

PS
19815

Proceedings of the 6th International Coral Reef Symposium, Australia, 1988, Vol. 2

BENTHIC AND PLANKTONIC PRIMARY PRODUCTION OF AN OPEN ATOLL LAGOON (TIKEHAU, FRENCH POLYNESIA)

C.J. CHARPY-ROUBAUD¹, L. CHARPY¹ and L. LEMASSON²

¹ ORSTOM, Tahiti, PO BOX 529, Papeete, FRENCH POLYNESIA

² ORSTOM PO BOX 5045, Montpellier, 34032, FRANCE

ABSTRACT

Phytoplanktonic and microphytobenthic production of Tikehau lagoon were studied from 1983 to 1987. Phytoplanktonic production estimated by the ¹⁴C method is relatively high ($0.44\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) in spite of a low biomass ($0.19\text{mg}\cdot\text{m}^{-3}$), especially at the surface ($4.1\text{mgC}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$). It is correlated with the percentage of organisms of a size of less than $5\mu\text{m}$ which is of 61% on the average.

Microphytobenthic production of sands, estimated by O_2 budget, is strongly related to light energy and does not show any photo-inhibition. The mean production of the lagoon was calculated to $0.25\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, i.e. lower than phytoplanktonic production with a factor of 1.8. The microphytobenthic biomass presents an important micro-heterogeneity; the efficiency of the benthic photosynthetic system is not as good ($2.6\text{mgC}\cdot\text{mgChlorophyll}^{-1}\cdot\text{h}^{-1}$) as that of phytoplankton ($9.6\text{mgC}\cdot\text{mgChlorophyll}^{-1}\cdot\text{h}^{-1}$).

INTRODUCTION

The atolls of French Polynesia are located in one of the least productive ocean of the world; in fact, they are situated in a large anticyclonic gyre (BLACKBURN, 1981), the waters of which are low in nutrients. The load of organic particles of atoll lagoons is three to five times higher than that of the neighboring ocean waters (CHARPY, 1985); the origin of this organic matter may be to the primary production of the lagoon (phytoplankton and phytobenthos) or the production of detritus by the reef.

The goal of this work is to make an estimate of phytoplankton and sand microphyte production; it has been carried out within the framework of the ATOLL program by the ORSTOM Center of Tahiti.

MATERIAL AND METHODS

Sampling stations

We have chosen the atoll of Tikehau as a study site since it can be considered, due to its geomorphology, as being representative of the "open" atolls of the Tuamotu Archipelago. Its lagoon has an average depth of 25 metres and a volume of 10^{10}m^3 (LENHARDT, 1987); its bottom is mainly composed of fine to very fine sand (INTES & ARNAUDIN, 1987) and has an important bioturbation.

The investigated stations are mainly in the southern part of the lagoon, in the immediate neighborhood of the laboratory (Fig.1). Measurements of phytoplanktonic production covered the 1983-1987 period and microphytobenthic production the 1985-1987 period.

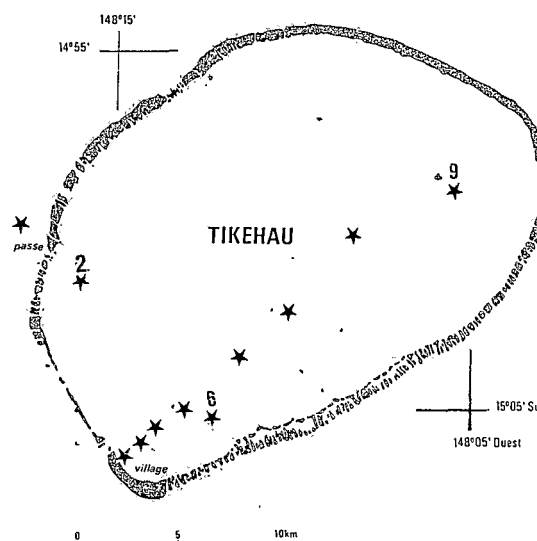
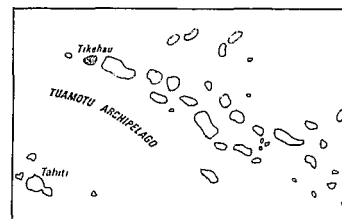


Figure 1. Locations of in situ productivity measurements.

