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Photosynthetic picoplankton in French Polynesian atoll lagoons: estimation of taxa contribution to biomass and production by flow cytometry

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ABSTRACT: Picophytoplankton was studied by flow cytometry in 11 Tuamotu (French Polynesia) atoll lagoons and in the surrounding ocean. The respective contribution of *Prochlorococcus*, *Synechococcus* and picoeukaryotes on biomass and primary production was evaluated. Red fluorescence was demonstrated to be a proxy for chlorophyll. The relative sizes of the 3 picoplankton groups were estimated using forward light scattering measured in Takapoto lagoon on living cells. The average diameters for *Prochlorococcus*, *Synechococcus* and picoeukaryotes were estimated as 0.62 ± 0.08 (SD), 0.89 ± 0.09 and 3.11 ± 0.22 µm, respectively. The lowest values occurred before sunrise and the highest in the afternoon. Cellular carbon content was estimated using C/biovolume ratios from the literature. The average biomass for *Prochlorococcus*, *Synechococcus* and picoeukaryotes was calculated as 60 ± 20, 178 ± 52 and 4695 ± 834 fg C cell^{-1} respectively. *Synechococcus* formed the predominant group in terms of abundance and carbon biomass and had the highest planktonic primary production in most lagoons. As it is generally scarce in deep water with limited light availability, its biomass contribution was reduced in deep lagoons. Average lagoonal picoplankton abundance varied by a factor of 200 for the different populations and was affected by the geomorphology of the atolls. In very shallow lagoons, no general trend could be observed, as the dominant group appeared to depend on the water renewal rate within the lagoon. In the surface layer of the surrounding ocean the community structure was dominated by *Prochlorococcus*. However, the observed percentage of *Synechococcus* (>10%) is usual for the coastal zone. In the upper 120 m of ocean waters surrounding Takapoto, the integrated picoplankton biomass (1242 mg C m^{-2}) consisted of 65% *Prochlorococcus*, 1% *Synechococcus* and 34% picoeukaryotes.

KEY WORDS: Flow cytometry · Cyanobacteria · *Prochlorococcus* · Chlorophyll · Primary production · Atoll lagoons · Diurnal cell size variations

INTRODUCTION

In its intertropical zone, the Pacific Ocean harbors hundreds of coral atolls and the profusion of life is noteworthy in these oligotrophic waters. A number of these islands are located in the South Pacific. In the Tuamotu archipelago (French Polynesia), many atolls are inhabited and sea farming of black pearl oyster *Pinctada margaritifera*, which feed on phytoplankton, is a major economic activity. Much research has studied the community structure of phytoplankton, evaluated primary production and investigated the nature of the food particles aggregated by oysters. In these coral reef lagoons, small phytoplankton cells identified as prokaryotic *Synechococcus* sp. (Blanchot et al. 1989, Charpy et al. 1992) dominate larger cells both in terms of biomass and primary production (Charpy 1996). Nevertheless the heterogeneity in the water column can lead, under certain circumstances, to the local dominance in biomass and primary production of picoeukaryotes (Charpy & Blanchot 1996). In addition, small populations of *Prochlorococcus* in the lagoon waters of the closed atoll Takapoto have been

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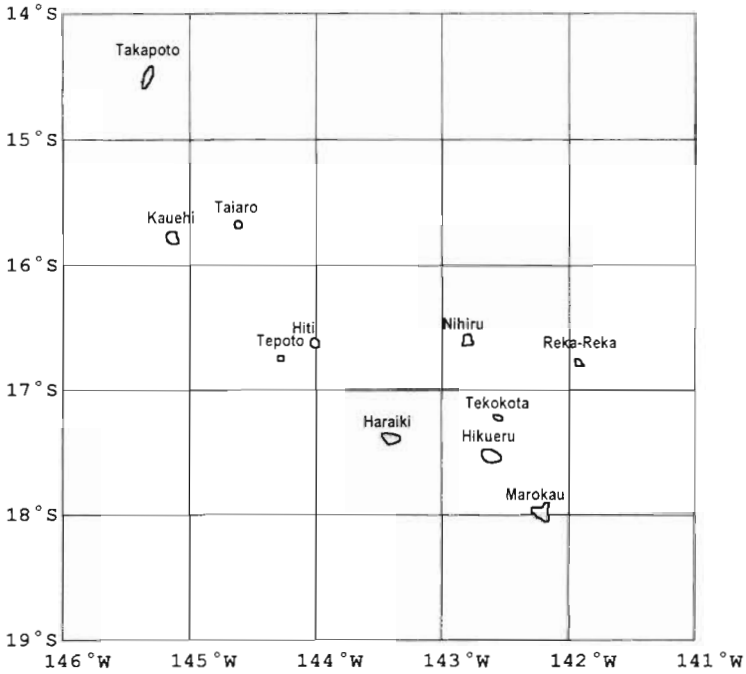

Fig. 1. Location of investigated atolls in French Polynesia

described (Charpy & Blanchot 1996). These reports show a diversity of community structure in several atoll lagoons and raise the question as to which biological or geomorphological force drives this system. Several studies in Tuamotu Archipelago (CYEL: Charpy 1992; TYPATOLL: Dufour & Harmelin-Vivien 1997) have contributed to our understanding of the relationships among picoplankton populations and of their distribution patterns, as well as the relationships between atoll geomorphology and picoplankton community structure. A classification of phytoplankton cell number, carbon biomass, chlorophyll biomass and primary productivity by size was established according to Li's method (1995). As cell abundance does not take into consideration the large difference in cell size of the 3 groups, we estimated the relative size of cells by using forward scatter as an index of size. We then computed the carbon content of cells using the relationship between cell volume and carbon. In order to estimate the contribution of each photosynthetic group to total chlorophyll biomass and production, we considered total red fluorescence to be a proxy for chlorophyll *a*. We used chlorophyll size fractionation to calculate the contribution of each population to primary productivity.

MATERIAL AND METHODS

Sampling. The location of the 11 investigated atolls appears on Fig. 1 and their characteristics are given in Table 1. Water samples were collected with acid-cleaned Niskin bottles at the surface and at 5 m depth intervals down to a maximum depth of 30 m. Phytoplankton biomass in Takapoto was sampled in November 1994 at 6 (Stns 1, 2, 3, 6, 7 and 8) of the 8 stations investigated during the CYEL program within the lagoon (Charpy 1996) and at 1 ocean site for a total of 15 + 1 profiles (Fig. 2). Sampling in the ocean was at 5, 20, 30, 50, 60, 80, 90, 100, 110, 120 and 150 m depth. Within the TYPATOLL program 10 atoll lagoons were studied in November 1995 and March 1996. For each lagoon, surface samples were collected at triplicate sites in 5 areas located in the north, south, east and west quad-

Table 1. Characteristics of the 11 investigated atolls during the PGRN, CYEL and TYPATOLL programs. S_{at} = atoll area; S_{lag} = lagoon area (km^2); NP = number of inlets into the lagoon; EAD = estimated average depth (m); Ope = Opening = linear extent of channels/linear extent of barrier reef; Inh. = no. of inhabitants; Expl. = marine commercial exploitation

Atoll	Latitude	Longitude	S_{at}	S_{lag}	NP	EAD	Ope	Inh.	Expl.	Source
Haraiki	17° 28' S	143° 26' W	24.6	10.4	1	10	19	20		
Hikueru	17° 35' S	142° 38' W	107	82	0	25	18	300	Pearl	
Hiti	16° 43' S	144° 06' W	25	15	0	10	19	0		
Kauehi	15° 50' S	145° 09' W	343	315	1	45	22	200	Pearl	
Marokau	18° 03' S	142° 16' W	256	217	1	30	17	50		
Nihiru	16° 41' S	142° 50' W	100	80	0	20	25	20		
Reka-Reka	16° 50' S	141° 55' W	52	7.4	0	1	2	0		
Taiaro	15° 45' S	144° 38' W	17.3	11.8	0	15	1	3		Chevallier & Salvat (1976), Poli & Salvat (1976)
Takapoto	14° 30' S	145° 20' W	104	81	0	25	2	500	Pearl	Salvat & Richard (1985)
Tekokota	17° 19' S	142° 34' W	7.3	5.1	1	3	59	0		
Tepoto Sud	16° 49' S	144° 17' W	6.2	1.6	1	5	15	0		

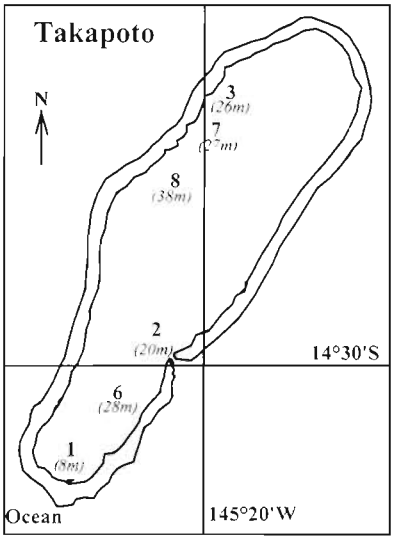

Fig. 2. Location of sampling stations investigated during the CYEL program in Takapoto lagoon (Stns 1 to 8) and the surrounding water (Stn 'Ocean')

rants as well as at the center of each lagoon in the morning. In addition, bottom samples were collected in the central area and surface samples at 6 ocean sites.

