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

November 15, 2021

Prepared for
UNDP Marshall Islands Ridge to Reef
Project ID 00104152

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Executive Summary

This report analyses and summarises data collected from benthic surveys of Likiep Atoll in October 2020, and compares those results to benthic surveys collected in 2001, to provide data that will be integral for future monitoring and conservation efforts.

- Overall hard coral cover has declined for all reef types between 2001 and 2020, and the declines were particularly pronounced for *Acropora* species. In 2001, *Acropora* accounted for 42% of all coral cover in the lagoon and 21% of all coral cover on the ocean, but by 2021, these numbers had dropped to 27% in the lagoon and only 2% on the ocean. We are unaware of any major stressors that may have driven this change, although it is possible that reefs in Likiep experienced bleaching during the 2014-2017 global mass bleaching event. The genus *Acropora* is known to be sensitive to heat stress and is often considered one of the 'losing' taxa after bleaching events (Loya *et al.*, 2001; Van Woesik *et al.*, 2011).

- Sites on the ocean side were healthy, with a higher percent cover of hard coral (24.86%) and greater diversity (as measured by coral genera richness, 14.33) on average than sites in the lagoon. Ocean sites were categorized by high percent cover of massive *Porites* and *Stylophora*, CCA, and *Halimeda*.

- Lagoon sites had low coral cover overall (6.02%) and low genera richness on average (6.71) when compared to ocean sites. Lagoon sites were characterized by high percentages of blue-green algae/cyanobacteria and sand.

- Scientists have estimated that coral reefs must have at least 10% cover of hard corals in order to keep up with future sea level rise (Perry *et al.*, 2015). All but one of the sites on the ocean side met this threshold, while only one of the sites in the lagoon (the MPA site) had more than 10% total coral cover.

- The low diversity of corals at lagoon sites, coupled with the lower percent cover of hard coral overall, may mean that sites within the lagoon are less resilient to future stressors than sites on the ocean.

- The MPA site had the highest prevalence of hard coral of all the lagoon sites (12.41%), almost all of which was *Acropora* (Fig. 6). This site also had low genera diversity (4), which may make it vulnerable to future disturbances. However, this site could be a good source of *Acropora* for a potential future coral gardening project, which may help to restore *Acropora* populations on other sites across the atoll. Because *Acropora* is density dependent, populations may not recover on their own without a nearby source of larvae.

- Fish surveys conducted concurrently (October 2020) found that sites in the lagoon had lower fish biomass than sites on the ocean, and recommended that management focus on lagoon fisheries.

These data informed the **following recommendations for marine resource managers, local leadership, and communities in Likiep:**

- 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 greenhouse gas emissions locally, will be integral to ensuring a future for coral reefs as the climate warms, in the Marshall Islands and elsewhere.

- Establishing or improving current protected areas with the goal of limiting fishing in the lagoon may help increase fish biomass. Importantly, as noted by Pinca et al. (2001), effective management must be led by the communities in Likiep, and they should also be responsible for enforcement. Rotated closures could be a way to ensure that the citizens of Likiep are able to access fishing grounds while giving reef fish populations a chance to recover. Gear restrictions may also be effective (for example, limiting the use of throw nets that target small herbivorous fish).

- Coral gardening for *Acropora* may be possible at the MPA site, where *Acropora* cover was comparatively high and the benthic communities appeared healthier than other lagoon sites. This would provide juvenile *Acropora* that could be transplanted at other sites around the atoll, potentially facilitating the recovery of *Acropora* populations atoll-wide (although their long-term survival may depend on future stressors, such as bleaching events).

- Water quality tests would help assess whether water quality within the lagoon is degraded by pollution from land. In the meantime, communities in Likiep could take steps to limit pollutants from entering the water, including solid waste and wastewater from households and agriculture. This is important on both the lagoon and ocean sides, but may be especially integral on the lagoon side of the islands, because flushing rates in the lagoon are lower than in the ocean and nutrients and pollutants may accumulate over time.

