Vol. 157: 109–117, 1997 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published October 16

Seasonal variation of primary productivity and skeletal $\delta^{13}C$ and $\delta^{18}O$ in the zooxanthellate scleractinian coral *Acropora formosa*

A. Juillet-Leclerc[1,*], J.-P. Gattuso[2,3], L. F. Montaggioni[4], M. Pichon[3,5]

[1]Centre des Faibles Radioactivités, Laboratoire mixte CNRS-CEA, F-91180 Gif-sur-Yvette Cedex, France
[2]Observatoire Océanologique Européen, Centre Scientifique de Monaco, Avenue Saint-Martin, MC-98000 Monaco
[3]Australian Institute of Marine Science, PMB no. 3, Townsville MC, Queensland 4810, Australia
[4]UPRESA-CNRS 6019, Centre de Sédimentologie/Paléontologie, Université de Provence, F-13331 Marseille Cedex 3, France
[5]Laboratoire de Biologie Marine, EPHE, URA-CNRS 1453, Université de Perpignan, F-66860 Perpignan Cedex, France

ABSTRACT: Carbon and oxygen isotopic ratios, measured along the growth axis of branches from colonies of the scleractinian coral *Acropora formosa* collected at 2 and 12 m depth at Yonge Reef (Northern Great Barrier Reef, Australia), were compared to metabolic rates. Measurements of primary production, respiration, temperature and irradiance were carried out *in situ* twice, in winter and in summer, and skeletal isotopic analyses were performed at 2 reference points corresponding to metabolic measurements. There was no evidence of any relationship between oxygen isotopic ratio and productivity. Skeletal $\delta^{13}C$ values and the rates of productivity showed a statistically significant positive relationship as predicted by the model proposed by Goreau (1977a: Proc 3rd Int Coral Reefs Congr 1: 395–401); $\delta^{13}C$ increased as a function of increasing productivity. The scattering of $\delta^{13}C$ observed particularly during summer demonstrates that the relationship between $\delta^{13}C$ and primary productivity is not very tight and that other internal and external parameters probably operate to explain the $\delta^{13}C$ variability.

KEY WORDS: *Acropora formosa* · Productivity · Skeletal $\delta^{13}C$ and $\delta^{18}O$

INTRODUCTION

The sensitivity of reef-building corals to environmental changes has enabled their use as potentially reliable monitors of reefal environment histories. Geochemical proxies, such as isotopic composition or trace elements, appear to be the most promising paleoenvironmental recorders (Beck et al. 1992, Quinn et al. 1993, Dunbar et al. 1994, Guilderson et al. 1994).

As stressed by McConnaughey (1989), the partitioning of oxygen and carbon isotopes is controlled by an isotopic disequilibrium often observed in biological carbonates. Although the accumulated aragonite of coral skeletons is in isotopic disequilibrium with respect to ambient seawater, the oxygen isotopic ratio ($^{18}O/^{16}O$) is regarded as an accurate index of changes in seawater temperature and/or isotopic composition (see McConnaughey 1989, Aharon 1991, Leder et al. 1996, Wellington et al. 1996). The environmental significance of the carbon isotopic composition is much more controversial and results have led to opposite conclusions (Swart 1983).

The isotopic composition of skeletal carbon depends on the isotopic composition of dissolved inorganic carbon (DIC) (Nozaki et al. 1978, Swart et al. 1996). It is also considered to be an indicator of the metabolic activity of zooxanthellate corals and it is commonly assumed that photosynthesis should increase skeletal $\delta^{13}C$ whereas respiration should decrease it (Swart 1983, McConnaughey 1989). Based on experiments showing that aragonite, coral tissue and zooxanthellae become increasingly depleted in $\delta^{13}C$ with increasing depth (Weber & Woodhead 1970, Land et al. 1975, Weber et al. 1976, Goreau 1977b), Goreau (1977a) pro-

*E-mail: anne.juillet-leclerc@cfr.cnrs-gif.fr

posed a theoretical model in which the animal and the algae share a common carbon pool affected by photosynthesis, respiration and calcification. Erez (1978) reported results showing a relationship between $\delta^{13}C$ and photosynthetic activity, and concluded, unlike Goreau's model, that the carbon isotopic composition of the skeleton becomes lighter when photosynthesis increases. Very recently Swart et al. (1996) demonstrated that changes in skeletal $\delta^{13}C$ are strongly linked with changes in the $\delta^{13}C$ of DIC. They found that skeletal $\delta^{13}C$, corrected for changes in $\delta^{13}C$ of DIC, is not correlated with productivity and that it is negatively correlated with the theoretical ratio of daily gross primary production to daily respiration (P/R).

As pointed out by Fairbanks & Dodge (1979), well marked annual periodicity of the $\delta^{13}C$ signal recorded on the same colony could suggest a relationship between $\delta^{13}C$ and insolation that is controlled by the rate of photosynthesis of the algal symbionts: $\delta^{13}C$ increases with increasing insolation. As $\delta^{18}O$ depends upon temperature and $\delta^{13}C$ depends upon irradiance, the isotopic signals are negatively or positively correlated according to meteorological conditions prevailing in each study site (McConnaughey 1989).

Carriquiry et al. (1994) explained that the variability of $\delta^{13}C$ could be due to shifts of the symbiosis from autotrophy to increased heterotrophy modulated by seasonal solar irradiance; however, their suggestion lacked experimental support.

