

INVESTIGATIONS OF ENERGY DYNAMICS IN CORAL REEF ECOSYSTEMS

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ABSTRACT

Understanding the processes, quantities and rates of energy fluxes in coral reefs is essential in the rational management of these ecosystems. With the application of certain methods and conceptual approaches, progress has been made in the investigation of the energy dynamics of a reef flat in northwestern Philippines. *In situ* enclosures are employed to study the contributions to productivity of major ecological components of the reef flat. The use of closed chambers ensures that measurements may be referred to a specific entity, and enables proper replication on both spatial and temporal scales. Some aspects of physiology characterized at this level may be extrapolated to the whole community. Open flow respirometry is a technique used to study processes at the community level where closed system measurements are inadequate to encompass the range of interactions and ensuing complexity that emerge on that scale. Concomitant measurements of critical environmental parameters allow the interpretation of metabolic trends. Experiments conducted in the laboratory serve to verify field observations, particularly on the effects of environmental factors on organismal physiology. Data obtained are used in determining spatial and temporal patterns of productivity, as well as the status or "health" of the ecosystem.

INTRODUCTION

This review paper highlights research efforts in the field of coral reef energy dynamics that started in 1989 with initiatives taken at the Marine Science Institute of the University of the Philippines. Studies of energy dynamics find their greatest application in questions dealing with productivity – what critical processes underlie net production of community biomass, which environmental factors (or combinations of these) are key regulators of function and what levels of biomass yield a coral reef can sustain under both normal and stressed conditions.

At the Marine Science Institute, investigations on environmental effects have focused on the factors light and water movement. Experiments are designed around aspects of organismal physiology as a response to variations in these parameters.

It is hoped that certain trends in individual behavior may be extrapolated to the community level to infer underlying mechanisms of patterns reflected at that level.

In the study of the ecosystem, a reductionist approach was adopted initially wherein a reef flat (Lucero in Bolinao, Pangasinan) was conceptually broken down into its major substrate components. The metabolism of each component over an annual cycle was measured using closed respirometry techniques. The basic premise of such approach is that energy is divided up among the different ecological units or compartments, starting with the solar input and ending with the harvested biomass, and as such can be quantified. Periodic measurements over an annual cycle or longer provide indications as to the stability of the system, which is helpful in interpreting or even predicting the effects of environmental perturbations (Yap, 1991a).

The justification for studies on productivity is that a firmer understanding of the biological as well as physico-chemical processes driving it (Hatcher, 1990; Kinsey, 1983) could lead to better management of the harvestable resources of a reef. For example, if long term measurements provide an indication of the amount of energy normally allocated by a community for routine maintenance, this information should serve as a guide as to limits of biomass extraction that the system could tolerate. Beyond such limits, a system may collapse, leading to a series of succession stages that would culminate in a different community which is not necessarily useful for man.

METHODS IN REEF ENERGETICS

A detailed description of methods used in the study of energy flow in coral reef ecosystems is given in Yap (1991b). Energetics studies on reef components may be carried out in the field or in the laboratory. Whole system experiments are usually performed *in situ*, unless adequately-sized and representative microcosms for such investigations are constructed in the laboratory. In all cases, monitoring of the relevant environmental parameters should closely accompany measurements of metabolism in both time and space.

Field measurements of energy flow traditionally make use of either closed system or open-flow techniques (Kinsey, 1985b; Yap, 1991b). In the Philippines, both approaches have been applied on a reef flat (Lucero in Bolinao, Pangasinan). Closed system measurements make use of a Plexiglas cylinder enclosing an organism or a patch of substrate in a watertight manner. A stirrer or similar device is installed to ensure that the enclosed water is well-mixed or homogeneous. A dissolved oxygen probe is attached to the chamber to measure increases or decreases in dissolved oxygen with photosynthesis or respiration, respectively. Respiration is partitioned from photosynthesis by covering the metabolic chamber with a black material to exclude light. Photosynthesis is then measured in the light. Gross and net primary production and respiration are computed for using the widely used conventional equations (Lederman, 1983).

