Energy flow and seasonality in a tropical coral reef flat

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ABSTRACT: Different substrates in a Philippine coral reef – sand, rubble, and living coral of the family Fungiidae – were monitored over a 2 yr period to compare their energy turnover and to determine possible diurnal and seasonal patterns. The metabolism of all 3 components did not vary significantly over the times of day between 09:00 and 15:00 h, and showed relatively small fluctuations with season. Within the narrow ranges of variation, light was positively correlated with primary production of coral, rubble and sand. Temperature increased coral respiration significantly. Higher production of rubble and sand communities occurred during times of lowered salinity, and was probably due to increased levels of nutrients associated with the rainy season. Respiration of all 3 substrates was elevated during the wet months, indicating stress related to lowered salinities. The various substrates differed significantly in terms of energy production and consumption, with coral showing the highest metabolic rate and P/R > 1, followed by rubble with P/R ≈ 1, then sand with P/R slightly less than 1 These results indicate that the net productivity of the system is made possible by the coral contribution, a finding which confirms previous studies.

KEY WORDS: Energy flow · Seasonality · Coral reef flat

INTRODUCTION

Coral reefs are complex ecosystems composed of a variety of organisms distributed in distinct zones (Done 1983). Such zones are typically distinguished by the predominant species inhabiting them or by the dominant substrate types. Because of its accessibility, the part of the reef that has received the most scientific attention is the reef flat (Kinsey 1985). The reef flat by itself is also characterized by different zones, being a combination of habitats for plants such as algae and seagrasses, for organisms inhabiting sand and rubble, and for the corals themselves.

In this study, the major patterns of energy production and consumption in a shallow tropical reef flat are determined, both in terms of contributions of the major components and in terms of variation over time. The natural complexity of coral reefs, deriving from their topography as well as from their biotic diversity, can render detailed investigations extremely difficult, although energy flow studies in reefs have a relatively long history (reviewed in Kinsey 1985 and

Wiebe 1988). It is for this reason that a reef flat with a relatively simple physical structure was selected.

The reef flat in question had the following major substrate types: sand, rubble and living coral. It was both logical and practical to consider reef-flat energy dynamics in terms of the relative contributions of each of these substrate types. Previous investigations have shown these reef components to have different levels of productivity and energy consumption, and hence, varying degrees of importance in total energy flow. For example, rubble substrates were found to contribute significantly to lagoonal productivity at French Frigate Shoals in Hawaii, USA (Atkinson & Grigg 1984). This is due to the activity of epilithic (e.g Klumpp & McKinnon 1989, 1992) and endolithic (Hawkins & Lewis 1982) algal populations. Sand substrates, though devoid of conspicuous plant or animal cover, may also be relatively active areas (Kinsey 1985). That the living corals themselves are highly productive and may account for the net positive production of a reef is well established (McCloskey et al. 1978, Kinsey 1985).

A second aspect of this study considers variation in metabolic performance of each of the substrate types over relatively short (i.e. within a day) and long (annual) time periods. One insight that could be drawn from such observations pertains to the stability of the system (Pomeroy et al. 1988). Simultaneous recording of physico-chemical variables allows inferences as to possible environmental influences on energy production and consumption. An understanding of the factors regulating coral reef productivity could then be derived.

In the text, 'production' refers to gross photosynthesis, unless specified otherwise, and 'energy consumption' refers to dark respiration.

MATERIALS AND METHODS

Study site. The area chosen for study is a 0.5 km wide reef flat on the western side of Santiago Island in Bolinao, Pangasinan, in the northwestern Philippines (approximately 16° 24' 41" N, 119° 54' 25" E). Depth averages about 1 m. A seagrass zone stretches from the shore about halfway across the flat, where it abruptly gives way to a sand-rubble substrate associated with coral, predominantly large microatolls of *Porites* spp. Other conspicuous corals are members of the Fungiidae and the Faviidae. The term 'reef flat' will be used below to refer only to the sand-rubble-coral section. Sand and rubble comprise about 85 % of the total area of the reef flat (as estimated from transect surveys by P. M. Aliño et al. unpubl.).

