

NOTE

Phytoplankton nutrient control in the oligotrophic South Pacific subtropical gyre (Tuamotu Archipelago)

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ABSTRACT: The identification of the nutrients likely to limit phytoplankton in the Tuamotu Archipelago ocean (South Pacific subtropical gyre) is deduced from DIN ($\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$), PO_4^{++} , and SiO_2 *in situ* concentrations and strengthened by the results of 4 other studies on the same area: (1) ϕ_{\max} , the maximum quantum yield of photosynthesis, (2) phytoplankton cell size, (3) nutrient enrichment on natural populations, (4) bacterial biomass and nutrient limitation of bacteria. The low ϕ_{\max} and the small size of phytoplankton support the idea of nutrient control. Low DIN concentrations (mean = 0.02 μM), low average DIN:P- PO_4^{++} ratios = 0.3 at:at, low average DIN: SiO_2 = 0.04 at:at, and significant increases of phytoplankton standing stock and bacterial production after N enrichments point to N as the main limiting nutrient. P is the second limiting nutrient as evidenced by the relative low phosphate concentrations (0.2 μM) and by the synergistic effect of DIN + PO_4^{++} enrichments. Silicon concentrations appear to limit the proliferation of siliceous taxa as evidenced from its average concentration of 1 μM and from the scarcity of diatoms. Natural concentrations of vitamins, Mo, Mn, Fe and chelators are sufficient to support the increase of phytoplankton standing stock induced by N and P additions and therefore are not limiting.

KEY WORDS: Phytoplankton · Nutrient control · South Pacific · Central gyre · Oligotrophy

The oligotrophic area constitutes more than 75% of the surface of the world's ocean. Within this vast area, nitrogen has been, for a long time, considered as the limiting nutrient of phytoplankton production and standing stock (Howarth 1988). However, the oligotrophic ocean cannot be considered as homogeneous and other nutrients should control phytoplankton: P (Eppley et al. 1973), Si (Brzezinski & Nelson 1996), Fe (Lindley et al. 1995). This note presents a comprehensive study on the phytoplanktonic nutrient control in the South Pacific central gyre where the control of

phytoplankton has never been studied, to our knowledge. It was conducted in the oceanic area of the Tuamotu Archipelago where extremely low concentrations of nutrients are maintained in surface waters by a permanent thermal stratification between 150 and 200 m depth (Rancher & Rougerie 1995).

Fisher et al. (1988) argued that concentrations $< K_s$ are associated with reduced uptake rates, potentially lowered enough to reduce phytoplankton growth rates or phytoplankton biomass accumulation. Indeed, in such environments with constant low limiting nutrient supply, nutrient luxury consumption and storage (Droop 1983) are unlikely to occur, and growth depends on the uptake of the limiting nutrients. In this note, we compare the concentrations of the major nutrients N, P and Si, measured in the oceanic area of the Tuamotu Archipelago, with their half-saturation constants for uptake (K_s), reported in the literature. The conclusions issued from these comparisons are improved by the results of 4 other studies in the same area: (1) light-photosynthesis curves (Pagès pers. comm.), (2) cell size and taxonomic composition of phytoplankton (Charpy & Blanchot 1998), (3) enrichment experiments (Dufour & Berland 1999) and (4) nutrient control of bacterial production (Torréton et al. 1998).

Materials and methods. The study took place during 2 oceanographic cruises, Typatoll 3 and Typatoll 4, on the RV 'Alis' in November 1995 and March 1996. Surface water (0.5 m depth) was sampled at 12 oceanic sites located between $15^\circ 30' - 18^\circ 30'$ S and $142^\circ - 145^\circ$ W (Fig. 1). Sampling was done leeward from a small plastic boat and at more than 1 km away from the RV. Water was sampled in acid-cleaned polyethylene bottles and processed within 1 h.

Analyses for PO_4^{++} and NH_4^+ were performed according to Murphy & Riley (1962) and Koroleff (1969) with a precision of 0.02 μM . $\text{NO}_2^- + \text{NO}_3^-$ and SiO_2 measurements were done according to Wood et al.

