

Structural complexity shapes the behavior and abundance of a common herbivorous fish, increasing herbivory on a turf-dominated, fringing reef

Judith Santano^a, Isaiah A. Milton^{b,1}, Bianca Navarro^{c,1}, Raines M. Warren^{d,1}, Paul H. Barber^c, Peggy Fong^c, Caitlin R. Fong^{e,*}

^a Stanford University, Earth Systems Program, 371 Serra Mall, Stanford, CA 94305, United States of America

^b Hampton University Department of Marine and Environmental Science, 100 Queen Street, Hampton, VA 23664, United States of America

^c University of California Los Angeles, 621 Charles E. Young Drive South, Los Angeles, CA 90095, United States of America

^d Howard University Department of Biology, 415 College Street NW, Washington, DC 20059, United States of America

^e California State University Northridge, Department of Biology, 18111 Nordhoff St, Northridge, CA 91330, United States of America

ARTICLE INFO

Keywords:

Coral reefs
Herbivory
Herbivore behavior
Complexity
Resource
Refuge

ABSTRACT

Coral-dominated reefs typically have abundant refuges and limited resources for herbivores; conversely, algal-dominated reefs have abundant resources but often have limited refuges. This difference results in a trade-off between risk and reward for herbivorous fishes. However, disturbances that kill coral but retain topographic complexity can decouple this tradeoff, challenging this paradigm. Many fringing reefs in Moorea, French Polynesia are algal-dominated with heterogeneous structural complexity likely driven by disturbances associated with crown-of-thorns predation and typhoons, which occurred between 2006 and 2010. Short turfs are a good recruitment surface for coral larvae, and thus has a greater potential to recover to coral dominance than long turfs. To explore how variation in complexity impacts the behavior of herbivorous fishes, we compared abundance, residence time, and time budgets of *Acanthurus nigrofuscus*, a common herbivore species, in paired high versus low complexity areas. We chose areas in close proximity to maximize the likelihood fish could choose between complexity types. We also measured turf height in high versus low complexity plots. Fish were $\sim 3\times$ more abundant, spent roughly double the time in, and budgeted more than $4\times$ as much time to hiding in high complexity reef areas. Although, on average, individual herbivores spent the same proportion of time foraging in both areas, their greater abundance and longer residence time suggests their local herbivory rates could be 7.5 times higher in high complexity areas. We also found turfs in high complexity plots were roughly 75% the height of turfs in low complexity plots. This provides some evidence for stronger overall herbivory pressure in high complexity areas, albeit differences in absolute turf height were modest (~ 0.5 mm). Combined, these results suggest reefs that retain structural complexity following disturbance may be more likely to recover due to the higher localized herbivory rates resulting from uncoupling of the tradeoff between structural complexity and resource limitation.

1. Introduction

Worldwide, tropical reefs are shifting from coral to algal dominance (Bellwood et al., 2004; Hughes et al., 2017) with concomitant shifts in trade-offs between availability of resources and refuges from predators (Randall, 1965; Steele, 1999; Almany, 2004; Fong et al., 2018). For example, coral-dominated areas have high complexity that provides ample refuge for herbivores but low algal resources (e.g. food). While large, stand-forming macroalgae can provide both food and shelter (e.g.

Hoey and Bellwood, 2011; Bittick et al., 2018), algal turfs are early colonizers post disturbance (Pratchett et al., 2008; Adjeroud et al., 2009; Gilmour et al., 2013) and typically have lower complexity with limited refuge for herbivores, but support higher algal resources (Randall, 1965; Steele, 1999; Almany, 2004). This separation of food and shelter creates a trade-off between resources and refuge that is tightly coupled to the structure of the benthos, which can vary at the meter scale.

Among other factors, trade-offs based on benthic complexity can reinforce the stability of both coral and algal-dominated states (Graham

* Corresponding author.

E-mail address: cat.r.fong@gmail.com (C.R. Fong).

¹ Equal middle authors.

and Nash, 2013; Muthukrishnan et al., 2016). This connection exists because benthic structure can drive patterns in both fish abundance (Almany, 2004) and fish behavior (Fong et al., 2018), directly shaping local rates of herbivory (Madin et al., 2011). For example, high complexity reefs attract herbivorous fishes, resulting in ‘reef halos’, areas adjacent to the reefs that are denuded of primary producers (Madin et al., 2011). Therefore, reduced complexity in algal-dominated versus coral-dominated reef areas could provide a mechanism that contributes to the empirically-quantified positive feedbacks of high herbivory in coral states and low herbivory in algal states (Muthukrishnan et al., 2016). This positive feedback with the benthic community on the critical controlling force of herbivory may be one reason some reefs are governed by alternative stable state dynamics (Muthukrishnan et al., 2016). In short, trade-offs between resources and refuge that are tightly coupled to the structure of the benthic community could influence whether a community recovers following disturbance by shaping local patterns of herbivory.

