# BIOGEOCHEMICAL BUDGETS IN CORAL REEF SYSTEMS

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## INTRODUCTION

The term "model" in ecosystem analysis refers to the systematic conceptualization of the myriad components within an ecosystem. A high degree of mathematical sophistication is desirable as an ultimate goal of ecosystem analysis. Until that sophistication can also obtain sufficient realism, less sophisticated constructs in the form of mass-balance budgets provide considerable insight into the dynamics of ecosystems.

Budgets, like their more complicated counterparts, involve the identification of simple "functional units," or "compartments," within the ecosystem; budgets also require the identification of likely pathways of material flow through the system. However, budgets do not require that mathematical functions describing the characteristics of material flux be devised. Budgets of carbon flux have been developed for several coral reef systems or portions thereof, and carbon budgets for hypothetical reefs will be the primary subject of this discussion.

## GENERAL BUDGETARY CONSTRUCT

The primary subject of discussion here will be a coral atoll of hypothetical, but realistic, dimensions. Imagine a circular atoll with a lagoon of 100 $km^2$ area, a reef flat of 20 $km^2$, and a fore-reef (to a depth of about 50 meters) of 10 $km^2$. This atoll would have a lagoon about 11 km in diameter, a reef flat about 500 meters wide, and fore-reef about 250 meters wide. Data given by Wiens (1962) suggest these dimensions to be realistic. In addition to treating each of the above physiographic units as compartments in the budgets, we will consider the two further compartments of carbon dioxide and fixed carbon in the ocean water. There is thus the following 5-compartment budget: oceanic $CO_2$ and fixed carbon, lagoon, reef flat, and fore-reef.

The connectivity describes material transfer from one compartment to another. For the most part in a physiographic budget, that connectivity is two-way. That is, if material is transported from any one compartment A to compartment B, it probably can also go from B to A. Arrows on a compartment diagram show interpretations of the direction of net flux. Probably _any_ compartment pair can be connected. The diagram describes only the connectivities which seem likely to be quantitatively significant.

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Clearly, there is net flux from oceanic $CO_2$ to all three reef compartments in the form of $CaCO_3$ precipitation. We assume that net organic carbon flux is in the same direction, that is, that atolls are sites of net $CO_2$ uptake in the form of primary production. This point will be discussed in more detail later in the presentation. With respect to $CaCO_3$, most of the other arrows are fairly obvious. $CaCO_3$ is stripped off the reef and is transported either to the lagoon or to the oceanic fixed carbon pool, and material is also lost from the fore-reef to that pool. Deposits of fore-reef material piled on reef flats argue that there is net transfer from the fore-reef to the reef flat. It seems likely that this direction of net transfer is equally valid for organic carbon. Material carried from the fore-reef to the reef flat or delivered to the lagoon has a relatively good chance of settling out in these environments; material transported oceanward is likely to drift away from the atoll. Thus, the fore-reef is inherently an ineffectual trap for particulate material in comparison with the reef flat or lagoon.

## $CaCO_3$ BUDGET

The next step is to quantify the transfer rates associated with the arrows and the accumulation (or loss) rates in the boxes. First consider $CaCO_3$-C (Figure 1). Lagoon $CaCO_3$ production rates have been measured between about 5 and 10 moles $m^{-2}yr^{-1}$ (Smith and Pesret, 1974; Smith and Jokiel, 1975). The higher value is used here. Thus, the hypothetical lagoon produces 10 X $10^8$ moles C/yr. The production rate in shallow, well-flushed environments such as reef flats has been measured to be about 40 to 50 moles $m^{-2}yr^{-1}$ (Smith, 1973; Kinsey, 1972). Again, the higher value is taken for a total reef-flat production of 10 X $10^8$ moles C/yr. No $CaCO_3$ production rate data are available for fore-reefs. Such environments have high standing crops of calcareous organisms, so a production rate comparable to that of the reef flat is assumed--a total production of 5 X $10^8$ moles C/yr. $CaCO_3$-mediated loss from the $CO_2$ pool is simply the sum of the fluxes to the reef compartments, or 25 X $10^8$ moles C/yr.

