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**NITROGEN FIXATION IN THE
MARINE ENVIRONMENT:
A LITERATURE REVIEW**



**DEPARTMENT OF CONSERVATION AND ENVIRONMENT
PERTH WESTERN AUSTRALIA**

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NITROGEN FIXATION IN THE MARINE ENVIRONMENT :

A Literature Review

S Creagh

DEPARTMENT OF CONSERVATION AND ENVIRONMENT

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INTRODUCTION

Recent research on the role of fixation of atmospheric nitrogen (N_2) in the oceans has centred on the accepted conclusion that nitrogen is the limiting nutrient for growth and productivity of marine plants (Beers et al. 1968; Thomas 1969; Goldner 1980; Ryther & Dunstan 1971; Webb et al. 1975; Wiebe et al. 1975; Capone & Taylor 1977; Mague et al. 1977; Bohlool & Wiebe 1978; Capone & Carpenter 1982). Dissolved nutrients are generally in low concentrations in surface waters of the open oceans and in waters adjacent to coral reefs (Mague & Holm-Hansen 1975; Webb et al. 1975; Capone et al. 1977; Potts & Whitton 1977; Goldner 1980). Although the total combined nitrogen (includes NH_4^+ , NO_3^- , NO_2^- and urea) in the oceans exceeds the requirements of phytoplankton alone by a factor of about 100, most total combined nitrogen is contained in deep waters far below the photic zone (Ryther & Dunstan 1971; Goldman et al. 1979; Walsh et al. 1981, Capone & Carpenter 1982).

Nitrogen:phosphorus (N:P) ratios in nutrient-poor waters are also characteristically low, <10:1, compared with the 16:1 ratio required for maximum growth of phytoplankton (Redfield 1958; Redfield et al. 1963; Smith & Atkinson 1984) and 30:1 ratio necessary for optimum growth of benthic plants (Atkinson & Smith 1983; Smith & Atkinson 1984). This indicates that nitrogen rather than phosphorus is the limiting nutrient, provided the actual quantities of nitrogen and phosphorus in the water column are not so small that both nutrients are limiting. Banse (1974), however, points out that low N:P ratios (e.g. 5:1) for phytoplankton may not be indicative of low relative

concentrations of nitrogen in the water column, owing to different rates of elemental cycling.

Further evidence of nitrogen limitation comes from observations of increased primary productivity on reefs, and in coastal regions subject to inputs of fertilisers and nitrogen-enriched waters from rivers and land runoff (Ryther & Dunstan 1971; Kinsey & Domm 1973).

In an environment where nitrogen is viewed as a limiting nutrient, biological N_2 - fixation can provide an important source of combined nitrogen for the nitrogen cycle. The contribution of biological N_2 - fixation to the productivity of the oceans, however, has not been determined (Stewart 1971; Fogg 1978), although estimates have been made by Capone & Carpenter (1982). This review of N_2 - fixation in the marine environment is intended to summarise the numerous and dispersed works in the literature. The principal source of information was Biological Abstracts.

BENTHIC AND NEARSHORE ENVIRONMENTS

Many studies have been carried out in the benthic environment of the deep sea (Hartwig 1976), estuarine sediments (Stewart 1965, 1967; Bohlool & Wiebe 1978; Lipschultz et al. 1979) and coastal sediments (Dahl 1974; Maruyama 1975; Burris 1976; Hartwig 1976; Capone et al. 1977; Potts & Whitton 1977; Wickstrom 1980), seagrasses (Goering & Parker 1972; McRoy & Goering 1974; Lipschultz et al. 1979; Capone & Taylor 1975, 1977, 1980; Smith & Hayasaka 1982; Capone 1983), coral reefs (Johannes et al. 1972; Dahl 1974; Mague & Holm-Hansen 1975; Webb et al. 1975; Wiebe et al. 1975; Burris 1976; Capone et al. 1977; Potts & Whitton 1977;

Goldner 1980), algal mats (Paling 1985), salt marshes (Valiela & Teal 1979; De Laune & Patrick 1980), and mangrove communities (Zuberer & Silver 1975; Gotto & Taylor 1976; Floredelis & Aspiras 1981; Boto 1982; Van der Valk & Attiwill 1984). Limited work has also been done on N_2 - fixation associated with bacteria (Maruyama et al. 1970) and floating diatom mats (Martinez et al. 1983).

