Variability in composition of parrotfish bite scars across space and over time on a central Pacific atoll

Jonathan A. Charendoff[1] · Clinton B. Edwards[1] ·
Nicole E. Pedersen[1] · Vid Petrovic[2] · Brian Zgliczynski[1] ·
Stuart A. Sandin[1] · Jennifer E. Smith[1]

Abstract Parrotfishes are conspicuous herbivores, microvores, and detritivores in coral reef ecosystems, and the impacts of their feeding, particularly their capacity to expose reef carbonate, have received much attention. In many cases, parrotfish assemblages have been shown to control algal proliferation and promote the settlement of corals and crustose coralline algae (CCA). In extreme cases, high densities of parrotfishes may negatively affect net reef accretion through bioerosion and targeted coral predation. Most evidence describing the impacts of parrotfish foraging on benthic community structure is based upon correlations between benthic composition and parrotfish behavior or abundance, with much less known about process-based change of individual parrotfish bite scars through time. Here, we estimated parrotfish bite selectivity and determined the change in benthic composition within parrotfish bite scars relative to change in the overall reefscape using data collected over a 12-month duration from the fore reef habitat at Palmyra Atoll. We identified 2150 parrotfish bite scars which appeared most frequently on turf algae covered substrata but also on coral, CCA, and encrusting macroalgae. Of those bites taken on live coral, 96% of scars returned to live coral within 12 months. Notably, adult coral survivorship in bite scars was higher than at randomly sampled coral-covered locations not affected by parrotfish bites. The exposed substrate within bite scars was most commonly colonized by the dominant benthic functional group in the area immediately surrounding the scar. We found little evidence of coral recruitment to bite scars (1/2150); however, CCA growth on bites initially on turf algae increased from 18.4 to 32.9% across the two time intervals. Our results suggest that benthic areas affected by parrotfish bites were more likely to undergo a successional shift to a more calcified state relative to unaffected benthic areas, indicating that parrotfish grazing helps maintain highly calcified coral reef ecosystems.

Keywords Parrotfish · Grazing · Herbivory · Succession · Structure-from-motion

✉ Jonathan A. Charendoff
jonathan.charendoff@noaa.gov

1 Scripps Institution of Oceanography, UC San Diego, 9500 Gilman Dr., La Jolla, CA, USA

2 Department of Computer Science and Engineering, UC San Diego, 9500 Gilman Dr., La Jolla, CA, USA

Introduction

Herbivores in coral reef ecosystems constitute a highly diverse suite of organisms that consume primary producers as their main food source (Ogden and Lobel 1978; Hay and Taylor 1985; Steneck 1988). Over the last several decades, the roles of specific herbivore functional groups have been an important focal area within coral reef research (Belliveau and Paul 2002; Hoey and Bellwood 2008; Bonaldo et al. 2014; Ruttenberg et al. 2019). Parrotfishes (Scarinae) are a group of herbivores, microvores, and detritivores (Nicholson and Clements 2020) known to perform a wide range of ecological functions including algal removal (Bellwood and Choat 1990; Mumby 2006; Burkepile and Hay 2010), bioerosion (Bruggemann et al. 1996; Hoey and Bellwood 2008), and coral predation (Rotjan and Lewis 2005; Rotjan et al. 2006). Each of these processes can have important impacts on benthic community structure; however, the diversity of these functions has introduced debate regarding the

net positive (or negative) role that parrotfishes have on reef health and recovery from disturbance (McCauley et al. 2014; Russ et al. 2015).

The specialized beak-like feeding structure of parrotfishes enables excavating and scraping feeding activities that remove epilithic and endolithic algae, calcium carbonate, and cyanobacteria from the reef benthos, often resulting in distinctive visible bite scars (Bellwood and Choat 1990; Bonaldo and Bellwood 2009). These grazed patches of "bare space"—consisting of functionally bare carbonate (Bonaldo and Bellwood 2008)—have been suggested to be potential settlement locations for slower growing calcifying groups such as crustose coralline algae (CCA) and corals (Bellwood and Choat 1990). Parrotfish grazing is an important process for controlling algal standing stock (Bellwood et al. 2006; Mumby 2006; Burkepile and Hay 2008), and the top-down influence exerted by parrotfishes on fast-growing turf and other 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—either direct facilitation of coral recruitment to bite scars or promotion of crustose coralline algal growth and coral competitive dominance by the removal of turf algal competitors (Barott et al. 2012; Bonaldo et al. 2014; Shantz et al. 2020)—are not well-studied at the reefscape scale across year-long time series.

Coral reef benthic communities in areas that are both exposed to oceanic swell and largely free of direct human impact are often dominated by corals and calcifying algae, especially CCA (Williams et al. 2015; Smith et al. 2016; Robinson et al. 2018). Parrotfish grazing on algal substrates and resulting benthic succession may facilitate the settlement and growth of CCA and corals (Littler and Littler 1984; Lewis 1986; Steneck 1988; Burkepile and Hay 2006, 2010; Smith et al. 2010). The relative selectivity for certain benthic groups by parrotfishes may also drive reefscape level change in community structure (Hamilton et al. 2014; Streit et al. 2019). For instance, preferential grazing on benthic surfaces covered with fast-growing turf algae may create opportunities for growth of CCA, which is a preferred settlement space for coral recruits (McCook et al. 2001; Price 2010). Succession inside bite scars following parrotfish grazing may begin with colonization by turf algal communities in the short term, followed by an incremental growth of CCA into those grazed areas, helping to maintain calcifier dominance (Hixon and Brostoff 1996). While the aggregate effects of parrotfishes on coral reef benthic succession are well-understood, there is opportunity to learn from the succession of organisms that colonize "bare spaces" created by parrotfish grazing.

While parrotfishes primarily target substrata covered in turf algae through their feeding activities (Bellwood and Choat

1990; Hamilton et al. 2014; Kelly et al. 2016), some species will occasionally graze on coral colonies (Rotjan and Lewis 2005). As a result, it has been proposed that reefs with high parrotfish biomass or particular assemblages of parrotfishes (e.g., overrepresentation of noted coral predators (corallivores) *Bolbometopon muricatum* and *Chlorurus microrhinos*, (Bellwood and Choat 1990; Bellwood et al. 2003, 2012; McCauley et al. 2014)) may have a net negative impact on coral communities when combined with modern human stressors (Rice et al. 2019; Rotjan et al 2022). Some corals have been shown to recover rapidly from parrotfish grazing wounds, suggesting that parrotfish grazing does not always result in coral tissue loss or declines in coral abundance over time (Bonaldo and Bellwood 2011; Rempel et al. 2020). However, energy expenditure from healing grazing scars may reduce coral growth and fecundity (Meesters et al. 1994; Van Veghel and Bak 1994). Negative impacts may be exacerbated for certain coral taxa (e.g., *C. microrhinos* grazing on *Porites* spp.) or colonies that experience routine parrotfish grazing leading to long-term impacts on coral growth and fitness (Rotjan et al. 2006; Hoey and Bellwood 2008; Bonaldo and Bellwood 2011; Bellwood et al. 2012; Burkepile 2012; McCauley et al. 2014; Welsh et al. 2015). Importantly, there remain critical gaps in our understanding of the natural history of parrotfish grazing scars across the reefscape.

Difficulty in following small benthic features through time has limited the spatial and temporal extent of studies that address succession on bite scars. Using structure-from-motion technology (SfM), we can now generate highly detailed and geometrically accurate three-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). Here, we aim to document benthic succession on parrotfish bite scars from the fore reef habitat on Palmyra Atoll. We first located parrotfish bite scars across 700 m^2 of reefscape and track benthic succession on these bite scars using time series mapping with repeated imaging of sites over a year-long time series. We then determine the benthic group on which bites were taken and evaluate evidence for selectivity of certain benthic groups based upon their abundance across the reef. This study examines how benthic composition on space opened by parrotfish bite scars changed over time in comparison with change in benthic community composition across the overall reef reefscape.

Materials and methods

Study site

We conducted this study at Palmyra Atoll (5° 52′ N, 162° 06′ W), a National Wildlife Refuge within the Pacific Remote

Islands National Marine Monument, USA. Palmyra's coral reef ecosystem is generally free of local human impacts and provides a natural baseline to understand coral reef ecosystem function in the relative absence of direct anthropogenic impacts (Brainard et al. 2005; Sandin et al. 2008). We selected four plots at the 10-m isobath on the fore reef (FR3, FR5, FR7, and FR9), spaced roughly 4 km apart on the north and south shores (Fig. 1), from which we collected imagery to generate 3D models and derived 2D orthoprojections. SCUBA divers collected imagery in September–October 2015, June 2016 and September–October 2016. Each plot covered an area of 200 m^2. (With the exception, the 100 m^2 plot at FR9 as field conditions in 2015 did not allow for image collection across the entire survey area.) We installed steel pins marked by GPS coordinates within each plot to allow for resurveys across the time series.

