Coral Reef Benthic Communities of Wotho Atoll, Republic of the Marshall Islands

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Executive Summary

- The taxa found on Wotho's reefs (regardless of the reef types; e.g. inner reef, outer reef, patch reef) are all commonly associated with reefs that are healthy, but the percent cover of live coral was less than the 10% threshold necessary to keep up with sea level rise at all but three of the reefs surveyed. This suggests that Wotho's reefs may have undergone a bleaching event prior to the survey, although this is only a hypothesis. Still, this hypothesis is supported by the high percentages of rubble found on many of the inner reefs, which could suggest a past disturbance event. Future surveys will be useful to provide evidence for bleaching (if the percent cover of macroalgae and coral taxa have remained stable over time, this may indicate that the state of the reefs from these surveys is not their natural state).

- The benthic communities differed significantly across reef types, but the taxa found at each reef type varied. Outer reefs tended to be characterised by *Pocillopora*, and either massive *Porites* and *Goniopora* or *Microdictyon* (macroalgae genera). Inner and patch/back reefs were characterised by rubble, *Acropora*, and *Stylophora,* and either *Halimeda* or sand. The most important taxa in distinguishing between the benthic communities at inner versus outer reefs were *Microdictyon*, sand, turf, CCA, and rubble, followed by *Halimeda*, massive *Porites*, sponges, *Goniopora*, and *Acropora*.

- Bleaching was observed for less than 3% of all hard corals, suggesting that at the time of the surveys there was not widespread, ongoing bleaching. However, about 10% of *Acropora*, 21% of *Astreopora*, and 4% of *Pocillopora* observed were bleached. Both *Acropora* and *Pocillopora* are important reef-building corals, and both are known to be sensitive to heat stress. The majority of the bleaching observed during the surveys occurred in the lagoon sites (both inner sites along the lagoon side of the islands, and patch/back reefs).

- We also observed what may be a coral disease on several *Pocillopora* colonies in the photo quadrats, although this is another hypothesis because the observed patterns are not known to be caused by any specific disease. The affected patches were not quantified in these surveys and none fell underneath the randomly assigned points in our photo quadrats. Further surveys could seek to quantify the prevalence of this 'disease' (see Recommendations).

Introduction

Wotho is one of 29 atolls and 5 islands in the Republic of the Marshall Islands (RMI) (Beger et al., 2010). Wotho is composed of 13 islands with a total land area of 4.33 km^2 (1.67 mi^2) enclosing a lagoon of 94.92 km^2 (36.65 mi^2) (United Nations Environmental Programme, n.d.). It is a part of the Ralik Island Chain, and is approximately 660 km (410 mi) northeast of the capital of the RMI, Majuro Atoll.

Wotho Atoll is home to a population of 97 people as of the most recent census collected in 2011, which is 0.2% of the RMI’s total population of 53,158 (Secretariat of the Pacific Community, 2012). In 2011, the census report estimated that the population of Wotho was shrinking by about 3.4% per year. Wotho is one of the least populated atolls in the Marshall Islands, along with Bikini, Rongelap, Jabat, and Lib.

Because of its remote nature, there are no published studies (to our knowledge) of the benthic communities of the coral reefs in Wotho Atoll. In June 2016, a team of marine resource managers and scientists from the Marshall Islands Marine Resources Authority (MIMRA) and the College of the Marshall Islands (CMI), conducted benthic surveys of the coral reefs in Wotho Atoll, visiting 12 sites (Table 1, Fig1). This report provides analyses of the benthic quadrat photos collected by the survey team in order to provide a baseline estimate of relative coral reef ecosystem health in Wotho Atoll.

Fig 1. Survey sites in Wotho Atoll.

There is a dearth of information about potential local threats to coral reefs in Wotho, although local pressure on marine resources from people is likely to be minimal because of the small population size. However, in 2014, coral reefs in the Marshall Islands experienced the most severe bleaching event in their recorded history, and due to an extended central-Pacific El Niño event, the Marshall Islands experienced higher-than-average sea surface temperatures (SSTs) off and on through at least 2017 (Fig 2). Bleaching in the RMI had happened before;

observations of bleaching in Majuro Atoll were reported between 1998-2000, and in 2001, 2003, and 2006 (Beger et al., 2010).

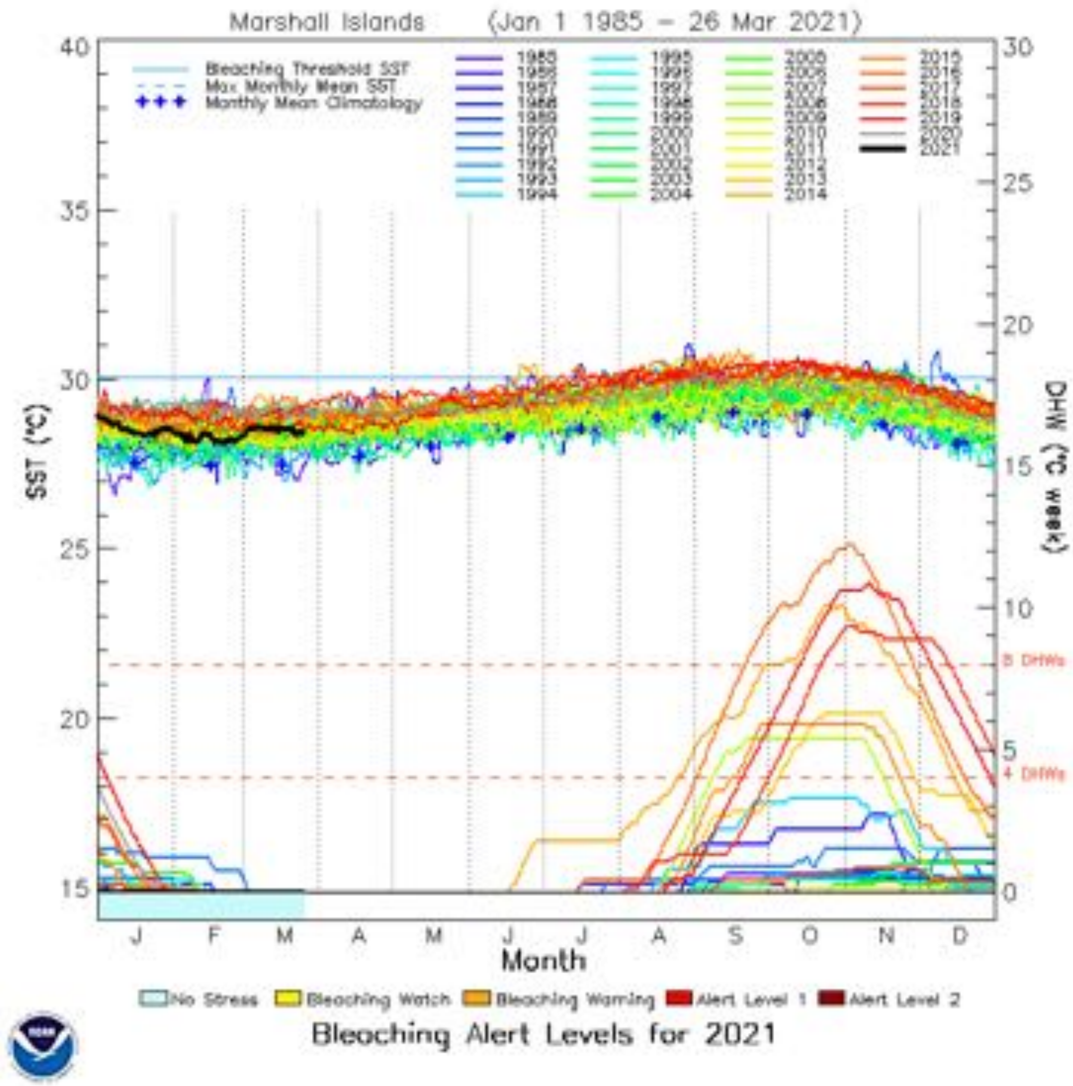

Fig 2. Degree heating weeks and sea surface temperatures in Majuro Atoll, Republic of the Marshall Islands, from 1985 - 2021 (NOAA Coral Reef Watch, 2019).

There are no reports of bleaching in 2014 from Wotho specifically, although there were bleaching alerts in both 2014 and 2015 (Fig 2). During the surveys, the RMI was under a bleaching watch, but there were no warnings in place. However, in September 2016 (three months after the data analysed here were collected), an Alert Level 2 Bleaching Warning was issued for the RMI, and maps suggest that some bleaching-level heat stress likely reached Wotho Atoll both before and after the surveys (Fig 3). While it is not possible to estimate the amount or severity of bleaching (and whether there was coral mortality), these data suggest that some bleaching likely occurred in Wotho Atoll between 2014 - 2017. As described further in the results and discussion section below, the photos captured some bleaching and potential evidence that bleaching (or another disturbance event) may have occurred prior to the surveys at some sites.

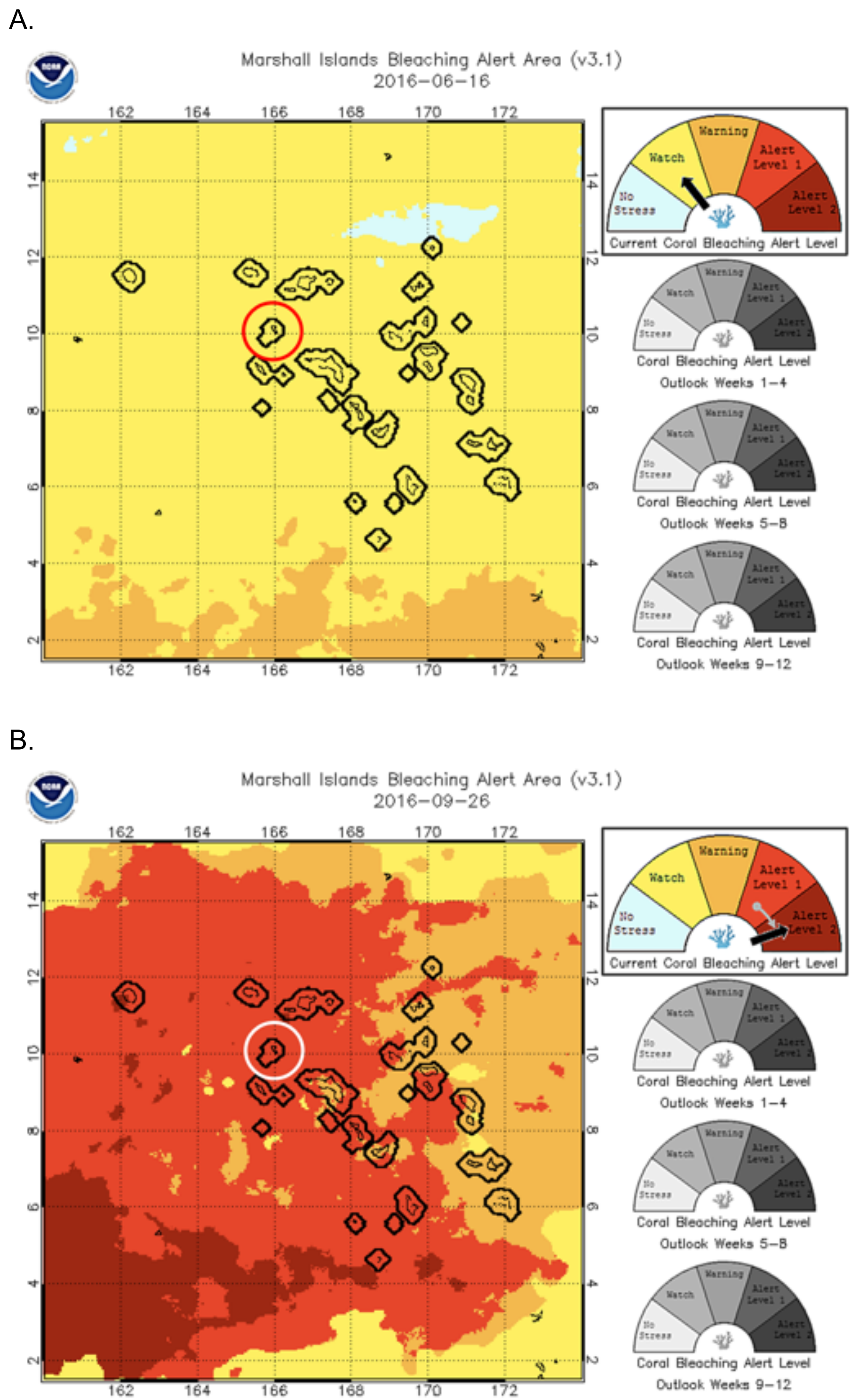

Fig 3: Bleaching alert areas in the Marshall Islands, (A) during the survey period and (B) three months following the surveys.

