KANSAS GEOLOGICAL SURVEY

OPEN-FILE REPORT SERIES 95-56

INFORMAL COMMUNICATIONS OF SCOR WORKING GROUP 104.

Kansas Geological Survey Open-File Report 95-56a: REFLECTIONS ON THE MEASUREMENT AND SIGNIFICANCE OF CARBON METABOLISM ON CORAL REEFS

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Kansas Geological Survey Open-File Report 95-56b: CORAL REEF CARBON CYCLE RESEARCH: CONCEPTUAL AND EXPERIMENTAL DESIGN

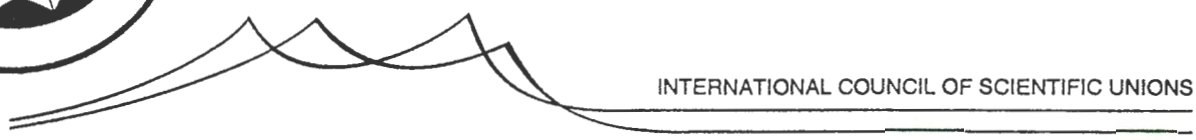
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OCTOBER 1995





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Preface:

This paper is an expanded version of an abstract submitted to the International Workshop on Carbon Cycling and Coral Reef Metabolism, Miyakojima, Japan, October 16-25, 1995; because it addresses the relationships among coral reef community structure, function, and the carbon cycle, it is also being circulated as a working paper of SCOR Working Group-104. Although it is a stand-alone document, it is best read in conjunction with the working paper of Smith (1995), which addresses the history and significance of reef community metabolism measurements in much more detail than the summary treatment presented here. As a working paper it is intended to be conceptually complete, but does not necessarily contain the level of citation and literature review appropriate to a formal publication.

Introduction:

In spite of the likelihood that carbon fluxes due to coral reef metabolism can only be a minor component of the global carbon cycle, there is persistent interest in exploring the question of whether coral reefs represent sources or sinks for atmospheric carbon dioxide. This paper examines the methods and requirements for making such a determination.

Two definitions are critical, and often ignored in the design and interpretation of individual experiments: what is a source or sink, and what is a coral reef.

Sources, Sinks, Inventories, and Fluxes:

A source of atmospheric CO_2 is any process (or reservoir) that produces a transfer of CO_2 into the atmosphere from another compartment of the exchangable

carbon cycle; the term sink is normally used to refer to the material where carbon resides after it is extracted from the atmosphere (e.g., terrestrial biomass, soil organic matter, etc.). Any flux of CO_2 into or out of the atmosphere can be called a source or sink, but a critical component of the definition is the time scale. The mixing time of the atmosphere is a few years, so definition of a source or sink is problematic unless it results in a net change over that time scale. From a climatic standpoint, material removed from the atmosphere must be sequestered for a minimum of many decades (more realistically, centuries to millennia) before it can be considered a sink. Because the atmosphere is the reference reservoir and because its carbon dioxide dynamics are relatively well known, the problem of source definition is less critical.

Figure 1 presents a simplified schematic of some of the major pathways and reservoirs of carbon related to reef systems. Net community production (the difference between photosynthesis (P) and respiration (R), also termed "excess" production: E = P - R) is a potential sink for atmospheric CO2, just as net calcification (precipitation - dissolution) is a potential source. The simplified relevant reactions are $CO_2 + H_20 \longrightarrow H_2O + O_2$ (P, or -R), and $2HCO_3^- + Ca^{++} \longrightarrow CaCO_3 + CO_2$. Neither sink nor source are actual, however, unless the integrated net reactions proceed as written, and the products are protected from further reaction and re-exchange with the atmospheric carbon cycle. In an actual reef system, organic and inorganic production tend to counterbalance each other in terms of atmospheric fluxes; the degree to which they counterbalance each other in source/sink behavior is more difficult to assess.

Figure 1 shows three possible destinations for the net organic and inorganic products of reef metabolism. They may end up in the local reef or reef-derived, or they may be exported to other oceanic compartments (here simplified as the shallow and deep ocean). To a first approximation, sediments are usually considered to be out of exchange with the atmosphere, but in actuality they are the site of active biogeochemical reactions and cannot be treated as inert (Tribble et al., 1989; Tribble et al., 1990; Walter et al., 1993); these issues are discussed further below.

