Latitudinal variability in phosphate uptake in the Central Atlantic

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ABSTRACT: The role of P in regulating planktonic production in Atlantic waters was assessed by the examination of the phosphate turnover time and uptake rate along a latitudinal transect across the Central Atlantic Ocean (27°N to 36°S). Phosphate uptake rates and the affinity for phosphate were higher for small (<0.8 µm) organisms, compared with those >0.8 µm. Phosphate uptake rates were relatively low, resulting in long phosphate turnover times (days), except in the surface waters south of 25°S, which were also characterized by the highest uptake rates and affinity for phosphate, and the smallest total P pools observed along the transect. The organisms were found to realize their maximal phosphate uptake rates at ambient phosphate concentrations, suggesting the adequacy of the P supply to support the requirements of organisms. These findings suggest that inorganic P was not limiting community production in most of the Central Atlantic, except for the area south of 25°S, where P uptake could possibly be limited by P supply. The long turnover times generally observed in the Central Atlantic Ocean are in agreement with previous observations in oceanic systems elsewhere, suggesting that the observation that P is unlikely to be a limiting resource for planktonic growth can be extrapolated to most of the open ocean. The combined rate of P excretion from planktonic organisms and their microbial grazers as dissolved organic phosphorus (DOP) represented 75% of the total phosphate uptake. This DOP does not reach a sufficient accumulation as to drive an important downward flux of DOP, which represents a loss of only 9% of the P inputs into the biogenic layer. Hence, the high P uptake rate of the planktonic community in the Central Atlantic provides P in excess to support primary production, leading to a release as DOP, which appears to be rapidly recycled in the biogenic layer, thereby maintaining an adequate P supply to fuel primary production.

KEY WORDS: Phosphate · Uptake · Atlantic · Excretion · Turnover · Picoplankton · Microplankton

INTRODUCTION

The quantification of the uptake of phosphorus by oceanic plankton has received limited attention (e.g. Carpenter & Capone 1983) relative to the dominant interest in nitrogen, the element most frequently limiting marine production (Downing 1999). Even if the belief that P does not play a limiting role in the ocean is correct, knowledge of the phosphorus uptake by plankton is needed to effectively model the biogeochemical cycling of P, which has been suggested to exert an important control on the long-term changes in

the production of the oceans (Redfield 1958, Broecker 1982). While N limitation has only been demonstrated for autotrophs, P limitation has been demonstrated for both marine autotrophic (e.g. Smith 1984, Krom et al. 1992, Thingstad & Rassoulzadegan 1995, Thingstad et al. 1998) and heterotrophic plankton (e.g. Cotner et al. 1997, Rivkin & Anderson 1997, Thingstad et al. 1998). Moreover, available information points to a prominent role of picoplankton, both autotrophic and heterotrophic, on P uptake (Currie & Kalff 1984, Bratbak & Thingstad 1985, Vadstein et al. 1993). Because these organisms are important contributors to the plankton biomass of the tropical ocean (e.g. Gasol et al. 1997), they may be hypothesized to play a dominant role in the cycling of P within the biogenic layer there.

The limited number of studies on P uptake and cycling by plankton since the early work of Pomeroy

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(1960) have been largely focused on estuaries and coastal waters (e.g. Taft et al. 1975, Harrison et al. 1977, Krempin et al. 1981, Lebo 1990, Thingstad et al. 1993, 1998, Björkman & Karl 1994), whereas studies of oceanic communities are still few and largely focused on the Pacific Ocean (Perry 1976, Perry & Eppley 1981, Harrison 1983, Laws et al. 1984) and the Sargasso Sea (Cotner et al. 1997). The available information suggests that P limitation is particularly important in warm, oligotrophic waters, but the empirical basis on the rates of P uptake and P requirements by oceanic plankton communities is still too meager to test this notion. Moreover, most studies report the incorporation of P into the particulate organic pool, but do not address its possible release to the dissolved organic pool. The dissolved organic matter (DOM) pool is an important reservoir of nutrients and carbon in warm, oligotrophic waters (Vidal et al. 1999). Given the high rates of phytoplankton carbon (e.g. Karl et al. 1998) and nitrogen (e.g. Bronk et al. 1994) release (often exceeding 50% of the uptake) to DOM, we hypothesize that phosphorus release as DOM should also encompass a significant fraction of the total phosphate consumed.

