DEVELOPMENT OF ALGORITHMS FOR REMOTE SENSING OF *TRICHODESMIUM* BLOOMS

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ABSTRACT. *Trichodesmium* is a major component of the global carbon cycle, but because of its sporadic occurrence it is extremely difficult to study by conventional shipboard methods. Information on the variability and spatial extent of this cyanobacterium is essential for calculation of its contribution to carbon and nitrogen fluxes. Intense surface blooms of *Trichodesmium* have been observed in satellite imagery from the Coastal Zone Color Scanner and in color photography from the space shuttle, but such reports are rare. To date it is difficult to differentiate *Trichodesmium* from other species by remote sensing measurements alone.

A consideration of the spectral reflectance and absorption measurements on natural and concentrated populations of *Trichodesmium* shows that at moderate concentrations, *Trichodesmium* and other cyanobacteria should be distinguishable from diatoms and dinoflagellates where high spectral resolution data are available. This paper discusses optical data collected from freshly collected *Trichodesmium*, focussing on narrow spectral absorption features resulting from the nitrogen containing pigments at 495 and 545 nm by phycoerythrin, and at 625 nm by phycocyanin. The specific absorption spectra are used in an optical model to generate reflectance spectra corresponding to different concentrations of *Trichodesmium*. The detection limits of algorithms based on these features are assessed. The model spectra are also compared to actual reflectance data from a series-dilution experiment. This treatment illustrates the potential to use existing and planned airborne and space craft water color sensors to map *Trichodesmium* and other cyanobacterial blooms.

1. Introduction

The cyanobacterium *Trichodesmium* spp (= *Oscillatoria*) is the most abundant and active nitrogen fixing species in the plankton of tropical and sub-tropical seas (Carpenter, 1983). The organism plays an important role in the global flux of nitrogen and carbon. However, its appearance in infrequently travelled tropical seas far from major research laboratories, combined with the difficulty of keeping it alive in culture, has made it difficult to study.

E. J. Carpenter et al. (eds.), Marine Pelagic Cyanobacteria: Trichodesmium and other Diazotrophs, 193–210.

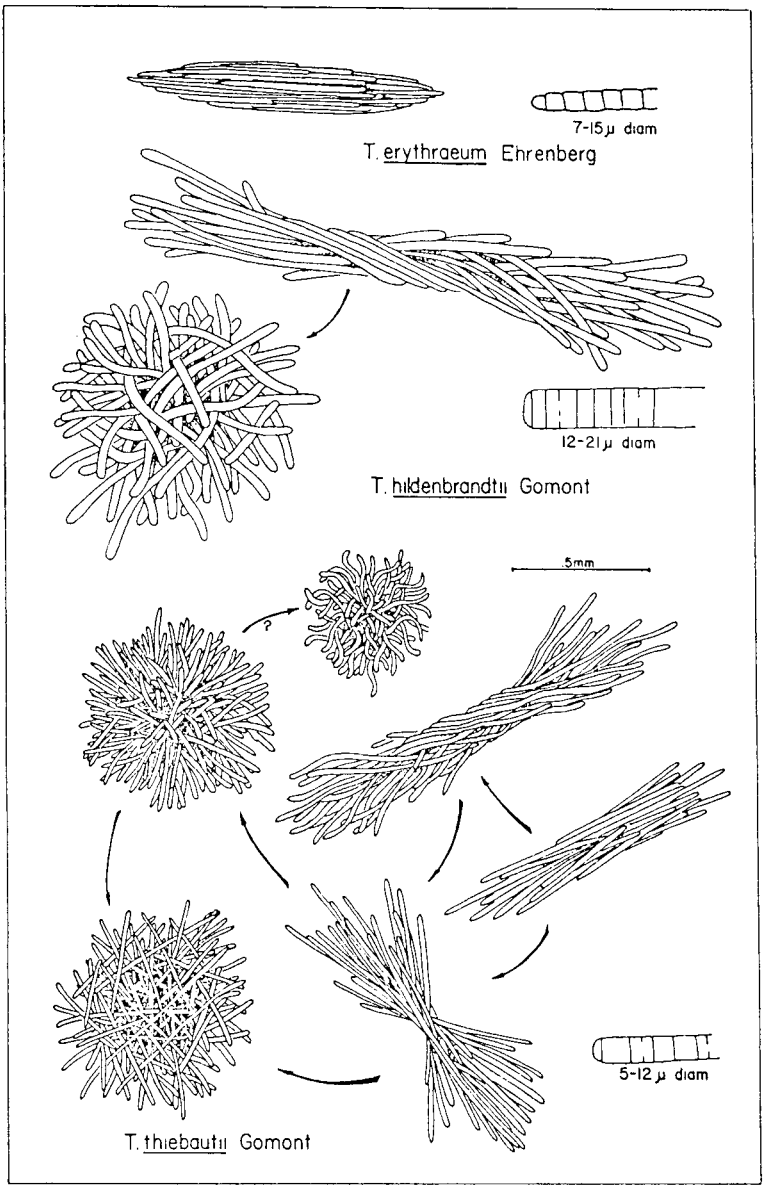

Figure 1. The colonial forms and relative sizes of Trichodesmium spp., (with speculations concerning relationships between forms; from Borstad, 1978).

Trichodesmium is non-uniformly distributed on all space scales. At the largest scales, the organism can form massive concentrated blooms stretching over hundreds of kilometers (Devassy et al., 1978). Gas vacuoles cause it to float on or near the surface, and convergence in the surface layers of the ocean can concentrate blooms into linear surface slicks. At the smallest scales, some variable and unknown fraction of the population of individual filaments (trichomes) of 100 or so cells (of 5 to 10 μm in length) are concentrated into colonies of tens to thousands of trichomes (figure 1). This colony-forming characteristic will also cause its concentration to be underestimated in remote sensing measurements.

The global distribution of the species, frequency of blooms and estimates of rate of N_2 fixation and primary production could be assessed more accurately by the use of remote sensing, especially if quantitative methods can be developed which differentiate *Trichodesmium* from other phytoplankton. Similarly, differentiation of cyanobacteria from other bloom-forming species in fresh water bodies would also be a significant improvement to present capabilities. In this chapter we discuss preliminary measurements of the organism's *in vivo* optical properties, made on artificially concentrated samples. The chlorophyll specific absorption spectra are then used to model reflectance spectra of *Trichodesmium* and a reference diatom species. Reflectance spectra are also compared to measurements made on serial dilutions of artificially concentrated *Trichodesmium*.

