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Primary productivity of the Palmer Long Term Ecological Research Area and the Southern Ocean

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Abstract

A major objective of the Palmer Long Term Ecological Research (Palmer LTER) project is to obtain a comprehensive understanding of the various components of the Antarctic marine ecosystem. Phytoplankton production plays a key role in this so-called high nutrient, low chlorophyll environment, and factors that regulate production include those that control cell growth (light, temperature, and nutrients) and those that control cell accumulation rate and hence population growth (water column stability, grazing, and sinking). Sea ice mediates several of these factors and frequently conditions the water column for a spring bloom which is characterized by a pulse of production restricted in both time and space. This study models the spatial and temporal variability of primary production within the Palmer LTER area west of the Antarctic Peninsula and discusses this production in the context of historical data for the Southern Ocean. Primary production for the Southern Ocean and the Palmer LTER area have been computed using both light-pigment production models [Smith, R.C., Bidigare, R.R., Prézelin, B.B., Baker, K.S., Brooks, J.M., 1987. Optical characterization of primary productivity across a coastal front. Mar. Biol. (96), 575–591; Bidigare, R.R., Smith, R.C., Baker, K.S., Marra, J., 1987. Oceanic primary production estimates from measurements of spectral irradiance and pigment concentrations. Global Biogeochem. Cycles (1), 171–186; Morel, A., Berthon, J.F., 1989. Surface pigments, algal biomass profiles and potential production of the euphotic layer—relationships reinvestigated in view of remote-sensing applications. Limnol. Oceanogr. (34), 1545–1562] and an ice edge production model [Nelson, D.M., Smith, W.O., 1986. Phytoplankton bloom dynamics of the western Ross Sea ice edge: II. Mesoscale cycling of nitrogen and silicon. Deep-Sea Res. (33), 1389–1412; Wilson, D.L., Smith, W.O., Nelson, D.M., 1986. Phytoplankton bloom dynamics of the Western Ross Sea ice edge: I. primary productivity and species-specific production. Deep-Sea Res., 33, 1375–1387; Smith, W.O., Nelson, D.M., 1986. Importance of ice edge phytoplankton production in the Southern Ocean. BioScience (36), 251–257]. Chlorophyll concentrations, total photosynthetically available radiation (PAR) and sea ice concentrations were derived from satellite data. These same parameters, in addition to hydrodynamic conditions, have also been determined from shipboard and Palmer Station observations during the LTER program. Model results are compared, sensitivity studies evaluated, and productivity of the Palmer LTER region is discussed in terms of its space time distribution, seasonal and interannual variability, and overall contribution to the marine ecology of the Southern Ocean.

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Résumé

Un objectif majeur du projet Plamer Long Term Ecological Research (Palmer LTER) est de comprendre de façon approfondie les différentes composantes de l'écosystème antarctique marin. La production phytoplanctonique joue un rôle clé dans cet environnement dit HLNC (fortes valeurs d'éléments nutritifs, faible chlorophylle) et les facteurs qui régulent cette production comprennent ceux qui contrôlent la croissance des cellules (lumière, température, éléments nutritifs) et ceux qui contrôlent leur taux d'accumulation, et de ce fait la croissance de la population (stabilité de la colonne d'eau, broutage, chute en profondeur). La glace de mer agit sur plusieurs de ces facteurs et conditionne fréquemment la colonne d'eau pour une poussée printanière caractérisée par un épisode de production limité dans le temps et dans l'espace. La présente étude modélise la variabilité spatiale et temporelle de la production primaire dans la zone Palmer LTER, à l'ouest de la Péninsule Antarctique, et discute cette production dans le contexte des données historiques relatives à l'océan Austral. La production primaire a été calculée, pour l'Océan Austral et la zone Palmer LTER, en utilisant à la fois des modèles de production lumière-pigments [Smith, R.C., Bidigare, R.R., Prézelin, B.B., Baker, K.S., Brooks, J.M., 1982. Optical characterization of primary productivity across a coastal front. Mar. Biol. (96), 575–591; Bidigare, R.R., Smith, R.C., Baker, K.S., Marra, J., 1987. Oceanic primary production estimates from measurements of spectral irradiance and pigment concentrations. Global Biogeochem. Cycles (1), 171–186; Morel, A., Berthon, J.F., 1989. Surface pigments, algal biomass profiles and potential production of the euphotic layer—relationships reinvestigated in view of remote-sensing applications. Limnol. Oceanogr. (34), 1545–1562] et un modèle de production de bordure des glaces [Nelson, D.M., Smith, W.O., 1986. Phytoplankton bloom dynamics of the western Ross Sea ice edge: II. Mesoscale cycling of nitrogen and silicon. Deep-Sea Res. (33), 1389–1412; Wilson, D.L., Smith, W.O., Nelson, D.M., 1986. Phytoplankton bloom dynamics of the Western Ross Sea ice edge: I. primary productivity and species-specific production. Deep-Sea Res. (33), 1375–1387; Smith, W.O., Nelson, D.M., 1986. Importance of ice edge phytoplankton production in the Southern Ocean. BioScience (36), 251–257]. Les concentrations de chlorophylle, la radiation photosynthétiquement utilisable totale (PAR) et le taux de couverture par la glace de mer ont été obtenus à partir de données satellitaires. Ces mêmes paramètres, ainsi que les conditions hydrodynamiques, ont aussi été obtenus sur le terrain lors du programme LTER. Les résultats des modèles sont comparés entre eux, les études de sensibilité évaluées, et la productivité de la région Palmer LTER est discutée eu égard à sa distribution spatio-temporelle, sa variabilité saisonnière et interannuelle, et sa contribution générale à l'écologie marine de l'Océan Austral.

