Does the nutrient enrichment of the equatorial upwelling influence the size structure of phytoplankton in the Atlantic Ocean ?

Chlorophyll
Phytoplankton
Equatorial upwelling
Atlantic

Chlorophylle
Phytoplancton
Upwelling équatorial
Atlantique

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ABSTRACT

A study of the size structure of chlorophyll *a* (Chl*a*) covering the major part of the equatorial Atlantic Ocean from 5°N to 5°S leads to the conclusion that seasonal nutrient enrichment in the open Eastern equatorial Atlantic does not drastically affect the size distribution of the primary producers : 90 % of the total Chl*a* is everywhere contained in the < 10 μm fraction on the average. In the coastal upwelling near Dakar, this percentage is less than 60 %, for the same range of Chl*a* concentrations. In the equatorial region the percentage of < 1 μm Chl*a* is the same in the deep chlorophyll maximum located at the top of the nitracline during the warm season and in the subsuperficial maximum of the upwelling. Therefore, from an ecological point of view, the term "upwelling" is misleading : the seasonal equatorial upwelling seems to be nothing other than the movement towards the surface of the deep chlorophyll maximum, with no appreciable increase of its value and some slight modification of its trophic organization.

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RÉSUMÉ

La présence de l'upwelling dans l'Océan Atlantique équatorial influence-t-elle la dimension des cellules du phytoplancton ?

Une étude de la structure de la taille des particules contenant la chlorophylle *a* (Chl*a*) recouvrant la majeure partie de l'Océan Atlantique équatorial de 5°N à 5°S, conduit à la conclusion que l'enrichissement saisonnier en sels nutritifs dans l'Atlantique équatorial oriental n'affecte pas de façon importante la distribution de la taille des producteurs primaires : 90 % de la Chl*a* est en moyenne contenue dans des cellules inférieures à 10 μm. Dans l'upwelling côtier près de Dakar, et pour la même gamme de concentration en Chl*a*, ce pourcentage est inférieur à 60 ; le pourcentage de Chl*a* < 1 μm est le même dans le maximum profond situé au sommet de la nitracline pendant la saison « chaude » et dans le maximum subsuperficiel de l'upwelling (saison « froide »). Par conséquent, d'un point de vue écologique, le terme « upwelling » est trompeur : l'upwelling équatorial semble n'être rien d'autre que la remontée en surface du maximum profond de chlorophylle sans augmentation appréciable de sa valeur et avec des modifications mineures de son réseau trophique toujours dominé par des organismes de très petite taille.

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INTRODUCTION

The trophic organization of pelagic ecosystems has long been recognized as an important consideration in assessing the ultimate yield of the oceans in terms of fisheries. It is generally agreed that the larger the plant cells at the beginning of the food chain the fewer the trophic levels that are required to convert the organic matter into forms useful to man (Ryther, 1969 ; Landry, 1977). Therefore, the first factor to be examined in this context is the size of photosynthetic organisms.

Coastal environments, and especially upwellings where nutrients are available in high concentration, are characterized by episodic pulses in phytoplankton biomass caused by large-celled diatoms and dinoflagellates or chain-forming diatoms that are retained by 10-20 μm mesh screens (*i.e.* netplankton). Accordingly, the volume of fish production in the coastal upwellings would appear to result not only from higher values of net primary production, but also from the small number of trophic levels between phytoplankton and fish.

In contrast, small solitary forms passed by 10-20 μm mesh screens (*i.e.* nanoplankton) account for most phytoplankton biomass in the open ocean, where about 80 % of the global marine phytoplankton production occurs (Malone, 1980). Recently, it has become increasingly apparent that very small organisms less than 2 μm in diameter called " picoplankton " (Sieburth *et al.*, 1978) contain an important fraction of the autotrophic biomass comprising cyanobacteria (Johnson, Sieburth, 1979) and eucaryotes (Johnson, Sieburth, 1982) in both the tropical and subtropical open ocean (Burney *et al.*, 1982 ; Li *et al.*, 1983 ; Platt *et al.*, 1983 ; Herbland *et al.*, 1985 ; Davis *et al.*, 1985).

