

ARE BENTHIC CYANOBACTERIA INDICATORS OF NUTRIENT ENRICHMENT? RELATIONSHIPS BETWEEN CYANOBACTERIAL ABUNDANCE AND ENVIRONMENTAL FACTORS ON THE REEF FLATS OF GUAM

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ABSTRACT

While benthic, filamentous cyanobacteria can be common on coral reefs, the factors influencing their distribution are poorly understood. Cyanobacterial blooms, like macroalgal blooms, may result from a combination of coastal eutrophication and reduced herbivory. Because benthic cyanobacteria are unpalatable to generalist herbivores, there may be little top-down control of cyanobacterial abundance. Since bottom-up factors may exert more influence on cyanobacterial populations, we hypothesized that high cyanobacterial abundance may be an indicator of high nutrient availability. In addition, cyanobacteria may compete with macroalgae for light and nutrients. Thus, we also hypothesized that cyanobacterial abundance may be negatively associated with macroalgal abundance. Since many strains of cyanobacteria wash ashore during periods of high wave action, we hypothesized that cyanobacterial abundance is negatively associated with wave height. We monitored cyanobacterial abundance, macroalgal abundance, nitrogen availability, phosphorus availability, salinity, and water temperature at nine reef flat locations around Guam. Average wave height for eastern and western shores, rainfall, minutes of sunshine, and wind speed were also monitored. Stepwise regression was used to determine which variable or combination of variables best explained variation in cyanobacterial abundance. Although nutrient availability was not significantly associated with cyanobacterial abundance, a positive association with macroalgal abundance explained 11.5% of the observed variation in total cyanobacterial abundance. At one site, negative relationships with macroalgal abundance and wave height explained 79.4% of the observed variation in the abundance of the cyanobacterium *Oscillatoria margaritifera*. Variation in cyanobacterial abundance can be best explained by examining individual strains of cyanobacteria, rather than by treating all cyanobacteria as a single ecological unit. Physical disturbance can be a more important influence on cyanobacterial abundance and distribution than either nutrient availability or interactions with macroalgae.

Most ecological studies of marine cyanobacteria have focused on planktonic forms (Kirk and Gilbert, 1992; Haney et al., 1995; Sellner, 1997), while benthic cyanobacteria have generally been grouped with turf or filamentous algae (Klumpp and McKinnon, 1992; Steneck and Dethier, 1994; Williams and Carpenter, 1997). Blooms of macroalgae are thought to result from a combination of nutrient enrichment associated with coastal eutrophication and decreased grazing by fishes and invertebrates due to overfishing and mass mortalities (Hughes, 1994; Littler and Littler, 1994; Lapointe, 1997). However, it is unclear whether cyanobacteria respond to these environmental factors in the same way as macroalgae (Fong and Zedler, 1993; Cowell and Botts, 1994). The nitrogen-fixing ability of some cyanobacteria may decrease their dependence on the availability of nitrogen in the water column (Larkum, 1988). Thus, nitrogen availability may not control the growth or abundance of some cyanobacteria (Cowell and Botts, 1994).

Cyanobacterial blooms are becoming more frequent around the island of Guam, and we often see mats of cyanobacteria covering thousands of square meters of reef flat and

washing up on shore (Limtiaco, 1994; Knuckles, 1995). These blooms can be single species or mixed-species assemblages, frequently containing *Oscillatoria* spp. and *Lyngbya* spp. These blooms can be unsightly for tourists and have been implicated in the death of juvenile siganids (rabbitfishes; Nagle et al., 1996). Secondary metabolites produced by benthic, marine cyanobacteria have also been cited in human poisonings (Carmichael et al., 1990; Nagai et al., 1996, 1997). To anticipate potentially harmful cyanobacterial blooms, we are studying top-down and bottom-up factors associated with spatial and temporal variation in cyanobacterial abundance. Chemical defenses render cyanobacteria highly unpalatable to generalist herbivores (Pennings et al., 1996, 1997; Thacker et al., 1997; Nagle and Paul, 1998). Caging experiments have shown that large, generalist herbivores play a limited role in determining cyanobacterial abundance (Thacker and Paul, unpublished data). However, some strains of cyanobacteria are the preferred foods of specialist sea hares (Nagle et al., 1998).