Of material entering the fore-reef compartment, we assume a sufficient amount remains to account for a net vertical accretion of about 1 mm/yr. This is equivalent to about 1 X $10^8$ moles C/yr. This figure is based primarily on $^{14}C$ age dating to obtain deposition rates on the fore-reef in Jamaica (Land, 1974). It thus appears that 4 x $10^8$ moles/yr, or 80% of the material produced in the fore-reef is lost from that environment. We assume that 75% of this loss is to the ocean and the remainder is to the reef flat.

Transport from the fore-reef plus $CaCO_3$ production on the reef flat account for 11 X $10^8$ moles C/yr input to the reef flat. The upward growth of the reef flat is obviously limited by sea level, and long-term world-wide sea level presently does not show a change of more than about

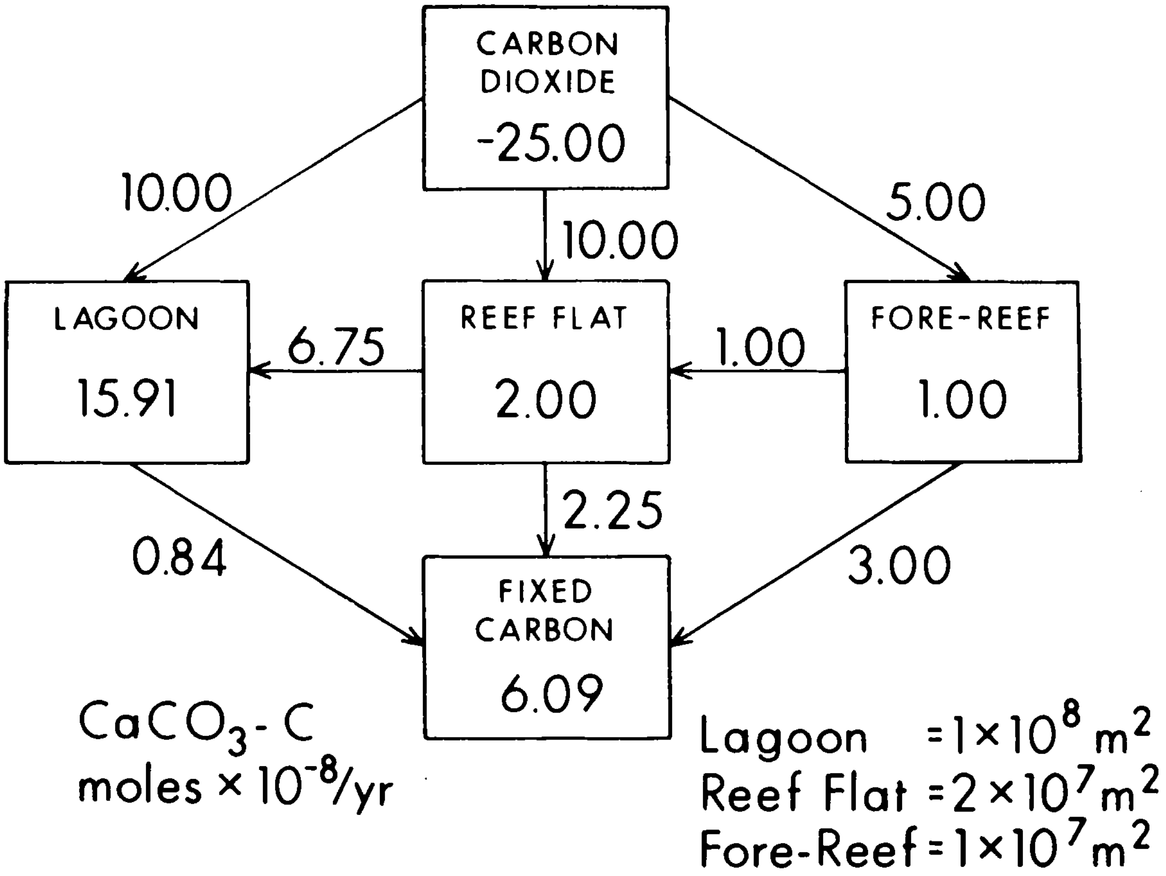

Figure 1. Compartment diagram of $CaCO_3$-C flux in a coral atoll.

