LAGOONAL WATER CHEMISTRY CHANGES INDUCED BY PINNACLES IN TIKEHAU ATOLL (FRENCH POLYNESIA)

L. Charpy and C. Charpy-Roubaud

ORSTOM, Centre d'Océanologie de Marseille, traverse de la Batterie des Lions, F-13007 Marseille, France.

ABSTRACT

Pinnacles are a common feature of many lagoons. We investigated their influence on the water chemistry in the lagoon of Tikehau atoll, French Polynesia. Concentrations of O_2, alkalinity, particulate organic matter and nutrients were measured upstream and downstream of water flowing past a representative coral head. A decalcification rate of -37 gCaCO$_3$ m^{-2} day^{-1} was calculated. No excess pinnacle production was noted. The gross primary production by the pinnacle community was estimated to be 4 gC m^{-2} day^{-1}

INTRODUCTION

Lagoon pinnacles may contribute an important portion of total lagoon productivity. Plant and animal biomass on patch reefs is high compared to bottom sediments. Indeed, most lagoon resources (pearl oysters, fish) are located close to the pinnacles. As water flows over and around the pinnacles, the characteristic of lagoonal water is modified by the metabolism of pinnacle benthic communities.

The questions discussed in this paper are :

What is the gross primary production and net calcification of lagoon pinnacles?

Are lagoon pinnacles a source or a sink for major nutrients ?

MATERIALS AND METHODS

Study site

The pinnacle chosen (referred to as the reference pinnacle) is located in the south part of Tikehau lagoon (Charpy and Harmelin-Vivien 1992, Peyrot-Clausade et al. 1995a). It is almost circular with a near surface diameter of 70 m. It rises from the floor of the lagoon (20 m depth) to within 0.5 m of the lagoon surface (Fig. 1). Four other pinnacles (Pin 2 to Pin 5, Fig. 2) were studied in January 1991 for comparison with the reference pinnacle.

Fig. 1: Reference pinnacle

The upper zone (0 to 2 m) of pinnacle is colonized by algae (*Halimeda, Pocockiella, Caulerpa, Liagora ceranoides*, algal turfs). Coral along the windward side are mainly colonies of *Porites lobata* and *Millepora platyphylla* and the leeward side by *Acropora variabilis, A. hyacinthus* and *A. hemprichii*. At mid depth (2 to 6 m), algae (*Halimeda, Caulerpa*) compete with corals (*Montipora, Astropora, Psammocora, Porites, Platygyra, Pavona*) for space. The lower zone (6 to 15 m) is occupied by patches of the corals *Montipora verrucosa, Stylocoeniella, Platygyra daedalea, Acropora formosa, Stylophora pistillata* and *Favia favus*, growing on a detrital or sandy gentle slope (Faure and Laboute 1984, Harmelin-Vivien 1985).

Sampling

The sampling at the reference pinnacle was conducted in January 1991, and March 1992. Nutrients (NO$_2$, NO$_3$, NH$_4$, PO$_4$, SiO$_2$, DON and DOP), alkalinity, dissolved O$_2$, biological oxygen demand, particulate organic carbon (POC), nitrogen (PON) and phosphorus (POP), chlorophyll (Chl), phaeophytin (Pha) , ATP and current speed were measured in the water column at 0.5 m depth on the windward side and at 0.5, 1.5 and 2.5 m depth to leeward of the reference pinnacle. Sampling was conducted at 4 hours intervals during the day and the night. In March 1992, the above nutrients and current speed were measured at 0.5 m depth on the windward and leeward sides of the reference pinnacle.
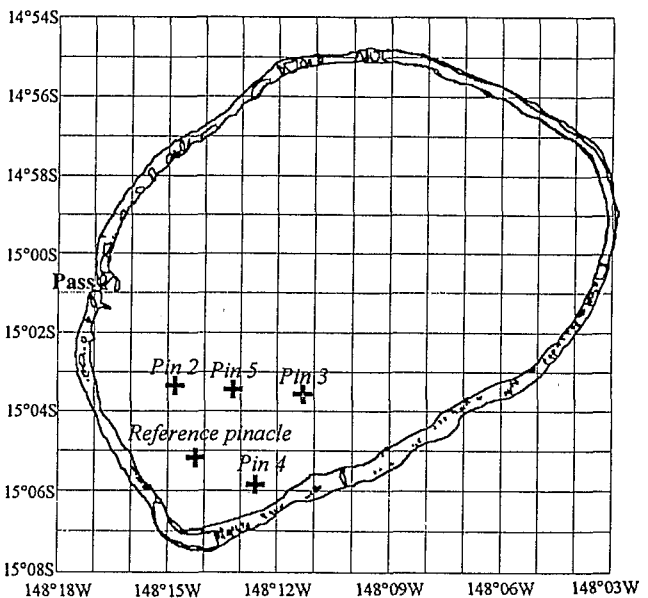

