Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region

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Abstract—Studies on phytoplankton were one component of the multi-disciplinary RACER program which had 69 stations within a 100 × 250-km rectangle in the southwestern Bransfield Strait and contiguous waters. Data were acquired during eight cruises between December 1986 and March 1987.

All deep stations north of the continental shelf break were low in phytoplankton biomass (<41 mg Chl a m⁻²) and in rates of primary production (mean of 0.34 g C m⁻² day⁻¹) as compared to stations in continental shelf waters. Phytoplankton biomass exceeded 700 mg Chl a m⁻² at some stations in shelf waters, with rates of primary production in December exceeding 3.0 g C m⁻² day⁻¹. The mean rate of primary production at the shelf stations for the 4-month period was 1.05 g C m⁻² day⁻¹. Greatest phytoplankton biomass was found at stations in Gerlache Strait and in nearby Bransfield Strait. Dramatic seasonality in phytoplankton crop size was observed, as massive blooms during December to January declined abruptly to low levels in February to March. As the decrease in phytoplankton biomass was much more abrupt than the corresponding decrease in incident solar irradiation, light does not appear to be the major factor involved in decline of the bloom. Except for stations in Gerlache Strait, nutrient levels remained sufficiently high (>10 μM inorganic nitrogen) that nutrient depletion is not likely to have caused the rapid decline of the phytoplankton bloom. Grazing, sinking and advection all appear to be important mechanisms of massive bloom decline. Phytoplankton populations appeared to be light-adapted, as they showed low $P_{\text{max}}$ values (1.1 mg C mg Chl a⁻¹ h⁻¹), low saturating light values ($k_\text{s} = 18.4 \text{Ein m}^{-2} \text{s}^{-1}$), high initial slope [$\alpha = 0.06 (\text{mg C mg Chl a}^{-1} \text{h}^{-1} /\text{μEin m}^{-2} \text{s}^{-1})$] and a compensation point for net light-activated fixation of CO₂ of ~1.0 μEin m⁻² s⁻¹.

INTRODUCTION

The Southern Ocean is commonly thought of as being very productive, largely because of reports on the high biomass of krill. Most oceanographic studies in Antarctic waters during the past 25 years, however, have shown that rates of primary production are low and in the range of 0.10–0.30 g C m⁻² day⁻¹ (HOLM-HANSEN et al., 1977; EL-SAYED, 1988). These rates are generally obtained during the austral summer period, and hence represent the period of maximal productivity. These low rates are surprising in that Antarctic waters usually have very high nutrient concentrations, with inorganic nitrogen generally exceeding 20 mmol m⁻³. No nutrient limitation has ever been documented in Antarctic phytoplankton (HAYES et al., 1984), although various authors have speculated about this...
possibility (Holm-Hansen et al., 1977, 1989; Jacques, 1983; Nelson and Smith, 1986). This situation of low primary production in spite of high nutrient concentrations has prompted some researchers to call it the major biological “paradox” of the Southern Ocean (El-Sayed, 1987).

Recently Martin and Fitzwater (1988) have speculated that iron may limit rates of primary production in pelagic Antarctic waters, but they specifically mentioned that this effect may not apply in coastal waters close to the continent. Recent studies close to Elephant Island were in agreement with this, as no effect of iron on phytoplankton growth rates could be discerned (Holm-Hansen, unpublished data). This hypothesis therefore does not seem to be applicable to the RACER study area.

Two other factors which are sometimes invoked to explain the low productivity in Antarctic waters are light intensity and low ambient temperatures. Solar irradiance over Antarctic waters is, however, sufficiently high (Krebs, 1983) that light cannot be viewed as a limiting factor in the upper water column during the summer months. Although low temperatures do limit specific growth rates of phytoplankton to values of µ = 1.0 or less (Neori and Holm-Hansen, 1982; Tilzer and Dubinsky, 1987; Spiess, 1987), this effect can not explain the paucity of phytoplankton biomass in most waters. Unless cells are removed or limited by some biological or physical process, the high nutrient concentrations in Antarctic waters should result in substantially higher standing crops of phytoplankton. A model proposed by Mitchell and Holm-Hansen (1991a) predicts that deep wind mixing can lead to insufficient light for development of blooms in the upper mixed layer. However, this mechanism which limits bloom formation for exposed waters probably can not explain the rapid decline of the blooms which develop in more sheltered waters. Nevertheless, it may be one component of the overall mechanism of bloom demise.

There are many scattered reports in the literature indicating that continental shelf waters in the Antarctic often have substantially higher phytoplankton biomass and therefore increased rates of primary production (El-Sayed, 1988) as compared to deep pelagic areas. Shelf waters in the Antarctic are generally 200–500 m deep, and hence the mechanism(s) which cause such elevated productivity in Antarctic waters may not be the same as those which have been described for shallow (5–50 m) shelf waters off the eastern coast of North America (Postma and Zijlstra, 1988) or coastal shelves off the Alaskan coast (Sater, 1974; Alexander and Niebauer, 1981). Reports in the Antarctic literature on phytoplankton biomass and rates of primary production in shelf waters generally are based on few station locations and often do not have sufficient physical, chemical, and optical data to interpret the causes for the elevated plant biomass. Furthermore, only a few studies have described the temporal aspects of bloom development and decline (e.g. Hart, 1942; Clarke, 1988; Wefer et al., 1988).

