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COMMUNITY STRUCTURE
CROCOSPHAERA
PICOEUKARYOTIC ALGAE
PROCHLOROCOCCUS
SYNECHOCOCCUS
TRICHODESMIUM

ABSTRACT. – Phytoplankton composition and community structure in the southwestern Pacific Ocean were examined at sea using flow cytometry and epifluorescence microscopy to explore the relationships among distributions of picophytoplankton populations and a variety of nitrogen fixing cyanobacteria. The cruise track began in New Zealand, extended north via New Caledonia to 13ºS, and continued east to 13.9ºS 173.2ºW. The track crossed a large bloom of the filamentous nitrogen-fixing cyanobacteria *Trichodesmium* centered around New Caledonia. Within *Trichodesmium* blooms, abundances of *Synechococcus* were elevated 10-fold; however, there was no significant enrichment of *Prochlorococcus,* picoeukaryotic algae, or heterotrophic bacteria. Unicellular coccoid cyanobacteria (> 2 µm), which resemble the nitrogen-fixing *Crocosphaera* spp., were observed in waters > 27 ºC along the eastward track and were most abundant at the deep oceanic stations where *Trichodesmium* was absent or present at very low abundances. These *Crocosphaera*-rich, *Trichodesmium*-poor stations were characterized by lower dissolved iron concentrations compared to coastal stations where *Trichodesmium* tended to be more abundant. Given the apparent mutually exclusive distributions of these two groups of cyanobacteria, further examination of N_2 fixation within the pico- and nanoplankton components of the phytoplankton community is needed.

STRUCTURE DU PEUPLEMENT
CROCOSPHAERA
ALGUES PICOEUCARYOTIQUES
PROCHLOROCOCCUS
SYNECHOCOCCUS
TRICHODESMIUM

RÉSUMÉ. – La composition du phytoplancton et la structure des populations du sud-ouest de l'Océan Pacifique ont été étudiées en mer par écoulement cytométrique et microscopie d'épifluorescence afin d'explorer les relations entre la distribution des populations de picophytoplancton et d'une variété de cyanobactéries fixatrices d'azote. L'expédition est partie de Nouvelle Zélande vers le Nord via la Nouvelle-Calédonie jusqu'à 13ºS, puis s'est prolongée vers l'Est jusqu'à 13.9ºS 173.2ºW. Ce parcours a croisé un large bloom de cyanobactéries filamenteuses fixatrices d'azote, *Trichodesmium,* au large de la Nouvelle-Calédonie. Dans ce bloom de *Trichodesmium*, de fortes abondances de *Synechococcus* ont été relevées ; cependant, il n'y avait aucun enrichissement significatif en *Prochlorococcus*, algues picoeucaryotiques, ou en bactéries hétérotrophes. Les cyanobactéries coccoïdes unicellulaires (> 2 µm), qui ressemblent aux espèces de *Crocosphaera* spp. fixatrices d'azote, ont été observées dans les eaux à plus de 27ºC le long du parcours vers l'est et étaient plus abondantes dans les stations les plus profondes où *Trichodesmium* était absente ou en faible abondance. Ces stations riches en *Crocosphaera* et pauvres en *Trichodesmium* sont caractérisées par des concentrations en Fe dissous inférieures à celles des stations côtières où *Trichodesmium* est plus abondant. Etant données les distributions apparentes, mutuellement exclusives, de ces deux groupes de cyanobactéries, une étude plus approfondie de la fixation d'azote dans les compartiments pico- et nano-planctoniques du peuplement phytoplanctonique est nécessaire.

INTRODUCTION

The recognition of nitrogen (N_2) fixation as a major source of new N to the oceanic ecosystem has prompted the need for a better understanding of the abundance and dynamics of N_2-fixing organisms. *Trichodesmium* spp. (*TRICHO*) can form extensive blooms throughout oligotrophic tropical and subtropical waters and are major contributors to N_2 fixation in the ocean (Capone *et al.* 1997, 2005). These non-heterocystous cyanobacteria grow in long filaments (trichomes) that often aggregate in colonies. One unique aspect of *TRICHO* is that healthy colonies appear to release NH_4^+, amino acids, and dissolved organic N (Capone *et al.* 1994, Glibert & Bronk 1994). This N release may have a direct impact on the surrounding phytoplankton community, especially in N-limited regions (Santhanam *et al.* 1994*,* Karl *et al.* 1997). In the North Pacific, increases in *TRICHO* were observed in response to decreased frequency of deep mixing events during the ENSO event of 1992/93 (Letelier & Karl 1996). Concurrently, increased abundance of picoplankton was observed, which supports a link between *TRICHO* and nitrogen dynamics of other phytoplankton (Campbell *et al.* 1997*,* Karl *et al.* 1997). Subsequently, another group of N_2-fixing cyanobacteria, *Crocosphaera* (*CROCO*) spp., was recently discovered in the North Pacific (Zehr *et al.* 2001) and this group may make an equal contribution to new N in the North Pacific, although the fate of this new N is not known (Montoya *et al.* 2004).

The southwest (SW) Pacific is undersampled by sea-going researchers, yet large persistent blooms of *TRICHO* have been observed by ocean color observations in this highly oligotrophic region of the ocean (Dupouy *et al.* 1988*,* 2000). The objectives of this project were to examine phytoplankton composition and community structure in this region where surface waters are chronically low in nitrogen and to explore the relationship among distributions of picophytoplankton groups, N_2 fixing cyanobacteria, and water column physical (temperature, mixed layer depth) and chemical (dissolved nitrate, silicate, iron) parameters. Do *TRICHO* blooms influence picoplankton community structure? Specifically, we hypothesized one major ecosystem response to TRICHO blooms would be seen as an increase in the abundance of *Prochlorococcus* (*PRO*) and picoeukaryotic algae (PEUK), as observed in the North Pacific (Campbell *et al.* 1997).

MATERIAL AND METHODS

Study Area: Seawater samples were collected in the southwest Pacific Ocean aboard the *R/V Roger Revelle* during Mar-April 1998. The cruise track began west of New Zealand (40°S 173°E), followed north to 13°S 163°E via New Caledonia, east to Fiji (18.30°S 178.37°E), north to American Samoa and returning south from 173.2°W to 176.1°E (Fig. 1). Water samples were collected from 6 - 15 depths within the upper 120 m using a Seabird CTD-rosette system equipped with 12-l Niskin bottles.

