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RELATIVE CONTRIBUTIONS OF *PROCHLOROCOCCUS* AND *SYNECHOCOCCUS* TO PICOPHYTOPLANKTON BIOMASS AND PRODUCTION OF ELEVEN TUAMOTU ATOLL LAGOONS (FRENCH POLYNESIA)

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ABSTRACT

The contributions of *Prochlorococcus* and *Synechococcus* to phytoplankton biomass and production were measured in eleven atoll lagoons of the Tuamotu archipelago. Both taxa were present in all lagoons. Their average abundances ranged from 1×10^3 to 280×10^3 *Prochlorococcus* ml^{-1} in Reka-Reka and Hiti respectively and 7×10^3 to 278×10^3 *Synechococcus* ml^{-1} in Reka-Reka and Tepoto Sud respectively. The shallow atoll lagoons showed a predominant influence of eukaryotes probably due to the suspension of micophytobenthic cells. *Synechococcus* was the major contribution to primary production in nine of the eleven atolls, contributing up to 70% of the primary production in six of them. The observed phytoplankton community structure was the same as in Tikehau atoll but differed from the open ocean where *Prochlorococcus* were dominant in term of biomass and production.

INTRODUCTION

By using different techniques the great abundance of prokaryotic phytoplankton was reported in the open and coastal waters of temperate and intertropical areas. Epifluorescence microscope was found to be an efficient tool to study the abundance and the extent of *Synechococcus* (Murphy and Haughen 1985; Blanchot et al. 1992). Later shipboard application of flowcytometry led to the discovery of a new free-living Prochlorophytes, *Prochlorococcus* (Chisholm et al. 1988).

We have applied the same techniques in the Tuamotu atolls of French Polynesia to study the abundance and the extent of prokaryotic phytoplankton. Using epifluorescence microscopy, our laboratory first recognized the great abundance of *Synechococcus* in closed (Takapoto : Charpy et al. 1992) and open (Tikehau : Blanchot et al. 1989) atoll lagoons. We found that the <1µm fraction was responsible for more than 60% of the phytoplanktonic biomass and production (Charpy et al. 1992).

The first descriptions of *Prochlorococcus* in coral reef environments were done in the Pacific ocean, specifically in Fijians waters and the Tuamotu archipelago (Blanchot 1996; Charpy and Blanchot 1996).

Our aims in this study are :

1) To determine the relationship between the geomorphology of atolls and the phytoplankton biomass and community structure
2) To quantify the relative contributions of *Prochlorococcus* and *Synechococcus* to total phytoplankton production.

MATERIAL AND METHODS

Samples of phytoplankton from eleven Tuamotu atoll lagoons (Fig. 1) waere counted and identified in November 1994 (Takapoto) and November 1995 (Kauehi, Tairao, Tepoto, Hiti, Haraiki, Tekokota, Hikueru, Marokau, Reka-Reka and Nihiru). Characteristics of the atolls appear in Table 1.

Sampling were collected from 6 stations in the Takapoto lagoon at 5 m depth intervals and at 5 stations in other atolls (surface and near the bottom). One oceanic station was sampled in 1994 (5, 20, 30, 50, 60, 80, 90, 100, 110, 120 and 150 m) and surface samples were collected at five oceanic stations in 1995.

Water samples were taken with a 5 l Niskin bottle fitted with a Teflon spring.

Table 1: Characteristics of the eleven prospected atolls. S = lagoon surface (km^2), NP = number of passage, EAD = Estimated average depth (m).

Atoll	Latitude	Longitude	S	NP	EAD
Kauehi	15°50'S	145°09'W	320.0	1	50
Taiaro	15°45'S	144°38'	9.2	0	15
Tepoto Sud	16°44'S	144°17'W	2.0	1	5
Hiti	16°43'S	144°17'W	24.0	0	10
Haraiki	17°28'S	143°26'W	11.0	1	10
Tekokota	17°19'S	142°34'W	3.0	1	3
Hikueru	17°35'S	142°38'W	79.1	0	25
Marokau	18°03'S	142°16'W	219.7	1	30
Reka-Reka	16°50'S	141°55'W	3.3	0	1
Nihiru	16°41'S	142°50'W	88.0	0	20
Takapoto	14°30'S	145°20'W	77.5	0	23