The overall objective of this study, which was one component of the multi-disciplinary RACER program (Huntley et al., 1991), was to document the biomass and productivity of phytoplankton throughout the RACER grid of 69 stations over a 4-month period. As the sampling grid included stations both in continental shelf waters and deep waters of the Drake Passage, it was anticipated that our studies should provide a good database to document any differences in shelf vs offshore waters and hopefully to furnish some insight as to the mechanisms which result in any observed differences in these environments. In this paper we describe spatial and temporal distributions of phytoplankton and rates of production during the cruise from the peak bloom period in December and January through the decline in March. Some of the data regarding specific questions, such as the
fate of the phytoplankton crop, are discussed in other manuscripts (e.g. KARL et al., 1991; HUNTLEY et al., 1991). In a separate paper (MITCHELL and HOLM-HANSEN, 1991a) we assess mechanisms of bloom formation and model the maximum crop size in relation to surface mixed layer depths and irradiance.

MATERIALS AND METHODS

Studies were performed at 69 stations in a 100 × 250-km sampling grid in the southwestern Bransfield Strait and contiguous waters (Fig. 1). Most of the stations were within the confines of the continental shelf where depths ranged from 84 to over 1000 m. Nine stations in Drake Passage were north of the continental shelf break and had depths ranging from 1000 to 4000 m. Eight cruises were completed between December 1986 and March 1987. There was one “fast” cruise each month (limited work at all 69 stations), followed by one “slow” cruise which involved intensive studies at 25 stations, including the five stations where in situ primary production measurements were made (Fig. 1).

Profiling instrumentation

An integrated unit with sensors for measurement of physical, biological and optical parameters was mounted on a General Oceanics rosette holding ten 10-liter PVC Niskin bottles equipped with Teflon-covered springs. All sensors were interfaced to a MER 1012F underwater spectroradiometer (Biospherical Instruments, see description of optics below) where the data were frequency coded for transmission via a single conductor hydrographic cable. The frequency data were converted with a deck control box interfaced to a personal computer where the data were digitally stored and selected parameters were displayed and plotted in real-time. Besides the optical measurements discussed below, the system had sensors for conductivity and temperature (Sea Bird Electronics, Inc.). Routine profiling with this system was conducted to 200 m. Water samples between 5 and 200 m were obtained at standard depths in the Niskin bottles during the “up” casts. Whenever a bottle was closed, selected physical and light data were printed out so a record was available of the precise depth and conditions of each sample. As all 10 Niskin bottles were generally used to obtain water samples between 5 and 200 m, water from the upper 1 m was obtained with a clean bucket. At those special stations where a Niskin bottle sample also was obtained in the upper 1–2 m of the water column, Chl a and ATP concentrations in the two water samples were in good agreement.

Light and optical measurements

The MER 1012F included measurement of depth, photosynthetically available radiation (PAR), seven channels of downwelling spectral irradiance and five channels of upwelling spectral radiance. Details of the spectral irradiance measurements may be found in MITCHELL and HOLM-HANSEN (1991b). Incident PAR was measured continuously with a 2-μ sensor (Biospherical Instruments QSR-240) mounted in a shade-free area on the ship’s superstructure. This permitted data from the underwater irradiance sensors to be corrected to compensate for any rapid changes in cloud cover. A submersible fluorometer and transmissometer (Sea Tech Inc.) were also integrated into the profiling system.
Fig. 1. Station locations during the 1986–87 RACER program. All 69 stations were occupied during the 5-day “fast grid”. The 25 circled stations were occupied during the 10-day “slow-grid”, including the five 24-h stations indicated by double circles. The cruise pattern was repeated four times between 15 December 1986 and 31 March 1987. The dashed line in Drake Passage indicates the location of the continental shelf break, north of which depths exceed 1000 m.

**Primary production**

Samples of water from any depth were poured into two clear and one black 250-ml borosilicate glass bottles with Teflon-lined screw caps. After injecting 5.0 μCi of 14C-bicarbonate into each bottle, they were returned to depth on a drifting buoy array for 8–24 h. After recovery of the bottles, samples were filtered through 25 mm glass fiber filters (Whatman GF/F) at a vacuum differential <20 cm Hg. The filters were placed
directly into scintillation vials, exposed to concentrated HCl fumes for 6–8 h, dried, and the incorporated radiocarbon determined by standard liquid scintillation procedures.

**Chlorophyll**

Samples for Chl $a$ measurements (50–100 ml) were filtered through 25 mm glass fiber filters (Whatman GF/F) at a vacuum differential <20 cm Hg and immediately extracted in 10 ml of absolute methanol (Holm-Hansen and Riemann, 1978). After extraction, the samples were shaken and centrifuged and concentrations of Chl $a$ were determined by measurement of fluorescence in a Turner Designs fluorometer (Holm-Hansen et al., 1965). For size fractionation studies, water samples were poured through Nitex netting of 20 μm mesh size, and the pigments in the filtrate determined as described above.