A core assumption of this paradigm is that resources and refuge are trade-offs; however, that assumption may not be true for all types of disturbances. Specifically, disturbances that leave the physical structure of the reef intact may decouple the relationship between benthic state, refuge, and resources. For example, when reefs lose coral cover due to crown-of-thorns outbreaks or bleaching, the underlying structure can persist for years (Sano et al., 1987; Garpe et al., 2006), resulting in a structurally complex, algal turf-dominated landscape that is both high in food resources and refuge availability. This greatly contrasts physical disturbances like hurricanes that flatten reef structure. Thus, disturbances that leave structure intact disrupt the paradigm that resources and refuge present a trade-off on reefs, potentially impacting herbivory rates on algal communities, a key process in facilitating recovery from an algal to coral dominated state (e.g. Bellwood et al., 2004; Adam et al., 2011; Muthukrishnan and Fong, 2018).

Algal turfs are important early colonizers following disturbances on coral reefs (Pratchett et al., 2008; Adjeroud et al., 2009; Gilmour et al., 2013), and represent transitional communities that mediate shifts to either coral or macroalgal dominance (Bellwood et al., 2004; Muthukrishnan et al., 2016; Fong et al., 2020). Closely-cropped algal turfs are highly productive and are the preferred food resource for many herbivores (Adey and Goertemiller, 1987; Bellwood et al., 2004; Vroom, 2011). Importantly, coral larvae can colonize short, cropped turfs (Jompa and McCook, 2003; Birrell et al., 2005), facilitating coral recruitment and subsequent recovery to coral dominance (Pratchett et al., 2008; Adjeroud et al., 2009; Gilmour et al., 2013). However, when ungrazed and/or sediment-laden, longer turfs may transition into macroalgae (Hughes et al., 2007; Lewis, 1986; Fong et al., 2020) that inhibit coral recruitment and compete with coral for space, potentially delaying or precluding coral recovery (McCook et al., 2001; Bellwood et al., 2004; Fong and Paul, 2011). Crucially, transitions between short and long turfs occur on the scale of millimeters in height; for example, productivity of algal turfs drops sharply with increasing height, with the most precipitous declines in the first few increases in millimeters (Tebbett and Bellwood, 2020). Thus, understanding how the structural complexity of disturbed reefs affects utilization by herbivorous fishes and localized herbivory rates is key to understanding the potential capacity of reefs to recover.

To examine the relationship between structural complexity, fish abundance and behavior, and localized herbivory rates, we quantified turf height and herbivorous fish abundance, residence time, and time budgets in adjacent patches of high and low complexity within a turf-dominated coral reef community following a period of biological and physical disturbance on the island of Moorea, French Polynesia.

2. Methods

Reefs of Moorea are recovering from two major disturbances. From 2006 to 2010, an outbreak of the corallivore *Acanthaster planci* killed

much of the coral while leaving reef structure intact; this outbreak was followed by a tropical cyclone in 2010 (Adjeroud et al., 2009; Adam et al., 2011; Kayal et al., 2012; Edmunds et al., 2019). Combined, it is likely these disturbances are what caused this algal turf-dominated landscape, with variation in topographic complexity where some areas retained higher topographic complexity while others became a lower complexity mix of rubble, hard bottom, and sand. Importantly, the herbivorous fish community remained relatively unchanged following these disturbances (Han et al., 2016), and there was even a boom in the abundance of juvenile parrotfishes (Adam et al., 2011), resulting in increased herbivory potential.

To determine how fish foraging behavior may vary across the resulting areas of high and low structural complexity, we quantified 1) fish abundance, 2) fish residence time, and 3) fish behavioral budgets. Our fieldwork was conducted during the first week of July 2018 on a fringing reef in the lagoon along the north shore of Moorea, French Polynesia that is proximal to the town of Maharepa (17°28.94S, 149°48.88 W: same site as Fong et al., 2018, Fig. 1). This reef is dominated by short algal turfs, macroalgae, and by small patches of remnant corals, as are many fringing reefs of Moorea (Adam et al., 2011) and globally (Vroom, 2011). This site was close to the Moorea Long Term Ecological Research site 2, and we were able to compile annual averages of benthic cover for this site to contextualize our study (Edmunds, 2020) (Fig. 2). We chose this site because it was dominated by short algal turfs (~ 1 mm, see results), a critical state that can mediate transitions to macroalgae on reefs (Fong et al., 2020). Further, due to a series of disturbances, this site is comprised of areas of lower complexity immediately adjacent to areas of higher complexity, allowing for a paired experimental design. Pairing helped us maximize the likelihood that individual fish could choose between complexity types within their home ranges.

To compare fish behavior and abundance in high versus low complexity states, we established three pairs of 2 × 2 m plots where each high complexity plot was adjacent to and within 1 m of a low complexity plot ($n = 3$ of each type); paired plots were at least 10 m apart from each other and were between 2 and 3 m in depth (Fig. 3). This size plot was also easily observable by an individual on snorkel. Following Fong et al. (2018), these plots were small enough and close enough together for individual fish to move between plots, which we observed, providing fish the opportunity to choose between pairs.