Methods

Phytoplanktonic production

Carbon incorporation rates were estimated by measuring the ¹⁴C incorporated after in situ incubation in transparent and dark vials of borosilicate of 300ml in capacity. The total content of the vials was filtered on GF/F filters and the filter rinsed with 10ml of HCl (0.1N). Radioactivity was measured by liquid scintillation with quenching correction. The total concentration of CO_2 was calculated from alkalinity (STRICKLAND & PARSONS, 1972); we used the reading $24\text{gC}\cdot\text{m}^{-3}$, a mean of 12 measures. Incubations were duplicated and results, in general, showed a difference of no more than 10% between duplicates.

Phytobenthic production

Primary production has been estimated by O_2 budgets, measured within clear and dark plexiglass domes. For depths less than 12m, we used a YSI probe

equipped with a high sensitivity membrane; for larger depths, 120ml of water was taken by a syringe in the domes and dissolved O₂ measured using the WINKLER method. Reproducibility of results had been tested in a previous work (CHARPY-ROUBAUD, 1986a).

Phytoplankton biomass

Chlorophyll and phaeophytin were measured by fluorescence after filtering 100 to 300 ml of water on GF/F filters (YENTSCH & MENZEL, 1963).

Microphytobenthic biomass

The preliminary measurements made to define the strategy for sampling and analysis are set out in a previous work (CHARPY-ROUBAUD, 1986b). Sampling were done by divers using a core (2.7cm diameter); the extractions were performed on fresh sediment with 90% acetone. Measurements were made by fluorimetry for functional chlorophyll and by spectrophotometry for total chlorophyll. Results are expressed in mg.m⁻² for each 0.5cm thick layer of sediment.

RESULTS AND DISCUSSION

Phytoplanktonic production

Table 1 gives an account of the averages of mean Carbon Assimilation rates (AC) by depth; we observe that AC is clearly higher at the surface than other depths.

Table 1 : Averages of carbon assimilation (AC) and assimilation number (AN) in relation with depth.

depth (m)	n	AC (mgC·m ⁻³ ·h ⁻¹)	AN (mgC·mgChl ⁻¹ ·h ⁻¹)
0 - 2	52	3.92 ± 1.02	21.1 ± 7.5
2 - 5	22	2.27 ± 0.67	13.0 ± 5.1
5 - 10	42	2.68 ± 1.33	13.5 ± 4.9
10 - 15	21	2.00 ± 0.72	11.2 ± 5.6
15 - 20	7	1.17 ± 1.15	4.7 ± 3.5
20 - 24	2	0.54	4.2

This lack of photoinhibition has already been observed in other atolls of Tuamotu: SOURNIA & RICARD (1976) in Takapoto and DELESALLE *et al* (1985) in Mataiva. The AC reading (average of the first 15 metres): 2.7mgC.m⁻³.h⁻¹, can be compared to other lagoon production data in the Pacific in Table 2 (extract in part from GORDON *et al*, 1971).

In Figure 2 we have shown phytoplankton production integrated up to 15 metres, according to the month of the year. We note that production drops sharply during May, June and August. This decrease is correlated with the reduction of light energy.

Table 2: Summary of production and chlorophyll data from Pacific Lagoons. R&Y= RYTHER and YENTH (1957).