**Inorganic nutrients**

Water samples were filtered through a 47 mm glass fiber filter (GF/F) and the filtrate stored in acid-cleaned polyethylene bottles at -70°C. The samples were kept on dry ice during transport to the Instituto Antartico Argentino in Buenos Aires, where they were processed in an autoanalyser using standard colorimetric procedures (Strickland and Parsons, 1972).

**RESULTS**

**Seasonal and spatial distribution of chlorophyll $a$**

The distribution of Chl $a$ in surface waters throughout the RACER grid during the four “fast” cruises is shown in Fig. 2. Phytoplankton biomass was highest in December, still relatively high in January, and decreased markedly in February and March, with the means ± S.D. being 6.5 ± 4.7, 4.6 ± 4.7, 1.4 ± 1.3 and 1.2 ± 0.8 mg Chl $a$ m$^{-3}$, respectively. Waters of the northern Gerlache Strait and contiguous waters close to Brabant, Hoseason and Trinity Islands were particularly rich in December and January, reaching a maximum of 25 mg Chl $a$ m$^{-3}$ at Sta. 43 during January. Stations in Drake Passage to the north of the continental shelf break (Fig. 1) always had less than 2.0 mg Chl $a$ m$^{-3}$, and generally were less than 1.0 mg Chl $a$ m$^{-3}$. All stations where Chl $a$ concentrations were over 10 mg m$^{-3}$ in surface waters were characterized by relatively stable upper mixed layers which were less than 20 m in depth (Mitchell and Holm-Hansen, 1991a). These data on Chl $a$ concentrations relative to water column stability support the original hypothesis of the RACER program (Huntley et al., 1991).

The patterns of integrated Chl $a$ values (0–50 m) during these four “fast” cruises were very similar to those found for surface concentrations (Fig. 3). The overall mean values for December to March were 291, 176.58 and 50 mg Chl $a$ m$^{-2}$, respectively. The richest areas were those in or close to Gerlache Strait, with values of over 700 mg Chl $a$ m$^{-2}$ in December, and over 500 mg Chl $a$ m$^{-2}$ in January. The deep stations in Drake Passage never exceeded 41 mg Chl $a$ m$^{-2}$. There were still significant concentrations of Chl $a$ at 50 m depth at all stations, but time constraints during the “fast” cruises did not permit detailed water sampling below 50 m.
Fig. 2. Surface Chl $a$ concentrations (mg Chl $a$ m$^{-3}$) contoured from data collected at 69 stations (shown by asterisks) during each of the four fast survey grids of the RACER investigation, 1986-87.
Fig. 3. Integrated Chl $a$ concentrations (mg Chl $a$ m$^{-2}$, 0-50 m) contoured from data collected at 69 stations (shown as asterisks) during each of the RACER fast grids, 1986-87.
During the "slow" cruises each month, time permitted determination of Chl \(a\) concentrations down to 200 m at each of 25 stations (see Fig. 1 for station locations). The relationship between Chl \(a\) concentrations when integrated to 50 m as compared to 200 m is shown in Fig. 4. The correlation between these sets of values is good \((r^2 = 0.94, n = 63)\), and the slope of the line indicates that approximately 55\% of the Chl \(a\) in the water column is found in the upper 50 m. As 50 m is approximately the depth of the average photosynthetic light compensation point, about 45\% of the total Chl \(a\) in the upper 200 m of the water column is found below the light compensation depth for net photosynthesis. Since most of this deep biomass is below both the mixed layer and the compensation depth, deep transport of phytoplankton by sinking and/or physical processes (vertical mixing or lateral advection) appears to be a significant feature of Antarctic ecosystems where blooms form (see also discussions in Huntley et al., 1991; Karl et al., 1991 and Niler et al., 1991). From our data on profiles of water column density (Mitchell and Holm-Hansen, 1991a) and the amount of Chl \(a\) recovered in sediment traps at 100 m depth (Karl et al., 1991) at the more productive RACER stations (Stas 43 and 13), it appears that passive sinking of phytoplankton during bloom conditions is responsible for much of the phytoplankton biomass below the euphotic zone. This conclusion is also supported by microscopic observations of the material in the sediment trap samples, which showed intact phytoplankton cells.

For interpretation of remotely sensed or mooring data, or for ship-based oceanographic studies where time does not permit documentation of the vertical distribution of phytoplankton biomass in the upper water column, it is of interest to know whether surface Chl \(a\) measurements may be used to estimate integrated Chl \(a\) values. Data in Fig. 5 show that, for the RACER study, surface Chl \(a\) correlated very well to Chl \(a\) integrated to 50 m \((r^2 = 0.91, n = 331)\), with the best-fit line having a slope of 0.89. These results suggest that phytoplankton biomass measurements in these Antarctic surface waters permit reliable estimation of the total phytoplankton biomass within the euphotic zone. This conclusion is in agreement with data of Comiso et al. (1990), who also found that Chl \(a\) concentrations were nearly uniform in the upper 30 m of the water column.
Representative water samples from Stas 13, 20, 39, 43 and 48 have been examined by standard inverted microscope techniques (Reid, 1983) to permit estimation of total organic carbon in phytoplankton cells. Preliminary examination of these data, when compared to our Chl a values and total particulate organic carbon (D. M. Karl, unpublished data), indicates that the ratio of cellular carbon to Chl a is close to that described by Hewes et al. (1990) for Antarctic phytoplankton. We thus consider it reasonable to estimate phytoplankton biomass in terms of carbon and to use a C:Chl a ratio of approximately 50 for this purpose.

