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Herbivore and Nutrient Impact on Primary Producer Assemblages in a Tropical Marine Environment

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HERBIVORE AND NUTRIENT IMPACT ON PRIMARY PRODUCER

ASSEMBLAGES IN A TROPICAL MARINE ENVIRONMENT

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by

Elizabeth Anne Lacey

2012

To: Dean Kenneth G. Furton
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This dissertation, written by Elizabeth Anne Lacey, and entitled Herbivore and Nutrient Impact on Primary Producer Assemblages in a Tropical Marine Environment, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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ABSTRACT OF THE DISSERTATION

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Globally, human populations are increasing and coastal ecosystems are becoming increasingly impacted by anthropogenic stressors. As eutrophication and exploitation of coastal resources increases, primary producer response to these drivers becomes a key indicator of ecosystem stability. Despite the importance of monitoring primary producers such as seagrasses and macroalgae, detailed studies on the response of these benthic habitat components to drivers remain relatively sparse.

Utilizing a multi-faceted examination of turtle-seagrass and sea urchin-macroalgae consumer and nutrient dynamics, I elucidate the impact of these drivers in Akumal, Quintana Roo, Mexico. In Yal Ku Lagoon, macroalgae bioindicators signified high nutrient availability, which is important for further studies, but did not consistently follow published trends reflecting decreased $\delta^{15}N$ content with distance from suspected source. In Akumal Bay, eutrophication and grazing by turtles and fishes combine to structure patches within the seagrass beds. Grazed seagrass patches had higher structural complexity and productivity than patches continually grazed by turtles and fishes.

Results from this study indicate that patch abandonment may follow giving-up density theory, the first to be recorded in the marine environment. As *Diadema antillarum* populations recover after their massive mortality thirty years ago, the role these echinoids will have in reducing macroalgae cover and altering ecosystem state remains to be clear. Although *Diadema antillarum* densities within the coral reef ecosystem were comparable to other regions within the Caribbean, the echinoid population in Akumal Bay was an insufficient driver to prevent dominance of a turf-algal-sediment (TAS) state. After a four year study, declining coral cover coupled with increased algal cover suggests that the TAS-dominated state is likely to persist over time despite echinoid recovery. Studies on macroalgal diversity and nutrients within this same region of echinoids indicated diversity and nutrient content of macroalgae increased, which may further increase the persistence of the algal-dominated state.

This study provides valuable insight into the variable effects of herbivores and nutrients on primary producers within a tropical coastal ecosystem. Results from this work challenge many of the currently accepted theories on primary producer response to nutrients and herbivory while providing a framework for further studies into these dynamics.

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CHAPTER I: Introduction

Human populations are rapidly increasing and altering nearshore marine

environments, particularly as 60% of the population is concentrated within 100km of the

coast (Vitousek et al. 1997). With these high densities, record high levels of nitrogen and

phosphorus are being introduced to the coastal ecosystems and resources such as

fisheries are becoming increasingly exploited (Cloern 2001, Halpern et al. 2008). As

41% of marine ecosystems are impacted by multiple drivers (e.g., both eutrophication

and overharvesting), rates of ecosystem loss have increased for nearshore ecosystems

such as seagrasses, mangroves and coral reefs (Vitousek et al. 1997). These losses are of

great importance both ecological and economically as shallow marine ecosystems

provide tourism and fisheries income, stabilize sediment, protect shorelines and cycle

nutrients, among many other important roles (Costanza et al. 1997, Waycott et al. 2009).

For these reasons, marine ecosystem managers have an urgent need to identify indicators

and quantify responses of primary producers to these drivers over time, as it is the

primary producers which form the base of the food web and can efficiently indicate

ecosystem health. There is also a need to assess ecosystem status and determine the

influence of these drivers on ecosystem status or the potential for a phase shift to a

different ecosystem state.

A phase shift is what occurs when an ecosystem experiences a fundamental

change in core processes in response to drivers (Figure 1; Scheffer et al. 2001, Collie et

al. 2004, Andersen et al. 2008). Each ecosystem has a unique capacity to buffer

perturbations and return to the original state without experiencing a permanent phase shift

to an alternative state (Nystrom et al. 2000). This capacity, termed resilience, can be

influenced by the relative dominance of each ecosystem component as it changes with different ecosystem processes (e.g., resource availability, herbivore disturbance), further examples are explored in Scheffer et al. (2001). Dominance of one species can be driven by the abundances of other species as they interact through factors such as population dynamics, competition and predation (Knowlton 1992), which may also operate as positive feedback mechanisms. Positive feedback mechanisms are self-stabilizing actions that serve to increase the resilience of the system's current state (Scheffer et al. 2001). In addition to external drivers, removal or reduction of these internal positive-feedbacks is often necessary for a phase shift to an alternative state to occur (Petraitis & Latham 1999).
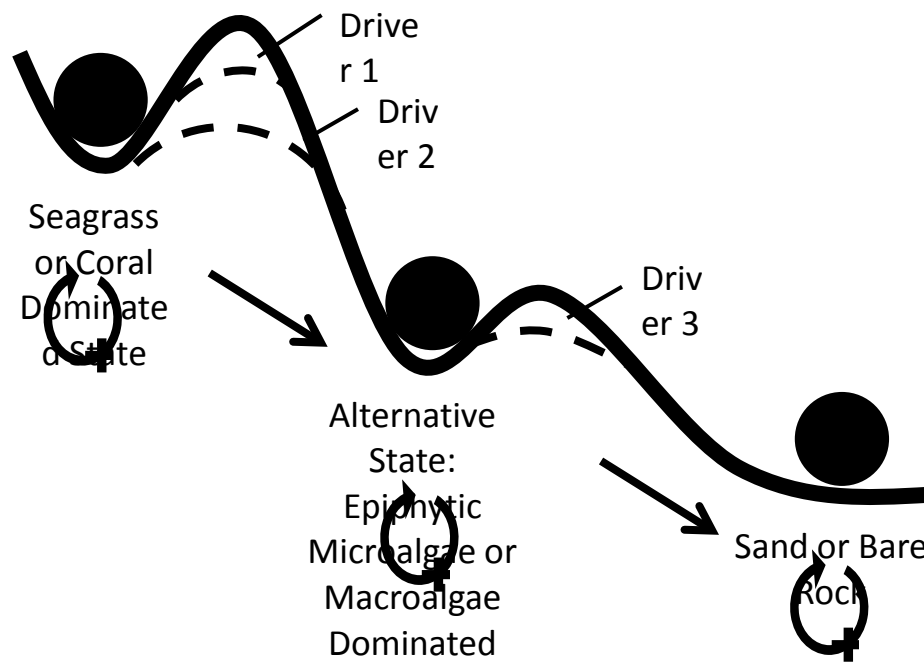
Figure 1: Drivers to phase shifts on coral- or seagrass-dominated ecosystems. Drivers (dashed lines) decrease the resilience of the current state while positive feedbacks (arrows with plus signs) increase the resilience of the current state.

Coastal marine ecosystems

Seagrasses are marine vascular plants common in coastal waters worldwide. They are the base of marine food webs, forming a trophic connection including sirenians (manatees and dugongs), turtles, herbivorous fish, sea urchins and waterfowl (Valentine & Heck 1999). Seagrass bed state dynamics include a clear, seagrass dominated state and a turbid, epiphytic microalgae dominated state characterized by phytoplankton blooms (Gunderson 2001). The epiphytic microalgae state is used to refer to those conditions in which seagrass have high epiphyte loads and the water is turbid with high phytoplankton biomass. The relative dominance of each of these alternative states is driven by nutrient availability and herbivory. For shifts from seagrass dominated states to epiphytic states, perturbations from eutrophication alter seagrass abundance, resource use and productivity (Borum 1985, Orth et al. 2006), parameters that can be monitored to indicate ecosystem state. Positive feedbacks to the resilience of a clear, seagrass dominated state occur through the stabilization of sediments by seagrass rhizomal mats (Ginsburg & Lowenstam 1958, Scoffin 1970). In a nutrient replete system, the benthos would be expected to exist as a turbid, epiphytic microalgal-covered state rather than a clear water, seagrass dominated state. In Florida Bay, nutrients have driven the seagrass system from a clear to turbid state with frequent sediment resuspension and algal blooms as the positive feedback mechanisms by which this turbid state exists (Fourqurean & Robblee 1999). Opportunistic epiphytic overgrowth reduces light penetration to seagrass blades and limits successful seagrass recolonization (Ferreira et al. 2007), thus increasing the resilience of this alternative turbid state as seagrasses are competitively excluded (Tomasko & Lapointe 1991).

An additional driver is through herbivore grazing disturbance. In the absence of

herbivory, areas experiencing high nutrient loads would be expected to shift from

relatively clean seagrass blades to blades dominated by epiphytic microalgae (Neckles et

al. 1993, McGlathery 1995). However, grazing stimulates seagrass productivity from the

extensive networks of belowground biomass to offset the loss of aboveground biomass

(Valentine et al. 1997). Resource allocation is mobilized from storage in rhizomes to the

production of new leaves aboveground. The status of the seagrass ecosystem is reflected

in rates of primary production, seagrass abundance and measurements of nutrient reserves

in rhizomes (carbon, nitrogen, phosphorus and soluble carbohydrates), but the direct

effects of grazing behaviors on these parameters is not well known although it has been

modeled in mesotrophic environments (Figure 2).
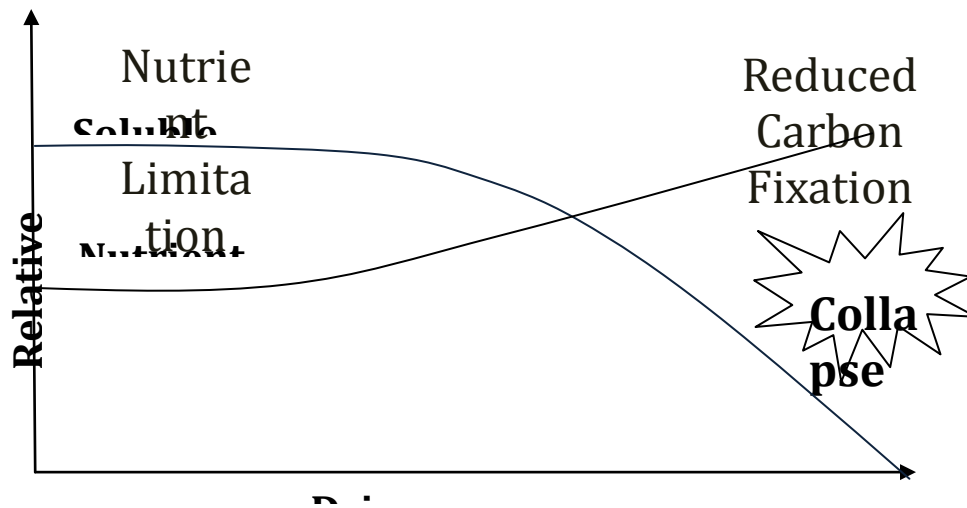
Figure 2: Grazer disturbance model for seagrass ecosystems (modeled after a

mesotrophic environment; Fourqurean et al. 2010). Low grazing intensity leads to

seagrasses that are nutrient limited with higher soluble carbohydrate content relative to

aboveground nutrient content. High grazing intensity results in reduced carbon fixation and declining soluble carbohydrates with the potential for seagrass bed collapse.

Relative dominance of coral reef alternative states is also driven by nutrient availability and herbivory (Hughes 1994, Lapointe 1999, Szmant 2002). These ecosystems are also impacted by coral diseases and ocean acidification but as it is not feasible for marine ecosystem managers to mitigate for these indirect drivers (McManus & Polsenberg 2004), it become more important to focus on these top-down (herbivory) and bottom-up (nutrient) drivers. Shifts from coral- to algal-dominated states can occur when there is an increase in nutrients to the system, which favors the growth of macroalgae as they competitively exclude corals (Idjadi et al. 2006). Nutrients impact macroalgal productivity and this can be measured in tissue concentrations of nitrogen and phosphorus. For many macroalgae species, their relationship with nutrients is not well established and warrants further consideration. Information on nutrient dynamics will be of particular interest as a parameter by which to monitor the effects of nutrient enrichment on the coral-algal relationship. Positive feedbacks to the macroalgae state include reductions in habitat complexity (Lee 2006), decreased coral recruitment from the Allee effect, and increased turbidity and sedimentation that commonly occurs in algal-dominated systems (Knowlton 1992).

Alterations in grazers impact the dominant benthic cover and therefore the state of the coral reef ecosystem. Herbivores directly impact macroalgal dominance through the removal of biomass, which provides space for coral recruitment. Events like the massive mortality of the herbivore *Diadema antillarum* throughout the Caribbean in the 1980s, released macroalgae from herbivory pressure, which increased algal abundance. After

the loss of this herbivore, many reefs experienced a dramatic shift to increased

macroalgal cover from formerly coral-dominated reefs (Lessios et al. 1984a, de Ruyter

van Steveninck & Bak 1986). As the sea urchin population begins to recover, their

grazing may serve as a buffer to excessive nutrients in a similar manner as sea turtles in

seagrass beds. Correlations between parameters such as sea urchin density and

macroalgal abundance and distribution are especially important when considering these

ecosystems are under an additional stress of high nutrient availability.
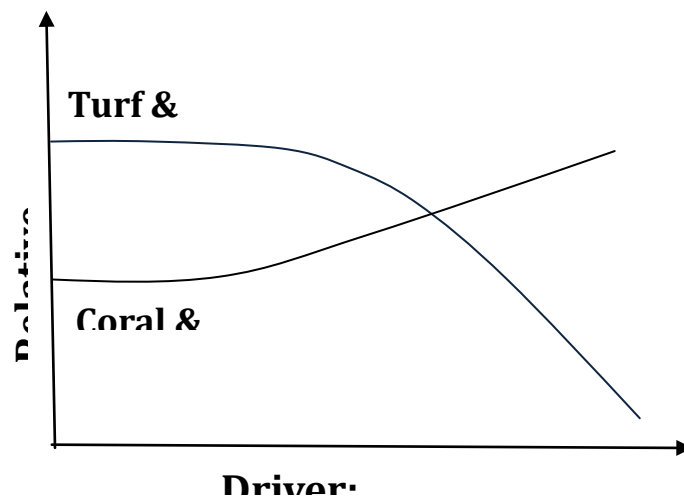
Figure 3: Grazer disturbance model for coral reef ecosystems based upon the

Littler and Littler Relative Dominance Model (Littler et al 2006). Benthic covers turf and

frondose macroalgae are prevalent at low grazing intensities while high grazing

intensities reduces these covers and provides space for coral and crustose coralline algae

cover. In a high nutrient environment, the Relative Dominance Model would predict

frondose macroalgae and crustose coralline algae be present rather than turf and coral.

Understanding the drivers underlying resilience in nutrient replete environments

is crucial to preventing continued degradation. There are many gaps in the ecological

theory of herbivore- and nutrient-induced changes to primary producer assemblages and

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no known studies which consider multiple systems (seagrass and coral) within the same shallow marine environment. Studying multiple systems provides interesting insight into the responses of primary producers to similar nutrient scenarios and is a mechanism by which similar questions can be asked in these different ecosystems. An expansion in our understanding of the mechanisms affecting dominant benthic habitat and potentially ecosystem resilience can be beneficial for marine park management decisions and priorities. During this research, I first considered the macroalgal response to nutrients and the importance of their use as nutrient bioindicators within my study region of Akumal, Mexico (Chapter II). These data can determine the relative nutrient availability to the primary producer community within the Mesoamerican coastal region and the accuracy in designating this system as nutrient replete rather than nutrient limited. I then sought to evaluate the impact of green sea turtles, *Chelonia mydas*, and herbivorous fish on dominant seagrass state as the primary producers are impacted by high nutrient availability (Chapter III). There are many unanswered questions regarding the physiological and morphological response of seagrasses to grazing in a eutrophic environment as well as how these parameters relate to observed grazer behavior. In a similar manner to herbivores in seagrass beds, I also considered the role of herbivorous black-spined sea urchins, *Diadema antillarum*, on structuring the algal dominant state in Akumal Bay (Chapter IV). Beginning with a consideration of the recovery dynamics of the sea urchin, I also sought to analyze the impact of this driver on benthic cover functional groups and what changes in benthic cover over time mean to overall coral reef ecosystem state. Finally, I analyzed how high nutrient availability could impact changes in generic diversity and nutrient content of macroalgae (Chapter V). These data are

considered with results on herbivory found during Chapter IV in order to determine the

trajectory of this highly impacted coral reef ecosystem as it is impacted by the

increasingly common drivers of eutrophication and fishing exploitation. Results from the

research produced during these studies answers ecological questions on the relative

importance of these drivers on primary producer assemblages in nutrient-replete

ecosystems. Results can also provide important information to assist marine park

managers in their quest to protect these important ecosystems.

CHAPTER II: Challenges in using marine macroalgae tissue chemistry for assessing nutrient pollution in the Mexican Caribbean

Abstract

Rising coastal populations are rapidly driving changes in nearshore marine environments through increased anthropogenic nutrient loading. Monitoring the response of primary producers such as macroalgae to these nutrients is an important management priority yet data are lacking on even the most basic ranges to be expected for tissue nutrients. My study was designed to add to the paucity of nutrient literature as well as utilize two different bioindicator methodologies to determine the fate of nutrients on $\delta^{15}N$, nitrogen and phosphorus content within Yal Ku Lagoon, Akumal, Quintana Roo, Mexico, an ecosystem considered to be heavily impacted by anthropogenic nutrients. Bioindicators are continuous samplers of the aquatic environment and provide data on the bioavailability of nutrients to primary producers, such as macroalgae. In July 2009 and 2010, nitrogen, phosphorus and $\delta^{15}N$ content of *Acanthophora spicifera* were used as an active bioindicator bioassay to record nutrients within the water column while a collection of macroalgae was also completed as passive macroalgae indicators to record nutrients available at the benthos. While the bioassay of *A. spicifera* did signify some dilution of nutrient content with distance in 2010, clear isotopic indications of this pattern were absent in 2009. Tracking nitrogen (maximum 4% dry weight) and phosphorus (maximum 0.18% dry weight) tissue content in both active and passive macroalgal bioindicators suggest Yal Ku Lagoon is a nutrient replete ecosystem but data are highly variable. While macroalgae bioindicators can indicate the relative nutrient status and bioavailability within the system, the diffuse sources of nutrients coming from this karstic

environment may not allow clear tracking of gradients in nutrient pollution. My study

contributes valuable data which can be used to increase our understanding on the

fluctuating ranges of $\delta^{15}N$ and nitrogen content within marine macroalgae. My study also

illustrates the variability between bioindicator methodologies and parameters and

therefore their use and interpretation for management purposes.

Introduction

Globally, human populations are rapidly increasing and altering nearshore marine

environments with anthropogenic nutrient loading (Cloern 2001). Increased nutrients,

such as nitrogen from fertilizers and sewage, increases primary productivity (Doering et

al. 1995, Thornber et al. 2008) and can cause the formation and proliferation of

macroalgal blooms (Lapointe 1997, Stimson et al. 2001). Effective monitoring of

indicators preceding such macroalgal blooms could allow for corrective actions to reduce

nutrient loading prior to detrimental blooms. Traditionally, testing of the water column

has been used to monitor levels of nutrients available within an ecosystem (Burford et al.

2003, Biao et al. 2004). However, when terrestrial nitrogen arrives in spatially or

temporally variable pulses, measurements of short-term water column chemistry do not

represent the long-term influence or bioavailability of these nutrients (Fong et al. 1998,

Fong et al. 2004). Measurements of primary producer tissue chemistry represent time-

integrated nutrient availability which dampens short-term fluctuations (Fourqurean et al.

1997). These primary producer measurements also allow an understanding of

eutrophication to be developed in an ecologically relevant way (Savage & Elmgren

2004).

While macroalgal response may differ depending on species as there are physiologically different uptake rates and storage capacities (Wallentinus 1984), internal content generally reflects external conditions (Gerloff & Krombholz 1966, Lyngby 1990, Lapointe et al. 1992). As such, tissue chemistry is a function of spatial and temporal patterns in nutrient availability and the demand from the primary producer for those nutrients for growth (Redfield 1958, Gerloff & Krombholz 1966, Atkinson & Smith 1983). Macroalgae are also easy to collect and prepare, can integrate available nutrients over time (Cohen & Fong 2005, Costanzo et al. 2005) and their fast uptake rates make them ideal for bioassay techniques (Wallentinus 1984, Costanzo et al. 2001). Tissue nitrogen and phosphorus concentration, $\delta^{15}N$ and productivity are part of the suite of parameters considered in the use of macroalgae as a method by which to estimate relative availability of nutrients within an ecosystem (Horrocks et al. 1995, Fong et al. 1998, Umezawa et al. 2002, Lin & Fong 2008, Dailer et al. 2010). Algal tissue chemistry can be used passively through the sampling of species present naturally within the environment or actively through the deployment of bioassay species that are transplanted from their natural environment and incubated in areas under observation (Costanzo et al. 2000). As passive bioindicators have holdfasts within the sediment, these indicate the benthic availability of nutrients while the positioning of active bioindicators above the substrate more accurately sample water column nutrient availability. The use of both techniques can provide a more accurate understanding of the temporal and spatial pattern in nutrient availability within an ecosystem and could be used to infer potential nutrient-driven macroalgal blooms.

Specific stable isotope signatures can be used to trace sources of nutrients within an ecosystem (Heaton 1986, Peterson & Fry 1987). For instance, high ratios of ^{15}N: ^{14}N can indicate the presence of sewage while naturally high $\delta^{15}N$ can also occur through denitrification, fractionation during nitrate uptake and overlapping or multiple nutrient sources (Heaton 1986, Fourqurean et al. 1997). For this reason, interpretation of $\delta^{15}N$ data should be done utilizing corroborating data for perceived trends and potential sources. For instance, spatial patterns comparing nitrogen content and $\delta^{15}N$ can indicate variation in signals arising from nutrient sources rather than differences in nutrient uptake processes (Leichter et al. 2003, Savage & Elmgren 2004). While research does suggest that many macroalgal species do not fractionate nitrogen isotopes (Cohen & Fong 2005), interpretation of $\delta^{15}N$ data requires corroboration with other nutrient data.

I examined nitrogen, phosphorus and $\delta^{15}N$ content of macroalgae in both an active and passive bioassay methodology to determine the impact nitrogen loading had on the benthic assemblages in a region where nitrogen impact had been recorded in octocorals (Baker et al. 2010). I ask the question: Do parameters of macroalgae tissue chemistry (nitrogen, phosphorus, $\delta^{15}N$) in active and passive macroalgae bioindicators reflect spatial patterns in reference to suspected nutrient source? Utilization of both active and passive bioindicator methodology allowed me to determine if trends differed between methods as both have been presented in literature but no comparisons have been previously published. I also wanted to contribute to the paucity of literature reporting nitrogen and $\delta^{15}N$ values for marine macroalgae. Despite the prevalence of literature suggesting ^{15}N isotopic data can be used to detect anthropogenic nutrients, isotopic data with corroborating nitrogen content are lacking.

Methodology

Study system

Millions of tourists visit the Mayan Riviera region of Mexico's Yucatan Peninsula and rapid coastal development has intensified sewage inputs to coastal areas (Murray 2007). The Yucatan Peninsula is characterized by karstic geology, where stream flow of pollutants directly into the water is uncommon and groundwater is conducted from inland into the nearshore environment through submarine groundwater discharge. While most resorts have on-site wastewater treatment, many residences lack proper sewage disposal methods (Pacheco et al. 2001) and groundwater is commonly contaminated with pollutants indicative of human waste (Baker et al. 2010, Metcalfe et al. 2011). Yal Ku Lagoon, Akumal, Quintana Roo, Mexico (20º 24.702 N, -87º 18.27 W) is a popular tourist destination as clear water and submerged aquatic vegetation provide a suitable habitat for abundant fish and frequent visits by manatees, stingrays and turtles. The L-shaped lagoon has a rocky coast interspersed with red mangroves (*Rhizophora mangle*). Yal Ku Lagoon is 300 meters in length and turns sharply east before continuing 300 meters to the ocean entrance (Figure 1). Within my study region, *Thalassia testudinum* and *Gorgonia ventalina* isotopic ratios, phosphorus and nitrogen concentrations, as well as water quality of the underground cave system, indicate groundwater sources of nutrients and pollutants (Carruthers et al. 2005, Mutchler et al. 2007, Baker et al. 2010, Metcalfe et al. 2011). Previous research in Yal Ku Lagoon has documented decreasing δ^{15}N of octocorals, and water column *Enterococcus coliform* bacteria, an organism indicative of human sewage, with increasing distance from the suspected lagoon spring source (Baker et al. 2010).

