

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 Torrétton 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 at $^{-1}$, P will be depleted first, whereas ratios < 10 at at $^{-1}$ 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 at $^{-1}$, indicating N limitation before P limitation (Table 2). In Tikehau and Takapoto, NH_4 concentrations were not available. In Tikehau, the very low $\text{NO}_2^- + \text{NO}_3^-$ to P- PO_4 ratios of < 0.4 at at $^{-1}$ 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 at $^{-1}$ in November suggested P limitation. In March, the average DIN/P- PO_4 ratio of 24 at at $^{-1}$ is less than the con-

Table 1. Characteristics of the 12 atolls ordered by increasing area.

Atoll	Latitude	Longitude	S _{at}	S _{lag}	EAD	Aper.	Inh.	Expl.	Main characteristics of the choice
Reka-Reka	16°50'S	141°55'W	5.2	0.7	1	0.02	0	No	small size, low aperture
Tepoto Sud	16°49'S	144°17'W	6.2	1.6	5	0.15	0	No	small size, medium aperture
Tekokota	17°19'S	142°34'W	7.3	5.1	3	0.59	0	No	small size, high aperture
Haraiki	17°28'S	143°26'W	25	10.4	10	0.19	20	No	small to medium size, medium aperture
Taiaro	15°45'S	144°38'W	17.3	11.8	15	0.01	3	No	small to medium size, low aperture
Hiti	16°43'S	144°06'W	25	15	10	0.19	0	No	small to medium size, medium aperture
Nihiru	16°41'S	142°50'W	100	80	20	0.25	30	No	medium size, medium aperture
Takapoto	14°30'S	145°20'W	104	81	25	0.02	612	Pearl	medium size, low aperture
Hikueru	17°35'S	142°38'W	107	82	25	0.18	134	Pearl	medium size, medium aperture
Marokau	18°03'S	142°16'W	256	217	30	0.17	65	Pearl	big size, medium aperture
Kauehi	15°50'S	145°09'W	343	315	50	0.22	302	Pearl	big size, medium aperture
Tikehau	15°00'S	148°10'W	448	394	25	0.20	400	Fish	big size, medium aperture

S_{at}, atoll area; S_{lag}, lagoon area (km²); EAD, estimated average depth (m); Aper., degree of hydrodynamic aperture (or the relative length of communication between a lagoon and the ocean) quantified by the ratio (length of submerged reef flats + reef-flat spillway + passes)/(perimeter of atoll rim); Inh., number of inhabitants in 1996; Expl., marine commercial exploitation.

servative limit we admit for P limitation, 30 at at⁻¹, so we cannot conclude firmly for P limitation.

From concentration levels, it generally appears that DIN concentrations were below 0.5 μM, the presumed limiting threshold for phytoplankton growth (Table 2), except at Tekokota and Tepoto in November and Reka-Reka in both March and November. In all the lagoons except Tepoto and Tekokota, P-PO₄ concentrations were below the 0.2-μM threshold.

Confirmation of N and P limitations from other approaches—Previous studies confirm the resource limitation of Tu-

amotu phytoplankton by nutrients and the relative importance of N or P.

More than 60% of chlorophyll and ¹⁴C uptake are in the class size < 3 μm in Tuamotu atoll lagoons (Charpy 1996). The small size, thus the large surface to volume ratios, of autotrophic picoplankton is an advantage over larger algae in taking up low concentrations of limiting nutrients (Chisholm 1992). The dominance of this class of plankton may be an indicator of nutrient limitation.

Bacterioplankton carbon exceeds phytoplankton carbon in most of the 12 lagoons at both seasons (Torréon pers. comm.). Because bacterioplankton has higher N to C and P

Table 2. Nutrient concentration (μM) means and standard errors for each lagoon and season.*

