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Phytoplankton spring bloom of the Gironde plume waters in the Bay of Biscay: early phosphorus limitation and food-web consequences

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Abstract – During the spring 1995 (2–25 May), a cruise was carried on the *RV Poseidon* (Germany) on the continental shelf of the south Bay of Biscay. The objective was a comprehensive study of the planktonic food web within the Gironde plume waters. In these waters phosphate was present at very low concentrations (undetectable to < 0.1 µmol·L^{-1}), whereas nitrate, silicate and ammonium concentrations were much higher (several µmol·L^{-1} for nitrate and silicate and 0.5 to 1.0 µmol·L^{-1} for ammonium). The size distribution of the phytoplankton biomass (estimated from chlorophyll *a* measurements by high performance liquid chromatography) and primary production (measured by ^{14}C in situ method) showed a great proportion of small (40 to 70 % < 3 µm) and active autotrophic cells (growth rates estimated from 0.4 to 0.8 d^{-1} for the entire euphotic layer). Considering the very high values of NO_3-N:PO_4-P ratios and the high C:P and N:P ratios for the particulate organic matter, it is suggested that an early phosphorus depletion limits the spring bloom phytoplankton and particularly the new production (nitrate uptake coming from the Gironde waters).

From these results and other simultaneous observations on the heterotrophic processes (such as grazing of microzooplankton), we can conclude that the planktonic food web would be close to a maintenance system as defined by Platt et al. The possible generalisation of these results for each spring is discussed with respect to the scarcity of previous and reliable phosphate data. © Elsevier, Paris

phosphate / phytoplankton / limiting factor / estuarine water / coastal water

Résumé – Floraison phytoplanctonique printanière des eaux du panache de la Gironde : limitation par le phosphore et conséquences. Au cours du printemps 1995 (2–25 mai), une campagne océanographique a été réalisée à bord du *NO Poséidon* (Allemagne) sur le plateau continental Sud-Gascogne. L'objectif était l'étude de la structure et du fonctionnement du réseau trophique planctonique des eaux issues de l'estuaire de la Gironde. Les concentrations en phosphate dans ces eaux étaient extrêmement faibles (indécelable à moins de 0,1 µmol.L^{-1}) tandis que celles du nitrate, du silicate et de l'ammoniaque étaient beaucoup plus élevées (quelques µmol.L^{-1} pour le nitrate et le silicate et de 0,5 à 1 µmol.L^{-1} pour l'ammoniaque). La distribution des tailles du phytoplancton, aussi bien en biomasse qu'en production, révèle l'importance des petites formes (entre 40 et 70 % < 3 µm).

A la lumière des rapports NO_3-N:PO_4-P élevés et des rapports C:P et N:P de la matière organique particulaire également élevés, il est suggéré que le phosphore limite précocement le bloom phytoplanctonique printanier et plus particulièrement la production nouvelle qui s'établit à partir de la consommation du nitrate provenant des eaux de la Gironde.

Ces résultats et d'autres observations simultanées sur les activités hétérotrophes (comme le broutage du microzooplancton) conduisent à la conclusion que le réseau trophique planctonique tourne sur lui-même avec de faibles exportations. La généralisation éventuelle de ces résultats à l'ensemble des eaux du panache de la Gironde à chaque printemps est suggérée mais ne peut être affirmée compte tenu de la rareté des valeurs antérieures fiables de phosphate. © Elsevier, Paris

phosphate / phytoplancton / facteur limitant / estuaire / eau côtière

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1. INTRODUCTION

For many years, a current dogma in aquatic sciences was that marine and estuarine phytoplankton tend to be nitrogen limited, while freshwater phytoplankton tend to be phosphorus limited [18, 41, 43]. If the phosphorus limitation in freshwaters environments has been rigorously demonstrated at several hierarchical levels of system complexity (from algal cultures to whole lakes) a similar rigorous demonstration has not been achieved for marine waters [23].

On the contrary, it seems that an increasing number of studies conclude to nutrient limitation other than nitrogen in diverse marine ecosystems. For example, silicates can be the first nutrient to be exhausted in the upwelling [11, 24] and also in coastal zones where high nitrate inputs from agricultural activities can modify the nutrients ratios (i.e. decrease of Si:N ratio) which increases the risk of shift from diatoms to dinoflagellates algae [10]. Phosphorus limitation has also been noted in different marine systems: along the east coast of the United States, notably the Chesapeake Bay and Hudson River [34, 46]; at the outer edge of the estuary of two of China's largest rivers, the Changjiang and the Huanghe Rivers [22]; in the Mediterranean [3] and finally in an oligotrophic zone of the open central North Pacific [35] and north-eastern tropical Atlantic Ocean [37]. At last, iron has been hypothesised to be a factor limiting the phytoplankton standing crop in the ocean for decades [20] reported by Martin [31], but iron was recently the object of a vigorous debate about its role in the paradoxical phenomenon constituted by the large high-nutrient, low-chlorophyll systems (HNLC areas) in the open ocean [8, 9].

The objective of this study is to show some evidence that phosphorus is the first limiting nutrient of the phytoplankton spring bloom in the waters coming from the Gironde estuary on the continental shelf of south Bay of Biscay. Some observations on the phytoplankton (standing stock, size distribution, growth rates), and particulate organic matter composition associated with other observations on the heterotrophic processes (such as grazing of microzooplankton), lead to the conclusion that the planktonic food web would be a maintenance or regenerative system [36].

2. MATERIALS AND METHODS

The results have been obtained during spring 1995, on the *RV Poseidon* (Germany). The cruise (BIOMET, i.e. BIOlogy and METals) was designed to study the interaction between metal contaminants coming from the Gironde estuary (principally cadmium and arsenic) and the planktonic food web. The cruise consisted of two legs: the first leg (2 to 10 May) was a transect from the coast to the continental slope (seven stations) and during the second leg (18 to 25 May) we followed a drogue equipped with a particles trap (PPS 5), for 8 days (*figure 1*).

Temperature and salinity were measured with a CTD probe (Sea Bird, SBE-25). Seawater was sampled with Niskin bottles (8 L) washed with HCl at the beginning of each leg; samples for nutrients (NO_3-N, NO_2-N, NH_4-N, PO_4-P, and Si $(OH)_4$-Si) were deep frozen and analysed in the laboratory at the end of each leg, on an autoanalyser apparatus (Skalar), according to the standard methods [44]. For phosphate and ammonia, which are not exempt of problems with deep frozen samples [5], analyses were also achieved on board, immediately after sampling, on a spectrophotometer (Shimadzu UV 160) with a 10 cm optical path.