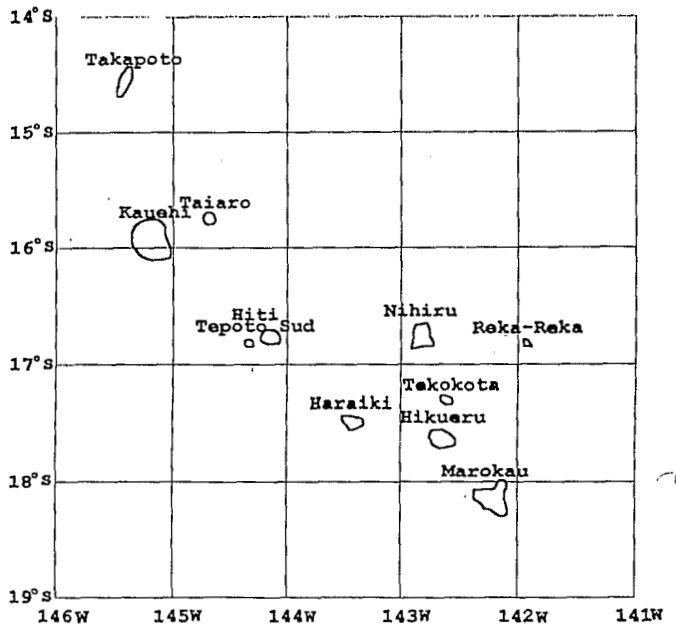

Fig. 1: Location of prospected atolls

Samples for population enumerations and for chlorophyll-a analyses (Chl) were stored in an ice box and kept in the dark. Filtrations and size separations (total, >3µm, >1µm) were completed within an hour after sampling. Nuclepore (3µm and 1µm) and GF/F filters were used. Chl was estimated by fluorimetry (Yentsch and Menzel 1963).

The methods used for enumeration of populations has been described by Partensky et al. (in press) and Blanchot and Rodier (in press). Briefly, samples were counted with a Becton-Dickinson FACScan flow cytometer. Takapoto samples were counted when live (November 1994) and the other samples were fixed with paraformaldehyde to give a final concentration of 1%, then were kept for 10 minutes in the dark, frozen in liquid nitrogen and stored at -20°C until analysed. The analysis of the fixed material was done within a month after sampling. The excitation source was a blue laser beam (15 mV, 488 nm), the red fluorescence (RF) of the chlorophyll was analyzed with wave lengths >650nm. In order to calibrate the fluorescence and estimate the volume counted, known quantities of fluorescent beads (Polyscience, 2µm) were added to each sample.

Sub-samples used for measuring primary production were incubated between 10:00 hr and 14:00 hr in 200 ml polycarbonate bottles with 2 µCi of ^{14}C. In Takapoto, samples were incubated *in situ* at 0, 5, 10, 15, 20, 25 m depth. In the other atolls, all incubations were made in a deck incubator with flowing water and natural light, using the clean technique (Fitzwater et al. (1982). Filtrations and size fractionations used the same filters and filtering protocoles as for chlorophyll. Radioactive counts were made using a liquid scintillation spectrometer (Packard).

RESULTS AND DISCUSSION

The eleven atolls may be separated into 4 groups according to phytoplankton biomass as estimated by chlorophyll (Table 2, Fig. 2) : Reka-Reka (0.566 µg l^{-1}), Takapoto, Taiaro, Hiti, Haraiki (0.234 - 0.268 µg l^{-1}), Kauehi, Tepoto Sud, Hikueru, Marokau, Nihiru (0.156 -0.193 µg l^{-1}) and Tekokota (0.018 µg l^{-1}).