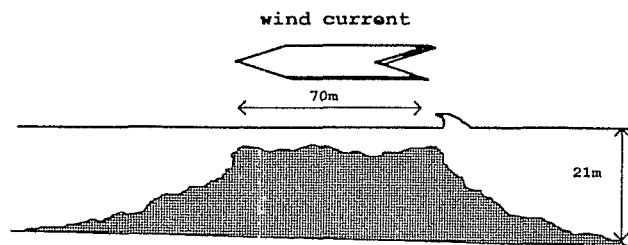Fig. 2: Location of the prospected pinnacles

Analytical methods

Dissolved inorganic nutrient (NH$_4$, NO$_2$, NO$_3$, SiO$_2$, PO$_4$) concentrations were determined immediately in the field laboratory using the standard techniques described by Strickland and Parsons (1972). Dissolved organic nitrogen (DON) and phosphorus (DOP) were determined after UV-oxidation in presence of H$_2$O$_2$.

Oxygen was determined in the traditional manner using modified Winkler procedures on samples. BOD was calculated after an incubation of 72 hours.

Total alkalinity (TA) determinations (Smith and Kinsey, 1978) were performed on acidified seawater samples by the method of Perez and Fraga (1987). The standard error given by the authors is: $\pm$ 0,003 meq l^{-1}. Total alkalinity data were not corrected for changes in nutrient concentration (Chisholm and Gattuso, 1991). Carbonate alkalinity was calculated by the equation:

$$CA \ (meq \ l^{-1}) = TA - BA$$

with: BA = borate alkalinity (meq l^{-1}):

$$BA = \Sigma B \left[\frac{a_H K_{1b} + 2K_{1b} + 2K_{1b}K_{2b}}{a_H^2 + a_H K_{1b} + 2K_{1b}K_{2b}} \right]$$

ΣB = total boron (mmol l^{-1}) = 0.01$\times$S; a$_H$ = hydrogen ion activity (10^{-pH}); K$_{1b}$, K$_{2b}$ = first and second

dissociation constants for boric acid. Values for these constants are tabulated as functions of temperature and salinity in Riley and Skirrow (1975).

Total CO_2 (ΣCO_2) was calculated from the equation:

$$\Sigma CO_2 = CA\left[\frac{K_{1c}a_{II} + K_{1c}K_{2c} + a_{II}^2}{K_{1c}a_{II} + 2K_{1c}K_{2c}}\right]$$

K_{1c}, K_{2c}= first and second dissociation constants for carbonic acid (Riley, Skirrow, 1975).

Chemical analyses of POM
Sea water samples were first prefiltered through a polyamide screen with 35 µm mesh. Then, 1) 100 to 300 ml were filtered through a Whatman GF/F filter for pigment analysis; 2) 500 to 1000 ml were filtered through a GF/F processed filter (precombusted 4 h at 450°C and precleaned with 1N HCl) for POC, PON and particulate organic phosphorus (POP) analysis and 3) 250 to 500 ml were filtered through a Millipore 0.45 µm filter for ATP analysis.

