C. R. Acad. Sci. Paris, Sciences de la vie/Life sciences, 1994; 317 : 937-42
Écologie/Ecology

Benthic respiratory and photosynthetic quotients in a tropical lagoon

Quotients respiratoire et photosynthétique benthiques dans un lagon corallien

JACQUES CLAVIER [1], GUY BOUCHER [2], CLAIRE GARRIGUE [3]

[1] *Centre ORSTOM, BP 70, 29280 Plouzané, France.*
[2] *URA CNRS 699, BIM, Muséum National d'Histoire Naturelle, 57, rue Cuvier, 75231 Paris, France.*
[3] *Centre ORSTOM, BP A5, Nouméa, Nouvelle-Calédonie.*

RÉSUMÉ

Les flux de gaz carbonique et d'oxygène ont été mesurés dans des enceintes de 0,2 m^2 placées à l'interface eau-sédiment, dans le lagon SW de Nouvelle-Calédonie. Les travaux ont été menés sur plusieurs sites représentatifs d'une large gamme de milieux. Les incubations ont été réalisées à l'obscurité pour estimer la respiration, puis à la lumière ambiante, afin de suivre les effets de la production primaire. Les quotients respiratoire (QRC = production de CO_2/consommation d'O_2) et photosynthétique (QPC = production brute d'O_2/consommation brute de CO_2) des communautés ont été calculés par régressions linéaires fonctionnelles (modèle II). La valeur de QRC estimée à partir de 61 incubations est de 1,14 (E.S. 0,05) et la valeur de QPC obtenue sur 18 incubations est de 1,03 (E.S. 0,08). La linéarité des relations entre les flux d'O_2 et de CO_2 nous permet de considérer les valeurs obtenues comme représentatives de l'ensemble du lagon. ▲

***Mots clés** : gaz carbonique, oxygène, métabolisme, coefficients respiratoires et photosynthétiques de communauté.*

ABSTRACT

Carbon dioxide and oxygen fluxes were measured in 0.2 m^2 enclosures placed at the water sediment interface in the SW lagoon of New Caledonia. Experiments, performed at several stations in a wide range of environments, were carried out both in darkness to estimate respiration and at ambient light, to assess the effects of primary production. The community respiratory quotient (CRQ = CO_2 production rate/O_2 consumption rate) and the community photosynthetic quotient (CPQ = gross O_2 production rate/gross CO_2 consumption rate) were calculated by functional regressions. The CRQ value, calculated from 61 incubations, was 1.14 (S.E. 0.05) and the CPQ value, obtained from 18 incubations, was 1.03 (S.E. 0.08). The linearity of the relationship between the O_2 and the CO_2 fluxes suggests that these values are representative for the whole lagoon. ▲

Key words : carbon dioxide, oxygen, metabolism, community respiratory and photosynthetic quotient.

VERSION ABRÉGÉE

La mesure des transferts de carbone organique entre les compartiments fonctionnels des réseaux trophiques est un élément nécessaire à l'estimation des flux d'énergie dans les écosystèmes marins. Ces flux sont souvent mesurés par les échanges de gaz carbonique, qui sont à la fois le produit ultime de la dégradation aérobie et anaérobie de la matière organique et la source de carbone pour l'élaboration des tissus végétaux. Les flux de CO_2 à l'interface eau-sédiment représentent donc le bilan des phénomènes de respiration et de photosynthèse. Au cours de la respiration, la quantité d'O_2 est liée à celle de CO_2 par le quotient respiratoire ($|\Delta CO_2/\Delta O_2|$) ; de même, l'O_2 rejeté et le CO_2 absorbé pendant la photosynthèse sont liés par le quotient photosynthétique ($|\Delta O_2/\Delta CO_2|$). Le but de ce travail a été d'estimer les quotients métaboliques de communautés qui permettent de calculer les flux de carbone à partir de mesures d'O_2, plus aisées à obtenir dans le milieu naturel que celles de CO_2.

