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Biomass, production and heterotrophic activity of bacterioplankton in the Great Astrolabe Reef Lagoon (Fiji)

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Abstract

Biomass, production and heterotrophic activity of bacterioplankton were determined over a 2 weeks cruise in the Great Astrolabe Reef lagoon (Fiji). Biomass (determined by epifluorescent microscopy), production (assessed by ^{3}H-thymidine incorporation into DNA) and growth rates are distributed homogeneously over the water column (20 to 40m deep). Bacterial variables do not differ significantly from site to site inside the lagoon. Bacterioplankton biomass and production vary little over a diurnal period with coefficients of variation of 9 and 22%, respectively. On average, over the whole study bacterial abundance is 0.77 10^9 cell l^{-1} (15.5 µgC l^{-1}) and bacterial production averages 4.3 µgC $l^{-1}d^{-1}$. Attached bacteria were distinguished in selected samples and on average 10.4% of the bacteria are attached to particles while they contribute for 14.1% to total production. Growth rates for bacterioplankton differ significantly for the free (0.19 d^{-1}) and attached (0.30 d^{-1}) communities. Fixation seems to provide an advantage for bacterial growth into this lagoon. Carbon growth yield (CGY) was determined experimentally into two dilution cultures by comparing the net increase of bacterial biomass and the net decrease of dissolved organic carbon (DOC). Both determinations led to a very low growth yield (average 5.7%). By applying the average CGY value to bacterial production rates into the lagoon, heterotrophic activity was estimated to average 76 µgC $l^{-1}d^{-1}$. The turn-over rate of DOC (average 1572 µgC l^{-1}) is therefore estimated to average 0.048 d^{-1} during that period. Both bacterioplankton abundance and production values appear to be greater than in oceanic water surrounding the Great Astrolabe Reef lagoon.

1. Introduction, objectives

Planktonic bacteria play an important role in most of the ecosystems studied. The development of epifluorescent microscopy and tracer approaches have led to better understand their contribution to cycle of energy and matter in various pelagic ecosystems. However, little is known about their importance in coral reef lagoons because most of the results in coral reefs environments have focused on water overlying coral reefs (Sorokin, 1974, Pascal & Vacelet, 1981, Moriarty *et al.* 1985, Linley & Koop, 1986, Hoppe *et al.* 1988, Ducklow, 1990, Moriarty *et al.* 1990) with only few exceptions in atoll lagoons (Sorokin, 1974, Yoshinaga *et al.* 1991, Torréton & Dufour, 1996), and Island lagoons (Sorokin, 1974, Landry *et al.* 1984, Yoshinaga *et al.* 1991). Coral reefs areas are characterized by high and efficient recycling processes and low inputs of new nutrients (Crossland & Barnes, 1983). Atoll and island lagoons may represent large bodies of water where heterotrophic bacterioplankton could contribute for an important part of total carbon, nitrogen and phosphorus. Thus the description and comprehension of bacterioplankton dynamics is essential in the studies of carbon and nutrient cycling in coral reefs environments.

This study intends to describe bacterioplankton biomass, productivity and heterotrophic activity in the water column of the coral lagoon of the Great Astrolabe Reef (Fiji). Bacteriobenthos biomass and productivity has been described previously in *Syringodium isoetifolium* seagrass beds in an area of this lagoon (Pollard & Kogure 1993). But very little is known in the water column of this lagoon. Vertical and horizontal distribution and short term variations of bacterioplankton parameters were investigated during a 2 week campaign in April 1994.

Two distinct microbial communities can be identified. One is attached to the substrate, forming epifloral community and the other occurs as free bacteria suspended in the water column. Free and attached bacterial communities do not present the same fate. Free bacteria are mostly exported *via* grazing by phagotrophic nanoplankton and attached bacteria may be exported by sedimentation or by grazing by larger organisms including mesozooplankton. They do not either present the same metabolic properties (Hoppe et al. 1988). Moriarty (1979) reports that up to 50% of the bacteria are attached in some coral reef environments. An objective of that study was therefore to estimate the contribution of attached bacteria to biomass and activity of the whole community and to investigate if fixation was an advantage in the Great Astrolabe Reef lagoon.

The importance of standing stocks and fluxes across bacterioplankton will be further compared to other components of the planktonic trophic network obtained during the same survey (Charpy 1996 and Blanchot 1996, this volume).

2. Material and methods

2.1. Study sites and sampling

The Great Astrolabe Lagoon lies in the South of Viti Levu the main island of Fiji. The general characteristics of this lagoon were summarized by Naqasima et al. (1992).

This work was performed during a campaign on the ORSTOM R/V Alis from 18 to 29 May 1994. Bacterioplankton parameters were determined every day through the lagoon water column. A total of 10 sampling stations (20 to 40 m deep, see Fig. 1 and Tab. 1) were investigated over the whole water column.

Bacterioplankton parameters were also recorded along a diurnal cycle on station 5 (at 10m depth) in order to appreciate the representativeness of a single measurement at this scale and to detect any trend in the diurnal evolution of bacterial biomass and activity. An oceanic station (OC), Northeast of the lagoon (Fig. 1) was also visited during the cruise.

Water samples were collected using acid-washed Niskin bottles and treated on board immediately after sampling. All sample handling was performed using either disposable sterile hardware or acid-washed Polycarbonate bottles.

2.2. Abundance, biovolume

Water samples received 0.2 µm filtered and buffered formalin (2% final concentration) and were stored at 2°C in the dark until filtration within 6h after sampling. Bacteria were then collected onto 0.2 µm Nuclepore membranes after staining with DAPI (Porter & Feig, 1980). Membranes were mounted on microscopic slides and stored at -20°C until counting within one month. Bacterial cells were counted under epifluorescence (magnification 1000). At least 400 cells on at least 20 fields were counted. Replicate filters of the same sample differ on average by 11.7% of the mean.

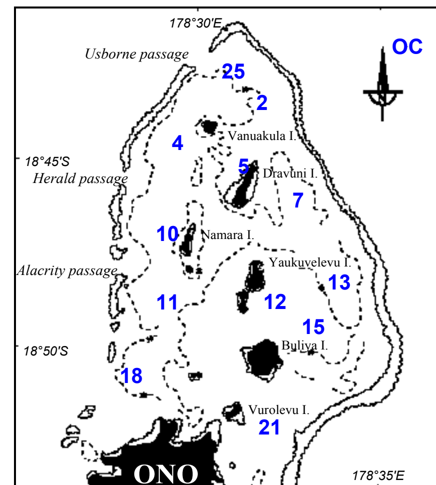

Figure 1: Map of the Great Astrolabe Reef lagoon. Sampling locations are figured by station numbers. OC designs the oceanic station.