Methods

Data Collection

Data were collected by the Marshall Islands Marine Resources Authority in June 2016 using the methods described by Houk et al (2013). Three to five 50m-long transects (depending on the site) were placed along the benthos between 8 and 10m depth, and about 50 photographs (covering 0.5 x 0.5m) were collected along each of the transect lines (at 1m intervals, Table 1).

Table 1: Site information.

Site	LocalName	Latitude	Longitude	Reef Type
WTHO-1	W IN 1	10.140523	165.978462	Patch/back
WTHO-2	W IN 2	10.155317	165.965328	Patch/back
WTHO-3	W IN 3	10.168879	165.935502	Inner
WTHO-4	W IN 5	10.096612	165.985439	Inner
WTHO-5	W IN 6	10.079942	165.979553	Inner
WTHO-6	W IN 7	10.061037	165.980255	Inner
WTHO-7	W IN 8	10.051706	165.999982	Inner
WTHO-8	W OUT N2	10.17906	165.950452	Outer
WTHO-9	W OUT W1	10.171265	165.918946	Outer
WTHO-10	W OUT W3	10.096247	165.94712	Outer
WTHO-11	W OUT W4	10.067521	165.959773	Outer
WTHO-12	W OUT W5	10.031001	165.996688	Outer

Data Analysis

Photo Identification

Photos from the transects were processed to calculate the benthic percent cover using the open-source web tool CoralNet (Beijbom *et al.*, 2012), which overlaid 10 random points per photo for 150-250 photos per site, depending on the number of transects (between 1,430 and 2,570 points per site). Each point was manually identified to the genus level for hard coral (including the octocoral *Heliopora*, because it is common in the region) and macroalgae, and to the functional group for sponges, soft corals, turf algae, crustose coralline algae, invertebrates, and cyanobacteria. When possible, corals and soft corals with signs of bleaching were identified to the genus level.

The categories and codes for benthic analyses were adapted from those provided by Martin Romain, R2R Chief Technical Advisor. These codes had been used by MICS and MIMRA for previous analyses of coral reefs at different atolls and sites (the updated codes are in the supplementary materials, S1). Using these code files will allow local stakeholders to compare the results from this analysis to those from other atolls and/or time periods. The results from the analyses presented here have consolidated many of the codes for ease of interpretation, but in the future, these higher resolution codes may allow more detailed or higher resolution analyses without redoing the photo identification.

To allow comparisons to other data using these same taxa, these analyses relied on (scleractinian) taxonomy that is currently out-of-date. Specifically, the analyses in this report comply with the taxonomy as described by Veron (2000). Since this taxonomy was published, the genera and species within the Faviidae family have changed considerably, with some species being moved into different genera and the species within genera being split among one or more other genera (Huang *et al.*, 2011). However, again, using the older taxonomy will allow comparison across atolls and time periods for which data are collected by MIMRA and others in the Marshall Islands. The functional groups of the corals that are affected by these taxonomic changes have not changed and thus are not likely to influence any estimates of relative reef health or degradation.

Statistical Analyses

All statistical analyses were conducted using R Statistical Software version 4.0.2 (R Core Team, 2020) and RStudio Version 1.3.1093 (RStudio Team, 2020). Plots were created using the R packages ggplot2 (Wickham, 2016) and ggbiplot (Vu, 2011).

Descriptive statistics of the coral reefs at each site and for each key taxa were calculated, along with the Genera Richness (number of distinct genera) for hard coral genera at each site and reef type, as a way to estimate diversity of hard corals (because more diverse reefs are thought to be more resilient to stressors (Richards *et al.*, 2008)).

Principal Component Analysis (PCA) (Jolliffe, 2002) was used as a tool for visualizing patterns in the data across sites and reef types based on the benthic community composition. Similarity Percentages (SIMPER) analysis is useful in that it calculates the contribution of each genera (by percent) to the difference between two groups. Here, SIMPER (999 permutations) was used to analyze drivers of benthic community differences across the two different reef types using the R package vegan (Oksanen *et al.*, 2019). Finally, the percent of corals that were bleached by genera were calculated and compared across reef types.

Results

Overview

Macroalgae had the highest cover of all functional groups across sites, followed by turf algae, sand, then hard coral cover; however, the large standard deviations of each of these functional groups show that the community compositions varied across sites (Table 2).

Table 2: Percent cover of functional groups (including all sites), sorted from highest to lowest overall percent cover. Photos of functional groups are in Figs 3-5.

Functional Group	Mean	Median	Minimum	Maximum	Standard Deviation
Macroalgae	25.61	20.38	5.64	58.04	17.20
Turf algae	24.23	24.82	9.80	44.32	10.94
Sand	13.40	12.56	0.60	36.68	11.25
Coral	9.57	8.46	2.44	26.28	6.49
CCA	9.47	5.18	0.44	24.28	9.30
Rubble	8.40	7.22	0.80	20.96	6.97
Sponge	7.46	7.02	3.04	13.80	3.14
Cyanobacteria	0.81	0.50	0.08	3.39	0.96
Other Non-Living/ Unidentifiable	0.55	0.44	0.04	1.84	0.53
Soft corals	0.36	0.24	0.04	1.40	0.44
Invertebrates	0.25	0.16	0.08	0.72	0.20

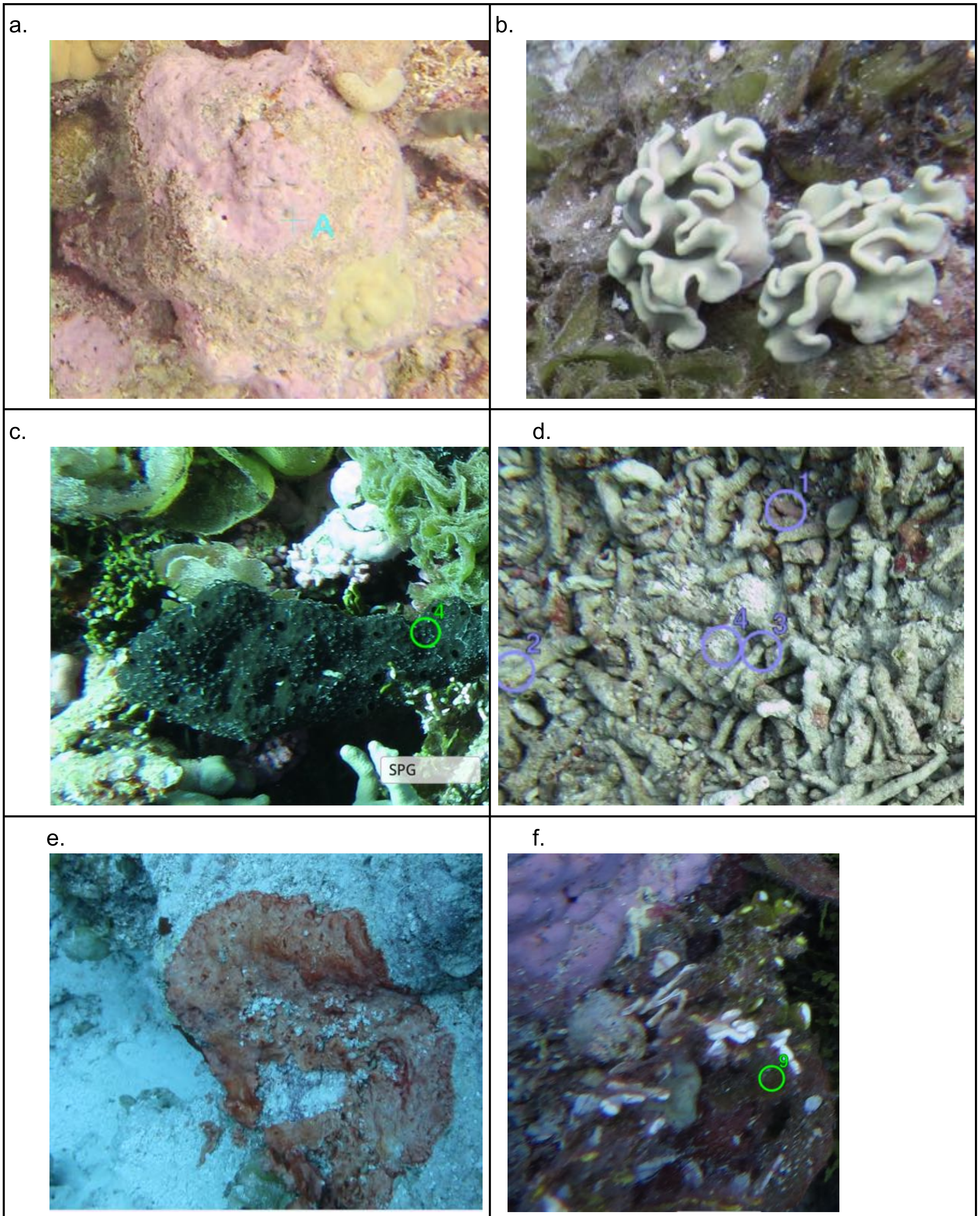

Figure 3. Most common benthic categories, including (a) CCA surrounded by turf algae, (b) soft corals, (c) a sponge (black) surrounded by Halimeda, Microdictyon, and CCA, (d) rubble covered by turf algae, (e) a cyanobacteria mat, and (f) cyanobacteria growing over Halimeda.

Macroalgae across all sites was composed almost entirely of the genera *Microdictyon*, *Halimeda*, and *Caulerpa*. Overall, *Microdictyon* alone accounted for 74.69% of all macroalgae across the entire atoll, while *Halimeda* accounted for 23.03% and *Caulerpa* accounted for 1.50% (Fig 4).

