FISH RESPONSE TO MACROALGAL REMOVAL

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FISH RESPONSE TO MACROALGAL REMOVAL

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[To all who aspire to use knowledge to better the world around them]

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SUMMARY

Coral reefs are rapidly degrading into macroalgae dominated systems sustained through positive feedback loops. Macroalgae can harm corals directly via competition and indirectly via suppression of recruitment and increasing susceptibility to disease. This suppresses coral resilience, enhances macroalgal resilience and abundance, and decreases fish herbivory and recruitment. To break macroalgal feedback loops manual macroalgae removal may be an option. This study removed macroalgae in paired $4m^2$ removal and control plots (n=12-14) in a backreef lagoon of Moorea, French Polynesia, and (1) analyzed fish responses to macroalgal removal at days 0, 7, 30, and 55, and (2) measured macroalgal recovery at day 55. Immediately following removal (day 0), total fish visitations per minute and bites per minute increased by 232% and 575% respectively. Herbivore visitations increased by 172% at day 0 and remained elevated by 26-63% from day 7 through 55 post removal. In contrast, after an initial 588% increase in invertivore visits, there were no significant differences in invertivore visits at later dates. These results support the argument that dense macroalgae deter herbivory, create refuges from herbivores and invertivores, and create feedback loops enhancing macroalgal resilience. Total macroalgal abundance did not recover over the 55 day duration of monitoring; at day 55, total cover of macroalgae was 21% lower and barren substrate was 25% higher than at day 0. Thus, at these spatial and temporal scales of manipulation, manual removal of macroalgae allows fishes to maintain low macroalgal cover. These results suggest that manual removal of macroalgae prior to coral recruitment seasons may allow herbivores to maintain lower cover or algae, greater cover of bare substrate, and possibly facilitate coral recruitment – potentially enhancing coral resilience and reef recovery. The spatial scales over which manual

macroalgae removal can be used for long-term phase shift reversal are uncertain and an area for further evaluation.

1. INTRODUCTION

Coral reefs are complex, species rich habitats that provide critical ecosystem services including fisheries, tourism, protection from storm surge, and useful natural products (Hoegh-Guldberg et al 2007). Recently coral reefs have declined due to multiple stressors, with reefs in the Caribbean losing about 80% of coral cover (Gardner et al. 2003) and reefs in the Pacific about 50% over the last 3-4 decades (Bruno & Selig, 2007). Even the Great Barrier Reef (GBR), the largest, and one of the most intensively managed and economically incentivized reefs, lost ~ 50% of its coral cover between 1985 and 2012 (De'ath et al. 2012), and lost 30% of the remaining cover in 2016 alone due to severe warming *(*Hughes et al. 2018). As corals decline, coral reefs commonly transition into macroalgal dominated systems, which may be maintained by positive feedbacks. Macroalgae exacerbates coral decline by producing allelopathic chemicals that harm corals upon contact (Rasher et al 2011) and release of dissolved organic carbon that can disrupt beneficial coral microbes and cause anoxic conditions within coral mucus (Smith et al. 2006, Gershenzon & Dudareva 2007). Additionally, increased macroalgal cover suppresses coral growth (Clements et al. 2018), alters coral microbiomes (Thurber et al 2012), exacerbates coral disease, suppresses larval survival (Nugues et al. 2004, Beatty et al. 2018), and suppresses coral recruitment (Hughes et al. 2007, Burkepile & Hay 2008, Kuffner et al. 2006, Vermeij et al 2009, Dixson et al. 2014).

Although reversal of macroalgal dominated states is possible (Idjadi et al 2006), especially if there is adequate herbivore grazing (Bellwood et al 2006, Rasher et al 2013), the presence of macroalgae may deter fish recruitment (Dixson et al. 2014), and overfishing may reduce the ability for herbivory to keep pace with macroalgal growth. This may be especially true in situations with limited herbivore redundancy, where only a few browser species ingest macroalgae. Hoey & Bellwood (2009) found one species, *Naso unicornis*, was responsible for nearly 90% of bites on macroalgae in the genus *Sargassum*, and Rasher et al. (2013) found that only 4 of 29 species of larger herbivorous fishes were responsible for consuming common macroalgae, with some chemically-rich algae being consumed by only one herbivore species. Even for macroalgal consuming herbivores, dense macroalgal patches can deter feeding or use as opposed to low density patches (Hoey & Bellwood 2011, Dell et al. 2016). Once macroalgae become abundant, this abundance may suppress herbivore feeding and facilitate the stability of macroalgal dominated areas. Unpalatable macroalgae also can serve as a refuge from herbivory for more palatable macroalgae (Hay 1986, Pfister & Hay 1988, Bittick et al. 2010). Thus, once adequately established, macroalgal dominated reefs may be resilient and resist removal even if some herbivores remain. If so, removing established macroalgae may be necessary to break macroalgal feedbacks that suppress herbivory and stabilize macroalgal dominance.

Previous studies on how macroalgae impact herbivory and herbivore behaviors have commonly focused on brown algae in the genus *Sargassum* (Hoey & Bellwood 2011, Chong-seng et al. 2014, Dell et al. 2016, Bauman et al. 2017). This alga is common on degraded reefs and generates positive feedbacks that both suppress herbivory and increase algal growth in dense versus sparse stands (Hoey & Bellwood 2011, Dell et al. 2016, Davis 2018). Whether the suppression of herbivores by *Sargassum* density is specific to that genus, or is a trait of macroalgae in general, is not clear. Full macroalgal removal studies have been conducted in the Caribbean on patch reefs of approximately $1000m^2$

(McClanahan et al. 2000), finding that bites of Acanthurids were approximately three times higher on the removal than control reefs while parrotfish bites did not differ. Similar studies in the Indian Ocean off the coast of Kenya (McClanahan 1999) also found greater *Acanthurid* and *Scaridae* biomass in removal plots. However, the effects of macroalgae on fish herbivory may vary with environments. In contrast to these tropical studies, investigations in temperate waters indicate that fish densities and species richness are positively associated with density of *Sargassum* (Levin & Hay 1996), or are largely unaffected by differing densities of larger macroalgae *(*Holbrook et al. 1990*).*

To evaluate whether macroalgal abundance could suppress herbivory and enhance hysteresis once macroalgae becomes abundant, we removed macroalgae from multiple $4m^2$ areas in a backreef tropical lagoon dominated by mixed species of macroalgae and evaluated the effects of this on fish visitation and biting rates over a two-month period. Our goal was to determine whether mixed assemblages of macroalgae could produce positive feedbacks that suppressed herbivory, facilitated continuing algal dominance, and helped explain the hysteresis common on many modern coral reefs (Mumby et al. 2007). We also aimed to determine whether manual removal of macroalgae on this scale would attract sufficient fish grazing to prevent macroalgal recovery for a considerable period.

2. METHODS

2.1 *Macroalgal removal*

Fourteen pairs of 2m x 2m plots in a backreef lagoon on the north coast of Moorea were marked with flagging tape (locations - approximately from 17°28'39.2"S 149°50'26.0"W to 17°28'46.9"S 149°50'47.3"W). Plots were paired based on visual similarity of coral and macroalgal abundance, species content, and topographic complexity. Plots within a pair were separated by approximately 2-3m, different pairs were separated by >7m, and plots within a pair were haphazardly assigned to control or removal treatments. Upright macroalgae were removed by hand from removal plots.

2.2 *Video analysis*

After macroalgae were removed in the treatment plots, GoPro Hero 4 cameras were positioned on plot edges to record fish activity in each separate plot. Videos were taken at days 0, 7, 30, and 55 after macroalgal removal, with all videos occurring between June and August of 2018. Analysis of videos began 1 minute after the diver left the field of view, and continued for 5 to 15 min depending on the frequency of fish visitation and feeding. Videos from day 0 were analyzed for 5 minutes because the strong response by fishes allowed adequate assessment within this interval; videos from days 7, 30, and 55 had reduced visitation rates, making longer assessments necessary. Responses (visits and bites) were recorded per time length to standardize comparisons across time. Macroalgal removal and video recordings were conducted between 9 and 4pm and videos of spatially paired control and treatment plots were conducted simultaneously to ensure spatial and temporal pairing of plots. Due to camera placement errors or dislodgment, sample size varied from 10-12 (day 0, n = 10; 7days, n = 11; 30 days, n=12; 55 days, n=12).

