Variability of Primary Production in an Antarctic Marine Ecosystem as Estimated Using a Multi-scale Sampling Strategy[1]

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SYNOPSIS. A major objective of the multidisciplinary Palmer Long Term Ecological Research (LTER) program is to obtain a comprehensive understanding of various components of the Antarctic marine ecosystem—the assemblage of plants, animals, ocean, sea ice, and island components south of the Antarctic Convergence. Phytoplankton production plays a key role in this polar ecosystem, and factors that regulate production include those that control cell growth (light, temperature, nutrients) and those that control cell accumulation rate and hence population growth (water column stability, advection, grazing, and sinking). Several of these factors are mediated by the annual advance and retreat of sea ice. In this study, we examine the results from nearly a decade (1991–2000) of ecological research in the western Antarctic Peninsula region. We evaluate the spatial and temporal variability of phytoplankton biomass (estimated as chlorophyll-a concentration) and primary production (determined *in-situ* aboard ship as well as estimated from ocean color satellite data). We also present the spatial and temporal variability of sea ice extent (estimated from passive microwave satellite data). While the data record is relatively short from a long-term perspective, evidence is accumulating that statistically links the variability in sea ice to the variability in primary production. Even though this marine ecosystem displays extreme interannual variability in both phytoplankton biomass and primary production, persistent spatial patterns have been observed over the many years of study (*e.g.,* an on to offshore gradient in biomass and a growing season characterized by episodic phytoplankton blooms). This high interannual variability at the base of the food chain influences organisms at all trophic levels.

INTRODUCTION

The Antarctic marine ecosystem is globally significant (Harris and Stonehouse, 1991). Mounting evidence suggests that the world climate is changing and that polar regions, with their associated ecosystems, may be especially sensitive to this change. In particular, the western Antarctic Peninsula (WAP) region (Fig. 1) has experienced a statistically significant warming trend during the past half century (King, 1994; Stark, 1994; Smith *et al.*, 1996b; King and Harangozo, 1998; Smith and Stammerjohn, 2001). Thus, this region is proving to be an exceptional area to study ecological response to climate variability (Ross *et al.*, 1996; Smith *et al.*, 1996a, 1999). Ecosystem research in the marine system (Fraser *et al.*, 1992; Trivelpiece and Fraser, 1996; Quetin and Ross, 2000), and paleoecological records from this area (Emslie, 1995; Emslie *et al.*, 1998), show that ecological transitions have occurred in response to climate change.

Primary production in the WAP area follows closely the distribution of phytoplankton biomass measured as chlorophyll a (chl-a) concentration, and published values show a wide range of spatial and temporal variability (Smith *et al.*, 1996a, 1998a; Dierssen *et al.*, 2000; Moline and Prezelin, 1996). Concentrations are greatest nearshore with an onshore/offshore gradient of decreasing biomass towards the continental
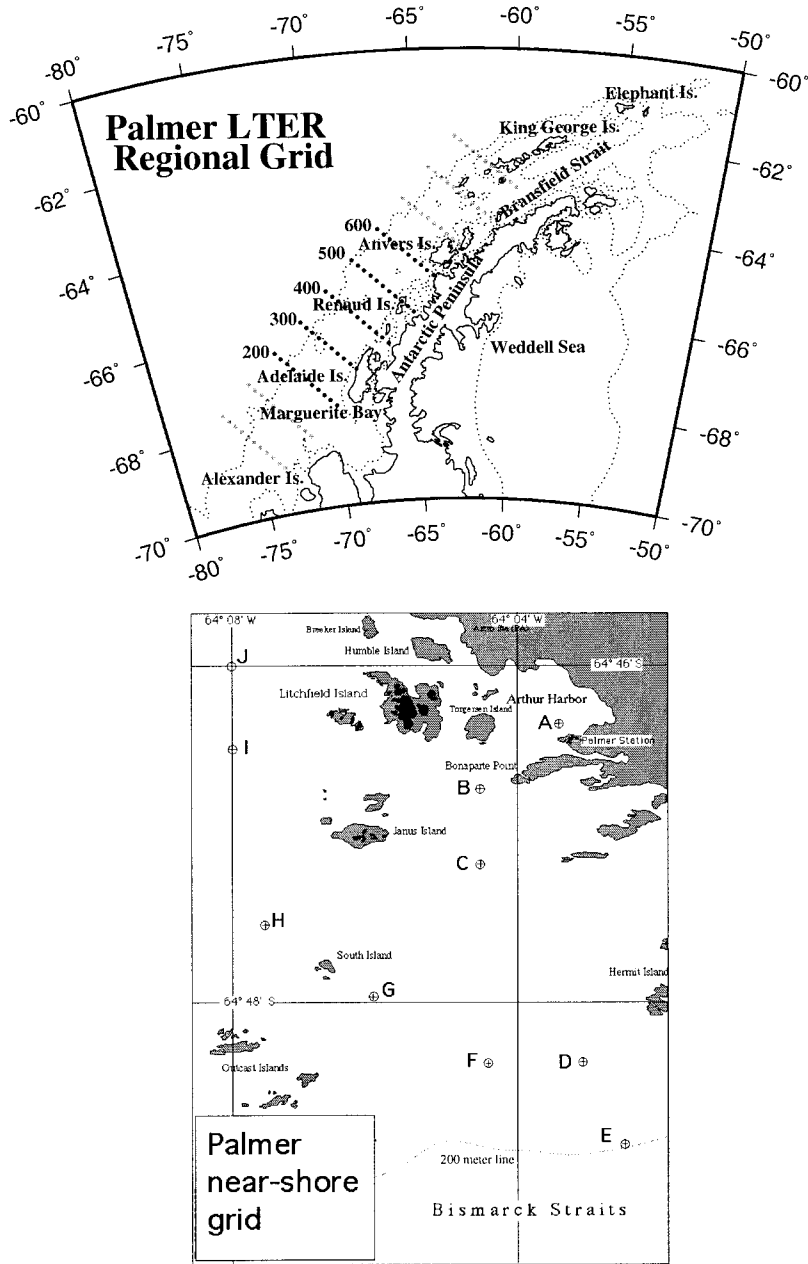
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FIG. 1. The Palmer LTER region. (A) Sampling grid visited every January/February, at the peak of the growth season. The 200 to 600 lines are shown in bold and include the sampling stations occupied during January cruises. The 200 m and 1,000 m bathymetric contours are indicated by the dotted lines. (B) Palmer LTER nearshore grid southwest of Anvers Island. The 200 m depth contour is indicated by the dotted line.

slope that follows a gradient in bottom to-pography and physical and optical proper-ties (Smith *et al.*, 1996*a*, 1998*c*). While many physical and biological factors (*e.g.,* light, temperature, nutrients, water column stability, advection, grazing, sinking) have been hypothesized as controls of cell and population growth, it is likely that no single

factor dominates, and environmental variability can significantly influence these various factors.