Open flow respirometry has been carried out following the techniques of Kinsey (1985b). A dissolved oxygen probe is employed to monitor dissolved oxygen changes in a water mass as it flows over the bottom. From such changes, primary production and respiration are computed for, and assumed mainly to represent activity of the benthic community. The metabolism of the plankton is usually insignificant compared to the benthos. Atmospheric diffusion is corrected for.

Laboratory measurements of metabolism essentially make use of the same equipment, like dissolved oxygen probes, incubation chambers and other support equipment such as water baths to maintain temperature, a light source, stirrers. Measurement set-ups may be either closed or flow-through systems (von Oertzen, 1984). The latter are more ideal, as the accumulation of toxic wastes in the metabolic chamber is prevented, and a constant and adequate supply of oxygen, nutrients and essential trace elements can be assured. Flow-through systems are, however, more difficult to construct. One such set-up has been developed by A. Rex F. Montebon of the Marine Science Institute.

Measurements of environmental factors that are known to influence metabolism are essential to studies on productivity. These must be made with sufficient frequency and replication so that the data may be properly used to help explain metabolic trends. Environmental factors of interest include light, temperature, salinity, water motion, the various nutrient species (particularly of phosphorous and nitrogen) and particulate loading of the water column.

RESEARCH THEMES AND APPLICATIONS

Energy Budget of a Coral Reef

A recently completed study (Yap, Montebon and Dizon, 1992b; 1993) involved the investigation of the energy production and consumption of three reef flat substrate components, namely, coral (of the family Fungiidae), rubble and sand. Of these substrates, the coral had the highest production-to-respiration ratio ($P/R > 1$) over a diurnal period. The rubble component had a P/R ratio approximating 1, while sand was heterotrophic ($P/R < 1$).

This result confirms previous findings that corals in general sustain a net positive primary production (Gladfelter, 1985). In contrast, combined sand and rubble zones in reef flats tend to be heterotrophic, and probably consume the organic carbon produced in the more productive parts of a reef (Kinsey, 1985a). The preliminary picture that emerges is one of energy flow from the autotrophic to the net energy-consuming compartments of a reef, effectively maintaining the whole system. The flow of energy constitutes a number of trophic and detrital pathways, which remain subjects for future study in the Philippines.

Temporal Patterns of Energy Flow

In an investigation of seasonality in metabolism and its stability over time, the three substrates mentioned above were monitored at monthly intervals over an approximately two-year period (The exact duration of monitoring varied for each substrate.) (Yap, Montebon and Dizon, 1992a; 1993). The production and respiration rates of coral, rubble and sand fluctuated only within narrow ranges over an annual cycle, displaying a kind of constancy or stability. A certain stability in function is expected at the ecosystem level (Pomeroy et al., 1988) and it constitutes an emergent property.

Within the relatively narrow ranges of variation in metabolic rates, however, significant effects of the environmental factors light, temperature and salinity were detected. These parameters exhibited significant variations over the seasons into which a year was arbitrarily divided based on temperature and salinity data, namely, dry-cool (December-February), dry-warm (March-April) and wet (May-November). Despite its location at a low latitude, the reef flat studied still underwent a certain seasonality in productivity (Hatcher, 1990).

Environmental Effects on the Physiology of Reef Organisms

One of the most important controlling influences on coral productivity is still that of light (Gladfelter, 1985). In addition to light being important on its own, its effects are also manifested in the influence of an environmental disturbance such as siltation. In such a case, silt in the water column reduces the intensity of light penetrating to the benthos, thus causing a reduction in photosynthesis. This is in addition to physical impacts such as smothering. Light in relation to productivity is thus one of the major points of investigation in studies of coral reef energetics in the Philippines (Montebon and Yap, 1992b; Yap and Montebon, 1992; Yap et al., 1993).