Since bottom-up factors may exert more influence on cyanobacterial populations than top-down factors, we hypothesized that (1) cyanobacterial abundance is positively associated with nutrient availability (Fong et al., 1993). In addition, cyanobacteria may compete with macroalgae for light and nutrients (Fong and Zedler, 1993). Thus, we also hypothesized that (2) cyanobacterial abundance is negatively associated with macroalgal abundance. Since many strains of cyanobacteria are fragile and do wash ashore during periods of high wave action, we hypothesized that (3) cyanobacterial abundance is highest when disturbance from wave action is lowest. We examined these three hypotheses by measuring cyanobacterial abundance and nine environmental variables at nine reef flat locations around Guam over 14 sampling periods. Associations among these variables and cyanobacterial abundance were examined using stepwise regression. Although previous studies of benthic, marine cyanobacteria have treated diverse assemblages as a single ecological unit (Klumpp and McKinnon, 1992; Williams and Carpenter, 1997), all strains of cyanobacteria may not show the same responses to environmental conditions. Thus, we also examined the associations between environmental variables and the dominant strain of cyanobacteria at one site.

METHODS

We monitored cyanobacterial abundance, macroalgal abundance, nitrogen availability (as nitrate and nitrite concentration), phosphorus availability (as ortho-phosphate concentration), salinity, and temperature at nine reef flat locations around Guam. Ammonium concentrations were not monitored regularly because a pilot study found that 70% of total nitrogen was represented by nitrate and nitrite, while only 8% was represented by ammonium, agreeing with previous reports of low ammonium concentrations around Guam (Matson, 1991). The nine locations were chosen to allow access in most weather conditions throughout the year and included Tanguisson Beach Park, Pago Bay, Togcha River, Cocos Lagoon, Fingers Reef, Piti Bombholes, and three sites in Tumon Bay: Sails, Pia, and Ypao Beach Park (Fig. 1). All sites were 0.5 to 2 m deep, depending on tidal height, with high light availability. We surveyed each site 14 times, approximately 6 wks apart.

We measured cyanobacterial and macroalgal abundance by sampling 0.5×0.5 m quadrats spaced 6 m apart along fixed transect lines. At the Tumon Bay and Tanguisson Beach Park sites, we sampled two 60 m transect lines, for a total of 20 quadrats. At the remaining sites, we sampled three 30 m transect lines, for a total of 15 quadrats. These sampling schemes were chosen to ensure an adequate representation of species diversity in each area. The quadrat was divided by strings into 100 cells, 5×5 cm each. We noted the presence or absence of each species in each cell of the quadrat