Flow cytometry: Picoplankton cell abundances were enumerated from live samples (0.2 to 0.3 ml) analyzed immediately following collection using a FACSCalibur (Becton Dickinson, San Jose, CA) flow cytometer equipped with a 488 nm 15 mW laser and standard filter setup as described previously (Campbell 2001). Replicate samples were also preserved with 0.2% paraformaldehyde for heterotrophic bacteria (HBac) analysis using SYBR (Marie *et al.* 1999) and cell cycle analyses for growth rates estimates of *PRO* (Liu *et al.* 1997). Purple-Yellow 0.98 µm fluorescent bead standards (Sphereotech, Libertyville, IL) were run with each sample. Sample flow rate was determined by gravimetric analysis and verified by comparing flow cytometric counts with known concentrations of beads and cell cultures determined by microscopy (Campbell *et al.* 1997, 2001). Data was analyzed using CYTOWIN (Vaulot 1989) to distinguish the three major groups of picoplankton, *PRO, Synechococcus (SYN)*, and PEUK, as well as the 2 - 3 µm orange-fluorescing cells (identified as *Crocosphaera*-like cyanobacteria). Identification of this population of unicellular cyanobacteria as putative *Crocosphaera* sp., hereafter p*CROCO,* was based on estimated size and phycoerythrin fluorescence characteristics (Zehr *et al.* 2001), as well as microscopic observation. Based on flow cytograms, observed p*CROCO* were similar in size to N. Atlantic isolates (Falcón *et al.* 2004).

Microscopy: *TRICHO* were enumerated by epifluorescence microscopy using 575 +/– 15 nm excitation at 100 X magnification. Ten liters of water from 6 - 8 sampling depths were filtered by gravity onto a 10 µm pore, 47 mm diameter Nuclepore filter (Poretics Corp.).

Nutrients: Samples for nutrient analyses were collected directly into clean bottles and concentrations determined by standard colorimetric techniques [Parsons *et al.*, 1984] using a Technicon II autoanalyzer.

Iron Analysis: Trace metal clean techniques were employed for all stages of dissolved seawater collection and analyses. A Zodiac was deployed from the ship and samples were taken at least 1 km upwind of the ship. Samples were collected from 5 m depth using teflon tubing (and 75 cm C-flex silicone tubing) and a battery operated peristaltic pump. Samples were filtered through a precleaned CalyxTM polypropylene 0.22 µm cartridge filter (Millipore) and collected in 1 L LDPE bottles. Before each sample was collected, >12 L seawater was passed through the Teflon tubing system and an additional >4 L was passed through the Teflon tubing and cartridge filter. Samples were double-bagged and transported for analysis on shore. In a class 100 cleanroom, samples were acidified for >1 month and then metals were concentrated 167-fold using organic extraction methods (Bruland *et al.* 1979). Fe was analyzed on a Hitachi Z-8100 graphite furnace atomic absorption spectrophotomer with Zeeman correction, using standard addition methods. The detection limit of these extractions, defined as

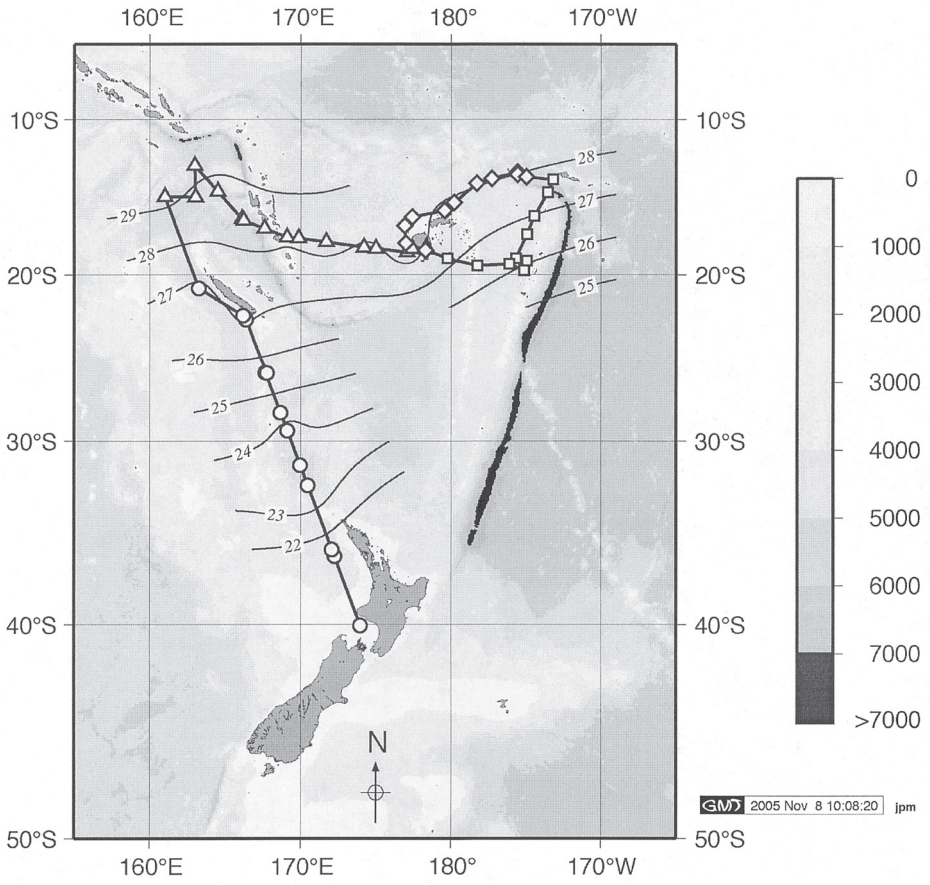

Fig. 1. – Station locations along four tracks in the Southwestern Pacific Ocean: track 1 (circles); track 2 (triangles); track 3 (diamonds); track 4 (squares). Bathymetry for the region from ESRI (Ormsby *et al.* 2004). Temperature contour lines (22 – 29 ºC) indicate average surface mixed layer temperates.

three times the standard deviation of blank (Milli-Q) values, was 60 pmol Fe L^{-1}.