Location	Method	Production (mgC·m ⁻³ ·h ⁻¹)	Chlorophyll (mg·m ⁻³)	Reference
Marshall				
Eniwetok	O ₂	1.67	0.33	SARGENT & AUSTIN (49)
Eniwetok	¹⁴ C	0.75		DOTY & CAPURRO (61)
Rongelap	O ₂	0.42	0.17	SARGENT & AUSTIN (49)
Rongelap	¹⁴ C	0.44		DOTY & CAPURRO (61)
Palau				
Iwayama Bay	R&Y	(7)	-	MOTODA (69)
Anchorage	R&Y	(8)	-	"
Hawaii				
Kaneohe Bay	¹⁴ C	5.39	0.93	DOTY & CAPURRO (61)
Line Islands				
Fanning	¹⁴ C	9.29	0.55	"
Tuamotu				
Takapoto	¹⁴ C	0.4-3.1	0.46	SOURNIA & RICARD (76)
Mataiva	¹⁴ C	2.3-9.0	0.7	DELESALLE & al. (85)
Tikehau	¹⁴ C	2.72	0.18	This paper
Rangiroa	¹⁴ C	3.1	0.20	CHARPY (unpublis.)
Toau	¹⁴ C	0.64	0.14	CHARPY (unpublis.)
Moorea	¹⁴ C	4-22	0.05	SOURNIA & RICARD (82)
Tahiti	¹⁴ C	9-17	0.08	"

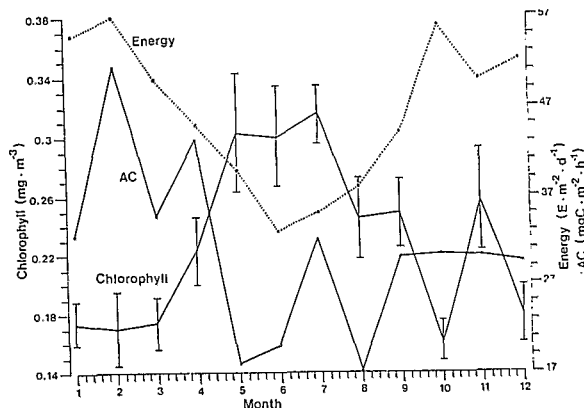


Figure 2. Integrated phytoplankton production AC (depth 15m)

Phytoplankton biomass is low: 0.19±0.01mg·m⁻³ but this average is typical of coral reef waters (JEFFREY, 1968); contrary to production, biomass is higher in May, June and July; LE BORGNE *et al*, (in press) have shown that zooplankton can ingest all daily phytoplanktonic production, especially when the salpa *Thalia democratica* is abundant as observed in summer. The increase of phytoplankton in coldest months could therefore be due to a decrease in the activity of zooplankton.

Phytoplanktonic production is correlated with light energy (Eh: E·m⁻²·h⁻¹) with a correlation coefficient equal to 0.38 where n=43; we can estimate AC using the multiplicative model (Fig.3):

$$AC = 0.39 \cdot Eh^{0.25} \quad (1)$$

Daily production in the lagoon (PPKJ) is obtained by using the bathymetric edges provided by LENHARDT (1987) by the equation:

$$PPKJ = P_{0-5} \cdot S_{0-5} + P_{5-10} \cdot S_{5-10} + \dots + P_{35-40} \cdot S_{35-40}$$

where $P = \text{mgC} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ for the intermediary depth of bathymetric edges (2.5m, 7.5m, 12.5m, 17.5m, 22.5m, 27.5m, 32.5m, 37.5m) and $S =$ surface of bathymetric edges.

Deeper than 24m, AC values were calculated using equation 1 and annual means of light energy at different depths.

Therefore, for the entire lagoon, phytoplankton production is $176 \cdot 10^6 \text{gC} \cdot \text{d}^{-1}$; i.e. a mean production of $0.44 \text{gC} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$.

