# The relationship between macroalgae taxa and human disturbance on central Pacific coral reefs

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## Abstract

Climate change and human disturbance threatens coral reefs across the Pacific, yet there is little consensus on what characterizes a "healthy" reef. Benthic cover, particularly low coral cover and high macroalgae cover, are often used as an indicator of reef degradation, despite uncertainty about the typical algal community compositions associated with either near-pristine or damaged reefs. In this study, we examine differences in coral and algal community compositions and their response to human disturbance and past heat stress, by analysing 25 sites along a gradient of human disturbance in Majuro and Arno Atolls of the Republic of the Marshall Islands. Our results show that total macroalgae cover indicators of reef degradation may mask the influence of local human disturbance, with different taxa responding to disturbance differently. Identifying macroalgae to a lower taxonomic level (e.g. the genus level) is critical for a more accurate measure of Pacific coral reef health.

## Keywords

Coral reef; macroalgae; coral and macroalgal cover; monitoring and assessment; diagnostics; Republic of the Marshall Islands (RMI)

## Highlights

- Benthic composition differed by atoll, level of disturbance and exposure. Degraded sites were dominated by turf algae, sponges, and cyanobacteria.
- Different genera of macroalgae were associated with high and low human disturbance.
- Macroalgal genera may be better indicators of human-caused reef degradation than overall quantity of macroalgae.
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**Body of Paper**

**1. Introduction**

The health of coral reef ecosystems is declining worldwide (Aswani et al., 2015; Fenner, 2012; Hoegh-Guldberg et al., 2018; Hughes et al., 2019; Williams et al., 2015). Threats to coral reefs include both global pressures (such as climate change and ocean acidification) and local pressures (such as overfishing, sedimentation, and eutrophication). In addition to threatening the livelihoods and source of food for millions of people (Cinner, 2014), many of these threats can kill coral and reduce habitat complexity, influencing the ability of reefs to protect shorelines (Alvarez-Filip et al., 2009; Ferrario et al., 2014). Additionally, the potentially additive properties of these impacts may make corals and coral reef ecosystems less resilient to natural disturbances like storms (Scheffer et al., 2015, but see Côté and Darling, 2010).

Global sea temperatures have been rising for the past century and are projected to continue to rise (IPCC, 2014). This is leading to more frequent and severe heat waves and heat stress (Easterling et al., 2000; Donner et al., 2005; Maynard et al., 2015a) which can cause coral bleaching, coral mortality, and a reduced resilience to other stressors (Carpenter et al., 2008; Hughes et al., 2007; Magris et al., 2015; Toth et al., 2015). As a result, ongoing research is aiming to identify management actions that could confer coral reef resilience to climate change (e.g.; Bruno et al., 2019; Guest et al., 2018; Maynard et al., 2015b; McClanahan et al., 2012; Van Oppen and Gates, 2006). Applying these actions, however, depends on robust estimators of reef status. There has been disagreement in the literature about the relative role of local human activities in coral reef degradation with some articles reporting that local

impacts are important (e.g. Fabricius et al. 2005; Scheffer et al. 2015; Williams et al. 2015; Crane et al. 2017), and other articles finding that local impacts are negligible in comparison to the impacts of climate change (e.g. Aronson and Precht 2006; Carpenter et al. 2008; Bruno and Valdivia 2016).

The debate about the relative role of local and global threats may in part stem from disagreements over the metrics of reef health, as well as the very definition of a healthy reef. Total macroalgae cover is commonly used to indicate that reefs are 'unhealthy' or have a different benthic composition than what was found prior to disturbance (e.g. McCook et al. 1997; Mumby et al. 2005; Hughes et al. 2007; Bruno and Valdivia 2016). However, the broad category of "macroalgae cover" used in many field studies includes a variety of alga with different sensitivities to disturbance and life history strategies (Diaz-Pulido et al., 2010). The use of this coarse category could lead to the mischaracterization of reefs as unhealthy versus healthy. It neglects the differences within algae communities, overlooks other key reef organisms such as cyanobacteria and turf algae which are common on degraded reefs, and disregards the important role some algal assemblages may play in reef ecosystem function (e.g. Perry et al., 2016). Some reefs with high macroalgae cover are not necessarily degraded; in fact, some reefs far from human disturbance may have high percentages of macroalgae cover (Vroom et al. 2006; Vroom and Braun 2010; Williams et al. 2015).

The difficulties in defining 'healthy' reefs are also influenced by the debate about what reefs may have looked like before the Industrial Revolution. Some studies argue that some reefs may have naturally high macroalgae cover (Howe, 1912; Setchell, 1928; Vroom, 2011;

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Finnegan et al., 2015), while others argue that macroalgae has increased at the expense of live coral even on the most remote reefs due to recent climate change (Aronson and Precht 2006; Carpenter et al. 2008; Bruno and Valdivia 2016). However, while phase shifts from hard coral- to macroalgae-dominated reefs after disturbances are well documented in the Caribbean (Hughes, 1994; Hughes et al., 2007; Suchley et al., 2016), these may be uncommon in the Indo-Pacific (Bruno et al., 2009; Smith et al., 2016). It is possible that disturbances may instead cause coral reefs to shift towards other dominant taxa, such as sponges (Bell et al., 2013; Powell et al., 2014), corallimorphs (Work et al., 2008), or corals with 'weedy' life history strategies (Darling et al., 2012; Davenport and Haner, 2015; Crane et al., 2016).

The existence of remote Pacific atolls with negligible local impacts has allowed researchers to contrast coral and fish communities between pristine and more disturbed Pacific reefs (Houk and Musburger, 2013; Martin et al., 2017; Pecl et al., 2017; Sandin et al., 2008; Williams et al., 2013). The atolls of Majuro and Arno in the Republic of the Marshall Islands (RMI) provide a unique opportunity for targeted analysis of possible indicators of reef health and the relative threats posed by climate change and human disturbance. Only 19 km apart, the two atolls have comparable climatic and oceanographic experiences but a diversity of local human disturbance histories. In 2014, the most extensive thermal stress event in recorded history impacted the RMI. Abnormally high sea surface temperatures from July through December 2014 led to Bleaching Alert Level II warnings from NOAA Coral Reef Watch for September through November for the entire country, although heat stress was not as high in the southern atolls, including Majuro and Arno (Coral Reef Watch, 2017). There

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were some reports of possible shallow water bleaching-related coral mortality based on limited observations in Majuro and Arno (Fellenius, 2014), but the overall effect of the heat stress event on coral and algal communities remains unclear.

In this study, we examined how human disturbance impacts the composition of coral and algae communities across the more populated Majuro Atoll and more pristine Arno Atoll to explore the local impact of these disturbances and their effect on the recovery of reefs after the 2014 thermal stress event. We first investigated patterns in percent cover of key coral and alga taxa and their relationship with metrics of human influence across 25 sites in Majuro and Arno. We then examined how size structure of the coral communities varies across sites within each atoll and between the two atolls. Finally, we assessed the recovery from the recent (2014) thermal stress event by comparing percent cover surveys of key benthic life forms from 2007 in Arno and 2014 in Majuro to our data from 2016, at a subset of the original sites. The results provide insight into the limitations of macroalgae as an indicator of reef health and the impacts of human activities on coral communities in the central Pacific.

## 2. Methods

### 2.1 Background

The RMI is a nation of 29 atolls and five oceanic islands in the northwest tropical Pacific, just north of the Gilbert Islands of Kiribati and east of the Federated States of Micronesia. The Marshallese people depend heavily on surrounding coral reefs for food, as fishing is a major source of sustenance (Gillett, 2008; Martin et al., 2017), and for protection from storms and rising seas (Pinca et al., 2005).
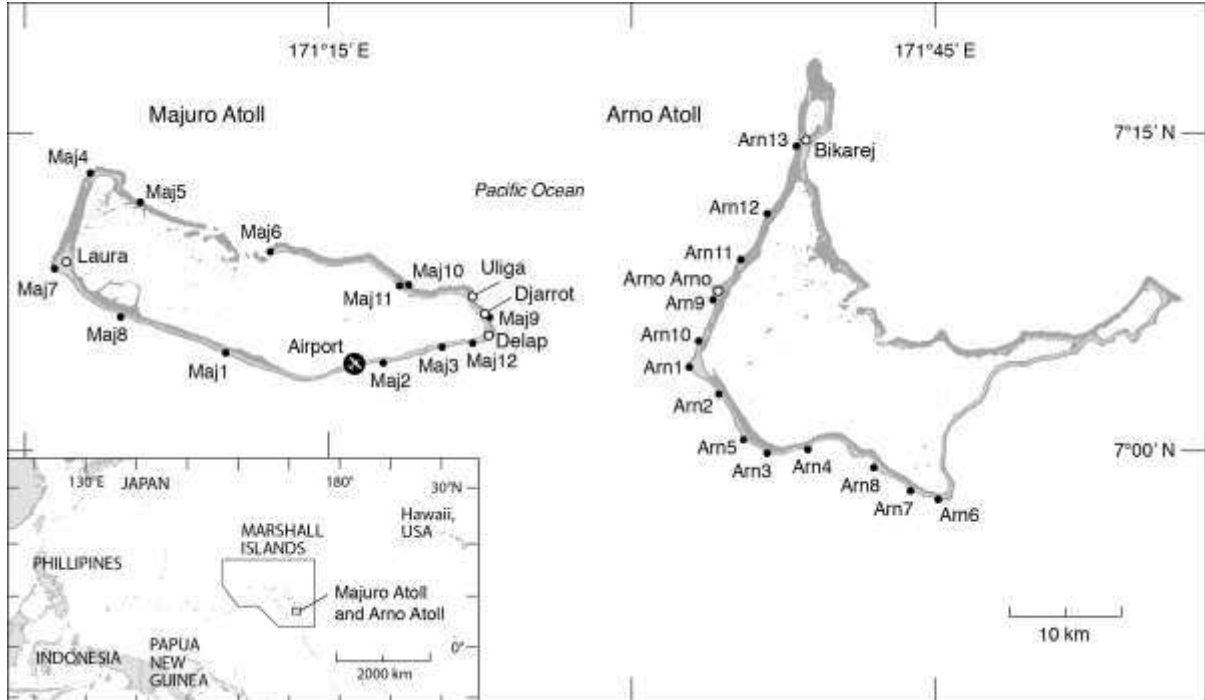
**Figure 1: Map of the RMI including study sites (black circles) and key towns and villages (white circles).**

The RMI have been inhabited for approximately 3,000 years (Ratzel, 1896). Majuro Atoll,

the capital of the RMI and home to over half of the country's approximately 53,000 people

(Secretariat of the Pacific Community, 2012), was subjected to extensive modifications and

population growth after its occupation by the American military during World War II

(Spennemann, 1996). In the 1970s, a series of causeways were built to connect the islands of

Djarrot and Laura in Majuro, which interrupted water flow between the lagoon and the ocean

and encouraged shoreline development along eastern and southern Majuro. An artificial

channel was then built to connect the lagoon and the ocean between Majuro Wharf and the

east part of Rairok in the 1980s (Xue, 2001). Over the past few decades, immigration from

outer atolls and a high birth rate has increased the population density especially in the eastern

population center of Delap-Uliga-Djarrot (Secretariat of the Pacific Community, 2012;

Spennemann, 1996). Coastal management challenges brought about by population growth, waste generation, and shoreline construction are placing pressure on the local coral reef ecosystems; for example, untreated sewage is concentrated and pumped from an outfall pipe near field site Maj12 that has corroded and leaks sewage directly onto the reef flat (MIMRA, 2016), and garbage often accumulates inside the lagoon (Richards and Beger, 2011).

Arno Atoll, located only about 19 km east of Majuro, has remained largely undisturbed by population growth and human modifications. Arno is larger than Majuro in area (12.96 km$^2$ of land, versus 9.72 km$^2$ in Majuro) but is home to fewer than 2,000 people, a number that is shrinking annually due to emigration to Majuro. The population of Arno is also spread more evenly throughout the atoll; the most populated island, Arno Arno, was home to 281 people as of the most recent census (Secretariat of the Pacific Community, 2012).

To date, there have only been a few published studies of the RMI's coral reefs (e.g.; Houk and Musburger, 2013; Martin et al., 2017; Pinca et al., 2005; Richards et al., 2008; Richards and Beger, 2011), none of which have included Arno Atoll. Because of the close proximity to Majuro, Arno is subject to some fishing pressure by fishermen who travel from Majuro, but this is almost entirely pelagic; access to reefs is controlled by the local iroij (chief) (Hess, 1999). While there is some reef fishing pressure in Arno, it is decidedly lower than in Majuro, and closely monitored by the central government. The Outer Island Fish Market Center in Majuro, a government sustainable development initiative that provides resources to outer island fishers, reports receiving only 33 boatloads (approximately 2,500 pounds each) of fish (pelagic and reef) from Arno Atoll in 2015 (MIMRA, 2015).

**2.2 Study Sites**

A total of 24 outer reef and one lagoon site across Majuro and Arno Atolls (12 in Majuro, 13 in Arno) were sampled between June 25 and July 7, 2016 (Table 1). We analyzed all data both with and without the lagoon site (Maj11), but we ultimately included that site in our analyses because it did not alter the statistical significance of any of the analyses. Sites were selected to cover the range of habitats, population density, and coastal infrastructure around each atoll. We prioritized sites with previous data (before the 2014 thermal stress event), which included sites Maj03, Maj04, Maj06 through Maj09, and Maj11 in Majuro visited by in 2014 (M. Beger, unpub. data), and Arn03 through Arn08 in Arno visited by MIMRA in 2007. Sites in Arno were restricted to the western and southern rim due to difficulties accessing the distant northeast and southeast outer reefs.

