



Net community production in "High Nutrient-Low Chlorophyll" waters of the tropical and Antarctic Oceans: grazing vs iron hypothesis

Nutrients
New production
Grazing
Tropical Ocean
Antarctic

Nutriments
Production nouvelle
Broutage
Océan tropical
Antarctique

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ABSTRACT

An analysis of tropical upwelling systems shows a great range in the rate of increase of the standing stock expressed in terms of the water column chlorophyll content.

Grazing appears to be the main factor responsible for lowering the rate of increase, especially in moderate and strong High Nutrient-Low Chlorophyll (HNLC) waters. A simple model comparing Net Community Production (NCP) rates with observed chlorophyll increase rates, leads us to conclude that phytoplankton population must present high specific growth rates on a daily rhythm in order to overcome grazing. Maximum specific growth rates (V_{max}) calculated for daily total production (TP) are, in the two main upwelling areas, 1.57 d^{-1} off NW Africa and 1.04 d^{-1} off Peru. For extreme HNLC conditions in the Costa Rica Dome, V_{max} remains high, 0.98 d^{-1} .

The Atlantic equatorial upwelling in the Gulf of Guinea is characterized by moderate HNLC conditions. From an analysis of a nutrient-temperature diagram and heat fluxes, we deduce a nitrate-based new production (NP) rate of $0.368 \text{ g C m}^{-2} \text{ d}^{-1}$, corresponding to a f -ratio of 0.3. The Peruvian coastal upwelling, during the strongest upwelling period in austral winter, shows HNLC conditions extending far offshore and reaching the Galapagos Islands. NCP could not be determined in these waters.

Antarctic nutrient consumption diagrams are also presented. An overall consumption evaluation along a 1,550 km North-South section leads to atomic assimilation ratios of $\Delta\text{Si}/\Delta\text{N}/\Delta\text{P} = 55.9/12.3/1$. From the end of winter to end of summer, the average nitrate consumption is 0.38 mol m^{-2} . For this five month period, the calculated NP is $0.2 \text{ g C m}^{-2} \text{ d}^{-1}$. From the silicon-nitrogen ratios during nutrient consumption and those in the particulate material, we deduce a f -ratio slightly lower than 0.5. This f value confirms earlier data derived from ^{15}N uptake studies. The model application leads to a V_{max} (TP) value of 0.54 d^{-1} , which does not seem excessively low in the low temperature regime of the Southern Ocean. We discuss an Antarctic scenario starting with "grazing" limitation and finishing with iron limitation.

Despite evidence in favour of the grazing hypothesis which allows us to classify regions geographically into "high and low" speed areas of phytoplankton deve-

lopment, a global chart of dust inputs into the ocean strongly supports the iron limitation hypothesis. This observation constitutes a challenge to the "grazing only" hypothesis and militates in favour of more detailed future studies.

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RÉSUMÉ

Production communautaire nette des eaux «Riches en Nutriments-Pauvres en Chlorophylle» dans les océans tropical et antarctique : le broutage face à la limitation par le fer

L'analyse des systèmes tropicaux de remontées d'eaux met en évidence l'existence de toute une gamme de taux d'accroissement de la biomasse autotrophe exprimée par le contenu en chlorophylle dans la colonne d'eau.

Le broutage s'avère être le principal facteur responsable du ralentissement du taux d'accroissement, ceci particulièrement dans les conditions «Riches en Nutriments-Pauvres en Chlorophylle» (RNPC).

La construction d'un modèle simple prenant en compte les effets réciproques phyto-zooplancton au cours du cycle nyctéméral, permet de comparer les taux de Production Communautaire Nette (PCN) à ceux des accroissements observés de chlorophylle, et conduit à la conclusion que le phytoplancton, face à la pression de broutage, possède nécessairement des vitesses de croissance spécifique élevées.

Les taux maximaux de croissance spécifique (V_{max}) calculés pour la production totale (PT) journalière dans les deux principales zones de remontée sont de $1,57 \text{ j}^{-1}$ devant les côtes NW-africaines et de $1,04 \text{ j}^{-1}$ devant celles du Pérou. Dans la situation extrême de grande richesse nutritive associée à des biomasses faibles caractérisant le dôme de Costa-Rica, V_{max} garde une valeur élevée de $0,98 \text{ j}^{-1}$.

L'upwelling équatorial atlantique dans le golfe de Guinée est marqué par des conditions RNPC. A partir de diagrammes éléments nutritifs-température, et des flux d'apport de chaleur, on déduit une consommation de nitrate qui, en termes de carbone, représente une production nouvelle (PN) de $0,368 \text{ gC m}^{-2} \text{ j}^{-1}$ et correspond à un facteur f de 0,3. L'upwelling côtier péruvien, observé pendant la période principale de remontée en hiver austral, a des propriétés RNPC qui s'étendent très au large des côtes et atteignent les abords des îles Galapagos. La PCN n'a pu être déterminée dans ces eaux.

Des diagrammes de consommation nutritive sont également présentés. Une évaluation générale de l'utilisation nutritive tout au long des 1550 km d'une section nord-sud, conduit à des valeurs de rapports atomiques de $\Delta\text{Si}/\Delta\text{N}/\Delta\text{P} = 55,9/12,3/1$. Entre la fin de l'hiver et celle de l'été suivant, la consommation moyenne de nitrate est de $0,38 \text{ mol m}^{-2}$. Pour une période de cinq mois, la PN est de $0,2 \text{ gC m}^{-2} \text{ j}^{-1}$. A partir des rapports de consommation silicium-azote et de ceux du matériel particulaire, on peut déduire un facteur f légèrement inférieur à 0,5. Cette valeur confirme d'anciennes estimations de f obtenues à partir de mesures d'assimilation d'azote-15.

L'application de notre modèle aux conditions antarctiques conduit à un V_{max} (PT) de $0,54 \text{ j}^{-1}$. Cette valeur ne semble pas exagérément faible compte tenu des basses températures du régime antarctique. La discussion évoque un «scénario antarctique» dans lequel la limitation débute par les effets de broutage, mais finit par la limitation par le fer.

En dépit de l'évidence de l'hypothèse du broutage, qui nous permet de classer les régions selon une gamme de régimes de développements phytoplanctoniques lents ou rapides, une carte de l'océan mondial présentant les apports d'aérosols plaide également en faveur de l'hypothèse du fer. Cette observation constitue un avertissement sérieux face à la théorie du «broutage seul» et implique la nécessité de futurs travaux plus détaillés.

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INTRODUCTION

Historical considerations

The iron limitation hypothesis presented recently by Martin (1990) and Martin *et al.* (1990 *a*; 1990 *b*) has had a considerable impact on the oceanographic community, insofar as the idea leads to the exciting possibility of conducting experiments and human interventions at large scales in the open ocean. This will be "un tournant dans l'histoire" (as we say in French) for oceanography. Despite numerous recent critical comments (Banse, 1990; 1991 *a*; 1991 *b*; Broecker, 1990; Dugdale and Wilkerson, 1990), the iron limitation hypothesis has enough merit to induce a critical reevaluation of the so-called "grazing hypothesis".

We must ask ourselves to what extent grazing by the heterotrophic community keeps the autotrophic standing stock low, and whether this can be the only factor explaining long residence times of unused nutrients in the euphotic zone. There seems no *a priori* reason to consider that iron limitation, in addition to grazing, might contribute to the control of slow nutrient evolution. But one may expect that this control occurs at the end of the residence time period of the water body, *i. e.* at a time before other events are able to change the properties of the water. According to Martin, iron in small quantities is available at an early stage in the surface waters, mainly in the Antarctic after winter mixing. We all believe that the mechanisms of planktonic dynamics in polar waters will probably be different from those in the warmer waters of the tropical ocean. One major difference between the two systems is that tropical nutrients, unlike antarctic nutrients, are not lost to the deep sea after their stay in the euphotic zone. In the tropics nutrients are only removed by photosynthesis, however it has not been very well established where and under which conditions this photosynthesis occurs.

Historically, some of the earliest observations and considerations dealing with the paradox of High Nutrient-Low Chlorophyll (HNLC) were made when Strickland *et al.* (1969) described two types of nutrient regimes in the Peruvian coastal zone and explained nutrient-rich, transparent waters by grazing. Barber and Ryther's (1969) investigations led to the "biological conditioning" hypothesis for upwelling zones (Barber *et al.*, 1971). The "Barber effect" was, for all of us in the French upwelling research team, the possible explanation for the slow increase of productivity in nutrient-rich upwelling systems. During the Cineca-program off the NW African coast, we described once relatively High Nutrient-Low Chlorophyll waters associated with relatively high surface temperatures ($t > 18^{\circ}\text{C}$) in a limited area off Nouakchott (Groupe Médiproduct, 1974; Minas *et al.*, 1974). But, as we shall see later, HNLC conditions seem to be rare off NW Africa. It is important to point out here, that the slow increase in productivity observed and discussed at that time was for processes observed in NW African coastal waters, while the first Barber and Ryther (1969) observations were at the equator. Therefore, the retarded planktonic bloom in the NW African coastal upwelling was probably not due to a lack of iron. Martin

(1990) writes: "Meeting biological Fe requirements is relatively easy in neritic waters, where resuspended bottom sediments and associated Fe-rich oxides, colloids, *etc.*, occur together with elevated concentrations of Fe. Hence excess NO_3 is never observed in coastal upwelling environments such as those off the west coasts of Africa and North and South America".

In Antarctic waters, the "biological conditioning" has been taken into account in our discussions of possible controlling factors, such as light, temperature, turbulence (Jacques and Minas, 1981) and grazing (Le Corre and Minas, 1983).

The "grazing" hypothesis, formulated by Walsh (1976), has become increasingly accepted as the principal explanation. In the tropical Pacific, the most important contribution describing the problem of the HNLC anomaly was made by Thomas (1979), after his earlier observations of nutrient inversions (Thomas, 1972), due to massive advection of nutrient-rich waters from the Peruvian coast. We shall show here how our French colleagues (*e. g.*, Voituriez *et al.*, 1982; Herbland *et al.*, 1983) also considered grazing as the main explanation of the relatively low productivity during the principal upwelling season along and in the vicinity of the equator in the Gulf of Guinea.

Minas *et al.* (1986), in a comparative study of tropical upwelling systems, came to the conclusion that grazing could explain the existence of different rates in the development of the autotrophic standing stock. HNLC situations, mainly characteristic of the equatorial Pacific, appear ultimately to be nothing other than repressed standing stock development under conditions of high heterotrophic activity.

Warm HNLC waters at the sea surface in the tropical ocean are an obvious indicator of longer residence time in the euphotic zone, because at their origin the waters ascending into the euphotic zone were cold. We shall endeavour to show here in greater detail how Net Community Production (NCP) studies provide arguments supporting the grazing hypothesis. We should remember that NCP determinations are mostly based on nutrient consumption evaluations deduced from field observations. Oxygen production or CO_2 consumption can also be used (Codispoti *et al.*, 1986). It has been recognized that NCP is almost equivalent to the New Production (NP) (Minas *et al.*, 1986; Eppley, 1989; Platt *et al.*, 1989). Our statement is that despite a slow, very slow, or even zero, specific increase in the rate of the autotrophic standing stock in the water, phytoplankton growth at itself actually takes place at a fast rate. The main objective is to demonstrate that the phytoplankton specific growth is normal or even high. The determination of nutrient consumption permits calculation of the total amount of chlorophyll produced by new production. The difference to the observed chlorophyll content in the water gives an indication of the part removed by grazing. It has been shown that in coastal upwelling zones, more than 60 % of the chlorophyll produced disappeared from the water (Minas *et al.*, 1982 *b*; 1986). The fate of the removed planktonic biomass is to fuel the integration of organic matter in the higher trophic levels, the dissolved organic pool, and the exportation by fecal pellet sedimentation and other large sinking particles.

THE GRAZING HYPOTHESIS IN THE TROPICAL OCEAN

Growth kinetics in tropical upwelling systems: can grazing explain different rates of increasing autotrophic standing stock ?

A detailed diagram analysis (Minas *et al.*, 1982 *b*; 1986) has permitted us to determine photosynthetic nutrient consumption (and oxygen production) in upwelled water bodies during their advection from an upwelling source area. In addition, an analysis of T-S diagrams can lead to residence time evaluations according to a heat budget model established by Bowden (1977). A combination of the two methods (Minas *et al.*, 1986) allows NCP determinations for steady state upwelling systems with these results. It is possible to study the growth kinetics of the autotrophic standing stock.

Two types of growth curves for coastal upwelling off both NW Africa and Peru are shown in Figure 1. The thin curves show the observed increase in the phytoplankton standing stock ($\Sigma\text{Chl}_{\text{obs}}$), expressed as integrated chlorophyll per square meter (ΣChl mg m⁻²). The thick curves show the increase in $\Sigma\text{Chl}_{\text{NCP}}$, *i. e.* the amount of chlorophyll deduced from the nutrient consumption (or biological O₂ production). This quantity has been calculated using the Redfield conversion ratio and a carbon/chlorophyll ratio of

55/1 (given by Ketchum and Corwin, 1965, and often used by other authors; *see* Minas *et al.*, 1986; 1990; Marra *et al.*, 1990). Table 1 contains all numerical information such as equations, growth constants, specific growth rates, *etc.* The difference between the two types of curves shows how much of the chlorophyll originally produced has been removed by some process.

