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**REVIEW OF LITERATURE CONCERNING
BLUE-GREEN ALGAE OF THE
GENUS *Trichodesmium***



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

Bulletin 197 July 1985

REVIEW OF LITERATURE CONCERNING BLUE-GREEN
ALGAE OF THE GENUS Trichodesmium
(Order Nostocales : Family Oscillatoriaceae)

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ISBN 0 7309 0402 4

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INTRODUCTION

This review is part of a major study being undertaken by the Department of Conservation and Environment, of primary production in the tropical, coastal marine communities of the Dampier Archipelago (20⁰40'S; 116⁰40'E).

Nitrogen has been viewed as a limiting nutrient in the marine environment (Ryther & Dunstan 1971; Mague et al. 1974), and biological nitrogen (N₂) fixation could be an important source of combined nitrogen for the nitrogen cycle. Trichodesmium, the most widespread and conspicuous of the planktonic blue-green algae, (Plate 1) is most likely to contribute significant amounts of nitrogen to local areas (Mague et al. 1974; Fogg 1978; Capone & Carpenter 1982).

Trichodesmium is widespread in the Dampier Archipelago and elsewhere in Western Australian coastal waters (Table 2 p22), and this review was compiled to give some perspective of the contribution of Trichodesmium to N₂-fixation.

THE GENUS TRICHODESMIUM

The marine genus, Trichodesmium, is closely related to the freshwater genus, Oscillatoria. There have been suggestions that the two genera should be classified as one, Oscillatoria (Drouet 1968; Carpenter & Price 1976); however, some authors prefer to retain the genus name Trichodesmium as it has historical precedence and the taxonomic problems with this genus, and most other blue-green algae, are yet to be resolved (Fogg et al. 1973; Borstad 1978, 1982). At present, four Trichodesmium species are recognised.

Trichodesmium is a planktonic, filamentous alga which, although it lacks heterocysts, is able to fix atmospheric nitrogen under aerobic conditions, and to a lesser degree anaerobically (Goering et al. 1966; Taylor et al. 1973; Pearson et al. 1979; Ohki & Fujita 1982). It is a bloom-forming genus (Desikachary 1959; Bowman & Lancaster 1965). During blooms red-pigmented trichomes (filaments) aggregate into rafts or bundles, each bundle with about 6-25 trichomes (Fogg et al. 1973 Plate 1). These bundles float to the surface where they are commonly seen in long windrows which may vary from a metre to many kilometres in length (Fogg et al. 1973, Plate 1). Wood (1965) records large Trichodesmium blooms, covering areas of up to 52 000km² off the Western Australian coast. Cell densities of up to 300 x 10⁶/m³ have been recorded in the Carribean Sea (Carpenter & Price 1977). These blooms are commonly known as "sea sawdust" or "red tides", though the colour of the blooms may vary from red to brown, green or yellow (Smith 1972).

DISTRIBUTION

Trichodesmium is found usually at depths of 0-200 m in open sea areas poor in nutrients. Maximum cell concentrations are generally at the surface or at depths of 15 to 25 m (Kovaleva 1976; Carpenter & Price 1977; McCarthy & Carpenter 1979). Such oligotrophy is unusual in a marine blue-green alga: the only other species known to occur in large quantities in oceanic waters is the unicellular Synechococcus sp. (Waterbury et al. 1979). The majority of blue-greens occur in littoral or coastal areas with higher nutrient levels (Fogg et al. 1973; Ohki & Fujita 1982).

The genus is widely distributed in tropical and sub-tropical waters of the Indian, Pacific and Atlantic Oceans. Desikachary (1959) described three species from the Indian Ocean:

Trichodesmium erythraeum, T. thiebautii, and T. hildenbrandii.

Wood (1965) described a fourth species, Trichodesmium rubescens.

Trichodesmium is known from the Philippines, East Indian Archipelago, east coast of South America, the Red Sea (which may have received the name from Trichodesmium blooms) and the Arabian Sea (De Toni 1864; Ballantine & Abbott 1957; Desikachary 1959; Bowman & Lancaster 1965; Wood 1965; Ramamurthy 1970; Chellam & Alagaraswami 1978; McCarthy & Carpenter 1979; Aleem 1980). It has also been recorded in the East China Sea and off the coast of Japan (Nagasawa & Marumo 1967, Marumo & Asaoka 1974a, b). In

summer, the alga extends into temperate regions, extending northward from the Sargasso Sea to the continental shelf of North America (Fogg et al. 1973) and off the south coast of Ireland (Farran 1932).

Trichodesmium rubescens has been recorded off the south coast of New Zealand and even in Antarctic waters, although it is not known whether the alga is metabolically active at these high latitudes (Wood 1965).

In Australia Trichodesmium blooms occur off the New South Wales coast (May 1978) and Great Barrier Reef (Revelante & Gilmartin 1982; Revelante et al. 1982). In Western Australia blooms have been recorded during autumn and winter months (April-August) at Cottesloe, off Rottnest Island and Cockburn Sound in the south west (Smith 1972; Kenneally 1973) and in summer (November-March) in waters off the Dampier Archipelago in the northwest of the State (Table 2, p22).

ENVIRONMENTAL FACTORS AND BLOOM FORMATIONS

The environmental factors which initiate bloom formation are not known, but it is likely that many factors contribute to the phenomenon.

Nutrients

Phytoplankton biomass of the open oceans is low and is believed to be limited by the availability of plant

nutrients (Borstad 1978). In areas where the physical environment is relatively stable and permanent stratification of the water column occurs, large spatial or temporal fluctuations in phytoplankton abundance and productivity are unusual (Borstad 1978, 1982). Even in these areas, however, relatively large fluctuations in abundance of Trichodesmium have been noted, with blooms occurring when water is thermally stratified, nutrient impoverished ($1.5-3.1 \mu\text{gP/L}$ and $1.4-7.0 \mu\text{gN/L}$), and when other phytoplankton are at their minimum seasonal abundance (Steven et al. 1970; Marumo & Nagasawa 1976; Kimor Golandsky 1977; Borstad 1982; Revelante & Gilmartin 1982).

Steven & Glombitza (1972) suggested such fluctuations may result from rapid growth of "seed populations" in deeper nutrient-rich waters, with decline in surface populations occurring when cellular reserves are depleted. Conversely, Carpenter & Price (1976) suggested blooms occur in calm, sunny weather when nitrogen fixation can occur unhindered. This suggestion was based on the assumption that N_2 -fixation provides nearly all the alga's nitrogen requirement, and that this process is adversely affected by sea turbulence. In this instance the growth and decay cycle of Trichodesmium would be determined by physical factors affecting N_2 uptake. Borstad (1982), however, found no direct relationship between sunny weather and bloom formation, and suggested lateral

transport may determine the timing of bloom events: that is, blooms could be patches advected in low salinity, neritic surface water from productive regions.