**Table 1: Biodiversity and thermal stress experienced in 2014 by the 25 study sites.**

| Site name | lat | long | mean NDVI[1] | mean SST[1,2] | SST sd[1,2] | max DHW[1,2] | Shannon-Weaver[3] | genera richness[3] |
|---|---|---|---|---|---|---|---|---|
| Arn01 | 7.063 | 171.545 | 0.47 | 29.37 | 0.60 | 4.84 | 1.88 | 17 |
| Arn02 | 7.041 | 171.569 | 0.35 | 29.38 | 0.60 | 5.14 | 2.38 | 18 |
| Arn03 | 6.992 | 171.608 | 0.36 | 29.39 | 0.60 | 4.86 | 2.06 | 14 |
| Arn04 | 6.995 | 171.642 | 0.26 | 29.39 | 0.60 | 4.86 | 1.55 | 18 |
| Arn05 | 7.004 | 171.589 | 0.38 | 29.37 | 0.60 | 5.14 | 1.55 | 16 |
| Arn06 | 6.955 | 171.748 | 0.41 | 29.36 | 0.59 | 4.03 | 2.07 | 14 |
| Arn07 | 6.962 | 171.725 | 0.38 | 29.36 | 0.59 | 4.03 | 1.89 | 17 |
| Arn08 | 6.981 | 171.695 | 0.40 | 29.38 | 0.60 | 4.52 | 2.04 | 17 |
| Arn09 | 7.117 | 171.564 | 0.45 | 29.35 | 0.60 | 4.68 | 2.11 | 24 |
| Arn10 | 7.084 | 171.552 | 0.40 | 29.36 | 0.60 | 5.28 | 2.14 | 19 |
| Arn11 | 7.150 | 171.587 | 0.46 | 29.33 | 0.60 | 4.39 | 2.51 | 23 |
| Arn12 | 7.188 | 171.608 | 0.43 | 29.33 | 0.60 | 4.24 | 2.00 | 14 |
| Arn13 | 7.243 | 171.632 | 0.40 | 29.32 | 0.60 | 4.21 | 2.38 | 23 |
| Maj01 | 7.074 | 171.166 | 0.38 | 29.40 | 0.61 | 5.55 | 2.09 | 25 |
| Maj02 | 7.066 | 171.295 | 0.25 | 29.38 | 0.60 | 4.54 | 1.64 | 15 |
| Maj03 | 7.079 | 171.343 | 0.31 | 29.38 | 0.59 | 4.39 | 2.31 | 13 |
| Maj04 | 7.221 | 171.056 | 0.44 | 29.38 | 0.61 | 4.16 | 1.57 | 20 |
| Maj05 | 7.197 | 171.097 | 0.35 | 29.39 | 0.61 | 4.68 | 1.97 | 17 |
| Maj06 | 7.157 | 171.203 | 0.43 | 29.37 | 0.61 | 4.55 | 2.27 | 11 |
| Maj07 | 7.143 | 171.027 | 0.45 | 29.41 | 0.61 | 5.37 | 2.02 | 20 |
| Maj08 | 7.103 | 171.081 | 0.37 | 29.40 | 0.61 | 5.04 | 2.47 | 20 |
| Maj09 | 7.103 | 171.382 | 0.14 | 29.37 | 0.59 | 4.52 | 2.72 | 25 |
| Maj10 | 7.130 | 171.316 | 0.39 | 29.37 | 0.59 | 4.23 | 2.72 | 23 |
| Maj11 | 7.129 | 171.308 | 0.41 | 29.37 | 0.59 | 4.23 | 1.21 | 6 |
| Maj12 | 7.082 | 171.368 | 0.19 | 29.38 | 0.59 | 4.26 | -- | -- |

[1] Normalized Difference Vegetation Index (NDVI), Sea Surface Temperature (SST), Degree Heating Weeks (DHW)
[2] Mean SST and SST standard deviation (sd) were calculated from daily SST values from July 2014 – June 2015. MaxDHW is the maximum DHW value in the same time period.
[3] Calculated using size frequency data of coral genera, which we did not collect at Maj12.

In Majuro, sites in Delap-Uliga-Djarrit are exposed to the most human influence (Figure 1, Maj09 through Maj01, clockwise) (Secretariat of the Pacific Community, 2012). Maj02 is located just east of a controversial expansion of the airport runway, which began in 2011 (Johnson, 2012; RMIPA, 2013) and is underway as of October, 2017 (RMIPA, 2017). Construction projects in Majuro like the airport runway depend on dredging of the reefs to supply materials (Ford, 2015; Richards and Beger, 2011). Islands in the northwest of the atoll are either uninhabited or home to fewer than 100 people, and are therefore less affected by run-off and eutrophication, although these sites are still fished, both for sustenance and the aquarium trade (Pinca et al., 2005). The sites in north Majuro have the highest exposure to wind and waves (with the exception of Maj11, which is inside the lagoon) from the prevailing northeast trade winds.

In Arno Atoll, sites Arn03 through Arn08 were identified based on previous surveys by MIMRA and the Secretariat of the Pacific Community (SPC). The other sites (Arn01, Arn02, Arn09 through Arn13) were selected based on distance and availability of accessible shallow (<15 m) reef flats. Arn01 was located directly offshore from Arno Arno, the island with the largest population (281 as of 2011) in Arno Atoll (Secretariat of the Pacific Community, 2012), and Arn08 and Arn13 were located offshore of slightly smaller wetos (townships). Arn12 was just north of a small boat passage that allowed boats to travel from the outer reefs to the lagoon. Because of Arno's orientation, all of the sites we visited there were relatively unexposed.

Each site was assigned a category of exposure based on the direction perpendicular to the shoreline (north, south, east, west, northeast, southwest, etc.). We later incorporated this into our statistical analysis to account for any potential effects of wind and wave exposure on benthic composition at each site.

**2.3 Survey Methods**

All data were collected between June 25 and July 7, 2016. A 50-m transect tape was laid randomly at 10-m depth at each site. We took 0.33 $m^2$-sized quadrat photos (50.0 cm width by 66.7 cm length) at 50 cm intervals along the transect, for a total of 100 photos per site. These photos were later analyzed to calculate the percent cover of macroalgae and coral genera (see section 1.2.6 below) at each site.

We also measured the length (in cm) of corals in situ along the transect, including all coral colonies ≥1 cm that lay at least partially within 25-cm on both sides of the tape. We considered corals with separate patches of living tissue greater than 3-cm apart from each other independent and measured them individually. All corals were identified to the genus level, with the exception of Porites rus.

Maj12 is located at Majuro's sewage outfall; RMI-EPA coliform and enterococci tests consistently exceed safe levels at this site (Doig, 1996; MIMRA, 2016), and we were therefore unable to sample there because of health concerns. Instead, we obtained 250 quadrat photos taken over an area of 250-m (five transects at 50m each), collected eight weeks later than data from our other sites by Karl Fellenius of Hawaii Sea Grant and Martin

Romain of the College of the Marshall Islands when the sewage pipe was temporarily turned off. Therefore, Maj12 is included in the benthic cover analysis but not the size frequency analysis.

We obtained the limited available data from past benthic surveys to evaluate the change in benthic composition since before the 2014 thermal stress event. In Majuro, benthic surveys were conducted in July and August 2014 for Maj03, Maj04, Maj06 through Maj09, and Maj11, six sites in total (M. Beger, unpublished data). Here, researchers recorded the percent cover at each site using three point-intercept 20-m transects at 3m and 10m depth (60-100 points per transect). Each point was categorized within 17 key functional groups. At the same time, coral abundance was recorded to the species level within a 100-m long belt transect (i.e. 100m$^2$) area (Maj03, Maj04, Maj06) or 50m$^2$ area (Maj07, Maj09, Maj11). These methods are described in Richards 2009.

Past taxa-level survey data was not available for Arno. The most recent surveys were conducted in Arno in summer 2007 at sites Arn03 through Arn08 (Marshall Islands Marine Resources Authority, unpublished data), following the Secretariat of the Pacific Community (SPC) underwater visual census, which includes broad benthic categories. Researchers delimited ten 5x5-m quadrats on each side of a 50-m transect, for a total of 20 quadrats per transect per site. The depth of surveys was variable; measured via a dive computer, the average depth at the center of each quadrat was 7.7 m, shallower than the 10 m depth of our 2016 surveys. Sixteen substrate components (including nine abiotic components and seven live coral shapes) were estimated on a semi-quantitative scale (0, 1-10%, 11-30%, 31-50%,

51-75%, and 76-100%), adding up to 100% coverage. These data were then summarized by site and benthic category by the SPC, and provided to us by MIMRA.

**2.4 Human Disturbance**

We estimated human influence at each site using the Normalized Difference Vegetation Index (NDVI), which is calculated using satellite imagery from the United States Geological Survey's Land Satellite 8. NDVI measures the amount of green terrestrial vegetation within a 60-meter pixel on a scale of -1.0 to +1.0 and is commonly used to represent the extent of human disturbance on terrestrial ecosystems (e.g., Vaidyanathan et al. 2010; Lambert et al. 2015). We used NDVI instead of more traditional measurements such as human population (e.g., Houk and Musburger 2013; Bruno and Valdivia 2016) in order to access a higher spatial resolution than that of the available census data and account for disturbances occurring where there are no permanent residents, such as the construction and dredging at the airport.

Satellite data were obtained from November 26, 2015, selected due to the low cloud cover on that day. Using ArcGIS ArcMap 10.4.1, we cast a circle with a 1-km diameter (chosen to minimize overlap of the circles) around each site and traced the landmass that fell within the circle. We then calculated the average NDVI of the landmass, giving us a proxy to rank human influence at each site (Table 1). For Arn12, no land was located within a 1-km radius; instead, we used the same NDVI as Arn13, the next closest site, which was uninhabited and therefore similarly undisturbed.

**2.5 Oceanographic Data**

Sea Surface Temperatures (SST) and Degree Heating Weeks (DHW; Liu et al., 2008) for all sites covering the period June 3, 2013 through April 30, 2017 were obtained from 0.05° x 0.05° resolution V3 satellite-derived data developed by the NOAA Coral Reef Watch program. We calculated the maximum DHW value for the bleaching year (July 2014 – June 2015) for each site, and these were later incorporated into our statistical analysis to account for any differences in heat stress between sites.

**2.6 Data Analysis**

Photos from the transects were processed in the lab to calculate benthic percent cover using Coral Point Count with Excel Extensions Research Software version 4.1 (Kohler and Gill, 2006), which overlaid 20 random points per photo for 100 photos per site (for a total of 2,000 points per site). Each photo covered 0.33 m$^2$ (50.0 cm width by 66.7 cm length). We identified each point to the genus level for coral and macroalgae and to functional group for sponges, soft corals, turf algae, crustose coralline algae (CCA), and cyanobacteria. We also identified the coral Porites rus, which has a 'weedy' life history strategy (Darling et al., 2012) and the encrusting sponge Terpios hoshinota, which can overgrow and kill corals, to the species level.

All statistical analysis was done using R i386 version 3.2.4 (R Core Team, 2016). We first investigated the relationship between NDVI and percent cover of specific benthic categories with a series of simple linear regressions. Next, we calculated the Shannon-Weaver diversity index (H') and genera richness per site (Table 1) using vegan package 2.4-2 (Oksanen et al.,

2017) and tested these indices against the NDVI with a linear regression to look for a

relationship between diversity and human influence. We also tested if the NDVI and the

Shannon-Weaver diversity index or genera richness were significantly different between

Majuro and Arno using Welch two-sample t-tests.

We visualized differences in benthic community composition by site and atoll using Principal

Component Analysis (PCA) on a subset of the percent-cover data (99% of all observations)

of coral and macroalgae taxa using the R stats package (R Core Team, 2016). We then used

SIMPER analysis (999 permutations) with the vegan package version 2.4-2 (Oksanen et al.,

2017) to identify the key taxa driving differences in benthic taxa  between atolls. We also

used permutational-based multivariate analysis (PERMANOVA, 99,999 permutations,

Anderson 2001) with the vegan package to test for variation in means of all benthic taxa and

also only macroalgae taxa caused by four environmental variables: atoll, NDVI, maximum

DHW, and wind and wave exposure. We used the direction perpendicular to the shoreline at

each site as a categorical variable to account for exposure (for example, north, south, east,

west, northeast, southwest, etc.). The prevailing winds in this region come from the

northeast, such that sites in the north and east (Maj05 through Maj09, clockwise, Figure 1,

except Maj11) of the atoll are most exposed to winds and greater wave activity. All of these

sites in the north and east, with the exception of Maj09, are also relatively undisturbed by

human influence. For example, Arn01 and Arn02 were assigned to exposure category

"West", while Maj01 was assigned to "Southwest".  The order of these variables in the

PERMANOVA test did not affect the results.