Concentrations of Chl and Pha were determined by fluorescence (Yentsch and Menzel 1963) using a Turner 111 fluorimeter.

POC and PON concentrations were determined after rinsing the filter with 20 ml of HCl (0.1N) with a 185-B Hewlett-Packard CHN analyzer (Gordon and Sutcliffe 1973).

POP was oxidized with persulfate at 110° C for 1.5 h (Menzel and Corwin 1965) and phosphate concentrations subsequently analyzed by spectrophotometry (Strickland and Parsons 1972).

ATP extractions were performed immediately in 5 ml of boiling Tris (0.02 M, pH = 7.85); ATP extracts were frozen at -20°C until analysis in the Tahiti laboratory. ATP concentrations were measured using the method described by Holm-Hansen and Booth (1966), with a LKB Luminometer and Luciferine-Luciferase preparations from Sigma (FLE 50).

Flux from the reef pinnacle calculations
Fluxes (moles m^{-1} h^{-1}) are the product of volume transport per unit width of reef perpendicular to the direction of water flow (m^2 h^{-1}) and change in O_2, TA, nutrient or POM concentration between upstream and downstream stations. Division by the distance (m) between upstream and downstream stations yields the rate per unit area : moles m^{-2} h^{-1} (Marsh and Smith, 1978). The volume transport rate (V_t) is the product of the current velocity and water depth (Maragos 1978). The diffusion correction was applied to oxygen budgets according to the principles outlined by Odum and Hoskin (1958). No diffusion correction was applied to CO_2 budgets.

RESULTS

Thirty oxygen, alkalinity, nutrient and POM budgets were calculated in January 1991 and March 1992. The average current speed above the reef pinnacle was 6.2±0.3 m s^{-1}.

Oxygen and alkalinity fluxes
Oxygen production or respiration rates varied between - 1.7 and +1.0 g O_2 m^{-2} h^{-1} and were positive during the daylight (between 8 hr and 16.00 hr) and negative during the night (Fig. 3).

TA changes varied between -0.2 and +0.2 eq m^{-2} h^{-1} and were close to 0 during daylight and negative during the night (Fig. 4).

Therefore, we could calculate O_2 and TA budget averages for night and day time and during 24 h period (Table 1).

Table 1: Average ± Standard Error of oxygen production and respiration (g m^{-2} h^{-1}), total alkalinity changes (eq m^{-2} h^{-1})and ΣCO_2 changes (moles m^{-2} h^{-1})between windward and leeward part of the reference pinnacle

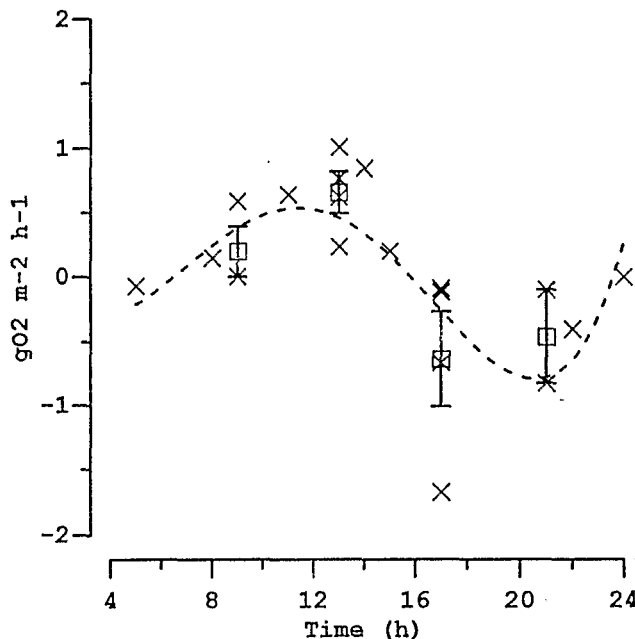|	O_2	TA	ΣCO_2
night 17:00-5:00	-0.44±0.18 n=9	-0.073±0.040 n=9	-0.063±0.035
daylight 5:00-17:00	+0.46±0.11 n=11	+0.012±0.011 n=9	+0.010±0.009
m^{-2} day^{-1}	+0.23	-0.73	-0.63