Table 1: Characteristics of the sampling sites

station	latitude (S)	longitude (E)	depth (m)	sampling date
2	18°43'29"	178°31'45"	28	04-18-94
4	18°44'34"	178°29'28"	39	04-20-94
5	18°45'11"	178°31'15"	17	04-27-94
7	18°46'05"	178°32'44"	43	04-19-94
10	18°46'59"	178°29'11"	37	04-18-94
11	18°48'49"	178°29'11"	39	04-20-94
13	18°48'17"	178°33'50"	38	04-19-94
15	18°49'28"	178°33'08"	29	04-22-94
18	18°50'46"	178°26'38"	34	04-21-94
21	18°52'08"	178°21'58"	30	04-22-94
25	18°42'40"	178°30'58"	31	04-29-94
OC	18°41'12"	178°35'12"	3000	04-26-94

Station 5 was studied only for the diurnal pattern of bacterioplankton variables and dilution cultures (no vertical profile). OC : oceanic station

Mean cell volume was estimated by delimiting bacterial contours on photographic slides projected on a sheet at a final magnification of 10000. Length and width of individual cells were determined with a digitizing tablet. Bacterial volume was computed by assimilating bacteria to a cylinder with an hemisphere at both sides. At least 2 photographic slides were used per sample for a total of at least 150 cells. Mean cell volume estimation differs on average by less than 20% on the 2 slides of the same sample (Torréton & Dufour, 1996).

2.3. Bacterial production using TdR incorporation

2.3.1 Routine measurements

Bacterial production of biomass was determined by following the rate of [*methyl*-^{3}H]thymidine incorporation into DNA (TdR, Fuhrman & Azam, 1982).

TdR incorporation was performed routinely on freshly collected samples (within 1 hour) using 10 nM [methyl-^{3}H]thymidine (Amersham, 1.74 TBq/mmol). After 30 min incubation at 28°C (±1°C in situ temperature), duplicate 10 ml samples were chilled in a 2°C water bath. Samples were filtered onto 0.2 µm Nuclepore membranes and rinsed with 5 ml of 0.2 µm filtered lagoon water. Vacuum was disconnected and filters received 15 ml ice-cold 5% TCA. After 15 min vacuum was reapplied and the membranes were rinsed 3 times with 5 ml of ice-cold 5% TCA. Membranes were stored at -20°C in scintillation vials before radioactivity determination (within 2 weeks). DNA was hydrolyzed by adding 0.5 ml of 0.5N HCl into the vials. The vials were then heated at 100°C during 30 min in a water bath. Radioactivity was determined after allowing samples to stay with scintillation cocktail overnight. Quench correction was made with external standards. Incorporation was calculated after subtraction of a zero time blank.

The proportion of TdR incorporation in the > 3 µm size class was determined at every station on 10m deep samples using the procedure described above and by replacing 0.2 µm membranes by 3 µm ones.

2.3.2. Saturation kinetics

Saturation kinetics were assayed regularly in order to check if 10 nM was sufficient to saturate incorporation process and limit isotope dilution. Every assay was performed on 15 replicate subsamples (5 ml each). Each concentration of the label (2, 5, 10, 20 and 30 nM) was applied to duplicate samples and a zero time blank.

2.3.3. Isotope dilution

Isotope dilution assays (Pollard & Moriarty 1984) were performed at different stations in order to determine the contribution of labeled TdR to total incorporation. Every assay was performed on 8 replicate subsamples (5 ml each). All the subsamples received 10 nM of labeled thymidine and increasing amounts of unlabeled thymidine (0, 20, 40 and 60 nM). A zero time blank was performed for every concentration and was subtracted from the signal. Maximum incorporation rate were computed from the regression of [total TdR added] versus 1/observed incorporation rate: [L+A] = Vmax.L/Vobs - P, where L and A are the concentrations of labeled and unlabeled TdR, P is the "pool" of thymidine inducing intra and extra cellular isotope dilution, and Vobs and Vmax are observed and maximum TdR incorporation rates respectively. Of course this procedure gives a correct estimate of isotope dilution only if incorporation into the target molecule is the rate limiting step.

2.3.4. Extraction of DNA

A total of 15 additional TdR incorporation assays were done in triplicates as described in section 2.3.1. After incubation, precipitation and filtration steps, membranes were stored at -20°C until analysis at the laboratory. Labeled DNA was extracted enzymatically from these membranes following a modification of Wicks & Robart's (1987) procedure as described in Torréton & Bouvy (1991). Recovery of the label into the DNA fraction was then compared with the label recovered on the same samples using the standard TCA precipitation procedure.

2.3.5. Calibration of TdR incorporation against cell production

The conversion factor of TdR incorporation into cell production was estimated in dilution cultures of lagoon water. These cultures are described in § 2.6.

2.4. DOC determinations

Samples were filtered through burnt (440°C, 4h) Whatman GF/F glass fiber filters to remove particulate carbon greater than 0.7 µm. The filtrate was then dispatched into replicate Teflon capped glass tubes previously acid washed and burnt (550°C, 4h). Ten ml samples receive $HgCl_2$ (10 ppm final concentration) to prevent bacterial growth during the storage of the samples. The tubes were then stored in the dark at 4°C until analysis. After elimination of CO_2 by adding 0.1ml HCl 1N and bubbling 10 min with CO_2 free air, DOC was analyzed using HTCO technique (Sugimura & Suzuki, 1988) on a Total Organic Carbon analyzer (Shimadzu TOC 5000). Blank value average 200 µgC l^{-1} and was not subtracted from the signal.

2.5. Bacterioplankton growth yield and heterotrophic activity

Bacterioplankton carbon growth yield was estimated in the lagoon water cultures used to calibrate [*methyl*-^{3}H]thymidine incorporation into cell production (see 2.6.). DOC consumption was estimated and related to bacterial biomass production into the cultures. Growth yield of bacterioplankton was defined as the slope of the regression line of bacterial biomass versus DOC decrease. Production divided by carbon growth

yield was used to assess DOC consumption by heterotrophic bacteria into this lagoon.

2.6. Lagoon water cultures

Two dilution cultures were realized by inoculating 10 and 30% of 1µm filtrate of lagoon water (station 12, 04-23-95) into 0.2 µm filtered lagoon water in order to remove potential limitation of bacterial growth by available nutrients and grazing by eukaryotes greater than 1 µm. The absence of flagellates in the cultures was verified during microscopic enumeration of bacteria. Bacteria were allowed to grow in the dark at 30°C under gentle agitation. Periodically (1.5 to 2 hours) water samples were removed and bacterial abundance, biovolume, DOC and ^{3}H-TdR incorporation were recorded as described above excepted that TdR was added at 20nM in order to prevent isotope dilution and/or unsaturation of incorporation into fast growing populations in these cultures. Comparison of rates with 20nM and 40 nM were made occasionally and showed no significant differences showing that maximum incorporation was achieved at 20nM. Recovery of the label into the DNA and TCA fractions was estimated systematically in the dilution cultures.

3. Results and discussion

3.1. Methodological background

3.1.1. Saturation kinetics

Saturation kinetics showed that 10 nM was sufficient to saturate the incorporation process (Fig. 2).