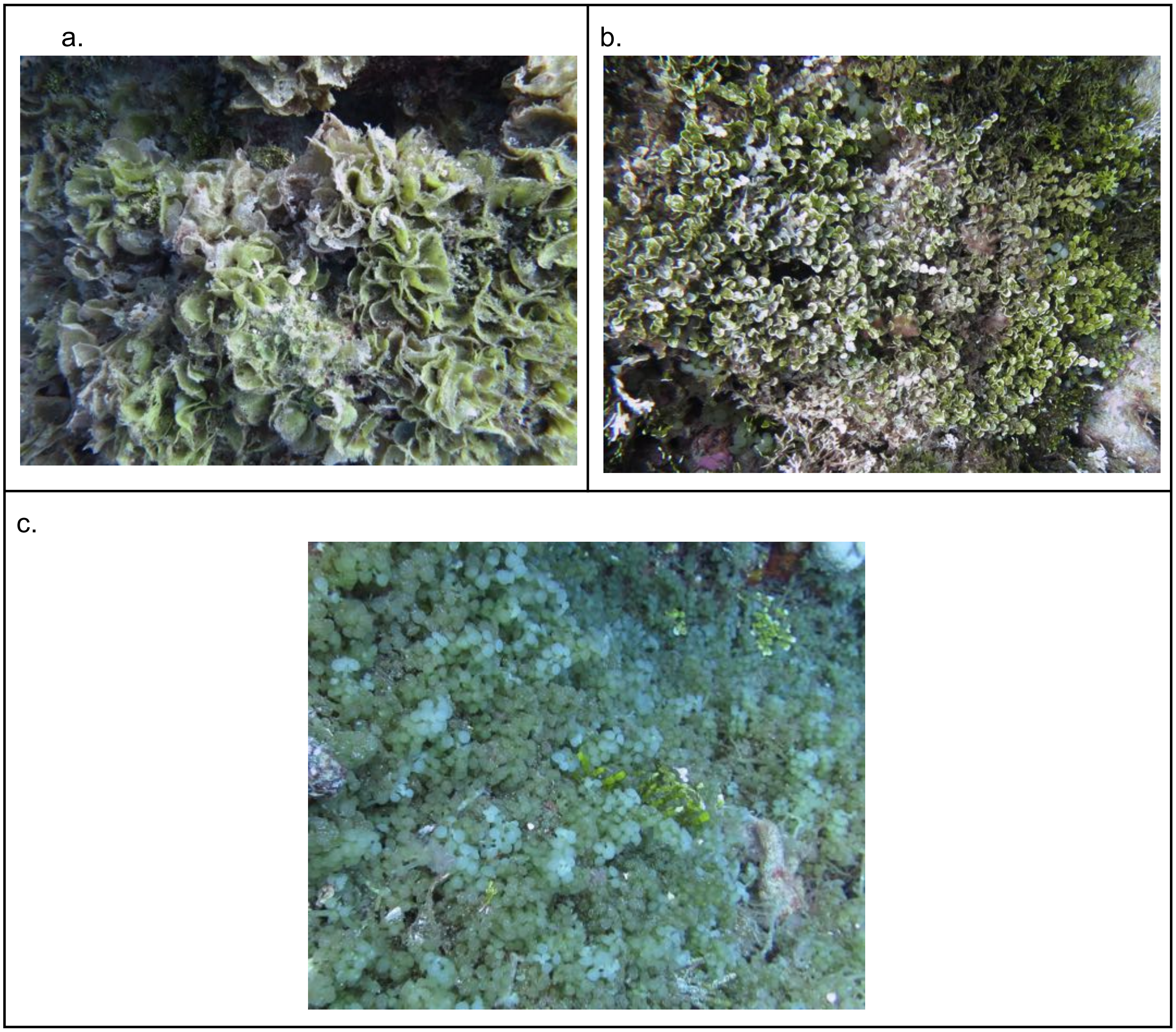

Figure 4. The three most common macroalgae genera in Wotho. Microdictyon (a) was the most common, accounting for almost three-quarters of all the macroalgae across the atoll, while Halimeda (b) accounted for almost a quarter. Caulerpa (c) was less common, accounting for less than 2% of all macroalgae across the atoll.

Of the hard coral genera, massive *Porites* was the most common, accounting for 22.52% of all hard coral cover across the entire atoll. The second most common coral genera was *Acropora*, accounting for 16.88% of all coral cover, followed by *Isopora* (15.11%), *Goniastra* (11.98%), *Stylophora* (5.49%), and *Pocillopora* (4.73%) (Fig 5).

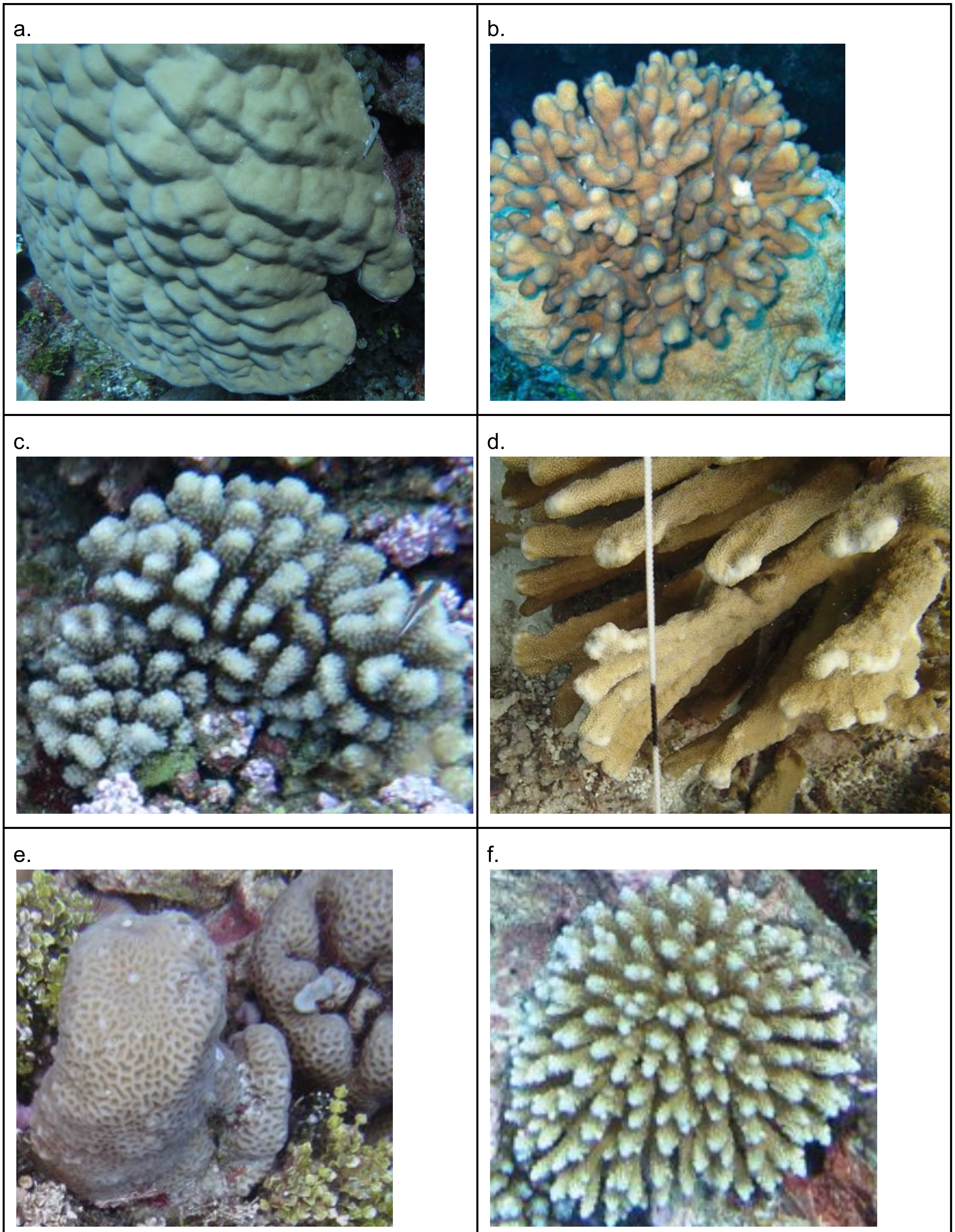

Figure 5. Most common coral genera found in Wotho Atoll: (a) massive Porites, (b) Stylophora, (c) Pocillopora, (d) Isopora, (e) Goniastrea, and (f) Acropora.

Benthic Communities By Site

The benthic communities varied widely across sites (Fig 6). Some sites had more hard coral cover than others (for example, 4_Out had the highest percent coral cover at 26.28% of benthic cover while 3_Out had the lowest at 2.44%) (Table 3). The total percent cover of live coral does not seem to depend on the reef type, although the different genera of hard coral differed by reef type (discussed further in the *Comparison of Benthic Communities by Reef Type* section below). Almost all reefs surveyed had less than 10% live hard coral cover (all but 3 out of 12 sites). Studies from other parts of the Pacific have found that coral reefs must maintain a hard coral cover of greater than 10% to produce enough carbonate to withstand erosion and to grow fast enough to keep up with sea level rise (Perry et al., 2015). The low percent cover of hard coral cover in Wotho could have important implications for shoreline protection (discussed further in the conclusions).

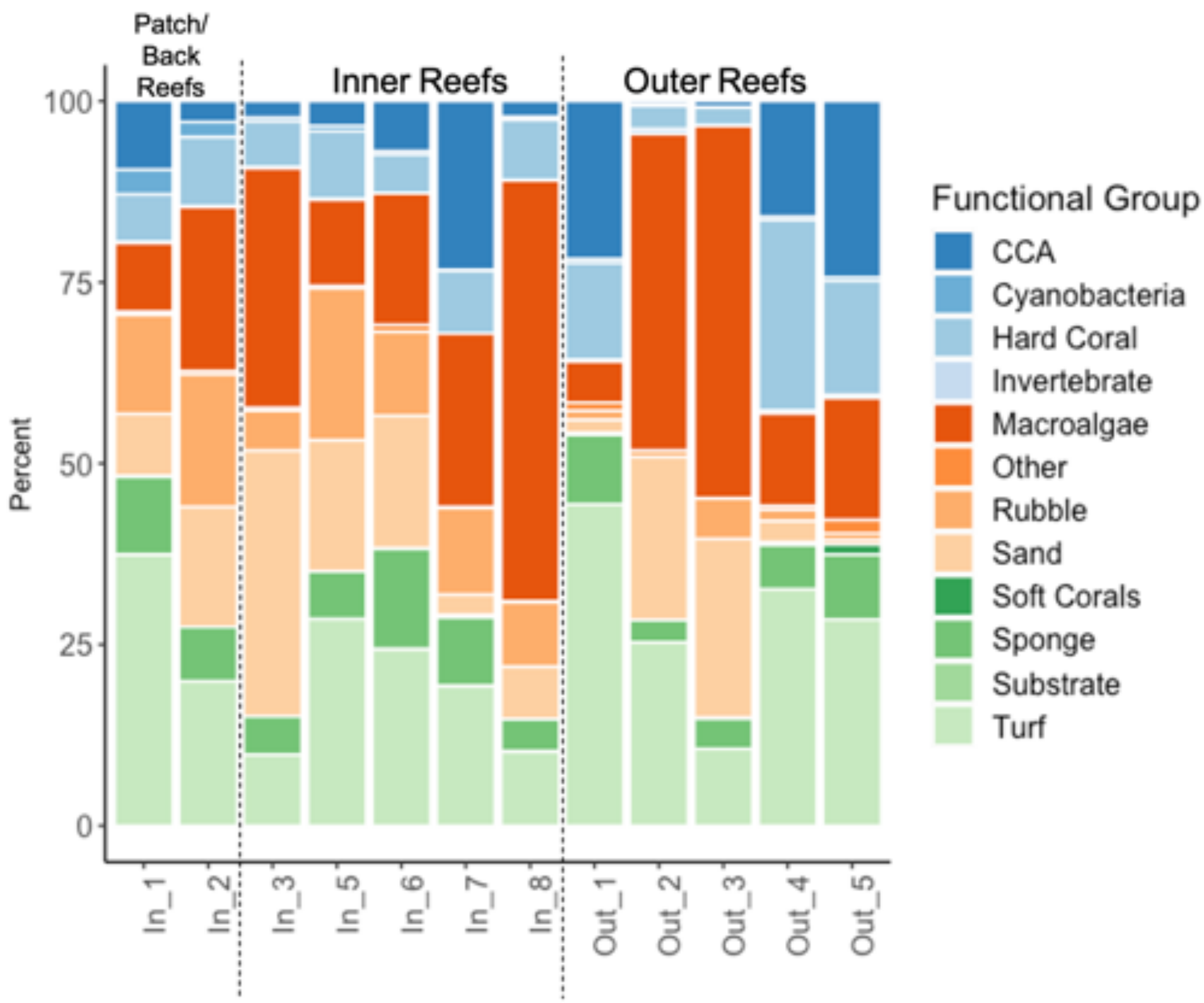

Fig 6. Percent cover of key functional groups by site.

Table 3. Percent cover of key taxon and hard coral genera richness by site.

