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Size structure of phytoplankton biomass in the equatorial Atlantic Ocean

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Abstract—The size structure of chlorophyll *a* (Chl *a*) and phaeopigments (<20, <10, <3, <2, and <1 μm) has been studied along three transects (4°, 23°, and 35°W) covering the entire equatorial Atlantic Ocean, with special attention to the small sizes (<3 μm). Everywhere in the studied area, even in the equatorial upwelling, the bulk of Chl *a* is within organisms which pass through a 3 μm Nuclepore filter. The vertical distribution of the <1 μm Chl *a* is closely related to the depth of the nitracline. In the nitrate-depleted mixed layer, the <1 μm Chl *a* always dominates, and represents 71% of the total Chl *a* on the average. At the top of the nitracline, the <1 μm Chl *a* concentration is maximum but represents only 50% of the total Chl *a*. In the nitrate-rich waters, whatever the depth, the percentage of <1 μm Chl *a* is everywhere <50% and decreases downwards. At the bottom of the photic zone, the <1 μm Chl *a* values are nearly zero. When integrated over the whole euphotic layer, the <1 μm Chl *a* represents about 25% of the total Chl *a* when nitrate is present at surface; this percentage reaches 60% when the top of the nitracline deepens to 100 m depth.

Preliminary measurements of photosynthetic activity (light gradient and time course experiments) indicate that the <1 μm fraction contains actively photosynthetic organisms but also organisms which are able to fix CO_2 in the darkness in a significant proportion.

The roles of sinking, nutrients, and light in the vertical distribution of picoplankton are discussed.

Our results indicate that the size distribution of Chl *a* (and especially the relationship between abundance of picoplankton and nitrate distribution) is the same throughout the whole equatorial Atlantic belt, from Brazil to the Gulf of Guinea. From an ecological point of view, the open equatorial Atlantic, in spite of large variations in hydrological structure, can be considered as a unique ecosystem. Probably the same is true for the entire open tropical Atlantic zone.

INTRODUCTION

THE SMALL solitary forms of phytoplankton passing through 10 to 20 μm mesh screens (nanoplankton) account for most phytoplankton biomass in the open ocean where about 80% of the marine phytoplankton production occurs (MALONE, 1980). Recent studies have focused attention on a smaller size class of autotrophic organisms—the picoplankton (<2 μm, according to SIEBURTH *et al.*, 1978). WATERBURY *et al.* (1979) and JOHNSON and SIEBURTH (1979) show the existence of small unicellular cyanobacteria (procaryotes) with a widespread geographical distribution and the ability to achieve considerable densities. Recently, LI *et al.* (1983) in the eastern tropical Pacific, and PLATT *et al.* (1983) in the tropical North Atlantic (west of Azores) concluded that autotrophic picoplankton (<1 μm) are capable of supplying 60% (range 20 to 80%) of the total primary production in the open ecosystem.

These two last results are extremely important because they modify our concepts on the biological structure of the pelagic ecosystem, but they are limited in space and time. We

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report here the results of a study of the vertical size distribution of phytoplankton biomass in the photic zone of the entire equatorial Atlantic Ocean. We pay special attention to the small classes (<3 and <1 μm) and their relation to the hydrological structure. The great number of size fractionations (≃1000) presented here allows some conclusions with high statistical significance.

MATERIALS AND METHODS

Sampling was performed during two similar cruises of the R.V. *Capricorne* in the equatorial Atlantic (Fig. 1): FOCAL 4 during July to August 1983 and FOCAL 6 during January to February 1984, with three north–south transects (between 15°N and 5°S at 23°W, and between 5°N and 5°S at 4° and 35°W). Sampling depths (8 to 10 in the euphotic zone) were chosen from temperature, salinity, and oxygen profiles recorded with a STDO system. Seawater was collected with 5 l PVC bottles on a "rosette sampler". Nitrate and nitrite were analyzed immediately on an autoanalyzer (Technicon A II) by methods described by STRICKLAND and PARSONS (1972). Chlorophyll *a* was determined by fluorimetric analysis in methanol extracts: 250 ml of seawater were filtered on a glass fiber filter (Whatman GF/F25 mm) under low vacuum (<75 mm Hg). GF/F filters showed a better chlorophyll retention efficiency (≃13% on the average, 27 measurements) than the GF/C filters in the equatorial waters. Immediately after the end of filtration, the filter was transferred in a glass

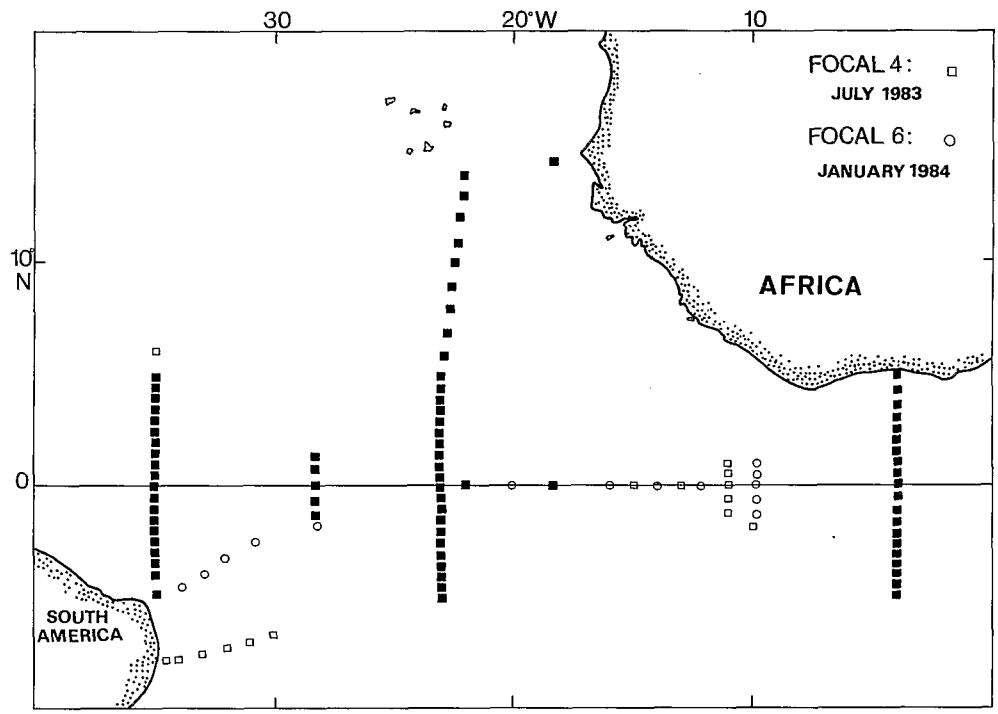

Fig. 1. Map of the equatorial Atlantic showing the location of sampling stations. The solid squares are the stations sampled during both cruises.