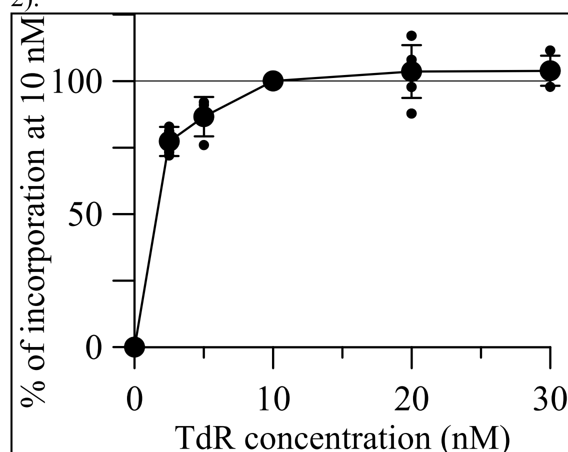

Figure 2: Evolution of TdR incorporation rate with increasing concentrations of labeled TdR. Five experiments were performed. Rates are normalized by giving 100% to the 10 nM value

3.1.2. Isotope dilution

On average the "dilution pool" was not significantly different from zero, representing 0.7 nM (SE = 1.0 nM, n = 6) using the isotope dilution plots method (Tab. 2, Fig. 3). Thus labeled TdR constitutes nearly 100% of TdR incorporated according to this procedure and it was not necessary to correct TdR incorporation for isotope dilution.

Table 2: Dilution pool of TdR determined using the isotope dilution procedure

Station	Depth (m)	Vobs	Vmax (pMh^{-1})	Vobs/Vmax (%)	Dilution Pool (pM)
5	10	18.08	25.97	69.60	1.59
5	10	24.26	28.38	85.47	0.77
25	0	10.19	14.12	72.15	3.89
25	5	7.91	9.91	79.84	0.26
25	10	11.20	13.47	83.15	1.17
25	20	11.27	11.20	100.65	-3.30
		Average		81.81	0.73
		SE		4.53	0.96

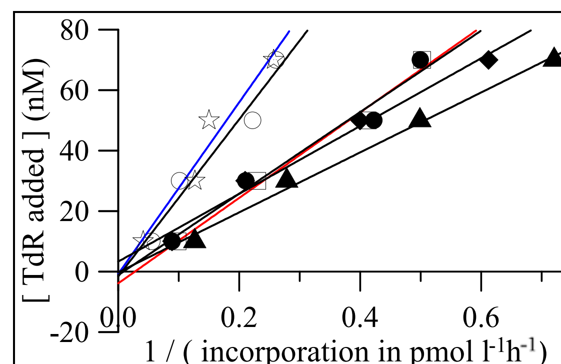

Figure 3 : Isotope dilution plots of TdR incorporation. Y-intercept represents the opposite of the dilution pool. Six experiments were performed on stations 2 ( ), 5 (○), 7 (☆), 10 (●), 11 (▲), and 13 (◆).

3.1.3. Incorporation into DNA versus cold TCA precipitate

In the water column samples, label recovered into DNA averages 75.0 % with minor fluctuations (SE=1.3 %, n=15, see Tab. 3). This shows that TdR is not extensively catabolized but incorporated preferentially in the DNA like in other atoll lagoons (Torréton & Dufour, 1996). Thus, on the remaining *in situ* samples, incorporation into DNA was calculated by multiplying incorporation into cold TCA precipitable material by 0.75.

During bacterial growth into the dilution cultures, recovery of the label into the DNA and TCA fractions was stable (mean 90.5 %, SE=3.1 %, n=8, see Tab. 3) and significantly higher than in situ (P<0.001, Student's t-test). This has already

been observed in other coral reef lagoons (Torréton & Dufour, 1996). This difference, although limited in importance during that study, is of particular interest as TdR incorporation is basically an estimation of DNA synthesis. DNA is not the only macromolecule labeled by ^{3}H-TdR, but usually for commodity only incorporation into cold TCA precipitate (including DNA, RNA and proteins) is determined. TCA derived production estimate ($Prod_{TCA}$) is therefore estimated by:

$$Prod_{TCA} = \text{Incorporation into TCA} \times TCF_{TCA} \quad (1)$$

Where TCF_{TCA} is the Thymidine Conversion Factor based on incorporation into TCA precipitate. However, the real bacterial production value ($Prod_{DNA}$) should be given by incorporation into DNA: $Prod_{DNA} = \text{Inc. into DNA} \times TCF_{DNA}$ (2).

Where TCF_{DNA} is the Thymidine Conversion Factor based on incorporation into DNA. But DNA constitutes on average 75.0% and 90.5% of labeled TCA precipitated macromolecules on *in situ* sample and in lagoon water cultures, respectively. This can be resumed by :

$$\text{Inc. into TCA} = \text{Inc. into DNA} / 0.75 \quad (3)$$

$$\text{and } CF_{TCA} = 0.905\ CF_{DNA} \quad (4)$$

Therefore using (3) and (4), (1) comes :

$$Prod_{TCA} = \text{Inc. into DNA} / 0.75 \times 0.905\ CF_{DNA} \quad (1')$$

And using (2), (1') comes :

$$Prod_{TCA} = Prod_{DNA} \times 0.905/0.75$$

Cell production calibrated against TdR incorporation into cold TCA precipitate would therefore lead to a 1.21 fold overestimation of the real bacterioplankton production. This artifact is not very important in that ecosystem as the percent of labeled incorporated into DNA is rather high for *in situ* samples. But in waters showing a stronger catabolism pathway for ^{3}H-TdR, this difference of incorporation pattern between *in situ* and cultured bacteria may lead to a much greater overestimation (Torréton & Bouvy, 1989).

3.1.4. Calibration of TdR incorporation against cell production

After a lag phase of less than 10 hours, bacterial cells and TdR incorporation grew exponentially (Fig. 4). Four different methods usually yielding slightly different results were proposed to relate cell multiplication and TdR incorporation (Ducklow *et al.* 1992). However, if care is taken to account for the proportion of inactive cells, all the four methods lead to the same conversion factor (Torréton & Dufour, 1996).

Table3 : Proportion of TdR incorporated into DNA using DNase extraction method.