- Communities in Likiep can also collect their own data to guide future decision making about how best to conserve local reefs and ensure that they still provide ecosystem services in the future. The Likiep Fisheries Management Advisory Committee recommended this as a part of the Fisheries Management Plan for Likiep (Likiep Atoll Local Government, 2006), but it is unclear whether the data were ever collected. 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, for example, this could be a place that might need to be temporarily closed for fishing.

- Communities in Likiep 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, when conditions allow), and estimating the percent-cover of certain taxa or coral morphologies. These data would 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 the percent cover of *Acropora* over time).

- Protecting the physical integrity of reefs in Likiep will be important to ensure that they continue to grow fast enough to keep up with rising sea levels, particularly in the lagoon where coral cover is low. Educational programs that describe the harms of damaging live coral colonies and rubble through acts like mining or anchoring will help to limit these activities and to keep coral reefs intact, while also possibly providing more substrate where corals 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 contribute to preserving the physical structure of coral reefs on Likiep.

- Finally, repeating these surveys of reefs in Likiep (every 3-5 years) will be important for further untangling the patterns observed in this report and the changes occurring over time, including the key drivers of the patterns documented in this report (for example, the low cover of *Acropora*).

Introduction

Likiep Atoll is composed of 65 islands and islets surrounding 164 square miles of lagoon, two of which – Likiep Likiep and Jebal – are home to the majority of its population. The eastward side of the atoll is the windward side, while the westward side is the leeward side (Pinca *et al.*, 2001). The island is within the Ratak Chain (the eastern of the two island chains composing the RMI), and is about 81 miles (130 km) northeast of Wotje Atoll and 219 miles (353 km) north of Majuro Atoll, the nation's capital.

As of the last census in 2011, Likiep was home to 401 people, and the population had declined from the 1999 census, when 527 people lived on the island (Secretariat of the Pacific Community, 2012). The Government of the Marshall Islands' Economic Policy, Planning and Statistics Office (EPPSO) started collecting data for the 2021 census on August 23, 2021 (Johnson, 2021) and an updated population estimate will be available when the census report is released.

In October 2020, the Marshall Islands Conservation Society (MICS) traveled to Likiep to conduct benthic surveys of the coral reefs surrounding Likiep Atoll, visiting 14 sites total, seven on the ocean side and seven on the lagoon side (Fig. 1). The MICS team conducted benthic surveys and fish surveys at all sites except L-OS-3, where they only collected fish data because of local weather conditions. This report provides analysis of the benthic quadrat photos they collected in order to assess the overall health of coral reef communities around Likiep Atoll. Previous surveys from Likiep provide us with a snapshot of what coral reefs around the atoll were like in 2001 (Pinca *et al.*, 2001), which allows us to also investigate whether the benthic communities have changed in the last decade.