Light energy was measured with a LI-COR sensor (LI-190SA) fitted with a spherical probe.

Biomass and production measurements. Takapoto samples (November 1994) for population enumeration of live cells and for chlorophyll *a* (chl *a*) analyses were stored in an isotherm container in the dark. Filtration and size fractionation (total and <1 µm) were completed within an hour of sampling. Enumeration of populations was performed according to Partensky et al. (1996) and Blanchot & Rodier's (1996) methodology. Samples were counted with a Becton-Dickinson FACScan flow cytometer. The excitation source was a blue laser beam (15 mW, 488 nm). The red fluorescence of the chlorophyll was analyzed at wave lengths >650 nm. In order to calibrate the optical measurements and to check the flow rate, known quantities of fluorescent beads (Polyscience, 2 µm) were added to each sample. List mode files were transferred to a microcomputer and analyzed on CYTOPC software (Vaulot 1989).

During TYPATOLL expeditions, we could not have the flow cytometer on board and samples were fixed with paraformaldehyde to a final concentration of 1% (modified from Vaulot et al. 1989). These samples were then kept in the dark for 10 min, frozen in liquid nitrogen and stored at −20°C for a few days, which can cause loss of cells. The analysis of the fixed material was conducted within a month of sampling. Partensky et al. (1996) estimated that most *Prochlorococcus* and *Synechococcus* were well preserved by this fixation method (loss ca 3 to 4%) while picoeukaryotes were poorly preserved, with a cell loss of up to 23%. They considered that the other flow cytometric parameters such as forward scatter were differently affected by the fixation, depending on the population type. In near-surface nitrate-depleted samples, *Prochlorococcus* populations are too dim to be completely resolved by the FACScan system, as has already been mentioned in the literature (Olson et al. 1990, Campbell & Vaulot 1993, Shimada et al. 1993, Dusenberry & Frankel 1994). Therefore, underestimation of dim *Prochlorococcus* was corrected in surface samples as reported by Blanchot & Rodier (1996) and Charpy & Blanchot (1996). Nevertheless an underestimation of cells could have occurred. In offshore cruises the dim *Prochlorococcus* were always restricted to oligotrophic areas, where divinyl chl *a* concentrations were weak. The weak red fluorescence is linked to a low cellular pigment content. The primary consequence of this is a possible underestimation of the fraction of biomass attributed to the *Prochlorococcus*.

Primary production measurements (clean technique; Fitzwater et al. 1982), chlorophyll determination and size fractionation (Nuclepore filters) were conducted according to Charpy (1996). All sub-samples used for measuring primary production were incubated between 10:00 and 14:00 h in 200 ml polycarbonate bottles with 2 µCi of $H^{14}CO_3$. In Takapoto, samples were incubated *in situ* at 0, 5, 10, 15, 20 and 25 m depth at Stn 6. At the other atolls, a deck incubator was used with flowing water and natural light. Incubation bottles were filtered successively through 3 µm and 1 µm Nuclepore filters and then 25 mm Whatman GF/F glass fiber filters. One bottle was filtered directly through GF/F filters for an estimate of total production. To remove inorganic carbon 250 µl of 0.5 N HCl were added to the filter in the scintillation vial. After 12 h, 100 µl of Protosol were added to the filter. Radioactivity on the filters was measured with a liquid scintillation counter and corrected for quench using an internal standard and the channels ratio method.

Chl *a* concentrations were determined by fluorometry (Yentsch & Menzel 1963). The vacuum during fractionation never exceeded 0.004 atm. Fluorescence was measured before and after acidification with 50 µl of 1 M HCl. The fluorometer was calibrated using the SIGMA chl *a* standard. For chl *a* determinations a 250 ml water sample was size fractionated using the same methods as for the productivity samples.

Estimating biomass and production from flow cytometry. Assuming that fluorescence is a proxy for chl *a*, we can estimate the picophytoplankton biomass as chl *a* from *in vivo* red fluorescence (RF) (Yentsch &

Campbell 1991, Li et al. 1993, Shimada et al. 1993):

$$\text{chl}\,a = \sum_{i=1}^{3} n_i \times f_i \times \psi_i \quad (1)$$

where i refers to the 3 recognizable groups (i.e. *Prochlorococcus*, *Synechococcus* and picoeukaryotes); n = cell concentration; f = mean cell RF; ψ = fg chl *a* per relative unit of RF.

Assuming that the <1 µm fraction consists primarily of prokaryotic cells (Charpy & Blanchot 1996), we can also estimate the chlorophyll <1 µm using Eq. (2):

$$\text{chl}\,a\,{<}1\ \mu\text{m} = \sum_{i=1}^{2} n_i \times f_i \times \psi_i' \quad (2)$$

where ψ' = fg chl *a* <1 µm per relative unit of RF.

It is also possible to estimate the picophytoplankton biomass as carbon. Indeed, it is commonly accepted that cellular carbon content is directly related to cell volume (Strathmann 1967):

$$C = \sum_{i=1}^{3} n_i \times v_i \times \alpha_i \quad (3)$$

where n = cell concentration; v = mean average cell volume; α = carbon biomass to biovolume ratio.

In flow cytometric analyses of phytoplankton, it is common practice to regard forward (narrow angle) light scatter (FSC) as an index of cell size (Olson et al. 1993). A strong empirical correlation between FSC and Coulter volume using a wide variety of algae was demonstrated by Olson et al. (1989). These authors suggested that, at the low angles used by the flow cytometer to measure FSC, the influence of cell shape and refractive index was minor compared to that of cell size. We can therefore use FSC measured in Takapoto to estimate the cell sizes of the 3 picoplankton groups, assuming that they have a spherical shape and similar refractive indexes. The relation between FSC and the size of spherical particles in the size range of picophytoplankton (0.3 to 3 µm) can be written as (Morel 1991):

$$\frac{\text{FSC}_{\text{Cell}}}{\text{FSC}_{\text{Beads}}} = \left(\frac{\text{Diameter}_{\text{Cell}}}{\text{Diameter}_{\text{Beads}}}\right)^{x} \quad (4)$$

Assuming that, in a given biotope (lagoon, ocean), the exponent x is the same for the 3 picoplankton groups, it can be estimated from a known value of cell diameter.

RESULTS

Takapoto

The averaged light profile from Takapoto lagoon is shown in Fig. 3. At 25 m depth (average depth of the lagoon) light energy was on average 7% of the surface light energy.

Picoplankton distribution was heterogeneous in the water column in the 11 profiles performed between November 4 and 9 at Stns 6 and 7. In the upper 10 m, total biomass was lower (0.2 µg chl *a* l^{-1}) with 14.1 ± 1.1 × 10^3 *Prochlorococcus* ml^{-1}, 68.7 ± 2.3 × 10^3 *Synechococcus* ml^{-1} and 2.7 ± 0.01 × 10^3 picoeukaryotes ml^{-1}. Below 10 m, biomass was higher (0.3 µg chl *a* l^{-1}) with 33.4 ± 1.5 × 10^3 *Prochlorococcus* ml^{-1}, 141.1 ± 7.7 × 10^3 *Synechococcus* ml^{-1} and 2.3 ± 0.1 × 10^3 picoeukaryotes ml^{-1}. In the entire column, 57 ± 2% of the carbon assimilation rate was due to particles <1 µm.