The aim of this paper is to compare metabolic activity and skeletal isotopic composition in the same branching coral colonies in order to check whether the $\delta^{13}C$ is or is not controlled by the photosynthesis rates of the symbionts. We report on *in situ* effects of depth and seasonal changes in temperature and light intensity on primary productivity, skeletal growth and skeletal chemistry of oxygen and carbon isotopes in the zooxanthellate scleractinian coral *Acropora formosa*. We will focus on the following 2 questions: (1) Is the oxygen isotopic composition affected by the rate of metabolic activity? (2) Is the carbon isotopic composition an accurate indicator of the metabolic activity, as claimed previously?

MATERIAL AND METHODS

Study site and environmental setting. The reef site studied (Yonge Reef) is located in the northern section of the Great Barrier Reef (14° 35' S, 145° 37' E); it belongs to the outer shelf reef type. Surface seawater temperature in the open ocean varies between a maximum of 29 to 30°C in summer (January and February) and 23 to 24°C in winter (July and August). Temperatures on the reef flat were recorded by the temperature probe of an Interocean S4 current meter and by regular measurement with a Technitemp probe. The temperatures on the reef are similar to those of the open ocean; however, a diurnal variation of up to 2°C was recorded, resulting from variations in the water depth above the reef flat due to the tides.

Salinity measurements were carried out near the study site (14° 42' S, 145° 29' E) by the Commonwealth Scientific and Industrial Research Organization from 1979 to 1982. There is little variation throughout the year and typical values for surface seawater are in the range 34.5 to 35.5 psu. Major cyclonic events or heavy monsoonal rainfall in the area during the summer season do not affect water salinity significantly in the vicinity of offshore reefs.

The reef flat is subjected to waves and swells generated by the trade winds which blow persistently at 15 to 25 knots for approximately 9 months of the year. Since the trade winds originate generally from the SE, the reef flat, oriented N-S to SSE-NNW, does not take the full brunt of the swell. At high tide, waves break on the inner reef flat, whereas at low tide the breaker line is close to the reef front. The SE swell is refracted around the south horn of Yonge Reef and may affect the northern half of the back reef margin.

Records of current speed and direction were obtained on the reef flat (ca 1 to 2 m depth) using an Interocean Systems S4 current meter. During the trade wind season, currents result from the combination of a tidal flow oriented NE-SW and a wind driven flow in SE-NW direction, with a maximum velocity of 0.25 m s^{-1}.

Biological material. Eleven sets of branches (length ranging from 65 to 165 mm) were sampled from different colonies of *Acropora formosa* (Dana 1846) at each site using bone cutting pliers; the branches were then attached to concrete bases and finally were cemented onto dead corals. Preparation of the samples was performed in November 1988 at 2 m depth on the reef flat and at 12 m on the back reef slope.

Productivity measurement. Rates of oxygen flux were measured *in situ* in July 1989 and January 1990 using a 6-chamber respirometer comprising 6 galvanic oxygen sensors (EIL, Kent, UK), a stainless steel thermistor (Analog Devices model AC 2626 K4) and a cosine corrected quantum sensor (LI-192SA). The oxygen sensors were calibrated every day from air-saturated seawater and a saturated solution of sodium dithionite (zero oxygen). Irradiance, dissolved oxygen and temperature were logged every minute. Epiphytes were carefully removed, especially on the cement bases, which were thoroughly cleaned with a metallic brush. All specimens and their respective bases were incubated for 24 h in UV-transparent perspex chambers. Chamber volumes (2.9 or 6.7 l depending on the

size of the specimens) were corrected by the volume of specimens and bases. Seawater in each chamber was stirred continuously using a small-sized propeller. The chambers were flushed for 2 to 4 min every 30 min. Rates of photosynthesis and respiration were first estimated by regressing oxygen data against time, normalized to the branch length of the specimens, and expressed in µmol O_2 m^{-1} h^{-1}. The following exponential function was fitted to the photosynthesis-irradiance data using a non-linear, least squares regression (program AR of the BMDP statistical package, Health Sciences Computing Facility, University of California, Los Angeles, CA, USA):

$$p = p_m^g(1 - e^{-I/I_k}) + r$$

where p = rate of net productivity; p_m^g = maximal rate of gross productivity; I = irradiance (µmol m^{-2} s^{-1}); I_c = irradiance at which $P = -R$; I_k = irradiance at which the initial slope and the horizontal asymptote intercept; and r = rate of dark respiration. The definition of all metabolic parameters used in the present paper can be found in Gattuso & Jaubert (1988). Daily rates of gross primary production (P_c gross) and respiration [R_c (24 h)] were estimated by numerically integrating (1 min intervals) the data for the fitted lines against irradiance measured during the experiments.

Rates of photosynthesis and respiration are usually normalized using biomass parameters, such as chlorophyll or protein contents, which requires the destruction of the samples. None of these parameters were available since replicate measurements were required on the same sets of colonies at 2 different times in order to correlate primary productivity to skeletal isotopic ratios. We chose to normalize rates to length of branches, which could be easily measured under water and minimized manipulation of the specimens. Branch length is a relatively good indicator of coral biomass in *Acropora formosa* since the protein content per unit of branch length is not statistically different between 2 and 12 m depth (data not shown).

Upon completion of measurements in July 1989, coral skeletons were stained twice on 2 consecutive days. Colonies were incubated during the day for 3 to 4 h in 6 l plastic bags containing Alizarin Red S (final concentration ca 8 mg l^{-1}). Specimens were then cemented back in their original location. After the second series of measurements, in January 1990, the specimens were dried for subsequent determination of growth rate and skeletal isotopic ratios. Care was taken to avoid breaking the branch tips. The number of data available was 5 at 2 m and 6 at 12 m; the other specimens were lost or broken during the 20 mo of the experiment.

