



Assessment of Elkhorn Coral Populations and Associated Herbivores in Akumal, Mexico

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OPEN ACCESS

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Specialty section:

This article was submitted to
Coral Reef Research,
a section of the journal
Frontiers in Marine Science

Received: 15 February 2019

Accepted: 22 October 2019

Published: 12 November 2019

Citation:

Mudge L, Alves C, Figueroa-Zavala B
and Bruno J (2019) Assessment of
Elkhorn Coral Populations and
Associated Herbivores in Akumal,
Mexico. *Front. Mar. Sci.* 6:683.
doi: 10.3389/fmars.2019.00683

Coral decline in the Caribbean is marked by the loss of habitat-forming corals, such as elkhorn coral (*Acropora palmata*). Elkhorn coral recovery has been isolated and patchy, but recently a “re-sheeting” phenomenon, in which elkhorn tissue grows over standing dead coral skeletons, was observed along the reefs in the Mexican Yucatán peninsula. Little is known about the ecological factors contributing to “re-sheeting,” but it is hypothesized that grazing from herbivores provides top-down control of algal growth and promotes coral recovery. The purpose of this study was to evaluate the status of elkhorn populations in Akumal, Mexico and determine if *Diadema* urchins or parrotfish populations are associated with higher elkhorn abundance and lower algal cover. To achieve this objective, we surveyed 12 spur and groove reef sites in Akumal, where re-sheeting was recently observed, and measured elkhorn coral and herbivore population metrics. We found that both herbivore groups are associated with increasing elkhorn coral presence and cover, and lower macroalgal cover. Additionally, we tested for sampling bias in counting *Diadema* urchins and found that a significant difference in urchins counts between paired day and night transects on shallow, high complexity reefs. Our results suggest that historically important herbivore groups may be contributing to the recovery of elkhorn coral in Akumal by facilitating tissue re-sheeting.

Keywords: *Acropora palmata*, Caribbean, *Diadema antillarum*, parrotfishes, herbivory

INTRODUCTION

Coral decline over the last few decades has greatly changed the structure and functioning of coral reef ecosystems. In the Caribbean, an important component of this decline was the loss of habitat-forming acroporid corals, particularly elkhorn coral (*Acropora palmata*). Elkhorn coral dominated shallow reef habitats until the 1980s when an outbreak of white-band disease decimated populations region-wide (Aronson and Precht, 2001). The recovery of elkhorn coral is a conservation priority because its unique branching structure provides habitat for countless other reef organisms, its critical role in reef accretion due to fast growth, and its role in buffering coastlines from wave action (Aronson and Precht, 2001; Bellwood et al., 2004; National Marine Fisheries Service, 2015). A second critical component of reef change in the Caribbean has been the decline of herbivore populations. Regionally, parrotfishes have been removed from reefs via overfishing (Hughes, 1994) and the long-spined sea urchin, *Diadema antillarum*, was nearly extirpated regionally by a pathogen outbreak in the 1980s (Lessios et al., 1984). The reduction of herbivory has led to an increased

cover and biomass of macroalgae (Hughes, 1994; Aronson and Precht, 2000). This in turn, when extreme, can reduce coral settlement and recruitment and slow population recovery (Knowlton, 1992; Hughes, 1994; Edmunds and Carpenter, 2001; Mumby, 2009).

Despite the region-wide declines in major reef-building corals, there are some instances of patchy and isolated coral recovery documented in the Caribbean (Macintyre and Toscano, 2007; Zubillaga et al., 2008; Larson et al., 2014; Muller et al., 2014). Recently, a “re-sheeting” phenomenon, in which elkhorn tissue grows over relict coral skeletons (Bonito and Grober-Dunsmore, 2006), was observed along the reefs in the Mexican Yucatán peninsula (Bruno, 2014; Rodríguez-Martínez et al., 2014). Re-sheeting can be identified in the field (**Figure 1**) whereby thin, healthy tissue takes the shape of the substrate beneath it (in this case, usually the smoothed or flattened edges of relict skeletons) and the edge is not overgrown by another spatial competitor. Little is known about the ecological factors contributing to this re-sheeting phenomenon, and more generally, to the establishment of individual colonies and the regrowth of new populations (Graham et al., 2011). Coral recovery, in general, is complex and any number of ecological or environmental mechanisms can contribute to the recovery of coral species, including recruitment and post-settlement survival (Ritson-Williams et al., 2009), capacity to cope with additional stressors (Mora et al., 2016), interactions with predators and competitors (Grober-Dunsmore et al., 2006), or variation in geographic area and management status (Graham et al., 2011). However, we do know that grazing of benthic algae by herbivorous fishes and urchins is one mechanism of coral recovery which generally facilitates the survival and growth of juvenile or remnant corals (Edmunds and Carpenter, 2001; Hughes et al., 2007). This top-down control by herbivores suppresses the growth of macroalgae, enabling corals to settle and grow by reducing competition for space (Knowlton, 1992; Edmunds and Carpenter, 2001; Carpenter and Edmunds, 2006; Kuempel and Altieri, 2017). Increasing herbivore populations (Kramer et al., 2015; McField et al., 2018), and thus increased grazing activity, may be contributing significantly to the regrowth of elkhorn coral observed in Mexico, where it appears recovery is restricted to locations with numerous herbivores and little seaweed.

Scientists have been calling for management initiatives that will aid in the recovery of herbivore populations as one way to boost coral recovery. In the Caribbean, much of this focus is placed on increasing the populations of herbivorous parrotfish species (Jackson et al., 2014; Adam et al., 2015a; Cramer et al., 2017). Understanding the impacts of multiple grazer populations is important for management, and an ongoing debate of the relative importance of parrotfish and urchin populations in controlling macroalgal growth, specifically, has not been resolved (Adam et al., 2015a; Russ et al., 2015; Bruno et al., 2019). *Diadema* populations remain low throughout the Caribbean, but locally high populations may contribute more grazing pressure to the top-down control of macroalgae. However, we may not have an accurate understanding of the contribution of *Diadema* to coral recovery on contemporary coral reefs. *Diadema* can be hard to detect on structurally complex reefs due to their nocturnal

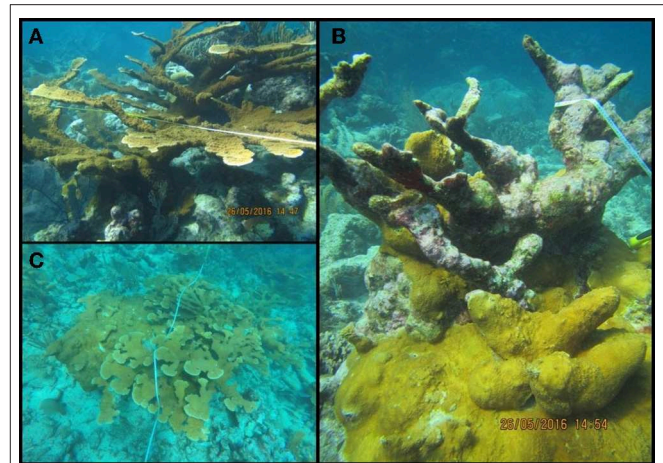


FIGURE 1 | Examples of elkhorn coral (*Acropora palmata*) growth forms. **(A)** Typical branching colony growth form. **(B)** An example of re-sheeting growth over a relict elkhorn colony. **(C)** An elkhorn thicket, and in this case contains both growth forms, with re-sheeting regrowth on the left side of the thicket and more typical branching colonies on the right and upper side of the thicket.

feeding behavior, as they are known to seek refuge from predators during the day (Ogden, 1976; Levitan and Genovese, 1989). If urchins are left out of management interventions, we may miss out on a critical component for coral reef recovery.