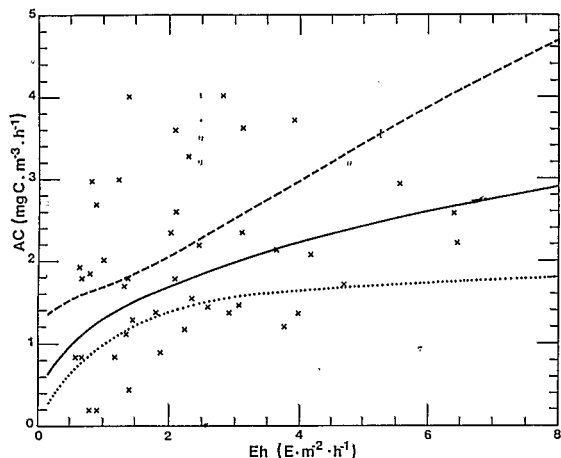


Figure 3. Multiplicative model AC versus Eh (hourly light energy at incubation depth level).

The representative assimilation number (AN) for the entire lagoon can be estimated by using the average of hourly production ($44 \text{mgC} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) and the average of integrated chlorophyll over 25m ($4.86 \text{mg} \cdot \text{m}^{-2}$): it is equal to $9 \text{mgC} \cdot \text{mgChlorophyll}^{-1} \cdot \text{h}^{-1}$. This value is of the same order as that given by TAKAHASHI & BIENFANG (1983) for picoplankton in Hawaiian waters, but lower than that given by GRIFFITHS (1976) for the Great Barrier Reef (14.4); it is characteristic of small-sized phytoplankton. The works by CHARPY (1985) and BLANCHOT *et al* (in press) has previously shown that an important part of the phytoplankton of Tikehau lagoon is made up of cells, the size of which is less than $5 \mu\text{m}$, with cyanobacteria dominating. FURNAS & MITCHELL (1986) observed that picoplankton frequently made up more than 50% of the chlorophyll standing crop.

Table 3 allows one to compare the phytoplanktonic production of waters pre-filtered on NUCLEPORE $5 \mu\text{m}$ (AC<5) with that of non pre-filtered waters (ACT). We observe that the percentage of total production due to phytoplankton of a size of less than $5 \mu\text{m}$ varies between 13% to 90% with a mean of $38 \pm 10\%$ whereas the percentage of chlorophyllian organisms of a size of less than $5 \mu\text{m}$ is of $61 \pm 12\%$ on the average in non pre-filtered waters. One observes a significant correlation between ACT and the percentage of chlorophyll passing through a filter with a pore size of $5 \mu\text{m}$ (%Chl<5): $R=0.51$; the equation of the regression line of ACT versus %Chl<5 is (Fig.4) :

$$ACT = 0.024 \cdot 10^{-3} (\pm 4 \cdot 10^{-3}) \cdot \%Chl < 5 + 1.1 (\pm 0.2)$$

Table 3: Phytoplankton Carbon assimilation ($\text{mgC} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) in samples filtered on $5 \mu\text{m}$ (AC<5) and without filtration (ACT); AN=assimilation number ($\text{mgC} \cdot \text{mgChlorophyll}^{-1} \cdot \text{h}^{-1}$); %AC=AC<5 \cdot 100/ACT; %Chl<5=percent of chlorophyll passing $5 \mu\text{m}$.

date	st.	depth	ACT	AC<5	%AC	AN t	AN<5	%Chl<5
07/24/83	2	0	4.9	2.3	47	13.3	7.3	86
		5	2.8	2.3	82	7.4	6.4	95
		10	3.2	1.8	56	9.0	4.9	99
07/26/83	9	0	4.0	2.6	65	14.7	14.0	68
		5	3.1	2.8	90	10.0	12.4	73
		10	3.7	2.0	53	11.8	8.6	74
11/23/84	6	0	5.6	2.5	44	18.7	12.4	67
11/24/84	6	0	2.6	1.5	58	11.7	8.3	81
		2	2.5	1.3	51	12.4	7.2	90
		10	3.6	1.5	42	17.2	8.3	86
		15	2.5	1.1	44	13.2	6.1	95
		4	0.5	0.2	45	3.1	1.4	89
10	2.4	0.3	13	19.5	2.6	94		
01/27/85	6	0	2.2	0.4	18	10.0	3.9	47
07/12/85	6	0	4.5	0.6	14	15.4	3.8	54
08/13/85	6	0	2.1	0.3	14	10.2	4.9	30
		2	1.4	0.2	14	5.5	4.5	17
		4	1.5	0.3	20	7.9	5.7	28
		6	1.4	0.2	15	8.2	4.5	26
		8	1.1	0.2	18	7.0	4.1	31
		10	0.9	0.2	28	4.7	5.7	18
15	0.7	0.1	18	3.3	2.6	18		
08/14/85	6	0	1.2	0.3	25	5.5	3.1	44
average					38		61	