Sea ice coverage in the WAP area also shows high spatial and temporal variability (Stammerjohn and Smith, 1996) which has important implications for the marine ecosystem (Smith *et al.*, 1998*b*). Therefore, a central hypothesis of the Palmer LTER is that the advance and retreat of sea ice is a major physical determinant of spatial and temporal changes in the structure and function of the Antarctic marine ecosystem. For example, air temperature and sea ice are strongly linked in the WAP area (Jacka, 1990; Jacka and Budd, 1991; Weatherly *et al.*, 1991; King, 1994; Smith *et al.*, 1996*b*), and there is evidence for decreasing trends in sea ice that correspond to the statistically significant warming trends (Smith and Stammerjohn, 2001). In addition, the high variability in the frequency of storm events in the WAP region explains a significant amount of the variability in sea ice (Harangozo *et al.*, 1997; Marshall and King, 1998; van den Broeke, 2000; Stammerjohn *et al.*, 2001). The hydrography of the WAP area is poorly known (Hofmann *et al.*, 1996); however, the variability in circumpolar deep water intrusions onto the continental shelf (Fig. 1A) mediates sea ice formation and decay as well as influences the supply of nutrients to the shelf (Domack *et al.*, 1992; Jacobs and Comiso, 1997). It is within this context of a highly variable physical environment that we consider the spatial and temporal variability of pigment biomass and phytoplankton production.

Our goal is to estimate the spatial and temporal variability of primary production in the western Antarctic Peninsula (WAP) region. The need to synoptically characterize physical and biological properties of this large, inhospitable and remote ocean (*i.e.,* Southern Ocean) over long time periods leads to the use of satellite data. We use a multiplatform sampling approach (Smith *et al.*, 1987) whereby surface shipboard observations are used to develop in-water bio-optical algorithms, and these algorithms are used with ocean color (SeaWiFS) satellite data to estimate pigment biomass (Dierssen and Smith, 2000). We then use a depth-in-

tegrated primary production model that was developed specifically for these waters to estimate primary production from the satellite derived chl-a data (Dierssen *et al.*, 2000). Results are compared with independent shipboard observations to optimize in-water and satellite algorithms for estimation of primary production in the WAP region. The objective of this work is to determine the interannual variability of phytoplankton production, making use of our multi-scale sampling approach, and to discuss the role of sea ice in mediating this variability.

METHODS

Sampling strategy

Our long-term regional observations are structured by a sampling grid (Waters and Smith, 1992) that lies along the west coast of the Antarctic Peninsula (Fig. 1A). This fixed grid provides station locations that can be visited repeatedly over time scales of many years. The length of this grid runs roughly parallel to the peninsula (from southwest to northeast), and transect lines perpendicular to the peninsula are spaced every 100 km and numbered 000.xxx to 900.xxx. Along these transect lines, cardinal stations are spaced 20 km apart from nearshore (xxx.000) to 200 km offshore (xxx.200). Thus, cardinal station 600.140 would be located along the 600 line approximately 140 km offshore from the coast of the peninsula. It should be noted that some of the nearshore cardinal stations are located on or between islands (*e.g.,* Anvers, Renaud, Adelaide) and the peninsula. Thus, when sampling ''outside'' the islands, we typically occupy stations from xxx.040 to xxx.200 (*i.e.,* from 40 km to 200 km along a transect line). Further, the summer study area typically encompasses only the 200 to 600 transect lines. Within this portion of the grid we have had eight January cruises (1993–2000). The annual January cruises are timed to match a critical period in the breeding chronology of an apex predator, the Adelie penguine (*Pygoscelis adeliae*), within this marine ecosystem. In addition, there have been several process cruises that had a specific seasonal focus (March 1993, August 1993, June 1999). The geographi-

cally-fixed sampling grid also simplifies seasonal and interannual comparisons and facilitates modeling of multidisciplinary data sets. Surface observations within the large scale grid are limited by time and resources and, for our sampling strategy, are complemented by mooring, satellite and finer scale observations.

Within the large-scale peninsula grid we have embedded a smaller sampling grid (Fig. 1B) in the area adjacent to Palmer Station (*i.e.,* within the small-boating limit of 3.7 km of Palmer Station). Stations within this smaller grid are visited at least weekly (weather and sea ice conditions permitting) throughout the period of maximum phytoplankton production (typically October to March). Thus our surface sampling strategy includes spatial sampling during annual cruises in portions of the regional grid (Fig. 1A) and temporal sampling during the growth season in the area adjacent to Palmer Station (Fig. 1B). These surface observations are then complemented by satellite observations as discussed below.

Pigment biomass

Shipboard phytoplankton biomass is characterized by (1) total chl-a concentration using standard fluorometer techniques (Smith *et al.*, 1981), (2) photosynthetic pigments analyzed by high-pressure liquid chromatography (Kozlowski *et al.*, 1995), and (3) taxonomic analysis by microscopy. In this work we discuss only the fluorometer results, and total chl-a is used as a proxy measure of phytoplankton biomass. Water samples were processed either onboard ship while at sea or at Palmer Station, using Millipore HA filters that are subsequently extracted in the dark in a freezer for 24 hr in 90% acetone. Readings were made using a digital Turner Designs Fluorometer that is periodically calibrated using purified chlorophyll solutions (Sigma Co.) of known concentrations as confirmed by independent spectrophotometer measurements. Chl-a concentration is calculated by subtracting the phaeopigment concentration determined by sample acidification.

For the estimation of pigment biomass, satellite observations of ocean color have been used now for over two decades (Smith and Baker, 1978; Gordon and Morel, 1983; Hovis *et al.*, 1980). Basically, the spectral reflectance (or ocean ''color'') is determined by the backscattering and absorption of the dissolved and suspended materials within the upper layers of the water column. In waters dominated by increasing concentrations of phytoplankton, the color shifts from blue to green with increasing concentrations of chl-a. Bio-optical algorithms quantitatively relate chl-a to the spectral reflectance observed by an ocean color satellite sensor (*e.g.,* SeaWiFS). Here we utilize monthly SeaWiFS Level-3 Standard Mapped Images of chl-a provided from the NASA Goddard Space Flight Center's Distributed Active Archive Center (Version 2, Hooker and McClain, 2000). These images are global-area coverage data that have been averaged over each month using the maximum likelihood estimator mean. The resolution of each pixel in the image is approximately 0.088 degrees latitude and longitude, which translates roughly to a resolution of 9.77 km per pixel in the north-south and 4.2 km per pixel in the east-west direction. Land, clouds and sea ice have been masked from the SeaWiFS images shown here.