Here we report the uptake rate and turnover time of inorganic phosphorus along a latitudinal transect (27°N to 36°S) across the Central Atlantic Ocean

(Fig. 1). This area is characterised by permanent stratification, which leads to generally low inorganic nutrient concentrations and low plankton biomass in the biogenic zone, with a subsurface (down to 180 m) autotrophic biomass maximum (Agusti & Duarte 1999). However, the doming of the pycnoclines from the equator towards the African coast leads to enhanced nutrient supply and higher plankton biomass (cf. LeBouteiller 1986, Agusti & Duarte 1999), as can be readily observed from an examination of ocean color (Campbell & Aarup 1992). Hence, the study comprised a gradient of phytoplankton biomass and nutrient supply, thereby allowing for a greater range in the expected uptake and turnover rates of inorganic phosphorus. We first characterised the nutrient contents of the plankton through bulk measurements of particulate organic C, N and P (POC, PON, and POP). We then conducted tracer ($^{33}\text{P-PO}_4$) addition experiments in surface and DCM (deep chlorophyll *a* maximum) waters along the transect to determine the incorporation of dissolved inorganic phosphorus (DIP) into different size fractions (<0.8 μm and 0.8–240 μm) of particulate organic matter (POM). In addition, we conducted experiments to determine the rate of release of dissolved organic phosphorus (DOP), thereby allowing the estimation of the net production of DOP and the total consumption of DOP.

METHODS

The present study was conducted from October to November 1995 on board the Spanish RV 'BIO Hespérides' as part of the 'Latitud-II' cruise, which examined latitudinal changes in the control of planktonic production in the Central Atlantic Ocean. A total of 11 stations between the Canary Islands (27°13'N) and Argentina (36°21'S) were sampled in this study (Fig. 1). Water samples were collected between 06:00 and 10:00 h local time, from the surface and/or the DCM (see Table 1) using 12 to 30 l Niskin bottles mounted on a rosette frame fitted with a CTD profiler. Large particles and mesozooplankton were excluded using a 240 μm Nifex mesh when transferring the seawater into 5 l polypropylene bottles.

Four replicate samples (0.5 to 1.5 l) were collected on glass fiber filters (Whatman GF/F) for duplicate measurements of POC, PON and POP in

Fig. 1. Stations sampled during the 'Latitud-II' cruise

the microplankton (<240 µm) size fraction. To collect the picoplanktonic fraction (<0.8 µm) we first removed larger plankton using a 0.8 µm Nucleopore filter (4 replicates), collecting the remaining particles on GF/F filters. Duplicate filters of each fraction were analyzed for POC, PON and POP determinations. The filters used for C and N analyses were combusted, and those for P analysis were acid-washed (HCl 10%) before use. The samples were preserved frozen until analyzed. POC and PON were measured using a Carlo Erba CHN analyzer Model 1104, after removing inorganic carbon with HCl fumes. POP was determined as soluble reactive P (SRP) following oxidation of the sample in acidic persulfate at 120°C for 30 min (Koroleff 1983). After oxidation, the sample was filtered through a GF/C filter to remove debris.

Total dissolved phosphorus in the water was determined as SRP following oxidation in acidic persulfate of the filtrate of 20 ml subsamples filtered through 0.2 µm membrane filters (Koroleff 1983). Dissolved inorganic P (DIP) was measured directly as SRP (Koroleff 1983). The concentration of DOP was estimated as the difference between total dissolved P and DIP.

Samples (2 ml) for enumeration of bacteria were preserved with 1.5% glutaraldehyde. The samples were filtered at low pressure onto black Nucleopore filters (0.2 µm nominal pore size), and stained with DAPI (4',6-diamino-2-phenylindole) for 5 to 10 min (Martinussen & Thingstad 1991). Filters were rinsed with filtered seawater, mounted on glass slides and stored frozen until examination. Bacteria collected on the filters were examined at 1000× magnification under a Zeiss Axioplan microscope equipped with an epifluorescence unit fitted with a UV Zeiss filter 487701. The volume of individual bacterial cells was estimated from measurements of the dimensions of 170 cells, using a video camera adapted to the microscope at 1000×, and computing the volume by approximation to the nearest simple geometric shape. The biovolume of phytoplankton (pico- and microautotrophs >0.2 µm) was derived from epifluorescence counts and size estimates, obtained by examination of 50 to 100 ml subsamples collected on 0.6 µm black Nucleopore filters and illuminated with blue light to high chlorophyll a autofluorescence (Agustí & Mura unpubl. results). At least 40 cells of bacteria, picoplankton and microphytoplankton were measured to estimate their average cell volume and, when multiplied by their density, their biovolume.