A key issue for this discussion is the question of whether the transport of material fractionates the inorganic and organic products in such a way as to enhance either source or sink behavior. Transport of material to the deep ocean can effective removal from the short-term carbon cycle; although both inorganic and organic products are likely to react at depth, there re-equilibration with the atmosphere will be postponed for hundreds to thousands of years (oceanic turnover times). Downslope transport of material is known to occur at shelf edges and on atoll slopes, but the fraction of total production following this path is very poorly known. Because of the extensive sediment trapping on shallow shelve, banks and lagoons and the approximate equivalence of reef accretion and reef production rates (Buddemeier and Smith, 1988) it

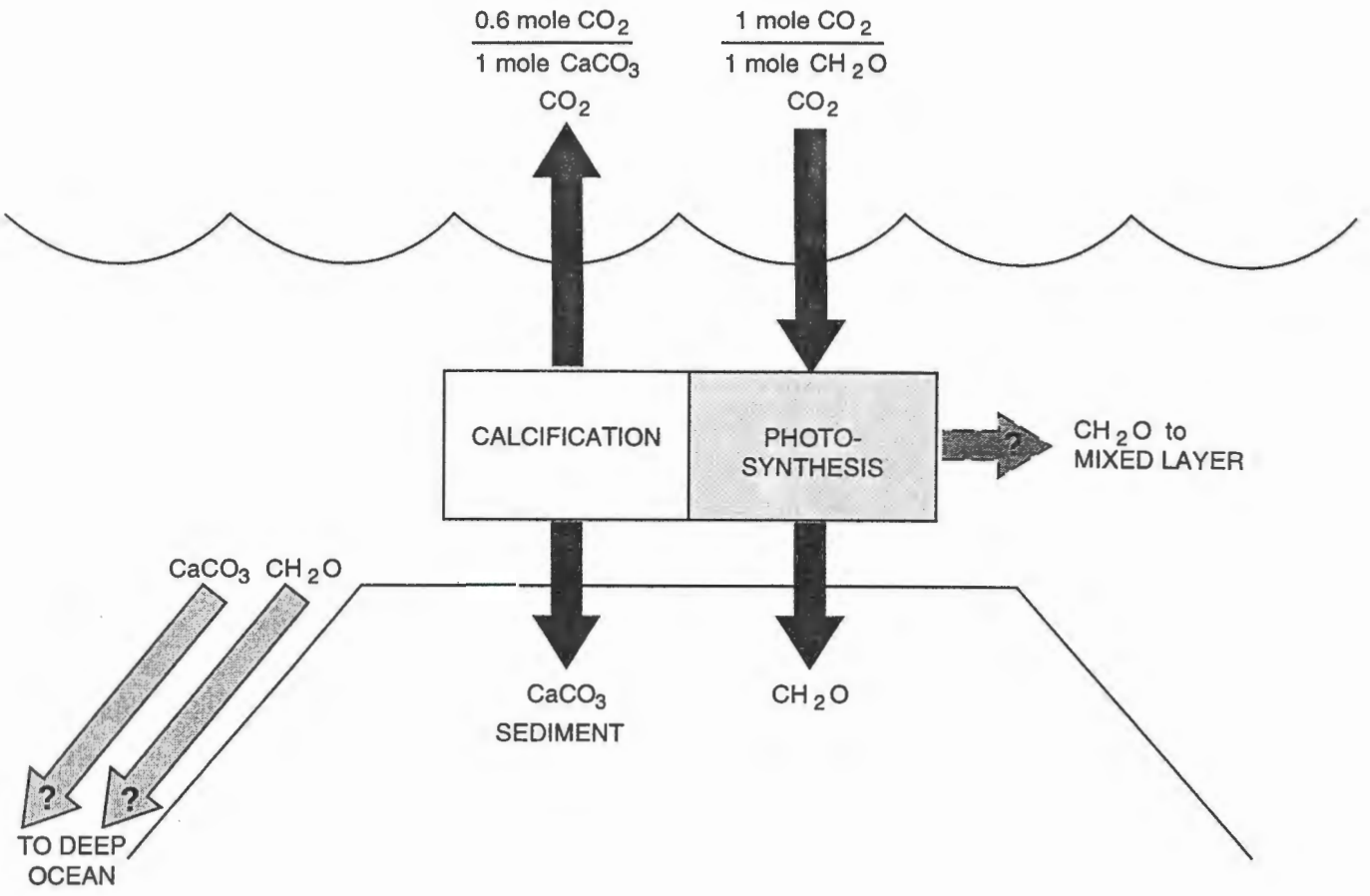


Figure 1: A schematic representation of reef-related carbon fluxes and reservoirs. If net calcification and net photosynthesis are positive, then their products must be transported to one of the reservoirs indicated (sediment, deep ocean, or surface ocean). Only in the case where the amount of organic carbon buried in the sediment or transported to the deep ocean is > 0.6 x the amount of carbonate carbon similarly transported can reef metabolism be considered a sink for atmospheric CO_2.

is normally assumed that a substantial majority of shallow water production is retained within the depth range of the oceanic mixed layer. For the material transported downslope, density will be a factor; solid carbonates will sink more readily than free organic matter. The carbonates removed will carry with them included or attached organic matter, so to a first approximation we can assume that transport to the deep ocean will remove organic and inorganic carbon in the same proportions as burial in the shallow sediments.

A more significant potential fractionating mechanism is transport of material out of the reef system to the surface ocean. Although oceanic "alkalinity plumes" around reef areas testify to some off-reef transport of carbonate materials, loss of organic material in the form of POC and DOC is probably proportionally more important because of the buoyancy and reactivity of organic material. Mobilization of reef organic matter has been reported by a numerous authors (Coles and Strathman, 1973; Marshall, 1965; Marshall et al., 1975). Indications of the significance of this flux are reported by Johannes (1967), who estimates that the carbon exported from reefs by coral mucus production is equivalent to about 40% of the coral respiration; he also cites studies reporting that normal oceanic phytoplankton/zooplankton ratios are shifted dramatically in favor of zooplankton in the vicinity of coral reefs. If it is correct that the net productivity of reef systems is of the same order of magnitude as the surrounding oceans (Crossland et al., 1991), this observation implies that a significant fraction of the reef primary production is exported to and consumed in locations away from the reef. This is an important consideration in metabolic estimates of fluxes; if respiration is separated in time or space from photosynthesis, local or short-term measurements may suggest a sink where, on a more realistic scale, none actually exists.

