AN ABSTRACT OF THE THESIS OF Rodney C Camacho for the Master of Science in Biology presented Oct 21, 2016

Title: DRIVERS OF MACROALGAL CANOPY DYNAMICS WITHIN SAIPAN LAGOON SEAGRASS HABITATS

Approved:

Peter C. Houk, Chairman, Thesis Committee

Seagrass habitats provide essential goods and services to coastal societies in the form of fisheries, filtering nutrients from watershed runoff, and stabilization of shorelines. However, seagrass beds are in decline globally. Managing seagrass habitats for ecosystem resilience requires a better understanding of how seasonal and temporal trends interact to determine future projections. This thesis examined *Halodule uninervis* beds and associated macroalgae canopies across a 10-year period in the Saipan Lagoon, Commonwealth of the Northern Mariana Islands, to quantify both seasonal and temporal dynamics from photo-quadrat datasets. Within each year, seasonal cycles were the strongest drivers of macroalgal dynamics. The cooler and dryer winter months were associated with blue-green algae canopies, mainly *Lyngbya* sp. and *Phormidium* sp. with an inverse relationship between sea-surface temperatures (SST) and coverage. In contrast, the warmer and wetter summer months were associated with red algae canopies, predominantly *Acanthophora spicifera*, which were positively related to rainfall. Interestingly, seasonal influences were not spatially consistent. Both blue-green algae emergence in the winter months and red algae emergence in the summer months were greatest in the central area of the lagoon, and gradually diminished moving to the north and south as watershed size and pollution diminished, and watershed geology shifted from being volcanic to limestone. The karst, limestone watersheds in the southern part of the lagoon displayed no direct relationship with red algae and rainfall, but did show a weak relationship with groundwater that was predicted by tidal heights and lunar periods, that together served as a proxy to freshwater discharge. Once controlling for the expected seasonal dynamics in statistical models, the persistence of macroalgal canopies through time was predicted by two watershed characteristics, size and developed land within. Persistent macroalgal canopies existed in the central, urbanized lagoon over the past decade. However, when moving to the north or south of this central region, low macroalgal canopy coverage initially existed, but these have become more pronounced through time. The northernmost region appears to represent a disturbance mediated system, whereby macroalgal canopies become increasingly prolific during summer months, but large wave event during the winter months typically remove the macroalgal build-up. In sum, the majority of the *Halodule* seagrass beds in the lagoon had a growing tendency for the long-term persistence of macroalgal canopies, while only a few regions had non-significant trends with watershed characteristics, mainly in the south lagoon. The collective results were used to prioritize local management strategies in Saipan, but also offer guidance to similar programs dealing with complex seasonal-and-temporal cycles that exist in seagrass systems.

TO THE OFFICE OF GRADUATE STUDIES

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DRIVERS OF MACROALGAL CANOPY DYNAMICS WITHIN SAIPAN LAGOON SEAGRASS HABITATS

BY

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A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

IN

BIOLOGY

UNIVERSITY OF GUAM
OCTOBER 2016

Acknowledgments

I would like to thank first my committee chair, Dr. Peter Houk, for sticking by me through this whole process even before it began. Many thanks to the rest of my committee Dr. Tom Schils, Dr. Jason Biggs, and Dr. Ryan Okano. This committee has kept me has always had the best interest in this study and even though they played a devil’s advocate, I know they meant well and they want the best research paper I can produce. I would like to thank Frances Castro and the Marine Monitoring Team for providing logistical help in data collection. To my parents, thank you for all your support and sacrifices that you made in order for me to achieve this milestone in my life. To the rest my family, I thank you for your support and guidance throughout my time during this research. Lastly, I dedicate this thesis to my daughter, Malina Mae, it was because of her that I pushed myself to complete this thesis.

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Introduction

Saipan Lagoon Seagrass Beds

Seagrass habitats provide essential ecosystem services that support the economy, culture, and livelihood of tropical island nations (van Beukering et al. 2006, Houk et al. 2012). Productive seagrass habitats are well known to support a variety of fisheries (Jackson et al. 2001, Gillanders 2007), but also play a key role in trapping sediments and removing nutrients from watershed discharge, and stabilizing shorelines (Houk & van Woesik 2008, Houk & Camacho 2010, Houk et al. 2013). Despite the beneficial ecosystem services that seagrass habitats provide, they remain threatened by coastal development projects that can directly impact seagrass through removal and modification of nearshore environments, and indirectly through growing non-point source pollution associated with watershed development. In many island nations, hotels and tourism industries often view seagrass habitats as a nuisance, because tourists prefer swimming in clear waters with sandy bottoms (Jenks & Coulson 1963). Clearly there is a need to better translate the benefits of seagrass habitats to the economic and urban development sector. Equally, science is needed to evaluate the current status and temporal changes within seagrass ecosystems to inform managers and guide policy. The present thesis builds upon the science by investigating representative seagrass habitats in the Saipan Lagoon, Commonwealth of the Northern Mariana Islands, to better appreciate how environmental drivers lead to predictable seasonal and temporal changes through time, with the overall goal of improving the information available to managers.

Distribution, Function, and Importance of Seagrass Beds

The estimated global coverage of seagrass is approximately 177,000 km^2 with the highest density of seagrass habitats located in the Indo-West Pacific region. Extensive seagrass habitats also exist within temperate regions (Larkum et al. 2006). In total, there are five temperate species in the North Atlantic, 10 species in the Tropical Atlantic, nine subtropical and temperate species in the Mediterranean, 15 temperate species in the North Pacific, 24 species in the tropical Indo-Pacific, and 18 temperate species in the southern oceans (Short et al. 2007). Large coverage of seagrass beds in coastlines and shorelines constantly being affected by overexploitation, physical modification, nutrient and sediment pollution, introduction of non-native species, and global climate change (Norse 1993). From 1879 to 2006, an estimated 65% of seagrass has been lost globally, making seagrass habitats one of the most threatened ecosystems in the world (Lotze et al. 2006, Short et al. 2007, Waycott et al. 2009).

Like terrestrial plants, seagrasses require sunlight, nutrients, and carbon dioxide, but unlike terrestrial plants, seagrasses are able to survive in saline waters through an extensive root system (Larkum et al. 2006). Depending on the genus, pollination occurs either on the water surface (*Enhalus*) or in the water column (*Halodule*) (McMillan 1976, Ackerman 2006). Generally, the majority of tropical species are found growing on soft-bottom substrates, and in turn, their roots help to directly stabilize the soft substrates. Larger seagrass species will also reduce water movement allowing sediments to settle and reduce the amount of sediments that can form a layer on corals (Orth et al. 2006). Their role of stabilizing soft-bottom substrates is also beneficial to stabilizing sandy shorelines (Christianen et al. 2013, Blake et al. 2014). Seagrasses also act as nutrient sinks by buffering and up-taking nutrients and chemicals draining into the marine environment from watersheds (Duarte et al. 2005, Romero et al. 2006, McGlathery et al. 2007). By increasing the deposition of sediments, and through the ensuing uptake of nutrients attached to sediments and in freshwater discharge, seagrass ecosystems serve to lower nutrient levels reaching the oligotrophic outer reef habitats. Once removed, these nutrients can then be released slowly through a process of decomposition and consumption, transforming pulsed releases of nutrients from watersheds, to more steady and continuous releases that are beneficial to seagrass ecosystem diversity (Hutchings et al. 1991, Burkholder et al. 2007). Ecologically, seagrass beds provide foraging habitat, refuge, and nursery grounds for many (juvenile) fish and other marine biota (Unsworth et al. 2007, Horinouchi 2008, Unsworth et al. 2008, Unsworth et al. 2009). When considering the collective role that seagrass habitats play in governing physical, chemical, and ecological processes that together provide essential ecosystem services, it becomes obvious that attention should be given to their monitoring and management in understanding the temporal dynamics of competing macroalgae that occur within seagrass beds.

Prior to understanding temporal dynamics within seagrass habitats, it is desirable to first appreciate the seasonal cycles that have the potential to mask temporal change. Seasonal cycles are associated with numerous environmental regimes, but shifting rainfall, wind-speed and associated wave energy, sea-surface temperature, sunlight intensity, and tides are most influential to seagrass ecosystems. The influence of rainfall was highlighted in Biscayne Bay, Florida, where the onset of the rainy season decreased salinity values of nearshore marine waters, corresponding to increase in the proliferation of macroalgal stands (Lirman et al. 2008). Wave energy has influenced seagrass beds in Australia, where a cyclone generated 12 m wave swells that uprooted 70% of the seagrass beds (Poiner et al. 1989). Sea-surface temperatures (SST) can also shift seagrass habitat dynamics, as Potouroglou et al. (2014) reported an increase in the density of flowering shoots of *Z. marina*, while a lowering of SST during the winter months in CNMI promoted the growth of seasonal red macroalgae that competed with *Halodule uninervis* for sunlight (Houk & Camacho 2010). In addition to, Houk and Camacho (2012) reported that seasonal temperatures, land-based runoff, and wave energy combined to dictate the dynamics of seagrass habitat plots over a two-year period in the Saipan Lagoon. Interestingly, watershed runoff during rain events appears to affect seagrass habitats seasonally, while groundwater seepage is more continuous, magnified during low tides associated with full/new moons (i.e., lunar cycles) (Fourqurean et al. 1992, Rutkowski et al. 1999, Kamermans et al. 2002, Carruthers et al. 2005, Houk et al. 2013). Indeed, the presence of groundwater discharge has been associated with both the extent and composition of seagrass habitats, most notably among *Thalassia* and *Halodule* (Fourqurean et al. 1992, Kamermans et al. 2002, Slomp & Van Cappellen 2004, Carruthers et al. 2005, Houk & Camacho 2010, Houk et al. 2013). In East Africa, there was a negative relationship between groundwater discharge and seagrass bed diversity, and a positive relationship between groundwater discharge and ^{15}N that was found in the leaves of the *Thalassodendron ciliatum* (Kamermans et al. 2002). Yet, there is a limit to seagrasses' abilities to dominate nutrient-laden environments, both groundwater and surface discharge can lead to eutrophication and macroalgal proliferation within seagrass beds. Thus, in order for healthy seagrass beds to exist, some nutrient contribution from watersheds must occur; but too much can lead to their demise as macroalgae are more efficient in rapid nutrient uptake in comparison and can quickly overgrow the shorter *Thalassia* and *Halodule* species for light. There is a delicate balance in nutrient contribution between coastal zones and their watersheds that must be maintained for healthy seagrass systems, similar to coral reefs.

Watershed development is one of the most severe threats to the ecosystem services provided by seagrass beds. Excess nutrients delivered to nearshore marine waters can shift the competitive edge away from seagrasses, which can sustain longer-periods of low nutrient regimes in between pulsed releases due to their roots, unlike macroalgae, which respond rapidly to the increased frequency of nutrient pulses (McGlathery 2001, Ferdie & Fourqurean 2004, Burkholder et al. 2007). Over longer time periods, habitats can shift from seagrass-to-macroalgal dominance (Dunton 1990), but because there are few studies that have conducted time-series monitoring, the mechanisms remain poorly understood. The decline of seagrass habitats has secondary implications for nutrient cycling rates, fish habitat provisioning, and even shoreline stabilization. For instance, Tuya et al. (2014) reported that mats of *Caulerpa prolifera* contain less density and biomass in both predatory and prey fishes, less primary productivity, and less stabilization on sediments compared with a *Cymodocea nodosa* seagrass bed. Increases in the sediment loads and nutrients being supplied to coastal waters from farms and urban infrastructure leads to increase in turbidity, that reduces the sunlight available for photosynthesis, and provides an influx of excess nutrients at higher-frequency intervals (Peierls et al. 1991, Turner & Rabalais 1991, Lapointe & Clark 1992, Schaffelke et al. 2005, Rivera-Guzmán et al. 2014). The end result can be a complete loss of seagrass beds associated with watershed urbanization and industrial waste discharge (Olinger 1975, Livingston 1987).

