Fine-scale spatial patterns of parrotfish herbivory are shaped by resource availability

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ABSTRACT: 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. Spatially constrained grazing by herbivores, particularly parrotfishes, may foster coral recruitment by creating a spatially continuous refuge of bare substrate for settlement and survival. However, frequent bouts of concentrated feeding potentially remove newly settled corals. Understanding the frequency and intensity of parrotfish foraging behavior at appropriate scales (months and meters) is essential for connecting herbivory with benthic processes. We documented the foraging behavior of a large, mobile coral reef herbivore (the steephead parrotfish *Chlorurus microrhinos*) on Palmyra Atoll using various techniques (observational follows, fish surveys, and bite scar tracking) across 2 habitat states (one dominated by algal turfs, one dominated by live coral and crustose coralline algae) that are representative of reefs throughout the Central Pacific. Large differences in the abundance of a preferred resource were associated with major differences in feeding behavior. Where resources were abundant and regrew quickly, foraging areas were small and spatially focused, resulting in dense patches of bite scars (>100 bites m^{-2}). Feeding behavior also showed a temporal periodicity, with individuals defending and regrazing the same area after regrowth occurred. In areas where resources were less abundant and recovered more slowly, parrotfish movements and foraging areas were significantly larger and bites were distributed sparsely across food patches. The large variability we observed within a single atoll suggests that characterizing species-specific foraging patterns from small-scale studies may not be appropriate.

KEY WORDS: Herbivory · Parrotfish · Coral reefs · Turf algae · Coral–algal interactions · Bite scar · Palmyra Atoll · *Chlorurus microrhinos*

INTRODUCTION

Herbivory plays a formative role in structuring the distribution, settlement, and survival of foundational species in marine systems (Carpenter 1986, Estes et al. 1998), where the mere presence of corals and macroalgae increase niche space by modifying physical conditions (Bruno & Bertness 2001, Bruno et al. 2003). Changes in the abundance or behavior of herbivores can disrupt this process and can have profound, often negative, effects on the ecosystem function, biodiversity, and resilience (Duffy & Hay 2001, Altieri et al. 2012, Moore & Duffy 2016). Therefore,

mechanisms that underpin herbivore behavior and abundance and their subsequent connections to the success of foundational species have become an important focus of marine ecology (Byrnes et al. 2006, Rasher & Hay 2010, Poore et al. 2012).

Herbivory on coral reefs can remove algae that compete with reef-building corals for space, and thus may indirectly promote coral recruitment, growth, and survival (Edmunds & Carpenter 2001, Mumby et al. 2006, Burkepile & Hay 2008). This process is particularly important in the wake of disturbances such as bleaching events, predator outbreaks, and powerful storms that may expose bare substrate and leave

reefs vulnerable to algal overgrowth (Edmunds 2002, Adam et al. 2011, Gilmour et al. 2013). Filamentous algal turfs are often the first to colonize newly exposed bare space (Diaz-Pulido & McCook 2002, Bonaldo & Bellwood 2009) and are fierce spatial competitors that retard coral recovery by inhibiting coral settlement and survival (McCook et al. 2001, Vermeij et al. 2009, Arnold et al. 2010). The reduction in herbivore biomass on coral reefs through human activities such as fishing has been linked to increases in filamentous algal turf cover (Bellwood et al. 2004, Smith et al. 2010), and researchers now recognize algal turf as a stable benthic state on many Indo-Pacific reefs (Smith et al. 2016). This trend is particularly worrisome because reefs that were once dominated by calcifying corals are now inhabited by fleshy non-accreting flora.

Directly following disturbances to coral reefs, the abundance of mobile herbivores, particularly parrotfishes, has been shown to respond positively to increases in the availability of algal resources (Adam et al. 2011, Gilmour et al. 2013). On decadal time scales, parrotfish abundance has been shown to track changes in benthic habitat that were the result of typhoons and coral bleaching events (Russ et al. 2015). Currently, it is not well understood how resource-induced responses in parrotfish behavior and distribution affect the fine-scale spatial and temporal patterns of algal removal and the creation of bare space. Variation in the fine-scale movement of parrotfish has been linked to numerous abiotic and biotic factors including proximity to shelter, intraspecific competition, changes in coral cover, as well as the particular life stage of the fish (Mumby & Wabnitz 2002, Maciá & Robinson 2005, Bonaldo et al. 2006, Nash et al. 2012, Davis et al. 2017a). However, the degree to which fine-scale foraging behavior changes in response to variation in preferred resources is not well documented. Modeling studies suggest that the spatial patterning of feeding by individual herbivores has the potential to influence coral–algal competition and thus the trajectory of a reef's benthic state (Sandin & McNamara 2012, Eynaud et al. 2016). In the Sandin & McNamara (2012) model, grazing by spatially constrained herbivores resulted in dense patches of bare space (i.e. bite scars) within a foraging territory. Conversely, homogeneous foraging by mobile herbivores resulted in single bite scars that are more uniformly distributed, isolated, and abut algal turfs or other space competitors on all sides. When modeled through time, these contrasting spatial patterns of grazing can result in different dominant benthic states (Sandin & McNamara 2012). Spa-

tially constrained grazing was predicted to be more beneficial to the long-term growth and recruitment of corals because the dense patches of bite scars alleviated the competitive pressure on coral recruits from invading algal turfs. However, it has been shown that incidental grazing by parrotfish is likely fatal to coral recruits and the abundance of scraping parrotfish has been linked to spatial differences in coral recruit mortality (Bak & Engel 1979, Penin et al. 2010). Therefore, a trade-off in parrotfish herbivory exists between the creation of bare space and the incidental removal of coral recruits (Mumby 2009).

