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# Size distribution patterns of phytoplankton in the western Pacific: towards a generalization for the tropical open ocean

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**Abstract**—The size distribution of chlorophyll *a* (Chl *a*) was comprehensively investigated during four cruises along 165°E from 20°S to 6°N, with cell counts by epifluorescence microscopy and nutrient analysis being performed at the same stations. Observations took place in two contrasting periods, an El Niño Southern Oscillation event in 1987 and a non ENSO period in 1988 and 1989. One micrometre Nuclepore filters proved to separate efficiently cyanobacteria from eucaryotic microalgae, in nutrient-rich water masses as well as in poor ones, and whatever the depth or the cell abundance. The Chl *a* distribution in the <1 $\mu$m and >1 $\mu$m fractions resulted from the relative contribution of procaryotic and eucaryotic cells to the total Chl *a*. In a stratified system, the euphotic zone was found to be divided into two parts: (1) an upper nitrate-depleted layer in which cyanobacteria were always numerically predominant, closely linked with Chl *a* in the <1 $\mu$m fraction which accounted for 60% of total Chl *a* on average; (2) a lower nutrient-rich layer in which Chl *a* > 1 $\mu$m dominated, belonging mainly to eucaryotic microalgae, as confirmed by the correlation between Chl *a* > 1 $\mu$m and the number of eucaryotes. The rapid change of the Chl *a* size pattern repeatedly observed at the top of the nitracline, whatever the depth, clearly demonstrated the major effect of nutrient increase on the size structure of phytoplankton. In systems such as the equatorial upwelling, where there is no oligotrophic mixed layer, Chl *a* > 1 $\mu$m predominated from the top to the bottom of the euphotic layer, in spite of very numerous cyanobacteria in the surface waters. Below the deep Chl *a* maximum, relatively large amounts of Chl *b* in the <1 $\mu$m fraction can be attributed to minute cells such as prochlorophytes. These results were compared with Chl *a* fractionations previously performed in the tropical Atlantic Ocean. Analysis of 230 profiles of Chl *a* in the <0.6, <0.8, <1, <2, <3, <10 and <20 $\mu$m fractions did not reveal any significant difference between the two areas. Since the Chl *a* size structure properties with respect to nutrient are common to both oceanic systems, the relationship evidenced in the western Pacific between the Chl *a* size pattern and the distribution of procaryotic and eucaryotic algal cells is likely to be similar in the tropical Atlantic: phytoplankton over wide areas has certain well-defined size distribution properties, probably typical of the whole of the tropical open ocean.

## INTRODUCTION

THE structure and functioning of the pelagic ecosystem has had to be reconsidered after the discovery of the widespread occurrence of minute (0.2–2.0 $\mu$m) algal picoplankton (JOHNSON and SIEBURTH, 1979; AZAM *et al.*, 1983; STOCKNER and ANTIA, 1986; JOINT, 1986). A large part of primary production in subtropical and tropical open oceans is henceforth

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attributed to picophytoplankton (SIEBURTH *et al.*, 1978) composed of procaryotic chroococcoid cyanobacteria assigned to the genus *Synechococcus*, and minute eucaryotic microalgae (LI *et al.*, 1983; PLATT *et al.*, 1983; ITURRIAGA and MARRA, 1988). The ecological role of picophytoplankton, especially with respect to global ocean fluxes of biogenic material, points to the need to determine not only their spatio-temporal distribution but also the environmental factors that govern their abundance and species composition.

HERBLAND and VOITURIEZ (1979) first described the main properties of the so-called Typical Tropical Structure (TTS). Although not verified everywhere, especially outside the true tropical zone (23°27′N, 23°27′S), the properties established in the open Atlantic Ocean by these authors are consistent with many recent studies in similar regions. One of the most general features of the TTS is the virtually permanent occurrence of the deep chlorophyll maximum, the depth of which is strongly linked to the depth of the nitracline (CULLEN, 1982; HERBLAND, 1983; HAYWARD, 1987; EPPLEY *et al.*, 1988). Moreover, LE BORGNE (1981) found that in the eastern tropical Atlantic zooplankton dry weights were negatively correlated with the depth of the nitracline, and positively correlated with the chlorophyll content in the 0–150 m layer, in the TTS as well as in the equatorial divergence. This indicates that the zooplankton and phytoplankton standing crops are closely related, even in upwelled waters of the open ocean (WALSH, 1976). Furthermore, HERBLAND *et al.* (1985) showed that the properties of the size distribution of Chl *a* were the same throughout the equatorial Atlantic belt, from Brazil to Africa: in the nitrate-depleted mixed layer, Chl *a* in the $<1\ \mu$m fraction always dominates. At the top of the nitracline, the $<1\ \mu$m Chl *a* concentration is maximum, representing about 50% of the total Chl *a*. In nutrient-rich waters, whatever the depth, the percentage of $<1\ \mu$m Chl *a* is <50%. This is also true of equatorial upwelling (HERBLAND *et al.*, 1987).

These results show that, from an ecological point of view, the open equatorial Atlantic Ocean, despite wide variations in hydrological structure, presents certain common properties which suggest a close relationship between hydrology, biomass and production of phytoplankton and zooplankton, exactly as if the whole area behaved as a single ecosystem. One major task is therefore to fix the limits of the system, both spatially and temporally. Since the size distribution of Chl *a* is a particularly significant index of the structure of the planktonic community, we have studied the Chl *a* size properties in the western tropical Pacific as part of the PROPPAC (PROduction Pélagique PACifique) programme. Our aim was to determine some possible particularity of the area that might, for example, be related to the oligotrophic waters of the so-called warm pool, or to the equatorial upwelling, or to the convergence zones. Comparison was possible with results from the equatorial Atlantic but also with observations reported from the eastern and central Pacific by CHAVEZ (1989) and PEÑA *et al.* (1990). Furthermore, epifluorescence microscopy was used for counting two of the main forms of cells containing the bulk of the phytoplankton biomass, i.e. cyanobacteria and eucaryotic microalgae, allowing an interpretation of Chl *a* size structure in terms of cell communities.

## METHODS

### *Sampling*

Four similar cruises were carried out on R.V. *Coriolis* and *Le Suroit* in the western Pacific (Fig. 1), in September 1987 (PROPPAC 1), April 1988 (PROPPAC 2), September

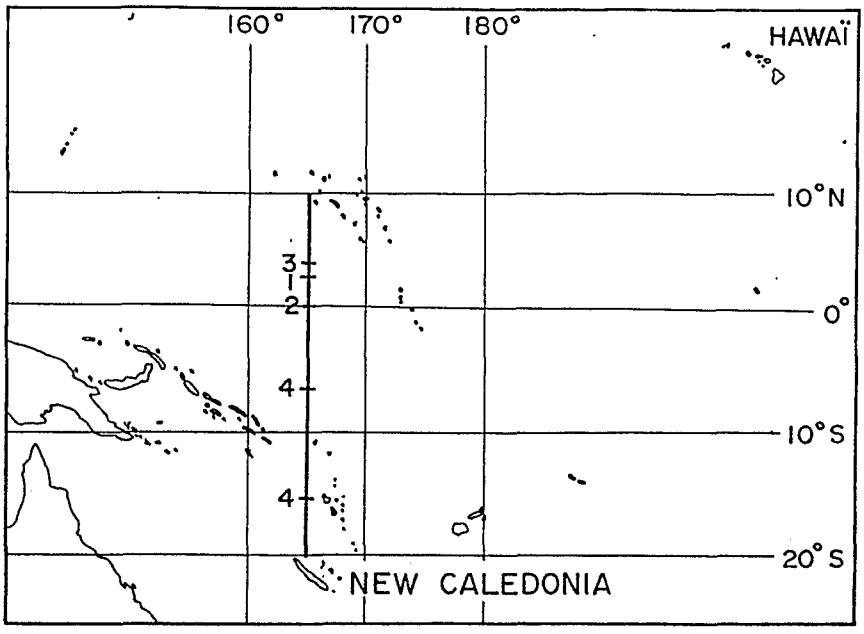


Fig. 1. Location of the five fixed position studies performed during four cruises along the transect at 165°E. Nutrient-rich waters were observed at surface at 9° and 10°S (September 1987), from 3°S to 5°N (April 1988) and from 5°S to 2°N (September 1988).