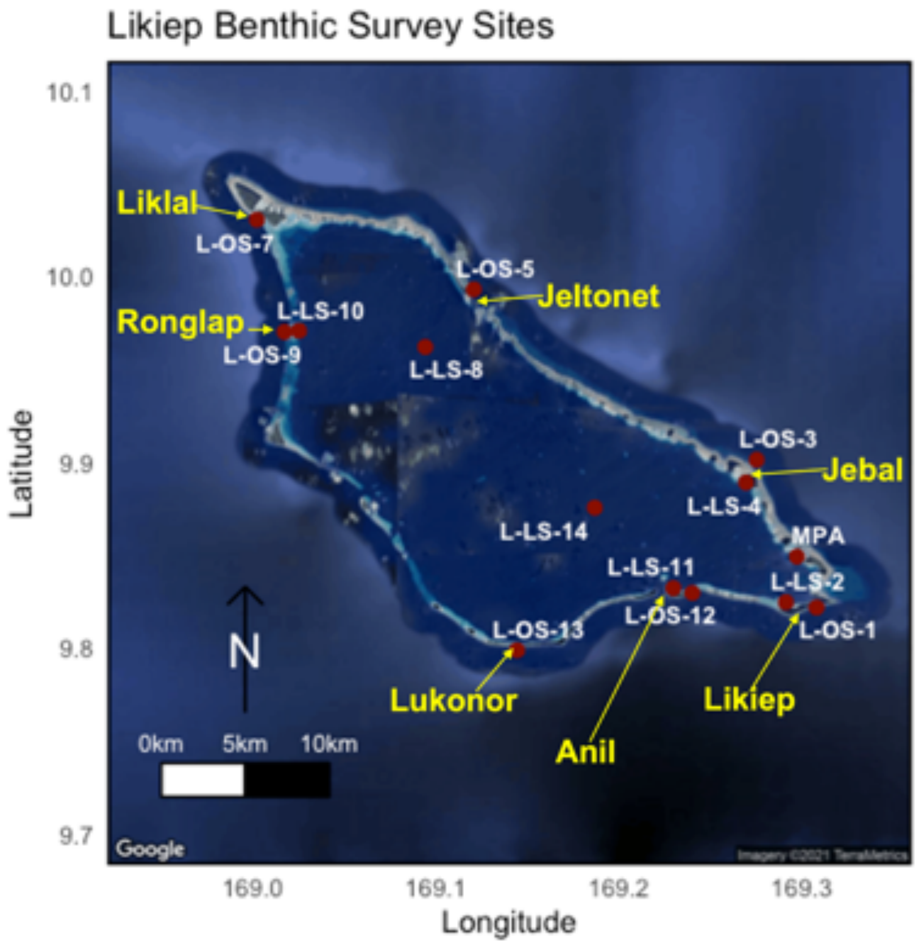

Fig. 1. 2021 survey sites from Likiep Atoll. Benthic survey data were collected at all sites except L-OS-3, where only fish surveys were done due to local conditions.

The previous surveys from Likiep Atoll provide some indication of local threats to reefs, although the authors found that the health of coral reefs in Likiep was 'quite good'. The threats facing reefs at the time of previous surveys (2001) were minimal, and were all related to subsistence and small-scale fisheries. It is possible that these local threats may have declined over time in correlation with the declining local population (although it remains to be seen if the population continued to decline since the most recent census in 2011). However, fishing pressure may be decoupled from the local population size due to external markets for reef fish. When Pinca et al. visited Likiep to conduct reef surveys, they also conducted interviews with local fishers, and their findings suggest that this may have been the case locally; the authors mentioned that improved access to communication technology may have increased fishing pressure around Likiep because local fishermen were able to sell their catches to outer markets. Of the 20 fishermen interviewed by Pinca et al (2001), five stated that they sold over half of their catches to outer markets in Majuro and Ebeye. This is consistent with recent research showing how reef fisheries in the Marshall Islands have shifted from subsistence-only fisheries to small-scale commercial fisheries over time (Vianna *et al.*, 2020). However, the majority of fish caught in Likiep were kept for local consumption (Pinca *et al.*, 2001).

The 2001 report ended with recommendations for the future management of marine resources around Likiep Atoll, including the establishment of protected areas (alongside efforts to educate students and local communities on the importance of coral reefs and the resources they provide; educating local people in how to manage resources based on both traditional and scientific methods; enforce local legislation regulating marine resource use through local people; and, finally, to institute a routine assessment plan to monitor the state of coral reef ecosystems on a regular basis).

These recommendations led to the creation of a Marine Protected Area (MPA), although it is unclear exactly when the protected area was established and what its boundaries are. The surveys from 2001 showed that the majority of fishers in Likiep were enthusiastic about establishing regulations on local fisheries, and in 2006, after several meetings and discussions, the Likiep Local Government created a Fisheries Management Plan, which limited access to local fishing sites to members of the Likiep community, and established a local Fisheries Management Advisory Committee that would draft future rules on fishing (Likiep Atoll Local Government, 2006). Some marine resource assessments were apparently conducted in 2003, including reef surveys and a survey of MPA(s), but we did not have access to those reports. We know that they exist because they were listed among the documents that were reviewed by the authors of the Republic of the Marshall Islands National Strategic Plan, 2015 - 2017 (EPPSO, 2014). Surveys of other marine resources have been conducted since 2001, including a survey of marine invertebrates in 2009 (Chapman, 2009).

Sites in Likiep Atoll may have also faced non-local threats such as bleaching caused by rising global sea surface temperatures, and these threats were not discussed in the previous reports. For example, in 2014, coral reefs in parts of the Marshall Islands experienced the most severe bleaching event in their recorded history, and due to an extended central-Pacific type El Niño event, the Marshall Islands experienced higher-than-average sea surface temperatures intermittently 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).