Seasonal and spatial distribution of primary production

The magnitude of daily primary production at each of the five “intensive” stations (Fig. 1) is shown in Fig. 6A. It is seen that the highest rates of production were found in December (mean of 2.2 g C m\(^{-2}\) day\(^{-1}\)), with rates decreasing each month to a mean of 0.163 g C m\(^{-2}\) day\(^{-1}\) in March. Although Sta. 20 showed a higher rate of fixation in March as compared to the other stations, the average daily production at Sta. 20 from January to March (it was ice covered during December) was considerably lower (0.34 g C m\(^{-2}\) day\(^{-1}\)) than the average of the other four stations (0.51 g C m\(^{-2}\) day\(^{-1}\)) during the same time period. The average rate of production for all stations during the 4-month period was 0.86 g C m\(^{-2}\) day\(^{-1}\).

As such daily rates are very dependent upon light conditions during the in situ incubation period, pertinent data are presented in Table 1 so that rates may be scaled to the irradiance during the day of the incubation or scaled to the mean daily irradiance during the month of the observation. The latter approach minimizes day-to-day variations due to clouds and provides a more ecologically relevant measure of the typical production of a station. When primary production is expressed on the basis of the mean (Fig. 6B) rather than the daily irradiance (Fig. 6A), some data shift by as much as 2 times (e.g. Stas SA13 and SA48). The overall spatial and temporal trends and conclusions remain the same. The overall rate of primary production based on daily mean irradiance over the 4-month period was 1.03 g C m\(^{-2}\) day\(^{-1}\), with the average each month for December to March being 2.53, 0.99, 0.51 and 0.25 g C m\(^{-2}\) day\(^{-1}\), respectively. If one excludes Sta. 20
in Drake Passage, the rate of primary production for the four continental shelf stations averaged 1.85 g C m\(^{-2}\) day\(^{-1}\) during the months of December and January when the maximum crop was observed.

**Light and photosynthetic response**

In order to see if the photosresponse of phytoplankton varied significantly during the 4 months of our study, rates of primary production integrated to the 1% depth of penetration of PAR were divided by the product of Chl a integrated over the same depth interval and the surface PAR during the incubation (Table 1). This "ecological photosynthetic efficiency" parameter has units of mg C (mg Chl a)\(^{-1}\) (Ein m\(^{-2}\))\(^{-1}\). There is no seasonal trend in this parameter, and data from Sta. 20 are similar to those of other stations. During the entire cruise, six *in situ* stations (SA43, SA48, SB20, SB43, SC20 and SD43) had daily irradiance which exceeded the mean daily irradiance of the month of sampling. These stations include the smallest values for the photosynthetic efficiency parameter and correspond to the data in Fig. 7 where we observed light saturation of *in situ* photosynthesis. Although we noted light saturation, photoinhibition did not appear to be significant even for daily surface irradiance of approximately 100 Ein m\(^{-2}\) day\(^{-1}\). The other 12 values fall in the range of 0.21–0.57 mg C (mg Chl)\(^{-1}\) (Ein m\(^{-2}\))\(^{-1}\). This range is surprisingly narrow considering the great variations in biomass and light conditions during this 4-month period, resulting in a 50-fold variation in integrated production.

The overall rate of primary production will be a function of solar irradiance, phytoplankton biomass throughout the euphotic zone, and the rate of attenuation of scalar irradiance throughout the upper water column. Incident solar irradiation in Antarctica is dependent upon weather conditions, with the irradiance on a stormy day often being only
| Sta. No. | Date      | Hours | Ein m\(^{-2}\) | g C m\(^{-2}\) | Note 1 | Note 2 | Note 3 | Euphotic zone | Note 4 |
|         |           |       |                |                |        |        |        |              |        |
| Cruise A: mean light flux = 55.1 Ein m\(^{-2}\) day\(^{-1}\) |     |       |                |                |        |        |        |              |        |
| 43      | 12/22/86  | 12.0  | 42.5           | 1.37           | 60.3   | 1.95   | 1.78   | 14           | 150    | 0.20 |
| 13      | 12/27/86  | 21.5  | 15.9           | 1.60           | 18.4   | 1.85   | 4.32   | 25           | 175    | 0.57 |
| 48      | 12/20/86  | 12.0  | 66.7           | 2.12           | 108    | 3.44   | 1.74   | 30           | 142    | 0.22 |
| 39      | 12/25/86  | 12.0  | 37.1           | 1.53           | 41.1   | 1.70   | 2.27   | 17*          | 95     | 0.43 |

Cruise B: mean light flux = 57.4 Ein m\(^{-2}\) day\(^{-1}\)

| Sta. No. | Date      | Hours | Ein m\(^{-2}\) | g C m\(^{-2}\) | Note 1 | Note 2 | Note 3 | Euphotic zone | Note 4 |
|         |           |       |                |                |        |        |        |              |        |
| 43      | 1/26/87   | 21.5  | 77.3           | 0.65           | 103    | 0.86   | 0.48   | 20           | 92     | 0.09 |
| 13      | 1/28/87   | 20.3  | 25.6           | 0.80           | 44.8   | 1.39   | 1.78   | 31           | 112    | 0.28 |
| 48      | 1/25/87   | 19.7  | 30.0           | 1.02           | 31.0   | 1.06   | 1.96   | 25           | 123    | 0.28 |
| 39      | 1/31/87   | 22.6  | 27.9           | 0.23           | 29.1   | 0.24   | 0.48   | 40*          | 26     | 0.32 |
| 20      | 1/30/87   | 20.3  | 94.8           | 0.39           | 98.8   | 0.41   | 0.24   | 58           | 32     | 0.13 |

