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Spatial and temporal distribution of *Trichodesmium* spp. in the stratified Gulf of Aqaba, Red Sea

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ABSTRACT: Phytoplankton (>100 µm) abundance was studied in the open waters of the Gulf of Aqaba during the summer stratification period of 1996. A succession took place among the major phytoplankton groups, with diatom numbers decreasing throughout the summer. The diazotrophic cyanobacteria *Trichodesmium* spp. became more prominent as the stratification period progressed; 5 *Trichodesmium* species were identified: *T. thiebautii*, *T. erythraeum* with tuft-shaped colonies and *Trichodesmium* sp. with puff-shaped colonies were common at ~10^2 colonies m^{-3} throughout the stratification period, whereas *T. tenue* and *T. hildebrandtii* were more rare. A bloom of *T. thiebautii* and *T. erythraeum* with >10^6 tuft colonies m^{-3} was observed in coastal waters of the Gulf during fall 1997. Tuft-shaped colonies were dominant near the surface, while puff-shaped colonies of *Trichodesmium* sp. were mainly found in the bottom half of the photic zone. These depth distributions were maintained for more than 2 mo, suggesting that the 2 colony types occupied distinct niches. Puff-shaped colonies were found to have higher chlorophyll *a* contents than tufts, but their photosynthetic activities were not significantly different. Fatty acid analysis of dominant plankton species yielded new trophic relationships for *Trichodesmium* spp. The *Trichodesmium* spp.-specific fatty acid C22:2ω6 was found in *Macrosetella gracilis* (the sole copepod to graze on *Trichodesmium* spp.) and in chaetognaths, suggesting that these carnivorous zooplankton fed on *M. gracilis*. Furthermore, this fatty acid was observed in the filter-feeding *Salpa maxima*, which was abundantly present in the Gulf of Aqaba during June 1997.

KEY WORDS: Red Sea · Phytoplankton · Cyanobacteria · *Trichodesmium* · Nitrogen fixation

INTRODUCTION

The Gulf of Aqaba is an extension of the northern Red Sea, located between the Sinai (Et Tih) Desert and the Western Arabian (An Nefud) Desert. It is a deep basin (1800 m) approximately 165 km in length and an average of 15 km wide. It is separated from the northern Red Sea by a shallow sill (240 m) at the Straits of Tiran. High evaporation rates drive a thermohaline circulation with a continuous advection of nutrient-poor surface waters from the Red Sea into the Gulf, counterbalanced by an efflux of more dense deep waters (Klinker et al. 1976, Murray et al. 1984, Wolf-Vecht et al. 1992). Surface waters are characterized by a shallow but stable thermocline in summer. Lower air temperatures in fall cause a rapid erosion of the thermo-

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cline, leading to deep convective mixing during the winter months. Convective mixing may reach down to depths of 600 m or more in the northern part of the Gulf (Klinker et al. 1976, Wolf-Vecht et al. 1992, Genin et al. 1995, Lindell & Post 1995).

Phytoplankton chlorophyll *a* in the Gulf of Aqaba is low in summer, with surface concentrations fluctuating between 0.02 and 0.04 µg l^{-1} (Klinker et al. 1978, Genin et al. 1995, Yahel et al. 1998), considered characteristic for oligotrophic conditions. Chlorophyll *a* reaches its maximum concentration (1.2 µg l^{-1} on average) at the end of the winter mixing period (Genin et al. 1995). Phytoplankton is made up mostly of ultraphytoplankton, species with a cell diameter of less than 8 µm, which contribute >90% to chlorophyll *a* standing stock (Lindell & Post 1995, Yahel et al. 1998). The deep mixing in winter drives a seasonal succession among the ultraphytoplankton (Lindell & Post 1995). Eukaryotic algae dominate during the mixing event, whereas the cyanobacteria *Synechococcus* spp. and *Prochlorococcus* spp. are dominant during spring and late summer respectively (Lindell & Post 1995). Likewise, one would expect the composition of larger phytoplankton to be affected by water body structure and nutrient availability. Studies of larger phytoplankton in the Gulf of Aqaba have been limited in scope with a focus on symbiotic associations of nitrogen-fixing cyanobacteria with diatoms and dinoflagellates (Kimor et al. 1992, Gordon et al. 1994). Temporal and spatial distribution of microplankton in the Gulf of Aqaba was studied in 1974-1975 and the presence of nitrogen-fixing, bloom-forming *Trichodesmium* spp. colonies in early and late summer was documented (Kimor & Golandsky 1977, Gordon et al. 1994). *Trichodesmium* spp. has been the subject of intense study over the last 2 decades, since it is considered a major contributor to primary production and a significant source of new nitrogen in the ocean surface layers (Capone et al. 1997, Carpenter & Romans 1991). Summer populations and especially blooms of *Trichodesmium* spp. may contribute significantly to the carbon and nitrogen budget of the Gulf of Aqaba during summer stratification. The purpose of this study was to establish temporal and spatial distribution patterns of *Trichodesmium* spp. among the >100 µm phytoplankton size fraction. We further report on chlorophyll contents, photosynthetic activities, nitrogen fixation and trophic relationships of *Trichodesmium* spp. populations in the Gulf of Aqaba.

