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Deep-Sea Research I 51 (2004) 173–203
DEEP-SEA RESEARCH PART I
www.elsevier.com/locate/dsr

Biomass and primary productivity of the cyanobacterium *Trichodesmium* spp. in the tropical N Atlantic ocean

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Received 7 August 2002; received in revised form 15 April 2003; accepted 6 October 2003

Abstract

Primary production and standing crop, as chlorophyll-*a* (chl-*a*), of *Trichodesmium* spp., and other phytoplankton as well as the abundance and depth distribution of *Trichodesmium* were measured on three cruises to the tropical North Atlantic Ocean. *Trichodesmium* abundance was greatest on a cruise in May–June 1994, with average surface densities of 2250 trichomes l^{-1} and depth integrated abundance of 91×10^6 trichomes m^{-2}. Average surface densities were 292 and 222 trichomes l^{-1} and depth integrated abundance 21 and 8.6×10^6 trichomes m^{-2} for the April 1996 and October 1996 cruises, respectively. Total (phytoplankton plus *Trichodesmium*) chl-*a* standing crop and the percentage as *Trichodesmium* averaged 47 (62%), 22 (13%) and 30 (11%) mg chl-*a* m^{-2} for May–June 1994 and April and October 1996. On the May–June 1994 and April and October 1996 cruises 89%, 93% and 92% of the trichomes were in colonies, and the remainder occurred as free trichomes. Peak abundances of *Trichodesmium* were generally in the upper water column, with an average biomass maximum at 12 m on the May–June 94 and October 96 cruises and at 40 m during the April 96 cruise. The average C:N ratio (atomic) of *Trichodesmium* was 6.5.

Mean rates of total primary production (*Trichodesmium* and other phytoplankton together) for May–June 1994, and April and October 1996 were 1080, 932 and 804 mg C m^{-2} d^{-1}, and *Trichodesmium* accounted for an average of 47%, 7.9% and 11%, respectively, of the total primary production for each cruise. These primary production rates exceed those typically reported at oligotrophic open ocean sites. *Trichodesmium* C assimilation numbers (mg C fixed mg chl-a^{-1} h^{-1}) were highest at the surface and were always lower than those of other phytoplankton. Average nitrogen demand, as calculated from the mean *Trichodesmium* C fixation from all three cruises, was about 40 mg N m^{-2} d^{-1}, about 10% of concurrently determined rates of N_2 fixation.
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Keywords: *Trichodesmium*; Primary productivity; Tropical Atlantic Ocean; N_2 fixation

1. Introduction

The planktonic marine diazotroph *Trichodesmium* spp. is thought to be important in fixation of both carbon (C) and nitrogen (N) in many tropical seas (Capone et al., 1997). For example, Carpenter

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doi:10.1016/j.dsr.2003.10.006

and Romans (1991) summarized previous *Trichodesmium* biomass measurements for the SW North Atlantic Ocean, applied relatively conservative (10 day) C and N doubling times, and estimated that species in this genus were the most important primary producers and the largest contributor of new N to the oceanic euphotic zone in this region. However, to verify these estimates, comprehensive studies on rates of euphotic zone C and N turnover are needed. Here we report on the standing crop and rate of C fixation of *Trichodesmium* spp. and compare these data with productivity rates for the general phytoplankton community. A companion paper (Capone et al., manuscript pending) reports on rates of N_2 fixation and the estimated flux of NO_3^- to the euphotic zone from deep water.

The tropical Atlantic Ocean shows a large seasonal variability and is influenced by many different local physical and chemical forcing factors such as equatorial and coastal upwelling, large inputs of freshwater, and Saharan dust, that make it spatially variable as well. Perhaps because of its smaller size or because it does not exhibit dramatic basin-wide phenomena like the El Nino, it has not received the attention given to the tropical Pacific Ocean. There have been few multi-seasonal basin-wide oceanographic field studies of the tropical Atlantic (CIPREA in 1978–79, FGGE in 1979, AMASSEDS in 1989–91, AMT in 1995–98 being exceptions). Most of these studies were conducted along the eastern side of the basin, and very few included examination of water samples with a microscope for enumeration of plankton species and abundances. Thus, while it is known that *Trichodesmium* is important as a primary producer in the Caribbean Sea, and Carpenter and Price (1977) observed that it constituted 60% of the euphotic zone chlorophyll-*a* (chl-*a*) and accounted for 20% of the primary production, there are no comparative data for the tropical Atlantic outside of the Caribbean. The goal of our study was to determine the contribution of *Trichodesmium* to primary production and standing crop in the tropical Atlantic Ocean. Because *Trichodesmium* was ignored or missed by much of the previous work in the region, its impact is also missing from the modeling of this region. This paper details the impact of *Trichodesmium* on the total biomass and primary production in the tropical Atlantic.

2. Methods

Sampling was carried out on three cruises in the tropical Atlantic Ocean: R.V. *Gyre*, 23 May–18 June 1994, R.V. *Seward Johnson*, 29 March–25 April 1996 and 12 October–6 November 1996 (Fig. 1). Water samples for primary productivity, chl-*a*, and *Trichodesmium* abundance measurements were collected with a CTD rosette system with 10 l Niskin bottles. For the ^{14}C primary productivity measurements, samples were collected at specific light levels (100%, 55%, 28%, 10%, 1%) in the water column at 0700 with the rosette system. Extinction coefficients were determined daily at noon with a Biospherical Instruments Co. spectral radiometer (Model MER 1010), and the coefficient from the previous day was used to select bottle sampling depths.

Water for primary productivity measurements on phytoplankton other than *Trichodesmium* was first pre-screened through 105 μm mesh nylon netting in order to remove colonies of *Trichodesmium* and larger zooplankton, and then poured into 500 ml clear polycarbonate bottles. Bottles were pre-cleaned for contaminant removal (Fitzwater et al., 1982). To each, 20 μCi of ^{14}C bicarbonate was added, and two light and one dark bottle were incubated on deck from 0800 to 1200 in an open Plexiglass incubator with temperature maintained by surface seawater pumped through the incubator and with layers of plastic window screening used to attain desired irradiance levels. To terminate the incubation, the contents of each bottle were filtered through a 0.22 μm pore size 25 mm diameter cellulose nitrate filter. Filters were rinsed with ca. 3 ml of filtered seawater. Time zero samples were run to subtract for any background activity remaining on the filter. All filters were exposed to fuming HCl for 20 min in a desiccator in order to dissolve any carbonates. Samples were then placed in a 5 ml mini scintillation vial with Opti-fluor scintillation cocktail, and activity was determined with a scintillation counter aboard ship. All counts were quench corrected.

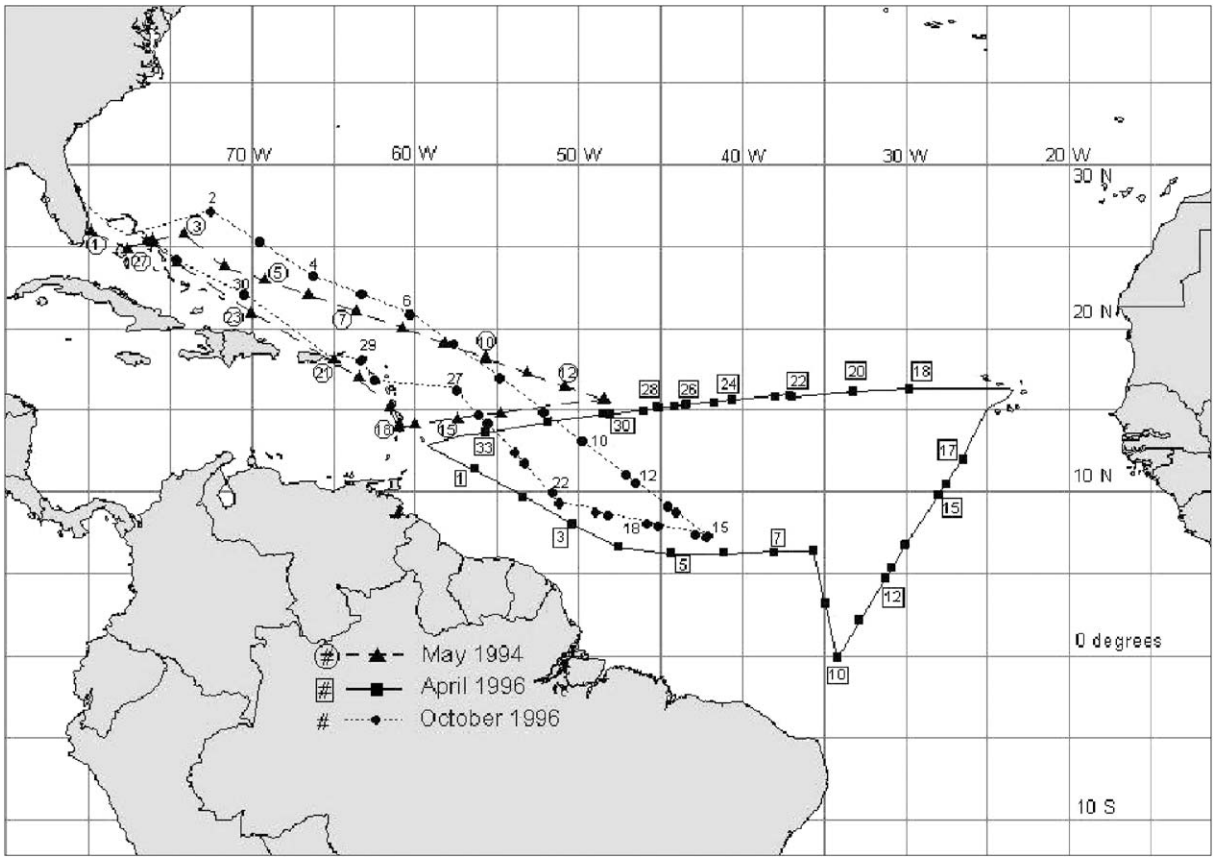

Fig. 1. Station locations for cruises.

To measure *Trichodesmium* productivity, colonies were first collected in a 202 μm mesh 1 m diameter net towed at 10–20 m depth. Colonies were selected with a plastic bacteriological transfer loop and rinsed in filtered seawater. Ten colonies were then placed in a 20 ml glass vial, and 1 μCi of ^{14}C sodium bicarbonate was added. Two light and one dark bottle were incubated from 0800 to 1200 for each irradiance level (100%, 50%, 25%, 10% and 1%), and incubations and sample handling were as described for phytoplankton. In plotting the data, depths were rounded to the nearest 5 m depth. For both bulk phytoplankton and *Trichodesmium*, daily carbon fixation was scaled by multiplying the hourly C fixation rate by ten hours.

Phytoplankton chl-*a* concentration was determined by filtering 1000 ml of seawater first through a 105 μm mesh to remove *Trichodesmium* colonies and zooplankton and then on to a 25 mm diameter GF/F filter, which was then placed in 7 ml of cold (ca. −5°C) methanol and held in the dark in a freezer overnight. Chl-*a* concentration was determined with a Turner Designs 10-005-R fluorometer. The fluorometer was periodically calibrated against a sample which also had its pigments measured with a spectrophotometer according to trichromatic equations (Porra et al., 1989). Since shipboard productivity measurements were done on a per colony basis and in situ biomass estimates were done as counts of trichomes, a conversion factor was necessary to compare *Trichodesmium* chlorophyll biomass to that of other phytoplankton and for comparison of chlorophyll specific estimates of primary productivity. For the first cruise (*Gyre*, May–June 1994), the value assumed

was based on literature values for this region for chlorophyll content and the numbers of trichomes per colony (Carpenter and Price, 1977). For most stations, values of 50 ng chl per colony and 250 trichomes per colony were used. However, for several stations (*Gyre* 15–21) in mid-cruise, much smaller colonies were observed and the conversion was scaled to 100 trichomes per colony and 20 ng chl per colony. For both 1996 cruises, a conversion factor was empirically determined every 2–3 days, to relate colonies, trichomes and chl-*a* content of *Trichodesmium*. Care was taken to select the same size colonies as used for shipboard primary production measurements. Three samples of 10 colonies each were used for determining the colony-specific chl-*a* concentration, and three samples of 10 colonies each were used for the enumeration of trichomes per colony with a microscope. The colony count samples were shaken to disperse the trichomes, and trichome content was determined by placing 1 ml of the dispersed trichomes in a Sedgwick Rafter chamber and counting at 100× magnification.

Concentrations of free trichomes and colonies of *Trichodesmium* at each station were determined by filtering ten liters of seawater from the Rosette casts onto an 8 or 10 μm pore size, 47 mm diameter Nuclepore or Poretics filter. A Millipore Swinnex 47 filter holder containing the filter was attached to the spigot of the Rosette bottle with tubing, and the water was filtered by gravity. Direct filtration by gravity allowed minimal disturbance to colonies and permitted counts of trichomes in the colonial and free state. The filter was mounted on an oversize (75 mm × 50 × 1 mm) glass microscope slide, a drop of immersion oil was put on the filter, then a # 1 coverslip ($45 \times 50\,mm^2$) was placed on it. The free trichomes and colonies of *Trichodesmium* were then enumerated on ship within 24 h of collection. Counts were done at 400× magnification with a Zeiss Axioskop microscope with epifluorescence and green excitation.

The particulate carbon and nitrogen content of *Trichodesmium* was determined with a Carlo Erba Model EA-1108 elemental analyzer. For each measurement, ten colonies were rinsed in filtered seawater and placed on a pre-combusted (490°C) glass fiber filter, which was then desiccated and stored prior to measurement.