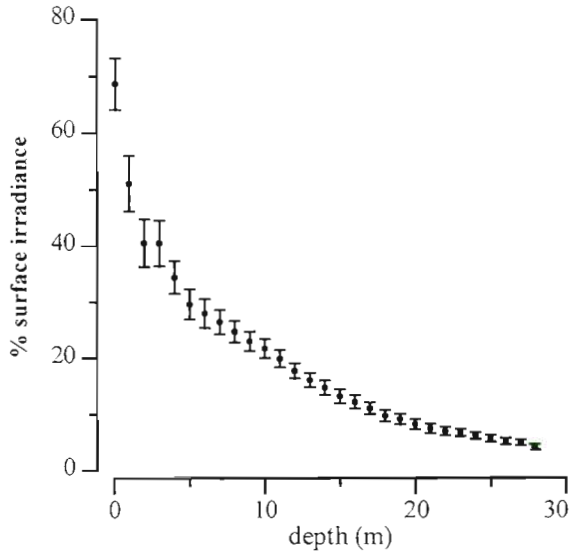

Fig. 3. Average ± SE of the percentage of surface irradiance measured in Takapoto lagoon

In the 4 remaining profiles, the water column was homogeneous.

Estimating the contribution of the picoplankton groups to biomass as chl *a*

The chl *a* content per unit of RF, ψ_i and ψ_i' were estimated for 2 depth layers by regression using measured values of chl *a*, chl *a* <1 µm, n_i and f_i and using Eqs. (1) & (2) (Table 2). Values of ψ_i and ψ_i' differed according to depth. The fit of data for individual layers was

Table 2. ψ (fg chl *a* per unit RF) and ψ' (fg chl *a* <1 µm per unit RF) of the 3 picoplankton groups

	Takapoto (0–10 m)	Takapoto (15–30 m)	Nov 1995 (10 atolls)	Mar 1996 (10 atolls)
$\psi_{Prochlorococcus}$	13.7	111.0		
$\psi_{Synechococcus}$	10.8	3.3		
$\psi_{picoeukaryotes}$	9.3	8.6		
$\psi'_{Prochlorococcus}$	15.6	128.5	43.7	49.3
$\psi'_{Synechococcus}$	13.4	2.8	4.7	7.4

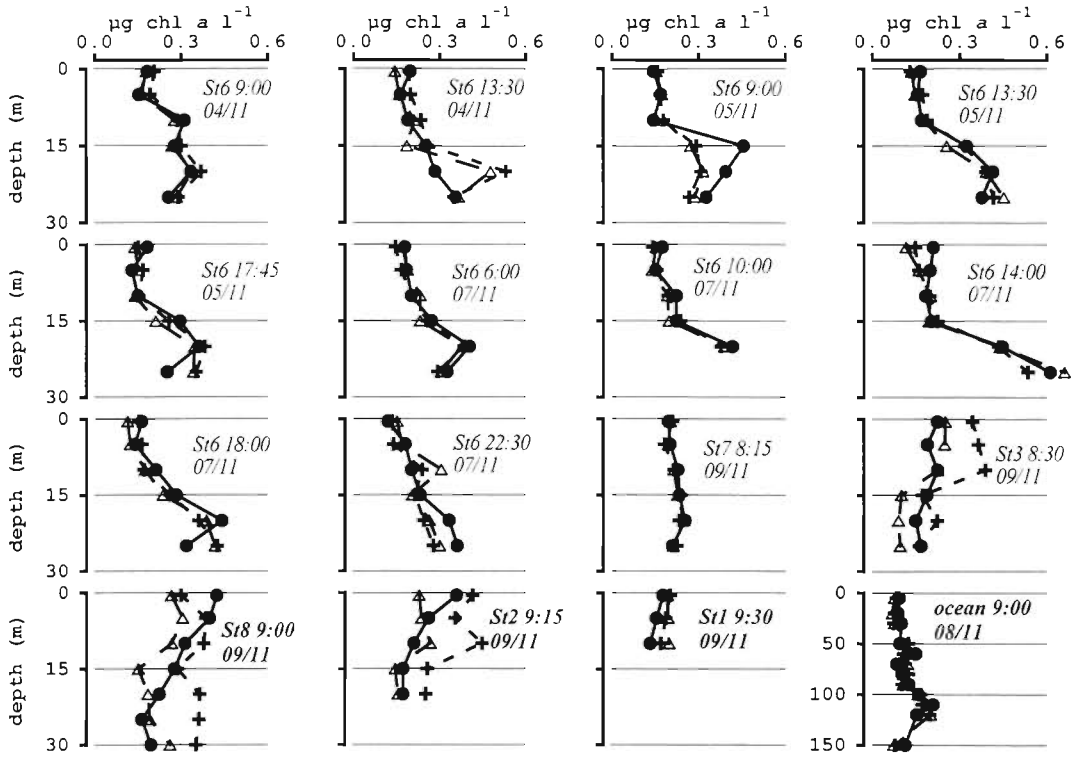

Fig. 4. Depth profiles of (●) measured chl *a*, (+) fitted values of $\sum_{i=1}^{3} n_i \times f_i \times \psi_i$ and (△) fitted values of $\sum_{i=1}^{2} n_i \times f_i \times \psi_i' + \text{chl } a > 1$ µm in Takapoto lagoon (November 1994)

extremely good in the first 11 profiles for total chl *a* ($R^2 = 97.5$ and $p < 0.01$ in both layers) and chl *a* <1 µm [$R^2 = 92.6$ in the upper layer (0 to 10 m) and 92.7 in the deeper layer (15 to 30 m), $p < 0.01$]. The agreement between measured chl *a* and fitted values of

$$\sum_{i=1}^{3} n_i \times f_i \times \psi_i$$

and between measured chl *a* and fitted values of

$$\sum_{i=1}^{2} n_i \times f_i \times \psi_i' + \text{chl } a > 1 \text{ µm}$$

(Fig. 4) was very good. Using regression estimated values of ψ_i and ψ_i', the percentage contributions to chl *a* and chl *a* <1 µm from each picoplankton group were calculated. In terms of total chl *a*, picoplankton in the upper layer consisted of 54 ± 2% picoeukaryotes, 45 ± 2% *Synechococcus* and 2 ± 0% *Prochlorococcus*. In the same layer *Synechococcus* contributed 86 ± 1% of chl *a* <1 µm and *Prochlorococcus* 14 ± 1% of chl *a* <1 µm. In terms of total chl *a*, picoplankton in the deeper layer consisted of 32 ± 2% picoeukaryotes, 33 ± 1% *Synechococcus* and 35 ± 1% *Prochlorococcus*. In this deeper layer, *Prochlorococcus* and *Synechococcus* contributed 59 ± 1 and 41 ± 1% of chl *a* <1 µm, respectively.

In the surrounding ocean waters, the 0 to 120 m integrated chl *a* (13.8 mg chl *a* m^{-2}) consisted of 11% *Prochlorococcus*, 34% *Synechococcus* and 56% picoeukaryotes.

Estimating the sizes and cellular carbon contents of picoplankton groups

Following Morel (1991) and Binder et al. (1996), we estimated the exponent x of Eq. (4) using cytometric measurements and the average diameter of *Synechococcus* (0.8 µm) measured at Takapoto with an optical microscope. Eq. (4) becomes:

$$\frac{FSC_{Cell}}{FSC_{Beads}} = \left(\frac{Diameter_{Cell}}{Diameter_{Beads}}\right)^{X} = \left(\frac{0.8}{1.98}\right)^{X}$$

We found for lagoonal waters $x = 3.94$ and in the upper 100 m of oceanic waters $x = 4.34$.

