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Photosynthetic Parameters, Irradiance, Biooptical Properties and Production Estimates in the Western Ross Sea

L. Lazzara¹, V. Saggiomo², M. Innamorati¹, O. Mangoni³, L. Massi¹, G. Mori¹, and C. Nuccio¹

ABSTRACT

The primary production characteristics of phytoplankton coenoses were investigated during three summer periods (1987–88, 1989–90 and 1994–95), in Terra Nova Bay. The basic photosynthetic parameters of the P vs. E curves were analyzed, as well as the *in vivo* spectral absorption and fluorescence properties, which allow the maximum quantum yield for carbon uptake and for PSII fluorescence to be appreciated and compared, in order to evaluate the physiological conditions and the photoacclimation performance of this phytoplankton. Low light acclimation features (elevated values of α^B , P_{max}^B and ϕ_{mv} with E_k between 11 and $102 \mu E m^{-2} s^{-1}$) are clearly present in these natural populations. High daily productions of the water column have been estimated through a biooptical model ($0.1\text{--}3.1 g C m^{-2} day^{-1}$), and a seasonal integrated value of $125 g C m^{-2}$ has been appreciated at Terra Nova Bay, for the period from December through February.

Introduction

The western Ross Sea is being recognized, in the past few years, as a site of elevated primary production and extensive phytoplankton blooms (Smith et al. 1990, 1996; Innamorati et al. 1992a,b), mainly after the use of satellite visible imagery (Sullivan et al. 1993; Arrigo and McClain 1994; Arrigo and Weiss 1996). Nevertheless, a lack of studies on primary production distribution, biooptics and photophysiology of phytoplankton coenoses in the Southern Ocean and especially in the Ross Sea, is still evident. The biooptical models of primary production used for remote sensing applications (Platt and Sathyendranath 1988; Morel and Berthon 1989; Morel 1991; Antoine and Morel 1996) are essentially based at present on photosynthetic parameters obtained on tropical or temperate phytoplankton and still few biooptical data (Mitchell and Holm-Hansen 1991) have been directly measured on antarctic coenoses.

Collection of data concerning distribution of phytoplankton biomass and production, together with photosynthetic parameters and biooptical properties of natural populations, was performed

throughout three austral summers (Innamorati et al. 1992a; Lazzara et al. 1997) in the western Ross Sea. Objectives of this study are: the local validation of a biooptical model of primary production and the eventual identification of photosynthetic and optical parameters specific for the western Ross Sea phytoplankton; the spatial and temporal extension of primary production estimates in this region with the consequent contribute to the characterization of the western Ross Sea ecology.

Methods

Sampling

Investigations have been carried out in a large area of the Ross Sea, diversified in the course of three campaigns, as detailed in Innamorati et al. (this Vol.; Fig. 1). In 1988 the sampling area covered a grid extending 40×50 miles, centred around latitude $75^\circ S$ and $165^\circ E$ longitude, while in 1989–90 and 1995, respectively, three (BTN, SMN, MERG) and two (BTN, TIB) stations were sampled in Terra Nova Bay, in order to follow the temporal trend of

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phytoplankton biomass and production and the related environmental factors. In 1989–90 a cruise was carried out over a much larger area of the western Ross Sea between the latitudes of 60° and 75°S and the longitudes of 165° and 177°E. Moreover, during the 1995–96 season, in Terra Nova Bay, four stations were sampled (stations 32, 33, 36, 38) for primary production measurements, as detailed by Saggiomo et al. (this Vol.).

Pigments

The concentrations of liposoluble pigments were determined after filtration of 2 to 3 dm³ of seawater on Whatmann GF/F filters, and extraction in acetone 100% (diluted to 90% for measurements), by means of both spectrophotometric analysis (Kontron, Uvikon 930) for chlorophaeopigments (chlorophyll a and phaeopigments, hereinafter named Chl) using the specific absorption coefficient of Jeffrey and Humphrey (1975), following Lorenzen (1967) modified by Riemann (1978) for separate determination of chlorophyll a and phaeopigments and by means of spectrofluorometric analysis (Perkin Elmer, LS-5b) for chlorophyll a and phaeophytin a determination, with purified chlorophyll a (Sigma Chemical) as standard (cf. Lazzara et al. 1997, for further details).

Irradiance and Biooptical Properties

Measurements of surface global irradiance were performed by means of solarimeters (Kipp & Zonen, CM5) and of PAR quantum meters (LI-Cor, LI-192SB) continuously recorded (chart recorder) or stored every 10 min (data logger) during the three seasons (1987–88, 1989–90 and 1994–95) at Terra Nova Bay and in the Western Ross Sea in 1989–90. Out of the period of the campaigns, daily irradiance has been measured by solarimeters (Kipp & Zonen) at the meteorological stations ARGOS ID n. 7351 and n. 7353 of the Antarctic Meteorological Observatory (PNRA). Intercomparison between sensors used in the different years, during days of minimum atmospheric attenuation (clear sky), gives less than 1.5% differences in daily integrated irradiances. A clear-sky irradiance curve has been interpolated with these maxima which gives, with respect to the theoretical values outside the atmosphere, a minimum atmospheric attenuation of 24%, whereas the real attenuation including clouds effect, over the period from

December through February, averaged over the 3 years, was of 39% (see Fig. 5). In-water vertical profiles of downwelling, upwelling and scalar quantum PAR irradiance were measured by means of a photoprobe (Innamorati et al. 1994b) equipped with cosine and spherical quantum meters (LI-Cor), depth meter and reference surface sensor, for the three expeditions, in both Terra Nova Bay and in the western Ross Sea. Spectral downwelling and upwelling irradiances have been measured by means of a spectroradiometer (LI-Cor, 1800-UW) for several stations at different depths during the three seasons. The photosynthetically available part of global irradiance was considered to be 43% of total solar radiation (Mobley 1994), the ratio used to convert irradiance from energetic to quantic units was $Q/E = 2.77 \times 10^{18}$ (Morel and Smith 1974). The average loss for surface reflectance was considered to be 7%, as calculated by Morel (1991) for the summer solstice at 75°N, and an average ratio of the downwelling to scalar irradiance was found to be, from all our measurements, as $E_d/E_0 = 0.70$, and was used to obtain scalar PAR just below the surface [$PAR_0(0^-)$].

Spectral Absorption of Phytoplankton

Spectral absorption of phytoplankton (a_{ph}) was derived from that of total particulate matter (a_p) after methanol extraction (Kishino et al. 1986). Seawater samples up to 2 dm³ were filtered on Whatman GF/F filters previously soaked in filtered seawater. Absorption of wet filters was immediately measured by means of a LI-COR spectroradiometer (LI-1800UW-12) equipped with an integrating sphere (LI-1800-12S). Detritus absorption (a_d) was measured on the same filters after methanol extraction of pigments for 24 h at 4°C. Before measurements the bleached filters were soaked again for 1 h in filtered seawater to allow the extraction (even if partial) of the water soluble pigments (Bricaud et al. 1995). Finally phytoplankton absorption was calculated subtracting a_d from a_p . The spectra are blank-subtracted and corrected for the pathlength amplification (β factor), following Bricaud and Stramski (1990).

