

Phosphate uptake in the euphotic layer of the Equatorial Atlantic Ocean Methodological observations and ecological significance

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ABSTRACT

Rates of phosphate uptake (ΔP) were measured with in situ incubations in natural assemblages of plankton using ^{32}P -phosphorus and were compared with rates ^{14}C - CO_2 assimilation (ΔC), measured in the same conditions.

The measurements were performed at two opposite seasons in the Equatorial Atlantic Ocean: during the "cold season" when the equatorial upwelling occurred and during the "warm season" when the typical structure (TTS) was established, i.e. when a warm oligotrophic mixed layer existed.

The validity of applying the method to measure the net assimilation of phosphate by living particulate matter in these waters was tested on the following points: (1) the filter blanks values, (2) the reproducibility of the method, (3) time courses studies which show no rapid initial phosphate uptake and was approximately linear over the experiment time (8 hours), (4) the volume of filtration, which had no effect from 0.5 l to 4.3 l, and (5) the effect of light intensity which was variable and difficult to foresee.

From the in situ incubations, it appears that the phosphate uptake rates would be always maximal in the superficial waters (0-30 m layer), i.e. in the chlorophyll maximum layer during the upwelling season and in the oligotrophic mixed layer of the TTS during the warm season ($\Delta P \approx 1.25 \text{ ng-at P l}^{-1}\text{h}^{-1}$). But, the lack of precision in determining the low values of phosphate in the mixed layer of the TTS makes accurate determination difficult.

The vertical distribution of the assimilation ratio $\Delta C/\Delta P$ was different in the two hydrological structures: the ratio decreased from the surface to the bottom of the euphotic layer in the upwelling, but was maximum at the level of the chlorophyll maximum (within the thermocline) in the TTS.

The Turn Over Rate (TOR: $\Delta P/\text{PO}_4$) does not require the knowledge of the ambient phosphate concentration and can be measured with satisfactory precision in the oligotrophic mixed layer; the values were high: more than 0.5 d^{-1} whereas they ranged between 0.15 and 0.35 d^{-1} in the chlorophyll maximum layer of the two seasons: with such high values of TOR, the length of the incubation could be a possible bias in the mixed layer.

Simultaneous measurements of particulate phosphorus (POP) allowed the calculation of the phosphorus-containing particles growth rates ($\Delta P/\text{POP}$). They would be very high in the mixed layer ($> 1 \text{ d}^{-1}$) whereas the values did not exceed 0.8 d^{-1} elsewhere (chlorophyll maximum included).

Zooplankton ($> 50 \mu\text{m}$) regeneration (via organic and inorganic excretion) accounted for 17.5 to 29 % of the daily phosphate uptake in the TTS and 24-76 % in the upwelling structure. Such a great difference between the measured uptake and the measured regeneration may be due to the activity of the microzooplankton ($< 50 \mu\text{m}$). The main conclusion is that the mixed layer, during the warm season would be a very dynamic system in spite of its low biomasses.

KEY WORDS : Phosphorus — Phytoplankton — Primary production — Tropical Atlantic.

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RÉSUMÉ

ASSIMILATION DU PHOSPHATE DANS LA ZONE EUPHOTIQUE DE L'Océan ATLANTIQUE ÉQUATORIAL.
OBSERVATIONS MÉTHODOLOGIQUES ET CONSÉQUENCES ÉCOLOGIQUES

Les taux d'incorporation de phosphate (ΔP) ont été mesurés sur des populations naturelles de plancton avec le traceur ^{32}P et comparés avec les taux d'incorporation du $^{14}\text{CO}_2$ (ΔC) mesurés dans les mêmes conditions (incubations in situ).

Ces mesures ont été réalisées à deux saisons différentes dans l'Océan Atlantique Équatorial : pendant la « saison froide », en période d'activité de l'upwelling équatorial et pendant la « saison chaude », quand la structure tropicale typique (STT) est établie, c'est-à-dire lorsqu'une couche homogène d'eau chaude et épuisée en sels nutritifs existe.

La validité de la méthode a été testée sur les points suivants : (1) la valeur des blancs de filtre, (2) la reproductibilité des mesures, (3) l'incorporation en fonction du temps, qui est plus ou moins linéaire pendant la durée des incubations, (4) le volume de filtration, qui n'a aucun effet entre 0,5 et 4,3 l, et (5) l'influence de l'éclairement, qui est variable et difficile à interpréter.

A partir des incubations in situ, il apparaît que ΔP est toujours maximum dans la couche superficielle (0-30 m), c'est-à-dire dans le maximum de chlorophylle pendant la saison d'upwelling et dans la couche homogène pendant la saison chaude ($\Delta P \approx 1,25 \text{ natg P l}^{-1} \text{ h}^{-1}$). Mais la difficulté pour déterminer précisément la concentration en phosphate dans la couche homogène rend les résultats incertains pour cette dernière.

La distribution verticale du rapport d'assimilation $\Delta C/\Delta P$ est différente dans les deux structures. Il décroît (comme la chlorophylle) de la surface vers le fond en période d'upwelling tandis qu'il est maximum au niveau du maximum de chlorophylle en saison chaude.

Le taux de renouvellement du phosphate ($\Delta P/PO_4$) n'exige pas de connaître la concentration en phosphate pour être calculé. Il a donc pu être mesuré avec une précision satisfaisante dans la couche homogène. Les valeurs y sont très élevées : plus de $0,5 \text{ j}^{-1}$ tandis qu'elles sont plus faibles, comprises entre 0,15 et $0,35 \text{ j}^{-1}$ dans le maximum de chlorophylle aux deux saisons. Avec des valeurs si élevées, les durées d'incubation ne doivent pas dépasser quelques heures dans la couche homogène.

Des mesures simultanées du phosphore organique particulaire (POP) ont permis de calculer les taux de croissance des particules contenant du phosphore ($\Delta P/POP$). Ils seraient très élevés dans la couche homogène ($> 1 \text{ j}^{-1}$) tandis qu'ils n'excéderaient pas $0,8 \text{ j}^{-1}$ ailleurs.

La régénération par le zooplancton ($> 50 \mu\text{m}$) ne rend compte que de 17,5 - 29 % de la consommation journalière du phosphate dans la TTS et 24-76 % dans l'upwelling. Une telle différence entre l'assimilation et la régénération pourrait être due à l'activité du microzooplancton ($< 50 \mu\text{m}$).

La principale conclusion est que la couche homogène de l'Atlantique tropical oriental serait, malgré des biomasses faibles, un système très dynamique où les microorganismes se renouvellent rapidement.

MOTS-CLÉS : Phosphore — Production primaire — Atlantique tropical.

1. INTRODUCTION

Phosphorus is frequently considered as the most important nutrient in both the regulation of productivity and limitation of biomass in freshwaters and the waters of estuaries (KETCHUM, 1969). In contrast direct and indirect evidence supports the contention that nitrogen is often the element most likely to limit plant productivity in the sea (THOMAS, 1966; EPPLEY *et al.*, 1973 and others). Probably for that reason, the phosphorus metabolism of natural plankton has been studied extensively in lake waters (HUTCHINSON and BOWEN, 1947; RIGLER, 1956, 1964; LEAN, 1973) and more recently in coastal marine environments (CORRELL *et al.*, 1975; TAFT *et al.*, 1975; HARRISON *et al.*, 1977). But to my knowledge, the studies on the phosphorus cycle, including measurements of uptake and release by the organisms in marine offshore waters are scarce. PERRY (1976)

and more recently PERRY and EPPLEY (1981) have examined the dynamics of phosphorus utilization in the Central North Pacific Ocean (CNPO) an extreme oligotrophic environment, characterized by low concentrations of plankton biomass and of dissolved nitrogen and phosphorus compounds. Their main conclusions were the following: (1) the phytoplankton of these waters was nitrogen limited rather than phosphorus limited, (2) the mean values of turnover times for phosphate ranged between 19 and 31 days according to the season, and (3) the growth rates of phytoplankton in the mixed layer averaged $0.14 \text{ doublings d}^{-1}$, i.e. the low values found by EPPLEY *et al.* (1973) and SHARP *et al.*, (1980) by other methods in the same waters and among the lowest values in the marine waters.

