PART II. NUTRIENTS, PARTICULATE ORGANIC MATTER, AND PLANKTONIC AND BENTHIC PRODUCTION OF THE TIKEHAU ATOLL (TUAMOTU ARCHIPELAGO, FRENCH POLYNESIA)

BY

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NUTRIENTS IN OCEANIC AND LAGOONAL WATERS

Matter and energy budgets for coral reefs, their components, and the world around them can, do, and must balance in a theorical context (Smith and Kinsey, 1988). In this paper, we will try to establish nitrogen, phosphorus and silica budgets between ocean and lagoon waters of Tikehau atoll in the purpose to learn more about the functioning of coral reef lagoons. Nutrient concentrations (dissolved components and particulate organic matter) were measured in the lagoon and in the surrounding oceanic surface waters between 1983 and 1987.

DISSOLVED COMPONENTS

Ocean waters

Five oceanic stations shown on Fig. 1 have been sampled to a 500 m depth. At the most remote ocean station, OS7 (considered as representative of oceanic conditions), the upper 50 m surface layer displayed the characteristic temperature (29.5 °C) and the salinity (35.5 ‰) of oceanic waters. Below this superficial layer (120 to 150 m) a temperature of 25 °C and a maximum salinity of 36.2 ‰ were recorded. Nutrient profiles were typical of offshore oceanic waters, with a very low nutrient concentration down to 200 m depth. As summarized in Fig. 1, nutrient concentrations increased to 15 mmol NO_3 m^{-3} and 2.5 mmol PO_4 m^{-3} at 500 m.

The nitrite concentration displayed a maximum at 175 m (0.1 mmol m^{-3}). Nutrient concentrations in the upper 200 m proved to be higher at the stations located in the immediate vicinity of the atoll.

The atoll therefore seems to disturb the standard vertical profiles of nutrient observed at station OS7, which in turn, results in an enrichment of nitrogen and phosphorus in the euphotic layer. The enrichment is probably due to a turbulent vertical mixing caused by the atoll mass effect, i.e. by internal waves (so, Andrews and Gentien , 1982, consider upwelling to be a source of nutrients for the Great Reef ecosystem) and also, perhaps, by an up surge of deep waters from the atoll coral base as hypothesized by Rougerie and Wauthy (1986).
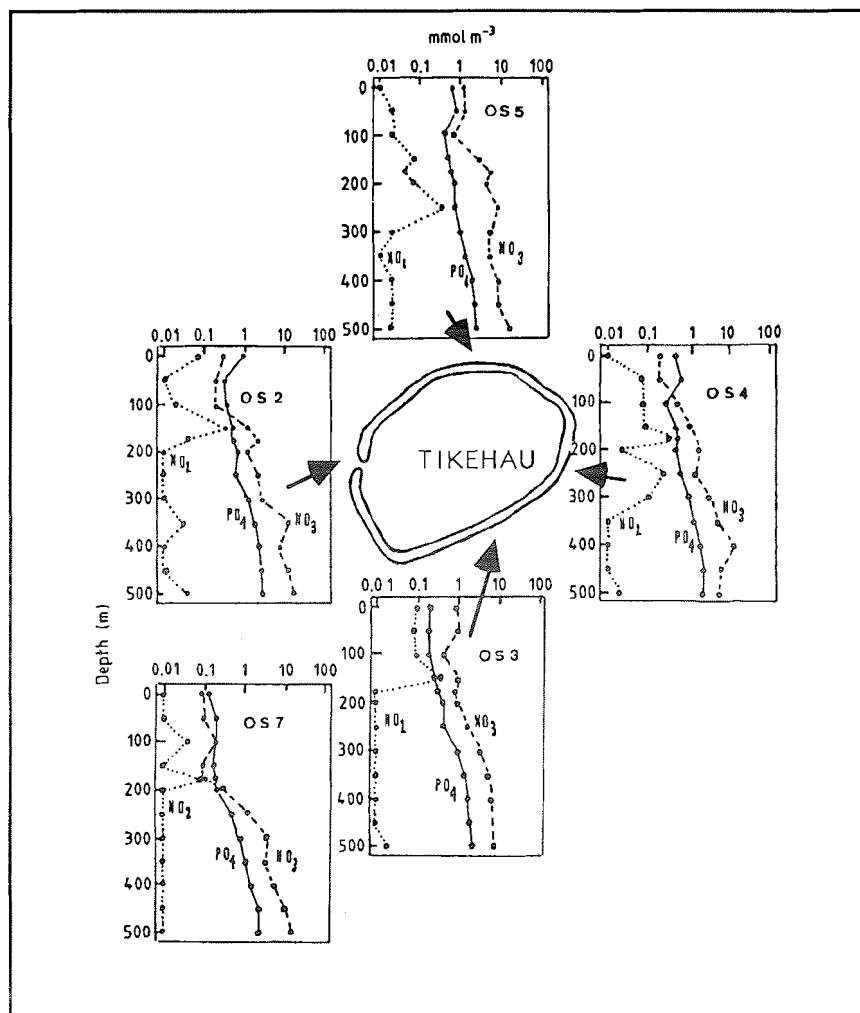
Fig. 1 : Inorganic nutrient concentration profile (mmol m^{-3}) at oceanic stations near the Tikehau Atoll (from Charpy-Roubaud *et al.*, 1990).

Table 1 : Summary of concentrations (mmol m^{-3}) of nutrients, dissolved organic phosphorus (DOP), and dissolved organic nitrogen (DON) in the lagoon of Tikehau (s : standard deviation, (n) : number of samples) (from Charpy-Roubaud *et al.*, 1990).

Variable	Range	Mean	s	(n)
NH_4	0.14 - 9.11	2.10	1.95	(96)
NO_2	0.01 - 0.18	0.02	0.03	(180)
NO_3	0.01 - 0.83	0.08	0.12	(184)
DON	0.40 - 8.20	1.80	2.39	(93)
PO_4	0.01 - 0.89	0.16	0.13	(232)
DOP	0.01 - 1.47	0.39	0.24	(142)
SiO_2	0.07 - 1.72	0.83	0.42	(130)

Lagoonal waters

The average nutrient concentrations listed in Table 1 were not unusual, being of the same order of magnitude as the standing stock nutrient concentrations in coral-reef waters as reviewed by Crossland (1983).

Nutrient concentrations vary considerably with time. NH_4, PO_4 and SiO_2 concentrations were twice as high in 1985 as in other years. The average monthly NO_3 count lays close to the detection limit (between 0.01 and 0.1 mmol m^{-3}), except in February (0.24 $\pm$ 0.06 mmol m^{-3}) and August (0.14 $\pm$ 0.05 mmol m^{-3}). The monthly average value of PO_4 varies in a spread of 0.1 to 0.2 mmol, except in January (0.4 $\pm$ 0.1 mmol). Concentrations of nutrients were found to be homogeneous throughout the lagoon.

PARTICULATE ORGANIC MATTER (POM)

Charpy (1985) emphasized that the particulate organic matter (POM) content of the water column appears to be a good indicator of lagoon productivity. Measurements of deposition rates of organic material are very important. Nutrient requirements for lagoonal production may be met partially through recycling autochthonous material in sediments. One of the principal factors which governs the rate of nutrient regeneration from sediments is the amount of organic matter incorporated into these sediments from the overlying waters (Koop and Larkum, 1987).

POM in oceanic waters

Table 2 : Cruises between 1983 and 1985 in oceanic waters near Tikehau Atoll.

date	July 1983	November 1983	March 1984	November 1985
Name	TIK3	TIK5	TATI	TATU
Stations	OS2, OS5	OS2, OS3, OS4, OS5	OS2, OS3, OS4, OS5	OS2
Depths (m)	0, 25, 50, 100, 150, 200	0, 25, 50, 75, 100, 125, 150, 175, 200, 250	0, 50, 100, 125, 150, 175, 200	0, 25, 50, 75, 100, 125, 150, 200
Parameters	Chl a, Phaeo a	Chl a, Phaeo a, ATP	Chl a, Phaeo a, ATP, POP	Chl a, Phaeo a, ATP, POP, POC, PON

ATP concentrations are greatest in the upper 100 m of ocean waters ranging from 0.05 to 0.12 mg m^{-3}. No significant differences among sampling stations were detected.

Chlorophyll profiles displayed in Fig. 2 show a deep maxima between 100 and 200 m depth. Concentrations recorded in March 1984 reached 0.24 mg m^{-3} at these depths whereas surface concentrations were five time smaller (0.05 mg m^{-3}).

Particulate organic phosphorus, carbon and nitrogen (respectively POP, POC and PON) profiles are shown on Fig. 3. Concentrations generally decrease with depth. The high concentration values that were observed in surface waters in March 1984 were probably due to abundant detritus export from the reef flat and thus overestimated.
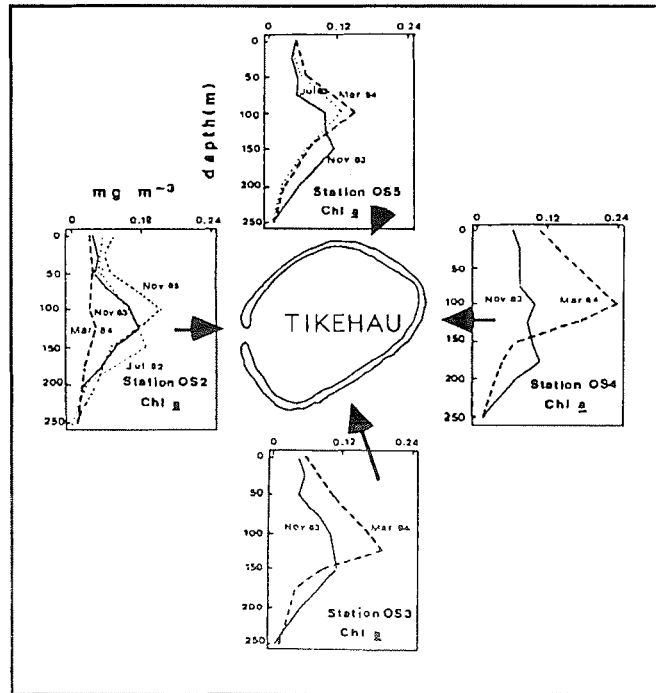
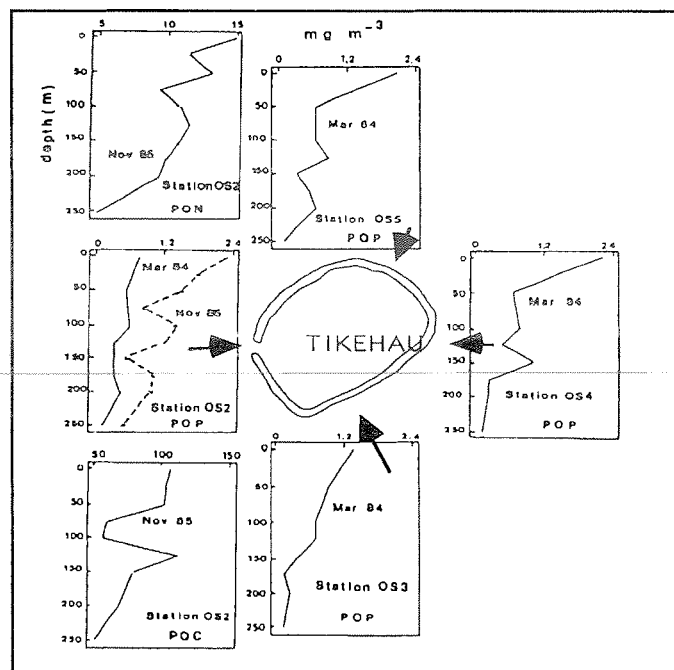Fig. 2 : Chlorophyll a (chl a) concentration profiles (mg m^{-3}) at oceanic stations near Tikehau .

Fig.3 : Particulate organic phosphorus, carbon and nitrogen (POP, POC and PON) concentration profiles (mg m^{-3}) at oceanic stations near Tikehau (from Charpy and Charpy-Roubaud, 1991).

POM in the lagoon and oceanward the pass.