Subsampling from coral branches. Several branches from every colony were sawn carefully into halves along the growth axes. Great care was taken to avoid any damage of the branch tips. Around 80 µg of carbonate (referred to as subsamples) was removed from the growth axis for isotopic analysis, using low-speed drilling (drill diameter: 0.6 mm) to avoid any mineralogical conversion (Gill et al. 1995). The alizarin-stained zone and the tip were subsampled very carefully (these are used as reference points, representing days of alizarin staining and of collection). The apical part of the branches is very fragile and was sometimes broken during sampling. In such cases, an apex was removed from another branch of the same colony. Subsequent measurements demonstrated that all apices from the same colony provided similar results. Subsampling was carried out as close as possible to the growth axis.

Isotopic measurements. Determination of $\delta^{18}O$ and $\delta^{13}C$ was performed on all subsamples using a FINNIGAN MAT 251 mass spectrometer, coupled with a standard FINNIGAN 'Bremen Carbonate Device'. This allows automatic processing of the subsamples with an individual acid bath. Reproducibility of $\delta^{18}O$ and $\delta^{13}C$ measurements is, respectively, 0.07‰ and 0.05‰ (2σ). The isotopic compositions are expressed in delta notation with PDB (Pee Dee Belemnite) as standard:

$$\delta^{18}O = [(^{18}O/^{16}O)_{sample}/(^{18}O/^{16}O)_{standard} - 1] \times 10^3$$
$$\delta^{13}C = [(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard} - 1] \times 10^3$$

Organic matter was eliminated prior to the determination of $\delta^{18}O$ and $\delta^{13}C$ by roasting the aragonite powder under partial vacuum for 20 min at 400°C. As we know that such a treatment may convert aragonite into calcite, isotopic composition of some subsamples was compared before and after heat treatment in order to assess the effect of oven-drying. There was no noticeable difference.

Statistics. Results were analysed using the statistical packages SuperAnova v. 1.11 and StatView v. 4.01 (Abacus Concepts Inc., Berkeley, CA, USA). Analyses of variance from repeated measures were used to study the effects of depth and season on metabolic parameters and skeletal isotopic composition. The effects of these factors on growth rate were tested using standard 2-way ANOVAs for depth and season and 1-way ANOVAs for skeletal isotopic composition. Preliminary testing (on $P/-R$ ratios) showed that the use of arcsine transformation to normalize the distribution of percentages or ratios (Zar 1984) did not change the conclusions drawn from ANOVAs. Predictive regression (simple linear regression) could not be used to investigate the relationship between 2 sets of parameters since (1) the 2 variables are not independent and (2) fluxes show a natural variability and are subject to measurement errors (Ricker 1973). Functional regression was therefore applied to our data sets as

described by Jacques & Pilson (1980). There is a simple relationship between the slopes of the functional (b_f) and predictive (b_p) regression: $b_f = b_p/r$; with r = coefficient of correlation. Results are expressed as mean ± standard error of the mean when applicable.

RESULTS

Biological and physiological data

Seasonal seawater temperature and daily irradiation varied widely (Table 1). Temperature increased by 4.5 to 5°C between July 1989 and January 1990, but varied very little according to depth (0.2 to 0.4°C). The duration of the daylight period was 15 to 26% higher in summer than in winter. The daily irradiation in summer increased by 69 and 34%, respectively, at 2 and 12 m.

The average growth rate of *Acropora formosa* at 2 and 12 m was 21.7 ± 2.1 and 25.3 ± 2.0 mm (7 mo)$^{-1}$. Assuming that there was no seasonal variation in linear extension rate (see Gladfelter 1984) these values may be extrapolated to annual extension rates of 37.2 and 43.4 mm yr^{-1} respectively. The effect of depth on linear extension was not statistically significant (p = 0.24).

Mean estimates of the photosynthesis-irradiance curves are given in Table 2. p_m^g varied significantly according to season (p = 0.05) but did not vary significantly with depth (p = 0.14). Season had a significant effect on the initial slope α (p = 0.0009) but depth had no effect on α (p = 0.10). Rates of dark respiration did not vary with depth (p = 0.10) or season (p = 0.34). I_k and I_c both changed with depth (p = 0.001 and p < 0.0001) and season (p = 0.003 and p < 0.0001).

Daily metabolic budgets are shown in Table 3. Depth had a significant effect on the rate of gross photosynthesis (P_c gross; p = 0.016) but was less important for daily respiration rate [R_c(24 h)]. In most samples, P_c gross was higher in winter than in summer while R_c(24 h) was lower in winter than in summer. No statistically significant seasonal effect on these parameters could, however, be detected (p = 0.09 to 0.34). The $P/-R$ ratio varied significantly with depth (p = 0.04) and season (p = 0.0004).

Isotopic data

The average oxygen and carbon isotopic composition at 2 and 12 m depth, in winter and summer, is given in Table 3. Analyses of all subsamples extracted from every branch are given in Table 4. There is a significant correlation between $\delta^{18}O$ and $\delta^{13}C$ in summer (functional regression: $y = -6.26 - 0.5x$; r = −0.69; p = 0.02; n = 10) and in winter (functional regression: $y = -5.11 - 0.39x$; r = −0.83; p = 0.001; n = 11) (Fig. 1).

