12. ATMOSPHERIC NITROGEN FIXATION BY REEF COMMUNITIES

Coral reefs within the Cairns and Tully boxes act as both sources and sinks of nitrogen and phosphorus. While a wide range of nutrient related processes occurring on coral reefs have been investigated over the years (summarized by D'Elia, 1988), few of these types of investigations have been carried out on reefs within the study area. The most comprehensive summary of nutrient fluxes onto or off a reef biologically comparable to those in the study area comes from the work of Crossland and Barnes (1983) at Lizard Island, with the proviso that the hydrodynamics of the Lizard Island reef may be significantly different from those on platform reefs in open shelf waters. In contrast to earlier studies (Wiebe et al., 1975), the work of Crossland and Barnes suggested that the reef flat and small lagoonal habitats of this system were not major sources of nitrogen and phosphorus to surrounding waters. More recently, Capone et al. (1992) have reported measurements of a variety of nitrogen transformations in unconsolidated coral reef sediments on central GBR (19°S) reefs. Estimates of potential fluxes associated with specific nutrient processes must therefore be extrapolated from a small number of experimental studies done elsewhere in the GBR.

The spatial extent and distribution of habitat (substratum) types on individual reefs is highly heterogeneous. The calculation of substrate-weighted nutrient processes for entire reefs is therefore dependent upon reliable estimates of area-averaged rate processes within different habitat types and the relative contributions of different substratum types to total reef area. A detailed census of substratum types for all reefs within the study area is beyond the scope of the present study. The analysis of spatial information in the satellite imagery of a large sample of reefs throughout the GBR (Figures 2 and 3) suggests that shallow (< 2 m) substrate, largely reef flat and reef flat sand patches, comprises approximately 18 percent of total reef area, with considerable variations between individual reefs. Sandy substrate similar to that found in reef lagoons at depths < 5 m comprised an additional 33 percent of area of the reefs classified.

Fixation of atmospheric nitrogen (Wiebe et al., 1975) has been identified as one of the major nutrient processes occurring on coral reefs. A variety of measurements of nitrogen fixation by reef communities have been carried out in the GBR (e.g. Burris, 1976; Wilkinson and Sammarco, 1983; Wilkinson et al., 1984; Larkum et al., 1988; Capone et al., 1992), but only the data of Wilkinson et al. (1984), Larkum et al. (1988) and Capone et al. (1992) can be extrapolated to larger scales. Wilkinson et al. (1984) demonstrated that community nitrogen fixation rates are highest on outer shelf reefs where the reef substratum is dominated by actively grazed turfs of cyanobacteria. Analytical considerations dictate that direct measurements of nitrogen fixation must be made with small pieces of reef substratum. The difficulty with using data derived from such experiments revolves around extrapolating measurements made at a very small scale to larger substratum-based habitat structural units. The most detailed study, incorporating estimation of nitrogen fixation rates for a variety of reef substratum types and seasonal fluctuations is that of Larkum et al. (1988). They derived roughness-corrected annual fixation rates of 366 and 9.6 kmol N km^{-2} $year^{-1}$ for hard substrate reef flat and shallow lagoonal sand habitats, respectively. Fixation rates were derived for other structural/substratum types, but the classification of those habitat types in the satellite imagery is less well resolved and will not be included herein. More recently, Capone et al. (1992) estimated average annual nitrogen fixation rates on unconsolidated sediment to be 69.2 kmol N km^{-2}. On an areal and rate-specific basis, the shallow hard substrate rate measurements are the most important.

Using the imagery derived estimates of reef flat and shallow sand areas (Table 2), annual atmospheric nitrogen fixation by reef associated cyanobacteria in the Cairns and Tully boxes is estimated to be 89 x 10^3 and 90 x 10^3 kmol, respectively. Despite the lower area-specific rate of fixation in unconsolidated sand substrates, fixation in this habitat appears to account for half of the total fixation. The data available do not allow us to reliably estimate the proportion of this

newly fixed nitrogen which is either rapidly or ultimately exported from reefs to surrounding waters, nor the contribution of this newly fixed nitrogen to the net nitrogen balance of the reefs.

Coral reefs are active centers of nutrient transformation with dissolved nutrients being actively taken up and released by coral reef animals, plants and microbial communities associated with different substratum types. Apart from the results of Crossland and Barnes (1983), there is no information on reef-scale annual fluxes of nitrogen and phosphorus from reef flat systems in the central GBR from which regional scale estimates can be made. Results from measurements made at Lizard Island, which has a geometry considerably different from most shelf reefs, suggest that net exchanges with surrounding waters may be small at times. By area, lagoonal sands, both shallow and deeper, constitute the largest substratum type by area. Measurements by Hansen et al. (1987) indicated that dissolved nutrient fluxes into or out of reef lagoon sands of reefs were small and given the relatively small contribution of reefs to total shelf area (< 15 percent), was therefore unlikely to be significant on the shelf scale. More recent measurements by Capone et al. (1992) indicate that a range of active microbially mediated nitrogen transformations occur in reef sediments. Measurements made on mid- and outer-shelf reefs in the central GBR indicated relatively high rates of NO_3 reduction (34 ± 23 µmol N m^{-2} hr^{-1}) and NH_4 utilization (38 ± 18 µmol N m^{-2} hr^{-1}). Nitrogen fixation rates in outer-shelf reef sediments averaged 7.9 ± 3.7 µmol N m^{-2} hr^{-1}. Rates of NH_4 eflux from reef sediments (0.51 ± 0.64 µmol N m^{-2} hr^{-1}) and denitrification (1.56 ± 1.28 µmol N m^{-2} hr^{-1}) were considerably slower. Overall, a considerable proportion of the nitrogen fixed in reefal sand substrates is taken up by microbial populations in the sand and transformed further.

The major unknown benthic flux associated with coral reefs is the extent of denitrification occurring within reef sediments and the reef matrix following the deposition of particulate organic matter. While mineralization, nitrification and denitrification are known to occur in reef sediments, the magnitude of these processes at the shelfscale in the Great Barrier Reef is unknown.