# Photosynthetic parameters of phytoplankton from 50° N to 50° S in the Atlantic Ocean

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ABSTRACT We conducted 150 photosynthesis-irradiance (P-E) experiments along 2 Atlantic meridional transects from 50° N to 50° S in April-May and October-November 1996. The latitudinal and vertical distributions of the maximum chlorophyll $a$-normalized rate of photosynthesis ($P_m^B$) and the initial slope of the P-E curve ($\alpha^B$) were examined in relation to the variations in relevant physical, chemical and biological variables. $P_m^B$ ranged from <1 mg C mg chl$^{-1}$ h$^{-1}$ in the central oligotrophic gyres to >10 mg C mg chl$^{-1}$ h$^{-1}$ in temperate regions and the upwelling area off Mauritania. The dynamic range of the observed variations in the P-E parameters was 3 to 4 times higher than assumed in productivity models that divide the ocean into biogeochemical provinces. Variability in the physiological parameters of phytoplankton was as high as that of chlorophyll concentration. We obtained a model of multiple linear regression to calculate integrated primary productivity from data of surface temperature, chlorophyll $a$ and $P_m^B$. Changes in $P_m^B$ accounted for 30% of the total variability in productivity, whereas variations in chlorophyll $a$ explained only 5%, which indicates that phytoplankton photophysiology is more relevant than biomass in the control of primary productivity. We found a significant, negative correlation between the latitudinal changes in $P_m^B$ and those in the depth of the nitracline, suggesting an important role for the nutrient supply from below the thermocline in the regulation of photosynthetic efficiency over large spatial scales. A large degree of temporal variability was observed in the subtropical gyres: $P_m^B$ and $\alpha^B$ varied by a factor of 3 between the 2 cruises, whereas phytoplankton biomass remained constant. The differences in the photosynthetic parameters between seasons were larger than between biogeochemical provinces. We emphasize the need to include nutrient-driven changes of phytoplankton photophysiology in models of primary productivity.

KEY WORDS: P-E relationships · Photosynthesis · Phytoplankton · Nutrients · Temporal variability · Atlantic Ocean

## INTRODUCTION

Knowledge of the variability in the relationship between photosynthesis and irradiance in natural phytoplankton populations yields a double outcome for the study of primary production in the ocean. First, it allows the determination of the influence of different environmental constraints on the efficiency with which microalgae convert light into chemical energy (Platt et al. 1992, Lindley et al. 1995, Babin et al. 1996). Secondly, it provides the parameters needed to compute estimates of marine productivity from remotely sensed data of phytoplankton pigments (e.g. Longhurst et al. 1995, Sathyendranath et al. 1995, Antoine et al. 1996). In the absence of photoinhibition, a photosynthesis-irradiance (P-E) curve is defined by 2 parameters: $P_m^B$, the maximum rate of chlorophyll-normalized photosynthesis, and $\alpha^B$, the initial slope of the curve, which is an index of light-limited photosynthetic efficiency. Estimation of local water column production requires the development of an algorithm that, in addition to the parameters of the P-E curve, takes into account the irradiance field and the pigment profile (Platt & Sathyendranath 1988). In order to extrapolate the local production estimates to regional and basin scales, it is essential to know the temporal and geographical vari-

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ability of the P-E parameters (Sakshaug et al. 1997). However, there is a significant lack of P-E observations over many areas of the open ocean, constituting what has been defined as 'a serious gap in phytoplankton ecology' (Longhurst et al. 1995).

In addressing our deficient knowledge of the distribution of phytoplankton physiological responses, it has been assumed that most of the variability in primary production is due to changes in first-order factors such as pigment concentration and irradiance, leaving a less important role for the physiology-dependent changes in the chlorophyll-specific rate of photosynthesis (Platt et al. 1991, Sathyendranath et al. 1995). This assumption is supported by the fact that phytoplankton pigments often have a wider dynamic range of variation compared to that of the photosynthetic parameters. However, while excellent coverage of the chlorophyll distributions has been attained using satellite observations, no comparable data exist for the distribution of photosynthetic parameters over large spatial scales and models of global productivity often rely on P-E observations that are geographically unbalanced (e.g. Sathyendranath et al. 1995). Furthermore, studies suggesting that phytoplankton production in the ocean is mainly controlled by irradiance are based on laboratory experiments (Goldman et al. 1979) or have a limited spatial coverage (Bidigare et al. 1987, Marra & Heinemann 1987). Large-scale measurements are clearly required in order to assess the variability of phytoplankton photophysiology, its connection to physical forcing (Balch et al. 1997) and its importance in the control of oceanic primary production.

The significance of second-order factors (sensu Platt & Sathyendranath 1988) for the response of algal photosynthesis to light has recently been illustrated by the findings of Behrenfeld & Falkowski (1997a), who described a non-linear relationship between temperature and the ratio of chlorophyll per unit carbon fixed. Similarly, it has been proved that the availability of micronutrients (Lindley et al. 1995) and macronutrients (Platt et al. 1992) affect significantly the parameters of the P-E curve. However, Cullen et al. (1992b) showed a lack of consistency in the relationship between P-E parameters and nutrient-limited growth of phytoplankton, cautioning against the use of $P_m^B$ as an indicator of nutritional status. Their analysis was nevertheless based on results from monospecific, continuous cultures and therefore the applicability of their conclusions to real situations depends on the extent to which (1) balanced growth exists in the ocean (Balch & Byrne 1994) and (2) community responses of photoadaptive responses can be equated to that of a single species (see Harris 1986). The study of multispecific phytoplankton assemblages over a large range of oceanographic regimes avoids these uncertainties, providing

the potential to determine if natural variations in $P_m^B$ can tell us anything about the physiological state of phytoplankton.

Here we present the results of a basin-scale survey of phytoplankton photosynthetic parameters carried out as a part of the Atlantic Meridional Transect (AMT) programme. Although other workers have previously described the distributions of the quantum yield of photosynthesis (Olaizola et al. 1996) and the P-E parameters (Hood 1995, Kyewalyanga et al. 1998) over large spatial scales, this is to our knowledge the first study that combines measurements of water column productivity and photosynthetic parameters over a range of temperate, tropical and equatorial environments on an ocean-wide basis (50° N to 50° S). Observations from 2 contrasting seasons are considered in order to evaluate the temporal variability in the photosynthetic responses of phytoplankton. We aim (1) to quantify the role of phytoplankton photophysiology versus phytoplankton biomass in the control of integrated primary production over large spatial scales and (2) to investigate the importance of second-order factors for the regulation of the spatial and temporal variability in the light-saturated rate of chlorophyll-normalized photosynthesis.

## METHODS

Two cruises were conducted on board RRS 'James Clark Ross' on a passage between UK and the Falkand Islands during 22 April to 22 May 1996 (AMT-2) and 16 September to 25 October 1996 (AMT-3). The 11 000 km long cruise track follows the 20° W meridian from 47° N to 10° N and then bears SW until ~40° S. The southern part of the cruise track follows the 56° W meridian until ~50° S.

