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Hydrological structure analysis for estimating the primary production in the tropical Atlantic Ocean

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ABSTRACT

The vertical distribution of the parameters involved in primary production was studied on a large number of stations of the tropical Atlantic Ocean. A statistical analysis and an ecological interpretation are used to point out a typical tropical structure (TTS) of the tropical ecosystem in the euphotic layer.

The TTS has the following characteristics:

The depths of the nitracline, oxycline and chlorophyll maximum are statistically the same. A maximum of photosynthetic activity occurs at the level of the chlorophyll maximum where the nitracline is shallower than 60 m. The nitracline position is correlated with the thermal maximum gradient, according to its value and depth. The nitrite primary maximum is located ten to twelve meters below the top of the nitracline, in the decreasing concentrations of chlorophyll, where light conditions are limited.

An inverse relationship exists between the depth of the chlorophyll maximum and its value.

The integrated chlorophyll and primary production values are negatively correlated with the depth of the nitracline.

The analysis allows the rough estimation of the integrated biomass and production of the phytoplankton in the water column from any vertical profile of nitrate, nitrite, *in vivo* fluorescence, oxygen and temperature.

1. Introduction

In a recent paper, Herbland and Voituriez (1977) found that in tropical situation (absence of nitrate in the mixed layer) the top of the nitracline (= nitrate gradient) divides the euphotic zone into two layers: the upper layer which is nitrate depleted and the lower layer which is light limited. The top of the nitracline is a level, where the net primary production (Dugdale, 1967) would be maximum and the light conditions are such that the vertical nutrient flux balances the nutrient uptake. Then, the nitracline appears to be an important ecological level in the vertical distribution of the parameters involved in the primary production processes.

In addition Herbland and Voituriez (1977) showed that in the typical tropical situations of the Atlantic Ocean, the integrated primary production was highly cor-

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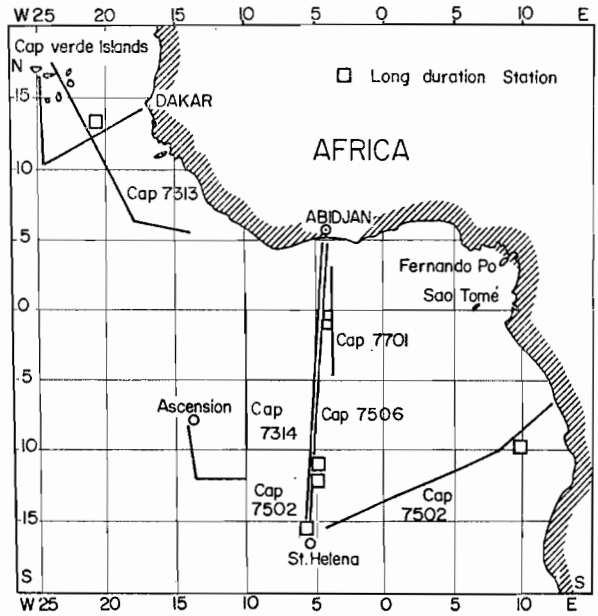

Figure 1. The different cruises of the R.V. *Capricorne* used in this study.

related with the depth of nitracline. When there are no direct *in situ* measurements of primary production the knowledge of the depth of the nitracline is sufficient for a rough estimate of the primary production in the water column. Unfortunately the historical nitrate data are scarce in the oceanic tropical Atlantic compared to oxygen or temperature data.

The aim of this paper is to describe the relationships that enable us in most cases to define the chlorophyll and primary production profiles and to estimate the integrated values of phytoplankton biomass and production from the vertical distribution of oxygen, nutrients or temperature. These relationships also facilitate the analysis of the ecological significance of the vertical distribution of these parameters.

2. Materials and methods

Data were collected on a series of five cruises of the R.V. *Capricorne* (Fig. 1): CAP 7313 in the Guinea Dome, during July and August 1973; CAP 7314 in the equatorial area during October 1973; CAP 7502 and CAP 7506 respectively in February and August 1975 from Abidjan to St. Helena Island, with three long duration stations in each cruise; CAP 7701 in January 1977 from 4N to 4S.

The sampling depths were chosen from temperature profiles; within the thermocline the sampling intervals were reduced to five or ten meters in order not to miss the key-points of the vertical distribution. Temperature, salinity and oxygen were

recorded *in situ* with a STDO probe system (Bisset Berman), coupled with a Hewlett Packard computer. Oxygen was also measured by the Winkler method at all sampling depths during CAP 7502, CAP 7506 and CAP 7701.