To represent the coral component, specimens of the Fungiidae were selected since they consist of a single polyp, regardless of size of the corallum. In contrast to colonial corals, there is not much interference by epilithic and endolithic organisms in metabolic measurements of the coral-zooxanthellae complex, rendering the interpretation of physiological results more straightforward.

Metabolic experiments. The metabolic experiments performed in this study made use of oxygen measurements in *in situ* enclosures (Wells 1977, Zeitzschel 1981). Primary production and respiration were measured by the degree of oxygen evolution or consumption respectively.

Field measurements made use of an acrylic cylinder (volume ca 9 l) bolted onto an acrylic platform on which the coral was placed, forming a watertight enclosure. In the case of sand or rubble, patches were chosen at random and were enclosed with a metal cylinder (diameter ca 20 cm, height ca 10 cm), driven into the sediment to a depth of about 5 cm. The acrylic cylinder was then fitted over the metal cylinder. Dye experiments performed in an aquarium showed the enclosure to be impervious to water exchange between the internal and external environments.

The top end of the acrylic cylinder was fitted with a dissolved oxygen probe (Nester Instruments model 8500x) and a battery-operated bilge pump for stirring the enclosed water.

Respiration was first measured by covering the setup with a black canvas material to exclude light, and hence, prevent photosynthesis. Production was then assessed in the light when the cover was removed. The runs were started with the dark incubation to bring the initial oxygen levels down, thus avoiding the occurrence of supersaturation during the photosynthetic measurements in the light. Prior to a series of measurements in a day, the probe was air-calibrated according to manufacturer's instructions. During photosynthetic and respiration measurements, oxygen readings were recorded every minute until enough data points were obtained to produce a significant regression over time. This was usually achieved within 10 to 15 min.

Temperature inside a chamber was monitored during an entire incubation by means of the probe's thermistor. Ambient water temperature was taken with a mercury thermometer against which the probe's sensor had been calibrated in the laboratory. Internal chamber temperature was usually higher than external temperature by less than 1 °C.

Light values were registered simultaneously by a LI-COR 193SA spherical quantum sensor attached to an LI-1000 data logger The sensor was mounted on a tripod support and was thus situated about 1 m below the water surface.

Bottom salinity readings with a refractometer were made at various times of the day. Measurements of light, temperature and salinity were averaged to yield mean daily values. Based mainly on temperature and salinity profiles, a year was divided into 3 'seasons': dry-cool (December to February), dry-warm (March and April) and wet (May to November).

Metabolic runs were carried out from approximately October 1989 to November 1991 (the exact starting and ending month differed for each substrate; see 'Results'). One day during each monthly visit was devoted to measurement of each reef flat component. For each incubation, a coral specimen or a patch of substrate was selected anew at random.

Measurements were usually performed between 09:00 and 15:00 h, and a 'day' was divided into 'morning' (09:00 to 11:00 h), 'noon' (11:00 to 13:00 h), and 'afternoon' (13:00 h and later). During each time of day, 2 replicate runs of respiration and then production were carried out.

In order to obtain data on fungiid metabolism at other times of the day and night, 24 h measurements

were performed on 3-4 July 1991 at the site. Three replicate incubations were done at roughly 3 h intervals between sundown and dawn. Daytime measurements for this particular exercise were made just after sunrise and at noon.

Production and respiration rates are expressed per unit surface area of the substrate. In the case of the fungiids, projected surface area was used (detailed procedure for measurement and formula for computation are given in Yap et al. 1992). This has the advantage of providing information on the area available for gathering incident light, which is important in productivity studies (Davies 1980).

Statistical analyses. Significant differences among the groups of each environmental parameter (light, temperature and salinity) according to season were tested using the Tukey-Kramer method (Sokal & Rohlf 1981) which is an *a posteriori* test. Differences in production and respiration among substrates, times of day or seasons were assessed using a 3-way analysis of variance (Sokal & Rohlf 1981, Zar 1984). Where the data did not meet the criteria for normality and homoscedasticity, they were transformed using log transformation, power transformation or natural log transformation as appropriate. Where significant differences were detected, Tukey's multiple comparisons test was employed to determine where the differences lay. Possible effects of light, temperature and salinity on production and respiration were determined for each substrate by pooling all data gathered over the monitoring period and applying multiple linear regression analysis.

