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Trichodesmium in coastal waters of Tanzania: diversity, seasonality, nitrogen and carbon fixation

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Abstract

Seasonal distribution, nitrogen fixation and primary productivity of *Trichodesmium* species were intermittently studied in the coastal waters of Tanzania. Samples were collected in 1975/6, 1980, 1993/4, 1994/5 and 1998/9. Four colony forming species were found, i.e. *T. erythraeum*, *T. tenue*, *T. thiebautii* and one unidentified *Trichodesmium* sp. while *T. contortum* was rarely encountered, and only as individual trichomes. *T. erythraeum* was most abundant, although other *Trichodesmium* species dominated during particular periods of the year. The occurrence of *Trichodesmium* showed a consistent seasonal pattern. High *Trichodesmium* biomass was promoted by the NE monsoon (December–April) while it was low or absent during the SE monsoon (June–October). The biomass was highest at the surface especially during calm weather periods. The NE monsoon was characterized by elevated rainfall, temperature and nitrate concentrations while salinity, light intensity and turbidity tended to decrease. Phosphate concentrations did not show systematic variations with season. The rate of nitrogen fixation by *Trichodesmium* species in surface waters was 1.8 ± 1.6 pmol N trichome^{-1} h^{-1} giving an average N_2 fixation of 42.7 mmol N m^{-3}y^{-1}. The mean rate of carbon fixation was 1.15 ± 0.3 ng C trichomes^{-1} h^{-1} in the upper 5 m depth. It is estimated that *Trichodesmium* contributes about 0.03–20% of the total CO_2 fixation in the coastal surface waters during the SE and NE monsoon, respectively.

Introduction

Cyanobacteria are important contributors to benthic and open ocean primary production through photosynthesis and nitrogen fixation (Hoffmann, 1999). *Trichodesmium,* a planktonic nitrogen-fixing cyanobacterium, is particularly abundant and occurs in tropical and sub-tropical seas where it contributes a major fraction of new nitrogen input to the oligotrophic surface waters (Carpenter & Romans, 1991; Gallon et al., 1996; Capone et al., 1997; Karl et al., 1997). *Trichodesmium* is a filamentous, non-heterocystous cyanobacterium often forming colonies (Bergman et al., 1997). *Trichodesmium* colonies may be abundant in surface waters where it often forms conspicuous blooms during calm periods (Steven & Glombitza, 1972; Carpenter & Price, 1976; Bryceson, 1982; Karl et al., 1992). In addition, *Trichodesmium* colonies form a substratum that other organisms, such as diatoms, dinoflagellates, fungi, protozoans, hydrozoans and copepods colonize. It has been suggested

that *Trichodesmium* serves as organic resources on which these biota depends (O'Neil & Romans, 1992; Siddiqui et al., 1992; O'Neil, 1999). On the other hand, at least one *Trichodesmium* species produces toxins that may negatively affect marine invertebrates (Hawser et al., 1992; Hawser & Codd, 1992).

Studies on cyanobacteria such as *Trichodesmium* in the western Indian Ocean and along the Tanzanian coast are few. Previous studies in the area include those of Bryceson (1982) who noted higher *Trichodesmium* biomass during December–May. Also, in the adjacent areas off the Kenyan coast, Kromkamp et al. (1997) observed a higher *Trichodesmium* biomass during the intermonsoon period from November to December 1992 as compared to the preceding south-east monsoon (SE) period. Furthermore, Bryceson & Fay (1981) reported a mean ethylene production (ARA) of 3.5–10.8 nmol C_2H_4 $(10^3$ trichomes$)^{-1}$ h^{-1} in coastal waters off Dar es Salaam (Tanzania). Here we present data on *Trichodesmium* diversity, seasonal distribution and on its nitrogen and carbon fixation potentials aimed at providing baseline information on selected aspects of the ecology and physiology of *Trichodesmium* species in the coastal waters of Tanzania.

Materials and methods

Sampling sites

Data from 1975/6 and 1980 were collected at the Dar-es-Salaam coast at an offshore station (with a depth of about 60 m) located at approximately 6° 40′ S and 39° 17′ E outside Mbudya and Bongoyo island, here referred to as site D (Fig. 1). During 1993/4, 1994/5 and 1998/9 the sampling was conducted at an offshore station located at approximately 6° 9′ S and 39° 9′ E, west of Zanzibar town (referred to as site Z) with a depth of about 25 m. The climate of the region is tropical; with air temperatures at sea level rarely falling below 20 °C. Seawater temperature fluctuates between 25 and 30 °C. The air is humid with an annual average precipitation of about 1100–1500 mm. The dominant factors determining the hydrography of the East African Indian Ocean are the monsoon trade winds. The northeast (NE) monsoon persists from December to April and the SE monsoon from June to October (Newell, 1959). Climatic characteristics during the NE monsoon are higher temperature, lower wind speed and calmer sea. Tides in this area are semi-diurnal with a spring tidal range of approximately 3 m (Lwiza & Bigendako, 1988).

Trichodesmium *abundance*

In 1975/6, sub-surface water samples (125 ml) were collected at two-week intervals and immediately fixed in 1% Lugol's solution and the trichomes were counted after a 24 h settling period (Utermöhl, 1931; Lund et al., 1958). In 1993/4, 1994/95 and 1998, triplicate samples were collected two to four times per month by concentrating 10–20 l of seawater from the desired depths (varying from 0 to 20 m) through a 20 μm mesh size net. The samples were immediately preserved in 4% borax buffered (pH 8.0) formalin. Counting of trichomes was done under a light microscope (Olympus BH2, Japan) using a Sedgewick rafter cell. Trichome number in colonies was enumerated after disruption of the colonies. Colonies were picked using a plastic loop and transferred into filtered seawater (FSW, 0.22 μm membrane filters) for rinsing. Then individual colonies were transferred into eppendof tubes containing one ml FSW and vigorously shaken to disrupt the colonies. Further disruption was sometimes aided by teasing the colonies using plastic loops. Following disruption, individual trichomes were counted using a Sedgewick rafter cell. In 1975/6, *Trichodesmium* species were not identified to species level but were all regarded as *Oscillatoria* (*Trichodesmium*) *erythraea*. In 1993/4, *Trichodesmium* species were identified according to Carpenter & Janson (per.com to T.J. Lyimo). In 1994/5 and 1998, identification was done following the descriptions given by Janson et al. (1995). In order to get the relative abundance of the different *Trichodesmium* species, integrative net samples were collected by vertically hauling plankton net (90 μm mesh size) from a depth of 20 m. In the laboratory, 100 *Trichodesmium* trichomes were identified to species level using light microscopy and the respective numbers of each species recorded.