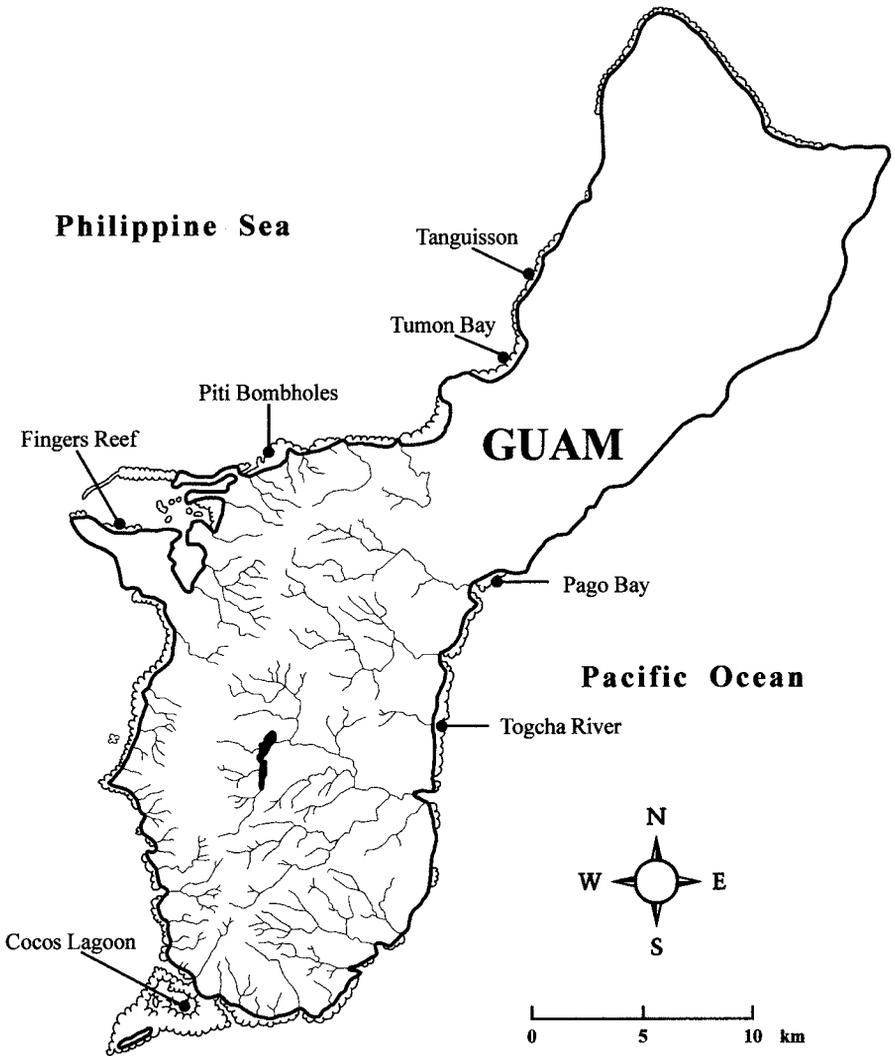


Figure 1. A map of Guam showing the nine sampling locations.

and scored the total as percent cover (Pennings and Callaway, 1996; Sutherland, 1996). The mean percent cover was then determined for each site. For this study, we summed the mean percent cover of all cyanobacterial species and all macroalgal species to estimate total cyanobacterial and macroalgal abundance at each site. Monthly total rainfall and monthly average minutes of sunshine, peak wind speed, and average wave height were obtained from a National Weather Service monitoring program.

Every 6 wks, we collected three replicate water samples 5 cm above the bottom from each study site. Nutrient analyses were contracted to the Guam Water and Environment Research Institute. Nitrate and nitrite were measured together in Jones's (1984) modification of the cadmium reduction method described in Parsons et al. (1984). Standards were run at 0, 7.14, 17.9 and 35.7 μM . A second source control (a control from a separate stock solution) was run at 3.57 μM . Ortho (reac-

Table 1. Correlation of environmental variables with cyanobacterial abundance at nine locations around Guam. n = 126. Bonferroni alpha = 0.006.

Variable	r	r ²	P
Phosphorus	0.034	0.001	0.706
Nitrogen	-0.196	0.038	0.028
Salinity	0.102	0.010	0.254
Water temperature	-0.029	0.001	0.748
Rainfall	-0.142	0.002	0.113
Minutes of sunshine	0.032	0.001	0.723
Peak wind speed	-0.042	0.002	0.640
Average wave height	0.007	<0.001	0.940
Macroalgal abundance	0.339	0.115	<0.001

tive) phosphate was measured by the method described in Parsons et al. (1984). Standards were run at 0, 1.61 and 3.23 μM , while a second source control was run at 0.81 μM . When water samples were collected, we also measured salinity and temperature using a Water Checker U-10 (Horiba Instruments, Irvine, California).

Pearson correlation coefficients were used to determine the relationships between the nine environmental variables and cyanobacterial abundance. Macroalgal abundance and cyanobacterial abundance were square-root transformed ($y = (x + 0.5)^{1/2}$) to meet the assumptions of normality (Sokal and Rohlf, 1995). Since many of the variables may be correlated with one another, stepwise regression (Wilkinson et al., 1992; Sokal and Rohlf, 1995) was used to determine which variable or combination of variables best explained the variation observed in cyanobacterial abundance. P-to-enter and P-to-leave the model were set at 0.05. Both forward and backward selection procedures were used to find the best model.