Average POC, PON, POP, ATP and pigments concentrations in samples taken between 1983 and 1987 in the lagoon (all stations and depths included) are presented in Fig. 4. The level of POM concentration observed at OS1 is correlated with the level of POM concentration observed in lagoonal waters. This is more evident for POC ($r = O.94$, $p = 0.0005$) and PON ($r = 0.86$, $p = 0.006$) but is also true for chl a ($r = 0.59$) and POP ($r = 0.50$). Therefore, the POM water content of OS1 was influenced by the lagoonal discharge. Quasim and Sankaranaryanan (1970) observed a similar feature : POC concentration in surface oceanic waters at 2 km from the Karawatti atoll (Laccadives) was 3 times higher than POC concentration 12 km seawards. We can estimate the average POC and PON concentrations in oceanic waters when the lagoonal discharge is zero by the intercepts of the regression lines : POC concentration at OS1 versus POC concentration in the lagoon (58 ± 26 mg C m^{-3}), and PON concentrations at OS1 versus PON concentration in the lagoon (6 ± 3 mg N m^{-3}). The POP concentration in oceanic waters can be calculated from the POP average concentration measured in the upper 100 m (0.7 ± 0.3 mg P m $^{-3}$)

Table 3 : Average concentrations of POM in the lagoon of Tikehau and oceanward the pass.

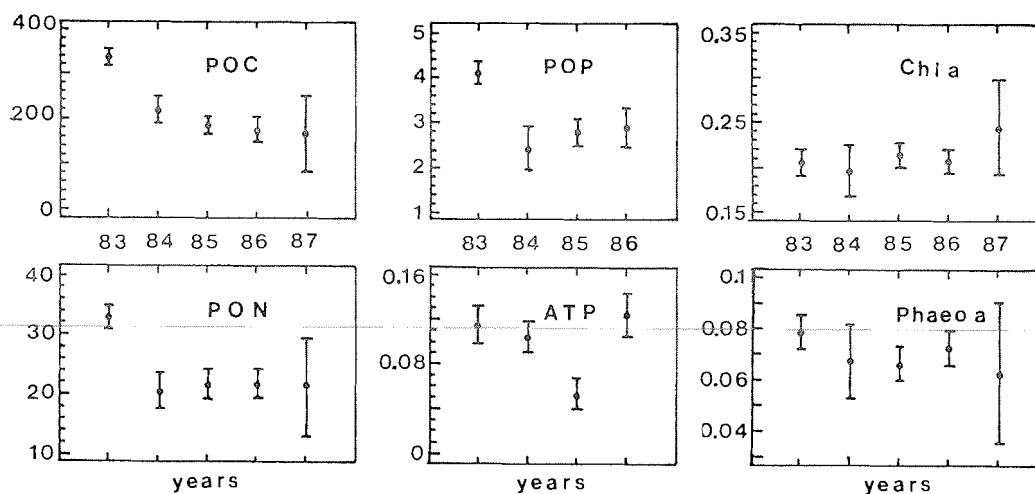|	Chl a mg m^{-3}	Phaeo a mg m^{-3}	ATP mg m^{-3}	POC mmol m^{-3}	PON mmol m^{-3}	POP mmol m^{-3}	C/N at : at
Ocean							
Mean	0.06	0.03	0.02	52	6	0.7	8.7
SE	0.004	0.003	0.004	3	0.5	0.1	0.4
(n)	58	58	13	31	31	41	31
Lagoon							
Mean	0.18	0.07	0.11	192	21	2.7	9.1
SE	0.003	0.002	0.005	5	1	0.1	0.2
(n)	409	409	162	290	289	224	289

Fig 4 : Mean ($\pm$ SE) POC, PON, POP, ATP and pigment concentrations in the lagoon of the Tikehau atoll as function of year (expressed in mg m^{-3}).

Concentrations are found to vary with depth in response to a resuspension of detritus that accumulates in deep waters. On the average, POC concentrations recorded near the lagoon floor were 37% higher than those measured in surface water, whereas PON were 27% greater, 31% for POP, 32% for Chla, 43% for phaeo a and 1% for ATP. The average POM concentrations in the lagoon may be strongly influenced by climatological events such as storms or hurricanes. The average POC concentration in the lagoon was unusually high in July 1983 (466 mg m^{-3}) after cyclones that occured at Tikehau in early 1983.

POM size and composition

Size repartition of the POM is summarized in Table 4. On the average, 50% of the POM is made up of suspended particles smaller than 5 µm but this percentage can vary considerably : *i.e.* : 72 to 90% of the POM was in the 0.7-3 µm size class in April 1986. This discrepancy is probably due to the use of Nucleopore filters instead of Millipore filters. New results at different times have shown that 80 % of the POM pass through a Nucleopore 3 µm. Therefore, the average POM passing through 5 µm is probably much higher than 50 %.

Table 4 : Means (± SE) of POM passing through a 5 µm (1984 and 1985) or 3µm (1986) pore filter as a percentage of total POM at the Faufaa station, south of the Tikehau lagoon. Standard error of samples taken at same dates are given (from Charpy and Charpy-Roubaud, 1991).

Date	Chl a (%)	Phaeo a (%)	ATP (%)	POC (%)	PON (%)	POP (%)
23 Nov 1984	-		47 ± 2	35 ± 0	24 ± 1	75 ± 19
24 Nov 1984	66 ± 5	-	48 ± 26	61 ± 7	57 ± 3	88
2 Apr 1985	57 ± 25	-	-	43 ± 14	55 ± 23	27 ± 7
9 Apr 1985	32 ± 6	40 ± 35	68 ± 11	33 ± 11	46 ± 16	47 ± 20
12 Jul 1985	57	29 ± 17	30	35	32	29
13 Aug 1985	25 ± 4	34	20 ± 5	-	-	24 ± 12
7 Apr 1986	92 ± 5	74 ± 3	75 ± 24	81 ± 1	77 ± 13	99 ± 2
Average ± SE	50 ± 6	45 ± 8	46 ± 6	50 ± 6	54 ± 5	49 ± 6

Phytoplankton account for 35% of the living carbon with a strong dominance of cyanobacteria while heteroflagellates and ciliates account for 6% of the living carbon (fig.5) (Blanchot *et al.*, 1989).
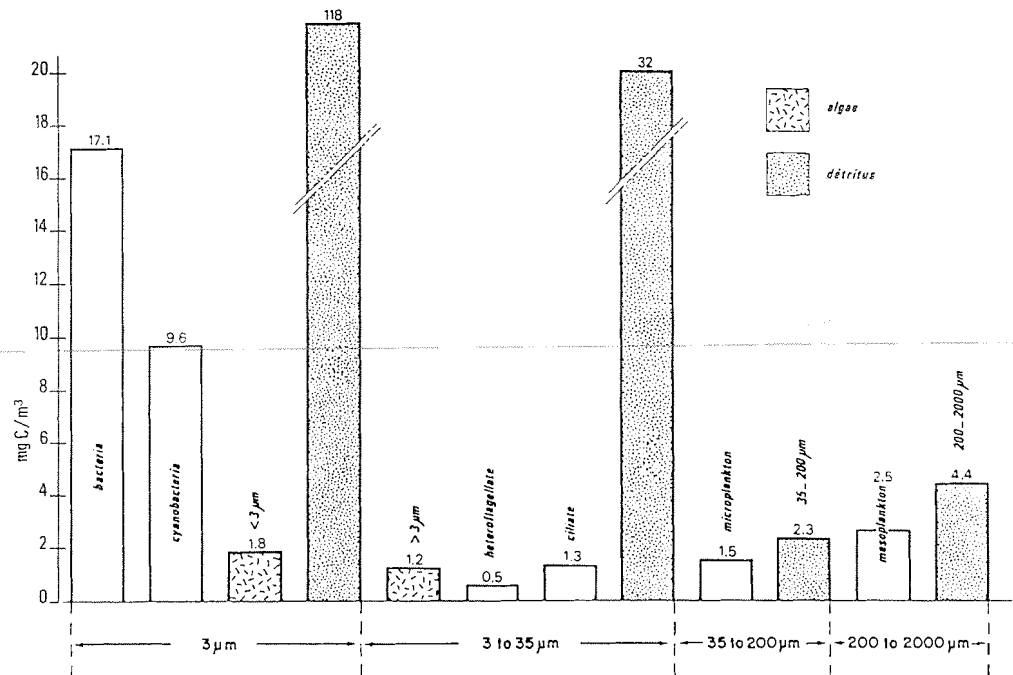

Fig. 5 : Size distribution of organic seston weight (mg C m⁻³) for different size-classes of seston (<3 µm, 3 to 35 µm, 35 to 200 µm, 200 to 2000 µm) in the Tikehau lagoon. Data for living C of 35 to 200 µm and 200 to 2000 µm size class were calculated using ATPx125 (from Blanchot *et al.*, 1989).

Sedimentation of Particles

Sedimentation rates as well as settling velocities of POM were studied by setting a sediment trap far enough from the bottom (5 m) to collect only materials sinking from surface layer. Results listed in Table 5 show that the sedimentation rate of POC and PON (*i.e.* : 350 and 36 mg m^{-2} d^{-1}) are close to the values given by Taguchi (1982) in Hawaii. Sedimentation rates at Tikehau are however four times lower than the values for organic deposition in the lagoon of One Tree Island (Australia) given by Koop and Larkum (1987) and are also 2.4 times lower than the POC deposition rate found by Chardy and Clavier (1989) in New Caledonia.

The mean sedimentation rate of total pigments (*i.e.* : 0.23 mg m^{-2} d^{-1}) is four times lower than sedimentation rate given by Taguchi (1982) in Hawaii and four times lower than Chl a deposition rate calculated from Chardy and Clavier (1989) in New Caledonia.

The average POC:PON:POP ratio on a mass basis in trapped material was 117:12:1 while the ratio in suspended material estimated during trapping experiment was 68:7:1. The loss of phosphorus in trapped particles indicates that organic matter was dead and that a non-negligible part of POM is mineralized in the water column. This was latter confirmed by ATP measurements in trapped materials which were all zero.

Table 5 : Mean (16 data) trapping rate (TR ; mg m^{-2} d^{-1}), settling velocities (SV ; m d^{-1}) and C:N:P ratio (w/w) of trapped material measured at Faufaa station, south of the Tikehau lagoon.
In brackets, coefficient of variation (%)

Chl a		Phaeo a		POP		POC		PON		C:N:P
TR	VS	TR	VS	TR	VS	TR	VS	TR	VS	
0.11	0.6	0.12	1.4	3.2	1.7	350	2.6	36	2.2	117:12:1
(66)	*(72)*	*(67)*	*(74)*	*(78)*	*(25)*	*(94)*	*(116)*	*(97)*	*(104)*	

Origin of lagoonal POM

Findings of Charpy and Charpy-Roubaud (1990b) indicate that the detritus pool (84% of POC) originates in lagoonal primary production whereas detritus reef flat export toward the lagoon is insignificant. The phytoplankton production ingested and then excreted as fecal pellets by zooplankton cannot alone explain the levels of POC sedimentation rate. Export of POM from lagoon pinnacle reefs may thus be the other major POC source.

NUTRIENT BUDGET

Fluxes between lagoon and ocean can be estimated by :

$$\text{Flux (mmol m}^{-2}\text{ d}^{-1}) = F \setminus f(Cl\text{-}Co,Ls)$$

Where F is the annual average flow through the pass and the reef-flat spillways (6 10^8 m^{-3} d^{-1} in Lenhardt, 1991), Ls is lagoon surface (4.2 10^8 m^2) and Cl and Co are concentration of total nitrogen (ΣN), total phosporus (ΣP) or silicate in the lagoon - Cl -and ocean - Co - ($\Sigma N = NO_2+NO_3+NH_4+DON+PON$ and $\Sigma P = PO_4+DOP+POP$ where DON and DOP are dissolved organic nitrogen and phosphorus concentrations). Average concentrations in the lagoon and ocean are recapitulated in Table 6.

If we compare this data with the water composition at Christmas Island given by Smith *et al.* (1984), we observe that Tikehau surrounding waters present similar ΣP concentration but lower ΣN and silicon concentrations. Inside the lagoon, nutrient concentrations are quite similar exept for the silicon which was 3.5 times higher in Christmas Island.

Table 6 : Average concentrations ± 95% confidence intervals (mmol m^{-3}) of total nitrogen (ΣN), total phosphorus (ΣP) and silicate in oceanic (Co) and lagoonal waters (Cl) (from Charpy-Roubaud et al., 1990).

Nutrient	Ocean waters	Lagoon waters
NH$_4$	0.80	1.90
NO$_2$	0.04	0.02
NO$_3$	0.30	0.09
DON	2.30	4.60
PON	0.40	1.40
ΣN	3.80 ± 1.30	8.01 ± 0.90
PO$_4$	0.38	0.16
DOP	0.26	0.39
POP	0.02	0.10
ΣP	0.66 ± 0.12	0.65 ± 0.06
SIO2	1.00± 0.20	0.80± 0.40

Nitrogen budget

During their crossing over the reef-flat and their residence in the lagoon, oceanic waters become impoverished in NO$_2$ and NO$_3$ and enriched in NH$_4$ and organic nitrogen. The total nitrogen concentration in the lagoon is roughly twice as great than in the ocean (i.e. : 8.0 mmol N m^{-3} vs 3.8 mmol N m^{-3} in ocean). Therefore, according to the flux equation, the nitrogen concentration of oceanic water increases at a rate of 0.6 mmol N m^{-2} d^{-1} during its residence time in the lagoon.