Data Analysis: Depth distributions of each picoplankton group and *TRICHO* were contoured using Surfer (Golden Software, Sandy, UT). Multidimensional scaling (MDS) analysis was used to identify clusters of stations based on similarity of community structure. Correlations of log(x+1) transformed abundance data were performed (after Field *et al.* 1982), and the resulting dissimilarity index was analyzed using SYSTAT 8.03 (SSI, Richmond, CA, USA). Only stations for which all groups were enumerated were included in MDS analysis (see Fig. 2). T-tests for log transformed data were performed to determine significance of differences between groups.

RESULTS

Results from this cruise are presented as four separate tracks which are identified in Figure 1. Stations near island coasts and in < 200 m water were considered coastal. Open ocean stations were defined as those at least 50 km beyond the 200 m isobath (see Table I, Fig. 1). The first track began west of New Zealand where the surface water temperature was cool (17 ºC) and high levels of major nutrients were present (Table I). At Sta. 1, community structure of the picoplankton was typical of coastal, temperate regions in that *PRO* was absent, *SYN* was abundant (12.7×10^3 cell ml^{-1}), and PEUK were found at the highest densities observed (17.8×10^3 cell ml^{-1}). *TRICHO* and p*CROCO* cells were also absent (Fig. 2).

At Stas. 2 - 6, the community structure was more typical of offshore, oceanic waters. *PRO* abundance increased to $>100 \times 10^3$ cell ml^{-1} and profiles displayed a subsurface maximum. Abundance of *SYN* ($2 - 5 \times 10^3$ cell ml^{-1}) was ~100-fold lower than *PRO*. PEUK distributions showed the characteristic oceanic depth profile with maximum abundances at or below deep chlorophyll fluorescence maximum (DCM; Table I). Abundance of *PRO* increased as temperature of the surface mixed layer (SML) increased and surface concentrations of NO_3^- and PO_4^{3-} decreased towards New Caledonia (Table I). High concentrations of SiO_4 (>6 µM) were limited to coastal stations, and levels de-

Table I. – Environmental parameters for each station; average values within the Surface Mixed Layer (SML). DCM, Deep chlorophyll fluorescence maximum depth; Station Type, coastal (C) or oceanic (O), based on bathymetry and distance from islands (see Fig. 1); na, data not available.

Sta	SML (m)	DCM (m)	Salinity	Temp °C	$NO_3 + NO_2$ (µM)	PO_4^{-3} (µM)	Si (µM)	Station Type
1	44	S	na	17.2	0.610	0.220	6.700	C
2	44	60	na	21.2	0.169	0.151	1.350	O
4	44	100	35.88967	24.1	0.165	0.080	1.425	O
5	42	60-80	35.86477	23.7	0.016	0.080	1.913	O
6	42	75	35.43250	23.6	0.144	0.084	1.290	O
7	50	70	35.65793	24.5	0.183	0.098	1.633	O
8	75	100	35.48003	25.6	0.118	0.062	2.158	O
10	42	80	35.53467	27.1	0.169	0.054	1.808	C
11	40	S	35.61125	27.2	0.079	0.057	0.573	C
12	50	80	35.42802	26.8	0.223	0.094	0.919	O
13	30	75	34.58794	29.3	0.250	0.127	0.867	O
14	35	70	34.92966	28.8	0.124	0.149	0.758	O
15	35	90	35.13594	29.3	0.057	0.140	0.700	O
16	55	65	35.13779	28.5	0.133	0.131	0.733	O
18	40	90	35.13369	28.6	0.043	0.158	0.975	O
19	50	60	35.12844	28.6	0.190	0.101	0.413	C
20	30	40	35.12179	28.1	0.153	0.152	1.056	C
22	45	120	35.12900	28.4	0.139	0.140	0.650	O
23	40	120	35.27021	27.9	0.150	0.111	0.587	O
24	50	120	35.36220	27.9	0.167	0.100	0.500	O
25	50	120	35.20738	28.5	0.192	0.115	0.683	O
26	43	100	35.32959	28.6	0.234	0.123	0.657	C
27	48	100	35.42118	28.7	0.210	0.140	0.200	C
29	50	S	35.49548	27.9	0.204	0.130	0.704	C
30	50	S	35.53641	27.8	0.160	0.100	1.400	C
31	58	60-80	35.46892	28.6	0.126	0.108	0.740	C
32	60	80	35.45786	28.5	0.133	0.132	0.710	C
33	60	na	35.49125	28.2	na	na	na	C
34	75	100	35.66143	27.8	0.193	0.112	0.575	C
35	45	130	35.78901	27.9	0.160	0.153	0.333	O
36	40	90	35.65340	28.5	0.186	0.173	0.717	O
37	55	125	35.66494	28.5	0.155	0.148	0.500	O
39	40	80	35.58083	29.0	0.233	0.170	0.875	O
40	40	100	35.68467	28.8	0.215	0.218	0.550	O
41	40	110	35.63896	28.7	0.181	0.197	0.905	O
42	45	110	35.74912	28.5	0.083	0.167	0.800	O
43	55	130	35.59012	28.2	0.130	0.184	0.650	O
44	30	130	35.60507	27.4	0.160	0.157	0.733	O
45	55	120	35.91350	26.4	0.130	0.183	0.671	O
46	80	110	35.93468	26.5	0.230	0.136	0.330	O
47	60	120	35.85990	26.4	0.172	0.156	0.940	C
48	80	80	35.86173	26.9	0.150	0.123	0.500	O
51	50	60-90	35.66586	27.7	0.144	0.121	0.464	C

creased to < 2 µM farther along Track 1. SiO_4 remained well below 1 µM throughout most of the remaining stations, although was slightly elevated near islands (e.g., Sta. 20, 30, 47).

TRICHO was present at very low densities (<10 trichome L^{-1}) at Sta. 4 - 6 and increased to ~1000 trichome L^{-1} at Sta. 10 and 11, the coastal stations south of New Caledonia, where water was warmer (>27 °C). At Sta. 12, northwest of New Caledonia, *TRICHO* decreased (<250 trichome L^{-1}) concurrently with very low abundances of the picoplankton (Fig. 2).