To quantify the topographic complexity of these 6 plots, we measured rugosity by laying a flexible chain over the benthos for two planar meters. We laid three replicates across the length and three across

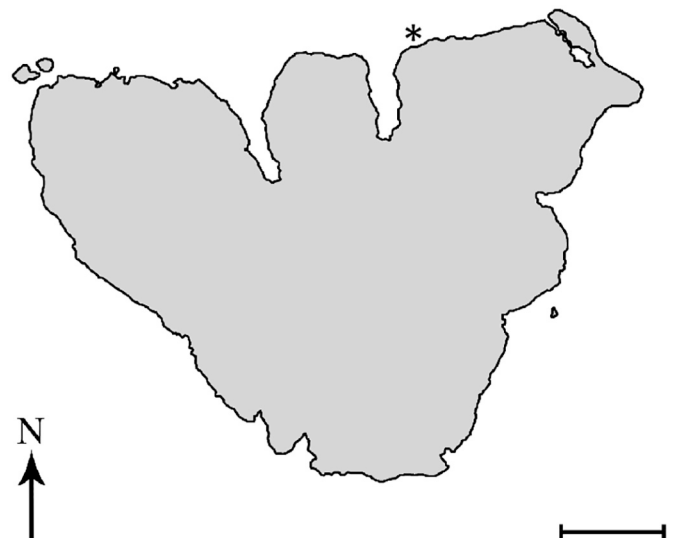


Fig. 1. Map of Moorea with study site indicated with a *. Scale bar is 3 km.

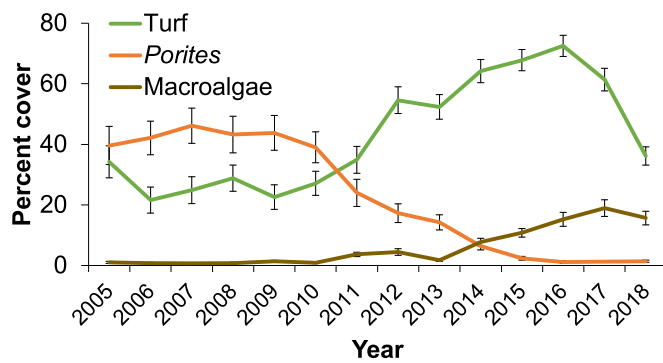


Fig. 2. Abundances of *Porites* spp., turf, and macroalgae from the closest LTER site on the fringing reef.

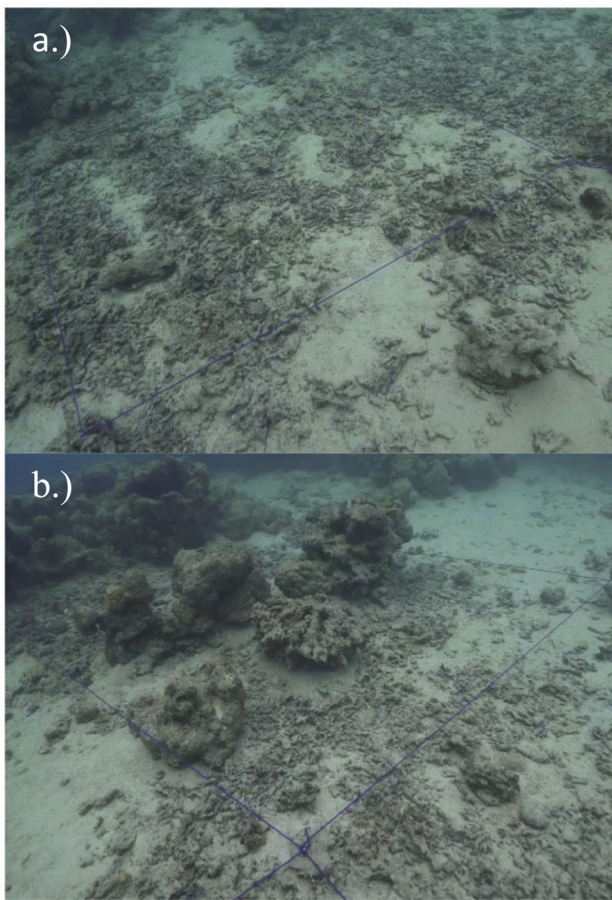


Fig. 3. Photos of a.) low and b.) high complexity plots. Plots were marked off in purple line.

the width of each plot using random starting points along the plot edge ($n = 6$ per plot). We calculated rugosity as the ratio of the fitted chain length divided by the planar length; thus, the lowest possible value of 1 indicates a completely flat benthos, with higher values indicative of greater rugosity (videos of plots can be found in the Supplement).

After testing the data for the relevant assumptions, we compared variation in rugosity among the plots using a nested ANOVA, with topographic complexity nested within plot.

To characterize the composition of the benthos, we surveyed the entire plot area ($n = 4$ per plot) using the point intercept technique, employing a 1x1m quadrat with 81 intercepts. At each point, we categorized the benthic community as algal turfs (<1 cm), macroalgae

(either *Turbinaria ornata* or *Dictyota bartayresia*), or sand, the only benthic groups within the experimental plots. We then tested for differences in turf abundance with a nested ANOVA framework, following confirmation that the data met the relevant assumptions.