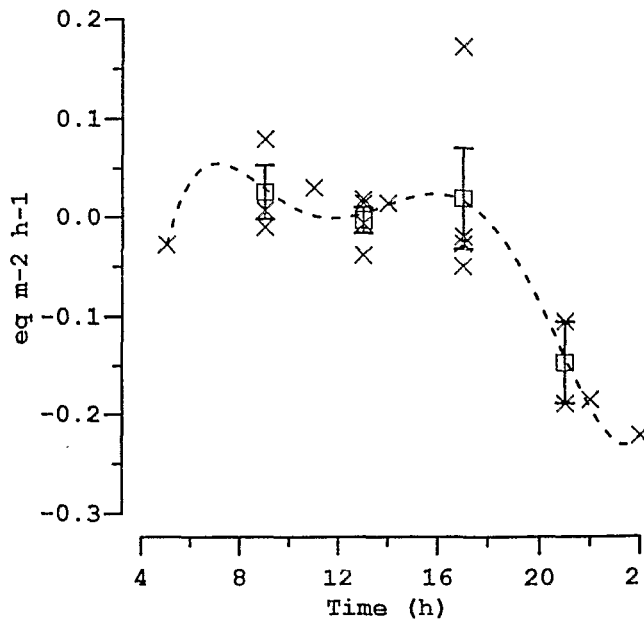Fig. 3: Oxygen production and respiration between the windward and leeward part of the reference pinnacle

Fig. 4: TA changes between the windward and leeward part of the reference pinnacle

Table 2: Average (± SE) nutrient concentrations (µM) to windward (WW) and leeward (LW) of the reference pinnacle in January 1991 and March 19921

Stat	PO$_4$	NO$_2$	NO$_3$	NH$_4$	SiO$_2$	DON	DOP
WW	0.10±0.01	0.01±0.00	0.02±0.00	0.48±0.04	0.74±0.08	0.83±0.12	0.24±0.03
LW	0.11±0.02	0.02±0.00	0.04±0.01	0.38±0.03	0.74±0.08	0.95±0.16	0.24±0.03

Table 3: Average (± SE) of nutrient budgets between windward and leeward part of the reference pinnacle (mmol m^{-2} h^{-1})

	PO$_4$	NO$_2$	NO$_3$	NH$_4$	SiO$_2$	DON	DOP
January	+0.02±0.04 n=19	+0.02±0.00 n=20	+0.06±0.01 n=20	-0.32±0.13 n=20	-0.1±0.1 n=19	+0.26±0.52 n=19	+0.03±0.05 n=19
March	-0.06±0.02 n=10	+0.02±0.00 n=10	+0.15±0.05 n=10	-1.74±0.18 n=10	-1.7±0.1 n=10	-4.6±0.6 n=10	-0.46±0.07 n=10
pooled	+0.00±0.03 n=29	+0.02±0.00 n=30	+0.09±0.02 n=30	-0.79±0.16 n=29	-0.6±0.2 n=29	-1.4±0.6 n=29	-0.14±0.06 n=29

Table 4: Average ± SE POM concentrations (mg m^{-3}) and BOD$_{72h}$ (mmol m^{-3}) on the windward (WW) and leeward (LW) sides of the reference pinnacle

Stat	POP	POC	PON	BOD	Chl	Pha	ATP
WW	2.2±0.1	142±10	29±3	17.4±2.4	0.37±0.03	0.21±0.02	0.08±0.01
LW	2.0±0.1	131±7	27±3	12.1±2.2	0.36±0.04	0.21±0.01	0.010±0.01

Table 5: Average ± SE POM budgets between windward and leeward sides of the reference pinnacle (mg m^{-2} h^{-1})

	POP	POC	PON	Chl	Pha	ATP
Average	-0.93±0.26	-26±15	-3.8±2.0	+0.07±0.16	+0.02±0.11	+0.02±0.05
n	19	19	19	18	18	13

Nutrient budgets

Mean nutrient concentrations observed on the windward and leeward sides of the reference pinnacle are summarized in Table 2. Concentrations of all species were very similar.