Results presented here support the hypothesis that vertical motion in the equatorial upper Atlantic does not disrupt the size structure of the phytoplankton community. In other words, the expression " upwelling " does not, from a biological point of view, have the same meaning in the coastal and the open Atlantic Ocean.

MATERIAL AND METHODS

Data were collected during the cruises FOCAL 4, 6 and 8 respectively in July-August 1983, January-February 1984 and July-August 1984. For comparison, some samples were collected near Dakar (Senegal) during the period of upwelling (early 1985).

The fluorometric method used for chlorophyll *a* analysis has been described in detail elsewhere (Herbland *et al.*, 1985). 100 % methanol was used for extraction instead of 90 % acetone. This allows a total and rapid extraction without grinding and avoids the centrifugation step (Holm-Hansen, Riemann, 1978). Nuclepore polycarbonate filters (porosities of 10 μm and 1 μm in the present study) were used for fractionation. Total chlorophyll *a* was measured on Whatman GF/F fibre glass filters. These filters have approximately the same capacities of retention as the 0.2 μm Nuclepore polycarbonate filters (Li *et al.*, 1983, and unpublished data).

RESULTS

Influence of the equatorial upwelling on the Chl*a* distribution

Results presented in Figure 1 (sections at 23 and 4°W) show clearly that seasonal variations of the vertical distribution of nitrate affect the Chl*a* distribution. In January 1984 (*i.e.* during " warm season "), the bulk of Chl*a* was found in a layer about thirty metres thick located within the upper part of the nitracline (Fig. 1 *a*). This is the typical tropical structure as described by Herbland and Voituriez (1979), in which the deep chlorophyll maximum (DCM) is principally governed by turbulent mixing and nutrient supply rate from below, with an active balance of nitrate fluxes (Cullen, 1982 ; Abbott *et al.*, 1984). In July 1984 (*i.e.* during the " cold season "), the vertical motion of the nitracline causes the rising of the DCM which reached the surface between 0°30N and 3°30S (Fig. 1 *b*). It must be noted that at 4°W, in July 1984, the nitracline did not reach the surface, except at 3°S, when a few tenths (0.34-0.39 μgat l^{-1}) were measured in the 0-30 m layer. But the nitracline was close to the surface and probably induced a phytoplankton development that reached it.

Size structure of Chlorophyll *a*

Netplankton (> 10 μm)

Size separations on a 10 μm filter were carried out at 9 stations for 8-10 levels. Four representative structures are selected in Figure 2, from the weak and deep chlorophyll maximum located at the bottom of the nitrate-depleted layer (but not uniform in temperature) at 35°W (Fig. 2 upper left) to the typical Chl*a* distribution in the upwelling with values greater than 1 μg.l^{-1} in the subsurface layer (Fig. 2 bottom right). It is clear that the percentage of > 10 μm Chl*a* rarely exceeds 15 %. Similarly, the percentage of > 10 μm Chl*a* is not affected by the total Chl*a* value (Fig. 3) : the percentate of netplankton does not increase with increasing total Chl*a* values.

In contrast, for the same range of Chl*a* concentrations (0-2 μg.l^{-1}), the percentage of < 10 μm Chl*a* is significantly lower in the surface upwelled water near Dakar. Moreover the percentage seems to slowly decrease when the total Chl*a* values increase.

Picoplankton (0.2-1 μm)

On Figure 4, we have selected 4 categories of samples according to their position in the water column and in the nutrient structure. Although there is a small overlapping it clearly appears that the deep and weak chlorophyll maxima located at the bottom of the nitrate-depleted layer at 35 and 28°W (open circles) contain the highest proportion of picoplankton. In contrast, it is not possible to separate, on the basis of this size criterion, the samples in the deep chlorophyll maxima located at the top of the nitracline during the warm season (crosses) from those of the subsuperficial maximum of the equatorial upwelling (dots). In the coastal samples (c) the percentage of picoplankton never exceeds 20 %.

