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Trichodesmium, a Globally Significant Marine Cyanobacterium

Douglas G. Capone, Jonathan P. Zehr, Hans W. Paerl, Birgitta Bergman, Edward J. Carpenter

Planktonic marine cyanobacteria of the genus *Trichodesmium* occur throughout the oligotrophic tropical and subtropical oceans. Their unusual adaptations, from the molecular to the macroscopic level, contribute to their ecological success and biogeochemical importance. *Trichodesmium* fixes nitrogen gas (N_2) under fully aerobic conditions while photosynthetically evolving oxygen. Its temporal pattern of N_2 fixation results from an endogenous daily cycle that confines N_2 fixation to daylight hours. *Trichodesmium* colonies provide a unique pelagic habitat that supports a complex assemblage of consortial organisms. These colonies often represent a large fraction of the plant biomass in tropical, oligotrophic waters and contribute substantially to primary production. N_2 fixation by *Trichodesmium* is likely a major input to the marine and global nitrogen cycle.

Trichodesmium, a colonial marine cyanobacterium (*1*) (Fig. 1), has intrigued naturalists, biologists, and mariners for well over a century (*2*). These cyanobacteria have been reported throughout the tropical and subtropical Atlantic, Pacific, and Indian oceans, as well as the Caribbean and South China seas (Fig. 2) (*3*, *4*). Modern interest in *Trichodesmium* dates to the early 1960s with the recognition that the biological productivity of large expanses of the ocean is often limited by the availability of nitrogen (*5*) and the observation that *Trichodesmium* is diazotrophic (that is, an N_2 fixer). The current focus in assessing the global role of the upper ocean in assimilating atmospheric CO_2 has elevated the importance of quantifying marine N_2 fixation.

Although major advances in understanding the biology of *Trichodesmium* have recently occurred on diverse fronts, several important questions remain largely unresolved: (i) Where does *Trichodesmium* fit in the broader scheme of cyanobacterial phylogeny? (ii) How does *Trichodesmium* sustain simultaneous photosynthetic O_2 evolution with nitrogenase activity, and why does it fix N_2 only during daylight periods? (iii) What physiological, morphological, and behavioral adaptations contribute to *Trichodesmium*'s ecological success in the oligotrophic marine environment? (iv) What environmental and ecological factors control production and N_2 fixation in *Trichodesmium* in situ, and to what extent does it contribute to productivity, nutrient cycling, and trophodynamics in tropical and subtropical seas? (v) What is the over-

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all importance of *Trichodesmium* N_2 fixation and primary production in the global marine N and C cycles?

Molecular and Physiological Features

Open-ocean marine N-cycle studies and basic N_2 fixation research converged in 1961 when Dugdale *et al.* first identified *Trichodesmium* as a putative light-dependent N_2 fixer (*6*). However, as a nonheterocystous N_2 fixer, *Trichodesmium* represented a clear exception to the prevailing dogma (*7*) and, in the absence of a pure culture or other definitive evidence, its ability to fix N_2 was viewed with some caution (*8*). A comparison of the DNA sequence of the gene that codes for the Fe protein of nitrogenase (*nifH*) obtained from natural populations of *Trichodesmium* with that from a *Trichodesmium* isolate (*9*) provided the first direct evidence of the cyanobacterial origin of the nitrogenase activity associated with *Trichodesmium*. Later immunolocalization studies showed that the nitrogenase protein occurs within *Trichodesmium* cells (*10*–*12*).

The diversity among forms of *Trichodesmium* with respect to cellular and colonial morphology has prompted extended debate concerning its taxonomy and phylogenetic position within the cyanobacteria. With the relatively recent isolation and maintenance of cultures of the organism (*13*, *14*) and the development of structural and molecular biological approaches to characterizing natural populations, the taxonomic status of *Trichodesmium* populations has gained firmer footing. Sequence analysis of *nifH* and 16S ribosomal DNA (rDNA) has enabled inference of the taxonomic identity of the *Trichodesmium* sp. isolates and has provided additional bases for distinguishing *Trichodesmium* species as well as the means to determine the relative phylogenetic relation of *Trichodesmium* to other bacteria and cyanobacteria (*15*, *16*). The data are consistent with differences in trichome dimensions and colony morphology that had been used in previous taxonomic schemes (*15*). The nitrogenase DNA sequences of field samples of *T. thiebautii* and both field and culture samples of *T. erythraeum* were very similar (98% over 325 nucleotides), in contrast to comparisons of nitrogenase *nifH* gene sequences between species of other cyanobacterial genera, which are as low as 75% similar. *Trichodesmium nifH* sequences from three species form a deeply branching cluster within the cyanobacteria (Fig. 3), implying a very early radiation in cyanobacterial evolution. Although the *nifH* sequence indicates that *Trichodesmium* sp. NIBB 1067 is distantly related to other cyanobacteria, it appears relatively closely related to an oscillatorian on the basis of its 16S rDNA sequence (*17*). The reason for the differences in phylogenetic association based on the two genes is not yet clear but could involve convergent evolution (in *nifH*) or lateral transfer (of *nifH* or 16S ribosomal RNA genes). The rather distant relation of the *Trichodesmium nifH* gene to that of other cyanobacteria suggests that *Trichodesmium nifH* evolution may be constrained by the structural requirements for aerobic N_2 fixation.

One of the most intriguing aspects of *Trichodesmium* biology is the simultaneous occurrence of N_2 fixation and photosynthesis. Several hypotheses explaining how *Trichodesmium* might fix N_2 aerobically have been proposed. First, it is possible that the properties of *Trichodesmium* nitrogenase are unique with respect to their resistance to O_2 inactivation. Second, nitrogenase may be transiently modified to protect it from permanent O_2 deactivation, or it may be continually synthesized to replace protein being inactivated by O_2. Third, there may be intracellular O_2-consumptive processes that maintain O_2 at concentrations compatible with N_2 fixation. Finally, N_2 fixation and photosynthesis may be spatially segregated in some manner—for instance, either within specific regions in a colony or by cell differentiation within a trichome—such that N_2 fixation and photosynthesis are mutually exclusive within individual cells.

Mapping of the *Trichodesmium* nitrogenase operon and subsequent sequencing of nitrogenase structural genes demonstrated

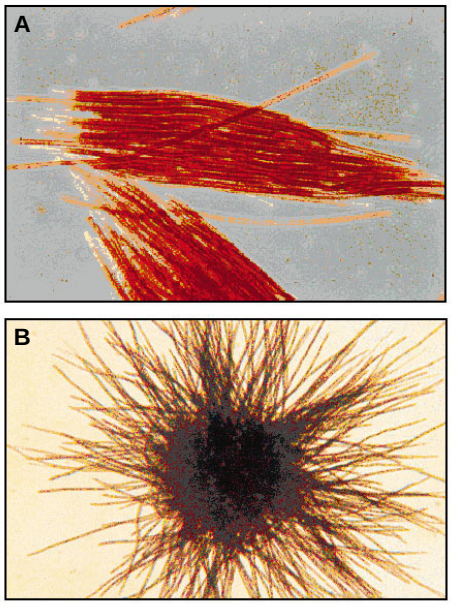

Fig. 1. Examples of *Trichodesmium* colonies. (**A**) Fusiform or tuft of *Trichodesmium* culture IMS 101; (**B**) radial or puff colony of *T. thiebautii*. Colonies are typically ~2 to 5 mm in length (fusiform) or diameter (radial) and are composed of tens to hundreds of aggregated filaments (trichomes). Each trichome consists of tens to hundreds of cells (typically ~100); cells are generally 5 to 15 μm in diameter but can range up to 50 μm in length (*15*) (photos by H. Paerl).