Large area imaging and coregistration of 3D models

Underwater imagery was collected following methods described by Edwards et al. (2017). Briefly, we mounted two Nikon D7000 16.2-megapixel DSLR cameras onto a custom frame, capturing imagery with differing angles of view. We set one camera to an 18-mm focal length to provide high image overlap required for 3D model generation and the second camera to a 55-mm focal length to provide high image resolution ($\leq$ 1 mm) for identifying benthic organisms (Pedersen et al. 2019).

We processed images to create 3D models of each plot using the SfM software *Metashape* Pro 1.3.5 (Agisoft LLC., St. Petersburg, Russia). Details of model generation have been discussed in detail elsewhere (Westoby et al. 2012; Burns et al. 2015).

To track changes in benthic composition over time, we exported 3D point clouds generated in *Metashape* to the custom visualization software *Viscore* (Petrovic et al. 2014). We scaled and oriented relative to the plane of gravity using the depth and scale measurements collected within each plot during image collection (Sandin et al. 2020). We manually coregistered (aligned in 3D space) the time series of 3D models for each plot in *Viscore*. We created 2D projections orthogonal to the plane of gravity (so-called "orthoprojections") directly from the coregistered point clouds (Fig. 2a, b) and exported as individual. tiff files for each year. Importantly, using orthoprojections generated directly from the coregistered point clouds facilitates precise mapping of plots through time (Kodera et al. 2020; Sandin et al. 2020), as opposed to orthophotomosaics which can suffer image distortion resulting from the blending and distortion of photographs during orthorectification (Nicosevici et al. 2009).
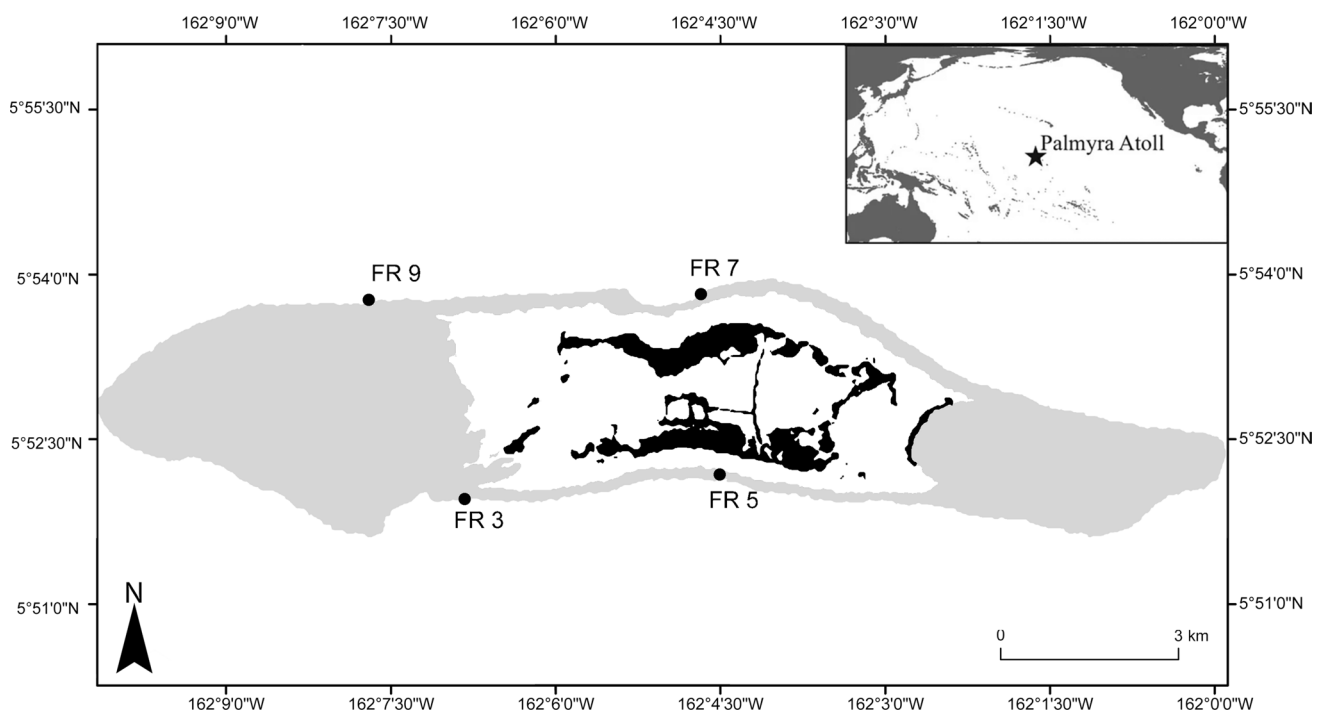

Fig. 1 Map of Palmyra atoll with marked locations of study sites (FR3: N 5.86654, W-162.11359; FR5: N 5.86965, W-162.07520; FR7: N 5.89715, W-162.07831; FR9: N 5.89651, W-162.12813). Land is shown in black, and fore reef is shown in gray
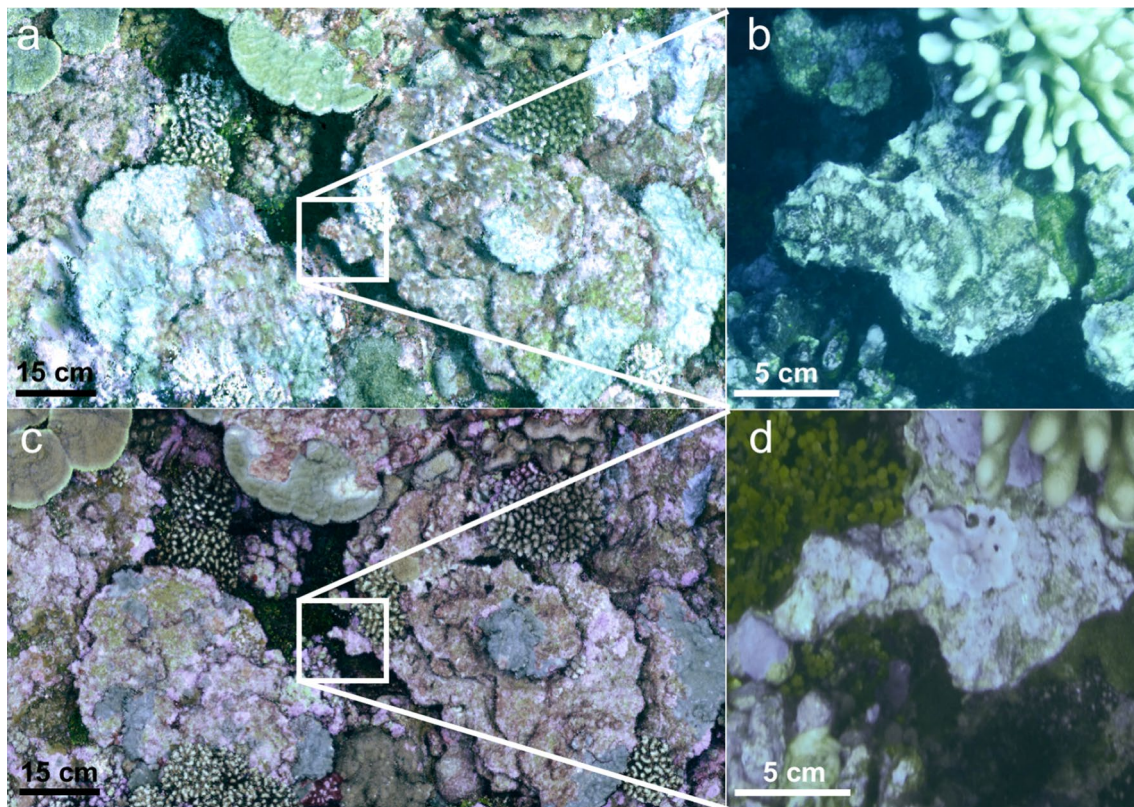
Fig. 2 Close-up of orthoprojections from the coregistered three-dimensional reef model for site FR3 from **a** September 2015 and **b** September 2016. **c** High-resolution image used to find parrotfish bite scars in September 2015 and **d** to track their fate to September 2016

Ecological post-processing

Identification of bite scars

We defined parrotfish bite scars as either singular bare patches or patches with two to many parallel lines of exposed carbonate on the reef substrate of roughly 1 to 3 cm in length (Fig. 3), which are distinctive of scraper and excavator parrotfish grazing, respectively (Bellwood and Choat 1990; Jayewardene et al. 2009). We identified bite scars from orthoprojections collected at the beginning of the time series (t_0, September 2015) with the aid of spatially linked, high-resolution raw imagery collected from each plot (Fig. 2c, d) and segmented in Adobe *Photoshop CC*. We estimated the initial benthic group on which bites were taken from a 1-cm wide buffer radius surrounding each bite scar. Within each buffer, we segmented and identified the benthic organisms to the finest taxonomic resolution possible, and then grouped them into eight functional categories: 1. hard coral (Scleractinia), 2. CCA, 3. mixed matrices of CCA and turf algae (mixes between 30% CCA/70% turf algae and 70% CCA/30% turf algae covered substrata, hereafter referred to as mixed CCA/turf algae), 4. turf algae covered substrata (hereafter turf algae), 5. encrusting macroalgae (*Lobophora*

spp., and *Peyssonnelia* spp.), 6. other invertebrates (including Octocorallia and Corallimorpharia), and 7. *Halimeda* spp.. We grouped other erect macroalgae and non-biological substrata (e.g., sand), all of which are rare on the fore reef at Palmyra atoll (< 2% of benthic cover), into 8, the final category, "other." For the purpose of analysis, we included encrusting macroalgae, soft corals, and *Halimeda* in the "other" category as bites were absent or rare on these groups. In cases where buffers contained multiple groups, we determined the composition of that bite scar as the group which constituted the greatest proportion of area within each buffer. Bites with more than three functional groups in their respective buffer were uncommon ($n = 5$).