Table 1. Seawater temperature, underwater daily irradiation and duration of daylight and darkness during the field experiments. Means ± SE; n: sample size

	Temperature (°C)	Daily irradiation (mol m^{-2} d^{-1})	Daylight (min)	Darkness (min)
Austral winter (Jul 1989)				
2 m (n = 2)	26 ± 0.01	21.4 ± 2	676 ± 3	763 ± 3
12 m (n = 1)	25.6	7.5	666	773
Austral summer (Jan 1990)				
2 m (n = 5)	30.5	36.3	782	657
12 m (n = 5)	30.6 ± 0.2	10.4 ± 1.1	768 ± 2	671 ± 2

Table 2. Curve fitting parameters for photosynthesis-irradiance curves for *Acropora formosa*. The model equation is shown in the text ('Material and methods—Productivity measurements'). Means ± SE; n: sample size

	p_m^g (mmol m^{-2} h^{-1})	I_k (µmol m^{-2} s^{-1})	r (mmol m^{-2} h^{-1})	α [mmol m^{-2} h^{-1} (µmol m^{-2} s^{-1})$^{-1}$]	I_c (µmol m^{-2} s^{-1})
Austral winter (Jul 1989)					
2 m (n = 6)	1392 ± 250	245 ± 14	−322 ± 47	6 ± 1	67 ± 5
12 m (n = 6)	991 ± 130	117 ± 12	−203 ± 25	9 ± 1	27 ± 3
Austral summer (Jan 1990)					
2 m (n = 5)	665 ± 99	308 ± 19	−212 ± 22	2.2 ± 0.3	123 ± 7
12 m (n = 5)	555 ± 216	245 ± 30	−190 ± 75	2.7 ± 0.9	75 ± 7

Table 3. *Acropora formosa*. Daily integrated metabolic parameters and averaged isotopic data as a function of depth and season. $P/-R = P_c$ gross/$-R_c$ (24 h). Means ± SE; n: sample size

	P_c gross (mol m^{-1} d^{-1})	R_c (24 h) (mol m^{-1} d^{-1})	$P/-R$	$\delta^{18}O$ (‰ vs PDB)	$\delta^{13}C$ (‰ vs PDB)
Austral winter (Jul 1989)					
2 m (n = 6)	11 ± 2	−8 ± 1	1.4 ± 0.1	−4.28 ± 0.06	−2.09 ± 0.02
12 m (n = 6)	7 ± 1	−4.9 ± 0.7	1.4 ± 0.03	−3.90 ± 0.03	−3.12 ± 0.12
Austral summer (Jan 1990)					
2 m (n = 5)	7 ± 1	−5.1 ± 0.5	1.3 ± 0.1	−4.99 ± 0.08	−2.58 ± 0.13
12 m (n = 5)	4 ± 1	−5 ± 2	0.9 ± 0.1	−4.60 ± 0.04	−3.31 ± 0.16

Oxygen isotopic composition

The oxygen isotopic composition varied significantly according to depth ($p = 0.0005$) and season ($p < 0.0001$). Though only 2 temperatures were tested (corresponding to season of metabolic measurements), we verified that $\delta^{18}O$ decreased as a function of temperature (functional regression: $y = 0.44 - 0.17x$, $r = 0.85$, $p < 0.001$, $n = 21$; Fig. 2; for the same values the predictive regression is: $y = -0.15 - 0.27x$, $r = 0.85$).

There is no evidence of any relationship between the oxygen isotopic ratios and productivity. $\delta^{18}O$ values varied widely according to season and to depth, even when the rates of productivity remained within the same range. The oxygen isotopic composition of the corals is clearly not controlled by the metabolic activity.

Carbon isotopic composition

$\delta^{13}C$ varied significantly as a function of depth ($p = 0.0002$) and season ($p = 0.011$). It was lower at 12 m than at 2 m, with a shift of 0.73‰ in summer (−3.31 vs −2.58‰) and 1.04‰ in winter (−3.12 vs −2.09‰).

There are large isotopic differences for similar levels of productivity obtained at different seasons and depths. The carbon isotopic data display a large range (−2.04 to −3.76‰) and are quite scattered with respect to productivity of individual colonies (Fig. 3). Winter $\delta^{13}C$ are roughly constant at each depth (except for 1 value obtained at 12 m depth) while summer $\delta^{13}C$ display a large scatter. There is a statistically significant correlation between skeletal $\delta^{13}C$ and gross primary production (functional regression: $y = -3.77 + 0.14x$; $p = 0.03$; $R^2 = 0.22$; $n = 21$).

DISCUSSION

Metabolic parameters

Large amounts of photosynthetically fixed carbon are translocated from zooxanthellae to the animal host and are a major source of energy for coral tissues (Muscatine et al. 1989). This makes the plant-animal symbiotic unit very much light-dependent. Both the animal and the symbiotic algae respond to a decrease in irradiance in order to maximize photosynthetic efficiency and decrease energy expenditure. These photoadaptative processes result in profound changes in the shape of the photosynthesis-irradiance (PI) curves according to light regime (Barnes & Chalker 1990). Typical changes with increasing depth are (1) an

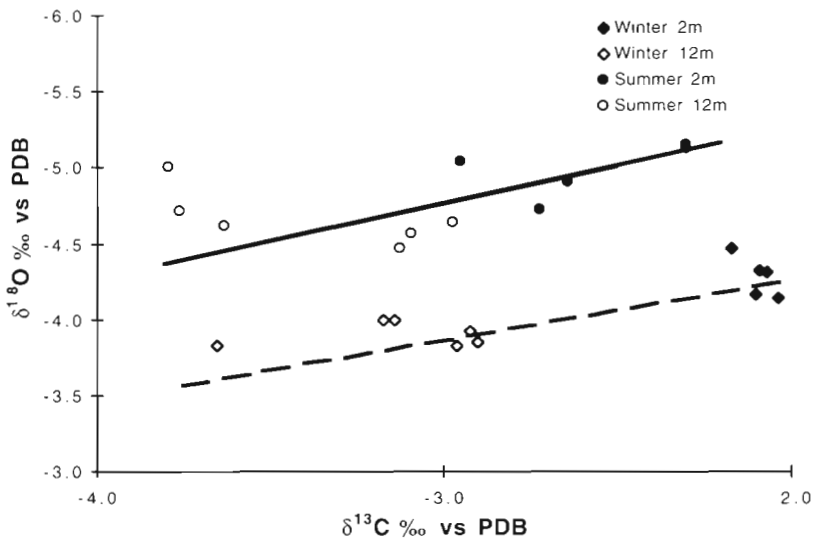

Fig. 1. *Acropora formosa*. Relationship between skeletal $\delta^{18}O$ and skeletal $\delta^{13}C$ in winter and summer. The functional regression lines computed for each season for colonies studied at 2 and 12 m are shown. ($\delta^{18}O$ values are plotted with an inverse scale, as is usual in geochemical studies)