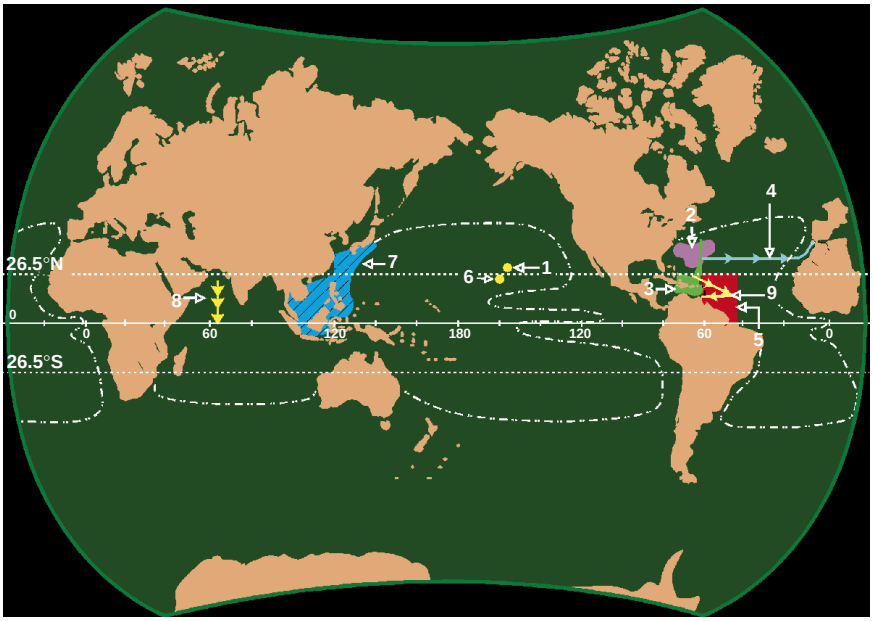

Fig. 2. Location of process-oriented studies and distribution of *Trichodesmium* in the world's oceans based on maps compiled by Carpenter (*3*) with reference to surface nutrient and productivity distributions from Berger *et al*. (*85*) to exclude areas of coastal upwelling and equatorial divergence. Dashed line indicates approximate extent of *Trichodesmium* penetration into subtropical waters. Although *Trichodesmium* is found in waters colder than 20°C, growth and activity are usually restricted to waters above 20°C (*3*, *4*). See Table 1 for key to study locations.

that the gene size and organization were similar to those of other heterocystous and nonheterocystous cyanobacteria (*16*). Modeling of the three-dimensional structure of the Fe protein from the deduced amino acid sequence did not reveal unique or unusual features of the *Trichodesmium* nitrogenase Fe protein, relative to those of other cyanobacteria, that might explain a higher O_2 tolerance (*18*). Moreover, elevated O_2 concentrations lead rapidly to inhibition of N_2 fixation, whereas decreased partial pressure of O_2 often stimulates activity (*19*); hence, nitrogenase activity in *Trichodesmium* is O_2-sensitive.

Continuous nitrogenase synthesis, as observed in other nonheterocystous cyanobacteria (*7*), could replace nitrogenase inactivated by O_2 and thereby provide a mechanism for simultaneous N_2 fixation and photosynthesis. However, nitrogenase activity in *Trichodesmium* is sustained for several hours in the presence of the protein synthesis inhibitor chloramphenicol (*19, 20*) and well after the disappearance of *nifH* messenger RNA (*21*), which indicates a relatively low turnover rate of nitrogenase protein during the active period of N_2 fixation. In some diazotrophs, nitrogenase may be protected from permanent inactivation by O_2 through conformational changes or covalent modification (*7*). The Fe protein of *Trichodesmium* nitrogenase can be modified in response to O_2 stress (*19, 22*), although the nature of the modification and whether this modification confers protection have yet to be determined.

Experimental evidence exists for the role of O_2 removal processes in maintaining low intracellular O_2 concentrations and thereby facilitating contemporaneous N_2 fixation and photosynthesis. Respiration rates in *Trichodesmium* appear high relative to other cyanobacteria, resulting in high compensation points (typically 100 to 200 μmol m^{-2} quanta s^{-1}) (*23*). Several other biochemical or physical means of O_2 consumption have been suggested (*24*).

Fogg (*25*) first offered the provocative hypothesis that a spatial segregation of O_2 evolution and nitrogenase activity (analogous to that between vegetative cells and heterocysts) occurs within *Trichodesmium* colonies. He postulated that photosystem II (PS II)–associated O_2 production took place in trichomes near the periphery of the colony, whereas nitrogenase activity was confined to the inner portions of the colony that lacked PS II. Experimental evidence supporting this idea was provided (*26, 27*) soon after Fogg's original suggestion. However, other findings suggest that nitrogenase and oxygenic photosynthesis may co-occur in cells and that colony integrity is not an absolute prerequisite for activity (*28*). Early suggestions that *Trichodesmium* might differentiate N_2-fixing and photosynthesizing cells along individual trichomes have recently gained support (*29*). If cellular delegation of activity through differentiation is conclusively demonstrated as a general mechanism in *Trichodesmium*, it would provide an invaluable model for molecular-level studies of a simple differentiated system.

The proposed mechanisms summarized above are not mutually exclusive. *Trichodesmium* most likely uses several strategies to permit nitrogenase activity during photosynthesis. Other mechanisms that enable the co-occurrence of nitrogenase activity and oxygenic photosynthesis in this organism may yet be identified. Regardless of how *Trichodesmium* is able to fix N_2 in the light, it is equally curious that in natural populations N_2 fixation occurs only during the day and is not performed during the night, as is characteristic for other nonheterocystous cyanobacteria (*7*). Saino and Hattori (*30*) first observed that nitrogenase was only active in samples of *Trichodesmium* collected during daylight hours: Samples collected at night were incapable of N_2 fixation under artificial light. They suggested, 8 years before circadian rhythms were identified in any prokaryote (*31*), that the daily cycle of N_2 fixation in *Trichodesmium* might be attributable to an endogenous rhythm. Research into the dynamics of the nitrogenase pool and *nifH* transcription in natural populations revealed a dynamic daily cycle of synthesis, activity, and degradation, directly coupled to the light cycle (*19–21*), thus providing a mechanistic explanation for the original observations.

A primary criterion for establishing the endogenous nature of N_2 fixation in *Trichodesmium*—its persistence over several cycles in constant light—has recently been provided in *Trichodesmium* sp. IMS 101 (*32*). The circadian clock, which appears to be set by illumination patterns, is likely to be of adaptive significance in ensuring that synthesis is induced in anticipation of the light period, thus optimizing the efficiency of light-driven N_2 fixation in the relatively stable environment of tropical and subtropical seas. This is the first endogenous rhythm to be confirmed in a prokaryote other than a coccoid cyanobacterium (*31*).

Ecology

Trichodesmium primarily inhabits surface waters of oligotrophic, tropical, and subtropical oceans, and is encountered in high abundance in western boundary currents (for example, the Gulf Stream, Kuroshio), in tropical portions of the central gyres, and in several ocean margin seas (*3*) (Fig. 2). The water column of these environments is generally very stable, with the upper mixed layer often around 100 m. This zone is characterized by low nutrient concentrations, very clear waters, and deep light penetration.

In an environment where the densities of microorganisms are very low and the waters highly transparent, *Trichodesmium* is unusual in that it is visually prominent, especially during surface blooms. The observed abundance of *Trichodesmium* in nutrient-depleted waters prompts the question of how it is uniquely adapted to this environment. Characteristics of *Trichodesmium* that appear to contribute to its success in the oligotrophic open ocean include its capability to fix N_2; its natural buoyancy, which positions it in the upper water column; a photosynthetic apparatus adapted to a high-light regime; and a relatively low growth rate, which, coupled with a lack of major grazers, allows it to maintain relatively high biomass.

Despite its ability to fix N_2 and its hab-

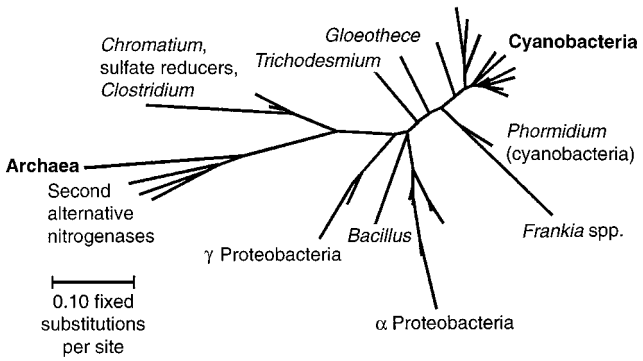

Fig. 3. Evolutionary relation of the genus *Trichodesmium* to other diazotrophs on the basis of *nifH* amino acid sequence data. The evolutionary distances between deduced amino acid sequences were used to create a phenogram using the neighbor-joining method of PHYLIP (*96*). The Fe protein gene (*nifH*) of *Trichodesmium* was amplified from cultures by means of the polymerase chain reaction (*9*). *Trichodesmium nifH* sequences cluster relatively distantly from other cyanobacterial genera, implying that the *Trichodesmium* genus diverged early in evolution. The *nifH* DNA sequences obtained from field collections of *T. erythraeum* and *T. thiebautii* are very similar (98%) and could be distinguished by only a few signature nucleotides (short distances among *Trichodesmium* species *nifH* sequences cannot be distinguished here).

itation in the high-light environment of the near surface, *Trichodesmium* has growth rates that are low relative to those of many eukaryotic phytoplankton (*4*). Even in culture, the doubling times of *Trichodesmium* are slow (~3 to 5 days), which suggests that a relatively low growth rate may in fact be an adaptation for exploiting the high-energy but low-nutrient conditions of the oligotrophic oceans (*33*). Because of its diazotrophic capacity, *Trichodesmium* growth rates are presumably limited by the availability of non-N nutrients. Field and laboratory data suggest that Fe is a key factor limiting *Trichodesmium* N_2 fixation and growth rates (*34–36*).

