Energetic Role of Algae in Reef Ecosystems[1]

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Reef communities are recognized for their high productivity, but there is little information on the particular populations of primary producers responsible for this. There has as yet been no satisfactory attempt to rank the producer populations in a reef community according to their relative importance, and it is not clear whether community productivity is dominated by one or a few such populations or is distributed fairly evenly over a number of populations. There is also little information on how productivity varies spatially and temporally, nor is it yet known if there are basic differences between different types of reefs. Metabolic studies of reefs have tended to focus more on the community approach than on the study of individual populations.

Visual inspection of relative standing crops is not necessarily a reliable indicator of the relative importance of various populations as primary producers. Populations through which energy is flowing rapidly may not be visually dominant or even obvious. Algae which achieve large standing crops may do so because they are not being directly utilized as energy sources by consumers, and this gives no hint as to their metabolic activity. Less obvious forms such as fine filaments growing close to the substrate may be responsible for a larger share of total community productivity. Standing-crop observations serve as a useful starting point but should be followed up by careful observations of metabolism before statements can be made about the role of various populations in the functioning of reef ecosystems.

Meaningful comparisons between various reef populations, between populations and whole reef communities or particular zones, and between reef communities or populations and other communities or populations can best be made on the basis of projected surface area (flat map area) rather than on the basis of actual (irregular) reef area or on the basis of biomass and other considerations. Systems which may thus be compared range from phytoplankton to forests. This is an important consideration in examining various literature sources for comparative information.

Various productivity studies of reef communities and populations are presented in Table 1. The community productivity values are among the highest

Table 1. Productivity values (g C m^{-2} hr^{-1}) for benthic reef communities and populations.

	Net P	Gross P	Reference
Communities			
Rongelap coral-algal	0.18	0.33	Sargent & Austin (1949, 1954)
Enewetak coral-algal	0.40	0.80	Odum S Odum (1955)
Enewetak coral-algal[1]	0.25	0.50	Smith & Marsh (1973)
Enewetak algal[1]	0.72	0.97	Smith & Marsh (1973)
Hawaii coral-algal	0.36	0.60	Kohn & Helfrich (1957)
Guam coral-algal	0.32	0.58	Marsh (1974)
Enewetak substrate samples[2]		0.06–0.33	Marsh (unpubl.)
Populations			
Intertidal blue-greens[3]	0.054–0.18		Bakus (1967)
Crustose Corallinaceae[4]	0.11	0.14	Marsh (1970)
Crustose Corallinaceae, range for 5 spp.	0.042–0.22	0.05–0.28	Littler (1973)
Schizothrix mats		0.24	Marsh (unpubl.)
Halimeda	0.19	0.34	Hillis-Colinvaux (1974)
H. discoidea[5]	0.0044–0.017	0.005–0.019	Doty (1969, 1971)
Lyngbya majuscula[5]	0.0005–0.021	0.0005–0.021	Doty (1969, 1971)
Sargassum echinocarpum[5]	0.057–1.95	0.062–2.15	Doty (1969, 1971)
S. polyphyllum[5]	0.065–0.32	0.067–0.33	Doty (1969, 1971)
S. obtusifolium[5]	0.039–0.20	0.042–0.22	Doty (1969, 1971)
14 spp. corals		0.22–0.85	Kanwisher & Wainwright (1967)

[1] Determined by upstream-downstream changes in O_2 and CO_2; all other community values determined from O_2 changes only.

[2] Contained mixed algal populations and smaller fauna.

[3] Hourly values reduced from long-term harvest data and therefore underestimated with respect to other values, which are based on O_2 exchange of samples in respirometers.

[4] Based on an assumed photosynthetic quotient of 1.25 for converting O_2 to C, resulting in an underestimate with respect to other values (which assume a PQ of 1.0).

[5] Values calculated by the author from Doty's separate standing crop and respirometry values; range of values reflects seasonal changes in standing crops. Doty's AEC contract AT–(04–3)–235 is hereby acknowledged.