It has been shown for Antarctic waters that there is a relatively tight coupling between surface chl-a and chl-a integrated to depth within the euphotic zone (Morel and Berthon, 1989; Comiso *et al.*, 1990; Holm-Hansen and Mitchell, 1991; Smith *et al.*, 1996a). Since ocean color satellite observations effectively sample the upper layers (Gordon and McCluney, 1975; Smith, 1981), the derived signal is generally well correlated with integrated chl-a within the water column. This is an important advantage for remote sensing in Antarctic waters. A significant disadvantage, however, is the high percentage of clouds that obstruct visible and infrared wavelengths.

Recent research with ocean color data of the Southern Ocean (SO) (Mitchell and Holm-Hansen, 1991; Mitchell, 1992; Sullivan *et al.*, 1993; Tilzer *et al.*, 1994; Arrigo *et al.*, 1998; Dierssen, 2000) indicates that bio-optical properties are significantly different in the SO when compared to other regions. Consequently, Dierssen *et al.*

(2000) using a large *in-situ* data set (>1,000 stations from the Palmer LTER program) assessed the general processing algorithms for ocean color satellites and then created a revised SO-algorithm for use in Antarctic waters (Dierssen and Smith, 2000). These authors discuss in detail both the biological and optical methods used in their work. A validation of the SO-algorithm using SeaWiFS data (Version 2) shows that satellite-derived chl-a can be used to accurately estimate chl-a in these waters (Dierssen, 2000). For this analysis, all satellite-derived chl-a is adjusted using the SO-algorithm.

Primary production

Shipboard samples for determining primary production were collected at depths corresponding to the following percent surface irradiance: 100%, 55%, 27%, 11%, 5%, and 2%. Duplicate production samples were estimated for each light level by 24-hr simulated *in situ* incubations with ^{14}C-bicarbonate. The incubations were conducted on deck, and temperature was controlled by running seawater (from the ship's seawater intake located at 3 m depth) through the incubation apparatus. These shipboard production data were then used to optimally parameterize a production model so as to enhance model performance for the WAP area.

Behrenfeld and Falkowski (1997) provide a summary of phytoplankton primary production models and show that such models equate depth-integrated primary production to the product of: surface phytoplankton biomass, a photoadaptive variable, euphotic depth, an irradiance-dependent function and daylength. Our formulation of this model (Dierssen *et al.*, 2000) is as follows:

$$PP_{eu} = P_{opt}^{B} D Z_{eu} C_o F, \qquad Z_{eu} = 46.8 C_o^{-0.36}$$

where PP_{eu} is daily integrated primary production [mg C m^{-2} day^{-1}], D is daylength [h], Z_{eu} is the euphotic depth [m], F is the irradiance-dependent function taken as a constant and equal to 0.64, P^B_{opt} is the photoadaptive variable and set to 1.09 [mg C mg chl-a^{-1} hr^{-1}] for these waters, and C_o is the satellite-derived chl-a (*i.e.,* a measure of the surface phytoplankton biomass). In our formulation of the model we investigated the possibility that environmental factors (*e.g.,* sea surface temperature, incident irradiance, chlorophyll, day length, mixed layer depth, etc.) may influence the variability of P^B_{opt}. However, no parameter (in particular sea surface temperature) produced a statistically significant relationship to P^B_{opt} that would increase predictability of the model over a constant value. Parameterization of the model in the context of environmental variability remains a subject of further research.

This standard production model was optimized using Palmer LTER bio-optical data to fit the relatively uniform chl-normalized production profile and low photoadaptive variable (characteristic of low-light adapted phytoplankton) found in Antarctic waters. It was developed using Palmer LTER 1994/95 and 1995/96 field data and then tested using other Palmer LTER data and historic data from the WAP region. This model explained 72% of the variability in WAP primary production (Dierssen *et al.*, 2000; Dierssen, 2000).

Sea ice

Passive microwave remote sensing of the Southern Ocean provides one of the most complete space/time records of the annual advance and retreat of sea ice, because microwaves are neither limited by clouds nor winter polar darkness. Consequently, these data are exceedingly valuable in both describing and understanding the highly variable physical environment affecting the marine ecology of polar regions. The passive microwave data used in this study are from the Defense Meteorological Satellite Program's (DMSP) Special Sensor Microwave/Imager (SSM/I) and were provided by the EOS Distributed Active Archive Center (DAAC) at the National Snow and Ice Data Center, University of Colorado in Boulder, Colorado (http://nsidc.org). Methods and details regarding these data are given elsewhere (Stammerjohn and Smith, 1996; Smith *et al.*, 1998*b*; Smith and Stammerjohn, 2001; Stammerjohn, 1993). The satellite-derived estimates of sea ice extent (*i.e.,* the area enclosed by the ice edge) are

provided on a daily basis with a pixel resolution of 25 km^2.

RESULTS AND DISCUSSION

Spatial and temporal variability based on discrete field observations

A dominant and distinguishing characteristic of Southern Ocean marine ecology is sea ice, which ranges from a minimum extent of about 4×10^6 km^2 in February to a maximum extent of about 19×10^6 km^2 in September (Gloerson *et al.*, 1992). This seasonal sea ice zone is roughly the size of the Antarctic continent itself. In the Palmer LTER region, sea ice can cover the entire grid during winter and be completely absent during summer. However, the annual curves of sea ice extent for the past decade (Fig. 2) demonstrates that both the timing and magnitude of sea ice coverage are variable from year to year. For example, 1991 is a year when sea ice arrived early and remained above average for the entire winter period whereas, in contrast, 1998 is a year when sea ice was below average for most of the winter period. In addition, the timing of sea ice advance and retreat is important (*e.g.,* 1992 *vs.* 1999), since the freezing and melting of sea ice affect the salinity, and hence density gradients, of the upper ocean. This, in turn, influences the vertical structure of phytoplankton distributions and abundance. In particular, the melting of sea ice induces water column stability which restricts and concentrates phytoplankton in the well illuminated upper layer, thus establishing favorable conditions for phytoplankton blooms (Smith and Nelson, 1986; Nelson *et al.*, 1987; Nelson and Smith, 1991). Therefore, sea ice dynamics can mediate the timing and areal extent of production at the base of the food web. Furthermore, sea ice is a habitat, feeding site, refuge and/or breeding ground (Hunt, 1991) for many marine organisms at various trophic levels, so that the variability of sea ice is coupled to the variability in the marine ecosystem (*e.g.,* Quetin and Ross, 2001).

