Journal of Marine Systems 17 (1998) 229–243

JOURNAL OF MARINE SYSTEMS

Seasonal and interannual variability of phytoplankton biomass west of the Antarctic Peninsula

R.C. Smith [a,*], K.S. Baker [b], M. Vernet [b]

[a] Institute for Computational Earth System Science, University of California Marine Bio-Optics (UCMBO), Department of Geography, University of California, Santa Barbara, Santa Barbara 93106 CA, USA

[b] UCMBO, MRD, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093-0218, USA

Received 15 October 1995; accepted 15 June 1996

Abstract

The spatial and temporal variability of phytoplankton biomass, estimated as chlorophyll-a (chl-a) concentration, is examined in the continental shelf-slope region west of the Antarctic Peninsula. Relationships between temporal observations in the nearshore Palmer Station grid (64°46.77′S, 64°04.36′W) and spatial observations in a larger regional grid 200 km on/off-shore and 900 km alongshore are presented. Average chl-a concentrations in the upper layers of the water column in the immediate vicinity of Palmer Station show strong seasonal and interannual variability. Biomass accumulation typically starts during mid-November, while strong blooms develop from December through January. The 1991/1992 and 1994/1995 seasons developed higher overall chl-a concentrations (average maximum water column values reaching 8 and 16 mg chl-a m^{-3}, respectively) than the 1992/1993 and 1993/1994 seasons (average maximum water column values of less than 3 mg chl-a m^{-3}). The 1994/1995 season of extremely high chl-a concentrations also showed a prolonged bloom period into February, while the 1991/1992 season did not. Similar interannual variability was observed in the regional grid. Average chl-a concentration in the top 30 m was 0.91, 1.24 and 1.66 mg chl-a m^{-3} for January of 1993, 1994 and 1995, respectively. The regional grid contains an on/off-shore gradient in bottom topography, measured physical and optical characteristics, as well as chl-a concentrations. Regional inshore grid stations in January had, on average, almost four times more chl-a biomass than off-shore stations (2.18 vs. 0.59 mg chl-a m^{-3}, respectively). There is evidence that this on/off-shore gradient is modulated alongshore by latitudinal variability which follows the annual advance and retreat of sea ice.

Résumé

La variabilité spatiale et temporelle de la biomasse phytoplanctonique, exprimée en termes de concentration de chlorophylle a, est examinée dans la région du plateau continental et du talus à l'ouest de la Péninsule Antarctique. Les observations temporelles sur la grille côtière de la Station Palmer (64°46.77′S, 64°04.36′W) sont mises en relation avec les observations spatiales réalisées sur une plus vaste grille régionale de stations (900 km en parallèle à la côte et 200 km selon la perpendiculaire). La teneur moyenne en chlorophylle dans les couches supérieures de la colonne d'eau présente une forte variabilité saisonnière et interannuelle au voisinage immédiat de la Station Palmer. L'accumulation de biomasse commence typiquement à la mi-novembre et de fortes floraisons se développent de décembre à janvier. En 1991–1992 et 1994–1995 ont été atteintes des teneurs chlorophylliennes beaucoup plus fortes (moyenne maximale sur la colonne d'eau 8 et 16 mg

* Corresponding author. Tel.: +1-805-893-4709; Fax: +1-805-893-2578; E-mail: ray@icess.ucsb.edu

PII: S0924-7963(98)00040-2

m^{-3}, respectivement) qu'en 1992–1993 et 1993–1994 (moyenne maximale sur la colonne d'eau < 3 mg m^{-3}). Outre sa biomasse chlorophyllienne extrêmement élevée, la saison 1994–1995 se caractérise par une période de floraison prolongée jusqu'en février, ce qui n'a pas été observé en 1991–1992. Une variabilité interannuelle comparable s'observe sur la grille régionale. Les teneurs chlorophylliennes moyennes pour les 30 m supérieurs sont de 0.91, 1.24 et 1.66 mg m^{-3} pour janvier 1993, 1994 et 1995, respectivement. La grille régionale montre un gradient côte-large, pour la topographie du fond et les caractéristiques physiques et optiques mesurées comme pour la biomasse chlorophyllienne. Les stations côtières de la grille régionale présentent en moyenne des biomasses chlorophylliennes près de quatre fois plus fortes en janvier que les stations du large (2.18 contre 0.59 mg m^{-3}, respectivement). Il apparaît que ce gradient est modulé, parallèlement à la côte, par une variabilité latitudinale qui suit l'avance et le retrait annuels de la glace de mer.

Keywords: phytoplankton; LTER; Antarctic Peninsula

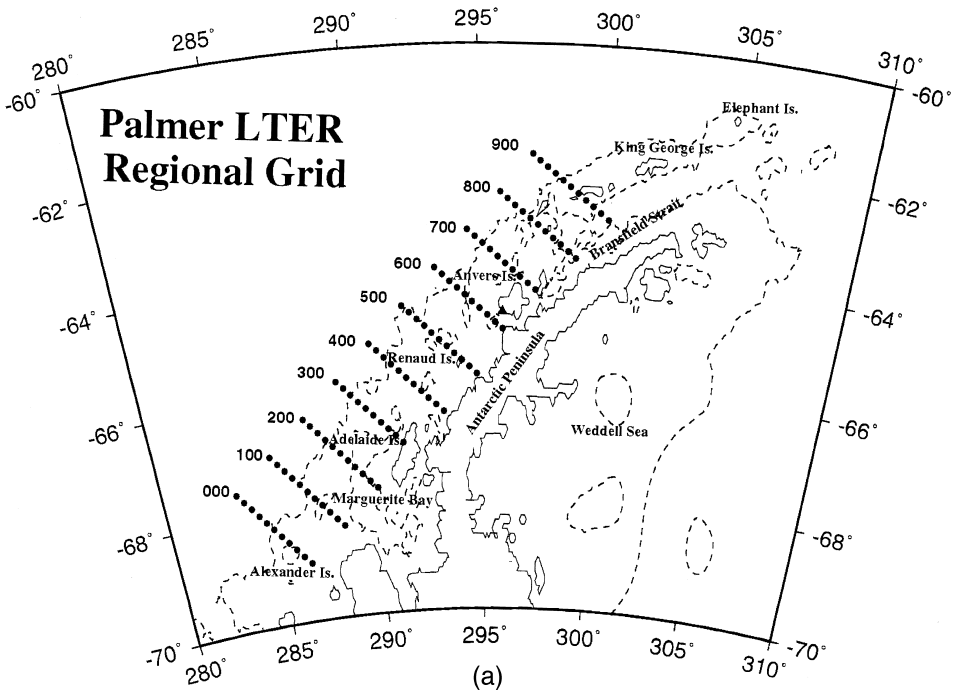
1. Introduction

Since 1991 the Palmer Long Term Ecological Research (LTER) program has included spatial sampling during annual cruises in portions of the regional grid (Fig. 1a) and temporal sampling during the growth season (October to March) in the area adjacent to Palmer Station (Fig. 1b). The Palmer LTER study area west of the Antarctic Peninsula is a shelf-slope system (1) swept by the seasonal sea ice zone, (2) influenced by melt water from glaciers and abundant icebergs, (3) inclusive of areas providing some protection from wind and storms, and (4) potentially enriched by essential micronutrients from processes associated with proximity to the peninsula. Bordering on, and presumably influenced by, the Permanently Open Ocean Zone (POOZ) to the northwest, the Palmer LTER area is a complex combination of two distinctive and relatively productive subdivisions of the Antarctic marine ecosystem (Tréguer and Jacques, 1992): the Coastal and Continental Shelf Zone (CCSZ) and the Seasonal Ice Zone (SIZ). We refer to this segment of the Antarctic marine ecosystem as the west Antarctic Peninsula coastal ecosystem.