Cruise C: mean light flux = 34.5 Ein m\(^{-2}\) day\(^{-1}\)

| Sta. No. | Date      | Hours | Ein m\(^{-2}\) | g C m\(^{-2}\) | Note 1 | Note 2 | Note 3 | Euphotic zone | Note 4 |
|         |           |       |                |                |        |        |        |              |        |
| 43      | 2/28/87   | 5.8   | 14.4           | 0.44           | 22.6   | 0.69   | 1.05   | 19           | 143    | 0.21 |
| 13      | 3/2/87    | 8.8   | 21.5           | 0.35           | 24.2   | 0.39   | 0.56   | 38           | 49     | 0.33 |
| 48      | 2/26/87   | 4.8   | 10.4           | 0.12           | 33.3   | 0.39   | 0.40   | 45           | 40     | 0.29 |
| 39      | 3/5/87    | 9.9   | 17.5           | 0.12           | 19.3   | 0.13   | 0.24   | 22*          | 14     | 0.41 |
| 20      | 3/3/87    | 4.8   | 13.5           | 0.13           | 42.7   | 0.40   | 0.33   | 56           | 34     | 0.28 |

Cruise D: mean light flux = 23.1 Ein m\(^{-2}\) day\(^{-1}\)

| Sta. No. | Date      | Hours | Ein m\(^{-2}\) | g C m\(^{-2}\) | Note 1 | Note 2 | Note 3 | Euphotic zone | Note 4 |
|         |           |       |                |                |        |        |        |              |        |
| 43      | 3/21/87   | 8.2   | 31.7           | 0.16           | 35.2   | 0.18   | 0.12   | 60           | 36     | 0.14 |
| 48      | 3/31/87   | 9.3   | 13.8           | 0.18           | 14.0   | 0.19   | 0.31   | 70           | 43     | 0.31 |
| 39      | 3/25/87   | 8.3   | 10.6           | 0.07           | 11.2   | 0.07   | 0.15   | 25*          | 13     | 0.50 |
| 20      | 3/23/87   | 9.3   | 10.6           | 0.20           | 11.6   | 0.21   | 0.43   | 80           | 33     | 0.56 |

Note 1: total incident light flux during day of incubation.
Note 2: photosynthetic rate per measured light flux that day.
Note 3: photosynthetic rate per mean light flux measured during each cruise.
Note 4: photosynthetic efficiency within the euphotic zone, expressed as mg C (mg Chl a\(^{-1}\)) (Ein m\(^{-2}\))\(^{-1}\).
* This station had much glacial "flour", and hence the depth of the euphotic zone was shallower than would be expected on basis of Chl a concentrations.
Fig. 7. Photosynthetic assimilation numbers as a function of the mean irradiance to which the samples were exposed during the in situ incubation periods. Estimates of mean irradiance were based on integrated surface irradiance scaled by the observed attenuation coefficient to each sample depth. Points shown include samples from all five RACER productivity stations from December to March. The inset is an enlargement of the data showing the response to low irradiance levels.

15–20% of that on a bright day (Table 1). An important consideration in this context, however, is the photosynthetic response of phytoplankton throughout the water column as a function of the mean ambient irradiance to which they are exposed during the incubation period. Data in Fig. 7 were fit with the equation proposed by Platt and Jassby (1976) using an iterative non-linear parameter estimation routine. The estimated $P_{\text{max}}$ value is 1.1 mg C (mg Chl h)$^{-1}$, $\alpha$ is 0.06 mg C (mg Chl a h)$^{-1}$ (\(\mu\)Ein m$^{-2}$ s$^{-1}$)$^{-1}$. The light saturation parameter ($I_k$) is 18 \(\mu\)Ein m$^{-2}$ s$^{-1}$ and the apparent compensation point for light-activated radiocarbon incorporation is in the range of 0.5–1.0 \(\mu\)Ein m$^{-2}$ s$^{-1}$ (see inset in Fig. 7). Our $P_{\text{max}}$ is higher than those reported by Tilzer et al. (1985), but similar to the mean value reported for the same region by Brightman and Smith (1989) and Arctic waters (Harrison and Platt, 1986). Our observed $\alpha$ is higher and our $I_k$ is lower than the values of Tilzer et al. (1985), Sarsaug and Holm-Hansen (1986) and Brightman and Smith (1989). As discussed by Mitchell and Holm-Hansen (1991a) we believe our $\alpha$ value, which is based on in situ observations, may be higher since the spectral distribution of PAR will be narrowed to blue–green irradiance which is more optimal for photosynthesis than the more red-rich spectrum of surface solar energy or tungsten–halogen lamps. Since our $P_{\text{max}}$ is similar to previous reports, our higher $\alpha$ results in low values for $I_k$. The magnitude of the $\alpha$ and $I_k$ suggests that these populations were low-light adapted (Sarsaug and Holm-Hansen, 1986), but not to the extent as reported for ice algae by Palmisano et al. (1985) for which very low values of $P_{\text{max}}$ resulted in low $I_k$. The upper limit of $P_{\text{max}}$ for Antarctic phytoplankton (typically 0.5–3) may be more indicative of temperature limitation of the population (Tilzer and Dubinsky, 1987; Holm-Hansen et al., 1987), although the very low values for ice algae are probably due to extreme shade adaptation.

