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Pico- and nanoplankton biomass and production in the two largest atoll lagoons of French Polynesia

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ABSTRACT: Pico- and nanoplankton concentrations were measured in the lagoonal waters of the 2 largest atolls of French Polynesia (Fakarava and Rangiroa). Growth, production and grazing rates were estimated using diffusion chambers near the reef flat spillways and near the main channels of the atolls. The overall microbial biomass was dominated by picoplankton, with very high abundances of bacteria and cyanobacteria, these 2 groups representing each 20 to 50% of the total carbon. Nanoplankton (auto- and heterotrophic flagellates) constituted only 10 to 15% of the total biomass. Microbial concentrations were 1.5 to 3-fold lower near the reef flat spillways than near the channels. This suggests an important biomass production inside the lagoon. At Rangiroa, growth rates varied from 0.02 to 0.06 h^{-1} for bacteria and from 0.01 to 0.04 h^{-1} for the other groups (cyanobacteria, auto- and heterotrophic flagellates). At Fakarava, growth rates were in the same range except for the heterotrophic flagellates (0.05 to 0.17 h^{-1}). Growth rates were significantly higher near the reef flat spillways than near the channels. More than 50% of both bacterial and cyanobacterial production was grazed by the higher trophic levels in both atolls. Bacterial production was enhanced by a nitrogen enrichment whereas production of cyanobacteria and flagellates was enhanced by both a nitrogen and a phosphorus enrichment.

KEY WORDS: Atoll lagoon · Picoplankton · Nanoplankton · Growth · Nutrient limitation

INTRODUCTION

Microbes are an important component of the living biomass of oceanic communities and play major roles in biogeochemical cycles (Cho & Azam 1990). Autotrophic cells <20 µm in size constitute a significant fraction of the primary production in many systems (Olson et al. 1990). Heterotrophs such as bacteria and protozoa are the major consumers of the dissolved organic matter and their biomass may be the largest of any planktonic assemblage (Cho & Azam 1990). Protozoa are also the link between microbes and higher trophic levels for the transfer of material and energy (Azam et al. 1983). In coral reef ecosystems, however, the interactions between bacteria, phytoplankton and protozoa are poorly known (Gonzalez et al. 1998), and only few papers have assessed the contribution of microbial populations to the reef productivity (Ducklow 1990, Charpy & Blanchot 1998, Ferrier-Pagès & Gattuso 1998, Torréton 1999). Measurements of protozoan growth and grazing rates are also scarce (Landry et al. 1984, Ferrier-Pagès & Gattuso 1998, Gonzalez et al. 1998).

Among coral reef systems, Tuamotu atolls (French Polynesia) are of great interest because they are very productive compared to the surrounding ocean (Torréton & Dufour 1996a, Charpy 1996), and they host numerous pearl oysters farms in their lagoons, with a high economic value. Since oysters feed on plankton, the functioning of plankton communities in lagoons has attracted attention, but so far, it has only been poorly described. Extensive measurements have been performed in the atolls of Tikehau and Takapoto on the biomass and growth rates of bacteria (Torréton & Dufour 1996a, Gonzalez et al. 1998) and phytoplankton (Blanchot et al. 1989, Charpy et al. 1992, Charpy 1996, Charpy & Blanchot 1998). However, few data have

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been collected on microbial productivity in other Tuamotu atolls (Delesalle & Sournia 1992, Charpy & Blanchot 1998, Hollibaugh et al. 2001). The extrapolation of data from one atoll to another is also unsatisfactory due to a high geomorphological diversity (Andrefouët 1998). Atolls can be closed with almost no exchange with the ocean (e.g. Takapoto) or possess large channels and reef flat spillways (hoas) allowing exchange of large amounts of oceanic waters.

The aim of this study was to measure pico- and nanoplankton production in the 2 largest atolls of French Polynesia, Rangiroa and Fakarava, during an oceanographic cruise in October 1998. These atolls are 4 to 15 times bigger than those usually investigated and have large connections with the ocean, through numerous reef flat spillways and channels. Except for 2 studies performed in Rangiroa on macrozooplankton and particulate organic matter (Michel et al. 1971, Charpy et al. 1997), no data are available to our knowledge on this type of atoll. The experiments were undertaken with several objectives: (1) to estimate the contributions of pico- and nanoplankton groups to community productivity at the beginning of the dry season, (2) to compare the concentrations and growth rates of pico- and nanoplankton with those measured in other atolls or reef systems, and (3) to compare the biomass, growth and production rates measured in 2 different areas within each lagoon: the reef flat spillways (oceanic water influence) and the channels (lagoon water influence).

Coral reefs are also characterised by oligotrophic waters where primary productivity is limited by the availability of inorganic nutrients such as phosphorus (Entsch et al. 1983, Littler et al. 1991) and nitrogen (Laws & Redalje 1979, Kimmerer & Walsh 1981). Few studies have investigated the effect of nutrient enrichment on the phytoplanktonic communities of Polynesian atoll lagoons (Vacelet et al. 1996, Dufour & Berland 1999, Dufour et al. 1999, Sakka et al. 1999). Since these atolls have a high morphological diversity affecting nutrient concentrations in their lagoons (Andréfouët 1998), the effect of nitrogen and phosphorus enrichment on the phytoplanktonic populations of Rangiroa and Fakarava was also investigated.

MATERIAL AND METHODS

Study sites. Experiments were carried out in October 1998 in the 2 largest atolls of the Tuamotu Archipelago during an oceanographic cruise on board the MY 'Golden Shadow'. Rangiroa (147° 40′ W, 15° 05′ S), with a surface area of 1640 km^2 and a maximal depth of 34 m, is one of the largest atolls in the world, representing 12% of the total area of the Archipelago

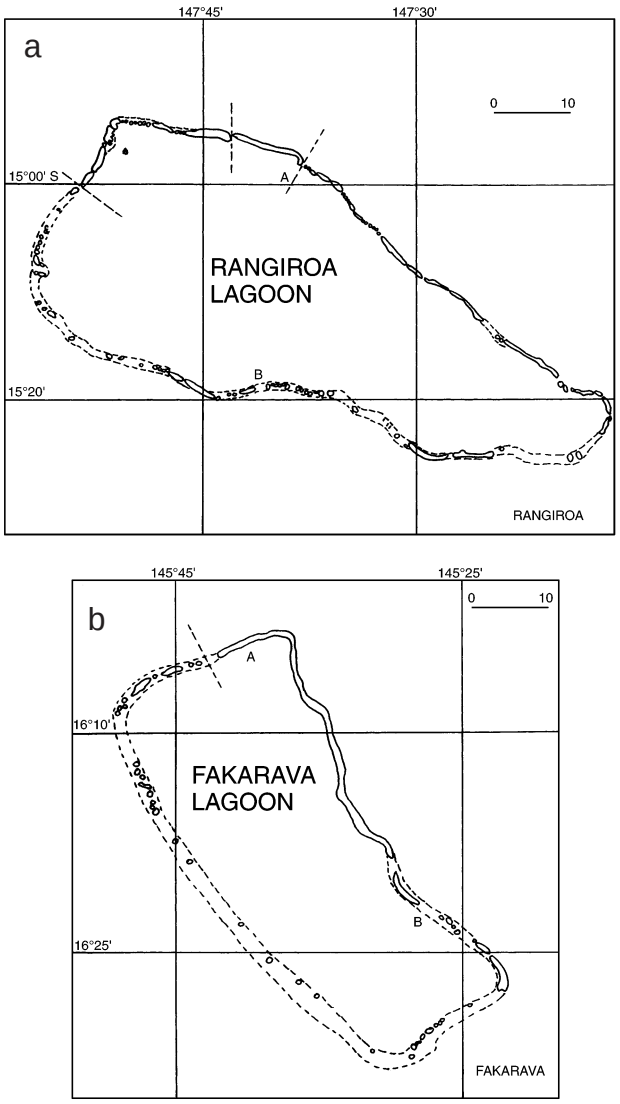

Fig. 1. Location of the study site and sampling points. (a) Atoll of Rangiroa; (b) atoll of Fakarava. A: incubations near the channels; B: incubations near the reef flat spillways

