Peninsula. Other fish, primarily the myctophid, Electrona antarctica, were found throughout the region in low abundances. In March/May 1993 the sampling design reflected what we had learned about the hydrography and fish distributions and was based on concurrent hydrographic measurements. The midwater trawl was primarily fished in waters landward of the continental water boundary, in either continental zone or shelf water, the supposed habitat of silverfish. However, silverfish were again restricted to 'shelf' waters within 40 to 50 km of the mainland (Fig. 18).

Midwater trawls yield large spatial scale sampling over a short time scale that does not include the critical time for egg laying for the south polar skuas. During the first two seasons south polar skuas were evaluated as 'collectors of fish' over a longer time frame. Otoliths from the guano of about 20 pairs of south polar skuas on Bonaparte Point were sorted from weekly guano collections, and otoliths identified, counted and measured. Results were compared to less frequent diet samples from skua pairs monitored for reproductive success by the seabird component to verify that similar fish populations were being preyed upon by all south polar skuas. Otolith species composition and relative abundance represents the fish community available to these seabirds within their foraging range of about 160 km. The combination of large spatial scale sampling over a short time scale and a long temporal sampling regime over a spatial scale defined by the foraging range and depth of the south polar skua has proven valuable in understanding possible factors affecting fish distribution, and in developing an approach to test our hypothesis on interannual variability in fish availability.

Two fish species dominate catches, both from nets and from guano, but the patterns for the two differ, both in time and in space. Antarctic silverfish are restricted in their spatial distribution, whereas Electrona antarctica is found over the entire grid in both the same areas as silverfish and further offshore (Fig. 18). Silverfish are also more restricted in their temporal availability (Fig. 19). In both years, E. antarctica was the most abundant species

(a) 1991-1992 season



(b) 1992-1993 season

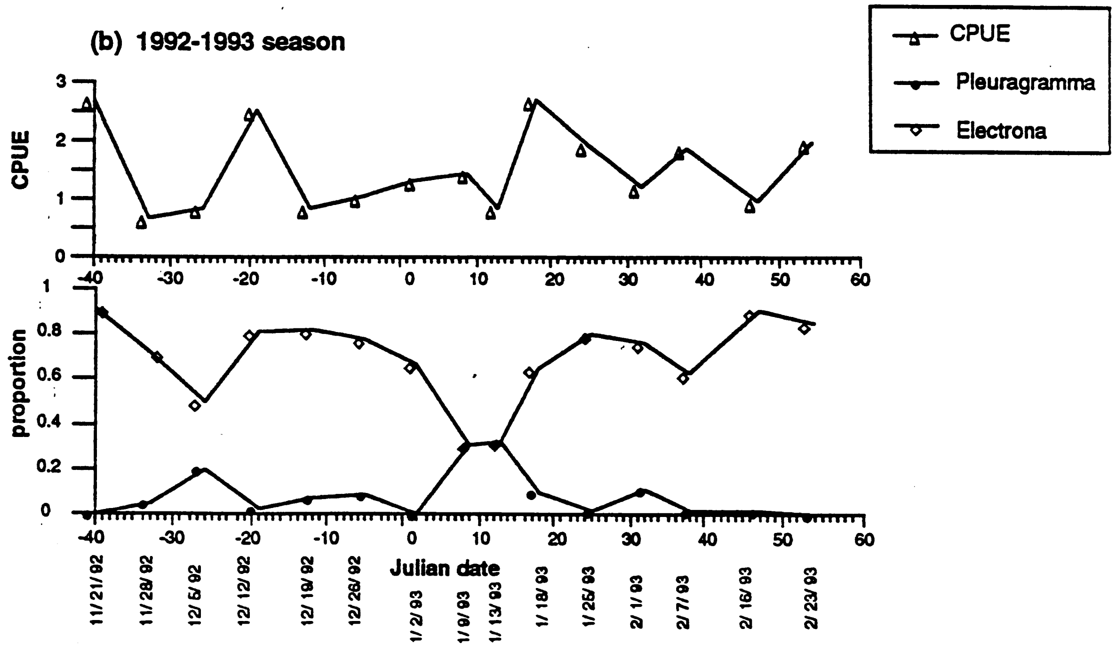


Figure 19. Fish community composition within the foraging range of the south polar skua, as calculated from guano samples collected near Palmer Station during the 1991-1992 and 1992-1993 seasons. CPUE is catch per unit effort, or total number of sagittal otoliths per guano sample. Proportion is the proportion of the total sagittal otoliths per collection date contributed by each of two species, Pleuragramma antarcticum and Electrona antarctica.

in guano samples in spring and early summer. Antarctic silverfish were a significant proportion of the total catch in early summer, although 1992-1993 proportions never reached the levels of 1991-1992, and did not increase throughout the season (Fig. 19). Thus silverfish distributions were variable on all scales measured (temporal, spatial and interannual), whereas E. antarctica has a more homogeneous distribution.

Our approach to testing the hypothesis about the mechanism underlying interannual variability in silverfish availability to south polar skuas requires both net and guano collections, and age analysis of silverfish otoliths. The age composition of silverfish in the guano samples will tell us if recruitment or distribution shifts is behind the variability observed in the proportion of silverfish in the fish community available to skuas. If the age distribution remains the same each year, then physical factors controlling horizontal or vertical movements in silverfish that in turn affect their availability to south polar skuas is the most likely explanation for a 'poor silverfish year'. Alternatively, if the age composition changes, and we can follow a decrease in a certain year class through several years, then a recruitment failure of that year class is the most likely explanation. We are in the process of evaluating several methods for otolith analysis for the adults, an essential part of our approach.

Otolith analysis will not only help distinguish causes of interannual variability in fish availability to a particular group of birds, but also be useful for physiological measurements. Condition factor and percent lipid are estimates of the more recent nutritional history of the fish, whereas standard otolith analysis (Hubold and Tomo 1989) will yield the relative growth rates of the fish during the last 8 years or so. Since growth of fish of AC2+ and older is restricted to summer months, the otolith rings record the effect of environmental conditions, and represent a record of the past nutritional history. Such patterns may help us establish a relationship between recruitment success and growth rates in silverfish and prey availability for the south polar skuas and environmental factors such as timing of the ice retreat.

E. Seabird ecology and vertebrate predators. (William R. Fraser and Wayne Z. Trivelpiece, Montana State University)

Two seabird species were selected to represent the LTER apex predators. These are Adélie penguin (Pygoscelis adeliae) and south polar skua (Catharacta maccormicki). Adélie penguins and south polar skuas hold different trophic positions in the region, with the former being essentially a planktivore that feeds almost exclusively on the antarctic krill (Euphausia superba), and the latter being a piscivore that relies primarily on the antarctic silverfish (Pleuragramma antarcticum). Adélie penguins are year-round residents within the region of interest to the LTER, and winter in association with the pack ice. South polar skuas, however, are only summer residents that winter in arctic waters. These two wintering strategies have important implications to aspects of the data being obtained on the ecology of each species, and in particular on the effects of pack ice on these predators. Four hypotheses guide the predator research:

H1: Winter-over survival and physiological condition of adult Adélie penguins upon their return to the rookeries to breed is a function of winter and early spring food availability in the pack ice and on the location of winter pack ice relative to the rookeries (sea ice extent). Adult winter- over survival, physiological condition and 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 and catastrophic summer storms, is linked to the extent of sea ice through its effects on spring and summer krill availability. Krill availability will be lower during cold summers and higher during warm summers. Fledgling weights and the number of chicks fledged per pair will thus increase during warm summers, while the duration of foraging trips will decrease.

H3: The physiological condition of south polar skuas during the pre-egg stage is a function of the availability of the antarctic silverfish within the skua's spring

Table 5. Parameters for which databases are being developed by the LTER Seabird Component for Adelie Penguins and South Polar Skuas.

Reproductive Biology

Breeding population size
Arrival dates/chronology
Onset of reproduction
Egg weights and volumes
Egg weights and volumes
Ratio of 1:2 chick broods
Chick growth
Chicks fledged/pair
Chicks fledged/colony
Chick fledging weights
Chick fledging chronology
Breeding chronology

Foraging Ecology

Adult diet composition
Chick diet composition
Prey caloric value
Prey characteristics
Prey characteristics
Foraging trip duration
Ptylochronology

Demographic Studies

Adult overwinter survival
Annual cohort survival
Recruitment
Cohort banding

Pelagic Studies

Seabird distribution
Seabird abundance
Seabird biomass
Seabird diets

foraging range. Territory occupancy will be earlier and more constant, and the onset of reproduction earlier when silverfish are more available.

H4: Breeding success of the south polar skua will exhibit cycles different from those of Adélie penguins. Recruitment of their primary prey, the antarctic silverfish, is affected negatively by pack ice during the spring of cold years. Because south polar skuas primarily eat subadult fish, breeding success will be a function of ice conditions 8-10 years prior to the current breeding season.

The approach in testing these hypotheses capitalizes on abundant, easily accessible Adélie penguin and south polar skua breeding populations (12,000 and 1,000 pairs, respectively), and on the measurement of ecological variables (Table 5) that are likely to be sensitive indicators of change in the marine system. These data are obtained using protocols that have been instrumental in the development of long-term databases in the region since 1977. These methods, now standardized as part of the CCAMLR Ecosystem Monitoring Program, are implemented annually in both apex predator species as part of a terrestrial, colony-based research effort that covers the October-March period. A marine-based complement to the terrestrial work occurs each January coincident with peak food demands by these predators. The key objectives are to examine variability in pelagic abundance and distribution, reproductive success, foraging ecology and winter-over survival and recruitment relative to annual changes in sea ice conditions, and within the broader context of change in other physical and biological features of the marine environment.

The pattern emerging as the predator research develops continues to support the view that sea ice may be critical not only to the ecology of Adélie penguins and south polar skuas, but to a host of other southern ocean, upper-trophic level predators as well (Fraser et al. 1992). Coupling the current LTER predator data with data obtained as part of complementary research programs initiated in the mid-1970's and 1980's suggests that, in effect, sea ice mediates the abundance and availability of prey (Fraser et al. 1989, 1992).

Long-term changes in predator populations, and in the diets of a select group of predators, can be linked to changing sea ice conditions during the last two decades within the LTER sampling area. These findings may have broad implications to the function of Antarctic marine ecosystems (Ainley et al. 1988), to the direction of future research initiatives, and to the management and use of antarctic marine living resources (Fraser and Trivelpiece in preparation; Fraser et al. in preparation).

F. Modeling (Eileen Hofmann and John Klinck, Old Dominion University; Barbara Prezelin and Ray Smith, University of California at Santa Barbara)

The modeling component of the Palmer LTER program is designed to provide an approach for integrating and analyzing the many and varied data sets that are now becoming available from the program and to test the program core hypotheses. Consequently, the modeling component consists of a hierarchy of models. These models consider the physical environment, primary production, krill distribution and higher predator effects. The efforts in the modeling component during the first part of the Palmer LTER program have been directed towards identifying and formulating the models that will be used.

The models being developed for the physical environment consist of a regional scale circulation model and a coupled sea-ice and mixed layer model. The circulation model considers the three-dimensional, time-dependent flow in the LTER grid region. This model is based upon a semi-spectral primitive equation model (Haidvogel et al. 1991) that has been applied successfully to a variety of oceanic environments. This model is now being configured for the LTER region. The model allows for bottom bathymetry, surface wind stress and thermodynamic effects on the flow. The simulated circulation fields obtained from this model will be calibrated and analyzed using the hydrographic data sets collected as part of the LTER field program. The simulated circulation fields will provide a basis for understanding the patterns observed in the the water mass and property distributions seen in the hydrographic distributions as well as providing input to the biological models described below.

Table 6. Spatial and temporal scales of the Palmer LTER.