Trichodesmium contains both chlorophyll a and the bilin pigments phycoerythrin and phycocyanin which have characteristic absorption spectra. These features should become visible in remotely observed spectra at some cell concentration. Our studies were undertaken with a view to determining the detection limits for these features and, in general, to prepare for the higher spectral resolution remote sensing instruments now becoming available. The present family of space-borne water-color sensors is not optimal for this purpose, but as will be discussed below, improved sensors are being launched in the next decade.

2. Observations of *Trichodesmium* from Space

The Coastal Zone Color Scanner (Hovis et al., 1980) collected global data on near-surface phytoplankton biomass during its lifetime from 1978 to 1986. The CZCS was a mechanical scanner with a spatial resolution of about 1 km that made high sensitivity measurements of water-leaving radiance in four bands, each 20 nm wide, centred at 443, 520, 550 and 670 nm. Algorithms for deducing chlorophyll concentrations from ratios of blue and green radiance values have been developed and tested (Gordon et al 1983). With correction for atmospheric effects calculated from the longer wave bands and under so-called "Case 1" conditions in which the optical properties of the water are dominated by the presence of phytoplankton (Morel and Prieur, 1977), the algorithms have been shown capable of accuracy to better than a factor 2.

However, the algorithms were calibrated using more accessible diatom and dinoflagellate species. There have been few reported cases in which *Trichodesmium* was the dominant species in the water, and where ship measurements were made of its concentration at the time of a CZCS overpass. Moreover, the colonial behaviour of *Trichodesmium* suggests that self-shading may reduce the effect of pigments present on the optical properties of the water. Exact calculation of this effect requires knowledge of the effective optical depth of the pigment in a single cell (including increase of the path length in the cell by scattering), and a good statistical description of the clustering properties of colonies. At low cell numbers however, water color is dominated by absorption by water itself and by chlorophyll a. In spite of gas vesicles and auxiliary pigments, single cells of *Trichodesmium* are probably sufficiently similar to diatoms and

dinoflagellates that the CZCS algorithms could be expected to apply if the individual *Trichodesmium* cells were dispersed.

However, pigment in colonies may be seriously underestimated. If it is assumed that the optical depth of the pigment in a cell is significant, i.e of the order of unity or greater, then clustering of cells results in some being shadowed by others and an overall reduction of light absorption for a given pigment concentration. The gathering of about 100 *Trichodesmium* cells roughly 10 μm across into linear chains, trichomes about 1000 μm long, should not result in significant shadowing, since the cell axis will on average make an angle of 60 degrees to the direction of incoming and outgoing photons. The 100 cells would still have roughly their entire area 100 x 10 x 10, or 10^4 μm^2 , available for intercepting light.

Clustering of the trichomes into colonies can result in a more significant shadowing. If 10,000 trichomes were stacked evenly to form a cube 1,000 μm on a side, then shadowing would be by a factor of 100. That is, the area available to intercept light would be 10^6 μm^2, equivalent to that of 100 trichomes, instead of to the 10,000 trichomes actually present.

The actual clustering of trichomes is much more random and variable, roughly falling into two configurations: "radial, or puff" and "parallel, fusiform or tuft" forms (figure 1). The colony nomenclature differs between authors. A factor of 3-10 for the effect of shadowing appears a reasonable assumption. This effect will seriously reduce visibility of moderate concentrations of *Trichodesmium* in CZCS surveys.

However, the gas vesicles in *Trichodesmium* tend to increase its visibility, since they can bring the alga to the surface where blooms may accumulate under appropriate conditions. Marine and fresh-water cyanobacterial blooms have been well studied, but have not been the subject of much remote sensing effort to date. There are only three papers describing detection of blooms of fresh water cyanobacteria with the multi-spectral scanner on the LANDSAT series satellites. Horne and Wrigley (1975) reported early studies of *Anabaena* and *Microcystis* blooms using the near infra-red bands. Horstmann et al. (1978) and Ulbricht (1983a, b) have detected *Amphanizomenon* and *Nodularia* blooms in the Baltic, also using LANDSAT MSS band 6. In the late 1980's, there have also been two papers discussing remote sensing of *Trichodesmium* blooms from space. Kuchler and Jupp (1988) presented a natural color photograph taken from the US Space Shuttle using a hand-held camera, showing a massive *Trichodesmium* bloom off the coast of Australia. DuPouy et al, (1988; and this volume) have shown an example of a bloom imaged by the Coastal Zone Color Scanner at a time when high concentrations of *Trichodesmium* are common in surface waters near New Caledonia. In their example of a surface scum, the CZCS shows an increase in radiance in all bands, but with a smaller increase in the blue band at 440 nm.

We have studied a series of CZCS images collected in the spring of 1979 covering the west coast of India during March, during the time period (February to May) when Devassy et al (1978) report regular occurrence of *Trichodesmium* blooms along a coastal strip normally between the 5 m and the 25 m isobaths, with more detailed observations in 1977 and 1978. Devassy notes that this pre-monsoon season is characterized by clear skies, low winds and little coastal runoff. The CZCS images cover large cloud-free areas stretching 1500 km offshore and about 800 km along the coast centred on the region from Bombay to Goa. The images show a persistent pattern which is well illustrated by figure 2. Over most of the area the radiance back-scattered to the satellite at 520 and 550 nm is low. This is the type of water referred to as Case 1 by Morel and Gordon (1983). Radiance variations at 443 nm show the effects of absorption by varying amounts of chlorophyll pigment, and the chlorophyll image in figure 2d shows the quantitative pigment concentrations which should be accurate to within a factor 2 for common phytoplankton species.

