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Dynamics of seagrass and macroalgal assemblages in Saipan Lagoon, Western Pacific Ocean: disturbances, pollution, and seasonal cycles

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Abstract

Despite a wealth of laboratory experiments describing seagrass growth and competitive interactions with macroalgae under varying nutrient concentrations, there is limited information available from field studies conducted in complex natural environments. We examined ecological change over time in the Saipan Lagoon, Western Pacific Ocean. Here, seagrass (*Halodule uninervis*) canopy cover was quantified monthly at relatively small spatial scales over a 3-year period. Where watershed size and human population were low, there was a significant relationship with seasonal environmental cycles; cooler temperatures correlated with increased drift, red algal abundance and freshwater input increased green algae. Following cyclical macroalgal overgrowth, however, seagrass again became the dominant canopy. Conversely, in the presence of high human population and urbanization, seasonal cycles were absent and a seagrass-to-macroalgal transition was evident. Adjacent to a large watershed with moderate pollution, significant ties were found between seagrass emergence and winter-time disturbance events (large swells), as detached macroalgae that formed during summer months were removed annually. In summary, seagrass systems associated with Saipan Lagoon appear to be hierarchically controlled, following: 1) disturbances, 2) land-based pollution, and 3) seasonal environmental cycles.

Keywords: disturbance; dynamics; *Halodule uninervis*; pollution; seagrass.

Introduction

Seagrass beds throughout tropical lagoons in the Pacific cover much smaller areas than their continental shelf counterparts where much of the existing research has been conducted. In both systems, the meadows have functional roles in nutrient filtration (Stapel et al. 1996, Udy and Dennison 1997, Terrados and Duarte 2000) and provision of habitat that enhances harvestable fish and invertebrate resources (Heck et al. 2003, Dorenbosch et al. 2005). Further, many Pacific island communities have a disproportional, high social reliance upon their relatively small seagrass systems (Johannes 1978). Accordingly, improvements in understanding the processes driving the dynamics of seagrass assemblages are desirable as increased watershed pollution continues to be strongly related to reductions in seagrass diversity (species and genotypic, Duffy 2006), abundance, and biomass (Davis and Fourqurean 2001, Daby 2003, Burkholder et al. 2007), threatening the resources that depend upon them (Mumby et al. 2005, Nakamura and Sano 2005, Verweij et al. 2008).

Physiologically, it is becoming clear that seagrass growth can be directly reduced by nitrogen enrichment as cellular assimilation occurs faster than processing, altering metabolic balances (Burkholder et al. 1992, 1994, Touchette and Burkholder 2001). However, the individualistic, halted growth response of seagrass to increased nitrogen loading does not account for the rapid seagrass-to-macroalgal transitions that have been reported (Robblee et al. 1991, Short and Burdick 1996, Cardoso et al. 2004). Clearly, as ecological complexity increases (defined as the number of interacting species) our ability to predict a generalized change over time decreases (Armitage et al. 2005). Seasonal cycles, driven mainly by freshwater input and temperature (Biber and Irlandi 2006, Lirman et al. 2008) confound straight forward relationships with proxy indicators of pollution (e.g., *Enterococcus* bacterial densities) that might otherwise be extrapolated from the wealth of manipulative experiments.

The end result is that high macroalgal abundances are often reported where nutrient concentrations are high and/or herbivory is low (Deegan et al. 2002, Boyer et al. 2004). However, managers would benefit from indicators of negative change that become evident on intermediate timescales, between the extreme states of seagrass versus macroalgal dominance.

Recently, Houk and van Woesik (2008) showed that watershed size and human population density explained 60–90% of the variance in *Halodule uninervis* (Forssk.) Aschers. habitat size and integrity (integrity being defined as a ratio of *Halodule* to macroalgae) throughout Saipan Lagoon. Seagrass-dominated habitats were found where low-to-moderate watershed development and human population sizes existed; however, persistent stands of macroalgae became evident where human influences were high. In drawing these relationships, the authors used a 1-year dataset encompassing abundance estimates from ninety-four 50-m transects

throughout Saipan Lagoon (30 km^2). These high spatial, but low temporal resolution data provide supporting evidence that a sand-seagrass-macroalga shift is probable under increasing nutrient loads at landscape scales (100–1000 m^2) over long time periods (>10 years) (Udy et al. 1999, Kendrick et al. 2002). Yet, our understanding of the mechanisms driving ecological change remain limited.