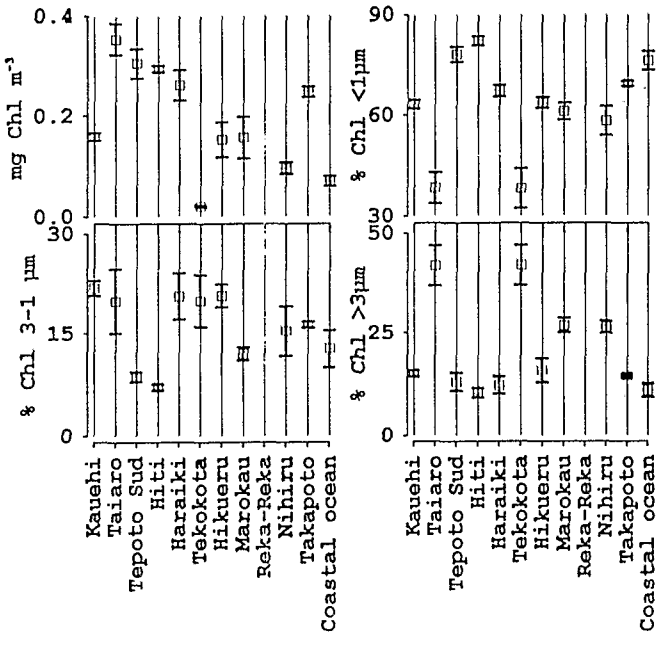

Fig. 2: Average ± SE of chlorophyll concentrations (Chl) and percentages of Chl in the 3 size fractions in the eleven atoll lagoons.

The high chlorophyll concentration observed in the Reka-Reka lagoon can be explained through the resuspension of benthic microphytes due to the shallowness of the lagoon (1 m).

The second group of atolls is heterogeneous, composed of one medium-sized lagoon with average depth > 20 m (Takapoto) and two small lagoons with an average depth ≅ 10 m (Tairao and Haraiki), all with one (Haraiki) or no passage.

The third group of atolls is also heterogeneous, comprised of large (Kauehi and Marokau), medium (Hikueru and Nihiru) and small (Tepoto Sud) lagoons with one passage.

The low chlorophyll content of the Tekokota lagoon can be readily explained by its open exchange with the ocean. Previously, Delesalle and Sournia (1992) observed a linear relationship between residence time and phytoplankton chlorophyll concentrations.

With two exceptions (Tairao 38% and Tekokota 38%), the percentage of Chl passing through the 1µm filter was between 58% (Nihiru) and 82 % (Hiti) in all the lagoons (Fig. 2). Similar higher percentages were previously observed in Tikehau (Blanchot et al. 1989) and in Takapoto atolls (Charpy et al. 1992; Charpy and Blanchot 1996).

Differences in phytoplankton community composition can be observed between atoll lagoons : *Prochlorococcus* were particularly abundant in Hiti lagoon (280 10^3 ± 19 10^3 cells ml^{-1}),and *Synechococcus* in Tepoto Sud and Haraiki, (280 10^3 and 190 10^3 cells ml^{-1}). Picoeukaryotes were considerably less abundant, with maxima in Takapoto, Tairao and Tepoto (2.4, 2.5 and 1.8 10^3 cells ml^{-1}) (Fig. 3).

The sizes of the two dominant photoautotrophic prokaryotes, *Prochlorococcus* and *Synechococcus* was less than 1µm (Charpy et al. 1992; Charpy and Blanchot 1996) and their summed abundances were correlated (R = 0.67, n = 144) with the Chl<1µm concentration (Fig. 4)