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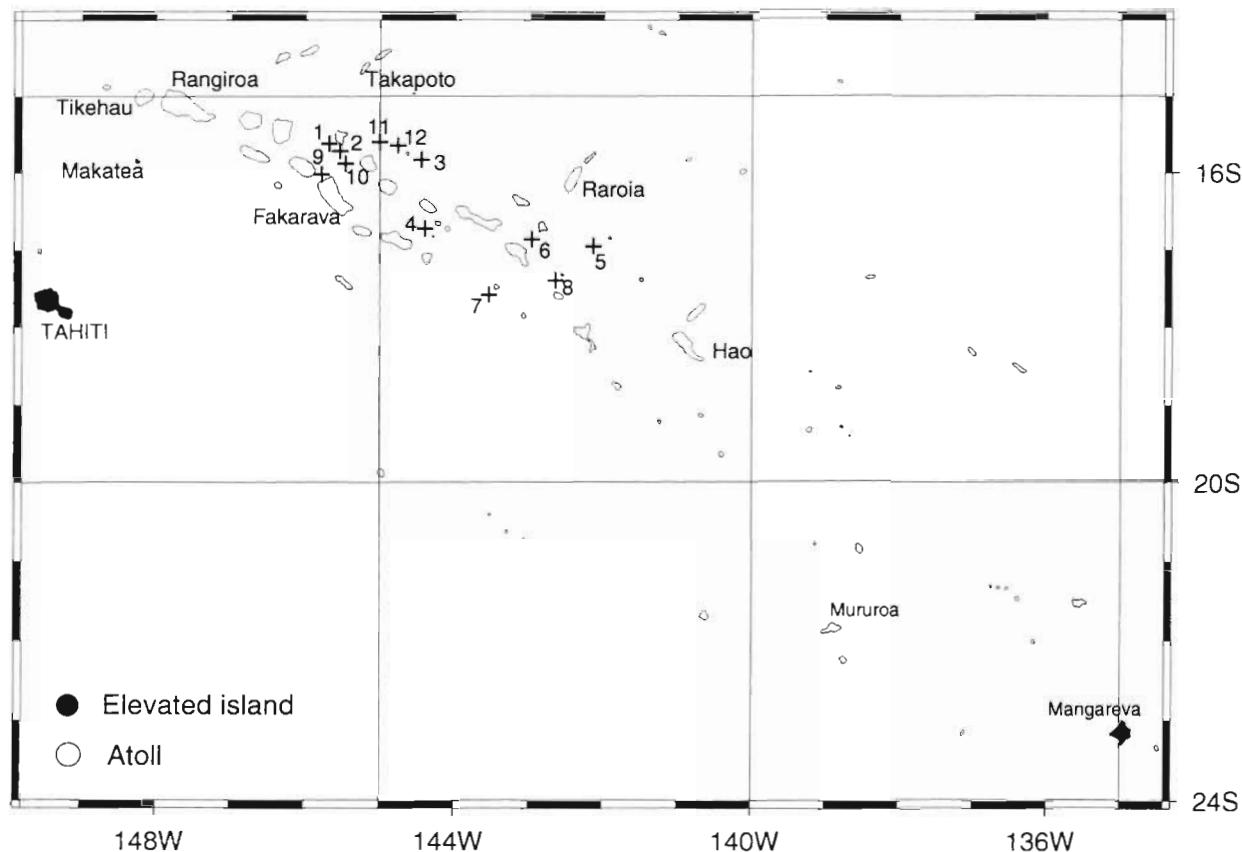


Fig. 1. Location of the 12 ocean sites sampled in the Tuamotu Archipelago (French Polynesia)

(1967) and Mullin & Riley (1955) with a Technicon autoanalyzer following Tréguer & Le Corre's (1975) protocol with a precision of 0.01 μM for $\text{NO}_2^- + \text{NO}_3^-$ and 0.10 μM for SiO_2 .

Results and discussion. Evidence of nitrogen limitation from nutrient concentrations in sea water: All the DIN (dissolved inorganic nitrogen) concentrations are $<0.05 \mu\text{M}$ (average = 0.02 μM , Table 1). Such low DIN concentrations were reported in surface waters of the North Pacific Central gyre and of the South-West