Akumal, Mexico, is a small coastal Caribbean town, located approximately 105 km south of Cancún, along the Riviera Maya in Quintana Roo. Patterns of coral ecosystem degradation in Akumal mirror past Caribbean region-wide decline of herbivores and corals from overfishing, hurricanes, and disease (Roy, 2004). Additionally, heavy coastal development and remarkable increases in tourism-based activities over the past decade are associated with deteriorating reef conditions in Akumal Bay, particularly in the backreef lagoon that is frequently visited by tourists (Gil et al., 2015; Figueroa-Zavala and Munoz Arroyo, 2018). Conservation efforts resulted in a fish sanctuary being announced in 2015 (Yucatan Times, 2019) and a larger (1,653 hectare) Marine Refuge for Protected Species in 2016 (Official Gazette of the Federation, 2016), yet formal protection and management measures are still being developed. Despite deteriorating conditions from coastal development, ecological monitoring along the Mesoamerican Barrier Reef indicated recent increases to elkhorn coral (Rodríguez-Martínez et al., 2014; McField et al., 2018) and herbivore populations (Kramer et al., 2015; McField et al., 2018). Yet, little is known about the abundance of elkhorn populations in Akumal and what factors may be contributing to the re-sheeting phenomenon observed on these spur-and-groove reefs.

The purpose of this study was to evaluate the status of elkhorn populations in forereef habitats of Akumal, Mexico and determine if historically important herbivore groups, namely *Diadema* urchins or parrotfishes, are associated with higher elkhorn abundance and less macroalgae. Specifically, we tested hypotheses that higher local density or biomass of herbivores corresponds to increased elkhorn presence, higher elkhorn

live area index (LAI), and lower macroalgal percent cover. Additionally, we investigated the sampling bias of *Diadema* density by conducting paired day/night transects.

MATERIALS AND METHODS

Research Site

We conducted this study on the coral reefs of Akumal, Mexico (Figure 2), where elkhorn re-sheeting was observed in recent years. There are three distinct sets of spur-and-groove reefs in Akumal, moving perpendicular from the shoreline. The shallowest spur and groove set has a depth range generally ≤ 11 m, the middle set is ~ 12 –16 m deep, and the deepest set is > 16 m deep. We sampled in the first two spur and groove sets (referred to as “shallow” and “deep” throughout), as the third deepest set is beyond the expected depth range of elkhorn coral. Survey locations were chosen based on published locations of previous elkhorn coral assessments (Rodríguez-Martínez et al., 2014) and monitoring sites used by a local non-governmental organization, Centro Ecológico Akumal (CEA). Due to rarity of elkhorn coral presence across Akumal, we surveyed some locations known to have elkhorn coral to ensure that we would find spurs with elkhorn colonies, but there was no pre-determined surveying gradient of low-to-high abundance. Table 1 documents the total number of transects and which transects contained elkhorn colonies. We conducted 55 transect surveys from May to August 2016 at 12 reef sites, covering approximately 2,200 m² of benthic habitat over a 10 km stretch of coastline. Transects were 20 m long, with all benthic information recorded within 1 m on each side and parrotfish observed within 2 m on either side.

Live Area Index of Elkhorn Coral

For each elkhorn colony or patch observed, we measured the colony size (length, width, and height in cm); estimated percent mortality; and documented observations of lesions from disease or predation, bleaching, fish bites, worms, and overgrowth. Colonies and patches were measured if the center or base of a colony was inside the 2 m belt. The calculation used for live area index (LAI) is: $(W * L * \% \text{ Live tissue})/100$ in units cm² (Larson et al., 2014). Elkhorn colonies and patches were grouped into three size classes (< 60 , 60–1,600, and $> 1,600$ cm²) based on reproductive potential (Larson et al., 2014). For patches or thickets of elkhorn coral in which it was not possible to delineate individual colonies, the total width and length of the thicket was measured, and estimated percent coverage of live tissue documented (similar to the estimation of percent mortality).

Herbivore Abundance, Biomass, and Density

We recorded parrotfish species, number of individuals of each species, initial or terminal phase, and estimated size (cm). Parrotfish biomass was calculated from published length-weight ratios found on www.fishbase.org (see Table 2 for coefficient values used), using the equation: $W = a \times L^b$ (Froese and Pauly, 2000). In the equation, W represents weight (g), L represents length (cm) and the letters a and b represent standard coefficients

based on the species. Parrotfish biomass for all species was pooled together for a biomass value for each transect (g/m²). Parrotfish species were assigned functional groups based on feeding strategy and the proportion of biomass and total individuals observed was calculated for each group (browser, scraper, and excavator). Browsers typically feed on fleshy macroalgae, grazers on turf algae, and excavators on endolithic algae but take large bites that usually excavate the reef framework (Adam et al., 2015b, 2018). The biomass (g/m²) and density (individuals per m²) of browser species was also calculated for each transect.

We counted all *Diadema antillarum* urchins observed within the 2 m belt, and density of *Diadema* was calculated for each transect (individuals/m²). We searched for urchins under crevices and included them in a count even if only the spines were visible. Transects were geolocated using surface GPS waypoints and starting points marked with flagging tape so we could return to the exact same spurs at night to recount *Diadema* urchins, for a total of 16 paired day-night *Diadema* surveys. On the paired transects only, reef topography was visually assessed by divers, whereas “complex” spurs had relatively higher reef relief and more available crevices or overhangs for organisms to seek refuge (Wilson et al., 2007).

Benthic Cover

Go-Pro cameras (Hero 4) in underwater housings were used to record benthic images along each transect, remaining ~ 25 cm above the benthos. A total of 30–35 images were collected per transect and uploaded to CoralNet for analysis (Beijbom et al., 2015). Ten points were randomly assigned to each image and we manually identified the benthic component for each tag. Identification was made to species level when possible and all ID tags were pooled into relevant functional groups (hard coral, soft coral, gorgonian, macroalgae, turf algae, crustose coralline algae (CCA), coralline-turf-bare (CTB), etc.). CTB refers to a combined category of coralline algae, turf algae, and bare substrate, and is used when the identification at the specific point cannot be resolved in the images.