Reefs, Reef Communities, and Reef Organisms:

The term "coral reef" is applied to many structures and communities, and the terminology used by other disciplines is not necessarily appropriate for "reef" classification in terms of carbon cycle behavior. The most rigorous and traditional definition might be an community in which the benthos is dominated by calcifying reef organisms, living on top of a carbonate structure produced by that community or its predecessors. Examples of this are oceanic atolls (especially those with relatively small emergent areas) and outer shelf barrier reefs, as in the central Great Barrier Reef. Such communities are normally found to be primarily autotrophic, although this is not an intrinsic requirement of the definition.

However, geologists may focus on the carbonate structure without close attention to its presently living community, and ecologists apply the term to mixed communities in which there may be net heterotrophy, terrigenous influences, or other communities (e.g., seagrasses) that are not an obligate part of the "pure" coral reef community. Figure 2 depicts a gradient in "reef community" types from seaward to

landward. Stressed or coastal coral communities often contain a much higher ratio of non-calcifying to calcifying organisms, and therefore may exhibit a higher organic to inorganic production ratio, making them appear to be larger potential CO_2 sinks (Gattuso et al., 1995). This may in some cases be true, but the error lies in ascribing this behavior to a "coral reef community;" the actual sink behavior is the product of (for example) a seagrass or algal community that not only is not an intrinsic part of the coral reef community, but may even be competing with or replacing it.

Approaches to Source/Sink Determination:

At present, we can classify three basic approaches to the determination of sink behavior in terms of the methods available for experimental assessment. Two of them involve determination of production rates and/or the disequilibria that drive fluxes, and one directly measures the reaction products. All have specific -- and different -- limitations and disadvantages. The experimental approaches, which will be discussed with regard to their limiting uncertainties and applications to date, are:

1. Site-specific community metabolism
2. System-level community metabolism
3. Characterization of sequestered materials

All of the methods require some level of regionalization of local (or "point") data, and/or site selection for "representativeness," in order to generalize specific measurements to the global and climatic levels. These processes -- selection and regionalization -- depend critically on the conceptual design, the definition of a coral reef or coral reef community, and the limitations of the methods employed.

