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Resource Availability Drives Large Differences in the Fine-Scale Spatial Pattern of
Parrotfish Herbivory on a Coral Reef

A Thesis submitted in partial satisfaction of the

requirements for the degree Master of Arts

in Ecology, Evolution & Marine Biology

by

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March 2016

The thesis of Peter Miles Carlson is approved.

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ABSTRACT

Resource Availability Drives Large Differences in the Fine-Scale Spatial Pattern of Parrotfish Herbivory on a Coral Reef

By

Peter Miles Carlson

Herbivory by fishes and sea urchins is a powerful mechanism on coral reefs that mitigates coral-algal competition by physically removing algae and creating bare space. The fine-scale spatial patterning of herbivory has the potential to foster coral recruitment by creating a spatially continuous refuge for coral settlement and survival. The temporal nature of grazing also has the potential to influence competitive outcomes between coral and algae by preventing algal dominance and consistently exposing bare substrate at a particular location. Here we explore the intraspecific variability in the fine-scale feeding behavior of a large, mobile coral reef herbivore on a small, pristine Central Pacific atoll. We document how two different resource regimes appear to drive differences in the social structure and the spatial and temporal feeding behavior of the Steephead Parrotfish, *Chlorurus microrhinos*. We report that feeding behavior is spatially focused when resources are abundant and regrow quickly, resulting in dense patches of bite scars (>100 bites m^{-2}). There also appears to be a temporal periodicity to feeding behavior when resource are abundant and predictable, although our study duration did not allow for the precise timing between feeding bouts to be detected. We found that movement increases and feeding

behavior is distributed sparsely across food patches when resources were scarce and recovered more slowly. The differences we report here occur at sites that are only a few kilometers away from one another, but result in dramatically different impacts to the benthos that could alter the survival of corals at their earliest life stages.

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INTRODUCTION

Coral reefs are one of the most diverse marine ecosystems on the planet and provide countless ecosystem goods and services for people throughout the world. These services do not come without costs and decades of anthropogenic pressure from overfishing, pollution, and physical habitat destruction have left many of the world's coral reefs in decline (Hughes 1994, Jackson et al. 2001, Bellwood et al. 2012). Additionally, natural disturbances such as coral disease, hurricanes, bleaching events and predator outbreaks augment the stressors facing coral reefs today (Nystrom et al. 2000, Adam et al. 2011). Declining or dead reefs are often characterized by an abrupt regime shift from calcifying, reef-building corals to large stands of macroalgae and dense mats of algal turf. Reefs that are dominated algae lack the natural diversity that underpins the ecosystem services that humans rely on (Moberg & Folke 1999). After years of documenting declines, coral reef research has begun to focus on understanding reef resilience and resistance, that is, what factors influence a reef's ability to withstand and recover from human and natural disturbances alike (Graham et al. 2006, Mumby et al. 2006, Norström et al. 2009). A central topic in coral reef resilience research has been the competitive balance between coral and algae and the factors that mediate that balance (Hughes & Tanner 2000, Edmunds & Carpenter 2001, Bellwood et al. 2004, Vermeij et al. 2009). On reefs that have undergone macroalgal phase shifts, factors such as poor water quality, limited coral larval supply, and coral disease have been suggested as reasons why competition often favors algal growth (Hughes & Tanner 2000, Fabricius et al. 2005, Aronson & Precht 2006).

Among the various explanations, the most well documented mechanism has been depletions in herbivore biomass (Hughes 1994, Cheal et al. 2010, Jackson et al. 2014).

Herbivory on coral reefs is primarily carried out by sea urchins and fishes (such as parrotfish and surgeonfish) (Carpenter 1986) and is a powerful mechanism in altering the competitive advantage in favor of the growth and recruitment of corals through the direct removal of algal turf and macroalgae (Bellwood et al. 2004, Mumby 2006, Bonaldo et al. 2014). Studies have shown that phase shifts to macroalgae have been correlated with declines in parrotfish abundance and sea urchin die-offs due to disease(Hughes 1994). A comprehensive review of the status and trends of Caribbean coral reefs concluded that the removal of herbivores, particularly parrotfish, resulted in a region-wide decline in coral cover on Caribbean reefs(Jackson et al. 2014). Large and small-scale herbivore exclusion experiments have resulted in increased algal cover compared to their grazed counterparts (Hughes et al. 2007, McCauley et al. 2010, Adam et al. 2011). There is also evidence that calcium carbonate space exposed by the physical impact of parrotfish feeding promotes coral settlement(Mumby et al. 2007). This feeding also creates micro-habitats that could potentially foster the settlement and growth of new corals. All of this evidence supports the idea that the removal of parrotfish by fishing enables the establishment of macroalgae. If macroalgae do become predominate on reefs, it may be difficult to reverse the trajectory back to a coral-dominated state (Mumby 2009).

Despite correlative and experimental evidence for the control of algae by herbivores, there is also evidence that suggests that this relationship might be too simplistic of a view of reef dynamics (Cote et al. 2013, Adam et al. 2015, Smith et al. 2016). Competitive interactions

between corals and algae are complex and the presence and/or protection of herbivores does not guarantee the cascading effects that result in the increase, recovery, or resilience of corals (Ledlie et al. 2007, Sandin et al. 2008a, Cheal et al. 2010, Carassou et al. 2013). Similarly, reductions in herbivore biomass, particularly parrotfishes, do not necessarily result in a macroalgal phase shift (Russ et al. 2015). Furthermore, the majority of studies supporting the control of macroalgae by parrotfish come primarily from the Caribbean (Hughes 1994, Jackson et al. 2014) and it appears this relationship may not be as strong in other oceans (Bruno et al. 2009).

Macroalgal phase shifts are not as prevalent on Indo-Pacific reefs as in the Caribbean and it appears that in this region the abundance of low lying, fleshy algal turfs may be a more appropriate indicator of reef health(Bruno et al. 2009, Smith et al. 2016). Algal turfs (generally <2cm tall) are being recognized as a stable benthic state (Jouffray et al. 2015, Smith et al. 2016) that inhibits the recruitment of calcifying, reef building organisms. Algal turfs are usually the first to colonize bare space (Bonaldo & Bellwood 2009) and have been shown to inhibit coral settlement and survivorship through various processes (McCook et al. 2001, Vermeij & Sandin 2008, Vermeij et al. 2009). Research from pristine reefs in the Central Pacific has shown that even in remote regions with minimal human impacts (i.e., fishing and nutrient inputs), coral-algal competition is strong and that algal turfs are fierce space competitors that can kill living coral tissue (Sandin et al. 2008b, Barott et al. 2009).

Herbivores that target algal turfs are hypothesized to be important agents that can reduce turf abundance and indirectly promote coral recruitment, growth, and survival (Ceccarelli et al. 2011). Many parrotfish appear to target algal turfs as a large proportion of their diet

(Hamilton et al. 2014), and their method of feeding can expose bare calcium carbonate structure on the reef (Bellwood & Choat 1990). Studies have shown that parrotfish abundance can respond positively to sudden increases in algal turf, and that this is a potentially powerful behavioral response that inhibits the proliferation of algae post-disturbance (Adam et al. 2011, Gilmour et al. 2013, Tootell & Steele 2015). A long-term study of population dynamics in the Philippines showed parrotfish populations appear to track differences in benthic composition and that the nature of benthic resources can predict parrotfish abundance (Russ et al. 2015). If parrotfish are indeed necessary for reef resilience and recovery, these findings are positive because herbivores are able respond to sudden increases in algal turfs and thus may be able to ameliorate the negative effects of turf algae on the earliest life stages of settling corals.

Currently, it is not well understood how the nature of how resource-induced responses in parrotfish behavior and distribution affect the spatial and temporal patterns of algal removal and the creation of bare space. Specifically, the degree to which fine-scale foraging behavior changes when preferred resources are abundant compared with when they are rare has not been documented. As implied above, there is potential for the spatial patterning of feeding by an herbivore to influence coral-algal competition and, thus the trajectory of a reef's benthic state (Sandin & McNamara 2011). Spatially constrained foraging results in dense clusters of bite scars (i.e., bare space) within a foraging territory. Conversely, homogenous foraging results in single bite scars that are uniformly distributed, isolated, and immediately abutting algal turfs or other space competitors on all sides. When modeled through time these contrasting spatial patterns of foraging behavior have different

outcomes: spatially constrained grazing was predicted to be more beneficial to the long term growth and recruitment of corals. The dense patches of bite scars created by spatially constrained grazing alleviated the competitive pressure of invading algal turfs on coral recruits.

In this study we examine how two different algal resource regimes alter the fine-scale foraging strategies of a single species of excavating parrotfish, *Chlorurus microrhinos,* on a remote Central Pacific atoll. We asked whether differences in the abundance and growth of a preferred food source (algal turf) altered the spatial and temporal patterns of feeding, using direct observations of fish foraging behaviors and space use. We also monitoring the spatial and temporal distribution of bite scars across the benthos under these different conditions. We collected data across two different resource regimes; one with high availability and fast regrowth rate of a preferred food source, and the other with low availability and slow regrowth of the same resource. We found notable differences in the fine-scale foraging strategies of *C. microrhinos* between these two resource regimes, leading to dramatic differences in the temporal and spatial patterns of algal removal and the creation of bare space.

METHODS

Mixed Algal Turf Classification

The term algal turf is a broad classification that includes a diverse assemblage of filamentous algae, detritus, and cyanobacteria and is often referred to as epilithic algal

matrix (EAM) (Wilson et al. 2003, Smith et al. 2016). Algal turf assemblages are typically highly productive and quickly colonize dead coral skeletons (McCook et al. 2001). Many large excavating parrotfish show a preference for feeding on assemblages of mixed algal turfs (Hamilton et al. 2014)and, because of the nature of their feeding mode, remove the deal coral skeleton and the associated endolithic bacteria and detritus (Le Campion-Alsumard et al. 1995, Green et al. 2009, Charpy et al. 2012). For this study, we did not measure the exact species composition present in the EAM. Therefore we will be referring to this diverse group of short (<2cm) filamentous turfs as 'mixed algal turfs'.