Statistical Analysis

A two-step hurdle modeling approach was used to evaluate the relationship between elkhorn coral and six predictor variables: total parrotfish biomass, biomass of parrotfish browser species, density of parrotfish browser species, *Diadema* density, maximum depth, and site. Due to low sample size ($n = 16$), we could not include night time urchin density as a predictor in the models. This approach was used over other strategies to (1) aid in determining if either herbivore is associated with the presence/absence of elkhorn coral in addition to the amount of live tissue measured; (2) account for the existence of zeros in the response variable, as elkhorn coral is considered a rare species and was not observed on every transect. This is a well-accepted approach in ecological statistics for measuring the abundance of rare species (Welsh et al., 2002; Fletcher et al., 2005; Zuur et al., 2009). Prior to analysis, raw data were analyzed for normality, heteroscedasticity, outliers, and collinearity. Two outlier observations were removed prior to analysis. Total parrotfish density was not used as a predictor

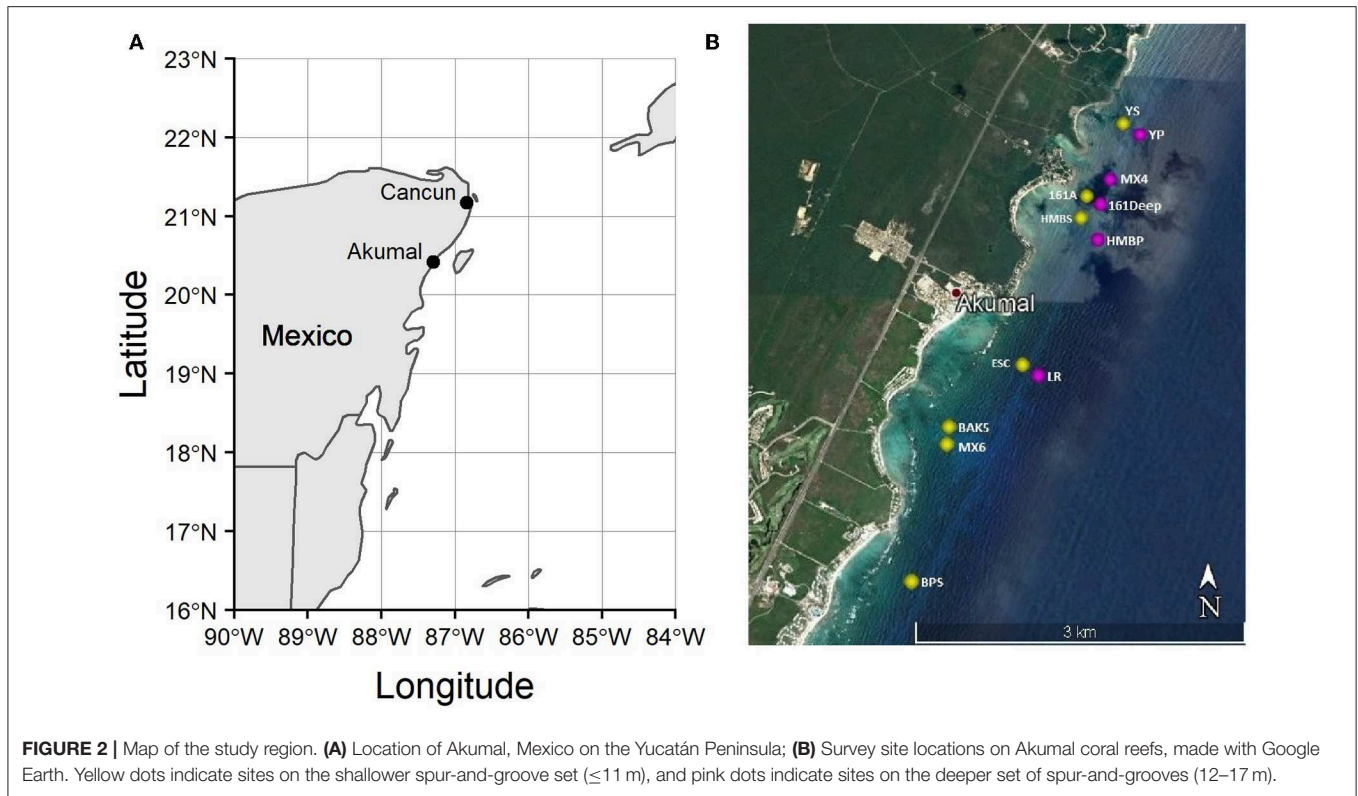


TABLE 1 | Elkhorn coral survey and demographic information.

| Site | Latitude | Longitude | Max depth (m) | Site depth category | # transects completed | # transects with elkhorn | Elkhorn LAI (cm ²): mean (SD) | Percent elkhorn cover: mean (SD) |
|----------|----------|-----------|---------------|---------------------|-----------------------|--------------------------|---|----------------------------------|
| 161ACROP | 20.40559 | -87.30202 | 9.14 | Shallow | 6 | 6 | 105,809.45 (160867.48) | 5.96 (10.91) |
| 161DEEP | 20.40478 | -87.30074 | 12.19 | Deep | 5 | 5 | 66,576.97 (74302.57) | 4.33 (5.61) |
| BAK5 | 20.38302 | -87.31755 | 7.31 | Shallow | 4 | 3 | 28,700.06 (42725.79) | 6.57 (7.54) |
| BPS | 20.37073 | -87.322 | 10.67 | Shallow | 4 | 4 | 11,706.43 (10205.53) | 3.57 (4.12) |
| ESC | 20.38927 | -87.3102 | 13.72 | Deep | 4 | 1 | 1,766.33 (3532.65) | 0 |
| HMBP | 20.4012 | -87.30149 | 16.15 | Deep | 3 | 0 | 0 | 0 |
| HMBP | 20.40339 | -87.30288 | 9.75 | Shallow | 4 | 3 | 15,368.76 (15814.95) | 4 (4.69) |
| LR | 20.38829 | -87.30881 | 15.24 | Deep | 4 | 0 | 0 | 0 |
| MX4 | 20.40732 | -87.29943 | 13.41 | Deep | 6 | 4 | 39,895.78 (60556.80) | 2.12 (5.2) |
| MX6 | 20.38264 | -87.31803 | 8.23 | Shallow | 4 | 2 | 38,736.63 (76344.12) | 0.75 (1.5) |
| YP | 20.41203 | -87.29575 | 15.54 | Deep | 5 | 0 | 0 | 0 |
| YS | 20.41321 | -87.29728 | 10.67 | Shallow | 4 | 4 | 64,076.05 (69338.72) | 0 |

Reported for each site is: latitude, longitude, maximum depth in meters, depth category of the site, number of transects completed, number of transects in which elkhorn coral was observed at that site, average live area index (LAI) of elkhorn colonies or patches that were measured, and average percent cover of elkhorn coral calculated from the benthic photo analysis.

variable due to high collinearity with biomass and fish biomass is the more ecologically relevant variable for this study. Only *Diadema* density from day-time surveys was included in the models. Maximum depth, measured in meters, was used as the fixed effect because depth category of the spurs (deep or shallow) is confounding with site: meaning that sites were either deep or shallow, but not both. In all models, total parrotfish biomass, biomass of parrotfish browser species, density of parrotfish

browser species, *Diadema* density, and depth were treated as fixed effects and site used as a random effect.