The historical data (MAZEIKA, 1968; MERLE, 1978), and the results of the more recent cruises show that there are two main seasons in the equatorial Atlantic

Ocean: a "warm season", from October to end of May, and a "cold season" from June to September. During the warm season, there is a nitrate-depleted mixed layer, with very low nutrients and chlorophyll concentrations. The chlorophyll maximum lies in the thermocline and it is frequently associated with the nitracline (HERBLAND and VOITURIEZ, 1979). During the cold season, the nutrients reach the surface layer where higher chlorophyll values are measured. Thus, the equatorial area of the Atlantic Ocean shows two contrasted situations: one situation approaches to the upwelling system. From a biological point of view, this contrast is worth studying since the distribution of the plankton organisms and the nature and the intensity of the rate processes are expected to be different.

In this paper, we report the results dealing with the phosphorus cycle of a multiphasic study of the photic zone of the Eastern Equatorial Atlantic Ocean (Program CIPREA: Circulation et Production à l'Équateur dans l'Atlantique supported by O.R.S.T.O.M.), covering the two seasons.

2. MATERIAL AND METHODS

The first cruise, CIPREA 1 (CA 7802) was in August 1978 when the equatorial upwelling was active; the second SOP 1 (CA 7903) and the third CIPREA 2 (CA 7906) were respectively in February and March 1979 during the warm season.

— Temperature and salinity were recorded *in situ* with an STD multisensor (Bisset Berman) coupled with a Hewlett Packard computer.

— Light measurements includes: (1) a continuous record on the deck of total irradiance with a calibrated Eppley pyranometer or Kipp an Zonen solarimeter; integrating over the period of the entire day yielded the total daily irradiance ($J\ m^{-2}d^{-1}$) for the spectral range 300-2 800 nm; (2) at 5 m intervals the downwelling quantum irradiance was measured for the 370-700 nm spectral region, at about 13 h local time, with a Lambda quantum meter.

Sampling levels were chosen according to the temperature and salinity profiles in order not to miss the expected gradients and maxima of the nutrients and biological parameters. Samples from discrete depths for chemical and biological analyses were collected with PVC bottles of two capacities: 12 small Niskin bottles of 1.7 l on a rosette sampler (General Oceanic) for oxygen, nutrients and chlorophyll measurements and a 30 l Niskin bottle for particulate matter and assimilation studies at 5 to 8 levels, each morning before the sunrise.

Nutrients were immediately analysed with an autoanalyser (Technicon A 11) following the analytical methods described in STRICKLAND and PARSONS

(1972) and Dissolved Organic Phosphorus (DOP) was determined after UV oxydation in silice tubes (ARMSTRONG *et al.*, 1966).

Chlorophyll *a* was measured by fluorometry according to procedure of YENTSCH and MENZEL (1963) as modified by Holm HANSEN *et al.* (1965): 175 ml of sea water was filtered through a Whatman GFC glass fiber filter (\varnothing 25 mm) with a very low suction pressure (\approx 75 mm Hg.) Calibration of the fluorometer was made with chlorophyll *a* (Sigma) on a spectrophotometer (Beckman 25).

Particulate Carbon, Nitrogen and Phosphorus was collected on precombusted Gelman Type A glass fiber filters by filtration of 1 or 2 l of sea water. The sea water was prefiltered through a 200 μ m mesh size net. The C.N. samples were kept frozen, after dessication at 60 °C, until analysis with a CHN analyser (Hewlett Packard 185 B). The particulate phosphorus was immediately analysed after persulfate oxydation (MENZEL and CORWIN, 1965).

Rates of photosynthetic carbon fixation by phytoplankton were determined by the ^{14}C method of STEEMANN-NIELSEN (1952). Each morning before sunrise 8 levels were sampled within the euphotic zone and the samples (300 ml) were incubated *in situ* in sterile glass bottles with 8 μ Ci of ^{14}C for 11 h, the length of the day light. After incubation, the samples were filtered through 0.45 μ m membrane (Sartorius) filters. The filters were rinsed with 10 ml of filtered sea water (not acidified), dried at 55-60 °C for 8-10 h in a scintillation vial and their radioactivity determined with a liquid scintillation counter (Packard, PRIAS).

Phosphate uptake was determined by the use of ^{32}P - PO_4 as a tracer. The ^{32}P - PO_4 concentration in the sample was very low ($< 0.02\ \mu$ gatP l^{-1} , 0.1-0.2 μ Ci per sample) to prevent a change in the dynamics of the phosphate uptake (WILLIAMS and ASKEW 1968; WRIGHT 1973).

Time zero and formalin treated samples incubated for the duration of the experiment were used as controls (see below the paragraph: "methodological problems with PO_4 uptake"). Samples were treated identically to those for ^{14}C uptake.

Other samples were incubated in a deck incubator cooled with surface sea water. The light effect was investigated with nickel screen around each bottle, corresponding to about 50 %, 30 %, 10 %, 3 % and 1 % of the surface light. These simulated *in situ* incubations were carried out for 4-6 h around midday.

Estimates of the input of regenerated phosphorus, both dissolved organic (DOP) and PO_4 were obtained from excretion rates of zooplankton captured within the euphotic layer by two nets: A WP_2 net with 200 μ m mesh size and a small net (50 cm diameter) with 50 μ m mesh size, to collect the microzoo-

plankton (50-200 μm size animals). The excretion rates were calculated as the difference between the concentration of total DOP and PO_4 , at the end of the incubation in the bottles with and without animals, for a known weight of unsorted animals. Incubations were run in the dark, in 2 l and 1 l bottles, at two temperatures for 20-23 hours. The input of regenerated phosphorus was then calculated from the dry weight biomass of zooplankton larger than 50 μm and 200 μm according to the vertical distribution of zooplankton and temperature profiles (see LE BORGNE, 1977 for details).

3. METHODOLOGICAL PROBLEMS WITH PHOSPHATE UPTAKE

Since the use of ^{32}P was a new method for our laboratory, it was necessary to test the validity of applying the method to measure net assimilation of phosphate by living particulate matter in the waters of the equatorial Atlantic Ocean.

3.1. The "blanks of filters": sensitivity in the measurement of low phosphate uptake is limited by the precision with which non biological retention of radioactivity can be determined. Thus we have to try and determine with the best accuracy the blank values in our experiments.

Controls killed with formalin were prepared and incubated for the duration of the experiment for each station during the cruise CIPREA I. The filters rinsed with filtered sea water have lower values (1 340 against 5 760) with lower standard deviation (630 cpm against 1 162) than the not rinsed samples. But the problem of adsorption remains, even with rinsing: for comparison, the blank in $^{14}\text{CO}_2$ uptake experiments, with the same bottles and same filters gave a much lower mean value ($m = 166$ cpm, $\sigma = 31.6$ with 8 replicates) whereas the added radioactivity was very much higher (7-8 μCi per sample).

3.2. Problems with the low-level phosphate in the mixed layer of the warm season

The determination of the phosphate uptake rate with the ^{32}P technique requires the knowledge of the ambient phosphate concentration. STRICKLAND and PARSONS (1972) indicates that the smallest amount than can be detected with certainty with the standard method of MURPHY and RILEY (1962) is about 0.03 μg at P l^{-1} . FROELICH and PILSON (1978) recommended that users of T.A. II for low-level phosphate in sea water calibrate each colorimeter for the refractive index effect. The mean

value, with our apparatus is 0.1 μg at l^{-1} (range 0.06-0.125). Then we have corrected all the phosphate values, prior to calculation of phosphate uptake rates. But, sometimes, we obtained negative values, specially for the cruise CA 7903 (14 days at $0^\circ\text{-}4^\circ\text{W}$ in February 1979).