Change in bite scar composition over time

To quantify change in the functional group composition of the benthos at the location of the bite scars through time, we relocated scars in the coregistered orthoprojection time series (June 2016, t_1; September–October 2016, t_2). We determined the composition of bites scars as the benthic group occupying the centroid of the bite scar (defined from t_0) in each subsequent time point (t_1 and t_2; Fig. 2) to create a point estimate of benthic change within
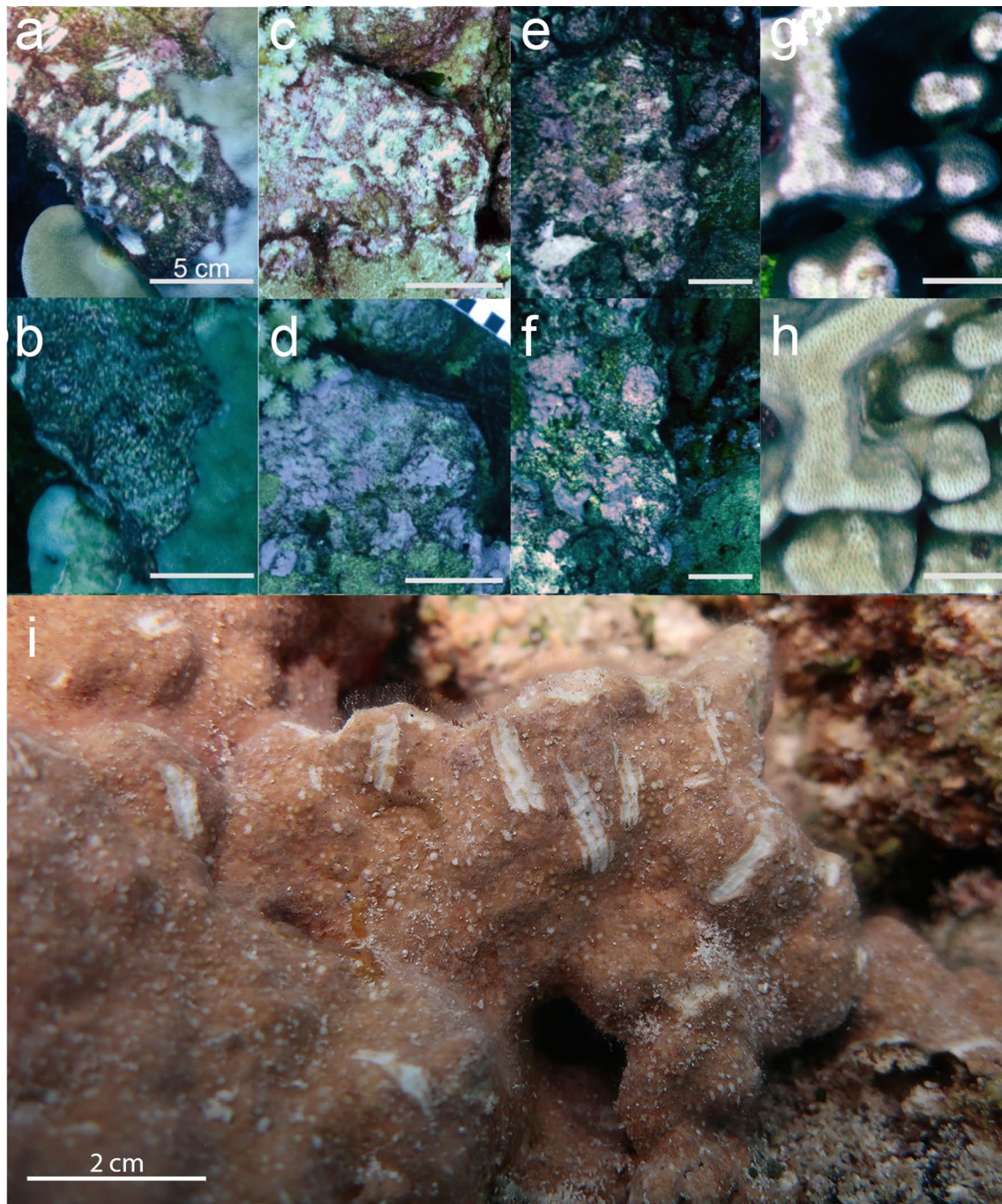
Fig. 3 Examples of parrotfish bite scars trajectories on focal benthic functional groups. Turf algae covered substrata **a**, **b** in September 2015, and June 2016, respectively. Mixed matrices of crustose coralline algae (CCA)/turf algae (**c**, **d**), CCA (**e**. **f**), and hard coral (**g**, **h**). **i** Close up image of individual bite scars on CCA. Scale bars are 5 cm (**a**–**h**) or 2 cm (**i**)

each bite scar, using the groups defined above. The ending functional group identity of transition 1 was the starting identity for transition 2. As such, it was possible that bites starting on CCA could change to turf algae after transition 1 and subsequently return to CCA after transition 2. We removed any bite scars located in t_0 that could not be relocated (e.g., due to dislodgement of the substrate) from

the study ($n = 41$) for a total of 2150 bites scars included in this analysis.

Overall changes in benthic composition

To estimate benthic composition in each plot, we used random point sampling in *Viscore* (Fox et al. [2019]). *Viscore*

distributed a stratified random sample of 4000 points across the 3D model of the 200 m² plots (with 2000 points for the 100 m² plot), and we labeled each point to the finest taxonomic level possible and grouped to the functional groups listed 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 the raw images for the most detailed view of the point in question when making taxonomic designations. To determine how non-bite scar points in the reef changed across the time series, we placed the points in t_0 at the same location on the reef in t_1 and t_2, with the point again designated to the finest taxonomic resolution and grouped to the described functional group level.

Quantitative analysis

Grazing selectivity

We used Vanderploeg and Scavia's electivity index (Vanderploeg and Scavia 1979; Lechowicz 1982) to determine if parrotfish grazed on certain benthic functional groups more than expected based on that functional group's abundance in the reefscape. Chesson's α is first calculated as:

$$\alpha_i = \frac{r_i/p_i}{\sum_i^m r_i/p_i}, \quad i = 1, \dots, m$$

where r_i is the number of bite scars on functional group type i of $m = 8$ functional groups present in each plot, and p_i represents the relative proportion of functional group i in each plot (Chesson 1983). Electivity is then calculated as:

$$E_i^* = \frac{\left[\alpha_i - \left(\frac{1}{m}\right)\right]}{\left[\alpha_i + \left(\frac{1}{m}\right)\right]}$$

A value of 0 represents neutral grazing preference for any functional group as the instances of grazing are proportional to the abundance of that functional group. Values of E_i^* significantly above 0 indicate a positive grazing preference, while values of E_i^* significantly below 0 indicate a negative grazing preference. We calculated selectivity indices for each reef site.

Bite scar succession and overall benthic change

We used a three-way Chi-squared (χ^2) contingency table analysis to determine if change in functional group identity inside bite scars was different from changes in random locations on the reef. This analysis allowed us to estimate if any change in the functional group inside each bite scars was dependent on the initial composition of the bite scar in

the transition from t_0 to t_1 (time interval 1, $T1$), and from t_1 to t_2 (time interval 2, $T2$). We grouped transitions from t_i to t_{i+1} as either "different" or "same" depending on whether the benthic group in question did or did not change, respectively. For example, we grouped bites on turf algae in t_0 that were colonized by hard coral or CCA by t_1 as "different"; in contrast, we grouped bites on turf algae that were colonized by turf as "same." Similarly, we grouped all random points which remained the same functional group in t_i and t_{i+1} as "same," while we grouped those that became different functional groups as "different." We conducted two-way contingency table post hoc analyses for both bite scars and random points to determine if change in functional group identity was independent of starting functional group for either case. To directly compare benthic change of ungrazed coral tissue and bite scar succession on grazed coral, only coral from grazed taxa (massive *Porites* spp., sub-massive *Goniastrea stelligera*, and *Pavona* spp.) were included in the analysis as hard coral. We labeled corals that did not belong to the three focal taxa as "other hard coral." We conducted all analyses in *R* version 4.0.2 (R Core Team 2020).