Site-specific community metabolism:

Studies of community metabolism typically depend on measurements of the changes in carbon and/or oxygen chemistry in either isolated bodies of water or along a well-defined flow trajectory. Time scales of measurement are typically of hours to a few days, and spatial scales may be meters to a few hundred meters.

Advantages: Relatively high precision and direct measurement of the metabolic reactants and products are possible; determinations can be made of the function of specific communities. Although technologically demanding, the methods can readily be carried out in the field.

Disadvantages: Because of the inherent small spatial and temporal scales, variability is difficult to assess, and extrapolating or regionalizing measurements to larger scales of time and space is almost certainly the limiting uncertainty in the method. The method cannot assess the loss of fixed carbon from the local system, and sediment metabolism

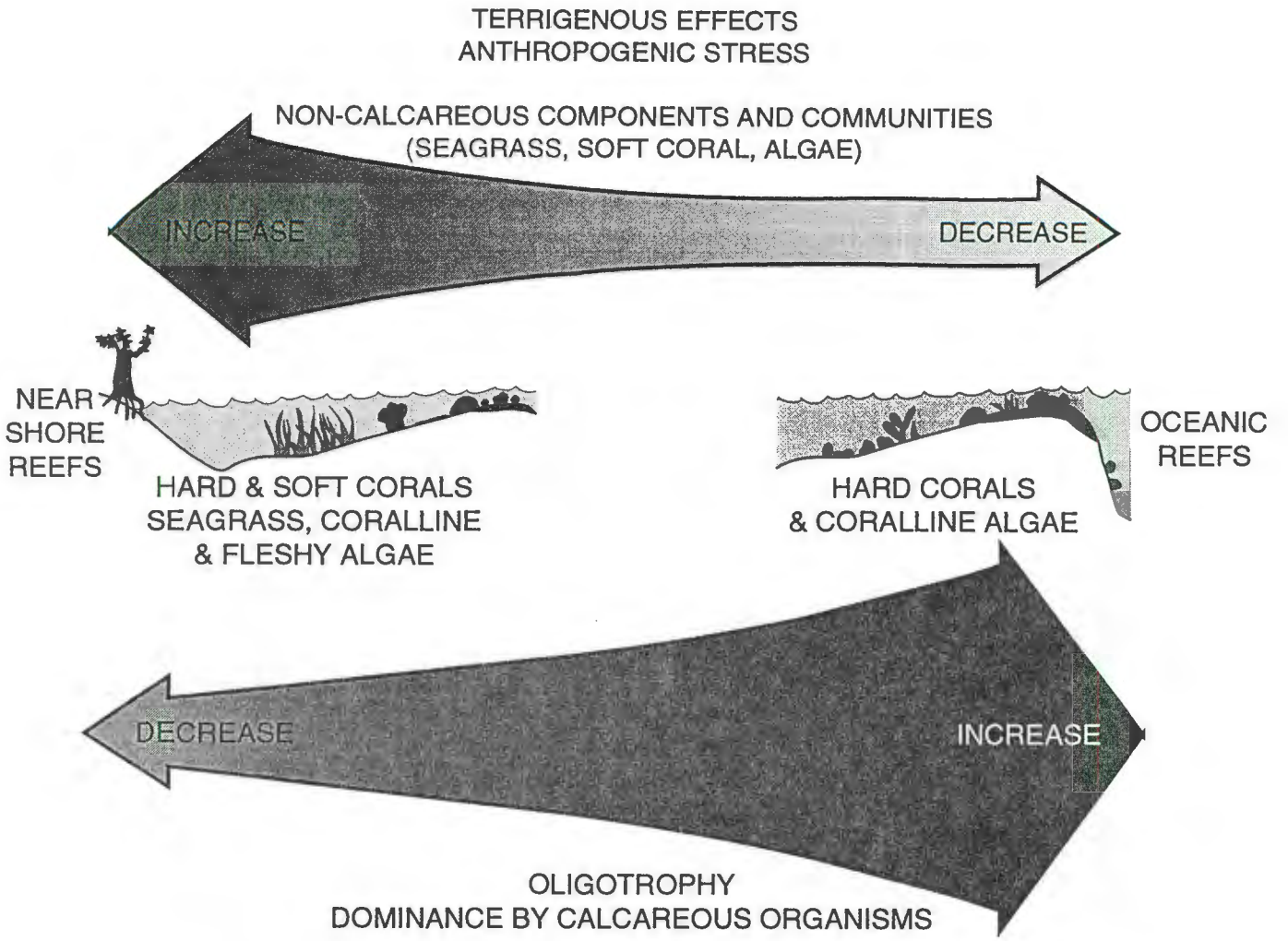


Figure 2: Environmental trends in "coral reef" communities. Terrigenous and human influences are commonly associated with communities having a lower proportion of calcifying organisms. Non-calcifiers may be intimately associated with corals and coralline algae, but are not an obligate part of a strictly defined "coral reef community" such as occurs in many oceanic settings.

contributions may vary on time scales long compared to the period of observation. The method is difficult to apply in high energy environments or in areas where the water volume cannot be defined, both of which may be important to the total flux of CO_2.

Applications to date: Perhaps as many as 50 such studies have been carried out at a wide variety of locations in all oceans. Results are usually expressed as relevant to a specific community type (e.g., reef flat, reef slope, lagoon, etc.). Calcification, and especially photosynthesis and respiration, are highly variable between sites of the same type and at individual sites over time. Gross rates of P