Table 1. Variability in the Chl a and phaeopigments analysis with methanol. FOCAL 6 cruise

		Total Chl *a*			<3 µm
		Sta. 35	Sta. 27	Sta. 44	Sta. 26
Chlorophyll *a*	*n*	10	7	8	8
	m	0.108	0.146	0.146	0.224
	Cv	1.9%	3%	6.4%	3.4%
Phaeopigments	*n*	10	7	8	8
	m	0.067	0.157	0.097	0.092
	Cv	5.8%	7%	3.6%	12%

test tube containing 7 ml of 100% methanol. With the residual seawater retained by the filter (0.15 ml, Cv = 4.8%, $n = 15$), the extraction solvant was 97 to 98%. The tubes were plugged and placed in darkness at 4°C; no difference could be observed between the results with and without grinding in methanol, agreeing with conclusions by HOLM-HANSEN and RIEMANN (1978). At the end of extraction, completed after 30 min, the tubes were shaken gently and fluorescence was measured directly in the test tubes with a Turner 112 fluorometer. Correction for phaeopigments was made by acidification (HOLM-HANSEN *et al.*, 1965), by addition of 50 µl HCl 0.5 N. The coefficients of variation for replicate analysis were usually <6% (Table 1). No significant difference was found with samples ground and extracted in acetone 90% (26 comparisons). Calibration of the fluorimeter was made with pure Chl *a* (Sigma) in 97% methanol with its concentration first measured on a spectrophotometer.

Size fractionation

A 20 µm mesh net was used to separate netplankton from nanoplankton. Size fractionations of 1, 2, 3, and 10 µm were made with polycarbonate filters (Nuclepore, 47 mm diameter). A very low vacuum (<25 mm Hg) was necessary for the filtration on 1 and 2 µm filters; gravity was sufficient for the 3 µm and 10 µm filters. Only two filters of the same porosity were used at each station (8 to 10 samples) without measurable clogging after the filtration of 5 samples, even in the chlorophyll maximum: replicates filtered on the same 3 µm Nuclepore filter did not show any trend for chlorophyll and phaeophytin in the <3 µm fraction from the first to the fifth sample.

Each Nuclepore filtrate was immediately filtered on a Whatman GF/F glass fiber filter. Comparisons between 0.2 µm Nuclepore and Whatmann GF/F filters show no statistical difference in the retention capacity of the two filters. As LI *et al.* (1983), our operational definition of picoplankton is particles that pass 1 µm Nuclepore filters (at <25 mm Hg instead of 135) but are retained on Whatman GF/F filters. We have adopted the formula "<1 µm Chl *a*" for convenience, although it does not mean that all particles of picoplankton are smaller than 1 µm (SHELDON, 1972). The remark is valid for the other porosities of the Nuclepore filters.

$^{14}CO_2$ uptake in a light gradient

A linear incubator was used, illuminated at one end by a 500 W light pressure lamp (Philips). Temperature was controlled by circulating surface seawater. The incubator was divided into 12 compartments along its axis by transverse glass partitions. The

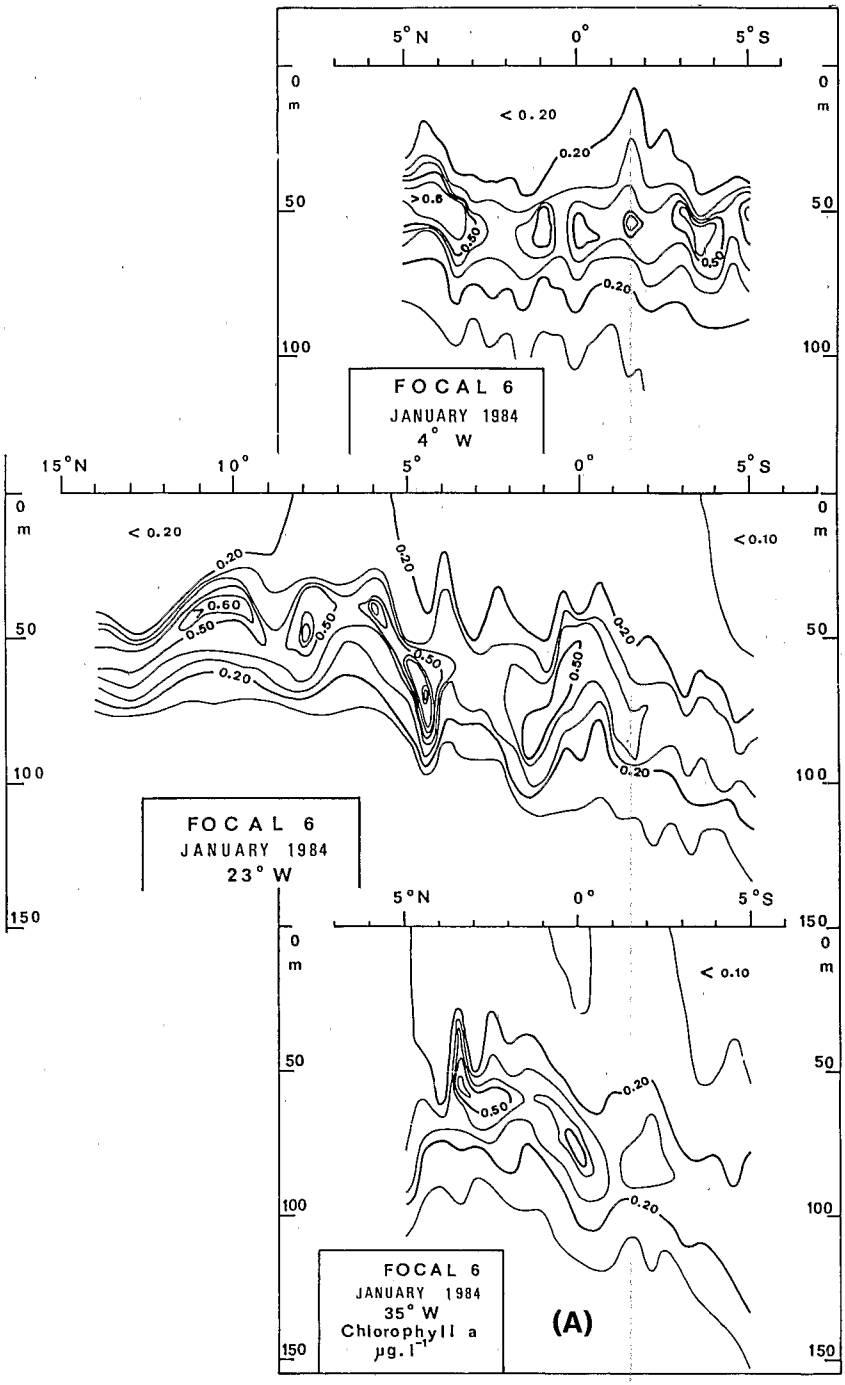
5° N
0°
5° S
0
m
50
100
< 0.20
0.20
> 0.6
0.50
0.5
FOCAL 6
JANUARY 1984
4° W
15°N
10°
5°
0°
5° S
< 0.10
FOCAL 6
JANUARY 1984
23° W
150
FOCAL 6
JANUARY 1984
35° W
Chlorophyll a
µg.l⁻¹
(A)

Fig. 2A.