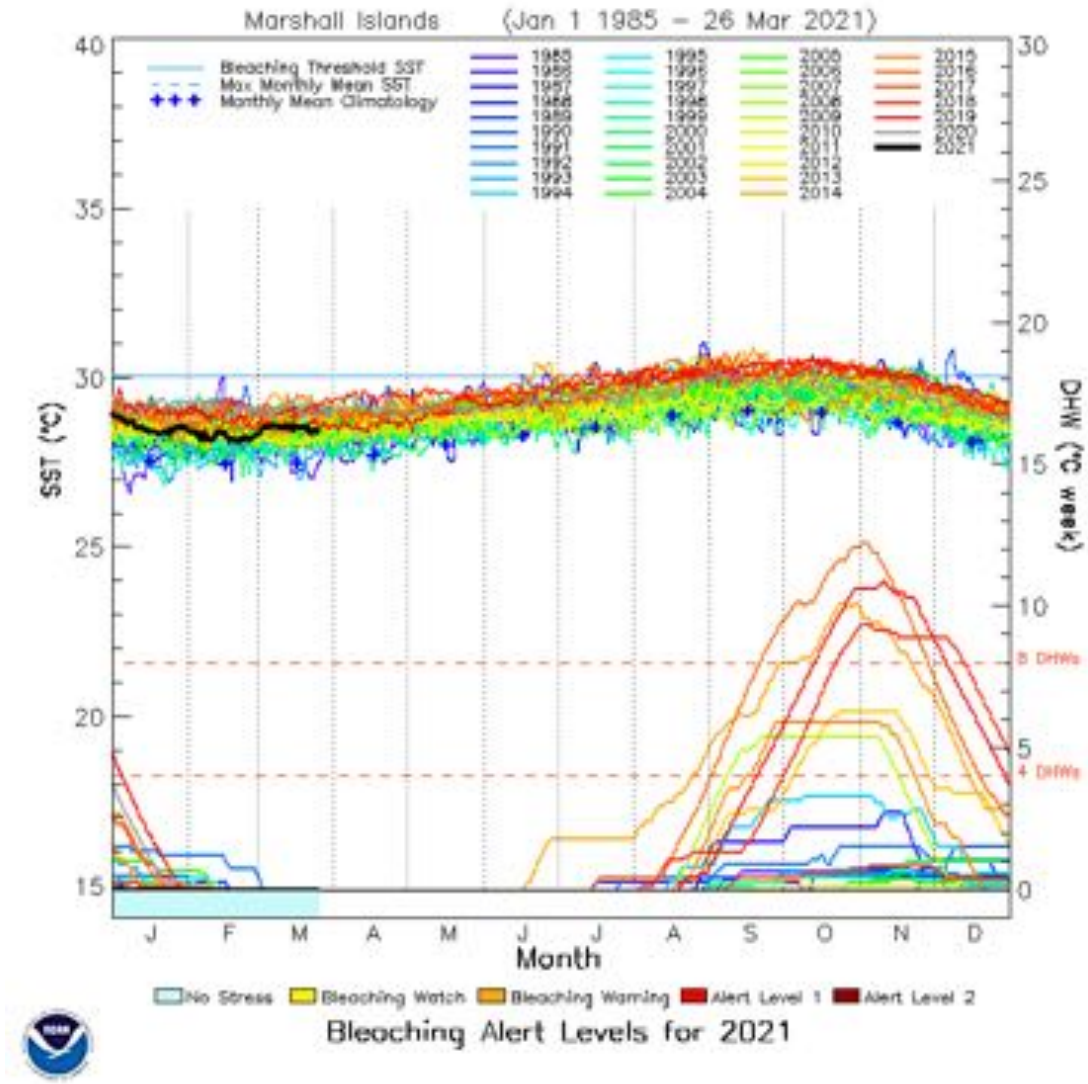

Fig. 2. Degree heating weeks and sea surface temperatures in Majuro Atoll, Republic of by the Marshall Islands, from 1985 - 2021 (NOAA Coral Reef Watch, 2019).