In each video, we assessed: i) the number of visits per species, ii) the number of bites per individual during each visit, iii) bites/cover of that substrate type, and iv) aggressive behaviors. Aggressions were counted as a sudden rapid swimming directed towards another fish that resulted in immediate fleeing by the target fish. In some instances of densely packed parrotfish schools with 5 or more individuals, bites for the school were estimated based on the bites of the individuals that were more clearly visible. Only fish over 5cm were included in our counts, due to difficult of seeing smaller fish at the back of the plots. Statistics employed a generalized linear mixed model with time and status (control or treatment) as fixed effects, and paired post-hoc t-tests run in JMP 13 Pro. Aggressions were analyzed using a Wilcoxin Signed Rank Test due to control plots having many plots that experienced 0 aggressions.

2.3 Benthic cover within plots:

Percent cover of benthic species in each plot was assessed at day 0 and 55 after macroalgal removal by haphazardly looping a 3m metal link chain with pre-marked randomized points into the plot, photographing this, and assessing what occurred beneath each point. This was repeated three times for each plot, resulting in an average of 87 points per plot for day 0 plots, and 78 points for day 55 plots. (Variation in points was due to points occasionally being obscured in the photographs). Day 0 determinations were conducted approximately 24 hours after macroalgal removal (to avoid suppression of initial fish response immediately after removal and to allow debris to clear). Percent cover assessments were conducted again on day 55 to evaluate the degree to which our removal treatments remained different from the control plots. Removals occurred only on day 0 and were not maintained throughout the experiment.

3. RESULTS

3.1 *Algal reduction*:

Macroalgal removal resulted in an immediate reduction of 40% in total macroalgal cover, with a 51% reduction remaining after 55 days (Table 1). For the day 0 time point, the less than complete reduction was due to remaining basal portions for some species (primarily *Amansia*) that were difficult to remove completely. Our visual assessment indicated that these basal portions that were previously in the understory bleached rapidly and were lost within days of initial overstory removal (note the non-significant reduction at day 0, but the significant 75% reduction that remained at day 55). At day 0, the major losses in macroalgal cover in removals was due to the decrease of brown algae (*Turbinaria*, *Sargassum,* and *Dictyota*). After 55 days for potential recovery, *Sargassum, Amansia*, and *Turbinaria* were still 93%, 75%, and 57% lower, respectively in removal versus control plots. *Dictyota* no longer differed significantly. Bare areas were 192% and 345% higher in removal versus control areas at 0 and 55 days, respectively.

Table 1 –
Benthic Cover (% ± SEM) "P-values" indicates values obtained by comparing removal and control plots within a time point, * indicate difference (p < .025) for the same plots between time points, at day 0 and day 55. "Other" refers to other living substrates such as CCA, and animals such as urchins and giant clams.

	Day 0 n=14			**Day 55** n=12		
Substrate	**Removal**	**Control**	**P-value**	**Removal**	**Control**	**P-value**
Sargassum	0.51 ± 0.20	7.50 ± 2.37	**0.01**	0.62 ± 0.24	9.29 ± 2.21	**0.002**
Dictyota	0.64 ± 0.27	5.11 ± 2.11	0.05	1.10 ± 0.52	0.98 ± 0.59	0.88
Amansia	20.32 ± 3.45	22.99 ± 3.04	0.43	6.87 ± 1.42*	27.92 ± 3.45	**<0.001**

Table 1 continued

Turbinaria	8.96 ± 1.16	35.70 ± 2.68	**<0.001**	15.59 ± 1.57*	36.38 ± 2.84	**<0.001**
Total Macroalgae	32.25 ± 3.17	72.42 ± 3.04	**<0.001**	25.55 ± 1.93*	76.11 ± 2.32	**<0.001**
Turf	3.65 ± 1.57	1.67 ± .66	0.17	0.21 ± 0.21	1.44 ± 0.98	0.26
Coral	2.57 ± 0.74	1.94 ± .57	0.56	2.79 ± 0.41	3.20 ± 0.88	0.58
Barren	46.98 ± 1.84	16.08 ± 2.11	**<0.001**	58.64 ± 2.05*	13.19 ± 1.55	< **0.001**
Rubble	5.96 ± 1.86	5.23 ± 1.57	0.76	5.73 ± 1.94	3.31 ± 1.40	0.13
Sand	1.80 ± 0.98	1.04 ± 0.37	0.43	2.24 ± 0.56	1.27 ± 0.46	0.15
Other	0.09 ± 0.01	6.38 ± 0.86	**<0.001**	5.90 ± 1.60*	2.69 ± 0.65*	0.07

3.2 *Fish visits and species diversity*:

A total of 7,385 fish visits and 22,553 fish bites were observed in the 562.5 minutes of video analyzed. Following macroalgal removal, total fish visits were significantly higher in the removal versus control plots, with visits increasing by 232% on day 0 and remaining 47-55% higher across days 7, 30, and 55 (Fig.1). On day 0, increases in total fish visits to removal versus control plots were due to significant increases of 172% for herbivores and 588% for invertivores. During later dates, only herbivore visits remained significantly elevated, by 26-63% in removal versus control plots. Average species richness of visiting fishes was significantly elevated in removal (12.3 species) versus control plots (6.8 species) on day 0 (p= <.001, Paired t-test), but this difference did not persist for days 7, 30, or 55 (P > .05 Table S1). Both the Shannon-Weiner Index of diversity and an assessment of evenness of visits were significantly higher at day 0 and day 7 in removal plots but this difference did not persist for days 30 and 55 (Table S1). Although 65 identifiable species were recorded across all plot types, over 50% of fish visits after day 0 were by the surgeonfish *Ctenochaetus striatus* and the parrotfish *Chlorurus sordidus*. The most common invertivore visits were by the wrasses *Thalassoma hardwicke* and *Halichoeres hortulanus* and the triggerfish *Balistapus undulates*. None of the invertivore species comprised more than 7% of visits at any monitoring time.