Diurnal averages of light plotted over more than an annual period indicate a range of variation of from 500 to over 2000 microEinsteins $m^{-2} s^{-1}$ (Fig. 1). A laboratory experiment in which corals of the species *Fungia (Danafungia) horrida* in the size range 5-9 cm (average diameter) were exposed to stepwise increments in light intensity, showed significant increases in gross photosynthetic rates (Fig. 2; Yap et al., 1993). The values obtained were used to generate a light saturation curve (Fig. 3) based on the hyperbolic tangent function following the method of Chalker (1981).

A light saturation curve yields useful insights into the ecology of the species. For example, saturation of the coral's photosynthetic machinery by light is shown to occur at an irradiance of approximately 800 microEinsteins $m^{-2} s^{-1}$ (Yap et al., 1993). This is a relatively high value when compared to results of other investigators (e.g., Chalker 1981; Chalker et al., 1983). This is probably due to the relatively shallow depths at which the species is situated and the consequent high light

intensities to which it is normally exposed. If this finding is applicable to other coral species in the tropics, it could be used, for example, in predicting rates of productivity that could be expected in shallow, well-lit waters at various times of the day.

Another environmental factor that has been identified as being an important determinant of coral reef function is hydrodynamics (Hatcher, 1990). Experiments at the Marine Science Institute have started at the organismal level, and a look at the effects of water motion on the photosynthesis, respiration and calcification of a hermatypic coral species, *Porites cylindrica* (Montebon and Yap 1992a). Water motion can exert significant influences on both photosynthetic and respiration rate (Dennison and Barnes, 1988; Montebon and Yap, 1992a). The degree of turbulence on particular reef zones can thus serve as a predictor of relative levels of activity of the primary producers.

The Reductionist versus the Systems Approach

Rates of productivity as they are measured may vary depending on the spatial scale encompassed by the experimental protocol (Hatcher, 1990). The reason is that more numerous and complex (as well as interacting) processes come into play as the space of interest is scaled up. This involves both biotic (e.g., competition) and abiotic (physico-chemical, hydrodynamic) factors. This is why metabolic measurements of organisms or communities within chambers do not necessarily yield data representative of total system function.

For purposes of comparison, *in situ* chamber metabolic runs were immediately followed by open system flow respirometry measurements of the same community in one field experiment (Yap, Dizon, and Montebon, 1992). Trends in photosynthesis and respiration, as well as the flux of the major nutrients, were assessed on both scales. The work is currently ongoing, and it takes into account possible seasonal patterns. Thus, measurements are made during the dry-warm and wet seasons.

DISCUSSION AND CONCLUSIONS

The more fundamental questions in coral reef energy dynamics, such as with respect to the effects of environmental factors on metabolism, are most effectively addressed at the level of the individual organism. It is the basic physiological processes at this scale, as they respond to environmental forcing, that ultimately underlie the complex of phenomena that occur at the level of the community or ecosystem. However, as the level of organization goes up the ecological hierarchy, interactive processes involving both biotic and abiotic factors become more important, and system behavior becomes more complex. One result is in the form of so-called "emergent phenomena" (Pomeroy et al., 1988) that cannot be satisfactorily understood using an entirely reductionist approach.

This is the reason why current research efforts in the Philippines address both levels simultaneously: that of the individual, and that of the whole system. It is hoped that the interpretation of processes observed at each of the above scales would coverge into a rational picture of productivity.

At the level of the organism, the effects of important environmental factors, such as light and water turbulence, are clearly elucidated. Results could be used to explain trends in community behavior on larger scales, such as why net community production might vary among different zones of a reef, or with time (i.e., diurnally, seasonally). Many other processes at the organismal level could be extrapolated to the larger system in this way.

At the level of the ecosystem, broad patterns in productivity in both space and time emerge. As discussed, some of these could be explained by invoking processes at lower levels. This includes energy budgets in reefs, where quantities of materials and energy can be compartmentalized among functionally defined ecological components.

Other system processes are clearly emergent, and they result from interactions at levels higher than the organism. An example is the appearance of system stability in terms of both energy production and consumption over an annual cycle. Such a result provides a clear message about reef function. Quantitative assessments, in addition, give an indication of the amount of energy produced and consumed by the system for maintenance.