RESULTS

Seasonal variation in light, temperature and salinity

In Fig. 1, the daily mean values for light, water temperature and salinity are plotted across time from October 1989 to November 1991. Light intensity fluctuated over an annual cycle from 500 to >2000 μE m^{-2} s^{-1}. These intensities were measured during the 'window' from 09:00 to 15:00 h. Low values were due to reduced penetration in the water column at times of high cloud cover, particularly during the rainy season.

Water temperature, measured during the same hours as light, varied from a minimum value of 23°C in December 1989 to a maximum of 33°C during the summer months of April to August (different years). Salinity also fluctuated throughout an annual cycle (Fig. 1), with minimum values (29 to 30 ppt) being reached in October (1990 and 1991). During other times of the year, values remained more or less stable at 34 ppt.

On the basis of observations of temperature and rainfall, the months of the year were grouped according to 'season' (see 'Methods'). When values of light, temperature and salinity were grouped into the different seasons, and the groups compared using the Tukey-Kramer method ($\alpha = 0.05$), mean light levels of all 3 seasons were found to differ significantly from each other. Dry-cool season water temperatures were different from those of the dry-warm and wet seasons, while wet season salinity readings significantly varied from those taken during the dry-cool and dry-warm months.
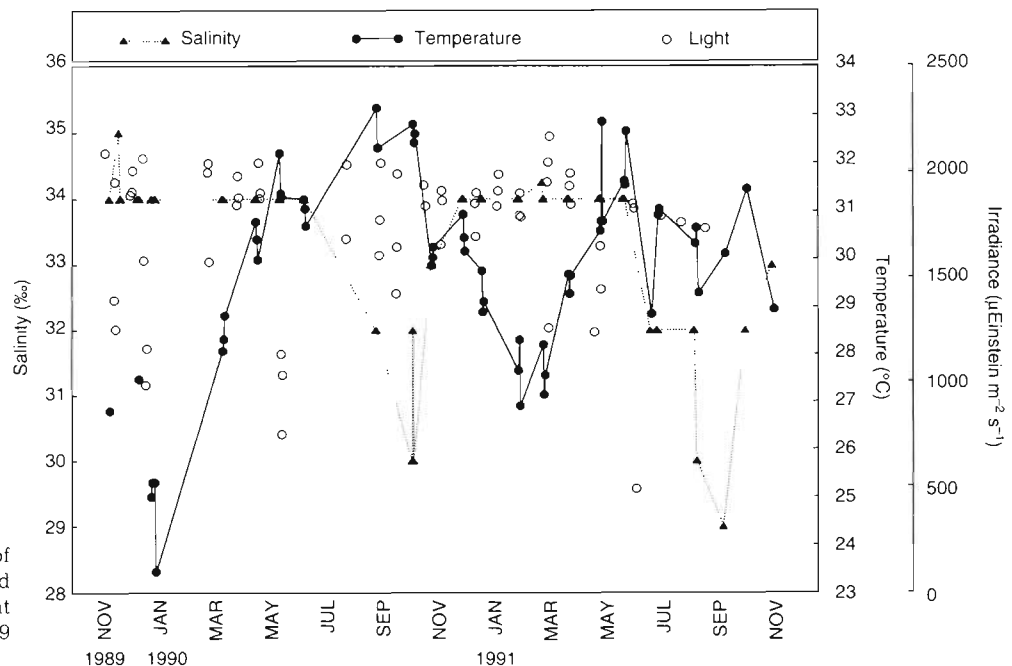