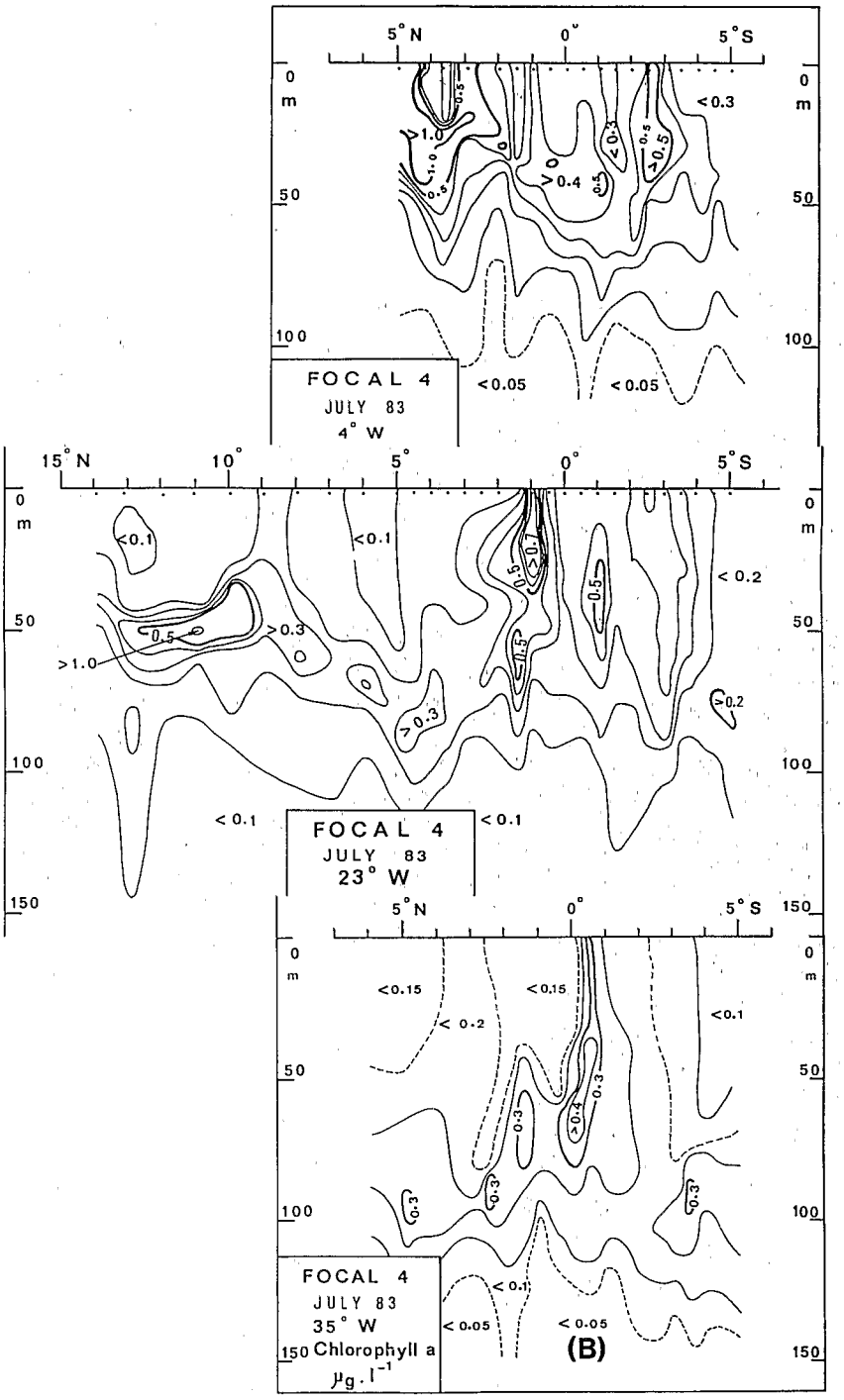

Fig. 2. Vertical distribution of total Chl *a* on the three transequatorial transects shown in Fig. 1. (A) FOCAL 6 cruise, January to February 1984; (B) FOCAL 4 cruise, July to August 1983.

photosynthetic available radiation (PhAR) was measured in each compartment with an underwater quantum sensor (LiCOR Li 192 SB). The range of the irradiances was 6 to 750 $\mu E\ m^{-2}\ s^{-1}$, i.e., approximately the range of PhAR from the bottom of the euphotic zone to 4 to 5 m below the surface in full sun at midday. The incubation time varied between 4 and 7 h.

Uptake of CO_2 was measured in 300 ml BOD bottles, according to conventional procedures: counting of the introduced radioactivity; immediate filtration for a blank substraction; low vacuum (<75 mm Hg) during the filtration; decontamination of the filter (Whatman GF/F) with 200 µl HCl 0.1 N in the scintillation vial, and drying at 50°C over a night. Liquid scintillation counting with the channel ratio method was used to measure the activity of the filters (Philips PW 4700 liquid scintillation counter).

In offshore water of the tropical ocean, this conventional method may induce inhibition of carbon uptake by the presence of 'inhibitory' materials such as metals (CARPENTER and LIVELY, 1980; FITZWATER *et al.*, 1982). MARRA and HEINEMANN (1984) found no difference between noncontaminating incubation procedures and conventional methodology. It is difficult to determine whether metal contamination affects our results. The use of a similar procedure in the same waters gave very high assimilation numbers (HERBLAND and LE BOUTEILLER, 1983) and the results of the experiments presented here are used more for internal comparison than for accurate determination of the primary productivity values in the water column.

RESULTS

Total chlorophyll a *distribution in the equatorial Atlantic Ocean: zonal and seasonal variations*

The impact of the geographical and seasonal hydrological variations is clearly visible in the vertical distribution of Chl *a* during the cruises FOCAL 4 and FOCAL 6 used in this study. In winter (January to February 1984, Fig. 2A), the chlorophyll maximum layer (values >0.25 $\mu g\ l^{-1}$) was located in the thermocline, with a maximum value close to the top of the nitracline (i.e., the depth where the nitrate concentration was >0.10 to 0.15 µg-at. l^{-1}). In the equatorial band (5°N to 5°S) it progressively sank from east to west, from 45 to 60 m at 4°W to 50 to 90 m at 23°W and 55 to 110 m at 35°W. Between 6° and 12°N at 23°W, the chlorophyll maximum followed the rising thermocline and nutricline due to the North Equatorial Countercurrent (NECC). In summer (July to August 1983, Fig. 2B), as expected during the season of the equatorial upwelling (VOITURIEZ *et al.*, 1982), the chlorophyll maximum layer frequently reached the surface at 4° and 23°W in the equatorial divergence (1°N to 5°S), while it was deep, with low values at 35°W (except at 0°30'S where nitrate was detectable in surface water). At 23°W the influence of the Guinea Dome was visible between 9° and 14°N, where Chl *a* maximum followed the doming of the nutriclines with higher values (VOITURIEZ and DANDONNEAU, 1974).

Vertical distribution of the <1 µm *size class*

In the upper part of the nitrate-depleted layer, the <1 µm Chl *a* concentrations were low, between 0.05 and 0.10 $\mu g\ l^{-1}$. A subsurface <1 µm Chl *a* maximum of 0.18 $\mu g\ l^{-1}$ on the average, appeared either at the bottom of the nitrate-depleted layer (26 times) or at the top of the nitracline (28 times). Discrete sampling did not show any difference between values of the <1 µm Chl *a* maximum with or without nitrate in the water. Nowhere did the <1 µm Chl *a* value exceed 0.30 $\mu g\ l^{-1}$, even in the coastal waters off Ivory Coast where the total Chl *a*