The status of seagrass beds in the Saipan Lagoon

Much of Saipan's economy and culture is dependent on the lagoon system and the resources it provides to hotels, tourist operations and the local people. Within the Commonwealth of the Northern Mariana Islands (CNMI), the Saipan Lagoon represents the only extensive shallow-water habitat with an abundance of nearshore seagrass beds that include three species: *Halodule uninervis*, *Enhalus acoroides,* and *Halophila minor*. Among these, *Halodule* and *Enhalus* seagrasses are the most abundant, spatially-extensive, and form structural habitats. Both have macroalgal stands mixed within the seagrass canopy, with dominant genera including *Acanthophora*, *Dictyota*, *Halimeda*, *Padina*, and *Phormidium*. Studies examining the spatial distribution patterns of seagrass and macroalgae began shortly after WWII using aerial photography and limited in-situ transects (Cloud 1959). Historic images and data showed that prolific macroalgae stands often existed in areas where seagrass habitats now reside (Cloud 1959, Houk & van Woesik 2008). As time passed, urbanized watersheds returned to vegetated counterparts, and the nearshore habitats returned to a mixture of seagrass and macroalgae by the mid 1960's and early 1970's. Amesbury et al. (1979) conducted fish surveys in 24 habitats within the Saipan Lagoon and found that seagrass stands again dominated nearshore habitats, which in turn supported the most extensive fisheries compared with other habitats. Follow-up work in the 1970's supported these conclusions, and reported that seagrass beds had greater sea cucumber diversity compared with those of reef margins and mid lagoon sand locations (Chandran 1988, Duenas and Associates 1997). Yet, in modern times the growing development of hotels and other infrastructure appear to be reverting seagrass habitats back to macroalgal dominance in certain locales (pers. obs., aerial photographs).

Houk and van Woesik (2006) compared ecological habitat maps between 1959 and 2002 and reported a decrease in both seagrass and staghorn coral habitat. Interestingly, this study described positive relationships between the large seagrass species, *Enhalus acoroides,* and watershed size, with no added variance explained by urbanization within the watersheds. In contrast, *Halodule uninervis* habitats had a strong, negative association with human development, leading to macroalgae outcompeting the *Halodule*. A follow-up study by Houk and Camacho (2010) examined the biological mechanisms responsible for seagrass-to-macroalgal regime shifts in the Saipan Lagoon. Their findings suggested that the eventual persistence of macroalgal growth within *Halodule* seagrass beds was a consequence of extended seasonal dynamics. Seasonally high abundances of various species of macroalgae persisted for longer periods of time, often linking the proliferation of two or more species in areas adjacent to urbanized watersheds, eventually shading the *Halodule* understory for much of the year. Their study also defined two distinct seasons, based upon environmental regimes, which predict macroalgal dynamics in less-urbanized watersheds. Low temperatures and rainfall, along with high wind-driven waves characterized the winter months, while high temperatures and rainfall, with calmer waters characterized the summer months. However, the spatial scale of that investigation was limited.

The present thesis builds upon past efforts in Saipan Lagoon to better evaluate both seasonal dynamics and longer-term trends across *Halodule* seagrass habitats. Specifically, the present research will: (i) examine if the seasonal dynamics of temperature, rainfall, and large-wave events suggested by the small-scale seagrass plots (20 m^2, 3 replicate stations, Houk and Camacho 2010) are consistent across larger scales of investigation (500 m^2, 10 replicate stations) and (ii) use this improved understanding of seasonal dynamics to evaluate trends in seagrass and macroalgal abundances with respect to land-use in adjacent watersheds using a 10-year dataset (2006 to 2015). The first part of the study will investigate seasonality using spatially-extensive snapshots of canopy cover within *Halodule* habitats throughout the lagoon during the wet and dry seasons. Using two initial datasets, the present thesis will first determine how canopy cover and algal composition change seasonally. Appreciating seasonal dynamics is necessary prior to analyzing long-term data that were not always collected during the same months. The second part of the study will focus on the temporal trends in seagrass and macroalgal dynamics with respect to land-use within adjacent watersheds. These investigations will build upon Houk and van Woesik (2008), who hypothesized a relationship between watershed size, development, and the integrity of *Halodule* seagrass habitats. Specifically, null hypotheses are grouped into two themes, seasonal dynamics (i.e., wet versus dry) and temporal dynamics, which both have a spatial component nested within them.

Null Hypotheses

Seasonal Dynamics

$H0_1$: Macroalgal canopy cover within *Halodule* beds across wet and dry seasons does not differ. $H0_1$ will be proven false if a multivariate test of comparison for canopy cover show differences. In the instance that $H0_1$ is found to be false then species-based correlations with PCO axes will be utilized to determine which algae have the strongest seasonal growth cycles.

$H0_2$: Macroalgal canopy cover within each season does not differ spatially across the lagoon. $H0_2$ will be proven false if multivariate tests of comparison for canopy cover show spatial differences within either season. If significant differences are found, species-based correlations with PCO axes will be utilized to determine which algae have predictable spatial patterns.

Temporal dynamics

$H0_3$: Seasonal trends depicted in $H0_1$ and $H0_2$ were not persistent through time. $H0_3$ will be proven false if linear models support that seasonal relationships with macroalgal canopies were persistent through time. If significant models are found, the variance associated with seasonality will be removed by using the residuals from a forward stepwise regression.

$H0_4$: The persistence of the macroalgal canopies have been consistent through time across the study regions. $H0_4$ will be falsified if ANOVA tests find significant differences in seasonally-adjusted macroalgal canopy cover through time. If significant differences are found, post-hoc tests will be conducted to determine which time frames are distinct within each region, and if there is any consistent trend.

$H0_5$: Locations with persistently high or significantly increasing macroalgal canopy cover are not related to watershed characteristics or environmental factors associated with each site. $H0_5$ will be proven false if logit models predict “high” macroalgal canopy states are related to watershed characteristics or environmental factors. If significant, current estimates of macroalgal canopies will be examined using linear models with the same watershed characteristics and environmental variables to see if temporal trends and current canopy abundances were driven by similar factors.

Methods

Study Site Description

The Commonwealth of the Northern Mariana Islands (CNMI) is located in the Western Pacific between the Philippine Sea and the Pacific Ocean. The CNMI is comprised of 14 islands where the four southernmost islands are populated. Of the four islands, Saipan is the largest and contains a unique lagoon different from the other islands. The Saipan Lagoon is located on the western side of the island and is divided into two by the main channel with the northern section known as the Tanapag Lagoon and the southern section known as the Garapan Lagoon. The lagoon stretches the entire length of the island from north to south. Narrowing (<100 m) at the northern and southern ends, it reaches its greatest width (5 km) near the center of the island. The depth of the lagoon varies from less than one meter to 15 m, though most of the lagoon is shallow (1 m) (Duenas and Associates 1997). Progressing away from land, lagoon habitats begin with seagrass beds, transition to sand flats, which eventually give way to back-reef coral habitats, dominated by staghorn *Acropora*, *Isopora*, and *Porites*. While seagrass and macroalgal habitats exist along most of the shoreline, they achieve greatest abundance and diversity in the central lagoon, an area which has the largest watersheds and most extensive urban development (Houk & van Woesik 2008, Houk & Camacho 2010).

For the present study, the lagoon was divided into 6 regions (A – F**,** Figure 1), representing lagoon sub-sections exposed to similar environmental regimes, yet differing in watershed size and human population (ranging from 0.5-4.0 km^2, and 209-3,983 people). Monitoring using standardized protocols described below has been ongoing within each

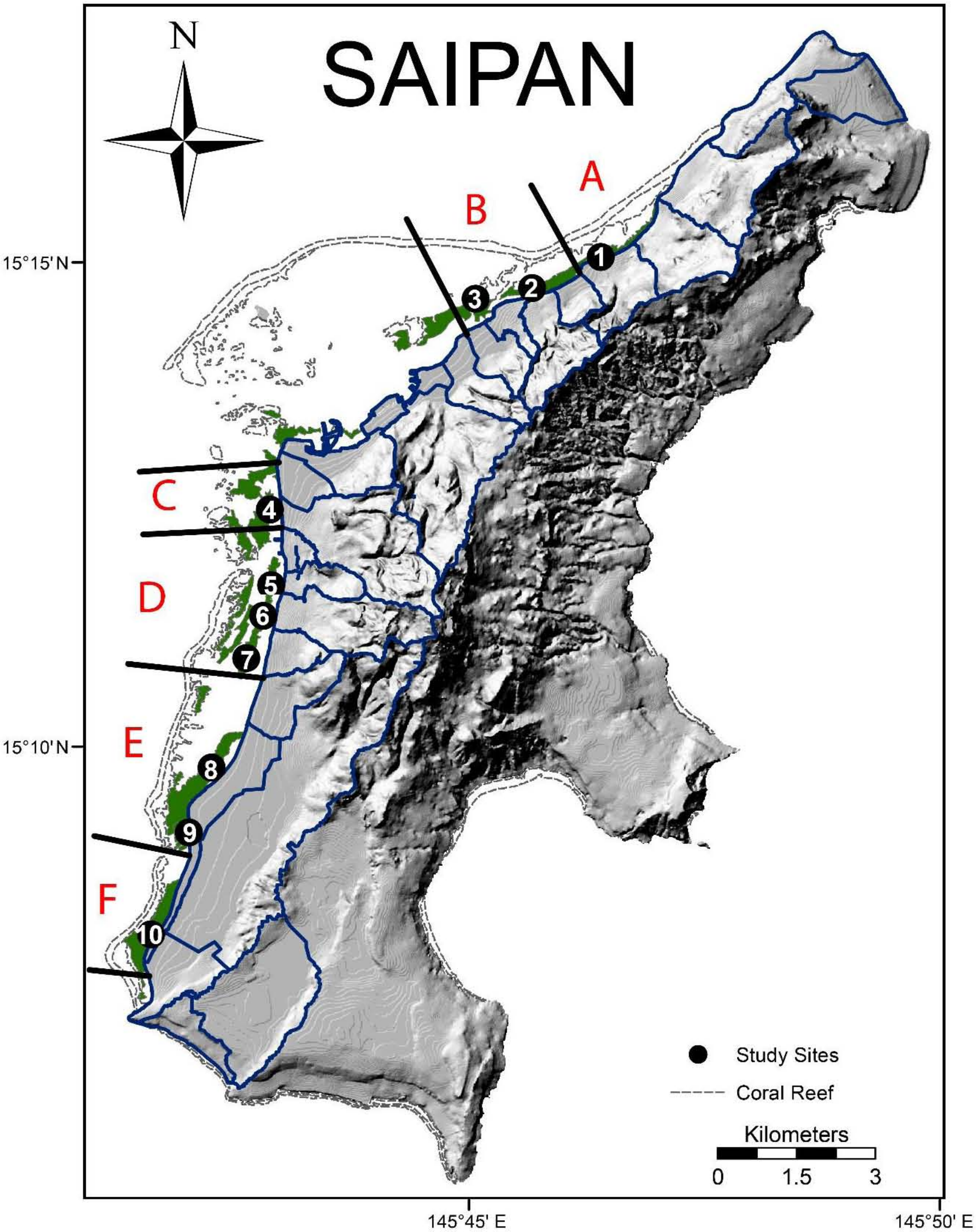

Figure 1. Map of Saipan. The blue polygon outlines depict the major watersheds located on the western side of the island. The green polygons are Halodule beds based on 2006 habitat mapping. The red letters are the regions associated with watersheds and the current study. The numbered dots are the study sites used in seasonal analyses.

region since 2000. However, the timing and frequency of monitoring has shifted annually, a caveat which provided the incentive for the initial hypotheses for examining seasonal variability by controlling for these variables. Houk and Camacho (2010) have reported that the northern-most section of the lagoon experienced large (>2.5 m) wave events in 2006 leading to the assumption that wave-induced disturbance events may be common to this section of the lagoon during winter months. They also found that there is an influence of groundwater in the southern sections of the lagoon but it was not determined if it was a driver through time.