MATERIALS AND METHODS

During the 1996 summer stratification period we collected samples on board the RV 'University I' at monthly intervals at Sampling Station A (29°28′N, 34°55′E) at the northern tip of the Gulf of Aqaba. During a research cruise from 2 to 10 June on board the same vessel, we visited additional sampling sites with a more central location in the Gulf of Aqaba: Stns B (29°06′N, 34°46′E) and M (28°47′N, 34°43′E), along with Stn R (27°25′N, 34°25′E) in the northern Red Sea (see map in Li et al. 1998). Samples were collected with 100 µm mesh plankton nets. The nets were fitted with a Tsurumi-Seiki flow meter (model #5197) in order to obtain estimates of the total volume of water passed through the net. Vertical hauls were made at a rate of 0.8 m s^{-1}, and a mechanical closing mechanism allowed sampling of desired depth ranges: 0–5, 5–10, 10–30, 30–50, 50–75 and 75–100 m. Horizontal tows were made at a speed of approximately 0.5 m s^{-1} for 7 min duration. Samples were resuspended in 300 to 500 ml filtered seawater. Diel change in the vertical distribution of *Trichodesmium* spp. was studied on samples taken at 00:00, 07:00, 13:00 and 19:00 h local summer time; 50 ml samples were taken for immediate analysis of *Trichodesmium* spp. populations, and colonies were enumerated using a Nikon SMZ-2B dissecting microscope. Colony size was estimated in replicates of 20 colonies suspended in 50 ml GF/F-filtered seawater. Colonies were gently vortexed for 10 to 30 min, until all colonies had disassembled into individual trichomes without disrupting them. Trichomes were counted in a 1 ml Sedgwick-Rafter cell using a Nikon Labophot 2 microscope equipped with an epifluorescence attachment and a B2 filter set (excitation range 450 to 490 nm, a 510 nm dichroic mirror and a 520 nm barrier filter). A 250 to 450 ml sample from each tow was preserved in 2.5% glutaraldehyde and stored in darkness at room temperature. Diatom and dinoflagellate species in these samples were identified and enumerated using both a bright-field inverted microscope (Nikon TMS-F) and a phase-contrast microscope (Nikon Labophot 2).

Analyses. Chlorophyll *a* was determined on samples of 10 to 20 colonies of *Trichodesmium* spp. collected on Whatman GF/F filters and extracted in 90% acetone for 12 to 24 h in the dark at 4°C. Chlorophyll *a* concentrations were determined on a Turner Design model 10-000A fluorometer following the procedure of Venrick et al. (1987). On the June 1996 cruises, samples were also taken to measure the carbon and nitrogen content of *Trichodesmium* colonies and that of the particulate fraction in the water column. For the individual colony contents, between 50 and 70 colonies were collected on precombusted Whatmann GF/F filters which were rinsed in 0.2 µm-filtered seawater. Water-column particulate organic carbon/nitrogen (POC/PON) samples were collected by filtering onto precombusted GF/F filters between 0.5 and 1.5 l samples collected by Niskin bottles or from surface bucket hauls. All POC/

PON filters were acid-fumed (concentrated HCl) overnight to remove carbonate, dried at 40°C, and then stored in a desiccator prior to analysis. POC and PON concentrations were determined with a Europa Scientific CHN analyser, using acetanilide as a standard. Photosynthetic carbon fixation was measured on 10 to 20 *Trichodesmium* spp. colonies collected in glass vials with 20 ml GF/F-filtered seawater while basically following established procedures (Carpenter et al. 1993, Roenneberg & Carpenter 1993, Villareal 1995). Samples were spiked with 10 µCi of $NaH^{14}CO_3$ (Amersham) and immediately transferred to a 24°C incubator for 4 h. Light was provided by 'warm-white' fluorescent tubes at 300 µmol quanta m^{-2} s^{-1}. Light was measured with a Li-COR LI 185 light meter with a LI-195SA quantum sensor. Temperature was maintained at approximately 24°C with running seawater. Dark control bottles were run alongside the samples in each incubation. Samples were filtered on 25 mm GF/F filters, then washed with 10 ml filtered seawater. Thefilters were fumed overnight with HCl in desiccators. The filters were supplied with 5 ml scintillation cocktail (Insta-GelII Plus, Packard) and ^{14}C incorporation was determined during 10 min readings per vial using a Tri-Carb 1600 TR (Packard) scintillation counter. The nitrogen fixation potential of *Trichodesmium* spp. was measured by the acetylene reduction method (Capone et al. 1990). Twenty colonies were placed in darkened 22 ml tubes containing 18 ml of GF/F-filtered seawater. Tubes were crimp-sealed with a teflon/silicon septum (National Scientific), 2 ml of acetylene-saturated seawater was injected through the septum, and the tubes were transferred to the light. Incubation conditions were identical to those of photosynthesis measurements, and the incident light allowed both photosynthesis and nitrogen fixation to occur at their maximal rates. Controls were tubes with GF/F-filtered seawater spiked with acetylene, and dark-incubated samples. Incubations were terminated by injecting either 10^{-6} M DCMU (Sigma) or transfer to darkness. Headspace samples (100 µl) were drawn with a 250 µl gas-tight syringe (Precision Sampling Corporation Pressure-Lock) and analysed on a gas chromatograph (Hewlett 5890, Packard Series II) with a 30 m semi-capillary column of 0.53 mm internal diameter. The contribution of *Trichodesmium* spp. to the marine food web of the Gulf of Aqaba was studied from comparative lipid analyses of both phytoplankton and zooplankton species. Zooplankton samples were taken by vertical tows of a 100 µm mesh plankton net from 150 m depth to the surface. Salps were sampled from surface waters with a bucket. Samples for lipid analysis were taken by picking individual animals from the net sample, placing them on precombusted 45 mm Whatman GF/F-filters, and quickly freezing them in liquid nitrogen. The sample size for calanoid copepods and for the harpacticoid *Macrosetella gracilis* amounted to 15 adult individuals, chaetognaths and doliolids to 8 individuals each, and salps to 5 individuals. The zooplankton samples were lyophylized prior to analysis. Samples for the lipid analysis of cyanobacteria were obtained from exponentially growing pure cultures of *Synechococcus* sp. Strain C129 and *Trichodesmium* sp. Strain RS9602 (Gulf of Aqaba isolates) along with the Sargasso Sea isolates *Synechococcus* sp. Strain WH7803 and *Trichodesmium* sp. Strain IMS101. Fatty acids were extracted and processed according to standard methods (Christie 1982, Kattner & Fricke 1986, Müller-Navarra 1995, Müller-Navarra & Lampert 1996). Known concentrations of synthetic fatty acids of odd chain length (11:0, 13:0, 15:0, 17:0, 19:0, 21:0) were added to the samples to serve as internal standards. Samples were analysed by thin-layer chromatography flame-ionisation detection on a Iatroscan MARK II gas chromatograph with a 30 m DB-FFAP column. Fatty acid composition was expressed as the percent contribution of each individual fatty acid to the total natural (even chain length) fatty acid mass of each sample.