Table 4. *Acropora formosa*. Carbon and oxygen skeletal isotopic composition and gross primary production of individual colonies

Colony	$\delta^{13}C$ (‰)		$\delta^{18}O$ (‰)		P_c gross (mol m^{-1} d^{-1})	
	Winter	Summer	Winter	Summer	Winter	Summer
2 m						
42	−2.09	−2.95	−4.32	−5.04	7.65	7.88
45	−2.07	−2.3	−4.31	−5.13	7.57	5.14
61	−2.1	−2.72	−4.17	−4.72	10.11	9.26
63	−2.17	−2.3	−4.47	−5.15	8.41	6.44
66	−2.04	−2.64	−4.14	−4.91	19.83	3.85
12 m						
17	−2.92	−3.76	−3.92	−4.71	6.00	1.61
18	−3.65	−3.63	−3.82	−4.72	10.22	3.08
67	−2.96	−3.09	−3.83	−4.57	7.93	1.58
68	−2.9	−2.97	−3.85	−4.64	4.04	8.38
69	−3.17	−3.79	−3.99	−5.00	9.04	–
70	−3.14	−3.12	−4.00	−4.47	5.20	4.68

increase of the initial slope (α) of the PI curve, (2) a decrease of I_k and (3) a decrease in the rate of respiration (r). *Acropora formosa* displays similar changes, although these are not significant due to its limited bathymetric distribution (approximately 2 to 12 m), suggesting that the photosynthetic efficiency increases and energy expenditure decreases with increasing depth.

There are marked seasonal differences in the parameters of the PI curves as well as in the daily metabolic budgets. The daily gross production decreased according to increasing depth and was lower in summer than in winter. This result contrasts with data collected by Chalker et al. (1984) on *Acropora granulosa*, which displays a gross production at 1 m depth lower than at 10 and 15 m and a gross production higher in summer (December) than in winter (June).

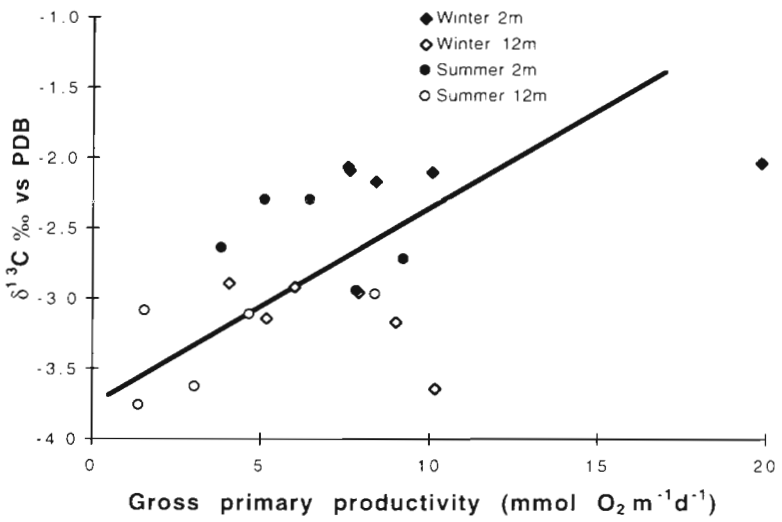

Fig. 3. *Acropora formosa*. Skeletal $\delta^{13}C$ as a function of gross primary production. The significant functional regression line is shown

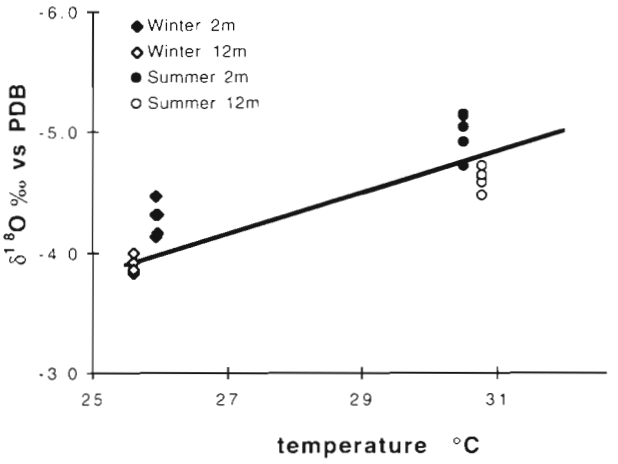

Fig. 2. *Acropora formosa*. Skeletal $\delta^{18}O$ versus temperature. The functional regression line is shown. Temperature dependence of $\delta^{18}O$ and consequences of the aragonite deposition mechanism for $\delta^{18}O$ are discussed in Juillet-Leclerc et al. (1997). ($\delta^{18}O$ values are plotted with an inverse scale, as is usual in geochemical studies)

Comparison between physiological data and isotopic ratio

Physiological measurements were carried out during 1 or 2 consecutive days, while isotopic data integrated several days of calcium carbonate deposition. We previously demonstrated (Juillet-Leclerc et al. 1997, see also Gladfelter 1982, 1983, 1984) that calcification takes place through 2 successive steps: formation of a framework followed by a progressive infilling of residual intercrystalline space, according to the Gladfelter model. The duration of the second step (i.e. infilling) is not well known but accretion of aragonite could last several months in species of the genus *Acropora* (Gladfelter 1984).