In January, PO$_4$, NO$_3$, NH$_4$ and SiO$_2$ net export and uptake varied respectively between -0.3 and +0.4, -0.05 and +0.19, -1.7 and +1.2, -1.3 and +2.0 mmol m^{-2} h^{-1}. In March, they varied respectively between -0.15 and 0, - 0.12 and +0.34, -3.0 and +1.0, -2.3 and -1.1 mmol m^{-2} h^{-1}. In January, DON and DOP budgets varied respectively between -3.4 and +4.8, -0.4 and +0.5 mmol m^{-2} h^{-1}. In March, they varied respectively between -8.2 and -2.0, -0.9 and -0.2 mmol m^{-2} h^{-1}. As no relationships were observed between sampling time and nutrient fluxes, we averaged these fluxes (Table 3).

POM budgets

Averages POM concentrations and BOD$_{72h}$ measured on the windward and leeward sides of the reference pinnacle are summarized in Table 4. We observed that POM concentrations were higher to the windward of the pinnacle and were lower than averages given by Charpy and Charpy-Roubaud (1991) for the 1982-1987 period.

POP, POC and PON budgets varied respectively between - 4.1 and +0.6, -115 and +142, -15 and +22 mg m^{-2} h^{-1}. Chl, Pha and ATP budgets varied respectively between - 0.8 and +1.8, -1.2 and +1.0 and -0.3 and +0.4 mg m^{-2} h^{-1}. As no relationships were observed between sampling time and POM budgets, we calculated the average of these budgets using all data.

Other pinnacles

We observed in the 4 other pinnacles surveyed during the daylight an O$_2$ production, a NO$_3$ export and a NH$_4$ uptake (Table 6).

DISCUSSION

Calcification and decalcification rates

For each mole of CaCO$_3$ precipitated, TA is lowered by 2 equivalents; the converse is true for CaCO$_3$ dissolution (Smith and Kinsey 1978). Therefore, calcification or decalcification rates (mg h^{-1}) can be calculated by the equation

$$\frac{dCaCO_3}{dt} = \frac{dTA}{dt} \times 50 \cdot$$

We calculated a calcification rate of +0.59 g Ca m^{-2} h^{-1} during the daylight and a decalcification rate of -3.64 g Ca m^{-2} h^{-1} during the night. Over a full 24h period, the pinnacle showed a net decalcification rate of -37 g Ca m^{-2} day^{-1}. The low level of calcification during the daylight may reflect the low rates of coral growth. Indeed, the proportion of living coral was very low in the lagoon pinnacles.

Table 6: Current velocity (CV : m h^{-1}), Nitrogen (mmol m^{-2} h^{-1}) and Oxygen (g m^{-2} h^{-1}) fluxes between windward and leeward part of four pinnacles.

station	CV	NO$_2$	NO$_3$	NH$_4$	O$_2$
Pin2	300	0.01	0.02	-0.61	0.11
Pin3	400	0.05	0.15	-0.51	0.12
Pin4	424	0.04	0.11	-0.68	0.22
Pin5	462	-0.10	0.34	-0.47	0.23

Table 7: Rate of calcification and accretion (*) in French Polynesian reefs.