Les quotients respiratoire et photosynthétique du benthos ont été étudiés en septembre-octobre 1993 sur 7 stations représentatives

Note présentée par Claude Levi.
Note remise le 20 mai 1994, acceptée après révision le 26 septembre 1994.

Corresponding author : J. Clavier.

des fonds du lagon SW de Nouvelle-Calédonie. Les flux d'O_2 et de CO_2 à l'interface eau-sédiment ont été estimés simultanément à l'intérieur d'enceintes de 0,2 m^2 constituées d'une base en PVC coiffée d'une demi-sphère transparente. Les incubations (3 réplicats) ont d'abord été réalisées à la lumière pendant 2 h ; après renouvellement de l'eau, elles ont été poursuivies 3 h à l'obscurité pour simuler les conditions nocturnes. Les valeurs des mesures de sondes pH et polarographiques placées dans l'eau enclose ont été relevées toutes les 10 s et les moyennes par minute ont été stockées sur mémoire numérique. Elles ont évolué en fonction de l'éclairement dans les enceintes claires, tandis qu'elles ont diminué linéairement à l'obscurité. Des dosages de l'alcalinité totale ont été réalisés sur des échantillons d'eau filtrés, prélevés en début et en fin d'incubation. Les flux de CO_2 ont été calculés à partir des données de pH, alcalinité totale, température et salinité. Les quotients respiratoire et photosynthétique ont été calculés par régression (méthode des moindres rectangles).

A l'obscurité, les flux d'O_2 ont varié de 0,42 à 2,78 mmol m^{-2} h^{-1} et ceux de CO_2 entre 0,60 et 3,01 mmol m^{-2} h^{-1}. A la lumière, les flux bruts d'O_2 ont varié de 1,40 à 11,86 mmol m^{-2} h^{-1} et ceux de CO_2 entre 0,71 et 11,95 mmol m^{-2} h^{-1}. Aucune photo-inhibition de la photosynthèse n'a pu être constatée sur l'évolution des concentrations en O_2 à la lumière. La valeur estimée du quotient respiratoire de communauté est de 1,06 ($n = 19$, $r^2 = 0,84$, E.S. = 0,10) alors qu'une précédente étude réalisée sur le même lagon selon des techniques identiques, mais à une autre saison, fournit une valeur de 1,17 [5]. Cette valeur ne différant pas significativement de celle obtenue pendant la présente étude, nous avons fusionné les deux groupes de données et obtenu une valeur de 1,14 ($n = 61$, $r^2 = 0,90$, E.S. = 0,05). La valeur estimée du quotient photosynthétique est de 1,03 ($n = 18$, $r^2 = 0,91$, E.S. = 0,08).

La technique développée dans le milieu naturel permet une mesure simultanée des flux d'O_2 et de CO_2 à l'interface eau-sédiment et autorise un calcul précis des quotients métaboliques du benthos. Nous avons estimé de tels coefficients sur des stations de caractéristiques distinctes représentant les principaux types de fonds du lagon. Le quotient respiratoire a été calculé sur deux saisons et le quotient photosynthétique a été obtenu sur une large gamme d'éclairements (0,33 à 0,91 mol m^{-2} h^{-1}). La linéarité des relations entre les flux d'O_2 et de CO_2 nous permet donc de considérer les quotients respiratoire et photosynthétique obtenus comme des constantes représentatives de l'ensemble des substrats meubles du lagon. ▲

Energy fluxes through marine benthic ecosystems are usually investigated by means of organic carbon transfers through the water-sediment interface as reflected by changes in the chemistry of the overlying water. CO_2 is the ultimate product of organic matter degradation through both aerobic and anaerobic metabolisms [1] and is the carbon source for the production of plant tissues by photosynthesis [2]. CO_2 flux at the water-sediment interface is the result of the balance of respiration and photosynthesis, the two processes operating in light, whereas photosynthesis stops in the dark.