Large seasonal variability of phytoplankton biomass in polar regions has long been noted as a consequence of the extreme seasonal variability in solar radiation. Time se-
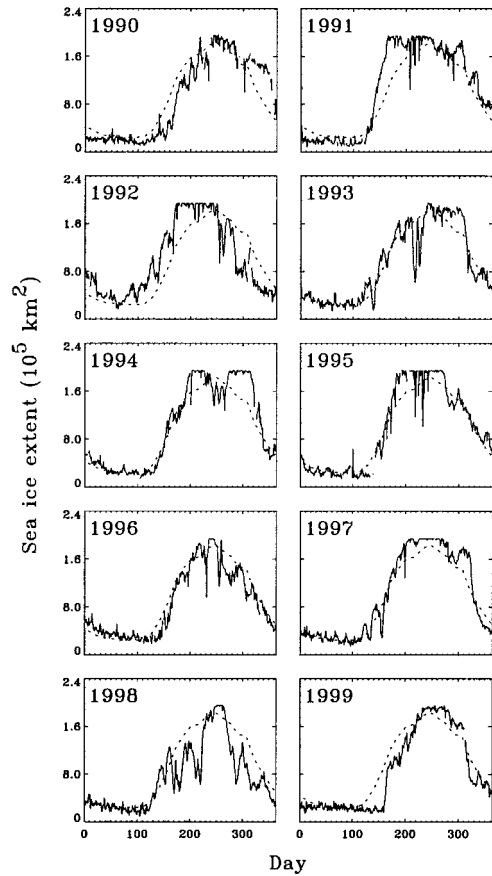

FIG. 2. Annual curve of sea ice extent for the period 1990 through 1999. Thin dashed line gives the monthly mean for these data for this ten-year period.

ries data taken in the vicinity of Palmer Station (Fig. 3) illustrate this variability and show both the timing and magnitude of phytoplankton biomass and primary production for each growing season (October to April). Note that the data points in Figure 3 reflect the quasi-weekly sampling frequency (weather-permitting) of nearshore stations B and E; no temporal averaging was made. Figure 3 also illustrates the interannual variability in the magnitude of biomass accumulation in the water column throughout the season, as well as in the differences in the timing of blooms (peak concentrations). In general, primary production follows closely the distribution of chlorophyll. Between one to three blooms can occur per season, often during fall (Nov/Dec), summer (Jan) and/or late summer/early fall
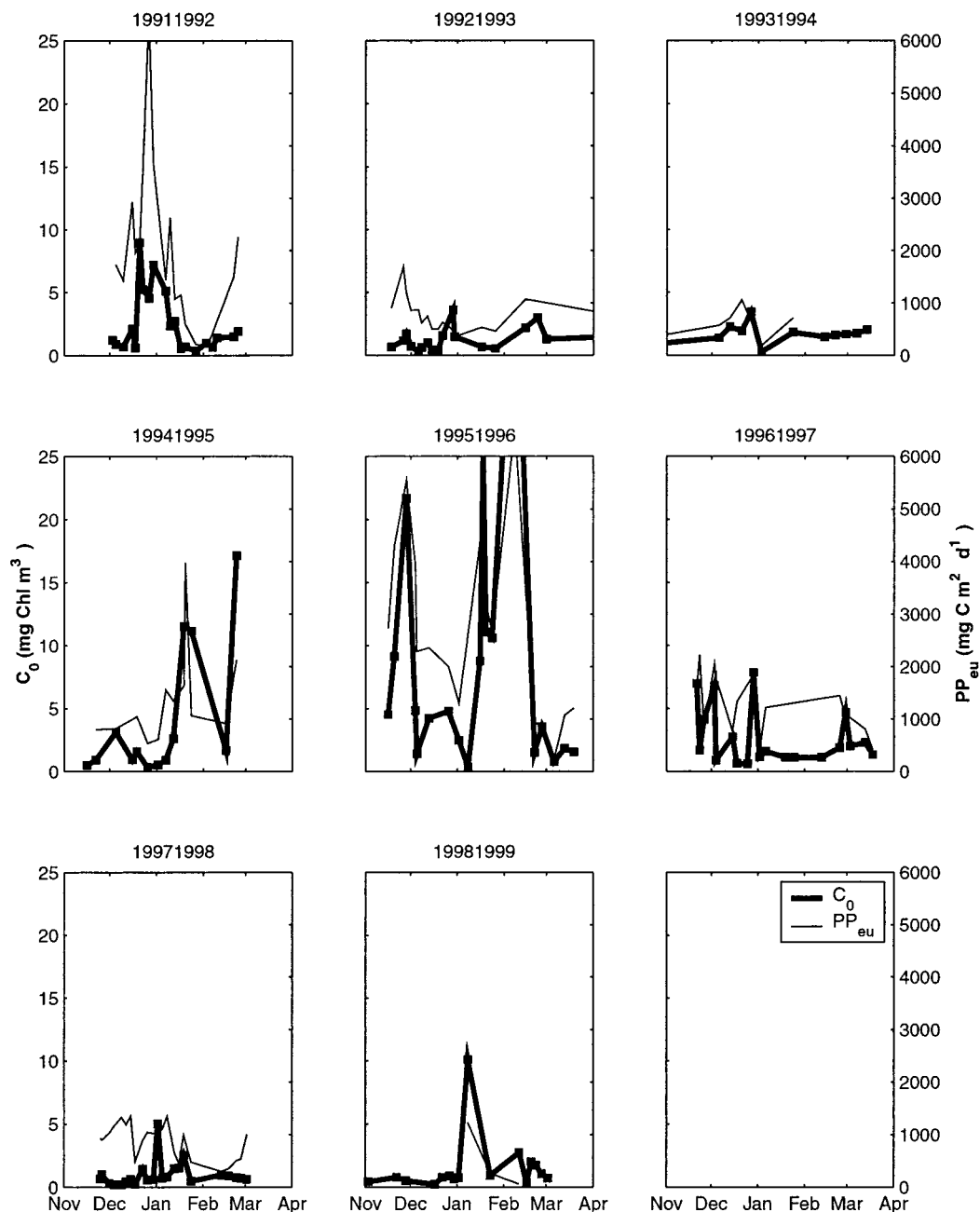
FIG. 3.   Surface chl-a (mg chl-a m^{-3}, thick line) and water column integrated primary production (mg C m^{-2} day^{-1}, thin line). Data averaged for nearshore stations (B & E) and presented as a function of time during the growing season from 1991/92 through 1998/99. Data for the 1991/92 through 1993/94 season are estimated using photosynthesis irradiance curves integrated to 60 m (Moline and Prezelin, 1996). Data from 1994/95 through 1999/00 estimated from simulated *in situ* observations (SIS), as described in the text, integrated to the depth representing 2% of surface irradiance.