Fig. 1. Mean daily values of irradiance, temperature and salinity at the Lucero reef flat over the period October 1989 to November 1991
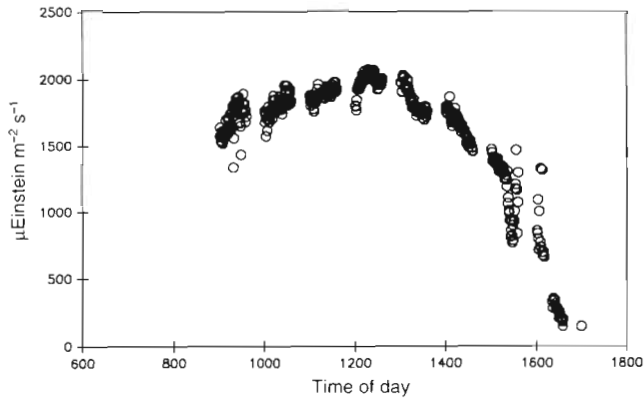
Fig. 2. Irradiance at the Lucero reef flat over the time interval 09:00 to 17:00 h. Measurements from October 1989 to April 1990 pooled
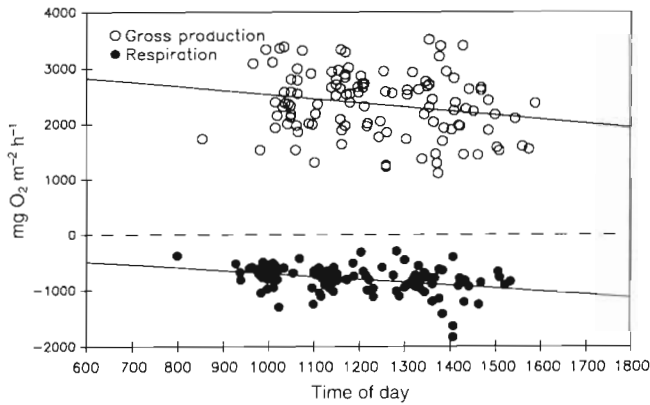

Fig. 3. Gross primary production and respiration of fungiid corals over a diurnal period. Measurements from October 1989 to August 1991 pooled. Lines through points are regression lines
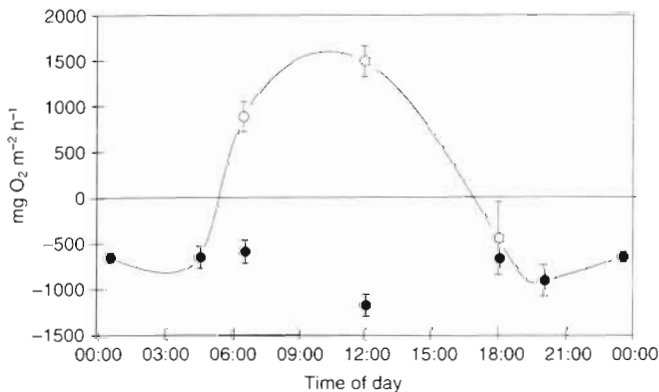

Fig 4. Net primary production (O) and respiration (●) of fungiid corals measured at intervals over a 24 h period on 3–4 July 1991. Values are means of 3 replicates ± SD

Temporal trends in metabolism

Diurnal patterns

In Fig. 2, light values were pooled from observations from October 1989 to April 1990 and plotted across time of day. For purposes of generating the graph, measurements between 09:00 and 17:00 h were included. Peak values around 2000 μE m^{-2} s^{-1} occurred at midday. Light levels were relatively constant from 10:00 to 14:00 h.

Values of gross primary production and respiration of fungiids were pooled from the entire observation period of October 1989 to August 1991 and similarly plotted against time of day (Fig. 3). For purposes of the ANOVA, the data from each season were grouped into batches of 'morning', 'noon' and 'afternoon' values (see 'Methods'). For each season, no significant differences with respect to time of day between 09:00 and 15:00 h were detected (Table 1).

Since data gathered only from 09:00 to 15:00 h were used to infer trends on production and respiration over the 2 yr monitoring period, it is useful to know what the values were like during the times outside of this interval. This information was obtained for coral from measurements made of production and respiration at other times of the day and night during a 24 h period in the summer (see 'Methods'). In this particular case, *net* photosynthetic rates are depicted. Net primary production (± SD) at dawn (06:00 h) was about ⅔ the value at 12:00 h of 1490 ± 170 mg O_2 m^{-2} h^{-1} (Fig. 4). Respiration during the dark hours was in the range 650 to 900 mg O_2 m^{-2} h^{-1}. Maximal respiration (1180 ± 120 mg O_2 m^{-2} h^{-1}) was observed at noon.

