

Reprinted from

# JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

---

Journal of Experimental Marine Biology and Ecology,  
225 (1998) 269–283

Contribution of soft-bottoms to the community metabolism  
(primary production and calcification) of a barrier reef flat  
(Moorea, French Polynesia)

G. Boucher<sup>a,\*</sup>, J. Clavier<sup>b</sup>, C. Hily<sup>c,d</sup>, J.-P. Gattuso<sup>e,f</sup>

<sup>a</sup>URA 699 CNRS, Biologie des Invertébrés Marins, MNHN, 47 rue Cuvier, 75231 Paris, France

<sup>b</sup>Centre ORSTOM de Brest, BP 70, 29280 Plouzané, France

<sup>c</sup>UBO, URA CNRS 1513, Laboratoire d'Océanographie, BP 452, F-29275 Brest Cedex, France

<sup>d</sup>Centre ORSTOM de Tahiti, BP 529, Papeete, French Polynesia

<sup>e</sup>Observatoire Océanologique Européen, Centre Scientifique de Monaco, Avenue Saint-Martin, MC-98000  
Monaco, Monaco

<sup>f</sup>EPHE, Laboratoire de Biologie Marine et Malacologie (URA 1453 CNRS), Université de Perpignan,  
F-66860 Perpignan Cedex, France

Fonds Documentaire ORSTOM



010014163



Fonds Documentaire ORSTOM  
Cote : B 4 14163 Ex : 1

# JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

Harold Barnes, Founder Editor

## Aims and Scope

The journal provides a forum for work in the biochemistry, physiology, behaviour, and genetics of marine plants and animals in relation to their ecology; all levels of biological organization will be considered, including studies of ecosystems and ecological modelling. The main emphasis of the journal lies in experimental work, both from the laboratory and the field. Descriptive studies will, however, be acceptable if they elucidate general ecological principles. Papers describing important new techniques, methods, and apparatus will also be considered. All papers will be refereed by experts before acceptance for publication. In all cases proofs will be sent to authors. The editors, referees, and publisher will make every effort to expedite publication and the cooperation of authors in this task is welcomed.

## Managing Editors

**Ecophysiology, biochemistry, microbiology, genetics:** John Vernberg, Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, Columbia, SC 29208, USA, E-mail: vernberg@biol.sc.edu

**Community ecology, benthos of soft sediments, zooplankton & phytoplankton, pelagos, modelling, satellite imagery:** Richard Warwick, Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth, Devon, PL1 3DH, UK, E-mail: jembe@wpo.nerc.ac.uk

**Population ecology, experimental design, rocky shore and subtidal animals and plants, fish and fisheries, behaviour:** Tony Underwood, Centre for Research on Ecological Impacts of Coastal Cities, Marine Ecology Laboratories, A11, University of Sydney, Sydney, NSW 2006, Australia, E-mail: aju@bio.usyd.edu.au

## Associate Editors

**Molecular Marine Biology:** Ron Burton, Marine Biology Research Division O, Scripps Institution of Oceanography, University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0202, USA, E-mail: rburton@ucsd.edu

**Ecophysiology, biochemistry, microbiology, genetics:** Steve Stancyk, Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, Columbia, SC 29208, USA, E-mail: stancyk@sc.edu

## Consulting and Book Review Editor

Margaret Barnes, Dunstaffnage Marine Laboratory, P.O. Box 3, Oban, Argyll PA34 4AD, UK

## Editorial Board

J. Agard, St. Augustine, Trinidad and Tobago  
R. Aronson, Dauphin Island, AL, USA  
D. Ayre, Wollongong, Australia  
S.S. Bell, Tampa, FL, USA  
B.E. Brown, Newcastle upon Tyne, UK  
L.E. Burnett, Charleston, SC, USA  
C.A. Butman, Woods Hole, MA, USA  
M.G. Chapman, Sydney, Australia  
J.H. Christy, Balboa, Panama  
A. Clarke, Cambridge, UK  
C.M. Duarte, Blanes, Spain  
T. Ebert, San Diego, CA, USA  
K.J. Eckelbarger, Walpole, ME, USA  
J. Field, Cape Town, South Africa  
R.N. Gibson, Argyll, UK  
J. Gray, Oslo, Norway  
J. Grant, Halifax, NS, Canada  
M.E. Hay, Morehead City, NC, USA

D. Hedgecock, Bodega Bay, CA, USA  
P.M.J. Herman, Yerseke, The Netherlands  
R.E. Hodson, Athens, Georgia, USA  
I.R. Joint, Plymouth, UK  
P. Mladenov, Dunedin, New Zealand  
G.S. Moreira, Sao Paulo, Brazil  
J.A. Pechenik, Medford, MA, USA  
N. Polunin, Newcastle upon Tyne, UK  
D. Raffaelli, Aberdeenshire, UK  
B. Santelices, Santiago, Chile  
J.R. Sargent, Stirling, UK  
D.R. Schiel, Christchurch, New Zealand  
R. Seed, Menai Bridge, UK  
V. Smetacek, Bremerhaven, Germany  
A. Tamaki, Nagasaki, Japan  
S.F. Thrush, Hamilton, New Zealand  
C.D. Todd, St. Andrews, UK

**Submission of articles:** Manuscripts should be sent (in triplicate) directly to the relevant Section Editor.

**Publication information:** *Journal of Experimental Marine Biology and Ecology* (ISSN 0022-0981). For 1998 volumes 216-227 are scheduled for publication. Subscription prices are available upon request from the Publisher. Subscriptions are accepted on a prepaid basis only and are entered on a calendar year basis. Issues are sent by surface mail except to the following countries where Air delivery via SAL mail is ensured: Argentina, Australia, Brazil, Canada, Hong Kong, India, Israel, Japan, Malaysia, Mexico, New Zealand, Pakistan, PR China, Singapore, South Africa, South Korea, Taiwan, Thailand, USA. For all other countries airmail rates are available upon request. Claims for missing issues should be made within six months of our publication (mailing) date.

**Orders, claims, and product enquiries:** please contact the Customer Support Department at the Regional Sales Office nearest you:

**New York:** Elsevier Science, P.O. Box 945, New York, NY 10159-0945, USA; Tel. (+1)212-633-3730; [Toll free number for North American customers: 1-888-4ES-INFO (437-4636)], Fax (+1)212-633-3680; E-mail usinfo-f@elsevier.com

**Amsterdam:** Elsevier Science, P.O. Box 211, 1000 AE Amsterdam, The Netherlands; Tel. (+31)20-4853757, Fax (+31)20-4853432, E-mail nlinfo@elsevier.nl

**Tokyo:** Elsevier Science, 9-15 Higashi-Azabu 1-chome, Minato-ku, Tokyo 106, Japan; Tel. (+81)3-5561-5033, Fax (+81)3-5561-5047, E-mail info@elsevier.co.jp

**Singapore:** Elsevier Science, No. 1 Temasek Avenue, #17-01 Millenia Tower, Singapore 039192; Tel. (+65)434-3727, Fax (+65)337-2230, E-mail asiainfo@elsevier.com.sg

**Back volumes:** Please contact the Publisher.



## Contribution of soft-bottoms to the community metabolism (primary production and calcification) of a barrier reef flat (Moorea, French Polynesia)

G. Boucher<sup>a,\*</sup>, J. Clavier<sup>b</sup>, C. Hily<sup>c,d</sup>, J.-P. Gattuso<sup>e,f</sup>

<sup>a</sup>URA 699 CNRS, Biologie des Invertébrés Marins, MNHN, 47 rue Cuvier, 75231 Paris, France

<sup>b</sup>Centre ORSTOM de Brest, BP 70, 29280 Plouzané, France

<sup>c</sup>UBO, URA CNRS 1513, Laboratoire d'Océanographie, BP 452, F-29275 Brest Cedex, France

<sup>d</sup>Centre ORSTOM de Tahiti, BP 529, Papeete, French Polynesia

<sup>e</sup>Observatoire Océanologique Européen, Centre Scientifique de Monaco, Avenue Saint-Martin, MC-98000 Monaco, Monaco