Study Site

This study was conducted at Palmyra Atoll (5° 53' N, 162° 07' W) located in the remote Northern Line Islands chain (Fig 1). In 2001 Palmyra came under the protection of the US Fish and Wildlife Service and The Nature Conservancy and all non-scientific collection and fishing thereafter was prohibited. Decades prior to formal regulations, Palmyra's remoteness and lack of an indigenous population afforded it some level of protection. Palmyra provides a unique predator-dominated coral reef system with a high biomass of apex predators compared to other reefs in Line Island chain and around the world (Sandin et al. 2008b). Additionally, there is a high biomass of primary consumers, including large-bodied parrotfish, which are becoming increasingly rare on other Indo-Pacific reefs (Edwards et al. 2014). Palmyra's 'pristine' levels of predators and competitors provide rare insight into the factors driving the space use and feeding of an important coral reef herbivore.

In order to investigate the spatial patterns of foraging behavior, we selected two sites on Palmyra's extensive back reef habitat (Fig 1; Penguin Spit and Western Terrace). Penguin Spit (PS) is characterized by a high abundance of mixed algal turfs, while Western Terrace (WT) is dominated by hard corals and crustose coralline algae (CCA). Fish surveys from the two sites show that PS has a higher density and biomass of the target species, *Chlorurus microrhinos,* than WT. The sites were similar in their depth and rugosity.

Historical information on Palmyra's coral reefs is difficult to find prior to the establishment of a research facility in 2001. However, there is evidence for a mild bleaching event in 2009 following a larger event in 1998 that resulted in extensive coral mortality and appeared to affect the shallow Penguin Spit site particularly (Williams et al. 2010). The large amount of dead coral covered in mixed algal turfs compared to other sites around Palmyra suggest that Penguin Spit did undergo a major coral die off in its recent history (20 years) and may be in a stable algal turf state or a transitional state between coral and algal dominance.

Study Species

The Steephead parrotfish, *Chlorurus microrhinos,* is a large bodied (TLmax = 70cm) parrotfish that is found throughout the Indo-Pacific. Their gape and strong jaw musculature allow them to excavate large sections (approx. 118 mm^2 area) of algae and dead coral with each bite (Bonaldo & Bellwood 2009, Green et al. 2009). Despite being widespread on Indo-Pacific reefs, threats such as subsistence spearfishing and habitat destruction are making them increasingly rare in some regions of their historical range.

As is common within the family Scaridae, *C. microrhinos* has two morphological phases, with an initial phase (IP) that includes male and female individuals, and a terminal phase (TP) that consists of larger males. TP males are visually distinguishable from IPs by the large hump on the head and they often dominate several IPs in a socially localized group or harem. TP males often compete with other TP males for territory and mates, leaving individuals with distinguishing scars and markings.

Fish Surveys

Fish community surveys: To characterize the entire fish community at each site, we conducted visual surveys during the summer of 2013 and 2014 using a belt transect method (n= 18 transects per site). Divers swam and recorded identity (to species), number, and the total length of each fish greater than 20cm TL in a 25 x 4m swath that extended to the surface. Upon completion of this 25m swath, the diver swam back along the same transect line and counted all fish less than 20cm TL in a 25 x2m swath extending to the surface. Fishes were later assigned to broad trophic categories (primary consumer, secondary consumer, planktivore, and piscivore) and total length was converted to biomass using trophic classifications and length-weight conversion factors compiled by the NOAA Coral Reef Ecosystem Division (Heenan et al. 2014).

To assess the differences in predation risk between the two sites, we calculated piscivore biomass (kg/m^2) for each transect as well as the mean for each. We log transformed biomass to improve the spread of the data and a student's t-test was used to test for significance.

Targeted C. microrhinos *surveys*: We conducted targeted *C. microrhinos* surveys three times at Penguin Spit and three times at Western Terrace during summer of 2014. Each survey consisted of six, 50m X 4m belt transects. Transect locations were not fixed between surveys, but the relative placement of transects was kept consistent in reference to a fixed boat mooring at each site. All transects were done by the same observer (KD) to ensure consistency. The observer recorded the number, total length, and color phase of all *C. microrhinos*. We calculated the density and biomass for each color phase at each site and calculated biomass as above.

We used targeted *C. microrhinos* survey data to assess the differences in conspecific competitor size and phase structure as a proxy for differences in the social structure at Penguin Spit and Western Terrace. We first compared the biomass for each phase between the two sites using the Welch's two sample t-test. We then compared the biomass between phases within a site using Welch's two sample t-test. We used this approach to assess whether the overall TP and IP biomass was different between sites and whether the relative TP to IP biomass was different within a particular site.

Benthic Surveys

We used a uniform point contact (UPC) technique to characterize the benthic community composition at each site. Points were located at 1m intervals along a 25m. At each site, in each of the two years (2013, 2014) we conducted eight transects for a total of 16 transects and 400 total benthic data points per site. At each point we recorded benthic cover, rugosity and depth. Benthic cover was recorded as one of nine categories; live coral, mixed algal turf, crustose coralline algae (CCA), *Halimeda* spp., *Lobophora* spp., Corallimorph,

bare, *Dictyosphaeria* spp, or fleshy macroalgae. The 'live coral' category included hard and soft corals. 'Mixed algal turf' is a nominal category that represents low lying (<2cm tall), fleshy, filamentous algae and cyanobacteria (*see above*). Larger algal species (>2cm) were categorized as 'fleshy macroalgae'. The 'bare' category represents areas that had recently been grazed leaving the calcium carbonate structure exposed. We measured rugosity at each point by measuring the change in depth between the highest and lowest point within a 1.0m x 0.5m box around the point.

We used benthic survey data to quantify and compare the availability of resources for *C. microrhinos* at Western Terrace and Penguin Spit. We calculated percent cover from the points on each transect, then calculated the mean percent cover for each site with standard error.

To test for differences in benthic assemblages at the site level, we used a multinomial approach to characterize the resources available. We plotted each benthic transect in multi-dimensional space, with each axis representing a cover category and the percent cover determining its position along that axis. Conceptually, plotting this way creates a cloud of points for Western Terrace and a cloud of points for Penguin Spit. The centroid of each cloud was calculated and the Euclidean distance between the centroid was computed. The Euclidean distance between centroids is a relative measure of differences in the benthic resources available for *C. microrhinos* at each site. A randomized resampling technique was then employed to develop a null distribution of Euclidean distances to test the observed data for significance. To do this, the site name was randomly assigned to each transect and the centroids and Euclidean distance between the randomly assigned clouds

was calculated. This process was repeated 10,000 times and used as the null distribution of Euclidean distances to test against the observed data. From the null distribution, a 95% confidence interval was calculated and if the observed data fell outside of that null 95% confidence interval, the resulting difference was considered significant.

Only the benthic categories that were observed in *C. microrhinos* diet were considered resources for this multinomial analysis (see Diet Preference below). We plotted each benthic transect (n =32) in 6–dimensional space according to the benthic categories (CCA, *Halimeda*, Live Coral, *Lobophora*, Bare, and Mixed Algal Turfs).

Mixed algal turf clustering and patch size: We analyzed the UPC transect data to detect differences in the spatial heterogeneity and patch size of mixed algal turfs between the two sites. We recorded the number of consecutive points of mixed algal turf for each benthic transect at Western Terrace and Penguin Spit as a proxy for patch size and calculated the distribution of these patch sizes for each site. The reported distributions include only non-zero values, including single, isolated points of mixed algal turf. We tested the distributions for the effect of site using the Wilcoxon rank-sum test in R.

Bite Composition Surveys

Diet selectivity: We quantified preference for each food type in the diet in relation to its availability in the environment. We performed timed bite composition surveys, on snorkel, that were between 5mins and 1hr long. We recorded a total of 5,669 bites taken by 11 individuals at Western Terrace and 13 individuals at Penguin Spit. We pooled bite data by site and we calculated the proportion of bites on a particular substrate type.

We calculated the diet preference for all substrate types that we observed fish feeding on during the targeted bite composition surveys (mixed algal turfs, CCA, live coral, *Halimeda*, *Lobophora,* and bare) using Manly's Alpha of selectivity (Chesson 1983) as follows:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j} \quad i = 1, ..., m$$

Where r_i is the proportion of bites on substrate type i to m *(m= 6 in this case)*. The proportion of substrate-specific bites is then divided by the proportion, n, of substrate i available for consumption. Site specific α's were calculated for each substrate present in the diet. We used the null index of $\alpha = 0.1667$, representing equal preference for the 6 substrate categories. Values significantly greater than the null index indicate a preference and values significantly lower than the null index indicate an 'avoidance' of a particular substrate. Values not significantly different from the null index indicate 'no preference' for a particular substrate.

We constructed confidence intervals around the null index using a randomized process that represented uniform feeding across all substrates. In the randomization, we allowed bites to occur on any one of the 6 substrates, with the probability of a bite occurring on a particular substrate equal to its observed proportion in the environment. We calculated the randomized Manly's alpha for each substrate and repeated the process 10,000 times. We calculated the 95% confidence intervals around the null index ($\alpha = 0.166$) from the resulting distributions and used them as the threshold value indicating a significant preference, avoidance, or no preference for a particular substrate.

Spatial and Temporal Patterns of Bite Scars

Spatial trends in bite scars between sites: To assess the nature of bite scar patterning across space we placed a 0.5m x 0.5m quadrat at each point along a benthic transect (described above, UPC methods) and counted the number of fresh (2-3 days old) bite scars from *C. microrhinos*. *Chlorurus microrhinos* was the most common large excavating parrotfish observed at each site and their feeding scars were easily distinguishable from other parrotfishes because of the scar's depth and length. We converted the bite scar counts to a bite scar density and reported the bites/m^2. We tested for significant site effect in the observed bite density distributions using a Wilcoxon rank sum test in R.