The variation in gross primary production and respiration of the rubble substrates over time of day is depicted in Fig. 5 using values from February 1990 to November 1991. Sand metabolism treated in a similar fashion is shown in Fig. 6, with values from February 1990 to August 1991. In both instances, measurement times were between 09:00 and 15:00 h. As in the case of the coral, the data were grouped into 'morning', 'noon' and 'afternoon' values per season. There were no significant variations in production nor respiration in both substrates over time of day between 09:00 and 15:00 h for all seasons (Table 1).

Seasonal patterns

For purposes of discerning trends in production and respiration with season, data for each of the substrates were averaged over the months comprising each season as described previously. Results are shown in Fig. 7. From the data spanning almost 2 yr for each

substrate, it is apparent that no significant fluctuations in production nor respiration occurred that could be related to particular seasons.

The ANOVA confirmed the absence of seasonal differences in gross primary production of coral, rubble and sand (Table 1). On the other hand, significant differences in respiration with respect to season were apparent for coral and sand (Table 1). Tukey's multiple comparisons test showed that, for coral, respiration during the wet months was higher than in the dry-cool season. For sand, wet season respiration was higher than during the dry-warm period. This apparent seasonality, however, may be an artifact due to the significant substrate-season interaction shown by the statistical analysis (Table 1).

Effects of environmental factors on metabolism

In order to help explain differences in metabolism over 'season' in the 3 reef flat components, production and respiration were regressed on the environmental parameters light, temperature and salinity. All data from the 2 yr monitoring period were pooled for the analyses. Results are given in Table 2.

The production of coral, rubble and sand was significantly and positively influenced by light, despite the relatively narrow

Table 1. Summary of ANOVA results testing for effects of substrate, season and time of day. $p < 0.05$; $p < 0.01$

Source of variation	df	MS	F
Production (data power transformed)			
Main effects	6	221.815	378.335**
Substrate	2	661.679	1128.584**
Season	2	0.729	1.244
Time of day	2	2.205	3.761*[a]
2-way interactions	12	0.887	1.514
Substrate × Season	4	1.914	3.265*
Substrate × Time of day	4	0.307	0.524
Season × Time of day	4	0.568	0.968
3-way interactions	8	0.189	0.322
Explained	26	51.656	88.106**
Residual	286	0.586	
Respiration (data natural log transformed)			
Main effects	6	16.957	171.402**
Substrate	2	49.320	498.527**
Season	2	1.380	13.953**[b]
Time of day	2	0.255	2.579
2-way interactions	12	0.251	2.541**
Substrate × Season	4	0.560	5.661**
Substrate × Time of day	4	0.122	1.231
Season × Time of day	4	0.047	0.479
3-way interactions	8	0.112	1.135
Explained	26	4.064	41.076**
Residual	286	0.099	

[a] Tukey's multiple comparisons test showed differences to lie among times of day from *different* seasons, but not among times of day from *within* the same season

[b] Tukey's multiple comparisons test showed significant differences in coral respiration between the dry-cool and wet seasons, and in sand respiration between the dry-warm and wet seasons
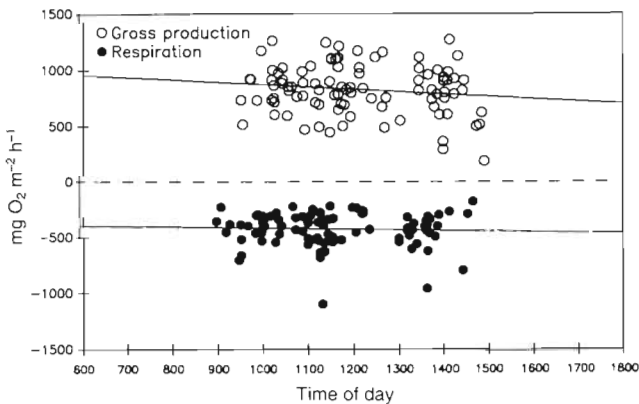