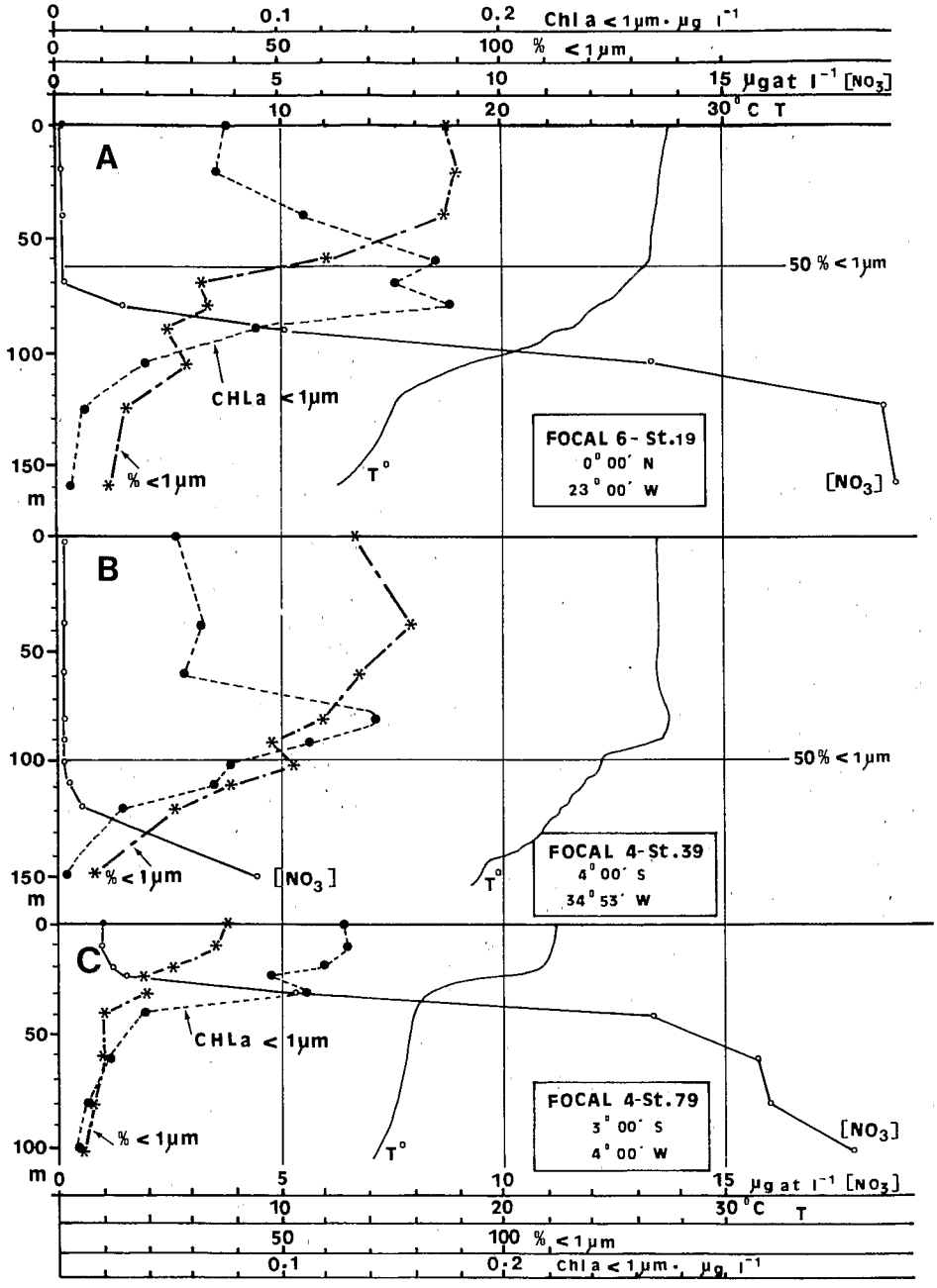

Fig. 3. Examples of typical vertical distribution of temperature, nitrate, <1 µm Chl *a*, and % of Chl *a* in the <1 µm fraction. (A), (B) No detectable nitrate (<0.1 µg-at. l^{-1}) in the upper layer; (C) nitrate detectable in the upper layer.

concentration reached 2 to 3 μg l^{-1}. At the bottom of the photic zone, the <1 μm Chl *a* values were nearly zero (Fig. 3).

The relative importance of the <1 μm Chl *a*, expressed by its percentage in the total Chl *a*, has also a strong consistency in its vertical distribution. In the nitrate-depleted mixed layer, most of the chlorophyll biomass (mean value = 71%, Table 2) was in the <1 μm size fraction. The percentage of <1 μm Chl *a* decreased above the nitracline (Fig. 3A and B). The value 50% of <1 μm Chl *a* followed the depth of the top of the nitracline (Fig. 4) irrespective of the total Chl *a* concentration. In the eastern equatorial upwelling, when nitrate reached the surface (Fig. 3C), the <1 μm Chl *a* concentration was maximum at surface and represented <50% of the total Chl *a*, like in the deep chlorophyll maximum layer. Therefore vertical and seasonal variations in the nutrient (i.e., nitrate) distribution seem to affect both the vertical distribution of the <1 μm Chl *a* and its relative abundance to the total Chl *a*. In the nitrate-depleted mixed layer, most of the Chl *a* was associated with particles smaller than <1 μm, whereas the opposite occurred in the chlorophyll maximum layer located in the nitracline, whatever the depth at which nitrate became detectable, up to and including surface (Fig. 4).

In the nitrate-depleted layer, the percentage of <1 μm Chl *a* can be inversely related to the total Chl *a* concentration (Fig. 5). Thus, the percentage of <1 μm Chl *a* would be a sensitive indicator of oligotrophy. This is also suggested by the fact that for a given total Chl *a* value (at least between 0.1 and 0.25 μg l^{-1}), the percentage of <1 μm Chl *a* increases from the east to the west (Fig. 5), and the western Atlantic equatorial ocean is known to be more oligotrophic than the eastern Atlantic.

The nitracline depth effect on the <1 μm Chl *a* percentage in the water column (integrated values from surface to the bottom of the photic zone) is clearly shown in Fig. 6: when the nitracline is deeper than 70 m, i.e., a frequent situation all the year round in the western tropical Atlantic (VOITURIEZ and HERBLAND, 1981), more than 50% of the integrated Chl *a* is associated with particles <1 μm.

Table 2. Mean, number, and standard deviation of Chl a *percentages in the different size classes (<1 to <20 μm) of the photic zone in the equatorial Atlantic Ocean. The two asterisks indicate that at 4° and 23°W the nitrate concentration is not always <0.1 μg-at. l^{-1}*

	%Chlorophyll *a* <1 μm			% Chlorophyll *a* <3 μm		% Chl <10 μm	%Chl <20 μm
Cruise	FOCAL 6	FOCAL 6	FOCAL 4	FOCAL 4	FOCAL 4	FOCAL 6	FOCAL 6
Transect	4°W	23°W	35°W	4°W	23°W		
Above the chlorophyll maximum (NO_3 < 0.1 μg-at. l^{-1})	m=70.0	71.6	74.7	66.0	82.0	86.4	94.4
	σ=19.5	10.1	13	10.7	11.8	7.3	2.7
	n=32	43	41	7	46	17	6
				(*)	(*)		
In the maximum chlorophyll layer (>0.25 μg l^{-1}) (NO_3 >0.1 μg-at. l^{-1})	m=34.9	38.0	48.0	61.1	65.0	89	92.0
	σ=13	12.8	11.3	7.7	15.9	6.24	2.2
	n=43	69	22	21	71	13	6
Below the chlorophyll maximum (NO_3 >0.1 μg-at. l^{-1})	m=17.3	19.25	30.5	64.0	74	87.1	90.0
	σ= 6.4	8.1	13.3	14.7	11	5.3	5.1
	n=16	44	52	55	79	13	7

