Carbon fixation and productivity index in relation to chlorophyll and light in the equatorial Atlantic Ocean

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ABSTRACT

During a 14 day study at a fixed position at the Equator (4° W) in February, 1979 (SOP cruise), concentrations of chlorophyll a *measured in samples taken between 25 and 50 m depth showed marked changes from day to day. Similarly, the amounts of carbon fixed during* in situ *incubations also varied. Hence, highly significant regression lines can be calculated between production and chlorophyll for each sampling depth.*

These equations make it possible to calculate easily the primary production from the sole chlorophyll data, provided that the available light intensities are of the same order of magnitude. They are used to predict the production for 17 stations carried out during three other cruises at the same place (0°, 4° W): CIPREA 2 (3 stations, Apr., 1979), CIPREA 4 (13 stations, Oct., 1979) and CIPREA 5 (1 station, Jan., 1980). 72 values of production are so calculated: they are not statistically different from the measured values of in situ *carbon fixation.*

If the profile of chlorophyll is mainly regulated by the nitrate availability, in contrast the nitrate concentration has no direct effect upon the pattern of the vertical profile of the productivity index (mg C.mg Chla^{-1}.h^{-1}*) which presents always a maximum between 5 and 15 m, and decreases regularly downwards. Consequently for an incident radiation close to the average, the vertical distribution of production, and in particular the depth of production maximum, are entirely defined by the chlorophyll profile.*

The productivity index varies approximately twofold at a given value of available radiation. Our observations support the hypothesis that these variations would be related to the concentration of chlorophyll. The mean cell size would also vary as a function of the chlorophyll content: in a chlorophyll poor water, cells would be very small and the productivity index is then very high.

A good adaptation to the environment, added to a specially high photosynthetic efficiency, characterize the natural assemblages of phytoplankton in the deep-sea tropical Atlantic Ocean. Effectively, a single relationship between productivity index and depth or available light allows to describe the primary production of the four cruises, even when two opposite situations are compared: the mixed layer is nitrate depleted in one case, not in the other, due to the input of nutrient rich waters by the equatorial divergence.

KEY WORDS : Primary production — Chlorophyll — Light — Equatorial Atlantic Ocean.

RÉSUMÉ

FIXATION DE CARBONE ET INDICE DE PRODUCTIVITÉ EN FONCTION DE LA CHLOROPHYLLE ET DE LA LUMIÈRE DANS L'ATLANTIQUE ÉQUATORIAL

Lors d'une étude de 14 jours en position fixe à l'Équateur (4° W) en février 1979 (Campagne SOP), les concentrations de chlorophylle a *mesurées dans les échantillons prélevés entre 25 et 50 m de profondeur ont présenté des changements importants d'un jour à l'autre. De même, les quantités de carbone fixé pendant les incubations* in situ *ont varié également, de sorte que des droites de régression hautement significatives peuvent être calculées entre production et chlorophylle pour chaque profondeur d'échantillonnage.*

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Ces équations permettent de calculer aisément la production primaire à partir des seules données de chlorophylle, dans la mesure où les quantités de lumière disponible sont du même ordre de grandeur. Elles sont utilisées pour prévoir la production de 17 stations réalisées lors de trois autres campagnes au même endroit (0° ; 4° W) : CIPREA 2 (3 stations, avr. 1979), CIPREA 4 (13 stations, oct. 1979) et CIPREA 5 (1 station, jan. 1980). 72 valeurs de production sont ainsi calculées : elles ne sont pas statistiquement différentes des quantités de carbone fixé mesurées in situ.

Si le profil de chlorophylle est principalement contrôlé par la disponibilité en nitrate, en revanche la concentration de nitrate dans l'eau n'a aucun effet direct sur la forme du profil vertical de l'indice de productivité (mg C.mg Chla^{-1}.h^{-1}) qui présente toujours un maximum entre 5 et 15 m, et décroît régulièrement vers le bas. En conséquence, pour une radiation incidente proche de la moyenne, la distribution verticale de la production, et en particulier la profondeur du maximum de production, sont entièrement définis par le profil de chlorophylle.

L'indice de productivité varie approximativement du simple au double pour une valeur donnée de lumière disponible. Nos observations supportent l'hypothèse que ces variations seraient reliées à la concentration de chlorophylle. La taille moyenne des cellules varierait également en fonction du contenu chlorophyllien : dans une eau pauvre en chlorophylle, les cellules seraient en moyenne très petites et l'indice de productivité est alors très élevé.

Une bonne adaptation au milieu, ajoutée à une efficacité photosynthétique particulièrement élevée, sont caractéristiques des peuplements phytoplanctoniques de l'océan Atlantique tropical du large. En effet, une seule relation entre indice de productivité et profondeur ou lumière disponible est suffisante pour décrire la production primaire des quatre campagnes, même lorsque deux situations opposées sont comparées : la couche homogène est épuisée en nitrate dans un cas, et pas dans l'autre, grâce à l'apport d'eaux riches en sels nutritifs par la divergence équatoriale.

MOTS-CLÉS : Production primaire — Chlorophylle — Lumière — Océan Atlantique équatorial.

INTRODUCTION

In every ecological study of primary production in the sea, the major factor to be considered is the phytoplankton biomass. Production is of course proportional to the biomass if variations of the latter are only quantitative, and not qualitative. One measurement of production for one given biomass would be theorically sufficient for knowing the production for any other biomass of the same nature in the same environmental conditions.

As a matter of fact, reality is much more complex, particularly because of the numerous possible physiological changes of the plankton, and because of imperfect production and biomass measurements. The two classical methods are indeed remarkably sentitive and precise (chlorophyll *a* by fluorimetry on acetone extracts, ^{14}C method with liquid scintillation counting), but their actual significance is still poorly known (GIESKES *et al.*, 1978, LORENZEN and JEFFREY, 1980, JEFFREY and HALLEGRAEFF, 1980, for chlorophyll, EPPLEY, 1980, and the PETERSON's revue, 1980, for the ^{14}C method).

Phytoplankton chlorophyll *a* represents only about 1 % of the cell dry weight (SHUTER, 1979) and the chlorophyll cell content is known to change with species, their physiological state, the measurement time (SOURNIA, 1974; OWENS *et al.*, 1980; HITCHCOCK, 1980; HUNTER and LAWS, 1981) and the light level or depth (ANDERSON, 1969; EPPLEY *et al.*, 1973; BANNISTER and LAWS, 1980).

Then, if the significance of the chlorophyll as a biomass index is so variable, the production by chlorophyll unit is expected to change in a wide range when the environmental factors fluctuate. Effectively, from *in situ* measurements in the eastern equatorial Pacific, the Sargasso sea and the Mauritanian upwelling area, MOREL (1978) reported that, from one station to another, the production by chlorophyll unit varied approximately in a ratio 10/1 at a given value of available light. However, in many cases, a certain correlation is nevertheless found in plankton between the light saturated rate of photosynthesis and the concentration of chlorophyll (STEELE and BAIRD, 1961; STEEMANN NIELSEN and HANSEN, 1961), or between the daily gross production and the euphotic zone content of chlorophyll (LEMOALLE, 1981). Necessarily, the environmental conditions must be similar (STEEMANN NIELSEN and JORGENSEN, 1962).

In order to get a good description of the primary production in a given area and above all an accurate estimate of this production, it is of prime importance to establish such relationships between carbon fixation and concentration of chlorophyll. This means that the collected set of data is then coherent and homogeneous enough to be considered as representative of a single plankton community for certain conditions of environment. It is then possible to study the problem of the actual significance of the biomass and production index on a statistically satisfying basis. In addition, measurements of chlorophyll concentration and available light allow a simple calculation of the carbon production (RYTHER and YENTSCH, 1957). PLATT *et al.* (1977) have shown that pigment concentration and light comprise the minimum data set which can be used for the prediction of primary production. To achieve this, a great number of measurements are needed.

The main difficulty is data collection: a complete day is necessary to get a single value of primary production at a given place. Approximately 12 days are required to calculate a significant mean, provided that the environmental properties did not vary excessively during sampling.

The distinguishing feature of the present work lies on the data used: 31 stations of *in situ* primary production, all of them carried out with the same methodology at the same position in the Equatorial Atlantic Ocean during four different cruises of the RV "Capricorne" in 1979.

METHODS

Four studies at a fixed position at the Equator (4° W) were performed with the RV "Capricorne":

- 14 days (from 5 to 18 Feb., 1979) during SOP cruise which formed a part of the First G.A.R.P. Global Experiment (F.G.G.E.).
- 3 days (from 22 to 24 Apr., 1979) during CIPREA 2 cruise.
- 13 days (from 20 Oct. to 1 Nov., 1979) during CIPREA 4 cruise.
- 1 day (18 Jan., 1980) during CIPREA 5 cruise.

Water sampling for measurements of nutrients, chlorophyll, particulate matter and primary production was performed at 8 levels, before sunrise, using a 30 l Niskin PVC bottle.

Nutrients (NO^-_3, NO^-_2, NH^+_4, PO^{--}_4) were immediately analyzed with a Technicon Autoanalyzer (Strickland and Parsons, 1972). For chlorophyll *a* measurement, each 180 ml sample was immediately filtered through a Whatman GF/C filter, ground and extracted in 90 % acetone for at least 2 h in a refrigerator. Samples were then analyzed on a fluorometer TURNER model 111 (Yentsch and Menzel, 1963) calibrated with pure chlorophyll *a* (Sigma) by spectrophotometric measurement.