(Fig. 1a). Fakarava (145° 30′ W, 15° 10′ S) has a surface area of 1220 km^2 and a maximal depth of ca 30 m (Fig. 1b). These atolls are huge compared to the others (with a surface area between 5 and 700 km^2), and their characteristics are described in Bonvallot et al. (1994) as well as in Dufour & Harmelin-Vivien (1997). Compared to smaller atolls, they have deep lagoons (often considered as an inland sea) as well as large channels (1 and 3 for Rangiroa and Fakarava respectively). They are situated in the central part of the Tuamotu Archipelago whereas smaller atolls are located in the eastern part. Oceanic waters usually enter the lagoons through the reef-flat spillways and exit via the channels (Michel et al. 1971). Two different experiments were carried out in each atoll. In the first set of experi-

ments, the abundance, growth and production rates of pico- and nanoplankton were measured near both the main channel and the reef flat spillways (Fig. 1, Sites A and B respectively). In the second set of experiments, limiting nutrients were identified by the effect of nutrient additions on pico- and nanoplankton assemblages. All experiments were run in triplicate.

Growth, production and grazing rate measurements. Seawater was collected between 07:00 and 09:00 h at 1 m depth near the channel (Fig. 1a,b, Site A) or the reef-flat spillways (Fig. 1a,b, Site B) and brought back to the laboratory. Particles were size-fractionated, by gravity filtration and reverse flow, through nylon screens and Nuclepore™ filters to avoid cell breakage (Furnas & Mitchell 1986). Five filtrations were performed to remove different size classes of predators: <0.8 µm (mostly bacteria and *Prochlorococcus*), <2 µm (previous cells, chroococcoid cyanobacteria and picoflagellates), <5 µm (previous cells and nanoflagellates), <10 µm (previous cells and small ciliates) and non-fractionated samples (entire population). Each size-fraction was transferred into 3 Perspex chambers (1 l) closed at each end by a dialysis membrane (Spectra/Por, cut off 14 to 20 000 dalton) and incubated *in situ* for 24 h near the channels (A) or the reef flat spillways (B). This incubation technique has already been described and used in several studies (Landry et al. 1984, Furnas 1990, Ferrier-Pagès & Gattuso 1998). Dialysis membranes allow exchanges of dissolved organic and inorganic nutrients between the external seawater and the incubated medium and prevent container-induced nutrient limitation. Incubations started within 2 h after water sampling. The water column depth was ca 5 m and incubation chambers were set at 1 m depth.

Samples (2 l) from the different size-fractions were taken at the beginning of each incubation, filtered onto Whatman GF/F glass fibre filters under low vacuum pressure and frozen (–20°C) for subsequent determination of chlorophyll *a* by fluorometry (Strickland & Parsons 1972). Triplicate samples (10 to 20 ml) were also taken at the beginning and end of each incubation for pico- and nanoplankton density estimation. They were fixed with borax buffered formaldehyde (2% v:v), stained with DAPI (Porter & Feig 1980), filtered onto 0.2 µm black Nuclepore™ filters and stored at –20°C. Organisms were counted and measured under ×1000 magnification with a Leica epifluorescence microscope using UV and blue light excitation.

Microbial abundance was converted into carbon biomass (B, µg C l^{-1}) using the following equations:

$$B = N \times C$$

where N = cell density (cells ml^{-1}); C = estimated cell carbon content (fg C $cell^{-1}$). We chose, according to Charpy & Blanchot (1998), a carbon content of 178 fg C $cell^{-1}$ for cyanobacteria and 4700 fg C $cell^{-1}$ for nanoflagellates. We assumed 15 fg C $cell^{-1}$ for bacteria according to Caron et al. (1995). The carbon content for picoflagellates (260 fg C $cell^{-1}$) was calculated using the conversion factor of Børsheim & Bratbak (1987) equal to 0.22 pg C μm^{-3}. The average size of picoflagellates in this study was determined using a calibrated ocular micrometer and a binocular microscope (1.20 μm^3).

Growth rates (μ, h^{-1}) of bacteria, cyanobacteria and flagellates were calculated in the different size fractions according to the following equation:

$$\mu = (\ln N_f - \ln N_i) / (T_f - T_i)$$

where N_f and N_i are cell numbers (cells ml^{-1}) at the beginning (T_i) and end (T_f) of the incubation period.

Production rates (µg C l^{-1} d^{-1}) of bacteria, cyanobacteria and flagellates were estimated using the following relation:

$$P = B_i \times \mu \times 24$$

where B_i is initial biomass (µg C l^{-1}); μ is growth rate (h^{-1}).

Community consumption rates (G, µg C l^{-1} d^{-1}) of 1 size fraction by the larger size fractions were obtained according to the following relationship:

$$G = P_1 - P_2$$

where P_1 and P_2 are the production rates (µg C l^{-1} d^{-1}) of 2 fractions during an incubation. Grazing rates (cells ml^{-1} h^{-1}) were estimated from: (1) the difference in cell increase in 2 fractions at the end of the incubation; (2) the equations of Marin et al. (1986). Both techniques provided similar results.

Nutrient enrichment experiments. Batch experiments were performed to assess nutrient limitation of microbial populations. This method is the easiest way to determine an index of the potentially limiting nutrient during oceanic cruises. Samples were collected in acid cleaned polyethylene jars in the center of each lagoon. Due to low intra-lagoonal variations in Tuamotu atolls (Charpy et al. 1997), this site was considered representative of mean conditions. Samples were size-fractionated as described above into 3 size classes (<0.8, <5 and <10 µm) to avoid grazing according to Cushing & Horwood (1998). Each fraction was transferred into 12 acid cleaned polycarbonate bottles (500 ml). Triplicate bottles were enriched either with 5 µm ammonium (NH_4Cl), 2 µm phosphorus (NaH_2PO_4) or with both nutrients. Three control bottles in each size class were kept without nutrient enrichment. Nutrient concentrations in control bottles, measured as in Tréguer & Le Corre (1975), were identical to *in situ* (i.e. from 0.7 to 1.3 µm for dissolved inorganic nitrogen and from 0.20 to 0.46 µm for dissolved inorganic phos-

phorus). Final nutrient concentrations in the enriched bottles were comparable to enrichments performed in previous studies (Dufour & Berland 1999, Torréton et al. 2000). The main advantages and drawbacks of such enrichment are described in Dufour & Berland (1999). Bottles were incubated for 24 h *in situ*, at 2 m depth. Samples (10 to 15 ml) were taken at the beginning and end of the incubation for density measurements as described above. Growth rates were determined for each group in each fraction as described above.

Analysis. All results are expressed as mean and standard deviation of the mean. Statistical analysis of the differences between atolls or between reef flat spillways and channels were performed on StatView using 1-factor ANOVAs. When a significant effect was found, means were compared with a Bonferroni/Dunn post-hoc test.