First of all, it can be seen that the Peru curves display a distinctly lower growth kinetics than those for NW Africa. As given in Table 1, the specific rates of increase (V_i) of the chlorophyll stock ($\Sigma\text{Chl}_{\text{obs}}$) are 0.221 d⁻¹ for NW-Africa, *i. e.* six times greater, and 0.036 d⁻¹ for Peru. For purposes of comparison, a reference curve (dashed) is shown in Figure 1 for a $V_i = 1$ d⁻¹, *i. e.* one doubling per day (equation $y = y_0 \cdot 10^{0.301T}$, with $y_0 = 16.11$, which is the initial ΣChl_0 value for Peru). It is important to remark that the specific rate of increase is called V_i , *i. e.* V-integrated, because it concerns the increase of standing stock in the whole water column, which at least contains the euphotic zone. This problem will be discussed later in more detail. The comparison of the three curves (Peru, NW Africa, Reference) suggests that stronger grazing off Peru is probably the reason for the slower observed increase of the amount of chlorophyll. As we explained more fully in Minas *et al.* (1986), the bloom off Africa can initially start over the continental shelf, and by the time larger animals (Euphausiids) at the shelf break begin their grazing pressure, it is too late, because the phytoplankton biomass is already overwhelming and its rapid

Table 1

Summary of data shown in Figure 1. Numerical characteristics concerning the observed increase rate of chlorophyll standing stock and that deduced from NCP rates. Specific increase rates are given on an integrated basis (V_i), and at the depth of the photosynthetic maximum, like classical assimilation numbers of the production curve. Principal attention should be paid to the characteristics of the Chl_{obs} curve showing the "apparent" increase controlled by grazing. Corresponding NCP curve constants have also been calculated, but they have not the same significance because, as we shall see later in the theoretical paragraph, the NCP curve is a cumulative curve demonstrating nutrient consumption.

Equation (see Fig. 1)	PERU		NW-AFRICA		REFERENCE
	obs	NCP	obs	NCP	
	$\Sigma\text{Chl}_{\text{obs}} = 16.11 \cdot 10^{0.0154T}$	$\Sigma\text{Chl}_{\text{NCP}} = 29.79 \cdot 10^{0.0198T}$ derived from $\Sigma\Delta\text{O}_{2\text{bio}} = 3.98 \cdot 10^{0.0198T}$	$\Sigma\text{Chl}_{\text{obs}} = 26.30 \cdot 10^{0.0867T}$	$\Sigma\text{Chl}_{\text{NCP}} = 47.23 \cdot 10^{0.1012T}$ derived from $\Sigma\Delta\text{O}_{2\text{bio}} = 6.31 \cdot 10^{0.1012T}$	$\Sigma\text{Chl} = 16.11 \cdot 10^{0.301T}$ or $\Sigma\text{Chl} = 16.11 e^{0.693T}$
V_i (d ⁻¹) Specific increase rate (integrated)	0.036	0.047	0.221	0.262	1.0
AN_i (mgC mgChl ⁻¹ d ⁻¹) C/Chl = 55/1 Assimilation number (integrated)	0.20	0.26	1.22	1.44	5.5
$\text{AN}_{\text{max}} = 1.86 \text{AN}_i$	0.37	0.48	2.27	2.68	10.23
AN_{max} (TP) for $f^* = 0.5$ for $f^* = 0.2$ for $f^* = 0.64$	0.74 1.85	0.96 2.40	3.55	4.19	
V_{max} (d ⁻¹) (TP) for $f = 0.5$ for $f = 0.2$ for $f = 0.64$	0.135 0.336	0.175 0.436	0.646	0.762	

* from Minas *et al.* (1986).

increase can no longer be brought under control. Off Peru, zooplankton are more abundant in the euphotic zone, because of the anoxic water just below. This results in more intense grazing pressure at the beginning of the bloom, keeping the phytoplankton growth under control from the outset. Another possibility is that during the weak upwelling season off Peru, relaxation periods of upwelling create zooplankton excess, which is conserved near the coast by the flow pattern of water masses (subsurface onshore flow).

In Figure 1, we also compare the shapes of the $\Sigma\text{Chl}_{\text{NCP}}$ and $\Sigma\text{Chl}_{\text{obs}}$ curves. The (NCP) curve increases slightly faster than the (obs) curve for both Peru and NW Africa. It is also interesting to compare the values of the productivity index ($\text{mgC mg Chl}^{-1} \text{h}^{-1}$), here called the assimilation number (AN). The values of AN given in the literature are the best inter-comparison term, representing a specific uptake rate. Since AN_i constitutes the integrated value, we can estimate AN_{max} (light saturation value) by multiplying AN_i by the factor 1.86. This value was statistically established by Minas *et al.* (1982 *a*). Almost the same value (1.89) resulted from a similar evaluation by Cullen *et al.* (1992). Considering the Peru data, the values of AN for both curves (NCP and obs) are low. This is not surprising, as $\text{AN}_{\text{maxNCP}}$ can be considered as an approximation of the new production value. But the values still remain relatively low when the f -ratios are applied (see AN_{max} (TP) in Tab. 1). This demonstrates that the values of V_i , as well as AN, are only apparent characteristics of the grazing controlled slow speed curve. In fact, the real physiological specific growth rate must be higher. In order to show this, we address the problem in the following paragraph.

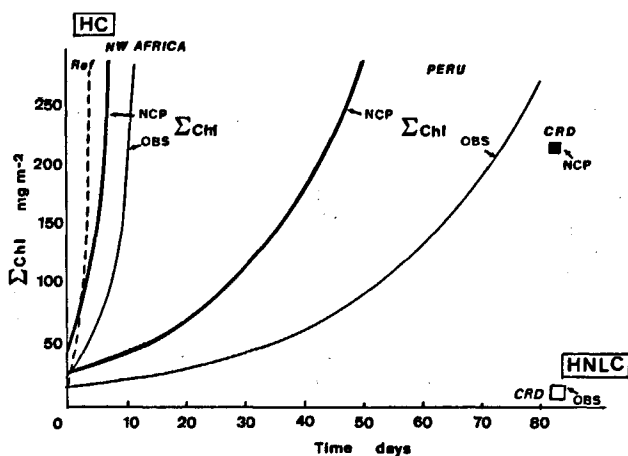


Figure 1

Kinetic characteristics of the increasing standing stock of chlorophyll from two coastal upwellings off NW-Africa and Peru (redrafted from Minas *et al.*, 1986). The exponential equations and specific increase rates are given in Table 1. Curve $\Sigma\text{Chl}_{\text{obs}}$ represents the increase in water column chlorophyll vs time. Curve $\Sigma\text{Chl}_{\text{NCP}}$ represents the total amount of chlorophyll produced as calculated from the nutrient consumption. In our interpretation, the slower evolution of Peru is due to grazing. NW-Africa, less controlled by grazing, grows faster. For comparison, a reference curve displaying a higher specific growth rate (1.0 d^{-1}) is shown (see data on Tab. 1). The points representing the Costa Rica dome (CRD) upwelling are typical for HNLC conditions, and contrast with the fast-growing high chlorophyll (HC) system off Peru. The CRD points correspond to average values resulting from a model established by Broenkow (1965) and discussed by Minas *et al.* (1974; 1986).

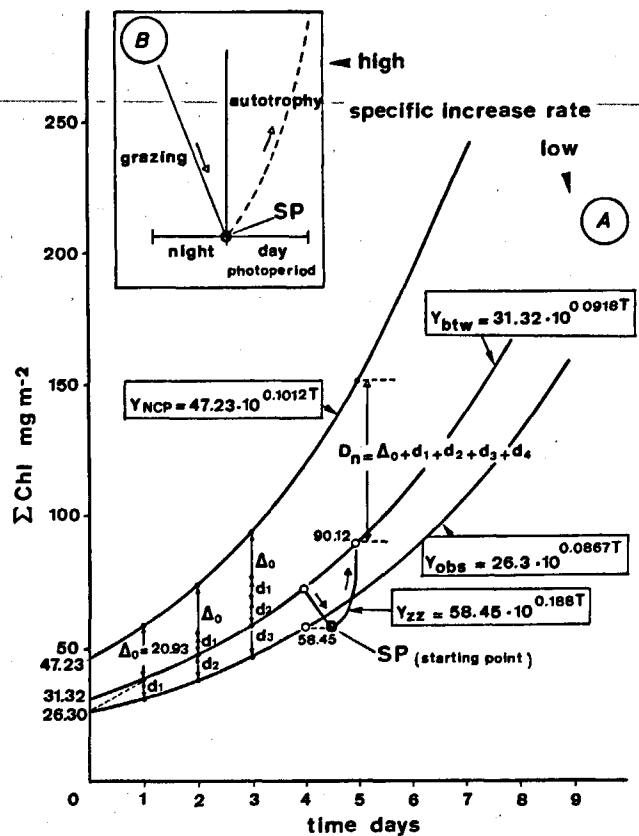


Figure 2

Application of the zz model to the Chl_{NCP} and the Chl_{obs} curves in the case of the NW African upwelling. The principle of the model is to construct a daily exponential curve ($Y_{zz} = Y_{z0} \cdot 10^{\mu_{zz} T}$) which, during the photoperiod (Fig. B), reaches the Y_{btw} curve. The latter is obtained by subtracting from the NCP curve the cumulative day-to-day difference $\Delta n = \Delta_0 + d_1 + d_2 + \dots + d_n$, as shown by Figure A. Daily curve is presented at the 5th day. The objective is to evaluate the μ_{zz} value for each day and to derive from this the corresponding $V_{zz\text{max}}$ value. Equations and data are given in Table 2. The figure for the Peruvian system is not shown but, for purposes of comparison and better understanding, the reader may construct the Peruvian curve and verify the data of Table 2.

The day-night "zigzag model" (zz model)

As a possible explanation for the retarded growth curves of the standing stock shown in Figure 1, we propose that the day-night rhythm of the activity of the autotrophic vs heterotrophic community leads to a zigzag movement of the autotrophic standing stock. Circadian periodicities in natural populations of marine phytoplankton are a well known fact (see review done by Sournia, 1974). We are inspired by several studies in recent literature dealing with day-night effects on the water properties of planktonic activity. Oudot (1989) was able to detect during time series diel changes in the concentration of O_2 and CO_2 . A zigzag variation displays biological oxygen production and CO_2 consumption during the day, and the contrary during the night, due to respiration. Le Bouteiller and Herbland (1982) observed during similar studies such day-night variations in chlorophyll concentration. Grazing by diel migrant zooplankton and necton and associated nitrogen fluxes below the euphotic zone received much attention in two papers by Longhurst and Harrison (1988) and Longhurst *et al.* (1989). Cullen *et al.* (1992) summarize:

Table 2

The day-night "zigzag model": equations and results of calculations leading to assimilation numbers and finally to the highest specific increase rates, in the areas off Peru and NW-Africa.

Equations (see also Tab. 1)	PERU			NW-AFRICA		
	$Y_{btw} = 16.876 \cdot 10^{0.01575T}$			$Y_{btw} = 31.32 \cdot 10^{0.0918T}$		
The daily NCP-curve equation is $Y_{zz} = Y_{zz0} \cdot 10^{\mu_{zz}T}$						
	n = T = 1	n = T = 30	n = T = 60	n = T = 1	n = T = 5	n = T = 10
$\mu_{zz} = \log \frac{Y_{btwn} - D_n}{Y_{obsn} - 1}$	0.0359	0.0460	0.0566	0.168	0.188	0.214
V_{zzi} (d ⁻¹) specific increase rate (integrated)	0.086	<u>0.112</u>	0.139	0.471	<u>0.542</u>	0.635
AN_{zzi} (mgC mgChl ⁻¹ h ⁻¹) assimilation number (NP) (integrated)	0.473	0.616	0.765	2.59	2.98	3.49
$AN_{zzmax} = 1.86 AN_{zzi}$ (NP)	0.880	1.146	1.423	4.817	5.543	6.491
AN_{zzmax} (TP) for f* = 0.5	1.760	2.292	2.846			
for f* = 0.2	4.400	5.730	7.115			
for f* = 0.64				7.527	8.610	10.142
V_{zzmax} (d ⁻¹) (TP) specific increase rate for f = 0.5	0.32	0.42	0.52			
for f = 0.2	0.80	<u>1.04</u>	1.29			
for f = 0.64				1.37	<u>1.57</u>	1.844

* from Minas et al. (1986); see also Eppley (1989).

"Diel variability of beam attenuation also indicated high specific growth rates of phytoplankton and a strong coupling of production with grazing".