1988 (PROPPAC 3) and November 1989 (PROPPAC 4). The studies were conducted on south to north transects along 165°E, with stations at every degree from 20°S to 6°N. Twelve levels were sampled between 0 and 160, 180 or 200 m depth with 5-l Niskin bottles on a "rosette sampler" coupled with a Seabird CTDO system. Fixed positions were occupied successively for 8 days at 3°N (September 1987), 0° (April 1988), 4°N (September 1988) and 7°S and 15°S (November 1989), with samplings at 5.30 a.m., 12.00 a.m. and 6.00 p.m. (local time).

*Nutrients, light and pigments*

Nitrate, nitrite and phosphate were analysed immediately on-board ship on an auto-analyzer (Technicon A II) using the methods described by STRICKLAND and PARSONS (1972). The detection limit for $NO_3$ was 20 nM, and good accuracy was achieved above 50 nM (OUDOT and MONTEL, 1988). Underwater light intensity was determined at noon with a LiCor quantameter mounted on the CTDO frame so that depth and light could be measured simultaneously. Chlorophyll *a* was determined fluorometrically as described by HERBLAND *et al.* (1985) with some slight modifications. Pigments were extracted within 3 h by methanol (95%) from 100 ml samples filtered on GF/F filters. The coefficients of variation for 10 replicates ranged from 2 to 5%. Calibration of the TURNER 112 fluorometer equipped with a high-sensitivity sample holder was performed with pure Chl *a* (Sigma) titrated on a spectrophotometer. A mixture of pure Chl *a* and Chl *b* was prepared to test for potential bias on the Chl *a* estimation arising from the presence of Chl *b* in natural samples (NEVEUX and DE BILLY, 1986). As long as the ratio Chl *b*/Chl *a* did not exceed 1, the Chl *a* determination was not significantly biased with the precise method used here. Field measurements of Chl *b* reported in the literature indicate that the ratio

Chl *b*/Chl *a* is usually low, i.e. <1, especially in the tropical open ocean (LORENZEN, 1981; GIESKES and KRAAY, 1986; EVERITT *et al.*, 1990).

*Size fractionations*

Nuclepore polycarbonate filters (0.6, 0.8, 1, 2 and 3 $\mu$m) were used for size fractionations, always at <30 mm of Hg vacuum pressure. Total Chl *a* was systematically measured on GF/F filters. Chlorophyll *a* in the fractions was estimated on a subsample, either in the fraction retained on the Nuclepore filter or in the filtrate after a second filtration, or in both (Table 1). The methanol method of analysis was found to be precise enough to detect small but significant differences in size fractions of both Chl *a* and pheophytin *a*. Thus, the estimate of total Chl *a* was not found to be significantly different from the sum of Chl $a > 1$ $\mu$m and Chl $a < 1$ $\mu$m measured on subsamples (see Table 1). Screening is a delicate operation, especially on 1 $\mu$m porosity in tropical ocean waters, because most of the ultraplanktonic cells have a diameter close to 1 $\mu$m. Furthermore, Nuclepore filters being very fine, a leaking of cells can occur at the periphery of the filter without any leakage of water being apparent at the base of the funnel. Results of the methanol method also were compared with pigment determinations on a spectrofluorometer. At three stations (12°S, 2°S and 5°N; September 1988), screened seawater (<1 $\mu$m and >1 $\mu$m fractions and total) from 12 sampling levels was separated into two aliquots for immediate extraction and analysis on the fluorometer on the one hand, and for freezing and later analysis on a spectrofluorometer at the laboratory on the other, according to the procedure of NEVEUX and PANOUSE (1987).

Table 2 shows that the estimates of Chl *a* by the two different methods of extraction and analysis were similar and independent of the depth or the accessory pigment concentrations. The regression coefficient is lower than 1, possibly because of different standardizations or, more likely, because of a slight pigment loss due to conservation of samples. However, the most important result is that the percentages of Chl $a < 1$ $\mu$m are virtually the same with both methods. A striking relationship between Chl *b* (spectrofluorometry) and the so-called "pheophytin *a*" (fluorometry) is also evident (Table 2), which suggests that these two pigments, if not the same, are at the very least closely related (HERBLAND, 1988). This conclusion is also supported by direct comparison of pheophytin *a* with Chl *b* as estimated on board in acetone extracts with a spectrophotometer, according to the method of JEFFREY and HUMPHREY (1975). On four occasions at the fixed position 3°N, 165°E (September 1987), duplicate samples were taken at four depths with a 30 l Niskin bottle. Seawater (8 l) was filtered on GF/F 47 mm filters for the spectrophotometer. Chlorophyll *b* ranged from 0.01 mg $m^{-3}$ at 20 m to 0.31 mg $m^{-3}$ at 80 m. Results are presented in Table 2.

*Epifluorescence microscopy*

Samples (50 or 100 ml) for epifluorescence enumeration were fixed with buffered formalin at a final concentration of 1–2/1000 and immediately filtered on black 0.2 $\mu$m Nuclepore filters at <125 mm of Hg vacuum pressure, then frozen until counting in the laboratory within 2 months. Cells (200–800) were counted on 20–80 fields at each depth with a Leitz Dialux 20 microscope (HOBBIE *et al.*, 1977). In this paper, cyanobacteria designate the orange-fluorescing picocyanobacteria, and eucaryotic microalgae designate

*Table* 1. *A typical depth distribution of Chl* a *and pheophytin* (Pheo) *in total*, <1 μm *and* >1 μm *fractions*, *nutrients*, *temperature*, *cyanobacteria and microalgae*. *Station at* 3°S, 165°E (*September* 1987). *Concentration of Chl* a *and pheophytin*: mg $m^{-3}$

| Depth (m) | $NO_3$ | $NO_2$ (mmole $m^{-3}$) | $PO_4$ | $T$ (°C) | Total (measured) | | (1) <1 μm | | (2) >1 μm | | Total (1) + (2) | | Cyanob. (cells $ml^{-1}$) | Microalg. (cells $ml^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Chl *a* | Pheo | Chl *a* | Pheo | Chl *a* | Pheo | Chl *a* | Pheo | | |
| 0 | 0.006 | 0.003 | 0.05 | 29.34 | 0.093 | 0.037 | 0.062 | 0.030 | 0.032 | 0.010 | 0.094 | 0.040 | 1130 | 10 |
| 20 | 0.006 | 0.003 | 0.05 | 28.71 | 0.070 | 0.042 | 0.047 | 0.024 | 0.030 | 0.015 | 0.077 | 0.039 | 1140 | 50 |
| 40 | 0.009 | 0.000 | 0.05 | 28.41 | 0.070 | 0.040 | 0.043 | 0.024 | 0.036 | 0.012 | 0.079 | 0.036 | 1440 | 90 |
| 60 | 0.008 | 0.001 | 0.05 | 28.32 | 0.094 | 0.055 | 0.060 | 0.030 | 0.043 | 0.017 | 0.103 | 0.047 | 1600 | 160 |
| 80 | 1.029 | 0.061 | 0.17 | 27.63 | 0.489 | 0.274 | 0.228 | 0.128 | 0.247 | 0.142 | 0.475 | 0.270 | 5800 | 720 |
| 100 | 8.69 | 0.203 | 0.60 | 24.00 | 0.357 | 0.435 | 0.140 | 0.250 | 0.232 | 0.215 | 0.372 | 0.465 | 60 | 1150 |
| 120 | 10.52 | 0.060 | 0.74 | 21.36 | 0.200 | 0.300 | 0.070 | 0.160 | 0.150 | 0.130 | 0.220 | 0.290 | 10 | 620 |
| 140 | 10.54 | 0.039 | 0.75 | 19.71 | 0.122 | 0.193 | 0.038 | 0.107 | 0.104 | 0.086 | 0.142 | 0.193 | 10 | 370 |
| 160 | 12.81 | 0.017 | 0.94 | 15.65 | 0.019 | 0.040 | 0.003 | 0.010 | 0.018 | 0.030 | 0.021 | 0.040 | — | — |
| 180 | 14.56 | 0.013 | 1.07 | 14.56 | 0.003 | 0.025 | 0.001 | 0.002 | 0.002 | 0.015 | 0.003 | 0.017 | — | — |
| 200 | 16.00 | 0.010 | 1.16 | 13.47 | 0.002 | 0.024 | 0.001 | 0.009 | 0.001 | 0.016 | 0.002 | 0.025 | — | — |

*Table 2. Linear relationships* (Y = A + BX) *between Chl* a (*spectrofluorometer*) *and Chl* a (*fluorometer*), *and between Chl* b (*spectrofluorometer and spectrophotometer*) *and pheophytin* (*fluorometer*)

| *Y* | *X* | *A* | *B* | *r* | Degrees of freedom | Number of stations |
|---|---|---|---|---|---|---|
| Chl *a* (Total) Spectrofluorometer | Chl *a* (Total) Fluorometer | 0.0025 | 0.772 | 0.978 | 34 | 3 |
| % Chl $a < 1\,\mu m$ Spectrofluorometer | % Chl $a < 1\,\mu m$ Fluorometer | 7.5 | 0.958 | 0.971 | 18 | 2 |
| Chl *b* (Total) Spectrofluorometer | Pheo (Total) Fluorometer | −0.0080 | 0.380 | 0.946 | 34 | 3 |
| Chl *b* (Total) Spectrophotometer | Pheo (Total) Fluorometer | −0.02 | 0.930 | 0.881 | 11 | 4 |

the chlorophyll red-fluorescing algal cells, irrespective of their size. Results from these counts are presented in detail elsewhere (BLANCHOT *et al.*, in press).