RESULTS

Population dynamics

The phytoplankton (>100 µm) community in the Gulf of Aqaba during summer 1996 was made up by representatives of diatoms, dinoflagellates and cyanobacteria. Both pennate and centric diatoms were observed, the latter group being the most abundant. The diatoms consisted mostly of *Chaetoceros* and *Leptocylindrus* species found throughout the photic layer down to 100 m depth. *Proboscia alata* dominated the phytoplankton community in the upper 10 m, with densities of 30 000 cells m^{-3} recorded at Stn R. Less abundant species included those of the genera *Rhizosolenia* and *Hemiaulus.* Dinoflagellates belonged mostly to the orders Gonyaulacales (genera *Ceratium* and *Protoperidinium*) and Dinophysiales (genera *Dinophysis* and *Ornithocercus*). The genus *Ceratium* was best represented with at least 7 species, of which *C. fusus* and *C. trichoceros* were the most abundant. Cyanobacteria were represented by various species of the genus *Trichodesmium*.

Identification of *Trichodesmium* species is less straightforward than that of diatoms and dinoflagellates because of the lack of distinct and unique morphological characteristics. We distinguished 3 colony types (Table 1): (1) spherically shaped colonies, (2) bow-tie-shaped colonies of trichomes that were densely arranged (puffs), and (3) colonies with trichomes arranged in

Table 1. *Trichodesmium* spp. Morphological characteristics of colonies and trichomes from the Gulf of Aqaba. For the spherical colonies, dimensions are for the central section (core of densely packed trichomes) and the diameter of the colony as a whole; for bow-tie colonies, dimensions are for the central section (center point where trichomes are in tight association) and the exterior section (polar ends of the colony where the trichomes are separated). nd: not determined; l: length; w: width

	Colonies			Trichomes			
Colony shape	Color	Dimensions (µm)		No. per colony	Dimensions (µm)	Cells per trichome	Cell shape (µm)
Spherical (puffs), *Trichodesmium* sp.	Dark-brown to reddish-brown	Central section Colony diam.	150–300 1000–2500	30–150	800–2000 (l) 5–7 (w)	110–270	7.5–15 (l) 5–7 (w)
Bow-tie (*T. tenue*)	Yellow-brown	Central section Exterior section Colony length	20–40 200–250 >1000–2500	nd	1000–2000 (l) 5–6.5 (w)	80–310	8–12 (l) 5–6.5 (w)
Parallel-straight (*T. erythraeum*)	Dark-brown to reddish	Colony diam. Colony length	50–150 1000–2000	35–190	300–800 (l) 6.5–8 (w)	40–130	6–7.5 (l) 6.5–8 (w)
Parallel-twisted (*T. thiebautii*)	Yellow-brown	Colony diam. Colony length	50–300 1800–2500	35–190	1000–2200 (l) 6–7 (w)	55–180	12–17.5 (l) 6–7 (w)

parallel bundles or rafts (tufts). The former 2 colony types were each made up of unitypical trichomes and cells. The bow-tie-shaped colonies were identified as *T. tenue* and the puff-shaped colonies as *Trichodesmium* sp. sensu Janson et al. (1995). Among the tuft-shaped colonies we observed 2 different trichome types with cells that differed in shape and dimensions (Table 1). These types were identified as *T. thiebautii* and *T. erythraeum*. *T. erythraeum* colonies were made up of 35 to 190 trichome bundles arranged parallelly; the colonies were smaller in cross-section, than those of *T. thiebautii*, and contained shorter trichomes with cells that were approximately as long as wide (Table 1). *T. thiebautii* colonies were larger in diameter, with winding trichomes up to 2 mm in length and cells that were significantly longer than wide. On one occasion we found a different trichome type of distinctly larger diameter. This type was tentatively identified as *T. hildebrandtii*.

