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UNIVERSITY OF CALIFORNIA SAN DIEGO

**VARIABILITY IN COMPOSITION OF PARROTFISH BITE SCARS ACROSS SPACE  
AND OVER TIME ON A CENTRAL PACIFIC ATOLL**

A thesis submitted in partial satisfaction of the  
requirements for the degree Master of Science

in

Marine Biology

by

Jonathan Aaron Charendoff

Committee in charge:

Professor Jennifer E. Smith, Chair  
Professor Stuart A. Sandin  
Professor Brice X. Semmens

2021



The thesis of Jonathan Aaron Charendoff is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2021

## EPIGRAPH

Perhaps knowledge is more like a trail—a hybrid of map and territory, artifice and nature—wending through a vast landscape. While science may provide a reliable route to certain answers, it remains narrow; it can reduce the environment to a navigable line, but it cannot encompass it. ... Great mysteries surround us all, like beasts slinking silently through the night—their presence can be intuited, or imagined, but never fully illuminated.

Robert Moor

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ABSTRACT OF THE THESIS

**VARIABILITY IN COMPOSITION OF PARROTFISH BITE SCARS ACROSS SPACE  
AND OVER TIME ON A CENTRAL PACIFIC ATOLL**

by

Jonathan Aaron Charendoff

Master of Science in Marine Biology

University of California San Diego, 2021

Professor Jennifer E. Smith, Chair

Robust parrotfish assemblages have been shown to control algal proliferation and promote the settlement of corals and crustose coralline algae (CCA). At relatively high densities, parrotfish have been suggested to negatively affect net reef accretion through bioerosion and targeted corallivory. Most evidence describing the impacts of parrotfish grazing are based upon correlations benthic change and behavior or abundance, with less known about process-based change of individual parrotfish bite scars through time. We estimated parrotfish grazing selectivity and determined the change in composition of parrotfish bite scars relative to change in the overall landscape using data collected from the fore reef habitat at Palmyra Atoll. We identified over 2100 parrotfish bite scars estimated the substrate they were taken on, and

described the change in benthic composition within the scar area identified over the 12 month duration of the study. Bite scars were most abundant on turf algae, but were found on all dominant benthic functional groups. Of bites taken on coral, 96% of scars returned to complete coverage of live coral by the end of the study, while only 67% of points on coral remained alive during this study across the overall reef. Further, coral recruitment to bite scars was virtually nonexistent (n=1). Change within bite scars was dependent on the composition of the surrounding substrate, but 33% and 38% of bites on turf and mixed turf/CCA, respectively, progressed to CCA. Successional trajectories on bite scars, compared with change on the overall reef landscape, suggest parrotfish grazing maintains a calcifier-rich benthos.

## **Introduction**

Herbivores in coral reef ecosystems constitute a highly diverse suite of fishes and invertebrates that consume algae as a primary food source (Ogden and Lobel 1978; Hay and Taylor 1985; Steneck 1988). In recent decades, the roles of specific herbivore functional groups have become a focus of coral reef research (Belliveau and Paul 2002; Hoey and Bellwood 2008; Bonaldo et al. 2014; Ruttenberg et al. 2019). Within the herbivorous fish community, parrotfishes (Scarinae) are known to perform a wide range of functions in benthic reef community ecology from bioerosion (Bruggemann et al. 1996; Hoey and Bellwood 2008) to algal removal and control (Bellwood and Choat 1990; Mumby 2006; Burkepile and Hay 2010) and coral predation (Rotjan and Lewis 2005; Rotjan et al. 2006). Each of these processes can have an important impact on benthic community structure, however, the diversity of these functions has introduced debate on the net positive (or negative) role that parrotfishes have on reef health and recovery (McCauley et al. 2014; Russ et al. 2015).

The specialized beak-like feeding structure in parrotfish enables excavating and scraping feeding activities that remove both epilithic algae and calcium carbonate from the reef benthos, often resulting in a distinctive bite scar visible on the reef substrate (Bellwood and Choat 1990; Bonaldo and Bellwood 2009). Parrotfish grazing on turf algae is an important process for controlling algal standing stock (Mumby 2006; Burkepile and Hay 2008), and the top-down influence exerted by parrotfish on fast-growing algae has been suggested to drive positive correlations between parrotfish abundance and coral abundance and recruitment (Mumby et al. 2007; Cramer et al. 2017; Adam et al. 2018). However, the processes proposed to drive these correlations – direct facilitation of coral recruitment to bite scars or promoting coral competitive

dominance by removing turf algae (Barott et al. 2012; Bonaldo et al. 2014; Shantz et al. 2020) – is not well studied on the landscape scale.

While parrotfishes primarily target turf algae through their feeding activities (Bellwood and Choat 1990; Hamilton et al. 2014; Kelly et al. 2016), some species will occasionally graze directly on coral colonies (Rotjan and Lewis 2005). As a result, it has been proposed that reefs with high parrotfish biomass, or particular assemblages of parrotfish may have a negative impact on coral communities negatively. This has been especially noted for coral species known to be preferentially targeted, such as *Porites* spp. (Hoey and Bellwood 2008; Bonaldo and Bellwood 2011; Burkepile 2012; McCauley et al. 2014; Welsh et al. 2015). Some corals have been shown to recover rapidly from parrotfish grazing wounds, suggesting that parrotfish grazing does not ubiquitously result in net negative impacts on coral health and abundance (Rempel et al. 2020). Importantly, there remain critical gaps in our understanding of the natural history of parrotfish grazing across the reef landscape.

The scraping and excavating activities of parrotfish on fast growing algal substrates expose small patches of “bare space” on reefs which are often considered to be potential settlement locations for slower growing calcifying groups such as CCA and corals (Bellwood and Choat 1990; Hughes et al. 2007). As grazing activities are known to maintain turf algae and macroalgae in a cropped and less competitive state (Burkepile and Hay 2010), parrotfish may also have an indirect impact on benthic succession by facilitating the growth of CCA and corals (Smith et al. 2010). On the other hand, exposed carbonate inside bite scars taken on turf algae substrates may quickly be colonized by turf algae, thus preventing establishment of other organisms (Bonaldo and Bellwood 2009; Carlson et al. 2017). Further, the relative selectivity for certain benthic types by parrotfishes may also drive landscape-wide change in community

structure (Wismer et al. 2009; Hamilton et al. 2014; Streit et al. 2019) as preferential grazing on fast growing algae may provide a benefit to corals and CCA – a known preferred settlement space for coral recruits (McCook et al. 2001; Price 2010). To understand the net positive or negative effects of parrotfishes on coral reefs, there is a complementary opportunity to learn from the natural history of the “bare space” created by parrotfish grazing activities.

Difficulty in following small benthic features through time has limited the spatial extent at which studies addressing succession on bite scars occurs. Further, little direct data exist that explore the ability of herbivory to drive benthic reef succession towards CCA across the reef landscape (Hixon and Brostoff 1996; Hughes et al. 2007; Burkepile and Hay 2010; Smith et al. 2010). Using structure-from-motion technology (SfM) we can now generate highly detailed and geometrically accurate 3-dimensional (3D) models from imagery collected from natural reefscapes (Westoby et al. 2012; Burns et al. 2016; Ferrari et al. 2016; Torres-Pulliza et al. 2020). Further products derived from 3D models, such as 2-dimensional (2D) orthorectified planar projections (orthoprojections), can then be used to accurately map and extract organism level data of coral reef communities (Kodera et al. 2020; Sandin et al. 2020).