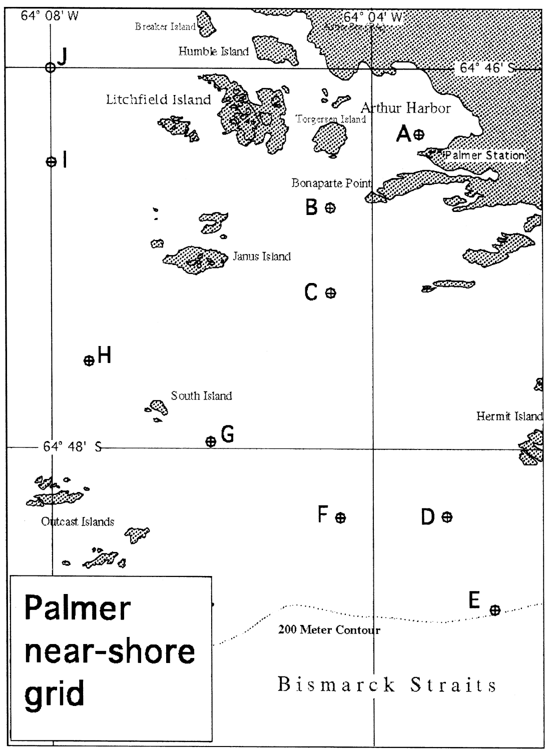
A central hypothesis of the Palmer LTER program is that the annual advance and retreat of the pack ice is a major physical determinant of spatial and temporal changes in the structure and function of Antarctic marine communities. In addition to enhanced productivity associated with the retreat of the marginal ice zone, these coastal waters of Antarctica show, on average, a higher rate of primary production and chl-a accumulation than the POOZ waters of the Antarctic circumpolar current (El-Sayed, 1968; Holm-Hansen et al., 1977; El-Sayed, 1984). A review of published phytoplankton biomass and primary production data (Smith et al., 1996) 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), shows that January chl-a concentrations near the coast average > 2 mg chl-a m^{-3} and decline to < 0.6 mg m^{-3} at the shelf break.

Until the Palmer LTER program, most data available for this region originated from short-term programs (1 to 2 years) focused on specific processes and concentrated to the north of Anvers Island (Fig.

Fig. 1. (a) Palmer LTER regional grid to the west of the Antarctic Peninsula (Universal Transverse Mercator projection). The cardinal stations at 20-km intervals are indicated by solid dots. Cardinal grid lines at 100-km intervals are labelled from 000 to 900. 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. (b) Palmer LTER nearshore grid (A–J) southwest of Anvers Island (Mercator projection). The 200-m contour is indicated by the dotted line.


Palmer LTER
Regional Grid
Elephant Is.
King George Is.
Bransfield Strait
Anvers Is.
Renaud Is.
Antarctic Peninsula
Adelaide Is.
Marguerite Bay
Alexander Is.
Weddell Sea
900
800
700
600
500
400
300
200
100
000
280°
285°
290°
295°
300°
305°
310°
-60°
-62°
-64°
-66°
-68°
-70°

(a)


64° 08' W
64° 04' W
64° 46' S
64° 48' S
Breaker Island
Humble Island
Litchfield Island
Torgersen Island
Arthur Harbor
Palmer Station
Bonaparte Point
Janus Island
South Island
Hermit Island
Outcast Islands
200 Meter Contour
Bismarck Straits
A
B
C
D
E
F
G
H
I
J
Palmer
near-shore
grid

(b)

Table 1
(a) LTER cruise identifier information, dates and cardinal lines sampled

Cruise	Ship[a]	Begin	End	Year	Lines
Nov 91	PD91-9	07 Nov	21 Nov	1991	600–700
Jan 93	PD93-1	05 Jan	08 Feb	1993	200–600
Mar 93	NBP93-2	25 Mar	15 May	1993	200–600
Aug 93	PD93-7	29 Aug	25 Sep	1993	200–600
Ice 93	PD93-8	08 Oct	05 Nov	1993	200–600
Jan 94	PD94-1	11 Jan	07 Feb	1994	200–600
Jan 95	PD95-1	07 Jan	08 Feb	1995	200–600

(b) Annual monthly distribution of LTER cruises (indicated by month and year) and field seasons at Palmer Station (indicated by ×'s)

Month	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
1991/1992				×	Nov 91	×	×	×	×			
1992/1993				×	×	×	Jan 93	×	Mar 93	*	*	
1993/1994		Aug 93	*	×	×	×	Jan 94	×	×			
1994/1995				×	×	×	Jan 95	×				

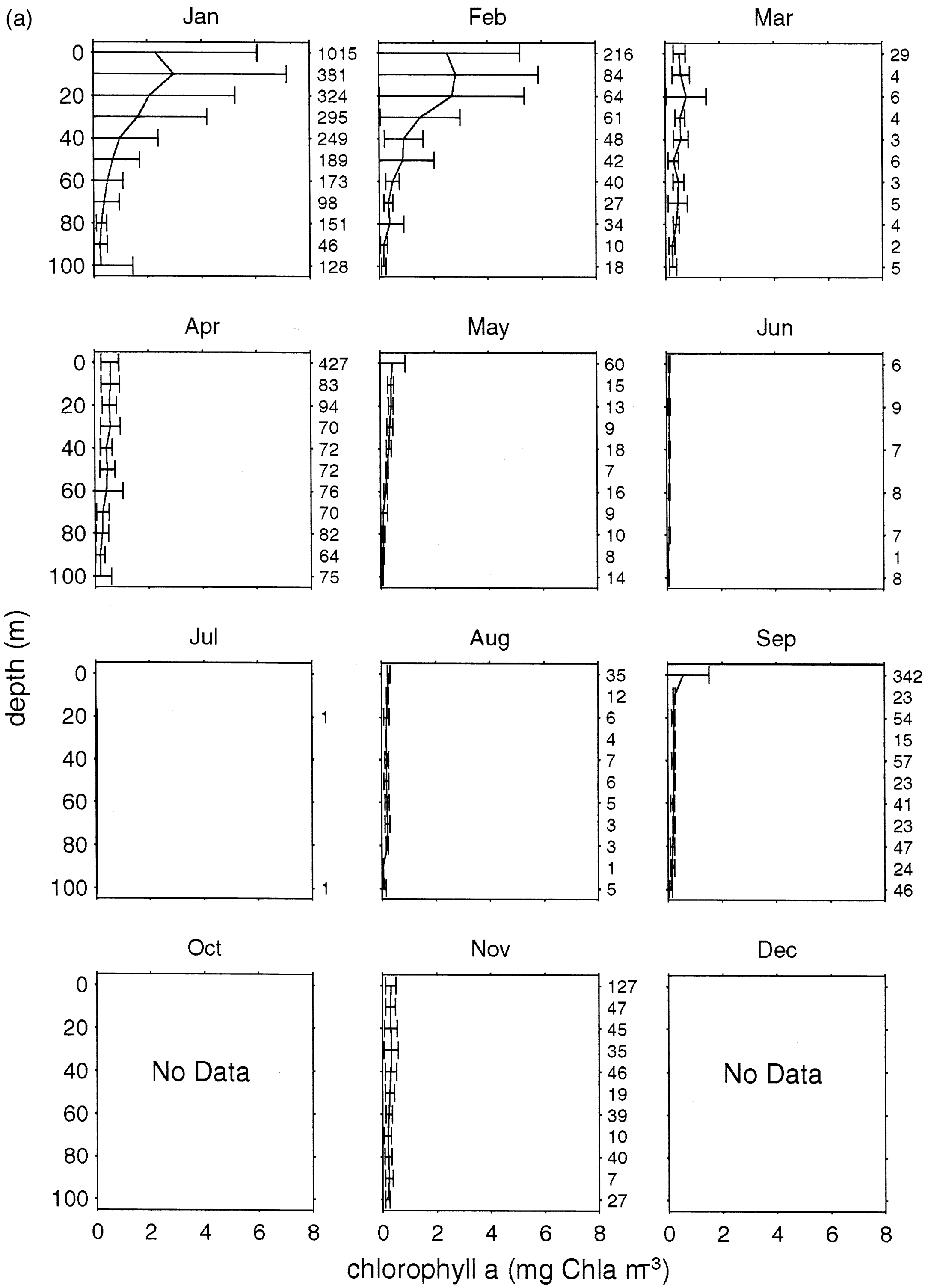
[a] PD = R/V *Polar Duke*; NBP = *Nathaniel B. Palmer*.
Cruises extending beyond one month are indicated by '*'.