A key characteristic of *Trichodesmium* is the presence of gas vesicles, which provide buoyancy (*37*) and help maintain *Trichodesmium* populations in the upper surface waters. As has been noted in other planktonic cyanobacteria, the buoyancy of *Trichodesmium* is a dynamic property: A daily cycle of rising and sinking of colonies is often observed, and this may be a result of cell ballasting through the progressive increase of relatively dense carbohydrate and protein accumulating from photosynthesis through the day (*38*).

Wind stress at the surface affects the qualitative distribution of *Trichodesmium* populations. Relatively high and steady winds of the Trade Wind belts mix plankton populations throughout the upper euphotic zone, but natural buoyancy counteracts mixing to the bottom of the mixed layer; population densities are generally greatest at relatively shallow depths (20 to 40 m) in the upper water column (*3*, *4*) (Fig. 4).

Localization of the population in the high-irradiance upper water column is an adaptation that may provide a solution to the constraint of high compensation points (*23*) (equivalent to compensation depths of ~50 to 70 m in oligotrophic waters) and the added energetic demands of N_2 fixation. Pigment composition and photosynthetic parameters indicate a photosystem adapted for both maximum efficiency and photoprotection at high light (*4*, *39*). Moreover, Fe enters the open ocean primarily through atmospheric deposition, and location of these organisms in the upper water column may be advantageous with respect to Fe acquisition (*35*).

When wind stress is low for an extended period, the intrinsic buoyancy of *Trichodesmium* can have striking consequences, leading to the development of extensive surface blooms or "red tides" (*3*, *39*, *40*). These phenomena, which range in actual color from yellow to brown, are easily observed by satellite (Fig. 5) (*41*, *42*). The accumulation of the population at the surface for an extended period may result in photoinhibition (*43*) and, possibly, photooxidative damage (*3*, *4*, *39*); however, bloom organisms appear to be metabolically active, growing (*40*, *41*), and relatively resistant to photoinduced damage (*39*).

Although physical processes most often dominate oceanic plankton distributions, large surface accumulations of *Trichodesmium* may affect the bulk physical and chemical properties of surface waters. Mesoscale sea-surface features of the extent and intensity characteristic of some *Trichodesmium* blooms likely modify light penetration and the quality of the in situ light field (*43*) as well as heat and gas transfer across the ocean-atmosphere interface (*44*). Organic and inorganic nutrients accumulate during blooms and can affect subsequent phytoplankton succession and productivity (*40*).

Ecologically, *Trichodesmium* affects the structure and function of the oligotrophic ocean by contributing to its productivity and trophodynamics, as well as by providing a unique pelagic habitat. Upon close inspection, many colonies reveal a microcosm including bacteria, other cyanobacteria, protozoa, fungi, hydrozoans, and copepods (45). Nitrogen and carbon fixed by *Trichodesmium* enters the food web, but not necessarily through increased C and N flux into classical food chains. Some species of *Trichodesmium* produce a toxin that deters grazing by calanoid and cyclopoid copepods, considered to be the major grazers in these systems (*46*). A specialized group of harpacticoid copepods appear adapted to the toxin and are capable of directly grazing *Trichodesmium* (*47*), although their quantitative role in the consumption of *Trichodesmium* is unknown. Although there are anecdotal reports of the presence of *Trichodesmium* in the guts of gelatinous zooplankton and fish (*4*), this does not appear to be a quantitatively important fate for *Trichodesmium* biomass, and much of the C and N fixed by *Trichodesmium* likely enters upper trophic levels by other pathways. In natural populations of *Trichodesmium*, a large proportion of recently fixed N is released as organic N (*48*). Besides providing a means of exchange between N_2-fixing and non–N_2-fixing cells in the colonies, this exudation may be an important source of C and N for microbes inhabiting the colonies (*49*) or free-living in the water column, and ultimately may be a source of inorganic N for phytoplankton.

Biogeochemistry

With its cosmopolitan distribution throughout much of the oligotrophic tropical and subtropical oceans (*3*) and its capacity to form extensive surface blooms (*40–42*), *Trichodesmium* may be one of the most globally important cyanobacteria and phytoplankton. However, there is insufficient quantitative information to substantiate this inference, possibly because of the unique problems associated with assessing the biomass and productivity of *Trichodesmium* by traditional methods as well as the inherent difficulty in sampling ephemeral blooms (*50*). As a result, the contribution of *Trichodesmium* to marine C and N input has generally been considered relatively small (*51*). Recent data, however, suggest otherwise.

Accurately quantifying N_2 fixation in the seas has direct bearing on our understanding of C flux in the tropical oceans. According to the "new production" concept

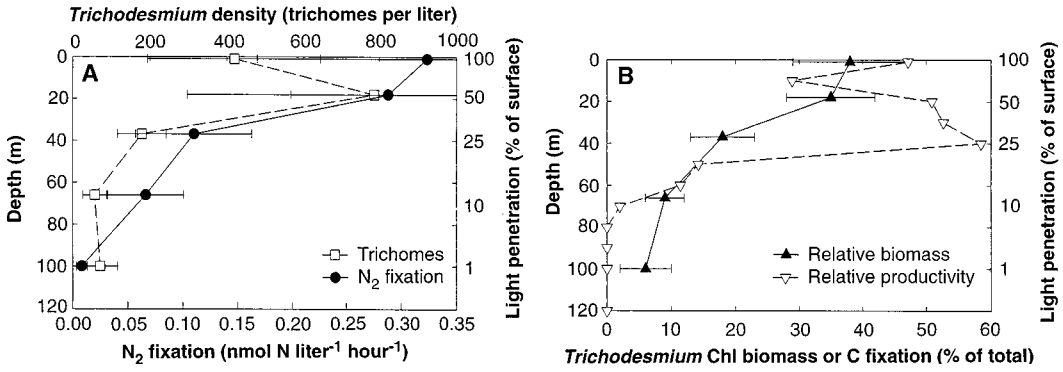

Fig. 4. Average depth distributions of trichomes of *T. thiebautii* and volumetric N_2 fixation (**A**), and chlorophyll a (Chl a) biomass and primary productivity relative to microplankton (**B**), for a series of stations taken in the southwestern tropical North Atlantic in May 1994 (Fig. 2, map code 9) (*97*). Bars indicate ±SE of the mean.

(52), in steady-state marine systems the amount of organic N removed from the system (that is, the euphotic zone) should equal external ("new") N inputs entering that system. Although N_2 fixation is a potential source of new N, NO_3^- from depth is generally considered the quantitatively dominant source of new N in most open-ocean systems (52). Areal rates of total production in tropical oligotrophic regions are typically very low (53), and the relative amount of production dependent on new N (that is, "new" production) is thought to be small; nonetheless, the export of organic N and C from the upper water column of oligotrophic regions is important in the marine C and N budgets because the total area involved is vast (53).

The increase in atmospheric CO_2 has provided added impetus to the quest to quantify oceanic primary production and its rate of removal to depth (54). N_2 fixation and vertical NO_3^- flux from depth have different potentials for supporting primary production and effecting net removal of CO_2 from the atmosphere. Vertical NO_3^- flux occurs with a concurrent upward flux of CO_2 and PO_4^{3-} from depth, often close to the stoichiometric requirement of phytoplankton. Thus, relative to N_2 fixation, NO_3^- derived from depth has limited capacity for effecting net removal of atmospheric CO_2. N_2 fixation represents a source of new N entering the system that can account for a net sequestering of atmospheric CO_2 into export production (55).

Recently, several independent lines of evidence have prompted speculation that marine N_2 fixation has been severely underestimated and may play a larger role in global C and N fluxes. Large imbalances in the estimated N budgets for the North Atlantic, central North Pacific, Indian, and global oceans have prompted speculation as to unknown or poorly quantified N inputs, and N_2 fixation may provide the missing source of N (56).

For nonupwelling regions of the tropical and subtropical North Atlantic, the vertical flux of NO_3^-, assumed to represent the bulk of the influx of new N into the euphotic zone (52), is estimated to range from 30 to 150 μmol N m^{-2} day^{-1} (57). However, such estimates of new N inputs are often insufficient to satisfy the calculated demand for new N and organic export from the euphotic zone (57), which suggests the existence of sources of combined N in addition to vertical NO_3^- flux. Other biogeochemical approaches also reveal N demand in, or losses from, the upper water column exceeding current estimates of N inputs, further indicating unquantified inputs (58).

Independent evidence that N_2 fixation may be of greater relevance than currently believed derives from studies of the natural isotopic abundance of ^{15}N in surface particulate organic nitrogen (PON). *Trichodesmium* has a low $\delta^{15}N$, typical of N_2-fixing organisms (59). Relative to the isotopic composition of PON in more nutrient-rich areas, the $\delta^{15}N$ of suspended particles and zooplankton in surface waters of the western and central tropical Pacific and in the Caribbean is often low and inversely related to the abundance of *Trichodesmium*. This suggests that the isotopically light PON in these waters is a result of N_2 fixation by *Trichodesmium* (59).