Subsamples (1.2 ml) for counts of *Prochlorococcus* cells were preserved with 1% paraformaldehyde + 0.05% glutaraldehyde (final concentration), frozen in liquid nitrogen and later stored at -20°C. The samples were later thawed and run through a Becton & Dickinson

FACScalibur flow cytometer with laser emission at 488 nm. Samples were run at low speed (approx. 12 µl min⁻¹), and data were acquired in log mode until around 10000 events had been recorded. We added 10 µl per sample of a 10⁻⁵ ml⁻¹ solution of yellow-green 0.92 µm Polysciences latex beads as an internal standard, to be able to effectively detect *Prochlorococcus* with a low FL3 (red fluorescence) signal and no FL2 (orange fluorescence) signal. Surface prochlorophytes could not be unambiguously identified because of their low fluorescence. Their concentrations were approximated as being twice the cell density of the population with the highest red fluorescence, following Partensky et al. (1996).

Water samples (1 l) were prefiltered through a 240 µm mesh and transferred to acid-washed glass bottles. The incorporation of ³³P-PO₄ in 2 different size fractions (>0.2 and >0.8 µm) after the addition of 10 µCi of carrier-free isotope (ICN Biomedicals) was followed by collecting the particulate material in 5 to 10 ml subsamples on Nucleopore filters of 0.2 and 0.8 µm pore size, respectively. Sampling frequency decreased progressively, with a total of 8 to 16 samples, depending on uptake velocity, drawn for each experiment. Duplicate samples were drawn whenever sampling intervals exceeded 2 h. The experimental units, enclosed in neutral screens to reduce irradiance to levels approaching those received *in situ*, were incubated for about 24 h (range 13 to 46 h) in large (1 m³) tanks placed on deck, and continuously flushed with seawater to maintain a constant temperature. A pair of formalin-killed (12.5% formaldehyde) controls were included with each set of water samples (Ammerman 1993) in order to control for non-biological uptake. Samples for analyses of DOP and DIP concentrations were collected from the experimental bottles at the beginning and end of the experiments. The radioactivity of the particles collected on the filters was assayed in a Beckman LS6000IC scintillation counter with CytoScint ES as scintillation cocktail. A 10% solution of ethyl acetate was added to the cocktail. The radioactivity of the samples was corrected for the ³³P decay with time when the radioactivity measurements of samples from any 1 experiment lasted more than 13 h (error in the disintegrations per minute [DPM] ≤ 2.3%).

The P incorporated into the <0.8 µm size class was calculated as the difference between the activity retained on the 0.2 µm filter and that retained on the 0.8 µm filter. The DIP turnover time (*T*) was determined from the time course of the percent ³³P-PO₄ incorporated by the organisms (for example Fig. 2). The time course of the percent ³³P-PO₄ removed showed a rapid initial rate of ³³P-PO₄ incorporation, which declined over the course of the experiment. The

Fig. 2. Time course of the percent of ^{33}P taken up by planktonic organisms (<240 and <0.8 μm) in surface waters at $33^{\circ}20' \text{ S}$, $45^{\circ}20' \text{ W}$

initial, linear portion of the curve (initial 4 to 10 h of incubation) was used to fit the equation:

$$\frac{{}^{33}\text{P}_t}{{}^{33}\text{P}_A} = \frac{{}^{33}\text{P}_0}{{}^{33}\text{P}_A} + k \cdot t \quad (1)$$

where ${}^{33}\text{P}_A$ is the total ${}^{33}\text{P}$ - PO_4 added, and ${}^{33}\text{P}_0$ and ${}^{33}\text{P}_t$ are the ${}^{33}\text{P}$ - PO_4 incorporated into particles at time 0 and at time t , respectively. The slope of the equation (k , h^{-1}) provides an estimate of the phosphate turnover rate. The DIP turnover time (T , days) was estimated as the inverse of k (extrapolated to 24 h) and the uptake rate of phosphate (V , $\mu\text{mol P l}^{-1} \text{ h}^{-1}$) was estimated as the product of the ambient DIP concentration in the water and the phosphate turnover rate. An independent estimate of the net phosphate uptake rate (V_{net} , $\mu\text{mol P h}^{-1} \text{ l}^{-1}$) was calculated from the reduction in DIP between the beginning and end of the experiments. Because the incubation bottles may have contained protozoan grazers, which may have released some of the incorporated P back to the dissolved pool, V_{net} represents a minimum estimate of the gross P incorporation rate. The specific uptake rate per unit of particulate phosphorus (U , h^{-1}) provided an estimate of the turnover rate of POP. In addition, we measured the accumulation of DOP during the course of the experiments at 7 of the stations, providing an estimate of the net rate of DOP release, which, when combined with the estimate of P uptake into the particulate fraction, provided an estimate of the total phosphate uptake by the community.