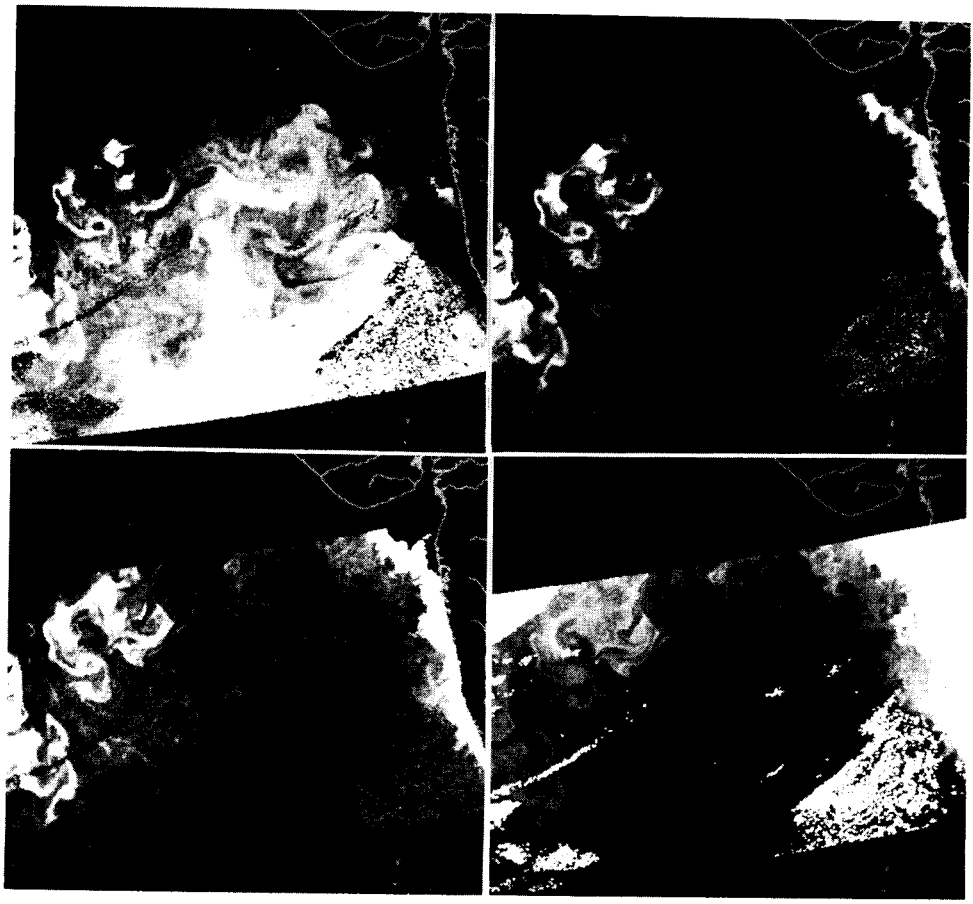

Figure 2 (a to d). CZCS images of water-leaving radiance at 443 nm (upper left), 520 nm (upper right) and 550 nm (lower left) and chlorophyll pigment distribution (lower right) in the Arabian Sea for March 29 1979.

Close to the coast of India, higher radiances are observed in the 520 and 550 nm bands, while in the 443 nm band, reduced radiances are observed, implying high pigment concentrations with high back-scatter. This is the type of signature that should be expected for a *Trichodesmium* bloom. In such "Case 2" waters the chlorophyll pigment concentrations may not be accurate, and pigment concentrations due to *Trichodesmium* will tend to be underestimated as noted above. The region of high radiance in figure 2 covers an area of about 20,000 km^2 over the continental shelf of western India. These case 2 waters extend into deeper water than reported by Devassy for the occurrence of *Trichodesmium*. However, the accuracy and coverage of Devassy's surveys are not clear. Without further in-situ measurements it is not possible to definitely identify the source of the scattering, but the coincidence is suggestive.

Reduced radiances at 433 nm are observed in Figure 2a to distances farther from the coast of India than the region of high backscatter at 520 and 550 nm. The additional area of elevated pigment values (compared to farther offshore) is about 7,000 km^2, and may be related to fertilization via nitrogen fixation by the *Trichodesmium* closer to shore.

On the left side of Figure 2 are distinct regions, covering a total of about 10,000 km^2, showing high radiance in all 3 CZCS bands at 433, 520 and 550 nm. This is the signature expected from a strongly-scattering bloom such would be caused by coccolithophores, which are known to be common in this area.

From this example it can be seen that CZCS images can be useful in determining the area of intense blooms. Alternatively, improved airborne senors are available now. While satellite sensors have relied on broad spectral bands to image the scattering or chlorophyll absorption, new technology is making available sensors with higher spectral resolution (Borstad et al., 1985; Vane, 1987), which in combination with studies of the pigment specific absorption properties of different classes of alga promises to significantly advance remote sensing of phytoplankton through increased pigment differentiation, pigment ratios and chlorophyll fluorescence.

3. Optical Measurements

While there are a few relative *in vivo* absorption spectra for *Trichodesmium* in the literature (Shimura et al., (1975), McCarthy and Carpenter, (1979), and Ohki et al., (1986), there is only one report of chlorophyll specific absorption coefficients (Lewis et al., 1988) which are required for optical modelling. No information has been available concerning the reflectance spectrum of the cyanobacterium and how this changes with changing pigment concentration.

We made optical measurements of above-water reflectance, in water vertical profiles of downwelling radiance and of absorption by isolated and concentrated *Trichodesmium* colonies on cruise number 18 of the University of Miami vessel RV Columbus Iselin, between November 4 and November 24, 1988. The cruise track, from Miami through the Bahamas to the Honduran Island of Roatan, and on to Limon, Costa Rica crossed a wide area of the Caribbean where *Trichodesmium* occurs at relatively low concentrations and where blooms have been observed. Several interrelated experimental programs were also conducted, providing supporting measurements of carbon and nitrogen fixation, nutrient uptake and cell counts.

3.1. SPECTRAL ABSORPTION COEFFICIENT

Individual *Trichodesmium* colonies were picked out of the contents of a surface plankton tow using pipettes, washed through filtered sea water, and dispersed in small volumes of filtered water by mechanical stirring. The suspension of trichomes was then collected on moist GF/F filters papers. Absorption was measured according to the method of Mitchell and Kiefer (1988), using the Institute of Ocean Sciences spectrometer (Walker et al 1975) looking through the dispersed colonies on GF/F filter paper at an Osram halogen bulb. Experiments on serial dilutions of the same sample showed that Mitchell and Kiefer's Beta factor could be applied to our samples, since all serial dilutions gave within 5% absolute absorption when normalized by the ratio (sample volume/filter area of the filter) and Beta. Beta is the so-called 'path length amplification factor', which is defined as the ratio of absorption of cells on a filter paper, which itself is highly scattering, to the same number of cells in a minimally scattering suspension. Bricaud and Stramski (1990) have also confirmed the applicability of Mitchell and Kiefer's (1988) Beta factor where optical densities of the sample are greater than about 0.20. Figure 3 shows typical chlorophyll specific spectral absorption coefficients (a_{ph}) for dispersed trichomes

of *Trichodesmium* (probably *T. theibautii* and *T. hildenbrandtii*), in this case for station 14 in the Eastern Caribbean at approximately 17° 01.8' N 82° 08.2' W.