There is recent evidence that Trichodesmium requires considerably higher concentrations of ammonium, nitrate and phosphate than do other phytoplankters, and that it is not able to metabolise efficiently the usual ambient concentrations of these nutrients (Carpenter & McCarthy 1975; Wade & Matsamoto 1975; Carpenter & Price 1976; McCarthy & Carpenter 1979; Borstad 1982). For example, half saturation constants (K_s) for ammonium uptake ($6.7 \mu\text{g-atoms NH}_4^+-\text{N/L}$) are nearly an order of magnitude greater than K_s values reported for other oceanic phytoplankters (Eppley et al. 1969; Carpenter & Guillard 1971; Carpenter & McCarthy 1975). Evidence obtained for cellular-N doubling times also indicates that Trichodesmium cannot take up nitrogen rapidly enough, at concentrations found in the open ocean, to sustain rapid growth (Carpenter & McCarthy 1975; McCarthy & Carpenter 1979). Assuming blooms are indeed the result of rapid growth, such growth is most likely initiated in deeper waters where nutrients are available, or in coastal areas subject to land runoff or local upwelling of nutrient rich water. Trichodesmium blooms from these regions would then be carried by ocean currents (Borstad 1982; Isouchi 1982) to nutrient-poor areas where they are sustained by their ability to fix atmospheric nitrogen.

An alternative explanation is that stimulation of N_2 -fixation may lead to blooms, although how it is stimulated is unknown (Carpenter & McCarthy 1975). Reports of large and actively N_2 -fixing blooms in areas with slightly increased phosphate concentrations (Carpenter & Price 1976; 1977) may be because that N_2 -fixation is limited by ATP and metabolites from photosynthesis, which in turn is limited by nutrient supply (Borstad 1982).

Temperature and Light

Trichodesmium has optimum growth at 22-29°C and 33-36‰ salinity (Carpenter & Price 1977; Goldman 1977; Kimor & Golandsky 1977). For example, in the Gulf of Eilat, Israel, blooms occur when upper layer temperatures of sea water begin to decline in November, or when they begin to rise in June (Kimor & Golandsky 1977).

Carpenter & McCarthy (1975) found little effect of light on the uptake of ammonium, nitrate or urea at concentrations of 2 μ gN/L.

Severe photoinhibition at sea surface irradiance, probably caused by photorespiration and photochemical inhibition of electron transport, may reduce N_2 -fixation rates: N_2 -fixation and C-assimilation processes compete for energy and reductants generated under the effects of light (Mague et al. 1977; Foy & Smith 1980; Li et al. 1980).

Rates of photosynthesis are further inhibited at high light intensities of 600-700 $\mu\text{E}/\text{m}^2/\text{h}$ (McCarthy & Carpenter 1979). Photoinhibition may thus explain apparent dependence of acetylene reduction (and hence N_2 -fixation) on light intensities (Taylor et al. 1973; Saino & Hattori 1978).

Surface blooms, however, do occur when there is little or no cloud cover. Trichodesmium may be able to regulate buoyancy using gas vesicles to avoid prolonged exposure at the surface (McCarthy & Carpenter 1979).

Oxygen and Sea Turbulence

Trichodesmium, like most members of the Oscillatoriaceae, does not possess heterocysts (thick-walled cells) that protect nitrogenase from oxygen inactivation (Fogg 1974). The mechanism for protecting nitrogenase is not known.

Fogg (1974) suggested that oxygen concentrations may be decreased in the middle of the trichome bundles to allow N_2 -fixation to take place. This hypothesis has been supported by Carpenter & Price (1976) using ^{14}C autoradiography to demonstrate the presence of $^{14}\text{CO}_2$ incorporation in differentiated (highly pigmented) cells located in the centre of the colony. Differentiated cells may not evolve O_2 in photosynthesis and thus may function as heterocysts in N_2 -fixation. Further evidence, for the

segregation of photosynthesis and N_2 -fixing processes along trichomes, is presented by Bryceson & Fay (1981) who found morphological differentiation of trichomes into granulated and non-granulated regions according to the presence or absence of carboxysomes (polyhedral bodies). Reducing conditions (tetrazolium reduction) were also very evident in the non-granulated regions. Saino & Hattori (1982) suggested that uptake of hydrogenase from hydrogen metabolism protects the nitrogenase by removing oxygen.

Saino & Hattori (1982) report that when central cells are exposed to oxygen after disruption of colonies, N_2 -fixation drops sharply even though individual trichomes remain intact. Thus, in the sea, turbulence from wave action which separates trichomes and allows oxygen to enter will result in decreased nitrogenase activity. If bloom formation is related to N_2 -fixation rates, maximum blooms may be expected to occur at the sea surface in calm weather, or, with slightly increased wave turbulence, at depths of 15 to 20 m (Carpenter & Price 1976). Bryceson & Fay (1981) noted an inverse relationship between size of trichome bundles and wind speed: the latter factor determines wave turbulence. Maximum bundle size was also observed to increase with maximum nitrogenase activity.

Giberellic Acid and Vitamin B₁₂

Ramamurthy (1972) found giberellic acid stimulated growth of a Trichodesmium sp. in culture medium; however, the levels used were far in excess of levels found in natural conditions.

Vitamin B₁₂ is required for maintenance of Trichodesmium in the laboratory (Ohki & Fujita 1982) and under natural conditions it is produced in abundance by estuarine bacteria (Fogg et al. 1973). It may be that the numerous bacterial populations observed to be associated with Trichodesium bundles (Taylor et al. 1973; Carpenter & McCarthy 1975; Bryceson & Fay 1981) supply this requirement in the open oceans. In the marine environment, vitamin B₁₂ is known to be excreted by a large range of phytoplankters (Carlucci & Bowes 1970; Aaronson et al. 1971).

Discussion

Although Trichodesmium has been viewed as a bloom-forming species, the lack of understanding of causal factors for bloom formations and the apparent paradox of excessive growth in nutrient-poor marine waters, has given support to an alternative hypothesis concerning "bloom" formation. This hypothesis suggests the putative Trichodesmium blooms are not the result of rapid growth over a short period, but

rather are the result of accumulations of algae along frontal systems owing to physical oceanographic processes (Borowitzka personal communication). This process could be similar to "red-tide" formation by toxic dinoflagellates, Gymnodinium or Gonyaulax, where blooms are viewed as the result of interactions between natural population growth and a concentration both vertically and horizontally, through buoyancy and converging currents (Devassy, 1979).

In conclusion increased population densities of Trichodesmium are thus associated with numerous environmental factors: low wind speed, minimal cloud cover, low nutrient levels and warm ambient water temperatures (Taylor et al. 1973; Mague et al. 1977; Eleuterius et al. 1981). Wyatt (1975) also suggested that any number of integrated environmental factors which allow algae to selectively concentrate in upper regions of the eutrophic zone, by decreasing vertical mixing rates through the water column, will result in increased average reproduction rates and thus increased population densities. Such factors are likely to include heavy rainfall, influx of estuarine waters, the meeting of dissimilar water masses, and calm, sunny weather.

GAS VACUOLES

Trichodesmium, like freshwater planktonic blue-green algae, possesses gas vacuoles. The common occurrence of these gas vacuoles suggest a mechanism by which Trichodesmium can maintain itself at optimum depth in the water column (Stevens and Van Baalen 1970). Cellular regulation of buoyancy may enable the alga to obtain nutrients from deeper waters (Walsby 1977, 1978; McCarthy & Carpenter 1979). The difficulty encountered in culturing Trichodesmium suggests that surface blooms are largely moribund, with actively growing filaments containing vacuoles below the surface maintaining the bloom (Fogg et al. 1973).