3. Results

3.1. Hydrography

Average surface water temperature of the 22 stations taken on the May–June 1994 cruise was 27.2°C (±0.2 SE), and mean surface salinity was 35.4 (±0.4) PSS (Table 1). Winds were relatively strong at all stations, and average wind speed in the trade winds of the North Equatorial Drift Current was 17.3 (±1.4) knots. Average mixed layer depth was 31.0 (±3.0) m. A lens of slightly lower salinity water was encountered at stations 9–11, and 15–21 (Table 1).

At the 29 stations sampled in April 1996, surface water temperature averaged 26.5°C, (±0.2) and salinity averaged 36.0 (±0.1) PSS (Table 2). Wind speeds averaged 15.1 (±1.3) knots and mixed layer depths were 58 (±4) m. Surface water temperature were warmest at the 28 stations sampled on the October 1996 cruise and averaged 28.5°C (±0.1), with mean surface salinity lowest among all cruises, averaging 34.2 (±0.2) PSS because of freshwater input in the study area from the Amazon River (Table 3). Mixed layer depth averaged about 28.3 (±2.4) m while wind speeds averaged 11.3 (±1.3) knots.

3.2. Speciation

As previously reported (Carpenter and Price, 1977) for the Caribbean and southwest Sargasso Sea, the populations of *Trichodesmium* we encountered through most of the tropical N. Atlantic were predominantly composed of *Trichodesmium thiebautii*. Individual cells of *T. thiebautii* were relatively large, typically about 10 μm in dia. (range ca. 8–15 μm). Cells are as wide as they are long, and trichomes typically have about 100 cells.

3.3. Trichome density

May–June 1994: The average densities of trichomes were highest for all stations at about

Table 1
Trichodesmium densities and productivity in the tropical Atlantic in May–June 1994

Date	Station #	Latitude	Longitude	Surface temp (°C)	Surface salinity PSS	Mixed layer depth (m)	Surf bio density (trichomes l^{-1})	Max den (trichomes l^{-1})	Depth of max (m)	Int biomass × 106 trichomes m^{-2}	Fraction above 20 m (%)	Fraction above 50 m (%)	Tricho (mg C m^{-2} d^{-1})	Phyto (mg C m^{-2} d^{-1})	Tricho % prod	Tricho % prod
24-May-94	4	23.87	71.67	27.05	36.43	33	4	nd[a]	nd	0.18	33	100	1.2	391	0.3	
	6	22.07	66.54	27.40	36.29	38	6.6	6.6	1	0.13	100	100	1.2	340	0.4	
27-May-94	7	21.04	63.60	26.89	36.48	43	132	132	1	7.0	55	67	59	496	11	
28-May-94	8	20.05	60.82	26.72	36.45	37	64	3941	23	95.8	83	97	773	538	59	
29-May-94	9	19.12	58.23	26.62	35.18	15	193	193	1	5.6	72	82	44	401	10	
30-May-94	10	18.23	55.68	26.46	35.41	15	2017	2017	1	57.5	35	99	466	291	62	
31-May-94	11	17.31	53.17	26.27	35.30	22	150	5465	26	146.5	73	96	1149	530	68	
1-Jun-94	12	16.47	50.82	25.68	36.73	44	15.7	1307	38	38.5	6	90	677	458	60	
2-Jun-94	13	15.67	48.46	25.49	36.64	32	1009	2572	20	88.1	70	100	nd	283	nc[b]	
4-Jun-94	15	14.88	54.74	26.66	35.45	31	988	988	1	11.9	82	97	108	370	23	
5-Jun-94	16	14.51	57.44	27.43	29.55	19	11,932	20,621	11	320.3	98	100	4533	263	95	
6-Jun-94	17	14.16	60.04	27.21	34.30	11	10,867	10,867	1	95.8	99	100	1114	126	90	
7-Jun-94	18	14.00	61.09	27.34	34.66	19	2954	2954	1	60.1	92	99	669	259	72	
10-Jun-94	19	15.24	61.57	27.81	35.06	31	5476	6675	20	298.4	63	95	nd[b]	nd	nd	
11-Jun-94	20	17.06	63.41	29.00	34.11		5518	5518	1	229.2	52	100	649	309	68	
12-Jun-94	21	18.14	64.94	27.72	35.73	27	1372	1372	1	85.0	19	99	nd	nd	nd	
14-Jun-94	23	20.91	70.07	27.89	36.25	57	20.9	2641	38	154.4	19	75	nd	nd	nd	
16-Jun-94	25	24.06	74.57	27.98	36.40	47	20.9	1318	13	18.9	98	100	143	230	38	
18-Jun-94	27	24.89	76.61	28.58	36.17	37	10.5	1323	16	25.1	88	94	408	397	51	
Average				27.17	35.40	31.0	2250	3884	11.9	91.5	65	94	720	355	47.0	67.0
SE				0.21	3.0	3.0	840	1181	3.1	22.5	7	2.2	290	39	8.1	
n				19	19	18	19	18	18	19	19	19	15	16	15	

[a] nd = not determined.
[b] nd = not calculated.

Table 2
Trichodesmium densities and productivity in the tropical Atlantic in Apr 1996

Date	Station #	Latitude	Longitude	Surface temp (°C)	Surface salinity PSS	Mixed layer depth (m)	Surf Bio density (trichomes l^{-1})	Max den (trichomes l^{-1})	Depth of max (m)	Int Biomass × 106 trichomes m^{-2}	Fraction above 20 m (%)	Fraction above 50 m (%)	Tricho (mg C m^{-2} d^{-1})	Phyto (mg C m^{-2} d^{-1})	Tricho % prod	Tricho % prod
29-Mar-96	1	11.35	56.47	27.00	34.92	43	1074	3063	25	68.0	49	98	nd	nd	nd	
30-Mar-96	2	9.69	53.45	27.00	36.08	65	55	157	10	3.4	52	82	nd	1608	0	
31-Mar-96	3	8.00	51.40	27.10	36.13	75	1	42	32	2.1	34	88	nd	1193	0	
1-Apr-96	4	6.65	47.56	27.6	16.08	107	7	37	50	0.38	20	77	0[a]	1371	0	
2-Apr-96	5	6.27	44.31	27.31	36.02	106	2	20	112	1.41	2	9	0[a]	1295	0	
3-Apr-96	6	6.23	44.33	27.44	35.99	70	108	288	54	15.5	18	80	36	916	3.8	
4-Apr-96	7	6.23	38.04	27.00	35.98	53	1915	3130	15	148.2	40	98	786	1253	39	
5-Apr-96	8	6.36	35.68	27.40	35.77	63	411	606	30	34.3	46	73	167	961	15	
6-Apr-96	9	3.16	34.93	27.80	35.68		4	17	40	0.36	23	95	0[a]	890	0	
7-Apr-96	10	0.00	34.14	28.30	36.15	20	8	35	71	0.75	7	7	0[a]	853	0	
8-Apr-96	11	2.06	32.89	28.02	35.50	34	118	137	8	4.7	51	89	6.6	876	0.8	
9-Apr-96	12	4.69	31.26	27.90	35.57	39	1311	2378	35	61.9	42	93	189	861	18	
9-Apr-96	13	5.31	30.88	27.64	35.62	51	237	369	10	14.4	47	84	nd	nd	nd	
10-Apr-96	14	6.50	30.03	27.14	35.71	46	67	131	65	6.2	30	70	15	1099	1.3	
11-Apr-96	15	9.72	27.99	25.88	35.92	52	38	116	10	4.8	47	63	nd	892	0	
12-Apr-96	17	11.88	26.50	25.80	35.98		55	88	25	4.0	41	99	5.0	768	0.7	
17-Apr-96	18	16.26	29.81	23.53	36.38	52	0	114	80	2.4	0	0	nd	nd	nd	
18-Apr-96	20	16.08	33.18	24.10	36.27	52	1	33	100	1.1	1	5	0a	500	0	
19-Apr-96	22	15.76	37.97	24.60	36.34	57	22	201	70	7.1	8	22	5.9	349	1.7	
20-Apr-96	24	15.55	40.61	25.30	36.16	67	174	213	7	15.1	27	73	74	330	18	
20-Apr-96	25	15.44	41.72	25.40	36.45	51	8	198	30	10.9	17	50	nd	nd	nd	
21-Apr-96	26	15.25	43.49	25.40	36.17	55	105	1008	50	25.6	13	78	103	327	24	
21-Apr-96	27	15.18	44.19	25.76	36.22	76	79	252	30	14.7	24	59	nd	nd	nd	
22-Apr-96	28	15.09	45.09	25.50	36.17	76	176	187	50	12.0	29	70	nd	216	nc	
22-Apr-96	29	14.97	46.00	25.63	36.37	67	71	378	50	13.6	13	64	nd	nd	nd	
23-Apr-96	30	14.73	48.10	26.20	36.17	53	290	432	16	19.9	34	54	44	421	9.4	
23-Apr-96	31	14.55	48.47	26.30	36.32	45	39	286	40	9.0	30	87	nd	nd	nd	
24-Apr-96	32	14.26	51.88	26.3	36.20	41	286	446	25	15.5	52	85	116	324	26	
26-Apr-96	33	13.62	55.69	26.90	325.57	46	1799	2016	28	89.9	54	96	nd	nd	nd	
Average				26.46	36.00	57.9	292	565	40	20.9	29	67	91	824	7.9	9.9
SE				0.22	0.06	3.7	98	165	5.0	6.1	3.2	5.6	46	87	2.6	
n				29	29	27	29	29	29	29	29	29	17	21	20	

nd = not determined.
nc = not calculated.
[a] 0 assumed because of low ($<2\times10^6$) trichome density.

Table 3
Trichodesmium densities and productivity in the tropical Atlantic in October 1996

Date	Station #	Latitude	Longitude	Surface temp (°C)	Surface salinity PSS	Mixed layer depth m	Surf bio density (trichomes l^{-1})	Max den (trichomes l^{-1})	Depth of max (m)	Int Biomass × 106 trichomes m^{-2}	Fraction above 20 m (%)	Fraction above 50 m (%)	Tricho (mg C $m^{-2} d^{-1}$)	Phyto (mg C $m^{-2} d^{-1}$)	Tricho % prod	Tricho % prod
12-Oct-96	2	27.05	72.52	27.80	36.19	35.0										
13-Oct-96	3	25.19	69.53	27.56	35.22	25.0	46	46	1	1.0	87	87	19	59.3	24	
14-Oct-96	4	23.13	66.25	27.92	36.29	31.0	27	27	1	0.3	79	92	13	497	2.5	
15-Oct-96	5	22.01	63.31	28.10	34.00	42.0	723	723	1	1.4	67	84	96	223	30	
16-Oct-96	6	20.73	60.41	28.25	34.00	50.0	39	134	1	4.7	47	98	31	562	5.3	
17-Oct-96	7	18.90	57.64	28.06	34.21	41.0	295	295	1	5.5	73	94	55	364	13	
18-Oct-96	8	16.85	54.87	28.23	34.40	41.0	74	160	20	4.9	62	88	18	297	5.7	
19-Oct-96	9	14.82	52.19	28.21	35.77	47.0	204	204	1	11.5	44	80	127	510	20	
20-Oct-96	10	13.05	49.85	28.03	33.80	44.0	1356	1356	1	9.7	60	89	55	750	6.8	
21-Oct-96	11	10.99	47.16	28.64	35.85	22.0	105	499	1	24.0	17	70	nd	979	nc	
21-Oct-96	12	10.49	46.51	29.40	34.30	9.0	492	566	30	22.2	28	82	nd	nd	nd	
22-Oct-96	13	9.02	44.60	29.04	33.64	20.0	19	58	30	4.2	21	87	7.2	942	0.8	
23-Oct-96	15	7.18	42.22	28.80	34.50	39.0	116	159	20	6.2	58	94	nd	1785	nc	
23-Oct-96	16	7.34	42.84	28.70	33.26	9.0	145	197	20	10.2	42	63	nd	nd	nd	
24-Oct-96	17	7.85	45.17	29.17	33.77	22.0	42	65	10	4.3	33	97	nd	1543	0	
24-Oct-96	18	8.00	45.88	29.00	33.06	29.0	456	456	1	4.9	82	100	nd	nd	nd	
25-Oct-96	19	8.53	48.26	29.10	32.85	15.0	0	391	30	6.2	27	100	nd	1279	0	
25-Oct-96	20	8.69	48.98	29.30	30.60	11.0	0	6	10	0.1	67	92	nd	nd	nd	
26-Oct-96	21	9.17	51.17	28.32	35.05	15.0	0	1	10	0.0	100	100	0[a]	457	0	
26-Oct-96	22	9.82	51.61	29.27	32.97	15.0	0	6	30	0.2	46	100	nd	nd	nd	
27-Oct-96	23	11.66	53.31	28.70	33.16	30.0	312	312	1	17.2	32	78	79	1215	6.1	
27-Oct-96	24	12.09	53.67	28.71	35.49	35.0	99	327	20	12.7	40	64	nd	nd	nd	
28-Oct-96	25	14.14	55.64	28.21	35.85	47.0	582	895	20	19.9	66	99	401	865	32	
28-Oct-96	26	14.63	56.12	28.38	34.02	17.0	1	89	20	2.9	36	85	nd	nd	nd	
29-Oct-96	27	16.10	57.47	28.11	32.92	24.0	0	298	1	3.6	60	94	54	911	5.6	
1-Nov-96	28	16.71	62.54	28.80	33.26	26.0	349	492	10	18.9	55	100	103	1032	9.1	
2-Nov-96	29	17.95	63.33	28.36	33.95	23.0	417	1584	20	30.2	81	97	235	1284	15	
4-Nov-96	30	21.94	70.53	28.16	35.35		103	366	10	5.1	95	100	80	308	21	
Average				28.51	34.20	28.3	222	360	12	8.6	56	89	86	793	11.0	9.8
SE				0.09	0.24	2.4	59	76	2.1	1.6	4.4	2.1	26	105	2.5	
n				28	28	27.0	27	27	27	27	27	27	16	20	18	

nd = not determined.
nc = not calculated.
[a] 0 assumed because of low ($<2 \times 10^6$) trichome density.