## RESULTS

### *Size distribution of Chl* a

Size fractionations were performed during two contrasting climatic periods in the western tropical Pacific Ocean. The first one (September 1987) was an El Niño event without equatorial upwelling at 165°E, the other, in 1988 and 1989, being a non-El Niño period with strong equatorial upwelling (BLANCHOT *et al.*, 1989). A variety of situations were observed: the top of the nitracline (defined as the first level where $NO_3 > 0.1\,\mu M$) varied from 140 m in the most oligotrophic regions around 15°S, to the surface in upwelled waters. The concentration of Chl *a* in the Chl *a* maximum varied from 0.22 to 0.68 mg $m^{-3}$. Temperature at the depth of the Chl *a* maximum ranged from 22.9 to 29.0°C depending on the season, latitude or hydrological structure. In spite of the great diversity of situations encountered, the Chl *a* size distribution was clearly related to nutrients. In the oligotrophic layer ($NO_3 < 0.1\,\mu M$), whose depth varied from 40 to 130 m, Chl $a < 1\,\mu m$ always dominated and represented 60% of total Chl *a* on the average, whatever the latitude or the depth (Fig. 2). The peak of Chl $a < 1\,\mu m$ typically occurred just at the top of the nitracline, with the greatest Chl $a > 1\,\mu m$ or just above. Within the nitracline and below it, Chl $a > 1\,\mu m$ invariably predominated and was about 62% of total Chl *a* (Fig. 2). In nutrient-rich waters, no clear relationship was established between percentage of Chl $a < 1\,\mu m$ and nitrate concentration for any given depth. However, a slight but significant decrease with depth appeared in the smaller fractions ($<1\,\mu m$, $<0.8\,\mu m$), irrespective of nitrate concentration (Fig. 2). This also was observed in the equatorial Atlantic (HERBLAND *et al.*, 1985) and in the central Pacific (PEÑA *et al.*, 1990).

The only exception encountered to this general pattern of chlorophyll size distribution was due to the blooming of *Oscillatoria* spp. (Syn. *Trichodesmium*), observed by eye and epifluorescence microscopy in the upper layer (Fig. 2, stations at 8° and 10°S in April 1988 and at 15°S in November 1989). In this particular case the trichomes of *Oscillatoria* were retained on the 1 $\mu m$ pore size Nuclepore filters, and hence Chl $a > 1\,\mu m$ was well above 50% in surface nutrient-poor waters. *Oscillatoria* often was observed in surface waters

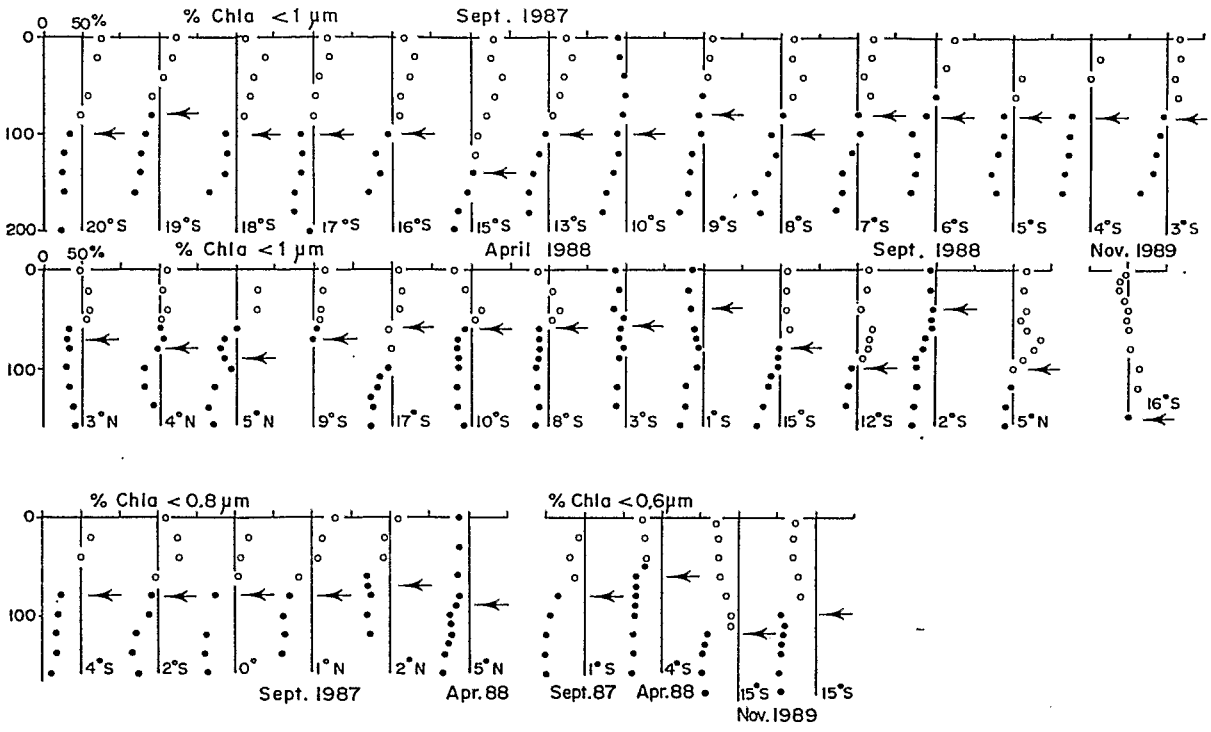


Fig. 2. Depth distribution of Chl *a* (in % of total) at 165°E in the <1 µm, <0.8 µm and <0.6 µm fractions. Open circles: $NO_3$ < 0.1 µM. Full circles: $NO_3$ > 0.1 µM. Arrows: depth of the chlorophyll maximum.

from 16° to 8°S in April 1988 and November 1989, but neither in September 1987 nor in September 1988. The genus *Oscillatoria* is regarded as rather common in tropical open oceans (CARPENTER, 1983) and would therefore constitute a significant exception to the Chl *a* < 1 µm dominance in oligotrophic waters of the tropical regions.

At 10°S in September 1987, nitrate-rich waters reached the surface ($NO_3$ = 0.56 µM). Chlorophyll *a* > 1 µm was dominant in the whole photic zone (Fig. 2). Exactly the same size distribution was observed in the equatorial upwelling which extended from 3°S to 5°N in April 1988 and from 5°S to 2°N in September 1988, and which brought to the surface, waters containing up to 4 µM of nitrate (Fig. 2, see BLANCHOT *et al.*, 1989, for details on nutrient distribution). A similar chlorophyll size pattern was observed in the equatorial upwelling of the Atlantic Ocean by HERBLAND *et al.* (1987).

When the concentration of Chl *a* < 1 µm is directly compared to that of Chl *a* > 1 µm without any space, time or hydrological considerations, two groups of points appear to be clearly separated by a line close to $Y = X$ (Fig. 3a). Above this line, the points represent the relative Chl *a* size distribution in the oligotrophic upper layer, and below this line the points represent the situation in the nutrient-rich lower layer or in the upwelling. Thus, a striking coincidence is observed between chlorophyll dominance in the <1 µm and >1 µm size classes and nitrate concentration below and above 0.1 µM. Exactly the same pattern was obtained from size fractionations in the open tropical Atlantic (Fig. 3b and c).