1a). While such data can be brought together to obtain information on seasonal variability, long-term studies are required to address processes on interannual, decadal and longer time scales. The Palmer LTER project (Smith et al., 1995) was designed to sample at multiple spatial scales within one regional scale grid, permitting repeated sampling on both seasonal and annual time scales, thus addressing both short and long-term ecological phenomena. In this paper, we describe seasonal, interannual and spatial variability in total chl-a distribution, as was observed during the first four Palmer LTER field seasons. The data follow two modes of sampling: temporal observations made during the growth season (November to March of each year) in the Palmer nearshore grid, and spatial observations made during yearly cruises in the LTER regional grid (Fig. 1a,b; Table 1a,b). Methods are presented in Section 2, results and discussion in Section 3, and conclusions are given in Section 4.

2. Methods

Phytoplankton biomass is estimated by (1) total chl-a concentration using standard fluorometer techniques (Smith et al., 1981), (2) photosynthetic pigments analyzed by high-pressure liquid chromatography (Moline et al., 1994; Kozlowski et al., 1995), as well as by total carbon and nitrogen in seston (Mordy and Carlson, 1991), and (3) taxonomic analysis by microscopy. In this work only the fluorometer results are discussed, where we use chl-a as a proxy measure of phytoplankton biomass. Samples were run either aboard ship at sea or on station, using Millipore HA filters in 90% acetone after a 24-h extraction by freezing without mechanical disruption.

Fig. 2. (a) Mean (solid line) and standard deviation (bars) profiles of chl-a (mg chl-a m^{-3}) vs. depth (m) for LTER cruises by month. Values on the right axes are the number of samples at each depth that were used to compute the mean and standard deviation. June and July values are from Quetin and Ross (unpublished data). (b) Mean depth frequency distribution of maximum chl-a concentrations for LTER cruises. Chl-a maxima are defined as values greater than 50% of the mean concentration for each vertical profile. (c) Surface chl-a C_0 (mg chl-a m^{-3}) vs. integrated water column chl-a C_{50} (mg chl-a m^{-3}), where integrated water column chl-a was determined to 50 m then divided by the depth of integration. Least squares regression gives $\log(C_{50}) = 0.849\log(C_0) - 0.0719$, with a coefficient of determination $r^2 = 0.88$ and $n = 449$.


(a)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
No Data
No Data
depth (m)
0
20
40
60
80
100
0 2 4 6 8
1015
381
324
295
249
189
173
98
151
46
128
216
84
64
61
48
42
40
27
34
10
18
29
4
6
4
3
6
3
5
4
2
5
427
83
94
70
72
72
76
70
82
64
75
60
15
13
9
18
7
16
9
10
8
14
6
9
7
8
7
1
8
1
1
35
12
6
4
7
6
5
3
3
1
5
342
23
54
15
57
23
41
23
47
24
46
127
47
45
35
46
19
39
10
40
7
27
chlorophyll a (mg Chla m⁻³)

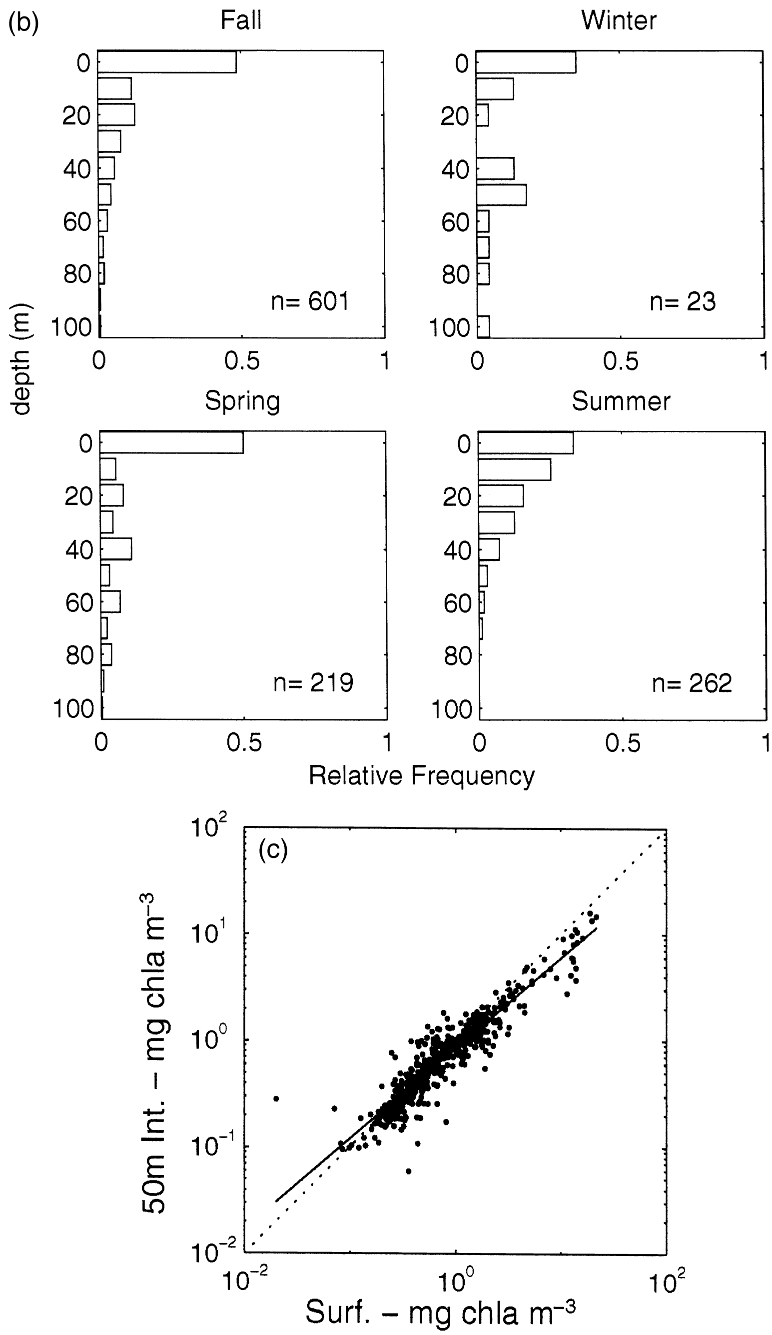


Fig. 2 (continued).