Bohlool & Wiebe (1978), working on intertidal mud and sand flats, found blooms of Oscillatoria and Euglena contributed nearly 50% (73 kg N/ha/yr) of the estimated nitrogen input by biological fixation, although these blooms covered only 1% of the total surface of the sediments. Nitrogen fixation rates for Enteromorpha communities in the same area were about 4 kg N/ha/yr, whereas uncolonised sand and mud flats, and Zostera communities, showed very low nitrogen fixing activity (0.4 kg N/ha/yr).

Seagrass communities in temperate waters generally show low rates of N_2 - fixation. It has been estimated that biological N_2 - fixation, associated with the rhizosphere and phyllosphere of temperate zone Zostera marina meadows, supplies 3 to 8% of the total nitrogen demand (McRoy & Goering 1974; Capone 1983), whereas in tropical, Thalassia testudinum communities, N_2 - fixation may represent between 20 and 50% of the total nitrogen requirements (Patriquin 1972; Capone & Taylor 1975, 1977, 1980). The low fixation rates of temperate compared with tropical seagrass systems may result from the ready availability of nitrogen, in either the water column or sediments, of temperate waters (Lipschultz et al. 1979; Smith & Hayasaka 1982).

Guerinot et al. (1977) considered N_2 - fixation, by

micro-organisms associated with sea urchins feeding on algae and eelgrass (Zostera), to be significant; however, the extent to which the fixed nitrogen is used by the animals is not known.

Much interest in coral reef research has been generated by the apparent paradox of high productivity in characteristically, nutrient-poor tropical waters (Johannes et al. 1972; Mague & Holm-Hansen 1975; Webb et al. 1975; Capone et al. 1977; Goldner 1980). Nitrogen fixation is considered to be the main reason for the high productivity of reef communities. Burris (1976) estimated annual input of 6.8-30.6 kg N/ha/yr for the benthic blue-green alga Calothrix on the Great Barrier Reef, Australia. These results approximate those of Stewart (1967, 1971) who found 25 kg N/ha/yr (representing 41% of the mean nitrogen present per annum) to be fixed by benthic algae on temperate sublittoral fringes of rocky coasts.

On Enewetak (Eniwetok) Atoll in the Marshall Islands, rates of N_2 - fixation for blue-green algae show considerable variation: Mague & Holm-Hansen (1975) calculated an input of 0.2-4.0 kg N/ha/yr for Nostoc, whereas Wiebe et al. (1975) estimated a mean rate of 657 kg N/ha/yr for Calothrix, one of the highest rates reported for marine or terrestrial communities.

In mangrove communities, high rates of N_2 - fixation have been found to be associated with root tissues and soils. For example, Boto (1982) estimated an annual input of between 4 and 8.8 kg N/ha/yr for mangrove communities in North Queensland. From such a high rainfall area, loss by leaching, into adjacent coastal waters, may be substantial.

Salt marshes may lose as much as 1.295 kg N/ha/yr, in particulate form carried by tides, to surrounding coastal waters, (Valiela & Teal 1979). On a global scale, Capone & Carpenter (1982) suggest that coastal salt marshes, followed by coral reefs, may be the most important sites of N_2 - fixation in marine environments. Although coral reefs have similar N_2 - fixation rates to salt marshes these reefs cover a smaller overall area. One major problem with such large-scale estimates is the difficulty in determining areas accurately.