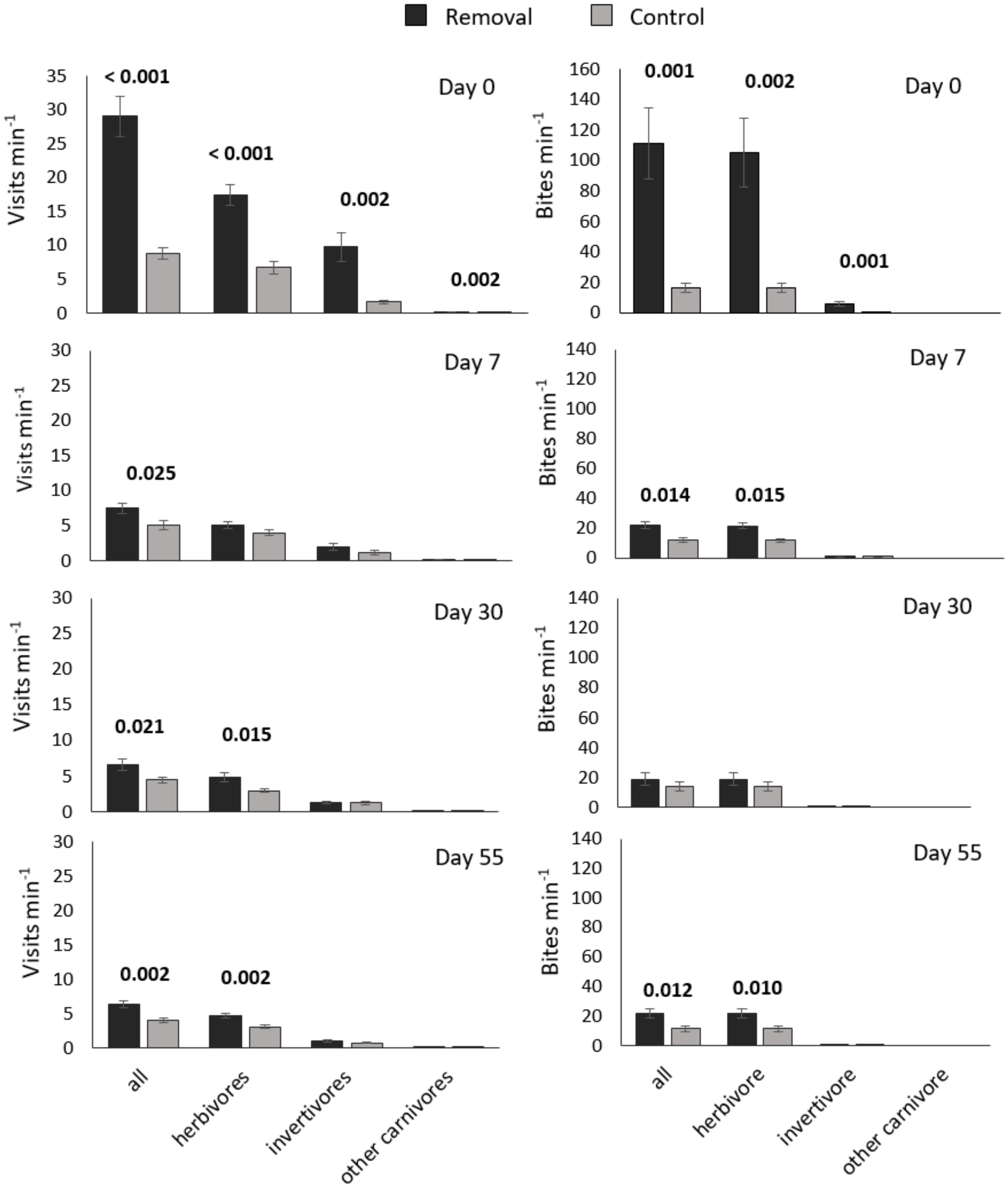

Figure 1 – Fish visitations and bites per minute at day 0, 7, 30, and 55 post macroalgae removal, bars represent $\bar{x}$ ± SEM, n = 12-14, p-values determined from generalized linear mixed model.

3.3 *Feeding behaviors*:

Bite rates across all fishes were elevated by a significant 575%, 88% and 90% in removal versus control plots on days 0, 7, and 55, respectively (Fig. 1). Mean bite rate was 34% greater in removal versus control plots on day 30, but this was not significant (p=.34). These differences were driven primarily by herbivore feeding, with invertivore feeding adding a minor component at day 0, but not on days 7, 30, or 55 (Fig. 1). Herbivore feeding was primarily due to *Acanthuridae* and *Scaridae*. Invertivore feeding was modest in contrast to herbivore feeding and was primarily due to triggerfishes, wrasses, butterflyfishes, and goatfish.

The Acanthurids *C. striatus* and *Acanthurus nigrofuscus*, and the parrotfish *C. sordidus* were responsible for $\geq$94% of total fish bites, except for the initial removal plots where they comprised 82% of bites. *C. striatus* in particular accounted for $\geq$80% or more of all bites for both removal and control plots at all time points and plots except the initial removal plots. Bite rates were significantly elevated in removal versus control plots for *C. striatus* at days 0, 7, and 55, but not at day 30 (Fig. 2). *C. sordidus* showed a similar trend, with significantly greater bite rates on days 0 and 7, but not on days 30 and 55 – though the trend was still in that direction. For both of these species, the higher bite rates in removal plots appeared to be the result of a combination of more frequent visits, more visits that involved feeding, and more bites per feeding visit (Fig. 2). Feeding behavior by *A.*

nigrofuscus did not differ significantly as a function of macroalgal removal, but both visit rates and feeding rates were low for this species (Fig. 2).

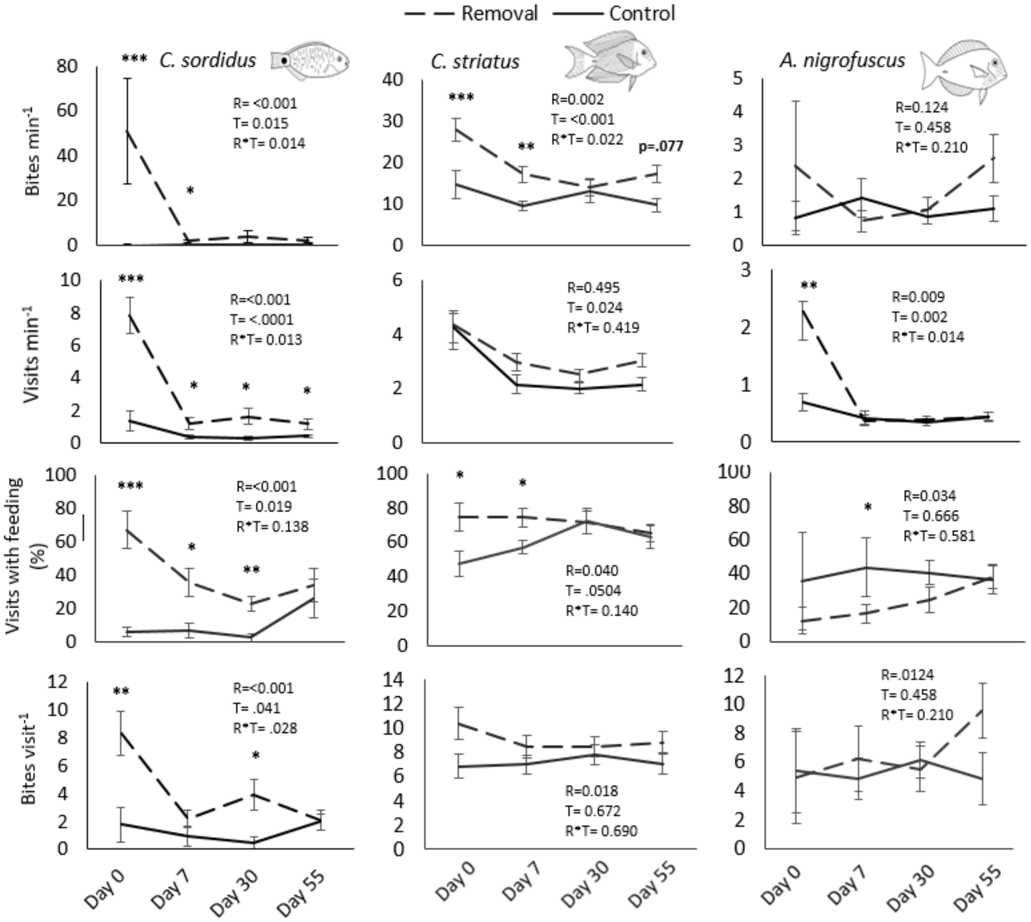

Figure 2 Biting and visiting behaviors of common herbivores over time after macroalgal removal. Bars represent x̄ ± SEM. Inset statistical values obtained from generalized linear mixed model with R = removal and T = time; significance of post-hoc t-tests is indicated with *= $p< 0.05$, ** = $p <0.01$, *** = $p < 0.001$. n = 9-12

3.4 *Aggressive behaviors*

We commonly noted *C. striatus* and *A. nigrofuscus* chasing *C. sordidus*. These interactions made up 73.3% of all observed aggressions, and except for day 7, aggressions per minute and aggressions per individual *C. sordidus* were significantly higher in removal versus control plots (Fig. 3). *C. striatus* and *A. nigrofuscus* chases towards other *Scarus* sp.

parrotfishes made up 10.1% of observed aggressions. No other aggression type made up more than 3% of aggressive observations.