Water column samples

Station	Depth (m)	TCA (pmol l^{-1} h^{-1})	DNA (pmol l^{-1} h^{-1})	% in DNA
2	0	18.97	15.54	81.9
4	30	17.85	12.70	71.1
5	10	12.84	9.81	76.4
5	10	14.09	11.38	80.8
7	0	13.11	9.72	74.1
10	0	4.75	3.57	75.2
11	0	12.77	9.40	73.6
13	30	8.73	5.89	67.5
15	0	9.31	6.47	69.5
18	29	10.84	8.06	74.4
21	0	9.58	8.05	84.0
21	5	11.59	8.33	71.9
21	10	11.29	8.86	78.4
21	20	12.47	8.43	67.6
25	20	11.27	8.84	78.4
		Average		75.0
		SD		5.0
		SE		1.3

Dilution cultures

Culture	Day-time	TCA (pmol l^{-1} h^{-1})	DNA (pmol l^{-1} h^{-1})	% in DNA
A	12	6.23	6.60	105.9
A	14	19.50	15.58	79.9
A	16	39.01	37.14	95.2
A	18	37.84	30.24	79.9
B	8	7.84	7.45	94.9
B	10	34.61	31.55	91.2
B	12	113.47	95.63	84.3
B	14	122.13	112.96	92.5
		Average		90.5
		SD		8.8
		SE		3.1

TCA : ^{3}H-TdR recovered into the TCA precipitable fraction, DNA : ^{3}H-TdR recovered into the DNA fraction. % in DNA : DNA x 100 / TCA. Each value is the average of duplicate determinations. Culture A: 10% inoculum, culture B: 30% inoculum (4-24-94).

Cells multiplication and TdR incorporation were then related using the cumulative method proposed by Bjornsen & Kuparinen (1991). This method claims the advantage to be « model free », *i.e.* to not require assumptions about the proportion of active cells.

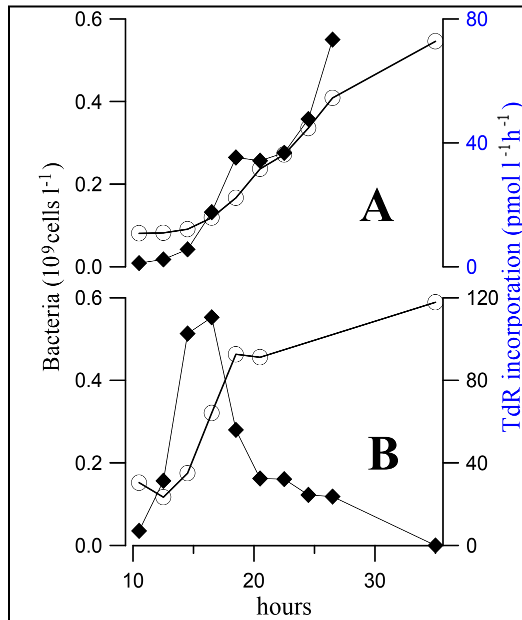

Figure 4: Evolution of bacterial abundance (○) and TdR incorporation into DNA (◆) along the seawater cultures. A: 10% inoculum, B: 30% inoculum.

Least squares linear regressions were used to compute the thymidine conversion factor (TCF) assuming the relation : Cells = TCF (ΣTdR)+ ß where: Cells is the net increase of bacterial cells cumulated over the successive time intervals, ΣTdR is the integral of TdR incorporation cumulated over the successive time intervals and ß is the intercept of the regression of cells versus ΣTdR.

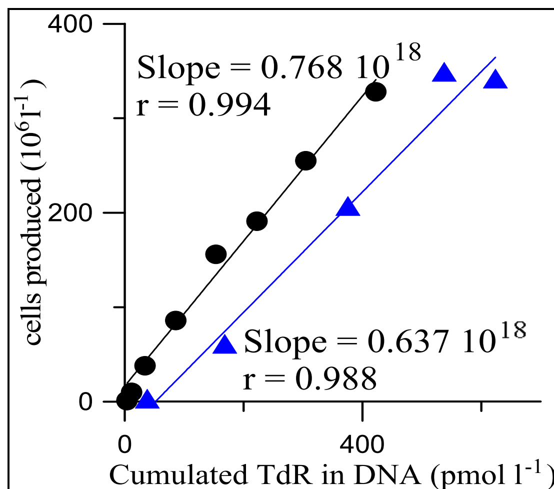

Figure 5: Cells produced vs integral of TdR incorporation cumulated over successive time intervals. The slope of the regression lines represent the conversion factor (CF) for TdR incorporation into cell production. ●: 10% inoculum, ▲: 30% inoculum

The two independent determinations lead to similar results (see Fig. 5). The average conversion factor, 0.7 10^{18} cells per mol of TdR incorporated into DNA is close to the average CF determined in Tikehau lagoon (1.0 10^{18}, Torréton & Dufour, 1996). Incorporation of TdR into DNA (in mol $l^{-1}h^{-1}$) was thus multiplied by 0.7 10^{18} to obtain bacterial production in cell $l^{-1}h^{-1}$. These production values were multiplied by 20 fgC $cell^{-1}$ (Lee & Fuhrman, 1987) in order to obtain production values in gC $l^{-1}h^{-1}$.

3.1.5. Bacterial growth yield into the seawater cultures

Although limited by the precision inherent to the method, DOC decreased significantly within the cultures ($P < 0.05$, see Fig. 6) while bacterial carbon increased. Cells multiplication and DOC consumption were related using a cumulative method as described above for TdR incorporation. Least squares linear regressions were used to compute the carbon growth yield (CGY).

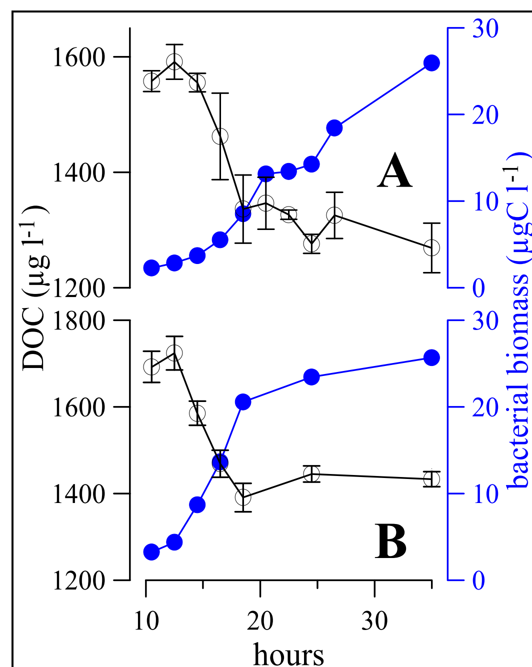

Figure 6: Evolution of bacterial carbon (●) and DOC (○) within the seawater cultures. A: 10% inoculum, B: 30% inoculum

The relation : δBC = CGY (δ DOC)+ ß was assumed, where, δBC is the net increase of bacterial carbon cumulated over the successive time intervals, δ DOC is the net decrease of DOC and ß is the intercept of the regression. The two independent determinations lead to very convergent results (see Fig. 7) with an average CGY of 5.7 %.

This very low growth yield has been observed in Tikehau and Takapoto lagoons (Torréton & Dufour, unpublished data) and a comparable CGY was determined during the North Atlantic bloom with the same method for seawater culture realization and for DOC determination (Kirchman *et al.* 91). This CGY is thus very unlikely to be a methodological artifact but rather an index of severe bottom-up limitation of bacterioplankton.