To evaluate the differences in size frequency distributions for major coral taxa between sites and atolls, we grouped the size frequency data into eight taxonomic groups representing the most ecologically important and prevalent taxa: Acropora, Heliopora, Isopora, Montipora, Pavona, Pocillopora (genera), Faviids (family), massive Porites (morphology of genus Porites), and Porites rus (species). For each of these groups, at each site and for each atoll, we calculated demographic statistics on coral abundance and size, including: mean size, standard deviation, coefficient of variation, skewness and skewness standard error, and kurtosis and kurtosis standard error. We considered skewness and kurtosis values greater than two times the standard error significantly different from normal (McClanahan et al., 2008).

Despite transformations (including log, square root, power, and reciprocal transformations) of the size distribution data for each taxon at each atoll, none of the distributions met the assumptions of normality (Shapiro-Wilk test) or homogeneity of variance (Levene's test), so comparisons of size frequency distributions between sites were conducted using untransformed data. Critical values for all tests were adjusted using the Bonferroni correction to avoid Type I errors across multiple comparison tests. We used the Kolmogorov-Smirnov test to compare size frequency distributions between Arno and Majuro (Adjeroud et al., 2007). We tested size frequency distributions across atolls instead of across sites because the PERMANOVA results showed that the benthic composition differed more between atolls than by NDVI across sites. We used Welch's analysis of variance (ANOVA) tests to examine whether the mean size, coefficient of variation, skewness, or kurtosis for each of the nine categories varied between Majuro and Arno (Adjeroud et al., 2007).

Finally, we tested whether percent cover of key benthic taxa had changed after the 2014 thermal stress event using a series of Welch's two-sample t-tests for all benthic categories and key coral taxa with Bonferroni corrections. The data were tested for normality using the Shapiro-Wilk test and for homogeneity of variance using Levene's Test, and all assumptions were met. In Majuro, using unpublished data from 2014, we combined the percent cover (from point-intercept transects) with abundance data (from belt transects) to calculate percent cover of individual coral genera. We tested for changes between 2014 and 2016 in key live coral genera percentage of both total benthic cover and live coral cover. In Arno, we did not have data at the genus level, and were therefore only able to test the overall change in the percent of major benthic categories (comparing 2007 and 2016 surveys).

## 3. Results

### 3.1 Benthic Cover

Macroalgae (including Halimeda spp.) cover ranged from 0% to 88% (Figure 2a) across all sites. Halimeda spp. was the most commonly observed macroalgae, ranging from 0% to 77% of all benthic cover across all sites. Live coral cover ranged from 1% to 54% across all sites (Figure 2a). In Arno, massive Porites were common, while in Majuro, Acropora was more prevalent (Figure 2b). In general, sites in Arno had more macroalgae cover than sites in Majuro (Figure 2c). Halimeda was common in both Majuro and Arno, although it was found consistently at all sites in Arno. Microdictyon was more commonly found in Arno, while Lobophora was more common in Majuro (Figure 2c).
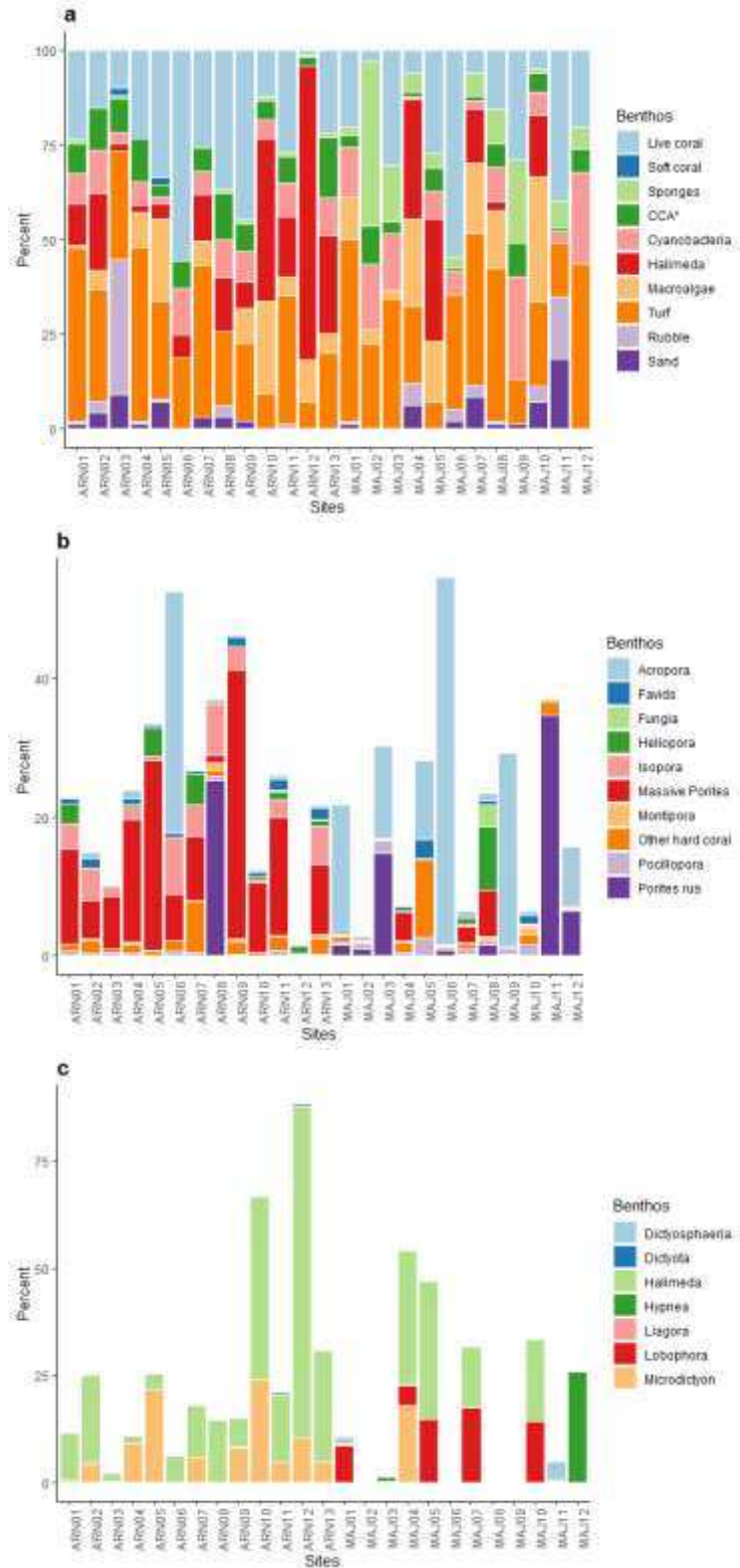
**Figure 2: Percent cover of (a) key benthic categories, (b) live coral and (c) macroalgae genera at each study site. *Crustose coralline algae (CCA)**

The PCA of key coral taxa by site suggested some differences in the typical coral community compositions between sites in Majuro and sites in Arno (Figure3a), with the sum of the first and second principal components in both PCAs greater than 0.50. Porites rus and Acropora (in both table and branching morphologies) were more common at sites in Majuro. By contrast, sites in Arno were more likely to be dominated by massive Porites. The PCA of key coral taxa suggests less distinct grouping of sites by exposure; there is less dissimilarity between the exposed northern sites (Fig 3a, triangles) and the less exposed southern and western sites (Fig 3a, circles, squares) than between the Majuro (white symbols) and Arno (dark symbols) sites.

The PCA of only the macroalgae genera showed that the macroalgae communities were distinct, with very little overlap in the plots between the two atolls, with the exception of sites Maj04 and Maj08 (Figure3b), which were more similar to the Arno sites than to the other Majuro sites. These sites are located on the north side of the atoll where there was relatively little human influence. Majuro sites were dominated by the macroalgae genera Hypnea, Dictyota, Liagora, Lithothamnion, and Lobophora, while Arno sites had higher prevalence of Halimeda, Dictyosphaeria, and Microdictyon. Similar to the PCA of key coral taxa, the PCA of macroalgae genera suggests less distinct grouping by exposure, with some similarity between the north facing-sites (Fig 3b, circles) and some south-facing sites (Figure 3b, triangles).
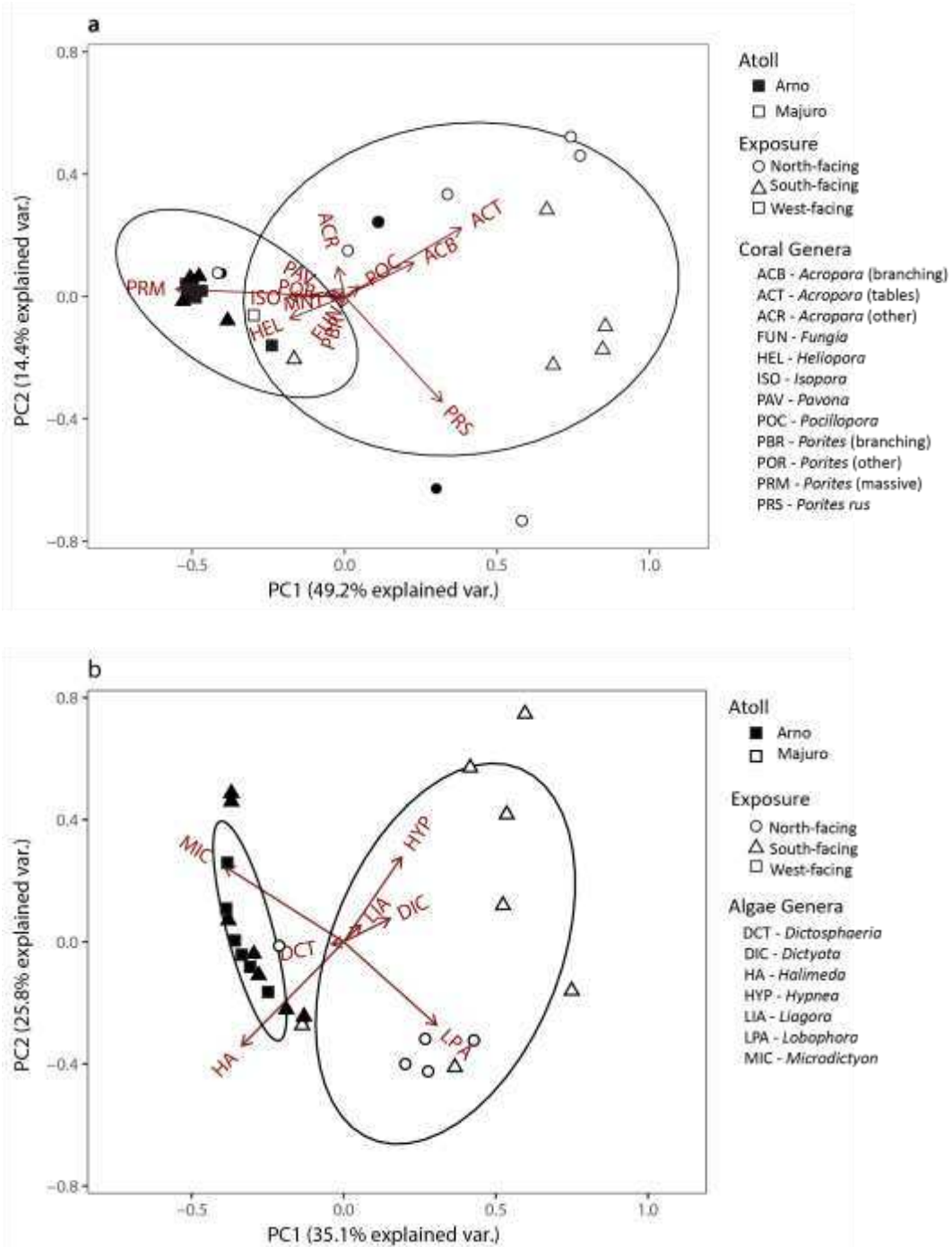
**Figure 3: Principle components analysis of (a) observed coral taxa and (b) macroalgae genera, by atoll (dark=Arno, clear=Majuro) and exposure (circles=north, triangles=south, squares=west). Genera that comprised <1% of observations are excluded. Ellipses indicate 95% confidence intervals of the coral taxa or macroalgae genera by atoll.**

The SIMPER analysis identified ten key taxa driving almost 80% of the differences in benthic communities between Majuro and Arno Atolls (Table 2). The results show that three different macroalgae genera drove over 25.67% of the difference in benthic community composition between atolls, while coral taxa collectively drove 21.72% of the difference, and other taxa, including turf algae, cyanobacteria, rubble, and crustose coralline algae together drove 31.93% of the difference between atolls. As expected, these results are similar to the key drivers of difference between atolls identified by the PCA (Figure 3).

