

Atoll morphometry controls lagoon nutrient regime

Abstract—Nutrient control of phytoplankton was studied in 12 atoll lagoons of contrasting morphology in the Tuamotu Archipelago in the South Pacific. In large lagoons and in small lagoons well open to the ocean, N limitation was indicated by dissolved inorganic N (DIN, $\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) $< 0.5 \mu\text{M}$, by DIN/P- PO_4 ratios < 3 atom atom $^{-1}$, and by increased phytoplankton and bacterioplankton productivity after N enrichment. This trend shifts to P limitation for shallow, enclosed lagoons. N or P limitations are empirically predictable and explainable according to atoll-scale morphometric factors.

It is generally accepted that inorganic nutrient concentrations exert major control over phytoplankton biomass, productivity, and species composition (i.e., Dugdale and Wilkerson 1992). It was suggested that the conflict between nitrogen or phosphorus limitation of net community production in aquatic systems could be resolved by considering extrema of degrees of aperture (Smith and Atkinson 1984). Basically, a confined system should be P limited because of accumulation and recycling of internally fixed N until P is exhausted. Conversely, open systems should be N limited because they export N before P is lowered.

In atoll lagoons, Kimmerer and Walsh (1981) and Rayner and Drew (1984) suggested that N is limiting in Tarawa, Peros Banhos, and Salomon because of the low dissolved inorganic N to P ratios. Conversely, in Astove and Saint Joseph atolls, Littler et al. (1991) claimed a P limitation according to nutrient enrichment experiments and concentrations in seawater and macroalgal tissues. In Christmas Island and Canton atoll lagoons, primary production was limited because of reactive P concentrations below oceanic concentrations (Smith 1984). In Takapoto, Sakka et al. (1999) deduced from enrichment experiments that N, followed by P, regularly limits phytoplankton biomass and growth, whereas Fe may be in short supply at times. Finally, in other studies, nutrients did not seem to be limiting for primary production (Smith 1984; Sorokin 1995). Therefore, the trend in nutrient limitations and regimes in atoll lagoons worldwide is not clear.

In this study, we aim to test the hypothesis that the degree of confinement controls the type of nutrient limitation encountered in atoll lagoons. For this, we have considered a set of atolls bathed by a similar oceanic environment (Dufour et al. 1999), but with various morphological configurations in area, aperture, and depth. These configurations imply that the physical processes of water renewal (due to wave, wind, and tide; Kraines et al. [1999]) vary in efficiency from one atoll to another, providing a gradient of confinement inside this set of atolls.

The morphological features of the 12 studied atolls are in Table 1. These 12 atolls represent different types of atolls that can be defined according to the morphometry of the 77 atolls encountered in the Tuamotu Archipelago (Andréfouët

1998). In all the atolls, anthropogenic pressures (pollution, agriculture) are virtually nil.

Nutrient concentrations were measured at the end of the dry (November 1995) and rainy (April 1996) seasons during weather conditions typical of this region, with moderate east to southeast wind and a moderate southeastern swell. Sampling and methods are presented in Torrétion et al. (2000). Data for Takapoto and Tikehau atolls are from Charpy (1996).

Nutrient limitation was tested using concentration thresholds and DIN to P- PO_4 ratios. Published data indicate that uptake and growth of phytoplankton in coral reef waters are limited by N when DIN ($\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) $\leq 0.5 \mu\text{M}$ and by P when P- $\text{PO}_4 \leq 0.1\text{--}0.2 \mu\text{M}$ (Sorokin 1995). The mean intracellular N to P ratios of healthy phytoplankton generally do not deviate much from the 16 atom atom $^{-1}$ Redfield ratio. However, some marine phytoplankters depart from this average ratio. Moreover, because many species of picoplankton meet their needs for nutrients from dissolved organic matter and because DIN to P- PO_4 ratios in nutrient fluxes may differ from ratios in nutrient standing stocks, it is admitted that if DIN/P- $\text{PO}_4 > 30$ at atom $^{-1}$, P will be depleted first, whereas ratios < 10 at atom $^{-1}$ indicate N limitation (e.g., Smith 1984). In situ concentrations and DIN/P- PO_4 ratios can be compared with these thresholds to determine whether P or N is in shorter supply.

Evidence of nutrient control from in situ concentrations and ratios—DIN and P- PO_4 concentrations did not vary significantly within atoll lagoons (ANOVA, not shown; Dufour and Harmelin-Vivien 1997). Conversely, the concentrations of both nutrients varied significantly between atoll lagoons, and the concentrations of P- PO_4 varied seasonally. We therefore spatially averaged the data acquired for each lagoon and for each season (Table 2).

Oceanic water around Tuamotu atolls typically have average nutrient concentrations of $0.02 \mu\text{M}$ and $0.21 \mu\text{M}$ for DIN and P- PO_4 , respectively (Dufour et al. 1999). Assuming that the limiting thresholds given above are reliable, phytoplankton growth in atoll lagoons with a very fast flushing rate should be limited by DIN. However, this prediction is not only valid for well open atolls; the general trend is a limitation by N. In Haraiki, Hikueru, Hiti, Kauehi, Marokau, Nihiru, Taiaro, Tekokota, and Tepoto Sud, DIN/P- PO_4 ratios were regularly ≤ 3 at atom $^{-1}$, indicating N limitation before P limitation (Table 2). In Tikehau and Takapoto, NH_4 concentrations were not available. In Tikehau, the very low $\text{NO}_3^- + \text{NO}_2^-$ to P- PO_4 ratios of < 0.4 at atom $^{-1}$ indicate N rather than P limitation during both seasons. In Takapoto, we cannot presume which of N or P was less available for phytoplankton. In Reka-Reka, an average DIN/P- PO_4 ratio of 54 at atom $^{-1}$ in November suggested P limitation. In March, the average DIN/P- PO_4 ratio of 24 at atom $^{-1}$ is less than the con-