

FUNCTIONAL ASPECTS OF NUTRIENT CYCLING ON CORAL REEFS

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ABSTRACT

Coral reef waters are generally very low in nutrients, yet benthic productivity is among the highest in the world. A general concern of reef ecologists has been to identify the sources of nutrients for reef productivity and the processes responsible for nutrient recycling on reefs. One potentially important process that has been poorly studied is the recycling of regenerated nutrients from sediments and feces trapped in reef holes and crevices. These nutrients, if available to the benthos in concentrated form, could have a major influence on reef productivity.

INTRODUCTION

Coral reef communities are extremely diverse and variable, and we should not expect that the relationships between reef organisms or the dynamics of the system to be simple to understand. On the other hand, by analyzing these complex systems in terms of functional groups, we may gain a better understanding of important processes, and identify research areas that need our attention. In this paper, I will try to identify processes and functional groups involved in nutrient dynamics on coral reefs.

Understanding nutrient dynamics on coral reefs is important because, as in any other ecosystem, primary production is controlled by the availability of nutrients, and primary production is one of the main factors that determines community biomass and secondary production.

Coral reefs occur in tropical areas, where oceanic waters are generally very low in nutrients, yet these complex ecosystems have some of the highest biomasses and productivity that have been reported (Lewis, 1977). This dilemma can be termed the 'paradox of the coral reef'. There has been a great interest in identifying mechanisms that could explain this paradox. Two important ones that have been well studied are the recycling of nutrients between algal/invertebrate symbionts and the fixation of N_2 by blue-green algae and bacteria. Another approach has been to identify additional sources of dissolved nutrients, such as from ground water seepage or upwelling of nutrient enriched deepwater. A final approach has been to examine the reef ecosystem for structural and functional properties that lead to enhanced conservation of nutrients. This is the approach that will be emphasized here.

SOURCES OF NUTRIENTS

There are two general sources of nutrients for primary production: New nutrients and regenerated (recycled) nutrients. If only regenerated nutrients were available, gross photosynthesis could not exceed respiration (i.e., P/R ratios could not exceed 1.0) unless there was a change in elemental ratios (e.g., an increase in the C/N and C/P ratios). Net production (growth) requires the input of new nutrients into the system, as does net export from the system. It is important to point out that nutrient recycling mechanisms, even when 100% efficient, cannot supply nutrients for a positive net production. Furthermore, if recycling mechanisms are inefficient it will take an input of new nutrients to maintain a steady state biomass.

New Nutrients:

New nutrients can enter reef systems from both terrestrial and oceanic sources and, in the case of nitrogen, by in situ N_2 fixation. Nutrient input to reefs from terrestrial sources remain poorly studied. However, we can make several general statements. Coral reefs located off the coasts of high volcanic islands or on continental shelves may receive a considerable supply of nutrients via terrestrial runoff (Marsh, 1977). However, coastal areas with high runoff are usually devoid of coral reefs unless estuarine systems, such as mangrove forests, trap the nutrients near shore. It is not clear at this time whether the negative effect of runoff on reef development is due to siltation stress, salinity stress or nutrient stress (in the latter case, high nutrient concentrations can promote high phytoplankton and macroalgal growth rates, which in turn can result in unfavorable environmental conditions for reef-building corals). Most likely, all three stresses contribute to the effect. In any case, the on-shore current patterns that generally dominate coral reef circulation should limit the amount of terrestrial runoff that reaches most offshore reefs. One interesting phenomenon that has been reported recently is the submarine seepage of NO_3 enriched fresh water inshore of a fringing reef (D'Elia, et al., 1981; Johannes, 1980). It is unlikely that this kind of seepage will reach offshore reefs, and there is little or no information on how frequently this phenomenon occurs. Reefs located offshore of low carbonate islands should receive little input of terrestrial nutrients because runoff from these terrains are usually low in nutrients unless fertilizer has been applied for agricultural purposes. Atoll reefs generally have no significant land masses nearby from which to receive terrestrial runoff.

Oceanic sources of nutrients will be dependent on the concentration of nutrients in the source water, the rate of flow of water over the reef, and the ability of primary producers to take up the nutrients at the given concentration. Nutrient concentrations in tropical oceanic waters are generally near limits of detection, but there are reports that upwelling may occasionally result in higher concentrations (Thompson and Golding, 1981; Andrews and Gentien, 1982). The rates of water flow over the reef are high, and several species of reef coral have been found to be able to take up nutrients from these low concentrations (Franzisket, 1974; D'Elia, 1977; D'Elia and Webb, 1977; Webb and Wiebe, 1978). Atkinson (1981) has estimated that there was a sufficient uptake of dissolved phosphorus from water crossing the reef flat to account for the measured primary production (ΔO_2) if a Redfield ratio (C:P) of 490 was assumed (the oceanic C:P ratio is 106). He also found that marine algae from a variety of sources had C:N:P ratios much higher than the Redfield ratio (Atkinson and Smith, 1983), a possible indication of an evolutionary adaptation to low nutrient conditions. An alternative explanation is that macroalgae need a greater amount of C-rich structural material than phytoplankton, which results in higher C:N:P ratios for the former. It should be instructive to measure the C:N:P ratio of other reef organisms, especially the microcrustaceans, which have body structures similar to planktonic organisms.