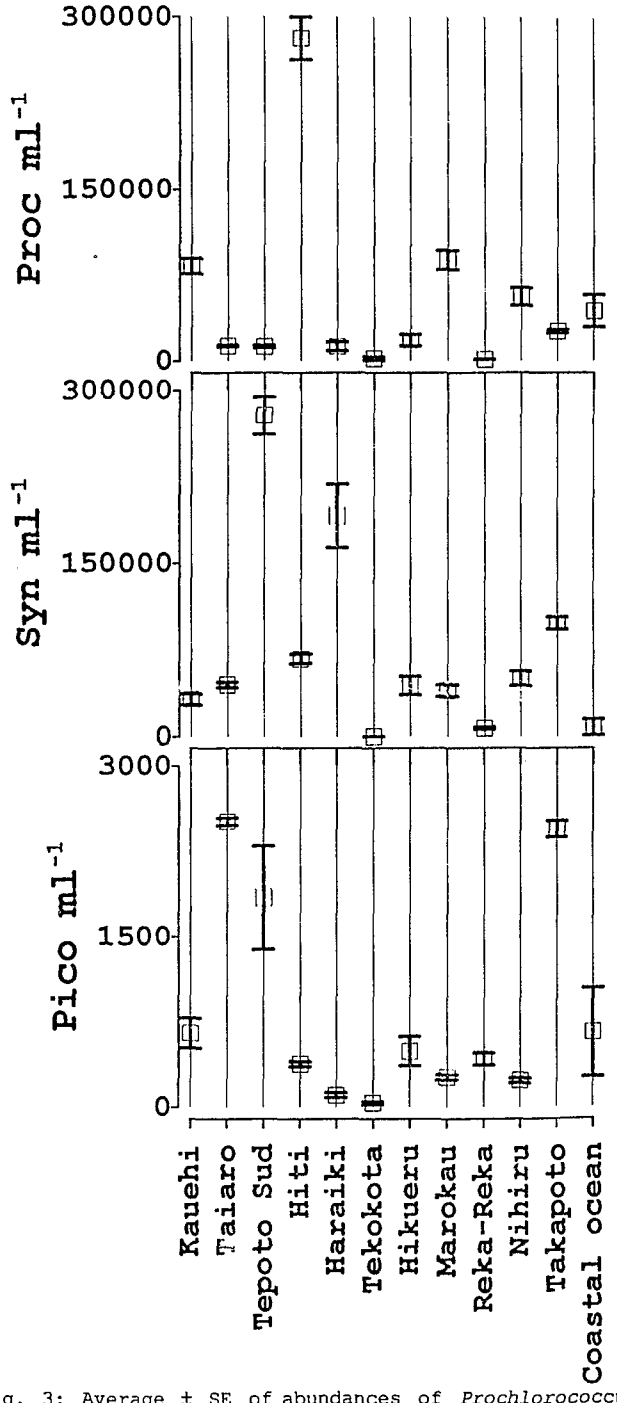

Fig. 3: Average ± SE of abundances of *Prochlorococcus* (Proc), *Synechococcus* (Syn) and picoeukaryotes (Pico) in eleven atoll lagoons and coastal ocean.

Table 2: Average ± SE of chlorophyll concentration, percentages of Chl in different size fractions, phytoplankton abundance and percentage of *in vivo* red fluorescence (RF) in 11 Tuamotu atoll lagoons and surrounding surface oceanic waters.

Atoll		Chlorophylle-a				*Prochlorococcus*		*Synechococcus*		Picoeukaryotes	
		µg l^{-1}	% <1µm	% 1-3µm	% >3µm	cell/ml	% RF	cell/ml	% RF	cell/ml	% RF
Kauehi		0.156	63.2	21.8	15.0	82756	11.3	32094	75.9	650	12.8
	S.E.	*0.012*	*1.3*	*1.1*	*0.8*	*6572*	*1.9*	*4819*	*4.7*	*130*	*2.9*
Taiaro		0.268	38.3	19.8	41.8	12890	2.1	44180	52.8	2500	45.1
	S.E.	*0.022*	*4.6*	*4.8*	*5.1*	*1036*	*0.2*	*2297*	*2.3*	*35*	*2.2*
Tepoto Sud		0.193	78.3	8.7	13.0	12297	0.4	277687	93.8	1835	5.8
	S.E.	*0.013*	*2.3*	*0.7*	*2.1*	*1130*	*0.1*	*16554*	*1.2*	*450*	*1.2*
Hiti		0.234	82.3	7.2	10.5	280668	40.2	66288	53.5	378	6.4
	S.E.	*0.041*	*1.4*	*0.4*	*1.1*	*18967*	*1.6*	*4027*	*1.6*	*22*	*0.5*
Haraiki		0.260	67.1	20.6	12.3	12630	2.2	190148	96.6	105	1.3
	S.E.	*0.037*	*1.7*	*3.5*	*2.0*	*3762*	*1.0*	*26768*	*1.1*	*22*	*0.4*
Tekokota		0.018	38.2	19.9	41.9	2015	14.3	105	17.3	35	68.4
	S.E.	*0.004*	*5.9*	*3.9*	*5.1*	*1510*	*5.3*	*16*	*4.1*	*14*	*6.0*
Hikueru		0.192	63.7	20.6	15.7	17888	3.6	43775	82.9	490	13.4
	S.E.	*0.052*	*1.6*	*1.7*	*2.9*	*5020*	*0.5*	*7579*	*3.3*	*125*	*3.7*
Marokau		0.175	61.1	12.0	26.9	88272	16.4	39133	75.4	265	8.1
	S.E.	*0.043*	*2.5*	*1.0*	*1.8*	*8238*	*3.1*	*4778*	*5.9*	*23*	*3.1*
Reka-Reka		0.566	67.3	18.4	14.3	1147	1.0	7140	26.3	423	72.7
	S.E.	*0.055*				*267*	*0.3*	*1049*	*4.3*	*52*	*4.5*
Nihiru		0.158	58.2	15.3	26.4	55850	9.2	49708	86.8	237	4.0
	S.E.	*0.016*	*4.3*	*3.7*	*1.6*	*7669*	*0.9*	*6219*	*1.5*	*23*	*0.7*
Takapoto		0.250	69.5	16.2	14.2	25714	2.0	97116	56.7	2433	41.3
	S.E.	*0.010*	*0.8*	*0.5*	*0.5*	*1474*	*0.1*	*5091*	*1.8*	*72*	*1.9*
Ocean		0.056	76.3	12.7	11.0	43560	36.1	7832	35.4	656	28.5
	S.E.	*0.007*	*2.9*	*2.7*	*1.6*	*13888*	*11.9*	*6812*	*12.9*	*389*	*7.9*