Relative to conventional assessments of planktonic standing crop, primary productivity, and inorganic N uptake, there are few direct estimates of *Trichodesmium* biomass and its rate of N_2 fixation (50) (Table 1) and even fewer estimates of its contribution to primary production. The most comprehensive studies to date have been made in the subtropical Sargasso Sea and in the tropical Caribbean and far western Pacific (Kuroshio, South and East China Sea) (Fig. 2), ocean margin regions that may not be representative of the tropical oceans. More limited data are available for the tropical North Atlantic and the vicinity of Hawaii. Virtually no information exists for large expanses of the tropical oceans, particularly in the Southern Hemisphere. Nonetheless, several of the studies conducted over the past two decades have provided direct evidence of the importance of *Trichodesmium* relative to other phytoplankton (60). With

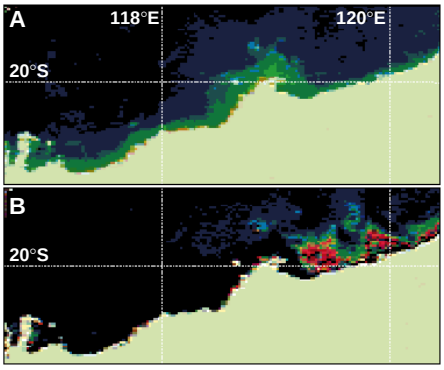

Fig. 5. (**A**) Image of chlorophyll and (**B**) relative *Trichodesmium* abundance derived from a coastal zone color scanner (CZCS) image of the northwestern coast of Australia in the vicinity of the Dampier Archipelago and confirmed by contemporaneous sea-truth data [adapted from (42)]. A protocol based on reflectivity and absorption at 550 nm was used. Chlorophyll is reported as detected by CZCS, with lowest to highest chlorophyll a concentrations ranging from purple (<0.05 mg m^{-3}) to red (>3.0 mg m^{-3}). For *Trichodesmium*, dark colors indicate its absence; lighter colors (light blue through orange) indicate its presence. Differences in color represent varying responses to the protocol, not necessarily differences in *Trichodesmium* concentration.

Table 1. Summary of direct areal estimates of N_2 fixation, as originally reported or as derived. Studies based on C_2H_2 reduction determinations of N_2 fixation used a 3:1 conversion from C_2H_2 reduced to N_2 fixed, unless otherwise noted. *N*, number of discrete observations.

Location	Areal estimates			Map code	Reference
	Date	Average ± SE (μmol N m^{-2} day^{-1})	*N*		
	Subtropical				
28°N, 155°W (North Pacific)	Aug 73	33	1	1	(95)
27° to 34°N (NW Sargasso Sea)	Sep–Oct 73	1.4* ± 0.47	9	2	(93)
22° to 36°N (Sargasso Sea)	Aug 74	6.2* ± 4.0	7	3	(92)
22° to 23°N (Caribbean passages)	Feb–Mar 74, Aug 74	4.2* ± 4.0	10	3	(92)
30°N (Atlantic transect)	May–Jun 75	0.29* ± 0.13	5	4	(94)
	Tropical				
0° to 24°N, 45° to 66°W (SW North Atlantic)	Fall 64	41† ± 7.6	19	5	(65)
	Spring 65	108† ± 24	15	5	(65)
21°N, 159°W (North Pacific)	Oct, Dec 72	134	2	6a	(62)
12° to 22°N (Caribbean)	Feb–Mar 74, Aug 74	77* ± 9.7	12	3	(92)
10° to 25°N (SE East China Sea)	Summer 77	126	32	7	(63)
23°N, 158°W (North Pacific)	Jun 90, Feb 91	85	2	6b	(89)
7° to 10°N (Arabian Sea)	May 95	35 ± 7.4	9	8	(81)
14° to 22°N (SW North Atlantic)	May 94	73 ± 22	12	9	(64)
NE Caribbean	May 94	278 ± 129	3	9	(64)
Tropical, grand average		106 ± 24			

*Data as originally presented using a 6.3:1 conversion ratio. †Data based on direct $^{15}N_2$ uptake. Average rates from 0 and 15 m are assumed over the top 20 m and have been increased by 50% to account for activity below 20 m, on the basis of data for the region from Fig. 4 and (64).

respect to subtropical waters such as the Sargasso Sea, previous studies have detected appreciable populations of *Trichodesmium* only for limited periods during the summer, and the calculated contributions of *Trichodesmium* to C and N input were relatively small (Table 1) (*61*).

In tropical studies, despite low growth rates, the relatively high biomass of *Trichodesmium* in these regions implies that it may account for a quantitatively important input of organic C, and data from several studies have provided support for this idea (*60*) (Fig. 4). Not surprisingly, the most data exist for estimates of N_2 fixation (Table 1). The average rate of N_2 fixation reported for a suite of stations throughout the Caribbean Sea was 77 μmol N m^{-2} day^{-1}. One station in the tropical North Pacific yielded an N_2 fixation rate of 134 μmol N m^{-2} day^{-1} (*62–65*). We calculated 126 μmol N m^{-2} day^{-1} on the basis of data (*63*) for the China Sea and Kuroshio current near the southern tip of Japan (Table 1). Our recent results from the open tropical Atlantic Ocean (Fig. 4) are generally consistent with earlier data from this and other tropical regions (Table 1). Scaling the average (nonbloom) tropical rate of 106 μmol N m^{-2} day^{-1} to tropical oligotrophic waters that cover about 150×10^6 km^2 (*53*) yields an annual input of ~80 Tg N, considerably greater than previous estimates of pelagic N_2 fixation input (*3, 40*).

These estimates of N input through N_2 fixation in tropical areas are roughly equivalent to the estimates of vertical NO_3^- flux given above and suggest that these two processes are of comparable importance in new N input. Moreover, recent evidence indicates that actual eddy diffusivities are at the lower range of those values currently assumed (*66*). If this is correct, it would lower the estimate of N input by vertical flux of NO_3^- and correspondingly increase the relative importance of upper water column N_2 fixation to overall N input. The extreme depth of the euphotic zone in the oligotrophic open ocean (>100 m), and the absence of measurable NO_3^- throughout much of the upper water column of the highly oligotrophic tropical areas, imply an uncoupling between the reservoirs of NO_3^- at depth and productivity in the near surface. Any NO_3^- that penetrates up from depth is likely to be assimilated at the chlorophyll maximum, typically located near the 1% light level near the nitracline.

Although numerous blooms have been documented and their spatial extent and biomass density have been estimated (*40–42*), the effect of a given bloom on C and N input has been determined only on a few occasions. For three studies that directly measured N_2 fixation in surface blooms, the input of N in the bloom was about three times that occurring throughout the rest of the water column (*67*).

Taken together, these observations strongly indicate that N_2 fixation is an important component of the marine N budget that needs to be considered in basin-scale studies of N cycling and in calculations of global N budgets. In addition to N_2 fixation, other potentially significant "new" N inputs, such as atmospheric deposition of dissolved inorganic and organic N, have been poorly quantified or ignored in the past (*68*). More accurate assessment of their contributions to the oceanic N cycle will further help to rectify current discrepancies in basin-scale and oceanic N budgets.

Future Research and Prospects

Research efforts from a molecular to a global perspective provide a new basis for understanding the biology and ecology of *Trichodesmium* and inferring its role in global biogeochemical cycles. Physiological, genetic, and immunological evidence have confirmed *Trichodesmium*, rather than associated microorganisms, as the main N_2 fixer in its colonial aggregates. *Trichodesmium* fixes N_2 aerobically, possibly in the same cell and at the same time as it evolves O_2 through photosynthesis, making it a unique and valuable model organism for the study of N_2 fixation in photosynthetic organisms. As one of the few prokaryotic systems identified as having an endogenous rhythm, *Trichodesmium* has a relative biochemical simplicity that makes it an attractive system for identifying the genetic and physiological factors regulating components of its biological clock.

Multiple characteristics have been identified that contribute to the ability of *Trichodesmium* to fix N_2 aerobically, but a single critical component that allows simultaneous photosynthesis and nitrogenase activity of nitrogenase has yet to be found, and seemingly conflicting results need to be reconciled. The dichotomy in growth rate estimates based on C or N in natural populations needs also to be resolved. The availability of robust cultures will greatly improve our knowledge of the biochemical functioning of these unusual diazotrophs.

A variety of recognized morphological and functional features demonstrate *Trichodesmium* to be well adapted to the N-poor oligotrophic ocean environment. Of particular ecological relevance may be its cyclic patterns of vertical migration, N_2 fixation, and photoprotective processes. However, we have yet to develop an integrative physiological model directly linking these ecological behaviors in cultures or in natural populations. More rigorous definition of the interplay of physical and chemical limiting factors will provide important constraints for modeling and predicting the in situ dynamics of these populations.