If the correction is ignored, doubtful values of $\Delta\text{C}/\Delta\text{P}$ and $\Delta\text{P}/\text{POP}$ are obtained in the mixed layer (mean value of $\Delta\text{C}/\Delta\text{P} = 30$ and mean value of $\Delta\text{P}/\text{POP} = 4,7 \text{ day}^{-1}$). That is why the phosphate uptake rates were not calculated for the cruise CA 7903.

3.3. The reproductibility of measurements of rate of phosphate uptake

It was estimated in several occasions.

(1)—Four replicates of surface sea-water were incubated *in situ* for 11 h at station 31 (CIPREA II). The results were surprisingly good (mean = 10 618 cpm, $\sigma = 209$, $\text{Cv} = 2.0 \%$); (2)—Five replicates of surface water were incubated for 5 h in the deck incubator during CIPREA I. The coefficient of variation was higher (26,3 %); (3)—During the experimental studies

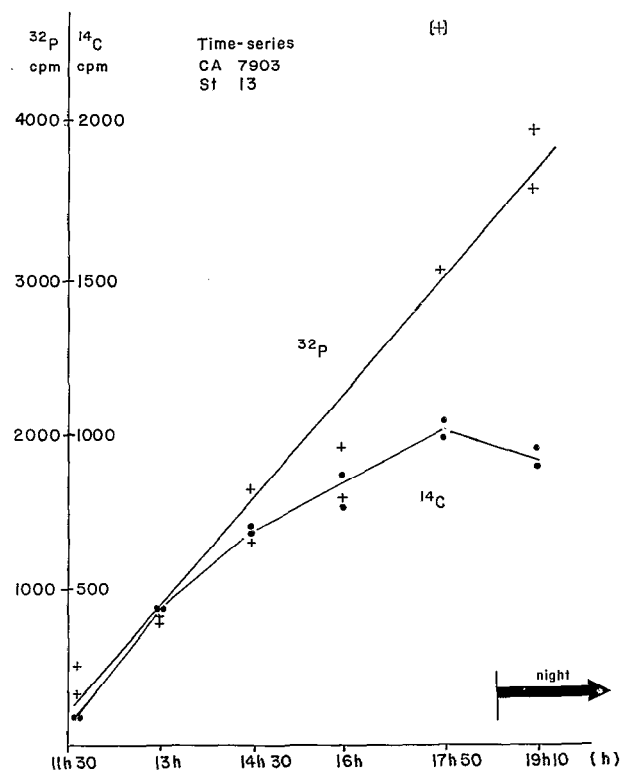


FIG. 1. — An example of phosphate uptake in a time course experiment.

Un exemple d'assimilation du phosphate en fonction du temps.

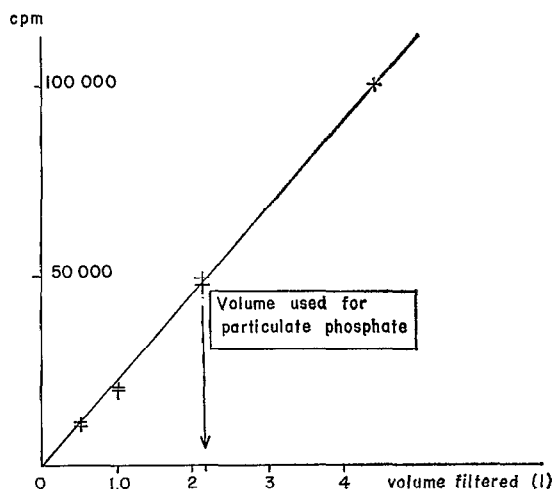


Fig. 2. — The effect of volume of filtration upon the measurement of phosphate uptake.

Influence du volume de filtration sur la mesure de l'assimilation du phosphate.

on the deck, samples have been incubated in duplicates. The replicates counts are generally in good agreement (fig. 1, fig. 2, fig. 3 c) but occasionally (fig. 1, point in brackets) some values are high, without obvious explanation. Similar results were found by PERRY (1976) with 12 replicates bottles. Therefore we intuitively rejected the rare anomalously high values.

3.4. Time course of $^{32}\text{PO}_4$ uptake

Several authors (TAFT *et al.*, 1975; MC CARTHY *et al.*, 1975; BERMAN and STILLER, 1977; LEMASSON and PAGÈS, 1981) demonstrated that ^{32}P (or ^{33}P) uptake occurred initially at a rapid rate which could not, from comparison with photosynthesis measured by $^{14}\text{CO}_2$ fixation and heterotrophic activity measured by labelled glucose, be equated with net uptake associated with growth. Other authors (HARRISON *et al.*, 1977) found a linearity over 2 hours and PERRY (1976) who worked in the oligotrophic waters of the Central North Pacific found a linearity over 24 h of phosphate uptake under natural light/dark photoperiod conditions.

Two time courses were run in the equatorial waters with $^{14}\text{CO}_2$ and $^{32}\text{PO}_4$ simultaneously (fig. 1). Similar shapes of curves were obtained with both compounds, and no rapid initial PO_4 uptake was observed, the uptake was approximately linear over 8 h. PERRY (1976) concluded that the linearity implied that the PO_4 concentration was not drastically reduced during the 24 h period within the

microcosm of the incubation bottle. In our time series experiments, the number of cpm on the filter after 8 hours was low compared to the added radioactivity; but, several times, with the *in situ* incubations (samples in the warm mixed layer), the part of the uptaken radioactivity was important (45-60 % of the initial radioactivity). It is likely that the incubation period is too long for such samples (see "RESULTS") if organic excretion is taken into account (LEMASSON and PAGÈS, 1981). Thus, if *in situ* incubations from sunrise to sunset would be the best method to determine the true daily net production of particles in the water column (dark loss not included) through the $^{14}\text{CO}_2$ uptake, the same method must be applied with caution to the $^{32}\text{PO}_4$ uptake in the oligotrophic waters of the tropical Atlantic Ocean.

3.5. Effect of the volume filtered

In the course of routine primary production experiments with phytoplankton, the volume of sea water filtered through the membrane or glass fibre filter is one of the factor which can affect the results (BERMAN, 1973). In order to make feasible the comparison of the phosphate uptake results with those of particulate organic phosphorus in which the filtered volume was greater (2 000 ml against 300 ml) the volume effect has been tested. Five flasks of 3 l were filled with water of the thermocline (60 m) and incubated for five hours in the deck incubator (the light was reduced to 3 % of surface light with a nickel screen). It is clear (fig. 2) that no volume effect can be detected from 0.5 l to 4.3 l, in these waters.

3.6. The light influence

In a recent study, RESHKIN and KNAUER (1979) found a light dependence of phosphate uptake by phytoplankton in coastal natural assemblages, the relationship approximately fitting a Michaelis Menten kinetic function. In contrast, PERRY (1976) for oligotrophic sea water, TAFT *et al.*, (1975) for coastal waters of the Chesapeake Bay Estuary and BERMAN and STILLER (1977) for lake water did not find significant differences between rates of phosphate uptake in the light and dark period.

Phosphate uptake as a function of light intensity was measured in 8 experiments, the data from five being presented in fig. 3; three times, the PO_4 uptake rates were compared to the $^{14}\text{CO}_2$ uptake rates simultaneously measured in the same conditions.

During the SOP cruise (fig. 3 a and 3 b) the water was sampled in the chlorophyll maximum layer, where the light was 3-6 % of the surface light.