(Feb/Mar). Neither the timing nor magnitude is consistent from year-to-year with blooms often lasting from several days to a few weeks.

Regional seasonal variability of chl-a, as determined by shipboard measurement, is illustrated in Figure 4 for each January cruise from 1993 to 1999. The contoured concentration maps are produced from shipboard point measurements made throughout the sampling grid during a given January cruise period, thus the data have been spatially (but not temporally) smoothed. These cruise data display an interannual variability consistent with the higher temporal resolution data from the nearshore Palmer area (Fig. 3). From the eight years of January cruise data collected to date, the average chl-a for the entire grid varies from 0.59 (in January 1997) to 1.66 mg chl-a m^{-3} (in January 1995). To illustrate the onshore to offshore gradient in phytoplankton biomass, Figure 5A shows surface chl-a averaged for each station (*i.e.,* xxx.040 to xxx.200) across the 200 to 600 transect lines. Even with the high interannual variability, chl-a concentrations for nearshore stations 40–60 km (*i.e.,* those stations just offshore of the islands along the peninsula) are consistently three to ten times higher than for stations 180 to 200 km offshore. We also analyzed the variability from the northernmost (600.xxx) to the southernmost (200.xxx) lines (Fig. 5B). Although the trends are less defined, the highest biomass tends to occur in the northern part of the grid along the 500 and 600 lines, while biomass tends to be lower in the southern portion of the grid (200–300 line) where sea ice is more persistent.

The Ackley and Sullivan (1994) conceptual model of the annual cycle of sea ice formation during autumn (with possible entrainment of phytoplankton as a seed population), followed by sea ice decay during spring (with potential bloom inoculum and sedimentation of particulate organic matter), is a framework within which to test ice-ecosystem hypotheses. According to this model, the seasonal timing of sea ice coverage is a critical factor in determining subsequent primary productivity within the system, and Smith *et al.* (1998*b*) presented

preliminary evidence for such an ice-ecosystem connection (see their Table 1). In the Smith *et al.* (1998*b*) study, subregions within the Palmer LTER grid were defined as follows: (a) onshore is the average of all cardinal stations from 40 km to 100 km; (b) offshore is the average for cardinal stations from 120 km to 200 km; (c) central is the average of all stations along the 500 and 600 line transects; and (d) southern is the average of all stations along the 200 and 300 line transects (see Fig. 1a). The chl-a biomass measured for each January survey of the grid was spatially averaged into these four sub-regions, and those values were compared to previous winter and spring sea-ice extents in the Palmer LTER region. The Smith *et al.* (1998) study used 4 yr (1993–1996) of data, and we updated the comparison with 3 more years (1997–1999). The comparisons show that high (low) sea-ice extent in the previous winter and spring is associated with high (low) chl-a biomass in the onshore/central and offshore/southern subregions, respectively. The time-series of January data is still too short to determine statistically robust correlations, but the patterns are suggestive of ice-ecosystem connections.

Several possible relationships between sea ice forcing and ecosystem response can be inferred from the spatial relationships found between chl-a biomass and sea-ice extent. For example, higher correlation of biomass in the onshore/central sub-region with previous winter sea ice extent suggests that in this area, which in some years has relatively little sea ice, biomass responds to increased sea ice extent. This is expected in the context of the hypothesis that an increase in the areal extent of the marginal ice zone increases the spatial and temporal extent of water column stability, ice algae inoculation, and consequent phytoplankton blooms (Smith and Nelson, 1986). In contrast, the higher correlation of biomass in the offshore/southern sub-region with previous spring sea ice extent references an area that is typically covered with sea ice each year and which retains sea ice well into the spring. Here, in the context of the Ackley-Sullivan conceptual model, the higher biomass concentrations in this sub-
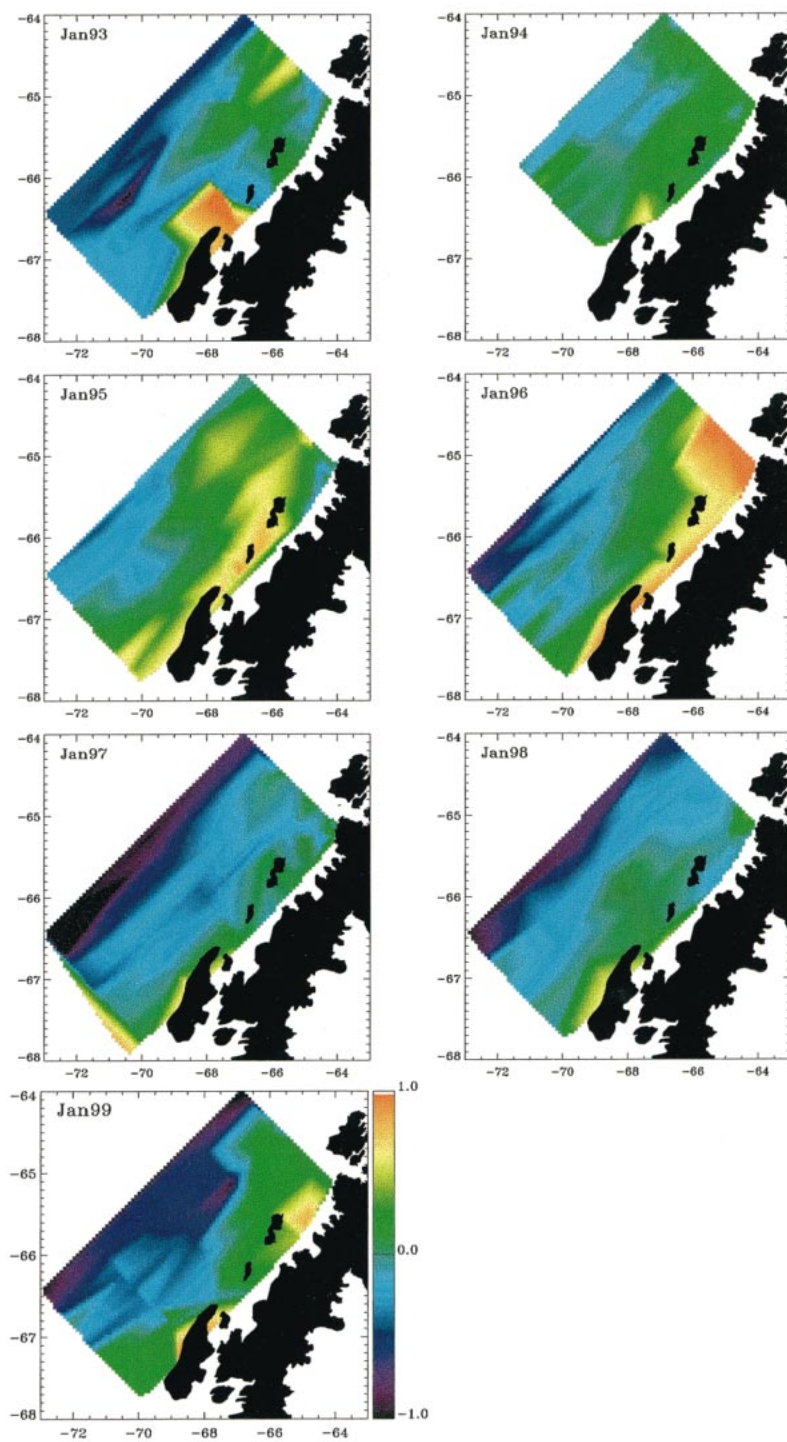
Fig. 4.   Chl-a concentration (mg chl-a m^{-3}) averaged within the euphotic zone in the Palmer LTER grid for each January cruise from 1993 to 1999.