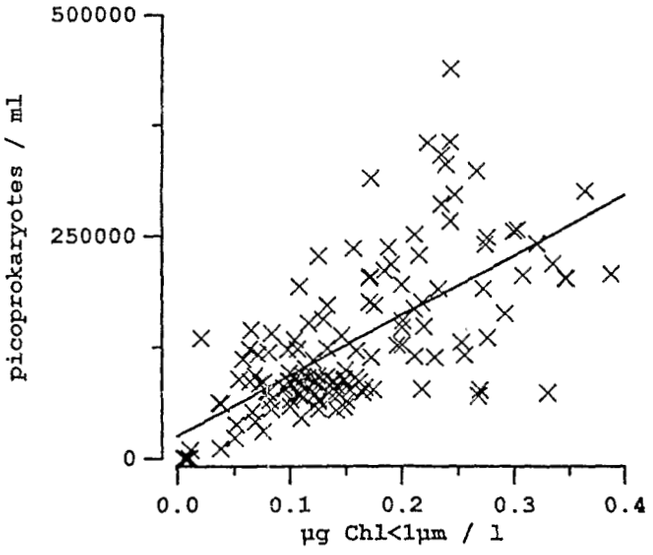

Fig. 4: Abundances of picoprokaryotes *vs* chlorophyll (Chl) < 1µm in Tuamotu atoll lagoons.

The percentage of cells with red autofluorescence (RF) (Fig. 5) was poorly correlated with the percentage of Chl<1µm (R=0.34). This poor correlation was probably due to the fact that RF was measured in fixed samples during the November 1995 expedition (Partensky et al. in press). Indeed, the correlation was better (R=0.46) if we use only data from Takapoto, where the RF was measured *in vivo*.

Therefore, we have to cautiously use the % of RF to estimate the contribution of each taxa to phytoplankton biomass.

In most of atolls, prokaryotic phytoplankton dominated. The two notable exceptions were the atypical atolls, Tairao and Tekokota, where the contribution of RF by the picoeukaryotes was high, 45% and 68% respectively. The shallow lagoon of Reka-Reka was also an exception haven 67% of Chl in the <1µm fraction, presumably prokaryotes, but with 73% of RF due to picoeukaryotes. At this stage we cannot interpret this contradiction.

In surrounding oceanic waters, *Prochlorococcus* and *Synechococcus* dominated the phytoplankton at the surface with 36.1% and 35.4% of RF respectively. For the 150 m water column close to Takapoto (Fig. 6), *Prochlorococcus*, *Synechococcus* and picoeukaryotes had effective dominances of 42.3%, 5.3% and 52.4% respectively.

The percentage of primary production in the <1µm fraction varied between 32% (Reka-Reka) and 72% (Kauehi) (Table 3) and was correlated (R=0.60, n=86) with the percentage of Chl in cells smaller than 1µm (Fig. 7).