The sea-water was collected with 1.7 l PCV bottles on a rosette sampler at 12 levels. Nitrate and nitrite analysis were made on an auto-analyser (Technicon) adapted from Strickland and Parsons (1972). Chlorophyll *a* was measured in two ways: by *in vivo* fluorescence with spectrophotometric calibrations at different levels for each station, for CAP 7313 and CAP 7314, and by extracted fluorescence with calibrations with pure chlorophyll *a* (Sigma) for CAP 7502, CAP 7506 and CAP 7701; a Turner fluorimeter (model 111) was used for all measurements. In extracted fluorescence samples, chlorophyll *a* was corrected for interference by phaeophytin with acidification (Holm Hansen *et al.*, 1965). The primary production was measured by the *in situ* ^{14}C method with incubation of 8 hours, centered on midday at 8 or 10 levels. Special precautions have been observed during filtration (low vacuum < 100 mm Hg) and scintillation counting eludes the under estimation problem.

For the statistical analysis, the orthogonal regression lines have been calculated, i.e. the variables are supposed to be interdependent. From an ecological point of view, it is not always true, (for example, the pycnocline and nitracline depths are not interdependent whereas nitracline and oxycline are) but it is more convenient to run the regression in reverse.

3. Results and discussion

a. Nitracline, chlorophyll and primary production. Chlorophyll maxima at subsurface depths in the sea have long been known to occur, and processes regulating their distribution have been subject to discussions (Steele, 1964; Goering *et al.*, 1970); Venrick *et al.* (1973) have summarized a large amount of data accumulated over 8 years, all of which indicate that a deep chlorophyll maximum layer is a regular and continuous feature of much of the Pacific Ocean. Although the development of this layer appears not to be a localized feature, there have been few attempts to measure it with accuracy in oceanic areas of the tropical Atlantic Ocean.

Our analysis was carried out upon 126 chlorophyll profiles; it showed a regular deep maximum occurring at each station, near the bottom of the mixed layer and the concentration was sometimes as great as 10 times those of the surface layer; (the values range between 0.05 to 0.15 $\mu g/l$ in the mixed layer and can reach 1 $\mu g/l$ in the maximum). Hobson and Lorenzen (1972) wrote that this localization is probably caused by the distribution of nutrients near the pycnocline and Anderson (1969) and Goering *et al.* (1970) have associated the chlorophyll maximum with gradients of density.

Chlorophyll maximum and nitracline. Anderson (1969) showed that below the seasonal pycnocline (seasonal, because it was at high latitude) nitrate was only detect-

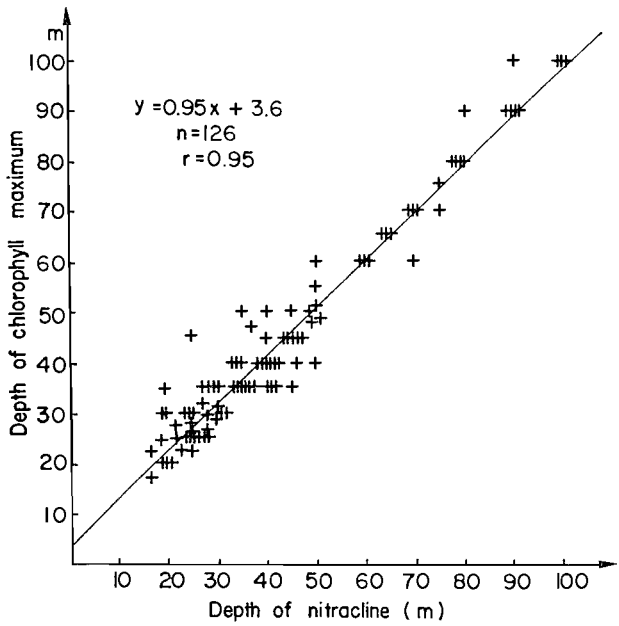

Figure 2. Linear regression between the depth of the nitracline (first level where the nitrate is not equal to zero) and the depth of chlorophyll *a* maximum.