The accumulating evidence strongly indicates a much more important role of *Trichodesmium* in oceanic biogeochemistry than it is currently afforded. Synoptic estimates of the areal and temporal extent of *Trichodesmium* populations and, particularly, blooms by new and planned satellite sensors [for example, the ocean color and temperature scanner (OCTS) and the sea-viewing wide field-of-view sensor (SeaWiFS)], coupled with the development of in situ methods of enumerating these populations (for example, fluorescence-based optical plankton counters and laser-induced fluorescence imagers), will further refine and advance our knowledge of occurrence in tropical and subtropical seas. This information will be useful in determining the potential role of blooms in the modification of system-scale features such as heat, material flux, and albedo. The more comprehensive database on *Trichodesmium* population biomass and distribution derived from satellite studies, along with expanded direct information on its in situ contributions to C and N cycling, will also allow for more precise extrapolation of its oceanic contributions to new N inputs as well as the inclusion of *Trichodesmium* as an explicit component of large-scale modeling of oceanic productivity.

Variations in oceanic productivity over glacial-interglacial time scales have been directly related to subtle variations in the extent of denitrification and cyanobacterial (that is, *Trichodesmium*) N_2 fixation in the sea (*69*). The possibility exists for use of nucleotide probes of *nifH* to examine paleoecological trends of *Trichodesmium* populations in oceanic sediment cores (*70*). Developing a firm understanding of the dynamics and controls of *Trichodesmium* populations in the contemporaneous ocean, along with information on its population trends over geological time scales, will lead to important new insights about controls of oceanic productivity.

REFERENCES AND NOTES

1. The genus *Trichodesmium* is composed of a small number of marine cyanobacterial species within the order Oscillatoriales and was first described by Ehrenberg (*71*). As the name *Trichodesmium* implies (from the Greek, *tricho*: hair, *desmos*: chain), they are filamentous. *Trichodesmium* species are most often observed as fusiform or spherical colonies, although they also occur as single trichomes (*72, 73*). They notably lack heterocysts, the morphologically and biochemically differentiated cells specialized for fixing N_2, which characterize filamentous cyanobacteria of the orders Nostocales and Stigonematales [R. W. Castenholz and J. B. Waterbury, in *Bergey's Manual of Determinative Bacteriology*, J. T. Staley,