Spatial scale	km^2
Southern Ocean ice cover	10^7
Bellingshausen/Amundsen Sea	10^6
Large gyres	10^6
Antarctic Peninsula Region	10^5
Palmer Basin (near field, 100 × 100 km)	10^4
Seabirds (Adélie penguins, south polar skuas)	
Summer foraging (50 × 50 km)	10^3
Winter range	10^5
Eddies	10^2
Silverfish population (*Pleuragramma antarcticum*)	$\sim 10^5$
Krill (*Euphausia superba*) population	10^6
aggregations	$< 10^0$

Temporal scale	Min
Climate	
Seasonal cycle, year	0.5×10^5
Episodic weather, hours to days	$10^1 - 10^4$
Ice movements, hours to weeks	$10^1 - 10^5$
Optical variability, min to hours	10^{-1}
Phytoplankton	
Diel cycles, hours	$10^1 - 10^3$
Blooms (turnover times), days	10^4
Secondary Producers (life span)	
Krill, 5–7 years	3×10^5
Antarctic silverfish, ~25 years	10^6
Seabirds (life span)	
Adélie penguin, ~12 years	5×10^5
South polar skua, 40 years (70 max)	10^6

The coupled sea-ice and mixed layer model is based upon existing models described by Price et al. (1986) and Hakkinen (1990). This model will be used to simulate the temperature and salinity structure of the upper part of the water column. Analysis of the LTER hydrographic data has shown that this part of the water column exhibits considerable seasonal variability. Also, the episodic nature of the forcing within the LTER region (e.g. storms) results in erosion and re-establishment of the mixed layer several times within a given season, such as the austral summer. The seasonal and within-season variability will be investigated with the coupled sea-ice and mixed layer model. This model will also be used to analyze and interpret patterns that are observed in primary production and pigment measurements made in the LTER region. Stability (or not) is considered to be one of the major factors regulating primary production in antarctic waters. Once the coupled sea-ice and mixed layer model is implemented and calibrated, it is anticipated that it will be interfaced with bio-optical model being developed by Smith and Prezelin.

As briefly discussed in Section II A, marine systems span such a large range of space/time scales that remote sensing and modeling are essential in order to cover this range of scales (Table 6). Smith et al. (1987) compares the sace/time domains of several physical and biological processes with sace/time samling regimes of various measurement platforms (Fig. 7). For the LTER, an understanding of the space/time distributions of our key indicator species and the environmental and biological processes that affect these distributions, is fundamental to a complete understanding of and linkage between the various trophic levels.

Further, the harsh environment and limited resources for sampling require that we develope a robust and accurate method for estimating primary production over a range of space/time scales. Development of the primary production model has several components: a model of production for the marginal ice zone which can provide a temporal estimate for the entire LTER region as well as the Southern Ocean; high-latitude ocean color algorithms for use with the SeaWiFS ocean color satellite sensor for high spatial (but limited temporal) estimation of pigment biomass and primary production; and local and mesoscale bio-optical estimates of pigment biomass and primary productivity based upon ship and Palmer Station area data. A key objective will be to apropriately link the resolution of these productivity models to circulation models and the higher trohic level models at space/time scales best suited to the objectives of the LTER. We have already shown that bio-optical models can be used to predict rates of light-dependent carbon fixation from field measurements of water-column optical properties and phytolankton absorption properties combined with verifiable assumptions regarding photosynthetic quantum yield (Smith et al. 1990). Adaptation of these models to the high-latitude and low temperature polar environment is another key objective and is in progress.

The modeling efforts underway for the prey (krill) component are focused on understanding the processes that contribute to the spatial distribution of krill swarms that have been observed in the acoustic data sets collected during the LTER cruises. This modeling effort will build upon models developed for krill swarming, which are described in Levin et al. (1988) and Morin et al. (1988). Results from the circulation and coupled sea-ice and mixed layer model as well as the results from the bio-optical and primary production modeling efforts will be interfaced with the output of the coupled sea-ice and mixed layer model.

The modeling effort for the higher predators (penguins) consists of an energetics-based model for the Adélie penguin. This model has been implemented and is now at the point of doing simulations for calibration purposes. It is anticipated that the results from the krill swarming model will eventually be interfaced with the penguin energetics model. A second modeling effort that considers the effects of the size class structure of the prey (krill) on penguin foraging is currently under development. This model builds upon the size class models described in Hofmann et al. (1992) and Dekshenieks et al. (in press). The krill size frequency distributions obtained from stomach content analysis of penguins in the Palmer Basin area and those at King George Island provide the observational basis for implementing and calibrating this model. The model will be used to investigate the effect of fishing krill for a particular krill size class on penguin survivability.

III. Relationship of research to the five core areas

Core area 1. Pattern and control of primary production

One of the objectives of the Palmer LTER is to better define the seasonal pattern and control of primary productivity in antarctic waters near Palmer Station. To do this we are gathering data from several spatial and temporal scales and using many approaches. Remote sensing techniques provide geographic and temporal/spatial data on scales that would otherwise not be available. Several satellite derived products are or will provide coverage of sea-ice extent and thickness, pigment biomass and primary productivity, and hydrographic characteristics of near surface layers of the ocean. Direct measurements of nutrient, biomass, and primary production are determined weekly or biweekly near Palmer Station, annually during summer in a 200 by 300 km area of the LTER grid, and periodically in the austral spring and autumn of winters with different sea ice extent in an area of the LTER grid larger than in summer. The contribution of sea-ice phytoplankton to the total carbon budget of the Southern Ocean is unknown. We are approaching this difficult problem presently by pursuing an accurate estimate of sea-ice distribution, selectively collecting samples of phytoplankton biomass from the underside of sea ice (available to grazers), and making light measurements to develop bio-optical models for the estimation of under-ice production. Understanding the seasonal control of primary productivity will come from the integration of the field data with experimental studies conducted in the field and laboratory to define the physiological characteristics of phytoplankton at different times during an annual cycle. Variability of some of the physiological characteristics of phytoplankton are presently being analyzed as a first step to developing a regional bio-optical model of primary production.

Core area 2. Spatial and temporal distribution of populations selected to represent trophic structure

Based on our understanding of the antarctic pelagic marine food web, two pairs of predator/prey species have been chosen for detailed studies within the Palmer LTER study region: the Adélie penguin and antarctic krill pair is thought to be positively impacted by winters of extensive ice cover, and the south polar skua and antarctic silverfish pair negatively impacted. One prey item, Euphausia superba, or antarctic krill, is an herbivorous macrozooplankter that is widespread and abundant, dominates the diets of many predators, and is an important grazer of the phytoplankton community. The other, Pleuragramma antarcticum or antarctic silverfish, although a dominate member of the sparse epipelagic fish fauna and an important component of the diet of several seabirds and seals, is not abundant and is reported to be restricted in its distribution.

The research program for antarctic krill covers multiple spatial and temporal scales. The larger spatial scales are important for understanding the population dynamics of the species, and the smaller scales of more interest to specific food web interactions, with krill either as prey or consumer. Temporal scales are both interannual, such as the indices for reproductive effort and post-winter status, as is appropriate for a long-lived species, and also seasonal to understand the impact of interannual variability in phytoplankton bloom dynamics on secondary production in krill. Antarctic krill have a circumpolar distribution and are not genetically different throughout their range. However, population centers may be aligned with the series of large gyres around the continent, for example the gyre(s) found off the west coast of the Antarctic Peninsula within the Palmer LTER grid. The gyre off Adelaide Island includes the 300.* and 200.* transect lines (Fig. 6), areas that are consistently covered with ice in the winter (Stammerjohn 1993), and where we believe reproduction occurs every year, possibly because of a more dependable food supply. Reproduction and larval survival may or may not be successful in the northern region of the LTER Peninsula grid, depending on ice dynamics and food availability. Given the potential impact of interannual variability in winter ice cover on population dynamics, and the implications of a possible population center off Adelaide Island, sampling for parameters vital to understanding population dynamics of krill must be on the mesoscale, and include regions that exhibit consistent and variable ice cover in the winter, i.e. from the 600.* to 300.* lines (Fig. 6). Finer spatial scale sampling is conducted within the foraging range of the Adélie penguins during the critical period for chick rearing, as part of a joint exploration of predator/prey interactions. In addition, the finer temporal sampling possible from zodiacs over the Palmer grid yields estimates of growth in the krill population. These growth estimates, determined both experimentally and by following modal lengths over time, represent the sum of food availability in the area during the season. We anticipate that these growth rates will show interannual and within season variability dependent on the timing and availability of food which in turn is linked to both ice dynamics and climate variables like wind and clouds.

The sampling approach and design to generate both relevant annual measurements of the fish populations within the LTER grid and to test the hypothesis about silverfish availability within the foraging range of the south polar skuas from Palmer Station has changed during our first two years of sampling. The current sampling scheme reflects what we have learned about silverfish distributions, the understanding that south polar skuas have a maximum foraging range during chick raising of about 160 km, some preliminary observations of south polar skuas from near Palmer Station foraging behind the islands near the Peninsula, and the analysis of otoliths from two years of south polar skua guano samples. Stations sampled for fish populations include all those within 160 km of Palmer Station to include the fish community that may be available to the skuas, and those for silverfish dynamics include all stations on the shelf and within 60 km of the Peninsula on the standard transect lines plus additional stations within the known habitat of silverfish (shelf) and where south polar skuas have been observed foraging. Depths sampled with the midwater trawl are consistent with our objective of understanding silverfish population dynamics, not just the availability of those size fish preyed upon by the south polar skuas. South polar skuas serve as collectors over the longer temporal or seasonal scale important to understanding patterns of fish availability to the seabirds, and these samples yield adequate otoliths to test the hypothesis concerning a narrow size range of fish. Whether the narrow size/age range of fish found in south polar skua guano is due to behavior of the fish or of the seabird is not yet known.

Adélie penguins and south polar skuas have a circumpolar distribution, and throughout Antarctica tend to be the dominant components of avian communities in terms of both abundance and biomass. Within the LTER region of interest on the Antarctic Peninsula, populations of these two predators represent approximately 80% of the avian biomass, and are thus two of the region's key avian consumers. As current LTER hypotheses suggest, the ecology of these predators is tied to sea ice dynamics and the availability of krill and silverfish. Issues related to the spatial and temporal scales over which sea ice impacts prey abundance and/or availability, and thus the ecology of these predators, have been addressed by selecting parameters for measurement (Table 5) with inherent response times that accommodate the desired range of spatial and temporal scales potentially important to these predators. The measurement of chick growth rates, for example, provides an index of prey availability in the marine environment every 3-5 days within the predator's summer foraging range. The measurement of over-winter survival, on the other hand, provides a similar index, but it represents an intergrated value encompassing a minimum of 6 months within the predator's winter foraging range. The data being obtained thus encompass temporal scales covering days to years, and spatial scales covering meters to thousands of kilometers.

Core area 3. Pattern and control of organic matter accumulation in surface layers and sediments

Organic matter accumulation in the surface layers and sediments is the most difficult of the six core research areas to directly compare to the other LTER sites. In the subtidal in the immediate vicinity of Palmer Station accumulation of sediments is rare. Because this is a high energy environment and scour from icebergs is common, most beaches are composed of pebble-size rocks or larger. This trend continues subtidally. Sediments are found at depth (500 m) in Palmer Basin, but interaction between these sediments and surface waters is one-way, from the pelagic to the benthic realm. For the Palmer LTER we consider the "surface layers" to mean the surface layers of the ocean and the associated sea ice, a seasonal component.

Particulate organic matter does not accumulate in these surface layers permanently. In cold winters pack ice forms early and sea ice microbial communities (SIMCO's) develop, and significant accumulation and production of particulate organic matter (both living and detritus) in sea ice occurs. When the pack ice melts in the spring, the accumulated organic matter (algal cells, bacteria, protozoans, detritus, fecal pellets) is released into the water column. How much of this material is recycled within the surface layers and how much reaches the bottom is unknown. Downward vertical flux of particulate organic matter was only 8% of integrated water column production in this region in the summer (RACER overview 1987). Many investigators believe that the melting sea ice provides the seed stock for the ice-edge plankton blooms (Garrison et al. 1987). Although the same close link between algal and bacterial production exists in SIMCO's as in the water column (Garrison et al. 1986), algal biomass and presumably primary production is much less in the ice than in the ice-edge blooms, so production of detritus and microbial activity will also be less.

Core area 4. Patterns of inorganic inputs and movements of nutrients through soils, groundwater and surface waters

In the surface waters of Antarctica, most of the inorganic nutrients are derived from upwelling of nutrient-rich water masses. By comparison to other coastal regions worldwide, terrestrial inputs to the Palmer LTER region are relatively minor. The upwelled waters contain high concentrations of dissolved inorganic carbon (C=2 mM), nitrate (N=30-40 uM) and phosphate (P=2-3 uM). By comparison, partially reduced forms of N (i.e., NH4 and NO2) are negligible (<0.5 uM). The C:N:P molar stoichiometry is generally constrained within narrow limits and approximates the "Redfield"ratio of 106C:16N:1P. This empirical relationship and elemental consistency derives from the fact that the nutrient composition of the deep water masses is the result of the accumulated regeneration at depth of particulate organic matter that is exported from the near surface waters. In this way, the inorganic and organic nutrient flows of the polar ocean are closely linked.