Particulate organic carbon (POC) and particulate organic nitrogen (PON) were measured by filtration of 550 mL of seawater on precombusted (400 °C during 8 h) 25 mm fibre glass filters (Whatman GFF). The filtration procedure was the same for particulate organic phosphorus (POP), except that the volume filtered was 1 100 mL and the filters (47 mm) were acid (HCl ~ 2 N) washed before being combusted. Immediately after filtration, all the filters were deep frozen; they were respectively analysed, within a delay of 1 month after the cruise, on a carbon and nitrogen analyser (Carlo Erba 1500) for POC and PON and after a persulphate oxidation procedure [32] for POP.

The total and size fractionated chlorophyll *a* (> 20, 3–20 and < 3 μm Chl*a*) have been respectively estimated by filtration of 500 mL of seawater on 47 mm Whatman GFF filters, 20 μm sieves and 3 μm Nuclepore polycarbonate filters. The filters were deep frozen and analysed at the end of the cruise both by high performance liquid chromatograhy (HPLC) [29] and a classical acidification fluorometric method [25]. Primary production was measured by the ^{14}C method, with in situ incubations from morning (8.00 hours) to evening (20.00 hours), in 320 mL polycarbonate bottles. The same size fractionation procedure as for chlorophyll *a* was achieved after incubation with the following partition of seawater volume: 100 mL for the unfiltered fraction, 120 mL for the < 20 μm fraction and 100 mL for the > 3 μm fraction. Low vacuum was applied (< 50 mmHg) in order to mini-

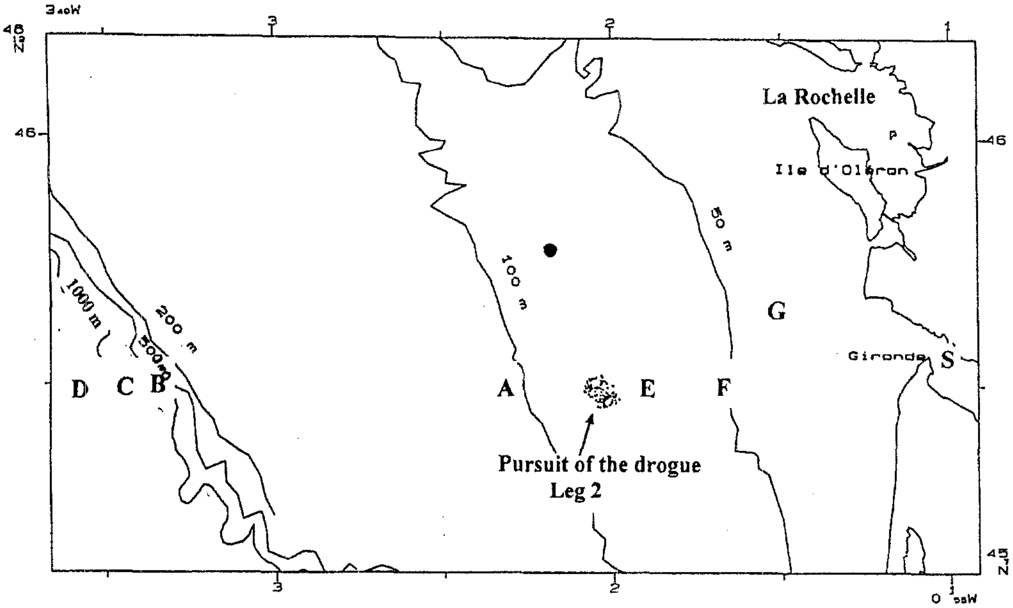

Figure 1. Position of the stations during the BIOMET cruise. Leg 1: Stations A to G and S, from 2 to 10 May 1995; leg 2: track of the drogue from 18 to 25 May 1995. The dark dot is the location of the study in spring 1994.

Figure 1. Position des stations pendant la campagne BIOMET. 1^{ere} partie: Stations A à G et S, du 2 au 10 mai 1995; 2^{eme} partie: Poursuite de la drogue du 18 au 25 mai 1995. Le point noir représente la localisation de l'étude en 1994.

mise the cell damage during filtration; the filters were placed into 7 mL scintillation vials, wetted with 200 µL of 1.0 N HCl, dried overnight at 55 °C, after which 5 mL of scintillation cocktail was added and the samples counted on board (Packard Instrument). Counting of the introduced radioactivity and immediate filtration for a blank substraction were also achieved.

The phytoplankton growth rates are rarely estimated in natural populations because they need the determination of the phytoplanktonic carbon (C_{phy}), which is not easy to assess. Thus, we calculated the 'assimilation numbers' (AN), defined as the ratio primary production/Chl*a* (ΔC/Chl*a*), which is commonly used as an index of growth rate even if we know that the C_{phy}/Chl*a* ratio may be highly variable from the top to the bottom of the euphotic layer or from one area to the other, depending on physiological adaptation and species composition [7 and references herein].

3. RESULTS

3.1. Hydrological context

The salinity distribution along the transect reveals the large extension of the Gironde plume at this period: salinity as low as 34.5 has been recorded on the slope (100 miles from the coast). The vertical distribution of the salinity during the second leg confirms clearly the importance of the plume, since a 25 m deep layer of salinity lower than 33.8 lies over the typical seawater mass of the Bay of Biscay (*figure 2*). The low salinity water was slightly warmer (13.5–14 °C) than the bottom water (12.3 °C) with a clear trend to increase on the last days of the cruise (*figure 2*).