Ed. (Williams and Wilkins, Baltimore, 1989), pp. 1710–1727].
2. The Red Sea obtained its name from the coloration imparted by *T. erythraeum* (*71*) [H. J. Carter, *Ann. Mag. Nat. Hist.* **3**, 182 (1863)]. Darwin, while aboard the H.M.S. *Beagle* [C. Darwin, *Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyages of the H.M.S.* Beagle *Round the World Under the Command of Capt. Fitz Roy, R.N.* (Clowes, London, 1845)], as well as Captain J. Cook and his naturalist, J. Banks, aboard the H.M.S. Endeavour, each commented on *Trichodesmium's* appearance and abundance in tropical seas [J. C. Beaglehole, Ed., *The* Endeavor *Journals of Joseph Banks 1768–1771* (Angus and Robertson, Sydney, Australia, 1962), vol. II: *The Journals of Captain James Cook on His Voyages of Discovery*, vol. I: *The Voyage of the* Endeavor *1768–1771* (Cambridge Univ. Press, Cambridge, 1955), pp. 404–405]. Because of its buoyancy and tendency to form colonies, it is easily observed near the sea surface by the naked eye. The colonies, long referred to by mariners as "sea sawdust," aggregate at the surface during periods of low wind stress to form conspicuous surface slicks or blooms.
3. E. J. Carpenter, in *Nitrogen in the Marine Environment*, E. J. Carpenter and D. G. Capone, Eds. (Academic Press, New York, 1983), pp. 65–103.
4. _____, *Mar. Biol. Lett.* **4**, 69 (1983); J. R. Gallon *et al.*, *Arch. Hydrobiol. Suppl.* **117**, 215 (1996).
5. See (*74*) for a summary of historical data on N limitation. Iron (Fe) availability has been shown to limit the growth of phytoplankton in some oceanic regions characterized as high nutrient, low chlorophyll (HNLC) [J. Martin *et al.*, *Nature* **371**, 123 (1994)].
6. R. C. Dugdale, R. D. W. Menzel, J. H. Ryther, *Deep Sea Res.* **7**, 297 (1961). In parallel with the expansion of interest in the marine N cycle, a revolution in fundamental research on N_2 fixation also occurred [R. W. F. Hardy and U. D. Havelka, *Science* **188**, 633 (1975)].
7. At the time, nitrogenase was recognized to be inactivated by O_2. It was generally held that cyanobacteria protected nitrogenase from O_2 evolved through photosynthesis by spatial segregation of nitrogenase into specialized cells named heterocysts, which lacked PS II and did not evolve O_2. Nonheterocystous forms were thought to be incapable of N_2 fixation. After 1970, several other nonheterocystous cyanobacteria were found to have nitrogenase; however, unlike *Trichodesmium*, their nitrogenase was only active under conditions of reduced O_2 concentration, or by temporally segregating N_2 fixation to nonphotosynthetic periods (that is, at night) [P. Fay *et al.*, *Nature* **220**, 810 (1968); P. Fay, *Microbiol. Rev.* **56**, 340 (1992); J. R. Gallon, *New Phytol.* **122**, 571 (1992); B. Bergman, J. R. Gallon, A. N. Rai, L. Stal, *FEMS Microbiol. Rev.* **19**, 139 (1997)].
8. G. E. Fogg, *Ecol. Bull.* **26**, 11 (1978); B. F. Taylor *et al.*, *Arch. Microbiol.* **88**, 205 (1973).
9. J. P. Zehr and L. A. McReynolds, *Appl. Environ. Microbiol.* **55**, 2522 (1989); J. P. Zehr *et al.*, *ibid.* **56**, 3527 (1990).
10. H. W. Paerl, J. C. Priscu, D. L. Brawner, *ibid.* **55**, 2965 (1989).
11. B. Bergman and E. J. Carpenter, *J. Phycol.* **27**, 158 (1991).
12. C. Fredriksson and B. Bergman, *Microbiology* **141**, 2471 (1995).
13. Two cultures are currently available, both apparently strains of *T. erythraeum* [J. P. Zehr, S. Braun, Y. Chen, M. T. Mellon, *J. Exp. Mar. Biol. Ecol.* **203**, 158 (1996)]: strain NIBB 1067, isolated by K. Ohki and Y. Fujita [*Mar. Ecol. Prog. Ser.* **7**, 185 (1982)], and *Trichodesmium* IMS 101, isolated by Prufert-Bebout *et al*. (*14*). The former has been resistant to transplantation, whereas the latter has been disseminated to several laboratories. Additional isolates may now be available.
14. L. Prufert-Bebout, H. W. Paerl, C. Lassen, *Appl. Environ. Microbiol.* **59**, 1367 (1993).
15. The abundance and location of intracellular structures such as gas vacuoles, as well as the form and size of cells and of aggregates or colonies, varies substantially; taxonomic identifications are based on such characteristics [K. Anagnostides and J. Komarek, *Arch. Hydrobiol. Suppl.* **80**, 327 (1988)]. Detailed cytomorphological analysis of natural populations of *Trichodesmium* in the Caribbean and Sargasso seas, which concluded that there are several distinct morphotypes of *Trichodesmium* [S. Janson *et al.*, *J. Phycol.* **31**, 463 (1995)], is supported by both *nifH* (16) [J. Ben-Porath, E. J. Carpenter, J. P. Zehr, *ibid.* **29**, 806 (1993)] and 16*S* rDNA (S. Janson, K. Virgin, B. Bergman, S. Giovannoni, in preparation) sequence analysis.
16. J. P. Zehr, K. Ohki, Y. Fujita, *J. Bacteriol.* **173**, 7055 (1991); G. Sroga, U. Landegren, B. Bergman, M. Lagerstrom-Fermer, *FEMS Microbiol. Lett.* **136**, 137 (1996).
17. A. Wilmotte, J.-M. Neefs, R. De Wachter, *Microbiology* **140**, 2159 (1994).
18. J. P. Zehr, D. Harris, B. Dominici, J. Salerno, *FEMS Microbiol. Lett.*, in press.
19. J. P. Zehr, M. Wyman, V. Miller, L. Duguay, D. G. Capone, *Appl. Environ. Microbiol.* **59**, 669 (1993).
20. D. G. Capone, J. M. O'Neil, J. Zehr, E. J. Carpenter, *ibid.* **56**, 3532 (1990).
21. M. Wyman, J. P. Zehr, D. G. Capone, *ibid.* **62**, 1073 (1996).
22. K. Ohki, J. P. Zehr, Y. Fujita, *J. Gen. Microbiol.* **138**, 2679 (1992).
23. E. J. Carpenter and T. Roenneberg, *Mar. Ecol. Prog. Ser.* **118**, 267 (1995); (*75, 76*). The compensation point is the light intensity at which photosynthetic O_2 production equals respiration.
24. These include the Mehler reaction [photoreduction of O_2 by PS I and a source of adenosine triphosphate (*76*)]; uptake hydrogenase [S. Saino and A. Hattori, *Mar. Biol. (Berlin)* **70**, 251 (1982)]; elevated cytochrome oxidase [B. Bergman, P. J. A. Siddiqui, E. J. Carpenter, G. A. Peschek, *Appl. Environ. Microbiol.* **59**, 3239 (1993)]; photorespiration [W. Li, H. Glover, I. Morris, *Limnol. Oceanogr.* **25**, 447 (1980)]; and superoxide dismutase activity (K. Cunningham and D. G. Capone, in preparation).
25. G. E. Fogg, in *Algal Physiology and Biochemistry*, W. D. P. Stewart, Ed. (Blackwell, Oxford, 1974), pp. 650–682.
26. Autoradiographic localization of photosynthetic $^{14}CO_2$ incorporation in both natural and cultured *Trichodesmium* provided evidence for spatial segregation in colonies [E. J. Carpenter and C. C. Price IV, *Science* **191**, 1278 (1976); H. W. Paerl and P. T. Bland, *Appl. Environ. Microbiol.* **43**, 218 (1982); H. W. Paerl, *J. Phycol.* **30**, 790 (1994)]. Moreover, microelectrode measurements of small-scale O_2 gradients in actively photosynthesizing *Trichodesmium* colonies at times revealed distinct internal hypoxic or anoxic microzones (*27*) [H. W. Paerl and B. M. Bebout, *Science* **241**, 442 (1988)].
27. H. W. Paerl and B. M. Bebout, in *Marine Pelagic Cyanobacteria: Trichodesmium and Other Diazotrophs*, E. J. Carpenter, D. G. Capone, J. Rueter, Eds. (Kluwer Academic, Dordrecht, Netherlands, 1992), pp. 43–59.
28. The fluorescence signature of PS II light-harvesting pigments was found in all cells [E. J. Carpenter *et al.*, *Mar. Ecol. Prog. Ser.* **65**, 151 (1990)]; nitrogenase occurs with carboxysomes, ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO), and phycoerythrin in the same cell (*77, 78*). Paerl *et al*. (*10*) detected nitrogenase by immunolocalization in a high proportion of cells within the colonies they examined; more recent studies of several species of *Trichodesmium* species collected in various waters consistently found that nitrogenase is synthesized in a smaller subset (10 to 40%) of cells, randomly spread through the colony (*11, 12, 77*). Free trichomes occur in nature [for example, (*73*)], although the specific rate of nitrogenase activity associated with free filaments in situ may be considerably less than in intact colonies (*72*). Colonies disaggregated under N_2 and returned to aerobic conditions, or colonies disaggregated under air and assayed under N_2, exhibited nitrogenase activity comparable to whole colonies (D. G. Capone *et al.*, in preparation). Cultures of *Trichodesmium* growing aerobically as individual trichomes fix N_2 at relatively high rates (*14*) [K. Ohki and Y. Fujita, *Mar. Biol. (Berlin)* **98**, 111 (1988)]. However, cultures that exhibit concurrent nitrogenase activity with photosynthesis in single filaments (*13, 14*) are grown at present at subsaturating light levels, which may allow for cellular respiration to maintain sufficiently low O_2 concentrations for nitrogenase activity.
29. Bryceson and Fay (*79*) first suggested spatial segregation of nitrogenase activity and photosynthesis in cells along a trichome, noting the absence of carboxysomes (sites of RuBisCO) in three to five zones along trichomes of *T. erythraeum*, which also had higher reducing potentials. Recent immunolocalization studies of several species of field-collected *Trichodesmium* (*78*) [C. Fredriksson and B. Bergman, *Protoplasma* **197**, 76 (1997)] and the *Trichodesmium* IMS 101 isolate (C. Fredriksson, H. Paerl, B. Bergman, in preparation) reported that within individual trichomes, nitrogenase is localized along each trichome in subsets of several cells with distinct ultrastructural features.
30. T. Saino and A. Hattori, *Deep Sea Res.* **25**, 1259 (1978). Subsequent examination of nitrogenase protein dynamics in field populations found active protein only present in the cells during the day (*20*). Nitrogenase synthesis was initiated in the morning, and activity commenced with the onset of photosynthesis. The daily cycle of synthesis is regulated at the level of transcription, as *nifH* transcripts were detected before the beginning of the light period preceding the appearance of the protein and were present only until midday in natural populations and in *Trichodesmium* sp. IMS 101; this indicated that the diel cycle of synthesis was cued by a factor other than light (*21*). Moreover, there appears to be a subcellular process that results in cessation of activity during the late afternoon. The extant Fe protein component of nitrogenase is converted to an inactive form through an as yet uncharacterized posttranslational protein modification mechanism and "turned off." Immunolocalization studies confirmed that nitrogenase was synthesized and degraded over the day-night cycle (*12*).
31. For N_2 fixation in a coccoid cyanobacterium, see N. Groebblaar, T. C. Huang, H. Y. Lin, T. J. Chow, *FEMS Microbiol. Lett.* **37**, 173 (1986). Circadian clocks have also been found in association with photosynthetic genes of another *Synechococcus* strain [for example, T. Kondo *et al.*, *Science* **266**, 1233 (1994)]. L. Stal and W. Krumbein [*Arch. Microbiol.* **143**, 67 (1983)] reported persistence of N_2 fixation in constant light for one cycle in a filamentous benthic oscillatorian that normally confines nitrogenase activity to dark periods.
32. Y. Chen, J. P. Zehr, M. Mellon, *J. Phycol.* **32**, 96 (1996). A daily cycle of nitrogenase induction and activity persisted for up to six cycles in constant light with a free-running clock of about 26 hours. A diel variation in the compensation point has also been reported; this may be driven by an endogenous rhythm in respiration, because photosynthetic parameters do not exhibit a comparable daily cycle under continuous illumination (*75*).
33. C. S. Reynolds, in *Molecular Ecology of Aquatic Microbes*, I. Joint, Ed. (NATO ASI Series, vol. G 38; Springer-Verlag, Berlin, 1995), pp. 115–132. Low growth rates and high biomass are common strategies for algae inhabiting physically stable, nutrient-poor environments. Interestingly, growth rates of natural populations of *Trichodesmium* based on CO_2 assimilation are generally somewhat more rapid than those based on N_2 uptake (*3, 4*).
34. It had been speculated that molybdenum was a primary limiting factor for *Trichodesmium* [R. W. Howarth and J. J. Cole, *Science* **229**, 653 (1985)], although no substantial evidence has been provided. In contrast, because nitrogenase is an Fe-rich protein, the cell quota for Fe of *Trichodesmium* is considerably higher than in other phytoplankton (*35*). *Trichodesmium* is capable of rapid Fe uptake, although it does not appear to produce siderophores (*35*). Fe additions can stimulate *Trichodesmium* growth and activity [J. G. Rueter *et al.*, *J. Phycol.* **26**, 30 (1990); H. W. Paerl, L. Prufert-Bebout, C. Guo, *Appl. Environ. Microbiol.* **60**, 1044 (1994)]. *Trichodesmium* growth in situ also requires phospho-