Field and laboratory studies indicate that gas vacuolation (RGV) and buoyancy of Trichodesmium are controlled by light and limiting nutrients, that affect the relative rates of photosynthesis, growth and gas vesicle synthesis (Carpenter & Walsby 1979; Klemer et al. 1982). Klemer et al. (1982), working with the freshwater species Oscillatoria rubescens, found that limiting concentrations of nitrogen resulted in decreased RGV, while decreased levels of inorganic carbon resulted in increased RGV. Similarly, if nitrogen was not limiting, decreased light intensity increase RGV. If Trichodesmium responds in a similar manner to high light intensities and nutrient depletion near the surface, subsurface blooms may be expected to occur when nitrogen is limiting, and surface blooms when inorganic carbon is limiting.

As nitrogen decreases in surface layers, the greater pressure of the cells would increase as photosynthate is accumulated rather than assimilated, leading to the collapse of pressure sensitive gas vesicles. Protein required for gas vesicle synthesis also appears to decrease with decreasing levels of ambient nitrogen (Klemer et al. 1982). Conversely, low light and decreased inorganic carbon favour relative protein synthesis (Carpenter & Walsby 1979; Klemer et al. 1982).

Two other functions have also been attributed to Trichodesmium gas vesicles: gas storage (Kolkwitz 1928; Canabaeus 1929), and light shielding (Fogg et al. 1973).

It is unlikely that the vesicles are used for gas storage as they are readily permeable to gas; hence, this early suggestion was discounted in subsequent papers (Fogg et al. 1973; Carpenter & Walsby 1979). Whether gas vesicles can function as a light shielding mechanism remains undetermined: it is not known whether the apparent scattering of light caused by the vesicles can produce significant shielding, or whether it merely redirects the light (Fogg et al. 1973).

PIGMENTS

Feldman (1932) considered Trichodesmium to be a bottom dwelling form that occasionally floats to the surface, and hence may be

recorded in the plankton. The red pigmentation of the trichomes may thus be explained in terms of chromatic adaptation, although in some areas Trichodesmium has been recorded from such depths in the waterbody as to cast doubt on the suggestion that it is predominantly benthic (Fogg et al. 1973).

The red pigmentation results primarily from the phycobilin, 0-phycoerythrin, which shows peak absorption activities at 500, 547 and 565 nm wavelengths (Fujita & Shimura 1974; Shimura & Fujita 1975). Colour variations observed in the field are the result of varying environmental conditions causing changes in the relative proportions of component pigments: chlorophyll a, B-carotene, zanthophylls and phycobilins (c-phyocyanin and c-phycoerythrin) (Smith 1972).

In Western Australia, Trichodesmium blooms off the south west coast are generally coloured deep rusty-red, while those off the north west coast are characteristically cream (Plate 1).

EFFECTS OF BLOOMS ON MARINE FAUNA

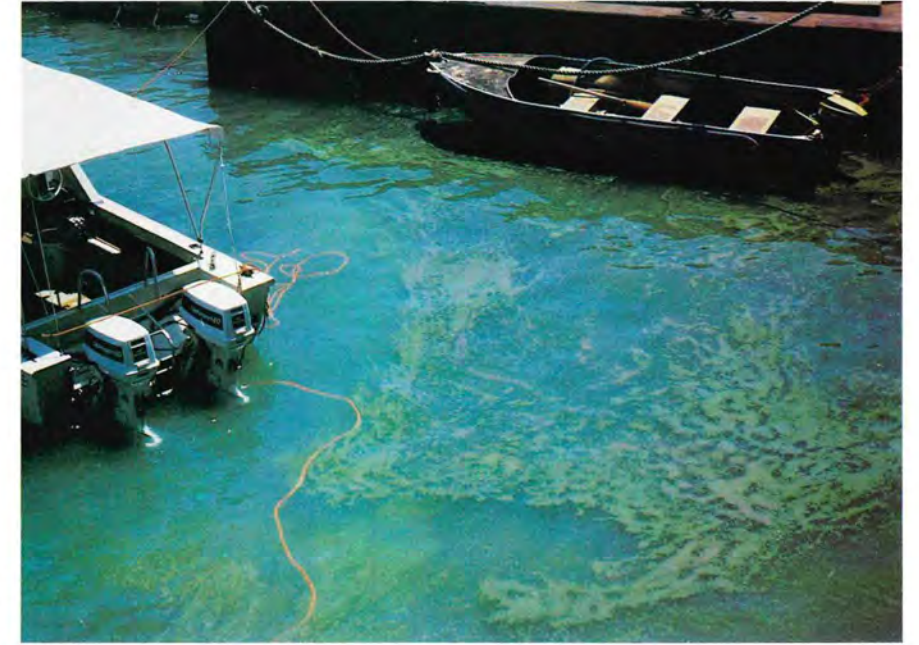
There is much information available on the effects of Trichodesmium blooms in marine waters (Chidambaram 1942; Chidambaram & Mukundan Unny 1944; Nagabhushanum 1967; Daniel et al. 1978). The blooms in general are non-toxic, and Ramamurthy (1970) reported no ill effects after "accidental drenching" in a

PLATE 1.
TRICHODESMIUM BLOOMS OFF WESTERN AUSTRALIA
 AND QUEENSLAND COASTS



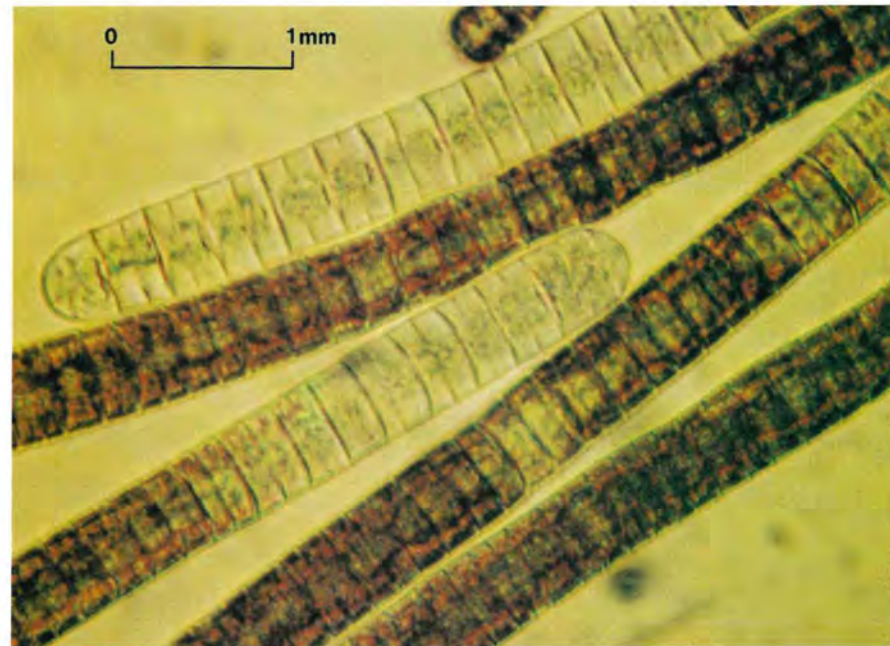
R.G. Chittleborough

Trichodesmium bloom accumulated on the shore immediately north of No-Name Bay, Dampier Archipelago, 6 November, 1980. Dead and dying fish were seen in the bay at the time.