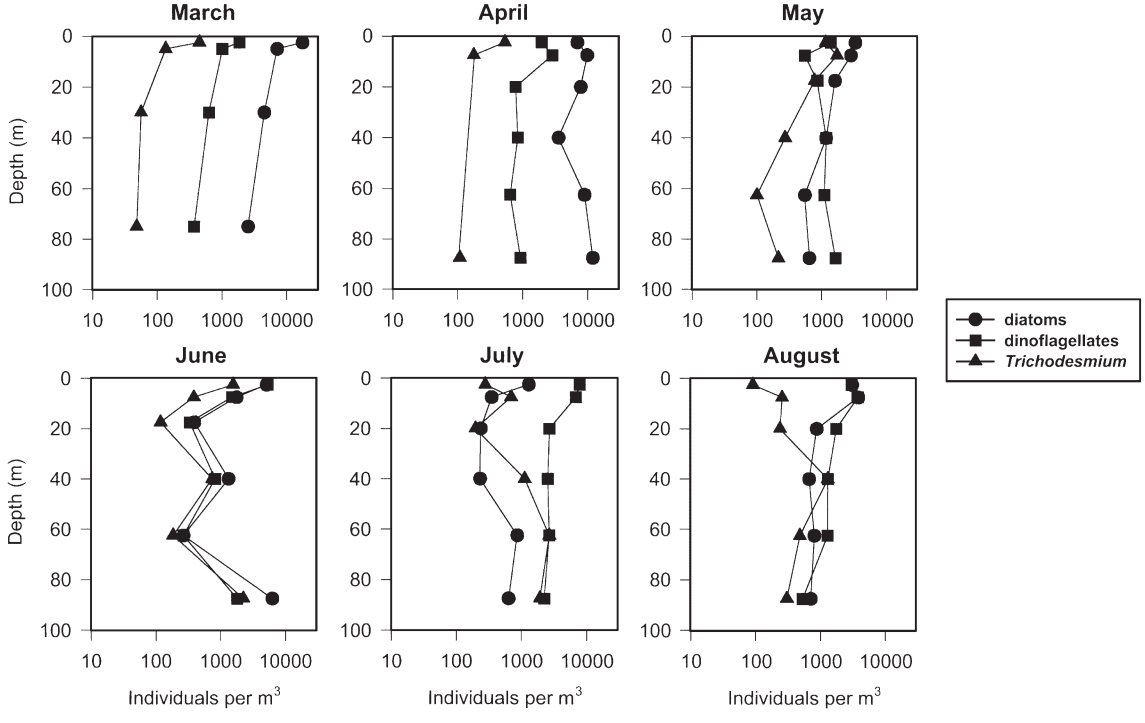

Fig. 1. Depth distributions of diatoms, dinoflagellates and the filamentous cyanobacterium *Trichodesmium* spp. in the open waters of the Gulf of Aqaba during the summer stratification period of 1996

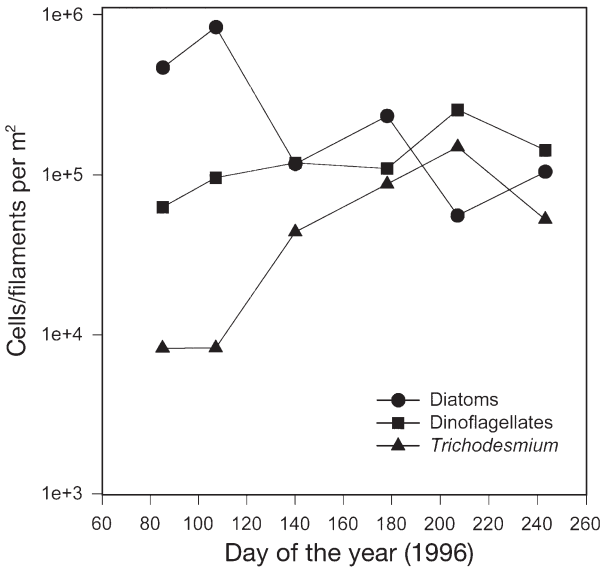

Fig. 2. Changes in total integrated number of diatoms, dinoflagellates cells and filaments of the cyanobacteria *Trichodesmium* spp. in the open waters of the Gulf of Aqaba during summer 1996

Throughout the upper 100 m of the water column, dinoflagellates and diatoms were found at all depths, with their highest numbers near the surface (Fig. 1). *Trichodesmium* spp. trichome numbers were most abundant in the upper 10 m in May and June. During July and August they were found mostly in the 50 to 100 m layer. Depth profiles further indicate a decreasing contribution of diatoms to the phytoplankton community as the summer progressed (Fig. 1). Total integrated numbers show that a succession among the major phytoplankton groups took place during summer stratification (Fig. 2). Diatoms, the most abundant group in the early stage of stratification, decreased in abundance by an order of magnitude. Specifically, *Proboscia alata* declined in May-June, whereas *Rhizosolenia* and *Hemiaulus* sp. appeared during this period. Dinoflagellates maintained their population size throughout the stratification period. *Trichodesmium* spp. populations clearly developed during this period of nutrient-deplete conditions and their trichome numbers increased by an order of magnitude to >100 000 filaments m^{-2} (Fig. 2). The development of *Trichodesmium* spp. was expressed as an increase in colony number. Of the 3 colony types (spherical puffs, bow-tie and parallel tufts) only the latter 2 were quantitatively important. *T. tenue*, with its bow-tie-shaped colonies, was the first to appear in late March, when deep mixing ceased, and was found in low numbers only. This species was rapidly replaced by larger populations of tuft- and puff-shaped colonies of *Trichodesmium* spp. Tuft colonies in the Gulf of Aqaba contained 45 ± 7 trichomes and were significantly smaller those from Stn R in the northern Red Sea, which were made up of 186 ± 6 trichomes. Puff colonies were not observed in samples from Stn R in the northern Red Sea.