rus, and the source of its phosphorus requirement has been the focus of some attention (*4, 36*).
35. J. G. Rueter *et al.*, in (*27*), pp. 289–306.
36. D. M. Karl *et al.*, *ibid.*, pp. 219–237.
37. C. VanBaalen and R. M. Brown, *Arch. Microbiol.* **69**, 79 (1969); A. Walsby, *Br. Phycol. J.* **13**, 103 (1978); E. Gantt *et al.*, *Protoplasma* **119**, 188 (1984). *Trichodesmium* gas vesicles, which can survive pressures at depth in excess of 200 m, have the highest collapse pressure of any cyanobacterial vesicles yet examined.
38. T. Villareal and E. J. Carpenter, *Limnol. Oceanogr.* **35**, 1832 (1990); K. M. Romans, E. J. Carpenter, B. Bergman, *J. Phycol.* **30**, 935 (1994).
39. M. Lewis, O. Ulloa, T. Platt, *Limnol. Oceanogr.* **33**, 92 (1988). Phycobiliproteins, which have a high efficiency of transfer of light energy, appear to be the primary light-harvesting pigments of photosynthesis (*4*) [S. Shimura and Y. Fujita, *Mar. Biol. (Berlin)* **31**, 121 (1975)]. *Trichodesmium* also has relatively high concentrations of carotenoids (*3, 4*) [K. Hogetsu and M. F. Watanabe, in *Studies on the Community of Marine Pelagic Blue-Green Algae*, R. Marumo, Ed. (Ocean Research Institute, Tokyo, 1975), pp. 36–40], as well as ultraviolet (UV)-absorbing compounds that may each confer protection from photooxidative damage (*80*) [A. Subramaniam, thesis, State University of New York, Stony Brook (1995)]. Phycobiliprotein complexes may also play a photoprotectant role under high-light conditions by reducing their quantum efficiency and by converting some phycourobilin (λ_{max} = 495 nm) to phycoerythrin (λ_{max} = 595 nm), thereby reducing absorption at lower wavelengths (*80*).
40. V. P. Devassy, P. M. Bhattathiri, S. Z. Qasim, *Indian J. Mar. Sci.* **7**, 168 (1978); R. Santhanam *et al.*, *ibid.* **23**, 27 (1994); (*36*). For a summary of historical reports of extensive blooms over the last several decades, see E. J. Carpenter and D. G. Capone, in (*27*), pp. 211–217.
41. The high reflectivity of gas vesicles and the high concentrations of phycobiliproteins in the cells provide useful features for remote sensing (*42*) [S. Tassan, *Int. J. Remote Sens.* **16**, 3619 (1995); C. Dupouy, in (*27*), pp. 177–191]. Capone *et al.* (*81*) recently encountered a bloom in the Arabian Sea that lasted about 7 days and was retrospectively observed in images from AVHRR satellite overpasses in the morning but not in the afternoon, consistent with shipboard observations that the bloom sank slightly (to ~0.5 m) each afternoon. From the satellite imagery, the areal extent of this bloom was conservatively estimated to be ~1 × 10^6 km^2. *Trichodesmium* blooms have also been observed from the U.S. space shuttle [for example, D. A. Kuchler and D. Jupp, *Int. J. Remote Sens.* **9**, 1299 (1988)].
42. A. Subramaniam and E. J. Carpenter, *Int. J. Remote Sens.* **15**, 1559 (1994).
43. R. L. Oliver and G. G. Ganf, *J. Plankton Res.* **10**, 1155 (1988). *Trichodesmium*, with its UV-absorbing compounds and phycobiliproteins, displays higher absorption than eukaryotic phytoplankton in the UV and blue regions of the spectrum (*80*).
44. Episodic phytoplankton blooms may contribute to feedback in the warm water pool climate system in the Pacific [D. A. Siegel *et al.*, *J. Geophys. Res.* **100**, 4885 (1995)]. Cyanobacterial blooms in the Baltic Sea increase sea surface temperature locally by 1.5°C [M. Kahru, J.-M. Leppanen, O. Rud, *Mar. Ecol. Prog. Ser.* **191**, 1 (1993)]. Phytoplankton biomass may influence the flux of moisture [S. Sathyendranath *et al.*, *Nature* **349**, 54 (1991)]. The dense accumulation of planktonic biomass at the interface may increase viscosity [I. R. Jenkinson, *Oceanol. Acta* **16**, 317 (1993)] providing turbulent damping and increasing diffusion rates across the air-sea interface.
45. J. O'Neil and M. Roman, in (*27*), pp. 61–73.
46. S. Hawser *et al.*, *J. Appl. Phycol.* **4**, 79 (1992).
47. Some harpacticoid copepods are able to graze *Trichodesmium* to >75% of their body weight per day [J. O'Neil and M. Roman, *Hydrobiologia* **292–293**, 235 (1994)] and can consume 33 to 45% of colony N per day [J. O'Neil, P. M. Metzer, P. Glibert, *Mar. Biol. (Berlin)* **125**, 89 (1996)].
48. From 25 to 50% of recently fixed N by freshly collected colonies could be accounted for by the net release of amino acids [D. G. Capone, M. D. Ferrier, E. J. Carpenter, *Appl. Environ. Microbiol.* **60**, 3989 (1994)] or by the accumulation of ^{15}N-dissolved organic N (P. Glibert and D. Bronk, *ibid.*, p. 3996).
49. H. W. Paerl, B. M. Bebout, L. E. Prufert, *J. Phycol.* **25**, 773 (1989).
50. Cruises through regions in which *Trichodesmium* blooms occur are infrequent, and conventional oceanographic cruises seldom allow time for opportunistic sampling of blooms. Moreover, because of their size and buoyancy, traditional methods of microplankton sampling are strongly biased against accurate assessment of *Trichodesmium* even under nonbloom conditions. *Trichodesmium* is often viewed as a nuisance organism in plankton net–based sampling focused on microplankton collection and quantitation, as high densities clog nets. Net sampling, unless performed carefully at low towing speeds and with fine-mesh nets (≤100 μm), will disrupt the relatively delicate colonies. Routine protocols for plankton counting, measuring chlorophyll and primary productivity on samples drawn from water bottles, may also impose biases. Because colonies are buoyant, they rapidly rise to the top of water sample bottles (sample water is drawn from the bottom). Relatively small sample volumes are used in most of these procedures (~300 ml and often less) and would likely undersample large colonial phytoplankton, such as *Trichodesmium*, that typically occur at concentrations at or below one colony per liter (under nonbloom conditions). Prescreening of water, commonly performed to remove large zooplankton, also removes *Trichodesmium* colonies, thereby eliminating their contribution to estimates of biomass or C fixation. Moreover, unless discharged by acid treatment, gas vesicles prevent cells from sinking in Utermohl settling chambers (used for counting phytoplankton) or sedimenting during centrifugation. Results from conventional oceanographic phytoplankton surveys in tropical areas should therefore be viewed cautiously with regard to their accuracy in quantitatively estimating *Trichodesmium* abundance and total C and N fixation unless sampling and handling protocols were specifically adapted to account for these organisms. Recent satellite evidence (*41, 42*) reinforces the proposition that planktonic diazotrophs are undersampled.
51. D. G. Capone and E. J. Carpenter, *Science* **217**, 1140 (1982); J. N. Galloway *et al.*, *Global Biogeochem. Cycles* **9**, 235 (1995). The relatively small global estimate is attributable to the general acceptance of Carpenter's (*3*) calculation for *Trichodesmium* N input by N_2 fixation, which, for large expanses of the ocean, depended on historical plankton surveys that likely underestimated abundances of *Trichodesmium* (*50*).
52. Primary productivity is dependent on two distinct sources of N: "recycled" N, which results from the cycling of autochthonous organic and inorganic material, and "new" N, which is defined as allochthonous N that arrives de novo into a system. Sources of new N include NO_3^- advecting or diffusing up from the large reservoirs of NO_3^- at depth, combined forms of N from wet or dry atmospheric deposition, and N entering into the system through N_2 fixation [R. C. Dugdale and J. J. Goering, *Limnol. Oceanogr.* **12**, 196 (1967)]. Relative to other sources of new N, nitrate from depth is generally considered the most important (*82–84*).
53. D. G. Capone, *Mitt. Int. Ver. Theor. Angew. Limnol.* **25**, 105 (1996); (*82, 85*).
54. The oceans likely play a key role in the global C cycle [U. Siegenthaller and J. Sarmiento, *Nature* **365**, 119 (1993)]. It is postulated that the marine biota serve as a "biological pump" for sequestering C into the deep ocean [A. R. Longhurst and W. G. Harrison, *Prog. Oceanogr.* **22**, 47 (1989)].
55. D. M. Karl *et al.*, *Nature* **373**, 230 (1995); (*82*). If PO_4^{3-} limits *Trichodesmium*, its supply from depth would co-occur with deep CO_2. However, Fe is currently thought to be the most critical limiting nutrient for *Trichodesmium* (*34–36*). In this regard, the atmospheric supply of Fe would ultimately constrain *Trichodesmium's* capacity to sequester CO_2.
56. A budget for the upper water column of North Pacific waters near Hawaii (*36*) required an input by N_2 fixation about equivalent to vertical N flux in order to achieve balance. Michaels *et al*. (*86*) estimated an input of N between 50 and 75 Tg $year^{-1}$ to account for observed excesses of combined N in the North Atlantic; M. Furnas *et al*. [*Great Barrier Reef Research Commission Res. Pub. 36* (1995)] invoked extensive N_2 fixation to balance nutrient budgets for two sections of the Australian shelf–Coral Sea along the Great Barrier Reef. The Arabian Sea budget presented by K. Somasundar *et al*. [*Mar. Chem.* **30**, 363 (1990)] indicates a deficit of ~28 Tg N, which they suggest may be partially offset by N_2 fixation. Global budgets generally reveal an excess of losses over inputs (*51*) [J. Christensen *et al.*, *Global Biogeochem. Cycles* **1**, 97 (1987); D. G. Capone, in *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides and Halomethanes*, W. B. Whitman and J. E. Rogers, Eds. (American Society for Microbiology, Washington, DC, 1991), pp. 255–275]. D. Hansell and T. Y. Waterhouse [*EOS* (suppl.) **76**, OS17 (1996)] reported an anomaly in surface total organic N in the oligotrophic North Pacific, which they attributed to N_2 fixation.
57. Vertical NO_3^- flux is computed as the product of the NO_3^- gradient at the nitracline and the vertical eddy diffusivity (K_z). Nitrate gradients used to calculate this term do not vary widely within the major oceanic basins (*74*). Although there is considerable debate regarding appropriate values for diapycnal eddy diffusivities, values in the range of 1 × 10^{-5} to 5 × 10^{-5} m^{-2} s^{-1} are commonly reported or used (*74, 83, 86*). Eddy diffusivities for open-ocean systems have been estimated by various approaches, and larger values have been reported [for example, (*74, 88*)]. Depth-integrated uptake of $^{15}NO_3^-$, used to estimate new N demand in the euphotic zone, often exceeds NO_3^- flux into the upper water column in tropical waters (*83, 87*) [F. King and A. H. Devol, *Limnol. Oceanogr.* **24**, 645 (1979)]. However, tracer incubation methods may cause a substantial nutrient perturbation in highly nutrient-depleted waters, thereby artificially stimulating NO_3^- uptake [P. M. Glibert and D. G. Capone, in *Nitrogen Isotope Techniques*, R. Knowles and T. H. Blackburn, Eds. (Academic Press, New York, 1993), pp. 243–272]. Moreover, although it is often assumed that photoinhibition of nitrification prevents recycling of NH_4^+ to NO_3^- within the euphotic zone [R. Olsen, *J. Mar. Res.* **39**, 227 (1981)], nitrification occurs in the lower euphotic zone and some NO_3^- uptake may be considered recycled production [B. B. Ward, K. A. Kilpatrick, E. H. Renger, R. W. Eppley, *Limnol. Oceanogr.* **34**, 493 (1989)].
58. Estimates of net productivity inferred from O_2 dynamics in the upper water column exceed estimates of input fluxes (*88*); PON export can exceed conventional inputs (*36, 89*).
59. Typically a $\delta^{15}N$ of 0 to 2 per mil, where $\delta^{15}N$ equals $[(^{15}N{:}^{14}N_{sample}/^{15}N{:}^{14}N_{air}) - 1] \times 1000$. Organic production dependent on N_2 fixation results in biomass with an N isotopic ratio relatively low in ^{15}N and similar to that of the available pool of N_2 (that is, $\delta^{15}N$ near zero). This is distinct from organic matter production dependent on fixed forms of N, which are usually heavier (that is, a greater relative ratio of ^{15}N to ^{14}N), and thereby provides a distinct signature for tracing the movement of recently fixed N into the food web. Light PON is most often found in areas where *Trichodesmium* is abundant (*84, 90*) [E. Wada and A. Hattori, *Nitrogen in the Sea: Forms, Abundances, and Rate Processes* (CRC Press, Boca Raton, FL, 1991); M. A. Altabet *et al.*, *Nature* **354**, 136 (1991); S. A. Macko, L. C. Entzeroth, P. L. Parker, *Naturwissenschaften* **71**, 374 (1984); M. M. Mullin, G. H. Rau, R. W. Eppley, *Limnol. Oceanogr.* **29**, 245 (1984)]. Recently, L. Tupas, M. P. Sampson, and D. M. Karl [*Eos* (suppl.) **76**, OS86 (1996)] reported an input of light surface PON settling into deep (for example, 1500 m) sediment traps during the summer at the Hawaiian Ocean Time Series (HOT) station north of Hawaii, which they attributed to *Trichodesmium*. Surface PON had a substantially lighter signal,