**Nutrients**

Inorganic nitrogen and phosphate concentrations in the upper 100 m of the water column at three stations, which are representative of stations with high, intermediate and
low phytoplankton biomass (Stas 43, 48 and 20, respectively) are shown in Fig. 8. Nutrients were reduced to low levels (1.9 mmol m\(^{-3}\) inorganic nitrogen; 0.37 mmol m\(^{-3}\) phosphate) during January at Sta. 43 and increased during February and March to relatively high concentrations. There was very little seasonal depletion of nutrients at Sta. 20, as inorganic nitrogen was above 22 mmol m\(^{-3}\) at all times, and phosphate exceeded 1.6 mmol m\(^{-3}\) during all months. Nutrients at Sta. 48 were intermediate between these two stations, but inorganic nitrogen and phosphate concentrations did not fall below 12 and 1.0 mmol m\(^{-3}\), respectively. Values of PO\(_4^{-3}\) at 100 m at Sta. 43 approach typical deep-water values for all cruises but this is not true for NO\(_3^{-}\). Stations SB43 and SC43 had 100 m values less than half of typical deep-water or winter-time levels. The deep depletion of NO\(_3^{-}\) at a station, which apparently stayed stratified at depths less than 30 m during December and January (MITCHELL and HOLM-HANSEN, 1991a), suggests that vertical transport of nutrients to the highly productive surface waters may occur. The observation that PO\(_4^{-3}\) values at 100 m do not show similar depletion provides support for the argument.

![Fig. 8. Inorganic nitrogen (NO\(_3^{-} + NO_2^{-}\)) and phosphate concentrations at stations with high biomass (Sta. 43), intermediate values of biomass (Sta. 48), and low biomass (Sta. 20). Data are from the months of December (line A), January (B), February (C), and March (D). There were no data from Sta. 20 in December as it was covered by sea ice.](image-url)
presented by Karl et al. (1991) that $\text{PO}_4^{3-}$ is more rapidly regenerated in the water column than is $\text{NO}_3^-$, leading to anomalous ratios of C:N:P in sediment trap particulates for some RACER stations.

**Size distribution of phytoplankton**

During the 4 months of the RACER investigation the phytoplankton population in the coastal region showed a change in cell size distribution from predominantly microplankton ($>20 \mu m$ in effective cell diameter) in December to predominantly nanoplanckton ($<20 \mu m$ in cell size) in February and March. In December the nanoplanckton at Sta. 43 accounted for about 15% of the total Chl a in the upper 50 m (Fig. 9). By January the size distribution of the phytoplankton had changed considerably, as the nanoplanckton accounted for over 90% of the phytoplankton biomass in the upper 10 m of the water column, but only 25% at 50 m depth. At Sta. 20 in Drake Passage, January populations were 50% nanoplanckton. Ice cover prevented us from sampling this region in December. By February and March, the entire RACER grid was dominated by nanoplanckton. During "fast" cruises C and D (February and March, respectively) surface water samples were size fractionated at all stations. During February nanoplanckton accounted for 90% of the total Chl a ($n = 66$), and during March the corresponding figure was 92% ($n = 64$). During February and March the only stations where microplankton accounted for more than 60% of the total Chl a were in or close to Gerlache Strait (Stas 44, 55 and 56), where the Chl a concentrations were still relatively high ($2.4-5.3 \text{ mg m}^{-3}$) in surface waters. These data are consistent with previous information showing that high phytoplankton biomass is usually associated with microplankton, whereas low biomass waters are generally dominated by nanoplanckton (Bröckel, 1981; Hewes et al., 1990).

**DISCUSSION**

Our data on phytoplankton distribution and photosynthetic rates demonstrate the richness of continental shelf waters as compared to deep waters lying north of the shelf break. Of the nine stations lying north of the shelf break, Chl a concentrations slightly in

![Fig. 9. Chl a content in nanoplanckton ($<20 \mu m$ in size) as a percentage of the total Chl a content in the upper 50 m of the water column at Sta. 43 in December and January.](image-url)
excess of 2.0 mg m\(^{-3}\) were recorded on just two occasions, with most Chl \(a\) concentrations being less than 1.0 mg m\(^{-3}\). Comparison of these data with the data from the rest of the RACER grid (Figs 2 and 3) clearly demonstrate the relative biological paucity of these Drake Passage stations. Similar data in other areas of the Antarctic often show that such differences in phytoplankton distribution and primary production are related to different water masses (Rönner et al., 1983; Lutjeharms et al., 1985). This does not appear to be the case in the RACER grid as indicated by the data in Fig. 10. It is seen that the “rich” stations (i.e. those stations which had surface Chl \(a\) concentrations over 5.0 mg m\(^{-3}\) at least one time during our study) overlap all but one of the six water masses described for this area (Niiler et al., 1991) and that the low production waters occupy approximately 50% of the areas of type II and III waters. It is thus not likely that the chemical constituents in different water masses in this area are responsible for the marked gradients in primary production. Mitchell and Holm-Hansen (1991a) have demonstrated that region I had significantly lower Chl \(a\) as compared to all other regions in December and January. As the season progressed, the high bloom regions declined in crop size so that there was little regional differentiation by March.