Our spectrum shows a maximum absorption peak at 435 nm and a second peak at 675 nm, due to chlorophyll a. Peaks at 494 nm and 541 nm are ascribed to phycoerythrin and that between 619 and 624 nm to phycocyanin. Our spectra are of similar shape to the relative absorption spectra for *Trichodesmium* reported by Shimura et al., (1975), McCarthy and Carpenter, (1979), and Ohki et al., (1986), but we did not observe the peak at 565 nm (phycoerythrobilin chromophore) as reported by Shimura et al., 1975 or Ohki et al (1986) for *T. erythraeum.* Our spectra are very different both in shape and absolute value from those reported by Lewis et al., (1988) from the western Sargasso at 35° 35'N 65° 45'W. Lewis' spectra show very low absorption across the 500 to 600 nm region (perhaps related to a phycoerythrin deficit relative to chlorophyll), and have not been normalized to zero at 750 nm. His samples were collected by reverse filtration from a bucket from a concentrated bloom while ours were picked individually out of the contents of a plankton tow.

Variations in chlorophyll specific absorption in other types of phytoplankton have been found to be related to senescence (Kiefer et al., 1979); growth irradiance (Dubinsky et al., 1984) as well as cell size, intercellular pigment concentration and presence of auxiliary pigments (Sathyendrenath et al., 1987). How much of the difference between our measurements and those of others is due to pigmentation and physiological differences and how much is due to variation in technique is unclear. More detailed investigation of these differences is needed.

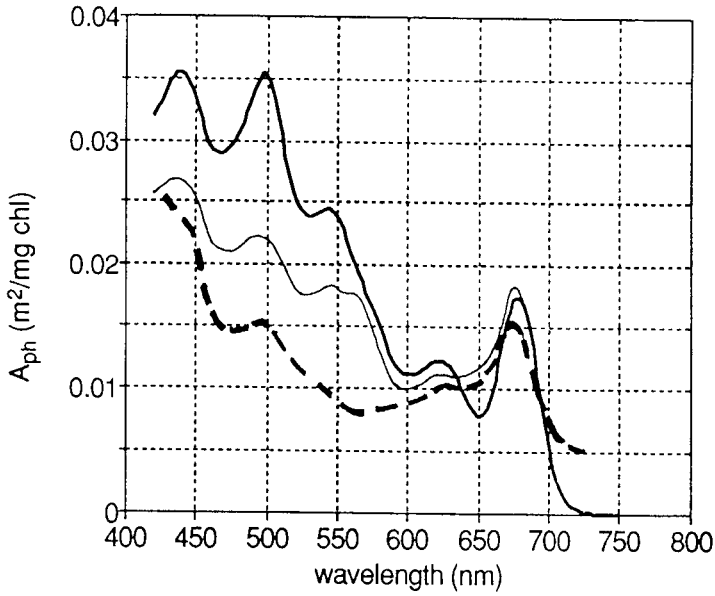

Figure 3. Chlorophyll specific spectral absorption coefficients (a_{ph}) for dispersed trichomes of *Trichodesmium* from the Caribbean (heavy line) , compared to a_{ph} reported by Lewis et al (1988) for *Trichodesmium* from the Sargasso (dashed line) and a relative absorption of *Trichodesmium* from the Kuroshio, normalized to the 670 nm peak (Ohki et al., 1986).

Our absolute value at the 440 nm absorption peak (.035 m^2mg^{-1} chlorophyll m^{-3}) falls within the range reported by Mitchell and Kiefer (1988) for various cultures, especially those grown at high light intensities, and within the upper part of the range shown by Sathyendranath et al. (1989) for cultures of diatoms and dinoflagellates. It is lower than reported by Bricaud et al., 1983, and by Morel and Bricaud (1981) for *Coccolithus huxleyi*. Our values do not agree with the absolute absorption coefficients published by Lewis et al. (1988), especially below 600 nm. Lewis used a constant value of 2.45 for Kiefer's Beta term which describes the optical path length amplification caused by scattering (Kiefer and Soohoo, 1982; Mitchell and Kiefer, 1988) and does not seem to have normalized absorption to zero at 750 nm.

Lewis et al. measured a decrease of photosythesis by about a factor 3 at high light in *Trichodesmium* samples which were mechanically disrupted, compared to samples with intact colonies. They concluded that this was due to an increase in the diffuse attenuation coefficient of the algae *in situ* because of the self shading which would normally be present due to colony formation. We noted above that self shading of this order of magnitude might be expected. In one case we measured a 2 to 4 times increase in attenuation when intact colonies suspended in seawater in an Utermöhl cell were dispersed. However, this was for a very high concentration (7785 trichomes ml^{-1}) so that Beers law does not apply (Sathyendrenath et al., 1987).

3.2. MODELLED REFLECTANCE SPECTRA

3.2.1 *The model.* A simple model of the spectral irradiance reflectance was proposed by Morel and Prieur (1977), and has since been developed by Prieur and Sathyendranath (1981), (Morel 1980 and 1988), Gordon and Morel (1983) and Sathyendranath et al. (1989). The basic model is:

$$R_i = 0.33\, B_t/A_t \qquad (1)$$

where B_t is the total backscattering from the water and A_t is the total absorption in the water. Both B and A are due to water itself, to suspended material and to dissolved organics (known as Gelbstoff). All constituents make independent, additive contributions. When modified for the reflectance factor observed in remote sensing (Carder and Steward, 1985), the equation becomes:

$$R_L = .1076\, (b_w + b_c C' + b_m M)/(a_w + a_c C + a_y Y) \qquad (2)$$

All terms have units of m^{-1}. The a and b absorption and scattering coefficients all have their own characteristic variation with wavelength, and are multiplied by the appropriate concentrations of the different constituents. The a_C and b_C, and to some extent the associated b_m, will vary with phytoplankton species and physiological state, but mean "normal" spectral curves are usually assumed.

The total absorption is due to water (a_W), to phytoplankton (a_c), and to dissolved yellow organic matter, or gelbstoff (a_y). Water gives a constant Rayleigh scatter (b_w) to which is added scatter from the phytoplankton (b_w) and from other suspended material (b_m). Morel (1980 and 1988) has suggested a relation for these backscatter contributions in which the coefficient C' varies non-linearly with C, the chlorophyll concentration in mg m^{-3}.

We have also added a term to include solar-stimulated fluorescence centered at 685 nm, taking account of absorption of both the stimulating and the emitted radiation (Neville and Gower, 1977, Spitzer and Dirks, 1986). The amount of fluorescence will depend on the absorption in the water. Absorption of stimulating light by phytoplankton gathers the energy to be emitted at longer wavelengths; any other absorption reduces the emitted fluorescence. The total emission is

controlled by a single yield parameter which is not necessarily dependent on chlorophyll concentration or other water properties, but which is expected to vary with growth phase and physiological state of the plankton. Typical values are 0.3 to 1%.

