

# Primary Production and Nutrient Fluxes in the Gulf of Biscay

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## Abstract.

Since the roles of continental shelves and coastal areas in the global biochemical carbon cycle are nowadays a leading concern in oceanographic research programmes, this study aims to define the specific effect of nutrients on the onset and development of the phytoplankton bloom at the ocean margins. Comparison experiments of the carbon, nitrogen and phosphorus assimilation rates were carried out from 1989 to 1991 in the English Channel and the Gulf of Biscay. New production were obtained from the traditional approach using *f*-ratio values, *i.e.* the ratios of directly measured nitrate to carbon uptakes and/or the ratios of nitrate to nitrate plus ammonium uptakes. Values of *f* agree well on the shelf, slope and deep basin regions of the Gulf of Biscay but are most likely overestimated in the coastal zone of the English Channel. The C/N/P uptake ratios exhibit, furthermore, great spatial variability that can reflect variations in the nutrient status of phytoplankton during its growth.

## 1.- Introduction.

The measurement of <sup>14</sup>C primary production alone is generally insufficient to assess the capacity of phytoplankton to support production at higher levels in the food web. This shortcoming and the need to understand the processes shunting transfer and behaviour of organic matter and the pelagic food web led to the introduction and development of the concepts of "new" and "regenerated" production. Their difference is based on the partitioning of primary production according to the nitrogen source (Dugdale and Goering, 1967). New production is the fraction of autotrophic production sustained by an external input of N-nutrients, mainly nitrate, while regenerated production refers to the uptake of *in situ* recycled nutrients, mostly ammonium and urea. Both ecological categories are not strictly separated in nature, but confine the frame for an

adequate understanding of the oceanic productivity (Goldman, 1988). The relative contributions of new and regenerated nitrogen to primary production are commonly estimated by the so-called *f*-ratio, *i.e.* the ratio of  $^{15}\text{N}$ -nitrate to  $^{14}\text{C}$  carbon uptakes (Eppley, 1989). A similar and almost equivalent expression uses the sum of nitrate and ammonium based production in stead of the  $^{14}\text{C}$  primary production. This second equation refers to an open ocean system, where nitrate is the main allochthonous nitrogen source and ammonium the main autochthonous one. It should be pointed out, however, that while new production is usually supported by nitrate, the basic distinction is between nitrogen supplied by local photic zone regeneration and that supplied from elsewhere. For instance, near sewage outfall, considerable new production could be supported by ammonium (Eppley *et al.*, 1979), while in coastal and shelf regions, depending on the rate of nitrification, a significant part of the recycled nitrogen may be released as nitrate + nitrite and not as ammonium (Wollast, 1993). Therefore, *f*-ratio expressions may vary according to each situation or context (Harrison *et al.*, 1987; Knauer, 1993).

There are at least four general methods of measuring new production (Eppley, 1989; Knauer, 1993): (a) sediment traps at the bottom of the photic zone, (b) incubation experiments for assessing nitrate and carbon dioxide assimilation rates, (c) nutrient, oxygen, carbon dioxide and tracer gas distributions in the context of circulation models, and (d) the disequilibrium ratio of dissolved  $^{234}\text{Thorium}/^{238}\text{Uranium}$ . Besides incubation measurements, the increasing number of literature concerning the  $^{15}\text{N}$  methodology, updated in a review by Harrison (1983), gives evidence on the present interest of stable isotope techniques. On the other hand, the use of radioactive phosphorus ( $^{32}\text{P}$ ) on natural marine samples has also shown to provide easy measurements of the regenerated production by isotopic dilution techniques (Sorokin, 1985; Veldhuis *et al.*, 1991). Unlike nitrogen studies, use of radioactive phosphorus (carrier-free) may be less subject to methodological problems related to the addition of large amounts of stable isotopes and the analytical difficulties in measuring low ambient concentrations of substrate such as ammonia. Furthermore, since there is a close relationship between nitrogen and phosphorus in the production of organic matter (Codispoti, 1989), combined studies of both nitrogen and phosphorus assimilation rates may lead to the understanding of the role of these nutrients in the regulation of the carbon cycle.

In the present paper, short-time measurements of  $^{15}\text{N}$ ,  $^{32}\text{P}$  and  $^{14}\text{C}$  uptake rates by phytoplankton are used to illustrate the concepts of new and regenerated production in the Gulf of Biscay. The area, investigated during September 89, July 90 and June 91 in the framework of the Belgian Impulse Programme Global Change, allows the sampling in shelf, slope and deep basin regions and, therefore, presents a potential for the evaluation of exchanges at the ocean