12 m depth, with a mean of 3900 (±1200 SE) trichomes l^{-1} (Fig. 2B). A subsurface maximum at between 10 and 40 m was evident at most stations on all three cruises and this is reflected in the average pattern for all cruises (Fig. 2) This pattern was observed previously by Carpenter and McCarthy (1975) and Carpenter and Price (1977) in vertical profiles taken in the sub-tropical Atlantic and Caribbean Sea. The upper 20 m contained 65% of the total *Trichodesmium* standing stock and the upper 50 m contained 94% (Table 1).

Along the cruise track, spatial variability of these populations was evident. A section sampled during the cruise shows a boundary for population densities of greater than 100 trichomes l^{-1} at 70–90 m with higher densities at shallower depths (Fig. 3). Mid-depth maxima were evident at many stations, although at a series of stations in mid-cruise (stations 15–21), maximal densities were at or very near the surface, coincident with a low salinity lens (Table 1). Depth integrated abundances were less than 10^6 trichomes m^{-2} at the first two stations where biomass observations were made, and increased to greater than 10^8 for most stations (Table 1, Fig. 4).

For the 19 stations where *Trichodesmium* biomass was sampled the *Trichodesmium* population averaged 91.5×10^6 trichomes (SE = 22.5×10^6) m^{-2}. Fifteen of the stations had depth integrated populations greater than 10×10^6 trichomes m^{-2}.

April 1996: *Trichodesmium* standing crop averaged 21×10^6 ($\pm 6.1 \times 10^6$) trichomes m^{-2}. Peak density in the composite profile occurred at about 25 m and averaged 468 (±158) trichomes l^{-1} (Fig. 2). The biomass maximum averaged across all stations was somewhat deeper, however, at 40 m (Table 2). This value was skewed by several stations with very low overall densities of *Trichodesmium* which had peaks deeper in the water column (e.g. stations 5, 10 and 20). The mean proportion of the population in the upper 20 m was 29%, with 67% within the upper 50 m. Using the grand average densities, this amounted to 39% of the population above 20% and 71% above 50 m. Fourteen of 29 stations had populations of less than 10×10^6 trichomes m^{-2}.

Spatial variability in populations can be seen in the bubble plots and in the sections along the cruise track (Fig. 4). Highest depth integrated standing crop and surface densities occurred near

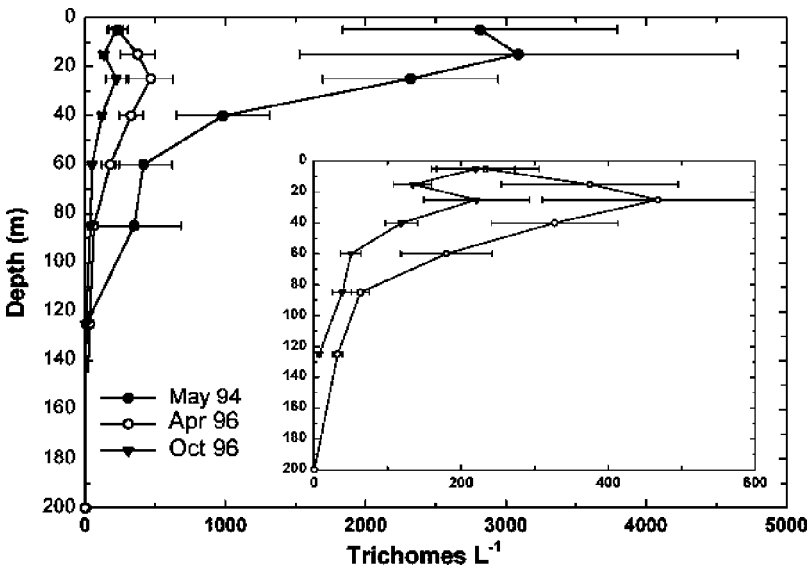

Fig. 2. Average vertical profiles of *Trichodesmium* trichome concentration for all three cruises. Error bars represent standard error of the mean. Inset: expanded scale for last two cruises.

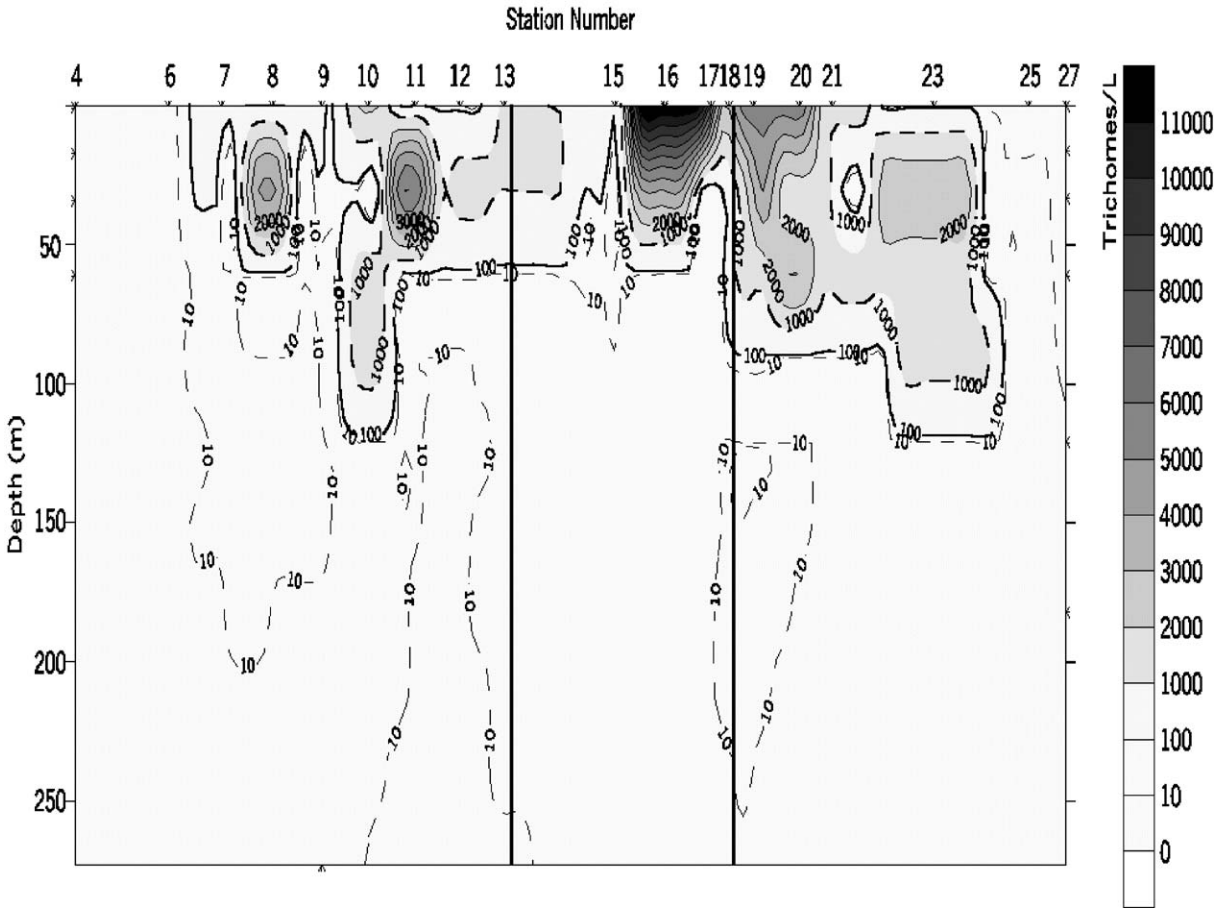

Fig. 3. Section (log scale) of trichome abundance (trichomes l^{-1}) along cruise track for June 1994 R.V. *Gyre* cruise. Vertical lines indicate three legs of cruise (see Fig. 1).

5°N between 30° and 40°W and at the more westerly stations on the transect along 15°N (Fig. 4). Density maxima at most stations were between 20 and 40 m, and the 100 trichome l^{-1} boundary was generally found near 60 m (Figs. 5A and B).

October 1996: *Trichodesmium* abundance was lowest during the October 1996 cruise. Average *Trichodesmium* concentration was highest over the top 25 m (Fig. 2), averaging about 220 trichomes l^{-1} (Table 3) and falling to about one quarter of that at 50 m depth (Fig. 2). The upper 20 m held 56% of the population, while 89% of the population was found within the upper 50 m. *Trichodesmium* concentration averaged 8.6×10^6 (± 1.60 SE) trichomes m^{-2} with 18 of the 27 stations having integrated populations less than 10×10^6 trichomes m^{-2} and 4 with populations less than 100,000 trichomes m^{-2} (Table 3).

The 100 trichome l^{-1} boundary was often much shallower than on the first two cruises, (Fig. 6). At stations 13 and 14, and 17–22, very high densities of *Hemiaulus hauckii* with its symbiont *Richelia intracellularis* largely displaced *Trichodesmium* (Carpenter et al., 1999).

3.4. Abundance of free trichomes

On the three cruises, the relative abundance of free trichomes to trichomes in colonies was determined. Paired observations were made at discrete depths, with typically 5–8 depths sampled per station. At stations with relatively low overall

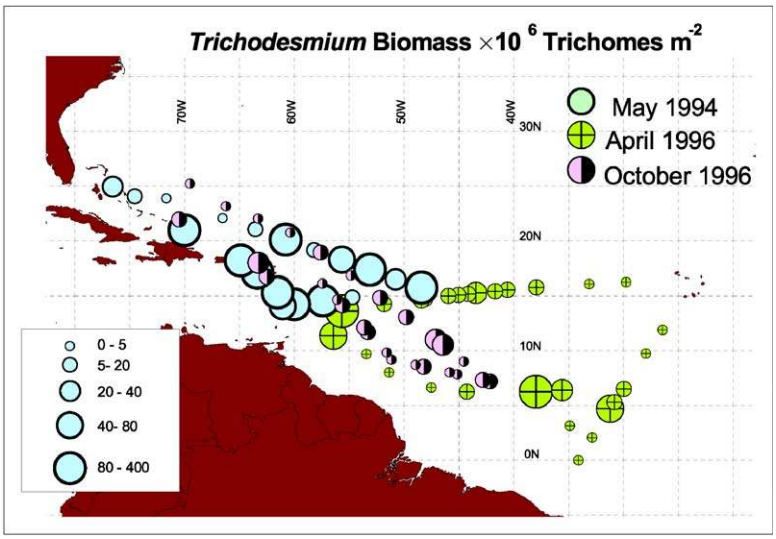

Fig. 4. Depth integrated trichome standing crop for all three cruises.

densities of *Trichodesmium*, there were depths where all the *Trichodesmium* was present only as free trichomes. It was somewhat rarer to encounter samples with only colonies and no free trichomes (Table 4). In all three cruises only two stations were sampled which had no *Trichodesmium* at all (October 1996) while only free trichomes were detected at 5 stations on the May–June 1994 and at 3 stations on the October 1996 cruise.

Thus, at stations with low *Trichodesmium* densities, free trichomes often dominated while at stations with appreciable colony densities, the bulk of trichomes were in colonies. For example, the average percent of free trichomes was 60% of total trichomes for 91 discrete paired observations in which some *Trichodesmium* was observed for the May–June 1994 cruise. However, if observations are restricted to samples with a minimum of 100 or 1000 total trichomes l^{-1}, the average relative free trichome density fall to 28% and 21%, respectively. Across the whole cruise, for 114 paired observations, the average free trichome concentration was 141 trichomes l^{-1} while the density of trichomes in colonies averaged 1175 trichomes l^{-1} (Table 4). On this basis, the average abundance of free trichomes was about 10.7% of total trichomes.

For the April 1996 cruise, the average free trichome density for 255 discrete observations was 16 trichomes l^{-1}, while trichomes in colonies averaged 215 trichomes l^{-1}. For 237 paired observations with measurable *Trichodesmium*, the average percent of free trichomes was 29% (Table 4). This drops to 10% and 4% for samples which had at least 100 or 1000 total trichomes l^{-1}. Considering the average density of free and total trichomes across all stations, free trichomes represented 7.1% of total trichomes on this cruise.

For the October 1996 cruise, for 215 discrete observations where *Trichodesmium* was detected, the average percent of free trichomes was 28%. For samples having at least 100 or 1000 total trichomes, this percentage dropped to 7.8% and 8.2%. If the average densities of trichomes over the whole cruise are used, the average abundance of free trichomes was 8.3%.

