NOTE

Measurement of oxygen metabolism in open-top aquatic mesocosms: application to a coral reef community

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ABSTRACT· A new experimental and analytical protocol enabling the measurement of the metabolism of aquatic communities in open-top mesocosms is described. It involves estimation of air-water gas exchange and use of a polynomial regression to estimate metabolic parameters from measurements of dissolved oxygen concentration. Sample data is provided for a coral reef community. Its major advantage compared to the standard respirometry technique is that the community is not subject to great variations of physical and chemical parameters such as dissolved oxygen concentration or pH during the experiment. Changes in the concentration of dissolved oxygen were measured over 24 h periods and used to derive community gross photosynthesis (P_g) and respiration (R). Experiments performed on the same community with 2 differents light intensities (360 and 250 μmol m^{-2} s^{-1}) provided consistent estimates of P_g (208 $\pm$ 50 and 73 $\pm$ 20 mmol O$_2$ m^{-2} d^{-1}) and R (−219 $\pm$ 55 and −79 $\pm$ 29 mmol O$_2$ m^{-2} d^{-1}). The air-water oxygen transfer velocities, K_{O_2}, varied between 34 $\pm$ 5 and 84 $\pm$ 12 cm h^{-1} This approach provided estimates of community metabolism that are not significantly different from those obtained using the standard respirometry technique.

KEY WORDS: Primary production · Respiration · Mesocosms · Coral reef community · Aquatic ecosystem

Mesocosms and microcosms are artificially constructed ecosystems maintained in containers isolated from natural ecosystems (Beyers & Odum 1993). They have been used in ecological studies for many years (Woodruff 1912, Gause 1934) and enable the running of small-size ecosystems for days, months or years (Adey 1983, Jaubert et al. 1995, Luckett et al. 1996). They are tools for experiments that could not be carried out on natural systems, such as effect of changes in environmental parameters (e.g. light, temperature,

salinity, pCO$_2$ and water motion) on community structure and function (Parsons 1981, Oviatt 1994). The use of mesocosms in experimental ecology has been criticized by several authors (Heath 1980, Kinsey 1985, Hendrey 1992, Carpenter 1996, Nijs et al. 1996), who pointed out limitations such as variability between mesocosms, low species diversity, low environmental variability and small-scale approach. Mesocosms are, nevertheless, powerful tools to investigate system behavior when field experiments cannot be performed or when the system under investigation is too complex (Oviatt 1994, Lawton 1996).

Community metabolism of an aquatic mesocosm can be measured using various techniques, depending on the type of mesocosm under investigation. Flow-through mesocosms are open systems continously supplied with 'new' water, the exchange rate being adjusted to be able to measure a significant change of selected parameters. Community metabolism of such systems can be investigated using an adaptation of the flow respirometry technique (Marsh & Smith 1978) by measuring differences in the water chemistry between the inflowing and the outflowing seawater (Henderson & Smith 1980, Henderson 1982, Griffith et al. 1987). Mesocosms which are closed in terms of seawater supply can be open or closed to the atmosphere. Open-top mesocosms have seldom been used to investigate the community metabolism of aquatic systems (Jaubert et al. 1995, Langdon & Sweeney 1995). It is indeed difficult to estimate the gas exchange across the air-water interface but this problem can be avoided by sealing the mesocosm and using it as a respirometer (Kinsey 1978, McCloskey et al. 1978). This method is, however, difficult to implement because it requires that the container be completely filled, in order to avoid the presence of air, and that regular partial flushing be carried out in order to avoid great variation in, for example, dissolved oxygen and carbon dioxide.

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Coral reefs comprise several communities, making this ecosystem one of the most diverse, complex and productive ecosystems on earth. Field studies of community metabolism began in the late 1940s (Sargent & Austin 1949, Odum 1956) and considerable information is now available on community productivity and calcification of coral reef flats (Smith 1995, Gattuso et al. 1998). Additionally, Smith & Buddemeier (1992) suggested that community metabolic parameters could be used as a tool to investigate the response of coral reefs to environmental stress. However, relatively few studies have used mesocosms for investigating coral reef metabolism (Henderson & Smith 1980, Henderson 1982, Adey 1983, Griffith et al. 1987, Atkinson et al. 1995, Jaubert et al. 1995, Luckett et al. 1996).