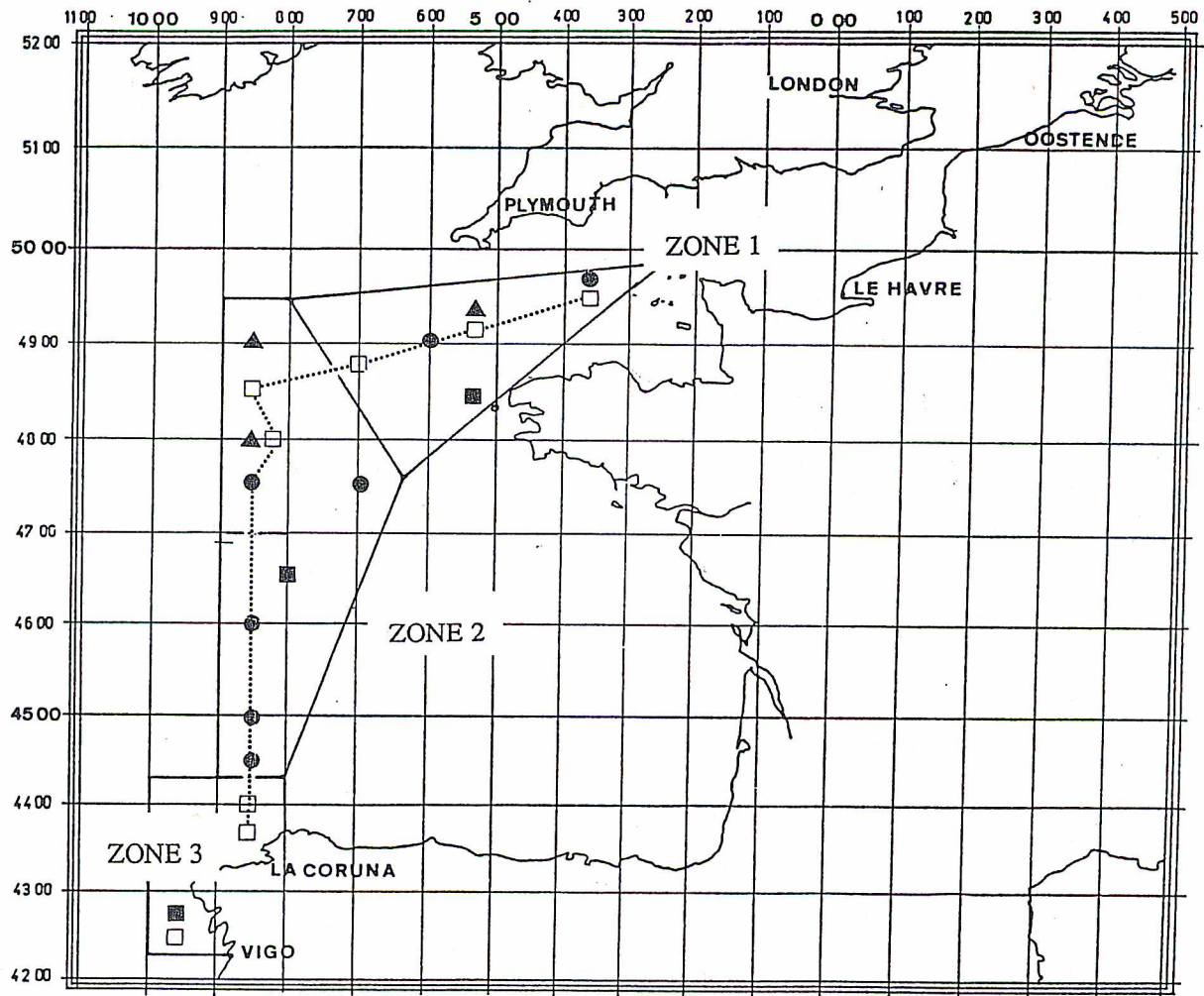


Fig. 1.— Cruise track (□) and location of the sampling stations during September 89, July 90 and June 91: (●)  $^{14}\text{C}$ , (▲)  $^{15}\text{N}$ ,  $^{14}\text{C}$  and (■)  $^{32}\text{P}$ ,  $^{15}\text{N}$ ,  $^{14}\text{C}$ .

margins (figure 1). In the first section, a comparison of the nitrogen (nitrate and ammonium) and carbon uptake regimes in different functional subunits of the Gulf of Biscay, based on chlorophyll *a* and nutrient distribution patterns, is presented. The second section is mainly devoted to the problematic aspect of the measurements of phosphorus incorporation.

## 2.- Methods.

### 2.1.- C, N, P assimilation experiments.

For the carbon and phosphorus assimilation rates, samples were incubated in 600 ml flasks, spiked respectively with 0.6 ( $^{14}\text{C}$ ) or 3.3 ( $^{32}\text{P}$ ) Mbq. After incubation, samples were filtered using GF/F glass-fibre filters and the particulates were analyzed for  $^{14}\text{C}$  or  $^{32}\text{P}$  by liquid scintillation. The incubations for the nitrogen assimilation rates were started immediately after the addition of  $^{15}\text{N}$  labelled nitrate or ammonium (99%  $^{15}\text{N}$ ) to samples in 2.7 l polycarbonate bottles. Spike solutions increased the ambient concentrations by about 10%. The particulate material was collected using Whatman GF/F glass fiber filters and the particulate nitrogen was subsequently converted to  $\text{N}_2$  by a modified Dumas method according to Goeyens *et al.* (1985). The  $^{14}\text{N}/^{15}\text{N}$  ratio was measured by emission spectrometry.

### 2.2.- Nutrient analyses.

The analysis of nutrients was carried out immediately on board after sampling. Ammonium was determined according to the manual method of Koroleff (1969) with a detection limit of  $\pm 0.05 \mu\text{M}$ . Nitrate, nitrite and phosphate were measured using the automated method described by Elskens and Elskens (1989) with detection limits of  $\pm 0.1 \mu\text{M}$  for  $\text{NO}_3$  and  $\text{PO}_4$ .

### 2.3.- Calculation of productivity, nutrient stock concentrations, *f*-ratios and relative preference index.

A simple model, considering the evolution of light intensity, nutrient concentrations and the depth of the mixed layer was used to estimate the primary production measured by the  $^{14}\text{C}$  and  $^{15}\text{N}$  isotopic methods, in terms of  $\text{mg}(\text{C or N})\text{m}^{-2}\text{d}^{-1}$ . Mean values for the global solar irradiance and the extinction coefficient were obtained from quantametric profiles performed during the different cruises according to Parsons *et al.* (1984). The influence of nutrients was taken into account by carrying out incubation experiments at at least two different depths (-10 and -40 m). Assimilation rates of nitrogen and carbon were corrected with respect to the mean value of the light intensity at these depths using field calibration curves of productivity *versus* light intensity. Values of primary production, chlorophyll *a*, and nutrient concentrations were finally integrated over the thickness of the mixed layer, whose depth was determined from the density data.

Two different expressions of the *f*-ratio have been used throughout this study. The first one is based upon results obtained from both  $^{15}\text{NO}_3$  and  $^{14}\text{C}$  incubation experiments according to the definition of Eppley (1989). It assumes

Table 1  
 Primary production in the Gulf of Biscay.  $\rho$  represent the absolute uptake rate in  $\text{mM h}^{-1}$

Subunits	Primary production		f-ratios		RPI <sub>(NH<sub>4</sub>)</sub> $\frac{\rho_{\text{NH}_4}}{\text{NH}_4 / \sum \text{N}_{\text{inorg.}}}$ (3)	RPI <sub>(NO<sub>3</sub>)</sub> $\frac{\rho_{\text{NO}_3}}{\text{NO}_3 / \sum \text{N}_{\text{inorg.}}}$ (4)
	$\text{mg C m}^2 \text{ d}^{-1}$	$\text{mg N m}^2 \text{ d}^{-1}$	$\frac{\rho_{\text{NO}_3} * 6.6}{\rho_{^{14}\text{C}}}$ (1)	$\frac{\rho_{\text{NO}_3}}{\rho_{\text{NO}_3} + \rho_{\text{NH}_4}}$ (2)		
Zone 1	500 - 900 816 ± 117	95 - 187 140 ± 70	0.56	0.78 - 0.82 0.80	1.5 - 2.3 1.9	0.9 - 1.0 0.95
Zone 2	47 - 220 123 ± 54	17 - 135 76 ± 58	0.12 - 0.95 0.46	0.12 - 0.95 0.48	1.0 - 7.8 3.5	0.8 - 1.4 1.0
Zone 3	2100	744	> 1	0.93	0.9	0.9

a constant Redfield ratio of 6.6 by atoms for the C/N uptake rates (Eqn. 1, Table 1). The second one, defined as the ratio of nitrate to the total inorganic nitrogen transport rates (Eqn. 2, Table 1), provides a better insight regarding the nitrogen uptake regime (Eppley and Peterson, 1979). As will be discussed later, the comparison of both  $f$ -ratio values allow us to derive an estimate of the recycled production supplied by the dissolved organic nitrogen which is not measured in this study.  $f$ -ratios inform on the relative importance of the nitrogen source for the phytoplankton nutrition, the preference of the phytoplankton for one nutrient or another is indicated by the relative preference index RPI (McCarthy *et al.*, 1977). This index is defined as the ratio of the  $f$  value for the particular nutrient to its concentration fraction (Eqns 3 and 4, Table 1). A RPI value greater than 1 indicates preference, smaller than 1 rejection, and equal to 1 reflects that utilization of the nutrient is equitable with its availability.