Temporal trends in bite scars between sites: To track bite scar patterns across time we tracked the origination of new bite scars on designated dead coral heads using a 2-month photo time series. We first identified coral heads on which *C. microrhinos* bite scars were present and mapped their locations so they could relocated. We tracked each coral head for 2 months, taking a photograph every 4-5d to document the appearance of new bite scars. Our sampling included fifteen coral heads at Penguin Spit and eleven coral heads at Western Terrace. We recorded new bite scars and followed them through time using simple image analysis techniques. We derived bite density calculations from prescribed area boundaries on the photos that were consistent throughout the study. We took care not to over/under estimate the area tracked through time and only included new bite scars in the bite density calculation. For more information about the photography and image analysis see appendix section 1.

We plotted the bite scar density through time and measured the number of days between 'peaks' of bite density. We defined a 'peak' in bite density as any case where the absolute value of the difference between the time point and the preceding and/or the following time point was greater than the mean value of all bites recorded for that photo plot. This definition identified times when heavy feeding had either just started or had just stopped.

We calculated the variance in bite scar density for each photo plot and pooled the data by site as a measure of consistency in bite scar density over time. A high variance in bite scar density is evidence of a more periodic foraging pattern that consists of episodes of high feeding followed by periods of no feeding. A low variance in bite scar density indicates a more homogenous foraging pattern across time. We log transformed and categorized the variances by site and used student's-t test to test for a significance difference between sites.

Artificial bite scar recovery rate: We measured the bite scar recovery (turf regrowth) rates over 14d during September 2015. Access to the study site at Western Terrace was prevented because of large swell, so we selected the nearest site possible (less than 500m from Western Terrace) that had a similar depth profile and similar benthic cover. A single observer (PC) etched artificial bite scars into dead coral heads covered in mixed algal turfs to the approximate dimensions, 0.66cm x 3.3cm, for approximately 2.00 cm^2 bare area. We made three sets of three parallel scars (for a total of nine scars) on each coral head and caged them within one 0.5m X 0.5m cage. There were a total of five cages at each site, each containing three groups of scars for a total of 15 groups of scars per site. Cages were designed to exclude large excavating parrotfish such as *C. microrhinos* so that recovery could be measured without further grazing. We took photos of each group of scars

immediately after etching (day zero) and every two days after with a Canon G15 digital camera set to 'underwater' mode inside an underwater housing. We placed a 5cm measuring tape directly next to the group of scars and the tape was pressed flush against the benthos for each photo so that accurate area measurements could be made for each scar using image analysis software.

We adapted image analysis techniques to track the recovery of mixed algal turf within the artificial scars by comparing the color of the scar to the color of the surrounding, undisturbed mixed algal turf. We calculated an Earth Mover Distance (EMD) cost (Rubner et al. 2000, Andoni et al. 2008) to compare the pixel intensity histograms (i.e. grey scale color values) of the recovering scar and the undisturbed mixed algal turf immediately adjacent to the scar. Larger EMD costs values indicate a greater difference between the artificial scar and the surrounding turf (i.e., less recovered). For more information on the pixel intensity histogram calculation, EMD cost theory, the EMD calculation, and the error and correction calculation associated with this approach, see appendix section 2. All EMD values used for analysis include the error correction that was calculated for each photo.

We tested the EMD values at day 6 and day 12 at Penguin Spit and Western Terrace for significance between sites and days using a linear mixed effects model. We used this model to account for the lack of independence of data because each 0.5 X 0.5m cage contained three groups of artificial scars. With cage denoted as a random effect, nested within site, we tested for a significant site effect. To attain a probability (p-value) of a difference between sites, we compared the full model (with a site effect) and the reduced model (without a site effect). We ran a Likelihood ratio test between the full and reduced

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model using the 'anova' function in R and report the resulting p-value as the likelihood that EMD values are different between Western Terrace and Penguin Spit. We calculated the least squares means for both sites using the 'lsmeans' package and 'ref.grid' function in R to estimate the magnitude and direction of the difference between sites.

The adjusted EMD values were also used to estimate the percentage recovered by day 6 and day 12 using the following equation, where d is the day and 0 is the day zero EMD value:

$$\frac{(EMD_0 - EMD_d)}{(EMD_0)}$$

Focal Animal Follows

We identified individual TP *C. microrhinos* by their unique coloring, specific markings, and distinguishable scars (e.g. missing scales and cut fins). We consistently relocated five TP individuals at each site from July to September 2014 for repeated 2h spatial follows. During each focal follow, the location of the fish was recorded every 5 seconds on a Garmin GPSMap 78sc handheld GPS, set to 'track' mode. The GPS unit was secured to a float with a waterproof case carried by the snorkeler. Each observer synchronized their wristwatch with satellite time on the GPS before every trial. Upon entering the water, the snorkeler located, identified and observed an individual *C. microrhinos* for 3-5 minutes before starting the trial to ensure that the fish was unaffected by their presence. If the individual *C. microrhinos* was behaving normally (e.g. feeding, defending territory), the observer would begin a 2h following bout. In most cases, fish were unaffected within a minute of the snorkeler's presence.

Once the trial begun, the snorkeler positioned the GPS float over the focal fish or as close as possible without disrupting their behavior (usually <1m). Then the observer recorded the start time and end time of each activity. We categorized activity into feeding, territorial defense, defecating, cleaning, and swimming. After the trial was complete, observer downloaded the spatial point data from the GPS and categorized each point into one of the five activities. We complete a total of 57 2h trials, 29 from Penguin Spit and 28 at Western Terrace.

Patterns of Space Use

We used the 2h focal follow data to characterize the movement, space use, and foraging behavior of *C. microrhinos* at Western Terrace and Penguin Spit. We calculated all spatial data metrics in the Geospatial Modeling Environment (GME) 0.7.3.0 platform that interacts with the open source statistical software R version 3.1.0.

95% kernel utilization distribution: We calculated the 95% Kernel Utilization Distribution (KUD) space use metric for each 2h trial; the area calculated represents the space used during that 2h follow. The 95% KUD is a common space use metric that calculates the 95% probability that an animal will be found in a given area (Steury et al. 2010, Welsh & Bellwood 2012). Details about the parameters and protocol that we used to calculate the 95% KUD can be found in appendix 3. We refer to the 2h 95% KUD area as the '2h area'.

Pathway length: To compare the foraging behavior of *C. microrhinos* between Penguin Spit and Western Terrace, we measured the distance an individual fish swam ('pathway length') during each 2h GPS track. Within the GME platform, we used the 'pathmetrics'

tool to calculate the distance between each successive point (every five seconds) and we summed those distances to estimate the distance swam in one 2h period.

Site fidelity: We calculated the centroid (center position) of every 2h trial and measured the distances between all centroids for an individual to quantify the site fidelity of each fish. Smaller inter-centroid distances indicate a higher site fidelity while larger values indicate greater movement between trials, indicating less site fidelity. Each site fidelity value was divided by the average 2h area for each individual fish so that we could control for the overall area.

Estimating the amount of mixed algal turf within the two hour area: We were not able measure the benthic composition (i.e., resource availability) within each individually delineated 2h 95% KUD area but we did quantify a site-level estimate of the mixed algal turf present. We multiplied the proportion of mixed algal turf at the site (from the UPC benthic data) by each 2h 95% KUD area to get an estimate of the amount of mixed algal turf present.

Average feeding foray time: We estimated the amount of time an individual's feeding forays lasted at a particular location from the spatial behavioral 2h follow data. The end of a feeding episode was considered anytime a fish ceased feeding and started another behavior (i.e. directed swimming, territorial defense, cleaning, etc.).

Statistical Model: We tested the effect of site on the above derived metrics (95% KUD area, pathway length, site fidelity, area of mixed algal turf, and average feeding foray time) for significance using mixed effects model framework(R package lmer4) to overcome the

repeated measures in the experimental design (i.e., we did multiple 2h follows on the same individuals). We structured the models so each individual fish was nested within site and treated as a random effect. We log-transformed the 2h 95% KUD area data and the mixed algal turf per 2h area data to improve the spread of the residuals and reduce the influence of outliers. A p-value was attained for each data set by comparing the full model, with site, and reduced model, without site. We ran a likelihood ratio test between the full and reduced model using the 'anova' function within R. We calculated the least squares means of the untransformed data for both sites using the 'lsmeans' package and 'ref.grid' function in R to estimate the magnitude and direction of the difference between sites.

RESULTS

Fish Survey Data

Chlorurus microrhinos *biomass and density:* The density and biomass of TP *C. microrhinos* was much greater at Penguin Spit compared to Western Terrace (Table 1). The size and color phase data across all transects plotted in 8-dimensional space showed that the two sites separate strongly and were significantly different from the randomized null distribution (observed value = .709; null 95% CI = 0.01317 – 0.615).

Piscivore biomass: We found no significant difference in the predator biomass between Penguin Spit and Western Terrace (Fig. 2, p= 0.86, Mean biomass ± SE: PS = 2.63 ± 0.69 kg/m^2; WT = 3.06 ± 1.38 kg/m^2).

Benthic Community Structure and Habitat

Percent cover: We found a significant difference in the major resources available for *C. microrhinos* between Western Terrace and Penguin Spit (Fig. 3). Penguin Spit consists of mixed algal turfs (45.5%), live coral (21.0%), and Corallimorph (14.0%), while Western Terrace is characterized by live coral (35.5%), CCA (22.2%) and *Lobophora* (20.2%), with mixed algal turfs only comprising 10.0% of the benthic cover (Fig. 3).The multinomial analysis of the percent cover data showed that Penguin Spit and Western Terrace separated strongly and were significantly different from one another. The observed Euclidean distance of 0.477 fell well outside the randomized null distribution 95% CI [0.036, 0.240].

Mixed algal turf clustering and patch size: Patches of mixed algal turf at Penguin Spit were larger and occurred more frequently than patches observed at Western Terrace. Differences between the sites were significant, with the longest chain of consecutive points at Penguin Spit and Western Terrace being 11 and 3 points, respectively (Fig. 4, p = 0.025).

Physical characteristics: Western Terrace and Penguin Spit show similarities in the depth and rugosity indicating that habitat structure at each site was similar. The mean depth at Western Terrace and Penguin Spit were 3.2 ±.79m SE and 2.6 ±.86m SE, respectively. Relief was also similar between the sites with the majority of relief points falling in the 0.5 - 1.0m and 1.0 – 2.0m categories for both sites (Fig. 5).