In order to improve our ability to predict change in Saipan Lagoon, this study followed the growth dynamics of three seagrass plots differing in environmental regime (Houk and van Woesik 2008). We argue that improved insight into functional relationships can benefit monitoring strategies and management targets.

Materials and methods

Study area

Saipan Lagoon resides upon a submerged Pleistocene (or earlier) shelf that extends along the west coast of Saipan, the capital of the Commonwealth of the Northern Mariana Islands, Western Pacific Ocean (Cloud 1959, Figure 1). Seagrass plots adjacent to three watersheds differing in physical characteristics and human population were selected for temporal investigation: 1) Pau Pau (1.59 km^2, 2500 individuals, 15.2557° N, 145.7794° E, WGS 1984), 2) Garapan (0.74 km^2, 15,000 individuals, 15.2114° N, 145.7147° E), and 3) Kilili (0.59 km^2, 3000 individuals, 15.1663° N, 145.7080° E) (Figure 1). The lagoon adjacent to Pau Pau watershed is the narrowest and is most exposed to large swells that increase surface current velocities in nearshore seagrass beds (Houk and van Woesik 2008). The Garapan watershed has the highest human population density and is associated with Saipan's growing urban and tourist center. Kilili watershed is the smallest in size and height; with numerous freshwater springs observable along the coastline during low tides.

Data collection

Seagrass and macroalgal abundance data were collected monthly from June 2005 to March 2008. At each site, permanent markers were installed at both ends of a single 10-m transect line, 250 m from shore, using a global positioning system (GPS). Along each transect line, a 0.5 m×0.5 m quadrat, broken up into 25 equal sub-quadrats using intersecting strings, was placed at every 2-m mark, and a digital photograph was taken. The photographs were analyzed by recording the dominant seagrass [*Halodule uninervis* or macroalgae (genus level)] that resided within each sub-quadrat based upon a 2-dimensional plan view from above. This method was selected for its repeatability, non-destructive nature, facilitation of grouped observer analyses to reduce error, and best focused upon the dynamics and persistence of ''canopy'' cover that can change within the monthly time frames used for examination. Means and standard deviations (SD) were calculated based upon benthos abundances within replicate quadrats.

In order to assess the nature of freshwater discharge, continuously recording conductivity-temperature sensors (Star-Oddi DST-Mini, Reykjavik, Iceland) were deployed from November 2005 to March 2006. These sensors collected hourly conductivity measurements that were converted to salinity values (PSU). At Pau Pau, gaps in data collection occurred due to sensor fouling and damage; only 40 days of data were collected. Mean, maximum, and minimum tide data were collected from the Saipan Harbor tide station. Mean daily tide heights were calculated from 30-min interval measurements, inclusive of 48 readings for each day. Extreme swells, considered here as ''disturbances'', were identified by reviewing the CNMI Emergency Management Office daily wave height database (compiled by the authors and available at http://www.cnmicoralreef.net/rp/pubs.htm). Disturbances were considered to have occurred if average wave heights were ≥2.5 m within 1 month prior to ecological data collection. Rainfall data were collected from the Saipan airport rain gauge (http://www7.ncdc.noaa.gov) located on the southern part of the island, while wave and tide data are reported above.

Proxies to watershed pollution and human health, i.e., *Enterococcus* bacterial densities, were examined for correlations with rainfall, tide, and wave heights, using the CNMI Division of Environmental Quality weekly beach water quality monitoring database (http://www.cnmicoralreef.net/rp/pubs.htm). Although nutrient concentrations would be a more desirable measure of pollution loading with direct relations to submerged aquatic vegetation growth, these data were not available. Bacterial densities are considered useful indicators of organic material and nutrients (Herrera and Suarez 2005, Haller et al. 2009).

Data analyses

In order to gain insight into the nature and magnitude of freshwater input, regressions were conducted between the daily variance of salinity measurements, rainfall, and the mean tide height (R-statistical package, Crawley 2007). To examine pollution loading, binomial logit regressions between weekly *Enterococcus* bacterial density transgressions and rainfall, tide, and wave height were employed. Transgressions were indicated when weekly bacterial densities were above 104 colony forming units (cfu), in accordance with local water quality standards designed to reduce risk to human health.