Atoll	Season	DIN		P-PO ₄		DIN/P-PO ₄	
		Mean	SE	Mean	SE	Mean	SE
Reka-Reka	Nov	0.54	0.047	0.01	0.000	53.80	4.663
Reka-Reka	March	0.85	0.144	0.04	0.005	23.51	2.903
Tepoto	Nov	0.63	0.164	0.27	0.016	2.65	0.685
Tepoto	March	0.12	0.024	0.25	0.012	0.47	0.088
Tekokota	Nov	0.59	0.055	0.26	0.004	2.27	0.203
Tekokota	March	0.33	0.058	0.30	0.016	1.08	0.157
Haraiki	Nov	0.25	0.078	0.08	0.011	3.02	0.914
Haraiki	March	0.22	0.115	0.18	0.023	1.00	0.427
Taiaro	Nov	0.06	0.020	0.14	0.012	0.40	0.119
Taiaro	March	0.04	0.008	0.13	0.016	0.30	0.061
Hiti	Nov	0.08	0.016	0.11	0.020	0.83	0.076
Hiti	March	0.15	0.029	0.10	0.010	1.46	0.304
Nihiru	Nov	0.10	0.026	0.13	0.005	0.74	0.156
Nihiru	March	0.10	0.015	0.16	0.013	0.66	0.102
Takapoto	Nov	0.20*	0.049	0.04	0.005	5.48*	1.130
Takapoto	March	0.28*	0.057	0.02	0.003	15.46*	3.728
Hikueru	Nov	0.02	0.006	—	—	—	—
Hikueru	March	0.09	0.014	0.03	0.011	1.00	0.427
Marokau	Nov	0.06	0.015	0.12	0.002	0.51	0.127
Marokau	March	0.14	0.014	0.16	0.010	0.93	0.095
Kauehi	Nov	0.05	0.013	0.07	0.004	0.79	0.207
Kauehi	March	0.05	0.009	0.21	0.010	0.25	0.046
Tikehau	Nov	0.05*	—	0.13	—	0.39*	—
Tikehau	March	0.03*	0.003	0.10	0.008	0.26*	0.030

* DIN = NO₂⁻ + NO₃⁻ + NH₄⁺ except where designated by an asterisk, where DIN = NO₂⁻ + NO₃⁻.

Table 3. Nutrient controls by N or P, according to in situ concentrations and to bioassays. Results of phytoplankton bioassays from Dufour and Berland (1999). Results of bacterioplankton bioassays from Torr eton et al. (2000).*

Atoll	November			March		
	Nutrients in situ†	Bioassay		Nutrients in situ†	Bioassay	
		Phytoplankton	Bacterioplankton		Phytoplankton	Bacterioplankton
Reka-Reka	P>N	P=N	P	P or N	P>N	P
Tepoto Sud	N	N>P	G	N	N>P>Si	N>G
Tekokota	N	N>Si=P	—	N	N>P>Si	—
Haraiki	N>P	N>P	N	N>P	N>P>Si	N
Taiaro	N>P	N>P	N	N>P	N>P	—
Hiti	N>P	N=P	G	N>P	N=P	G
Nihiru	N>P	N>P	N	N>P	N>P>Si	N
Takapoto	N or P	?	?	N or P	N>P‡	?
Hikueru	N, P	N=P	N=P	N>P	N>P	P>N
Marokau	N>P	N	—	N>P	N>P>Si	—
Kauehi	N>P	N=P	N	N>P	?	N
Tikehau	N>P	?	?	N>P	?	?

* G, glucose; ?, no data; —, no or inconsistent response to nutrient amendment.

† N limitation when $\text{DIN/P-PO}_4 < 10$ at at^{-1} and $\text{DIN} \leq 1 \mu\text{M}$; P limitation when $\text{DIN/P-PO}_4 > 30$ at at^{-1} and $\text{P-PO}_4 \leq 0.2 \mu\text{M}$.

‡ From Sakka et al. (1999) in April 1996 and April 1997.

to C ratios than phytoplankton (e.g., Kirchman 1994), a large part of the N and P standing stock is sequestered in bacterial biomass and is likely not available for phytoplankton.

To test the response of phytoplanktonic standing stock to nutrient limitations, enrichment experiments with N, P, Si, chelators, Fe, Mo, Mn, vitamins, and their combinations were carried out on water samples coming from the same 12 lagoons, Tikehau excepted (Dufour and Berland 1999; Sakka et al. 1999). Selected conclusions of these bioassays are reported in Table 3. Nitrogen appears clearly as the first limiting nutrient, except in Reka-Reka, where it is phosphorus in March. In all lagoons, natural concentrations of Si, chelators, Fe, Mo, Mn, and vitamins were sufficient to support increases of phytoplankton biomass induced by N and P additions and therefore were not limiting.