The aim of the present study was to develop a new experimental and analytical protocol enabling the measurement of the community metabolism of an open-top aquatic mesocosm. This method, which estimates the air-sea O_2 transfer velocity (K_{O_2}), was applied to a coral reef open-top mesocosm. Comparison of the derived metabolic parameters with those obtained both in the field and in the laboratory demonstrated the usefulness of the open-top mesocosm in community metabolism measurements and experimental ecology.

Materials and methods. The reef community studied was settled in an 0.58 × 0.58 × 0.58 m aquarium. The substratum (surface area = 0.34 m²) was a live sand system: a carbonate sand layer (5 cm thick) separated the main seawater reservoir (90 l) from a small volume (15 l) of confined water (Jaubert 1989). The aquarium contained Mediterranean seawater (salinity = 38.3) passed through a sand filter and heated to 27 ± 0.1°C using a temperature controller (EliWell-PC 902T). The water was renewed between experiments at a rate of 5% h⁻¹. Light was provided by a 400 W/Daylight metal halide lamp (Philips HPI-T) that could be moved up and down in order to control irradiance as required. The lamp ran on a 12:12 h photoperiod. Irradiance (= photosynthetic photon flux density) was measured using a 4π quantum sensor (LI-193SA, LI-COR Inc.). Water motion was ensured by a 1000 l h⁻¹ centrifugal pump (Aquarium System, Maxijet 1000) and gas exchange was promoted by air pumps (Réna Alizé and Réna 301) fitted to 1 or 2 air stones. The glass windows of the tank were cleaned daily to prevent algal growth.

The reef community used for the experiments comprised coral sand and calcareous live rocks on which small (5 to 15 cm in diameter) scleractinian coral colonies (2 *Acropora* spp., 1 *Favia* sp.) and several sea anemones (*Aiptasia* sp.) were growing. The microfauna usually associated with a coral reef community include small crustaceans, polychaetes and gastropods (*Stomatela* sp.). The hard substratum covered approximately one-third (0.11 m²) of the total surface area. Most organisms of the community were collected in the Red Sea and were introduced in the mesocosm 3 yr prior to the present study.

Water temperature was measured (±0.1°C) and logged every minute using a temperature recorder (Seamon, Hugrùn). The concentration of dissolved oxygen was measured using an amperopolarographic electrode (Ponselle, oxythermometric model OXY TS). The electrode was calibrated daily, before and after each experiment. One liter of air-saturated sea water, stirred (magnetic stirrer) and aerated (air pump, Réna Alizé, running with 1 air stone) in a beaker, was allowed to cool slowly (30 to 40 min) from 26 to 20°C. The variation of water temperature resulted in a variation of oxygen content. The electrode was calibrated against the theoretical values of the oxygen content, which were determined with an empirical relationship using the temperature, the salinity and the atmospheric pressure (Wanninkhof 1992). All the data were averaged and logged every minute with a data-logger (LI-1000, LI-COR Inc.).

Three experiments were carried out on the same reef community under different irradiance and water regimes (see Table 1). The first experiment was performed under a high photon flux density (360 µmol m⁻² s⁻¹) and an oxygen transfer velocity (K_{O_2}) varying from 20 to 87 cm h⁻¹. The second one was set under the same photon flux density but K_{O_2} was set to 2 ranges by controlling the water regime. The third experiment was performed under a lower photon flux density (250 µmol m⁻² s⁻¹) and 2 fixed water regime surfaces.

The mesocosm was always kept open to the atmosphere except during measurements of community metabolism using the respirometry technique. It was then filled with heated Mediterranean seawater (S = 38.3; 27°C), kept at 360 µmol m⁻² s⁻¹ and sealed using a glass cover and a neoprene gasket. Oxygen concentration was measured as described above. Net community production (*NCP*) was measured several hours after the light went on and several hours after the light went off. Night respiration (*R*) and gross primary production (P_g) were compared using Student's *t*-tests.

Data are reported as mean ± standard deviation of the mean.