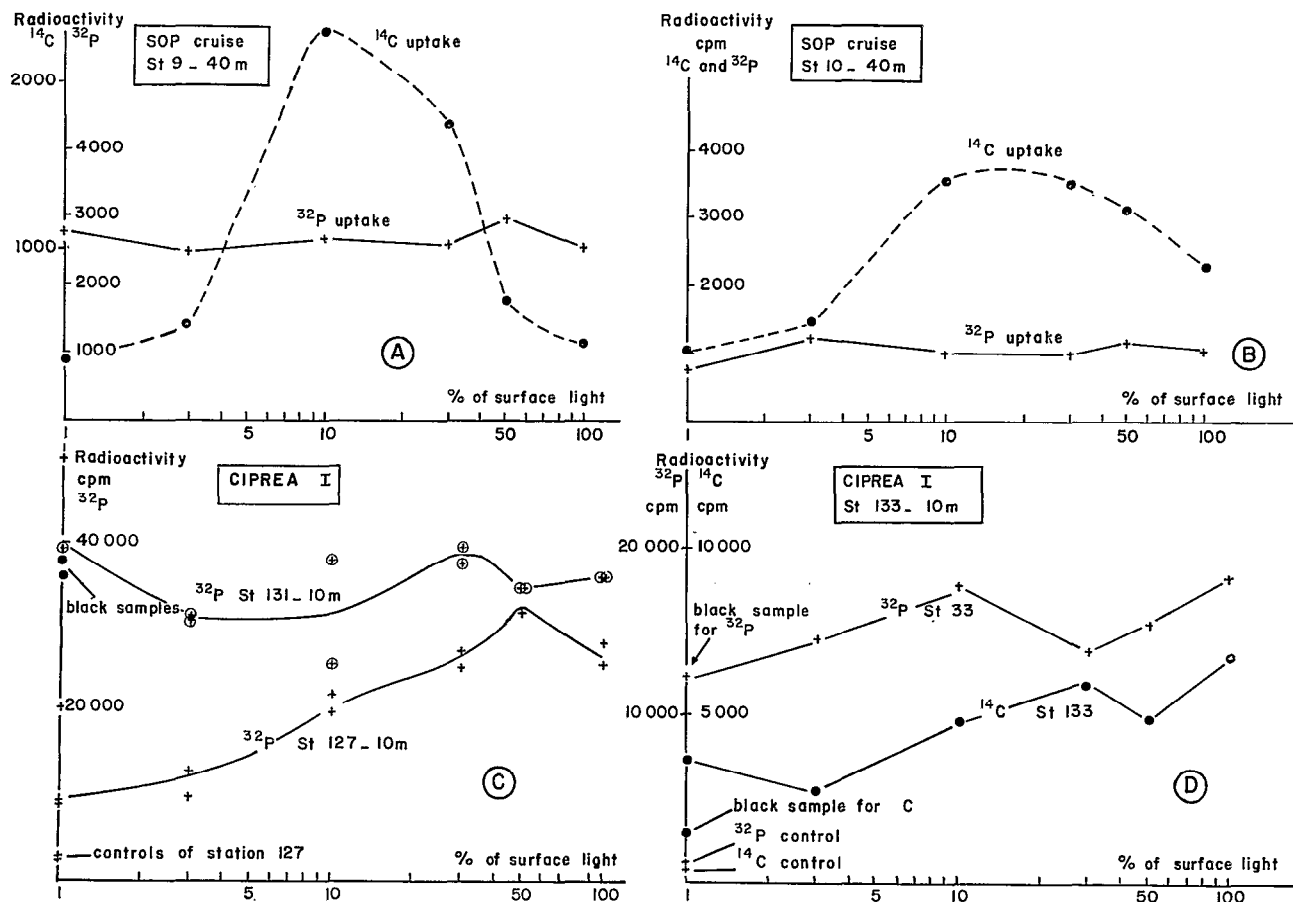


Fig. 3. — The influence of light intensity on the $^{14}\text{CO}_2$ and $^{32}\text{PO}_4$ uptake. (Simulated *in situ* incubations)
 Influence de l'intensité lumineuse sur l'assimilation simultanée du $^{32}\text{PO}_4$ et du $^{14}\text{CO}_2$. (Incubations *in situ* simulé)

There was a clear inhibition for $^{14}\text{CO}_2$ uptake in the 50-100 % range and no appreciable effect for $^{32}\text{PO}_4$ uptake on the whole range.

During CIPREA I (fig. 3 c and 3 d), water was sampled at 10 m near the well lighted chlorophyll maximum (it was an upwelling situation with nutrients in surface waters). There was again no significant trend for $^{32}\text{PO}_4$ uptake, station 127 excepted, in which the maximum of uptake occurred for the 30-100 % range. The dark samples did not differ from the others.

The light influence on phosphate uptake rates has been studied in an other way in February 1979 (cruise CA 7903): in addition to the *in situ* incubated samples, two samples located within or near the chlorophyll maximum layer were incubated 10 meters above their initial depth, during the same time, with $^{14}\text{CO}_2$ and $^{32}\text{PO}_4$. The results of the experiment are presented in table I. They clearly show

that the photosynthetic activity is always increased when the samples are incubated 10 meters above their sampling level. The mean value is 24.5 % with a low standard deviation (12.7); on the contrary, the phosphate uptake rate shows erratic results. At two stations (9 and 14) very high increases were induced whereas no significant effect was visible at the two others (8 and 10).

Then the direct light influence seems unpredictable. In most cases, there was no influence (7 over 8). Hence, the hourly phosphate uptake rates have been multiplied by 24 to obtain the daily phosphate uptake rates.

But, as TAFT *et al.* (1975), said dial periodicity is not specially a function of the quantity of light, and all our experiments have been performed during the day time. We have no results on short term experiments for 24 h like HARRISON *et al.* (1977) who showed a circadian periodicity with this technique.

TABLE I

Indirect estimation of light influence on the $^{14}\text{CO}_2$ and $^{32}\text{PO}_4$ uptake: samples have been incubated at their original level and ten meters above.

Estimation indirecte de l'influence de la lumière sur l'assimilation simultanée du $^{14}\text{CO}_2$ et du $^{32}\text{PO}_4$: Échantillons incubés in situ à leur niveau d'origine et 10 mètres au-dessus.

Station Sampling level (PO_4)			CO_2 uptake rate $\mu\text{gC l}^{-3} \text{h}^{-1}$			PO_4 uptake rate $\mu\text{gat m}^{-3} \text{h}^{-1}$		
n°	m	$\mu\text{gat l}^{-1}$	In situ incubation	10 m above In situ inc.	% of variation	In situ incubation	10 m above In situ inc.	% of variation
8	40	0.17	3.27	4.99	+ 52.6	1.84	2.19	+ 16.7
	45	0.25	2.12	2.73	+ 28.8	1.86	1.75	- 6.4
9	40	0.20	4.60	5.68	+ 23.5	3.52	4.88	+ 40.5
	45	0.28	4.08	4.83	+ 18.4	5.03	9.96	+100.0
10	40	(0.11)	2.24	2.86	+ 27.7	3.17	3.41	+ 7.2
	45	(0.19)	3.57	*	-	3.96	3.10	- 18.6
14	40	0.17	2.76	3.15	+ 14.1	1.35	2.14	+ 57.9
	45	0.22	2.12	2.42	+ 14.2	1.10	2.00	+ 83.3
Mean value			-	-	+ 24.5	-	-	+ 34.5
Standard deviation			-	-	12.7	-	-	42.5

4. RESULTS OF *in situ* INCUBATIONS

4.1. Hydrological structure (fig. 4)

The hydrological conditions met from 5°N to 10°S at 4°W in August 1978 (cruise CIPREA I) and in April 1979 (cruise CIPREA II) agree with the expected situations: in summer there was a large cooling (surface temperature 22°C) between $0^\circ30'\text{S}$ and 5°S with nutrients increase in superficial waters ($\text{NO}_3 > 2 \mu\text{gat l}^{-1}$ and $\text{PO}_4 > 0.40 \mu\text{gat l}^{-1}$) between the same limits. High values ($6 \mu\text{gat l}^{-1}$ of NO_3) were measured at $2^\circ30'\text{S}$ in surface waters. The "equatorial upwelling" was not centered on the equator as already noted by VOITURIEZ and HERBLAND (1977). The chlorophyll distribution followed the hydrological structure: low values ($< 0.2 \mu\text{g l}^{-1}$) were measured in the warm mixed layer on each side of the upwelling. Low values of chlorophyll were also measured in the middle part of the upwelling (around 3°S); the highest values ($> 0.7 \mu\text{g l}^{-1}$) were located at the boundary of the upwelling area.