We also surveyed the height of turfs within our experimental plots. In each plot we measured the turf height using steel wire marked at 1 mm intervals at 10 haphazardly chosen points within a 10 by 10 cm quadrat (points were averaged for each quadrat, with $n = 4$ replicate quadrats per plot) (sensu Fong et al., 2018). We tested for differences in turf height using a nested ANOVA after confirming that data met relevant assumptions; quadrat averages were used as replicates in the ANOVA.

To evaluate the relationship between topographic complexity and fish abundance and behavior, we chose *Acanthurus nigrofuscus* as our focal fish species. This species is the most abundant non-site attached acanthurid on this reef (Fong et al., 2018), making it useful for estimating abundance and behavior across topographic treatments. Further, this species is widely distributed across the Indo-Pacific and Indian oceans. We chose an acanthurid instead of a scarid because scarids at this site are very small (<5 cm, Fong et al., 2018), making species identifications challenging. Finally, Fishelson et al. (1987) showed this fish can have a narrow range no more than a few meters, making it appropriate for our experimental plot design. All observational data were taken while floating on snorkel, rather than SCUBA, to minimize movement and noise that might disrupt fish behavior (Lindfield et al., 2014; Emslie et al., 2018). While the presence of the observer likely impacted fish behavior to an extent, disruptions would be equal across study plots as all were surveyed using the same method. There were 3 fish observers, and we reduced inter-observer variability to below 5% before we collected any data.

To test whether reef complexity shaped patterns of fish abundance, we recorded the total number of *A. nigrofuscus* that occupied plots in 3-min windows ($N = 31$ focal periods for each complexity type ($n = 10, 10, 11$ per pair), $N = 62$ total focal periods) and analyzed the data with a nested PERMANOVA because data did not meet assumptions of parametric statistics.

To test whether reef complexity influenced the residence time of individual fish in the experimental plots, we calculated the average amount of time an individual spent within a given plot. To do this, we haphazardly selected individual fish as they entered a plot and then recorded the time, in seconds, that it stayed in the plot ($N = 240$, ranging from 29 to 51 individuals per plot; $n = 128$ high complexity, $n = 113$ low complexity). We then tested for significant differences among plot types in a nested PERMANOVA because data did not meet assumptions of parametric statistics.

We followed the behavior of individual fish within our 6 plots and constructed time budgets based on focal observations of individual fish to determine the relationship between behavior and topographic complexity. We selected individual fish haphazardly as they entered our plots and recorded behavior for the entire duration that the fish remained in the plot (average = 38.0 ± 0.16 SE, max = 150 s).

Following similar methods of Fong et al. (2018), we recorded fish behavior as one of four categories: foraging, swimming, hiding, or other. Foraging included when fish took a single bite of algae as well as forays, which are multiple bites taken in rapid succession. Swimming was defined as active movement through the water column without stopping to forage. Hiding was defined as fish moving slowly while staying close to the structure of the benthos (<10 cm) but not foraging. The 'other' category was included to document any behaviors not encompassed in the other categories, such as being still in the water column (Fong et al., 2018), and comprised <0.5% of the average time budget. To minimize diurnal variation in behavior, we only collected observations between 0900 and 1500 h, when herbivorous reef fish are most active and which is most comparable to other studies (e.g. Fong et al., 2018).

In our analysis, we only included data for fish that were in our plots >15 s ($N = 151$; $n = 74$ high complexity, 77 low complexity). We used this cut off to exclude individuals that rapidly passed through without

interacting with the benthos. To test for differences in time budgets among the low and high complexity plots, we calculated the proportion of time each individual spent engaged in each behavioral category, and then analyzed these data in a MANOVA framework, as the response variables were not independent. We next examined individual behavior categories (foraging, swimming, hiding) in a nested PERMANOVA because data did not meet assumptions of parametric statistics.

In order to quantify how differences in abundance, residence time, and time budgets came together to impact differences in total herbivory pressure, we calculated an estimate of total seconds fish spent foraging in high and low complexity plots on average as [average number of fish in a 3 min period (abundance) * average total time spent in the plot (residence time) * average time spent foraging (time budget)].

3. Results

High complexity plots were significantly more rugose than low complexity plots (Supplementary Video, Table 1A), where rugosity was 1.61 ± 0.05 SE and 1.32 ± 0.03 SE respectively. Because a value of 1 represents a completely flat surface, the observed difference is almost 2-fold. High and low complexity plots were both dominated by algal turfs. On average, high complexity plots were 81.28 ± 3.5 SE % algal turfs while low complexity plots were 77.4 ± 3.5 SE % algal turfs (Table 1B). Turf height was significantly shorter in high complexity plots than in low complexity plots (Table 1C). On average, turf height was more than 30% taller in low complexity plots, with heights of 1.08 ± 0.16 (SE) mm and 1.45 ± 0.11 (SE) mm in high and low complexity plots, respectively (Fig. 4a).

