REPORT

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Effects of monsoon-driven wave action on coral reefs of Guam and implications for coral recruitment

Abstract Benthic cyanobacteria can respond rapidly to favorable environmental conditions, overgrow a variety of reef organisms, and dominate benthic marine communities; however, little is known about the dynamics and consequences of such cyanobacterial blooms in coral reef ecosystems. In this study, the benthic community was quantified at the time of coral spawnings in Guam to assess the substrate that coral larvae would encounter when attempting settlement. Transects at 9, 18, and 25-m depths were surveyed at two reef sites before and after heavy wave action driven by westerly monsoon winds. Communities differed significantly between sites and depths, but major changes in benthic community structure were associated with wave action driven by monsoon winds. A shift from cyanobacteria to crustose coralline algae (CCA) accounted for 44% of this change. Coral recruitment on Guam may be limited by substrate availability if cyanobacteria cover large areas of the reef at the time of settlement, and consequently recruitment may in part depend upon wave action from annual monsoon winds and tropical storms which remove cyanobacteria, thereby exposing underlying CCA and other substrate suitable for coral settlement.

Keywords Community structure dynamics ·
Coral recruitment · Crustose coralline algae ·
Cyanobacteria · Pacific Ocean reefs · Storm effects

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Introduction

With coral reefs degrading worldwide (Gardner et al. 2003; Hughes et al. 2003; Pandolfi et al. 2003), much attention has been focused on phase shifts from coral- to algal-dominated communities (Hughes 1994; Shulman and Robertson 1996; McClanahan and Muthiga 1998; McCook 1999; McCook et al. 2001). As coral communities are disturbed with increasing frequency, some populations appear to be unable to recover leaving benthic communities that are increasingly algal dominated (Brown 1997; Nystrom et al. 2000). Intense grazing and low nutrient levels are critical in maintaining coral-dominated communities (Littler and Littler 1984; Birkeland 1988), and there are abundant data and much debate over the relative importance of herbivory and eutrophication in structuring benthic algal communities and causing phase shifts (Hay 1984; Lessios 1988; Lapointe 1997, 1999; McCook 1999; Aronson and Precht 2000; Thacker et al. 2001). Yet, the role of other potentially important factors, such as substrate availability, interspecific competition, and wave action, in structuring algal communities have received less attention (Shulman and Robertson 1996; Aronson and Precht 1997; Blanchon and Perry 2004). Wave action can have significant effects on coral reef community structure (Rosen 1975; Adey and Burke 1977; Dollar 1982; Dollar and Tribble 1993; Cheroske et al. 2000) affecting not only species composition, but also the morphology of sessile organisms (Hay 1981; Palumbi 1984; Palumbi 1986). Wave action can also drastically alter benthic algal communities by either enhancing algal growth by bringing in nutrient-rich water and removing waste (Kingsbury 1962) or reducing cyanobacteria and macroalgal abundances by the mechanical effects of waves on the algal community and substrate (FitzGerald 1978; Dudgeon and Johnson 1992; Cheroske et al. 2000).

It is widely assumed that algae can outcompete corals under high nutrient and low herbivory conditions, although competitive outcomes may vary depending on

algal groups (Miller and Hay 1996; Miller and Hay 1998; Lirman 2001; McCook 2001). Cyanobacteria can be extremely abundant on coral reefs (Thacker and Paul 2001; Thacker et al. 2001), forming dense mats that may have negative consequences for the covered organisms due to possible anoxia and allelopathic effects of the abundant natural products produced by cyanobacteria (Nagle and Paul 1999; Paul et al. 2001). Benthic algae and cyanobacteria can also negatively affect coral recruitment and juvenile survivorship (Miller et al. 2000; Kuffner and Paul 2004), critical steps in maintaining diverse, coral-dominated communities. If blooms of macroalgae, turf algae, or cyanobacteria dominate the benthos, coral larvae may not find appropriate space to settle or may be overgrown by the algae if they do find a place to settle (Birkeland 1977; Hughes 1989). On the other hand, larvae from *Acropora*, *Agaricia*, and other genera of corals have been shown to metamorphose in response to chemical cues found in certain species of crustose coralline algae (CCA) (Morse and Morse 1996; Morse et al. 1996; Heyward and Negri 1999; Harrington et al. 2004). Thus, reef areas with high CCA cover and low cover of other algae may facilitate coral recruitment if larvae are present. Conversely, the presence of cyanobacteria may inhibit the recruitment of coral larvae even when suitable substrate, including CCA, is available (Kuffner and Paul 2004).