All topics treated in this paper have ultimate relevance with respect to the management of coral reef resources. As mentioned earlier, the basic natural process that underlies the usefulness of reefs to man in terms of products, physical protection of the coast and amenities (i.e., recreational activities based on the aesthetic value of these habitats) is productivity. The studies discussed in this paper have as a unifying objective the understanding of the dynamics of productivity of reef ecosystems. The field is ripe for future studies on a diversity of themes, particularly in the tropics.

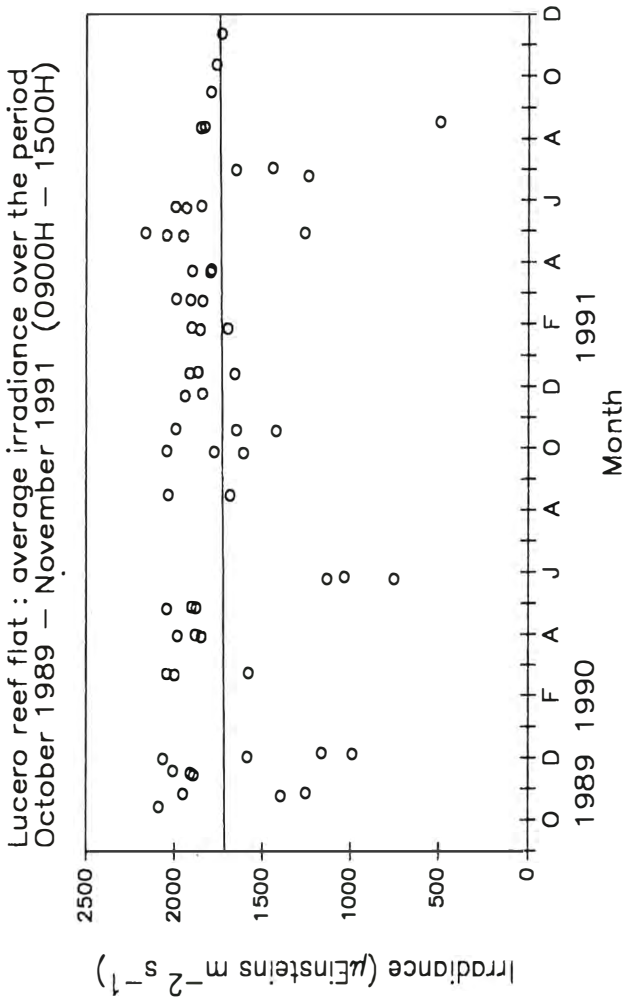


Figure 1. Variation in light intensity over an annual cycle in a reef flat (Lucero) in Bolinao, Pangasinan at a water depth of about 1 m. Values in $\mu\text{Einstein m}^{-2} \text{s}^{-1}$ are averages of daily values taken between 0900-1500H during monthly visits to the site from October 1989-November 1991 (See Yap, Montebon and Dizon, 1993).