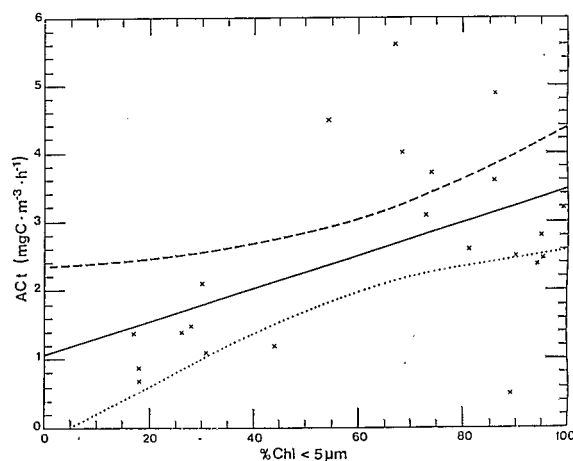


Figure 4. Regression line of carbon assimilation (ACT) versus percentage of chlorophyll passing through $5 \mu\text{m}$ filter (%Chl<5).

It seems to be that the smallest cells are being differentially ruptured to a greater degree than the larger cells, thus leading to an underestimate of C uptake (but not chlorophyll content) of the smallest cells. This fact was yet described by FURNAS (1987). The rupture of larger cells containing

more chlorophyll per cell can increase the chlorophyll concentration in the filtered sample, however microscopic examinations in april 1986 (BLANCHOT *et al.*, in press) confirm the dominance of smallest cells.

Microphytobenthic Production

In order to observe the influence of light energy on the net oxygen production in transparent tanks, measurements of O_2 budgets were realized in a continuous manner at depth. One observes when one groups the experiences together a very high significant correlation ($R = 0.7$, $n = 91$) between the energy and net production. This very high linear correlation allows one to make use of the equation by LEACH (1970) and RIZNYCK (1978) in order to estimate daily production (PBJ) using incubations of short duration.

$$PBJ \text{ (mgO}_2 \cdot \text{m}^{-2}) = P_{t-t_0} \cdot E_j \cdot E_{t-t_0}^{-1}$$

where :

P_{t-t_0} = Net production during the incubation period ($t-t_0$) ($\text{mgO}_2 \cdot \text{m}^{-2}$).

E_j = Incidental daily energy ($\text{E} \cdot \text{m}^{-2} \cdot \text{j}^{-1}$).

E_{t-t_0} = Incidental energy during the incubation period ($\text{E} \cdot \text{m}^{-2}$).

Fifty incubations of short duration (2 to 4 hours) were made at different stations and times ; the factor explaining the most variance is the depth of the station with 15 %, followed by light energy with 11 %. PBJ and depth are linked by the relation.

$$PBJ = -25.5 (\pm 2.5) \cdot \text{Depth} + 1005 (\pm 28.6) \quad (2)$$

The standard estimation error in the estimation of PBJ with equation (2) is $390 \text{ mgO}_2 \cdot \text{m}^{-2} \cdot \text{j}^{-1}$, i.e. 106 % of the net production corresponding to an average depth of 25 metres.