In this study, we examined the benthic community across three depths on two reef slopes on Guam to determine the benthic composition of coral reefs during the time that larvae generated from the summer mass coral spawning events would be recruiting. The occurrence of strong westerly monsoon winds between sampling periods allowed us to examine how wave action driven by these annual events can affect benthic communities and thus, potentially coral recruitment. We hypothesized that cyanobacteria would dominate the noncoral substrate in the absence of recent strong monsoon winds and that the wave action generated by those winds would reduce cyanobacterial cover exposing underlying organisms. We expected any changes in the benthic community would be less pronounced with depth.

Methods

Two reefs on Guam's leeward western coastline were selected for this study. Gun Beach is a Marine Protected Area located along the karst, river-free northern coastline and is characterized by relatively low macroalgal and high coral cover and richness. Fouha Bay is located along the southern coastline just outside of an embayment into which drains a flood stream from a small watershed and is characterized by high levels of nutrients and sediments (Wolanski et al. 2003). Because of their sheltered exposure on the island from the dominant trade winds, these sites remain free from wave action throughout most of the year except for brief periods during the passage of tropical storms and during monsoon events, i.e., seasonal reversal in wind direction (Asami et al. 2004). Both events may bring strong southwest winds that generate a substantial westerly swell.

Five replicate 10-m line transects along the 9, 18, and 25-m depth contours were permanently established at each site. The ends of each transect were marked with masonry nails so that transect tapes could be placed across the same area when reefs were resurveyed. Some nails marking transects at 9-m depth at Fouha Bay could not be located when sampling the second time, so new transects were placed across the same reef area at the same depth. The benthic composition was recorded every 25 cm along each transect in the categories: coral, crustose coralline algae (CCA), cyanobacteria, macroalgae (algae >1 cm height), rock, sand, sponge, and turf algae (algae <1 cm height). All biota were recorded to the lowest taxonomic unit possible; however, categories were kept for the analyses and data presentation because they represent ecologically distinct and relevant groups allowing us to examine overall changes in benthic community structure. Gun Beach was first sampled on June 24, 2001 and again on July 20, 2001; Fouha was first sampled on June 30, 2001 and again on August 22, 2001. Mass coral spawning events occurred between June 11–15th and July 10–14th, 2001 and included *Acropora* spp., *Montipora* spp., *Porites* spp., *Favia* spp., *Goniastrea* spp., and *Platygyra* spp. among others.

A variety of multivariate methods available in the PRIMER software (Clarke and Warwick 2001) were used to analyze differences in the benthic communities as a function of site (Gun Beach and Fouha Bay), depth (9, 18, and 25 m), and time (before and after the wind-driven wave action). Log-transformed cover data were used to calculate Bray–Curtis similarity, and analysis of similarities (ANOSIM) was used to test for differences in community structure across sites, depths, and time. ANOSIM calculates a global R statistic that reflects the differences in variability between groups as compared to within groups (so R values are proportional to differences between the groups) and checks for the significance of R using permutation tests (Clarke and Warwick 2001). Given the differences in community composition between Gun Beach and Fouha Bay and the non-availability of a three-way ANOSIM in the PRIMER software, data were analyzed by a two-way ANOSIM with depth and time for each location. Nonmetric multidimensional scaling (MDS) was also used to further analyze our communities. Based on a similarity matrix, MDS generates plots in which the distance between points is proportional to their degree of similarity; so closer points are more similar than points farther away (Clarke and Warwick 2001). An exploratory similarity breakdown using the SIMPER procedure available in the PRIMER software was used to quantify the relative contribution of each of the eight categories to dissimilarities in community

structure (Clarke and Warwick 2001). Additionally, a two-way repeated measures analysis of variance (ANOVAR) was used to check for differences in cyanobacterial cover (after rank transformation) with site, depth, and time as factors.