Data Collection

Ecological Data

In total, 12 sites have been examined since 2006, spread across the six sub-sections of the lagoon (Table 1). Survey Sites were all associated with CNMI's Marine Monitoring Program. Each site was selected based upon the presence of extensive *Halodule* seagrass beds adjacent to the shoreline (referred to as *Halodule* habitats herein). Depths within this habitat range from 0.5-1.5 m below MLLW. Data collection was initiated by laying 5 x 50 m transects parallel to shore, traversing the *Halodule* habitats. Quadrats were placed at 1m intervals and either *in-situ* data collection or digital photographs were taken. The benthos under each of five random points, either in-situ or from photographs, were assigned a pre-defined category. Photos were processed using the computer software Coral Point Count (Kohler & Gill 2006). These methods yielded a total of 250 data points per transect. The benthic categories chosen for analysis were seagrass (to genus level), corals (to genus level), turf algae (less than 2 cm), macroalgae (greater than 2 cm, to genus level if abundant), crustose coralline algae, sand, and other invertebrates (genus level if abundant).

Table 1. List of long-term monitoring sites and the years they were surveyed. Sites with an asterisk (*) were not included in the temporal analyses because they were inconsistently surveyed by the CNMI long-term monitoring program (i.e., sites labelled NA).

Unique Site ID	Region	Local Site Name	Disturbance (2004-2008)	Post Disturbance (2009-2013)	Present Study (2014-2015)
NA	A	Pau Pau*	x	x	
1	A	San Roque	x	x	x
NA	B	Achuago*	x		
2	B	Iguel Ranch	x	x	x
3	B	Tanapag	x	x	x
4	C	Fiesta Drainage		x	x
5	C	Hafa Adai Drainage		x	x
6	D	13 Fishermen		x	x
NA	D	Moylans*			x
7	D	Quartermaster		x	x
8	E	Kilili	x	x	x
9	E	Sugar Dock	x	x	x
10	F	San Antonio	x	x	x

Means, standard deviations, and standard errors were calculated based on the five 50 m replicates, with n = 250 points per transect, n= 1250 data points per site.

Environmental Data

A suite of site-based environmental data were collected to evaluate both seasonal cycles and temporal trends in macroalgal canopies. Watershed characteristics were developed from geographic information system (GIS) layers pertaining to topography, land-use, and human population. Digital elevation models (i.e., topographic data) were first used to define watershed boundaries. Land-use data were then overlaid upon the watershed boundaries, and a measure of disturbed, or altered land, was calculated by summing the coverage of barren land, urbanized vegetation, and developed infrastructure. In addition, human population data within each watershed were obtained from the 2010 US census (www.census.gov) administered by the CNMI Department of Commerce (commerce.gov.mp). *Enterococcus* bacterial violations from nearshore waters were also examined as a proxy for water quality based upon the CNMI Division of Environmental Quality weekly beach water quality monitoring database (http://www.becq.gov.mp). The percentage of bacteria violations within each year was calculated between 2006 and 2015, and mean across the years was used for predictive modeling described below. A proxy for groundwater influence was determined by taking the lowest minimum tide for two months prior to each ecological survey date. This approach and timeframe have previously been used to capture groundwater influences on macroalgal canopies in the Saipan lagoon (Houk and Camacho 2010). Tide data were collected from the software Wtides (http://www.wtides.com). Sea-surface temperature data were obtained from NOAA's

OceanWatch (http://oceanwatch.pifsc.noaa.gov/). Last, rainfall data were obtained from the Saipan airport weather station (www7.ncdc.noaa.gov/).

Data Analyses

H01 and H02

Algal composition data were analyzed using the multivariate software packages Primer and Permanova+ (Anderson et al. 2008). Canopy cover data were first log transformed, and then used to create a Bray-Curtis similarity matrix. Bray-Curtis matrices described the ecological similarity between each pair of sites based upon summed differences in pairwise species abundances (Anderson et al. 2008). Here, Bray-Curtis matrices described the similarity in canopy cover data from the same sites across the wet and dry season. Before examining comparisons between seasons, tests for homogeneity of variances of the similarity matrix were performed using PERMDISP, analogous to a univariate variance test. Given homogeneous variance structures between the two groups, PERMANOVA tests were used to assess seasonal and spatial differences. PERMANOVA tests are evaluated based upon pseudo F-statistics (analogous to ANOVA F-statistics), and t-statistics for post-hoc comparisons, both with P-values that were assessed by a bootstrapping procedure that removed one data point at a time, and reassessed the results. Finally, a principal coordinate ordination (PCO) was performed on the similarity matrices to depict the PERMANOVA results in two-dimensional space. Each PCO axis represents an eigenvector and has an associated eigenvalue that describes the maximum amount of variation in the multivariate assemblages that could be explained by a single axis. The resulting PCO plots retain the two leading eigenvectors and eigenvalues. In order to appreciate which species contributed most to the PCO plot structure, species-based vector overlays were placed on the PCO plots to highlight species/genera that had the strongest

Pearson's rank correlation coefficients with the PCO axes, with vector length describing the strength of the correlation.

H03 and H04

Prior to assessing how macroalgal canopies have shifted through time in the Saipan Lagoon, predictable seasonal variation in macroalgal canopies was removed using the above analyses as a foundation. Significant differences in algal composition existed across the wet and dry season. These included relationships between: (i) cooler sea-surface temperatures and blue-green algae during the winter months, (ii) rainfall and *Acanthophora* red algae during summer months, and (iii) minimum tidal height and several brown and green alga in the karst watersheds of the southern lagoon. Thus, seasonal cycles were dependent upon the study region. Therefore, regressions between each of the seasonal environmental factors and the noted macroalgae were conducted within each region. A forward, stepwise regression modeling process was then undertaken using the base packages in R (Crawley 2007). The first step in the modeling process was to remove the seasonal component of macroalgal canopy dynamics by developing best-fit models with seasonal cycles, with and without log transformations to ensure residual normality. In order to partition seasonal variation, canopy cover estimates were replaced with their residual values from the first step in the regression modeling. This process served to remove the component of macroalgae cover that could be explained by seasonal cycles alone, and focus upon the temporal trends of interest.

ANOVA and pairwise comparison tests were used to test for changes in macroalgal canopies through time. Temporal comparisons were based upon seasonally-adjusted macroalgal canopy cover data. Data available for temporal analysis differed for each site based upon historical sampling (Table 1). In all instances, data were inspected for normality prior to ANOVA and linear models.

H05

To understand the possible causes underlying the changes in macroalgal persistence in the seagrass habitats, logit models were used to test whether high or low macroalgal canopy states were predicted by watershed characteristics on temporal trends (Crawley 2007). The temporal analyses noted above characterized the study regions into three categories, those that had (i) a consistent and high presence of macroalgal canopies above 10% of seasonally adjusted values, (ii) significant increases in macroalgal canopies with present estimates above 10%, and (iii) no significant changes or static macroalgal canopies less than 10%. The relevance of these categories for site-based characterizations was furthered examined using natural breaks in the distribution of present macroalgal canopy estimates. Jenks Natural Breaks Optimization procedures (hereafter referred to as Jenk's breaks) defined 3 class breaks for canopy cover: 0 to 7.1, 7.2 to 19.5, and greater than 19.5 (Jenks & Coulson 1963). These breaks corresponded with the categories used to assess trends through time. Therefore, sites with either persistently high or significantly increasing macroalgal canopies were grouped (i.e., "high" macroalgal canopy states), and sites with non-significant increases and low present canopies were grouped (i.e., "low" macroalgal canopy states). Similar to linear models, logit models have P-values as well as intercepts and slopes. The difference being that logit models fit a logarithmic curve that predicts the odds of the dependent variable based on the independent variable. Linear models using only the present macroalgal canopies were also conducted to support the logit regression models. Together, these final models helped to understand the drivers of change through time and current states.

Results

Seasonal and Spatial Dynamics

Seasonal differences in the canopy cover of macroalgae and seagrasses were consistent across all study regions in the Saipan Lagoon (Pseudo-F = 55.527, p-value 0.0001, PERMANOVA, Fig. 2). *Halodule uninervis* was the most abundant canopy taxon during both seasons, accounting for approximately 30% of the cumulative cover. However, there were consistent differences in the seasonal growth of macroalgae that led to inter-annual trends. Higher cover of the red alga *Acanthophora spicifera,* the green algae *Halimeda* spp., and the brown algae *Dictyota* spp. were consistently found during the warmer, wet season (July to December), across all study regions (Fig. 3). In contrast, mixed species of blue-green algae, *Hydroclathrus* spp., and *Padina* spp. became more prolific during the cooler, dry season (January to June). Nested within these overarching trends were site-specific differences in numerous macroalgae whose abundances varied uniquely at the site level (several different *Halimeda* and *Caulerpa* species, *Hydroclathrus clathratus*, and *Acanthophora spicifera*; Fig. 3). In support, spatial differences across the study regions were pronounced once accounted for seasonal trends in nested designs (Pseudo F = 7.39, P=0.0001, Nested PERMANOVA). Within each season, spatial differences were generally consistent across the entire lagoon (Fig. 4). During the dry

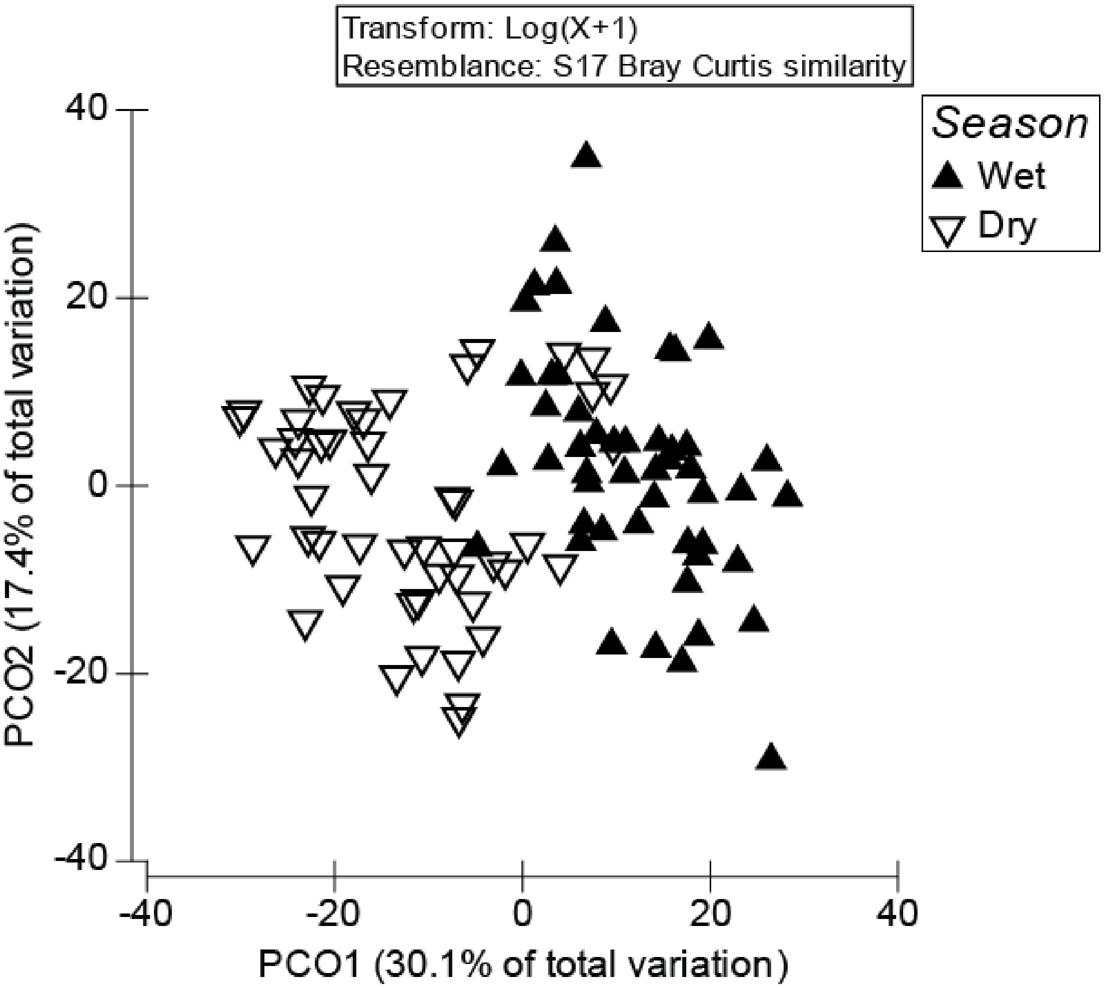

Figure 2. Principle Component Ordination (PCO) plot showing the seasonal difference within the Saipan Lagoon. Solid triangles represent the surveys conducted during the wet season and the inverted, hollow triangles represent surveys conducted during the dry season.