Increase in the nitrogen content of water flowing above the reef-flat is attributed to gaseous nitrogen fixation mostly by cyanobacteria of which a great variety occur on limestone substrata of coral reefs. At Tikehau, large quantities of cyanobacteria (i.e. : 150,000 cells ml^{-1}) were recorded in the lagoon water column by Blanchot et al. (1989). Charpy-Roubaud et al. (1989) have estimated that their productivity, added to that of benthic cyanophycean communities, is 0.69 g C m^{-2} d^{-1}. This carbon production would require nitrogen assimilation of approximately 3.6 mmol N m^{-2} d^{-1}, part of which could originate from dissolved molecular nitrogen.

Phosphorus budget

Mineral phosphorus (PO$_4$) water content decreases and organic phosphorus (DOP+POP) content increases during crossing of oceanic waters over the reef edge and during the residence time in the lagoon. Depletions of reactive phosphorus below oceanic levels were also observed by Smith (1984) and Smith and Jokiel (1975) in Christmas Island and Canton Atoll lagoons, both located in the Pacific. The total phosphorus concentration in the lagoon (ΣP = 0.65 mmol P m^{-3}) is of the same order of magnitude than phosphorus in the surrounding oceanic waters (ΣP = 0.66 mmol P m^{-3}). The phosphorus budget therefore appears to be well balanced.

The pattern of production emerging from all the foregoing discussion is that the high primary production over the reef and in the lagoon results from an input of nitrate and phosphate from enriched oceanic waters, from a great gaseous nitrogen fixation by cyanobacteria and from the mineralization of organic compounds in the lagoon.

NUTRIENTS IN SEDIMENTS OF THE LAGOON : FIRST RESULTS

Nutrient mineralization may occur in the water column (excretion and bacterial metabolism), at the sediment-water interface (hereafter expressed SWI) or within the sediments. The importance of recycling of autochtonous material at SWI and within sediments was estimated by measuring nutrient fluxes at the sediment-water interface. Two different approaches were used in order to assess these fluxes. These were : 1) direct measurement which uses a benthic chambers technique described by Hall (1984), carrying out the experiments in oxic (supply with oxygen) and anoxic (asphyxiation) dark conditions and 2) calculations through measurements of chemical gradients close to SWI, in peeper, following method previously described by Hesslein (1976). The results presented here have to be considered as preliminar.

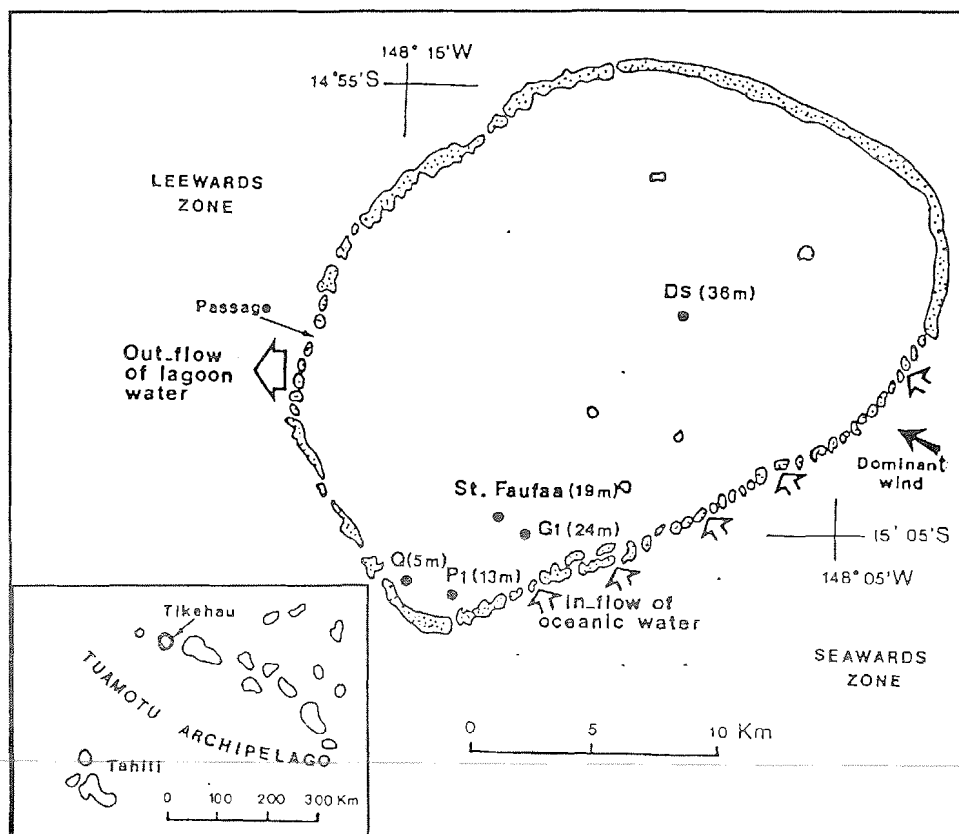Nutrients in sediment were studied at four sampling stations shown in Fig. 6.

Fig. 6 : Location of sediment flux sampling stations (e.g. : Ds, G1, Q, P1 and Station Faufaa).

Dark benthic chambers were used at stations Q and P1 because of the shallowness of these sites. In order to compare fluxes measured in oxic and anoxic conditions, the only analytical results taken into account are those obtained after oxygen depletion was achieved in the non-O_2 supplied chamber (hereafter termed asphyxiated chamber). Fluxes (F in μmol m^{-2} d^{-1}) can be estimated from the slope dC/dt of a plot of concentrations versus time multiplied by the ratio of supernatant-water volume V to chamber area S (V = 0.025 m^3; S = 0.11m^2). The formula is :

$$F = \f(dC,dt) \times \f(V,S)$$

The *in situ* peeper sampling method was used at three stations (DS, G2 and P1 see Fig. 6)

Benthic chambers

Variations of the chemical composition of water enclosed in the benthic chambers *vs* time is shown on Fig. 7. NO_3 and NO_2 concentrations do not appear because they were below the detection limit (<1 mmol m^{-3}).
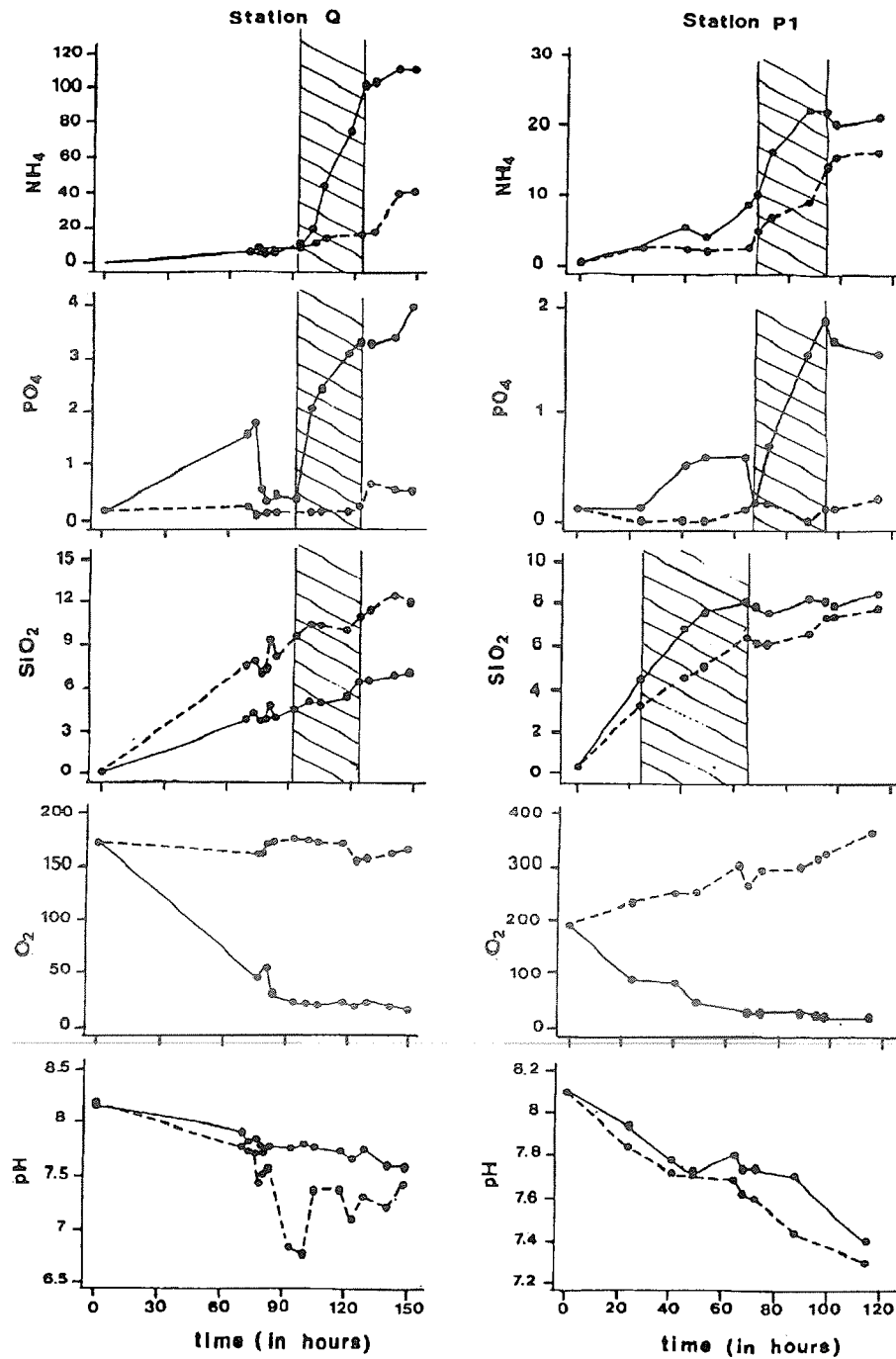

Fig. 7 : Evolution of inorganic nutrients (mmol m^{-3}), dissolved O_2 (mmol m^{-3}) and pH of overlying water inside asphyxiated and oxygenated dark benthic chambers at station Q and P1. Nutrient fluxes are calculated in the shaded area.

Station Q : In the asphyxiated chamber, O_2 concentration decreases with time and was less than 30 mmol m^{-3} after 90 hours of incubation while nutrient concentrations sharply increased. In the oxygenated chamber, a slight increase in concentration was observed for NH_4 and SiO_2 , but the PO_4 concentration remained nearly constant at a very low level. The concentration plateau that was observed after 125 hours was most likely due to a steady state occuring between enclosed and interstitial waters. Therefore fluxes are calculated between 90 and 120.25 hours, figured by the shaded area on Fig. 7.

Station P1 : Oxygen depletion in asphyxiated chambers occured after 69 hours. The same trends were observed for PO_4 and NH_4 like at station Q in both chambers. Silica concentrations exhibit a plateau after 65 hours of incubation. NH_4 and PO_4 fluxes were therefore calculated between 68.75 and 95.25 hours while the SiO_2 flux was calculated between 24 and 64.5 hours.

The foregoing drives to notice that an increase in NH_4 and PO_4 occurs in asphyxiated chambers at both sites. When oxygen concentration is preserved, a slight increase occurs in NH_4 while PO_4 remains constant at a very low level. Dissolved silica exhibit similar patterns at both sites and do not seem to be related to oxic/anoxic conditions. Calculations of nutrient fluxes are summarized in Table 7.

Table 7 : Dissolved nutrient concentration increases (dC in $\mu mol\ m^{-3}$) during dt = 30.25 hours at station Q and dt = 26.5 hours at station P1 and fluxes (F in $\mu mol\ m^{-2}\ d^{-1}$) from the sediments of the Tikehau lagoon. asph. = asphyxiated chamber; oxy. = oxygenated chamber.