Keywords: primary productivity; Southern Ocean; LTER; remote sensing

1. Introduction

Waters of the Southern Ocean are characterized by extreme seasonal variability in incident solar radiation, near freezing temperatures and the influence of sea ice. Phytoplankton production within this system supports abundant higher trophic level populations in an environment high in macronutrients relative to other large ocean environments (Llano, 1977; Priddle et al., 1986; Jacques, 1989; Smith, 1990; Tréguer and Jacques, 1992). Oceanic and atmospheric processes and biogeochemical fluxes within this system are presumed to be globally significant, sensitive to perturbation and are poorly understood relative to more accessible marine ecosystems (Harris and Stonehouse, 1991; Anderson, 1993; Johannessen et al., 1994). We currently do not have an adequate understanding of the chemical, optical, physical and biological processes regulating primary production and of the subsequent carbon fluxes within this ecosystem, nor do we fully understand the fundamental similarities and differences between this important marine system and those in more temperate latitudes. Further, data for the Southern Ocean are poorly distributed in both space and time.

The Antarctic marine ecosystem has long been viewed in terms of zonal biogeographical (Hart, 1942) and, more recently, hydrographic and biogeochemical subdivisions. Tréguer and Jacques (1992) have identified four functional subdivisions which are delineated by major frontal systems, and which are based on mechanisms controlling nutrient dynamics and hence phytoplankton production: (1) a highly productive Coastal and Continental Shelf Zone (CCSZ), (2) a relatively productive Seasonal Ice Zone (SIZ), (3) a less productive Permanently Open Ocean Zone (POOZ) and (4) a Polar Front Zone (PFZ). These subdivisions of the Southern Ocean are, in part, consistent with the blue ocean/green ocean dichotomy (Berger et al., 1989), where two pathways, one for pelagic conditions, the other for neritic conditions, transfer organic carbon from near-surface photosynthesis to burial in sediment. The Southern Ocean, especially the POOZ north of the pack ice and south of the Polar Front, has been characterized as a high nutrient, low chlorophyll (HNLC) area, where phytoplankton apparently lack the capacity to fully utilize abundant macronutrients (Minas et al., 1986). In contrast, phytoplankton biomass and productivity within the SIZ, which is swept by the relatively narrow (50 to 250 km wide) marginal ice zone (MIZ), is often significantly higher (Smith and Nelson, 1986; Nelson et al., 1987) and, as we show below, is subject to relatively large regional interannual variability. Coastal areas of the Southern Ocean, or the CCSZ, often exhibit relatively large blooms, may partially exhaust the supply of macronutrients (Holm-Hansen et al., 1989) and show the highest levels of pigment biomass and phytoplankton productivity (El-Sayed, 1968; Holm-Hansen et al., 1977; Priddle et al., 1986; Jacques, 1989; Smith and Sakshaug, 1990).

The Palmer Long Term Ecological Research (Palmer LTER) area west of the Antarctic Peninsula (Fig. 1) is a complex combination of two of these distinctive subdivisions, the coastal and continental

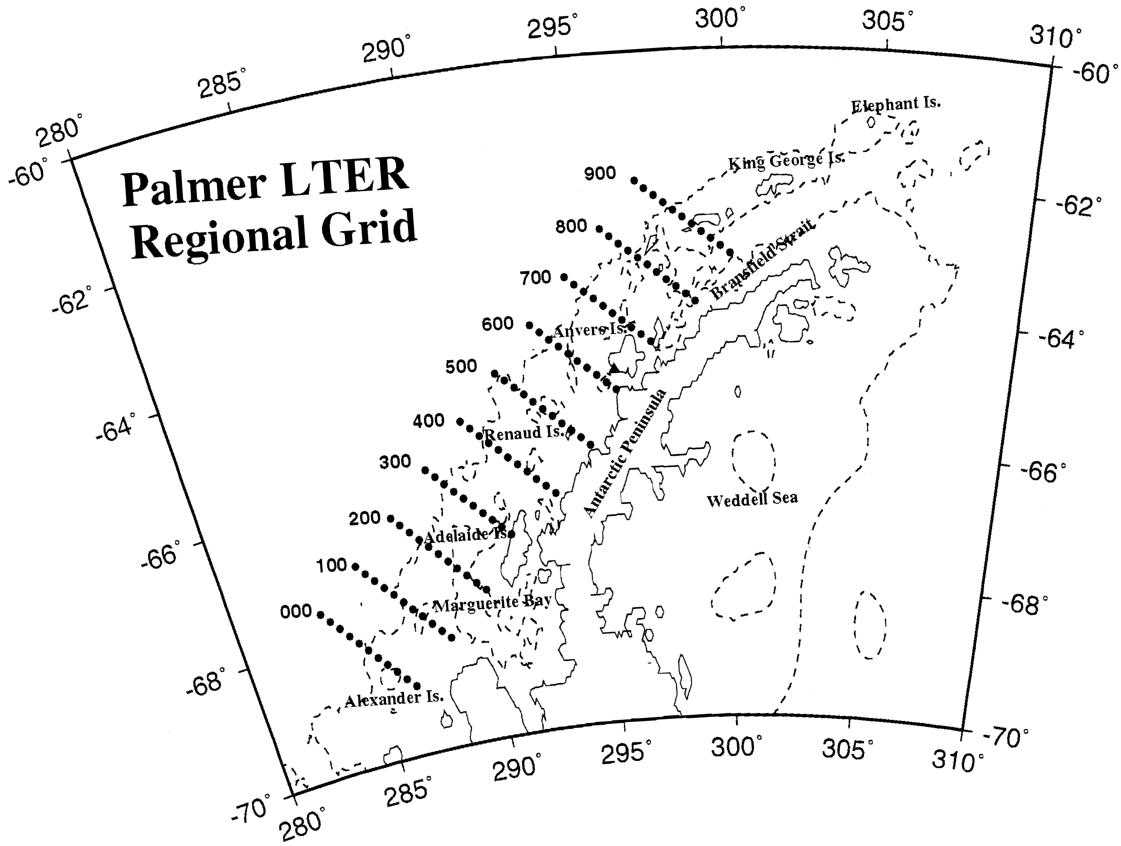

Fig. 1. Palmer LTER regional grid to the west of the Antarctic Peninsula (Universal Transverse Mercator projection). The Palmer LTER regional grid is a 900 km by 200 km rectangular area along the peninsula composed of stations '*xxx.yyy*', where the *x*-axis runs roughly parallel to the peninsula and the *y*-axis runs on/offshore. Within this grid, cardinal lines spaced every 100 km along (*xxx*) the peninsula and cardinal points spaced every 20 km on/offshore (*yyy*) comprise the basic sampling stations for the Palmer LTER program. The 500-m contour, a rough indicator of the shelf break, is shown by the dotted line. Palmer Station is indicated by a triangle on the southwest corner of Anvers Island.