± 1 mm/yr. For the budget, we assume that there is a 1 mm/yr deposition rate on the reef flat, or 2 X $10^8$ moles C/yr. We further assume that 75% of the loss from the reef flat is to the lagoon, and that the remainder is exported to the ocean.

Deposition in the lagoon is not ordinarily limited by sea level. Moreover, available data (Smith et al., 1971; Smith and Jokiel, 1975) suggest that sediment loss from the lagoon to the open ocean is small; we assume this loss to be 5% of the total lagoon input. Thus, about 16 X $10^8$ moles C/yr remain in the lagoon and about 1 X $10^8$ moles/yr are lost to the ocean.

Export of $CaCO_3$ to the open ocean is obtained by summing terms. For the budget as a whole to balance, the sum of the numbers in the various compartments must equal 0.

What are the inorganic budgetary characteristics of our hypothetical atoll? The lagoon is obviously the major repository for $CaCO_3$, accounting for about 65% of the total inorganic carbon fixed. The loss from the atoll is the next process in quantitative importance, at 25%, and the fore-reef and reef-flat areas are small sinks for inorganic carbon, accounting for only about 10% of the total production.

It is possible to investigate the consequences of changing the compartment sizes--that is altering the size of the atoll. Atoll reef flats and slopes are fairly constant in width (Wiens, 1962), so altering the atoll size primarily involves manipulation of lagoon diameters. For the following analysis, the lagoon area has been varied by powers of 10, and the reef-flat and fore-reef areas have been adjusted to maintain constant width. All production rates per unit area and depositional rates on the fore-reef and reef flat are held constant; proportional partitioning of flux from one compartment to another is maintained. As the atoll size decreases, the lagoon deposition rate increases, and the carbon loss increases towards 50% (Figure 2). As the lagoon fills in (or diminishes in horizontal dimensions to 0), the deposition rate will then necessarily vanish; there will be no further lagoon production; all excess sediments will then be exported from the atoll.

The change of sea level also has dramatic effects on the expected depositional characteristics of an atoll. To construct the budget so far, we have assumed that the reef-flat deposition rate is proportional to the rate of sea-level change. Fore-reef deposition is 1 mm/yr but in our budget is not controlled by changing sea level. Lagoons accept most of the sediments delivered to them. Modifying the budget to account for sea level change thus merely involves altering retention on the reef flat.

Figure 3 shows the results of such alterations. Up to a sea-level rise of about 5 mm/yr, deposition on the reef flat would keep pace with that rising sea level. On a faster rise, reef flat deposition rate would stabilize, if the environment retained all of its products. The