Station	param.	NH4 asph.	NH4 oxy.	PO4 asph.	PO4 oxy.	N/P asph.	N/P oxy.	SiO2 asph.	SiO2 oxy.
Q	dC	92.7	6.6	2.9	0.21			1.8	1.5
	dt	30.25	30.25	30.25	30.25			30.25	30.25
	F	16.71	1.18	521	38	32	31	329	274
P1	dC	12.2	9.2	1.7	0.0			4.7	3.1
	dt	26.5	26.5	26.5	26.5			40.5	40.5
	F	2.25	1.89	356	0	7		630	411

As a general trend, fluxes of nutrients are higher in anoxic than in oxic conditions. This is more obvious for PO_4, of which fluxes were close to 0 when oxygen was present but when the oxygen level was less than 0.30 mmol m^{-3}, they reach between 356 and 521 $\mu mol\ m^{-2}\ d^{-1}$. These differences can be interpreted as the result of biological and/or chemical processes. The biological process can be summarized as follows : the onset of anoxia allows some micro-organisms to metabolize organic material in the upper part of the sediment column (i.e. : increase in NH_4 flux may be due to amnonifier metabolism). Anoxia can possibly kill aerobic micro-organisms at SWI which in natural conditions have a dark uptake of N and P without any silica requirement. The chemical process can be that in oxic conditions, scavenging of P onto $FeOOH_2$ is commonly observed in marine sediments. Therefore, fluxes measured in asphyxiated chambers probably overestimate actual fluxes while those obtained when oxygen is present can estimate a nutrient availability for lagoonal primary producers.

Pore water

Pore-water profiles of nutrients display significant concentration gradient with depth as shown in Fig. 8. These gradients are maximum within the first top centimeters and correlated with the decrease in pH. Pore-water nutrient concentrations increase with depth, being greater at deep sampling stations. H_2S appears to be below the SWI, at about 1 cm depth at station DS and 5 cm at P1 and G2.
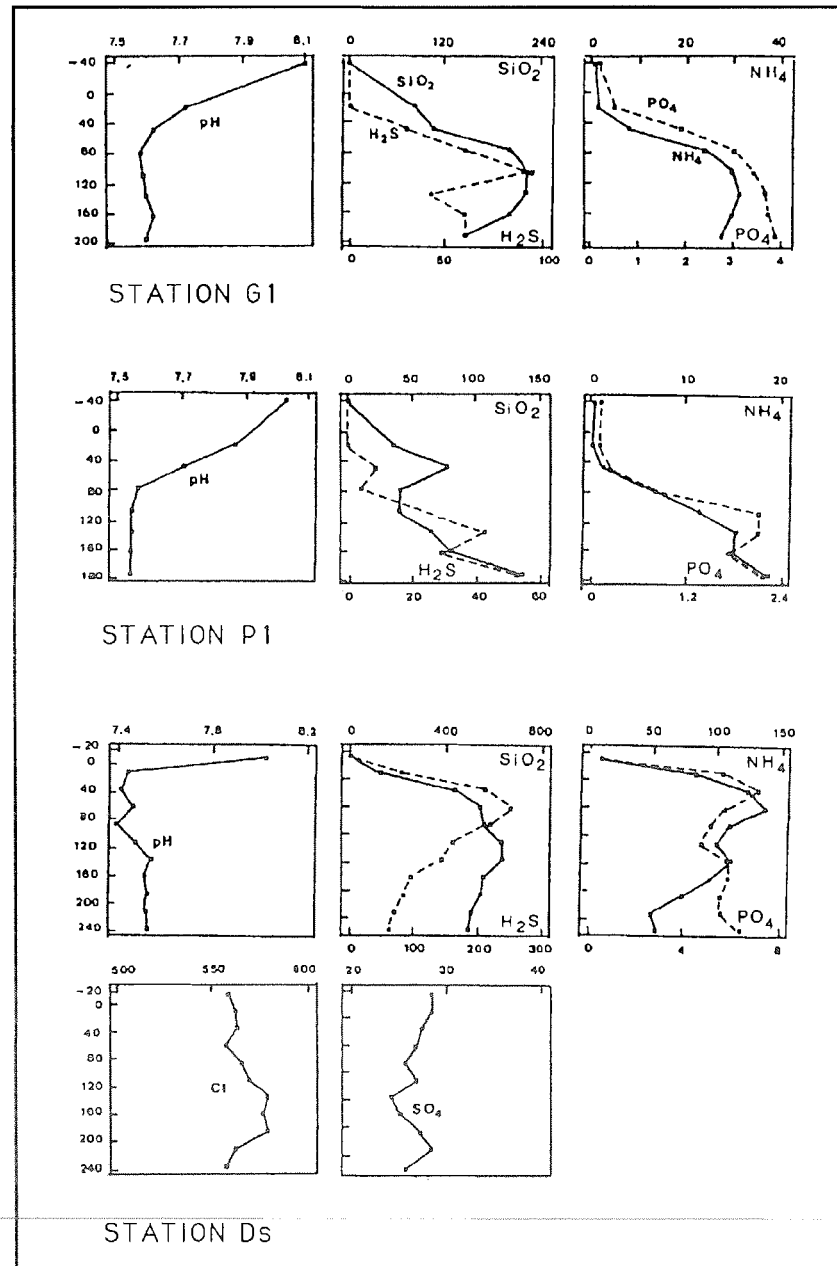
Fig. 8 : Variations of pH, inorganic nutrients (μmol m^{-3}), hydrogen sulphide (μmol m^{-3}), chloride (mmol m^{-3}) and sulphate (μmol m^{-3}) in sediment pore-waters at various stations (G1, P1 and Ds) in Tikehau lagoon .

The acidification of pore water downward in the sediment core, reflects the increase in total dissolved CO_2 related to mineralization processes. At the top of the sedimentary column, dissolved O_2 is the main electron acceptor. Oxygen is replaced downward by sulfate and H_2S appears in profiles owing to sulfate reduction. Deeper, there is a decrease in H_2S concentrations which is probably linked to a chemical control by FeS precipitation.

Positive gradient of concentrations close to SWI allow diffusion of nutrients from medium pore water to overlying sea water. PO_4 concentrations are lower than NH_4 concentrations (*i.e.* : 7 mmol m^{-3} PO_4 against 137 mmol m^{-3} NH_4). However, phosphate has been shown to strongly adsorb on calcium carbonate. This has been used to explain why calcium carbonate-rich sediments contain low concentrations of dissolved phosphate in their pore waters (Krom and Berner, 1980).

The calculation of fluxes (F in μmol m^{-2} d^{-1}) using pore water data can be calculated after Fick 1st law. The equation can be written :

$$F = \emptyset \times Ds \times \backslash f(dC,dz)$$

where $\emptyset$ is the interconnected porosity estimated at 0.70 ± 0.01, Ds is the *in situ* diffusion coefficient in m^2 d^{-1} where tortuosity is taken into account, dC/dz is concentration gradient in μmol m^{-4} when z tends toward zero. Results are presented in Table 8. They show that for each nutrient, flux increases with lagoon depth.

Table 8 : Average $\pm$ SE of dissolved nutrient fluxes calculated with pore-water gradient concentrations (μmol m^{-2} d^{-1}).

Station	NH_4	PO_4	SiO_2
Ds	493 ± 192	13 ± 5	466 ± 164
G1	11 ± 5	0.5 ± 0.3	164 ± 68
P1	0	0	68 ± 27

Comparisons between calculated fluxes with pore water data and observed fluxes in benthic chamber

Observed fluxes for ammonium in oxygenated and asphyxiated chambers are much greater than fluxes calculated using pore water data (which are close to 0). Observed fluxes for PO_4 are higher in asphyxiated chambers. Observed fluxes for Si are 6 to 9 times higher than calculated fluxes. Therefore, diffusion processes through SWI are unable to explain NH_4, PO_4 and Si fluxes observed in an asphyxiated chamber, but can explain the light PO_4 flux and 17% of Si flux measured in oxygenated chamber. The enhancement of transport across the interface may be due to bioturbation of sediment located in the upper part of sedimental layer. Nutrients coming into benthic chambers are then uptaken following different rates depending on oxygen conditions and on the elements considered ; P is probably uptaken more quickly than N and Si. So in this kind of environment, it seems more realistic to define a dispersion coefficient rather than a diffusion one. For dissolved silica, the dispersion coefficient is 5.7×10^{-5} cm^2 s^{-1}, about 10 times greater than difusion coefficient Ds (*i.e.* : Ds = 6.5×10^{-6} cm^2 s^{-1}). Therefore, nutrient fluxes measured in oxygenated chamber are assumed representative of real fluxes.

LAGOON PRIMARY PRODUCTION

PHYTOPLANKTON PRODUCTION

Phytoplankton of coral-reef ecosystems have often been considered as a low primary producer since the overwhelming majority of coral-reef studies were carried out in shallow ecosystems. In atoll lagoons, the reef area *vs* the total area (reef and lagoon) ratio is low. Lagoonal plankton may thus be a major contributor to total primary productivity of the ecosystem as a whole.

Carbon production

Table 9 gives an account of the average of mean carbon assimilation rates (hereafter expressed AC) by depth intervals measured through an estimation of ^{14}C and ^{32}P assimilation rates. The average AC is clearly related to depth, being higher in the surface layer than at other depths. No photoinhibition at high light intensity occur.

Table 9 : Average carbon assimilation rate (AC ; mg C m^{-3} h^{-1}) and assimilation number (AN ; mg C mg^{-1} Chl-a h^{-1}) in relation with depth (n = number of samples) (from Charpy-Roubaud *et al.*, 1989).

Depth (m)	n	AC	AN
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

Phytoplankton production integrated up to 15 m depth drops during May, June and August. This decrease is correlated with light energy reduction that occurs in winter of the southern hemisphere. Phytoplankton biomass is low (*e.g.* : 0.18 ± 0.01 mg Chl-a m^{-3}) but this is typical of coral reef ecosystems. Biomass is greater in May, June and July while conversely, production rates are lowest. Concentrations in the lagoon are approximately three times greater than those found in surface oceanic waters.

Daily phytoplankton production estimated for each bathymetric intervals reaches an average of 0.44 g C m^{-2} d^{-1} for the entire lagoon, equivalent to 0.012 g P m^{-2} d^{-1}. This value is high compared to the low phytoplankton biomass measured. The representative assimilation number estimated from the average hourly production (*i.e.* : 44 mg C m^{-2} h^{-1}) and the average chlorophyll integrated over 25 m (4.86 mg m^{-2}) is 9.8 mg C mg Chl a^{-1} h^{-1}, a value characteristic of small-sized plankton. The assimilation number is conspicuously high in the surface layer (*i.e.* : 21 mg C Chl-a h^{-1}). Approximately 1.4% of daily production is lost by sedimentation of organisms while the exit of particles out of the lagoon represents a loss of 0.2%.

Phytoplankton biomass and composition

Charpy (1985) and Blanchot *et al.* (1989) had previously shown that a great part of lagoon phytoplankton is made up of cells smaller than 5 µm with cyanobacteria dominating. Cyanobacteria can contribute to up to 75% of the carbon production of plankton primary producers. Table 10 allows comparison between phytoplankton production of waters pre-filtered on Nucleopore 5µm and of waters unfiltered. The percentage of total production due to phytoplankton of a size smaller than 5µm varies in a spread of 13 to 90% with average at $38 \pm 10\%$, whereas the percentage of 0-5 µm chlorophyllian organisms is $61 \pm 12\%$ on the average in unfiltered waters. It appears that the smallest cells are being differentially ruptured to a greater extent than large cells, leading to an underestimation of carbon uptake (but not chlorophyll content) by the smallest cells.

Table 10 : Phytoplankton Carbon assimilation (mg m^{-2} h^{-1}) in samples filtered on 5µm (AC<5µ) and without filtrations (ACt); AN = assimilation number (mg Chl a^{-1} h^{-1}); %AC = AC<5µx100/ACt; %Chl = percent of chlorophyll passing through 5 µm filter (from Charpy-Roubaud *et al.*, 1989).

Date	St.	Depth	ACt	AC<5µ	%AC	ANt	AN<5µ	%Chl
24 Jul 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
26 Jul 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
23 Nov 83	6	0	5.6	2.5	44	18.7	12.4	67
24 Nov 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
27 Jan 85	6	0	2.2	0.4	18	10.0	3.9	47
12 Jul 85	6	0	4.5	0.6	14	15.4	3.8	54
13 Aug 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
14 Aug 85	6	0	1.2	0.3	25	5.5	3.1	44

Relationship between phytoplankton production and light energy

Phytoplankton production is significantly correlated with light energy. Phytoplankton production (PP in mg C m^{-3} h^{-1}) can be estimated from the equation :

$$PP = 1.29\ Eh^{0.39}$$

where Eh is incidental light energy in E m^{-2} h^{-1}.

