

# Phytoplankton chlorophyll *a* distribution and water column stability in the central Atlantic Ocean

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**Abstract** – The relationship between the vertical distribution of phytoplankton chlorophyll *a* and the physical structure of the upper central Atlantic Ocean was investigated based on results from a cruise across the tropical Atlantic (27° N to 36° S). The thermocline was very sharp and shallow in the northern part of the transect, off the coast of Mauritania and Senegal, and deepened progressively to reach > 150 m deep between 20° S and 30° S. There was a deep chl *a* maximum associated with the thermocline throughout the transect, reaching chl *a* concentrations up to 50 fold greater than those in surface waters. The chl *a* concentration was greatest off the NW African coast and declined towards the south, parallel to a progressive deepening of the chl *a* maximum closely tracking that in the thermocline. The maximal and the integrated chlorophyll *a* concentrations varied as the 1/2 and 1/5 power of the surface chl *a*. The correlation between the depth where the maximum chl *a* concentration was observed and the depth where the thermocline was strongest accounted for 87.2 % of the variance in the depth of the maximum chl *a* concentration along the transect. The maximum chl *a* concentration tends, on average, to be shallower than the depth where the maximal vertical stability is found when the thermocline deepens below 60 m depth, and the maximum chl *a* concentration tended to decline as the depth at which the Brunt-Väisälä buoyancy frequency was highest increased. Because the position of the thermocline in the tropical Atlantic Ocean may be predicted from climatology, the results reported may be useful to improve the predictions on phytoplankton biomass and production. © Elsevier, Paris / Ifremer / Cnrs / Ird

**chlorophyll / phytoplankton / water column stability / central Atlantic Ocean**

**Résumé** – Répartition de la chlorophylle *a* du phytoplancton et stabilité de la colonne d'eau dans le centre de l'océan Atlantique. La répartition verticale de la chlorophylle *a* du phytoplancton est comparée à la structure physique de la colonne d'eau (fréquence de Brunt-Väisälä) dans l'Atlantique tropical, entre 27° N et 36° S. La thermocline, très marquée et peu profonde dans le nord de la radiale, au large des côtes de Mauritanie et du Sénégal, plonge progressivement au-delà de 150 m entre 20° S et 30° S. La teneur maximale en Chl *a* est associée à la thermocline, où elle peut être 50 fois plus forte que dans les eaux de surface ; le maximum prend sa plus grande valeur au large de la côte nord-ouest de l'Afrique et décroît progressivement vers le sud en plongeant avec la thermocline. Les concentrations maximale et intégrée varient selon une loi-puissance 1/2 ou 1/5 de la concentration en surface. La corrélation entre la profondeur du maximum de Chl *a* et la profondeur de la thermocline est de 87,2 % tout au long de la section. La maximum de Chl *a* se trouve, en moyenne, à une profondeur inférieure à celle de stabilité maximale lorsque la thermocline plonge au-delà de 60 m, et la concentration maximale en Chl *a* diminue lorsque augmente la profondeur du maximum de la fréquence de Brunt-Väisälä. Comme la profondeur de la thermocline dans l'océan Atlantique tropical peut être déterminée à partir de la climatologie, les résultats présentés ici contribuent à une meilleure prédiction de la biomasse phytoplanctonique et de la production primaire. © Elsevier, Paris / Ifremer / Cnrs / Ird

**chlorophylle / phytoplancton / stabilité verticale / océan Atlantique central**

## 1. INTRODUCTION

The distribution of phytoplankton in the permanently stratified tropical ocean is characterized by low biomass in surface waters and the presence of a subsurface chlorophyll *a* maximum [3, 10, 22]. The depth at which subsurface chl *a* maxima (DCM) develop varies widely, and may reach considerable depths [3, 4, 7, 16, 19]. Because a disproportionate fraction of the phytoplankton biomass and production occurs at the DCM in these waters, estimates derived from remotely-sensed surface properties may underestimate the areal biomass and production of phytoplankton [3, 22]. As a consequence, there is great interest, stemming from both practical and theoretical concerns, in the prediction of the vertical distribution of phytoplankton biomass in the tropical ocean.

The causes for the development of a DCM appear to be multiple, involving the interaction of physical and biological processes [21]. The nutrient depletion that characterizes the upper layer of permanently stratified tropical oceans renders primary production closely dependent on the diffusive nutrient flux across the thermocline [12–14]. Hence, algal cells located closer to the thermocline would benefit more directly from the diffusive flux before it is diluted within the upper layer [5, 9, 12, 13]. In addition, the density stratification at the thermocline further promotes the accumulation of algal cells [1]. While the bottom of the mixed layer represents an appropriate environment for algal nutrition, it is also a shaded one, triggering adaptative responses by the algae. An increase in the chl *a* per cell due to photoadaptation at this shaded ambient has been identified as a possible explanation for the development of the DCM [1, 2, 19, 20]. The importance of these adaptative responses has been, however, overestimated due to the neglect of picophytoplankton, whose high abundance in the DCM has been described recently [4, 7]. In summary, the depth and size of the DCM are believed to be largely constrained by the trade off between the stimulatory effect of an adequate nutrient supply from the diffusive flux across the thermocline, and the limitations on growth imposed by the shaded nature of the environment [7, 15].