These values agree well with the theoretical expected values of Morel (1991), who reported that in the size range of picophytoplankton FSC varies from approximately d^6 to d^4 (d = dimension); thus, they were used to calculate cell size in lagoonal and oceanic populations. The carbon content of cells (Table 3) was estimated using the following volume to carbon conver-

Table 3. Estimated diameter (µm) and carbon content (Cc, fg C cell^{-1}) of the 3 picoplankton groups in Takapoto lagoon. SD: standard deviation

Time	*Prochloro-coccus*		*Synecho-coccus*		Pico-eukaryotes	
	Size	Cc	Size	Cc	Size	Cc
06:00 h	0.54	39	0.81	129	2.93	3999
10:00 h	0.60	53	0.90	180	3.18	4970
14:00 h	0.73	94	0.99	239	3.26	5289
18:00 h	0.67	73	0.96	218	3.33	5571
22:00 h	0.56	43	0.80	124	2.83	3645
Lagoon average	0.62	60	0.89	178	3.11	4695
SD	0.08	23	0.09	52	0.22	834
Ocean (surface)	0.6	53	0.92	191	2.47	2568
Ocean (5–100 m)	0.6	53	0.82	135	2.34	2232

sion factors (Verity et al. 1992): 470 fg C µm^{-3} for prokaryotes and 0.433(cell volume)$^{0.863}$ fg C µm^{-3} for eukaryotes. During the period of our study picoplankton size and carbon content peaked at the beginning of the afternoon for prokaryotes and at the end of the afternoon for eukaryotes. This pattern of diurnal cell size variations appeared to be relatively independent of depth (Fig. 5). We calculated the carbon biomass of the 3 picoplankton groups by multiplying their cellular C content by their abundance. In the upper layer of the lagoon, the picoplankton C biomass (26 µg l^{-1}) consisted of 3% *Prochlorococcus*, 47% *Synechococcus* and 50% picoeukaryotes while in the deeper layer, the picoplankton C biomass (38 µg l^{-1}) consisted of 5% *Prochlorococcus*, 65% *Synechococcus* and 30% picoeukaryotes. In the upper 120 m of the ocean, integrated picoplankton biomass (1242 mg m^{-2}) consisted of 65% *Prochlorococcus*, 1% *Synechococcus* and 34% picoeukaryotes.

Estimating the contribution of picoplankton groups to primary production

The contribution of prokaryotic cells to total production can be estimated as the percentage of carbon assimilation rate in the <1 µm size fraction. Prokaryotic cells contributed 50.0 ± 1.6% of carbon assimilation rate in the upper layer and 63.2 ± 2.5% in the deeper layer. If we assume that the contributions of *Prochlorococcus* and *Synechococcus* to chl *a* <1 µm reflect their contributions to carbon assimilation rate <1 µm, we can estimate their contributions to primary production by multiplying their contribution to chl *a* <1 µm by the proportion of carbon assimilation rate <1 µm. The contribution of picoeukaryotes was estimated as the percentage of carbon assimilation rate >1 µm. In the upper layer, *Prochlorococcus*, *Synechococcus* and picoeukaryotes contributed 5.8 ± 0.5, 44.1 ± 1.4 and 50.0 ± 1.6% respectively to primary production, whereas in the deeper layer they contributed 38.0 ± 1.6, 25.2 ± 1.1 and 36.8 ± 2.5% respectively to primary production.

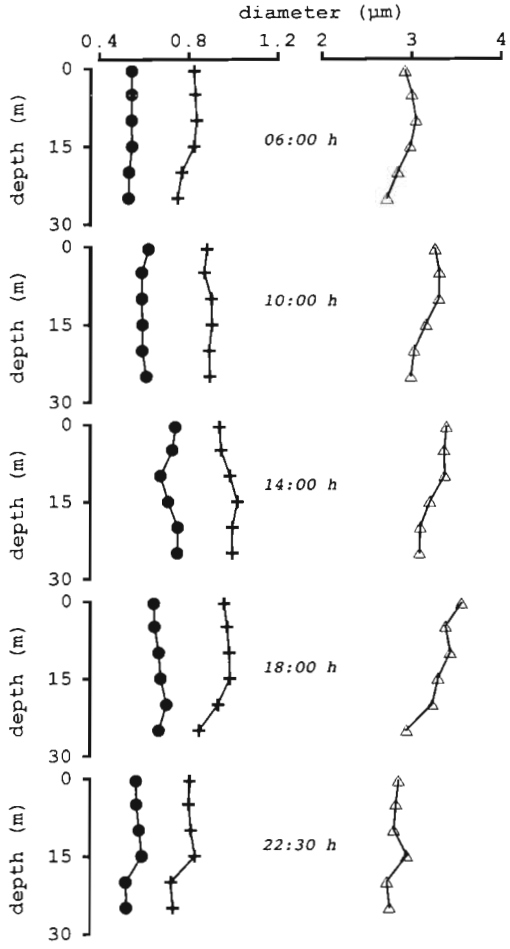

Fig. 5. Size of *Prochlorococcus* (●), *Synechococcus* (+) and picoeukaryotes (△) at different hours of the day in Takapoto lagoon

Other atolls

Picoplankton biomass and production in the 10 atolls investigated during TYPATOLL

Highest phytoplanktonic chl *a* was observed in Reka-Reka atoll (0.42 µg l^{-1} in March and 0.57 in November). In the lagoons of Taiaro and Haraiki chl *a* concentrations were twice as high in March (0.46 µg l^{-1}) as in November (0.26 µg l^{-1}). The lowest chl *a* concentration was observed in Tekokota (0.02 to

Table 4. Average ± standard error of chlorophyll concentration (Chl *a*), percentage of chl *a* in the <1 µm size fraction, picoplankton carbon biomass (Cpico), and *Prochlorococcus* (Proc), *Synechococcus* (Syn), and picoeukaryote (Peuk) abundances and their percentage contributions to chl *a* and Cpico in surface atoll lagoon waters. nm: no measurements