Active bioindicator bioassay

   Acanthophora spicifera was used as an active bioindicator as this species is ubiquitous on the adjacent reefs and has proven hardy to these types of bioassay experiments taking place within the water column (Lin & Fong 2008). *Acanthophora spicifera* was collected in Akumal Bay and gently cleaned of epiphytes. In order to reduce macroalgal initial nutrient content, macroalgae were placed in a plastic tub with two electric air stones while water was changed every two days for six days (Fong et al. 2003, Lin & Fong 2008, Dailer et al. 2010) with water collected offshore. The bucket of macroalgae was placed inside a larger plastic bin of water to decrease the potential for overheating from ambient temperatures and received diffuse natural light for approximately ten hours each day. Thirty-six *A. spicifera* replicates were created with six replicates retained in order to determine the initial concentrations of nitrogen, phosphorus and δ^{15}N. Six replicates per site were sewn inside mesh bags and placed at five locations throughout the lagoon at increasing distances from the suspected lagoon source in July 2009 and twice in July 2010 (Figure 1, black stars). All bags were placed along the bottom at the same depth and attached to rocks using cable ties. After seven days, samples were recovered, removed from the mesh bags and gently cleaned of epiphytes. Seven days was determined to be adequate deployment length on the basis of previous studies (Fong et al. 1998, Lin & Fong 2008). Samples placed at the lagoon source (0m) and at the juncture of the ocean entrance and source lagoon (300m) were lost therefore only the samples at 400m, 550m and 700m are presented (sample sizes are indicated in Table 1). My initial design included increased spatial coverage and productivity measurements utilizing Alizarin Red S dye (Wefer 1980), however the reality of working

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in this tourist destination precluded data collection as these samples were removed from the lagoon before researchers could retrieve them.

All samples were dried to a constant weight at 60ºC and ground to a fine powder using a mortar and pestle. Samples were analyzed in duplicate for nitrogen content using a CHN analyzer and for phosphorus using dry-oxidation acid-hydrolysis extraction followed by colorimetric analysis. Dry weight elemental content was calculated as (mass of element/dry weight of sample) x 100%. As simple measures of tissue nutrients do not take into consideration initial nutrient concentrations (Fong et al. 1998), percent change of nitrogen and phosphorus was also calculated. Isotopic analysis ($\delta^{15}N$) was completed with a CN analyzer and Finnigan MAT 252 mass spectrometer and are expressed using the standard $\delta^{15}N$ notation (Peterson & Fry 1987). Samples from both bioassay deployments in July 2010 were pooled because samples were not significantly different from each other (Student's t-test, p = 0.889). An ANOVA was used to test for significant differences between bioassay sites during each sampling event after examination of standardized residuals showed data conformed to assumptions of normality.

Passive bioindicator survey

To determine if trends in nitrogen, phosphorus and $\delta^{15}N$ differed depending on bioindicator methodology, a passive bioindicator survey was also completed. A survey of all macroalgae present along the lagoon was completed. Four to five samples of each macroalgae species present were collected at the source and along a sampling transect in 50 m increments from the juncture of the ocean entrance and source lagoon (400m) to the ocean entrance (700m) in July 2009 and 2010 (Figure 1, solid black line). For *Caulerpa* species, only three replicates could be collected because of the paucity of samples and the

relatively small size of these macroalgae. Samples were processed in an identical manner for nitrogen, phosphorus and δ^{15}N as during the bioassay. When the same genera were found along the transect in the same year and standardized residuals established that data conformed to normality assumptions, an ANOVA was used to test for significant differences between locations. When the same genera only appeared twice along the transect, a Student's t-test was used to test for significant differences.

Results

Macroalgae within the first 400 meters from the suspected source of Yal Ku Lagoon were limited to sparse *Halimeda opuntia* and *Caulerpa verticillata*. From 400m – 700m, the benthos changed and included other calcareous green macroalgae (e.g., *Udotea, Penicillus*), red macroalgae (e.g., *Laurencia*) and brown macroalgae (e.g., *Stypopodium, Dictyota*). From 550m to the ocean entrance (700m), there were octocorals, *Gorgonia ventalina*, and zoanthids, *Palythoa caribaeorum*.

Active bioindicator bioassay

In 2009, tissue chemistry of the active bioindicator bioassay increased significantly from 400 – 550m from the suspected source before values significantly decreased (Table 1) and this pattern was reflected in all measured nutrient parameters (P, N and δ^{15}N). During the 2010 bioassays, nitrogen content, nitrogen: phosphorus and δ^{15}N decreased away from the suspected source while phosphorus content did not change significantly (Table 1). *Acanthophora spificera* tissue nitrogen (N) ranged from 0.8 – 1.0 (%DW), tissue phosphorus (P) ranged 0.04-0.06 (%DW), nitrogen:phosphorus (N:P) were 39-57 and δ^{15}N values were 2.4-6.2‰ (Table 1). In 2010, there was a positive trend between change in nitrogen content and change in δ^{15}N as nutrient and δ^{15}N decreased

with increasing distance from suspected source. The trend was not observed in 2009 (Figure 2).

Passive bioindicator survey

During the 2009 and 2010 passive benthic bioindicator survey, Caulerpales (*Caulerpa* and *Halimeda*) were the common macroalgae present. Trendlines of nitrogen content and $\delta^{15}N$ along transect length are presented for these macroalgae genera to determine trends in these parameters with increasing distance from suspected source. In 2009, *Halimeda* tissue nitrogen significantly decreased with distance from source ($p < 0.05$) while *Caulerpa* tissue nitrogen content did not significantly change ($p = 0.977$; Figure 3a). In 2010, *Caulerpa* tissue nitrogen significantly decreased with distance from source ($p < 0.05$) while *Halimeda* did not significantly change ($p = 0.897$; Figure 3b). Further trends could not be determine because of a lack of replicate genera along the transect. In 2009, $\delta^{15}N$ of *Caulerpa* and *Halimeda* significantly increased with distance from source ($p < 0.05$; Figure 4a) while in 2010, *Caulerpa* $\delta^{15}N$ significantly increased with distance from source ($p < 0.05$; Figure 4b).

Discussion

Tracking nitrogen, phosphorus and isotopic content through the use of *Acanthophora spicifera* active bioindicators and a diversity of macroalgae genera as passive bioindicators indicate macroalgae response to nutrients in Yal Ku Lagoon is highly variable. However, as distance from suspected nutrient source increased, a decrease in nutrient content of both bioassay and sampled macroalgae occurred, but patterns were year and genera specific. In 2010, the bioassay of *A. spicifera* within the water column indicated a decrease in nitrogen availability and $\delta^{15}N$ with distance from

the suspected source of anthropogenic nutrient input but this trend did not occur in 2009. Data from this study can be used to provide evidence for the macroalgal uptake of nitrogen and phosphorus nutrients and the importance of using both tissue nitrogen and isotopic data to understand the fate of anthropogenic nutrients into a system. My study contributes valuable data which can be used to increase our understanding on the fluctuating ranges of $\delta^{15}N$ and nitrogen content within marine macroalgae.

Tissue content of nutrients and ratios of these nutrients when compared to standards can determine nutrient limitation to macroalgae growth. In general, macroalgae nitrogen content greater than 1.2 percent dry weight (% DW), phosphorus content less than 0.02 (% DW) and nitrogen:phosphorus higher than 30 can indicate a phosphorus-limited system (Atkinson & Smith 1983, Duarte 1992). However, macroalgae have proven to be highly variable rather than conforming to these established 'baselines.' Prior to this study, few studies have reported nutrient content on such a diverse group of macroalgae within the Mexican Caribbean from which to infer relative nutrient status. For those references within the literature in Akumal Bay Mutchler and Dunton (2007) reported *Halimeda* nitrogen of 1 (% DW) while my sampled *Halimeda* had nitrogen maximum 1.6 (% DW). Tissue nitrogen content of *Acanthophora spicifera* used in a bioassay directly adjacent to shrimp farms was 1.2 (% DW) and decreased to 0.8 (% DW) 400m from the shrimp farm (Lin & Fong 2008). In this study *A. spicifera* peaked at 1.0 (% DW), which while not greater than those measured next to the shrimp farm, are comparably higher than those areas deemed 'less impacted' by the shrimp effluent. Records of marine macroalgae nutrient content are sparse and this study adds to

our understanding on the ranges of nutrients possible within an ecosystem considered impacted by anthropogenic effluent.

Use of $\delta^{15}N$ in bioindicators has frequently been cited as clear evidence to the presence of sewage near outfalls and an effective way to measure increased pollutant dilution with increased distance from source (Costanzo et al. 2001, Costanzo et al. 2005, Lin & Fong 2008, Dailer et al. 2010). Elevated $\delta^{15}N$ values can occur through spatial differences in NO_3^- enrichment, denitrification and the mixing that occurs during groundwater transport (Fourqurean et al. 1997) in addition to the presence of sewage (Heaton 1986). In some research, $\delta^{15}N$ was the most sensitive indicator when compared to other parameters such as tissue nitrogen (Lin & Fong 2008), while in other published datasets, parameters such as tissue nitrogen, amino acids and chlorophyll a concentrations have provided adequate indicators of nutrient status (Costanzo et al. 2000). For studies on marine macroalgae, values of 3‰ have previously been reported for Akumal Bay *Halimeda* and 3.0-8.0‰ for multiple genera in southeast Florida with global ranges from 4-25.7‰ in reported sewage impacted areas (Lapointe et al. 2004, Mutchler et al. 2007, Dailer et al. 2010). Most often, as was found during my study, it is a combinations of multiple parameters that should be used to make statement regarding nutrient status and impacts (Fong et al. 2001).

Interpretation of data from passive bioindicators can be difficult as differential responses of each macroalgae species impact the nutrient signature. Differences in nitrogen content can be driven by chemical defenses, pigmentation (Delgado et al 1996) or growth morphologies (Littler & Littler 1980, Fong et al. 2001). These types of relationships are unknown for many of the genera found during this study and pooling

data by genera may mean important nuances to trends are missed. In addition, species or genera were not consistently present along the entire length of the sampling transect, making determinations of any nutrient dilution with distance difficult to establish. When the same genera was present at multiple locations along the sampling transect (e.g., *Halimeda*, *Caulerpa*), trends in nitrogen content did not clearly indicate a dilution of nutrients with increasing distance from suspected source. Despite the multitude of factors that can influence any comparisons between macroalgae genera within an ecosystem, it is important to note that nitrogen content was sensitive enough to detect changes at short distances through time while $\delta^{15}N$ did not detect these same changes.

In karstic environments such as the Mexican Caribbean, fissures can create a diffuse delivery of nutrients into the environment rather than creating distinct point sources (Metcalfe et al. 2011). The identification of the sources is important not only to the interpretation of nutrient data, but also to the management strategies developed to address the sources of these nutrients. It is conceivable that because the underground cave system beneath Yal Ku Lagoon is not completely mapped, fissures away from my suspected source location may contribute nutrients along the transect. Although this hypothesis is compounded by the fact that a distance effect was recorded in 2010 and in previous studies (Baker et al. 2010). As shoreline development continues along the Mayan Riviera (Murray 2007), the importance of each of these potential sources into the adjacent coastal ecosystem increases. The lack of baseline information mapping all potential sources and the pathways through subterranean cavern systems may limit our understanding of nutrients within Yal Ku Lagoon, and therefore the ability to manage these influences.

In highly eutrophic locations, macroalgae sensitivity to nitrogen availability is compromised as the macroalgae is saturated with nutrients (Cohen & Fong 2005). Alternatively, in some studies macroalgae indicators failed to respond to low levels of nutrient pollution (Costanzo et al. 2000). The ideal scenario at which these bioindicators can be used is highly variable and dependant on the questions being asked and the historic information available regarding the study system. In order to determine the dilution of nutrient sources in Yal Ku Lagoon, the ideal usage of macroalgae may be to use genera such as *Acanthophora* or *Enteromorpha* in active bioassay methodology rather than passive sampling of benthic communities, which differed in presence along the transect. The active bioassay sampled the water column and detected trends in $\delta^{15}N$ and nitrogen content that passive bioindicators sampling along the benthos did not detect. It may be that processes occurring within the sediment reduce ^{15}N and therefore its presence in macroalgae. Many factors exist that can influence nitrogen and phosphorus of macroalgae within an ecosystem including actual differences in nutrient availability from localized nutrient sources and variations in macroalgal nutrient uptake mechanisms. In using a bioassay approach, factors can be standardized although this methodology may require more work than passive bioindicator surveys. My study utilized a comparison between these different methodologies and nutrient parameters to illustrate the important role variability of macroalgal response have in the interpretation of data on nutrient impact within an ecosystem.

Table 1: Yal Ku Lagoon nutrient content (nitrogen, phosphorus, N:P) and isotopic content of *Acanthophora spicifera* bioassay in July 2009 and 2010. DW: dry weight. Values are means ± SE. Significant differences between sites were assessed with ANOVAs and differences determined by pairwise comparisons. Superscripted letters indicate significant difference ($p < 0.01$).

	Site	% Nitrogen (DW)	% Phosphorus (DW)	N:P	$\delta^{15}N$ (‰)
	Initial	0.7 ± 0.01^a	0.02 ± 0.00^a	38 ± 0.2^a	4.0 ± 0.02^a
July	400m (n=5)	0.7 ± 0.04^a	0.04 ± 0.00^b	42 ± 0.4^b	5.3 ± 0.04^b
2009	550m (n=6)	1.3 ± 0.03^b	0.06 ± 0.01^c	52 ± 0.8^c	6.2 ± 0.04^c
	700m (n=6)	0.8 ± 0.02^a	$0.05 \pm 0.00^{b,c}$	$39 \pm 0.3^{a,b}$	5.4 ± 0.02^b
	Initial	0.7 ± 0.02^a	0.04 ± 0.00^a	42 ± 1.2^a	4.1 ± 0.03^a
July	0m (n=8)	1.5 ± 0.04^b	0.06 ± 0.00^b	57 ± 0.4^b	6.0 ± 0.04^b
2010	550m (n=11)	1.0 ± 0.03^c	$0.05 \pm 0.01^{a,b}$	49 ± 0.1^c	5.3 ± 0.03^c
	700m (n=10)	$0.8 \pm 0.03^{a,c}$	$0.05 \pm 0.01^{a,b}$	39 ± 0.2^a	2.4 ± 0.83^a

Figure 1: Map of Yal Ku Lagoon, Quintana Roo, Mexico

Figure 2: Percent change in nitrogen content and $\delta^{15}N$ of *Acanthophora spicifera* bioassay [(final-initial)/initial] x 100% (bars indicated standard error).

Figure 3: Nitrogen content of all macroalgal species in 2009 (A) and 2010 (B). Bars indicate standard error.

Figure 4: d15N of all macroalgal species in 2009 (A) and 2010 (B). Bars indicate standard error.
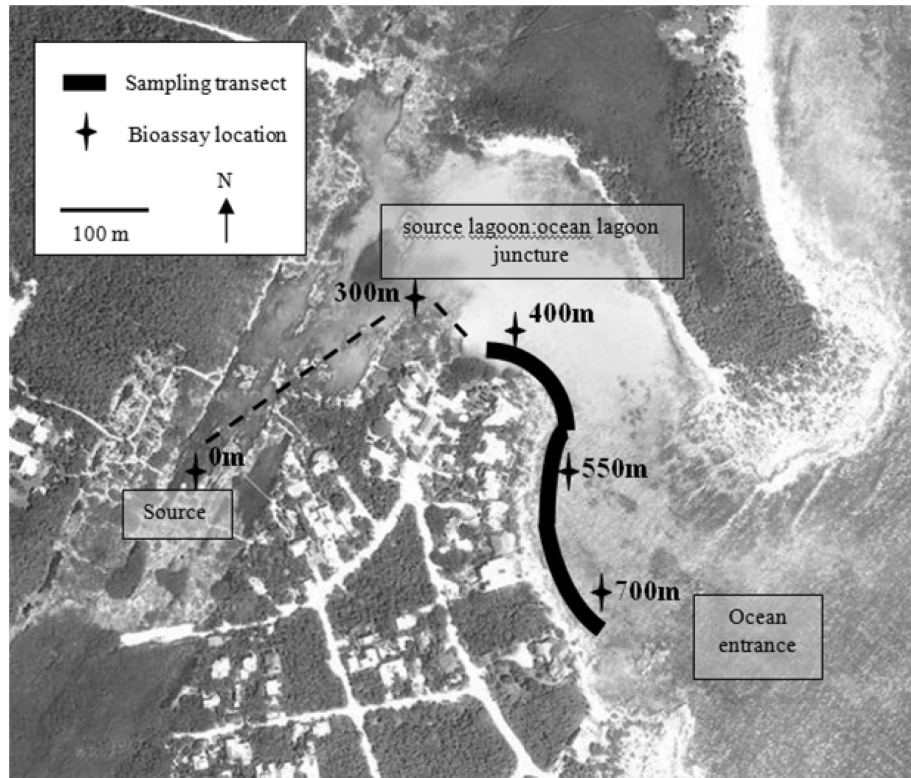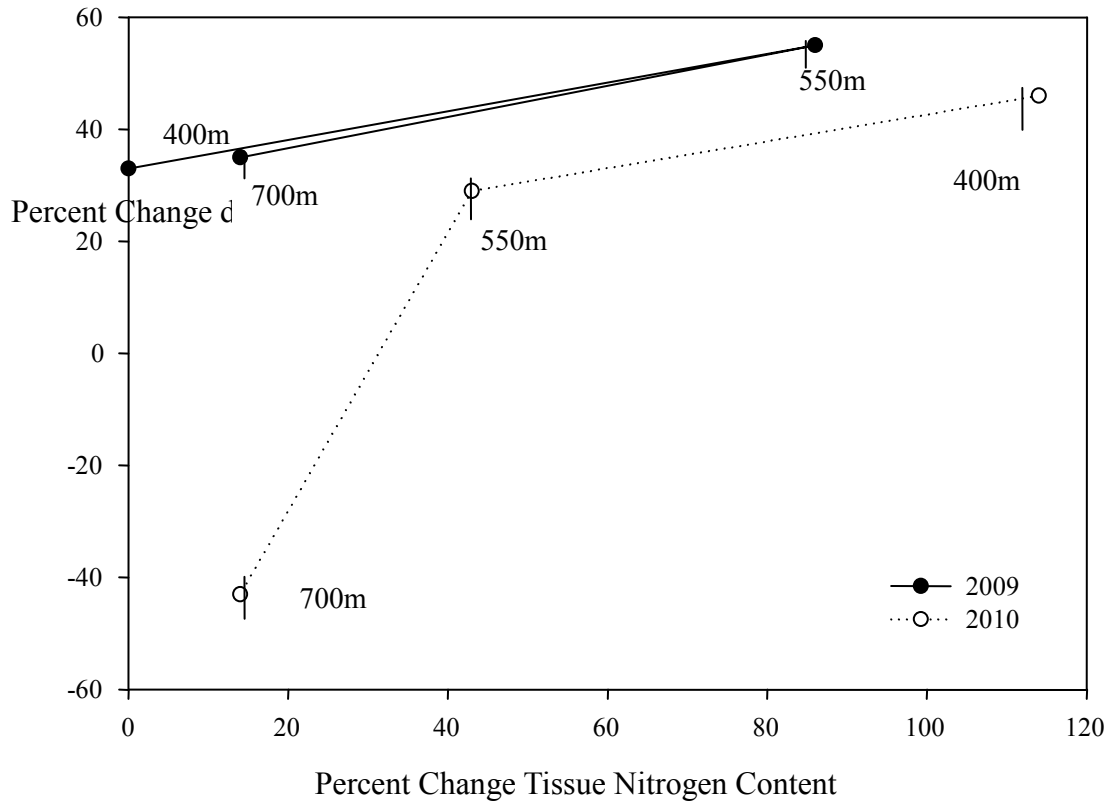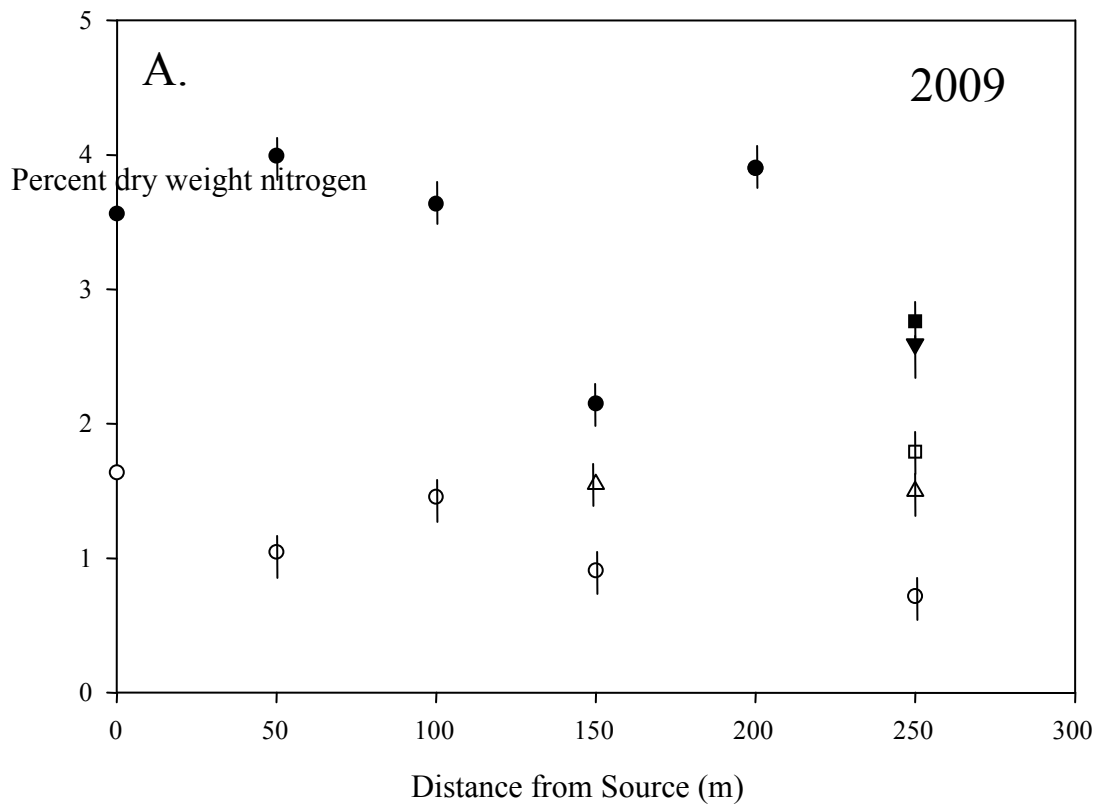
Percent Change d

Percent Change Tissue Nitrogen Content

25

A.   2009

Percent dry weight nitrogen

Distance from Source (m)

● Caulerpa
○ Halimeda
▼ Udotea
△ Rhipocephalus
■ Laurencia
□ Stypopodium

B.   2010

Percent dry weight nitrogen

Distance from Source (m)

- ● *Caulerpa*
- ○ *Halimeda*
- ▼ *Udotea*
- △ *Rhipocephalus*
- ■ *Laurencia*
- □ *Stypopodium*
- ◆ *Ulva*
- ◇ *Penicillus*
- ▲ *Dictyota*
- ▽ *Digenia*

A.   2009

Legend:
- ● *Caulerpa*
- ○ *Halimeda*
- ▼ *Udotea*
- △ *Rhipocephalus*
- ■ *Laurencia*
- □ *Stypopodium*