The concentration of silicic acid in upwelled waters varies considerably from water mass to water mass. In the Palmer LTER region, silicic acid (Si) is always found in excess of that needed for diatom growth (typically concentrations in upwelled waters exceed 75 uM). At the point of total exhaustion of N or P from the water column, a residual Si of 30-50 uM is generally observed. Nevertheless, the sediments of the Southern Ocean are known to be a major sink for Si compared to C or N. The reason(s) for this uncoupled burial stoichiometry are not known. Other required inorganic trace nutrients appear to be poresent in sufficient concentrations to sustain high rates of primary production, especially in the seasonal ice pack and, subsequently, injection into the water column during spring melting may comprise an important mechanism. Finally, for selected regions trace elements may be supplied from glacial runoff or for regions of Bransfield Strait from hydrothermal venting.

As antarctic phytoplankton (eg. diatoms) grow and reproduce in the water column inorganic nutrients are assimilated in an approximate molar ratio of 106C:16N:1P:16Si. The amount of Si uptake will depend to a large extent on the species composition and growth rate. For example, under conditions of diatom spore formation more Si may be removed from the water column per mole of C than during exponential growth. If diatoms are not present in the water column, then very little Si is removed. The accumulated plant biomass in part sinks out of the water column either as whole inactive cells or as egestion, an end product of zooplankton grazing processes. Grazing also leads to the formation of ammonium, a metabolic by-product. Because ammonium is taken up in preference to nitrate, the accumulation of ammonium acts to supress nitrate assimilation. Consequently, even though nitrate may exceed ammonium by a factor of 10, phytoplankton derive nitrogen largely from ammonium.

Our inorganic nutrient sampling strategy in the LTER program to date has been to obtain data on the concentrations of the major inorganic nutrient pools at all stations where we collect phytoplankton biomass and species composition data, or where we measure the light dependent uptake of 14C. In this way we can quantify the net nutrient removal rates and independently determine net primary production. In addition, the measurement of the dissolved inorganic carbon pool and water column alkalinity allow us to calculate the partial pressure of carbon dioxide and the derived flux of CO2 into or out of the ocean surface. Previous research in the coastal region of the Antarctic Peninsula has documented strong CO2 sink in coastal waters. Additional nutrient samples are collected from deep hydrocasts in order to characterize the independent water masses.

Core area 5. Patterns and frequency of disturbance to the research site

With the exception of tourism and research, the LTER region of interest on the Antarctic Peninsula has not been subjected to any disturbance originating with human commercial interests or activities. Where disturbance has occurred, it has almost exclusively been the result of sharp increases in the populations of southern fur seals

(Arctocephalus gazella) and southern elephant seals (Mirounga leonina), which in the last 20 years have increased, respectively, by 800% and 300% (Fraser et al. in preparation b). Because these seals use terrestrial sites as loafing and haul-out areas, two types of impacts have been recorded. The most obvious have been the effects on vegetation and terrestrial freshwater ecosystems. Some islands, for example, have lost 80% of their original vegetation, and virtually all freshwater ponds now exhibit high turbidity and a loss of the original flora and fauna. Less obvious but equally apparent, have been the effects on some colonies of Adélie penguins and other seabirds, where competition from seals for space has effectively divided the colonies into significantly smaller units. This effect has in some cases increased chick and egg exposure to predators, and accelerated the rate at which colonies move towards extinction (Fraser and Patterson 1993). The primary cause for these changes in seal populations appears to be linked to changing climate and sea ice conditions (Fraser et al. 1992; Fraser and Patterson 1993; Fraser et al. in prep)

IV. Data Management

Data management has been a consideration for the Palmer LTER since its inception three years ago because of the certainty of a continuing stream of related data. Further, as the eighteenth LTER site we benefit from the collective experience of the other LTER sites and the funding agency which encourages data planning. It is recognized that there is both a need to facilitate current research as well to provide for the long-term aspects of the program. Further, our data management is designed to take advantage of the existing strengths of the team members and foster an integration of data as well as data handling. The Palmer LTER data management is organized around several distinct concepts including: 1) acceptance of a diversity of computer platforms and tools, 2) establishment of a distributed system of communication, 3) development of an electronically available central database.

Table 7.

Site Computing Capabilities for Palmer LTER

site code: PAL
site: Palmer Station
location: Antarctica
update: jul93
#years as an LTER site: 2
#years there has been datamanagement at site: 1
data manager(s): Karen S. Baker
data manager(s) specialty: oceanographic data analysis, remote sensing
hardware/central server: unix/sun
hardware/other platforms: sun, dec, mac, pc
hardware/archive media: tape, optical disk, diskettes
hardware/local area network: ethernet, fddi
internet connectivity: node (crseo.ucsb.edu:128.111.254.81)
software/communication protocols: unix/tcpip,appleshare; mac/appletalk
software/wordprocessing: unix/groff,tex,latex; mac/microsoft word
software/bibliographic: unix/bibiX,bibtex; mac/procite, endnote
software/spreadsheets: unix/asteriX; mac/excel
software/statistics: unix/ s, imsl; mac/statviewII, systat, superanova
software/graphics: unix/idl, matlab, gmt; mac/excel, wingz, deltagraph, cricketgraph, macdrawII, superpaint
software/database: unix/postgres, pc/dbase
software/GIS:
software/dataentry:
software/other: unix/gopher, rolodex; mac/macproject, fetch, sam, udora
documentation forms(y/n/begin): y
metadata archival format: ascii, menu browser
data archival format: ascii, heirarchical directory

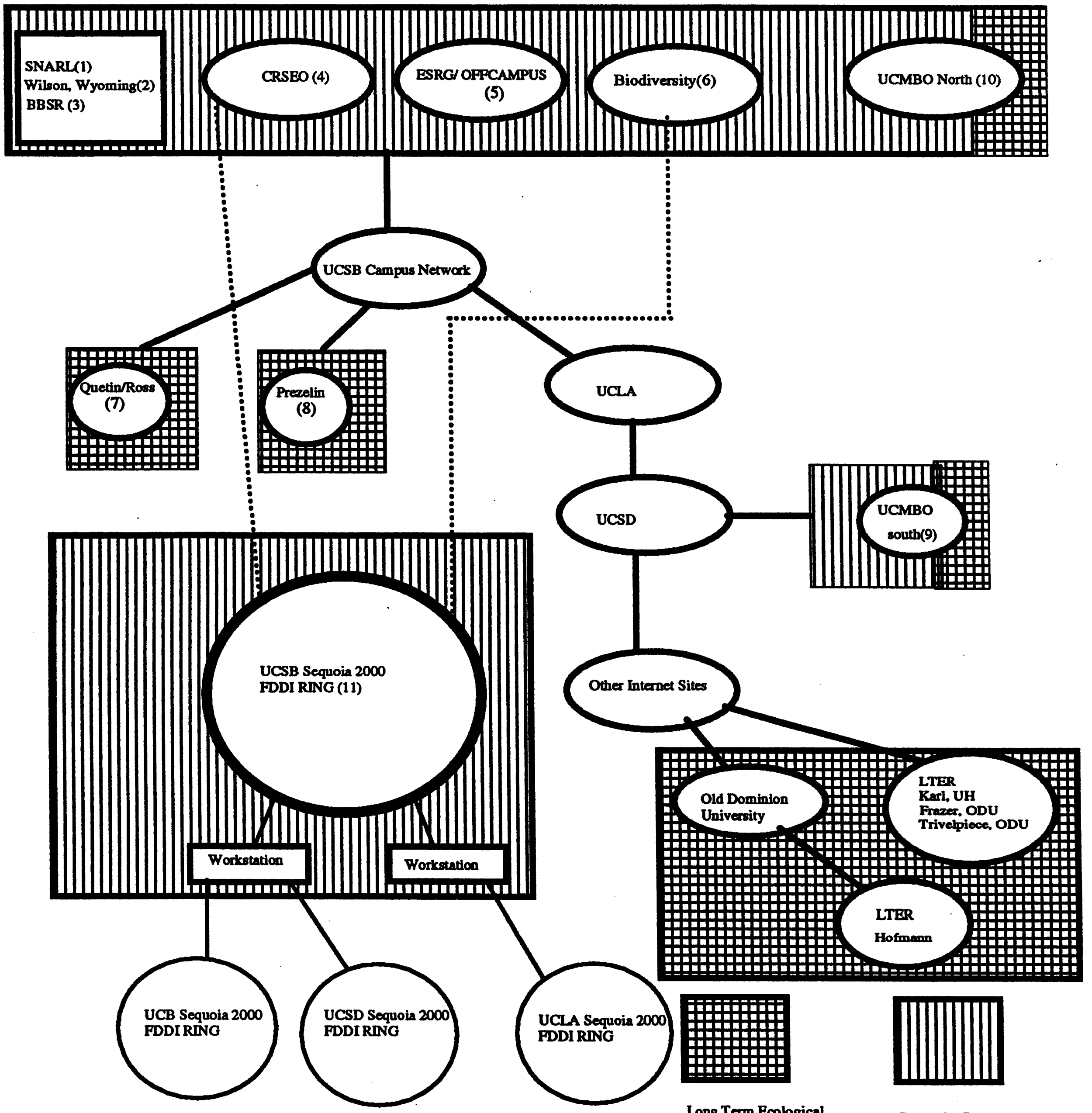
Personnel. Currently there is one half-time position which is the data manager who develops and maintains the central data structure in co-ordination with the individual investigators' data analysts who reside at their home sites. The data manager was made a member of the Executive Committee this year in recognition of the significant role data management must play in the development of an LTER site. The data manager, Karen Baker, has been a member of the marine bio-optics research team of Raymond C. Smith for eighteen years as a research participant and data analyst. Two of the CRSEO computer system analysts, Steve Miley and Jim Davidson, have been available on an as-needed basis and have provided significant input on networking, software tools as well as hardware configurations.

History. The Palmer LTER participants joined together with diverse scientific backgrounds permitting consideration of a significant portion of the antarctic food web from light to microbial activity to phytoplankton to krill to silverfish and birds. Each group has undergone development of a unique, independent hardware and software organization specifically optimized for their own particular research questions over a long period of time. Each group had adapted computer technology with reference to the local environment prior to joining together as the Palmer LTER team. Accepting the reality of these diverse computer platforms (unix, mac and pc) and tools means leaving local environment development in the hands of the individual research group and accepting the challenge of providing the methods for such a variety of systems to communicate (Table 7). Thus the data management is mandated with providing as powerful a connectivity as possible rather than promoting a standardization of equipment. Indeed a variety of platforms creates an enrichment of options in terms of data analysis and display.

The Palmer LTER participants reside in different physical locations including UC Santa Barbara (CA), Scripps Institution of Oceanography (CA), Old Dominion University (VA,MN and CA), University of Hawaii (HA) while the field work is conducted at Palmer Station (Antarctica) and aboard the research vessels *R/V Polar Duke* and *Nathanial B.*

Figure 20.

Center for Remote Sensing and Environmental Optics Computer Network Map



1) SNARL: Sierra Nevada Aquatic Research Lab: PI Jeff Dozier
2) Wilson Wyoming: PI Jeff Dozier
3) BBSR: Bermuda Biological Station for Research: PI Dave Siegel
4) CRSEO: Main Lab: Director Ray Smith
5) ESRG: Earth Space Research Group: PI Catherine Gautier
6) Biodiversity: PI Frank Davis
7) Quetin/Ross: PIs Robin Ross, Langdon Quetin
8) Prezelin Lab: PI Barbara Prezelin
9) UCMBO south: UCSD Scripps: PI Ray Smith
10) UCMBO north: UCSB CRSEO: PI Ray Smith

Palmer (Fig. 20). Given such a distribution, the development of the internet and the recent increase in reliable network software has played a critical part in the flow of data between individuals.

In order to gain an overview, a list was generated of the Palmer LTER software and hardware (Table 7). This simple survey was valuable enough that a Site Capability List was created by each LTER site at the data managers' group meetings. This list is maintained by the Palmer LTER as part of the LTER network online database (gopher lternet.edu; (2) Basic LTER documentation; (4) SiteCapabilities).