The ratio between the turnover rate (k) and the POP within each of the size fractions analyzed was used as an estimate of the affinity for orthophosphate of each fraction. The DIP uptake rate (V , $\mu\text{mol P h}^{-1} \text{ l}^{-1}$) for each size fraction was estimated as the product of k for the respective fractions and the DIP concentration of the water, whereas their P-specific uptake rate (U , h^{-1}) was

estimated as the product of the k :POP ratio and the DIP concentration.

At 3 of the stations, tracer-addition experiments were conducted to provide a rough estimate of the maximum uptake rate (V_{max}) of the natural communities, by measuring the initial uptake rate of ^{33}P under saturating concentrations. These experiments differed from those described above in that both 10 μCi of ^{33}P - PO_4 isotope and unlabeled phosphate (^{31}P) were added to 1 l of water (prefiltered through a 240 μm mesh) to yield a final phosphate concentration of 8 μM PO_4 . Because uptake rates were measured at a high phosphate concentration (phosphate concentration $\gg$ half saturation constant), the uptake rate obtained should approach the maximum uptake rate (U_{max}) for the community (Olsen et al. 1989).

RESULTS

The concentration of DIP in surface waters was rather low, especially in the area between 5°S and 36°S , where the DIP concentration was $<0.2 \mu\text{mol P l}^{-1}$ in the upper waters ($<150 \text{ m}$) (Fig. 3). Most of the P was

Fig. 3. Latitudinal variation of the partitioning of phosphorus among dissolved organic P (DOP), dissolved inorganic P (DIP) and particulate organic P (POP) (<240 μm) in surface and deep chlorophyll maximum (DCM) waters

Table 1. Position and depth (*z*) of the stations for phosphorus uptake experiments, the concentrations of particulate organic C, N and P (POC, PON and POP), chlorophyll *a* (chl *a*), and dissolved inorganic P (DIP) and the biovolume of bacteria and phytoplankton

Lat. (°N, -°S)	Long. (°W)	<i>z</i> (m)	POC ($\mu\text{mol C l}^{-1}$)	PON ($\mu\text{mol N l}^{-1}$)	POP ($\mu\text{mol P l}^{-1}$)	Chl <i>a</i> ($\mu\text{g chl a l}^{-1}$)	DIP ($\mu\text{mol P l}^{-1}$)	Bacteria ($10^3 \mu\text{m}^3 \text{ml}^{-1}$)	Phytoplankton ($10^3 \mu\text{m}^3 \text{ml}^{-1}$)
25.2	19.1	85	8.17	0.51	0.021	0.25	0.15	4.66	4.75
19.8	18.3	5	15.8	1.31	0.033	0.23	0.23	11.3	32.89
11.3	20.4	50	10.2	0.75	0.022	0.36	1.32	3.26	7.67
0.95	24.4	5	8.19	0.74	0.020	0.13	0.16	9.98	29.28
0.95	24.4	65	18.0	1.62	0.039	0.71	0.29	11.6	20.85
-5.72	27.1	5	8.33	0.72	0.034	0.08	0.23	12.2	21.43
-5.72	27.1	105	8.42	0.67	0.024	0.31	0.66	6.52	6.76
-15.0	31.0	5	6.30	0.51	0.022	0.02	0.27	6.83	0.16
-15.0	31.0	150	6.04	0.61	0.029	0.17	0.25	5.64	4.70
-20.8	33.4	5	7.07	0.41	0.023	0.04	0.13	9.10	6.44
-20.8	33.4	160	5.49	0.46	0.018	0.19	0.19	4.54	5.94
-24.3	36.4	120	7.40	0.65	0.030	0.24	0.14	5.01	2.87
-28.1	40.1	5	7.78	0.67	0.021	0.08	0.07	7.84	11.27
-30.6	42.5	5	7.46	0.70	0.025	0.05	0.12	6.97	8.82
-30.6	42.5	110	9.48	0.68	0.025	0.29	0.07	4.69	8.04
-33.3	45.3	5	8.17	0.70	0.037	0.07	0.07	9.50	9.53

in the dissolved pool, with an average of $30.2 \pm 7.4\%$ of the total P in the surface water being in the dissolved organic pool, and an average of $59.9 \pm 6.9\%$ of the total P in the DIP pool. The total P pool at the DCM ($0.51 \pm 0.21 \mu\text{mol P l}^{-1}$) was on average about twice as high as that in surface waters ($0.28 \pm 0.05 \mu\text{mol P l}^{-1}$). The high DOP and DIP concentrations observed around 10°N (Fig. 3) were ascribed to the proximity to the NW African upwelling (cf. Vidal et al. 1999, Duarte et al. unpubl.).