**Table 2: Most influential taxa in benthic community difference between Majuro and Arno Atolls, as identified by SIMPER analysis.**

| taxa | contribution (%) |
|---|---|
| **macroalgae** | |
| Halimeda | **15.10** |
| Microdycton | **6.35** |
| Lobophora | **4.22** |
| **coral** | |
| Massive Porites | **9.99** |
| Tabulate Acropora | **6.42** |
| Porites rus | **5.31** |
| **other** | |
| Turf algae | **12.39** |
| Cyanobacteria | **5.62** |
| Rubble | **4.30** |
| Crustose Coralline Algae | **9.62** |
| **total** | **79.32** |

The PERMANOVA analysis (Table 3) found significant differences in benthic community composition based on atoll ($p < 0.01$), NDVI ($p = 0.01$) and exposure ($p = 0.02$), but not for maximum DHW for the bleaching year ($p = 0.52$). Exposure (PERMANOVA $p = 0.24$) and maximum DHW (PERMANOVA, $p = 0.11$) were not key drivers of macroalgae composition across sites, while atoll (PERMANOVA, $p < 0.01$) and mean NDVI (PERMANOVA, $p = 0.01$) were statistically significant (Table 4). In order to test the significance of exposure in the absence of the atoll affect, we also ran the PERMANOVA analyses without the "atoll" factor. For all benthic categories, we found that NDVI ($p < 0.001$) and exposure ($p = 0.01$) were both statistically significant exploratory variables, while when testing only macroalgae genera, mean NDVI was

the only statistically significant exploratory variable (p < 0.01).  NDVI did not differ

significantly between atolls (Welch two-sample t-test, p = 0.11).

**Table 3: PERMANOVA of predictors of benthic composition (significant values are underlined).**

| source | df | ss | ms | $r^2$ | psuedo-f | p-value |
|---|---|---|---|---|---|---|
| atoll | 1 | 0.66 | 0.65 | 0.18 | 6.02 | $\leq 0.01$ |
| mean NDVI | 1 | 0.33 | 0.33 | 0.09 | 3.04 | 0.01 |
| exposure | 6 | 1.13 | 0.19 | 0.30 | 1.73 | 0.02 |
| max DHW (bleaching year) | 1 | 0.10 | 0.10 | 0.03 | 0.87 | 0.52 |
| residuals | 14 | 1.79 | 0.13 | 0.47 | | |
| **Total** | **23** | **3.7502** | | **1.00** | | |

**Table 4: PERMANOVA of predictors of macroalgae genera (significant values are underlined).**

| source | df | ss | ms | $r^2$ | psuedo-f | p-value |
|---|---|---|---|---|---|---|
| atoll | 1 | 0.99 | 0.99 | 0.22 | 7.93 | <u>$\leq 0.01$</u> |
| mean NDVI | 1 | 0.47 | 0.47 | 0.11 | 3.74 | <u>0.01</u> |
| exposure | 6 | 0.98 | 0.16 | 0.22 | 1.31 | 0.24 |
| max DHW (bleaching year) | 1 | 0.25 | 0.25 | 0.06 | 1.99 | 0.11 |
| residuals | 14 | 1.75 | 0.13 | 0.39 | | |
| **Total** | **23** | **4.45** | | **1.00** | | |

Least squares linear regressions showed significant relationships between NDVI and some of the major coral and algal cover categories, but not total live coral cover or total macroalgae cover. Halimeda ($p < 0.01$, $r^2=0.30$) and massive Porites ($p = 0.02$, $r^2 = 0.20$) were each significantly positively correlated with NDVI, which means they were more likely to be found in places with less human disturbance (Table 3). Conversely, Acropora ($p = 0.03$, $r^2 = 0.19$), cyanobacteria ($p < 0.01$, $r^2 = 0.54$), Hypnea ($p = 0.02$, $r^2 = 0.21$) and sponges ($p < 0.01$, $r^2 =0.30$) were negatively correlated with NDVI and were therefore more likely to be found in places with higher disturbance (Table 5). Variation in NDVI across sites explained about 20% or less of the variance across sites for Acropora, Isopora, massive Porites, and Hypnea. By contrast, NDVI explained about 54% of the variance of cyanobacteria across sites, and for Halimeda and sponges, NDVI explained approximately 30% of the variance of each. We found no relationship between Shannon Weaver diversity index (H') for each site (Table 1) and NDVI (linear regression, $p > 0.80$), or by atoll (Welch two-sample t-test, $p > 0.90$). We similarly did not find a relationship between genera richness (Table 1) and NDVI (linear regression, $p > 0.70$), or by atoll (Welch two-sample t-test, $p = 0.90$).

**Table 5: Results of simple linear regressions of NDVI and relative abundance of benthic taxa across all sites in Majuro and Arno Atolls (values significant at the 0.05 level are underlined).**

| | benthic category | slope[1] | n | $r^2$ | f-stat | p-value |
|---|---|---|---|---|---|---|
| **Live Coral** | All live coral | -- | 8968 | 0.02 | 0.38 | 0.55 |
| | Acropora | -435.00 | 3066 | 0.19 | 0.57 | <u>0.03</u> |
| | Heliopora | -- | 415 | 0.04 | 0.86 | 0.37 |
| | Isopora | -- | 837 | 0.16 | 1.80 | 0.05 |
| | All Favids | -- | 216 | 0.07 | 1.85 | 0.19 |
| | Montipora | -- | 97 | 0.01 | 0.19 | 0.67 |
| | Pocillopora | -- | 248 | 0.03 | 5.82 | 0.39 |
| | Massive Porites | +564.12 | 3259 | 0.20 | 0.20 | <u>0.02</u> |
| | Porites rus | -- | 1445 | 0.00 | 0.00 | 0.96 |
| **Macroalgae** | All macroalgae | -- | 9660 | 0.09 | 2.20 | 0.15 |
| | Dictyosphaeria | -- | 51 | 0.03 | 0.63 | 0.44 |
| | Dictyota | -- | 102 | 0.01 | 0.18 | 0.67 |
| | Halimeda | +1352.10 | 5873 | 0.30 | 3.73 | <u>0.01</u> |
| | Hypnea | -477.42 | 458 | 0.21 | 6.06 | <u>0.02</u> |
| | Liagora | -- | 39 | 0.00 | 0.01 | 0.94 |
| | Lithothamnion | -- | 69 | 0.11 | 2.75 | 0.11 |
| | Lobophora | -- | 978 | 0.03 | 0.66 | 0.43 |
| | Microdictyon | -- | 2038 | 0.04 | 0.90 | 0.35 |
| **Other** | CCA | -- | 2809 | 0.06 | 1.39 | 0.25 |
| | Cyanobacteria | -904.20 | 3731 | 0.54 | 26.88 | <u>< 0.01</u> |
| | Turf algae | -- | 11,849 | 0.00 | 0.02 | 0.88 |
| | Soft coral | -- | 38 | 0.00 | 0.03 | 0.87 |
| | Sponges | -1032.71 | 2191 | 0.30 | 9.94 | <u>< 0.01</u> |

[1]NDVI has an inverse relationship with disturbance. Therefore, a negative slope indicates an association with more disturbance and vice versa.

Almost half of the sponge cover in Majuro (48.1%) was Terpios hoshinota, an encrusting sponge often found in highly degraded areas that has the ability to overgrow and kill corals. Because this sponge closely resembles cyanobacteria, it is easily misidentified (Rutzler and Muzik, 1993). Maj02, a site with high turbidity located close to the airport dredging site, had 29.6% cover of Terpios hoshinota and only 4.2% macroalgae cover (Figure 4). We found no Terpios hoshinota in Arno.
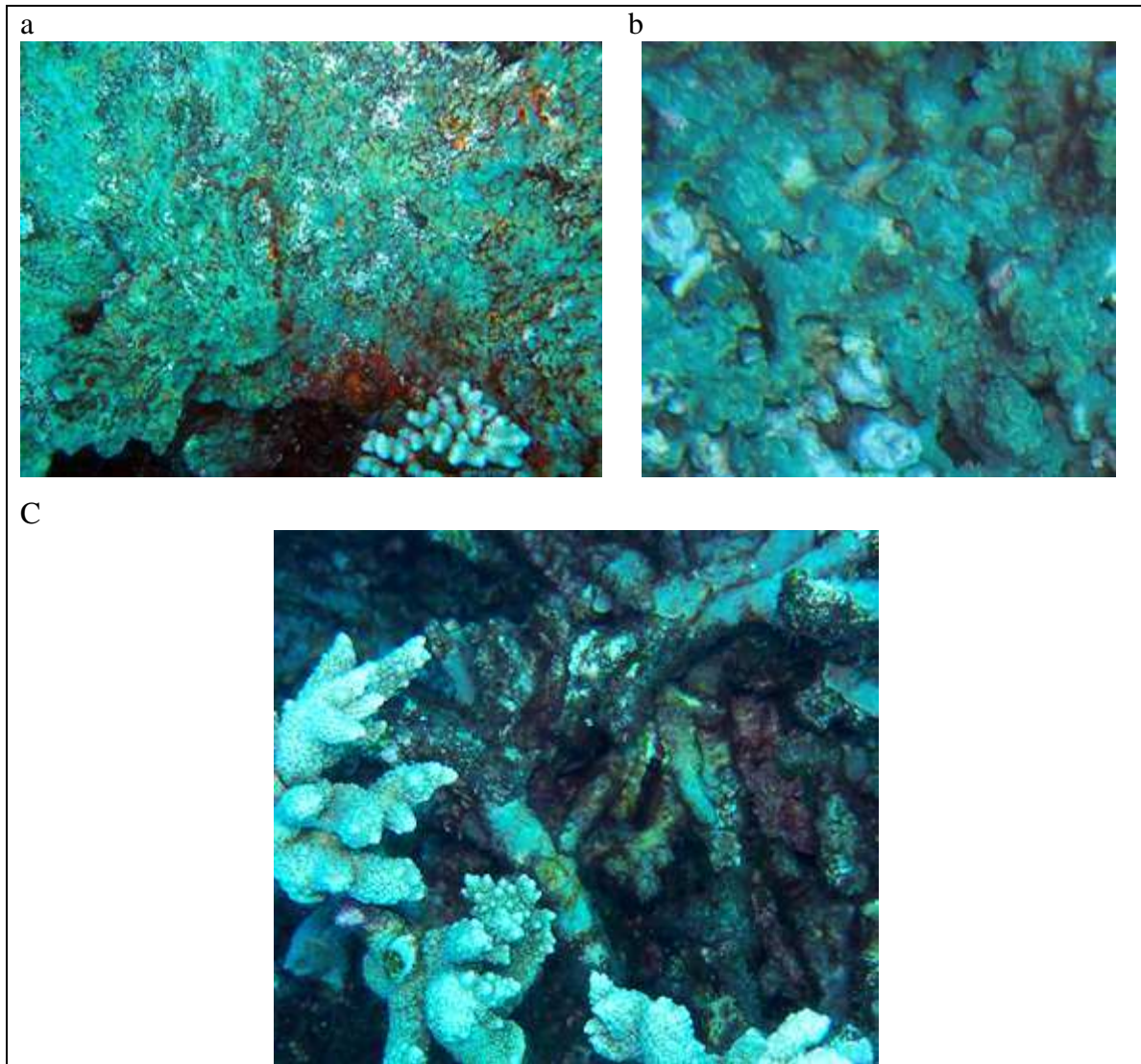
**Figure 4: From Maj02, (a) Terpios hoshinota covering a table of Acropora sp., (b) Zoomed-in view of Terpios hoshinota, (c) Terpios hoshinota and cyanobacteria growing on a branching Acropora sp.**

### 3.2 Coral Size Structure

The size-structure data show that corals in Arno were on average smaller than those in Majuro.

Across all sites, massive Porites were the most common coral in the size-structure data

(n=1887), with an overall mean size of 15.41 cm, the vast majority of these in Arno (Supplement

1). Acropora followed closely (n = 1381, mean size = 16.05 cm) followed by Faviids (n = 1042, mean size = 8.09 cm) (Figure 5).
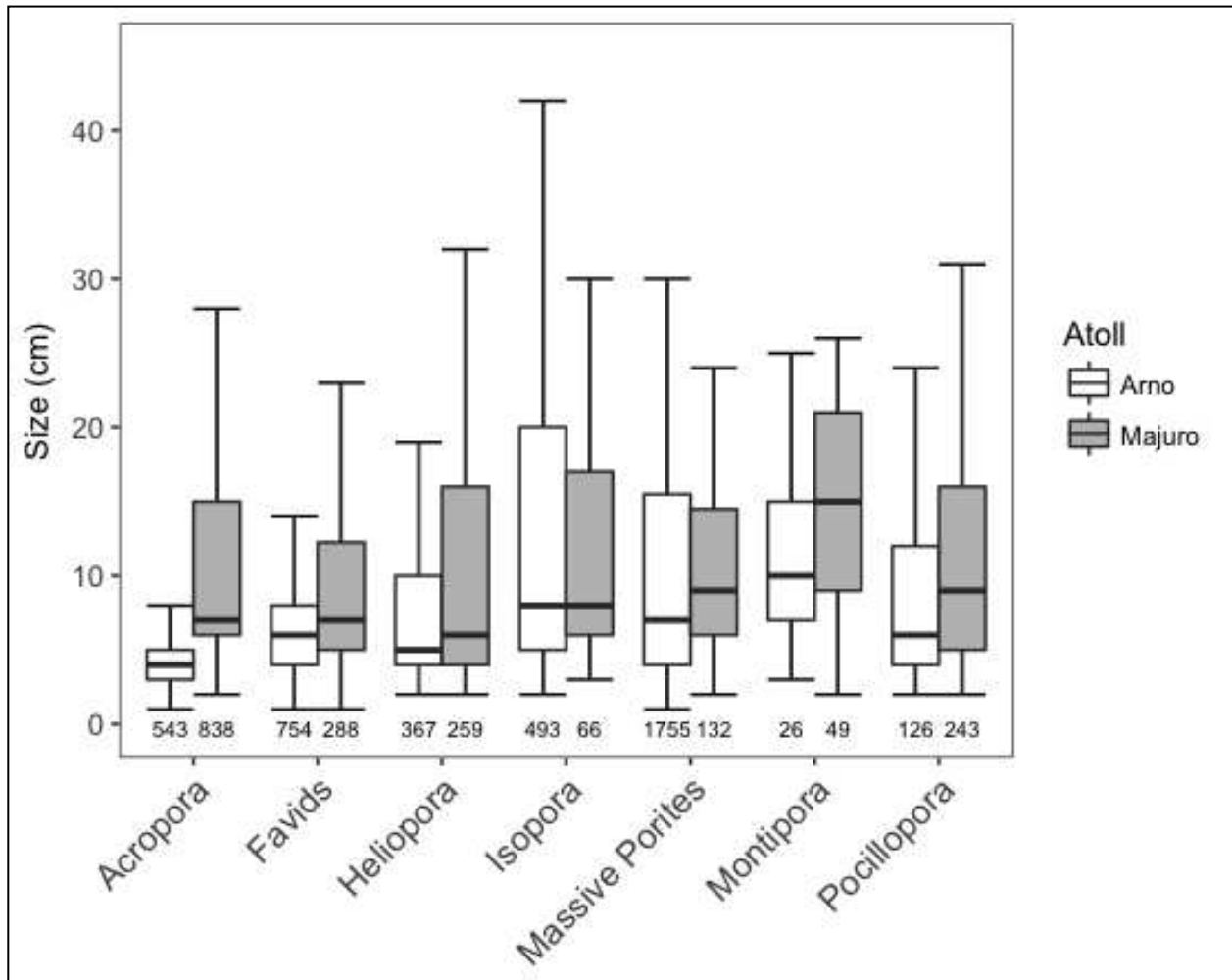