reported for natural systems. Ratios of gross productivity to respiration on a 24-hour basis are 1.0 or slightly higher for most communities studied. See Kinsey and Domm (1974), Marsh (1974), and Smith (1974) for a further discussion of this point. An exception to the commonly observed ratio was reported by Smith and Marsh (1973) for a community at Eniwetok that was dominated almost exclusively by algae and had very few corals; their reported ratio was 1.9. This implies that free-living algae rather than the symbiotic algae of corals are the most important producers making energy available to non-coral consumers on the reef. Furthermore, if the ratio observed by Smith and Marsh for the algal community applies to the algal zones of mixed coral-algal communities as well, then these zones would be by far the most productive zones of such communities. This was also suggested by Marsh (1974) for a Guam community. Community studies have generally not partitioned productivities into values for various zones because of problems with

methodology, but such a partitioning would obviously be desirable.   In any case, the algal community studied by Smith and Marsh is the most productive reef community yet examined.   Most reef communities studied to date have been Pacific ones, but Quasim and Sankaranarayanan (1970) and Milliman and Mahnken (1971) studied Indian Ocean and Caribbean reefs, respectively.   Reef productivities are among the highest reported for natural communities.   However, they may be no greater than for other tropical marine communities.   The turtle-grass beds studied by Odum (1957) had a gross productivity value of $0.83 \text{ g C m}^{-2} \text{hr}^{-1}$.

There have been fewer studies of individual reef populations than of reef communities.   This may be accounted for by the fact that population studies are generally the more difficult, requiring estimates of standing crop in the field (with temporal and spatial variations) combined with respirometry of individual samples. For the most part, the population values in Table 1 are lower than the total community values.   However, this is not surprising since total community productivity is the sum of individual population productivities.   Where productivity of a given reef zone may be dominated by a particular population or group of populations, as in the case of the calcareous algal ridge on some atoll reefs or the *Sargassum* zone on some fringing reefs, it should be easier to evaluate the contribution of such populations to overall reef productivity.   This was attempted by Marsh (1970) and Littler (1973) for calcareous red algae.   They found comparable productivity values (Table 1) but reached somewhat different conclusions concerning the significance of these organisms in total community productivity for atoll reefs and a Hawaiian fringing reef, respectively.

Table 1 includes one set of values for corals, those reported by Kanwisher and Wainwright (1967).   Their values suggest that productivity per unit area in corals (with their contained zooxanthellae) is as high or higher than that for free-living algal populations.   They reported ratios of maximum rates of photosynthesis to respiration (P: R) ranging from 1.9 to 2.8.   These ratios were based on short-term incubation experiments.   More recently, McCloskey (*in* Johannes *et al.*, 1972, and unpublished) has carried out experiments lasting for 24 hours and concluded that the earlier reported ratios were too high.   This implies that the reported productivity values were also too high.   While more work is called for, it is likely that the symbiotic algae of corals are less important in total community productivity than are free-living algae.

Reef populations fall within the same productivity range as other populations. For instance, Pomeroy's (1963) tabulated net productivity values from a number of earlier studies yield a range of 0.017 to $0.75 \text{ g C m}^{-2} \text{hr}^{-1}$, with most values falling between 0.17 and $0.42 \text{ g C m}^{-2} \text{hr}^{-1}$.   Kanwisher (1966) found gross productivity values as high as $1.7 \text{ g C m}^{-2} \text{hr}^{-1}$ in Woods Hole seaweeds.   Whatever accounts for high productivities in reef communities, the explanation is not likely to be higher productivities of individual populations.

A useful way to consider primary producers in reef communities is to discuss them in three groups: macroalgae, symbiotic forms, and fine filamentous forms.

Sea grasses are often abundant where fringing and barrier reefs occur but will not be considered part of the "reef community" here.

The macroalgae are the most obvious forms. These include various genera of reds, browns, and greens, as well as blue-greens which have a large enough biomass accumulation to form mats. The important consideration is functional rather than taxonomic. Generally the macroalgae may be taken to be anything that develops individual thalli or colonies large enough to be collected as discrete samples or that form distinct clumps (e.g., *Entermorpha*) or turfs (e.g., *Jania* and *Amphiroa*). The calcareous red algae may also be included in this category, both those which form crusts overgrowing the substrate and those which form distinct upright thalli. It is possible to remove discrete samples of macroalgae from the reef and measure metabolic rates in a respirometer, extract chlorophyll, determine dry and wet weights, etc., according to the usual approach. It may not be possible to separate these algae into separate taxa in any one sample, since individual species are often found growing intermixed on the reef. This is particularly true of turfs, which may have a complex association of reds and greens and possibly blue-greens growing intertwined with each other; they may contain assemblages of animals as well. One may be able to estimate percentages of various taxa present in a discrete sample, however. Considered from the standpoint of metabolic activity and the transfer of energy to higher trophic levels, the macroalgae constitute a functional grouping.