POC, PON, and POP concentrations differed by about 1 order of magnitude among stations (Table 1). The highest concentrations of POC, PON and POP were found in the surface waters near the upwelling region off NW Africa and in the DCM of the equatorial area, where POC concentrations reached 16 and $18 \mu\text{mol C l}^{-1}$, respectively (Table 1). These maximum concentrations were twice as high as the average POC (average $\pm \text{SE} = 8.82 \pm 0.27 \mu\text{mol C l}^{-1}$), which tended to be higher at the DCM, which was found between 50 and 160 m (Agustí & Duarte 1999), than in surface waters. The contribution of the 2 size fractions examined (<0.8 and $0.8\text{--}240 \mu\text{m}$) to the POC, PON and POP concentrations differed considerably. The $0.8\text{--}240 \mu\text{m}$ fraction dominated the pools of POC, PON and POP (76% of POC, 71% of PON and POP, on average), except in

Fig. 4. Latitudinal variation of the distribution of POC, PON and POP in the 2 sestonic size fractions examined (<0.8 and $0.8\text{--}240 \mu\text{m}$) in surface and DCM waters

Table 2. Coefficient of determination (r^2), slope and significance (p) of least-squares, linear regression analyses between the concentrations of particulate organic C, N and P for the total (i.e. <240 μm) community, and each of the 2 size fractions (<0.8 and 0.8–240 μm) considered in surface and DCM waters. The regression slopes provide estimates of the average atomic C:N, C:P and N:P ratios

	Size fraction (μm)	POC versus PON			POC versus POP			PON versus POP		
		r^2	Slope	p	r^2	Slope	p	r^2	Slope	p
5 m	Total (<240)	0.9	10.7	0.001	0.2	179.5	0.36	0.2	16.5	0.35
	0.8–240	0.7	24.7	0.017	0.1	<0	0.59	0.1	6.2	0.63
	<0.8	0.0	<0	0.97	0.1	<0	0.52	0.5	18.9	0.08
DCM	Total (<240)	0.9	10.3	0.000	0.5	426.4	0.04	0.7	46.8	0.009
	0.8–240	0.1	3.7	0.57	0.1	118.6	0.54	0.6	22.6	0.027
	<0.8	0.7	12.3	0.012	0.2	252.1	0.35	0.3	23.1	0.19

Fig. 5. Average ($\pm$ SE) C:N, C:P and N:P ratios in the 2 sestonic size fractions examined (<0.8 and 0.8–240 μm) in surface and DCM waters. Sample size for each mean and standard error value = 8

the DCM near the equator (1°S), where the fraction <0.8 μm showed an important contribution (Fig. 4).

The biomass of microplankton was evenly distributed between that of autotrophs ($53 \pm 4.8\%$ of the biovolume, on average) and bacteria ($46 \pm 4.5\%$ of the biovolume, on average), although autotrophs clearly dominated the biomass near the NW African upwelling and in DCM waters near the equator (Table 1). The autotrophic biomass was dominated by eukaryotic nano- and microplankton near the NW African upwelling, whereas prochlorophytes and cyanobacteria were significant components of the autotrophic biomass in the most oligotrophic waters, with prochlorophytes representing, on average, $32 \pm 2.1\%$ of the biovolume across the transect. The size fraction <0.8 μm contained most (70 to 80%) of the picoplankters (bacteria, cyanobacteria and prochlorophytes), while the larger fraction also included the nano- and microphytoplankton biomass, as well as heterotrophic protozoa and detrital particles.

The concentrations of POC and PON were closely correlated in both surface and DCM waters (Table 2), and declined from the Canary Islands towards the equator in surface waters, whereas they increased in DCM waters. In contrast, the concentration of POP was rather independent of those of POC and PON, both in the DCM and particularly in surface waters (Table 2), indicative of a highly variable C:P ratio compared to the C:N ratio (Fig. 5). The particulate C:N, C:P and N:P ratios tended to exceed the Redfield ratios. The high values observed for the C:P ratios suggest a high contribution of detrital particles, which are depleted in P and N relative to C compared to living plankton (e.g. Knauer et al. 1979, Olsen et al. 1986). The size fraction <0.8 μm (which includes bacteria and cyanobacteria) showed the lowest average C:P and N:P ratios, particularly in surface waters (Fig. 5). The C:P ratio of the larger size fraction (0.8–240 μm) and the N:P ratio of the smaller fraction (<0.8 μm) were highest at about 30°S as well as close to the equator (Fig. 4), indicating the seston of these waters to be P-depleted.