J.R. Ottaway

Trichodesmium bloom at Abbot Point, Queensland, 23 October, 1982. Extensive blooms were common between Mackay and Townsville from November to March in 1981, 1982 and 1983.



Photomicrograph of Trichodesmium trichomes. Sample taken from shallow water on the shore of Withnell Bay, Dampier Archipelago, 25 November, 1984.

S. Creagh



J.R. Ottaway

Trichodesmium bloom washed up on the beach and after decomposing for several days had formed thick, black, tar-like accumulations, 24 October, 1982. This phenomenon, at Abbot Point, Queensland, was often coincident with large numbers of dead fish (> 500/km) washing ashore.



J.R. Ottaway

Trichodesmium bloom near Gidley Island, Mermaid Sound, 24 November, 1984. Subsequent microscopic examination of trichomes, collected from the surface water, indicated that many were moribund. Trichodesmium blooms are very common and widespread in Mermaid Sound during summer months.

Aerial photograph of Trichodesmium windrows taken from 900m altitude near Cape Preston (55km southwest of Dampier), 2 April, 1985. Northeast Regnard Island is in the background. Individual windrows may reach several kilometres in length, and collectively cover many hundreds of square kilometres.



C. Nicholson

bloom of the alga. Deaths of fish and planktonic organisms associated with heavy blooms are most likely caused by decreased oxygen levels and clogging of gills (Qasim 1970; Fogg et al. 1973; Chellam & Alagaraswami 1978). Adult fish may actively avoid blooms because of bloom density and the 'offensive' odour (Qasim 1970). In some circumstances the blooms appear to provide an important food source for some fish; for example, sardines, mackerel (Chacko 1942; Ramamurthy 1970) and milkfish (Chanos chanos) larvae (Wood 1965).

Numerous invertebrate species are also found in close association with Trichodesmium blooms. The harpacticoid copepod, Macrosetella gracilis, present in Trichodesmium thiebautii bundles can ingest between 90-125% body weight carbon/day feeding on Trichodesmium (Calef & Grice 1966; Roman 1978). M. gracilis thus provides a pathway by which carbon and nitrogen from the blue-green algae are incorporated into the food web via secondary production (Roman 1978). There are numerous reports of tintinnids (Marumo 1975), colonial hydroids (Geiselman 1977; Borstad & Brinckman-Voss 1979) and amoebae (Anderson 1977; Nair et al. 1980) found in tightly woven trichomes of pelagic Trichodesmium colonies. Madhupratap et al. (1980) also noted the phenomenon of tunicates in the Bay of Bengal in association with Trichodesmium erythraeum blooms. In general, spherical Trichodesmium colonies tend to contain greater numbers of micro-organisms, such as bacteria, fungi, ciliates and diatoms, than do bundle colonies (Ohki & Fujita 1982).

CULTURING TRICHODESMIUM SPP

Evidence of the ability of Trichodesmium to fix atmospheric nitrogen is considered inconclusive by some authors. Until the algae can be grown and tested in axenic culture, this doubt is likely to persist, but, to date, all attempts at culturing have been unsuccessful (see Bryceson & Fay 1981; Ohki & Fujita 1982).

Ramamurthy (1972) was the first to report successful axenic culture of Trichodesmium erythraeum in modified Erdschreiber medium; however, the antibiotic levels used may have caused genetic mutation, and it has not been possible to repeat the experiment successfully (Ohki & Fujita 1982). Carpenter & McCarthy (1975) and Ohki & Fujita (1982) succeeded in keeping bundle colonies of T. thiebautii alive in the "f"-medium of Guillard & Ryther (1962) for over 100 days, but failed to obtain active growth.

Difficulties encountered in culturing this alga may be caused by one or more of the following: very specific vitamin B₁₂ requirements; grazing by living contaminants such as M. gracilis; the fact that it is stable only at low nutrient concentrations; reagents, that are used as nutrients, being toxic (Ohki & Fujita 1982). Such problems may be further exacerbated by the ready lysis of the alga. Furthermore surface blooms from which algae are collected for laboratory culture may be largely moribund. The alga lyses lengthwise as a result of bursting gas

as a result of bursting gas vacuoles, which occupy most of the cell in surface filaments (Borowitzka personal communication), and also as a result of junctions between cross walls and longitudinal walls of the filaments.

IMPORTANCE OF TRICHODESMIUM TO THE HYDROGEN CYCLE

Work by Scranton (1983) indicates that Oscillatoria (Trichodesmium) thiebautii produces significant amounts of hydrogen and has the potential to maintain hydrogen supersaturation typically observed in the open oceans. Preliminary results from this work also suggest hydrogen production and nitrogen fixation may not be strongly coupled.

NITROGEN FIXATION

Dugdale et al. (1961) first reported nitrogen fixation to be associated with Trichodesmium, in the Sargasso Sea. Subsequent work has substantiated this report (Dugdale et al. 1964; Goering et al. 1966; Mague et al. 1974; Carpenter & McCarthy 1975; Carpenter & Price 1976, 1977; Mague et al. 1977; Saino & Hattori 1978). Bryceson & Fay (1981) presented evidence, suggesting $^{15}\text{N}_2$ incorporation by T. erythraeum rather than by any associated micro-organisms.

Comparisons of estimated N_2 -fixation rates given in the literature, are made difficult by the wide variety of units used

to express the rates; however, earlier works suggested N_2 -fixation by Trichodesmium constitutes an important component of the nitrogen supply for nutrition of oceanic phytoplankton (Dugdale et al. 1964; Goering et al. 1966; Taylor et al. 1973). Goering et al. (1966) using the ^{15}N technique, found maximum N_2 -fixation rates per volume for Trichodesmium in the Atlantic to be $0.32 \mu\text{gN}/\text{m}^3/\text{h}$. Rates of NH_3 and NO_3^- uptake were also found to be greater than those for N_2 uptake. Acetylene reduction values for the Caribbean Sea indicate that this alga may contribute major inputs of nitrogen in the region (Carpenter & Price 1977; Li et al. 1980). Maximum N_2 -fixation rates occurred at a depth of 20 m, with 25% surface light intensity and decreased turbidity. Trichodesmium was found to constitute 60% of total chlorophyll a and 20% of primary production values recorded in the upper 50 m, with a maximum range for nitrogen input of $54\text{--}179 \mu\text{gN}/\text{m}^2/\text{h}$ (representing 8–27% of the daily nitrogen demand of phytoplankton in the euphotic zone). Average fixation rates per volume in the Caribbean Sea were estimated to be $7.0 \mu\text{gN}/\text{m}^3/\text{h}$ at 10–15 m, decreasing to only 2.3% of this rate at 75 m (Carpenter & Price 1977).