The increasing understanding of the factors that determine the occurrence of deep chlorophyll maxima in the tropical and temperate ocean has led to the development of numerical models that adequately reproduce the observed vertical distributions [8, 11, 17, 21]. These models are, however, highly demanding in terms of the number and complexity of input parameters required

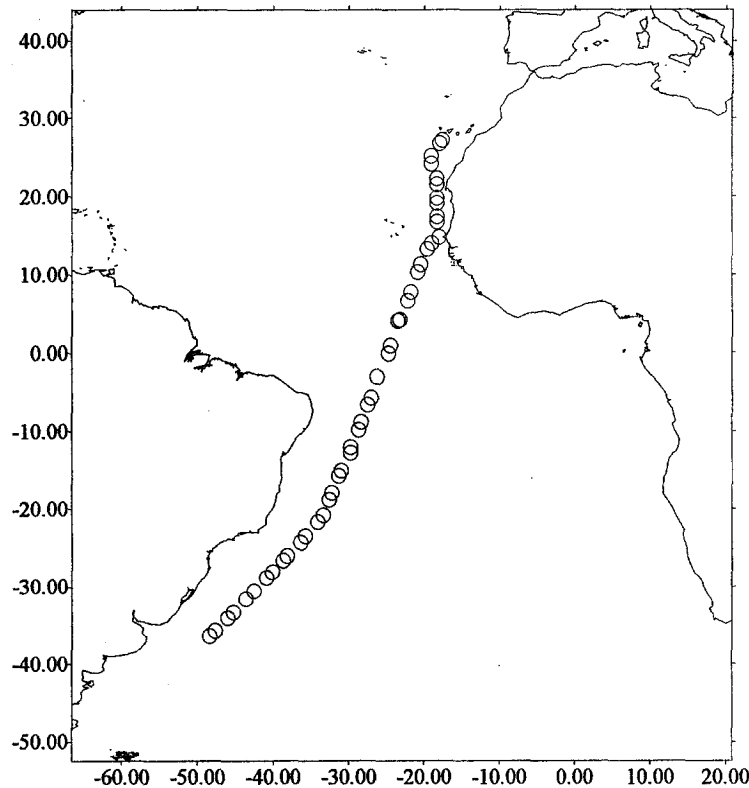
(e.g. up to 13 [21]) and are, therefore, more useful for heuristic than for predictive purposes. There is, therefore, a need to produce simple, reliable models predicting the vertical distribution of phytoplankton biomass in the tropical ocean. These models would, once available, improve our ability to predict ecosystem structure and help correct present flaws in the prediction of phytoplankton biomass and production.

Here we provide a simple statistical analysis of the relationship between the vertical distribution of phytoplankton chl *a* and the physical structure of the upper central Atlantic Ocean. Although empirical by nature, the relationships developed are based on an appropriate understanding of the casual link between the dependent and independent variables and, once tested, will allow the prediction of the vertical distribution of phytoplankton biomass from available seasonal models of the upper ocean. Previous research in the area has suggested close relationships between the vertical distribution of chl *a* and the physical structure of the water column [9, 10]. These observations lead us to hypothesize that (i) the depth of the chl *a* maximum should be coupled with the depth of the upper thermocline, (ii) the size of the vertical chl *a* maximum should decline, due to increased shading, as the depth of the thermocline increases, and (iii) the increase in phytoplankton biomass at the DCM relative to that in the surface water must be greatest when the thermocline is shallow, which leads to a better balance between the benefit of the proximity to the diffusive nutrient flux across the thermocline and that of an optimal illumination for algal growth.

The empirical relationships hypothesized were developed based on data collected in the *Latitude II* cruise along the central Atlantic Ocean (27° N to 36° S, *figure 1*). The transect made offered optimal opportunities to test the relationships hypothesized because the entire cruise spanned areas of nutrient-depleted surface waters with upper thermocline depths ranging from relatively shallow (23 m) to considerably deep (230 m).

## 2. MATERIALS AND METHODS

This study was conducted during the *Latitude II* cruise across the central Atlantic Ocean (from the Canary Islands (Spain) to Mar del Plata (Argentina, *figure 1*), aboard the Spanish R.V. *BIO-Hespérides*. The cruise was conducted between 21 October and 16 November 1995, and 46 oceanic stations were occupied along the studied