In April 1979, the hydrological situation was very different: a warm mixed layer (temperature = 28 - 29°C) was present on the whole section; nitrate was frequently undetectable ($< 0.10 \mu\text{gat l}^{-1}$) in the

mixed layer, and phosphate values were lower than $0.10 \mu\text{gat l}^{-1}$. The chlorophyll maximum ($> 0.4 \mu\text{g l}^{-1}$) was located in the nitracline.

4.2. Phosphate uptake rates (ΔP)

In the two situations, maximum uptake rates were measured in the superficial layer (0-30 m) i.e. in the chlorophyll maximum layer in the upwelling situation and in the mixed layer during the warm season. There was no seasonal difference in the 0-30 m layer: ΔP (in $\text{ng-at P l}^{-1} \text{h}^{-1}$) = 1.28 ($\sigma = 0.51$) during the cold season and 1.23 ($\sigma = 0.47$) during the warm season. Below the chlorophyll maximum, ΔP decreased (fig. 5).

4.3. Assimilation ratios $\Delta\text{C}/\Delta\text{P}$

Atomic ratio (at/at) of assimilation rates for carbon and phosphorus were computed for each depth in each situation. The vertical distributions of the mean values were very different in the two structures (fig. 5). They decreased from the surface to the bottom of the euphotic layer in the upwelling, but were maximum at the level of the chlorophyll maximum layer in the TTS. High

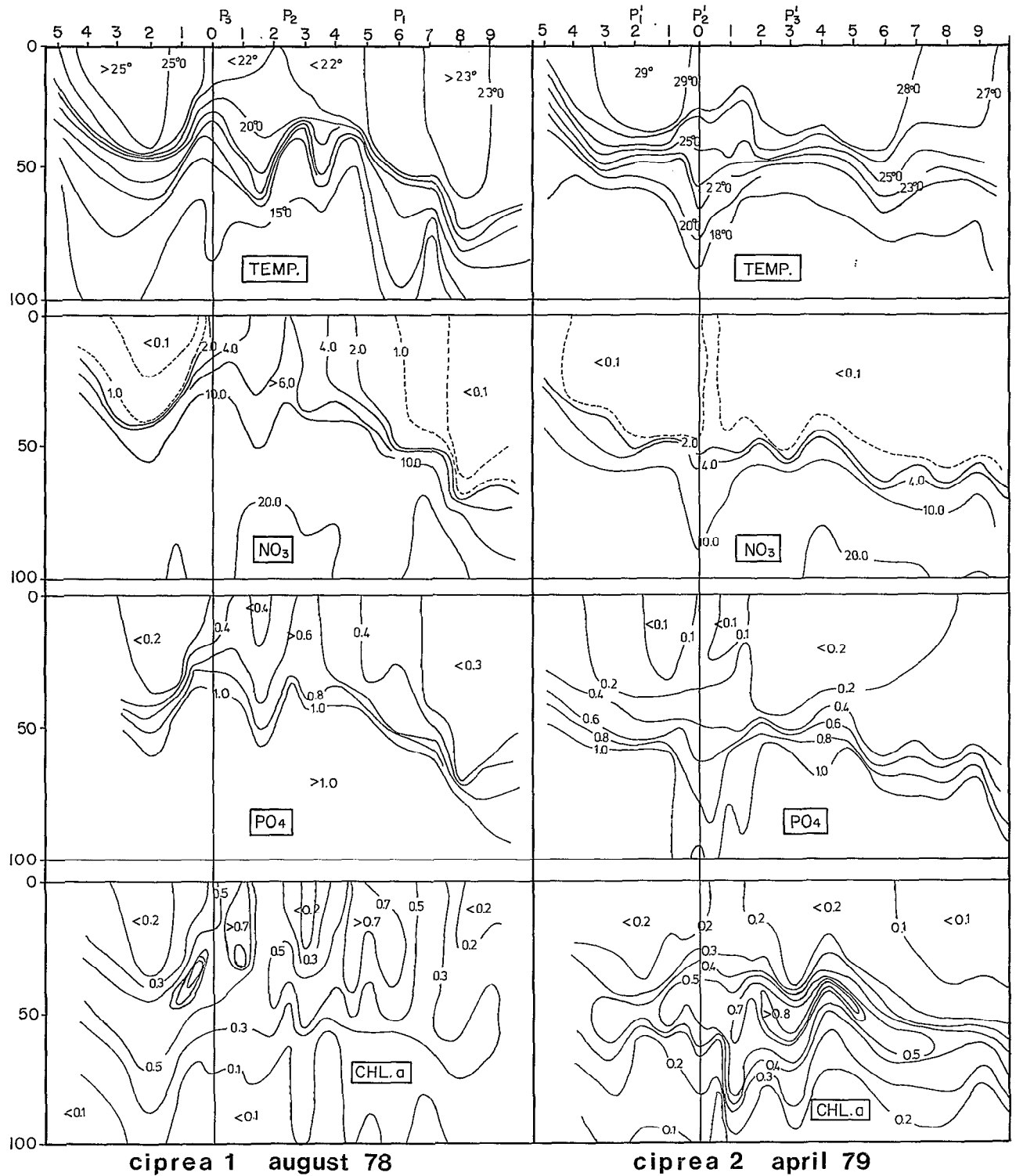


FIG. 4. — Temperature, nitrate, phosphate and chlorophyll a distribution from 5° N to 10° S at 4° W in August 1978 (cold season) and April 1979 (warm season).

Température, nitrate, phosphate et chlorophylle a : distribution entre 5° N et 10° S à 4° W en août 1978 (« saison froide ») et avril 1979 (« saison chaude »).

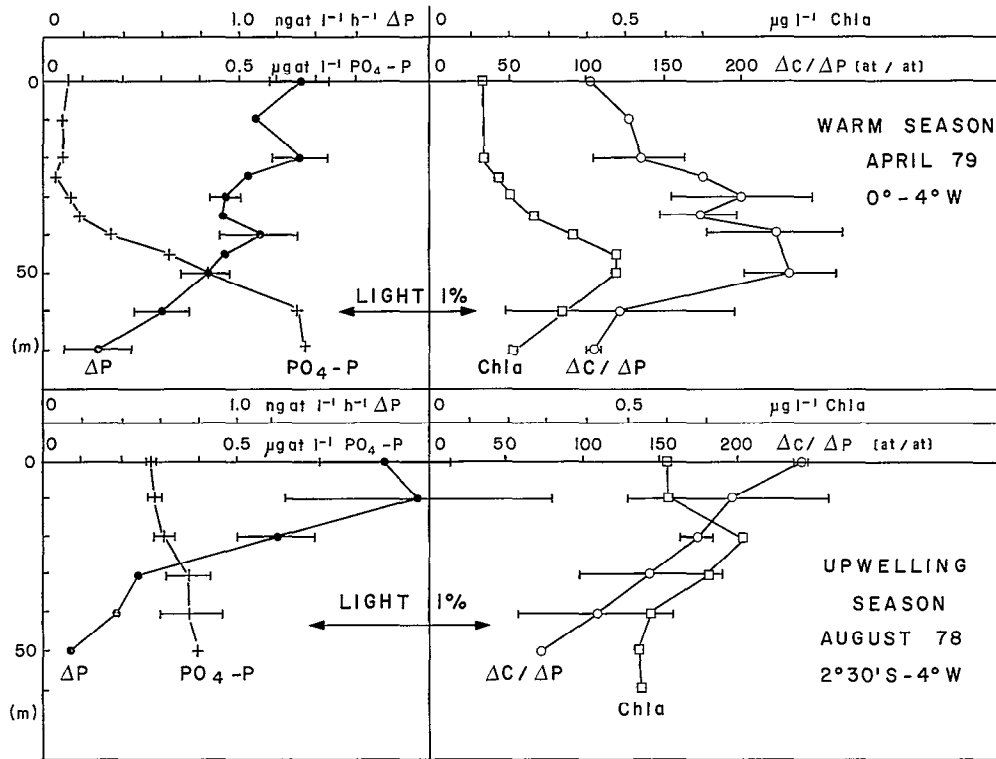


FIG. 5. — Vertical distribution of phosphate (PO₄), phosphate uptake rate (ΔP), chlorophyll a (chl a) and assimilation ratios (ΔC/ΔP) in the two different hydrological structures (upwelling and Typical Tropical Structure).