#### 2.4.- Nitrate depletions.

Summer stratification in the upper layer is usually characterized by seasonally warmed and high salinity surface waters with low amounts of nutrients. The integrated differences, over the thickness of the mixed layer, between the winter nitrate level and the *in situ* observed concentrations are defined as depletions. The term depletion signifies in this context the amount of nitrate removed from the water column during the ongoing growth season and leads to an estimate of the seasonally integrated new production. The winter reference levels of nitrate in the surface waters were taken from Morin *et al.* (1991). It should be stated that this winter value is usually in good agreement with the *in situ* value measured at the base of the photic zone.

### 3.- Carbon and nitrogen assimilation.

During September 1989, vertical distributions of salinity and dissolved inorganic nitrogen from a north to south transect (September 1989) along 8°30' W demonstrated the existence of a central high salinity lens with significantly decreased surface nitrate and ammonium concentrations, which extended approximately from 48° N to 45° N (figure 2). The potential temperature data shows that the northern border agrees with the summer thermal front of Ushant (Pingree *et al.*, 1975) and follows almost the outline of the haline fronts identified by Morin *et al.* (1991). The origin of these haline fronts resides mainly in the outflow, towards the English Channel, of the river Loire on the South Brittany shelf. In the winter, a conservative mixing is observed between the offshore waters with low nutrient concentrations and the coastal waters enriched by the river inputs (Morin *et al.*, 1991). To the south, the high salinity and low nitrogen surface

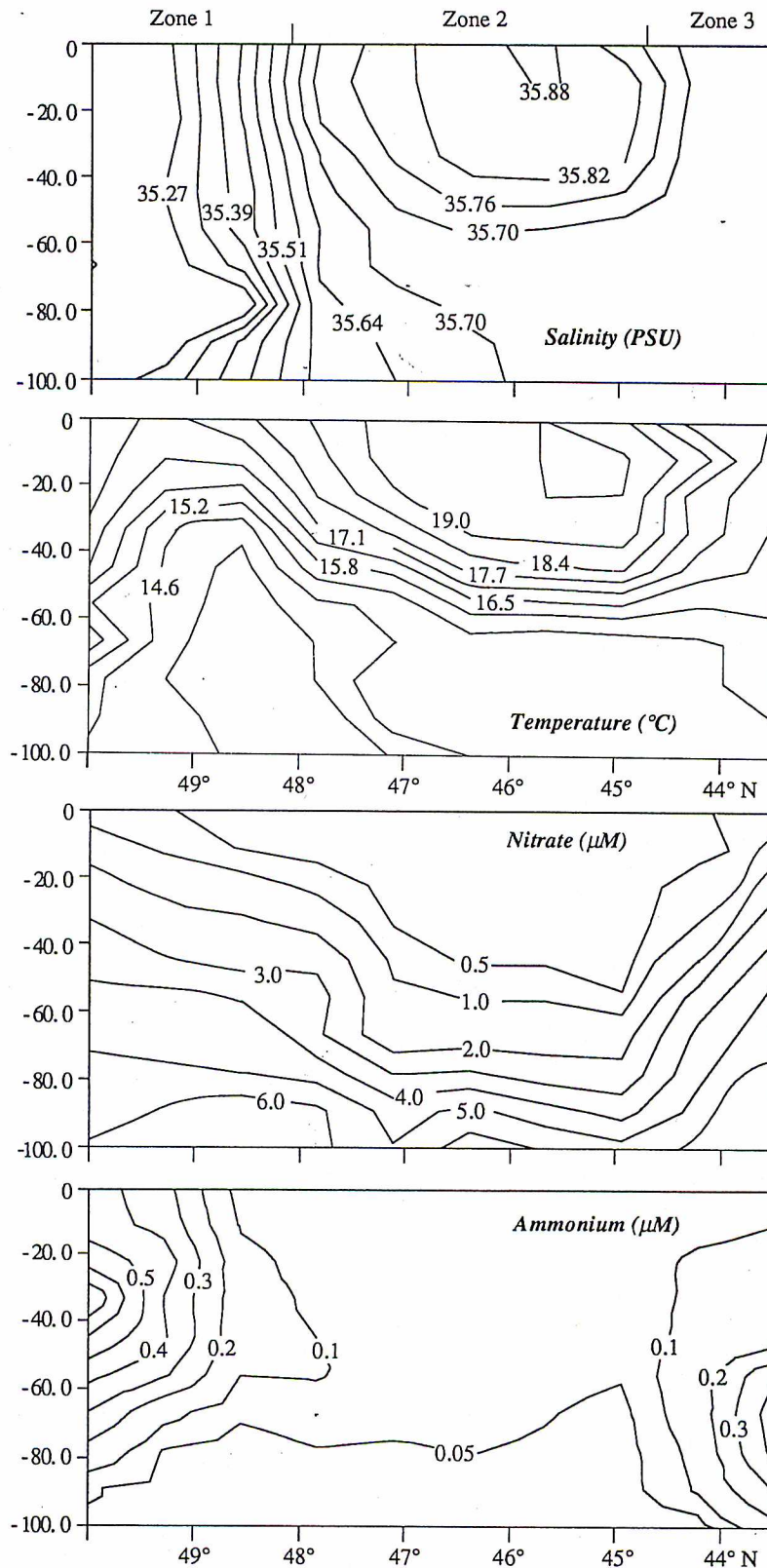


Fig. 2.— Vertical distributions of salinity (psu), potential temperature (°C), nitrate ( $\mu\text{M}$ ) and ammonium ( $\mu\text{M}$ ) along a north to south transect 8°30' W (Global Change Cruise September 1989). The cruise track is illustrated in figure 1.

water lens is confined by intense upwelling processes occurring in the vicinity of the Northern Spanish coast.

During July 1990 and June 1991, similar spatial variabilities were pointed out for the distribution of nutrients, salinity and temperature. Therefore, the Gulf of Biscay was divided into three different functional subunits according to the scheme of figure 1.