In our following demonstration, the amplitude of the day-night oscillation is controlled by the intensities of algal growth vs herbivorous grazing (Fig. 2B). By means of the following simple model, which we call the day-night "zigzag" model, we propose to extract from the position in the diagram of the Chl_{NCP} curve relative to the position of the Chl_{obs} curve, a specific increase rate of the standing stock during the daily photoperiod. The extracted value will become nearer to, or even represent the true specific algal growth rate. As demonstrated by Figures 2A and 2B, the principle of the model is to determine for each day, the exponential growth function necessary to satisfy a geometrical position dictated by the Chl_{NCP} curve. The growth coefficient μ of this daily equation will be called μ_{zz} , and the deriving assimilation numbers and specific increase rates will be designed also with the zz index. Figures 2A and 2B show the treatment of the Chl_{NCP} and Chl_{obs} curves in the case of the NW African upwelling system. The same treatment has been applied to the Peru curves. The results for the two upwellings regimes are given in Table 2. The treatment procedure is the following: the NCP curve at the

origin has already the value $(Chl_{NCP})_0 = 47.23$, which means that at the beginning there is a signature of nutrient consumption in the water. The first day curve has to reach a point below the NCP curve at a vertical distance of $\Delta_0 = (Chl_{NCP})_0 - (Chl_{obs})_0 = 20.93$. For the following equation and l_{zz} calculation (2nd day), the first night grazing difference d_1 is cumulated with the initial Δ_0 . The third day, d_2 is added to $\Delta_0 + d_1$, etc. The caption of Figure 2 describes in greater detail the operations for day T = 5. All points reached by the daily Y_{zz} curves can be connected by a line which will be called the Y_{btw} curve because of its position between (btw) the (NCP) and the (obs) curves (equations for all curves are given in Table 2). The two Y_{btw} relations concerning Peru and NW Africa are obtained by approximation because, as analysed in the following theoretical paragraph, the (btw) line cannot correspond to a purely exponential curve. This approximation has almost no influence on the second decimal of the V_{zz} values. Results of the zz model are contained in Table 2. As for Figure 1 and Table 1, we also calculated the assimilation indexes which we then used to calculate values of V by taking into account the f -ratios. As announced before, we conclude that the model allows us to extract and to define from respective positions of the (NCP) and (obs) curves a second specific increase rate V_{zz} , in addition to the apparent

increase rate given in Figure 1 and Table 1. Let us call these apparent rates (A)V and compare them to the V_{zz} . At the integrated level, and concerning "new production", we have on average the following values [V_{zzi} for T=5 (NW-Africa) and T = 30 (Peru) in Table 2] compared with the data in Table 1:

NW Africa: $V_{zzi} = 0.54 \text{ d}^{-1} > (A) V_i = 0.26 \text{ d}^{-1}$,
i. e. 2.1 times greater.

Peru : $V_{zzi} = 0.11 \text{ d}^{-1} > (A) V_i = 0.047 \text{ d}^{-1}$,
i. e. 2.4 times greater.

In order to obtain highest V values concerning total production (TP) at light saturation, we transformed first V_{zzi} into assimilation numbers and then back to $V_{zzmax}(TP)$ as done for the calculation in Table 1. We finally obtain:

$V_{zzmax}(TP) - \text{NW Africa} = 1.57 \text{ d}^{-1} > V_{zzmax}(TP) - \text{Peru} = 1.04 \text{ d}^{-1}$.

These values show that the specific growth rate evaluated by the model reaches a high value off Peru and therefore is not fundamentally different from the value for NW Africa. The slightly lower value in the tropical Pacific is perhaps a signal of some iron limitation as we shall see later in Figure 6C. The difference could be due to a greater activity of microzooplankton keeping the value of V at a lower level. The grazing mechanism of microheterotrophs is still poorly understood. In regard to migrant macrobiota, their influence is permanent, *i. e.* day and night, because they are intimately associated with the algae. On the other hand, Martin (1990) argues that coastal upwelling systems are not lacking in iron because the sediments provide a sufficient supply. As a global conclusion resulting from our model application, we believe that grazing is mainly responsible for the much lower apparent increase rate of the phytoplankton standing stock observed off Peru.

Some theoretical remarks concerning the zz model

Instead of analysing the system, let us now build up and simulate the phenomena by establishing from the daily basic function, *i. e.* $Y_{zz} = Y_{zZo} \cdot 10^{\mu_{zz}T}$, the three other functions, *i. e.* Y_{obs} , Y_{btw} and Y_{NCP} . It is useful to show how different levels of grazing (Gr) and specific increase rates (V_{zz}) lead to the main characteristics of the different curves as defined in Figure 2. In Table 3 we present the equations for some simple values of the model parameters (we do not present the figures of the curves, which can easily be constructed). In the first case (case 1), grazing is kept constant at a relatively high value in regard to the initial chlorophyll content, *i. e.* 90 % of Y_{zZo} ; the daily μ_{zz} is chosen at a constant value of 0.301, corresponding to one doubling per day ($V = 1 \text{ d}^{-1}$). It is interesting to note that the equation concerning the apparent increase of chlorophyll standing stock has the form of $Y_{obs} = a \cdot 10^{\mu T} + b$. The same is true for the equation Y_{btw} . All the equations contain the same value of μ (*i. e.* 0.301), but on the other hand the addition in the equation of the constant grazing term is responsible for a shift up of the specific increase rates (V) with time. For example, for the Y_{obs} curve, V_{obs} is initially 0.1 d^{-1} (first day) and then steadily increases towards 1 d^{-1}

(*i. e.* the V_{zz} value) for high values of T. This demonstrates that a constant grazing leads very rapidly to negligible grazing effects. In case 2, we choose a relatively low initial grazing but allowed it to increase exponentially. We choose μ_{zz} to correspond to a high specific rate of increase ($V = 1.5 \text{ d}^{-1}$). In this case Y_{obs} remains a simple exponential function resulting in a constant ($V_{obs} = 1 \text{ d}^{-1}$). The Y_{btw} is also reduced to a simple exponential form, but the Y_{NCP} equation becomes more complex. The specific rate of increase changes with time, starting from an initial value of V_{NCP} of 1.5 d^{-1} (first day) and decreasing towards 1 d^{-1} for longer time values.

Returning to the functions given in Figure 2, we can now mention that grazing increases exponentially ($Gr = 6.581 \cdot 10^{0.112T}$). We can also state that μ_{zz} has an exponential function ($\mu_{zz} = 0.1677 \cdot 10^{kT}$, with $k = 0.012$). The upwards shift of μ_{zz} and V_{zz} with time is probably not a mathematical artifact because it is known from the literature that the specific growth rates of phytoplankton increase with temperature. According to Eppley (1972), $V = \text{doubling d}^{-1} = 0.851 \cdot 10^{0.0275\theta}$ (equation given under this form by Frost, 1987). As given in Table 2, our increase of V (from 1.4 to 1.8, *i. e.* $\Delta V = 0.4$ for NW Africa, and for Peru from 0.8 to 1.3, *i. e.* $\Delta V = 0.5$) is of the same order of magnitude as that calculated from Eppley's formula. A temperature change from 15 to 19°C (the increase of θ is about the same in the two upwelling zones) leads to an increment ΔV of 0.6 d^{-1} . We are at present conducting a theoretical study of this model, which will be supplemented by additional observations from upwelling systems.

The HNLC conditions of the Costa Rica dome

The diagram in Figure 1 shows values of ΣChl_{NCP} and ΣChl_{obs} from the Costa Rica dome (CRD) upwelling. These are average values, for a steady-state system corresponding to the observations of Wyrтки (1964) and

Table 3

Equations of V vs time curves for several values of grazing (Gr) and daily growth coefficients (μ_{zz}). Figures of the different curves are not presented, but they can easily be constructed.

Case 1	Equations
Grazing is constant Example: Gr = 9 $\mu_{zz} = 0.301$ (<i>i. e.</i> $V_{zz} = 1 \text{ d}^{-1}$) $Y_{zZo} = 10$	$Y_{zz} = 10 \cdot 10^{0.301T}$ $Y_{obs} = 10 \cdot 10^{0.301T} + 9$ $Y_{btw} = 10^{0.301T} + 18$ $Y_{NCP} = 9(T + 1) + 10^{0.301T}$
Case 2	Equations
Grazing increases exponentially Example: $Gr = Gr_0 \cdot 10^{\mu T}$ with $Gr_0 = 5$ and $\mu = 0.301$ $\mu_{zz} = 0.39794$ (<i>i. e.</i> $V_{zz} = 1.5 \text{ d}^{-1}$) $Y_{zZo} = 10$	$Y_{zz} = 10 \cdot 10^{0.39794T}$ $Y_{obs} = 10 \cdot 10^{0.301T}$ $Y_{btw} = Y_{obs} \cdot 10^{0.301T} + Gr_0 \cdot 10^{0.301T-1}$ $Y_{NCP} = Y_{btw} \cdot 10^{0.301T} + 10 \cdot 10^{0.301T-2} \cdot 5$

Broenkow (1965). These values are considered to be representative of typical HNLC conditions (Minas *et al.*, 1986). In the dome, where nutrients are high, the chlorophyll concentration stays at a permanently low level near 10 mg Chl m⁻² during the upwelling period. The NCP point in Figure 1 corresponds to a value of 218 mg Chl m⁻² with a residence time of 83 days. The ratio of $\Sigma\text{Chl}_{\text{obs}}/\Sigma\text{Chl}_{\text{NCP}}$ is 0.046 which is a low value, but appears to be typical of HNLC waters. As we shall later show, similar values are observed in the Antarctic section of our study.

The "zz model" described earlier can be used for evaluation of the specific increase in the rate of daily production (*i. e.* V_{zz}). If the grazing rate compensates the daily autotrophic chlorophyll production, 218/83 = 2.63 mg Chl are involved in the day-night oscillation. The daily growth constant according to the model is $\mu_{zz} = \log 12.63/10 = 0.1014$ and the corresponding value of V_{zzi} is 0.263 d⁻¹. Following the same mode of calculation as before and using a *f*-ratio of 0.5, the final specific rate of increase at optimal light conditions reaches a relatively high value of $V_{zz\text{max}} = 0.98$ d⁻¹. This is almost the same value as previously calculated for Peru. In HNLC waters with a higher background of chlorophyll, Cullen *et al.* (1991) concluded that high (about 1.5 d⁻¹) to extremely high (>1.5 d⁻¹) specific growth rates of phytoplankton suggest vigorous growth of phytoplankton, effectively controlled by grazing. We shall return to same question in our final paragraph devoted to the NCP study in the Antarctic waters.

Our observations of high specific rates of increase, which are perhaps still lower than the true physiological phytoplankton growth rates, could be discussed in detail within the context of an analysis done recently by Banse (1991 *a*; 1991 *b*). We agree with Banse's arguments and his conclusion that shipboard culture work on natural populations suffers from incubation artifacts by modifying the natural open-water grazing environment.

NCP and grazing in the Atlantic equatorial upwelling

The Atlantic equatorial upwelling has been studied during a several-year programme in the Gulf of Guinea and surrounding oligotrophic areas. One of the principal conclusions was that planktonic productivity does not increase during the main upwelling season at the equator, despite a significant input of nutrients into the photic zone (Voituriez *et al.*, 1982; Herbland *et al.*, 1983). Zooplankton grazing was considered as the principal factor for keeping primary production at moderate levels. A North-South section of temperature, nitrate and chlorophyll crossing the equator in the Gulf of Guinea, south of Abidjan (4°W) is shown in Figure 3. The centre of the upwelling is situated slightly south of the equator. Cold water with a temperature of 21 to 22°C occupies a large area and has a southern boundary near 5°S. Upwelled waters result in surface nutrient levels between 3 and 6 μM NO₃, but chlorophyll concentrations never reach high values and are generally less than 1 μg l⁻¹. We are at present conducting an evaluation of nutrient consumption by diagram analysis. Since complex mixing occurs in this area, this is a difficult process because non-

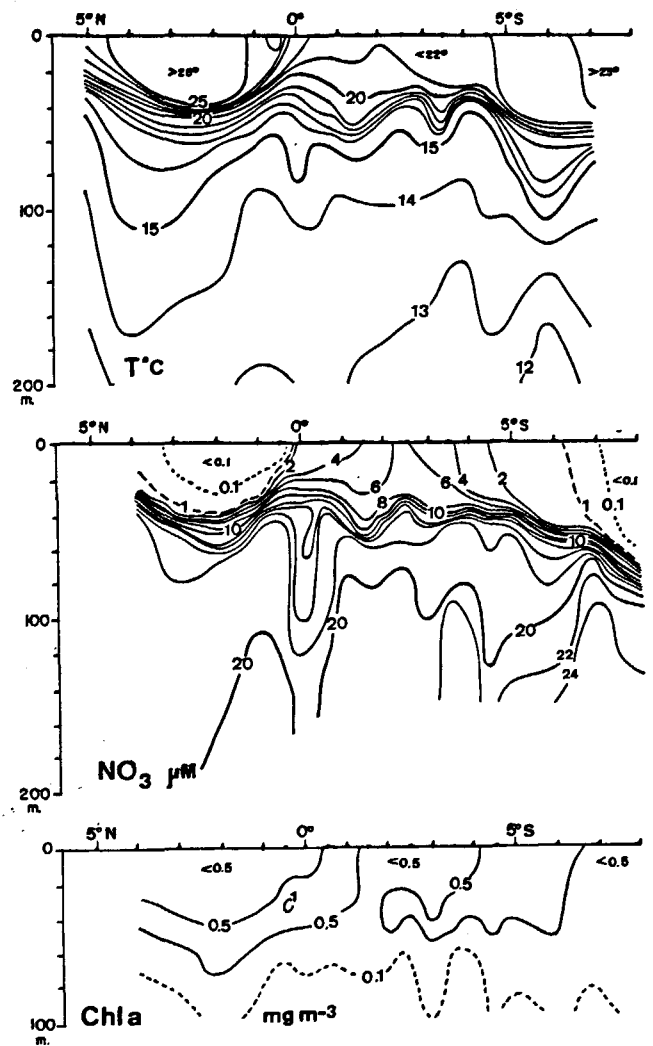


Figure 3

North-South equatorial section along 4°W, showing the distribution of temperature (°C), nitrate (μM) and chlorophyll (μg l⁻¹) during the main upwelling season (August 1978), drafted from Voituriez and Herbland (1984) and Voituriez *et al.* (1982). In the Gulf of Guinea, upwelling is covering a large band reaching 5°S.

conservative properties cannot be determined easily. Minas *et al.* (1991), encountered such difficulties in analysing a three-component mixing system.