**Figure 1.** The location of the stations sampled (21 Oct. to 16 Nov. 1995) in the tropical Atlantic Ocean.

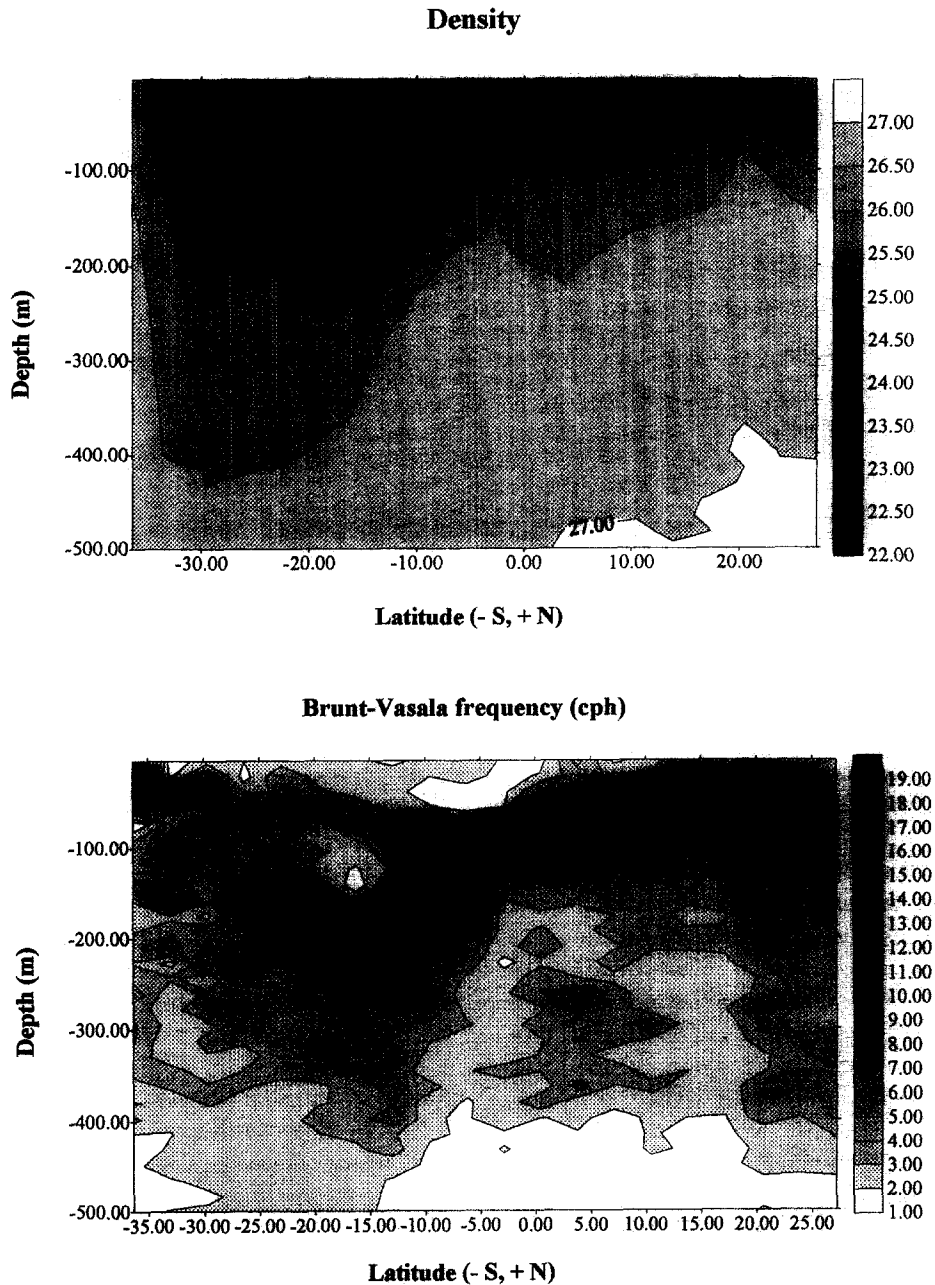
area (figure 1). At each station, the physical structure of the water column was profiled from the surface down to 1000 m, with a vertical resolution of 0.1 m, using a Sea-Bird MARK V or MARK III CTD fitted with a fluorometer. Salinity and temperature estimates derived from both CTD were calibrated during the cruise using direct salinity measurements from a Guildline Autosol salinometer calibrated with IAPSO standard seawater (34.993), and a highly accurate reversible thermometer, respectively. The vertical distribution of phytoplankton biomass, represented by the chl *a* concentration, was measured in water samples collected using 12 L Niskin bottles attached to the CTD by a Rosette sampler system. Subsamples of 250 mL from each sample were filtered through Whatman GF/F filters for fluorometric analysis of chl *a* concentration [18]. The filters were homogenized and kept refrigerated in the dark while pigments were extracted in 90 % acetone for ca. 1 h. Fluorescence was measured, following extraction, in a Turner Designs fluorometer.

Profiles of underwater spectral irradiance were obtained at the stations using a Licor LI-1800UW spectroradiometer, and integrated over 400–700 nm to estimate the irradiance within the photosynthetically active radiation (PAR) band.

The vertical distribution of the chlorophyll *a* concentration at each station was constructed based on samples collected at 18 different depths, allocated on the basis of the signal derived from the fluorometer attached to the CTD. Observations from a previous cruise across the area indicated that induced fluorescence tends to overestimate the depth of the DCM (Duarte, unpubl. observations), so that waters somewhat shallower than the deep fluorescence maximum were also sampled. Moreover, although induced fluorescence represented an appropriate proxy of phytoplankton biomass within any one station, the relationship between induced fluorescence and chl *a* concentration varied greatly during the cruise, due to differences in fluorescence yield of the different communities present

across the wide area studied. Chlorophyll *a* concentrations were, however, found to be adequate descriptors of phytoplankton biomass, as reflected in good correlations with microscopically-determined phytoplankton biovolume in these stations (Agustí, in prep.).

Vertical profiles of salinity and temperature derived from the (corrected) CTD data were screened for errors. We then calculated the density anomaly,  $\sigma_t$ , from temperature and salinity following the algorithms of Fofonoff and Millard [6], and then averaged the data at 1 m intervals.



**Figure 2.** Contour plot of the vertical variation in density (upper panel) and in the Brunt-Väisälä buoyancy frequency (lower panel) along the meridional transect across the tropical Atlantic Ocean.

The vertical gradient in  $\sigma_t \left( \frac{\Delta \rho}{\Delta z} \right)$  was then used to calculate the Brunt-Väisälä buoyancy frequency ( $N$ ) according to the equation:

$$N = \frac{-g}{\rho} \frac{\Delta \rho}{\Delta z} \quad (1)$$

where  $g$  is the gravitational acceleration, and  $\rho$  is the mean density averaged over  $\Delta z$  depth interval. The Brunt-Väisälä buoyancy frequency represents the strength of the density stratification and, therefore, the stability of the water column. The depth at which the Brunt-Väisälä buoyancy frequency was estimated to be maximal represents, therefore, the depth of maximum stability, and was selected to represent the thermocline depth.