In any case, a quick calculation shows that for the following average conditions: dissolved inorganic nitrogen (DIN) concentrations in the range of 0.5 to 1.0 μM , current velocities in the order of 0.06 to 0.50 cm/s, annual gross productivity of $3,220 \text{ gC} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, P/R ratio of 1.4 and net productivity of $950 \text{ gC} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, the first m^2 of reef substrate to make contact with oceanic water would need to strip out 0.08 to 1.3% of the DIN to support net production and maintain a C:N of 6.6. This assumes a mixed layer 1 m deep; twice that percentage would have to be taken up if the organisms can only strip nutrients from the bottom-most 0.5 m of water. Uptake of nutrients to support all of gross production (i.e., if no recycling occurred) would require stripping somewhere between 0.25 to 8.5% of DIN. This means that for many reef flats, where the water column is usually less than a meter deep, waters flowing over downstream areas may be significantly depleted in nutrients. In fore-reef zones, vertical mixing should prevent this type of depletion from being as important, but it is still apparent that at low concentrations and at slow current velocities it is unlikely that uptake of new oceanic nutrients could account for much more than net productivity. Otherwise, we should see a much greater drop in DIN and dissolved

inorganic P concentrations during upstream-downstream experiments (Pilson and Betzer, 1973). In fact, DIN and dissolved organic N (DON) concentrations generally increase as oceanic waters cross the reef, and a net export of N has been found for some reefs (Johannes, et al., 1972; Webb, et al., 1975). This implies a source of fixed N from within the reef community, which can be attributed to N₂ fixation by benthic blue-green algae and N₂-fixing bacteria (Mague and Holm-Hansen, 1975; Burris, 1976; Capone, et al., 1977; Wiebe, et al., 1975). Rates of N₂ fixation on coral reefs have been found to exceed those of alfalfa fields, the terrestrial community with the highest reported rates of N₂ fixation. These high rates have led many investigators to conclude that fixed N is plentiful on reefs, and that concentrations of P must be controlling reef productivity. However, measurements of N₂ fixation generally have been restricted to shallow reef flats or back reef areas and denitrification rates have not been adequately measured in any reef environment. Until they are, any conclusions about N availability are premature.

Regenerated Nutrients:

It generally is believed that the main evolutionary adaptation to low nutrient conditions in reef environments has been the evolution of relationships that lead to efficient recycling of nutrients. The foremost example of this type of relationship is the endosymbiosis between algae and invertebrates. Present day coral reefs are physically dominated by a variety of orders and classes of coelenterates and virtually all of them have symbiotic dinoflagellates (zooxanthellae) in their tissues. It has been repeatedly demonstrated that these animals do not excrete waste products as do other nonsymbiotic animals (Kawaguti, 1953; Pomeroy and Kuenzler, 1969) and that there is even a measurable uptake of dissolved nutrients by them attributable to the presence of the algae (see earlier references). Other invertebrate groups, including sponges, molluscs and ascidians, also have some species with algal symbionts. This form of recycling is the most efficient possible (often 100%) as the nutrients are available to the algae in concentrated form. It should cost the algae much less energy to take up the nutrients they need from a concentrated source than to take them up once they had been excreted and diluted.

As important as this type of relationship may be, there are still many groups of algae and many more of vertebrates and invertebrates living on the reef that are not involved in endosymbiotic relationships. These plants and animals need nutrients and excrete nutrients, respectively, and depending on their biomass these fluxes may be quite large. There are few estimates of the absolute and/or relative biomasses of reef organisms. Odum and Odum (1955) found that zooxanthellae make up roughly 15% of the biomass of primary production on a Enewetak reef flat and that coral polyps make up about 50% of the biomass of consumers. However, they had very poor estimates for the biomass of reef fishes and their samples were from the reef flat, which is topographically and biologically less diverse than most forereef areas. Measurements of biomass on a Caribbean fore reef (Szmant-Froelich, 1972) show a greater percentage of the algal biomass to be made up of zooxanthellae and a smaller percentage of the consumer biomass to be made up of symbiotic coelenterates. In order for the reef as a whole to be efficient in recycling nutrients, there must be mechanisms for recycling nutrients among these free-living plants and animals. The main problem arises when one considers that the same high water flow over the reef that assures a large source of low-nutrient oceanic water also assures that any nutrients excreted into the water by animals will be rapidly diluted and carried away. Therefore, what is needed is a mechanism to prevent dilution and loss.