Readings were made using a digital Turner Designs (10-AU-005) Fluorometer, periodically calibrated using standard chlorophyll solutions checked with a spectrophotometer. Chl-a concentration is calculated by subtracting phaeopigment concentration determined by sample acidification.

For the time series data obtained in the vicinity of Palmer Station, samples were taken once or twice a week using an outboard driven rubber boat (Zodiac) to occupy a nearshore grid of stations (Fig. 1b). Stations A through J are within the 2-mile (3.7 km) boating limit of Palmer Station and were sampled weekly to a depth of 30 m, while stations B and E were sampled more frequently. In the following work, time series of pigment biomass for austral spring and summer, during the field seasons of 1991/1992, 1992/1993, 1993/1994, and 1994/1995 are presented for stations B and E. Cruise samples were obtained from twelve go-flo bottles of a rosette sampler on a bio-optical profiling system (Smith et al., 1984) deployed to a maximum of 500 m.

In order to structure our long-term regional observations, we created a sampling grid along the west coast of the Antarctic Peninsula (Waters and Smith, 1992), analogous to the well-known CalCOFI (California Cooperative Oceanic Fisheries Investigations) grid along the west coast of North America (CALCOFI, 1963). Establishing a fixed sampling grid was motivated by the need for station locations that could be visited repeatedly over time scales of many years, and that were regularly spaced to simplify comparisons and modelling efforts of multidisciplinary data. Spacing of cardinal lines and stations was a compromise between biogeochemical spatial gradients within the area and available resources for periodic sampling. The regional (Fig. 1a) and nearshore (Fig. 1b) grids were created so that key stations on the inshore grid could be routinely visited during annual/seasonal sampling of the larger grid. As a consequence, sampling dates between the two grids are often only a few days apart. The Palmer LTER regional grid (Fig. 1a) 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/off-shore (*yyy*) comprise basic sampling stations. For example, grid location 600.040 is 600 km from the southern end of the sampling grid and 40 km off-shore. This particular station (600.040) is also closest to the Palmer nearshore grid that is routinely sampled during annual/seasonal cruises. Table 1a shows cruise identifier information, dates and region sampled. To date, there have been six regional LTER cruises which provide data with respect to interannual variability in summer (Jan 93, Jan 94, Jan 95) and seasonal variability in winter (Aug 93), spring (Nov 91), summer (Jan 93, Jan 94, Jan 95), and fall (Mar 93) (Table 1b).

3. Results and discussion

3.1. Vertical distribution

Inspection of the vertical distribution of chl-a based on compiled historical data for this region (Smith et al., 1996) shows that, on average, maximum biomass is usually at or near the surface. Four years of Palmer LTER cruise data are in basic agreement with this finding (Fig. 2a). Mean depth frequency distributions of maximum chl-a concentrations (Fig. 2b) show that during summer months roughly 30% of the maxima are near surface with the remainder between 10 and 40 m, and that during fall months over 40% are near surface. Winter and spring profiles often show a bimodal distribution, with maximum chl-a concentrations at either the surface or at depths of 40 to 50 m. Future analyses will attempt to link these depth distributions to physical, chemical and optical characteristics of the water column.

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., 1996). Results from Palmer LTER cruise data (Fig. 2c) are consistent with these earlier findings, including comparable slope values of 0.89 obtained from RACER1 (Holm-Hansen and Mitchell, 1991) and of 0.92 obtained from a summary of historical data (1968–1993) (Smith et al., 1996). Indeed, the regression coefficients are also similar to those found for more temperate waters, where integration was performed to one attenuation length, and slopes of 0.96 (Smith and Baker, 1978) and of 0.95 (Brown et al., 1985) were found. For seasons that were sampled historically (late spring, summer and fall), this relationship is also found to hold true (Smith et al., 1996).

3.2. Temporal variability

Large seasonal variability of phytoplankton biomass in polar regions is widely recognized as a consequence of the extreme seasonal variability in solar radiation. Data taken in the vicinity of Palmer Station illustrate this variability and show both the timing and magnitude of biomass development (Fig. 3a,b). Initial accumulation of chl-a most often began early- to mid-December, followed by a peak in concentration (bloom) towards the end of December. This peak was then often followed by a secondary peak in mid-February, but in years with higher chl-a accumulation (1991/1992, 1994/1995), there were additional peaks between the two typical bloom periods. Timing of events at stations B (Fig. 3a) and E (Fig. 3b) tracked closely, but not exactly, indicating significant small scale (< 1 km) spatial variability.

Average chl-a concentrations in the top 30 m at station B were higher during 1991/1992 and 1994/1995 seasons than during 1992/1993 and 1993/1994 seasons. Values ranged from 0.5 to 8 mg chl-a m^{-3} during 1991/1992 and 0.5 to 16 mg chl-a m^{-3} during 1994/1995 and were consistently less than 3.0 mg chl-a m^{-3} during 1992/1993 and 1993/1994. Typically, biomass was higher at station B (off Bonaparte Point) than at station E (further off-shore) during years of high chl-a accumulation (1991/1992 and 1994/1995), with this trend slightly reversed during years of lower chl-a accumulation (1992/1993 and 1993/1994). Surface chl-a concentrations followed similar patterns observed for the average chl-a in the top 30 m (data not shown). However, higher chl-a concentrations were sometimes slightly subsurface (1–2 m), suggesting a highly variable surface layer inshore during a bloom. Magnitude and temporal variability in chl-a concentrations observed at the outer stations (F–J, Fig. 1b) were similar to those observed at station E.

In the vicinity of Palmer Station we observed a distinct interannual variability not only in the timing and magnitude of blooms but also in integrated biomass over the growing season (November to February). Monthly chl-a averages, for combined nearshore stations B and E, for each annual growing season are summarized in Table 2. Four-month (November to February) mean chl-a concentrations for each growing season are also given and show more than a twofold annual variability.

Regional seasonal variability is illustrated in Fig. 4 which shows average chl-a concentration within the top 30 m for each LTER cruise. These cruise data display a seasonal variability consistent with the higher temporal resolution data from the Palmer nearshore grid (Fig. 3). The average chl-a for the