Here, we use a large area imaging approach to first describe benthic community composition from the forereef habitat on Palmyra Atoll. We then locate and track the fate of parrotfish bite scars across the reef landscape using time series mapping with repeated imaging of the same sites over time. We then determined the substrate on which bites were taken and evaluated evidence for selectivity of certain benthic groups based upon their abundance across the reef. Finally, we examined how community composition on space opened by parrotfish bite scars changed over time in comparison to change in the benthic community composition across the landscape.

## **Materials and Methods**

### **Study Site**

The study was conducted at Palmyra Atoll (5° 52' N, 162° 06' W), a National Wildlife Refuge within the Pacific Remote Islands National Marine Monument, located approximately 1,600 km south of Oahu, HI. Palmyra's coral reef ecosystem is largely undisturbed by local human impacts and provides a natural baseline to understand coral reef ecosystem function in the relative absence of anthropogenic influences (DeMartini et al. 2008; Sandin et al. 2008; Williams et al. 2013; Hamilton et al. 2014; McCauley et al. 2014; Carlson et al. 2017). We selected 4 fore reef plots along the 10 m isobath, roughly spaced 4 km apart on the north and south shores (Fig. 1) from which imagery was collected to generate 3D models and associated 2D orthoprojections. Imagery was collected in September-October 2015, June 2016 and September-October 2016. Each plot covers an area of 200 m<sup>2</sup> (with the exception of the 100 m<sup>2</sup> plot at FR9) and was imaged by divers on SCUBA. Plots were established with geo-referenced steel pins marked by GPS allowing for resurveys across the time series.

### **Large area imaging & coregistration of 3D models**

Raw imagery was collected in the field following methods described by Edwards et al. (2017). Two Nikon D7000 16.2-megapixel DSLR cameras were mounted onto a custom frame. One camera is set to an 18mm focal length to provide high image overlap (>80%) required for 3D model generation. The second camera is set to a 55mm focal length to provide high image resolution ( $\leq 1$  mm) for identifying benthic organisms (Pedersen et al. 2019).

Images were processed to create 3D models of each plot using the SfM software *Metashape Pro 1.3.5* (Agisoft LLC., St. Petersburg, Russia). Details of the model generation have been discussed in detail elsewhere (Westoby et al. 2012; Burns et al. 2015). Importantly, in the present study both sets of images were used in the alignment step, while only images from the 18mm camera are used to generate the dense cloud. Using both sets of images in the alignment step allows us to interactively ‘fetch’ the high resolution 55mm images during later steps of visualization and analysis.

To track change over time for small ( $\sim 1 \text{ cm}^2$ ) benthic areas, 3D point clouds generated in *Metashape* were exported directly to *Viscore* (Petrovic et al. 2014), and each was scaled and oriented relative to plane of gravity using the depth and scale measurements collected within each plot (Sandin et al. 2020). The 3D model timeseries of each plot was then coregistered, and finally 2D orthoprojections orthogonal to the plane of gravity were created directly from the coregistered point clouds (Fig. 2a, b). Importantly, generating geometrically accurate orthoprojections directly from the point cloud (Kodera et al. 2020; Sandin et al. 2020) facilitates precise mapping and coregistration to track small areas through time, as opposed to using orthophotomosaics which are confounded by the need for blending and distortion (Nicosevici et al. 2009).

## **Ecological Post-Processing**

### *Identification of bite scars and change in substrate composition over time*

Parrotfish bite scars were defined as at least two parallel lines of exposed carbonate on the reef substrate (Fig. 3), which are distinctive of scraper and excavator parrotfish grazing (Jayewardene et al. 2009). Bite scars were identified from orthoprojections collected at the



beginning of the timeseries ( $t_0$ , September 2015) with the aid of spatially-linked, high-resolution raw imagery associated with each plot (Fig. 2c, d) and annotated in Adobe *Photoshop CC*. The starting composition of bite scars was then estimated from a 1 cm wide buffer surrounding each bite scar. Within each buffer, the benthic organisms were digitized to the finest taxonomic resolution possible and then grouped to the following functional groups: hard coral (Scleractinia), CCA, mixed matrices of CCA and turf algae (approximate even mix of turf and CCA, hereafter referred to as mixed CCA/turf algae), turf algae, encrusting macroalgae (*Lobophora* spp., and *Peyssonnelia* spp.), soft corals (Octocorallia and Corallimorpharia), and *Halimeda* spp.. Other erect macroalgae, invertebrates, and non-biological substrata, all of which are rare on the fore reef at Palmyra atoll (< 2% of benthic cover), were grouped into the final category, ‘other’. In cases where buffers contained multiple groups, the composition of the bite scar was determined as that group constituting the greatest proportion of pixel area within the buffer. Bites with more than 3 functional groups in their respective single buffer were uncommon ( $n = 5$ ).

To quantify change in the substrate composition of scars through time, bite scars were first relocated in the coregistered orthoprojection time series (June 2016,  $t_1$ ; September – October 2016,  $t_2$ ). The substrate composition of bites scars was then determined as the benthic group occupying the greatest proportion of the bite scar in each of these subsequent time points (Fig. 3), using the groups defined above. Any bite scars located in  $t_0$  that could not be relocated were removed from the study ( $n = 41$ ).

### *Overall changes in benthic composition*

To estimate the benthic composition in each plot, we used random point sampling in *Viscore* (Fox et al. 2019). A sample of 4000 points were distributed in a stratified random fashion across the 200-m<sup>2</sup> 3D model and each point was designated to the finest taxonomic level possible and grouped as above for analysis. A key feature of the point sampling tool is the efficient access to the raw imagery associated with a given point allowing the user to interactively “flip” through images for the most detailed view of the point in question when making taxonomic designations. To determine the trajectory of the overall reef through time, points placed on the reef in  $t_0$  were replicated across the coregistered placed on the same location of reef area again in  $t_1$  and  $t_2$ , to track how non-bite scar locations in the reef changed across the same time series.

## **Statistical analysis**

### *Grazing selectivity*

To determine if parrotfish bites were found on certain benthic functional groups more than expected based on that functional groups’ abundance in the landscape, we used Manly’s  $\alpha$  selectivity index (Chesson 1983) calculated as:

$$\alpha_i = \frac{r_i/n_i}{\sum_j^m r_j/n_j}, i = 1, \dots, m$$

where  $r_i$  is the number of bite scars on functional group type  $i$  of  $m = 8$  functional groups present in each plot and  $n_i$  represents the relative proportion of functional group  $i$  in each plot. The null index,  $\alpha_{\text{null}} = 0.125$ , represents no grazing preference for any functional group as the instances of grazing are proportional to the abundance of that functional group. Values of  $\alpha$  significantly above  $\alpha_{\text{null}}$  indicate that bite scars were found more often than expected if each functional group were present in the plot in equal proportion. Alternatively, values of  $\alpha$  significantly below  $\alpha_{\text{null}}$

indicate an avoidance of that functional group. Selectivity indices were calculated for each reef site.