Diet Preference

Selectivity: *Chlorurus microrhinos* showed a significant avoidance of CCA, *halimeda*, live coral, and *lobophora* at Penguin Spit (Manly's α = 0.03, 0.006, 0.059, 0.0019 respectively) and Western Terrace (Manly's α = 0.111, 0.007, 0.034, 0.108 respectively). Fish appeared to avoid bare substrate at Penguin Spit (Manly's α = 0.028) but showed a neutral preference at Western Terrace (0.179). In contrast, there was a significant preference for mixed algal turfs at both Penguin Spit and Western Terrace (Fig. 6, Manly's α PS = 0.873; WT= 0.511).

Bite Scar Patterns

Spatial trends in bite scars between sites: The distribution of bite scar density showed that the majority of quadrats contained zero bite scars at both sites (Fig. 7). However, at Penguin Spit, the distribution of bite scar densities had long tail, indicating that areas of high bite scar density (>100 bites m^{-2}) were present at the site. The proportion of quadrats with bite scar densities greater than 100 bite m^{-2} was 0.08 of the total observations from Penguin Spit, with the highest recorded bite density 320 bites m^{-2}. The highest recorded bite density from Western Terrace was 76 bites m^{-2}. We use a Wilcoxon rank sum text to test for a difference between sites and found that the effect was significant (Fig. 7, p = < .0001).

Temporal trends in bite scars between sites: Penguin Spit was characterized by sharp spikes in new bite density followed by periods of little activity (Fig. 8a). Western Terrace was characterized by a steadier, more consistent new bite densities over time that indicated

more homogenous feeding pattern across time (Fig. 8b). The sample variance in bite scar density was significantly larger at Penguin Spit and difference between sites was highly significant (Fig. 8a, Fig. 8b, p = 0.0001).

Using our definition of a 'peak', only the bite densities at Penguin Spit exhibited such behavior. The number of days between each 'peak' of bite density at Penguin Spit shows a considerable amount of variability. The shortest and longest intervals were 7 and 56 days. The median peak interval was 19.0 days, the mean was 23 days, and the sample standard deviation was 12 days (Fig. 9).

Bite scar recovery comparison: Using the adjusted Earth Mover Distance (EMD) image analysis approach, bite scars at Penguin Spit recovered faster and the recovery was significantly greater by day 12 of undisturbed growth. At day 6, the recovery response estimate between the two sites was not significantly different (Table 2; p = 0.1702, LS Means ± SE: PS = 43.33 ± 1.8; WT = 39.59 ± 2.06), but by day 12, Penguin Spit was significantly 'more recovered' than Western Terrace (Table 2; p = 0.0001, LS Means ± SE: PS = 12.03 ± 2.1; WT = 32.25 ± 2.1).

Using the adjusted EDM values to estimate recovery for each artificial scar showed a similar pattern, with much faster recovery at Penguin Spit (Table 2, Fig. 10; Day 6 mean PS = 44.21%; WT= 16.10%, Day 12 mean PS= 84.96%; WT = 31.45%). Three of the artificial scars at Penguin Spit were estimated as 100% recovered at day 12, while the greatest recovery at Western Terrace was estimated at 45.3%.

Space Use Patterns

95% kernel utilization distribution: There were significant differences between sites in the 2h 95% KUD area measurements, with Western Terrace areas approximately 3 times larger than areas at Penguin Spit (Fig. 11a: $p = 0.0094$, LS Means: PS= 251.7 m^2 ;WT= 797.0 m^2).

Pathway length: We found that the pathway length was significantly different between sites, with fish at Western Terrace swimming 41.0% further over a two hour period. (Fig. 11b: $p = .006$, LS Means: PS = 1148.0m; WT = 1619.5m).

Site fidelity: The inter-centroid distances between an individual's 2h territory were low and we did not find a significant difference in fine-scale site fidelity once we had controlled for the size of each territory ($p = .38$).

Mixed algal turf within territories: The estimated amount of mixed algal turf within a fish's 2h 95% KUD area was not significantly different between Penguin Spit and Western Terrace, indicating that *C. microrhinos* maintains similar access to its preferred resource at both sites. Using a mixed effects model, the effect of site was not significant ($p = .95$, LS Means ± SE: PS = 103.73m^2 ±25.16; WT = 105.02m^2 ±25.17).

Average feeding foray time: We found a significant difference between sites in the time an individual spent feeding at a particular locations. We found that fish at Penguin Spit had significantly longer feeding forays than fish at Western Terrace ($p= .0364$, LS Means ± SE: PS = 101 secs ± 11; WT = 66 secs ± 9).

DISCUSSION

Feeding by herbivores, both fish and sea urchins, has been shown to have a net positive effect on coral by removing algae and creating bare space that potentially fosters coral recruitment and early survival. Predictive models have suggested that the fine-scale spatial patterning of herbivory could be essential in accurately forecasting competitive outcomes between corals and algae (Sandin & McNamara 2011). Spatially constrained feeding by sea urchins, for example, was predicted to be more beneficial for coral recruitment and growth because this type of foraging creates clustered patches of bare space for coral settler refuge. Mobile herbivores (such as many fish species) created a discontinuous, intermittent feeding pattern across the model domain. This pattern was less conducive to coral recruitment and growth because algae could quickly outcompete new corals for space by quickly filling in these smaller, isolated patches. In the Sandin and McNamara (2011) model, the clustered feeding pattern was designed to mimic sea urchin feeding behavior, but in nature we found evidence that a large mobile parrotfish can also feed in a spatially constrained manner that creates dense patches of bites scars with low levels of algae and an abundance of bare space.

For *C. microrhinos* at Palmyra there were dramatic site level differences in social structure and feeding behavior that appeared to be unrelated to predator abundance, rugosity, nor depth. We found that when resources were abundant, *C. microrhinos* minimized movement and focused feeding on patches of preferred resources. When resources were more scarce, *C. microrhinos* increased the scales of movement, and feeding behavior was spread over a greater area. This foraging behavior resulted in a dispersed distribution of bite scars. Even

in areas of low resource abundance feeding activity was somewhat clustered within resource patches, but we only observed areas of high bite scar density (>100 bites m^{-2}) where resources where abundant. Our results are congruent with other studies that reported constrained grazing behavior by *C. microrhinos* despite their large size and mobility (Welsh & Bellwood 2012), but here we document large-scale variability in this feeding behavior over small spatial scales on one localized reef. The spatial pattern of herbivory is clearly important for the creation of bare space and potentially coral settlement, but the temporal patterns of clearing and overgrowth by algae will also determine the extent to which herbivory might mediate coral settlement and survival. Here, we also tracked the arrival and succession of *C. microrhinos* bite scars through time and detected a temporal periodicity to feeding when resources were abundant and regeneration was rapid and predictable.

The social structure of *C. microrhinos* differed between these two different resource regimes. Social systems in parrotfishes are generally characterized by a dominant TP male that defends a territory associated with a harem of IPs, with whom mating frequently occurs (Mumby & Wabnitz 2002). Researchers have also documented parrotfish with single-male and multi-male groups on the same reef, but the multi-male groups are composed of smaller males with overlapping foraging ranges (van Rooij et al. 1996). TP males that are haremic will maintain territories with IP females for mating purposes, but studies have found indirect evidence that there are some resources benefits (e.g. reduced grazing pressure, higher algal abundance, exploitation of high yield food patches) to territoriality (Bruggemann et al. 1994, Mumby & Wabnitz 2002). At Penguin Spit we documented a social system in *C. microrhinos* that consisted of TP males that maintained

exclusive territories containing high yield food patches. IP individuals were rare at Penguin Spit and yet the TP males were among the largest seen in our study. Acoustic telemetry data collected in conjunction with this project show that both TP and IP individuals would regularly leave their feeding area and travel offshore, most likely for mating purposed (Davis et al. *in prep*). Similarly, in our 2h focal observations we would occasionally be forced to abort a 2h focal follow because the individual would cease feeding and swim in a directed fashion offshore. The potential offshore mating excursions and lack of IP females suggests that the territoriality exhibited by TPs at Penguin Spit was driven by access to preferred resource patches and not by access to mates as commonly reported in other parrotfish species. A few km away, the social system at Western Terrace contrasts strongly with that seen at Penguin Spit, and is characterized by socially localized groups often composed of one dominant TP and 4-5 IPs. The two different social systems we report here both occur on Palmyra's reef terrace habitat and both result in dramatically different spatial and temporal patterns of turf algae removal and the creation of bare space.

Penguin Spit is dominated by algal turfs, a situation that is not typical for other areas at Palmyra atoll. There is evidence for a mild bleaching event in 2009 following a larger event in 1998 that resulted in extensive coral mortality that appeared to strongly reduce coral cover at the shallow Penguin spit site (Williams et al. 2010). Other studies of coral reef systems that have undergone major coral die-offs have reported increases in herbivore biomass in response to algal turf increases (Adam et al. 2011, Gilmour et al. 2013). The high density of *C. microrhinos* at Penguin Spit could be a similar response to high levels of cover of algal turf.

Spatial Grazing Pattern

We showed that the feeding patterns of *C. microrhinos* at fine spatial scales can result in dense patches of feeding scars (>100 bites/m^2) where turf algae are removed and calcium carbonate substrate is exposed (Bellwood & Choat 1990). Coral recruit density has also been shown to be highest when algal cover is lowest (Edmunds & Carpenter 2001, Vermeij et al. 2009), suggesting that dense patches of bite scars, like the ones observed at Penguin Spit, could potentially provide a more favorable habitat for coral at the earliest life stages opposed to a substrate covered in algal turfs. Coral planulae are particularly susceptible to algal-induced, microbe-mediated mortality during their benthic exploration and settlement phase (Vermeij & Sandin 2008). Thus, these dense patches of bite scars could potentially ameliorate the negative effects that fleshy turf algae exerts on coral planulae survival during their most vulnerable phase by creating a more spatially extensive refuge of bare space for settlement and growth.