Distribution verticale du phosphate (PO₄-P) de l'assimilation du phosphate (ΔP), de la chlorophylle a (chl a) et du rapport d'assimilation (ΔC/ΔP) dans deux structures hydrologiques différentes; en haut: structure tropicale typique; en bas: upwelling équatorial.

values were recorded (> 200) where the chlorophyll values were high; it would indicate that the high phosphate uptake rates would not be overestimated.

4.4. Phytoplankton and/or particles growth rates

The growth rate is defined as the rate of increase of cell substance per unit cell substance:

$$\mu = \frac{1}{S} \times \frac{dS}{dt}$$

With natural samples, the difficulty is to measure S, the biomass (i.e. carbon, nitrogen or phosphorus), because the measurements of particulate organic matter in the sea generally include phytoplankton, microzooplankton, detritus and bacteria. Hence, direct estimate of growth rate of phytoplankton by measuring the incorporation of C, N or P with radio-tracers technique may be underestimated if non phytoplanktonic biomass is included in the S compartment.

However, PERRY and EPPLEY (1981) pointed out that in the Central North Pacific Ocean, particulate phosphorus does not include detritus unlike POC and PON, and it can be used as a valuable detritus-free biomass measurement. In a recent study, we found that POP was more associated with chlorophyll than PON and overall POC in the euphotic layer of the Equatorial Atlantic Ocean (HERBLAND and LE BOUTELLER, 1981): in the chlorophyll maximum layer POP would include approximately only 20 % of organisms without chlorophyll. In the nitrate depleted mixed layer the determination is more complicated because the regression technique which has been used to evaluate the particulate organic matter not associated with chlorophyll, gave an overestimated value of that compartment.

Therefore, the ratios ΔP/POP, which have been calculated for each depth at each station have probably not the same significance from the top to the bottom of euphotic layer (fig. 6). These ratios are an acceptable lower limit for the chlorophyll maximum layer in both seasons, whereas they are probably

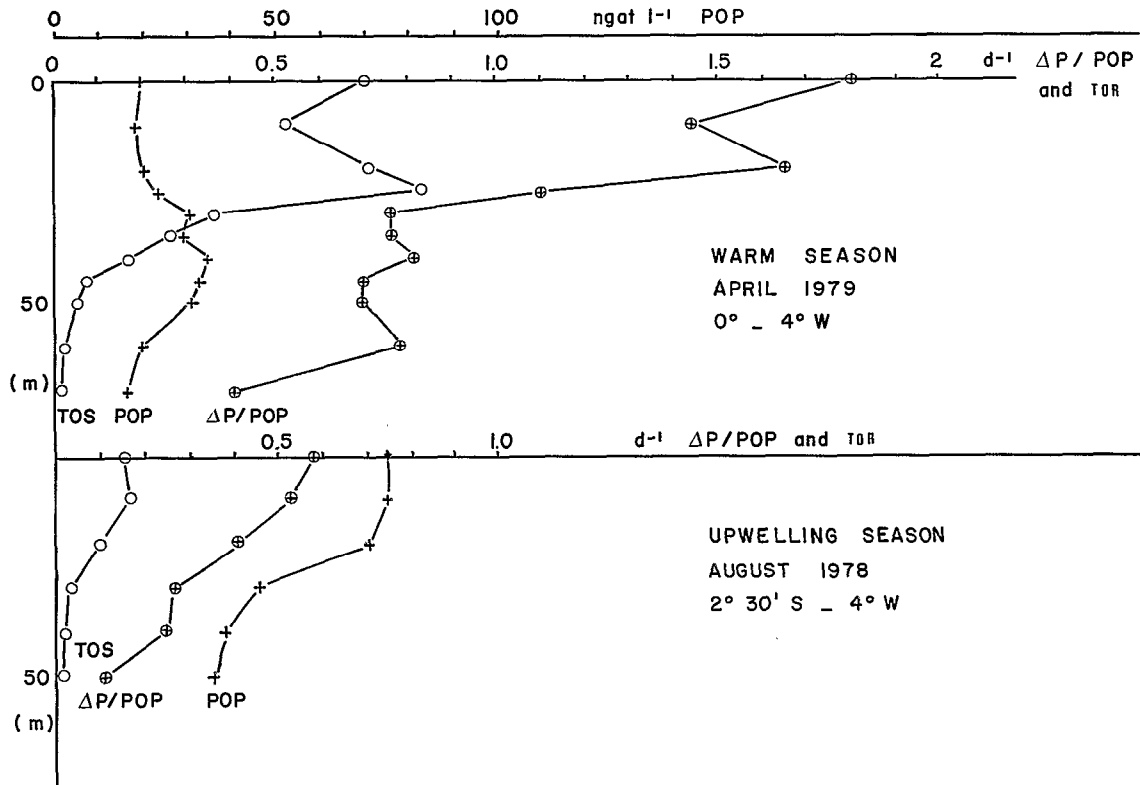


FIG. 6. — Vertical distribution of particulate organic phosphorus (POP) particles growth rate ($\Delta P/POP$) and Turn Over Rate of phosphate ($TOR = \Delta P/PO_4$) in the two different hydrological structures. Same stations as in fig. 5.

Distribution verticale du phosphore organique particulaire (POP), du taux de croissance des particules ($\Delta P/POP$) et du taux de turn over (TOR) dans deux structures hydrologiques différentes; en haut: structure tropicale typique; en bas: upwelling équatorial.

more underestimated in the mixed layer during the warm season. The highest values were measured in the mixed layer ($> 1 \text{ d}^{-1}$) whereas the values in the chlorophyll maximum did not exceed 0.8 d^{-1} . They were lower again in the upwelling season since ΔP did not change and POP was higher (1).

4.5. Turn Over Rate of phosphate (TOR)

With the tracer method, the calculation of PO_4 turn over time does not require the knowledge of the ambient phosphate concentration. We only have to know the percentage uptake of $^{32}PO_4$ per unit time because the total radioactivity added is proportional to the ambient PO_4 concentration. Nevertheless, the steady state is implicitly assumed (PERRY and EPPLEY, 1981). The inverse of the turn over time is the Turn Over Rate which has a dimension of rate (T^{-1}), like a growth rate. In order to facilitate

the comparison with the particulate growth rate, we have calculated the TOR for each depth in each situation. We assumed a dark uptake equal to the light uptake (see above).