I would like to bring attention here to a little studied mechanism, that of particle entrapment and nutrient regeneration within the reef framework.

REGENERATIVE SPACES

Coral reefs are riddled with holes and tunnels of all sizes. From 50 to 75% of the reef volume can be made up of these voids (Ginsburg, 1983). These holes contain varying amounts of sediment which comes from a variety of sources, including carbonate sediments

generated by degradation of the reef structure by borers, fecal material from fishes and invertebrates that use these holes as shelters or encrust the walls of the holes, and non-reefal material (including terrestrial and pelagic) that is trapped inside the reef as seawater percolates through the porous structure. Organic materials in these sediments are metabolized by microorganisms, and in the process, nutrients are regenerated. Elevated concentrations of nutrients have been measured in waters from reef cavities (Di Salvo, 1969; Andrews and Muller, 1983; Szmant-Froelich, 1983).

I suggest that 'burps' of nutrient enriched water exit these holes and provide benthic primary producers with short episodes of exposure to higher nutrient concentrations. During Hydrolab Mission 83-10, whose objective was to study the role of herbivorous fish in nutrient regeneration, we measured nutrient (NH_4 , NO_3 and total dissolved N) concentrations of surface and bottom waters at two sites, one near shore ("Habitat" site), the other less protected and more offshore (East Slope site), as well as waters from about 400 m offshore of the reef, and from inside caves at the East Slope site (Table 1). The results of these measurements show that reef water is 3 to 4 times higher in NO_3 and slightly higher in NH_4 and organic N concentrations than oceanic waters. The most dramatic difference in nutrient concentration, however, can be seen between the offshore water and the cave water. Cave water concentrations are 13 times higher in NO_3 , 2 times higher in NH_4 and 3 times higher in organic N than offshore waters. These enrichments in the caves represent a significant increase in nutrients for any primary producers that might have access to them. Dye injections into caves showed that there was rapid outwelling of cave waters onto the reef, and, importantly, that these cave waters flowed within 1 m of the bottom for 10-15 min or longer before mixing upwards. This indicates that there is a process that restricts vertical mixing and dilution of nutrient enriched outwelled cave waters, such that benthic primary producers would have sufficient time to strip the nutrients from these waters before they mix upwards. Corollary evidence that 'burps' of enriched water exist near the reef bottom were obtained from fish excretion experiments during which fishes were incubated inside PVC pipes. Concentrations of NO_3 were always constant during each incubation but varied considerably between incubations (Table 1). Since these were short incubations (30 min) replicated repeatedly with new fish during 4 to 5 hour periods, and conducted at various locations over the reef, the differences in NO_3 concentration reflect true spatial and temporal differences in NO_3 concentrations of reef bottom waters. The rapid outwelling of the dye from the caves further indicates that rates of nutrient regeneration in cave sediments must be fairly high in order to maintain the observed enrichments in spite of the high water flow.

Table 1. Mean nutrient concentrations at various sites in Salt River Canyon, St. Croix (Hydrolab Mission 83-10) during August 4-10, 1983 (mean \pm 1 std. dev.).

Site	Depth (m)	No. Sampling periods	μM			
			NH_4	NO_3	DIN	DON
Offshore	0	2	0.40 \pm 0.04	0.07 \pm 0.03	7.7 \pm 0.2	7.2
	15	2	0.28 \pm 0.06	0.07 \pm 0.04	8.2 \pm 0.4	7.8
East Slope	0	8	0.49 \pm 0.19	0.24 \pm 0.12	7.8 \pm 1.4	7.1
	15	17	0.45 \pm 0.27	0.30 \pm 0.13	9.2 \pm 3.3	8.4
"Habitat"	0	9	0.57 \pm 0.25	0.27 \pm 0.05	9.0 \pm 1.8	8.2
	15	16	0.53 \pm 0.24	0.31 \pm 0.11	8.6 \pm 1.8	7.8
Caves	15-30	15	0.67 \pm 0.26	0.93 \pm 0.42	24.6 \pm 11.0	23.0
Fish Incubation	15	49	-	range 0.14 - 0.40	-	-

Nutrient regeneration also occurs in lagoon sediments (Entsch, *et al.*, 1983) where nutrients are utilized by extensive macroalgae and turtle grass beds. These beds are heavily grazed upon by reef fish. Many of these fish exhibit diel migration patterns, whereby they graze on the backreef and in the lagoons by day but shelter in the deeper forereef by night. Material that they transport in their guts at dusk is defecated over the forereef or in their nocturnal shelters. This form of transport may be an important means of upstream nutrient recycling on coral reefs. The reverse cycle of migration (nocturnal feeding, daytime sheltering) by juvenile grunts has been shown to have measurable impact on nutrient concentrations around coral heads (Meyer, *et al.*, 1983).