shelf zone (CCSZ), which is swept by the seasonal ice zone (SIZ). It is a region where factors giving rise to highly productive near-shore blooms are modified and modulated by the annual advance and retreat of sea ice. A variety of factors control phytoplankton growth (light, temperature, nutrients) and accumulation (water column stability, grazing, and sinking) in this complex environment, and it is unlikely that any single factor dominates. Here we draw upon historical data, both surface (Smith et al., 1996a) and satellite, to estimate net primary productivity (NPP) for the Palmer LTER region and the Southern Ocean as a whole. In Section 2, we describe two models for the estimation of net primary productivity (NPP) and the data sources used in these models. Section 3 presents results and discussion, which is followed by conclusions in Section 4.

2. Models

2.1. Light-chlorophyll production (LCP) model based on satellite observations

A series of improved bio-optical models (Bidigare et al., 1992) now make it possible to estimate phytoplankton production using satellite data (Smith et al., 1982; Platt et al., 1988; Balch et al., 1989; Morel and Berthon, 1989; Sathyendranath et al., 1989; Balch et al., 1992) and consequently create global maps of ocean productivity (Byers, 1994; Antoine et al., 1996). Here we use the model by Morel and Berthon (1989) to estimate net primary productivity (NPP, mg C m^{-2} d^{-1}) by:

$$NPP = (1/39)\,\rho\,PAR(0+)\langle Chl\rangle_{tot}\Psi* \quad (1)$$

where (1/39) is a factor converting 39 J energy into 1 mg C, ρ is the ratio of active pigments to all pigments, PAR(0+) is daily integrated photosynthetically available radiation incident above the air–water interface (J m^{-2} d^{-1}), $\langle Chl\rangle_{tot}$ is water column chlorophyll concentration integrated to the euphotic depth (g Chl m^{-2}), and $\Psi*$ is the cross section of photosynthesis per unit of areal chlorophyll (m^2 $(g\ Chl)^{-1}$). This model is a simplification of full spectral and depth-dependent models and is valuable for a first-order assessment of the spatial distribution, on regional scales, of carbon fixation.

For chlorophyll concentration we first use historical data from the Coastal Zone Color Scanner (CZCS) which flew from late 1978 to mid 1986. Second, we use chlorophyll data obtained from a series of LTER cruises. Goddard Space Flight Center (GSFC) has processed usable images taken by the CZCS of which we use level 3 chlorophyll concentrations (binned on a 20 km by 20 km grid). We implement the Southern Ocean pigment retrieval algorithm developed by Sullivan et al. (1993) to create seasonal and annual chlorophyll maps, which corrects Southern Ocean CZCS data roughly by a factor of two. We then accept the error analysis of Feldman (1989) who gives uncertainties for CZCS chlorophyll of $\pm 35\%$ for Case 1 waters and a factor of two for other waters. These CZCS data are highly averaged over both time and space, incompletely understood in terms of Southern Ocean bio-optical properties (Mitchell and Holm-Hansen, 1991), but permit a first-order estimation of regional variability (Sullivan et al., 1993; Smith et al., this volume). Further, these satellite data are generally consistent with ship observations, because historical chlorophyll data were used to develop the Southern Ocean pigment algorithm (Sullivan et al., 1993).

PAR is estimated using radiance data preprocessed by the International Satellite Cloud Climatology Project (ISCCP). The ISCCP C1 product gives values for radiance, atmospheric constituents and cloud cover on a 2.5° latitude by 2.5° longitude grid. PAR was computed from ISCCP radiance data using the method of Gautier et al. (1980) as improved by Diak and Gautier (1983). The formulation for PAR for all sky conditions is given as:

$$PAR = \frac{PAR_{clr}(1 - A_{cdy})}{(1 - A_{cdy}\,A_{clr})} \quad (2)$$

where PAR_{clr} is clear sky PAR (cloudless), A_{cdy} is a cloud albedo, and A_{clr} is the clear sky surface albedo. Clear sky PAR was determined using a simplifying parameterization by Frouin et al. (1989), which is based on a complete radiative transfer model and allows a significant reduction in computation time. Based on comparisons with surface data (Gautier and Frouin, 1992), uncertainties in monthly PAR have been estimated at $\pm 15\%$ for regions where aerosols are not well quantified and $\pm 5\%$

elsewhere. Since this algorithm degrades with increasing solar angles, a correction factor (Pinker and Laszlo, 1992) was applied for Southern Ocean regions poleward of 60°S. We compared ISCCP results with directly measured PAR at Palmer Station and found agreement within 11% for months from December to March and disagreement by about a factor of two during September to November. For the work reported herein, we correct the ISCCP data using surface measurements from Palmer Station.

For waters of the Southern Ocean we take the ratio of active to total pigments (ρ) equal to 0.9. This is based on a series of global total pigment regressions for a study of SeaWiFS CZCS-type pigment algorithms (Aiken et al., 1995). The factor $\Psi*$ is related to the light utilization index Ψ of Falkowski (1981). A significant characteristic of this factor is that the variance of $\Psi*$ is smaller than the individual variances of its physiological components (Morel, 1978; Platt, 1986; Morel, 1991; Antoine and Morel, 1996). However, it should be noted that Siegel et al. (1995) have recently challenged the concept that $\Psi*$ is a biogeochemical constant. For the LCP model we use high latitude values (spring, summer and autumn, 0.059, 0.047 and 0.070 m^2 (g Chl)$^{-1}$, respectively) as suggested by Antoine et al. and Antoine and Morel (Antoine et al., 1996; Antoine and Morel, 1996) and which are also consistent with values obtained by Marotti (1992).