Site	Genera Richness	Hard Coral	Macro-algae	Turf Algae	CCA	Cyano-bacteria	Sponges	Soft Corals	Sand	Rubble
1_In	21	6.57	9.48	37.37	9.48	3.39	10.72	0.16	8.57	13.63
2_In	18	9.56	22.60	19.96	2.84	2.12	7.48	0.00	16.56	18.28
3_In	11	6.32	33.04	9.80	2.36	0.52	5.28	0.00	36.68	5.48
5_In	15	9.36	11.88	28.52	3.44	0.68	6.58	0.00	18.12	20.96
6_In	21	5.28	18.16	24.32	6.96	0.48	13.80	0.12	18.32	11.56
7_In	24	8.64	23.92	19.24	23.24	0.20	9.44	0.36	2.80	11.96
8_In	18	8.28	58.04	10.20	2.20	0.40	4.44	0.04	7.24	8.88
1_Out	25	13.28	5.64	44.32	21.80	0.56	9.60	0.32	1.76	1.24
2_Out	11	3.16	43.68	25.32	0.44	0.24	3.04	0.00	22.56	0.80
3_Out	13	2.44	51.36	10.64	0.80	0.08	4.12	0.12	24.72	5.56
4_Out	26	26.28	12.76	32.64	15.96	0.48	6.08	0.40	2.92	1.52
5_Out	29	15.72	16.80	28.48	24.28	0.52	8.92	1.40	0.60	0.96

The reefs surveyed also differed by coral composition (Fig 7). The genera *Acropora*, which is known to be sensitive to heat stress, was more common on inner sites and patch/back reefs, while another heat-sensitive genera, *Pocillopora,* was more common on outer reefs. The branching corals *Isopora* and *Stylophora* were also more common on inner and patch/back reefs. Massive *Porites*, a mounding coral with a 'hardy' life history strategy that is considered less sensitive to heat stress than other corals, were more common on outer reefs, along with *Goniopora*, which also has a mounding morphology.

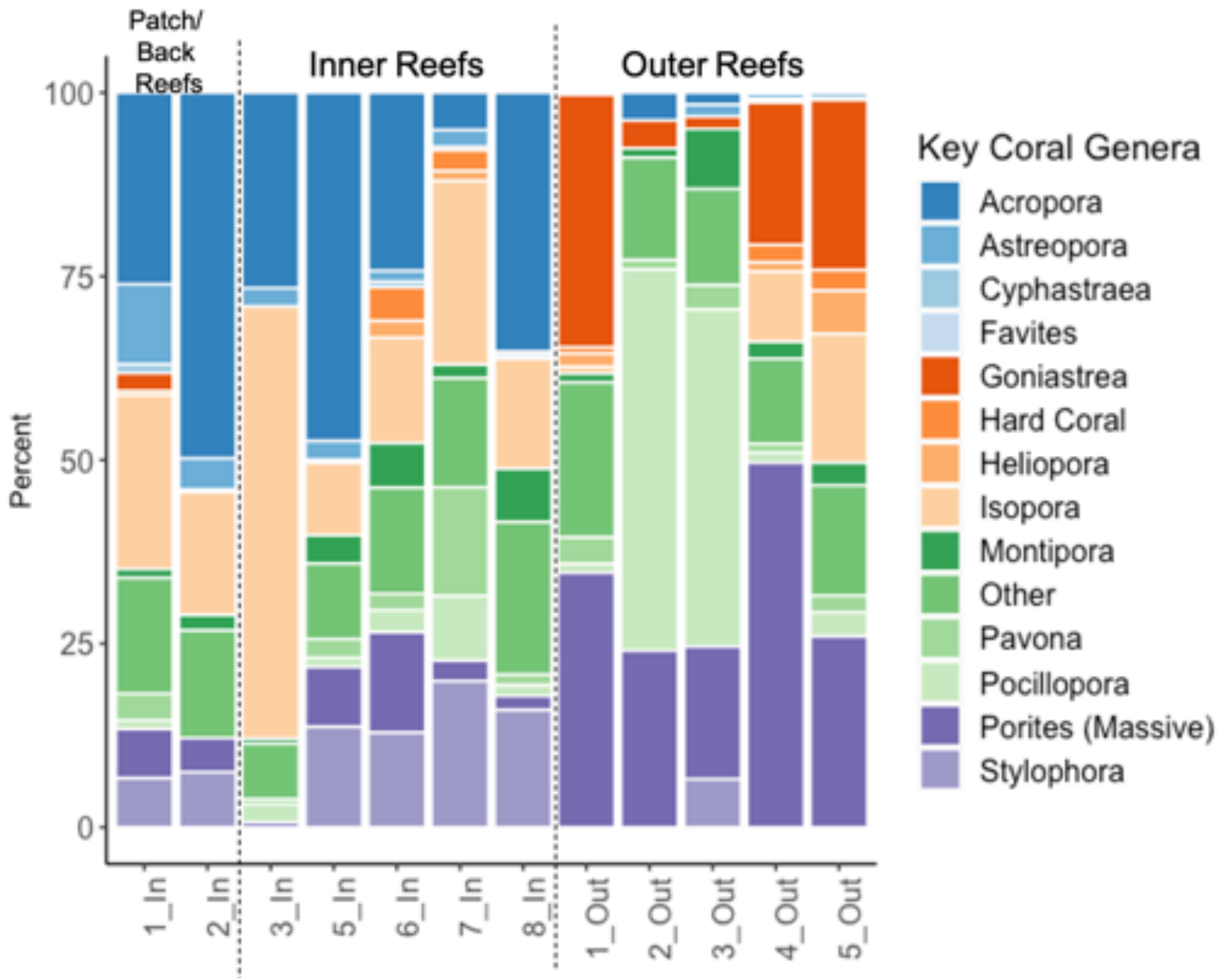

Figure 7. Percent of hard coral cover genera in Wotho Atoll. The genera listed here collectively composed of >90% of all coral cover across sites in Wotho.

Comparison of Benthic Communities by Reef Type

Coral communities often differ depending on environmental factors, such as reef type, exposure to wind and waves, and whether they are located within an enclosed lagoon or on the ocean side of an atoll or island. We investigated the different community compositions of the reefs in Wotho by comparing across different reef types, including lagoon patch reefs ('patch/back reefs'), reefs on the inside of the atoll's lagoon ('inner reefs'), and reefs along the ocean side of the atolls ('outer reefs'). The overall genera richness of inner and outer reefs was similar (35 for inner reefs versus 37 for outer reefs), while the richness of the patch/back reefs was lower at 28 coral genera per reef type.

The PCA showed that the benthic communities of the reefs differed significantly by reef type, with the exception of the patch/back reefs, which were more similar to inner reefs than outer reefs (this is not surprising given that the patch reefs were inside of Wotho's lagoon). PCA is a statistical analysis that seeks to reduce the variability in a dataset (in this case, the percent cover of benthic taxa at each site) without sacrificing any of the complexity by creating new variables, called Principal Components (PCs). A PCA plot as shown in Figure 8 only shows the first two PCs, and when these two PCs (representing each of the axes in Fig 8) sum to greater than 50%, the PCA is created statistically significant (Jolliffe, 2002). Here, the first two PCs sum to 78.8%, indicating that the majority of the difference in benthic communities across sites and reef types (almost 80%), was captured by the first two PCs. Therefore, the PCA is statistically significant and it did capture differences across reef types, although again, community compositions varied within reef types as well (as indicated by the wide spread of the ellipses).

Oceanic (outer) sites on the outside of the atolls tended to be characterised by massive *Porites*, *Goniopora* on one end and the macroalgae *Microdictyon* on the other end. By contrast, the inner sites (including the patch reefs) were more characterised by rubble, *Stylophora*, and *Acropora* overall, while some were also explained by sand, and others were more explained by the macroalgae *Halimeda.* Some sites within both outer and inner reefs seemed to be explained by crustose coralline algae (CCA), which is an important structural component of coral reefs (it is an encrusting algae that cements reefs together), and also provides substrate that allows coral larvae to settle and grow.

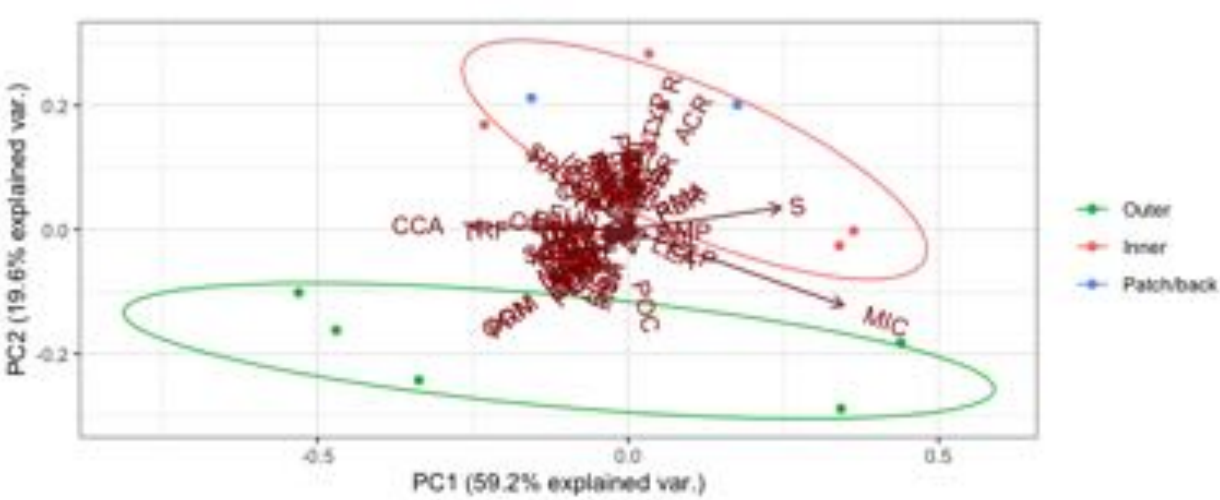

Figure 8. Principal Component Analysis (PCA) of benthic percent cover data by reef type. Each point represents a site, and the arrows represent the percent taxa. The length of each arrow indicates how much of the difference across the sites is explained by that variable (with longer arrows having greater explanatory power). The closer the points are to each other, the more similar those sites are.

SIMPER analysis was used to identify the taxa that were the most important when explaining the difference across reef types (Table 4, full results in the supplementary materials). Because the patch/back reefs were similar to the inner reefs according to the PCA, this table only shows the key taxa explaining difference across inner and outer reefs, although the comparisons between patch/back reefs and outer reefs, and patch/back reefs and inner reefs are also in the supplementary materials. The results of the SIMPER analysis are similar to the results of the PCA, in that they indicate that the same key taxon drove the differences across inner and outer reefs.

Table 4. Results of SIMPER analysis, indicating the percentage of key taxon contributing the most to differences across outer and inner reefs. Only the taxon accounting for 90% of the difference across sites are listed here. For the full SIMPER results (including differences across inner and back reefs and outer and back reefs), please see the supplementary materials.

Category	Average % (Outer Reefs)	Average % (Inner Reefs)	Individual Contribution to Differences (%)	Cumulative Sum of Contribution (%) to Differences
Microdictyon	20.05	20.40	21.86	21.86
Sand	10.51	16.63	14.17	36.03
Turf	28.28	18.42	13.68	49.71
CCA	12.66	7.64	11.62	61.33
Rubble	2.02	11.77	10.01	71.34
Halimeda	5.26	8.06	6.11	77.45
Massive *Porites*	4.61	0.38	4.38	81.83
Sponges	6.35	7.90	3.69	85.52
Goniopora	2.70	0.01	2.76	88.28
Acropora	0.06	2.42	2.43	90.71

Bleached Hard Corals

The benthic photos revealed some bleaching of several genera of hard corals, specifically the genera *Acropora*, *Astreopora*, *Leptastrea*, *Pocillopora*, *Turbinaria, Galaxea, Seriatopora,* and massive *Porites*. Overall, 2.75% of all hard corals were bleached, suggesting there was likely not an ongoing bleaching event at the time of the surveys.

Acropora, *Astreopora*, and *Pocillopora* were the taxa most affected by bleaching; 10.10% of *Acropora* (out of 485 total observations) were bleached, compared to 21.54% of *Astreopora* (out of 65 total) , and 4.41% of Pocillopora (out of 136 total). Both *Acropora* and *Pocillopora* are known to be sensitive to heat stress. They are both also important taxa ecologically and functionally on reefs because of their branching morphologies. *Acropora* in particular is widely recognized as one of the regular 'losers' after bleaching events because of its sensitivity (Van

Woesik et al., 2011). However, because it is a fast-growing, competitive genera, if there are nearby larvae sources, *Acropora* may be able to recover quickly after bleaching events (Darling et al., 2012).

By comparison, <1% of massive *Porites* observed (out of 647 total) bleached, which is not surprising given that massive *Porites* is often one of the 'winners' after bleaching events (Van Woesik et al., 2011). Some bleaching was also observed in *Leptastrea* (one of two total observed, or 50%), *Turbinaria* (one of five total observed, or 20%), *Seriatopora* (two out of 15 observed, or 13.33%), and *Galaxea* (two out of 10 observed, or 20%), although these corals were less common and the percent bleached is likely skewed because there were so few observations.