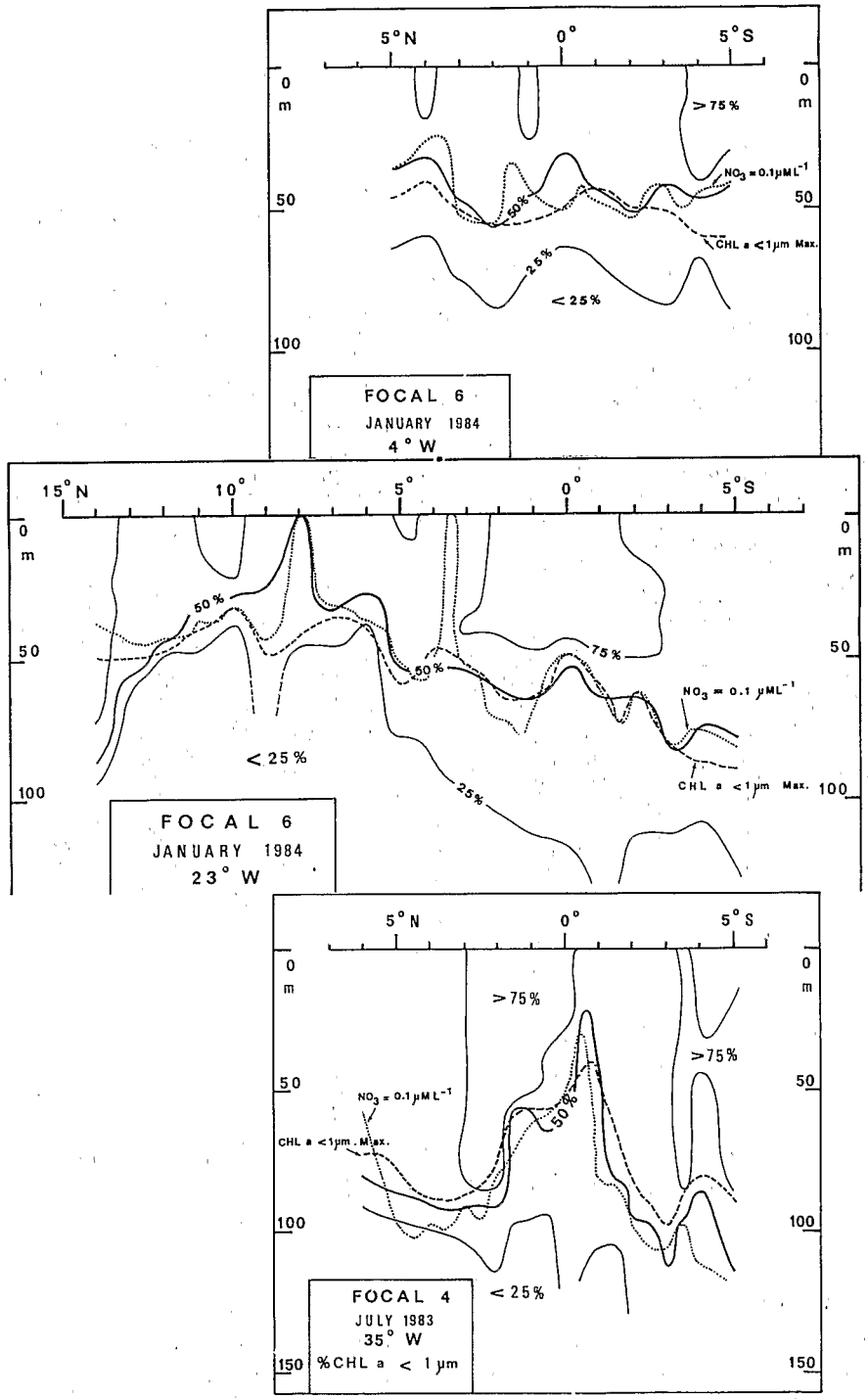

Fig. 4. Vertical distribution of the percentage of Chl *a* in the <1 µm fraction along the three transects of Fig. 1. The isoline 50% follows the top of the nitracline (dotted line); the <1 µm Chl *a* maximum (broken line) is roughly at the same depth.

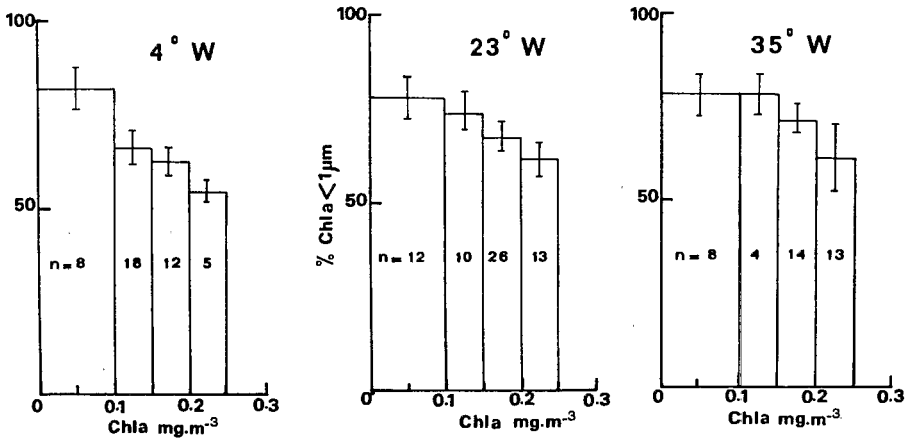

Fig. 5. The relationship between the total Chl *a* concentration and the percentage of Chl *a* in the <1 µm fraction for samples in the nitrate-depleted mixed layer (NO_3 <0.1 µg-at. l^{-1}). *n* = Number of samples in each interval.

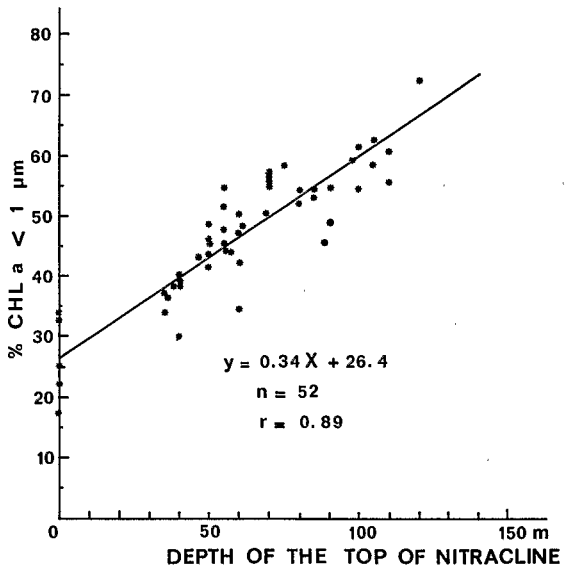

Fig. 6. Relationship between percentage of <1 µm Chl *a* (integrated values over the photic layer) and depth of the top of nitracline.