3.5. Average colony size, C and N and chlorophyll content

Mean number of trichomes per colony for the two 1996 cruises was 135 ± 14 (7) in April and 98 ± 11 (8) in October 1996 (Table 5). The chl-*a* content per colony averaged 21 ± 4 ng ($n = 13$) and

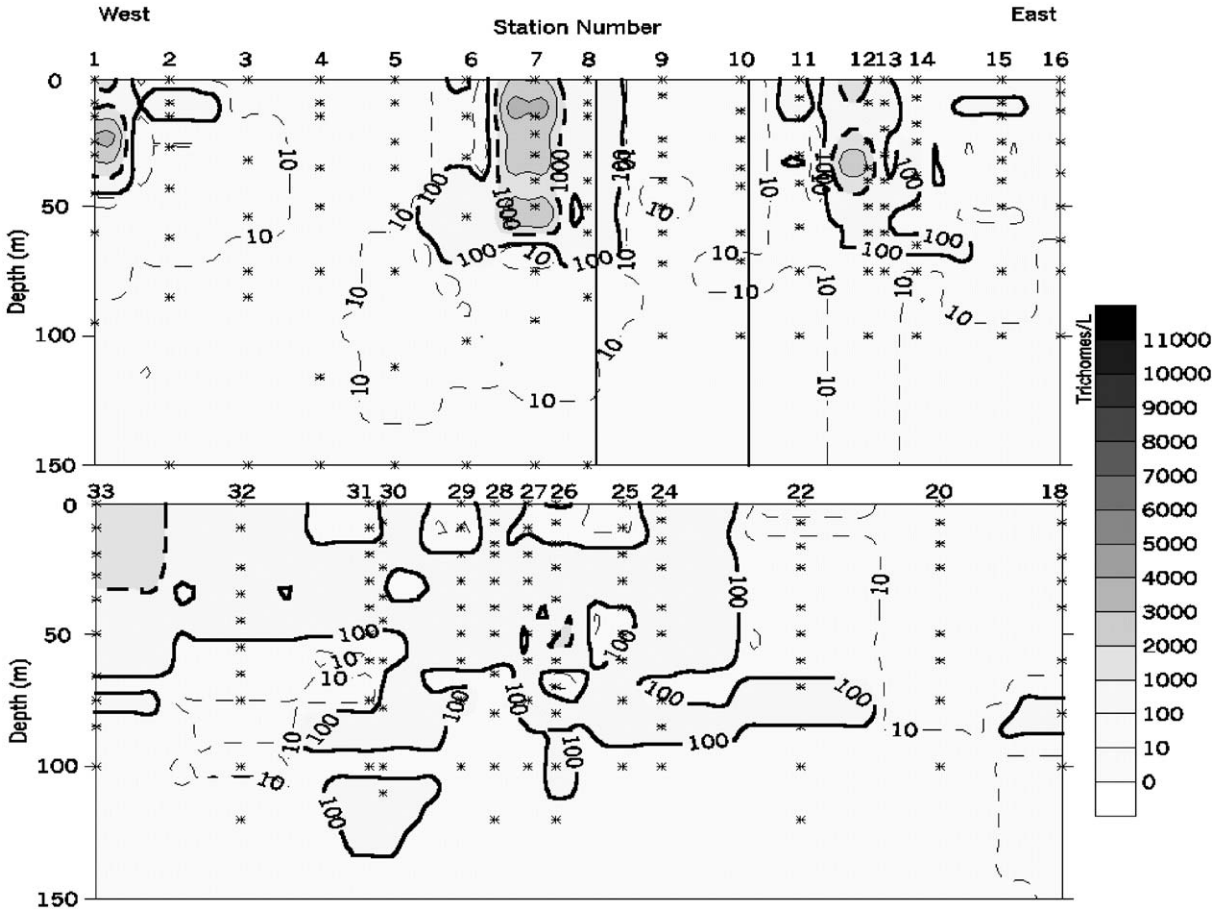

Fig. 5. Section of trichome abundance (trichomes l^{-1}) along cruise track for April 1996 R.V. *Seward Johnson* cruise. Upper panel: eastbound leg with divergence to equator indicated by vertical lines. Lower panel: westbound leg (see Fig. 1).

38 ± 5 ($n = 9$) in April and October 1996, respectively (Table 5).

The C:N ratio of *Trichodesmium* was relatively constant through the three cruises and averaging 6.5, 5.6 and 7.3 for May–June 94, April 96 and October 96, respectively (Table 5). A regression analysis of all values of C vs. N yielded a slope of 5.83 and an r^2 of 0.93. Colony C content varied from about 2–15 μg and N content between 0.2 and 2.9 μg.

3.6. Chlorophyll-a distributions

Trichodesmium dominated the vertical distribution of chl-*a* during the May–June 1994 cruise (Figs. 7A and B, Table 6) with maximum chlorophyll occurring near the surface. As for trichome abundance, the bulk of the *Trichodesmium* chlorophyll was concentrated close to the surface, with most residing within the upper 50 m, while the largest fraction of the other phytoplankton were found deeper, typically between 50 and 100 m (Fig. 7B).

Bubble plots of depth integrated chlorophyll again indicate both the highest relative and absolute concentrations of *Trichodesmium* encountered during the May–June cruise with the highest densities on all cruises localized in the SW Sargasso Sea and NE Caribbean (Fig. 8). Total chlorophyll standing stock (< 105 μm phytoplankton plus *Trichodesmium*) integrated to 200 m averaged 47 mg m^{-2} (± 0.9) on the May–June 94

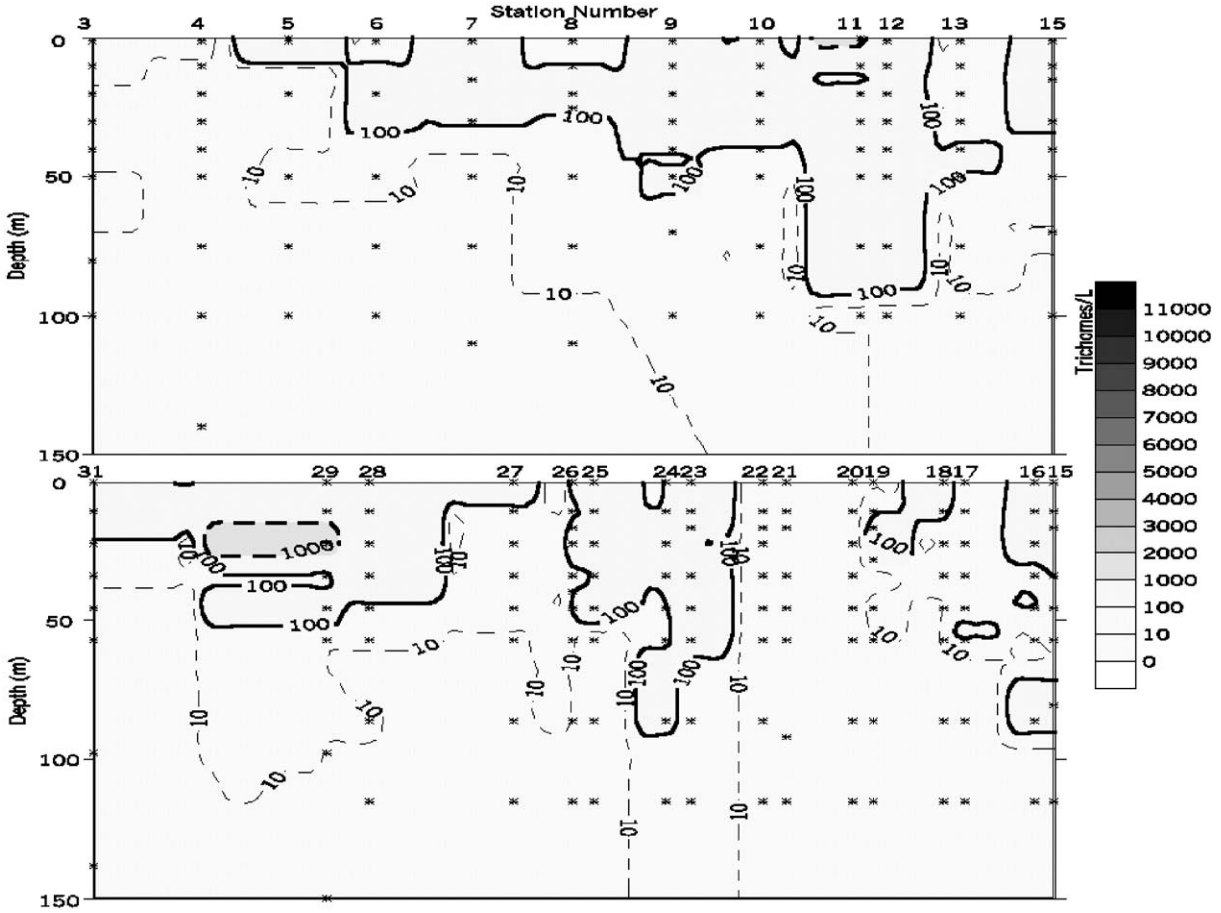

Fig. 6. Section of trichome abundance (trichomes l^{-1}) along cruise track for October 1996 R.V. *Seward Johnson* cruise. Upper panel: southeastbound leg. Lower panel: northwestbound leg (see Fig. 1).

cruise, 22 mg m^{-3} (± 2) during the April 96 cruise and 30 mg m^{-2} (± 3.3) during the October 1996 cruise. *Trichodesmium* averaged 62% of the total (depth integrated) chl-*a* in May 1994 and 13% and 11% in April and October 1996. At several stations on all cruises, *Trichodesmium* accounted for more than 20% of depth integrated chlorophyll.

3.7. Primary productivity

May 1994: Carbon fixation per colony was highest during the May–June 94 cruise averaging about 0.22 μg C colony^{-1} h^{-1} at full surface irradiance, falling off slightly at the 50% and 25% light levels and more sharply at lower irradiances (Fig. 9, Table 6). Average volumetric C fixation was maximal at the 50% light level at 3.2 mg C m^{-3} h^{-1} (± 2) decreasing rapidly at greater depths (Fig. 10, Table 6). The variability in the volume-specific productivity of *Trichodesmium* was high, especially at the 50% light level because of the high variability in the standing crop (Figs. 2 and 7, Table 6). The average vertical profiles of production of *Trichodesmium* (Fig. 11) indicated maximal rates of primary production at the 50% depth which on this cruise was at about 17 m (Table 6). Phytoplankton production decreased from the surface to depth (Fig. 11A, Table 6). Averaged across the stations, at the 50% irradiance level, about a half of the total production was from *Trichodesmium* (Fig. 11B). For

Table 4
Relative abundance of free trichomes and trichomes in colonies

	Free trichomes		Trichomes in colonies (trichomes l^{-1})		Total	Total paired obs	# of observations of 0			% Free trichomes			
	Average	SE	Average	SE	*n*		Discrete obs with no free trichomes	Whole stations with no trichomes	Discrete obs with no colonies	Whole stations with no colonies	Based on average densities for whole cruise	Average of discrete obs	For stations with > 100 trichomes l^{-1}	For stations with > 1000 trichomes l^{-1}
Gyre 94	141	32	1175	240	1316	114	23	0	73	5	10.7	60.0	28.0	21.0
Sj Apr 96	16	1	215	31	232	255	22	0	57	0	7.1	29.0	10.0	4.0
Sj Oct 96	9	1	103	13	113	215	30	2	60	3	8.3	28.0	7.8	8.2
Average	79		695		774						8.7	39.0	15.3	11.1
Sum						584	75	2	190	8				

Trichodesmium, virtually all photosynthesis took place in the upper 50 m (Table 6).

Areal rates of C fixed by *Trichodesmium* varied widely along the cruise track (Fig. 12, Table 1), ranging from 1 to over 4500 mg C m^{-2} d^{-1} at station 16 with a strong surface bloom (Table 1, Fig. 12). Productivity of *Trichodesmium* averaged 720 (±290) mg C m^{-2} d^{-1}, and of other phytoplankton 356 (±27) mg C m^{-2} d^{-1} (Table 1; Fig. 10). For all stations, *Trichodesmium* accounted on average for about 47% of total depth integrated primary production.

April 1996: Colony specific rates were substantially less during the April 1996 cruise than during the June 94 cruise, averaging about 0.07 μg C colony^{-1} h^{-1} near the surface and decreasing rapidly at light levels below 10% of surface irradiance (which was typically at about 50 m depth) (Fig. 9, Table 6). Volumetric C fixation by *Trichodesmium* was also much less and averaged about 0.25 mg C m^{-3} h^{-1} at the 100% and 50% irradiance depths (Figs. 10A and B, Table 6). Phytoplankton productivity was about 1 mg C m^{-3} h^{-1} in the upper water column (Fig. 11A) and dominated overall water column productivity at most stations.

Overall, areal rates of primary production by *Trichodesmium* were much lower in April 96 than in May–June 94 (Fig. 12, Table 2). Primary production by *Trichodesmium* and other phytoplankton averaged 91 (±46) and 824 (±87) mg C m^{-2} d^{-1}, on this cruise. Across the stations, *Trichodesmium* accounted for an average of 7.9% of total primary production.

October 1996: Colony specific rates of C fixation by *Trichodesmium* were slightly higher compared to those observed in April 1996, or about 0.09 μg C colony^{-1} h^{-1} (Fig. 9, Table 6). Volumetric rates were similar at about 0.2 mg C m^{-3} h^{-1} in the upper water column. Phytoplankton productivity was elevated during the October 96 cruise, with average volumetric rates well above 1.0 mg C m^{-3} h^{-1} in waters at and above the 25% light level falling off at lower irradiances (Fig. 11A, Table 6). Much of this enhanced C fixation was associated with an extensive *Hemiaulus* bloom (Carpenter et al., 1999).