### *Bite scar succession & benthic change*

To determine if changes in substrates inside bite scars differed from changes in random locations on the reef, we used a three-way  $\chi^2$  contingency table analysis. This analysis was used to determine if the change in substrate inside bite scars was dependent on the initial estimate of the bite scar substrate composition in the transition from  $t_0$  to  $t_1$  (transition 1), and on the substrate within the bite scar from  $t_1$  to  $t_2$  (transition 2). Transitions from  $t_i$  to  $t_{i+1}$  were grouped as either ‘same’ or ‘different’ depending on whether the substrate in question did not change or changed, respectively. For example, bites on turf algae in  $t_0$  that were colonized by hard coral or CCA by  $t_1$  were grouped as ‘different’; in contrast, bites on turf algae that were colonized by turf were grouped as ‘same’. Similarly, all random points which remained the same substrate in  $t_i$  and  $t_{i+1}$  were labeled as ‘same’ while those becoming different substrates were grouped together as ‘different’. Two-way contingency-table *post hoc* analyses were conducted for both bite scars and random points to determine if change in benthic functional group was independent of starting substrate for either case. All analyses were conducted in *R*, version 4.0.2 (R Core Team, 2020).

## **Results**

### **Bite scars**

A total of 2150 bite scars were found across Palmyra in September 2015 creating a total of 0.14 m<sup>2</sup> of bare carbonate space across 900 m<sup>2</sup> of reef surveyed. The majority of parrotfish bite scars were found on turf algae (45.9%  $\pm$  12.1, mean  $\pm$  SE), but were also found commonly

on CCA ( $16.6\% \pm 3.6$ ), hard corals ( $16.5 \pm 7.3$ ), and mixed CCA/turf algae ( $11.1\% \pm 1.8$ ). The remaining percentage of bite scars was made up of encrusting macroalgae (mostly *Lobophora* and *Peyssonellia*,  $9.9\% \pm 4.1$ ) (Fig. 4a). Bite scars were not found on the other substrates (*Halimeda* spp., other corals, other fleshy macroalgae and invertebrates) despite their presence at our study sites. All bite scars on coral were taken on adult colonies ( $> 5\text{cm}$  diameter) and no juvenile corals ( $< 5\text{cm}$ ) were found in the 1cm buffer surrounding bite scars at any site. Parrotfish grazing most frequently targeted massive (*Porites* spp., 45.6% of hard coral bite scars) and sub-massive (*Goniastrea stelligera*, 30.5%, and *Pavona* spp., 23.9%) coral taxa.

### **Grazing selectivity**

The majority (70.0%) of bite scars were found on turf or mixed turf/CCA communities despite the fact they only occupy a combined total 27.9% of the benthos at our sites. Therefore, we observed a significant selective preference for turf algae ( $\alpha = 0.31 \pm 0.15$ ,  $\alpha \pm 95\%$  CI) or mixed CCA/turf algae ( $\alpha = 0.24 \pm 0.10$ ) assemblages (Fig. 4b). Hard coral ( $\alpha = 0.10 \pm 0.09$ ), CCA ( $\alpha = 0.11 \pm 0.04$ ) and encrusting macroalgae ( $\alpha = 0.24 \pm 0.14$ ) were grazed in proportion to their abundance across the landscape. No bite scars were found on the other functional groups indicating an avoidance ( $\alpha_i < \alpha_{\text{null}}$ ) of those groups.

### **Bite scar succession & benthic change**

Change in the benthic composition within bite scars was dependent on what the bite was originally on. Recall that change in benthic composition is defined by comparing benthic composition in  $t_1$  within the bite scar area relative to the benthic composition in the 1 cm buffer around the same area in the first time point,  $t_0$  (referred to as ‘transition 1’), and subsequently the

comparative composition from  $t_1$  and  $t_2$  ('transition 2'). Note that the ending substrate at the end of transition 1 is the starting substrate for transition 2. As such, it is possible that bites starting on CCA could change to turf algae after transition 1 and subsequently return to CCA after transition 2. Bites on CCA changed to a different substrate type less frequently than turf algae and mixed CCA/turf algae. Across the entire time series ( $t_0 - t_2$ ) only 45.9% of bites initially on CCA in  $t_0$  changed to a different substrate (123/268), while 62.4% (766/1228) and 74.5% (207/278) of bites initially on turf algae and mixed CCA/turf algae in  $t_0$ , respectively, changed composition (Table 1,  $X^2 = 358.6$ ,  $p \ll 0.01$ ). The proportion of substrate change was variable between transition intervals for bite scars on algal substrates (see Table 2 for all transition proportions). In transition 1, 51.4% of bites on CCA (138/268) became a different substrate, while only 33.9% of bites on CCA (145/425) changed substrate over transition 2. Conversely, a lower proportion of bites on turf algae changed substrate in transition 1 relative to transition 2 (39.0% [479/1228] and 63.6% [548/936], respectively).

Bite scars largely transitioned towards CCA and mixed CCA/turf algae over the course of the study regardless of starting substrate type (Fig. 5a, c, e). For example, turf algae filled in bite scars in greatest proportion during transition 1, with 49.7% of bites on mixed CCA/turf algae (138/278) being colonized by turf algae, and 56.8% of bites on turf algae (697/1228) being recolonized by turf algae. Turf algae filled in bite scars on CCA in second greatest proportion (32.6% [87/268], Fig. 5a). However, there were fewer bites colonized by turf algae (936) than bites initially taken out of turf algae (1228). As such, the majority of bites scars that became mixed CCA/turf algae (71.5%, 203/284) and CCA (53.4%, 227/425) were initially on turf algae.

Bite scars on coral did not lead to notable reductions in coral cover nor did bite scars induce detectable coral mortality, with 95.9% of bites on hard corals (259/270) returning to

healthy coral tissue within 12 months of being recorded. Change from starting substrate was negligible for coral during each transition (93.7% [252/270] and 98.8% [260/264] no change in substrate for transitions 1 and 2, respectively). Only one bite scar had a coral recruit, from the genus *Acropora*, settle (0.04% of the total bite scars) across this time series. Nearly all bites taken on corals occurred within the interior of coral colonies (where coral was the sole occupant within the respective buffer for a bite scar, [97.0%, 262/270]) and these bites all returned to live coral within a year of observation.

Change in percent cover across the reef landscape over the course of the study were also found to be dependent on starting substrate ( $X^2 = 2158.3$ ,  $p \ll 0.01$ ). 67.4% of randomly sampled points (2793/4144) landed on hard corals and remained as hard coral over the course of the study. The changes in random points that transitioned to a different substrate were as follows: 42.5% of points on CCA (1152/2712), 75.8% of points on turf algae (2283/3012), and 87.0% of points on mixed CCA/turf algae (937/1077), respectively. Points on algal substrates largely transitioned towards CCA (CCA to CCA: 57.5%, [1560/2712]; mixed CCA/turf algae to CCA: 41.3%, [445/1077]; turf algae to CCA: 35.6%, [1072/3012]), with little variation over the course of the study (Fig. 5b, d, f).