Data on wind speed and direction for westerly winds affecting Guam between 1962 and 1994 were acquired from the Water and Environmental Research Institute (WERI) in Guam. These data were used to quantify the number of days each month of every year with strong westerly winds (winds blowing at least 20 knots). Winds of this speed generate swells of approximately 3 m that affect the western coast of Guam, including the two localities investigated in our study. During our study period, strong westerly winds occurred on July 3, 8–11, 14–15 (National Weather Service, average maximum and peak speeds of 17 and 22 knots) and on August 3–4 and 13–18 (WERI, average maximum and peak speeds of 21 and 42 knots). The WERI also noted large westerly swell on August 16–19; up to 4 m swell inside Fouha Bay as quantified by Wolanski et al. (2003).

Results

Benthic communities on Guam differed significantly between sites both before (one-way ANOSIM, global $r = 0.552$, $P = 0.001$) and after (global $r = 0.531$, $P = 0.001$) wave action from wind events (see Fig. 1 for percent cover of each benthic category). At both sites, communities differed significantly as a function of time and depth (two-way ANOSIM, Gun beach: time: global $r = 0.636$, $P = 0.001$, depth: $r = 0.627$, $P = 0.001$, Fig. 2a; Fouha Bay: time: global $r = 0.953$, $P = 0.001$, depth: $r = 0.511$, $P = 0.001$, Fig. 2b). Cyanobacteria and crustose coralline algae (CCA) contributed the most to the overall community dissimilarities before and after the monsoon winds (SIMPER analysis, Table 1). At each site, the combined contributions of these benthic categories were greatest at 9 and least at 25 m (see relative contributions of cyanobacteria and CCA in Table 1). At Gun Beach, the community at 9 m was significantly different from those at 18 and 25 m (pairwise test comparisons, $P = 0.001$ for any pair comparison), which
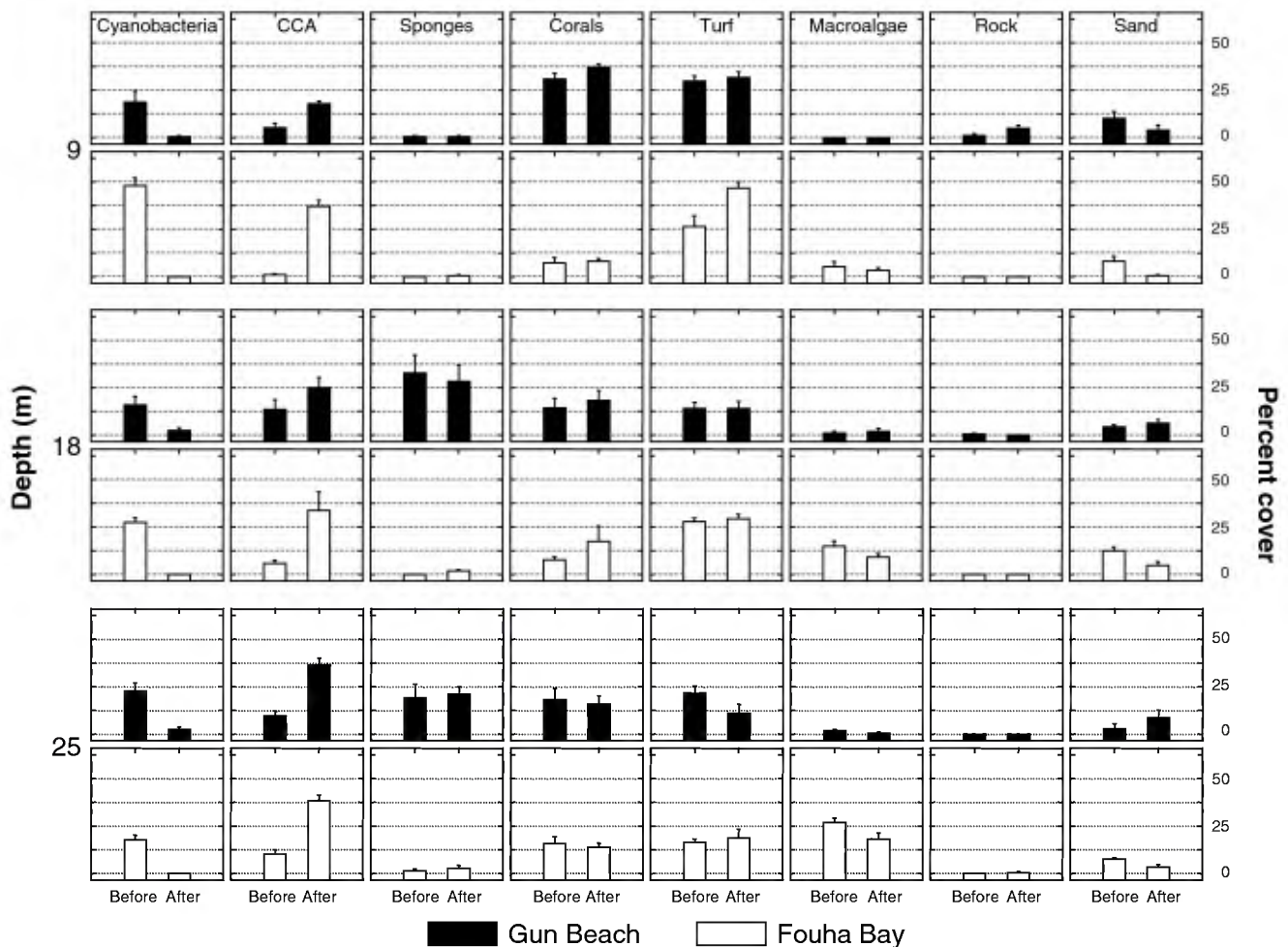