The above equation, even with the fluorescence term added, is simple in form, but is limited in practice by uncertainties in the spectral values of the coefficients. The terms b_w, a_w and a_y are relatively well defined, though measurements of Y (absorption m^{-1} at 350 nm) are often lacking in practice. The spectral form of the term b_c may be taken from the spectral reflectance of phytoplankton deposited in sufficiently high concentration on filter papers (Mitchell and Kiefer, 1988). The spectral form of the inorganic component is usually taken as having a uniform power law, typically (wavelength)$^{-1}$, across the visible spectrum. The dominant effect of the phytoplankton is through the term a_c, which can be measured in concentrated in-vivo conditions, or (with suitable corrections) from measured transmission through phytoplankton deposited on a filter paper.

3.2.2 *Modelled reflectance spectra.* We use the specific absorption coefficient of *Trichodesmium* shown in Figure 3, and the corresponding curve for the diatom *Skeletonema*, (figure 4) also measured with the IOS spectrometer in a laboratory culture to compute reflectance spectra with the above model.

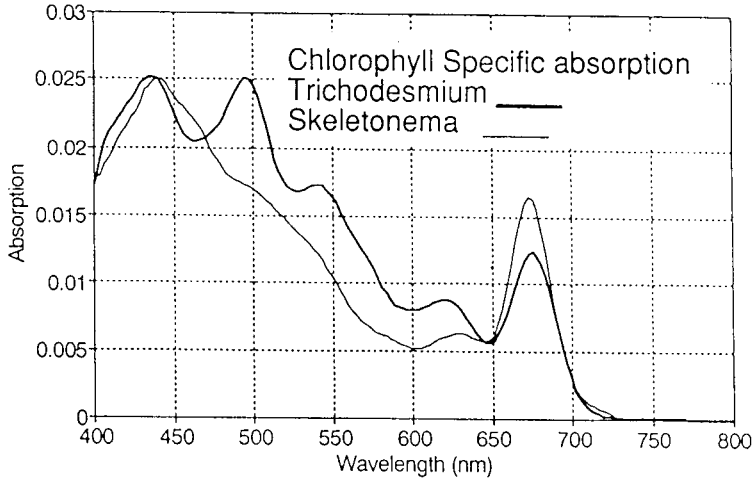

Figure 4. Normalized absorption coefficients for *Trichodesmium* and the diatom *Skeletonema* used in the reflectance modelling in figure 5 a to e.

Predicted pairs of reflectance spectra are shown in Figure 5a to 5f. The four pairs of spectra cover conditions ranging from relatively clear, oligotrophic water to fairly concentrated near-bloom conditions. In Figure 5a the two spectra in clear water (C = .1 mg m^{-3}, b = .1 m^{-1}, Y = .005 m^{-1}) are indistinguishable. In Figure 5b (C = 1 mg m^{-1}, b = .5 m^{-1}, Y = .01 m^{-1}) the differences start to become appreciable, and should be easily measurable with a sensor having sufficient spectral resolution in cases illustrated in Figures 5c (C = 10 mg m^{-1}, b = 2 m^{-1}, Y = .02 m^{-1}) and 5d (C = 25 mg m^{-1}, b = 2 m^{-1}, Y = .02 m^{-1}).

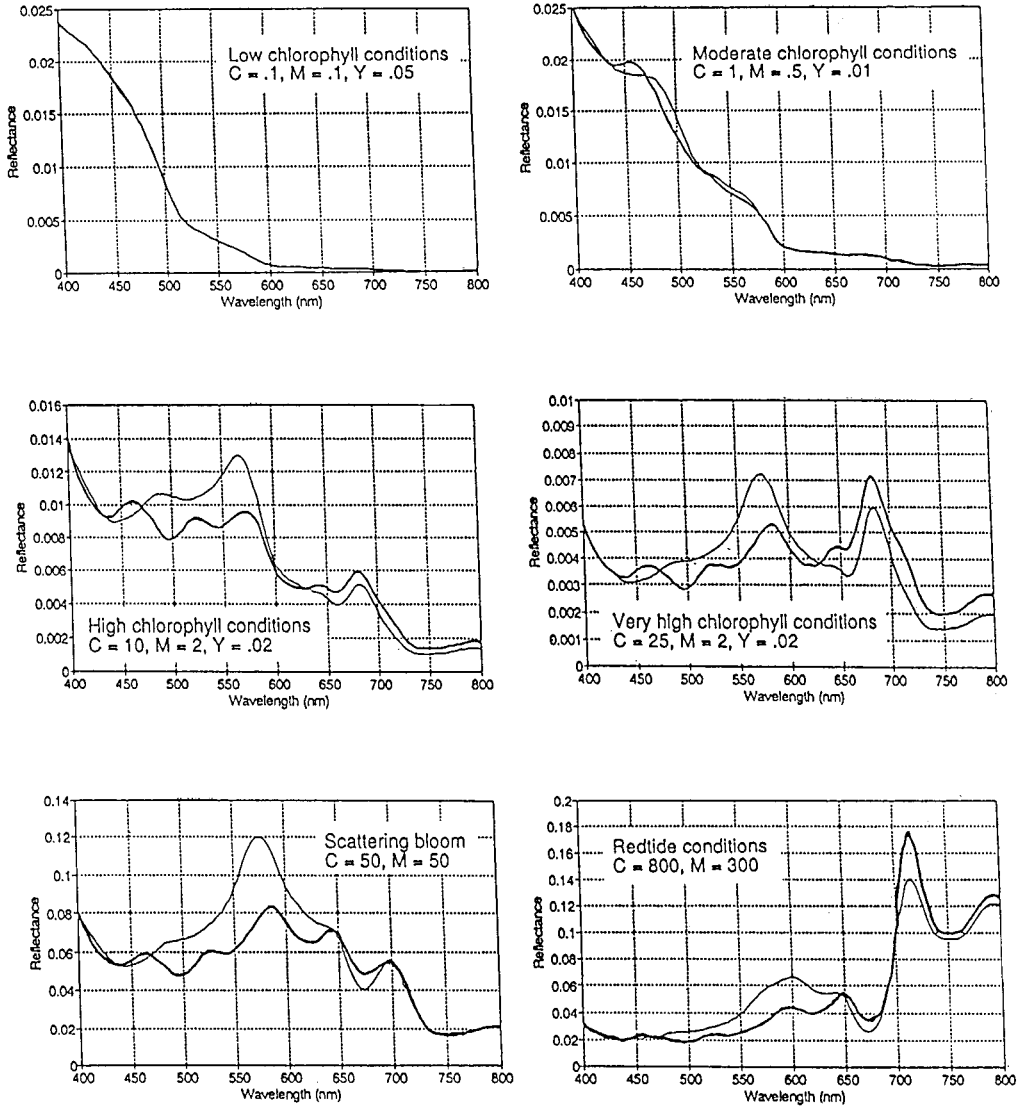

Figure 5a to e. Modelled reflectance spectra for *Trichodesmium* (heavy line) and *Skeletonema* (thin line) for varying concentrations of chlorophyll (C), scattering (M) and Gelbstoff (Y).