The second track began NW of New Caledonia at the edge of the South Pacific Subtropical Gyre (SPSG) (Longhurst 2000). Surface water temperatures were extremely warm (>28 °C) and the SML was relatively shallow (35 - 50 m). The cruise track led into the path of Cyclone *Zuman*. This typhoon with maximum winds of 85 kts originated at 14.3°S 167.4°E and moved west over the northernmost island of Vanuatu and along ~16°S latitude toward our Sta. 13 and 14 (*http: //www.metoffice.com/sec2/ sec2cyclone/ tctracks/shem97_8/zuman.gif*). Directly ahead of the cyclone path there was considerable rainfall and lower salinity surface waters were observed at Sta. 13 and 14. Surface nitrate was low throughout this region, although higher than expected at Sta. 13 where the nitracline was at 150 m (Table I). Concentrations of PO_4^{3-} in the SML were low (<0.1 µM), except at coastal Stas. 18, 19, 41, and at Sta. 51 southeast of Fiji (0.2 - 0.3 µM).

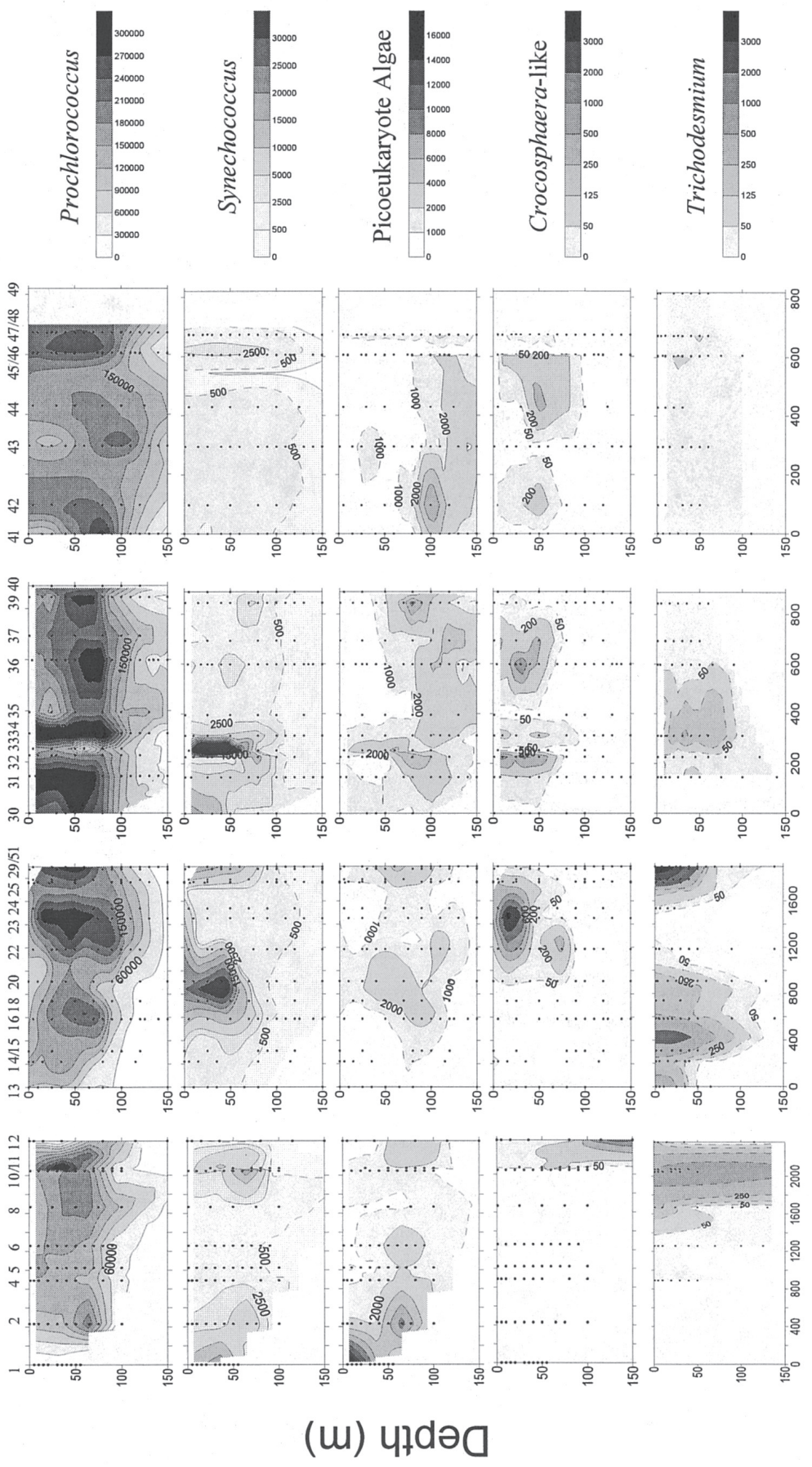

Fig. 2. – Depth distributions for phytoplankton abundance along Tracks 1 – 4. Top row: *Prochlorococcus* (cell ml^{-1}); Second row: *Synechococcus* (cell ml^{-1}); Third row: picoeukaryotic algae (cell ml^{-1}); Fourth row: *Crocosphaera*-like cells (cell ml^{-1}); and Fifth row: *Trichodesmium* (trichome L^{-1}). Data for *Trichodesmium* were not available for stations 2, 5, 7, 26, 30, 35, 40, 50; picoplankton data were not available at 49.

Picoplankton abundances in the vicinity of the storm, and north to Sta. 15, were approximately two-fold lower than observed at other oceanic stations along track two. Stas. 16 and 18 were occupied in the wake of the storm and although *PRO* and PEUK cell densities remained low, *SYN* abundance increased to 8-10 × 10^3 cell ml^{-1}, which is 3-4 fold higher than is typically found in oceanic waters. At all deep ocean stations of Track 2 (see bathymetry Fig. 1), two populations of *PRO* could be distinguished by flow cytometry (Campbell & Vaulot 1993) at depths below the SML.