Atoll	Date	Chl *a* ($\mu g\ l^{-1}$)	Chl *a* <1 µm (%)	Cpico ($\mu g\ l^{-1}$)	Proc ($10^3\ ml^{-1}$)	Chl *a* Proc (%)	C Proc (%)	Syn ($10^3\ ml^{-1}$)	Chl *a* Syn (%)	C Syn (%)	Peuk ($10^3\ ml^{-1}$)	Chl *a* Peuk (%)	C Peuk (%)
Haraiki	Nov 1995	0.26 ± 0.04	67.1 ± 1.7	35.4 ± 5.0	12.6 ± 3.8	6.5 ± 2.7	1.8 ± 0.4	190.1 ± 2.7	60.1 ± 3.8	96.7 ± 0.6	0.11 ± 0.02	33.4 ± 1.6	1.4 ± 0.2
	Mar 1996	0.46 ± 0.06	82.0 ± 0.1	78.9 ± 18.0	210.2 ± 45.1	34.6 ± 2.7	14.7 ± 0.7	369.7 ± 87.6	47.4 ± 2.7	82.9 ± 1.7	0.24 ± 0.04	18.1 ± 0.1	2.4 ± 1.0
Hikueru	Nov 1995	0.19 ± 0.05	63.7 ± 1.6	11.3 ± 2.1	17.9 ± 5.0	17.5 ± 2.2	8.1 ± 0.9	43.8 ± 7.6	46.8 ± 2.1	70.4 ± 3.4	0.49 ± 0.13	36.7 ± 2.0	21.5 ± 3.7
	Mar 1996	0.19 ± 0.02	63.7 ± 0.9	8.1 ± 0.9	12.9 ± 1.2	15.4 ± 2.7	8.7 ± 1.0	17.3 ± 3.6	48.8 ± 2.5	37.4 ± 4.7	0.87 ± 0.08	35.8 ± 0.3	53.9 ± 3.9
Hiti	Nov 1995	0.23 ± 0.04	82.4 ± 1.4	28.7 ± 1.8	280.7 ± 19.0	72.7 ± 1.0	51.8 ± 0.5	66.3 ± 4.0	10.8 ± 0.9	41.6 ± 0.5	0.38 ± 0.02	16.6 ± 1.1	6.6 ± 0.3
	Mar 1996	0.26 ± 0.02	55.1 ± 1.3	22.2 ± 1.2	69.0 ± 4.6	19.1 ± 0.9	16.8 ± 1.0	86.6 ± 8.1	37.2 ± 0.9	70.7 ± 1.7	0.55 ± 0.06	43.7 ± 0.1	12.5 ± 1.2
Kauehi	Nov 1995	0.16 ± 0.01	63.2 ± 1.3	13.4 ± 1.1	82.8 ± 6.6	36.4 ± 3.1	33.3 ± 2.8	32.1 ± 4.8	27.9 ± 3.3	42.9 ± 4.7	0.65 ± 0.13	35.7 ± 0.9	23.8 ± 3.7
	Mar 1996	0.20 ± 0.03	71.0 ± 2.3	16.3 ± 1.2	104.3 ± 8.0	40.4 ± 2.8	34.5 ± 2.2	43.8 ± 4.3	32.8 ± 2.8	48.3 ± 2.0	0.57 ± 0.06	26.7 ± 0.1	17.3 ± 0.7
Marokau	Nov 1995	0.17 ± 0.04	61.2 ± 2.5	13.0 ± 1.2	88.3 ± 8.2	37.6 ± 3.6	36.4 ± 2.4	39.1 ± 4.8	22.8 ± 6.3	53.3 ± 2.6	0.27 ± 0.02	37.8 ± 2.8	10.3 ± 0.8
	Mar 1996	0.24 ± 0.01	61.0 ± 1.3	24.6 ± 1.9	146.2 ± 14.8	29.3 ± 3.2	31.8 ± 3.1	79.0 ± 8.5	32.4 ± 3.2	57.5 ± 3.2	0.54 ± 0.06	38.3 ± 0.5	10.8 ± 0.9
Nihiru	Nov 1995	0.16 ± 0.02	58.2 ± 4.3	13.1 ± 1.5	55.9 ± 7.7	27.9 ± 3.6	22.8 ± 2.0	49.7 ± 6.2	30.0 ± 3.7	67.8 ± 2.6	0.24 ± 0.02	42.1 ± 5.3	9.4 ± 1.2
	Mar 1996	0.19 ± 0.00	63.9 ± 0.3	19.9 ± 0.9	102.9 ± 8.5	35.7 ± 3.5	27.6 ± 2.4	50.0 ± 3.3	27.8 ± 3.5	45.1 ± 1.6	1.1 ± 0.12	36.4 ± 0.1	27.4 ± 2.5
Reka-Reka	Nov 1995	0.57 ± 0.06	67.2 ± 0.1	(3.5 ± 0.4)	1.4 ± 0.1	nm	2.1 ± 0.2	7.1 ± 1.0	nm	37.0 ± 3.1	0.42 ± 0.05	nm	60.8 ± 3.2
	Mar 1996	0.42 ± 0.03	59.2 ± 0.5	(6.8 ± 0.7)	0.9 ± 0.1	nm	0.7 ± 0.1	0.5 ± 0.1	nm	1.4 ± 0.2	1.3 ± 0.14	nm	97.9 ± 0.2
Taiaro	Nov 1995	0.27 ± 0.02	38.3 ± 4.6	21.1 ± 0.5	12.9 ± 1.0	10.9 ± 1.6	3.2 ± 0.2	44.2 ± 2.3	28.6 ± 4.3	37.6 ± 1.2	2.50 ± 0.35	60.4 ± 5.4	59.1 ± 1.3
	Mar 1996	0.45 ± 0.04	39.3 ± 3.2	43.8 ± 2.8	28.8 ± 6.7	23.5 ± 2.0	3.4 ± 0.8	32.1 ± 5.9	19.1 ± 2.0	12.7 ± 1.9	7.35 ± 0.34	57.5 ± 0.2	84.0 ± 2.5
Takapoto[a]	Nov 1994	0.19 ± 0.01	66.6 ± 0.2	25.4 ± 0.4	12.1 ± 0.9	1.4 ± 0.1	2.8 ± 0.2	71.5 ± 3.5	45.9 ± 1.8	46.9 ± 1.1	2.67 ± 0.05	52.8 ± 1.8	50.3 ± 0.9
Tekokota	Nov 1995	0.02 ± 0.01	38.2 ± 5.9	0.3 ± 0.1	2.0 ± 1.5	33.0 ± 7.4	25.8 ± 6.4	0.1 ± 0.0	7.1 ± 2.2	10.6 ± 2.1	0.04 ± 0.01	59.8 ± 6.8	63.6 ± 5.7
	Mar 1996	0.03 ± 0.01	22.6 ± 2.7	0.2 ± 0.0	1.0 ± 0.2	19.4 ± 0.8	23.8 ± 3.4	0.1 ± 0.0	1.4 ± 0.4	4.7 ± 1.3	0.03 ± 0.01	79.2 ± 0.9	71.5 ± 2.9
Tepoto Sud	Nov 1995	0.19 ± 0.01	78.3 ± 2.3	59.8 ± 4.1	12.3 ± 1.1	3.4 ± 0.5	1.1 ± 0.1	277.7 ± 16.6	73.4 ± 2.0	84.0 ± 2.9	1.84 ± 0.45	23.2 ± 2.2	14.9 ± 2.9
	Mar 1996	0.21 ± 0.02	4.5 ± 0.1	14.4 ± 1.8	8.8 ± 0.5	1.2 ± 0.2	3.4 ± 0.4	25.7 ± 4.2	3.3 ± 0.2	32.1 ± 3.9	1.88 ± 0.30	95.5 ± 0.2	64.5 ± 3.8
Ocean	Nov 1995	0.06 ± 0.01	76.3 ± 2.9	5.5 ± 1.8	43.6 ± 13.9	67.0 ± 5.0	50.7 ± 12.7	7.8 ± 6.8	9.9 ± 7.4	15.5 ± 10.2	0.66 ± 0.39	23.1 ± 4.2	33.8 ± 14.2
	Mar 1996	0.05 ± 0.01	60.4 ± 8.0	1.2 ± 0.4	11.9 ± 6.2	56.4 ± 9.2	41.6 ± 8.4	0.8 ± 0.5	8.1 ± 4.2	12.0 ± 4.2	0.17 ± 0.05	35.5 ± 7.5	46.5 ± 11.0

[a]0–10 m

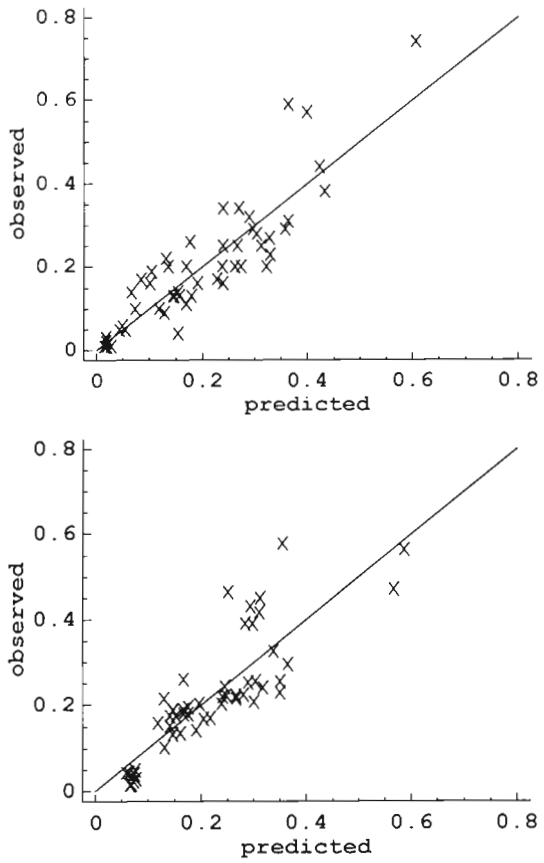

Fig. 6. Observed versus predicted values of chl *a* in 10 atoll lagoons in November 1995 (top) and March 1996 (bottom)

0.03 µg l^{-1}). In both seasons, the percentages of chl *a* in the <1 µm size fraction were usually above 50% in the studied atolls. The exceptions were Taiaro (38 to 39%), Tekokota (23 to 38%) and Tepoto Sud in the dry season (4.5%) (Table 4).

Large differences in relative picoplankton group abundance were observed between the 2 sampling periods in some lagoons. *Prochlorococcus* were particularly abundant in Hiti lagoon (281×10^3 cells ml^{-1}) during the rainy season (November) and in Haraiki (210×10^3 cells ml^{-1}) during the dry season (March). *Synechococcus* were very abundant in Haraiki lagoon during both seasons but especially in March, when average abundance reached 370×10^3 cells ml^{-1}. A large number of *Synechococcus* were also observed in Tepoto Sud lagoon in November 1995 (278×10^3 cells ml^{-1}). Highest picoeukaryote abundances were recorded in Taiaro during both seasons, particularly in March (7.4×10^3 cells ml^{-1}). The densities of the 3 picoplankton groups in surface coastal ocean waters ranged from 12×10^3 to 44×10^3 *Prochlorococcus* ml^{-1}, 0.8×10^3 to 7.8×10^3 *Synechococcus* ml^{-1} and 0.2×10^3 to 0.7×10^3 picoeukaryote ml^{-1}.