Table 5
Some *Trichodesmium* colony properties from the 3 Atlantic cruises

May-94 station	N (μg colony^{-1})	C (μg colony^{-1})	C:N (M)	Apr-96 station	N (μg colony^{-1})	C (μg colony^{-1})	C:N (M)	Trichomes/ colony	ng chl colony	Oct-96 station	N (μg colony^{-1})	C (μg colony^{-1})	C:N (M)	Trichomes/ colony	ng chl colony	
3	1.33	7.66	6.71	1	nd	nd	nd	91.2	16.1	1	0.80	4.47	6.52			
4	1.30	7.52	6.75	6	1.12	4.38	4.56			2	0.58	3.39	6.82			
5	1.49	8.23	6.46	7	1.38	5.93	5.01		8.3	3	1.23	6.62	6.28	56		
6	2.90	15.23	6.12	8	0.93	3.64	4.57		12.8	5	1.62	8.28	5.96			
7	1.68	9.60	6.68	11	nd	nd	nd	172	7.9	6	0.60	3.76	7.31	105		
8	1.64	8.82	6.26	12	nd	nd	nd			7	0.64	4.24	7.73			
9	1.40	8.10	6.74	13	nd	nd	nd		9.6	8	1.03	3.64	4.12	153		
10	1.77	9.82	6.46	14	nd	nd	nd	186	11.6	9	1.55	9.71	7.31	96		
11	1.70	9.05	6.22	15	nd	nd	nd		12.1	10	0.82	4.47	6.36			
12	1.92	9.84	5.97	17	0.98	4.94	5.88		14.4	23	0.22	2.04	10.82	53	37.6	
15	0.92	5.21	6.61	22	0.75	3.84	5.97			25	0.45	3.24	8.40		29.6	
16	0.46	2.81	7.21	23	nd	nd	nd		29.5	27	0.44	2.86	7.58	93	31.4	
17	0.91	5.57	7.12	24	0.87	4.48	6.01	109	19.1	28	0.58	4.92	9.90		37.6	
18	0.73	4.31	6.93	25	nd	nd	nd		50.1	29	0.95	6.46	7.93	116	60.1	
19	0.90	4.88	6.32	26	1.10	4.46	4.73	103	27.8	30	nd	nd	nd		51.9	
20	1.39	7.94	6.67	28	1.87	9.78	6.10		51.9	31	0.59	3.32	6.56	111	34.0	
22	1.65	8.64	6.12	30	1.25	6.62	6.18			32	1.01	5.51	6.36		48.4	
23	1.61	8.88	6.42	31	nd	nd	nd			33	nd	nd	nd		10.7	
24	1.95	10.35	6.19	32	1.39	7.37	6.19	136								
25	0.38	2.47	7.54	33	1.25	6.64	6.20	149								
27	0.99	5.46	6.42													
Avg	1.38	7.64	6.57		1.17	5.64	5.58	135	21		0.82	4.81	7.25	98	38	6.47
SE	0.13	0.63	0.09		0.09	0.56	0.21	14	4		0.10	0.52	0.39	11	5	
n	21	21	21		11	11	11	7	13		16	16	16	8	9	

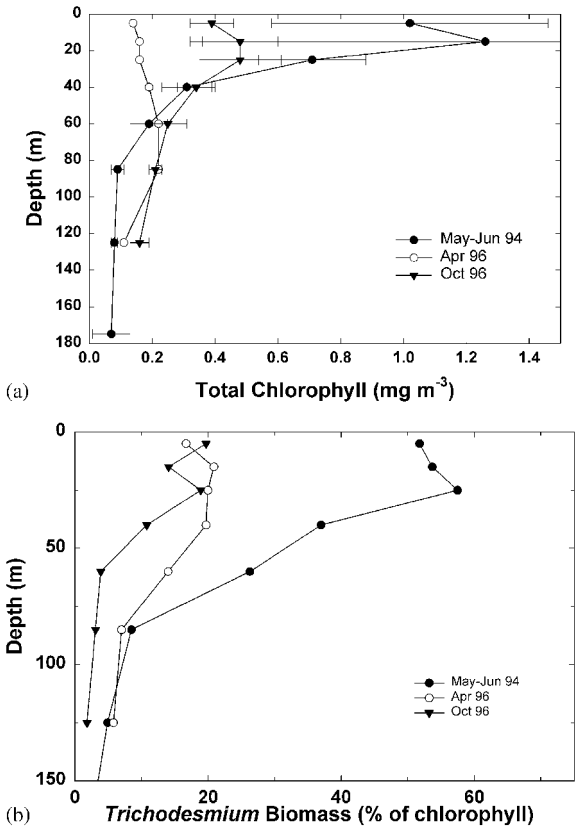

Fig. 7. Average depth profiles of total chlorophyll for all three cruises (a). Lower panel (b): percent of total chlorophyll accounted for by *Trichodesmium* on each cruise.

The October 1996 cruise, which found the lowest overall densities of *Trichodesmium* (Table 3), also recorded the lowest areal rates or primary production by this cyanobacterium (Fig. 12). *Trichodesmium* was responsible for an average of 86 (± 26) mg C m^{-2} d^{-1}, and other phytoplankton fixed 793 (± 105) mg C m^{-2} d^{-1}. Thus *Trichodesmium* contributed 11% of total production (Table 3).

Assimilation numbers: During all three cruises, mean *Trichodesmium* assimilation numbers were highest at the surface, and averaged between about 4 and 5 (mg C mg chl-a^{-1} h^{-1}) for the surface, 50% and 25% light levels, falling off rapidly at lower irradiances (Fig. 13A). In general, assimilation numbers for bulk phytoplankton were substantially higher at all depths (Fig. 13B).

4. Discussion

Trichodesmium is a predominant component of the phytoplanktonic flora in the central tropical North Atlantic, particularly in the upper reaches of the euphotic zone. Its abundance and contribution to primary productivity varies greatly both spatially and seasonally. The contribution of *Trichodesmium* to primary production appears to be greater in the tropical N. Atlantic than in many other tropical oceans where it is found (e.g. Dupouy et al., 2000).

4.1. Standing stock

Intrabasin trends: Relative to the brief, late summer appearance and low densities of *Trichodesmium* generally reported in the subtropical N. Atlantic (e.g., McCarthy and Carpenter, 1979, Orcutt et al., 1997), high densities of *Trichodesmium* were encountered on all three of our cruises to waters largely below 20°N, with the greatest densities generally noted on the May–June 1994 cruise. There also appears an east–west gradient with the highest densities seen in the western portion of the basin, between 45° and 65°W (Fig. 4).

However, many stations sampled were proximal among the 3 cruises (Table 7, Fig. 1) and the large differences between cruises at many of these stations indicates a seasonal component to the variability in these populations in the tropics as well. Two studies near Barbados (Steven and Glombitza, 1972, Borstad, 1982) have shown strong variability in *Trichodesmium* populations associated with the variation in major currents. Similarly, Navarro et al. (2000) have noted a strong seasonal signal at the Caribbean Ocean Time Series (CaTS) station with maxima during the summer, and have found *Trichodesmium* to be absent in Caribbean waters strongly influenced by the Orinoco River.

Surface currents may have been a factor in our studies. During the May–June 94 cruise, the highest densities of *Trichodesmium* were associated with lower salinity surface waters (Table 1) which may have derived from Amazonian inflow into the basin. In contrast, *Trichodesmium* densities were

Table 6
Average depth distributions of *Trichodesmium* and phytoplankton chlorophyll and primary productivity

Light depth %	Depth	SE	Tricho (mgchl-$a\,m^{-3}$) Avg	SE	n	Phyto (mgchl-$a\,m^{-3}$) Avg	SE	n	Tricho % total (of average)	Tricho % total (of discrete obs) Avg	SE	n	Tricho µg C fixed per colony h^{-1} Avg	SE	n	Tricho mg C fixed $m^{-3}\,h^{-1}$ Avg	SE	n	Phyto mg C fixed $m^{-3}\,h^{-1}$ Avg	SE	n	Tricho % total (of average)	Tricho % total (of discrete obs) Avg	SE	n
May–June 94																									
100	1		0.38	0.16	19	0.09	0.02	19	80	47	9%	17	0.22	0.04	17	2.06	1.11	15	1.27	0.33	17	62	31	8%	15
50	17	1.0	0.52	0.24	17	0.10	0.02	20	84	54	9%	18	0.21	0.03	17	3.15	2.00	15	0.91	0.26	17	77	50	10%	15
25	34	1.9	0.15	0.04	18	0.11	0.02	20	58	33	7%	19	0.20	0.03	17	0.90	0.47	16	0.90	0.21	17	50	21	7%	16
10	64	4	0.08	0.03	16	0.11	0.02	20	41	22	7%	18	0.06	0.01	17	0.06	0.04	15	0.26	0.06	17	19	10	5%	15
1	121	6.3	0.10	0.07	12	0.08	0.01	20	54	14	7%	16	0.00	0.00	17	0.00	0.00	14	0.07	0.03	17	6	0.06	0.3%	5
0.1	182	11.1	0.09	0.09	6	0.01	0.00	3	91	39	30%	3	nd			nd			nd						
Apr-96																									
100	1		0.03	0.01	21	0.12	0.01	21	23	28	7%	12	0.07	0.01	12	0.23	0.08	12	1.09	0.09	21	18	15	4%	12
50	14	2.2	0.04	0.01	20	0.11	0.01	20	25	27	7%	11	0.07	0.01	11	0.28	0.14	11	1.15	1.10	20	20	14	5%	11
25	27	2.9	0.04	0.02	21	0.11	0.01	21	28	30	8%	12	0.06	0.01	12	0.22	0.07	12	1.09	1.10	21	17	16	5%	12
10	49	2.9	0.03	0.01	21	0.16	0.03	21	17	26	6%	12	0.04	0.01	12	0.15	0.09	12	0.80	0.08	21	16	14	5%	12
1	80	3.4	0.01	0.01	21	0.23	0.03	21	6	7	3%	9	0.01	0.00	12	0.00	0.00	12	0.37	0.07	21	1	3	2%	9
0.1	116	5.5	0.01	0.00	21	0.10	0.01	21	7	6	4%	11	0.00	0.00	13	0.00	0.00	13	0.16	0.03	21	1	1	1%	11
Oct-96																									
100	1		0.05	0.01	31	0.31	0.07	21	15	19	4%	21	0.09	0.01	17	0.25	0.07	16	1.24	0.20	21	17	24.8	7.0%	16
50	19	1.2	0.05	0.02	27	0.33	0.07	21	13	17	4%	21	0.09	0.01	17	0.25	0.10	16	1.81	0.33	20	12	14.7	4.1%	15
25	36	2.6	0.03	0.01	22	0.32	0.08	20	10	9	2%	20	0.07	0.01	17	0.09	0.03	15	1.24	0.26	20	7	7.3	2.0%	15
10	53	3.1	0.02	0.01	28	0.25	0.04	21	7	3	1%	21	0.03	0.01	15	0.01	0.00	13	0.72	0.15	21	1	1.3	0.4%	13
1.0	82	2.6	0.01	0.00	26	0.23	0.03	21	4	2	1%	21	0.00	0.00	15	0.00	0.00	13	0.13	0.02	21	0	0.9	0.6%	11
0.1	112	2.8	0.00	0.00	20	0.10	0.02	20	2	1.7	0.7%	18	0.00	0.00	12	0.00	0.00	9	0.07	0.02	20	0	0.02	0.0%	7

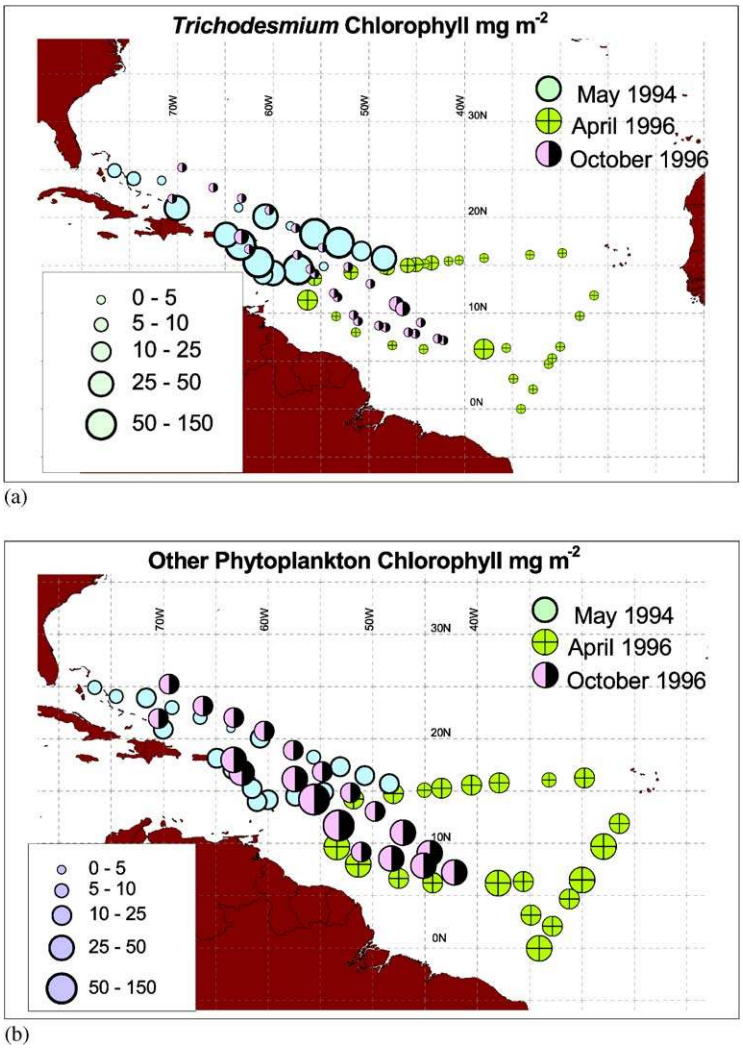

Fig. 8. Depth integrated chlorophyll for each cruise for *Trichodesmium* (a) and other phytoplankton (b).

very reduced in the much lower salinity waters closer to the northeast coast of South America encountered on the October 96 cruise, where high concentrations of *H. hauckii* with endosymbiotic *R. intracellularis* were found (Carpenter et al., 1999). Data from more recent cruises (Subramaniam et al., manuscript in preparation) suggest that there is a succession in the species of the dominant organism associated with the Amazon River plume as the water ages and nutrient pools associated with the plume are successively depleted. *Trichodesmium* was usually found at the edges of the plume, in waters that were depleted of nitrate and silicon.