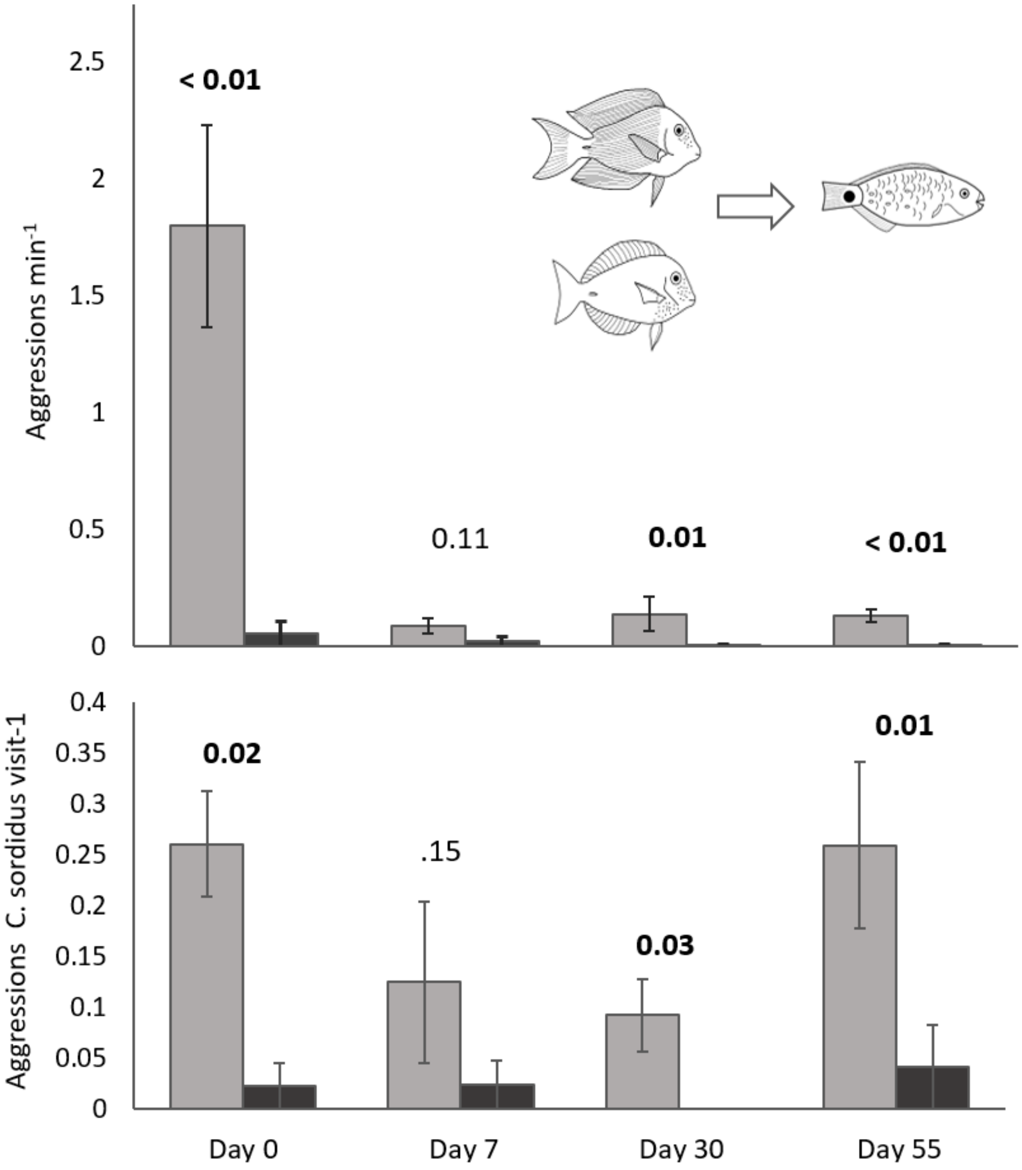

Figure 3 Aggressions per minute and per individual *C. sordidus* by *C.striatus* and *A. nigrofuscus* towards *C. sordidus C. sordidus*. Aggressions by the two surgeonfishes were combined because rapid movements prevented distinguishing between species in several instances. Bars represent $\bar{x} \pm$ SEM. Per individual means are only based on plots that had at least 1 *C. sordidus* visit. N= 6-8 plot pairs, due to excluding plots with no visits.

3.5 *Substrate preferences*

In removal plots, *C. striatus* was responsible for 40% of total observed bites at day 0, and 80-83% for the later monitoring points. In control plots, *C. striatus* was responsible for 82-88% of bites at all monitoring points. Because *C. striatus* had the majority of bites, and bites on *Sargassum, Amansia*, and *Dictyota* comprised < 9% of bites in either removal or control plots, we thus assessed the relative frequency of biting on barren substrate versus on *Turbinaria*, as a function of the 2-dimensional cover of each substrate type for both the initial and final monitoring period. For both time periods, *C. striatus* focused its feeding on the barren benthos rather than on the fouling communities on *Turbinaria* in both treatment and control plots. Relative bite rates ranged from 5.6 - 22.9X greater on barren benthic substrates versus *Turbinaria* (Fig. 4).

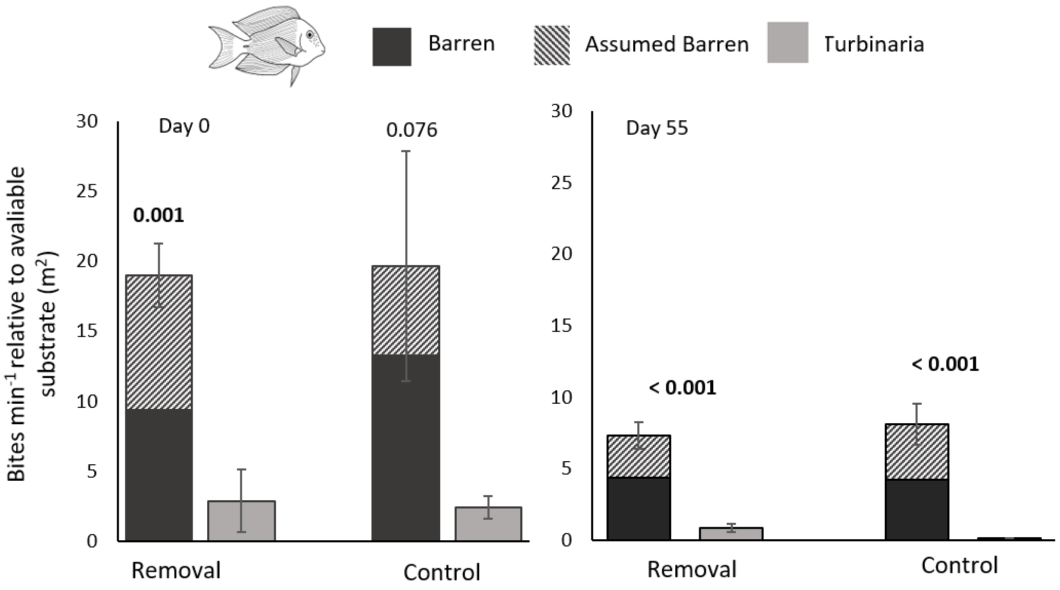

Figure 4 Bites by *C. striatus* at day 0 and day 55 after macroalgal removal on barren benthos versus the macroalga *Turbinaria*. “Assumed barren” bites were mildly obscured by uneven surfaces but likely barren substrate. Bars represent x̄ ± SEM. for combined barren and assumed barren totals.

4. DISCUSSION

Coral reefs are increasingly impacted by global and local stressors that can cause a “death spiral” of coral loss, macroalgal proliferation, further loss of coral and herbivores, and reinforcement of the macroalgal dominated states (Mumby & Steneck 2008, Hay & Rasher 2010). Herbivorous fishes can facilitate reef recovery by removing macroalgae (Mumby et al. 2007, Rasher et al. 2013), but once macroalgae dominate reefs, they may generate feedbacks that enhance macroalgal resilience, suppress fish and coral recruitment (Dixson et al. 2014), and suppress the potential positive effects of herbivores on coral recovery. The mechanism generating the positive feedback for macroalgae include enhanced growth and reduced herbivory within dense assemblages of macroalgae. Dell et al. (2016) reported higher survival and growth of juvenile and mature *Sargassum* when surrounded by conspecifics, and Hoey & Bellwood (2011) found that experimental plots with greater *Sargassum* density experienced less grazing by not only species that consumed *Sargassum,* but also other cropping, excavating, and scraping herbivores that did not consume adult *Sargassum.* Davis (2018) also found that *Turbinaria* recruit survival was greater in the presence of a high density of adults. Thus, Sargassum, or other common macroalgae, may produce an associational refuge for conspecifics as well as for other more palatable, macroalgae, as has been documented for both tropical (Hay 1981, Littler et al. 1986) and temperate reefs (Hay 1986, Pfister and Hay 1988).