Trends in seagrass and macroalgal abundances were analyzed in accordance with disturbance events, water temperature, periodical tidal fluctuations associated with lunar phases, rainfall, and through time. Mixed effect multiple regression models were constructed to define functional relationships between environmental variables and seagrass and macroalgal coverages (R-statistical package, Crawley 2007). In all instances, the regression terms quantifying the temporal dependence of sequential monthly samples for seagrass and macroalgae were not significant throughout the study period. Thus, regressions were reduced to linear models as these terms became omitted. The independent, environmental variables were standardized (by subtracting the means and

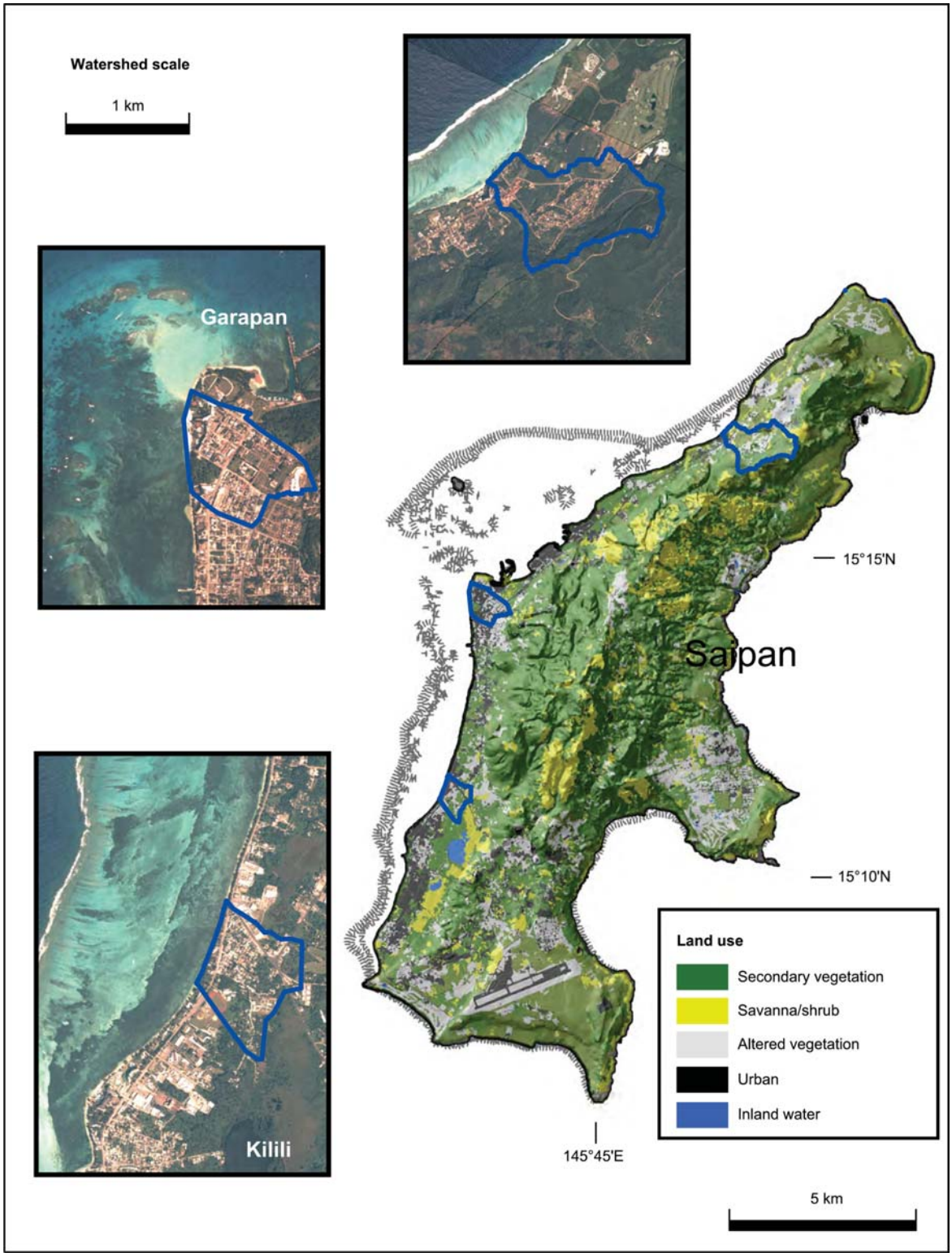

Figure 1 2006 satellite image of Saipan overlain with watershed topography and land-use. Insets show the three study regions.

dividing by the SDs) to allow equal weightings. To meet the requirements of normality of residuals (Box and Cox 1964), power transformations using the maximum-likelihood estimate of lambda ($y=x^k$) were conducted if normality assumptions were not met for dependent variables. This study examined the best fit models using Akaike's Information Criterion. Briefly, the selected models explained the greatest proportion of the variance while using the least number of explanatory

variables to ensure the greatest precision, accuracy, and repeatability.