**Figure 5: Quartile plots of coral size for major coral categories across both Arno and Majuro Atolls, where the lower and upper hinges correspond with the first and third quartiles, the center line represents the median, and the whiskers indicate 95% confidence intervals. Porites rus was omitted due to the low number of observations in Arno.**

Within each atoll, skewness and kurtosis were positive and significantly different from normal for all categories, indicating a peaked distribution dominated by small corals (Supplement 2). The one exception was Montipora in Arno Atoll. Skewness was more positive in Arno for all categories except Porites rus, which was more than twice as common in Majuro as Arno. Greater

positive skewness may indicate that there are more juveniles present at sites in Arno, but could also result from partial mortality during the 2014 heat stress event. The shape of the size distributions differed significantly between Majuro and Arno for five of the eight categories (Komogorov-Smirnov test, Table 6).

**Table 6: Kolmogorov-Smirnov (ks) test results comparing across atolls, with Bonferroni correction. Significant results are underlined.**

| Category | ks test statistic (w) | ks p-values | Bonferroni correction |
|---|---|---|---|
| Acropora | 0.54 | < 0.01 | < 0.01 |
| Favids | 0.24 | < 0.01 | < 0.01 |
| Heliopora | 0.12 | 0.03 | 0.06 |
| Isopora | 0.18 | 0.04 | 0.09 |
| Montipora | 0.31 | 0.08 | 0.16 |
| Pocillopora | 0.22 | < 0.01 | < 0.01 |
| Massive Porites | 0.17 | < 0.01 | < 0.01 |
| Porites rus | 0.30 | < 0.01 | < 0.01 |

Mean size was greater in Majuro for six of the eight coral categories (Table 7); only Isopora was larger in Arno, where they were also more common (Figure 5). The difference in mean sizes were significant for Isopora (Welch's ANOVA, $p < 0.01$, Table 7), but not for any other coral categories.

**Table 7: Results of Welch's ANOVA of size-frequency statistics between atolls, with significant results underlined.**

| category[3] | mean[1] | | | coefficient of variation | | | skewness | | | kurtosis | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | f | df[2] | p-value | f | df[2] | p-value | f | df[2] | p-value | f | df[2] | p-value |
| Acropora | 1.76 | 20.41 | 0.20 | 2.18 | 21.97 | 0.15 | 1.01 | 18.63 | 0.33 | 0.65 | 16.89 | 0.43 |
| Favids | 3.49 | 11.34 | 0.09 | 9.30 | 20.48 | <0.01 | 12.37 | 15.91 | <0.01 | 5.45 | 12.10 | 0.04 |
| Heliopora | 2.16 | 12.61 | 0.17 | 1.85 | 12.99 | 0.20 | 3.51 | 7.39 | 0.10 | 1.50 | 5.72 | 0.27 |
| Isopora | 14.38 | 17.12 | <0.01 | 22.78 | 16.18 | <0.01 | 3.90 | 13.00 | 0.07 | 1.90 | 15.61 | 0.19 |
| Montipora | 0.56 | 13.81 | 0.46 | 6.41 | 13.58 | 0.02 | 2.52 | 10.17 | 0.14 | 0.20 | 11.71 | 0.67 |
| Pocillopora | 1.44 | 17.15 | 0.25 | 0.07 | 19.76 | 0.79 | 0.02 | 16.17 | 0.90 | 0.12 | 13.29 | 0.74 |
| Massive Porites | 0.07 | 10.81 | 0.80 | 0.02 | 7.07 | 0.90 | 0.43 | 8.61 | 0.53 | 0.63 | 17.87 | 0.44 |

1Mean size in cm
2 df is the denominator degrees of freedom. Numerator degrees of freedom equals 1.00 for all tests.
3 Porites rus was not included because it was only observed at one site in Arno, and we did not have enough observations for this test.

The size-frequency distribution statistics by atoll (Supplement 1) appear to be representative of the statistics within sites (Supplement 3), with overwhelmingly positive skewness and kurtosis. Most coral categories had positive skewness and kurtosis at each individual site, with the exception of Acropora, Isopora, and Pocillopora. Kurtosis was negative for Acropora at four out of 24 sites, indicating that the Acropora at this site tended to be close in size to the mean, but these kurtosis values were all very close to zero, with none equal to or greater than -1.0. Kurtosis was also negative at four of the 23 sites where Isopora was found, with these values slightly further from zero, ranging from -0.8 to -2.2. The size distribution for Pocillopora had negative kurtosis at seven of the 23 of sites, the most of all coral categories, with values ranging from -0.1 to -2.1. By contrast, only one coral category at one site had a negative skewness value (Faviids at Maj05, -0.3, Supplement 3).

### 3.3 Comparison with Previous Surveys

Maximum DHW only varied by 1.52°C·week across sites (4.03°C·week at Arn06 and Arn07 to 5.55°C·week at Maj01) during the bleaching year (June 2014 – July 2015), while mean SST varied by less than 0.1°C (Table 1). The maximum DHW values surpassed the Bleaching Alert Level I threshold but not the Alert Level II threshold; this indicates that the heat stress event was less pronounced around the southern RMI than in the rest of the country, where maximum DHW values exceeded 12°C·week (Coral Reef Watch, 2017).

There were no significant changes in the percent cover of major benthic categories (live coral, CCA, dead coral, cyanobacteria or macroalgae) between the pre-thermal stress 2014 surveys and

our 2016 surveys at the six Majuro sites for which data were available (Supplement 4). There was significantly higher sponge cover in 2016 (9.6%, up from 0.2%; Welch two-sample t-test, p $< 0.05$), however that could be in part due inconsistencies in identification of benthic taxa between the 2014 and 2016 surveys (see Discussion). There was also no significant change in the percent cover of individual coral taxa or of coral taxa as a percent of living coral cover; the one exception was Pavona which decreased from already low value of 2% to 0.25% of benthic cover (Welch two-sample t-test, p-value $< 0.01$, Supplement 4). We also detected no significant changes in major benthic categories (live coral, CCA, dead coral, cyanobacteria or macroalgae) in Arno between the much earlier 2007 surveys for sites Arn03 through Arn08 and our 2016 surveys (Supplement 5). Cyanobacteria did increase from 0 to 6.31% (p=0.08 with the Bonferroni correction) but that may be due to aforementioned inconsistencies in identification between surveys.

## 4. Discussion

The results indicate that differences in benthic composition and coral size-structure across Majuro and Arno may be related to a combination of local human disturbance and exposure to wind and waves. However, total macroalgae cover, a metric commonly used for characterized unhealthy or disturbed reefs, is not correlated with local human disturbance. Instead, local human disturbance is a predictor of the composition of the macroalgae community across sites and the presence of particular taxa of macroalgae, as well as sponges, cyanobacteria and coral. To our knowledge, this paper is the first to suggest a relationship between genera of macroalgae and differing levels of human impacts on coral reefs. Below we explore the drivers of differences in

coral and algal taxa across sites, the use of NDVI as an indicator of human disturbance, and the implications of the findings for research on Pacific coral reef resilience.

The key patterns in benthic composition and size-structure across sites and atolls were explained by a combination of local human disturbance and exposure to wind and waves (Table 3). Wind and wave exposure is a known predictor of coral community structure, especially on shallow reef flats where corals may be susceptible to breakage, scouring, and abrasion (Dollar, 1982; Grigg, 1998; Storlazzi et al., 2005). Although exposure also influences macroalgae cover (e.g., Williams et al., 2013), the PERMANOVA indicated exposure was not a driver of differences in macroalgae community composition between sites (Table 4). Because of difficulty accessing the north side of Arno, all of the exposed (north or northeast facing) sites were in Majuro, which could account for some of the differences in benthic composition and specifically in macroalgae composition observed across the two atolls.  Analysis of such additional exposed sites would provide a more complete test of whether exposure may explain some of the differences in macroalgae community across sites.

The differences in the benthic community between the two atolls are reflected in the varying sizes and abundances of particular coral taxa. The corals in Majuro were on average larger than those found in Arno, with the exception of Isopora and Porites rus, which had larger mean sizes in Arno (Table 7). Massive Porites were more prevalent in Arno than in Majuro and were significantly more likely to be found at sites with lower disturbance, but had a slightly larger mean size in Majuro, although this was not statistically significant. In addition to smaller mean coral sizes for most categories of corals in Arno, the population size distributions were more

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positively skewed in Arno than Majuro (with the exception of Porites rus, Table 7), which indicates the presence of proportionately more small corals in Arno. Previous studies have shown that small corals are more likely to be found at exposed sites compared to those unexposed to waves (Caballero Aragon et al., 2016; Victor et al., 2009); however, in this case we found the opposite, suggesting the differences in size distributions cannot be attributed solely to wind and wave exposure.

Research has shown that smaller coral colonies are more vulnerable to mortality (Bak and Meesters, 1998; Connell, 1973; Hughes and Connell, 1987; Wittenberg and Hunte, 1992). One potential explanation is that it is rare for small corals to experience partial mortality; because small colonies have less surface area, mortality is more likely to be total (Bak and Meesters, 1998). It is therefore possible that higher local human disturbance in Majuro has caused mortality among smaller corals, contributing to their paucity in Majuro compared to Arno; also, in Majuro, nutrient pollution has also caused outbreaks of disease, which can disproportionately affect small coral colonies (Sussman et al., 2008).

There were more Acropora in Majuro than in Arno, and an inverse relationship between cover of Acropora and NDVI, showing that higher Acropora cover was correlated with high levels of disturbance (Table 5). This was surprising because most species of Acropora are competitive, fast-growing corals that tend to be sensitive to environmental fluctuations and local disturbances (Darling et al., 2012). Acropora in Majuro were on average larger than those in Arno (21.32 cm in Majuro vs 7.94 cm in Arno), although again, this was not statistically significant. In this case, the differences in mean size could be explained by morphology; large tables were common in

Majuro (76.7% of all Acropora cover) but rare in Arno (0.01%). This is unlikely to be caused by exposure because there was no statistical difference in the presence of tabulate Acropora at exposed and unexposed sites within Majuro (Welch's two-sample t-test, p = 0.29).

To our knowledge, this is the first study to use NDVI as a proxy for human influence on coral reefs, although NDVI is commonly used in land-based studies (e.g. Lambert et al., 2015; Leu et al., 2013; Vaidyanathan et al., 2010). It is well suited to characterizing human disturbance to coral reefs in the Pacific Islands for two reasons. First, human population data is often not available at a high enough resolution to estimate how human population differs between sites. Second, NDVI may serve as a more accurate indicator of the effects of human activities on coral reefs (e.g. nutrification, land-based runoff) than population, because it accounts for anthropogenic features that may be distant from population centers. For example, one of the most degraded sites, Maj02 (Figure 1), was located near the airport expansion site, where the human population is low but sedimentation from human activity is high because of dredging. NDVI is a consistent way to account for any human activities that could have a detrimental effect on reefs despite low populations living nearby, like roads, bridges, farms, and landfills.

While there was no relationship between all live coral or macroalgae cover and NDVI, some genera of macroalgae were more likely to be associated with high disturbance, and vice versa (Table 5). The SIMPER analysis found that some macroalgae genera were key drivers of differences in benthic community composition between the atolls, particularly Halimeda, which accounted for 15.10% of all variation in benthic communities across Majuro and Arno (Table 2). Regression analyses found that Halimeda was more likely to be found at sites with low

disturbance while Hypnea was more prevalent at disturbed sites. This is consistent with studies that have found different taxa of macroalgae respond to disturbance in different ways (Clausing and Fong, 2016; Mumby et al., 2005; Stimson et al., 2001), however, to our knowledge, there have been no prior studies specifically examining how Hypnea and Halimeda respond to human influence on reefs.