At the Togcha River reef flat, we studied a strain of *Oscillatoria margaritifera* in more detail. *O. margaritifera* was present at this site throughout this study, although it was not always present inside the sampling quadrats. Each week, we sampled the percent cover of *O. margaritifera*, other cyanobacteria, and macroalgae. Inorganic nitrogen availability, phosphorus availability, and salinity were measured every 6 wks, as described earlier. Water temperature was measured by a submerged StowAway Tidbit temperature logger (Onset Computer Corporation, Bourne, Massachusetts) located at a depth of 2 m in one transect. For these analyses, we noted the maximum temperature recorded on the day prior to the quadrat sampling. Rainfall, minutes of sunshine, peak wind speed, and wave height were obtained from a National Weather Service monitoring program. Rainfall and minutes of sunshine were summed for the 3 d prior to sampling, while peak wind speed and wave height were averaged for the 3 d prior to sampling. Pearson correlation coefficients were used to determine the relationships between the nine environmental variables and the abundance of *O. margaritifera* (Sokal and Rohlf, 1995). Stepwise regression (Wilkinson et al., 1992) was used to determine which variable or combination of variables best explained the variation observed in the abundance of *O. margaritifera*, with P-to-enter and P-to-leave the model set at 0.05. Both forward and backward selection procedures were used to find the best model.

RESULTS

Cyanobacteria present at our study sites included *Oscillatoria* spp., *Lyngbya* spp., *Symploca* spp., and *Tolypothrix* sp. Our data revealed no relationship between phosphorus availability or nitrogen availability and cyanobacterial abundance (Table 1, Fig. 2A,B). Macroalgal abundance was positively associated with cyanobacterial abundance (Table 1, Fig. 2C). Only the positive association with macroalgal abundance significantly contributed to the stepwise regression model, which explained 11.5% of the variation in

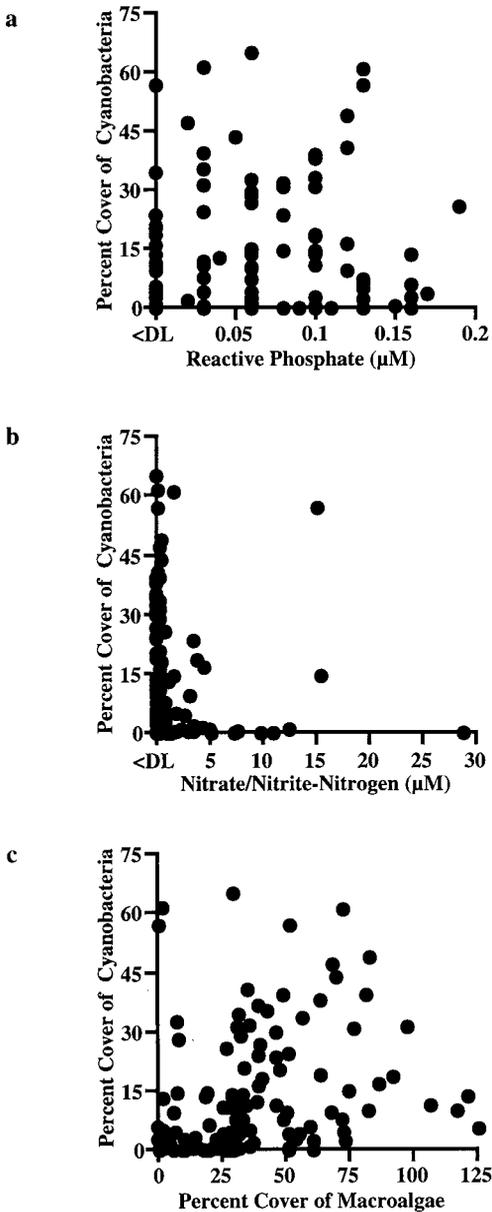


Figure 2. Associations between cyanobacterial abundance and (a) phosphorus availability (reactive phosphate), (b) nitrogen availability (nitrate and nitrite nitrogen), and (c) macroalgal abundance. Correlation coefficients and significance values are presented in Table 1.

cyanobacterial abundance ($n = 126$, $r^2 = 0.115$, $P < 0.001$, Table 2). Once macroalgal abundance was in the model, the partial correlations of the remaining variables were not significant (Table 2). Forward and backward selection procedures yielded the same model.