Connectivity. It was necessary first to insure physical connections to internet for each group. This has been accomplished in several different manners (Fig. 20):

1) direct campus broadband connection;

2) for two of the groups with heavy mac use, gatorboxes provide tunneling across the internet permitting appletalk networks to interface with the CRSEO unix network and providing remote disk mounting;

3) for those depending upon dial-up modems, tools such as gopher for browsing and ftp for file transfer are being used.

Such connectivity makes electronic mail and file transfer immediately available, but as the connectivity becomes exercised, we find also a transfer of both computer knowledge and computer resources which makes a significant contribution toward integrating the group and the data.

The principal investigators for the group, Robin Ross and Langdon Quetin, are located at UC Santa Barbara as are two of the other co-investigatorsincluding Raymond C. Smith who is also director of the Center for Remote Sensing and Environmental Optics (CRSEO) which is a research unit at UC Santa Barbara organized by earth scientists interested in making available a state-of-the-art computer technology to address their scientific pursuits. Further, several CRSEO investigators and many UC scientists have formed a multiyear collaboration with Digital Computer Company to investigate an EOS-era database project

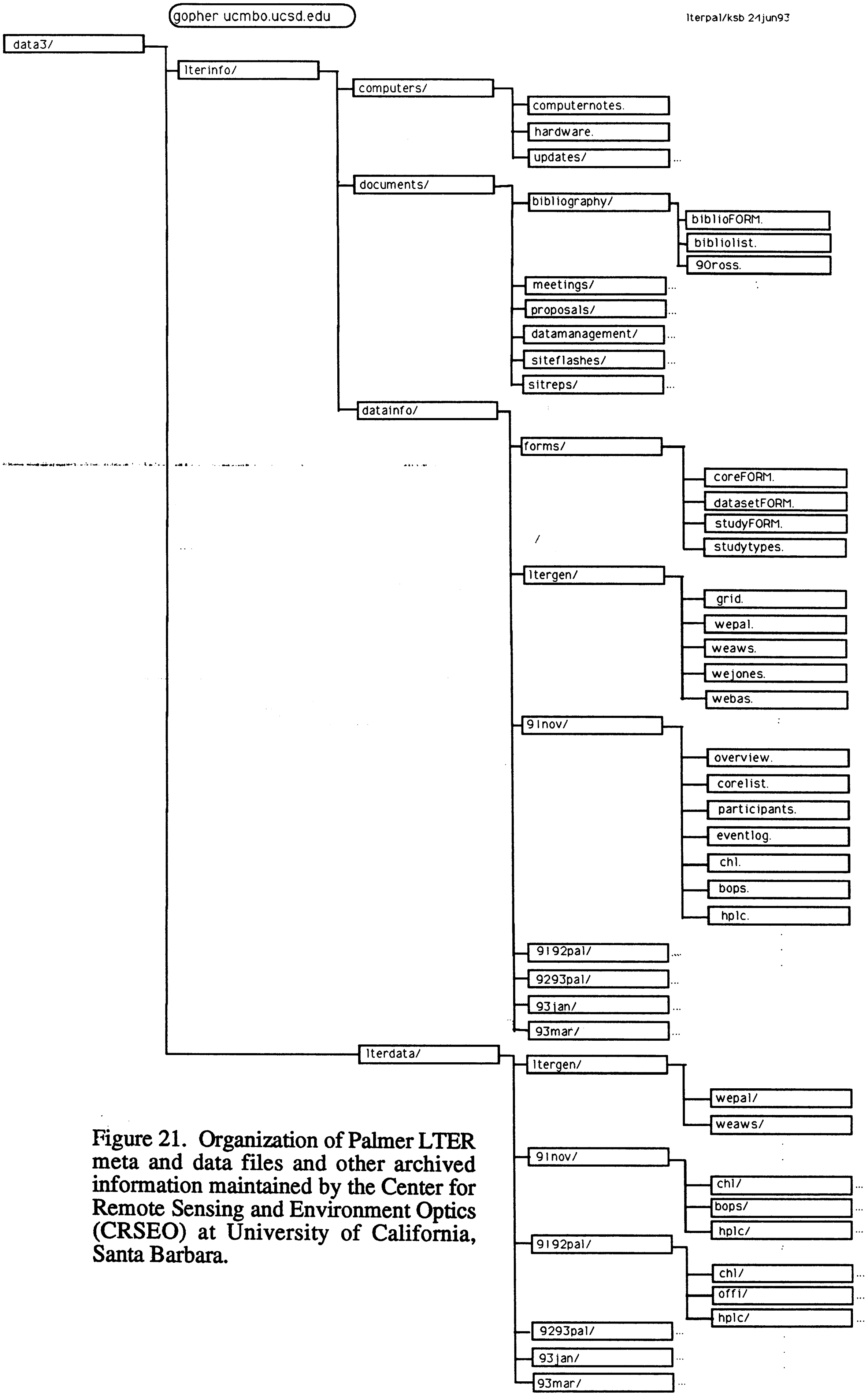


Figure 21. Organization of Palmer LTER meta and data files and other archived information maintained by the Center for Remote Sensing and Environment Optics (CRSEO) at University of California, Santa Barbara.

called Sequoia 2000. The Palmer LTER benefits from this effort in terms of available hardware, software, personnel and database planning. While storage of large datasets such as satellite data is available at Berkeley, a 500 Megabyte disk is available to serve as an initial local data hub.

Database. The goal of the centralized documentation and data storage is to make data and information available easily regardless of platform. To further this goal, all Palmer LTER investigators have accounts on the CRSEO server to provide direct access to the Palmer LTER central archive. The central data disk is divided in two sections: datainfo and data (Fig. 21). Information in both sections is maintained in flat ascii files so they are easily available to all investigators with their current hardware capabilities. Quality control for both metadata and the data itself is the responsibility of the individual investigator. The central data archive is itself a backup of each individual investigator's dataset but is itself backed up on a regular schedule. After considering the other LTER site data policies, the Palmer LTER group developed a data policy this year in order to help define the rules of data sharing.

The datainfo section contains general information pertinent to the LTER as well as the metadata which is documentation describing the data taken for each field study. The datainfo section is available to the general internet users through a gopher connection:

gopher lter.crseo.ucsb.edu

choosing (6) Palmer LTER datainfo. This internet gopher provides a menu driven browse for selecting resources, viewing and accessing from most platforms with internet access. By enlarging the base of information from metadata about the data to include LTER bibliographies, reports, and lists this information is available not only for investigator reference but also for student education.

In order to organize the metadata, a common vocabulary was developed and documented (Table 8). A study consists of a ship cruise or a season at Palmer Station. Within each study, data sets exist either as part of the predefined core data sets or as part of

Table 8.

COREFORM Definitions

STUDY
- annual cruise
- annual short cruise
- fall cruise
- general
- other
- spring cruise
- station

CATAGORY
- BO-biooptics
- BR-birds
- HY-hydrography
- KR-krill
- MICRO-microbial
- MO-modeling
- OV-overview
- PH-phytoplankton

DATASETS
- ACOU-Simrad acoustic transect; 38 kHz transducer
- ADBND-Adelie banding
- ADBRSUC-Adelie breeding success estimate (chicks fledged/pr; chicks fledged/colony)
- ADCENS-Adelie pair formation and breeding population census
- ADCP-acoustic doppler current profiling system
- ADDIET-Adelie diets; chick diet composition
- ADEGG&CHICK-Adelie egg and chick develop (onset of repro; hatch; fledg chrono; egg wts/vol; 1:2 chick broods; chick growth; chick fledg wt)
- ADPYTL-Adelie ptylochronology
- ADSTOM-estimates of ad krill LF in stomachs of Adelie penguins (AMLR) from eye diameter
- ADTELE-Adelie telemetry
- ATCTD-along track ctd & fluorometry
- ATK-along track position; time; depth; pyro
- ATP-microbial biomass (adenine tri-phosphate activity)
- BAC#-bacterial cell numbers
- BIOFISH-acoustic transects with 120kHz transducer with towed biofish
- BOPS-bio-optical profiling system with rosette (cond;temp;fluor;trans;irrad;rad;PAR)
- BRCENS-seabird census, transect or stationary from ship
- BRDIET-Adelie diets; chick diet composition from ship
- CHL-chlorophyll and phaeopigments (discrete fluorometer)
- CHN-carbon,hydrogen,nitrogen ratios
- CTD-conductivity; temperature; depth
- DIC/ALK-dissolved inorganic carbon, alkalinity
- DIVSUR- underice diving survey
- DOC-dissolved organic carbon
- DON-dissolved organic nitrogen
- DOP-dissolved organic phosphorous
- EXOGLU-bacterial exoenzyme activity of B-glucosidase
- EXOLEU-bacterial exoenzyme activity of luecine aminopeptidase
- FINGEST-field ingestion of adult and larval krill
- GRID-LTER grid information
- H2O2-hydrogen peroxide
- HIST-historical

DATASETS (continued)
- HPLC-high pressure liquid chromatography 6 pigments(chla;chlb;chlc;hex;fuco;perid;silica)
- KRILLTAR-targetted tows on schools of adult krill or for krill larvae
- KRINGEST-experiments on krill/phytoplankton interaction
- LEU-microheterotrophic production estimated by 3H-leucine
- LPS-total and soluble lipopolysaccharide (TLPS and SLPS)
- MMCENS-census of marine mammals within 2 mi limit of Palmer Station
- NUT-nutrients; 5 macro (silica; phosphate; nitrite; nitrate; ammonia)
- O2-dissolved oxygen
- OVIEW-overview of dataset along with corelist,participants,eventlog
- PARTSIZE-particle size
- PHYCONA-physiological condition of adult krill (IGR(instant growth rate); chemcomp; condition fact)
- PHYCONL-physiological condition of larval krill (IGR(instant growth rate); chem comp; condition factor)
- POC/PON-particulate organic carbon and nitrogen
- PRODIS-primary production in situ
- PRODPI-productivity vs irradiance measurements in photosynthetrons
- PRODSIS-primary production simulated in situ
- PUV-profiling uv irradiance
- SALPPIG-phytoplankton pigment in salps
- SALT-discrete salinometer measurements
- SEDTRAP-sediment trap in nearshore waters; near sta B
- SFISH-silverfish chemical composition; otolith analysis; gonadal index; stomach contents
- SKBND-south polar skua banding
- SKBRSUC-south polar skua breeding success estimate (chicks fledged/pr)
- SKDIET-south polar skua diet; adults and chicks
- SKEGG&CHICK-south polar skua egg and chick development
- SKCENS-south polar skua pair formation and breeding population census
- SKTELE-south polar skua telemetry
- SKQUANO-collection of skua guano as source of prey hard parts (otoliths)
- SPF-spawning frequency of adult krill
- TRMETZO-trace metal content of zooplankton
- TRWL1M-species composition and abundance in 1-m net
- TRWL2M-species composition and abundance in 2-m net
- TRWLMW-species composition and abundance in midwater trawl
- UV-NSF Palmer station monitoring system irradiance data
- WEAWS-automated weather system
- WEBAS-weather british antarctic survey
- WEJONES-weather jones
- WEPAL-palmer station weather
- XBT-expendable bathythermograph
- ZODTRWL-zodiac tows 1-m 500um mesh ring net for comp and abund of zoopl including krill larvae

the non-core-opportunity data sets. The study types and dataset definition list is maintained online (Coreform Definition Table). Describing each study is a corelist listing the measurements made (Table 9), a participant list describing who was on site for the study and an eventlog listing chronologically the type and location of measurements made during the study. Efforts are still underway to streamlineand simplify documentation in order to make sure it gets done, which includes providing forms while at sea or on station so documentation may be done while data is being taken.

The data itself is stored in a directory to which only the LTER investigators have access. The plan is to facilitate data storage and exchange in order to promote more rapid data assimilation between groups. There is ongoing discussion as to what stage of analysis the data should be before being entered onto this common data disk.