Pacific Ocean by Eppley et al. (1973), Perry & Eppley (1981), and Le Borgne et al. (1995, 1997). In the South Pacific subtropical gyre, DIN concentrations reported by Raimbault et al. (1999) at 15° S, 140° W were close to 0 (mean = 0.0013 μM , SD = 0.0025 μM , n = 5). In the surface waters of the Tuamotu Archipelago, Charpy-Roubaud et al. (1990) measured average $\text{NO}_2^- + \text{NO}_3^-$ concentrations of 0.07 μM (SD = 0.04, n = 11). All these DIN concentrations are inside the range of K_s , from 0.01 to 10.3 μM , for nitrate and ammonium uptake reported by Goldman & Glibert (1983). Recent studies tend toward lower values in oligotrophic waters. Indeed, a certain degree of physiological adaptation has been found for nutrient K_s controlling phytoplankton. K_s values of short-term nutrient uptake are generally much larger than the corresponding half-saturation of long-term (steady-state) uptake and growth (Morel 1987). In oligotrophic surface waters of the North Atlantic, K_s for NO_3^- and NH_4^+ uptake were as low as 0.02 to 0.03 μM (Harrison et al. 1996). In the oligotrophic tropical Pacific, Lindley et al. (1995) admitted a phytoplankton limitation for $\text{DIN} \leq 0.5 \mu\text{M}$. Finally, the DIN concentrations that we measured are close or below these K_s values for N uptake and a limitation by N is therefore expected.

Table 1. Dissolved nutrient concentrations. Mean for all stations. n = number of samples, DIN = dissolved inorganic nitrogen

Nutrient	Unit	Mean	SE	n
NH_4^+	μM	0.016	0.0041	19
$\text{NO}_2^- + \text{NO}_3^-$	μM	0.010	0.0036	24
DIN	μM	0.023	0.0048	19
PO_4^{3-}	μM	0.21	0.015	24
SiO_2	μM	1.03	0.109	24
DIN:P-PO_4^{3-}	at:at	0.14	0.028	19
DIN:Si	at:at	0.036	0.008	19
$\text{P-PO}_4^{3-}: \text{Si}$	at:at	0.24	0.022	24

The average PO_4^{++} concentration we measured (0.21 μM , Table 1) is much higher than the surface PO_4^{++} concentrations (from undetectable to 0.09 μM) reported for the surface waters of the Central North Pacific by Eppley et al. (1973) and Perry & Eppley (1981) and for the Central South-West Pacific by Le Borgne et al. (1995, 1997). PO_4^{++} concentrations like ours have been measured in the surface Pacific at the longitude of the Tuamotu Archipelago: on average 0.39 μM ($SD = 0.11$, $n = 13$) at 12° S by Garside (US JGOFS data system: nutrients; <http://www1.whoi.edu/jgofs.html>, with permission), 0.12 μM at 15° S ($SD = 0.06$, $n = 6$) by Raimbault et al. (1999) and 0.20 to 0.23 μM at 15° to 16° S by Reverdin et al. (1991). In the Tuamotu Archipelago oceanic waters, Charpy-Roubaud et al. (1990) reported PO_4^{++} average concentrations of 0.33 μM ($SD = 0.10$, $n = 33$) while Rancher & Rougerie (1995) reported an average of 0.15 μM ($SD = 0.05 \mu\text{M}$, $n = 5$). Such concentrations are close to the K_s for P uptake of 0.14 to 0.18 μM in the oligotrophic Central North Pacific (Perry & Eppley 1981) and, therefore, P is a potential limiting nutrient.

Our mean SiO_2 concentrations (1.03 μM , Table 1) are in the range of the concentrations (0.4 to 1.6 μM) reported for surface waters of Central South and North Pacific by Eppley et al. (1973), Perry & Eppley (1981) and Garside (JGOFS data system: nutrients). In the surface waters of the Tuamotu Archipelago, Charpy-Roubaud et al. (1990) observed Si concentrations identical to ours (mean = 1.08, $SD = 0.5$, $n = 19$). A wide range of K_s for Si uptake by diatoms, from 0.3 up to 22 μM , was reported by Brzezinski & Nelson (1996). However, from the data of Nelson & Brzezinski (1990), Brzezinski & Nelson (1996) and Nelson & Dortch (1996), we may deduce a reasonable limit of 1.5 μM under which the growth of natural assemblages of diatoms should be limited. Our mean SiO_2 concentration is under this threshold (Table 1). This should be the cause of the scarcity of diatoms in the Tuamotu oceanic waters dominated by non-siliceous taxa of *Prochlorococcus* and *Synechococcus* (Charpy & Blanchot 1998). Such a limitation of diatoms by Si was evidenced in other oligotrophic areas (Nelson & Brzezinski 1990, Brzezinski & Nelson 1996).