2.2. Sea ice model for primary productivity

A key hypothesis of the Palmer LTER program proposes that interannual and annual variability in sea ice coverage is a major determinant in spatial and temporal changes in Antarctic marine communities, an idea supported by many previous studies. For example, phytoplankton blooms have been observed both in the vicinity of retreating ice edges in spring (Smith and Nelson, 1985; Wilson et al., 1986; Nelson et al., 1987; Sullivan et al., 1988; Smith and Nelson, 1990; Comiso et al., 1993) and along stationary ice edges in summer and winter (Dieckmann, 1987; Nelson et al., 1989; Comiso et al., 1990), and it is believed that ice-edge blooms contribute significantly to the total production of the Southern Ocean (Smith and Nelson, 1985, 1986). In addition, the contribution from sea ice algal and bacterial production on total productivity appears to be significant as well (Grossi et al., 1987; Kottmeier et al., 1987; Kottmeier and Sullivan, 1987; SooHoo et al., 1987; Garrison, 1991).

As a consequence, a direct, bottom-level impact on the ecosystem is stimulation of primary production by a receding marginal ice zone. Given that interannual variability in Palmer LTER ice coverage is known from October 1978 to August 1994, interannual variability in ice edge production can be estimated using an approach similar to Smith and Nelson (1986) and Smith et al. (1988). This approach assumes that productivity in the region of the melting ice edge is enhanced due to stratification of the water column caused by low saline water from the melting ice. This stratification stabilizes phytoplankton in a light- and nutrient-rich environment, thus supporting primary production. Prediction of ice edge productivity therefore assumes that production is enhanced throughout the length of the melting ice edge, and the area uncovered by the receding ice edge each month is the areal extent of ice edge enhanced production.

The relatively few estimates of ice edge productivity are primarily from the Ross and Weddell Seas. To estimate ice edge productivity in the Palmer LTER region, we averaged production rates (1.6 g C m^{-2} d^{-1}) observed in the Bransfield and Gerlache Straits (Bodungen et al., 1986; Holm-Hansen and Mitchell, 1991) and designate this estimated as an 'upper limit' production rate associated with the spring pack ice retreat in the Palmer LTER study area. We also carry out a sensitivity analysis using several lower MIZ production rates. Thus, production associated with the spring ice retreat can be estimated as follows: area uncovered each month × production rate × number of days in that month.

2.3. Production estimate based on biogeochemical subsystems

Table 1 presents a summary of selected productivity data for the Southern Ocean in terms of major functional units (Tréguer and Jacques, 1992). Here we emphasize historical data within the Palmer LTER region (Smith et al., 1996a, 1998, this volume) and only consider areas south of the Polar Front (i.e., we exclude the PFZ). The data show a considerable

Table 1
Primary production in the Southern Ocean for the three subdivisions of the Antarctic marine ecosystem

Zone	Area ($\times 10^6$ km^2)	Minimum	C uptake (g C m^{-2} y^{-1}) ave	Maximum	Ref.[a]	C total ($\times 10^{15}$ g C y^{-1})
CCSZ	0.9	12	143	420	a	
			118		b	
		55	148	331	c	
CCSZ value used			140			0.13
SIZ	16		(21)		d	0.33
POOZ	14	5	16	35	e	
			< 40		f	
			< 50		g	
		10	23	44	h	
POOZ value used			20			0.28
TOTAL						0.74

[a](a) Smith et al. (1995), (b) Vernet et al. (in press), (c) El-Sayed (1968), (d) Smith et al. (1988), (e) Holm-Hansen et al. (1977), (f) Tréguer and Jacques (1992), (g) Jennings et al. (1984), (h) Miller et al. (1985).

range of variability for each zone but allow first order estimates of productivity for the Palmer LTER area and, more tentatively, for the area of the Southern Ocean south of the Polar Front.

3. Results and discussion

3.1. Published historical results

Data summarized in Table 1 provides a context in which to consider model results. Estimates of global ocean productivity have long been determined by estimating average production from oceanographic provinces which are then multiplied by the respective areas (Ryther, 1969; Koblentz-Mishke et al., 1970; Platt and Subba Rao, 1975; Berger et al., 1987). Here we adopt a similar strategy by using the biogeochemical subdivision suggested by Tréguer and Jacques (1992) as a basis for estimating production within the Palmer LTER area of the Southern Ocean. A comprehensive review of phytoplankton biomass and productivity data for the west Antarctic Peninsula coastal ecosystem gave a mean value for the CCSZ area of 143 g C m^{-2} y^{-1} (Smith et al., 1996a) which is based on an average daily rate of 1.17 g C m^{-2} d^{-1} and the assumption of a growing season of 120 days per year. That review summarizes published data for this region, including large programs such as the Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) (El-Sayed, 1994; Thorley and Trathan, 1994) and Research on Antarctic Coastal Ecosystems Rates (RACER) (Holm-Hansen and Mitchell, 1991). The Smith et al. (1996a) value is consistent with a value of 118 g C m^{-2} y^{-1} which was obtained by averaging weekly observations near Palmer Station over a 4-month period from 15 November 1994 through 15 March 1995 (Vernet et al., in press) and with an earlier published average of 148 g C m^{-2} y^{-1} by El-Sayed (1968). We subjectively selected 140 g C m^{-2} y^{-1} as a mean productivity rate for this area.

The published values of MIZ related production from the Ross and Weddell Seas show relatively high values for daily production (0.91 to 0.20 g C m^{-2} d^{-1}) (El-Sayed and Taguchi, 1981; El-Sayed et al., 1983; Wilson et al., 1986; Smith and Nelson, 1990). Jennings et al. (1984), using nutrient depletion to estimate productivity in the Weddell Sea, found an average value of 0.32 ± 0.10 g C m^{-2} d^{-1}. Marotti (1992), making use of productivity data from Prézelin (unpublished), found values of 0.18 ± 0.05 g C m^{-2} d^{-1} for spring time observations in the Bellingshausen Sea. These daily rates may hold for the MIZ, which is typically 50 to 250 km wide, and stratified by low saline water from the melting pack-ice, but not necessarily for the whole SIZ. In Table 1, we use an estimate for the whole SIZ as given by Smith et al. (1988) to be representative of this zone. We vary this value in the sensitivity analysis dis-

Table 2
Annual primary production in the Southern Ocean

Ref.	$\times 10^{15}$ g C y^{-1}
El-Sayed (1968)	3.3
Holm-Hansen et al. (1977)	0.5
Berger et al. (1987)	5.2
Smith (1991)	1.2
Antoine et al. (1996)	4.0
Legendre et al. (1992)[a]	0.3
Bio-optical model	2.1
Table 1	0.7

[a] Based on SIZ and CCSZ areas only.

cussed below. For the POOZ we cite several recent reviews and subjectively assume 20 g C m^{-2} y^{-1} as a representative value. Table 2, which is far from all inclusive, lists several estimates of total annual production for the Southern Ocean, here taken as that area south of the Polar Front (roughly 31×10^6 km^2). Estimates vary by an order of magnitude and illustrate that global numbers need to be cautiously considered. Clearly, a key issue in regional and global estimates is the space/time variability of the environment, the necessary compromises made in sampling this environment and the corresponding assumptions used to extrapolate limited data over space and time. Various, often subjective, assumptions permit a wide range of results.