Results

Initial bite scar composition and grazing electivity

We found a total of 2150 parrotfish bite scars on Palmyra Atoll in September 2015 from initial sampling across 700 m² of reef surveyed. While hard coral comprised an average of 29.5% of reef cover, an average of 16.5% of bite scars was observed on this functional group (Fig. 4a). Based on the electivity analysis (Fig. 4b), we found evidence of neutral electivity for hard coral ($E_i^* = -0.253$, 95% CI = [−0.743, 0.237]). CCA comprised an average of 19.6% of reef cover, while an average of 16.6% of bite scars were observed on this functional group. Based on the electivity analysis, we found evidence of neutral electivity for CCA ($E_i^* = -0.070$, 95% CI = [−0.230, 0.089]). Mixed CCA/turf algae comprised and average of 7.2% of reef cover, while an average of 11.1% of bite scars was observed on this functional group. Based on the electivity analysis, we found evidence of positive electivity for mixed CCA/turf algae ($E_i^* = 0.261$, 95% CI = [0.061, 0.461]). Turf algae comprised and average of 19.8% of reef cover, while an average of 45.9% of bite scars was observed on this functional group. Based on the electivity analysis, we found evidence of positive electivity for turf algae ($E_i^* = 0.353$, 95% CI = [0.055, 0.651]). Encrusting macroalgae comprised and average of 5.4% of reef cover, while an average of 9.9% of bite scars was observed on this functional group. Based on the electivity analysis, we found evidence of neutral electivity for encrusting macroalgae ($E_i^* = 0.161$, 95% CI = [−0.343, 0.665]). We found no bite

Fig. 4 **a** Mean relative percent composition of bite scars (light gray) and reef plots (dark gray) across the four study sites at Palmyra. **b** Mean relativized electivity 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 0
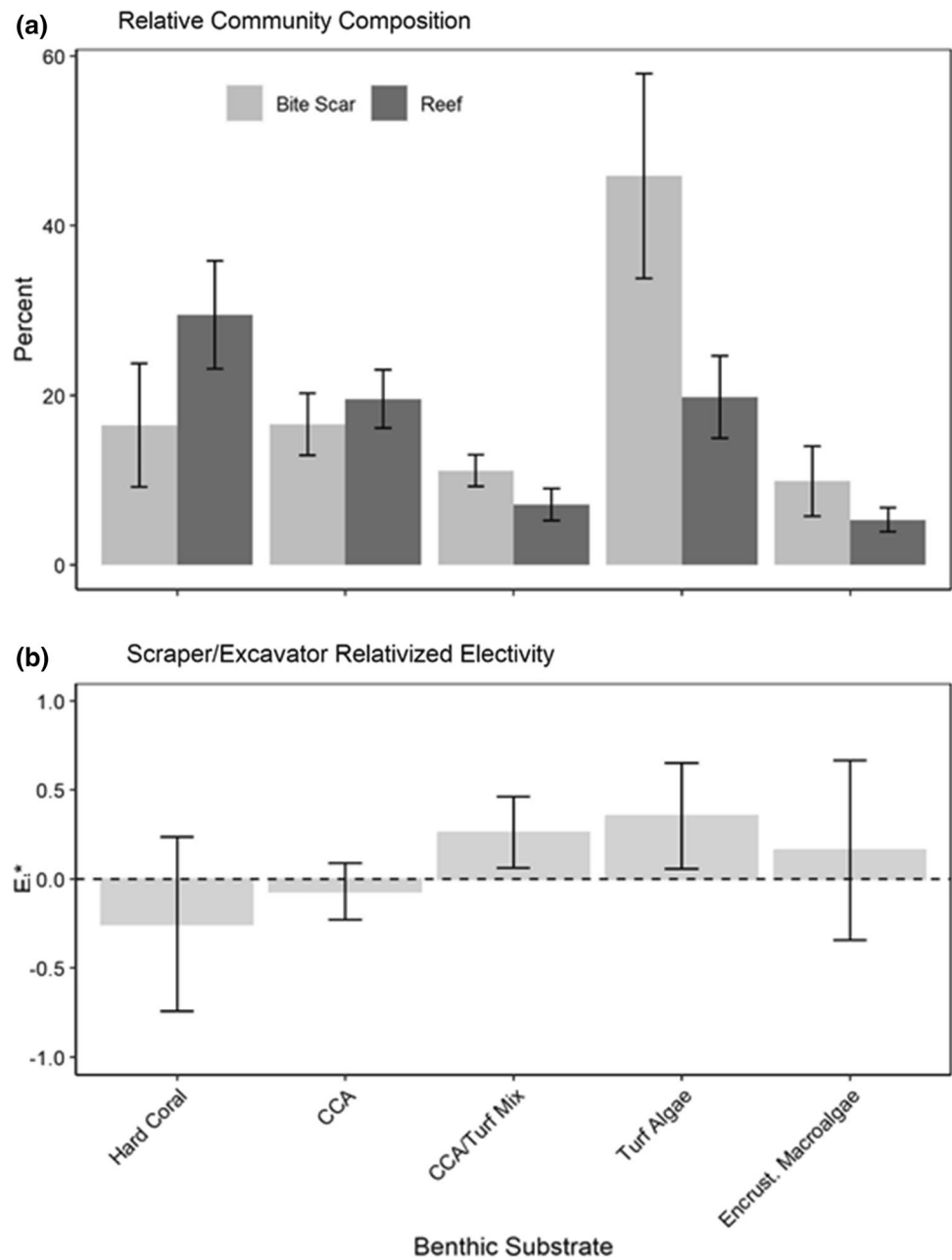
scars on the other functional groups, indicating a negative electivity ($E_i^* < 0$) for those groups.

All bite scars on coral were on adult colonies (> 5 cm diameter), and we did not find any juvenile corals (< 5 cm) in the 1-cm buffer surrounding bite scars at any site. We observed parrotfish predation scars on several coral taxa: massive *Porites* spp. and sub-massive *Goniastrea stelligera* and *Pavona* spp. Massive *Porites* spp. corals comprised an average of 13.0% of the coral community at these sites, but had 45.6% of all detected bite scars on corals. In comparison, *Goniastrea stelligera* and *Pavona* spp. corals comprise 9.0% and 6.1% of the coral community but contained 30.5% and 23.9% of bites on hard coral, respectively.