Particulate matter was collected by filtration of 2 l samples through Gelman Type A filters. For carbon and nitrogen, a C H N analyzer (Hewlett Packard) was used, and the method of Menzel and Corwin (1965) was applied for phosphorus assessment. Seawater for production measurement (^{14}C method: Steemann Nielsen, 1952) was filtered through a 200 µm mesh net, poured in 300 ml bottles previously sterilized, and incubated *in situ* from sunrise to sunset (mean duration: 11 h). The radioactivity introduced (from 5 to 10 µCi per flask) was counted by liquid scintillation technique according to recommandations of Herbland (1977). After incubation, samples were collected on Sartorius filters, rinsed with filtered seawater and dried at 60 °C. At each station, two samples were filtered just after addition of $^{14}CO_2$. Their radioactivity was substracted from that of the samples.

The downwelling quantum irradiance was measured every day at about 13 h 00 (U.T.) with a Lambda quantameter. Data are given in percent of available light having passed through the sea surface (Jitts *et al.*, 1976). Total incident radiation was recorded from a pyranometer (Kipp and Zonen). Light received by samples during incubation (PAR: Photosynthetically Available Radiation) was computed according to Jitts *et al.* (1976).

RESULTS AND DISCUSSION

Relationship between production and chlorophyll

During the 14-day study of the SOP cruise, the vertical distribution of physical and chemical properties has shown important variations in the euphotic zone, due to the south-north fluctuation of the equatorial current system (Herbland and Le Bouteiller, 1982). So, depth of thermocline and nitracline varied from about 25 to 40 meters (Fig. 1). Presently abundance and distribution of phytoplankton are known to be strongly related to hydrological and chemical structure in that region (Herbland and Voituriez, 1979). As a matter of fact, vertical profiles of chlorophyll and carbon fixation effectively changed much from day to day, so that a wide range of values were obtained at several depths. Because of the relatively small variations of PAR received by the samples at each incubation level during the same time (Table I), pairs of chlorophyll and carbon fixation data can be gathered for each sampling depth (Fig. 2). Then the relationship between these two variables can be studied by depth for only small ranges of light. From 25 to 50 meters, computation of the least square linear regressions (Table II) shows that the relation between amount of fixed carbon and concentration of chlorophyll measured at the beginning of the incubation, is very good: coefficients of correlation range between 0.92 and 0.97 for the best described levels, *ie* those with numerous data and a wide range of chlorophyll concentrations. Station 12 data are not used in computation: the corresponding points evidently do not belong to the regression lines (Fig. 2, c, d, e), which can be interpreted as due to light deficiency (Table I). Above 25 m depth, all samples belonged to the nitrate depleted mixed layer, and below 50 m, only some data are available.

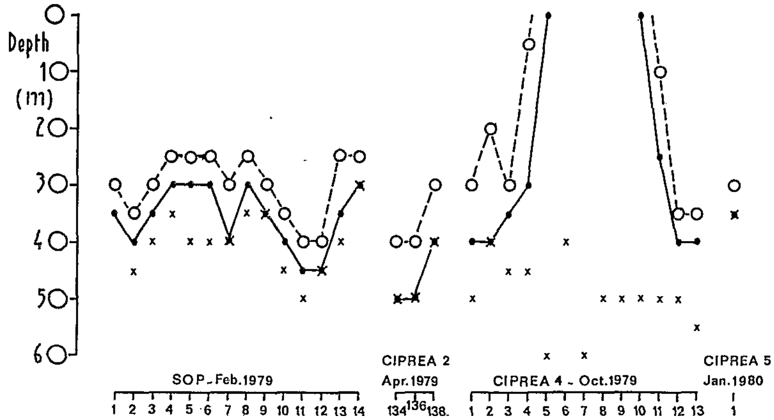

FIG. 1. — Depths of the chlorophyll maximum and of the top of the nitracline, for 31 stations at (0°; 4° W). Open circle: lower level. where $NO_3 < 0.05$ mM.m^{-3}. Filled circle: upper level where $NO_3 > 0.05$ mM.m^{-3}. Cross: depth of the maximum of Chlorophyll *a*
Profondeurs du maximum de chlorophylle et du sommet de la nitracline pour les 31 stations à (0°, 4° W). Point clair : *niveau inférieur où $NO_3 < 0.05$ mM.m^{-3}.* Point sombre : *niveau supérieur où $NO_3 > 0.05$ mM.m^{-3}.* Croix : *profondeur du maximum de chlorophylle* a.

TABLE I

$\overline{PAR}$ (Mean value of the photosynthetically available radiation, 10^{22}q.m^{-2}.h^{-1}) received by each sample during *in situ* incubation. SOP cruise

$\overline{PAR}$ (Valeur moyenne du rayonnement disponible pour la photosynthèse, 10^{22}q.m^{-2}.h^{-1}) reçu par chaque échantillon au cours de l'incubation in situ. *Campagne SOP*

Depth-(m)	Station number													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
0.....	189.8		172.3				255.6	161.5						
5.....				96.8	115.7	106.1			90.6	92.0		8.1	82.6	102.0
10.....	61.9			67.0		65.8	97.4	61.5			17.1			
15.....				49.1	57.8	50.9			52.8	46.0		4.7	45.0	52.0
20.....	2.1	44.8	35.9	38.7	46.3	40.3	67.0	42.3			12.8			
25.....				31.3	34.7	31.8		32.3	34.7	27.6			27.8	32.5
30.....	25.3	28.4	24.4	23.8	29.7	20.2	34.1	22.3	26.4	22.6	10.5			26.0
35.....	21.1	22.4	15.1	14.9	16.5	11.5	11.5	12.3	17.4	12.7	8.7	2.4	18.0	21.3
40.....	16.8	14.9	7.9	8.3	9.6	5.9		7.4	10.0	11.0	7.0	1.7	14.0	13.5
45.....		9.3						4.9	6.0	8.1	4.9	1.1		10.8
50.....	7.7	6.6	3.4				5.0		4.2		2.4	0.6	6.7	8.3
55.....												0.3	3.4	
60.....		3.9	2.0							2.1	1.5	0.1		
70.....			1.3											

The least square regression (model I) provides a predictive model, whereas the geometric mean method (model II) would be theorically more suitable to describe observations in the case of interdependant variables (LAWS and ARCHIE, 1981). Nevertheless, since all correlation coefficients calculated in the present work are particularly high, the two types of linear regression equations do not differ very much. This is why only the least square regression will be used below.

The slopes of regression lines decrease from 25 to 50 m depth, excepted at 45 m with only 5 data (Fig. 2, f, Table II). Nevertheless, not all slopes are significantly different from each other (Table III), whereas the relative radiation at each depth on one hand, amounts of light effectively received by samples on the other hand, decrease regularly from 25 to 50 m and are statistically different from one sampling depth to another (Table IV). The y-intercepts are positive (45 m excepted) but are statisti-

TABLE II

Regression lines equations computed between carbon fixation ($mg.m^{-3}.h^{-1}$) and chlorophyll *a* ($mg.m^{-3}$) for the SOP cruise (stat. 12 excepted). Number of data (n), slope (a), y-intercept (b), coefficient of correlation (r) and level of significance (p)

Équations des droites de régression calculées entre fixation de carbone ($mg.m^{-3}.h^{-1}$) et chlorophylle a *($mg.m^{-3}$) pour la campagne SOP (sauf stat. 12). Nombre de données (n), pente (a), ordonnée à l'origine (b), coefficient de corrélation (r) et son degré de signification (p)*

Depth (m)	n	a	b	r	p
25........	8	9.94	0.47	0.96	< 0.001
30........	11	7.39	0.83	0.97.	< 0.001
35........	11	6.47	0.75	0.96	< 0.001
40........	12	5.29	0.76	0.92	< 0.001
45........	5	8.06	− 1.33	0.94	< 0.05
50........	7	3.27	0.19	0.85	< 0.05

TABLE III

Regression lines of Figure 2. Tests for answering the following questions: is the y-intercept (b) significantly different from zero? Is the slope (a) of the regression line for z_1, depth different from the slope for z_2? (Tests from DAGNELIE, 1969, for level of significance 5 %)

Droites de régression de la Figure 2. Tests destinés à répondre aux questions suivantes : l'ordonnée à l'origine (b) est-elle significativement différente de zéro? La pente de la droite pour le niveau z_1 est-elle différente de celle pour le niveau z_2? (Tests d'après DAGNELIE, *1969, au risque 5 %)*

Depth (m)	$b \neq 0$	z_1	z_2	$a(z_1) \neq a(z_2)$
25........	n.s.	25	30	n.s.
30........	yes	30	35	n.s.
35........	n.s.	35	40	n.s.
40........	n.s.	25	35	n.s.
50........	n.s.	25	40	n.s.
		30	40	yes
		25	50	yes
		30	50	yes
		35	50	yes
		40	50	yes

cally different from 0 only at 30 m (Table III). Since the regression lines calculated for 6 sampling depths, those occupied by the major part of the biomass (HERBLAND and LE BOUTEILLER, 1982, fig. 7), are not statistically different from each other (Table III), it is not possible to demonstrate

TABLE IV

Tests for answering the following questions: is the light (expressed in percentage of surface irradiance, and in $\overline{PAR}$) at depth z_1 significantly different from light at z_2? SOP cruise data. MANN-WHITNEY U test at level of significance 1 %

Tests destinés à répondre aux questions suivantes : la lumière (exprimée en pourcentage de radiation incidente et en $\overline{PAR}$) à la profondeur z_1 est-elle significativement différente de la lumière en z_2? Données de la campagne SOP. Test U de MANN-WHITNEY *au risque 1 %*

z_1	z_2	% light (z_1) $\neq$ % light (z_2)	$\overline{PAR}$ (z_1) $\neq$ $\overline{PAR}$ (z_2)
25	30	yes	n.s.
30	35	yes	yes
35	40	yes	yes
40	50	yes	yes

rigorously that one given datum point belongs to one or the other of these regressions. Nevertheless, values obtained at the same place (0°, 4° W) during CIPREA 2, CIPREA 4 and CIPREA 5 cruises are plotted on figures 2. Distributions of these dots are very close to those of the SOP cruise, so that they can be considered, at first approximation, as being part of the same relationships. Therefore, equations from the SOP cruise (Table II) were used for computing the photosynthetic production of all the stations performed at the equator (4° W) during the CIPREA program from only chlorophyll data according to their sampling depth. Results show clear evidence that calculation provides a very good estimate of the production (Table V) since no statistical difference appears between computed and measured values. Accordingly, from the SOP cruise data, the primary production of the CIPREA 2, 4 and 5 cruises is accurately predicted. Conversely, data of the CIPREA 4 cruise would not allow accurate prediction of the production of the SOP cruise because the regression line between production and chlorophyll is not well defined by CIPREA 4 data.