The underlying mechanism allowing a continuous, highly clustered feeding patterns appears to be the availability and rapid growth of mixed algal turfs at Penguin Spit. Here we show that the density of *C. microrhinos* increases with resource abundance, as would be expected under most foraging models (Fretwell & Calver 1969, Schoener 1971, Charnov 1976, 1989). This also conforms to other studies that relate the abundances of parrotfishes to their response to preferred food (Adam et al. 2011, Tootell & Steele 2015). We also show that fine-scale space use appears to be most closely related to preferred resource abundance, in that other key characteristics were similar between sites (e.g., rugosity, depth, and apparent predation risk). Interestingly, despite very different algal

densities at the two sites, the estimated amount of algal resource contained in the 2h foraging areas was the same between sites due to much smaller foraging areas at Penguin Spit relative to the Western terrace. This finding suggests that fish at both sites maintain access to similar amount of a preferred resource, and that resource abundance influences fish movements and space use.

Fish at Penguin Spit used smaller 2h foraging areas and spatially focused their feeding even within those areas, but to infer that the higher bite densities observed at Penguin Spit are simply a function of a smaller foraging area maybe an oversimplification of the mechanisms at play. Fish at Penguin Spit would continually bite on dead coral heads covered in mixed algal turfs during a 2h trial, despite excursions to check territorial boundaries and visit cleaning stations (Davis et al. *in prep*). This observation is supported by the photo plot time series data from Penguin Spit that showed peaks in bite density that appeared to occur during one spatially constrained feeding episode (Fig 8a). Also, fish at Penguin Spit spend a significantly longer time feeding at one location than fish at Western Terrace. This supports the idea that *C. microrhinos* is capable of feeding in a highly spatially constrained manner despite the capability of moving large distances (Welsh & Bellwood 2012), and that spatially constrained foraging patterns that were previously ascribed to sea urchins or other localized foragers can actually occur in fish if conditions allow (Sandin & McNamara 2011).

Temporal Pattern of Spatial Grazing

Past studies have shown that on reefs where herbivory was excluded or infrequent, algae become the dominant space holder: however, consistent grazing is able to control algal

abundance and prevent overall algal dominance (Mumby et al. 2006, Hughes et al. 2007).

Consistent grazing by large parrotfish has been suggested to be more beneficial for coral

recruitment compared to situations where herbivory has been excluded or impeded

(Steneck et al. 2014). We tracked bite scar densities through time for particular locations at

Penguin Spit and Western Terrace and showed that at Penguin Spit, patches of high bite

scar density have some temporal periodicity (Fig 8a). Here show 'peaks' of high bite scar

density appear to come in short, concentrated bouts. Following these peaks, there are

periods of inactivity where no new bite scars are recorded and mixed algal turf recovers.

Importantly, these high bites scar density patches occur in area where algal turf recovery is

rapid, so the temporal window for coral recruitment may be relatively small.

An additional complications is that these high bite scar density patches appear to be re-

grazed on a regular basis. Our study and others have shown that TP *C. microrhinos* show

high site fidelity and will defend territories against conspecifics (Welsh & Bellwood 2012)

(*Davis et al. in prep*), so that feeding sites are likely be revisited by the same individual.

Here we show repeated peaks occur on the same coral heads despite a relatively short time

series, indicating that individual fish revisit coral heads within their territories at an

interval of approximately 16d to 34d. Future research over longer time periods may detect

a regular periodicity to the bites, perhaps related to growth rates of algae. High grazing

frequency, similar to what we found here, has been shown to result in highly productive,

early successional algal turf communities compared to areas with a lower grazing

frequency (Carpenter 1986). This 'cropping' may be a key factor contributing to the very

high density *C. microrhinos* present at Penguin Spit. The re-grazing behavior at Penguin

Spit could also be related to the highly site-attached nature of *C. microrhinos* (Welsh &

Bellwood 2012) combined with the particularly small foraging areas, such that resource locations and conditions are predictable at the time scale of weeks. Patches of mixed algal turfs were larger and more frequent at Penguin Spit than at Western Terrace, also allowing more spatially constrained foraging.

The spatially constrained feeding behavior and frequent re-visitation of feeding sites by *C. microrhinos* at Penguin Spit is particularly interesting in the context of algal-induced mortality during the earliest recruitment stages of coral planulae. The earliest life stages of corals appear to be particularly sensitive to the presence of algal turfs and it appears that a large majority of mortality occurs during the benthic exploration and settlement phase stage (2-7 days post spawn)(McCook et al. 2001, Vermeij & Sandin 2008). Thus, the interplay of grazing (which can remove coral recruits), re-grazing, and algal regrowth (which can lead to coral recruit mortality) could be particularly important to coral recruitment success. The shortest interval between grazing bouts from the bite scar time series data was 7 days and the median was 19 days. We estimated artificial bite scar recovery, relative to their surroundings mixed algal turf, to be 44.21% recovered with mixed algal turfs after 6 days. Although we were not able to directly measure coral planulae survival success under different frequencies of parrotfish feeding bouts, it appears that grazing return time, mixed algal turf recovery time, and published data on coral planulae temporal susceptibility to algal turfs are all at similar temporal scales. Thus while the creation of large grazed spaces (as modeled by Sandin & McNamara 2011) in high-production areas might be considered as conducive to coral recruitment, the associated rapid algal recovery and frequent re-grazing in these same areas can have the opposite

effect. This an intriguing area of future research that could clarify the connection between spatial patterns of herbivory and coral recruitment success.

CONCLUSION

Here we show that small-scale spatial differences in underlying productivity and turf algal growth are associated with dramatic differences in social structure and benthic use in a large, excavating parrotfish. In the high-productivity area, large individuals held small individual territories, and feeding was characterized by intense grazing over small areas that recovered quickly and were subsequently re-grazed at high frequency. This spatially and temporally intense foraging behavior has the potential to strongly influence coral-algal competition at the earliest, most vulnerable stage in coral life history, but the effects are paradoxical: intense grazing opens space for coral recruitment, but rapid algal recovery and repeated re-grazing inhibits coral recruitment.

TABLES & FIGURES
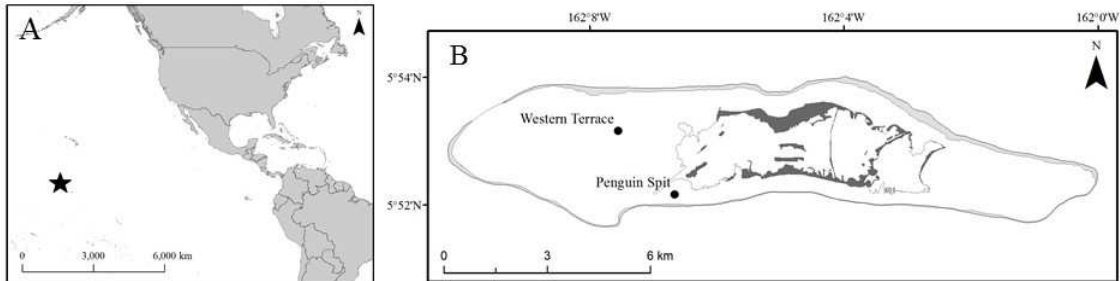
Figure 1. (A) The location of Palmyra Atoll (★) in the Central Pacific, approximately 1500km south of the Hawaiian Archipelago. (B) Palmyra Atoll, with the location of Penguin Spit and Western Terrace. The light grey shading is the 30m isobaths and the dark grey shading represents land.

Table 1. Biomass and density of *Chlorurus microrhinos* at Penguin Spit and Western Terrace, Palmyra atoll. Surveys targeting *C. microrhinos* were conducted three times during summer of 2014. Each survey consisted of 6 transects and covered 1200 m^2 area.