Bite scar succession

At the end of the first 9 months (t_1), 6.7% of bites on hard corals transitioned to a new functional group (Fig. 5a, 5.2% to turf algae, 0.7% to mixed CCA/turf algae, and 0.7% to CCA). Between t_1 and t_2, 1.2% bites colonized by hard coral transitioned to a new functional group (0.4% to turf algae, and 0.8% to other). At the end of the 12 months (t_2), 4.1% of bites on hard coral transitioned to a new functional group (3.3% to turf algae, 0.4% to mixed CCA/turf algae, and 0.4% to CCA). Nearly all bites taken on coral (97.0%) occurred within the interior of coral colonies (100% of buffer occupied by coral), with a majority of
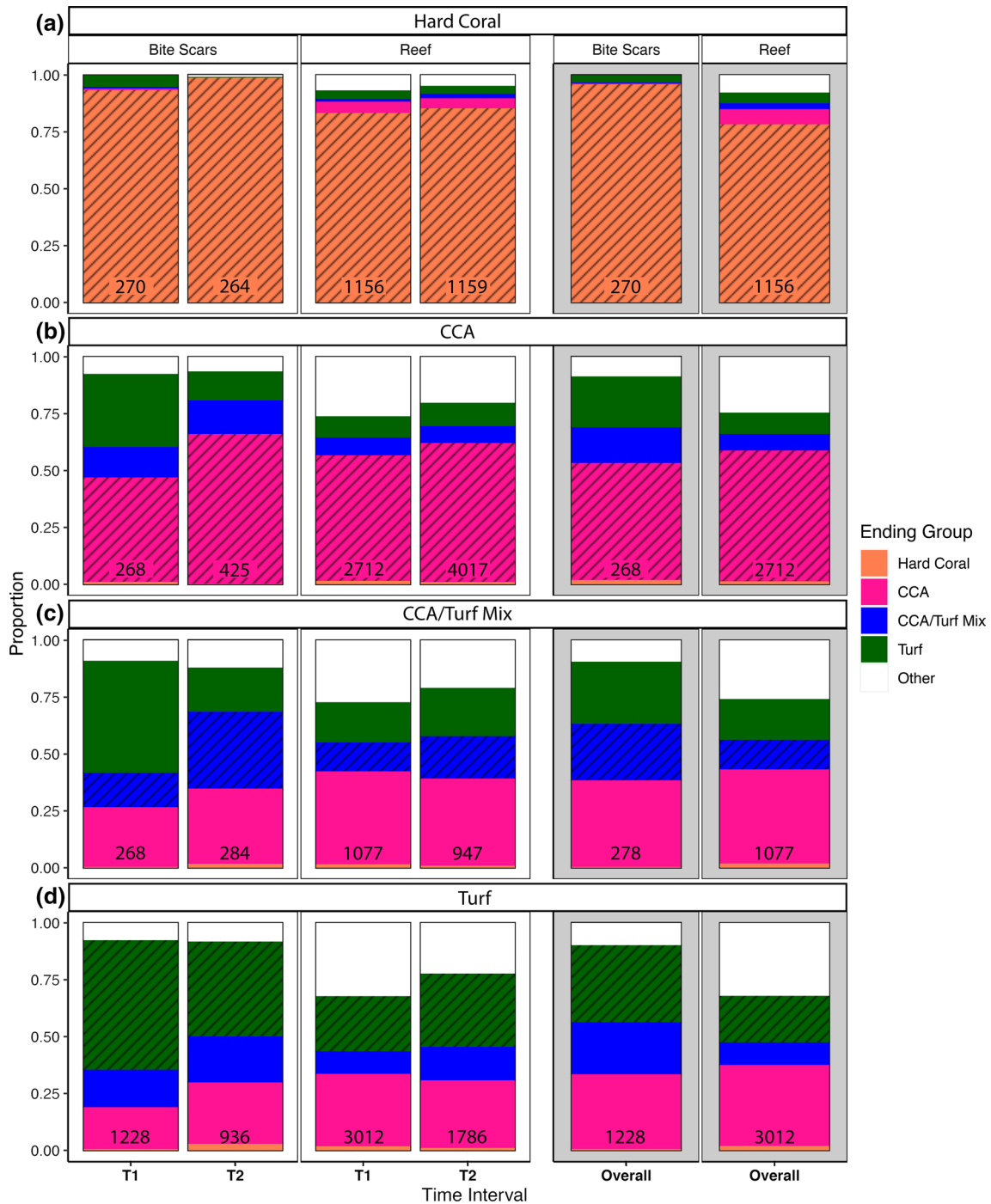
Fig. 5 Change in substrate composition starting on focal benthic functional groups. Proportion of substrate type at the end of each time interval (*T*1: t_0–t_1, *T*2: t_1–t_2, Overall: t_0–t_2) for bite scars and random points starting on **a** hard coral, **b** coralline algae (CCA), **c** mixed CCA/turf algae, and **d** turf algae covered substrate (turf algae).

"Other" includes substrates such as soft corals, and other macroalgae. Hash marks highlight the proportion of no change in substrate composition across a time interval. Numbers for each bar are the number of bites or random points of the starting substrate at the start of the time interval, values are presented in Supplementary Table 1

those bites returning to live coral by the end of the study (95.9%). See Supplemental Table 1 for complete summary of transition proportions. By t_1, 54.1% of observed bites on CCA transitioned to a new functional group (Fig. 5b,

32.1% to turf algae, 13.4% to mixed CCA/turf algae, 1.1% to hard coral, and 7.5% to other). Between t_1 and t_2, 34.1% of bites colonized by CCA by t_1 transitioned to a new functional group (12.7% to turf algae, 14.8% to mixed CCA/

Table 1 Results from X^2 analyses of independence for successional trajectories between bite scars and reef landscapes

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	$p < <0.01$

Bite scar and reef refer to *post hoc* analyses of independence of successional trajectories across starting substrates for those respective point types

turf algae, 0.2% to hard coral, and 6.4% to other). At the end of the 12 months (t_2), 48.5% of observed bites initially on CCA transitioned to a new functional group (22.4% to turf algae, 15.7% to mixed CCA/turf algae, 1.9% to hard coral, and 8.6% to other).

By t_1, 84.9% of observed bites on mixed CCA/turf algae transitioned to a new functional group (Fig. 5c, 49.3% to turf algae, 26.3% to CCA, 0.4% to hard coral, and 9.0% to other). Between t_1 and t_2, 66.2% of bites colonized by mixed CCA/turf algae by t_1 transitioned to a new functional group (19.4% to turf algae, 33.1% to CCA, 1.8% to hard coral, and 12.0% to other). At the end of the 12 months (t_2), 75.1% of observed bites on mixed CCA/turf algae transitioned to a new functional group (27.3% to turf algae, 38.1% to CCA, 0.4% to hard coral, and 9.4% to other).

By t_1, 43.0% of observed bites on turf algae covered substrata transitioned to a new functional group (Fig. 5d, 16.5% to mixed CCA/turf algae, 18.4% to CCA, 0.6% to hard coral, and 7.6% to other). Between t_1 and t_2, 58.3% of bites colonized by turf algae by t_1 transitioned to a new functional group (20.2% transitioned to mixed CCA/turf algae, 27.0% to CCA, 2.9% to hard coral, and 8.2% to other). At the end of the 12 months (t_2), 66.1% of observed bites on turf algae transitioned to a new functional group (22.9% to mixed CCA/turf algae, 32.9% to CCA, 0.6% to hard coral, and 9.8% to other).

We found limited evidence of coral growth over bites initially taken on algal functional groups (t_0–t_1: algae to coral: 0.6% [11/1774 bites]; t_1–t_2: 2.0% [33/1645]; t_0–t_2: 0.7% [13/1774]). Of the coral growth within bite scars initially taken on algal substrates, there was only one bite scar with an observed coral recruit, from the genus *Acropora*, (0.04% of the total bite scars) across the entire time series.

Differences in transition proportions on bite scars were statistically significant between starting groups for each transition (See Table 1 for full results from Chi-squared (χ^2) analyses).

Overall benthic change

Across the reefscape, randomly sampled points that were classified as hard coral at t_0, 16.6% transitioned to a new functional group by t_1 (Fig. 5a, 3.7% to turf algae, 1.2% to mixed CCA/turf algae, 4.9% to CCA, and 6.7% to other). Between t_1 and t_2, 14.6% points on hard coral transitioned to a new functional group (3.5% to turf algae, 2.0% to mixed CCA/turf algae, 4.4% to CCA, and 4.7% to other). At the end of the 12 months (t_2), 21.6% of points on hard coral transitioned to a new functional group (4.7% to turf algae, 2.6% to mixed CCA/turf algae, 6.7% to CCA, and 1.3% to other).

By t_1, 44.8% of randomly sampled points on CCA transitioned to a new functional group (Fig. 5b, 9.4% to turf algae, 7.8% to mixed CCA/turf algae, 1.6% to hard coral, and 26.1% to other). Between t_1 and t_2, 39.9% of points colonized by CCA by t_1 transitioned to a new functional group (10.2% to turf algae, 7.4% to mixed CCA/turf algae, 1.0% to hard coral, and 20.2% to other). At the end of the 12 months (t_2), 42.5% of points on CCA transitioned to a new functional group (9.4% to turf algae, 7.3% to mixed CCA/turf algae, 1.3% to hard coral, and 24.5% to other).

By t_1, 87.3% of randomly sampled points on mixed CCA/turf algae transitioned to a new functional group (Fig. 5c, 17.6% to turf algae, 40.9% to CCA, 1.6% to hard coral, and 27.2% to other). Between t_1 and t_2, 81.4% of points colonized by mixed CCA/turf algae by t_1 transitioned to a new functional group (21.2% to turf algae, 38.3% to CCA, 1.0% to hard coral, and 20.9% to other). At the end of the 12 months (t_2), 87.0% of points on mixed CCA/turf algae transitioned to a new functional group (17.9% to turf algae, 41.3% to CCA, 1.9% to hard coral, and 25.8% to other).

By t_1, 75.8% of randomly sampled points on turf algae transitioned to a new functional group (Fig. 5d, 9.9% to mixed CCA/turf algae, 31.8% to CCA, 1.9% to hard coral, and 32.2% to other). Between t_1 and t_2, 68.8% of points colonized by turf algae by t_1 transitioned to a new functional group (14.7% to mixed CCA/turf algae, 29.7% to CCA,

1.1% to hard coral, and 22.3% to other). At the end of the 12 months (t_2), 79.6% (2397/3012) of points on turf algae transitioned to a new functional group (9.9% to mixed CCA/turf algae, 35.6% to CCA, 2.0 to hard coral, and 32.1%to other).