In each case in Figure 5 a constant fluorescence yield of 1% has been used. This fluorescence emission, centered on about 685 nm, overlaps the absorption band of chlorophyll a centered on 670 nm. Under low-scattering conditions the fluorescence peak provides a clear and useful signal for estimation of chlorophyll concentrations in the range 0.5 - 25 mg m^{-3} (Gower and Borstad, 1981).

We also show the results for more extreme conditions in Figure 5e (C = 50 mg m^{-1}, b = 50 m^{-1}, Y = .02 m^{-1}) where a bloom with high scattering is modelled, and 5f (C = 800 mg m^{-1}, b = 300 m^{-1}, Y = .02 m^{-1}), which was designed to duplicate the form of reflectance spectra observed in a red tide of the dinoflagellate *Gonyaulax spinifera* off the west coast of Vancouver Island in August and September 1990 (Gower and Borstad, 1991). In these two cases the fluorescence signal is lost in the larger effect of chlorophyll absorption. As the amount of scattering near 670 nm increases, the absorption will cause an increasing dip, which compensates for the fluorescence peak and then dominates the spectrum

3.3. MEASURED REFLECTANCE SPECTRA

3.3.1. *Reflectance Spectra of a Serial Dilution of Concentrated Trichodesmium.* Because a natural bloom was not encountered on the November 1988 Iselin cruise, we created bloom-like conditions by pouring the contents of a near-surface plankton tow into a small, clear plastic container suspended in the sea off the sunny side of the ship. While this artificial situation will not mimic the real optical behaviour of a *Trichodesmium* bloom, we feel that it a good first approximation since in a bloom the concentrations near the surface would be very high.

At one station off Roatan Island, (Honduras) the contents of a 64 μm mesh plankton tow were poured into the container, which was 10 cm diameter and 25 cm deep, with a rounded bottom which helped avoid reflection from the container itself. Upwelling radiance spectra were obtained by pointing the spectrometer vertically into the container from the deck of the ship. A file of 100 or more individual spectra were obtained for each dilution, from which averages of 10 to 20 spectra from inside the container were later selected to represent that dilution. After each raw radiance data file was obtained, the contents of the container was diluted with an equal volume of sea water, and another file of spectra were measured. After the first two spectra were obtained (0 and 1 in Figure 6), the plankton was gently screened through a 64 μm mesh plankton net in an attempt to wash out some of the contaminating diatoms and nannoplankton. Samples at each dilution were counted using a microscope and Sedgwick-Rafter cell, and chlorophyll and phycoerythrin concentrations were obtained for most dilutions.

The raw upwelling radiance spectra were transformed into reflectance factor spectra by dividing by a radiance spectrum of a white card obtained at the same time. A very small correction for the reflectance contribution of the container itself was calculated by viewing the container containing ambient seawater and subtracting the reflectance of the nearby sea itself. The corrected spectra obtained are shown in Figure 6.

3.3.2. *Above Water Reflectance of Trichodesmium.* Reflectance spectra were also measured on *Trichodesmium* samples concentrated on 2.54 cm GF/C filters by viewing them from above under solar illumination. In order to avoid further bleaching (since samples were collected from surface plankton tows, they perhaps already exhibited some bleaching), this measurement was made within a few seconds after the cells on the filters were first exposed to sunlight, though no evidence of bleaching was observed in subsequent measurements. The observed radiance spectra were normalized by the spectrum from a moistened, white filter viewed immediately afterwards in order to provide reflectance factor spectra.

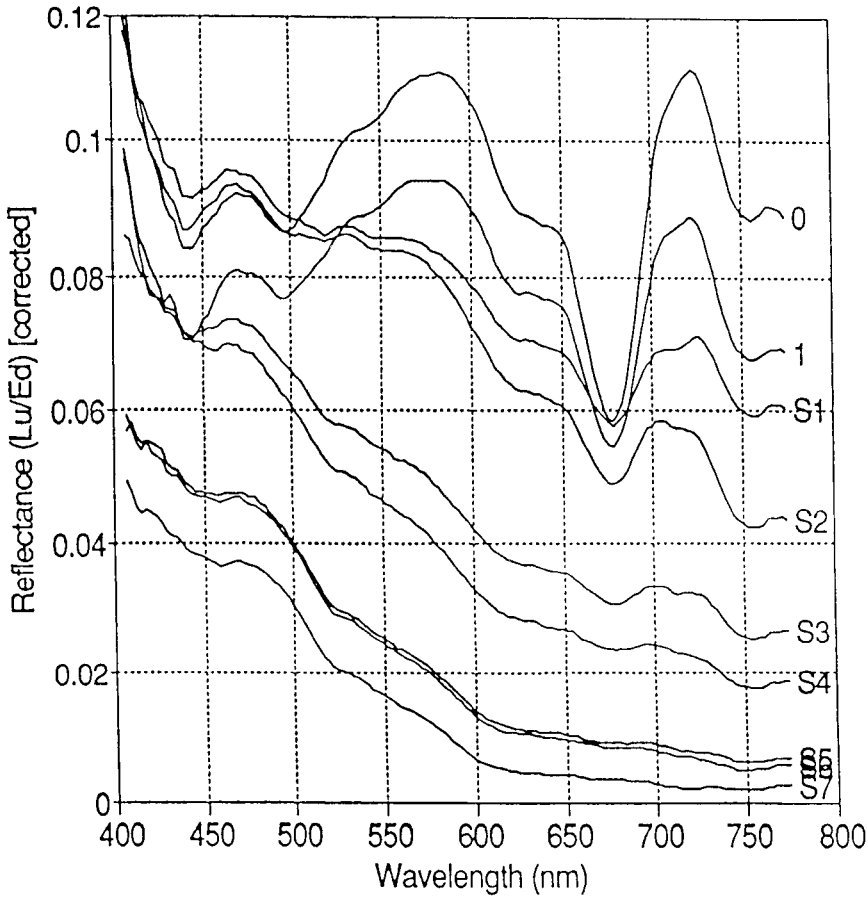

Figure 6. Spectral reflectance of a serial dilution of *Trichodesmium* measured in a small transparent container suspended at the surface of the sea in deep water. Dilutions 0 to S6 are 1441, 949, 858, 696, 359, 216, 144 and 46 trichomes ml^{-1}.