B.   2010

Distance from Source (m)
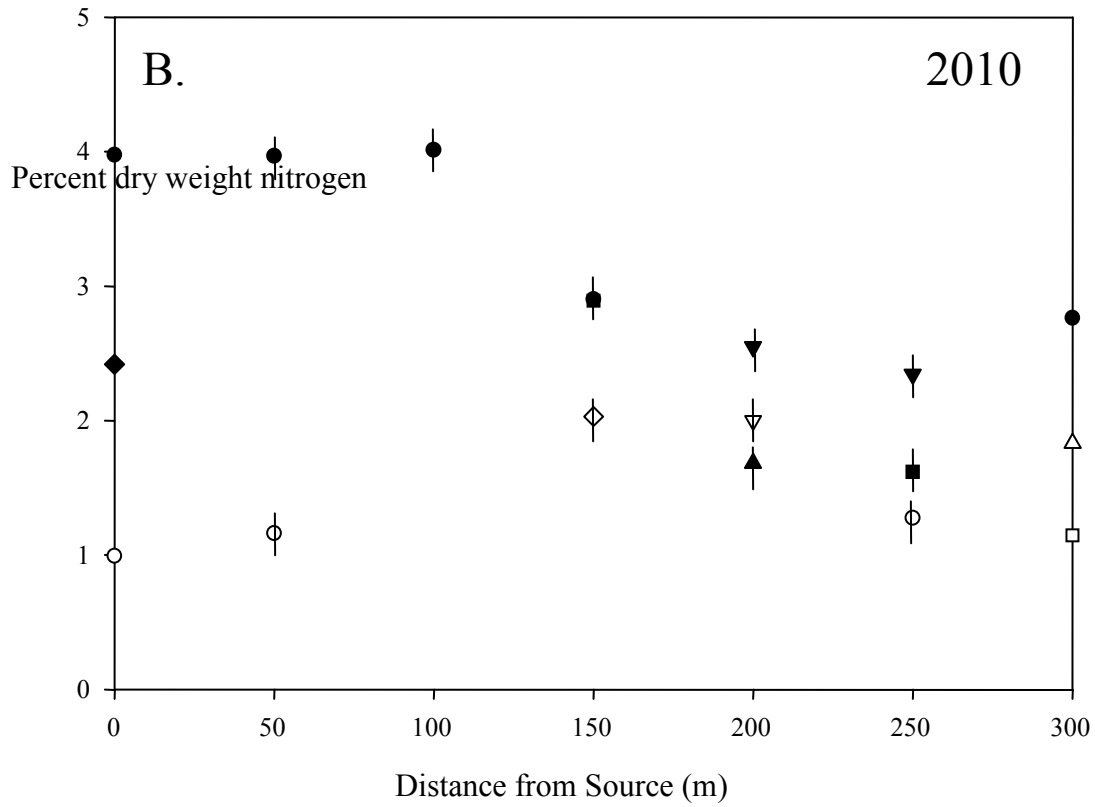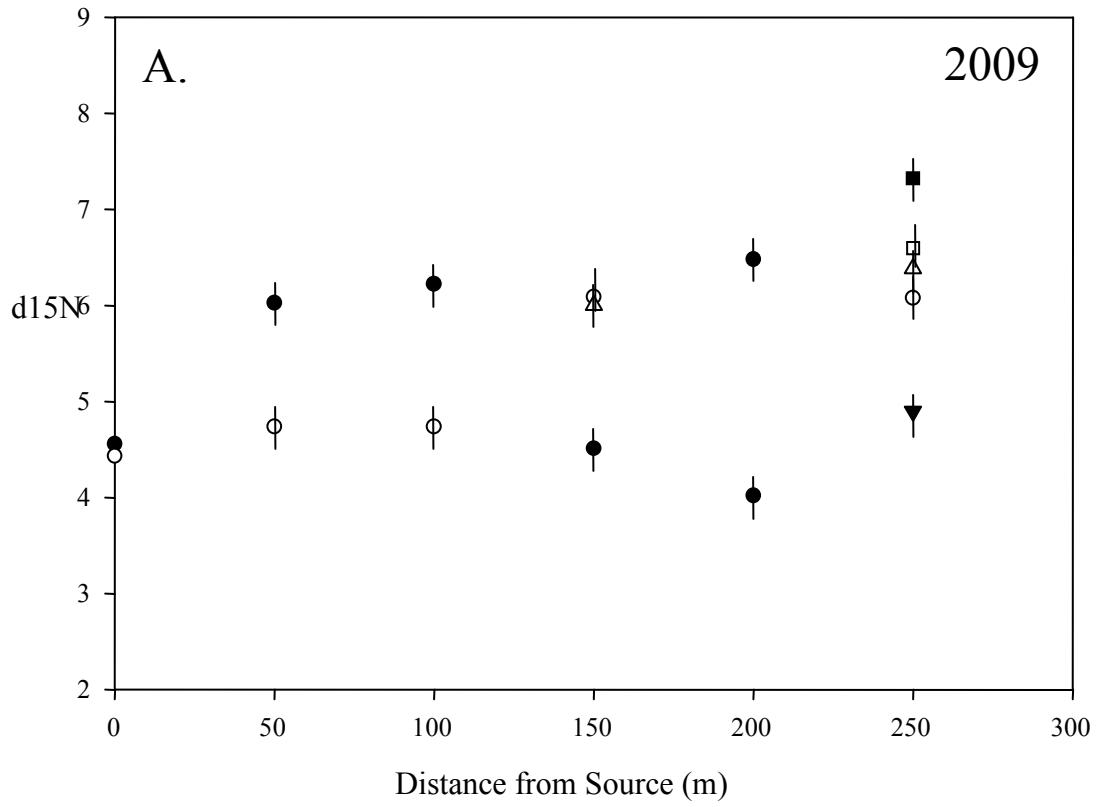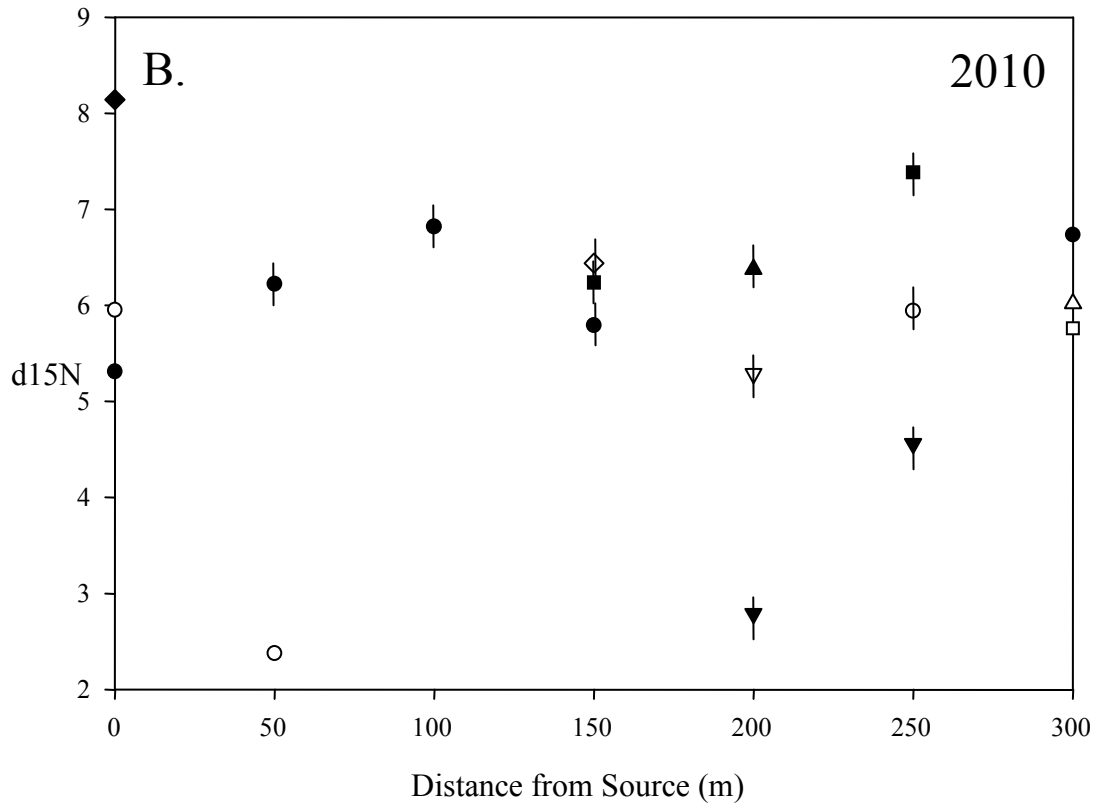
- ● *Caulerpa*
- ○ *Halimeda*
- ▼ *Udotea*
- △ *Rhipocephalus*
- ■ *Laurencia*
- □ *Stypopodium*
- ◆ *Ulva*
- ◇ *Penicillus*
- ▲ *Dictyota*
- ▽ *Digenia*

CHAPTER III: Morphological and physiological responses of seagrasses to grazers and their role as patch abandonment cues

Abstract

Monitoring seagrass patches grazed by the green sea turtle, *Chelonia mydas*, reveal that a 'giving up density' predicts patch abandonment rather than previous theories on leaf nutrient or rhizomal soluble carbohydrate content. The morphological and physiological responses (productivity, plant morphology and nutrient storage) potentially influencing seagrass recovery from grazing disturbances were monitored for one year under three different grazing scenarios (turtle grazed, fish grazed and ungrazed) in a nutrient-replete environment. Significantly less soluble carbohydrates and increased nitrogen and phosphorus content in the structurally important *Thalassia testudinum* were indicative of the stresses placed on macrophytes during herbivory. To determine if these physiological effects, and their impact on *C. mydas* nutrition and therefore patch use, were the drivers of this heterogeneous grazing behavior, patches were mapped throughout the bay and monitored over a six-month interval. The presence of ungrazed patches provided refuge for *Halodule wrightii* and *Syringodium filiforme* within the ecosystem and are important propagule source to recolonize abandoned areas. This study is the first to document the responses of a eutrophic ecosystem to these natural grazing processes and apply terrestrial theories on 'giving up density' to explain marine herbivore grazing behavior.

Introduction

Herbivores are important drivers of ecosystem dynamics (Valentine & Duffy 2006, Heck & Valentine 2007) and seagrass productivity (Zieman et al. 1984, Valentine

et al. 1997), reducing canopy cover and freeing space for competitive interactions between macrophytes (Heck & Valentine 2006). In high nutrient environments, macroalgal blooms increase the sensitivity of seagrasses to grazing as light availability affects carbohydrate storage in rhizomes and therefore the energy available to compensate for grazing disturbances (Macia 2000, Valentine et al. 2000) or higher summer productivity (Lee & Dunton 1997). Studies considering herbivores in conjunction with eutrophication are of particular importance as coastal ecosystems worldwide are increasingly impacted by anthropogenic disturbances (Waycott et al. 2009) and interactions of grazers with nutrient-replete systems becomes more common.

Cultivation grazing is the process by which grazing by turtles creates patches of new leaves, optimizing food quality as new leaves have higher nutrient content than old leaves (Bjorndal 1980, Aragones et al. 2006). The drivers behind the creation of these grazing patches, particularly the cues for herbivores to abandon a grazing patch in favor of a new patch, are not well known. Thayer et al. (1984) hypothesized that decreases in aboveground nutrient content precede bed collapse, but more recent studies suggest otherwise (Moran & Bjorndal 2005, 2007). An alternative theory proposed by Fourqurean et al. (2010) as an extension on research by Dawes et al (1979), suggests that rhizomal soluble carbohydrates may decrease prior to seagrass bed abandonment. These reductions result in low rates of productivity and decreased biomass from thinning leaves, cueing herbivore abandonment. In addition, indices of shoot density, blade width and leaf growth are also used as early indications of chronic stress (Zieman et al. 1984, Lee & Dunton 1997, Lal et al. 2010). These may be visual cues to induce abandonment and represent a 'giving up density' corresponding to a harvest rate that balances the

associated metabolic costs of foraging (Brown 1988). Giving Up density theory extends

the optimal foraging theory and includes balancing the harvest rate to metabolic costs,

predation risk and missed opportunity costs of not engaging in alternative activities.

While this theory has never been applied to marine herbivores, it may be an alternative to

the theory of rhizomal soluble carbohydrate cues. No studies have monitored these

physiological parameters important to seagrass recovery and growth in natural rather than

simulated grazed seagrass beds (Moran & Bjorndal 2005, Kuiper-Linley et al. 2007,

Moran & Bjorndal 2007) as they are abandoned by green sea turtles in order to elucidate

patterns and cues.

My study was designed to evaluate the effect of different types of herbivory (fish

and turtle) on morphological and physiological characteristics of seagrasses and which of

the monitored characteristics may cue patch abandonment by green sea turtles as patch

dynamics in the entire seagrass bed are monitored over time. I predict that grazed

patches will have higher nutrient content (carbon, nitrogen and phosphorus) in

aboveground leaf tissue than ungrazed patches, regardless of herbivore presence. I

predict that summer nutrient content of aboveground biomass will be lower than winter

following the hypothesis that plants increase rhizomal soluble carbohydrate storage

during optimal summer growing conditions, even in a nutrient replete environment.

Should soluble carbohydrate content be the cue to *C. mydas* patch abandonment, I predict

that patches abandoned will have significantly lower soluble carbohydrates than patches

remaining grazed. I hypothesize the paucity of storage in belowground nutrient reserves

will cause leaf thinning and decreased productivity, the mechanism cueing herbivore

patch abandonment. Should a giving up density be the cue, I would predict that patches

with the lowest biomass, as measured through the leaf area index, will be abandoned.

Methodology

Study site

Akumal ("Place of the Turtles" in Mayan) is located in Quintana Roo, Mexico on

the Yucatan Peninsula along the Caribbean Sea (Latitude: 20° 23' 45" N Longitude: 87°

18' 52" W). Akumal Bay is the northern 400 meter portion of a 2 km half moon-shaped

lagoon connected to Jade Bay and South Akumal Bay. A barrier reef exists 300 m

offshore and variable-sized patch reefs are sparsely distributed throughout the entire

lagoon. Highly porous, karstic geology delivers terrestrially-derived nutrients into the

coastal zone through submarine groundwater discharge (Mutchler et al. 2007).

Measurements of nitrogen, phosphorus and isotopic content of macrophytes, in addition

to high epiphyte loads, indicate the high availability of anthropogenically derived

nutrients to this ecosystem (Baker et al. 2007, Mutchler et al. 2007, Metcalfe et al. 2011).

Seagrass herbivores include the green sea turtle *Chelonia mydas* and near the interspersed

patch reefs, members of the family *Scaridae* (parrotfish) and *Acanthuridae* (surgeonfish).

Seagrass beds consist of *T. testudinum*, *H. wrightii* and *Syringodium filiforme* with few

intermixed macroalgae typified by calcareous Chlorophytes (e.g., *Halimeda*, *Udotea*) and

calcareous Rhodophytes (e.g,. *Neogoniolithon*).

Seagrass response

To determine the species specific response of seagrass to herbivory, physiological

responses were monitored in grazed and ungrazed patches in the seagrass beds.   Distinct

regions exist where seagrass beds have been grazed (by turtle or fish) or not grazed

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(Figure 1), and within these regions small cages (20 cm diameter) were placed for six days at a time during two distinct growing seasons (winter and summer) to sample productivity, leaf morphology, tissue nutrients and soluble carbohydrates. These cages were not intended to be experimental exclosures; rather, they allowed us to measure the production of material in the short-term without having biomass lost to fish or turtle grazers. Cages were deployed on two separate occasions during each season and samples were pooled within season after statistical analysis determined there was no significant difference between deployments within each patch (Student's t-test, $p = 0.897$). Areas targeted as fish grazed were surrounding a 50 m^2 patchreef within the same seagrass beds where turtle grazing occurred. Fish herbivory was confirmed by the patterns of bite marks on leaves, which were indicative of parrotfish grazing. Cages were created with vinyl-coated hardware mesh (ca. 1 cm mesh) and four 3mm diameter stakes secured the cage into the substrate.

To measure productivity and morphometrics within these cages, all *T. testudinum* blades were punched using a modified leaf marking technique (Zieman 1974, Fourqurean et al. 2001). At the end of six days, aboveground and belowground biomass was collected for all seagrass species present from which to measure carbon, nitrogen, phosphorus and soluble carbohydrates. Six randomly selected shoots of *T. testudinum* were measured for length, width and elongation rate (mm/shoot/day), from which elongation area (width x length of new growth at base of leaf) was calculated. All seagrass samples were cleaned of epiphytes, dried to a constant weight at 60ºC and ground to a fine powder using a mortar and pestle. Samples were analyzed in duplicate for carbon and nitrogen content using a CHN analyzer and for phosphorus using dry-

oxidation acid-hydrolysis extraction followed by colorimetric analysis. Dry weight

elemental content was calculated as (mass of element/dry weight of sample) x 100%.

Rhizome tissue for all species was cleaned of adhering sediments, dried to a constant

weight at 60ºC and ground to a fine powder using a mortar and pestle. Because of the

smaller size and paucity of *H. wrightii* and *S. filiforme* rhizomes, samples were pooled

from three cages to provide an adequate amount of sample material. Samples were

analyzed for soluble carbohydrates using the seagrass tissue adaptation (Lee & Dunton

1997) to the MBTH (3-methyl-2-benzothiazolinone hydrazone hydrochloride) method

(Pakulski & Benner 1992).

In order to test for the hypothesized differences between herbivory patches and

seasons on nutrient content, carbohydrate content and growth rates, a randomized

complete block ANOVA was used for morphometric and productivity data, where shoots

within cage were nested within combinations of patch (fish grazed, turtle grazed,

ungrazed) x season (winter, summer). Data were analyzed to establish they conformed to

all normality assumptions. Differences among patches for all seagrass species were

determined through Least Squares Difference pairwise comparisons with Bonferroni

corrected significance levels (0.008). Because of the variability in presence of *H.

wrightii* and *S. filiforme* in grazed cages, sample sizes varied between patches and

seasons. Therefore, to test for differences between herbivory patches and between

seasons, nutrient content and soluble carbohydrate data were analyzed via three-way

ANOVA (*T. testudinum*), two-way ANOVA (*S. filiforme*) or via a student's t-test or

Mann-Whitney nonparametric test (*H. wrightii*), depending on how the data met

normality assumptions. No *S. filiforme* was collected during the winter in the fish grazed

patch and no *H. wrightii* was collected in the fish (either season) or turtle grazed (winter season) patches.

Patch dynamics

To monitor changes in seagrass patch location and seagrass morphological and physiological changes over time in relation to changes in patch designation (grazed and ungrazed), patch locations in the seagrass ecosystem were tracked using belt transects. These transects were established between pre-existing navigational buoys in Akumal Bay initially (January 2011) and six months later (June 2011). The belt transects differed in length and cardinal ordination, and covered a combined length of 860 meters within the northern portion of Akumal Bay where sea turtles are present in the highest densities (authors' *pers obs*). All surveys were completed by the same diver in order to minimize any confounding errors in patch differentiation. Patches were labeled as grazed when leaf apexes were incomplete and seagrass blade length was 5 cm or less from the blade sheath junction. Ungrazed patches were those with seagrass blade length greater than 5cm and complete apexes. A modified Braun-Blanquet (BB) index was used to calculate abundance for each macrophyte present (Fourqurean et al. 2001) within a 0.25 m^2 plot within each patch. For each macrophyte BB score, 1 indicated coverage less than 5% of the plot, 2 indicated 5-25% cover, 3 indicated 25-50% cover, 4 indicated 50-75% cover; and 5 indicated 75-100% cover. The presence of a different patch was recorded when grazing status (grazed or ungrazed) or when BB score differed from adjacent patches.

Braun-Blanquet scores were converted to abundances using the mean abundance within each score (e.g. 2.5% cover for score 1, 87.5% cover for score 5) and then averaged across similarly designated patches (e.g., all grazed patches). Mean abundances

are presented for all grazing statuses during both surveys for comparisons between surveys. A Student's t-test was used to test for differences between grazed and ungrazed seagrass abundances as no data was available to determine newly grazed or abandoned status during the initial time period. An ANOVA was used to test for differences in species abundance among patch status (ungrazed, grazed, abandoned, newly grazed) within the second sampling after examination of standardized residuals showed the data conformed to all normality assumptions. Within each patch, epiphyte presence/absence, grazing status (blade apex complete or incomplete) of *T. testudinum* and seagrass blade length for all species was recorded. After the second survey patches labeled ungrazed had been ungrazed for six months or more while abandoned patches were recently ungrazed (less than six months since being grazed). Following the second survey, a Student's t-test was used to test for differences in proportions of each transect in each status between sampling events.

At 15 randomly chosen patches within the study area, aboveground and belowground biomass of *T. testudinum* was collected to determine the change in response variables between sampling intervals as a function of patch status. Six randomly selected shoots of *T. testudinum* were measured for length and width and cleaned of epiphytes, dried to a constant weight at 60ºC and ground to a fine powder using a mortar and pestle. Samples were processed for carbon, nitrogen, phosphorus and soluble carbohydrates using the same methods as for cage samples. An ANOVA was used to test for hypothesized differences in all parameters (width, carbon, nitrogen, phosphorus, soluble carbohydates) among patch status in the second survey (remain ungrazed, remain grazed, abandoned) after examination of standardized residuals showed the data conformed to all

normality assumptions. A Student's t-test was used to test for differences in initial

survey data between patches designated during the second survey as grazed and

abandoned. Means are presented for each of the three statuses in the initial survey for

comparisons between surveys. None of the patches sampled changed from an ungrazed

to a grazed status during the sampling interval.

Results

Seagrass response

Ungrazed patches had the widest *Thalassia testudinum* blades (ANOVA F =

12.06, p < 0.001) with fastest elongation rate (ANOVA F = 16.99, p < 0.001) and largest

new growth area (ANOVA F = 10.22, p = 0.002) when compared to fish and turtle grazed

patches (Figure 2 and 3). The difference was greater in the summer months and

significantly higher in ungrazed patches compared to grazed patches regardless of grazer

identity in both seasons (p < 0.001 for all three parameters). Fish grazed and turtle

grazed patches were significantly different from each other in width during the winter (p

< 0.001), but were not significantly different for other parameters or within the same

patch between seasons. Grazed shoots had a maximum of three leaves while ungrazed

shoots had a maximum of six leaves. Fish grazed leaves appeared less pigmented and

curled. All three species of seagrass were present in ungrazed patches while only *T.

testudinum* and occasionally *S. filiforme* were present in grazed patches.

Ungrazed patches of *T. testudinum* had lower nitrogen and phosphorus content

than turtle and fish grazed patches in both seasons (Figure 4). Carbon content was not

significantly different from turtle or fish grazed patches in the winter or summer,

respectively (p = 0.178 and 0.912, respectively). Differences between C:N:P ratios

among patches were the result of nitrogen and phosphorus differences as well as temporal decreases in nutrient availability. Ungrazed patches changed winter (542:29:1) to summer (635:31:1), fish grazed patches changed winter (446:32:1) to summer (544:35:1) and turtle grazed patches changed winter (388:30:1) to summer (426:30:1). Soluble carbohydrates were significantly higher in the ungrazed patches for both seasons and were significantly higher in summer compared to winter for all three patches (Figure 4).

Similar significant differences to those of *T. testudium* were found in *Syringodium filiforme,* where ungrazed patches had significantly less nitrogen and phosphorus content than turtle grazed patches (Figure 5, sample size was too small to test for differences to fish grazed patches). For *Halodule wrightii*, significant differences between ungrazed and turtle grazed patches in the winter occurred only in nitrogen and phosphorus content (Figure 6, Patch Mann-Whitney $p = 0.010$ for both). There was significantly higher carbon, nitrogen and phosphorus content in winter compared to summer in the ungrazed patches, similar to the trend found in *T. testudinum* and *S. filiforme*. Soluble carbohydrates of rhizomes were significantly higher in ungrazed patches than turtle grazed patches (t-test $p < 0.001$), similar to *T. testudinum*. Grazed shoots had a maximum of three leaves while ungrazed shoots had a maximum of seven leaves.