Despite an overall trend toward CCA, substrate change on bite scars and random points was significantly different across the time series (for Sept. 2015 – Sept. 2016:  $X^2 = 3326.9$ ,  $p \ll 0.01$ ), and in the intermediate time intervals (Table 1 for full  $X^2$  results). Across the entire time series, the largest difference in change in substrate between bite scars and randomly sampled points was in the proportion of points that remained as hard coral. From  $t_0 - t_2$ , 95.9% of bite scars returned to healthy coral tissue, while only 67.4% of points on coral remained as such. There were marginal differences in the percent of CCA colonization on algal substrates (CCA to

CCA: 6.0%, random points - bite scars; mixed CCA/turf algae to CCA: 3.3%; turf algae to CCA: 2.7%). However, the percent of turf colonization on algal substrates was greater on bite scars than on random points (CCA to turf algae: -13.0%, random points - bite scars; mixed CCA/turf algae to turf algae: -9.6%; turf algae to turf algae: -13.5%). CCA growth was marginally higher on random points than bite scars and turf algae colonization was higher on bite scars, however, CCA was still the dominant organism that colonized or increased in abundance in both bite scars and random points (Fig. 5e, f).

## **Discussion**

Parrotfish bite scars are often described as potential settlement space for coral recruits and other calcifying organisms, but there is little data that track the fate of bite scars over time. Adding valuable data about the natural history of parrotfish grazing, we described the fates of 2150 parrotfish bite scars over a year-long time series in 4 plots at Palmyra Atoll in order to examine the direct impacts of substrate removal by parrotfish grazing. Parrotfish bite scars were found on turf algae more often than expected relative to the proportion of turf algae available on the reef. We tracked bite scars and a series of random points on the reef landscape, and noted any changes in composition to determine the direct impact of parrotfish grazing on coral reef benthic community structure. The proportion of substrate change within both bite scars and random points was dependent on the substrate at the start of the time series. We show that 95.9%, (259/270) of bites taken on live coral transitioned back to live coral by the end of the study, and demonstrate an increasing tendency of bite scars to transition towards crustose coralline algae (CCA), and away from fleshy algal functional groups over the course of the study. This suggests that benthic succession moves from fleshy to calcifying groups within parrotfish bite scars, at

least within the time course observed here. These results provide direct support for previous work examining the impact of parrotfish grazing on algal growth and benthic succession indicating that parrotfish help to maintain a cropped turf algal community allowing for growth of CCA across the reef landscape (Mumby 2006; Bonaldo and Bellwood 2009; Burkepile and Hay 2010; Ceccarelli et al. 2011). However, our results contrast with previous work that showed a distinctly negative impact of parrotfish corallivory on coral survival (Rotjan et al. 2006; Welsh et al. 2015).

While grazing selectivity was consistent with other studies showing an overwhelming preference of parrotfishes for turf algae (Hamilton et al. 2014; Kelly et al. 2016)), we show that effectively all benthic functional groups (hard coral, CCA, encrusting macroalgae) are subject to the scraping and excavating of parrotfish. Consistent with other studies of parrotfish grazing, we found no evidence that parrotfish bite scars were disproportionately found on hard corals indicating that parrotfishes are not actively targeting corals across the reef landscape (Hoey and Bellwood 2008; Mumby 2009; Adam et al. 2015). Bite scars on an unexpected algal substrate type (i.e. not turf algae) may result from a diverse parrotfish community (Adam et al. 2018) or competition between parrotfishes limiting foraging space use (Nash et al. 2012; Davis et al. 2017), especially as the reefs at Palmyra have relatively low abundance of turf algae and high parrotfish biomass (Hamilton et al. 2014; Smith et al. 2016). Recent work has also suggested that targeted grazing on coral by parrotfish may in fact be a side effect as parrotfish seek to access to endolithic algae or other boring organisms growing inside specific coral colonies as they seek to meet nutritional requirements (Choat et al. 2002; Rotjan and Lewis 2005; Clements et al. 2017).

Exposure of reef carbonate by parrotfish grazing has been proposed as a mechanism for facilitating coral recruitment by providing a clear, open space for recruits while also providing a



depression that would create a micro habitat that could be protected from future grazing activities (Bellwood and Choat 1990; Arnold et al. 2010; Steneck et al. 2014). However, we tracked bare space associated with bite scars and found that coral recruitment into these habitats was virtually nonexistent. Out of the 2150 bites we tracked over the course of one year, we recorded only one coral recruitment and survivorship event. This result is perhaps not surprising, given that bite scars occupied only 0.14 m<sup>2</sup> of the studied reef area and past work at Palmyra has shown densities of 1 recruit per 0.17 m<sup>2</sup> of reef (Pedersen et al. 2019). However, our observations are limited based upon image resolution and so we may have missed early recruits but are confident that anything over 1 mm in size would have been picked up in our data set. Nonetheless, recruitment to bite scars we observed appears to match the null expectation of recruitment across the reef landscape suggesting that bite scars are likely not creating enhanced settlement space for coral recruits despite the benefit that grazing has on removing fleshy algal competitors from the benthos (McCook et al. 2001; Mumby et al. 2007).

Some studies have found negative correlations between parrotfish abundance and coral recruitment as it has been proposed that incidental grazing on exposed coral recruits could limit survivorship (Brock 1979; Box and Mumby 2007; Venera-Ponton et al. 2011). We observed no evidence of incidental grazing but did not explicitly track coral recruits outside of bite scars. The limited coral recruitment to bite scars observed here is likely a result of rapid recolonization (approx. 2 weeks) of bare space by turf algae thus preventing persistence of bare space across the landscape long settle to promote recruitment (Bonaldo and Bellwood 2009; Sandin and McNamara 2012; Carlson et al. 2017). There were some cases (13 bite scars) of established corals expanding over bite scars where the bare space generated here may have allowed corals to expand in the absence of competitors in these cases (Barott et al. 2012). Further, as bite scars

transitioned more frequently to CCA than any other functional group over the course of the study, our results suggest that the parrotfishes at Palmyra provide an indirect benefit on coral recruitment by controlling fleshy algal proliferation but not directly opening settlement substrates on any functional scale.