For both seasons, the TOR was higher in the superficial waters, but the values were much higher in the mixed layer of the TTS (0.5 d^{-1} or more). In the upwelled waters, the mean values ranged between 0.15 and 0.30 d^{-1} (fig. 6). Since the phosphate concentration is not required, the results collected during the SOP cruise (14 days at 0° - 4° W in February 1979) can be used here (fig. 7). In the mixed layer, where the nutrient concentration were low, the $\Delta P/PO_4$ ratios were again high (0.86 d^{-1} , $\sigma = 0.26$, $n = 34$) and they were lower in the chlorophyll maximum layer (0.29 d^{-1} , $\sigma = 0.17$, $n = 23$). Moreover, as it has been seen before, the incubations of 5 hours (instead of 11) gave higher values in the mixed layer (1.56 d^{-1} , $\sigma = 0.46$, $n = 5$) but did not

(1) ΔP was measured with Sartorius membrane filters ($0.45 \mu\text{m}$) and POP with Gelman fiber glass filters (type A/E). We know to day that the Gelman filters have a weak retention capacity in the nitrate-depleted mixed layer (HERBLAND *et al.*, in prep.). Thus, the ratios $\Delta P/POP$ are probably overestimated in this layer.

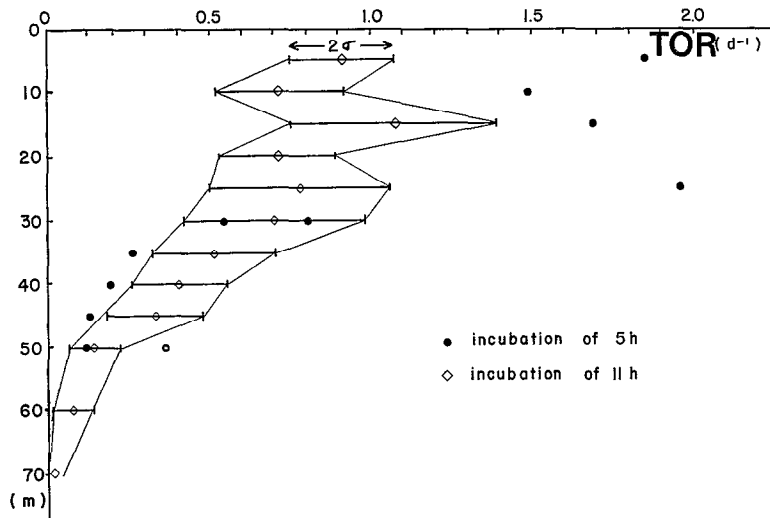


FIG. 7. — Vertical distribution of the Turn Over Rate of phosphate in the euphotic layer during the SOP cruise (CAP 7903) a 14 day-station at 0°-4° W.

Distribution verticale du taux de turn over (TOR) du phosphate dans la zone euphotique au cours d'une station de 14 jours à 0-4° W (CAP 7903 en février 1979).

TABLE II

Comparison between phosphate uptake (ΔP) and phosphorus excreted by zooplankton (50-5 000 μm). PO_4 excr. is the phosphate excreted and P_{Tot} is the total phosphorus (organic+inorganic) excreted in the euphotic layer.

Comparaison entre l'assimilation du phosphate (ΔP) et le phosphore excreté par le zooplancton (50-5 000 μm). PO_4 excr. : « phosphate réactif » excreté; P_{Tot} : phosphore total excreté (minéral+organique). Valeurs intégrées sur la couche euphotique.

	ΔP	PO_4 excr.	P_{Tot} excr.	PO_4 excr. P_{Tot} excr.	
				$\frac{\text{PO}_4 \text{ excr.}}{\Delta P}$ %	$\frac{P_{\text{Tot}} \text{ excr.}}{\Delta P}$ %
Upwelling (0-50m) m	1 205	305	566	26.7	49.7
2°30'-4°W σ	216	77	144	12.3	22.9
0° - 4°W m	1 222	193	325	15.8	26.7
σ	92	12	20	1.7	2.9
Warm season(5-60m)					
0° - 4°W m	1 468	187	337	12.8	23.0
σ	70	41	76	3.0	5.6

differ in the chlorophyll maximum layer (0.21 d^{-1} , $\sigma = 0.10$, $n = 5$) presumably because incubations from sunrise to sunset are too long for such warm waters.

4.6. Phosphate uptake and phosphorus regeneration

In table II we show the results of phosphorus excretion by the zooplankton (micro-+mesozooplankton, i.e. from $50 \mu\text{m}$ to $5\,000 \mu\text{m}$). Each value is the mean of three stations. Phosphate regeneration is small compared to the phosphate uptake especially during the warm season where it accounts for only 13 % of the uptake; even if we suppose that the organic phosphorus is, for a great part, immediately mineralized by the bacteria, a gap remains between the measured uptake and the measured excretion. How to explain such a difference? Firstly we can be suspicious of the two methods: ΔPO_4 (for 24 hours) can be overestimated because the incubations ran during the day and again, we are ignorant of the uptake during the night. At least, it seems that the hourly rates are not overestimated because the assimilation ratio $\Delta\text{C}/\Delta\text{P}$ have high values. ΔC could be overestimated, because very high values of assimilation number have been measured in the nitrate depleted layer (HERBLAND and LE BOUTEILLER, 1981), but they are confirmed by the large *in situ* increases of chlorophyll during the day (LE BOUTEILLER, pers. comm.).

But, in other hand, the phosphate uptake could be underestimated: bacteria are very small organisms and the filters used in our study probably did not retain all the phosphate-consuming organisms.

Values of zooplankton excretion in table II are those of LE BORGNE. His method has been tested in detail (see, for example, LE BORGNE, 1982). Probably the results are nearly correct for that fraction of zooplankton.

5. DISCUSSION

It is clear from the work of many authors (for example FAUST and CORRELL, 1976, and HARRISON *et al.*, 1977) that both photosynthetic and heterotrophic microorganisms took up radiophosphate. But PERRY (1976) and PERRY and EPPLEY (1981) presented evidence that phosphate assimilation in the North Pacific Ocean was primarily by phytoplankton.

We tried to investigate the question by the size fractionation technique with Nuclepore filters of $3 \mu\text{m}$ pore size. Although the separation of algae from bacteria is not totally achieved (BERMAN, 1975), it gives valuable information for elucidating the flux of nutrients into various components of the microplankton and in characterizing different aquatic environments (BERMAN and STILLER, 1977). Although

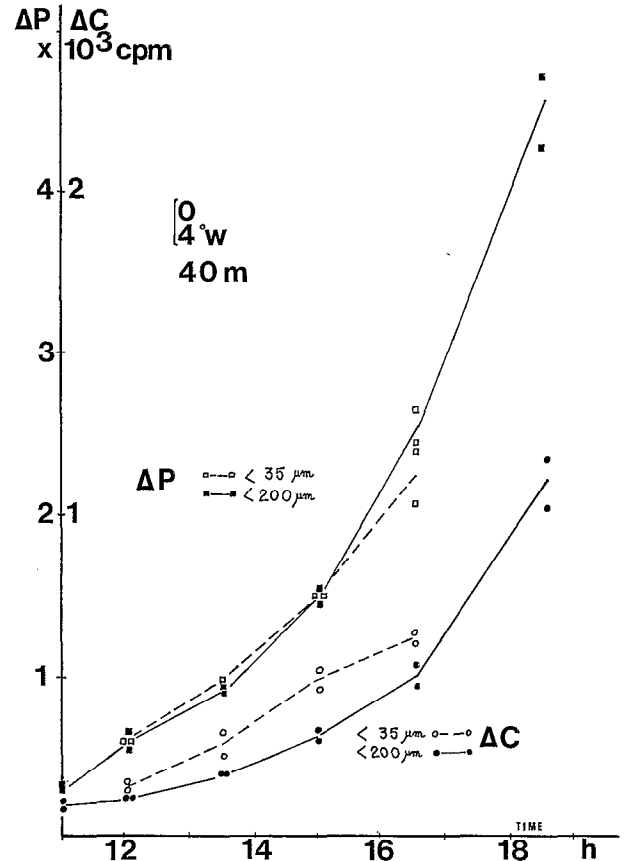


Fig. 8. — A time series experiment on simultaneous phosphate and carbonate uptake comparison between the $35 \mu\text{m}$ and $200 \mu\text{m}$ prefiltered samples.