Physical and chemical parameters

Temperature and turbidity were measured *in situ* by a thermometer attached to the water sampler and a 20 cm diameter Secchi disc, respectively. In 1993, light intensity was measured with a light meter (QSI-140B Integrating Quantum Scalar Irradiance Meter, Biospherical Instruments Inc., California) while in

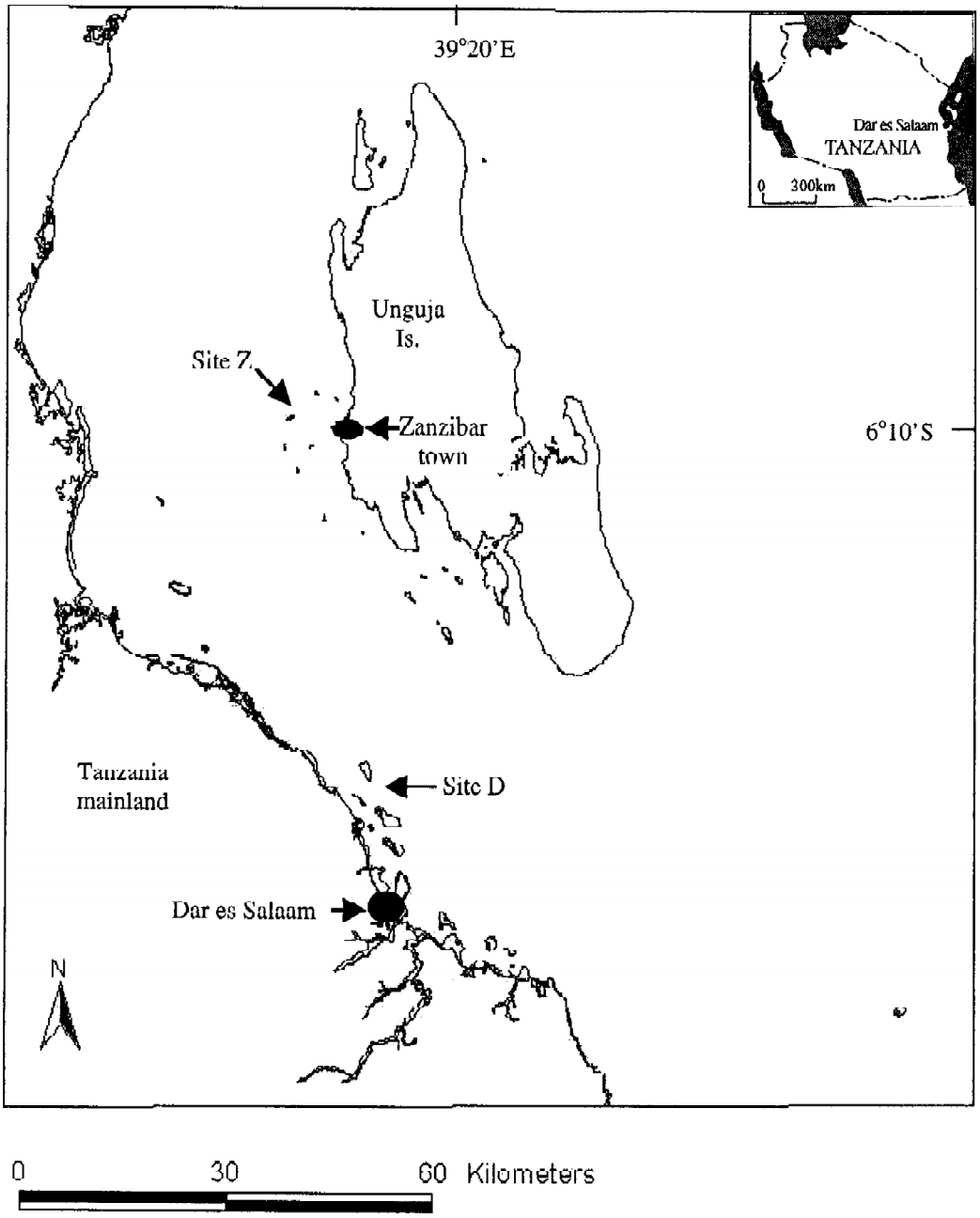


Figure 1. Map of the study area with the sampling sites marked by the letter D for Dar es Salaam site and Z for Zanzibar site.

1994/5 and in 1998 light was measured using a LI-COR (LI-189) photometer. Salinity was measured in the field by a hand refractometer (ATAGO S/MILL, Japan). Rainfall and wind speed data were obtained from meteorology department at Zanzibar airport.

Surface water samples for nutrient analyses (PO_4^+ and NO_3^-) were filtered through glass fiber filters (GF/F) into 20 ml acid washed plastic vials and kept cool on ice for transport to the laboratory. Samples were kept frozen (−20 °C) if not immediately analyzed. Phosphate and nitrate were in 1975/6 determ-

ined according to Strickland & Parsons (1968), and according to Parsons et al. (1984) in 1993/4, 1994/5 and 1998. However, in 1998, nitrate was measured using a Technicon 2 auto-analyzer.