The majority of the bleached corals were observed on the inner (n = 47) or patch/back (n = 22) reef sites, collectively accounting for 87.34% of the bleached corals observed (Table 5). Only 12.66% of the bleached corals were found on outer reef sites.

Table 5. Number of bleaching observations by taxon and reef type.

Genus	Inner (Lagoon) Reefs	Outer (Oceanic) Reefs	Patch/back reefs	Total
Acropora	34	2	13	49
Astreopora	6	1	7	14
Galaxea	2	0	0	2
Leptastrea	0	1	0	1
Pocillopora	3	3	0	6
Massive *Porites*	0	3	1	4
Seriatopora	2	0	0	2
Turbinaria	0	0	1	1
Grand Total	**47**	**10**	**22**	**79**

Finally, we observed an example of what may be a coral disease on several *Pocillopora* colonies in the photo quadrats. While none of these potential patches fell underneath the randomly assigned points (and were therefore not counted as part of the percent cover), we counted eleven individual colonies with these distinctive markings (brown and white patches near the tips of the branches). These patterns are not currently known to be caused by a specific disease, and the brown patches do not appear to kill the tissue of the *Pocillopora*. The white patches may be something separate and could also be caused by disease (D. Fenner, personal communication, 18 May 2021), or potentially predation from corallivorous fish, although in the latter case we would expect to see similar patterns on other coral genera and not just *Pocillopora*.

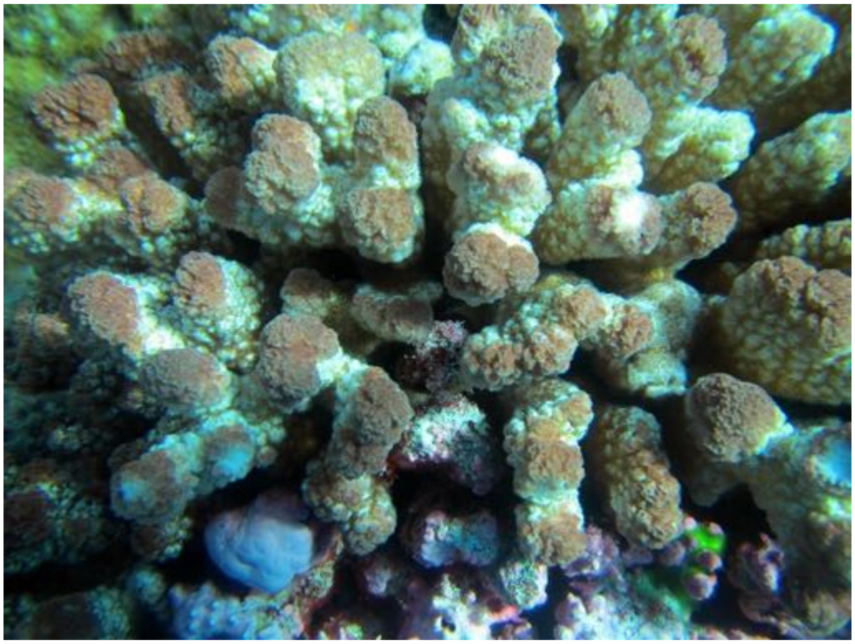

Fig 8. Pocillopora with brown and white patches on the ends of the branches.

Conclusions

The data collected and analysed in this report provide the first baseline of Wotho Atoll's benthic habitat. While these reefs were likely exposed to heat stress both before and after the surveys (Fig 2, Fig3), to our knowledge, there have been no bleaching reports from Wotho specifically. These surveys documented some bleaching as of June 2016 when the region was under a Bleaching Watch (Fig 3), although the bleaching was at low levels overall; less than 3% of all corals were bleached per our estimates from the quadrat photos. The diver who took the photo quadrats reported that about 10% of corals were bleaching during the surveys, including coral colonies found at various depths (K. Fellenius, personal communication, 19 May 2021). Our estimate of 3% bleached at the time of surveys may be lower than the bleaching that actually occurred.

About 10% of all *Acropora*, 22% of *Astreopora*, and 4% of *Pocillopora* were bleached at the time of the surveys. Both *Acropora* and *Pocillopora* are important reef-building corals that contribute to overall reef complexity, and both are often disproportionately affected by temperature stress. Both *Acropora* and *Pocillopora* were also among the top ten most common genera across sites, accounting for 16.88% and 4.73% of all hard coral cover, respectively. By contrast, *Astreopora* was less common, accounting for 2.26% of all hard coral cover. Because *Acropora* are fast-growing and competitive species (Darling *et al.*, 2012), *Acropora* populations have the potential to recover quickly after thermal heat stress or other acute stressors. Recovery depends on several factors, including the magnitude and duration of the heat stress, the amount of mortality, and whether there is a healthy source population to provide larval recruits post-disturbance. *Acropora* are broadcast spawners, which makes them vulnerable to allele effects if their population falls below certain levels (Teo and Todd, 2018).

The photos also showed some instances of bleaching in the genera *Galaxea, Leptastrea*, *Seriatopora,* and *Turbinaria*. The number of total observations of these genera were very low. These low numbers of observations likely misrepresent the amount of bleaching and its impact on these genera. Therefore, we do not consider it likely that these species were disproportionately impacted by temperature stress during the surveys.

Finally, almost a quarter of the mounding coral *Astreopora* were bleached. To our knowledge, *Astreopora* is not known to be especially susceptible to temperature stress so we are unaware of any reason why this genus would be disproportionately impacted by heat stress during the surveys. In general, mounding morphologies of corals are usually thought to be more resistant to heat stress. Future surveys will show whether *Astreopora* survived after the 2016 surveys or whether its overall prevalence has decreased over time.

The observed bleaching was almost all within the lagoon; almost 90% of observed bleaching was on either patch/back reefs or along the lagoon side of islands. Reefs in lagoons may be more susceptible to heat stress than those on outer reefs if water within the lagoon has low flushing rates and/or if the lagoon is shallow. Again, it is unclear whether there was bleaching (and if there was, its severity and duration) in Wotho prior to this study, although reefs likely experienced some heat stress (NOAA Coral Reef Watch, 2019).

Training community members living in Wotho to recognize and identify bleaching so that they can report it in the future would be useful. The impacts of bleaching could influence both human populations in Wotho and the local ecosystem. Outer reef complexity from branching corals is integral for protecting shorelines against erosion from large waves. By contrast, reefs in the lagoon are not usually exposed to high wind and waves, so any potential loss of reef complexity at these sites from bleaching-related coral mortality will not likely affect these reefs' ability to protect shorelines from erosion. Reef complexity from branching corals is still important even within lagoons as they provide valuable habitat for reef fish and invertebrates. In some cases, for example, certain invertebrate species may co-occur only with specific species of *Acropora* and *Pocillopora*. One example of this is the *Trapezia* crab, which guards its host coral from predation and contributes to increased survival (Samsuri et al., 2018; Stier et al., 2010).

Fig 9. Trapezia crab inside of a Pocillopora colony (NOAA, 2021).

In addition to bleaching, we also observed some examples of a potential, unconfirmed coral disease that only impacted *Pocillopora* (Fig 8). We cannot definitively attribute this pattern to any specific cause from just the photos, although a conversation with coral reef scientist Douglas Fenner suggested that it could have been caused by a yet-unidentified disease (D. Fenner, personal communication, 18 May 2021). We recommend that future surveys quantify coral disease at each site, specifically among *Pocillopora* colonies. This could be done, for example, by counting the number of *Pocillopora* colonies within a given distance from the transect tape, and differentiating between the numbers that exhibit symptoms and those that don't, to come up with an estimated percent of colonies affected. It would also help to distinguish whether these symptoms are widespread across the whole atoll or are specific to a given area (inner reefs versus outer reefs, for example).

The benthic communities in Wotho were different between lagoon reefs (including patch/back reefs and those along the lagoon side of the islands) and oceanic reefs, although there were wide differences in percent cover of coral taxa even within reef types. Oceanic (outer) sites on the outside of the atolls tended to be characterised by massive *Porites*, *Goniopora*, *Pocillopora* and the macroalgae *Microdictyon.* Massive *Porites* is a slow-growing, hardy genera of coral that is less sensitive to heat stress than many other taxa (Van Woesik et al., 2011). By contrast, the inner sites (including the patch reefs) were more characterised by rubble, *Stylophora*, and *Acropora* overall, while some were also explained by sand, and others were more explained by the macroalgae *Halimeda.* Some sites within both outer and inner reefs were explained by crustose coralline algae (CCA), which is an important structural component of coral reefs (it is an encrusting algae that cements reefs together), and also provides substrate that allows coral larvae to settle and grow.

Coral reefs found within lagoons are often home to different benthic communities than outer reefs because there is less water flow between the lagoon and the ocean, which can result in higher productivity and nutrients. That may be the case in Wotho, although it appears that the lagoon is largely open along the western rim (Fig 1). The lagoon sites were characterized by low percent cover of hard coral (below 10%) compared to outer reefs, although most outer reefs also had less than 10% hard coral cover (only sites 1_Out, 4_Out and 5_Out had higher than 10% coral cover, with live hard corals accounting for 13.28%, 26.28% and 15.72% of the total benthos, respectively). The benthic community compositions could potentially be partially explained by exposure to wind and waves; sites 1_Out, 4_Out and 5_Out are both along the western rim of the atoll, which (depending on the prevailing wind direction) may be more sheltered than the north or eastern rims. However, site 3_Out is also along the western rim of the atoll and it had the lowest coral cover of all the sites surveyed, with only 2.44%.

Studies from other parts of the Pacific have found that coral reefs must maintain a hard coral cover of greater than 10% to produce enough carbonate to withstand erosion and to grow fast enough to keep up with sea level rise (Perry et al., 2015). Future surveys will be integral for evaluating whether the coral cover at these reefs has remained low or has increased, which could have important implications for management; for example, if coral cover has remained low, these sites may need more direct intervention such as a coral gardening project to ensure that they continue to grow fast enough to keep up with rising sea levels, although it is important to recognize that coral gardening is only effective in the long-term in the absence of future bleaching events, which is not guaranteed. However, increasing the percent cover of hard coral to above 10% will be integral, particularly around the ocean side of reefs, to ensure that they can keep up with sea level rise and protect the shorelines from increased erosion.

Many of the sites in Wotho had notably high coverage of macroalgae (with some sites having over 50% cover composed entirely of macroalgae). It may be tempting to consider the sites unhealthy, but previous work has found that the percent cover of macroalgae is not an effective indicator of reef health. In some cases, high algae cover may be natural (Cannon et al., 2019). The macroalgae that were most common at these sites, *Halimeda* and *Microdictyon*, have been associated with low human influence and healthy coral reefs in other places (including sites in the Marshalls), and calcareous green algae like *Halimeda* also play an important role in sediment production on coral reefs (Perry et al., 2016). Cannon et al. (2019) found, for example, that the percent cover of *Halimeda* declined with increasing human influence in Majuro and Arno Atolls, while Berger et al. (2010) noted that *Microdictyon* and *Halimeda* are both found at healthy reef sites across the Marshall Islands. In contrast, genera that were not common from our analysis in Wotho were often found at degraded sites, such as *Hypnea*, *Dictyota*, and *Padina* (Photos in S3, Supplementary Materials), along with cyanobacteria (Fig 5).

An unpublished report investigating the health of fish stocks in the northern Marshall Islands notes that Wotho is also home to a traditional protected area called a ‘mo’ in the southern part of the lagoon that appeared to contribute to increased fish biomass in that part of the lagoon (Jarrett and Houk, 2018). Within the boundaries of the *mo,* fishing is only allowed for rare special occasions. One of the sites surveyed here, Site 8_in, was inside of the *mo*. This site had low coral cover (8.28%) and the highest cover of macroalgae of all sites surveyed (at 58.04%). High macroalgae cover could be caused by high piscivore biomass because of predation of herbivores and grazers (top-down drivers) (Houk and Musburger, 2013), which could be the case here given that fish surveys reported high biomass of piscivores (Jarrett and Houk, 2018).