| Site	Color Phase	Biomass (g/m$^2 \pm$ SE)	Density (#/1200m$^2 \pm$ SE)
Penguin Spit	TP	21.72 $\pm$ 2.57	7.67 $\pm$ .88
	IP	2.11 $\pm$ 2.03	1.67 $\pm$ 1.2
Western Terrace	TP	4.39 $\pm$ 1.61	1.33 $\pm$ .33
	IP	2.09 $\pm$ 0.52	2.33 $\pm$ .88
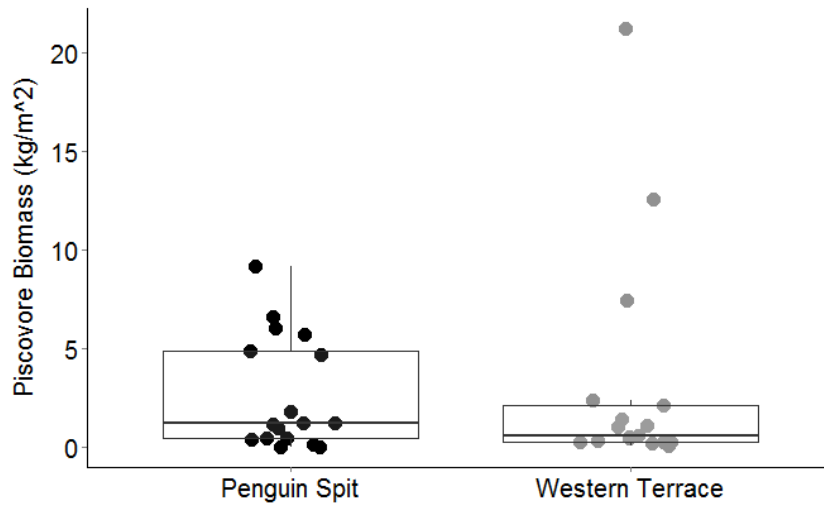
Figure 2. Biomass of piscivores at Penguin Spit and Western Terrace from fish community surveys. Data were taken during the 2013 and 2014 June – September seasons. Each point represents the biomass of piscivores along a 25m belt transect, N=17 at each site.
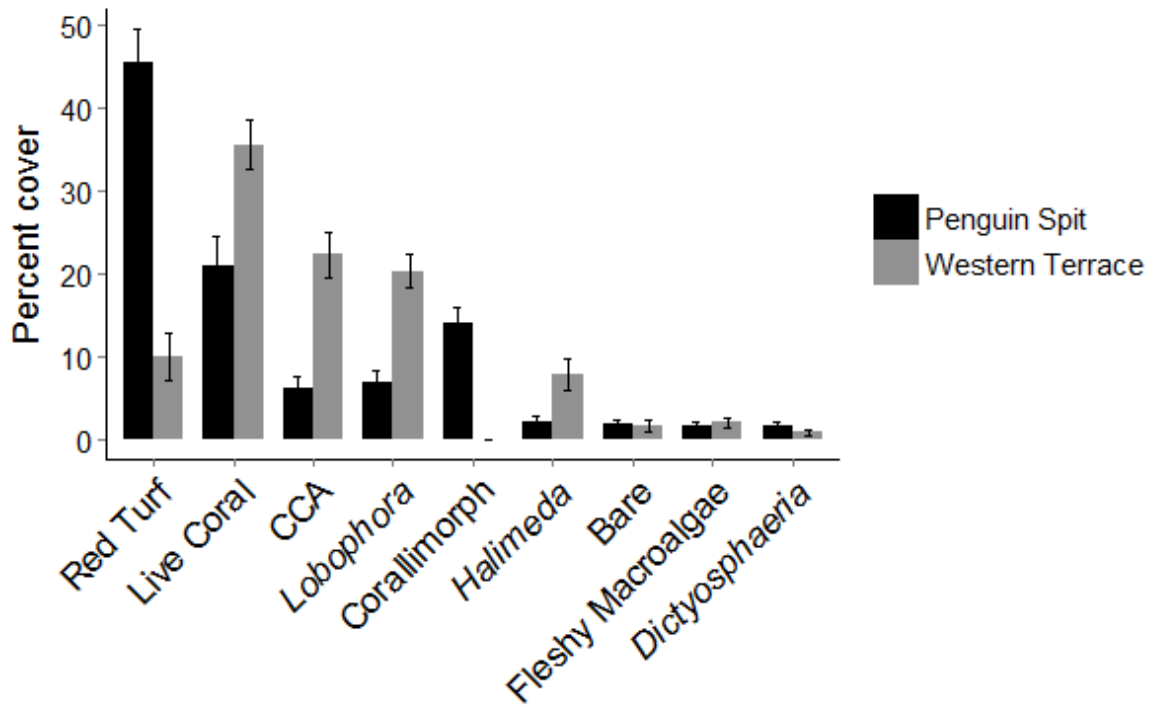
Figure 3. Percent cover of benthic substrate at two sites on Palmyra atoll, Penguin Spit and Western Terrace. Penguin Spit consists of mixed algal turfs (45.5%), live coral (21.0%), and Corallimorph (14.0%), while Western Terrace is characterized by live coral (35.5%), CCA: crustose corraline algae (22.2%) and *Lobophora* (20.2%), with mixed algal turfs only comprising 10.0% of the benthic cover.
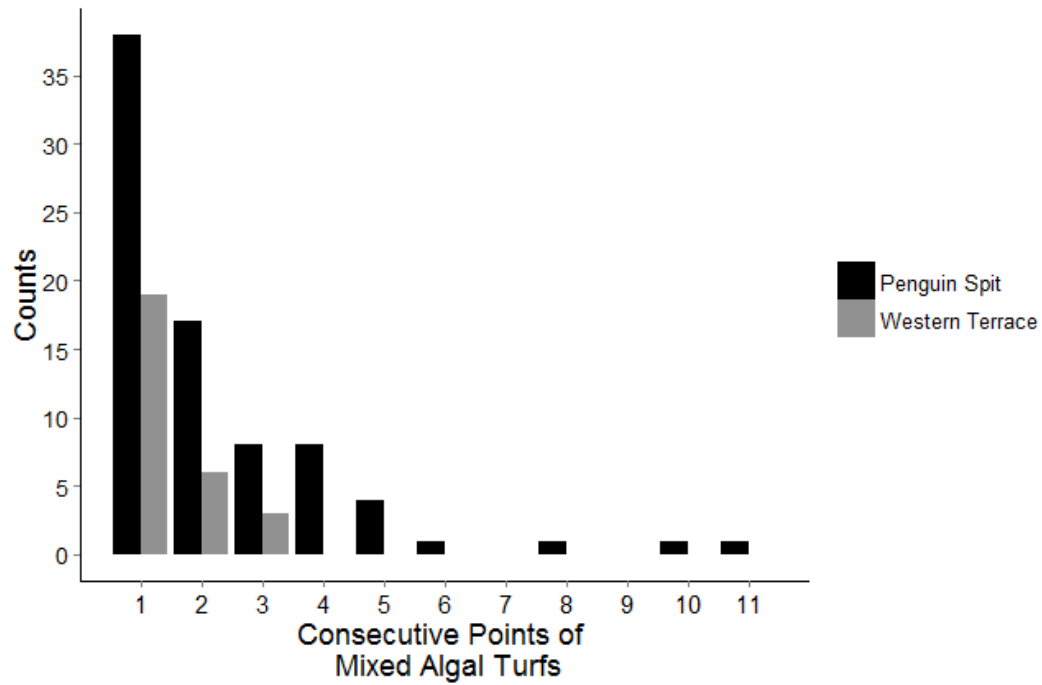
Figure 4. The total number and the number of consecutive points of mixed algal turfs recorded on benthic transects at Penguin Spit and Western Terrace. Only non-zero values are shown, with 79 and 28 individual turf clusters from Penguin Spit and Western Terrace, respectively. Differences between the sites were significant, with the longest chain of consecutive points at Penguin Spit and Western Terrace being 11 and 3 points, respectively ($p = 0.025$).
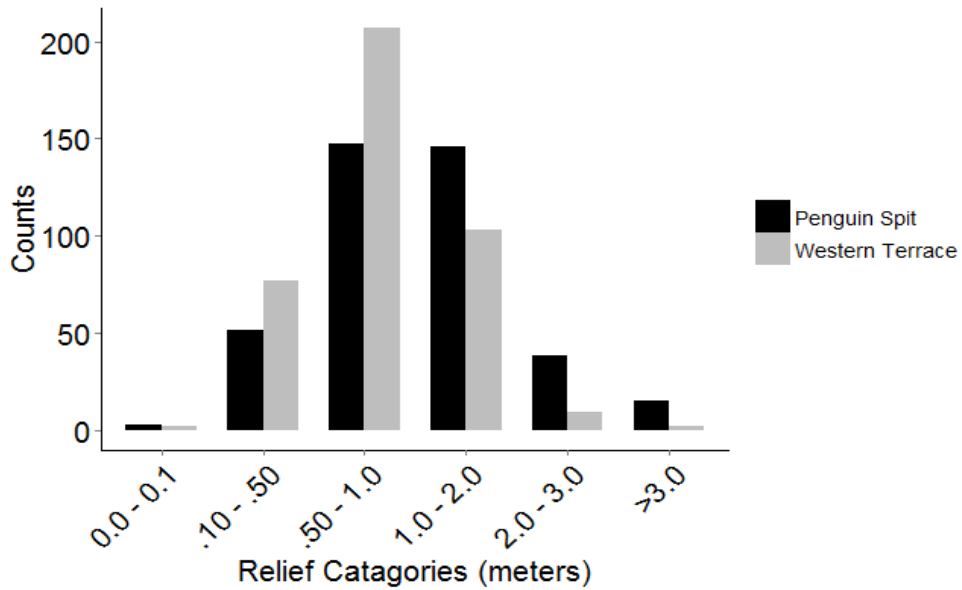
Figure 5. Distribution of the number of points in each relief category from two sites at Palmyra atoll, Penguin Spit and Western Terrace. Relief was measured as the height between the lowest and highest point within a 0.5 x 0.5 m box. Data were taken from 25 m point contact surveys, taking a measurement every m. Each site had a total for 16 transects over two years, for a total of 400 points per site.
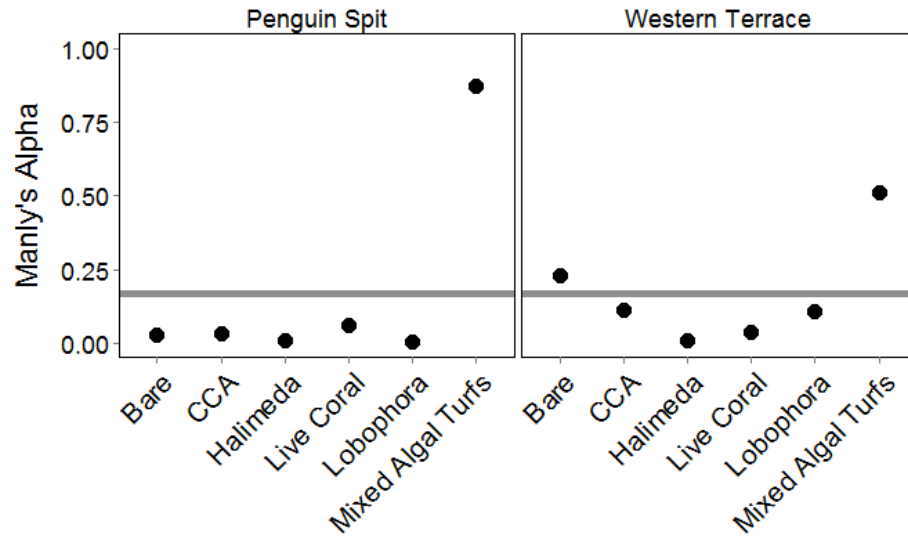
Figure 6. Manly's α selectivity index for *C. microrhinos* feeding on six different substrate types at Penguin Spit and Western Terrace. Grey line at α = 0.166 ± .018 is the null expectation of equal selectivity for each substrate based on its availability in the environment. A value above the α threshold indicates preference for a particular substrate. We found a significant preference for mixed algal turfs at both Penguin Spit and Western Terrace (Manly's α PS = 0.873; WT= 0.511).
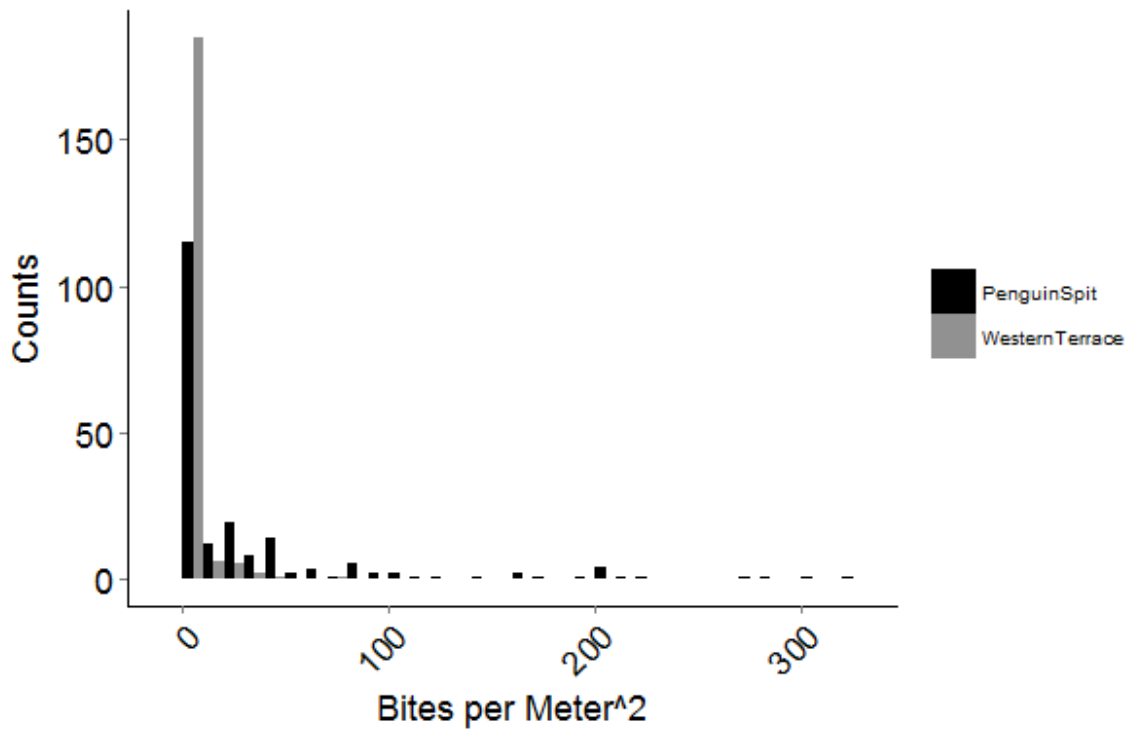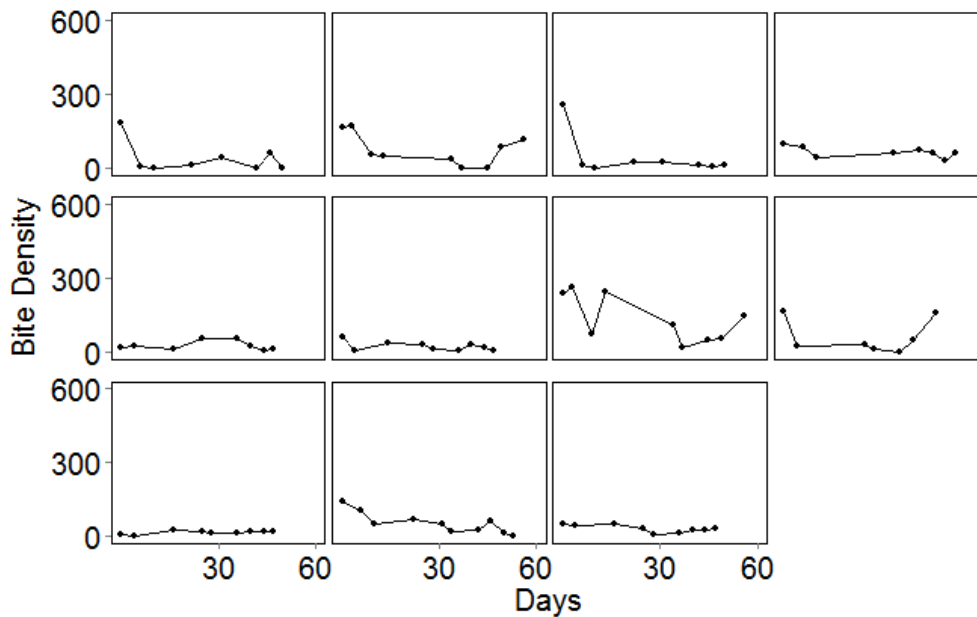
Figure 7. Distribution of *Chlorurus microrhinos* bite scar density on the benthos at Penguin Spit and Western Terrace. Bite density was recorded every meter along a 25m belt transect and is calculated as bites m^{-2}. We found that the effect of site was highly significant (p < 0.0001), with the highest areas of bite scar density at Penguin Spit.

