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Distribution of the cyanophyte *Trichodesmium* (Oscillatoriaceae) in the eastern Caribbean Sea: influence of the Orinoco River

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Abstract: Orinoco River influence in the Caribbean Sea, characterized by high nutrient input, causes a decrease of *Trichodesmium* populations. The Caribbean Time Series (CaTS) station, south of Puerto Rico (17°36'N 67°00'W), was monitored for 25 months in order to observe the *Trichodesmium* abundance pattern and the presence of the river plume. In general, mean *Trichodesmium* abundance was higher at the surface and decreased with depth. The mean upper water column (surface to 20 m) abundance was 54.1±32.6 col/m ^{3}. Within the sampling period, abundance was highly variable (1–700 col/m^{3}). Correlation between *Trichodesmium* abundance and wind speed (p=0.002), chlorophyll a concentration (p=0.001), nitrate (p=0.02) and silicate (p=0.003) concentrations were statistically significant. However, *Trichodesmium* abundance was not correlated with salinity (p=0.70), temperature (p=0.16) and seawater density (p=0.71) variations at CaTS. Eastern Caribbean regions highly influenced by the Orinoco River discharge were devoid of *Trichodesmium* colonies.

Key words: *Trichodesmium*, Orinoco River, cyanophytes, Caribbean Sea, time series station

Trichodesmium Ehrenberg species are nitrogen-fixing colonial cyanobacteria that occur frequently in tropical oligotrophic waters. There are five identified species of *Trichodesmium*; the most common in tropical seas are *T. thiebautii* Gomont ex Gomont and *T. erythraeum* Ehrenberg ex Gomont (Carpenter *et al.* 1993, Jason *et al.* 1995). Blooms of *Trichodesmium* are common in tropical and subtropical seas of all oceans, particularly when winds are calm and the water temperature is above 26°C. At least 20 blooms per year have been reported in the oceans, lasting up to 15 days (Carpenter and Capone 1992). Letelier and Karl (1996) noted that *Trichodesmium* contribute at least the 27% of the new primary production in the North Pacific Ocean. In the tropical North Atlantic Ocean it is the most important primary producer (about 165 mg C m^{-2} d^{-1}) (Carpenter and Romans 1991). Recently, Capone *et al.* (1997) attributed global importance of *Trichodesmium* populations to the nitrogen budget in the oligotrophic gyres where it is dominant. They argued that nitrogen fixation by *Trichodesmium* is of equal importance as the vertical nitrate flux as a new nitrogen source. Since oligotrophic regions are dominated by *Trichodesmium* species, its importance in the nitrogen balance will be reviewed.

The Caribbean and other major tropical and subtropical seas exhibit maximum *Tri-*

chodesmium abundance and calm wind conditions during the summer. Méndez (1984) noted the highest *Trichodesmium* abundance in the Caribbean during the summer (June to August) with an mean of 515 col/m^3. The lowest value was during the winter (2 col/m^3). Variations in *Trichodesmium* abundance were observed throughout the sampling period (52 weeks) ranging from 1 to 3 762 col/m^3, with an mean of 171 col/m^3. Similar variations were reported previously by Steven and Glombitza (1972), Carpenter and Price (1977), Borstad (1982), Letelier and Karl (1996). Carpenter and McCarthy (1975) reported 566 *Trichodesmium* col/m^3 (using the conversion of 30 000 cells per colony) in the Caribbean and, two years later, Carpenter and Price (1977) noted values between 90 and 343 col/m^3. Recently, Navarro (1998) observed similar variability in the Mona Passage waters. Abundance varied from 0 to 33 col/m^3 (or ca. cero to 33 *Trichodesmium* cells/m^3) over a one-week sampling period. Previously, Carpenter and Price (1977) also reported similar variability in the Mona Passage, where abundance varied from 178 to 1 083 *Trichodesmium* cells/m^3 in the upper water column.

Reports of *Trichodesmium* abundance in the Caribbean Sea during the Orinoco River (hereafter OR) influence are scarce. Fresh water is particularly significant because each year from July through November, this region receives a massive riverine discharge from the OR. After July, the OR plume disperses over a large area, reaching the northern Caribbean Sea and the south coast of Puerto Rico between August and October (Muller-Karger *et al.* 1989). Some of the most recent reports on the OR discharge in the Caribbean are available in Volume 98 of the Journal of Geophysical Research (1993). There, Bidigare *et al.* (1993) established that the OR modifies the vertical distribution and composition of the phytoplankton community during periods of high freshwater outflow (August-October). Large number of *Trichodesmium* colonies in the upper water column were observed during low river discharge. During maximum discharge, diatoms are the major component of the surface phytoplankton community due to the high input of silicates and nutrients (Sánchez *et al.* 1995). Also, significant amounts of dissolved organic matter (DOM) and sediments are introduced by the river into the Caribbean Sea, which reduce light penetration and consequently the euphotic zone (Farmer *et al.* 1993). This reduction affects phytoplankton abundance, and an inverse relationship between salinity and phytoplankton abundance has been observed in the Caribbean waters (Sánchez *et al.* 1995, Borstad 1982).