In the Sargasso Sea, however, with maximum population density similarly occurring at 25 m depth, average nitrogen input from Trichodesmium N_2 -fixation has been estimated at only $2 \mu\text{gN}/\text{m}^2/\text{h}$ (maximum rate $\approx 12 \mu\text{gN}/\text{m}^2/\text{h}$) with average N_2 -fixation rates per volume of $0.1 \mu\text{gN}/\text{m}^3/\text{h}$ (maximum rate $\approx 0.64 \mu\text{gN}/\text{m}^3/\text{h}$) (Carpenter & McCarthy 1975). Low rates for the Sargasso Sea were also recorded by Carpenter & Price (1977).

Carpenter & McCarthy (1975) estimate that the rate of incorporation of nitrogen into the first trophic level through phytoplankton uptake of NO_3^- and NH_3 is greater by a factor of 2 000 than the rate of N_2 -fixation by T. thiebautii.

Thus, on a small scale, N_2 -fixation by Trichodesmium may be of considerable significance to the nitrogen budget of an ecosystem; however, in broader oceanic terms, at least for the central North Pacific and western Sargasso Sea, it is a negligible component of nitrogenous nutrition for phytoplankton (Mague et al. 1974, 1977; Carpenter & McCarthy 1975; McCarthy & Carpenter 1979).

The wide variations in N_2 -fixation rates recorded in the literature may be attributed, in part, to genetic differences in growth phases of Trichodesmium cultures and to diel variation. Fixation rates characteristically show a mid-day depression followed by an increase later in the afternoon (Stewart et al. 1971; Mague et al. 1977; Saino & Hattori 1978; Bryceson & Fay 1981). Differences in techniques employed to measure fixation rates may also add to the discrepancies; e.g. in situ acetylene reduction assays carried out under argon atmospheres yield higher estimates for nitrogen fixation rates than artificial air mixtures, probably because of increased oxygen partial pressures on the seabed (Bunt et al. 1970).

TRICHODESMIUM IN THE DAMPIER ARCHIPELAGO

Is Trichodesmium significant in the nitrogen budget of the Dampier Archipelago? Blooms of varying density and size are frequently observed in this area during summer months (see Tables 1 and 2).

TABLE 1. Approximate density measurement and bundle counts of Trichodesmium blooms in the Dampier Archipelago, 25 November 1984. Weights are after drying collections over silica gel for >2 days at $\approx 25^{\circ}\text{C}$.

BLOOM DESCRIPTION	BUNDLE COUNT ($\times 10^6/\text{L}$)	DENSITY (g dry wt/L)
individual trichomes, bloom just visible in water	0.12	0.064
forming windrows clearly visible	2.93	0.542
dense bloom in shallow (0.5 m) water	38.90	7.211

Before the ecological importance of N_2 -fixation to primary production can be estimated, the following must be known:

- (a) the extent and biomass of Trichodesmium blooms with respect to total phytoplankton biomass;
- (b) the frequency of occurrence of Trichodesmium blooms;
- (c) the nitrogen turnover in the euphotic zone;

- (d) the input of nitrogen into the system from sources other than N_2 -fixation by Trichodesmium; e.g. from land runoff
- (e) the loss of nitrogen through sedimentation, burial, denitrification, and grazing; and
- (f) the average N_2 -fixation rates of Trichodesmium in the Dampier Archipelago.

It is, however, possible to make gross estimates of nitrogen budgets from available literature. In Mermaid Sound, for example, if a relatively high, 24-hour average fixation rate, e.g. $108 \mu\text{gN}/\text{m}^2/\text{h}$ is assumed to occur throughout a euphotic zone 10 m deep, over three months of the year, then, for a bloom covering most of the $162 \times 10^6 \text{ m}^2$ Mermaid Sound, the upper limit for annual nitrogen input into the Sound may be estimated at $39 \times 10^3 \text{ kg}$ nitrogen per year. Thus, for a carbon demand of $110 \text{ mg C}/\text{m}^2/\text{d}$ (Carpenter & Price 1977) and C:N ratio of 5.8:1 (average based on values from Fogg 1978), representing a phytoplankton nitrogen demand of about $19 \text{ mg N}/\text{m}^2/\text{d}$, N_2 -fixation by Trichodesmium has the potential to contribute 14% of the total phytoplankton nitrogen demand. However, if a high carbon demand of $477 \text{ mg C}/\text{m}^2/\text{d}$ over an average 11 m depth (Revelante & Gilmartin 1982) is assumed, N_2 -fixation by Trichodesmium represents only 3.2% of the total nitrogen demand in the euphotic zone.

TABLE 2. Observations of *Trichodesmium* blooms in the Dampier Archipelago and elsewhere along the coast of Western Australia

DATE	LOCATION	BLOOM DESCRIPTION	OBSERVER
04.11.80-06.11.80	Withnell Bay; Noname Bay (Dampier Archipelago)	Dense windrows to extremely dense (yellow-green) blooms	R.G. Chittleborough
31.03.84	Mermaid Sound (Dampier Archipelago)	Just visible near Conzinc Is and Noname Rocks, Dampier Archipelago (pale brown bloom)	J.R. Ottaway
30.10.84-06.11.84	200 m south of Withnell Bay	Very dense, (milky bloom) about 100-200 m wide, extending along coast	D.A. Mills
13.11.84	Port Hedland to Karratha	Relatively dense, almost continuous bloom along this entire section of coast	C.J. Simpson
14.11.84-15.11.84	Mermaid Sound	Scattered blooms	C.J. Simpson
22.11.84	Mermaid Sound to at least North Rankin A gas platform	Dense windrows, each many kilometres in length, from coast to 140 km seawards	A. Chegwiddden
24.11.84	Mermaid Sound	Visible, occasional small, high density (brown) windrows; Gidley to East Lewis Island	J.R. Ottaway
25.11.84	Mermaid Sound	Extremely dense (yellow brown) bloom along east shore (water < 1 m depth) of Withnell Bay	J.R. Ottaway
27.03.85	Ledge Point, \approx 35 km east of Albany	0.5 km offshore, low to moderate density; windrows covering about 1 km ² area	J.R. Ottaway
27.03.85	Cape Vancouver, \approx 50 km east of Albany	Nearshore windrows: low density, covering about 0.25 km ² area	J.R. Ottaway
02.04.85	Very widespread between Reynard Is, Eaglehawk Is and Cape Preston	Dense windrows clearly visible from 900 m altitude	C.J. Nicholson
15.04.85-17.04.85	5 km west of Marmion Beach, Perth	Low density bloom with scattered bundles, windrows 400-500 m wide perpendicular to coast	S. Creagh
17.04.85	5 km west of Sorrento Beach, Perth	Dense, narrow windrows (about 50 m wide) extending along coast	S. Creagh

Thus, such literature-based estimates may well result in either marked overestimates or underestimates of the importance of N₂-fixation by Trichodesmium. It is also difficult to find values for fixation rates that have been measured at similar latitudes under similar conditions to those occurring in the Dampier Archipelago.