3.2. LCP model results

Fig. 2a shows a log plot of Southern Ocean productivity (mg C m^{-2} d^{-1}) as derived using the model of Morel and Berthon (1989) described above. Data were first averaged seasonally, then annually, to obtain an average daily rate. As noted previously, the CZCS data used as input to this model have been heavily averaged over both space and time. Nevertheless, the CZCS data show significant variability in the distribution of phytoplankton biomass in the Southern Ocean as discussed in detail by Sullivan et al. (1993) and Comiso et al. (1993). The productivity estimates displayed here follow the general distribution of biomass but is modified (via Eq. (1)) by the average distribution of PAR incident on the Southern Ocean. Integrated production over the area south of 55°S, which is a rough geographic approximation of the area south of the Polar Front, gives a value of 2.14 g C m^{-2} y^{-1} assuming an effective 365-day year. This demonstrates how assumptions affect value, since a significantly shorter growing season will proportionally reduce the annual estimate accordingly. The relative spatial distribution shown in Fig. 2a is likely to be a more robust evaluation of Southern Ocean annual production than the absolute values.

Fig. 2b is a close-up view of the longitudinal area between 55° and 80°W and inclusive of the Antarctic Peninsula and the Palmer LTER regional grid (shown by red triangles), while Fig. 2c shows productivity by season for the Palmer LTER grid only. There are no CZCS or PAR data during winter (Jun, Jul, Aug), hence no production could be calculated for the top plot. The springtime data (Sept, Oct, Nov) show a gradient in production from high values in the northeast (lower right hand corner of the grid), to low values in the mid peninsula region, to zero values in the predominantly ice covered southern region. Summer values (Dec, Feb, Mar) show relatively high and patchy distribution throughout the grid, likely a feature of very uneven CZCS coverage, while relatively low and more uniform distributions are seen in fall (Mar, Apr, May). Mean daily rates of productivity, as computed with the bio-optical model, using CZCS and ISCCP data, are roughly a factor of 3 to 4 times lower than the average (1170 mg C m^{-2} d^{-1}) found from shipboard data (Table 1) for this CCSZ region.

Fig. 3 shows primary production computed with the bio-optical model using chlorophyll data (Smith et al., 1996b), from each Palmer LTER regional cruise. These data also illustrate the spatial and seasonal variability of productivity within the Palmer LTER grid. As with the CZCS-derived estimates, these data are consistent in showing a gradient in productivity from northeast (lower right on the grid plots) to southwest (upper left), which is associated with an on/offshore gradient and the alongshore seasonal progression of biomass accumulation (Smith et al., 1996b). August 1993 (winter) ship observations show values which are low and relatively uniform. November 1991 (spring) ship observations were limited by above average ice coverage for this time of year (Stammerjohn and Smith, 1996; Fig. 4 in Smith et al., 1996b; Smith et al., this volume). However, the springtime pattern shows productivity