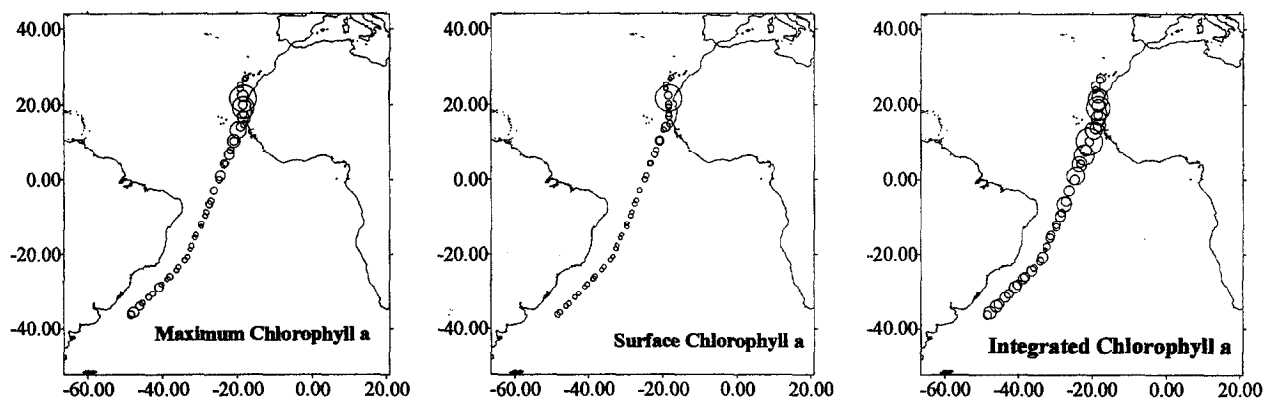
The extent of heterogeneity in the vertical distribution of chl  $a$  was represented by the ratio between the surface and the maximum concentrations. The hypothesized relationships between chl  $a$  distribution and the depth of maximum vertical stability was modeled using least-squares regression analysis.

### 3. RESULTS

The waters studied were stratified along the entire transect across the tropical Atlantic Ocean (figure 2). The thermocline was very steep in the northern part of the transect, off the coast of Mauritania and Senegal, where there was evidence of upwelling (figure 2). The Guinea

dome was clearly reflected in the density profiles, with a secondary doming of the pycnoclines being evident near the Equator. In general, the thermocline deepened progressively from the Canary Islands towards the Equatorial dome, and then deepened considerably to constitute a weakly stratified water column, with a very gradual increase in density with depth between 20° S and 30° S (figure 2). The change in the Brunt-Väisälä buoyancy frequency with depth clearly reflected the N-S deepening of the thermocline along the transect, and an associated decline in the maximal Brunt-Väisälä buoyancy frequency, indicative of a reduction in stability as the thermocline deepened (figure 2). The deep thermocline observed south of 15° S was weak and ill-defined.

Chlorophyll  $a$  concentrations ranged widely along the meridional transect, with the highest concentrations found in the upwelling area off NW Africa, as well as in the southernmost waters sampled, whereas chl  $a$  concentrations and areally-integrated chl  $a$  pools were much lower in equatorial waters (figure 3). There was a clearly defined deep chlorophyll maximum throughout the transect, which closely followed the thermocline (figure 4). The chl  $a$  maximum deepened towards the subtropical gyre, and was located at a depth receiving, on average, 3%  $\pm$  0.5 ( $\pm$  SE) of the irradiance incident on the surface. The variability in surface and maximal chl  $a$  concentration among stations ( $>$  10-fold) was much greater than that in areally-integrated pools (4-fold, figure 3). The reason for this difference was that the photic layer ( $>$  1% of surface irradiance) extended much deeper in unproductive waters, allowing the development of phytoplankton communities across a thicker water



**Figure 3.** The variation in the maximal chl  $a$  concentration, the chl  $a$  concentration in surface waters, and the integrated chl  $a$  pool along the tropical Atlantic Ocean. The diameter of the circles is scaled to the value of the variable represented: min. and max. diameters for the maximal and surface chl  $a$  concentrations are 0.15–2.5 and 0.015–2.0 mg m<sup>-3</sup>, respectively, and those for the integrated chl  $a$  pool are 15–60 mg m<sup>-2</sup>.

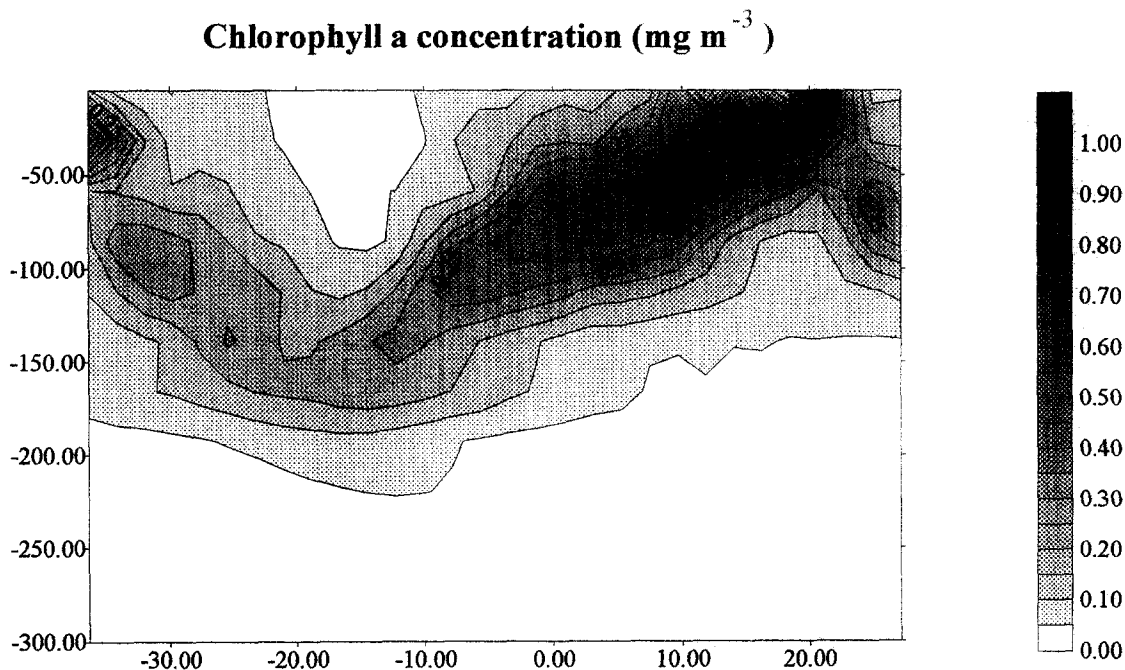


Figure 4. Contour plot of the vertical variation in the chl *a* concentration along the meridional transect across the tropical Atlantic Ocean.