Island	Year	g Ca m^{-2} day^{-1}	Reference
Moorea (Outer reef)	1981	0.8	Sournia et al (1981)
Moorea (Outer reef)	1984	6.3	Payri (1987)
Moorea (Outer reef)	1985	7.4	Pichon (1985)
Moorea (Outer reef)	1988	5.5	Le Campion-Alsumard et al (1993)
Moorea (Outer reef)	1992	24.3	Gattuso et al. (1993)
Tikehau (Porites)	1989	7	Charpy and Harmelin-Vivien (1992)
Tikehau (Algal rim)	1989	1	Charpy and Harmelin-Vivien (1992)
Moorea (Fringing reef)	1990	0.4*	Peyrot-Clausade et al. (1995a)
Tikehau 1	1990	1.5*	Peyrot-Clausade et al. (1995a)
Tikehau 2	1990	0.2*	Peyrot-Clausade et al. (1995a)
Takapoto	1990	2.6*	Peyrot-Clausade et al. (1995a)
Tikehau (pinnacle)	1991-1992	-37	This study

Data regardless calcification and accretion rates measured in French Polynesian reefs are summarized in Table 7. Daily values for calcification on a Polynesian reef directly exposed to the ocean at Moorea Island, varied greatly according to the period of the year (Payri, 1987).

The rate of decalcification observed in Tikehau lagoon pinnacle was high and may reflect its active destruction by endolite organisms and fishes (Peyrot-Clausade et al. 1995b). Values of accretion observed by Peyrot-Clausade et al. (1995a) in Tikehau were positive, but they were measured on experimental substrates made of blocks cut from living *Porites* colonies. Strong coral destructions were also observed in Galapagos Islands 68 g m^{-2} day^{-1} (Reaka-Kudla et al. 1996) and in Uva Island, Panama 52 g m^{-2} day^{-1} (Eakin 1996).

Organic carbon production and respiration

The average respiration rate measured during the night was -0.44 ± 0.18 g O_2 m^{-2} h^{-1} and the average net oxygen production measured during daylight was $+0.46\pm0.11$. g O_2 m^{-2} h^{-1}. The net daily oxygen production was $+0.23$ g O_2 m^{-2} and the gross daily O_2 production was 10.8 g O_2 m^{-2}.

TA measurements alone are sufficient for the determination of changes in CO_2 due to calcification (dCO_{2c}): dCO_{2c}=dTA/2. Therefore, changes in CO_2 due to photosynthesis (dCO_{2y}) can be calculated by : dCO_{2y}=dCO_2-dCO_{2c}=dCO_2-dTA/2 and the net carbon production or respiration (dCO_{2y}/dt) is obtained by (dCO_{2y}/dt)=(dCO_2-dTA/2)/dt. We observed a net production of +0.051 g C m^{-2} h^{-1} during the daylight and a net respiration of -0.316 g C m^{-2} h^{-1} during the night. Over a 24h period, the net C respiration rate was -3.2 g C m^{-2}. Corresponding gross carbon production was 4.4 g C m^{-2} day^{-1}.

Organic carbon production can also be calculated from dO_2/dt measured during daylight (dO_{2ll}/dt) and dO_2/dt measured during the night (dO_{2nl}/dt):

$$dCO_{2p}/dt=(dO_{2ll}/dt\times PQ)+(dO_{2nl}/dt\times RQ)$$

Using PQ=RQ=1, the gross C production calculated with O_2 data was equal to 4.1 g C m^{-2} day^{-1}, very similar to the value obtained with TA data.

Nutrient and POM export and import from the pinnacle

Nutrient concentrations in the water column were very low. Nutrient fluxes from pinnacles calculated from upstream downstream difference were close to zero. Uptake of NH_4 and SiO_2 could be noted, probably by benthic algae covering dead corals. Pinnacles exported on average 2 mmol NO_3 m^{-2} day^{-1} probably due to the presence of nitrifying organisms within the pinnacle. POM concentrations were on average higher to the windward side of the pinnacle. This is confirmed by the BOD$_{72h}$ which was higher also. POM fluxes were negative, indicating that the pinnacle imported more organic matter than were exported (Table 5). Most of the organic matter produced by pinnacle communities would be consumed by benthic animals and those trapped inside the reef structure. However, measurements were made on normal windy period, and, during storm events, the export of organic matter from pinnacles may be much more important.