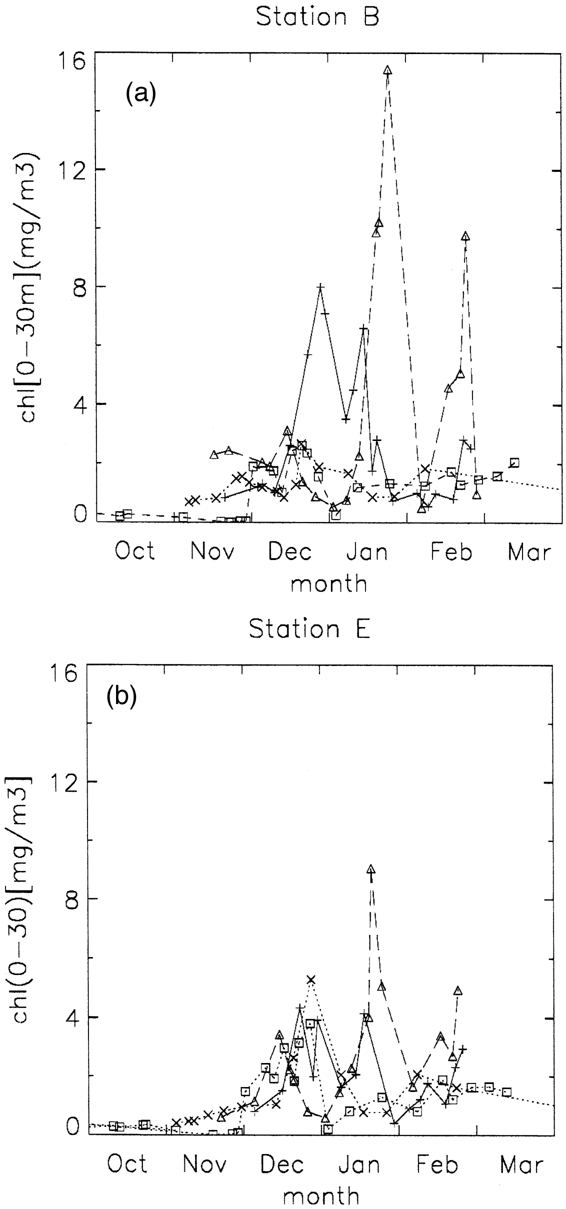


Fig. 3. (a) Average chl-a concentration (mg chl-a m^{-3}) in the top 30 m as a function of time during the growth season for station B (+ = 1991/1992; × = 1992/1993; square = 1993/1994; triangle = 1994/1995). (b) Average chl-a concentration (mg chl-a m^{-3}) in the top 30 m as a function of time during the growth season for station E. Symbols as in Fig. 3a.

Table 2
Average chl-a concentration (mg chl-a m^{-3}) in top 30 m for combined inshore stations B and E

Month	Oct	Nov	Dec	Jan	Feb	Mar	Mean	Jan600.040	Jan600line	Jangrid
1991/1992	–	0.85	2.75	2.42	1.68	–	1.92	–	–	–
1992/1993	–	0.82	1.90	1.24	1.85	–	1.45	2.35	1.73	0.91
1993/1994	0.28	0.08	2.20	0.97	1.36	1.72	1.15	1.04	1.16	1.24
1994/1995	–	1.49	1.84	5.36	3.16	–	2.96	4.96	1.66	1.66

The mean represents a growth season average (November to February).
The last three columns represent cruise data.

entire grid varies from 0.91 to 0.56 to 0.22 mg chl-a m^{-3} for Jan 93 (summer), Mar 93 (fall), and Aug 93 (winter) cruises, respectively.

Regional interannual variability can be seen by comparing chl-a concentrations for each of the three January cruises shown in Fig. 4 and in Table 2 (last column). The highest regional pigment biomass was during the Jan 95 cruise, which is also consistent with the high value for the 1994/1995 growing season average from the Palmer nearshore grid (Table 2, column 8). In contrast, regional pigment biomass during the Jan 94 cruise was higher than during the Jan 93 cruise, which is opposite to the growing season averages from the Palmer nearshore grid in 1993/1994 and 1992/1993. However, the regional grid line closest to the Palmer nearshore grid (600) does show the same pattern of interannual variability in pigment biomass as the growing season averages from the Palmer nearshore grid (Table 2, columns 8–10).

The Palmer LTER group have hypothesized (Smith et al., 1995) that sea ice mediates several factors regulating phytoplankton cell growth and accumulation and, hence, the space/time variability in phytoplankton biomass. Pigment biomass, particularly under heavy grazing pressure, may vary independently from phytoplankton production. Consequently, linkages between chl-a and sea ice are expected to be complex and may not always show a tight coupling. Nevertheless, evidence to date suggests that there is a linkage between the timing and extent of sea ice and that of the abundance and distribution of phytoplankton. Springtime ‘conditioning’ of the water column by sea ice may be an important factor in determining phytoplankton biomass levels in January. The interannual variability in winter (August) sea ice coverage for these 4 years is shown by the ice contour in the January plots in Fig. 4 and in greater detail by the ice images in Fig. 5. The ice images indicate that 1991 and 1994 had above average winter ice coverage, while 1992 and 1993 had average and below average winter ice coverage, respectively (Stammerjohn and Smith, 1996). These figures are suggestive of a linkage between the phytoplankton and the extent and timing of sea ice, a theme that we will develop more fully elsewhere.

3.3. Spatial variability

Regional spatial variability in pigment biomass within the LTER grid during each cruise is also illustrated in Fig. 4. Inspection of the spatial chl-a patterns for each cruise shows both an on/off-shore gradient and an alongshore gradient in pigment biomass. To investigate the presence of an alongshore gradient within the LTER grid, the average chl-a for a cardinal line was determined from station averages, integrated to a depth of 30 m (units of mg chl-a m^{-3}), for stations 040 to 180. The results, summarized in Table 3 and plotted in Fig. 6, show that the 1993 and 1995 cruises display the most notable alongshore gradients.

The winter cruise (Aug 93), distinguished by a relatively low and uniform distribution of pigment biomass (Table 3; Fig. 6), occurred when the distribution of sea ice was unusually low in August 1993 (Fig. 5). In addition, the timing of maximum sea ice within the LTER grid during that year was anomalous, occurring several months later (during September/October) than on average (August) (Stammerjohn and Smith, 1996). Pigment biomass in the spring of 1991 (Nov 91) was also relatively low (Table 3) for the two cardinal lines sampled. (Further