The model. The dissolved oxygen concentration in the mesocosm depends on the metabolism of the aquatic organisms (photosynthesis and respiration) as well as on the air-sea gas exchange. It was assumed that the water body present underneath the sand-water interface acted as interstitial water and was part of the community. Air-sea gas exchange is determined by Fick's law:

$$\Phi_d = \frac{K_{O_2} \cdot (C_{sat} - C_t)}{6} \tag{1}$$

where Φ_d: air-sea oxygen flux (μmol O_2 m^{-2} min^{-1}); K_{O_2}: oxygen transfer velocity (cm h^{-1}); C_{sat} and C_t: concentration of dissolved oxygen of air-saturated seawater and of the mesocosm seawater at a given time (μmol l^{-1}); and 6 is a constant required to express Φ_d in μmol O_2 m^{-2} min^{-1}.

C_{sat} varies as a function of temperature, salinity and atmospheric pressure (Wanninkhof 1992). K_{O_2} is often estimated in the field from wind speed data using an empirical relationship (Liss & Merlivat 1986, Wanninkhof 1992). This method cannot be used in a mesocosm since there is no wind, although O_2 is definitely exchanged at the air-water interface. Langdon & Sweeney (1995) proposed a method that they successfully used in the Biosphere II ocean mesocosm. The oxygen concentration is raised to 250 μmol l^{-1} by bubbling the seawater with oxygen-rich air. The oxygen then decreases for 6 d before reaching a new steady state, close to the concentration of air-saturated seawater. The decrease of oxygen concentration is used to estimate K_{O_2}. A simulation carried out with Stella software (version II, High Performance Systems) showed that this method can only be used with very large mesocosms where the water column is large (several m). We provide below an alternate method, based on a polynomial regression technique, to estimate K_{O_2}.

The O_2 concentration in our reef mesocosm was constant at night, increased steeply when light was switched on, reached a new steady state during the light period and decreased to reach the nighttime steady state concentration when the lamp was switched off (Fig. 1A). A polynomial regression is used to explain these changes in O_2 concentration. It is based on the following theoretical model: at each time t, the variation of dissolved oxygen concentration (Fig. 1B) in the coral reef mesocosm is a function of the air-sea gas exchange, the respiration rate (R, O_2 consumption; R is considered to be negative throughout the paper) and the rate of gross primary production (P_g, gross O_2 production). NCP ($P_g + R$) is measured during the daylight period. P_g was estimated by adding R to NCP, assuming that it is constant throughout the 24 h experi-

ments. This assumption is often used in studies of reef community metabolism (e.g. Odum 1956, Kinsey 1978) although there is no experimental evidence to support it. The model can be described by the following equation:

$$\frac{\Delta O_2}{\Delta t} = \Phi_d + R + \begin{cases} P_g \text{(light period)} \\ 0 \text{ (dark period)} \end{cases} + e \tag{2}$$

where $\frac{\Delta O_2}{\Delta t}$: dependent variable, variation of dissolved oxygen concentration as a function of time (μmol O_2 m^{-2} min^{-1}); Φ_d: air-sea oxygen flux (μmol O_2 m^{-2} min^{-1}); P_g: rate of gross primary production (μmol O_2 m^{-2} min^{-1}); R: rate of respiration (μmol O_2 m^{-2} min^{-1}); and e: residuals.

Eq. (2) can be expanded as follows:

$$\frac{\Delta O_2}{\Delta t} = \frac{K_{O_2} \cdot (C_{sat} - C_t)}{6} + \begin{cases} P_g \text{(daylight)} \\ 0 \text{ (night)} \end{cases} + R + e \tag{3}$$

For the sake of convenience,

$$F = \frac{K_{O_2} \cdot (C_{sat} - C_t)}{6} \quad \text{and} \quad \Delta = \frac{\Delta O_2}{\Delta t}$$