During each cruise, 25 productivity stations were sampled at intervals of approximately 270 nautical miles. At each station, water samples were taken from 5 to 10 depths in the upper 200 m of the water column using a rosette equipped with 12 metal-clean, Teflon® Niskin bottles that were provided with silicone O-rings and seals. Sampling depths were selected according to the vertical distribution of fluorescence. Vertical profiles of photosynthetically active irradiance (PAR, 400 to 700 nm) were obtained with a SeaOPS Satlantic sensor, whereas incident PAR was continuously measured and recorded using a Delta-T Instruments PAR sensor. Temperature profiles were measured with a Neil Brown Mark IIIB CTD instrument. The concentration of inorganic nutrients was determined colourimetrically on fresh samples using a Technicon AAII Autonalyser. Chlorophyll a concentration was determined fluorometrically on 250 ml samples after low vacuum

pressure (<100 mm Hg) filtration through 0.2 μm polycarbonate filters and overnight extraction in 90% acetone. The fluorometer was calibrated before and after each cruise using pure chlorophyll a (Sigma) as a standard. For the identification and counting of phytoplankton, duplicate 100 ml samples were preserved in Lugol's iodine and 0.5% buffered formalin, respectively. Samples were examined under an inverted microscope and cell numbers converted into carbon (C) biomass as in Holligan et al. (1984).

Three P-E experiments were carried out at each station with water samples taken from the surface (7 m), the deep chlorophyll maximum and an intermediate depth. A total of 150 P-E curves were obtained during the 2 cruises. Sampling was conducted every day at 10:00 to 10:30 h local time. All $^{14}$C-uptake experiments started within 30 min of sampling. For the P-E experiments, we used 3 bench incubators equipped with 100 W halogen lamps and cooled by running surface seawater provided by the ship's continuous non-toxic water suply. Temperature in the incubators was within 0.5°C of that at the sea surface. Each incubator held 20 samples that were exposed to an irradiance gradient from 5 to 2500 μmol m$^{-2}$ s$^{-1}$. Light was attenuated by neutral density filters and the incubation bottles. Irradiance at each position of the incubator was checked regularly during the cruises using a LiCOR 2π PAR sensor. Working under dim light conditions, seawater samples were dispensed into 70 ml polycarbonate bottles, inoculated with 370 kBq (10 μCi) of NaH$^{14}$CO$_3$ and incubated for 2.5 h. Incubation bottles were cleaned by soaking them in 1 N HCl overnight and then rinsing 3 times with deionized water. For each curve, 1 bottle was wrapped with aluminium foil prior to incubation and the corresponding dark DPM value was subsequently substracted from the $^{14}$C activity of each light sample. At the end of the incubations, samples were filtered under low vacuum pressure (<100 mm Hg) through 0.2 μm polycarbonate filters. Filters were exposed to concentrated HCl fumes overnight and then placed in scintillation vials together with 4 ml of scintillation cocktail. Radioactivity of each sample was measured with a Beckman LS6000 SC scintillation counter. Counts were corrected for quenching using the channel ratio method.

The results of each P-E experiment were fitted to the continuous exponential model by Platt et al. (1980) using non-linear least squares regression:

$$P^B = P_s [1 - \exp(-\alpha I/P_s)] [\exp(-\beta I/P_s)]$$

where $P^B$ [mg C mg chl$^{-1}$ h$^{-1}$] is the chlorophyll-normalized rate of carbon incorporation; $P_s$ [mg C mg chl$^{-1}$ h$^{-1}$] is the maximum rate of chlorophyll-normalized carbon incorporation without photoinhibition; $\alpha^B$ [mg C mg chl$^{-1}$ h$^{-1}$ (μmol m$^{-2}$ s$^{-1}$)$^{-1}$] is the initial slope of the

P-E curve, $I$ is the irradiance (μmol m$^{-2}$ s$^{-1}$) and $\beta$ [mg C mg chl$^{-1}$ h$^{-1}$ (μmol m$^{-2}$ s$^{-1}$)$^{-1}$] is the photoinhibition parameter. The realized maximum rate of carbon incorporation ($P_m^B$, mg C mg chl$^{-1}$ h$^{-1}$) was calculated according to Platt et al. (1980). In order to avoid any bias in the choice of the model, we systematically used the continuous exponential equation for all the curves even if photoinhibition was not apparent. In previous experiments where $\beta$ was not significantly different from zero, we compared the P-E parameters obtained using the continuous exponential model with those obtained with the hyperbolic tangent model, which does not include a photoinhibition parameter. The differences between the estimates of $P_m^B$ and $\alpha^B$ produced by both models were not significant (paired $t$-test, p > 0.05) and amounted to less than 10% of the mean (Marañón & González 1997).

In addition to the determination of P-E parameters, simulated in situ $^{14}$C experiments were conducted at each station in order to obtain vertical profiles of primary productivity. Within 30 min of sampling, seawater samples from 5 to 7 depths were transferred under dim light conditions to acid-washed, 70 ml polycarbonate bottles, inoculated with 370 kBq (10 μCi) of NaH$^{14}$CO$_3$ and incubated for 7 to 8 h in a deck incubator cooled by pumped surface seawater. Three light bottles plus one dark bottle were incubated for each sampling depth. Light profiles were simulated using a set of neutral density and blue plastic filters and according to the vertical PAR distribution measured before the incubation. Filtration, decontamination and counting of the samples were carried out as described previously for the P-E experiments. Dark bottle values were subtracted from the counts in the light samples.

## RESULTS

### The structure of the water column

The latitudinal distributions of temperature from 50° N to 50° S during the 2 cruises reflect the changes in the structure of the water column along the transect as well as the differences between seasons (Fig. 1). In temperate North Atlantic waters, the upper water column was relatively well mixed during April-May 1996 (AMT-2) (Fig. 1A), in comparison to the conditions during September-October 1996 (AMT-3) (Fig. 1B). Conversely, strong thermal stratification observed in the South Atlantic central gyre during AMT-2 gave way to a well-mixed upper water column during AMT-3. During both cruises, a marked outcropping of the isotherms between 25° and 20° N indicated the cooling of subsurface waters as the transect crossed the margin of the upwelling area off Mauritania. A reduction in
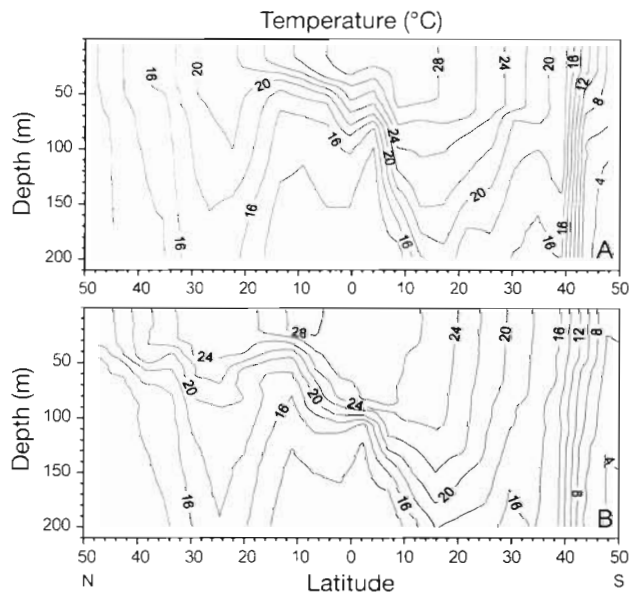
Temperature (°C)



Fig. 1 Latitudinal distributions of temperature during (A) April-May 1996 (AMT-2) and (B) September-October 1996 (AMT-3)

the thickness of the upper mixed layer was also observed as a result of the equatorial upwelling. During both cruises, the thermocline in the northern subtropical gyre was shallower than in the southern subtropical gyre. The differences we observed between the physical and biological conditions of the north and south oligotrophic regions reflect the different location of the cruise track relative to the gyre centre in each hemisphere, and are not intended to represent differences between the gyres as a whole. The vertical distribution of nutrients followed closely that of temperature. Excluding temperate waters, nitrate was undetectable (<0.05 µM) in the upper mixed layer throughout the transect. Reflecting the position of the thermocline, the nitracline in the southern central gyre was deeper than it was in the northern central gyre.