Tuft and puff colonies at Stns B and M in the northern part of the Gulf maintained depth distributions, with little overlap between the 2 types (Fig. 3). The vast majority (>95%) of the tuft colonies were localized in the upper 50 m at both locations (Fig. 3) mostly in the upper 10 m; in contrast, 62 to 81% of the puff colonies (41 ± 5 trichomes) were confined to the lower half of the photic zone between 50 and 100 m (Fig. 3). These depth distributions were maintained over the diel cycle, suggesting that both populations were neutrally buoyant.

The depth distribution of the tuft and puff populations described above was maintained throughout the summer at Stn A (Fig. 4). The tuft population appeared in early April. It reached maximum densities/concentrations at the end of May, after which it rapidly declined. The deep puff populations of *Trichodesmium* sp. appeared towards the end of May, later than the tuft colony, but its population maintained itself throughout June and July until its decline at the end of the stratification period (Fig. 4). Since the more

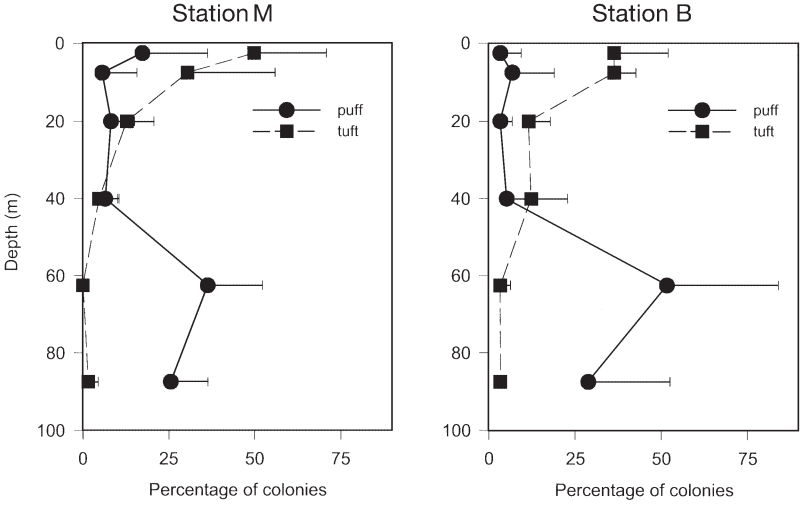

Fig. 3. *Trichodesmium* spp. Depth distributions puff- and tuft-shaped colonies at 2 sampling sites in the northern Gulf of Aqaba (June 1996). Typical colony densities were 15 to 24 colonies m^{-3} for each vertical haul

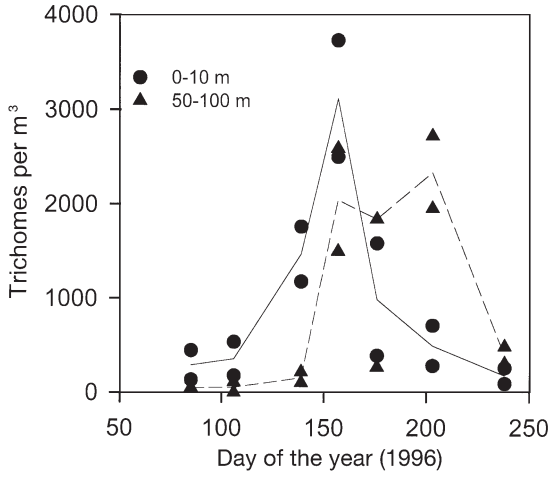

Fig. 4. *Trichodesmium* spp. Succession of shallow (0 to 10 m) and deep (50 to 100 m) populations at Sampling Stn A in the northern Gulf of Aqaba (summer 1996). Shallow populations consisted mainly of tuft-shaped colonies and free filaments of *T. thiebautii/erythraeum* and the deep population of puff-shaped colonies and free filaments of *Trichodesmium* sp. (see also Fig. 3). Lines connect mean values of duplicate samples for each depth range

buoyant tuft colonies accumulate in the surface layer, they were subject to wind action. This caused *Trichodesmium* spp. to accumulate in adjacent coastal waters, and their total population in the Gulf of Aqaba would be underestimated if sampling were to take place in the open waters only. Coastal waters near the Marine Biology Station in Eilat were monitored for *Trichodesmium* spp. populations during the 1996 and 1997 summers (Fig. 5). Modest maxima in late spring and early fall were recorded for 1996, with colony numbers not exceeding 10^2 m^{-3}. A spring maximum was not observed in 1997. However, a *Trichodesmium* spp. bloom with occasional densities of $>10^6$ tuft colonies m^{-3} occurred in early fall of 1997 (Fig. 5). Bloom conditions lasted about 2 wk, after which colony numbers declined, becoming insignificant towards winter.