Calculations of total CO_2 concentration from field pH measurements in seawater are currently used [3-5] but they involve cumbersome total alkalinity measurements [6, 7]. Knowledge of metabolic quotients allows organic carbon flux to be calculated from O_2 flux alone, which is less difficult to measure *in situ* than CO_2 flux. In light, O_2 production and CO_2 consumption by microphytes or plant tissues are related by the photosynthetic quotient ($PQ = |\Delta O_2/\Delta CO_2|$) and, in the dark, O_2 consumption and CO_2 production are related by the respiratory quotient ($RQ = |\Delta CO_2/\Delta O_2|$). As these fluxes result from organism metabolic pathways and biogeochemical processes as well at the water-sediment interface of undisturbed communities, it has been proposed to use benthic community respiratory (CRQ) and community photosynthetic (CPQ) quotients [8].

The aim of this study was to calculate these community metabolic quotients on the same undisturbed sediment area from representative stations sampled in a tropical lagoon at ambient light and dark conditions.

Materials and methods

Field measurements were performed in the south-west lagoon of New Caledonia (SW Pacific) in September-October, 1993. Triplicate incubations at the water-sediment interface were conducted at 7 stations ensuring a wide range of biotic and abiotic conditions (*Fig. 1* and *Table I*).

Oxygen and carbon dioxide fluxes at the water-sediment interface were simultaneously estimated in the water trapped in enclosures [3]. At each sampling station, 3 PVC tubes, covering 0.2 m^2 of bottom surface, were carefully pushed about 10 cm into the substrate by SCUBA divers ensuring a minimum of sediment disturbance. They were covered with clear acrylic hemispheres to trap a known volume of water (from 52.7 to 58.9 l, depending to the depth of core insertion into the substrate). Incubations

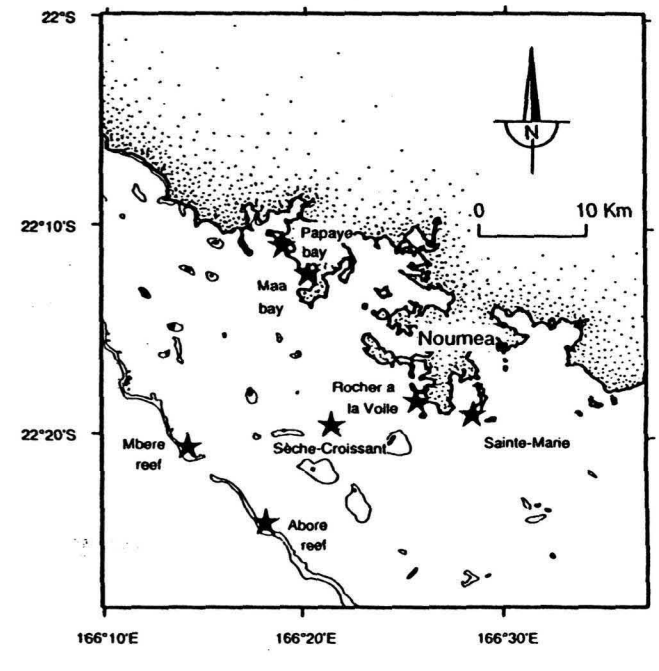

Figure 1. ***Location of sampling stations in the SW lagoon of New Caledonia.***

Table I
Characteristics of the sampling stations. Temp : water temperature ; Plant AFDW : ash free dry weight of macrophytes ; Chl *a* : quantity of chlorophyll *a* ; % Chl *a* : percentage of chlorophyll *a* in total photosynthetic pigments. Sediment types are according to Wenworth scale [28] : FS, fine sand ; VFS, very fine sand ; MD, mud

Station name	Depth (m)	Temp °C	Light ($mol.m^{-2}.h^{-1}$)	Plant AFDW ($g.m^{-2}$)	Chl *a* ($mg.m^{-2}$)	% Chl *a*	Sediment type	% mud
Sainte-Marie	9.2	22.2	0.33	0.00	35.46	42.26	FS	36.04
Sèche-Croissant	10.2	22.7	0.60	65.38	34.68	37.25	FS	8.62
Mbere reef	8.5	22.6	0.68	0.00	17.67	66.00	FS	1.34
Aboré reef	5.0	22.9	0.73	0.00	54.03	71.13	VFS	1.96
Rocher à la Voile	7.5	23.7	0.70	51.80	60.29	51.20	FS	7.52
Maa bay	8.5	23.9	0.91	40.31	28.92	36.26	MD	82.73
Papaye bay	9.5	23.5	0.40	43.95	34.34	38.04	VFS	61.50