Although *O. margaritifera* was consistently present at the Togcha River reef flat, its abundance varied greatly and showed a general decline over time (Fig. 3). This

cyanobacterial strain spread over soft and hard substrates, and overgrew coral rubble, live coral, and macroalgae. Several environmental variables were significantly correlated with the abundance of *O. margaritifera*, including average wave height, water temperature, and macroalgal abundance (Table 3). A combination of negative relationships with wave height and macroalgal abundance significantly contributed to the stepwise regression model, which explained 79.4% of the observed variation in the abundance of *O. margaritifera* ($n = 25$, $r^2 = 0.794$, $P < 0.001$; Fig. 4, Table 4). Once these two variables were in the model, the partial correlations of the remaining variables were not significant (Table 4). Forward and backward selection procedures yielded the same model.

Table 2. Stepwise regression model and partial correlations for environmental variables associated with total cyanobacterial abundance.

Variables entered into stepwise regression model			
Variable	Coefficient	F	P
Constant	1.643	14.336	<0.001
Macroalgal abundance	0.281	16.142	<0.001
Variables excluded from stepwise regression model			
Variable	Partial Correlation	F	P
Phosphorus	-0.037	0.169	0.682
Nitrogen	-0.105	1.364	0.245
Salinity	0.012	0.017	0.895
Water temperature	0.019	0.044	0.835
Rainfall	-0.124	1.906	0.170
Minutes of sunshine	-0.027	0.091	0.763
Peak wind speed	-0.092	1.042	0.310
Average wave height	-0.076	0.710	0.401

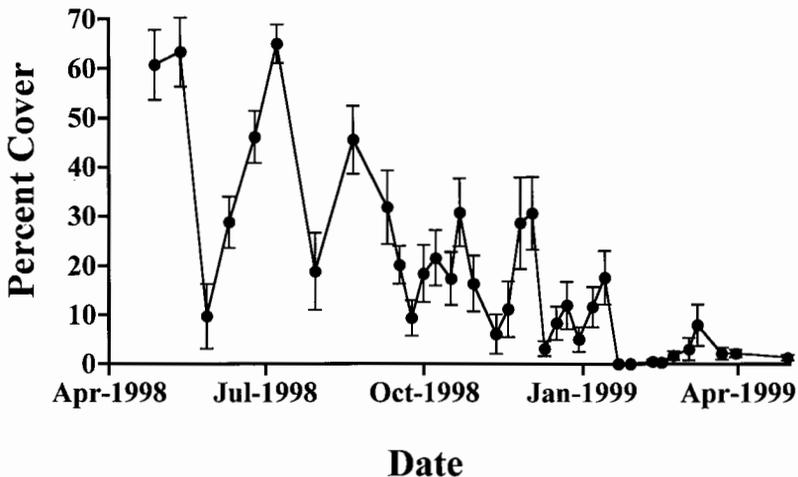


Figure 3. Variability in the abundance of *Oscillatoria margaritifera* at the Togcha River reef flat between April, 1998 and April, 1999.

Table 3. Correlation of environmental variables with the abundance of *Oscillatoria margaritifera* at the Togcha River reef flat. Bonferroni alpha = 0.006.