The macroalgae account for some rather obvious differences between fringing and barrier reefs on the one hand and atolls on the other. For instance, *Sargassum* is found only on the fringing and barrier reefs of high islands in the Pacific and not on atolls. Furthermore, as reported by Tsuda (1972), there are rather obvious seasonal changes of standing crops of this genus on some fringing reefs. A seasonal productivity pattern is implied by the annual accumulation of a large amount of biomass which eventually dies, breaks away from the substrate, and drifts about as detritus. Similar gross seasonal changes in turfs composed of *Amphiroa* and other mixed algal species are also obvious. Gross observation of the fringing reefs of Guam suggests seasonal changes in the standing crops of macroalgae generally. There must be a seasonal pulse in the productivity of these forms as well. Kohn and Helfrich (1957) found some seasonal variation in total community productivity of a Hawaiian fringing reef but did not, however, note changes in standing crops of any particular algae. On atolls there are few such obvious variations in the standing crops of macroalgae, but there may nevertheless be significant changes which are not obvious in total standing crops or in relative species composition. There is no particular evidence to suggest seasonality in productivities, although this possibility cannot be denied.

Much less obvious but potentially more significant in total reef productivity, are the fine filamentous forms. These are often overlooked on casual inspection, yet they can be found almost everywhere upon closer examination. Such fine filamentous algae include a number of green and blue-green taxa and often reds and browns as well. Many of these are forms which may potentially grow into

macroalgae if not prevented from doing so by grazing organisms. The algae may be scattered and recognizable as individual filaments, or they may be dense enough to form a fine fuzz. Obviously, any dividing line between macroalgae and fine filamentous forms is somewhat arbitrary since one gradually intergrades into the other. However, the distinction seems valid nevertheless. From the practical standpoint, it is not usually feasible to obtain a discrete sampling unit of the fine filaments for productivity measurements in a respirometer or discrete analyses of wet and dry weights, chlorophyll, or organic carbon. It is usually necessary to break away a portion of the substrate bearing these algae and treat such a substrate unit as the "sample." Unfortunately, there have been no in-depth studies of the metabolic activity of such filamentous forms, yet their possible importance is suggested by several considerations.

Grazing organisms such as acanthurid and chaetodon fishes often appear to be feeding on, or at least picking at, visually barren substrates. Such substrates can usually be seen to contain large numbers of small algal filaments on closer examination. Examinations of gut contents of fishes often reveal masses of fine filaments which appear to have been ingested in small units. Sea urchins and grazing gastropods often appear to be occupying relatively barren substrate for long periods of time and apparently feeding. If grazers are excluded from certain areas by cages, there quickly grow up extensive standing crops of macroalgae (Mathieson et al., 1971), suggesting that grazing pressure prevents this from happening in the absence of exclosures. Even when small filaments cannot at first be seen on the substrate, fanning away of loose sediments often reveals such forms.

Preliminary observations on filament-occupied substrate broken away and placed in a respirometer (Marsh, unpubl.) and observations of oxygen exchange in hemispherical domes placed over loose or solid substrates occupied by filamentous forms (M. Wells, unpubl.) suggest high rates of productivity. Upstream-downstream studies of oxygen exchange which have attempted to partition overall changes into various reef zones have suggested that "sand-rubble" or "sand-shingle" zones, composed of the kind of substrate referred to here, may be metabolically active. Odum and Odum (1955) extracted cholorophyll from samples of this substrate and found significant levels of the pigment, although their methods (which were the only ones available at the time) may be subject to question.

Yet another consideration is the well known inverse relationship between biomass amount and metabolic activity in individual organisms. Recent views of phytoplankton productivity place great emphasis on nannoplankton (Pomeroy, 1974), a size class which had been previously ignored. It now appears that these forms are at least as significant in photosynthesis and respiration of most water masses as is net plankton, the traditionally studied primary producers in the sea. It is reasonable to suggest that benthic microalgae which can grow into macroalgae may be more metabolically active as microalgae. When all the points in the foregoing discussion are considered, it seems obvious that workers studying reef productivity should focus more attention on small filamentous forms and the reef

zones dominated by them.

The third group of primary producers considered here has the longest history of study and has generated the most controversy. This group is the symbiotic algae, or zooxanthellae, enclosed in the tissues of corals and some other reef organisms such as tridacnid clams. Despite a number of earlier and recent studies on the metabolism of corals containing zooxanthellae, there continues a lively debate as to the relative part played by these algae in total coral metabolism. The question of coral nutrition has recently been reviewed by Muscatine (1973) and Johannes (1974). The role of corals and their zooxanthellae in community productivity was considered earlier in this paper.

Another type of algae in reef communities can now be dismissed as unimportant from the standpoint of community energetics. These are the filamentous forms of green algae (*Ostreobium*) which are commonly found imbedded in the skeletons of corals and other reef-building organisms. It was originally suggested by Odum and Odum (1955) that these forms are important not only in meeting the energy requirements of individual coral colonies but also in contributing to overall reef productivity. The work of Halldal (1968), Kanwisher and Wainwright (1967), and Franzisket (1968) has eliminated these algae from consideration as significant primary producers on reefs.