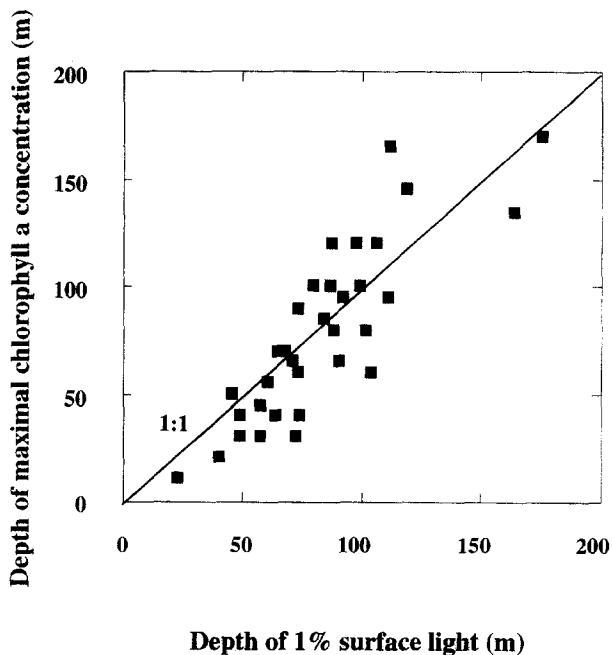


Figure 5. The relationship between the depth of the maximal chl *a* concentration and the depth at which the 1% of the light (PAR) in surface was found. The solid line represents the 1:1 line.

column. This is indicated by the close relationship ( $R^2 = 0.70$ ,  $P < 0.0001$ ) between the depth of the maximum chl *a* and the depth receiving 1 % of the irradiance incident in the surface (figure 5).

Closer examination of the relationships between the maximal (Chl  $a_{max}$ ,  $mg\ m^{-3}$ ) and the integrated (Chl  $a_{int}$ ,  $mg\ m^{-2}$ ) chlorophyll *a* concentrations and the surface chl *a* (Chl  $a_{sur}$ ,  $mg\ m^{-3}$ ) concentration (figure 6) revealed these relationships to be strongly non-linear, as described by the regression equations:

$$Chl\ a_{max} = 1.36 \cdot Chl\ a_{sur}^{0.49 \pm 0.06}$$

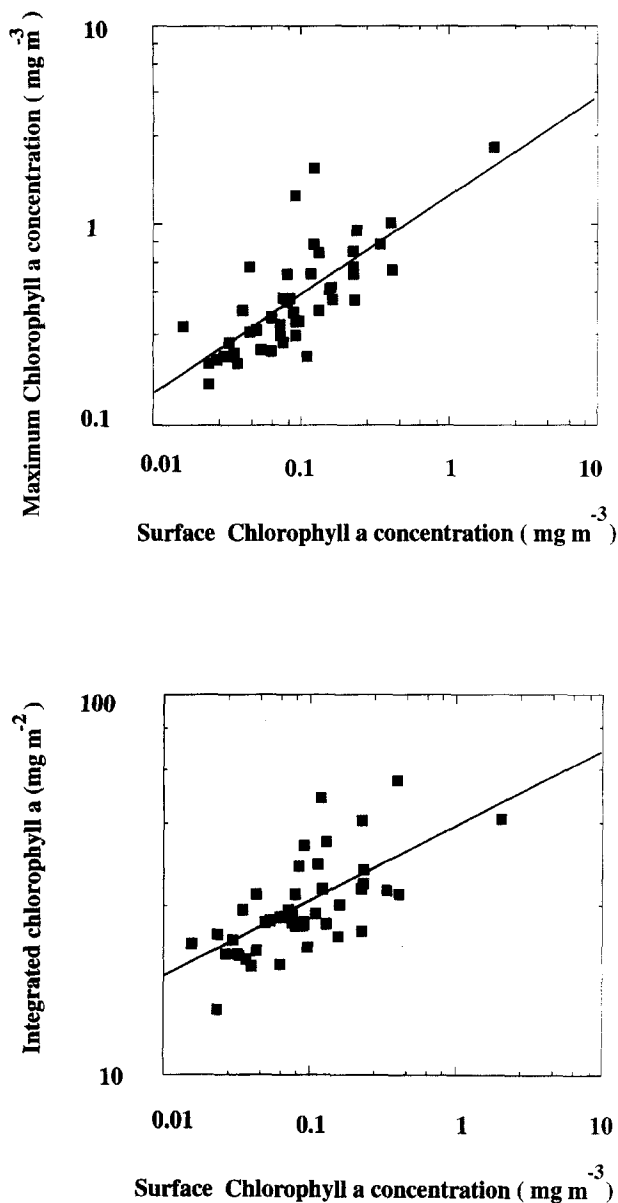
( $R^2 = 0.55$ ,  $N = 46$ ,  $P < 0.0001$ )

and

$$Chl\ a_{int} = 43.6 \cdot Chl\ a_{sur}^{0.20 \pm 0.03}$$

( $R^2 = 0.55$ ,  $N = 46$ ,  $P < 0.0001$ )

which show that the maximal and the integrated chlorophyll *a* concentrations change as the 1/2 and 1/5 power of the surface chl *a*. Hence, both the maximal and, particularly, the integrated chl *a* change slower than the surface concentration does. The difference between the chl *a* concentration in the DCM and that in the surface waters was



**Figure 6.** The relationships between maximal chl *a* concentration (upper panel) and the integrated chl *a* pool (lower panel) with the chl *a* concentration in surface waters. The solid lines represent the fitted regression equations.

greatest (Chl  $a_{\max}$  over 50 fold greater than Chl  $a_{\text{sur}}$ ) just south of the Equator (figure 7), where examination of the density profiles revealed doming of intermediate waters (figure 2), which bring nutrient-rich waters close to the photic layer, allowing the development of a deep, dense