The <3 µm *size class*

The methodology used in the present study does not allow direct comparison of the <1 µm with the 1 to 3 µm group, since there were no systematic simultaneous screening on the 1 and 3 µm Nuclepore membrane filters of the same sample. As previously observed with the <1 µm Chl *a*, the maximum percentage of <3 µm Chl *a* occurred in the nitrate-depleted waters (Table 2), but although they tended to decrease in the chlorophyll maximum layer (65% at

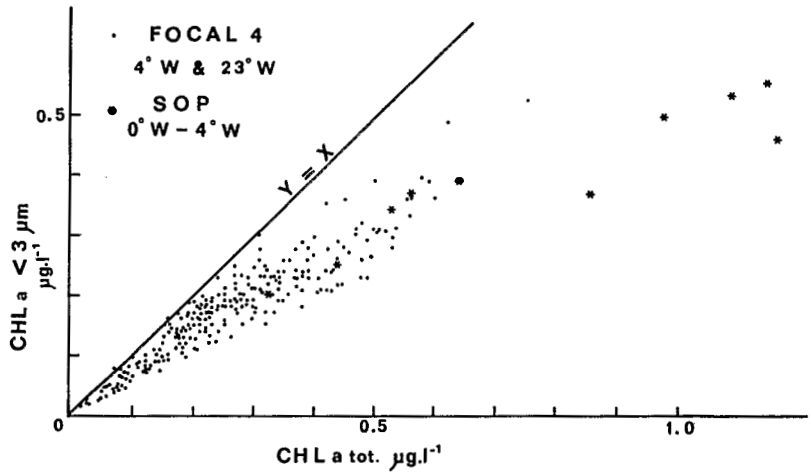

Fig. 7. Relationship between <3 µm Chl *a* and total Chl *a* values in the equatorial Atlantic Ocean. Dots: FOCAL 4 cruise, from 5°N to 5°S at 4°W and from 14°N to 5°S at 23°W. Asterisks: Special Observation Period (SOP) of the GARP, a 14-day study at 0° to 4°W where higher Chl *a* values were measured.

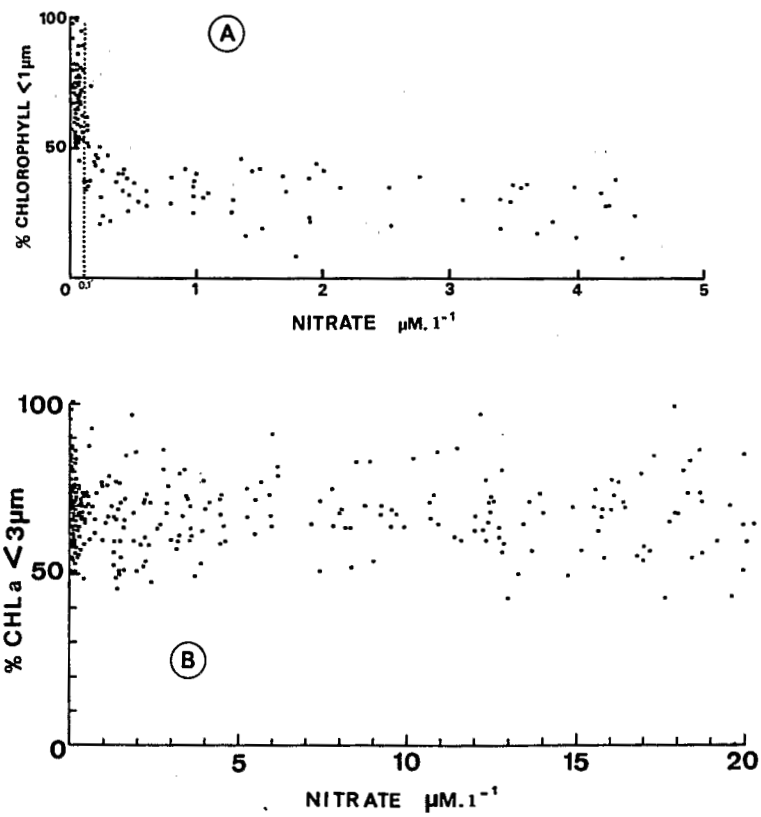

Fig. 8. Relationship between nitrate concentration and (A) percentage of Chl *a* in the <1 µm fraction; (B) percentage of Chl *a* in the <3 µm fraction. Data of FOCAL 4 and FOCAL 6.

Table 3. *Size distribution of Chl* a *in the upwelled waters off Ivory Coast. The bulk of Chl* a *is associated with particles* >10 μm (*distance from the shore:* 100 km, *bottom:* 3100 m)

Date	Position	Depth (m)	Chlorophyll *a* (μg l^{-1}) Total	<1 μm	1 to 3 μm	3 to 10 μm	>10 μm
6.8.83	4°20'N 4°W	15	0.923	0.072	0.066	0.158	0.627
		20	1.23	0.053	0.143	0.204	0.83
		40	3.06	0.046	0.055	0.073	2.88

23°W), the values were rarely smaller than 50%. At 4°W, in the nitrate-rich surface water, the percentage of <3 μm Chl *a* was roughly uniform (60 to 65%) throughout the photic zone, corresponding to values measured in the nitracline at 23°W (Table 2).

The relationship between the total Chl *a* and <3 μm Chl *a* values shows clearly that the percentage of <3 μm Chl *a* decreases when the total Chl *a* increases (Fig. 7).

A clear difference between the <3 and <1 μm Chl *a* appears when the percentage of each size class is plotted against the nitrate concentration: the percentage of <1 μm Chl *a* exceeds 50% when the nitrate concentration is lower than 0.1 μg-at. l^{-1}, and is <50% with increasing nitrate concentration (Fig. 8A). Although the <1 μm Chl *a* is included in the <3 μm Chl *a*, such a relationship does not exist with the <3 μm Chl *a* (Fig. 8B). This suggests that the vertical distribution of the <1 and 1 to 3 μm Chl *a* are very different (see Discussion).

The net picoplankton: >10 *and* >20 μm

Measurements confirm the secondary importance of the net chlorophyll biomass in the oceanic waters: the 10 μm screen rarely removes more than 20% of the total Chl *a*, whatever the location and the depth (Table 2). No vertical and geographical trend could be pointed out except at one station off Ivory Coast during the seasonal upwelling (August 1983, Table 3).

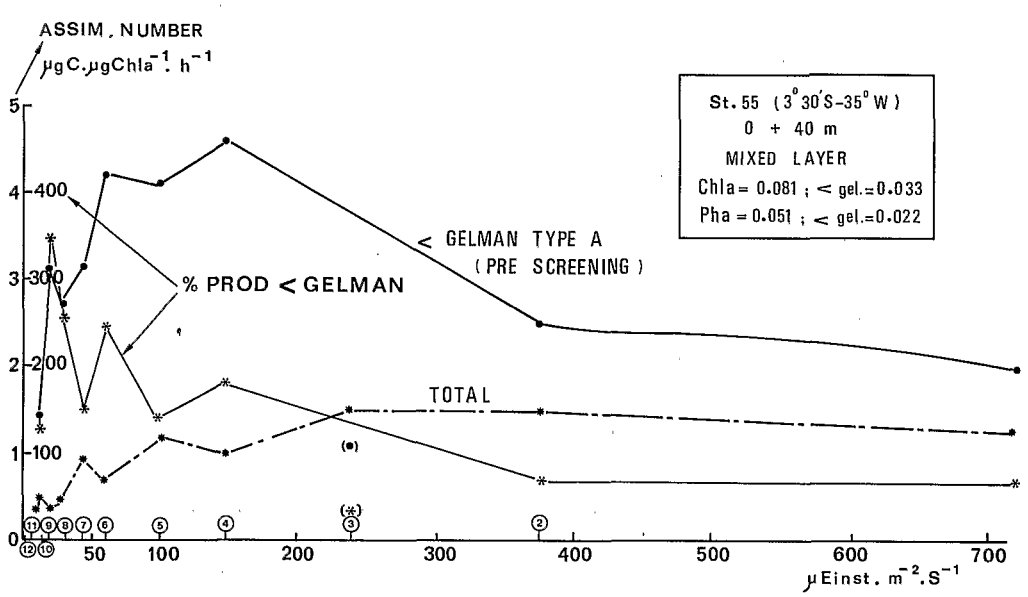

Fig. 9. Example of photosynthesis response in a light gradient of non-fractionated and prescreened samples of the mixed layer. Direct comparisons with 1 μm Nuclepore filters lead to the conclusion that the Gelman type A glass fiber filter retains a little more Chl *a* than does the 1 μm Nuclepore filter.