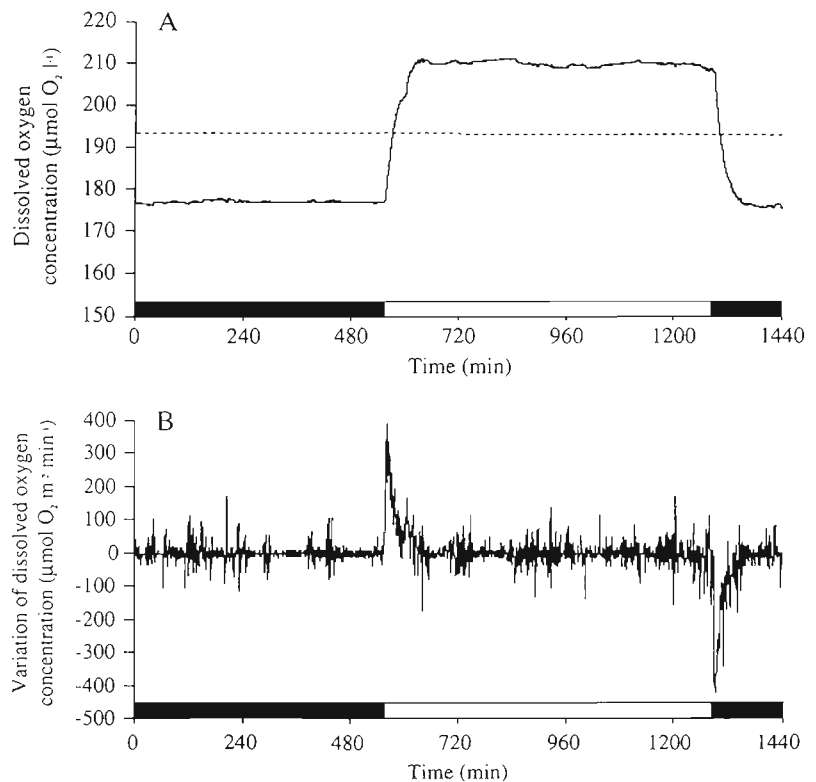The model presented in Eq. (3) can be expressed as a matrix equation:

Fig. 1. (A) Concentration of dissolved oxygen in the coral reef mesocosm during a 24 h experiment. The dashed line shows the dissolved oxygen concentration of air-saturated seawater. (B) Changes in dissolved oxygen. These data represent the best example of the trend observed

$$\begin{bmatrix} \delta_1 \\ \delta_2 \\ . \\ . \\ \delta_n \end{bmatrix} = \begin{bmatrix} f_1 \\ f_2 \\ . \\ . \\ f_n \end{bmatrix} \cdot K_{O_2} + \begin{bmatrix} 1 \\ 1 \\ . \\ 0 \\ 1 \end{bmatrix} \cdot P_g + R + \begin{bmatrix} e_1 \\ e_2 \\ . \\ . \\ e_n \end{bmatrix} \qquad (4)$$

$$\Delta = F \cdot K_{O_2} + Xp_g \cdot P_g + R + e$$

with n varying from 1 to 1440 and $Xp_g = 1$ during the light period and $Xp_g = 0$ in darkness.

P_g and Φ_d can be split into $Xp_g \cdot P_g$ and $F \cdot K_{O_2}$. K_{O_2} and P_g are the partial regression coefficients (i.e. constants). Xp_g and F are the independent variables and are known since the photoperiod, C_{sat} and C_t are known. So, the polynomial regression leads to the estimation of K_{O_2}, P_g and R.

Polynomial regressions are carried out on the daily records of dissolved oxygen variation. The following conditions for the use of polynomial regression have been checked: normality of the residuals, or at least symmetry of their distribution; homoscedasticity and no correlation between residuals and predicted values (Zar 1984). This estimation of the oxygen transfer velocity and metabolic parameters was carried out by fitting Eq. (4) to the variation of dissolved oxygen using JMP 3.1 (SAS Institute Inc.).

Results and discussion. K_{O_2}, the oxygen transfer velocity: The oxygen transfer velocity ranged from 20 to 87 cm h^{-1}, depending on the water motion (Table 1). These values are within the range of the oxygen transfer velocities described in the literature for wind tunnel experiments (Liss & Merlivat 1986, Wanninkhof 1992) and *in situ* determinations (Frankignoulle et al. 1996). They correspond to the 'Rough Surface Regime' conditions provided in the field by a wind speed of 5 to 13 m s^{-1} (Liss & Merlivat 1986). We did not attempt to reach a maximum oxygen transfer velocity but our results suggest that it could be possible to simulate, using additional pumps, air stones

or even a wave-making device, any kind of surface regime.