The proportion of primary production associated with cells <1µm was also correlated (R=0.77, n=30) with the proportion of living RF of picophotoprokaryotes (*Prochlorococcus* + *Synechococcus*) measured in Takapoto (Fig. 8).

This correlation was lower with RF measured in fixed samples (R=0.64, n=60), but was good enough to use as an estimation of the taxonomic contribution to primary production. Using the % of RF from Table 2, *Synechococcus* was the dominant taxon in the majority of the lagoons, contributing for more than 70% of the primary production in Kauehi, Tepoto Sud, Haraiki, Hikueru, Marokau and Nihiru. Picoeukaryotes were dominant in Tekokota primary production (68%) and Reka-Reka (73%). *Prochlorococcus* were dominant in the primary production of coastal oceanic waters (36%) and were also important in the Hiti lagoon (40%).

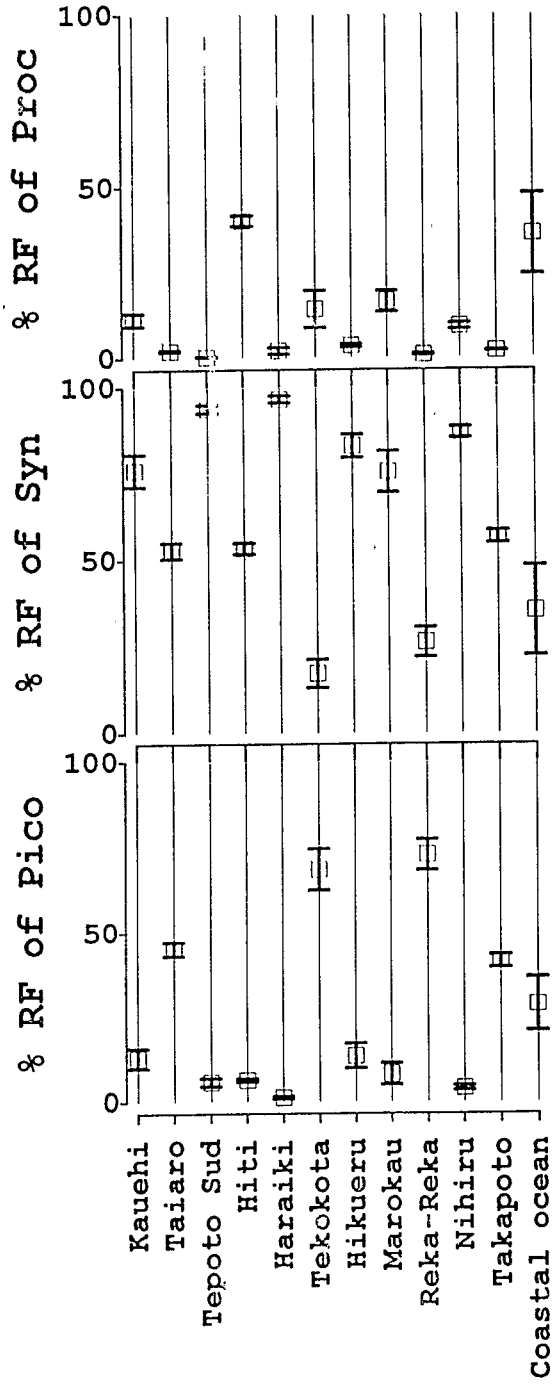

Fig. 5: Average ± SE contribution of *Prochlorococcus* (Proc), *Synechococcus* (Syn) and Picoeukaryotes (Pico) to the red autofluorescence (RF).