3.2. Nutrients

At the same stations, nitrate, silicate and phosphate exhibited similar shapes in their vertical distribution however, drastic differences existed in the absolute values (*figure 3*): if nitrate and silicate concentrations were on the order of a few micromoles per liter in the mixed layer (mean values, respectively, 3.4, standard deviation [SD] = 0.54 and 1.9 $\mu mol \cdot L^{-1}$, SD = 0.39), for 32 samples, the phosphate concentrations were extremely low (mean value = 0.017 $\mu mol \cdot L^{-1}$, SD = 0.013, n = 32). The ammonia distribution was totally different: significant concentrations (mean value = 0.63 $\mu mol \cdot L^{-1}$, SD = 0.19, n = 32) were measured in the mixed layer with a frequent maxi-

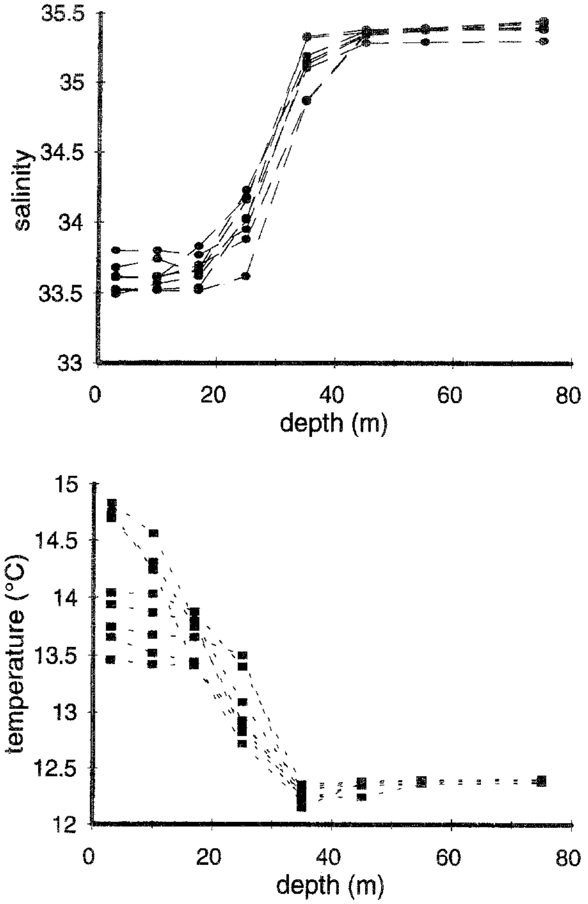

Figure 2. Vertical distribution of salinity and temperature at the eight stations from leg 2 (the depth of the bottom was 80–85 m).

Figure 2. Distribution verticale de la salinité et de la température aux 8 stations pendant le suivi de drogue sur les fonds de 80–85 m.

mum at the bottom of this layer, whereas values close or equal to zero occurred in the bottom layer.

It follows that the ratios N:P reached very high values in the plume waters (*figure 4*): NO_3-N:PO_4-P ratios were very variable in the 0–25 m layer, but the mean value of 196 (at/at, SD = 117, n = 32) showed clearly the excess of NO_3 versus PO_4 in that layer, whereas the ratios were close to 16 (mean value = 17.5, SD = 2.8, n = 24) in the marine water below.

Moreover, if we consider only ammonium, the reduced mineral form of nitrogen, we find again high values of N:P ratios in the mixed layer (mean value = 33.1, SD = 19.1, n = 32), with a maximum that can reach 80 near 25 m. By comparison, the ratios NO_3-N:$Si(OH)_4$-Si had a smooth vertical distribution (*figure 4*), with slightly higher values in the mixed layer than below (mean value = 2.0, SD = 0.55, n = 32 in the mixed layer versus 1.6, SD = 0.2, n = 24 in the bottom layer).

Along the transect, we again observe very high NO_3-N:PO_4-P ratios, from the coast to the 100 m line (stations S to A, *figure 1*), within the euphotic zone (*table I*). The highest mean value (161) was reached far from the coast (~ 50 miles), i.e. in the offshore part of the plume. Below, in the aphotic zone, the NO_3-N:PO_4-P ratios were of the same order of the Redfield value. Far offshore, on the slope (stations C and D, *figure 1*), the NO_3-N:PO_4-P ratios were much lower because of low nitrate concentrations in the mixed layer.

3.3. Particulate organic matter

The vertical distribution of particulate carbon, nitrogen and phosphorus show a clear maximum in the superficial plume waters (*figure 5*). Below 40 m, in the marine waters, the concentrations were low and uniform. The mean values and the particulate C:N:P ratios of each layer are reported in *table II*. In the mixed layer the C:N ratios were not significantly different from the classical Redfield value (6.5 versus 6.6 with a low variability: SD = 2.8). On the contrary, the C:P and N:P ratios are much higher (approximately twice the Redfield value) with a higher variability due to a greater scattering of the POP values.

3.4. Chlorophyll *a*, primary production, size distribution and 'growth rate' of phytoplankton

Chlorophyll *a* values were approximately uniform in the mixed layer (between 0.8 and 1.25 $\mu g \cdot L^{-1}$), with a regular decrease below (*figure 6*, top); primary production was maximum at the surface and decreased sharply below 10 m to reach values close to zero at 35 m, which was the depth of the bottom of the euphotic zone (the depth of 1 % of the surface PAR, measured just below the surface, varied between 30 and 35 m).

The size distribution of Chl*a* was characterised by the dominance of small forms: 50–70 % of the Chl*a* was contained in organisms smaller than 3 µm and 25–35 % in the 3–20 µm size fraction (*figure 6*, bottom). It means that only 5–15 % of the total Chl*a* was greater than 20 µm. The picture for the primary production was not very different (*figure 6*, bottom): even if the < 3 µm fraction was less pronounced (35–60 %), the 3–20 µm size class