In this study, we examined how 2 common coral reef habitat states, one dominated by algal turfs and one dominated by live coral and crustose coralline algae (CCA), influence the fine-scale foraging behavior of an important species of large, excavating parrotfish, *Chlorurus microrhinos*, on a remote Central Pacific atoll. We first quantified differences in habitat state using a variety of survey methods and measurements of algal turf recovery time post scraping (i.e. artificial parrotfish bite) across sites. We then quantified differences in foraging behavior through direct observations of fish as well as the spatial and temporal distribution (over meters and months) of bite scars across the benthos at each site. There were notable differences in the fine-scale foraging patterns of *C. microrhinos* between these 2 habitat states, leading to striking differences in the temporal and spatial patterns of algal removal and the creation of bare space. We report large swaths of continuous bare space that could potentially benefit coral settlement and survival. However, we also report frequent and intense bouts of regrazing that are likely fatal to newly settled recruits. We document 2 distinct foraging behaviors for a single species of herbivorous parrotfish at the scale of a backreef on a single atoll and consider how these differences in foraging behavior might affect the settlement and survival of foundational organisms such as corals.

MATERIALS AND METHODS

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 thereafter was prohibited. Decades prior to formal regulations, Palmyra's remoteness and lack of
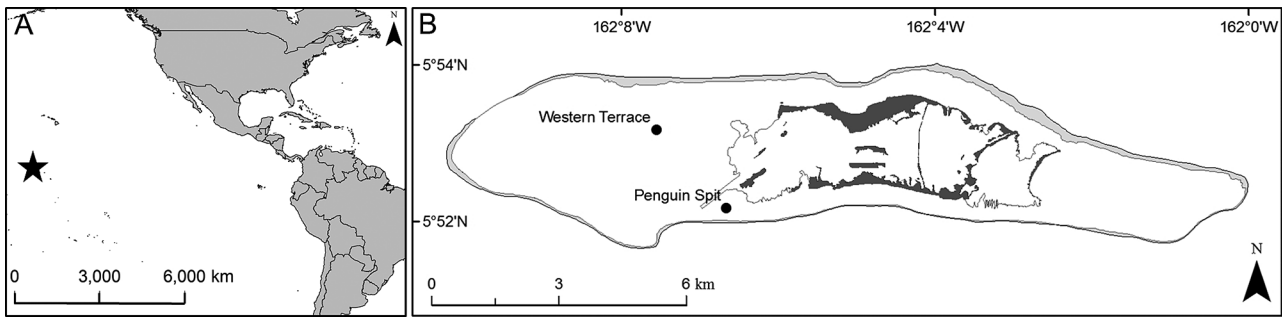
Fig. 1. (A) The location of Palmyra Atoll (★) in the Central Pacific, approximately 1500 km south of the Hawaiian Archipelago. (B) Palmyra Atoll, with the location of Penguin Spit and Western Terrace. The light grey shading marks the 30 m isobath and the dark grey shading represents land

an indigenous population afforded it a high level of protection. Palmyra provides a unique predator-dominated coral reef system with a high biomass of apex predators compared to other reefs in the Line Islands chain and around the world (Sandin et al. 2008). Additionally, there is a high biomass of primary consumers, including large-bodied parrotfish species, that are becoming increasingly rare on other Indo-Pacific reefs (Edwards et al. 2014).

In order to investigate the spatial patterns of foraging behavior, we selected 2 sites on Palmyra's extensive backreef habitat (Penguin Spit [PS] and Western Terrace [WT]; Fig. 1); one site exemplifies Palmyra's high level of live coral cover and CCA (WT), and the other represents a potentially more disturbed system dominated by low-lying algal turfs (PS). In Palmyra, there is some evidence for a mild bleaching event in 2009 following a larger event in 1998 that resulted in extensive coral mortality, and these events appeared to affect the shallow PS site particularly strongly (Williams et al. 2010). These sites were also selected because of similarities in depth and structural complexity (Carlson 2016) and are representative of 2 common benthic states found throughout the Line Islands chain (Sandin et al. 2008, Smith et al. 2016).

Study species

The steephead parrotfish *Chlorurus microrhinos* is a large-bodied (max. total length = 70 cm) parrotfish that is found throughout the Indo-Pacific. Their gape and strong jaw musculature allow them to excavate large sections (approximately 118 mm² 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 have led to rarity in some regions of their historical range (Edwards et al. 2014).

As is common within parrotfishes, *C. microrhinos* has 2 morphological phases, with an initial phase (IP) that includes male and female individuals, and a terminal phase (TP) that consists of larger males (Ebisawa et al. 2016). 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.

Habitat state

We characterized differences in habitat state between PS and WT in 2013 and 2014 to help explain observed variation in parrotfish foraging behavior. We quantified depth, rugosity, percent cover, and predator abundance between the 2 sites as potential explanatory variables. Additionally, in 2015 we manually etched artificial bite scars on substrates covered in mixed algal turf and tracked algal turf regrowth as a proxy for the differences in the recovery of benthic resources between the 2 sites.