Fig. 5. Gross primary production and respiration of rubble substrates over a diurnal period. Measurements from February 1990 to August 1991 pooled. Lines through points are regression lines
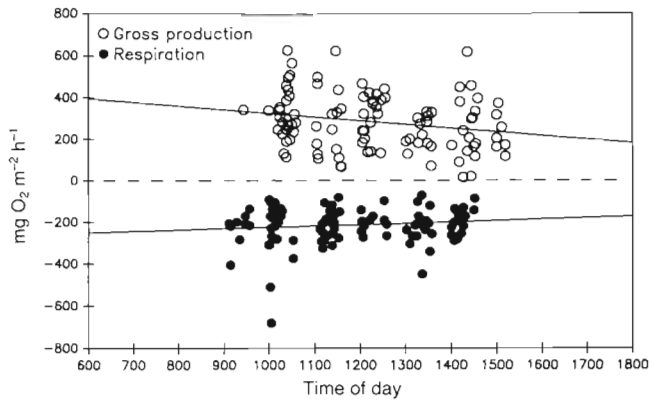

Fig. 6. Gross primary production and respiration of sand substrates over a diurnal period. Measurements from February 1990 to November 1991 pooled. Lines through points are regression lines
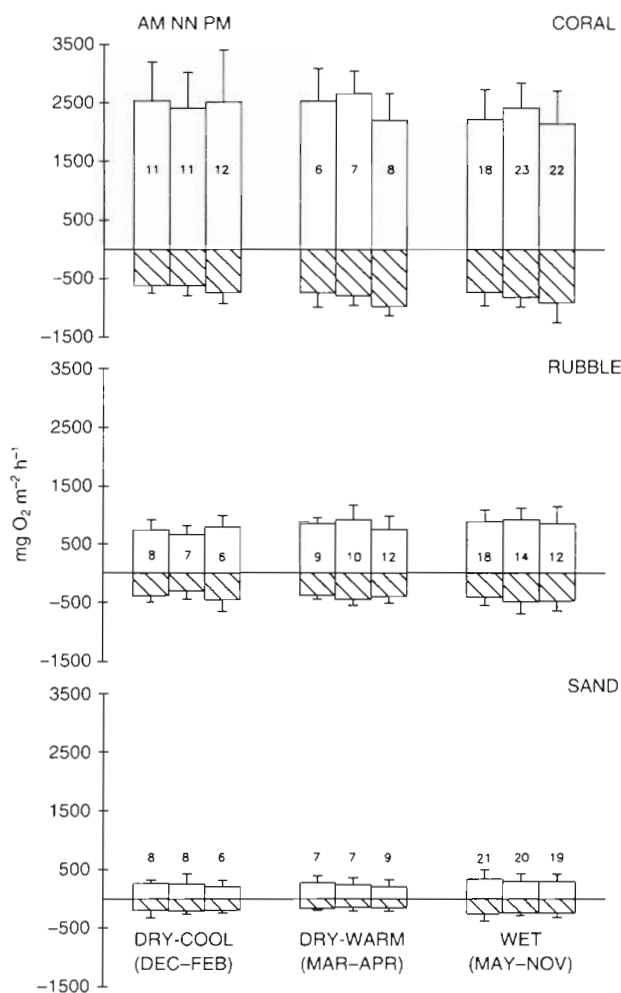
Fig. 7. Gross primary production (open bars) and respiration (hatched bars) of 3 reef flat substrates (coral, rubble and sand) over 3 times of day per season (AM: 09:00 to 11:00 h; NN: 11:00 to 13:00 h; PM: 13:00 h and later). Numbers inside or above the bars indicate replicates

Table 2. Results of regression analysis of production and respiration of coral, rubble and sand against light, temperature and salinity. Only significant results are given. Data are from October 1989 to November 1991 *p < 0.05