Zone 1 represents stations located at the Channel entrance on both sides of the Ushant front. In the summer, the vertical distribution of chlorophyll *a* shows a broader maximum with stock concentrations usually exceeding  $60 \text{ mg m}^{-2}$ . Primary production measurements average  $816 \pm 177 \text{ mg C m}^{-2} \text{ d}^{-1}$  and  $140 \pm 70 \text{ mg N m}^{-2} \text{ d}^{-1}$ , that classify zone 1 among eutrophic ecosystems (Table 1). The maximum value remains lower than that observed in the Bay of Brest ( $1200 \text{ mg C m}^{-2} \text{ d}^{-1}$ , Quéguinier and Tréguer, 1986), but is close to the estimated yearly average production for continental shelves ( $800 \text{ mg C m}^{-2} \text{ d}^{-1}$ , Wollast, 1991). In the summer, nitrate was the main source of nitrogen production, although the relative preference index (RPI) showed that ammonium is apparently the preferred nutrient for phytoplankton. It should be noted that our *f*-ratios for the uptake of inorganic nitrogen (0.78–0.82, Eqn. 2, Table 1) are high in comparison with those reported for coastal waters (0.30–0.46) by Eppley and Peterson (1979). On the other hand, they are in good agreement with those (0.70–0.80) measured in the Bay of Brest during the spring bloom (Dauchez *et al.*, 1991). Such high values can be related to relatively high inputs of new nitrogen (nitrate) in zone 1. However, one cannot exclude the possibility that dissolved organic nitrogen (DON) represents a significant fraction of the total nitrogen assimilation. It has been reported that urea uptake accounts on an annual basis for about 25% of the total nitrogen utilization in Californian coastal waters (McCarthy *et al.*, 1977) and supplies approximately 27% of the nitrogen requirement for the surface water community in the Southern Ocean during autumn (Probyn and Painting, 1985). Therefore, if urea uptake occurs in similar proportion in the Channel entrance area, our *f*-ratio would be lowered to  $\pm 0.6$ . This value is close to the mean annual value of  $\pm 0.5$  documented for the coastal regions and upwelling areas (Paasche, 1988) and even closer to the *f*-ratio of 0.58 calculated from the nitrogen and carbon assimilation experiments (Eqn. 1, Table 1). From these results and the comparison of both *f*-ratio values, it is suggested that about 58, 20 and 22% of the nitrogen production are supplied by nitrate, ammonium and DON, respectively (see also figure 3).

The inorganic nitrogen stock concentrations in the mixed layer remain in the summer close to  $2.6 \pm 0.7 \text{ g N m}^{-2}$ , so that any limitation of the phytoplankton production by this nutrient can probably be ruled out in this zone. For July 1990 and September 1989, the calculated nitrate depletions range from 2.3 to  $3.9 \text{ mg N m}^{-2}$ . Assuming that the growth season begins in March and neglecting



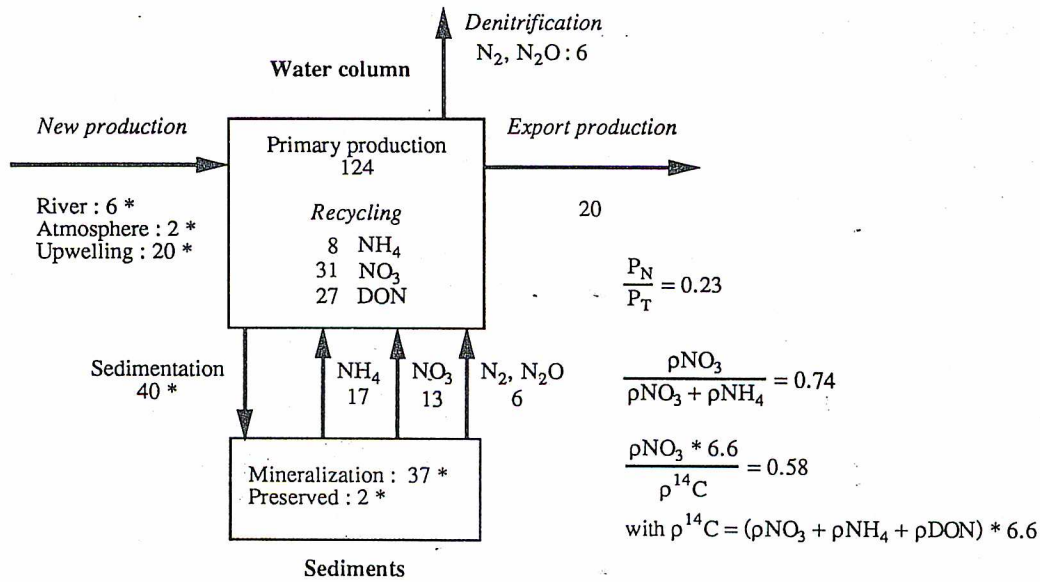


Fig. 3.— Tentative N-budget for zone 1. Fluxes are given in  $\text{mg N m}^{-2}\text{d}^{-1}$ . The incoming fluxes (\*) at the boundaries of the system are taken from Wollast (1993).

effects such as nitrification and turbulent diffusion through the mixed layer, a daily nitrate deficit of  $21 \pm 5 \text{ mg N m}^{-2} \text{ d}^{-1}$  was calculated for the different sampling periods. On the basis of a Redfield ratio of 6.6 by atoms, the corresponding new production rate of  $118 \text{ mg C m}^{-2} \text{ d}^{-1}$  represents less than 15% of the instantaneous primary production measurements in zone 1 and, as a consequence, is significantly lower than the value predicted by the  $f$ -ratio of 0.58. This suggests that primary production in the Channel entrance has to be sustained by continuous inputs of new or recycled nitrate at the boundaries of the system. Considering the average yearly fluxes of nitrogen in the coastal zone calculated by Wollast (1993) from the continental, benthic, atmospheric and oceanic sources and combining these data to the measurements of primary production in zone 1, a tentative N-budget was established. According to the fluxes presented in figure 3, new production would account for about 25% of the total primary production, the remaining 75% being supported by recycling processes. Approximately 50% would be supplied by recycled nitrogen in the water column and 25% by the sediments. In the latter case, since most of the remineralization occurs close to the water-sediment interface and as the nutrients released are rapidly available for photosynthesis, it seems reasonable to incorporate these fluxes, for both nitrate and ammonium, in the evaluation of the regenerated production and not as an external source of nutrients (Jickells, 1991). The nitrogen speciation was calculated to fit the experimental values for both expressions of the  $f$ -ratios (figure 3). The recycled amounts of nitrate and ammonium in the water column were then estimated by subtraction knowing the incoming fluxes at the boundaries of the system (Wollast, 1993). It is interesting to note that the value obtained for nitrate, using this approach, is consistent