able at a depth beneath the level of the chlorophyll maximum, and he supposed that nutrients which might normally be supplied to surface waters by diffusion and mixing processes from below, are mostly used by photosynthetically active phytoplankton communities. The association of the chlorophyll maximum with the beginning of nitrate (i.e. the top of the nitracline) has been fitted in our data. The depth of the first nitrate value different from zero (*D* N03, in meters) versus the depth of chlorophyll maximum (*D* Chla max, in meters) is plotted in Figure 2. There is a highly significant correlation coefficient ($r = 0.95$, $p = 0.99$), and the equation of the linear regression is

$$D \text{ Chla max} = 0.95\, D\text{N03} + 3.6 \qquad (1)$$

The slope is not significantly different from one and the intercept with Y axis is not significantly different from zero. Then, the depth of the maximum of chlorophyll and that of the top of the nitrate gradient are statistically the same.

Chlorophyll and primary production maxima. Few *in situ* primary production measurements have been made in the tropical Atlantic area; moreover when the data exist sampling was often not adequate to resolve the peak of maximal photosynthetic activity.

Our data take into account 28 stations of *in situ* primary production measure-

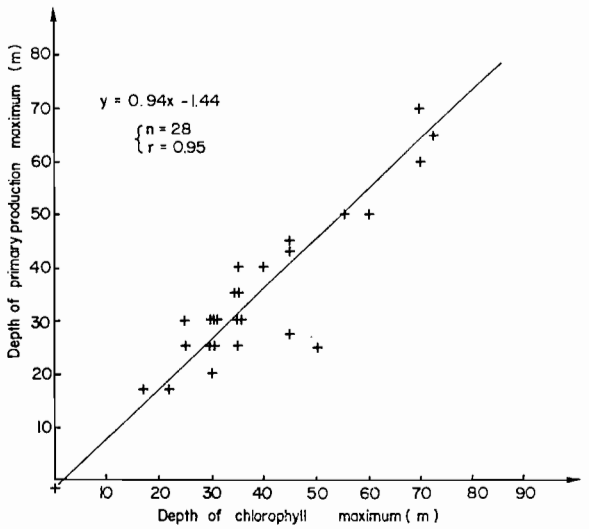

Figure 3. Linear regression between the depth of the chlorophyll *a* maximum and the depth of primary production ($^{14}CO_2$ uptake) maximum.

ments. The depth of maximal photosynthetic activity (*D pp* max, in meters) was well localized and plotted against the depth of chlorophyll maximum (Fig. 3). The coefficient of correlation is highly significant ($r = 0.95$, $p = 0.99$) and the equation of the linear regression is

$$D_{pp\ \max} = 0.94\ D_{\text{Chla max}} - 1.44 \qquad (2)$$

The slope is not significantly different from one and the intercept with Y axis is not significantly different from zero. Hence, the depth of the chlorophyll maximum and that of the maximum of photosynthetic assimilation of carbon are statistically the same.

The permanent association in the tropical Atlantic of the chlorophyll maximum with the nitracline and the primary production maximum gives evidence of the importance of the nitracline which is the rich nutrient layer the best lighted in the water column. The phytoplankton in this layer would not only account for a major portion of the phytoplankton standing crop but would also contribute significantly to the total primary production in the water column (Jamart *et al.*, 1976) since the overall production depends on the new production which occurs in the nitracline.

When the nitrate depleted layer is deep (> 60-70m), the primary production maximum becomes undetectable and there often are constant values from the surface to the nitracline without increase at this level. Sometimes a weak maximum can occur in the mixed layer (Goering *et al.*, 1970).

The light being a limiting factor in the deep maximum, it does not allow the de-

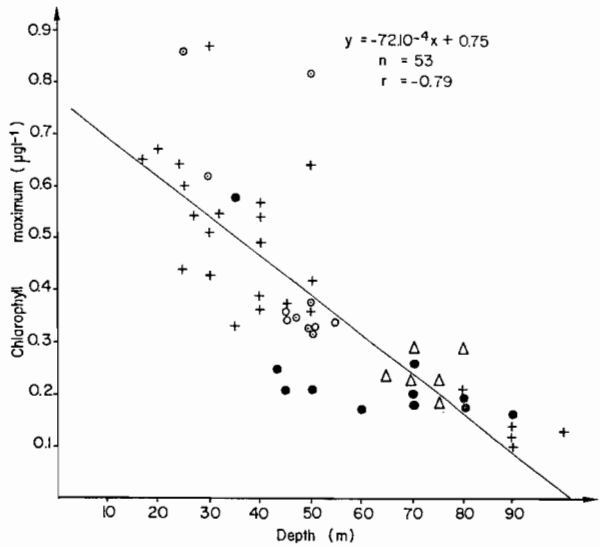

Figure 4. Linear regression between the depth of the chlorophyll *a* maximum and the value of this maximum.

velopment of a large chlorophyll maximum. But in contrast to the maximum of primary production, the chlorophyll maximum is always detectable and its value is at least twice the value in the mixed layer.