Community metabolism: The estimates of the metabolic parameters were not significantly different over the range of water motion (and K_{O_2}) used (Student's *t*-tests, p > 0.1) (Fig. 2A,B); they were therefore averaged for each light level. Results of the comparison between respirometric measurements and the method presented here (Table 1, Fig. 3) allowed us to conclude that both methods provide the same estimations for the community metabolic parameters (Student's *t*-tests, p > 0.2). Those results emphasize the validity of the new method we set up for the measurements of the community metabolism and K_{O_2}.

The ranges of P_g and R measured during the experiments were, respectively, 33 to 300 mmol O$_2$ m^{-2} d^{-1} and –50 to –366 mmol O$_2$ m^{-2} d^{-1}. The average daily metabolic parameters measured during each experiment are shown in Table 1. P_g was higher during the 2 experiments carried out under the high irradiance (360 µmol m^{-2} s^{-1}; 208 ± 50 mmol O$_2$ m^{-2} d^{-1}, N = 22) than under low irradiance (250 µmol m^{-2} s^{-1}; 73 ± 20 mmol O$_2$ m^{-2} d^{-1}, N = 13). R was also higher during the first 2 experiments (–219 ± 55 vs –79 ± 29 mmol O$_2$ m^{-2} d^{-1}). These metabolic performances compare well with those obtained for shallow lagoons (Kinsey & Domm 1974, Kinsey 1979, Atkinson & Grigg 1984), for sandy areas (Kinsey 1977, 1979) and for a coral patch (Gattuso et al. 1996). Thus, we conclude that the functional aspect of the community under investigation matches its structure and composition: a community composed of a sandy area with less than 50% of the hard substratum covered by autotrophic organisms (zooxanthellate scleractinian corals, sea anemones and algae).

The daily P_g/R ratio displayed very little change under different light regimes. The ratios obtained at 360 and 250 µmol photons m^{-2} s^{-1} (0.96 ± 0.11, N = 22 vs 0.97 ± 0.14, N = 13) did not differ significantly (Stu-

Table 1 Oxygen transfer velocities (K_{O_2}) and community gross primary production (P_g) and respiration (R) estimated using the open-top and the respirometric approaches. The respirometric and open-top methods were compared using data collected within one month. Mean ± SD values are given; the sample size is shown in parentheses

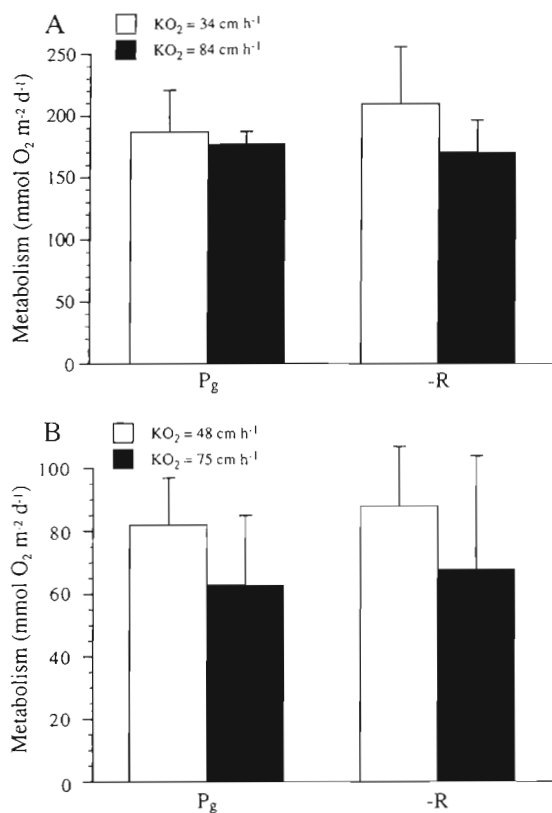|	Irradiance (µmol m^{-2} s^{-1})	K_{O_2} (cm h^{-1})	P_g (mmol O$_2$ m^{-2} d^{-1})	R (mmol O$_2$ m^{-2} d^{-1})
Open-top				
Expt no. 1	360	Between 20 and 87	217 ± 54 (16)	–227 ± 58 (16)
Expt no. 2	360	34 ± 5 (4) 84 ± 12 (2)	184 ± 27 (6)	–196 ± 43 (6)
Expt no. 3	250	48 ± 10 (7) 75 ± 16 (6)	73 ± 20 (13)	–79 ± 29 (13)
Respirometry vs	360	–	276 ± 28 (4)	–209 ± 17 (3)
Open-top		Between 27 and 87	241 ± 53 (9)	–252 ± 56 (9)