Fish abundance was approximately 3 times greater in high complexity plots than low complexity plots (Table 2A, Fig. 4b). On average, we observed 4.3 ± 0.3 SE fish per 3 min in high complexity plots compared to 1.5 ± 0.3 SE fish in low complexity plots. Moreover, individual fish spent about twice as much time in the high complexity plots than the low complexity plots (Table 2B, Fig. 4c). On average, an individual spent 41.3 ± 3.7 SE seconds in high complexity plots compared to 22.0 ± 2.7 SE seconds in low complexity plots.

Results show significant differences in how fish allocate their time in the two complexity treatments (Table 3). This difference in time budget was driven by differences in the proportion of time spent hiding in high and low complexity plots (Fig. 5a). Fish spent more than 4 times the proportion of time hiding in high complexity plots than low complexity plots (Table 4A). On average, individual fish spent 18.3 ± 3.1 SE % of their time hiding in high complexity plots compared to 4.3 ± 1.2 SE % of their time hiding in low complexity plots. In contrast, fish spent similar proportions of their time swimming and foraging in high and low complexity plots (Table 4B,C) (Fig. 4 b,c), with ~30% of an individual's time allocated to swimming and ~ 50% of their time allocated to foraging.

We found fish exerted ~7.5 times as much total herbivory pressure in high complexity plots than low complexity plots (4469.29 s and 596.85 s respectively).

Table 1

Results of nested ANOVA on rugosity data (A), turf cover (B), and turf height (C) where plot ID was nested within complexity.

NESTED 1-F ANOVA	df	SS	MS	F-ratio	p
A.) Rugosity					
Plot ID: Treatment	1	0.5202	0.5202	25.776	0.0148*
Residuals	3	0.0606	0.0202		
B.) Turf Cover					
Plot ID: Treatment	1	2.3	2.3	0.015	0.903
Residuals	21	3141.9	149.6		
C.) Algal Turf Height					
Complexity	1	0.8437	0.8437	5.625	0.0279*
Residuals	20	3.0000	0.1500		

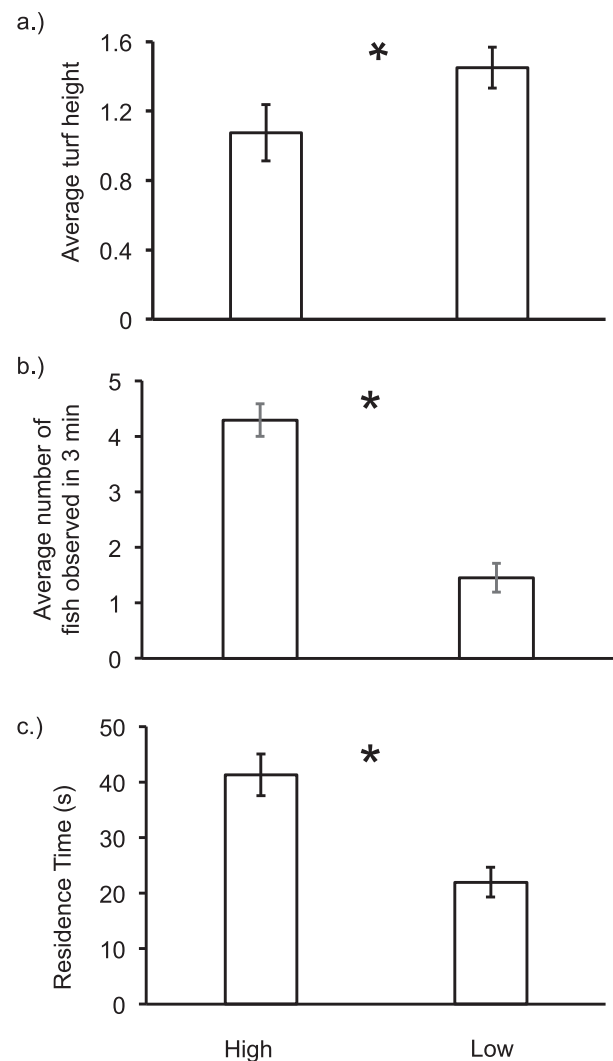


Fig. 4. Average a.) algal turf height, b.) number of *Acanthurus nigrofuscus* visiting a plot in a 3-min interval, and c.) amount of time (in seconds) spent by *A. nigrofuscus* in high versus low complexity plots. Error bars are \pm SE and significant differences are indicated with *.

Table 2

Results of nested PERMANOVA on abundance surveys (A) as well as residence time (B) of our focal fish, *Acanthurus nigrofuscus*, in high versus low complexity plots.