An inverse relationship has been found between the depth of the maximum and its value (Chla max in $\mu g/1$), (Fig. 4) according to the following equation in which $r = -0.79$ ($p = 0.99$):

$$\text{Chla}_{\max} = -72.10^{-4} \quad D\text{Chla max} + 0.75 \tag{3}$$

Nitracline, integrated chlorophyll and integrated primary production. Since the chlorophyll maximum, which coincides with the top of the nitracline, decreases when its depth increases, for a lack of light, and since it accounts for a major portion of standing crop in the water column, the integrated chlorophyll values are expected to decrease when the nitracline deepens: such a relationship has been found between D_{NO3} and the integrated chlorophyll values (Chla_i in mg/m^2) according to the following equation (Fig. 5) in which $r = -0.80$ ($p = 0.99$)

$$\text{Chla}_i = -0.17\, D_{NO3} + 22.5 \tag{4}$$

In the same way, a highly significant negative linear regression has been recently found between the depth of the nitrate depleted layer ($D_{NO3\text{-}0}$) and the integrated primary production of the water column (PP_I in $mgC/m^2/h$) (Herbland and Voituriez, 1977), according to the following equation

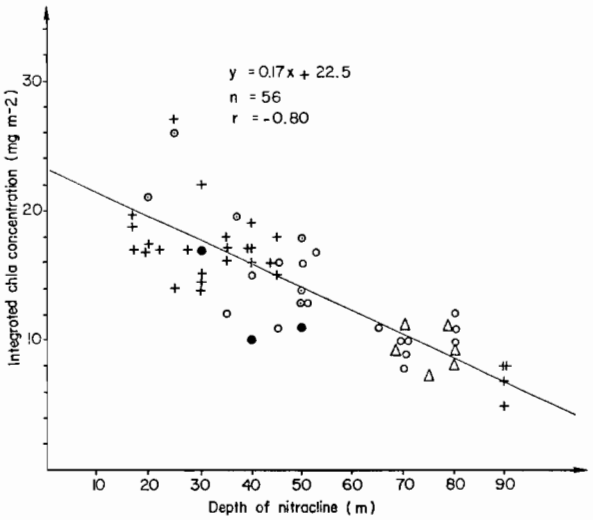

Figure 5. Linear regression between the depth of the nitracline and the integrated value of chlorophyll *a* in the water column.

$$PP_I = -0.91\ D_{NO3\text{-}0} + 85 \tag{5}$$

If the depth of the nitrate depleted layer is replaced by the depth of the first value of nitrate different from zero (D_{NO3}) which has a more crucial ecological position, and if we add two new values of *in situ* primary production obtained during the cruise CAP 7701, the equation is slightly modified (Fig. 6):

$$PP_I = -0.87\ D_{NO3} + 90.2\ (r = -0.84) \tag{6}$$

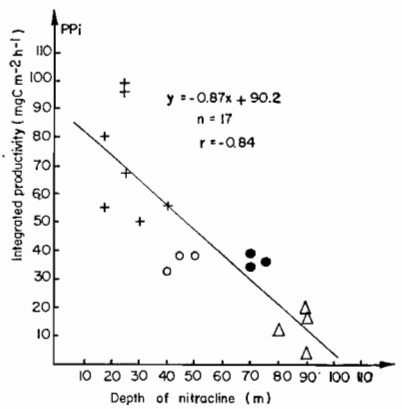

Figure 6. Linear regression between the depth of the nitracline and the depth of integrated value of primary production in the water column.