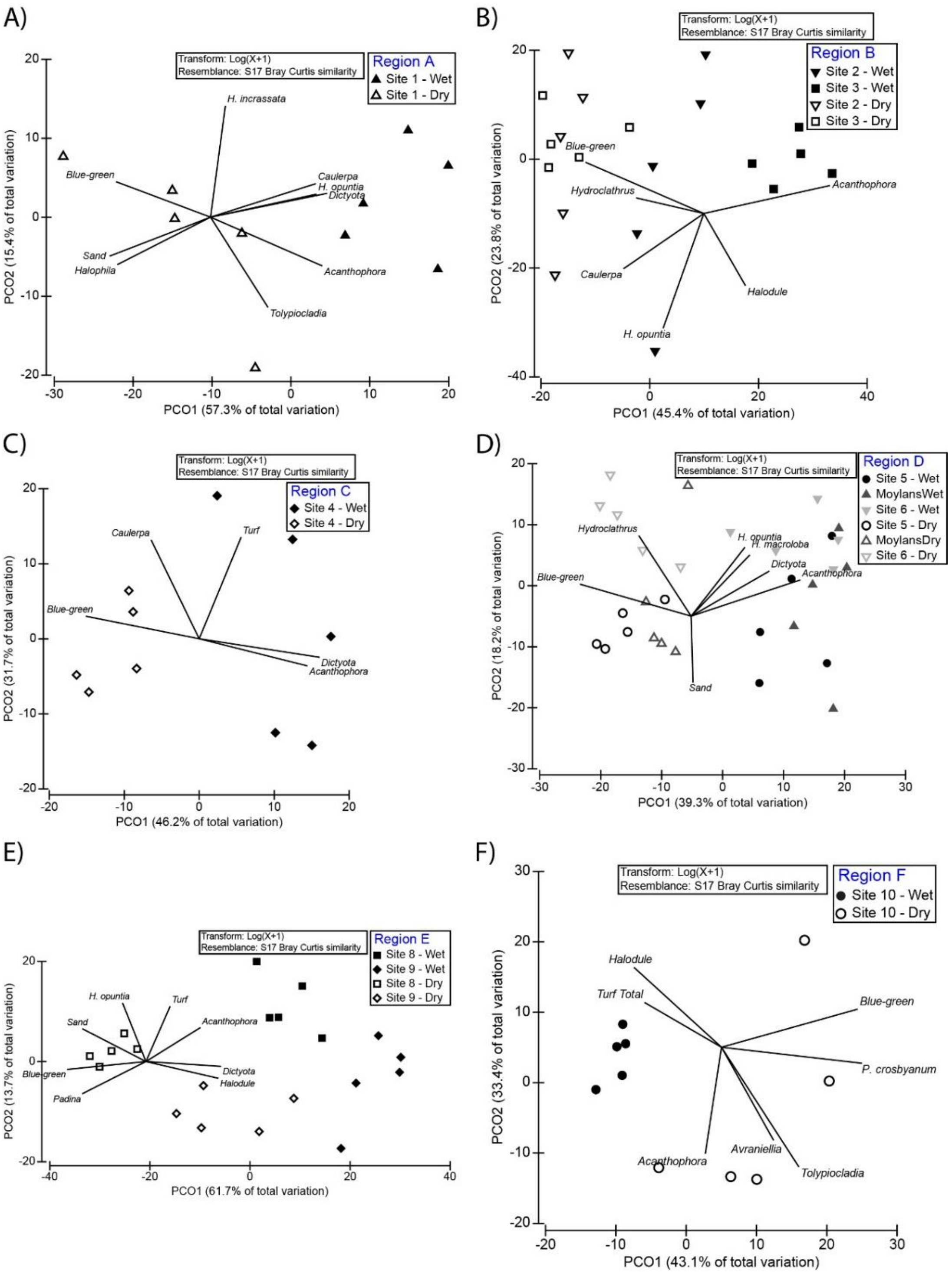

Figure 3. PCO plots of the seasonal variation by study region and site. Solid points correspond to surveys conducted during the wet season and hollow points correspond to surveys conducted during the dry season. The plots show that there is a separation in canopy cover over the seasons and that each site is also different from each for each season.

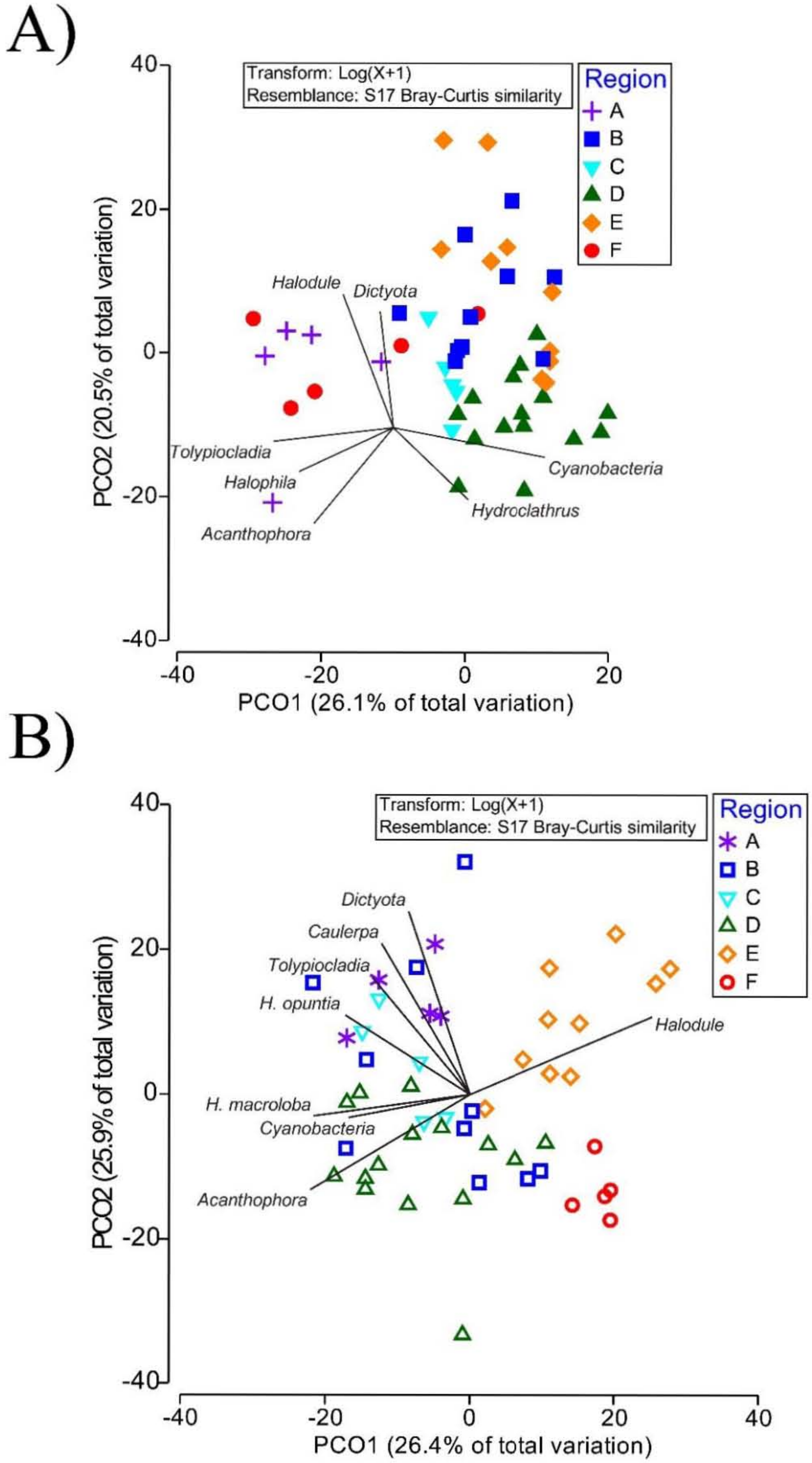

Figure 4. Principle Component Ordination (PCO) plot of the spatial variations by regions for (A) dry and (B) wet seasons in the Saipan Lagoon.

season, lagoon regions associated with disproportionally low human populations were separated along the primary axis of the principle components ordination (PCO x-axis, watersheds in the furthest north and south, away from the population center, regions A and F, Figure 4A). These regions had significantly lower abundances of seasonal blue green algae and *H. clathratus* compared to others, confirmed by pairwise multivariate testing among sites (Pseudo t-statistic >1.94, P<0.026). Seasonal macroalgal enrichments within the remaining regions (B, C, D, and E) followed a predictable pattern, with highest coverage in the central lagoon seagrass habitats where human population density was highest, and gradually declining when moving away from this central area in both directions, north and south (PCO y-axis, Fig. 4A). During the wet season, there was also clear separation along the primary PCO axis, but the wet season differences were associated with watershed geology. Regions with small, limestone watersheds in the south of the lagoon were distinct from others based upon disproportionally lower seasonal influences of *Acanthophora*, *Halimeda*, and *Dictyota* (Pseudo t-statistic >2.36, P<0.016). After accounting for watersheds with significant groundwater discharge, remaining regions followed a similar trend revealed during the dry season (PCO y-axis, Fig. 4B).

Global regression models, inclusive of all sites and all years, supported that the main seasonal trends in the Saipan Lagoon were sea-surface temperature, rainfall, and groundwater, respectively (Figs 5 A and B). There was a consistent inverse relationship between temperature and blue-green algae canopy cover, as cooler temperatures persisted there was an increase in blue-green algae across all regions (Fig. 5A). In support of the multivariate analyses, the tightest relationships were found in the center of the lagoon, Region D, and gradually decreased moving both north and south (regression slopes, Fig.