In situ measurements of N₂-fixation rates may yield additional information concerning the Dampier Archipelago ecosystem. For example, unusually high N₂-fixation rates in the Caribbean Sea served to emphasise the importance of phosphorus input into the area via the Gulf Stream (Carpenter & Price 1977).

SUMMARY AND CONCLUSIONS

- (1) Trichodesmium spp. are marine, planktonic, blue-green alga widely distributed throughout the tropical and subtropical waters of the world's oceans.
- (2) The known species are thermosensitive, and there are numerous, environmental factors likely to be involved in bloom formation, e.g. light, turbidity, wind, and nutrient availability. Generally, maximum bloom densities are observed between 0 and 25 m depth, under calm, sunny weather conditions. Gas vacuoles may provide a mechanism by which Trichodesmium maintains itself at optimum depths in the water column.

- (3) According to the literature surveyed, blooms seem to be non-toxic. Associated death of marine organisms is probably due to lowered oxygen concentrations and clogging of respiratory structures. Under some conditions Trichodesmium blooms may provide an important source of food for a variety of invertebrates and fish.
- (4) Trichodesmium, although it lacks heterocysts, is capable of N_2 -fixation. The mechanism may be the segregation of photosynthetic and N_2 -fixing processes in differentiated cells along trichomes.
- (5) Estimates of the relative contribution of Trichodesmium to nitrogen budgets, in marine environments, range from negligible to 27% of the total nitrogen demand in the euphotic zone. While Trichodesmium blooms occur frequently in the Dampier Archipelago, it is impossible to make any conclusive statements on the importance of Trichodesmium in the nitrogen cycle until detailed measurements of density and N_2 -fixing activity have been made.

ACKNOWLEDGEMENTS

Dr J.R. Ottaway (DCE), Dr R.G. Chittleborough (DCE) and Dr M.A. Borowitzka (Murdoch University) constructively criticised various drafts of the manuscript and provided unpublished data or observations. Additional data and photographs were provided by Dr D.A. Mills (DCE), Mr C.J. Simpson (DCE), Mr C.J. Nicholson (DCE) and Mr A. Chegvidden (Woodside Petroleum Pty. Ltd.). This work was supported by a grant from the Commonwealth Employment Programme to the Western Australian Department of Conservation and Environment. Professor A.J. McComb (Botany Department, University of Western Australia) kindly made office facilities available.

REFERENCES

- AARONSON, S.; DE ANGELIS, B.; FRANK, O. & BAKER, H. (1971)
Secretion of vitamins and amino acids into the environment by
Ochromonas danica. Journal of Phycology 7 : 215-218.
- ALEEM, A.A. (1980)
Marine cyanophyta from Sierra Leone, West Africa.
Botanica Marina 23 : 49-52.
- ANDERSON, O.R. (1977)
Fine structure of a marine amoeba associated with a blue-green
alga in the Sargasso Sea.
Journal of Protozoology 24 : 370-376.
- BALLANTINE, D. & ABBOT, B.C. (1957)
Toxic marine flagellates; their occurrence and physiological
effects on animals.
Journal of General Microbiology 16 : 274-281.
- BORSTAD, G.A. (1978)
Some aspects of the occurrence and biology of Trichodesmium
(Cyanophyta) in the western tropical Atlantic near Barbados,
West Indies. (Unpublished Ph.D. thesis, Marine Science
Centre, McGill University, Montreal.)
- BORSTAD, G.A. (1982)
The influence of the meandering Guiana current on surface
conditions near Barbados - temporal variations of
Trichodesmium (Cyanophyta) and other plankton.
Journal of Marine Research 40 : 435-452.
- BORSTAD, G.A. & BRINCKMANN-VOSS, A. (1979)
Pelagiana trichodesmium n. gen., n. sp., family Pandeidae
(Anthomedusae/Athecatae, Cnidaria), a new hydrozoan associated
with the planktonic cyanophyte Trichodesmium thiebautii.
Canadian Journal of Zoology 52 : 1232-1237.
- BOWMAN, T.E. & LANCASTER, L.J. (1965)
A bloom of the planktonic blue-green alga, Trichodesmium
erythraeum, in the Tonga Islands.
Limnology and Oceanography 10 : 291-292.
- BRYCESON, I. & FAY, P. (1981)
Nitrogen fixation in Oscillatoria erythraea in relation to
bundle formation, and trichome differentiation.
Marine Biology 61 : 159-166.
- CALEF, G.W. & GRICE, G.D. (1966)
Relationship between the blue-green alga Trichodesmium
thiebautii and the copepod Macrosetella gracilis in plankton
off north-eastern South America.
Ecology 47 : 855-856.
- CANABAEUS, L. (1929)
Über die Heterocysten und Gasvakülen der Blaualgen und ihre
Beziehung zueinander. Pp 1-48 in R. Kolkowitz [ed]
"Pflanzenforschung" 13 (Fischer, Jena).

- CAPONE, D.G. & CARPENTER, E.J. (1982)
Nitrogen fixation in the marine environment.
Science 217 : 1140-1142.
- CARLUCCI, A.F. & BOWES, P.M. (1970)
Production of vitamin B₁₂, thiamin and biotin by
phytoplankton. Journal of Phycology 6 : 351-357.
- CARPENTER, E.J. & GUILLARD, R.R.L. (1971)
Intra specific differences in nitrate half-saturation
constants for three species of marine phytoplankton.
Ecology 52 : 183-189.
- CARPENTER, E.J. & McCARTHY, J.J. (1975)
Nitrogen fixation and uptake of combined nitrogenous nutrients
by Oscillatoria thiebautii in the western Sargasso Sea.
Limnology and Oceanography 20 : 389-401.
- CARPENTER, E.J. & PRICE, C.C. (1976)
Marine Oscillatoria spp. and Trichodesmium spp. : explanation
for aerobic nitrogen fixation without heterocysts.
Science 191 : 1278-1280.
- CARPENTER, E.J. & PRICE, C.C. (1977)
Nitrogen fixation, distribution and production of
Oscillatoria (Trichodesmium) spp. in the western Sargasso
and Caribbean Seas. Limnology and Oceanography 22, 60-72.
- CARPENTER, E.J. & WALSBY, A.E. (1979)
Gas vacuole collapse in marine Oscillatoria thiebautii
Cyanophyta and the effect on nitrogenase activity and
photosynthesis.
Journal of Phycology 15 : 221-223.
- CHACKO, R.I. (1942)
An unusual incidence of mortality of marine fauna.
Current Science 11 : 404.
- CHELLAM, A. & ALAGARSWAMI, K. (1978)
Blooms of Trichodesmium thiebautii and their effect on
experimental pearl culture at Jeppalodai, India.
Indian Journal of Fisheries 25 : 237-239.
- CHIDAMBARAM, K. (1942)
On the alleged inhibitory influence of Trichodesmium
Current Science 11 : 406-407.
- CHIDAMBARAM, K. & MUKUNDAN UNNY, M. (1944)
Note on the swarming of the planktonic alga Trichodesmium
erythraeum in the Panbam area and its effect on the fauna
Current Science 13 : 263.
- DANIEL, A. NAGABHUSHANAM, A.K. & KRISHNAMURTHY, P. (1978)
On the occurrence of greenish yellow water phenomenon caused
by the swarming of Trichodesmium erythraeum in the sea off
Madras, India, and its effect on the local marine fauna.
Journal of the Bombay Natural History Society 75 : 88-95.