In the oligotrophic layer, Chl *a* < 0.6 µm and Chl *a* < 0.8 µm, respectively, accounted for 27 and 45% of total Chl *a* on the average, as against 8 and 23% in nutrient-rich waters (Table 3). Results of all the size fractionations performed with the same method in both the Atlantic and the western Pacific (Table 3) provided no evidence of any major Chl *a* size

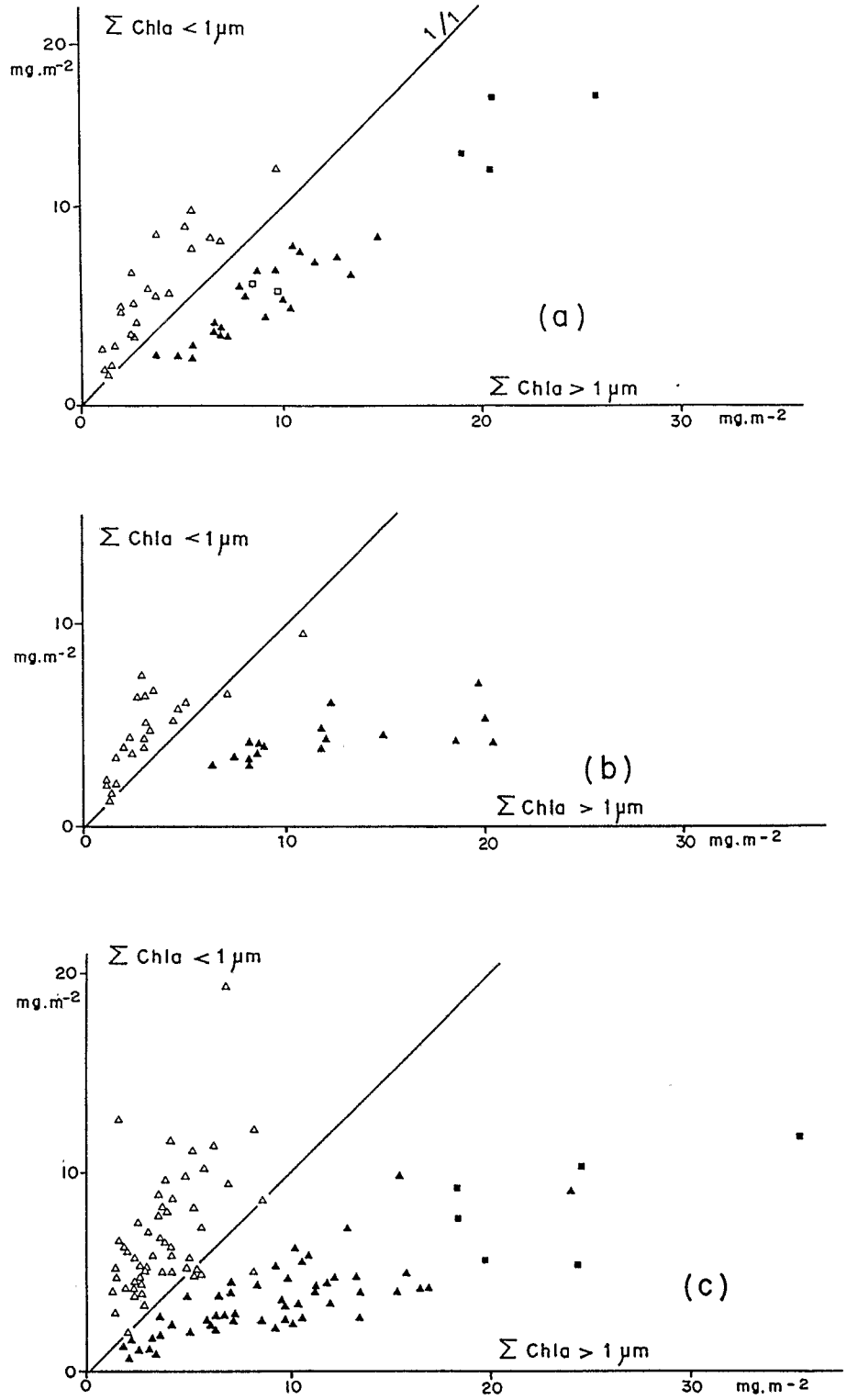


Fig. 3. Depth-integrated values of Chl $a < 1\ \mu m$ vs Chl $a > 1\ \mu m$. (a) PROPPAC data (165°E); Pacific Ocean; 29 profiles. (b) PIRAL data (5°N, 20°W and 12°N, 22°W; June, July and August 1986); Atlantic Ocean; 21 profiles (data not published). (c) FOCAL data (transects at 4°W, 23°W and 35°W from 13°N to 7°30'S, July 1983, January and July 1984). Redrawn from HERBLAND *et al.* (1985); Atlantic Ocean; 61 profiles. Open triangles: upper layer ($NO_3 < 0.1\ \mu M$). Open squares: the same, but with *Oscillatoria* (see text). Shaded triangles: deeper layer ($NO_3 > 0.1\ \mu M$). Shaded squares: upwelling ($NO_3 > 0.1\ \mu M$ at surface).

*Table* 3. *Size structure of Chl* a *in the two different situations, with and without nitrate in the layer. All data were collected by the ORSTOM Group (methanol method): FOCAL, PIRAL and PROPPAC programmes (nine cruises, 230 stations). Mean relative concentrations (%), standard deviation (S.D.) and number of vertical profiles* (n)

| Size class ($\mu$m) | Cruises | Nitrate-poor layer ($NO_3 < 0.1\ \mu M$) | | | Nitrate-rich layer ($NO_3 > 0.1\ \mu M$) | | |
|---|---|---|---|---|---|---|---|
| | | % | S.D. | *n* | % | S.D. | *n* |
| <0.6 | FOCAL | 32.8 | 13.5 | 14 | 10.3 | 8.4 | 13 |
| | PROPPAC | 27.3 | 2.8 | 3 | 8.4 | 5.3 | 3 |
| <0.8 | FOCAL | 50.0 | 10.4 | 17 | 14.0 | 5.6 | 19 |
| | PROPPAC | 44.7 | 6.0 | 3 | 22.5 | 7.0 | 7 |
| <1.0 | FOCAL | 64.5 | 9.7 | 53 | 29.1 | 7.0 | 57 |
| | PIRAL | 59.5 | 7.2 | 20 | 27.3 | 5.0 | 17 |
| | PROPPAC | 60.3 | 8.6 | 24 | 37.8 | 4.5 | 26 |
| <2.0 | FOCAL | 72.0 | 6.1 | 8 | 58.3 | 8.6 | 9 |
| <3.0 | FOCAL | 74.1 | 11.4 | 26 | 66.9 | 8.1 | 42 |
| | PIRAL | 65.8 | — | 1 | 57.1 | — | 1 |
| | PROPPAC | — | — | — | 69.3 | 8.0 | 2 |
| <10.0 | FOCAL | 84.0 | 9.3 | 7 | 87.2 | 6.4 | 8 |
| <20.0 | FOCAL | 93.2 | 1.5 | 5 | 93.0 | 1.6 | 2 |

difference between the two oceans, especially within the best sampled size classes: thus, 120 profiles of size fractionation on 1 $\mu$m filters show that the contribution of Chl $a < 1\ \mu$m in the oligotrophic upper layer is of the same magnitude everywhere. The greatest decrease in Chl *a* contribution between the nutrient-poor and nutrient-rich waters, was observed in the <0.6 and <0.8 $\mu$m fractions. Conversely, the 1–3 $\mu$m fraction increases from 10% of total Chl *a* in the poor top layer, to about 40% in the rich deeper layer (Table 3). One extreme situation was encountered in the Dome of Guinea where chlorophyll maximum concentrations reached values as high as 1.42 mg $m^{-3}$ between 30 and 50 m: up to 80% of total Chl *a* there belonged to the >1 $\mu$m fraction. This result is consistent with the general trend of a relative enhancement of the mean cell diameter when Chl *a* concentration increases, as previously noted by LE BOUTEILLER and HERBLAND (1984) and HERBLAND *et al.* (1985).