A.
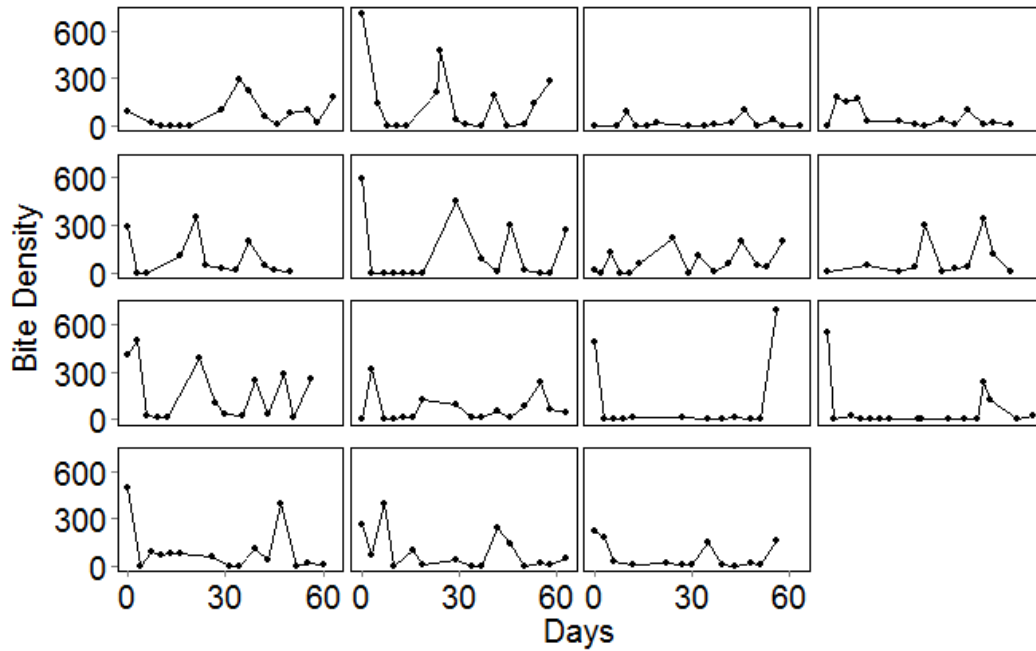
B.

Figure 8. Bite Density (bites/meter^2) through time measured at two sites, Penguin Spit (A) and Western Terrace (B). Each frame is a unique location at each site. Each location was photographed every 4-5 d and only new bites were recorded and are shown here.
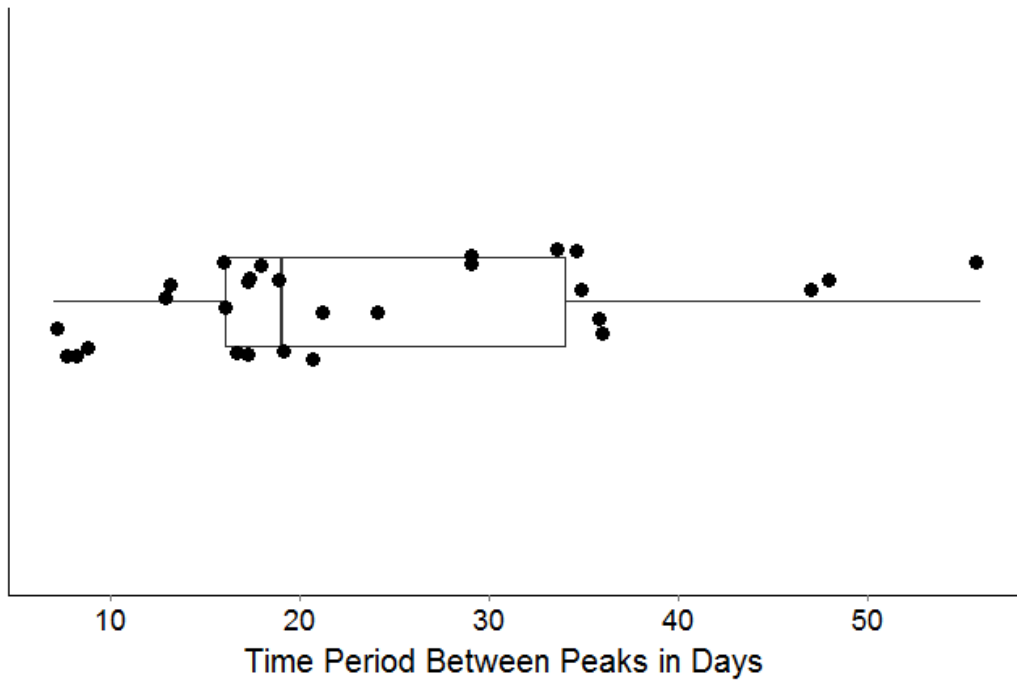
Figure 9. Number of days between consecutive 'peaks' in bite density from photo plots time series at Penguin Spit. (Q1 = 16 days, Median = 19 days, and Q2 = 34 days)

Table 2. Earth Mover Distance (EMD) values as a proxy for the recovery of artificial scrapes on dead coral heads covered with mixed algal turfs at Penguin Spit and Western Terrace. Lower EMD values indicate a greater similarity to the surrounding, undisturbed mixed algal turfs and represent a greater amount of recovery. Percent recovered was calculated in relation to the Day 0 EMD value for each unique scrape.