## Phytoplankton biomass and primary production

The distribution of phytoplankton abundance as estimated from the concentration of chlorophyll a (chl a) showed similar major vertical and latitudinal patterns during both seasons (Fig. 2). Low chl a concentrations (<0.2 mg m$^{-3}$) characterized the upper mixed layer of the central gyres, whereas concentrations above 0.5 mg m$^{-3}$ were encountered in surface and subsurface waters at temperate regions and also in the upwelling area off NW Africa. Relatively high chl a concentrations (>1 mg m$^{-3}$) were measured north of 45°N during AMT-2, indicative of the late stages of the

North Atlantic spring bloom (Fig. 2A). Similarly, highest chl a levels in the southern end of the transect were found during the austral spring (Fig. 2B). Phytoplankton biomass was dominated by cyanobacteria and small flagellates in low productivity areas, with higher contributions by diatoms in temperate and upwelling waters (Marañón et al. unpubl.).

A distinct deep chlorophyll maximum (DCM) was present at low latitudes, with chl a concentrations ranging between 0.2 and 0.4 mg m$^{-3}$. An analysis of the distribution of phytoplankton carbon biomass showed that, rather than representing a real biomass maximum, the DCM was largely the result of a decrease with depth in the C to chl a ratio (Marañón et al. unpubl.). Reflecting the location of the nutricline, the chl a maximum was subsuperficial in the upwelling area off Mauritania and deepest in the southern subtropical gyre.

Primary production was higher in temperate waters towards both ends of each transect and in the upwelling region off NW Africa, whereas very low rates of photosynthesis were measured in the subtropical gyres. Highest rates of productivity (>2 mg C m$^{-3}$ h$^{-1}$) were measured in surface and subsurface waters north of 40°N during AMT-2 and south of 30°S during AMT-3. Relatively high levels of productivity (>1 mg C m$^{-3}$ h$^{-1}$) were also found in the upwelling region during AMT-3. Although the main latitudinal patterns of
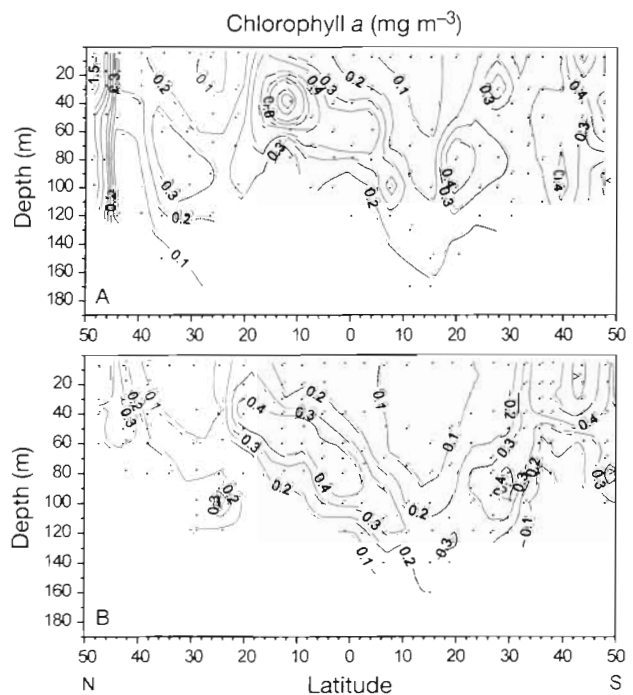
Chlorophyll a (mg m$^{-3}$)



Fig. 2. Latitudinal distributions of chlorophyll a concentration during (A) AMT-2 and (B) AMT-3. Contouring levels are 0.1, 0.2, 0.3, 0.4, 0.6, 0.8, 1.0, 1.5 and 2.0 mg m$^{-3}$

distribution of productivity were similar to those of chl *a* concentration, the depth-integrated photosynthesis to chl *a* ratio exhibited a >10-fold range of variability during this study (Fig. 3). Very low ratios (<0.4 mg C mg chl$^{-1}$ h$^{-1}$) were measured between the Equator and 12°S during AMT-2, whereas values as high as 5 mg C mg chl$^{-1}$ h$^{-1}$ were calculated for North Atlantic waters during the same cruise. We observed a relative increase in the depth-integrated photosynthesis to chl *a* ratio in temperate waters during spring and also in the upwelling area near 20°N. Low values were always found in the oligotrophic areas, and the southern central gyre tended to show lower rates than the northern central gyre. A large increase in photosynthesis to chl *a* ratios took place during AMT-3 in major sections of the transect, especially the equatorial and subequatorial regions, although comparable values were found in both ends of the transect.

## Photosynthetic parameters

The light-saturated rate of chlorophyll-normalized photosynthesis ($P_m^B$) varied by a factor of >40 during this study (range: 0.3 to 14 mg C mg chl$^{-1}$ h$^{-1}$), and the main patterns of vertical and latitudinal distribution of this parameter were similar during April-May and September-October 1996 (Fig. 4). $P_m^B$ decreased with depth along the transect, which indicates photoadaptation of the phytoplankton populations. Relative vertical homogeneity in $P_m^B$ was found only in areas with enhanced mixing of the upper water column, namely the temperate regions during spring. Lowest values of $P_m^B$ were measured in deep waters of the southern subtropical gyre, whereas an increase in $P_m^B$ was found between 20° and 5°N as the transect crossed the upwelling region off NW Africa. Surface and subsurface values of $P_m^B$ in the northern central gyre were significantly higher than in the southern central gyre.
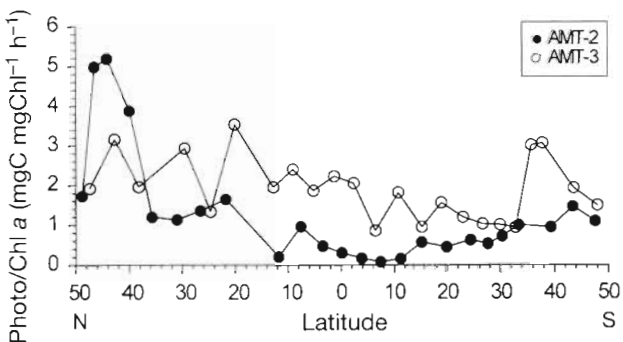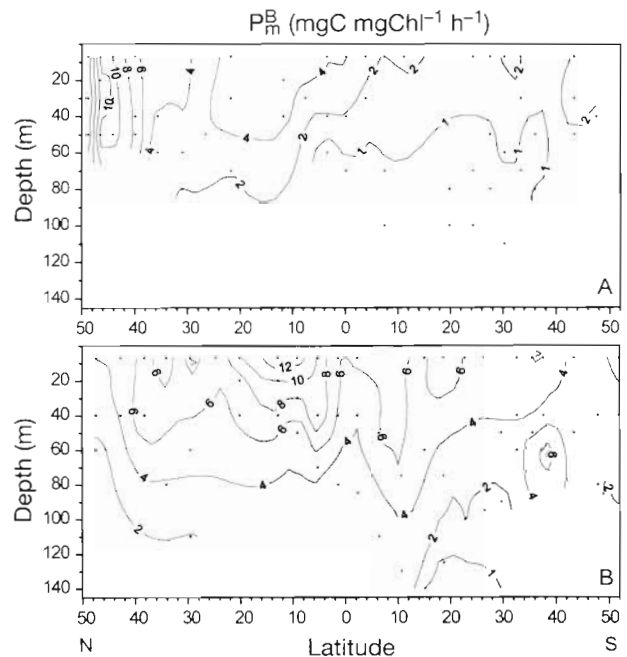