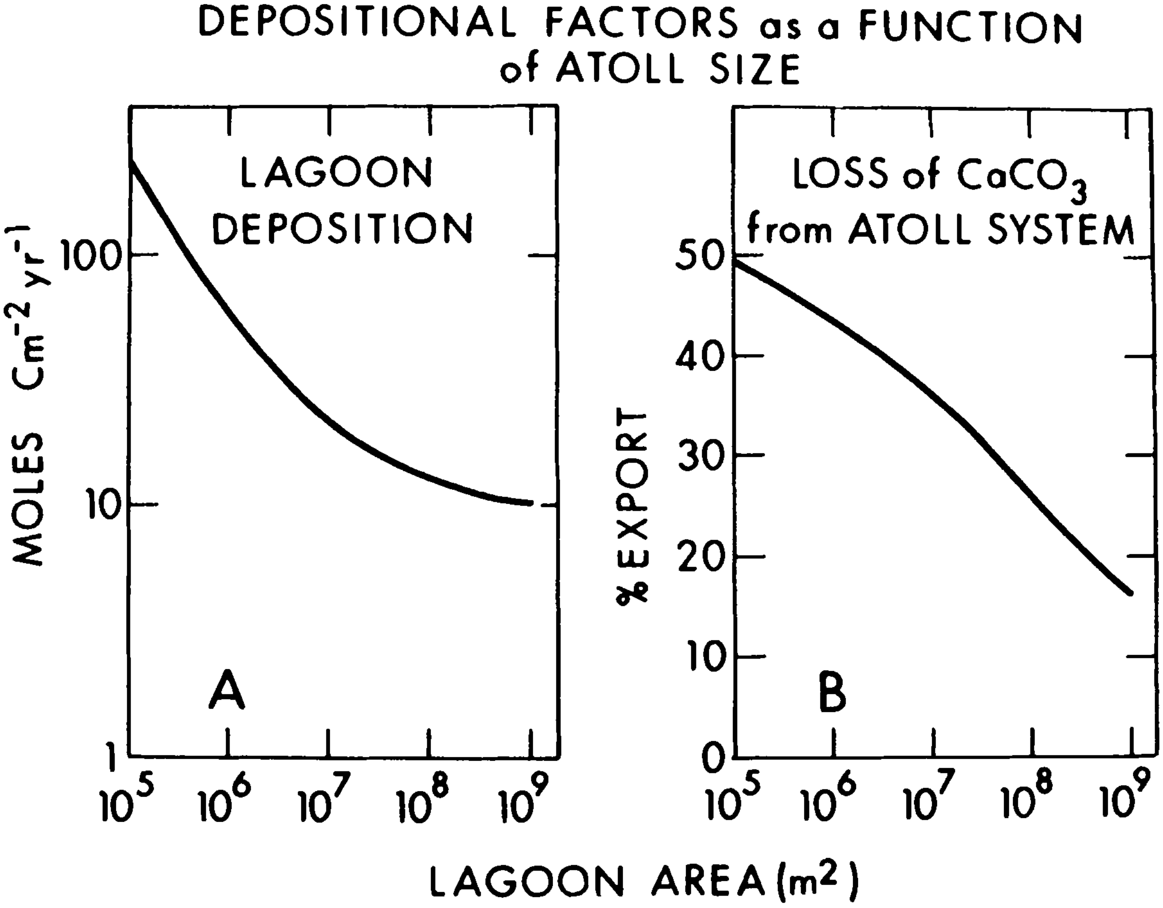

Figure 2. $CaCO_3$-C flux as a function of atoll size.