The apical zone of a branch is the only part exhibiting an 'instantaneous' isotopic composition. The older the sample, the larger is the bias in the measured proxy due to the 2-step deposition mechanism. As a result, a discrepancy between physiological data and isotopic composition becomes more likely, with the isotopic signal of the older parts of the colonies depending upon the magnitude

of the infilling process (Juillet-Leclerc et al. 1997). The effect of the mechanisms of calcium carbonate deposition has been demonstrated using measurements of skeletal $\delta^{18}O$, but they also control the carbon isotopic composition. Therefore, carbonate from the apex is the only subsample which may be rigourously compared with physiological measurements. In contrast, comparison between the isotopic ratio and rates of productivity of the alizarin-stained zone (July 1989, 6 mo before collection) must be performed with caution since the isotopic ratios of the subsamples integrate approximately 6 mo of infilling.

Effects of calcification pattern on isotopic oxygen and carbon ratios

$\delta^{18}O$-temperature relation

The temperature dependence of $\delta^{18}O$ deduced from these data displays a significant discrepancy from the calibration reported by Weber & Woodhead (1972) for the same genus. The difference in the slopes of the $\delta^{18}O$-temperature relation (0.15 vs 0.28‰ $°C^{-1}$) can be explained by secondary aragonite deposition which reduces the annual isotopic amplitude corresponding to the annual temperature difference (see Juillet-Leclerc et al. 1997). Weber & Woodhead (1972) did not take into account the isotopic composition of sea water. Their data were corrected by estimating the average salinity (Levitus 1982), which was converted into isotopic composition using the relationship between salinity and $\delta^{18}O$ corresponding to the tropical Pacific Ocean, calculated from the GEOSECS Atlas (Östlund 1987): $-\delta^{18}O = 3.43 - 0.28\,T°C$. Using this relation, the isotopic measurements obtained for the apex (considering a mean $\delta^{18}O_{water} = 0.35$‰ vs SMOW)—the only location corresponding to an 'instantaneous' aragonite formation—are in very good agreement with the calculation (the isotopic composition calculated for 2 m depth is −4.96‰, compared with an average measured value of −4.99‰).

Variation of $\delta^{18}O$ according to depth

The comparison between the measured isotopic profile from colonies which grew at 12 m depth and the isotopic profile simulated on the basis of the aragonite deposition mechanism (Juillet-Leclerc et al. 1997) suggests that the magnitude of the secondary infilling is less important at 12 m than at 2 m depth (20% vs 60 to 80% of aragonite deposited at the base of the branches after 1 yr growth). This high primary aragonite content could be ascribed to a less active infilling by secondary aragonite, due to reduced light. In this case, oxygen and carbon isotopic values measured for deeper colonies could be less biased by secondary infilling.

Effects of calcification on $\delta^{13}C$ and the $\delta^{18}O$-$\delta^{13}C$ relationship

The scattering of the $\delta^{13}C$ values is large in summer (i.e. branch tips) but is much lower in winter (i.e. the alizarin-stained zones) at both 2 and 12 m (except for colony no. 18 at 12 m depth), including colony no. 66 for which productivity is very high. This difference may result from progressive infilling which smooths initial $\delta^{13}C$ differences.

Such a process may also explain why the correlation between $\delta^{18}O$ and $\delta^{13}C$ is stronger in winter than in summer (Fig. 1); the progressive infilling smooths variability within each colony and reduces the initial scattering observed between $\delta^{18}O$ and $\delta^{13}C$. In winter, the relationship between oxygen and carbon isotopic composition is roughly linear.

Relationship between isotopic ratio and gross primary production

The productivity/$\delta^{13}C$ relationship shows a significant correlation; this result is in agreement with previous studies (Land et al. 1975, Goreau 1977a, Swart 1983). According to the model proposed by Weber & Woodhead (1970), the animal cells and the zooxanthellae use the same carbon pool. Zooxanthellae preferentially use light CO_2 when the rate of photosynthesis is high. The carbon available for calcification is therefore enriched in ^{13}C and skeletal carbon becomes heavier. As the authors suppose that oxygen and carbon are fractionated by a similar mechanism, $\delta^{18}O$ and $\delta^{13}C$ should be correlated. $\delta^{18}O$ and $\delta^{13}C$ do indeed show a depletion as depth increases, but the correlation is very weak.

Goreau (1977a) interpreted $^{13}C/^{12}C$ changes in the light of the Weber & Woodhead model (1970) just described; but although CO_2 released by respiration increases when coral grows faster, CO_2 uptake increases as well and coral is forced to take up a greater amount of isotopically heavier HCO_3^- from water to build its skeleton. As Goreau supposed that oxygen fractionation and carbon fractionation are probably carried out through different mechanisms, this model does not imply any correlation between $\delta^{18}O$ and $\delta^{13}C$ and seems more appropriate for explaining the results of the present paper.

The discrepancy of $\delta^{13}C$ observed between colonies grown in winter and summer at 2 m and 12 m depth and

showing similar rates of gross primary production may be due to changes in the concentration of DIC, but no DIC data are available for our study site. However, DIC supply cannot explain the $\delta^{13}C$ variability observed in colonies grown within a given season, especially during summer during which there is no isotopic effect due to progressive infilling (assuming that DIC-$\delta^{13}C$ variability between 2 and 12 m depth is negligible).