The spatial and temporal abundance of *Trichodesmium* populations during riverine discharge has not been studied in the Caribbean Sea. This work documents the distribution, abundance and the influence of the OR discharge in *Trichodesmium* populations in the upper water column at the Caribbean Time Series (CaTS) station in the eastern Caribbean Sea.

MATERIALS AND METHODS

The Caribbean Time Series (CaTS) station, located 26 miles off the south coast of Puerto Rico (17°36'N 67°00'W), was monitored from February 1995 through November 1997. All collections were taken in the morning aboard the R/V Isla Magueyes or the R/V Pezmar (Department of Marine Sciences-University of Puerto Rico). Temperature, salinity, total chlorophyll a fluorescence and seawater density were determined using a Sea Bird SBE 19 conductivity-temperature-depth profiler and a fluorometer located in a rosette sampler system. Wind speed was recorded using an anemometer.

Nutrient concentrations (nitrate and silicate) were determined by the method described by Parsons *et al.* (1984). Water samples were collected in 100 ml Nalgene bottles and refrigerated until analyzed (24 hours after collection). Nitrate was reduced to nitrite through a Cd-Cu column and nitrite was determined spectrophotometrically (543 nm) using sulfanilamide and N-(1-naphthyl)-ethylenediamine as coupling chemicals. Silicates was determined spectrophotometrically (810 nm) through the formation of the silicomolybdate complex.

Plankton samples were taken at the surface, 10 m and 20 m depths using a 0.5 m diameter conical net with 202 μm mesh operated using a double-trip opening and closing mechanism (General Oceanics). A five-minute tow was performed at each depth at approximately 2 knots (Méndez 1984). A mechanical flowmeter (General Oceanics R-2030) was installed at the net opening to measure water volume filtered by the net. The concentrated sample was rinsed with filtered (64 μm mesh size) seawater and placed in a 500 ml polypropylene bottle (Fisher Scientific). Samples obtained for colony counts were preserved in a 4% formalin-filtered seawater solution and transported to the laboratory. The preserved samples were sieved through a plankton net (64 μm) to eliminate excess water. The concentrate was resuspended in filtered seawater (150 - 800 ml depending on biomass abundance), subsampled with a Stempel pipette (10 ml) and counted in a Bogorov chamber (Aquatic Research Instruments). A Nikon 137 245 stereoscope was used to count *Trichodesmium* colonies. The whole sample was preserved afterwards in 4% formalin-filtered seawater solution.

Water samples, from an oceanographic cruise in the eastern Caribbean Sea, were analyzed in order to document *Trichodesmium* abundance in relation to riverine influence. The cruise was carried out during October 23 to November 1, 1996 (Ori-4 cruise) aboard the R/V Isla Magueyes. Temperature, salinity, total Chl a fluorescence, seawater density, nutrient concentrations and wind speed were recorded (as described previously). Cruise samples were from surface waters. Four samples were from the Gulf of Paria, Trinidad (G1-G4) and seven from the eastern Caribbean Sea (C1-C13).

RESULTS AND DISCUSSION

The prevailing *Trichodesmium* abundance pattern at CaTS was of higher concentrations at the surface (72% of the total measurements) decreasing with depth (Fig. 1); a pattern observed previously by Steven and Glombitza (1972), McCarthy and Carpenter (1979), Borstad (1982) and Lewis *et al.* (1988). However, abundance was higher at 10 m than at the surface on 5/18 occasions (28%) and higher at 20 m than at 10 m on 7/18 occasions (39%) (Table 1). Sample variability (error) was unknown because no replicates were taken.

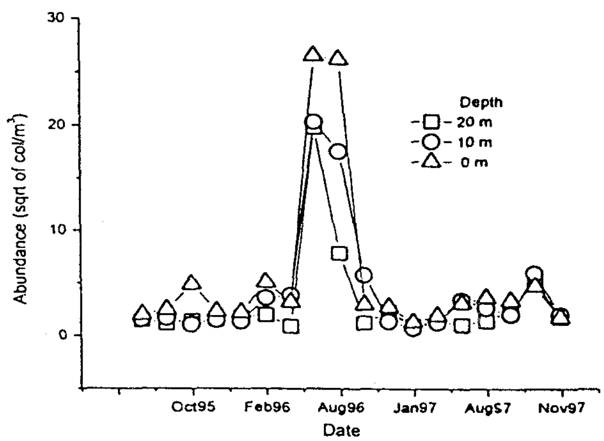

Fig. 1. Time series for *Trichodesmium* abundance at CaTS.

Mean colony concentration at the surface was 86.0±52.3 col/m^3, 47.6±27.3 col/m^3 at 10 m and 28.7±21.7 col/m^3 at 20 m depth. The mean colony concentration in the upper water column (surface, 10 m and 20 m) was 54.1±32.6 col/m^3 (over 25 month investigation). Temporal abundance was highly variable throughout the year. Upper water abundance varied from 1 to 704 col/m^3. Such variability was also observed by Letelier and Karl in 1996 (0.02 to 140 col/m^3) and Méndez in 1984 (2 to 3.762 col/m^3).