Now, four groups of chlorophyll and production data (Fig. 2), collected during four different cruises at the same position between February, 1979 and January, 1980, are gathered into a remarkably homogeneous set. Regressions between photosynthetic production and chlorophyll biomass can then be computed with all available data for each incubation depth (Table VI). For the 3 best described levels, 30, 35, 40 m, from 82 to 87 % of the variance of the production can be explained by changes of the chlorophyll content, for 23 or 24 degrees of freedom.

As a direct consequence of these regression equations computed for each sampling depth, the

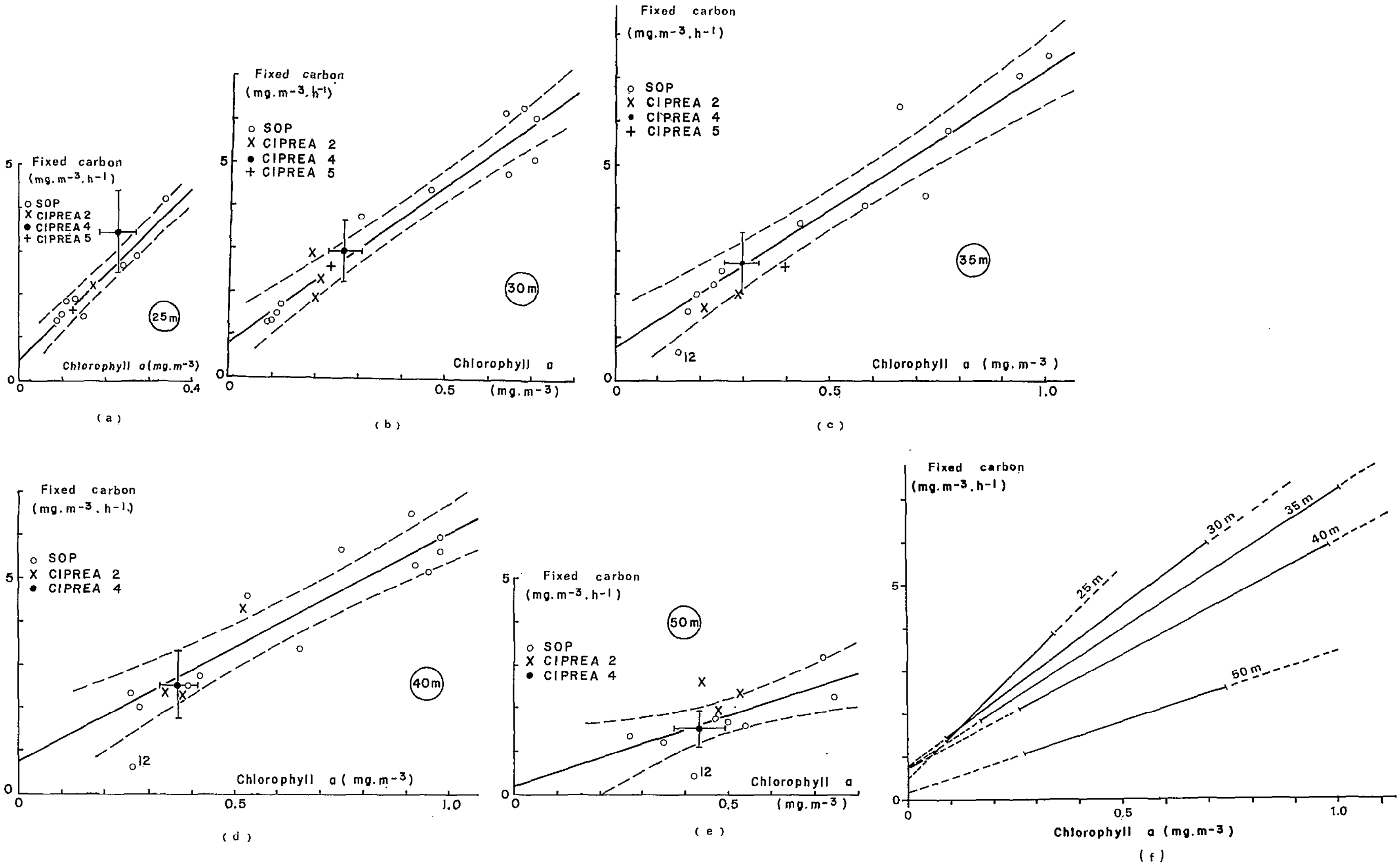

FIG. 2. — Fixed carbon from sunrise to sunset plotted versus concentration of chlorophyll *a* at the beginning of the incubation. Each point represents one *in situ* incubation. The regression line and the confidence limits (level of significance 5 %, according to DAGNELIE, 1969) were computed with SOP data, Stat. 12 excepted
(a) at 25 m. CIPREA 4: means and standard deviations for 5 pairs of values. *(b)* at 30 m. CIPREA 4: 11 pairs of values. *(c)* at 35 m. CIPREA 4 : 11 pairs of values. *(d)* at 40 m. CIPREA 4: 12 pairs of values. *(e)* at 50 m. CIPREA 4: 12 pairs of values. *(f)* the same from 25 to 50 m

Carbone fixé en fonction de la concentration de chlorophylle a *en début d'incubation. Chaque point représente une journée d'incubation* in situ. *La droite de régression et ses intervalles de confiance (au risque 5 %, selon* DAGNELIE, *1969) sont calculés avec les données de la campagne SOP, sauf la station 12*
(a) *à 25 m. CIPREA 4: moyennes et déviations standard pour 5 couples de valeurs.* (b) *à 30 m. CIPREA 4: 11 couples de valeurs.* (c) *à 35 m. CIPREA 4: 11 couples de valeurs.* (d) *à 40 m. CIPREA 4: 12 couples de valeurs.* (e) *à 50 m. CIPREA 4: 12 couples de valeurs.* (f) *les mêmes droites de 25 à 50 m*

TABLE V

Comparison of values of primary production measured during CIPREA 2, 4 and 5 cruises with values calculated from chlorophyll data and relationships computed with SOP cruise data (table 2)

Comparaison des valeurs de production primaire mesurées lors des campagnes CIPREA 2, 4 et 5 avec celles calculées à partir des données de chlorophylle et des relations obtenues avec les données de la campagne SOP (tabl. 2)

Depth (m)	CIPREA 2 cruise				CIPREA 4 cruise				CIPREA 5 cruise			
	n	mean production (mgC.m⁻³.h⁻¹)			n	mean production (mgC.m⁻³.h⁻¹)			n	mean production (mgC.m⁻³.h⁻¹)		
		measured	calculated	differ. in %		measured	calculated	differ. in %		measured	calculated	differ. in %
25......	1	2.20	2.16	− 2	5	3.43	2.78	− 19	1	1.64	1.69	+ 3
30......	3	2.36	2.31	− 2	11	2.97	2.79	− 6	1	2.61	2.57	− 2
35......	2	1.87	2.37	+ 27	11	2.75	2.68	− 3	1	2.62	3.31	+ 26
40......	3	2.99	2.95	− 1	12	2.52	2.72	+ 8				
45......	1	3.87	2.62	− 32	4	2.15	1.97	− 8	1	1.67	1.69	+ 1
50......	3	2.30	1.77	− 23	12	1.53	1.61	+ 5				
Mean Difference				− 4.5 (n = 13)				− 1.3 (n = 55)				+ 7 (n = 4)

TABLE VI

Regression lines equations between carbon fixation ($mg.m^{-3}.h^{-1}$) and chlorophyll *a* ($mg.m^{-3}$) for all available data (stat. 12, SOP, excepted). Number of data (n), slope (a), y-intercept (b), correlation coefficient (r) and level of significance (p), range of chlorophyll values, mean percentage of surface irradiance and mean $\overline{PAR}$. Data from SOP, CIPREA 2, 4 and 5 cruises

Équations des droites de régression entre fixation de carbone ($mg.m^{-3}.h^{-1}$) et chlorophylle a ($mg.m^{-3}$) pour toutes les données disponibles (sauf stat. 12, SOP). Nombre de données (n), pente (a), ordonnée à l'origine (b), coefficient de corrélation (r) et niveau de signification, gamme de valeurs de chlorophylle, pourcentage moyen de lumière incidente et $\overline{PAR}$ moyen. Données des campagnes SOP, CIPREA 2, 4 et 5