We used uniform point contact (UPC) surveys to characterize benthic community composition and the physical habitat state at each site. Points were located at 1 m intervals along a 25 m transect. At each site, in each of the 2 years (2013, 2014) we conducted 8 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 assigned to one of 9 categories; live coral, mixed algal turf (see below), CCA, the green alga *Halimeda opuntia* (*Halimeda*), the brown alga *Lobophora variegata* (*Lobophora*), the corallimorph *Rhodactis howesii* (Corallimorph), bare calcium carbonate (bare), the

green alga *Dictyosphaeria cavernosa* (*Dictyosphaeria*), or other fleshy macroalgae. The term mixed 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). For this study, we did not measure the species composition present in the EAM, and therefore we will be referring to this diverse group of short (<2 cm) filamentous turf algae as 'mixed algal turfs'. The 'bare' category represents areas that had recently been grazed, leaving the calcium carbonate structure exposed. For further descriptions of the rugosity measure and cover categories, see Supplement 1 (all supplementary materials in this article can be found at www.int-res.com/articles/suppl/m577p165_suppl.pdf).

To test for differences in benthic assemblages at the site level, we used the percent cover transect data and treated each transect as a replicate within a multinomial framework to characterize the available resources at the site level (Barott et al. 2012). Each transect is represented by a point in multinomial space with the observed percent cover determining its position along that particular cover category's axis. Conceptually, this creates a cloud of points for each site, and we computed the Euclidean distance between the observed cover data for each site in multinomial space. To estimate the probability of a site effect, we tested this distance against a randomized resampled null distribution, where the site name was randomly assigned to each point in multinomial space and a null Euclidean distance was calculated. This process was repeated 10 000 times to create a null distribution against which we could test whether our observed Euclidean distance fell within the 95% confidence intervals (for further details, see Supplement 2). Only the benthic categories CCA, *Halimeda*, live coral, *Lobophora*, bare, and mixed algal turfs, which we observed in the diet of *C. microrhinos* (see 'Fish abundance and behavior', below), were included in the multinomial analysis.

Predator abundance has been shown to influence the foraging patterns of marine and terrestrial species (Preisser et al. 2005); thus, to characterize the relative risk of predation on TP *C. microrhinos* at a particular site, we calculated the biomass and density of piscivores greater than 30 cm total length (as kg ha^{-1}). We conducted visual surveys during the summer of 2013 and 2014 using a belt transect method (n = 9 transects site^{-1} yr^{-1}; see Hamilton et al. 2014 for a description of methods). We log transformed the resulting data and used Student's *t*-test to test for differences between sites.

To investigate the regrowth rate of benthic food resources at PS and WT, we measured bite scar recovery (i.e. mixed algal turf regrowth) rates from artificial disturbance over 12 d during September 2015. Access to the study site at WT was prevented because of large swell, so we selected the nearest site possible (<500 m from WT) that had a similar depth profile and benthic assemblage. A single observer (P. M. Carlson) etched artificial bite scars (approximately 0.66 × 3.3 cm) into dead coral heads covered in mixed algal turfs using a standard flathead screwdriver to create a 2.2 cm^2 bare area that removed only the top 3–4 mm of mixed algal turf and associated dead coral skeleton. In all cases, the top layer of algal turf and dead coral skeleton was easily removed and scars were consistently the same depth and length. Prior to etching, we preformed extensive *in situ* assessments of natural bite scars to ensure that our artificial bite scars matched the depth and length of natural scars at Palmyra. Three sets of 3 parallel scars (for a total of 9 scars) were made on each coral head and caged within one 0.5 × 0.5 m PVC cage that was open on all sides. Cages were topped with a soft plastic mesh with large-diameter openings (10 × 10 cm) and cleaned every 3 d to minimize the effects of shading. Cages were designed to exclude large excavating parrotfish such as *C. microrhinos* so that recovery could be measured without further grazing. There were a total of 5 cages at each site, each containing 3 sets of scars for a total of 15 sets of scars per site.

A single observer (P. M. Carlson) photographed each group of scars along with a 5 cm measuring tape. We analyzed photos by adapting existing image analysis techniques within ImageJ 1.48V to track the recovery of mixed algal turf within the artificial scars by comparing the pixel intensity histogram (i.e. color values) of the scar to the pixel intensity histogram of the surrounding, undisturbed mixed algal turf. We compared the color values for the artificial scar and undisturbed mixed algal turf within a single photo using an Earth Mover Distance (EMD; Rubner et al. 2000, Andoni et al. 2008) metric and estimated the percent recovered (i.e. how closely the color of the artificial scar matched the adjacent undisturbed algal turf) at Day 0, 6, and 12. For more information on the pixel intensity histogram calculation, EMD cost theory, and the EMD calculation, see Supplement 3.

Fish abundance and behavior

In 2014 we characterized the abundance and foraging behaviors of *C. microrhinos* at PS and WT to

understand how differences in habitat state relate to differences in herbivory and the creation of bare space. We quantified *C. microrhinos* abundance, social structure, and diet preference, tracked the spatial and temporal trends of bite scars, and calculated numerous spatial metrics derived from repeated 2 h behavioral observations.

To quantify the abundance of our study species, we conducted targeted *C. microrhinos* density surveys 3 times at PS and 3 times at WT during the summer of 2014, with approximately 10 d between each survey. Each survey was conducted by a single observer (K. Davis) and consisted of six 50 × 4 m belt transects that were not fixed but were in approximately the same location relative to a fixed boat mooring. The observer recorded the number, total length, and color (morphological) phase of all *C. microrhinos*. We calculated the density and biomass for each color phase at each site using length–weight conversion factors compiled by the NOAA Coral Reef Ecosystem Program (Heenan et al. 2014). We used targeted *C. microrhinos* survey data to assess the differences in conspecific competitor size and color phase structure as a proxy for differences in the social structure between PS and WT.