Future. Future efforts will include continuing to find ways to encourage connectivity and to facilitate the submission of dataset forms and datasets. Since the gopher connection has proven useful, a wais type server will be considered to enhance the search/browse capabilities. Also, consideration will be given as to whether data should be made available online through a gopher link which has the advantage of bypassing any personnel time needed to fulfill data requests. Although we have been primarily concerned in these first years with the establishment of data taking, organization, storage, and availability, it is recognized that as the amount of data in the database increases, we need to consider the possibility of a relational database such as the Sequoia 2000 postgress or the Digital rdb, especially as user interfaces are evolving rapidly. The database now is organized in such a way as to facilitate conversion to a relational database. There will continue to be attention paid to maintaining as robust and powerful a system as possible while requiring as little maintenance and support as possible. An emphasis on publically available software will continue with an eye toward maintaining data convertibility, meaning data is available to be entered into whatever software package any particular user wishes to use.

Table 9.

CORELIST 93AUG								
STUDY	CATAGORY	DATASET	CORE	DOC	DATA	PI	FREQUENCY	
spring cruise	BO	BOPS	c	y	n	Smith	1/station	
spring cruise	BO	CHL	c	y	n	Smith	12/bops	
spring cruise	BO	PUV	*	y	n	Smith		
spring cruise	BR	BRCENS	c	y	n	Frs/Tri	1/station;3/20km;sp., numbers, distrib	
spring cruise	BR	BRDIET	c	y	n	Frs/Tri	1/40-60km;seabird diets	
spring cruise	HY	ATCTD	c	y	n	Smith	1/15sec	
spring cruise	HY	ATK	c	y	n	Smith	1/minute	
spring cruise	HY	CTD	*	y	n	Klinck		
spring cruise	HY	XBT	c	y	n	Klinck	between stations	
spring cruise	KR	BIOFISH	c	y	n	Ros/Que	1/net tow	
spring cruise	KR	DIVSUR	*	n	n	Ros/Que		
spring cruise	KR	FINGEST	*	n	n	Ros/Que		
spring cruise	KR	PHYCONA	c	n	n	Ros/Que	(1 igr,45cc+cf)/trans	
spring cruise	KR	PHYCONL	c	n	n	Ros/Que	(1 igr, 4-5cc/stg, 40-50cf/stg)/trans	
spring cruise	KR	SFISH	c	n	n	Ros/Que	on trawl	
spring cruise	KR	TRWL1M	c	n	n	Ros/Que	1/station	
spring cruise	KR	TRWL2M	c	n	n	Ros/Que	1/station	
spring cruise	KR	TRWLMW	c	n	n	Ros/Que	1/selected stations	
spring cruise	MICRO	ATP	c	n	n	Karl		
spring cruise	MICRO	BAC#	c	n	n	Karl	?/station	
spring cruise	MICRO	DIC/ALK	c	y	n	Karl	?/station	
spring cruise	MICRO	DOC	c	n	n	Karl	?/station	
spring cruise	MICRO	DON	c	y	n	Karl	selected profiles(3-4)	
spring cruise	MICRO	EXOGLU	n	n	n	Karl	?/station	
spring cruise	MICRO	EXOLUE	c	y	n	Karl	?/station	
spring cruise	MICRO	H2O2	c	n	n	Karl	?/station	
spring cruise	MICRO	LEU	c	y	n	Karl	?/station	
spring cruise	MICRO	LPS	c	n	n	Karl	?/station	
spring cruise	MICRO	O2	c	n	n	Karl	?/station	
spring cruise	PH	CHN	c	y	n	Prezelin	6-8/station	
spring cruise	PH	HPLC	c	y	n	Prezelin	6-8/station	
spring cruise	PH	NUT	c	y	n	Prezelin	6-8/station	
spring cruise	PH	PRODPI	c	y	n	Prezelin	4-6/station	
spring cruise	OV	OVIEW	c	y	n	chief sci	per event	

V. Educational activities

A. Graduate student thesis topics

Nicolas Boucher, Ph.D. student

University of California at Santa Barbara

Advisor Barbara Prezelin

The thinning of the stratospheric ozone layer is predicted to continue into the next century. Due to atmospheric current patterns, ozone depletion is most prominent over Antarctica during the austral spring and leads to increased levels of UVB radiation reaching the surface of the earth. During the austral spring 1990, I participated in a study that measured the impact of UVB radiation on the water column primary production (Icecolors '90). Preliminary results showed that phytoplankton photosynthesis was decreased by 6-12% due to the increased levels of UVB radiation over the Marginal Ice Zone in the Bellinsghausen Sea, Antarctica (Smith et al. 1992). The approach used in this study also allowed us to quantify the effects of background levels of UVA radiation on primary production in natural communities. I propose to use existing data from two austral spring cruises (Icecolors '90, LTER '91) to develop and test a UVA and UVB dependent bio-optical model of primary production in antarctic waters.

The specific aims are:

1) to combine a PAR dependent model with UV dependent fractional inhibition algorithms into a single UVB, UVA and PAR dependent bio-optical model of <u>in situ</u> rates of primary production in antarctic waters and

2) to use the model to estimate measured rates of production in the presence and absence of UVA and/or UVB radiation over the time and space scale of the LTER '91 austral spring cruise.

The results of such a modeling effort with 'real world' data should advance significantly any attempt to estimate the temporal and spatial variability of <u>in situ</u> primary production in antarctic waters. It is also likely that advancing a predictive approach to UV dependent primary productivity in antarctic waters would benefit similar attempts in other marine environments where UV radiation is a significant environmental factor.

Thomas Frazer, Ph.D. student

University of California at Santa Barbara

Advisors Robin Ross Langdon Quetin

The larvae of Euphausia superba are found feeding on the underside of sea ice during the austral winter. This observation has been observed many times in the past decade and the presence of sea ice and the food sources associated with it may be important to the winter-over survival of larval krill (Ross and Quetin 1991). My thesis will focus on the winter ecology of larval krill and contribute to a more detailed and quantitative understanding of the role of ice-associated food resources in their winter diet. The results of the research will be of interest to krill biologist as well as those with an interest in direct and indirect interactions between biotic and physical components of food webs.

The thesis will consist of four related chapters. The first will provide a quantitative characterization of the abundance and distribution of krill larvae under annual sea ice during early and late winter. The second and third chapters will evaluate the use of stable isotopes as a chemical tool to quantify the long-term assimilation of ice-associated food resources consumed by larval krill during winter. The second chapter will rely heavily on field collected data. The third chapter will make use of laboratory experiments to more rigorously assess the conclusions drawn from the field. The final chapter will make use of a suite of physiological measures, e.g. growth, ingestion and respiration, to investigate the energetics of larval krill during early and late winter.

Karen L. Haberman, Ph.D. student

University of California Santa Barbara

Advisors Robin Ross and Langdon Quetin

Previous studies suggest that growth and reproduction of antarctic krill, Euphausia superba, are food limited in the Southern Ocean. However, a knowledge of whether certain phytoplankton types or groups are better utilized by krill is important to understanding how patterns of phytoplankton abundance and species composition affect the krill's food availability and thus, overall fitness in krill. This thesis is designed to compare the ingestion and assimilation of different types of phytoplankton by the antarctic krill, and to determine whether they selectively feed on certain types or physiological stages of phytoplankton, with an emphasis on the prymnesiophyte Phaeocystis, and diatoms. The reason for this focus is twofold: first, both Phaeocystis and diatoms occur in large blooms in the Southern Ocean, and both are in the size range grazed most effectively by krill; second, available evidence suggests that the edibility and nutritional value of Phaeocystis for various grazers are low compared to diatoms.

During preliminary experiments, krill did not ingest Phaeocystis colonies (mean diameter 100-µm) in stationary growth phase. In a Phaeocystis/ diatom mixture, total ingestion rate was negligible when the mix contained Phaeocystis from a culture not ingested as a unialgal food source. Visual observations indicate that this lack of feeding may be due to clogging of the feeding basket by a mucousy exudate from the Phaeocystis colonies. The importance of Phaeocystis' physiological state to its ingestion and assimilation by krill will be examined in detail. I also intend to evaluate immunochemical techniques to compare gut contents of field-caught krill to the phytoplankton pigment profiles collected concurrently as part of the LTER core data set. This comparison will enable me to determine whether krill are selective feeders.

One major objective is to determine whether species composition and physiological state of phytoplankton influence ingestion and assimilation by krill. I will conduct long-term grazing experiments during which krill growth will be measured to assess the impact of different phytoplankton community composition on secondary production, and facilitate more accurate modeling of krill growth and reproduction based on phytoplankton distribution. Information from this thesis will also help us assess the influence of krill grazing on the composition of the phytoplankton community.

Cathy M. Lascara, Ph.D student

Old Dominion University

Advisor Eileen Hofmann

The PhD research project being undertaken will focus on investigation of processes important to the distribution and dynamics of antarctic krill in waters west of the Antarctic Peninsula. The approach will be multi-phase, involving several specific objectives and require synthesis of field observations, literature review and simulation modeling experiments. Analysis of a multi-disciplinary data set collected by the LTER will form the foundation of the first phase of this dissertation research. The objective is to quantitatively map the spatial and temporal distribution of krill and to interpret krill distribution patterns in relation to other habitat characteristics; in particular, the concentration and composition of food resources, ice history, large-scale flow regimes, and hydrographic and optical properties of the upper ocean. The second phase will be to develop a conceptual model which illustrates the biological and physical processes that determine the environmental variability experienced by krill. This model will be formulated as a set of modules or sub-models that consider specific processes. It is envisioned that the entire model will be too complicated to tackle as a single problem. However, understanding of krill dynamics may be greatly improved through simulation models designed to examine single processes. But the frame work of a complete conceptual model is necessary so that sub-modeling efforts can be interpreted in the context of the entire system. The final phase of this research project will concentrate on the development of a series of time- and space-dependent modules to determine appropriate mathematical formulations and coefficient parameterizations for several key processes identified in the conceptual model. Initial modeling efforts will focus on the processes of growth and biological diffusion in a variable environment.

Mark A. Moline, Ph.D. student

University of California at Santa Barbara

Advisor Barbara Prezelin

Although macronutrients in the Southern Ocean are in ample supply to sustain a large phytoplankton standing stock, the region is typically one of low primary productivity and large episodic blooms account for the majority of the annual productivity. Mechanisms and processes explaining both the 'Antarctic Paradox' and the formation and dissipation of 'megablooms' have emerged (Sullivan et al. 1988, Smith et al. 1990, Mitchell et al. 1991, Sakshaug et al. 1991, Smetacek et al. 1992). Most of these studies, however, have been conducted shipboard and as a result have been restricted to describing the above in a spatial context. A few have concentrated on the temporal variability of phytoplankton dynamics but have either limited there studies to a few parameters of interest or to time scales too large for the processes themselves.

With the existing datasets (including hydrographic, optical, and primary productivity components) collected over the first three LTER field seasons (9192PAL, 9293PAL, 9394PAL), I propose to develop and advance the understanding of the mechanisms controlling primary productivity in Antarctica. Specific goals working with the data sets are:

(1) To examine the multiple feedback mechanisms between the physical, chemical, and biological systems and to determine the time scales on which they occur (9192PAL dataset).

(2) To examine the above mechanisms on annual time scales using the data collected from 1991-1994 and to identify the major determinants driving phytoplankton biomass and primary productivity.

(3) To test existing models of antarctic productivity with the LTER 9192PAL dataset and to develop a temporal model based on integrating the hydrography, optics, and primary production.

(4) To verify the predictive strength of the developed model using the 9293PAL and 9394PAL datasets.

Results from the PAL datasets should significantly advance present knowledge of the time scales of processes governing antarctic primary productivity. They will also provide the Palmer LTER and others a criterion to increase the efficiency of future sampling efforts.

David A. Smith, PhD student

Old Dominion University

Advisor John Klinck

The research project being done will consider the hydrography and circulation in the LTER region. This analysis will consist of three general sub-studies: analysis of historical observations of water properties, analysis of time and space dependence of surface exchanges that force the circulation and numerical modelling of the circulation.

The analysis of historical data will be accomplished with observations from three general data sources, which contain some overlap: National Ocean Data Center, Southern Ocean Atlas (Arnold Gordon) and Southern Ocean Atlas (Dirk Olbers). Attempts will be made to obtain hydrographic observation from other sources such as the British Antarctic Survey and the RACER project. These historical observations will be combined with the hydrographic and nutrient measurements taken as part of the various LTER cruises. Analysis of this data will focus on tracking the path of Circumpolar Deep Water as it moves onto the shelf and on an estimation of the depth of the mixed layer during various seasons.