From (4) and (6) it becomes possible to express the index of productivity of the water column (PP_I/Chla$_t$ in mg carbon fixed/mg Chla/h) in terms of D_{NO_3}, according to the following equation:

$$\frac{PP_I}{\text{Chla}_t} = \frac{-0.87\, D_{NO_3} + 90.2}{-0.17\, D_{NO_3} + 22.5} \tag{7}$$

The index of productivity is indicative of the photosynthetic efficiency of the phytoplankton population of the water column. According to equation (7) it varies hyperbolically from 4 when the nitracline reaches the surface ($D_{NO_3} = 0$) to 0.6 when the nitracline reaches 100m ($D_{NO_3} = 100$).

This result fits with our data.

Photosynthesis is more efficient when the nitracline is shallow. In the upwelling of North West Africa, Barber and Huntsman (1975) have found a mean value of 3.1 for the water column (0-25m) with incubations under simulated *in situ* light conditions. Consequently, the typical tropical ecosystems, in spite of their low biomasses compared to those of upwelling regions, have a photosynthetic efficiency of the same order of magnitude, when the nitracline is close to the surface. Automatically, D_{NO_3} is never equal to zero and PP_I and Chla$_t$ are never equal to zero when the nitracline deepens. Equations (4), (5), (6) and (7) are only valid between the interval of the nitracline observed depths (15 and 100m in this part of the Atlantic Ocean).

b. Nitracline and pycnocline. Anderson (1969) and Goering *et al.* (1970) have associated the chlorophyll maximum with gradients of density. The thermal gradient (as an expression of density gradient) has two ecological effects on the phytoplankton community. In terms of production, the first is a positive effect in increasing the static stability which allows the development of a phytoplankton population not much eroded by turbulent mixing processes. The second effect is a negative one, in decreasing nutrients flux through the thermocline. The distribution of chlorophyll and primary production will be regulated by the interactions of this double effect. Then, it is interesting to find a relationship between the thermal gradient and nutrient (= nitrate) gradient.

In Figure 7, we have plotted the depth of the nitracline (D_{NO_3}) versus the depth of the maximal thermal gradient $D_{GT\max}$; the equation of the linear regression is:

$$D_{NO_3} = 0.77\, D_{GT\max} + 11.2 \tag{8}$$

The coefficient of correlation is highly significant ($r = 0.90$; $p = 0.99$) the slope is significantly different from one and the Y axis intercept is significantly different from zero. It means that when the depth of thermal gradient maximum is less than 49m ($D_{NO_3} = D_{GT\max}$ when $D_{GT\max} = 49$m) the level of the nitracline is statistically below the level of the thermal gradient maximum. When it is greater than 49m, nitrate crosses the barrier of stability.

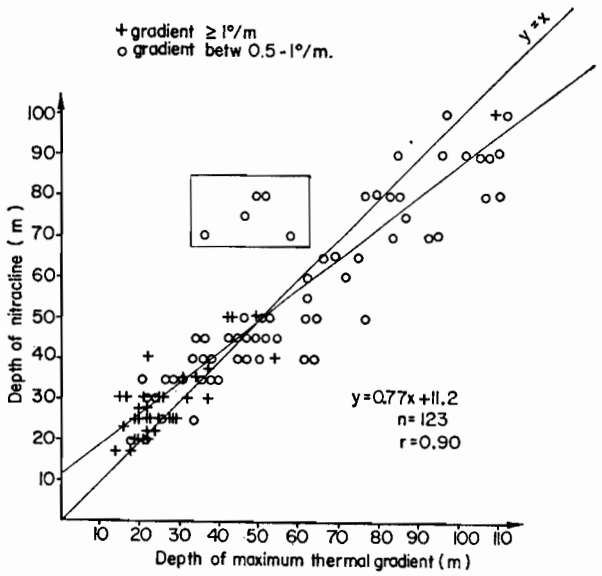

Figure 7. Linear regression between the depth of the thermal maximum gradient and the depth of the nitracline. Open circles in the square are those of the tropical convergence (see text).