There are two striking aspects regarding the distribution and photosynthetic rates of phytoplankton within the RACER stations in continental shelf waters during the period

![Fig. 10. Map of the RACER sampling grid, showing the area (cross hatched) where Chl \(a\) concentrations exceeded 5.0 mg m\(^{-3}\) at least once during the period from December to March as compared to the different water masses (I–VI) which can be distinguished in this area. The water mass data are from Niiler et al. (1991).](image-url)
December to March. These are (1) that the seasonality in magnitude of production is far greater than would be expected on the basis of incident solar radiation, and (2) certain locations, particularly in and around Gerlache Strait and contiguous waters close to Brabant, Hoseason and Trinity Islands, are very rich as compared to other nearby stations which are also representative of shelf environments. During December in Bransfield and Gerlache Straits (excluding Sta. 20), the mean rate of production scaled to the mean surface PAR observed during the month, was 2.5 g C m$^{-2}$ day$^{-1}$. The mean value for January was 1.2. The mean value in this region reported by Bodungen et al. (1986) for November to December was 0.88 g C m$^{-2}$ day$^{-1}$. It is evident that an extensive coastal region of the Antarctic Peninsula sustains blooms for more than 2 months which equal or exceed the rates of production previously reported for very productive ice-edge blooms (El-Sayed et al., 1983; Wilson et al., 1986).

Chl$\alpha$ data showed that phytoplankton biomass was greatest in December, and declined each month through March. Our observational data do not permit us to specify when the spring bloom started to develop nor what the maximal bloom concentrations were. Clarke (1988) observed peak phytoplankton concentrations at Signy Island in December to January after a 60-day growth period, so we believe that the RACER program sampling began in the peak bloom period. Furthermore, nutrient data suggest that our December measurements were most likely close to the time when the phytoplankton crop reached its maximum size, as nutrient concentrations were still moderate in late December and then declined sharply before the next measurements in late January (Fig. 8). Although seasonality has been recognized in Antarctic phytoplankton (Clarke, 1988; Wefer et al., 1988) and often compared to the “spring bloom” of Arctic waters, the factors responsible for such pronounced seasonality are not known. It is certainly related, however, to seasonal variation in solar radiation combined with stabilization of the upper water column as discussed by Mitchell and Holm-Hansen (1991a). Grazing pressure and ontogenetic development of phytoplankton species also can be assumed to play important roles in the demise of the spring bloom. As shown by the data in Table 1, the incident light flux in March was 42% of that in December, whereas integrated Chl$\alpha$ values in March were only 17% of that in December, and integrated primary production was only 9.8% of that in December. Nutrient data (Fig. 8) indicate that the rapid decline of the bloom throughout most of the RACER stations in Bransfield Strait was not caused by nutrient limitation. Data presented by Karl et al. (1991) indicate that vertical flux at 100 m is typically only about 1% of the standing stock of ATP or DNA. Mitchell and Holm-Hansen (1991a) found similar rates of sinking loss of Chl$\alpha$ for the same trap deployments, while the mean carbon flux was only 31% of the rate of primary production. Even if the typical rate of production from regenerated nutrients is high (70%), sinking flux would only balance new production, on average, for the 1-day flux and production experiments. Unless sinking is extremely pulsed, so that 24-h deployments are subject to severe statistical sampling error, it appears that sinking rates of the crop can not account for the rapid decline of the bloom we observed between January and March.

At Sta. 43 the value of Chl$\alpha$ integrated to 100 m declined from 724 mg m$^{-2}$ in December to 42 mg m$^{-2}$ in March. A maximum contribution by sinking to bloom decline can be estimated by assuming there is no new production and that the Chl$\alpha$ sinking rate is equal to the maximum rate we measured (2%, Mitchell and Holm-Hansen, 1991a). With this extremely conservative proviso, sinking would account for 83% of the decline in Chl$\alpha$ we observed. Assuming no new production and the mean rate of Chl$\alpha$ flux (0.8%), which is
probably still conservative, sinking would account for only 50% of the Chl a decline. Since we expect some new production (NO₃ based) during the period, these estimates are considered upper limits of sinking losses for the phytoplankton and we believe that sinking probably accounts for less than 50% of the bloom decline from the observed peak values to the values in March. As solar irradiation was still adequate, and temperature varies by only a few degrees within the area, the decline of the bloom to very low levels in February and March appear to be related either to grazing and/or to advective transport processes in addition to sinking.