PERMANOVA	df	SS	MS	Pseudo-F	p
A.) Abundance					
Complexity	1	104.908	42.386	42.386	<0.001
Residuals	59	146.028	2.475		
Total	61	264.968			
B.) Residence Time					
Complexity	1	31,781	31,781	24.5513	<0.001*
Residuals	237	306,791	1294		
Total	239	339,841			

4. Discussion

High complexity, turf-dominated reef states on Moorea, French Polynesia provided both resources and refuge to a common species of herbivorous fish, a notable exception to the paradigm that resources and refuge are a trade-off on reefs. This result matches general predictions that fish abundance and species richness is higher in complex structure

Table 3
Results of MANOVA of time budget, where behaviors were our multivariate responses.

MANOVA	df	SS	MS	Pseudo-F	p
Time Budget					
Complexity	1	0.912	0.9118	4.5943	0.0249*
Residuals	148	29.372	0.1985		
Total	150	31.634			

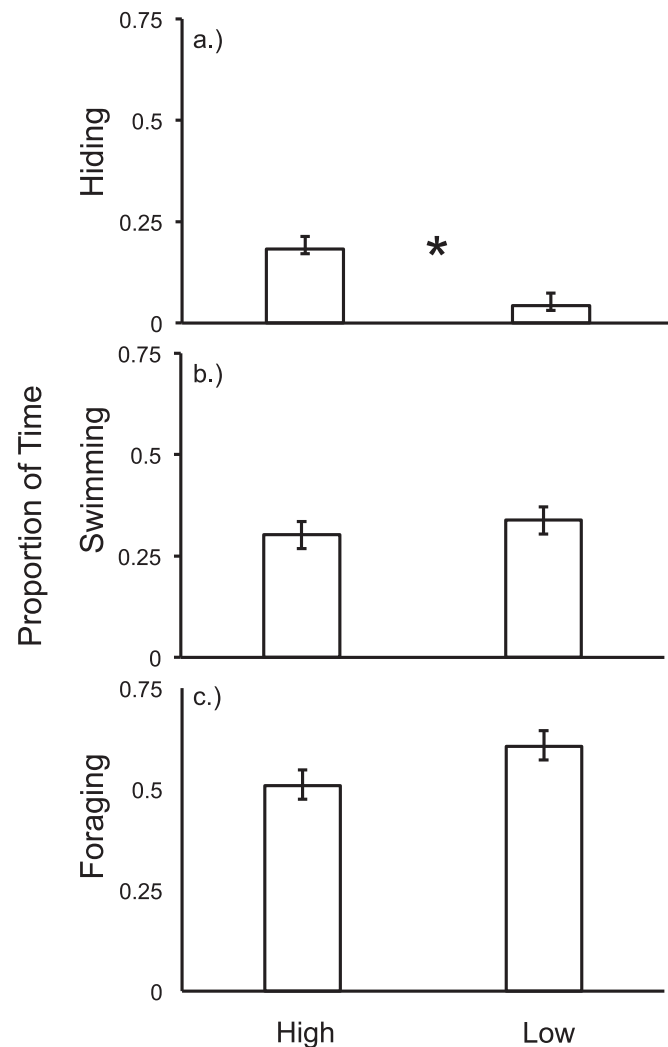


Fig. 5. Time budgets for *Acanthurus nigrofuscus* in high and low complexity plots. Bars represent means while errors are \pm SE. Significant differences are indicated with *.

because of decreased risk provided by increased refuge (Randall, 1965; Risk, 1972; Steele, 1999; Gratwicke and Speight, 2005a, 2005b; Graham and Nash, 2013; Rogers et al., 2014). However, a novel component to our research is the coupling of resources and refuges. The tradeoff between resources and refuge in coral-dominated versus algal-dominated areas was proposed over 50 years ago (Randall, 1965) and has become a foundational paradigm of coral reef ecology (reviewed in Graham and Nash, 2013). Our findings show that this paradigm does not always hold, particularly post-disturbance when the normal ecological dynamics of reefs are disrupted. Specifically, when physical structure is retained with algal domination, resources and refuges co-occur (Sano et al., 1987; Garpe et al., 2006), dissolving this classic trade-off.

In contrast to our results, previous studies on the recovering reefs of

Table 4
Results of nested PERMANOVA on individual behaviors of swimming (A), hiding (B) and foraging (C).

PERMANOVA	df	SS	MS	Pseudo-F	p
A.) Hiding					
Complexity	1	0.4623	0.46225	11.439	< 0.001*
Residuals	148	5.9806	0.0404		
Total	150	6.6787			
B.) Swimming					
Complexity	1	0.0877	0.087707	1.03891	0.2922
Residuals	148	12.4944	0.084422		
Total	150	12.608			
C.) Foraging					
Complexity	1	0.1314	0.13144	1.2876	0.2177
Residuals	148	15.1077	0.10208		
Total	150	15.4428			

Moorea found herbivore abundance remained relatively constant across a gradient of physically intact reefs across all reef types (Han et al., 2016). An important difference is that Han et al. (2016) was on a much larger scale than ours; the transects used to estimate fish abundance could have easily encompassed all of our experimental plots. Further, our study only considered one species; other species of herbivores may display different patterns. The scale-dependent nature of these two studies suggest that herbivory rates on disturbed reefs is likely locally patchy, and may vary even on very small spatial scales. In turn, such fine-scale spatial variation in herbivory rates may influence local recovery dynamics.