RESULTS

Growth, production and grazing rate experiments

The <0.8 µm fraction contained small bacteria (ca 0.3 to 0.4 µm) and microscopic examinations revealed few cells attached to particles (5 to 8% of the total). *Prochlorococcus* cells contained in this first fraction were not counted, due to their low fluorescence. The <2 µm fraction contained the majority of microbial cells, with bacteria, cyanobacteria, auto- and heterotrophic picoflagellates (Figs. 2 & 3). Cyanobacteria were mainly represented by the genus *Synechococcus* and cells were very small (1 µm size). Heterotrophic nanoflagellates were also small (mean size of 3 to 3.5 µm), passing through the 5 µm filter. Concentrations of heterotrophs were higher in Fakarava, whereas concentrations of pico- and nano-autotrophs were higher in Rangiroa (Figs. 2 & 3; statistical analysis in Table 1). Bacterial abundances ranged from 9 to 14×10^8 cells l^{-1} in Fakarava and from 4 to 18×10^8 l^{-1} in Rangiroa (from the reef flat spillways to the channel). Total heterotrophic flagellates (pico- and nanoflagellates) were twice as abundant in Fakarava (12 to 28×10^5 l^{-1}) as in Rangiroa (7 to 14×10^5 l^{-1}). Finally, cyanobacterial abundances ranged from 5 to 7 $\times$ 10^7 cells l^{-1} in Fakarava and from 9 to 18×10^7 cells l^{-1} in Rangiroa. Pico- and nanoplankton concentrations were also different according to the sampling site (Figs. 2 & 3), being 1.5 to 3 times more elevated near the channels than near the reef flat spillways (Table 1).

In terms of biomass, picoplankton was predominant (Figs. 2 & 3), with cyanobacteria as the most important group (26 to 49% of the total biomass), followed by heterotrophic bacteria (20 to 39%). Nanoplankton (both auto- and heterotrophic nanoflagellates) represented only 6 to 25% of the total biomass. Chloro-

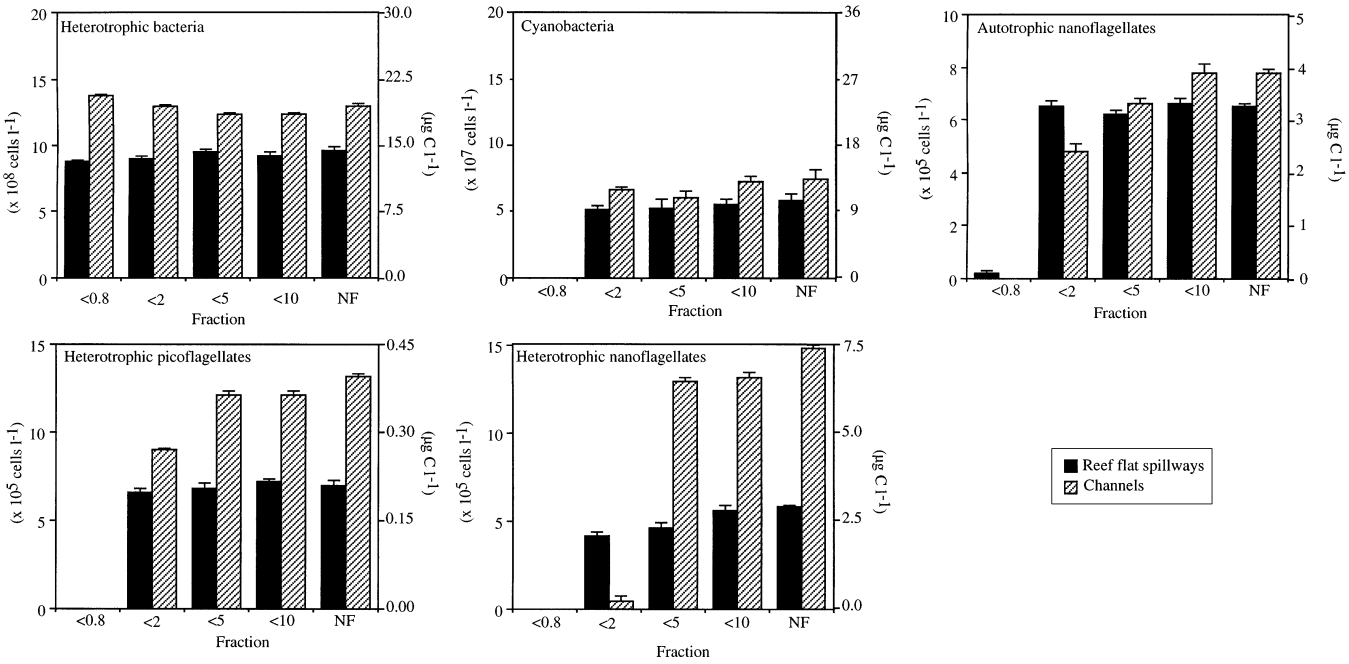

Fig. 2. Concentrations (cells ml^{-1}) in the different fractions at the beginning of experiments performed in the lagoon of Fakarava. Black and hatched bars represent samples taken near the reef-flat spillways and the channels respectively. NF is the non-fractioned sample. Mean ± standard deviation of the 3 incubations. When vertical bars do not appear in 1 fraction, it means that the group was not detected

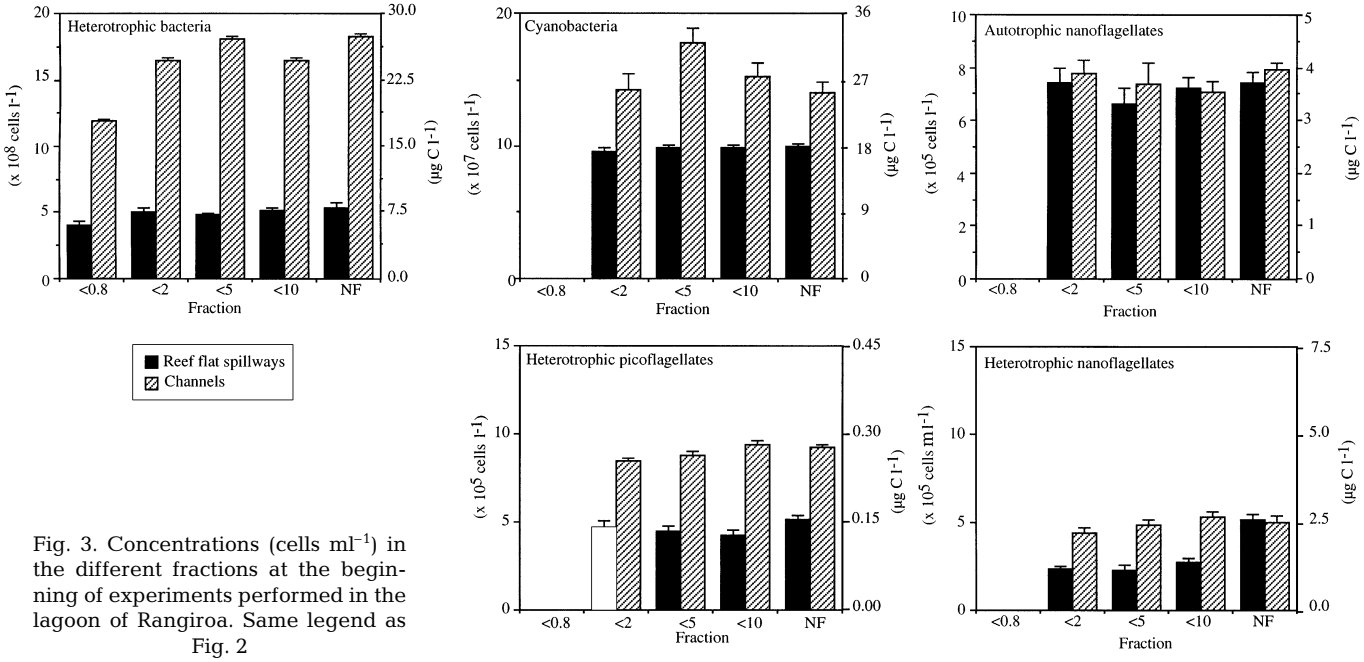

Fig. 3. Concentrations (cells ml^{-1}) in the different fractions at the beginning of experiments performed in the lagoon of Rangiroa. Same legend as Fig. 2

phyll *a* concentrations varied between 0.008 to 0.25 µg l^{-1} according to the experiment and the size class considered. Organisms <10 µm represented 75 to 85% of the total planktonic chlorophyll *a*. *Prochlorococcus* (<0.8 µm fraction) contributed to only 5 to 9% of the total chlorophyll *a* (0.008 to 0.03 µg l^{-1}).