Table 2. *Trichodesmium* spp. Average (±SD) chlorophyll content (ng colony^{-1}), photosynthetic carbon fixation (nmol C colony^{-1} h^{-1}) and ethylene reduction (nmol colony^{-1} h^{-1}) for puff- and tuft-shaped colonies from the Gulf of Aqaba during the 1996 and 1997 stratification periods. Number of observations in parentheses; nd: not determined

Parameter	1996		1997	
	Puff	Tuft	Puff	Tuft
Chlorophyll *a*	7 ± 1 (5)	3 ± 2 (20)	14 ± 4 (6	4 ± 3 (35)
Photosynthesis	0.3 ± 0.3 (18)	0.4 ± 0.2 (22)	0.8 ± 0.02 (4)	0.5 ± 0.1 (24)
Acetylene reduction	nd	nd	0.004 (1)	0.01 ± 0.01 (5)
C/N ratio	4.3 ± 0.3 (5)	4.1 ± 0.4 (9)	nd	nd

Physiological properties

Surface populations of the tuft and puff colony types differed in chlorophyll content as well as rates of carbon and nitrogen fixation at ambient light (Table 2). Puff colonies had higher chlorophyll contents and higher carbon fixation rates than tuft colonies in both 1996 and 1997. Tuft colonies attained rates of acetylene reduction ranging between 2 and 5% of carbon-fixation rates (Table 2). Cultures of *Trichodesmium* sp. Strain RS9602, which was isolated from the Gulf of Aqaba, had rates of carbon fixation and acetylene reduction of 0.56 nmol C ng^{-1} chlorophyll *a* h^{-1} and 0.017 nmol ethylene ng^{-1} chlorophyll *a* h^{-1} respectively. These rates were similar to those of ethylene reduction and carbon fixation of the tuft colonies among natural populations of *Trichodesmium* spp. in the Gulf. The resulting C/N ratios of *Trichodesmium* spp. colonies did not reflect their carbon and nitrogen fixation potential. The tuft and puff colony types from surface waters had a C/N ratio of 4.1 to 4.3 (Table 2). Such ratios were observed in plankton samples from near the nitracline, whereas C/N ratios of surface plankton samples at the same sites ranged between 7.7 and 8.9 (Fig. 6). Plankton samples taken at 5 to 20 m depth (wind-mixed layer) along a longitudinal transect in the Gulf had C/N ratios of 8.0 ± 1.2 (n = 13), whereas C/N ratios of 10.4 ± 2.2 (n = 4) were determined for the open waters of the northern Red Sea.

Trophic relationships

During spring 1997, *Trichodesmium* spp. were not observed, and the Gulf of Aqaba carried atypically large populations of the jellyfish *Aurelia* (>1 m^2), and the tunicates *Salpa maxima* (>100 m^2) and *Doliolum denticulatum*. This raised the question whether these observations were related. So far, *Macrosetella* has been regarded as the sole grazer of *Trichodesmium* spp.; and we therefore studied the fatty acid signatures of the cyanobacteria *Trichodesmium* spp. and *Synechococcus* and potential grazers to elucidate whether chaetognaths, copepods and tunicates directly or indirectly fed on *Trichodesmium* spp. during spring 1997. The fatty acid analyses revealed interesting differences between the different plankton organisms (Table 3). Both *Synechococcus* spp. strains had an extremely low content of long-chain (>18 C-at.) polyunsaturated fatty acids, which were represented only by 20:5ω3. This is in agreement with the published

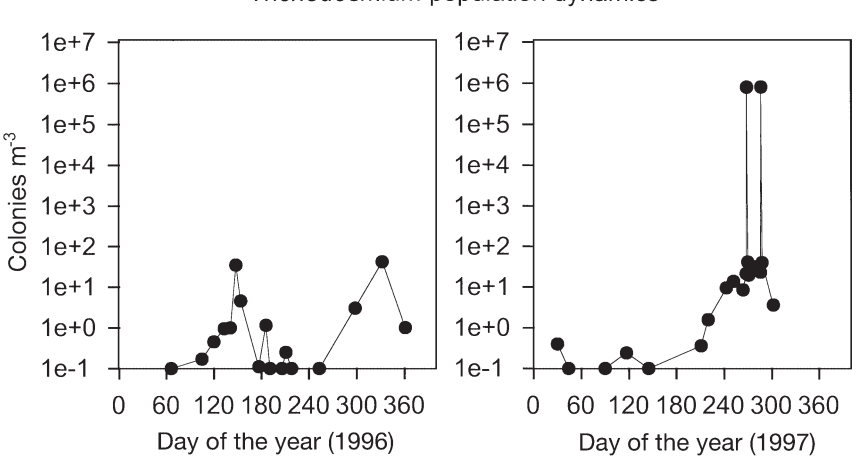

Fig. 5. *Trichodesmium* spp. Seasonal variation in colony numbers of tuft colonies in coastal surface waters (0 to 5 m) near the Marine Biology Station, Eilat, during the summer stratification periods of 1996 and 1997