- DESIKACHARY, T.V. (1959)
 "Cyanophyta"
 (Academic Press, New York). 686pp
- DE TONI, G.B. (1864)
 "Sylloge algarum omnium hucusque cognitarum", 5.
 (Sylloge myxophycearum, Padua).
- DEVASSY, V.P., BHATTATHIRI, P.M. & QASIM, S.Z. (1978)
Trichodesmium erythraeum phenomenon
Indian Journal of Marine Science 7 : 168-186.
- DEVASSY, V.P., BHATTATHIRI, P.M. & QASIM, S.Z. (1979)
 Succession of organisms following Trichodesmium phenomenon
Indian Journal of Marine Science 8: 89-93.
- DROUET, F. (1968)
 Revision of the classification of the Oscillatoriaceae.
Monographs of the Academy of Natural Science, Philadelphia
 15, 370pp.
- DUGDALE, R.C. & GOERING, J.J. (1964)
 High nitrogen fixation rates in the Sargasso Sea and the
 Arabian Sea.
Limnology and Oceanography 9 : 507-510.
- DUGDALE, R.C., MENZEL, D.W. & RYTHER, J.H. (1961)
 Nitrogen fixation in the Sargasso Sea.
Deep-Sea Research 7: 297-300.
- DUGDALE, R.C., GOERING, J.J. & RYTHER, J.H. (1964)
 High nitrogen fixation rates in the Sargasso Sea and the
 Arabian Sea.
Limnology and Oceanography 9: 507-510
- ELEUTERIUS, L., PERRY, H., ELEUTERIUS, C., WARREN, J. &
 CALDWELL, J. (1981)
 Causative analysis on a nearshore bloom of Oscillatoria
erythraea Trichodesmium in the northern Gulf of Mexico.
Northeast Gulf Science 5 : 1-12.
- EPPLEY, R.W., ROGERS, J.N. & McCARTHY, J.J. (1969)
 Half saturation constants for uptake of nitrate and ammonia by
 marine phytoplankton.
Limnology and Oceanography 14 : 912-920.
- FARRAN, G.P. (1932)
 The occurrence of Trichodesmium thiebautii off the south coast
 of Ireland.
Rapports et Proces-Verbaux des Reunions, Conseil International
pour le Exploration de la Mer 77 : 60-64.
- FELDMAN, J. (1932)
 Sur la biologie des Trichodesmium Ehrenburg
Revue Algologique 6 : 357-358.

- FOGG, G.E. (1974)
 Nitrogen fixation. Pp. 560-582 in .W.D.P. Stewart [ed].
 "Algal Physichology and Biochemistry" (Blackwell, Oxford).
- FOGG, G.E. (1978)
 Nitrogen fixation in the oceans.
Ecological Bulletin 26 :11-19.
- FOGG, G.E. STEWART, W.D.P. FAY, P., & WALSBY, A.E. (1973)
 "The Blue-green Algae." (Academic Press, London).
- FOY, R.H. & SMITH, R.V. (1980)
 The role of carbohydrate accumulation in the growth of
 planktonic Ocillatoria species.
British Phycological Journal 15 : 1139-150.
- GEISELMAN, J.A. (1977)
 Marine colonial hydroid inclusion discovered within planktonic
Oscillatoria colonies.
Bulletin of Marine Science 27 : 821-824.
- GOERING, J.J. DUGDALE, R.C. & MENZEL, D.W. (1966)
 Estimates of in situ rates of nitrogen uptake by Trichodesmium
 in the tropical Atlantic Ocean.
Limnology and Oceanography 11 : 614-620.
- GOLDMAN, J.C. (1977)
 Biomass production in mass cultures of marine phytoplankton at
 varying temperatures.
Journal of Experimental Marine Biology and Ecology 27 :
 161-169.
- GUILLARD, R.R. & RYTHER, J.H. (1962)
 Studies of marine planktonic diatoms I. Cyclotella nana
 Hustedt, and Detonula confervacea (Cleve) Gran.
Canadian Journal of Microbiology 8 : 229-239.
- ISOUCHI, T. (1982)
 Relationship between distribution of surface plankton
 communities and coastal water of Southern Honshu and Shikoku
 Islands and in the Seto Inland Sea, Japan, in Summer 1980.
Journal of the Tokyo University of Fisheries : 49-74.
- KENNEALLY, K.F. (1973)
 An occurrence of the planktonic blue-green alga Oscillatoria
erythraea at Cottesloe.
Western Australian Naturalist 12 (7) : 168.
- KIMOR, B. & GOLANDSKY, B. (1977)
 Microplankton of the Gulf of Eilat : aspects of seasonal and
 bathymetric distribution.
Marine Biology 42 : 55-68.
- KLEMER, A., FEUILLADE, J. & FEUILLADE, M. (1982)
 Cyanobacterial blooms : carbon and nitrogen limitation have
 opposite effects on the buoyancy of Oscillatoria.
Science 215 (4540) : 1629-1631.

- KOLKWITZ, R. (1928)
 Uber Gasvakuolen bei bakterien.
Berliner Botanische Gesellschaft 46 : 29-34.
- KOVALEVA, T.M. (1976)
 Vertical distribution of phytoplankton in the tropical region
 of the Atlantic Ocean.
Hydrobiological Journal 12 : 1-6.
- LI, W.K.W., GLOVER, H.E. & MORRIS, I. (1980)
 Physiology of carbon assimilation by Oscillatoria thiebautii
 in the Caribbean Sea.
Limnology Oceanography 25 : 447-456.
- MADHUPRATAP, M., DEVASSY, V.P., NAIR, S.R. & RAO, T.S. (1980)
 Swarming of pelagic tunicates associated with phytoplankton
 bloom in the Bay of Bengal, India.
Indian Journal of Marine Science 9 : 69-71.
- MAGUE, T.H., MAGUE, F.C. & HOLM-HANSEN, O. (1977)
 Physiology and chemical composition of nitrogen-fixing
 phytoplankton in the central north Pacific Ocean.
Marine Biology 41 : 213-227.
- MAGUE, T.H., WEARE, N.M. & HOLM-HANSEN, O. (1974)
 Nitrogen fixation in the North Pacific Ocean.
Marine Biology 24 : 109-119.
- MARUMO, R. (1975)
 An outline of studies on the community of marine pelagic
 blue-green algae. Pp. 1-16 in R. Marumo [ed] "Studies on the
 Community of Marine Blue-Green Algae". (Technical Report of
 the Ocean Research Institute of the University of Tokyo,
 Tokyo).
- MARUMO, R. & ASAOKA, O. (1974)a
 Distribution of pelagic blue-green algae in the North Pacific
 Ocean.
Journal of the Oceanographic Society of Japan 30 (6) :
 77-85.
- MARUMO, R. and ADSAOKA, O. (1974)b
Trichodesmium in the East China Sea. Part I. Distribution of
Trichodesmium thiebautii during 1961-1967.
Journal of the Oceanographic Society of Japan 30 (6) :
 298-303.
- MARUMO, R. & NAGASAWA, S. (1976)
 Seasonal variation of the standing crop of a pelagic
 blue-green alga, Trichodesmium in the Kuroshio waters, Japan.
Bulletin of the Plankton Society of Japan 23 : 19-25.
- MAY, V. (1978)
 New records for Australian algae
Telopea 1 : 315-318.