We propose, therefore, an approach inspired by a study of temperature-nutrient diagrams (Voituriez and Herbland, 1984) of the equatorial divergence. Such diagrams can be used to indicate the intensity of nutrient uptake in upwelling zones.

Figure 4 contains a simple scheme showing how three types of diagrams can be formed as a consequence of different intensities of simultaneous surface heating and nutrient assimilation. When nutrient uptake is very fast relative to heating, the data points fall below the theoretical straight line of mixing, connecting here the end members A and B of non-conservative properties. A rapid assimilation system, as described in Figure 4B, shows such a distribution. If the opposite situation occurs, data points fall above the AB line. Such diagrams characterize strong HNLC conditions. As examples, we show diagrams for the Costa

Rica dome (Fig. 4C) and equatorial Pacific (Fig. 4D) during HNLC conditions.

Linear temperature-nutrient relationships are encountered in the surface water of upwelling zones more frequently than deviations from the straight line. This suggests that surface heating and nutrient uptake occur at similar rates or, rather at rates compensating each other, in order to keep straight the AB line. It is evident that in this case, mixing which normally occurs in all these systems does not produce any change in the straight line relationship. With a few noteworthy exceptions (e. g. Traganza *et al.*, 1983; Dugdale *et al.*, 1989), these relationships have not received enough attention in remote sensing studies. All surface temperature-nutrient relationships in our coastal upwelling studies (Minas *et al.*, 1986) show linear relationships described by:

$$T = -0.16 [NO_3] + 17.53; r = 0.96^{**} (n = 48) \text{ for NW Africa}$$

$$T = -2.26 [PO_4] + 21.30; r = 0.97^{**} (n = 48) \text{ for Peru}$$

$$T = -2.40 [PO_4] + 17.48; r = 0.87^{**} (n = 63) \text{ for SW Africa.}$$

Voituriez and Herbland (1984) observed that there is no change in the temperature-nitrate relationship between the upwelling and the non-upwelling seasons at, and near the equator (see diagram of Fig. 4E). They concluded that there is no increase in the nitrate uptake during the upwelling season (July-August-September). We do not fully agree with this statement. The principal reason is that a higher heat input should occur during the upwelling regime, coinciding

with a higher nitrate assimilation, thus maintaining the straight line relationship. The following simple approach can lead to a nitrate flux evaluation, and therefore to a new production (NP) determination. Hastenrath and Lamb (1978), in their "Climatic Atlas", indicate a net heat gain of $100 \pm 20 \text{ W m}^{-2}$ in the upwelling area of the Gulf of Guinea during August, *i. e.* during the principal upwelling period. Since there is in this area a relatively mixed water body within the upper 30 m, one can consider that the daily heat input is absorbed in this upper layer. An average heat flux of 100 W m^{-2} (*i. e.* $207 \text{ cal cm}^{-2} \text{ d}^{-1}$), is sufficient to increase the temperature of the upper 30 m by 0.07°C per day. The linear NO_3 -temperature relationship given by Voituriez and Herbland is described by $NO_3 = -1.88T + 45.5; r = 0.95^{**}$ ($n = 540$). Thus a temperature change of 0.07°C corresponds to a change in NO_3 of $0.1316 \mu\text{M } NO_3$. The daily change in a 30-m water column would therefore be $3.948 \times 10^{-3} \text{ mol N}$, *i. e.* $\sim 4 \times 10^{-3} \text{ mol N m}^{-2} \text{ d}^{-1}$. ^{14}C productivity curves from the same area show that most of the production takes place in the upper 30 metres (Voituriez *et al.*, 1982). Lewis *et al.* (1990) have shown that in the equatorial Pacific, most of the net heat fluxes reach the deeper part of the euphotic zone below the upper mixed layer. In a system of constant linear temperature-nutrient relationship, this would mean a more intense nitrogen uptake in the deeper part of the euphotic zone. Such deeper thermal effects may also occur along the Atlantic equator. In fact, they do not change the average estimation of nitrate consumption on

Figure 4

Nutrient-temperature diagram properties in upwelling zones.

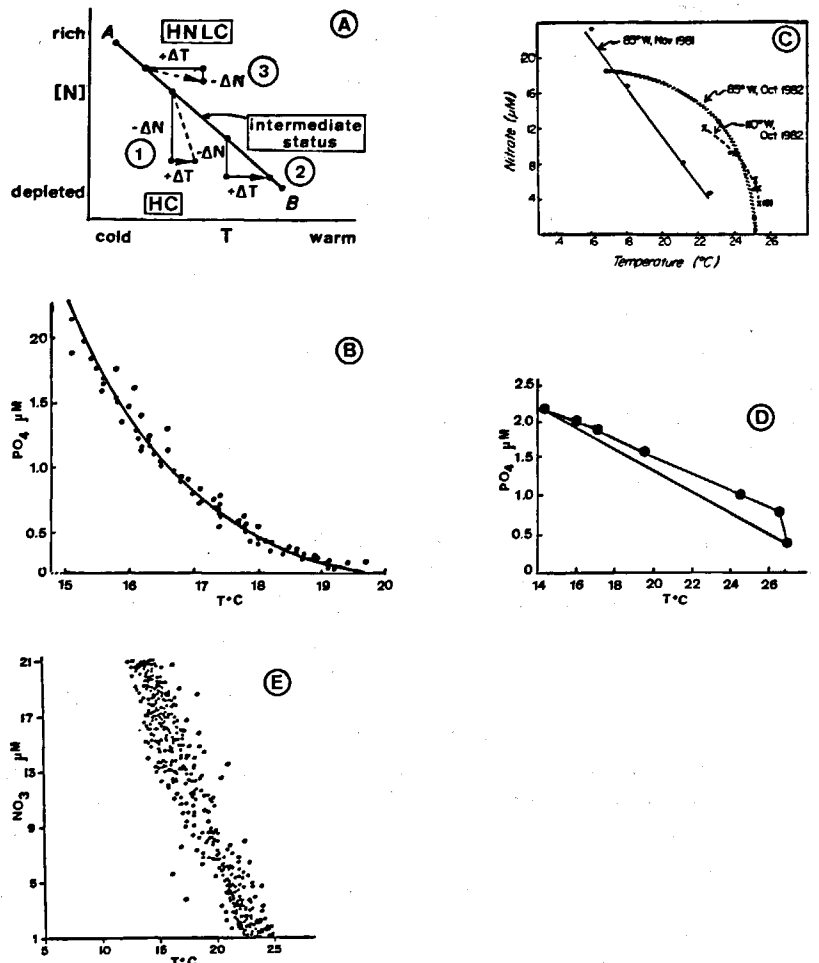
A) Theoretical explanation: three cases can be observed: 1) Nutrient assimilation moves the data points below the AB straight line, and simultaneous heating is not sufficient to bring the points back to the AB line ($-\Delta N > +\Delta T$). This type of diagram depicts fast-growing production systems, leading to high chlorophyll (HC) concentrations. An example is given in Figure 4B; 2) Nutrient consumption is small or negligible in regard to heating. Such a diagram indicates HNLC conditions (Fig. 4C and 4D); 3) Heating on the average compensates nutrient consumption. The straight line relationship is conserved (Fig. 4E).

B) PO_4 vs T diagram showing fast-growing autotrophs (from Minas *et al.*, 1986) in the Peruvian coastal upwelling.

C) NO_3 vs T diagram belonging to the equatorial Pacific upwelling (from Barber *et al.*, 1983), showing HNLC conditions.

D: PO_4 vs T plot, indicating HNLC and corresponding to the average data of the Broenkow (1965) model, drafted from Data Report Scripps Institution of Oceanography (1960).

E) General scatter diagram combining all data collected along 4°W , from 0 to 5°S [Gulf of Guinea (from Voituriez and Herbland, 1984)]. The equation given by the authors is: $NO_3 = -1.88T + 45.49; r = 0.95 (n = 540)$.



the square metre basis. Special attention has to be paid to this problem in future more detailed studies. In terms of carbon, the calculated NP represents $318 \text{ mg C m}^{-2} \text{ d}^{-1}$. Voituriez *et al.* indicate an average value of ^{14}C production (total production) of $1069 \text{ mg m}^{-2} \text{ d}^{-1}$. The corresponding *f*-ratio expressed in terms of carbon is $318/1069 = 0.3$. This is a first approach which seems reasonable. Since zooplankton are active, a regenerated production of 70 % appears realistic. Modern trace metal clean methods would probably result in a lower *f*-ratio, since ^{14}C uptake measurements were somewhat underestimated in the past (Martin *et al.*, 1989). This daily NP represents a yearly rate of $9.67 \text{ mol C m}^{-2} \text{ yr}^{-1}$ (yearly rates are often used by geochemists).

Garçon *et al.* (1989) have recently conducted a theoretical evaluation of NP for this region. Mathematical box model calculations, using the kinematics of CO_2 fluxes along the equatorial Atlantic divergence, lead to a nitrate based NP of near $17 \text{ mol C m}^{-2} \text{ yr}^{-1}$. They indicate a *f*-ratio of 0.3 for the Gulf of Guinea. This *f* value is in fact largely underestimated because total production was overestimated by factor 2 to 2.4 (hourly ^{14}C uptake rates have been erroneously converted into daily rates). One may argue that the biological part of the model does not take into account "grazing", which seems to become a key problem for equatorial zones. We can conclude that because of the relatively low chlorophyll content of the waters associated with relatively high nutrients, the Atlantic equatorial upwelling may be considered as a moderate HNLC system. It seems to turn out that such systems have low *f*-ratio tendencies, supporting the idea of more regenerated production due to a dominant heterotrophic activity. Similar low *f*-ratios 0.1 to 0.3 were observed by Murray *et al.* (1989), who compared and discussed the results of several NP approaches in the eastern equatorial Pacific.