and R may fluctuate by factors of 3-4 or even more, making calculation of net rates, extrapolations, and regionalizations highly uncertain. An overview of results (Kinsey, 1985; Smith, 1995) indicates a wide variation in the inferred source or sink behavior of individual sites, but suggests that an overall system average is probably close to zero.

System-level community metabolism:

System-level studies have commonly used nutrient (phosphorus) depletion as an indicator of net organic fixation in combination with alkalinity and salinity changes to assess the metabolism of relatively enclosed, long residence time systems (see discussion by Smith, 1995).

Advantages: This approach integrates over most of the spatial variability of the system, which is probably the greatest uncertainty in combining site-specific studies. It also integrates over longer time scales than most site-specific studies, although it will not (unless repeated) characterize major seasonal or interannual variations.

Disadvantages: The method can be applied only in cases where system geometry and residence times produce a detectable and interpretable signal. Probably the major disadvantage is the need to use assumptions about C:P ratios or other large-scale chemical estimators in order to calculate productivity; because of natural variability in this ratio, there is significant uncertainty in the absolute value of the calculated results.

Applications to date: System-level studies have been carried out at six atoll or island lagoons, plus three other carbonate-producing but not coral reef environments. Results consistently indicate that the carbon flux is either approximately neutral or a small net source to the atmosphere.

Figure 3 provides some perspective on the results of both local and system-level metabolic measurements. It was prepared by pooling all of the P, R, and G values listed by in Table 2 of Kinsey (1985) to produce a mean and standard deviation for each of the indicated reef categories. This calculation implies that each measurement is an