The production of O_2 can be transformed into the gross production of carbon (PBCJ) by the equation of McCLOSKEY *et al.* (1978) :

$$PBCJ \text{ (gC} \cdot \text{m}^{-2} \cdot \text{j}^{-1}) = (PBJ \cdot 0.375 \cdot PQ) + (R \cdot 0.375 \cdot RQ) \quad (3)$$

where R = Respiration during daytime ; we have taken the mean of hourly respiration measured in the dark tanks : $31 \pm 7 \text{ mgO}_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$, multiplied by 10 hours. PQ and RQ = photosynthetic and respiratory coefficients chosen as being equal to 1 as RAVEN (1976) & McCLOSKEY *et al.* (1978) advise.

We can therefore calculate the PBJ of the intermediary depths of the bathymetric edges (0-5, 5-10, 10-15, 15-20, 20-25, 30-35, 35-40) by equation (2) and transform them into PBCJ by equation (3). The production of bathymetric edges is obtained by multiplying the PBCJ by the bathymetric surface areas provided by LENHARDT (1987); the total represents overall microphytobenthos production of the lagoon, i.e. : $100 \cdot 10^6 \text{ gC} \cdot \text{j}^{-1}$, which gives a mean PBCJ of $0.25 \text{ gC} \cdot \text{m}^{-2} \cdot \text{j}^{-1}$. This value is of the same order as the production values for tropical marine sediments (refer to table in CHARPY-ROUBAUD, 1986a).

The biomass of microphytobenthos was measured on 185 samples, at different stations and at different times. No significant trend can be seen, probably because of the high intra-station heterogeneity. In fact, the coefficients of variation of total and active chlorophyll were estimated on 34 samples at

same station at respectively 41 % and 73 % of the biomass average. The general averages are : $19.7 \pm 1.6 \text{ mg} \cdot \text{m}^{-2}$ for total chlorophyll and $9.6 \pm 1.4 \text{ mg} \cdot \text{m}^{-2}$ for functional chlorophyll. The assimilation number calculated by using the latter mean is equal to $2.6 \text{ mgC} \cdot \text{mgChlorophyll}^{-1} \cdot \text{h}^{-1}$.

Comparison of phytoplankton - phytobenthos.

Figure 5 allows comparison of benthic (PBCJ) and planktonic productions (PPKJ). PBCJ exceeds PPKJ in the 0-10 metre bathymetric edge (2.7% of the surface area of the lagoon), whilst both of these productions are equivalent for depths of between 10 to 15 metres (5.7% of the lagoonary surface area) and PPKJ exceeds PBCJ in the remaining 92% of the lagoon). On the average, PPKJ therefore exceeds PBCJ by a factor of 1.8. This fact is due to the relatively importance of depth of the lagoon where 92% of the bottom are over 15 metres in depth. However, this comparison should be treated with caution since the methodologies used to estimate PPKJ and PBCJ are totally different (assimilation of ^{14}C and O_2 budget).

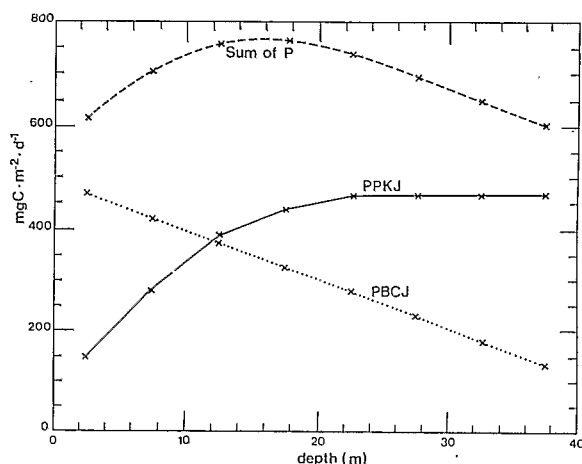


Figure 5. Comparison between phytoplanktonic (PPKJ) and Phytobenthic (PBCJ) production.