Patch dynamics

The majority of seagrass patches surveyed during the initial survey were ungrazed (63%) with epiphyte present while the remaining patches were grazed and epiphytes were absent. The percent of ungrazed patches did not significantly change during the second survey (Student's t-test, $p = 0.911$) while significant reductions in grazed patches occurred (Student's t-test, $p < 0.003$). From the initial 318m of grazed patches, 27%

continued to be grazed while 73% were abandoned in the second survey (Figure 7).

From the initial 542m of ungrazed patches, 97% remained ungrazed while 3% were

newly grazed in the second survey. During initial surveys, ungrazed patches had

significantly higher abundances of all three seagrass species than grazed patches (t-test p

< 0.001, Table 1).

In the second survey, comparisons could only be made between ungrazed, grazed

and abandoned patches as sample size of newly grazed patches was too small (n = 1) for

statistical comparison. Ungrazed patches had the highest abundance of *T. testudinum* and

S. filiforme than grazed and abandoned patches (ANOVA p = 0.015 and p = 0.037,

respectively) while *H. wrightii* abundance was highest in abandoned patches (ANOVA p

= 0.008) and increased significantly from initial to second survey (t-test p < 0.001). *H.

wrightii* was also significantly different from both ungrazed and continually grazed plots.

S. filiforme and *T. testudinum* abundance did not significantly change for abandoned

patches from initial to second survey (t-test p = 0.912). There were two new species of

macroalgae within the one abandoned plot that had macroalgae but because of the small

sample size, significant differences could not be determined. In the one newly grazed

patch, there was one less seagrass species present but small sample size did not allow

statistical comparisons.

Within the fifteen patches of *T. testudinum* sampled for nutrients, soluble

carbohydrates and morphometrics during the initial survey, ungrazed patches had

significantly lower nitrogen and phosphorus content (t-test p-value < 0.001 for both

parameters) and significantly higher soluble sugar content (t-test p-value = 0.044) than

grazed patches, similar to those results found in the cages. During the second survey,

carbon content and nitrogen:phosphorus were not significantly different between patch

status (ungrazed, grazed and abandoned, Figure 8). Phosphorus content, soluble

carbohydrates and carbon:phosphorus were not significantly different between abandoned

and ungrazed patches while nitrogen content and carbon:nitrogen were not significantly

different between abandoned and grazed patches. Therefore, I detected no differences in

carbon, nitrogen, phosphorus or soluble carbohydrates in *Thalassia testudinum* that

seemed to serve as cues for abandonment of grazed plots. Plotting leaf length and width

for each patch status illustrated a clumping of patches prior to abandonment and a distinct

shift in these parameters following abandonment (Figure 9). Leaf biomass was calculated

(length x width x 2) and multiplied by the BB density score to incorporate both biomass

and density in the determination of a threshold at which patches may be abandoned

(Figure 10).

Discussion

My study determined that in seagrass beds with high nutrient availability, patches

grazed by fish or turtles had higher nutrient content in aboveground tissue and depleted

belowground energy reserves than those patches that were ungrazed. Herbivore-specific

responses of *Thalassia testudinum* in grazed patches were reflected in tissue nutrient

content ratios and leaf morphology, where patches grazed by fish had significantly

narrower leaves and significantly higher nutrient content than those patches grazed by

turtles. The *Halodule wrightii* and *Syringodium filiforme* present in the ungrazed beds

may provide a source for recolonization by these species once patches are abandoned. I

determined that seagrass patches abandoned in the second survey did not contain the

lowest content of carbon, nitrogen, phosphorus and soluble carbohydrate, contrary to

predictions. Instead, my data suggest that a 'giving up density' similar to found in terrestrial ecosystems is the mechanism by which patches are abandoned.

Herbivory in a nutrient-replete seagrass ecosystem

The relative physiological and morphological effects (productivity, tissue nutrients and soluble carbohydrates) of grazing on macrophytes were similar to those previously measured from simulated grazing or exclosure experiments in sites with lower nutrient availability (Moran & Bjorndal 2005, 2007, Fourqurean et al. 2010). Overall values of nitrogen and phosphorus content of *T. testudinum* in this study (maximum 3.4 and 0.26 percent dry weight, nitrogen and phosphorus respectively) were higher than those found in Bermuda (maximum 2.5 and 0.15 percent dry weight, nitrogen and phosphorus, respectively, see Fourqurean et al. 2010). High nutrient availability shifted N:P ratios in all patches towards the taxon specific Redfield ratio of 30:1 (Duarte 1992). During the summer, C:N:P ratios were higher as more carbon was fixed in all three patches and in winter only turtle grazed patches were significantly below the taxon specific Redfield ratio for C:P (Duarte 1992).

Contrary to the typical response of macrophytes to the increased favorable growing conditions in the summer (Lee & Dunton 1997) and as recorded in the ungrazed patches during this study, neither fish nor turtle grazed patches had higher productivity in summer compared to winter. Leaf widths of fish grazed (4.9-5.4mm) and turtle grazed (5.0-5.9mm) patches in this study were narrower than some other studies on grazing (6.3 – 6.3mm; Zieman et al. 1984) but not as narrow as other published studies (5.6 – 6.3mm, Moran & Bjorndal 2005; 3.3 – 4.7mm, Williams 1988; 1.4 – 3.0mm, Fourqurean et al. 2010). Differences in leaf widths further emphasizes the detrimental effects of high

grazing to seagrass photosynthetic leaf tissue and rhizomal storage morphological and physiological parameters, which are necessary components to consider for seagrass recovery and survival. My study is the first to record these parameters in response to grazing behavior in a nutrient-replete environment.

Smaller sample sizes for *Syringodium filiforme* and *Halodule wrightii* limited the determination of significant differences in nutrient and soluble carbohydrate content between patches but their absence in grazed patches may indicate herbivore preference (Armitage & Fourqurean 2006). The absence of certain species may also indicate a lower tolerance to these repeated or prolonged grazing behaviors as they are unable to recover sufficiently to remain in the ecosystem (Kuiper-Linley et al. 2007). The lower soluble carbohydrate in the ungrazed *S. filiforme* during the winter may decrease the ability of this species to recover from grazing. Larger species with thicker rhizomes, such as *T. testudinum*, may also be better at translocating their stored carbohydrates longer distances and are therefore better able to compensate for loss than those species with thinner rhizomes, e.g., *H. wrightii* and *S. filiforme* (Marba et al. 2006). The reduced productivity and amount of leaves for all three species when compared to ungrazed leaves reflects a significant decrease in aboveground biomass and increases the plant's reliance on belowground biomass as a energy reserve (Williams 1988). As these reserves are depleted to replace leaves lost to grazers, the lower soluble carbohydrate content of the rhizomes reduces the ability of the plant to counter prolonged or future disturbances until the reserves can be replaced (Thayer et al. 1984, Kuiper-Linley et al. 2007, Moran & Bjorndal 2007). More importantly, considering this relationship was found at a eutrophic study site further indicates that high nutrient availability cannot counter the biomass loss

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caused by grazing as these macrophytes become carbon starved through similar

mechanisms as those found in mesotrophic seagrass beds (Fourqurean et al. 2010). My

data also support the recent relationship established between nutrient-replete

environments and reduced soluble carbohydrates as seagrasses utilize available nutrients

for growth rather than rhizomal storage (Campbell et al. 2012).

Grazer behavior and patterns

Over a six month interval, the location of grazed patches was largely stable, with

only a small fraction of area changing status. My data indicate grazing patches were

long-lived enough to affect soluble carbohydrate storage, morphology and nutrient

content of seagrass leaves. As expected, during the initial survey turtle herbivory

reduced seagrass abundance and canopy complexity (macrophyte species diversity and

blade length and width). During the second survey, after patches were abandoned,

increased leaf lengths, widths and the occurrence of pioneering species (*Halodule

wrightii*) increased canopy complexity. The abundance of this species in recently

abandoned patches is consistent with successional dynamics reported for other types of

seagrass ecosystems, especially in nutrient-replete systems (Duarte 1995, Fourqurean et

al. 1995). Although I cannot test statistically changes in macroalgae as a result of the

small sample size, the one patch that had *Udotea* and *Halimeda* during the initial study

did have a new genus, *Penicillus*, during the second survey. It was surprising that

macroalgae was scarce throughout grazed patches, where canopy cover was decreased

and competitive interactions may be favored, or in ungrazed patches, where macroalgae

may potentially find refuge from selective removal by 'pruning' grazers. Slow

colonization by macroalgae may be due to a limited reproductive potential into the area

and is an interesting area for further study on macrophyte dynamics in this unique system.

Different impacts of grazers on seagrass species may also be an important determinant of primary producer distribution, as found in other studies (Armitage & Fourqurean 2006). Fishes such as members of the family Scaridae preferentially feed on faster-growing, early successional seagrass species such as *Halodule wrightii* over slower-growing, climax species such as *T. testudinum* (Armitage & Fourqurean 2006), thus impacting the diversity of seagrasses found within these grazed patches. Macrophyte preference is less evident for green sea turtles in the Caribbean as their diet largely consists of *T. testudinum* (Mortimer 1981), which may be an artifact of the lower availability and abundance of *H. wrightii* relative to other species as well as spatial variability between grazing populations and habitat types (Bjorndal 1997). This is the first study to simultaneously consider the impact of different grazing behaviors on morphological and physiological parameters important to seagrass growth and recovery (e.g., productivity, blade width).

Ungrazed portions of the seagrass bed provided refugia for *H. wrightii* and *S.filiforme* within the ecosystem, which may allow recolonization by these species once patches are abandoned by grazers. Similar responses have been reported after other disturbances (Armitage et al. 2011). While *H. wrightii* can replace *T. testudinum* under conditions of high nutrient availability (Fourqurean et al. 1995), if no source for *H. wrightii* propagules exists, the ecosystem could collapse to become bare sand. This study indicates that heterogeneous grazing may promote a more species-rich seagrass community in a eutrophic ecosystem.

Giving Up Density as a driver to patch abandonment

Monitoring of patch status provided an opportunity to look at the changes in response variables (nutrient content, morphology, physiology) as a function of patch type. The driver(s) behind these changes in patch use are elusive as monitoring of *Chelonia mydas* patch use through time can be challenging in the field. My results did not conform to my hypothesized association to soluble carbohydrates or with the previously hypothesized driver of nutrient content. However, those patches abandoned had the smallest biomass and therefore density of leaves (Figure 5), indicating that a giving up density or a 'giving up biomass' may be the mechanism by which patches are abandoned. When a patch is composed of these much smaller leaves, the effort required by *C. mydas* to consume enough plant biomass to fulfill their nutritional needs far outweighs the cost and therefore induces abandonment, similar to the mechanism reported in terrestrial ecosystems (Brown 1988). This theory refers to the density of resources within a patch at the point an herbivore discontinues grazing. In this system, patch abandonment is not driven by the quality of seagrass as would be reflected in the soluble carbohydrate or nutrient content, but by the low quantity provided by the sparse, thin seagrass blades of the heavily grazed patches. This is supported by the abandonment of only those patches with leaf area/biomass less than 350mm^2. I would expect that once a patch reaches this 'abandonment threshold,' the patch will be abandoned by mesograzers in search of higher quantity yields for their grazing effort.

My research is the first to apply the 'giving up density' theory to the grazing behavior of marine herbivores. The application of this theory provides novel insight on the behavior of mesograzers and the crossover between terrestrial and aquatic theories,

which provides a platform for additional inquiries on the behavior of other mesograzers (e.g., manatees, dugongs). While sea turtles in this study site are not at risk of predation because of the paucity of predators, Brown's original theory included predation cost. Where predation is higher, there may be a greater risk to continued grazing when available food biomass and density are low. I therefore might predict this abandonment threshold to be at a higher density than my study site as costs of predation risk outweigh low harvest rates. The application of giving up density theory should be examined in other sites where the drivers behind patch abandonment by green sea turtles have yet to be determined and predation may be a consideration.

Table 1: Average percent abundance of seagrass in patches within each grazing designation.

		Patch Status				
	Sampling	Ungrazed n = 20	Newly Grazed n = 1	Grazed n = 6	Abandoned n = 11	Statistic
Thalassia testudinum abundance	Initial	31%		1%		t-test $p < 0.001$
	Second	32%[a]	25%	12%[b]	10%[b]	ANOVA $p = 0.015$
Syringodium filiforme abundance	Initial	10%		1%		t-test $p < 0.001$
	Second	23%[a]	5%	10%[b]	10%[b]	ANOVA $p = 0.037$
Halodule wrightii abundance	Initial	23%		1%		t-test $p < 0.001$
	Second	22%[a]	5%	1%[b]	31%[c]	ANOVA $p = 0.008$

Figure 1: Patch differentiation as ungrazed (left) and turtle grazed (right). Note the thinner, less dense seagrass in the grazed plot with exposed sediment when compared to the denser, longer *Thalassia testudinum* blades in the ungrazed plot.

Figure 2: *Thalassia testudinum* width in all three grazing patches for both seasons winter and summer. Values are patch means ± SE. Significant differences were assessed with a randomized complete block ANOVA and differences among patches determined through pairwise comparisons with Bonferroni corrected significance levels (0.008). Superscripted letters indicate significant difference between patches in the same season (ANOVA F = 12.063, p < 0.001).

Figure 3: *Thalassia testudinum* elongation rate and new growth area for both seasons winter and summer. Values are patch means ± SE. Significant differences were assessed with a randomized complete block ANOVA and differences among patches determined through pairwise comparisons with Bonferroni corrected significance levels (0.008). Superscripted letters indicate significant difference among patches in the same season (Elongation rate ANOVA, F = 16.993, p < 0.001; New Growth Area ANOVA, F = 10.224, p = 0.002).

Figure 4: *Thalassia testudinum* carbon (a), nitrogen (b), phosphorus (c) and soluble carbohydrates (d). Values are patch means ± SE. Significant differences were assessed with 3-way ANOVAs, and differences among patches determined by pairwise comparisons with Bonferroni corrected significance levels (0.008). Superscripted letters indicate significant difference among patches in the same season (corresponding to the Patch ANOVA F and p-value). Samples sizes are summer, winter: ungrazed (12, 11), fish grazed (6, 10) and turtle grazed (12, 8).

Figure 5: *Syringodium filiforme* carbon (a), nitrogen (b), phosphorus (c) and soluble carbohydrates (d). Values are patch means ± SE (ungrazed and turtle grazed only). Significant differences were assessed with 2-way ANOVAs and differences between patches determined by pairwise comparisons with Bonferroni corrected significance levels (0.008). Superscripted letters indicate significant difference between patches in the same season (corresponding to the Patch ANOVA F and p-value). Samples sizes are summer, winter: ungrazed (4, 11), fish grazed (0, 1) and turtle grazed (4, 8).

Figure 6: *Halodule wrightii* carbon (a), nitrogen (b), phosphorus (c) and soluble carbohydrates (d). Values are patch means ± SE (ungrazed and turtle grazed only). Significant differences between winter and summer ungrazed samples were assessed with a student's t-test. Significant differences between summer ungrazed and turtle grazed were assessed with student's t-test (t-test) or Mann-Whitney t-test (M-W), depending on normality of data from the small sample size. Samples sizes are summer, winter: ungrazed (4, 11), fish grazed (0, 0) and turtle grazed (0, 3).

Figure 7: Percentage of patch area in each patch status. Patches that remained ungrazed or remain grazed are the same color as those patches ungrazed or grazed.

Figure 8: *Thalassia testudinum* within the monitored patches carbon (a), nitrogen (b), phosphorus (c) and soluble carbohydrates (d). Values are patch means ± SE. Significant differences were assessed with 3-way ANOVAs, and differences among patches determined by pairwise comparisons with Bonferroni corrected significance levels (0.008). Superscripted letters indicate significant difference among patches during the second survey only (corresponding to the Patch ANOVA F and p-value).

Figure 9: Scatterplot of *Thalassia testudinum* width by length for initial survey (A) and second survey (B) of patches at three different grazing statuses.

Figure 10: Leaf area biomass and density (mm^2/m^2) by patch type.

Thalassia testudinum Width (mm)

Patch Status

Thalassia testudinum
Elongation Rate (mm/shoot/day)

Thalassia testudinum New Growth Area (cm^2/shoot/day)

Legend: Winter, Summer

Elongation Rate categories: Ungrazed Grazed, Fish Grazed, Turtle

New Growth Area categories: Ungrazed Grazed, Fish Grazed, Turtle

Elongation Rate

New Growth Area

a.

Carbon content (percent dry weight)

Patch Status

b.

Nitrogen Content (percent dry weight)

Patch Status

c.

Phosphorus Content (percent dry weight)

d.

Soluble Carbohydrate Content (mgC -1 rhizome dry weight)

Patch Status

a.

Carbon Content (percent dry weight)

Patch Status

b.

Nitrogen Content (percent dry weight)

Patch Status

c.

Phosphorus Content (percent dry weight)

Patch Status

d.

Soluble Carbohydrate Content (mg C -1 rhizome dry weight)

Patch Status

c.

Phosphorus Content (percent dry weight)

d.

Soluble Carbohydrate Content (mgC-1 rhizome dry weight)

a.

Carbon Content (percent dry weight)

b.

Nitrogen Content (percent dry weight)

c. Phosphorus Content (percent dry weight)

d. Soluble Carbohydrate Content (mgC -1 rhizome dry weight)

Leaf Area: Density Index (mm-2/m-2)

Patch Status

Ungrazed   Grazed   Abandoned

CHAPTER IV: Increased algal dominance despite presence of *Diadema antillarum*
populations on a Caribbean coral reef

Abstract

Following the Caribbean-wide massive mortality of *Diadema antillarum* (Philippi, 1845), many coral ecosystems experienced a shift to a benthos dominated by algal assemblages. Populations of *D. antillarum* herbivore have been slow to recover, and further impacts on local and regional-scales have severely threatened the health of coral reefs. From 2008-2011 the population of *D. antillarum* and structure of the benthic community were monitored within Akumal Bay, Mexico as a heavily impacted ecosystem. Across the four years of the study, densities of adult *D. antillarum* did not significantly change and were highest on backreef sites (mean $1.30/m^2$ and $1.44/m^2$). Coral cover remained low at all sites (maximum 14%) and decreased during the four years of the study. Changes in crustose coralline algae (CCA) cover varied by year but cover was significantly higher on forereef sites while cover by turf-algal-sediment (TAS) increased at all four sites. *Diadema antillarum* densities correlated positively with coral and CCA cover in the backreef sites where sea urchin densities were higher but no correlation occurred with TAS and turf. Where *Echinometra lucunter* (Linnaeus, 1758) sea urchins were more prevalent, their densities correlated negatively with coral and positively with crustose coralline algae (CCA). Although densities of adult *D. antillarum* were comparable to other regions of the Caribbean, increases in TAS over the four years of this study may be evidence that even an important herbivore cannot prevent continued decline of a reef in an impacted ecosystem.

Introduction

Coral reefs in the Caribbean have experienced major disturbances over the past few decades and continue to be under a combination of stressors including bleaching, overexploitation of herbivores, coral diseases and declining water quality which has resulted in an increase in macroalgae cover (Knowlton 1992, Aronson & Precht 2001, Hughes et al. 2003, Bellwood et al. 2004). The importance of *D. antillarum* in removing macroalgae cover became evident after their massive mortality in 1983, when algal biomass abruptly increased (de Ruyter van Steveninck & Bak 1986, Carpenter 1988, Hughes 1994). As the populations of long-spined sea urchin *Diadema antillarum* (Philippi, 1845) recover after their 1983 Caribbean-wide massive mortality (Lessios et al. 1984b, Lessios 2005), it remains unclear if grazing by this herbivore provides a suitable driver from which to expect a decrease in macroalgal cover on impacted coral reefs. Modeled scenarios indicate that sea urchins impart significant resilience to Caribbean reefs such that continued decline is inevitable when sea urchins are scarce (Mumby et al. 2006). However, abundant literature indicate it is a combination of factors which impacts the benthic dynamics on coral reefs and the propensity for shifts between dominant states (e.g., competition for space (Sandin & McNamara 2012), herbivore diversity (Cheal et al. 2010), biotic histories (Aronson et al. 2004), global climate change and marine diseases (Aronson & Precht 2006).

Nearly thirty years after this mortality event, the *D. antillarum* population recovery dynamics along with concomitant changes in benthic cover have been reported for many sites within the Caribbean basin (summarized in Ruiz-Ramos et al. 2011). Adult *D. antillarum* densities currently being reported within the Caribbean (e.g.,

Jamaica) are still lower than previously recorded densities but are beginning to slowly increase (Carpenter 1988, 2005, Carpenter & Edmunds 2006). The lack of a robust population recovery is attributed to three main causes. First, the loss of cover by corals has decreased habitat complexity necessary for successful recolonization and survival by the echinoids (Lee 2006). Second, *D. antillarum* recovery is constrained through Allee effects since reproduction of sea urchins is density-dependent and requires close proximity to conspecifics for successful external fertilization (Levitan 1991). While larvae may recruit into the system (Eckert 1998), settlement typically requires a cue from high adult densities. Lastly, recovery may also be affected through the presence of other populations of echinoids or urchin predators (Lessios 1995). Research suggests an escape size does exist where large echinoids are less susceptible to predation but there are multiple factors which can reduce the probability of successful survival to that size (Hereu et al. 2005, Clemente et al. 2007), including direct predation on sea urchin larvae and subadults. Adult urchin predators (e.g., triggerfish, Randall et al. 1964) are highly prized commercial species whose densities have declined dramatically throughout the Caribbean. In systems heavily impacted by fishing, predation on adult *D. antillarum* is lower and sea urchin densities subsequently increase (Clemente et al. 2010), which may serve to increase the potential for recovery of these echinoids.

As sea urchin populations slowly recover, it is necessary to reassess their importance and role in driving the relative dominance of macroalgal benthic cover on coral reefs. For ecological studies of macroalgal cover, various classification strategies have been developed by which to categorize groups of macroalgae based upon their form and function in reference to the experimental questions being posed (Littler & Littler

1980, Steneck & Dethier 1994, Steneck 1997). Form functional groups as developed

under the relative dominance model include coral, crustose coralline algae (CCA) and

turf algae and are based upon the relative disturbance (e.g., herbivory) and productivity

(e.g., nutrients) experienced on a reef (Littler & Littler 1984). Crustose coralline algae

are the 'cementers' of the reef and produce an encrusting, calcifying skeleton which can

cue coral settlement (Morse et al. 1988). Turf algae are attached to the substratum with

rhizoids and have upright microfilamentous branches less than 2 cm tall. Because many

species of macroalgae are phenotypically plastic, the turf functional group may include

species that are considered frondose macroalgae during other portions of their life cycle

(Hay 1981). Turf can be further divided into turf-algal-sediment (TAS) with

identification as such determined by the presence of sediments bound within the turf mat

(Airoldi & Virgilio 1998). Turf-algal-sediment communities are strong competitors for

space on the reef (McCook et al. 2001), and it has been suggested that TAS may also

suppress herbivory, at least for alternative herbivores such as fish (Bellwood & Fulton

2008), because of the presence of sediment bound within the turf.

When considering these macroalgae functional groups in study sites where *D.

antillarum* populations are recovering, one expects decreased cover of turf and TAS algae

and increased cover by CCA and coral (Littler & Littler 1984, Edmunds & Carpenter

2001, Carpenter & Edmunds 2006, Jordan-Garza et al. 2008). In these sites, coral cover

is higher while TAS and turf cover has decreased. For systems with high nutrient levels

and high grazing rates, a benthos dominated by CCA is to be expected, as CCA is

adapted to resist grazing pressures (Steneck 1983). The echionid-benthos relationship

would be reflected in a positive correlation of *D. antillarum* to coral and CCA and a

negative relationship to TAS and turf. Studies tracking the relationship between these different benthic covers in relatively nutrient replete sites over longer time scales are lacking but can provide interesting insight into this dynamic.

The goals of this study were to determine: (1) if the population of *D. antillarum* on a reef with high nutrient availability was recovering, producing larvae and if they were susceptible to predation by any sea urchin predator (2) if significant correlations occurred between sea urchin densities and coral reef benthic communities (3) if cover by these benthic communities changed with time and (4) the role of any other fish herbivores, if any, within the study system on these same benthic covers. The question remains if the implications for the slow recovery of *D. antillarum* herbivore will have the significant results in a nutrient-replete reef, where macroalgal cover is much higher. I hypothesize that while *D. antillarum* populations may be recovering at this study site and driving shifts towards increased CCA cover, turf and TAS biomass removal by the herbivore population in a resource-rich environment will fail to control or decrease cover by these algal functional groups.