The most disturbed sites (lowest NDVI: Maj09, Maj12, Maj03, Maj02, all of which except for Maj09 had low exposure to wind and waves) had low total macroalgae cover (ranging from 0.2% to 4.7%), and high cover of other benthic taxa such as turf algae, sponges, and cyanobacteria. Sites in Majuro had higher sponge cover on average than sites in Arno (0.6% average sponge cover in Arno compared to 10.9% in Majuro), and were home to different sponge taxa. Almost half (48.1%) of all sponges in Majuro were Terpios hoshinota, an encrusting sponge sometimes called "black disease" because of its ability to quickly overgrow and kill corals (Shi et al., 2012). Terpios hoshinota was absent from our surveys from Arno. This sponge is a natural part of coral reef ecosystems, but may be able to outcompete corals in degraded conditions (Rutzler and Muzik, 1993). Terpios hoshinota was most prevalent at site Maj02 (covering 29.6% of the substrate, compared to 2.0% live coral and 4.7% macroalgae), which was near the airport expansion project and dredging. This is consistent with previous studies, which have found that Terpios hoshinota tends to be found near areas of coastal development and with high turbidity (Reimer et al., 2011a; Rutzler and Muzik, 1993). Terpios hoshinota may be attracted to sites with high coral cover (Lin and Soong, 2009), specifically those with branching corals (Elliott et al., 2016), and is able to persist for long periods of time (Reimer et al., 2011b). Outbreaks of Terpios

hoshinota may be reversible and coral may be able to recover, but data are lacking to estimate the length of outbreaks (Reimer et al., 2011a).

These results suggest that using cover of macroalgae as a single category to evaluate reef degradation and not considering other potential indicator taxa (such as T. hoshinata or other sponges that can outcompete corals) could mask the impacts that human activities have on reefs. Percent cover of macroalgae is often used as a proxy for coral reef health (assuming sites with higher cover are more degraded, e.g. McCook et al. 1997; Mumby et al. 2005; Hughes et al. 2007), but other studies have also determined that macroalgae have limitations as an indicator of reef health. In Hawaii's uninhabited French Frigate Shoals, for example, Vroom et al. (2005) found that macroalgae cover was higher than that of coral at 46% of their study sites, with considerable heterogeneity across sites, even around the same island. A subsequent study indicated that macroalgae community composition was dependent on latitude (Vroom and Braun, 2010). There have also been studies identifying high macroalgae cover at undisturbed sites (e.g. Williams et al. 2013). While exposure to wind and waves was not a significant driver of macroalgae community composition across our sites, exposure has influenced the distribution of macroalgae genera in other places (e.g. Williams et al., 2013); this sensitivity to physical environmental conditions is another potential confounding factor further illustrating that macroalgae as a single category is not a suitable indicator of human disturbance to reefs.

The use of macroalgae as an indicator stems from evidence of phase shifts from coral to macroalgae dominance in the Caribbean (Hughes, 1994; Hughes et al., 2007), but other studies found little to no evidence of this in the Indo-Pacific (Bruno et al., 2009; Smith et al., 2016).

Instead, degraded reefs in the Pacific may see shifts to other taxa, including sponges (Bell et al., 2013; Norström et al., 2009; Powell et al., 2014) or "weedy" corals (Crane et al., 2016; Darling et al., 2013), with the outcomes varying by oceanographic conditions, local factors, and latitude. For example, in Yap, Federated States of Micronesia (FSM), researchers found that disturbed sites had low macroalgae cover (Crane et al., 2017). This is consistent with the results here, in which degraded sites were not dominated by macroalgae, but instead had high cover of sponges, cyanobacteria, and turf algae.

It may be more appropriate to use metrics like the taxon-specific cover of particular sponges like Terpios hoshinota, cyanobacteria and/or particular macroalgae taxa like Hypnea, rather than total macroalgae cover, to characterize reef degradation in the Pacific. One obstacle to developing such a metric will be accurate identification in the field. The increases in cyanobacteria and especially sponge cover between the past surveys and our 2016 surveys may, for example, be due to inconsistencies in identifying different taxa between the different research teams. The sponge Terpios hoshinota accounted for almost half of the sponges found in Majuro (48.10%), and it is notoriously hard to identify, particularly in photo quadrats, because it resembles cyanobacteria (Rutzler and Muzik, 1993).

We did not detect differences in benthic cover after the 2014 thermal stress event, likely because the event was least intense in the southern RMI. Despite a Level II Bleaching Alert from NOAA Coral Reef Watch for the whole of the RMI in 2014 (maximum DHW reached 11.71 °C·week, averaged across the region), Majuro and Arno did not experience severe heat stress (maximum DHW reached 4.03 – 5.55 °C·week at our sites). The comparison of 2014 pre-thermal stress

benthic cover data and our 2016 data suggest that any bleaching which may have occurred in 2014 had a limited effect on total coral cover. While bleaching did not appear to alter overall coral cover, it is possible that past disturbances such as bleaching or disease outbreaks may have caused some fragmentation, which would cause the size-frequency distributions to shift towards smaller corals (Buglass et al., 2014). Unfortunately, this could not be tested because the earlier data did not include size-frequency measurements.

A number of recent studies have emphasized the effectiveness of locally-run or citizen science coral reef monitoring programs (Forrester et al., 2015; Loerzel et al., 2017; Roelfsema et al., 2016; Schläppy et al., 2017; Stuart-Smith et al., 2017). However, these programs commonly use broad categories such as "hard coral", "soft coral", "macroalgae", or other (e.g. Hill 2006). Our results suggest such programs would be more effective if they included training and identification of common coral and macroalgae genera (e.g. Roelfsema et al., 2016), as well as more difficult organisms to identify such as Terpios hoshinota. Including these categories would provide managers and researchers alike with a more complete picture of the current state of coral reefs in the Indo-Pacific.

## 5. Conclusion

This study identifies a relationship between local human disturbance, exposure, and the benthic community composition and coral size structure in reefs across Majuro and Arno Atolls. Degraded sites were dominated by turf algae, cyanobacteria, and sponges (particularly Terpios hoshinota) and in general had low cover of macroalgae. We also found variation in which genera of macroalgae were found at disturbed sites. Hypnea was statistically correlated with high

disturbance, while Halimeda was more likely to be found at sites with low disturbance, independent of the exposure to wind and waves. More research is needed from other parts of the Indo-Pacific to further test the hypothesis that different taxa of macroalgae respond differentially to human impacts. Our results illustrate that the commonly-used metric total macroalgae cover may be a misleading indicator of the level of disturbance experienced by reefs. It is important for researchers and monitoring teams in the Pacific to use sampling protocols that identify coral and macroalgae to the genus level, and to consider identifying other indicator taxa that are commonly found on degraded reefs, such as the encrusting sponge Terpios hoshinota.

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**Supplement 1. Coral size data by coral category for each atoll.**
Includes number of colonies (n), mean size in centimeter (μ), standard deviation (sd), coefficient

of variation (cv), skewness (sk), and kurtosis (k). The skewness and kurtosis values that are

significantly different from normal are underlined.

| | | Acropora | Favids | Heliopora | Isopora | Montipora | Pocillopora | Massive Porites | Porites rus |
|---|---|---|---|---|---|---|---|---|---|
| **Arno Atoll** | n | 543 | 754 | 367 | 493 | 26 | 126 | 1755 | 119 |
| | μ | 7.9 | 7.5 | 10.7 | 17.9 | 11.9 | 10.2 | 15.3 | 33.5 |
| | sd | 54.7 | 7.8 | 14.0 | 21.8 | 6.9 | 9.5 | 20.3 | 43.9 |
| | cv | 688.2 | 103.4 | 131.0 | 121.8 | 58.1 | 93.0 | 133.3 | 131.1 |
| | sk | 16.4 | 7.3 | 3.2 | 2.6 | 1.9 | 1.9 | 3.9 | 2.3 |
| | k | 268.0 | 87.3 | 12.6 | 8.2 | 0.5 | 3.4 | 29.4 | 5.6 |
| **Majuro Atoll** | n | 839 | 288 | 259 | 66 | 49 | 243 | 132 | 300 |
| | μ | 21.3 | 9.6 | 12.3 | 11.6 | 16.0 | 11.7 | 17.5 | 23.1 |
| | sd | 46.5 | 6.3 | 13.4 | 7.6 | 9.4 | 8.9 | 25.8 | 76.2 |
| | cv | 218.6 | 65.8 | 109.4 | 54.3 | 59.1 | 75.7 | 147.7 | 329.3 |
| | sk | 5.0 | 1.3 | 2.0 | 1.6 | 1.4 | 1.6 | 3.4 | 12.1 |
| | k | 30.8 | 1.3 | 3.9 | 3.3 | 3.6 | 2.8 | 11.7 | 170.9 |
| **All** | n | 1382 | 1042 | 626 | 559 | 75 | 369 | 1887 | 419 |
| | μ | 16.0 | 8.1 | 11.3 | 17.2 | 14.6 | 11.2 | 15.4 | 16.1 |
| | sd | 50.3 | 7.5 | 13.8 | 20.8 | 8.8 | 9.1 | 20.8 | 68.7 |
| | cv | 313.4 | 92.1 | 121.5 | 120.9 | 60.5 | 81.3 | 134.8 | 263.4 |
| | sk | 10.6 | 6.1 | 2.7 | 2.7 | 1.5 | 1.7 | 3.8 | 11.8 |
| | k | 155.2 | 73.4 | 9.0 | 9.4 | 3.6 | 2.9 | 27.1 | 182.7 |

**Supplement 2.      Size frequency of key coral taxa by atoll.**
Boxplot and mean colony size (white dots) for the dominant hard coral taxa at each atoll, with n-

values specified above the x-axes.
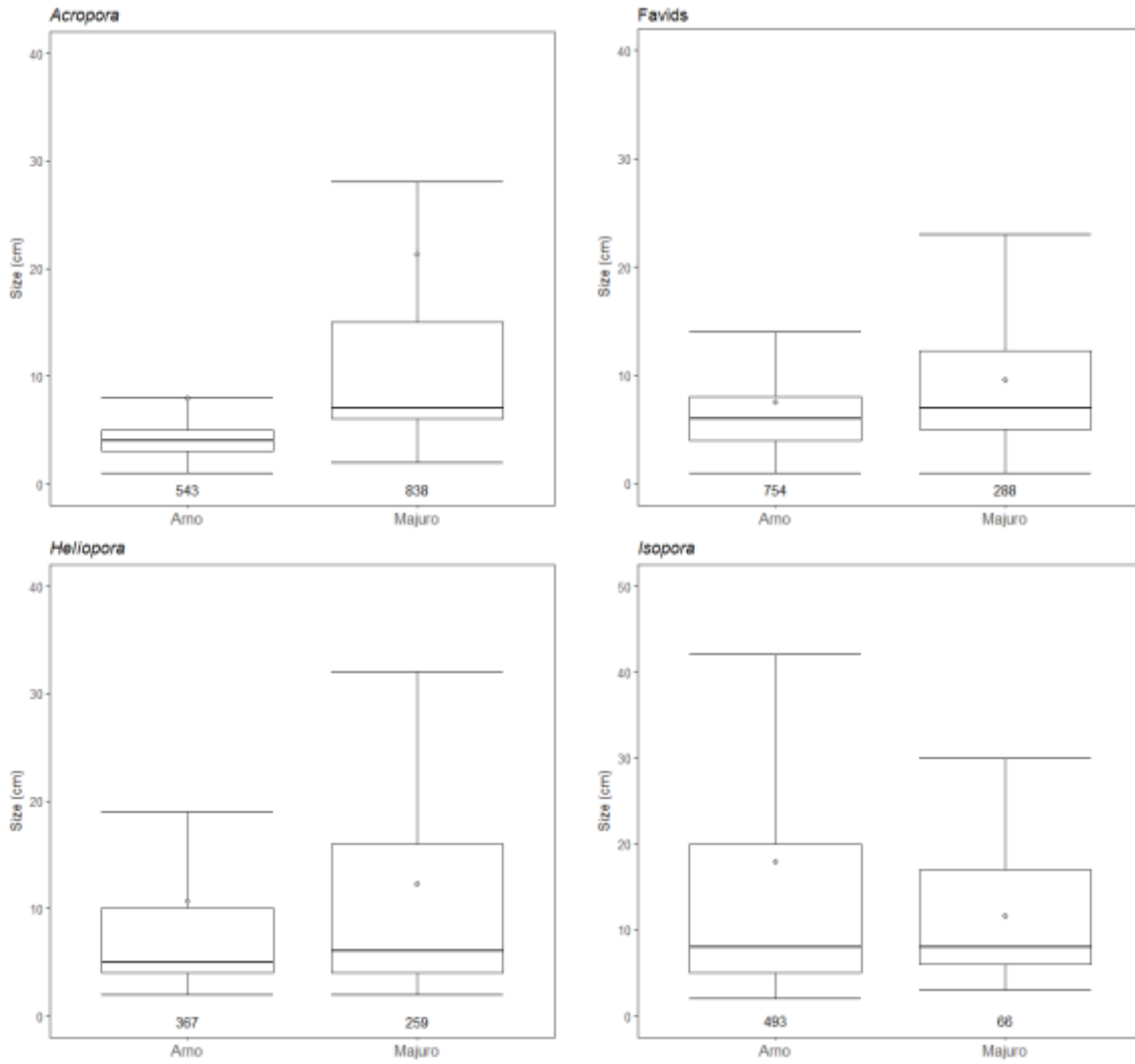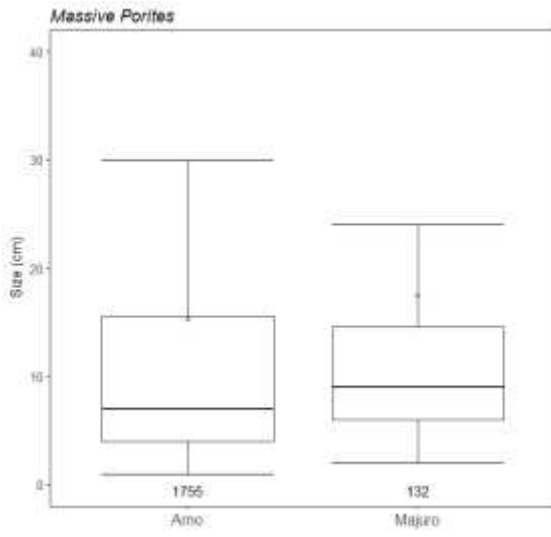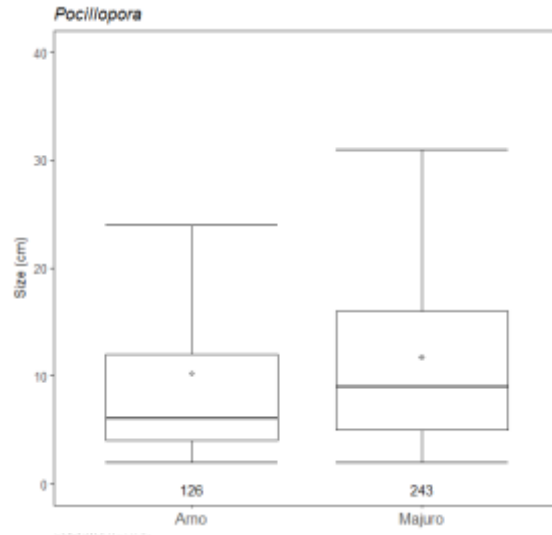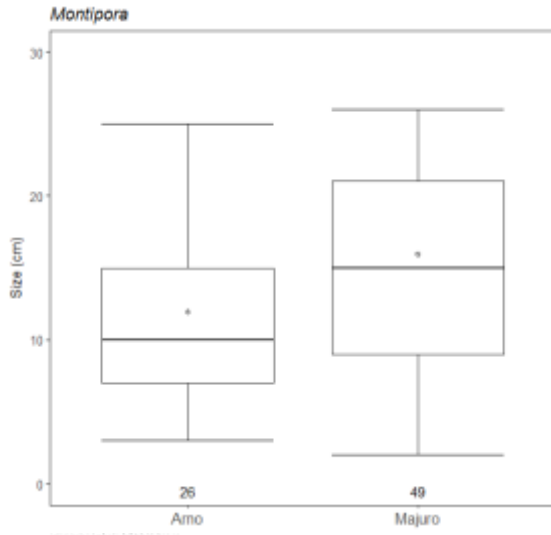
**Supplement 3.**        **Coral size frequency values by site.**