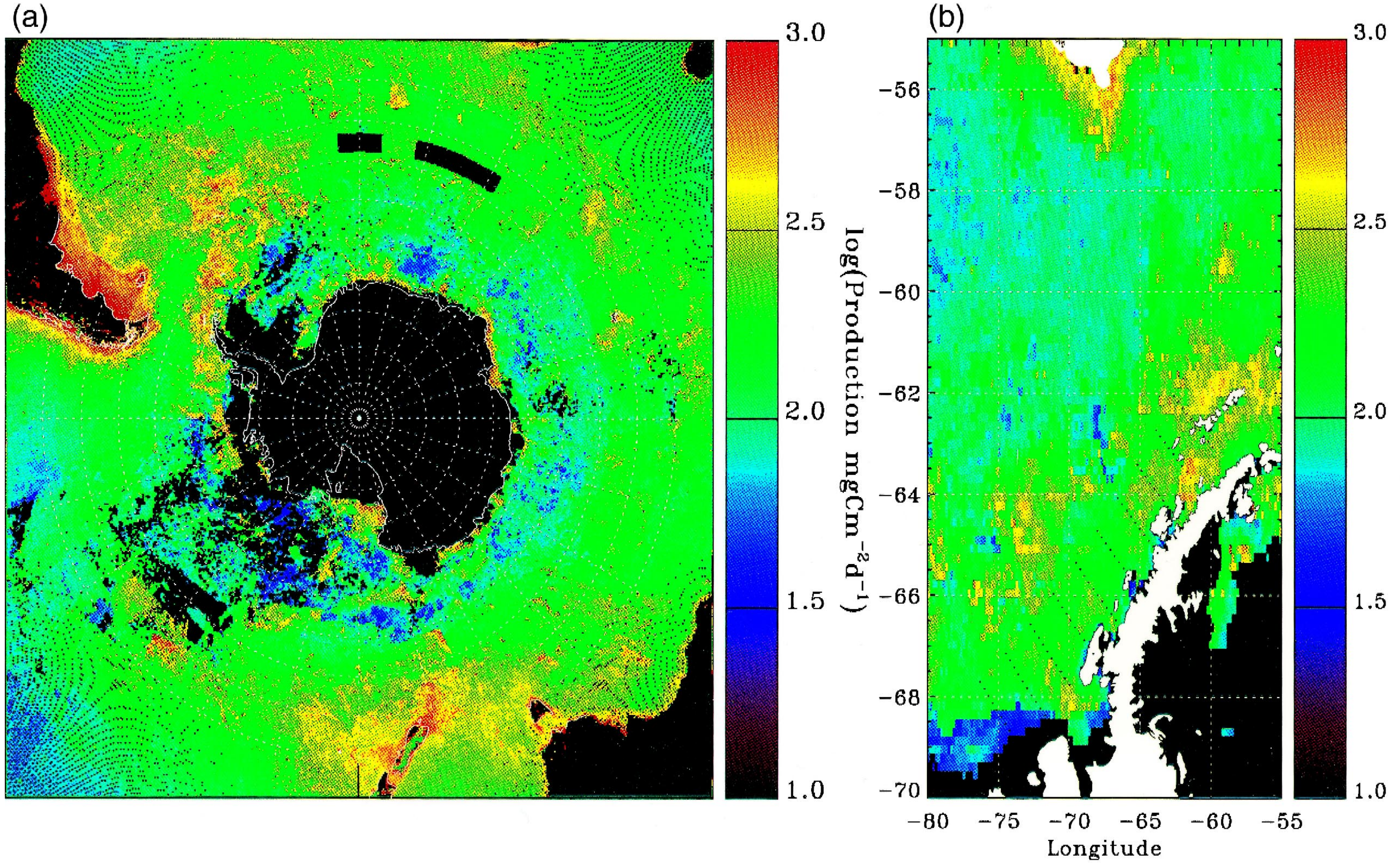

Fig. 2. (a) Southern Ocean Net Primary Productivity (NPP) (g C m^{-2} d^{-1}), estimated using satellite CZCS and ISCCP data. Integrated yearly NPP for all waters south of the Polar Front (55°S) is 2.14 Gton C y^{-1}. (b) NPP (mg C m^{-2} d^{-1}) as in (a) for the region west of the Antarctic Peninsula (55° to 80°W). Palmer LTER sampling grid lines are demarcated by the yellow triangles. (c) NPP (mg C m^{-2} d^{-1}) as in (a) for the Palmer LTER grid and for each season: winter (Jun, Jul, Aug), spring (Sep, Oct, Nov), summer (Dec, Jan, Feb), and fall (Mar, Apr, May). Mean daily rates of productivity for spring, summer and fall are 198, 351 and 147 mg C m^{-2} d^{-1}, respectively.

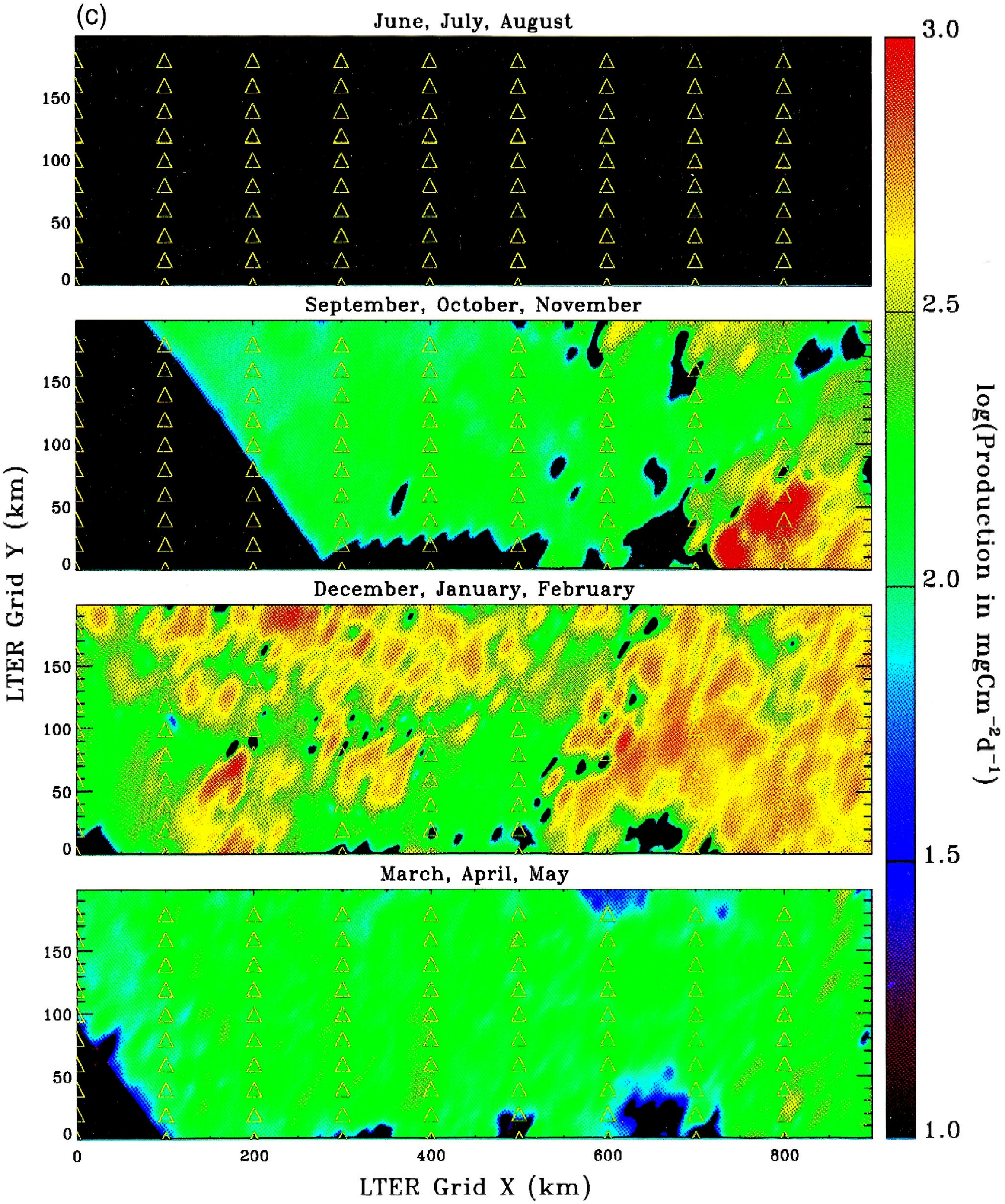

Fig. 2 (continued).