Our study corroborated this trend, finding that bite rates by herbivores increased by 547% in removal plots compared to control plots at day 0, and remained 90% greater at day 55. The dramatic increase in feeding on the benthos on day 0 was due primarily to herbivores, with much of the increase being due to *C. striatus,* and to a lesser extent *A. nigrofuscus* (Fig2), both of which feeds on or off of small filamentous algae and detritus (the epilithic algal matrix or EAM), rather than browsing on macroalgae. The dramatic day 0 increase in herbivory could likely have resulted from palatable algae that had been sheltered below the macroalgal canopy becoming suddenly available and fishes rapidly grazing more heavily in, these resource-rich patches. The lack of significant increase in bite rates in removal plots at day 30 (though still 35% higher) may result from overconsumption of resources in the removal plots sometime between day 7 and 30. A previous study in the Caribbean observed a similar overcompensation effect, where once cages were removed, feeding rates in previously caged areas were 7-12 times greater than in previously grazed areas (Burkepile & Hay 2011). As a result, the herbivores removed all seaweeds to levels below those of surrounding areas (ME Hay personal observation). However, the prolonged grazing increase of 90% at day 55 in this study, without us maintaining the macroalgal removal and the lack of macroalgal recovery (Table 1) both supports the notion that high densities of macroalgae, such as >70% total macroalgal benthic cover found in the control plots, deters feeding by herbivores, even those species that consume macroalgae (Hoey & Bellwood 2011, Dell et al. 2016, Davis 2018).

Previous studies document less palatable macroalgae serving as herbivory refuges for more palatable species. Examples include *Sargassum* protecting *Hypnea musciformis* and *Gracilaria tikvahiae* from fish and urchin grazing, respectively in temperate areas (Hay 1986, Pfister & Hay 1988), or *Stypopodium* and *Turbinaria* reducing grazing on more palatable macroalgae on coral reef (Littler et al. 1986, Bittick et al. 2010). Some of the increased herbivore activity in our removal treatment could be related to canopy removal exposing smaller and more palatable species of macroalgae, but most responses appeared to be due to the increased access to algal turfs and EAM, which can serve as a collector of organic detritus. Herbivores that visited removal plots on day 0 included species, such as *A. Nigrofuscus, Zebrasoma scopas, C. striatus, and C. sordidus* that commonly feed on the EAM (Choat et al. 2002). In addition to herbivores, feeding by invertivores also increased by 224% on day 0, suggesting that macroalgae also serves as a refuge for invertebrates (Clements & Hay 2015). Increased feeding by invertivores in removal plots did not persist past day 0, but increased feeding by herbivores persisted through the 55 days of the experiment- possibly due to the rapid re-accumulation of material into EAM or the ability of clonal EAM to re-sprout rapidly from refuging basal sections, a trait that many invertebrates either lack or do more slowly.

The increases in herbivory following algal removal on the Pacific reef we investigated is similar to patterns documented by McClanahan et al. (2000, 2001) in similar studies conducted in the Caribbean; however algae was removed from larger patch reefs and monitored for a longer time period in McClanahan's studies, and the impact of algal removal on fish feeding rates appeared modest compared to the impacts seen here (McClanahan et al. 2001). A similar study in Kenya, detected a modest, 40% increase in feeding rates by two surgeonfishes following macroalgal removal, but no differences among other herbivorous fishes (McClanahan 1999).

Effects on macroalgal removal on herbivory might vary as a function of the spatial scale of the removal areas and the local density or diversity of herbivorous fishes. Our 4m^2 removal areas were small relative to the expansive, macroalgal dominated system surrounding our plots. Thus, herbivorous fishes that preferred macroalgal-free substrate for grazing could easily migrate from surrounding areas and concentrate feeding in cleared areas; this may artificially raise the apparent impact of macroalgal removal in our experiment. Although we physically removed macroalgae on day 0 only, macroalgal abundance did not recover over the next 55 days, suggesting that fish grazing may have been sufficient to suppress recovery once macroalgae were removed. The ability of herbivores to control macroalgae may vary as a function of the area available for macroalgal growth (Mumby & Steneck 2008*)*, so it is possible that the effects we document here may weaken with larger spatial scales of macroalgal removal. However, McClanahan et al. (2000, 2001) noted qualitatively similar effects in the Caribbean when conducting removals on patch reefs of ~1000 m^2 (~250x larger than the plot areas we manipulated) Additionally, when evaluating effects of macroalgal cover on fish across scales of $1m^2$, $100m^2$, and $1000m^2$, results from small scale manipulations in a warm temperate reef scaled-up well in one the few studies designed to assess the effects of scale (Levin & Hay 2002).

4.1 *The role of Herbivore Identity*:

Both removal and control plots were dominated in visits and bites by only a few herbivorous species. *C. striatus* is thought to use its comb-like teeth to feed on detritus and microalgae within algal EAM (Tebbett et al 2017). Studies using measures of algal height (Tebbett et al. 2017), bite morphology (Purcell & Bellwood 1993, Tebbett et al. 2017), and stomach content analysis (Choat et al. 2002) suggest *C. striatus* primarily consumes detritus and inorganic matter while leaving algal turfs intact. However, another similar study found *C. striatus* had greater algal turf removal than *A.* nigrofuscus, a species believed to have greater cropping impact (Marshell & Mumby 2012). Our results do not clarify the impact of *C. striatus* on turfs, but provide some distinction between the two species in terms of feeding behaviors. *C. striatus* had significantly higher bites per minute in removal plots, whereas *A. nigrofuscus* did not show a clear preference (fig 2). *C. striatus* and *C. sordidus* also had differences in feeding behavior. Both *C. striatus* and *C. sordidus* had time points with greater bites per minute in removal plots. However, this was driven by different behaviors. *C. sordidus* had significantly higher visits per minute, and at some time points, significantly higher bites per visit and percentage of visits that had feeding. Greater *C. striatus* bites per minute was driven partially by significantly higher percentages of visits in which feeding occurred, and smaller, nonsignificant changes in other metrics that may sum to an overall change in bites per minute (fig. 2).

These results differ from some other studies. McClanahan (1999) found *C. striatus* did not have significantly higher bites per minute in removal plots, and actually had significantly greater visits per minute to control plots, and greater numbers of bites per visit in removal plots. Also, in contrast to our results, *A. nigrofuscus* had significant preferences, and had significantly higher bites per minute, and bites per visit in removal plots. These divergent findings suggest that herbivore feeding behavior may be context-dependent, varying with environmental conditions, level of initial macroalgal cover, recent history of herbivore feeding, or other conditions.

4.2 Aggressive Behaviors:

In the Caribbean, when McClanahan et al. (2000) removed macroalgae, they found an immediate increase in aggression among herbivorous fishes. *Acanthurus coeruleus, A. bahianus, Stegastes fuscus, S. planifrons*, and *Sparisoma viride,* all increased aggressions towards other herbivorous fishes in removal plots. Our removal plots also had significantly higher aggressions by surgeonfishes (*C. striatus* and *A.nigrofuscus*) against the parrotfish *C. sordidus* (Fig 3). *C. striatus* and *C. sordidus* have similar diets (characterized by bacteria, meiofauna, and unidentified organic matter; Choat et al. 2002), suggesting that they may compete for food. *C. soridus* had higher bites per visit in removal plots at day 30, which was the date with the least feeding in this treatment by *C. striatus* (Fig 2). Similar resource usage may explain the aggressive behaviors, with the frequency of aggressions being much higher on day 0 when valuable, newly exposed, resources would have presumably been greatest. Aggressive behaviors of Acanthurids have been reported for *Acanthurus lineatus* (Robertson et al 1979, Choat & Bellwood 1985), *Acanthurus zineutus*, and *Zebrasoma scopes* (Robertson et al 1979), however to our knowledge, this is the first report of aggressions by *C. striatus* towards *C. sordidus.*

4.3 Implications for conservation

Coral dominated reefs have a low standing stock of highly productive filamentous algae, most of which are consumed by herbivores (Carpenter 1986, Burkepile & Hay 2006). As reefs degrade, they become dominated by a high standing stock of macroalgae with lower mass specific productivity, with most of algal productivity no longer being cycled through herbivores. Thus, macroalgae may dominate degraded reefs not just because there are not enough herbivores (Hughes et al. 2007, 2010), or the right diversity of herbivores (Burkepile & Hay 2008, Rasher et al. 2013) to remove them, but also because once macroalgae achieve some critical density, they alter habitat characteristics so that herbivores are discouraged from foraging. This will alter food webs, energy and nutrient transfer, and enhance macroalgal dominance at the expense of coral recovery.