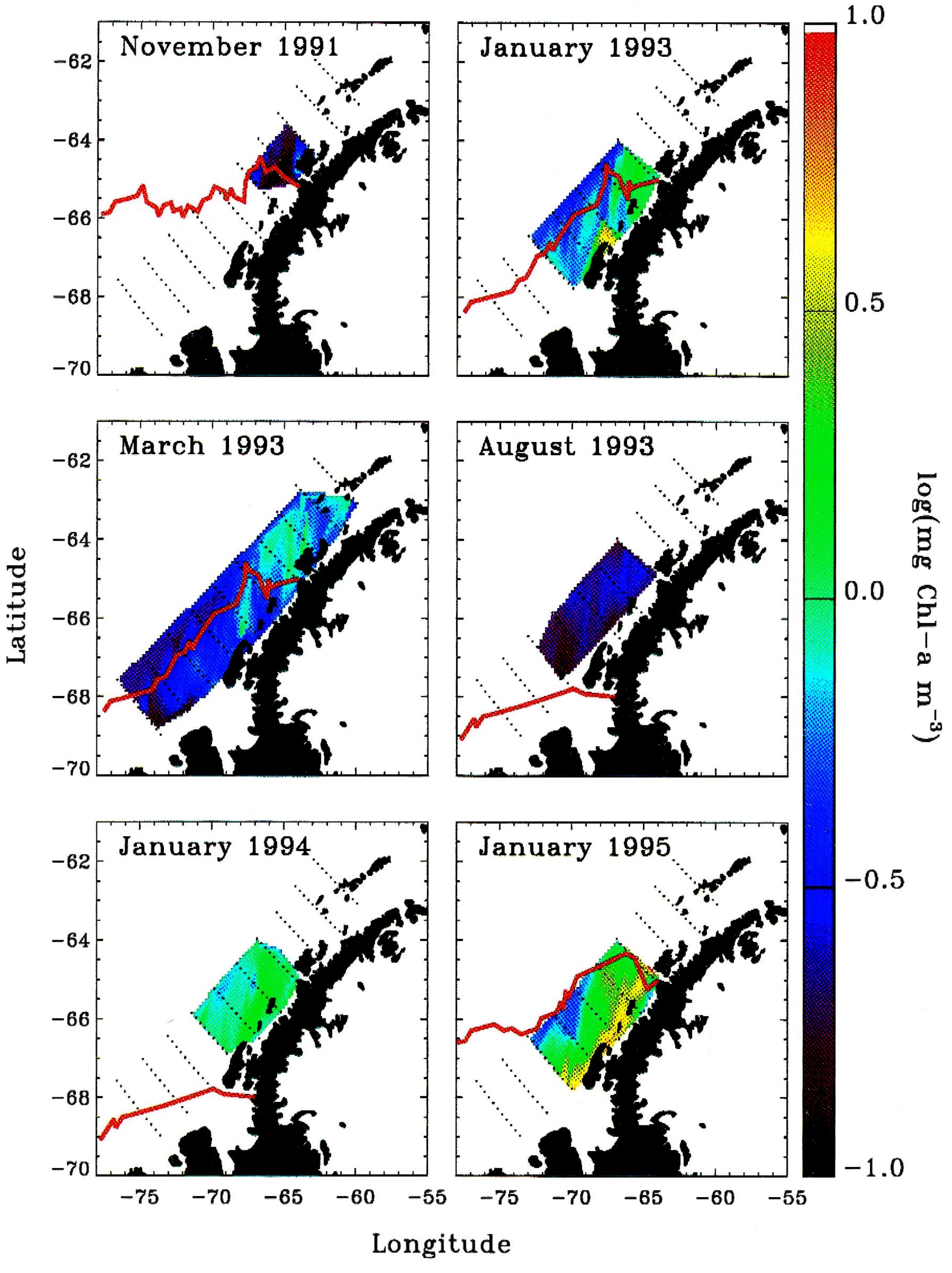


Fig. 4. Average chl-a concentration (mg chl-a m^{-3}) in the top 50 m within the LTER grid for each cruise. Log chl-a concentration is indicated by the color bar. Small dots indicate the cardinal stations within the LTER grid. The solid red line shows the location of the mean 80% sea ice concentration contour for August, which best reflects the interannual variability in maximum winter ice coverage. The January and March subplots show the previous winter's August 80% ice concentration contour, while the August and November subplots show the contemporaneous August 80% ice concentration contour.

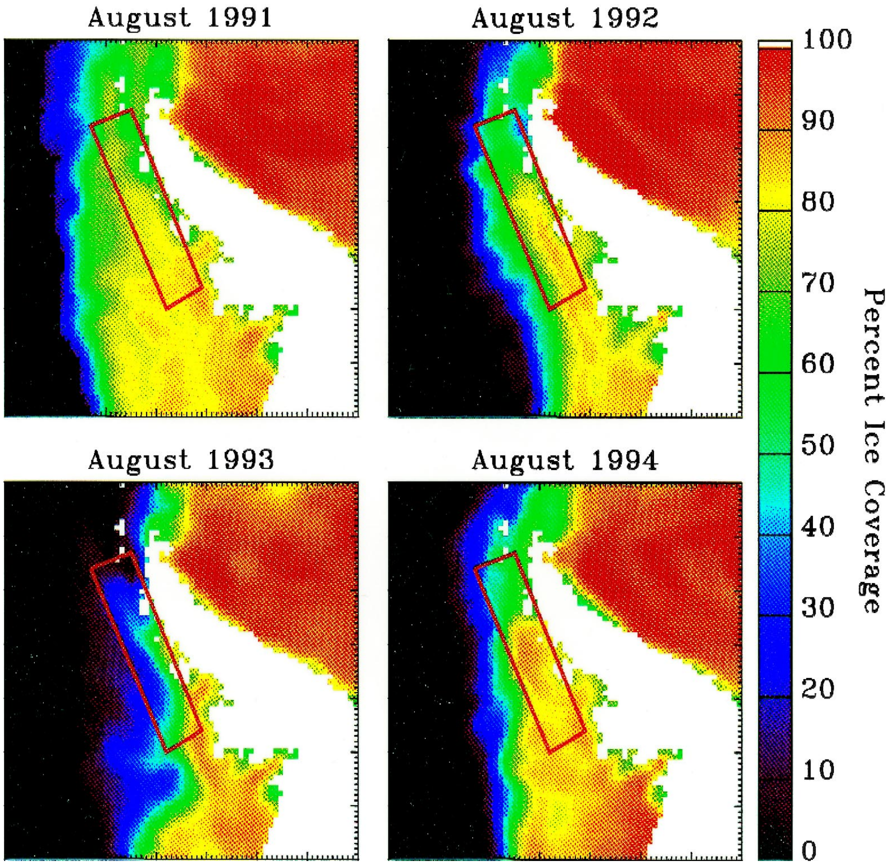


Fig. 5. Average August sea ice concentration for each of the LTER field seasons to date. The Antarctic Peninsula is shown in white, the boundary of the LTER grid is the red rectangle west of the Peninsula, and percent ice coverage is indicated by the color bar. Sea ice concentrations were estimated from passive microwave satellite (SSM/I) data.

Table 3
Average chl-a concentration (mg chl-a m^{-3}) in top 30 m over each grid line from station 040 to 180. Lines 200 to 600 were averaged to give a grid mean, standard deviation (std) and coefficient of variation (cv)

Line	Nov 91	Jan 93	Mar 93	Aug 93	Jan 94	Jan 95	Mean Jan	Std
100	–	–	0.32	–	–	–	–	–
200	–	0.68	0.40	0.17	–	1.36	1.02	0.48
300	–	0.50	0.37	0.19	1.39	0.78	0.89	0.45
400	–	0.67	0.63	0.22	1.13	1.33	1.04	0.34
500	–	1.08	0.53	0.26	1.30	3.18	1.30	0.31
600	0.18	1.63	0.88	0.25	1.16	1.66	1.48	0.28
700	0.27	–	0.89	–	–	–	–	–
800	–	–	0.56	–	–	–	–	–
Mean		0.91	0.56	0.22	1.24	1.66	1.15	
std		0.45	0.21	0.04	0.12	0.91	0.24	
cv		49%	37%	18%	10%	55%	21%	

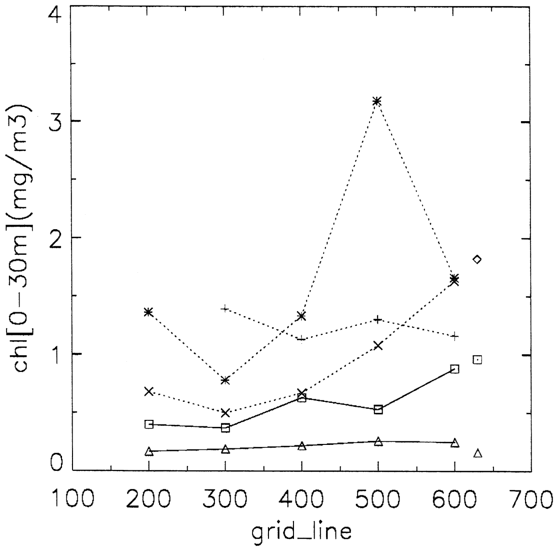


Fig. 6. Average chl-a concentration (mg chl-a m^{-3}) in the top 30 m over each grid line for each LTER cruise (× = Jan 93; square = Mar 93, triangle = Aug 93; + = Jan 94; ∗ = Jan 95). Average chl-a values from combined Palmer nearshore grid stations B and E, which were sampled during each respective cruise, are shown at grid line position 600.030 (square = Mar 93; triangle = Aug 93; diamond = mean Jan).