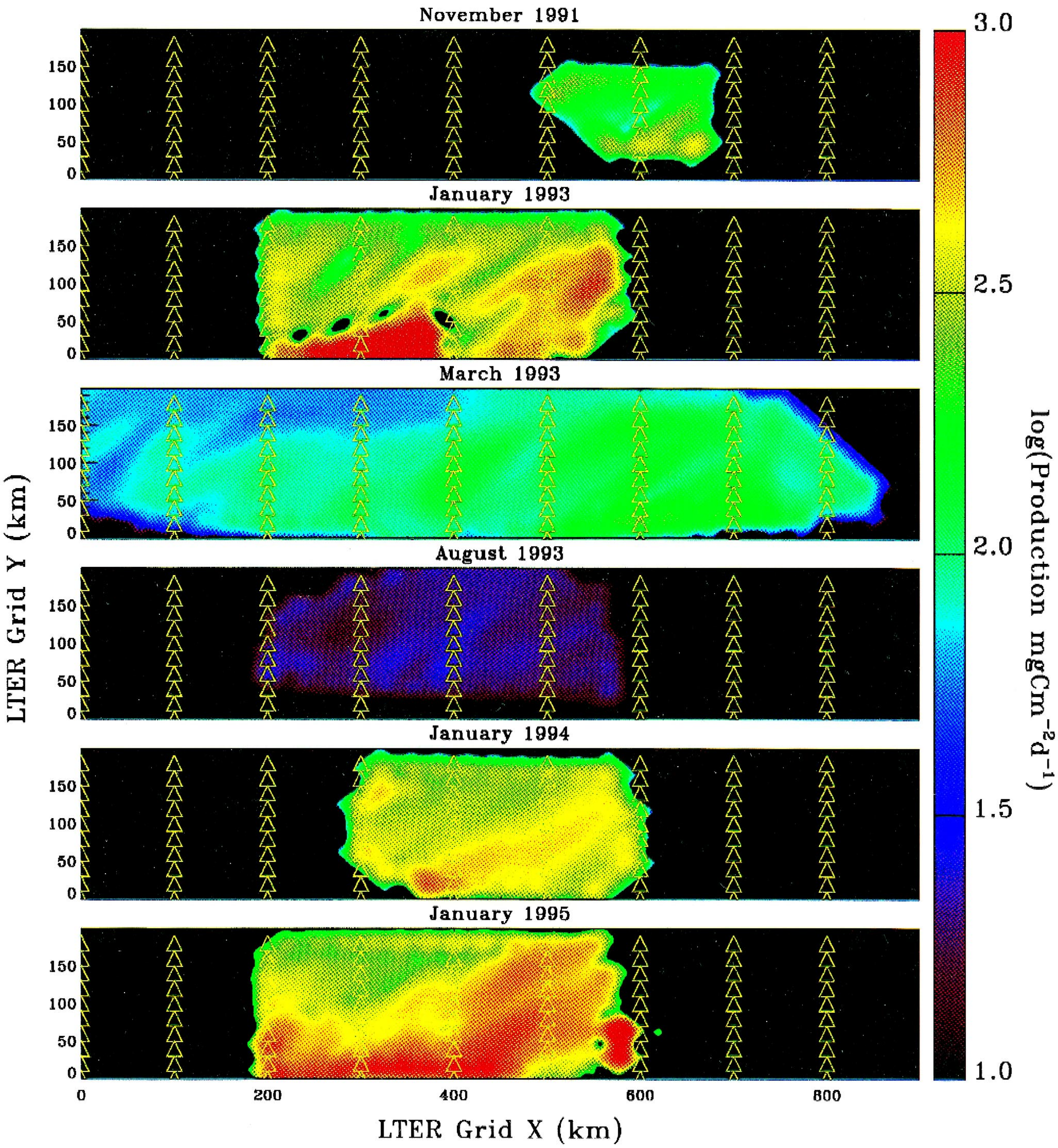

Fig. 3. NPP (mg C m^{-2} d^{-1}), estimated using surface chlorophyll and PAR data for the Palmer LTER grid area and for each LTER cruise. Mean daily productivity (mg C m^{-2} d^{-1}) for each cruise are: Nov 91, 23; Jan 93, 172; Mar 93, 85; Aug 93, 7; Jan 94, 109; Jan 95, 216.

beginning near-shore, and following the retreat of sea ice, but the relative contribution of nearshore vs. sea ice influence is uncertain. January (summer) ship observations (Jan 1993, Jan 1994, Jan 1995) show interannual variability in the strength of on/offshore and alongshore gradients. March 1993 (fall) ship observations show low productivity throughout the Palmer LTER grid, although values slightly increase both nearshore and alongshore. On average, and as was true when using CZCS derived chlorophyll con-

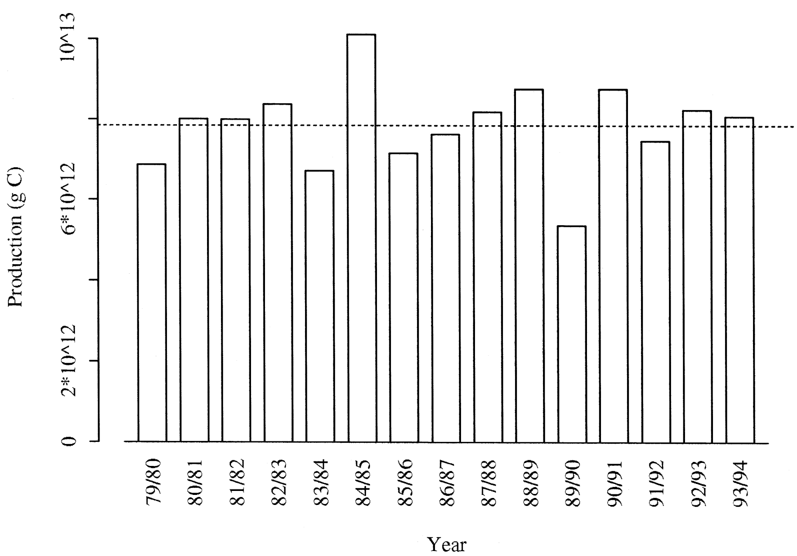

Fig. 4. Estimated Palmer LTER production associated with the annual retreat of pack ice, assuming a mean primary production rate of 1.6 g C m^{-2} d^{-1} an 'upper limit' estimate for MIZ related production. Dashed line represents the 15-year mean (7.85×10^{12} g C y^{-1}). Coefficient of variation is 14% and is independent of the assumed production rate.

centrations, these results using the LCP model are low by a factor of 3 or 4 compared to average shipboard determinations of production.