Spectral Fluorescence and Quantum Yield of Photosynthesis

In vivo fluorescence was measured directly on suspensions, for nearly the same amount of samples

as for absorption, using a spectrofluorometer (Perkin-Elmer LS-5b) equipped with a red-sensitive photomultiplier tube and a quantum correction device (rhodamine B) which allows fluorescence excitation spectra to be corrected up to 630 nm. The measurements were performed with excitation / emission at 440/684 nm, after addition of the photosynthesis inhibitor DCMU (final concentration 20 μM) and 30 s of exposure to saturating irradiance, so that maximal fluorescence (F_{max}) was measured. Spectral values were measured on samples concentrated by gentle filtration in dim light on a 0.22- μm Nuclepore filter, to record the entire spectra with sufficient accuracy, and the spectra were scaled to the signal measured at fixed λ (440 ex/684 em). For each sample the signal of the filtered suspension was subtracted to avoid interference of Raman scattering (further details and discussion on the whole procedure are given in Lazzara et al. 1996). The spectral *in vivo* fluorescence yield of phytoplankton in relative values was calculated as the ratio of $F_{\text{max}}(\lambda)$ to $a_{\text{ph}}(\lambda)$, for the spectral domain 380–630 nm. An index of the photosynthetic conversion efficiency was also calculated, as $\text{FRI} = (F_{\text{max}} - F_0)/F_{\text{max}}$, being F_0 the fluorescence measured before the DCMU addition.

The maximum quantum yield of photosynthesis (ϕ_m) was estimated from the ratio:

$$\phi_m = P_{\text{max}}/AQ, \quad (1)$$

where P_{max} ($\text{mol C m}^{-3} \text{ day}^{-1}$) is the maximal production in the light limited portion of the P vs E curve, and AQ (Morel et al. 1987) is the total amount of absorbed quanta estimated from:

$$AQ = \int_{400}^{700} E(\lambda) a_{\text{ph}}(\lambda) d\lambda \quad (2)$$

and expressed in $\text{mol quanta m}^{-3} \text{ day}^{-1}$, with $\int E(\lambda)$ being equivalent to the irradiance at the onset of saturation (E_k).

Primary Production

Primary production processes were investigated in the Ross Sea, in summer 1990, 1995 and 1996. A temporal series (from January 12 to February 8, 1990), with sampling intervals of about 4 days, was performed at stations MERG and SMN in Terra Nova Bay. The measurement of primary production rates were performed on samples incubated *in situ* at 0, 5, 10, 25 m, as well as at the level of the

deep fluorescence maximum, for 4 h, around noon. A second set of measurements was carried out during the austral summer 1995 and 1996 (February 2 to 10). Stations TIB, 33, 36 and 38 were located in the same area of 1990 while station 32 was located in the southernmost part of Terra Nova Bay. At each station, profiles of down- and upwelling underwater PAR were obtained using the above-mentioned photoprobe. Sampling depths were selected according to the optical levels (50, 20, 10, 5, 1 and 0.13% of incident irradiance) and a surface sample was also included. The measurement was performed by *in situ*-simulated conditions. Each sample collected from surface and the optical depths listed above was enclosed in light and dark polycarbonate (Nalgene) 450-ml bottles and incubated with 1 ml (20 μCi) of $\text{NaH}^{14}\text{CO}_3$ for 4–6 h on deck, in running surface seawater, at the different light levels obtained by means of neutral light screens (Electroformed Nickel screens, Veco Int. Co. USA). The radioactive content was measured, after acidification, within 24 h from filtration, in a Beckman LS 1801 liquid scintillator, using 10 ml of Aquasol II scintillation cocktail. In all stations sampled during February 1996, the P vs. E relationship was measured on four depths using a radial photosynthetron as in Babin et al. (1994). The photosynthetic parameters were calculated according to Platt et al. (1980).

Depth-Integrated Biomass

The depth-integrated values of biomass for the euphotic zone were obtained, through trapezoidal integration, from chlorophyll profiles and underwater PAR measurements. From the underwater PAR profiles carried out during the four cruises, a good relationship was established (Fig. 1a; $r = 0.91$, $N = 54$) between z_{eu} , the depth of the euphotic zone (1% of surface PAR) and its chlorophaeopigment content $\text{Chl}_{z_{\text{e}}}$, described by the regression $Z_{\text{eu}} = 34 \text{Chl}_{z_{\text{e}}}^{-0.502}$. Thus, when the depth of the euphotic zone had not been directly measured, it was estimated through the above-mentioned relationship and an iterative procedure. This started from an estimate of z_{eu} , based on surface values of Chl , which gives a first integrated value of Chl , and consequently a second estimate of z_{eu} and so on, thus reaching convergence towards a final stable value of z_{eu} and of its depth integrated value of chlorophaeopigments (Chl_{tot}).

The relationship between the mean concentration of chlorophaeopigments in a layer of one

penetration depth (Chl_{pd}) and Chl_{tot} is described by the regression: $Chl_{tot} = 52.4 C_{pd}^{0.502}$ ($r = 0.91$, Fig. 1b). This relationship is slightly different from that described by Morel and Berthon (1989) for high latitude waters and uniform profiles. In fact, our samples are, in most cases, from stratified conditions (see Fig. 6, in Innamorati et al., this Vol.), where the biomass has a subsurface maximum in

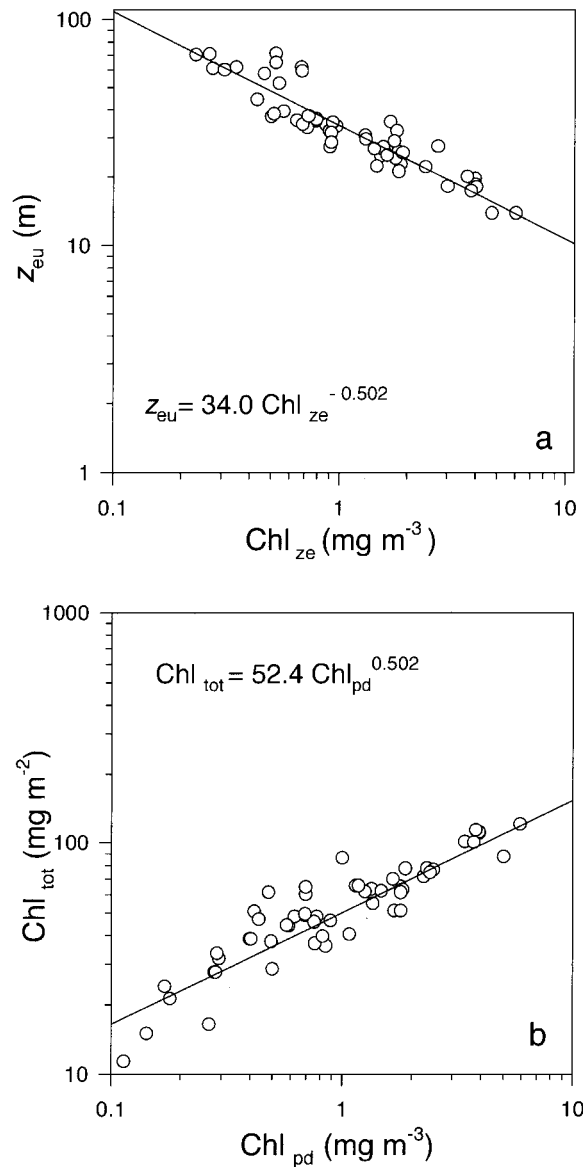


Fig. 1. a Relationship between depth of the euphotic zone (z_{eu}) and its chlorophaeopigments mean concentration (Chl_{ze}). b Relationship between Chl_{tot} (integrated Chl content in the euphotic layer) and Chl concentration in the layer of one penetration depth (Chl_{pd}). The regression equations are given

the euphotic layer and only a few samples are from well mixed waters, as in the previously quoted work. Therefore, the value of Chl_{tot} has been estimated through the previous regression, when only surface samples had been collected.