Fig. 4. Latitudinal distributions of the maximum rate of chlorophyll *a*-normalized photosynthesis ($P_m^B$) during (A) AMT-2 and (B) AMT-3

Despite the similar distribution patterns encountered during both cruises, absolute rates of light-saturated photosynthesis during AMT-3 were, particularly at low latitudes, significantly higher than those observed during AMT-2. Given that the same experimental procedures were used during both cruises, methodological differences cannot be responsible for the observed temporal variability.

The vertical distribution of the initial slope of the P-E curve ($\alpha^B$) was generally characterized by an increase with depth, indicating an enhanced photosynthetic efficiency of deep phytoplankton assemblages adapted to low irradiance levels (Fig. 5). During AMT-2, $\alpha^B$ ranged between >0.05 mg C mg chl$^{-1}$ h$^{-1}$ (µmol m$^{-2}$ s$^{-1}$)$^{-1}$ in temperate North Atlantic waters and <0.01 mg C mg chl$^{-1}$ h$^{-1}$ (µmol m$^{-2}$ s$^{-1}$)$^{-1}$ at low latitudes. The highest $\alpha^B$ values measured during AMT-3 took place between 0° and 10°N, whereas lower values were found in the southern subtropical gyre.

The latitudinal distribution of the calculated saturation parameter $I_k$ ($P_m^B/\alpha^B$) showed contrasting patterns during this study (Fig. 6). During AMT-2, $I_k$ decreased from north to south, whereas the the opposite was true for AMT-3. This pattern of variation closely reflected the latitudinal distribution of incident irradiance (see Fig. 8A). The increased values of $I_k$ in the southern part of the transect during AMT-3 were the result of a reduction in $\alpha^B$, as $P_m^B$ showed a similar latitudinal pattern during both cruises (Figs. 4 & 5). The highest val-



Fig. 3. Latitudinal distributions of the depth-integrated photosynthesis to chlorophyll *a* ratio within the euphotic zone during AMT-2 and AMT-3

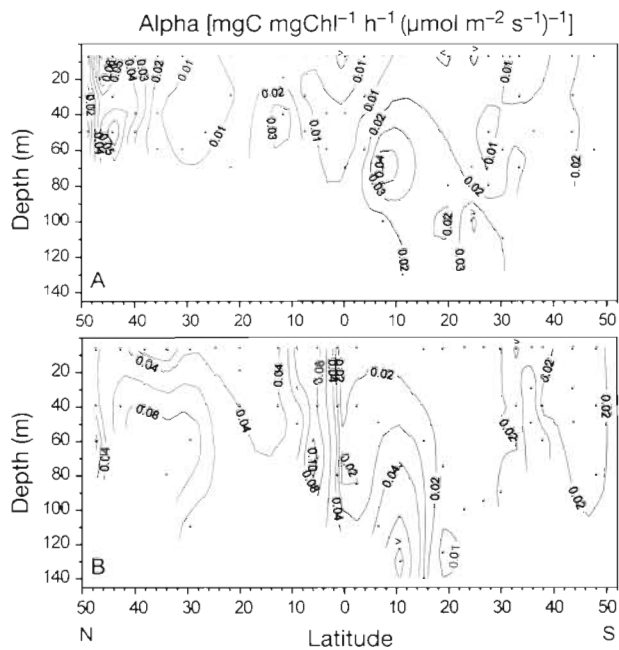Alpha [mgC mgChl$^{-1}$ h$^{-1}$ (µmol m$^{-2}$ s$^{-1}$)$^{-1}$]



Fig. 5. Latitudinal distributions of the initial slope of the photosynthesis-irradiance curve ($\alpha^B$) during (A) AMT-2 and (B) AMT-3

ues of $I_k$ (>400 µmol m$^{-2}$ s$^{-1}$) were calculated for surface and subsurface waters of the tropical regions, where high irradiances concurred with increased stability of the upper mixed layer. Phytoplankton photoadaptation caused a strong vertical gradient in $I_k$, which decreased systematically with depth reaching values <50 µmol m$^{-2}$ s$^{-1}$ at the base of the euphotic layer.

Fig. 7 illustrates the range of P-E relationships observed during this study at the surface and the DCM. In temperate waters, enhanced vertical mixing during spring prevented phytoplankton photoadaptation so that the surface and the DCM populations showed very similar photosynthetic responses (Fig. 7A, F). By contrast, assemblages from the DCM at low latitudes exhibited reduced $P_m^B$ and significant photoinhibition at irradiances above 500 µmol m$^{-2}$ s$^{-1}$ (Fig. 7B, C, D, E), which indicates that the turnover time for vertical mixing was longer than the time required for phytoplankton photoadaptation. Given that the light-saturated rate of photosynthesis is sensitive to temperature, and considering that all the P-E incubations were carried out at surface temperature, $P_m^B$ of phytoplankton from the DCM may have been overestimated at low latitudes, where vertical differences in temperature were large. However, this effect is likely to be of minor importance in view of the large magnitude of the vertical differences in $P_m^B$ at low latitudes. Carbon fixation rates under high irradiance were in some cases

reduced by a factor of >5 as compared to photosynthesis at optimal light levels (Fig. 7D, E).