Methodology

Study site

The coast of Quintana Roo, Mexico on the Yucatan Peninsula consists of multiple bays and lagoons along the periphery of the Mesoamerican barrier reef, the second largest coral reef system in the world. The area is experiencing a dramatic increase in tourism pressure as development projects increase land use (Murray 2007). Stream flow of pollutants directly into the water is uncommon because of the highly porous, karstic geology characteristic of this region. Instead, terrestrially-derived nutrients enter the

coastal zone via submarine groundwater discharge and influence coastal coral, seagrass and macroalgae ecosystems. The nitrogen and phosphorus concentrations and isotopic ratios of macrophytes indicate the land-based sources of nutrients (Carruthers et al. 2005, Mutchler et al. 2007) and coral diseases have become increasingly common from eutrophication of coastal waters (Harvell et al. 2007). Studies of nitrogen isotopic content of gorgonians from Akumal established significant enrichment when compared to other sites along the MesoAmerican reef (Baker et al. 2007).

Akumal Bay reef is located approximately 300 meters from shore and is characterized by a semi-enclosed lagoon sloping towards the 3 – 4 meter deep backreef, a shallow northern and southern reef crest and a 3 – 4 meter deep forereef (Figure 1). The reef has low coral cover (13.8%, E. Jordán-Dahlgren unpubl.) with 50% loss of coral cover over the last twenty years (Harvell et al. 2007) and high fishing pressure (Garcia-Salgado et al. 2008). For this study, Akumal's barrier reef was divided into the northern and southern portions, separated by approximately 400 meters of patchy rather than continuous reef structure, with backreef and forereef areas for a total of four sites (Figure 1). In 1998, these reefs suffered massive 'El Niño' bleaching and outbreaks of disease, after which coral cover dramatically declined (Steneck & Lang 2003). The North Forereef (NF) is characterized by dead stands of *Acropora palmata* (Lamarck, 1816) and occasional live *Porites asteroides* (Lamarck, 1816) and *Montastraea sp.* colonies while the South Forereef (SF) is predominantly dead stands of *A. palmata*. Both NF and SF are exposed to more wave action than the back reef areas, as is typical of barrier reefs. The North Backreef (NB) and South Backreef (SB) sites are characterized by live *Agaricia tenuifolia* (Dana, 1848), *Montastraea sp.* and occasional *P. asteroides* colonies. Backreef

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sites are intermixed with octocorals, *Gorgonia ventalina* (Linnaeus, 1848) (NB and SB) and *Plexaurella nutans* (Duchassaing, 1860) (NB). Recently, the SB and SF sites have been increasingly colonized by the zooxanthid, *Palythoa caribaeorum* (Duchassaing and Michelottie, 1861). The NB and NF sites are adjacent to the navigation channel, where water exchange from inside the bay occurs.

Sampling methodology

At each site in July from 2008 – 2011, thirty meter long transects were sampled parallel to the reef crest (n = 6 – 10) and ten 1 m^2 quadrats were placed randomly along each transect to quantify percent benthic cover and adult *D. antillarum* density. Depths among all sites ranged 2 - 3 m. Benthic cover was classified as: turf (mix of filamentous algae less than 2 cm high), turf-algal-sediment (TAS) matrix, crustose coralline algae (CCA), macroalgae, live coral, open substrate (e.g., dead coral, bare rock) and sand. As habitat structural complexity can be a driver of *D. antillarum* distribution (Lee 2006), rugosity measurements were made every 5 m using the Atlantic and Gulf Rapid Reef Assessment (AGGRA) line intercept transect methodology (www.aggra.org). The difference between the highest and lowest relief portions of the reef within a 1 meter sweep of the 5 meter interval were recorded, providing a spatial index of the reef and a ratio of reef surface contour distance. Within the same 1 m^2 quadrat where percent cover was recorded, density of *D. antillarum* with test diameter greater than 4 cm was determined. These surveys were completed during the daylight relying on the assumption that daytime locations were an adequate representation of individual sea urchin foraging areas (Carpenter 1986).

Diadema antillarum larval recruitment into the system was measured using the methods described in Miller et al. (2009), modified from (Bak 1985). A total of 25 plates were deployed, 5 per buoyed line, along the backreef (North and South), where larval retention is highest (Hernandez et al. 2008) and at a distance 0.5-2m above the substrate. Following recommendations from *D. antillarum* recruitment studies done in Puerto Rico (Miller et al. 2009, Williams et al. 2010), settlement plates were moved to the North Backreef site during the winter after rugosity was found to be significantly higher than both forereef sites (Table 1). The plates were visually surveyed *in situ* for recruits monthly in April and May 2010, biweekly in June and July 2010, and biweekly in January and February 2011, seasonal periods when sea urchin settlers have been reported in other parts of the Caribbean (Miller et al. 2009, Williams et al. 2010). After each visual survey, the larval settlement plates were replaced with clean plates to avoid settlement-preventive fouling. Used larval plates were placed in plastic bags and transported to the laboratory where they were further surveyed under magnification to count any settled larvae that may have been missed during the *in situ* surveys.

In 2011, each of the four sites was surveyed using a modified AGGRA method (www.aggra.org) to identify and quantify all fishes present. Six 25 m long x 2 m wide belt transects were completed in each of the study sites where data on fish length, density and identity were quantified. Following the survey, fishes were placed in groups based on whether they were considered an herbivore or sea urchin predator (e.g., triggerfish, hogfish, grunts, snapper). After determining that the majority of fish surveyed could be placed in three main herbivore groups (parrotfish, damselfish and surgeonfish) and insufficient predators precluded forming a predator group, mean counts in the three

herbivore groups were normalized to a density of 100-m^2 census area per size class (0-5

cm, 6-10 cm, 11-20 cm, 21-30 cm). Mean lengths per each size class (e.g., 2.5 cm for

size class 0-5 cm) were converted to estimated biomass using length-weight relationships

(Bohnsack & Harper 1988, Paddack et al. 2006). After the first year of the study, when it

was determined that there was a small, rock-boring echinoid *Echinometra lucunter*

(Linnaeus, 1758) at the sites, density measurements of these urchins were made in the

same quadrat and with the same methodology as was used for *D. antillarum*.

Statistical analysis

To test for significant differences in *D. antillarum* and *E. lucunter* densities and

benthic covers between the four sites each year, one-way Kruskal-Wallis tests were

performed in SPSS (PASW). Mann-Whitney U tests were used for post-hoc pairwise

comparisons between sites with Bonferroni corrections for experiment-wide Type I error

rates. To test for significant differences in *D. antillarum* densities and benthic covers at

each site over the four years of the survey, one-way Kruskal-Wallis tests were performed

in SPSS (PASW). Mann-Whitney U tests were used for post-hoc pairwise comparisons

between years with Bonferroni corrections for experiment-wide Type I error rates.

Spearman rho correlations were calculated to determine the relationship between the

areas of high density *D. antillarum* (South and North Backreef) and *E. lucunter* (South

and North Forereef) with the benthic cover categories (TAS, turf, CCA, coral). Because

sea urchin populations did not significantly change at any of the sites for the four years of

the study, data were not segregated by year but were pooled for a single correlation.

Quadrat-level comparisons were utilized rather than transect or site averages as the *D.*

antillarum exhibited aggregative behavior on the meter-scale, as found in other studies

(Macia et al. 2007). To test for significant differences between sites for total fish density and biomass, an ANOVA was performed after examination of data determined it was homoscedastic.

Results

Diadema antillarum *density*

Akumal Bay reef sites were characterized by isolated, high-density aggregations of *D. antillarum* with maximum 16 adults per m^2 in plots containing sea urchins, but 77% of surveyed quadrats had no sea urchins (Table 1). Across all sites there was no significant difference in sea urchin density through time (Table 2) while a significant difference in density occurred each year across sites (Figure 2). The significant difference occurred in North and South Forereef sites, which had lower sea urchin densities (mean: 0.24, 0.20/sea urchins/m^2, respectively) than North and South Backreef sites (mean: 1.07, 1.31/sea urchins/m^2, respectively) (Figure 2). Forereef sites had an average 85% of quadrats without *D. antillarum* and, when present, mean abundance of sea urchins was 1.52/sea urchins/m^2.   Backreef sites had an average 68% of quadrats without *D. antillarum* and, when present, mean abundance of sea urchins were 3.53/sea urchins/m^2.

Benthic habitat and correlations with Diadema antillarum *density*

Across all sites the dominant benthic cover was turf-algal-sediment (TAS), which over time significantly increased while coral and turf cover significantly decreased, regardless of *D. antillarum* presence. Positive correlations of *D. antillarum* to crustose coralline algae (CCA) cover occurred in the backreef, while CCA cover increased significantly on the South Forereef, despite lower densities of *D. antillarum*.

Coral cover significantly decreased over time across all sites (Table 2) and the largest decrease in cover occurred at the South Backreef and North Backreef sites, where cover decreased 8% and 13%, respectively (Figure 3a). There was a significant difference in coral cover between all sites in 2008 ($\chi^2 = 5.093$, p = 0.024) and 2009 ($\chi^2 = 5.217$, p = 0.022), when backreef sites had significantly higher cover than forereef sites. By 2011 all sites were not significantly different from each other ($\chi^2 = 1.026$, p = 0.311) and mean coral cover was 2% ($\pm$ 0.3 SE). At these backreef sites where *D. antillarum* densities were highest, there were positive correlations of *D. antillarum* with coral and CCA cover (Table 3). Significant differences in CCA cover occurred between sites in time ($\chi^2 \geq 3.760$, p $\leq$ 0.042), which was caused by the 2 – 6 times more CCA cover on forereef sites compared to backreef sites in 2010 and 2011. At the forereef sites, over 20% of the benthos was covered in CCA by 2011 and South Forereef CCA cover more than doubled (11-26%) over the period 2008 – 2011 (Table 2, Figure 3b). The CCA cover was positively correlated to *D. antillarum* densities on the backreef sites (Table 3). The TAS cover became the dominant benthic cover at all four sites, having increased significantly over the course of the study (Table 2). Backreef sites had significantly less TAS than forereef sites ($\chi^2 \geq 14.486$, p < 0.001, Figure 3c) yet negative correlations between TAS and *D. antillarum* density were not significant (Table 3). Across all sites, there was a significant effect of time on turf cover as sites NB, SF and NF experienced a significant decrease in turf while SB did not differ significantly from initial cover (Table 2, Figure 3d).

Diadema antillarum *larval recruitment*

No *D. antillarum* larval recruits were found on the settlement plates during summer *in situ* or magnified surveys in the laboratory. There were also no *E. lucunter* larvae found on settlement plates *in situ* or during magnified surveys in the laboratory. After relocation of the plates within the backreef based on more recent literature recommendations, settlement plates still did not yield recruits.

Other faunal densities and correlations

Population densities of *Echinometra lucunter* did not change with time ($\chi^2 \geq$ 3.846, p-value $\geq$ 0.061), but each year North and South Forereef sites (7.5 sea urchins / m^2) had significantly more *E. lucunter* than North and South Backreef sites (0.4 /m^2; $\chi^2 \geq$ 13.331, p-value < 0.001; Figure 4). *E. lucunter* populations on the South and North Forereef and benthic cover categories were negatively correlated, while turf and coral exhibited positive correlations to CCA (Table 3). *Diadema antillarum* predators were scarce throughout the duration of the study and there were no significant variation among sites for the three fish herbivore species: damselfish, surgeonfish and parrotfish (ANOVA, p = 0.873, 0.799, 0.521, respectively; Table 4). Throughout the entire reef, no lobsters and no more than three triggerfish were seen in the four years of the study. No triggerfish were recorded during the 2011 surveys and other potential sea urchin predators (e.g., grunts, snapper and hogfish) were absent or occurred at densities less than 1 per 100 m^2 at all sites. Fish herbivores such as *Acanthurus coeruleus* (Bloch & Schneider, 1801) (blue tang), *Acanthurus chirurgus* (Bloch, 1787) (doctorfish) and *Stegastes adustus* (Troschel, 1865) (dusky damselfish) were present at densities averaging 19.5 per 100 m^2 across all four sites and the majority were less than 10cm in

length with mean biomass of 14.2 g / m^2 (Table 4). *Scarus taeniopterus* (Desmarest, 1831) (Princess), *Sparisoma viride* (Bonnaterre, 1788) (Stoplight), *Scarus iserti* (Bloch, 1789) (Striped) and *Sparisoma rubripinne* (Valenciennes, 1840) (Yellowtail) parrotfish across all four sites were present at lower densities (13.9 per 100 m^2) with 14% greater than 20 cm in length and a mean biomass of 9.7 g / m^2 (for all parrotfish).

Discussion

Population densities of *D. antillarum* in Akumal Bay, Mexico at the beginning of this survey were low but comparable to current densities found at other sites within the Caribbean. Expected correlations (positive relationships between *D. antillarum* and crustose coralline algae (CCA) and coral cover) were found at backreef sites where *D. antillarum* densities were highest although coral cover significantly decreased at all sites. Temporal trends do not indicate the system has experienced a decrease in prevalence of an algal-dominated state as turf-algal-sediment (TAS) cover significantly increased. Herbivore populations of both sea urchins and fish remain low and the prevalence of this epilithic TAS cover within the Bay may deter feeding by these herbivores and prevent adequate control of algal biomass on the reefs of Akumal Bay.

Diadema antillarum *abundance*

Diadema antillarum populations in Akumal Bay did not significantly increase from 2008-2011, which is consistent with results reported during surveys from other sites in previous years, Panama (Lessios 2005) and the Florida Keys (Chiappone et al. 2002). Although historic sea urchin density data is not available for Akumal Bay, the highest average densities recorded during this survey (1.44/m^2 NB 2008) are within range of those currently reported for many other areas within the Caribbean region, where these

populations have not yet recovered (summarized in Ruiz-Ramos 2011). The significantly higher populations of *D. antillarum* in the North Backreef may have been due to the significantly higher rugosity at this site. Previous research has shown that *D. antillarum* use physical structures as refuge (Ogden 1976, Levitan & Genovese 1989). In field manipulations, alterations in structural complexity significantly decreased macroalgal cover and significantly increased *D. antillarum* densities (Lee 2006). Habitat-complexity therefore facilitates the removal of macroalgae and has important consequences on both the recovery of this important herbivore and the efficacy at which macroalgal cover is reduced. The lower topographic complexity at some of our sites may act as a positive feedback to the resilience of the algal dominated state at these sites.

Successful sexual reproduction is required if local populations of sea urchins are to increase in the absence of immigration. Maximum densities of adult *D. antillarum* (16 sea urchins / m^2) were more than twice mean densities reported for another MesoAmerican Reef site in Mahahual Bay (7 sea urchins / m^2; Jordan-Garza et al. 2008), yet in Akumal there was an absence of *D. antillarum* larvae on settlement plates. Even if a proportion of larvae produced in Akumal Bay are lost due to planktonic predators or other factors, it is a reasonable expectation that some local larvae would settle on the substrate made available on the settlement plates. If adults are successfully reproducing upstream, settlers may also arrive during the 3-5 week planktonic stage (Eckert 1998). It could be that fewer reproducing adults in Akumal Bay as well as upstream locations results in inadequate larval supply from which to sustain recruitment. Sperm limitation to successful fertilization, as quantified in other studies, often leads to extremely low larval production and these Allee effects (review in (Levitan 1995) as indicated by an absence

of settlers. The methodology and placement of larval settlement plates were ideal to detect available larvae (e.g., successes in Puerto Rico and the Florida Keys, Miller et al. 2009) but perhaps studies on a larger spatial or temporal scale may impact results. Additional studies into the demographics of sea urchins in this area may yield important information on the mechanisms preventing successful larval production and retention into the system as well as inferences towards other impacted systems within the Caribbean.

In addition, the forereef sites do host a population of *Echinometra lucunter* sea urchins, which may aggressively attack *D.antillarum* as a burrow defense strategy (Grunbaum et al. 1978), increasing juvenile mortality and preventing successful *D. antillarum* larvae recruitment on the forereef. *E. lucunter* densities are significantly higher on the forereef as they prefer microhabitats with greater exposure to wave action and currents (McGehee 1992), thus limiting habitat overlap with *D. antillarum* as physical forcing determines where each sea urchin exists. Perhaps because of this, studies on the competitive outcomes of *D. antillarum* as an intruder as well as defender with *E. lucunter* are limited (Shulman 1990). Despite the perceived minimal interactions between these two echinoids, Akumal Bay *E. lucunter* populations on the forereef are on average higher than those found on other Caribbean reefs (1.24 / m^2, Lessios et al. 1984a), thus potentially increasing their relative importance in structuring the benthos at this study site. It may be that as populations of *E. lucunter* are established on the forereef, they competitively exclude other echinoids similar to original hypotheses behind interactions studied between *E. viridis* and *D. antillarum* (Williams 1981)*,* rather than through later theorized mechanisms of settlement facilitation (McClanahan 1999, Lessios 2005).

Benthos relationships

Although *D. antillarum* densities were within ranges found at other sites and suggest a positive relationship between sea urchin density and CCA/coral cover in the backreef environment, the system is still experiencing an overall increase in TAS cover. Sea urchins may be removing some turf and TAS algal cover, providing space for CCA to settle and cue coral settlement, yet sea urchins are not decreasing TAS cover. Prior to the massive mortality event, *D. antillarum* densities of 16 / m^2 were shown to completely clear algae from the reef while 4 / m^2 densities correlated to the highest coral spat densities (Sammarco 1980). More recent research suggests densities as low as 1 / m^2 can maintain a cropped algae patch (Dahlgren, C., personal communication in Mumby et al. 2006). My densities along the backreef were > 1 / m^2 yet the population of *D. antillarum* was unable to maintain a cropped algae substrate and an increase in coral cover did not occur. Decline in coral cover may be caused by a multitude of factors including stresses the coral experiences in competition with the increased epilithic TAS cover (McCook et al. 2001), reproductive restrictions within the coral population itself, historic disturbances from diseases throughout the MesoAmerican region (Aronson & Precht 2001) and many other factors impacting coral reef health (Mumby & Steneck 2008). Like sea urchins, corals are impacted by the Allee effect and the highest coral cover found at the end of the study (1% at NB) is incredibly low compared to other regions of the MesoAmerican Reef, which report an average of 22% cover by live coral (Schutte 2010). Small scale disturbances from the low level of herbivory or from wave action may be providing substrate for coral larvae settlement but coral populations within Akumal may have decreased to the extent that they are unable to successfully produce enough planulae to

counter their mortality. There are a multitude of unknown factors in addition to herbivory which should be considered when addressing causes of coral reef decline. While there is some research to suggest a more direct correlation between sea urchins and coral growth (Myhre & Acevedo-Gutierrez 2007, Idjadi et al. 2010), in Akumal this relationship does not seem to be as direct.

Considering those characteristics of macroalgal functional groups, potentially higher rates of herbivory from sea urchin populations should be reflected in a benthos dominated by CCA. In areas with fewer sea urchins and less herbivory, macroalgae should dominate the benthos. A positive correlation between *D. antillarum* and coral and CCA did occur on the backreef, where these sea urchin populations were highest, yet CCA was not the dominant cover at these sites. In fact, overall cover by CCA on the total reef area surveyed during all four years of the study was low (<17%). Despite low densities of *D. antillarum* on the forereef, CCA cover was higher than backreef sites, contrary to my hypothesized outcomes. This may be a response to *E. lucunter* populations present there or may be representative of recently explored negative effects of *D. antillarum* on CCA (O'Leary & McClanahan 2010). In addition to herbivory as a source of disturbance, forereefs are typically highly influenced by wave action (Roberts 1983), which can influence epilithic cover. Cover by CCA is highly resistant to mechanical stress and research on TAS mats suggest they may be characteristic of high-energy environments (Bellwood & Fulton 2008), despite decreased sedimentation rates in these areas (Airoldi & Virgilio 1998). This consideration of wave action as a disturbance in addition to herbivory is not often considered when predicting dominate benthic cover on coral reefs.

The population of *Echinometra lucunter* sea urchins may add to the overall level of herbivory at the forereef sites, increasing the amount of substrate available for CCA colonization and growth. For *E. lucunter,* intra- and interspecific aggression increases the dispersion of this species relative to resources (Shulman 1990). This dispersion can control the spatial distribution of not only the echinoids, but also of the benthic cover resistant to their herbivory, perhaps as is evident by the significant increase in CCA cover on the south forereef. As *E. lucunter* dominate the forereef environment, their presence had a positive correlation with CCA cover similar to *D. antillarum* correlations with CCA cover in the backreef. Of note is the significant negative correlation of *E. lucunter* densities with coral cover on the forereef, the mechanisms behind which are unknown. *E. lucunter*, similar to *D. antillarum*, did not have a significant correlation to TAS cover and therefore cannot be categorized as an adequate controller of this algal cover. With further study, this relationship may prove to play an interesting new ecological role in these echinoid/benthos dynamics.

Akumal Bay herbivorous fish populations were not significantly different at the four sites and therefore cannot explain differences in benthic cover. Their low biomass (22-72% less than other Caribbean reefs (Paddack et al. 2009), may explain the increase in algal cover, particularly as the high-sediment content in TAS mats has been shown to suppress herbivory by fish (Bellwood & Fulton 2008). Caribbean-wide reef fish population densities are decreasing (Paddack et al. 2009) and modeled scenarios on the resilience of Caribbean coral reefs indicate that while herbivorous fish may be able to compensate for the loss of urchins, reefs with low coral cover have less resistance to grazer loss and reef decline may be inevitable (Mumby et al. 2006). Low herbivore

biomass may be caused by a dominance of smaller-sized fishes within the herbivore guild and results in decreased algal consumption (Paddack et al. 2006). With 86% of parrotfish less than 20 cm in length, the decreased herbivore biomass may decrease the ability of this guild of herbivores to control macroalgal cover. These factors, in addition to variable densities of *D. antillarum*, have an important role in the interpretation of changes to benthic cover on Akumal reefs.

In summary, Akumal reefs experienced a decline in coral cover and an increase in TAS cover despite *D. antillarum* densities comparable to other sites reported within the Caribbean. While coral and CCA covers were highest where densities of *D. antillarum* were highest along the backreef, this relationship did not hold universally across Akumal Bay. This suggests that grazing by *D. antillarum* has not decreased the dominance of an algal-dominated state and supports those modeled scenarios which indicate a disproportionate decrease in resilience as coral reefs with low coral cover continue to decline (Mumby et al. 2006). A snapshot in 2008 rather than over the four years of this survey may have resulted in a far different conclusion regarding the fate of this reef, which illustrates the importance of tracking temporal trends during studies involving herbivores (both sea urchin and fish) in coral-algal dynamics. In Akumal Bay, declines in coral cover may be evidence that the presence of *D. antillarum* cannot prevent the decline of the reef as it has been impacted by high TAS cover and a paucity of suitable herbivores.

Table 1: Maximum density of *Diadema antillarum* per m^2, frequency of plots without *Diadema antillarum* and rugosity index by site. ANOVA results for comparisons between all sites each year are given as chi-square value (p-value) with similar sites separated by '-'.

		2008	2009	2010	2011
South Forereef (SF)	**Max Density (per m^2)**	4	4	1	1
	Frequency of plots without *D. antillarum*	74%	84%	98%	92%
	Rugosity	Index: 60		SE: 4	
North Forereef (NF)	**Max Density (per m^2)**	3	5	0	1
	Frequency of plots without *D. antillarum*	72%	66%	100%	95%
	Rugosity	Index: 61		SE: 4	
South Backreef (SB)	**Max Density (per m^2)**	7	8	8	9
	Frequency of plots without *D. antillarum*	87%	63%	58%	73%
	Rugosity	Index: 82		SE: 5	
North Backreef (NB)	**Max Density (per m^2)**	16	11	12	8
	Frequency of plots without *D. antillarum*	67%	68%	64%	67%
	Rugosity	Index: 111		SE: 11	

Table 2: Kruskal-Wallis Chi-square (χ^2) and p-values across all years for each site (df 3; independent variable: year).   Years not significantly different are presented with a '-' between years (2008 = 1, 2009 = 2, 2010 = 3; 2011 = 4).