This report found that fish biomass of all classes was among the highest of several atolls surveyed in the region (both inside and outside of the lagoon), and fishing pressure is not likely to be a threat to local reefs because of Wotho's small population size (Jarrett and Houk, 2018). If a commercial export fishery has since been established, future reef surveys (in addition to fish surveys) would help to evaluate any potential impacts of the fishery on local ecosystems.

Overall, these results suggest that reefs in Wotho at the time of the survey were in a concerning state because of the low coral cover at most sites, but this was likely due to bleaching prior to the surveys and not local threats. The taxa of macroalgae and corals that were found locally are all common on healthy coral reefs, although at almost all sites the percent of coral cover was lower than expected (all except for two sites were below 10%). The number and level of threats experienced locally is likely very low; the human population is small enough that it likely does not create much nutrient pollution, and fish stocks appear to be healthy. This also suggests that coral reefs at these sites have a high likelihood of recovery.

The hypothesis we have proposed, that coral bleaching had likely occurred prior to the surveys, is supported by the high percentages of rubble within lagoon sites, in particular. Further evidence that these reefs will be able to recover from a past stress event is the high prevalence of crustose coralline algae (CCA) at some sites. This encrusting algae provides an important substrate for coral larvae to settle on and grow. However, the site with the lowest coral cover (3_Out) also had <1% total cover of CCA, indicating again that this site may need further intervention in order to increase the total coral cover. Importantly, while recovery from bleaching is likely for Wotho's reefs, it could take several years to a decade or longer. These sites could be good candidates for coral gardening projects, given the low levels of local disturbance, which could help to increase reef complexity, regardless of the presence or absence of prior bleaching (Boström-Einarsson et al., 2020). Again, it is important to caution that coral gardening is only likely to be successful in the long term in the absence of future bleaching events.

This report analyzes data from the first benthic surveys of Wotho Atoll, conducted in 2016. Subsequent surveys of benthic community composition (ideally every 3-5 years, and prior to establishing or expanding any local protective measures) would show if the reefs have changed over time and whether the percentages of hard coral cover (and branching coral in particular) have increased. Future surveys should also specifically consider the location of additional protected areas (e.g. no-take, special reserves) with particular attention to sites that have low percentages of hard coral and CCA, and with permission from local leaders.

Summary of findings

- The taxa found on Wotho's reefs (regardless of the reef types) are all commonly associated with reefs that are healthy, but the percent cover of live coral was less than the 10% threshold necessary to keep up with sea level rise at all but three of the reefs surveyed. This suggests that Wotho's reefs may have undergone a bleaching event prior to the survey, although this is only a hypothesis. Still, this hypothesis is supported by the high percentages of rubble found on many of the inner reefs, which could suggest a past disturbance event. Future surveys will be useful to provide evidence for bleaching (if the percent cover of macroalgae and coral taxa have remained stable over time, this may indicate that the state of the reefs from these surveys is not their natural state.

- The benthic communities differed significantly across reef types, but the taxa found at each reef type varied. Outer reefs tended to be characterised by *Pocillopora*, and either massive *Porites* and *Goniopora* or *Microdictyon* (macroalgae genera). Inner and patch/back reefs were characterised by rubble, *Acropora*, and *Stylophora,* and either *Halimeda* or sand. The most important taxa in distinguishing between the benthic communities at inner versus outer reefs were *Microdictyon*, sand, turf, CCA, and rubble, followed by *Halimeda*, massive *Porites*, sponges, *Goniopora*, and *Acropora*.

- Bleaching was observed for less than 3% of all hard corals, suggesting that at the time of the surveys there was not widespread, ongoing bleaching. However, about 10% of *Acropora*, 21% of *Astreopora*, and 4% of *Pocillopora* observed were bleached. Both *Acropora* and *Pocillopora* are important reef-building corals, and both are known to be sensitive to heat stress. The majority of the bleaching observed during surveys occurred in the lagoon sites (both inner sites along the lagoon side of the islands, and patch/back reefs).

- We also observed what may be a coral disease on several *Pocillopora* colonies in the photo quadrats, although this is another hypothesis because the observed patterns are not known to be caused by any specific disease. The affected patches were not quantified in these surveys and none fell underneath the randomly assigned points in our photo quadrats. Further surveys could seek to quantify the prevalence of this 'disease' (see Recommendations).

Recommendations

- The RMI has long been a global leader in the fight against climate change, which is the greatest threat to coral reefs around the world. Continuing this advocacy, while continuing efforts to reduce local greenhouse gas emissions, will be integral to ensuring a future for coral reefs as the climate warms, in the Marshall Islands and elsewhere.

- Training of local community members, in particular fishers, to recognize coral bleaching, estimate its severity, and then report it to scientists at MIMRA would be helpful in identifying when bleaching has occurred and the severity of occurrence.

- Protecting the physical integrity of reefs in Wotho will be important to ensuring that they can continue to grow fast enough to keep up with rising sea levels, particularly in the lagoon where coral cover is low. Limiting or banning the mining of live coral colonies and coral rubble will help to keep coral communities intact and also may provide more substrate where coral recruits can settle and grow. Also, establishing anchoring regulations (such as prohibiting boats from dropping their anchors on or within a certain distance from coral reefs) could also contribute to preserving the physical structure of coral reefs in Wotho.

- The report on fish biomass prepared in Wotho includes its own list of recommendations, including potentially increasing the size of the *mo*. While that report suggests that fish populations are healthy (indeed, they are among the highest of any atolls in the northern Marshall Islands), it also made suggestions to establish a commercial fishery, in which case increasing the size of the *mo* could help to offset any potentially negative impacts that could be associated with increased fishing pressure (Jarrett and Houk, 2018).

- Another suggestion that is reiterated from Jarrett and Houk (2018) is for communities in Wotho to collect their own data to guide future decision making about how they can best conserve and protect local reefs and the services they provide. For example, local fishers can keep a log of the fish they catch, their size, and the location, which might reveal trends in fish populations that could inform management. If the catch is low in a given area of the lagoon, this could be a place that may need to be temporarily closed for fishing. People in Wotho could also establish their own benthic monitoring programs by snorkeling at each of these sites on a semi-regular basis (once every 3-6 months) and estimating the percent-cover of certain taxa or morphologies. These data would also contribute to adaptive management (if there is a sudden increase in macroalgae at a given site, for example, communities could decide to limit fishing there; they could also monitor for changes in *Acropora* or other ecologically important taxa over time).

- While fishing pressure is unlikely a threat to reefs in Wotho (unless a commercial fishery was established prior to the surveys), pausing fishing of herbivores temporarily at sites with extremely low coral cover (Sites 2_out and 3_out, for example) may help to reduce the total cover of macroalgae and provide more substrate where corals could settle and grow, which would encourage recovery of coral populations.

- Future surveys should be conducted regularly (every 3-5 years), which will be important for further untangling the patterns observed here and changes occurring over time. In particular, future surveys will be helpful in establishing whether some direct intervention such as coral gardening projects may be necessary to increase the overall percent of hard coral cover. In addition:

- Future surveys should specifically seek to quantify instances of potential coral disease, particularly among *Pocillopora*. This could be done, for example, by counting the number of *Pocillopora* colonies within a given distance from the transect tape, and differentiating between the numbers that exhibit symptoms and those that don't, to come up with an estimated percent of colonies affected.

- Future surveys should also consider the boundaries of the *mo* and, with permission from local leaders, seek to compare the benthic communities and fish biomass of at least one site from within the *mo* to sites outside of it.

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Supplementary Materials

S1. Identification codes used in CoralNet, compared to MIMRA's codes.

LabelID	ShortCode	MIMRA_code	FuncGroup	FullName
5332	BCM	MBGMA	BG	Mat Blue-Green Macroalgae
2543	BG	BG	BG	Other Non-Coralline Blue-Green Macroalgae
1324	BMA	NBMAO	BG	Other
1440	RBG	RBG	BG	Cyanobacteria on rubble
2455	SCZ	SCHIZ	BG	Schizothrix
1765	STBA	SBGMA	BG	Stringy Blue-Green Macroalgae
1458	CCA	CCA1	CCA	Crustose coralline algae
1115	FCA	FCA	CCA	Fleshy Coralline Algae
2654	RCA	RCA	CCA	Rubble CCA
58	ACA	ACAN	Coral	Acanthastrea
204	ACB	ACROPARB	Coral	Acropora - Branching
5457	ACD	ACROST	Coral	Acropora - Digitate
59	ACR	ACROP	Coral	Acropora
603	ACT	ACROTBL	Coral	Acropora - Table
2037	ALV	ALVE	Coral	Alveopora
4101	ANA	ANA	Coral	Anacropora

60	AST	ASTRP	Coral	Astreopora
2485	BACR		Coral	Bleached Acropora
	BGON		Coral	Bleached Goniastrea
2491	BISO		Coral	Bleached Isopora
2490	BPOC		Coral	Bleached Pocillopora
2605	BPRM		Coral	Bleached PRM
607	CAU	CAUL	Coral	Caulastrea
3464	COE	COE	Coral	Coeloseris
190	COS	COSC	Coral	Coscinaraea
608	CTE	CTEN	Coral	Ctenactis
3232	CYC	CYCL	Coral	Cycloseris
61	CYP	CYPH	Coral	Cyphastraea
164	DIP	DIPLO	Coral	Diploastrea
2049	DIS	DIST	Coral	Distichopora
99	ECH	ECHPO	Coral	Echinopora
192	ECY	ECHPHY	Coral	Echinophyllia
610	EUP	EUPH	Coral	Eupyllia
174	FAV	FAVID	Coral	Favidae-Mussidae massive/meandroid
970	FST	FST	Coral	Favia stelligera (now Goniastrea stelligera)
63	FUN	FUNG	Coral	Fungia
62	FVA	FAV	Coral	Favia
115	FVT	FAVT	Coral	Favites

760	GAL	GAL	Coral	Galaxea
64	GAR	GARD	Coral	Gardineroseris
130	GNP	GONIO	Coral	Goniopora
117	GON	GON	Coral	Goniastrea
175	HCO	UNSC	Coral	Other hard coral
633	HEL	HELIO	Coral	Heliopora
65	HER	HERP	Coral	Herpolitha
624	HLM	HALO	Coral	Halomitra
554	HYD	HYD	Coral	Hydnophora
150	ISO	ISOP	Coral	Isopora
66	LEA	LEPT	Coral	Leptastrea
623	LEO	LEPTOR	Coral	Leptoria
67	LEP	LEPTOS	Coral	Leptoseris
68	LOB	LOBOPH	Coral	Lobophyllia
201	MER	MERU	Coral	Merulina
79	MIL	MILL	Coral	Millepora
70	MNT	MONTI	Coral	Montipora
69	MST	MONT	Coral	Montastraea
194	MYC	MYCED	Coral	Mycedium
3461	OUL	OULO	Coral	Oulophyllia
193	OXY	OXYP	Coral	Oxypora
71	PAC	PACHY	Coral	Pachyseris
72	PAV	PAV	Coral	Pavona
1413	PBR	PBR	Coral	Porites (branching)
132	PCL	PORCYL	Coral	Porities-cylindric a
196	PEC	PECT	Coral	Pectinia

594	PHY	PHYSO	Coral	Physogera
116	PLA	PLAT	Coral	Platygyra
1615	PLE	PLSIA	Coral	Plesiastrea
609	PLER	PLERO	Coral	Plerogyra
3467	PLP	PLP	Coral	Polyphillia
73	POC	POC	Coral	Pocillopora
2048	POD	POD	Coral	Podobachia
74	POR	POR	Coral	Porites (other)
4929	PRE		Coral	Encrusting Porites
1974	PRM	PORMAS	Coral	Porites (massive)
88	PRS	PORRUS	Coral	Porites rus
75	PSA	PSAM	Coral	Psammocora
1964	SCA	SCAP	Coral	Scapophyllia
197	SCL	SCOL	Coral	Scolymia
3531	SDL	SANDO	Coral	Sandolitha
189	SER	SERIA	Coral	Seriatopora
474	SID	SID	Coral	Siderastrea
77	STYC	STYLC	Coral	Stylocoeniella
185	STYP	STYLO	Coral	Stylophora
200	SYM	SYMP	Coral	Symphillia
2427	TBA		Coral	Tubipora
199	TRB	TURBIN	Coral	Turbinaraea
2373	TRC		Coral	Trachyphyllia
78	TUB	TUB	Coral	Tubastrea
134	CRL	CMO	Corallimorph	Corallimorphia - general