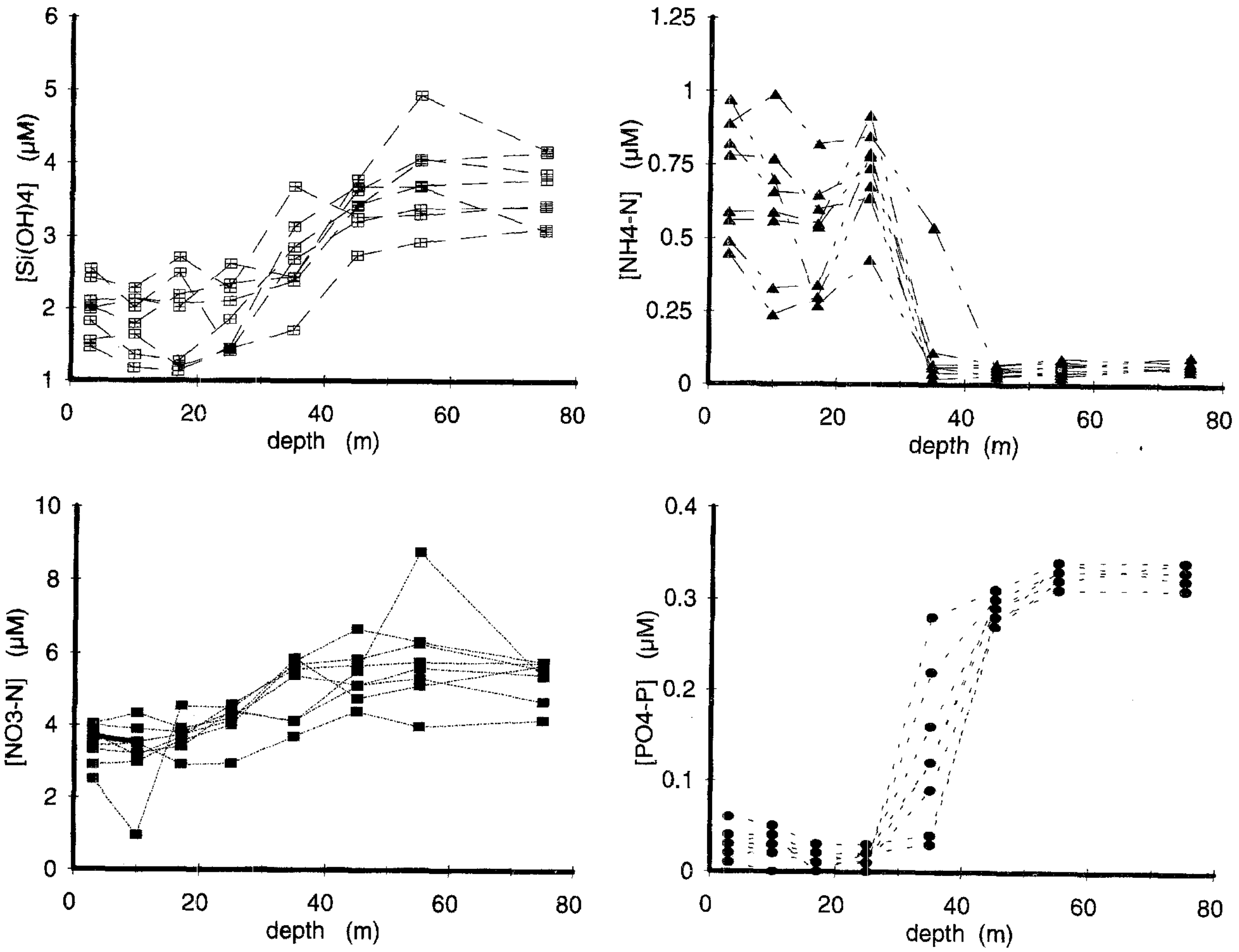

Figure 3. Vertical distribution of nutrients: nitrate, silicate, ammonium and phosphate at the same stations as *figure 2*.

Figure 3. Distribution verticale des sels nutritifs: nitrate, silicate, ammoniaque et phosphate aux mêmes stations que celles de la *figure 2*.

remained high; thus, the > 20 µm fraction represented typically 5–20 % of the total production.

To gain a global picture of the phytoplankton standing stock, its dynamics and importance compared to the POC within the whole photic zone, we calculated the integrated values of variables dealing with these aspects for the 0–35 m layer (*table III*). A striking result is the low variability during the 8 days (one station per day) for the different variables. The mean value of integrated AN is 21.3 mgC·mgChla^{-1}·d^{-1} (SD = 3.1, n = 8), which would be equivalent to a growth rate of 0.42 d^{-1} if we assume a mean Cphyt/Chl*a* ratio equal to 50. (The relationship between Chl*a* and POC in the euphotic zone not being linear, it was impossible to calculate a mean slope; according to Banse [2] and Furnas [15], 50 is considered as a realistic value.) Thus, the turnover time of the whole phytoplankton community was close to 2.5 days for the entire photic layer.

The phytoplanktonic carbon would represent 25–33 % of the total carbon and the mean ratio C:POC being 0.121, it would take approximately 8 days for the phytoplankton to renew all the particulate organic carbon of the photic layer.

Finally, the main results reported here can be summarised as follows: the Gironde plume had a great extension offshore at this period of the year in 1995. In these waters, phosphate was the first nutrient to be exhausted in the euphotic layer, whereas nitrate, silicate and ammonium