The circulation and physical environment in the Bellingshausen Sea is affected by surface wind stress, heat exchange with the atmosphere, solar heating and ice cover. Each of these processes can be estimated from climatologies or atmospheric analyses (or forecasts). The monthly variability of ice cover is being considered by other investigators in the LTER project, so these results will be used without further analysis. The twice daily analyses of the Australian Meterological Service will be obtained to estimate surface wind stress, air temperture, humidity and cloud cover. These values will allow an estimation of the heat flux at the ocean surface. The crudest analysis will be to use the values of pressure and temperature at the ocean surface to estimate fluxes. If possible, we will obtain the estimated surface flux values that are used in the boundary layer part of the atmospheric model. These should provide better estimates of the twice daily fluxes of heat and momentum.

The final part of this study will be the implementation of a 3-d circulation model, specifically, SPEM (semi-spectral primitive equation model) written by Dale Haidvogel for the Bellingshausen Sea. This model includes at thermodynamically active mixed layer and ice. A series of experiments will be used to see the influence on the physical properties in this area of offshore ocean circulation, surface wind stress, ice cover, redistribution of ice by wind and circulation, surface thermodynamic exchanges and ice production. The offshore circulation will be estimated from the monthly solutions from FRAM (fine resolution antarctic model) which has been run by British scientists. This is a full model of the Southern Ocean which is forced by seasonally varying wind and heat fluxes. Forcing for the other model cases will come from estimates obtained in the second part of this study.

Sharon Stammerjohn, M.A. student (completed thesis December 1993)

University of California at Santa Barbara

Advisor Ray Smith

Abstract. Spatial and temporal variability in Southern Ocean sea ice coverage is analysed from October, 1978 to December, 1991. Sea ice coverage is calculated from passive microwave satellite data, using Scanning Mulit-Channel Microwave Radiometer (SMMR) and Special Sensor Microwave/Imager (SSM/I) data. Spatial variability in sea ice coverage was based on the following eight regions: Southern Ocean, Weddell, Indian, West Pacific, Ross, Amundsen and Bellingshausen regions, as well as the subregion of the Bellingshausen, the Long term Ecological Research (LTER) study area located west of the Antarctic Peninsula. The six adjacent Southern Ocean regions all show unique interannual

variability which is confirmed by cross spectral analysis of monthly anomalies, and no two regions have the same anomalous years of extreme maximum or minimum ice coverage. Regional interannual variability appears to be a yearly re-distribution of near constant ice coverage for the whole Southern Ocean, and in extreme high or low ice years there are asymmetries in southern ocean ice coverage. Spectral analysis of monthly anomalies confirmed that most of the variance in regional ice coverages is due to interannual variability. Several patterns in interannual and annual variability are observed in the 13.25-year time series of southern ocean ice coverage, and possible climatic forcings contributing to these patterns are discussed. A thorough characterization of LTER ice coverage in comparison to the other regional ice coverages is provided, and possible ice-ocean-air and ice-ecosystem dynamics in the LTER region are explored.

B. Research Experience for Undergraduates (REU) Site

The Palmer LTER was an REU site during the 1991-1992 and 1992-1993 austral seasons, years two and three of the Palmer LTER. We recruited undergraduates to become integral members of four research teams within the Palmer LTER. The research areas included: hydrography, optical characteristics of the water column, primary production and phytoplankton physiology, and secondary production (pelagic zooplankton and fish). The overall objective was to provide an educational experience to acquaint students with all aspects of the research process and to encourage them to continue their education in science. The experiences included: a seminar series, pre-season training in the advisor's laboratory, 10 weeks in Antarctica as an essential member of a research team, and independent research projects with data analysis and preparation of publications in the home laboratory. One of the benefits to the student participants was the integrative aspects of the LTER as an interdisciplinary research program. Seven undergraduates joined three research teams in 1991-1992 and eleven undergraduates four research teams in1992-1993, joining the Palmer LTER research teams for research either at Palmer Station or on one of two research vessels. Students evaluated the program at the end of their award and the majority believe that their experience was beneficial in either helping them find a focus within aquatic science or deciding to continue in science as either technicians or graduate students.

VI. Evidence of historical literature being considered and incorporated; intersite and network activities; leadership, management and organization

A. Historical Literature.

The existing long-term databases on upper-trophic level predators in the vicinity of Palmer Station stem from research on the ecology of seabirds initiated in the early 1970's by Parmelee et al. 1977. Originally focusing on species other than penguins, this research established the earliest evidence linking aspects of the ecology of south polar skuas with antarctic silverfish. Subsequent work by Neilson (1983) and Pietz (1986, 1987) demonstrated that sea ice may also be important to the foraging ecology of south polar skuas, and thus play a role in determining reproductive success. Intensive studies on Adélie penguins did not begin in the area until the CCAMLR (Convention for the Conservation of Antarctic Marine Living Resources) Ecosystem Monitoring Program (CEMP) was established in 1987 (Fraser and Ainley 1988). The United States component of CEMP is known as AMLR (Antarctic Marine Living Resources) and is discussed in another section. Although focused on Adélie penguins, this program provided the vehicle for continued studies on south polar skuas and other predators, inluding marine mammals and terrestrial ecosystems. As a result, and particularly in view of the recent establishment of the Palmer LTER, the databases developed at Palmer Station on upper-trophic level predators include some of the oldest, most complete, coincident terrestrial, pelagic and environmental records available for the Southern Ocean.

American Geophysical Union (AGU) volume, "Foundations for Ecological Research in the Western Antarctic Peninsula Region", by the Palmer LTER accepted. Manuscripts are due in late March. The Preface and Table of Contents are are provided below.

Preface

The LTER (Long-Term Ecological Research) Program was established in 1981 by the National Science Foundation of the United States because of the need to study some ecological processes that occur over longer time spans than the normal three year grant duration. Today the LTER Network consists of 18 sites that span a variety of ecosystem types in the continental United States, Alaska, Puerto Rico and Antarctica. The addition of the Palmer LTER at Palmer Station, Antarctica in October of 1990 extended the geographical and ecological range of the LTER Network, and provided the opportunity to link physical and ecological processes in the northern hemisphere to those in the southern hemisphere.

One of the criteria for establishment of an LTER site is the existence of historical data and observations that serve to guide future research programs. In this monograph we bring together in one place the meteorological, hydrographic, biological and ecological observations made in the general area of the Bellingshausen Sea and Antarctic Peninsula, and discuss the natural processes underlying those observations. This compilation of available data and observations in conjunction with our present understanding of processes provides the foundation for long-term studies of the ecosystem west of the Antarctic Peninsula. In this context this monograph also provides a place for informal historical observations often so important to our understanding of long-term variability and change.

The area of study of the Palmer LTER is bounded by the southern end of the Bransfield Strait extending south to Marguerite Bay, and from the Antarctic Peninsula seaward for 200 km. The northern end of the area of discussion is the southern edge of a gap in the distribution of Adélie penguin (Pygoscelis adeliae) populations that extends to Livingston Island. The seaward limit of the area is at the seaward limit of krill (Euphausia superba) distributions, includes probable spawning grounds for antarctic silverfish (Pleuragramma antarcticum) in the Biscoe Islands, and contains hydrographic features of the Southern Ocean that are uniquely antarctic. The Palmer LTER has as its central hypothesis that interannual variability in the annual extent of the pack ice has major impacts on all levels of the marine ecosystem, and interannual variability in the extent of winter ice cover is high in the chosen region. This monograph does not contain reviews of the larger geographic distributions, but instead restricts the geographical breadth of the data summaries and extends the depth and multidisciplinary nature of the coverage. Even with the stated geographical restrictions and our intent to look at a small area in depth, there will be limitations. For example, the monograph is primarily marine oriented, a choice made to accurately reflect differences in habitat area and species richness between the marine and terrestrial ecosystem. The geographically restricted observations on patterns and distributions are placed in the context of our knowledge to date of the underlying processes that affect them, and this knowledge comes from many regions in the Southern Ocean. To achieve this aim, the chapters are organized around several general themes introduced by a historical overview of research and more informal observations in the region. Chapters describing the various habitats precede chapters describing the distribution of biological populations. Chapters reviewing and evaluating the current state of our knowledge of processes controlling the distributions follow. The role of man's impact on the region, whether commercial fishing or tourism, is another feature and must be included in the context of this long-term multidisciplinary program. A final chapter summarizes the state of our knowledge and the design and objectives of the Palmer LTER with comments about other large research initiatives such as GLOBEC and BOFS in the area.

Draft Table of Contents - one author has not yet confirmed

Preface authors - R. Ross, E. Hofmann, L. Quetin

Part I. Historical Description and Perspective

author - S. El-Sayed, Texas A and M University

Part II. Habitat Description

Chapter 1. Terrestrial Habitat

author - D. Walton, British Antarctic Survey

Chapter 2. Terrestrial Biotic Components

author - R. Lewis Smith, British Antarctic Survey
(invited, decision pending)

Chapter 3. Water Mass Distributions and Circulation

authors - E.E. Hofmann, J.M. Klinck, C.M. Lascara, D. Smith, Old Dominion University

Chapter 4. Sea Ice Distribution

authors - R. Smith and S. Stammerjohn, University of California, Santa Barbara

Chapter 5. Climate and Meteorology

authors - R. Smith and K. Baker, University of California, Santa Barbara

Chapter 6. Benthic Habitat

authors - M. White and A. Clarke, British Antarctic Survey

Chapter 7. Sedimentary Record

author - E. Domack, Hamilton College

Part III. Distributions of Biological Populations (Horizontal and Vertical)

Chapter 1. Microbial communities

author - Dave Garrison, National Science Foundation and University of California at Santa Cruz

Chapter 2. Standing Stock of Phytoplankton

author - Greta Fryxell, Texas A and M University, and others

Chapter 3. Standing Stock of Zooplankton plus Krill

authors - L. Quetin, R. Ross of University of California at Santa Barbara, C. Lascara of Old Dominion University, and V. Marine, University of Chile

Chapter 4. Benthic Communities

author - M. White, British Antarctic Survey

Chapter 5. Standing Stock of Fish

author - A. Kellerman, Nationalparkamt Wattenmeer
(invited, decision pending)

Chapter 6. Marine Birds

authors - W. Fraser and W. Trivelpiece, Old Dominion University

Chapter 7. Marine Mammals

authors - ?

Part IV. Control of Biological Distributions (Horizontal and Vertical)

Chapter 1. Microbial Processes

author - D. Karl, University of Hawaii at Manoa

Chapter 2. Primary Production

authors - B. Prézelin and R. Smith, University of California at Santa Barbara

Chapter 3. Pelagic Secondary Production

authors - R. Ross and L. Quetin, University of California at Santa Barbara, and others

Chapter 4. Benthic Production (fish, macroalgae, invertebrates)

author - A. Clarke, British Antarctic Survey

Chapter 5. Marine Birds

authors - W. Trivelpiece and W. Fraser, Old Dominion University

Chapter 6. Marine Mammals

authors - D. Costa, ONR and University of California at Santa Cruz

Part V. Human Disturbance

Chapter 1. Terrestrial Disturbances

Ron Naveen, Oceanites, and Wayne Trivelpiece, Old Dominion University

Chapter 2. Marine Disturbances - Hydrocarbons

author - C. Kennicutt, Texas A and M University

Chapter 3. Marine Disturbances - Commercial Fishing

authors - S. Nicol, Australian Antarctic Division, and D. Agnew, CCAMLR

Part VI. Summary and Synthesis

authors - Palmer LTER Group

B. LTER Coordinating Committee meetings, All Scientists Meetings

LTER Network All Scientists Meeting

The Palmer LTER participated in both the 1990 and 1993 All Scientists Meetings. For each meeting, five people attended and we presented posters about our site and ongoing research. One strong difference between the 1990 and 1993 All Scientists Meetings is that there is a more widespread acceptance of the antarctic LTERs as having relevant things to