Torr eton et al. (2000) simultaneously tested the effect of glucose, ammonium, and phosphate additions on the growth of bacterioplankton in the same lagoons. Their results (Table 3) point to N as the principal limiting inorganic nutrient for bacterioplankton growth, except in Reka-Reka and Hikueru, where it is P. The N and P phytoplanktonic limitation is likely reinforced by the competition with bacterioplankton, itself nutrient limited, and by the expected higher affinity of bacteria for inorganic nutrients (e.g., Kirchman 1994).

Average N/P ratios in the suspended particulate organic matter, again in the same lagoons, ranged between 5.1 and 14.9 at at^{-1} (Charpy et al. 1997). These values have to be used cautiously as indicators of phytoplankton limitation since this particulate organic matter is mainly composed (82–95%) of detrital materials. Generally, detrital materials have N/P ratios higher than living materials because of rapid P recycling. Therefore, low N/P (below Redfield ratios) reveals N rather than P deficiency in the sestonic fraction.

Enrichment experiments using the protocol of Dufour and Berland (1999) indicate a potential limitation of phytoplankton standing crop by nutrients. In situ nutrient concentrations point to a limitation of nutrient uptake and specific growth

rate of natural phytoplanktonic communities. Bioassays on bacteria suggest a competition for limiting nutrients. The three approaches inform about different aspects of nutrient control. We note that they are in close agreement about N and P limitations (Table 3).

The shift from N to P limitation with atoll morphology—The results listed above point to a general N limitation, except in the case of the Reka-Reka atoll, which seems P limiting for phytoplankton (this study) and bacterioplankton (Torr eton et al. 2000). Reka-Reka is representative of the group of atolls with small, confined, and shallow lagoons. A dozen of these atolls are encountered in the remote eastern part of the Archipelago. It was not possible to include other atolls of this group to confirm this unique behavior because of their limited accessibility.

Despite a total number of only 12 atolls sampled in 1995–1996, their contrasting morphology allows assessment of the continuum of changes in DIN and P-PO_4 concentrations when lagoon size and aperture vary (Figs. 1, 2). DIN concentrations were negatively correlated with lagoon size (DIN vs. log of the average depth: $r^2 = 0.88$, $n = 10$, Fig. 1; DIN vs. log surface: $r^2 = 0.69$, $n = 10$), but not with aperture. Conversely, P-PO_4 concentrations were not related to lagoon size or depth, but rather to aperture ($r^2 = 0.45$, $n = 12$, Fig. 2) and therefore to the degree of exchange between lagoon and ocean. DIN/P-PO_4 ratios tend to be higher in the shallowest lagoons and in enclosed lagoons ($\text{DIN/P-PO}_4 = -29.7[\text{aperture}] - 0.35[\text{average depth}] + 17.2$, $r^2 = 0.56$, $n = 10$). These trends strongly suggest that the results for Reka-Reka are not random chance but that this atoll is well representative of an end-member in term of nutrient regimes in atoll lagoons.

The shift from N to P limitation envisioned for a shallow, enclosed lagoon could result from a combination of the four following processes. 1. The highly oxygenated upper layer of the carbonate-rich sediments of atoll lagoons should

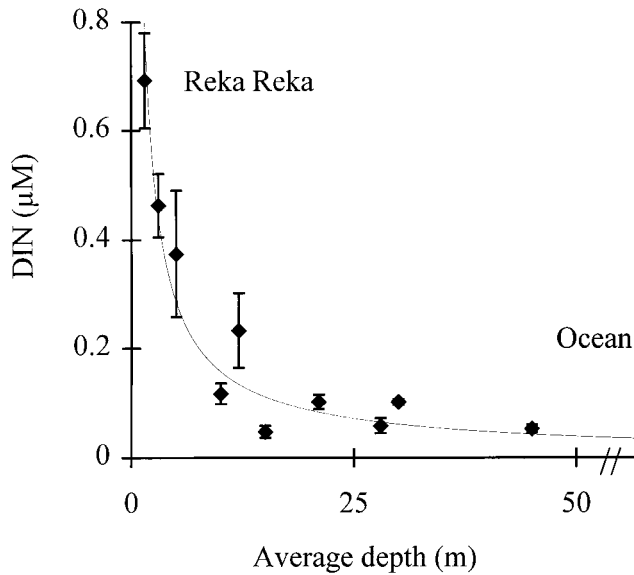


Fig. 1. Relation of DIN ($\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) concentrations with average depth of lagoon. Mean \pm SE for each lagoon.