HNLC in the Peruvian coastal upwelling

The Peruvian coastal upwelling, which during austral winter appears to belong to the HNLC conditions, has been studied for pelagic productivity mostly during the weak upwelling season (Barber and Smith, 1981; Codispoti *et al.*, 1982). During this weak upwelling season, a great variability in the chlorophyll vs nutrient regime exists, showing aspects of HNLC tendencies as explained above and also very high chlorophyll concentrations associated with high production rates (Ryther *et al.*, 1971; Simpson and Zirino, 1980; Boyd and Smith, 1983). Only a few descriptions are available when strongest winds induce the main upwelling during the austral winter (June to September) (Guillén *et al.*, 1973; Walsh *et al.*, 1980). Long sections were carried out during the French Paciprod cruise of R.V. Jean-Charcot in 1986 [August 8 to September 18 (Coste *et al.*, 1989; Minas *et al.*, 1990)]. High nutrients are observed in the surface water ($\text{NO}_3 > 10 \mu\text{M}$) along a section between the Galapagos Islands and the Peruvian coast near 15°S (Fig. 5). Chlorophyll is very low, mostly between 0.5 and $1 \mu\text{g l}^{-1}$, with some higher values near the coast. ^{14}C productivity is in general below $0.5 \text{ g C m}^{-2} \text{ d}^{-1}$. These characteristics classify these waters as HNLC waters. Murray

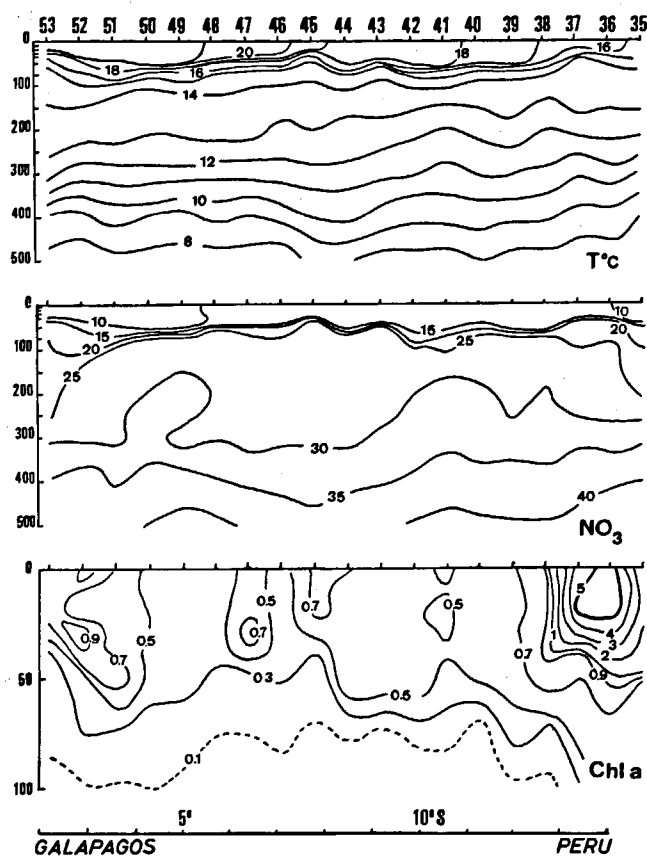


Figure 5

Temperature, nitrate (μM) and chlorophyll ($\mu\text{g l}^{-1}$) on the connection section between the coast of Peru (15°S) and the Galapagos Islands. The section shows a great extension offshore, with high nitrate and low chlorophyll ($< 1 \mu\text{g l}^{-1}$), with one exception at a coastal station (T and NO_3 distributions from Minas *et al.*, 1990).

et al. (1989) measured primary productivity with the ^{14}C method in June of the same year at some stations south of the equator, between Ecuador (2°S) and the Galapagos. They judged this productivity (0.3 to $0.4 \text{ g C m}^{-2} \text{ d}^{-1}$) "anomalously low, especially considering the nutrient concentration available". In our first approach (Minas *et al.*, 1990), we were cautious with "grazing" arguments, since other important factors such as turbulence, light and perhaps now iron limitation may play a role, especially in the offshore waters. A NCP analysis, as done by Minas *et al.* (1986), appears to be very difficult or even impossible for this season (Minas *et al.*, 1990).

Some thoughts and concluding remarks dealing with large scale features in the tropical Atlantic and Pacific

Global productivity charts displaying total and export production (Berger *et al.*, 1987), as well as satellite images of sea surface chlorophyll distribution, are frequently exhibited within the framework of Global Change Programs. From our review of the main upwelling systems and the kinetics of growth characteristics, we conclude that the NW-African coastal upwelling, which is one of the best known area of the world ocean through the Cineca programme, appears to be a rapidly growing, and therefore highly productive zone with high chlorophyll concentra-

tions as a permanent characteristic. Export to the offshore oligotrophic regime seems to occur by transport of particulate and dissolved organic matter. On the other hand, in the Pacific South American upwelling (mainly Peru), growth appears to be more controlled by grazing. During austral winter, the HNLC conditions, associated with very low productivity, allow an extension of nutrient-rich water towards the open ocean, following the general circulation pattern (Peru and South Equatorial Current). During the weak upwelling season off Peru, productivity, as shown by many observations, also frequently exhibits a high chlorophyll pattern, like NW Africa. The upwelling along the equatorial Pacific is the most expressive emanation of HNLC characteristics, with almost the same properties as the Costa Rica dome upwelling (Fig. 6B and Tab. 3). Global CZCS sea surface chlorophyll charts generally clearly demonstrate the different patterns between the tropical Atlantic and Pacific Oceans (Fig. 6A). The more extensive chlorophyll, particularly off NW Africa, contrasts with less chlorophyll-producing Peruvian and equatorial zones in the Pacific Ocean. Unfortunately, global charts often give average situations, obliterating seasonal events. One of the greatest unsolved questions for oceanographers concerned with biological productivity is to know and understand the fate of nutrients transported away from Peru during austral winter, and all those nutrients upwelling along the equator. Where and how are they consumed (Minas and Minas, 1990)? Almost nothing is known about the dynamics of the nutrient utilization far from the upwelling source areas. This large-scale problem, existing since the work of Thomas (1972; 1979), will be addressed by the US-J-GOFS EqPac Process Study. The most important contribution, more clearly elaborated by observation than by nutrient dynamic explanation, is due to Feldman *et al.* (1984) and Feldman (1986 *a*; 1986 *b*). There are blooms observed off Peru, and even far SW of the Galapagos islands. Some blooms have been studied already in greater detail (Bender and McPhaden, 1990). Pisiyas and Lyle (1988) noted, on the basis of Eastropac Atlas, that "the Costa Rica dome is the locus of the highest surface productivity of any open ocean region in the equatorial Pacific". This demonstrates that the Costa Rica dome can switch from a HNLC site to a normal situation. The remaining question concerns the reason of such phytoplankton outbursts. The washout effect of the great dilution during an upwelling event allows the autotrophs to outgrow their grazers. Are atmospheric iron inputs, or simply iron availability increased by dilution with old oligotrophic surface waters, the key elements for launching these events? The

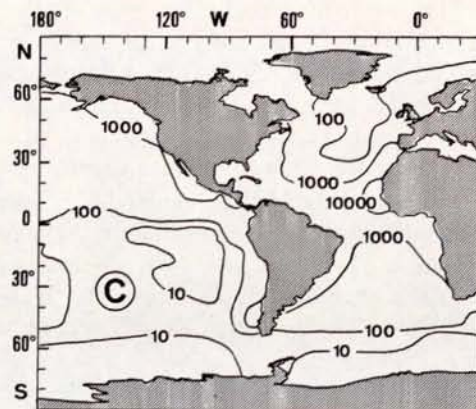
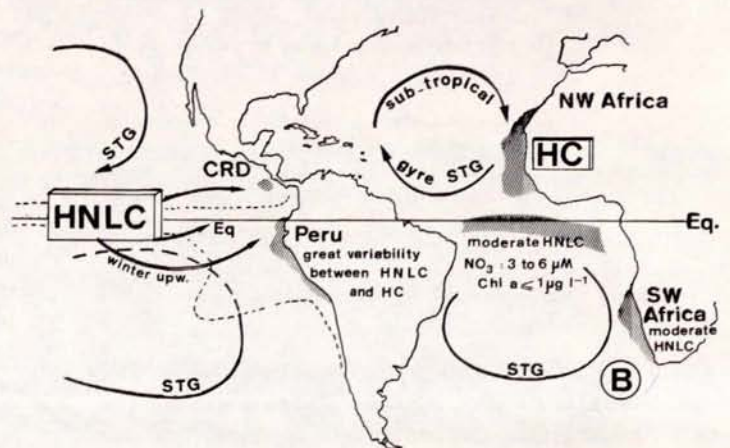
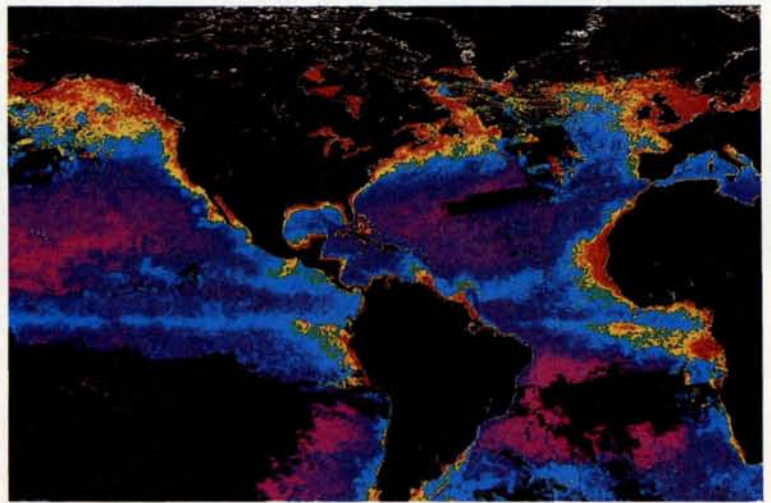


Figure 6

A) CZCS images of tropical upwelling systems (Feldman, 1989) disclose generally a greater development and extension of near-surface chlorophyll, especially off NW Africa. This fact agrees with our geographical classification of fast- to slow-growing systems under the influence of more or less grazing pressure (see Tab. 3 and Fig. 6B).
 B) Location of HNLC zones well developed along the equatorial Pacific, and seasonally in the Costa Rica dome and off Peru. The tropical Atlantic displays only moderate HNLC situations, especially during the equatorial upwelling. NW Africa is showing almost permanently high chlorophyll situations.
 C) Global fluxes of mineral aerosol to the ocean in $\text{mg m}^{-2} \text{yr}^{-1}$, according to Duce *et al.* (1991). This chart supports greatly the iron limitation hypothesis, and therefore constitutes a challenge to the "only grazing" explanation.

Table 4

Classification of tropical upwelling systems between extreme HC and HNLC conditions. Seasonal characteristics are very important; the same upwelling, like that off Peru, can belong to all types between HC and HNLC.

HC	fast-growing standing stock with high chlorophyll
	<ul style="list-style-type: none"> - NW-Africa, mostly permanent situation, with possible local exceptions - Peru, coastal upwelling, frequent during the weak upwelling season - SW-Africa, coastal upwelling, frequent during the weak upwelling season
	<ul style="list-style-type: none"> - Peru, coastal upwelling during the weak upwelling season - SW-Africa, coastal upwelling during the main upwelling season (Probyn, 1988)
	<ul style="list-style-type: none"> - Atlantic Equatorial Upwelling (Gulf of Guinea), with moderate HNLC conditions during the main upwelling period (July-August-September)
	<ul style="list-style-type: none"> - Peru, coastal upwelling, HNLC situation during the main upwelling season (austral winter)
	<ul style="list-style-type: none"> - Pacific Equatorial Upwelling with extreme HNLC conditions - Costa Rica dome

HNLC very low or stationary chlorophyll standing stock

global chart of dust inputs to the ocean published by Duce *et al.* (1991) is a welcome addition to this discussion (Fig. 6C). At first glance, this seems, from a geographical point of view, to provide strong support for the iron limitation hypothesis. This is true not only for the Antarctic Ocean, but also for the tropical Atlantic and Pacific features, particularly if one considers NW Africa vs the eastern equatorial Pacific and its HNLC zones. This constitutes a challenge to the "grazing only hypothesis" and suggests that we need to be cautious. Even the Atlantic equatorial upwelling, which we earlier called "moderate HNLC" might be partly influenced by a greater iron availability. The most recent publication (Young *et al.*, 1991; Betzer, pers. comm.) shows that even oligotrophic zones may respond by sporadic productivity increases to atmospheric iron inputs in the North Pacific.

At present, arguments in favour of "grazing" seem more convincing, mainly due to the fact that in iron-rich freshly upwelled coastal water, production can start slowly. In very slow growing regimes, there is evidence that high specific uptake rates must be inferred or even directly observed (Cullen *et al.*, 1992). In our view, the strongest argument supporting the grazing explanation is that, in a Chl vs time diagram, the whole spectrum of growth velocities can be observed, from very fast to extremely slow (*see* classification of Tab. 4). Iron limitation should not allow such a variety of intermediate status. Despite these arguments, it is clear that iron, and other metals which play such an important role in algal physiology (Martin and Gordon, 1988; Morel, 1991), may also exercise their limitation or fertilization effects, especially during the final stage of longer

residence times in the photic zone. Great attention will have to be paid to these aspects in the future. Studies should focus also on the regional dynamics of the herbivores. Dominant grazing pressure should result from excess zooplankton. It is tempting to suggest that transport of zooplankton by surface circulation (Peru Current, South Equatorial Current), from the coastal upwelling areas towards the equator, induces grazing pressure in the water upwelling along the equator. Charts of zooplankton abundance (Reid, 1962; 1977) seem to support this idea.