It appears (Fig. 8) that the high thermal gradients ($\geqslant 1$ °C/m) are nearly all located above 50 m, whereas the mean and low gradients are rather below this limit. The ecological consequences are important: (1) When the thermocline is near the surface, the thermal gradient has a propensity to increase, making up a barrier of

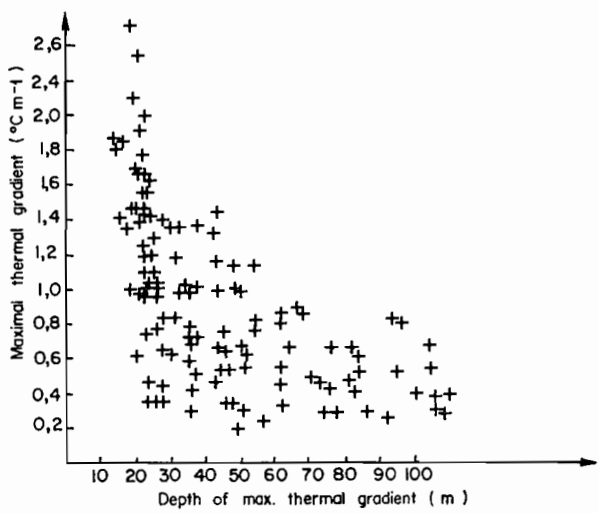

Figure 8. Relationship between the thermal maximum gradient and its depth.

stability which is not easily crossed by the nutrients. The phytoplankton maximum which stands at the top of the nitracline (equation 1) is below this barrier. This level is well lighted and phytoplankton may exhaust the nitrate, making up a nitrate depleted layer in the thermocline. (2) In contrast, when the pycnocline is deep the thermal gradient has a propensity to decrease; the NO_3 crosses this weak barrier, allowing the phytoplankton to concentrate in a shallower, better illuminated strata, producing a shallower nitracline. Since the chlorophyll maximum stands below the thermal maximum gradient of density precisely when the latter is shallow, high and well illuminated, it is probable that the sinking of active or senescent cells from shallower depth is not a prime cause of the chlorophyll maximum formation.

Meanwhile, exceptions to this pattern can occur, as is the case for five stations made at 10S in the tropical convergence during CAP 7502. These stations are marked off by a weak maximum thermal gradient and an anomalous distance between the nitracline and the maximal thermal gradient (Fig. 7). There are also irregular oxygen oversaturations (114% at 50m) but the relative positions of the nitracline, oxygen and chlorophyll maximum remain the same. This is due to a convergence occurring at around 10S between the westward equatorial current and the eastward south equatorial counter-current (Lemasson and Rébert, 1973) and creating a downwelling of the high salinity subtropical waters which bring oxygen rich and nitrate depleted waters below the discontinuity layer. A similar exception was observed in a convergence at the northern boundary of the equatorial upwelling (Voituriez and Herbland, in preparation). It can be concluded that the thermal gradient maximum is a good indicator of the primary production only when the vertical advection is negligible, excluding upwelling and active convergence.

c. Nitracline and oxygen. During summer, over large areas of the North Pacific Ocean, Anderson (1969) found a surface oxygen maximum beneath the seasonal pycnocline. Likewise, Gallardo *et al.* (1974) in Angola dome, Voituriez and Dandonneau (1974) in the Guinea Dome, and Herbland and Voituriez (1977) in the Gulf of Guinea (Angola Dome), have found numerous oxygen maxima between the bottom of the mixed layer and the nitracline. Anderson (1969) suggested that these oxygen maxima are formed largely by photosynthesis, at least in areas where a chlorophyll maximum was present.

The good relationship between the chlorophyll maximum, and the maximum of photosynthetic activity is in favor of this hypothesis. It is likely that the high supersaturations found in dome areas by Gallardo *et al.* (1974) and Voituriez and Dandonneau (1974) are due to *in situ* primary production, all the factors controlling the primary production being favorable (light and nutrients, in a well stratified layer).

Above the oxygen maximum, the water is saturated, or slightly oversaturated, and below, there is an oxycline more or less sharp according to the hydrological structure. Herbland and Voituriez (1977) pointed out a very high correlation ($r =$

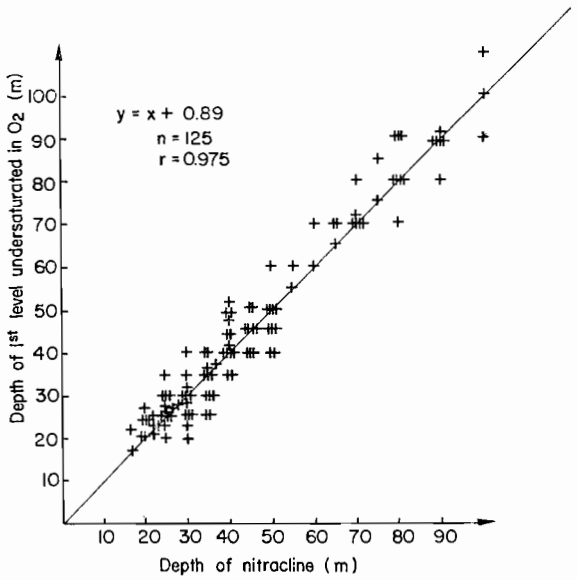

Figure 9. Linear regression between the depth of nitracline and the depth of the oxycline (first level undersaturated).