Growth rates (Figs. 4 & 5) varied according to the sampling site and the size-class considered. Bacterial growth was maximal in the <0.8 µm fraction where all predators were removed (equivalent to gross growth rates). It decreased in the higher size fractions, with the increasing number of predators (equivalent to net growth rates). Growth rates were maximal in the <2 and <5 µm fractions for cyanobacteria and autotrophic flagellates, and in the <5 and <10 µm fractions for the heterotrophic nanoflagellates. In Fakarava, both bacteria and heterotrophic flagellates had fast growth rates (Fig. 4), which varied from 0.06 to 0.15 h^{-1} for picoflagellates (2.4 to 5 doublings d^{-1}), 0.05 to 0.17 h^{-1} for nanoflagellates and 0.02 to 0.04 h^{-1} for bacteria

Table 1. Statistical tests (ANOVAs) were performed to check the difference in biomass and growth rates between the atolls of Fakarava and Rangiroa and between the reef flat spillways and channels in each atoll; $p < 0.05$ significant. F > R or F < R: biomass and growth rate in Fakarava (F) are higher or lower respectively than in Rangiroa (R). C > RFS or C < RFS: biomass and growth rate measured near the channels (C) are higher or lower respectively than those measured near the reef flat spillways (RFS). AF: autotrophic flagellates; HPF, HNF: heterotrophic pico- and nanoflagellates respectively. ns: non-significant

	Differences between the atolls of Fakarava and Rangiroa				Differences between channels and reef flat spillways			
	Reef flat spillways		Channels		Atoll of Fakarava		Atoll of Rangiroa	
	p	Observation	p	Observation	p	Observation	p	Observation
Biomass								
Bacteria	<0.0001	F > R	= 0.010	F < R	<0.0001	C > RFS	<0.0001	C > RFS
Cyanobacteria	<0.0001	F < R	<0.0001	F < R	= 0.007	C > RFS	= 0.001	C > RFS
AF	= 0.010	F < R	= 0.320	ns	= 0.70	ns	= 0.20	ns
HPF	<0.0001	F > R	= 0.030	F > R	= 0.002	C > RFS	<0.0001	C > RFS
HNF	= 0.040	F > R	= 0.001	F > R	= 0.002	C > RFS	= 0.005	C > RFS
Growth rates								
Bacteria	= 0.005	F < R	= 0.003	F < R	<0.001	C < RFS	= 0.020	C < RFS
Cyanobacteria	= 0.001	F > R	= 0.640	ns	<0.001	C < RFS	<0.001	C < RFS
AF	= 0.20	ns	= 0.003	F > R	= 0.003	C < RFS	= 0.003	C < RFS
HPF	= 0.001	F > R	= 0.001	F > R	<0.001	C < RFS	= 0.30	ns
HNF	<0.001	F > R	<0.001	F > R	<0.001	C < RFS	<0.001	C < RFS

(0.7 to 1.4 doublings d^{-1}). Growth of the autotrophic nanoflagellates was lower (0.00 to 0.04 h^{-1}). In Rangiroa, bacteria showed the fastest growth rates (0.02 to 0.06 h^{-1}) corresponding to 1.4 to 2.1 doublings d^{-1} (Fig. 5), whereas the growth of the other groups was lower and varied between 0.00 and 0.04 h^{-1} (0.35 to 1.4 doublings d^{-1}). Growth rates of the heterotrophic pico- and nanoflagellates were significantly higher in

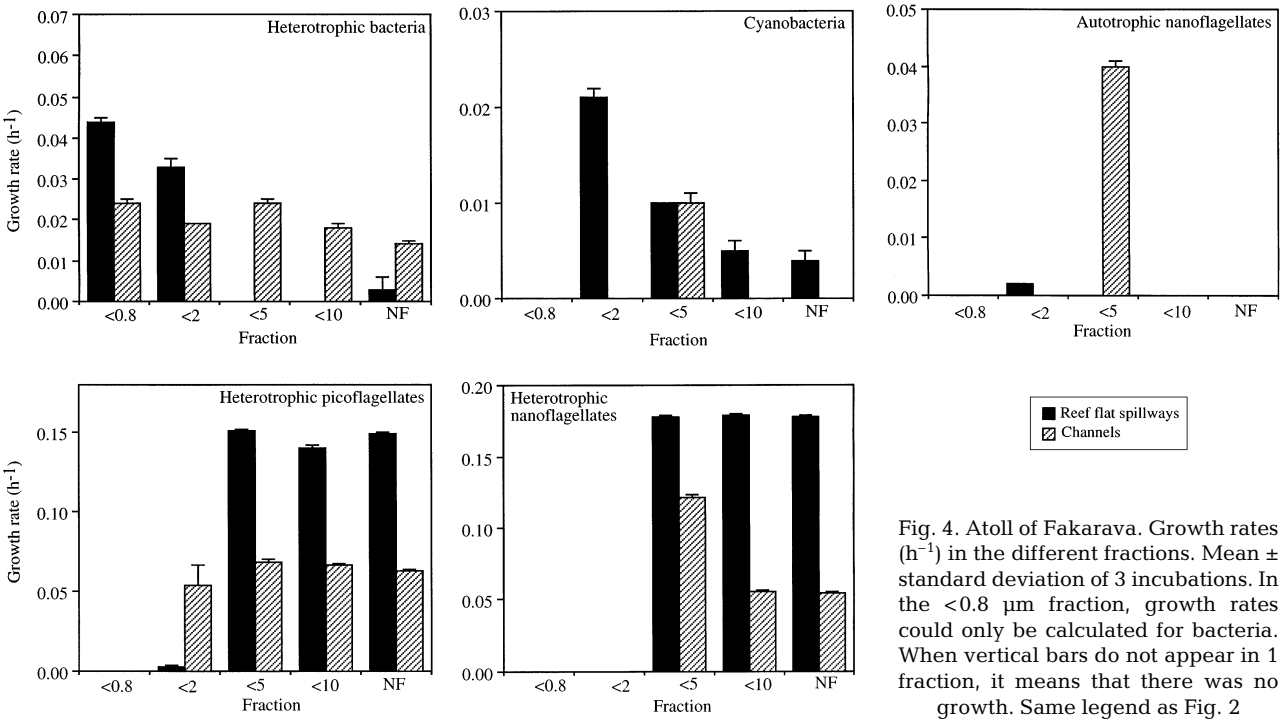

Fig. 4. Atoll of Fakarava. Growth rates (h^{-1}) in the different fractions. Mean ± standard deviation of 3 incubations. In the <0.8 µm fraction, growth rates could only be calculated for bacteria. When vertical bars do not appear in 1 fraction, it means that there was no growth. Same legend as Fig. 2