1603	DSC	DISCO	Corallimorph	Discosoma
1397	PYT	PAZ	Corallimorph	Palythoa
3208	ANE	ANEM	Invertebrate	Anemone
227	ASC	ASC	Invertebrate	Ascidian
3154	BCH	CHRYOBRN	Invertebrate	Brown Chysophyte
1853	BRZ	BRZ	Invertebrate	Bryozoan
2423	CHR	CHR	Invertebrate	Chrysophyta
424	CHRY	CHRYS	Invertebrate	Chrysophyte
637	CLM	CLM	Invertebrate	Giant clam (Tridacna)
1648	COT	COT	Invertebrate	Crown-of-Thorns Seastar
3840	CRS	CRU	Invertebrate	Crustaceans
1799	HDN	HDN	Invertebrate	Hydrozoa
456	HDR	HDR	Invertebrate	Hydroid
2482	INV	NoIDINV	Invertebrate	Not Identified Invert
4584	MSK	MLC	Invertebrate	Mollusc
145	SEA	SEA	Invertebrate	Sea cucumber
1914	SPR	SPI	Invertebrate	Spirobranchus
231	WRM	WMO	Invertebrate	Other Worm
133	ZOA	Z	Invertebrate	Zoanthid
1591	AMP	AMP	Macroalgae	Amphiroa
218	ASP	ASP	Macroalgae	Asparagopsis
3640	BCA	BCA1	Macroalgae	Other Branching Coralline Algae
4938	BOO	Bood	Macroalgae	Boodlea
3598	BRY	BRYP	Macroalgae	Bryposis

780	CHL	CHLDES	Macroalgae	Chlorodesmis
423	CLP	CLP	Macroalgae	Caulerpa
3828	DCT	DYCTY	Macroalgae	Dictyosphaerea
401	DIC	DICT	Macroalgae	Dictyota
1868	GLA	GLXU	Macroalgae	Galaxaura
403	HA	HALI	Macroalgae	Halimeda
3209	HYP	HYP	Macroalgae	Hypnea
2562	JAN	JAN	Macroalgae	Jania
1791	LIA	LIAG	Macroalgae	Liagora
1708	LIT	LIT	Macroalgae	Lithothamnion
138	LPA	LOBO	Macroalgae	Lobophora
81	MA	NOIDMAC	Macroalgae	Non-Coralline Green Macroalgae - Other
2539	MIC	MICDTY	Macroalgae	Microdictyon
5359	MSO	MAST	Macroalgae	Mastophora
418	NEO	NEOM	Macroalgae	Neomeris
428	PAD	PAD	Macroalgae	Padina
1325	RMA	NRMAO	Macroalgae	Non-Coralline Red Macroalgae - Other
429	SRG	SARG	Macroalgae	Sargassum
435	TBI	TURB	Macroalgae	Turbinaria (algae)
3930	TYD	TYDM	Macroalgae	Tydemania
2057	COT_DC	COT_DC	Other	CoTs scar
3525	DBS	TOD	Other	Terrestrial Organic Debris
460	FISH	FISH1	Other	Fish

1827	TAPE	Tape	Other	Tape-Wand-Shadow
638	TRA	AWD	Other	Trash
1647	UNK	SHADOW	Other	Shadow - Unknown
2545	Wand	Wand	Other	Wand
2230	R	RBL	Rubble	Rubble
84	S	Sand	Sand	Sand
2608	BSCO		SCO	Bleached Soft Coral
3831	DND	DEN	SCO	Dendronephthya
1802	GOR	GSC	SCO	Gorgonian Soft Coral
151	LOSI	SC	SCO	Lobophyton/Sinularia
128	SAR	SARC	SCO	Sarcophyton
177	SCO	LSCO	SCO	Other Leather Soft Coral
683	SRC	NLSCO	SCO	Other Non-Leather Soft Coral
285	CUP	CUPS	Sponge	Sponges, hollow forms, cups and alike
2142	DYS	DYS	Sponge	Dysidea sp.
3191	OLV	OLV	Sponge	Olive sponge
2168	SPG	SP1	Sponge	Sponge (other)
3726	TER	TERPS	Sponge	Sponges: Terpios
515	RCK	RCK	Substrate	Rock
1807	SLT	SLT	Substrate	Silt
1439	BGTA	BGTA	Turf	Cyanobacteria

				Turf Algae
82	TRF	TURF	Turf	Turf algae mix

S2. Full results of the SIMPER analysis.

Patch/back vs. Outer Reefs

	average	sd	ratio	Ave (patch / back reef)	Ave (outer reef)	cumsum	p
MIC	0.0947066	7.72E-02	1.2275	10.25339	20.048	0.1986	0.697
R	0.0696837	1.55E-02	4.5042	15.95275	2.016	0.3447	0.010 **
TRF	0.0597958	3.81E-02	1.5709	28.66526	28.28	0.47	0.584
CCA	0.054639	3.24E-02	1.6888	6.16104	12.656	0.5846	0.443
S	0.0545629	2.17E-02	2.5109	12.56287	10.512	0.699	0.72
PRM	0.0207829	2.39E-02	0.8694	0.45904	4.608	0.7426	0.204
HA	0.0202273	1.75E-02	1.1593	5.24908	5.264	0.785	0.705
SPG	0.0172928	1.16E-02	1.4921	9.09857	6.352	0.8212	0.539
ACR	0.0172009	8.35E-03	2.0599	3.49618	0.056	0.8573	0.029 *
GON	0.0132803	1.14E-02	1.1688	0.07968	2.704	0.8851	0.080 .
BG	0.0118861	3.48E-03	3.4183	2.75323	0.376	0.9101	0.005 **
ISO	0.0067369	1.31E-03	5.1299	1.57689	1.08	0.9242	0.521
POC	0.003720	2.91E-03	1.2803	0.03984	0.784	0.932	0.18

	8						
AST	0.0032524	4.37E-04	7.4417	0.69849	0.048	0.9388	0.001 ***
Other	0.002941	2.23E-03	1.3174	0.49896	0.736	0.945	0.401
STYP	0.0027356	8.16E-04	3.3545	0.57912	0.032	0.9507	0.781
CLP	0.0020388	2.63E-03	0.7758	0.2396	0.392	0.955	0.476
PLA	0.00168	1.59E-03	1.0551	0	0.336	0.9585	0.205
SCO	0.0015603	1.97E-03	0.7916	0.07968	0.344	0.9618	0.406
INV	0.0014807	9.77E-04	1.5158	0.11976	0.4	0.9649	0.195
HEL	0.0014601	1.71E-03	0.8549	0.01992	0.296	0.9679	0.236
LEO	0.00124	1.34E-03	0.9281	0	0.248	0.9705	0.294
FST	0.0012	1.35E-03	0.8868	0	0.24	0.9731	0.417
DCT	0.0010806	7.89E-04	1.369	0.19936	0.336	0.9753	0.56
PAV	0.0010405	7.10E-04	1.4653	0.11952	0.256	0.9775	0.642
MNT	0.0010205	9.17E-04	1.1132	0.13984	0.296	0.9796	0.714
MST	0.00102	1.04E-03	0.9777	0.02	0.208	0.9818	0.286
LOB	0.00072	1.12E-03	0.6427	0	0.144	0.9833	0.313
PRE	0.0005584	2.26E-04	2.4763	0.11968	0.008	0.9845	0.667
GOR	0.00052	5.10E-04	1.0207	0	0.104	0.9855	0.211
POR	0.000498	5.25E-04	0.9487	0.0996	0	0.9866	0.166

ECH	0.00046	4.01E-04	1.1484	0.02	0.096	0.9876	0.384
PBR	0.0004	3.89E-04	1.029	0.08	0.008	0.9884	0.156
TRB	0.0004	3.89E-04	1.029	0.08	0.008	0.9892	0.156
FAV	0.0004	3.53E-04	1.1339	0	0.08	0.9901	0.291
FVA	0.0004	3.89E-04	1.029	0.04	0.088	0.9909	0.561
HCO	0.0003602	2.95E-04	1.2202	0.03984	0.096	0.9917	0.387
COE	0.00032	2.86E-04	1.119	0	0.064	0.9923	0.198
ANA	0.0002996	1.06E-04	2.831	0.05992	0	0.993	0.011 *
PSA	0.00028	2.86E-04	0.9791	0	0.056	0.9936	0.386
CYP	0.0002598	1.34E-04	1.9388	0.05984	0.04	0.9941	0.251
GAL	0.0002598	3.54E-04	0.7346	0.01992	0.04	0.9946	0.582
COS	0.0002192	1.47E-04	1.4914	0.05984	0.016	0.9951	0.112
FUN	0.0002	1.63E-04	1.2247	0.04	0.016	0.9955	0.187
MIL	0.0002	4.22E-04	0.4743	0	0.04	0.9959	0.589
OUL	0.0002	1.33E-04	1.5	0	0.04	0.9964	0.198
HYD	0.0001996	4.20E-07	475.2903	0.03992	0	0.9968	0.017 *
DIC	0.0001992	2.10E-04	0.9487	0.03984	0	0.9972	0.166
HER	0.00018	1.99E-04	0.905	0.02	0.04	0.9976	0.482
FVT	0.00016	1.58E-04	1.0142	0	0.032	0.9979	0.229
LEP	0.00016	3.37E-04	0.4743	0	0.032	0.9982	0.589

ACA	0.0000996	1.05E-04	0.9487	0.01992	0	0.9985	0.166
GAR	0.0000996	1.05E-04	0.9487	0.01992	0	0.9987	0.166
HYP	0.0000996	1.05E-04	0.9487	0.01992	0	0.9989	0.166
JAN	0.0000996	1.05E-04	0.9487	0.01992	0	0.9991	0.166
LPA	0.0000996	1.05E-04	0.9487	0.01992	0	0.9993	0.318
SER	0.0000996	1.05E-04	0.9487	0.01992	0	0.9995	0.939
CAU	0.00008	1.03E-04	0.7746	0	0.016	0.9997	0.795
GLA	0.00004	8.43E-05	0.4743	0	0.008	0.9997	0.581
GNP	0.00004	8.43E-05	0.4743	0	0.008	0.9998	0.856
LEA	0.00004	8.43E-05	0.4743	0	0.008	0.9999	0.854
MER	0.00004	8.43E-05	0.4743	0	0.008	1	0.589

Patch/back vs. Inner Reefs

	average	sd	ratio	Ave patch/ back reefs	Ave Inner Reefs	cumsum	p
MIC	8.01E-02	7.42E-02	1.0798	10.25339	20.4	0.2348	0.826
TRF	6.42E-02	4.47E-02	1.4347	28.66526	18.416	0.4228	0.482
S	5.05E-02	4.34E-02	1.1644	12.56287	16.632	0.5708	0.82
CCA	3.15E-02	3.22E-02	0.9773	6.16104	7.64	0.663	0.948
R	3.09E-02	1.76E-02	1.7594	15.95275	11.768	0.7536	0.869
HA	1.74E-02	2.24E-02	0.7754	5.24908	8.064	0.8045	0.832
SPG	1.73E-02	9.98E-03	1.7364	9.09857	7.904	0.8553	0.546
BG	1.15E-02	3.44E-03	3.3403	2.75323	0.456	0.889	0.008 **
ACR	9.98E-03	7.60E-03	1.3128	3.49618	2.424	0.9182	0.596
ISO	4.54E-03	3.36E-03	1.3506	1.57689	1.76	0.9315	0.951
STYP	3.30E-03	1.83E-03	1.8014	0.57912	1	0.9412	0.575
AST	2.53E-03	5.77E-04	4.3869	0.69849	0.192	0.9486	0.012 *
PAV	1.64E-03	2.24E-03	0.7327	0.11952	0.36	0.9534	0.543
CLP	1.56E-03	2.46E-03	0.6337	0.2396	0.424	0.958	0.821
PRM	1.50E-03	3.66E-04	4.0998	0.45904	0.384	0.9624	0.992
Other	1.26E-03	7.09E-04	1.7741	0.49896	0.432	0.9661	0.963
POC	1.24E-03	1.39E-03	0.896	0.03984	0.288	0.9697	0.944
MNT	1.02E-03	7.92E-04	1.2887	0.13984	0.296	0.9727	0.709
DCT	9.17E-04	6.38E-04	1.4381	0.19936	0.016	0.9754	0.806
PRE	7.20E-04	8.13E-04	0.8852	0.11968	0.216	0.9775	0.6