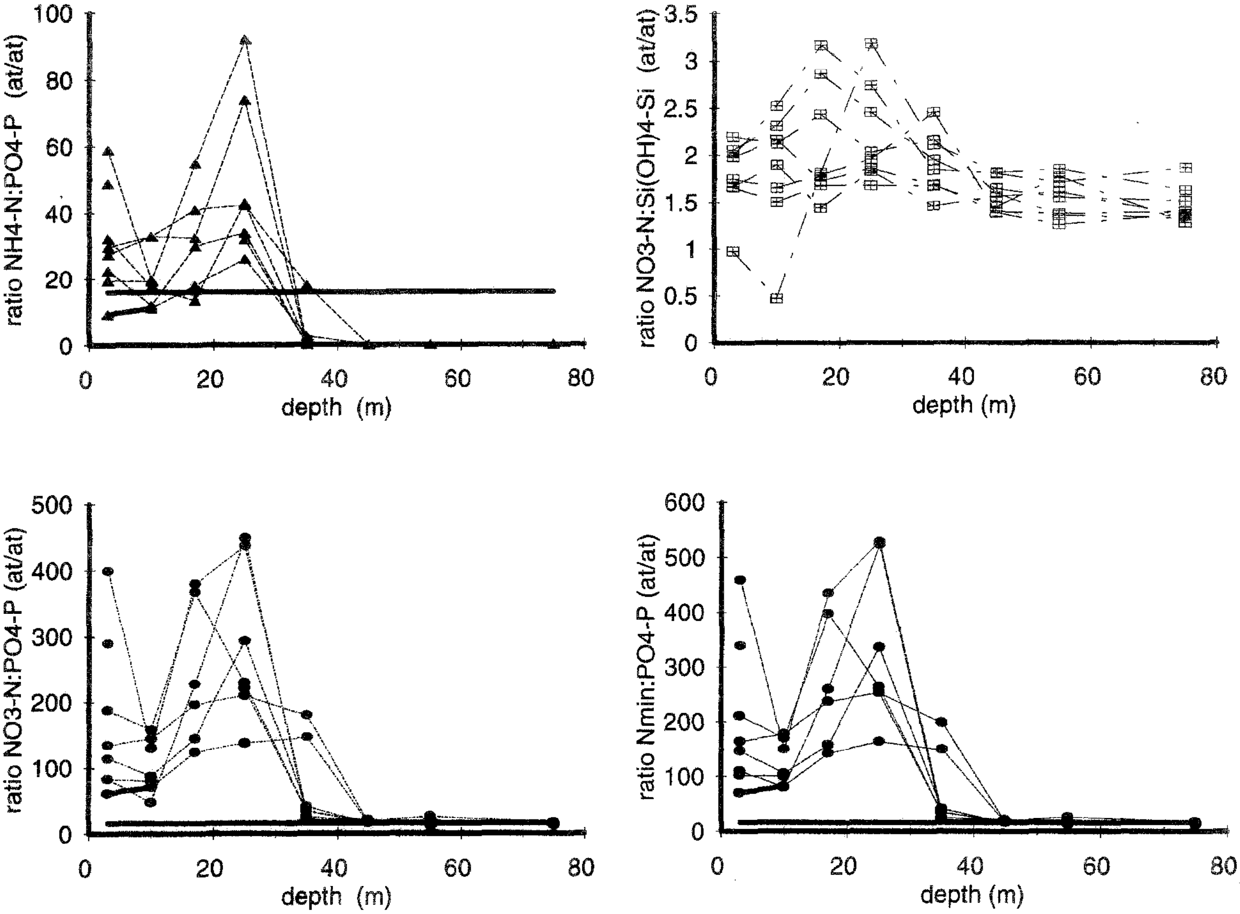

Figure 4. Vertical distribution of the nutrient ratios nitrate/phosphate, ammonium/phosphate, inorganic nitrogen/phosphate and nitrate/silicate; the vertical line is the N:P ratio equal to 1 (same stations as *figure 2*).

Figure 4. Distribution verticale des rapports nitrate/phosphate, ammonium/phosphate, azote inorganique/phosphate et nitrate/silicate; la ligne verticale figure le rapport N/P égal à 16; (mêmes stations que celles de la *figure 2*).

were at much higher concentrations with respect to the phytoplankton needs for growth. The phytoplanktonic biomass and production was dominated by small cells (< 10–20 μm), with relatively high assimilation numbers and probably high growth rates.

4. DISCUSSION

4.1. Nutrients ratios, particulate matter composition and phytoplankton growth rates

Several signs of phophate limitation of the spring phytoplankton production have been observed in the offshore Gironde plume waters: 1) very low PO_4-P concentrations, which were sometimes at the lower limit of detection; 2) very high NO_3-N:PO_4-P ratios, whereas relatively low NO_3-N:Si $(OH)_4$-Si ratios have been measured; and 3) high C:P and N:P ratios in the particulate organic matter, whereas the C:N ratio values were close to the Redfield ratios (6.5, SD = 0.44).

Phosphate limitation in the marine environment under the Gironde influence may be explained by the nutrients ratios at the outer part of the Gironde estuary (station S, *figure 1*). Within the salinity range 18 to 27 (the limits of our observations), there were inverse relationships between salinity and nitrate, silicate and phosphate, respectively. Nitrate values varied between 80 and

Table I. Mean nutrient concentrations (µM) and nutrient ratios within the 0–25 m layer along the transect (stations G to D from *figure 1*) during the first leg of the BIOMET cruise.

Tableau I. Concentrations moyennes des sels nutritifs (µmol.l^{-1}) et rapports de ces sels dans la couche 0–25 m le long de la radiale de BIOMET (stations G à D de la *figure 1*). Les valeurs entre parenthèses sont les écart-types relatifs à ces moyennes, calculées sur 3, 4 ou 5 mesures selon le cas dans cette couche d'eau; (-): pas de mesure.

	Stations						
	D	C	B	A	E	F	G
Distance from the coast (miles)	100	95	90	50	30	21	13.5
Depth of bottom (m)	2 000	1 000	200	100	75	50	35
[NO_3-N]	0.29 (0.06)	0.17 (0.21)	1.48 (1.08)	4.63 (2.19)	4.37 (0.36)	4.05 (0.73)	4.45 (1.48)
[$Si(OH)_4$]	0.87 (0.15)	0.78 (0.10)	1.19 (0.56)	0.92 (0.17)	1.41 (0.36)	1.19 (0.21)	3.41 (2.6)
[NH_4-N]	0.11 (0.06)	0.11 (0.02)	0.39 (0.16)	0.48 (0.24)	0.71 (0.24)	0.80 (0.53)	0.42 (0.24)
[PO_4-P]	0.045 (0.02)	0.04 (0.02)	0.09 (0.04)	0.07 (0.07)	0.035 (0.023)	0.035 (0.025)	0.05 (0.01)
$\frac{[NO_3\text{-N}]}{[PO_4\text{-P}]}$ (euphotic)	7.0 (1.4)	3.2 (3.4)	15.4 (7.1)	89.0 (81.8)	161 (76.9)	88.0 (37.0)	62.0 (52.8)
$\frac{[NO_3\text{-N}]}{[PO_4\text{-P}]}$ (aphotic)	(-) (-)	12.7 (0.95)	15.1 (2.2)	11.5 (1.25)	16.6 (1.41)	17.9 (0.78)	14.9 (-)

Values in parentheses are the standard deviation, each number being the mean of three, four or five measurements at different depths in that layer; (-): no measurement.

40 µmol·L^{-1} and the mean NO_3-N:PO_4-P and NO_3-N:Si $(OH)_4$-Si ratios were, respectively, 70.1 (SD = 8.9, $n = 9$) and 1.78 (SD = 0.27, $n = 9$). It would mean that the Gironde waters had a large nitrate excess relative to phosphate, according to the typical N and P phytoplankton requirements (ratio near 16), but no large excess relative to silicate since ratios NO_3-N:Si $(OH)_4$-Si close to 1 may be considered as equilibrated for the growth of diatoms [27]. Therefore, with such nutrient ratios at the mouth of the estuary, it is not surprising that phosphate was the first nutrient to be exhausted by phytoplankton communities growing at N:P ratios close to the Redfield values as long as phosphate is available. Along the transect, in spite of a great variability, the highest NO_3-N:PO_4-P values (mean = 161) were reached at ~ 30 miles from the coast, which could be interpreted as an increasing phosphorus limitation from the estuary to the outer part of the plume. Below the plume (in the marine aphotic layer) the NO_3-N:PO_4-P ratios were of the same order as the Redfield value. Far offshore (on the continental slope, stations C and D, *figure 1*) the NO_3-N:PO_4-P ratios were much lower than 16, reflecting a probable nitrogen limitation in these marine waters (*table I*).