Depth (m)	n	a	b	r	p	Range of chla values ($mg.m^{-3}$)	Mean percentage of incident radiation	Mean $\overline{PAR}$ ($10^{22}q.m^{-2}.h^{-1}$)
0......	9	10.61	0.29	0.80	< 0.02	0.08 − 0.29	100	186.9
5......	17	11.27	0.60	0.82	< 0.001	0.08 − 0.27	50	88.9
10......	8	12.13	0.53	0.92	< 0.01	0.07 − 0.27	33.6	62.5
15......	14	10.34	0.67	0.79	< 0.001	0.09 − 0.29	26.2	46.1
20......	14	11.88	0.26	0.95	< 0.001	0.07 − 0.29	21.1	38.5
25......	15	10.80	0.52	0.80	< 0.001	0.09 − 0.34	16.4	28.9
30......	26	7.06	1.02	0.91	< 0.001	0.09 − 0.70	12.3	22.7
35......	25	6.51	0.70	0.93	< 0.001	0.17 − 1.07	8.3	14.7
40......	26	5.73	0.38	0.92	< 0.001	0.26 − 0.98	5.86	10.8
45......	11	7.26	− 0.76	0.85	< 0.001	0.34 − 0.77	4.77	8.3
50......	22	3.21	0.25	0.64	< 0.01	0.27 − 0.74	3.00	5.8
60......	17	1.90	0.10	0.61	< 0.01	0.25 − 0.58	1.68	3.2
70......	8	3.59	− 0.42	0.83	< 0.02	0.18 − 0.26	0.85	1.6

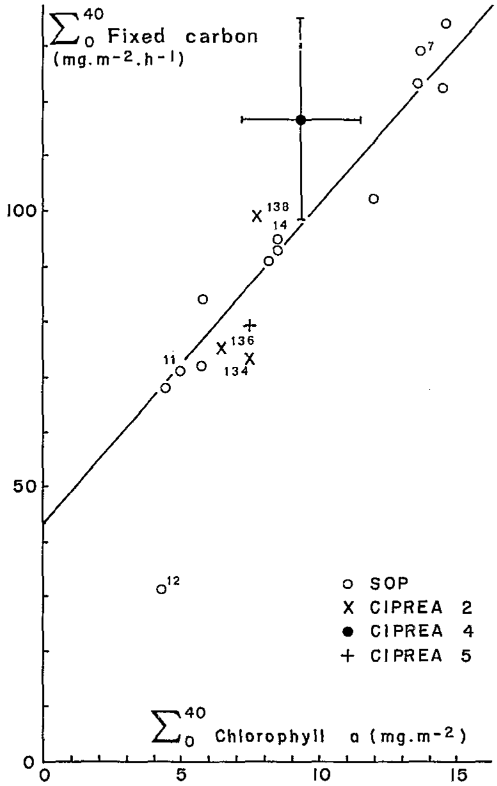

Fig. 3. — Fixed carbon as a function of chlorophyll *a*. Values integrated by linear interpolation from 0 to 40 m. The regression line was computed with SOP cruise data, sta. 12 excepted. CIPREA 4: means and standard deviations for 13 pairs of values. Station numbers identify some of the representative points (see text)

Carbone fixé en fonction de la chlorophylle a. *Valeurs intégrées par interpolation linéaire de 0 à 40 m. La droite de régression est calculée avec les données de la campagne SOP (stat. 12 exceptée). CIPREA 4: moyennes et déviations standard calculées avec 13 couples de valeurs. Quelques numéros de station sont reportés près des points représentatifs (voir texte)*

integrated values of production and chlorophyll are also strongly correlated, whatever layer may be considered. For instance, for the most often and well described layer, 0-40 m, the following correlation is obtained for the SOP cruise (Fig. 3):

$$\Sigma_0^{40} \text{ (fixed carbon)} = 5.76\ \Sigma_0^{40} \text{ Chla} + 43.8$$

(fixed carbon in $mg.m^{-2}.h^{-1}$ and chlorophyll *a* in $mg.m^{-2}$; $n = 12$, $r = 0.975$).
The experimental points which represent measurements of the CIPREA 2 and 5 cruises may be also considered to belong to the regression line, whereas those of CIPREA 4 cruise are slightly different because of the special vertical distribution of the chlorophyll during this cruise (Le Bouteiller and Herbland, 1982a). As could be expected from the results reported above, the y-intercept is positive and high.

Light conditions at each depth

We have shown that to study the relationship between production and chlorophyll for each incubation level, the data could be divided into classes very conveniently defined by depth. Since light is the major factor acting on the process of photosynthesis, it would be meaningless to rank production data by sampling depth if PAR varies much from day to day and from one cruise to another. During the SOP cruise, only PAR of the station 12 is very different from the mean PAR (Table I). For the other cruises, the amounts of PAR are of the same order of magnitude (Table VII), even if slight differences occur at 25 and 30 m between data of SOP cruise and CIPREA 4 cruise.

The nitrate effect

Abundance of nitrate in sea-water is one of the main factors which act on the primary productivity. However, comparison of Figure 2, c and Figure 4 evidences that, for one light level, production as a function of chlorophyll is not influenced by the nitrate concentration: higher values of production are obtained for higher concentrations of chlorophyll (SOP stations), not for nitrate richer waters. This result also appears on Figure 3: points which represent stations 10 and 11 (SOP), 134 and 136 (CIPREA 2) without nitrate in the 0-40 m layer, belong to the same linear regression as the other stations which contain more or less nitrate in the integration layer (Fig. 1). For a given value of PAR, carbon fixation is strongly correlated with chlorophyll concentration, at any nitrate concentration. This conclusion is also supported by analysis of Figure 5. The vertical profiles of chlorophyll, production, productivity and nitrate are outlined for three typical stations from three different cruises. The productivity index is defined as the amount of carbon fixed during the incubation *in situ* from sunrise to sunset, thereafter averaged per hour and referred to chlorophyll unit (initial value). It should be noted that the vertical profiles of the productivity index present a maximum always between 5 and 15 m depth. In addition, the profiles are never deformed significantly at the depth where nitrate appears (Fig. 5): surface (station 9), 30 m (station 14) and 50 m (station 134). Furthermore, these profiles of productivity index seem to be typical not only of the equatorial area near 4° W, but also of all the central part of Gulf of Guinea. Among 54 stations with *in situ* incubations of primary production

TABLE VII

Amount of radiation received by samples during the *in situ* incubation. All available data, stat. 12 (SOP) excepted. Mean value (m) and standard deviation (st. d.). Difference of PAR from one cruise to another tested with the MANN-WHITNEY U test (level of significance 5 %)

Quantité de lumière reçue par les échantillons au cours de l'incubation in situ. *Toutes données disponibles, sauf stat. 12 (SOP). Moyenne (m) et déviation standard (st. d.). Différence de $\overline{PAR}$ entre les campagnes testée à l'aide du test U de* MANN-WHITNEY *(au risque 5 %)*

Depth (m)	$\overline{PAR}$ $(10^{22}q.m^{-2}.h^{-1})$									Difference	
	SOP cruise (Feb.)			CIPREA 2 (Apr.)			CIPREA 4 (Oct.)			SOP-CIP. 2	SOP-CIP. 4
	n	m	st.d.	n	m	st.d.	n	m	st.d.		
25.........	8	31.6	2.7	1	23.8	—	5	24.1	5.7	—	yes
30.........	11	24.4	6.0	3	22.5	7.5	10	17.9	4.6	n.s.	yes
35.........	11	15.5	4.2	2	13.1	5.3	10	13.1	3.3	n.s.	n.s.
40.........	12	10.1	2.9	3	11.9	5.2	11	9.5	2.2	n.s.	n.s.
45.........	5	7.8	2.4	1	11.6	—	3	7.9	0.2	—	n.s.
50.........	7	5.3	2.1	3	6.3	2.9	11	4.6	1.0	n.s.	n.s.

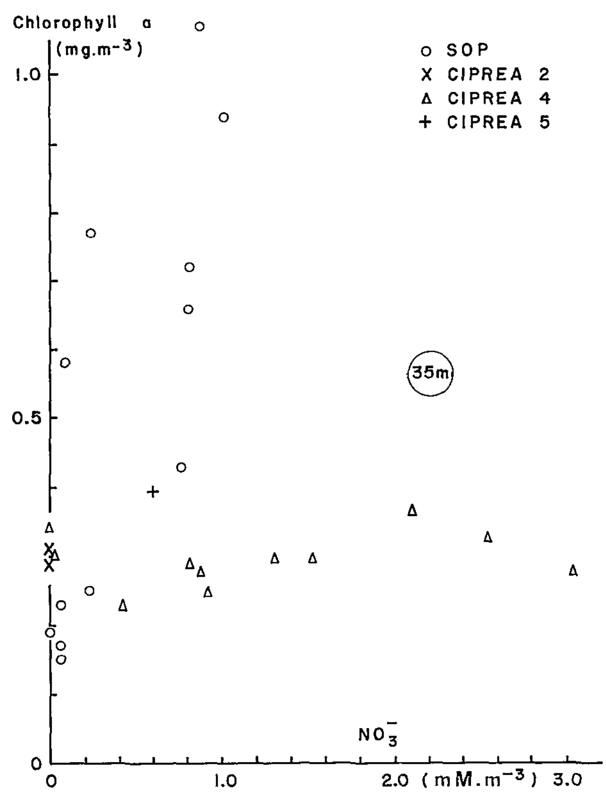

FIG. 4. — Concentrations of chlorophyll *a* and nitrate at the beginning of each incubation at 35 m. A similar figure would be obtained from carbon fixation data, because of the relationship between carbon fixation and chlorophyll *a* (Fig. 2, c)

Concentrations de chlorophylle a *et de nitrate en début d'incubation à 35 m. Une figure semblable serait obtenue à partir de la fixation de carbone grâce à la relation directe entre fixation de carbone et chlorophylle* a *(Fig. 2, c)*

performed at 4° W from 5° N to 10° S (CIPREA programm, RV Capricorne), 50 stations have complete data showing a maximum productivity index between 0 and 20 m, and most often between 5 and 15 m. For these stations, depth of the nitrate depleted mixed layer ranges from 0 to 70 m. Therefore, productivity as we have measured it, is not directly related to nitrate concentration and not significantly higher in the presence of nitrate (HERBLAND and LE BOUTEILLER, 1983). With respect to productivity, there is no reason to divide the euphotic zone into two layers, one with and the other without nitrate.