Interbasin differences: Recent attention has been focused on possible systematic differences among the major ocean gyres, and in particular between the N. Atlantic and N. Pacific. The studies of Gruber and Sarmiento (1997) and Deutsch et al. (2001) suggest a greater degree of new nitrogen creation, presumptively through biological N_2 fixation, in the N. Atlantic gyre, compared to the N. Pacific (Capone, 2001). The cell quota for iron of diazotrophs appears to be much higher than

that of non-diazotrophs (e.g. Berman-Frank et al., 2001; Kustka et al., 2002). Aeolian dust is a major source of iron to the upper ocean (Duce et al., 1991), and this flux is greatest in the N. Atlantic (Gao et al., 2001). High dust flux likely accounts for the 10 fold higher concentrations of "dissolved" iron in the N. Atlantic compared to the N. Pacific (Wu et al., 2000).

Consistent with the supposition that N_2 fixation, and by extension diazotrophs, may be a more predominant component of the planktonic flora of the N. Atlantic, compared to the N. Pacific gyre, densities of the most conspicuous diazotroph, *Trichodesmium*, appear much greater in the central tropical N. Atlantic than the N. Pacific. Letelier and Karl (1996) reported average densities of 46 trichomes l^{-1} for a 3 year study at Station Aloha. Similarly, Marumo and Asaoka (1974a) reported about 2 trichomes l^{-1} in the central Pacific in the vicinity of Hawaii. Higher concentrations are encountered in the western portion of the Pacific (see Carpenter, 1983a). For instance, Marumo and Asaoka (1974b) found an average of about 1000 trichomes l^{-1} in the Kuroshio between 1961 and 1967. In the west equatorial drift, concentrations ranged from 100 to 1000 trichomes l^{-1} (Nagasawa and Marumo, 1967).

For all three of our cruises, which included stations across the basin, surface trichome densities averaged about 763 trichomes l^{-1} with a maximum of about 20,000 trichomes l^{-1}. However, it should be noted that the sampling density in the N. Atlantic for this organism is probably the greatest for any ocean basin (e.g. Carpenter, 1983a).

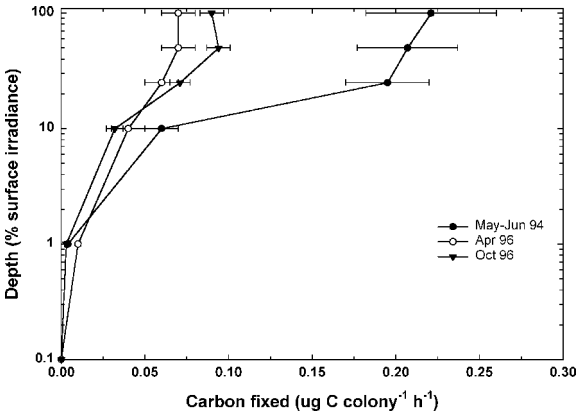

Fig. 9. Average depth profile of *Trichodesmium* colony specific carbon fixation rate for each cruise.

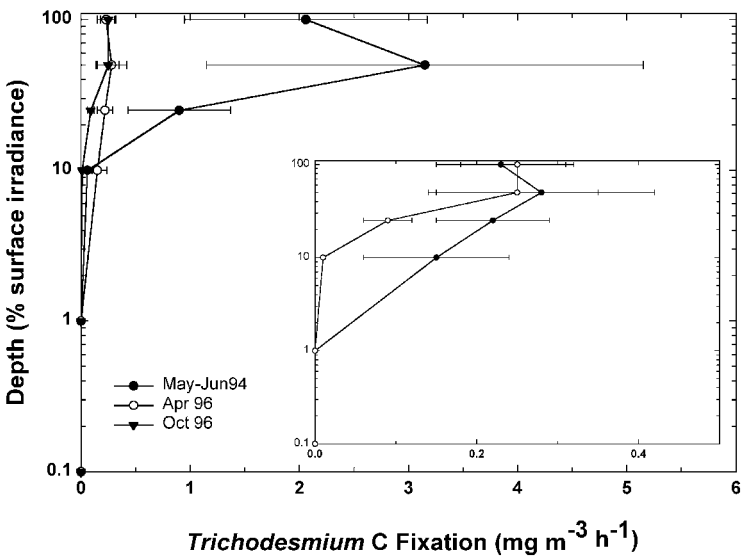

Fig. 10. Average depth profile of *Trichodesmium* volumetric carbon fixation rate for each cruise. Inset: expanded scale for April and October 96 cruises.

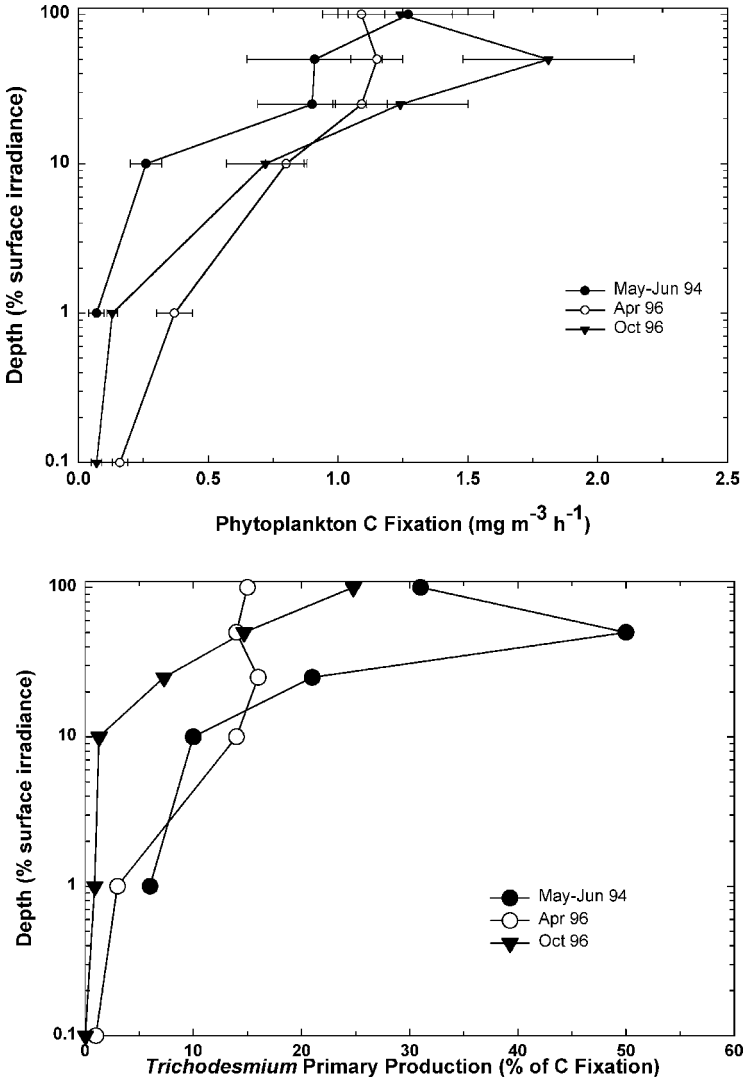

Fig. 11. Average depth profile of phytoplankton volumetric carbon fixation rate for each cruise. Lower panel: percent of total primary production accounted for by *Trichodesmium* on each cruise.

Chlorophyll comparisons: In order to compare the relative abundance of *Trichodesmium* to microplankton chlorophyll, trichome counts were also expressed in terms of chlorophyll. Although the chl-*a* content ranged from 8 to 60 ng chl-*a* per colony, with a grand average of 28 ± 4 ng chl-*a* per colony, these measurements represent samples taken across the entire basin from different seasons with extremely different chemical and physical forcing factors and thus can be taken to be representative of the tropical North Atlantic as a whole. It should be noted that all the samples were obtained by near surface net tows (5–20 m). While the colony size (trichomes per colony) also exhibited a large range, going from 53 to 186 trichomes per colony, the grand average was 117 ± 9 trichomes per colony. Again, this is a small variance considering that the measurements are from across the basin and from all seasons. We did not find any apparent relationship between colony size and physical parameters such as wind speed and mixed layer depth ($r^2 < 0.1$)(data not shown).

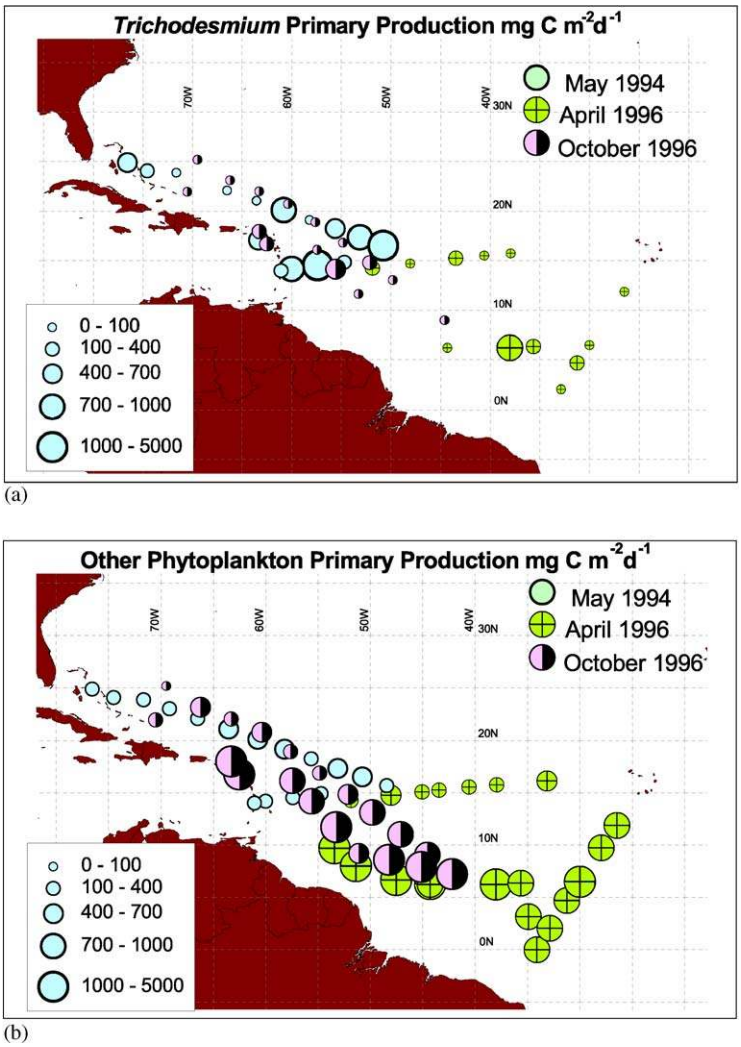

Fig. 12. Depth integrated primary production for each cruise for *Trichodesmium* (a) and other phytoplankton (b).

Trichodesmium chlorophyll accounted for 62%, 13% and 11% of depth integrated total chlorophyll (i.e. *Trichodesmium* plus microplankton) on the three cruises (see also Table 6). Carpenter and Price (1977) found *Trichodesmium* to account for, on average, about 61% of total chlorophyll in the Caribbean Sea and about 5% in the Sargasso Sea during several cruises. Letelier and Karl (1996) found *Trichodesmium* chlorophyll to account for about 18% of total chl-*a* at Station Aloha, and that this fraction had increased during the period 1988–1995 (Karl et al., 1995). In contrast, on a cruise to the southwest Pacific, *Trichodesmium* was a relatively small component of total chlorophyll (Dupouy et al., 2000).

Free trichomes: Reports from different locations have reported very different distributions of *Trichodesmium* with respect to its occurrence as aggregates versus free trichomes, and this has implications with respect to the ability and approach used to accurately quantitate these populations. Furthermore, this aspect of the life

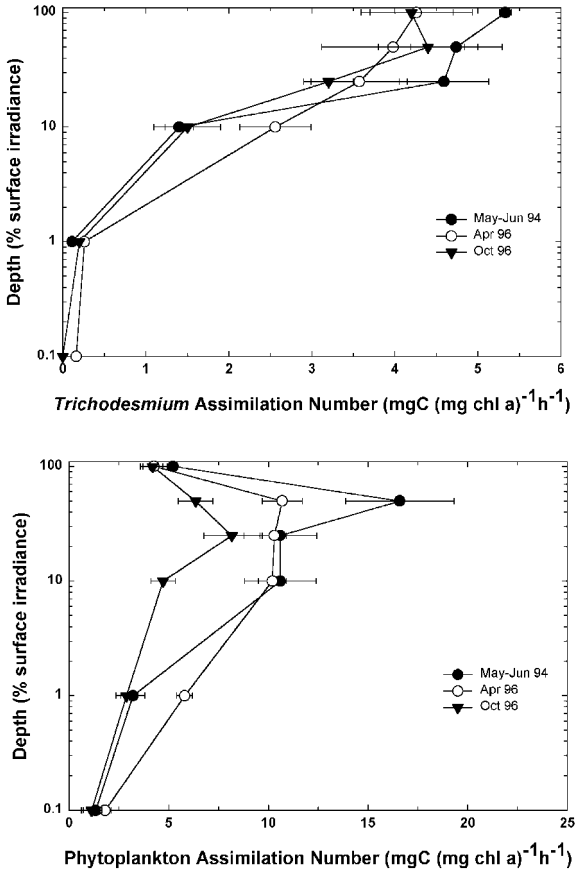

Fig. 13. Mean assimilation numbers of *Trichodesmium* and other phytoplankton on each cruise.

style of *Trichodesmium* may have bearing with respect to vertical movement and physiological ecology.

We observed that, based on the grand average densities of free trichomes and trichomes in colonies for each cruise, 90%, 93% and 92% of all trichomes were present in colonies for the June 94, April 96 and October 96 cruises (Table 4). The averages based on discrete, paired observations were 40%, 71% and 72%. However, at stations with low trichome densities, the probability of encountering a colony is very low. When stations with concentrations greater than 100 trichomes l^{-1} are considered the percentage of trichomes found in colonies increases to 72%, 90% and 92%, while at stations with populations greater than 1000 trichomes l^{-1}, it increases further to 79%, 96% and 92% for the three cruises. Hence, when colonies are present and are effectively sampled, they dominate the distribution of *Trichodesmium* biomass.