- McCARTHY, J.J. & CARPENTER, E.J. (1979)
Oscillatoria (Trichodesmium) thiebautii (Cyanophyta) in the
 central north Atlantic Ocean.
Journal of Phycology 15 : 75-82 (1979).
- NAGABHUSHANAM, A.K. (1967)
 On an unusually dense phytoplankton "bloom" around Minicoy
 Island (Arabian Sea), and its effect on the local tuna
 fisheries.
Current Science 36 : 611-612.
- NAGASAWA, S. & MARUMO, R. (1967)
 Taxonomy and distribution of Trichodesmium (Cyanophyceae) in
 the Kuroshio waters. Information Bull., Planktol. Japan:
 139-143. (Commemoration number of Dr Y. Matsue. Tokyo, Japan.)
- NAIR, V.R., DEVASSY, V.P. & QASIM, S.Z. (1980)
 Zooplankton and Trichodesmium phenomenon.
Indian Journal of Marine Science 9 :1-6.
- OHKI, K. & FUJITA, Y. (1982)
 Laboratory culture of the pelagic blue-green alga
Trichodesmium thiebautii : conditions for uni-algal culture.
Marine Ecology Progress Series 7 : 185-190.
- PEARSON, H.W., HOWSLEY, R., KJELDSSEN, C.K. & WALSBY, A.E. (1979)
 Aerobic nitrogenase activity associated with a non-hetero-
 cystous filamentous cyanobacterium.
Federation of European Microbiological Societies,
Microbiological Letters 5 163-167.
- QASIM, S.Z. (1970)
 Some characteristics of a Trichodesmium bloom in the
 Laccadives.
Deep Sea Research 17 : 655-660.
- RAMAMURTHY, V.D. (1970)
 Antibacterial activity of the marine blue-green alga
Trichodesmium erythraeum in the gastro-intestinal contents of
 the seagull Larus brunicephalus.
Marine Biology 6 : 74-76.
- RAMAMURTHY, V.D. (1970)
 Experimental study relating to red tide.
Marine Biology 5 : 203-204.
- RAMAMURTHY, V.D. (1972)
 Procedures adopted for the laboratory cultivation of
Trichodesmium erythraeum.
Marine Biology 14 : 232-234.
- RAMAMURTHY, V.D. & KRISHNAMURTHY, S. (1968)
 Nitrogen fixation by the blue-green alga, Trichodesmium
erythraeum (Ehr.).
Current Science 37 : 21-22.

- REVELANTE, N. & GILMARTIN, M. (1982)
Dynamics of Phytoplankton in the Great Barrier Reef Lagoon.
Journal of Plankton Research 4 : 47-76.
- REVELANTE, N., WILLIAMS, W.T. & BUNT, J.S. (1982)
Temporal and spatial distribution of diatoms, dinoflagellates
and Trichodesmium in waters of the Great Barrier Reef.
Journal of Experimental Marine Biology and Ecology 63 27-45.
- ROMAN, M.R. (1978)
Ingestion of the blue-green alga Trichodesmium by the
harpacticoid copepod, Macrosetella gracilis.
Limnology and Oceanography 23 : 1245-1248.
- RYTHER, J.H. & DUNSTAN, W.M. (1971)
Nitrogen, phosphorus and eutrophication in the coastal marine
environment.
Science 171 : 1008-1013
- SAINO, T. and HATTORI, A. (1978)
Diel variation in nitrogen fixation by a marine blue-green
alga, Trichodesmium thiebautii.
Deep-Sea Research 25 : 1259-1264.
- SAINO, T. & HATTORI, A. (1982)
Aerobic nitrogen fixation by the marine non-heterocystous
cyanobacterium Trichodesmium (Oscillatoria) spp. : its
protective mechanism against oxygen.
Marine Biology 70 : 251-254.
- SCRANTON, M.I. (1983)
The role of the cyanobacterium Oscillatoria thiebautii in the
marine hydrogen cycle.
Marine Ecology Progress Series 11 : 79-88.
- SHIMURA, S. & FUJITA, Y. (1975)
Phycocerythrin and photosynthesis of the pelagic blue-green
alga Trichodesmium thiebautii in the waters of Kuroshio,
Japan.
Marine Biology 31 : 121-128.
- SMITH, G.C. (1972)
A red tide of Trichodesmium in coastal waters of Western
Australia.
Western Australian Naturalist 12 : 81-83.
- STEVEN, D.M., BROOKS, A.L. & MOORE, E.A. (1970)
Primary and secondary production in the tropical Atlantic.
ONR Report contract N00014-67-A-10432-0001. Bermuda
Biological Station Special Publication 124 pp.
- STEVEN, D.R. & R. GLOMBITZA (1972)
Oscillatory variation of a phytoplankton population in a
tropical ocean.
Nature 237 : 105-107.

- STEVENS, S.E. & VAN BAALEN, C. (1970)
 Growth characteristics of selected mutants of a coccoid
 blue-green alga.
Archives of Microbiology 72 : 1-8.
- STEWART, W.D.P., MAGUE, T.; FITZGERALD, G.P. & BURRIS, R.H.
 (1971)
 Nitrogenase activity in Wisconsin lakes of differing degrees
 of eutrophication.
New Phytologist 70 497-509.
- TAYLOR, B.F.; LEE, C.C. & BUNT, J.S. (1973)
 Nitrogen fixation associated with the marine blue-green alga,
Trichodesmium, as measured by the acetylene-reduction
 technique.
Archives of Microbiology 88 : 205-212.
- WADE, E. & MATSAMOTO, A. (1975)
 Ammonium uptake in Trichodesmium colonies. Pp. 62-64 in
 R. Marumo [ed] "Studies on the Community of Marine Pelagic
 Blue-Green Algae". (Ocean Research Institute, University of
 Tokyo, Tokyo).
- WALSBY, A.E. (1977)
 Gas vacuoles in sea sawdust.
British Phycological Journal 12 : 123.
- WALSBY, A.E. (1978)
 The properties and buoyancy providing role of gas vacuoles in
Trichodesmium.
British Phycological Journal 13 : 103-116.
- WATERBURY, J.B. WATSON, S.W. GUILLARD, R.R.L. & BRAND, L.E.
 (1979)
 Widespread occurrence of a unicellular marine planktonic
 cyanobacterium.
Nature 277 (5694) : 293-294.
- WOOD, E.J.F. (1965)
 "Marine Microbiol Ecology". (Chapman & Hall, London).
- WYATT, T. (1975)
 Further remarks on red tide models
Environmental Letters 9 : 217-224.