began at between 9 to 10 a.m. according to the station and lasted for 2 h at ambient light (light incubations). The enclosures were then opened for 15 min to renew the incubated water in order to restore ambient conditions. The clear hemispheres were relocked and sheltered with black polyethylene plastic sheets and aluminium covers for light exclusion and thermic isolation, respectively. Dark incubations were then conducted for 3 h, a lengh of time which allowed the O_2 saturation percentage to remain above 80 %.

Enclosed water was gently stirred using submersible pumps powered by waterproof batteries to prevent the formation of concentration gradients and to allow good irrigation of the oxygen and pH probes placed in a water closed-circuit connected to the enclosures. Details on probes deployments are given in [5, 9]. Incubation water was collected by SCUBA divers using 100 ml syringes, at the beginning and at the end of light and dark incubations. The water was filtered on GF/C Whatman membranes to remove particulate material and stored in the dark at 4 °C pending analysis. Total alkalinity (TA) was measured, within 2 days, on 50 ml subsamples by the potentiometric automatic method [10] using a Tacussel Titrator (TT-processor 2600S) and an automatic burette (EBX2 20 ml).

Oxygen flux (ΔO_2 mmol m^{-2} h^{-1}) was calculated as the difference in values recorded at the beginning and at the end of light incubations, and as the slope of oxygen concentrations vs. time during dark incubations. The total carbon dioxide concentration (ΣCO_2) was calculated using pH, TA, temperature and salinity data [11]. The total carbon dioxide flux ($\Delta\Sigma CO_2$) is the difference in CO_2 concentrations at the beginning and at the end of light and dark incubations. $\Delta\Sigma CO_2$ not only depends on biological activity but also on total alkalinity shift related to the variation of $CaCO_3$ and to the effects of anaerobic metabolism. Biological carbon dioxide flux (ΔCO_2 mmol m^{-2} h^{-1}) was calculated as : $\Delta CO_2 = \Delta\Sigma CO_2 - 1/2\,\Delta TA$ [3, 12].

During dark incubations, O_2 and CO_2 fluxes (ΔCO_2D and ΔO_2D respectively) depend mainly on respiration processes. The community respiratory quotient is therefore : $CRQ = |\Delta CO_2D/\Delta O_2D|$. In light incubations, net O_2 and CO_2 fluxes (ΔCO_2L and ΔO_2L respectively) result both from photosynthetic activity (ΔCO_2P and ΔO_2P) and respiration or other processes. The flux related to primary production is thus : $\Delta CO_2P = \Delta CO_2L - \Delta CO_2D$ and $\Delta O_2P = \Delta O_2L + \Delta O_2D$. The community photosynthetic quotient corresponds to : $CPQ = |\Delta O_2P/\Delta CO_2P|$. As oxygen and carbon dioxide fluxes are both affected by natural variability and measurement error, the metabolic quotients are calculated by means of functional regressions [13].

Some parameters that can influence benthic metabolism were also measured. As zoobenthic biomass in the lagoon, mainly involved in respiration, has already been studied [14, 15], the experiments were particularly focused on photosynthesis. Photosynthetically active radiation (PAR, 400-700 nm) was measured with a quantum sensor (LiCor, LI-192SA) placed inside one of the enclosures. Data were integrated over the experiment duration (mol m^{-2} h^{-1}). Microphytobenthos biomass was indirectly assessed through sediment chlorophyll *a* measurements. The top centimetre from five 5.31 cm^2 cores, manually collected by SCUBA divers inside each enclosure, was carefully separated and deep-frozen in darkness for later analysis. The samples were later lyophilised [16] and pigments were extracted by 90 % acetone for 18 to 24 h. After filtration of the extract, optical densities were assessed on a spectrophotometer at 750 and 665 nm. Equations derived from Lorenzen [17] were used to calculate chlorophyll *a* concentrations (mg m^{-2}). Macroflora was collected by hand in each enclosure. Ash free dry weights were calculated from dry weights and ash weights measured after oven-drying (60 °C) until the weight was constant and then heated again at 550 °C for a futher 3 h. Plant biomasses are expressed in grams of ash free dry weight per m^2 (gAFDW m^{-2}). The mud fraction (< 63 µm) percentage was determined by granulometry.