<sup>f</sup>EPHE, Laboratoire de Biologie Marine et Malacologie (URA 1453 CNRS), Université de Perpignan, F-66860 Perpignan Cedex, France

Received 4 April 1997; received in revised form 30 August 1997; accepted 9 September 1997

### Abstract

The relative contribution of soft bottoms to the community metabolism (primary production, respiration and net calcification) of a barrier reef flat has been investigated at Moorea (French Polynesia). Community metabolism of the sedimentary area was estimated using in situ incubations in perspex chambers, and compared with estimates of community metabolism of the whole reef flat obtained using a Lagrangian technique (Gattuso et al., 1996). Carbon flux in coral reefs. 1. Lagrangian measurement of community metabolism and resulting air-sea CO<sub>2</sub> disequilibrium. Mar. Ecol. Prog. Ser. 145, 109–121). Net organic carbon production (*E*), respiration (*R*) and net calcification (*G*) of sediments were measured by seven incubations performed in triplicate at different irradiance. Respiration and environmental parameters were also measured at four randomly selected additional stations. A model of Photosynthesis-irradiance allowed to calculate oxygen (O<sub>2</sub>), organic carbon (CO<sub>2</sub>) and calcium carbonate (CaCO<sub>3</sub>) evolution from surface irradiance during a diel cycle. As chlorophyll *a* content of the sediment was not significantly different between stations, primary production of the sediment was considered as homogeneous for the whole lagoon. Thus, carbon production at the test station can be modelled from surface light irradiance. The modelled respiration was two times higher at the test station than the mean respiration of the barrier reef, and thus underestimated sediment contribution to excess production. Sediments cover 40–60% of the surface and accounted for 2.8–4.1% of organic carbon excess production estimated with the modelled *R* and 21–32% when mean *R* value was

\*Corresponding author.

considered. The sedimentary  $\text{CaCO}_3$  budget was a very minor component of the whole reef budget. © 1998 Elsevier Science B.V.

**Keywords:** Coral reef; Community metabolism;  $\text{O}_2$  and  $\text{CO}_2$  budgets; Calcification; Sediment

## 1. Introduction

High gross primary production ( $P_g$ ) of coral reefs is generally attributed to coral and algal structures and little attention has been paid to the contribution of sediment patches around coral heads (Sorokin, 1993). However, coral cover seldom exceeds 70% in most barrier reefs and soft-bottoms constitute large areas in most lagoons, sometimes covered by seagrass beds. Sediments could have a significant contribution to reef biogeochemistry as sinks of carbon (Buddemeier, 1996), as they are sites of organic matter storage, active bacterial activity and diagenesis. Carbonate sands result from the mechanical degradation of reef structures, and bioerosion of coral heads and calcareous algae (Harmelin-Vivien et al., 1992; Le Campion-Alsumard et al., 1993; Peyrot-Clausade et al., 1995). However, coral debris never constitutes a dominant element of lagoonal sediments and most sands are characterized by molluscs, foraminifers and *Halimeda* biofacies (Chevillon, 1996). Sediments are also subjected to passive (Tribble et al., 1990; Walter et al., 1993) or active dissolution of  $\text{CaCO}_3$  via microbiota activity (Peyré-Venec, 1987). However, they can also display significant  $\text{CaCO}_3$  deposition as sand grains are sometimes covered with a dense coating of calcareous microalgae and harbour large populations of foraminiferans (Le Calvez and Salvat, 1980).

Studies on community metabolism typically rely on measurements of changes of dissolved inorganic carbon, total alkalinity and dissolved oxygen of a water mass as it flows above the system of interest (Lagrangian method) or in isolated bodies of water (incubation method). The first method enables the measurement of community metabolism of shallow-water reef systems (reviewed by Kinsey, 1985a,b; Smith, 1995). The reef flat is characterized by different physiographic zones and represents a combination of habitats for corals, plants and for organisms inhabiting sand and rubble. The second method allows measurement *in situ* of the community metabolism of the various components of a reef system (corals, algae, rubble, sediment: Payri, 1987; Gattuso and Jaubert, 1990; Boucher et al., 1994; Clavier et al., 1994; Yap et al., 1994). The reef metabolic budget is sometimes reconstructed from the sum of the different components weighted by their areal surface cover (Nakamori et al., 1992). Both methods seek to measure net or excess community production ( $E$ ), and respiration ( $R$ ) in order to calculate gross production ( $P_g = E + R$ ) as well as the inorganic carbon production also termed net calcification ( $G$ ).

The aim of this study is to estimate the relative contribution of soft bottoms to global production of organic carbon and calcium carbonate of the Tiahura barrier reef flat (Moorea, French Polynesia). Data related to the community metabolism of the whole barrier reef were published in a companion paper (Gattuso et al., 1996).

## 2. Methods

### 2.1. Study site

The Tiahura barrier reef (Fig. 1), located on the NW coast of the Island of Moorea ( $17^{\circ}29'S$ ,  $149^{\circ}54'W$ ), has been intensively studied during the past 25 years. Descriptions of the spatial variability of benthic assemblages can be found in Richard (1982) and Galzin (1985). The barrier reef flat is separated from the fringing reef by a narrow drainage channel (about 6 m deep and 100 m wide) exhibiting rather strong currents. The barrier reef at Tiahura is ca. 490 m wide and 1.3 m deep (0–3 m) and the fringing reef is ca. 250 m wide and less than 1 m deep. The tidal range is lower than 0.4 m. Oceanic water crosses the front reef and drains the barrier reef up to the drainage channel where a strong current flushes the lagoon through the Taotoi Pass.

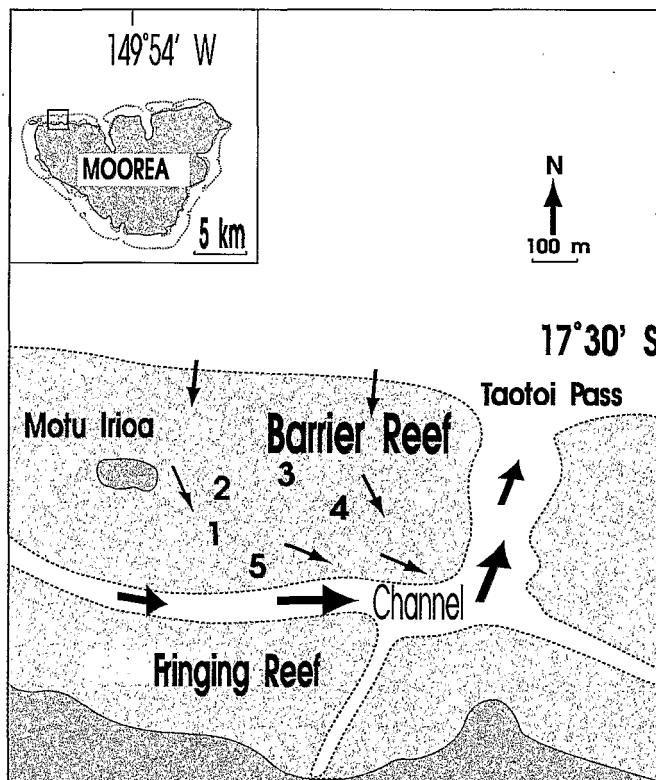


Fig. 1. Location of the investigated stations and logger deployment on the Tiahura transect (Moorea Island, French Polynesia). St 1–4, DCMU-inhibited incubations at light; St 5, test diel cycle station at ambient light. Arrows indicate the transit of oceanic water through the barrier reef.

## 2.2. Sediment production and respiration

### 2.2.1. Experimental set up

One test station was selected on the barrier reef in an area of bare medium sand called 'La patte d'Oie' representative of the average depth of the lagoon (1.4 m). The estimation of sediment metabolism was obtained by the incubation procedure previously described by Boucher et al. (1994) and Clavier et al. (1994). A known volume of bottom water was incubated in three enclosures deployed on the bottom at ca. 2 m apart. The surface area was 0.2 m<sup>2</sup> and the enclosed volume of sea water varied between 57 and 59 l. Seven successive runs of triplicated incubations, lasting between 77 and 100 min, were performed during a diel cycle (07:30 to 19:42) in order to get the whole range of irradiance. Between each incubation series, the domes were opened for 10 min in order to flush the water trapped in the enclosure.