Results

Site characteristics

Mean *Enterococcus* densities were highest in Garapan [159 colony forming units (cfu) ±455 (SD)], followed by Pau Pau (41 cfu±163), and Kilili (31 cfu±89), following human populations but not watershed sizes. An interactive term associated with the transport of pollution from land and the re-suspension of coastal sediments (rainfall×wave height) had the best functional relationship with weekly bacterial concentrations at Garapan (p=0.01, AIC=103.8, logit regression), while no relations emerged elsewhere. No significant regressions were found between salinity, rainfall, and mean tide height; however non-linear, repeated trends were noted. Kilili had the greatest variation in salinity over the study period, with one or more high-variance events typically recorded during each month when mean tide height was lowest, representing the time frame between the full and new moons (Figure 2). In contrast, rainfall seemed to have had the greatest influence upon salinity at Garapan where two periods of intense rainfall during December 2005 and January 2006 corresponded with high salinity variance.

Seagrass–macroalgal dynamics

The three sites had differing dynamics of seagrass and macroalgal abundances throughout the study. Garapan initially had 40% seagrass cover, which decreased to 10% as macroalgal canopy increased following the 2006 wet season, with no subsequent reduction (Figure 3). An interaction term (time×rain) accounted for ~50% of the variance in the declining seagrass abundance, a trend driven by the establishment of persistent stands of *Caulerpa*, *Acanthophora*, and *Laurencia* to a lesser degree (Figure 3, Table 1). Significant increases in *Caulerpa* abundance were noted during the wet season, while the attached macroalga *Halimeda macroloba* Decaisne dominated canopy cover during the dry season when temperatures were higher and the tidal regimes were of lower magnitude (R^2=0.36, regression between time×tide×rainfall×temperature and *H. macroloba* cover, p=0.01) (Table 1). However, the cyclical seasonal trends noted were small in comparison with the multi-year temporal trends. No relationships with disturbances were evident at Garapan.

In contrast, the seagrass and macroalgal assemblages at Kilili followed cyclical patterns of growth, emergence, and removal corresponding to varying temperature, tidal regimes, rain, and large-swell events. *Tolypiocladia* increased seasonally with the onset of lower temperatures in the fall and winter, but was removed during disturbance events (R^2=0.48, p=0.008, combined regression model, Figure 4, Table 1). In contrast, *Halodule uninervis* cover was significantly greater when mean daily tides were higher and rainfall was lower (R^2=0.57, p=0.002, two-variable regression model), factors that are proxies of lower ground and surface water discharge,

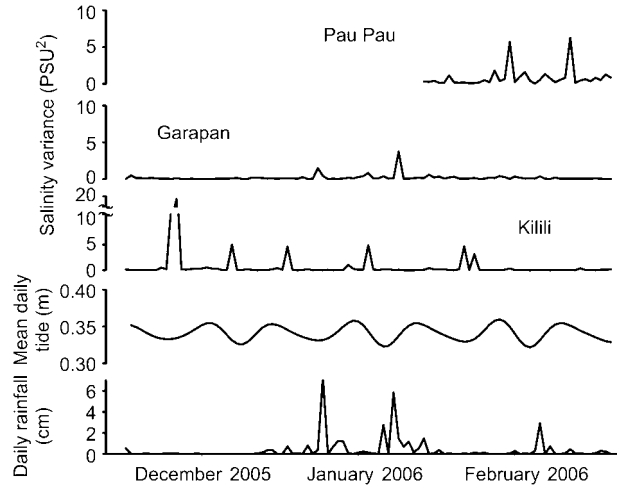

Figure 2 Mean daily rainfall and tide height for Saipan. Variance in salinity is shown for each study region, as recorded by *in-situ* data loggers from June 2005 to March 2008.