MICROPHYTOBENTHIC PRODUCTION

Carbon production

Primary production was estimated by O_2 budget, measured within clear and dark plexiglass domes. In order to assess the influence of light energy on net oxygen production, measurements of O_2 budgets were carried out continuously at various depths. Net O_2 production and light energy were positively correlated (r=0.7, n=91) and thus, daily production (DBP) was estimated by equation :

$$DBP\ (mg\ O_2\ m^{-2}\ d^{-1}) = P_{t-to} \times \backslash f(Ej, Et\text{-}to)$$

where P_{t-to} = net production in mg O_2 m^{-2} during incubation period t-to

Ej = Daily incidental light energy in E m^{-2} d^{-1}

E_{t-to} = Incidental light energy in E m^{-2} d^{-1} during incubation period t-to

The mean hourly respiration rate measured in dark domes was 31 ± 7 mg O_2 m^{-2} with a respiratory and photosynthetic coefficient chosen as being equal to 1 for latter conversion in carbon production. By averaging production by depth intervals, the overall lagoon microphytobenthos production was found to be equal to 0.25 gC m^{-2} d^{-1}. This value is of the same order of magnitude as production values for tropical marine sediments reviewed by Charpy-Roubaud (1988).

Benthic carbon production (BP) can thus be related to incidental light energy (Eh in E m^{-2} h^{-1}) by the equation :

$$BP\ (mg\ C\ m^{-2}\ h^{-1}) = 28.78\ Eh^{0.45}$$

Biomass

Microphytobenthic biomass was measured in 185 samples taken at different stations and at different time of the year. There are considerable variations among sampling stations. The average total chlorophyll biomass is 19.7 ± 1.4 mg m^{-2} whereas the average active chlorophyll is 9.6 ± 1.4 mg m^{-2}. The mean hourly assimilation number estimated from the latter biomass is of 2.6 mg C mg chlorophyll^{-1} h^{-1}. Biomass is significantly higher in the 0-3 m depth interval than in deeper intervals.

COMPARISON BETWEEN PHYTOPLANKTON AND MICROPHYTOBENTHIC PRIMARY PRODUCTION

Fig. 9 shows phytoplankton, microphytobenthic and total primary production by a 5 m depth interval. Total primary production is slightly the same whatever the depth interval is. Phytobenthic production is greater than phytoplankton production within the first 10 meters, being 25 times higher in the 0-5 m depth interval. From 20 m downward, phytoplankton is the major contributor to total primary productivity of the whole ecosytem. On the average, phytoplankton primary production is 1.8 times greater than phytobenthic production.
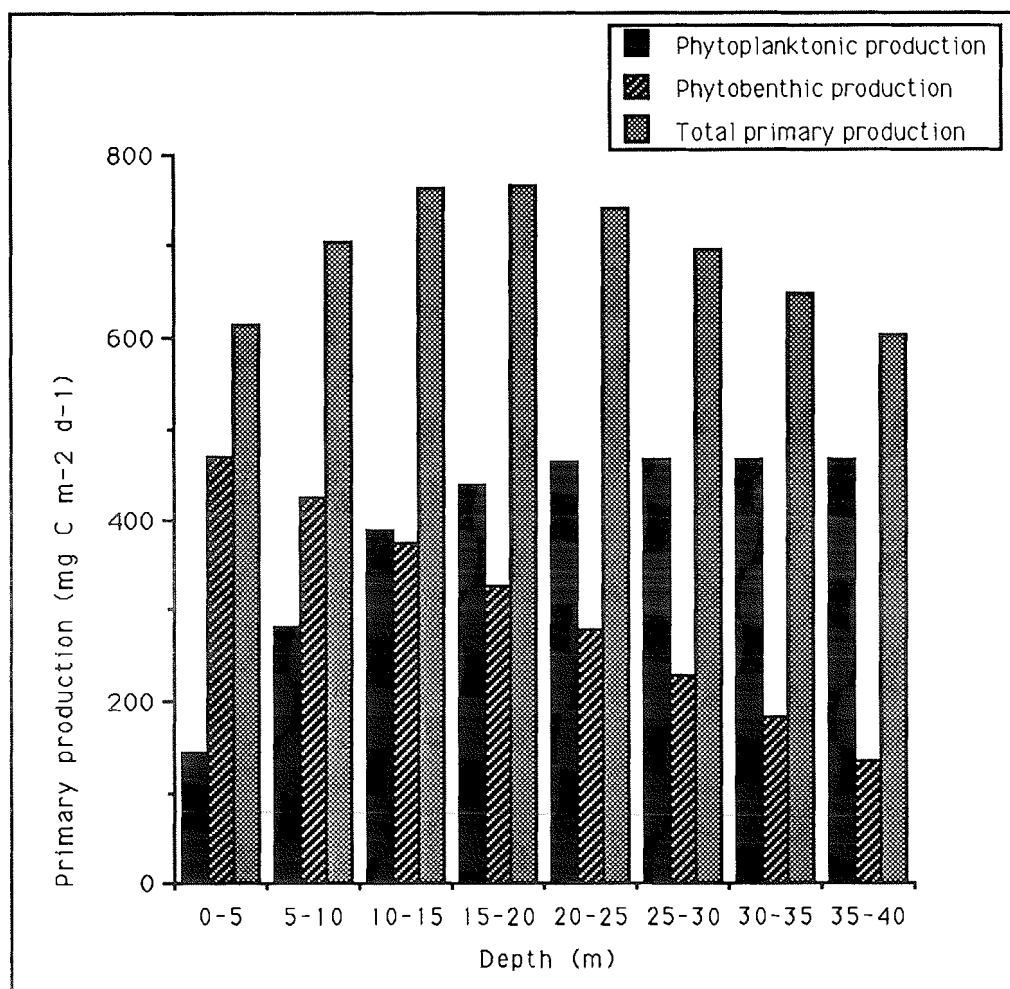
Fig. 9 : Benthic, planktonic and total primary productions in the Tikehau lagoon by a 5 m depth interval (from Charpy-Roubaud, 1988).

RELATIONSHIP BETWEEN LIGHT AND PRIMARY PRODUCTION IN THE LAGOON.

Light energy

Percentages of light energy measured at surface decreases with depth d (m) according to the equation :

$$\% \text{ of incident energy} = e^{(4.45 - 0.06d)}$$

It was measured that 17% of surface light energy reached 25 m (average depth of the lagoon).

Phytobenthos and phytoplankton production

According to the foregoing sections, phytoplankton production (PP) can be related to incidental light energy (Eh) with a standard error of 0.6 mg C m^{-3} h^{-1} by the equation :

$$PP = 1.29 \, Eh^{0.39} \qquad (1)$$

Phytoplankton production per unit volume can then be converted into production per unit area according to the equation :

$$PPd = \int_0^d PPz \, dz \qquad (2)$$

where PPd (mg C m^{-2} h^{-1}) = production at depth d per unit area, PPz (mg C m^{-3} h^{-1}) = production at depth z per unit volume.

Using equation (1) and (2), phytoplankton production is related to light by the equation :

$$PPd = \int_0^d e^{0.254} \, [e^{(4.45-0.06z)}E_{hs} / 100 \,]^{0.39}$$

where Ehs (E m^{-2} h^{-1}) is light energy at the surface.

Similary, the relationship between phytobenthos production at depth d (BPd in mg C m^{-2} h^{-1}) and light energy Ehs at surface level can be written :

$$BPd = 28.78 \, (e^{(4.45-0.06d)}\backslash F(Ehs,100))^{\,0.454} \qquad (3)$$

Predicted plankton and benthic production were calculated at depths between 0 and 36 m (*i.e.* : maximum depth of the lagoon) for different Ehs values observed in natural conditions (1 - 8 E m^{-2} h^{-1}). Results presented in Fig. 10 indicate that phytobenthos production exceeds phytoplankton production in the upper 18 m. The total primary production (PT) is relatively constant with depth and depend primarily on light energy reaching the surface. Therefore, an average PT can be obtained for each Ehs value and subsequently, a linear relation linking PT and Ehs, *i.e.* :

$$PT = 6.5 \, Ehs + 31.5$$

Therefore, daily total production PTd can be calculated assuming a sun time of 10 hours a day by the equation :

$$PTd \, (mg \, C \, m^{-2} \, d^{-1}) = 6.5 \, Eds \, (E \, m^{-2} \, d^{-1}) + 315 \qquad (4)$$

The PTd value for Eds = 0 is 315 mg C m^{-2} d^{-1}; may be interpreted as the respiration in the water column and sediments. Daily light energy data obtained in 1986 can be converted into daily primary production using equation (4). Monthly averages of PTd are plotted in Fig. 11. Over the entire year, the surface lagoon received a total of 15,550 E m^{-2} of which water column and sediments produced a total of 216,709 mg C m^{-2}, equivalent to a daily average of 0.59 mg C m^{-2} d^{-1}, not very different of the value of 0.69 mg C m^{-2} d^{-1} estimated through field experiments.
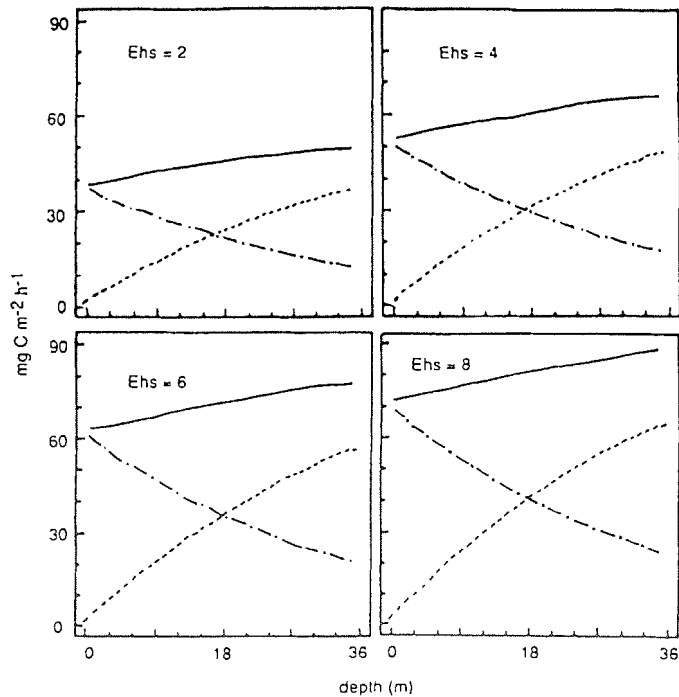
Fig. 10 : Predicted phytoplankton production (dashed line), phytobenthic production (dotted line) and total production for different surface light energy levels (Ehs : E m^{-2} h^{-1}) in Tikehau lagoon from Charpy and Charpy-Roubaud (1990a).

The photosynthetic efficiency of lagoonal communities can be summarized as follows :

- One mg of Chl a allows an hourly growth production of 4.2 mg carbon

- One Einstein reaching lagoon surface allows the growth production of 14 mg of organic carbon in the water column and sediments.
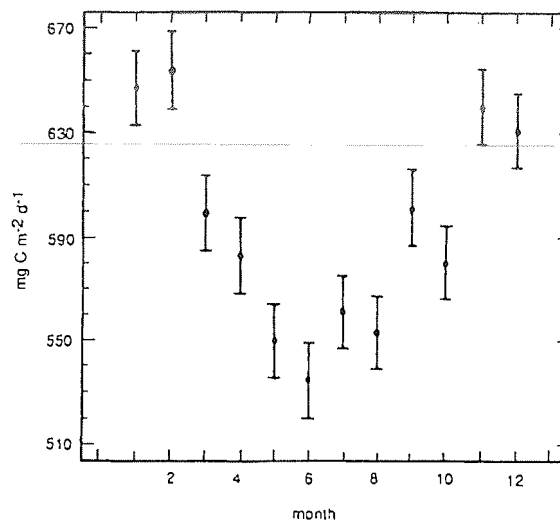

Fig. 11 : Monthly averages and confidence intervals (p=95%) of predicted total primary production (plankton and benthos) in 1986 in Tikehau lagoon (from Charpy and Charpy-Roubaud, 1990a).
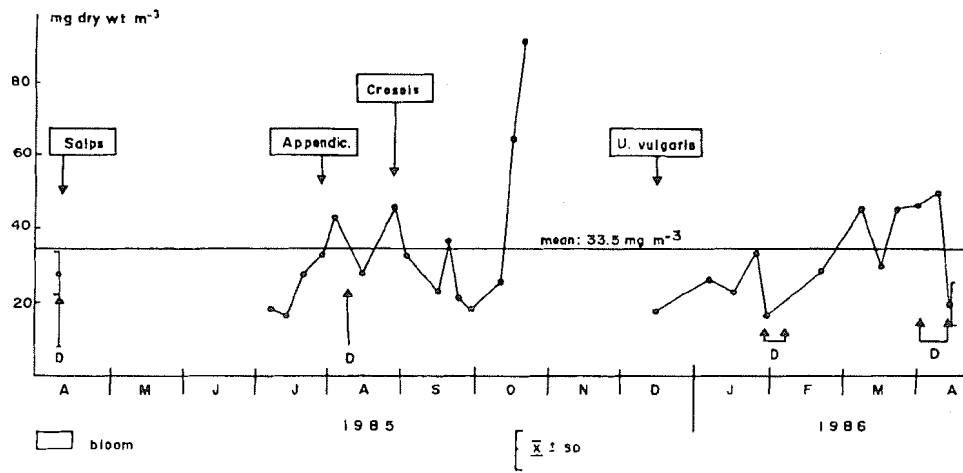
Fig. 12 : Variations in mesozooplankton dry weight from April 1985 to April 1986 in the Tikehau lagoon. Blooms of *Thalia democratica* (Salps), appendicularians (Appendic.), the pteropod *Creseis chierchiae* and the copepod *Undinula vulgaris* are shown. D : large amount of detritus (from Le Borgne *et al.*, 1989).