The first step tested the effect of these predictor variables on the presence of elkhorn colonies, using glmer generalized linear mixed-effects models from the lme4 package in R (Bates et al., 2015), with presence/absence of elkhorn colonies as a binomial response. In step two, for transects in which elkhorn colonies were present, we used mixed-effect lmer models from

TABLE 2 | Parrotfish species observed and coefficient values used in biomass calculations.

| Common name | Scientific name | Functional group | Value of coefficient a | Value of coefficient b | Total number fish observed | Average length of individual (cm) | Average mass of individual (g) |
|-------------|---------------------------------|------------------|------------------------|------------------------|----------------------------|-----------------------------------|--------------------------------|
| Redband | <i>Sparisoma aurofrenatum</i> | Browser | 0.00468 | 3.4291 | 174 | 14.89 | 83.42 |
| Stoplight | <i>Sparisoma viride</i> | Excavator | 0.025 | 2.921 | 93 | 21.16 | 259.39 |
| Striped | <i>Scarus iserti</i> | Scraper | 0.0166 | 3.02 | 74 | 15.79 | 76.73 |
| Princess | <i>Scarus taeniopterus</i> | Scraper | 0.0135 | 3 | 9 | 17.54 | 81.42 |
| Redtail | <i>Sparisoma chrysopterygum</i> | Browser | 0.0099 | 3.1708 | 2 | 24 | 236.92 |
| Yellowtail | <i>Sparisoma rubripinne</i> | Browser | 0.0156 | 3.0641 | 16 | 21.56 | 198.22 |
| Queen | <i>Scarus vetula</i> | Scraper | 0.0138 | 3.03 | 3 | 32.67 | 565.06 |

Summary of parrotfish species observed across all transects, species functional group assignment, the values of coefficient a and b used to calculate biomass, and the average length of an individual fish for each species. Functional groups assigned based on analysis from Adam et al. (2018).

the lme4 package to test for the effect of these predictor variables on elkhorn LAI (a continuous response variable). Macroalgae was observed on every transect, so the step two mixed-effects structure was used to estimate the effect of the predictor variables on percent cover of macroalgae. All predictor variables were centered and scaled prior to modeling. Values are centered by subtracting variable means and scaled by standard deviations, using the center and scale functions, respectively, from base R. This results in standardized coefficients that can be compared directly. Chi-squared tests were used to evaluate if predictors could be dropped from the full model. Akaike information criterion (AIC) values were used to evaluate competing models. We used paired *t*-tests to evaluate the difference in *Diadema* density between day and night surveys. All statistical analyses were completed using R version 3.5.0.

RESULTS

Description of Elkhorn and Herbivore Populations in Akumal

The heterogeneity of the spur and groove reef ecosystem in Akumal, Mexico, was indicated by the high variability in the presence and abundance of elkhorn coral and herbivores across sampling sites (Figure 3). Elkhorn coral was most common and had the highest live area index in shallow areas (Table 1) and was not found on the deepest transects (~15 m) at sites LR, YP, and HMBP (Figure 3, Table 1). We measured 85 elkhorn colonies or patches and found that a majority ($n = 60$) had a LAI >1,600 cm² (Figure 4). Of those in the larger size class, we documented 15 colonies of a typical branching form, 25 observations of continuous re-sheeting over relict elkhorn skeleton, 12 observations of patchy re-sheeting colonies, and 8 thickets which contained a series of branching colonies (see Figure 1 for examples of form classification). Average percent cover of elkhorn coral was determined from the point-count image analysis and ranged from 0 to 6.5% (Table 1). At two sites, ESC and YS, elkhorn coral did not appear under the transect tape where images were taken for point-count analysis, but colonies did originate within the 2 m belt, which explains why there is a 0% cover but positive LAI value for these sites. The average percent cover of major benthic categories are: 32.56% for macroalgae,

23.5% for turf algae, 13.02% for CTB, and 11.65% for scleractinian corals (including elkhorn coral).

The abundance and density of herbivores also varies by site and depth (Figure 3). *Diadema* density recorded in the day-time ranged from 0 to 1.2 individuals per m², with an average of 0.18 individuals/m² across all sites. *Diadema* urchins were more common in shallow sites (max density: 1.2/m², mean density: 0.35/m²) and present but rare at sites deeper than 12 m (Figure 3, mean density: 0.017/m²). *Diadema* were not observed in belt transects in 3 out of our 12 sites (BPS, LR, HMBP).

We observed seven different species of parrotfishes, with species, average length (cm), and average weight (g) reported in Table 2. Parrotfish biomass ranged from ~2–43 g/m², with an average of 12 g/m². Parrotfish were observed in all transects but had higher average biomass in deeper sites (15 g/m²) compared to shallower sites (9 g/m²; Figure 3). Browser species, which typically feed on fleshy macroalgae, comprised the largest proportion of biomass and individuals observed (42 and 51%, respectively), although excavator species made up a comparable 39% of the total biomass (Figure 5).

Herbivore Populations and the Presence of Elkhorn Coral

Herbivore population metrics of total parrotfish biomass and *Diadema* density have a positive statistical effect on the presence of elkhorn coral and accounted for 73.7% of variance explained in the model (Figures 6A,B and Table 3, marginal $R^2 = 0.737$, conditional $R^2 = 0.929$). The significance of *Diadema* density (estimate = 5.7, $p = 0.023$) was slightly higher, yet comparable to parrotfish biomass (estimate = 2.33, $p = 0.046$). Model selection revealed that browser density, browser biomass, and maximum depth were not significant predictors and were not included in the final model (Table 4).

Herbivore Populations and the Amount of Elkhorn Coral Tissue (LAI)

Linear mixed-effects models revealed that *Diadema* urchins have a statistically significant positive correlation on the amount of live elkhorn tissue (estimate = 1.66, $p = 0.032$) and total parrotfish biomass has a small, nearly statistically significant correlation (estimate = 0.04, $p = 0.094$; Table 3, Figures 6C,D).

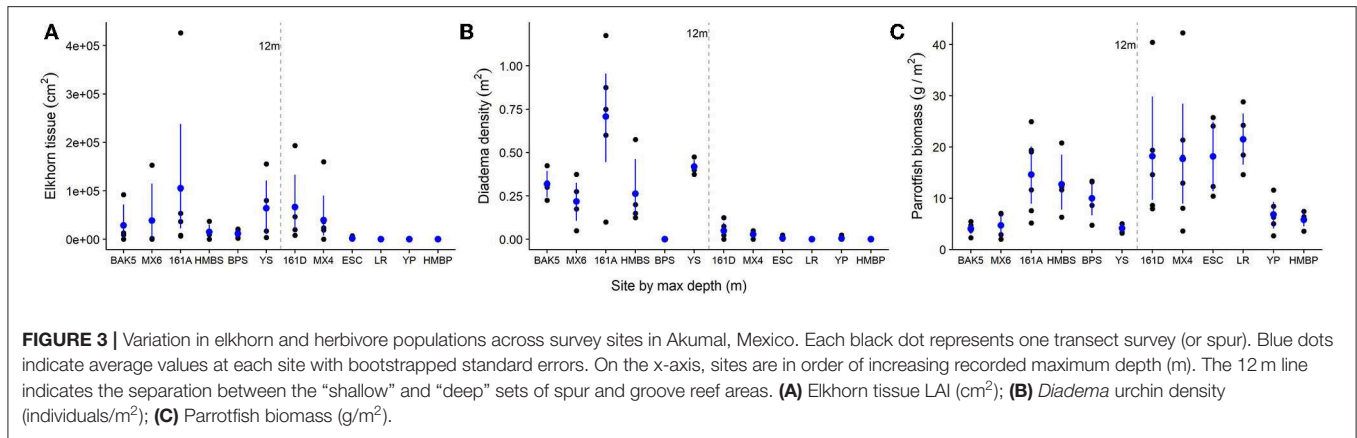


FIGURE 3 | Variation in elkhorn and herbivore populations across survey sites in Akumal, Mexico. Each black dot represents one transect survey (or spur). Blue dots indicate average values at each site with bootstrapped standard errors. On the x-axis, sites are in order of increasing recorded maximum depth (m). The 12 m line indicates the separation between the “shallow” and “deep” sets of spur and groove reef areas. **(A)** Elkhorn tissue LAI (cm²); **(B)** *Diadema* urchin density (individuals/m²); **(C)** Parrotfish biomass (g/m²).

