

Nitrogen Cycle on a Coral Reef¹

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While coral reefs are characterized by high rates of biological productivity, it has long been a puzzle to biologists as to how this is accomplished. Most reefs exist in oceanic deserts where phytoplankton production is extremely low. In nutrient poor waters of the tropical Pacific Ocean, nitrogen is believed to be the most limiting element (Thomas and Owen, 1971). Starting in 1971 on the Symbios expedition (Johannes *et al.*, 1972), a group of scientists examined the nitrogen flux of a windward reef at Enewetak Atoll, Marshall Islands. In this paper I wish to review these findings.

The studies on the nitrogen cycle at Enewetak made use of two important features of the reef. (See Webb *et al.*, 1975, for a complete description of the sampling sites.) First, water passing over the reef is unidirectional. This means that it can be treated as a continuous culture system, much as one would do in the laboratory. Input chemical and biological parameters can be measured and the changes that take place in these features examined as the water passes over the reef (output). Furthermore, since the different communities, *e.g.*, algal flat, zone of small corals, *etc.*, are arranged perpendicular to water flow (see Odum and Odum, 1955), it is possible to examine which communities are responsible for specific changes. For example, Smith and Marsh (1973) showed that the algal flats had a production to respiration ratio (P/R) much greater than 1 while the zones with coral showed a P/R ratio of about 0.75, although the overall P/R ratio was about 1.

The second important feature is that the activities of organisms in the water itself are insignificant compared to that of those in the benthos. Oxygen consumption is extremely low (Pomeroy, Alberts and Wiebe, unpubl. data). Bacteria as estimated by viable plate counts ranged from 50 to 200 cells per ml (Sottile and Wiebe, unpubl. data). While viable plate count procedures underestimate the total bacterial population, even if the numbers were 100 times higher, they would not exert a detectable effect on water quality that we could measure. Thus, for these two reasons flow studies can be conducted.

Initially (Johannes *et al.*, 1972), what surprised us most was that more nitrogenous compounds left the reef than were present at the initial (upstream) station.

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The greatest increase was in dissolved organic nitrogen (DON) followed by ammonia and nitrate in about equal concentrations. Nitrite was not detected in the flow studies. The presence of nitrate production was of particular interest since, while it appears to be the dominant fixed nitrogen compound in the world's oceans, no one had ever measured, *in situ*, its rate of production in any marine environment. Thus, in our studies we concentrated on two aspects of the nitrogen cycle: 1) the reason for the increase in nitrogen compounds as water passed over the reef and 2) the production of nitrate by natural marine communities.

As described by Webb *et al.* (1975) the increase in nitrogen compounds resulted from nitrogen fixation, mostly by blue-green algae. The average net fixed nitrogen production on the reef was 985 kg per hectare per year. The average value from all of the reef studies on nitrogen fixation (Wiebe *et al.*, 1975) was 730 kg per hectare per year. These values are as high as those reported for the richest alfalfa fields (Alexander, 1971). Three genera of blue-green algae were identified. The most important organism was *Calothrix crustacea*, a heterocystous alga which was found extensively on the algal flat and as an epiphyte on other algae (e.g., *Dictyosphaeria*). The other two organisms, found in lesser quantities, were *Rivularia* and *Hormothamnion*. *Rivularia*, in fact, appears to be a morphological variety of *Calothrix* and not a separate genus (R. Tsuda, personal communications). It is found in the upper intertidal regions and is subject to drying during each tidal cycle. *C. scopulorum* has been shown (Jones and Stewart, 1969) to release up to 40 percent of its fixed nitrogen into solution, largely in the form of peptides and amino acids. This might account for the large increase in DON in waters passing over the reef. Hanson (Ph. D. dissertation, University of Hawaii, 1974) has reported similar release from *C. crustacea* isolated from a coral lagoon.

Wiebe *et al.* (1975) reported on some of the major physiological controls on the *Calothrix* community nitrogen fixation including light, temperature and salinity. These features were chosen for investigation because they are major variables in this reef system. Details of experiments can be seen in Wiebe *et al.* (1975). The results may be briefly summarized as follows. Salinities of 2–45‰ had no detectable effect on the rate of nitrogen fixation. These organisms live in inter- and subtidal zones subject to both very high and low salinities. The organisms seem well-adapted for this type of fluctuation.