This distribution permits the tracing of a line (one point excepted) which represents the maximum excepted percentage of Chl*a* in the < 1 μm fraction for a given Chl*a* concentration; this line suggests that picoplankton blooms are unlikely in the equatorial Atlantic.

DISCUSSION

Our results show that at least in the eastern Atlantic, the commonly-termed " equatorial upwelling " does not bring about a phytoplanktonic development comparable either in intensity or in quality with blooms observed in coastal upwellings. In 1984, the Chl*a* values were significantly higher in July than in January, but if we refer to previous data, this would appear exceptional: from 1977 to 1979 (Voituriez *et al.*, 1982) and in 1983 (unpublished FOCAL data), between 5°S and 5°N at 4°W, there was no significant seasonal difference between winter and summer integrated values of Chl*a*. However, even in 1984, nowhere did the Chl*a* concentrations exceed 1,5 $\mu g\, l^{-1}$. Available CZCS images in that region confirm, at least for summer 1983 and 1984, the absence of values greater than 2-3 $\mu g\, l^{-1}$ for the sum Chl*a* + phaeopigments (Carder, pers. comm.).

Our results are consistent with earlier observations in the same region dealing with the size structure of zooplankton (Voituriez *et al.*, 1982), the relationship between phytoplankton and zooplankton biomasses (Le Borgne, 1981) the properties of diverse biochemical and physiological indices of zooplankton (Le Borgne, Roger, 1983) and the nitrate/temperature linear relationship (Voituriez, Herbland, 1984). All these observations failed to reveal any difference between the two seasons in the Eastern equatorial Atlantic Ocean. With a one-dimensional model, Osborn (pers. comm.) suggests that the changes in species composition in the equatorial Pacific at 110°W are due to a substantial decrease in both upwelling and mixing: relatively high productivity is associated