Large blooms of *TRICHO* were a prominent feature of Track 2. One bloom was centered on New Caledonia and the other near Fiji (Fig. 2). *TRICHO* was most abundant at stations with low surface salinity and a deeper SML. At both Sta.16, occupied 3 days after *Zuman*, and the island-influenced Sta. 19, *TRICHO* counts were approximately 1000 trichome L^{-1} and increased up to 4000 trichome L^{-1} near Fiji (Sta. 51). Away from these near-island sites in open water regions, p*CROCO* appeared at densities up to 1.6 × 10^3 cell ml^{-1} and were most numerous at Stas. 22 - 25, where water temperatures were > 28 °C.

The third track of the cruise began west of Fiji and extended northeast to 13.65°S 175.56°E. Surface waters of this transect had uniformly low N (Table I), with a fairly deep nitracline at ~100 m (data not shown), except at Sta. 39 where it shoaled to ~50 m. Average *PRO* abundance was highest along this track and reached a maximum of 346 × 10^3 cell ml^{-1} at Sta. 34. *PRO* was uniformly distributed in the SML (although may have been underestimated in surface waters at the northernmost stations due to extremely dim fluorescence of these cells). *SYN* abundance was several times higher at the coastal stations north of Fiji (30 - 34), and reached maximum abundance (60 × 10^3 cell ml^{-1}) at Sta. 33, but was uniformly low at oceanic stations (35 - 40). Large puffs of *TRICHO* were observed at Sta. 34, although abundance was only 10 - 100 trichomes L^{-1}. p*CROCO* were abundant at Stas. 32, 34, 36 and 37 (0.4 - 0.8 × 10^3 cell ml^{-1}) and < 0.2 × 10^3 cell ml^{-1} or absent at the other stations along the track. Due to the small volume of flow cytometry analyses, however, p*CROCO* could have been below the limit of detection at these stations.

The last leg of the cruise track began in the northeast edge of the study area. Thirty knot winds were encountered en route from Sta. 40 to 41, and the temperature of the SML was cooler (< 27 °C) from Sta. 45 - 48 (Table I). This section of the SPSG is primarily oligotrophic open ocean. The DCM occurred at depths > 100 m (Table I). Observed *PRO* abundances were >200 × 10^3 cell ml^{-1} along this track and were uniformly distributed in the SML. *SYN* abundance was 100-fold lower than *PRO* throughout (< 1 × 10^3 cell ml^{-1}) with several subsurface peaks (2 × 10^3 cell ml^{-1}) observed. Similarly, PEUK abundance was uniformly low throughout the SML with deep subsurface peaks in abundance at or below the DCM. Sta. 47 was an exception, perhaps due to its proximity to islands of Tonga, *SYN* increased to 5 - 7 × 10^3 cell ml^{-1} and PEUK abundance was ~two-fold higher. Neither *PRO* nor *TRICHO* showed a marked increase. Overall, *TRICHO* abundance was very low (<30 trichome L^{-1}) along this track, and was below detection at Sta. 42, but increased to 50-75 trichome L^{-1} at Sta. 45. p*CROCO* abundance was also very low (<0.1 × 10^3 cell ml^{-1} or absent) along this track, with the exception of Stas. 42, 44, and 46 where 0.2 - 0.4 × 10^3 cell ml^{-1} were observed within the SML only.

Dissolved Fe concentrations at stations along the cruise track ranged from < 60 to 1000 pM and showed a gradient between open ocean and coastal stations (Table II). Median open ocean and coastal Fe concentrations were 93 and 355 pM, respectively. The highest Fe concentrations was observed at Sta. 47, which, as noted above, was adjacent and leeward of several islands and a region of shallow (<200m) bathymetry. An apparent exception to this gradient occurred at open ocean Sta. 45, where dissolved Fe concentrations were relatively high at 622 and 762 pmol L^{-1}, measured from samples collected on two consecutive days. Likewise, some coastal stations (32, 36) had low Fe concentrations more similar to open ocean regions.

To examine community composition within and outside *TRICHO* blooms (defined as > 3000 trichomes cm^{-2}; Fig. 3), SML-integrated counts were compared among stations (Fig. 3). Depth-integrated *SYN* abundance was significantly higher within vs. outside *TRICHO* blooms (t-test, p = 0.003); this difference was approximately 10-fold higher. In contrast, p*CROCO* abundance was

Table II. – Dissolved Fe concentrations at coastal (C) and oceanic (O) stations in the SW Pacific. Level of detection (LD) was 60 pM.

Station	Station Type	Dissolved Iron (pM)
20	C	840
26	C	680
31	C	230
32	C	Below LD
34	C	480
36a	C	90
36b	C	110
47	C	1000
49	C	Below LD
51	C	510
15	O	Below LD
16	O	Below LD
18a	O	320
18b	O	Below LD
22	O	90
45a	O	620
45b	O	760