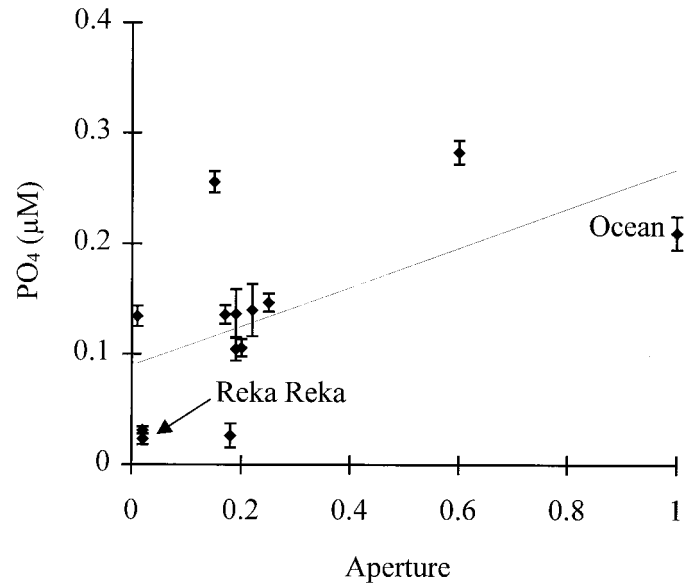


Fig. 2. Relation of dissolved phosphate concentrations with aperture of lagoon. Mean \pm SE for each lagoon.

strongly adsorb and precipitate P. Sorokin (1995) reported a net flux of P- PO_4 from water column to different bottom biotopes of coral systems. In Tikehau atoll, Charpy-Roubaud et al. (1996) demonstrated that diffusional fluxes from sediment to water column tend to be deficient in P, with a mean DIN/P- PO_4 ratio of 30 at at^{-1} . 2. Nitrogen fixation by benthic cyanobacterial communities and net export of DIN and dissolved organic N to the overlying water occur widely in coral reef environments (Larkum et al. 1988; Charpy-Roubaud et al. 1997). Smith (1984) estimated that about 60–85% of the N incorporated into organic material in Canton Atoll and Christmas Island lagoons originates from N_2 fixation. 3. Nitrogen enrichment via rainfall can shift nutrient limitation of phytoplankton growth from N to P in the surface ocean (Prospero and Savoie 1989) and thus could also do so in shallow atoll lagoons. 4. The high bacterial biomass in Tuamotu (*see above*) with N to P ratio content < 16 at at^{-1} (Kirchman 1994) sequesters more P than N compared to phytoplankton.

However, in most of the Tuamotu lagoons, these processes do not occur at rates high enough to prevent N depletion from the water column. Diffusional flux of ammonium from sediments in Tikehau is estimated to contribute only 0.1–6.8% of the N requirement for lagoon primary production (Charpy-Roubaud et al. 1996). Moreover, N losses can occur through denitrification (Smith 1984). In Tikehau lagoon, Charpy-Roubaud et al. (1997) estimated that planktonic and benthic N fixation does not contribute more than 13% of the N requirement for gross primary production. This percentage is coherent with the 9–14% provided by N_2 fixation at One Tree Island (Larkum et al. 1988). Prospero and Savoie (1989) have shown that the nitrate content of rainwater is three times lower in the South Pacific than in the North Pacific because of the scarcity of anthropogenic sources in the southern hemisphere. The surrounding ocean is likely the main source of nutrients for atolls (Atkinson 1992), and oce-