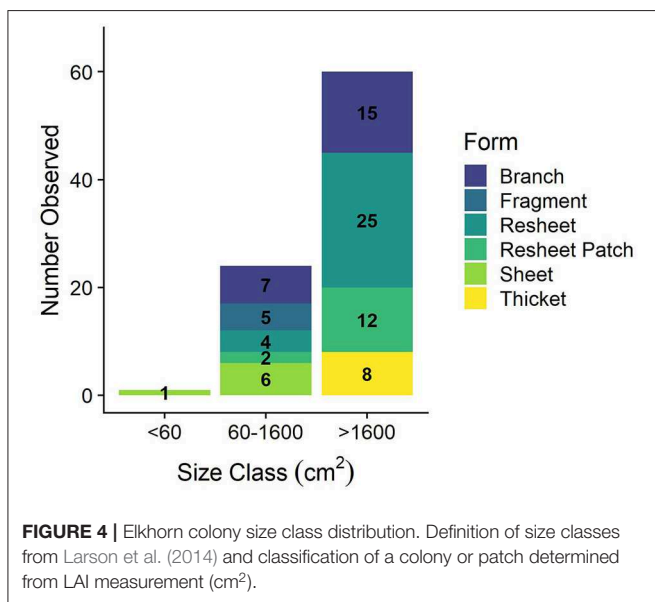


FIGURE 4 | Elkhorn colony size class distribution. Definition of size classes from Larson et al. (2014) and classification of a colony or patch determined from LAI measurement (cm²).

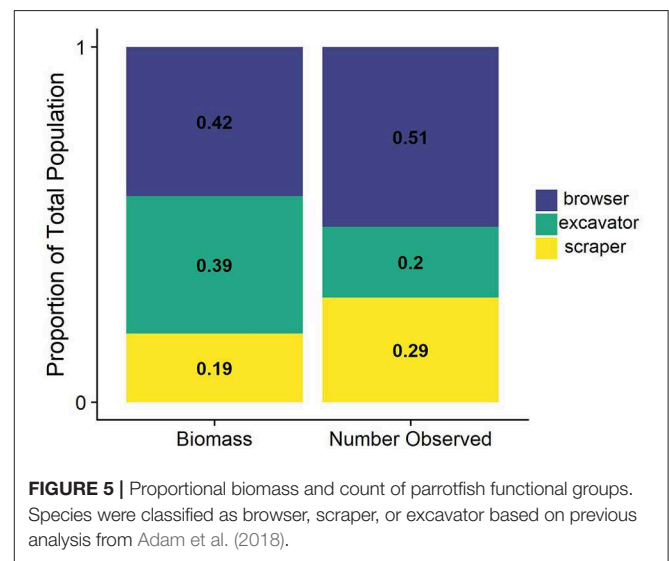


FIGURE 5 | Proportional biomass and count of parrotfish functional groups. Species were classified as browser, scraper, or excavator based on previous analysis from Adam et al. (2018).

Browser density, browser biomass, and maximum depth were not significant terms and dropped from the final model. However, model comparison indicated that the final model had a lower AIC but was only marginally different from the null model ($p = 0.06$; **Table 4**), which only had site as a random effect. Even though *Diadema* density was a significant predictor of elkhorn LAI, fixed effects in the final model did not account for a substantial amount of the variance (**Table 3**; marginal $R^2 = 0.158$).

Herbivore Populations and Macroalgal Cover

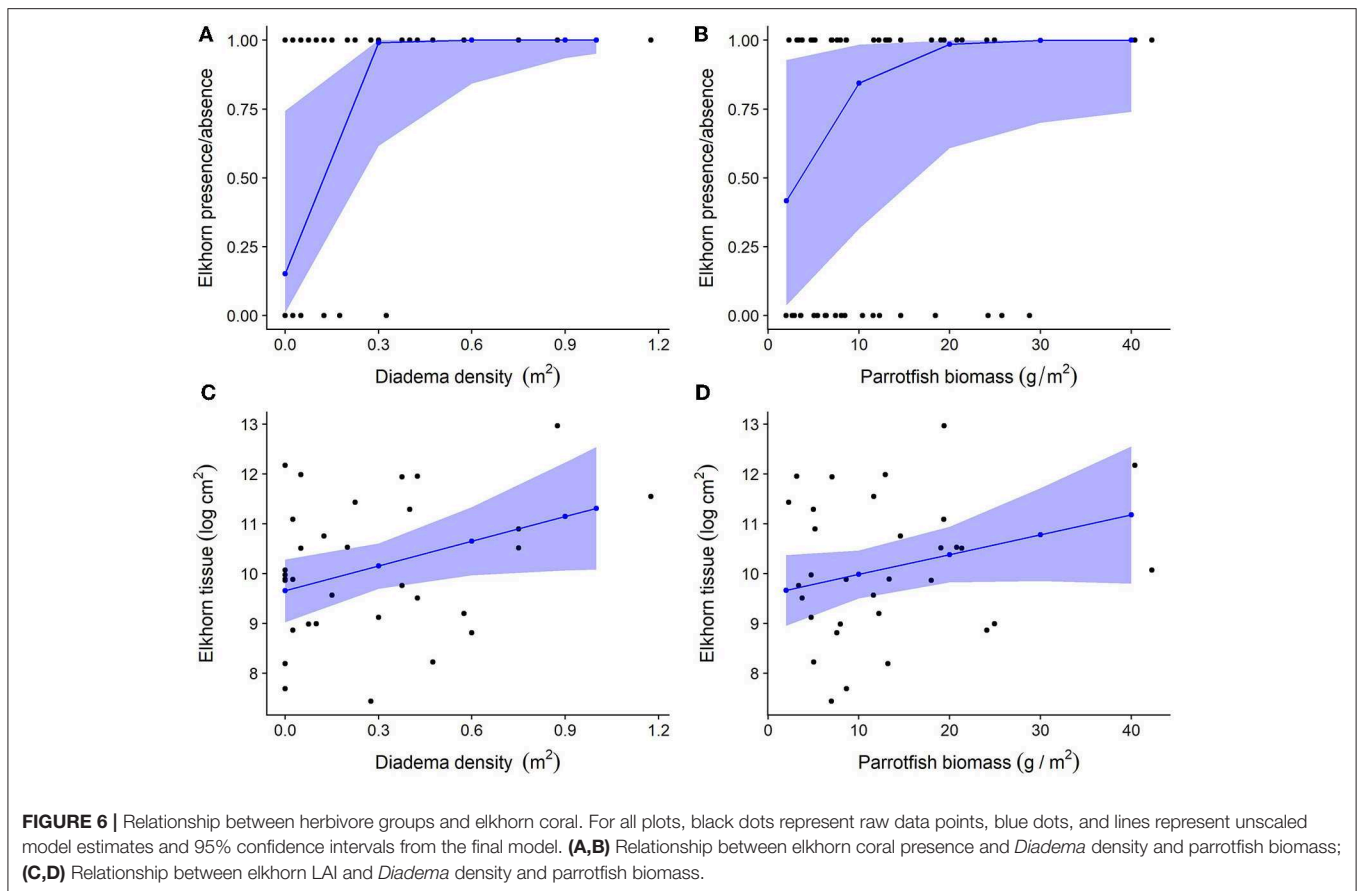
Diadema density (estimate = -5.84 ; $p = 0.001$) and browser species biomass (estimate = -3.95 , $p = 0.032$) had statistically significant negative correlations with macroalgal cover. Browser species density had a significant positive correlation to macroalgal cover (estimate = 4.0 , $p = 0.007$; **Table 3**, **Figure 7**). These predictors (fixed effects) accounted for 27.9% of the variance explained in the model (**Table 3**). Total parrotfish