with the mean annual rate of nitrification of  $12 \text{ g N m}^{-2} \text{ y}^{-1}$  given for the coastal zone by Henriksen and Kemp (1988). Moreover, the exported production flux, required to maintain the system at steady state, is almost equal to the rate of new production. A distinctive property of this cycle, as compared to the open ocean, is the intensive recycling of nitrogen derived from the sediments. In this study a daily flux of  $30 \text{ mg N m}^{-2} \text{ d}^{-1}$  was used according to the value selected by Wollast (1993). It should be stressed that this flux may be overestimated in regions where the water column is seasonally stratified. Since most of the stations in zone 1 appear to be in regions where summer stratification occurs, exchanges between the superficial and bottom waters could be reduced because of the presence of the thermocline. Nevertheless, to balance our N-budget in zone 1, as the benthic flux decreases, primary production has essentially to be sustained by larger inputs of new nitrogen at the boundaries of the system. Under extreme conditions, assuming a benthic flux equal to zero and keeping the remineralization rate in the water column at  $66 \text{ mg N m}^{-2} \text{ d}^{-1}$ , new production would then represent  $58 \text{ mg N m}^{-2} \text{ d}^{-1}$ , *i.e.* practically 46% of the total production. Since the total flux of nitrate in the system is  $72 \text{ mg N m}^{-2} \text{ d}^{-1}$  ( $P_T \times 0.58$ , figure 3), the amount of nitrate recycled in the water column by nitrification is  $14 \text{ mg N m}^{-2} \text{ d}^{-1}$ . Although this N-budget is rather speculative, it illustrates the complexity of the nitrogen cycle in the coastal zones. It suggests, furthermore, that with a benthic flux varying seasonally between 0 and  $30 \text{ mg N m}^{-2} \text{ d}^{-1}$ , new production would represent 46 to 23% of the total primary production in zone 1. The most important conclusion is certainly that in both situations, the regenerated production is underestimated by use of classical expressions of the *f*-ratio (Eqns 1 and 2, Table 1) and that the importance of the discrepancy increases depending on the nitrification rate.

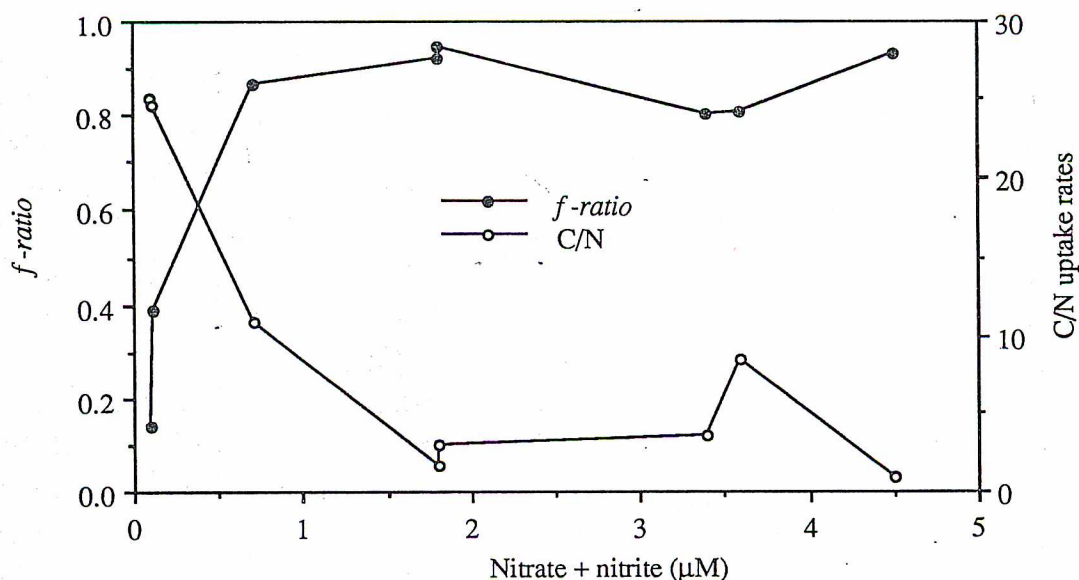


Fig. 4.— Evolution of the *f*-ratio (Eq. 2) and the C/N uptake rates *versus* nitrate concentrations for each incubation depth in zone 2. Combined data from July 1990 and June 1991.

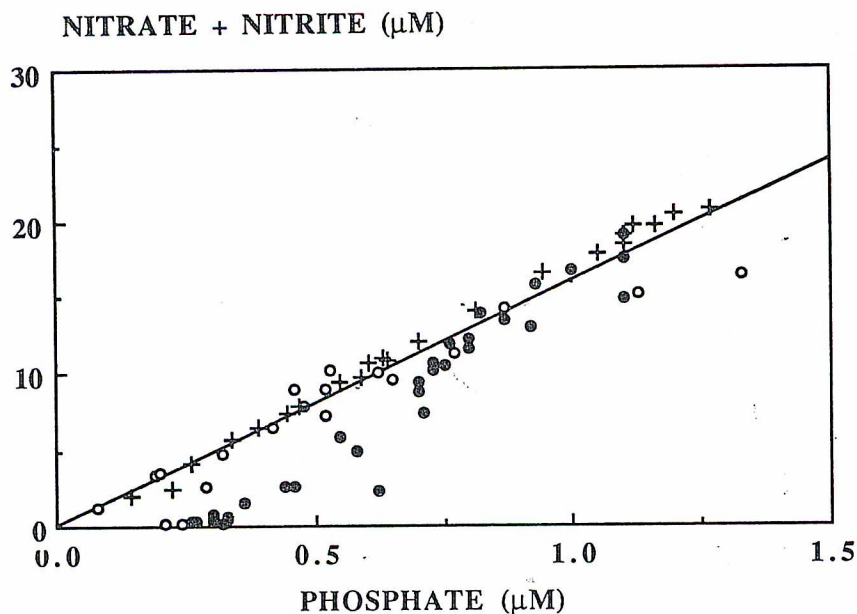


Fig. 5.— Evolution of nitrate + nitrite *versus* phosphate concentrations in zone 2: (●) September 89, (○) July 90, (+) October 92 and (—) Redfield ratio.

Zone 2 groups stations located in the vicinity of the margin on the shelf, slope and deep basin region. In the summer, it appears as a typical oligotrophic system with an average production of  $123 \pm 54 \text{ mg C m}^{-2} \text{ d}^{-1}$  (Table 1). At these stations, extremes in concentrations and gradients occur within shallow subsurface depth intervals, located between 30 and 70 m (figure 2). Chlorophyll *a* and  $\text{O}_2$  maxima are overlapping in the 60 to 65 m intervals, located just above the thermocline, in the nutricline. Stock concentrations of chlorophyll *a* average at  $20 \pm 8 \text{ mg m}^{-2}$ . Considerable fluctuations were observed for the nitrogen assimilation rates ( $17$  to  $135 \text{ mg N m}^{-2} \text{ d}^{-1}$ ) and the nitrogen uptake regime (*f*-ratios ranging from 0.1 to 0.9). Both of them were strongly influenced by the nutrient dynamics of the environment. The evolution of the *f*-ratio *versus* nitrate concentration shows clearly a system shift from new to regenerated production when the concentration of nitrate falls below  $1 \text{ } \mu\text{M}$  (figure 4). One should stress that the half-saturation constant for nitrate assimilation, is usually close to  $1 \text{ } \mu\text{M}$  (Collos and Slawyk, 1980). In September 1989, surface waters (above 100 m) typically showed a nitrogen deficit relative to the values predicted by the Redfield ratio N/P (16/1 by atoms) which applies for depths below 100 m (figure 5). Within the photic zone, extreme nitrogen to phosphate ratios can occur when either available P or N is exhausted, or is close to exhaustion. The tendency for a general low photic N/P ratio in most of the oceanic surface layers has been reported (Codispoti, 1989). Under N-limiting conditions, higher specific uptake rates of ammonium are found, but the absolute transport rates of total nitrogen decrease drastically. In these conditions, the C/N assimilation ratios reach a maximum of 20–25. Such high values are to be expected in nitrogen-limited environments