Results are shown in Figure 7 for concentrations of 1300 (upper curve), 2600, 5700, 6600, and 23000 (lowest curve) trichomes cm^{-2} referenced against a blank filter whose reflectance was assumed to be unity at all wavelengths. The centre curves show some variation in spectral form, but the samples show the expected trend from the thin covering of the filter at the lowest concentration to near optical thickness for the lowest curve. The reduction in reflectance of the filter for the numbers of trichomes cm^{-2} given above implies a cross-section area per trichome of 5×10^{-5} to $2 \times 10^{-4} cm^2$. This agrees very well with mean cell diameters of 10 μm and trichome lengths of 1 mm which gives an area of $10^{-4} cm^2$.

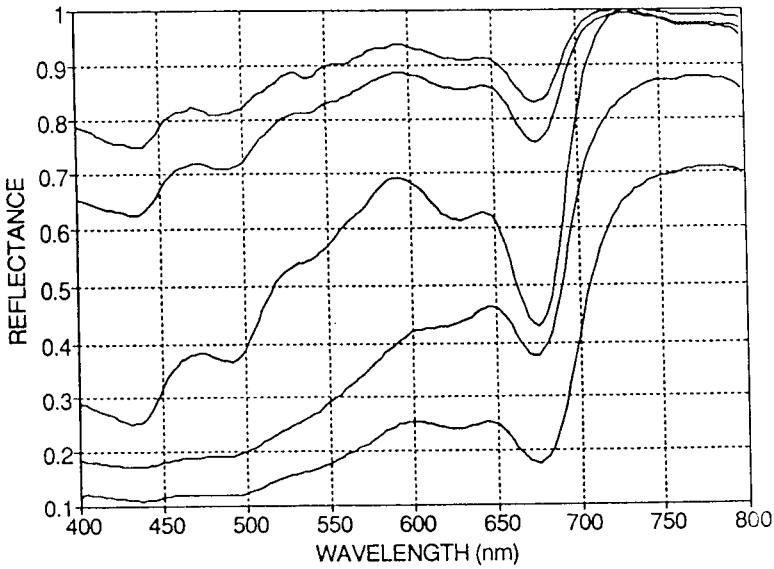

Figure 7. Reflectance of mats of *Trichodesmium* on white GF/C filter papers, to mimic surface scums of the alga without overlaying water.

4. Implications For Remote Sensing

4.1. SPECTRAL BAND REQUIREMENTS

The absorption spectrum in Figure 3 for *Trichodesmium* indicates sufficient similarity to other marine phytoplankton that measurements of "effective" pigment absorption using a ratio of blue and green upwelling radiances, for example with CZCS satellite data, will probably be satisfactory at "sub-bloom" conditions as suggested by Lewis et al 1988. However, the conversion of the "effective" pigment concentration to equivalent measurements in other species needs to take account of the self-shading noted above, since the colonial nature of *Trichodesmium* wm result in an underestimate of tropical and sub-tropical chlorophyll.

The three widely spaced CZCS spectral bands can not detect the spectral variations at 495 nm or the smaller variations at 545 nm due to the phycobilin pigments in cyanobacteria, and so can not begin to distinguish cases where these pigments occur. Higher spectral resolution imagers are required for this. The Seawifs scanner, due to be launched in 1995, will have additional bands which should make some distinction possible, but the model results in section 3 indicate that more bands are needed.

Minima in both the modelled and measured *Trichodesmium* reflectance spectra (figures 5 and 6 respectively), correspond to chlorophyll absorption at 440 and 670 nm, to phycoerythrin absorption at 495 and 545 nm and to phycocyanin absorption at 625 nm. In the red region of the spectrum of water-leaving radiance, we recognize solar-stimulated chlorophyll a fluorescence at 685 nm (Neville and Gower 1977, Gower and Borstad 1981, Borstad et al., 1985). In general at least two bands are needed (one in the absorption or fluorescence region and at least one other close by as a reference) to confirm the presence of such features, implying the need for 10 bands

in the spectral region 440 to 670 alone, with additional bands for atmospheric correction, gelbstoff determination and measurement of fluorescence. In combination with the need to make remote sensing observations in narrow and well-defined windows that minimize contamination by atmospheric absorption features, we are left with a requirement for nearly continuous coverage of the visible spectrum, suggesting that imaging spectrometers such as the Fluorescence Line Imager (Borstad et al, 1985) and the Compact Airborne Spectrographic Imager (Borstad and Hill, 1989) may be the appropriate technology.

The model spectra also indicate that measurements of solar-stimulated fluorescence should be a useful capability in a space sensor. In micro-photometric studies of *Trichodesmium* absorption and fluorescence Carpenter (unpublished) has recorded fluorescence at 560 - 575 nm (from phycoerythrin), 655 nm (from Phycocyanin) and 681 nm (from chlorophyll) with 490 nm stimulation. Relative to our modelled reflectance, and to reflectance of natural blooms of diatoms or dinoflagellates measured with the same instrument, our measured *Trichodesmium* reflectance spectra show a shoulder at 655 nm. We have seen this shoulder in remote sensing measurements of other blue-greens in freshwater lakes also, but it is not commonly seen in diatom or dinoflagellate blooms. This may be evidence of solar stimulated phycocyanin fluorescence, however, without detailed measurements we can not separate this feature from the effects of absorption occurring in the same region. We do not recognize fluorescence by phycoerythrin, presumably because it is included in the main green peak at 575 nm. Hoge and Swift (1983) have shown that it is possible to remotely measure phycoerythrin fluorescence using active laser stimulation from aircraft. Specific identification of *Trichodesmium* may have to rely on actively stimulated fluorescence of phycoerythrin (Hoge and Swift 1983), or on its absorption properties. Methods based on phycoerythrin fluorescence may be confounded by interference from *Synechococcus*, another abundant cyanobacterium.

4.2. RED REFLECTANCE OF AN ALGAL MAT OR SURFACE SCUM

The reflectance spectra in Figure 7 show the effect of increasing coverage by trichomes on the filters, with the spectra for the highest concentrations showing the "red edge" at 720 nm characteristic of terrestrial vegetation. The reflectance of the more concentrated samples are also similar to the upwelling radiance spectra of benthic cyanophyte mats shown by Jorgensen and De Marais (1988). Surface mats or scums of *Trichodesmium* and other blue-greens will show the characteristic chlorophyll "red edge" in their spectrum, a feature which should be detectable in remote sensing measurements over deep water by the radiance difference between 680 and 720 nm.