Fig. 1 Percentage cover (mean ± SE) of cyanobacteria, crustose coralline algae (CCA), sponges, hard corals, algal turf, macroalgae, rock, and sand found at Gun beach (*black bars*) and Fouha Bay (*white bars*) at 9, 18, and 25-m depth before and after wind-driven wave action
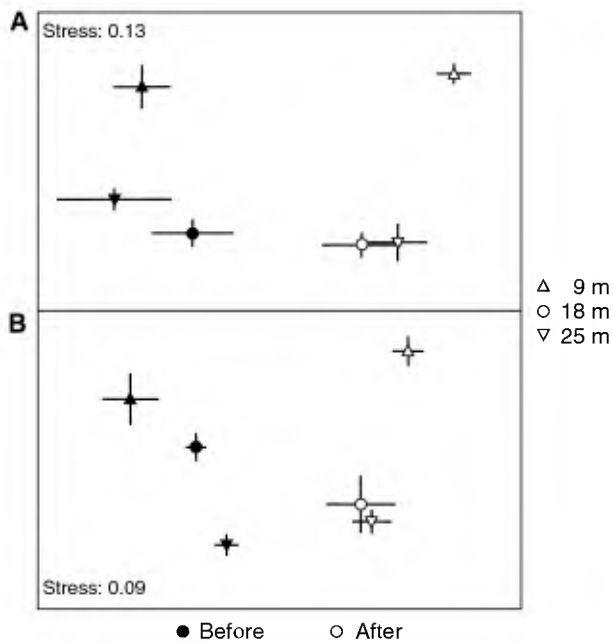
Fig. 2 Non-metric multidimensional scaling (MDS) performed separately for Gun Beach (**a**) and Fouha Bay (**b**) for the transects at 9 (*filled triangle*), 18 (*filled circle*), and 25 m (*filled inverted triangle*) sampled before (*black*) and after (*white*) strong westerly winds. MDS based on Bray–Curtis similarities from log-transformed abundances of the eight benthic categories used in our study. See text for more details