*Distribution of cyanobacteria and eucaryotic microalgae*

Cells were counted on two transects at 165°E and during the five fixed position studies. Picocyanobacteria were 5–20 times more abundant than eucaryotic microalgae in oligotrophic waters (see Fig. 6 later), as is generally the case in tropical and subtropical regions (MURPHY and HAUGEN, 1985; ITURRIAGA and MITCHELL, 1986; GIESKES and KRAAY, 1986; LI and WOOD, 1988). The relative abundances most often estimated from 20°S to 6°N were 1000 cyanobacteria for 100 microalgae (cells $ml^{-1}$) in the mixed layer. However, these abundances varied widely with depth and station location (BLANCHOT *et al.*, in press). The maximum cyanobacteria generally occurred just above the Chl *a* maximum, often in nitrate-depleted waters. The eucaryotic microalgae were scarce in surface waters

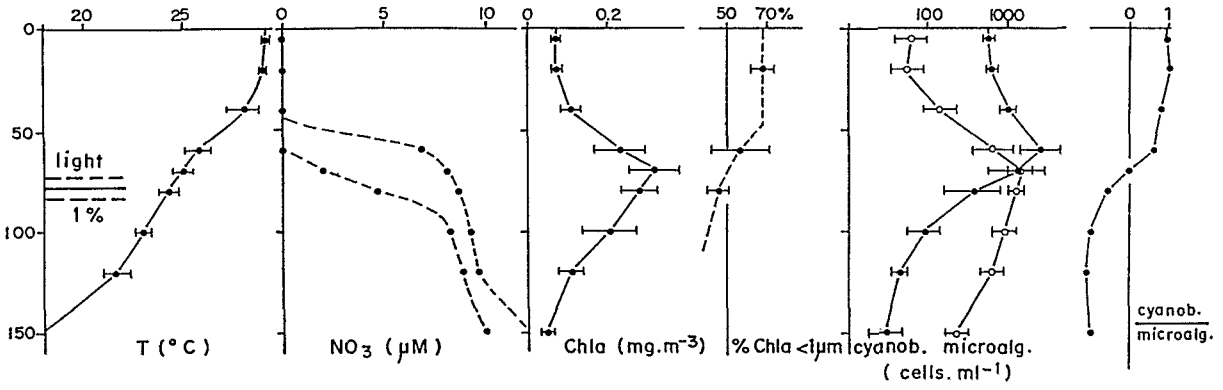


Fig. 4. Results of the 8 day study at 3°N, 165°E in a Typical Tropical Situation (PROPPAC 1 cruise, September 1987). Mean profiles (±S.D.) of temperature (°C), Chl *a* (mg $m^{-3}$), % Chl *a* < 1 µm, number of cyanobacteria and microalgae (cells $ml^{-1}$, log scale) and ratio cyanobacteria/microalgae (in log). The maximum and minimum limits of nitrate concentration are indicated, and also the mean depth of the euphotic zone (1% level, eight profiles of light penetration).

(<1000 cells $ml^{-1}$) and displayed a maximum at the depth of the Chl *a* maximum, as observed by GLOVER *et al.* (1986) in the Sargasso Sea and EPPLEY *et al.* (1988) in the North Pacific Central Gyre. The ratio of cyanobacteria to microalgae decreased from the lower part of the mixed layer to the bottom of the photic zone (Fig. 4). Similar patterns were noted in the northeastern tropical Pacific by MAKEYEVA (1988) and in the Sargasso Sea by GLOVER *et al.* (1988a). Microalgae numerically dominated only when cyanobacteria decreased below about 1000 cells $ml^{-1}$, which occurred in the lower part of the photic zone, generally below the 1% light depth. In upwelled waters, cyanobacteria predominated from the top to the bottom of the euphotic layer, but their numerical predominance steadily decreased downwards (Fig. 5).

Nitrate-depleted waters are relatively richer in cyanobacteria while nitrate-rich ones present a higher contribution of eucaryotic microalgae (Fig. 6). A typical distribution is given in Table 1. Points representing the most oligotrophic surface waters are near the *Y*-axis (high cyanobacteria/microalgae number ratios). Maximum cell abundance of both

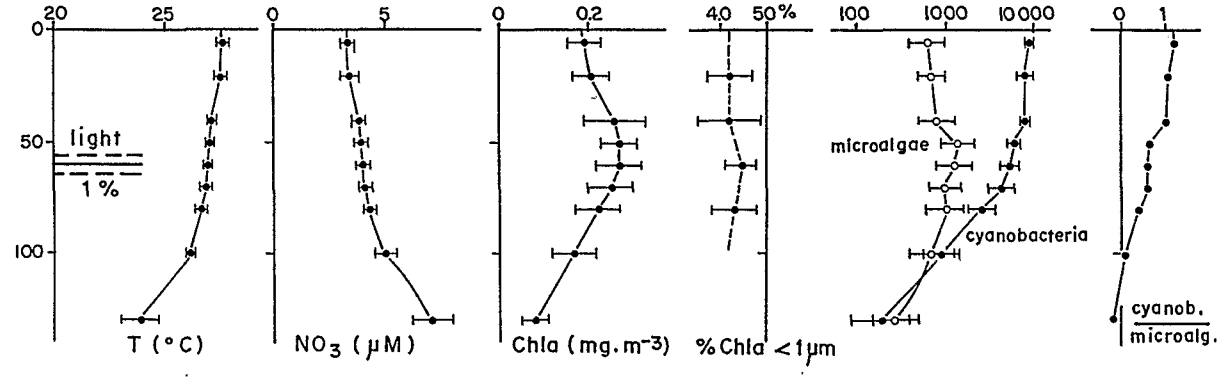


Fig. 5. Results of the 8 day study in the equatorial upwelling at 0°, 165°E (PROPPAC 2 cruise, April 1988). Same legend as Fig. 4.