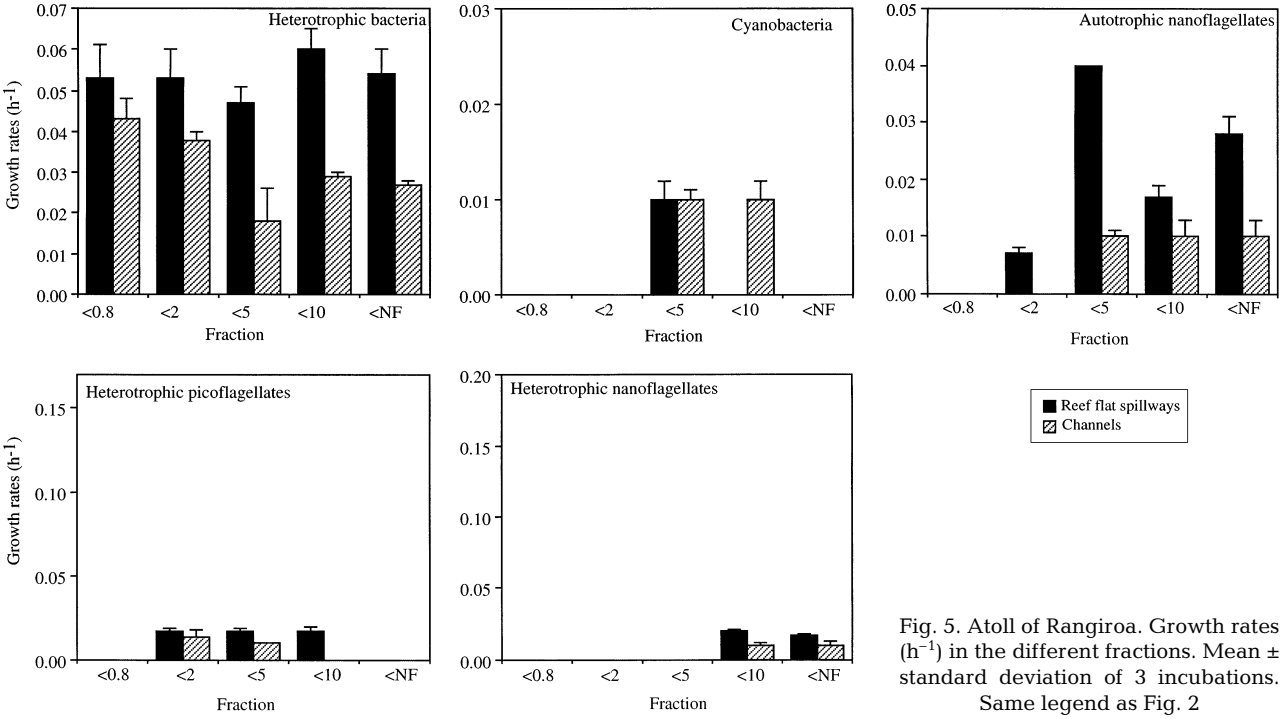

Fig. 5. Atoll of Rangiroa. Growth rates (h^{-1}) in the different fractions. Mean ± standard deviation of 3 incubations. Same legend as Fig. 2

Fakarava than in Rangiroa, whereas growth of bacteria was significantly lower (Table 1). In both atolls, growth rates were also different according to the sampling site (Table 1), being 1.5 to 3 times higher near the reef flat spillways than near the channels.

In Rangiroa, bacteria showed the highest production rates (from 7 to 18 µg C l^{-1} d^{-1}; Table 2). They represented 39 to 72% of the total microbial production. The difference between maximal and minimal production rates in each sampling site indicated that 25 to 39% of the bacterial production were grazed by the <5 µm fraction, containing mostly heterotrophic flagellates. This corresponds to a consumption rate of 0.6 to 1.4 × 10^4 bacteria ingested ml^{-1} h^{-1}. Cyanobacteria were the second most productive group, with up to 27% of the total production (Table 2). Almost all of this production was grazed by the >10 µm organisms, corresponding to 0.4 × 10^4 cyanobacteria ingested ml^{-1} h^{-1}. Auto- and heterotrophic flagellates had lower production rates. In Fakarava, both bacteria and heterotrophic flagellates showed the highest production rates (Table 2). The autotrophic production was much lower (between 0 and 15% of the total production). The difference between maximal and minimal production rates in each site indicated that 41 to 88% of the bacterial and 75% of the cyanobacterial productions were consumed by the <10 µm fractions. This is equal to 0.6 to 1.7 × 10^4 bacteria ml^{-1} h^{-1} and 0.05 to 0.5 10^4 cyanobacteria ml^{-1} h^{-1} ingested. The total pico- and nanoplanktonic production was higher in Fakarava than in Rangiroa (15 and 43% higher for the channel and the reef flat spillways experiments respectively, ANOVA, $p < 0.01$).

Nutrient enrichment experiments

The effect of nutrient enrichment on the pico- and nanoplankton growth is shown in Figs. 6 & 7 for the 2 atolls. In the <0.8 µm fraction, 25 to 50% increase in bacterial growth rates was observed in both atolls under nitrogen enrichment, with no specific effect of phosphorus (Figs. 6 & 7; statistical analysis in Table 3). In the larger size fractions, the enhancement in growth following nitrogen enrichment was smaller due to the

Table 2. Maximal and minimal production rates (µg C l^{-1} d^{-1}) measured in the atolls of Rangiroa and Fakarava. Fraction: size-class in which production rates have been measured; %: percentage of the total production; AF: autotrophic flagellates; HNF: heterotrophic nanoflagellates; NF: non-fractionated community; –: production rates too low to be measured

Group	Maximal production rates		Fraction	Minimal production rates		Fraction
	Reef flat spillways (%)	Channel (%)	(µm)	Reef flat spillways (%)	Channel (%)	(µm)
Rangiroa atoll						
Bacteria	9.5 ± 1.2 (50)	18.0 ± 1.2 (67)	0.8	7.1 ± 1.1 (72)	10.8 ± 1.2 (86)	5
Cyanobacteria	4.3 ± 0.7 (23)	7.2 ± 1.1 (27)	5	–	–	10
AF	4.1 ± 0.8 (23)	1.1 ± 0.2 (4)	5	1.4 ± 0.2 (15)	1.1 ± 0.3 (9)	10
HNF	1.2 ± 0.2 (5)	0.6 ± 0.4 (2)	NF	1.2 ± 0.1 (12)	0.7 ± 0.1 (5)	NF
Fakarava atoll						
Bacteria	16.3 ± 2.1 (48)	12.3 ± 1.1 (31)	0.8	1.8 ± 0.4 (12)	7.2 ± 1.15 (46)	5–10
Cyanobacteria	4.8 ± 0.9 (15)	3.4 ± 0.5 (9)	2–5	1.2 ± 0.2 (8)	–	5–10
AF	–	2.9 ± 0.3 (7)	5	–	–	
HNF	12.4 ± 1.5 (36)	21.1 ± 2.6 (54)	5–NF	11.5 ± 1.4 (79)	8.4 ± 1.3 (54)	10

Table 3. Statistical tests (ANOVAs) were performed to check the difference in growth rate measured in the control (C), nitrogen (N), phosphorus (P) and nitrogen + phosphorus (NP) enrichments for each microbial group. $p < 0.05$ significant. Post-hoc tests were also performed and $p \leq 0.008$ is significant. Significant values of p are reported in italics. AF: autotrophic flagellates; HF: heterotrophic flagellates

	Bacteria		Cyanobacteria		AF		HPF	
	Fakarava	Rangiroa	Fakarava	Rangiroa	Fakarava	Rangiroa	Fakarava	Rangiroa
ANOVA	*0.0006*	*0.0014*	*0.019*	*0.0001*	*0.0002*	*0.0001*	*<0.0001*	*<0.0001*
Post-hoc tests								
C,N	*0.0008*	*0.0080*	*0.0025*	*<0.0001*	*0.0001*	*<0.0001*	*<0.0001*	*<0.0001*
C,P	0.51	0.58	*0.0004*	*<0.0001*	*0.0006*	*0.0002*	*0.0017*	*0.0002*
C,NP	*0.0003*	*0.0004*	*0.0013*	*<0.0001*	*<0.0001*	*<0.0001*	*<0.0001*	*<0.0001*
N,P	*0.0020*	0.020	0.18	0.01	0.16	0.09	*<0.0001*	0.52
N,NP	0.44	0.05	0.64	0.03	0.46	0.84	0.38	0.49
P,NP	*0.0007*	*0.0008*	0.36	0.64	0.05	0.13	*<0.0001*	0.49