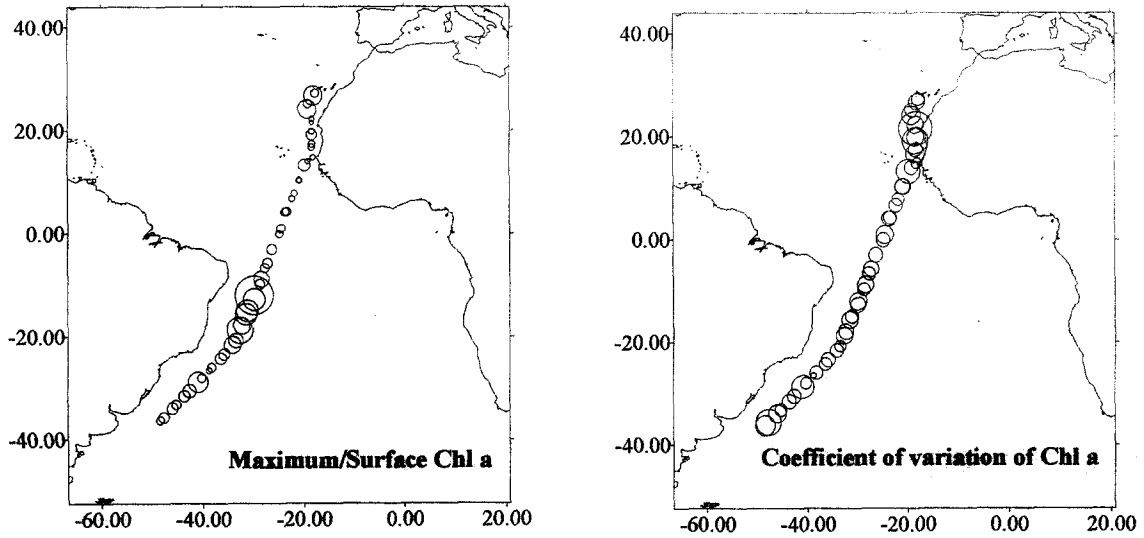
phytoplankton layer overlain by highly unproductive waters (see below). The extent of vertical heterogeneity in chl *a* concentrations was best reflected in the coefficient of variation of the concentration over depth (i.e. the ratio between the standard deviation and the mean concentration of the chl *a* profile at each station), which revealed the vertical distribution of chl *a* concentration in the tropical waters studied to be skewed (i.e. coefficient of variation  $> 0.7$ , figure 7). This inequality in chl *a* distribution with depth was greatest in the waters supporting the highest chl *a* concentrations (figure 7).

The chl *a* concentration was greatest off the NW African coast, where the thermocline was shallowest and upwelling was evident, and declined towards the south, parallel to a progressive deepening of the chl *a* maximum (figure 4), thereby closely tracking the change in the thermocline (figure 2). The close relationship between the distribution of chl *a* and the stability of the water column was apparent from the examination of the vertical variability of these properties along the stations sampled, where the depth of maximal induced fluorescence (a proxy of chl *a* concentration) corresponded to that of maximal vertical stability (figure 8). There were two stability maxima south of  $20^{\circ}$  S, but the DCM was associated with the deeper one, which was also the absolute maximum stability in the upper water column.

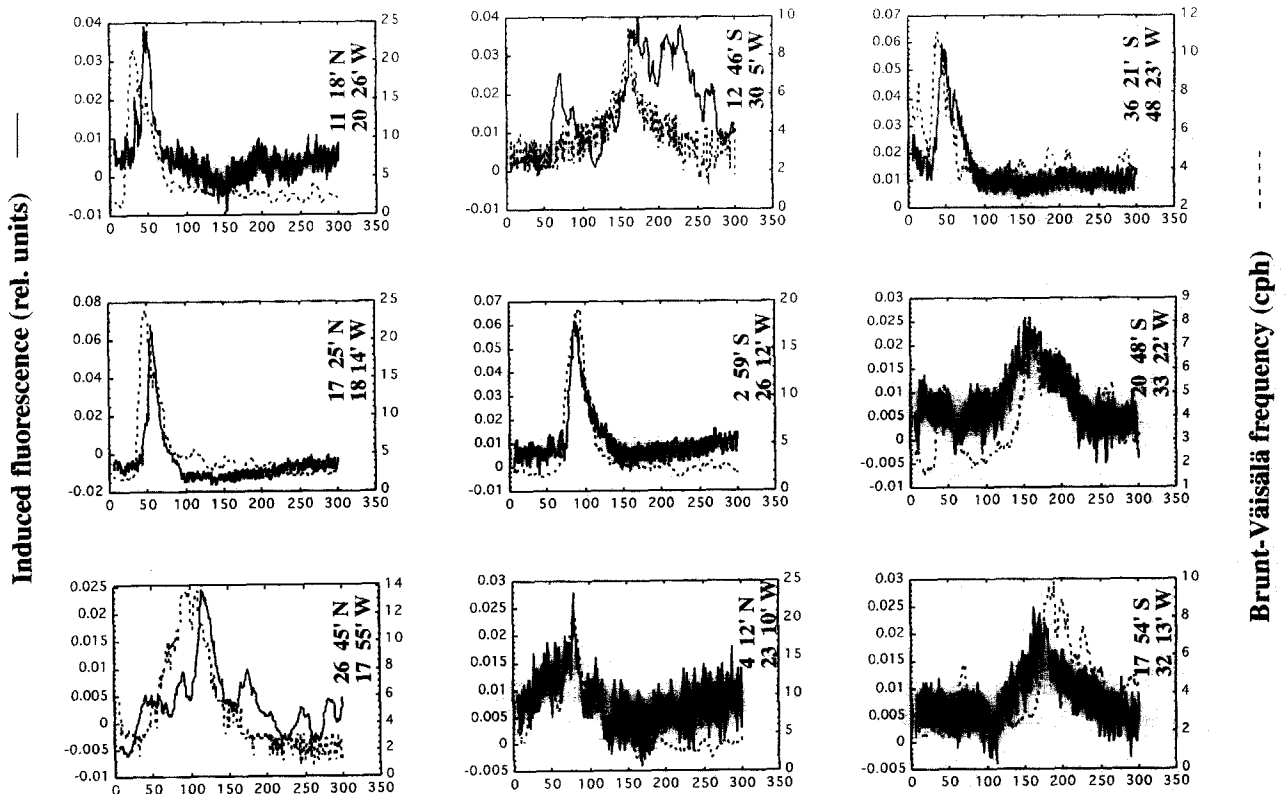
There was, therefore, a strong correlation ( $P < 0.0001$ ) between the depth where the maximum chl *a* concentration ( $Z_{\max \text{ Chl } a}$ ) was observed and the depth where the thermocline was strongest (i.e. the depth where the Brunt-Väisälä buoyancy frequency was highest,  $Z_{\max N}$ , figure 9). This relationship was best described by the regression equation,