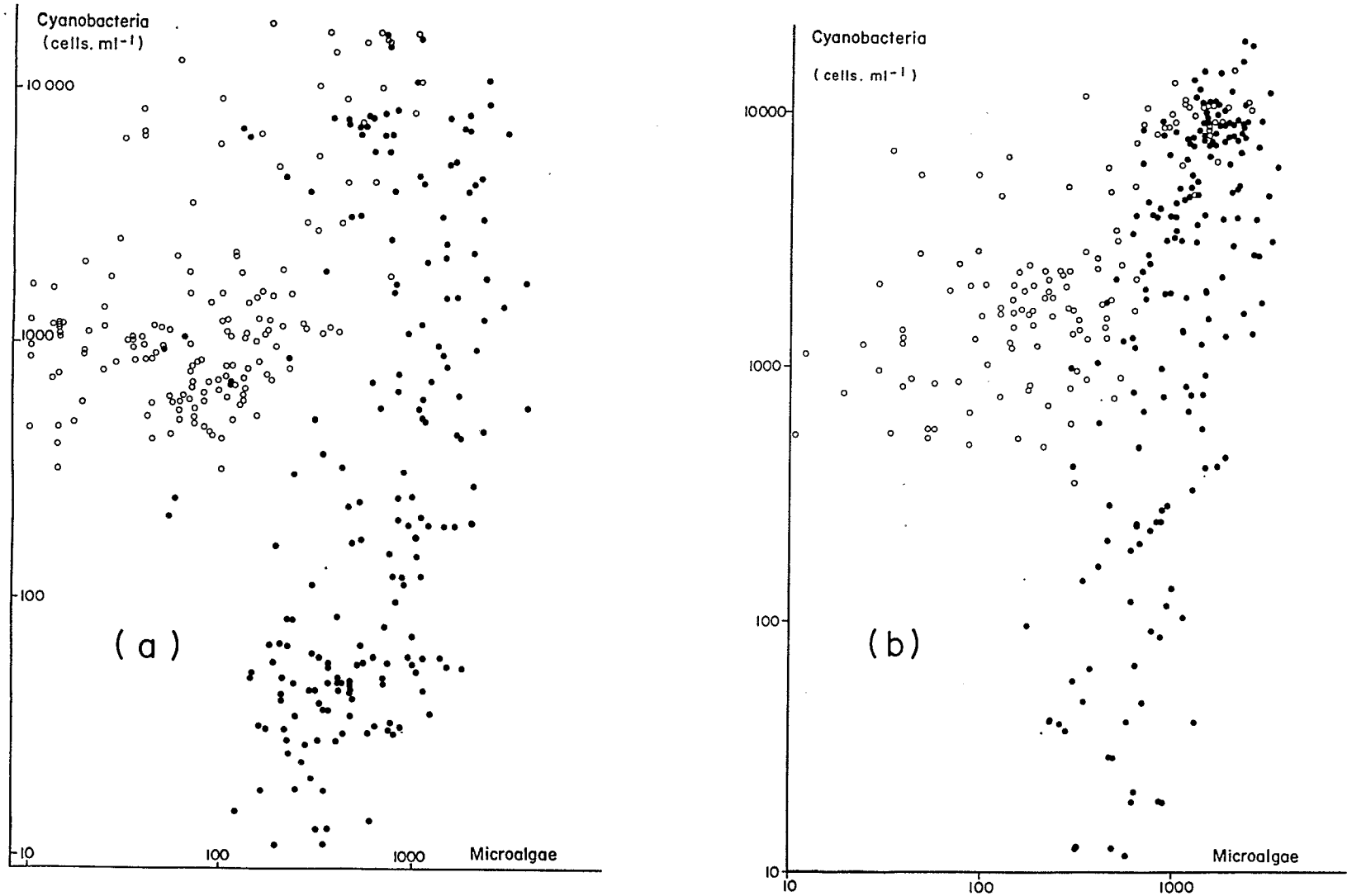


Fig. 6. Cyanobacteria vs microalgae at 165°E (log scales). (a) September 1987, ENSO event (PROPPAC 1); 41 profiles from 20°S to 5°N. (b) September 1988, non ENSO period (PROPPAC 3); 31 profiles from 19°S to 6°N. Open circles: $NO_3 < 0.1\ \mu M$. Shaded circles: $NO_3 > 0.1\ \mu M$.

cyanobacteria and microalgae correspond to the upper upwelled waters (see Fig. 5). Points from the deep Chl *a* maximum are just above or below the line $y = x$. Counts from the bottom of the photic zone are near the $X$-axis (low ratios).

Size fractionations were performed at seven different positions between 17°S and 5°N, including two stations in the equatorial upwelling (Fig. 7). Results show that an average of 75% of cyanobacteria passed through 1 $\mu$m filters ($n$ = 72, S.D. = 15%). A slight but significant decrease in the percentage of cyanobacteria in the <1 $\mu$m fraction was observed from the surface to about 100 m depth (Fig. 7), as also reported by GLOVER *et al.* (1985, 1986), LI and WOOD (1988), and OLSON *et al.* (1990a) in the Atlantic Ocean. An average of 94% of eucaryotic microalgae exceeded 1 $\mu$m size. Our cell counts did not show any significant change with depth of the contribution of microalgae in the >1 $\mu$m fraction, in contrast with the observations of GLOVER *et al.* (1988a) and LI and WOOD (1988) in the North Atlantic. The abundance of nutrients, at the surface or at whatever depth, induced higher cell numbers of both cyanobacteria and microalgae but did not change their respective size distributions below and above 1 $\mu$m (Fig. 7). Thus, in tropical ocean waters, the 1 $\mu$m Nuclepore filter appears to separate efficiently the eucaryotic microalgae from the procaryotes within the whole photic zone for both nutrient-rich waters and poor ones, and whatever the cell abundances may be. Schematically, the <1 $\mu$m fraction contains only about 6% of eucaryotic microalgae, but the bulk of cyanobacteria and prochlorophytes.

*Size distribution of Chl* b

The size distribution of Chl *b* was studied in September 1988 with a spectrofluorometer in three typical situations, at 2°S in the equatorial upwelling system, and at 9°S and 5°N in two Typical Tropical Structures. In the mixed layer at 5°N, the Chl *b* content in the <1 $\mu$m fraction was very low, in both absolute and relative terms (Fig. 8). Concentrations of Chl *b* also were relatively weak in the equatorial upwelling. On the contrary, Chl *b* was abundant at the depth of the nitracline, i.e. in the deep Chl *a* maximum, especially in the smaller fraction (Chl *b* < 1 $\mu$m = 68% of total Chl *b* in this layer on the average). Chlorophyll *b* is

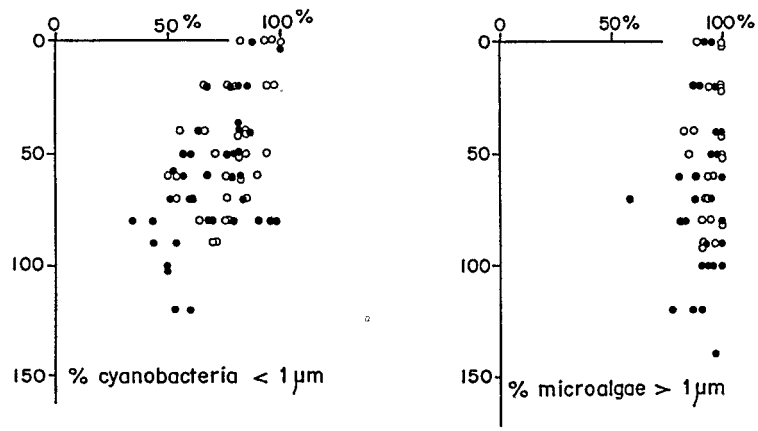


Fig. 7. Depth distribution of the relative concentration of cyanobacteria in the fraction <1 $\mu$m and of microalgae in the fraction >1 $\mu$m. Seven profiles collected at 165°E in April and September 1988. Open circles: $NO_3 < 0.1$ $\mu$M. Shaded circles: $NO_3 > 0.1$ $\mu$M.

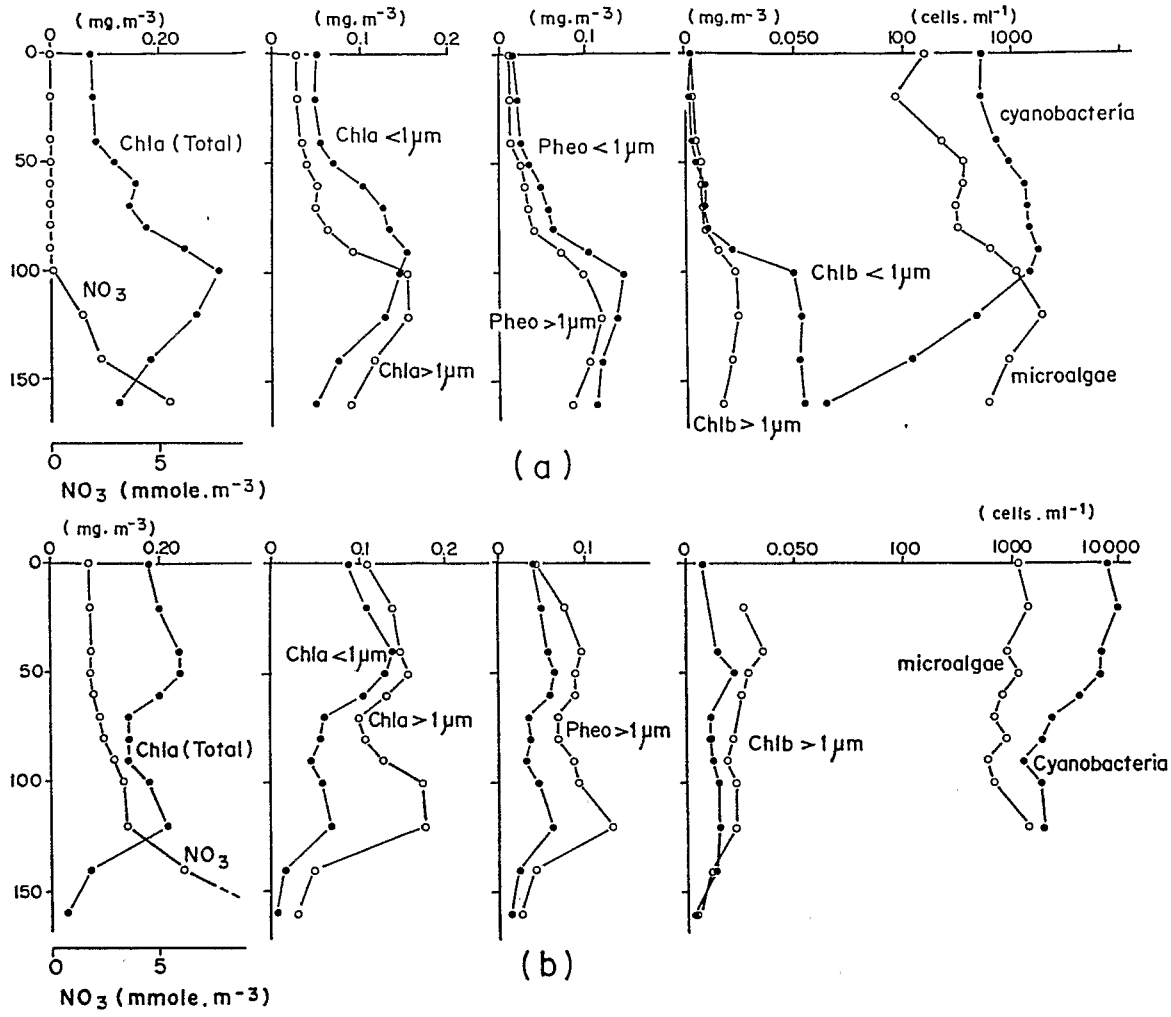


Fig. 8. Depth distribution of Chl *a* and pheophytin (fluorometer), Chl *b* (spectrofluorometer) in the <1 µm and >1 µm fractions, $NO_3$, cyanobacteria and microalgae (September 1988). (a) 5°N, 165°E (Typical Tropical Structure). (b) 2°S, 165°E (equatorial upwelling system).