The phosphate turnover rates (k , h^{-1}) were low, albeit highly variable, ranging from 0.001 to 0.026 h^{-1} . The maximum uptake rate (V_{max}) into the particulate fraction of the natural communities, estimated at 3 of the sampling stations, ranged from 0.0001 to $0.0033 \mu\text{mol P l}^{-1} \text{ h}^{-1}$, and was comparable to values measured in the carrier-free incubations. This indicates that the uptake rates realized at the *in situ* phosphate concentrations approach the maximal rates possible. The turnover time of DIP (T) ranged from 1.6 to 40.1 d, and, in surface waters, tended to be fastest at the southern-most stations (Fig. 6), tending to decrease as DIP concentrations

declined ($r = 0.5$, $p < 0.08$). The DIP uptake rates into the particulate fraction (V) varied between 0.0001 and $0.028 \mu\text{mol P l}^{-1} \text{ h}^{-1}$ and showed a contrasting latitudinal pattern between surface and DCM waters, involving high P uptake rates in the surface waters at the southern end of the transect and in the DCM waters off the NW African coast (Fig. 6). The specific uptake rate per unit of particulate phosphorus (U) ranged from 0.005 to 0.12 h^{-1} and followed a latitudinal pattern that mirrored that of the uptake rate (Fig. 6).

The proportion of isotope accumulated in the particulate fraction by the end of the incubations, which represents a minimum estimate of the total isotope incorporated, was generally low ($<45\%$), particularly in DCM waters (mean $\pm$ SE: $8 \pm 2\%$, Fig. 7). The proportion of isotope accumulated in the particulate fraction was significantly higher (mean $\pm$ SE: $19 \pm 5\%$) in surface waters (Fig. 7). The proportion of isotope accumulated in the particulate fraction decreased from the moderately high values observed at the northern end of the transect (10 to 25°N) to the low values between the equator and 20°S , followed by a considerable

Fig. 6. Latitudinal variation of the uptake rate constant (k), uptake rate (V) and POP turnover rate (U) in surface and DCM waters. The right axis of the top panel shows the DIP turnover time (T), calculated as the inverse of the uptake rate constant

Fig. 7. Latitudinal variation in the proportion of ^{33}P incorporated at steady state (13 to 46 h) into the 2 sestonic size fractions examined (<0.8 and $0.8\text{--}240 \mu\text{m}$) in surface and DCM waters

Fig. 8. Average ($\pm \text{SE}$) POP-specific uptake rate (U) and the affinity for P ($k:\text{POP}$) of the 2 sestonic size fractions examined (<0.8 and $0.8\text{--}240 \mu\text{m}$) in surface and DCM waters. Sample size for each mean and standard error = 8

increase towards the southern end of the transect (Fig. 7). The proportion of isotope incorporated increased as the DIP uptake rate increased ($r = 0.90$, $p < 0.0001$). The ^{33}P recovered in the 2 size fractions examined (<0.8 and $240\text{--}0.8 \mu\text{m}$) was roughly similar at the lowest latitudes, but showed some differences either in surface or DCM waters at the northern and southern ends of the transect (Fig. 7). The size fraction $<0.8 \mu\text{m}$ tended to show a higher specific uptake rate (U , h^{-1}) and affinity for phosphate ($k:\text{POP}$ ratio, Fig. 8) in surface waters than the size fraction $>0.8 \mu\text{m}$ did (t -test, $p < 0.01$). Moreover, surface communities tended to show a higher affinity for phosphate than those from the DCM (Fig. 8), with a clear tendency for the affinity for phosphate of both fractions to be highest in the surface areas at the southern end of the transect.

The partitioning of P into the different pools (DIP, DOP and POP) changed over the course of the experiments. The concentration of DIP declined by, on average, 44% during the incubations, yielding a net DIP uptake rate (V_{net}) in excess of that calculated from the initial rate of incorporation of ^{33}P into the particulate fraction (V , Fig. 9). This observation suggests a rapid release of ^{33}P to the dissolved pool, as supported by the

Fig. 9. Comparison of the average ($\pm \text{SE}$) phosphate uptake rate estimated from the initial increase in $^{33}\text{PO}_4$ in the particulate fraction (V) and from the reduction in DIP between the beginning and the end of the experiments (V_{net}) in surface and DCM waters. Sample size for each mean and standard error = 8