biomass and maximum depth were not significant terms and were dropped from the final model (**Table 4**). Significant temporal variance in *Diadema* urchin counts.

Analysis of paired day and night transect surveys revealed there is a significantly higher number of *Diadema* urchins observed at night (**Figure 8**; $df = 15$, $t = -3.36$, $p = 0.004$). This difference is more pronounced in the shallower, higher relief reefs ($df = 9$, $t = -4.6$, $p = 0.001$). *Diadema* were present on deeper, lower relief sites, yet there was no difference between *Diadema* counts during day and night surveys (**Figure 8**). Because of the mixture of variables (depth, complexity) we cannot statistically attribute the differences in *Diadema* count due to any covariates other than time of day.

DISCUSSION

The goal of this study was to evaluate the status of elkhorn populations in Akumal, Mexico and determine if *Diadema* urchin or parrotfish populations are associated with higher elkhorn abundance and lower algal cover. The majority of



elkhorn colonies observed were large in size ($>1,600 \text{ cm}^2$) and exhibited the re-sheeting growth form. We found that, overall, the presence of elkhorn coral and amount of live tissue increased with increasing herbivore density or biomass. Most strikingly, we found that both herbivore populations contributed significantly to the presence of elkhorn coral. Complementary linear mixed-effects models indicate that *Diadema* density was a better predictor than parrotfish biomass of total elkhorn tissue live area index, although the fixed effects only contributed to a small portion of the variance. We also found that higher *Diadema* density and parrotfish browser species biomass was correlated with lower macroalgal cover, even at low abundances. We observed higher *Diadema* density during our night surveys especially at shallower, high relief reef sites. While this result is not surprising because it corresponds to the expected nocturnal behavior of urchins (Carpenter, 1984), it suggests we may be underestimating population densities, and therefore grazing activity, of *Diadema* urchins when only considering day-time measurements. Our findings support the argument that recovering herbivore populations may be contributing significantly to controlling algal growth and facilitating high elkhorn abundance or resheeting on contemporary Caribbean shallow water forereef habitats (Morrison, 1988; Edmunds and Carpenter, 2001; Precht and Precht, 2015).

Top-down control of macroalgal growth is one ecological factor imperative for coral recovery, as this process provides

physical space on the benthos for corals to settle or grow (Knowlton, 1992; Edmunds and Carpenter, 2001). We hypothesized that the “re-sheeting” phenomenon of elkhorn coral observed in Mexico was related to this top-down control of algal growth, since coral tissue is growing over bare surfaces of relic corals, not up into newly formed 3D structures. Of the 85 colonies surveyed, 43 were classified as re-sheeting and 37 of those colonies were in the largest size class (Figure 4); indicating that re-sheeting is contributing to a large portion of the total LAI and elkhorn cover on Akumal reefs.

Our study revealed that even at low biomass, parrotfish browser species, which feed specifically on macroalgae, have a significant negative correlation with macroalgal cover. Parrotfish biomass in the Mesoamerican Barrier Reef has been increasing slightly in the past few years, and the populations observed here in Akumal are comparable to country and region-wide parrotfish population sizes (Jackson et al., 2014; McField et al., 2018), indicating that recovering populations may be reaching a threshold in which they can exert effective top down control of algal growth (Williams et al., 2016). Even though total parrotfish biomass was not correlated to lower macroalgal cover, fish grazing activity from non-browser species may have other positive benefits such as contributing to increased coral calcification (Suchley and Alvarez-Filip, 2017) or overall reef accretion (Cramer et al., 2017). Conversely, we found increasing macroalgal cover with increasing browser species density. The

TABLE 3 | Estimated regression parameters, standard error, z-value or t-value, and p-values from the final linear mixed-effects models.

| Approach and fixed effects | Estimate | Standard error | z or t-value | p-value |
|--|----------|----------------|--------------|----------------------|
| Presence/absence of elkhorn coral | | | | |
| (Intercept) | 2.135 | 1.3 | 1.63 | 0.103 |
| <i>Diadema</i> density | 5.7 | 2.51 | 2.27 | 0.023 * |
| Parrotfish biomass | 2.33 | 1.12 | 1.99 | 0.046 * |
| <i>Marginal R² = 0.737; Conditional R² = 0.929</i> | | | | |
| Amount of elkhorn tissue (LAI) | | | | |
| (Intercept) | 9.90 | 0.24 | 41.61 | <0.001 *** |
| <i>Diadema</i> density | 0.44 | 0.20 | 2.15 | 0.032 * |
| Parrotfish biomass | 0.37 | 0.22 | 1.68 | 0.094 |
| <i>Marginal R² = 0.158; Conditional R² = 0.158</i> | | | | |
| Percent cover of macroalgae | | | | |
| (Intercept) | 32.77 | 2.49 | 13.14 | <0.001 *** |
| <i>Diadema</i> density | -5.84 | 1.70 | -3.43 | 0.001 ** |
| Browser biomass | -3.05 | 1.42 | -2.15 | 0.032 * |
| Browser density | 4.00 | 1.49 | 2.69 | 0.007 ** |
| <i>Marginal R² = 0.279; Conditional R² = 0.676</i> | | | | |

All predictor variables were centered and scaled prior to modeling. Terms were dropped from models using chi-square test. Z-values are reported for the binomial presence/absence of elkhorn coral model, while all other models report t-values.

Signif. codes: 0; ***, 0.001; **, 0.01; *, 0.05; 0.1; 1.

Bold values indicate significant p-values.

high number of small bodied Redtail parrotfish species may be contributing to this trend (Table 2).