Results discussed above indicate a potential limitation of phytoplankton by N, P and Si. Nutrient atomic ratios can be used to determine the most limiting nutrient (Goldman et al. 1979). Measured DIN:P- PO_4^{++} ratios (on average 0.14 at:at, Table 1) are well below the optimal Redfield ratio of 16 at:at. The observed DIN:Si ratios (Table 1) are far below the value of 1 at:at considered as the optimal uptake ratio for diatoms (Nelson & Dortch 1996). From these low ratios we may deduce that N limits more than P and Si.

Such nitrogen limitation is questionable. Indeed, McCarthy & Goldman (1979) observed that some phyto-

planktonic cells can rapidly and efficiently utilize zooplankton and bacteria excreta before they are physically dispersed to the surrounding media. Therefore, other evidence of nutrient limitation is required.

Evidence of nutrient limitation from other kinds of studies in the same area: (1) The maximum quantum yield of photosynthesis, \varnothing_{\max} (maximum carbon dioxide fixed per photons absorbed at subsaturating irradiances), may be lowered by toxins, low temperatures or availability of a nutrient (Rabinowitch 1969, Lindley et al. 1995). \varnothing_{\max} was calculated from α , the initial slope of the chlorophyll-normalized primary production-irradiance curve (Pagès pers. comm., on the same samples as ours) and a_p , the chlorophyll absorption coefficient ($\varnothing_{\max} = \alpha/a_p$). For a_p , we used the mean value of 0.026 $\text{m}^2 \text{mg}^{-1}$ ($SE = 0.002$, $n = 8$) measured at 12° S, 140° W by Lindley et al. (1995). The average \varnothing_{\max} of 0.0069 mol C (mol photons) $^{-1}$ ($n = 6$, maximum of 0.013) was well below the operational maximum of 0.06 to 0.10 mol C (mol photons) $^{-1}$ (Cleveland et al. 1989) and indicated photosynthesis limitation. In the surface tropical waters of the Tuamotu Archipelago, phytoplankton metabolism is not submitted to thermal stress, nor toxicity, and nutrient limitation is likely to be the only factor affecting \varnothing_{\max} .

(2) Picoplankton largely dominates the algal biomass of the Tuamotu surface waters, as seen from the high proportion of chlorophyll in the class size <3 μm (86 %, $SE = 2$, $n = 11$, Charpy et al. 1997). According to Kiørboe (1993), cells smaller than 100 μm in diameter do not profit significantly, in terms of nutrient uptake, from natural water turbulence. However, the small size and, thus, the large surface to volume ratios of autotrophic picoplankton is an even greater advantage over larger algae for nutrient uptake (Chisholm 1992). Therefore, the low nutrient concentrations found in surface waters of the Tuamotu Archipelago are probably a powerful selective force favoring picoplankton. Conversely, the dominance of small cells in these areas may be used as an indicator of nutrient limitation.

(3) Nutrient enrichment experiments with N, P, Si, chelators, Fe, Mo, Mn and vitamins were carried out at Sites 1, 4, 6, 7 and 9 (Fig. 1). They allowed us to test the response of phytoplankton standing stock to the limiting nutrients and to their combination (Dufour & Berland 1999). Selected conclusions of these bioassays are reported in Table 2. A noticeable agreement with the conclusions deduced from *in situ* nutrient concentrations can be observed. Indeed, N appears clearly as the main limiting nutrient. However, the highest standing stock was obtained with N+P enrichments (data shown in Dufour & Berland 1999). This observation is consistent with a view that both N and P are in relatively short supply, so that enrichment by one nutrient without the other produces only a brief growth

Table 2. Nutrient controls according to *in situ* concentrations (this study) and to bioassays (Dufour & Berland 1999)

Site	<i>In situ</i> ^a	Bioassay ^b	Site	<i>In situ</i> ^a	Bioassay ^b
1	N>P>Si	N>P	7	N>P>Si	N>P>Si
2	N>Si		8	N>P>Si	
3	N>Si		9	N>P>Si	N>P
4	N>P	N=P	10	N>P>Si	
5	N>P		11	N>P>Si	
6	N>P>Si	N>P	12	N>Si	