anic waters in the Tuamotu Archipelago are clearly N depleted (DIN = $0.02 \mu\text{M}$, DIN to P- PO_4 ratios < 0.2 at at^{-1} , *see* Dufour et al. 1999). Rougerie (1995) suggested that deep nutrient-rich waters are convected upward within the atoll structures under thermal pressure. Interstitial waters in the Tuamotu reefs regularly have DIN to P- PO_4 ratios < 10 at at^{-1} (Rougerie 1995). Therefore, their efflux into lagoons should also cause a N rather than a P deficit. Finally, phosphorus can be recycled faster than N so that low residual concentrations of inorganic P can sometimes be observed when inorganic N is fully depleted (e.g., Sorokin 1995).

In the shallow and enclosed Reka-Reka lagoon, one mechanism likely explains the shift from N to P limitation. In shallow lagoons, enrichment of the water column in DIN by benthic N_2 fixation or NH_4^+ efflux from bottom sediments may occur (Charpy-Roubaud et al. 1996, 1997). Supply of DIN favors phytoplankton growth and creates a simultaneous demand for P. Because of P- PO_4 deficit influx from the sediment (Charpy-Roubaud et al. 1996; *see above*), P must be supplied by the water column. Consequently, in small, poorly flushed lagoons such as Reka-Reka, P concentration in the water column progressively decreases until it becomes limiting for phytoplankton growth. In other shallow lagoons with medium or large apertures (Tepoto Sud, Tekokota), water is renewed by oceanic fluxes in a few hours or days, according to swell conditions (Pagès and Andréfouët unpubl. data). Nutrient efflux from the bottom sediments is likely overwhelmed by the large volume throughput of oceanic water (which is N limited). In medium to large, deep (10–50 m) lagoons, benthic fluxes are not sufficient to sustain phytoplankton demand (Charpy-Roubaud et al. 1996), and N, rather than P, is limiting in spite of N_2 fixation or N efflux. Therefore, the shift from N to P limitation depends on the relative importance of benthic over pelagic processes. It reflects the increasing confinement of the lagoon, depending on degree of aperture, depth, and size.

Conclusions and generalizations—Considering N and P, the nutrient phytoplankton control of atoll lagoons appears to vary with morphology. In lagoons that are deep or well flushed, N is in shorter supply than P, as it is in the ocean. This scenario is the most usual. However in shallow and confined lagoons, net production tends to be limited by the exogenous oceanographic delivery of P, whereas N requirements should be satisfied by endogenous and mainly benthic N fixation. The processes and morphological factors we point to in the Tuamotu Archipelago could also explain the observed decrease in P-PO₄ concentrations from the ocean to the lagoons in Tarawa, Christmas Island, Canton, Uvea, Saint Joseph, Astove, and Uvea (Kimmerer and Walsh 1981; Smith 1984; Novozhilov et al. 1992; Le Borgne et al. 1997). Our findings are also consistent with N limitation of Tarawa (Kimmerer and Walsh 1981), Peros Banhos, and Salomon atoll lagoons (Rayner and Drew 1984), all deep or well-flushed, and P limitation of Christmas Island and Canton (Smith 1984), Saint Joseph, and Astove atolls (Littler et al. 1991), all shallow and confined lagoons.

This comparative study suggests that N is the main limiting factor, but this trend shifts to P limitation as confinement increases or depth decreases.

*Philippe Dufour*¹

Institut de Recherches pour le Développement
Station d'Hydrobiologie Lacustre de l'INRA
75 avenue de Corzent
74203 Thonon les Bains
France

Serge Andréfouët

Remote Sensing/Biological Oceanography
Department of Marine Science
University of South Florida
1407th Avenue South
St. Petersburg, Florida 33701

Loïc Charpy

Institut de Recherches pour le Développement
Centre d'Océanologie de Marseille
rue de la Batterie des Lions
F-13007 Marseille
France

Nicole Garcia

C.N.R.S.
Centre d'Océanologie de Marseille
case 901
University Luminy
F-13009 Marseille
France

¹Corresponding author (dufour@ird.fr).