Our results also revealed increased coral presence and cover with increasing urchin populations and confirmed previous studies demonstrating that higher *Diadema* densities are associated with coral recovery (Edmunds and Carpenter, 2001; Carpenter and Edmunds, 2006; Myhre and Acevedo-Gutiérrez, 2007) and lower macroalgal cover (Carpenter and Edmunds, 2006; Myhre and Acevedo-Gutiérrez, 2007; Williams et al., 2016; Rodríguez-Barreras et al., 2018) in the Caribbean. This correlation may also be due to positive feedbacks associated with structural complexity and *Diadema* populations (Lee, 2006). The physical structure of the reef, and elkhorn skeletons in particular, may provide enough refuge to support larger *Diadema* populations, which results in increased grazing pressure. A 2013 study in Akumal Bay also demonstrated a positive relationship between habitat structural complexity and *Diadema* density (Lacey et al., 2013).

The spatial extent of grazing pressure can also influence effectiveness of top-down control of macroalgal growth. Previous evidence suggests that herbivory from urchins is more effective for promoting coral growth due to the high grazing intensity and spatially constrained grazing behavior of *Diadema* urchins (Carpenter, 1986; Sandin and McNamara, 2012), particularly in shallow-water reef zones (Morrison, 1988). Additionally, herbivorous fishes have larger foraging ranges (up to 0.5 hectares) so the grazing pressure from fish is more diffuse due to their roaming behavior (Carpenter, 1986; Sandin and McNamara, 2012; Adam et al., 2015a). This is one potential explanation for higher *Diadema* estimates in our models.

Implications for Local Management

Our results support recommendations to enhance herbivore populations as one mechanism to promote coral recovery and control macroalgal growth on degraded coral reefs (Adam et al., 2015a; Williams et al., 2016). Efforts to protect and potentially enhance fish populations are already underway through designation of a fish sanctuary and marine reserve in Akumal (Official Gazette of the Federation, 2016; Yucatan Times, 2019). Consideration of the full life-history of parrotfish species is also critical to ensure that ecological functions from all parrotfish groups (browsers, scrapers, and excavators) are maintained (Adam et al., 2015a). A robust parrotfish guild can provide complementary functions to promote reef recovery, including removal of different species of algae (macro vs. turf) and removal of dead coral which can provide space for new coral settlement or growth (Cardoso et al., 2009). We demonstrated that browser species specifically contribute to reduced macroalgae cover, and other studies have found that browser foraging behavior may result in higher rugosity reefs, as bites from browser species typically do not erode reef substrate. Population metrics and behaviors of excavator species, however, should be monitored to prevent excessive substrate erosion or corallivory, which could lead to coral mortality of other reef-building corals (Rotjan and Lewis, 2006; Cardoso et al., 2009; Burkepille, 2012; Bruno et al., 2019).

Strong associations between elkhorn abundance and *Diadema* populations in Akumal suggest that *Diadema* reintroduction may be an appropriate tool for local managers when developing holistic coral recovery or restoration plans (Adam et al., 2015a; Precht and Precht, 2015). Managers and researchers could work together toward finding and cultivating ideal site-specific *Diadema* population sizes: large enough to exhibit top-down control of macroalgal growth and promote coral recovery, but not so dense that urchin grazing harming coral recruitment by consuming coral spat or further eroding the reef substrate (Sammarco, 1980; Korzen et al., 2011; Sandin and McNamara, 2012). *Diadema* urchins are known bioeroders, meaning they can remove the hard carbonate substrate of the reef; therefore, benthic habitats with poor or no coral recruitment can also be flattened by grazing of extremely high-density urchin populations (Bak, 1994). The role of grazing by smaller urchins, namely *Echinometra* spp., has been noted in other Caribbean locations (Sangil and Guzman, 2016; Kuempel and Altieri, 2017); however, *Echinometra* spp. are not common on the exposed spur-and-groove forereef habitats in Akumal. These urchins are typically found in shallow, intertidal zones or protected leeward reefs (Brown-Saracino et al., 2007; McClanahan and Muthiga, 2007) and a 2013 study in Akumal documented variable populations densities of *E. lucunter* (0–12 individuals per m²) in a shallow, lagoon portion of Akumal Bay. However, the bay area in Akumal is a distinctly different reef structure than the spur-and-groove forereef. The habitat and spatial heterogeneity of both coral and *Diadema* populations demonstrates the need for location-specific information for evaluating associations between herbivory and coral recovery. To address the issue of inaccurate population estimates of *Diadema* urchins, day-time survey protocols should be supplemented with evening

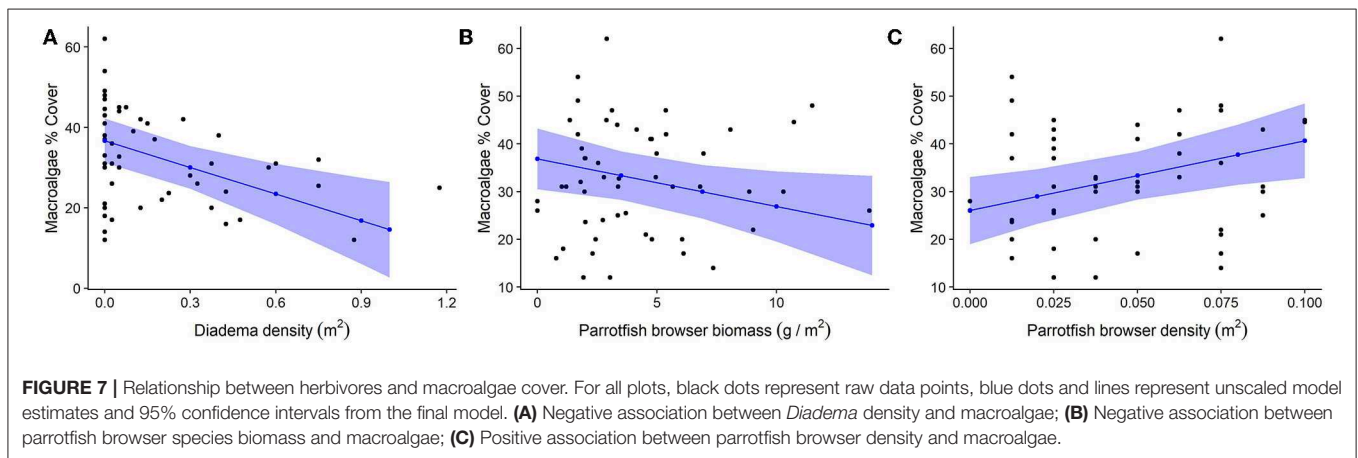
TABLE 4 | Summary of model comparisons.