The concentration of dissolved oxygen, pH and sea water temperature were measured in the chambers as described earlier. The oxygen sensor (YSI) and the pH electrode (Radiometer, GK 2401C) were calibrated daily. The oxygen sensor was calibrated against air-saturated seawater. The pH electrode was fitted in a pressure-compensating device similar to the one described by Chisholm et al. (1990). It was calibrated against N.B.S. buffers (pH 6.865 and 7.413 at 37°C; Radiometer). Replicate sea water samples were collected at the beginning and at the end of each incubation inside the chambers, filtered on Whatman GF/C membranes and stored in BOD bottles in darkness at 4–10°C pending subsequent potentiometric determination of total alkalinity (Gattuso et al., 1993). The difference in temperature between the enclosed and external seawater never exceeded 1°C.

Incident irradiance was measured continuously ashore and on some occasions underwater during all field experiments using an LI-192SA quantum sensor, averaged and logged every minute on an LI-1000 data-logger.

### 2.2.2. Community productivity and calcification

Calcification and partitioning of organic and inorganic carbon metabolism were computed using the alkalinity anomaly technique (Smith and Key, 1975). Net primary production and calcification during each incubation were calculated as follows:

$$p_{\text{net}}(\text{O}_2) = \frac{\Delta[\text{O}_2]v}{s\Delta t \times 10^3} \quad (1)$$

$$p_{\text{net}}(\text{CO}_2) = \frac{\Delta \text{DIC}v}{s\Delta t} - g \quad (2)$$

$$g = \frac{\Delta \text{TA}v}{2s\Delta t} \quad (3)$$

where:  $p_{\text{net}}$ =community net primary production (mmol m<sup>-2</sup> h<sup>-1</sup>);  $g$ =community calcification (mmol CaCO<sub>3</sub> m<sup>-2</sup> h<sup>-1</sup>);  $\Delta[\text{O}_2]$ =change in the concentration of dissolved oxygen during the incubation ( $\mu\text{mol l}^{-1}$ ) estimated by regressing [O<sub>2</sub>] versus time;  $v$ =chamber volume (l);  $s$ =sediment surface area (m<sup>-2</sup>);  $\Delta t$ =incubation time (h);

$\Delta DIC$ =change in total inorganic carbon ( $\text{mmol l}^{-1}$ );  $\Delta TA$ =change in total alkalinity (TA,  $\text{meq l}^{-1}$ ).

Dissolved inorganic carbon was calculated from measurements of pH and total alkalinity. The distribution of ionic species was computed using the  $\text{CO}_2$  acidity constants (Mehrbach et al., 1973), the  $\text{CO}_2$  solubility coefficient (Weiss, 1974), the borate acidity constant (Hansson and Jagner, 1973) and the water dissociation constant (Lyman, 1957). The total borate molarity was calculated using the Culkin (1965) ratio to salinity. Rates of productivity (expressed both in terms of  $\text{O}_2$  and  $\text{CO}_2$ ) and calcification were plotted as a function of the average atmospheric irradiance measured during the incubation. Several functions (exponential, Michaelis-Menten and hyperbolic tangent) were fitted to the community productivity (PI) and calcification (GI) data. An exponential function was chosen as it provided high  $r^2$  and low asymptotic standard errors. It was fitted to the data using the shareware package MacCurveFit 1.1:

$$p = p_{\max}(1 - \exp(-I/I_k)) + r$$

where:  $p$ =rate of net productivity (or calcification);  $p_{\max}$ =rate of maximal gross productivity (or calcification);  $I$ =irradiance;  $I_k$ =irradiance at which the initial slope intercepts the horizontal asymptote; and  $r$ =respiration rate (or net night-time calcification).

Night-time, day-time and daily (24-h) rates of gross production, respiration and net calcification were estimated by numerically integrating (1-min intervals) the data for the fitted lines against irradiance in air ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) measured during the experiment as well as during several subsequent days. By convention, small letters refer to instantaneous and hourly fluxes ( $g$ ,  $p$ ,  $r$ ) while capital letters ( $G$ ,  $P$ ,  $R$ ) refer to fluxes integrated over the day, night or 24 h. In accordance with earlier procedures (Gattuso et al., 1993), the sign of the daily metabolic parameters is shown in the figures and tables, but absolute values are reported in the text and when using weight units. All parameters related to the organic carbon metabolism were computed using net primary productivity measured according to the  $\text{CO}_2$  technique.

Total production of the reef ( $P_T$ ), simultaneously measured by Gattuso et al. (1996), was estimated as the sum of hard bottom production ( $P_{HB}$ ) and soft bottom production ( $P_S$ ), i.e.  $P_T = (xP_{HB} + yP_S)$  where  $x$ =hard bottom surface and  $y$ =soft bottom surface.

### 2.2.3. Spatial variability of respiration, alkalinity fluxes and environmental parameters

Four additional stations (St 1–4) were randomly selected between the coral heads of the barrier reef (Fig. 1) in order to obtain an estimate of spatial variability of environmental parameters, community respiration and net calcification. Runs of triplicate incubations were performed at the water-sediment interface as described above. Respiration ( $\text{O}_2$  and  $\text{CO}_2$  techniques) was measured during morning hours by inhibiting photosynthesis with DCMU (Garrigue et al., 1992). Sediment cores ( $5.31 \text{ cm}^2$ ) were collected by scuba divers inside each of the three enclosures for measurements of silt content (%) and median ( $\mu\text{m}$ ) of the sediment, organic matter content (weight loss at  $450^\circ\text{C}$ ), chlorophyll  $a$  and phaeophytin ( $\text{mg m}^{-2}$ ). The first centimeter of the core was

deep-frozen and later lyophilised pending analysis. Pigments were extracted using 90% (v/v) acetone and measured spectrophotometrically at 665 and 750 nm before and after acidification. Biomass was calculated using the equations of Lorenzen (1967).

### 2.3. Statistics

Statistical testing was carried out using the Statgraphics package. Data are reported as mean  $\pm$  standard error of the mean;  $N$  = sample size. Significant differences between parameters or processes measured at the different stations were tested using the Kruskal-Wallis test ( $H_0$  = no difference among the stations; significance at  $P < 0.05$ ). Significant differences between parameters or processes measured at test station 5 and at the other stations were tested using the Mann-Whitney test.  $H_0$  was that the medians of the samples are equal. If the  $P$  value for any of the alternative hypothesis (mean 1 greater or lower than mean 2) was less than 0.05 for a 95% confidence level, the null hypothesis was rejected.

The community respiratory quotient (CRQ) was estimated by regressing the  $\text{CO}_2$  fluxes against the  $\text{O}_2$  fluxes. Since both fluxes were subjected to natural variability and measurement errors, geometric mean regression was used to calculate the slope of the regression line.

## 3. Results

The mean values of the different environmental parameters and processes measured at the five stations investigated on the barrier reef are given in Table 1. Sediments were fine (St 1, 2, 5) to medium sand (St 3 and 4), with a quite similar silt fraction and a high organic content (4.1–5.5%). Sediment chlorophyll *a* and phaeophytin content were not significantly different between the five stations (Kruskal-Wallis test:  $P = 0.06$  and 0.26, respectively). The median biomass at the diel cycle station was not significantly different from the median biomass measured at the other stations (Mann-Whitney test,  $P = 0.20$ ).