Trichodesmium abundance at CaTS was relatively low throughout the year, except in the summer of 1996. Our mean surface value was lower than the values reported previously in

TABLE 1

Trichodesmium *abundance and chemical data at CaTS.*

Date	Depth (m)	Abundance (col/m³)	Nitrates (μM)	Silicates (μM)	Wind (knots)	Temp (°C)	Salinity (psu)	Chl *a* total (μg/L)	Density (g/cm³)
2/28/95	0	4	*	2.5	22	26.68	35.20	0.11	22.9758
3/23/95	0	9	*	*	4	*	*	*	*
5/19/95	0	4	*	2.4	3	28.12	35.95	0.06	23.0693
	10	2	*	*		28.11	35.94	0.08	23.0701
	20	2	*	2.4		28.11	35.94	0.08	23.0668
5/25/95	0	2	*	*	7	*	*	*	*
	10	2	*	*		*	*	*	*
	20	1	*	*		*	*	*	*
6/13/95	0	11	*	*	13	*	*	*	*
	10	6	*	*		*	*	*	*
	20	0	*	*		*	*	*	*
6/29/95	0	6	*	1.3	11	28.97	35.74	0.23	22.6328
	10	3	*	*		28.97	35.74	0.18	22.6341
	20	1	*	1.1		28.97	35.76	0.20	22.6429
7/11/95	0	20	*	*	7	*	*	*	*
	10	5	*	*		*	*	*	*
	20	17	*	*		*	*	*	*
7/26/95	0	2	*	3.7	10	28.93	35.91	0.10	22.7740
9/2/95	0	2	*	3.3	8	29.74	34.57	0.14	21.4913
9/26/95	0	18	*	*	4	*	*	*	*
	10	1	*	*		*	*	*	*
	20	1	*	*		*	*	*	*
10/18/95	0	23	*	*	19	*	*	*	*
	10	1	*	*		*	*	*	*
	20	2	*	*		*	*	*	*
11/3/95	0	5	*	*	15	28.94	34.63	*	21.8290
	10	2	*	*		28.95	34.66	*	21.8290
	20	2	*	*		28.95	34.66	*	21.8250
11/29/95	0	2	*	*	8	*	*	*	*
	10	5	*	*		*	*	*	*
	20	5	*	*		*	*	*	*
1/25/96	0	5	*	*	22	27.11	35.37	0.20	22.9662
	10	2	*	*		27.11	35.37	0.13	22.9660
	20	3	*	*		27.11	35.37	0.15	22.9662
2/8/96	0	2	*	*	5	*	*	*	*
2/22/96	0	25	0.07	3.4	11	26.80	35.56	0.09	23.2038
	10	12	0.01	2.9		26.80	35.56	0.08	23.2035
	20	4	0.02	2.8		26.80	35.56	0.11	23.2030
3/14/96	10	5	*	*	6	*	*	*	*
5/2/96	0	10	*	*	8	26.71	36.20	0.11	22.2910
	10	14	*	*		26.72	36.20	0.11	22.2912
	20	1	*	*		26.71	36.20	0.12	22.2888
6/26/96	0	107	0.21	0.9	8	28.12	35.29	0.29	22.5787
	20	31	0.15	2.1		28.05	35.29	0.33	22.5975
7/19/96	0	122	*	*	10	*	*	*	*
7/31/96	0	704	0.29	1.5	6	28.07	35.18	0.15	22.5062
	10	413	0.24	1.4		28.07	35.18	0.33	22.5084
	20	392	0.10	1.7		28.06	35.18	0.32	22.5118
8/16/96	0	81	*	*	10	*	*	*	*
8/22/96	0	687	0.00	1.8	8	28.47	34.94	0.29	22.1947
	10	308	0.07	1.8		28.47	34.93	0.16	22.1950
	20	61	0.05	1.8		28.46	34.93	0.22	22.1959
9/24/96	0	105	*	*	5	*	*	*	*