| Approach and model terms | df | AIC | BIC | LogLik | Deviance | Chisq | p-value |
|--|----|-------|-------|--------|----------|-------|--------------------|
| Presence/Absence of elkhorn coral | | | | | | | |
| Null model: (1 site) | 2 | 60.1 | 64.0 | -28.0 | 56.1 | - | - |
| Full model: <i>Diadema</i> density + Parrotfish biomass + browser biomass + browser density + depth + (1 site) | 7 | 47.2 | 60.9 | -16.6 | 33.2 | 4.58 | 0.205 |
| Final model: <i>Diadema</i> density + Parrotfish biomass + (1 site) | 4 | 45.8 | 53.7 | -18.9 | 37.8 | 18.3 | 0.0001*** |
| Amount of elkhorn tissue (LAI) | | | | | | | |
| Null model: (1 site) | 3 | 116.4 | 120.8 | -55.2 | 110.4 | - | - |
| Full model: <i>Diadema</i> density + Parrotfish biomass + browser biomass + browser density + depth + (1 site) | 8 | 120.1 | 131.9 | -52.1 | 104.1 | 0.98 | 0.80645 |
| Final model: <i>Diadema</i> density + Parrotfish biomass + (1 site) | 5 | 115.1 | 120.4 | -52.6 | 105.11 | 5.3 | 0.06972. |
| Percent cover of macroalgae | | | | | | | |
| Null model: (1 site) | 3 | 402.1 | 408.0 | -198.1 | 396.1 | - | - |
| Full: <i>Diadema</i> density + Parrotfish biomass + browser biomass + browser density + depth + (1 site) | 8 | 396.3 | 412.1 | -190.2 | 380.3 | 0.82 | 0.663973 |
| Final: <i>Diadema</i> density + browser biomass + browser density + (1 site) | 6 | 393.1 | 404.2 | -190.6 | 381.1 | 14.99 | 0.001825 ** |

For each linear mixed-effect model, the model terms, degrees of freedom, Akaike information criterion (AIC), Bayesian information criterion (BIC), log likelihood (LogLik), deviance, chi-square, and p-value are reported.

Signif. codes: 0; ***, 0.001; **, 0.01; *, 0.05; 0.1; 1.

Bold values indicate significant p-values.



or night surveying, especially on high relief reefs where more urchins may be completely hidden during daylight hours. More robust information on herbivore population dynamics may also benefit in-water conservation projects, such as coral nurseries, as knowledge of local herbivore densities can provide guidance on geographic areas where outplanted coral fragments might have a higher competitive advantage due to grazing of macroalgae (Sandin and McNamara, 2012; Adam et al., 2015a; Precht and Precht, 2015). This study demonstrates the importance for considering *Diadema* population metrics in coral recovery efforts.

Local management interventions may be limited in the scope of problems that can be addressed; however, without mitigation

of underlying causes of coral mortality such as ocean warming and coastal development, we should not expect herbivore protection or enhancement alone to increase coral resilience (Edmunds and Elahi, 2007; Adam et al., 2015a; Arias-González et al., 2017; Cox et al., 2017; Bruno et al., 2019).

Limitations and Other Considerations

Bottom-up forces, such as eutrophication from terrestrial runoff, which counter grazing pressure may also contribute to a shift toward algal dominance (Arias-González et al., 2017). This study did not test for bottom-up forcing from nutrients; although previous studies demonstrated a correlation between tourism, a proxy for nutrient influx, and declining reef condition in

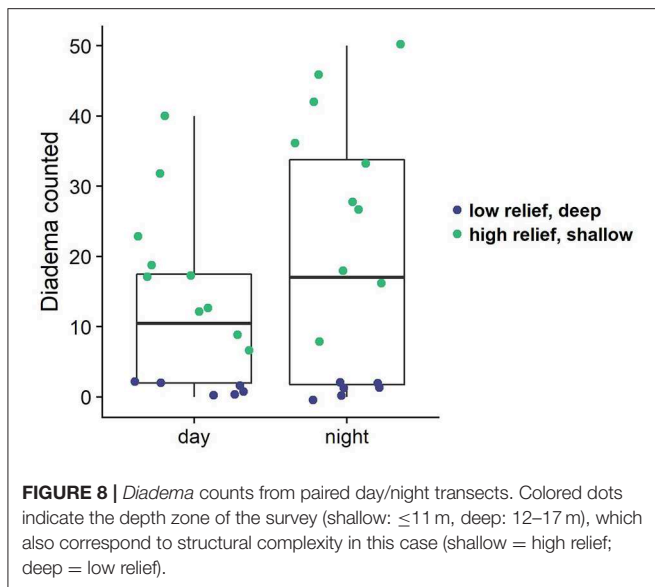


FIGURE 8 | *Diadema* counts from paired day/night transects. Colored dots indicate the depth zone of the survey (shallow: ≤ 11 m, deep: 12–17 m), which also correspond to structural complexity in this case (shallow = high relief; deep = low relief).

Akumal Bay (Gil et al., 2015; Renfro and Chadwick, 2017) and documented sources of anthropogenic nutrient input to Akumal waters (Hernández-Terrones et al., 2015).

While this study finds statistical correlations between *Diadema* density and parrotfish biomass with elkhorn live tissue cover, experimental manipulations of herbivore abundance and coral growth are needed to establish a causative effect. Herbivore exclusion studies have been conducted before (Lirman, 2001; Hughes et al., 2007; Sotka and Hay, 2009); however, in the Caribbean these particular studies involve “weedy” coral species that have different growth forms and rates and thus different ecological roles from “competitive” coral species, such as elkhorn coral (Bellwood et al., 2004; Darling et al., 2012). Additionally, we used a visual estimate for reef relief; however, studies quantifying rugosity and *Diadema* abundances would be more informative in quantifying the relationship not only between *Diadema* and reef complexity but also in developing predictions of accurate *Diadema* densities based on reef rugosity.

Lastly, even when elkhorn recovery is documented, tissue damage from predatory snails (e.g., *Coralliophila abbreviata*) and damselfish grazing (from the cultivation of turf algal “gardens”) may stifle the full potential for regrowth (Grober-Dunsmore et al., 2006). In Akumal, high damselfish density and turf algae cover has been observed the past few years (Figueroa-Zavala and Munoz Arroyo, 2018). These sources of tissue damage should be closely monitored.

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CONCLUSION

In summary, our results suggest that *Diadema* urchins and parrotfishes are associated with the presence and higher abundance of elkhorn coral in Akumal, Mexico, likely through the top-down control of macroalgae growth. We found that even at low abundances, these herbivore groups are associated with less macroalgal cover, although experimental grazing studies are needed to quantify the magnitude of this effect. While gaps in our knowledge persist regarding the ecological factors contributing to coral recovery, results here suggest that both herbivore groups contribute to elkhorn abundance. Additionally, we highlight the importance of estimating accurate urchin counts using night-time surveys in order to fully understand the influence of *Diadema* grazing on macroalgal growth and coral recovery on contemporary Caribbean reefs.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

LM and JB conceived of the study. LM, CA, JB, and BF-Z carried out the study and collected field data, made substantial contributions to the text, and interpretation of the final version of this manuscript. LM performed statistical analysis and wrote the first draft of the manuscript.

FUNDING

This work was supported by the Henry van Peters Wilson Memorial Fund from Department of Biology at UNC-Chapel Hill (LM), the Tinker Foundation via UNC Institute for the Study of the Americas (LM), and the Environment, Ecology and Energy Program (CA) at UNC-Chapel Hill.

ACKNOWLEDGMENTS

We would like to thank Jenny Hughes for her help in the first few days of conducting fieldwork in Akumal, the staff at CEA and Akumal Dive Centre for providing logistical support in the field, and Dr. James Umbanhowar for statistical assistance.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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