Site	*Diadema antillarum*		Coral		Crustose Coralline Algae (CCA)		Turf Algal Sediment (TAS)		Turf	
	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value
South Forereef	22.308	<0.001	80.22	<0.001	46.78	<0.001	121.09	<0.001	276.22	<0.001
	1-2-3-4		2-3-4		1-2 2-3 3-4		2-3-4		2-3-4	
North Forereef	34.971	<0.001	28.05	0.011	11.18	0.011	148.43	<0.001	193.68	<0.001
	1-2-4 2-3		2-3-4		1-2 1-3-4		1-2 3-4		3-4	
South Backreef	20.364	<0.001	60.62	<0.001	33.99	<0.001	54.09	<0.001	10.51	0.015
	1-4 2-3-4		1-2-3		1-2 2-3 3-4		1-2-3		1-3 3-4	
North Backreef	21.66	<0.001	21.66	0.186	4.81	0.186	8.45	0.038	42.06	<0.001
	1-2-3-4		2-3		1-2 2-3-4		1-2-3 3-4		1-2 2-3 3-4	

Table 3: Spearman rho correlations between *Diadema antillarum* density on the North and South Backreef with the benthic cover categories and *Echinometra lucunter* on the North and South Forereef with the benthic cover categories (*ns* = no significant correlation).

		Turf-Algal-Sediment (TAS)	Turf	Crustose Coralline Algae (CCA)	Coral
Diadema antillarum	Spearman Rho	*ns*	*ns*	0.484	0.322
	p-value			<0.001	<0.001
Echinometra lucunter	Spearman Rho	*ns*	-0.200	0.247	-0.116
	p-value		<0.001	<0.001	0.011

Table 4: Herbivorous fish densities (per 100 m^2 ± standard error) and biomass (g/m^2) at all four sites in 2011.

		0-5cm	6-10cm	11-20cm	21-30cm	Total Density	Total Biomass
Damselfish	South Forereef	3.0 ± 0.5	5.4 ± 0.6	7.4 ± 0.4	0.0 ± 0.0	15.8	11.8
	North Forereef	0.4 ± 0.2	5.0 ± 0.5	9.4 ± 0.8	0.0 ± 0.0	14.8	13.6
	South Backreef	3.0 ± 0.5	4.0 ± 0.5	9.4 ± 0.4	0.0 ± 0.0	16.4	13.5
	North Backreef	0.4 ± 0.2	5.0 ± 0.5	8.6 ± 0.7	0.0 ± 0.0	14.0	12.9
Surgeonfish	South Forereef	3.0 ± 0.3	10.0 ± 0.7	10.6 ± 1.1	0.0 ± 0.0	23.6	15.7
	North Forereef	3.0 ± 0.3	12.4 ± 0.9	9.4 ± 0.6	0.0 ± 0.0	24.8	14.9
	South Backreef	3.0 ± 0.3	9.0 ± 0.7	10.0 ± 0.8	0.0 ± 0.0	22.0	14.9
	North Backreef	3.0 ± 0.3	10.4 ± 0.5	11.4 ± 0.8	0.0 ± 0.0	24.8	16.5
Parrotfish	South Forereef	0.0 ± 0.0	6.4 ± 1.1	4.6 ± 0.6	1.6 ± 0.4	12.6	8.1
	North Forereef	0.0 ± 0.0	5.0 ± 1.2	7.6 ± 0.6	3.0 ± 0.6	15.6	10.5
	South Backreef	0.0 ± 0.0	4.4 ± 1.0	6.0 ± 0.6	2.4 ± 0.4	12.8	9.1
	North Backreef	0.0 ± 0.0	4.6 ± 0.8	8.2± 0.7	1.6 ± 0.4	14.4	10.9

Figure 1: Map of Akumal Bay, Quintana Roo, Mexico (Latitude: 20° 23' 45" N

Longitude: 87° 18' 52" W). Study sites indicated by boxes (SF = south forereef, NF =

north forereef, SB = south backreef, NB = north backreef).

Figure 2: Density of adult *Diadema antillarum* (letters indicate significant differences in

the same year between sites). Solid circle = south forereef, Open circle = north forereef,

solid triangle = south backreef, open triangle = north backreef.

Figures 3A-D: Percent benthic cover for each of the four sites over four years (letters

indicate significant differences in the same year between sites). Note the difference in

scale between 3A-B and 3C-D. Solid circle = south forereef, Open circle = north

forereef, solid triangle = south backreef, open triangle = north backreef.

Figure 4: Density of *Echinometra lucunter* (letters indicate significant difference in the

same year between sites). Solid circle = south forereef, Open circle = north forereef,

solid triangle = south backreef, open triangle = north backreef.

a. Coral

b. Crustose Coralline Algae (CCA)

c. Turf-Algae-Sediment (TAS)

d. Filamentous

South Forereef
North Forereef
South Backreef
North Backreef

Percent

Year

Percent Cover

Year

92
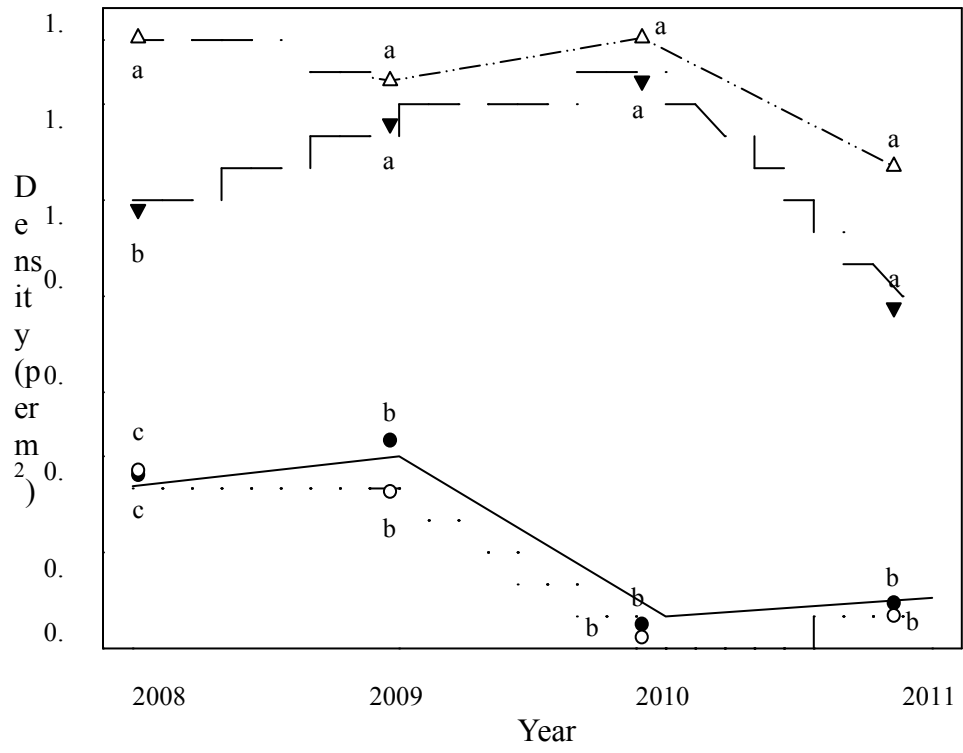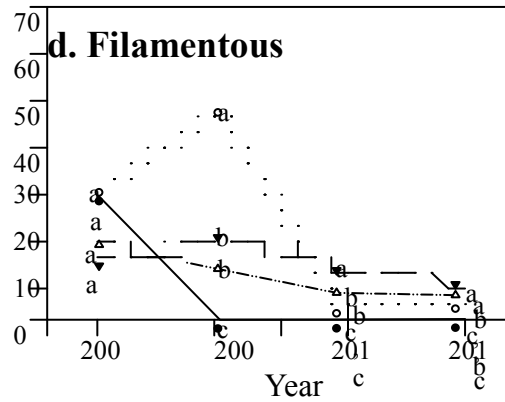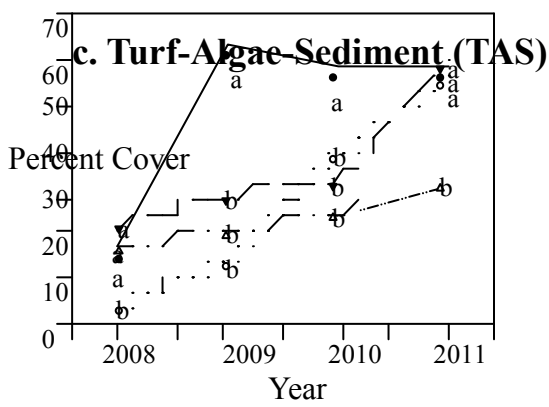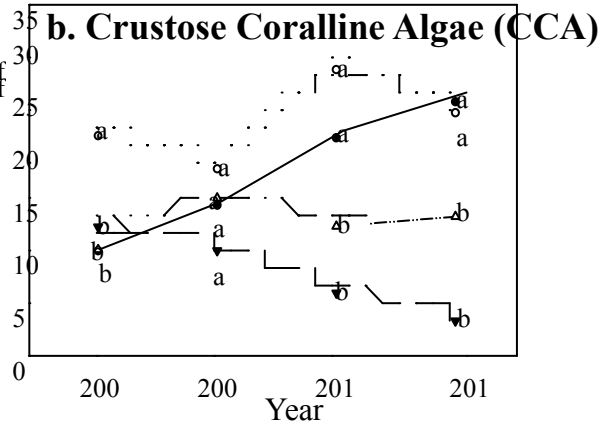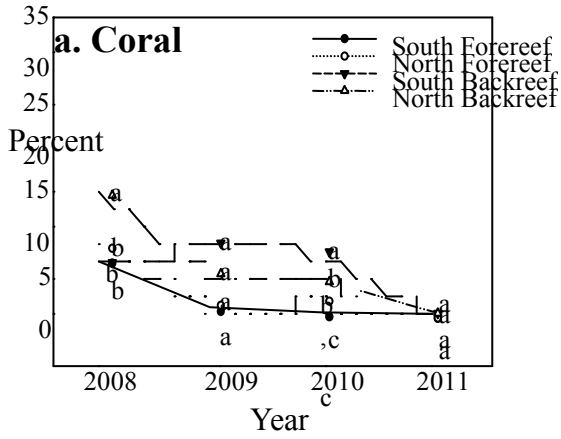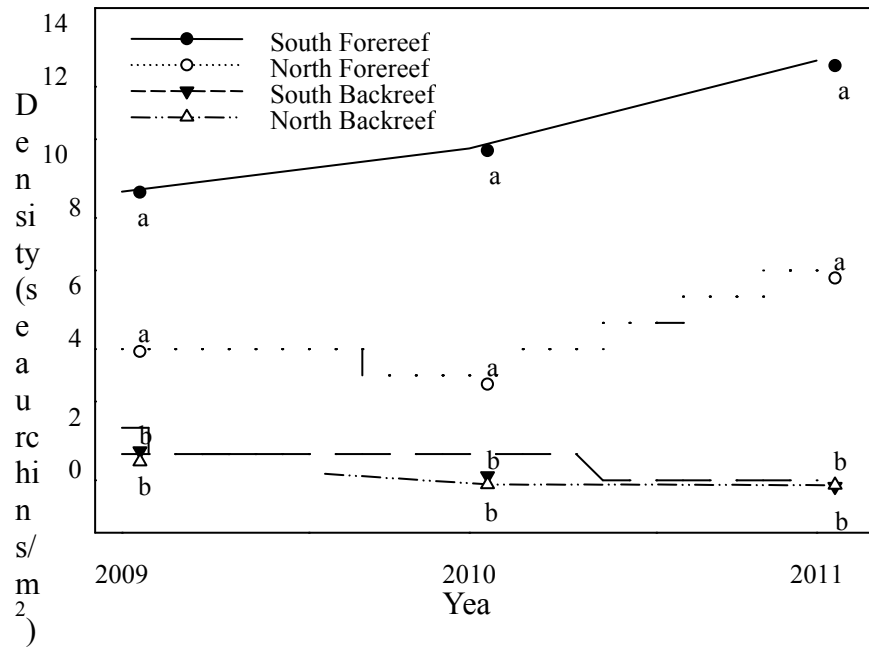
CHAPTER V: Macroalgae genera richness, diversity indices and nutrient content

relationships over time on an impacted Caribbean coral reef

Abstract

Examination of benthic functional groups previously studied (Chapter IV)

determined that reefs in Akumal were turf-algae-sediment (TAS) dominated and

Diadema antillarum densities have recovered to densities comparable to other regions

within the Caribbean. As disturbance by herbivores can drive changes to macroalgae

diversity, I monitored macroalgae generic richness and diversity indices in conjunction

with nutrient content as a proxy to productivity to determine how these factors may

impact macroalgae diversity. Using the dynamic equilibrium model, I hypothesized that

in conditions of high nutrient availability, I would expect higher diversity and richness at

higher *D. antillarum* density sites (North Backreef and South Backreef, Chapter IV) than

those sites with lower *D. antillarum* densities (North Forereef and South Forereef).

Detailed studies on macroalgae diversity and nutrient content, particularly within the

Mesoamerican region, are sparse and data reporting this information is vital for continued

work on these dynamics. My results indicate that generic diversity increased for three

sites and nutrient content remained enriched throughout the duration of this study.

Dominant genera present included *Halimeda*, *Galaxaura*, *Gelidiella* and *Dictyota*. South

Forereef was the only site which decreased in diversity and was also the only site to

experience an increase in crustose coralline algae (CCA) during previous studies. Data

on nutrient content within the various macroalgae sampled indicate highly variable

nitrogen (0.6-3.0 %DW) and phosphorus content (0.03-0.15 %DW) not previously

recorded and emphasizes the importance of continued studies on these macroalgae

nutrient dynamics. After considering general trends of increasing diversity over the four years of the study for three of the four sites, it may be both TAS and a diverse guild of macroalgae may continue to dominate the Akumal coral reef ecosystem.

Introduction

Diversity, richness and evenness are driven by a multitude of factors, the majority and extent of which in marine ecosystems are largely unknown (Stachowicz et al. 2007). Diversity encompasses taxa richness, the number of taxa present and evenness, the relative abundance of taxa within the community. Early research hypothesized that herbivory was important for maintaining diversity of marine plant communities as biomass removal decreases the probability of competitive exclusion (Paine 1966a, 1971, Lubchenco 1978). In further study, the Intermediate Disturbance Hypotheses (IDH) predicts a unimodal relationship between diversity and disturbance (grazing or abiotic forcing): at low disturbance rates, competitive exclusion can lead to community dominance by few superior competitors, but at high disturbance rate, few taxa can persist, such that diversity is at maximum at intermediate levels of disturbance (Paine 1966b, Grime 1973a, Connell 1978, Lubchenco 1978). Complexities to herbivore disturbance arise when differences in herbivore size, feeding modes, food preferences and mobility impact their effect on individual plant taxa (Lubchenco 1978). Primary producer response to herbivory is also an important factor as different competitive abilities for limiting resources and defense mechanisms can determine primary producer prevalence within the habitat (Gaines & Lubchenco 1982).

Continual nutrient enrichment impacts productivity and also creates a unimodal distribution of organisms as aggressive competitors for space and light displace

subordinate organisms (Mittelbach et al. 2001, Worm et al. 2002). For macroalgae,

effects of enrichment tend to be context-dependent and little is known about the

importance of morphological and physiological differences among macroalgae on

nutrient content (Fong et al. 2001). In marine ecosystems, some macroalgae (e.g., foliose

Chlorophytes) are opportunists with fast nutrient uptake and growth rates reflecting this

increased productivity afforded by enrichment (Waite & Mitchell 1972, Birch et al. 1981,

Gordon et al. 1981, Lapointe & Tenore 1981). There is typically a trade-off between

fast-growing colonizers and slow-growing superior competitors (Connell & Slatyer 1977,

Grime 1977), as per-capita nutrient and space availability decrease through a

successionary sequence, so that long-lived and slow-growing organisms dominate later

successional stages. However, early successional species (e.g., *Ulva*) can outcompete

species occurring during later successional stages under conditions of nutrient enrichment

(Lubchenco 1978).

Both productivity (Grime 1973a, Huston 1979) and disturbance (Paine 1966b,

Grime 1973a, b, Connell 1978) are central to those ecological theories surrounding our

understanding of the factors determining abundance, diversity and distribution of species.

In the dynamic equilibrium model, the identity and quantity of genera present can be the

result of disturbances and productivity over time (Huston 1979). This model suggests

that disturbances increase diversity when productivity is high and decrease diversity

when productivity is low. Understanding diversity is important in the context of overall

ecosystem status as a macroalgally-rich ecosystem may contain macroalgae of varying

tolerances to nutrient limitation or disturbances. The diverse assemblage of macroalgae

might then remain dominant as changes to productivity or levels of disturbance occur

over time (known as the insurance hypothesis (Yachi & Loreau 1999), provided I have an understanding on how both of these factors may have influenced diversity.

Diversity can be measured at different levels, e.g., species, genus, functional groups, depending on the type of information required to answer the ecological questions being asked. Functional groups can be created which categorize organisms based on body morphology, life history strategy or other traits that may be ecologically relevant to broader ecosystem questions, e.g., macroalgae form functional groups (Littler et al. 1983, Steneck & Dethier 1994). If an area is being monitored, for instance, to detect an invasive species or conserve an endangered species, species level surveys are necessary but they require specialist training and increased survey time. Species-level comparisons of diversity provide the highest resolution but can be too variable to demonstrate trends (Warwick 1988b, a) while genus or functional group analyses may provide more relevant ecological information (Konar & Iken 2009). Aggregating species composition data to genus level can provide similar results to functional group data (Konar & Iken 2009) however attributes determining functional groups can be disputed or vary between researchers and experimental questions. Because it is impossible to disaggregate data collected using functional groupings into species- or genera-specific information after the fact, recording of data in the field should be done at the highest practical level of taxonomic resolution. For marine macroalgae and the difficulty of field identification to the species level, genus level is the more practical choice and provides latitude to functional group assignation of individual taxa. In this manner, data collected at the genus level can not only be useful for those ecological questions being asked during the

survey, but can also provide important information to questions that arise from the survey results.

Previous survey data (Chapter IV) considered coral reef functional groups such as turf. Because many species of macroalgae are phenotypically plastic, the turf functional group may include multiple genera that are considered frondose macroalgae during other portions of their life cycle (Hay 1981) and may have vastly different impacts on coral reef ecosystem dynamics. The use of these functional groups was useful to answer the ecological questions posed during the previous survey while more specific questions on diversity, evenness and richness require genus-level surveys, the highest level of taxonomic resolution that can be used during *in situ* identification of macroalgae. It is helpful to consider both functional groups and genus-level information as genus level surveys can be scaled up to the most appropriate functional group and functional groups can give insight into attributes among genera that may be driving differences.

This study builds on conclusions drawn from a previous study (Chapter IV) where monitoring of benthic functional groups indicated that reefs in Akumal were increasingly turf-algae-sediment (TAS) dominated and *Diadema antillarum* densities were greatest at North Backreef and South Backreef sites. While benthic functional groups can provide information on the overall ecosystem status, a more detailed consideration of macroalgae genera and nutrient content can provide important information on the use of nutrients within the ecosystem and if macroalgae genera are likely to remain dominant through time. The goals of this study were to first complete a record of diversity and nutrient content of the macroalgae genera present within Akumal Bay. This is an important step as there is a paucity of literature reporting diversity and taxon-specific nutrient content in

the Mesoamerican (but for diversity see Collado-Vides et al. 1998 and for nutrient content see Mutchler and Dunton 2007). I also wanted to understand the drivers to macroalgal diversity (e.g., herbivore disturbance and nutrient content as a proxy for productivity) in the context of Huston's dynamic equilibrium model (1979). I hypothesized that sites where macroalgal productivity was not limited by nutrients, nitrogen and phosphorus content would be above those values indicated as minimum for aquatic marine plants (0.02% dry weight phosphorus, 1.2% dry weight nitrogen, 30:1 N:P; Atkinson & Smith 1992). For those sites with high productivity, I would expect higher diversity and richness at higher *D. antillarum* density sites (North Backreef and South Backreef, Chapter IV) than those sites with lower *D. antillarum* densities (North Forereef and South Forereef). Diversity would be expected to vary spatially among sites and temporally among years depending on changes in herbivore density and macroalgal productivity (e.g., if macroalgae nutrient content increases, I would expect diversity to increase at sites with higher *D. antillarum* density).

Methodology

Akumal Bay reef is located approximately 300 meters from shore and is characterized by a semi-enclosed lagoon sloping towards the 3 – 4 meter deep backreef, a shallow northern and southern reef crest and a 3 – 4 meter deep forereef (Figure 1). The reef has low coral cover (maximum 14%; Chapter IV) with 50% loss of coral cover over the last twenty years (Harvell et al. 2007) and high fishing pressure (Garcia-Salgado et al. 2008). Four 70m by 100m locations were targeted (Figure 1) to represent the different areas on Akumal Bay reef, two on the forereef (South Forereef and North Forereef) and

two on the backreef (South Backreef and North Backreef). Rugosity is significantly

higher in backreef than forereef sites (Chapter IV).

From 2008-2011, six to ten haphazardly-chosen locations within each area were

selected to place a 30 meter transect line parallel to the reef crest. Macroalgae generic

richness was assessed by recording percent cover and identify of all macroalgae genera

present within 60-100 random m^2 locations along the transect. All efforts were made to

identify macroalgae (greater than 3cm) to the genus level. For those specimens that I

were unable to identify in the field, samples were taken back to the lab for further

identification using Littler & Litter (2000). Shannon-Weiner diversity, which takes into

account richness and evenness, was calculated using PRIMER software (Clarke &

Warwick 2001) with the equation: $H' = -\Sigma\, p_i \ln\,(p_i)$, where p_i is the proportional cover of

the ith genera along the transect and Σ is sum of all i macroalgae genera. Pielou's

evenness was calculated as $J' = H'/\log(S)$ using PRIMER software (Clarke & Warwick

2001). Since macroalgal plants differ in size and it becomes difficult to calculate

numbers of 'individuals,' percent cover was used for the proportional data (p_i) to

calculate H' (Aronson et al. 1994). To determine if there were changes in diversity

through the four years of the survey and if diversity different by site, measures of

diversity were compared via a two-way ANOVA using SPSS after an examination of

standardized residuals determined that data conformed to assumptions regarding

normality. Differences between years were determined with post-hoc pairwise

comparisons.

Macroalgae tissue samples were collected within the four designated study areas,

both inside and outside of sampling quadrats. Samples were discarded when there was

inadequate biomass (less than 5 grams dry weight) to complete analytical sampling. All samples were gently cleaned of epiphytes, dried to a constant weight at 60ºC and ground to a fine powder using a mortar and pestle. Samples were analyzed in duplicate for nitrogen content using a CHN analyzer and for phosphorus using dry-oxidation acid-hydrolysis extraction followed by colorimetric analysis. Dry weight elemental content was calculated as (mass of element/dry weight of sample) x 100%. While some genera were found at multiple sites, *Halimeda* spp. was the only genus present in multiple sites over the four years. To determine if significant changes occurred over the four years of the survey, data across all sites were compared by year via an ANOVA using SPSS after examination of standardized residuals determined the data conformed to assumptions regarding normality.

Results

Twenty-two different genera were recorded during the surveys from 2008-2011 on Akumal reefs (Table 1). *Gelidiella* spp., *Halimeda* spp. and *Dictyota* spp. were the dominant macroalgae genera. Additional genera were noted on the reef (e.g., *Sargassum*) but did not fall within the study area. Over time, three of the four sites (North Forereef, South Backreef, North Backreef) experienced a significant increase in Shannon-Weiner diversity and Pielou's evenness while two of the sites had significant changes in richness (decrease in South Forereef and increase in South Backreef). Temporal variation also occurred in macroalgal nutrient content. While nitrogen and phosphorus content significantly increased in *Halimeda,* the only genera present in multiple sites through all four years, N:P in 2008 was not significantly different than the N:P observed in 2011. For genera not present across multiple sites, samples were largely phosphorus limited

(South Forereef: *Laurencia*; North Forereef: *Stypopodium*; South Backreef: *Stypopodium*; North Backreef: *Caulerpa*). For each of these genera present, nitrogen content was *Caulerpa* 2.5 – 2.8 percent dry weight (% DW), *Laurencia* 0.8 – 2.1 (% DW) and *Stypopodium* 1.1 – 2.0 (% DW). Maximum nutrient content was 3.1 (% nitrogen DW *Penicillus*) and 0.15 (% phosphorus DW *Caulerpa*).