Summary of colony size data collected for each key coral taxonomic categories at each site,

including number of colonies (n), mean size in centimeters (mean), standard deviation (sd),

coefficient of variation (cv), skewness (sk), and kurtosis (k). The skewness and kurtosis values

that are significantly different from normal are underlined.

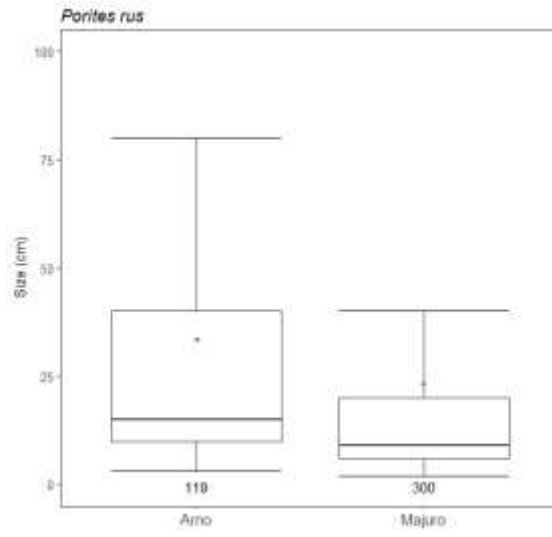| | category | n | mean | sd | cv | sk | k |
|---|---|---|---|---|---|---|---|
| **Arn01** | Acropora | 19 | 4.4 | 1.6 | 37.5 | 2.3 | 7.7 |
| | Favids | 34 | 6.1 | 5.8 | 95.6 | 4.2 | 19.5 |
| | Heliopora | 43 | 11.3 | 10 | 88.3 | 1.1 | -0.1 |
| | Isopora | 31 | 16.4 | 20.9 | 127.3 | 2.7 | 8.3 |
| | Pocillopora | 15 | 14.4 | 11.5 | 79.7 | 0.9 | -0.1 |
| | Massive Porites | 246 | 12.8 | 16.3 | 127.6 | 3.1 | 12.2 |
| | category | n | mean | sd | cv | sk | k |
| **Arn02** | Acropora | 29 | 5.0 | 2.3 | 45 | 0.0 | -0.3 |
| | Favids | 68 | 9.0 | 9.1 | 101.6 | 3.5 | 15.6 |
| | Heliopora | 2 | 25.0 | 14.1 | 56.6 | 0.0 | 0.0 |
| | Isopora | 23 | 25.0 | 20.1 | 80.2 | 0.7 | -0.8 |
| | Montipora | 6 | 7.5 | 4.4 | 58.9 | 1.0 | 0.7 |
| | Pocillopora | 9 | 13.0 | 11.6 | 89.0 | 1.4 | 0.4 |
| | Massive Porites | 52 | 20.7 | 34.2 | 165.0 | 3.3 | 12.2 |
| | category | n | mean | sd | cv | sk | k |
| **Arn03** | Acropora | 47 | 3.4 | 1.2 | 35.2 | 0.7 | 0.2 |
| | Favids | 47 | 10.5 | 13.8 | 131.6 | 3.1 | 9.1 |
| | Isopora | 11 | 24.1 | 16.8 | 69.8 | 1.1 | 0.6 |
| | Pocillopora | 3 | 8.3 | 1.5 | 18.3 | 0.9 | 0.0 |
| | Massive Porites | 75 | 14.5 | 16.7 | 115.3 | 2.5 | 6.6 |

| | category | n | mean | sd | cv | sk | k |
|---|---|---|---|---|---|---|---|
| **Arn04** | Acropora | 47 | 3.4 | 1.3 | 38.9 | <u>3.2</u> | <u>14.0</u> |
| | Favids | 50 | 3.7 | 1.6 | 44.4 | 0.8 | 0.6 |
| | Heliopora | 4 | 6.0 | 3.4 | 56.1 | 0.0 | -0.2 |
| | Isopora | 10 | 12.3 | 12.7 | 103.3 | 1.6 | 1.6 |
| | Montipora | 5 | 8.4 | 1.7 | 19.9 | -0.5 | -0.6 |
| | Pocillopora | 5 | 7.8 | 3.2 | 40.9 | 0.3 | -1.3 |
| | Massive Porites | 246 | 11.6 | 13.1 | 112.9 | <u>2.0</u> | <u>3.6</u> |
| | category | n | mean | sd | cv | sk | k |
| **Arn05** | Acropora | 19 | 6.3 | 4.8 | 76.5 | 2.0 | 3.5 |
| | Favids | 40 | 7.0 | 5.2 | 74.3 | <u>2.2</u> | <u>5.1</u> |
| | Heliopora | 48 | 19.0 | 19.0 | 99.9 | <u>1.4</u> | 1.5 |
| | Isopora | 11 | 26.6 | 16.9 | 69.4 | 0.5 | 0.2 |
| | Montipora | 1 | 7.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Pocillopora | 5 | 14.2 | 10.7 | 75.3 | 0.9 | -0.6 |
| | Massive Porites | 252 | 11.8 | 15.3 | 129.2 | <u>3.5</u> | <u>17.7</u> |
| | category | n | mean | sd | cv | sk | k |
| **Arn06** | Acropora | 32 | 61.2 | 221.4 | 362.1 | <u>3.8</u> | <u>13.2</u> |
| | Favids | 21 | 4.6 | 5.0 | 108.4 | 2.1 | 4.0 |
| | Isopora | 77 | 15.4 | 18.0 | 117.1 | <u>2.6</u> | <u>6.6</u> |
| | Pocillopora | 15 | 11.3 | 5.9 | 51.6 | 0.3 | -1.3 |
| | Massive Porites | 55 | 20.1 | 24.6 | 122.6 | <u>1.5</u> | 1.5 |
| | category | n | mean | sd | cv | sk | k |
| **Arn07** | Acropora | 16 | 4.0 | 1.7 | 42.8 | 0.8 | 0.3 |
| | Favids | 33 | 5.8 | 3.3 | 56.3 | <u>2.8</u> | <u>10.5</u> |
| | Heliopora | 27 | 24.7 | 25.9 | 104.7 | 1.5 | 1.7 |
| | Isopora | 118 | 10.5 | 11.7 | 111.0 | <u>2.8</u> | <u>8.1</u> |
| | Montipora | 2 | 20.0 | 14.1 | 70.7 | 0.0 | 0.0 |
| | Pocillopora | 5 | 16.8 | 20.0 | 118.9 | 1.6 | 2.3 |
| | Branching Porites | 202 | 10.0 | 11.0 | 109.6 | <u>4.7</u> | <u>29.1</u> |
| | Massive Porites | 95 | 22.0 | 24.9 | 113.4 | <u>1.9</u> | <u>3.3</u> |

| | category | n | mean | sd | cv | sk | k |
|---|---|---|---|---|---|---|---|
| **Arn08** | Acropora | 87 | 4.5 | 2.6 | 57.5 | <u>4.7</u> | <u>30.7</u> |
| | Favids | 35 | 5.7 | 2.4 | 42.2 | 0.7 | -0.8 |
| | Isopora | 50 | 34.3 | 39.2 | 114.2 | <u>1.5</u> | 1.5 |
| | Pocillopora | 14 | 15.9 | 11.9 | 74.7 | 0.9 | -0.3 |
| | Massive Porites | 42 | 9.9 | 11.7 | 118.3 | <u>2.4</u> | <u>5.5</u> |
| | Porites rus | 119 | 33.5 | 43.9 | 131.1 | <u>2.3</u> | <u>5.6</u> |
| | category | n | mean | sd | cv | sk | k |
| **Arn09** | Acropora | 55 | 5.4 | 3.2 | 59.2 | <u>3.3</u> | <u>15.8</u> |
| | Favids | 110 | 7.6 | 4.3 | 56.6 | <u>1.9</u> | <u>6.2</u> |
| | Heliopora | 4 | 16.3 | 13.2 | 81.1 | 0.1 | -5.2 |
| | Isopora | 29 | 14.8 | 14.5 | 97.9 | 1.3 | 0.4 |
| | Montipora | 1 | 11.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Pocillopora | 17 | 4.6 | 1.3 | 28.9 | 0.9 | 2.1 |
| | Massive Porites | 297 | 16.8 | 20.3 | 120.5 | <u>2.2</u> | <u>6.1</u> |
| | category | n | mean | sd | cv | sk | k |
| **Arn10** | Acropora | 65 | 4.5 | 1.9 | 42.4 | <u>1.6</u> | <u>3.4</u> |
| | Favids | 46 | 6.7 | 3.6 | 53.4 | <u>1.5</u> | 2.1 |
| | Heliopora | 21 | 4.2 | 0.7 | 17.9 | -0.3 | 4.1 |
| | Isopora | 6 | 23.2 | 26.7 | 115.3 | 2.0 | 4.0 |
| | Montipora | 1 | 25.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Pocillopora | 2 | 6.0 | 1.4 | 23.6 | 0.0 | 0.0 |
| | Massive Porites | 81 | 23.8 | 24.2 | 101.7 | <u>1.2</u> | 0.4 |
| | category | n | mean | sd | cv | sk | k |
| **Arn11** | Acropora | 54 | 5.8 | 3.5 | 61.5 | <u>3.3</u> | <u>16.0</u> |
| | Favids | 111 | 10.0 | 13.2 | 131.3 | <u>6.9</u> | <u>59.5</u> |
| | Heliopora | 67 | 8.9 | 9.6 | 107.8 | <u>3.7</u> | <u>17.9</u> |
| | Isopora | 33 | 19.1 | 27.3 | 142.7 | <u>2.7</u> | <u>7.6</u> |
| | Montipora | 9 | 14.6 | 6.3 | 43.1 | -0.1 | -1.9 |
| | Pocillopora | 25 | 8.2 | 8.4 | 102.0 | <u>2.3</u> | <u>5.0</u> |
| | Massive Porites | 132 | 21.1 | 33.3 | 157.9 | <u>5.2</u> | <u>37.8</u> |