To extend the temporal data set at Terra Nova Bay down to late spring, the phytoplankton cell density has been considered and the chlorophyll content of surface cells examined; it was found to undergo a relatively small change during the summer season, passing from 2 to 6 pg Chl/cell. More precisely, this ratio was remarkably stable around 2 pg/cell, from the end of December throughout January, whereas an increase was observed from the beginning of February. Considering that the phytoplankton community dominated by diatoms had not changed significantly during the first phase of the bloom, we could reasonably extend the value typical of the top of the bloom (2 pg Chl/cell) up to its beginning, on December 10 and calculate, from the cell density, the surface values of chlorophaeopigments (Chl_{pd}).

Integrated Production Estimates

The depth-integrated values of primary production were obtained applying the biooptical model of Morel (1991; Antoine and Morel 1996), which makes use of the daily surface irradiance and of the chlorophyll content of the euphotic layer. The daily carbon production (PP, in $g C m^{-2} day^{-1}$) was computed from the following equation:

$$PP = (1/39)\rho Chl_{tot} PAR(0^+) \Psi^*, \quad (3)$$

where 39 corresponds to the energy in kJ stored in 1 g of organic carbon, ρ is the average ratio of chlorophyll a / Chl, Chl_{tot} is here the depth-integrated Chl content ($g Chl m^{-2}$) up to 0.1% of surface PAR, $PAR(0^+)$ is the daily PAR irradiance impinging on the sea surface in energetic units ($MJ m^{-2} day^{-1}$), Ψ^* is the column photosynthetic efficiency or cross-section for photosynthesis ($m^2 g Chl^{-1}$).

The ratio of chlorophyll a / Chl generally showed no significant variation inside the euphotic zone and, when separately studied for each campaign, it was found to be sufficiently constant in Terra Nova Bay, for the 1987–88 campaign ($\rho = 0.88 \pm 0.05$) and for the 1989–90 campaign in the western Ross Sea ($\rho = 0.85 \pm 0.06$), with the only exception of much lower values ($0.45 < \rho <$

0.6) for three stations of each campaign. Therefore, these average values were used in Eq. (3) to compute daily primary production (PP). On the contrary, during the summer seasons of 1989–90 and 1994–95 in Terra Nova Bay, a regular variation was observed for ρ , progressing with the seasonal evolution of biomass from high values, during the bloom periods ($\rho = 0.90$) to minimum values ($0.4 < \rho < 0.5$) corresponding to periods of minimal biomass. For this reason, instead of an average ratio, as for 1987–88 and for the western Ross Sea, an interpolated time-dependent value of the ratio was applied in Terra Nova Bay during summer 1989/90 and 1994/95.

As far as concerns the photosynthetic cross-section, a reasonable mean value for the world ocean $\Psi^* = 0.07 \text{ m}^2 \text{ g Chl}^{-1}$ (Morel 1978; Platt 1986) was used in the standard calculation (Figs. 7, 8) of the integrated primary production (PP) for this summer antarctic phytoplankton (see below for discussion).

Results

The spectral absorption and fluorescence excitation properties of phytoplankton at Terra Nova Bay during 1989–90 and 1994–95 are well represented (Innamorati et al. 1994a; Lazzara et al. 1997, for a more detailed examination), by the sample shown in Fig. 2a (station TIB on February 4 1995) and used for production measurements. These spectra are typical of a diatom dominated phytoplankton community, as it was generally observed at Terra Nova Bay during summer in the euphotic layer (see Nuccio et al., this Vol.), and reveal the presence of chlorophyll a, chlorophyll c and fucoxanthin-like pigments. In Fig. 2b the fluorescence yield spectrum, with its nearly flat shape, accounts for a negligible presence of non-photosynthetic pigments in this phytoplankton, being so favourable to the simplifying assumption of coincidence between absorption and action spectrum for photosynthesis, adopted in the standard version of the biooptical model for integrated production (Antoine and Morel 1996).

The P^B vs. irradiance relationship explored for a time series carried out in austral summer 1990 at Terra Nova Bay shows two different trends. The first (Fig. 3a) is related to the late phase of a spring bloom characterized by a well-stabilized water column, high daily irradiance, low nutrient concentrations and an intense grazing activity

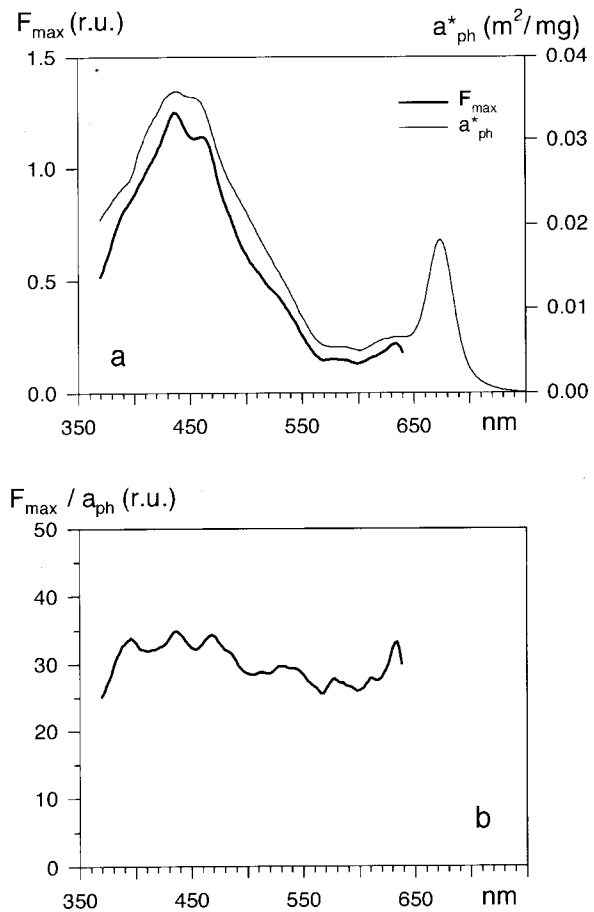


Fig. 2. a Absorption and fluorescence excitation spectra of phytoplankton at station TIB on February 4 1995. b Fluorescence yield spectrum (F_{\max}/a_{ph}) of the above sample

(Marino et al. 1995). The second (Fig. 3b) coincides with the probable beginning of a late summer bloom; in this period the mixed layer was deeper and nutrient concentrations were higher before a strong storm occurred at the end of January. The lower P^B_{\max} values are related, in our opinion, to the observed differences in water column structure and to the reduced daily irradiance. The P^B vs. E relationship measured in Terra Nova Bay during February 1996, represents the time evolution of photosynthetic parameters during a late summer bloom, when an integrated primary production up to $2.4 \text{ g C m}^{-2} \text{ day}^{-1}$ was measured (Mangoni et al. 1999). The mean P^B vs. E curves related to four depths for each station are reported in Fig. 3c,d,e, and f and show a quite similar trend. As for the off-shore areas of Ross Sea, as well as other Antarctic areas in austral summer, phytoplankton commu-