We found 95.9% of bite scars on live coral tissue regrew the over the scar within the 12 months of our study. This is in contrast to the landscape level observations where only 67.4% of random points on live coral survived across the same time interval. Previous research suggests that parrotfish grazing on corals can have a largely negative impact on colony survivorship and demography (Hoey and Bellwood 2008; McCauley et al. 2014). Parrotfishes in the Caribbean and Great Barrier Reef are known to be significant grazers on coral colonies (Rotjan and Lewis 2005; Mumby 2009; Bonaldo and Bellwood 2011) where repeated, intense parrotfish grazing has the capacity to induce coral mortality (Rotjan et al. 2006; Bonaldo and Bellwood 2011; Welsh et al. 2015). However, the ability of grazed corals to recover as we observed, could be because bites were only found on established, massive and sub-massive corals (*Porites* spp., *Goniastrea stelligera*, *Pavona* spp.) with stress-tolerant life history strategies (Darling et al. 2012); a small fraction of the high coral diversity seen at Palmyra atoll (Williams et al. 2008). Parrotfish grazing on corals is known to target coral taxa like *Porites* spp., therefore the targeted colonies observed in our study may have a history of parrotfish grazing and recovery (Rotjan and Lewis 2005; Welsh et al. 2015). Parrotfish grazing combined with environmental stressors, or grazing on non-favored corals, has the potential to cause excess coral mortality (Burkepile 2012) but Palmyra's reef exist largely free of local human impacts, removing possible confounding factors on the ability of corals to heal from parrotfish grazing wounds.

The bite scars tracked in this study generally progressed from fleshy turf algae to CCA within a 12-month interval from initial grazing on the benthic surface. Along with this overall trend towards CCA growth, we observed an increase in the magnitude of CCA colonization on bite scars (Fig. 5 c, e) from transition 1 (Sept. 2015 – June 2016) to transition 2 (June 2016 – Sept. 2016). Primary settlement of turf algae onto bare space (e.g. bite scars) is expected as turf algae generally grow more rapidly than CCA (Diaz-Pulido and McCook 2002; Bonaldo and Bellwood 2009). However, freshly colonized turf algae is part of a highly cropped algal assemblage which can allow for settlement and overgrowth of CCA (Hixon and Brostoff 1996). Furthermore, we observed the majority of bites that were by *t<sub>1</sub>* filled in with either CCA or mixed CCA/turf algae had originally started off as bites on turf algae. Therefore, growth of CCA from turf algae suggests that parrotfish grazing at Palmyra is creating space to maintain a calcifier rich benthos, consistent with other studies indicating that parrotfishes contribute to facilitating growth of CCA and corals over turf and other macroalgae (Ogden and Lobel 1978; Belliveau and Paul 2002; Burkepile and Hay 2006; Smith et al. 2010).

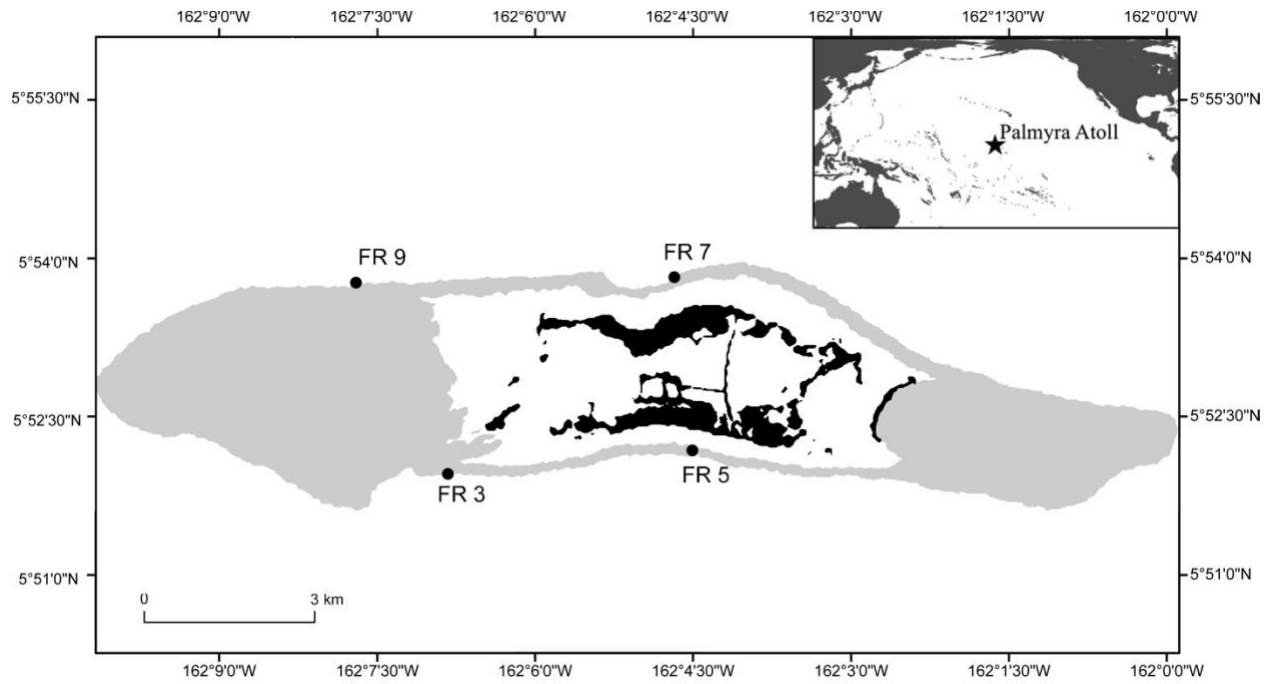
While successional trajectories were significantly different between bite scars and the reef landscape as a whole, there were small differences in the proportion of CCA colonization between the bite scars and random points. Instead, bite scars had a higher proportion of turf colonization than the random points (Fig. 5e, f). Further, the variability between transitions in the successional trajectories on bite scars was not observed on the random points across the reef landscape. These differences between bite scars and random points in the magnitude of succession towards turf algae and variability of trajectories across the time series likely result from bite scars starting from a bare carbonate space while the random points were mostly on established, undisturbed substrates. Space clearing and subsequent benthic succession from

parrotfish bite scars will likely combine with other processes – e.g. grazing from other herbivores, direct coral-algal competition – to structure the benthic community composition on coral reefs (Steneck 1988; Barott et al. 2012; Hamilton et al. 2014). Additionally, parrotfish grazing occurs across time and over large spatial scales as they seek out grazing substrates (Welsh and Bellwood 2012; Davis et al. 2017). As a result, CCA and turf algae dominated trajectories we describe here are likely to integrate over time and across space acting with other processes to maintain a CCA and coral rich benthos while limiting the proliferation of turf algae.