^aN limitation: DIN:P-PO₄^{**} < 10 at:at and Si-SiO₂:DIN > 1 at:at, DIN ≤ 1 µM; P limitation: DIN:P-PO₄^{**} > 30 at:at and Si-SiO₂:P-PO₄^{**} > 3 at:at, PO₄^{**} ≤ 0.2 µM; Si limitation: Si-SiO₂:DIN < 1 at:at and Si-SiO₂:P-PO₄^{**} < 3 at:at, SiO₂ ≤ 1.5 µM
^bBased on increase of chlorophyll

enhancement until the depletion of the other nutrient occurs. Si addition increased phytoplankton standing stock only when N and P requirements were preliminarily satisfied. Natural concentrations of chelators, vitamins, Mo, Mn and Fe were sufficient to support increases of phytoplankton standing stock induced by N and P additions and therefore were not limiting. A source of these nutrients could originate from the atolls. Indeed Dufour & Berland (1999) did not observe such limitation by these nutrients in atoll lagoons. Recently, Lindley et al. (1995) speculated Fe and N co-limitation at 12° S, 140° W in the oligotrophic Central Pacific some degree north and outside of the Tuamotu Archipelago. However, it appears that iron enrichment stimulates the net growth of microphytoplankton or nanophytoplankton but not of cyanobacteria dominated picophytoplankton which can compensate for growth-limiting levels of iron by producing extracellular siderophores (Wilhelm et al. 1996). Indeed, a lack of Fe limitation is consistent with the observation that cyanobacteria dominate in the area under study (Charpy & Blanchot 1998).

(4) It is now well established that bacteria make up more of the oligotrophic ocean biomass than phytoplankton do (Cho & Azam 1990, Dufour & Torréton 1996). Bacterial carbon at the 12 sites sampled (Fig. 1) was 2.8 times the phytoplankton carbon (SD = 0.9, n = 12, Torréton pers. comm.). On the other hand, it was shown that the N:C ratio is higher in bacteria than in phytoplankton (Goldman et al. 1987). Therefore, a large part of the N standing stock is immobilized by bacteria and is not available for phytoplankton. Moreover, Wheeler & Kirchman (1986) showed that bacteria are able to compete successfully with phytoplankton for NH₄⁺. Therefore, under conditions of extremely low concentrations of DIN (and not of PO₄^{**}, as seen above), bacteria are likely to maintain the phytoplankton in a state of N limitation. The excretion of N-

depleted organic compounds by the phytoplankton should continue to promote this situation. On the other hand, Torréton et al. (1998) observed, in one site of the Tuamotu Archipelago ocean, a positive effect of NH₄⁺ addition on bacterial production. This result, together with the knowledge of nutrient competition between bacterioplankton and phytoplankton, reinforces our hypothesis of N limitation of phytoplankton.

Summary and conclusions. Results of the *in situ* nutrient concentration measurements and of the 4 other approaches have different significances. The low quantum yield of photosynthesis and the small size of phytoplankton account for a nutrient control. The *in situ* nutrient concentrations which are indicative

of the nutrient uptake limitation and the *in vitro* enrichment experiments which identify the nutrients that limit the phytoplanktonic standing stock agree with N limitation (Table 2). Therefore, other sources of N, such as N₂ fixation (Smith 1984), dissolved organic N (Bonin & Maestrini 1981) and rain (Prospero & Savoie 1989), appear insufficient to supply the phytoplankton N requirements. The high bacterial biomass and the N limitation of bacterial production confirm the N deficiency. Even if phosphate is not totally exhausted *in situ*, P is the second limiting nutrient as evidenced by the synergistic effect of N+P enrichments. Silicon concentrations appear most often under the threshold level for siliceous taxa. However, Si is less limiting than N as evidenced by DIN:Si. Si additions increase phytoplankton standing stock when N and P requirements are preliminarily satisfied, probably inducing a shift from picoplankton to larger diatoms. Natural concentrations of vitamins, Mo, Mn, Fe and chelators are sufficient to support the increase of phytoplankton standing stock induced by N and P additions and therefore are not limiting. A lack of Fe limitation is consistent with the dominance of cyanobacteria but contradicts the N and Fe simultaneous limitation speculated by Lindley et al. (1995) for the oligotrophic South Pacific Ocean. Nevertheless, if not limiting the phytoplankton stock, Fe and other micronutrients may control the phytoplankton taxonomic composition (Bonin & Maestrini 1981, Zettler et al. 1996).

The synthesis of these different studies gives a synoptic view of phytoplanktonic nutrient control. It is a further step towards knowledge of the biochemical functioning of the oligotrophic Central South Pacific. It also should be used as a reference to studies considering the functioning of the 77 lagoons of the Tuamotu Archipelago which are fuelled by the oceanic water of the South Pacific central gyre (Dufour & Harmelin-Vivien 1997).

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