Estimating the contribution of picoplankton groups to biomass in November 1995 and March 1996

In November 1995 and March 1996, cytometric measurements were performed on fixed samples but the fit of the data was insufficient to estimate ψ_i. The picoeukaryotes were poorly preserved and as a result their RF were likely affected by the fixation. However, we were able to calculate ψ_i' (Table 2), as the fits of chl *a* <1 µm versus prokaryotic RF were good ($p < 0.01$) in all investigated lagoons except Reka-Reka (Fig. 6). The contribution of prokaryotic groups to total chl *a* was estimated by multiplying their contribution to the chl *a* <1 µm (calculated from Eq. 3) by the proportion of chl *a* <1 µm. The contribution of picoeukaryotes to total chl *a* was estimated as the percentage of chl *a* >1 µm.

Since all the samples were collected in the morning during TYPATOLL expeditions, the C biomass of the 3 groups was estimated using the average cellular C contents calculated from the morning samples collected in Takapoto: 53 fg C $cell^{-1}$ for *Prochlorococcus*, 180 fg C $cell^{-1}$ for *Synechococcus* and 4970 fg C $cell^{-1}$ for picoeukaryotes. For surface ocean waters, we used the values calculated for surface ocean waters surrounding Takapoto: 53 fg C $cell^{-1}$ for *Prochlorococcus*, 191 fg $cell^{-1}$ for *Synechococcus* and 2568 fg C $cell^{-1}$ for picoeukaryotes. The picoplankton carbon biomass (Table 4) varied from 0.2 µg l^{-1} in Tekokota to 79 µg l^{-1} in Haraiki (March). *Prochlorococcus* dominated the picoplankton biomass in only 1 lagoon: Hiti in November (73% of chl *a* and 52% of C). The contribution of *Synechococcus* to picoplankton biomass was important in all lagoons except Reka-Reka, Taiaro and Tekokota. Its contribution was also important in Tepoto Sud but only in November, when they contributed to 73% of chl *a* and 84% of C. Picoeukaryotes dominated the picoplankton biomass at Reka-Reka, Taiaro, Takapoto (in surface water) and Tekokota. They also dominated the picoplankton biomass at Tepoto Sud in March (96% of chl *a* and 65% of C). In surface ocean waters in November, *Prochlorococcus* contributed 51%, *Synechococcus* 16% and picoeukaryotes 34%, of picoplankton carbon, whereas in March their contributions were 42, 12 and 46% respectively.

Estimating the contribution of picoplankton groups to primary production in November 1995 and March 1996

As for Takapoto data, the contribution of prokaryotic cells to total production was estimated by the percentage of carbon assimilation rate in the <1 µm size fraction. In both seasons, the percentages of carbon assimilation rate in the <1 µm size fraction were above 45%

Table 5. Average ± standard error of percentage of carbon assimilation rate (CAR) in the <1 µm size fraction; percentage contributions of *Prochlorococcus* (Proc), *Synechococcus* (Syn), and picoeukaryotes (Peuk) to CAR in surface atoll lagoon waters; and estimated primary production (PP). nm: no measurements

Atoll	Date	CAR <1 µm (%)	CAR Proc (%)	CAR Syn (%)	CAR Peuk (%)	PP (g C m^{-2} d^{-1})
Haraiki	Nov 1995	70.7 ± 1.0	7.1 ± 3.0	63.6 ± 3.0	29.3 ± 1.6	0.34
	Mar 1996	81.1 ± 1.4	39.8 ± 1.4	40.4 ± 1.4	19.8 ± 2.8	0.60
Hikueru	Nov 1995	46.5 ± 4.4	13.1 ± 3.3	33.4 ± 2.6	53.5 ± 2.0	0.62
	Mar 1996	65.8 ± 3.7	10.5 ± 0.1	48.9 ± 0.4	40.6 ± 0.5	0.62
Hiti	Nov 1995	66.8 ± 0.8	58.2 ± 1.0	8.6 ± 0.6	34.2 ± 1.1	0.30
	Mar 1996	53.3 ± 1.1	16.1 ± 0.3	37.3 ± 0.8	46.6 ± 1.1	0.34
Kauehi	Nov 1995	71.7 ± 2.3	40.7 ± 3.7	31.1 ± 3.6	28.2 ± 0.9	1.04
	Mar 1996	74.9 ± 2.3	49.7 ± 1.5	25.2 ± 0.8	25.1 ± 2.3	1.30
Marokau	Nov 1995	50.3 ± 1.3	31.3 ± 3.9	18.4 ± 4.5	50.3 ± 2.8	0.66
	Mar 1996	57.7 ± 0.7	26.0 ± 0.3	31.1 ± 0.3	42.9 ± 0.6	0.94
Nihiru	Nov 1995	52.1 ± 2.1	25.1 ± 2.4	27.0 ± 2.1	47.9 ± 5.3	0.42
	Mar 1996	52.5 ± 8.5	24.5 ± 4.0	28.0 ± 4.6	47.5 ± 8.6	0.49
Reka-Reka	Nov 1995	45.4 ± 1.1	nm	nm	54.2 ± 1.0	0.07
	Mar 1996	34.7 ± 0.5	nm	nm	65.3 ± 0.6	0.05
Taiaro	Nov 1995	37.0 ± 6.1	10.7 ± 2.6	26.3 ± 3.6	63.0 ± 5.1	0.53
	Mar 1996	32.0 ± 5.1	16.5 ± 2.7	15.5 ± 2.5	68.0 ± 5.1	0.88
Takapoto	Nov 1994	50.0 ± 1.6	5.8 ± 0.5	44.1 ± 1.4	50.0 ± 1.6	0.81
Tekokota	Nov 1995	45.3 ± 3.1	36.4 ± 3.2	8.9 ± 2.7	54.7 ± 2.3	0.01
	Mar 1996	23.7 ± 0.7	20.9 ± 0.6	2.8 ± 0.1	76.3 ± 0.7	0.01
Tepoto Sud	Nov 1995	62.3 ± 1.1	2.8 ± 0.4	59.5 ± 1.0	37.7 ± 0.9	0.12
	Mar 1996	15.1 ± 0.3	2.7 ± 0.1	12.4 ± 0.3	84.9 ± 0.3	0.14
Ocean	Nov 1995	52.4 ± 0.8	nm	nm	47.6 ± 0.8	
	Mar 1996	57.4 ± 1.4	45.0 ± 5.2	12.4 ± 5.4	42.6 ± 2.4	

in all atolls except in Reka-Reka in March (35%), in Taiaro (37 and 32%), Tekokota in March (24%) and Tepoto Sud in March (15%) (Table 5). The estimated contributions of picoplankton groups to primary production could be calculated for all atoll lagoons except Reka-Reka using their contributions to chl *a* <1 µm and the percentage of carbon assimilation rate <1 µm. With some exceptions, picoplankton group contributions to carbon assimilation rate were very close to their contributions to chl *a* (Tables 4 & 5). In Takapoto, the contribution of *Prochlorococcus* to carbon assimilation rate was much higher than what their contribution to chl *a* indicated (Tables 4 & 5), but this value considers only the upper layer of the lagoon. In Tepoto Sud (March), the contribution of *Synechococcus* to carbon assimilation rate was 4 times their contribution to chl *a*. In Hiti (November), picoeukaryote contribution to carbon assimilation rate was twice their contribution to chl *a*.

Estimation of lagoon productivity

We attempted to estimate lagoon primary production using the average *in situ* biomass-specific production, P^B, measured in Takapoto and Tikehau lagoons between 1991 and 1994 (13 mg C mg^{-1} chl *a* h^{-1}; Charpy 1996), the average chl *a* concentration and the estimated average depth of lagoons (Table 5). Estimated lagoon productivity ranged between 0.01 g C m^{-2} d^{-1} (Tekokota) and 1.3 g C m^{-2} d^{-1} (Kauehi).

DISCUSSION

Picoplankton size

At Takapoto the sizes calculated for the 3 groups are within the range of the data given in the literature (Table 6). The size of prokaryote cells is for the most part under 1 µm in diameter for *Prochlorococcus* (0.54 to 0.73 µm) and *Synechococcus* (0.81 to 0.99 µm). Above 1 µm the cells are largely picoeukaryotes (2.83 to 3.26 µm). During the day, the size increased to a maximum value, then decreased. The average sizes of *Prochlorococcus*, *Synechococcus* and picoeukaryotes increased by 35, 22 and 14%, respectively.