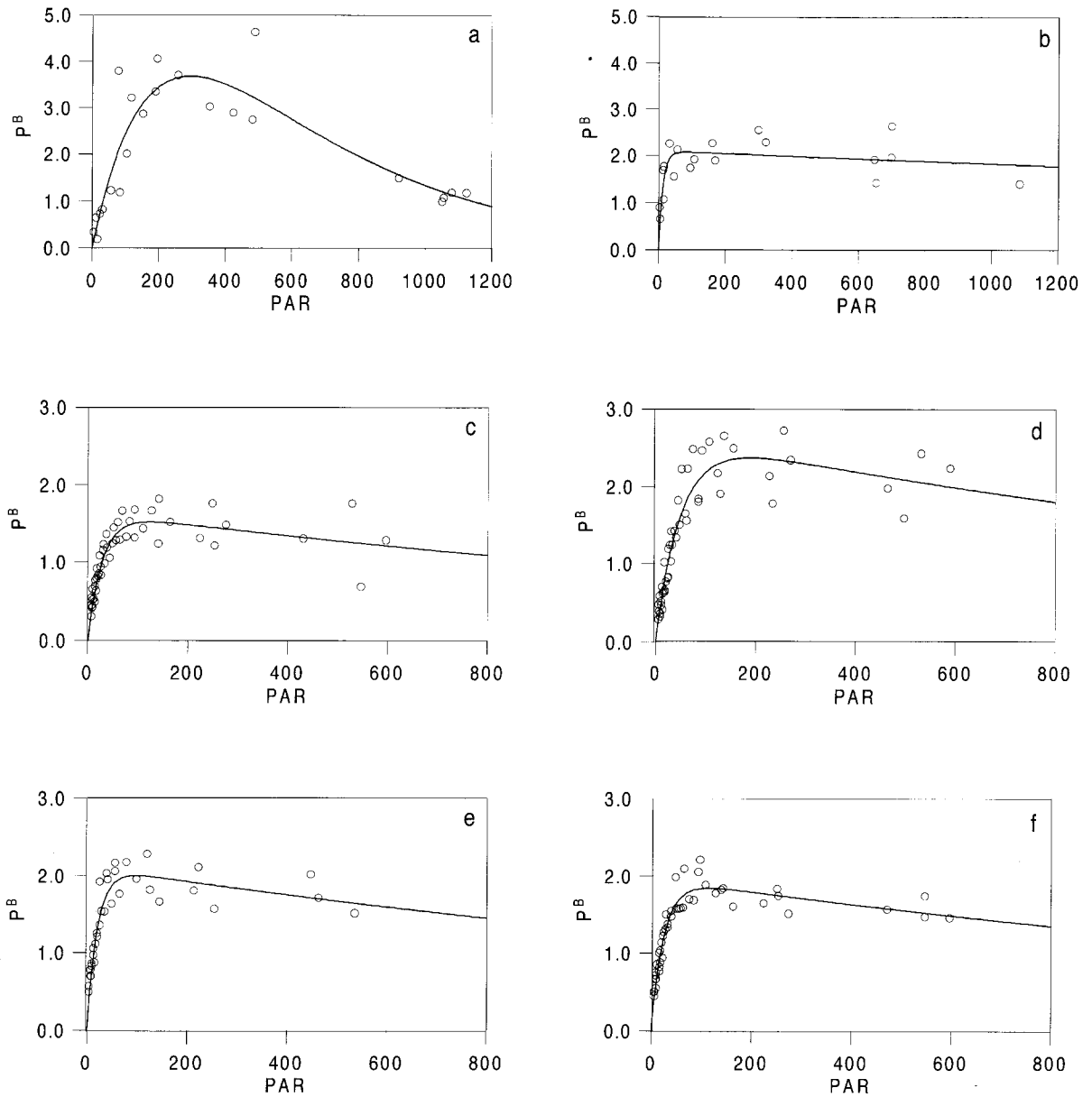


Fig. 3a-f. Time series of primary production normalized for chlorophyll *a* (P^B) vs. PAR during January (a) and February 1990 (b). P^B vs. E curves measured at stations 32 (c), 33 (d), 36 (e) and 38 (f) during February 1996; the mean curves were obtained from experiments carried out at four depths for each station

nities were well adapted to low light level (Saggiomo et al., this Vol.; Holm-Hansen and Mitchell 1991; Figueiras et al. 1994). The photosynthetic efficiency, α^B , is very high but lies in the same range of that reported for the Ross Sea and other regions in austral summer from the same authors. In contrast, P^B_{max} of the 1990 time series and of February 1996 are from two to three times higher than that reported for Bransfield Strait region by Holm-Hansen and Mitchell (1991), but

similar to that observed for the ice edge of Weddel Scotia Sea by Figueiras et al. (1994) and among the highest reported for the offshore Ross Sea by Saggiomo et al. (this Vol.).

The biooptical properties and the classical photosynthetic parameters describing the Pvs.E relationship for the phytoplankton coenoses of Terra Nova Bay are shown in Table 1. The maximum productivity (P^B_{max}) is always very high, up to 2.8 times of what would be expected at the

Table 1. Basic photosynthetic parameters from the P^B vs. E relationship and biooptical properties of summer phytoplankton coenoses at Terra Nova Bay

	P_{\max}^B g C/g Chl ⁻¹ d ⁻¹	α^B (g C/g Chl)(E/m ² s) ⁻¹	E_k $\mu\text{E m}^{-2} \text{s}^{-1}$	E_{\max} $\mu\text{E m}^{-2} \text{s}^{-1}$	a^*_{avg} m ² /g Chl	a^*_{max} m ² /g Chl	ϕ_m mol/mol
'90 January	3.67	9.8	102	287	22.8	49.6	0.051
'90 February	2.06	46.7	11	69			
Terra Nova Bay 1990	3.22	11.9	75	239			
TNB '94 st 30 January	1.60	13.3	33	102	(22.8)		(0.061)
TNB st.TIB 4.2.95	2.30	35.0	19	67	24.1	51.4	0.110
TNB '96 st 32 February	1.54 ± 0.2	16 ± 2.8	28	136	(24.1)		(0.059)
TNB '96 st 33 February	2.38 ± 0.4	15.6 ± 3.1	45	180	(24.1)		(0.058)
TNB '96 st 36 February	2.44 ± 0.7	31.6 ± 7.2	21	101	(24.1)		(0.096)
TNB '96 st 38 February	1.84 ± 0.1	21.5 ± 1.9	24	114	(24.1)		(0.079)
Claustre et al. '97 Cryp	1.40	7–9	50–53		14.2		0.091
Claustre et al. '97 Diat	3.80	12–14	76–86		15.3		0.112
Model 0°C ^a	1.30	6.4	50		16.0	35.5	0.070
Model 20°C ^a	4.60	6.4	180		16.0	35.5	0.070

^aFrom Morel (1991) and Antoine and Morel (1996).

temperature of 0°C, with a $Q_{10} = 1.88$ (Eppley 1972), whereas the irradiance at the onset of saturation (E_k) is often very low (11–102 $\mu\text{E m}^{-2} \text{s}^{-1}$) and consequently the values of the photosynthetic efficiency (α^B) are also generally high {10 – 47[gC(gChl)⁻¹(E m^{-2})⁻¹]. The maximum quantum yield of photosynthesis (ϕ_m) estimated from carbon production, spectral absorption and irradiance measurements, reaches rather high values for natural populations, in January ($\phi_m = 0.051$) and close to the theoretical maximum in February ($\phi_m = 0.110$). In 1994 and 1996 estimates of ϕ_m were made (values in parentheses) using the absorption values measured in the same months of 1990 and 1995, respectively and they lie in the same range (0.058–0.096 mol C/mol quanta). For a population of open water near the ice edge at McMurdo Sound, SooHoo et al. (1987) find quantum yields of photosynthesis ranging from 0.028 to 0.054 mol C (mol quanta)⁻¹, whereas Claustre et al. (1998) for two Antarctic coenoses dominated by diatoms and cryptophytes, respectively, report mean values for ϕ_m , of 0.112 and 0.091 mol C (mol quanta)⁻¹.