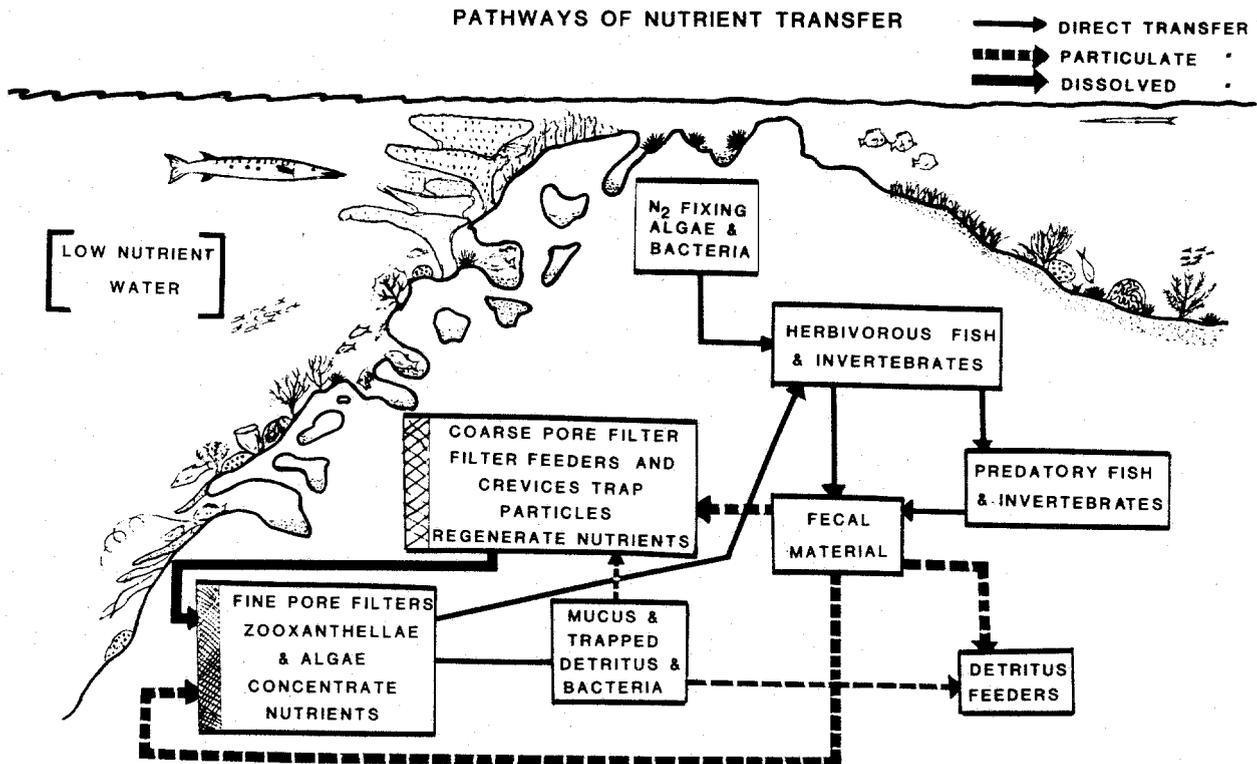


Figure 1. Diagrammatic representation of nutrient pathways on a coral reef.

FUNCTIONAL GROUPS

The various processes and functional groups involved in coral reef nutrient dynamics are diagrammatically represented in Figure 1.

New nutrients enter the system in both dissolved and particulate form, or are generated *in situ* by N_2 fixation. Dissolved nutrients and some particulates are taken up by the organisms included in the "fine-pore concentrators" group made up of algae and zooxanthellae. Other particulates are trapped by the reef framework and by filter-feeding organisms, which I call the "coarse-pore concentrators". Planktivorous fish also concentrate particulates and have been shown to excrete and defecate significant amounts of NH_4 and organic material in their nocturnal shelters (Bray, 1982). Herbivores graze on the algae and corals, and carnivores, in turn, feed on the herbivores. The fecal material from both of these groups, many of which spend about one-half of their time sheltering in reef crevices,

are deposited either into reef crevices or released just above the reef surface, where it rains onto what can be viewed as a benthic wall-to-wall carpet of mouths. I have observed particles of cardinal fish feces being consumed by Agaricia agaricites and by other fish. Fish feces contain a lot of mucus, and I believe that fish fecal material is the source of much of the "organic-aggregate" material reported from reef waters. Fecal particles that are eaten form a direct link in nutrient recycling. They are an important nutritional source for corals and other sessile invertebrates that previously has not been taken into account when considering questions of food availability. Regenerated nutrients outwelling from reef interstices form an indirect link in nutrient recycling on the reef, possibly a critical one in maintaining the high rates of reef productivity.

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