Fig. 2. Estimates of the community daily metabolism (P_g and R) using 2 differents oxygen transfer velocities (K_{O_2}) during the second (A) and the third (B) experiments

Fig. 3. Estimates of the reef community daily metabolism (P_g and R) using the respirometry method (mean values ± SD on 4 experiments for P_g and 3 experiments for R) and the polynomial regression method (mean values ± SD on 18 experiments for each parameter)

dent's t-test, p > 0.8). They were therefore averaged and the overall P_g/R ratio (0.96 ± 0.12, N = 35) is significantly different from 1 (Student's t-test, p = 0.03). This result is in agreement with the one obtained in another reef mesocosm (P_g/R = 0.91, Jaubert et al. 1995). Community gross primary production and respiration are usually closely balanced in coral reef communities, with P_g/R close to 1 (Kinsey 1983, Kinsey 1985, Gattuso et al. 1998). The ratio found in the present work is within the range of values reported for natural communities, and the community in the mesocosm exhibits a slightly heterotrophic metabolism. The daily net community productions (daily NCP) calculated at 360 and 250 µmol photons m^{-2} s^{-1} ($-11 ± 25$ mmol O_2 m^{-2} d^{-1}, N = 22 vs $-5 ± 11$ mmol O_2 m^{-2} d^{-1}, N = 13) were not different for the 2 light intensities (Student's t-test, p > 0.46) and the overall daily NCP ($-9 ± 21$ mmol O_2 m^{-2} d^{-1}, N = 35) is significantly different from zero (Student's t-test, p = 0.009). This daily NCP differs from the one found by Griffith et al. (1987) for a microcosm (56 mmol O_2 m^{-2} d^{-1}) and indicates that photosynthetically fixed carbon cannot supply the daily heterotrophic needs of the whole community. An external source of organic carbon is
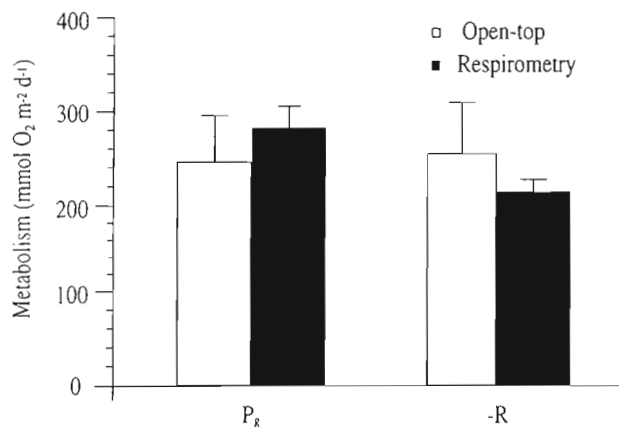
therefore required. It is likely supplied by the seawater renewal that occurs between experiments.

Conclusion. The method described in the present paper uses a polynomial regression and was set up to study metabolic performance of aquatic ecosystems enclosed in open-top mesocosms. It takes into account the air-water oxygen exchanges by estimating the gas transfer velocity and provides estimates of primary production parameters P_g and R by measuring the variation of dissolved oxygen concentration. This method has been successfully applied to a coral reef mesocosm. The metabolic performance was not significantly different from that determined using a standard respirometric approach and was within the range of those measured in the field. These results demonstrate that some natural communities can be mimicked, in terms of metabolism, in open-top mesocosms. Thus, we assume that this model coral reef community behaves as an analog for a natural reef system and is a potentially useful tool to perform experiments on the effect of environmental factors on coral reef metabolic parameters.

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