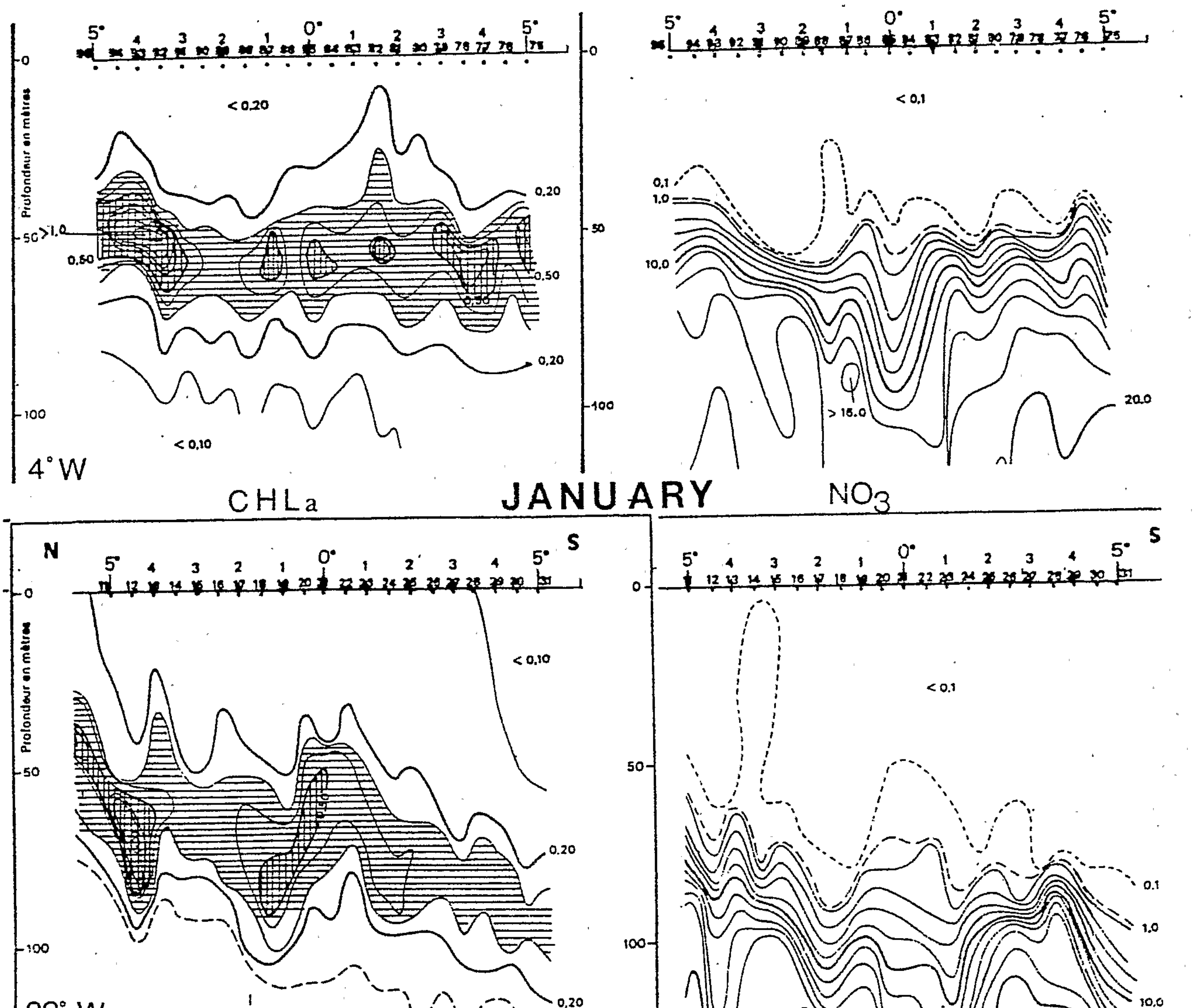

Figure 1 *a*

*Vertical distribution of Chl*a *(on the left) and nitrate (on the right) between 5°N and 5°S at 4°W (upper panel) and 23°W (lower panel) during the FOCAL 6 cruise (January 1984). Chl*a*:* $\mu g l^{-1}$; NO_3: $\mu gat\, l^{-1}$.

Distribution verticale de la Chl*a* (à gauche) et du nitrate (à droite) entre 5°N et 5°S à 4°W (partie supérieure) et à 23°W (partie inférieure) pendant la campagne FOCAL 6 (janvier 1984). Chl*a* en $\mu g l^{-1}$; NO_3 en $\mu atg l^{-1}$.