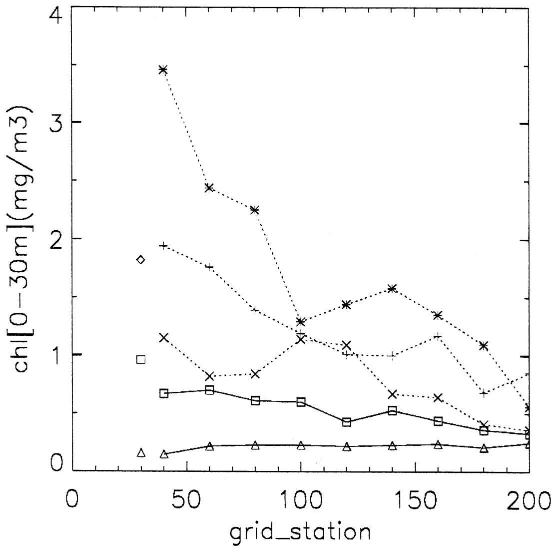


Fig. 7. Average chl-a concentration (mg chl-a m^{-3}) in the top 30 m, averaged over alongshore station position for each LTER cruise. Average chl-a values from combined Palmer nearshore grid stations B and E are plotted at grid station position 030. Symbols as for Fig. 6.

sampling during the Nov 91 cruise was prevented by the spatial extent of sea ice in the southern part of the grid.) It is possible that these low and uniform values of pigment biomass represent a winter time 'base level' prior to the development of late spring/early summer bloom conditions. In contrast, higher pigment biomass values were observed during each summer throughout the grid. Average chl-a concentration during the Jan 94 cruise was, like the Aug 93 cruise, relatively uniform (10% coefficient of variation, cv), yet nearly six times higher. Table 3 and Fig. 6 also show interannual variability in summer pigment concentrations with respect to the alongshore gradient, where the Jan 94 cruise is relatively uniform, in contrast to Jan 93 and Jan 95 cruises which show distinct alongshore gradients.

The on/off-shore variation of pigment biomass within the LTER grid is summarized in Table 4 and plotted in Fig. 7. There is a statistically significant ($p < 0.01$) and persistent on/off-shore gradient in chl-a concentration during summer and fall. For the

Table 4
Average chl-a concentration (mg chl-a m^{-3}) in top 30 m over alongshore station position

Station	Nov 91	Jan 93	Mar 93	Aug 93	Jan 94	Jan 95	Mean Jan	Std
040	–	1.15	0.67	0.15	1.94	3.46	2.18	1.17
060	–	0.82	0.70	0.22	1.76	2.44	1.67	0.81
080	–	0.84	0.61	0.23	1.39	2.25	1.49	0.71
100	–	1.14	0.60	0.23	1.19	1.29	1.21	0.08
120	–	1.09	0.43	0.22	1.01	1.44	1.18	0.23
140	–	0.67	0.53	0.23	1.00	1.58	1.08	0.46
160	–	0.64	0.44	0.24	1.17	1.35	1.05	0.37
180	–	0.41	0.36	0.21	0.68	1.09	0.73	0.34
200	–	0.36	0.33	0.25	0.85	0.56	0.59	0.25

Table 5
Average chl-a concentration (mg chl-a m^{-3}) in top 30 m for stations B and E and 600.040 during times of coincident sampling

Date	B	E	600.040	B/600.040	E/600.040	B/E
Nov 91–11/10/91	0.85	0.86	0.19	4.47	4.52	0.99
Jan 93–01/09/93	1.67	2.06	2.34	0.71	0.88	0.81
Jan 93–01/15/93	0.87	0.78	0.90	0.96	0.86	1.11
Jan 93–01/26/93	0.89	0.78	1.24	0.71	0.63	1.14
Jan 93–02/06/93	1.85	2.08	1.08	1.71	1.92	0.89
Mar 93–04/13/93	1.03	0.89	0.86	1.19	1.03	1.12
Aug 93–09/03/93	0.21	0.11	0.22	0.95	0.50	1.90
Jan 94–01/18/94	1.20	0.82	0.91	1.31	0.90	1.46
Jan 94–01/21/94	1.33	1.30	1.04	1.27	1.25	1.02
Jan 95–01/12/95	2.27	2.29	4.96	0.46	0.46	0.99
Jan 95–01/20/95	10.23	9.06	1.37	1.13	6.61	1.13
Jan 95–01/24/95	15.44	5.08	1.51	10.20	3.36	3.04
Jan 95–02/05/95	0.53	1.65	1.50	0.35	1.10	0.32
Mean				1.96	1.85	1.22
std				2.68	1.86	0.65

January cruise average (Table 4), values close to the coast (stations *xxx*.040) are 3.7 times higher than at the shelf break. These values are remarkably consistent with early results for the northern part of the grid (El-Sayed, 1968), where average January values of 2.12 and 0.42 mg chl-a m^{-3} were found for 'in-shore' and 'off-shore' waters, respectively. A similar on/off-shore gradient is observed for the standard deviations where there is more than a factor of four difference between the standard deviations for the onshore station vs. the shelf break station. The exception, with respect to an on/off-shore gradient, is the winter period (Aug 93), which shows consistently low values throughout the grid.

In addition to seasonal variability with respect to the presence of an on/off-shore gradient in chl-a biomass, there is interannual variability in the gradient strength observed among the three January cruises (Table 4; Fig. 7). Jan 93 differs from Jan 94 in having a lower on/off-shore gradient (about $\times 2$ in 1993 vs. $\times 3$ in 1994), and Jan 95 had the steepest gradient ($\times 6$) due to a disproportionately higher chl-a concentration nearshore.

3.4. Relation between nearshore and regional grids

Regional observations with respect to the on/off-shore gradient can be extended to include nearshore measurements made from Palmer Station. For this analysis we compare data from the Palmer nearshore grid stations B and E with the LTER grid station 600.040, since samples were taken relatively close in time (Table 5). On average, chl-a concentration at station B is higher than at station E, and nearly twice as high as at station 600.040. There is considerable spatial variability, but the variability observed in considering stations B and E as an inshore extension of the 600 line is similar to the variability observed along the 600 line itself. This is further verified by inspection of the on/off-shore gradients shown in Fig. 7, which include the average chl-a concentrations from combined stations B and E, during the respective seasonal periods, plotted at approximately the 030 position. Consistency in the interannual variability of pigment biomass is observed between stations B and E, station 600.040, and along the whole 600 line but not across the whole grid (Table 2).

4. Conclusions

The shelf-slope system west of the Antarctic Peninsula shows fundamentally different characteristics compared to pelagic areas of the Antarctic marine ecosystem. Regional coverage from the annual cruises show the on/off-shore gradient in pigment biomass to be an enduring characteristic (El-Sayed, 1968), with nearshore areas roughly four times higher than off-shore areas. Further, there is some evidence for an alongshore gradient, perhaps associated with the timing of the seasonal alongshore retreat of sea ice and/or latitudinal influences. This is consistent with the concept that the Palmer LTER area is a complex mix of a high productive Coastal and Continental Shelf Zone (CCSZ) and a relatively productive Seasonal Ice Zone (SIZ) (Tréguer and Jacques, 1992). The on/off-shore gradient blends into the relatively less productive Permanently Open Ocean Zone (POOZ) which lies west of the LTER regional grid. Within this west Antarctic Peninsula coastal ecosystem, concentrations and gradients in pigment biomass are highest during spring, summer and fall periods, while the winter period shows low and relatively uniform distributions.

Observations over the first four seasons of the Palmer LTER program show significant variation in both the timing (±several weeks) and magnitude (±a factor of 2) of annual biomass accumulation. The relatively high temporal sampling of the Palmer nearshore grid helps resolve seasonal variability, and results show that nearshore areas have (over four times) higher variability than off-shore areas, presumably due to the greater occurrence of episodic blooms which comprise a significant component of the annual accumulation of pigment biomass. Our 4-year time series suggests that generally two blooms occur, a relatively large spring bloom during December/January and a smaller secondary bloom in February/March. However, blooms appear to be more persistent in years of higher chl-a accumulation. Above average sea ice concentrations in spring appear to be associated with years with higher phytoplankton biomass, but this hypothesis remains to be quantitatively evaluated.