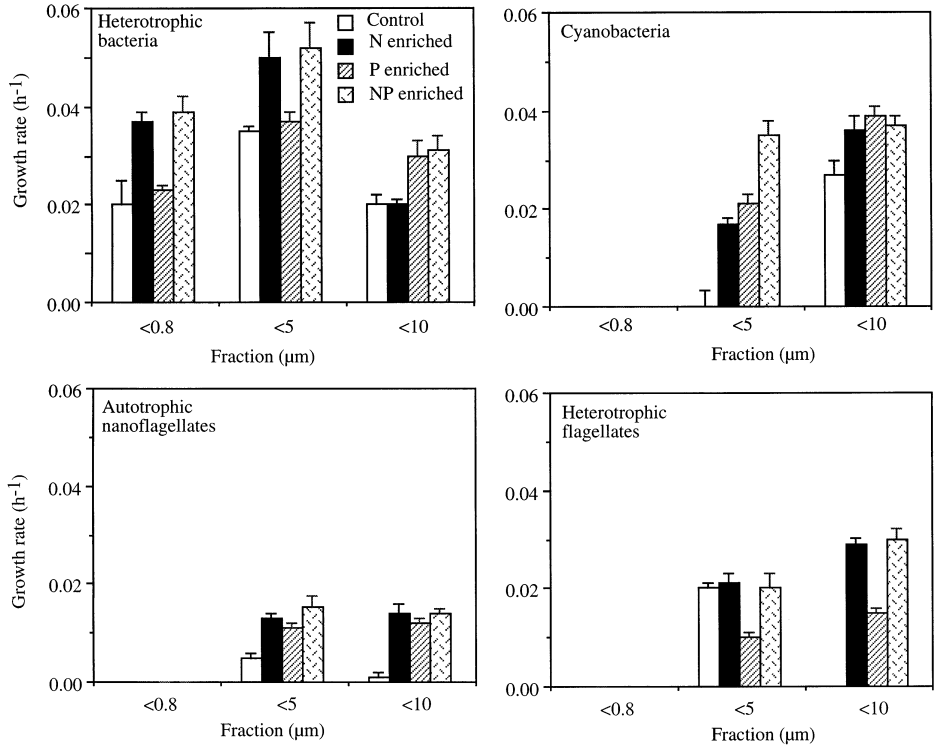

Fig. 6. Growth rates (h^{-1}) in the different size-fractions following nutrient enrichment. Atoll of Fakarava. Mean ± standard deviation of 3 incubations

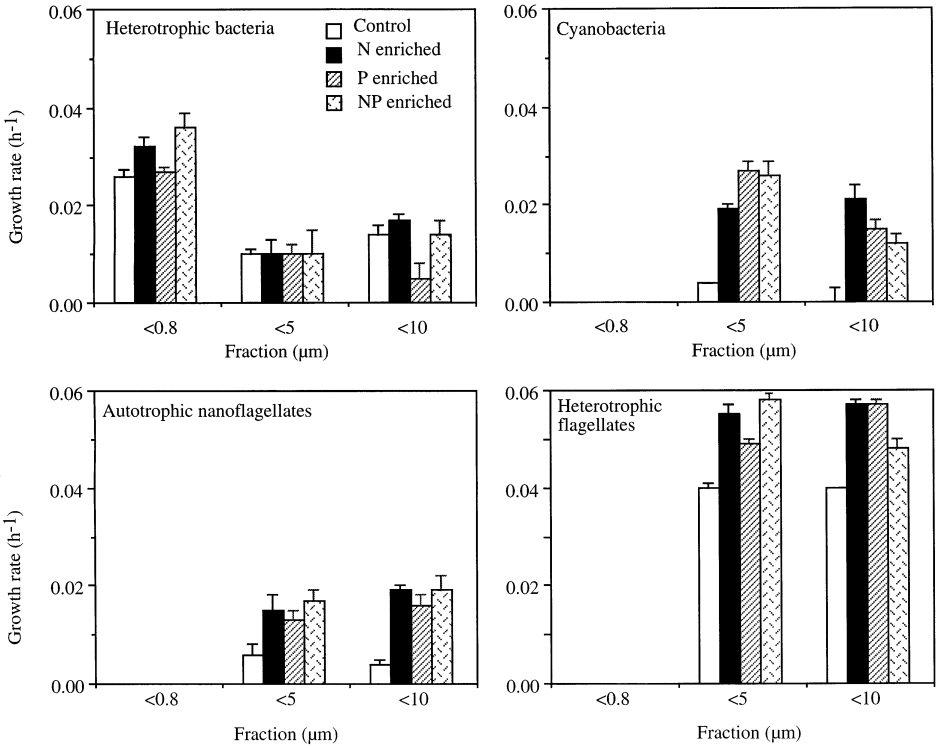

Fig. 7. Growth rates (h^{-1}) in the different size-fractions following nutrient enrichment. Atoll of Rangiroa. Mean ± standard deviation of 3 incubations

grazing pressure. For cyanobacteria, a large increase in growth rates was obtained in the <5 µm fraction under nitrogen enrichment, and an even larger one was measured under phosphorus enrichment (Figs. 6 & 7; statistical analysis in Table 3). In Fakarava, addition of both nitrogen and phosphorus induced the highest growth in cyanobacteria. This could not be observed in Rangiroa. Growth of the auto- and heterotrophic flagellates was also enhanced (from 20 to more than 50%) under nutrient enrichment (Table 3).

DISCUSSION

The planktonic food web of Polynesian atolls has become the focus of interest in recent years due to the development of pearl oysters farms; however, it remains poorly described (Charpy & Charpy-Roubaud 1990, Gonzalez et al. 1998, Niquil et al. 1999). This study is one of the first to compare simultaneously biomass and production rates of the auto- and heterotrophic microbial components.

There are uncertainties when converting microbial abundance into carbon biomass using carbon conversion factors (Dennett et al. 1999), because a wide range of factors exists in the literature. Microbial populations studied in this work are from the most oligotrophic waters in the world. Our approach was to select conversion factors already used for such environments, in order to compare the results with those obtained in previous studies. Carbon contents for cyanobacteria and nanoflagellates were therefore chosen according to Charpy & Blanchot (1998) and are in agreement with those used by Garrison et al. (2000) for oligotrophic waters. Carbon content for heterotrophic bacteria, chosen according to Caron et al. (1995), is also in agreement with those used in previous studies for bacteria sampled in oligotrophic waters (Simon & Azam 1989, Torréton & Dufour 1996a, Garrison et al. 2000).

Our results showed that autotrophic cells <20 µm accounted for 80% of the total chlorophyll *a*, confirming previous measurements performed in small Tuamotu atoll lagoons (Charpy & Charpy-Roubaud 1990, Charpy et al. 1992, Charpy 1996) and other lagoons (Furnas et al. 1990) that the dominant phytoplankton is very small. Chlorophyll *a* concentrations in the <0.8 µm fraction indicated that *Prochlorococcus* cells contributed to only 5 to 9% of the total biomass. Such low *Prochlorococcus* biomass is commonly observed when cyanobacteria are especially abundant (Charpy & Blanchot 1998), except on few occasions such as in the atolls of Hiti and Haraili (Charpy & Blanchot 1998).