region are hypothesized to be a result of the late sea ice retreat, whereby the recently inoculated meltwaters contribute to the high chlorophyll biomass observed in January. In contrast, an early retreat would contribute to a bloom that would be well dissipated by January, resulting in the lower chlorophyll biomass observed at that time. These observations are tentative, and will be tested with more complete satellite data, but display the critical nature of the spatial extent and the associated impacts on phytoplankton production.

Spatial and temporal variability based on satellite observations

The Palmer LTER field data show significant variation in the timing (+/− several weeks) and magnitude (roughly +/− a factor of 5) of annual biomass accumulation, both alongshore and on/offshore. Simple correlations (not shown) indicate that roughly 60% of the variability in production can be explained by biomass alone (Dierssen *et al.*, 2000). Therefore variability in biomass is generally related to variability in primary production (Fig. 3). Moreover, we can use estimates of chl-a to accurately model primary production for this region using a simple algorithm. Since our field observations are limited in time and space, a production model allows us to use satellite observations to extend estimates of the space/time variability of primary production.
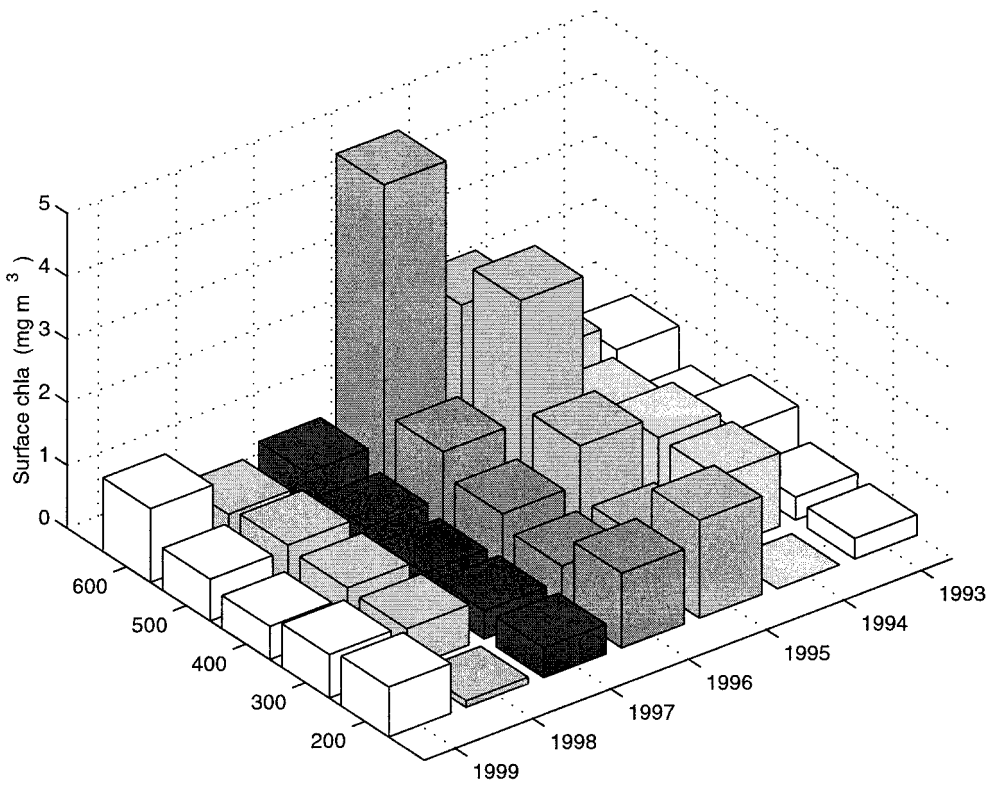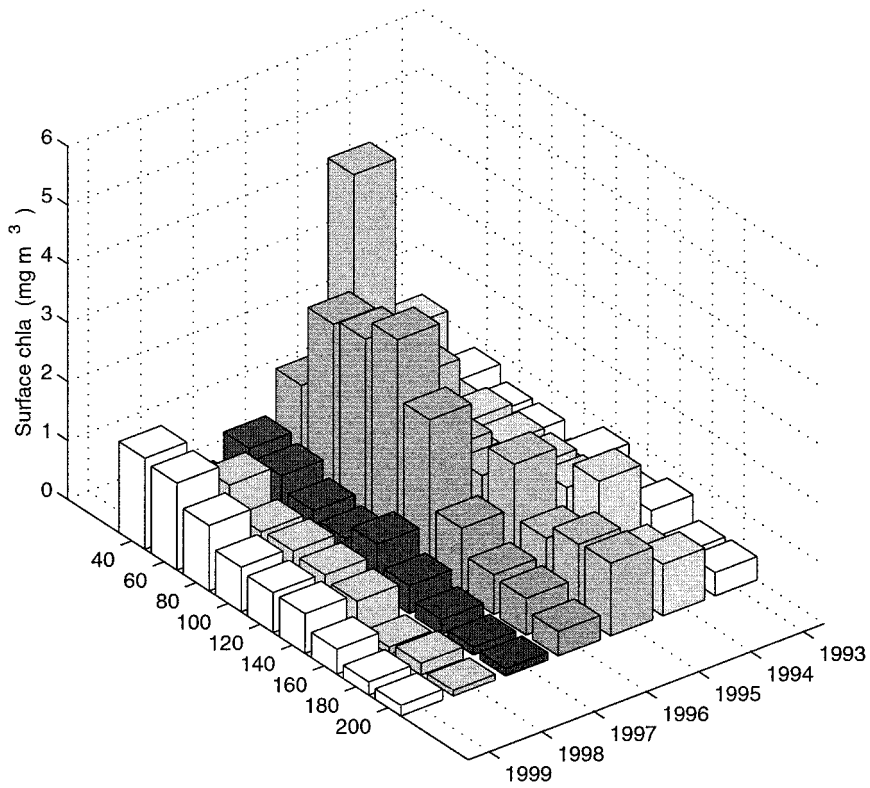
Making use of the production model described in the methods, production is calculated using estimates of chl-a from SeaWiFS and compared with shipboard primary production measurements. Figure 6 provides such a comparison and shows annual primary production (g C m^{-2} yr^{-1}), determined for the nearshore area of Palmer Station, estimated three different ways as described in the figure legend. As Figure 6 shows, there is good agreement between the three methods for estimating the high interannual variability (roughly seven-fold) in production for the Palmer area.