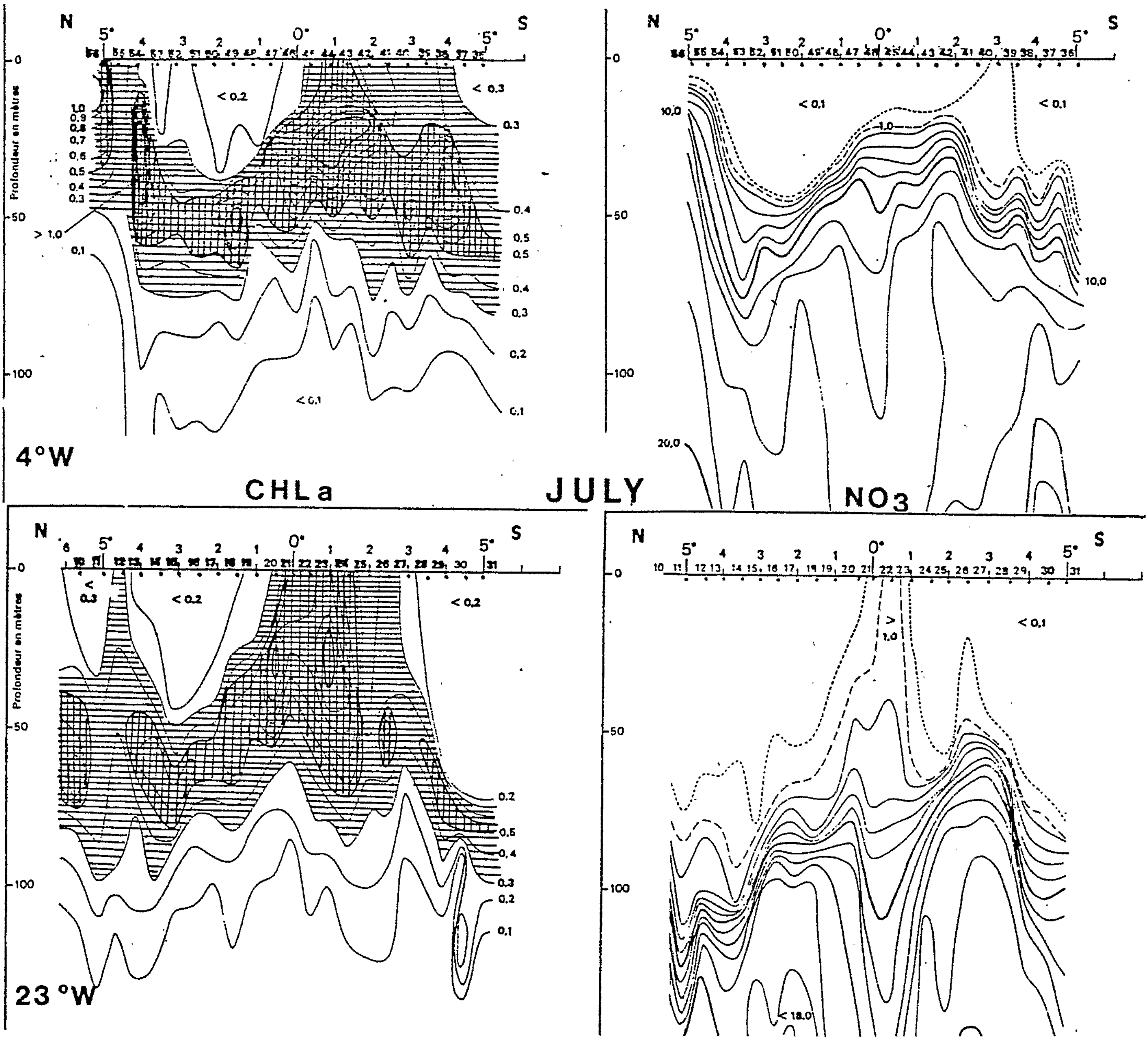

Figure 1 *b*
Same legend as Figure 1 a *for FOCAL 8 cruise (July 1984).*

Même légende que pour la figure 1 *a*, mais pour la campagne FOCAL 8 (juillet 1984).