Orcutt et al. (2001) recently reported on the distribution of *Trichodesmium* biomass at the Bermuda Atlantic Time Series (BATS) station, finding an average of 16% of trichomes in colonies. They collected colonies by gentle plankton tows with determination of volume filtered, and estimated free trichomes by filtering 3–41 of seawater from water bottles from discrete depths. Plankton tows may underestimate colony abundance by physical disruption of the colonies and passage of the trichomes through net meshes, as pointed out by them and others (e.g. Villareal, 1995). Orcutt et al. (2001) were unable to consistently observe colonies in Niskin bottles, but this is not surprising given the generally low density (typically less than 0.01 colony l^{-1}) of *Trichodesmium* at this station through most of the year. Bryceson and Fay (1981) reported that the percentage of trichomes found in colonies varied from 25% to 70% in their studies in the Indian Ocean off of Tanzania.

Several studies in the Pacific have also reported a preponderance of *Trichodesmium* biomass as free living trichomes rather than colonies (e.g. Saino and Hattori, 1980; Chang et al., 2000). Letelier and Karl (1996) reported that trichomes in colonies constituted only 12% of the total with the remainder of *Trichodesmium* being present as free trichomes, but pointed out that the net tows used could have led to an underestimation of colony density. Also, samples were preserved and held before counting. Letelier and Karl (1996) enumerated trichomes by concentration of 4–10 l volumes on 10 μm Nitex and back rinsed, with colonies picked out. Colonies disrupted during the concentration procedure would be tallied as free trichomes. Moreover, there were low overall colony densities through most of this study as well (average of 0.03 l^{-1}). Comparison of the colony concentrations determined by vertical tows with integrated results from horizontal tows showed them to be similar, despite differences in volume (43 m^3 in horizontal tows versus 16 m^3 for

Table 7
Biomass data from stations within approximately a degree of each other among the three cruises

	Station #	Lat	Long	trichomes l^{-1} surfaces	trichomes l^{-1} max	Depth max	Trichomes $m^{-2} \times 10^6$
26-May-94	6	22.07	66.54	6.6	6.6	1	0.1
14-Oct-96	4	23.13	66.25	27	27	1	0.3
27-May-94	7	21.04	63.60	132	132	1	7.0
15-Oct-96	5	22.01	63.31	723	723	1	1.4
14-Jun-94	23	20.91	70.07	21	2641	38	154
4-Nov-96	31	21.94	70.53	103	366	10	5.1
28-May-94	8	20.05	60.82	64	3941	23	95.8
16-Oct-96	6	20.73	60.41	39	134	1	4.7
29-May-94	9	19.12	58.23	193	193	1	5.6
17-Oct-96	7	18.90	57.64	295	295	1	5.5
12-Jun-94	21	18.14	64.94	1372	1372	1	85.0
11-Jun-94	20	17.06	63.41	5518	5518	1	229
1-Nov-96	28	16.71	62.54	349	492	10	18.9
2-Nov-96	29	17.95	63.33	417	1584	20	30.2
5-Jun-94	16	14.51	57.44	11932	20621	11	320
29-Oct-96	27	16.10	57.47	0	298	1	3.6
24-Apr-96	32	14.26	51.88	286	446	25	15.5
19-Oct-96	9	14.82	52.19	204	204	1	11.5
26-Apr-96	33	13.62	55.69	1799	2016	28	89.9
4-Jun-94	15	14.88	54.74	988	988	1	11.9
28-Oct-96	25	14.14	55.64	582	895	20	19.9
30-Mar-96	2	9.69	53.45	55	157	10	3.4
27-Oct-96	23	11.66	53.31	312	312	1	17.2
31-Mar-96	3	8.00	51.40	0.6	42	32	2.1
26-Oct-96	21	9.17	51.17	0	1	10	0.01

vertical tows), suggesting that colony disruption was not a function of filtration volume.

Thus, there may be a fundamental difference in the state of trichomes between the Atlantic and Pacific Oceans, or between the Atlantic tropics and sub-tropics. It will remain for more comprehensive sampling to resolve this issue.

4.2. Primary productivity

During the three cruises (May–June 1994, April and October 1996), total (*Trichodesmium* plus other phytoplankton) primary productivity averaged 1080, 932 and 804 (grand mean = 930) - mg C m^{-2} d^{-1} (Table 8). *Trichodesmium* spp. were responsible for an average of about 67%, 8.3% and 9.5%, respectively, of the total primary productivity in this region, based on the means from each cruise, or 47%, 7.9% and 11% based on the average derived from the individual paired observation (Tables 1–3, last column and Table 8).

We measured primary production rates on isolated colonies of *Trichodesmium* and scaled

Table 8
Summary of primary production values for the 3 cruises

Cruises		*Trichodesmium* (mg C m^{-2} d^{-1})	SE	*n*	Phytoplanlton (mg C m^{-2} d^{-1})	SE	*n*	Summed total	Total from avg from individual obs (mg C m^{-2} d^{-1})	SE	*n*	Tricho contrib.	SE	*n*
												From means (% of total)	Avg from individual obs (% of total)	
May–June 94		720		±290	15	356	±27	17	1076	1080	±285	15	67	47	8.0%	15
Apr 96		91		±46	17	824	±87	21	915	932	±99	20	9.9	7.9	2.6%	20
Oct-96		86		±26	16	793	±105	20	879	804	±107	18	9.8	11	2.5%	18
All cruises	Average of means	299		±211	3	658	±151	3	957	939	±80	3	29	22		
All cruises	Average of all obs	286		±100	48	676	±55	58	940	930	±95	53	30	21	3.6%	53

these rates to the population density directly determined at each depth. This component of primary production was added to separate determinations of microalgal CO_2 uptake, and this could also directly account for some of the differences between our primary productivity measurements and those of other investigators.

The use of isolated colonies in physiological studies would, of course, omit any contribution of free trichomes. However, as noted, in this system where *Trichodesmium* populations are substantial, the preponderance of its biomass appears to be in colonies. Isolation of colonies through the net tows and selection of colonies from the tow may also potentially induce artifacts by the handling of colonies, although studies assessing this effect for N_2 fixation have generally found good agreement between samples collected by gentle net tows and those carefully collected in situ by divers (Carpenter et al., 1987).

The tropical North Atlantic Ocean has had relatively few measurements made of primary production, and those in the literature show a wide range in values. Our overall rates of production are considerably higher than many previous observations in oligotrophic tropical waters, which usually range from about 200 to 500 mg C m^{-2} d^{-1}, in both the tropical and subtropical Atlantic Ocean. Our mean rate for the three cruises of primary production by bulk plankton of about 670 mg C m^{-2} d^{-1} and of total primary production (including *Trichodesmium*) of about 940 mg C m^{-2} d^{-1} (Table 8) is similar to oceanic bloom rates. For comparison, production during the N. Atlantic Spring Bloom, much farther north at 47°N averaged 1085 mg C m^{-2} d^{-1} (Martin et al., 1993).

However, most measurements in the oligotrophic tropical and sub-tropical Atlantic Ocean are lower than that which we observed. Ryther and Menzel (1961) measured primary production at 22 stations SE of Bermuda (between 30°N and 16°N) in winter, and production averaged 50 mg C m^{-2} d^{-1}. However, because their data were collected before the advent of clean sampling techniques, this rate is likely an underestimate. There is considerable new information on primary production at the BATS study, and mean daily

production rates for 1989 and 1990 were 302 and 394 mg C m^{-2} d^{-1} (Michaels et al., 1994). Mean integrated primary production at the BATS site between 1989 and 1997 averaged 154 (SD = 30) g C m^{-2} yr^{-1} (Steinberg et al., 2001), or 422 mg C m^{-2} d^{-1}. This rate is less than half the mean rate observed on our three cruise. However, this site is subtropical, and hydrographically different than the tropical Atlantic.

Several observations have been made in the eastern equatorial Atlantic. Bauerfeind (1987) noted a mean rate of production of 247 mg C m^{-2} d^{-1} between January and May 1979 over ten sections between 2°S and 3°N at the 22°W meridian. In March and April 1989 at 18°N, 30°W (NW of Cape Verde Islands) primary production over an 11 day period averaged about 500 mg C m^{-2} d^{-1} (Jochem and Zeitzschel, 1993). Claustre and Marty (1995) measured production at 20°N, 31°W in autumn 1991 and spring 1992 and rates averaged 352 ± 68 and 267 ± 53 mg C m^{-2} d^{-1}, respectively. At the oligotrophic station in the EUMELI JGOFS study on May and September–October cruises at ca. 22°N, 31°W, production was very constant and ranged from 289 to 376 mg C m^{-2} d^{-1} (Morel et al., 1996).

Observations on the western flanks of the basin are also relatively low. Steven (1971) reported an annual average of 288 mg C m^{-2} d^{-1} for a station off the NW coast of Barbados. Beers et al. (1968) found an annual mean of 110 mg C m^{-2} d^{-1} for a station in the Caribbean off of Jamaica. However, our rates are similar to those of Monger et al. (1997) who estimated 980 mg C m^{-2} d^{-1} and Voituriez and Herbland (1981) who reported 899 mg C m^{-2} d^{-1} (annual average) in the Eastern Tropical Atlantic. The explanation for the high primary production rates could partially be that many of our samples were collected in the west Equatorial Drift, and productivity in that region, as noted by Longhurst (1993) and Monger et al. (1997), is relatively high.

A further probable cause of general high productivity is the seasonal presence of the discharge plumes from the Amazon and Orinoco Rivers. The relatively high silicate and iron concentrations in Amazon water (Ryther et al., 1967; Milliman and Boyle, 1975) may have been a factor in promoting the growth of *Trichodesmium* and other phytoplankton.

Seasonality: Both biomass and productivity of *Trichodesmium* showed large apparent seasonality (Tables 1–3, 6–8), with an almost 10 fold difference, on average, between the maximum values in June 1994 and the minimum values observed in April and October 1996. Since the tracks were very different among the 3 voyages, the averages may be somewhat misleading. However, strong variability is also apparent at stations that were proximal to each other (Table 7).

This seasonality may, in part, derive from warmer summer temperatures and the relatively shallower mixed layer depth during June 1994 relative to April 1996. Mixed layer depth at many stations during October 1996 was often very shallow. However, at many stations this was a result of the inflow of the Amazon River, and at many of the stations with low surface salinity, the diatom *Hemiaulus hauckii* was dominant in the plankton (Carpenter et al., 1999).

Another important factor for the relative success of *Trichodesmium* may be a seasonally phased dust input into the tropical N. Atlantic. During late winter to spring, aeolian dust from northwestern Africa is deposited throughout this region (Husar et al., 1997; Gao et al., 2001). This input may provide a source of iron for diazotrophs such as *Trichodesmium* (Berman-Frank et al., 2001; Kustka et al., 2003). Indeed, tropical and subtropical Atlantic surface Fe concentrations are relatively high (Wu et al., 2001; Sañudo-Wilhelmy et al., 2001).

Assimilation numbers: Carbon assimilation numbers (P^B) for *Trichodesmium* on our three cruises showed a maximum between 4 and 5 mg C (mg chl-a^{-1}) h^{-1}, and were lower than those for microplankton (Fig. 13). However, these values are on the high side of all previous estimates. For instance (Letelier and Karl, 1996) found maximum assimilation numbers for *Trichodesmium* of about 3 at Station ALOHA during 2 different months, and also substantially less than the microalgal component of the phytoplankton. Lewis et al. (1988) reported carbon assimilation values of 3.8 mg C (mg chl-a^{-1}) h^{-1} for samples collected during a *Trichodesmium* bloom near 35°N,

65°W. Similarly (Li et al., 1980), found P^B values of about 3 C (mg chl-a^{-1}) h^{-1}.

The generally low carbon assimilation numbers for *Trichodesmium*, relative to eukaryotic algae, suggest a lower efficiency of assimilation of particulate organic carbon. Li et al. (1980) found between 33% and 66% of the ^{14}C assimilated in the soluble metabolite pool after a 2-h deck incubation. They speculated that the accumulation of carbon in the metabolite pool rather than a protein pool was indicative of some sort of nutrient stress in *Trichodesmium*. However, Kana (1993) found very high photorespiration rates for *Trichodesmium*, with a light compensation point around 200 μE m^{-2} s^{-1}. He suggested that this might be a mechanism to protect nitrogenase from oxygen produced during photosynthesis. Nitrogenase, the enzyme responsible for nitrogen fixation, is damaged by exposure to oxygen, and diazotrophs use various protection strategies such as heterocysts or temporal separation of oxygen evolution during photosynthesis and nitrogenase activity. *Trichodesmium* seems to be unique in its requirement to fix nitrogen during photosynthesis, and there are various hypotheses to explain this behavior. Mulholland and Capone (2001) studying the stoichiometry of nitrogen and carbon utilization in *Trichodesmium* cultures, found that C accumulation based on CO_2 fixation exceeded observed POC increases by more than 50% during late log and stationary phases of growth. They speculated that *Trichodesmium* could be releasing soluble organic carbon during these growth phases. Whatever the reason, the excess carbon assimilated by *Trichodesmium* that is not converted to particulate organic carbon would explain its low assimilation number compared to other organisms. The large range in assimilation values may reflect either the environmental differences between the tropical Atlantic and other sites where these values were obtained, or differences in growth stages.