Nitrogen fixation

In 1975/6 and 1980, nitrogen fixation rates were measured by the acetylene reduction assay (ARA) as described by Burris (1972). Twenty five ml water samples containing *Trichodesmium* colonies were sealed into 27.5 ml serum bottles. Then 0.6 ml acetylene gas was injected by a syringe to each bottle and the pressure allowed to equalize till the amount of the acetylene remained in the serum bottles was 20%. The samples were incubated *in situ* for ca. 2 h in full sunlight in a floating cage placed immediately below the surface and agitated gently by the waves. Samples of the headspace gas was withdrawn and stored in 8 ml evacuated tubes until analyzed by a gas chromatograph (GC). Ethylene production was normalized to biomass, taken as number of trichomes. In 1993 and 1999, nitrogen fixation rate was measured by ARA method as described by Capone (1993). *Trichodesmium* colonies were collected by plankton tows, picked using a plastic loop and transferred to FSW. The colonies were then transferred to 4 ml of FSW in 10-ml serum bottles, sealed by rubber stoppers and capped with aluminum caps. Ten percent of the air phase was withdrawn from the bottles and replaced with an identical volume of acetylene gas generated from calcium carbide. Samples were incubated *in situ* for ca. 1 h (in 1993) and for ca. 2 h (in 1999) in a floating cage as described above. In 1993, 0.55 ml of gas was withdrawn from the gas phase by gas tight syringes, sealed in a rubber stopper and within 1–2 h injected into a GC. The GC was equipped with a Porapack N column with airflow of 50 – 75 $cm^3 min^{-1}$. In 1999, 4 ml of the gas samples were withdrawn and stored in 4-ml pre-evacuated vacutainers and analyzed using a Chrompack CP-2002P GC (The Netherlands) equipped with a Hayesep A column at an oven temperature of 35 °C. The amount of ethylene produced was calculated as described by Capone (1993). In all cases, known concentrations of ethylene gas served as standard and ethylene production was normalized to the number of trichomes.

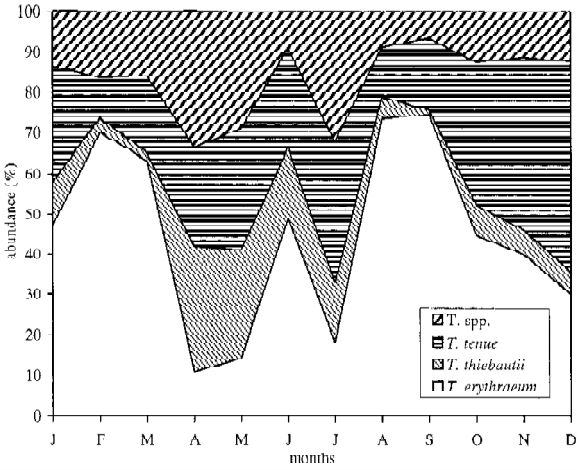


Figure 2. Seasonal variation of *Trichodesmium* species abundance collected from site Z during 1998. The values represent the average of triplicate samples collected twice per month.

Photosynthetic activity

Rates of carbon fixation were measured using the ^{14}C-bicarbonate technique as described by Strickland & Parsons (1968). *Trichodesmium* colonies were collected in July 1999 at around 10.00 am. In the laboratory, colonies of similar size were picked using a plastic loop and transferred to FSW for rinsing. One colony was transferred to a 20-ml glass scintillation vial containing 5-ml FSW. Three μl aliquots of $NaH^{14}CO_3$ (1 mCi/ml) were added to each vial, immediately transferred to a dark box and deployed at sea for *in situ* incubations. The incubations were done at 0 m, 1 m, 2 m, 3 m, 5 m, 10 m and 20 m depths and lasted ca. 6 h, from noon to 1800 hrs. Two types of controls were used during this experiment, (1) a bottle containing FSW without *Trichodesmium* colonies incubated in light near the surface (1 m), (2) a bottle covered with foil (dark) containing *Trichodesmium* colonies incubated at 18-m depth. The second control always showed higher C-uptake activity and these values were therefore subtracted from the light exposed experimental bottle when calculating productivity. Incubations were terminated by addition of ~15 μl of 6 m HCl to each vial. In the laboratory, samples were purged with air for approximately 30 min. This was followed by addition of 15 ml of Lumagel (Lumac, The Netherlands) scintillation fluid. Samples were then left in darkness for 12 h before counting using a TRI-CARB 2100TR liquid scintillation counter (Packard, Canberra). The biomass was estimated by counting trichomes of five

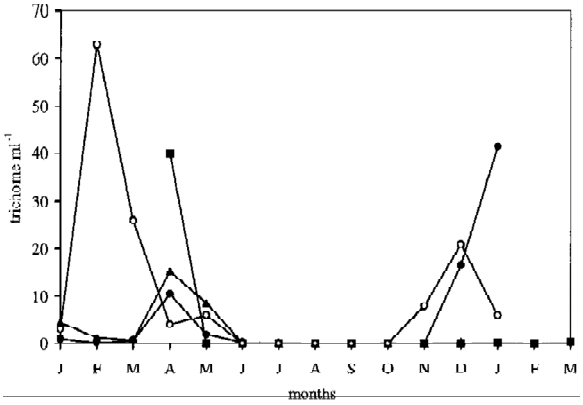


Figure 3. Seasonal variation of *Trichodesmium* total abundance in Tanzanian coastal surface waters collected from site D during 1975/6 (open circles), and from site Z, during1993/4 (closed circles), 1994/5 (closed squares) and 1998 (closed triangles). The values represent the average of triplicate samples collected twice per month in 1975/6, 1994/5 and 1998 and four times per month in 1993/4.

Trichodesmium colonies (as described above) of similar size as the ones incubated. The mean number of trichomes per colony obtained was taken as the number of trichomes in each experimental vial.

Results

Species composition

In 1975/6, all *Trichodesmium* species were regarded as *Oscillatoria* (*Trichodesmium*) *erythraea*. In 1993/4, four species were encountered and identified as *T. erythraeum*, *T. thiebautii*, *T. tenue* and *T. radians*. Also four species were encountered in 1994/5 and identified as *T. erythraeum*, *T. thiebautii*, *T. tenue* and one unidentified *Trichodesmium* species, while in 1998 five species were encountered: *T. erythraeum*, *T. thiebautii*, *T. tenue*, *T. contortum* and an unknown *Trichodesmium* species. The species identified as *T. radians* during 1993/4 is similar to that described by Janson et al. (1995) as of uncertain taxonomic position, hence *Trichodesmium* sp. During 1998, *T. erythraeum* dominated the biomass in February–March (>65%), June (~50%), and (~70%) in August–September (Fig. 2). However, other species such as *T. tenue*, *T. thiebautii* or *Trichodesmium* sp., could dominate at some period within the year. *T. contortum* was least common and was always observed as individual trichomes.