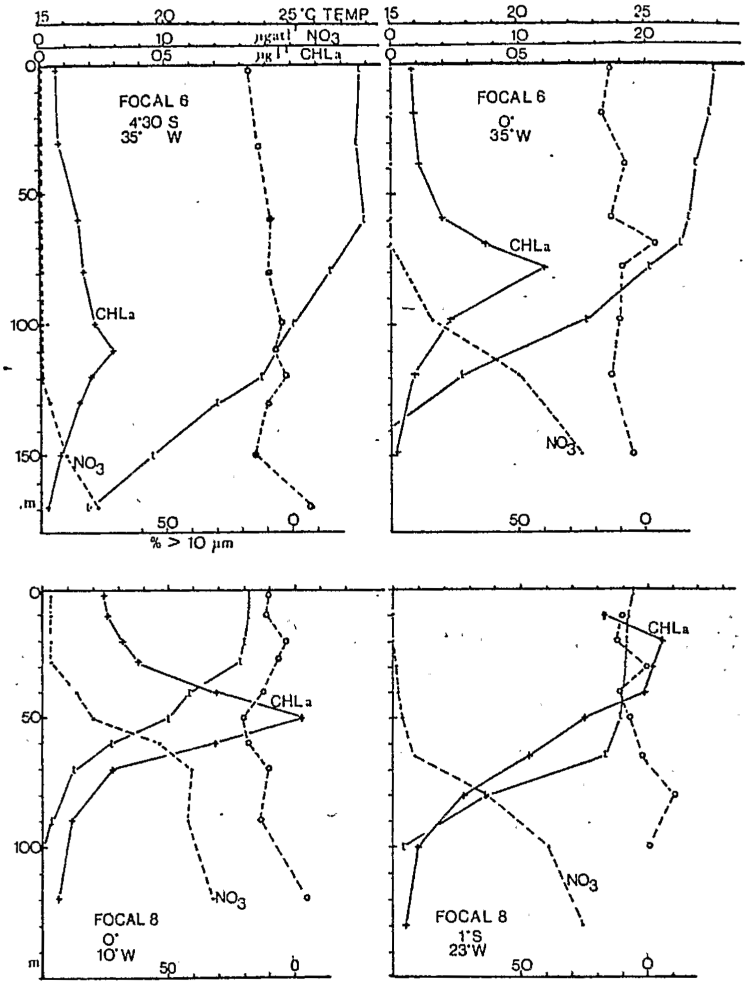

Figure 2

Vertical distribution of temperature (t), nitrate (.--.) Chla (+--+) and percentage of > 10 µm Chla (0--0) at four stations in the equatorial Atlantic. The apparent negative values of the percentage of > 10 µm Chla are due to the lack of precision of the method : in those cases more Chla was found after screening on 10 µm than without screening.

Distribution verticale de la température (t), du nitrate (.--.), de la Chl*a* (+--+) et du pourcentage de Chl*a* > 10 µm (0--0) à quatre stations dans l'Atlantique équatorial.

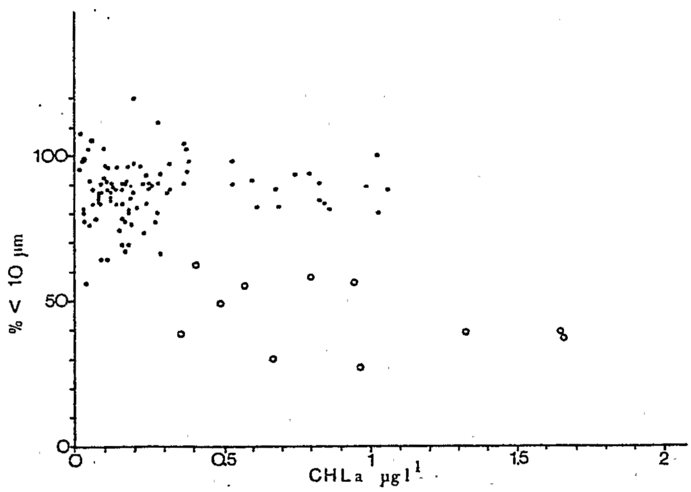

Figure 3

Relationship between total Chla concentration and the percentage of < 10 µm Chla between 0 and 2 µgl^{-1}. Dots : open equatorial Atlantic ; open circles : coastal upwelling near Dakar (Senegal).

Relation entre la concentration en Chl*a* totale et le pourcentage de Chl*a* < 10 µm entre 0 et 2 µgl^{-1}. Points : Atlantique équatorial du large ; cercles : upwelling côtier près de Dakar (Sénégal).