Temperature: *Trichodesmium* was active in photosynthesis at water temperatures from 23.5°C (May 1994) to 29.4°C (October 1996). However, on analysis, no relationship was observed between temperature and rates of production or standing crop (Table 9). This observation is in agreement with that of Carpenter and Capone (1992) who noted that all but one of fifteen blooms

Table 9
Results of correlation analysis

	Surface biomass triochomes l^{-1} slope	r^2	Max biomass triochomes l^{-1} slope	r^2	Depth int triochomes $m^{-2} \times 10^6$ slope	r^2	Areal C fix mg C m^{-2} d^{-1} slope	r^2
Salinity (PSS) versus								
Jun-94	−1906	0.718	−2715	0.804	−41.3	0.469	−567	0.816
Apr-96	−788	1.254	−1463	0.309	−38.2	0.156	−68.6	0.008
Oct-96	4.58	0.000	19.1	0.004	1.35	0.041	18.6	0.038
Temperature (°C) versus								
Jun-94	997	0.060	745	0.019	33.3	0.094	55.6	0.002
Apr-96	111	0.065	151	0.042	4.96	0.034	11.3	0.006
Oct-96	118	0.035	141	0.030	2.26	0.017	−44.6	0.039
Wind speed (knots) versus								
Jun-94	−310	0.250	−301	0.130	−3.337	0.041	−45.34	0.067
Apr-96	0.488	0.000	11.79	0.032	1.439	0.091	4.86	0.030
Oct-96	21.34	0.091	48.1	0.126	0.335	0.057	9.27	0.275
Mixed layer depth (m) versus								
Jun-94	−163	0.307	−165.2	0.172	−1.28	0.029	−34.9	0.134
Apr-96	−7.57	0.072	−13.9	0.086	−0.38	0.049	−1.154	0.019
Oct-96	9.79	0.16	7.87	0.062	−0.013	0.0004	3.134	0.13

of *Trichodesmium* reported in the scientific literature occurred at a water temperature above 26°C. It would appear that while *Trichodesmium* has previously been shown to be metabolically active at 18°C (Carpenter, 1983a), temperatures above 26°C are necessary for bloom development.

Salinity: Surface salinities from a high of 36.7 to as low as 26.5 were encountered across the three cruises. Low salinities were noted on the first cruise at some stations relatively removed from continental land masses, and on the last cruise during sampling in the Guiana Current. The salinity decrease is related to intrusions of freshwater from the Amazon River, and it has been noted previously that *Trichodesmium* abundance in the Barbados area is inversely related to salinity (Borstad, 1982). During the first cruise (June 94), there was a relatively strong relationship between salinity and the density of *Trichodesmium* at the surface and at the biomass density maximum ($r^2 = 0.72$ and 0.80). There was a weak negative relationship on the April 96 cruise, and no perceptible relationship between salinity and *Trichodesmium* density on the last cruise.

Wind speed: The tradewinds encountered on the cruises were relatively strong, typically 15–25 knots, and under such conditions, *Trichodesmium* populations are thought to be stressed (Carpenter and Price, 1976) since the ability of colonies to fix N_2 decreases when they are disturbed by wave action. However, the density and activity of the population was relatively high in regard to C and N_2 fixation (Capone et al., manuscript pending), particularly on the first cruise. As noted above, population density was low at the surface relative to the subsurface maximum at 10–25 m; however, assimilation numbers for *Trichodesmium* (Fig. 13) were relatively high at the surface, usually ranging from 2 to 4 mg C (mg chl-a^{-1}) h^{-1}, suggesting that populations were healthy. It thus appeared that calm sea conditions are not a requisite for an active *Trichodesmium* population. However, for a bloom or surface accumulation of *Trichodesmium*, calm sea conditions are most likely necessary because high winds mix the population to deeper water and prevent surface accumulations. The strongest correlation with wind occurred on the first cruise and had a negative slope (Table 9).

C:N ratio and N requirement: Cyanobacteria have a nitrogen content greater than that of eukaryotic phytoplankton. Nitrogen constitutes about 1–3% of the dry weight of eukaryotic phytoplankton (Wheeler, 1983), while it is 4–9% in cyanobacteria (Fogg et al., 1973). The C:N ratios (weight) previously observed for *Trichodesmium* are 5.2–5.4 in the sub-tropical Atlantic (McCarthy and Carpenter, 1979) and 5.6 in the western Pacific (Marumo, 1975). The mean ratio of 6.5 observed on our three cruises (Table 5) is closer to the classic C:N Redfield ratio of 6.0 (weight) and would indicate a lower nitrogen content than observed in these earlier studies. Assuming a mean rate of *Trichodesmium* primary production from all observations of 259 mg C m^{-2} d^{-1}, we can calculate an N requirement for *Trichodesmium* dependent primary production based on the C:N content of *Trichodesmium* of 6.5 of about 40 mg N m^{-2} d^{-1}. If all of this requirement is met by N_2 fixation, then this value is somewhat greater than the estimated rate of N_2 fixation of 30 mg N m^{-2} d^{-2} as calculated by Carpenter and Romans (1991) for the SW tropical Atlantic Ocean. However, concurrent determinations of depth integrated N_2 fixation by *Trichodesmium* on these cruises indicated an average input of about 4 mg N m^{-2} d^{-1} (Capone et al., manuscript pending), or about 10% of the demand of net photosynthesis. These are still substantial rates of N_2 fixation compared to those in the sub-tropics and are comparable to current estimates of diffusive nitrate flux in these permanently stratified tropical waters (e.g. Planas et al., 1999; Williams et al., 2000). With respect to the N demand of *Trichodesmium*, as shown by Mulholland and Capone (1999, 2000), *Trichodesmium* can satisfy much of its N demand by ammonium assimilation. As discussed earlier, there could be departures from Redfield stoichiometry because *Trichodesmium* fixes C in excess to N for oxygen protection via photorespiration (Kana, 1993; Mulholland and Capone, 2001).

4.3. Undersampling of Trichodesmium

At first glance, the relative contribution of *Trichodesmium* to standing crop and primary

production may seem extremely large. However, many earlier studies of primary production in tropical waters entirely overlooked the contribution of *Trichodesmium* either explicitly through pre-filtration and exclusion of *Trichodesmium* colonies (e.g. Strickland and Parsons, 1972), or implicitly by counting or assaying relatively small volumes of seawater, which would bias against inclusion of the colonial forms (see below).

For instance, Hulburt's classic studies (Hulburt, 1962) typically counted 50 ml of seawater to quantitatively enumerate phytoplankton, including *Trichodesmium*. In the BATS study, Lohrenz et al. (1992) incubated 250 ml volumes of seawater, then measured ^{14}C incorporation in only a 50 ml aliquot of that water. Similarly, Jochem and Zeitzschel (1993) incubated 250 ml and then assayed the ^{14}C uptake in only 75 ml. While these volumes are sufficient for estimates of picoplankton production, it is highly unlikely that any colonial *Trichodesmium* present would have been included in production measurements. The typical *Trichodesmium* concentration in these waters is about 1 colony per L and in the aforementioned studies, there is at most a 1 in 4 chance of sampling a colony in the primary production measurement.

In a study in the central Arabian Sea (Capone et al., 1998) during an extended period of surface accumulations (often referred to as a bloom) of *Trichodesmium*, surface slicks in the upper 0.5 m accounted for CO_2 uptake rates of about $12\,mg\,C\,m^{-3}\,h^{-1}$ and 25% of depth integrated primary production. However, because of the standard sampling protocols followed to account for the rolling of the ship and because of the length of Niskin bottles, the so called surface sample usually comes from depths >1 m, which would have completely missed this input.

Underestimation of *Trichodesmium* is an issue when remote sensing is used as well. Although bulk of the population resides within the first optical depth and therefore is visible to a satellite, the formation of colonies by *Trichodesmium* causes "self shading" or secondary packaging. Subramaniam et al. (1999) calculated that *Trichodesmium*'s contribution to the chlorophyll signal detected by a satellite could be underestimated by at least a factor of four. While current algorithms to detect *Trichodesmium* can identify blooms of this organism (Subramaniam et al., 2002), the algorithms have a threshold for uniquely identifying it and thus miss much of the background concentration.

To place the potential contribution of *Trichodesmium* in perspective, let us consider its relative biovolume and contribution to phytoplankton cell carbon. At most of our stations, the bulk of *Trichodesmium* biomass occurred in colonies or "clumps" each composed of about 100–200 trichomes in a colony. Average surface colony density was about 15, 2 and 2 colonies l^{-1} for the June 94, April 96 and October 96 cruises (assuming 150, 135 and 98 trichomes colony^{-1}) (Tables 1–3 and 5).

A typical trichome has about 100 cells (Carpenter, 1983b, Letelier and Karl, 1996). Thus, a single colony contains 10,000–20,000 photosynthesizing cells. *Trichodesmium* cells are relatively large. For instance, *T. thiebauti*, the most common form in the tropical N. Atlantic, has a cell diameter of about 10 μm, and therefore a cell volume (assuming a cylindrical cell shape) of about 785 μm^3. This compares to a coccoid cyanobacterium such as *Synechococcus* and *Prochlorococcus*, with diameters of about 1 and 0.7 μm (Durand et al., 2001), and cell volumes of 0.5 μm^3 (Table 10). Thus, while picoplankton may numerically

Table 10
Calculation of theoretical biovolume and carbon for phytoplankton and *Trichodesmium* in 1 L volume assuming 1 colony per liter

		Assumed diameter	Volume		Biovolume	Percent of total	C content		Percent of total
		μm	μm^3	cells l^{-1}	$\mu m^3\,l^{-1}$		fg C μm^{-3}	μg C l^{-1}	
Prochlorococcus	Sphere	0.68	0.165	30,000,000	4,939,087	21	325	1.6	17
Synechococcus	Sphere	0.87	0.345	10,000,000	3,447,914	14	325	1.1	12
Trichodesmium	Cylinder	10	785	20,000	15,707,965	65	424	6.7	71

dominate and account for 10^7–10^8 cells l^{-1} (Durand et al., 2001) and have a combined cell volume of 5×10^6 μm^3 and about 1.6 and 1.1 $\mu g C l^{-1}$ for *Prochlorococcus* and *Synechococcus*, respectively, a single colony of *Trichodesmium* in a liter could account for a cell volume of about 15×10^6 μm^3 and a carbon content of 6.7 $\mu g l^{-1}$, or the bulk of the cell volume and carbon when compared to picoplankton (Table 10).

To accurately scale *Trichodesmium* productivity to volume or area, robust population estimates are also needed and require that a sufficient volume of water be examined and filtered. For our studies in the tropics, we filtered 10 l for microscopic examination, and this appears to be an adequate volume for good population estimates. More might be required in waters of lower density. Alternatively, in waters of lower abundance, a corresponding larger volume would be needed for accurate biomass assessments. Furthermore, because of the presence of buoyant gas vesicles, the bulk of the *Trichodesmium* population tends to accumulate at specific depths. Sampling should be undertaken at sufficiently close intervals (e.g. 10 m), particularly in the upper 50 m, to assure that peaks in population are not missed.

4.4. Contribution of Trichodesmium

The contribution of *Trichodesmium* to overall standing crop and primary production in the central tropical N. Atlantic was substantial. Besides the incremental contribution to algal biomass and primary production, *Trichodesmium* may also contribute to the enhancement of overall primary and export production through N_2 fixation.

Measurements of the contribution of *Trichodesmium* to total primary production have also been made at station ALOHA north of Hawaii and indicated that *Trichodesmium* accounted for 4% of the total C assimilation between 1989 and 1992 (Letelier et al., 1996; Letelier and Karl, 1996). Recently, Chang et al. (2000) estimated the contribution of *Trichodesmium* to primary production in the Kuroshio near Taiwan to be from 0.2% to 2.3% of the total. Our study indicates a greater importance for *Trichodesmium* in terms of carbon assimilation in the tropical North Atlantic Ocean relative to the N. Pacific.

N_2 fixation by *Trichodesmium* introduces new nitrogen into the euphotic zone and, via recycling and excretion of nitrogen, can promote the growth of other phytoplankton. Indeed, despite a low contribution to primary production, Letelier et al. (1996) also concluded that 27% of new (or export) production could be supported by N_2 fixation by *Trichodesmium*.

The higher rates of primary production noted in our study area may therefore be partially a result of the enhanced N_2 fixation through the area (we will report on rates of N_2 fixation separately; Capone et al., manuscript pending). As pointed out earlier (Carpenter and Romans, 1991) and as reported here, densities of *Trichodesmium* are much greater in the tropical N. Atlantic, compared to the sub-tropical zone. Orcutt et al. (2001) recently made two N–S transects and also found that population density of *Trichodesmium* increased dramatically (up to 17 fold increase) south of Bermuda (ca. 32–34°N to ca. 26–29°N) from subtropical to tropical seas. The higher population density and resultant N_2 fixation in these waters likely both contribute to higher total rates of primary productivity in the tropical Atlantic. The overall contribution of *Trichodesmium* (and perhaps other diazotrophs, see Zehr et al., 2001; Capone, 2001) can be seen in the distinct isotopic signature in the food webs of the tropical North Atlantic (Montoya et al., 2002).

5. Conclusion

Our measurements on three cruises show a relatively high rate of primary production in the western tropical Atlantic Ocean. This is due, in part, to the inclusion of *Trichodesmium* in primary production measurements. The incorporation of this diazotroph in C cycling models may help to explain global imbalances in oceanic carbon budgets and causes of high chl-*a* concentrations in this region as detected by remote sensing (Wroblewski et al., 1988; Longhurst, 1993). The data also suggest that low wind speed is not a requisite for active *Trichodesmium* colonies.

Acknowledgements

We are grateful to Pilar Heredia, Andy Parrella, Kristen Romans Brown, Rachel Foster, Jay Burns and Erika Magaletti for assistance and technical support. Support for this research was from NSF grants OCE 9317738 and 9314252.

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