Table 1  
Mean values (SE) of the environmental parameters measured at five stations of the Tiahura barrier reef

Station	Date	Md	Silt	OM	Chloro	Pheo	$R_{\text{O}_2}$	$R_{\text{CO}_2}^\circ$	TA
ST1	23/08/1992	250	1.65	4.09 (0.16)	14.05 (1.90)	9.89 (1.5)	1.73	1.29	1.72 (0.74)
ST2	11/08/1992	250	2.14	4.20 (0.02)	22.53 (4.62)	14.68 (2.34)	2.47	2.36	1.02 (0.06)
ST3	21/08/1992	500	1.94	5.54 (0.67)	14.12 (1.72)	12.18 (1.36)	2.05 (0.16)	1.89 (0.24)	1.16 (0.08)
ST4	20/08/1992	500	1.85	5.03 (0.40)	15.30 (2.54)	11.95 (2.09)	2.16 (0.25)	1.61 (0.24)	1.01 (0.06)
ST5	14–15/08/1992	250	0.74	4.31 (0.04)	18.66 (2.05)	9.16 (2.21)	2.97 (0.15)	4.04 (0.21)	1.48 (0.24)
<i>N</i>		1	1	3	9	9	1–3	1–3	9

Md, median ( $\mu\text{m}$ ); silt, silt content (%); OM, organic matter content (%); Chloro and Pheo, chlorophyll *a* and phaeophytin content ( $\text{mg Chl m}^{-2}$ );  $R_{\text{O}_2}$  and  $R_{\text{CO}_2}^\circ$ , respiration estimated by the oxygen and carbon dioxide technique, respectively ( $\text{mmol m}^{-2} \text{ h}^{-1}$ ); TA, total alkalinity flux ( $\text{mEq m}^{-2} \text{ h}^{-1}$ ). *N*, number of replicates.

The pigment content of the test station (St 5) was thus considered as representative of the sediment of the whole barrier reef.

The average community respiratory quotient (CRQ) was 1.35 for the four barrier reef stations. When the respiration of the diel cycle station was taken into account, CRQ increased to 2.2. Respiration rate at St. 5 ( $4.04 \pm 0.21 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ,  $N=3$ ) was significantly higher (Mann-Whitney,  $P=0.001$ ), than respiration rate measured at St. 1–4 ( $1.77 \pm 0.16 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ,  $N=8$ ). Thus respiration at the test station cannot be considered as representative of the whole barrier reef.  $\text{CaCO}_3$  dissolution in darkness was not significantly different between the stations (Kruskal-Wallis test;  $P=0.29$ ) and St. 5 was not significantly different from the mean dissolution of St. 1–4 ( $0.74 \pm 0.12$  vs.  $0.60 \pm 0.07 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$  (Mann-Whitney test,  $P=0.35$ ).

The results of the diel cycle experiment at St. 5 are shown in Table 2. The duration of night and day were, respectively, 713 and 727 min. Irradiance in air varied from 0 to  $1853 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  and irradiance at the water-sediment interface was estimated to be 78% of surface irradiance. The rate of oxygen production and of photosynthetic  $\text{CO}_2$  fixation in the chambers increased as a function of increasing irradiance and then decreased until dawn. Photosynthetic processes prevailed during the whole day on sediment respiration. Changes in TA indicate a net precipitation of  $\text{CaCO}_3$  during the day and a net dissolution at night.

The PI and GI curves calculated from sediment incubations are shown in Fig. 2. The associated curve-fitting parameters are given in Table 3. The coefficients of determination were always higher than 0.8. The daily metabolic parameters are shown in Table 4 and compared to the results obtained for the whole reef flat. The  $\text{O}_2$  and  $\text{CO}_2$  techniques provided quite different results. The gross and excess production ( $P_g$  and  $E$ ) and the daily respiration ( $R$ ) estimated using the  $\text{O}_2$  technique were lower than the estimates derived from the  $\text{CO}_2$  technique. However, the  $P_g/R$  ratios obtained with the

Table 2  
Oxygen, carbon dioxide and total alkalinity fluxes measured during seven runs of triplicated incubations at station 5

Runs	Initial time	Final time	Surface irrad. ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	$N$	$\text{O}_2$ ( $\text{mmol m}^{-2} \text{ h}^{-1}$ )	$N$	$\text{CO}_2^\circ$ ( $\text{mmol m}^{-2} \text{ h}^{-1}$ )	TA (mEq $\text{m}^{-2} \text{ h}^{-1}$ )
1	7.33	9.00	860	3	2.52 (0.18)	2	-4.12 (0.05)	-1.15 (0.44)
2	9.13	10.35	1516	3	4.15 (0.20)	3	-7.23 (0.17)	-1.67 (0.08)
3	10.54	12.20	1853	3	4.42 (0.24)	3	-8.89 (0.48)	-2.86 (0.34)
4	12.41	14.23	1724	3	4.39 (0.24)	3	-6.93 (0.36)	-2.32 (0.26)
5	14.30	16.02	895	3	2.0 (1.28)	3	-5.81 (0.32)	-2.57 (0.66)
6	16.22	17.48	126	3	0.06 (0.18)	2	0.39 (0.44)	0.90 (0.35)
7	18.03	18.42	0	3	-2.97 (0.15)	3	4.04 (0.21)	1.49 (0.24)

$N$ , number of replicates; initial and final time, beginning and end of each run of incubation in decimal hours; surface irradiance, average surface irradiance during the series of incubation;  $\text{O}_2$ , oxygen metabolism;  $\text{CO}_2^\circ$ , carbon dioxide metabolism; TA, total alkalinity flux.

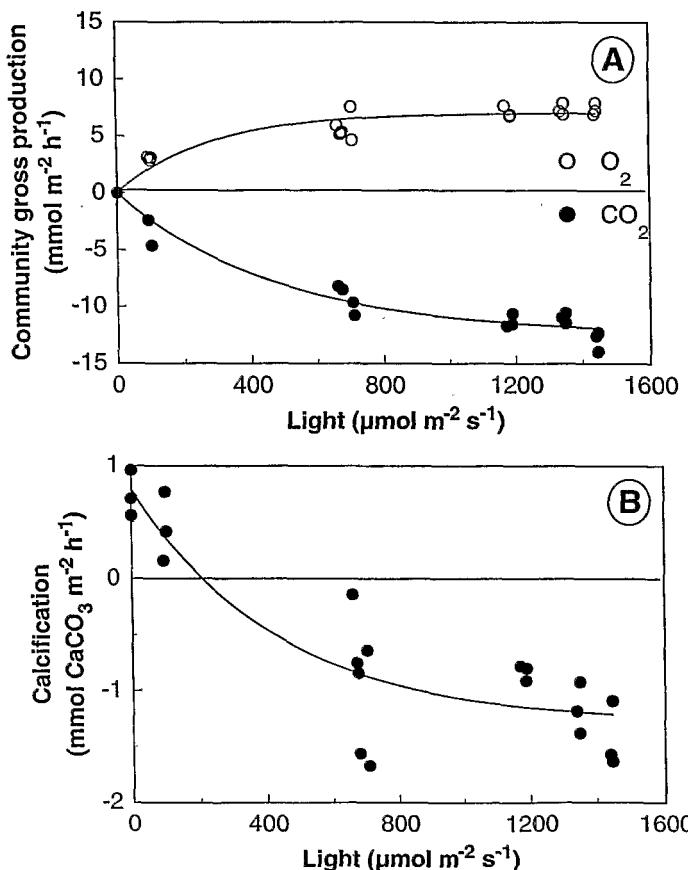


Fig. 2. Community photosynthesis (PI) and calcification (GI) irradiance curves. (A) Net primary productivity in mmol O<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> (○) or mmol CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> (●); (B) calcification in mmol CaCO<sub>3</sub> m<sup>-2</sup> h<sup>-1</sup>; incident surface irradiance in μmol photons m<sup>-2</sup> s<sup>-1</sup>.

two methods were similar (0.99 and 1.07) and close to 1. CaCO<sub>3</sub> dissolution at night exceeded CaCO<sub>3</sub> precipitation during the day and the daily budget indicated a slight dissolution (2.4 mmol CaCO<sub>3</sub> m<sup>-2</sup> day<sup>-1</sup>).