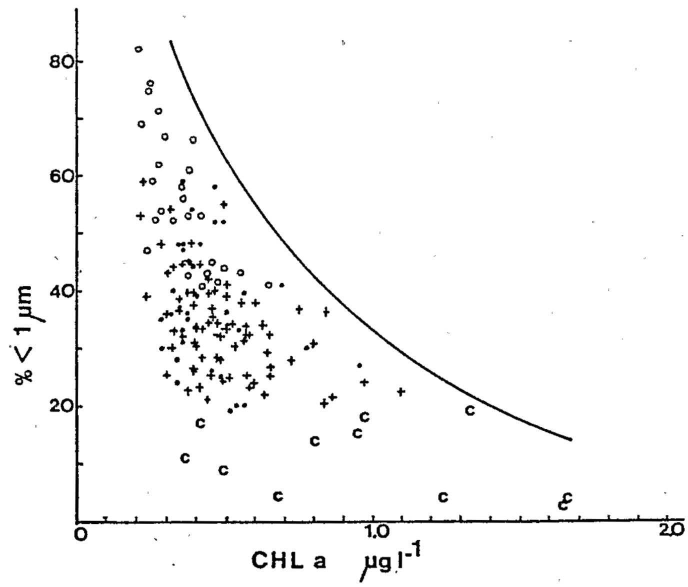

Figure 4

Relationship between total Chla concentration and the percentage of < 1 µm Chla between 0 and 2 µgl^{-1}. C : coastal upwelling near Dakar. Open circles : deep chlorophyll maxima in a nitrate-depleted layer ; crosses : deep chlorophyll maxima in the nitracline of typical tropical structure ; dots : subsuperficial maxima in the equatorial upwelling.

Relation entre la concentration en Chl*a* totale (entre 0 et 2 µgl^{-1}) et le pourcentage de Chl*a* < 1 µm. C : upwelling côtier près de Dakar. Cercles : maximums profonds de Chl*a* dans une couche épuisée en nitrate ; croix : maximums profonds de Chl*a* dans la nitracline de la structure tropicale typique ; points : maximums subsuperficiels dans l'upwelling équatorial.

with a diatom-rich collection ; at times of relatively low productivity the diatoms are absent and microflagellates are dominant. In the equatorial Atlantic we have no indication on species composition either in the deep chlorophyll maximum or when the upwelling occurs. But according to Voituriez *et al.* (1982), the level of productivity at 4°W between 0° and 5°S is not reduced when the upwelling ceases and since the size structure of Chl*a*-containing cells does not change we may draw the conclusion that the trophic organization of the water column is not drastically affected by the vertical motions. All year round, the pelagic ecosystem is dominated by very small organisms : the primary producers with high growth rates (Le Bouteiller, Herbland, 1982) would be continuously grazed by small herbivorous zooplankton, thus preventing any bloom of phytoplankton.

In a previous study, we pointed out that picoplankton dominates (71 % on average in terms of Chl*a*) in the nitrate-depleted layer, whereas its relative importance decreases in the Chl*a* maximum, where nanoplankton accounts for the bulk of the biomass (Herbland *et al.*, 1985).

It must be also mentioned that at present, we strongly favour the hypothesis that the deep phaeophytin maximum is mostly the result of an artefact due to the presence of chlorophyll *b* in picoplankton cells, well adapted to the low level and spectral quality of the light in the bottom of the stratified photic zone (Herbland, 1987). The proportion of apparent Ph*a* in the subsuperficial Chl*a* maximum is lower than in the DCM. The combination of these two effects (disappearance of the mixed layer and relative reduction of Chl*b*-containing picoplankton) leads us to expect an increase in the mean cell size of phytoplankton, but limited to the 0.5-10 μm range, when the upwelling occurs.

CONCLUSION

Ten years of intensive chemical and biological measurements in the Eastern equatorial Atlantic Ocean, lead us to the conclusion that the seasonal upwelling itself does not have an important effect on the intensity of primary production. During the warm season (8 months out of 12), the nitracline remains sufficiently close to the surface to allow the maintenance of a deep chlorophyll maximum in which the bulk of the primary production occurs. The seasonal upwelling seems to be nothing other than the movement towards the surface of the deep chlorophyll maximum with little, if any, enhancement of its value and only minor modification of its trophic organization. Since physical processes (advection, mixing, vertical motions) are evidently the major causes of the biological responses, we may advance the converse notions that the physical processes of the equatorial Atlantic are different from those of coastal upwelling, and that the knowledge of equatorial biology and chemistry might be used to obtain a better understanding of the horizontal and vertical circulation.

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