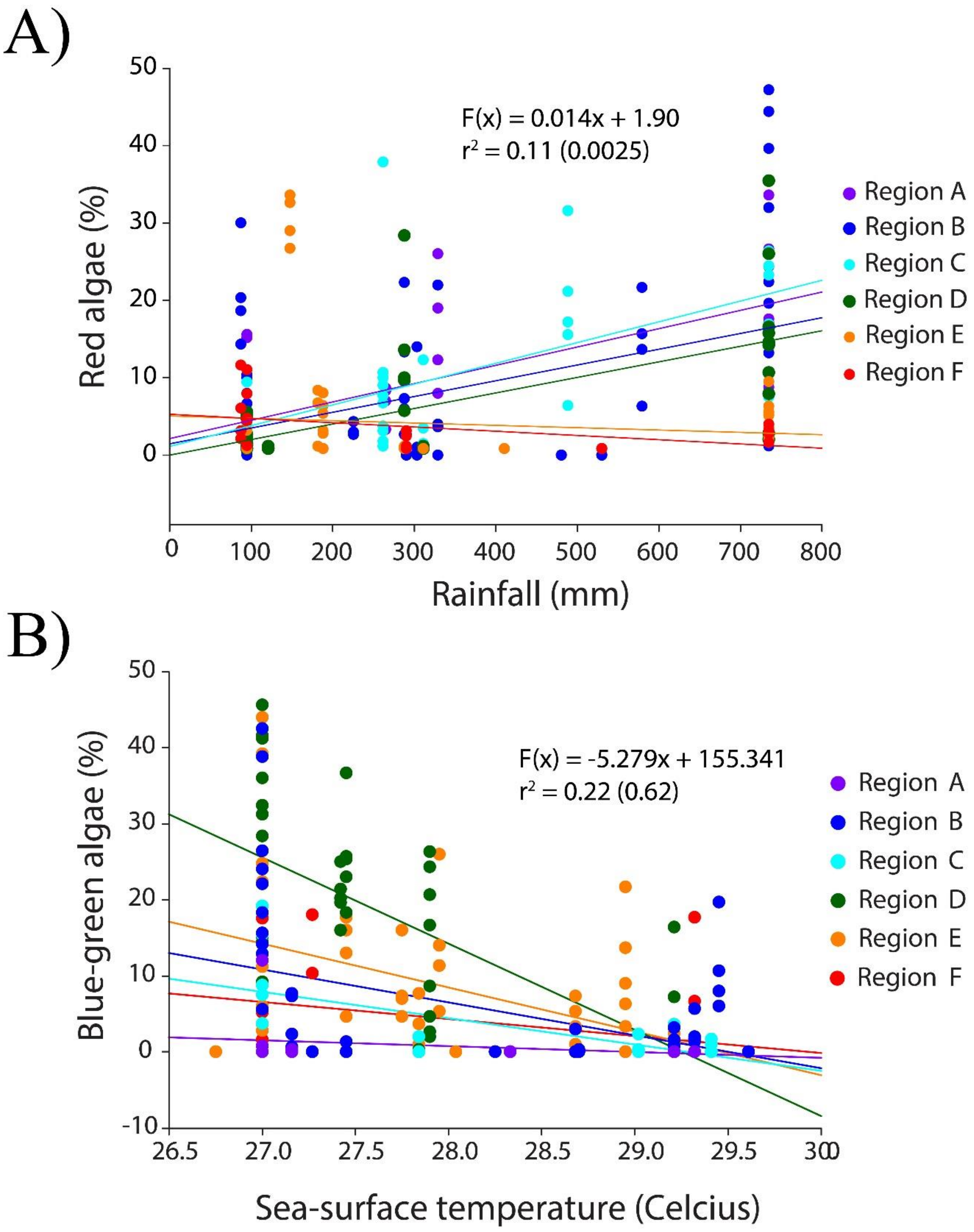

Figure 5. A regional scatterplot of the relationship between A**)** blue-green algae and sea surface temperature (SST) and B**)** red algae and rainfall. Based on the plots, there is a negative relationship between the blue-green algae and SST and a weak positive relationship between red algae and rainfall.

5A). In contrast, red algae showed a positive relationship with rainfall, which was amplified when removing the southernmost regions E and F where groundwater discharge existed with limestone watersheds (Figure 5B). Again, the slope of this relationship generally decreased with distance from the center of the lagoon, though not as strongly. Lastly, groundwater (GW) influence, as estimated by the two-month minimum low tide, had a consistent but weak influence on *Acanthophora* and *Dictyota*, whereby lower minimum tide heights predicted greater algal cover in regions E and F only.

Local regression models within each region provided further insight into the magnitude and spatial distribution of seasonal factors across the lagoon. The relationship between SST and blue-green algae cover was most pronounced (regions A to E), followed by the relationship between rainfall and red algae (regions A to D), and finally groundwater for both green and brown algae (regions E and F only) (Table 2). Local models therefore resonated with both multivariate tests and global models. Given the predictable nature of seasonal factors and algal cover within each region, it was possible to remove the estimated component of seasonal variation by extracting the residuals from local models, and replacing the algal cover values with these residuals prior to temporal analyses (i.e., the proportion of variation not accounted for by seasonal factors).

Temporal Trends

Temporal change in adjusted macroalgal canopies differed for each site and region, but were characterized into common response categories. Macroalgal canopies were consistently high across sites in the central lagoon through time, with no significant differences reported within region C (Fig. 6), the southernmost site in region B (Site 3**,** Fig. 7B), and the northernmost site in region D (Site 6, Fig. 10a) (≥10% adjusted macroalgal

Table 2. Regression models describing the relationship between natural environmental regime and algal phylums. These results were used to partition the variance in algal abundance by suppressing seasonal effects.

Region	Site	Model	Slope (SE)	P- value
A	1	lm(red~rainfall)	0.02 (0.008)	0.005
B	2 and 3	lme(log(bg+1)~sst, random= ~1|site)	-0.69 (0.14)	0
		lme(log(red+1)~rainfall, random= ~1|site)	2.0 E^{-3} (1.0 E^{-3})	0.01
C	4 and 5	lme(log(bg+1)~sst, random= ~1|site)	-0.69 (0.14)	<0.0001
		lme(log(red+1)~rainfall, random= ~1|site)	3.0 E^{-3} (1.0 E^{-4})	0.001
D	6 and 7	lme(log(brown+1)~sst, random= ~1|site)	0.88 (0.13)	0
		lm(bg~sst)	-11.33 (1.96)	<0.0001
		lm(log(red+1)~rainfall	3.0 E^{-3} (5.0 E^{-4})	<0.0001
E	8 and 9	lme(log(green+1)~gw, random= ~1|site)	-0.06 (0.11)	<0.0001
		lme(log(brown+1)~gw, random= ~1|site)	-0.23 (0.11)	0.05
		lm(log(bg+1)~sst)	-0.63 (0.18)	<0.001
F	10	lm(green~rainxgw)	4.19 (0.75)	<0.0001
		lm(log(brown+1)~rainxgw)	0.27 (0.06)	<0.0001

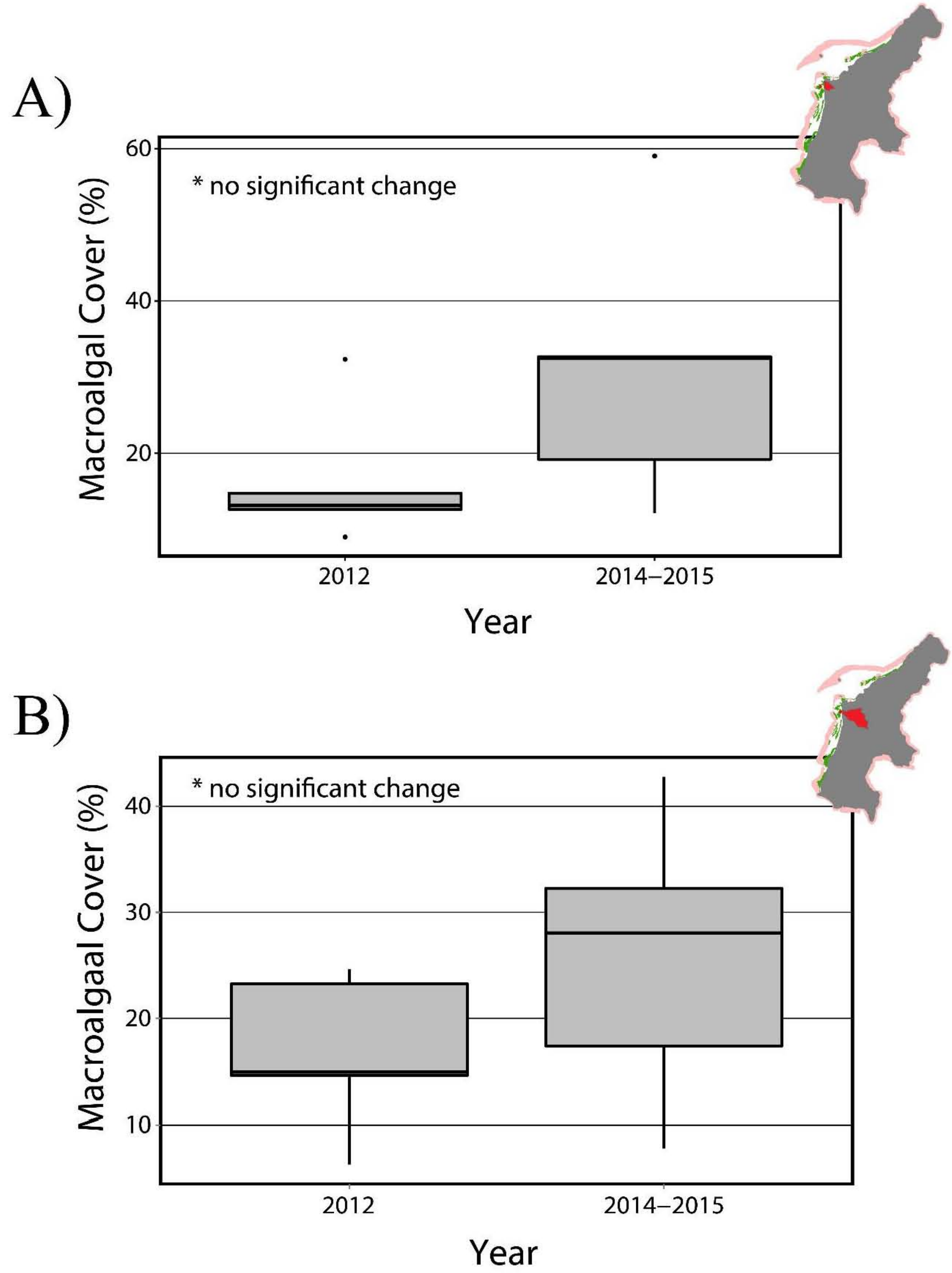

Figure 6. Box plot of macroalgal cover change through time in Region C. Macroalgal cover represents residuals (if significant from regression, Table 2) and raw values. A) Site 4. B) Site 5.

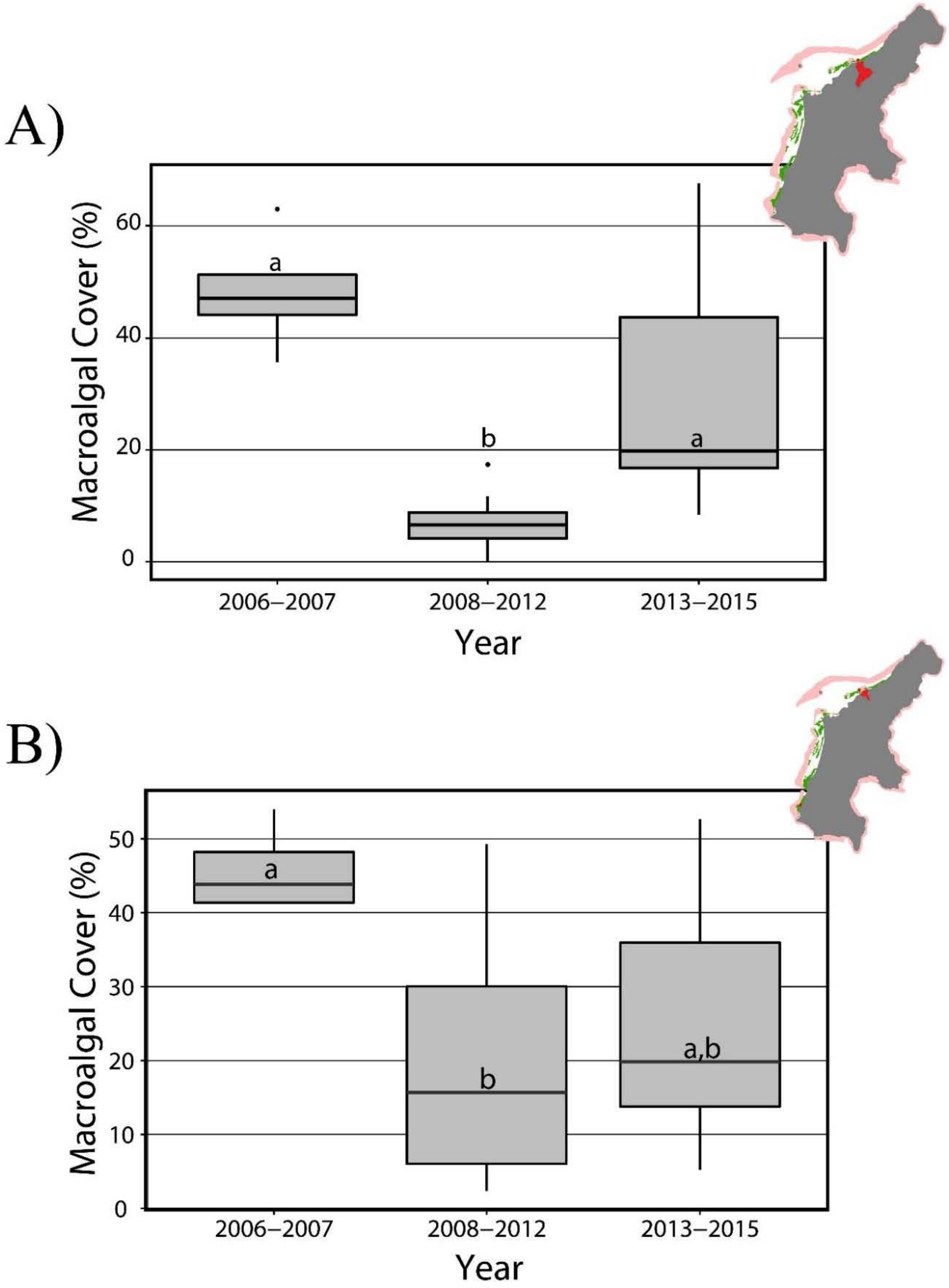

Figure 7. Box plot of macroalgal cover change through time in Region B. Macroalgal cover represents residuals (if significant from regression, Table 2) and raw values. A) Site 2. B) Site 3. Lowercase letters indicate statistical groupings.