The phytoplankton specific absorption coefficients from the whole data set, show spectral averages, a^*_{avg} (400–700 nm), ranging from 17.7 to 26.9 m² g Chl⁻¹ and maxima, a^*_{max} , in the range 37.4 – 57.8 m² g Chl⁻¹, although just the absorption spectra contemporary with the ¹⁴C measurements are reported in Table 1. These absorption data are of a typical summer phytoplankton assemblage of

the Western Ross Sea dominated by the diatom *Fragilariopsis*, as frequently observed in Terra Nova Bay (Nuccio et al., this Vol.). At McMurdo Sound SooHoo et al. (1987, see their Fig. 6 and Table II) with a population dominated by the prymnesiophyte *Phaeocystis pouchetii* find a mean specific absorption coefficient (irradiance-weighted and spectral average), a^* , ranging from 15 to 29 m² g Chl⁻¹. These a^* values are close to those measured at Terra Nova Bay and, under the realistic hypothesis of a similar spectral distribution of underwater irradiance, owing to the same Chl concentration and depth, the a^*_{avg} should be similar as well. Claustre et al. (1998), on the basis of the pigments concentrations and of their specific “in vivo” absorption coefficients, reconstructed the absorption spectra of antarctic coenoses dominated by diatoms and cryptophytes and find that the irradiance-weighted coefficients a^* are 9.7 and 7.1 m² g Chl⁻¹ respectively (Table 1) and the mean values of a^*_{avg} are 15.3 and 14.2 m² g Chl⁻¹ for the two coenoses (H. Claustre, pers. comm.). Unfortunately, the low absorption coefficients so estimated are not completely comparable with those obtained by the filter-pad method. Mitchell and Holm-Hansen (1991) estimated the specific absorption of phytoplankton of Antarctic Peninsula at high Chl concentration (0.5 ≤ Chl ≤ 50 mg m⁻³) using the particulate absorption normalized by the chlorophyll content. These spectra show high blue absorption with respect to the red, so that a detritus contribution, even if low,

has to be supposed. In spite of this, the values of these specific particulate spectra are very low, with an average maximum value at 435 nm of $18 \text{ m}^2 \text{ g Chl}^{-1}$. The authors attribute this low specific absorption to a high package-effect "typical of larger cells with high cellular pigment concentrations expected for chronic low light adaptation in high nutrient waters". On the contrary, at Terra Nova Bay small cells (Nuccio et al., this Vol.) with a relatively low Chl content let think of a weak package effect for this phytoplankton. Also measurements of the spectral irradiance attenuation coefficient $k(\lambda)$, and of the chlorophyll-specific attenuation $k_c(\lambda)$, [where $k_c(\lambda) = (k(\lambda) - k_w(\lambda)) / \text{Chl}$, with $k_w(\lambda)$ attenuation coefficient of pure water) were carried out at Terra Nova Bay and in the western Ross Sea during the three expeditions. These $k_c(\lambda)$ values, in accordance with the k_c definition and its properties for green waters of the case I, are slightly higher than a^*_{ph} [average (\pm s.d.) $k_c(440) = 88 \text{ g Chl m}^{-2} (\pm 20, \text{ with } n = 35)$], and so confirm the reliability of this phytoplankton specific absorption, measured through the filter-pad method.

The standard model of Morel (1991) for integrated production in cold waters ($0-1^\circ\text{C}$) at high latitudes, implies lower values of $P^{\text{B}}_{\text{max}}$ and E_k , which in turn implies low values of the photosynthetic cross section (Ψ^*). An average value for Ψ^* at 74°S , between December and February, can be estimated as $\Psi^* = 0.04 \text{ m}^2 \text{ g Chl}^{-1}$ for clear-sky conditions (Morel 1991; Antoine and Morel 1996) and has been used in a first application of the production model [Eq. (3)]. A comparison between the integrated primary production obtained from this procedure and the values resulting from ^{14}C production measurements gives the orthogonal regression: $\text{PP}(^{14}\text{C}) = 0.11 + 1.71 \text{ PP(mod)}$ ($r = 0.81, N = 17, p < 0.001$) which suggests a general underestimate (up to 50%) for the modelled values of integrated production. The simple regression of the integrated production from ^{14}C measurements with the product of $\text{PAR}(0^+) \times \text{Chl}_{\text{tot}}$, [see Eq. (3)] as shown in Fig. 4, after transformation of the production units in their energetic equivalent ($\text{MJ m}^{-2} \text{ day}^{-1}$) allows estimating with our data, from the angular coefficient of the regression, an average value for the photosynthetic cross section of $0.068 \text{ (m}^2 \text{ g Chl}^{-1})$, which is very close to the world ocean mean value (e.g. $0.07 \text{ m}^2 \text{ g Chl}^{-1}$ in Morel 1991). Claustre et al. (1998), with an extensive data set of primary production of

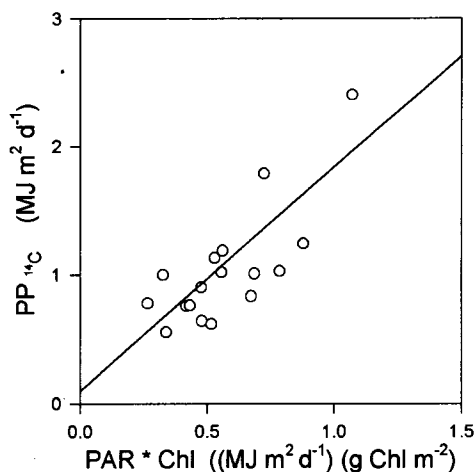


Fig. 4. Regression between integrated production from ^{14}C measurements ($\text{PP-}^{14}\text{C}$) and the product $\text{PAR}(0^+) \times \text{Chl}_{\text{tot}}$ (PP-mod); the slope of the regression gives an estimate of the photosynthetic cross-section Ψ^*

antarctic phytoplankton, also found for Ψ^* the average value of $0.069 \text{ m}^2 \text{ g Chl}^{-1}$, with maximal mean values of 0.114, when coenoses were dominated by diatoms and descending to 0.05, when dominated by flagellates or cryptophytes. As a consequence of the high values of $P^{\text{B}}_{\text{max}}$ and α^{B} which characterize this phytoplankton, also high values of the light utilization index Ψ^* can be expected (Platt 1986) especially in light-limited conditions. The use of higher values of Ψ^* , like the average value of $0.07 \text{ m}^2 \text{ g Chl}^{-1}$, is thus justified with this summer Antarctic phytoplankton, at least as a first approximation.