As greatly as salinity fluctuates, the temperature remains remarkably constant year around, between 26–39°C; the latter value having been measured in a small exposed tidal pool (E. Reese, personal communication). We examined the *Calothrix* community for its response to temperature. There was no nitrogen fixation at 24°C; the rate of fixation was temperature dependent up to 33°C. At 39°C the rate of fixation increased for about two hours but then fixation ceased. Jones and Stewart (1969) reported that *C. scopulorum* in cold Scottish water fixes nitrogen at 10°C.

Most of the nitrogen fixation was light dependent, but the shut-off time, when fixing cultures were placed in the dark, varied from a few minutes to several hours.

We do not know if the dark fixation represents algal or bacterial fixation, but dark algal fixation has been reported frequently. In fact these data while supporting the thesis that the *Calothrix* is the major nitrogen fixing organism on the reef do not exclude a major role by bacteria. For example bacterial nitrogen fixation could be intimately linked to the production of released algal photosynthate and thus appear to be "light dependent".

Rivularia (Calothrix) community reacted much like the *Calothrix* under the above conditions. Since it dries out daily we examined this effect on fixation. Dry, of course, it does not fix; when wetted it takes 30–40 minutes to begin and within a few minutes of beginning it establishes its maximal rate.

These experiments have provided us with a picture of some aspects of the nitrogen fixation process on the reef. Most of this activity occurs on the algal reef flat and the products (net) are exported to the coral and lagoon communities.

The other aspect of the nitrogen cycle we examined was nitrification, that is the biological oxidation of ammonia to nitrate. The results are reported in detail in two reports: Webb *et al.* (1975), and Webb and Wiebe (1975). Ammonia oxidation appears to be strictly a bacterially mediated phenomenon. While four separate pathways of oxidation have been described, only the autotrophic pathway of *Nitrosomonas sp.* oxidizing ammonia to nitrite and *Nitrosomonas sp.* oxidizing nitrite to nitrate have been reported to be important in nature. Initially, Webb and Wiebe (1975) isolated natural communities on the reef flat that showed net nitrate production averaging 1.35 nM per cm per hr. The communities responsible also contained nitrogen fixing blue-green algae. Utilizing a metabolic block, N-Serve (Dow Chemical Co.), which acts specifically against ammonia oxidase in *Nitrosomonas sp.*, it was demonstrated that nitrate production was via the classical autotrophic cycle. Further, using the same metabolic block, Webb and Wiebe (1975) established *in situ* nitrate uptake rates or community demand.

A schematic representation of the portions of the nitrogen cycle studied on the Enewetak reef is shown in Fig. 1. Four separate steps are involved, ending in the production of nitrate. While substantial quantities of DON and ammonia and nitrate are released into the water, nitrite production and utilization appear closely coupled. Denitrification, *i.e.*, the dissimilatory reduction of nitrate to nitrogen gas, probably is not an important process in view of the close correlation between exported nitrogen compounds and the rate of nitrogen fixation. If nitrogen fixation rates were much higher, then export denitrification could be important; but this is not the case. Nitrate assimilation could and does take place but again if the system is in a steady state, it should not affect the quantity of nitrogenous compounds leaving the reef.

These studies have provided us with a new understanding of how coral reefs maintain such high production in the face of impinging low nutrient waters. While the reef may have a P/R ratio of about 1, it certainly is exporting vast amounts of fixed nitrogen.

Finally, I would like to make a plea that these reef flat communities be given

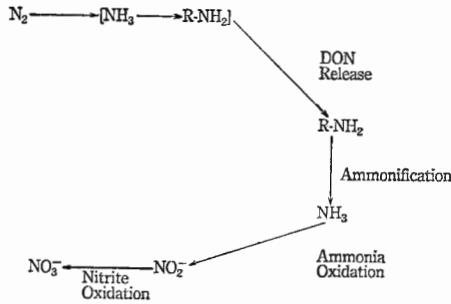


Fig. 1. Schematic representation of the portions of the nitrogen cycle studied on the Enewetak reef.

greater emphasis for study. They are drab looking compared to the corals and fish and have been accorded the lowest conservation priority vis a vis dredging, construction and sewage out-fall placement (Johannes, 1975). Yet the reef flats appear to be of great importance as a source of fixed nitrogen and carbon for the adjacent communities. The energy and nitrogen to support the rest of the system is derived from this much overlooked and disregarded reef habitat.

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