known to be an accessory pigment of Chlorophyceae, Prasinophyceae and Euglenophyceae, but also of prochlorophytes (CHISHOLM *et al.*, 1988; NEVEUX *et al.*, 1989). Since microscopic counts have indicated only very low numbers of eucaryotic microalgae in the <1 µm fraction (Fig. 7), high concentrations of Chl *b* < 1 µm in the nitracline of the TTS can be interpreted as being due to abundant prochlorophytes in this size class. Conversely, low concentrations of Chl *b* < 1 µm in the upper oligotrophic waters suggest only low prochlorophyte biomass in that layer, unless very numerous pigment-poor cells happen to be present in the surface waters, as was recently observed in the North Atlantic Ocean by OLSON *et al.* (1990b) and in the northwestern Mediterranean Sea by VAULOT *et al.* (1990).

In addition, results in Table 2 show a close relationship between the so-called pheophytin estimated fluorometrically (YENTSCH and MENZEL, 1963), and the Chl *b* measured on a spectrophotometer as well as on a spectrofluorometer. Maximum concentrations of "pheophytin" were measured systematically in the <1 µm fraction at the depth of the Chl *a* maximum or just below it in the western Pacific (see Table 1 and Fig. 8a) but also in the equatorial Atlantic (HERBLAND *et al.*, 1985). The distribution of "pheophytin" and Chl *b* thus would be similar (HERBLAND, 1988), which strongly suggests the presence of minute

cells such as prochlorophytes in the lower part of the photic zone. These cells would contribute significantly to the formation of the deep Chl *a* maximum.

## DISCUSSION

### *Chlorophyll a size distribution*

Chlorophyll fractionations clearly show the major effect of nitrate presence on the vertical distribution of the different size classes in the western Pacific, as in the equatorial Atlantic (Fig. 2, Table 3). Typically, either waters are nitrate-depleted ($NO_3 < 0.1\ \mu M$), in which case $<1\ \mu m$ chlorophyll predominates, or waters are richer in nutrients ($NO_3 > 0.1\ \mu M$) and then the major part of chlorophyll is contained in the $>1\ \mu m$ fraction. The $<0.6\ \mu m$ and $<0.8\ \mu m$ Chl *a* contribution also decreases rapidly below the top of the nitracline (Fig. 2).

Hence, a strict comparison of our data with results from similar environments requires size fractionations in the oligotrophic layer to have been separated from those in nutrient-rich waters. Such a requirement is seldom met. Nevertheless, our values are in the ranges reported by LI *et al.* (1983) in the eastern tropical Pacific, by PLATT *et al.* (1983) and GIESKES and KRAAY (1986) in the tropical Atlantic. More recently, PEÑA *et al.* (1990) reported that Chl $a < 10\ \mu m$ represented more than 75% of total Chl *a* in the central Pacific at 135°E from 15°S to 15°N, with a mean of 87% very close to the values found in the Atlantic Ocean (Table 3). Furthermore, PEÑA *et al.* (1990) found that Chl $a < 1\ \mu m$ predominated above the Chl *a* maximum north and south of the equator, within the oligotrophic mixed layer, while Chl $a > 1\ \mu m$ exceeded 50% in nearly all cases of high nutrient concentration and especially below the Chl *a* maximum.

These observations, added to the 120 profiles analysed in Table 3, lead us to the conclusion that chlorophyll presents a typical size distribution in both the Atlantic and the Pacific open tropical oceans. Any exceptions may be due to major coastal circulation and island mass effects (HERBLAND *et al.*, 1987) or to blooms of *Oscillatoria* in surface waters (Fig. 2). The numerous and diverse environmental structures analysed in the Atlantic and Pacific Oceans clearly bring out the rapid change occurring in the mean size distribution of chlorophyll at the top of the nitracline. All other environmental factors such as light, temperature, density or mixing seem of minor importance. To our knowledge, the only clear exception to the typical Chl *a* size distribution described above is the marked predominance of Chl $a < 1\ \mu m$ observed by CHAVEZ (1989) in the euphotic zone of the equatorial upwelling east of 140°W. Many data reported in the literature suggest that an increase rather than a decrease in the mean cell size of phytoplankton might be expected to occur in meso- or eutrophic waters, with some exceptions (SOURNIA, 1982). For example, a nitrate-dependent bloom of *Synechococcus* was observed in the Sargasso Sea by GLOVER *et al.* (1988b), whereas in the equatorial upwelling of the Atlantic Ocean, $>1\ \mu m$ cells always predominated, as indicated by the size distribution of Chl *a* (HERBLAND *et al.*, 1987). Futhermore, in the intense upwelling of the eastern equatorial Pacific, cells such as diatoms were observed in significant densities by DESROSIERES (1969) and CHAVEZ *et al.* (1990), certainly entailing an increase in the mean diameter of the phytoplankton cells and hence a change of the Chl *a* size structure. Based on more than 600 analyses of Chl $a < 1\ \mu m$ in the presence of nitrate, we assume that the predominance of Chl $a < 1\ \mu m$ observed by CHAVEZ (1989) in the Pacific upwelling reflects an atypical situation, and does not contradict our findings.

*Comparison of Chl a size distribution and cell abundances*

Since changes in the predominance of Chl $a < 1\ \mu m$ or Chl $a > 1\ \mu m$ in the absence or presence of nitrate have been observed in most studies dealing with pigment size fractionations, they very probably reflect two different structures of phytoplankton communities. We did not measure the Chl *a* content of each cell counted, but we were able to compare the Chl *a* concentration in each size class with the related cell abundances of both procaryotic and eucaryotic phytoplankton. Since the great majority of cyanobacteria passed through the 1 $\mu m$ filters, especially in the near-surface water samples, while the bulk of microalgae exceeded 1 $\mu m$ (Fig. 7), one may wonder what kind of relationship exists between Chl $a < 1\ \mu m$ and cyanobacteria abundance and between Chl $a > 1\ \mu m$ and eucaryotic microalgae.

Let us consider Figs 3 and 6. The oligotrophic layer appears to be dominated by both cyanobacteria and Chl $a < 1\ \mu m$ whereas the nutrient-rich waters contain mainly eucaryotic microalgae and Chl $a > 1\ \mu m$. Direct comparison of cyanobacteria with Chl $a < 1\ \mu m$ demonstrates that both indexes of biomass are significantly correlated (Fig. 9). Similarly, the number of microalgae is closely related to the Chl $a > 1\ \mu m$ content in the nitrate-rich layer (Fig. 9). These relationships prove that the variations of Chl $a < 1\ \mu m$ in the upper layer are partly explained by changes in the cyanobacteria, whereas Chl $a > 1\ \mu m$ reflects the abundance of microalgae in the lower layer.

In situations where the mixed layer becomes more and more oligotrophic and poor in chlorophyll, both cyanobacteria and eucaryotic algae decrease in number but the ratios cyanobacteria/eucaryotes and Chl $a < 1\ \mu m$/Chl $a > 1\ \mu m$ both tend to increase. Consequently, microalgae seem to disappear faster than cyanobaceria as oligotrophic conditions become more severe. This observation implies that cyanobacteria may be better equipped than eucaryotes to resist the depletion of nutrients in oceanic surface waters, as previously suggested by WYMAN *et al.* (1985).