However, a seasonal trend for Ψ^* , inverse to the irradiance availability with a minimum around the solstice, is predicted by the model of Morel (1991) and evident from the data of Claustre et al. (1998). It also appears from data at Terra Nova Bay, with an average value of $\Psi^* = 0.06 (\pm 0.01) \text{ m}^2 \text{ g Chl}^{-1}$ in January and of $0.09 (\pm 0.02)$ in February. Therefore, the integrated production (PP) has been calculated also with variable values of Ψ^* , obtained as a function of daily PAR (D. Antoine, pers. comm.) and enhanced so that their average was made equal to 0.068. The results in terms of modelled productions are quite similar, as averages, to the more rough estimates obtained with a constant value of Ψ^* , but their range of variation is slightly reduced (e.g. in 1989–90, instead of 0.35–3.14 it becomes 0.38–2.6 $\text{g C m}^{-2} \text{ day}^{-1}$).

The temporal evolution of daily integrated irradiances at Terra Nova Bay during three summer seasons is shown in Fig. 5 and compared with the curve of maximum irradiance empirically determined (see methods) and corresponding to clear-sky conditions. Values range from a maximum of $36 \text{ MJ m}^{-2} \text{ day}^{-1}$ (equivalent to $70 \text{ E m}^{-2} \text{ day}^{-1}$ of PAR) near the solstice of December 1987, to minima below $5 \text{ MJ m}^{-2} \text{ day}^{-1}$ in the second half of February. Generally high values have been measured with respect to clear-sky conditions (on average 80% for the three seasons), with fluctuations in the time scale of weeks, reflecting the average period for occurrence of storms or intense cloud coverages. In fact, relatively short periods (3–4 days) of maximal irradi-

ance at the sea surface were frequently present during each of the three seasons and, exceptionally, as during the late spring of 1987–88, also periods of 10 to 14 days occurred. During the first 40 days of the season 87–88, the highest relative irradiance reached the sea surface (on average 94.4% of maximum), whereas in February 1988 it was the minimal (62%) compared to the same period in 1990 (78%) and 1995 (85%).

The column-integrated values of chlorophaeopigments at Terra Nova Bay are shown in their temporal evolution in Fig. 6; they range between 10 and $170 \text{ mg Chl m}^{-2}$. The top of the summer bloom was clearly reached at the end of December in 1989–90, whereas it seems difficult to place the seasonal maximum for the integrated biomass

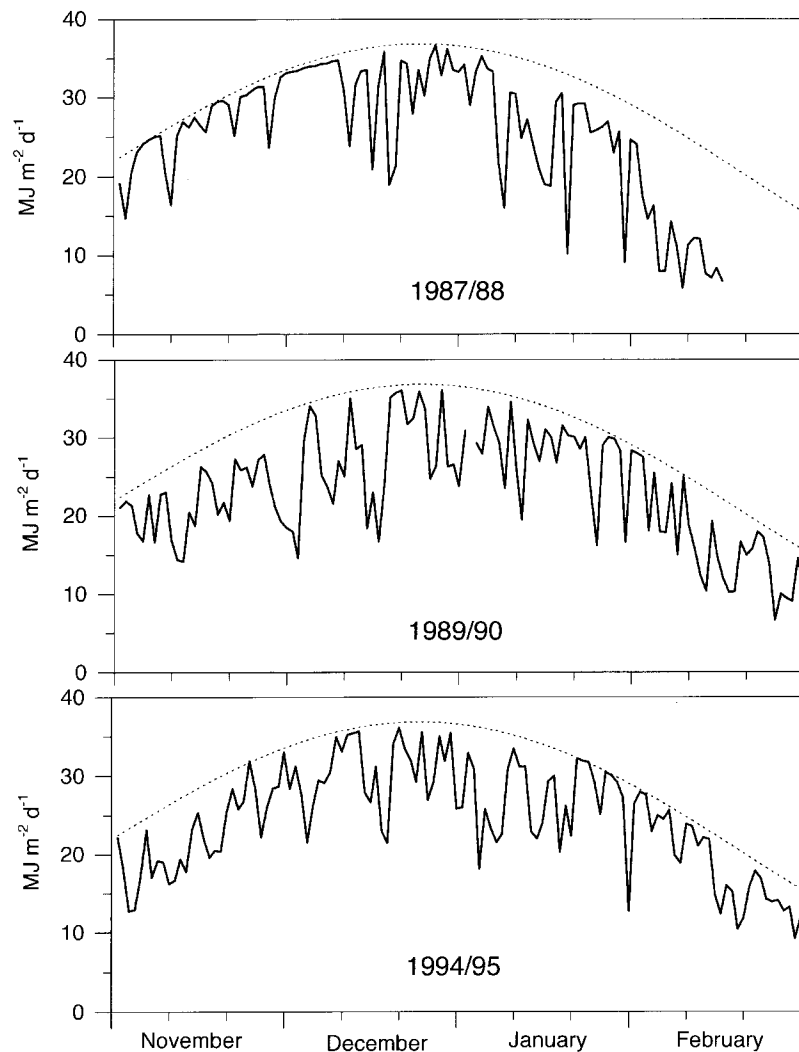


Fig. 5. Daily integrated irradiance at Terra Nova Bay during the years of investigations. The curve of maximum daily irradiance under clear-sky conditions (dotted line) is also reported

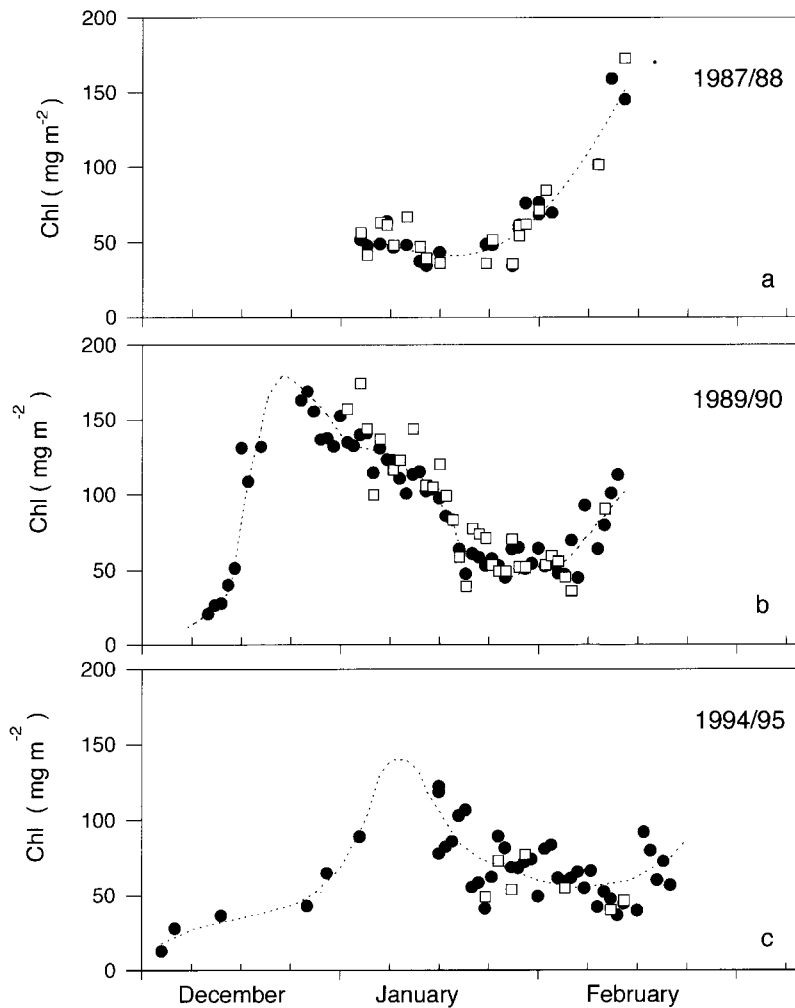


Fig. 6a-c. Temporal evolution of integrated chlorophaeopigments at Terra Nova Bay during the three summer seasons, as computed from C_{pd} (filled dots) and from Chl integration up to 0.1% of surface PAR (open squares)