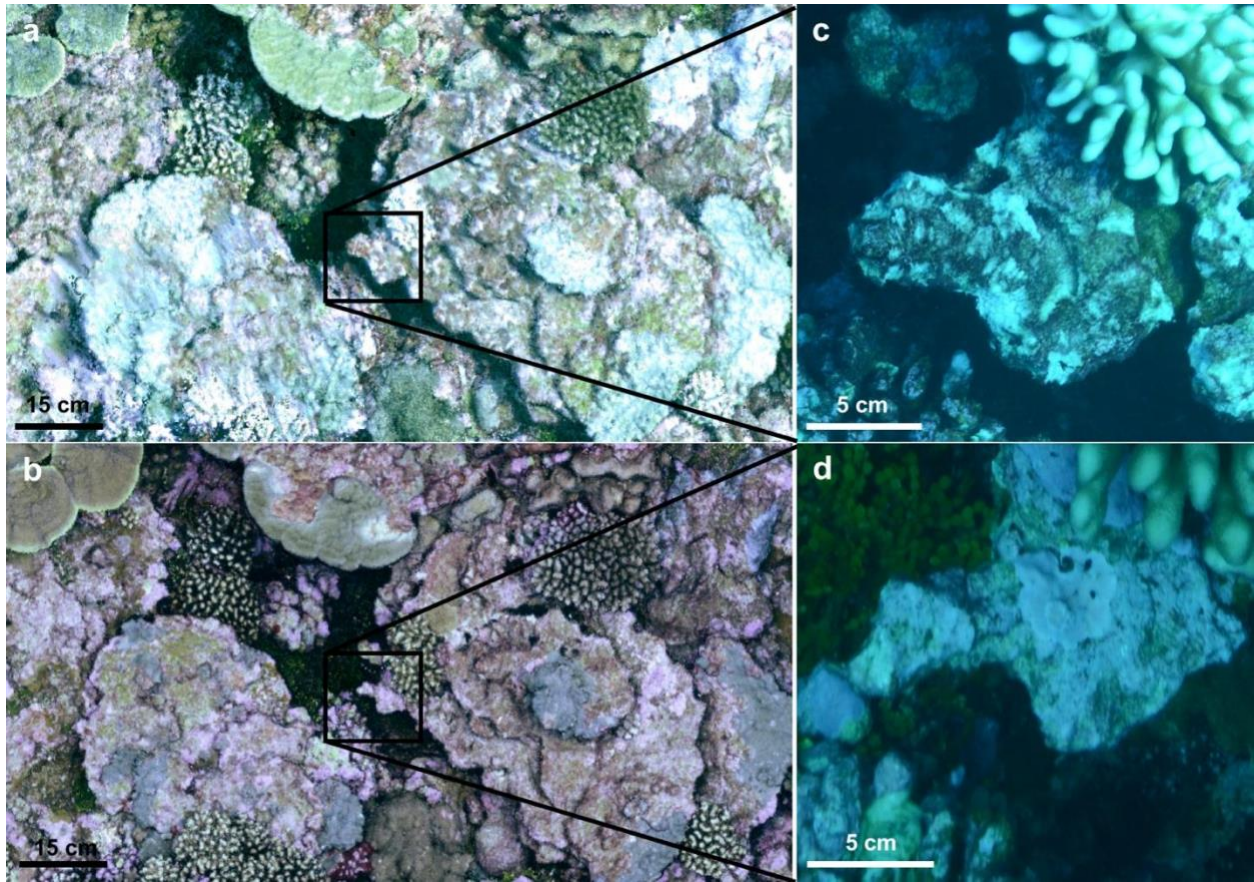
The use of spatially explicit reconstructions of coral reef time series allows for highly detailed examinations of the processes of benthic change. Although there was no functional impact from parrotfishes on coral mortality and recruitment, there was an enhancement of CCA recruitment and growth inside bite scars. Despite a significant difference between succession on parrotfish bite scars and succession across reef landscape, small differences in the proportion of CCA colonization on bite scars and random points indicate that parrotfishes contribute to the maintenance of the benthic community structure at Palmyra atoll by removing fleshy algae and facilitating colonization of CCA. Thus, while parrotfishes may not directly affect coral recruitment based upon our data there is evidence that they could indirectly facilitate it by promoting the abundance of their preferred settlement substrate. Given that Palmyra atoll represents an ecosystem largely free of local human impacts, further studies of landscape-wide succession on parrotfish bite scars across reef conditions could provide insight into how parrotfish communities structure and maintain benthic states across space and over time.

This thesis, in full, is currently being prepared for submission for publication of the material. Charendoff, JA; Edwards, CB; Pedersen, NE; Petrovic, V; Zgliczynski, B; Sandin, SA; Smith, JE. The thesis author was the primary investigator and author of this material.