Dominant Chlorophytes included *Caulerpa* (maximum cover 50%), *Halimeda* (maximum cover 60%) and *Udotea* (maximum cover 40%; Table 1). Dominant Rhodophytes included *Gelidiella* (maximum cover 80%), *Amphiroa* (maximum cover 40%) and *Galaxaura* (maximum cover 40%). Ochrophytes were dominated by *Dictyota* (maximum cover 60%). While there was no net change in generic richness for the North Forereef and North Backreef, macroalgal diversity and evenness did increase over time (Figure 2). These sites did not experience a significant change in crustose coralline algae (CCA) while coral cover significant decreased and turf-algal-sediment (TAS) cover increased (Table 2). Generic richness, evenness and diversity decreased significantly in the South Forereef while all parameters increased significantly in the South Backreef. The South Forereef was the only site to experience a significant increase in CCA while the South Backreef significantly decreased CCA. Coral cover significantly decreased and TAS significantly increased at both sites (Table 2).

Nitrogen and phosphorus content significantly increased in *Halimeda*, the only species present across all years and in multiple sites, while there were no significant changes in N:P of 2008 to 2011, which averaged 65 (Figure 3). Nutrient content in the genera collected was highly variable (Table 3) as nitrogen content was 0.6-3.4 (% DW) and phosphorus content was 0.03-0.15 (% DW). The high spatial and temporal

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variability in genera present do not make statistical comparisons of nutrient content between sites and years feasible.

Discussion

Conclusions drawn from the benthic functional groups examined previously in this dissertation indicated that reefs in Akumal are turf-algal-sediment (TAS) dominated and coral cover has significantly decreased. During this study, macroalgal diversity indices increased at three of the four sites as predicted by the dynamic equilibrium model (Huston 1979), where disturbance in a high nutrient environment increases diversity. When compared to the close to 100 genera recorded in other portions of the MesoAmerican reef (Collado-Vides et al. 1998), there were less genera found in Akumal during this survey. Although some disparity may be attributed to differences in sampling methodologies or intensities, some genera are less fecund under high nutrient conditions (Diaz-Pulido & McCook 2005) and may limit the genera present in Akumal to those which can tolerate nutrient-replete conditions. While nitrogen and phosphorus values were highly variable and for *Halimeda* tracked spatially and temporally, nitrogen and phosphorus content increased significantly and remained above the minimum nutrient content limiting to macroalgal productivity (Atkinson & Smith 1983, Duarte 1992). When considered in conjunction with previous functional group and herbivory data (Chapter IV), a decline in the algal dominated status does not seem a plausible prediction for Akumal Bay.

In coastal marine ecosystems, nitrogen and phosphorus loading are typically high from anthropogenic point and non-point sources existing in close proximity to these environments (Cloern 2001). Nitrogen:phosphorus above 30 indicate benthic marine

plant growth is phosphorus-limited and further consideration of nitrogen and phosphorus content is important to determine if specific nutrient content also indicates a limitation to growth (Atkinson & Smith 1983, Duarte 1992). In Akumal each site had at least one genus present for all four years and, in each of these site/genus combinations, nutrient ratios indicated macroalgae were phosphorus-limited. My data can also be considered in relation to the paucity of data on nutrient content of macroalgae reported for other areas within the Mexican Caribbean. For instance, in Akumal Bay Mutchler and Dunton (2007) reported *Halimeda* nitrogen values of 1 percent dry weight (% DW) while *Halimeda* in Yal Ku Lagoon, Akumal (Chapter II) had nitrogen maximum 1.6 (% DW).

Variability in nutrient content between genera could be caused by differences in morphologies and physiological requirements. Nutrient differences can occur between fleshy forms such as *Caulerpa* and *Avrainvillea* when compared to calcified forms such as *Halimeda*, *Udotea* and *Penicillus* (Demes et al. 2010). The calcifying behavior of some genera has an important role in phosphorus absorption and while samples can be decalcified to run analysis, this does not change the mechanism by which certain genera have acquired phosphorus. In this study (Table 3), fleshy *Caulerpa* nitrogen content was 2.5 – 3.0 (% DW) while calcareous *Udotea* was 0.09 – 0.115 (% DW). Phosphorus content for *Caulerpa* was 0.09 – 0.15 (% DW) and for *Udotea* was 0.07 – 0.10 (% DW). These variations could have been from differences in calcifying behavior. Other differences arise when considering growth forms such as epilithic versus psammophytic forms within the same genus (e.g., *Halimeda*) as photosynthesis among species is adapted to episodic delivery of nutrients and light limitation (Littler et al. 1988). Differences in growth morphologies between genera can also impact nutrient utilization as rhizophytic

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macroalgae utilize both water column and sediment nutrients, macroalgae with upright thalli and open-branching patterns utilize mostly water column nutrients and mat-forming species utilize mostly sediment nutrients (Fong et al. 2001). Those macroalgae genera morphologies characterized by high surface area-to-volume ratios and therefore growth rates may also have higher concentrations of nutrients than those slower growing genera (Bracken & Nielsen 2004). This study is important because it provides a more inclusive report of macroalgae nutrient content from which further work on the taxon-specific responses of macroalgae to nutrient availability can be made.

On the South Forereef, generic diversity, abundance and richness significantly decreased over the four years surveyed as the calcareous green genera *Halimeda* and *Udotea* were lost. The South Forereef experiences higher wave disturbance than backreef sites, yet this is the only site which did not follow my hypothesized results based on the dynamic equilibrium model (Huston 1979). Considering this data in conjunction with the increase in CCA and TAS cover found during previous studies, the increase in these functional groups may have increased competition for space needed for macroalgal propagule settlement and growth. The South Backreef was the only site to significantly increase genera richness through the addition of the genera *Avrainvillea*, *Bryothamnion*, *Padina* and *Turbinaria*. Some of these macroalgae do provide a more complex canopy structure (Steneck & Dethier 1994), which could provide refuge for other macroalgae genera as herbivores avoid highly dense macroalgal stands (Hoey & Bellwood 2011). Changes in macroalgal diversity could have also been impacted by the significantly higher rugosity provided at the South Backreef site than forereef sites. Structural complexity provides increased space for macroalgal propagule settlement, which could

drive the measured increases in diversity. The significant reduction in crustose coralline algae cover on the South Backreef could have also freed suitable substrate for settlement by new genera of macroalgae and the expansion of cover by the existing genera. While there was not an overall change in richness on North Forereef and North Backreef sites, genera diversity and evenness did significantly increase over time. Both of these sites experienced significant increases in TAS cover and no net change in the amount of CCA cover for the four years of the study. It is interesting to note that this is counter to what occurred on the south sites, where significant changes in CCA cover occurred when significant changes in genera richness occurred. The decrease in macroalgal genera richness where CCA was highest may have been caused by the shedding mechanism CCA utilizes to remove the epibionts attempting to recruit onto the thallus surface (Keats et al. 1997). As macroalgae are limited by available propagules and existing macroalgae fragmentation (Sousa 1985), the increasing cover by TAS mats may provide a source of these propagules and vegetative propagation for the persistence of existing genera (Airoldi 1998) while preventing the settlement or establishment of new genera.

In addition to nutrients, echinoid grazer disturbance was recorded within the sites and described in Chapter IV. In the South Forereef, the site with significantly higher densities of *Echinometra lucunter*, positive correlations between this echinoid and CCA cover may have contributed to decreased diversity through the CCA thallus shedding mechanism described previously. The decline in diversity at this site is counter to My hypothesis, which predicts that the disturbance caused by *E. lucunter* grazing would increase diversity in the high nutrient environment. In the North Forereef, *D. antillarum* was significantly lower than backreef sites and *E. lucunter* densities were significantly

lower than the South Forereef sites, yet diversity still increased. There is some disparity between the disturbances experienced at these sites which may be contributing to the inconsistencies in my measures of diversity. This study would greatly benefit from direct manipulation of the echinoids in order to elucidate some of these dynamics.

As Akumal's reefs are TAS dominated and macroalgae generic diversity has increased at the majority of sites, a reduction in macroalgal cvoer does not seem a practical prediction that can be supported within this ecosystem. Further, macroalgal identity, richness and diversity reduce temporal fluctuations in community biomass (Bruno et al. 2005, Bruno et al. 2006, Stachowicz et al. 2007) and can increase the stability of a macroalgal-dominated ecosystem. After considering general trends of increasing diversity over the four years of the study for three of the four sites, it may be both TAS and a diverse guild of macroalgae may continue to dominate the Akumal coral reef ecosystem.

Table 1: Macroalgal genera inventory for Akumal Bay, Quintana Roo, Mexico

Division	Genera	Maximum Percent Cover	Mean Percent Cover ± SE (across all four sites)
Chlorophyta	*Avrainvillea*	1	0.00 ± 0.00
	Caulerpa spp.	50	0.75 ± 0.10
	Dictyosphaeria cavernosa	20	0.16 ± 0.04
	Halimeda spp.	60	3.97 ± 0.21
	Neomeris annulata	10	0.12 ± 0.02
	Penicillus spp.	30	0.08 ± 0.04
	Rhipocephalus	10	0.03 ± 0.02
	Udotea spp.	40	0.38 ± 0.07
	Valonia ventricosa	10	0.06 ± 0.01
	Green other	10	0.17 ± 0.02
Rhodophyta	*Acanthophora spicifera*	1	0.00 ± 0.00
	Amphiroa	40	0.61 ± 0.09
	Bryothamnion	30	0.16 ± 0.05
	Coelothrix irregularis	20	0.17 ± 0.04
	Galaxaura	40	1.77 ± 0.14
	Jania	20	0.51 ± 0.06
	Gelidiella	80	1.05 ± 0.19
	Laurencia spp.	30	0.27 ± 0.05
	Liagora	20	0.06 ± 0.03
Ochrophyta	*Dictyota*	60	3.69 ± 0.22
	Lobophora	20	0.04 ± 0.02
	Padina	25	0.35 ± 0.05
	Stypopodium	15	0.36 ± 0.04
	Turbinaria	10	0.05 ± 0.02

Table 2: Change in benthic cover parameters and diversity indices over four years with average densities of echinoids (#/m^2) (↑ indicates significant increase in four years, ↓ indicates significant decrease in four years, -- indicates no significant change in four years)

Site	CCA	Coral	TAS	Turf	Diversity	Even ness	Rich ness	*Diadema antillarum*	*Echinometra lucunter*
South Forereef	↑	↓	↑	↓	↓	↓	↓	0.2	10.5
North Forereef	--	↓	↑	↓	↑	↑	--	0.2	4.5
South Backreef	↓	↓	↑	--	↑	↑	↑	1.3	0.5
North Backreef	--	↓	↑	↓	↑	↑	--	1.1	0.3

Table 3: N:P, nitrogen and phosphorus content for select macroalgae within Akumal

Bay, Quintana Roo, Mexico. Nitrogen and phosphorus values are percent dry weight and

N:P is expressed as the molar ratio.

2008	Genus	N	P	N:P
South Forereef	*Laurencia*	0.8	0.07	25
	Rhipocephalus	1.0	0.03	70
	Dictyota	1.4	0.07	45
North Forereef	*Dictyota*	1.4	0.06	50
	Halimeda	1.3	0.03	85
	Jania	0.8	0.07	27
	Liagora	0.8	0.03	75
	Rhipocephalus	1.2	0.04	68
	Stypopodium	1.5	0.07	48
South Backreef	*Caulerpa*	2.5	0.12	47
	Dictyota	1.3	0.04	81
	Galaxaura	1.1	0.06	39
	Halimeda	1.1	0.03	72
	Padina	2.7	0.06	92
	Stypopodium	1.1	0.04	68
	Udotea	2.1	0.08	59
North Backreef	*Caulerpa*	2.6	0.09	65
	Dictyota	1.7	0.07	56
	Halimeda	0.6	0.04	30
	Penicillus	1.3	0.04	73
	Stypopodium	1.4	0.03	95
	Udotea	2.1	0.08	59

2009	Genus	N	P	N:P
South Forereef	*Caulerpa*	3.0	0.12	54
	Halimeda	2.4	0.08	67
	Laurencia	2.1	0.06	74
	Stypopodium	1.2	0.04	73
North Forereef	*Dictyota*	1.7	0.05	78
	Galaxaura	1.0	0.03	71
	Halimeda	1.7	0.06	66
	Liagora	1.1	0.03	71
	Stypopodium	1.3	0.04	65
South Backreef	*Caulerpa*	2.9	0.13	52
	Galaxaura	1.2	0.03	75
	Halimeda	0.9	0.04	49
	Laurencia	2.3	0.07	75
	Stypopodium	1.6	0.05	76
	Udotea	1.7	0.07	56

North Backreef	*Caulerpa*	2.7	0.11	56
	Halimeda	1.9	0.06	76
	Laurencia	1.2	0.05	53
	Penicillus	3.1	0.09	79
	Rhipocephalus	1.7	0.07	56
	Stypopodium	1.5	0.05	67
	Udotea	2.2	0.10	51

2010	**Genus**	**N**	**P**	**N:P**
South Forereef	*Laurencia*	2.1	0.06	82
North Forereef	*Galaxaura*	1.1	0.04	56
	Halimeda	2.2	0.07	68
	Rhipocephalus	1.8	0.05	76
	Stypopodium	1.6	0.04	80
South Backreef	*Galaxaura*	1.3	0.04	70
	Halimeda	1.1	0.05	51
	Stypopodium	1.7	0.07	57
North Backreef	*Bryothamnion*	3.0	0.06	112
	Caulerpa	2.8	0.15	41
	Dictyota	2.2	0.07	70
	Halimeda	1.9	0.06	69
	Laurencia	2.3	0.06	92
	Penicillus	2.7	0.11	58
	Rhipocephalus	2.2	0.07	72
	Stypopodium	2.3	0.06	85
	Turbinaria	1.0	0.04	52
	Udotea	2.3	0.10	51

2011	**Genus**	**N**	**P**	**N:P**
South Forereef	*Laurencia*	1.9	0.06	69
North Forereef	*Dictyota*	1.5	0.06	54
	Galaxaura	1.2	0.03	78
	Halimeda	2.3	0.06	79
	Laurencia	1.1	0.05	53
	Stypopodium	2.0	0.05	82
South Backreef	*Caulerpa*	2.7	0.15	40
	Dictyota	1.8	0.05	79
	Galaxaura	1.1	0.03	99
	Halimeda	1.1	0.04	56
	Laurencia	1.8	0.06	67
	Stypopodium	1.3	0.04	76
	Turbinaria	1.1	0.04	63
	Udotea	2.5	0.09	61
North Backreef	*Caulerpa*	2.5	0.11	54
	Dictyota	1.1	0.05	48
	Galaxaura	1.0	0.03	76
	Halimeda	2.0	0.06	73

Laurencia	1.8	0.06	67
Penicillus	3.4	0.07	103
Rhipocephalus	1.8	0.05	75
Stypopodium	1.4	0.03	96
Turbinaria	0.9	0.03	69
Udotea	2.6	0.09	66

Figure 1: Map of Akumal Bay, Quintana Roo, Mexico (Latitude: 20° 23' 45" N

Longitude: 87° 18' 52" W). Study sites indicated by boxes (SF = South Forereef, NF =

North Forereef, SB = South Backreef, NB = North Backreef).

Figure 2a-c: Shannon-Weiner diversity (H'), species richness (d) and evenness (J) for all

four sites from 2008-2011 in Akumal Bay. Letters indicate significant difference at each

site among years.

Figure 3a-c: Nitrogen and phosphorus content (a) and N:P (b) of *Halimeda* spp. DW:

dry weight. Significant differences were assessed with an ANOVA across all sites to

detect differences among years. Letters indicate significant difference among years.
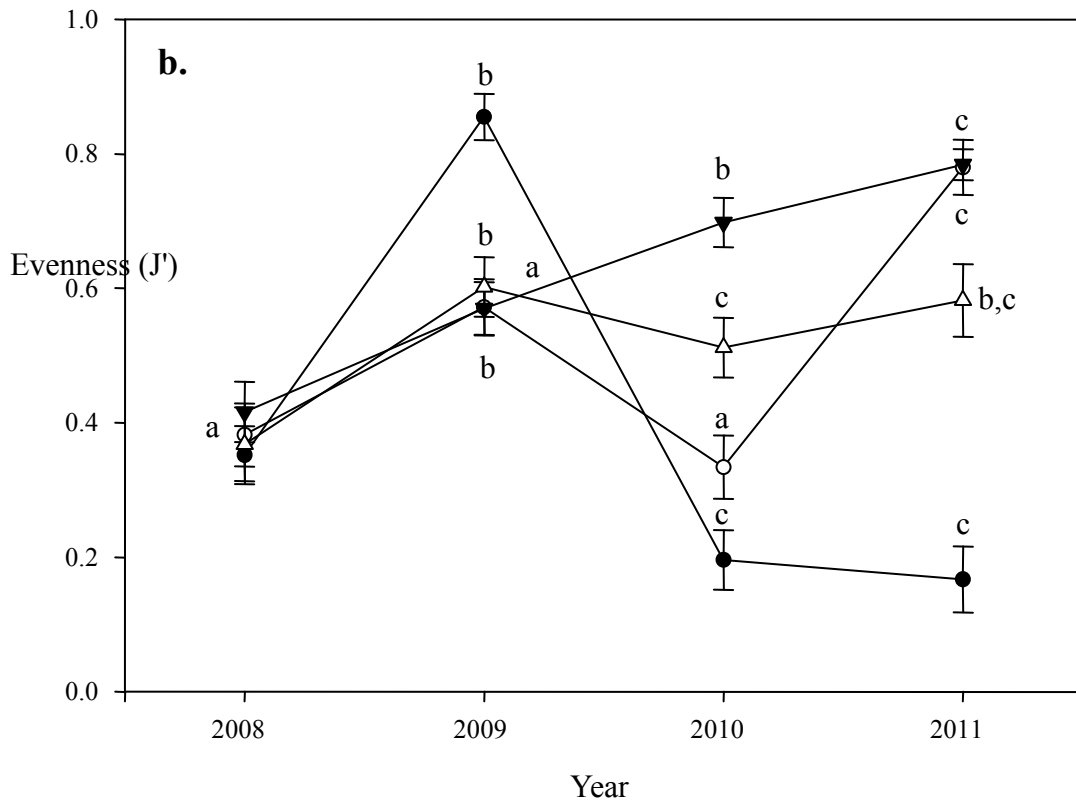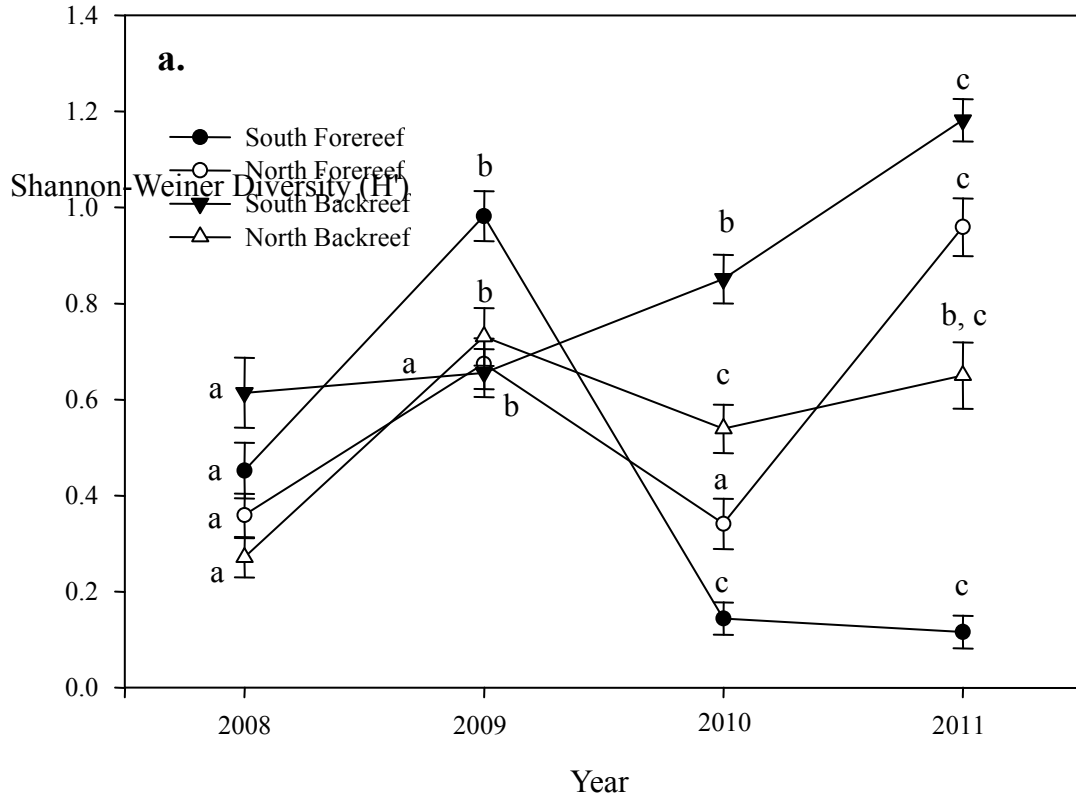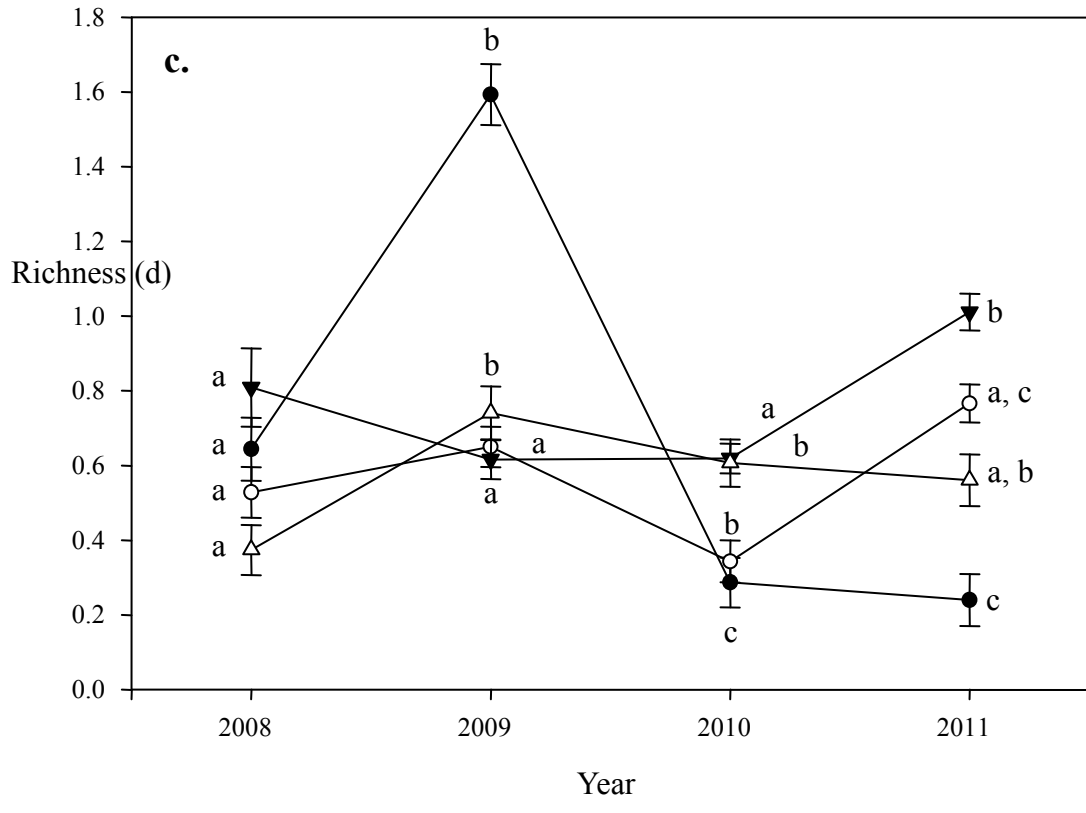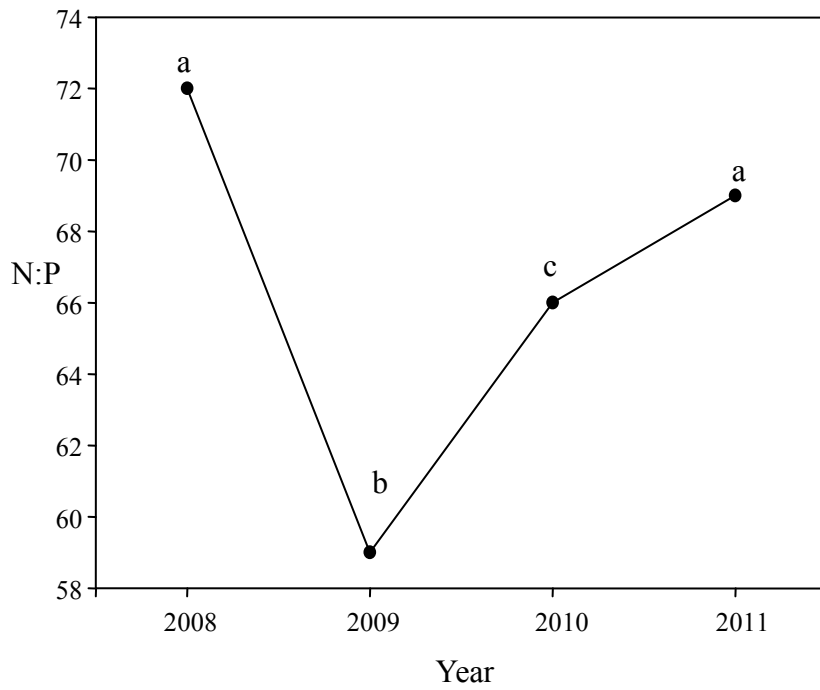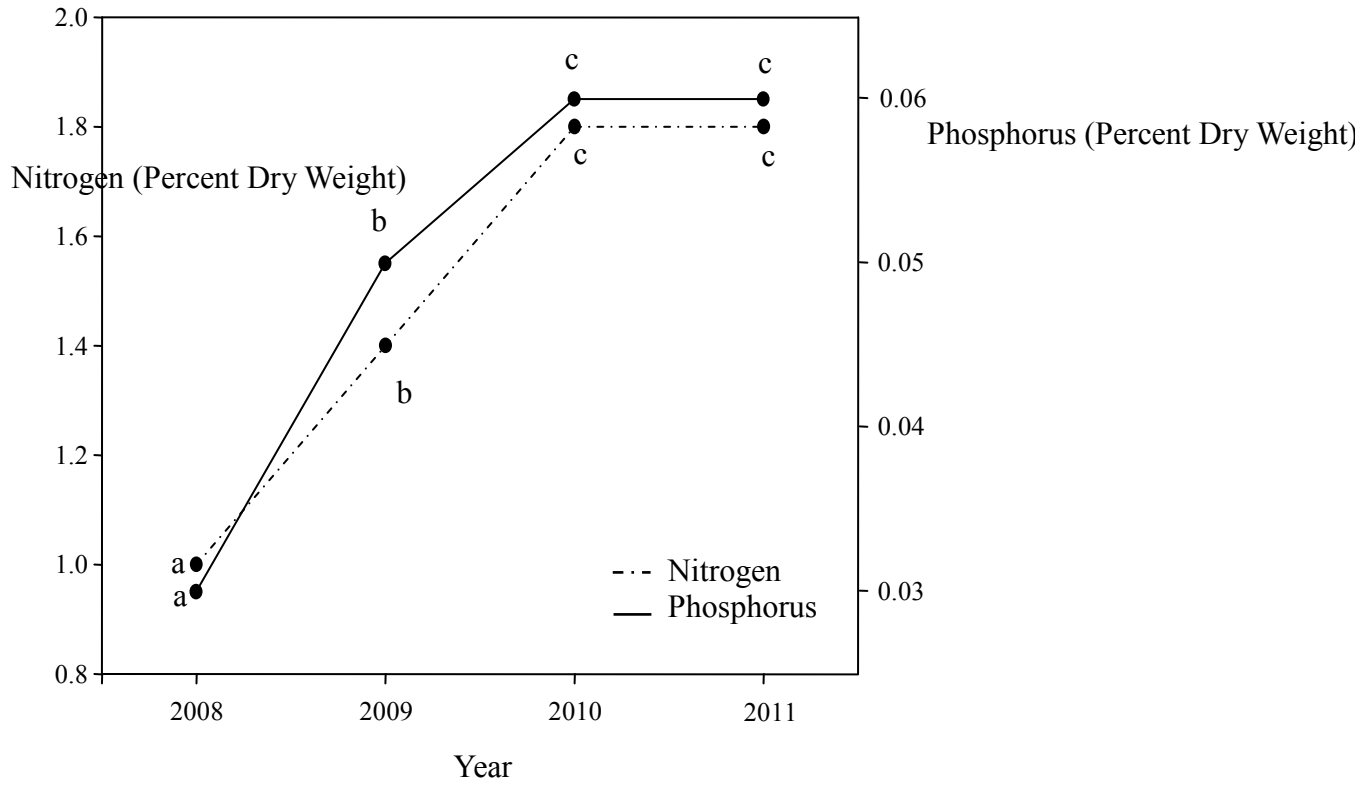
CHAPTER VI: Conclusion