THE ANTARCTIC OCEAN

NCP in the Antarctic HNLC waters

During the *Antiprod 1* cruise, carried out by the Médioprod Group on R.V. Marion-Dufresne at the end of austral summer in 1977, a section was made from 40°S to 62°S in the Indian Ocean (Fig. 7). Nutrient distribution has been studied along this section, and primary production has been measured with the ^{14}C method at each station. Nutrients in the surface waters decrease from south to north. Nutrient consumption has been evaluated from the concentration difference between the subsurface thermal minimum water and the surface waters (Le Corre and Minas, 1983). The nutrient concentration in the temperature minimum water represents the concentration of the mixed layer and, therefore, the concentration of the surface and near-surface waters at the end of winter. The following relationship between nitrate and silicate consumption has been established: $\Delta\text{NO}_3 = 0.25 \Delta\text{Si}(\text{OH})_4 - 0.55$. This relationship concerns only the sea surface consumption data. In order to use the

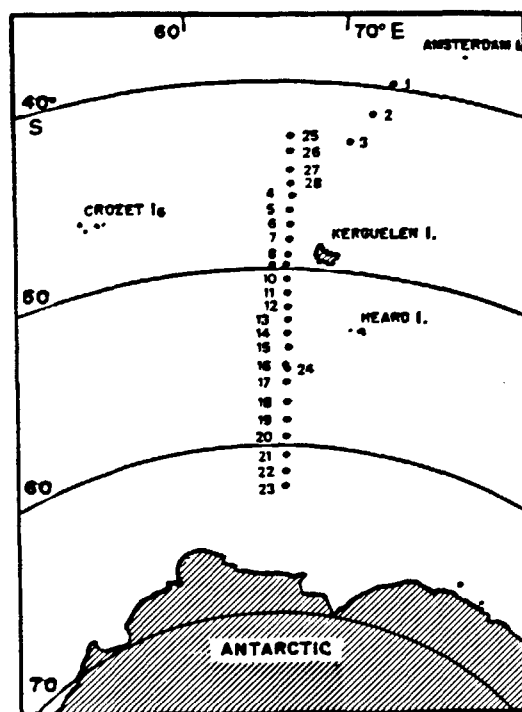


Figure 7

Station chart of the Antiprod-1 cruise.

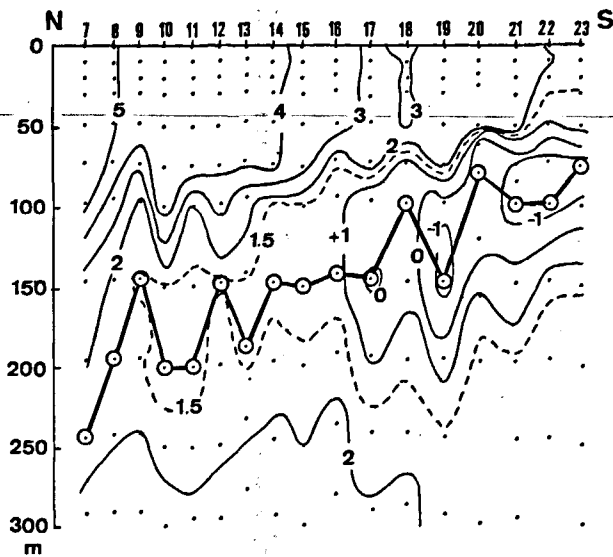


Figure 8
Distribution of temperature along the section of Figure 7, in the upper 300-metre layer, showing the thermal minimum (o).

Figure 9
Nitrate consumption (ΔNO_3 in μM) profiles at the Antiprod-1 cruise stations. ΔNO_3 is obtained by subtracting from the nitrate concentration at the thermal minimum the end-of-summer concentration observed at each depth. Water column integrated values ($\Sigma \Delta NO_3$ in $mmol\ m^{-2}$) are indicated for each station: $[\Delta NO_3 = (NO_3)_{min} - (NO_3)_{obs}]$.

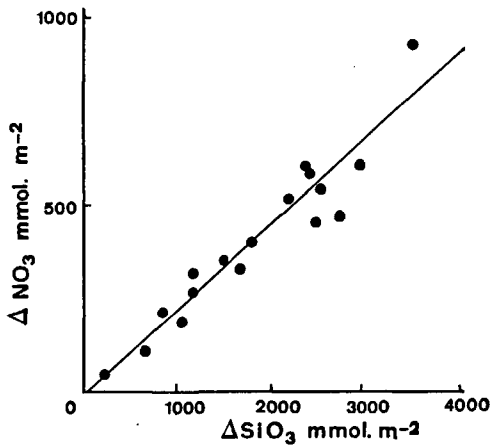


Figure 10
Water column integrated consumption of nitrate ($\Sigma \Delta NO_3$ in $mmol\ m^{-2}$) vs silicate (ΔSiO_3 in $mmol\ m^{-2}$), see Figure 9.

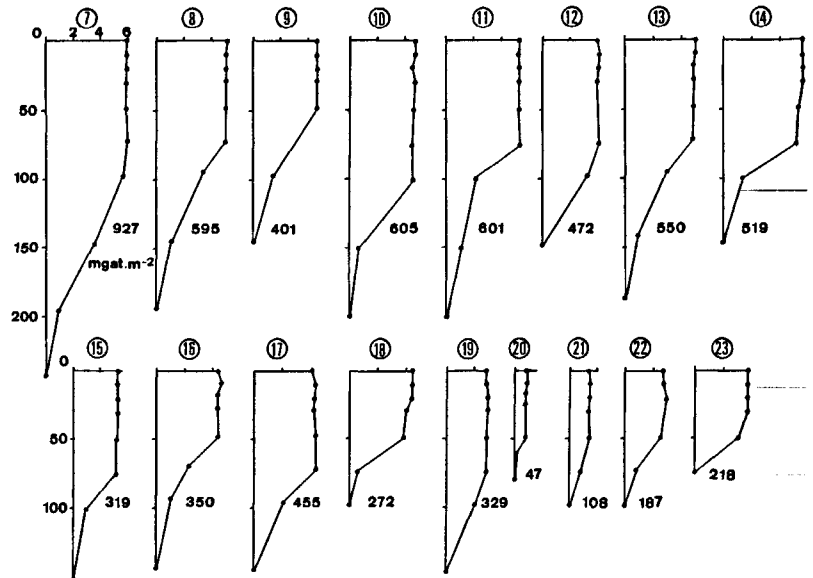
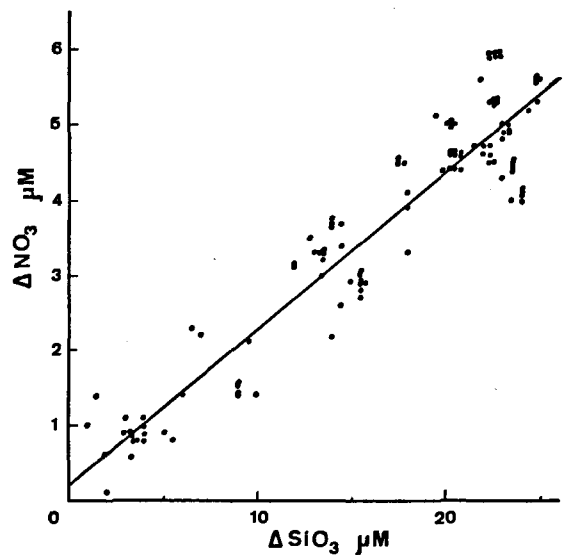


Figure 11
All-data diagram of consumption of nitrate (ΔNO_3 in μM) vs consumption of silicate (ΔSiO_3 in μM) at stations 7 to 23 of the Antiprod-1 cruise.

NCP approach and the zz model, we have also calculated the integrated nutrient consumption in the water column at each station. To illustrate our calculation, we show first, in Figure 8, the thermal structure of the upper 200 m, from which the depths of the temperature minimum have been determined. The nutrient content of this temperature minimum water is remarkably constant from south to north ($[NO_3] = 29.1 \pm 0.6$). The lapse of time corresponding to the nutrient consumption (Δt) is roughly six months, the primary productivity period in the Southern Ocean (Martin, 1990). The profiles of the ΔNO_3 at the different stations are shown in Figure 9. Profiles of ΔPO_4 and $\Delta Si(OH)_4$ (not shown) have almost the same shape. Regression calculations allow the establishment of the following relations between the changes in the consumption of the different nutrients.

Figure 10 shows the relationship between the integrated values of water column ΔSiO_3 and ΔNO_3 . The best fit equation is: $\Delta NO_3 = 0.23 \Delta SiO_3 - 11.38$; $r = 0.95$ ($n = 17$). The scatter diagram in Figure 11 contains all the individual data points, and regression calculation leads to the equation:



$\Delta\text{NO}_3 = 0.21 \Delta\text{SiO}_3 + 0.18$; $r = 0.94$ ($n = 116$). Integrated ΔNO_3 vs ΔPO_4 (diagram not shown) gives the relationship: $\Delta\text{NO}_3 = 13.32 \Delta\text{PO}_4 - 17.54$; $r = 0.87$ ($n = 17$).

In order to obtain an overall average of the nutrient consumption, we have integrated the whole nutrient consumption along the 1 553 km long North-South section (stations 7 to 23). The total annual consumption below a 1m-wide band having the same length is 594 kgmol for nitrate, 48 kgmol for phosphate and 2,712 kgmol for silicate. The overall average of the nutrient consumption per square metre is therefore:

for nitrate nitrogen $\Sigma\Delta\text{N-NO}_3 = 0.380 \text{ mol m}^{-2}$;
for mineral phosphorus $\Sigma\Delta\text{P-PO}_4 = 0.031 \text{ mol m}^{-2}$;
for silicate silicium $\Sigma\Delta\text{Si(OH)}_4 = 1.750 \text{ mol m}^{-2}$.

The average molar uptake ratios are:

$$\Sigma\Delta\text{N}/\Sigma\Delta\text{P} = 12.3$$

$$\Sigma\Delta\text{N}/\Sigma\Delta\text{Si} = 0.22.$$

or by taking phosphorus as the reference:

$$\Delta\text{Si}/\Delta\text{N}/\Delta\text{P} = 55.9/12.3/1.$$

The average amount of nitrate-nitrogen removed from these waters ($0.380 \text{ mol. m}^{-2}$) leads, according to Redfield ratios, to a nitrate based new production (NP), in terms of carbon, equal to $2.52 \text{ mol C m}^{-2}$, or 30.2 g C m^{-2} , which have been produced within the time interval from the end of winter (August-September) to the time of observation, at the end of summer (February-March). The time interval of the removal is not easy to determine; thus we have estimated the daily average NP using following time intervals:

$$5 \text{ months} = 0.20 \text{ g C m}^{-2} \text{ d}^{-1}$$

$$6 \text{ months} = 0.17 \text{ g C m}^{-2} \text{ d}^{-1}$$

$$7 \text{ months} = 0.14 \text{ g C m}^{-2} \text{ d}^{-1}.$$

The mean value of the ^{14}C uptake measurements carried out at each station is $0.14 \text{ g C m}^{-2} \text{ d}^{-1}$. This represents the new production which corresponds to a 7-month interval. Besides underestimation by the ^{14}C method, one may argue that the period of high production may have existed during the preceding time period. In fact, it is obvious that this new production is fairly low if one considers the luxurious abundance of nutrients available in the waters. A recent estimation of new production in the more productive marginal ice zone gives $49 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Smith and Nelson, 1990). In comparison with oligotrophic waters of the tropical ocean, our NP rate, which is practically the yearly value for these Antarctic waters (with nearly 6 months without production), is relatively higher. Martin *et al.*'s (1989) mean value of NP (sediment trap results in tropical Pacific) in the Vertex Program was $18.4 \text{ g C m}^{-2} \text{ yr}^{-1}$ while our NP in the Mediterranean Sea was $19.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Minas, 1970; Minas *et al.*, 1988).

If we convert the NP of carbon to equivalent amounts of chlorophyll using a $\text{C}/\text{Chl} = 55$, we obtain a chlorophyll production rate of $549 \text{ mg Chl m}^{-2} \text{ yr}^{-1}$. Since we have summarized the total amount of chlorophyll in the area in the same way as the nutrient consumption, we found an average content of 0.025 g m^{-2} . The ratio observed vs that actually produced is then $25/549 = 0.045$, *i. e.* 4.5 %. This

is similar to the value observed in the HNLC waters of the Costa Rica dome.

Grazing and the *f*-ratio problem

Silicon and nitrogen analyses of particulate matter from the same region of the Indian Ocean have been undertaken (Copin-Montégut and Copin-Montégut, 1978). Figure 12, as published by Le Corre and Minas (1983), shows the consumption values of silicate and nitrate along the North-South section (deltas of the surface waters). The values of particulate silicon and nitrogen are low in comparison with the consumption values of both elements. This demonstrates also that most of the elements assimilated by particulate matter are removed from the water column. Particulate silicon leaves the surface waters by sedimentation of fecal pellets or direct sedimentation of large diatoms.

An intriguing aspect of the consumption results is the high $\Delta\text{SiO}_3/\Delta\text{NO}_3$ ratio. The very strong correlation would suggest tight coupling between nitrogen assimilation and particulate silicon formation, probably by Antarctic diatoms, well known for their heavy skeleton. Particulate matter, on the

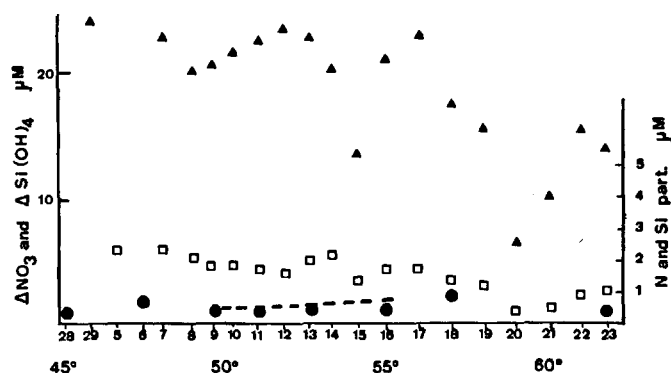


Figure 12

North-South distribution of surface nitrate and silicate consumption values (ΔNO_3 in μM and $\Delta\text{Si(OH)}_4$ in μM), for the Antiprod-1 cruise.