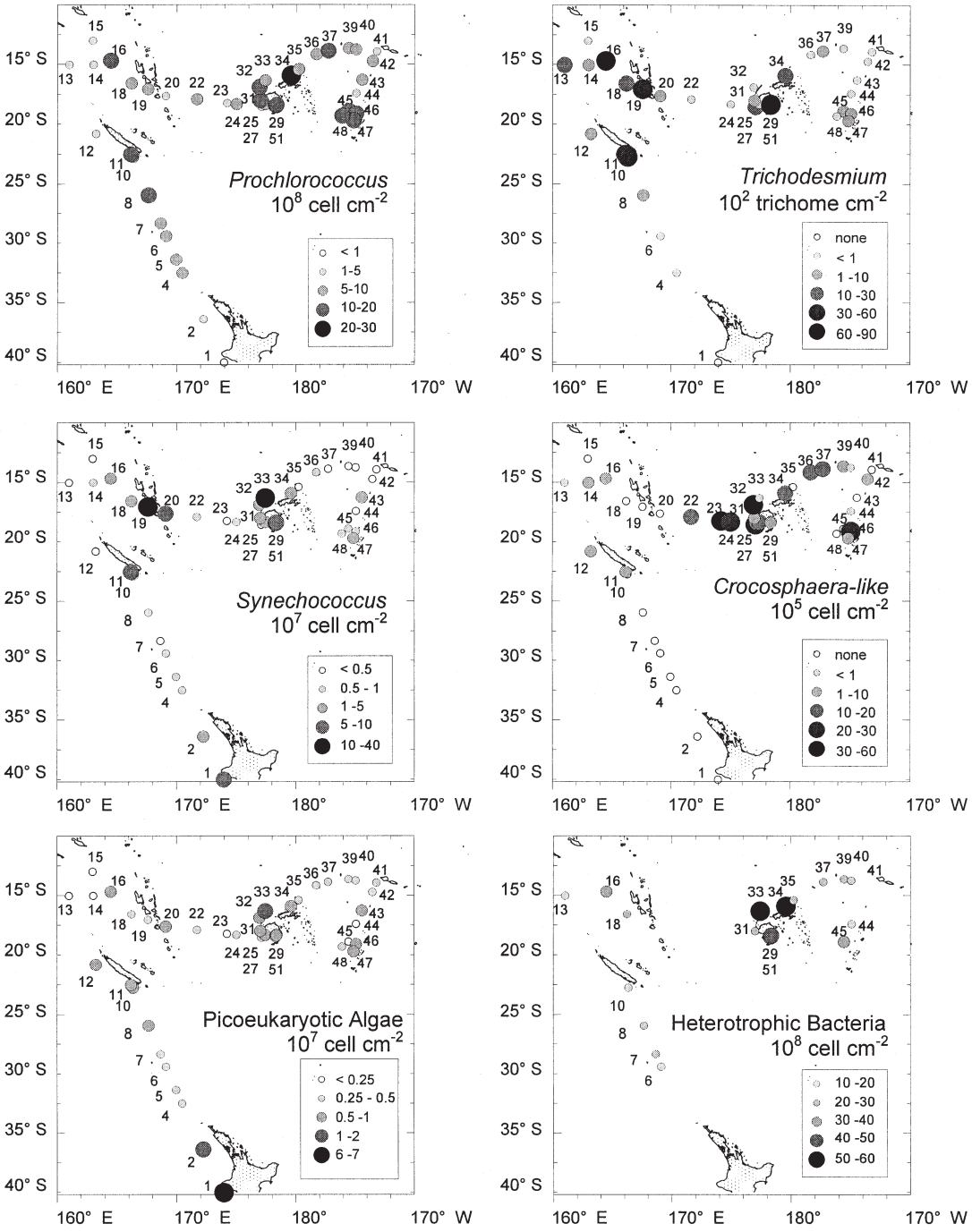

Fig. 3. – Maps of SML-integrated abundance for *Prochlorococcus* (× 10^8 cell cm^{-2}), *Synechococcus* (× 10^7 cell cm^{-2}), picoeukaryotic algae (× 10^7 cell cm^{-2}), *Trichodesmium* (× 10^2 trichome cm^{-2}), *Crocosphaera*–like cells (× 10^5 cell cm^{-2}), and heterotrophic bacteria (× 10^8 cell cm^{-2}).

ten-fold lower at stations with highest abundance of *TRICHO* (Fig. 3; $p < 0.05$). Assuming 100 cells $trichome^{-1}$, average depth-integrated *TRICHO* abundance was 5.45×10^5 cells cm^{-2} at bloom stations (10, 11, 16, 19, 29, and 51), where average p*CROCO* abundance was 2.54×10^5 cells cm^{-2}. At oceanic stations where *TRICHO* was absent, p*CROCO* averaged 2.57×10^6 cells cm^{-2}. *PRO* and PEUK abundances were slightly enriched at *TRICHO* bloom stations (average ~10% and 50% greater than the mean, respectively), but because of large variations among stations neither difference was significant. However, specific growth rates for *PRO* determined by cell cycle analysis were significantly higher at the *TRICHO* bloom stations (29 and 51; average = 0.54 d^{-1}; SD 0.025) than at open

ocean stations (30, 31, 33, 37, 40, 44; average = 0.44 d^{-1}; SD 0.078) ($p<0.01$). Growth rate could not be determined at Sta. 18 because the multiple *PRO* populations obscured patterns of DNA replication and subsequent analysis. Abundance of HBac was determined for only a subset of the stations and ranged from 4 - 11 × 10^5 cell ml^{-1} in the SML. HBac abundances were notably lower at the most oligotrophic stations, including the vicinity of Cyclone *Zuman* (Sta. 13), and were two to three-fold higher at stations with high picophytoplankton abundances (data not shown). Overall, HBac SML-depth integrated counts (Fig. 3) ranged ~3-fold and were significantly positively correlated with all 3 picophytoplankton groups ($p < 0.05$); however, HBac were not significantly different within *vs.* outside *TRICHO* bloom stations.

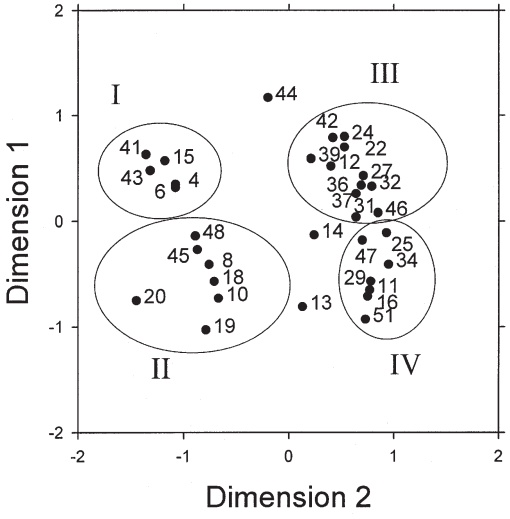

Fig. 4. – Similarity plot produced by multi-dimensional scaling (MDS) in 2D based on community structure. Axes are arbitrary distances. Clusters are proportional to dissimilarity among stations. Lines to identify clusters are added for clarity.

MDS analysis results (Fig. 4) indicated four main clusters among the stations that could be distinguished by community structure: (I) low abundance of all picoplankton, *TRICHO* and p*CROCO* absent; (II) *SYN* abundant, *TRICHO* present and p*CROCO* absent; (III) p*CROCO* abundant; (IV) *TRICHO* abundant. Outliers from these general groups include stations sampled during the cyclone (13 & 14) and Sta.44 where p*CROCO* is present. Sta. 1 lacked both *TRICHO* and p*CROCO* because temperature was below optimal range for these organisms, so was not included in analysis. Characteristic community structure of the p*CROCO* and the *TRICHO* clusters can be seen in the depth profiles of cell abundance (Fig. 5 A&B and C&D, respectively).