cover through time, $P_{adj}>0.05$ through time, multiple pairwise comparisons). Macroalgal in the northern lagoon was initially ≥30%, with large-wave disturbance events providing a significant, intermittent reduction, followed by subsequent increases until disturbances occurred again (i.e., a disturbance-mediated tendency for macroalgal persistence; Fig. 8). Moving towards the wave-sheltered, southern part of the lagoon, there was a significant increase in adjusted macroalgal canopy cover through time (Site 7 within region D, $P_{adj}<0.04$, pairwise comparisons) (Fig. 9B). Finally, there were non-significant changes through time and persistent, low macroalgal in the southern lagoon with limestone watersheds and associated groundwater influences **(**Figs. 10 and 11**)**. In sum, for regions A to D macroalgal canopies were either (i) persistently high, (ii) intermittently disturbed by large wave events that reduced canopies, but with subsequent increases to high states, >15%, or (iii) had significant increases through time to high states, >10%. In contrast, low macroalgal canopy cover remained within regions E and F, <10% (Table 3). In support of these generalized response categories, natural breaks in the present macroalgal canopy data also separated the sites into the same groupings. Thus, responses through time were evaluated with respect to the tendency for 'low' or 'high' macroalgal canopy states using logit models, while present macroalgal canopies were evaluated using linear models.

Watershed size and disturbed or altered land were the only significant predictors of macroalgal canopy responses through time (Fig. 12 A and B). Both variables were associated with non-overlapping, complete separation of macroalgal canopy states (i.e., perfect fits to the logit models). However, there was only a moderate correlation between watershed size and altered land of 0.62 (Fig. 13A), suggesting both were drivers of

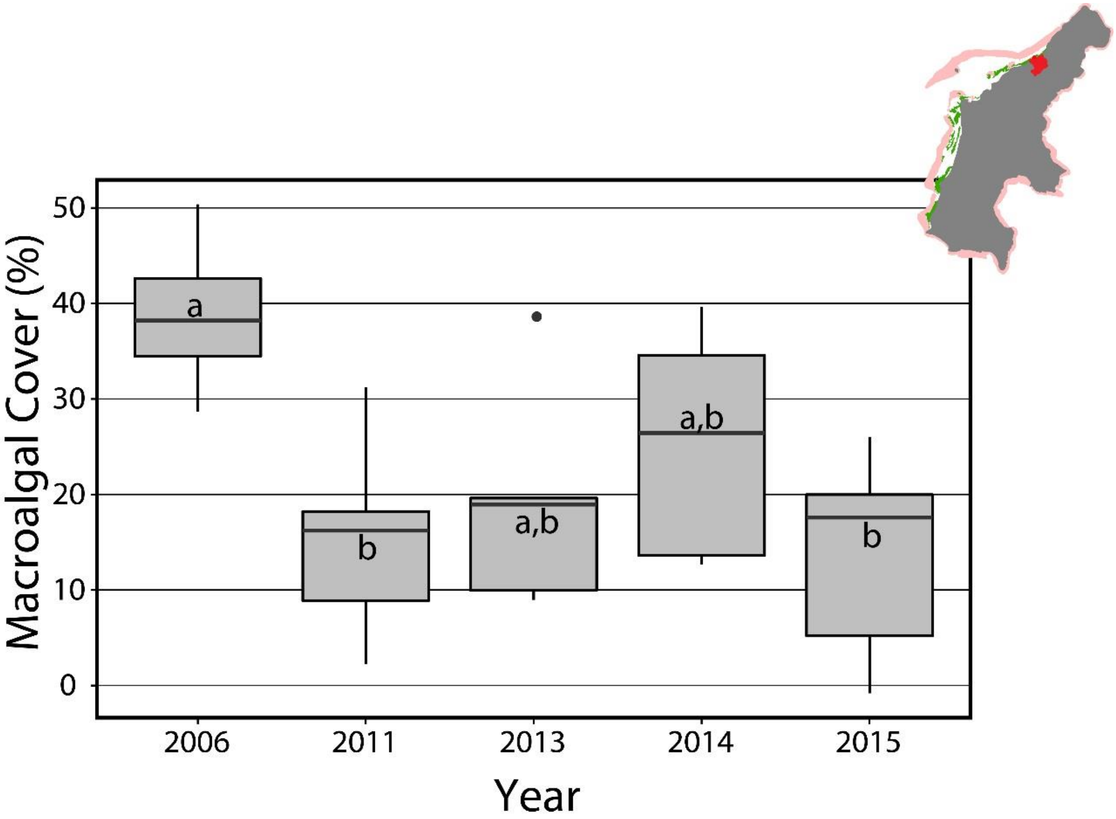

Figure 8. Box plot of macroalgal cover change through time in Region A, Site 1. Macroalgal cover represents residuals (if significant from regression, Table 2) and raw values. Lowercase letters indicate statistical groupings.

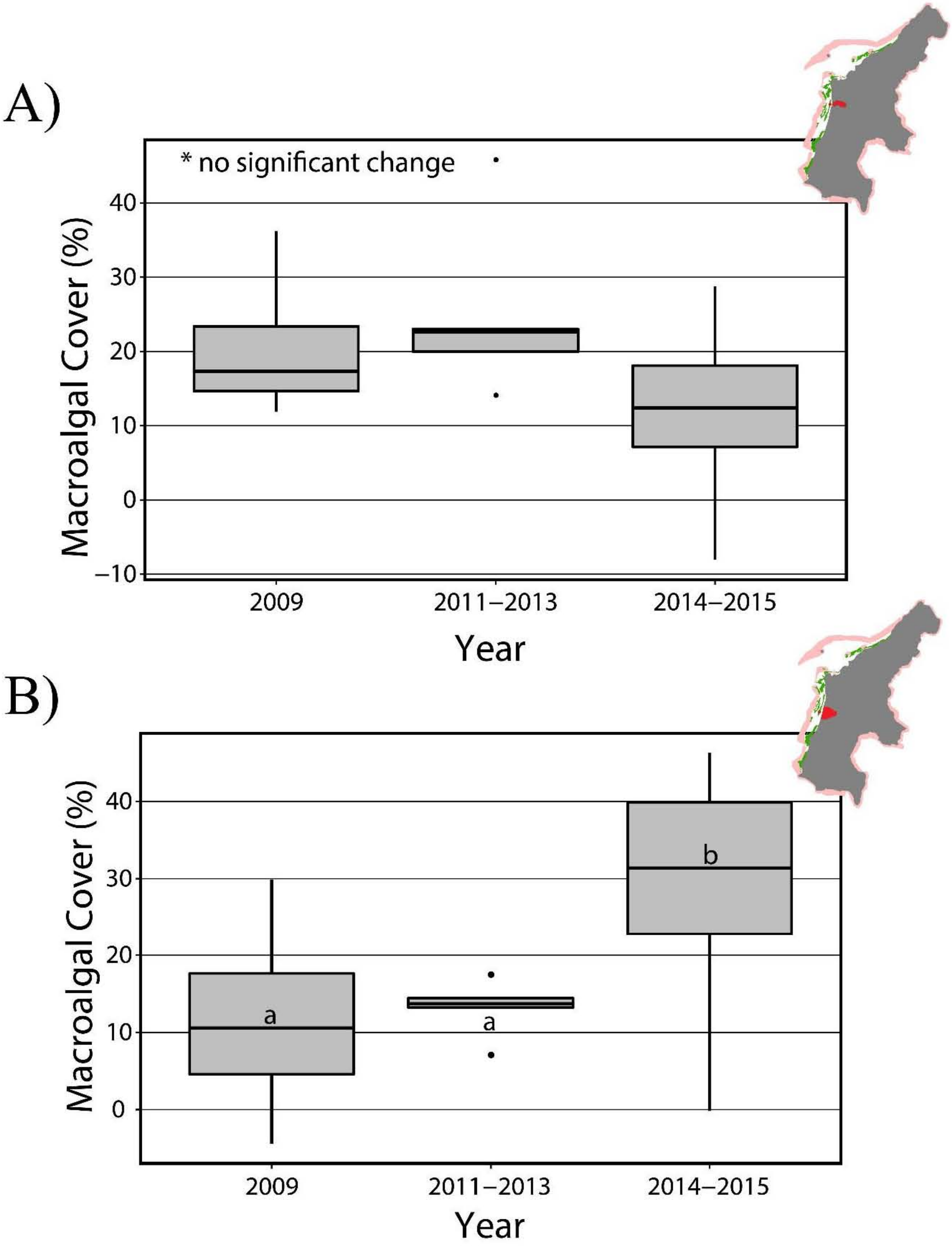

Figure 9. Box plot of macroalgal cover change through time in Region D. Macroalgal cover represents residuals (if significant from regression, Table 2) and raw values. A) Site 6. B) Site 7. Lowercase letters indicate statistical groupings.