CONCLUSIONS

Pinnacles lost -37 g Ca m^{-2} day^{-1} as a result of decalcification. The gross production based on oxygen and CO_2 fluxes was estimated to be 11 g O_2 m^{-2} day^{-1} and 4 g C m^{-2} day^{-1} but the net production was 0. As water flowed over the pinnacle, the lagoon water lost a small amount of silicate, ammonium and POM, but was enriched

Gross production: 4 g C m^{-2} day^{-1}

11 g O_2 m^{-2} day^{-1}

-37 g Ca m^{-2} day^{-1}

-0.6 g POC m^{-2} day^{-1}

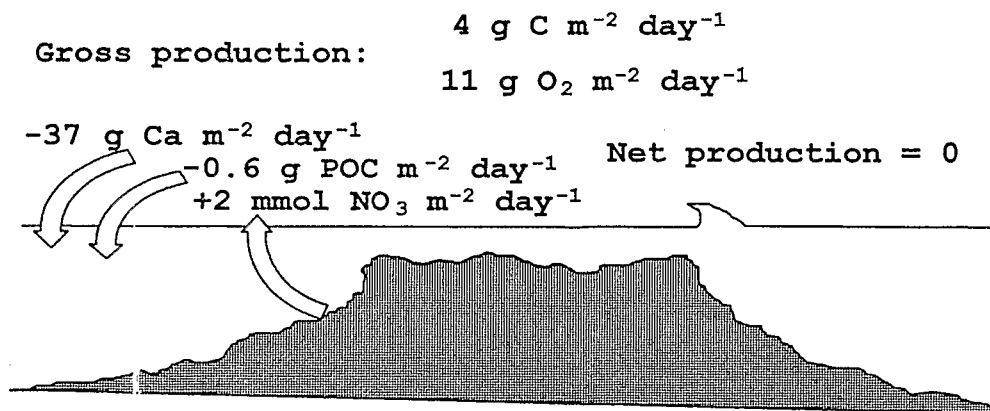+2 mmol NO_3 m^{-2} day^{-1}

Net production = 0

Figure 5: Primary production, calcification and C and nitrate budget

in nitrate (Fig. 5).

Therefore, we conclude that pinnacle community metabolism has little effect on lagoon water with no excess production and light nutrient uptake. However, during stormy conditions, it is possible that the organic matter trapped inside the pinnacle cavities would be exported to the water column and to the lagoon sediments.

REFERENCES

Charpy L, Charpy-Roubaud CJ (1991) Particulate Organic Matter fluxes in a Tuamotu Atoll Lagoon (French Polynesia). Mar Ecol Progr Ser 71 : 53-63

Charpy, L, Harmelin-Vivien M (1992) Preliminary results on production and calcification of coral reefs communities of Tikehau atoll. Notes et Doc Océanogr Tahiti 44 : 1-20

Chisholm JRM, Gattuso JP (1991) Validation of the alkalinity anomaly technique for investigating calcification and photosynthesis in coral reef communities. Limnol Oceanogr 36(6) : 1232-1239

Eakin CM (1996) Where have all carbonates gone ? A model of comparison of calcium carbonate budgets before and after the 1982-1983 El Niño at Uva Island in the eastern Pacific. Coral Reefs 15 : 109-119

Faure G, Laboute P (1984) Formations récifales: I Définition des unités récifales et distribution des principaux peuplements de Scléractinaires. In: Intes A (ed) L'atoll de Tikehau (archipel des Tuamotu, Polynésie Française). Premiers résultats. ORSTOM Tahiti, Notes et Doc Océanogr 22 : 108-136

Gattuso JP, Pichon M, Delesalle B, Frankignoulle M (1993) Community metabolism and Air-Sea CO_2 fluxes in coral reef ecosystem (Moorea, French-Polynesia). Mar Ecol Progr ser 96(3) : 585-590