Production values in gC l^{-1} h^{-1} were thus divided by 0.057 in order to obtain heterotrophic activity of the bacterioplankton community.

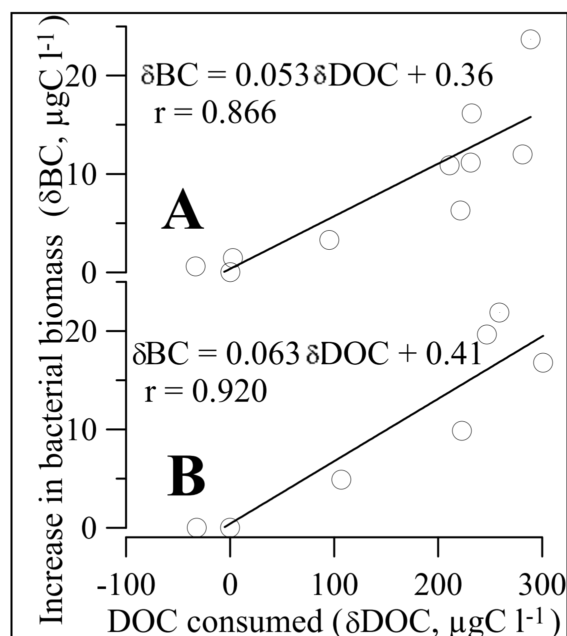

Figure 7: Plot of bacterial carbon produced versus DOC consumed over successive time intervals in the two cultures. The slope of the regression lines represent the carbon growth yield (CGY). A: 10% inoculum, B: 30% inoculum

3.2. Bacterioplankton biomass, production and growth rate in the Great Astrolabe Reef lagoon

3.2.1. Spatial variations

3.2.1.1. Vertical variations

Ten profiles of bacterioplankton parameters were realized from sub-surface to the bottom of the water column (25 to 45m). Bacterial parameters show little variations along the water column with coefficient of variation (CV%) representing 11, 18 and 17% for bacterial abundance, production and growth rate respectively (Tab. 4, see Fig. 8).

Water column may thus be considered roughly homogenous for bacterioplankton parameters observed during this cruise.

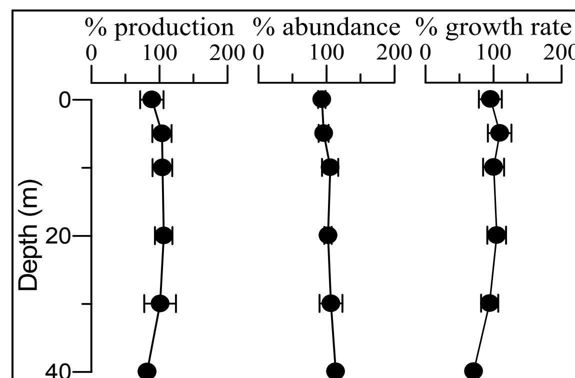

Figure 8: Average profiles of bacterial abundance, production and growth rate normalized to the average value per profile. Horizontal bars represent standard deviation.

3.2.1.2. Horizontal variations

Average values for vertical profiles do not differ very much from site to site into the lagoon. Coefficient of variation for averages of the 10 profiles are 10, 19 and 21 % for bacterial abundance, production and growth rate respectively (Tab. 5).

Variations are more important on integrated values as CV raise to 26 and 27 % for bacterial abundance and production respectively (Tab. 6). These weak differences, integrating both inter-station and day-to-day variations are thus mainly due to depth differences between the stations.

Table 4: Bacterial abundance, TdR incorporation and specific TdR incorporation per cell along vertical profiles.

Bacterial abundance (10^9 cells l^{-1})

Depth	2	4	7	10	11	13	15	18	21	25	ALL PROFILES		
0	0.73	0.68	0.62	0.77	0.72	0.64	0.70	0.62	0.70	0.58			
5	0.67	0.68	0.61	0.80	0.78	0.76	0.74	0.63	0.71	0.58			
10	0.84	0.70	0.59	0.95	0.85	0.74	0.66	0.84	0.85	0.64			
20	0.65	0.87	0.73	0.92	0.71	0.74	0.70	0.73	0.73	0.65			
30		1.03	0.84	0.98	0.58	0.74		0.64					
40			0.79								AVG	SD	CV%
AVG	0.72	0.79	0.70	0.89	0.73	0.72	0.70	0.69	0.75	0.61	0.73	0.07	9.7
SD	0.09	0.16	0.11	0.09	0.10	0.05	0.03	0.09	0.07	0.04			
CV%	12	20	15	10	13	7	4	13	9	6	11		

TdR into DNA (pmol l^{-1} h^{-1}) (a)

Depth	2	4	7	10	11	13	15	18	21	25	ALL PROFILES		
0	14.23	9.90	9.83	3.56	9.58	6.85	6.98	6.03	7.18	7.64			
5	12.64	10.37	11.07	7.93	11.25	7.83	7.10	10.98	8.69	5.93			
10	14.08	7.06	11.83	9.38	11.82	8.62	6.93	7.73	8.47	8.40			
20	11.52	8.91	10.18	9.23	9.59	9.93	9.42	7.82	9.35	8.45			
30		13.39	10.77	9.38	6.09	6.55		8.13					
40			8.42								AVG	SD	CV%
AVG	13.12	9.92	10.35	7.90	9.67	7.96	7.61	8.13	8.42	7.61	9.07	1.74	19.2
SD	1.28	2.31	1.17	2.50	2.24	1.38	1.21	1.79	0.91	1.18			
CV%	10	23	11	32	23	17	16	22	11	15	18		

TdR specific incorporation (10^{-21} mol $cell^{-1}$ h^{-1})

Depth	2	4	7	10	11	13	15	18	21	25	ALL PROFILES		
0	19.4	14.6	15.9	4.6	13.2	10.8	9.9	9.7	10.3	13.1			
5	18.8	15.3	18.1	9.9	14.5	10.3	9.6	17.4	12.2	10.2			
10	16.7	10.1	20.2	9.8	14.05	11.6	10.4	9.2	10.0	13.1			
20	17.7	10.2	13.9	10.0	13.5	13.5	13.4	10.7	12.8	13.1			
30		13.0	12.8	9.6	10.4	8.8		12.7					
40			10.7								AVG	SD	CV%
AVG	18.2	12.6	15.3	8.8	13.1	11.0	10.8	11.9	11.3	12.4	12.5	2.6	21
SD	1.2	2.4	3.5	2.3	1.6	1.7	1.7	3.3	1.4	1.4			
CV%	7	19	23	27	12	16	16	28	12	12	6		

(a): Incorporation into cold TCA precipitate was multiplied by 0.75 (average labeled DNA/labeled TCA ratio) to obtain incorporation into DNA.

Table 5: Average bacterioplankton biomass, productions and growth rates along the 10 vertical profiles.