We suggested above that $\delta^{13}C$ values could be biased by the aragonite deposition mechanism; by comparing the regression obtained for summer $\delta^{13}C$ values and for all the values, we obtain very similar relationships.

Metabolic data and isotopic measurements from colonies which grew under similar physical and chemical conditions (i.e. at a given depth and season) display significant differences. The scattering of data observed in Fig. 3 indicates that the mechanism of carbon incorporation into the skeleton is not as simple as Goreau (1977) suggested, and that his model is not fully supported by our results. Internal factors other than photosynthesis and respiration could be implied in C isotopic fractionation. Muscatine et al. (1989) measured the carbon isotopic composition of organic matter extracted from zooxanthellae and coral tissue. Their results indicated a strong correlation between $\delta^{13}C$ and productivity, which emphazises the fact that the scattering of our data is not only due to metabolic processes, but also involves mechanisms of carbon uptake and aragonite deposition.

Comparison between isotopic ratio and irradiation

Since photosynthesis is controlled by insolation, we also investigated a possible link between irradiance and carbon isotopic ratio as has been suggested by Fairbanks & Dodge (1979). The gross primary production (P_c gross) and respiration [R_c (24 h)] diminish sharply as depth increases due to the decline in both productivity and respiration rates per unit biomass. However P_c gross and R_c (24 h) tend to be lower in summer than in winter at 2 and at 12 m (Table 3). We attribute this decrease to the too-high temperature (exceeding 30°C) in summer at the 2 depths. Comparing productivity measurements in summer at 2 and 12 m depth, when the irradiance gradient is well marked but temperatures are similar, the small difference strongly suggests that photoinhibition occurs at the shallowest depth. A decrease in $\delta^{13}C$ induced by photoinhibition or by excessive temperature can be explained by Goreau's model: these factors imply weaker photosynthetic activity and, as a result, an increase of ^{12}C content in the common carbon pool.

Despite these features, skeletal $\delta^{13}C$ and productivity show a positive correlation. It appears therefore that the actual factor regulating $\delta^{13}C$ is photosynthesis and not irradiance *per se*. Productivity may be higher at deeper sites than at shallower ones (Chalker et al. 1984), due to excessive temperature and/or irradiance. Consequently skeletal $\delta^{13}C$ could be depleted in shallower waters.

CONCLUSION

The use of respirometers allowed direct comparison between metabolic processes and isotopic measurements. On the one hand, this study confirms that there is no apparent link between metabolic activity and $\delta^{18}O$, which seems to be primarily controlled by temperature. On the other hand, the functional regression applied between $\delta^{13}C$ and productivity on the scale of an individual colony shows a significant correlation: $\delta^{13}C$ increases with increasing productivity. This is in agreement with Goreau's model. The weakness of the relationship can be explained by several factors:

- the mechanism of skeletogenesis reduces an initially significant relationship between $\delta^{13}C$ and productivity. In addition, our metabolic measurements were restricted to only 1 or 2 consecutive days, thereby reflecting the environmental conditions partially or imperfectly compared to isotopic records, which integrate a longer period of time.
- the variability of the DIC isotopic composition, which could induce seasonal changes, is unknown.
- the conditions prevailing during this experiment were probably complex. Obviously, an excess of temperature, and possibly photoinhibition, limited productivity and confused our results.

Despite these special conditions, the relationship between $\delta^{13}C$ and productivity is stronger than between $\delta^{13}C$ and daily irradiance.

The large variability of both metabolic and isotopic data for colonies grown in identical environmental conditions, reveals that other internal and/or external factors probably induce different physiological activity and isotopic carbon fractionation.

What are the consequences of the results presented here on future $\delta^{13}C$ use as a proxy of paleoproductivity? Due to great intraspecific variability, no single isotopic profile can be considered to be a significant indicator in terms of reef paleoproductivity. But variation in productivity could be inferred from several isotopic profiles over the same time interval. High productivity does not always occur when solar radiation and/or temperature are high. High $\delta^{13}C$ could indicate simply that corals grew in more favorable conditions. In this regard, high $\delta^{13}C$ values could express fertility changes in distinct reef compartments during colder periods, as suggested by Aharon (1991). The trend of

isotopic profiles could be used as a guide for the qualitative assessment of environmental changes, particularly during the successive stages of holocene reef growth.

Acknowledgements. Assistance in the field was provided by the masters and crews of RVs 'The Harry Messel' and 'Lady Basten' as well as by R. Priest, J. Small, E. Shanahan, W. Darke, B. Musso and S. Romano. We thank P. Swart for reviewing an early draft of the manuscript. This study was carried out as part of an Australian-French cooperative research programme on Coral Reefs. It was supported by the French Ministry of Foreign Affairs, the *Programme National Récifs Coralliens* (PNRCO) and the Australian Institute of Marine Science (AIMS). We are grateful to the technicians of the AIMS workshops for constructing the 6-chamber respirometer This is a contribution of PNRCO.