Gordon DC Jr, Sutcliffe WH Jr (1973) A new dry combustion method for the simultaneous determination of total organic carbon and nitrogen in sea water. Mar Chem 1 : 231-241

Harmelin-Vivien M (1985) Atoll de Tikehau, Archipel des Tuamotu. Proc 5th int Coral Reef Congr, Tahiti 1: 211-268

Holm-Hansen O, Booth CR (1966) The measurement of adenosine triphosphate in the ocean and its ecological significance. Limnol Oceanogr 11 : 510-519

Le Campion-Alsumard T, Romano JC, Peyrot-Clausade M, Le Campion J, Paul R (1993) Influence of some coral reef communities on the calcium carbonate budget of Tiahura reef (Moorea, French Polynesia) Mar Biol 115 : 685-693

Maragos JE (1978) Measurement of water volume transport for flow studies. In Stoddart DR, Johannes RE (eds) Coral Reefs: research methods. UNESCO, Paris, pp 353-360

Marsh JA, Smith SV (1978) Productivity measurements of coral reefs in flowing water. In Stoddart DR, Johannes RE (eds) Coral Reefs: research methods. UNESCO, Paris, pp 361-378

McCloskey LR, Wethey DS, Porter JW (1978) Measurement and interpretation of photosynthesis and respiration in reef corals. In Stoddart DR, Johannes RE (eds) Coral Reefs: research methods. UNESCO, Paris, pp 379-396

Menzel D, Corwin J (1965) The measurement of total phosphorus in sea water based on the liberation of organically bound fraction by persulfate oxydation. Limnol Oceanogr 10(2) : 280-282

Odum HT, Hoskin CM (1958) Comparative studies on the metabolism of marine waters. Publ Inst Mar Sci Univ Texas 5 : 16-46

Payri CE (1987) Variabilité spatiale et temporelle de la communauté des macrophytes des récifs coralliens de Moorea (Polynésie Française). Contribution des algues au métabolisme du carbone de l'écosystème récifal. Thèse Univ Sciences et Techniques du Languedoc

Perez FF, Fraga F (1987) A precise and rapid analytical procedure for alkalinity determination. Marine Chemistry 21 : 169-182

Peyrot-Clausade M, Le Campion-Alsumard T, Hutchings P, Le Campion J, Payri C, Fontaine MF (1995a) Initial bioerosion and bioaccretion on experimental substrates in high island and atoll lagoons (French Polynesia). Oceanologica Acta 18(5) : 531-541

Peyrot-Clausade M, Le Campion-Alsumard T, Harmelin-Vivien M, Romano JC, Chazottes V, Pari N, Le Campion J (1995b) La bioérosion dans le cycle des carbonates : essais de quantification des processus en Polynésie Française. Bull Soc géol France 166(1) : 85-94

Pichon M (1985) Organic production and calcification in some coral reefs of Polynesia. In: Gabrie et al (eds) Proc 5th Internat Coral Reef Congr Tahiti French Polynesia 6 : 173-177

Reaka-Kudla ML, Feingold JS, Glynn W (1996) Experimental studies of rapid bioerosion of coral reefs in the Galápagos Islands. Coral Reefs 15 : 101-107

Riley JP, Skirrow G (eds) (1975) Chemical Oceanography. 2nd edit Academic Press London and New York

Smith SV, Kinsey DW (1978) Calcification and organic carbon metabolism as indicated by carbon dioxide. In Stoddart DR, Johannes RE (eds) Coral Reefs: research methods. UNESCO, Paris, pp 469-484

Sournia A, Delesalle B, Ricard M (1981) Premiers bilans de production organique et de calcification d'un récif barrière de la Polynésie Française. Oceanol Acta 4: 423-431

Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis (2nd ed). Bull Fish Res Bd Can 167 : 1-311

Yentsch CS, Menzel DW (1963) A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res 10 : 221-231