Table 11 : Relative contributions (%) of the main taxa to total zooplankton biomass in Tikehau lagoon. Percent contributions of non-living organisms (detritus) to total dry weight is also shown (from Blanchot and Moll, 1986 and Blanchot *et al.*, 1989).

[a]: Three samples of mesozooplankton were measured in April 1986 (from Le Borgne *et al.*, 1989).

Date	Size class	Taxon	% total biomass	% detritus
April 1985	Microzooplankton	nauplii	39.2	
	35-200 μm	copepods	30.6	70
		bivalve larvae	19.8	
		polychaete larvae	10.4	
	Mesozooplankton	copepods	68.4	
	500-2000 μm	chaetognaths	19.3	14
		salpids	8.8	
	Macrozooplankton	salpids	63.2	
	>2000 μm	copepods	22.8	
		chaetognaths	1.8	
April 1986	Mesozooplankton	copepods	73.8	
	200-2000 μm	larvaceans	5.0	3,10,49[a]
		brachyuran larvae	8.7	
		chaetognaths	5.6	

ZOOPLANKTON BIOMASS AND METABOLISM

The fate of the abundant particulate organic matter in the Tikehau lagoon and the level of efficiency of utilization by consumers are two aspects which are of primary importance to an understanding of the functioning of the lagoon pelagic food-web. Once sunk to the bottom, is seston consumed mostly by pelagic animals in the water column or by benthic ones ? Do they give rise to a significant predator biomass or is the efficiency of energy transfer between food and consumers low ? In order to provide answers to these questions, zooplankton have been studied at Tikehau during two 10 d periods in April 1985 and April 1986, and additionally by weekly samples taken in between.

ZOOPLANKTON BIOMASS

Fraction 3 to 35 μm (nanozooplankton)

An average number of 71 ± 14 heteroflagellates ml^{-1} and 7 ciliates ml^{-1} were found in samples taken in April 1986 in the lagoon. The mean individual volumes were of 542 ± 96 μm^3 for heteroflagellates and of $14\ 246 \pm 7\ 427$ μm^3 for cilates. In order to assess the relative biomass of these taxa, mean individual volumes were converted into carbon using a conversion factor chosen equal to 0.08 pg C μm^{-3} according to Sherr et al. (1984). The average biomass of heteroflagellates is approximately 3.1 ± 0.7 mg C m^{-3} while ciliate biomass is $7.6 \pm$ mg C m^{-3}. These values are of the same order of magnitude as those found by Hirota and Szyper (1976) in Hawaii though the method used does not make any difference between dead and live plankters.

Fraction 35 - 200 μm (microzooplankton)

Microzooplankton consists of 43% of organisms smaller than 100 μm of which 73% are protozoans (tintinnids Rhabdonella sp., Codonellopsis sp. and Epiplocyclis sp. accounting for 64% ; naked ciliates for 5%). Foraminifers and radiolarians are poorly represented (less than 1%). Metazoans account for only 27%. The second most abundant taxon smaller than 100 μm consists of naupliar copepods (18%) and the third of meroplankton bivalve larvae (8%). Out of organisms larger than 100 μm, protozoans account for 33% of total numbers of which 23% are tintinnids. Metazoans are noticeably dominant, accounting for 67% of the total. Copepod nauplii are the most abundant organisms (41%). Bivalve larvae do not exceed 7% of total numbers.

By using a C/ATP ratio of 125, live microzooplankton biomass can be estimated at 1.52 mgC m^{-3}. Together with nanozooplankton, biomass of heteroprophs smaller than 200 μm reaches a value of 3.3 mg C m^{-3}.

Fraction 200 - 2000 μm (mesozooplankton)

Variations in mesozooplankton dry weight were monitored as regularly as possible in the lagoon and displayed a measurement of two maxima in October 1985 (65 and 93 mg dry wt m^{-3}). Zooplankton at Tikehau are characterized by periodic blooms of copepods, larvae, pteropods and salpe. As shown in Fig. 12, the annual mean value is 33.5 mg m^{-3}, which is six times greater than the oceanic plankton concentrations measured in the vicinity of the pass (i.e. : 5.4 mg m^{-3}). Relative contributions of various size classes and taxa to zooplancton biomass are displayed in table 11.

Table 12 : Live biomass and detritus in terms of C, N, P estimated from the percentage of detritus in seston and from particulate organic carbon values in the Tikehau lagoon. - a : ATP x 125 b : POC - (ATP x 125)

Size class (μm)	year	Live			Dead		
		C	N	P	C	N	P
35-200	1985	0.36	0.07	0.03	0.84	0.16	0.06
	1986	1.02	0.19	0.08	2.37	0.45	0.18
	1986	1.5a			2.30b		
200-2000	1985	5.22	0.98	0.39	0.85	0.16	0.06
	1986	2.80	0.53	0.21	0.74	0.14	0.06
	1986	2.5a			4.4b		
> 2000	1985	3.23	0.61	0.24	0	0	0
	1986	0			0		

Table 13 : Metabolic atomic ratios and contribution of inorganic excretion to total excretion (%) in the Tikehau lagoon. $O:O_2$ respired; NH_4, Nt, PO_4, Pt : ammonia, total nitrogen, phosphate and total phosphorus excreted. nd : no data (from Le Borgne et al., 1989).

Date	Size class/species	$O:NH_4$	O:Nt	$O:PO_4$	O:Pt	$NH_4:PO_4$	Nt:Pt	$NH_4:Nt$	$PO_4:Pt$
April 1985	Microzooplankton	7.2	6.9	144	104	12.1	11.1	85.4	74.4
	Mesozooplankton	10.8	10.8	119	92	11.4	8.6	100.0	76.5
	Undinula vulgaris	18.4	13.2	132	100	7.9	7.9	48.2	43.1
	Thalia democratica	15.5	8.1	103	56	7.4	6.9	58.3	54.3
April 1986	Microzooplankton	nd	7.7	124	96	nd	12.5	nd	77.5
	Mesozooplankton	nd	7.1	144	110	nd	8.4	nd	76.3

Table 14 : Zooplankton. Net growth efficiencies (K_2) in terms of nitrogen and phosphorus for total populations and sorted species or taxa, calculated from N : P ratios of particles (a_1), zooplankton excretion (a_2), and body constituents (a_3). Number of replicates in (brackets) (from Le Borgne et al., 1989).

Date	Size class/species	a_1	a_2	a_3	$K_{2,N}$	$K_{2,P}$
1985	Mesozooplankton (9-10 April)	13.9 (25)	8.6 (4)	15.0 (2)	0.894	0.828
	Undinula vulgaris	13.9 (25)	7.9 (2)	25.7 (2)	0.623	0.337
	Thalia democratica	13.9 (25)	6.9 (12)	20.4 (2)	0.761	0.519
1986	Mesozooplankton (7-9 Apr.)	18.2 (4)	10.8 (2)	26.0 (1)	0.695	0.487
	(10-12 Apr.)	16.3 (4)	10.8 (2)	26.0 (1)	0.695	0.487
	(13-16 Apr.)	13.9 (4)	9.2 (2)	20.5 (1)	0613	0.416
	mean	16.1	8.4	23.3	0.748	0.517
	Mixed copepods	16.1 (12)	8.4	37.6 (1)	0.616	0.264
	Microzooplankton	16.1 (12)	12.5 (6)	16.7 (5)	0.889	0.857

Zooplankton biomass in terms of C, N, P

By removing detritus of samples and by calculating their relative contribution to seston dry weight, live zooplankton biomass can be estimated. Detritus dry weight represents 70% of 5-200 μm particles, between 1% and 21% of 200-2000 μm particles, and 0% of particles larger than 2000 μm. Contributions of carbon, nitrogen and phosphorus to dry weight of detritus and zooplankton taken separately were estimated by Le Borgne *et al.* (1989) enabling them to calculate biomass as shown in Table 12.

METABOLISM

Zooplankton respiration and excretion were measured in three organism size-classes and in species, *Undinula vulgaris* and *Thalia democratica*, which are abundant in the lagoon. Results of metabolic atomic ratios and contribution of inorganic excretion to total excretion are summarized in Table 13. Growth efficiency for the total population and sorted taxa are displayed in Table 14 and assimilation efficiencies of copepods are listed in Table 15. As a general pattern, efficiencies estimated for microzooplankton are greater than for mesozooplankton. Excreted nitrogen and phosphorus are mostly inorganic. They meet 32% and 18% of phytoplankton nitrogen and phosphorus requirements.

Production was then estimated. All P/B ratios presented in Table 16 are greater than 34% which is equivalent to a three day turnover time of the biomass. The turnover rate is shorter for mixed zooplankton, close to one day and even shorter for the salp *Thalia democratica* due to, in all probability, asexual reproduction, high water temperature (29.5 °C) and abundances of food as emphasized by Le Borgne and Moll (1986). On the average, P/B ratios for zooplankton are 5.7 times lower than P/B ratios estimated for phytoplankton.

The nitrogen and phosphorus assimilation rates in Table 17 are the sum of production and total excretion rates. Ingestion is calculated from assimilation and its relevant effficiency.

Table 15 : Assimilation efficiencies (D) of C, N, P and their ratios (a4=D_N:Dp a'4=D_C:D_N). Calculations made by the method of Conover (1966) using organic carbon, nitrogen and phosphorus percentages of dry weight in feces and food. nd : no data (from Le Borgne *et al.*, 1989).

Date	Species	Faeces			Food			D (%)			a_4	a'_4
		C	N	P	C	N	P	C	N	P		
1985	*Undinula vulgaris*	0.40	0.10	0.048	2.36	0.25	0.081	83.6	60.1	38.3	1.57	1.39
1986	Small copepods	0.59	0.17	0.025	15.4	1.86	0.258	96.8	91.0	90.2	1.01	1.06
		0.62	0.09		5.37	0.85	0.139	89.0	89.5	nd	nd	0.99

Table 16 : Production rates in terms of C, N, P (μg mg⁻¹ dry wt d⁻¹) and daily P:B ratios at Station 6. Body C, N and P, as percentages of dry weight, allows the conversion of rates into P:B (from Le Borgne *et al.*, 1989).

Date	Sizeclass /species	Production rates			Body constituents			P:B
		C	N	P	C	N	P	(%)
April 1985	Mesozooplankton	164	44.65	3.565	20.7	4.12	0.37	102.0
	Undinula vulgaris	108	29.97	2.604	31.4	8.73	0.76	34.3
	Thalia democratica	190	42.88	5.859	1.91	0.43	0.0725	816.0
April 1986	Mesozooplankton	331	73.64	7.061	38.4	8.50	0.81	86.4
	Mixed copepods	147	39.80	2.346	27.1	7.31	0.43	54.4

Table 17 : Zooplankton. Assimilation and ingestion rates (μg C, N or P mg⁻¹ dry wt d⁻¹) in the Tikehau lagoon (from Le Borgne *et al.*, 1989).