	Bacterial biomass		TdR incorporation	Bacterial production		Spec. Incorporation	Growth rate
Station	10^9 cell l^{-1}	µgC l^{-1}	pmol $l^{-1}h^{-1}$	10^6 cell $l^{-1}h^{-1}$	µgC $l^{-1}d^{-1}$	10^{-21} mol cell $l^{-1}h^{-1}$	d^{-1}
2	0.724	14.5	13.1	221	4.43	18.2	0.31
4	0.793	15.9	9.9	167	3.35	12.6	0.21
7	0.697	13.9	10.4	175	3.49	15.3	0.26
10	0.886	17.7	7.9	133	2.67	8.8	0.15
11	0.729	14.6	9.7	163	3.26	13.1	0.22
13	0.724	14.5	8.0	134	2.69	11.0	0.19
15	0.702	14.0	7.6	128	2.57	10.8	0.18
18	0.694	13.9	8.1	137	2.74	11.9	0.20
21	0.746	14.9	8.4	142	2.84	11.3	0.19
25	0.612	12.2	7.6	128	2.57	12.4	0.21
mean	0.731	14.6	9.1	153	3.06	12.5	0.21
SE	0.024	0.5	0.6	10	0.20	0.8	0.01
CV%	10	10	19	19	19	21	21

Table 6: Integrated bacterioplankton biomass and productions along the 10 vertical profiles.

	Bacterial biomass		TdR incorporation	Bacterial production	
Station	10^{12} cell m^{-2}	mgC m^{-2}	10^{-9} $m^{-2}h^{-1}$	10^{12} cell $m^{-2}d^{-1}$	mgC $m^{-2}d^{-1}$
2	18.0	360	320	5.39	108
4	29.4	588	352	5.95	119
7	32.6	652	462	7.80	156
10	32.1	642	305	5.15	103
11	25.0	500	326	5.49	110
13	25.8	516	286	4.82	96
15	17.5	350	199	3.36	67
18	24.8	496	287	4.85	97
21	18.9	378	218	3.69	74
25	15.6	312	196	3.31	66
mean	24.0	479	295	4.98	100
SE	2.1	41	27	0.45	9
CV%	26	26	27	27	27

3.2.2. Temporal variations

A diurnal cycle of abundance and activity was performed on 27 May at station 5 in order to estimate the representativity of single measurements to describe parameters at the scale of the day. Results (Tab. 7, Fig. 8) show that the variations are moderated at this time scale as CV% average 9 and 22 for bacterial abundance and production respectively (Tab. 7) with no significant trend along the day time (Fig. 8).

Table 7: Evolution of bacterial parameters along a diurnal cycle at 10m depth on station 5 (27-04-94 to 28-04-94).

Day time	BACT 10^9 cell l^{-1}	TdR pmol $l^{-1}h^{-1}$	Spec. Inc. 10^{-21}mol $cell^{-1}h^{-1}$
6.8	0.96	22.11	22.98
9.0	1.06	11.53	10.84
12.0	0.95	13.47	14.23
15.0	1.03	14.09	13.73
18.0	0.86	21.29	24.71
21.0	0.95	17.96	18.89
24.0	0.98	20.82	21.24
3.0	1.01	15.50	15.28
6.0	1.18	16.50	13.96
Mean	0.999	17.03	17.32
SE	0.030	1.25	1.60
CV%	9	22	28

Bacterioplankton variables determined using discrete sampling into the lagoon may thus be considered representative of the daily average value within around 20%. From day to day, during a two weeks period, fluctuation of bacterial parameters should not exceed the spatial fluctuations between stations as one or two stations were investigated every day.

3.2.3. Average values

Once, short term fluctuations has been established and eventual spatial fluctuations documented, it is possible to examine and compare average values with other ecosystems. Average parameters recorded in the lagoon and at the oceanic station are summarized in Table 8.

3.2.3.1. Bacterial biomass

With 0.77 10^9 cells l^{-1} (Tab. 8), average bacterial abundance is very similar to the values reported by Yoshinaga *et al.* (1991) in Majero Atoll and is about 1.5 - 2 times less the average values in Tikehau and Takapoto lagoons, Tuamotu, French Polynesia (Torréton & Dufour, 1996, Dufour & Torréton, 1993). Average cell volumes are small and stable in the lagoon, ranging from 0.042 to 0.065 $\mu m^3 cell^{-1}$ (average = 0.055, Tab. 8) and fall in the range (< 0.070 μm^3) where Lee & Fuhrman (1987), after direct estimations of carbon content per cell, proposed 20 fgC $cell^{-1}$ whatever the size. Based on this value, average bacterial biomass into the lagoon is 15.5 µgC l^{-1}.

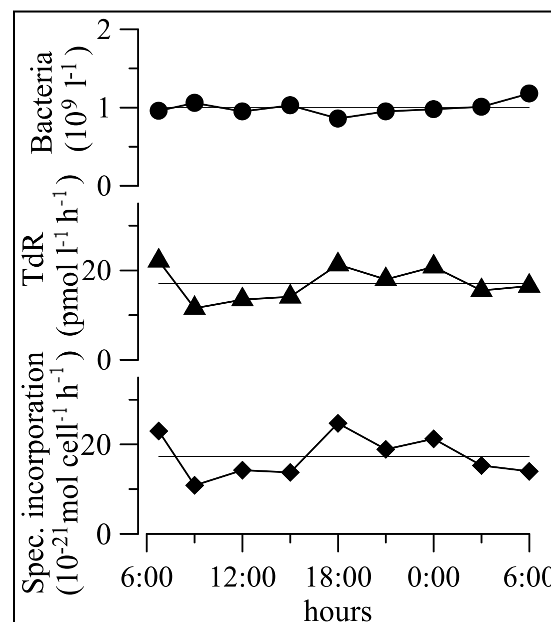

Figure 9: Diurnal evolution of bacterioplankton parameters at station 5 at 10m depth.

Table 8: Average bacterioplankton variables recorded during this study.

	biomass 10^9 cell l^{-1}	biovolume µm^3 $cell^{-1}$	TdR pmol $l^{-1}h^{-1}$	TdR/Cell 10^{-21}mol $cell^{-1}h^{-1}$	biomass attached % of total	TdR attached % of total
Mean	0.77	0.055	12.8	16.8	10.4	14.1
SD	0.14	0.015	3.6	4.3	0.9	0.9
N	56	12	56	56	12	12

Data include 10 vertical profiles (46 data, see Tab. 4) and a diurnal cycle on station 5 (9 data, see Tab. 7). Biovolume, attached bacteria and TdR incorporation by attached bacteria were determined only on 12 samples (see Tab. 9).