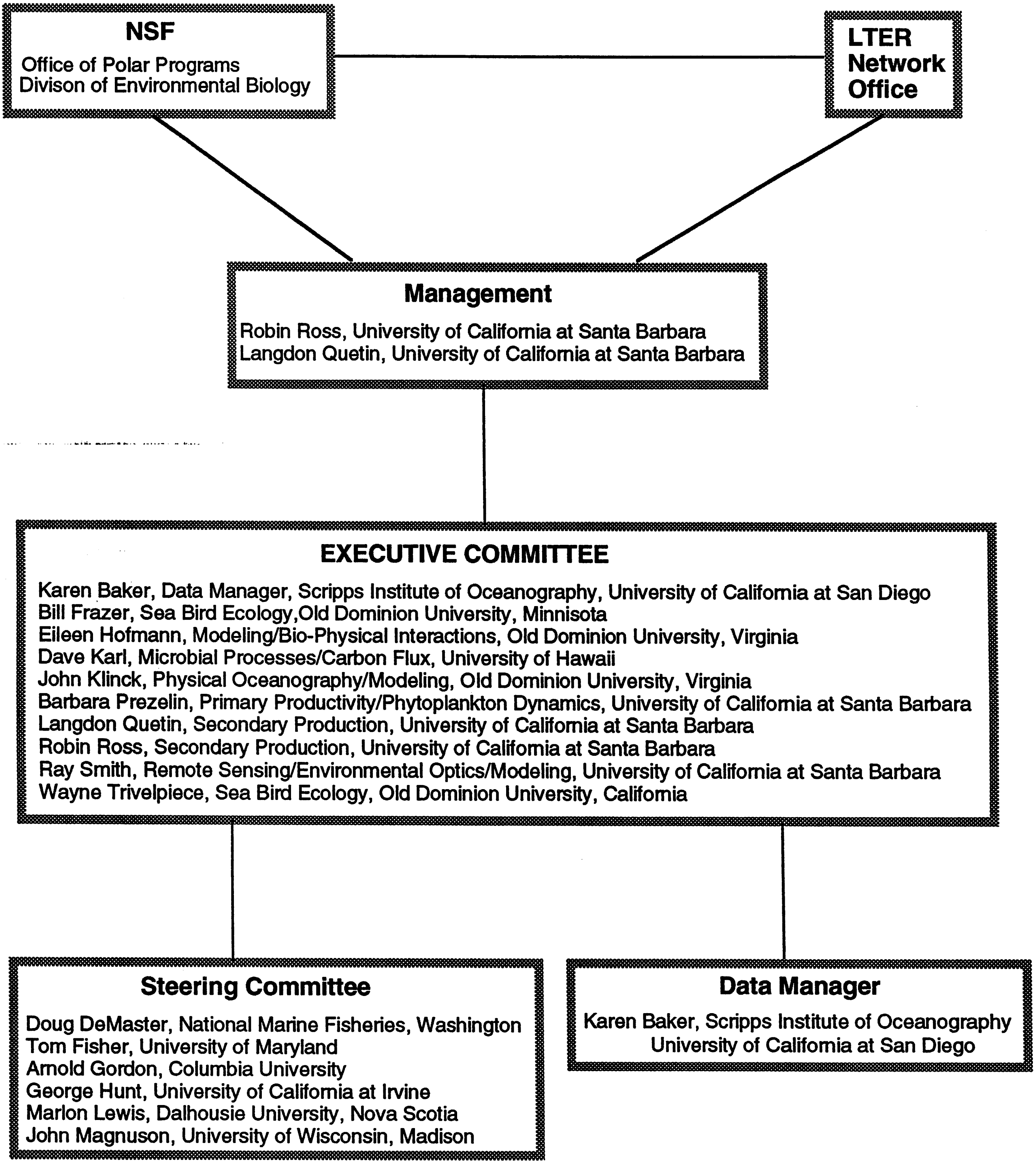


Figure 22. Administrative organization of the Palmer LTER

contribute to the Network. The ten minute site bite with pictures of the ecosystem at work and some sample data helped others see how antarctic LTERs (both Palmer and McMurdo Dry Valleys) might fit into the range of ecosystems. In September 1993 we actively participated in several of the workshops, and see intersite comparisions or studies developing in the following areas:

o El Nino - (Bruce Hayden from Virginia Coast Reserve is the leader.) Everyone agreed to look for possible effects in their ecosystems.

o Food Webs - (Robert Waide from Luquillo, Tom Frost from North Lakes) A small group will try a cross site comparison of food webs. The comparison will be in two parts: (1) construct food webs and compare basic food web parameters such as food chain length, (2) plan a cross-site experiment (a proposal will be necessary)

o LTER and NASA/EOS Collaborative Research - Karen Baker managed to obtain two of the four sun photometers from the NASA/EOS workshop committed to the Antarctic, one for Palmer and one for McMurdo Dry Valleys. They will switch out with the two arctic sites so all four sites have coverage for the spring and summer months.

o Biodiversity - also in several parts, and with no long time series yet, we can best participate at the level of looking at biodiversity and how increasing the spatial scale of sampling increases diversity.

C. Organization

The Executive Committee consisting of the ten principal investigators is the primary governing body of the Palmer LTER (Fig. 22). The committee provides general scientific direction and budget guidelines. Issues are decided in the Executive Committee by majority vote. Formal communication is maintained between principal investigators with a monthly agenda sent by email and two annual meetings. The co-managers of the LTER are the direct administrative contacts of the Palmer LTER to the LTER Network and the National Science Foundation. The co-managers coordinate the monthly agenda, Executive and Steering Committee meetings, the overall field season and perform other general administrative funcitions. The research, modeling and data management activities of the Palmer LTER are divided into several components with each administered by one to two principal investigators. The principal investigators of each component plan the detailed logistics for a field season and are responsible for the collecting specific data sets, and entry of data and results into the Palmer LTER data base. Field work at Palmer Station is often the responsibility of technicians or graduate students in the absence of the principal investigator. Undergraduate student volunteers comprise the majority of the field teams and are of great importance to our success.

D. International interactions

CCAMLR and SCAR

The Scientific Committee on Antarctic Research (SCAR) and the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) are international governing bodies that receive recommendations on a host of issues related to the Southern Oceans through a diverse network of specialists and working groups. Two LTER PI's, William R. Fraser and Wayne Z. Trivelpiece are, respectively, United States representatives to SCAR and CCAMLR, and address these bodies through participation in the Bird Biology Subcommittee of the Scientific Committee on Antarctic Research (WRF) and the CCAMLR Ecosystem Monitoring Program (WRF and WZT). The most direct interactions with the LTER occur primarily through the CCAMLR Ecosystem Monitoring Program (CEMP), which seeks annual data on the ecology of Adélie penguins as part of its efforts to develop long-term monitoring programs. These data are delivered to CEMP through the Antarctic Marine Living Resources Program (AMLR), which provides U.S. funding for its collection, analysis and the preparation of an annual report (see reports by Fraser et al. 1988-1993).

JGOFS (Joint Global Ocean Flus Study - Palmer LTER as a high latitude time series station

JGOFS may be interested in sponsoring the Palmer LTER as a high latitude time series station. A preposal is now being considered by NSF program managers, and if both the JGOFS Steering Committee and the program managers approve, a full proposal will be required. Most time-series stations for JGOFS are supposed to have biweekly or monthly sampling. However, our weekly sampling from station for spring and summer will satisfy requirements for a high latitude station.

VII. Related research projects

A. The Antarctic Marine Living Resources Program (AMLR).

Palmer Station is one of two active sites on the western side of the Antarctic Peninsula where proposed long-term monitoring of seabird populations has been initiated in support of U.S. participation in CCAMLR. The U.S. participates in CCAMLR through the United States Antarctic Marine Living Resources Program (AMLR), a national program of the National Marine Fisheries Service (NMFS) that emphasizes directed research on key component species in the Antarctic marine ecosystem. Recognizing that many Antarctic marine species are drawing increasing international interest due to their commercial fisheries potential, the principal objectives of directed research are to provide the U.S. and CCAMLR with the information needed to detect, monitor and predict the effects of fishing and associated activities on target and dependent populations in the marine ecosystem, including fish, squid, krill, seabirds and marine mammals.

AMLR research at Palmer Station, initiated in 1987, focuses on aspects of the ecology of Adélie penguins that are complementary to the scope of research and objectives outlined by CCAMLR. This research, which is independently funded, shares many objectives with the LTER, and, through cost-sharing, has facilitated long-term data collection on Adélie penguins on a scale that would otherwise have been difficult for any single program to fund. The result has been a mutually beneficial program with strong basic and applied components.

B. The Impacts of Tourism on Wildlife Populations at Palmer Station.

Tourism in Antarctica has been showing a steady increase since the late 1960's. However, despite rising concern that human activity may negatively impact wildlife populations, studies designed to address this issue have been lacking. The purpose of this study is to examine the feasibility of coupling research on the effects of tourism on Adélie penguin populations on Torgersen Island with two long-term ecosystem oriented programs already in existence in the area, namely the AMLR and LTER programs. The rationale for this approach is based on the premise that understanding and defining the natural variability inherent in the ecosystem is a necessary prerequisite for identifying and interpreting the effects of human activity. By employing identical technologies and methodologies, this study seeks to develop identical, coincident databases at sites visited by tourists to compare with databases developed as part of the two ecosystem studies at sites not visited by tourists. The latter will thus provide the background ecosystem data needed to discern and interpret the former. This arrangement is likely to establish the proposed research as one of the key studies addressing human impacts in Antarctica, and serve as a model for future research of a similar nature.

C. Icecolors II, 1993

The Antarctic Ozone Hole is recognized as an unambiguous example of how human activities in one part of the globe can influence processes in another part. The springtime stratospheric ozone layer over the Antarctic is thinning by over 50%, resulting in increased midultravioled (UVB) radiation reaching the surface of the Southern Ocean. Two LTER PI's, Barbara Prezelin and Ray Smith, are also co-PI's on a study to investigate the possible influence of ozone-related increases in UVB on phytoplankton communities. This work has been carried out in the LTER area, and many components of Prezelin's and Smith's research, both equipment and personnel, share common components between the LTER and Icecolors projects. For example, the LTER Aug/Sept 1993 cruise immediately preceeded the Ice'93 Oct/Nov cruise with some team members participating in both, providing a distinct savings in logistics and training of personnel. With this arrangement, the LTER cruise was able to provide exploratory information, having covered a significant part of the LTER grid, for the planning of Ice'93 while the latter cruise provided an additional month of selected hydrography and optics data to the LTER effort. The intellectual interactions are also strong, especially in understanding processes related to the spectrally dependent phytoplankton processes, including photoinhibition, photoreactivation, photoprotection, and photosynthesis. Further, the impact of UVB on phytoplankton communities, especially the possibility of long term effects, is clearly a concern for the LTER which will initially be addressed by the Icecolors research.

D. Energetics of adult and larval Euphausia superba (krill)

This research project with L. Quetin and R. Ross as co-PIs is focused on quantification of the role of ice biota in winter-over survival of krill larvae. Observed interannual differences in physiological condition of the larvae during the winter could lead to differences in survival of the young-of-the-year, and thus in the strength of any one year class. We proposed to investigate and compare the processes underlying such differences during early and late winter (June versus September). Low food availability in the fall after the summer phytoplankton blooms suggests that larvae in early winter will have experienced several months of near starvation conditions. Without an additional food source such as ice biota in the underside of the sea ice these larvae may not survive the winter. However, larvae under the ice in late winter of a heavy ice year will have had this additional food source, and may be in better physiological condition than the beginning of the winter. We will compare environmental conditions in open water and under ice, sample larval krill and determine their physiological condition, and quantify the nutritional contribution of the ice biota to total energy demand of the larvae on two month-long cruises to the Southern Ocean. In the laboratory at Palmer Station we will conduct experiments on the starvation tolerance of the late calyptopis and furcilia larvae, the stages present at the beginning of winter. We will establish what several measures of physiological condition (condition factor and lipid content) mean in terms of the nutritional history of the larvae, including the range of carbon content in a particular larval stage from close to the Point-of-No-Return (PNR) to well-fed. If larvae are starved beyond the PNR they can no longer recover, even if food subsequently becomes available. The proposed research will address several significant questions about the winter-over energetics of larval krill, in particular the role of ice biota in winter-over survival and subsequent recruitment.

E. Program for International Polar Oceans Research (PIPOR)

High resolution (30m) all weather sea ice data would be an enormously valuable asset to the Palmer LTER. Such data are now, in principle, available from an active microwave system on the European Remote Sensing Satellite (ERS-1). Ray Smith, with the recommendation of and collaboration with Dr. Frank Carsey at JPL, is a new member of the PIPOR team. This team includs the planning staff for the German SAR (Synthetic Aperature Radar) receiving station at O'Higgins on the Antarctic Peninsula who carry out field work on sea ice conditions in the Weddell and the Bellingshausen/Amundsen Seas. It is anticipated that this collaborative effort will make high resolution sea ice data available to the LTER in exchange for providing the PIPOR group with on site surface ice observations during the LTER season. A joint objective will be to enhance the accuracy of sea ice estimates from both active and passive microwave data in the Southern ocean.