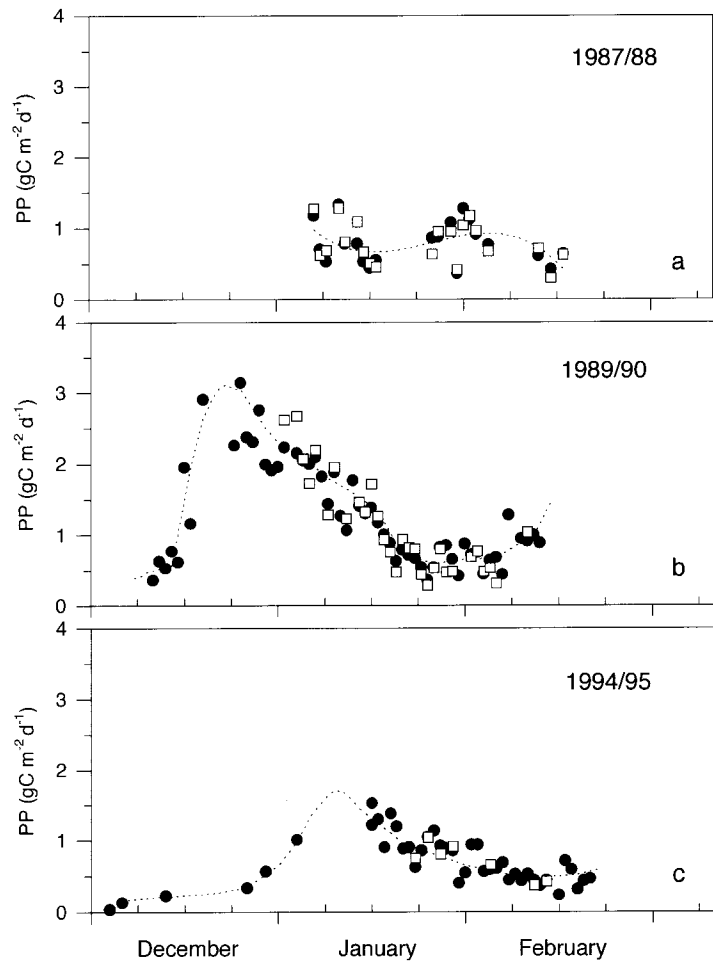
during 1987–88 and 1994–95, owing to the scarcity of sampling. On the other hand, it is more evident the position of the minimum biomass (less than 50 mg Chl m^{-2}) which occurs at mid January in 1987–88, at the end of January in 1989–90 and at the beginning of February in 1994–95. The presumably earlier season of 1987–88 can be related to the higher relative irradiance measured at the sea surface, during late spring 1987 (November and December, see Fig. 5).

The integrated production PP ($\text{g C m}^{-2} \text{ day}^{-1}$) calculated from the biooptical model, for the three seasons at Terra Nova Bay, is shown in Fig. 7. Values range from low to quite high daily productions ($0.1 - 3.1 \text{ g C m}^{-2} \text{ day}^{-1}$) reaching the top with the bloom of December 1989. A similar seasonal pattern is evident for the three data series, as it was for biomass (Fig. 6) in spite of the lack of completeness in sampling the whole seasons. It has

to be noted that the rise in biomass of late summer 1987–88 does not correspond to an increase in daily primary production (PP) owing to a double reason: the very low daily irradiance of that period, even less than $5 \text{ MJ m}^{-2} \text{ day}^{-1}$ in mid-February (Fig. 5), and the high proportion in phaeopigments which characterize the last three stations sampled in February 1988 (stations 49, 50, 51).

The integrated primary production values in the western Ross Sea during December 1989 (Fig. 8) exhibit more than a tenfold variation, from the lowest values of $0.21 \text{ g C m}^{-2} \text{ day}^{-1}$ (station 2) to the highest of $2.544 \text{ g C m}^{-2} \text{ day}^{-1}$ (station 22 along the 75°S transect). Three large areas show very high production ($>1 \text{ g C m}^{-2} \text{ day}^{-1}$): the first at Terra Nova Bay (stations 25, 26 and 27), the second nearly at the same latitude (75°S) but at 173°E (about 220 n miles offshore, stations 20–22) and

Fig. 7a-c. Temporal evolution of integrated production (PP) at Terra Nova Bay for the 3 years of investigations, as computed from C_{pd} (filled dots) and from Chl integration up to 0.1% of surface PAR (open squares)



the third at the latitude of 65°S approaching the Balleny Islands in a wide region of seasonal ice melting (stations 5, 6). The lower values of daily production ($<0.3 \text{ gC m}^{-2} \text{ day}^{-1}$) are observed to the north of the Antarctic convergence (62°S, station 2) and between 70° and 75°S in waters characterized by scarce biomass (less than 50 mg Chl m^{-2}), as was shown by Innamorati et al. (1992a).

Discussion

The primary production of the three years can be compared through the average values of the daily production obtained during the whole period (Table 2), which ranges from $0.73 \pm 0.21 \text{ gC m}^{-2} \text{ day}^{-1}$ in 1987–88 to $1.39 \pm 0.79 \text{ gC m}^{-2} \text{ day}^{-1}$ in 1989–90. When limited to the period common to the three seasons (6 Jan through 10 Feb) the average productions do not differ so much, ($0.79\text{--}0.98 \text{ gC m}^{-2} \text{ day}^{-1}$), despite the fact that

the seasonal cycles appear somewhat shifted from one year to the other by approximately 2 weeks.

These values of real and daily integrated productions appear high if compared to those even recently obtained in different antarctic waters, in the Weddell Sea (Dower et al. 1996) or in the Bellinghousen Sea (Savidge et al. 1995), but they are quite comparable to the direct measurements of primary production carried out in the whole Ross Sea. Wilson et al. (1986) obtained an average value in January and February 1983 of $0.962 \text{ gC m}^{-2} \text{ day}^{-1}$, Smith et al. (1990) for a transect at 72.5°S found an average value of $0.999 \text{ gC m}^{-2} \text{ day}^{-1}$ and of 1.37 at 76.5°S and more recently Smith et al. (1996) observed values ranging from 0.15 to $2.85 \text{ gC m}^{-2} \text{ day}^{-1}$, with the highest in January in the southernmost part of the Ross Sea.