Table 3

Curve fitting parameters for the oxygen metabolism (O<sub>2</sub>), organic carbon metabolism (CO<sub>2</sub>) and calcification (G) vs. surface irradiance

	p <sub>max</sub> (mmol m <sup>-2</sup> h <sup>-1</sup> )	I <sub>k</sub> (mmol m <sup>-2</sup> s <sup>-1</sup> )	r (mmol m <sup>-2</sup> h <sup>-1</sup> )	r <sup>2</sup>
O <sub>2</sub>	6.8±0.5	548±153	-2.3±0.4	0.92
CO <sub>2</sub> °	-12.3±0.9	696±149	3.5±0.5	0.96
G (CaCO <sub>3</sub> )	-2.1±0.3	560±242	0.8±0.2	0.82

The fitting equation is an exponential function [p = p<sub>max</sub>(1 - exp(-I/I<sub>k</sub>)) + r]. Mean±1 asymptotic standard error; r<sup>2</sup>, coefficient of determination.

Table 4

Comparison of the daily metabolic budget obtained by the oxygen and the carbon dioxide methods for sediments and for the barrier reef flat

Method	Parameters	O <sub>2</sub> (mmol m <sup>-2</sup> day <sup>-1</sup> )	CO <sub>2</sub> <sup>°</sup> (mmol m <sup>-2</sup> day <sup>-1</sup> )	CaCO <sub>3</sub> (mmol m <sup>-2</sup> day <sup>-1</sup> )
Sediment incubations <sup>a</sup>	R	-55.7	84.7	$G_{\text{night}}$ , 9.4
	P <sub>g</sub>	+54.9	-91	$G_{\text{day}}$ , -7.0
	E	-0.8	-6.3	$G_{24h}$ , 2.4
	P <sub>g</sub> /R	0.99	1.07	
Drifting logger <sup>b</sup>	R	-816	730	$G_{\text{night}}$ , -36
	P <sub>g</sub>	+818	-821	$G_{\text{day}}$ , -150
	E	+3	-91	$G_{24h}$ , -186
	P <sub>g</sub> /R	1.01	1.18	

<sup>a</sup>This study. <sup>b</sup>Gattuso et al., 1996; Gattuso, unpubl. data.

#### 4. Discussion

Carbon production of soft bottoms at Tiahura reef can be related to sediment surface, surface irradiance and microphyte biomass. Changes in the relative abundance of the major epibiotic components on the barrier reef are gradual from the crest to the drainage channel (Gattuso et al., 1993). At the back of the reef front, living and dead corals can cover up to 31 and 20% of the substratum, respectively. Sedimentary deposits are mostly represented by rubble (up to 20% of substratum cover) with less than 5% of coarse sand or gravel. When moving landwards, the percentage of live coral decreases to below 2% near the channel; some dead massive colonies are covered with *Turbinaria* and fine to medium sand may build up into hydraulic dunes. This spatial heterogeneity explains why estimates of sediment cover at the study site differ widely depending on authors: 61 (Richard, 1982) to 45% (estimation from measurements carried out on 10 replicated transects, in 1992; Galzin, pers. comm.).

Planktonic and benthic primary production in tropical lagoons can be predicted from the light energy received at the air-sea interface (Platt and Jassby, 1976; Charpy-Roubaud, 1988; Charpy and Charpy-Roubaud, 1990). The Tiahura barrier reef displays a very shallow reef flat where planktonic primary productivity was shown to be negligible (Delesalle et al., 1993). Total production mostly results from benthic hard- and soft-bottom activities (Sournia, 1976a,b, 1977; Sournia et al., 1981). No macroalgae or seagrass develop on sedimentary areas and soft-bottom primary production therefore derives exclusively from microphytobenthos activity. Primary production is known to be approximately proportional to the biomass of photosynthetic pigments (Rasmussen et al., 1983) as long as depth and turbidity are constant. The mean content of chlorophyll *a* in the first centimeter of sediment was low (16.5 mg m<sup>-2</sup>) compared to results previously reported for the Tiahura reef system (70 mg m<sup>-2</sup> in the first 2 cm: Vaugelas, 1982) and for other tropical sites (100–900 mg m<sup>-2</sup> in the first 3 cm: Sorokin, 1993). This may be due to the fact that only the pigments located within the first centimeter of the cores were extracted.

The rate of net photosynthesis does not decline at high irradiance at our study site. The lack of photoinhibition may be due to an acclimation of tropical microphytes to high

irradiance (Sournia and Ricard, 1975; Delesalle, 1985). Blanchard (1994) suggested that substrate bioturbation and active migration of the microphytes in the sediment enable the microphytobenthos to avoid photoinhibition. This turn-over of the microphytes could explain why the high level of primary production can be maintained even in shallow waters subjected to high irradiance.

Previous studies on the different components of a reef flat have demonstrated that sediment and rubble display a low excess production compared to coral- and algal-dominated reef communities (Odum and Odum, 1955; Marsh, 1974; Sournia, 1976a). Microbenthic diatoms, cyanobacteria and symbiotic foraminiferans are the major primary producers in most reef flat sediments. Their gross primary production in bare sands is generally 2–4 times lower than the production of symbionts on reef flats or patch reefs (Sorokin, 1993). As a result, net heterotrophic sand community have been reported when respiration related to organic matter degradation prevails on carbon production (Yap et al., 1994).

The large differences in the metabolic activity derived by the  $O_2$  and  $CO_2$  techniques suggest that the processes measured in enclosures may be different from those measured using a Lagrangian method. The daily metabolic budget obtained in the enclosures shows that respiration rate estimated by  $CO_2$  production was 1.52 higher than the respiration rate estimated by  $O_2$  uptake, whereas this ratio was only 0.89 for the Lagrangian method. Such a difference suggests the occurrence of a significant anaerobic metabolism at the water–sediment interface which increases  $CO_2$  release relative to  $O_2$  uptake. As a result, the estimates of excess production are one order of magnitude greater with the  $CO_2$  technique than with the  $O_2$  technique. A better estimation of carbon production can be anticipated from the carbon dioxide technique. Sediment gross production corresponds to  $P_g = 1.09 \text{ gC m}^{-2} \text{ day}^{-1}$  and excess production to  $E = 0.08 \text{ gC m}^{-2} \text{ day}^{-1}$ . These production estimates are within the range of the data ( $P_g = 0.4\text{--}1.4$ ;  $E = -0.5\text{--}0.78 \text{ gC m}^{-2} \text{ day}^{-1}$ ) known for coral sand dominated by diatoms and symbiotic foraminifera (Sorokin, 1993). With a  $P_g/R = 1.07$ , the sedimentary areas of the barrier reef flat at Tiahura are slightly autotrophic but less so than the whole barrier reef where photosynthesis by coral symbionts, macroalgae and turf algae is higher compared to the daily rate of respiration ( $P_g/R = 1.18$ ).

The rate of respiration was twice as high at the test site than in the other stations. This is a potential problem in interpreting the community metabolism data and deriving the contribution of soft-bottoms to whole reef processes. Such a discrepancy may be due to differences in the experimental design: respiration was measured at night at the main station, whereas it was measured during the day using DCMU to inhibit photosynthetic processes at the other stations. The two procedures were shown to provide similar values in a previous study (Garrigue et al., 1992). However, the assumption that areal respiration in darkness is equal to areal respiration in the light has been questioned because an increase of oxygen penetration in the sediment during the day stimulates organic matter oxidation (Revsbech et al., 1981; Hofman et al., 1991). Experiments carried out on tropical hypersaline mats and temperate intertidal sediments have shown that increased rates of areal gross photosynthesis are not only due to enhanced areal net photosynthesis, but also to enhanced areal respiration (Epping and Jørgensen, 1996). By assuming that areal respiration in darkness is equal to areal respiration in the light, bell

jar incubations may significantly underestimate areal respiration in the light and areal gross photosynthesis. Lastly, respiration at the beginning of the night tends to be higher than mid-night respiration (Kinsey, 1985b), a trend which could have explained the respiration overestimation obtained for the production experiment performed at the test station. Thus, the estimates of community respiration and sediment surface cover are the major sources of uncertainty for deriving the relative contributions of soft and hard bottoms to the community metabolism of the Tiahura barrier reef flat (Table 5). Soft bottoms contribute 2.8–32% of the barrier reef excess production. Uncertainties concerning sediment surface cover are far less important to the estimates of soft bottom contribution to global excess production than potential errors in respiration estimates. The low contribution of sediments derived from the modelled  $R$  appears to result from the overestimation of respiration discussed above. We tentatively suggest sediments contribute for 20–30% to the organic carbon metabolism of the Tiahura barrier reef flat.