Results

Experiments were performed at seven stations, allowing the measurement of metabolic quotients over a wide range of light levels, sediment characteristics, chlorophyll *a* contents and macrophyte biomasses *(Table I)*. During successive light and dark incubations, oxygen and pH changes were similar, and varied according to light intensity, linearly decreasing in darkness *(Fig. 2)*. During dark incubations, ΔCO_2D and ΔO_2D varied from 0.42 to 2.78 mmol m^{-2} h^{-1} and 0.60 to 3.01 mmol m^{-2} h^{-1} respectively. The CRQ value calculated from 19 incubations is 1.06 (S.E. 0.10). The regression explains 84 % of the variability of data *(Fig. 3)*.

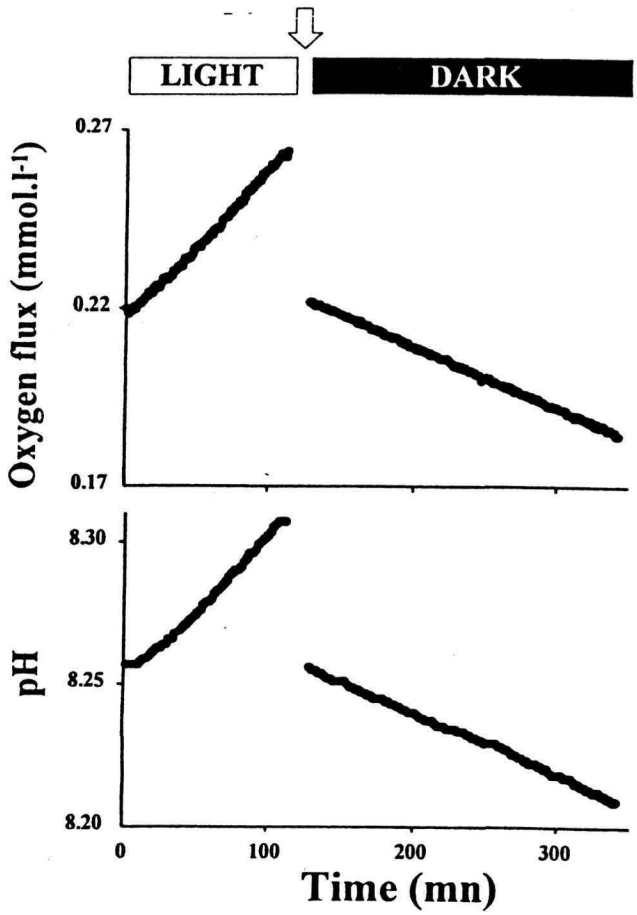

Figure 2. ***Oxygen and pH evolution over an incubation, in light and dark conditions.*** *Recording frequency is 1 mn. The arrow indicates the enclosure opening when enclosed water is renewed.*

CRQ has been estimated to be 1.17 during a previous study in the SW lagoon of New Caledonia [5]. The latter value was obtained, however, during the warm season (December 1991-January 1992) with a mean temperature of 25.8 °C whereas the present study was conducted at the end of the cool season with a mean temperature of 23.3 °C. As the two CRQ estimates do not differ significantly ($Z = 0.95$, $P > 0.05$), we calculated a mean CRQ considering the pooled values ($N = 61$). The slope of the functional regression is then 1.14 (S.E. 0.05) and the regression explains 90 % of the variability of data. The