This is in opposition with observations reported by THOMAS (1970) and by CURL and SMALL (1965) in the Pacific ocean, but in agreement with the results of a multivariate analysis applied to a great number of data from a coastal station (PLATT and SUBBA RAO, 1970; HARRISON and PLATT, 1980). They have shown that nutrients can explain only a minor part of variations of the relative production of phytoplankton. As suggested by HARRISON and PLATT (1980), ambient nutrient concentrations parameters may be inappropriate indices of nutrient availability due to rapid recycling (McCARTHY and GOLDMAN, 1979). This assumption is also supported by experiments which show that the productivity of samples enriched with nitrogen compounds is not enhanced significantly after one daytime *in situ* incubation (LE BOUTEILLER and HERBLAND, 1982a). In such an environment, the presence of nitrate is a *sine qua non* condition of abundance of phytoplankton, but seems to have no influence on the productivity index.

The shape of vertical profiles of production, and

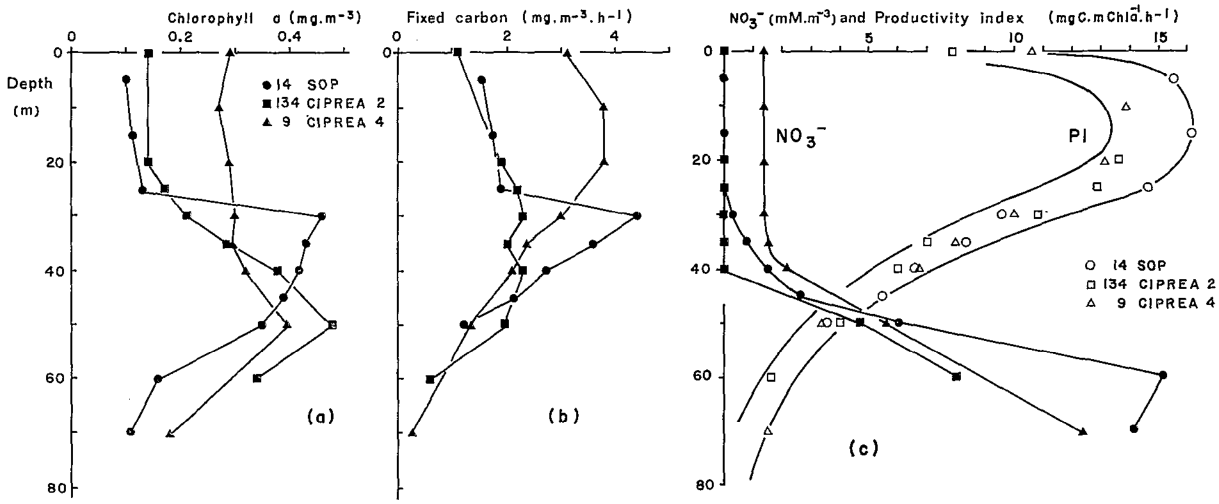

FIG. 5. — Depth distributions for 3 typical stations:
(a) chlorophyll *a*. *(b)* fixed carbon. *(c)* nitrate and productivity index

Distributions verticales pour 3 stations typiques :
(a) *chlorophylle* a. (b) *carbone fixé*. (c) *nitrate et indice de productivité*

especially the depth of the peak is a direct consequence of the above statement. Two stations characteristic of the "Typical Tropical Structure" (HERBLAND and VOITURIEZ, 1977), defined by the presence of a nitrate depleted mixed layer, are outlined on Figure 5: stations 14 and 134. Station 14 is very typical, since depths of chlorophyll and production maxima are equal (30 m), whereas the maximum of production of station 134 is well above the peak of chlorophyll. Station 9 represents an "atypical" situation: no nitrate depleted layer, and depth of the production maximum occurs 30 m above the chlorophyll maximum. These three stations are representative of the different situations observed during the 31 stations. In each case, production can be computed from chlorophyll and depth data by means of equations in table VI, without having to consider nitrate concentration. Finally, for an incident radiation close to the average, the vertical profile of production is entirely defined by the profile of chlorophyll. The presence of a sharp peak of chlorophyll, relatively well lighted, is the necessary and sufficient condition for that peaks of production and chlorophyll to appear both at the same depth. This is the case of station 14. Therefore, the peak of production is located at the top of the nitracline because of a great chlorophyll biomass at this depth, not because of a special productivity (see discussions of DANDONNEAU, 1979; CULLEN and EPPLEY, 1981; CULLEN, 1982; HERBLAND, 1983).

For less sharp peaks of chlorophyll, the production maximum is above the chlorophyll maximum. Since the productivity index increases from the bottom of the euphotic zone to about 5 or 10 m, a sample taken and incubated above the chlorophyll maximum, though less rich in chlorophyll, can fix more carbon than the sample taken within the chlorophyll maximum (Fig. 5, stations 134 and 9).

Another example can be taken from two stations during CIPREA 2 cruise at (2° 00 N; 4° 00 W). Nitrate and chlorophyll maximum both appeared at 60 m (Table VIII). Maximum of fixed carbon was measured at 40 and 35 m respectively. PAR data are very close to the mean values of table VI, so production can be computed from equations of table VI. Results are entirely consistent with measured values (Table VIII). These stations show evidence that a deep chlorophyll maximum is not a production maximum only because of the vertical gradient in the productivity index.

Relationship between productivity and chlorophyll

The empirical equations between carbon fixation and chlorophyll (Table VI) provide a good description of the production in the equatorial area. For this purpose, it is of minor importance that the y-intercepts of the regression lines are positive (Fig. 2 and 3, tables VI and X). But this observation could be very important from an ecological point of view: it means that the productivity index would depend on the amount of chlorophyll present in the water. Among the numerous causes likely to induce a variation of productivity according to the chlorophyll content, four of the most important factors will be discussed:

TABLE VIII

Comparison of values of primary production measured during CIPREA 2 cruise at (2° 00 N; 4° 00 W) with values calculated from chlorophyll data and relationships computed with data of SOP, CIPREA 2, 4 and 5 cruises at (0° 00; 4° 00 W) (Table VI)

Comparaison des valeurs de production primaire mesurées lors de la campagne CIPREA 2 à (2° 00 N; 4° 00 W) avec les valeurs calculées à partir des données de chlorophylle et des relations établies avec les données des campagnes SOP, CIPREA 2, 4 et 5 à (0° 00; 4° 00 W) (Tabl. VI)

Depth (m)	Chla ($mg.m^{-3}$)	NO_3 ($mM.m^{-3}$)	$\overline{PAR}$ $10^{22}q.m^{-2}.h^{-1}$	Fixed carbon ($mg.m^{-3}.h^{-1}$) measured	calculated
Station 140 (Apr. 25, 1979)					
0...	0.10	0.01	163	1.28	1.35
20...	0.11	0.00	37	1.59	1.57
40...	0.22	0.00	15	1.72	1.64
45...	0.22	0.00	11.6	1.31	0.84
50...	0.22	0.00	7.6	0.79	0.97
55...	0.25	0.00	5.2	0.67	—
60...	0.49	8.94	3.5	0.69	1.03
70...	0.23	15.98	1.9	0.15	0.40
Station 142 (Apr. 26, 1979)					
0...	0.10	0.00	177	1.55	1.35
10...	0.09	0.00	63	1.39	1.62
35...	0.15	0.00	18	1.91	1.68
50...	0.27	0.00	7.0	0.98	1.12
60...	0.46	11.22	2.8	0.77	0.97
65...	0.36	14.80	2.0	0.41	—
70...	0.21	17.05	1.4	0.17	0.33
80...	0.19	18.21	0.8	0.06	—

1 - A methodological artifact: the lower the chlorophyll concentration, the more under-estimated is chlorophyll content or the more over-estimated is the carbon fixation.

Chlorophyll *a* and ^{14}C methods were always used with the same rigour. However, both methods are imperfect, producing estimates that can be shifted as a function of chlorophyll concentration. This hypothesis may not be neglected, especially nowadays, when processes of the oligotrophic system appear so questionable (McCARTHY and GOLDMAN, 1979; GOLDMAN *et al.*, 1979; EPPLEY, 1980).

2 - Synthesis and accumulation of chlorophyll within the bottles during incubation: measurements of carbon fixation require several hours of incubation. If carbon fixation is related not only to the concentration of chlorophyll measured before incubation, but also to the amount of chlorophyll synthesized during incubation, a better production efficiency in chlorophyll poor waters could be due to a higher rate of chlorophyll synthesis during incubation. In reality, the rate of chlorophyll synthesis for one given irradiation seems not to depend on the chlorophyll concentration, at least for the area studied here (LE BOUTEILLER and HERBLAND, 1982a).

3 - The amount of PAR: if samples poorer in chlorophyll receive a more intensive radiation during incubation, then the amount of fixed carbon can be relatively greater. Extinction of light in the water is known to be related to the amount of phytoplankton (LORENZEN, 1972; MOREL and SMITH, 1974). Hence, chlorophyll poor waters are potentially best lighted. For the SOP cruise, however, the percentage of incident light received by chlorophyll-poor samples is not significantly higher than light received by rich waters (Table IX). The same holds true with respect to PAR (Table IX).