DISCUSSION

Phytoplankton communities of the Gulf of Aqaba in the summer of 1996 were made up of an assemblage of diatoms, dinoflagellates and the cyanobacteria *Trichodesmium* spp. as is usual for open seas of (sub)tropical regions. Dynamic changes in diatom and *Trichodesmium* spp. abundance have been noted previously for the Gulf of Aqaba (Kimor & Golandsky 1977). The phytoplankton underwent a succession whereby diatom numbers declined over summer, and the prokaryotic *Trichodesmium* spp. became more dominant. This succession is similar to the seasonal succession among ultraphyto-

fatty acid profiles of cyanobacteria (Sargent et al. 1987, Brett & Müller-Navarra 1997). Unlike other cyanobacteria, both strains of *Trichodesmium* spp. had a modest content of 20:5ω3 and of C22:2ω6. The latter fatty acid is either not found or found in very low concentrations (<1% of total fatty acids) in other groups of phytoplankton (Ackman et al. 1968, Harwood & Jones 1989, Reitan et al. 1994, Brett & Müller-Navarra 1997). Large calanoid copepods and the tunicate *D. denticulatum* (solitary gonozoids) contained considerable amounts of C:20ω3, but no C:22ω6. The harpacticoid copepod *Macrosetella gracilis* and the salp *Salpa maxima* (chain-forming blastozoids) contained both C20:5ω3 and C22:2ω6. Results were more ambiguous for chaetognaths: about one-third of the samples contained C22:2ω6 while the other two-thirds did not.

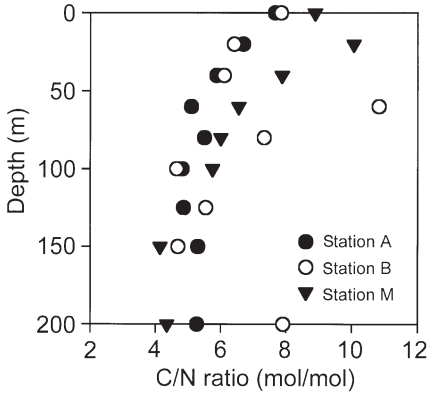

Fig. 6. Depth profiles of C/N ratios of plankton (<100 µm) populations at Sampling Stations A, B and M in the northern part of the Gulf of Aqaba, Red Sea

Table 3. Contents of polyunsaturated fatty acids as percentage of total fatty acids in cultured marine cyanobacteria and invertebrate species abundant in surface waters of the Gulf of Aqaba during the May 1997 cruise

Species	C20:5ω3 mean (min–max)	C22:2ω6 mean (min–max)	n
Trichodesmium sp. Strain RS9602	1.70	2.00	1
Trichodesmium sp. Strain WH9601	3.20	1.70	1
Synechococcus sp. Strain C129	0.22	0	1
Synechococcus sp. Strain WH7803	0.47	0	1
Salpa maxima	5.05 (2.43–11.90)	6.77 (0.65–23.3)	10
Macrosetella gracilis	11.41 (5.60–18.50)	3.33 (2.40–5.15)	5
Doliolum fasciculatum	2.89 (1.95–3.75)	0	4
Calanoid copepods	10.17 (2.50–24.40)	0	12
Chaetognaths	7.44 (2.57–22.80)	0.48 (0[a]–2.24)	10

[a]Seven samples contained no C22:2ω6

plankton (<8 µm) in these waters (Lindell & Post 1995). Both ultraphytoplankton and netphytoplankton successions in the Gulf of Aqaba are probably related to the characteristic, semi-annual variation in water body structure (Genin et al. 1995, Lindell & Post 1995). Such successions are typical of temperate waters (Smayda 1980), in contrast to the relative stability and slight inter-annual variability reported for other

warm, oligotrophic waters of the Sargasso Sea (Smayda 1980) and the Pacific Ocean (Venrick 1990). Phytoplankton composition in the central gyre of the Pacific shows a slow multi-annual trend of change, with *Trichodesmium* spp. populations becoming more prominent over recent years (Karl 1999). *Trichodesmium* spp. were the dominant nitrogen-fixing species in the Gulf of Aqaba, although diatoms such as *Rhizosolenia* sp. and *Hemiaulus* sp. as well as the heterotrophic dinoflagellate *Ornithocercus quadratus* contributed significantly to the phytoplankton in summer. These species often harbor cyanobacterial symbionts capable of nitrogen fixation (Kimor et al. 1992, Gordon et al. 1994), and their abundance is thus consistent with a progressing depletion of N-compounds (Gordon et al. 1994).

Here we report for the first time on the species composition and population dynamics of *Trichodesmium* spp. in the Gulf of Aqaba, Red Sea. Using the morphological characters of Janson et al. (1995) we identified *Trichodesmium* sp, *T. tenue*, *T. erythraeum*, *T. thiebautii* and *T. hildebrandtii* . The colony densities were low compared to reports from the Caribbean and Sargasso Sea (Hulburt 1968, Steven & Glombitza 1972, Carpenter & Price 1977, Villareal 1995), but consistent with reports of 10^3 trichomes m^{-3}, that are apparently typical for the Red Sea (Carpenter 1983). Distinctly different depth distributions for 2 *Trichodesmium* spp. colony types were observed. Puff-colony populations remained in deep parts of the photic zone, while tuft-colony populations were located in the wind-mixed layer (upper 10 to 30 m). While information on buoyancy regulation of colonies is extensive (Walsby 1978, Villareal & Carpenter 1990, Kromkamp & Walsby 1992, Romans et al. 1994), little is known about the capacity of natural populations of *Trichodesmium* spp. to regulate their position along the vertical. Our data suggest that vertical migration of the 2 *Trichodesmium* spp. colony types, if it occurred at all, was confined to bidirectional migration of low numbers of individual colonies. *Trichodesmium* spp. depth distributions at later dates in 1996 were consistent with the observations described above, suggesting that the 2 different *Trichodesmium* spp. types occupy different niches within the photic layer.