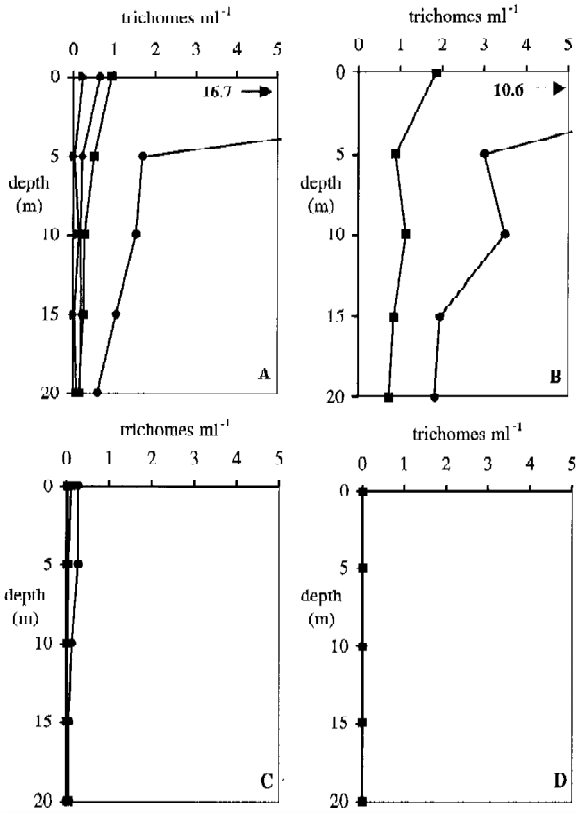


Figure 4. Vertical distribution of *Trichodesmium* total abundance at site Z in 1993, (A) During the NE monsoon period in December (closed circles), January (closed squares), February (closed triangles), and March (closed diamonds), (B) During the inter-monsoon period in April (closed circles) and May (closed squares), (C) During the SE monsoon period in June (closed circles), July (closed squares), August (closed triangles) and September (closed diamonds) and (D) During inter monsoon period in October (closed circles) and November (closed squares). The values represent the average of triplicate samples collected twice per month.

Biomass

Trichodesmium abundance varied with season ranging from zero, as recorded at site D in June–October (1975) and site Z in August–September 1998, to 63 000 trichomes l^{-1} at site D in February 1975 (Fig. 3). Although there were some inter-year variations in the abundance of *Trichodesmium*, higher numbers were recorded during the NE monsoon (December–April) while no or a few trichomes were detected during the SE monsoon (June – October). Distinct surface blooms of *Trichodesmium* were sometimes observed during the NE monsoon period with abundance ranging from 38 000 to 120 000 trichomes l^{-1}. The

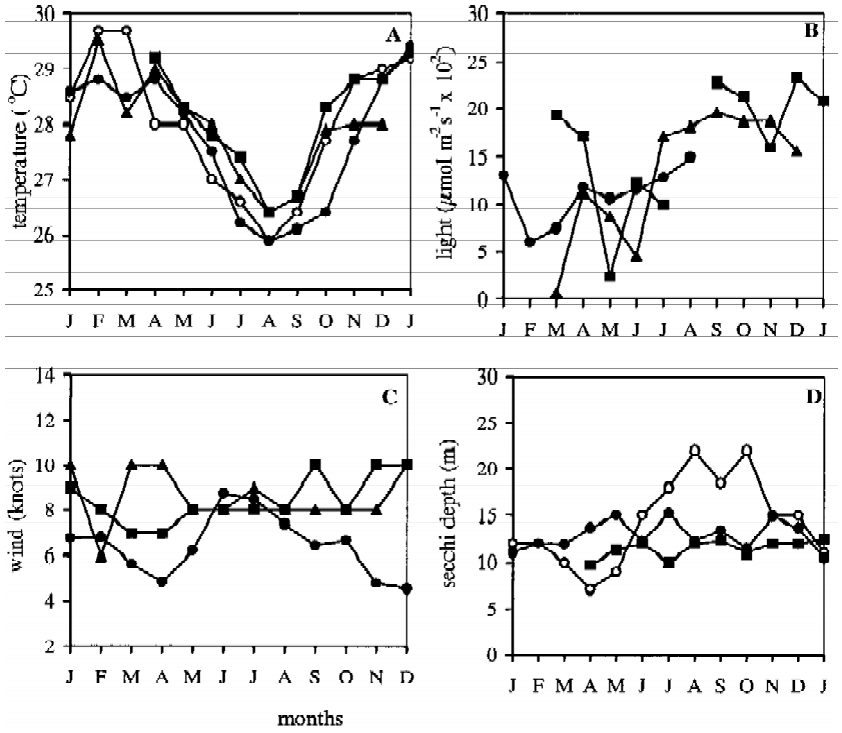


Figure 5. Seasonal variations in physical oceanographic parameters in the coastal area of Dar es Salaam and Zanzibar (Tanzania), (A) Surface water temperatures at site D during 1975/6 (open circles) and site Z during 1993/4 (closed circles), 1994/5 (closed squares) and 1998 (closed triangles), (B) Surface light intensity at site Z during 1993 (closed circles), 1994/5 (closed squares) and 1998 (closed triangles), (C) Wind speed in Zanzibar area during 1993 (closed circles), 1994 (closed squares) and 1998 (closed triangles) and (D) Turbidity, presented as secchi depth readings at site D during 1975/6 (open circles) and site Z during 1993/4 (closed circles) and 1994/5 (closed squares).

blooms often covered large surface areas or formed long streaks about 5–10 m wide. During bloom conditions, *T. erythraeum* colonies were sometimes found joined together by a colorless mucilaginous material. The depth distribution pattern down to 20 m of *Trichodesmium* species during 1993 is illustrated in Figure 4. Higher biomass was often restricted to the surface waters, i.e. the upper 5 m during the NE monsoon (Fig. 4A, B). During the SE monsoon, however, the biomass was low from surface down to 20 m (Fig. 4C, D).

Environmental parameters

Monthly values of physical oceanographic parameters are shown in Fig. 5. Water temperatures (Fig. 5A) were higher during the NE monsoon and ranged from 25.9 °C (site D and Z) to 29.7 °C (site D). The SE monsoon consistently offered lower temperatures, the lowest being in August. Surface light intensities (Fig. 5B) ranged from 60 μmol photons m^{-2} s^{-1} (site Z) to 2320 μmol photons m^{-2} s^{-1} (site Z). Wind speed was generally low during the NE monsoon (Fig. 5C) ranging from 4.5 knots (site Z) to 10 knots (site Z). The water was generally more turbid during the NE monsoon (Fig. 5D) with Secchi depth readings ranging from 7 m (site D) to 22 m (site D).