In addition to the temporal variability at Palmer Station (*i.e.,* Fig. 6), the SeaWiFS satellite data also can be used to estimate production over larger spatial scales. Figure

7 illustrates both the seasonal and interannual variability as well as the spatial variability of phytoplankton production in this region, and several observations can be made about primary production in this area. First, the spatial patterns within the Palmer LTER grid during those years for which there is ocean color satellite data (1998–2000) can be directly compared with the corresponding January cruise data shown in Figure 4. To first order, there is good agreement between the patterns observed in both the *in situ* and satellite data. (A full computational analysis of these spatial patterns is beyond the scope of this manuscript and will be published elsewhere). Second, within the larger WAP region (including the Drake Passage) we generally observe three separate zones that are a composite of Treguer and Jacques (1992) biogeochemical provinces:

1. a coastal shelf zone of consistently high biomass and a strong onshore to offshore gradient along the coastal Palmer LTER grid (Coastal Shelf Zone);
2. a pelagic region of low biomass northwest of the grid (Pelagic Zone); while biomass may be limited in this zone by factors such as iron, stability, or even silica concentrations, (Treguer and Jacques, 1992), phytoplankton blooms associated with the retreat of sea ice in the early spring (September–October) can occur;
3. a region of increasing biomass to the far north associated with the Polar Front (Frontal Zone); blooms in this region generally occur in the summer months from December through February.

Third, similar to our nearshore measurements, we also observe high levels of interannual variability throughout all three of the zones. Fourth, the spatial variability within the grid is high from year to year. For example, coastal biomass in Marguerite Bay (most southern inlet shown on the western side of the Peninsula) peaked in different months for all three seasons (February 1998, December 1998, and March, 2000). In December of 1997, we witnessed a massive bloom in the (more northward) frontal zone that is not evident in the later

two years. In November 1999, a large ice-edge bloom was evident in the pelagic zone that runs nearly the length of the Palmer LTER grid. Finally, the sub-regions show variable production rates ranging from 50 to 100 g C m^{-2} yr^{-1}. With the addition of more SeaWiFS data (and hence a longer satellite time series) we would like to investigate next the production of the various biogeochemical provinces, estimate their space/time variability and then sum these results to provide both Southern Ocean regional and total estimates of productivity. Preliminary estimates, making use of this multi-scale methodology (Smith *et al.*, 1998*a*; Dierssen, 2000), give values between 2.1 to 2.7 × 10^{15} g C yr^{-1} for the Southern Ocean (defined as non-ice covered area south of 50°S and north of the Antarctic continent). Previously published results (Ryther, 1963; Currie, 1964; El-Sayed, 1968; Holm-Hansen *et al.*, 1977; Berger *et al.*, 1987; Treguer and Jacques, 1992; Longhurst *et al.*, 1995; Antoine *et al.*, 1996; Behrenfeld and Falkowski, 1997; Smith *et al.*, 1998*a*) range from 0.6 to 8.3 × 10^{15} g C yr^{-1} for the SO. Clearly, the wide range in published estimates, along with the large spatial and temporal variability we observe, hinders our ability to define a ''typical'' biomass regime for the WAP region, much less for the SO as a whole. This emphasizes the need to continue to search for and understand mechanisms that may permit predictive estimates of this variability.