An adequate understanding of the energetic role of algae in reef ecosystems requires not only that we know what the major primary producers are, and the quantitative significance of their relative contributions to overall reef productivity, but also how the fixed energy is transferred to higher trophic levels. There is little quantitative information on pathways of energy flow. Certainly reef communities have large numbers of obvious grazing organisms such as herbivorous fishes, sea urchins, and gastropods. Other potentially significant pathways of energy transfer besides grazing are the indirect transfer of energy through dead plant material in detritus pathways and the transfer of energy through the release of dissolved organic material by primary producers and its subsequent heterotrophic utilization.

A number of studies of grazing organisms have demonstrated specific algal preferences by specific consumers (e.g., Earle, 1971; Randall, 1961, 1967). Many of these have indicated different preferences by the same species on different reefs. However, an analysis of gut contents, the usual method employed in such studies, is not sufficient to make statements about the quantitative aspects of energy flow for different populations of producers or herbivores. Exclosure experiments (*e.g.*, Earle, 1971) have demonstrated extensive algal growth on reef substrates when herbivores are excluded, but they are more useful for making statements about the effect of grazers on algal community structure than statements about energy flow.

A more basic consideration is that the large obvious consumers may not account for more than a small fraction of total community metabolism. Again, the inverse relationship between size and metabolic activity must come into consideration. It is likely that the organisms accounting for most significant energy flow on reefs are not the obvious fishes, urchins, etc. but hidden infauna in the various reef

substrates and smaller organisms ranging down to protozoans and bacteria. This generalization is presently gaining wider acceptance for all ecosystems.

The direct transfer of organic materials from zooxanthellae to their coral hosts has been demonstrated. However, the quantitative aspects of this transfer have not been studied in depth, and it is yet unclear how important this transfer is. See Muscatine (1973) for further discussion of this point. The transfer of energy from producers to consumers via dissolved organic compounds does not have to be exclusively a direct transfer such as that between the algal symbionts and their coral hosts. Dissolved organic material may be released into the ambient water and thereby made potentially available to any organisms in the community. That phytoplankton release significant portions of their total net primary productivion to their surrounding medium as dissolved organics is by now well known. Indeed a wide variety of dissolved organic compounds has been detected in sea water, although there has been little research done in reef waters. Nevertheless, the potential transfer of significant amounts of energy between producers and consumers via dissolved organics is a phenomenon worth examining in reef ecosystems.

The third pathway by which energy may be channeled between producers and consumers is the detritus pathway. This pathway has now been recognized as much more important than the direct grazing pathway in such marine systems as salt marshes. This would seem to be a potentially significant pathway on reefs also, but it is yet to be demonstrated. This presumption is particularly strong for the case of fringing reefs discussed above, where large seasonal variations in the standing crops of *Sargassum* have been found. As in salt marshes, there appears to be a minimal feeding of grazing organisms on the living plants, but they eventually die and break loose from the substrate to drift around on the reef flat or possibly to be washed off the reef flat. The exact fate of this detrital material is unknown, however. This represents a line of inquiry worth following up. Clearly, the production of detritus and its slow utilization throughout the year could be a factor tending to buffer or dampen seasonal pulses in productivity, so it is conceivable that reef community respiration has much less seasonal variation than does net community productivity.

Despite the lack of growth of large brown algae on atolls, detritus production may nevertheless be significant there. Johannes and Gerber (1974) measured the quantity of benthic algal fragments in waters flowing across an atoll reef community. Much of this was material such as the red alga *Asparagopsis*, which had a heavy growth on the reef face outside the surf zone, or on the algal ridge, and was continually torn off the reef by surf action to be carried downstream in the unidirectional current. Some of this material was recaptured by the reef-flat community and some of it passed into the lagoon.

Another source of detritus is the mucus which is shed from corals and may be exported from an atoll reef into the lagoon (Johannes, 1967; Marshall, 1965). This may be a pathway in which net productivity of symbiotic algae in excess of that required by the corals is made available to other reef organisms. Johannes

calculated that the amount of energy thus released by the coral-algal association could be a significant percentage of its total energy budget.

The relative significance of these three pathways of energy transfer from the primary producers to the consumers (and decomposers) in reef communities is unknown. It is not even possible to rank them in order of importance, much less to give quantative estimates of the total energy flow in each pathway. This lack of knowledge is not unique to reef systems, of course; but our ignorance is greater for such systems than for a number of other marine systems. This also·applies to the points discussed earlier in this paper.

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