	Environmental factor	Regression coefficient	R^2
Coral			
Production	Light	0.588*	0.250
Respiration	Temperature	51.312*	0.238
Rubble			
Production	Light	0.234*	0.250
	Salinity	−74.190*	
Respiration[a]	Salinity	−0.044*	0.058
Sand			
Production	Light	0.092*	0.178
	Salinity	−34.084*	
Respiration	–		

[a] Values log-transformed

the highest production and respiration rates, followed by the rubble, then the sand substrates. Averaging data gathered from the entire monitoring period yielded the following: mean gross primary production and respiration rates (± SD) for coral were 2355 ± 570 and 787 ± 252 mg O_2 m^{-2} h^{-1} respectively; for rubble, 827 ± 220 and 426 ± 150 mg O_2 m^{-2} h^{-1} respectively; and for sand, 283 ± 132 and 213 ± 90 mg O_2 m^{-2} h^{-1} respectively.

In the time interval between 09:00 and 15:00 h, coral production was seen to exceed respiration by a factor of more than 2 (sometimes 3 or greater). Rubble production was slightly greater than respiration during the same hours of the day, while sand production was more closely matched by respiration.

DISCUSSION

Comparison of substrates

This study is based, in part, on the assumption that fungiid metabolism, as expressed on the basis of projected surface area, is a reasonable representation of production and respiration of other corals on the reef flat. Projected surface area was considered to be a logical basis on which to express production and respiration, since fungiids have a greater horizontal than vertical extension (i.e. they are essentially flat) so that their upper surfaces are the main parts of the corallum exposed to incident light. It is assumed that the upper surfaces, as effectively measured by projected surface area, are the active portions of the corallum in terms of photosynthetic and respiratory processes. In the case of 3-dimensionally complex coral heads,

range in intensities commonly encountered between 09:00 and 15:00 h. The production of rubble and sand, as well as respiration of rubble, were negatively correlated with salinity. Coral respiration was positively correlated with temperature.

Comparison of substrates

The 3 substrates differed significantly in terms of their production and respiration (Fig. 7), as confirmed by ANOVA results (Table 1). The significant substrate-season interaction revealed by the statistical analysis is not considered to affect this conclusion seriously since the differences among substrates in terms of both production and respiration are clear and unambiguous for *all* seasons (see Fig. 7). The coral component displayed

more surfaces are exposed to incident light. But because of the reasons outlined above, expressions of metabolism per unit surface area for fungiids should be comparable with similar expressions for more complex colonies in which area is measured using different methods.

Values for gross primary production and respiration measured in this study were within the same orders of magnitude reported for *Acropora palmata* (Rogers & Salesky 1981), *Goniastrea aspera* (Motoda 1940 cited in McCloskey et al. 1978), *Porites furcata* (Beyers 1966 cited in McCloskey et al. 1978) and even entire coral outcrops (reviewed in Kinsey 1985). It is seen from this study that the coral component was a net producer, with a P/R ratio of approximately 1.5 (if the values obtained are extrapolated over a 24 h period, assuming a day:night cycle of 12:12 h). This is a well-established fact (reviewed in McCloskey et al. 1978).

Rates of gross photosynthesis and respiration of rubble were very similar to values obtained by Henderson (1981) for rubble in Hawaii. However, Henderson (1981) determined slightly higher respiration than production rates, yielding a P/R ratio of 0.7 to 0.9. In this study, the rubble had a P/R ratio close to 1 (ca 0.97).

The sand communities, on the other hand, were heterotrophic on the average (P/R ca 0.6 when extrapolated over 24 h). Both gross photosynthetic and respiration rates were consistently less than those of rubble, a finding similar to that of Henderson (1981) in Hawaii. Values in this study fall within the range reported by Kinsey (1985) in a review of several studies.