High C:P and N:P ratios in the particulate organic matter have been measured. However, particles in surface waters contain varying amounts of little or no phytoplankton material, which may affect the ratios [1]. Moreover, the elementary composition of phytoplankton is not only influenced by the chemistry of surrounding waters: high growth rates lead to typical C:N:P ratios of 106:16:1 irrespective of the medium N:P ratios [19]. So, it is not possible to determine the elementary composition of the phytopankton from field observations of the dissolved inorganic nutrients and total particulate organic pools alone. Its dynamics must also be considered.

In our study, the turnover time of the whole phytoplankton community was close to 2.5 days for the entire photic layer. However, the values within the 0–10 m layer were much shorter (the mean value on 17 samples was 1.2 d, SD = 0.18). Then, if we take into account the vertical movements of phytoplankton within the mixed layer [30], the integrated photosynthesis would be higher than estimates from the bottles suspended at fixed depths. Therefore, the actual integrated phytoplankton growth rates were somewhere between 0.4 and 0.8 d^{-1}. A growth rate of 0.8 d^{-1} corresponds to 1.2 doubling per day. If we

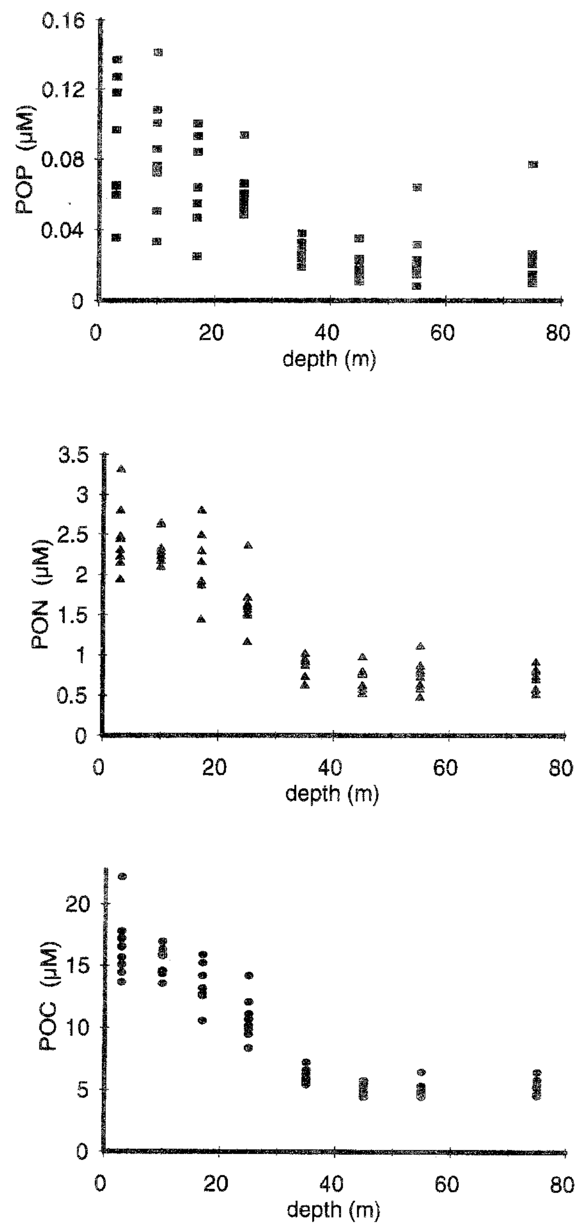

Figure 5. Vertical distribution of particulate organic matter concentrations and composition in terms of carbon (POC), nitrogen (PON) and phosphorus (POP) during the second leg of the BIOMET cruise (same stations as *figure 2*).

Figure 5. Distribution verticale de la matière organique particulaire en termes de carbone (POC), d'azote (PON) et de phosphore (PON) pendant la seconde partie de la campagne BIOMET; (mêmes stations que celles de la *figure 2*).

calculate the maximum growth rates (μ_{max}) predicted by Eppley's equation [13] at the temperature of the plume waters during BIOMET (~13.5–14 °C), the maximum expected phytoplankton μ_{max} in these waters could be near to two doublings per day. Even if both data are not strictly comparable (Eppley's data are all for laboratory cultures), it would be reasonable to speculate that the phytoplankton of the whole photic zone was growing approximately at 30–60 % of its μ_{max}. Such percentages of μ_{max} imply that the C:N:P ratios in phytoplankton are greatly influenced by the medium composition [19]. It would therefore mean that the high C:P and N:P ratios measured in the particulate organic matter could be the result of a phosphorus limitation for the phytoplankton standing crop.

4.2. Phytoplankton size and nature of the planktonic food web

It is actually paradoxical to find a dominant part of small cells in waters where nitrate and silicate are available. Although the dominance of larger cells in areas enriched with nitrate does not appear to be a result of a causal link between cell size and preference for either nitrate or ammonium [6], we have known for a long time that large cells dominate in areas that have relatively high supply rates of nitrate and can support a relatively large phytoplankton biomass [12, 14].

In a recent study, Chisholm [6] demonstrated the advantages of being small in a low nutrient environment. The above paradox, therefore, may be explained by the fact that phosphate uptake by large cells can be limited by molecular diffusion at very low concentrations. Chisholm's demonstration deals with nitrogen, but is valid for any nutrient. For example, Morel et al. [33] drew the same conclusion for iron and zinc availability in the ocean.

The negative consequence of decreasing size for algae is a change of food-web structure. Phytoplankton becomes increasingly the optimal food for smaller predator species (protozooplankton such as tintinnids and other ciliates) [4, 17, 45].