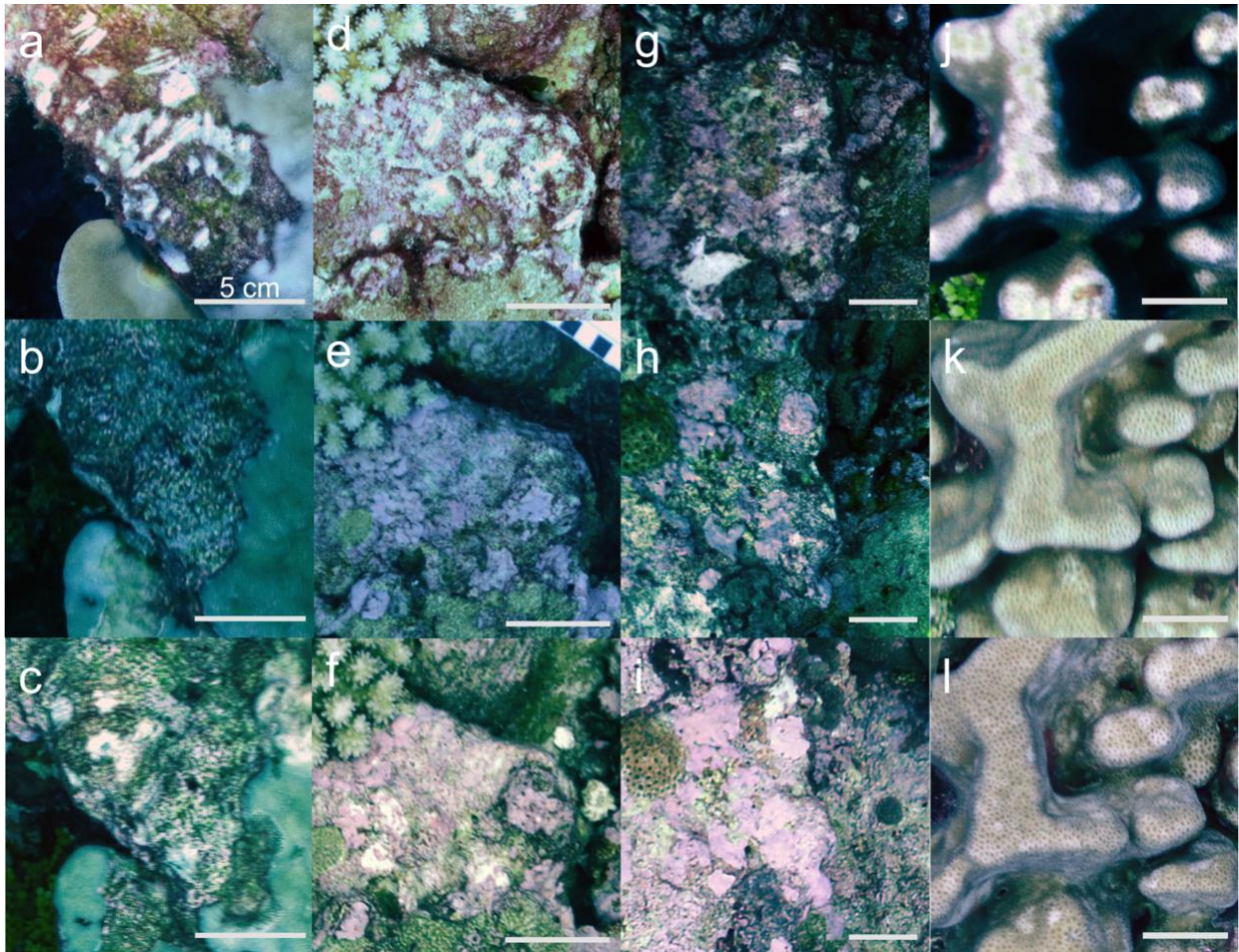
## Figures



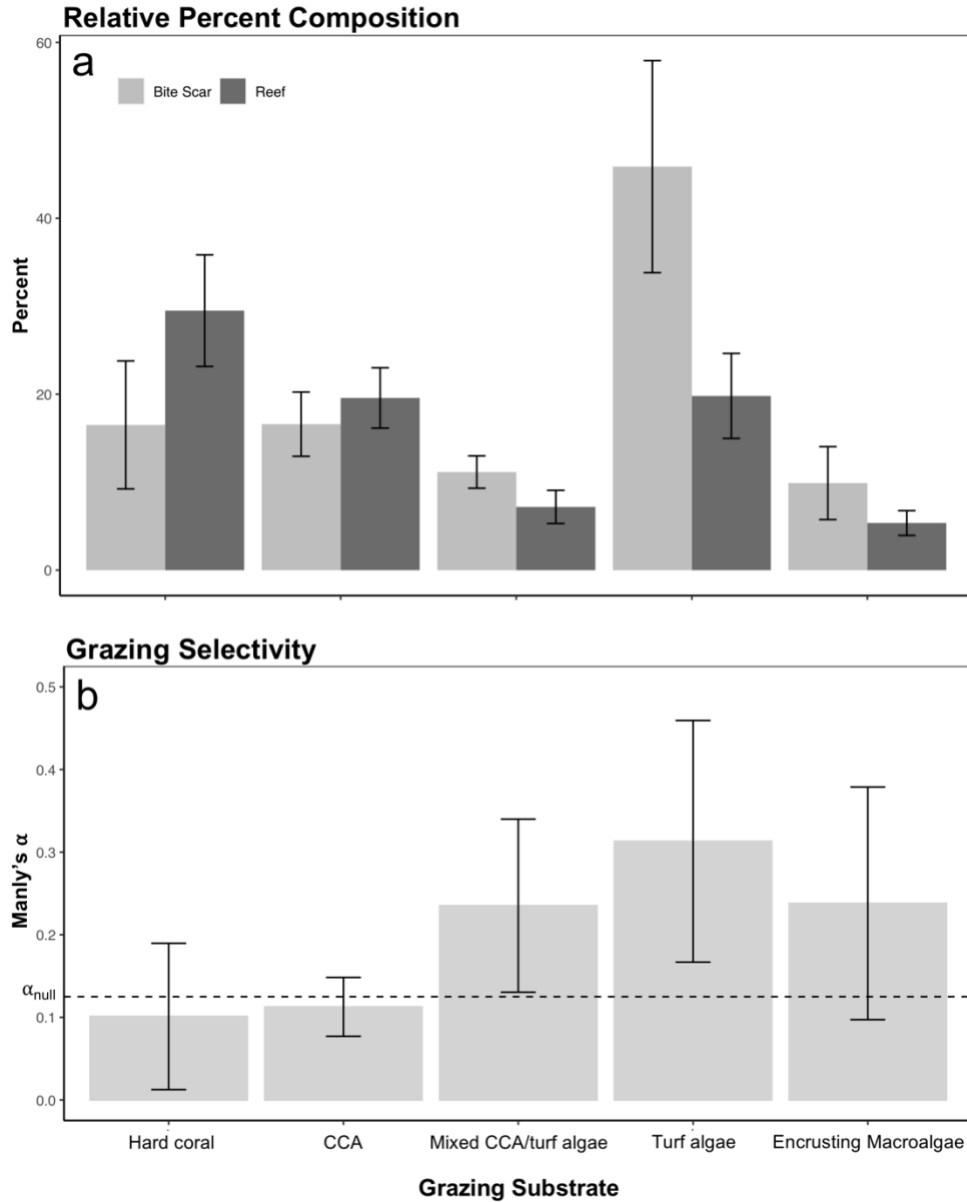
**Figure 1.** Map of Palmyra Atoll. Reef communities are shown in gray and land mass in black. Black circles are the approximate locations of fore reef survey sites (10m isobath) with corresponding site names.



**Figure 2.** Close up of orthoprojections from the coregistered 3-dimensional reef model for site FR3 from a) September 2015 and b) September 2016. c) High resolution image used to find parrotfish bite scars in September 2015 and d) to track their fate to September 2016.