Site	Day	EDM ± SE	Percent Recovered ± SE
Penguin Spit	6	43.33 ± 1.80	44.21% ± 4.1
	12	12.30 ± 2.10	84.96% ± 2.6
Western Terrace	6	39.59 ± 2.06	16.10% ± 2.60
	12	32.25 ± 2.30	31.45% ± 2.85
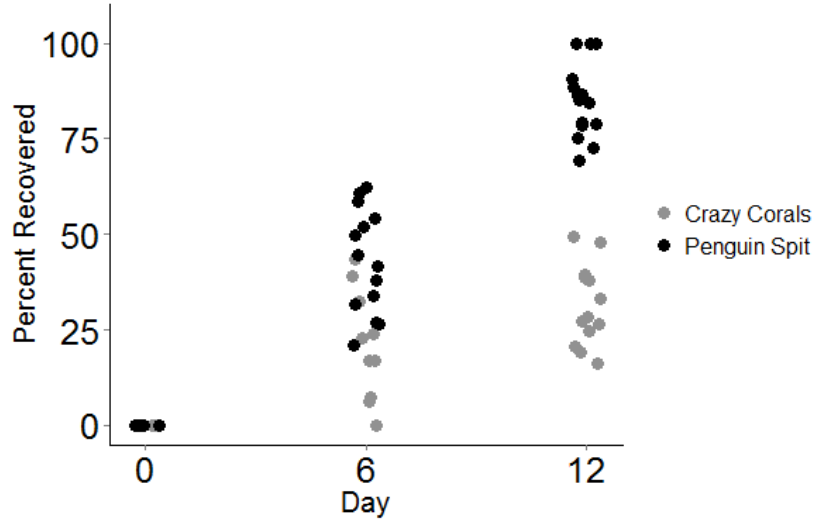
Figure 10. Percent recovered in artificial scrapes on dead coral heads covered in mixed algal turfs through time at Penguin Spit and a Western Terrace proxy (see methods). Percent recovered was calculated from Earth Mover Distance (EMD) differences between the artificial scrapes and the surrounding, undisturbed mixed algal turf at each time point. The difference in recovery was significant by 12d ($p < 0.0001$).
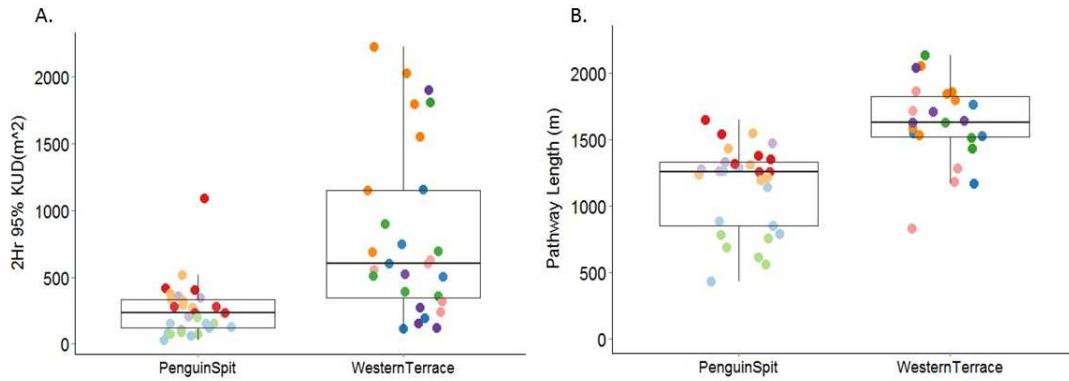
Figure 11. A. Area of the 95% Kernel Utilization Distribution (KUD) from 2h focal follows of *C. microrhinos* at Penguin Spit and Western Terrace. Each color represents a unique individual that was followed on at least 5 separate occasions over a three month period. **B**. The pathway length of a 2hr behavioral follow of *C. microrhinos* at Penguin Spit and Western Terrace.

APPENDIX

1 -- Bite Scar Photography and Image Analysis

We photographed designated areas of the benthos every 4-5 days to track the arrival of new *C. microrhinos* bite scars. A 0.5m X 0.5m PVC quadrat was included in each photo for scale. The distance above the reef was approximately the same for each photo but was not fixed because the photos only need to capture the arrival of new bite scars. We kept the location and position of the PVC quad constant for each photo plot through time. We took photos perpendicular to the face of coral head so that area measurements for bite scar density calculations were as accurate as possible. We used a Canon G15 digital camera set to 'underwater' mode inside an underwater housing

We analyzed the images from each plot using ImageJ 1.48V to track the arrival of new bite scars. For each image, we used one side of the 0.5m x 0.5m PVC frame to set the pixel/meter scale of each image. Once the scale was set, we traced the interior edge of the PVC quadrat and calculated the area to estimate the error of the pixel/m scale. We repeated this process until a pixel/m scale within $\pm$ 0.02m^2 of the 0.25m^2 PVC frame was achieved.

Using the acceptable pixel/m scale, we outlined the boundaries for each coral head in the photo using the 'Freehand' tool and calculated the area. We avoided areas of the benthos with high rugosity ensure an accurate area measurement. We established boundaries for each particular location and used the same boundaries for all photos in a series. We then recorded bite scars within the boundaries using the 'Multi-point' tool and tracked through time. We only recorded bite scars that had occurred during each respective time interval as

'new', and reported them for the bite density measurement. We calculated bite density as the number of new bite scars per unit area.

2 -- Bite Scar Recovery and the Earth Mover Distance (EMD) calculation

We analyzed the artificial bite scar images using ImageJ 1.48V photo analysis platform. First, we set the scale for each photo by drawing a 2 cm line on the measuring tape present in the photo. That line was used to set the pixel/cm scale for the entire image. To check the accuracy of that scale, we drew a 3cm line on the measuring tape and measured the length. To ensure accuracy, we only used scales within ± .02cm of the 3.0cm line. Once the scale of the photo was set, we outlined each scar from the day zero photos using ImageJ's 'freehand' tool and calculated the area. We measured all three scars from each of the 15 groups three times and calculated the average area for each scar, and selected the scar with the closest average area to 2.00cm^2 in each group for analysis and to track through time.

We defined recovery as the rate at which the etched scars 'filled in' and resembled the surrounding, undisturbed mixed algal turfs. We estimated recovery from photos taken on day 0, 6 and 12. Because the algal turf regrows from the sides as well as over the surface of the scar itself, simply outlining the scar and calculating the area is not appropriate. Instead, we calculated the pixel intensity histogram of each scar to track the change in color through time as a proxy for algal regrowth. We compared each pixel intensity histograms to pixel histograms of immediately adjacent, undisturbed mixed algal turfs in the same photo. We used the 'histogram' tool within ImageJ to calculate each pixel intensity histogram by converting each pixel of a RGB (Red Green Blue) image to greyscale using the formula.

$$gray = (red + green + blue)/3$$

We categorized the resulting grey pixel values into 255 bin histogram that represent the greyscale pixel intensity of the artificial scar. The lower values of the histogram represent darker/black pixel values, while higher values represent lighter/white pixel values.

With the scale on the photo set, we outlined the artificial scar at day 6 and calculated the area. We then compared the area to the day zero area to ensure we were capturing the entire scar. If the sample area and the day zero area did not match within $\pm$ .05 cm^2, we gradually expanded the outline until an acceptable area was achieved. This ensured that the entire artificial scar was included within the pixel histogram, capturing regrowth from the edges as well as on the surface of the scar. We calculated the pixel intensity histograms of the artificial scars using ImageJ's 'Histogram' tool. Additionally, we recorded the total number of pixels measured within the histogram. We then moved the exact outline of the artificial scar directly to the left and calculated the pixel intensity histogram for the adjacent, undisturbed mixed algal turf. We used the same outline to ensure that each histogram samples the same number of pixels and calculates accurate difference. We used that same outline to calculate the histograms for the undisturbed mixed algal turf to the right and above/below (depending on the location of the measuring tape in the photo) the artificial scar. Thus, for one photo, we computed three standard pixel histograms of undisturbed mixed algal turf and one pixel histogram of the artificial scar.

To compare the artificial scar to the undisturbed mixed algal turf, we calculated an Earth Mover Distance (EMD) cost between each histogram derived from a single photo (Rubner et al. 2000, Andoni et al. 2008). Conceptually, EMD calculates the smallest 'cost' or effort

that would be required to move one pile of dirt into another pile of dirt. In other words, EMD is the minimal cost that must be paid to transform a signature or histogram into the other (Rubner et al. 2000, Andoni et al. 2008). We calculated EMD in R using the 'emdist' package and the 'emd2d' function. We compared the experimental pixel histogram to each of the undisturbed pixel histograms from a single photo, and averaged the three (left, right, and top/bottom) EDMs or transformation 'costs'.

To estimate the error associated with each photo as well as the noise associated with the EMD approach, we calculated a value for a '100% regeneration'. To do this we calculated three pixel histograms of areas of undisturbed algal turf for each photo and from each time period and compared them to each other. We did this three times for each photo and we considered the average value the 'EMD error' for that particular photo. We subtracted the EMD error for each photo from the average EMD value and called it the error-adjusted EMD value. We used a linear mixed effects model and found that the effect site and day was not significant for distribution the of error values, indicating that the error associated with the EMD approach was consistent across space and time. We used the error-adjusted EMD values in all statistical comparisons and percent recovered estimations.

3 -- *95% Kernel Utilization Distribution*:

We calculated the 95% kernel utilization distribution (KUD) within the Geospatial Modeling Environment (GME) platform. To calculate the 95% KUD, the Kernel Density Estimation (KDE) raster is first calculated using the 'kde' command line in GME. We set the bandwidth to "PLUGIN" and we used a 0.25m cell size. After the KDE raster was calculated, we used the 'isopleth' command to draw a 95% isopleth around the KDE, with

the 'quantiles' command set to 0.95. We report the area of the isopleth as the 2h area. We

repeated the analysis for each two hour trial. We calculated the 95% KUD area for a total

of 57 2h follows, with 29 from Penguin Spit and 28 from Western Terrace.

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