To the extent that massive blooms are a significant component of this shelf ecosystem, a key question becomes one of more fully understanding bloom dynamics and regulation. These on/off-shore gradients suggest that conditions near the coast, in inlets and around islands are more conducive to higher phytoplankton population growth than open waters, although it is not clear if they also have higher specific growth rates (Banse, 1991). Nearshore conditions appear to be conducive in producing large phytoplankton blooms, but a full understanding of mechanisms associated with such blooms is lacking. Sea ice clearly plays a significant role in determining the abundance and distribution of phytoplankton biomass, but more complete space/time studies are necessary to fully elucidate these linkages. The high space/time variability of the more productive CCSZ and SIZ areas dictates mixed sampling strategies, including reliance on remote sensing, to optimally sample and characterize this area.

Results show that pigment biomass, which can be estimated by various proxy optical methods from satellite to in-water moorings, is generally distributed near surface in these waters. Consequently, there is a relatively tight coupling between surface chl-a and chl-a integrated to depth (Fig. 2c). This coupling is an important consideration when using ocean color satellite (e.g., CZCS, SeaWiFS, OCTS) and/or aircraft sensors to estimate water column chl-a concentrations, since the upwelling signal detected by these sensors is heavily weighted by the top attenuation length of the water column.

The combined temporal observations made in the Palmer nearshore grid and spatial observations made during yearly cruises in the regional grid demonstrate that the LTER sampling program is adequate for studying seasonal and interannual changes of biomass over time scales of interest (Smith et al., 1995). The initial 4-year time series of consecutive sampling in the LTER program already shows strong interannual variability as detected in several different ways: (1) timing and intensity of blooms, (2) strengthsin on/off-shore and alongshore gradients, (3) overall annual biomass accumulation, and (4) linkage between biomass and sea ice. Further, the regional gradients in phytoplankton biomass are consistent with temporal observations from Palmer Station, suggesting that the dynamics in chl-a accumulation in the vicinity of Palmer Station are representative of those within the shelf waters and that the seasonal nearshore variability is related to the LTER regional variability in chl-a biomass.

Acknowledgements

This work was funded by NSF/DPP Grant No. OPP90-1192 and NASA Grant No. NAGW-290-10 (RCS). We thank Charleen Johnson, Heidi Dierssen, and Sharon Stammerjohn for their invaluable help in manuscript preparation and helpful discussions.

References

Banse, K., 1991. Rates of phytoplankton cell division in the field and in iron enrichment experiments. Limnol. Oceanogr. 36, 1886–1898.

Brown, O.B., Evans, R.H., Brown, J.W., Gordon, H.R., Smith, R.C., Baker, K.S., 1985. Phytoplankton blooming off the US east coast: a satellite description. Science 229, 163–167.

CALCOFI, 1963. CALCOFI Atlas of 10-meter Temperatures and Salinities, 1949 through 1959. (California Cooperative Oceanic Fisheries Investigations Atlas No. 1), California. Marine Research Committee, California Cooperative Oceanic Fisheries Investigations.

Comiso, J.C., Smith, W.O., Sullivan, C.W., Maynard, N.G., 1990. Satellite ocean color studies of Antarctic ice edges in summer and autumn. J. Geophys. Res. 95, 9481–9496.

El-Sayed, S.Z. (Ed.), 1994. Southern Ocean Ecology: the BIOMASS Perspective. Cambridge Univ. Press, New York, 339 pp.

El-Sayed, S.Z., 1968. On the productivity of the Southwest Atlantic Ocean and the waters west of the Antarctic Peninsula. In: Llano, G.A., Schmitt, W. L. (Ed.s), Biology of the Antarctic Seas III, Antarctic Research Series, Vol. 11, pp. 15–47.

El-Sayed, S.Z., 1984. Productivity of the Antarctic waters: a reappraisal. In: Holm-Hansen, O., Bolis, L., Gilles, R. (Eds.), Marine Phytoplankton and Productivity (lecture notes on coastal and estuarine studies, 8). Springer, Berlin, pp. 19–34.

Holm-Hansen, O., Mitchell, B.G., 1991. Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. Deep-Sea Res. 38, 961–980.

Holm-Hansen, O., El-Sayed, S.Z., Franceschini, G.A., Cuhel, R.L., 1977. Primary production and the factors controlling phytoplankton growth in the Southern Ocean. In: Llano, G.A. (Ed.), Adaptations within antarctic ecosystems: Proc. 3rd SCAR Symp. on Antarctic Biology, Sponsored by the Scientific Committee for Antarctic Research (SCAR) and the International Union of Biological Sciences and held under the auspices of the United States National Academy of Sciences, Washington, DC, Aug 26–30, 1974. Gulf Publishing, Houston, pp. 11–50.

Kozlowski, W., Lamerdin, S., Vernet, M., 1995. Palmer LTER: Predominance of chryptomonads and diatoms in Antarctic coastal waters, Antarct. J. U.S., in press.

Moline, M.A., Prézelin, B.B., Schofield, O., Smith, R.C., 1994. Temporal dynamics of coastal Antarctic phytoplankton: physical/chemical/biological linkages through a summer diatom bloom. SCAR 6th Biology Symposium, Sponsored by the Scientific Committee for Antarctic Research (SCAR), et al., Venice, 30 May–3 June 1994, p. 189.

Mordy, D.W., Carlson, D.J., 1991. An evaluation of fluorescence techniques for measuring DNA and RNA in marine microorganisms. Mar. Ecol. Prog. Ser. 73, 283–293.

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.

Smith, R.C., Baker, K.S., 1978. The bio-optical state of ocean waters and remote sensing. Limnol. Oceanogr. 23, 247–259.

Smith, R.C., Baker, K.S., Dustan, P., 1981. Fluorometer techniques for measurement of oceanic chlorophyll in the support of remote sensing. SIO Ref. 81–17, Visibility Laboratory, Scripps Inst. Oceanography, Univ. California, San Diego, La Jolla.

Smith, R.C., Booth, C.R., Star, J.L., 1984. Oceanographic biooptical profiling system. Appl. Opt. 23, 2791–2797.

Smith, R.C., Baker, K.S., Fraser, W.R., Hofmann, E.E., Karl, D.M., Klinck, J.M., Quetin, L.B., Prézelin, B.B., Ross, R.M., Trivelpiece, W.Z., Vernet, M., 1995. The Palmer LTER: a long-term ecological research program at Palmer Station, Antarctica. Oceanography 8, 77–86.

Smith, R.C., Dierssen, H., Vernet, M., 1996. Phytoplankton biomass and productivity to the west of the Antarctic peninsula, in press. Foundations for Ecosystem Research West of the Antarctic Peninsula. AGU Antarctic Research Series.

Stammerjohn, S., Smith, R.C., 1996. Spatial and temporal variability in western Antarctic peninsula sea ice coverage, in press. Foundations for Ecosystem Research West of the Antarctic Peninsula. AGU Antarctic Research Series.

Thorley, M.R., Trathan, P.N., 1994. Biomass data set documentation, British Antarctic Survey, Natural Environment Research Council, Cambridge CB3 OET, UK.

Tréguer, P., Jacques, G., 1992. Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. Polar Biol. 12, 149–162.

Waters, K.J., Smith, R.C., 1992. Palmer LTER: a sampling grid for the Palmer LTER program. Antarct. J. U.S. 27, 236–239.