observation that the DOP concentrations increased greatly (>5 -fold) during the incubation in most of the experiments, leading to substantial (mean $\pm \text{SE} = 0.0055 \pm 0.002 \mu\text{mol P l}^{-1} \text{h}^{-1}$) net DOP production rates. Hence, the sum of the DOP and POP production rates was closely correlated ($r = 0.70$, $p < 0.05$) with our estimates of the net DIP uptake rate, thereby accounting for the loss of DIP during the incubations. The net DOP production rates accounted, on average, for $75 \pm 9.3\%$ of the total phosphate uptake, and were, on average, 4-fold greater at the DCM ($0.007 \pm 0.002 \mu\text{mol P l}^{-1} \text{h}^{-1}$) than those in surface waters ($0.002 \pm 0.0008 \mu\text{mol P l}^{-1} \text{h}^{-1}$), where DIP concentrations, and likely DIP supply, were lower. Indeed, the net DOP production rate increased significantly ($r = 0.97$, $p < 0.0001$; $r = 0.66$, $p > 0.05$ if the experiment at the highest DIP concentration is excluded) with increasing DIP concentration (Fig. 10).

DISCUSSION

DIP concentrations were low ($<0.04 \mu\text{mol P l}^{-1}$), but always above the detection limit, in the surface waters along the transect, but DIP concentrations tended to be somewhat higher in DCM waters, which receive the diffusive DIP flux across the thermocline. POP represented a small fraction (17.4%, on average) of the total P pool and was consequently low, particularly when compared to POC concentrations. The high POC:POP ratios observed (>200) suggest that detrital particles made an important contribution to POC. Most of the POP was contained in relatively large ($>0.8 \mu\text{m}$) parti-

Fig. 10. Relationship between the net rate of DOP production and the DIP concentration in the upper water

cles, but small ($<0.8 \mu\text{m}$) particles had lower C:P ratios, as expected from the importance of bacteria and cyanobacteria, which are characterized by low C:P ratios (Goldman et al. 1987, Vadstein et al. 1988), in this size fraction.

The rates of phosphate incorporation into the particulate fraction were relatively low, resulting in long phosphate turnover times (days), except in the surface waters at the southern end of the transect (25 to 36°S). These waters were also characterized by the highest phosphate uptake rates, and the smallest total P pools observed along the transect. The communities north of the equator were characterised by a relatively high biomass of DIP consumers, dominated by nano- and microplankton, and showed a rather high DIP uptake rate. This was in sharp contrast with the communities in the waters in the gyre area south of the equator, which showed the lowest biomass, phosphate uptake rates, and smallest proportion of P incorporation into the particulate pool. The communities growing in the waters at the southern end of the transect grew under very low phosphate concentrations, but showed high phosphate uptake rates, therefore leading to the fastest phosphate turnover rates observed. The proportion of ^{33}P incorporated into the particulate fraction during experiments was $<45\%$, and was again greatest at the southern end of the transect. These findings, together with the observations that the communities realized the maximal phosphate uptake rates possible at the *in situ* phosphate concentrations in the few stations where this was tested experimentally, suggest that the supply of inorganic P was sufficient to meet the demands of the planktonic communities growing in the Central Atlantic. Evidence of P limitation was, however, observed in the P-depleted waters at the southern end of the transect, where P-uptake rates appeared to be limited by P supply. This suggestion is

supported by the observation of a significant alkaline phosphatase activity, which was only detected in the southern-most area ($\sim 30^\circ\text{S}$; M. Vidal unpubl. data).

The smallest ($<0.8 \mu\text{m}$) components of the plankton, which dominated the most unproductive waters sampled here, were characterized by higher uptake rates and affinity for phosphate than larger ones, supporting previous conclusions (e.g. Currie & Kalff 1984, Olsen 1989, Thingstad et al. 1993) that picoplankton are superior competitors for P than larger plankton. The k:POP ratios measured in Atlantic waters, which provide rough estimates of the affinity for P of the communities, are within the lower range of previously reported estimates (e.g. Currie & Kalff 1984, Vadstein 1994, Cañellas et al. unpubl.), similar to those characteristic of P-saturated phytoplankton and bacteria (Olsen 1989, Vadstein & Olsen 1989).

Most analyses of size-fractionated phosphate uptake pointed to heterotrophic bacteria as major players in this process (e.g. Friebele et al. 1978, Berman 1983, Currie & Kalff 1984, Thingstad et al. 1993, Björkman & Karl 1994, Dolan et al. 1995). Yet, some reports point to a similar contribution of phytoplankton and bacteria (e.g. Harrison et al. 1977, Krempin et al. 1981) or to a dominant role of phytoplankton (e.g. Lebo 1990, Thingstad et al. 1996) in some areas. Bacterial dominance in P uptake has been proposed to be characteristic of systems with DIP turnover times much shorter than those observed in Atlantic waters (e.g. Krempin et al. 1981, Lean et al. 1987, Thingstad et al. 1993), whereas a greater contribution of phytoplankton to P uptake is often observed in waters with longer DIP turnover times (e.g. Thingstad et al. 1996).