Kinsey (1979) has previously demonstrated that reef sediment precipitates at least four to five times less  $\text{CaCO}_3$  than reef flats. Their contribution to community calcification of the Tiahura barrier reef flat is negative due to net dissolution of  $\text{CaCO}_3$  (Table 5). Incubations during the day clearly show that there is a light-induced  $\text{CaCO}_3$  precipitation, similar to that occurring in calcareous algae and zooxanthellate scleractinian corals. As a result, the decrease in total alkalinity observed during incubation in the light should be more related to the activity of calcifying organisms than to the anaerobic chemical reactions occurring in the sediment. In normal oxygenated water, non-conservative TA changes above the sediment are considered as almost exclusively due to  $\text{CaCO}_3$  precipitation or dissolution (Stumm and Morgan, 1981). The increase in TA observed in darkness could also result from the mineralization of organic matter and/or anaerobic production. Rapid reactions occurring in the interstitial water (aerobic respiration with nitrification and ammonification as well as reduction of manganese, iron and sulphate) are potential sources of alkalinity for the water column (Brewer and Goldman, 1976). Previous incubations in carbonate sand have shown that nitrogen fluxes at the water–sediment interface are very low in most tropical sediments (Boucher and Clavier, 1990). Therefore, the associated changes in TA during short-term incubations (90 min) are probably negligible. Sulphate reduction also produces a net flux of alkalinity in the anaerobic interstitial which may well be transferred into the overlying water, particularly for systems with lots of terrigenous material with iron (Smith, pers. comm.). In the low-turbulence organic sink areas of some lagoons, sulphate reduction

Table 5

Relative contribution of sediments (%) to total excess production ( $E$ ) and net calcification ( $G$ ) according to sediment cover and respiration estimates at Tiahura reef

Sediment cover (%)	$E$		$G$
	$R$ model	$R$ mean	
40	2.8	21.3	-0.52
50	3.4	26.7	-0.65
60	4.1	32	-0.77

$R$  model, respiration calculated from the PI model;  $R$  mean, mean respiration at St 1–4).

can explain up to 15% of TA change (Kinsey, 1978). At Tiahura, sediments comprise pure white coral sand on the barrier reef and there is no free iron available to bind any H<sub>2</sub>S which could be released.

Metabolic CO<sub>2</sub> produced at night causes a significant pH decrease which could dissolve CaCO<sub>3</sub>, but the enclosed sea water nevertheless remains supersaturated with respect to aragonite (Aller, 1982). Using saturation indices, Charpy-Roubaud et al. (1996) recently confirmed the hypothesis that the aerobic oxidation of organic matter at the water sediment interface leads to the dissolution of coral sand, although this release does not appear in the calcium profile. Supersaturation decreases in the anoxic zone but the carbonate phase precipitates and inhibits any increase in pH.

The chemical dissolution of carbonates cannot be considered as the only source of alkalinity at the water-sediment interface. Biological activity is also known to affect total alkalinity as observed for organisms boring coral skeletons (Lazar, 1991; Peyrot-Clausade et al., 1995). The activity of microboring organisms attached to the sand grains as well as the gut transit of sand grains in many benthic invertebrates are likely contributors to the dissolution process. Lastly, dissolution of foraminiferan tests has been identified as an important source of carbonate in many coastal environments (Green et al., 1993). The sedimentary CaCO<sub>3</sub> budget does not contribute significantly to the CaCO<sub>3</sub> budget of the Tiahura barrier reef flat.

## Acknowledgements

Thanks are due to Y. Chancerelle for assistance in the field, ORSTOM staff for assistance in the laboratory and to C. Bussi for help with data processing. This study was carried out at the CRIOBE field facility at Moorea (EPHE) and at the ORSTOM Center in Tahiti. This work was supported by grants from the Centre National de la Recherche Scientifique (moyens mi-lourds INSU), Programme National Récifs Coralliens (PNRCo), Programme Lagon ORSTOM and from the Muséum National d'Histoire Naturelle (Grande mission 1992). This is a contribution of PNRCo.