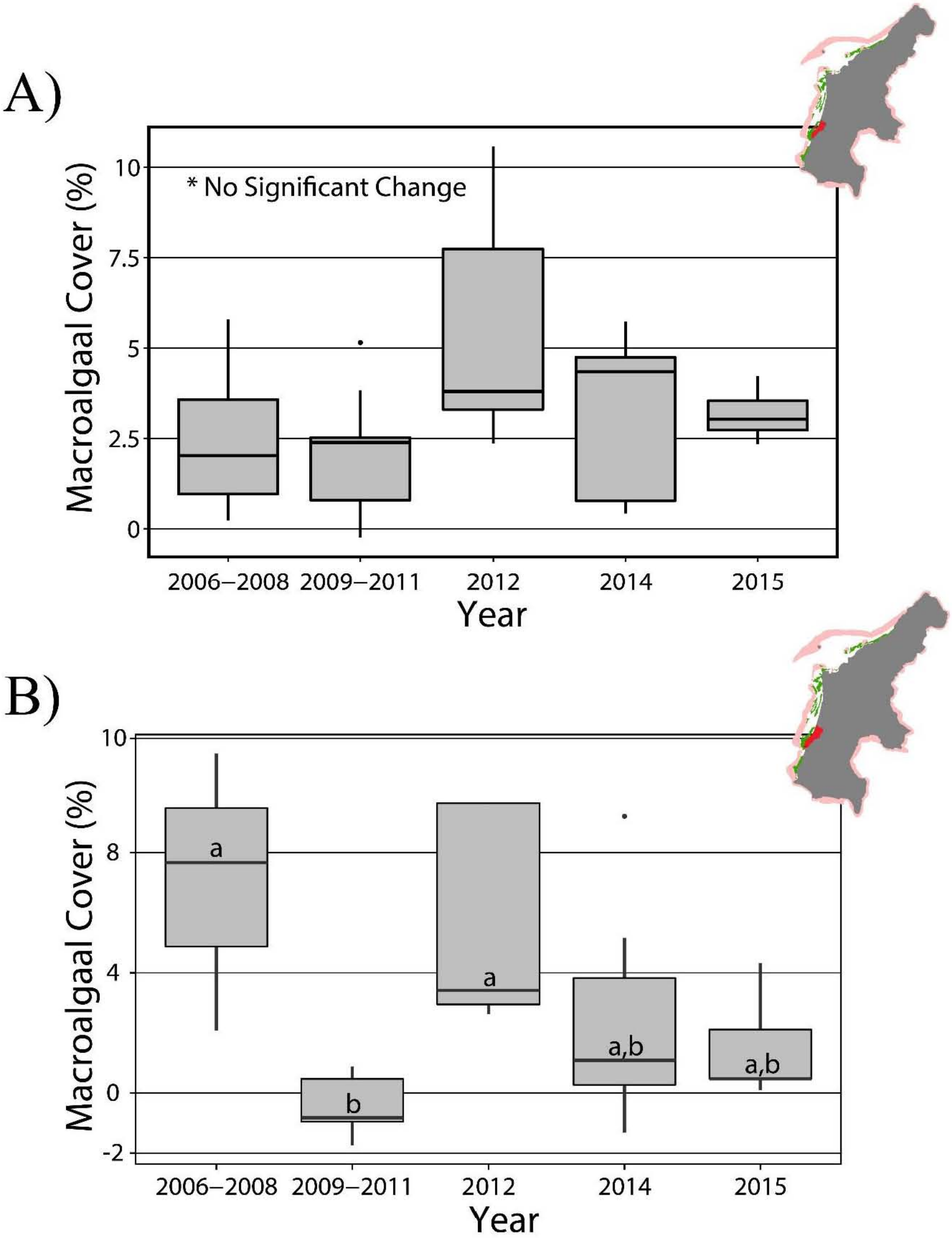

Figure 10. Box plot of macroalgal cover change through time in Region E. Macroalgal cover represents residuals (if significant from regression, Table 2) and raw values. A) Site 8. B) Site 9. Lowercase letters indicate statistical groupings.

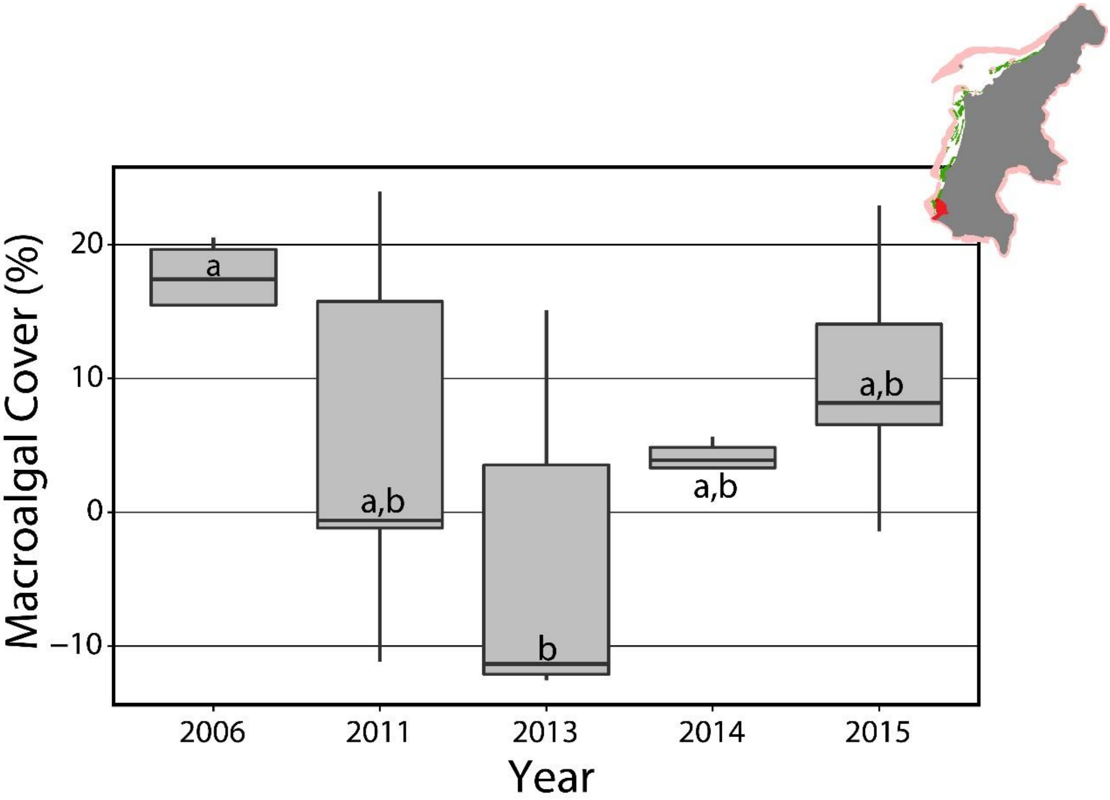

Figure 11. Box plot of macroalgal cover change through time in Region F, site 10. Macroalgal cover represents residuals (if significant from regression, Table 2) and raw values. Lowercase letters indicate statistical groupings.

Table 3. Summary table of ANOVA results and Tukey post-hoc comparisons for macroalgal canopy changes between 2006 and 2015. Macroalgal canopy state, defined in methods, was included to characterize sites as having either 'high' or 'low' macroalgal canopy cover through time. In addition, Jenk's breaks were used to characterize the present macroalgal cover across sites into three classes, which corresponded with the categories used to characterize temporal trends –(***>19.5, **>10%, and *<10% adjusted 2014-15 macroalgal canopy cover estimates)

Region	**Site**	**F-Statistic**	**P-value**	**Trends**	**Macroalgal canopy state**
A	1	3.64	0.02	Significant decrease from 2006 to 2011 (p_{adj} = 0.038). Algal cover remains the same with a non-significant increase in 2014 and a non-significant decrease in 2015. Change most likely caused by large-wave disturbances.	High***
B	2	11.54	$3 E^{-3}$	Significant decrease from 2006-2007 to 2008-2012 (p_{ad} = 0.0004) and a significant increase from 2008-2012 to 2013-2015 (p_{ad} = 0.0044)	High***
	3	4.30	0.03	Significant decrease from 2006-2007 to 2008-2012 (p_{ad} = 0.02). The algal cover change is non-significant in 2013-2015.	High**
C	4	2.77	0.14	No significant increase from 2012 to present with high algal cover.	High***
	5	2.95	0.10	No significant increase from 2012 to present with high algal cover.	High***
D	6	3.31	0.06	No significant change over the years, but constant high macroalgal cover.	High**
	7	4.11	0.04	No significant increases of macroalgal cover from 2009 - 2015. High algal cover	High***
E	8	2.09	0.12	Macroalgal cover is low and increases (non-significant) in 2012 and then decreases (non-significant) in the later years.	Low*
	9	4.34	$.9 E^{-3}$	Significant decrease in algal cover from 2006-2008 to 2009-2011 (p_{ad} = 0.02) and a significant increase from 2009-2011 to 2012. From 2012 to present, the algal cover then decreases (non-significant). Algal cover for all years <10%.	Low*
F	10	2.94	0.047	Algal cover has decreased from 2006 to 2013 and then increased in subsequent years. Algal cover for all years <20%	Low*

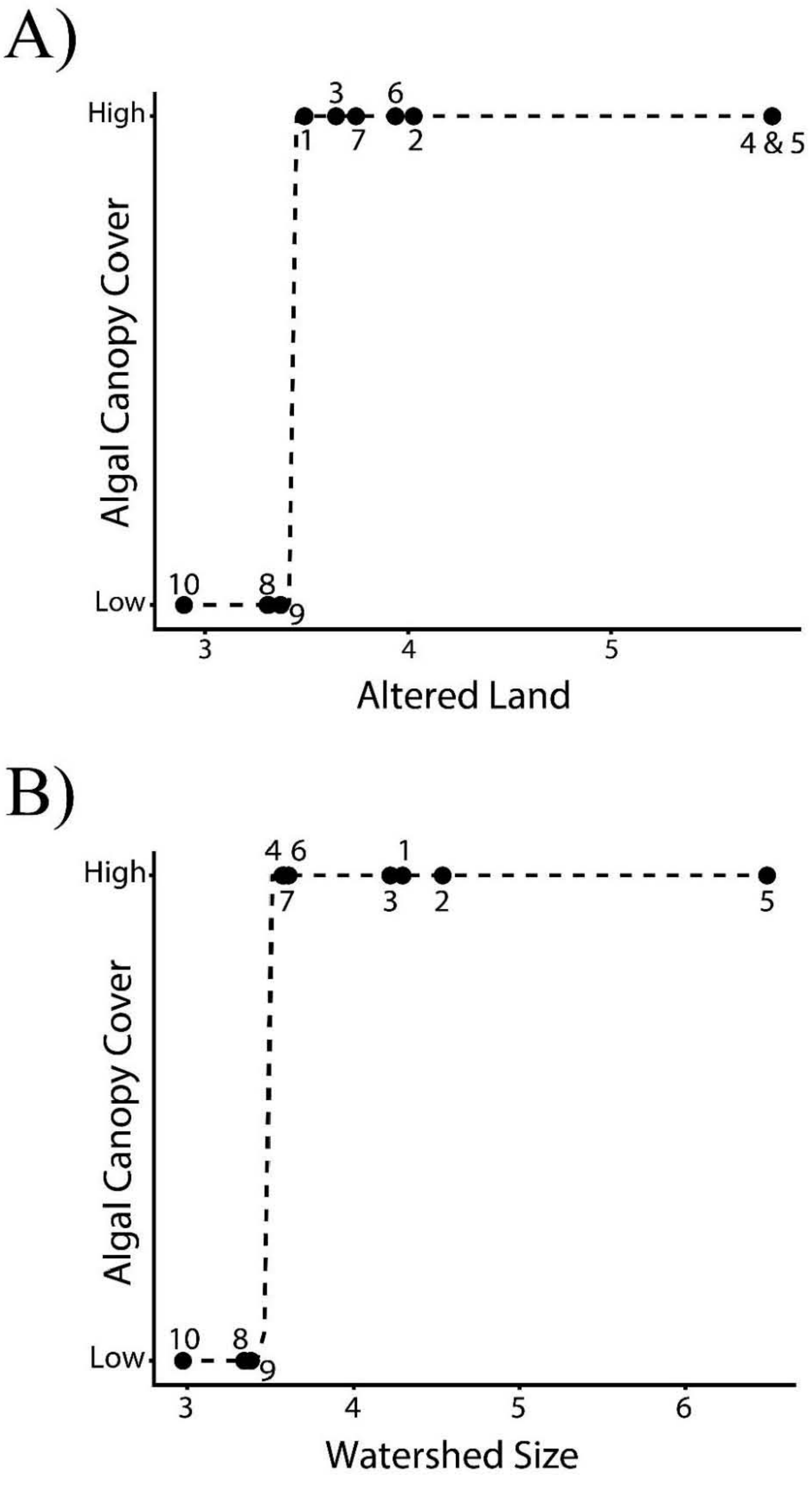

Figure 12. Logit models with logistic regressions of adjusted macroalgal canopy cover. Both models are good predictors for algal canopy cover in the Saipan Lagoon. However, the logit model for altered land (A) has a higher odds ratio when compared to watershed size (B).