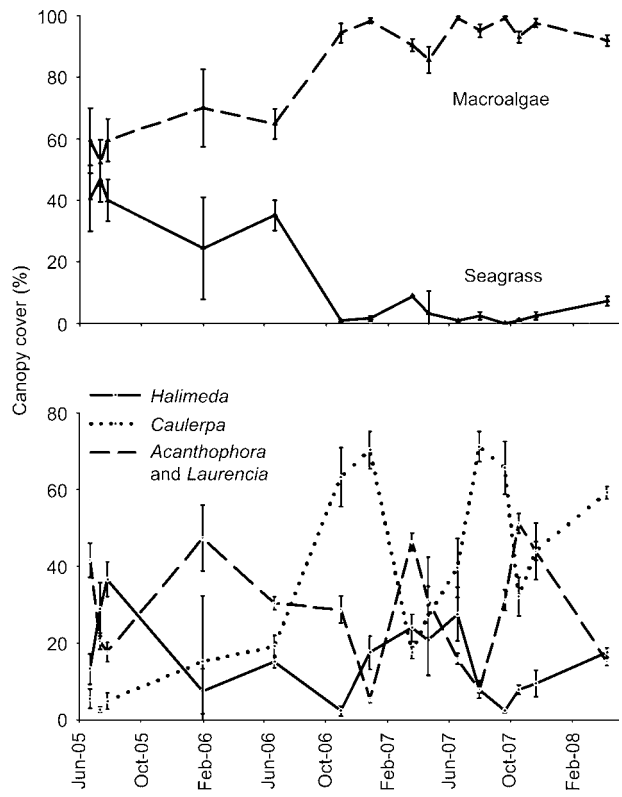

Figure 3 Percent coverage of seagrass (*Halodule uninervis*) and macroalgae (genus) at Garapan from June 2005 to March 2008. Values are means±SD (n=5 quadrats, consisting of 25 sub-quadrats each).

respectively. Time did not have a functional relationship with a substantial portion of the variance in seagrass or macroalgae cover at Kilili where seasonal cycles prevailed.

At Pau Pau, initial investigations documented the establishment of a large *Caulerpa racemosa* (Forsskål) J. Agardh bloom during the first wet season. *C. racemosa* overgrew

Table 1 Multiple regressions between standardized environmental variables and seagrass and macroalgal dynamics in Saipan Lagoon.

Dependent (y)	Equation	Slope 1 (SE)	Slope 2 (SE)	Slope 3 (SE)	Intercept	R^2	p-Value	AIC
Kilili								
Seagrass	Min. tide+rain+(min. tide×rain)	14.1 (6.2)	24.5 (8.2)	-10.1 (2.8)	37.4	0.57	0.002	131.5
Tolypiocladia	Temp.+max. wave+(temp.×max. wave)	-34.4 (9.2)	-38.2 (10.6)	13.1 (3.9)	103.6	0.48	0.008	142.2
Garapan								
Seagrass	(Time×rain)	-3.6 (1.0)			30.7	0.47	0.004	115.4
Halimeda	(Time×rain×temp.×min. tide)	-0.4 (0.1)			22.2	0.36	0.013	102.5
Pau Pau								
Macroalgae[a]	(Max. wave×time)	-5.9 (2.0)			66.9	0.35	0.01	162.1
Acanthophora	Rain	8.7 (1.9)			-8.5	0.55	>0.001	122.7

Slope number refers to the order in which the environmental variables are shown in the equations; SE represents the standard error of the slope estimate. [a] Indicates that all macroalgae except *Acanthophora* were grouped for the Pau Pau analyses. Environmental variables and AIC (Akaike's Information Criterion) values are defined in Methods section.

Halodule uninervis and dominated until a disturbance occurred in February 2006, displacing the macroalgal stand (Figure 5). A similar trend of smaller magnitude emerged the following year, as a wet-season bloom of *Acanthophora spicifera* (M. Vahl) Børgesen was removed following a February 2007 swell event. Accordingly, macroalgal canopy significantly decreased in concert with the occurrence of winter large-swell events that were common at Pau Pau throughout the study (R^2=0.35, p=0.01, Table 1). The *C. racemosa* bloom was noted only once; however, *A. spicifera* abundance was consistently higher during the wet season (R^2=0.55, p<0.001, regression between *A. spicifera* and rainfall), suggesting its greater persistence compared with other macroalgae at Pau Pau. There was a notable, though non-significant reduction in *Halimeda* and *Padina* with time, but low β-values (-0.01 to -0.05) suggest insignificant rates of change in comparison to other explanatory factors.