Below the chlorophyll maximum, cyanobacteria very often disappeared within less than 20 m (BLANCHOT *et al.*, submitted), so that the low but not negligible concentrations of

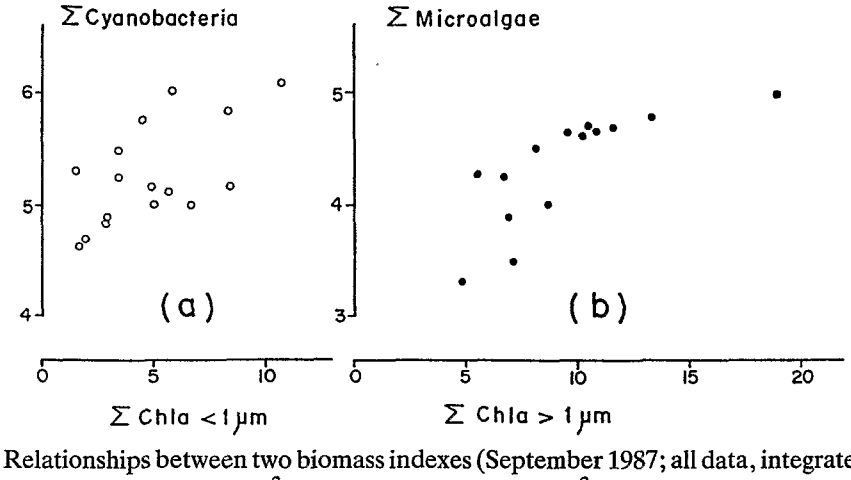


Fig. 9. Relationships between two biomass indexes (September 1987; all data, integrated values). (a) Cyanobacteria (log cells $cm^{-2}$) vs Chl $a < 1\ \mu m$ (mg $m^{-2}$) in the $NO_3$ <0.1 $\mu M$ layer. The regression equation is $y = 4.75 + 0.106x$; $r = 0.626$; $n = 16$; $P < 0.01$. (b) Microalgae (log cells $cm^{-2}$) vs Chl $a > 1\ \mu m$ (mg $m^{-2}$) in the nitrate-rich layer. The regression line equation is $y = 3.36 + 0.104x$; $r = 0.755$; $n = 14$; $P < 0.01$.

Chl *a* estimated in the <1 μm fraction in the lower layer would have to be contained by other minute cells. In most cases, a multitude of prochlorophytes may occur at the bottom of the euphotic layer (CHISHOLM *et al*, 1988; NEVEUX *et al.*, 1989; OLSON *et al.*, 1990b), as revealed here not only by high concentrations of Chl *b* (and "pheophytin") in the submicronic fraction (Fig. 8) but also by relatively high concentrations of Chl *a* < 1 μm in samples without cyanobacteria (see Table 1, 100 m depth). However, the biomass of prochlorophytes in terms of carbon would remain low in such waters, probably much below that of the eucaryotic phytoplankton (LI and WOOD, 1988).

Near the top of the nitracline, a transition zone successively contained the peaks of Chl *a* < 1 μm and cyanobacteria, and then the peaks of Chl *a* > 1 m and eucaryotic microalgae (see Fig. 8a).

When the concentration of Chl *a* in the fraction <1 μm is divided by the number of cyanobacteria, a range of 10–90 fg of Chl *a* per cyanobacterium is obtained using all the available data collected in nitrate-depleted waters at 165°E. These values only give an order of magnitude: they could well be more or less overestimated owing to the presence of some prochlorophytes and eucaryotes in the smaller fraction, or underestimated because of cyanobacteria retained on the 1 μm filters. Nevertheless, the values are consistent with the few estimates recently reported for similar regions. High values of cellular Chl *a* content, up to 100 fg Chl *a* per cyanobacterium, were considered possible by PREZELIN *et al.* (1986). GLOVER *et al.* (1988a) have found that Chl *a* concentration in *Synechococcus* cells could vary from 1 to near 24 fg Chl *a* per cell in the Sargasso Sea.

In the surface layer (0–20 m), a mean value of 80 fg Chl *a* per cyanobacterium ($n = 30$) was obtained from data collected during the field position study at 3°N (Fig. 4), whereas this value was only 8 fg Chl *a* per cyanobacterium in the equatorial upwelling ($n = 16$; Fig. 5). Similarly, when the Chl *a* > 1 μm concentration was divided by the number of eucaryotic microalgae, the estimated mean cell content was 330 and 180 fg Chl *a* per microalga outside and inside the upwelling respectively (layer 0–20 m, Figs 4 and 5). These changes of Chl *a* cell content show that the equatorial divergence induces a much larger increase in cell numbers (more than 11 times on the average) than in chlorophyll concentration (about 2.6 times) in the well-lit surface layer. All the profiles of Chl *a* size structure and cell counts show similar properties in the upwelled waters, at 10°S as well as in the equatorial belt. Cyanobacteria with the highest and lowest Chl *a* content are observed in the oligotrophic layer and in upwelled waters, respectively. Eucaryotic microalgae, very numerous in the upwelling, would be about twice as poor in Chl *a* per cell in this system as out of it. Because the Chl *a* cell content decreases much more within cyanobacteria than within microalgae, from oligotrophic to upwelled surface waters, the >1 μm fraction contains more chlorophyll than the <1 μm fraction. Cell abundance and Chl *a* concentration are thus proving to be two quite different biomass indexes. Cell counts give an overestimated image of the phytoplankton biomass in the upwelling system while, conversely, Chl *a* concentration would tend to underestimate the upwelling enrichment in comparison with the mixed layer of the TTS.

In upwelled waters, the ratio cyanobacteria/microalgae gradually decreased downwards (Fig. 5), as it did below the top of the nitracline of the two layered structure (Fig. 4). The increase that we observed everywhere in the relative number of microalgae from top to bottom of the nutrient-rich layer provides clear evidence of the effect of light on the vertical distribution of phytoplankton, while the other environmental factors seem of minor importance. This reflects the superiority of eucaryotes over cyanobacteria in

utilizing the deeply penetrating light for photosynthesis and growth, as noted previously by GLOVER *et al.* (1987) and LI and WOOD (1988).

## CONCLUSIONS

One of the most consistent features in our data was the typical depth distribution of Chl *a*, especially in the <1 μm and >1 μm fractions, which presented exactly the same pattern whatever the season, position or hydrological structure in the western Pacific at 165°E from 6°N to 20°S, as in the Atlantic between 4°W and 35°W and from 13°N to 7°30′S. Similar profiles also were observed in the central Pacific at 135°W from 15°N to 15°S by PEÑA *et al.* (1990). Furthermore, phytoplanktonic cells showed some well-defined vertical distributions, very similar to those previously observed in tropical and subtropical regions (BLANCHOT *et al.*, in press). In spite of numerous and diverse environmental conditions investigated, including an ENSO event, we never detected any clear atypical situation: chlorophyll size profiles as well as profiles of eucaryotic and procaryotic algae were always consistent with the typical ones, except when blooms of *Oscillatoria* occurred in oligotrophic surface waters.

Comparison between all the algal cell abundances and all the size distributions of Chl *a* and *b* and pheophytin, results in some well-substantiated conclusions. The size structure of Chl *a* proved to reflect the relative abundance of cyanobacteria and microalgae in the tropical regions. Typically, cyanobacteria would be the dominant component of phytoplankton in terms of Chl *a* biomass in the oligotrophic mixed layer. On the contrary, the Chl *a* biomass of eucaryotic microalgae would predominate in all the nutrient-rich water masses, irrespective to the depth of the nitrate appearance. The top of the nitracline would act as a boundary layer between the domain of the cyanobacteria upwards and the domain of the microalgae (and possibly prochlorophytes) downwards. Logically, the relationships established in the western Pacific between chlorophyll and cell numbers also should exist throughout the equatorial belt of the Atlantic Ocean. Therefore, results of Chl *a* fractionations performed in the Atlantic Ocean also can be interpreted in terms of cyanobacteria or microalgae predominance. The striking similarity of all the chlorophyll size profiles according to the nitracline in both the Atlantic and Pacific tropical oceans, strongly suggests that the size distribution of phytoplankton would be one of the most significant properties of the Typical Tropical Structure (HERBLAND and VOITURIEZ, 1979).

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