□ : ΔNO_3 values; ▲ : $\Delta\text{Si(OH)}_4$ values; ---: concentration level of particulate silicium; ● : concentration of particulate nitrogen (from Le Corre and Minas, 1983).

other hand, has a much lower Si/N ratio, with values near 2. This observation suggests that recycled nitrogen assimilation can make the difference. The high uptake ratio, *i. e.* 4.5 times more silicate than nitrate, suggests that more than half of the total productivity is regenerated production. This is also consistent with *f*-ratio values deduced from $^{15}\text{NH}_4$ and $^{15}\text{NO}_3$ uptake measurements by Olson (1980) and Glibert *et al.* (1982) who respectively calculated *f* values slightly higher and lower than 0.5. If we choose a photosynthetically active period of about five months, the total production deduced from the nutrient consumption study is therefore $\text{TP} = 2 \times 0.2 = 0.4 \text{ g C m}^{-2} \text{ d}^{-1}$. This value is 2.9 times greater than the ^{14}C uptake rate of $0.14 \text{ g C m}^{-2} \text{ d}^{-1}$. Simon (1986) in a similar study in a western area of the Indian Antarctic sector came to almost the same result. Without reopening the old ^{14}C -controversy, a main argument for the Antarctic region is to

imagine a scenario with the assumption of an initial productive episode during late winter-spring. Indeed, a higher NO_3 uptake was found by Olson (1980) and Glibert *et al.* (1982) during that period. Wheeler and Kokkinakis (1990) came to the same conclusion for the subantarctic Pacific.

Our principal objective here, the application of the "zigzag model" to Antarctic conditions, leads to the following calculations: on the basis of the average water column chlorophyll content, remaining at a constant level of 25 mg Chl m^{-2} , for a 5-month time interval, the daily increase (or decrease) of chlorophyll is $549/150 = 3.66 \text{ mg}$, μ_{zz} is 0.0593 and $V_{zzi} = 0.15 \text{ d}^{-1}$.

According to the same method of calculation as was used before and assuming a f -ratio of 0.5 for Antarctic waters, the final specific increase rate for total production is $V_{(TP)} = 0.54$. This value, consistent with the grazing hypothesis, appears to be reasonable within the low temperature regime of the Southern Ocean. Eppley's formula for a temperature of 3°C leads to a value for V of 1 d^{-1} . Smith and Nelson (1990) estimated doubling rates for Antarctic phytoplankton and found a mean doubling time of 0.3 d^{-1} with several values higher than 0.5 d^{-1} . Results of laboratory cultures of Antarctic species lead to values of 0.7 d^{-1} (Raimbault, 1984 and pers. comm.).

Despite satisfying results obtained from our NCP concept and model, it cannot be completely excluded that iron limitation may be involved, especially at the end of the time course, in the grazing scenario. If most of the NO_3 assimilation takes place in the upper 50 m , nearly 20% of the original $29 \mu\text{M NO}_3$ were consumed ($= 17\%$ for an average consumption of $5 \mu\text{M}$). According to Martin (1990), iron limitation starts at that point leaving the remaining 80% of nutrients unused. It is possible that our low ^{14}C -uptake estimations have been undertaken under such limitation conditions. A slightly different scenario could be imagined as follows: since frequent measurements are lacking in this region, some unobserved sporadic phytoplankton blooms may occur at an earlier period (springtime) quickly exhausting nutrients, down to the 20% limit, where iron limitation begins. Such a scenario acts against the Wheeler and Kokkinakis' concept founded basically on McCarthy's NO_3 uptake repression by ammonia and refuting the iron limitation. In the subantarctic waters, total N uptake ($84\text{--}732 \mu\text{M d}^{-1}$) seems to fall in the order of magnitude of our data. Unfortunately, there are no estimates of N uptake on a square metre basis, and thus comparison becomes difficult. We do not have enough experience to analyse grazing conditions as a function of algal population, size, and grazing capacities of micro- or macroheterotrophs (Banse, 1990; 1991 *a* and *b*; Frost, 1987; 1991). We have the feeling that turbulence is the greatest handicap for microalgae intimately associated with the microheterotrophs. Near the surface, stability is the best chance for the algae to win the battle of auto vs heterotrophy.

CONCLUSIONS

1) Our Net Community Production (NCP) analysis and study of the *in situ* development of the phytoplankton standing

stock in tropical upwelled waters during their transport away from the source area show that two kinds of specific increase rates (V) can be defined: a) the apparent V of the increasing standing stock which varies from high to very low values, or even to zero in HNLC waters; b) the actual V , which is deduced as being high everywhere in the tropical ocean.

Grazing by herbivores appears to be the principal factor responsible for the reduced apparent velocity.

2) NCP determinations should receive more attention, because they are the best indicator of the average past new production which remains as a signature of NO_3 consumption in the water body. NCP determinations are complementary to other new production (NP) methods (Eppley, 1989). In the Pacific HNLC waters along the equator, the application of Wyrki's (1964) NP calculation (Chavez and Barber, 1987) depends on the ascending water fluxes, which are highly variable (*see* Minas *et al.*, 1990). The weakest feature of this method is that nutrient dilution by mixing with oligotrophic waters is not taken into account. We hope to propose soon our own NCP method for more complex mixing processes near the equator.

3) An important open question concerns the fate of nutrients in HNLC waters, since they do not downwell as in the Antarctic Ocean. The CZCS data base can help to discover phytoplankton outbursts away from the upwelling source area (*see* all Feldman references), or within the source area, for instance the Costa Rica dome (Pisias and Lyle, 1988).

Why sudden outbursts? Iron input by dust, or cessation of grazing? We believe that short-time surface and near-surface stability under daily heat input favours the departure of autotrophs, overpowering the microheterotrophs because more light becomes available.

4) A principal consequence of HNLC situations is a fertilization of large-scale areas in the open ocean, because dissolved nutrients are transported more easily than particulate matter.

HNLC zones are also large CO_2 source areas, because biological CO_2 uptake favours CO_2 escape from the upwelled water to the atmosphere. In addition, CO_2 outgassing is accelerated by surface warming (Minas and Minas, 1990).

5) HNLC conditions in the coastal Peruvian upwelling provide perhaps less food to higher trophic levels (for instance, Anchoveta) than El Niño waters, as was shown by Feldman's (1986 *a* and *b*) observations.

6) If both the grazing and iron hypotheses are valid in the Antarctic Ocean, the iron limitation starts late, when most of the yearly photosynthesis period is over.

7) Attention has to be paid to the origin of the excess zooplankton. This excess has not to be necessary great, but great enough to maintain a permanent grazing pressure on a low biomass. We assume this excess is autochthonous in the Antarctic Ocean, but greatly allochthonous along the Pacific equator, especially in the area of its eastern boundaries.

8) The idea of iron fertilization of more or less greater zones of the open ocean seems excellent to us, but any intervention in the laboratory and at sea should also focus on the heterotrophic activity and its elimination ("Killing zooplankton since one cannot tell it to go on hunger-strike").

HNLC waters are perhaps nothing other than waters with an excess of animals; the principal question is becoming: Why?

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REFERENCES

- Banase K. (1990). Does iron really limit phytoplankton production in the offshore subarctic Pacific? *Limnol. Oceanogr.*, **35**, 772-775.
- Banase K. (1991 a). Iron availability, nitrate uptake, and exportable new production in the subarctic Pacific. *J. geophys. Res.*, **96**, 741-748.
- Banase K. (1991 b). Rates of phytoplankton growth, in: Control of phytoplankton production in nutrient-rich areas of the open sea, S.W. Chisholm and F.M.M. Morel, editors, *Limnol. Oceanogr.*, **36** (in press).
- Barber R.T. and J.D.H. Ryther (1969). Organic chelators: factors affecting primary production in the Cromwell Current upwelling. *J. expl mar. Biol. Ecol.*, **3**, 191-199.
- Barber R.T. and R.L. Smith (1981). Coastal upwelling ecosystems, In: *Analysis of marine ecosystems*, A.R. Longhurst, editor, Academic Press, New York, 31-68.
- Barber R.T., R.C. Dugdale, J.J. MacIsaac and R.L. Smith (1971). Variations in phytoplankton growth associated with the source and conditioning of upwelling water. *Investigación pesq., Barcelona*, **35**, 171-193.
- Barber R.T., S. Zuta, J. Kogelschatz and F. Chavez (1983). Temperature and nutrient conditions in the eastern equatorial Pacific, October 1982. *Tropic Oceanol.-Atmos. Newsletters*, **16**, 15-17.
- Bender M.L. and M.J. McPhaden (1990). Anomalous nutrient distribution in the equatorial Pacific in April 1988: evidence for rapid biological uptake. *Deep-Sea Res.*, **37**, 1075-1084.
- Berger W.H., K. Fisher, C. Lai and G. Fu (1987). Ocean productivity and organic carbon flux. Part 1: Overview and maps of primary production and export production. University of California, San Diego, SIO ref. 87-30, 1-69.
- Bowden K.F. (1977). Heat budget considerations in the study of upwelling, in: *A voyage of discovery*, M. Angel, editor. Pergamon Press, Oxford, 277-290.
- Boyd C.M. and S.L. Smith (1983). Plankton, upwelling, and coastally trapped waves off Peru. *Deep-Sea Res.*, **30**, 723-742.
- Broecker W.S. (1990). Comment on "iron deficiency limits phytoplankton growth in Antarctic waters" by John H. Martin *et al.* *Global biogeochem. Cycles*, **4**, 3-4.
- Broenkow W.W. (1965). The distribution of nutrients in the Costa Rica Dome in the eastern tropical Pacific Ocean. *Limnol. Oceanogr.*, **10**, 40-52.
- Chavez F.P. and R.T. Barber (1987). An estimate of new production in the equatorial Pacific. *Deep-Sea Res.*, **34**, 1229-1243.
- Codispoti L.A., R.C. Dugdale and H.J. Minas (1982). A comparison of the nutrient regimes off northwest Africa, Peru, and Baja California. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer*, **180**, 184-201.
- Codispoti L.A., G.E. Friederich and D.W. Hood (1986). Variability in the inorganic carbon system over the southeastern Bering Sea shelf during spring 1980 and spring-summer 1981. *Continental Shelf Res.*, **5**, 133-160.
- Copin-Montégut C. and G. Copin-Montégut (1978). The chemistry of particulate matter from the South Indian and Antarctic oceans. *Deep-Sea Res.*, **25**, 911-931.
- Coste B., H.J. Minas and M.-C. Bonin (1989). Production pélagique des côtes du Pérou et des îles Galapagos. Campagne *Pacipro*, 8 août-18 septembre 1986. Publ. IFREMER, Campagnes océanographiques françaises, **7**, 1-183.
- Cullen J.J., M.R. Lewis, C.O. Davis and R.T. Barber (1992). Photosynthetic characteristics and estimated growth rates indicate grazing is the proximate control of primary production in the Equatorial Pacific. *J. geophys. Res.*, **97**, 639-654.
- Duce R.A., P.S. Liss, J.T. Merrill, E.L. Atlas, P. Buat-Ménard, B.B. Hicks, J.M. Miller, J.M. Prospero, R. Arimoto, T.M. Church, W. Ellis, J.N. Galloway, L. Hansen, T.D. Jickells, A.H. Knap, K.H. Reinhardt, B. Schneider, A. Soudine, J.J. Tokos, S. Tsunogai, R. Wollast and M. Zhou (1991). The atmospheric input of trace species to the world ocean. *Global biogeochem. Cycles*, **5**, 193-259.
- Dugdale R.C. and F.P. Wilkerson (1990). Iron addition experiments in the Antarctic: a reanalysis. *Global biogeochem. Cycles*, **4**, 13-19.
- Dugdale R.C., A. Morel, A. Bricaud and F.P. Wilkerson (1989). Modeling new production in upwelling centers: a case study of modeling new production from remotely sensed temperature and color. *J. geophys. Res.*, **94**, 18119-18132.
- Eppley R.W. (1972). Temperature and phytoplankton growth in the sea. *Fish. Bull.*, **70**, 1063-1085.
- Eppley R.W. (1989). New production: history, methods, problems, in: *Productivity of the ocean: present and past*. W.H. Berger *et al.*, editors. J. Wiley and sons, 85-97.
- Feldman G.C. (1986 a). Variability of the productive habitat in the eastern equatorial Pacific. *Eos*, **67**, 106-108.
- Feldman G.C. (1986 b). Patterns of phytoplankton production around the Galapagos Islands, in: *Tidal mixing and plankton dynamics*. J. Bowman, M. Yentsch and W.T. Peterson, editors. Springer-Verlag, 77-104.
- Feldman G.C. (1989). CZCS images. NSF/NASA. US Global Ocean Flux Study Office, Woods Hole.
- Feldman G.C., D. Clark and D. Halpern (1984). Satellite color observations of the phytoplankton distribution in the eastern equatorial Pacific during the 1982-1983 El Niño. *Science*, **226**, 1069-1071.
- Frost B.W. (1987). Grazing control of phytoplankton stock in the open subarctic Pacific Ocean: a model assessing the role of mesozooplankton, particularly the large calanoid copepods *Neocalanus* spp. *Mar. Ecol.-Prog. Ser.*, **39**, 49-68.
- Frost B.W. (1991). High phytoplankton specific production, high nutrient concentration and low phytoplankton stock implies grazing control. *Limnol. Oceanogr., Special ASLO Symp.* (in press).