We quantified *C. microrhinos'* preference for biting on each benthic substrate type in relation to its availability in the environment through feeding observations conducted in 2013 and 2014 that were between 5 min and 1 h long. A feeding observation consisted of one observer, on snorkel, following an individual fish and recording the number of bites as well as the primary substrate bitten. A total of 5669 bites were observed during 11 and 13 bite composition observations at WT and PS, respectively. The data showed little variability between individual fish or years, thus the data were pooled by site. Diet preference was then calculated for mixed algal turfs, CCA, live coral, *Halimeda*, *Lobophora*, and bare using Manly's alpha of selectivity (Chesson 1983, Hamilton et al. 2014). In this analysis, an alpha level of 0.166 represents a preference threshold for 6 substrate types, with values below indicating avoidance and values above indicating preference for a particular substrate in relation to its availability in the environment.

In 2013 and 2014 we assessed the spatial distribution of *C. microrhinos* bite scars (i.e. clustered versus homogeneous feeding) across each site by recording the density of bite scars within a 0.5 × 0.5 m quadrat every meter along a 25 m benthic transect. We only recorded bite scars that were 2–3 d old (the benthos recovered from parrotfish feeding in a consistent fashion, with small filaments of red algal turf appearing within the surface of the feeding scar by Day 4,

documented in the bite scar time series discussed below). *C. microrhinos* was the most common large excavating parrotfish observed at each site and their feeding scars were easily distinguishable from those of other parrotfishes because of the scar's depth and length. We used the Bartlett test of homogeneity of variances and found that variance differed significantly between sites and that the distribution of both data sets was highly skewed, in many cases with zero or one bite scar present; thus, we used a Wilcoxon test for non-parametric data to test for a difference in bite scar density between sites.

We documented the timing and intensity of feeding episodes by tracking the origination of new bite scars on designated dead coral heads from July to August 2014. We first identified dead coral heads that had high densities of *C. microrhinos* bite scars and then photographed the exact same locations every 4–5 d over the course of 9 wk (n = 15 at PS; n = 11 at WT). The area surveyed was calculated using ImageJ 1.48V. We used a 0.5 × 0.5 m quadrat in the same position on the coral head in each photo to set the pixel per m^2 scale of the photo. We then traced distinct features on each coral head to create area boundaries that were kept consistent throughout the study. Each photo was taken at the same orientation to the coral head and we took care to avoid areas of high rugosity that would over- or underestimate the area surveyed. We only counted new bite scars that were not present in the preceding photo in the time series. We plotted the bite scar density through time and measured the number of days between calculated 'peaks' of bite density. All bite densities are presented as number m^{-2}. For further details about the bite scar photography, image analysis, and 'peak' calculation, see Supplement 4.

We generated numerous spatial data metrics to compare *C. microrhinos* space use and foraging behavior between PS and WT. We identified 10 individual TP *C. microrhinos* (5 at PS, 5 at WT) by their unique coloring and distinguishable scars (e.g. missing scales and cut fins) and conducted repeated 2 h spatial behavioral observations on the same individuals from July to September 2014 (n ≥ 5 obs. ind.$^{-1}$). For each observation, a snorkeler followed the fish and the location of the individual was recorded every 5 s on a Garmin GPSMap 78sc handheld GPS. Each observer synchronized their wristwatch with satellite time on the GPS before every track and recorded the exact start and stop time of the 5 most common activities (feeding, territorial defense, defecating, cleaning, and swimming). Territorial defense was defined as any interaction where a focal fish or conspecific

would swim aggressively towards another fish, often displacing one individual or posturing (e.g. raising dorsal fins and releasing excrement) along apparent boundary lines. We watched each individual *C. microrhinos* for 3–5 min before starting the observation to ensure that the fish was unaffected by the observer's presence. Once the observation began, the snorkeler positioned the GPS float above the focal fish or as close as possible without disrupting their behavior (usually <1 m). Fish were not disturbed by the observer's presence and consistently maintained normal behavior throughout each observation (e.g. consistent bite rate and regular trips to cleaning stations). Spatial point data were then categorized into one of the 5 activities.

The 2 h spatial behavioral data were used to characterize the movement, space use, and foraging behavior of *C. microrhinos* at WT and PS. We calculated the 95% kernel utilization distribution (KUD), pathway length, site fidelity, and average foray feeding time for each 2 h observation in the Geospatial Modeling Environment (GME) 0.7.3.0 platform that interacts with the open source statistical software R version 3.1.0. From the benthic surveys, we compared the standard deviation (SD) and the mean percent cover of mixed algal turfs at each site and found that the SD was less than the mean, indicating a fairly even distribution of mixed algal turfs across each site. Therefore, we used the site-level percent cover to calculate an estimate of mixed algal turf within each individual's 2 h 95% KUD.

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 a mixed-effects model framework (R package 'lmer4'; Bates et al. 2015) to account for repeated measures in the experimental design (multiple 2 h observations on the same individuals). We structured the models so that each individual fish was treated as a random effect nested within site. The 2 h 95% KUD area, the estimate of mixed algal turf per 2 h 95% KUD area, and the average feeding foray time data were log transformed to improve the spread of the residuals and reduce the influence of outliers in the model. We used the Bartlett test of homogeneity of variances to confirm homoscedasticity of the spatial data metrics between sites. We calculated the probability of a site effect for each metric by comparing the full model (with site) and the reduced model (without site). We ran a likelihood ratio test between the full and reduced model using the 'ANOVA' function within R and then calculated the least squares means of the untransformed data for both sites using the 'lsmeans' package and 'ref.grid' function in R (Lenth 2016) to estimate the magnitude and direction of the difference between sites for each metric. For complete descriptions on the spatial model parameters used and GPS error measurement, see Supplement 5.