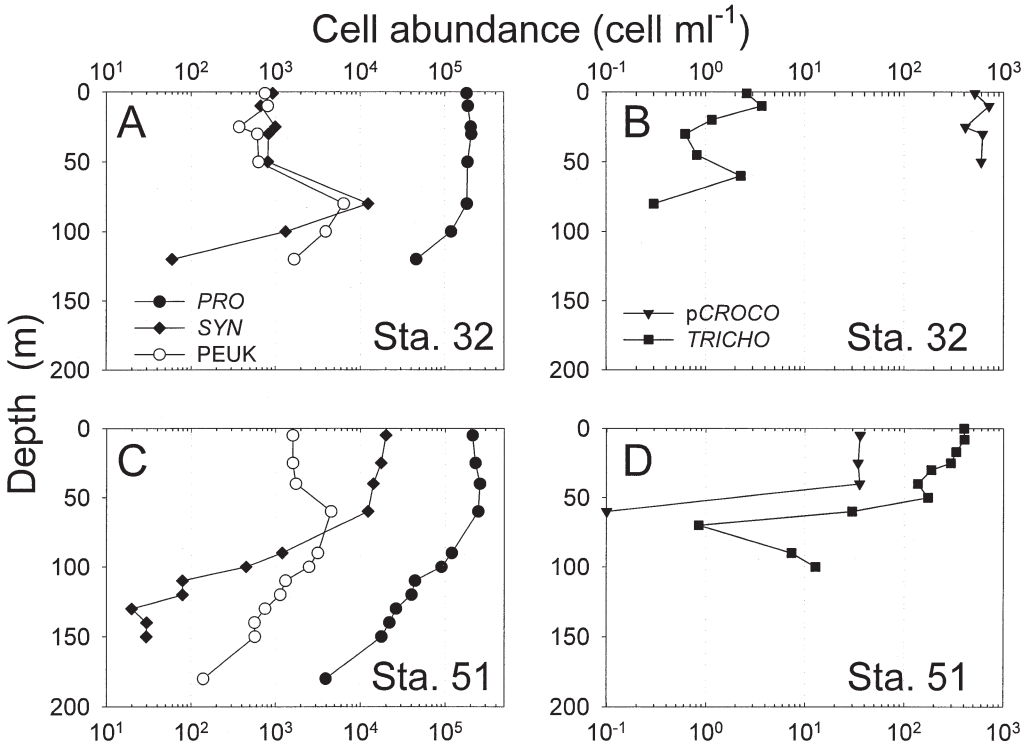

Fig. 5. – Vertical depth profiles of cell abundance (cell ml^{-1}) for Stations 32 and 51. *PRO*, *SYN*, and PEUK (A, C); *TRICHO* and p*CROCO* (B, D). The number of *Trichodesmium* cells was estimated assuming 100 cells/trichome.

DISCUSSION

The SW Pacific Ocean is one of the least studied areas of the ocean (Longhurst 2000) and consequently phytoplankton community structure in this region is not well characterized. Our cruise track included both the Archipelagic Deep Basin province (ARCH) and westernmost area of the SPSG province (Longhurst 2000), which are characterized by complex circulation. In the area centered on New Caledonia, Dandonneau *et al.* (2004) reported variability in chlorophyll *a* appears to be greater on an interannual rather than a seasonal scale due to the large *TRICHO* blooms that occur episodically. The dense chlorophyll feature that developed in late austral summer/early fall described by Dupouy *et al.* (2000) provided an opportunity to examine patterns of picoplankton distributions in the SW Pacific and compare distributions to *TRICHO* abundances.

Picoplankton are a major component of the phytoplankton community in oligotrophic waters. A previous report for the SPSG along 170°E, just east of our study area, showed *PRO* and *SYN* were the major contributors to chlorophyll biomass. Minor contributions from eukaryotic algae included one haptophyte group and chlorophytes, and diatoms were not detectable (DiTullio *et al.* 2003). Results from our study show a similar community structure. *PRO* were numerically dominant throughout the region and may have been at their seasonal maximum, when compared to recent studies in the SW Pacific (Dandonneau *et al.* 2004, DiTullio *et al.* 2003). This is similar to other regions, e.g., N. Pacific, Arabian Sea, and N. Atlantic, where highest *PRO* abundances typically occur in late summer/ early fall (Campbell *et al.* 1997, 1998, DuRand *et al.* 2001). Divinyl chlorophyll *a* was 40 - 60% of the total chlorophyll biomass at most stations along tracks 2 - 4 (Dupouy *et al.* 2000).

SYN generally are two orders of magnitude lower in abundance than *PRO* in subtropical gyres, but increase relative to *PRO* in coastal or mesotrophic regions (Partensky *et al.* 1996). *SYN* were present throughout much of the study area at low cell concentrations that were within the range of previous observations in the N. Pacific (Campbell *et al.* 1997) and along 165°E (Neveux *et al.* 1999), but lower than observations in the Arabian Sea and N. Atlantic (Campbell *et al.* 1998, DuRand *et al.* 2001). *SYN* appeared to be a single population of high phycourobilin (PUB) phycoerythrin type cells (based on cellular fluorescence), which also agreed with previous observations of a predominantly single high PUB-*SYN* population in the SW Pacific (Neveux *et al.* 1999). Overall, a typical oceanic picoplankton community structure dominated by photosynthetic prokaryotes was observed throughout most of the open waters of the SW Pacific; however, the abundance of both *PRO* and *SYN* increased at stations in close proximity to islands, and increases were positively correlated ($r = 0.44$, $p = 0.011$).