F. Long-Term Ecological Research (LTER) on the Antarctic Marine Ecosystem: Microbiology and carbon flux.

This research with David Karl as the principle investigator focuses on biogeochemical cycling of carbon and associated elements at the Palmer LTER. This grant comprises the microbiology and carbon flux component of the LTER and will provide measurements of a suite of core parameters related to the carbon cycle and will test several hypotheses pertaining to carbon fluxes, including bacterial productivity and nutrient regeneration.

VIII. Site description, structures and facilities

The LTER site region surrounds Palmer Station, located in a protected harbor on the southwest side of Anvers Island midway down the Antarctic Peninsula. Within a 9-km radius of Palmer Station are two exposed, prominent points, and groups of islands that extend to the edge of the Bismarck Strait to the southeast. These islands have a diverse topography which extends into the intertidal and subtidal zones surrounding and linking the islands. Palmer Basin, 22 km southwest of Palmer Station, is the only deep basin in the area. The maximum depth is 1,280 m, and the basin is connected to the open ocean on the west side of Anvers Island, and to the southern end of the strait between Anvers Island and the Antarctic Peninsula to the northeast. Both channels are about 450 m deep.

The climate is typically maritime antarctic, with snow and rain common any time of the year. The temperature at Palmer is relatively mild, averaging about -10°C in July and 2°C in January, with temperature extremes recorded at -31°C and 9°C. Annual rainfall averages about 20 inches and snowfall about 14 inches.

Palmer is especially well-situated for studies of birds, seals, and other components of the marine ecosystem, and it is equipped with a large, well-outfitted laboratory and seawater aquaria. The station consists of two major and several smaller buildings. Peak population is 43, including support personnel. Many Palmer-based research project are undertaken in conjunction with the research ship *Polar Duke*, a 205 foot ice-strengthened research vessel or the *Nathaniel B. Palmer*, a 310 foot ice class research vessel. Small boats support research near Palmer Station.

IX. National and international presentations on Palmer LTER research

Christian, J. R., and D. M. Karl. 1993. Bacterial exoenzymes in marine waters: implications for global biogeochemical cycles. American Society for Limnology Meeting xx:xx.

Fraser, W. and D. Patterson. 1994. Human disturbance and long-term changes in Adélie penguin populations: a natural experiment at Palmer Station, Antarctic Peninsula. Sixth SCAR Biology Symposium. Life History Strategies. May/June 1994. Venice, Italy. Accepted oral presentation.

Frazer, T. L., L. B. Quetin, R. M. Ross, and R. C. Smith. 1994 Poster: Palmer LTER: Larval antarctic krill, Euphausia superba, and winter ice. Sixth SCAR Biology Symposium. Life History Strategies. May/June 1994. Venice, Italy. Submitted abstract.

Haberman, K., R. M. Ross, and L. B. Quetin. 1993. Poster: Grazing by the antarctic krill Euphausia superba, on Nitschia spp. and Phaeocystis spp. monocultures. LTER All Scientists Meeting and International Summit. September 18-24, 1993. Estes Park, Colorado.

Hofmann, E. E., D. A. Smith, B. L. Lipphardt, Jr., J. M. Klinck, R. A. Locarnini, and R. C. Smith. 1994. Circulation and heat distributions on the continental shelf west of the Antarctic Peninsula. February 21-25, 1994. Ocean Sciences Meeting. San Diego, California. Submitted abstract.

Hofmann, E. E., D. A. Smith, B. L. Lipphardt, Jr., R. A. Locarnini, and R. C. Smith. 1994. Palmer LTER: Circulation west of the Antarctic Peninsula. Sixth SCAR Biology Symposium. Life History Strategies. May/June 1994. Venice, Italy. Submitted abstract.

Klinck, J. M. and R. C. Smith. 1994. Palmer LTER: Heat budgets and implications for circulation on the continental shelf west of the Antarctic Peninsula. Sixth SCAR Biology Symposium. Life History Strategies. May/June 1994. Venice, Italy. Submitted abstract.

Klinck, J. M., C. M. Lascara, and R. C. Smith. 1993. Hydrography and krill distributions in the Bellingshausen Sea as part of a long-term ecological research program. European Geophysical Society, May 3-7, 1993, Viesbaden, Germany. Annales Geophysicae, Supplement II 11(149):.

Lascara, C. M., E. E. Hofmann, R. M. Ross, and L. B. Quetin. 1992. Acoustically-derived distribution of krill (Euphausia superba) swarms off the Antarctic Peninsula during austral spring 1991 (LTER Program). EOS 73(43):319.

Lascara, C. M., E. E. Hofmann, R. M. Ross, and L. B. Quetin. 1993. Poster: Distribution of antarctic krill within the Palmer LTER study region based on bioacoustics. LTER All Scientists Meeting and International Summit. September 18-24, 1993. Estes Park, Colorado.

Lascara, C. M., E. E. Hofmann, R. M. Ross, and L. B. Quetin. 1994. Seasonal changes in the mesoscale distribution of Antarctic krill in the waters west of the Antarctic Peninsula. February 21-25, 1994. Ocean Sciences Meeting. San Diego, California. Submitted abstract.

Lascara, C. M., E. E. Hofmann, J. M. Klinck, R. M. Ross, and L. B. Quetin. 1994. Palmer LTER: Seasonal and geographic variability in the distribution of Antarctic krill, Euphausia superba, west of the Antarctic Peninsula. Sixth SCAR Biology Symposium. Life History Strategies. May/June 1994. Venice, Italy. Submitted abstract.

Lipphardt, Jr., C. M. Lascara, D. A. Smith, J. M. Klinck, E. E. Hofmann, R. A. Locarnini, and R. C. Smith. 1994. Palmer LTER: Seasonal Changes in the hydrographic structure of the upper 100 m of the water column. Sixth SCAR Biology Symposium. Life History Strategies. May/June 1994. Venice, Italy. Submitted abstract.

Quetin, L. B., R. M. Ross, and C. M. Lascara. 1994. Palmer LTER: Fine-scale distribution of Antarctic krill, Euphausia superba, within coastal waters near Palmer Station off the Antarctic Peninsula. Sixth SCAR Biology Symposium. Life History Strategies. May/June 1994. Venice, Italy. Submitted abstract.

Quetin, L. B., R. M. Ross, and T. A. Newberger. 1994. Palmer LTER: Variability in the distribution of length classes and maturity stages of adult antarctic krill, Euphausia superba, with season and environmental factors. Sixth SCAR Biology Symposium. Life History Strategies. May/June 1994. Venice, Italy. Submitted abstract.

Ross, R. M. 1993. Site presentation discussing research near Palmer Station. LTER All Scientists Meeting and International Summit. September 18-24, 1993. Estes Park, Colorado.

Ross, R. M., L. B. Quetin, and M. O. Amsler. 1994. Physiological condition of larval antarctic krill, Euphausia superba, throughout the year. Sixth SCAR Biology Symposium. Life History Strategies. May/June 1994. Venice, Italy. Submitted abstract.

Smith, D. A., E. E. Hofmann, J. M. Klinck, R. A Locarnini, and R. C. Smith. 1994. Palmer LTER: Water mass distribution west of the Antarctic Peninsula. February 21-25, 1994. Ocean Sciences Meeting. San Diego, California. Submitted abstract.

Smith, D. A., E. E. Hofmann, J. M. Klinck, B. L. Lipphardt, Jr., R. A Locarnini, R. C. Smith. 1994. Palmer LTER: Hydrography in the region west of the Antarctic Peninsula. Sixth SCAR Biology Symposium. Life History Strategies. May/June 1994. Venice, Italy. Submitted abstract.

Stammerjohn, S. 1993. Poster: Variability in sea ice areal coverage along the western Antarctic Peninsula. LTER All Scientists Meeting and International Summit. September 18-24, 1993. Estes Park, Colorado.

Trivelpiece, W., S. G. Trivelpiece, and W. Fraser. 1994. The impact of pack ice on the demography and distribution of Adélie penguin populations. Sixth SCAR Biology Symposium. Life History Strategies. May/June 1994. Venice, Italy. Submitted abstract.

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Education
B.S. (Physics), University of California at Los Angeles, 1969
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Education
B.S. (Wildlife Management), Utah State University, 1973
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Education

B.S. (Biology), Chestnut Hill College, 1974
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Selected Publications

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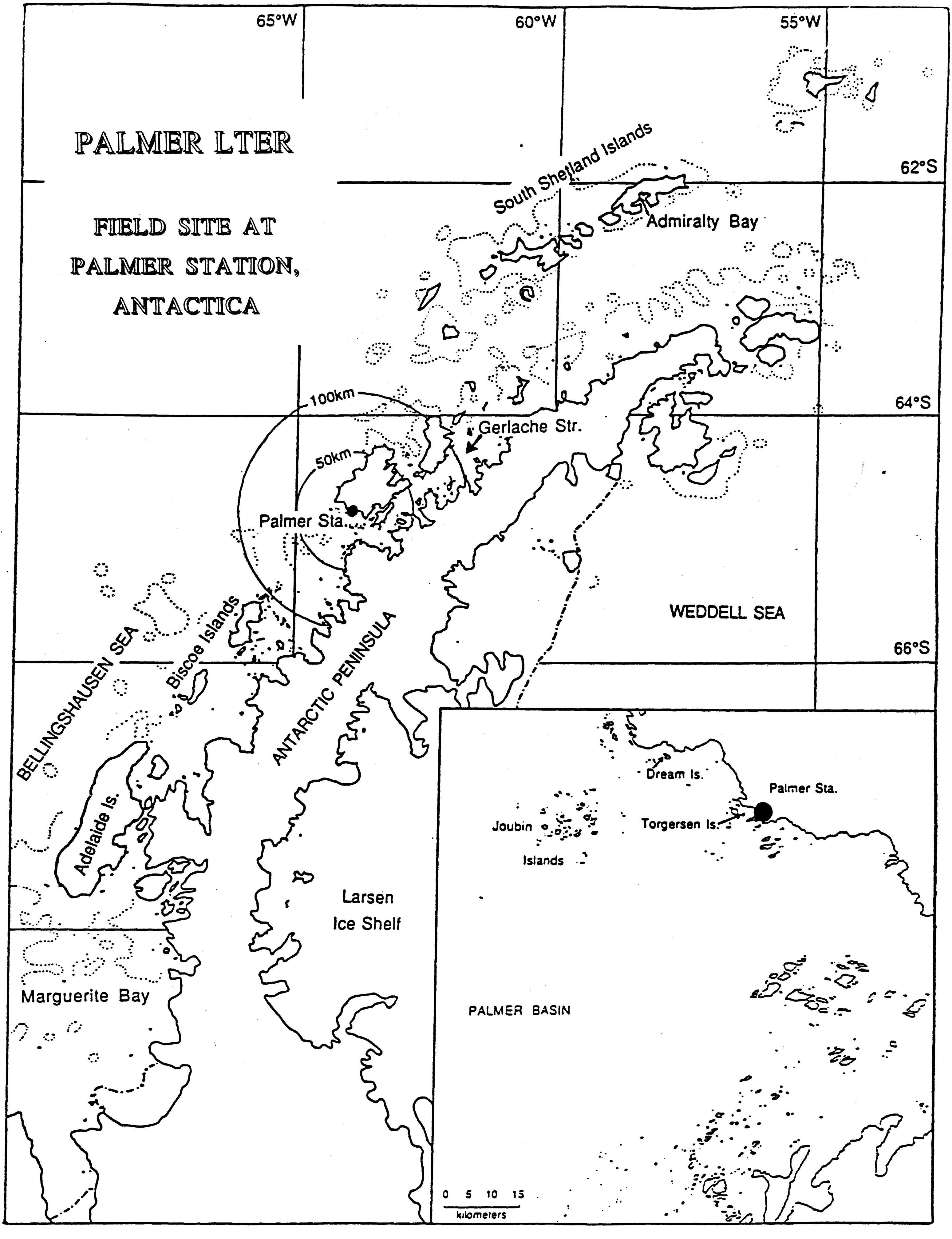

PALMER LTER

FIELD SITE AT PALMER STATION, ANTACTICA