There is some evidence to indicate that the LCP model requires significant modification for use in Antarctic waters (Marotti, 1992). In a relatively uniform MIZ environment in the Bellingshausen Sea, Marotti found that productivity was relatively independent of incident PAR. Also, saturation parameters, I_k, determined for Antarctic phytoplankton, are low relative to values found for phytoplankton in more temperate waters (Table 4 in Smith et al., 1996b). Further, these I_k values are frequently lower than in-water irradiance values found at the 10% PAR depth. As a consequence, a production model which is linear in PAR may be too simplistic to reflect the dynamics of production in this region.

3.3. Sea ice model

Fig. 4 shows a plot of the estimated production associated with the annual retreat of the pack ice within the Palmer LTER area using the sea ice model previously described (Wilson et al., 1986; Smith et al., 1988). Our purpose for presenting this model is twofold: (1) to illustrate the relatively large interannual variability (given in terms of a coefficient of variation, cv) associated with SIZ productivity, especially on a regional scale; and (2) to serve as the basis for a sensitivity analysis to estimate the relative contribution of MIZ related production as compared to production associated with the shelf-slope region per se.

Mean SIZ productivity for this area (dashed line in Fig. 4) is slightly less than 8×10^{12} g C y^{-1}, with significant variability about the 15-year mean. The sea ice data, and therefore the derived production, show some evidence of a persistent 6 to 8 year cycle (see e.g., Plate 1, Stammerjohn and Smith, 1996), where consecutive high ice years for the Palmer LTER area (1979–1982, 1986–1987 and 1991–1992) alternate with low ice years (1983–1985, 1988–1990, and 1993–1994). While the sea ice record is too short to show statistical significance of a possible sea ice periodicity (Stammerjohn and Smith, 1996), air temperature records for this area, which are inversely correlated with sea ice, have been shown to be significantly correlated with the Southern Oscillation Index (SOI) (Smith et al., 1996b) so that a potential mechanism for sea ice periodicity exists. While interannual variability in total Southern Ocean sea ice coverage is relatively small (cv of 1.7%), interannual variability, especially on a regional basis is significantly larger. For the LTER region a coefficient of variation in interannual sea ice coverage of 24.8% translates into a cv of 14% associated with SIZ phytoplankton production. Thus, relatively small ecological regions such as the Palmer LTER grid can experience large year to year variability in both sea ice and MIZ related production.

For the Palmer LTER area, which is a CCSZ within a SIZ, it is of interest to estimate the relative contributions from these two distinct subdivisions to the overall production within this area. A ‘base value’ productivity is first computed for the area by assuming (Table 1) an average value of 140 g C m^{-2} y^{-1} for CCSZ production (which could also contain some significant and unknown SIZ contribution). To compute this base value we correct for the fraction of time that the Palmer LTER area is ice covered (with an assumed zero productivity) to obtain an estimate for the annual Palmer LTER CCSZ production of 1.61×10^{13} g C y^{-1}. This ‘base value’ can then be compared with values computed by the sea ice model for a range of assumed MIZ daily production rates of 1.6, 0.8, 0.4 and 0.2 g C m^{-2} d^{-1}, where Fig. 4 shows a mean value of 7.85×10^{12} g C y^{-1} for the rate of 1.6. The ratio of SIZ to the base value CCSZ production is then found to be 48, 24, 12 and 6% for assumed rates of 1.6, 0.8, 0.4 and 0.2, respectively. The value of 1.6 g C m^{-2} d^{-1} may be viewed as an upper limit for the purpose of this sensitivity analysis. Values of 0.8 to 0.4 g C m^{-2} d^{-1} are within the range reported for the Ross and Weddell Sea marginal ice zones (Wilson et al., 1986; Smith et al., 1988), and 0.2 is close to the spring time value reported for the marginal ice zone in the Bellingshausen Sea (Marotti, 1992; Boyd et al., 1995). This suggests that the contribution of MIZ related production in this mixed CCSZ and SIZ region is likely between 5% and 50%.

4. Conclusions

Although estimates of oceanic regional production should be viewed with caution, these estimates do permit consideration of the relative contribution from distinct hydrographic/biogeochemical subdivisions of the Antarctic marine ecosystem which facilitate comparison among geographic regions. It is clear that better space/time data are required for each of these subdivisions if we are to increase the accuracy of global values, and there is the hope that satellite and aircraft data will aid in this effort in the coming years. Better estimates of the magnitude, timing and spatial extent of MIZ related production are needed in order to improve estimates associated with the SIZ. A sensitivity analysis of the Palmer LTER area shows that production associated with the annual retreat of the MIZ is likely to contribute between 5 and 50% to the productivity of this CCSZ/SIZ area and hence, also, to the interannual variability in this region. CCSZ related production shows significant space/time variability, where episodic blooms appear to be significant but mechanisms are not yet fully understood. The timing of blooms appear critical, and the relative importance of sea ice within the CCSZ remains a question.

Evidence suggests that considerable phytoplankton productivity within the Southern Ocean takes place under light-saturated conditions. Under these conditions a key assumption underlying LCP models for estimating productivity is seriously flawed, so that these models will need to be significantly revised and/or replaced with models that more accurately reflect the physiological conditions of phytoplankton within Antarctic waters. However, since the most effective (and perhaps only) way to adequately sample the space/time variability of the Southern Ocean is by means of remote sensing (Comiso, 1995), there is strong motivation for the development and use of bio-optical models that can accommodate ocean colour satellite and aircraft data as well as time series of ship and mooring observations.

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