Vertical variations

In Takapoto (November 1994), due to an unusual stratification of the water column in the lagoon envi-

Table 6. Picoplankton groups cell size in different areas. FCM: flow cytometric measurement

Group	Diameter (µm)	Source	Method	Area
Prochlorococcus	0.6–0.8	Chisholm et al. (1988)	Size fraction FCM	Atlantic and Pacific
	0.8	Vaulot et al. (1990)	Size fraction FCM	Mediterranean
	0.5–0.7	Morel et al. (1993)	Coulter Counter	Cultures
	0.6–1	Blanchot & Rodier (1996)	Size fraction FCM	Pacific
Synechococcus	0.9–2.2	Waterbury et al. (1979)	Microscopy	Atlantic
	0.8–1.0	Johnson & Sieburth (1979)	Microscopy	Atlantic
	1	Verity et al. (1992)	Microscopy	Cultures
	>0.6–1	Blanchot & Rodier (1996)	Size fraction FCM	Pacific
Picoeukaryotes	0.6–3	Blanchot & Rodier (1996)	Size fraction FCM	Pacific
	2.3	Campbell et al. (1994)	Microscopy FCM	Pacific
	1–2	Durand & Olson (1996)	Microscopy FCM	Pacific

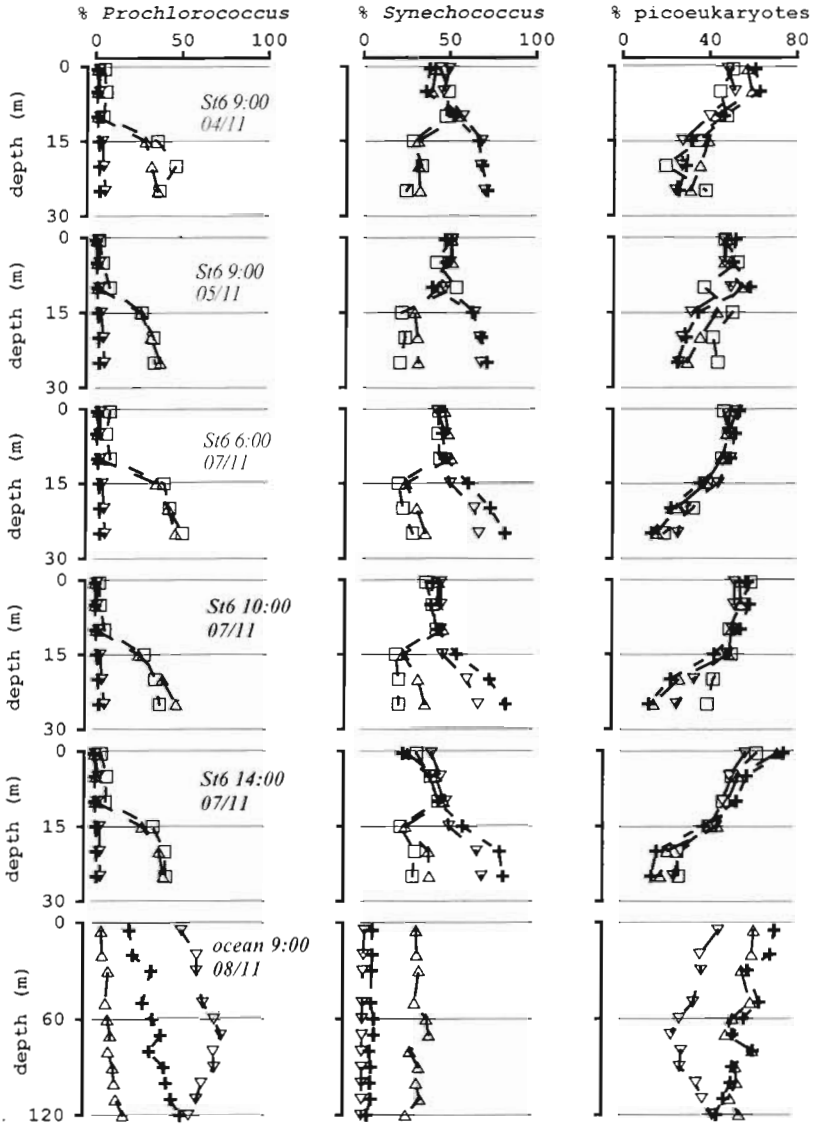

Fig. 7. Depth profiles of (+) percentage of red fluorescence, (△) percentage contribution to chl *a*, (▽) percentage contribution to picoplankton C and (□) percentage contribution to carbon assimilation rate in 8 depth profiles in Takapoto lagoon and in surrounding oceanic waters (November 1994)

ronment (Charpy 1996) the picoplankton community structure of the upper layer (0 to 10 m) was dominated by picoeukaryotes (54%). In the deeper layer (15 to 30 m) the 3 groups were equally abundant in terms of RF.

For *Prochlorococcus*, which are able to photoacclimate to low light intensity (large increase of divinyl chlorophyll *b*; Partensky et al. 1996), ψ values were 8 times higher in the deeper layer (111) than in the upper layer (14) (Table 2). However, for *Synechococcus* the trend was reversed: ψ values were 3 times lower in the deeper layer (3.3) than in the upper layer (10.8). Finally, for picoeukaryotes ψ values were similar in the upper and lower part of the water column. In the deeper layer, the higher chl *a* content and productivity of *Prochlorococcus* versus that of *Synechococcus* confirms the former's adaptation to low light environments (Moore et al. 1995). In contrast, during TYPATOLL experiments picophytoplankton was uniformly distributed in the water column due to frequent windy conditions. Surface samples were thus representative of the entire water column.

Comparison between different estimates of picoplankton group dominance

The dominance of the different picoplankton groups varied with the method used to estimate their relative

importance as reported by Li (1995): (1) percentage of red fluorescence (RF), (2) percentage of chl *a* calculated using regression estimated values of ψ_i, (3) percentage of carbon, (4) percentage of primary production. In the 5 depth profiles in Takapoto lagoon where picoplankton biomass and primary production were measured simultaneously (Fig. 7), firstly we observed that picoplankton group dominance estimated by flow cytometric analysis, i.e. percentages of RF and percentages of picoplankton C (via size/FSC estimations) are similar. Secondly, values estimated by their contribution to chl *a* were similar to values estimated by their contribution to primary production. This result concords with the observations of Li (1994, 1995) on the picoplankton of the central North Atlantic. Indeed, this author observed that differences between the contributions of picoplankton groups to chl *a* and primary production based on the measurements of ^{14}C uptake rate per cell obtained by flow sorting were small (28 vs 19% for *Prochlorococcus*, 11 vs 13% for *Synechococcus* and 61 vs 68% for picoeukaryotes).

Finally, *Prochlorococcus* dominance is strongly underestimated with methods (1) and (3) compared with method (2), whereas methods (1), (2), (3) and (4) appear equally efficient for picoeukaryotes. This is likely due to an underestimation of *Prochlorococcus* in near surface waters due to a lack of sensitivity of the FACScan. Prokaryotic cell estimations vary significantly at different depths. In the deeper layer of Takapoto lagoon, the pigment content and the carbon assimilation rate per cell of *Prochlorococcus* were high. Whereas with *Synechococcus*, the RF and C content per cell increased with depth without an increase in chl *a* content and productivity.

In ocean waters, *Prochlorococcus* dominance was overestimated with method (3) (carbon contribution) and method (1) (red fluorescence) compared with method (2) (chl *a* contribution). The opposite situation occurs for *Synechococcus*. The estimation of chl *a* content per unit fluorescence ψ_i in Takapoto oceanic waters was made using only 1 profile with all depths pooled, and was probably not reliable. Indeed, the ψ_i calculations in lagoonal waters have shown that this parameter varied with depth. In fact the pigment content of raised cells is known to increase when the light exposition decrease (Cailliau et al. 1996, Shimada et al. 1996). In addition there might have been variations in the carbon content of the 3 picoplankton groups with depth.