In order to assess the relative influence of the irradiance and nutrient fields on the variability of phytoplankton photophysiology, we examined the latitudinal changes in incident irradiance, the depth of the nitracline and $P_m^B$ both at the surface and at the DCM (Fig. 8). The depth of the nitracline was defined as the first depth where the concentration of nitrate was ≥1 µM. Although differing in their absolute value as a result of photoadaptation (see Fig. 7), $P_m^B$ values at the surface and at the DCM showed similar latitudinal distributions. The contrasting distributions of incident average irradiance during AMT-2 and AMT-3 (Fig. 8A) were not reflected in comparable, opposing patterns for the variations in $P_m^B$ during each season (Fig. 8B, C). We used the depth of the nitracline as a proxy for the rate of nutrient supply into the euphotic zone (e.g. Herbland & Voituriez 1979, Cleveland et al. 1989, Malone et al. 1993) and found a significant negative correlation between the latitudinal changes in this variable and those of $P_m^B$ (Fig. 8B, C; note inverted scale on the right Y axis). The depth of the nitracline decreased between the Equator and 20°N during both cruises, reflecting the effects of upwelling processes (see Fig. 1), and enhanced values of $P_m^B$ were concurrently measured in those regions (Fig. 8B, C). Conversely, the lowest values of $P_m^B$ were measured in the central oligotrophic gyres, where the nitracline was deepest. The differences between each subtropical gyre in the
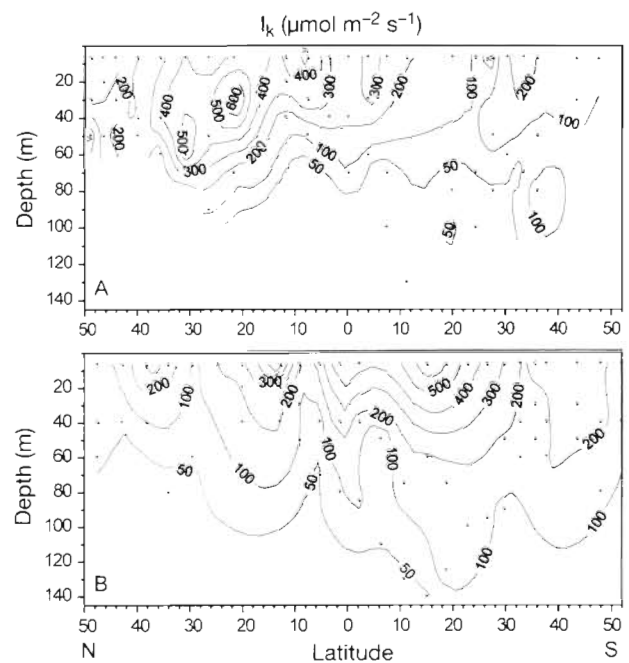
$I_k$ (µmol m$^{-2}$ s$^{-1}$)



Fig. 6. Latitudinal distributions of the saturation parameter $I_k$ ($P_m^B/\alpha^B$) during (A) AMT-2 and (B) AMT-3
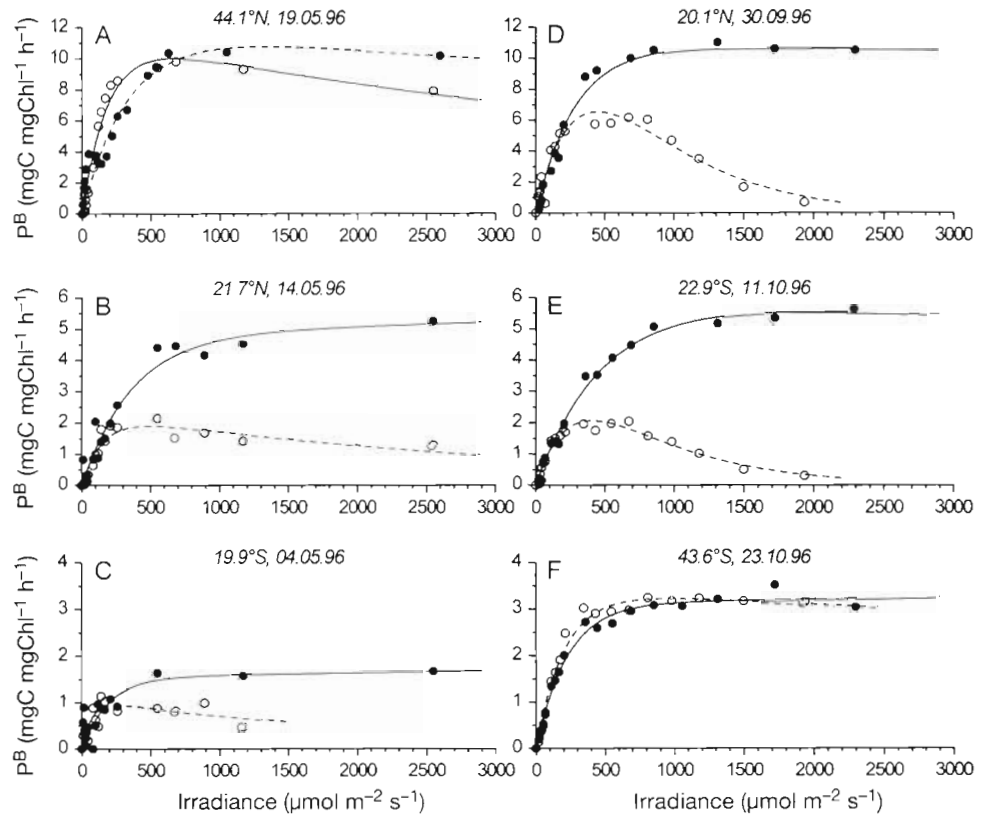
Fig. 7. Examples of photosynthesis-irradiance relationships of phytoplankton from the surface (●) and the deep chlorophyll maximum (○) in temperate and tropical waters of the Atlantic Ocean during (A, B, C) AMT-2 and (D, E, F) AMT-3. Lines represent best fits to the continuous exponential model (see 'Methods'). Sampling latitude and date (d/mo/yr) are indicated

thickness of the upper mixed layer (Fig. 1) were reflected in comparatively shallower nitracline depths at the northern central gyre. Accordingly, higher values of $P_m^B$ were usually measured in the northern subtropical gyre as compared to the southern subtropical gyre (see also Fig. 4).

A series of regression analysis was conducted between relevant physical, chemical and biological variables and surface $P_m^B$. We focused on the changes in $P_m^B$ at the surface in order to avoid the additional complications of the effects of photoadaptation. The depth of the nitracline was the only variable that showed a significant correlation with surface $P_m^B$, explaining 17% of its variability (Table 1). Neither temperature nor the taxonomical composition of phytoplankton were significantly correlated with surface $P_m^B$.