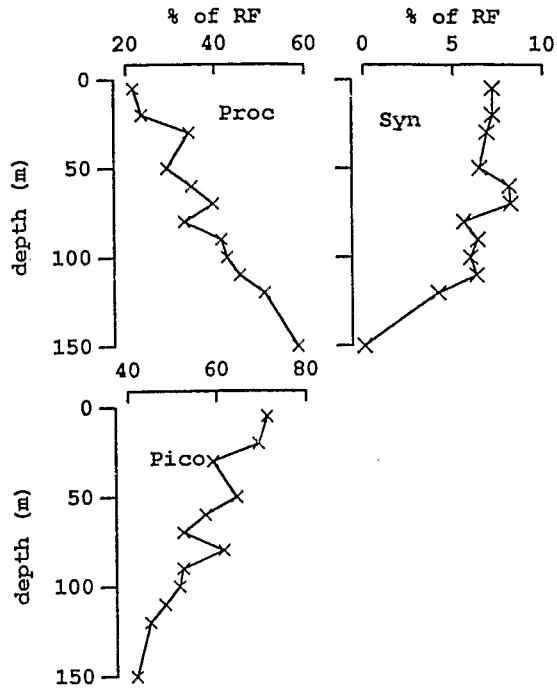

Fig. 6: Profiles of the contribution of *Prochlorococcus* (Proc), *Synechococcus* (Syn) and Picoeukaryotes (Pico) to the red autofluorescence in oceanic waters close to Takapoto atoll.

Table 3: Average of percentages of primary production in different size fractions in 11 Tuamotu atoll lagoons and surrounding surface oceanic waters. *S.E.* = Standard error.

Atoll		% <1µm	% 1-3µm	% >3µm	% <3µm
Kauehi		72.2	13.3	9.2	90.8
	S.E.	*2.5*	*2.3*	*0.7*	*0.7*
Taiaro		34.7	16.5	47.6	52.4
	S.E.	*5.2*	*1.4*	*6.1*	*6.1*
Tepoto Sud		62.1	24.6	12.3	87.7
	S.E.	*0.9*	*0.8*	*0.5*	*0.5*
Hiti		65.1	9.3	22.6	77.4
	S.E.	*1.2*	*0.8*	*1.1*	*1.1*
Haraiki		69.2	19.7	9.9	90.1
	S.E.	*1.5*	*1.4*	*0.3*	*0.3*
Tekokota		32.3	9.2	33.6	66.5
	S.E.	*3.7*	*1.9*	*5.3*	*5.3*
Hikueru		45.8	30.0	21.7	78.3
	S.E.	*3.7*	*5.3*	*2.5*	*2.5*
Marokau		47.2	8.3	39.3	60.7
	S.E.	*1.4*	*2.3*	*2.2*	*2.2*
Reka-Reka		45.5	39.1	15.0	85.0
	S.E.	*1.1*	*2.0*	*1.7*	*1.1*
Nihiru		50.8	13.4	33.1	66.9
	S.E.	*1.8*	*0.8*	*2.1*	*2.1*
Takapoto		57.0	23.0	20.0	80.0
	S.E.	*2.0*	*1.0*	*2.0*	*2.0*
Ocean		45.3	20.1	14.9	85.2
	S.E.	*0.2*	*1.5*	*2.6*	*2.6*

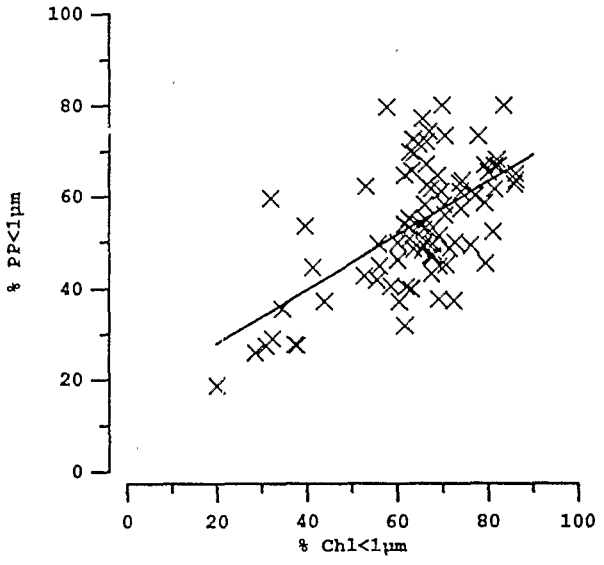

Fig. 7: Percentage of chlorophyll (Chl) *vs* percentage of primary production (PP) in the < 1µm fraction in eleven Tuamotu atoll lagoons