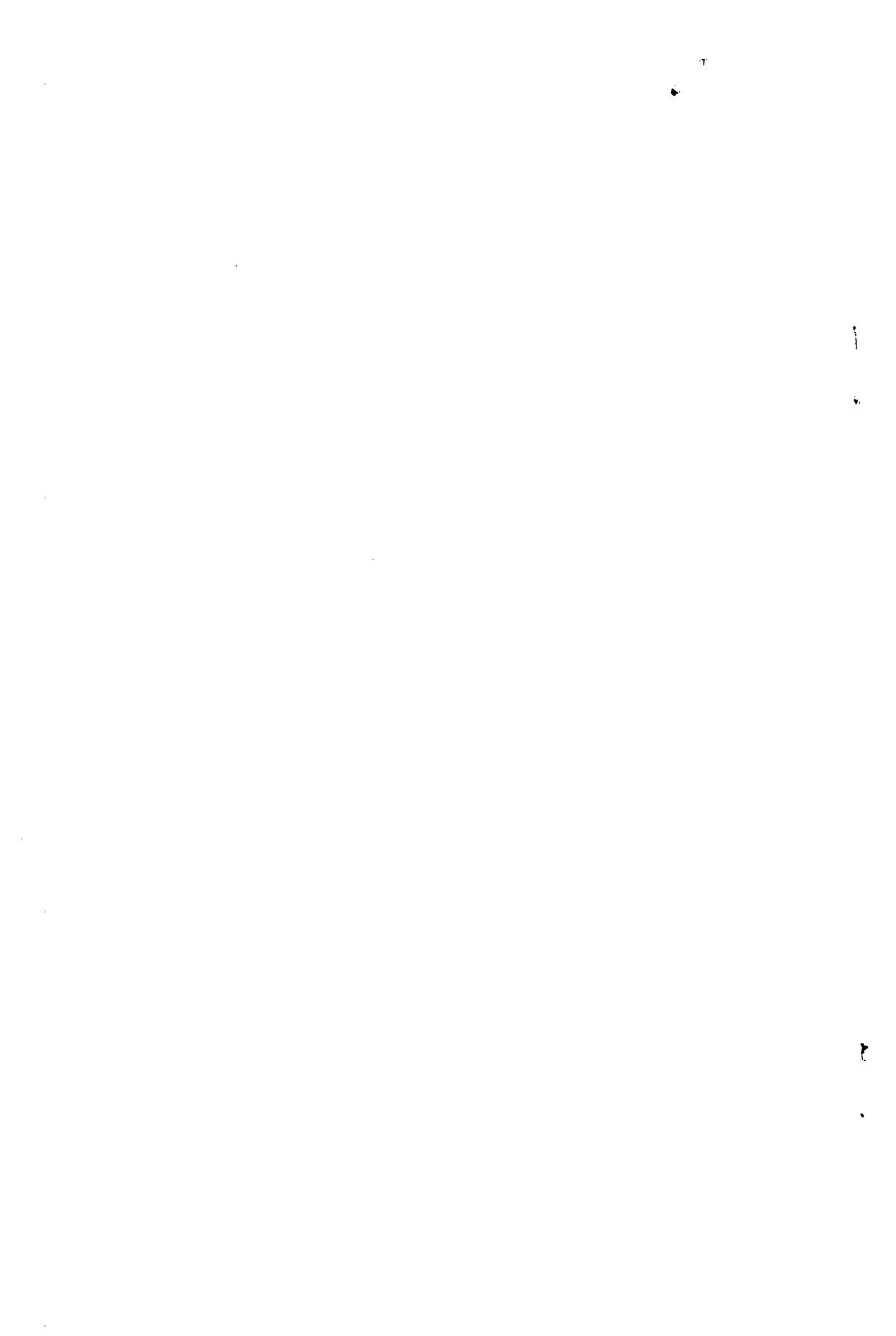
## References

- Aller, R.C., 1982. Carbonate dissolution in nearshore terrigenous muds: the role of physical and biological reworking. *J. Geol.* 90, 79–95.
- Blanchard, G., 1994. Caractéristiques photosynthétiques du microphytobenthos d'une vasière intertidale. *C.R. Acad. Sci. Paris Sci. Vie* 317, 633–637.
- Boucher, G., Clavier, J., 1990. Contribution of benthic biomass to overall metabolism in New Caledonia lagoon sediments. *Mar. Ecol. Prog. Ser.* 64, 271–280.
- Boucher, G., Clavier, J., Garrigue, C., 1994. Oxygen and carbon dioxide fluxes at the water-sediment interface of a tropical lagoon. *Mar. Ecol. Prog. Ser.* 107, 185–193.
- Brewer, P.G., Goldman, J.C., 1976. Alkalinity changes generated by phytoplankton growth. *Limnol. Oceanogr.* 21, 108–117.
- Buddemeier, R.W., 1996. Coral reefs and carbon dioxide. *Science* 271, 1299–1300.
- Charpy, L., Charpy-Roubaud, C.J., 1990. A model of light-primary production relationship in an atoll lagoon (Tikehau, Tuamotu Archipelago, French Polynesia). *J. Mar. Biol. Assoc. UK* 70, 357–369.

- Charpy-Roubaud, C.J., 1988. Production primaire des fonds meubles du lagon de Tikehau (Atoll des Tuamotu Polynésie Française). *Oceanol. Acta* 11, 241–248.
- Charpy-Roubaud, C., Charpy, L., Sarazin, G., 1996. Diffusional nutrient fluxes at the sediment-water interface and organic matter mineralization in an atoll lagoon (Tikehau, Tuamotu Archipelago, French Polynesia). *Mar. Ecol. Prog. Ser.* 132, 181–190.
- Chevillon, C., 1996. Skeletal composition of modern lagoon sediments in New Caledonia: coral, a minor constituent. *Coral Reefs* 15, 199–207.
- Chisholm, J.R.M., Collingwood, J.C., Gill, E.F., 1990. A novel in situ respirometer for investigating photosynthesis and calcification in crustose coralline algae. *J. Exp. Mar. Biol. Ecol.* 141, 15–29.
- Clavier, J., Boucher, G., Garrigue, C., 1994. Benthic respiratory and photosynthetic quotients in a tropical lagoon. *C.R. Acad. Sci. Paris* 317, 937–942.
- Culkin, F., 1965. The major constituents of seawater. In: Riley, J.P., Skirrow, G. (Eds.), *Chemical Oceanography*. vol. 1. Academic Press, London, pp. 121–161.
- Delesalle, B., 1985. Environmental survey of Mataiva atoll, Tuamotu Archipelago, French Polynesia. *Atoll Res. Bull.* 286, 1–41.
- Delesalle, B., Pichon, M., Frankignoulle, M., Gattuso, J.-P., 1993. Effects of a cyclone on coral reef phytoplankton biomass, primary production and composition (Moorea Island French Polynesia). *J. Plankton Res.* 15, 1413–1423.
- Epping, E.H., Jørgensen, B.B., 1996. Light-enhanced oxygen respiration in benthic phototrophic communities. *Mar. Ecol. Prog. Ser.* 139, 193–203.
- Galzin, R., 1985. Ecologie des poissons récifaux de Polynésie Française. Variations spatiotemporelles des peuplements. Dynamique des populations de trois espèces dominantes des lagons Nord de Moorea. Evaluation de la production ichthyologique d'un secteur récifo-lagonnaire. Thèse de Doctorat d'Etat, USTL, Montpellier, France, 195 pp.
- Garrigue, C., Clavier, J., Boucher, G., 1992. The use of photosynthetic inhibitor (DCMU) for in situ metabolic studies on soft bottom benthos. *Hydrobiologia* 246, 141–145.
- Gattuso, J.-P., Jaubert, J., 1990. Effect of light on oxygen and carbon dioxide fluxes and on metabolic quotients measured in situ in a zooxanthellate coral. *Limnol. Oceanogr.* 35, 1796–1804.
- Gattuso, J.-P., Pichon, M., Delesalle, B., Frankignoulle, M., 1993. Community metabolism and air-sea CO<sub>2</sub> fluxes in a coral reef ecosystem (Moorea French polynesia). *Mar. Ecol. Prog. Ser.* 96, 259–267.
- Gattuso, J.-P., Pichon, M., Delesalle, B., Canon, C., Frankignoulle, M., 1996. Carbon flux in coral reefs. I. Lagrangian measurement of community metabolism and resulting air-sea CO<sub>2</sub> disequilibrium. *Mar. Ecol. Prog. Ser.* 145, 109–121.
- Green, M.A., Aller, R.C., Aller, J.Y., 1993. Carbonate dissolution and temporal abundance of foraminifera in Long Island Sound sediments. *Limnol. Oceanogr.* 38 (2), 331–345.
- Hansson, I., Jagner, D., 1973. Evaluation of the accuracy of Gran plots by means of computer calculations. Application to the potentiometric titration of the total alkalinity and carbonate content of sea water. *Anal. Chim. Acta* 65, 363–373.
- Harmelin-Vivien, M., Peyrot-Clausade, M., Romano, M., 1992. Transformation of algal turf by echinoids and scarid fishes on french polynesia coral reefs. *Coral Reefs* 11 (1), 45–50.
- Hofman, P.A.G., de Jong, S.A., Wagenvoort, E.J., Sandee, A.J.J., 1991. Apparent sediment diffusion coefficients for oxygen and oxygen consumption rates measured with microelectrodes and bell jars: applications to oxygen budgets in estuarine intertidal sediments (Oosterschelde, SW Netherlands). *Mar. Ecol. Prog. Ser.* 69, 261–272.
- Kinsey, D.W., 1978. Alkalinity changes and coral reef calcification. *Limnol. Oceanogr.* 23 (5), 989–991.
- Kinsey, D.W., 1979. Carbon turnover and accumulation by coral reefs. PhD. dissertation, University of Hawaii, Honolulu, 248 pp.
- Kinsey, D.W., 1985a. Metabolism, calcification and carbon production. System level studies. In: Proceedings of the 5th International Coral Reef Symposium Tahiti (4), pp. 505–526.
- Kinsey, D.W., 1985b. Open-flow systems. In: Littler M.M., Littler, D.S. (Eds.), *Handbook Of Phycological Methods, Ecological Field Methods: Macroalgae*. Cambridge Univ. Press, London, pp. 427–460.
- Lazar, B., 1991. Bioerosion of coral reefs. A chemical approach. *Limnol. Oceanogr.* 36 (2), 377–383.
- Le Calvez, Y., Salvat, B., 1980. Foraminifères des récifs et lagons coralliens de Moorea, Iles de la Société. *Cah. Micropaléontol.* 4, 20–36.