Overall, change across the reef was dependent on starting functional group identity. Further, there were statistically significant differences in how functional groups changed over time on the reef in comparison with in the bite scars (Table 1). Despite these differences, the overall proportion of CCA increased across all bite scars (t_0: 12.5% CCA to t_2: 30.2% CCA) and randomly sampled points (t_0: 23.3% CCA to t_2: 35.4% CCA) across the survey period regardless of starting group identity (Fig. 6).

Discussion

While parrotfish bite scars are frequently invoked as potential settlement locations for coral recruits and other calcifying organisms (e.g., Bellwood and Choat 1990; Mumby et al. 2007), there are few empirical studies that provide data on the fate of bite scars over time (Bonaldo and Bellwood 2009; Bonaldo et al. 2011; Rempel et al. 2020). Here, we described the fates of 2150 parrotfish bite scars over a year-long time series of 700 m^2 of fore reef habitat on Palmyra Atoll. In general, we found little evidence of coral recruitment into bite scars ($n = 1$). Additionally, we found that the majority of bites on hard coral transitioned from bare carbonate back to hard coral (95.9%) within a
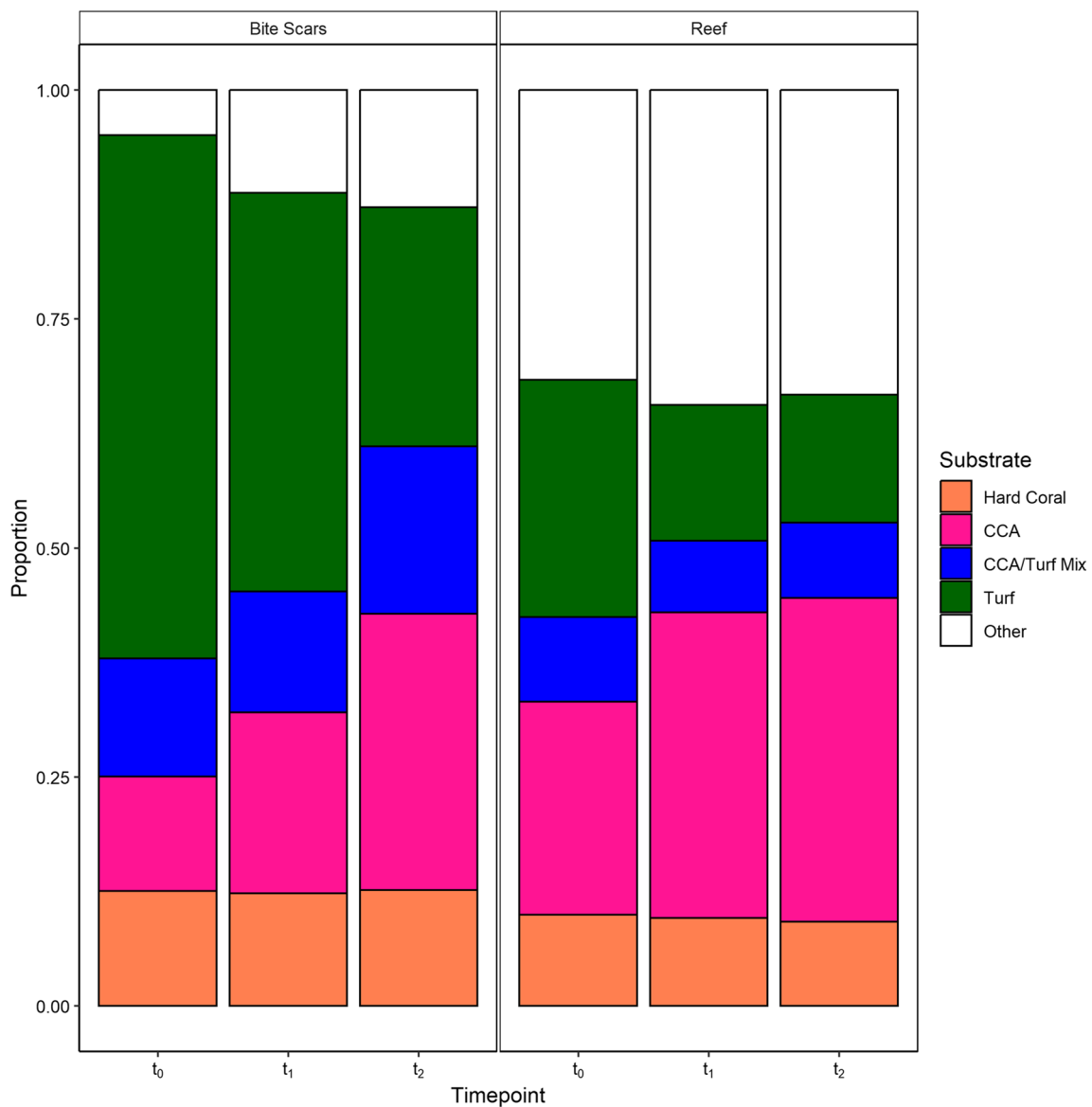

Fig. 6 Changes in community composition of all bite scars and random points across the survey period

year or less. Further, we found that bites on algal functional groups (turf algae, mixed CCA/turf algae and CCA) tended to transition more to CCA after a year than to other groups. As has been observed in other studies (Hamilton et al. 2014; Kelly et al. 2016), we found that parrotfish bites were found more frequently on turf algae covered substrate than would be expected based upon the abundance of this substrate type across the reefscape-indicating selectivity. We found statistically significant differences between the fates of parrotfish bite scars and the fates of randomly sampled points across the reefscape. Benthic change on random points starting on algal groups (i.e., turf algae, mixed CCA/turf algae, CCA) most consistently transitioned to CCA. However, the growth of benthic organisms within bite scars initially on algal functional groups showed primary colonization of fast-growing turf algae which progressed toward CCA colonization at the end of the third time point, a year after the grazing scars were identified.

The observed trajectories of succession within bite scars support as the premise that parrotfish grazing helps to enhance or maintain dominance by benthic reef builders (CCA and hard corals) that has been suggested and observed in previous studies (Littler and Littler 1984; Hixon and Brostoff 1996; Mumby 2006; Burkepile and Hay 2010; Ceccarelli et al. 2011). As a result, the parrotfish community at Palmyra may indirectly facilitate coral recruitment by enhancing CCA cover and mediating competition between fleshy macroalgae, turf algae, and other taxa rather than by directly opening settlement substrate for coral larvae.

We show that all major benthic functional groups (hard coral, CCA, encrusting macroalgae) aside from upright macroalgae are subject to the scraping and excavating activities of parrotfish grazing. However, turf algae covered substrata and mixed CCA/turf algae were the only benthic functional groups that was preferentially selected for as has been observed elsewhere (Hamilton et al. 2014; Kelly et al. 2016). As with other studies of parrotfish grazing, we found no evidence that parrotfish bite scars were disproportionately found on hard corals across the reef (Hoey and Bellwood 2008; Mumby 2009; Adam et al. 2015). Interestingly, it has been suggested that some parrotfish grazing on coral may not reflect active selectivity for corals, but rather a side effect as parrotfishes seek access to endolithic algae or other boring organisms growing inside coral colonies to meet nutritional requirements to support growth (Choat et al. 2002; Rotjan and Lewis 2005; Clements et al. 2017). Further, bite scars on non-turf algae covered substrata may be the result of having a diverse parrotfish community (Hamilton et al. 2014; 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).

Exposure of reef carbonate by parrotfish grazing has been proposed to facilitate coral recruitment by providing bare space or microhabitats into which larval corals can settle with reduced competition with other benthic organisms (Bellwood and Choat 1990; Steneck et al. 2014) or protection from incidental grazing (Arnold et al. 2010). Interestingly, while it is possible that some corals might have settled into our bite scars between sampling events, of the 2150 bites tracked over the course of one year in the present study, we observed only one successful coral recruitment event and found no dead recruits inside any of the bite scars. Limited coral recruitment to the bare space created by bite scars may be the result of rapid, complete recolonization (> 2 weeks) by turf algae (Bonaldo and Bellwood 2009; Sandin and McNamara 2012). However, as bite scars frequently transitioned to CCA over the course of the study, our results suggest that the CCA growth or recruitment into bite scars may provide enhanced settlement space for corals (Harrington et al. 2004; Price 2010). Ultimately, the level of recruitment we observed within bite scars at Palmyra atoll does not support a hypothesis of frequent coral recruitment into these areas.