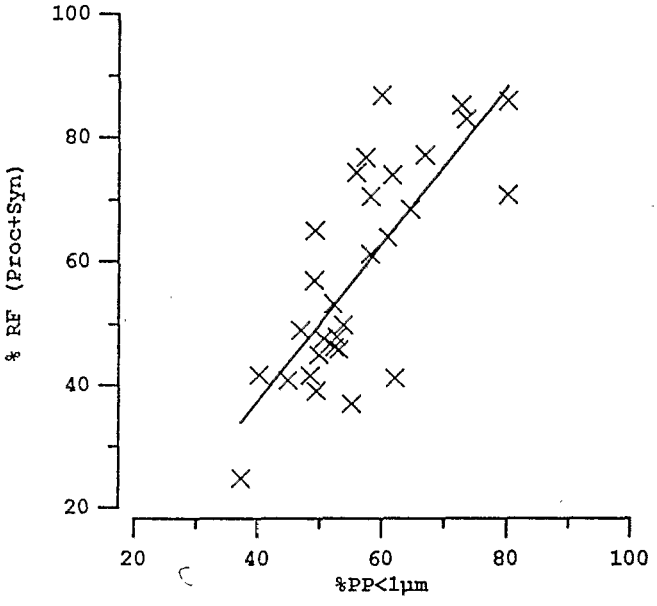

Fig. 8: Percentage of primary production (PP) < 1µm *vs* percentage of living red fluorescence (RF) of procaryotes in Takapoto atoll lagoons

SUMMARY CONCLUSIONS

Prochlorococcus and *Synechococcus* dominated phytoplankton biomass and primary production in 9 of 11 atolls sampled. Differences observed in the phytoplankton biomass and taxonomic composition are not yet explained, but they are likely to be related to the residence time of lagoon waters and/or nutrient contents.

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REFERENCES

Blanchot J (1996) Report of picophytoplankton study during the astro cruise In the Great Astrolabe Reef (18°45'S-178°30'E) Fiji. Notes et Doc Océanogr, 46 :69-77

Blanchot J, Charpy L, Le Borgne R (1989) Size composition of particulate organic matter in the lagoon of Tikehau atoll (Tuamotu archipelago). Mar Biol 102 : 329-339

Blanchot J, Rodier M (in press) Phytoplankton abundance and biomass in the western tropical Pacific Ocean along 165°E, during a weak El Nino (August 92) : new data from flow cytometry. Deep-Sea Res

Blanchot J, Rodier M, Le Bouteiller A 1992 Effect of El Nino Oscillation on the distribution and abundance of phytoplankton in the Western Pacific tropical Ocean along 165°E. J Plankton Res 14 : 137-156

Charpy L, Blanchot J (1996) Prochlorococcus contribution to phytoplankton biomass and production of Takapoto atoll (Tuamotu archipelago). C R Acad Sc Paris, Life sciences 319 : 131-137

Charpy L, Blanchot J, Lo L (1992) Contribution des cyanobactéries (Synechococcus spp.) à la production phytoplanctonique dans un lagon d'atoll fermé (Takapoto, Tuamotu, Polynésie Française). CR Acad Sci Paris, t 314, Série III : 395-401

Chisholm SW, Olson RJ, Zetttler ER, Waterbury J, Georicke R, Welschmeyer NA (1988) A novel free living Prochlorococcus occurs at high concentration in the oceanic euphotic zone. Nature 334 : 340-343

Courties C, Vaquer A, Troussellier M, Lautier J, Chretiennot-Dinet MJ, Neveux J, Machado C, Claustre H (1994) Smallest eukaryotic organism. Nature 370(6487): 255

Delesalle B, Sournia A (1992) Residence time of water and phytoplankton biomass in coral reef lagoons. Continental Shelf Res. 12(7/8) : 939-949

Fitzwater SE, Knauer GA, Martin JH (1982) Metal contamination and its effect on primary production measurements. Limnol Oceanogr 27(3) 544-551

Murphy LS, Haugen EM (1985) The distribution and abundance of phototrophic ultraplankton in the North Atlantic. Limnol Oceanogr 30 : 47-58

Partensky F, Blanchot J, Lantoine F, Neveux J, Marie D (in press) Vertical structure of picophytoplankton at different sites of the subtropical northeastern Atlantic Ocean. Deep Sea-Res

Yentsch CS, Menzel DW (1963) A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence, Deep-Sea Res 10 : 221-231