RESULTS

Habitat state

WT and PS show similarities in depth and rugosity, indicating that habitat structure at each site was similar (see Supplement 6). We also found no significant difference in the biomass of piscivores greater than 30 cm between the 2 sites ($t = 0.24$, df = 19, $p = 0.56$, mean biomass ± SE: PS = 359.3 ± 82.0 kg ha^{-1}; WT = 471.9 ± 216.5 kg ha^{-1}). The most numerically abundant piscivores at both sites belonged to the families Lutjanidae, Serranidae, and Carangidae.

The composition of benthic resources available for *Chlorurus microrhinos* feeding differed significantly between the sites. PS consisted of mixed algal turfs (45.5%), live coral (21.0%), and corallimorphs (14.0%), while WT was characterized by live coral (35.5%) and CCA (22.2%), with mixed algal turfs comprising only 10.0% of the benthic cover (Fig. 2A). Multinomial analysis of the percent cover data showed that PS and WT separated strongly and the availability of benthic resources was significantly different between the 2 sites.

We found that benthic food resources recovered from scarring more quickly at PS than at WT. Recovery of mixed algal turf after our experimental disturbance was significantly greater at PS, the site with greatest percent cover of this food resource, by Day 6 (Day 6 mean PS = 44.21%, WT = 16.10%, $\chi^2_1 = 15.745$, $p < 0.0001$) and continued to Day 12 (Day 12 mean PS = 84.96%, WT = 31.45%, $\chi^2_1 = 242.65$, $p < 0.0001$; Fig. 2B). Three of the artificial scars at PS were estimated as 100% recovered at Day 12, while the greatest recovery observed at WT was 45.3%.

Fish abundance and behavior

The biomass and density of TP *C. microrhinos* was much higher at PS (mean ± SE, 21.72 ± 2.57 g m^{-2} and 7.67 ± 0.88 ind. 1200 m^{-2}) compared to WT (4.39 ± 1.61 g m^{-2} and 1.33 ± 0.33 ind. 1200 m^{-2}), while the mean biomass and density of IPs at PS (0.032 ± 0.032 g m^{-2} and 0.33 ± 0.33 ind. 1200 m^{-2}) was much
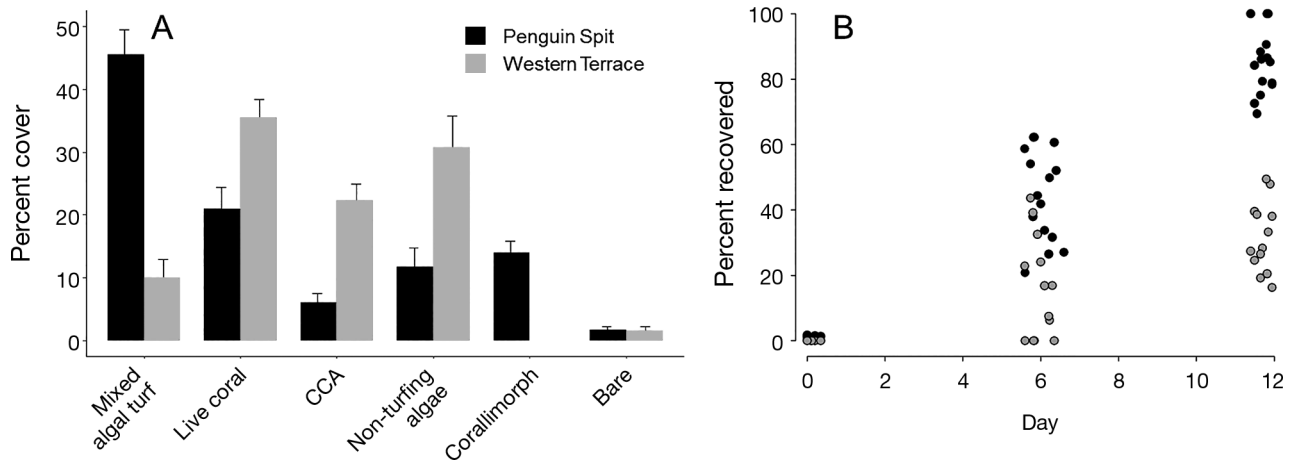
Fig. 2. Differences in habitat state between Penguin Spit (PS) and Western Terrace (WT) at Palmyra Atoll. (A) Differences in percent cover of benthic substrate (i.e. benthic resources) between PS and WT estimated from benthic point contact surveys (n = 400 points) done in 2013 and 2014 (error bars represent SE). CCA: crustose coralline algae. (B) Differences in the recovery rate of mixed algal turf within artificial bite scars on dead coral heads at PS and WT on Days 0, 6, and 12

less compared to WT (2.09 ± 0.93 g m^{-2} and 2.33 ± 0.88 ind. 1200 m^{-2}). Our observations at PS confirmed that IPs were relatively scarce compared to WT and other sites on Palmyra's backreef.

Diet selectivity analysis showed that *C. microrhinos* had a strong diet preference for mixed algal turfs compared to the other benthic resources present at each site (Manly's α = 0.166, PS = 0.873; WT = 0.511; see Fig. S1 in Supplement 7).

Bite scar densities were significantly greater at PS compared to WT (Wilcoxon rank sum $Z = -7.102$, p < 0.0001). The maximum recorded bite scar density was at PS (320 bites m^{-2}), and 8% of the quadrats surveyed along randomly placed benthic transects at PS had bite scar densities greater than 100 bites m^{-2} (Fig. 3). In contrast, the maximum recorded bite scar density at WT was 76 bites m^{-2}.