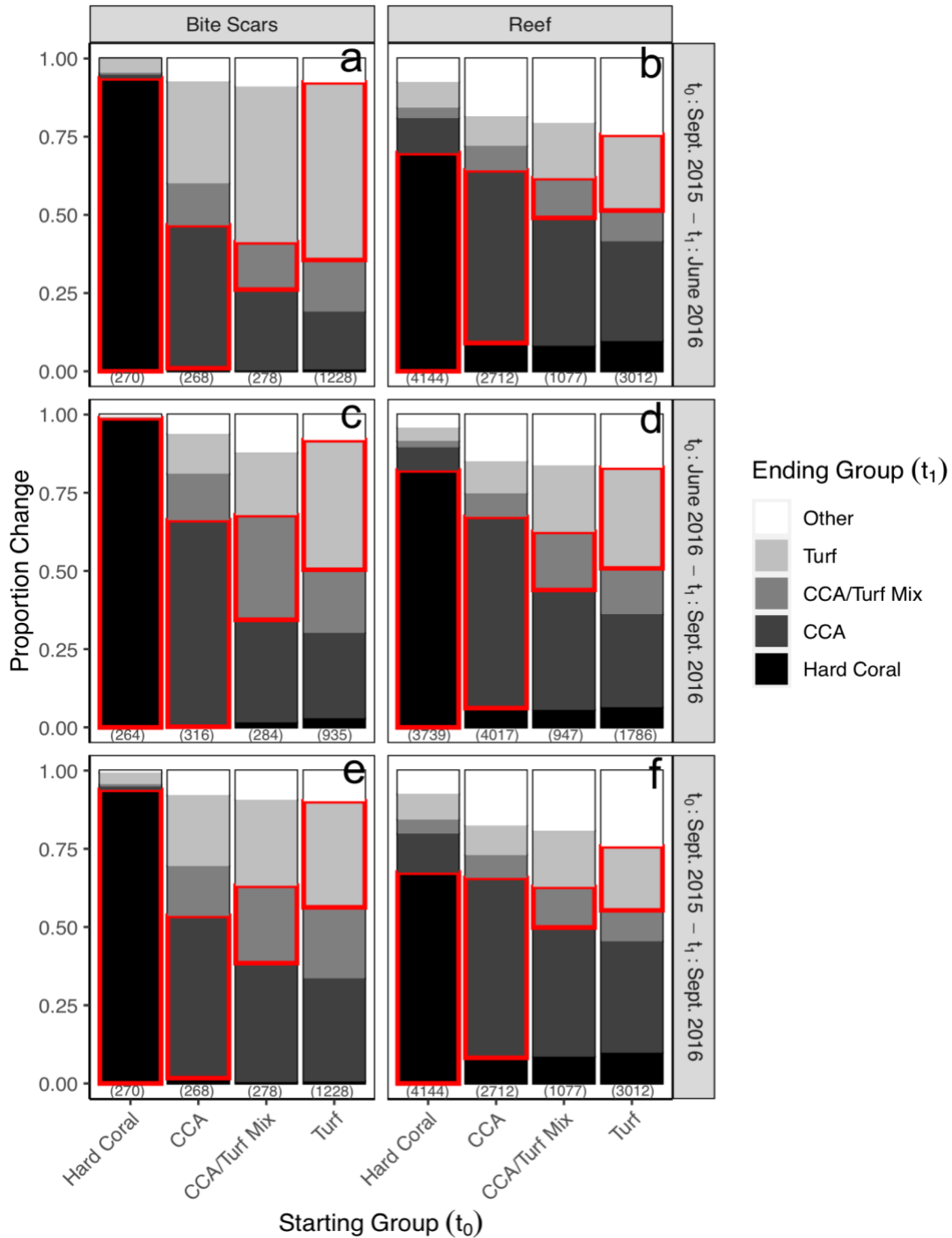


**Figure 3.** Examples of parrotfish bite scars trajectories on focal benthic functional groups. Turf algae (a-c) in September 2015, June 2016, and September 2016, respectively. Mixed matrices of Crustose coralline algae (CCA)/turf algae (d-f), CCA (g-i), and hard coral (j-l). All scale bars are 5 cm.



**Figure 4.** a) Relative percent composition of bite scars (light gray) and reef plots (dark gray) across Palmyra. b) Selectivity of Scraper and Excavator Parrotfishes for different substrate types. Error bars are 95% confidence intervals. Significant feeding selectivity for or against substrate type is indicated by 95% confidence interval completely above or below null selectivity (dashed line,  $\alpha_{null} = 1/8$ ).





**Figure 5.** Change in substrate composition starting on focal benthic functional groups including hard coral, crustose coralline algae (CCA), mixed CCA/turf algae, and turf algae. “Other” includes substrates such as soft corals, and other macroalgae. Proportion of substrate change across transition 1 (a-b), transition 2 (c-d), and whole time series (e-f) for bite scars (a, c, e) and random points (b, d, f). Column numbers are the number of points of each substrate at start of each transition. Red boxes highlight the proportion of no change in substrate composition across an interval

## Tables:

**Table 1.** Results from  $X^2$  analyses of independence for successional trajectories between bite scars and reef landscapes. Bite Scar and Reef refer to *post-hoc* analyses of independence of successional trajectories across starting substrates for those respective point types.

Time Interval	Association	$X^2$ Value	p-value
Sept. 2015 - June 2016	Point Type x Starting Substrate	3332.2	p << 0.01
	Bite Scars	359.6	p << 0.01
	Reef	2061.4	p << 0.01
June 2016 - Sept. 2015	Point Type x Starting Substrate	3817.4	p << 0.01
	Bite Scars	271.2	p << 0.01
	Reef	2014.8	p << 0.01
Sept. 2015 - Sept. 2016	Point Type x Starting Substrate	3326.9	p << 0.01
	Bite Scars	358.6	p << 0.01
	Reef	2168.3	p << 0.01

**Table 2.** Proportions of substrate change for bite scars and random points. Numbers in starting group column are the number of points for the above substrate at the start of each transition for bite scars and random points, respectively.

Transition	Starting Group	Ending Group	Bite Scar Transition Proportion	Number of Bites	Landscape Transition Proportion	Number of Points
Sept. 2015 - June 2016	Hard Coral (270, 4144)	Hard Coral	0.937	252	0.697	2890
		CCA	0.011	3	0.111	462
		CCA/Turf Mix	0.006	2	0.033	137
		Turf	0.047	13	0.083	343
		Other	0.000	0	0.075	312
	CCA (268, 2712)	Hard Coral	0.010	3	0.090	245
		CCA	0.457	122	0.552	1497
		CCA/Turf Mix	0.133	36	0.078	211
		Turf	0.326	87	0.094	254
		Other	0.074	20	0.186	505
	CCA/Turf Mix (278, 1077)	Hard Coral	0.002	1	0.082	88
		CCA	0.259	72	0.409	440
		CCA/Turf Mix	0.151	42	0.127	137
		Turf	0.497	138	0.176	190
		Other	0.090	25	0.206	222
	Turf (1228, 3012)	Hard Coral	0.006	7	0.097	291
		CCA	0.185	227	0.318	958
		CCA/Turf Mix	0.165	203	0.099	299
		Turf	0.568	697	0.242	729
		Other	0.076	94	0.244	735
June 2016 - Sept. 2016	Hard Coral (264, 3739)	Hard Coral	0.988	260	0.821	3071
		CCA	0.000	0	0.074	275
		CCA/Turf Mix	0.001	0	0.020	76
		Turf	0.003	1	0.042	157
		Other	0.007	2	0.043	160
	CCA (425, 4017)	Hard Coral	0.002	1	0.062	248
		CCA	0.661	280	0.611	2455
		CCA/Turf Mix	0.148	63	0.074	298
		Turf	0.127	54	0.102	411
		Other	0.062	27	0.151	605
	CCA/Turf Mix (284, 947)	Hard Coral	0.016	5	0.056	53
		CCA	0.328	93	0.383	363
		CCA/Turf Mix	0.334	95	0.186	176
		Turf	0.200	57	0.212	201
		Other	0.122	34	0.163	154
	Turf (936, 1786)	Hard Coral	0.029	27	0.064	115
		CCA	0.273	255	0.297	530
		CCA/Turf Mix	0.202	189	0.147	263
		Turf	0.414	388	0.322	575
		Other	0.082	77	0.170	303
Sept. 2015 - Sept. 2016	Hard Coral (270, 4144)	Hard Coral	0.959	259	0.674	2793
		CCA	0.004	1	0.124	515
		CCA/Turf Mix	0.004	1	0.045	187
		Turf	0.033	9	0.081	336
		Other	0.000	0	0.076	313
	CCA (268, 2712)	Hard Coral	0.019	5	0.082	222
		CCA	0.515	138	0.575	1560
		CCA/Turf Mix	0.157	42	0.073	197
		Turf	0.224	60	0.094	254
		Other	0.086	23	0.177	479
	CCA/Turf Mix (278, 1077)	Hard Coral	0.004	1	0.085	92
		CCA	0.380	106	0.413	445
		CCA/Turf Mix	0.247	69	0.130	140
		Turf	0.275	76	0.179	193
		Other	0.093	26	0.192	207
	Turf (1228, 3012)	Hard Coral	0.006	7	0.098	296
		CCA	0.329	405	0.356	1072
		CCA/Turf Mix	0.228	280	0.099	299
		Turf	0.339	416	0.204	615
		Other	0.098	120	0.242	730

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