(Carpenter and Dunham, 1985) and have been reported in the Bay of Brest at the end of the spring bloom when the ambient concentration of nitrate fell below  $1.6 \mu\text{M}$  (Dauchez *et al.*, 1991). When nitrogenous nutrients are non-limiting, N-production essentially originates from new production and the C/N uptake ratios approach values close to the C/N composition of the particulate organic matter (figure 4). No significant differences are detected between the two expressions of the  $f$ -ratio (Table 1) suggesting that the contribution of DON is negligible. This requires, however, further investigation. The nitrogen budget calculation within zone 2 is much more difficult to establish because little information is available. Nevertheless, the results presented here suggest that, during spring, the ecosystem evolves from a first phase where new production predominates into a second one dominated by regenerated production. The relationship between productivities (in  $\text{mg C m}^{-2} \text{ d}^{-1}$ ), biomasses (Chl. *a* in  $\text{mg m}^{-2}$ ) and nutrient stock concentrations ( $\text{NO}_3$  and  $\text{NH}_4$  in  $\text{mg N m}^{-2}$ ) for the different sampling periods is illustrated in figure 6. On an average basis, the highest productivity and biomass are observed in July 1990 with a system running on new production ( $f$ -ratios  $> 0.5$ ). June 1991 is characterized by a system shift from new to regenerated production ( $f$ -ratios  $\leq 0.5$ ) and by the highest accumulation of ammonium, an indication of intensive heterotrophic activity. During these productive periods, the nitrate uptake rate amounts on average to  $50 \pm 20 \text{ mg N m}^{-2} \text{ d}^{-1}$  and the nitrate depletions, calculated as previously mentioned, range from 1.3 to  $3.7 \text{ g N m}^{-2}$  (average of  $2.7 \pm 0.9$ ). Assuming that the nitrate uptake rate remains constant during this time, the length of the new production period is estimated to about 60 days from the nitrate depletions to the uptake rate ratio. Since nitrate is almost totally exhausted in the surface water (0–20 m) at the end of the spring time, it can be assumed that the initiation of the phytoplankton bloom, in zone 2, would start in mid-April. As will be discussed later, this is consistent with the model of Morin *et al.* (1991) for the prediction of the growth season development on the Armorican shelf. During September 1989, the low biomass and productivity were paralleled with low inorganic nitrogen stocks (figure 6), but the decline in primary production has also to be related to the day length and light.

Zone 3 groups stations located in the vicinity of the Northern coastal area of Spain (figure 1). As already stated, this area is seasonally influenced by intense upwelling processes occurring along the Spanish and Portuguese Atlantic coast. Regarding the  $T, S$  diagram for near-shore stations (Vigo), sampled in July 1990, the water column can be divided into three different layers: (1) the photic zone (0–80 m) where the variation of the salinity gradient is possibly due to fresh water inputs from the rias Vigo and Arosa, (2) an intermediate layer (80–400 m) where temperature and salinity are closely related and vary more or less linearly with depth, and (3) a deep layer (400–800 m) characterized by an inversion of

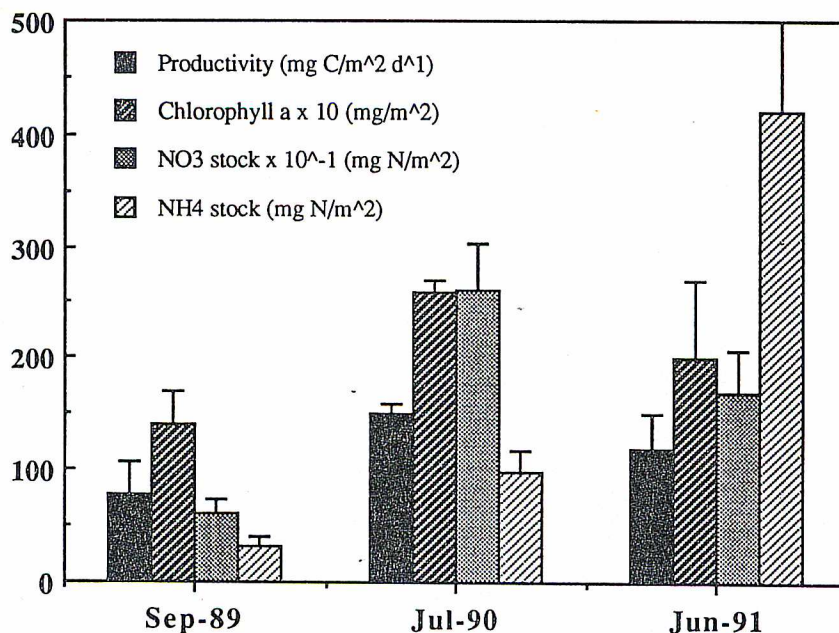


Fig. 6.— Mean values of productivity, biomass and nitrogen stock concentrations for the different sampling periods in zone 2.

the salinity and thermic gradients. At 800 m, salinity and temperature amount to 36‰ and 11.44°C respectively (figure 7a). The origin of this water mass probably resides from the outflow of Mediterranean waters through the Gibraltar Strait. Similar conclusions can be drawn from a plot of nutrients *versus* salinity. It should be stressed, however, that in July 1990, neither the thermocline, nor the nutricline were marked. A conservative behaviour of nutrients with temperature is found between 0 and 400 m (figure 7b). The N/P ratio remains almost constant on the whole profile of the water column and the slope of  $16.8 \pm 1$  is in agreement with data reported in the literature (figure 7c). Due to the upwelling processes, stock concentrations of nitrate in the surface water in July 1990 are extremely high, ranging from 2.9 to 4.5 mg N m<sup>-2</sup>. They support considerable biomass (136 mg Chl. *a* m<sup>-2</sup>) and productivity (2100 mg C m<sup>-2</sup> d<sup>-1</sup>). The *f*-ratio for the uptake of inorganic nitrogen amounts to 0.9 indicating a major importance of the nitrate assimilation (Table 1). However, its value calculated from the nitrogen and carbon assimilation experiments is greater than 1, because of a C/N uptake ratio of 3.1. This situation is not exceptional and has also been encountered in zone 2, when the nitrogen stock concentration was non-limiting (see Table 2). This suggests an active uptake of nitrogen by the heterotrophic community. The relative preference index (RPI) shows, furthermore, that both ammonium and nitrate are in fair equilibrium with their respective availabilities (Table 1).