Niiler et al. (1991) present evidence for a mean advective flow from the regions of highest biomass (Gerlache Strait, southwest Bransfield Strait) toward the northeast. Karl et al. (1991) discuss the potential role of advective processes in the anomalous depth distribution of mass flux for several sediment trap profiles during RACER. Based on a model of bloom development, Mitchell and Holm-Hansen (1991a) suggest that rates of grazing may be higher than traditionally estimated in order to limit crop size predicted by the model to values typical of observations. They also hypothesized that production based on regenerated nutrients may be substantial in blooms. Karl et al. (1991) speculate that a large pool of DOM may develop in order to account for biomass which is apparently lost from the particulate fraction but does not appear in the sediment traps. Accumulation of DOM presumably would be caused by microzooplankton that do not produce sinking fecal pellets, or rapid disruption and solubilization of macrozooplankton fecal pellets. If grazing is assumed to account for half of the decline not accounted for by sinking, then the mean rate of zooplankton grazing would have to be approximately 0.4 g C m⁻² day⁻¹ (assumptions: C:Chl a = 50 and zooplankton assimilate 50% of the food ingested) during the period December to March. This grazing rate is substantially higher than rates estimated from observed macrozooplankton stocks (excluding krill) by Huntley et al. (1991) but is similar in magnitude to the grazing rates predicted by a model which assumes no advective losses (Mitchell and Holm-Hansen, 1991a). The relative significance of these different mechanisms in demise of observed massive blooms must be tested.

Phytoplankton biomass measurements (Figs 2 and 3) show that the entire northern portion of Gerlache Strait and contiguous waters of Bransfield Strait attain very high biomass as compared to all other stations in the RACER grid. Chl a concentrations of 25 mg m⁻³ as found at Sta. 43 represent close to the maximal biomass that can be produced by Antarctic phytoplankton when grazing pressure has been reduced (Sakshaug and Holm-Hansen, 1986). Nutrient data from this station (Fig. 8) confirm that nutrients were reduced to very low levels and most likely were approaching concentrations where nutrient limitation of growth might ensue. Well-documented depletion of nutrients to very low levels has been described for a Ross Sea ice-edge bloom (Nelson and Smith, 1986) and for waters south and west of Palmer Station (Holm-Hansen et al., 1989). It was proposed that the richness and duration of the blooms close to Palmer Station were related to diminished vertical mixing processes, resulting in a continuously stratified upper water column. The Ross Sea ice-edge bloom showed good spatial coherence to near-surface stratification of the density field (Smith and Nelson, 1985). Our data from the RACER grid show that such rich phytoplankton blooms are not a sporadic and isolated phenomenon, but probably are representative of extensive areas of waters overlying the continental shelf in Antarctica.

The dramatic differences in productivity between such shelf waters and most of the deep waters of the Southern Ocean would partially explain the “paradox” of the apparent low
primary productivity of Antarctic waters and associated questions related to food web dynamics. Benthic biomass in many shelf areas of the Antarctic is reported to be rich and diverse, in spite of the fact that estimates of rates of primary production in Antarctic waters tend to be low. Recent data on nutrient depletion rates (Jennings et al., 1984; Holm-Hansen et al., 1989), sediment trap collections (Bodungen, 1986; Wefer et al., 1988), and rate of silicon deposition to the benthos (Dunbar et al., 1985) all indicate relatively high rates of production in waters over the continental shelf, in agreement with our measured high rates of primary production in the RACER sampling grid. It should be noted that the great bulk of primary production measurements available in the literature are usually from long cruise tracks in pelagic waters of the Antarctic, and hence reflect this tendency to obtain data predominantly for areas to the north of the continental shelf break. Even the blooms associated with receding ice edges over deep water generally represent relatively low biomass of 2–7 mg Chl a m\(^{-3}\) (Smith and Nelson, 1985; Nelson and Smith, 1986; Nelson et al., 1987; Sullivan et al., 1988) as compared to the concentrations of >20 mg Chl a m\(^{-3}\) found at many of the RACER stations. For one of the densest ice-edge blooms described, Wilson et al. (1986) observed mean daily production less than half the mean value we observed for coastal stations in December. There have been many smaller, more geographically restricted studies that have demonstrated the comparative richness of shelf waters (e.g. Burkholder and Sieburth, 1961; Krebs, 1983; El-Sayed, 1988). Our extensive RACER data set is supportive of such earlier studies, and suggests that the shelf areas of the Antarctic must be considered when attempts are made to relate rates of primary production to food requirements by grazers including krill. The formation and persistence of massive blooms in coastal waters of the Antarctic Peninsula may play a vital role for krill populations which are known to aggregate in the Peninsula region. Evidence is presented in Mitchell and Holm-Hansen (1991a) that massive blooms only form in regions with proximity to meltwater and reduced exposure to storm systems, conditions that are typical of the coastal regions of the Antarctic Peninsula. Similar conclusions regarding the importance of freshwater input and the degree to which the area is “protected” from storm events for the accumulation of high phytoplankton biomass have previously been described in Bransfield Strait by von Bodungen et al. (1986). In spite of one of the most intensive efforts to document planktonic processes controlling development and decline of the blooms, many questions remain unanswered. A detailed understanding of bloom decline awaits studies which will quantitate (a) the advective rates from the bloom locus; (b) the magnitude of production in massive blooms which is based on regenerated nutrients; (c) zooplankton (including microzooplankton) grazing rates; (d) the accumulation of DOM; and (e) the significance of episodic sinking.

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