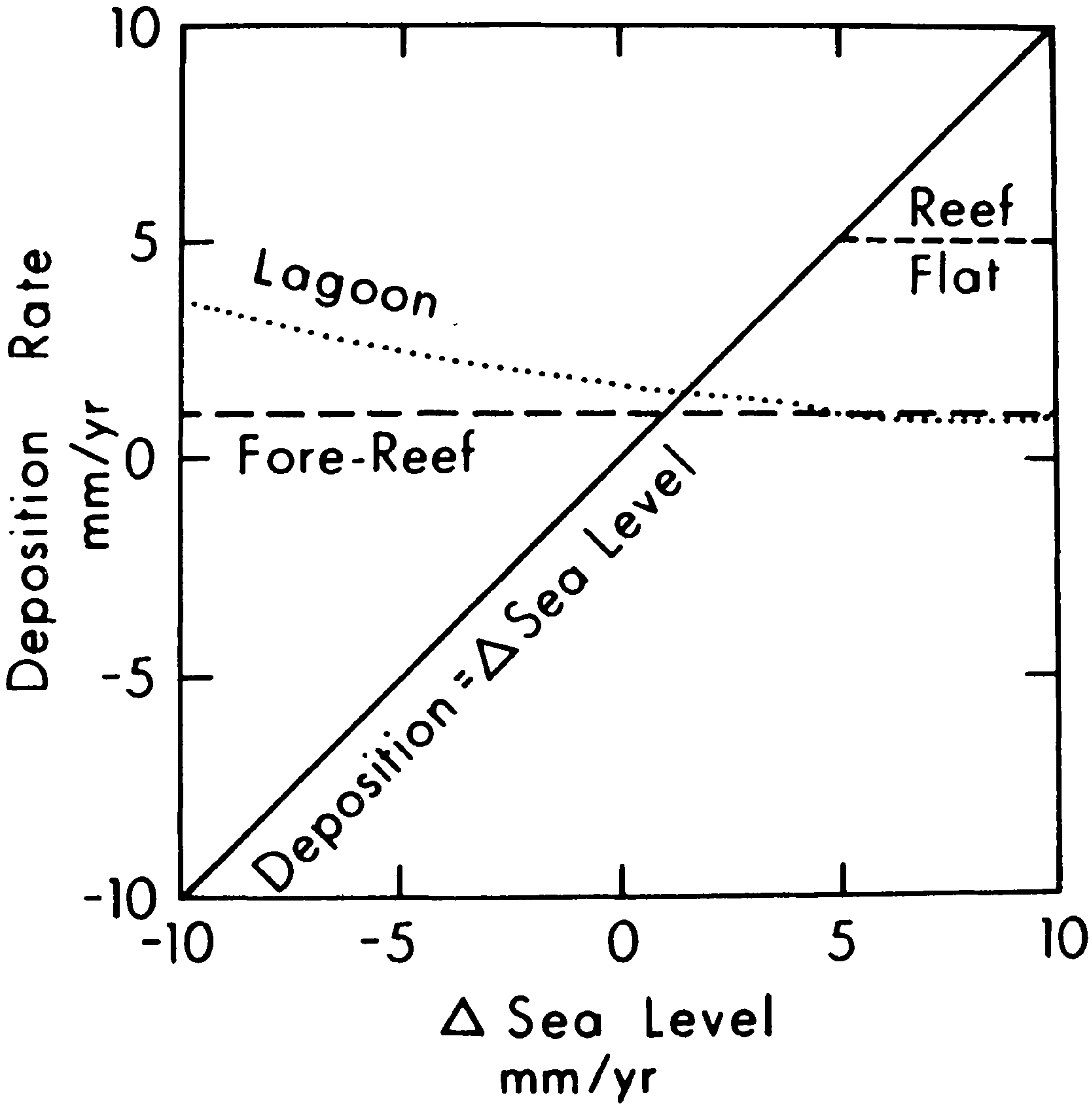

Figure 3. $CaCO_3$-C flux as a function of sea level rise.

fore-reef grows upward at 1 mm/yr, regardless of the rate of sea level change. The lagoon deposition rate would increase on a falling sea but would adjust to a deposition rate similar to that of the fore-reef during a period of rapidly rising sea level. This simple depositional model would break down as the atoll physiography is altered away from its starting geometry due to the change of sea level and depositional regime.

## ORGANIC CARBON BUDGET

Let us now turn our attention to the other major aspect of an atoll carbon budget: the production and consumption of organic carbon compounds. We will use our same hypothetical atoll for these calculations, as well as the same five compartment box model to represent that atoll.

Despite their very high gross production rates, coral reefs have a gross production to respiration ratio remarkably near 1.0. It is likely that reefs somewhat to either side of this unity P/R ratio can be found. Our own experience has been primarily with atoll which seem to be very slight net producers of carbon, so we give our hypothetical atoll a net community production rate of about 4 mmoles $m^{-2}day^{-1}$, or about 1.5 moles $m^{-2}yr^{-1}$. This corresponds to a P/R ratio of 1.007 if the gross production rate of the community is 6 g C $m^{-2}day^{-1}$. This value is very close to the net production rate reported by Smith and Jokiel (1975) for the lagoon at Canton Atoll. Lagoons are particularly useful for establishing the net production of a reef system, because they integrate reef community metabolism over a long time and a large area.