TABLE IX

Correlation coefficients and levels of significance computed between chlorophyll *a* and percentage of surface irradiance, and between chlorophyll *a* and PAR. Data from the SOP cruise, stat. 12 excepted

Coefficients de corrélation et niveaux de significativité calculés entre chlorophylle a *et pourcentage de lumière incidente, et entre chlorophylle* a *et $\overline{PAR}$. Données de SOP, sauf stat. 12*

Depth (m)	Between Chla and surface irradiance (%) r	p	Between Chla and $\overline{PAR}$ r	p
25......	0.58	n.s.	0.47	n.s.
30......	− 0.08	n.s.	0.31	n.s.
35......	− 0.48	n.s.	0.11	n.s.
40......	− 0.68	0.02	0.39	n.s.
50......	− 0.47	n.s.	− 0.48	n.s.

Pairs of production and chlorophyll data can be associated by sampling depth as done before, but also by using some classes of percentage of incident radiation, or according to PAR (Table X). Regression lines computed for samples taken above 45 m depth all exhibit an y-intercept notably above 0. Therefore, actual light availability may not be considered as the origin of the phenomenon.

4 - Nitrate and temperature: the nitrate influence has been studied earlier. As far as temperature is concerned, if chlorophyll poor waters are systematically warmer than rich waters, their productivity could be higher, because of the temperature effect

TABLE X

Equations of the regression lines between carbon fixation (mg.$m^{-3}.h^{-1}$) and chlorophyll *a* (mg.m^{-3}) for the SOP cruise (stat. 12 excepted) for different ranges of available radiation. Slope (a), y-intercept (b). The y-intercept is tested after DAGNELIE (1969)

Équations des droites de régression reliant fixation de carbone (mg.$m^{-3}.h^{-1}$) et chlorophylle a *(mg.m^{-3}) pour la campagne SOP (sauf stat. 12) pour différentes gammes de lumière disponible. Pente (a), ordonnée à l'origine (b). L'ordonnée à l'origine est testée selon* DAGNELIE *(1969)*

Percentage of surface irradiance	n	a	b	r	$b \neq 0$	Level of significance
]19-24]...........	9	10.03	0.45	0.97	yes	5 %
]15-19]...........	7	8.02	0.93	0.97	yes	5 %
]11.5-15].........	10	7.19	0.79	0.98	yes	2 %
]8.5-11.5].........	8	6.77	0.65	0.96	yes	5 %
]6.0-8.5]..........	8	6.42	0.20	0.91	n.s.	
]4.0-6.0]..........	9	5.74	0.38	0.89	n.s.	
]2.5-4.0]..........	7	5.20	− 0.51	0.86	n.s.	
]1.5-2.5]..........	6	3.40	− 0.19	0.89	n.s.	
$\log_{10} \overline{\text{PAR}}$ (10^{22}q.$m^{-2}.h^{-1}$)						
]1.6-1.3]..........	22	7.47	0.80	0.97	yes	1 ‰
]1.3-1.0]..........	17	6.01	0.82	0.94	yes	5 %

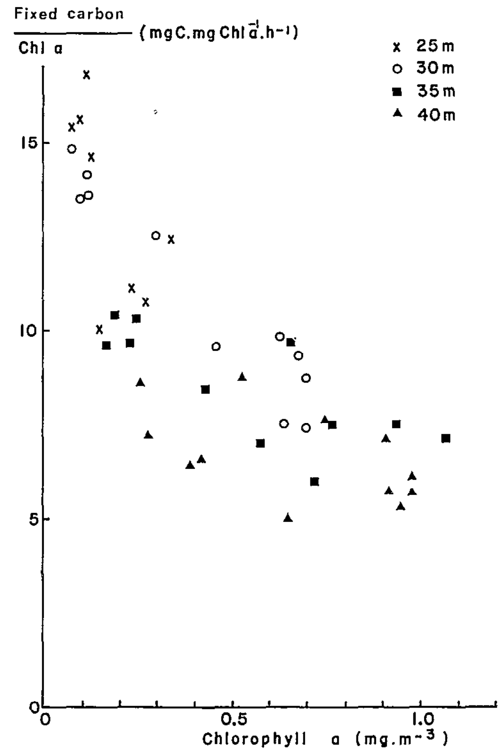

FIG. 6. — Productivity index plotted versus chlorophyll *a*, for 4 incubation depths. SOP cruise data, stat. 12 excepted

Indice de productivité en fonction de la chlorophylle a *pour 4 niveaux d'incubation. Données de la campagne SOP, sauf stat. 12*

on productivity (EPPLEY, 1972). In the Gulf of Guinea, temperature is related to the nitrate concentration. Thus, for the CIPREA 4 cruise, we have the relationship:

$[NO^-_3] = -1.349\ T + 33.59$
(computed for $[NO^-_3] > 0.5$ mM.m^{-3}; T in °C; $n = 184$; $r = -0.977$).

The lack of clear relationship between chlorophyll and nitrate (Fig. 4) as between productivity index and nitrate (Fig. 5, c) suggests that temperature is not the explaining factor.

Accordingly, the positive y-intercepts of the regression lines between production and chlorophyll would not be directly due to better environmental conditions when chlorophyll concentration is lower.

As a direct consequence, for a given irradiance, the productivity index varies as an inverse function of the chlorophyll concentration (Fig. 6). The same figure has already been obtained by TCHMIR (1971) in the Gulf of Guinea from experiments restricted to surface water. The integrated values for the water column by surface unit show the same trend (Fig. 7): the productivity index is maximal when the chlorophyll concentration is minimal, which has not been observed by STEELE and BAIRD (1961) in the North Sea, or LEMOALLE (1981) in Lake Tchad.

In the future, it will be essential to consider such a result when interpreting production data from chlorophyll rich or poor waters. If chlorophyll photosynthetic efficiency increases when chlorophyll concentration decreases, the production of oligotrophic waters would be relatively greater and the production of rich waters relatively lower. This would tend to reduce the seasonal and geographical differences of production, which are effectively rather small in the equatorial Atlantic Ocean (VOITURIEZ *et al.*, 1982).

Now, the experimental points of figure 2 can also fit on curves passing through the origin. The model is mathematically more complex but better from an ecological point of view, since production is non existing when chlorophyll is totaly absent. Calculation (Table XI) shows that, for SOP data, fitting on a power function curve is as good as fitting on a straight line (Table II). Therefore, our data reported here support the hypothesis that carbon fixation would vary as a power function of

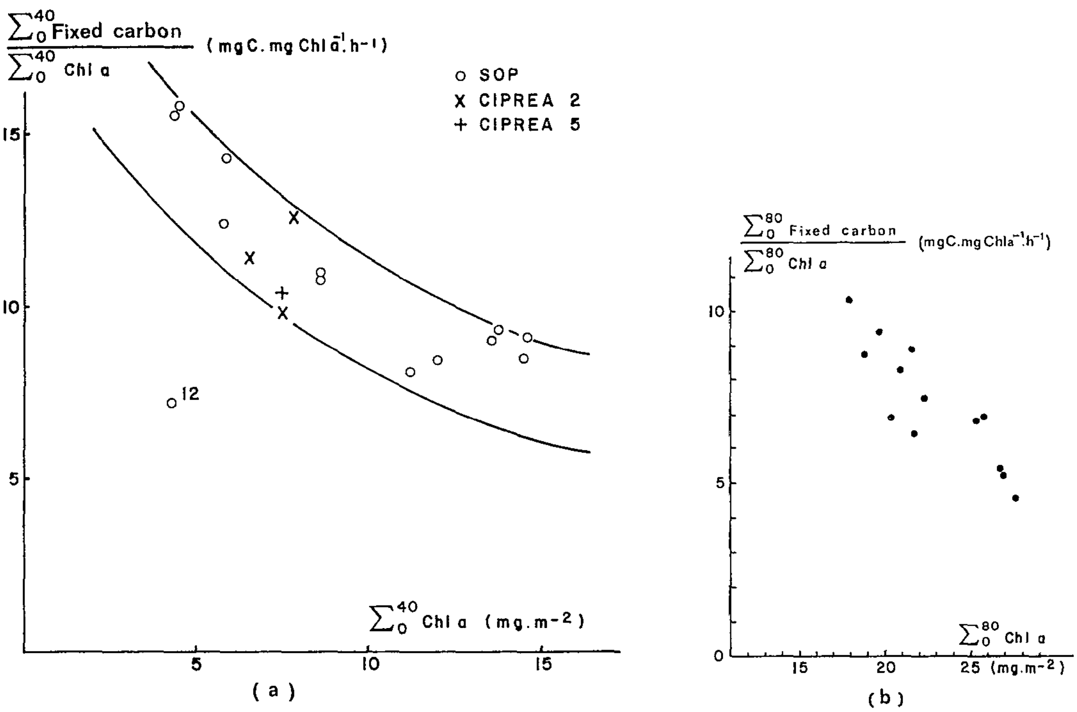

FIG. 7. — Productivity index plotted versus chlorophyll *a*
(a) Values integrated from 0 to 40 m for SOP, CIPREA 2 and 5 cruises. *(b)* Values integrated from 0 to 80 m for CIPREA 4 cruise
Indice de productivité en fonction de la chlorophylle a
(a) *Valeurs intégrées de 0 à 40 m pour les campagnes SOP, CIPREA 2 et 5.* (b) *Valeurs intégrées de 0 à 80 m pour CIPREA 4*

TABLE XI

Equations of the regression lines between carbon fixation and chlorophyll *a*, both expressed in logarithm. Symbols and data as in Table II

Équations des droites de régression reliant fixation de carbone et chlorophylle a, *toutes deux exprimées en logarithmes. Symboles et données* comme dans le tableau II

Depth (m)	n	a	b	r
25.....	8	7.84	0.72	0.93
30.....	11	7.76	0.73	0.99
35.....	11	7.03	0.78	0.98
40.....	12	5.97	0.81	0.94
50.....	7	3.10	0.77	0.86

the amount of chlorophyll *a* present in the water at the beginning of the incubation.