All chlorophyll containing plant species show this "red edge" when viewed directly with no water cover. This feature is a function of the low absorption of chlorophyll pigments at wavelengths longer than 700 nm. When dispersed in low concentrations in water, the increasing water absorption reduces the reflectance at wavelengths longer than 720 nm, leading to formation of a peak at wavelengths between 710 and 730 nm.

The effect of this "red edge" can be seen in images of surface mats of other bloom forming species acquired with the Advanced Very High Resolution Radiometer (AVHRR) on board the American NOAA weather satellites (Gower and Borstad, 1991). In extensive surface scums the ratio of radiance increases in the infrared to that in the red, above the radiances observed in nearby clear water, are close to the value for vegetation on land. The actual increases allow one to calculate the fraction of the sea surface within the sensor field of view which is covered with such vegetation. Similar measurements of *Trichodesmium* should be possible with the AVHRR where a sufficient fraction of the 1 km^2 pixel field of view of the scanner is covered. The AVHRR has the daily coverage needed to follow such blooms, and provides measurements in the

visible and near infrared with sufficient sensitivity. However, its spatial resolution limits its usefulness to cases where large areas (greater than several square km) are affected.

4.3. VARIATIONS OF COLOR WITH BLOOM PHASE

Not all *Trichodesmium* blooms are the silver-yellow color we saw in our serial dilution experiment. Daniel et al (1976) describe the moderate (200 - 450 trichomes ml^{-1}) concentrations as feeble to uniform greenish yellow in color. Devassy et al., (1978) describe the early stages of a bloom off Goa in India as grey in color, then... "As the bloom gets older, it begins to impart shades of reddish brown color and in bright sunlight it makes the sea look reddish in wavy lines. After some days, the bloom gets more and more concentrated and gives distinct reddish brown coloration to the water". Creagh (1986) summarizes reports of the color of *Trichodesmium* blooms off Australia as "extremely dense yellow green and brown; pale brown; high density brown; and very dense milky blooms."

These color variations are due to changing algal concentrations, but they must also relate to changes in the intra-cellular pigment concentrations and to the degree of vacuolation, which in many blue-green alga is under physiological control. Unfortunately absorption or reflectance spectra of trichomes with deflated gas vesicles have yet not been obtained. Walsby (1978) has reported a decrease in turbidity of about 35% using a nepholometer when *Trichodesmium* gas vesicles are collapsed using pressure. We did not measure scattering in our serial dilution experiment, but the model can be manipulated to show the effects of changes in scattering. The shape of the curves in Figure 6 and the increase in signal levels at all wavelengths with increasing *Trichodesmium* concentration indicates scattering over the full range of wavelengths plotted in our artificial "bloom". As expected, there was a very high correlation between reflectance at 780 nm and trichome concentration in our samples ($R_{780} = 6.2 \times 10^{-5}$ trichomes $ml^{-1} + .0068$; $r^2 = .98$).

The variation in bloom color will require different algorithms for different stages of a bloom. However, high reflectance at wavelengths greater than about 710 nm will allow surface scums of *Trichodesmium* and other algae to be visible in AVHRR and Landsat imagery regardless of the stage of the bloom. It should be noted however this scattering would be misinterpreted by the standard CZCS processing algorithm, which assumes zero water-leaving radiance at wavelengths longer than 670 nm. Higher spectral resolution and sensitivity with future sensors should give greater sensitivity, and permit positive identification of pigments such as phycoerythrin and phycocyanin.

5. Concluding Remarks

We have demonstrated that even with the cursory knowledge of spectral absorption and reflectance properties of *Trichodesmium* we have at present, it should be possible to design remote sensing algorithms specific to this cyanobacterium, especially when high spectral resolution devices are available. At present, some useful work can be done with data from conventional satellite sensors having broad spectral bands. Under conditions of intense blooms exhibiting surface scums, the long wavelength reflectance should provide a quantitative measure of abundance. Large area blooms can be mapped with the AVHRR, and smaller area events can sometimes be mapped with Landsat imagery. At very low concentrations, the conventional blue-green methods (Gordon et al, 1983) should suffice and CZCS data should be useful. However, algorithms will have to be altered to take into account the packaging or self shading occurring in colonies. At concentrations between about 5 and 200 mg, high spectral resolution

imaging spectrometers will provide the ability to detect and measure absorption from accessory pigments.

At present there are no satellite sensors in orbit designed for measuring ocean color. With the launch of Seawifs in 1995, the capabilities of satellite sensors will finally surpass those of the CZCS which provided data over the period 1978 to 1986. Seawifs will not however have the spectral bands needed to make a full study of the spectral information that should be available to satellite sensors. For this imaging spectrometers are required. Such instruments are now available on aircraft (AVIRIS, CASI, FLI, ROSIS) and will be available in space starting with the MERIS on the European EOS system in about 1998.

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Proceedings of the NATO Advanced Research Workshop on
Trichodesmium and other Marine Diazotrophs
Bamberg, Germany
May 26–31, 1991

Library of Congress Cataloging-in-Publication Data

NATO Advanced Research Workshop on Trichodesmium and Other Marine Diazotrophs (1991 : Bamberg, Germany)
Marine pelagic cyanobacteria : Trichodesmium and other diazotrophs / edited by E.J. Carpenter, D.G. Capone, and J.G. Rueter.
p. cm. -- (NATO ASI series. Series C, Mathematical and physical sciences ; vol. 362)
"Proceedings of the NATO Advanced Research Workshop on Trichodesmium and Other Marine Diazotrophs, Bamberg, Germany, May 26-31, 1991."
Includes index.
ISBN 0-7923-1614-2 (acid free paper)
1. Cyanobacteria--Congresses. 2. Trichodesmium--Congresses. 3. Water bloom--Congresses. I. Carpenter, Edward J. II. Capone, Douglas G. III. Rueter, J. G. (John G.), 1951- . IV. Series: NATO ASI series. Series C, Mathematical and physical sciences ; no. 362.
QR99.63.N38 1991
589.4'6'09162--dc20 91-46297
CIP

ISBN 0-7923-1614-2

Published by Kluwer Academic Publishers,
P.O. Box 17, 3300 AA Dordrecht, The Netherlands.

Kluwer Academic Publishers incorporates the publishing programmes of
D. Reidel, Martinus Nijhoff, Dr W. Junk and MTP Press.

Sold and distributed in the U.S.A. and Canada
by Kluwer Academic Publishers,
101 Philip Drive, Norwell, MA 02061, U.S.A.

In all other countries, sold and distributed
by Kluwer Academic Publishers Group,
P.O. Box 322, 3300 AH Dordrecht, The Netherlands.

Printed on acid-free paper

Printed in the Netherlands