Figure 4 summarizes the organic carbon budget. Reef sediments commonly average about 0.5% by weight organic carbon (Smith and Jokiel, 1975). This amounts to about 5% of the total carbon in the sediments, so organic carbon retained by each of the atoll compartments is fixed at this percentage of the inorganic carbon retention, which has already been established. There is no particular basis to argue for anything other than an even division of carbon transport from each atoll compartment to its various possible sinks. The budget turns out not to be particularly sensitive to this point.

While the magnitude of these various numbers might be altered somewhat, the budget clearly predicts a substantial export of even the miniscule net excess organic carbon produced by the atoll. Moreover, the proportional organic carbon export from the three reef subunits is considerably higher than the inorganic carbon export. It is tempting to ascribe this differential transport to an artifact of the budget; that does not seem to be the case. Broecker and Takahashi (1966) observed such a budgetary discrepancy for the Bahama Banks; they suggested that they had failed to obtain a mass balance among the terms. Smith and Jokiel (1974) ascribed a similar discrepancy at Canton Atoll to differential transport of organic material, and evidence for differential transport can be reconstructed for the Enewetak windward reef flat (Smith, 1973; Johannes and Gerber, 1974; Marshall, 1965). What are the mechanisms?

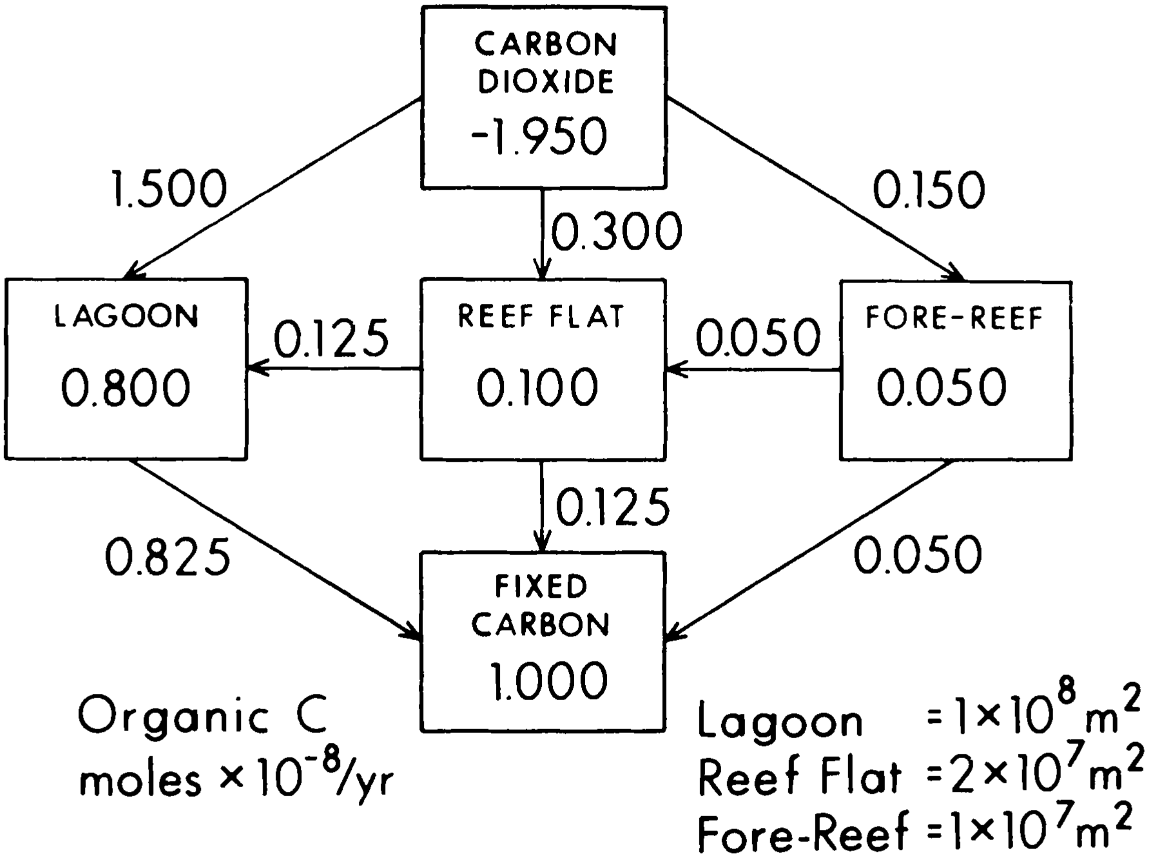

Figure 4. Compartment diagram of organic C flux in a coral atoll.