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Distribution and behavior of dissolved hydrogen sulfide in hydrothermal plumes

Abstract—Through the deep ocean, hydrothermal plumes disperse high concentrations of key chemical tracers including He-3, CH₄, Mn, Fe, H₂S, etc. This paper focuses on the distribution and behavior of total dissolved sulfide (sulfide hereafter) in hydrothermal plumes to show that its plume concentration decreases to subnanomolar a few kilometers from the vents. We also report on sulfide removal rates determined at in situ conditions; we observe that they are two orders of magnitude greater than for open ocean seawater, consistent with sulfide being detected only in the vicinity of hydrothermal vents. From our observations, we infer that the sole presence of sulfide in hydrothermal plumes locates active venting at the kilometer scale.

An exhaustive review of hydrothermal vent fluid chemistry data confirms that sulfide is vented at all known sites in concentrations from one to several tens of mmol L⁻¹ (Von Damm 1995). Conversely, little is known about hydrothermal plume sulfide concentrations since the few available water column data (i.e., Mottl and McConachy 1990; Radford-Knoery et al. 1998; Mandernack and Tebo 1999) do not constrain the lateral extent of sulfide in the plume. Here, we present two studies; the first one pertains to the distribution of total dissolved sulfide (sulfide hereafter) in the hydrothermal plume of an Atlantic ocean vent site, and the second one examines the kinetics of sulfide removal at conditions of temperature and concentration (nanomolar range) encountered in the plume.

We studied the Rainbow hydrothermal plume because its dispersion is well characterized (German et al. 1998; Thurnherr and Richards in press) and the end member vent fluids have been analyzed (Douville et al. 1997). We report on the data from four vertical hydrocast stations occupied during the Flame cruise (Fig. 1) for which sulfide measurements were performed. Three of these stations are within 2 km of each other, slightly downstream from the vent site (German et al. 1998; Thurnherr and Richards in press). The fourth station (Flame-HYD02) is located 4 km farther downstream.

Water samples collected in trace metal cleaned Niskin-type sampling bottles were subsampled for shipboard (sulfide) and shore-based (manganese, other parameters) analyses. Sulfide analyses were completed less than 40 min after the

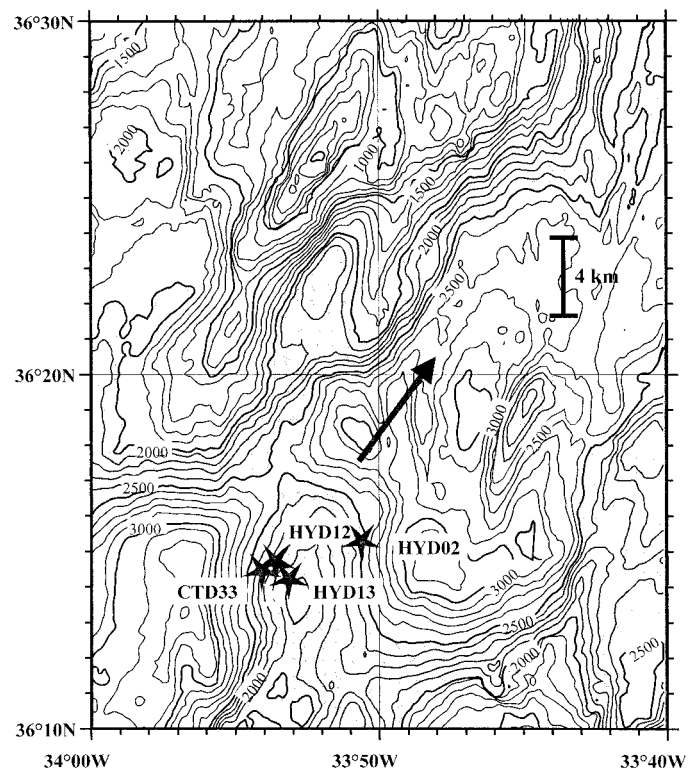


Fig. 1. Bathymetric map with station locations (stars) and the Rainbow hydrothermal vent field (cross). The arrow indicates the prevailing current direction at plume depth in the rift valley, and the scale bar indicates distance. For clarity, the ridge area between 2,500 and 2,000 m depth is grayed; the neutrally buoyant hydrothermal plume disperses between 2,100 and 1,900 m depth.