TABLE 1

Trichodesmium *abundance and chemical data at CaTS. (continued)*

	10	45	*	*		*	*	*	*
	20	9	*	*		*	*	*	*
10/3/96	0	9	0.27	4.0	9	28.75	34.59	0.09	21.8438
	10	33	0.29	3.6		28.74	34.59	0.10	21.8434
	20	1	0.38	4.1		28.74	34.59	0.14	21.8427
10/31/96	**0**	**1**	**1.29**	**5.3**	**13**	**28.76**	**33.72**	**0.11**	21.1874
11/26/96	0	7	0.2	3.7	15	27.79	34.21	0.08	21.8736
	10	2	0.21	3.5		27.79	34.21	0.09	21.8673
	20	5	0.15	3.5		27.80	34.20	0.13	21.8622
1/23/97	0	2	0.16	2.4	20	26.55	34.75	0.11	22.6726
	10	1	0.15	2.4		26.55	34.74	0.11	22.6696
	20	1	0.12	2.5		26.56	34.74	0.14	22.6646
2/25/97	0	4	0.75	2.1	17	25.85	35.42	0.06	23.3978
	10	2	0.62	2.1		25.85	35.41	0.07	23.3908
	20	2	0.68	1.9		25.85	35.41	0.08	23.3895
3/18/97	0	9	*	*	15	25.77	35.62	0.03	23.5758
	10	11	*	*		25.76	35.62	0.02	23.5746
	20	1	*	*		25.76	35.62	0.03	23.5754
8/21/97	0	13	0	2.2	13	28.81	35.63	0.03	22.6017
	10	7	0.33	1.9		28.81	35.63	0.05	22.6013
	20	2	0.13	2.4		28.81	35.63	0.04	22.6012
9/25/97	**0**	**11**	**0.56**	**3.3**	**14**	**29.02**	**34.70**	**0.04**	21.8293
	10	4	0.53	3.3		29.01	34.70	0.05	21.8340
	20	6	0.61	3.4		29.02	34.70	0.07	21.8294
10/21/97	0	22	0.45	2.2	3	28.96	35.94	0.12	22.7826
	10	35	0.41	1.7		28.99	36.10	0.12	22.8293
	20	27	0.42	1.8		28.81	36.44	0.04	23.2105
11/25/97	0	3	1.19	2.8	13	28.32	35.28	0.19	22.4982
	10	4	0.51	2.5		28.32	35.28	0.24	22.4994
	20	3	0.46	2.8		28.31	35.28	0.32	22.5007

* no data
Bold=Orinoco influence

Caribbean surface waters: 567 col/m^3 – autumn (Carpenter and McCarthy 1975), 343 col/m^3 – August and September (Carpenter and Price 1977), 835 col/m^3 – autumn (Carpenter and Romans 1991) and 171 col/m^3 – 52 weeks (Méndez 1984). Sampling period season can contribute to such differences. We estimated the mean *Trichodesmium* abundance on a monthly scale (over two years), however, many of the *Trichodesmium* distribution studies in the Caribbean Sea were performed during one season of the year.

During the summer period (June, July and August) of 1995 and 1996, low wind speed prevailed (6-10 knots) and during the winter (January and February) of 1995, 1996 and 1997 high wind speed were observed (17-20 knots). *Trichodesmium* abundance was higher in the summer (107-704 col/m^3) and lower in the winter (2-4 col/m^3) (Fig. 2). The minimum concentration in the upper water column (0-20 m) was observed during January and February 1997 (1 and 2 col/m^3) and the maximum during July and August 1996 (503 and 352 col/m^3) (Fig. 2 b). Méndez (1984) also found the highest and lowest counts in the summer (515 col/m^3) and in the winter (2 col/m^3). However, during the fall (September and October), when the OR influence in the Caribbean Sea was marked, we observed the same low *Trichodesmium* abundance pattern than in the winter.

During the fall (OR influence), *Trichodesmium* abundance decreased to 1 col/m^3 (October 1996) and nitrate and silicate concentrations increased to 1.3 μM and 5.3 μM, respectively (Figs. 3-4). In the spring (no OR influence), *Trichodesmium* abundance increased to 107 col/m^3 (June 1996), while nitrate and silicate concentrations dropped to 0.21 μM and 0.9 μM. August 1996 was not characterized by nitrate concentrations in surface waters and the highest *Trichodesmium* abundance value was observed (687 col/m^3). Similar patterns occur at 10 m and 20 m. Significant correlation among *Trichodesmium* abundance and nitrate (p=0.02) and silicate (p=0.003) concentrations were observed. Published oceanic measurements of silicates and nitrates during the fall in the southern Caribbean were 3.52 and 3.58 μM, but the concentrations changed to 1.50 μM -$Si(OH)_4$ and 4.12 μM -NO_3^- during the spring (Bonilla *et al.* 1993). Those concentrations were similar to our measurements in the CaTS station.

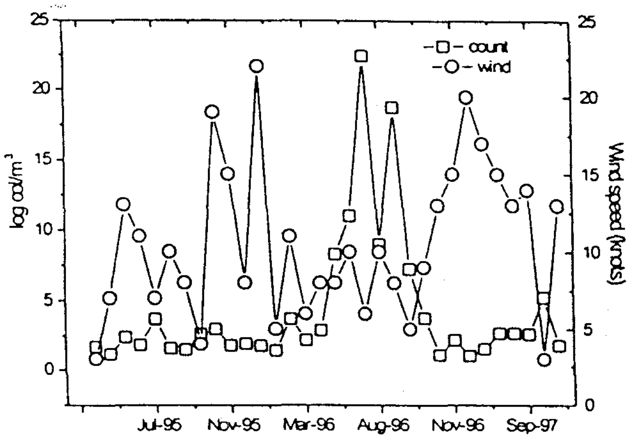

Fig. 2 Time series for *Trichodesmium* abundance and wind speed.