Macroalgae decrease coral settlement and recruitment, growth, and survival (Kuffner et al. 2006, Vermeij et al 2009, Dixson et al 2014, Beatty et al. 2018, Clements et al. 2018), so macroalgal removal, whatever the mechanism, may aid coral reef recovery and resilience. Total macroalgal cover in removal plots did not recover at all by day 55 of our experiment (Table 1), suggesting that elevated herbivory in these plots suppressed macroalgal recovery. McClanahan et al. (1999) found a similar pattern when removing macroalgae from 100m2 areas and monitoring for three months. Herbivory by scrapers and detritivores such as C. sordius and C. striatus may suppress macroalgal recovery by feeding on algal turfs and removing macroalgae propagules or germlings.

Macroalgae decrease coral settlement and recruitment, growth, and survival (Kuffner et al. 2006, Vermeij et al 2009, Dixson et al 2014, Beatty et al. 2018, Clements et al. 2018), so macroalgal removal, whatever the mechanism, may aid coral reef recovery and resilience. Total macroalgal cover in removal plots did not recover at all by day 55 of our experiment (Table 1), suggesting that elevated herbivory in these plots suppressed macroalgal recovery. McClanahan et al. (1999) found a similar pattern when removing macroalgae from $100m^2$ areas and monitoring for three months. Herbivory by scrapers and detritivores such as *C. sordius* and *C. striatus* may suppress macroalgal recovery by feeding on algal turfs and removing macroalgae propagules or germlings.

Herbivores that remove macroalgae and those that prevent macroalgal establishment are commonly different species (Bellwood et al. 2006, Rasher et al 2013, Chong-seng et al. 2014). Large brown macroalgae such as *Turbinaria* and *Sargassum* has increased dramatically in Moorea over recent decades (Payri 1987), as occurs on reefs world-wide when herbivores are removed or excluded experimentally (Lewis 1986, Hughes et al. 2007). If herbivores, like *Naso* sp, that typically consume the adult stages on Pacific reefs (Rasher et al. 2013) are too uncommon to remove the macroalgae, or if grazing becomes ineffective once dense beds develop and suppress herbivore feeding behavior (Hoey & Bellwood 2011, Dell et al. 2016), then macroalgal dominance may persist and corals may be unable to recover unless other forces remove the macroalgal beds (storms, human removal, etc.)

As reefs decline, intervention techniques, such as coral restoration and direct algal removal, are being increasingly employed (McClanahan et al. 1999, 2000, Rinkevich 2014). For future intervention efforts that involve macroalgal removal, it may be more efficient to remove most of the macroalgal canopy and allow light shock and intense fish feeding to remove the remaining pieces and holdfasts, rather than using more time and effort intensive techniques, such as scrubbing or chiseling of holdfasts. Macroalgal removal to encourage coral settlement may also be best performed a few weeks or months prior to expected coral settlement season. This will allow for the high initial feeding response to clear remaining macroalgae, possibly enhance cover of settlement stimulating encrusting coralline algae (Belliveau & Paul 2002, Ritson-Williams et al. 2010), but prevent corals from settling during high feeding periods when fish may inadvertently damage juvenile corals. Even light grazing on the EAM, such as that by *Salarias fasciatus*, can damage young corals (Christiansen et al. 2009). The higher preference for feeding on barren substrates (Fig 4) may also present a challenge for corals settling in uncleared areas. If there is very little barren space on a macroalgal dominated reef, and herbivores prefer feeding from barren areas, corals that settle in the lesser appropriate space that is available may be impacted by herbivore feeding.

APPENDIX A. SUPPLEMENTARY MATERIALS

Table 2

Richness, diversity, and evenness of fishes visiting plots			
Control Plots			
Time	**Richness**	**H (Shannon-Weiner Index)**	**Evenness**
Day 0	6.8 ± .71	0.89 ± .06	0.45 ± .02
Day 7	10.08 ± 1.57	1.01 ± .36	0.42 ± .15
Day 30	10.92 ± .95	1.16 ± .26	0.47 ± .10
Day 55	11.08 ± .90	1. 68 ± .07	0.45 ± .10
Removal Plots			
Time	**Richness**	**H (Shannon-Weiner Index)**	**Evenness**
Day 0	12.27 ± .81	1.72 ± .07	0.70 ± .02
Day 7	12.08 ± 1.54	1.70 ± .11	.68 ± .03
Day 30	12.92 ± .99	2.11 ± .29	0.57 ± .08
Day 55	10.92 ± .65	1.54 ± .09	0.44 ± .10
P-values	**Richness**	**H (Shannon-Weiner Index)**	**Evenness**
Day 0	0.001	<0.001	<0.001
Day 7	0.131	0.022	0.033
Day 30	0.126	0.435	0.467
Day 55	0.958	0.25	0.732

Table 3

Visits min^{-1} and Bites min^{-} after removal. Blank spaces in average visits min^{-1} or bites min^{-1} columns indicate 0 occurrences. Number of Pairs refers to number of pairs in which at least one of the plots in the pair had a visit or bite. Bites min^{-1} only shows data for species that bit in at least one the plots in more than 3 pairs. P-values were obtained from paired t-tests (*Ctenochaetus striatus, Acanthurus nigrofusucs, and Chlorurus sorididus* were tested globally first) except for italicized p-values which indicate a sign test was used due to control plots having all values being 0 for that species. “---" indicates that a global test was insignificant, so post-hoc p-values were not calculated. Herbivores included fish that consume primarily plant materials but may technically be omnivorous. Species were included as other carnivores if diet included invertebrates, but also potentially fish.

	Visits min-1				Bites min -1 (showing species that visited more than at least 1 plot in 3 pairs)			
7 DAYS	Removal	Control	P-value	Number of Pairs	Removal	Control	P-value	Number of Pairs
HERBIVORES	5.10 ± .49	4.00 ± .40	0.055	11	21.59 ± 2.26	11.62 ± 1.48	0.015	11
FAMILY: ACANTHURIDAE								
Acanthurus lineatus	0.02	0.01		1				
Acanthurus nigrofuscus	0.36 ± 0.07	0.42 ± 0.12	0.900	11	10.36 + 4.55	19.55 + 8.41	---	9
Acanthurus triostegus	0.01			1				
Ctenochaetus striatus	2.96 ± 0.31	2.55 ± 0.27	---	11	232.18 + 28.92	123.82 + 15.35	0.002	11
Naso lituratus	0.01			1				
Uncertain if *C. striatus* or *A. nigrofuscus*								
Zebrasoma rostratum	0.01			1				
Zebrasoma scopas	0.11 ± 0.03	0.2 ± 0.07	0.337	10				
FAMILY: POMACANTHIDAE								
Centropyge flavissima	0.4 ± 0.17	0.12 ± 0.05	0.184	10				
Pygoplites diacanthus								
FAMILY: POMACENTRIDAE								
Abudefduf septemfasciatus								
Abudefduf sexfasciatus	0.2 ± 0.13	0.12 ± 0.07	0.439	6				
Chromis margaritifer	0.06			1				
Stegastes fasciolatus	0.06 ± 0.06	0.01 ± 0.01						
Stegastes nigricans		0.18 ± 0.11	0.142	4				
FAMILY: SCARIDAE								