LITERATURE CITED

Aharon P (1991) Recorders of reef environment histories: stable isotopes in corals, giant clams, and calcareous algae. Coral Reefs 10:71–90

Barnes DJ, Chalker BE (1990) Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky Z (ed) Coral reefs. Elsevier, Amsterdam, p 109–131

Beck JW, Edwards RL, Ito E, Taylor FW, Recy J, Rougerie F, Joannot P, Henin C (1992) Sea-surface temperature from coral skeletal strontium/calcium ratios. Science 257: 644–647

Carriquiry JD, Risk MJ, Schwarcz HP (1994) Stable isotope geochemistry of corals from Costa Rica as proxy indicator of the El Niño/Southern Oscillation (ENSO). Geochim Cosmochim Acta 58:335–351

Chalker BE, Cox T, Dunlap WC (1984) Seasonal changes in primary production and photoadaptation by the reef-building coral *Acropora granulosa*, on the Great Barrier Reef. Lect Notes Coastal Estuarine Stud 8:73–87

Dunbar RB, Wellington GM, Colgan MW, Glynn PW (1994) Eastern Pacific sea surface temperature since 1600 A.D.: the $\delta^{18}O$ record of climate variability in Galapagos corals. Paleoceanography 9:291–315

Erez J (1978) Vital effect on stable-isotope composition seen in foraminifera and coral skeletons. Nature 273:199–202

Fairbanks RG, Dodge RE (1979) Annual periodicity of the $^{18}O/^{16}O$ and $^{13}C/^{12}C$ ratios in the coral *Montastrea annularis*. Geochim Cosmochim Acta 43:1009–1020

Gattuso JP, Jaubert J (1988) Computation of metabolic quotients in plant-animal symbiotic units. J Theor Biol 130:205–212

Gill I, Olson JJ, Hubbard DK (1995) Corals, paleotemperature records, and the aragonite-calcite transformation. Geology 23:333–336

Gladfelter EH (1982) Skeletal development in *Acropora cervicornis*: I. Patterns of calcium carbonate accretion in the axial corallite. Coral Reefs 1:45–51

Gladfelter EH (1983) Skeletal develoment in *Acropora cervicornis*. II. Diel patterns of calcium carbonate accretion. Coral Reefs 2:91–1100

Gladfelter EH (1984) Skeletal development in *Acropora cervicornis*. III. A comparison of monthly rates of linear extension and calcium carbonate accretion measured over a year. Coral Reefs 3:51–57

Goreau TJ (1977a) Carbon metabolism in calcifying and photosynthetic organisms: theoretical models based on stable isotope data. Proc 3rd Int Coral Reefs Congr 1:395–401

Goreau TJ (1977b) Coral skeletal chemistry: physiological and environmental regulation of stable isotope and trace metals in *Monstastrea annularis*. Proc Roy Soc Lond B 196:291–315

Guilderson TP, Fairbanks RG, Rubenstone JL (1994) Tropical temperature variations since 20,000 years ago: modulating interhemispheric climate change. Science 263: 663–665

Jacques TG, Pilson MEQ (1980) Experimental ecology of the temperate scleractinian coral *Astrangia danae*. 1. Partition of respiration, photosynthesis and calcification between host and symbionts. Mar Biol 60:167–178

Juillet-Leclerc A, Montaggioni LF, Pichon M, Gattuso JP (1997) Effects of calcification patterns on the skeleton's oxygen isotopic composition of the scleractinian coral *Acropora formosa*. Oceanol Acta 20:645–658

Land LS, Lang JC, Smith BN (1975) Preliminary observations on the carbon isotopic composition of some reef coral tissues and symbiotic zooxanthellae. Limnol Oceanogr 20:283–287

Leder JJ, Swart PK, Szmant AM, Dodge RE (1996) The origin of variations in the isotopic record of scleractinian corals: I. Oxygen. Geochim Cosmochim Acta 60:2857–2870

Levitus S (1982) Climatological atlas of the world ocean. NOAA Prof Pap 13

McConnaughey T (1989) C-13 and O-18 isotopic desequilibrium in biological carbonates: I. Patterns. Geochim Cosmochim Acta 53:151–162

Muscatine L, Porter JW, Kaplan IR (1989) Resource partioning by reef coral as determined from stable isotope composition. I. $\delta^{13}C$ of zooxanthellae and animal tissue vs. depth. Mar Biol 110:185–193

Nozaki Y, Rye DM, Turekian KK, Dodge RE (1978) A 200 year record of Carbon-13 and Carbon-14 variations in Bermuda coral. Geophys Res Lett 5:825–828

Östlund HG (1987) GEOSECS Atlantic, Pacific and Indian Ocean expeditions. Shorebased data and graphics. International Decade of Ocean Exploration. National Science Foundation, Washington, DC

Quinn TM, Taylor FW, Crowley TJ (1993) A 173 year stable isotope record from a tropical south Pacific coral. Quat Sci Rev 12:407–418

Ricker WE (1973) Linear regressions in fishery research. J Fish Res Bd Can 30:409–434

Swart PK (1983) Carbon and oxygen isotope fractionation in scleractinian corals: a review. Earth Sci Rev 19:51–80

Swart PK, Leder JJ, Szmant AM, Dodge RE (1996) The origin of variations in the isotopic record of scleractinian corals: II. Carbon. Geochim Cosmochim Acta 60:2871–2886

Weber JN, Deines P, Weber PH, Baker PA (1976) Depth related changes in the $^{13}C/^{12}C$ ratio of skeletal carbonate deposited by the Carribean reef-frame building coral *Montastrea annularis*: further implications of a model for stable isotope fractionation by scleractinian corals. Geochim Cosmochim Acta 40:31–39

Weber JN, Woodhead PMJ (1970) Carbon and oxygen isotope fractionation in the skeletal carbonate reef-building corals. Chem Geol 6:93–117

Weber JN, Woodhead PMJ (1972) Temperature dependence of Oxygen-18 concentration in reef coral carbonates. J Geophys Res 77:463–473

Wellington GM, Dunbar RB, Merlen G (1996) Calibration of stable oxygen isotope signatures in Galapagos corals. Paleoceanography 11:467–480

Zar JH (1984) Biostatistical analysis, 2nd edn. Prentice-Hall, Englewood Cliffs, NJ

Editorial responsibility: Otto Kinne, Oldendorf/Luhe, Germany

Submitted: September 23, 1996; Accepted: July 16, 1997
Proofs received from author(s): September 23, 1997