Photosynthesis in a light gradient

During FOCAL 6 cruise, 12 experiments were made of CO_2 uptake with water from the mixed layer and chlorophyll maximum, using the technique of pre- or/and post-screening. A detailed analysis of the data (and further experiments) will be the matter of another study. The results leave little doubt that the <1 μm fraction (or Gelman fiber glass filter in the present case) contains organisms which are actively photosynthetic (Fig. 9). It should be observed that in these experiments, the picoplankton carbon fixation rates expressed as a percentage of total activity generally had, in spite of a large scattering, a propensity to increase in low light intensities.

Time course of CO_2 fixation

Among the three time course experiments made during the FOCAL 6 cruise (and one other made during the recent FOCAL 8), we report the results of a representative experiment (Fig. 10). It leads to the following conclusions: the CO_2 fixation for the prescreened <1 μm fraction was linear over the first hours, reaching a plateau in the middle of the day with maximum light. Later, the CO_2 incorporation increased, even during the night. It follows that the percentage of CO_2 fixation in the <1 μm fraction increased with time, specially during the night.

The size distribution of phaeophytin (Phae a)

For the <20, <10, and <3 μm populations, there is no statistical difference in the respective percentage of Chl *a* and Phae *a* (Fig. 11). But it is clear that for the smaller sizes (<2 and specially <1 μm) the percentage of Phae *a* is greater than the percentage of Chl *a* in the same fraction. In other words, it means that the classical ratio of phaeophytin (Phae *a* + Chl *a*) in the <1 μm size class is much higher than the ratio of phaeophytin of the >1 μm size class.

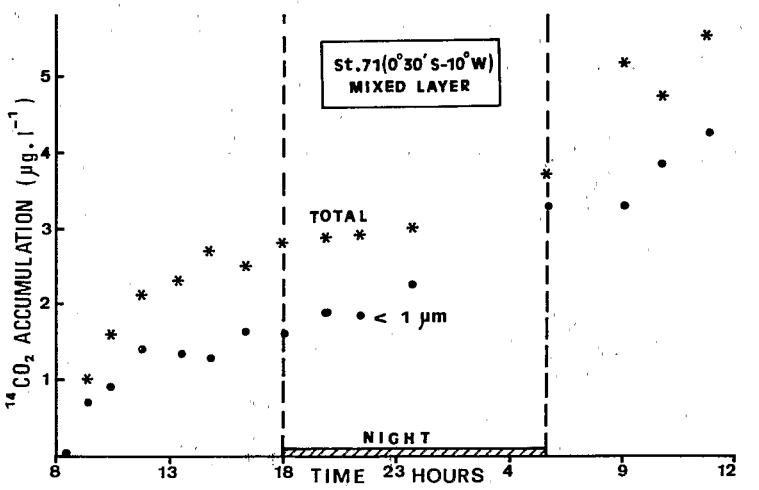

Fig. 10. Time course of $^{14}CO_2$ accumulation by plankton in a total and a prescreened (<1 μm) sample.

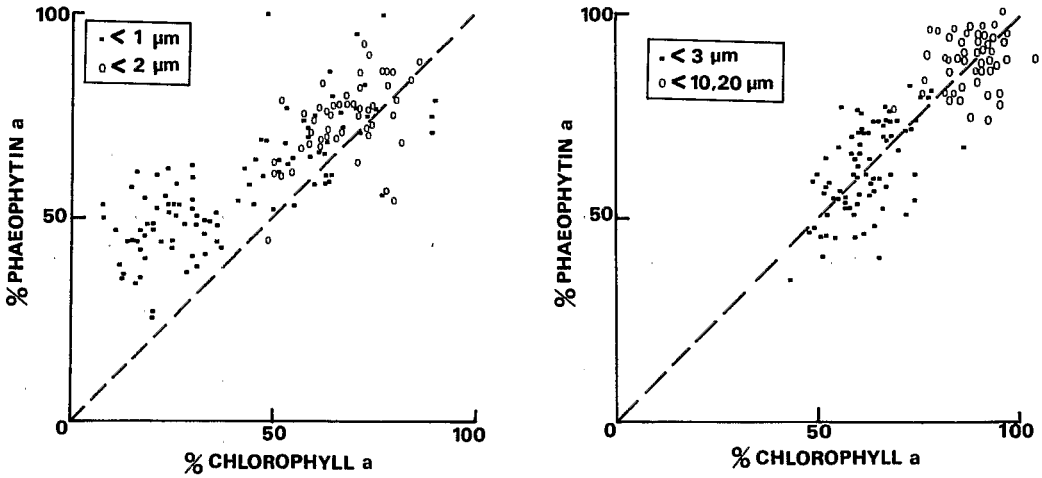

Fig. 11. Relationship between the percentage of Phae *a* and the percentage of Chl *a* in different size fractions. The broken line is $y = x$. There is a clear tendency for $y > x$ when the sizes decrease.

DISCUSSION

Although the different size fractionations were not made simultaneously on the same samples, the fairly constant size distributions of Chl *a* with time and space in the studied area allow us to summarize the vertical distribution of chlorophyll particles, with regard to the depth of both the nitracline and the photic zone (Fig. 12). In the nitrate-depleted mixed layer, the <1 µm Chl *a* is predominant (65 to 75%). Near the nitrate gradient, the percentage of <1 µm Chl *a* rapidly falls to 50% and decreases to a value close to zero at the bottom of the

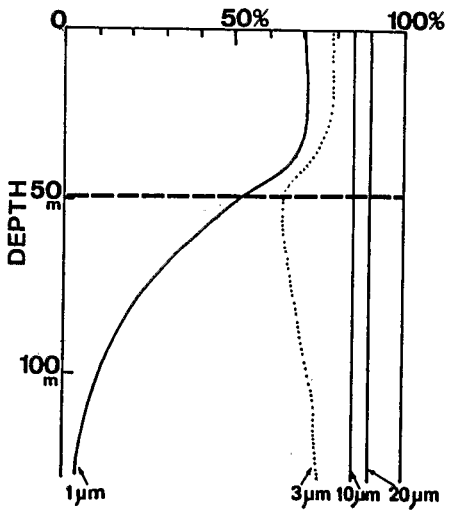

Fig. 12. Schematic and synthetic vertical distribution of the relative importance of the different size fractions in the euphotic zone (= 100 m in this example) according to the depth of the nitracline (horizontal broken line fixed at 50 m in this example).

photic zone. In contrast, the 1 to 3 μm size class does not exceed 5 to 10% in the mixed layer. It increases near the nitracline and becomes the dominant size class in the nutrient-rich layer of the photic zone. The 3 to 10 μm size class shows a slight but significant maximum in the maximum layer particularly when the total Chl *a* values are high. The >10 μm fraction is always small (≤15%), except at one station in the upwelling waters off Ivory Coast (Table 3).