During the BIOMET cruise, Sautour et al. (unpublished report) studied the grazing impact of micro- and mesozooplankton on the phytoplankton community. The integrated mesozooplankton consumption rates ranged from 54 to 281 $mgC{\cdot}m^{-2}{\cdot}d^{-1}$, corresponding to a grazing pressure comprised between 9 and 40 % on the total primary production. The integrated microzooplankton consumption ranged between 498 and 817 $mgC{\cdot}m^{-2}{\cdot}d^{-1}$ and this was equivalent to an average daily grazing pressure of 99 ± 23 % on the total primary production. Even if the

Table II. Mean particulate organic matter concentrations and composition in terms of carbon (POC), nitrogen (PON) and phosphorus (POP) in the mixed layer and the bottom marine water during the second leg of the BIOMET cruise.

Tableau II. Concentration et composition moyenne de la matière organique particulaire en termes de carbone (POC), d'azote (PON) et de phosphore (PON) dans la couche homogène et la couche d'eau marine sous-jacente pendant la seconde partie de la campagne BIOMET; (les valeurs entre parenthèses sont les écart-types, *n* = 32 pour chaque couche).

	POC **µM**	**PON** **µM**	**POP** **µM**	**C:N** **at:at**	**C:P** **at:at**	**N:P** **at:at**
Mixed	14.0	2.16	0.075	6.5	217	33.5
layer	(2.8)	(0.46)	(0.29)	(0.44)	(111)	(17.7)
Bottom	5.4	0.76	0.021	7.4	295	40.1
layer	(0.7)	(0.16)	(0.008)	(1.3)	(117)	(13.5)

Values in parentheses are the standard deviations, *n* = 32 for each layer.

Table III. Integrated values (0–35 m) on the whole photic zone during the second leg of the BIOMET cruise.

Tableau III. Valeurs intégrées sur l'ensemble de la couche euphotique (0–35 m) pendant la seconde partie de la campagne BIOMET (suivi de la drogue). POC: Carbone Organique Particulaire ; ΔC: production primaire; Cphyto: Carbone phytoplanctonique calculé à partir des valeurs de chlorophylle *a* (C_{phyto} = Chl*a**50).

Stations	H	I	J	K	L	M	N	O	Mean	SD
Date (May 95)	18	19	20	21	22	23	24	25		
POC ($mgC\cdot m^{-2}$)	5557	4898	5352	5427	5072	5732	4182	5448	5208	491
Chl*a* ($mg\cdot m^{-2}$)	29.5	26.6	28	29.8	26.6	29.4	31.5	35.6	29.6	2.9
ΔC ($mgC\cdot m^{-2}\cdot d^{-1}$)	577	542	590	608	767	625	606	699	627	72.4
ΔC/POC (d^{-1})	0.104	0.111	0.11	0.112	0.15	0.109	0.146	0.128	0.121	0.018
ΔC/Chl*a* ($mgC\cdot mgChla^{-1}\cdot d^{-1}$)	19.6	20.4	21.1	20.4	28.8	21.3	19.2	19.6	21.3	3.1
$\Delta C/C_{phyto}$ (d^{-1})	0.39	0.41	0.42	0.41	0.58	0.42	0.38	0.39	0.42	0.06
C_{phyto}/POC (%)	26.5	27.1	26.1	27.4	26.2	25.6	37.6	32.7	28.6	4.3

POC: particulate organic carbon; ΔC: primary production; C_{phyto}: phytoplankton carbon calculated from chlorophyll *a* values (C_{phyto} = Chl*a**50).

microzooplankton grazing was probably overestimated because incubations were run without mesozooplankton predators [26], the results indicate that grazing pressure of microzooplankton on phytoplankton was far higher than the pressure exerted by mesozooplankton. Moreover, if we assume that the picophytoplankton and small nanophytoplankton (i.e. < 5 µm) are the most available fractions for microzooplankton [16, 21, Sautour et al. (unpublished data)] calculated that microzooplankton grazed daily more than the < 3 µm of the food that is produced each day (213 ± 56 % of the < 3 µm primary production).

Other active regeneration processes have been observed during the same cruise: 1) rapid degradation of the small zooplankton fecal pellets (Sautour, personal communication); 2) high bacterial exoproteolytic activities in settling particles (Delmas, unpublished data); and 3) low sedimentation rates (Laborde et al., unpublished data).

All these characteristics of the planktonic food web and previous studies on grazing characteristics [42] lead to the conclusion that a 'maintenance' or 'regeneration' system, as defined by Platt et al. [36] and carefully analysed by Riegman et al. [40], could be applied to the Gironde plume. In such a system, the new production, elaborated