Variable	n	r	r ²	P
Phosphorus	8	-0.356	0.126	0.387
Nitrogen	8	0.405	0.164	0.320
Salinity	8	-0.188	0.035	0.655
Water temperature	36	0.605	0.366	0.001
Rainfall	36	-0.027	0.001	0.875
Minutes of sunshine	36	0.204	0.042	0.232
Peak wind speed	36	-0.362	0.131	0.030
Average wave height	36	-0.575	0.330	<0.001
Total macroalgae	25	-0.764	0.584	<0.001

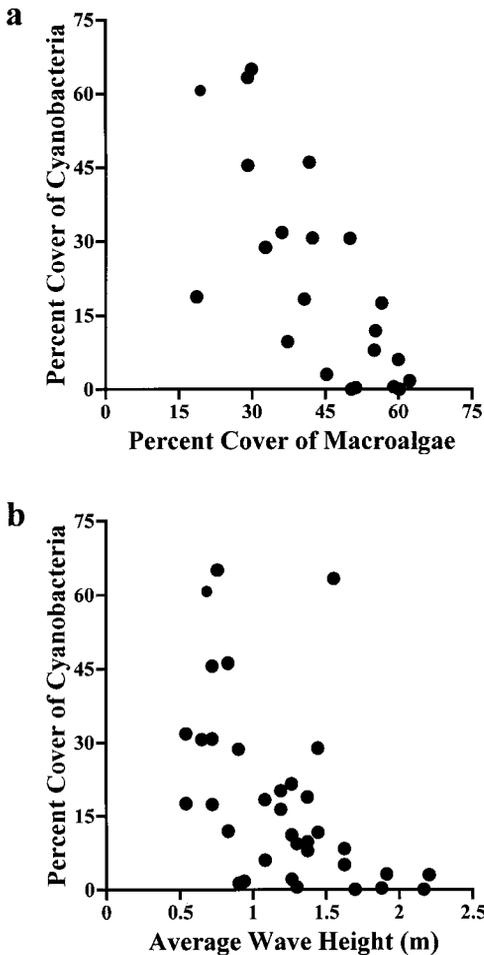


Figure 4. Associations between the abundance of *Oscillatoria margaritifera* and (a) macroalgal abundance and (b) average wave height at the Togcha River reef flat. Correlation coefficients and significance values are presented in Table 3.

Table 4. Stepwise regression model and partial correlations for environmental variables associated with the abundance of *Oscillatoria margaritifera* at the Togcha River reef flat.

Variables entered into stepwise regression model			
Variable	Coefficient	F	P
Constant	17.328	121.000	<0.001
Average wave height	-0.866	22.446	<0.001
Macroalgal abundance	-1.586	52.282	<0.001
Variables excluded from stepwise regression model			
Variable	Partial Correlation	F	P
Phosphorus	0.072	0.062	0.807
Nitrogen	0.192	0.458	0.511
Salinity	-0.225	0.642	0.439
Water temperature	-0.359	1.927	0.188
Rainfall	-0.185	0.460	0.510
Minutes of sunshine	-0.008	0.001	0.976
Peak wind speed	0.032	0.013	0.911

DISCUSSION

Contrary to our first hypothesis, when we examined all cyanobacterial taxa, we found no significant relationships between nitrogen and phosphorus availability and cyanobacterial abundance. The concentrations of both nutrients sometimes exceeded the thresholds that may sustain macroalgal blooms on Caribbean reefs (approx. 1.0 μM nitrogen and 0.1 μM phosphorus; Lapointe, 1997). A negative trend between inorganic nitrogen availability and cyanobacterial abundance may be related to the measurements of higher inorganic nitrogen in low salinity areas. Since Guam's freshwater aquifer contains high nitrate concentrations (Matson, 1991, 1993), freshwater seeps located on reef flats may provide both high inorganic nitrogen and low salinity habitats. In addition, the nitrogen-fixation abilities of some cyanobacteria may remove their dependence on water-column nitrogen (Larkum, 1988). The common genera of cyanobacteria in our surveys included *Tolypothrix*, which contains heterocysts and can fix nitrogen, and *Oscillatoria* and *Lynghya*, both of which lack heterocysts but can also fix nitrogen (Paerl, 1990). Cowell and Botts (1994) found that the biomass of the nitrogen-fixing, freshwater cyanobacterium *Lynghya wollei* was negatively associated with alkalinity, conductivity, and ammonium concentrations, but positively associated with phosphate concentrations. We found no significant relationships with phosphate concentrations in our study, possibly because phosphate concentrations were low at all sites.