September 1995 was characterized by low wind speed (8 knots), low salinity (34.57 psu), silicate concentration of 3.3 μM and *Trichodesmium* abundance of 2 col/m^3. October 1996 was the lowest *Trichodesmium* abundance month. Wind conditions were not calm (13 knots), salinity drops to 33.72 psu and silicate and nitrate concentrations increased to 5.3 and 1.29 μM, respectively (strong OR influence). On September and October 1997, OR influence was not as strong as the previous year and *Trichodesmium* abundance was higher than the previous reported value in the same season. Historically, calm wind conditions have been correlated

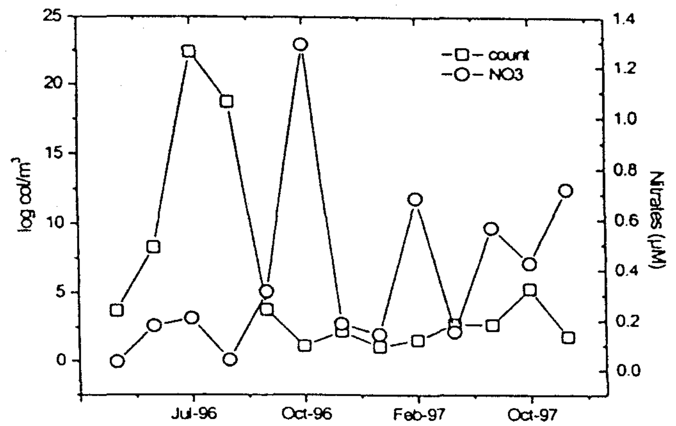

Fig. 3 Time series for *Trichodesmium* abundance and nitrates.

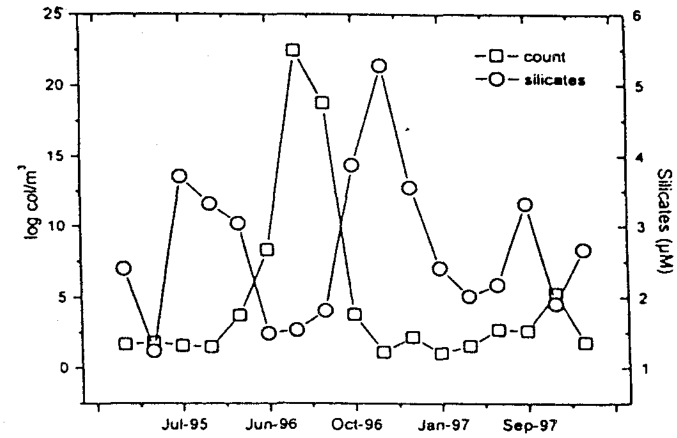

Fig. 4 Time series for *Trichodesmium* abundance and silicates.

with *Trichodesmium* abundance especially during the summer (Borstad 1982, Méndez 1984, Villareal 1995). However, Letelier and Karl (1996) and Villareal (1995) mentioned other environmental factors, such as solar insolation, grazing and physical removal, as conditions other than wind speed associated with abundance. We observed a significant correlation between abundance and wind speed (p= 0.002) at CaTS (Table 2). The maximum *Trichodesmium* abundance in CaTS coincided with low wind speed (less than 10 knots), low silicate concentration (less than 2 μM) and low nitrate concentration (less than 0.4 μM).

Trichodesmium abundance was not correlated with salinity (p=0.70), temperature (p=0.16) and seawater density (p=0.71) variability throughout the year. Since salinity and silicates are river indicators, silicates exert a strong influence on *Trichodesmium* abundance at CaTS (Fig. 5, 6 y 7). Temperature changes at CaTS (25–29 °C) did not affect *Trichodesmium* colonies. Thermal tolerance studies reveals that the maximum photosynthesis of *Trichodemsium* occur between 20 and 30 °C (Aruga *et al.* 1979 in Carpenter 1983). In a general pattern, salinity decreased

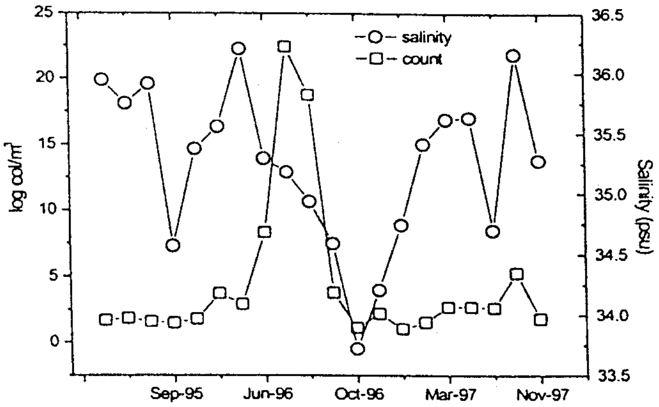

Fig. 5 Time series for *Trichodesmium* abundance and salinity.