Date	Size class/species	Assimilation			Ingestion		
		C	N	P	C	N	P
April 1985	Mesozooplankton	656	71.7	10.57	785	102	15.1
	Undinula vulgaris	515	48.3	7.75	616	80	20.2
	Thalia democratica		56.4	11.28	617	81	16.1
April 1986	Mesozooplankton	724	98.4	13.54	804	109	15.0
	mixed copepods	473	64.6	4.67	526	72	5.2

TROPHIC STRUCTURE AND PRODUCTIVITY OF THE ECOSYSTEM

With all data estimated in the foregoing sections of this chapter, biomass and fluxes of matter in plankton and in benthos can be assessed. In order to enable comparisons between benthic and planktonic ecosystems, standing stocks are in mg C m⁻² and fluxes in mg C m⁻² d⁻¹. The trophic web is illustrated in Fig. 13.

We did not measure directly the biomass of bacteria, but we think that we can obtain an order of magnitude by the difference between liv C estimated from ATP and the other biomasses measured or estimated. Therefore, free bacteria biomass (BB) may be calculated with the equation:

$$BB = \text{liv } C_{(< 5\,\mu m)} - \text{phy } C_{(< 5\,\mu m)}$$

with: liv $C_{(< 5\,\mu m)}$ = percentage of $ATP_{(< 5\,\mu m)}$ x ATP x 250

phy $C_{(< 5\,\mu m)}$ = percentage of chl $a_{(< 5\,\mu m)}$ x chl a x (C/chl-a ratio).

The average value C/chl a = 50 (Charpy and Charpy-Roubaud, 1990 b) lies within the range reported by Takahashi *et al.* (1985) for picoplankton and is very close to the ratio of 46 found by Laws *et al.* (1987) for oligotrophic Pacific waters. Therefore :

$$BB = (0.46 \times 0.11 \times 250) - (0.5 \times 0.18 \times 50) = 8.2 \text{ mg C m}^{-3}$$

The liv C$_{(5 - 35 \mu m)}$ is made up of heterotrophs and phytoplankton (4.5 mg C m^{-3}). It can be calculated using ATP$_{(5 - 35 \mu m)}$ data : 0.54 x 0.11 x 250 = 14.9 mg C m^{-3}. The carbon content of heterotrophs in the size range from 5 to 35 μm was therefore equal to : 14.9 - 4.5 = 10.4 mg C m^{-3}. The biomass of ciliates and heteroflagellates was equal to 1.8 mg C m^{-3} (Table 3), and the difference (= 8.6 mg C m^{-3}) was certainly due to bacteria adsorbed onto the detritus (Charpy, 1985).

The total biomass of bacteria was therefore equal to : free bacteria + adsorbed bacteria = 16.8 mg C m^{-3}. Such a biomass is commonly observed in waters over reefs ; Sorokin (1974) summarizes data for biomasses of bacteria which range from 11 to 170 mg C m^{-3}. More recently, Moriarty et al. (1985) reviewed the productivity and trophic role of bacteria on coral reefs. They give biomass values ranging from 19 to 150 mg C m^{-3}. Linley and Koop (1986) observed in the coral reef lagoon of One Tree Island (Great Barrier Reef) a biomass of heterotrophic bacteria ranging from 1.2 to 16.2 mg C m^{-3}, and Hopkinson et al. (1987) observed a bacterial biomass of 2 mg C m^{-3} in the water column of Davies Reef (Australia). In Tikehau, in April 1986, the biomass of bacteria was estimated at 17.1 mg C m^{-3} by Blanchot et al. (1989). The observed ratio free bacteria / adsorbed bacteria = 2 is consistent with the ratios given by Moriarty (1979) and Moriarty et al. (1985) in coral reef areas.

The estimated bacterial biomass was 2 times higher than the phytoplanktonic C in the Tikehau lagoon. Dominance of bacterial biomass was also observed in the oligotrophic waters of the Sargasso Sea by Fuhrman et al. (1989); the interpretation of these authors was that bacteria consume sigificant amounts of carbon probably released from phytoplankton directly or via herbivores.
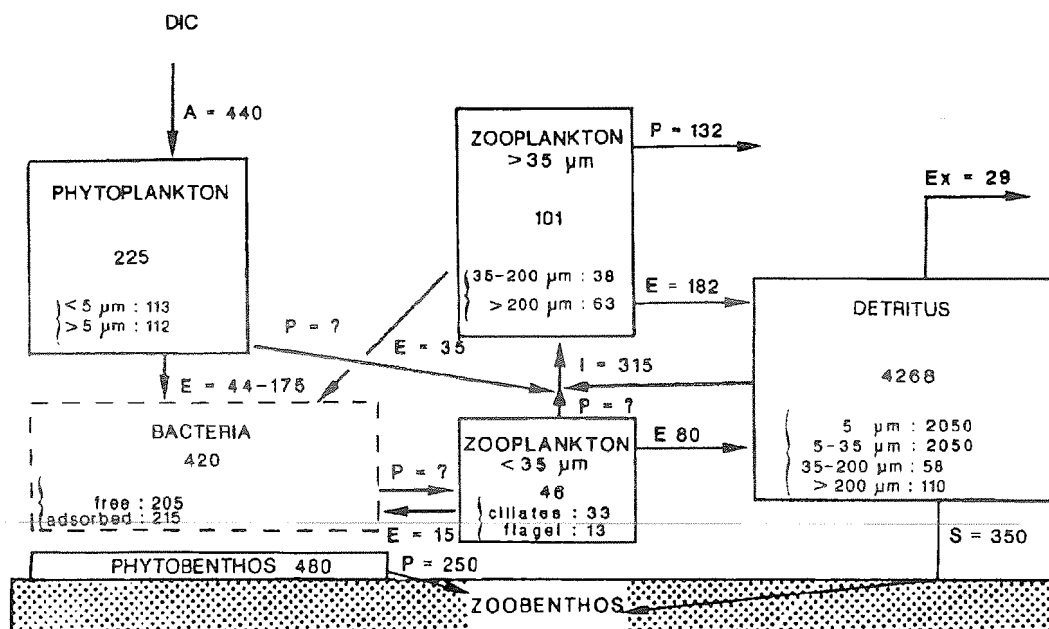

Fig. 13 : Trophic structure and productivity of the Tikehau lagoon communities. Standing stocks (mg C m^{-2}) are in boxes , and fluxes (mg C m^{-2} d^{-1}) are represented by arrows. A = assimilation, E = excretion, Ex = export, I = ingestion, P = production, S = sedimentation, DIC = dissolved inorganic carbon
(from Charpy and Charpy-Roubaud, 1990b).

Detritus, smaller than 35 μm, represent the most important particulate organic carbon pool in the lagoon. They originate from lagoonal primary production (Charpy and Charpy-Roubaud, 1990b) and their sedimentation onto the bottom exceeds benthic primary production. Plankton bacteria biomass is of same order of magnitude as microphytobenthos biomass and is equal to twice the phytoplankton biomass. Pelagic bacteria dominance can be interpreted by a microbial loop returning energy released as dissolved organic matter by phytoplankton and zooplankton, but also energy released as mucus from lagoon coral communities.

ZOOBENTHOS BIOMASS IN SEDIMENTS : FIRST RESULTS

A survey of 20 random stations was realised in the lagoon by A. Intes to provide a first assessment of the macro-zoobenthos of the soft bottoms. These unpublished data have to be considered as preliminary results.

Taxonomic structure - results (Fig. 14)

In terms of abundance, the Molluscs and the Polychaetes dominate the endofauna with a mean density of 11.3 and 10.4 ind m^{-2} respectively. The crustaceans count for less than 2 ind m^{-2} and the Echinoderms as well as the lancelets less than 1 ind m^{-2}. The abundance of the Crustaceans is probably under estimated as only large apparent Invertebrates were counted and no digging operations were carried out. Large Invertebrates burrowing in the sediment are not taken into account and their biomass remains unknown. However, the average density of the big burrowing species can be estimated to stand around 0.3 ind m^{-2} as revealed by hole density.

Regarding the epifauna, the Sponges clearly dominate with around 0.5 colony m^{-2}. The other organisms are generally scarce except in some very localised areas harbouring high densities of holothuroid (*Halodeima atra*).
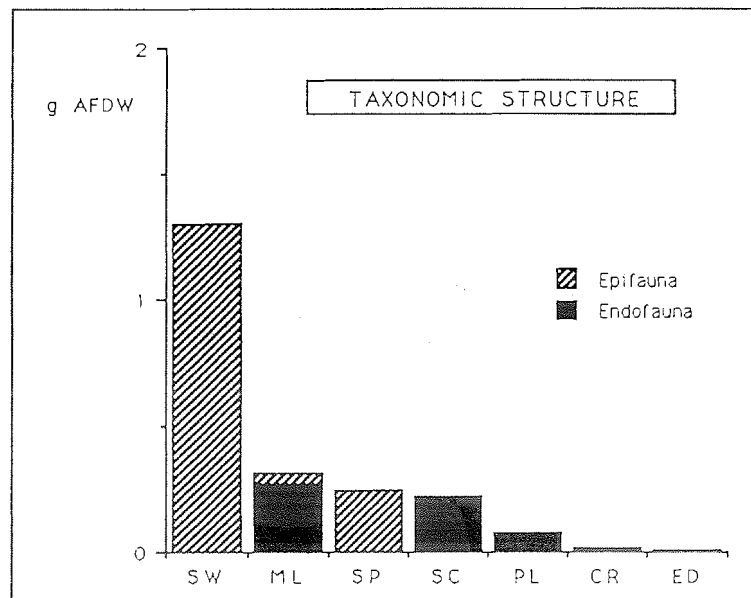

Fig. 14 : Taxonomic structure of zoobenthos biomass in sediment (SW : Sea weeds ; ML : Molluscs ; SP : Sponges ; SC : Sipunculids ; PL : Polychaetes ; CR : Crustaceans ; ED : Echinoderms) expressed in Ash Free Dry Weight (AFDW).

In terms of biomass, the global structure is not very different : the Molluscs remain at first rank with 36% of the animal organic matter (AOM), followed by the Sponges with 27% of AOM. The third class includes the Sipunculids, but also all the fauna living in the dead shells and in all probability some micromolluscs. This represents about 25% of AOM. The other groups stand far behind in importance : the Polychaetes are mainly small animals and contribute for only 9% to AOM. The crustaceans are essentially little species such as Tanaidacae or Mysidacae. Some crabs (mostly Portunids) are rarely collected in the endofauna and the contribution of the group to the biomass is poor : 2% of AOM. Once again, this is under estimated by the lack of information on the big burrowing forms. The Echinoderms are very few represented on the soft bottoms (Ophiuroids) with only 1% of AOM.

Considering the total living biomass, the primary producers largely dominate with about 60% of the total organic matter.

They are sea weeds such as *Halimeda* or *Caulerpa* belonging to several species, but they may also be Phanerogams *Halophila ovalis.* (the sole species encountered in this lagoon).

Trophic structure - results (Fig. 15)

The deposit feeders are considered as a unique group. No distinction between the surface deposit feeders and the burrowing deposit feeders is made. They are slightly the best represented with 46% of AOM, but it must be emphasized that they belong to the endofauna (except the Holothuroid *Halodeima atra*).
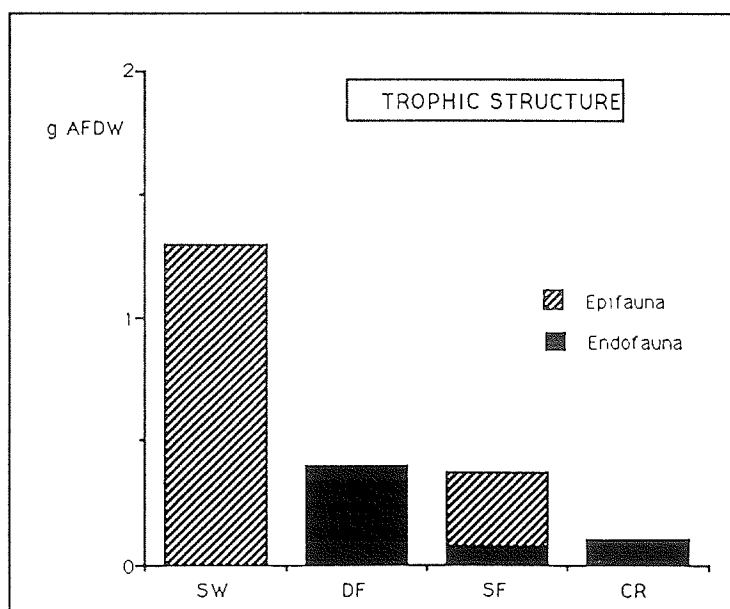

Fig. 15 : Trophic structure of zoobenthos in sediments (SW : Sea weeds ; DF : Deposit-feeders ; SF : Suspension -feeders ; CR : Carnivorous).

The suspension feeders stand in the same order of magnitude with 42% of AOM. Most of them belong to the same epifauna as Sponges do, but also some molluscs such as the bivalves *Pinna* are found.