We found 95.9% of bite scars on live coral tissue healed within the 12 months of our study. The observed recovery of live coral tissue into parrotfish bites occurred only on established, massive and sub-massive colonies of *Porites* spp*., Goniastrea stelligera* and *Pavona* spp.. While these taxa are known to be preferred for parrotfish grazing (Bonaldo and Bellwood 2011; Bonaldo et al. 2011), they have also been identified as having stress-tolerant life history strategies (Darling et al. 2012). Previous research suggests that repeated and intense grazing by parrotfish on corals can cause partial to complete coral mortality and limit colony growth (Rotjan et al. 2006; Hoey and Bellwood 2008; Bonaldo and Bellwood 2011; McCauley et al. 2014; Welsh et al. 2015). However, more recent work has shown certain stress-tolerant corals are able to survive most routine parrotfish grazing events (Rempel et al. 2020). Therefore, the majority of targeted colonies observed in our study may have long histories of parrotfish grazing and recovery (Rotjan and Lewis 2005; Welsh et al. 2015). The observations of coral mortality following grazing events in other studies may be the result of other confounding effects such as the presence of local impacts such as pollution or sedimentation which may have further decreased coral health and fitness (Bonaldo et al. 2011; Zaneveld et al. 2016; Rice et al. 2019; Rotjan et al. 2022).

Differences in changes within parrotfish bite scars relative to randomly sampled locations across the reef suggest that parrotfish grazing promotes the abundance of CCA and/or mixed communities of CCA and turf algae. We found

evidence that parrotfish grazing provided opportunities for CCA colonization and growth with 18.5% and 16.5% of bites taken on turf algae becoming CCA and mixed CCA/ turf algae, respectively. We also observed an increase in the proportion of transitions to CCA on bite scars starting on turf algae from the first transition across the entire study with 32.9% and 22.9% of bites taken on turf becoming CCA and mixed CCA/turf algae, respectively. A similar increase in proportion of transitions to CCA was not observed in the randomly sampled points on turf algae (first transition: 31.8% points to CCA; overall: 35.6% to CCA) suggesting active succession inside bite scars following parrotfish grazing events (Fig. 5d). The relative stability of the proportion of transitions toward CCA on the random points is expected as random points largely reflect the general trajectory of the heavily calcified benthic community mediated in part by parrotfishes at Palmyra. Additionally, bites initially taken on CCA were able to regrow or return to CCA in the greatest proportion (51.5% of bites on CCA) by t_2, despite turf algae primarily being the first colonizer to bare space (Diaz-Pulido and McCook 2002). There were few cases (13 bite scars) of established corals expanding into the bare space inside bite scars where grazing may have maintained algal competitors in cropped, competitively inferior states (Barott et al. 2012). Overall, parrotfishes appear to be facilitating succession toward CCA growth over time as trajectories from bite scars become more similar to background community across the reef surveyed in this study.

Disturbed space from parrotfish grazing activity progressed from initial colonization by fast-growing turf algae toward an increasing proportion of CCA over the duration of this study. We propose that the trajectories of CCA colonization and growth following grazing disturbances are a reflection of a healthy, intact herbivore community present on Palmyra atoll (Littler and Littler 1984; Hamilton et al. 2014). Further, as parrotfishes seek out additional turf algae dominated grazing locations through time (Welsh and Bellwood 2012; Carlson et al. 2017), the successional pathway will likely progress toward a community dominated by CCA and corals (Littler and Littler 1984; Hixon and Brostoff 1996). However, high parrotfish abundances are likely necessary to facilitate succession from fleshy macroalgae and/or turf to CCA (Steneck et al. 2014; Mumby et al. 2021); therefore, the successional pathways observed here may only be characteristic of the role of parrotfishes in the maintenance of highly calcified reefs with similar local conditions (Smith et al. 2016). The use of spatially explicit time-series reconstructions of coral reefs provides a powerful complement to previous studies of the top-down influence of parrotfish grazing on coral reef benthic community structure.

References

Adam TC, Kelley M, Ruttenberg BI, Burkepile DE (2015) Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. Oecologia 179:1173–1185

Adam TC, Duran A, Fuchs CE, Roycroft MV, Rojas MC, Ruttenberg BI, Burkepile DE (2018) Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. Mar Ecol Prog Ser 597:207–220

Arnold SN, Steneck RS, Mumby PJ (2010) Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. Mar Ecol Prog Ser 414:91–105

Barott KL, Williams GJ, Vermeij MJA, Harris J, Smith JE, Rohwer F, Sandin SA (2012) Natural history of coral-algae competition across a gradient of human activity in the Line Islands. Mar Ecol Prog Ser 460:1–12

Belliveau SA, Paul VJ (2002) Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. Mar Ecol Prog Ser 232:105–114

Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Environ Biol Fish 28:189–214

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol Lett 6:281–285

Bellwood DR, Hoey AS, Ackerman JL, Depczynski M (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Glob Chang Biol 12:1587–1594

Bellwood DR, Hoey AS, Hughes TP (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proc R Soc B Biol Sci 279:1621–1629

Bonaldo RM, Bellwood DR (2008) Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia. Mar Ecol Prog Ser 360:237–244

Bonaldo RM, Bellwood DR (2009) Dynamics of parrotfish grazing scars. Mar Biol 156:771–777

Bonaldo RM, Bellwood DR (2011) Parrotfish predation on massive Porites on the Great Barrier Reef. Coral Reefs 30:259–269

Bonaldo RM, Krajewski JP, Bellwood DR (2011) Relative impact of parrotfish grazing scars on massive Porites corals at Lizard Island, Great Barrier Reef. Mar Ecol Prog Ser 423:223–233

Bonaldo RM, Hoey AS, Bellwood DR (2014) The Ecosystem roles of parrotfishes on tropical reefs. Oceanogr Mar Biol Annu Rev 52:81–132

Brainard R, Maragos J, Schroeder R, Kenyon J, Vroom P, Godwin S, Hoeke R, Aeby G, Moffitt R, Lammers M, Gove J, Timmers M, Holzwarth S, Kolinski S (2005) The State of Coral Reef Ecosystems of the U.S. Pacific Remote Island Areas. State Coral Reef Ecosyst United States Pacific Free Assoc States 2005. Honolulu: NOAA Technical Memorandum NOS NCCOS. pp. 338–372

Bruggemann JH, Van Kessel AM, Van Rooij JM, Breeman AM (1996) Bioerosion and sediment ingestion by the caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode and habitat use. Mar Ecol Prog Ser 134:59–71

Burkepile DE (2012) Context-dependent corallivory by parrotfishes in a Caribbean reef ecosystem. Coral Reefs 31:111–120

Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128–3139

Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proc Natl Acad Sci U S A 105:16201–16206

Burkepile DE, Hay ME (2010) Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. PLoS ONE 5(1):e8963

Burns JHR, Delparte D, Gates RD, Takabayashi M (2015) Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. PeerJ 2015:e1077

Burns JHR, Delparte D, Kapono L, Belt M, Gates RD, Takabayashi M (2016) Assessing the impact of acute disturbances on the structure and composition of a coral community using innovative 3D reconstruction techniques. Methods Oceanogr 15–16:49–59

Carlson PM, Davis K, Warner RR, Caselle JE (2017) Fine-scale spatial patterns of parrotfish herbivory are shaped by resource availability. Mar Ecol Prog Ser 577:165–176

Ceccarelli DM, Jones GP, McCook LJ (2011) Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. J Exp Mar Bio Ecol 399:60–67

Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models.Ecology 64:1297–1304. https://doi.org/10.2307/1937838

Choat JH, Clements KD, Robbins WD (2002) The trophic status of herbivorous fishes on coral reefs 1: dietary analyses. Mar Biol 140:613–623

Clements KD, German DP, Piché J, Tribollet A, Choat JH (2017) Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. Biol J Linn Soc 120:729–751

Cramer KL, O'Dea A, Clark TR, Zhao JX, Norris RD (2017) Prehistorical and historical declines in Caribbean coral reef accretion rates driven by loss of parrotfish. Nat Commun 8:14160

Darling ES, Alvarez-Filip L, Oliver T, Mcclanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. Ecol Lett 15:1378–1386

Davis K, Carlson PM, Bradley D, Warner RR, Caselle JE (2017) Predation risk influences feeding rates but competition structures space use for a common Pacific parrotfish. Oecologia 184:139–149

Diaz-Pulido G, McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. Mar Ecol Prog Ser 232:115–118

Edwards CB, Eynaud Y, Williams GJ, Pedersen NE, Zgliczynski BJ, Gleason ACR, Smith JE, Sandin SA (2017) Large-area imaging reveals biologically driven non-random spatial patterns of corals at a remote reef. Coral Reefs 36:1291–1305

Ferrari R, Bryson M, Bridge T, Hustache J, Williams SB, Byrne M, Figueira W (2016) Quantifying the response of structural complexity and community composition to environmental change in marine communities. Glob Chang Biol 22:1965–1975

Fox MD, Carter AL, Edwards CB, Takeshita Y, Johnson MD, Petrovic V, Amir CG, Sala E, Sandin SA, Smith JE (2019) Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific. Coral Reefs 38:701–712