The monthly variations in chemical oceanographic parameters are shown in Figure 6. Seasonal variability in total rainfall pattern was obvious with two distinct rain seasons, a long rain period from March to May and a short rain period from November to December (Fig. 6A). Highest average rainfall at both sites during the study period occurred in April and the lowest in August. As expected, salinity tended to decrease during the rainy seasons (Fig. 6B) and ranged from 33 (site Z) to 36 (site Z). Phosphate concentrations did not show variations with seasons (Fig. 6C) and ranged from 0.8 nM (site Z) to 5.2 nM (site D). Nitrate concentrations were distinctly higher during the NE monsoon period, showing a maximum value of 77.4

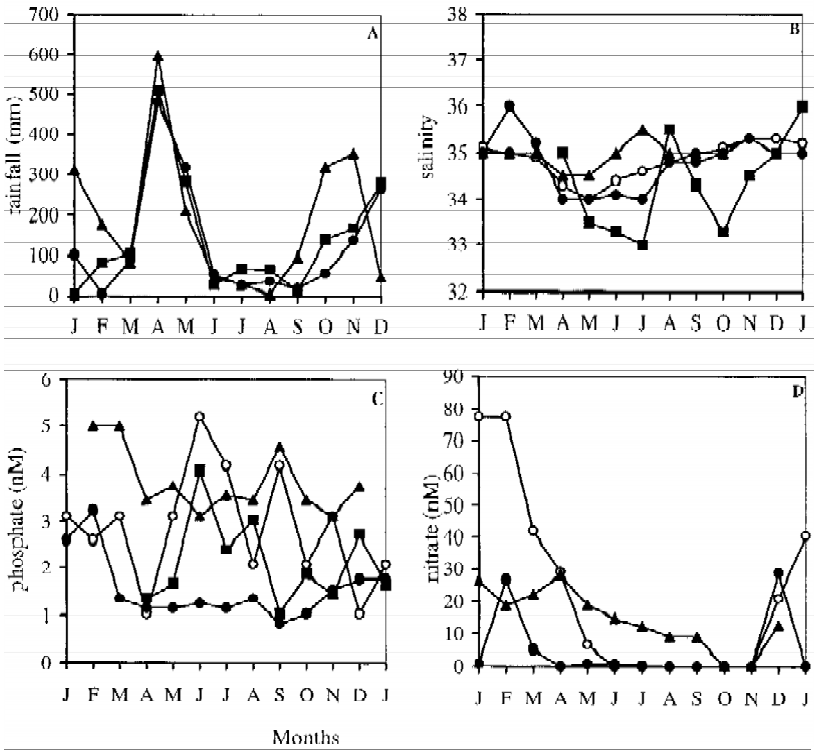


Figure 6. Seasonal variation of chemical oceanographic parameters in coastal areas of Dar es Salaam and Zanzibar (Tanzania), (A) Rainfall in Zanzibar area during 1993 (closed circles), 1994 (closed squares) and 1998 (closed triangles), (B) Salinity at site D during 1975/6 (open circles) and site Z during 1993/4 (closed circles), 1994/5 (closed squares) and 1998 (closed triangles), (C) Phosphate concentration at site D during 1975/6 (open circles) and site Z during 1993/4 (closed circles), 1994/5 (closed squares) and 1998 (closed triangles), and, (D) Nitrate concentration at site D during 1975/6 (open circles) and site Z during 1993/4 (closed circles) and 1998 (closed triangles).

nM (site D) and tended to decrease drastically towards zero during the SE monsoon period (Fig. 6D).

The relationship between the mean water temperature, wind speed, rainfall, nitrate concentrations, and *Trichodesmium* biomass (during the study period) is illustrated in Figure 7A–D. A significant positive correlation was seen between *Trichodesmium* biomass and water temperature ($r = 0.5$; $p = 0.000075$), rainfall ($r = 0.7$; $p = 0.000033$) and nitrate concentration ($r = 0.5$; $p = 0.001033$). However, there was no significant correlation between *Trichodesmium* abundance and wind speed ($r = 0.001$; $p = 0.994573$), STATISTICA 6.0.

Nitrogen fixation rates

High rates of nitrogen fixation occurred at around 10:00 am and generally persisted until around 04:00 pm (Fig. 8). In some cases, there was a drop in nitrogen fixation rate at mid-day. The nitrogen fixation activity was negligible from sunset (~07:00 pm) to

Table 1. Estimated seasonal variation in carbon fixation potential by *Trichodesmium* spp. at site Z based on average biomass during the NE monsoon (December–March), inter-monsoon (April–May), SE monsoon (June–September) and inter-monsoon (November–October) periods during 1993 applying the $^{14}CO_2$ fixation rates from July 1999

Depth (m) $^{14}CO_2$ fixation	*Trichodesmium*		$^{14}CO_2$ fixation ($\mu g\ C\ l^{-1}\ d^{-1}$)	
	NE	IM[a]	SE	IM[b]
0	6.1	4.4	0.07	0.005
5	1.1	2.1	0.09	0.007
10	1.1	3.0	0.05	0.006
15	0.4	1.0	0.01	0.003
20	0.1	0.4	0.01	0.001
Integrated production ($mg\ C\ m^{-2}\ d^{-1}$)	34.6	46.8	1.1	0.1

[a] April–May inter-monsoon period.
[b] November–October Inter-monsoon period.