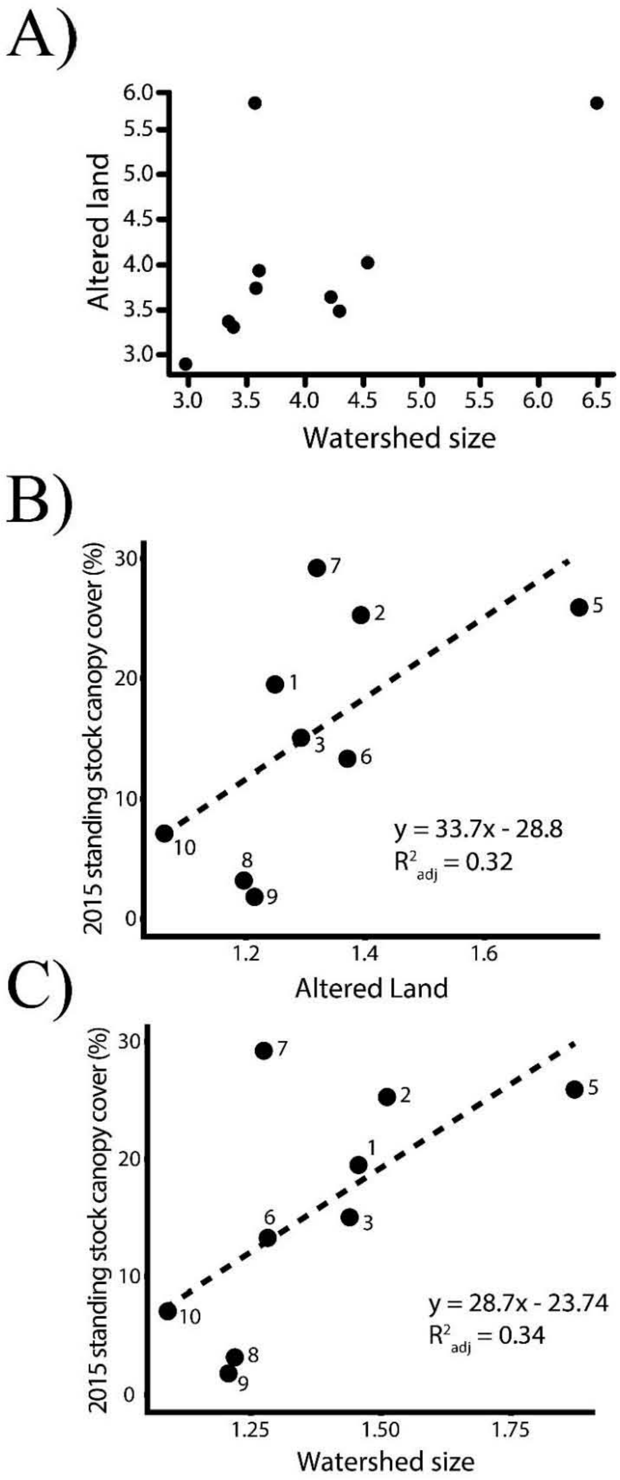

Figure 13. Scatterplots of 2015 standing stock and logit model predictors. A) Correlation plot of altered land and watershed size (cor=0.62). Linear regression model current standing stock showing the positive relationship of algal cover and altered land (B) and watershed size (C).

temporal trends. This trend was further supported by linear models describing watershed size and altered land as the only significant drivers of macroalgal canopy cover in 2015, with nearly identical amounts of variance explained and overall model fits (Fig. 13 B and C). The models summarized positive relationships between macroalgal canopy cover and both altered land and watershed size ($R^2_{adj} = 0.32$, $P = 0.06$, $R^2_{adj} = 0.34$, $P = 0.06$, Fig. 13 B and C).

Discussion

This study reported on the ecology of *Halodule* seagrass habitats within Saipan Lagoon over a 10 year period by first partitioning the variance associated with seasonal variation, and then examining trends through time in canopy cover with respect to watershed characteristics. Past studies examining temporal change in seagrass habitats have often focused on seagrass plant physiology, above-and-belowground plant biomass, and the overall productivity of seagrass beds across several years (Lanyon & Marsh 1995, Fourqurean et al. 2001). Generally, extensive seagrass meadows along continental shelves have greater biomass and production during the wet seasons when exposed to increased nutrients, as biomass within the root system becomes increased compared to the plant. However, across longer time periods or larger increases in nutrients, undesirable seagrass-to-macroalgal phase shifts can occur (Cardoso et al. 2004, Houk & Camacho 2010). Phase shifts leading to seagrass habitat loss have often been observed through aerial imagery across decades (Kendrick et al. 1999, Kendrick et al. 2002). The present study helped to uncover the processes and mechanisms behind long-term phase shifts in *Halodule* beds by focusing on macroalgal canopy dynamics that ultimately limit the amount of sunlight available for growth (Bell & Hall 1997, Hauxwell et al. 2001, Schaffelke et al. 2005).

Predictable seasonal cycles were first revealed by examining sea surface temperature and rainfall with respect to macroalgal growth. After accounting for the variance associated with seasonal cycles, temporal trends became clear, and were characterized with respect to watershed size and the amount of disturbed land.

The strongest seasonal cycle was associated with emergence of blue-green algae during the winter months with cooler sea surface temperatures. Blue-green algae were grouped for analysis, but mainly consisted of *Lyngbya* sp., with secondary contributions from *Phormidium* sp. (previously identified as *Schizothrix* sp.), and small contributions from *Calothrix* sp. Samples have been collected but no formal species identifications have been confirmed. These findings resonated with a previous study in Guam that reported *Lyngbya* sp. to be most abundant starting in January with cooler temperatures, with a localized presence remaining until June (Palmer 2003). Elsewhere, studies from both freshwater (McQueen & Lean 1987) and marine ecosystems (Fong & Zedler 1993, Kanoshina et al. 2003, Watkinson et al. 2005) have concluded that water temperature is one key factor promoting the growth of blue-green algae. Studies in temperate regions (Lake St. George and Baltic Sea) found that blue-green algal emergence was associated with warmer spring and summer temperatures, ranging between 19-22°C, alongside nutrient contributions from freshwater inputs (McQueen & Lean 1987, Kanoshina et al. 2003). In contrast, cooler waters during the winter months in Saipan have higher nutrient concentrations, particularly dissolved N and P (Eldredge & Center 1983). Thus, water temperatures and nutrient concentrations may act individually or in combination to promote blue-green algal growth, with differences across temperate and tropical regions attributed to the characteristics of local seasonal cycles.

Increased abundances of brown algae were also observed during winter months, with *Hydroclathrus clathratus* being the most dominant species. This also resonated with a local study on Guam where brown algae were present throughout most of the year, but were more abundant during winter months. Further, *H. clathratus* was only present during the dry months of February thru to the end of April (Tsuda 1974).

Nutrient-rich surface runoff and groundwater contributions also had predictable seasonal influences on macroalgal canopies. The average rainfall in Saipan during the dry and wet seasons differs substantially. Ten-year average rainfall during the dry season is 280 to 697 mm per year (January to June), while long-term averages during the wet season averages are well over twice as large (1040 to 1957 mm per year, July to December). The increase in precipitation during the wet season promotes freshwater runoff that is naturally higher in nutrients compared with tropical ocean waters (DiDonato et al. 2009). In addition, surface runoff carries pollutants from developed areas and fertilized farmlands to the lagoon through storm-drainages and groundwater seepages where karst limestone aquifers exist. Studies done in the past clearly show that excess nutrients promote algal growth (McGlathery 2001, Ferdie & Fourqurean 2004, Biber & Irlandi 2006, Burkholder et al. 2007), but the rate/ability at which algae can assimilate available nutrients differs between species (Biber et al. 2004). In this study, the most emergent alga during the wet season was the red algae, *Acanthophora spicifera,* but several others had seasonal contributions as well, including *Halimeda macroloba*, *Caulerpa spp*., and *Dictyota spp*. Past studies done in Hawaii, where *A. spicifera* is an invasive species, have also shown a strong response in growth with increased nutrients from storm-drains and sewage leaks (Eldredge & Smith 2001, Smith et al. 2002, Lapointe & Bedford 2011, Dailer et al. 2012). Though *A. spicifera* was abundant throughout most of the lagoon during the wet season, there was a notable absence or decreased abundance of this alga in the southern lagoon where karst aquifers and notable groundwater discharge existed (Houk and Camacho 2010). In support, Herrera-Silveira (1996) found that nutrient rich groundwater in the Celestun Lagoon (Gulf of Mexico) was influenced by the amount and frequency of rainfall, and that permeable soils in the aquifer allow for some filtration and nutrient reduction prior to discharge. Previous studies in the Saipan Lagoon have shown cyclical discharge of groundwater during extreme tides associated with full and new moon phases each month, providing for a slow, steady contribution of higher nutrients when averaged across the year (Houk and Camacho 2010). Yet, macroalgal enrichment in these areas was not as severe compared with larger watersheds where surface runoff existed. It appears that karst aquifers may serve to filter storm-water runoff during large rain events, and reduce pulsed contributions of nutrient rich runoff and sediment accumulation. The present study reveals that *Halodule* beds in the Saipan Lagoon associated with the smallest, karst watersheds were the only localities shown to have low macroalgal canopy cover through time.

While many studies have improved our appreciation for seasonal macroalgal growth cycles, fewer have attempted to formally account for seasonal influences when interpreting temporal trends. Monitoring programs might inherently account for seasonal cycles by sampling during the same month(s) each year, yet, annual differences in rainfall and sea surface temperature would still exist. Here, the inter-annual temperature difference for February was ±1.0 °C and September rainfall ranges between 375 mm and 514 mm over the study period. Based upon the global regression models, these differences could lead to a shift in macroalgal coverage across the Saipan study sites of up to 15%. This suggests that accounting for inter-annual seasonal variation in statistical models is essential prior to interpreting the nature and cause of temporal change. Because monitoring resources are limited in the CNMI, data collection events over the past decade have been conducted opportunistically during different months and seasons. Yet, by accounting for seasonal contributions, the last set of analyses were able to hypothesize whether seagrass beds were likely to: 1) remain in a low macroalgal canopy state, 2) continue shifting from low-to-high canopy cover, or 3) remain in a high macroalgal canopy state. In turn, these predictive states and 2014-15 adjusted coverage were both predicted by the size of the adjacent watershed and the amount of disturbed land within. Watershed factors served to increase the magnitude or extend the persistence of macroalgal canopies, or both. Logically, management would focus on the trends with disturbed land.

Management

The Saipan Lagoon Use Management Plan along with the local watershed impairment listing reports represent planning documents that help prioritize limited funding and resources that are available for watershed improvement projects. Seagrass habitats that had persistent and high macroalgal canopies were mainly associated with watersheds that have already been ranked as ”poor” (Bearden et al. 2014). Clearly restoration in these areas should be prioritized, but given the relative high urban development and economic interests, the cost of watershed restoration may be very high and socially contentious. Limited resources might alternatively focus on areas that gradually increased in macroalgal cover in recent years (Regions B and E). Watershed improvement projects in these regions could potentially gain more ecological value for less economic cost, and have less social conflict. Meanwhile, the central urbanized watersheds could remain as priorities areas for unique, intermittent management opportunities that attract more funding, but on an opportunistic basis. Last, the northernmost section of the lagoon (region A) was shown to have undesirable macroalgal build-up periodically, but large wave events common during winter months appeared to flush the seasonal macroalgal stands. These trends confirmed a shorter term study based upon smaller seagrass plots, whereby two large wave events removed dense *Caulerpa* stands that persisted for several months, as well as seasonal brown and red algae build-up (Houk and Camacho 2010). The other two regions with comparatively 'healthy' seagrass beds were associated with smaller watersheds and cyclical groundwater influence. These areas should not be ignored as they are still vulnerable to change with an increase in urbanization or agricultural-use that remains ongoing.

Conclusion

Seagrass habitats provide goods and services to coastal societies across the world, but are vulnerable to watershed pollution and habitat modification. Productive seagrass beds provide for fisheries, absorb nutrients from watershed runoff, and have roots that stabilize coastal shorelines. However, when inundated with excess sedimentation and nutrients from uncontrolled watershed development, seagrass beds and the benefits they provide to society erode. Indeed, the global decline in seagrass habitats has mainly been attributed to watershed and coastal development that provides excess nutrients to these habitats and disrupts the balance between seagrass and macroalgal canopies. Pulsed, seasonal dynamics complicate our ability to detect temporal trends and provide tangible guidance to managers in a timely manner. This study partitioned the seasonal and temporal variance in canopy cover across a 10-year period to predict the tendency for macroalgal versus seagrass dominance into the future, and determined causal relations with watershed size and urban development. The results offered tangible guidance for improved management strategies in Saipan Lagoon, and improved our understanding of how seasonal and temporal trends emerge in these complex ecological systems.

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