$$Z_{\max \text{ Chl } a} (\text{m}) = 15.62 (\pm 4.48) + 0.64 (\pm 0.037) Z_{\max N} (\text{m}) \quad (2)$$

which accounted for 87.2 % of the variance in the depth of the maximum chl *a* concentration along the transect. The equation indicates that the maximum chl *a* concentration tends, on average, to be shallower than the depth where the maximal vertical stability is found when the thermocline deepens below 60 m depth. The vertical distance between the thermocline (as depicted by the depth of maximal Brunt-Väisälä buoyancy frequency) and the overlying layer of maximum chl *a* concentration increases from 13 m when the thermocline is located 80 m deep, to over 50 m when the thermocline is located at 200 m depth, as observed between  $20^{\circ}$  S and  $30^{\circ}$  S (figure 2).

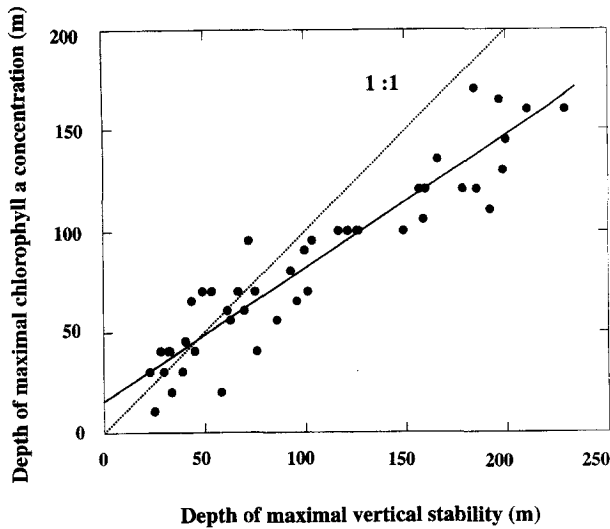


**Figure 7.** The vertical variation in the chl *a* concentration along the tropical Atlantic Ocean, as represented by the ratio between the maximal and surficial chl *a* concentrations, and the coefficient of variation of the profile of chl *a* concentration (18 depths sampled per station). The diameter of the circles is scaled to the value of the variable represented: min. and max. diameters for the maximal to surface chl *a* concentration ratio and the coefficient of variation of the profile of chl *a* concentration are 1–60 and 0.3–1.8, respectively.



**Figure 8.** Vertical profiles of induced fluorescence (a proxy of chl *a* concentration) and the Brunt-Väisälä buoyancy frequency, which indicates the vertical stability of the water column, in a subset of the stations sampled along the meridional transect studied.





**Figure 9.** The relationship between the depth where the maximum chl *a* concentration was observed and the depth of maximal vertical stability (i.e. where the Brunt-Väisälä buoyancy frequency was highest) along the meridional transect across the tropical Atlantic Ocean. The solid line represents the fitted linear regression equation, while the dotted line represents the 1:1 line.

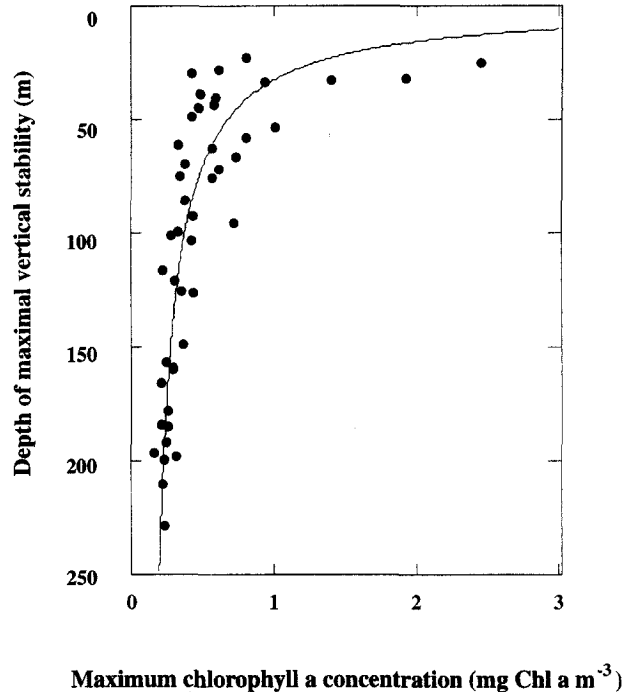
The maximal chl *a* concentration observed at the stations sampled declined as the depth where it was observed increased (figure 4), leading to a strong ( $P < 0.0001$ ) inverse relationship between the maximum chl *a* concentration and the depth where the Brunt-Väisälä buoyancy frequency was highest (figure 10), as described by the inverse equation,

$$\text{Chl } a_{\max} (\text{mg Chl } a \text{ m}^{-3}) = 0.078 + 29.9 / Z_{\max N} (\text{m}) \quad (3)$$

which accounted for 52 % of the variance in the maximum chl *a* concentration. Moreover, the vertical heterogeneity in chl *a* concentration was also associated with the depth where the Brunt-Väisälä buoyancy frequency was highest. The relative difference between the maximum and surface chl *a* concentration increased as the thermocline established deeper.