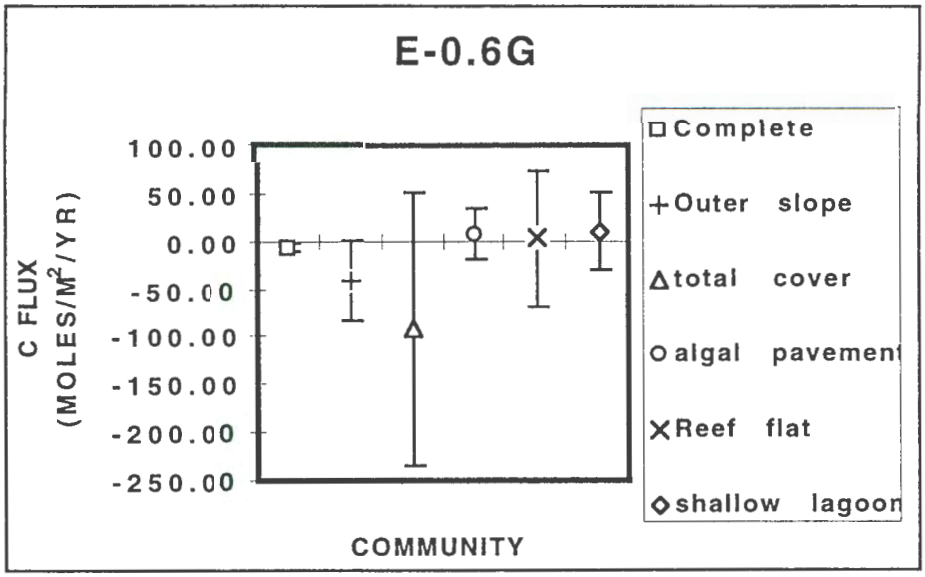


Figure 3: CO_2 flux estimates by community type, obtained by pooling all metabolic data reported by Kinsey (1985) for the indicated categories. Plot is of mean and stardard deviaion of the difference between net production (E=P-R) and 0.6 x net calcification (G). Positive numbers indicate a flux of CO_2 from sea to air; negative, from air to sea. None of the numbers are significantly different from zero, but whole-system values show the by far the smallest variance.

equivalent sample of a normal population; although we know that is not a reasonable assumption, the results are instructive nonetheless. The value E - 0.6G is an estimate of the net CO2 flux (negative is a release to the atmosphere, positive is an uptake).

The observations of interest from figure 3 are: (1) none of the categories show a mean that is significantly different from zero; (2) the most highly calcifying systems (outer slope and total coral cover) show the greatest tendency toward source behavior; and (3) the standard deviation for system-level measurements is strikingly less than the standard deviations of any of the more localized communities, and the values plotted graphically illustrate the basis for the conclusion (e.g. Smith (1995); Ware et al. (1992)) that reef systems are probably a very small net source of CO_2. These observations emphasize the importance of scale -- reef systems consist of variable component subcommunities whose functions are integrated over time and space scales much larger than those of the typical direct experimental observation.

Characterization of sequestered materials:

This method considers the chemical composition of reef sediments as indicators of source-sink behavior. Calcification releases 0.6 moles of carbon dioxide per mole of carbonate precipitated and photosynthesis takes up one mole of carbon dioxide per mole of carbon fixed. Therefore, if all of the products of the net metabolism are deposited in the sediments, a sedimentary ratio of organic to inorganic carbon >0.6 would indicate a source, while <0.6 would reflect sink behavior -- this ratio is equivalent to 5-6 weight % organic carbon in a sediment that is essentially all carbonate and organic matter.

Advantages: This method views the long-term process over the time scales of sediment deposition, which are generally appropriate to climate considerations. Sampling and analytical techniques are well established, and sediment samples can be taken in environments not amenable to metabolic study. Because extensive, distributed sampling is feasible, regionalization is less of a problem and can be supported with (e.g.) bathymetric and seismic surveys. Sediment analyses can also be used to assess terrigenous contributions or other factors.

Disadvantages: It is known that reefs export organic carbon as DOC and POC; while most of this is probably oxidized rapidly rather than sequestered elsewhere, it must be explicitly addressed in the budgetary estimates. Postdepositional organic inputs or diagenesis may alter the organic/inorganic ratio by pathways that do not imply the same source-sink relationships as primary deposition. Sediment samples integrate over time, but the time period sampled depends on the sediment accumulation rate, so samples from different locations will not necessarily represent the same time periods -- this dictates a long-term, steady-state assumption in combining results. Sampling of near-surface or recent sediments is complicated by possible inclusion of benthic biomass that

should not be considered truly sedimentary. Finally, if the community has undergone a recent change, the sediment results may not reflect current performance.

Applications to date: Although substantial data are available in the literature, there has been no systematic application of this to carbon cycle studies. This is probably in part due to the fact that the "source or sink" answer appears to be a foregone conclusion on the basis of sediment analyses -- most carbonate sediments in reef environments have organic/inorganic C ratios an order of magnitude lower than that required for a net carbon sink.