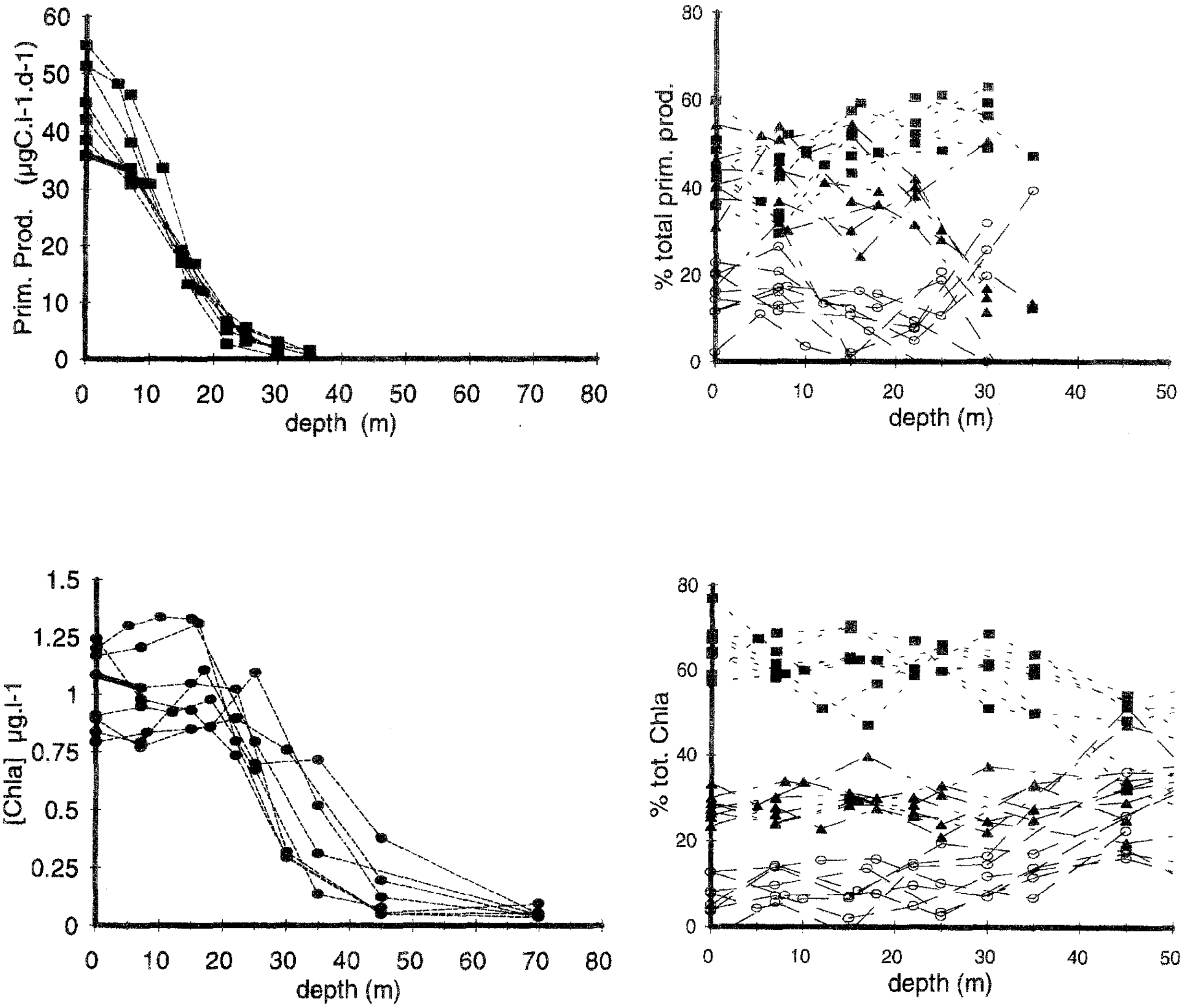

Figure 6. Top: Vertical distribution of chlorophyll *a* and primary production. Bottom: Vertical distribution of the size distribution of chlorophyll *a* and primary production: % < 3 µm; % 3–20 µm; % > 20 µm (same stations as *figure 2*).

Figure 6. Haut: Distribution verticale de la Chlorophyll *a* et de la production primaire; bas: distribution verticale de la structure de taille de la Chlorophyll *a* et de la production primaire : % < 3 µm ; % 3–20 µm ; % > 20 µm ; (mêmes stations que celles de la *figure 2*).

Table IV. Evolution of nitrate concentrations from mid-April to mid-June 1995 in the BIOMET area.

Tableau IV. Évolution des concentrations en nitrate de la mi-avril à la mi-juin 1995 dans la zone de la campagne BIOMET.

Cruises	**PreBIOMET**	**BIOMET**	**BIOMET**	**PostBIOMET**
		First leg	*Second leg*	
Dates	19/04/1995	7/05/1995	18–25/5/95	13/06/1995
[NO$_3$-N] Mean (µmol·L^{-1})	6.87	4.37	3.40	0.43
SD	1.10	0.36	0.54	0.38

from nitrate nitrogen coming from the Gironde waters or from the marine reservoir below, is very reduced.

One other argument in favour of phosphate limitation for the new production is the slow decrease of nitrate concentration within the BIOMET area between mid-April and mid-June 1995 (*table IV*): even if we know that the sampled water masses were not the same from one cruise to the other over the 2-month period and consequently that the NO_3-N decrease is not equivalent to a net NO_3-N uptake by phytoplankton community during this period, the seasonal trend is robust. Moreover, the same evolution has been already observed during the year 1994 in the same region on a larger scale (cruises 'AGIR', unpublished data).

5. CONCLUSIONS

Finally, the ecological characteristics for the spring planktonic food web on the continental shelf under Gironde's influence may be that, instead of an important and large cell (diatom) phytoplankton bloom, fuelled by nitrate (and silicate), the bloom would be limited in space and intensity because of early phosphate depletion. Then, the phytoplankton community is dominated by small cells, growing upon regenerated sources of nitrogen and phosphorus and actively grazed by microzooplankton.

Can we state as a rule that each year the spring phytoplankton bloom in the large plume of Gironde on the continental shelf is controlled by phosphorus availability? The answer is not evident because, to our knowledge, good historical data on phosphate distribution in the Gironde plume, if existing, are very scarce. Phosphate measurements on deep frozen samples must be considered as suspect. Some authors [28] found decreases in phosphate concentrations after freezing, whereas others [47] found the reverse; Chapman and Mostert [5] showed both: increases on short-term storage and decreases on long-term storage!

However, looking at our 'frozen nutrient data' from a previous cruise in the same area during the same season ('PNOCAT' cruise, in May 1994), there is some evidence that the same scenario occurred. For example, at the mouth of the Gironde, the mean NO_3-N:PO_4-P and NO_3-N:$Si(OH)_4$-Si ratios were, respectively, 45.5 (SD = 7.3, $n = 10$) and 1.15 (SD = 0.19, $n = 10$) within the salinity range 19–33 (versus, respectively, 70.1 and 1.78 in 1995). During a similar drogue exercise, same nitrate profiles were found and a great number of phosphate values were equal or close to zero in the mixed layer with few erratic values that could be attributed to freezing artefacts.

More generally, the results of the 'Réseau National d'Observation' (French National Net Monitoring of the marine environment quality) are similar [38, 39]. Over the period 1974–1984, the winter concentrations of phosphate in the Gironde estuary were low compared to those of the Loire and Seine, the two other great rivers of the French west coast (2.5 $\mu mol \cdot L^{-1}$ versus, respectively, 6.2 and 16.4 at salinity zero). Even if the NO_3-N concentrations were also low compared to these two rivers (respectively, 116, 192 and 313 $\mu mol \cdot L^{-1}$ at salinity zero for the rivers Gironde, Loire and Seine), the NO_3-N:PO_4-P ratios are always much higher than 16. More recent results for the years 1988 and 1989 [38] confirm this trend with variable but high N:P nutrient ratios in the Gironde estuary.

Further studies are planned to understand the phosphorus limitation processes: measurements of dissolved organic phosphorus pool and plankton phosphatase activities; use of ^{33}P as a tracer to evaluate the incorporation and regeneration of PO_4-P within the food web. If such a limitation of the spring planktonic production is confirmed, it would be interesting to study the implications of this atypical spring food web for the nutrition of fish larvae in a recruitment perspective.

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