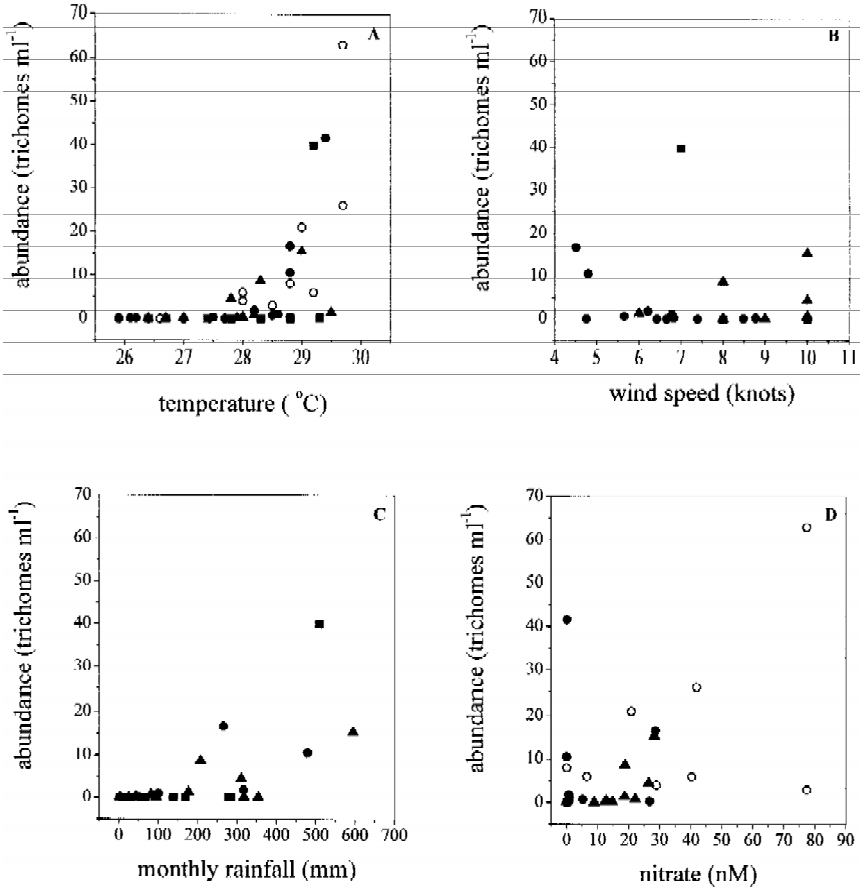


Figure 7. Relationship between *Trichodesmium* abundance and physical and chemical parameters in coastal areas of Tanzania, (A) *Trichodesmium* abundance and surface water temperatures at site D during 1975/6 (open circles), site Z during 1993/4 (closed circles), 1994/5 (closed squares) and 1998 (closed triangles), (B) *Trichodesmium* abundance at site Z and wind speed in the Zanzibar area during 1993/4 (closed circles), 1994/5 (closed squares) and 1998 (closed triangles), (C) *Trichodesmium* abundance at site Z and rainfall in the Zanzibar area during 1993/4 (closed circles), 1994/5 (closed squares) and 1998 (closed triangles), and, (D) *Trichodesmium* abundance and nitrate concentrations at site D during 1975/6 (open circles) and site Z during 1993/4 (closed circles) and 1998 (closed triangles).

early morning (~04:00 am) and the onset in activity was observed at daybreak (~06:00-0:700 am). The mean rates of ethylene production ranged from 3.5 to 10.8, 2 to 4 and 5 to 23 pmol C_2H_4 trichome^{-1} h^{-1} during the day (07.00 am to 06.00 pm) in 1975/80, 1994 and 1999, respectively. The average value recorded for all years was 7.2 ± 6.4 pmol C_2H_4 trichome^{-1} h^{-1}. By using a ratio of C_2H_4 produced to N_2 fixed of 4:1 (Capone, 1993), an estimated average nitrogen fixation rate of 1.8 ± 1.6 pmol N trichome^{-1} h^{-1} was apparent. Based on the average number of *Trichodesmium* trichomes counted in 1975, 1993/4, 1994/5 and 1998, it is estimated that *Trichodesmium* fixes up to 42.7 mmol N m^{-3}y^{-1} in the surface near shore waters of Tanzania.

Photosynthetic activity

The mean carbon fixation rates were generally low at the surface (<1 m) with a maximum occurring at 1–10 m depths and declining slowly down to 20 m depths where however still some activity was evident (Fig. 9A). Extrapolating the values from Figure 9A to natural population of *Trichodesmium* in July 1993 (Fig. 9B) and in various seasons during 1993 (Table 1), higher fixation rates at the surface were then obvious due to a higher biomass. The rate of *Trichodesmium*

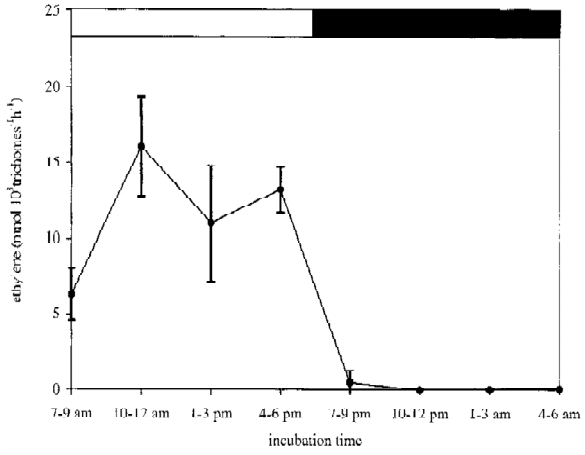


Figure 8. Diurnal nitrogen fixation rates by *Trichodesmium* in coastal areas of Zanzibar (Tanzania). Colonies were collected at site Z on 17th March 1999. Error bars indicate standard deviations (n = 4). The unfilled and filled bars above illustrate day (light) and night (darkness), respectively.

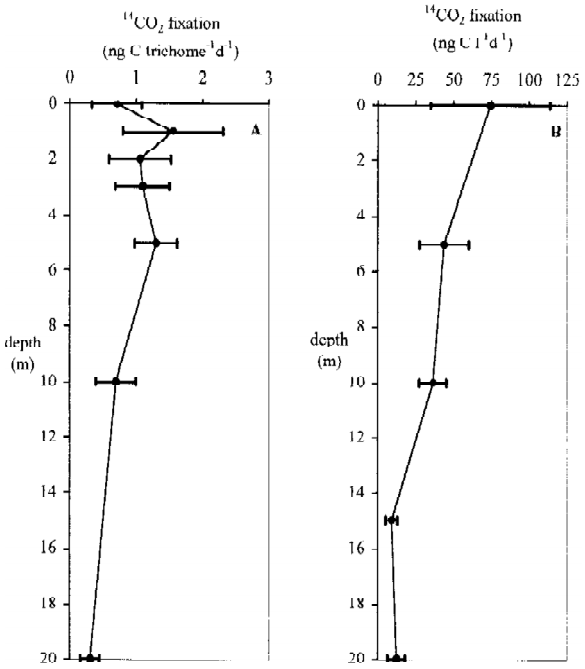


Figure 9. Vertical profile of *in situ* $^{14}CO_2$ fixation rates by *Trichodesmium*, (A) Collected from and incubated *in situ* at site Z in July 1999. (B) Values from (A) extrapolated to *Trichodesmium* biomass collected at various depths during July 1993. Error bars indicate standard deviations (n = 4).