CHLOROPHYLL AND PHYTOPLANKTON

Since fluctuations of the environmental factors do not seem to be directly at the origin of the inverse relationship between productivity index and chlorophyll concentration, then the hypothesis arises of changes in properties of the phytoplankton itself. By means of size fractioning, it is effectively possible to show evidence of a marked change in the size distribution of phytoplankton cells from chlorophyll rich to poor waters (Fig. 8). For 1 mg.m⁻³ of total chlorophyll *a*, about 50 % of the chlorophyll belongs to organisms passing through a 3 µm filter, and the percentage approximates 75 % when water contains 0.2 mg.m⁻³ of total chlorophyll *a*. Comparing figures 6 and 8 suggests that each concentration of chlorophyll *a* would correspond to a particular community of phytoplankton. The photosynthetic efficiency of the chlorophyll would be higher in chlorophyll-poor waters with dominant picoplankton, and lower in chlorophyll-rich waters. Production measurements showed that the productivity index of nanoplankton (< 35 µm) is systematically greater than the productivity of the total fraction (< 200 µm) (HERBLAND and LE BOUTEILLER, 1981). This is very consistent with results reported by MALONE (1971) and TAGUCHI (1980) in the Pacific Ocean. The efficiency of light-utilization is inversely related not only to the cellular pigment concentration (MOREL and BRICAUD, 1981), but also to the cell

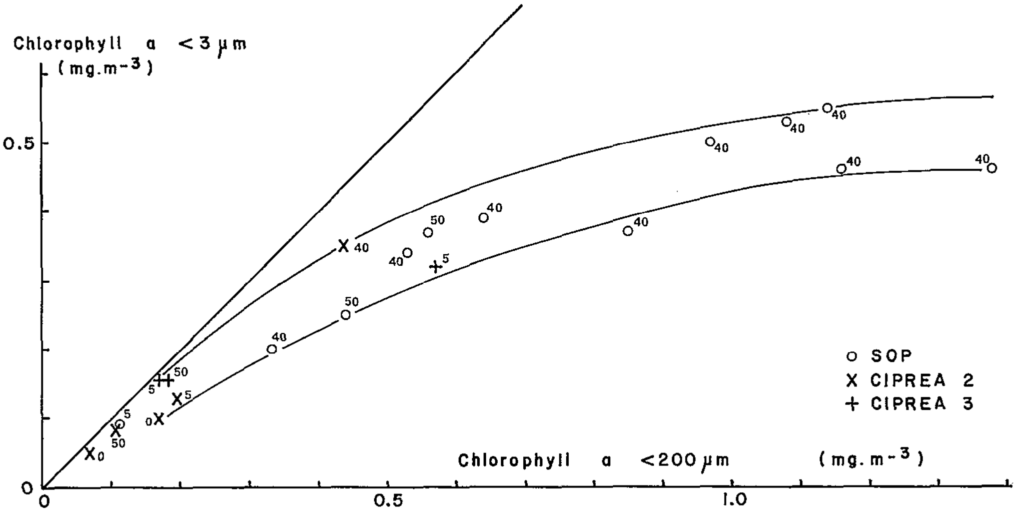

FIG. 8. — Amount of chlorophyll *a* passing through a 3 µm filter plotted versus total chlorophyll concentration. Data from HERBLAND and LE BOUTEILLER (1981). Sampling depths are reported for each station

Quantité de chlorophylle a *passant à travers un filtre de 3 µm en fonction de la concentration de chlorophylle totale. Données de* HERBLAND *et* LE BOUTEILLER *(1981). Les profondeurs de prélèvement sont indiquées pour chaque station*

size: the small cells, which have a higher surface/volume ratio, show a better productivity (TAGUCHI, 1976; CHRETIENNOT-DINET, 1981). Nevertheless, the < 3 µm fraction appeared to be very poorly productive (HERBLAND and LE BOUTEILLER, 1981). Accordingly, it is difficult to explain then how a water containing for example 0.2 mg.m^{-3} of chlorophyll *a*, of which nearly 75 % belongs to < 3 µm cells, could be so productive (Fig. 6). In fact, measurements of the chlorophyll content in flasks at the end of incubation suggest that the autotroph organisms (< 3 µm) would be inhibed or damaged by screening before incubation (LE BOUTEILLER and HERBLAND, 1982a), and consequently our direct measurements of productivity of the < 3 µm fraction may be suspected. Recently, LI *et al.* (1983) reported that, in the tropical Pacific Ocean, 20 to 80 % of the carbon fixation is attributable to < 1 µm autotrophic cells. PLATT *et al.* (1983), at the west of the Azores, found that picoplankton (< 1 µm) contributes about 60 % of the total primary production.

Finally, the higher productivity index plotted on figure 6 might well be due to the activity of very small phytoplanktonic cells. According to the chlorophyll concentration, which reflects changes of the size structure of the phytoplankton community, the productivity index varies approximately two-fold for one given light level (Fig. 6). In the same way, the productivity index of the whole photic layer increases from 5 to 10 when chlorophyll content decreases from 27 to 18 mg.m^{-2} during CIPREA 4 cruise (Fig. 7, b).

In nutrient rich or poor waters, phytoplankton activity as estimated by the productivity index appears in both cases to be very high, near maximal if compared to calculations of EPPLEY (1972). In the equatorial divergence, spatial and temporal variations of the environment properties exhibit a relatively small magnitude, characteristic of unperturbed regions (WALSH, 1976), so that biomass rather than growth rate would be controlled by nutrients (GOLDMAN *et al.*, 1979). The influence of the environmental conditions would be reflected not only in the chlorophyll concentration in sea-water, but also in some major properties of the phytoplankton, among which the mean cell size and the mean chlorophyll cell content, as pointed out by PLATT and SUBBA RAO (1973) and PLATT *et al.* (1977).

Relationship between production and light

In order to state precisely the effect of light on the photosynthetic fixation of carbon, three variables should be considered together: carbon fixation, chlorophyll and PAR.

Carbon fixation referred to unit light, both variables expressed in calories, corresponds to the K_b index proposed by PLATT (1969) for measuring the contribution of photosynthetic processes to the total optical attenuation coefficient of visible radiation in seawater. K_b was found to depend linearly on the chlorophyll concentration at each depth (PLATT, 1969; LE BOUTEILLER, 1982).

Carbon fixation per unit of chlorophyll *a*, which is the classical productivity index, will be considered below as a function of light.

Upon all available data of productivity index and PAR from the euphotic zone, a bilogarithmic transformation is applied so as to homogenize both variances, as MOREL (1978) did, and to minimize the influence of the chlorophyll concentration on the productivity index. Excluding surface and 5 m samples where photosynthesis was markedly inhibited by light excess, a linear regression equation is computed between productivity index and PAR (Table XII, fig. 9). It is noteworthy that this relationship is very similar for the SOP and CIPREA cruises, with highly significant correlation coefficients.

TABLE XII

Equations of the regression lines computed between productivity index (mgC.mgChla^{-1}.h^{-1}) and $\overline{PAR}$ (10^{22}q.m^{-2}.h^{-1}), both expressed in logarithm from all available data, excepted 0 and 5 m data and stat. 12 and 11 (SOP). Slope (a) and y-intercept (b)

Équations des droites de régression calculées entre indice de productivité (mgC.mgChla^{-1}.h^{-1}) et $\overline{PAR}$ (10^{22}q.m^{-2}.h^{-1}), tous deux en logarithme, à partir de toutes données disponibles, sauf données de 0 et 5 m et stat. 11 et 12 (SOP). Pente (a) et ordonnées à l'origine (b)

Cruises	Number of stations	Number of data	a	b	r
SOP...............	11	73	0.606	0.170	0.932
CIPREA 2 and 4....	14	95	0.675	0.140	0.936
SOP + CIP. 2 and 4.	25	168	0.631	0.166	0.933

The slope of the regression line, positive but less than one, means that the productivity index varies as a power function of PAR. Consequently, the quantum yield, as defined by plant physiologists, classically increases from surface to the bottom of the euphotic zone. Optimal radiative conditions for photosynthesis are observed near 10 m depth, with values of PAR ranging from 6 to 8 $\times 10^{24}$ q. m^{-2}.d^{-1}, which is very consistent with values reported by MOREL (1978). Then the maximal values of the productivity index lie near 150 g C. g Chla^{-1}.d^{-1}, an estimate close to the maximal value expected by EPPLEY (1972) for temperatures ranging from 25 to 30 °C, and also approximated by PLATT *et al.* (1980) off Peru. Data from stations 11 and 12 (SOP) were not used in the calculation because of their very high productivity index when referred to PAR (Fig. 9). This latter important result provides evidence that the relationships between productivity