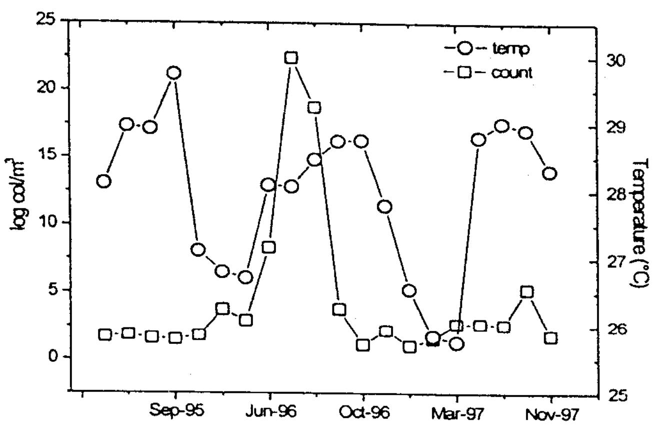

Fig. 6 Time series for *Trichodesmium* abundance and temperature.

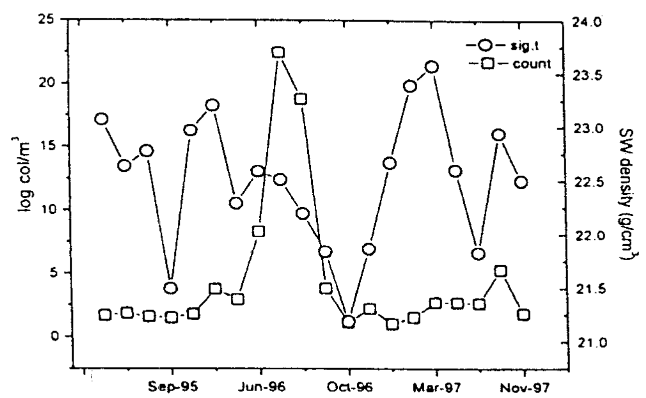

Fig. 7. Time series for *Trichodesmium* abundance and seawater density.

TABLE 2

Correlation coefficients for Trichodesmium *abundance and physical/chemical parameters.*

Parameter	n	df (error)	Correlation coefficient
Nitrates *	34	32	-0.4629
Silicates *	41	39	-0.4705
Chl a *	51	49	0.4479
Wind speed *	34	32	-0.2900
Salinity	54	52	0.0522
Temperature	54	52	0.1203
Density	54	52	-0.0540

* statistically significant ($p<0.05$)
(Rohlf and Sokal 1981)

and temperature increased during the time of OR influence (fall) and in the absence of the riverine discharge (winter, spring and summer), salinity increased and temperature decreased.

Total Chl a content was greatest during the months when *Trichodesmium* was most abundant (Fig. 8). Correlation between *Trichodesmium* abundance and Chl a content was significant ($p=0.001$). The highest and lowest Chl content were observed during the summer (highest *Trichodesmium* abundance) and the winter (lowest *Trichodesmium* abundance), respectively (Fig. 9). Steven and Glombitza (1972) noted the oscillatory variations between *Trichodesmium* abundance and Chl concentrations in the tropical western Atlantic. *Trichodesmium* filaments at 5m fluctuated regularly with Chl concentration with a periodicity of 3-4 months.

Trichodesmium was not observed in Caribbean waters strongly influenced by riverine inputs stations G1-G4 (Gulf of Paria) and C3. Although wind speed was low in the Gulf of Paria, nutrient concentrations were high and water samples were devoid of *Trichodesmium*. These stations were characterized by high silicate and nitrate concentrations (Table 3). Diatoms, dinoflagellates and zooplankton were very abundant. *Coscinodiscus*, *Chaetoceros*, *Noctiluca* and *Ceratium*

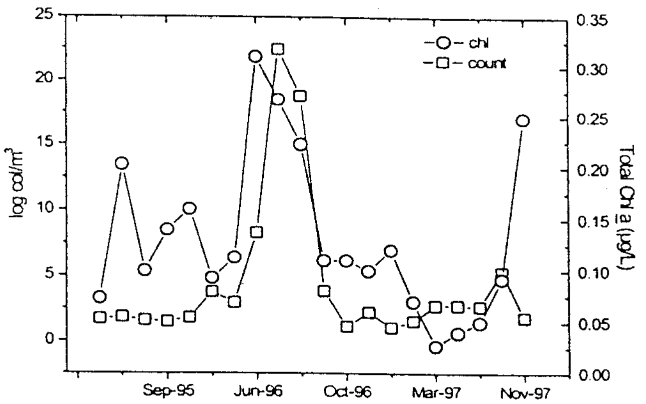

Fig. 8 Time series for *Trichodesmium* abundance and Chl a

were common in such samples influencing the high Chl fluorescence values in that station, while *Trichodesmium* biomass decreased to zero in highly fertilized areas. The mean NO_3^- and $Si(OH)_4$ concentrations in the Gulf of Paria were 1.95 µM and 39.8 µM, respectively. Bonilla *et al.* (1993) observed concentrations similar to our measurements in the Gulf of Paria NO_3^- = 3.25 µM and $Si(OH)_4$ = 40.75 µM. Dramatic decline in nutrient concentrations and a concurrent increment in *Trichodesmium* abundance were observed along a gradient toward the northern Caribbean basin (C1-C13). Bonilla *et al.* (1993) noted nitrate depletion before surface waters exit the Gulf. In contrasts, station C9, where oceanic conditions of high salinity prevailed, was characterized by a moderately high phytoplankton biomass, including *Trichodesmium* (highest abundance value), and the lowest nutrient concentrations measured during the cruise. The station farthest from the Gulf (CaTS) showed a nutrient increase and *Trichodesmium* abundance decrease compared to other Caribbean stations.