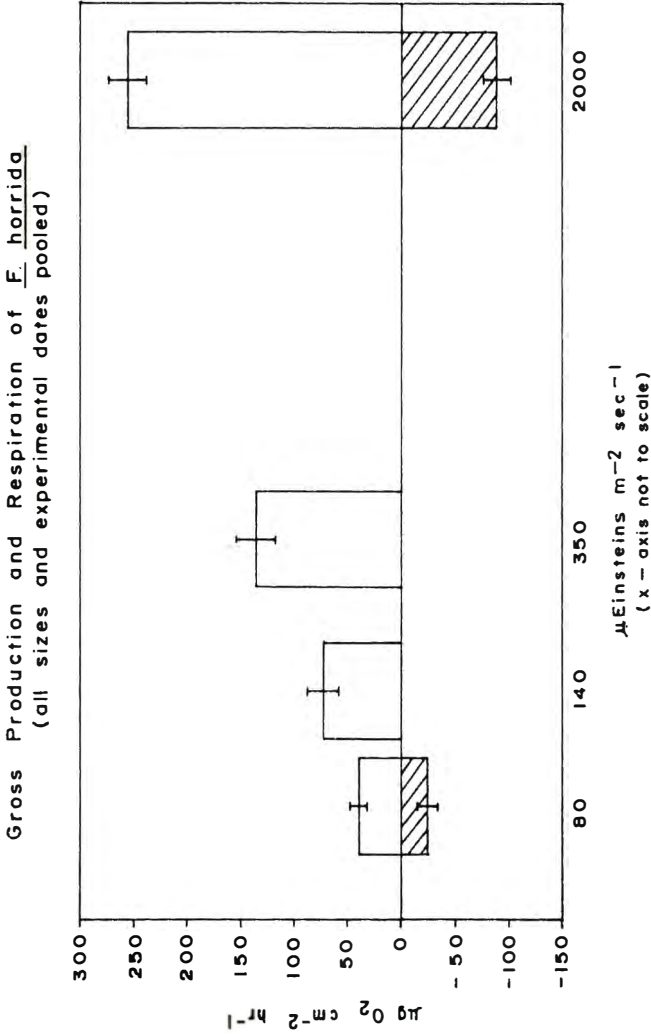


Figure 2. Gross photosynthesis and respiration of *Fungia (Danafungia) horrida* in response to increasing light intensities from 80 to 2000 $\mu\text{Einstein m}^{-2} \text{s}^{-1}$ (See Yap et al., 1993.)

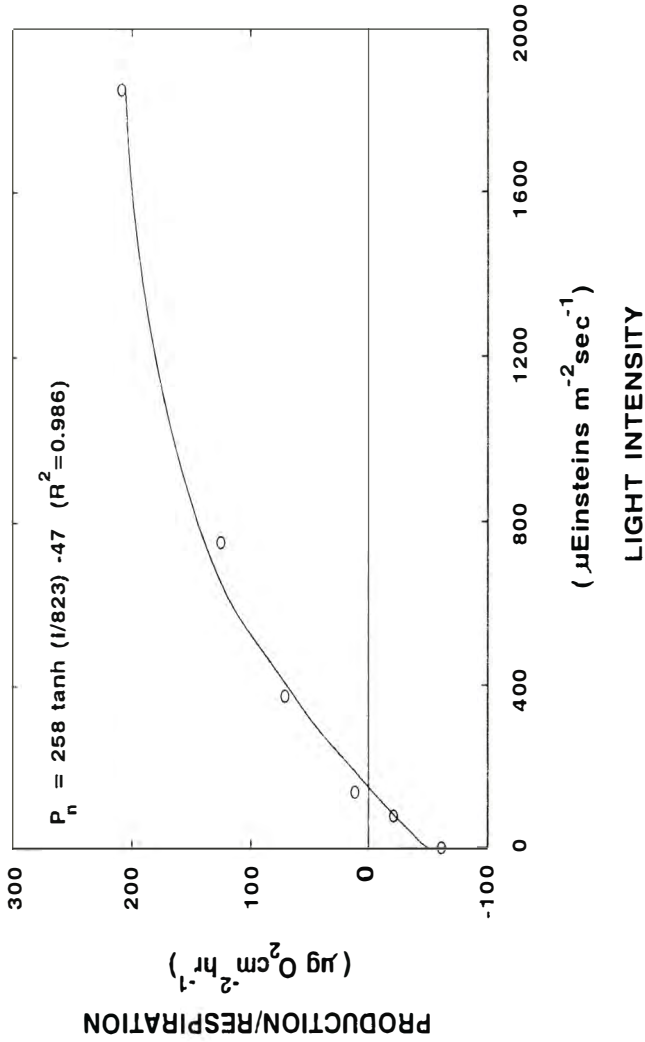


Figure 3. Light saturation curve constructed on the basis of data in Fig. 2 (from Yap et al., 1993.)

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