The bite scar time series dataset from PS was characterized by distinct peaks in new bite density followed by periods of little activity (Fig. 4A). WT was characterized by a steadier, more consistent appearance of new bites over time that indicated a more temporally homogeneous feeding pattern (Fig. 4A). Fig. 4 shows 3 locations from PS and WT that are representative of the entire bite scar time series dataset (for all bite scar time series plots, see Fig. S2 in Supplement 7). Only the bite density time series data at PS met our criteria of containing 'peaks'. Time between peaks in bite density showed a considerable amount of variability, with the minimum and maximum interval being 7 and 56 d, respectively. The median peak interval was 19.0 d and the first and third quartiles were 16 and 34 d, respectively (Fig. 4B).
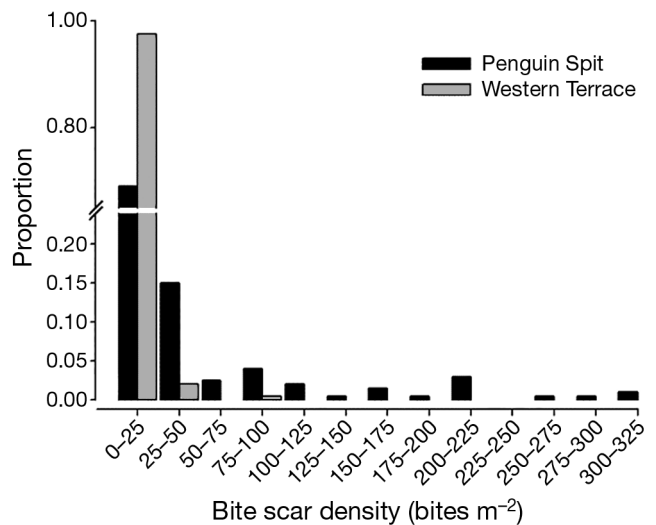

Fig. 3. Proportion of quadrats with *Chlorurus microrhinos* bite scars on the benthos at Penguin Spit and Western Terrace in 2013 and 2014

In general, fish moved more and foraged over greater areas at WT relative to PS. There were significant differences between sites in the 2 h 95% KUD area measurements, with WT areas approximately 3 times larger than areas at PS ($\chi^2_1 = 6.73$, p = 0.009, LS means ± SE: PS = 251.7 ± 150 m^2, WT = 797.0 ± 150 m^2; Fig. 5A). Pathway length was also significantly different between sites, with fish at WT swimming 41.0% further over a 2 h period ($\chi^2_1 = 7.5214$, p = 0.006, LS means ± SE: PS = 1148.0 ± 110 m, WT = 1619.5 ± 112 m; Fig. 5B). Site fidelity did not differ between sites; the inter-centroid distances between multiple measurements of an individual's 2 h foraging area were low
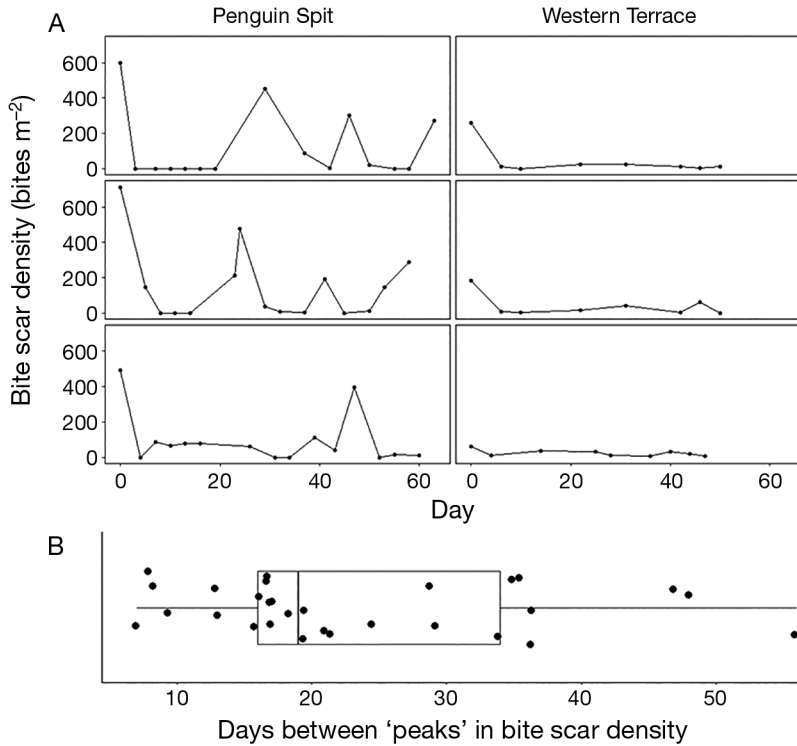
Fig. 4. (A) *Chlorurus microrhinos* bite scar density through time measured at 2 sites on Palmyra Atoll, Penguin Spit (PS) and Western Terrace (WT). (B) Box and whisker plot showing the time period between consecutive 'peaks' in bite scar density from photo plots of time series at PS. Only data from PS met our criteria of having 'peaks'. Boxes represent Q1 = 16 d, Q2 (median) = 19 d, and Q3 = 34 d. Points are offset for better visualization

The estimated amount of mixed algal turf within a 2 h 95% KUD area was not significantly different between PS and WT, indicating that *C. microrhinos* maintains a 2 h area containing the same amount of preferred resource at both sites ($\chi^2_1 = 0.1904$, p = 0.662, LS means ± SE: PS = 114.57 ± 28.16 m^2; WT = 106.02 ± 28.17 m^2); to do this, individuals maintain a much larger feeding area at WT (see above).