The long turnover time and slow phosphate uptake rates generally observed in the Central Atlantic Ocean are in agreement with previous observations in oceanic waters elsewhere (Fig. 11). This suggests that our conclusion that P is unlikely to be the primary limiting resource for planktonic growth in the Central Atlantic may be applicable to other regions of the open ocean. In contrast, however, estuarine and coastal systems often display short DIP turnover times (e.g. Taft et al. 1975, Thingstad et al. 1993; Fig. 11), although still generally longer than the very fast (minutes) turnover time characteristic of lakes (e.g. Rigler 1956, Lean et al. 1987), which approach those characteristic of strongly P-limited phytoplankton cultures (e.g. Fuhs et al. 1972, Healey 1973, Rivkin & Swift 1982). Yet, conclusive evidence of P limitation has been derived from the analysis of long-term studies in warm, oligotrophic waters (Michaels et al. 1996, Karl et al. 1997).

Our results suggest that P availability exceeded P demand across most of the Central Atlantic at the time the study was conducted. Whether this situation represents a transient phenomenon or, rather, a consistent

Fig. 11. Turnover rate of dissolved inorganic P in marine systems. (1) Thingstad et al. 1993; (2) Taft et al. 1975; (3) Friebele et al. 1978; (4) Lebo 1990; (5) Pomeroy 1960; (6) Berman 1983; (7) Björkman & Karl 1994; (8) Dolan et al. 1995; (9) Krempin et al. 1981; (10) Thingstad et al. 1996; (11) Nalewajko & Lee 1983; (12) Eppley et al. 1973; (13) Harrison et al. 1977; (14) Harrison 1983; (15) Perry & Eppley 1981; (16) This study. *Single values, rather than ranges, were available

feature of this area of the ocean cannot be resolved here, as the results presented were derived from a short-term study in which seasonal and interannual variation may be important. Although there are no previous estimates of P uptake and turnover for the area studied, a similar transect study conducted half a year before the study described here reported evidence of N limitation of the planktonic community (Planas et al. 1999), consistent with results from previous studies in the region (Le Bouteiller 1986, Metzler et al. 1997). Thus, excess P may be a consistent feature of this region of the ocean. The planktonic organisms take up inorganic P at considerable rates, but appear to be unable to convert the P incorporated into growth, suggesting an insufficient supply of other nutrients (e.g. N, Fe). This results in the high rates of DOP release, which represent the combined release by the DIP consumers and their microbial grazers, averaging about 75% of the uptake of DIP and supporting relatively high DOP concentrations in the upper Central Atlantic. These results are consistent with the importance of DOP as an integral component of the P pool in the upper ocean (e.g. Orret & Karl 1987, Vidal et al. 1999). The importance of DOP release in Central Atlantic waters is comparable to a similarly important release of

DOC and DON, thereby accounting for the large DOM pool accumulating in these waters (Vidal et al. 1999). In contrast, however, the P released as DOP is then rapidly recycled, as inferred from the high DON:DOP ratio (median ratio 28) in Central Atlantic waters (Vidal et al. 1999), leading to a relatively rapid turnover of the P contained within the plankton in the Central Atlantic as well as a relatively low downward flux of DOP compared to that of DON (Vidal et al. 1999). The planktonic community acts, therefore, as a pump system, mediating the transition between inorganic and organic phosphorus in the dissolved phase. As a result, vertical gradients of DOP concentration in the upper Central Atlantic (cf. Vidal et al. 1999) are not as strong as those reported elsewhere (Coste et al. 1988, Walsh 1989, Bethoux et al. 1992), supporting a modest downwelling flux of P, which accounts for only 9% of the upward phosphate supply (Vidal et al. 1999). The modest loss of P through the downward flux of DOM is in contrast with the important loss of N with sinking DOM, which often exceeds the upward nitrate supply (Vidal et al. 1999).

In summary, we conclude that P availability equalled or exceeded planktonic requirements over most of the Central Atlantic at the time of the study, except for the

southern end of the transect, where some evidence of P limitation was detected. The results support, when combined with other estimates available in the literature, the existence of a general trend towards a reduction in the importance of P as a limiting nutrient from freshwaters to the open ocean. Despite this situation, the high efficiency for P uptake by the pico-sized organisms dominating planktonic communities in the oligotrophic waters studied here allows them to play a major role in the geochemical processes involving P. The excess P relative to requirements fuels a luxury P uptake by the planktonic community in the oligotrophic waters studied here, leading, together with grazer-mediated release, to a rapid transformation of inorganic P into DOP, thereby minimizing P losses from the biogenic layer.

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