It is not known at present whether the deep populations of *Trichodesmium* sp. employ nitrogen fixation or if they meet their nitrogen demand through assimilation of dissolved N-compounds. A C/N ratio of 4.3 for both tuft and puff colony types in surface samples indicates that these were N-sufficient relative to the surrounding plankton community (C/N ratio of ~8). Deep populations of puff colonies do not necessarily depend on N-fixation, but may utilise combined N-sources. Plankton C/N ratios in the bottom half of the photic zone approached those of *Trichodesmium* spp., colonies, suggesting a higher N-supply at these depths. *Trichodesmium* spp. are capable of utilising ammonium and urea (Ohki et al. 1991) and could further explore the nitracline, as nitrate assimilation has previously been identified (Ohki et al. 1991, Wang et al. 2000).

According to the primary production data available for the Gulf of Aqaba (Iluz pers. comm.), *Trichodesmium* spp. contributed 13 to 35% of the surface production by other phytoplankton in early summer months. Primary production by *Trichodesmium* spp. exceeded surface primary production >7-fold during the short bloom period of September 1997. Since *Trichodesmium* spp. are largely limited to the surface layers, they do not contribute significantly to total annual primary production in the Gulf. However, it may impact significantly on C and N fluxes in coastal waters overlying coral reefs. Moreover, the C/N ratios of surface waters in the Gulf of Aqaba tend to be lower than those in the northern Red Sea, where the N-fixing *Trichodesmium* spp. were less abundant. High alkaline phosphatase activities among surface plankton and *Trichodesmium* spp. colonies from the Gulf of Aqaba measured during the same sampling period were indicative of low inorganic phosphate availability and, possibly, P-limitation (Li et al. 1998, Stihl et al. 2001). *Trichodesmium* spp. may thus play a pivotal role in the plankton ecology of the Gulf by alleviating N-depletion and driving the system to more P-deplete conditions.

Trophic relationships can be deduced from profiles of polyunsaturated fatty acids, since these are essential for metazoans, which have a very limited capacity for de novo synthesis (Sargent et al. 1987, Brett & Müller-Navarra 1997). Therefore, the fatty acid-composition of animals reflects the fatty acid composition of their food (Scott & Baynes 1978, StJohn & Lund 1996). In general, phytoplankton have a more constant composition of polyunsaturated fatty acids than organisms from higher trophic levels (Reitan et al. 1994, Brett & Müller-Navarra 1997). Until now, C20:5ω3 fatty acid has been reported as a marker of diatoms, C22:6ω3 as a marker of pigmented flagellates (Prymnesiophyceae, Chrysophyceae, Xanthophyceae, Cryptophyceae), while cyanobacteria and Chlorophyta were found to have negligible polyunsaturated fatty acid contents (Ackman et al. 1968, Sargent et al. 1987, Harwood & Jones 1989, Reitan et al. 1994, Pond & Harris 1996, Brett & Müller-Navarra 1997). Our results indicate that C22:2ω6 serves as a specific biomarker for *Trichodesmium* spp., since it is lacking in *Synechococcus*. We identified the C22:2ω6 marker in the known *Trichodesmium* spp.-feeder *Macrosetella gracilis* (Böttger-Schnack & Schnack

1989, O'Neil 1998) and in the salp *Salpa maxima*. However, it was not found in calanoid copepods which supposedly do not feed on *Trichodesmium* spp. Similarly, no C22:2ω6 was found in the tunicate *Doliolum denticulatum*. From this we conclude that *S. maxima* did feed on *Trichodesmium* spp. populations in the Gulf of Aqaba. It seems improbable that C22:2ω6 entered the food web via degradation of *Trichodesmium* spp., bacterial uptake and subsequent bacteriovory by protozoans. In such case, C22:2ω6 would have been either oxidised during degradation or would have shown up in the calanoid copepods as well. Its appearance in a portion of the chaetognath population is probably due to predation of some chaetognath individuals on *Macrosetellla gracilis*. *S. maxima* is too large to be fed upon by chaetognaths.

In spite of the virtual absence of *Trichodesmium* spp. from the Gulf of Aqaba during spring 1997, *Salpa maxima* must have ingested sufficient colonies to account for the C22:2ω6 signature among salps. Harbison & Gilmer (1976) provided a logarithmic regression of filtration rates on body size of *S. maxima* blastozoids that predict rates of 10.5 l d^{-1} for a mean 25 mm (body length) salp. During the 1997 cruise, several chains of 20 to 40 individuals were observed within 1 m^3 of the surface water. The individual filtration rate and a conservative estimate of 100 salps m^{-3} yields an estimated population filtration rate of 1 colony d^{-1}. This filtration rate cannot be met by the maximal growth rate of *Trichodesmium* spp., and therefore explains adequately why the anticipated *Trichodesmium* spp. spring maximum was lacking in 1997. Similarly, the high growth rates of pelagic tunicates such as *Doliolum denticulatum* (which has C22:2ω6 signatures) enable their populations to control algal blooms (Heron 1972). So far, feeding studies of salps and doliolids have concentrated on bacteria, small and medium-sized algae. The lower size limit of edible particles of ca. 0.5 µm has been well established through the morphology of the mucus filter (Silver & Bruland 1981), while little attention has been given to the upper size limit. However, there is no objective reason why salps and tunicates should not feed on a colonial cyanobacterium such as *Trichodesmium* spp. and thus form a new link in the trophic relationships of the marine food web.

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