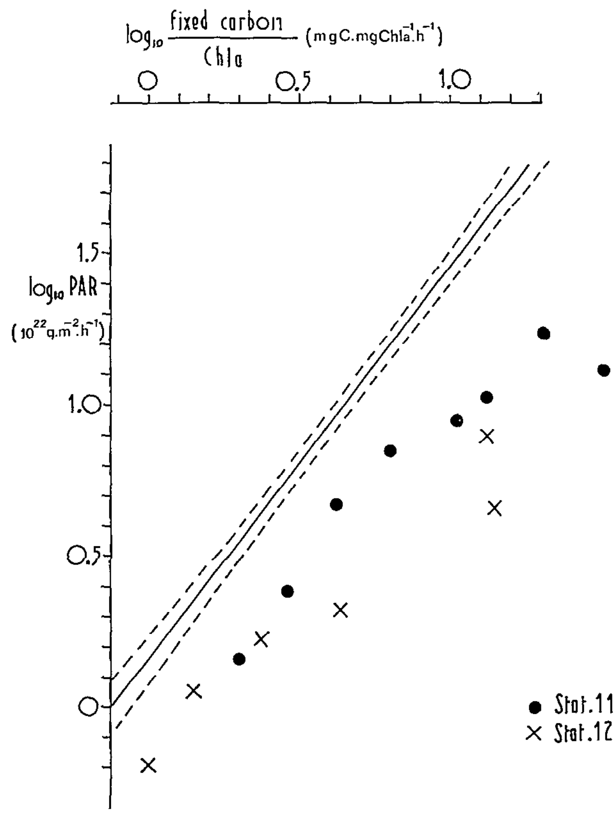

FIG. 9. — Productivity index as a function of PAR, both expressed in logarithm. Equation of the regression line is in table 12. Confidence limits computed according to DAGNELIE, 1969 (level of significance 1 %). Both scales are set by analogy with the depth distribution of the productivity index (Table XIII). Mean surface irradiance = 2 240 J.cm^{-2}.d^{-1} for a mean incubation time of 11 h 00. Productivity indexes of stat. 11 and 12 (surface irradiance = 970 and 250 J.cm^{-2}.d^{-1} respectively) are plotted for comparison

Indice de productivité en fonction de $\overline{PAR}$, tous les deux en logarithme. Équation de la droite dans le tabl. 12. Intervalles de confiance calculés selon DAGNELIE, 1969 (au risque 1 %). Les deux échelles sont disposées par analogie avec la distribution de l'indice de productivité en fonction de la profondeur (Tabl. XIII). Rayonnement global incident moyen = 2 240 J.cm^{-2}.j^{-1} pour une incubation moyenne de 11 h 00. Les indices de productivité des stat. 11 et 12 (rayonnement global incident = 970 et 250 J.cm^{2} j^{-1}; respectivement) sont représentés pour comparaison

and PAR (Table XII) are applicable only for amounts of radiation available at each depth close to the mean values (Table VI).

Furthermore, at a first approximation, PAR may be considered to decrease as an exponential function of depth. Effectively, for the SOP cruise (stations 11 and 12 excepted), the following equation has been computed:

$$\log_{10} \overline{PAR} = -0.030 \text{ Z} + 2.195$$

(PAR expressed as 10^{22} q.m^{-2}.h^{-1}, using 11 stations with 142 data — r = — 0.977). Accordingly, the productivity index is also well correlated to depth (Table XIII). Thus, an extremely simple description of the mean primary production as a function of chlorophyll biomass and depth is supplied by equations of table XIII. Obviously, such relationships are true only for incident radiation and depth of the euphotic layer rather close to the mean values calculated with our data. The variability of PAR, either due to day-to-day fluctuations of the incident radiation, or resulting from depth changes of the cells due to vertical stirring or mixing, is essential with respect to the capacity of adaptation of the phytoplankton, especially by changing the chlorophyll cell content.

TABLE XIII

Cruises	Number of stations	Number of data	a	b	r
SOP..........	12	81	— 0.0189	1.549	0.924
CIP.2, 4 and 5..	16	112	— 0.0189	1.548	0.915
SOP + CIP. 2, 4 and 5........	28	193	— 0.0189	1.547	0.925

Equations of the regression lines computed between productivity index (mgC.mgChla^{-1}.h^{-1}, in logarithm) and depth (m), from all available data, excepted 0 and 5 m data and stat. 12 (SOP). Slope (a) and y-intercept (b)

Équations des droites de régression calculées entre indice de productivité (mgC.mgChla^{-1}.h^{-1}, en logarithme) et profondeur (m), à partir de toutes données disponibles, sauf données de 0 et 5 m et stat. 12 (SOP). Pente (a) et ordonnée à l'origine (b)

In order to determine more precisely how the phytoplankton is adapted to PAR, some experiments of "light enrichment" were performed *in situ* at 21 of the 31 stations considered here: 117 samples for measuring carbon fixation, of which 90 were during CIPREA 4 cruise, were taken in duplicate: the ones incubated *in situ* at the sampling depth, the others 10 meters above (at times 5 or 20 m). The main advantage of this type of experiment is to allow comparison between samples for which errors and artifacts are very similar. Of the 117 samples taken from different depths and put upward for incubation on the incubation line, 112 fixed a greater amount of carbon than samples incubated at sampling depth. We may conclude that, in the experimental conditions, available light, surface excepted, always limits the amount of carbon fixed during the *in situ* incubation time, even if sea-water is nitrate-depleted. In other words, with respect to light, the *in situ* carbon fixation is never maximal.

On the other hand, below 25 m, the productivity index of a sample taken at depth "z" and incubated above, at depth "z — 10 m", is always lower than the productivity index of the sample taken and incubated at depth "z — 10 m" (Fig. 10). The contrary is observed above 25 m (Fig. 10). Therefore, two samples incubated at the same depth but taken at different depths, exhibit two different productivity indexes. These observations would result from the adaptation of phytoplankton by changing chlorophyll cell content, rates of photosynthesis and chlorophyll synthesis according to depth and PAR (LE BOUTEILLER, 1982).

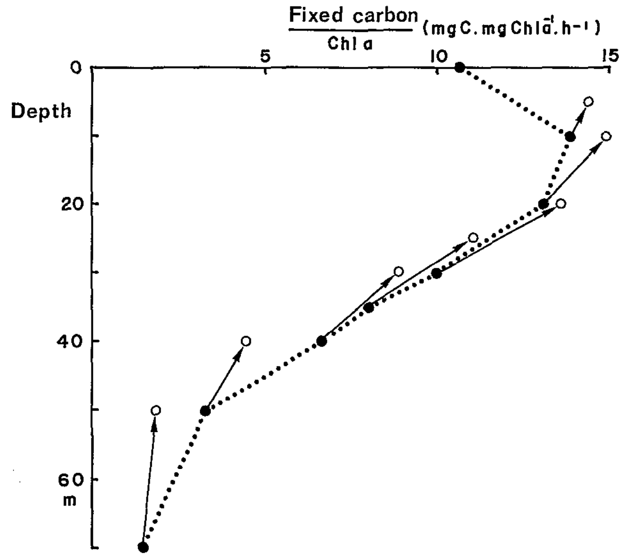

FIG. 10. — Depth distribution of the productivity index for a typical station (9, CIPREA 4, see Fig. 5). Each sample taken in duplicate: one incubated at sampling depth (solid circles), the other incubated above sampling depth (open circles)

Indice de productivité en fonction de la profondeur pour une station typique (9, CIPREA 4, voir Fig. 5). Points : *flacons incubés à la profondeur de prélèvement.* Cercles : *flacons incubés au-dessus du niveau de prélèvement*

Furthermore, figure 10 shows that between 25 and 60 m, the productivity index of "light enriched" samples increases only slightly. Thus putting a sample for incubation at 10 m above sampling depth will nearly equivalate to double PAR (Table VI). Stations 11 and 12 (SOP) have shown that conversely a decrease of the total incident radiation was partly balanced by a better quantum yield (Fig. 9). Schematically, there is a sort of damped reaction of the phytoplankton to variations of irradiance by which phytoplankton adapted to a light level, increases its efficiency for lower light and decreases it for higher one. Consequently, stations receiving half the light of the average (Stat. 11, SOP) or nearly 50 % more (Stat. 7 and 14, SOP) presented productions by chlorophyll unit close to the average (Fig. 2 and 3). A very significant decrease was observed only for one single station on a very cloudy day (Stat. 12, SOP. Fig. 2 and 3). Then, below the mixed layer, the phytoplankton is adapted at least to some extent, to the mean light level (FALKOWSKI, 1981).

CONCLUSION

In the eastern equatorial Atlantic ocean, a single determination of the chlorophyll *a* concentration provides an excellent description of the potential primary production of that sea-water. For an incident light intensity close to the average, the amount of carbon fixed during daytime can be precisely predicted from the chlorophyll content by means of very simple empirical relationships.

Undoubtedly, great homogeneity characterizes the structure and functioning of the tropical oceanic system. The amplitude of seasonal climatic variations is relatively small (HASTENRATH, 1978), most often sea-water temperature lies between 15 and 25°, and in addition the variability of the equatorial current system is of a low enough amplitude and frequency for primary production just to balance losses, mainly from herbivorous consumption (WALSH, 1976; LE BORGNE, 1981; VOITURIEZ *et al.*, 1982).

Because both depth of the euphotic layer and total incident radiation varied only within a small range from day to day and from one cruise to another, relationships between carbon fixation, chlorophyll and depth show very significant correlation coefficients, and are very similar for each cruise, in spite of differences in the hydrological and chemical structures (VOITURIEZ, 1981, and OUDOT, 1983, respectively).

How far such equations are applicable to predict the production in other areas is indeed to be determined. Because water masses move under the research vessel, the observations made at a fixed location during several days are obviously similar in the surrounding area. It was shown that these relationships were also true at the position (2° N; 4° W). They are probably applicable in the whole oceanic part of the Gulf of Guinea, provided that the incident radiation and the chlorophyll concentration are within the ranges of values used for establishing the relationships.

Since equations were calculated with data including numerous values pertaining to nitrate-depleted waters, there is hope that an extrapolation to the wide oligotrophic areas may be conceivable, which furthermore would constitute a possible approach for elucidating a part of the mystery of the oligotrophic system.

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