Since the main result of the present study is the coherent vertical distribution of the <1 μm Chl *a* and its dominance with regard to the other size classes, the discussion will be essentially restricted to the nature of the <1 μm 'picoseston' and to the factors which control its distribution.

Nature of the <1 μm 'picoseston'

In the previous study dealing with the size distribution of Chl *a* and particulate organic matter in the chlorophyll maximum layer of the equatorial Atlantic Ocean at 0° to 4°W, HERBLAND and LE BOUTEILLER (1981) concluded that the small fraction (<3 μm) was mainly (but not exclusively) composed of detritus or inactive phytoplankton, because of its low assimilation numbers (mg C mg Chl a^{-1} h^{-1}). On the other hand, LI *et al.* (1983) and PLATT *et al.* (1983) reached the opposite conclusion: the picoplankton is an important autotrophic component in an open ecosystem. In the same way, LE BOUTEILLER and HERBLAND (1985) found that the assimilation number increases when the total chlorophyll concentration decreases, at a given irradiance level, suggesting an especially high photosynthetic efficiency of the dominant very small cells. Recently, TAKAHASHI and HORI (1984) concluded that phytoplankton in the chlorophyll maximum layer in the western subtropical Pacific and South China Sea was composed of minute (0.22 to 3 μm) cells which would not be broken into small particles during the filtration process. The experiments reported here (CO_2 incorporation in a light gradient and time-course) suggest that the <1 μm fraction (or <Gelman fiber glass filter) contains photosynthetic organisms with high assimilation numbers, but also a significant amount of organisms which take up CO_2 during the night; LI *et al.* (1983) have observed the same trend (see their Fig. 3A and B).

Moreover, the higher percentage of CO_2 incorporation in the <1 μm fraction at low light intensity, and the 'plateau' at midday in the time-course experiments, seem to confirm the ability of picoplankton to use relative dim-light (MORRIS and GLOVER, 1981; LI *et al.*, 1983; PLATT *et al.*, 1983). On the other hand, the higher proportion of phaeophytin in the <1 μm fraction, compared to the Chl *a* in the same fraction, would mean that it includes relatively more detrital particles than the 3 to 10 and 10 to 20 μm fractions (Fig. 11).

We cannot affirm however, that the fluorimetrically determined phaeopigments in our study are free of Chl *b* interference (GIBBS, 1979; LORENZEN, 1981). YENTSCH (1983) was unable to demonstrate the presence of Chl *b* in the filtrate (Whatman GF/C filtered water) of Booth Bay Harbor water, but it does not necessarily mean that very small green algae (chlorophytes, prasinophytes, i.e., Chl *b* containing cells) do not occur in significant proportion in some oceanic waters (JEFFREY, 1974, 1976).

We are aware that the present study lacks data on the types of phytoplankton that were present in the different size classes. But the link between Chl *a* measurements and cell counts is not evident for the small size classes (LI *et al.*, 1983, their note No. 19).

Finally, the comparison between the different fractions (on different but similar samples) leads us to the conclusion that the <1 μm picoplankton has both similar and different properties than the other fractions: a higher percentage of phaeophytin or/and different

pigment composition, and an enhanced ability to take up the CO_2 at low light intensities and in the dark.

Factors controlling the distribution of picoplankton in the field

Sinking rates. In the mixed layer, the predominance of small forms with low intrinsic settling velocities could be explained by purely physical reasons (EPPLEY and WEILLER, 1979): Stokes equation predicts that a spherical particle of 1 μm diameter with a density of 1.2 will have a maximum sinking speed (S) of 3.3 cm d^{-1} in seawater. The application of the LAWS (1975) equation $S = 0.028\ V^{0.39}$ (V is the cell volume in μm^3) leads to $S = 2.22$ cm d^{-1}. TAKAHASHI and BIENFANG (1983) measured sinking rates not significantly different from zero for the <3 μm size fraction of natural phytoplankton in subtropical waters off Hawaii. This negligible settling rate indicates that there should be virtually no loss of picoplankton biomass from the mixed layer due to sedimentation. This could also partially explain why REID (1983), using the Utermöhl technique, found a very low percentage of total phytoplankton carbon in the picoplankton (<2 μm) fraction in the Sargasso Sea.

Nitrate. The fact that the <1 μm Chl *a* reaches a maximum at the top (or very near the top) of the nitracline (Figs 3 and 4) clearly indicates that nutrient availability is a driving force for the picoplankton abundance, unless the <1 μm Chl *a* maximum corresponds to an increase of intracellular chlorophyll concentration in presence of low light and nitrate (see the discussion by CULLEN, 1982). On the other hand, the presence of nitrate seems to favour the growth of nanoplankton rather than the growth of picoplankton. Effectively for a given total Chl *a* value, the percentage of <1 μm Chl *a* is always smaller with than without detectable nitrate in the water. This suggests that nanoplankton has a greater affinity for nitrate than picoplankton. The same trend was found by LE BOUTEILLER (unpublished data) with ^{15}N–NO_3 uptake experiments performed in the same area. In the subsurface chlorophyll maximum, the high Chl *a* concentrations would result from the enhanced growth and accumulation of cells >1 μm. In the same way, the inverse relationship between the percentage of <1 μm Chl *a* and the total Chl *a* in the nitrate-depleted layer (Fig. 5) suggests that when the oligotrophic conditions increase, the >1 μm size class is progressively eliminated before the <1 μm class.

Light. LI *et al.* (1983) found that the percentage contribution of picoplankton to the total uptake of $^{14}CO_2$ increased with depth. The relative enhancement of inorganic carbon uptake in the small size fraction at depth was attributed to the ability of the small phytoplankton to use relatively dim light efficiently. In our experiments, carbon uptake showed the same trend. However, the dominance of picoplankton in the well-lighted mixed layer suggests that the influence of the light can be hidden by the nutrient availability.

CONCLUSIONS

MALONE (1980) wrote that the nanoplankton accounts for most phytoplankton productivity and that episodic peaks in productivity are usually caused by increases in netplankton (>20 μm) productivity. In the offshore waters of the equatorial Atlantic a similar result is observed along the nutrient gradient between the picoplankton and the nanoplankton: the picoplankton accounts for most phytoplankton in the nitrate-depleted mixed layer, whereas sharp peaks in biomass (the deep chlorophyll maxima) are dominated by cells >1 μm but smaller than 10 μm, with a slight increase of the mean cell size when the total Chl *a* concentration increases (Fig. 12).

Finally, we stress the fact that the large and seasonal inputs of nutrients in the photic zone

of the open eastern equatorial Atlantic Ocean do not seem to affect drastically the size distribution within the phytoplankton community. In contrast, the net plankton (>10 and >20 μm) may dominate the upwelling waters off Ivory Coast and Senegal. This result confirms that from an ecological point of view (i.e., structure of the food web) equatorial upwelling is closer to the typical tropical structure (HERBLAND and VOITURIEZ, 1979) than a coastal upwelling. This suggests that the whole open equatorial (and probably tropical) Atlantic Ocean can be considered as a unique ecosystem, in spite of geographical and seasonal variations of hydrological structure.

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