$^{14}CO_2$ fixation ranged from an average of 0.02 μg C colony^{-1} d^{-1} recorded at 20 m depth to 0.27 μg C colony^{-1} d^{-1} recorded at the surface. Expressed on per trichome basis the mean carbon fixation rate in the upper 5 m was 1.15 $\pm$ 0.3 ng C trichome^{-1} d^{-1}. Extrapolating this mean CO_2 fixation rate to the mean number of *Trichodesmium* trichomes at site Z in 1993/4, 1994/5 and 1998, then carbon fixation rates at the surface waters ranged from 0.07 μg C l^{-1} d^{-1} when *Trichodesmium* biomass was low in September to 25.2 μg C l^{-1} d^{-1} in April.

Discussion

Although five *Trichodesmium* species were apparent, *T. erythraeum* was the most abundant species comprising up to 70% of the *Trichodesmium* population during certain parts of the year in the surface (down to 20 m) waters off Tanzania. The predominance of *T. erythraeum* agrees with previous observations from the Indian Ocean (Devassy et al., 1978). The more rapid floating velocity of *T. erythraeum* compared to *T. thiebautii* (Walsby, 1978) may prevent this species from being mixed as deeply as *T. thiebautii,* hence making it more easily encountered in surface waters. However, in the North Atlantic Ocean and the Japan Sea *T. thiebautii* is often reported to be generally more abundant (Marumo & Nagasawa, 1976) as compared to *T. erythraeum*. Also Orcutt (1999) reported few *T. erythraeum* in relation to *T. thiebautii* in the Sargasso Sea off Bermuda. Relatively large populations of *T. thiebautii* have also been noted in areas of the tropical and subtropical North Atlantic Ocean, Caribbean Sea, North Pacific gyre and Western Pacific Ocean. In contrast, *T. erythraeum* seems to predominate in the Southern Hemisphere including the Indian Ocean, SW Pacific and Australian waters (Capone & Carpenter, 1999). The reason for these differences in distribution is unclear. The predominance of *Trichodesmium* species at the water surface corresponds with earlier findings (Carpenter & Price, 1977; Orcutt, 1999). This is probably due to their need to live photoautotrophically in combination with their ability to regulate their buoyancy using gas vacuoles, apparently involving mechanism of carbohydrate loading (Villareal & Carpenter, 1990; Romans et al., 1994).

The Utermöhl settling method (Utermöhl, 1931) used to quantify *Trichodesmium* during 1975/6 may have underestimated the biomass as *Trichodesmium* have gas vacuoles used for buoyancy regulation (Walsby, 1978). Hence trichomes and/or colonies may have remained suspended in the settling cham-

bers as indicated by Chang (2000). The occurrence of *Trichodesmium* species in higher quantities during the NE monsoon is likely to be associated with the prevailing calmer weather conditions offered, as also suggested previously (Bryceson, 1982). During the NE monsoon, wind speeds are relatively low while water temperatures are higher, factors of importance for maintaining a stable water column and perhaps the physical integrity of *Trichodesmium* colonies. Water temperatures may also influence *Trichodesmium* photosynthetic activity as recently observed by Orcutt (1999). Maximum photosynthetic activities for natural populations of *Trichodesmium* species in the Atlantic Ocean were observed in water temperatures ranging from 25 to 28 °C. Also, rainfall may have an influence on the occurrence of *Trichodesmium* blooms. The blooms were mostly noted during dry spells of rainy seasons. Local fishermen, referring to the *Trichodesmium* blooms as 'vumbi la bahari' (sea dust), claim that the 'dust' sinks when it is raining and then reappear at the surface afterwards. In agreement with these observations, the biomass increased after rains when calm conditions resumed. Moreover, the wind gusts associated with rain often cause the ocean to become rough, which results in mixing. High *Trichodesmium* biomass was indeed observed following the short rains in October and in general it remained high until the end of the long rains in May.

During the NE monsoon period, the prevailing winds may also transport aeolian dust containing important nutrient that promote growth. Large quantities of continental material are often carried great distances over the oceans (see Duce et al., 1991). The dust may include key nutrients such as iron that has been demonstrated to stimulate both carbon and nitrogen fixation in cyanobacteria (Rueter, 1988; Rueter et al., 1990; Paerl et al., 1994). It has been hypothesized that the occurrence of *Trichodesmium* at the surface gives them a unique position to intercept, adsorb and solubilize iron from dust particles (Rueter et al., 1992). High correlation between aeolian Fe deposition and the occurrence of *Trichodesmium* colonies in the central Arabian Sea and Bermuda waters were recently reported by Capone et al. (1998) and Orcutt (1999), respectively. Also, Lenes et al. (2001) reported on the 100-fold increase in *Trichodesmium* biomass as a response to iron delivery in the offshore waters of the West Florida shelf following a July 1999 Saharan dust event.

It therefore appears that a cascade of environmental cues may be involved in the development and persistence of *Trichodesmium* populations in Tanzanian coastal waters through the NE monsoon. The following sequence of events is suggested based on the data obtained. The short rains possibly trigger the growth cycle of *Trichodesmium* in October and November (Fig. 6A) by accelerating terrestrial runoff and deposition of aeolian dust containing nutrients that stimulate growth. Higher water temperatures and low wind speed through the NE monsoon stabilizes the water column probably sustaining high *Trichodesmium* populations and initiating the development of *Trichodesmium* surface blooms. The long rain from March to May is likely to wash down additional atmospheric nutrients and cause terrestrial runoff, further sustaining growth of the *Trichodesmium* populations and later blooms. With a reduced atmospheric input following the end of long rain in May, *Trichodesmium* populations start to decline. Lower water temperature and higher wind speeds prevailing through the SE monsoon resulting in mixed and unstable water columns possibly exacerbate this situation. This hypothesis needs to be tested by continued monitoring of *Trichodesmium* populations and examination of possible regulatory factors such as atmospheric nutrient depositions in the area.