Perhaps the most conspicuous mechanism is the relative ease with which the biomass is dislodged by mechanical or biological erosion. Indeed, this dislodgement and subsequent transport of organic materials are apparently of considerable importance to the feeding patterns of reef organisms (Smith and Marsh, 1973). Even though erosion of $CaCO_3$ also occurs, this heavier material is likely to settle more rapidly. The second mechanism to be considered may be as important, or perhaps more so--the flux of dissolved organic material. Lacking any tendency to settle (short of adsorption to other materials), the dissolved organic compounds are readily transported from the system. Thus, despite initial concerns about a model suggesting significantly greater flux of organic than of inorganic reef products, we conclude that results to the contrary would be all the more surprising.

## OTHER BUDGETS

The discussion so far has involved carbon; but the carbon budgets, by implication, tell us a great deal about other materials. For example, some cations such as Mg or Sr have budgets which are very similar to that of $CaCO_3$. In polluted systems, one might predict pathways of the pollutant (e.g., trace metals) from a knowledge of their co-occurrence with carbon compounds. Alternatively, pollutant distribution in the ecosystem might carry significant clues about chemical behavior of the materials in question.

Net nutrient budgets must look somewhat like the organic carbon budget, although there may be differences in the details of gross sources, sinks, and intrasystem partitioning. Let us briefly consider two recent nutrient budget studies which have provided exciting insights into coral reefs. Webb *et al.*, (1975) reported on the flux of nitrogen through the windward reef flat community of Enewetak Atoll. The reef apparently exports all forms of fixed nitrogen, yet that community maintains its gross organic carbon production to respiration ratio near 1.0. The most obvious conclusion from the observation is that the community must offset the nitrogen export with an equivalent rate of nitrogen fixation. Subsequent studies (Wiebe *et al.*, 1975) not only verified this hypothesis but also isolated several of the important nitrogen-fixing organisms in the community. The high nitrogen-fixing capacity of that community has countered its location in the nitrogen-poor ocean waters of the Marshall Islands by exploiting an alternative, and large, nitrogen reservoir (air).

There is no such alternate phosphorus pool, and the phosphorus content of ocean waters impinging upon Enewetak Atoll is also low. Pilson and Betzer (1973) determined that the Enewetak reef-flat community retains phosphorus with great tenacity. These authors quoted Sargent and Austin (1949) as anticipating diurnal oscillations of phosphorus uptake and release in synchrony with oxygen production and consumption. That synchrony does not exist, and Pilson and Betzer point out that if it did, the reef community would have a requirement of up to 150% of the available phosphorus on a midday low tide in order to match the rate of organic carbon production.

Subsequent studies (Pomeroy et al., 1974) suggest that the strong retention and internal cycling of phosphorus represents a complex pattern of leakage by some members of the reef community and effective phosphorus capture by others. This pattern speaks to the complexity of the phosphorus cycle on a coral reef.

## SUMMARY

To summarize briefly, we hope that we have accomplished several objectives with these budgetary analyses. We have derived a $CaCO_3$ production, transportation, and deposition model which appears consistent with available data and with the characteristics of coral atolls. A similar budget for organic carbon suggests that while atolls show a very low net production rate, they export most of the organic material they do produce. Nutrient budgets have proven useful in suggesting the existence of various strategies of nutrient flux and cycling in the atoll ecosystem.

Such budgetary analyses are by no means ends in themselves, but they do provide a useful base on which to build further studies of coral reef processes and with which to evaluate the quantitative significance of those processes.

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