3.2.3.2. Bacterial production

With 12.8 pmol $l^{-1}h^{-1}$ on average, bacterial incorporation of TdR is 13 times more important in the lagoon than the average at the oceanic station. Using the TCF determined above (0.7 10^{18} cells per mol of TdR incorporated into DNA) and 20 fgC/cell this leads to 0.18 µgC $l^{-1}h^{-1}$ or 4.3 µgC $l^{-1}d^{-1}$. This value is about 1.5 fold less the average value determined by Pollard & Kogure (1993) in the same lagoon in 1989 (6.6 µgC $l^{-1}d^{-1}$, SE=1.2, n=6, using a theoretical conversion factor of 0.5 10^{18} cells per mol of TdR incorporated into DNA and 30 fgC/cell). However, their values were determined

only in the 5 m water column overlying a seagrass bed 100 m from the shore of Dravuni island. Considering these differences, bacterioplankton activity may be considered in good agreement between the two studies.

3.2.3.3. Bacterial growth rates

With 16.8 10^{-21} mol $cell^{-1}h^{-1}$ on average, bacterial specific incorporation rate per cell represent and average growth rate of 0.212 d^{-1}, therefore an average generation time of 1/0.212 = 4.7 days. This is quite long, considering the average temperature of about 28°C during the study and is an index of bottom-up limitation of bacteria.

3.2.3.4. Free and attached bacteria

The distinction between free and attached bacterioplankton has ecological consequences as free and attached bacterial production are not exported in the same way and do not present the same metabolic properties (Hoppe *et al.* 1988). Losses of attached bacteria may occur by sedimentation - very unlikely in free-living bacteria - or *via* grazing by higher trophic levels (mesozooplankton). Microscopy shows that a non negligible proportion of total abundance, 10.4% of the total on average (Tab. 9), is constituted by bacteria attached to particles. An even greater proportion of the total activity seems to be attributed to attached bacteria. TdR incorporation retained by 3 µm membranes represents, indeed, 14.1% of the total on average (Tab. 9).

Therefore, when the abundance and activity of the free community are calculated (by subtracting attached from the total), it can be seen that the average growth rate (0.19 d^{-1}) is significantly lower ($P<0.001$) than growth rate of the attached bacteria (0.30 d^{-1}). This shows that attachment seems to present an advantage for bacterioplankton community of the Great Astrolabe Reef lagoon. Particles are well known to present a favorable environment for microbial growth as bacterial exoenzymes activities release simple organic molecules directly taken up by attached bacteria (Hoppe *et al.* 1988). In oligotrophic systems where bacteria are likely bottom-up controlled (Dufour & Torréton, 1996), the attachment to particles seems to lead to a greater growth rate for the microbial community.

Table 9: Specific TdR incorporation rate per cell (10^{-21} mol $cell^{-1}h^{-1}$) for free and attached bacteria

Station	Date	------ total ------			---- attached ----			----- free -----			attached	attached
		cells 10^9 l^{-1}	Prod. 10^6 $l^{-1}h^{-1}$	µ d^{-1}	cells 10^9 l^{-1}	Prod. 10^6 $l^{-1}h^{-1}$	µ d^{-1}	cells 10^9 l^{-1}	Prod. 10^6 $l^{-1}h^{-1}$	µ d^{-1}	cells % total	Prod % total
2	04-18-94	0.841	9.90	0.28	0.050	1.18	0.56	0.791	8.71	0.26	6.0	12.0
4	04-20-94	0.699	4.97	0.17	0.048	0.62	0.31	0.650	4.34	0.16	6.9	12.5
5	04-27-94	1.063	6.08	0.14	0.163	0.74	0.11	0.900	5.34	0.14	15.3	12.2
5	04-28-94	1.182	8.70	0.18	0.189	1.41	0.18	0.992	7.29	0.18	16.0	16.2
7	04-19-94	0.587	8.31	0.34	0.055	1.45	0.63	0.532	6.87	0.31	9.4	17.4
10	04-18-94	0.955	6.59	0.17	0.088	0.59	0.16	0.866	6.00	0.17	9.3	9.0
11	04-20-94	0.847	8.31	0.24	0.076	0.85	0.27	0.772	7.46	0.23	8.9	10.2
12	04-23-94	0.550	4.96	0.22	0.045	0.79	0.42	0.505	4.17	0.20	8.2	16.0
13	04-19-94	0.742	6.06	0.20	0.075	0.98	0.31	0.667	5.08	0.18	10.1	16.2
15	04-22-94	0.663	4.87	0.18	0.087	0.92	0.25	0.576	3.95	0.16	13.1	18.9
18	04-21-94	0.837	5.43	0.16	0.097	0.71	0.18	0.740	4.72	0.15	11.6	13.1
21	04-22-94	0.845	5.96	0.17	0.081	0.90	0.27	0.765	5.06	0.16	9.5	15.1
	mean	0.818	6.68	0.20	0.088	0.93	0.30	0.730	5.75	0.19	10.4	14.1
	SE	0.054	0.49	0.02	0.013	0.08	0.05	0.043	0.44	0.01	0.9	0.9

3.3. DOC concentrations, heterotrophic activity and DOC turn-over

DOC concentrations determined in various areas of the lagoon show very little fluctuations with the sampling site. The coefficient of variation for determinations at 10m depth is only 6% around the mean value (1560 µgC l^{-1}, n=10). No significant vertical variation can be inferred from the vertical profile determined on station 25. Therefore, the average value for all the data (1582 µgC l^{-1}, Tab. 10). seems to be representative of the average conditions into the lagoon during the period of that study.

DOC turn-over due to bacterioplankton consumption may be estimated from bacterial production (BP) and bacterioplankton carbon growth yield (CGY) determined in the two dilution cultures. Bacterial carbon consumption (BCC) would thus equal BP/CGY.

With an average BP of 4.32 µgC $l^{-1}d^{-1}$ (see § *3.2.3.2.*) and a CGY of 5.7% (see § *3.2.5.*), BCC = 4.32 / 0.057 = 76 µgC $l^{-1}d^{-1}$. DOC turn-over rate would thus equal 1572 / 76 = 0.048 d^{-1} and DOC turn-over time: 1 / 0.048 = 21 days.

Table 10: DOC concentrations in the Great Astrolabe Reef lagoon

station	date	depth (m)	COD (µgC l^{-1})
2	04-18-94	10	1442
4	04-20-94	10	1498
5	04-23-94	10	1531
7	04-19-94	10	1698
11	04-20-94	10	1461
12	04-22-94	10	1655
18	04-21-94	10	1532
21	04-22-94	10	1509
22	04-22-94	0	1644
22	04-22-94	10	1631
25	04-27-94	0	1554
25	04-29-94	5	1650
25	04-29-94	10	1645
25	04-29-94	20	1563
	average		1572
	SE		22
	CV%		5

3.4. Comparison with open ocean

Determining bacterioplankton character-istics in the oceanic water column was not the main objective of that study. However, considering the weak variations observed into the lagoon one can guess that the unique profile performed at the oceanic station should be somehow representative of average oceanic conditions during the period of that study. Bacterioplankton characteristics show a classical vertical pattern with a maximum abundance in surface water and a maximum activity in deeper layers (Fig. 10), in relation with phytoplankton maximum production (Charpy, 1996, this volume). As a consequence this vertical pattern is even more pronounced for specific incorporation rate per cell (an index of bacterioplankton growth rate). Dissolved organic carbon decreases approximately regularly from surface to 100 m depth. No measurement of bacterioplankton variables were made below this level.