The carnivores are the least represented with only 12% of AOM. They are collected in the epifauna (Molluscs as *Strombus spp.* or *Nassarius spp.*) as well as in the endofauna (some Crustaceans and Polychaeta).

The deposit feeders are under estimated because the mud shrimps, or the Cardiidae for example, are not taken in account by the sampling method.

Discussion :

A first biocenotic survey carried out by Faure and Laboute (1984) concluded from the study of the coral species distribution that the whole lagoon belongs to a sole community inside which the species distribution depends on geomorphological or physical factors. The study of the fish community by Morize *et al.* (1990) leads to the same finding : there is only one fish community in the lagoon, but its observed structures (which varies in space and biomass) are greatly heterogenous without any evident explicative factor. The spatial heterogeneity of the benthic biomasses cannot be explained by the classic factors such as sediment characteristics, bathymetry, and distance to the rim.

Two hypothesis can be advanced nevertheless :

1 -The mapping of the biomasses matches the mapping of the bidimensional modelisation of the water circulation under the influence of the trade winds (see fig.12 of the first chapter). If the model can be considered as relevant, the vortex generated by the wind will be a facilitating factor for the organic matter sedimentation and consequently, would allow the development of the greatest amount of benthic biomass of bottom invertebrates.

2 - The sample distance from a lagoon reef construction may be the best explicative factor. These reefs, considered as a source of organic matter via the detritus released, may govern the bottom invertebrates distribution. This hypothesis will be tested in the forthcoming research program "Cyel".

As only the soft bottoms were investigated in this quantitative survey, no cnidarians were collected : the free living scleractinia as *Heteropsammia*, *Cycloseris*, or *Trachyphyllia* do not exist in French Polynesia. Apart from this, the general structure is close to the structure observed in the New Caledonia lagoon by Chardy and Clavier (1989). The three main groups in terms of biomass are the same, respectively the macrophytes, the sponges and the molluscs. The crustaceans and especially the echinoderms are relatively less represented in the Tikehau lagoon than in New Caledonia. Few species of crabs and quite no pagurids, no urchins, no asterids were collected in or on the sediment.

The biomass of the macrophytes is higher than the total animal biomass, but its trophic role in the bottom network cannot be appraised as few invertebrates seem to feed on them. Among the animals, the suspension feeders stand to the same order of magnitude of biomass than the deposit feeders in the Tikehau lagoon. Chardy and Clavier (1989), in New Caledonia, observed a suspensivores biomass about twice the one of the deposit feeders. The lack of soft bottom free living scleractinians may partly explain this fact.

The general trends of the trophic network described on the soft bottoms of the Tikehau lagoon may be summarised as :

A highly simplified fauna in which most of the zoological groups are represented, but with a little number of species (about 80 taxa).

The trophic network is basically highly dominated by the macrophytes production, but their consumers do not belong to the invertebrates fauna.

Among the animals, the suspension feeding guild is mainly represented on the sediment surface by the sponges, but also by some molluscs or polychaetes living in the sediment.

The deposit feeding guild is better represented among the zoological groups, where the molluscs and shell living organisms dominate in weight.

The two main guilds are quite equally represented at least on the soft bottoms. A first attempt to explain this may be the weakness of the currents in the lagoon, allowing a near vertical sedimentation on which only filter feeding organisms (*i.e.* actively pumping the sea water) may feed in sufficient quantity before bottom accumulation. This hypothesis mark a basic difference with the bottom network of New Caledonia, where the water circulation allows a higher contribution of the suspension guild to the benthic network.

Literature cited

ANDREWS (J.C.), GENTIEN (P.) - 1982 - Upwelling as a source of nutrients for the Great Barrier Reef eco-systems : a solution to Darwin's question ? **Mar. Ecol. Prog. Ser.,** 8 : 259 - 269

BLANCHOT (J.), CHARPY (L.), LE BORGNE (R.) - 1989 - Size composition of particulate organic matter in the lagoon of Tikehau atoll (Tuamotu Archipelago). **Mar. Biol.,** 102 : 329-339

CHARDY (P.), CLAVIER (J.) - 1989 - An attempt to estimate the carbon budget for the south west lagoon of New Caledonia. **Proceeding of the Sixth International Coral Reef Congress, Townsville, 1988,** 2 : 541-546

CHARPY (L.) - 1985 - Distribution and composition of particulate organic matter in the lagoon of Tikehau (Tuamotu archipelago, French Polynesia). **Proceeding of the Fifth International Coral Reef Congress, Tahiti, 1985,** 2: 353-357

CHARPY (L.), CHARPY-ROUBAUD (C.J.) - 1990a - A model of the relationship between light and primary production in an atoll lagoon. **J. mar. Biol. Ass. U.K.,** 70 : 357-369

CHARPY (L.), CHARPY-ROUBAUD (C.J.) - 1990b - Trophic structure and productivity of the lagoonal communities of Tikehau atoll (Tuamotu archipelago, French Polynesia). **Hydrobiologia,** 207 : 43-52

CHARPY (L.), CHARPY-ROUBAUD (C.J.) - 1991 - Particulate organic matter fluxes in a coral reef lagoon (Tikehau atoll, French Polynesia). **Mar. Ecol. Prog. Ser.,** 71 : 53-63

CHARPY-ROUBAUD (C.J.) - 1988 - Production primaire des fonds meubles du lagon de Tikehau (archipel des Tuamotu, Polynésie Française). **Oceanol. acta,** 11 (3) : 241-248

CHARPY-ROUBAUD (C.J.), CHARPY (L.), LEMASSON (L.) - 1989 - Benthic and planktonic primary production of an open atoll lagoon (Tikehau, Tuamotu archipelago, French Polynesia). **Proceeding of the Sixth International Coral Reef Congress, Townsville, 1988,** 2 : 551-556

CHARPY-ROUBAUD (C.J.), CHARPY (L.), CREMOUX (J.L.) - 1990 - Nutrient budget of the lagoonal waters in an open central South Pacific atoll (Tikehau, Tuamotu, French Polynesia). **Mar. Biol.,** 107 : 67-73

CONOVER (R.J.) - 1966 - Assimilation of organic matter by zooplankton. **Limnol. Oceanogr.,** 11 : 338-345

CROSSLAND (C.J.) - 1983 - Dissolved nutrients in coral reef waters. In : Perspectives on coral reefs. Barnes D.J. (eds) **Australian Institute for Marine Science, Townsville,** : 49-56

FAURE (G.), LABOUTE (P.) - 1984 - Formations récifales : I Définition des unités récifales et distribution des principaux peuplements de Scléractinaires. In : L'atoll de Tikehau (Archipel des Tuamotu, Polynésie Française), premiers résultats. **ORSTOM Tahiti, Notes et Doc. Océanogr.,** 22 : 108-136

FUHRMAN (J.A.), SLEETER (T.D.), CARLSON (C.A.), PROCTOR (L.M.) - 1989 - Dominance of bacterial biomass in the Sargasso Sea and its ecological implications. **Mar. Ecol. Prog. Ser.,** 57 : 207-217

HESSLEIN (R.H.) - 1976 - An in situ sampler for close internal pore water studies. **Limnol. Oceanogr.,** 21 : 912 -924

HALL (P.O.J.) - 1984 - Chemical fluxes at the sediment sea-water interface ; in situ investigations with benthic chambers. Ph. D. Thesis, **Chalmers university of technology, Goteborg, Sweden.**

HIROTA (J.), SZYPER (J.) - 1976 - Standing stocks of zooplankton size classes and trophic levels in Kaneohe bay, Oahu, Hawaiian islands. **Pacif. Sci.,** 30 : 341-361

HOPKINSON (C.S.), SHERR (B.F.), DUCKLOW (H.W.) - 1987 - Microbial regeneration in the water column of Davies Reef Australia. **Mar. ecol. Prog. Ser.,** 41 : 147-153

KOOP (K.), LARKUM (A.W.D.) - 1987 - Deposition of organic material in a coral reef lagoon, One Tree Island, Great Barrier Reef. **Estuar. coast. Shelf Sci.,** 25 : 1-9

KROM (M.D.), BERNER (R.A.) - 1980 - Adsorption of phosphate in anoxic marine sediments. **Limnol. Oceanogr.**, 25 : 797-806

LAWS (E.A.), Di TULLIO (G.R.), REDALJE (D.G.) - 1987 - High phytoplancton growth and production rates in the North Pacific subtropical gyre. **Limnol. Oceanogr.**, 32 : 905-918

LE BORGNE (R.), BLANCHOT (J.), CHARPY (L.) - 1989 - Zooplankton of Tikehau atoll (Tuamotu archipelago) and its relationship to particulate matter. **Mar. Biol.**, 102 : 341-353

LE BORGNE (R.), MOLL (P.) - 1986 - Growth rates of the salp in Tikehau atoll (Tuamotu is.) **Oceanogr. trop.**, 21 : 23-29

LENHARDT (X.) - 1991 - Hydrodynamique des lagons d'atoll et d'île haute en Polynésie Française. **ORSTOM Paris ed., Etudes et Theses** : 132 p

LINLEY (E.A.S.), KOOP (K.) - 1986 - Significance of pelagic bacteria in a coral reef lagoon, One Tree Island, Great Barrier Reef. **Mar. Biol.**, 92: 457-464

MORIARTY (D.J.W.) - 1979 - Biomass of suspended bacteria over coral reefs. **Mar. Biol.**, 53 : 193-200

MORIARTY (D.J.W.), POLLARD (P.C.), ALONGI (D.M.), WILKINSON (C.R.), GRAY (J.S.) - 1985 - Bacterial productivity and trophic relationships with consumers on a coral reef (MECOR I). **Proceeding of the Fifth International Coral Reef Congress, Tahiti, 1985**, 3 : 457-462

MORIZE (E.), GALZIN (R.), HARMELIN-VIVIEN (M.), ARNAUDIN (H.) - 1990 - Organisation spatiale du peuplement ichthyologique dans le lagon de l'atoll de Tikehau, Polynésie française. **ORSTOM-Tahiti, Notes et Doc Océanogr.**, 40 : 1-44

QUASIM (S.Z.), SANKARANARAYANAN (V.N.) - 1970 - Production of particulate organic matter by the reef of Karavatti atoll (Laccadives). **Limnol. Oceanogr.**, 15 : 574-578

ROUGERIE (F.) , WAUTHY (B) - 1986 - Le concept d'endo-upwelling dans le fonctionnement des atolls-oasis. **Oceanol. Acta**, 9 : 133-148

SHERR (B.F.), SHERR (E.B.), NEWELL (S.Y.) - 1984 - Abundance and productivity of heterotrophic nanozooplankton in Georgian coastal waters. **J. Plankton Res.**, 6 : 195-202

SMITH (S.V.) - 1984 - Phosphorus versus nitrogen limitation in the marine environment. **Limnol.Oceanogr.**, 29 (6) : 1149-1160

SMITH (S.V.), CHANDRA (S.), KWITKO (L.), SCHNEIDER (R.C.), SCHOONMAKER (J.), SEETO (J.), TEBANO (T.), TRIBBLE (G.W.) - 1984 - Chemical stoechiometry of lagoonal metabolism. U. Hawaii/U. South Pacificic Internat. Sea Grant Prog. Tech. Rept. UNIHI-SEAGRANT-CR-84-02, 30 p

SMITH (S.V), JOKIEL (P.L.) - 1975 - Water composition and biogeochemical gradients in the Canton atoll lagoon : 2 Budgets of phosphorus, nitrogen, carbon dioxide, and particulate materials. **Marine Science communications**, 1 (2) : 165-207

SMITH (S.V), KINSEY (D.W.) - 1988 - Why don't budgets of energy, nutrients, and carbonates always balance at the level of organisms, reefs, and tropical oceans ? an overview. **Proceeding of the Sixth International Coral Reef Congress, Townsville, 1988**, 2 : 551-556

SOROKIN (Y.I.) -1974 - Bacteria as a component of the coral reef community. **Proceeding of the Second International Coral Reef Symposium, Manilla**, 1 : 3-10

TAGUCHI (S.) - 1982 - Sedimentation of newly produced particulate organic matter in a subtropical inlet, Kaneohe Bay, Hawaii. **Estuar. coast. Shelf Sci.**, 14 : 533-544

TAKAHASHI (M.), KIKUSHI (K.), HARA (Y.) - 1985 - Importance of picocyanobacteria biomass (unicellular, blue-green algae) in the phytoplankton population of the coastal waters off Japan. **Mar. Biol.**, 89 : 63-69