Microbial biomass was therefore dominated by picoplankton, with very high concentrations of heterotrophic bacteria and cyanobacteria. Bacteria are very abundant in almost all atoll lagoons, included Rangiroa and Fakarava, and their concentrations ranged from 0.20 to 2.5×10^6 cell ml^{-1} (Table 4), depending on the depth, location and season considered. Picoplankton is known to be dominant in nutrient-poor waters because its small size and large surface to volume ratio are an advantage over larger size cells for nutrient uptake (Chisholm 1992, Dufour et al. 1999). Bacteria have moreover low C:N ratios relative to phytoplankton (Goldman et al. 1987) and can be an important contributor to particulate nitrogen standing stocks. Very few data exist on the abundance of the auto- and heterotrophic nanoplankton in lagoon waters (Table 4) as well as on their relative contribution compared to picoplankton. We showed in this study that nanoplankton (mainly auto- and heterotrophic flagellates) constituted only 10 to 15% of the total biomass. The microbial composition of atoll lagoons contrasts with open shallow reef environments such as the Great Barrier Reef. In these open shallow reefs, nano- and microplankton are more abundant (Revelante & Gilmartin 1982, Furnas & Mitchell 1986, Linley & Koop 1986, Ferrier-Pagès & Gattuso 1998) and cyanobacteria are at least one order of magnitude lower (Laws et al. 1984, Ayukai 1995, Le Borgne et al. 1997, Ferrier-Pagès & Gattuso 1998). In the Great Barrier Reef for instance, Linley & Koop (1986) demonstrated that autotrophic nanoflagellates could make up 78% of the total standing stock, whereas cyanobacteria constituted only 7% of the total. The difference in community composition between atoll lagoons and open reef systems may be due to a different coral coverage, atoll lagoons having few coral patches. It is well known that corals excrete large amounts of dissolved organic matter (Crossland 1987) which induce a nutrient enrichment of the surrounding waters and a higher growth of microbial populations. Tuamotu atolls are moreover located in the South Pacific Subtropical gyre, well known for its very oligotrophic waters (Dufour et al. 1999). The exceptionally high abundance of cyanobacteria in this study ($>10^8$ cells l^{-1}) has been reported twice for small Polynesian atolls (Table 4, Charpy et al. 1992, Charpy & Blanchot 1998) and seems to be consistent for bigger ones such as Rangiroa and Fakarava. High concentrations of cyanobacteria have also been reported in other lagoons such as the Great Astrolabe lagoon of Fiji (Charpy & Blanchot 1999). This group is able to fix molecular nitrogen (Charpy-Roubaud et al. 1997) and take advantage of low nutrient concentrations, such as those reported for atoll lagoons (Crossland 1983).

Previous studies performed in open reef systems have shown temporal and/or spatial variability of microbial biomass and activity, due to seasonal changes, diurnal rhythms (Moriarty et al. 1985) and

Table 4. Abundances and growth rates of pico- and nanoplankton groups measured in some previous studies of Polynesian atoll lagoons or in other reef lagoons. GBR: Great Barrier Reef

Location	Bacteria ($\times 10^6$ cells ml^{-1})	Cyanobacteria ($\times 10^4$ cells ml^{-1})	Autotrophic flagellates ($\times 10^3$ cells ml^{-1})	Heterotrophic flagellates ($\times 10^3$ cells ml^{-1})	Source
Abundances					
Tuamotu atoll lagoon		1.50	2.10	0.73	Blanchot et al. (1989)
Tuamotu atoll lagoon		5.10–19.2	1.50–6.40		Charpy et al. (1992)
Tuamotu atoll lagoon	0.30–0.60				Vacelet et al. (1996)
Tuamotu atoll lagoon	0.30–2.37				Torréton & Dufour (1996a)
Tuamotu atoll lagoon		1.60–3.50	2.30–2.50		Charpy & Blanchot (1996)
Tuamotu atoll lagoon		6.80–1.41	4.10–7.05		Blanchot et al. (1997)
Tuamotu atoll lagoon		11.0–40.0	2.30–2.70		Charpy & Blanchot (1998)
Tuamotu atoll lagoon	1.20–2.60		0.20–1.10	0.30–1.50	Gonzalez et al. (1998)
Tuamotu atoll lagoon	0.22–2.41				Torréton et al. (2000)
Majuro atoll lagoon	0.06–1.80				Sorokin (1978)
GBR lagoon	1.10–1.60				Moriarty (1979)
One Tree Island lagoon	0.12–1.30				Linley & Koop (1986)
Majuro atoll lagoon	1.06				Yoshinaga et al. (1991)
Sinton atoll lagoon	0.15–0.31			0.01–1.30	Sorokin (1991)
Seychelles island lagoon				0.20–3.10	Sorokin (1993)
GBR: Heron island lagoon	0.50–4.10				Sorokin (1994)
Mayotte atoll lagoon	0.21–0.43			0.02–0.10	Vacelet et al. (1999)
Great Astrolabe reef lagoon	0.77				Torréton (1999)
Great Astrolabe reef lagoon	1.80			5.30	Charpy & Blanchot (1999)
Growth rates (d^{-1})					
Tuamotu atoll lagoon	0.10–1.80				Torréton & Dufour (1996b)
Tuamotu atoll lagoon		1.10–1.30		1.50–1.70	Charpy (1996)
Tuamotu atoll lagoon				0.55	Blanchot et al. (1997)
Tuamotu atoll lagoon	0.11	0.19–3.02	0.21–0.48	0.12–0.68	Gonzalez et al. (1998)
Tuamotu atoll lagoon	0.28				Torréton (1999)
Tuamotu atoll lagoon	0.07–1.3				Torréton et al. (2000)
Lizard Island lagoon	0.12–2.16				Moriarty et al. (1985)
One Tree Island lagoon	0.72–3.80				Linley and Koop (1986)
Majuro atoll lagoon	0.12–0.70				Yoshinaga et al. (1991)

tidal currents (Linley & Koop 1986). Moriarty et al. (1985) measured a 7-fold change in bacterial growth rates at Lizard Island, depending on the ebb tide (temporal variability), whereas Linley & Koop (1986) observed a 15-fold variation along a transect over Davies Reef (spatial variability). Under such conditions, data obtained during discrete cruises are not representative of the system. In the other hand, studies performed in Tuamotu atoll lagoons (Torréton & Dufour 1996a,b, Charpy et al. 1997, Dufour & Harmelin-Vivien 1997) or in other atolls (Yoshinaga et al. 1991, Torréton 1999, Charpy & Blanchot 1999) always measured low variations for most variables, both spatially and temporarily. Torréton & Dufour (1996a) explained the vertical homogeneity in Polynesian atoll lagoons by a strong vertical mixing driven by regular trade winds. They also detected very limited day-to-day variations and seasonal trend, explained by constant hydrological characteristics of the oceanic waters around the atolls throughout the year and by constant seawater temperatures (Lenhardt 1991). Therefore, the important point of the atoll studies is that the weak variations observed would not strongly bias the estimations derived from discrete measurements.

Results obtained in this study showed that abundances of all groups were 1.5- to 3-fold lower near the reef flat spillways than near the channels, suggesting an important biomass production inside the lagoon (Charpy-Roubaud et al. 1990, Torréton 1999). Pico- and nanoplankton abundances were also different between the ocean and the lagoon. Bacterial concentrations measured during this cruise in oceanic waters around the atolls of Fakarava and Rangiroa (0.3 to 0.5×10^9 cells l^{-1}, data not shown) were 10- to 20-fold lower than those measured inside the lagoon and confirm the results of Torréton et al. (2000). This is presumably due to high predation rates of bacterioplankton by benthic reef organisms (Ayukai 1995).

Growth of all groups was also 1.5 to 3 times higher near the reef flat spillways than near the channels. This difference may be due to the 'atoll mass effect'

described by Charpy-Roubaud et al. (1990). This effect induces a turbulent vertical mixing of the waters along the slopes of the atolls with a subsequent nutrient enrichment. Oceanic waters are again enriched when they cross the reef flat due to the release of dissolved organic matter by reef organisms (Michel et al. 1971, Torréton & Dufour 1996a). These nutrient rich waters enter the lagoon via the reef flat spillways (Lenhardt 1991, Bonvallot et al. 1994) inducing high planktonic growth rates. During their transfer to the channel, waters become nutrient impoverished (transformation of inorganic nutrients into particulate organic matter; Charpy-Roubaud et al. 1990), thus limiting microbial growth. Starved oceanic cells, with very high affinities for dissolved substrates, should also be better nourished as they flow across the lagoon, with a subsequent decrease of their growth near the channel (Linley & Koop 1986).