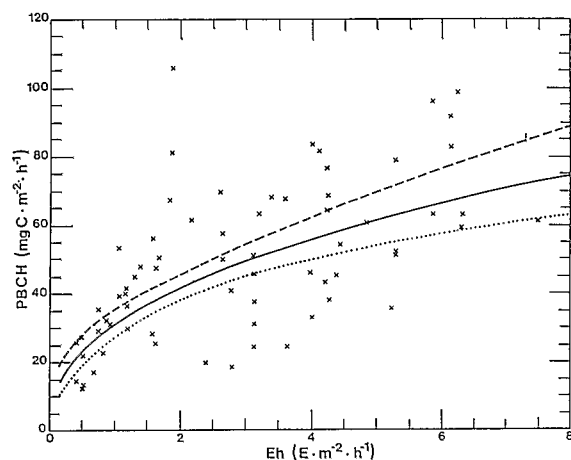


Figure 6. Phytobenthic production (PBCH) versus light energy (E_h).

The efficiency of the plankton photosynthetic system is better than that of the benthic system (9 against 2.6 mgC·mgChlorophyll⁻¹·h⁻¹), which indicates a turnover three times faster.

One can compare the response of both of these photosynthetic systems to light by comparing the regression AC versus Eh (Fig. 3) with that of hourly benthic production (PBCH : mgC·m⁻²·h⁻¹) in Eh (Fig. 6).

These curves have the same shape but the correlation between energy and production is higher for benthos (R = 0.66) than for plankton (R = 0.38).

CONCLUSION

In the lagoon of the atoll of Tikehau, daily phytoplanktonic production (average of 0.44 gC·m⁻²) decreases during the southern summer whereas biomass increases. Phytoplankton smaller than 5 µm represent an important part of the total phytoplanktonic production (61%). Total phytoplanktonic production is positively correlated with the percentage of small sized organisms. Measurements of the incorporation rate of carbon by phytoplankton in waters pre-filtered on 5 µm filters gives a mean production for these organisms equal to 38% of the total production ; therefore, a rupturing of cells probably occurs during the pre-filtration and the contribution of picoplankton to phytoplanktonic production may be at least of the same order as for biomass (61%). The mean daily production of microphytobenthos (0.25gC·m⁻²) is less than that of plankton by a factor of 1.8. It is strongly correlated to light energy and its assimilation number is 3.5 times lower than that of phytoplankton.