Large introduction of silicates, coming from the OR, stimulates growth of resident diatoms in the water column (Bidigare *et al.* 1993), apparently displacing *Trichodesmium* populations. McCarthy and Carpenter (1979) suggested that *Trichodesmium* is not a successful competitor for inorganic nutrients in the company of other oceanic phytoplankton. Phosphates can be the limiting nutrient when other phytoplankton are present in seawater and *Trichodesmium* will be excluded from the water column when high nutrient concentrations are present. Experimental work with phytoplankton (Hulbert and Corwin 1969 cited in Borstad 1982) has shown that diatoms respond readily to fertilization in batch cultures and nutrient inputs provide favorable conditions for diatom blooms

TABLE 3

Hydrographic and chemical data for cruise Ori/4.

Station	Latitude (°N)	Longitude (°W)	*Trichodesmium* abundance (col/m^3)	Nitrates (µM)	Silicates (µM)	Wind (knots)	Temp (°C)	Salinity (psu)
G-1	10.376	61.588	0	2.03	33.89	6	29.12	21.35
G-2	10.611	61.700	0	1.49	37.99	6	28.73	21.41
G-3	10.012	61.947	0	0.46	49.77	7	29.53	15.90
G-4	10.435	61.925	0	3.82	37.53	7	29.49	19.05
C-3	11.201	61.817	0	0.68	13.55	8	28.26	29.26
C-5	12.045	62.287	8.3	0.68	7.76	15	28.65	31.08
C-6	12.636	62.810	0	0.62	3.46	13	28.92	33.36
C-9	14.660	64.500	30.24	0.12	3.43	13	28.77	31.65
C-10	15.070	61.836	10.63	0.23	5.53	13	28.98	33.63
C-13 (CaTS)	17.360	67.000	1.49	1.29	5.28	15	28.74	33.15

(Sánchez *et al.* 1995). Santhanam *et al.* (1994) noticed minimal nitrate concentration (0.2-0.78 µg-at/L) during the maximum bloom of *Trichodesmium* in the Indian Ocean. However, Devassy *et al.* (1978) noted high nitrate concentrations when a *Trichodesmium* bloom was at its peak in the Indian Ocean and a decline in nitrate and phosphate concentrations when the bloom came to an end.

In summary, *Trichodesmium* abundance was related to wind speed and nutrient concentrations at CaTS. Salinity and temperature variability at CaTS did not exert an influence on *Trichodesmium* abundance. Caribbean regions highly influenced by the OR plume were devoid of *Trichodesmium* populations. Diatoms replaced *Trichodesmium* in those regions.

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RESUMEN

La influencia del Río Orinoco en el mar Caribe, caracterizada por un alto contenido de nutrientes, ocasionó una disminución en las poblaciones de *Trichodesmium*. La "Estación en Serie del Caribe" (CaTS), localizada al sur de Puerto Rico (17°36'N 67°00'W) fue monitoreada por 25 meses para determinar los patrones de abundancia de *Trichodesmium* y la influencia del Río Orinoco en esa región. En general, la abundancia promedio de *Trichodesmium* fue mayor en la superficie y disminuyó con la profundidad. El promedio de abundancia en la superficie (hasta los 20 m) fue de 54.1±32.6 col/m^3. Durante los 25 meses de muestreo, la abundancia fue altamente variable (1–700 col/m^3). Los análisis de correlación entre la abundancia de *Trichodesmium* y la velocidad de viento ($p= 0.002$), concentración de clorofila a ($p= 0.001$) y la concentración de nitratos ($p= 0.02$) y silicatos ($p= 0.003$) resultó estadísticamente significativa. Sin embargo, la abundancia no estuvo correlacionada con las variaciones en salinidad ($p= 0.70$), temperatura ($p= 0.16$) y densidad del agua ($p=0.71$) detectadas en CaTS. Las regiones del Caribe Oriental altamente influenciadas por la descarga del Río Orinoco estuvieron desprovistas de colonias de *Trichodesmium*.

REFERENCES

Bidigare, R.R., M.E. Ondrusek & J.M. Brooks. 1993. Influence of the Orinoco River outflow on distributions of algal pigments in the Caribbean Sea. J. Geophys. Res. 98(C2): 2259-2269.

Bonilla, J., W. Senior, J. Budgen, O. Zafiriou & R. Jones. 1993. Seasonal distribution of nutrients and primary productivity on the eastern continental shelf of Venezuela as influenced by the Orinoco River. J. Geophys. Res. 98(C2): 2245-2257.

Borstad, G.A. 1982. The influence of the meandering Guiana Current on surface conditions near Barbados - temporal variations of *Trichodesmium* (Cyanophyta) and other plankton. J. Mar. Res. 40: 435-452.

Capone, D., J.P. Zehr, H.W. Paerl, B. Bergman & E.J. Carpenter. 1997. *Trichodesmium*, a globally significant marine cyanobacterium. Science 276: 1221-1229.