DISCUSSION

Fine-scale space use and grazing patterns of *Chlorurus microrhinos* appear to be most closely related to the abundance and growth rate of their preferred resource, algal turf, while other key characteristics were similar between sites (rugosity, depth, and apparent predation risk). When resources were abundant (as at PS), *C. microrhinos* minimized movement and focused feeding on patches of algal turfs. When resources were more scarce (as at WT), *C. microrhinos* increased the scales of movement and feeding behavior was spread over a larger area, resulting in a dispersed distribution of bite scars. Our results are congruent with other studies that reported constrained grazing behavior by *C. microrhinos* despite their large size and mobility (e.g. Welsh & Bellwood 2012), but here

and not different between PS and WT once we had controlled for the size of each foraging area ($\chi^2_1 = 0.9882$, p = 0.38). Finally, fish at PS had significantly longer feeding forays than fish at WT ($\chi^2_1 = 4.4185$, p = 0.035, LS means ± SE: PS = 98 ± 12 s; WT = 68 ± 12 s).
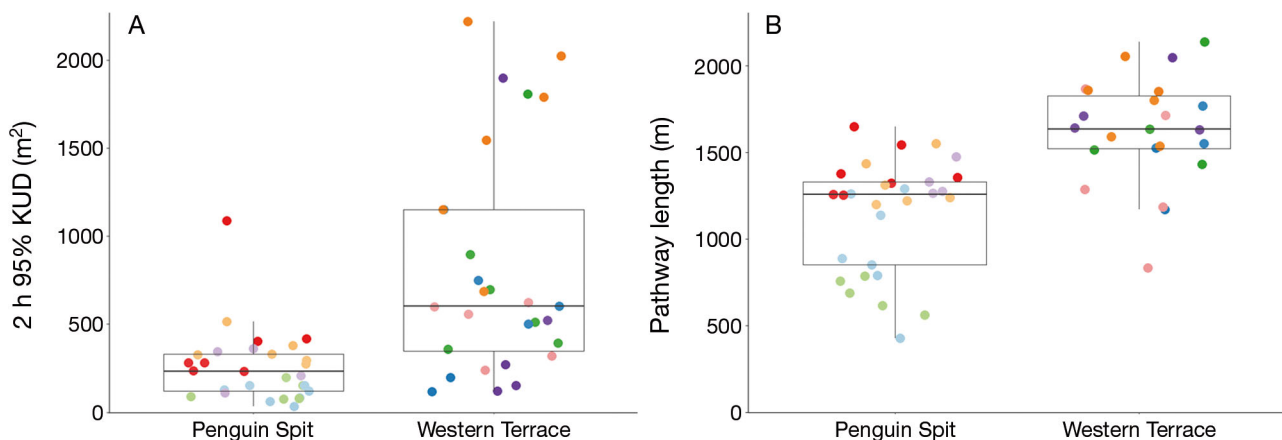

Fig. 5. Box plots showing (A) area of the 95% kernel utilization distribution (KUD) and (B) pathway length from 2 h focal following bouts of *Chlorurus microrhinos* at Penguin Spit and Western Terrace. Each color represents a unique individual that was followed on at least 5 separate occasions from July to September 2014, and the points are offset for better visualization. Boxes are 1st and 3rd quartiles, center line is median

we document strong variation in this feeding behavior at the scale of a backreef on a single atoll. This study, along with others, suggests that changes in benthic resource availability due to coral loss or recovery can potentially alter foraging behaviors; however, those responses may be species specific (Nash et al. 2012). The abundance of *C. microrhinos* also appears to be related to preferred food abundance, as would be expected under most foraging models (Fretwell & Calver 1969, Schoener 1971, Charnov 1976), and this observation agrees with other studies that relate the abundances of parrotfishes to the abundance or growth rates of preferred food (Adam et al. 2011, Gilmour et al. 2013, Tootell & Steele 2016).

Grazing by *C. microrhinos* at fine spatial scales can result in dense patches of feeding scars (>100 bites m^{-2}) where turf algae are removed and swaths of calcium carbonate substrate are exposed (Bellwood & Choat 1990). The density of bite scars recorded in this study is among the highest ever reported on algal turf and is almost twice as large as published values from Orpheus Island on the inner shelf of the Great Barrier Reef (Welsh & Bellwood 2012, but see Bonaldo & Bellwood 2011 for higher bite scar densities on living corals). These patches provide a potentially more favorable habitat for corals at the earliest life stages, as opposed to a substrate covered mostly in algal turfs with scattered, isolated bite scars (Arnold et al. 2010, Sandin & McNamara 2012). Coral recruit density has been shown to be highest when algal cover is lowest (Edmunds & Carpenter 2001, Vermeij et al. 2009), and coral planulae are particularly susceptible to algae-induced, microbe-mediated mortality during their benthic exploration and settlement phase (2–7 d post spawn; McCook et al. 2001, Vermeij & Sandin 2008). A large amount of mortality occurs during this time and this stage may represent a bottleneck for coral planulae survival. However, note that at PS, *C. microrhinos* revisit particular feeding locations at an interval of approximately 16 to 34 d. While the chronic grazing by parrotfish at particular locations may result in the consistent removal of algae and creation of bare space, the excavating nature of the bites (Bak & Engel 1979, Green et al. 2009) is likely fatal to a recently settled coral planula. The risk of incidental predation for young corals is likely dependent on species-specific growth rates and the size at which a coral is no longer susceptible to grazing. Further, coral settlement tends to occur in cryptic habitats (Price 2010), so the effects of incidental parrotfish predation may be location dependent. In those cases, the ability of grazing to keep surrounding, noxious algal turf at low levels could potentially outweigh the negative effects of incidental predation. Hence a trade-off in benefits to coral settlers through herbivory exists between settlement/recruitment facilitation and incidental grazing-induced mortality (Mumby 2009).