#### 4. DISCUSSION

The central Atlantic presents a distinct latitudinal pattern in the vertical density distribution, and the associated depth of the thermocline. The presence of a dome, the Guinea Dome, which results from the deflection in the direction of major currents off NW Africa is a character-



**Figure 10.** The relationship between the maximum chl *a* concentration observed at each station and the depth of maximum vertical stability (i.e. where the Brunt-Väisälä buoyancy frequency was highest) along the meridional transect across the tropical Atlantic Ocean. The solid line represents the fitted inverse equation.

istic feature of the (eastern) tropical Atlantic [23]. There is also a secondary doming of the pycnoclines at the Equator, resulting from divergence of water masses there, but where the thermocline remains deeper than in the Guinea Dome. The thermocline deepens and becomes poorly defined towards the south subtropical gyre located between  $20^\circ \text{ S}$  and  $30^\circ \text{ S}$ . As the depth of the thermocline increased, the stability of the water column declined, so that the domes off Guinea and at the Equator were characterized by sharp, highly stable thermoclines, while the deep thermocline in the subtropical gyre ( $20^\circ \text{ S}$  and  $30^\circ \text{ S}$ ) was a weak one.

These differences have important biological consequences, induced by associated differences in the diffusive flux of nutrients to the biogenic zone. On the one hand, the sharp thermocline is associated with similarly sharp gradients in nutrient concentrations, leading to a comparatively high diffusive flux to the overlying waters (Duarte et al., in prep.). On the other hand, the higher diffusive flux across sharp, shallow thermoclines is dis-

tributed within a thinner overlying volume of water, leading to an even higher volumetric nutrient supply (Duarte *et al.*, in prep.). As a consequence, there was, as observed in the past [9, 10], a close coupling between the structure of the thermocline and that of the phytoplankton communities.

The distribution of phytoplankton biomass was characterized by the presence of a deep chl *a* maximum along the transect. This DCM closely followed the thermocline, its concentration declining as the thermocline deepened towards the subtropical gyre, and was located at a depth receiving, on average,  $3\% \pm 0.5$  ( $\pm$  SE) of the irradiance incident on the surface (Agustí and Varela, unpubl. data). The coupling between the depth of the DCM and that of maximum stability was close in the dome areas and where the thermocline lay above 60 m. However, the DCM was positioned above the thermocline as this deepened, overlying the thermocline by about 50 m in the gyre area. Moreover, the concentration of phytoplankton within the DCM was closely associated to its depth, being greater in the dome area and comprising very sparse phytoplankton communities in the gyre areas. As a result, areally-integrated chl *a* concentrations remained more conservative along the transect than the volumetric concentrations did, leading to a strongly non-linear relationship between the integrated and the surface chl *a* concentrations. The prediction of the areal phytoplankton biomass and production of the tropical Atlantic Ocean from surface chl *a* concentration requires, therefore, the use of non-linear scaling terms.

The observations of the relationship between the depth of the thermocline and the depth and magnitude of the chl *a* are consistent with the hypothesized existence of a trade off between the beneficial effect of an adequate nutrient supply near the thermocline and the reduction of growth as light declines with depth [7, 15]. Although overlain by a sparser phytoplankton community, the considerable thickness of the water column (150 m) above the DCM of the gyre areas involves a substantial absorption of light by seawater, which dominates light absorption in these oligotrophic oceanic areas. As a consequence, the compensation depth for phytoplankton growth is well above the thermocline (about 50 m higher) in the gyre areas, preventing the development of a DCM associated with the thermocline.

The results obtained support our hypothesis that the depth and magnitude of the chl *a* maximum should be coupled with the depth of the upper thermocline. The average irra-

diance received at the depth of maximum chl *a* was  $3\% \pm 0.5$  ( $\pm$  SE) of that incident at the surface, slightly higher than the value of 1% of the surface irradiance conventionally used to define the limit of the biogenic layer. Previous attempts to establish simple patterns in the depth of the DCM focused on correlations between the depth of the nitracline and the depth of the DCM [10]. While significant correlations were reported for the eastern tropical Atlantic [10], the DCM often lay well above the nitracline, which tends to be located below the depth of maximum stability (Duarte *et al.*, submitted), in our study.

While there is support in the literature for the generality of our results [9, 10], there have also been unsuccessful attempts at finding similar relationships [5]. This contrast does not necessarily involve an inconsistency with our results, because they occurred in seasonally stratified areas, where the extent of nutrient limitation may be lower than that in the permanently stratified ocean, and where higher algal biomass in surface waters raises the compensation irradiance well above the depth of the seasonal thermocline. In addition, a poor correlation between the depth of the DCM and the depth of maximum water column stability may also result from the examination of relatively uniform areas of the ocean, where both the thermocline depth and that of the DCM show little variation. The standard error of the prediction of the depth of the DCM from the depth of maximum water column stability was  $\pm 15.2$  m, so that no significant correlation would be observed when comparing waters presenting thermocline depths ranging by less than about 30 m in depth.

In summary, our results provide support for the existence of a relationship between the size and depth of the chl *a* maximum and the depth and strength of the thermocline in the permanently stratified tropical ocean. However, these results do not imply that the depth and strength of the thermocline exert a direct control on the DCM, for the DCM depends on multiple processes and trade off [1, 5, 7, 9, 12, 13, 15, 21]. The importance of these multiple controlling processes should be, in turn, linked to the position and strength of the thermocline, rendering these reliable, simple predictors of the size and depth of the chl *a* maximum. Because the position of the thermocline in the stratified tropical ocean may be predicted from climatology, the results reported may be useful for improving predictions on phytoplankton biomass and production.

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