Temporal variations

The large differences of picoplankton community structure observed between the 2 TYPATOLL expeditions in some lagoons were independent of season. Indeed, *Prochlorococcus* were abundant in Haraiki, Marokau and Nihiru in March and in Hiti in November while *Synechococcus* were very abundant in Haraiki in March and in Tepoto Sud in November. A similar pattern was noted in Takapoto between 1991 and 1994 and in Tikehau (2 other Tuamotu atolls) between 1983 and 1985, where large differences in phytoplankton biomass as chl *a* were recorded independently of season (Charpy 1996). Therefore, we did not see the seasonal variations in picoplankton community structure observed by Campbell et al. (1997) in the subtropical North Pacific Ocean where the abundance of *Prochlorococcus* typically peaked in the summer, *Synechococcus* in the winter and picoeukaryotes in the spring. It seems that in the Tuamotu archipelago, small-temporal-scale stress (wind, storm, etc.) has a larger effect upon the community structure than the effect of season. Typically, strong winds can induce resuspension of sedimented particulate materials including benthic microalgae, which can lead to a change in the size fractionation of chl *a*. A significant relationship has been established between wind intensity and sediment resuspension (Clavier et al. 1995). Furthermore, the perturbation of the water-sediment interface induced by storms may release nutrients trapped in the sediments. In Tikehau lagoon, for instance, nutrient concentrations of sediment pore water reached maximum values of 130 µM NH_4, 7 µM PO_4 and 30 µM SiO_2 between 4 and 6 cm below the surface of the sediments (Charpy-Roubaud et al. 1997).

Relation between picoplankton biomass and community structure, and atoll geomorphology

In spite of the large variations in structure, some general trends can be observed. All atoll lagoons except Taiaro and Tekokota were dominated by prokaryotic plankton. With the exception of the deeper lagoons, Kauehi (45 m) and Marokau (30 m), where growth of *Prochlorococcus* appears to have been promoted, the dominant group was *Synechococcus*. *Prochlorococcus* are better adapted than *Synechococcus* for photosynthesis in blue-dominated light (Shimada et al. 1996). *Synechococcus* are well known to be abundant only in the upper part of the photic layer (Blanchot et al. 1992, Blanchot & Rodier 1996). The high chl *a* concentration observed in the Reka-Reka lagoon can be explained as a resuspension of benthic microphytes due to the shallowness of the lagoon (1.5 m). However, these benthic organisms were not considered when flow cytometric measurements were made, and therefore the contribution of picoplankton groups to chl *a*

could not be estimated. In a previous paper (Charpy et al. 1997), we demonstrated that phytoplankton biomass (chlorophyll concentration) was inversely related to the water exchange between lagoon and ocean. The decrease of chlorophyll concentration with the degree of openness of atoll lagoons may be related to a simple 'dilution' of the lagoon by the low-chlorophyll oceanic waters inside the open atolls. This may explain the very low phytoplankton biomass in Tekokota, a lagoon with high exchange with oceanic waters. The large dominance of picoeukaryotes observed in Taiaro may be due to the high salinity of the lagoon (>40 PSU).

Biotic factors can also affect the picoplankton biomass and community structure. There are a variety of macroinvertebrates that feed on ultra-plankton (Jørgensen et al. 1984, Vacelet 1984, Vacelet & Boury-Esnault 1995). Reiswig (1971) found that coral reef sponges are a significant sink for plankton. Indeed, Pile et al. (1996) observed that *Prochlorococcus* was filtered by sponges with the highest efficiency (93%), followed by *Synechococcus* (89%) and picoeukaryotes (72%). In coral reef waters sponges significantly decreased concentrations of *Prochlorococcus* and *Synechococcus* while increasing those of autotrophic picoeukaryotes (Pile 1997). Sponges are thus capable of altering community structure. In atoll lagoons, sponges and other filter feeders are mainly located on hard substrates: coral reef pinnacles or fringing reefs. The density of hard substrate varies between lagoons. Nihiru and Tekokota lagoons have a high percentage of hard substrate relative to surface area while Tepoto Sud and Taiaro have a low percentage (Dufour & Harmelin-Vivien 1997). The metabolism of cultivated pearl oysters, particularly abundant in Takapoto, can also affect the phytoplankton biomass (Charpy et al. 1997). Indeed, waste products from the reared *Pinctada margaritifera* stock in Takapoto lagoon enhanced the growth rates of phytoplankton by decreasing the regeneration time of the nutrients (Vacelet et al. 1996). Filtration experiments performed on Takapoto Pearl oysters demonstrated that *P. margaritifera* feed only on picoeukaryotes (Blanchot unpubl.). Zooplankton can also have a strong effect on picoplankton abundance and community structure. In Tikehau lagoon, animals >35 µm grazed more than 60% of primary production. Inorganic excretion constituted 32 and 18% of the phytoplankton nitrogen and phosphorus requirements (Le Borgne et al. 1989). Zooplankton biomass was studied in the investigated atolls but the data has not been processed yet.

Comparison between lagoon and open ocean waters

With the exception of Tekokota, picoplankton biomass was 2 to 10 times higher in atoll lagoons than in surrounding surface waters. On the other hand, integrated picoplankton biomass observed in Takapoto ocean waters (1242 mg C m^{-2} in the upper 120 m) was considerably higher than the integrated biomass found in lagoon waters. The picoplankton community structure was dominated by *Synechococcus* in atoll lagoons and *Prochlorococcus* in the surrounding ocean waters. This dominance of *Prochlorococcus*, already demonstrated in subtropical areas (Campbell & Vaulot 1993, Campbell et al. 1994, 1997) and tropical areas (Blanchot & Rodier 1996), would appear to be a common feature in the Pacific Ocean. This switch in dominance from *Prochlorococcus* to *Synechococcus* in lagoons may be due to 3 factors: (1) Photoinhibition in shallow lagoons. Photoinhibition of *Prochlorococcus* in shallow waters was observed in Takapoto. (2) Difference in nutrient availability. Differences in nutrient concentrations between lagoon and ocean were observed in Tuamotu Archipelago. In Takapoto and Tikehau, phosphate and silicate concentrations were lower in the lagoons than in the surrounding ocean water (Sournia & Ricard 1976, Charpy-Roubaud et al. 1990, Charpy 1996). N_2-nitrogen fixation by *Synechococcus* was reported in Tikehau lagoon by Charpy-Roubaud et al. (1997); this process requires extra P uptake and may therefore be responsible for phosphorus depletion. Data from the Great Astrolabe Reef (Fiji) and Tuamotu atoll lagoons (Blanchot & Charpy 1997) appear to indicate that when the photic layer is N depleted (NO_3 + NO_2 < 0.1 µM), *Prochlorococcus* is the major component of the integrated carbon biomass. In the layers where NO_3 + NO_2 concentration > 0.1 µM, picoeukaryotes constitute the major component in both atoll-lagoon and near-shore waters, whereas when NO_3 + NO_2 ≈ 0.1 µM, small concentrations of NH_4^+ appear to promote *Synechococcus* abundance. The turnover time of N and P might be lower in lagoon waters because part of the remineralization process occurs in the sediments and the pool of pore water nutrients is released during storms. (3) Difference in grazing. We argued above that grazing by benthic macroinvertebrates, organisms absent in ocean waters, could significantly affect the picoplankton abundance and community structure. In addition, lagoon zooplankton might be different from ocean zooplankton and therefore have a different grazing impact on picoplankton. Successive blooms of different groups of zooplankton can generate quantitative and qualitative differences in the control of the pico- and nanoplankton populations, and dominance of a specific group of grazers can alter the size distribution pattern of food particles. In a recent study G. Gorsky, M. J Dinet, J. Blanchot & I. Palazzoli (unpubl.) reported that the larvacean *Megalocercus huxleyi* efficiently filtered, assimilated and aggregated into fecal pellets pico- and nanoplankton

(submicronic particles included). Blooms of thaliaceans, larvaceans, pteropods and copepods were reported in Tikehau and Rangiroa lagoons (Michell et al. 1971, Le Borgne & Moll 1986, Le Borgne et al. 1989). Salps, larvaceans, doliolids and thecosome-pteropods are known to feed on particles at least 3.5 orders of magnitude smaller than their own size (Fortier et al. 1994). Such peculiar blooms of small particle feeders could alter the community structure from small-size-fraction dominance (prokaryotic) to large-size-fraction dominance (eukaryotic). Another hypothesis to explain the differences between oceanic and lagoonal picoplankton community structure is viral infection. Indeed, Blanchot & Rodier (1996) consider that viral infection could be responsible for controlling of the abundance of prokaryotic phytoplankton, and coastal waters are more suitable than ocean waters for cyanophage infection and growth (Boehme et al. 1993, Suttle & Chan 1994).

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