Our results also suggest that multiple facets of behavior need to be considered to understand any changes in local herbivory rates for *Acanthurus nigrofuscus*. Potential differences in herbivory rates were not evident in time budgeting data alone. This differs from similar research on this reef, which found fishes (both surgeonfish and parrotfish) spent more time foraging in coral versus algal dominated plots (Fong et al., 2018); in this case, differences in habitat use and herbivory pressure were evident in time budgets. In contrast, in this study, because fish spent more time in high complexity plots, equal budgets for individuals foraging in high and low complexity plots resulted in more total time foraging in high complexity plots. This was likely driven by the coupling of resources and refuge in this study, which contrasts the study comparing coral and algal dominated plots (Fong et al., 2018). Thus, a combination of time budgets, abundance, and residence time is required to mechanistically explain patterns of increased herbivory rates in high complexity, turf dominated reefs.

We found higher complexity plots had shorter turfs, which suggests these turfs may be under stronger overall top-down control. While we did not directly measure top-down control, we did document increased localized herbivory rates by our focal fish in high complexity plots. While the difference in turf height between treatments was small, closely cropped turfs are maintained by strong herbivory (e.g. Clausing et al., 2014; Fong et al., 2018), and even small changes of <1 mm can dramatically impact turf productivity and sediment load (Tebbett and Bellwood, 2020). Further, short turfs are a viable recruitment surface for coral larvae (Jompa and McCook, 2003; Birrell et al., 2005); thus, maintenance of short turfs may facilitate recovery of these reefs. This maintenance of short, cropped turfs in high complexity plots likely results from the unusual coupling of high algal density with removal of corals by crown-of-thorns predation and escape from physical damage from typhoons. While the specific combination of crown-of-thorns and typhoon damage in our study system may be relatively rare, the increased incidence and severity of coral bleaching (e.g. Hughes et al., 2017) suggests that high complexity, high algal cover will likely be an increasingly common outcome from reef disturbance, making this an important coupling to investigate.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

IM and RW were funded by the UC-HBCU Initiative funded through the UC Office of the President. BN and JS were funded through an NSF-PIRE award. This work was conducted as part of the Diversity Project, funded by an NSF-PIRE award to F Rohwer and PHB (OISE-1243541) and a UC-HBCU Initiative award to PHB and PF. CRF was funded by NSF PRFB Grant #1612308.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2021.151515>.