Évolution comparée en fonction du temps de l'assimilation du phosphate et du carbonate sur deux fractions différentes. Eau préfiltrée sur 35 ou 200 microns. Noter l'assimilation du carbonate supérieure pour l'eau filtrée sur $35 \mu\text{m}$.

the method gave satisfactory results for chlorophyll, phaeophytin, particulate carbon, nitrogen and phosphorus, and photosynthetic carbon fixation (HERBLAND and LE BOUTEILLER, 1981) the results were inconclusive for phosphate uptake.

Our results from *in situ* incubations would indicate that in the chlorophyll maximum layer phosphate uptake is primarily due to phytoplankton since the highest values of $\Delta\text{C}/\Delta\text{P}$ ratios were measured there. However, we have indirect evidence that, even in the chlorophyll maximum layer, phosphate and carbonate are not taken up by the same organisms. During a time series experiment, water filtered before incubation on a $35 \mu\text{m}$ net gave a higher photosynthetic fixation than the water filtered on $200 \mu\text{m}$; there was no difference in the phosphate uptake (fig. 8). That result is paradoxical, because

30 % of the chlorophyll was removed by filtration on the 35 μm net in the same sample.

One explanation may be the differential removal of the herbivores: we can suppose that the small herbivorous zooplankton is more removed than the phytoplankton, then the grazing pressure would be more reduced than the photosynthetic. But the difference does not appear with the phosphate uptake (fig. 8). The phosphate consuming organisms are perhaps smaller and a filtration on 35 μm would be ineffective in retaining the organisms which eat them. Unfortunately that experiment is single.

Four reasons for the discrepancy between P uptake and excretion measurements can be suggested: (1) the daily activity of the small microzooplankton ($< 50 \mu\text{m}$) could be an important part in the activity of the zooplankton in the water column; (2) the bacterial activity, through the organic excretion and spillage of phytoplankton, would also contribute to a significant part of the phosphorus regeneration; (3) during the night, large animals coming from the deep layers are a source of regenerated phosphorus, not measured in the experiments; (4) finally, additional nutrients are supplied by turbulent diffusion

TABLE III

Comparison between the Central North Pacific Ocean (PERRY and EPPLEY, 1981) and the nutrient depleted waters of the equatorial Atlantic Ocean (this paper).

Comparaison des résultats concernant le cycle du phosphore entre le Pacifique central nord (PERRY et EPPLEY, 1981) et les eaux de la couche homogène de l'Atlantique équatorial oriental (présente étude).

	Central North Pacific Ocean Perry and Eppley (1981)	Equatorial Atlantic Ocean Present study (mixed layer)
Phosphate uptake rate ($\text{ngat P l}^{-1}\text{d}^{-1}$)	0.7 - 1.2	10 - 30
Residence time of phosphate (days)	16 - 46	1 - 2 and < 1 with incubations of 5h.
Zooplankton excretion ($\text{ngat P l}^{-1}\text{d}^{-1}$)	0.9 - 2.8	5 - 10
Particles growth rates doubling d^{-1}	0.13 - 0.20	0.5 - 1.5

Nitrate + Nitrite Phosphate } $\mu\text{gat l}^{-1}$	0.03	0.02 - 0.06
Chla Phaeo } $\mu\text{g l}^{-1}$	0.04 0.02	0.10 0.05
POC PON POP } $\mu\text{gat l}^{-1}$	1.8 0.19 0.011	2.75 0.32 0.022

from below, but we are poorly informed about that processes.

In table III, we have reported the main results of PERRY and EPPLEY (1981) in the Central North Pacific Ocean (CNPO) and those of the present study for the mixed layer of the warm season. The phosphate uptake rates, the particles growth rates and the regeneration by zooplankton are much higher while the residence time of phosphate (for similar concentration) is much shorter in the equato-

rial Atlantic than in the CNPO. In the CNPO, the results are inconsistent with the notion of an active, rapidly growing and recycling microplankton in the incubation bottles whereas in the equatorial Atlantic the results suggest a highly dynamic system.

From our experimental work on the deck, there is no reason to believe that the results of the *in situ* incubations were overestimated specially the turnover time. But an undetected artifact is still possible, and although the cause is different, one finds again

with phosphorus a difficulty met with nitrogen : the accurate estimation of the nutrient fluxes in a nutrient-depleted mixed layer. However, the measure is theoretically possible with phosphorus if the salt error is carefully measured, while it is not with nitrogen, because the added ^{15}N is not at a concentration low enough to work like a tracer (SLAWYK, 1981).

Other measurements, including chlorophyll and oxygen increases in the water column and chlorophyll increases in the bottles (HERBLAND and LE BOUTEILLER, *in press* ; LE BOUTEILLER, pers. comm. ; OUDOT, *in press*) and urea turn over time (HERBLAND, 1976) agree with the idea of a high activity in the mixed layer.

The temperature in the mixed layer of the Atlantic was very high ($\approx 29^\circ\text{C}$). I did not find the temperature of the water column in the different papers dealing with the phytoplankton rate processes in the CNPO (EPPLEY *et al.*, 1973; SHARP *et al.*, 1980; PERRY and EPPLEY, 1981) but MC GOWAN and HAYWARD (1978) reported several temperature profiles near 28°N - 155°W . In the mixed layer the temperature was 24.5 - 27°C . Then, if it exists, the temperature effect is probably low: with a Q_{10} of 2.3 (EPPLEY, 1972), the metabolism would be increased by 1.35.

The word "oligotrophic" is probably not synonymous with ambient nutrient-depleted waters; for example the concentration of particulate organic matter in the CNPO was much lower (a factor two) than the concentration in the equatorial Atlantic, although the ambient nutrient content was the same (table III). Our waters were probably "less oligotrophic". In the CNPO, the nutricline is deep, and we found in the Atlantic a negative correlation between the depth of the nitracline and the chlorophyll values in the 0-20 m layer (fig. 9). Thus the depth of the nutricline influences not only the primary production processes at the level of the chlorophyll maximum (HERBLAND and VOITURIEZ, 1979; CULLEN and EPPLEY, 1981) but also the standing crop in the first meters of the water column, even if the ambient nutrient content is close to zero.

Between the results of PERRY and EPPLEY and ours, there is a factor two for the biomass, whereas there is one order of magnitude for the activities. Then a factor 5 remains unexplained. We touch the

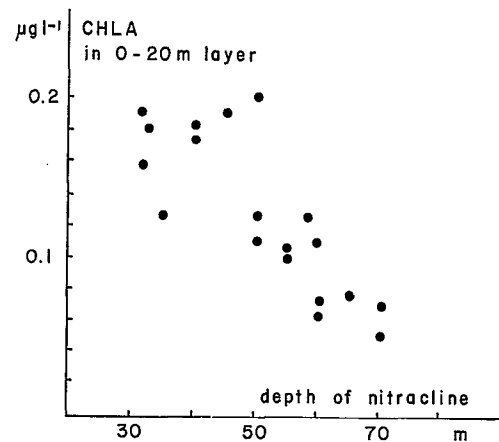


FIG. 9. — Relationship between the depth of the nitracline and the chlorophyll *a* concentration in the 0-20 m layer (nitrate-depleted mixed layer). Section at 4°W from 5°N to 10°S .

*Relation entre la profondeur de la nitracline et la concentration en chlorophylle *a* dans la couche 0-20 m (couche qui ne contient pas de nitrate). Section à 4°W de 5°N à 10°S .*

problem of the conflicting data in the oligotrophic oceans (see EPPLEY, 1980, and EPPLEY, 1981 and references herein). Is the mixed layer a kind of continuous culture in which the growth rates of the organisms are high and independent of the ambient concentration of limiting nutrient? Is phytoplankton and bacteria biomass being continually cropped by microzooplankton acting as in the overflow of a continuous culture? The data of the present paper are consistent with that new concept, at least for the eastern equatorial Atlantic Ocean.

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