## An empirical model of primary production

Using stepwise multiple regression, we evaluated the relative importance of several environmental and biological variables in explaining the latitudinal and temporal changes of integrated productivity. The independent variables included in the analysis were: surface temperature, incident irradiance, nitrate concentration at the base of the euphotic layer, surface chl $a$ concentration and surface $P_m^B$. Table 2 includes all

Table 1. Results of the regression analysis of surface $P_m^B$ (dependent variable) against several physical, chemical and biological variables. $^*p < 0.05$

| Variable | Intercept | Slope | $r^2$ | n | p |
|---|---|---|---|---|---|
| Temperature | 4.34 | 0.017 | 0.00 | 43 | ns |
| Salinity | 18.0 | −0.361 | 0.01 | 43 | ns |
| Depth of the nutricline | 7.11 | −0.031 | 0.17 | 34 | * |
| Diatom C (%) | 4.49 | 0.057 | 0.04 | 43 | ns |
| Dinoflagellate C (%) | 42.1 | 0.168 | 0.03 | 43 | ns |
| Cyanobacteria C (%) | 5.01 | −0.006 | 0.00 | 43 | ns |

Table 2. Results of the stepwise multiple regression analysis performed with the integrated rate of primary production as dependent variable and significant environmental and biological independent variables. Only those variables that explained more than 1% of the variance in primary production are shown

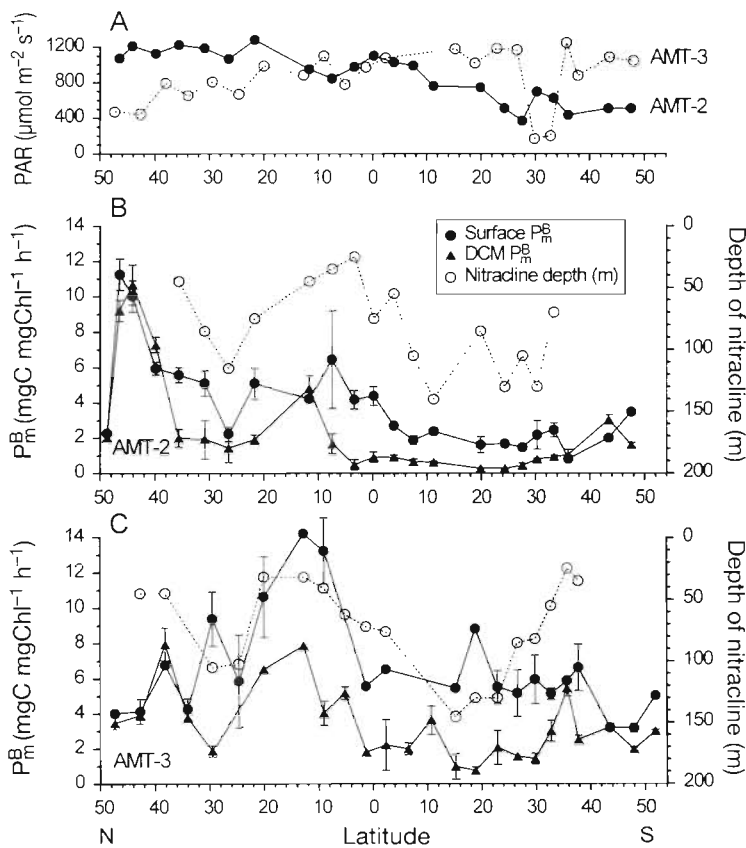| Variable | % variance | $F$ | $r^2$ | p |
|---|---|---|---|---|
| Temperature | 34.4 | 19.93 | 0.34 | 0.0001 |
| $P_m^B$ | 30.4 | 34.02 | 0.65 | 0.0000 |
| Chl $a$ | 4.9 | 27.60 | 0.70 | 0.0000 |

Fig. 8. (A) Latitudinal distributions of the daily averaged incident irradiance (PAR) during AMT-2 and AMT-3. (B and C) The maximum rates of chlorophyll-normalized photosynthesis ($P_m^B$) at the surface (7 m) and at the deep chlorophyll maximum (DCM) and the depth of the nitracline during (B) AMT-2 and (C) AMT-3. Bars indicate ±1 standard error

## Biogeochemical provinces and $P_m^B$

The AMT cruise track crosses 5 main biogeochemical provinces as defined by Longhurst et al. (1995): (1) the North Atlantic Drift (NADR, 60° to 40°N); (2) the North Atlantic Subtropical Gyre (NAST, 40° to 25°N); (3) the North Atlantic Tropical Gyre (NATR, 25° to 10°N), (4) the Western Tropical Atlantic (WTRA, 10°N to 5°S); and (5) the South Atlantic Tropical Gyre (SATL, 5° to 40°S). We calculated average values for surface chl *a* and $P_m^B$ in each biogeochemical region in order to summarize the main patterns of latitudinal and temporal change of phytoplankton abundance and photosynthetic performance (Fig. 10). The NADR province was characterized by increased chl *a* concentrations during both cruises, although the highest average values were measured during spring (AMT-2). Excluding NAST during AMT-3, the rest of the regions showed similar average chl *a* concentrations (0.1 to 0.2 mg m$^{-3}$) during both cruises. In contrast, significant differences in $P_m^B$ were found between regions and between cruises. During AMT-2, the NADR region showed the highest average $P_m^B$ (10.6 mg C mg chl$^{-1}$ h$^{-1}$), whereas a value of 1.8 mg C mg chl$^{-1}$ h$^{-1}$ was calculated for SATL. During AMT-3, $P_m^B$ was reduced in the NADR province, whereas it increased by a factor of >2 in the NATR, WTRA and SATL regions. Our results show that, partic-

those variables that explained more than 1% of the variability in the integrated productivity. The multiple linear regression model explained 70% of the variability in the integrated rate of primary production. Phytoplankton photophysiology, represented by $P_m^B$, accounted for 30% of the variability in primary production, whereas phytoplankton abundance, estimated by chl *a*, explained only 5%. Integrated primary production (IPP) during the 2 cruises could then be estimated as a linear function of surface temperature (Temp), $P_m^B$ and surface chl *a* according to:

$$\text{IPP} = -19.6\,(\pm 5.2) \times \text{Temp} + 59.7\,(\pm 9.5) \times P_m^B$$
$$+ 379.9\,(\pm 157.0) \times \text{chl } a + 458.7\,(\pm 150.5)$$

We compared the integrated primary productivity estimated using this empirical model with the integrated productivity rates measured at each station by $^{14}$C-uptake experiments (Fig. 9). A highly significant correlation ($r^2 = 0.70$, $p < 0.001$) existed between the measured and the estimated rates.
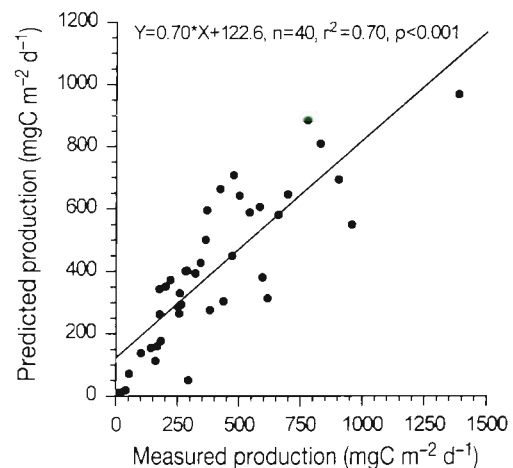