The distribution of PEUK in the SW Pacific was similar to recent observations in the SPSG and Archipelagic Deep Basin provinces (DiTullio 2003, Dandonneau *et al.* 2004) and other subtropical regions (Campbell *et al.* 1997, 1998, DuRand 2001). Highest abundances occurred at the surface at coastal stations (1, 33). At oceanic stations, abundances were typically $< 10^3$ cell ml^{-1} within the SML and increased to a subsurface maximum at or below the deep chlorophyll fluorescence maximum (DCM). Thus, subsurface peaks of PEUK were shallower along Tracks 1 and 2 than along most of Tracks 3 and 4.

Based on size estimates from flow cytograms, the population of orange-fluorescing cells larger than *SYN* observed in this study appeared to be similar to the N. Atlantic N_2-fixing *Crocosphaera* species (Falcón *et al.* 2004). The distribution of these p*CROCO* cells in the SW Pacific appears to be that of a truly tropical and open ocean organism. SML-depth integrated p*CROCO* was positively correlated with temperature ($r = 0.44$; $p = 0.003$) and negatively correlated with SiO_4 ($r = -0.48$; $p < 0.001$). We assume higher SiO_4 is characteristic of near-island or near-shore waters (Table I), thus this pattern is consistent with increased abundance of p*CROCO* in open water. In the North Pacific, abundance of p*CROCO* can vary from a few to 1000 cells ml^{-1} (Montoya *et al.* 2004); this range is equivalent to the observed abundances of *CROCO*-like populations in the SW Pacific (Fig. 2). It is not yet known if the unicellular p*CROCO* play a role similar to *TRICHO* in providing a N source to other organisms; however, p*CROCO* do appear to be an important component of oceanic ecosystems owing to the magnitude of their potential contribution to new N production (Montoya *et al.* 2004).

The most striking observation from this study was the inverse correlation between distributions of *TRICHO* and the p*CROCO* populations. This was most conspicuous at stations 23, 32, and 46 where p*CROCO* were most abundant and *TRICHO* was low or absent (Fig. 2). Church *et al* (2005) have suggested that p*CROCO* may be able to out compete larger cells for nutrients, e.g., PO_4^{3-} which may be limiting for *TRICHO* due to its high surface area: volume ratio (Sanudo-Wilhelmy *et al.* 2001, Moutin *et al.* 2005). In this region where the supply of iron via aeolian dust is very small (Duce & Tinsdale 1991), the higher surface area: volume ratio of p*CROCO* may very well provide an advantage over *TRICHO* in stations away from coastal inputs of iron. At coastal stations, the constraints imposed by Fe availability may be relaxed, thus allowing *TRICHO* to sequester Fe and bloom. For example, at Sta. 32 where dissolved Fe was below

60 pmol L^{-1} (the detection limit in this study; Table II), *TRICHO* abundance was much lower than p*CROCO* (Fig. 5). In contrast, at Sta. 51, dissolved [Fe] was 510 pmol L^{-1}, and *TRICHO* was much more abundant than pCROCO. However it is unclear what factors may be operating that seem to prevent p*CROCO* from dominating in near-shore stations. It is also interesting to note that the median coastal Fe concentration in this study (355 pmol L^{-1}) is similar to the ambient Fe concentration observed at a N. Australian station (290 pmol L^{-1}) where the ambient *TRICHO* population was photosynthetically and diazotrophically competent, but became Fe-limited during an on-deck incubation without added Fe (bottles with added Fe remained competent; Kustka *et al*. 2003). Thus, while these coastal regions in the SW Pacific may relax Fe limitation and allow bloom formation, a continued flux of Fe from coastal sources is of course necessary to sustain these blooms.

Average abundance for *TRICHO* in the SW Pacific determined in this study was 250 trichome L^{-1} (range 0-4000 trichome L^{-1}), which is much higher than was observed in the N. Pacific at Station ALOHA (46 trichomes L^{-1}; Letelier & Karl 1996). Water column stability is among the conditions conducive to formation of *TRICHO* blooms (Capone *et al.* 1997). Hansell & Feely (2000) suggested that high precipitation in the subtropical convergence zone and resulting salinity minimum lead to increased water stratification and conditions favorable to *TRICHO* growth in the SW Pacific. They attributed the higher than expected DON concentrations observed in the region centering on 10°S to *TRICHO* growth. We also noted that the average SML salinity was significantly lower for stations within *TRICHO* blooms than outside blooms ($p < 0.01$). Although *SYN* abundance was significantly enriched within *TRICHO* blooms, these blooms did not appear to fuel *PRO* or PEUK, as was hypothesized. *PRO* and PEUK abundances were instead positively correlated with salinity ($r = 0.53$; $r = 0.44$, respectively). We noted that the growth rate of *PRO* was significantly greater within blooms; however, grazing was not quantified, so perhaps grazing was enhanced at these near-island stations as well. Highest concentrations of *TRICHO* were "trapped" in the region between New Caledonia and Vanuatu and adjacent to the islands of Fiji (Dupouy *et al.* 2000). Perhaps because the *TRICHO* blooms observed in this region of the SW Pacific were closer to islands than were the blooms previously reported in the North Pacific, *SYN* populations, rather than *PRO* and PEUK, were more tightly correlated with *TRICHO* blooms. Consequently, it is not clear if *SYN* enhancement is linked to *TRICHO* directly, or if other factors, such as the proximity to islands coasts where higher Fe (median 355 pmol L^{-1}) or fixed N concentrations may stimulate growth.

CONCLUSIONS

In summary, picoplankton were an important component of an extensive bloom of *TRICHO* centered between New Caledonia and Vanuatu in the SW Pacific. Although *PRO* and PEUK abundance did not increase significantly within the bloom compared to outside the bloom as was hypothesized, *SYN* abundance was elevated significantly. Larger unicellular cyanobacteria, possibly N_2-fixing *Crocosphaera* spp., were most abundant at stations where *TRICHO* was absent or present at very low abundances. MDS analysis based on oceanic community structure distinguished bloom *vs*. non-bloom locations with p*CROCO* present. Given that N_2 fixation may provide ~ 50% of new nitrogen to the oceanic ecosystem (Karl *et al* 1997), the role of N_2 fixation in the marine N cycle is larger than previously thought. The newly recognized organisms, such as the unicellular cyanobacteria p*CROCO* we report here, play a crucial role in the N cycle if they can thrive in oceanic phytoplankton communities where *TRICHO* is absent.

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