Table 3 continued

Calotomus carolinus	0.01			1				
Chlorurus frontalis								
Chlorurus sordidus	1.19 ± 0.39	0.37 ± 0.12	0.040	11	22.55 + 8.1	1.55 + 1.09	0.025	7
Leptoscarus vaigiensis	0.1 ± 0.09	0.03 ± 0.01	0.391	5				
Scarus frenatus	0.04 ± 0.03	0.02		3				
Scarus oviceps								
Scarus psittacus & Scarus globiceps	0.09 ± 0.04	0.03 ± 0.02	0.169	6				
unidentified parrotfish IP (dark, uncertain)								
FAMILY: SIGANIDAE								
Siganus spinus	0.03 ± 0.02	0.02 ± 0.01	0.697	4				
Siganus argentus								
FAMILY: TETRADONTIDAE								
Canthigaster solandri								
FAMILY: ZANCLIDAE								
Zanclus cornutus	0.01	0.01		1				
INVERTIVORES	1.94 ± .50	1.12± .31	0.293	11	0.48 ± .29	0.10 ± .06	0.279	7
FAMILY: BALISTIDAE								
Balistapus undulatus	0.11 ± 0.05	0.16 ± 0.06	0.594	10				
Melichthys vidua	0.03 ± 0.03	0.02 ± 0.02		3				
Rhinecanthus aculeatus								
FAMILY: CHAETODONTIDAE								
Chaetodon auriga								
Chaetodon citrinellus	0.03 ± 0.02			2				
Chaetodon lunula								
Chaetodon lunulatus	0.01			1				

Table 3 continued

Chaetodon ornatissimus	0.01			1				
Chaetodon reticulatus	0.03 ± 0.01	0.01 ± 0.01	0.416	5				
Chaetodon vagabundus	0.02 ± 0.02	0.03 ± 0.02		3				
Orcipiger flavissimus								
FAMILY: LABRIDAE								
Bodianus axillaris	0.05	0.04		2				
Cheilinus trilobatus	0.04 ± 0.03	0.04 ± 0.01	0.988	6				
Cheilio inermis	0.01 ± 0.01	0.05 ± 0.02	0.112	5				
Coris aygula	0.03			1				
Coris gaimard								
Epibulus insidiator	0.02 ± 0.01	0.02 ± 0.01	0.975	4				
Gomphosus varius	0.06 ± 0.03	0.09 ± 0.04	0.597	7				
Halichoeres hortulanus	0.51 ± 0.11	0.17 ± 0.08	0.024	11				
Halichoeres marginatus	0.02 ± 0.01	0.04 ± 0.02	0.427	4				
Oxychelinus unifasciatus								
Stethojulis bandanensis	0.12 ± 0.06	0.02 ± 0.02	0.170	5				
Thalassoma ambylcephalum	0.03			1				
Thalassoma hardwicke	0.76 ± 0.37	0.39 ± 0.16	0.398	11				
unidentified wrasse								
FAMILY: MULLIDAE								
Mulloidichthys flavolineatus	0.01			1				
Parupeneus cyclostomus								
Parupeneus insularis		0.01		1				
Parupeneus multifasciatus		0.01		1				
FAMILY: TETRADONTIDAE								
Arothron hispidus								

Table 3 continued

Arothron meleagris								
Arothron stellatus								
Ostracion meleagris								
OTHER CARNIVORES	0.08 ± .04	0.04 ± .02	0.177	7				
FAMILY: AULOSTOMIDAE								
Aulostomus chiensis	0.01			1				
FAMILY: BLENNIIDAE								
Plagiotremus tapeinosoma	0.01			1				
FAMILY: CARANGIDAE								
Carangoides orthogrammus								
unknown carangidae		0.01		1				
FAMILY: CARCHARHINIDAE								
Carcharhinus melanopterus	0.01 ± 0.01	0.02 ± 0.01	0.330	4				
FAMILY: LETHRINIDAE								
Gnathodentex aureolineatus	0.01 ± 0.01			2				
Lethrinus olivaceus								
FAMILY: SERRANIDAE								
Cephalopholis argus	0.03 ± 0.02	0.01		2				
Epinephelus merra	0.01			1				
UNIDENTIFIED								
FAMILY: UNKNOWN								
total unknown fish species(not sure about what class, different for different videos)	0.02 ± 0.01			3				
total unidentified fish individuals	0.06 ± 0.04	0.01 ± 0.01	0.226	4				

Table 3 continued

	Visits min-1				Bites min -1 (showing species that visited more than at least 1 plot in 3 pairs)			
30 DAYS	Removal	Control	P-value	Number of Pairs	Removal	Control	P-value	Number of Pairs
HERBIVORES	4.92 ± .69	3.01 ± .20	0.015	12	19.00 ± 4.09	14.10 ± 2.75	0.355	12
FAMILY: ACANTHURIDAE								
Acanthurus lineatus	0.02			1				
Acanthurus nigrofuscus	0.39 ± 0.06	0.34 ± 0.06	.425	12	15.42 ± 5.89	12.33 ± 3.15	---	12
Acanthurus triostegus		0.01		1				
Ctenochaetus striatus	2.54 ± 0.29	2.01 ± 0.18	---	12	208.92 ± 31.64	175.17 ± 35.21	0.551	12
Naso lituratus								
Uncertain if *C. striatus* or *A. nigrofuscus*								
Zebrasoma rostratum								
Zebrasoma scopas	0.03 ± 0.01	0.15 ± 0.06	0.036	10	1.00	5.58 ± 4.41	0.317	4
FAMILY: POMACANTHIDAE								
Centropyge flavissima	0.46 ± 0.15	0.22 ± 0.1	0.861	12	1.25 ± 1.08	2.1 ± 1.91	1	4
Pygoplites diacanthus								
FAMILY: POMACENTRIDAE								
Abudefduf septemfasciatus	0.01			1				
Abudefduf sexfasciatus	0.14 ± 0.05	0.05 ± 0.02	0.074	8				
Chromis margaritifer	0.03 ± 0.02			2				
Stegastes fasciolatus								

Table 3 continued

Stegastes nigricans	0.02 ± 0.01	0.01 ± 0.01	0.082	4				
FAMILY: SCARIDAE								
Calotomus carolinus								
Chlorurus frontalis								
Chlorurus sordidus	1.59 ± 0.49	0.27 ± 0.11	0.016	12	53.75 + 38.7	1.17 + 1.17	.267	10
Leptoscarus vaigiensis	0.03 ± 0.01	0.02 ± 0.01	0.191	6				
Scarus frenatus								
Scarus oviceps	0.01 ± 0.01	0.02 ± 0.01		3				
Scarus psittacus & Scarus globiceps	0.06 ± 0.04	0.03 ± 0.02	0.551	4				
unidentified parrotfish IP (dark, uncertain)								
FAMILY: SIGANIDAE								
Siganus argentus		0.05		1				
Siganus spinus	0.02 ± 0.02	0.03 ± 0.02		2				
FAMILY: TETRADONTIDAE								
Canthigaster solandri								
FAMILY: ZANCLIDAE								
Zanclus cornutus	0.04 ± 0.02	0.02 ± 0.01	0.851	4				
INVERTIVORES	1.25 ± .15	1.22 ± .23	0.556	12	0.02 ± .02	0.09 ± .09		4
FAMILY: BALISTIDAE								
Balistapus undulatus	0.09 ± 0.05	0.16 ± 0.06	0.545	9				
Melichthys vidua	0.04 ± 0.03	0.01 ± 0.01	0.723	4				
Rhinecanthus aculeatus								
FAMILY: CHAETODONTIDAE								

Table 3 continued

Chaetodon auriga								
Chaetodon citrinellus	0.01			1				
Chaetodon lunula								
Chaetodon lunulatus		0.01		1				
Chaetodon ornatissimus	0.01 ± 0.01	0.04 ± 0.03	0.339	4				
Chaetodon reticulatus	0.01 ± 0.01			2				
Chaetodon vagabundus	0.01 ± 0.01	0.02 ± 0.01		3				
Orcipiger flavissimus	0.01			1				
FAMILY: LABRIDAE								
Bodianus axillaris	0.01	0.02 ± 0.02		2				
Cheilinus trilobatus	0.02 ± 0.01	0.02 ± 0.01	0.339	5				
Cheilio inermis	0.01	0.01		2				
Coris aygula	0.01			1				
Coris gaimard								
Epibulus insidiator	0.01 ± 0.01	0.02 ± 0.01	0.974	4				
Gomphosus varius	0.06 ± 0.03	0.05 ± 0.02	0.470	6				
Halichoeres hortulanus	0.23 ± 0.04	0.16 ± 0.05	0.257	12				
Halichoeres marginatus	0.12 ± 0.08	0.04 ± 0.03	0.210	8				
Oxychelinus unifasciatus	0.01			1				
Stethojulis bandanensis	0.02 ± 0.01			3				
Thalassoma ambylcephalum								
Thalassoma hardwicke	0.5 ± 0.11	0.6 ± 0.17	0.285	12				
unidentified wrasse		0.01		1				
FAMILY: MULLIDAE								
Mulloidichthys flavolineatus		0.01		1				