relative to deeper PON, during the bloom we observed in the Arabian Sea (*81*). Isotopically light PON may also result from other processes, such as uptake of recycled ammonium [D. M. Checkley and L. C. Entzeroth, *J. Plankton Res.* **7**, 553 (1985)], export of ^{15}N-enriched fecal material from the euphotic zone, or strong isotopic fractionation during nitrate uptake (*84*) [T. A. Villareal, M. A. Altabet, K. Culver-Rymsza, *Nature* **363**, 709 (1993)], or use of atmospherically derived anthropogenic N emissions, such as NO_x and NH_3/NH_4^+ (*91*). However, these processes are unlikely in the highly oligotrophic open ocean (*90*).

60. *Trichodesmium* spp. can represent a major fraction (~60%) of total chlorophyll and are important in primary production and N input in the Caribbean Sea (*92*). In the Indian Ocean, *Trichodesmium* can reach a biomass of up to 30 mg of chlorophyll a per cubic meter (*79*). E. J. Carpenter and K. Romans [*Science* **254**, 1356 (1991)] concluded that *Trichodesmium* is the most abundant phytoplankton in the tropical North Atlantic. C. S. Davis, S. M. Gallager, and A. R. Solow [*ibid.* **257**, 230 (1992)], using towed video microscopy, found very high abundance of *Trichodesmium* in North Atlantic waters. *Trichodesmium* accounted for a mean of 17% of total chlorophyll a throughout the year at the HOT station (*58*). *Richelia intracellularis* (a common endosymbiont of diatoms) [T. Villareal, in (*27*), pp. 163–175] can also contribute substantially to new N inputs (E. J. Carpenter *et al.*, in preparation).
61. Subtropical studies (*93–95*) found that even during the summer, when *Trichodesmium* was relatively abundant and active, areal rates of N_2 fixation were generally low compared with tropical waters.
62. K. R. Gunderson *et al*., *Pac. Sci.* **30**, 45 (1976).
63. T. Saino, thesis, University of Tokyo (1977).
64. D. G. Capone *et al.*, in preparation.
65. J. J. Goering *et al.*, *Limnol. Oceanogr.* **11**, 614 (1966).
66. T. Osborn, personal communication; K. L. Polzin, J. M. Toole, J. R. Ledwell, R. W. Schmitt, *Science* **276**, 93 (1997). J. R. Ledwell *et al*. [*Nature* **364**, 701 (1993)] estimated K_z values of 1.1×10^{-5} m^2 s^{-1} at a site 1200 km west of the Canary Islands during an extended (several months) SF_6 tracer experiment; K. A. VanScoy and D. E. Kelley [*Eos* (suppl.) **76**, OS40 (1996)] recently reported an integrated, basin-wide bulk K_z upper limit of 3×10^{-5} m^2 s^{-1} on the basis of a two-decade data set of tritium penetration.
67. For a bloom described in (*65*), we derived an input in the top 0.5 m of 115 μmol N m^{-2} day^{-1}, compared with the average of 41 μmol N m^{-2} day^{-1} for other, nonbloom stations during the same period. Similarly, a surface accumulation with input estimated to be ~300 μmol N m^{-2} day^{-1} was reported in (*62*). For a bloom encountered in the early spring intermonsoon in the central Arabian Sea (*81*), we estimated the bloom contribution of N through N_2 fixation to be ~100 μmol N m^{-2} day^{-1}, compared with 35 μmol N m^{-2} day^{-1} through the rest of the water column.
68. H. W. Paerl, *Nature* **316**, 747 (1985); R. Duce *et al.*, *Global Biogeochem. Cycles* **5**, 193 (1991); S. Cornell *et al.*, *Nature* **376**, 243 (1995); (*91*).
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89. D. M. Karl *et al.*, in preparation.
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95. T. Mague *et al.*, *Mar. Biol. (Berlin)* **41**, 213 (1977).
96. J. Felsenstein, PHYLIP Phylogeny Inference Package (version 3.5c), Department of Genetics, University of Washington, Seattle.
97. Water samples were collected at various depths over the upper 200 m by CTD (conductivity, temperature, depth)-rosette. *Trichodesmium* population abundance and depth distribution were obtained by filtering whole water bottles onto 5- or 10-μm filters, followed by direct counting by epifluorescent microscopy. For N_2 fixation, colonies of *Trichodesmium* were obtained by plankton tows at 10 to 15 m and assayed using the C_2H_2 reduction method. Samples were incubated on deck under full sunlight (100%) or with neutral density screening to approximate light levels of 1, 10, 28, and 55% of surface irradiance. For estimates of N_2 fixation, we assumed a conversion ratio of 4 mol of C_2H_4 produced per mole of N_2. Volumetric rates of N_2 fixation were estimated by scaling the rates determined on isolated colonies with reference to the population density observed at the depth corresponding to the light level of incubation. Chlorophyll of the <202-μm fraction was determined by standard methods, whereas *Trichodesmium* chlorophyll was estimated by determining chlorophyll a per cell and scaling that to total trichome counts at each depth. Primary productivity was determined using ^{14}C-bicarbonate on assays of <202-μm bulk water from each depth or, as for N_2 fixation, on isolated colonies and scaled to trichome concentrations at specific depth.
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