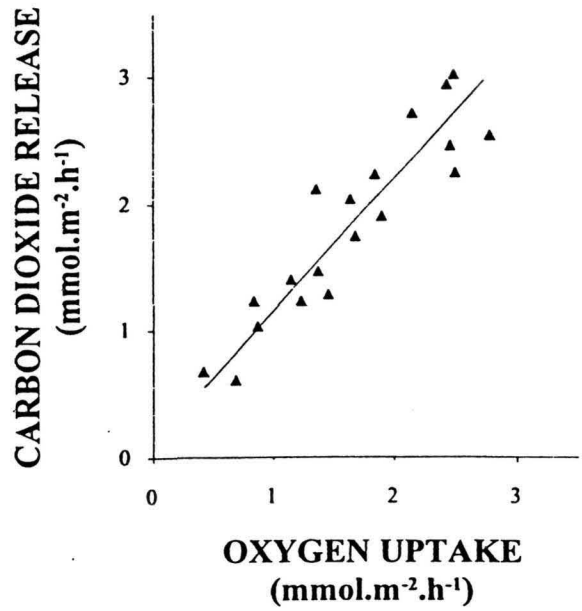

Figure 3. ***Relationship between CO_2 production and O_2 uptake (absolute values) during dark incubations on triplicated experiments at 7 stations.*** *Regression is Type II, geometric mean.*

global CRQ value is significantly greater than 1 ($Z = 2.79$, $P < 0.01$).

During light incubations, ΔCO_2P and ΔO_2P varied from 1.40 to 11.86 mmol m^{-2} h^{-1} and 0.71 to 11.95 mmol m^{-2} h^{-1} respectively. No photo-inhibition was noticed on data records during light incubations. ΔCO_2P and ΔO_2P *(Fig. 4)* were also well correlated ($r^2 = 0.91$) and the CPQ value obtained from 18 incubations is 1.03 (S.E. 0.08). CRQ does not differ significantly from 1 ($Z = 0.36$, $P > 0.05$). Variability of the ratio calculated for each experiment, which ranges from 0.51 to 1.28 for CPQ and 0.87 to 1.61 for CRQ respectively, demonstrates that the computation of functional regression on a representative sample is required to obtain reliable estimations of metabolic quotients.

Discussion

As a comprehensive discussion about CRQ has been published [5], we will focus our comments on the general significance of the quotient. During dark incubations, oxygen demand results from pooled effects of aerobic respiration and oxidation of dissolved reduced metabolic end-products of anaerobic respiration, reaching the sediment surface. However, some of the anaerobic respiration products are insoluble and cannot be transported to the oxidised layer of sediment. Thus, observed oxygen fluxes differ from the simple sum of all metabolic processes. CO_2 flux, on the other hand, corresponds to both aerobic and anaerobic respiration [1, 18]. CO_2 release could only be reduced by some particular procedures such as chemical action on carbonate by organic acid produced by fermentation, or chemolithotrophic CO_2 fixation, although the process is not likely to affect the CO_2 flux significantly [19]. CRQ could, therefore, not be regarded as a simple aerobic metabolic quotient, or as an estimate of the ratio of anaerobic and aerobic metabolisms. It is merely a

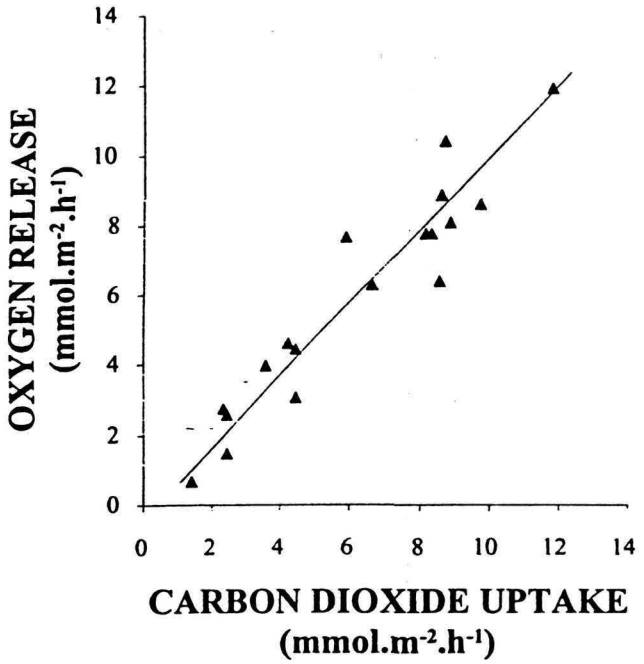

Figure 4. ***Relationship between gross O_2 production and gross CO_2 uptake (absolute values) during light incubations on triplicated experiments at 7 stations.*** *Regression is Type II, geometric mean.*