Table 3 continued

Parupeneus cyclostomus								
Parupeneus insularis	0.01 ± 0.01			2				
Parupeneus multifasciatus	0.03 ± 0.02	0.02 ± 0.02	0.389	4				
FAMILY: TETRADONTIDAE								
Arothron hispidus								
Arothron meleagris	0.01 ± 0.01	0.01		2				
Arothron stellatus		0.01		1				
Ostracion meleagris	0.01 ± 0.01	0.01		2				
OTHER CARNIVORES	0.05 ± .01	0.01 ± .01	0.179	7				
FAMILY: AULOSTOMIDAE								
Aulostomus chiensis								
FAMILY: BLENNIIDAE								
Plagiotremus tapeinosoma								
FAMILY: CARANGIDAE								
Carangoides orthogrammus	0.01			1				
unknown carangidae								
FAMILY: CARCHARHINIDAE								
Carcharhinus melanopterus		0.01		1				
FAMILY: LETHRINIDAE								
Gnathodentex aureolineatus								
Lethrinus olivaceus								
FAMILY: SERRANIDAE								
Cephalopholis argus	0.03 ± 0.01		0.053	4				

Table 3 continued

Epinephelus merra	0.02 ± 0.01			2				
UNIDENTIFIED								
FAMILY: UNKNOWN								
total unknown fish species(not sure about what class, different for different videos)	0.03 ± 0.01	0.01 ± 0.01	0.039	5				
total unidentified fish individuals	0.06 ± 0.02	0.01 ± 0.01	0.032	6				

	Visits min-1				Bites min -1 (showing species that visited more than at least 1 plot in 3 pairs)			
55 DAYS	Removal	Control	P-value	Number of pairs	Removal	Control	P-value	Number of Pairs
HERBIVORES	4.72 ± .34	3.14 ± .28	0.002	12	21.74 ± 2.97	11.46 ± 1.77	0.010	12
FAMILY: ACANTHURIDAE								
Acanthurus lineatus								
Acanthurus nigrofuscus	0.45 ± 0.07	0.44 ± 0.08	0.616	11	33.83 + 8.73	15.17 + 5.07	---	11
Acanthurus triostegus								
Ctenochaetus striatus	3.04 ± 0.22	2.16 ± 0.23	---	12	233.83 + 30.22	129.33 + 21.49	0.078	12
Naso lituratus								
Uncertain if *C. striatus* or *A. nigrofuscus*								
Zebrasoma rostratum								
Zebrasoma scopas	0.04 ± 0.03	0.06 ± 0.02	0.631	7				
FAMILY: POMACANTHIDAE								

Table 3 continued

Centropyge flavissima	0.44 ± 0.14	0.12 ± 0.04	0.042	10				
Pygoplites diacanthus								
FAMILY: POMACENTRIDAE								
Abudefduf septemfasciatus								
Abudefduf sexfasciatus	0.04 ± 0.03	0.04 ± 0.02	0.713	6				
Chromis margaritifer	0.03			1				
Stegastes fasciolatus								
Stegastes nigricans		0.01 ± 0.01		2				
FAMILY: SCARIDAE								
Calotomus carolinus								
Chlorurus frontalis	0.01 ± 0.01							
Chlorurus sordidus	1.15 ± 0.32	0.39 ± 0.11	0.033	10	30.33 + 20.45	3.92 + 1.98	0.217	10
Leptoscarus vaigiensis	0.02 ± 0.01	0.03 ± 0.01	0.023	6				
Scarus frenatus	0.02 ± 0.01	0.01 ± 0.01		3				
Scarus oviceps								
Scarus psittacus & Scarus globiceps	0.03 ± 0.02	0.03 ± 0.02	0.600	4				
unidentified parrotfish IP (dark, uncertain)								
FAMILY: SIGANIDAE								
Siganus argentus								
Siganus spinus	0.01 ± 0.01	0.01 ± 0.01		3				
FAMILY: TETRADONTIDAE								
Canthigaster solandri		0.01		1				
FAMILY: ZANCLIDAE								
Zanclus cornutus	0.02	0.02		2				
INVERTIVORES	1.08 ± .16	0.82 ± .10	0.216	12	0.16 ± .12	0.05 ± .04	0.393	6

Table 3 continued

FAMILY: BALISTIDAE								
Balistapus undulatus	0.09 ± 0.03	0.13 ± 0.04	0.647	10				
Melichthys vidua	0.04 ± 0.03	0.03 ± 0.02	0.857	4				
Rhinecanthus aculeatus		0.01		1				
FAMILY: CHAETODONTIDAE								
Chaetodon auriga		0.01		1				
Chaetodon citrinellus	0.03 ± 0.02	0.02 ± 0.02		3				
Chaetodon lunula								
Chaetodon lunulatus	0.01 ± 0.01	0.01 ± 0.01		2				
Chaetodon ornatissimus	0.02 ± 0.01	0.02 ± 0.01	0.732	4				
Chaetodon reticulatus	0.01			1				
Chaetodon vagabundus		0.01		1				
Orcipiger flavissimus								
FAMILY: LABRIDAE								
Bodianus axillaris								
Cheilinus trilobatus	0.05 ± 0.02	0.02 ± 0.01	0.567	6				
Cheilio inermis	0.02	0.01		2				
Coris aygula								
Coris gaimard	0.01			1				
Epibulus insidiator	0.02 ± 0.01	0.03 ± 0.01	0.416	5				
Gomphosus varius	0.06 ± 0.02	0.05 ± 0.03	0.780	8				
Halichoeres hortulanus	0.16 ± 0.04	0.11 ± 0.02	0.267	12				
Halichoeres marginatus	0.04 ± 0.02	0.09 ± 0.04	0.377	8				
Oxychelinus unifasciatus		0.01		1				
Stethojulis bandanensis	0.08 ± 0.04		0.091	4				
Thalassoma ambylcephalum								

Table 3 continued

Thalassoma hardwicke	0.45 ± 0.06	0.2 ± 0.04	0.001	12				
unidentified wrasse								
FAMILY: MULLIDAE								
Mulloidichthys flavolineatus								
Parupeneus cyclostomus	0.01			1				
Parupeneus insularis		0.01		1				
Parupeneus multifasciatus	0.01	0.01 ± 0.01		2				
FAMILY: TETRADONTIDAE								
Arothron hispidus		0.01		1				
Arothron meleagris								
Arothron stellatus								
Ostracion meleagris								
OTHER CARNIVORES	0.05 ± .02	0.04 ± .02	0.929	6				
FAMILY: AULOSTOMIDAE								
Aulostomus chiensis								
FAMILY: BLENNIIDAE								
Plagiotremus tapeinosoma								
FAMILY: CARANGIDAE								
Carangoides orthogrammus								
unknown carangidae								
FAMILY: CARCHARHINIDAE								
Carcharhinus melanopterus	0.01			1				
FAMILY: LETHRINIDAE								
Gnathodentex aureolineatus	0.01 ± 0.01	0.02 ± 0.01	0.053	4				
Lethrinus olivaceus								
FAMILY: SERRANIDAE								
Cephalopholis argus	0.04 ± 0.03	0.02 ± 0.02		3				

Table 3 continued

Epinephelus merra								
UNIDENTIFIED								
FAMILY: UNKNOWN								
total unknown fish species(not sure about what class, different for different videos)	0.01 ± 0.01	0.02 ± 0.02	0.974	4				
total unidentified fish individuals	0.01 ± 0.01	0.02 ± 0.02		3				

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