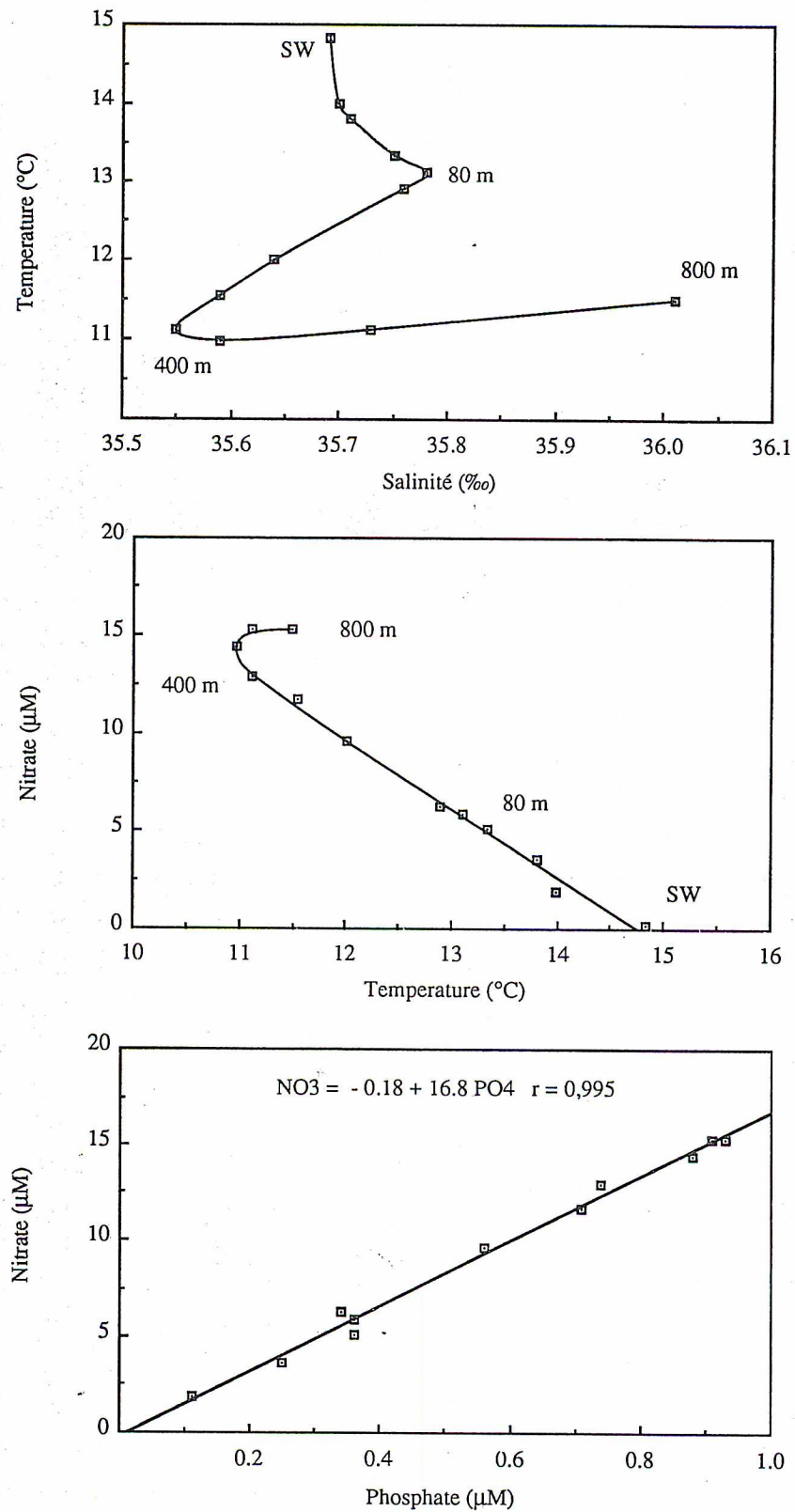


Fig. 7.— Hydrologic structure of the water column at a near-shore station (July 1990) in the upwelling region of the Northern coastal area of Spain: (A) T,S diagram, (B) and (C) variation of nitrate with temperature and phosphate.

Table 2  
C/N/P uptake rates in the Gulf of Biscay during July 90

	Depth (m)	Chl. <i>a</i> ( $\mu\text{g l}^{-1}$ )	$^{14}\text{C}$ uptake ( $\text{nmole l}^{-1}\text{h}^{-1}$ )	$^{15}\text{N}$ uptake ( $\text{nmole l}^{-1}\text{h}^{-1}$ )	$^{32}\text{P}$ uptake ( $\text{nmole l}^{-1}\text{h}^{-1}$ )	C/N	C/P	N/P
Zone 1 48°25 N - 05°21 W	-10	2.2	393	36	1.7	10.9	231	21
	-40	1.3	236	44	0.63	5.4	374	70
Zone 2 46°25 N - 08°00 W	-10	0.13	38	29	1.4	1.3	27	21
	-40	0.42	92	24	2.2	3.8	42	11
Zone 3 42°43 N - 09°18 W	-10	5	587	190	3.4	3.1	172	56

#### 4.- Phosphorus assimilation.

During July 1990, water samples collected in the offshore area (zone 2) were incubated under various conditions (figure 1). The uptake of  $^{32}\text{P}$  with time was followed under artificial light, dark and in the presence of sodium azide. Figure 8 shows that the cumulative uptake of  $^{32}\text{P}$  under constant light conditions increases more or less linearly with time. Furthermore, the rate of uptake after 30 hours reaches  $\pm 40\%$  which is extremely high, suggesting that this particular nutrient must be regenerated fairly rapidly in order to sustain the high rate of incorporation. Another interesting observation is that the uptake of phosphorus occurs also under dark conditions at a relatively high rate, although the pathway of this transfer is not yet clear. The azide sample indicates that there is a small amount of adsorption taking place. The high rate of uptake under dark conditions indicates that phytoplankton is able to make use of phosphorus during the night. Field measurements have shown that phytoplankton continues to synthesize protein during the night at the expense of intracellular low molecular weight compounds, polysaccharides and lipids produced during the day (Morris *et al.*, 1981; Cuhel *et al.*, 1984). It is thus possible that phytoplankton may utilize phosphate to produce ATP and DNA in the absence of light. Alternatively, the high uptake of phosphate can also be attributed to bacterial activity.