| | category | n | mean | sd | cv | sk | k |
|---|---|---|---|---|---|---|---|
| **Arn12** | Acropora | 34 | 3.8 | 1.6 | 42.0 | 0.9 | -0.3 |
| | Favids | 18 | 4.4 | 1.9 | 41.7 | 0.1 | -0.9 |
| | Heliopora | 101 | 4.8 | 3.0 | 62.5 | 2.2 | 6.9 |
| | Pocillopora | 9 | 4.0 | 1.0 | 25.0 | 1.0 | 0.8 |
| | Massive Porites | 24 | 5.1 | 4.2 | 82.4 | 4.3 | 20.1 |
| **Arn13** | category | n | mean | sd | cv | sk | k |
| | Acropora | 39 | 5.2 | 2.3 | 44.3 | 1.7 | 4.5 |
| | Favids | 141 | 7.6 | 5.0 | 66.1 | 2.9 | 12.7 |
| | Heliopora | 50 | 10.9 | 15.2 | 140.3 | 4.0 | 18.7 |
| | Isopora | 94 | 18.5 | 18.9 | 101.9 | 1.3 | 0.7 |
| | Montipora | 1 | 9.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Pocillopora | 2 | 5.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Massive Porites | 158 | 13.9 | 15.6 | 112.6 | 2.3 | 6.1 |
| **Maj01** | category | n | mean | sd | cv | sk | k |
| | Acropora | 64 | 20.9 | 50.0 | 239.6 | 3.4 | 10.5 |
| | Favids | 33 | 6.4 | 3.3 | 51.3 | 1.1 | 1.4 |
| | Heliopora | 4 | 6.3 | 6.5 | 104.0 | 2.0 | 4.0 |
| | Isopora | 2 | 16.0 | 12.7 | 79.5 | 0.0 | 0.0 |
| | Montipora | 3 | 8.3 | 10.1 | 121.4 | 1.7 | 0.0 |
| | Pocillopora | 14 | 8.5 | 4.3 | 50.5 | 0.3 | -1.4 |
| | Massive Porites | 3 | 10.0 | 4.4 | 43.6 | -1.6 | 0.0 |
| | Porites rus | 22 | 12.4 | 8.7 | 69.9 | 0.8 | 0.5 |
| **Maj02** | category | n | mean | sd | cv | sk | k |
| | Acropora | 29 | 9.9 | 13.0 | 130.9 | 3.5 | 12.8 |
| | Favids | 3 | 8.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Pocillopora | 13 | 21.3 | 15.4 | 72.2 | -0.2 | -1.9 |
| | Porites rus | 27 | 15.2 | 15.5 | 101.9 | 3.5 | 14.4 |
| **Maj03** | category | n | mean | sd | cv | sk | k |
| | Acropora | 86 | 26.7 | 48.6 | 181.8 | 3.3 | 11.0 |
| | Favids | 2 | 15.5 | 3.5 | 22.8 | 0.0 | 0.0 |
| | Montipora | 3 | 24.7 | 22.5 | 13.0 | 1.4 | 0.0 |
| | Pocillopora | 31 | 17.7 | 11.6 | 65.4 | 1.2 | 0.9 |
| | Porites rus | 107 | 19.7 | 33.9 | 172.4 | 4.6 | 24.6 |

| | category | n | mean | sd | cv | sk | k |
|---|---|---|---|---|---|---|---|
| **Maj04** | Acropora | 18 | 6.7 | 3.7 | 55.6 | 1.4 | 1.2 |
| | Favids | 31 | 7.9 | 3.7 | 46.7 | 1.1 | 1.2 |
| | Heliopora | 38 | 5.8 | 7.0 | 119.5 | 5.2 | 29.0 |
| | Isopora | 5 | 9.8 | 5.4 | 55.6 | 0.6 | -2.2 |
| | Montipora | 6 | 20.7 | 13.1 | 63.2 | 1.6 | 2.8 |
| | Pocillopora | 18 | 6.0 | 3.1 | 51.1 | 0.9 | 0.1 |
| | Massive Porites | 27 | 19.9 | 32.8 | 165.4 | 3.0 | 8.6 |
| | category | n | mean | sd | cv | sk | k |
| **Maj05** | Acropora | 213 | 14.9 | 18.0 | 121.1 | 4.0 | 20.6 |
| | Favids | 10 | 21.3 | 8.1 | 37.8 | -0.3 | 0.7 |
| | Heliopora | 21 | 4.8 | 3.5 | 73.3 | 4.6 | 21.0 |
| | Isopora | 12 | 15.8 | 8.6 | 54.1 | -0.1 | -1.0 |
| | Montipora | 2 | 13.5 | 13.4 | 99.5 | 0.0 | 0.0 |
| | Pocillopora | 31 | 15.6 | 6.9 | 44.6 | 0.2 | 0.0 |
| | category | n | mean | sd | cv | sk | k |
| **Maj06** | Acropora | 84 | 66.0 | 93.5 | 141.8 | 2.3 | 6.1 |
| | Favids | 2 | 2.5 | 0.7 | 28.3 | 0.0 | 0.0 |
| | Isopora | 7 | 7.7 | 4.4 | 56.9 | 2.0 | 4.3 |
| | Pocillopora | 6 | 20.2 | 4.6 | 22.7 | 0.3 | -2.1 |
| | Massive Porites | 7 | 7.7 | 6.2 | 80.5 | 2.1 | 4.7 |
| | Porites rus | 32 | 12.3 | 13.4 | 108.4 | 2.4 | 5.5 |
| | category | n | mean | sd | cv | sk | k |
| **Maj07** | Acropora | 69 | 7.4 | 6.1 | 82.3 | 6.3 | 46.9 |
| | Favids | 34 | 9.2 | 4.6 | 50.3 | 1.5 | 2.9 |
| | Heliopora | 37 | 10.0 | 10.4 | 104.1 | 1.9 | 3.4 |
| | Isopora | 16 | 12.2 | 9.4 | 77.2 | 2.6 | 7.9 |
| | Montipora | 11 | 16.0 | 6.6 | 41.2 | -0.6 | -0.8 |
| | Pocillopora | 27 | 9.3 | 9.2 | 98.2 | 2.5 | 7.2 |
| | Massive Porites | 47 | 13.3 | 15.1 | 113.5 | 2.9 | 9.4 |

| | category | n | mean | sd | cv | sk | k |
|---|---|---|---|---|---|---|---|
| **Maj08** | Acropora | 79 | 7.6 | 4.5 | 59.6 | 1.9 | 4.5 |
| | Favids | 22 | 9.6 | 5.3 | 55.3 | 0.9 | 0.4 |
| | Heliopora | 159 | 15.5 | 15.0 | 97.0 | 1.6 | 2.2 |
| | Isopora | 2 | 6.5 | 0.7 | 10.9 | 0.0 | 0.0 |
| | Montipora | 2 | 7.0 | 1.4 | 20.2 | 0.0 | 0.0 |
| | Pocillopora | 25 | 9.1 | 7.5 | 82.2 | 2.2 | 5.5 |
| | Massive Porites | 20 | 26.6 | 28.0 | 105.2 | 2.0 | 4.2 |
| | Porites rus | 7 | 25.3 | 19.5 | 77.0 | 2.1 | 4.8 |
| | category | n | mean | sd | cv | sk | k |
| **Maj09** | Acropora | 162 | 22.9 | 51.7 | 225.9 | 4.6 | 22.5 |
| | Favids | 81 | 10.0 | 6.6 | 66.4 | 1.1 | 0.3 |
| | Isopora | 13 | 9.8 | 6.0 | 61.9 | 1.2 | 0.5 |
| | Montipora | 11 | 15.5 | 6.6 | 42.3 | 0.3 | -1.0 |
| | Pocillopora | 50 | 9.5 | 5.4 | 56.4 | 0.9 | 0.2 |
| | Massive Porites | 14 | 18.8 | 33.9 | 180.6 | 3.6 | 13.0 |
| | Porites rus | 1 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | category | n | mean | sd | cv | sk | k |
| **Maj10** | Acropora | 28 | 8.9 | 4.0 | 45.3 | 0.7 | -0.6 |
| | Favids | 70 | 10 | 6.9 | 68.9 | 1.1 | 0.2 |
| | Isopora | 9 | 11.9 | 6.1 | 51.2 | 0.9 | -0.7 |
| | Montipora | 11 | 15.5 | 6.6 | 42.3 | 0.3 | -1.0 |
| | Pocillopora | 28 | 8.4 | 4.1 | 49.5 | 0.9 | 0.6 |
| | Massive Porites | 14 | 18.8 | 33.9 | 180.6 | 3.6 | 13.0 |
| | category | n | mean | sd | cv | sk | k |
| **Maj11** | Acropora | 7 | 6.6 | 2.8 | 42.9 | 0.0 | -1.0 |
| | Branching Porites | 103 | 8.5 | 11.8 | 138.9 | 4.8 | 27.4 |
| | Porites rus | 104 | 34.4 | 123.7 | 359.3 | 7.9 | 69.3 |

**Supplement 4.** **Benthic cover in Majuro Atoll in 2014 and 2016 surveys. Significant results are underlined.**

| | variable | t | df | p-value | Bonferroni correction | mean 2014 | mean 2016 |
|---|---|---|---|---|---|---|---|
| **key taxa** | Live coral | 0.50 | 9.52 | 0.63 | 1.00 | 33.35% | 27.32% |
| | CCA | 1.23 | 7.15 | 0.26 | 1.00 | 6.50% | 2.80% |
| | Dead Coral | 1.14 | 8.31 | 0.28 | 1.00 | 34.80% | 24.74% |
| | Cyanobacteria | -2.11 | 5.01 | 0.09 | 0.81 | 0.21% | 8.56% |
| | Macroalgae | 0.31 | 9.19 | 0.76 | 1.00 | 11.67% | 14.87% |
| | Sponges | -3.18 | 5.04 | <u>0.02</u> | <u>0.18</u> | 0.19% | 9.55% |
| | Sand | 0.71 | 5.79 | 0.50 | 1.00 | 12.37% | 5.54% |
| | Rubble | -1.22 | 7.46 | 0.26 | 1.00 | 1.37% | 4.58% |
| | Soft coral | -1.41 | 5.00 | 0.22 | 1.00 | 0.00% | 0.08% |
| **coral taxa (% all benthos)** | Acropora | 0.08 | 10.00 | 0.93 | 1.00 | 16.90% | 15.88% |
| | Favids | -0.07 | 9.96 | 0.95 | 1.00 | 0.08% | 0.09% |
| | Heliopora | 0.78 | 5.45 | 0.47 | 1.00 | 0.60% | 0.17% |
| | Isopora | 1.02 | 5.79 | 0.35 | 1.00 | 0.38% | 0.11% |
| | Pavona | 4.84 | 6.37 | <u><0.01</u> | <u><0.01</u> | 2.01% | 0.25% |
| | Pocillopora | 1.14 | 5.56 | 0.30 | 1.00 | 2.03% | 0.71% |
| | Porites rus | 0.21 | 9.65 | 0.84 | 1.00 | 9.92% | 8.37% |
| | Massive Porites | -1.54 | 5.00 | 0.18 | 1.00 | 0.00% | 0.64% |
| **Coral taxa (% live coral)** | Acropora | -0.38 | 9.71 | 0.71 | 1.00 | 33.39% | 42.49% |
| | Favids | 0.45 | 7.49 | 0.67 | 1.00 | 1.91% | 1.17% |
| | Heliopora | 0.87 | 5.86 | 0.42 | 1.00 | 7.82% | 2.47% |
| | Isopora | 0.44 | 10.00 | 0.67 | 1.00 | 2.08% | 13.63% |
| | Pavona | 1.63 | 5.46 | 0.16 | 1.00 | 17.90% | 3.12% |
| | Pocillopora | 0.46 | 9.27 | 0.65 | 1.00 | 6.00% | 4.63% |
| | Porites rus | -0.00 | 9.17 | 1.00 | 1.00 | 0.00% | 9.46% |
| | Massive Porites | 1.03 | 5.35 | 0.35 | 1.00 | 6.29% | 16.05% |

**Supplement 5.** **Change in benthic cover in Arno Atoll since previous available surveys. Significant results are underlined.**

| variable | t | df | p-value | Bonferroni correction | mean 2007 | mean 2016 |
|---|---|---|---|---|---|---|
| Live coral | 0.07 | 9.55 | 0.95 | 1.00 | 31.17% | 30.54% |
| CCA | -1.60 | 9.10 | 0.14 | 1.00 | 4.78% | 7.98% |
| Dead Coral | -1.13 | 9.03 | 0.29 | 1.00 | 23.54% | 29.42% |
| Cyanobacteria | -4.17 | 5.00 | <u>0.01</u> | 0.08 | 0.00% | 6.31% |
| Macroalgae | -1.85 | 6.90 | 0.11 | 0.99 | 6.14% | 12.97% |
| Sponges | 2.64 | 5.06 | <u>0.04</u> | 0.36 | 0.07% | 0.46% |
| Sand | 0.79 | 6.44 | 0.46 | 1.00 | 1.97% | 6.82% |
| Rubble | -1.22 | 7.46 | 0.26 | 1.00 | 1.37% | 4.58% |
| Soft coral | 2.78 | 6.09 | <u>0.03</u> | 0.27 | 3.46% | 0.63% |