Fig. 9. Relationship between the integrated primary production measured during AMT-2 and AMT-3 and the integrated production predicted by an empirical linear regression model with temperature, surface chl and surface $P_m^B$ as independent variables (see text for details)
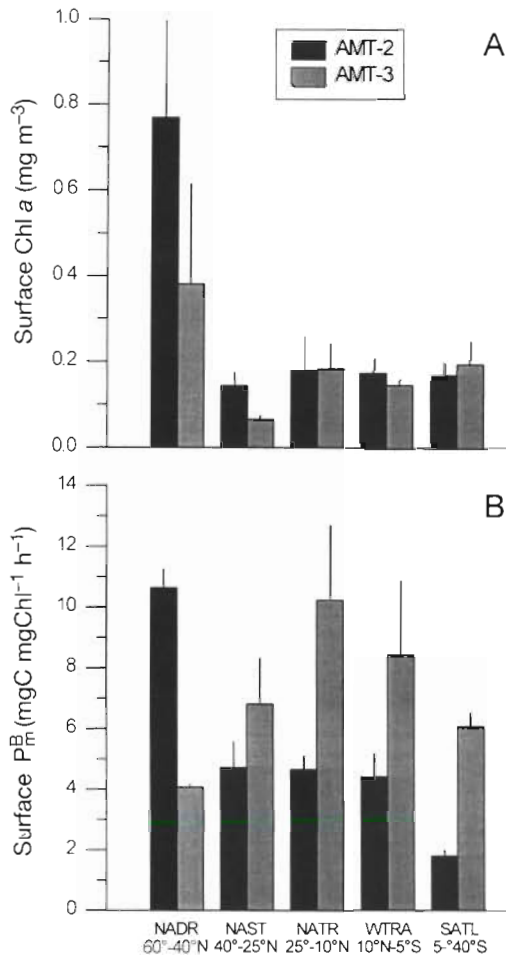
Fig. 10. Average surface values of (A) chlorophyll a concentration and (B) maximum rate of chlorophyll-normalized photosynthesis $(P_m^B)$ at each biogeochemical province sampled during AMT-2 and AMT-3. NADR: North Atlantic Drift (60°-40° N); NAST: North Atlantic Subtropical Gyre (40°-25° N); NATR: North Atlantic Tropical Gyre (25°-10° N); WTRA: Western Tropical Atlantic (10° N-5° S); SATL: South Atlantic Tropical Gyre (5°-40° S). Bars indicate 1 standard error

large-scale surveys that were restricted to the North (Kyewalyanga et al. 1998) and the South (Hood et al. 1995) Atlantic Ocean. Similarly, the values of $\alpha^B$ varied by a factor of ~30. The extensive spatial scales we covered during this study, together with the fact that we repeated the transect in 2 contrasting seasons, explain the larger variability we observed in the photosynthetic parameters. When considering only surface parameters (i.e. avoiding the effects of photoadaptation), we obtained a range of variation of about 1 order of magnitude, which agrees with the variability in normalized production found by Behrenfeld & Falkowski (1997a) in a large productivity dataset (see their Fig. 1). During our study, picoplankton generally accounted for >60% of total photosynthesis (Marañón unpubl. data). Accordingly, the absolute range of parameter values we obtained coincided with that reported for small phytoplankton in studies where the photosynthetic responses of size-fractionated assemblages have been determined (Platt et al. 1983, Joint & Pomroy 1986, Madariaga & Joint 1994).

The overall variability in $P_m^B$ (coefficient of variation, CV = 84%) was similar to that of chlorophyll concentration (CV = 102%). Moreover, when considering only tropical and equatorial regions (stations at latitudes below 25°), the observed variability in $P_m^B$ (CV = 63%) was even larger than the variability in chlorophyll concentration (CV = 46%). After comparing monthly estimates of biomass and productivity in different regions of the North Atlantic, Platt et al. (1991) concluded that in general there is a poor correlation between biomass and production, specially at high latitudes. Our data indicate this is also the case for low latitudes, where the regression coefficient ($r^2$) between integrated chlorophyll and integrated production was <0.012. These results contrast with the relatively narrow range of P-E parameters utilized in satellite-based models of primary productivity where the ocean is partitioned in biogeochemical provinces (Platt et al. 1991, Sathyendranath et al. 1995) and argue against the traditional view that variability in pigment concentration is greater than that in phytoplankton physiology and growth (see Platt & Sathyendranath 1988). The high variability in the phytoplankton photosynthetic parameters and the relative uncoupling between the chlorophyll and the production distributions have important consequences for the estimation of global primary productivity using remote sensing measurements of ocean colour.

ularly in the tropical and equatorial regions, the temporal variability in phytoplankton photophysiology was markedly higher than that of phytoplankton abundance.

## DISCUSSION

### Variability of the photosynthetic parameters

The large spatial extent of the present study allowed us to evaluate the natural range of variability in the photosynthetic parameters of phytoplankton in the open ocean. The dynamic range of $P_m^B$ during our cruises was ~40, compared with ~18 and ~4 during

### Importance of phytoplankton biomass versus photophysiology

In their analyses of temporal variability of primary production in the oligotrophic ocean, Bidigare et al.

(1987) and Marra et al. (1992) were able to obtain good agreement between *in situ* measurements of photosynthesis and estimates based on irradiance and pigment concentrations only. However, these studies were restricted to relatively small regions and therefore did not provide evidence for the validity of their approach over large spatial scales. In this regard, Platt & Sathyendranath (1988) stressed that 'chlorophyll and light account for such a high proportion of the variance in primary production that the influence of second-order factors is often obscured'. We tried to test the applicability of this statement to our observations in the Atlantic Ocean by conducting a multiple regression analysis on the integrated productivity, using several physical, chemical and biological independent variables. Our analysis showed no significant relationship between irradiance and productivity and suggested a relatively minor importance of chlorophyll concentration, which explained only 5% of the variability in integrated production (Table 2). In contrast, phytoplankton photophysiology represented by $P_m^B$ accounted for 30% of the variability in integrated productivity. The small temporal changes in chlorophyll concentration in the oligotrophic regions, despite the observed variability in productivity, suggest an important role for zooplankton grazing in the control of phytoplankton standing stocks (e.g. Cullen et al. 1992a).

Our results imply that 2 water masses containing similar amounts of chlorophyll under similar irradiance conditions may support dramatically different rates of photosynthesis as a result of a change in the photosynthetic efficiency of phytoplankton. From the point of view of the estimation of global ocean productivity using satelllite imagery, these observations come to emphasize the reservations recently expressed by Behrenfeld & Falkowski (1997a) and Sakshaug et al. (1997) about the use of elaborate models that relate productivity to chlorophyll concentration via irradiance, focussing too much attention on pigments and neglecting the importance of $P_m^B$. Following these authors' recommendation that more attention needs to be paid to phytoplankton photophysiology, we look now to the factors that may explain the large-scale variability in the light-saturated rate of photosynthesis.

## What controls the changes in $P_m^B$?

The fact that we conducted the same study during 2 contrasting seasons allowed us to test the influence of irradiance on the latitudinal distribution of surface P-E parameters. While 2 opposite patterns were observed in the latitudinal distribution of incident irradiance during each cruise (Fig. 8A), the changes in surface $P_m^B$ followed the same geographical trend in both

seasons (Fig. 8B, C). We found no evidence suggesting that irradiance was controlling the latitudinal variations in surface $P_m^B$, which argues against the view that light is the major factor that regulates phytoplankton photosynthesis and growth in the ocean (Marra & Heinemann 1987, Langdon 1988). In this connection, Behrenfeld & Falkowski (1997b) concluded, after reviewing several productivity models, that irradiance explains a minor portion of the variability in depth-integrated primary production. It is noteworthy that if the September-October cruise (AMT-3) had not been conducted then the similar distributions of PAR and $P_m^B$ during AMT-2 would have misleadingly suggested that irradiance was regulating surface maximum photosynthesis. This in an illustration of the importance of the repeatability of the observations, which is neglected in oceanographic studies based on single cruises.