Abundance values inside the lagoon studied are on average only 1.5 times higher than in surrounding oceanic surface waters (average from 5 to 40 m, Tab. 11), but production values are around 13 fold greater in lagoon than at the oceanic station sampled. Therefore, specific incorporation rate per cell, an index of bacterial growth rate, is 8 times greater in lagoon water than at the oceanic station at the same levels (Tab. 11). This specific incorporation rate per cell leads to an average growth rate of 0.285 d^{-1} when multiplied by the TCF determined above. This is equivalent to an average generation time of 1/0.285 = 3.5 days.

On the other side, DOC values do not appear significantly different in the ocean (0 to 40 m) and in the lagoon. However, the limited biodegradability of DOC into lagoon waters (reflected by the amount unaffected after bacterial growth in the seawater cultures) shows that a smaller fraction of the labile DOC pool, while undetected using the HTCO technique, could explain the large differences between oceanic water and lagoon bacterioplankton growth rates.

The main differences are (1) that bacterioplankton variables present a strong vertical pattern in the ocean while vertical homogeneity seems to be the rule into the lagoon and (2) that bacteria seems thus only slightly more abundant in lagoon waters but have a far greater activity than in the surrounding ocean. This later point has already been observed in surface oceanic waters surrounding Tikehau lagoon (Torréton & Dufour, 1996).

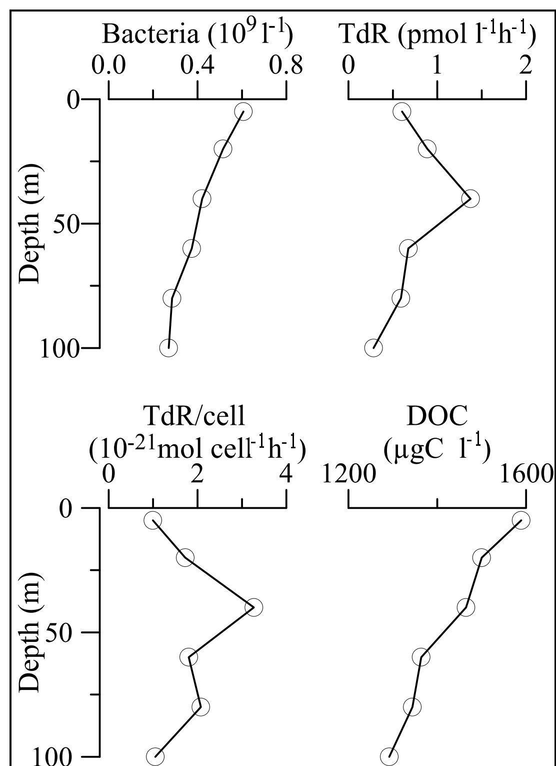

Figure 10: Abundance, TdR incorporation, specific incorporation rate per cell and DOC in the water column of the oceanic station.

Table 11: Average and standard error of bacterial variables recorded into the lagoon and at the oceanic station.

	Abundance 10^9 cell l^{-1}	TdR pmol $l^{-1}h^{-1}$	TdR/Cell 10^{-21}mol $cell^{-1}h^{-1}$	DOC µgC l^{-1}
	lagoon			
average	0.77	12.8	16.8	1572
SE	0.02	0.5	0.6	22
CV%	19	28	26	5
n	56	56	56	14
	ocean		**0 to 100 m**	
average	0.41	0.7	1.8	1426
SE	0.05	0.2	0.3	45
CV%	32	50	46	8
n	6	6	6	6
	ocean		**0 to 40 m**	
average	0.51	1.0	2.0	1518
SE	0.05	0.2	0.7	37
CV%	18	41	58	4
n	3	3	3	3

4. Conclusion

The use of ^{3}H-thymidine incorporation (10 nM final concentration) to estimate bacterioplankton production seems to be appropriate in the Great Astrolabe Reef lagoon as in other atoll lagoons (Torréton & Dufour, 1996). Most of the label is incorporated into DNA and isotope dilution is insignificant. Thymidine conversion factors determined in two dilution cultures average 0.7 10^{18} cell mol^{-1}, which is in the range of literature values.

Bacterioplankton biomass, production and growth rates are distributed homogeneously over the water column of the Great Astrolabe Reef lagoon. The comparison between average value over the ten profiles shows that bacterial variables do not differ significantly from site to site inside the lagoon.

At station 5, bacterioplankton biomass and production varied moderately over a diurnal period with coefficients of variation of 9 and 22%, respectively. And from day-to-day, variations of bacterioplankton biomass, production and growth rates should not exceed the moderate inter-stations variations (Tab. 5).

Fluctuations of bacterioplanktonic processes seem therefore very moderate both spatially and temporally over the 15 day period of the study.

Although less extensively studied, the proportion of attached bacterial abundance and activity shows also slight fluctuations from site to site, and thus, from day-to-day (Tab. 9). Dissolved organic carbon determined at least once every day also shows very moderate fluctuations around the mean value (Tab. 10).

On average, over the whole study bacterial abundance is 0.77 10^9 cell l^{-1} (15.5 fgC l^{-1}) with 10.4% attached to particles. Bacterial production averages 4.3 µgC l^{-1} with 14.1% due to attached bacteria. Over the 12 samples where they were distinguished, growth rates for bacterioplankton differs significantly for the free (0.19 d^{-1}) and attached (0.30 d^{-1}) communities. Therefore, in this low nutrient environment, attachment seems to provide an advantage for bacterial growth into this lagoon. The low average growth rate for the whole bacterioplanktonic community (0.21 d^{-1}, n=56) with an average temperature of *c.a.* 28°C suggests that bacterioplankton is resource limited into this lagoon.

Determined experimentally into two dilution cultures, the carbon growth yield (CGY) is very low (average 5.7%). This suggests that bacteria are limited by resource in the Great Astrolabe Reef lagoon. By applying the average CGY value to bacterial production rates into the lagoon, heterotrophic activity was estimated to average 76 µgC $l^{-1}d^{-1}$. Therefore, with a DOC concentration averaging 1572 µgC l^{-1} during that study, the turn-over rate of DOC is estimated to average 0.048 d^{-1} during that period. This low turn-over rate compared to the bacterial turn-over rate (0.21 d^{-1}) is another argument for a bottom-up limitation of bacterioplankton processes into this lagoon.

Bacterioplankton abundance, production and growth rate appear to be significantly greater than in oceanic water surrounding the Great Astrolabe Reef lagoon and confirm the more mesotrophic character of lagoon waters than their surrounding oceanic environment.

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The Great Astrolabe Reef Lagoon (Fiji) : Results of the French-Fijian ASTRO expedition

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