A variety of analyses from active reef systems suggest that typical organic C contents are <1% (organic/inorganic C ratios <0.1) (Emery, 1962; Emery et al., 1954; Smith, 1984; Tribble, 1990). Organic ratios may be higher in close proximity to a high productivity (and usually not coral-reef) source of organic materials. Systems-level surveys of sediments illustrate the effects of reef and other ecosystems. In the Bahamas (which is a carbonate platform of primarily non-coral origin with some coral reef communities) sediment organic levels are quite low except where they can be identified with mangroves, algal communities or seagrass beds (Morse et al., 1985). Brunskill (unpubl. data, pers. commun.) and colleagues at the Australian Institute of Marine Science have performed extensive sediment surveys in the Herbert River region of the Great Barrier Reef, in Exmouth Gulf in Western Australia, and in the Gulf of Papua. The first two locations provide a broad view of primarily reef-derived sediments over scales much larger than that of the reefs themselves. In both cases, sediment organic/inorganic ratios exceed 0.6 only in very limited areas close to the shore or strongly affected by streamflow. The organic/inorganic ratio remains low even in settings where carbonate material is less than 50% of the total sediment mass. These observations tend to reinforce the view of coral reefs as carbon dioxide sources except when they are influenced by or combined with other communities.

Two aspects in which sediments may contribute to some form of carbon sink deserve mention here, both relating to the fact that shallow reef sediments are sites of active bacterial metabolism and diagenesis (see above). When organic carbon is oxidized in the air or in surface ocean water which is in equilibrium with the atmosphere, CO_2 is returned to the atmosphere. However, when it is oxidized in carbonate-containing sediments the CO_2 may be neutralized by dissolution of solid carbonate, with the carbon transferred to the bicarbonate form ($CH_2O + O_2 + CaCO_3 \longrightarrow 2HCO_3^- + Ca^{++}$). If this simply canceled out the atmospheric effects of the original calcification and photosynthesis it would have no impact on source/sink considerations. However, because a mole each of organic and carbonate carbon formed represent a net withdrawal of 0.4 moles of atmospheric CO_2, the 1:1 neutralization in the sediment could be considered a net transfer of carbon from the atmospheric to the oceanic reservoir. Whether or not this represents a genuine sink has not been rigorously examined. However, because reef sediments are 5-10 times too depauperate in organic carbon to

represent a sink, and because this consideration could only change the ratio by a factor of about 2, it does not change the basic conclusion but may serve to somewhat reduce the discrepancy between the system metabolism and the sediment-based assessments.

A further related consideration has been pointed out by B. N. Opdyke (pers. commun.). The "titration capacity" of carbonate sediments could in principle convert terrestrial or marine organic carbon into an oceanic inorganic form if there were mechanisms for mixing the two "reactants." This could be a significant sink, but it is important to not that it is not a direct function of the metabolic activity of coral reef (or any other specific) communities; sedimentary microbes are the primary community, operating independently on the organic and inorganic products of other communities.

Evaluation and Conclusion:

Site specific studies are extremely useful for examining community function at small scales, but are generally inappropriate for extrapolating to whole-ecosystem performance, and especially to global and climatic scales. A broad overview of the results of many -- and variable-- site studies is consistent with the smaller number of more uniform findings of whole-system studies; on average, reefs are presently nearly in balance with respect to CO_2 flux, or are possibly a small net source of CO_2. A greater and more interesting discrepancy is between system studies and interpretation of sediment analyses, which suggest that either reefs have been a somewhat stronger CO_2 source over the recent past, or that there are carbon transport and reaction pathways in the present systems that have not been adequately characterized. Where sediment and whole-system metabolism studies are in reasonable agreement, the combined results might be used to calibrate the regionalization of site-specific studies, and to infer by difference the behavior of communities that are not directly measurable.

Identification of the actual -- as opposed to traditionally described -- communities and organisms involved in carbon fixation and transport, and determination of their functional behavior over appropriate scales of time and space, are critical to any effort to define true CO2 source or sink behavior.

The issues of carbon metabolism are not only (or not even primarily) of interest from a carbon-cycle standpoint; they are crucially important to present concerns about reef conservation and management. Many reefs have been damaged by overfishing, and others have been stressed or killed by high inputs of sediment, organic matter, and/or nutrients. If reefs have a higher net productivity than has been generally determined (as would be suggested by carbon sink behavior), they could sustain greater biomass harvesting and possibly higher nutrient or organic inputs. If managers and policy makers respond to an incorrect suggestion of higher productivity by relaxing environmental controls, the global loss of coral reefs could be accelerated. Careful experimental design and interpretation are essential in addressing this sensitive topic.

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