Table 2 Univariate repeated measures analysis of variance (ANOVAR) of cyanobacteria abundance before and after wind-driven wave action as a function of site and depth

| Source	SS	df	MS	F	P
Between subjects					
Site	2.400	1	2.400	0.057	0.813
Depth	29.025	2	14.512	0.347	0.710
Site × depth	432.325	2	216.162	5.165	0.014
Error	1,004.500	24	41.854		
Within subjects					
Time	13,470.017	1	13,470.017	429.666	< 0.001
Time × site	828.817	1	828.817	26.438	< 0.001
Time × depth	297.158	2	148.579	4.739	0.018
Time × site × depth	140.858	2	70.429	2.247	0.128
Error	752.400	24	31.350		

Westerly monsoon winds have a clear seasonal pattern and occurred most commonly during the months of July, August, September, and October from 1962–1994, these months also have the highest mean number of days per month with strong westerly winds (Fig. 3).

Discussion

Monsoon-driven wave action structures coral reef benthic communities on Guam. Irrespective of initial differences in community structure associated with sites and depths, wave action removed cyanobacterial cover off reefs up to a depth of 25 m, exposing the underlying substrate, which includes crustose coralline algae (CCA) and other substrates suitable for coral settlement. On Guam, monsoon winds have a strong seasonal pattern and occur most frequently during August and September, after the mass coral spawning events, which are usually in June and July (Richmond and Hunter 1990). The implications for coral recruitment loom large as blooms of cyanobacteria, mainly *Oscillatoria* spp. as found in this study, tend to proliferate during these months in Guam (Palmer 2003), especially on reef slopes.

Benthic cyanobacteria have generally been grouped with turf or filamentous algae in ecological studies (e.g., Steneck and Dethier 1994; Cheroske et al. 2000), but our current knowledge suggests that they may warrant separate consideration. Benthic cyanobacteria are quick

were not statistically different from each other ($P = 0.361$, Fig. 2a). At Fouha Bay, the communities at 9, 18, and 25 m were significantly different from each other (pairwise test comparisons, $P = 0.001$ for any pair comparison).

Despite differences in community structure between sites and across depths, a one-way ANOSIM with all data from Fouha Bay and Gun Beach together showed that communities differ significantly before and after the wind-driven wave action (global $r = 0.591$, $P = 0.001$). Decreases in cyanobacterial cover and increases in CCA cover contributed the most (SIMPER analysis, combined contribution of cyanobacteria and CCA 44.33%) to these changes. Further analysis showed cyanobacterial cover varied significantly as a function of time across sites and depths (ANOVAR significant interaction terms, Table 2).

Table 1 Average dissimilarity between the communities before and after the wind-driven wave action at Gun Beach and Fouha Bay at 9, 18, and 25-m depth and relative contribution of each benthic category to community dissimilarities

Depth	Site	Dissimilarity	Relative contribution							
			Cyanobacteria	CCA	Sponges	Corals	Turf	Macroalgae	Rock	Sand
9 m	Gun Beach	29.47	33.64	20.39	3.85	3.79	3.51	0.00	15.65	19.17
	Fouha Bay	49.84	34.72	28.90	1.53	6.23	6.66	7.58	0.00	14.39
18 m	Gun Beach	21.00	30.08	16.13	10.27	10.06	10.62	10.38	2.87	9.60
	Fouha Bay	32.54	36.51	23.84	8.09	9.71	2.26	7.05	0.00	12.54
25 m	Gun Beach	30.12	26.49	19.28	9.72	8.22	12.27	7.27	0.00	16.75
	Fouha Bay	25.93	36.19	21.24	10.02	6.22	5.52	7.07	2.24	11.51