The interplay of grazing, coral planulae settlement, and re-grazing (which can remove coral recruits) is further complicated by the fact that areas with the densest patches of bite scars also had the most rapid regrowth of algae. At PS we estimated that the benthos was 44 and 85% recovered from artificial bite scarring by Day 6 and 12 respectively, so the temporal window for coral settlement on bare calcium carbonate may be relatively short. However, the pattern of regrazing suggests that the window for settlement on bare substrate opens and closes frequently. Although we did not measure coral planulae survival success under different frequencies of parrotfish feeding bouts and algal recovery times, it is worth noting that time between peaks in grazing, mixed algal turf recovery time, and the time period when coral planulae are most susceptible to algal turfs are all at similar temporal scales (McCook et al. 2001, Vermeij & Sandin 2008). While the creation of large grazed spaces (as modeled by Sandin & McNamara 2012) in high-production areas might be considered conducive to coral recruitment, the associated rapid algal recovery after grazing and frequent re-grazing in these same areas can have the opposite effect. This is an intriguing area of future research that could clarify the connection between spatial patterns of grazing by large herbivores and coral recruitment success.

Our results indicated that the social structure of *C. microrhinos* can also vary at the scale of a single backreef. We observed that IP individuals were rare at PS, while TP males at that site were numerous and achieved some of the largest sizes we have observed across Palmyra. Social systems in many parrotfishes are characterized by a dominant TP male that defends a territory associated with a harem of IPs, with whom mating frequently occurs (Mumby & Wabnitz 2002), and fish at WT appeared to be associating in this more commonly reported haremic social structure. Although we did not directly test the differences in the social structure and mating system of *C. microrhinos* at Palmyra, there is evidence from acoustic telemetry done in conjunction with this project that *C. microrhinos* regularly leave their feeding area and travel offshore, likely for mating purposes (Davis et al. 2017b, this volume). This finding suggests that TP males at PS are exploiting high-yield food patches

and may be traveling to offshore locations for mating (Johannes 1978). These observations are discussed more in detail in Davis et al. (2017b) and provide an interesting framework for future research about reproductive behavior and social systems in pristine systems, where competition for food and mates is high.

The overall abundance of herbivores on Palmyra's reefs is high, hence our study site did not allow us to test whether the spatially constrained behavior and high bite scar densities reported here are a function of intense conspecific competition at PS, or whether an abundance of a preferred resource by itself reduces movement and concentrates foraging behavior. At PS we observed fish grazing on a particular patch of mixed algal turf and returning there to graze after trips to cleaning stations and bouts of territorial defense. It was our impression that *C. microrhinos* deliberately focused its feeding effort when resources were plentiful, and this closely matches the predictions of optimal foraging theory in patchy environments (Ford 1983). It has been shown that competition can structure space use in parrotfishes (Mumby & Wabnitz 2002, Davis et al. 2017a), and it is possible that intraspecific competition is important in species with highly specialized diets and that the large number of TP *C. microrhinos* at PS is perhaps related to the constrained movements and periods between intense grazing bouts that we report.

Sites dominated by mixed algal turfs that regrew quickly (similar to PS) were rare on Palmyra's reefs, and therefore we were limited by the number of replicate treatments we could test. However, at PS we documented recurring feeding behavior, with fish grazing, defending, and regrazing particular coral heads covered in mixed algal turf. While the interval between intense grazing episodes was highly variable, the timing of regrazing is potentially related to growth rates of epilithic and endolithic algae and bacteria (Clements et al. 2016). Similarly, the ability of the reef at PS to support a large biomass of *C. microrhinos* and elicit intense bouts of grazing by parrotfish is perhaps related to the community composition of epilithic and endolithic algae and bacteria (Clements et al. 2016). Specific dietary targets of *C. microrhinos* at Palmyra will be the focus of future studies.

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 which appeared to greatly reduce coral cover at the shallow PS site (Williams et al. 2010). Disturbance events such as these have been linked to increases in algal turf cover on other reefs around the world (Diaz-Pulido & McCook 2002, Gilmour et al. 2013), and this may

have been when PS switched from a predominantly coral-covered benthos to one covered by algal turfs. We do not know whether the PS site is on a trajectory of recovery towards a more coral-covered state or whether intense grazing is inhibiting coral recruitment and survival. However, understanding the potential conflict between grazing as an activity that opens space for coral settlement and grazing as a source of mortality for young corals will provide better assessments of reef recovery from disturbance and can better inform potential management strategies. We observed that in an unfished system, spatially and temporally intense foraging behavior of a large herbivore may influence coral–algal competition at the earliest, most vulnerable stage in the coral's life history. However, the potential effects are paradoxical: intense grazing opens space for coral recruitment, but rapid algal recovery and repeated re-grazing inhibits coral recruitment.

This study highlights the extreme variability that is possible over a small spatial scale and suggests that it may be misleading to use small-scale studies for broad characterizations of important ecosystem functions. Herbivory in marine systems can be a strong top-down control that ultimately determines the abundance and distribution of foundational ecosystem elements. Grazer behavior can be wide-ranging even at small spatial scales, and accurately forecasting the role herbivory plays in structuring the distribution of benthic biota requires a better understanding of the magnitude of variation in herbivore behavior and the potential for benthic resources to induce feedbacks between herbivores and herbs.

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