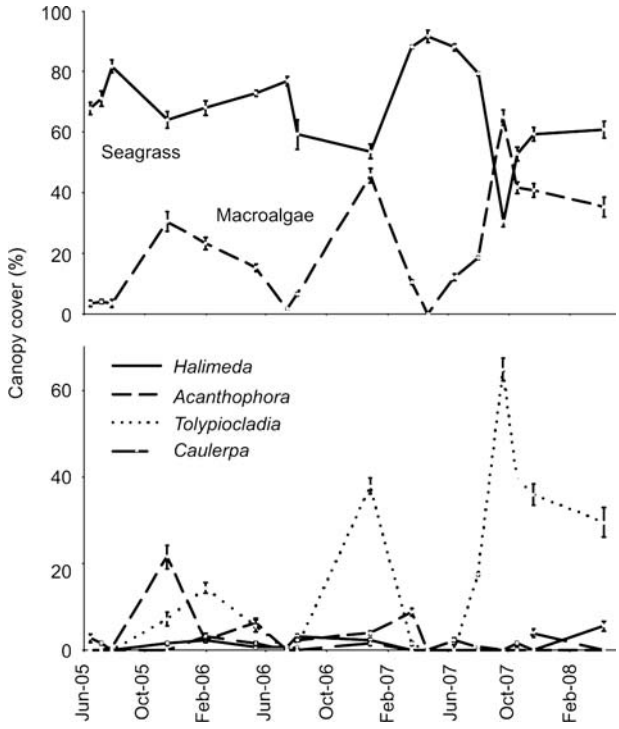

Figure 4 Percent coverage of seagrass (*Halodule uninervis*) and macroalgae (genus) at Kilili from June 2005 to March 2008. Values are means±SD (n=5 quadrats, consisting of 25 sub-quadrats each).

Discussion

We propose that the agents of change in the *Halodule* seagrass beds examined here act in a complex, hierarchical manner. At Kilili, where proxies of pollution had low values,

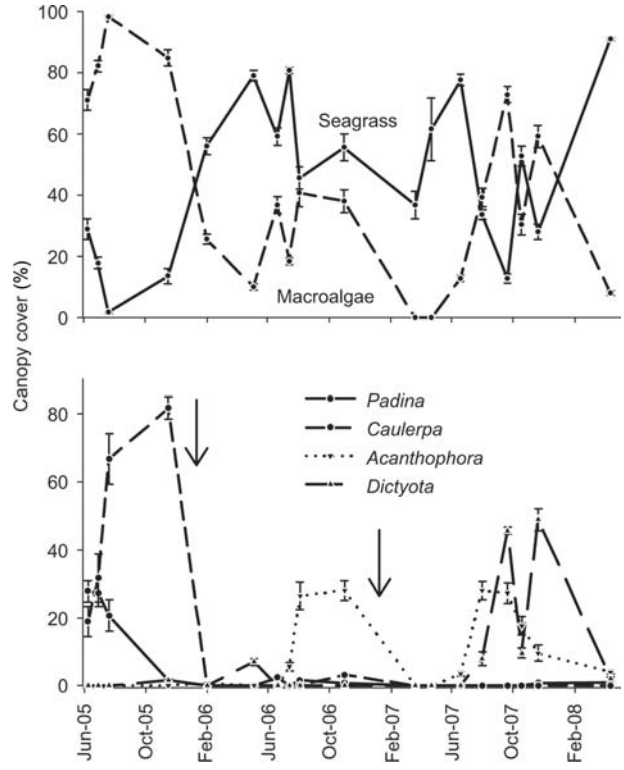

Figure 5 Percent coverage of seagrass (*Halodule uninervis*) and macroalgae (genus) at Pau Pau from June 2005 to March 2008. Arrows indicate large-swell events, as defined in the Methods section. Values are means±SD (n=5 quadrats, consisting of 25 sub-quadrats each).

temperature had the predominant functional relationship with drift macroalgal abundance (*Tolypiocladia*) (Biber and Irlandi 2006). The largest bloom of *Tolypiocladia* occurred during the fall of 2007, when temperatures were anomalously low for that season (27°C), ~1°C lower than average. Other than temperature-related blooms of *Tolypiocladia*, little persistent macroalgal growth occurred. Freshwater delivery to the seagrass plots through groundwater discharge (occurring during low minimum tide regimes) and rainfall was correlated with reduced seagrass canopy. However, the resultant multispecies growths of green and red algae were not persistent. It seems probable that low bacterial densities in the nearshore waters indicate lower nutrient enrichment for growth as compared to other sites.