The above findings on the respective contributions to total energy flow of the major components imply that if the reef flat is found to sustain an overall net production, or even an export of organic matter, a significant fraction of this would be due to the coral productivity (Kinsey 1985). Altogether, sand and rubble zones have been found to have a relatively low net productivity (Marsh 1974), probably due to the lower standing stocks of primary producers harbored by sand substrates, as already established early on by Odum & Odum (1955) in Eniwetok Atoll (Marshall Islands). Sand and rubble zones as a whole exhibit a P/R of less than 1, and probably act as heterotrophic sinks for the organic matter derived from the more productive reef components (Kinsey 1977, 1978). In this study, the areal coverage by sand was visibly greater than that of rubble, so that the combined sand-rubble areas probably also had P/R values less than 1.

Temporal variability and environmental effects

There were no significant differences in the metabolism of coral, rubble and sand over time of day between 09:00 and 15:00 h. The absence of large fluctuations on a daily basis, as well as over the seasons of the year, indicate a relative constancy in metabolism of this tropical ecosystem (cf. Moore 1972). This finding conforms to the observation that processes such as photosynthesis and respiration, when measured at the ecosystem level (as in the case of the sand and rubble communities in this study), exhibit 'remarkably stable' rates despite successional changes (Pomeroy et al. 1988).

In this particular study, the apparent constancy in metabolic rates is also probably due to the relatively narrow ranges of variation of environmental factors such as light, temperature and salinity. This is in contrast to the higher latitudinal limits of coral distribution (e.g. Crossland 1984, 1988). However, even within their small ranges, the above physico-chemical parameters showed significant differences over the dry-cool, dry-warm and wet seasons, thus exhibiting a certain 'seasonality' in the reef flat. They also appeared to significantly affect metabolic rates of the reef flat components. This would support Kinsey's (1985) view that seasonality is a 'marked feature of reefs at apparently all latitudes' (see also Moore 1972).

The positive influence of light on primary production of corals, within specified limits, is well known (reviewed in Gladfelter 1985). Primary producers in the rubble and sand substrates also responded to higher incident light intensity by increasing rates of photosynthesis. Charpy-Roubaud et al. (1988) established a significant relationship between light and microphytobenthic production of sands in Tikehau Lagoon, French Polynesia. Kinsey (1977) attributed the seasonality he observed over a wide latitudinal range to the effects of insolation rather than temperature.

The rate of primary production of rubble and sand was greater during times of lowered salinity, or when rainfall was higher. The apparent increase in primary production of the rubble and sand components with lowered salinity may not be a direct cause-effect relationship, but may be explained by an increase in nutrients in the water column through run-off during the rainy season. In other words, periods of relatively low salinity during the rainy months are associated with higher levels of nutrients in the water column which enhance photosynthesis (see Paerl et al. 1990). This possibility will be investigated further.

The respiration by the rubble community was also greater during periods of lowered salinity. Similar trends were indicated with respect to coral and sand where respiration rates were elevated during the wet months. Decreased salinity during the rainy season probably constituted a stress, with increased respiration reflecting additional metabolic work, particularly in terms of osmoregulation (Valiela 1984).

The positive correlation of respiration with temperature is a well-known response (Parsons et al. 1984, Valiela 1984). Significant effects of temperature on respiration have been documented for various species of corals (Coles & Jokiel 1977, Muthiga & Szmant 1987). In the Philippines, temperature elevations during the summer months have been shown to relate to lowered coral growth rates (Yap & Gomez 1984), in addition to other indications of stress such as mortality and bleaching (Yap et al. 1992). Jokiel & Coles (1990) found coral bleaching at abnormally high temperatures to correlate with respiratory rate. They proposed the hypothesis that any factor that increases respiration would accelerate bleaching at elevated temperatures. In the low-latitude locality of the present study, bleaching together with higher respiration rates may thus be seen as an integrated stress response during times of high temperature.

CONCLUSIONS

Organisms inhabiting sand and rubble in this tropical reef flat, as well as the corals represented by the Fungiidae, displayed relatively stable metabolic rates over time of day and with respect to season. Within the narrow ranges of variation, the environmental factors, light, temperature and salinity, still exerted significant effects on gross primary production and/or respiration. This accounted for a certain seasonality in productivity of the system, despite its location close to the equator. Of the reef flat components, the corals had a net autotrophy, making them likely candidates for export of organic matter to the more heterotrophic portions of the reef.

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