SUMMARY

Our planet may be viewed as a dynamic collection of interacting earth systems. While there is a growing understanding of the need to define the ecosphere as a whole (Strahler and Strahler, 1992; Longhurst, 1998; Bailey, 1998; Steele, 1995) and to identify the human impacts on its balance (Woodard, 2000), it remains difficult to quantify trends or system changes given the
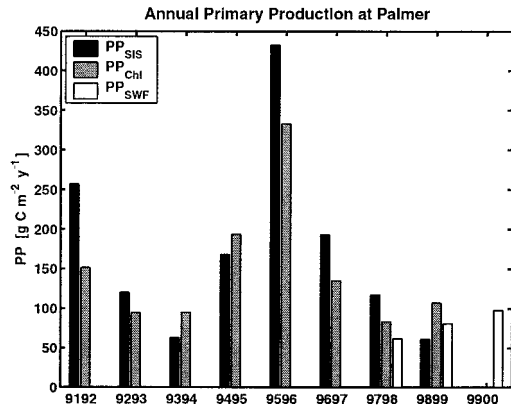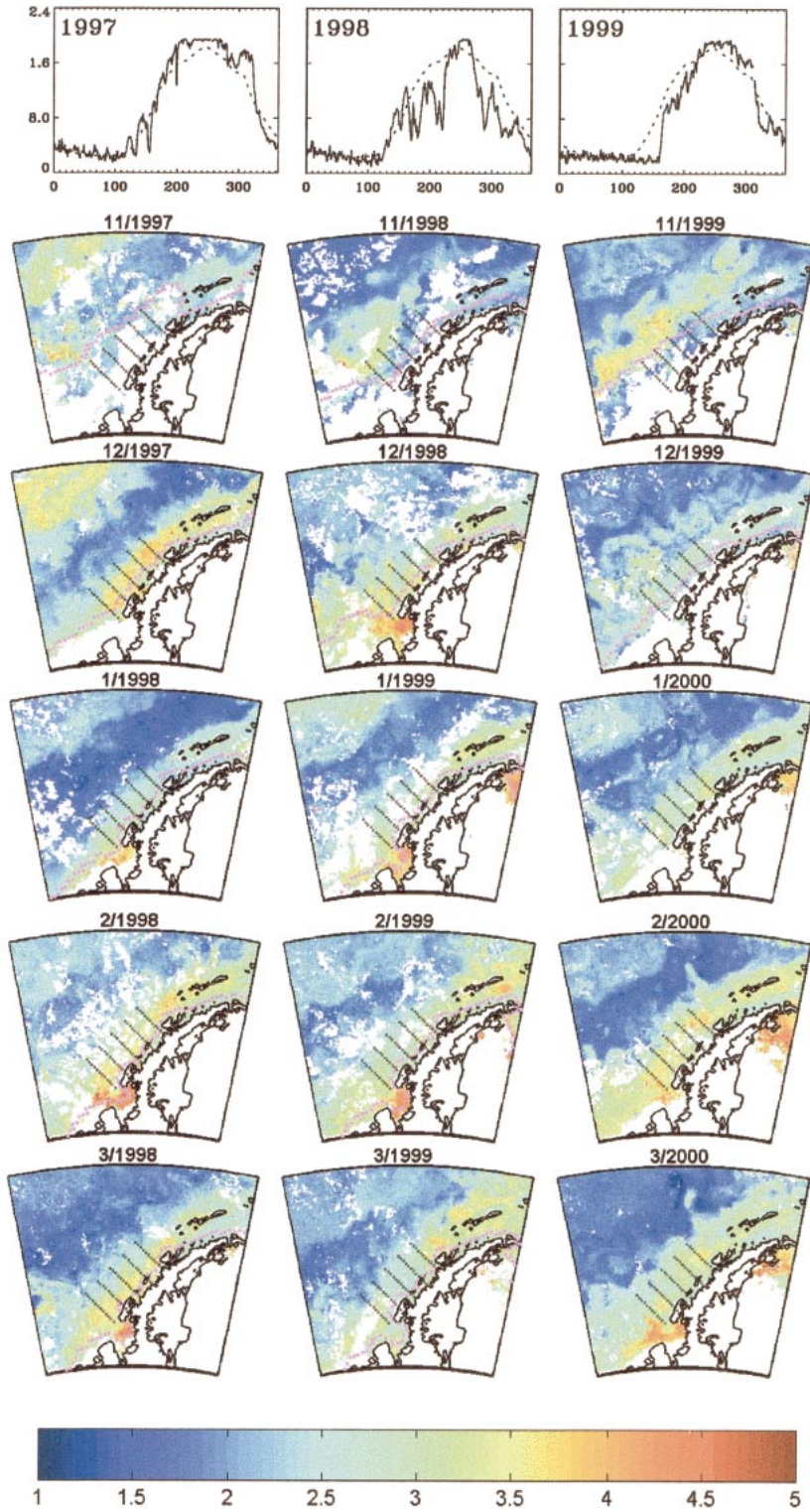

FIG. 6. Annual primary production (g C m^{-2} yr^{-1}) determined near Palmer Station for each growing season from 1991/92 to 1999/2000. First, annual estimate have been made from integrated near-weekly surface sampling over the growing season from November to March (152 days) at Palmer Station (PP$_{SIS}$). Production determined as described in Figure 3. Second, annual production estimated based on Palmer Station chl-a measurements using our production model and integrated over the same growing season (PP$_{CHL}$). Third, estimates from modeled primary production based on average monthly chl-a retrieved from SeaWiFS ocean color data (for the three years the satellite has been in orbit) (PP$_{SWF}$).

wide range of natural variability within each component (Likens, 1989; Magnuson, 1990). Specifically, the Antarctic marine ecosystem is composed of an interconnected system of hydrographic and biogeochemical sub-divisions (Treguer and Jacques, 1992) that includes open ocean, frontal regions, shelf-slope waters, sea ice and marginal ice zones. The processes associated with these distinct regions are subject to extreme seasonal variability, and in the context of this highly variable environment we have developed a sampling strategy which is sustainable over time in order to estimate phytoplankton biomass and production on several spatial and temporal scales so to understand the processes giving rise to the observed variability.

The Palmer LTER bio-optical data focus

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FIG. 5. Surface chl-a (mg chl-a m^{-3}) for each of the seven cruises averaged over the grid in two directions: A) cardinal stations averaged parallel to the coast showing average chl-a for each station from 40 km (nearshore) to 200 km offshore; B) cardinal stations averaged perpendicular (on/offshore) to the coast showing average chl-a from the northernmost transect (600.xxx line) to the southernmost (200.xxx) transect lines.

on the coastal continental shelf zone of the WAP region, an area swept by the annual advance and retreat of sea ice. Using shipboard observations we directly determined phytoplankton biomass and production. Concurrently we determined the relevant optical properties associated with the in-water dissolved and suspended constituents that have been used in turn as proxy measures of pigment biomass in order to make use of ocean color satellite sensors. The SeaWiFS satellite data extends our observations seasonally and regionally and shows a much larger temporal and spatial variability of biomass than previously thought. We developed a production model specifically for the Southern Ocean and use this model to estimate production from both shipboard and satellite estimates of chl-a. Most importantly, the SeaWiFS data provide estimates of production on temporal and spatial scales that would otherwise not be possible within this most inhospitable and remote environment. Also, the large interannual variability revealed by the satellite data requires a revision of past estimates of production. Production, within the Palmer LTER grid averages roughly 100 g C m^{-2} yr^{-1}, and preliminary estimates for the whole Southern Ocean (making use of our methodology) range from 2.1 to 2.7 $\times$ 10^{15} g C yr^{-1}. Importantly, these multiyear observations demonstrate again that the most effective (and perhaps only) way to adequately sample the space/time variability of the Southern Ocean is by means of remote sensing. Hence there is a strong motivation for the development and refinement of bio-optical models for ocean color satellite and aircraft data as well as for time series data from ship and mooring observations.

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FIG. 7. Monthly estimates of daily primary production (log (PP)) (mg C m^{-2} day^{-1}) for the WAP region from the SeaWiFS chl-a adjusted using our SO-algorithm (Dierssen and Smith, 2000) and a depth-integrated production model (Dierssen *et al.*, 2000). Pannels compare three years of available SeaWiFS data for the growing season from November through March. Purple contours show the average sea ice extent for each month. The top row shows the daily sea ice extent (Jan–Dec) for the preceding winter through the beginning of the field season depicted in the SeaWiFS images (see Fig. 2).

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