The increase in nitrate concentration during the NE monsoon may be attributed to accelerated terrestrial run off and/or atmospheric deposition of nutrients. Frequent episodic wet deposition of nitrogen has been registered in the North Atlantic and South Indian Oceans, which suggest that this route increases oceanic productivity (Owen et al., 1992). Besides terrestrial and atmospheric sources of new nitrogen in this system it is possible that another source of new nitrogen originates from N_2 fixation by diazotrophs particularly so from *Trichodesmium*. In the study area, phytoplankton (Bryceson, 1982) and zooplankton biomass (Okera, 1974) as well as fish catch (McClanahan, 1988) have been reported to be higher during the NE monsoon. Experiments using ^{15}N (Bryceson & Fay, 1981) demonstrated uptake of $^{15}N_2$ by *Trichodesmium* and a subsequent transfer of part of the fixed ^{15}N to bacterial fractions associated with colonies and to other phytoplankton. Similarly, O'Neil et al. (1996) demonstrated that the copepod, *Macrosetella gracilis* provides a direct link between atmospherically derived 'new' nitrogen and regenerated NH_4^+ in the oligotrophic systems. This was shown to be through feeding

Table 2. Comparison between nitrogenase activities (ARA) recorded for *Trichodesmium*

Study area	Ethylene production (pmol C_2H_4 trichome^{-1} h^{-1})	Reference
Indian Ocean, off Tanzania	3.5 – 10.8	Bryceson & Fay (1981)
Indian Ocean, off Tanzania	7.2 ± 6.4	This study
Indian Ocean, off Kenya	0.4 – 3.0	Kromkamp et al. (1997)
Caribbean Sea	6.4	Carpenter et al. (1987)
Sargasso Sea, off Bahamas	4.04	Carpenter et al. (1987)

on *Trichodesmium* colonies or mechanical breakage of cells while grazing. Also, Glibert & Bronk (1994) showed that approximately 50% of the nitrogen fixed by *Trichodesmium* is released as dissolved organic nitrogen (DON). This DON release is likely to stimulate microbial activity and phytoplankton primary production. These experiments support the contention that *Trichodesmium* enhances overall phytoplankton productivity by increasing the availability of assimilable nitrogen. Our data confirm that *Trichodesmium* populations in coastal areas of Tanzania are actively fixing nitrogen.

A comparison of nitrogenase activities recorded for *Trichodesmium* in different geographic regions is given in Table 2. The fixation rates are all within the same magnitude. The variations seen may be caused by differences in trichome or colony size or in bundleness (i.e. degree of trichome assembly into bundles). Trichome and colony size were noted to vary depending on *Trichodesmium* species and season. A direct relationship between bundleness and nitrogenase activity in *Trichodesmium* has previously been shown (Byrceson & Fay, 1981; Letelier & Karl, 1998). Higher bundleness gives rise to higher nitrogenase activities. Other factors may be type of species, physiological condition of *Trichodesmium* and abiotic factors such as nutrients availability, light and temperature. The decline in nitrogenase activity that was sometimes noted at mid-day might be due to photo-inhibition resulting in a lower supply of energy and electrons to sustain nitrogenase activity. A combination of a spatial and a temporal segregation of N_2 fixation from photosynthesis have recently been demonstrated to be major mechanisms deployed by *Trichodesmium* to protect its oxygen labile nitrogenase (Berman-Frank et al., 2001). This in turn enables N_2 fixation to take place during the day.

The mean values for *in situ* $^{14}CO_2$ fixation by *Trichodesmium* were lower at the surface, slightly increased from 1 to 5 m before declining again down to 20 m depths. However, the high standard deviations indicate that the differences noted are probably minor down to 10–15 m, and may be explained by fluctuations in irradiance during and between sampling dates. As suggested from Figure 9B, carbon fixation by *Trichodesmium* is possibly higher at the surfaces due to a local higher biomass. Our primary production values ranging 0.02–0.27 μg C Colony^{-1} d^{-1} are low compared to those reported previously from the Sargasso Sea off Bermuda (1.31–5.24 μg C colony^{-1} d^{-1}; Orcutt, 1999). The long incubation period used in this study may have underestimated the production rate due to recycling of the isotope through DO^{14}C. Other possibilities could be differences in colony size and variations in the physiological conditions of *Trichodesmium*. However, our data were similar to those reported from the Sargasso Sea (0.3 μg C colony^{-1} d^{-1}; Carpenter & Price, 1977) and from Central North Atlantic Ocean (0.042 μg C colony^{-1} d^{-1}; McCarthy & Carpenter, 1979). Based on average *Trichodesmium* counts in Zanzibar surface waters, we estimate carbon fixation rates to range from an average of 0.0075 μg C l^{-1} d^{-1} in September to 25.2 μg C l^{-1} d^{-1} in April. Previous overall primary production studies in the area suggested higher productivity during the rainy season (April) as compared to the dry season (August), with mean values of about 125 μg C l^{-1} d^{-1} and 25 μg C l^{-1} d^{-1}, respectively (Wallberg et al., 1999). Relating these values to our observation, the contribution to total CO_2 fixation by *Trichodesmium* in Tanzanian coastal surface waters ranges from 0.03 to 20.2% during the dry and rain seasons, respectively. Similarly, Carpenter & Price (1977) estimated that *Trichodesmium* contribute up to 20% of primary production in surface waters of

the tropics. Relating our estimate of *Trichodesmium* integrated water column production (Table 1) to previous integrated whole water production in the area (Ryther et al., 1966; Lugomela et al., 2001) a lower value of 4% and 8%, respectively, is obtained. This may perhaps be explained by the noted uneven vertical distribution of *Trichodesmium* colonies that tends to accumulate at the surface. Our estimates on integrated primary production for *Trichodesmium* in the western Indian Ocean (Table 1) are higher than those in the Sargasso Sea, ranging from about 0.2–0.9 mg C m^{-2} d^{-1} (Orcutt, 1999). This is probably due to higher *Trichodesmium* biomass in the Zanzibar coastal waters. In conclusion, it is apparent that *Trichodesmium* contributes substantially to primary production in the investigated area during the NE monsoon.

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