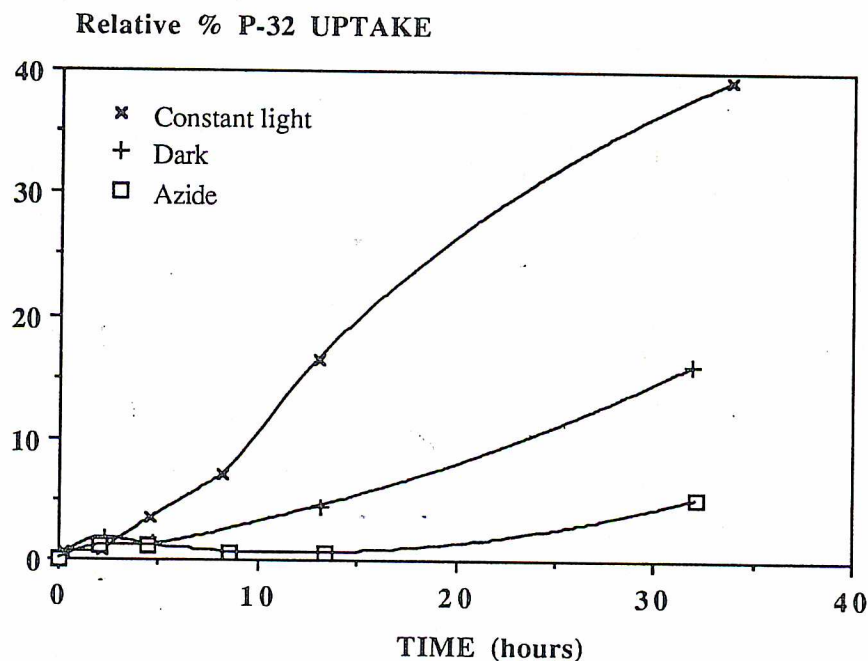


Fig. 8.- Relative uptake of  $^{32}\text{P}$  under artificial light, dark and in the presence of sodium azide

During June 1991, the influence of the bacterial activity on the uptake of phosphorus has been investigated. The method involves the use of antibiotics such as Penicillin-G and Streptomycin sulfate. Penicillin is known to inhibit



synthesis of bacterial cell wall and Streptomycin inhibits 30S ribosome function (Stanier *et al.*, 1976). Two series of samples were incubated under constant artificial light conditions during 24 hours with various amount of  $^{32}\text{P}$  added. One series was performed in the presence of antibiotics to inhibit the bacterial activity. The effect of antibiotic is demonstrated in figure 9, where the radioactivity in the solid phase is plotted against that in the dissolved phase. It is obvious that the addition of antibiotics lowered the percentage of  $^{32}\text{P}$  incorporation by about 7%. Parallel experiments were also conducted in the presence of sodium azide. The results show that the uptake due to non-biological action never exceeds 2%.

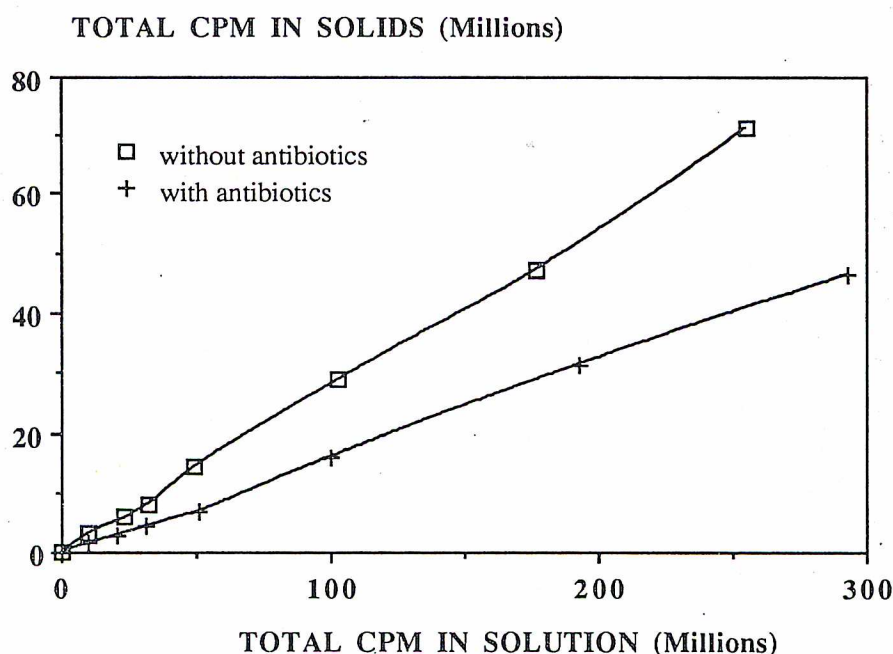


Fig. 9.— Comparison of  $^{32}\text{P}$  under artificial light conditions in samples with and without antibiotics

Knowing the phosphate concentration of the sample, the absolute rate of phosphorus uptake has been calculated (Table 2). It is noteworthy that marine phytoplankton has a C/P ratio of about 106/1 and a N/P ratio of about 16/1. The results obtained in this study indicate that C/P uptake rates varies from 42 to 374 and N/P from 11 to 70. However, we are not able at present to evaluate quantitatively the role of bacteria in the uptake and regeneration of phosphorus. It is obvious that in the future, we have to determine the rates of transfer of phosphorus through various biological pathways.

## 5.- Conclusions.

Because of its geographical extension and the diversity of its hydrologic structure, the Gulf of Biscay is an important area for the study of exchange processes at the ocean margins. Although there is a gradual decrease of primary production along a transect crossing the shelf edge from shallow to deep basin regions, spatial variation of primary production are best related to the outlines of the summer thermal front (Ushant front) which follows almost the haline fronts pointed out by Morin *et al.* (1991). Despite a difference of about two months between the sampling periods, it is interesting to note the similarities regarding the nitrogen and carbon assimilation rates, the fluctuations of the C/N uptake ratios and the *f*-ratio values observed in this study and those reported for the Bay of Brest by Dauchez *et al.* (1991). The apparent time-scale difference in the growth season maturity may be related to the establishment of a haline or thermal stratification which has been demonstrated to be important for the initiation of the phytoplankton development. Supporting this view, Morin *et al.* (1991) have shown that the nutrient assimilation and phytoplankton development take place sequentially on the Armorican shelf and that a time-lag of nearly three months may exist between the initiation of the bloom in South Brittany and in the central part of the continental shelf.

To summarize, the global trend of the studied ecosystem has shown the major importance of nitrate assimilation, a property which is in agreement with the observed high nitrate concentrations and the corresponding low ammonium availabilities. Nevertheless, on the shelf edge, the available nitrate stock was often depleted in the summer and, subsequently, primary production was fueled with recycled nitrogen, mainly ammonium. The C/N/P uptake ratios exhibit great spatial variability that can reflect variations in the nutrient status of phytoplankton during its growth. Interestingly, we note that the interval of fluctuations (minimum and maximum values) for C/N (1.3–10.9) and C/P (42–374) is of the same order of magnitude. This can be ascribed that to the fact that the uptake rates of nitrogen and phosphorus occur through various biological pathways including the auto- and heterotrophic communities. Large variations in C/P (47–115) have been reported previously for the Weddel-Scotia Seas by Tréguer *et al.* (1991). On the other hand the deviations of the N/P ratios from the Redfield one might suggest a temporary imbalance in the regeneration rate of both nutrients. Our data suggest that mineralization of phosphate might be higher than nitrogen as indicated by the general tendency for a low photic N/P ratio observed in the Gulf of Biscay. It is obvious that in the future, we have to determine the regeneration rates of both nitrogen and phosphorus through isotopic dilution techniques.

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