In contrast with natural fluctuations, the now-persistent macroalgal stands at Garapan are attributed to consistently high bacterial densities associated with nutrient enrichment (Deegan et al. 2002, Daby 2003, Boyer et al. 2004). The dependence of bacterial densities upon delivery (rainfall) and re-suspension (wave energy) gives rise to long lasting impacts of land-based pollution from this densely populated, urban watershed. Given these relations, it is not surprising that persistent stands of *Caulerpa* peaked during the first wet season, and remained dominant, as rain and wave events were common throughout the study. The cyclical relationship between cool wintertime temperatures and drift macroalgal abundance was masked by persistent *Caulerpa* growth. While studies indicate that nutrient-rich, freshwater discharge leads to an increased abundance of green algae (Kamer et al. 2001, Lapointe et al. 2004, Lirman et al. 2008), our results show that the transition can occur over short (months) time frames and may remain persistent over protracted periods (years).

At Pau Pau, the large watershed and moderate bacterial densities also indicate nutrient enrichment of the nearshore waters; thus macroalgal proliferation was expected over longer time periods than reported. However, high wave energy and faster surface currents are characteristic of the northern lagoon (Houk and van Woesik 2008). The wave-and-current mediated removal of a large *Caulerpa* bloom in 2005, coupled with similar removal of *Dictyota* and *Acanthophora* growths in 2006 and 2007, indicate that a disturbance mediated system may exist (Chambers 1987, Chambers et al. 1991). High values of pollution proxies related closely to rainy season growth of multi-species macroalgal assemblages; however, their persistence through time was consistently interrupted. Hence, the influences of pollution, at Garapan, and seasonal cycles at Kilili, were likely both masked by consistently high disturbance regimes (swell events).

Disturbance events represent physical impacts that caused rapid shifts in submerged vegetation dominance, preventing progress to, and stability at, a successional equilibrium (in the classic sense of the pendulum, Hollings 1973). We showed that predictable cycles of macroalgal growth and displacement were evident from seasonal perturbations (i.e., low temperatures and large swells); however, in the face of chronic human pollution, the initial phase shifts to macroalgal dominance remained stable throughout 3 years. These findings agree with an extensive 30-year examination of coral photo-quadrats at Heron Island, Australia, where successful recovery from acute disturbances was noted, but chronic disturbances led to permanent shifts in assemblages (Connell et al. 1997). Other studies comparing entire geographic regions for both marine and plant communities confirm these consistencies between the nature of disturbance and ecological resilience (Connell 1997, Laliberte et al. 2010). Yet, the literature provides less insight for assemblages that face chronic human pollution input and extremely high return rates of acute natural disturbances. Seagrass assemblages in the northern Saipan Lagoon appear to benefit from high disturbance frequencies, as the length of time required for predictable macroalgal persistence under high human pollution appears to be greater than disturbance rates dictate (Tanner et al. 1994). Clearly, both non-equilibrium and equilibrium theories of community assembly are equally relevant to our results (Norden et al. 2009), but the former provide a greater challenge for predicting resilience under future environmental regimes.

While it is straightforward to recommend enhanced management for seagrass assemblages where expected seasonal changes are masked by persistent macroalgal growth, it was more difficult to identify the range and magnitude of localized seasonal cycles. In Saipan Lagoon, appropriate locations for temporal investigations of seasonal dynamics were selected based upon previous habitat mapping and broad-scale transect data (Houk and van Woesik 2008), greatly benefiting our study design. Tracking ecological change over time, and drawing correlations with environmental regime, will undoubtedly assist managers in defining relevant targets and indicators of future change. While preferable targets include critical nutrient concentrations (Duarte 1995), rapid shifts in water quality over short time periods make monitoring, enforcement, and evaluation of policy laborious and expensive. Therefore, simultaneous efforts to establish ecologically-based criteria are warranted considering the ongoing accumulation of monitoring program data that encompass natural and human disturbance cycles.

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