Hamilton SL, Smith JE, Price NN, Sandin SA (2014) Quantifying patterns of fish herbivory on Palmyra Atoll (USA), an uninhabited predator-dominated central Pacific coral reef. Mar Ecol Prog Ser 501:141–155

Harrington L, Fabricius K, De G, Negri A (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. America (NY) 85:3428–3437

Hay ME, Taylor PR (1985) Competition between herbivourous fishes and urchins on Caribbean reefs. Oecologia 65:591–598

Hixon MA, Brostoff WN (1996) Succession and herbivory: effects of differential fish grazing on hawaiian coral-reef algae. Ecol Monogr 66:67–90

Hoey AS, Bellwood DR (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. Coral Reefs 27:37–47

Jayewardene D, Donahue MJ, Birkeland C (2009) Effects of frequent fish predation on corals in Hawaii. Coral Reefs 28:499–506

Kelly ELA, Eynaud Y, Clements SM, Gleason M, Sparks RT, Williams ID, Smith JE (2016) Investigating functional redundancy versus complementarity in Hawaiian herbivorous coral reef fishes. Oecologia 182:1151–1163

Kodera SM, Edwards CB, Petrovic V, Pedersen NE, Eynaud Y, Sandin SA (2020) Quantifying life history demographics of the scleractinian coral genus Pocillopora at Palmyra Atoll. Coral Reefs 39:1091–1105

Lechowicz MJ (1982) The sampling characteristics of electivity indices. Oecologia 52:22–30

Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol Monogr 56:183–200

Littler MM, Littler DS (1984) Models of tropical reef biogenesis: the contribution of algae. Prog Phycol Res 3:323–364

McCauley DJ, Young HS, Guevara R, Williams GJ, Power EA, Dunbar RB, Bird DW, Durham WH, Micheli F (2014) Positive and negative effects of a threatened parrotfish on reef ecosystems. Conserv Biol 28:1312–1321

McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19:400–417

Mumby PJ (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecol Appl 16:747–769

Mumby PJ (2009) Herbivory versus corallivory: are parrotfish good or bad for Caribbean coral reefs? Coral Reefs 28:683–690

Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, Blackwell PG (2007) Trophic cascade facilitates coral recruitment in a marine reserve. Proc Natl Acad Sci U S A 104:8362–8367

Mumby PJ, Steneck RS, Roff G, Paul VJ (2021) Marine reserves, fisheries ban, and 20 years of positive change in a coral reef ecosystem. Conserv Biol 35(5):1–11

Nash KL, Graham NAJ, Januchowski-Hartley FA, Bellwood DR (2012) Influence of habitat condition and competition on foraging behaviour of parrotfishes. Mar Ecol Prog Ser 457:113–124

Nicholson GM, Clements KD (2020) Resoling resource partitioning in parrotfishes (Scarini) using microhistory of feeding substrata. Coral Reefs 39:1212–1327

Nicosevici T, Gracias N, Negahdaripour S, Garcia R (2009) Efficient three-dimensional scene modeling and mosaicing. J F Robot 26:759–788

Ogden JC, Lobel PS (1978) The role of herbivorous fishes and urchins in coral reef communities. Environ Biol Fishes 3:49–63

Pedersen NE, Edwards CB, Eynaud Y, Gleason ACR, Smith JE, Sandin SA (2019) The influence of habitat and adults on the spatial distribution of juvenile corals. Ecography (cop) 42:1703–1713

Petrovic V, Vanoni DJ, Richter AM, Levy TE, Kuester F (2014) Visualizing high resolution three-dimensional and two-dimensional data of cultural heritage sites. Mediterr Archaeol Archaeom 14:93–100

Price N (2010) Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. Oecologia 163:747–758

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rempel HS, Bodwin KN, Ruttenberg BI (2020) Impacts of parrotfish predation on a major reef-building coral: quantifying healing rates and thresholds of coral recovery. Coral Reefs 39:1441–1452

Rice MM, Ezzat L, Burkepile DE (2019) Corallivory in the anthropocene: interactive effects of anthropogenic stressors and corallivory on coral reefs. Front Mar Sci 5:1–14

Robinson JPW, Williams ID, Yeager LA, McPherson JM, Clark J, Oliver TA, Baum JK (2018) Environmental conditions and herbivore biomass determine coral reef benthic community composition: implications for quantitative baselines. Coral Reefs 37:1157–1168

Rotjan RD, Lewis SM (2005) Selective predation by parrotfishes on the reef coral Porites astreoides. Mar Ecol Prog Ser 305:193–201

Rotjan RD, Dimond JL, Thornhill DJ, Leichter JJ, Helmuth B, Kemp DW, Lewis SM (2006) Chronic parrotfish grazing impedes coral recovery after bleaching. Coral Reefs 25:361–368

Rotjan RD, Ray NE, Cole I, Castro KG, Kennedy BRC, Barbasch T, Lesneski KC, Lord KS, Bhardwaj A, Edens M, Karageorge I, Klawon C, Kruh-Needleman H, McCarthy G, Perez R, Roberts C, Trumble IF, Volk A, Torres J, Morey J (2022) Shifts in predator behaviour following climate induced disturbance on coral reefs. Proc R Soc B Biol Sci 289:20221431

Russ GR, Questel SLA, Rizzari JR, Alcala AC (2015) The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. Mar Biol 162:2029–2045

Ruttenberg BI, Adam TC, Duran A, Burkepile DE (2019) Identity of coral reef herbivores drives variation in ecological processes over multiple spatial scales. Ecol Appl 29:1–16

Sandin SA, McNamara DE (2012) Spatial dynamics of benthic competition on coral reefs. Oecologia 168:1079–1090

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the Northern Line Islands. PLoS ONE 3:e1548

Sandin SA, Edwards CB, Pedersen NE, Petrovic V, Pavoni G, Alcantar E, Chancellor KS, Fox MD, Stallings B, Sullivan CJ, Rotjan RD (2020) Considering the rates of growth in two taxa of coral across Pacific islands. Adv Mar Biol 87:167–191

Shantz AA, Ladd MC, Burkepile DE (2020) Overfishing and the ecological impacts of extirpating large parrotfish from Caribbean coral reefs. Ecol Monogr 90:1–17

Smith JE, Hunter CL, Smith CM (2010) The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia 163:497–507

Smith JE, Brainard RE, Carter AL, Grillo S, Edwards CB, Harris J, Lewis LS, Obura D, Rohwer F, Sala E, Vroom PS, Sandin SA (2016) Re-evaluating the health of coral reef communities: baselines and evidence for human impacts across the central pacific. Proc R Soc B Biol Sci 283:1–9

Steneck RS, Arnold SN, Mumby PJ (2014) Experiment mimics fishing on parrotfish: insights on coral reef recovery and alternative attractors. Mar Ecol Prog Ser 506:115–127

Steneck RS (1988) Herbivory on coral reefs: A synthesis. Proc 6th Int Coral Reef Symp 37–49

Streit RP, Cumming GS, Bellwood DR (2019) Patchy delivery of functions undermines functional redundancy in a high diversity system. Funct Ecol 33:1144–1155

Torres-Pulliza D, Dornelas MA, Pizarro O, Bewley M, Blowes SA, Boutros N, Brambilla V, Chase TJ, Frank G, Friedman A, Hoogenboom MO, Williams S, Zawada KJA, Madin JS (2020) A geometric basis for surface habitat complexity and biodiversity. Nat Ecol Evol 4:1495–1501

Van Veghel MLJ, Bak RPM (1994) Reproductive characteristics of the polymorphic Caribbean reef building coral Montastrea annularis. 3.Reproduction in damaged and regenerating colonies. Mar Ecol Prog Ser 109:229–234

Vanderploeg HA, Scavia D (1979) Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecol Model 7:135–149

Welsh JQ, Bellwood DR (2012) How far do schools of roving herbivores rove? A case study using Scarus rivulatus. Coral Reefs 31:991–1003

Welsh JQ, Bonaldo RM, Bellwood DR (2015) Clustered parrotfish feeding scars trigger partial coral mortality of massive Porites colonies on the inshore Great Barrier Reef. Coral Reefs 34:81–86

Westoby MJ, Brasington J, Glasser NF, Hambrey MJ, Reynolds JM (2012) "Structure-from-Motion" photogrammetry: a low-cost, effective tool for geoscience applications. Geomorphology 179:300–314

Williams GJ, Gove JM, Eynaud Y, Zgliczynski BJ, Sandin SA (2015) Local human impacts decouple natural biophysical relationships on Pacific coral reefs. Ecography (cop) 38:751–761

Zaneveld JR, Burkepile DE, Shantz AA, Pritchard CE, McMinds R, Payet JP, Welsh R, Correa AMS, Lemoine NP, Rosales S, Fuchs C, Maynard JA, Thurber RV (2016) Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nat Commun 7:11833