conversion coefficient allowing a global CO_2 flux to be calculated from a total oxygen demand, easy to collect *in situ*. It is thus difficult to attach a proper biological signification to CRQ, given that it corresponds to a heterogeneous biogeochemical parameter. A value of CRQ close to 1 indicates, however, a benthic system where the bound and soluble pools of reduced material are close to steady state [20]. This is not the case in the SW lagoon of New Caledonia where a CRQ value significantly higher than 1 indicates the general importance of anaerobic metabolism processes in sediments [5].

CPQ corresponds to the ratio of community gross photosynthetic emission of oxygen on community gross fixation of carbon. Gross O_2 and CO_2 fluxes are calculated from net fluxes measured during light incubations, corrected for the effects of any biological or biogeochemical processes recorded during dark incubations. In our experiments, benthic primary production is mostly related to the joint activity of macrophytes and microphytes. The process also depends on the activity of symbiotic algae, mainly associated with foraminifera [21], which are abundant in the SW lagoon of New Caledonia. The ratio is, thus, a realistic measure of the rate of O_2 production divided by the rate of CO_2 utilisation by plants. The photosynthetic quotient can be influenced by various factors [11]. The main sources of error are photorespiration that reduces the photosynthetic quotient [22, 23], or chemo-autotrophic bacteria using hydrogen sulphide instead of water for the photosynthesis process [24]. Our results are close to the theoretical estimations of PQ, based on the general equation of photosynthesis, which predict a value of 1, except when the end products of photosynthesis are not carbohydrates [25]. Whereas typical values for marine phytoplankton lay in the region of 1.1 to 1.3 [2], with a generally accepted median value around 1.25, PQ for benthic communities varies greatly according to the experimental design and the calculation method. It is, however, accepted that this quotient is slightly more than unity in most coral reef environments (see [26] for a review). In our study, the excellent linearity of the regression between O_2 and CO_2 fluxes indicates that both a CPQ and a CRQ of around 1 are representative for the whole lagoon, and that the system is in autotrophic balance [27]. The calculated indices allow, thus, the estimation of global benthic carbon fluxes in the lagoon of New Caledonia, from O_2 measures easier to collect. ▼

Acknowledgements : this work is a contribution of PRCO 1993 (Programme national récifs coralliens). We would like to thank P. Joannot, Director of the aquarium of Noumea (New Caledonia), for assistance and Dr P. J. D. Lambshead (Museum of Natural History, London) for correcting the English.

References

1. Marty D., Bertrand J. C., Caumette, P. 1989. Les métabolismes bactériens dans les systèmes sédimentaires marins. In : *Micro-organismes dans les écosystèmes océaniques*, Bianchi M., Marty D., Caumette P., Bertrand J. C., Gauthier M., eds. Paris : Masson, 101-51.

2. Ryther J. H. 1956. The measurement of primary production. *Limnol. Oceanogr.* 1: 72-84.

3. 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.

4. Gattuso J. P., Pichon M., Delesalle B., Frankignoulle M. 1993. Community metabolism and air-sea CO_2 fluxes in a coral reef ecosystem (Moorea, French Polynesia). *Mar. Ecol. Prog. Ser.* 96: 259-67.

5. 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 (1-2): 185-93.

6. Smith S. V., Kinsey D. W. 1978. Calcification and organic carbon metabolism as indicated by carbon dioxide. In : *Coral reefs : research methods*, Stoddart D., Johannes R.E., eds. Manila : UNESCO, 469-84.