0.98) between the depth of the nitrate depleted layer and that of the oxygen saturated layer. This is the consequence of the stoichiometric relationship between the oxygen and nutrients, according to the empirical formula of the average composition of phytoplankton (Redfield *et al.*, 1963) in the processes of production and mineralization of organic matter.

In this paper, the first value of nitrate different from zero (D_{NO_3}) is plotted against the depth of the first level undersaturated in oxygen (D_{OX}) (Fig. 9).

The equation of the linear regression is:

$$D_{OX} = D_{NO_3} + 0.89 \tag{9}$$

with a very high significant coefficient of correlation $r = 0.975$, ($p = 0.99$).

Since the slope is equal to one, and the Y axis intercept is not significantly different from zero, there is a spatial coincidence between the depths of nitracline and oxycline in the tropical Atlantic ocean. This salient feature is very useful from a practical point of view: it becomes possible from an oxygen profile, given by an oxygen probe, to localize with accuracy the level of the nitracline, chlorophyll and primary production maxima, and consequently to estimate the integrated values of primary production and chlorophyll, from equations (4) and (6). Oxygen data of the cruises Equalant I and II have been used to map the integrated values of chlorophyll and primary production in the tropical Atlantic Ocean (Voituriez and Herbland, in preparation).

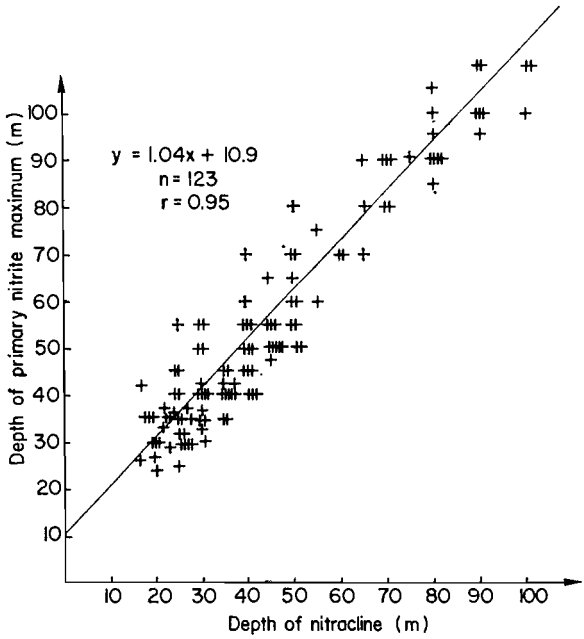

Figure 10. Linear regression between the depth of nitracline and the depth of primary nitrite maximum.

d. Nitracline and nitrite. The source of nitrite in the maximum has been ascribed to either bacterial or phytoplankton metabolism. Brandhorst (1958) suggested that nitrite originates from bacterial oxidation of ammonia, and recent observations that the rate of production of nitrite within the maximum increases in the dark upon the addition of ammonia seem to support Brandhorst's suggestion (Wada and Hattori, 1971; Hattori and Wada, 1971).

Vaccaro and Ryther (1960) first suggested that the appearance of nitrite near the compensation depth of open ocean was primarily caused by the reduction of nitrate by phytoplankton. Reasoning from laboratory studies they suggested that increases in nitrite concentration are expected when phytoplankton, starved of nitrogen, are exposed to both increased concentrations of nitrate and levels of irradiance. Recently, Kiefer *et al.* (1976) with a simple box model, assuming constant vertical mixing, indicated a sufficient uptake of upwardly diffusing nitrate to account for the appearance of nitrite.

In fields studies, Voituriez and Herbland (1977) have shown that in the tropical areas, nitrite never occurs when nitrate is absent, and the primary nitrite maximum is always associated with the nitracline. It agrees with the hypothesis of reduction of nitrate by phytoplankton.