References

- Adam, T.C., Schmitt, R.J., Holbrook, S.J., Brooks, A.J., Edmunds, P.J., Carpenter, R.C., Bernardi, G., 2011. Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS One* 6 (8), 23717.
- Adey, W.H., Goertemiller, T., 1987. Coral reef algal turfs: master producers in nutrient poor seas. *Phycologia* 26 (3), 374–386.
- Adjeroud, M., Michonneau, F., Edmunds, P.J., Chancerelle, Y., De Loma, T.L., Penin, L., Thibaut, L., Vidal-Dupiol, J., Salvat, B., Galzin, R., 2009. Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a south Central Pacific reef. *Coral Reefs* 28 (3), 775–780.
- Almany, G.R., 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* 106 (2), 275–284.
- Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. *Nature* 429 (6994), 827.
- Birrell, C.L., McCook, L.J., Willis, B.L., 2005. Effects of algal turfs and sediment on coral settlement. *Mar. Pollut. Bull.* 51 (1–4), 408–414.
- Bittick, S.J., Clausing, R.J., Fong, C.R., Scoma, S.R., Fong, P., 2019. A rapidly expanding macroalga acts as a foundational species providing trophic support and habitat in the South Pacific. *Ecosystems* 22 (1), 165–173.
- Clausing, R., Annunziata, C., Baker, G., Lee, C., Bittick, S., Fong, P., 2014. Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef. *Mar. Ecol. Prog. Ser.* 517, 121–129.
- Edmunds, P., 2020. MCR LTER: Coral Reef: Long-Term Population and Community Dynamics: Corals, Ongoing Since 2005. *KnB-Iter-mcr.4.38*. <https://doi.org/10.6073/pasta/10ee808a046cb63c0b8e3bc3c9799806>.
- Edmunds, P.J., Adam, T.C., Baker, A.C., Doo, S.S., Glynn, P.W., Manzello, D.P., Silbiger, N.J., Smith, T.B., Fong, P., 2019. Why more comparative approaches are required in time-series analyses of coral reef ecosystems. *Mar. Ecol. Prog. Ser.* 608, 297–306.
- Emslie, M.J., Cheal, A.J., MacNeil, M.A., Miller, I.R., Sweatman, H., 2018. Reef fish communities are spooked by scuba surveys and may take hours to recover. *PeerJ* 6.
- Fishelson, L., Montgomery, L., Myrberg, A.H., 1987. Biology of surgeonfish *Acanthurus nigrofasciatus* with emphasis on changeover in diet and annual gonadal cycles. *Marine ecology-progress series. Mar. Ecol. Prog. Ser.* 39, 37–47.
- Fong, C.R., Frias, M., Goody, N., Bittick, S.J., Clausing, R.J., Fong, P., 2018. Empirical data demonstrates risk-tradeoffs between landscapes for herbivorous fish may promote reef resilience. *Mar. Environ. Res.* 133, 1–5.
- Fong, C.R., Gaynus, C., Carpenter, R.C., 2020. Complex interactions among multiple anthropogenic stressors evolve over time to shift communities on reefs. *Ecosphere* 11 (5), e03130.
- Fong, P., Paul, V.J., 2011. Coral reef algae. In: *Coral Reefs: An Ecosystem in Transition*. Springer, Dordrecht, pp. 241–272.
- Garpe, K.C., Yahya, S.A., Lindahl, U., Ohman, M.C., 2006. Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Mar. Ecol. Prog. Ser.* 315, 237–247.
- Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H., Pratchett, M.S., 2013. Recovery of an isolated coral reef system following severe disturbance. *Science* 340 (6128), 69–71.
- Graham, N.A.J., Nash, K.L., 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32 (2), 315–326.
- Gratwicke, B., Speight, M.R., 2005a. Effects of habitat complexity on Caribbean marine fish assemblages. *Mar. Ecol. Prog. Ser.* 292, 301–310.
- Gratwicke, B., Speight, M.R., 2005b. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J. Fish Biol.* 66 (3), 650–667.
- Han, X., Adam, T.C., Schmitt, R.J., Brooks, A.J., Holbrook, S.J., 2016. Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia. *Coral Reefs* 35 (3), 999–1009.
- Hoey, A.S., Bellwood, D.R., 2011. Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecology Letters* 14 (3), 267–273.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschanivskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17 (4), 360–365.
- Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B., Kleypas, J., Van De Leemput, I.A., Lough, J.M., Morrison, T.H., Palumbi, S.R., 2017. Coral reefs in the Anthropocene. *Nature* 546 (7656), 82.
- Jompa, J., McCook, L.J., 2003. Contrasting effects of turf algae on corals: massive *Porites* spp. are unaffected by mixed-species turfs, but killed by the red alga *Anotrichium tenue*. *Mar. Ecol. Prog. Ser.* 258, 79–86.
- Kayal, M., Vercelloni, J., De Loma, T.L., Bosserelle, P., Chancerelle, Y., Geoffroy, S., Stievenart, C., Michonneau, F., Penin, L., Planes, S., Adjeroud, M., 2012. Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. *PLoS One* 7 (10), 47363.
- Lewis, S.M., 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol. Monogr.* 56 (3), 183–200.
- Lindfield, S.J., Harvey, E.S., McIlwain, J.L., Halford, A.R., 2014. Silent fish surveys: bubble-free diving highlights inaccuracies associated with SCUBA-based surveys in heavily fished areas. *Methods Ecol. Evol.* 5 (10), 1061–1069.
- Madin, E.M., Madin, J.S., Booth, D.J., 2011. Landscape of fear visible from space. *Sci. Rep.* 1, 14.
- McCook, L., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19 (4), 400–417.
- Muthukrishnan, R., Fong, P., 2018. Rapid recovery of a coral dominated eastern tropical Pacific reef after experimentally produced anthropogenic disturbance. *Mar. Environ. Res.* 139, 79–86.
- Muthukrishnan, R., Lloyd-Smith, J.O., Fong, P., 2016. Mechanisms of resilience: empirically quantified positive feedbacks produce alternate stable states dynamics in a model of a tropical reef. *J. Ecol.* 104 (6), 1662–1672.
- Pratchett, M.S., Munday, P., Wilson, S.K., Graham, N.A., Cinner, J.E., Bellwood, D.R., Jones, G.P., Polunin, N.V., McClanahan, T.R., 2008. Effects of climate-induced coral bleaching on coral-reef fishes. Ecological and economic consequences. *Oceanogr. Mar. Biol. Annu. Rev.* 46, 251–296.
- Randall, J.E., 1965. Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* 46 (3), 255–260.
- Risk, M.J., 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull.* 153, 1–7.
- Rogers, A., Blanchard, J.L., Mumby, P.J., 2014. Vulnerability of coral reef fisheries to a loss of structural complexity. *Curr. Biol.* 24 (9), 1000–1005.
- Sano, M., Shimizu, M., Nose, Y., 1987. Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Mar. Ecol. Prog. Ser.* 37, 191–199.
- Steele, M.A., 1999. Effects of shelter and predators on reef fishes. *J. Exp. Mar. Biol. Ecol.* 233 (1), 65–79.
- Tebbett, S.B., Bellwood, D.R., 2020. Sediments ratchet-down coral reef algal turf productivity. *Sci. Total Environ.* 713, 136709.
- Vroom, P.S., 2011. “Coral dominance”: a dangerous ecosystem misnomer? *Journal of Marine Biology* 2011, 164127.