7. Skirrow G. 1975. The dissolved gases : carbon dioxide. In : *Chemical oceanography*, Riley J. P., Skirrow G., eds. New York : Academic Press, 1-192.

8. Andersen F. O., Kristensen E. 1988. The influence of macrofauna on estuarine benthic community metabolism : a microcosm study. *Mar. Biol.* 99: 591-603.

9. Garrigue C., Clavier J., Boucher G. 1992. The use of photosynthesis inhibitor (DCMU) for *in situ* metabolic and primary production studies on soft bottom benthos. *Hydrobiologia* 246: 141-5.

10. Culberson C., Pytkowicz R. M., Hawley J. E. 1970. Seawater alkalinity determination by the pH method. *J. Mar. Res.* 28: 15-21.

11. Oviatt C. A., Rudnick D. T., Keller A. A., Sampou P. A., Almquist G. T. 1986. A comparison of system O_2 and CO_2 and C_{14} measurements of metabolism in estuarine mesocosms. *Mar. Ecol. Prog. Ser.* 28: 57-67.

12. Jacques T. G., Pilson M. E. Q. 1980. Experimental ecology of the temperate scleractinian coral *Astrangia danae*. I. Partition of respiration, photosynthesis and calcification between host and symbionts. *Mar. Biol.* 60: 167-78.

13. Ricker W. E. 1973. Linear regression in fishery research. *J. Fish. Res. Bd. Can.* 30: 409-34.

14. Boucher G., Clavier J. 1990. Contribution of benthic biomass to overall metabolism in New Caledonia lagoon. *Mar. Ecol. Prog. Ser.* 44: 229-38.

15. Chardy P., Clavier J. 1988. Biomass and trophic structure of the macrobenthos in the south-west lagoon of New Caledonia. *Mar. Biol.* 99: 195-202.

16. Hansson L. A. 1988. Chlorophyll *a* determination of periphyton on sediments : identification of problems and recommendation of method. *Freshwat. Biol.* 20: 347-52.

17. Lorenzen C. J. 1967. Determination of chlorophyll and pheo-pigments : spectrophotometric equations. *Limnol. Oceanogr.* 12: 343-6.

18. Hargrave B. T., Phillips G. A. 1981. Annual *in situ* carbon dioxide and oxygen flux across a subtidal marine sediment. *Estuar. Coast. Shelf. Sc.* 12: 725-37.

19. Hansen L. S., Blackburn T. H. 1992. Effect of algal bloom deposition on sediment respiration and fluxes. *Mar. Biol.* 112: 147-52.

20. Andersen F. Ø, Kristensen E. 1988. The influence of macrofauna on estuarine benthic community metabolism : a microcosm study. *Mar. Biol.* 99: 591-603.

21. Sournia A. 1976. Primary production of sands in the lagoon of an atoll and the role of Foraminiferan symbionts. *Mar. Biol.* 37: 29-32.

22. Burris J. E. 1981. Effects of oxygen and inorganic carbon concentrations on the photosynthetic quotients of marine algae. *Mar. Biol.* 65: 215-9.

23. Hackney J. M., Sze P. 1988. Photorespiration and productivity rates of a coral reef algal turf assemblage. *Mar. Biol.* 98: 483-92.

24. Kepkay P. E., Cooke R. C., Novitsky J. A. 1979. Microbial autotrophy : a primary source of organic carbon in marine sediments. *Science* 204: 68-9.

25. Rabinowitch E. I. 1945. Photosynthesis and related processes. New York : Wiley-Interscience. 599 p.

26. Kinsey D. W. 1985. Metabolism, calcification and carbon production. *Proc. 5th Int. Coral Reef Congr.* 4: 505-26.

27. Kinsey D. W. 1983. Standards of performance in coral reef primary production and carbon turnover. In : *Perspectives on coral reefs*, Barnes D. J., ed., AIMS Townsville, 209-20.

28. Wenworth C. K. 1922. A scale of grade and class terms for clastic sediments. *J. Geol.* 30: 377-92.