THE OPEN OCEANS

The blue-green Trichodesmium is the most widespread and conspicuous of planktonic algae in the open oceans, and it is considered to be the most likely organism to fix significant amounts of nitrogen (Mague et al. 1974; Fogg 1978; Capone & Carpenter 1982). Estimations show that Trichodesmium spp. have the potential to supply 2 to 30% of the average daily nitrogen requirement of phytoplankton in the euphotic zones of the Atlantic and North Pacific Oceans (reviewed by Creagh 1985). Richelia intracellularis, a N_2 - fixing blue-green alga endophytic in diatoms of the genus Rhizosolenia, is also believed to contribute to nitrogen input in the North Pacific gyre (Mague et al. 1977).

Although fixation by such algae may supply less than 2 to 5% of the total nitrogen demand of the euphotic zones, the input often occurs seasonally at times of stratification and isolation of upper mixed water layers, from deeper waters which have higher nutrient levels. At these times nitrogen input from potentially more important sources, such as denitrification and regeneration of ionic ammonium in sediments, would be

negligible (Mague et al. 1977). Smith & Atkinson (1984) believe that if nitrogen is limiting in a system where phosphorus is not, then nitrogen fixers could drive the system impoverished in nitrogen to a state of phosphorus limitation.

Although marine N_2 - fixation represents an estimated one fifth of that on land, and half of that produced from industrial synthesis of gaseous ammonia, it can supply only 0.3% of the total nitrogen demand of phytoplankton. Of this, 0.29% is supplied by benthic N_2 - fixation (Capone & Carpenter 1982). These estimates, however, have been calculated on a global basis, and therefore should be used with caution.

The estimate that total de novo nitrogen input from all sources, including fixation, supplies only 1% of total phytoplankton demand, would indicate that the bulk of the nitrogen requirement is met by rapid recycling of combined nitrogen within the euphotic zone, and from upwelling of deeper waters (Goldman et al. 1979; Walsh et al. 1981; Capone & Carpenter 1982).

Thus, the relative importance of biological N_2 - fixation in marine environments appears to be largely dependent on the scale of the system under consideration. For global marine nitrogen budgets, input from N_2 - fixation is of less importance than in smaller, local areas where nitrogen fixers may contribute significant amounts of nitrogen at certain times of the year. Although fixation in coastal regions may be high, it is unlikely to affect combined nitrogen levels in the upper mixed layers of deep oceanic waters (Mague et al. 1974).

McCarthy (1980) notes an additional problem of scale

with respect to the "something from nothing" paradox evident in coral reef systems. The suggestion here is that plants may respond to minute concentrations of nutrients (particularly ammonium, urea and amino acids), but conventional analytical techniques lack the resolution required to detect such nutrient levels (Allen 1977; Eppley et al. 1977). Consequently, for coral reefs at least, the problem may be under-estimation of available nitrogen. The patchy distribution of nutrients in space and time, and the rapid recycling and turnover rates of preferentially used compounds such as ammonia, urea and amino acids, also lead to further difficulties in estimating nitrogen available in the water column (McCarthy 1980).

CONCLUSION

The underlying question in the majority of recent works on N_2 - fixation in the oceans, and a question stated most clearly by Capone & Carpenter (1982), appears to be: "If de novo input through nitrogen fixation supplies very little of the total nitrogen demand in a system where nitrogen is assumed limiting, why are nitrogen-fixing phytoplankters not more prevalent?". The conclusion is that some other parameter, such as light, temperature, micronutrients or grazing limits phytoplankton growth or productivity.

It would seem more likely, however, that interactions between all such parameters, including nitrogen availability, are responsible for the control of growth and biomass. To assume a priori that nitrogen is the only major limiting parameter, given the wide range of environmental conditions likely to be encountered in the oceans, is unrealistic. By definition, an ecosystem consists of a complex of integrated

biological, chemical and physical parameters. Large blooms of marine N_2 - fixing phytoplankton are sporadic in space and time.² When they do occur controlling factors may be near-optimal for growth and productivity. In nutrient-impooverished waters, nitrogen fixers may be limited by the availability of phosphorus.

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