SCO	5.99E-04	5.50E-04	1.0892	0.07968	0.104	0.9792	0.921
SER	5.40E-04	5.66E-04	0.9537	0.01992	0.112	0.9808	0.27
POR	4.98E-04	5.25E-04	0.9487	0.0996	0	0.9823	0.166
FST	4.80E-04	6.20E-04	0.7746	0	0.096	0.9837	0.928
PBR	4.00E-04	3.53E-04	1.1339	0.08	0.016	0.9848	0.156
TRB	4.00E-04	4.22E-04	0.9487	0.08	0	0.986	0.156
GON	3.98E-04	3.87E-04	1.0292	0.07968	0.008	0.9872	0.967
INV	3.20E-04	1.68E-04	1.9044	0.11976	0.088	0.9881	0.995
ANA	3.00E-04	1.06E-04	2.831	0.05992	0	0.989	0.011 *
HCO	2.80E-04	2.15E-04	1.2989	0.03984	0.056	0.9898	0.74
HEL	2.60E-04	2.32E-04	1.12	0.01992	0.048	0.9906	0.983
FVA	2.40E-04	2.27E-04	1.057	0.04	0.04	0.9913	0.935
FUN	2.00E-04	1.89E-04	1.0607	0.04	0.008	0.9919	0.197
RMA	2.00E-04	3.27E-04	0.6124	0	0.04	0.9925	0.372
DIC	1.99E-04	1.88E-04	1.0607	0.03984	0.008	0.993	0.166
GAL	1.80E-04	1.99E-04	0.9047	0.01992	0.032	0.9936	0.739
COS	1.80E-04	1.47E-04	1.223	0.05984	0.032	0.9941	0.491
CYP	1.79E-04	1.47E-04	1.2193	0.05984	0.024	0.9946	0.798
HYD	1.60E-04	8.40E-05	1.9021	0.03992	0.008	0.9951	0.037 *
ECH	1.40E-04	1.35E-04	1.0371	0.02	0.024	0.9955	0.973
FAV	1.20E-04	1.03E-04	1.1619	0	0.024	0.9958	0.909
HLM	1.20E-04	1.69E-04	0.7115	0	0.024	0.9962	0.398
MST	1.00E-04	1.05E-04	0.9487	0.02	0.008	0.9965	0.972
HER	1.00E-04	1.05E-04	0.9487	0.02	0	0.9968	0.816

LPA	9.98E-05	1.05E-04	0.9502	0.01992	0.008	0.9971	0.245
ACA	9.96E-05	1.05E-04	0.9487	0.01992	0	0.9974	0.166
GAR	9.96E-05	1.05E-04	0.9487	0.01992	0	0.9977	0.166
HYP	9.96E-05	1.05E-04	0.9487	0.01992	0	0.998	0.166
JAN	9.96E-05	1.05E-04	0.9487	0.01992	0	0.9982	0.166
CAU	8.00E-05	1.69E-04	0.4743	0	0.016	0.9985	0.824
COE	8.00E-05	1.03E-04	0.7746	0	0.016	0.9987	0.998
AMP	8.00E-05	1.69E-04	0.4743	0	0.016	0.9989	0.587
LEO	4.00E-05	8.43E-05	0.4743	0	0.008	0.9991	0.991
OUL	4.00E-05	8.43E-05	0.4743	0	0.008	0.9992	0.999
PSA	4.00E-05	8.43E-05	0.4743	0	0.008	0.9993	0.99
GNP	4.00E-05	8.43E-05	0.4743	0	0.008	0.9994	0.853
LEA	4.00E-05	8.43E-05	0.4743	0	0.008	0.9995	0.84
MA	4.00E-05	8.43E-05	0.4743	0	0.008	0.9996	0.588
LEP	4.00E-05	8.43E-05	0.4743	0	0.008	0.9998	0.858
POD	4.00E-05	8.43E-05	0.4743	0	0.008	0.9999	0.602
SCL	4.00E-05	8.43E-05	0.4743	0	0.008	1	0.568

Outer vs. Inner Reefs

	average	sd	ratio	Ave outer reefs	Ave inner reefs	cumsum	p
MIC	0.106576	8.52E-02	1.2513	20.048	20.4	0.2186	0.498
S	0.069112	5.09E-02	1.357	10.512	16.632	0.3603	0.234
TRF	0.06668	4.96E-02	1.3436	28.28	18.416	0.4971	0.384
CCA	0.056648	4.10E-02	1.3825	12.656	7.64	0.6133	0.19
R	0.048792	2.78E-02	1.7584	2.016	11.768	0.7134	0.045
HA	0.029792	2.38E-02	1.2505	5.264	8.064	0.7745	0.22
PRM	0.02136	2.30E-02	0.9287	4.608	0.384	0.8183	0.019
SPG	0.018	1.41E-02	1.2757	6.352	7.904	0.8552	0.663
GON	0.01348	1.12E-02	1.2046	2.704	0.008	0.8828	0.007
ACR	0.01184	7.91E-03	1.4966	0.056	2.424	0.9071	0.13
ISO	0.007784	4.74E-03	1.6407	1.08	1.76	0.9231	0.133
STYP	0.004904	2.97E-03	1.6494	0.032	1	0.9331	0.003
Other	0.003168	2.48E-03	1.2772	0.736	0.432	0.9396	0.14
POC	0.00304	2.53E-03	1.2004	0.784	0.288	0.9459	0.154
CLP	0.002592	3.24E-03	0.8007	0.392	0.424	0.9512	0.414
PAV	0.001768	1.84E-03	0.9609	0.256	0.36	0.9548	0.585
PLA	0.00168	1.54E-03	1.0897	0.336	0	0.9583	0.018
INV	0.001624	1.01E-03	1.6019	0.4	0.088	0.9616	0.008
SCO	0.001616	1.86E-03	0.8701	0.344	0.104	0.9649	0.242
DCT	0.0016	9.76E-04	1.6387	0.336	0.016	0.9682	0.01
HEL	0.001432	1.59E-03	0.9029	0.296	0.048	0.9711	0.087

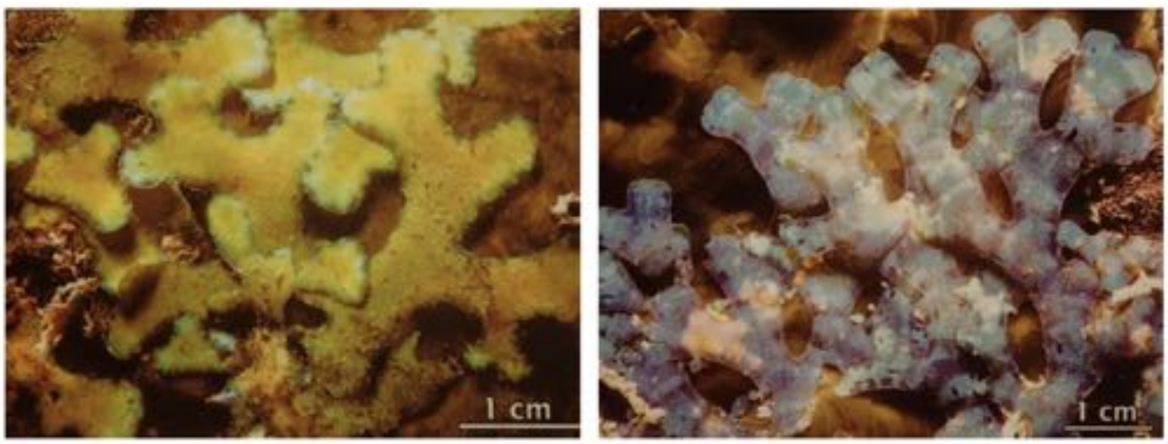
LEO	0.001232	1.26E-03	0.9743	0.248	0.008	0.9736	0.085
FST	0.0012	1.06E-03	1.1356	0.24	0.096	0.9761	0.275
MNT	0.001152	8.39E-04	1.3727	0.296	0.296	0.9785	0.558
PRE	0.00104	9.40E-04	1.1065	0.008	0.216	0.9806	0.007
MST	0.001032	1.06E-03	0.9785	0.208	0.008	0.9827	0.06
BG	0.001008	8.03E-04	1.2552	0.376	0.456	0.9848	1
AST	0.000752	5.14E-04	1.4628	0.048	0.192	0.9863	0.99
LOB	0.00072	1.09E-03	0.6638	0.144	0	0.9878	0.085
SER	0.00056	6.11E-04	0.9165	0	0.112	0.989	0.035
GOR	0.00052	4.93E-04	1.0542	0.104	0	0.99	0.015
ECH	0.000456	3.94E-04	1.158	0.096	0.024	0.991	0.145
FVA	0.000416	3.91E-04	1.0633	0.088	0.04	0.9918	0.479
HCO	0.000344	2.97E-04	1.157	0.096	0.056	0.9925	0.522
FAV	0.000328	3.10E-04	1.0571	0.08	0.024	0.9932	0.309
GAL	0.000296	3.66E-04	0.8094	0.04	0.032	0.9938	0.605
COE	0.000272	2.64E-04	1.031	0.064	0.016	0.9944	0.175
PSA	0.000272	2.57E-04	1.0566	0.056	0.008	0.9949	0.164
CYP	0.000224	1.76E-04	1.2709	0.04	0.024	0.9954	0.365
RMA	0.0002	3.16E-04	0.6325	0	0.04	0.9958	0.299
MIL	0.0002	4.08E-04	0.4899	0.04	0	0.9962	0.813
HER	0.0002	2.24E-04	0.8944	0.04	0	0.9966	0.086
LEP	0.000184	3.05E-04	0.6031	0.032	0.008	0.997	0.663
OUL	0.000176	1.33E-04	1.3217	0.04	0.008	0.9973	0.084
FVT	0.00016	1.53E-04	1.0474	0.032	0	0.9977	0.085

COS	0.000144	1.36E-04	1.0616	0.016	0.032	0.998	0.849
CAU	0.000128	1.40E-04	0.9143	0.016	0.016	0.9982	0.528
HLM	0.00012	1.63E-04	0.7348	0	0.024	0.9985	0.299
FUN	0.000088	1.01E-04	0.8685	0.016	0.008	0.9987	0.951
PBR	0.000088	1.01E-04	0.8685	0.008	0.016	0.9988	0.963
AMP	0.00008	1.63E-04	0.4899	0	0.016	0.999	0.827
GNP	0.000064	9.52E-05	0.6721	0.008	0.008	0.9991	0.655
LEA	0.000064	9.52E-05	0.6721	0.008	0.008	0.9993	0.687
DIC	0.00004	8.17E-05	0.4899	0	0.008	0.9993	0.986
HYD	0.00004	8.17E-05	0.4899	0	0.008	0.9994	0.983
LPA	0.00004	8.17E-05	0.4899	0	0.008	0.9995	0.827
GLA	0.00004	8.17E-05	0.4899	0.008	0	0.9996	0.832
TRB	0.00004	8.17E-05	0.4899	0.008	0	0.9997	0.976
MA	0.00004	8.17E-05	0.4899	0	0.008	0.9998	0.829
MER	0.00004	8.17E-05	0.4899	0.008	0	0.9998	0.813
POD	0.00004	8.17E-05	0.4899	0	0.008	0.9999	0.829
SCL	0.00004	8.17E-05	0.4899	0	0.008	1	0.842

S3. Macroalgae genera associated with degraded sites in Beger et al. (2010). Photos were taken from the CPCe Non-Coral Training Guide created for the Micronesia Conservation Trust (Fellenius, 2018).

Padina

Dictyota



Hypnea