Fig. 3 Number of years with at least 1 day of westerly winds over 20 knots (from a time series of 33 years). *Numbers* inside the bars represent the average number of days with winds over 20 knots for each month. *Asterisks* indicate months when mass coral spawnings occur on Guam (beginning ~5 days after the full moon)
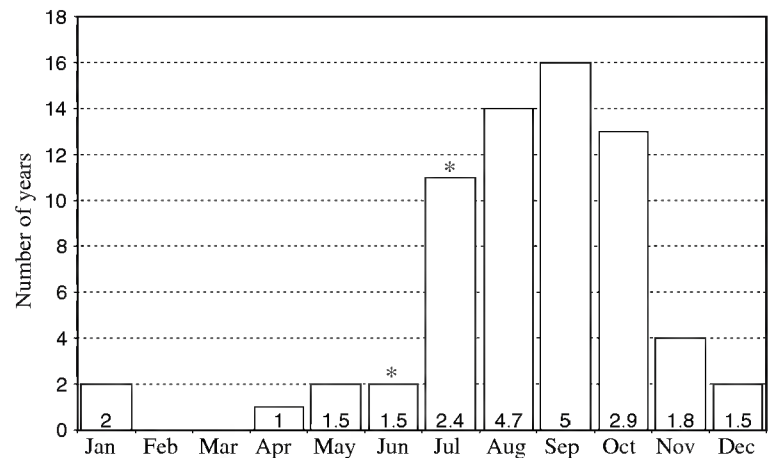
colonizers that are able to fix nitrogen and respond to phosphorous enrichment (Kuffner and Paul 2001; Elmetri and Bell 2004), are unpalatable to a variety of herbivores (Pennings et al. 1997; Thacker et al. 1997; Nagle and Paul 1999), and can bloom rapidly forming mats of fine filaments that overgrow and quickly dominate benthic communities (Cowell and Botts 1994; Doyle and Smart 1998; Thacker et al. 2001). Cyanobacteria can also inhibit coral recruitment even when appropriate substrate is available (Kuffner and Paul 2004). Cyanobacterial blooms are prevalent on Guam's reefs (up to 51% cover in our study) and proliferate over multiple substrates including CCA. Cyanobacteria cover much of the benthos of both reef flats and forereefs during the time when many important reef-building corals such as *Acropora* spawn and potentially recruit back to Guam.

Coral recruitment is dependent upon the availability of suitable substrate onto which coral larvae can settle and metamorphose (Richmond 1988). While CCA may facilitate the recruitment of some corals (Morse and Morse 1996; Morse et al. 1996; Heyward and Negri 1999) and are a significant benthic component on Guam's coral reefs, cyanobacteria may cover CCA or inhibit coral settlement even when appropriate substrate is available (Kuffner and Paul 2004). Our study illustrates that substrate conditions at the time that coral larvae are recruiting can vary widely depending on recent wave action. The more favorable substrate conditions (highest CCA cover and lowest cyanobacterial and macroalgal cover) were found after the occurrence of strong monsoon winds that generated heavy wave action. Thus, coral recruitment on Guam might be partially dependent upon the passing of early tropical storms (May–July) and monsoonal conditions to expose appropriate substrate at the time coral larvae may be present and ready to settle.

The timing of monsoon winds suggests that larvae from corals that spawn later in the summer and/or have longer larval competency periods may have a better chance of finding substrate suitable for settlement on reefs on the western side of Guam. Likewise, larvae from

corals that reproduce multiple times throughout the year, as many brooding corals do, may also have a better chance of finding suitable substrate to settle on. Recruitment shows high levels of spatiotemporal variation in many species including corals (Caley et al. 1996; Glassom et al. 2004; Sale et al. 2005), and stochastic processes may be important for coral larval recruitment and coral reef community development (Palmer et al. 1996; Sale 2004; Sandin and Pacala 2005). For example, recruitment patterns might differ depending on the actual conditions at the time of recruitment, which might in turn be affected by El Nino/Southern Oscillation (ENSO) events or variations in the monsoon system. Monsoon and storm events can also resuspend sediments (Wolanski et al. 2003), which may stress corals by smothering them and limiting the light and oxygen they receive. In Fouha Bay, these swell events resuspended and helped flush sediments trapped inside the bay (Wolanski et al. 2003) and removed algae/cyanobacteria from the forereef (our study). Clearly, more research is necessary to understand the dynamics of coral reefs, but given the worldwide favorable conditions for algal and cyanobacterial growth on coral reefs due to shifts in bottom-up and top-down forces over the last decades (increasing nutrient levels, declining herbivory, climate change), wave action might play a major role in controlling algal communities on coral reefs by reducing competition with established coral colonies and exposing substratum that is favorable for settlement of coral larvae.

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