This study provides valuable insight into the variable effects of herbivores and nutrients on primary producers within a tropical coastal ecosystem. In Chapter II, nitrogen and phosphorus tissue content in both active and passive macroalgal bioindicators supported the designation of the Akumal region as nutrient replete. These results support the findings of previous research in the region using seagrass, octocoral and water samples as tested for anthropogenic nutrients (Carruthers et al. 2005, Baker et al. 2007, Mutchler et al. 2007, Metcalfe et al. 2011). Only in 2010 did isotopic data from the bioassay of *Acanthophora spicifera* indicate a decrease in signature from source, which was corroborated with nitrogen content data.   In 2009 this trend was lacking in both isotopic and nitrogen content data as a peak in nitrogen and δ^{15}N occurred at mid-distance. Trends in isotopic and nitrogen content of passive bioindicators did not correlate with each other during any year or for any genera. There appears to be a decoupling of the δ^{15}N and nitrogen content signatures indicating that processes occurring in the benthos may be altering availability of these nutrients.   Studies are lacking which consider both active and passive bioindicators in the same system and over more than one sampling event. In general, data from this study establish the Akumal system is nutrient replete and macroalgae continue to be effective bioindicators of this high nutrient availability. However, if specific questions regarding nutrient dilution from source are required, as would be the case for marine park managers who seek to identify and reduced anthropogenic loading, active bioassay methodology could more accurately reflect water column nutrients. Higher spatial and temporal resolution is desirable to further utilize macroalgae as bioindicators and resolve variability found

during this study. This research emphasizes the importance of understanding limitations and confounding factors to the utilization and interpretation of bioindicator data. In any context, understanding the role and response of different macroalgae to this high nutrient availability is important for determining the likelihood that eutrophication will drive a regime shifts to a macroalgae dominated state.

Using this determination of the Akumal region as nutrient replete, in Chapter III I evaluated the impact of green sea turtles, *Chelonia mydas*, and herbivorous fish grazing on seagrass bed structure and ecosystem resilience under stressors of herbivory and enrichment. Data on seagrass patches grazed by *C. mydas* demonstrated that nutrient and soluble carbohydrate content were not predictive of patch abandonment, contrary to current theories (Thayer et al. 1984, Moran & Bjorndal 2007, Fourqurean et al. 2010). Higher nutrient content aboveground (carbon, nitrogen and phosphorus) and lower belowground (soluble carbohydrates) did follow previously reported trends in other grazed areas when compared to ungrazed areas. As in most ecological studies, increased spatial and temporal data as well as manipulative experimentation may further elucidate patterns. However, this study serves as an excellent platform from which to promote an understanding on the dynamics of herbivores in eutrophic ecosystems, a pairing not often considered (unlike peanut butter and jelly or beer and salty nuts). By completing a measurative study rather than a manipulation to mimic the behavior of these important mesograzers, I have provided evidence against a current hypothesis regarding rhizome carbohydrates and have opened a window for further study in this arena.

To revisit the conceptual model presented in the introduction, I propose a revised model (Figure 1) where eutrophication shifts the Akumal seagrass ecosystem to a highly epiphytized state, which is reversed by fish or turtle herbivory. The seagrass system shifts to a further degraded state when either herbivores are lost and the area is ungrazed or alternatively, when there are too many herbivores and continual herbivory shifts the system to bare sand. My research recorded evidence of this further degraded state in those fish grazed plots with much thinner leaves and less seagrass diversity. I would expect that over time, these areas would become completely devoid of seagrass and become sand barrens.
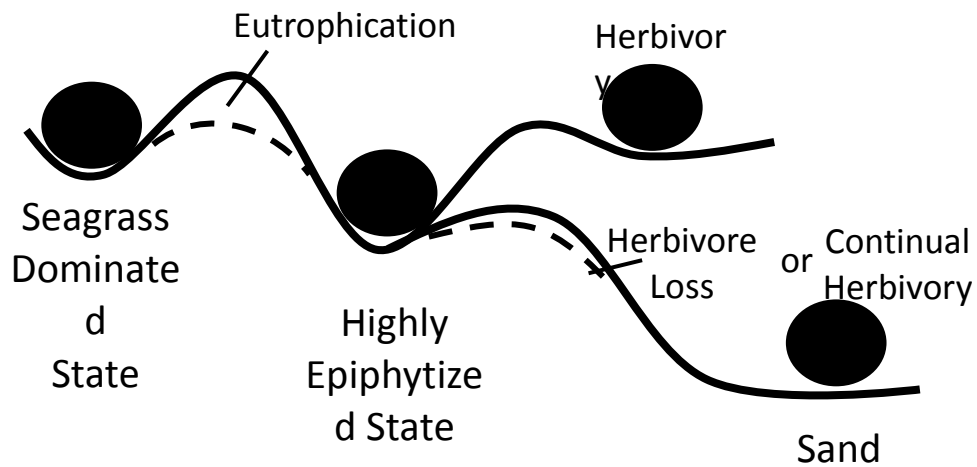
Figure 1: Conceptual model indicating the drivers to shifts within the seagrass ecosystem of Akumal Bay, Quintana Roo, Mexico. Dashed lines indicate the decreased resilience caused by the drivers eutrophication, herbivory and herbivore loss or continual herbivory.

To revisit the grazer disturbance model as I outlined in the Introduction, I propose some modifications based on the results of my research (Figure 2). While the original

model theorized it was the decline in soluble carbohydrates (dashed line) with increasing

grazing intensity which caused the seagrass patch abandonment, my data suggest that it is

the decline in biomass and the associated giving up density (Brown 1988), which cues

this abandonment. This is the first application of this giving up density theory to the

marine environment and provides an exciting platform for further work in the arena of

turtle grazing behavior.
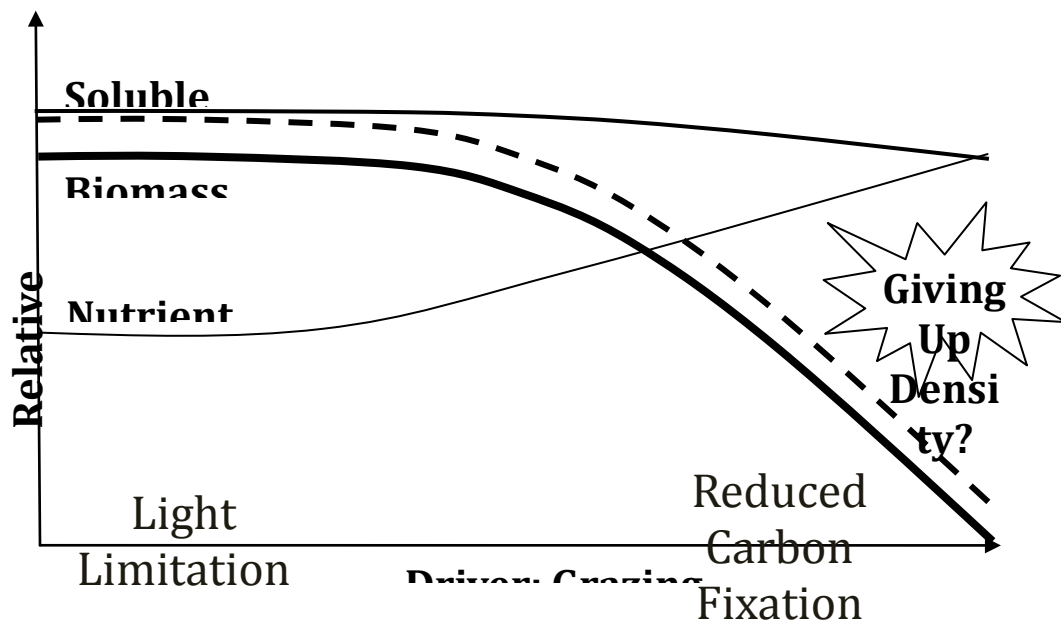
Figure 2: Grazer disturbance model for Akumal seagrass ecosystems. Low

grazing intensity leads to light limited seagrasses with higher soluble carbohydrate

content relative to aboveground nutrient content. High grazing intensity results in

reduced carbon fixation and an increase in relative nutrient content of aboveground

nutrient tissue and significantly less soluble carbohydrates (solid line as opposed to

originally theorized dashed line). Biomass may be the important driver to seagrass patch

abandonment as a potential giving up density is reached at high grazing intensities.

In a similar manner to herbivores in seagrass beds, in Chapter IV I considered herbivorous long-spined sea urchins, *Diadema antillarum*, as they consumed macroalgal biomass and influenced the dominant state of the coral reef in Akumal. Although densities of adult *D. antillarum* were comparable to other regions of the Caribbean, declines in coral cover and increases in turf-algal-sediment (TAS) over the four years of this study may be evidence that even a population of this important herbivore cannot prevent the decline of a reef with high nutrient availability. Similar to data published elsewhere, *D. antillarum* densities correlated positively with coral and crustose coralline algae (CCA) cover in the backreef sites where sea urchin densities were higher. These positive correlations and comparable sea urchin densities are important to consider in the context of a marine park manager utilizing data to predict ecosystem trajectory. If this study had been completed in 2008 only, the predicted trajectory would have considered densities of *D. antillarum* reducing macroalgal cover and a feasible coral recovery. However, when considering the trend in sea urchin populations and functional groups over four years, a different prediction occurs. On Akumal Bay's reefs, the high cover by TAS and the decline in coral cover indicate the system will likely remain algal dominated and a shift to coral dominance is unlikely.

To revisit the conceptual model presented in the introduction, I propose a revised model (Figure 3) where more specific information can be utilized to map the phase shifts that have occurred on Akumal coral reefs. In 1998, the area experienced both hurricane damage and El Niño bleaching followed by the massive mortality of *D. antillarum*. With the coral reef ecosystem in a macroalgae dominated state, further anthropogenic stressors such as nutrients and overfishing as well as incidences of disease have shifted the

community to one which is dominated by TAS. My research recorded the persistence of this TAS dominated state over time despite the presence of an echinoid population. The positive feedbacks to this TAS dominated state may have to do with the Allee effect as it reduces *D. antillarum* recovery rates, reduced reef rugosity as it restricts spatial distribution of echinoids and the suppression of herbivory that occurs with the high amounts of sediment incorporated into the TAS mats. My research is the first to record this alternative TAS-dominated state and its persistence over time when modeled scenarios would predict a decrease in macroalgal cover (Mumby et al. 2006).

Hurricane Mitch
El Niño
aching *D. antillarum*
Coral
Dominat
ed
lity
Nutrients &
Diseases
Macroalg
ae
Dominate
d
Overfish
Turf-Algae-
Sediment
(TAS)
Dominated
Allee Effect
Rugosity
Herbivory
Suppression
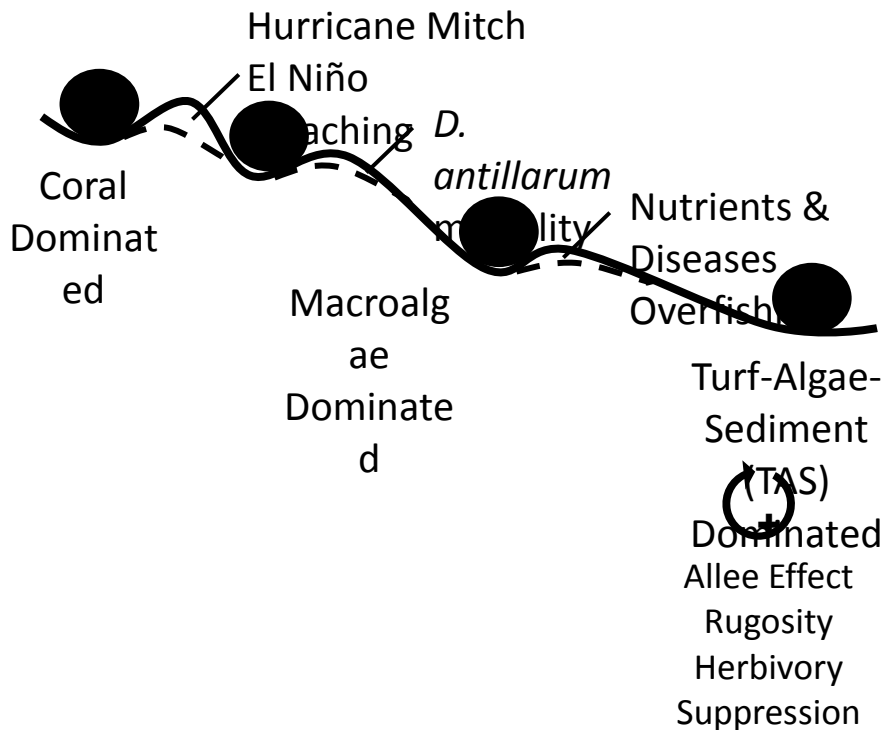
Figure 3: Conceptual model indicating the drivers to shifts within the coral reef ecosystem of Akumal Bay, Quintana Roo, Mexico. Dashed lines indicate the decreased resilience caused by drivers and the circular arrow with a plus sign indicates positive feedbacks to the TAS dominated state.

To revisit the grazer disturbance model as I outlined in the Introduction, I propose some modifications based on the results of my research (Figure 4). While the original model theorized turf and frondose macroalgae would decline with increased grazing intensity (dashed line), these macroalgal covers were largely absent in Akumal. Instead, TAS was present and dominated at sites regardless of grazing intensity. The original model theorized that either coral or CCA would increase with grazing intensity, depending on nutrient availability. In Akumal, a eutrophic system with high nutrient availability, I did record the expected result of increased CCA however these covers did not dominate, which has important ecological ramifications for marine park mangers hoping this cover will increase with echinoid recovery.
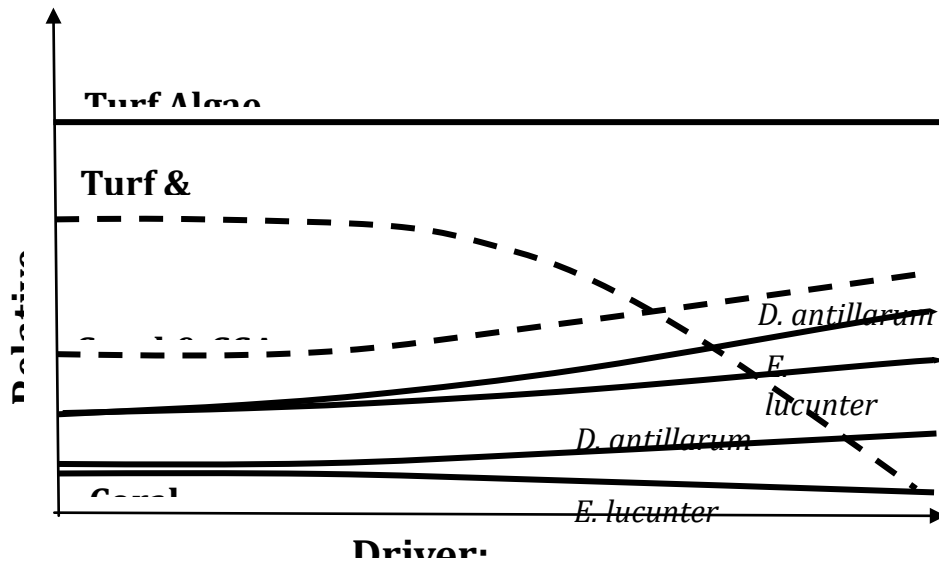
Figure 4: Grazer disturbance model for Akumal coral reef ecosystems. Dashed lines indicate the original model while solid lines indicate those results recorded during this survey. (CCA = crustose coralline algae)

An additional aspect to this study is that crustose coralline algae (CCA) as a coral settlement cue was significantly higher on the forereef sites where significantly more *Echinometra lucunter* occurred but this herbivore correlated negatively with coral cvoer. This echinoid species may have a further detrimental impact coral recovery not considered during other studies on echinoid dynamics. *E. lucunter* is not always present on other coral reefs and its relative *E. viridis* has been reported as a facilitator to coral recruitment. In the case of echinoids on Akumal reefs, their grazing behavior has not altered the dominance of a macroalgae state that is predicted under conditions of high nutrient availability.

In Chapter V I monitored macroalgae generic diversity, richness and evenness as well as considered factors such as nutrient availability over four years to determine if these measures varied temporally within an impacted, macroalgal-dominated ecosystem. These studies were done because measures of taxa richness, diversity and evenness are important to the overall structure of an ecosystem and when they are considered in conjunction with benthic functional groups examined in Chapter IV, a more integrated picture of ecosystem state can be established. Variability in macroalgae nitrogen and phosphorus concentrations precluded many determinations of significant trends, although nutrient content of *Halimeda*, the only genera present at multiple sites over time, did signify an increase in nutrients over time. Macroalgae nutrient data variability emphasizes the importance of continued studies on the effects of morphological differences between genera and the overall impact on these differences on nutrient uptake and assimilation. While I hypothesized that high nutrient availability would shift the ecosystem to one dominated by a single genera and therefore decrease diversity, richness

and evenness, generic diversity and evenness actually increased at three of four sites throughout the study duration. South Forereef, the site which experienced a decrease in diversity, was also the site which experienced a significant increase in crustose coralline algae during Chapter IV therefore this benthic cover may have an important role in overall coral reef macroalgal diversity. The population of echinoid herbivores monitored during Chapter IV may also have a role in macroalgal diversity and further manipulations of these parameters would be beneficial to data interpretation. As Akumal reefs are turf-algal-sediment dominated and macroalgae generic diversity has increased at the majority of sites, a recovery to the formerly coral dominated state does not seem a realistic expectation of this ecosystem.

Results from the research produced during these studies provide answers to not only ecological questions but also important information to be utilized in marine park managers' quest to protect these important ecosystems. In considering those bottom-up forces controlling dominant benthic assemblages, active bioassay techniques in both seagrass and coral reef ecosystems can provide important information on the availability of nutrients to these environments. Protecting the sea turtle population from anthropogenic stresses (e.g. harvesting and nest disturbance) may be an appropriate goal for Akumal Bay marine park managers as these herbivores seem to play an important role in the health of the seagrass beds. Compounding factors such as coral diseases, overfishing and eutrophication may have driven the coral reef community in Akumal Bay to such an algal-dominated state that even the recovery of an important echinoid herbivore cannot assist in the return of a coral dominated state. This same conclusion may be drawn from the increased macroalgae generic diversity, richness and nutrient

content as well. Protecting the coral reef habitat from further degradation could be the

only conservation option left for this important resource. With increased impacts to coastal

ecosystems through enrichment and overfishing, the response in primary producers reported

during these surveys is a key indicator of the larger issues affecting the stability of the seagrass

and coral habitats in Akumal Bay, Quintana Roo, Mexico.

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