- Le Campion-Alsumard, T., Romano, J.-C., Peyrot-Clausade, M., Le Campion, M., Paul, J., 1993. Influence of some coral reef communities on the calcium carbonate budget of Tiahura reef (Moorea, French Polynesia). *Mar. Biol.* 115, 685–693.
- Lorenzen, C.J., 1967. Determination of chlorophyll and pheopigments: spectrophotometric equations. *Limnol. Oceanogr.* 12 (2), 243–346.
- Lyman, J., 1957. Buffer mechanism of seawater. Ph.D. Thesis, Los Angeles
- Marsh, J.A. Jr., 1974. Preliminary observations on the productivity of a Guam reef flat community. In: Proceedings of the 2nd International Coral Reef Symposium Brisbane 1, pp. 139–145.
- Mehrback, C., Culberson, C.H., Hawley, J.E., Pytkowicz, R.M., 1973. Measurement of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. *Limnol. Oceanogr.* 18, 897–907.
- Nakamori, T., Suzuki, A., Iryu, Y., 1992. Water circulation and carbon flux on Shiraho coral reef of the Ryukyu Islands, Japan. *Continental Shelf Res.* 12 (7/8), 951–970.
- Odum, H.T., Odum, E.P., 1955. Trophic structure and productivity of a windward coral reef community. *Ecol. Monogr.* 1, 102–117.
- Payri, C., 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 Doctorat d'Etat de l'Université des Sciences Techniques du Languedoc, 149 pp.
- Peyré-Venec, M.T., 1987. Boring foraminifera in French Polynesia. *Coral Reefs* 11 (2), 205–212.
- Peyrot-Clausade, M., Le Campion-Alsumard, T., Harmelin-Vivien, M., Romano, J.-C., Chazotte, V., Pari, N., Le Campion, J., 1995. La bioérosion dans le cycle des carbonates: essai de quantification des processus en Polynésie française. *Bull. Soc. Géol. France* 166 (1), 85–94.
- Platt, T., Jassby, A.D., 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. *J. Phycol.* 12, 421–430.
- Rasmussen, M.B., Henriksen, K., Jensen, K., 1983. Possible causes of temporal fluctuations in primary production of the microphytobenthos in the Danish Wadden Sea. *Mar. Biol.* 73, 109–114.
- Revsbech, N.P., Jørgensen, B.B., Brix, O., 1981. Primary production of microalgae in sediments measured by the oxygen microprofile,  $H_{14}CO_3^-$  fixation, and oxygen exchange methods. *Limnol. Oceanogr.* 26 (4), 717–730.
- Richard, G., 1982. Mollusques lagonaires et récifaux de Polynésie Française. Inventaires faunistiques-Biométrie-Bilan quantitatif-Croissance-Production. Thèse de Doctorat d'Etat de l'Université de Paris 6, 313 pp.
- Smith, S.V., 1995. Reflections on the measurement and significance of carbon metabolism on coral reefs. Kansas Geological Survey, Open File Report Series 95-56, pp. 1–18.
- Smith, S.V., Key, G.S., 1975. Carbon dioxide and metabolism in marine environments. *Limnol. Oceanogr.* 20, 493–495.
- Sorokin, Y.I., 1993. *Coral Reef Ecology*. Springer-Verlag, Berlin.
- Sournia, A., 1976. Oxygen metabolism of a fringing reef in French Polynesia. *Helgolander Wissenschaft. Meeresuntersuch.* 28, 401–410.
- Sournia, A., 1976. Primary production of sands in the lagoon of an atoll and the role of foraminiferan symbionts. *Mar. Biol.* 37, 29–32.
- Sournia, A., 1977. Analyse et bilan de production primaire dans les récifs coralliens. *Ann. Inst. Océanogr. Paris* 53 (1), 47–74.
- Sournia, A., Ricard, M., 1975. Phytoplankton and primary productivity in Takapoto Atoll, Tuamotu Islands. *Micronesica* 11 (2), 159–166.
- 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 (4), 423–431.
- Stumm, W., Morgan, M.J., 1981. *Aquatic Chemistry*, 3rd ed. J. Wiley and Sons, Inc., New York.
- Tribble, G.W., Sansone, F.J., Smith, S.V., 1990. Stoichiometric modeling of carbon diagenesis within a coral reef framework. *Geochim. Cosmochim. Acta* 54, 2439–2449.
- Vaugelas, J.V. (de), 1982. Etude qualitative et quantitative de la matière organique vivante et détritique de sédiments coralliens dans les îles polynésiennes de Tahiti, Moorea et Takapoto. Thèse de 3eme cycle de l'Université de Paris 6, 150 pp.

- Walter, L., Bischof, S.A., Patterson, W.P., Lyons, T.W., 1993. Dissolution and recrystallization in modern shelf carbonates: evidence from pore water and solid phase chemistry. Phil. Trans. Roy. Soc. London A344, 27–36.
- Weiss, R.F., 1974. Carbon dioxide in water and seawater: the solubility of a non-ideal gas. Mar. Chem. 2, 203–215.
- Yap, H.T., Montebon, A.R.F., Dizon, R.M., 1994. Energy flow and seasonality in a tropical coral reef flat. Mar. Ecol. Prog. Ser. 103, 35–43.



# JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

## NOTES FOR AUTHORS

**Manuscripts:** Manuscripts (original and two copies) should be sent directly to the relevant Section Editor (see inside front cover). Manuscripts should be accompanied by title page, abstract and key words and the originals and photocopies of all figures. Authors should be sure to retain a copy of a submitted typescript.

**Electronic manuscripts:** Electronic manuscripts have the advantage that there is no need for the rekeying of text, thereby avoiding the possibility of introducing errors and resulting in reliable and fast delivery of proofs.

For the initial submission of manuscripts for consideration, hardcopies are sufficient. For the processing of accepted papers, electronic versions are preferred. After final acceptance, your disk plus three, final and exactly matching printed versions should be submitted together. Double density (DD) or high density (HD) diskettes ( $3\frac{1}{2}$  or  $5\frac{1}{4}$  inch) are acceptable. It is important that the file saved is in the native format of the wordprocessor program used. Label the disk with the name of the computer and wordprocessing package used, your name, and the name of the file on the disk. Further information may be obtained from the Publisher.

**Authors in Japan please note:** Upon request, Elsevier Science Japan will provide authors with a list of people who can check and improve the English of their paper (*before submission*). Please contact our Tokyo office: Elsevier Science Japan, 1-9-15 Higashi-Azabu, Minato-ku, Tokyo 106, Japan, Tel. (+81)3-5561-5032, Fax (+81)3-5561-5045.

**Enquiries concerning manuscripts and proofs:** Questions arising after acceptance of the manuscript, especially those relating to proofs, should be directed to: Elsevier Science Ireland Ltd., Bay 15K, Shannon Industrial Estate, Shannon, Co. Clare, Ireland. Tel.: (+353) 61 471944; Fax: (+353) 61 472144.

**For a full and complete Guide for Authors, please refer to *Journal of Experimental Marine Biology and Ecology*, Vol. 220, No. 1, pp. 161-167.**

The instructions can also be found on the World Wide Web: access under  
<http://www.elsevier.nl/locate/jembe> or <http://www.elsevier.com/locate/jembe>

***Journal of Experimental Marine Biology and Ecology* has no page charges.**

No responsibility is assumed by the Publisher for any injury and/or damage to persons or property as a matter of products liability, negligence or otherwise, or from any use or operation of any methods, products, instructions or ideas contained in the material herein.

Although all advertising material is expected to conform to ethical (medical) standards, inclusion in this publication does not constitute a guarantee or endorsement of the quality or value of such product or of the claims made of it by its manufacturer.

**US mailing notice:** *Journal of Experimental Marine Biology and Ecology* (0022-0981) is published in 24 issues by Elsevier Science B.V., Molenwerf 1, P.O. Box 211, 1000 AE Amsterdam, The Netherlands. Annual subscription price in the USA is US\$ 2931.00 (valid in North, Central and South America), including air speed delivery. Second class postage rate is paid at Jamaica, NY 11431.

**USA POSTMASTERS:** Send address changes to: Journal of Experimental Marine Biology and Ecology, Publications Expediting, Inc., 200 Meacham Avenue, Elmont, NY 11003. **Airfreight and mailing** in the USA by Publications Expediting.

© 1998 Elsevier Science B.V. All rights reserved

0022-0981/98/\$19.00

No part of this publication may be reproduced, stored in a retrieval system or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, without the prior written permission of Elsevier Science B.V., Copyright and Permissions Department, P.O. Box 521, 1000 AM Amsterdam, The Netherlands.

Printed in The Netherlands

US Library of Congress Catalog Card Number 68-26535

© The paper used in this publication meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper)