Carpenter, E.J. 1983. Physiology and ecology of marine planktonic *Oscillatoria* (*Trichodesmium*). Mar. Biol. Letters 4: 69-85.

Carpenter, E.J. & D.G. Capone. 1992. Nitrogen fixation in *Trichodesmium* blooms. 211-217 In: E.J. Carpenter and D. Capone (eds.) Nitrogen in the marine environment. Academic Press. New York.

Carpenter, E.J. & J.J. McCarthy. 1975. Nitrogen fixation and uptake of combined nitrogenous nutrients by *Oscillatoria* (*Trichodesmium*) in the western Sargasso Sea. Limnol. Oceanogr. 20: 389-401.

Carpenter, E.J., J.M. O'Neil, R. Dawson, D.G. Capone, P.J.A. Siddiqui, T. Roenneberg & B. Bergman. 1993. The tropical diazotrophic phytoplankter *Trichodesmium*: biological characteristics of two common species. Mar. Ecol. Prog. Ser. 95: 295-304.

Carpenter, E.J. & C.C. Price IV. 1977. Nitrogen fixation, distribution and production of *Oscillatoria* (*Trichodesmium*) spp. in the western Sargasso and Caribbean Seas. Limnol. Oceanogr. 22: 60-70.

Carpenter, E.J. & K. Romans. 1991. Major role of the cyanobacterium *Trichodesmium* in nutrient cycling in the North Atlantic Ocean. Science 254: 1356-1358.

Devassy, V.P., P.M.A. Bhattathiri & S.Z. Qasim. 1978. *Trichodesmium* phenomenon. Indian J. Mar. Sci. 7: 89-93.

Farmer, C.T., C.A. Moore, R.G. Zika & R.J. Sikorski. 1993. Effects of low and high Orinoco River flow on the underwater light field of the eastern Caribbean Basin. J. Geophys. Res. 98(C2): 2279-2288.

Jason, S., P.J.A. Siddiqui, A.E. Walsby, K.M. Romans, E.J. Carpenter & B. Bergman. 1995. Cytomorphological characterization of the planktonic diazotrophic cyanobacteria *Trichodesmium* spp. from the Indian Ocean and Caribbean and Sargasso Seas. J. Phycol. 31: 463-477.

Letelier, R.M. & D.M. Karl 1996. Role of *Trichodesmium* spp. in the productivity of the subtropical North Pacific Ocean. Mar. Ecol. Prog. Ser. 133: 263-273.

Lewis, M.R., O. Ulloa & T. Platt. 1988. Photosynthetic action, absorption and quantum yield spectra for a natural population of *Oscillatoria* in the North Atlantic. Limnol. Oceanogr. 33: 92-98.

Méndez, A. 1984. Nitrogen fixation by the bluegreen alga *Oscillatoria* (*Trichodesmium*) spp. M.S. Thesis. Department of Marine Science. University of Puerto Rico. Mayaguez Campus. 72p.

McCarthy, J.J. & E.J. Carpenter. 1979. *Oscillatoria (Trichodesmium) thiebautii* (Cyanophyta) in the Central North Atlantic Ocean. J. Phycol. 15: 75-82.

Müller-Karger, F.E., C.R McClain, T.R. Fisher, W.E. Esaias & R. Varela. 1989. Pigment distribution in the Caribbean Sea: Observations from space. Prog. Oceanog. 23: 23-64.

Navarro, A. 1998. Optical properties of photosynthetic pigments and abundance of the cyanobacterium *Trichodesmium* in the eastern Caribbean Sea. Ph.D. Thesis. University of Puerto Rico, Mayaguez Campus. 125 p.

Parsons, P., Y. Maita & C.M. Lalli. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon Press. New York.

Rohlf, F.J. & R.R. Sokal. 1981. Statistical tables. Second edition. W.H. Freeman and Company. New York.

Sánchez-Suárez, I., F.C. Troncone-Osorio & R. Díaz-Ramos. 1995. The phytoplankton from the Gulf of Paria, Venezuela (June 1984). Mar. Biol. 16: 192-205.

Santhanam, R., A. Srinivasan, V. Ramadhas & M. Devaraj. 1994. Impact of *Trichodesmium* blooms on the plankton and productivity in the Tuticorin Bay, southeast coast in India. Indian J. Mar. Sci. 23: 27-30.

Steven, D.M. & R. Glombitza. 1972. Oscillatory variation of a phytoplankton population in a tropical ocean. Nature 237: 105-107.

Stewart, WD.P. 1974. Algal physiology and biochemistry. Bot. Monogr.10: 194-204.

Villareal, T. 1995. Abundance and photosynthetic characteristics of *Trichodesmium* spp. along the Atlantic Barrier Reef at Carrie Bow Cay, Belize. Mar. Ecol. 16: 259-271.

Wyman, M., R.P.F. Gregory & N.G. Carr. 1986. Novel role of phycoerythrin in a marine cyanobacterium, *Synechococcus* Strain DC2. Science 230: 818-820.