REFERENCES

- Blanchot J., Charpy L., Le Borgne R. Seston composition in the atoll of Tikehau (Tuamotu archipelago) from 0.2µm to 2mm. *Mar. Biol.*, submitted.
- Blackburn, A. 1981. Low latitude gyral regions. In: *Analysis of Marine Ecosystems*. Longhurst A.R.(ed) Academic Press London pp 3-29.
- Charpy, L. 1985. Distribution and composition of particulate organic matter in the lagoon of Tikehau (Tuamotu archipelago, French Polynesia). *Proceed of the first intern coral reef Symp.* 3:353-357.
- Charpy, L. & Charpy-Roubaud, C.J. Particulate Organic Matter fluxes in a coral reef lagoon (Tikehau atoll French Polynesia). *Coral Reef*, submitted.
- Charpy-Roubaud, C.J. 1986b. Le microphytobenthos. I Biomasse (premiers résultats). In: *Contribution à l'étude de l'atoll de Tikehau:II(archipel des Tuamotu)*. ORSTOM-TAHITI, Notes et Doc. *Océanogr.*, 28:1-51.
- Charpy-Roubaud, C.J. 1986a. Le microphytobenthos. II Production Primaire (premiers résultats). In: *Contribution à l'étude de l'atoll de Tikehau:II(archipel des Tuamotu)*. ORSTOM-TAHITI, Notes et Doc. *Océanogr.* 28:52-81.
- Charpy-Roubaud, C.J. Production primaire des fonds meubles du lagon de Tikehau (Atoll des Tuamotu, Polynésie Française). *Océanologica Acta* in press.
- Delesalle, B. & Colleagues 1985. Environmental survey of Mataiva Atoll, Tuamotu Archipelago French Polynesia. *Atoll Res. Bull.* 286:1-34.
- Doty, M.S. & Capurro, L.R.A. 1961. Productivity measurements in the world ocean. *International Geophysical Year Oceanography Report* 4.
- Furnas, M.J. 1987. Effects of prescreening on productivity of size-fractionated phytoplankton. *Limnol. Oceanogr.* 32(2): 483-491.
- Furnas, M.J. and Mitchell, A.W. 1986. Phytoplankton dynamics in the central Great Barrier Reef-I. Seasonal changes in biomass and community structure and their relation to intrusive activity. *Continental Shelf Research*. 6(3): 363-384.
- Gordon, D.C.Jr., Fournier, R.O., Krasnick, G.J. 1971. Note on the Planktonic Primary Production in Fanning Island Lagoon. *Pacific Science* 25:228-233.
- Griffiths, D.J. 1976. The photosynthetic capacity of the phytoplankton in the waters of a coral reef. *Austr. J. Plant Physiol.* 3:53-56.
- Intes, A. & Arnaudin H. 1987. Esquisse sédimentologique du lagon de Tikehau. *Notes et Doc. ORSTOM Tahiti Ser. Oceanogr.* 35:71-100.
- Jeffrey, S.W. 1968. Photosynthetic pigments of the phytoplankton of some coral reef waters. *Limnol. Oceanogr.* 13:350-355.
- Leach, J.H. 1970. Epibenthic algal production in an intertidal mudflat. *Limnol. Oceanogr.* 15:514-521.
- Le Borgne, R.P., Blanchot, J., Charpy, L. Zooplankton of the atoll of Tikehau (Tuamotu Archipelago) and its relations with particulate matter. *Mar. Biol.* Submitted.
- Lenhardt, X. 1987. Etude bathymétrique du lagon de l'atoll de Tikehau. *Notes et Doc. ORSTOM Tahiti Ser. Oceanogr.* 35:53-70.
- McCloskey, L.R., Wethey, D.S., Porter, J.W. 1978. Measurement and interpretation of photosynthesis and respiration. In *Coral reef Research Methods*. Stoddart, D.R. & Johannes J.E.(ed), UNESCO Monographs on Oceanographic Methodology. Paris. 5: 581pp.
- Motoda, S. 1969. An assessment of primary productivity of a coral reef lagoon in Palau, Western Caroline Islands based on the data obtained during 1935-37. *Records of oceanogr. Works in Japan* 10:65-74.
- Raven, J.A. 1976. The quantitative role of "dark" respiratory processes in heterotrophic and photolithotropic plant growth. *Ann. Bot.* 40:587-602.
- Riznyk, R.Z., Edens, J.J., Libby, R.C. 1978. Production of epibenthic diatoms in a southern California impounded estuary. *J. Phycol.* 14:2-279.
- Ryther, J.H. & Yentsch, C.H. 1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. *Limnol. Oceanogr.* 2:281-286.
- Sargent, M.C. & Austin, T.S. 1949. Organic Productivity of an Atoll. *Trans. American Geophys. Union* 30:245-249.
- Sournia, A. & Ricard, M. 1976a. Données sur l'hydrologie et la productivité du lagon d'un atoll fermé (Takapoto, Iles Tuamotu). *Vie et Milieu* 26:243-279.
- Sournia, A. & Ricard, M. 1976b. Phytoplankton and its contribution to primary productivity in two coral reef areas of French Polynesia. *J. exp. mar. Biol. Ecol.* 21:129-140.
- Strickland, J.D.H. & Parsons, T.R. 1972. A practical handbook of sea-water analysis. *Fish. Res. Board of Canada* 167: 310 pp.
- Takahashi, M. & Bienfang, P.K. 1983. Size structure

of phytoplankton biomass and photosynthesis
in subtropical Hawaiian waters. *Mar. Biol.*
76: 203-211.

Yentsch, C.S. & Menzel, D.W. 1963. A method for the
determination of phytoplankton chlorophyll
and phaeophytin by fluorescence. *Deep-Sea*
Res. 10: 221-231.