Very few data exist on the growth rates of pico- and nanoplankton in Polynesian lagoons (Table 4, Charpy et al. 1992, Torréton & Dufour 1996a, Torréton et al. 2000). This study showed (Figs. 4 & 5) that either heterotrophic bacteria (in Rangiroa) or flagellates (in Fakarava) had the highest growth rates (a maximum of 2 and 5 doublings d^{-1} respectively). They are followed by cyanobacteria (0.5 to 1.5 doublings d^{-1}) and autotrophic flagellates (0.7 doubling d^{-1}). Bacterial growth rates are highly variable among studies (Table 4) and from one location to another, ranging from 0.70 to 2.20 doublings d^{-1} in this study and from 0.10 to 1.80 doublings d^{-1} in other Tuamotu atolls (Torréton & Dufour 1996a). This variability is likely due to the different structure of the atolls, to the grazing pressure and to the colonisation of the lagoon by coral pinnacles since it has been demonstrated that the release by corals of organic matter increase microbial growth (Ferrier-Pagès et al. 1998). In this work, the highest growth was obtained in the <0.8 µm fraction, containing no predators. If grazing is taken into account, bacterial growth at Fakarava and Rangiroa was very low (see growth rates measured in the >0.8 µm fractions, Figs. 4 & 5). This suggests that bacteria were largely ingested by the higher trophic levels. High grazing rates were indeed measured in both atolls since ca 50% of the daily bacterial production was at least consumed by the heterotrophic nanoflagellates (equal to 0.6 to 1.7×10^4 bacteria ml^{-1} h^{-1}). These results confirm the only existing value of grazing measured in Tuamotu atolls with a different technique (FLB) and equal to 0.5×10^4 bacteria ml^{-1} h^{-1} (Gonzalez et al. 1998). Likewise, cyanobacteria were highly grazed by nanoflagellates and more than 50% of the daily production was transferred to the higher trophic levels.

Pico- and nanoplankton production rates were relatively high suggesting a very dynamic microbial loop. As for biomass and growth rates, picoplankton (bacteria and cyanobacteria) showed the highest production rates. Microbial production was also significantly higher in Fakarava than in Rangiroa, especially for the heterotrophic flagellates. This may be due to a different hydrology between the 2 atolls. Delesalle & Sournia (1992) indeed showed that the amount of chlorophyll *a* was in close relationship with the residence time of the waters in the lagoon. Lagoons that have a very rapid (<40 d) exchange with the ocean are likely to become oligotrophic in terms of phytoplankton biomass. However, to our knowledge, residence time has never been measured in Fakarava and Rangiroa. The difference in biomass and production rates between the 2 atolls may also be due to the proximity of pearl farms near our experimental sites in Fakarava and a higher standing stock of pearl oysters in this atoll (T. Darius pers. comm.). Pearl oysters increase by 2 to 3 times the amount of suspended material in their surrounding environments (Vacelet et al. 1996), favouring the development of heterotrophic bacteria and flagellates.

This study also investigated nitrogen and phosphorus limitation by the phytoplanktonic populations of Rangiroa and Fakarava. Nutrient limitation may be assessed by different approaches (Elser et al. 1990, Bielefeld et al. 1996, Lavrentyev et al. 1998), based on cellular chemical composition, metabolic activity or direct response of phytoplankton to nutrient enrichment. Experiments with nutrient additions in bottles are subject to continuous controversy (Cushing & Horwood 1998), but are extensively used in marine and freshwater ecosystems (Elser et al. 1990). They indicate a potential for *in situ* nutrient limitation of algal growth in the absence of other limiting factors (Elser & Kimmel 1986) and allow testing the response of phytoplankton to the limiting nutrients and their combination. The main advantages and drawbacks of this method for atoll lagoons are described in Dufour & Berland (1999) and Torréton et al. (2000). Response of pico- and nanoplankton populations to nutrient enrichment may vary according to the method used but also to the season and the spatial heterogeneity within lagoons. Results obtained in this study therefore indicate a nutrient limitation at this time of the year. The prevalence of picoplanktonic cells is already an indicator of nutrient limitation (Chisholm 1992). Concentrations of inorganic nitrogen and phosphorus measured during this work are in the range of those previously obtained for such waters (Charpy-Roubaud et al. 1990, Rancher & Rougerie 1994, Dufour et al. 1999, Raimbault et al. 1999). They are close to the K_s of N and P uptake reported by Goldman & Glibert (1983) which argued for both a nitrogen and phosphorus limitation. Bacterial growth was limited by the amount of nitro-

gen, as during the Typatoll cruise (Torréton et al. 2000). Studies showing the direct stimulation of bacterial growth by nitrogen are scarce (Wheeler & Kirchman 1986, Selmer et al. 1993, Torréton et al. 2000), but have suggested that bacteria assimilate rather than regenerate ammonium when the organic substrate is nitrogen limited (Goldman & Dennett 1991). Growth was not enhanced following addition of phosphorus, suggesting that bacterioplankton at our study sites and during this period was not P-limited. This is maybe due to its high P-binding capacity (Jürgens & Güde 1990, Cotner & Wetzel 1992) and its ability to recycle phosphorus from detrital material (Clark et al. 1998). A phosphorus limitation of bacterial growth has however been observed in close and shallow atoll lagoons (Torréton et al. 2000). During this work, both nitrogen and phosphorus limited the growth of cyanobacteria and autotrophic flagellates (the addition of one nutrient inducing an increase uptake affinity for the other one). This dual limitation of phytoplankton was also shown in previous studies performed in Tuamotu lagoons (Vacelet et al. 1996, Dufour & Berland 1999, Dufour et al. 1999). Dufour et al. (1999) therefore hypothesised that the existing sources of nitrogen, such as nitrogen recycling in the sediment and N_2 fixation (Larkum et al. 1988) are not sufficient to supply phytoplankton requirements. Charpy-Roubaud et al. (1996) also demonstrated that diffusional nutrient fluxes from the sediment to the water column were weak in comparison to the primary productivity requirements. Moreover, phosphorus is known to be one of the main limiting nutrients in coral reef waters due to its adsorption on the carbonate rich sediments (Smith & Atkinson 1984). These conditions favour the development of picoplankton and especially bacteria, which are known to outcompete phytoplankton for nutrients when their concentrations are low (Wheeler & Kirchman 1986). Under nutrient enrichment, the growth of grazers such as heterotrophic flagellates was also quickly enhanced due to the increase in bacterial and pico-nanophytoplanktonic production.

Results obtained in this study have brought new insights on the abundance, growth and production rates of nanoplankton in atoll lagoon waters, and have allowed the comparison of these rates to those experienced by picoplankton. Measurements of growth rates of pico- and nanoplankton are also still scarce in such environments. They have also shown that both heterotrophic bacteria and autotrophic picoplankton (cyanobacteria) dominated the overall biomass due to their high growth and production rates and their high affinity for nutrients. Moreover, we noticed significant differences in biomass and growth rates between the reef flat spillways (oceanic waters influence) and the channels (lagoon influence). Higher biomass measured near the channels suggests a net microbial production inside the lagoon and an export to the ocean. Growth rates were however higher near the reef flat spillways, maybe due to an enrichment of seawater when crossing the reef flat. Finally, pico- and nanoplankton growth is nitrogen and phosphorus limited, with a competition between heterotrophic bacteria and phytoplankton for these 2 nutrients.

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