We also rejected our second hypothesis, since we found a strong, positive association between macroalgal abundance and total cyanobacterial abundance. The same factors that favor macroalgal growth may favor most cyanobacteria, indicating that these two taxonomic groups may respond to environmental conditions in the same way on tropical reefs. Studies in a freshwater estuary (Cowell and Botts, 1994) and a temperate marine lagoon (Fong and Zedler, 1993) found negative relationships between macroalgae and cyanobacteria, arguing that competition among these groups would be a major force in structuring their communities. Although many cyanobacteria can be epiphytes on macroalgae, the positive relationship that we found indicates that these two groups may

not necessarily compete with each other. Instead, cyanobacteria could facilitate the growth of macroalgae, through nitrogen fixation or associational defenses from herbivory (Pennings, 1997). However, macroalgal abundance explained only 11.5% of the variation in cyanobacterial abundance, indicating that other variables may be more important in determining the abundance and distribution of cyanobacteria, or that different strains of cyanobacteria respond to these variables in different ways.

When we examined the abundance of a single cyanobacterium, *O. margaritifera*, we found no significant associations with nutrient availability, again rejecting our first hypothesis. Since *O. margaritifera* was less abundant when there was greater macroalgal abundance, this cyanobacterium may compete with macroalgae, supporting our second hypothesis, and conflicting with our conclusions based on the abundance of all cyanobacterial species at all nine sites. However, since we made direct observations of *O. margaritifera* overgrowing several species of macroalgae, this association is not surprising. Wave height was also negatively associated with the abundance of *O. margaritifera*, indicating the importance of disturbance to the persistence of this cyanobacterial population and supporting our third hypothesis. Our best model for this single strain explained much more of the variation in abundance (79.4%) than the model for all strains (11.5%), which provides additional evidence that all cyanobacteria are not alike in their responses to environmental variables. For example, all cyanobacteria do not form the sprawling mats that are typical of *O. margaritifera*. Species that form more upright or ball-shaped colonies did not overgrow other substrates as extensively as *O. margaritifera*.

Although we found no relationships between cyanobacterial abundance and nutrient availability, measurements of nutrient availability were infrequent at each site. We may be unable to measure the possibly more important pulses of nutrient input from streams and shore run-off, e.g., after rainfall (Carpenter et al., 1998; Denton et al., 1998; Schaffelke and Klumpp, 1998). For example, the Togcha River reef flat is located near a river mouth that can have high levels of nitrate and phosphate due to a sewage outfall upstream (Guam Environmental Protection Agency, unpubl. data). These nutrients may be diluted before reaching our study site or occur in pulses that our sampling scheme was not able to detect. In addition, nutrient concentrations in sediment porewater may be more important than water column concentrations at our study sites (Larned, 1998). The use of biological indicators, such as tissue nutrient content (Frankovich and Fourqurean, 1997) and stable isotope concentrations in macroalgae and seagrasses (Mendes et al., 1997), may aid in determining the relative availability of nutrients among our sites.

In our future work, we will address the correlations we have found with manipulative experiments in laboratory aquaria and in the field (Thacker et al., in press). By examining both nitrogen-fixing and non-nitrogen-fixing strains of cyanobacteria, we may be able to determine which of these strains have positive or negative associations with macroalgae. In addition, studies of individual strains are needed to determine the different types of responses (including changing growth forms) that cyanobacteria may have to seasonal environmental conditions.

In contrast to our expectations, cyanobacteria are not necessarily associated with high nutrient availability and may not compete with macroalgae. The nitrogen fixation capabilities of some cyanobacteria may increase their abundance in low nutrient habitats. Both nitrogen fixation and associational defenses may create facilitative interactions with macroalgae. Although confirmed by only one site in this study, physical disturbance may be a more important influence on cyanobacterial populations than either nutrient avail-

ability or interactions with macroalgae. By combining a monitoring program with manipulative experiments, we hope to learn more about the factors influencing the distribution of cyanobacteria and to enhance our ability to anticipate harmful blooms.

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