An attempt to estimate the whole season production through a temporal integration (Table 2), for the months from December through February,

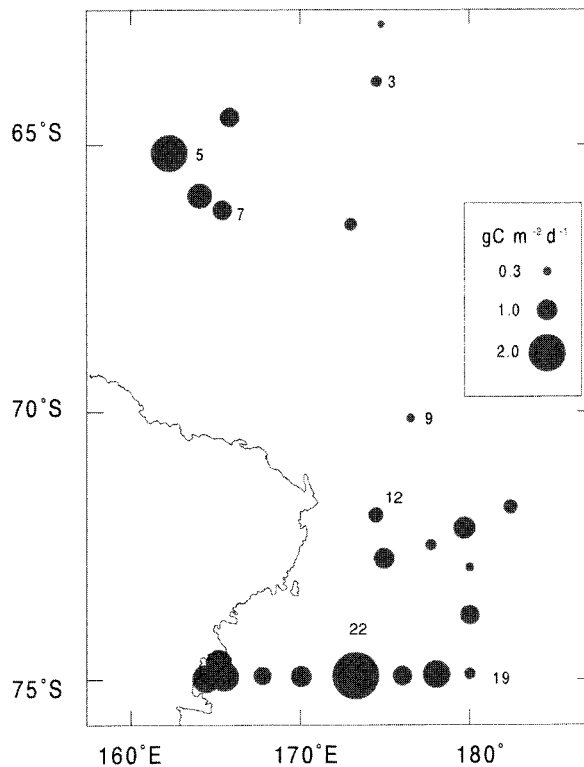


Fig. 8. Daily and column integrated primary production (PP) in the western Ross Sea during December 1989

Table 2. Time-integrated and average primary production (PP) at Terra Nova Bay for the 3 years of investigation. Data in brackets must be considered as underestimate of seasonal production

	Whole period gCm ⁻² day	Common period gCm ⁻² day	Dec-Jan-Feb gCm ⁻²
1987-88	0.79 ± 0.28	0.79 ± 0.28	(70.7)
1989-90	1.39 ± 0.79	0.98 ± 0.79	125
1994-95	0.76 ± 0.39	0.76 ± 0.39	(65.9)

gives values of 125 gCm⁻² (9 weeks) in 1989-90, of 70.7 over 6 weeks in 1987-88 and of 65.9 in 1994-95, the last ones being probably biased by under-sampling in the period of the bloom. A recent estimate of the Ross Sea production by CZCS imagery (Arrigo and McClain 1994) gives a value of 141 gCm⁻², between Dec. 10 and the Feb. 19 1979, in occasion of an intense and extensive bloom concerning the southern Ross Sea, which contrasts with the nearly ten fold lower values estimated for the entire Southern Ocean (Holm-Hansen et al. 1977; El-Sayed 1978) but also with values of 40 to 49 gCm⁻²year⁻¹ appreciated in the Bellinghausen

Sea (Boyd et al. 1995) or in the Weddell Sea (Smith and Nelson 1990). The high seasonal production of the Ross Sea seems now definitely assessed and has been recently confirmed by estimates of annual production from a several years study (Nelson et al. 1996), with values ranging from 216 gCm⁻² year⁻¹ in the southeastern part of the Ross Sea to 91 gCm⁻² year⁻¹ in the northern part. The annual production of the southwestern part, where Terra Nova Bay is included, is 142 gCm⁻² year⁻¹, but when limited to the period from December through February a value of approximately 105 gCm⁻² can be appreciated, which falls in the range of seasonal production estimated at Terra Nova Bay (Table 2).

The seasonality of phytoplankton production at Terra Nova Bay is characterized by a main peak occurring, depending on the year, from the second half of December through the beginning of January and eventually a second late summer bloom in February. December is the period of the main phytoplanktonic bloom in the Ross Sea, as reported also by Arrigo and McClain (1994) and Nelson et al. (1996). During February, a second rise of production is less evident than for phytomass (Fig. 6, and also Innamorati et al. 1992b) but it must be pointed out that even in mid February daily productions higher than 1 gCm⁻² day⁻¹ have been estimated. Similar, or higher, values of daily production during this month cannot be considered as exceptional in antarctic waters, having also been observed at Palmer station (Moline and Prezelin 1997) and in the Ross Sea (Nelson et al. 1996). In the latter case, the monthly average productions estimated do not show an evident second peak in February, probably owing to the interannual variability of this phenomenon.

As previously pointed out, the photosynthetic performance of this phytoplankton (see Table 1) reveals a general adaptation to low light regimes, as it is characterized by high values of the photosynthetic efficiency α^B , by low values of the saturation irradiance E_K , high values of the maximum assimilation number P_{max}^B and also by high values of the maximum quantum yield for photosynthesis, ϕ_m . Similar values of these photosynthetic parameters have been measured in the Weddell Sea (Figueiras et al. 1994; Claustre et al. 1998); and they are, indeed, consistent with the higher value of the column photosynthetic cross-section Ψ^* here observed (Fig. 4), which is suggested to be a general feature of Antarctic phytoplankton at Palmer Station (Claustre et al. 1998).

These features of phytoplankton production can be partially explained by a general low-light adaptation, but they could also be related to a low-temperature adaptation of the growth performance. In spite of low surface temperatures (-0.5 – 1.5 °C), the phytoplankton of Terra Nova Bay did reveal, from cell counts, quite high growth rates, at least during the initial phase of the bloom. Under the simplifying hypothesis of no losses due to grazing and sedimentation, a net growth rate of 0.8 doublings day^{-1} is reached by surface phytoplankton during a period of 5 days in December 1989 and still of 0.2 doublings day^{-1} at the beginning of the second bloom, in February 1990. Moreover, besides the high daily productions measured by ^{14}C assimilation (Mangoni et al. 1999) also high values of DCMU-induced variable fluorescence, with FRI higher than 0.70, were often observed at Terra Nova Bay, during the 1989–90 and 1994–95 expeditions.

Iron availability should not limit phytoplankton production in this area, as pointed out by Sullivan et al. (1993) owing to the important aeolian input of iron-rich dust from the coast to waters which are placed downstream of the dominant winds. Moreover, a 3-day incubation experiment on phytoplankton of Terra Nova Bay (Lazzara et al. 1997), with an iron-chelated addition (12 nM), led to generally high values of variable fluorescence and slightly lower (FRI = 0.44 ± 0.17) for the treated samples, than for the control (FRI = 0.61 ± 0.16).

The relationship between temperature and growth or productivity is obviously entailed by the temperature effects on the enzymatic activity of the Calvin cycle, but especially in the low-temperature domain, it is still debated whether and/or how much natural populations are limited in their growth by the depressed temperatures. Tilzer and Dubinsky (1987) pointed out that photosynthetic rates are less strongly affected by low temperatures than respiration rates are, so resulting in higher relative net productions for polar phytoplankton. Sullivan et al. (1993), using CZCS-satellite imagery, made the “counterintuitive conclusion that the highest phytoplankton crops occur in the coldest waters of the Southern Ocean”. More recently, Behrenfeld and Falkowski (1997) obtained a statistical relationship between maximal productivity and sea surface temperature, which, used as base of a production model for satellite images, made it possible to appreciate an enhanced production for polar phytoplankton

with respect to previous satellite estimates (Antoine et al. 1996; Longhurst et al. 1996).

The constant feature of a high production level for phytoplankton in the western Ross Sea is confirmed by the present study even at the seasonal time scale (3 months) and notwithstanding the presence of an interannual variability, which mainly concerns changes in the phase of the phytoplankton seasonal cycle (2 weeks, at least). Specific values of the photosynthetic parameters and of the biooptical properties seem to characterize the phytoplankton in the western Ross Sea, pointing out the need of further elaboration of specific regional algorithms to improve the estimate, through remote sensing, of phytoplankton biomass and production in this region.

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