Contrary to previous studies (Harrison & Platt 1980, Harrison & Platt 1986, Behrenfeld & Falkowski 1997a among others), we did not find sea surface temperature (SST) to be a significant factor governing the variations in $P_m^B$ during the AMT cruises (Table 1). Although $P_m^B$ may have been limited by low temperature at high latitudes, the warm temperatures encountered in tropical latitudes were not accompanied by consistently elevated rates of normalized maximum photosynthesis. This lack of correlation between SST and $P_m^B$ is probably reflecting the inverse relationship existing between temperature and nutrient supply in the open ocean (Kamykowski & Zentara 1986, Sathyendranath et al. 1991), which would confound the effects of temperature over the enzymatically controlled, dark reactions of photosynthesis (Eppley 1972, Kirk 1993). Furthermore, most of our measurements fall within the non-linear region of the temperature versus maximum photosynthesis curve (Behrenfeld & Falkowski 1997a), where significant relationships are more difficult to define.

A comparison between the changes in the hydrographic regime along the transect and the distribution of the P-E parameters strongly suggests that nutrient availability was the main factor controlling the large-scale variability in $P_m^B$ (Figs. 1, 4 & 8). The variations in surface $P_m^B$ were inversely correlated to the variations in the depth of the nutricline, which serves as a proxy for nutrient flux into the upper mixed layer (Herbland & Voituriez 1979, Cleveland et al. 1989, Malone et al. 1993). Thus, an increase in $P_m^B$ was observed during both cruises in association with the upwelling area off Mauritania and lower values of $P_m^B$ were measured at the stations in the southern central gyre as compared to those in the northern central gyre, presumably reflecting the enhanced stability of the water column in the former. The connections between nutrient

supply and phytoplankton photophysiology have been stressed by previous studies reporting on the distribution of P-E parameters (Thomas 1970, Platt et al. 1992, Hood 1995) and the maximum quantum yield of photosynthesis (Cleveland et al. 1989, Falkowski et al. 1991, Geider et al. 1993, Babin et al. 1996). However, this is the first study where these relations are assessed over a large spatial scale that encompasses temperate and tropical pelagic ecosystems and also during 2 different seasons, thus providing broader evidence for the critical role of nutrients in the control of phytoplankton photosynthesis. These results are in line with our study of growth rates during the AMT cruises (Marañón et al. unpubl.), where we concluded that nutrient supply was limiting not only the biomass but also the growth rate of phytoplankton in the oligotrophic gyres. Our observations highlight the need to incorporate nutrients into models of productivity based on satellite data sets of chlorophyll (Falkowski et al. 1992, Balch et al. 1997).

When discussing the distribution of the P-E parameters in the ocean, 2 additional factors should be taken into account: (1) the variability in the cellular carbon to chlorohyll (C:chl) ratio and (2) the relation between vertical mixing and the photoadaptive responses of phytoplankton. In their review of the relation between the P-E parameters and the physiological state of phytoplankton, Cullen et al. (1992b) cautioned against the interpretation of low values of $P_m^B$ as indicating nutrient defficiency. Several studies with continuous cultures (Eppley & Renger 1974, Herzig & Falkowski 1989) have shown that $P_m^B$ can be independent of the nutritional status because physiological adjustment of the C:chl ratio tends to match the changes in growth rate (Laws & Bannister 1980). In our study, however, we did not observe any significant pattern of latitudinal variation in the C:chl ratio, which was mainly dependent on the sampling depth (Marañón et al. unpubl.). Estimates of surface C:chl ratios based on cell counts showed a relatively small degree of variability and averaged 79.9 ± 4.2 (± 1 SE) during the first 3 AMT cruises, compared to 39.6 ± 2.9 at the DCM. Clearly growth irradiance appears as a major factor in the regulation of cellular C:chl ratios (Taylor et al. 1997). Our data indicate that the latitudinal variations in surface $P_m^B$ did not result from changes in cellular chl content, but could have been due to nutrient-induced differences in the turnover time of the photosynthetic units (Herzig & Falkowski 1989).

In a surface mixed layer, the photoadaptive responses of phytoplankton depend on the relation between the time scale for vertical mixing and the time scale for physiological acclimation (Cullen & Lewis 1988). If vertical mixing of phytoplankton is fast in relation to their photoacclimation rate, the average irradiance experienced by the cells will be a function of the depth of the upper mixed layer. This provides a potential, indirect link between the depth of the nitracline (which we use as a proxy for nutrient supply, but also covaries with the depth of the upper mixed layer) and the irradiance which phytoplankton actually experience. It could then be argued that, in those regions where the depth of the nitracline was shallower (e.g. the upwelling area off NW Africa), phytoplankton were exposed, on average, to higher irradiance levels, therefore confounding a possible relation between nutrient supply and the P-E parameters. However, we observed a very high vertical variability in $P_m^B$ in tropical and equatorial waters, which indicates that the vertical mixing of phytoplankton was slow in relation to their photoadaptation rates (Lewis et al. 1984), even under the effects of the upwelling (see Fig. 7B, C). It follows that surface phytoplankton were experiencing saturating irradiances ($I_0 \geqslant I_k$ during most of the transect, see Figs. 6 & 8) irrespective of the depth of the mixed layer, which leads us to conclude that the observed relation between the depth of the nitracline and $P_m^B$ is a true reflection of the effect of nutrient supply rates on the physiology of phytoplankton.

## Temporal variability and productivity models

The predictive capacity of provincially based productivity models (Sathyendranath et al. 1995, Longhurst et al. 1995) depends on the extent to which the chosen photosynthetic parameters are representative of the physiological conditions of phytoplankton on each region at each time. However, the applicability of the biogeochemical province approach is jeopardized if temporal variations are so large as to override the differences between provinces. In their study of the physiological parameters of phytoplankton in the North Atlantic, Kyewalyanga et al. (1998) found that the parameters were more variable between seasons than between provinces. Similarly, we found during our study that the variability in $P_m^B$ between cruises was often larger than between provinces (Fig. 10). Furthermore, $P_m^B$ at the low latitude regions showed a much higher temporal variability than chlorophyll, which remained relatively constant. We have not yet been able to define the mechanisms responsible for these temporal changes in phytoplankton photophysiology, which are likely to be the result of a combination of physical and biological factors over large spatial scales. In particular, the role of heterotrophs in supplying regenerated nutrients (Longhurst & Harrison 1989), the importance of atmospheric inputs of nitrate and ammonia (Legendre & Gosselin 1989) and the dynamics of $N_2$ fixation (e.g. Karl et al. 1997) deserve

additional research. The interactions between physical forcing, nutrient fluxes and phytoplankton physiology (Balch et al. 1997) should be included in primary productivity models, which are unlikely to reproduce the natural variability in photosynthesis if they just focus on pigments and the light harvesting processes.

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