- Garçon V.C., L. Martinon, C. Andrié, P. Andrich and J.-F. Minster (1989). Kinematics of CO₂ fluxes in the tropical Atlantic Ocean during the 1983 northern summer. *J. geophys. Res.*, **94**, 855-870.
- Gilbert P.M., D.C. Biggs and J.J. McCarthy (1982). Utilization of ammonium and nitrate during austral summer in the Scotia Sea. *Deep-Sea Res.*, **29**, 837-850.
- Groupe Médiprod (1974). Généralités sur la campagne *Cineca-Charcot II* (15 mars-29 avril 1971). *Téthys*, **6**, 1/2, 33-42.
- Guillén O., B. Rojas de Mendiola and R. Izaguirre de Rondán (1973). Primary productivity and phytoplankton in the coastal peruvian waters, in: *Oceanography of the South Pacific*. R. Fraser, editor, Unesco, Wellington, 405-418.
- Hastenrath S.L. and P. Lamb (1978). Climatic atlas of the tropical Atlantic and eastern Pacific Oceans. Univ. Wisconsin.
- Herbland A., R. Le Borgne and B. Voituriez (1983). Structure hydrologique et production planctonique dans l'Atlantique tropical oriental. *Thèse Doctorat ès Sciences, Université Aix-Marseille II*.
- Jacques G. and M. Minas (1981). Production primaire dans le secteur indien de l'Océan Antarctique en fin d'été. *Oceanologica Acta*, **4**, 1, 33-41.
- Ketchum B.H. and N. Corwin (1965). The cycle of phosphorus in a plankton bloom in the Gulf of Maine. *Limnol. Oceanogr., suppl.*, **10**, R148-R161.
- Le Bouteiller A. and A. Herbland (1982). Diel variation of chlorophyll *a* as evidence from a 13-day station in the equatorial Atlantic Ocean. *Oceanologica Acta*, **5**, 4, 433-441.
- Le Corre P. and H.J. Minas (1983). Distribution et évolution des éléments nutritifs dans le secteur indien de l'océan Antarctique en fin de période estivale. *Oceanologica Acta*, **6**, 4, 365-381.
- Lewis M.R., M.E. Carr, G.C. Feldman, W. Esaias and C. McClain (1990). Influence of penetrating solar radiation on the heat budget of the equatorial Pacific Ocean. *Nature*, **347**, 543-545.
- Longhurst A.R. and W.G. Harrison (1988). Vertical nitrogen flux from the oceanic photic zone by diel migrant zooplankton and nekton. *Deep-Sea Res.*, **35**, 881-889.
- Longhurst A.R., A. Bedo, W.G. Harrison, E.J.H. Head, E.P. Horne, B. Irwin and C. Morales (1989). NFlux: a test of vertical nitrogen flux by diel migrant biota. *Deep-Sea Res.*, **36**, 1705-1719.
- Marra J., R.R. Bidigare and T.D. Dickey (1990). Nutrients and mixing, chlorophyll and phytoplankton growth. *Deep-Sea Res.*, **37**, 127-143.
- Martin J.H. (1990). Glacial-interglacial CO₂ change: the iron hypothesis. *Paleoceanography*, **5**, 1-13.
- Martin J.H. and R.M. Gordon (1988). Northeast Pacific iron distributions in relation to phytoplankton productivity. *Deep-Sea Res.*, **35**, 177-196.
- Martin J.H., R.M. Gordon, S. Fitzwater and W.W. Broenkow (1989). Vertex: phytoplankton/iron studies in the Gulf of Alaska. *Deep-Sea Res.*, **36**, 649-680.
- Martin J.H., S.E. Fitzwater and R.M. Gordon (1990 a). Iron deficiency limits phytoplankton growth in Antarctic waters. *Global biogeochem. Cycles*, **4**, 5-12.
- Martin J.H., R.M. Gordon and S.E. Fitzwater (1990 b). Iron in Antarctic waters. *Nature*, **345**, 156-158.
- Minas H.J. (1970). La distribution de l'oxygène en relation avec la production primaire en Méditerranée nord-occidentale. *Mar. Biol.*, **7**, 181-204.
- Minas H.J. and M. Minas (1990). New productivity and CZCS Ocean Color Imagery. Considerations based on examples in upwelling systems of the tropical Ocean and the Mediterranean Sea. *Eos*, **71**, 160.
- Minas H.J., L.A. Romaña, T.T. Packard and M.-C. Bonin (1974). La distribution de l'oxygène dans un upwelling côtier (NW de l'Afrique) et dans celui d'une divergence au large (dôme de Costa Rica). *Téthys*, **6**, 1/2, 157-170.
- Minas H.J., L.A. Codispoti and R.C. Dugdale (1982 a). Nutrients and primary production in the upwelling region off Northwest Africa. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer*, **180**, 148-183.
- Minas H.J., T.T. Packard, M. Minas and B. Coste (1982 b). An analysis of the production-regeneration system in the coastal upwelling area off N.W. Africa based on oxygen, nitrate and ammonium distribution. *J. mar. Res.*, **40**, 615-641.
- Minas H.J., M. Minas and T.T. Packard (1986). Productivity in upwelling areas deduced from hydrographic and chemical fields. *Limnol. Oceanogr.*, **31**, 1182-1206.
- Minas H.J., M. Minas, B. Coste, J. Gostan, P. Nival and M.-C. Bonin (1988). Production de base et de recyclage ; une revue de la problématique en Méditerranée nord-occidentale, *Océanographie pélagique méditerranéenne*, H.J. Minas and P. Nival, editors, *Oceanologica Acta*, vol. sp. n°9, 155-162.
- Minas H.J., B. Coste, M. Minas and P. Raimbault (1990). Conditions hydrologiques, chimiques et production primaire dans les upwellings du Pérou et des îles Galapagos, en régime d'hiver austral (campagne *Paciprod*). *Actes du colloque Tour du Monde Jean Charcot, 2-3 mars 1989, Paris, Oceanologica Acta*, vol. sp. n°10, 383-390.
- Minas H.J., B. Coste, P. Le Corre, M. Minas and P. Raimbault (1991). Biological and geochemical signatures associated with the water circulation through the Strait of Gibraltar and in the western Alboran Sea. *J. geophys. Res.*, **96**, 8755-8771.
- Morel F.F.M. (1991). Micronutrient utilization by phytoplankton, in: Control of phytoplankton production in nutrient-rich areas of the open sea, S.W. Chisholm and F.M.M. Morel, editors, *Limnol. Oceanogr.*, **36** (in press).
- Murray J.W., J.N. Downs, S. Strom, C.-L. Wei and H.W. Jannasch (1989). Nutrient assimilation, export production and ²³⁴Th scavenging in the eastern equatorial Pacific. *Deep-Sea Res.*, **36**, 1471-1489.
- Olson R.J. (1980). Nitrate and ammonium uptake in Antarctic waters. *Limnol. Oceanogr.*, **25**, 1064-1074.
- Oudot C. (1989). O₂ and CO₂ balances approach for estimating biological production in the mixed layer of the tropical Atlantic Ocean (Guinea Dome area). *J. mar. Res.*, **47**, 385-409.
- Pisias N.G. and M. Lyle (1988). Eastern Equatorial Pacific: a prospectus for GOFs. Pacific Planning Report, *U.S. GOFs Plann. Rep.*, **9**, 47-60.
- Platt T., W.G. Harrison, M.R. Lewis, W.K.W. Li, S. Sathyendranath, R.E. Smith and A.F. Vesina (1989). Biological production of the oceans: the case for a consensus. *Mar. Ecol.-Prog. Ser.*, **52**, 77-88.
- Probyn T.A. (1988). Nitrogen utilization by phytoplankton in the Namibian upwelling region during an austral spring. *Deep-Sea Res.*, **35**, 1387-1404.
- Raimbault P. (1984). Influence of temperature on the transient response in nitrate uptake and reduction by four marine diatoms. *J. expl. mar. Biol. Ecol.*, **84**, 37-53.
- Reid J.L. Jr. (1962). On the circulation, phosphate-phosphorus content and zooplankton volumes in the upper part of the Pacific Ocean. *Limnol. Oceanogr.*, **7**, 287-306.
- Reid J.L. (1977). Some thoughts on the dependence of sound speed and the scattering layers upon ocean circulation, in: *Oceanic sound scattering prediction*, N.R. Andersen and B.J. Zahuranec, editors, Plenum Press, New York, 15-64.
- Ryther J.H., D.W. Menzel, E.M. Hulburt, C.J. Lorenzen and N. Corwin (1971). The production and utilization of organic matter in the Peru coastal current. *Investigación pesq., Barcelona*, **35**, 43-59.
- Scripps Institution of Oceanography, University of California (1960). Physical, chemical and biological data Costa Rica Dome cruise. *SIO Ref. Rep.*, **80-20**, 32 pp.
- Simon V. (1986). Le système assimilation-régénération des sels nutritifs dans les eaux superficielles de l'océan Austral. *Mar. Biol.*, **92**, 431-442.
- Simpson J.J. and A. Zirino (1980). Biological control of pH in the Peruvian coastal upwelling area. *Deep-Sea Res.*, **27**, 733-743.

- Smith W.O. Jr. and D.M. Nelson (1990). Phytoplankton growth and new production in the Weddell Sea marginal ice zone in the austral spring and autumn. *Limnol. Oceanogr.*, **35**, 809-821.
- Sournia A. (1974). Circadian periodicities in natural populations of marine phytoplankton. *Adv. mar. Biol.*, **12**, 325-389.
- Strickland J.D.H., R.W. Eppley and B.R. de Mendiola (1969). Phytoplankton populations, nutrients, and photosynthesis in Peruvian coastal waters. *Boln Inst. Mar Perú*, **2**, 4-45.
- Thomas W.H. (1972). Nutrient inversions in the southeastern tropical Pacific Ocean. *Fish. Bull.*, **70**, 929-932.
- Thomas W.H. (1979). Anomalous nutrient-chlorophyll interrelationships in the offshore eastern tropical Pacific Ocean. *J. mar. Res.*, **37**, 327-335.
- Traganza E.D., V.M. Silva, D.M. Austin, W.L. Hanson and S.H. Bronsink (1983). Nutrient mapping and recurrence of coastal upwelling centers by satellite remote sensing: its implication to primary production and the sediment record, in: *Coastal upwelling. Its sediment record. Part A*, E. Suess and J. Thiede, editors, Plenum Press, 61-83.
- Voituriez B. and A. Herbland (1984). Signification de la relation nitrate/température dans l'upwelling équatorial du golfe de Guinée. *Oceanologica Acta*, **7**, 2, 169-174.
- Voituriez B., A. Herbland and R. Le Borgne (1982). L'upwelling équatorial de l'Atlantique Est pendant l'Expérience Météorologique Mondiale (PEMG). *Oceanologica Acta*, **5**, 3, 301-314.
- Walsh J.J. (1976). Herbivory as a factor in patterns of nutrient utilization in the sea. *Limnol. Oceanogr.*, **21**, 1-13.
- Walsh J.J., T.E. Whitley, W.E. Esaias, R.L. Smith, S.A. Huntsman, H. Santander and B. R. de Mendiola (1980). The spawning habitat of the Peruvian anchovy, *Engraulis ringens*. *Deep-Sea Res.*, **27**, 1-27.
- Wheeler P.A. and S.A. Kokkinakis (1990). Ammonium recycling limits nitrate use in the oceanic subarctic Pacific. *Limnol. Oceanogr.*, **35**, 1267-1278.
- Wyrski K. (1964). Upwelling in the Costa Rica Dome. *Fish. Bull.*, **63**, 355-372.
- Young R.W., K.L. Carder, P.R. Betzer, D.K. Costello, R.A. Duce, G.R. DiTullio, N.W. Tindale, E.A. Laws, Uematsu M., J.T. Merrill and R.A. Feely (1991). Atmospheric iron inputs and primary productivity: phytoplankton responses in the North Pacific. *Global biogeochem. Cycles*, **5**, 119-134.