In order to localize with more precision the depth of primary nitrite maximum

($D_{NO2\ max}$) it has been plotted in our data, against the depth of the top of nitracline (D_{NO3}), (Fig. 10).

The equation of the linear regression is:

$$D_{NO2\ max} = 1.04\ D_{NO3} + 10.9 \text{ with } r = 10.95 \quad (10)$$

The slope is not significantly different from one but the Y intercept is significantly different from zero. It means that whatever the depth of the nitracline, the primary nitrite maximum is about ten to twelve meters deeper than the top of the nitracline, i.e. right in the middle of the nitracline; it is below the chlorophyll maximum which stands at the level of the top of the nitracline (equation 2). Then the primary nitrite maximum stands where the chlorophyll concentrations decrease in a light limited regime and where nitrate is abundant. This relationship agrees with the three ecological significances of the primary nitrite maximum proposed by Voituriez and Herbland (1977):

(1) Nitrite which is an indicator of nitrate uptake can be used as an indicator of "new production."

(2) The primary nitrite maximum layer defines precisely the deep layer of the euphotic zone in which light becomes a limiting factor of the primary production.

(3) The depth of the isoline $NO_2 - N = 0.1$ μgat/1 beneath the primary nitrite maximum can be used to define the depth of the production layer.

4. Conclusions

(1) In a typical tropical structure, where the mixed layer is nitrate depleted, the top of the nitracline has important biological signification. At this level, the light and nutrients combination is optimal. Then, the chlorophyll and the primary production maxima stand at this level, which also corresponds to the maximum uptake of nitrate. The upper layer is oxygen saturated, and the lower layer is undersaturated.

(2) Stability, which limits the vertical mixing, is a factor which controls the depth of the nitracline. When vertical advection is negligible there is a relationship between the depth of the nitracline and the depth of the thermal maximum gradient. This relationship shows that the top of the nitracline stands below the thermal maximum gradient when it is close to the surface (i.e. when it is high). When the thermal maximum gradient is deep, it has a propensity to decrease, and the top of the nitracline stands above the maximum thermal gradient.

(3) The chlorophyll maximum, and the primary production maximum, within certain limits follow the nitracline. They are below or above the maximum gradient of temperature according to the depth and the value of this gradient. The formation of the chlorophyll maximum by sinking processes in the typical tropical situation is not possible given this mode of formation. The value of the chlorophyll maximum decreases when its depth increases.

Table 1

Equation	r	n
$D_{NO3} = 0.77\ D_{\sigma T max} + 11.2$	0.90	123
$D_{Chla\ max} = 0.95\ D_{NO3} + 3.6$	0.95	126
Chla max $= -0.0072\ D_{Chla\ max} + 0.75$	−0.79	53
$D_{PPmax} = 0.94\ D_{Chla\ max} - 1.44$	0.95	28
$D_{ox} = D_{NO3} + 0.9$	0.975	125
D_{NO2} max $= 1.04\ D_{NO3} + 10.9$	0.95	123
$Chla_t = -0.17\ D_{NO3} + 22.5$	−0.80	56
$PP_t = -0.87\ D_{NO3} + 90.2$	−0.84	17

Legend: D_{NO3}, $D_{Chla\ max}$, D_{PPmax}, D_{ox} and $D_{NO2\ max}$ are expressed in meters (see text). Chla max is expressed in $\mu g/l$, PP_t in $mgC/m^2/h$ and $Chla_t$ in mg/m^2. r is the coefficient of correlation and n the number of values.

(4) The nitrite primary maximum is located about ten to twelve meters below the top of the nitracline in the decreasing concentrations of chlorophyll where the light is limiting primary production. It defines the bottom of the euphotic layer.

(5) From the set of relationships gathered in Table 1, it is possible to estimate the integrated values of chlorophyll and primary production by means of the depths of the nitracline, oxycline or chlorophyll maximum which are statistically the same. But the use of the depth of the thermal gradient maximum is more limited, since the relationship is only valid when the vertical motions are negligible.

(6) How universal for tropical waters are these relationships? Few data are available, especially for *in situ* primary production. In the Central South Pacific the respective positions of the nitracline, oxycline, chlorophyll and nitrite maxima seem to be conserved; but the sampling intervals were too large, and the "clines" and maxima were frequently missed. Work in other areas than the tropical Atlantic ocean should be strongly encouraged in order to determine the typical structure for the whole tropical ocean.

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