There were no reports of bleaching to my knowledge from Likiep specifically. Maps from the NOAA Coral Reef Watch program show that Likiep was exposed to alert-level bleaching in the past, but not for prolonged time periods as were experienced by reefs in the Ralak Chain (e.g. Fig. 3).

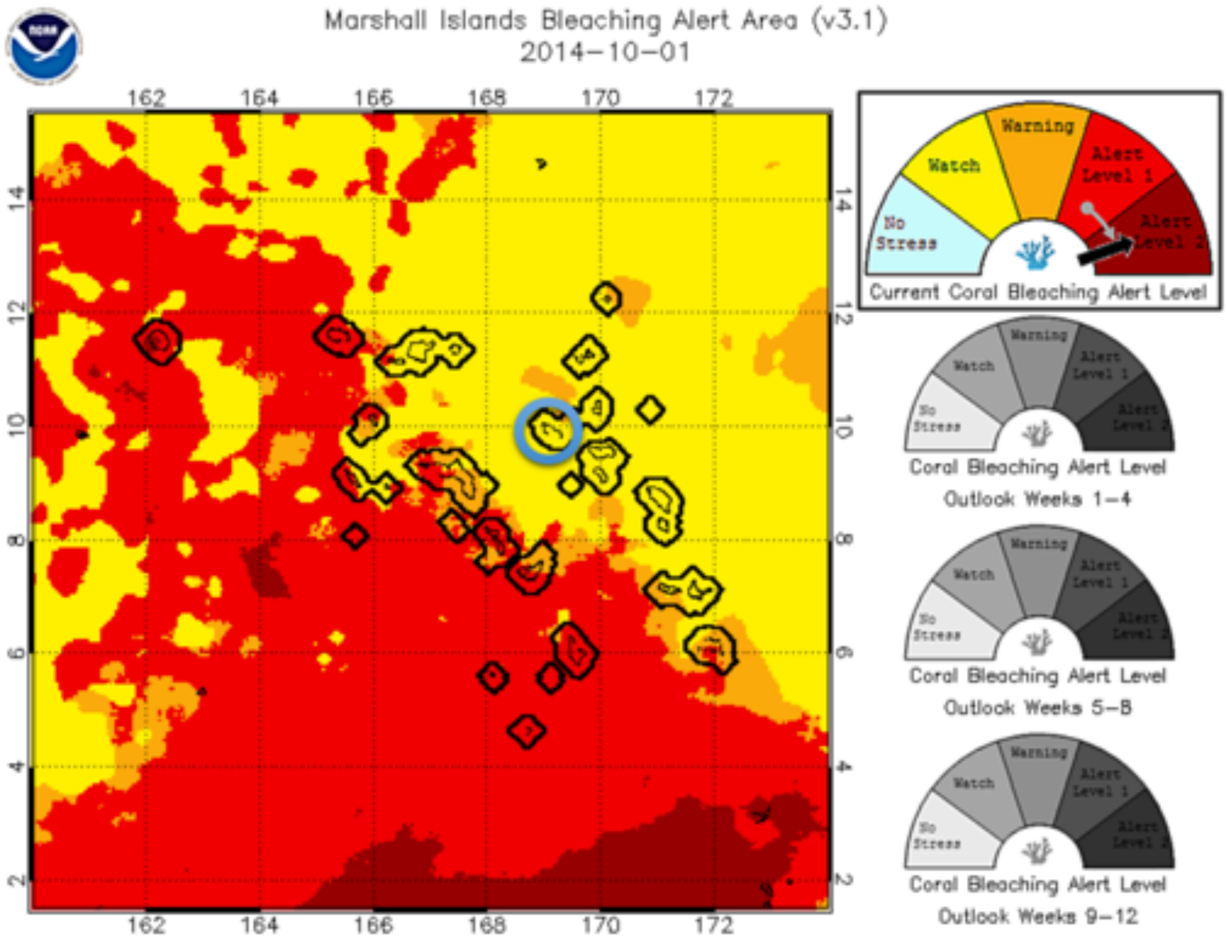

Fig 3. *Bleaching alert areas from NOAA's Coral Reef Watch on October 1, 2014 show that bleaching-level heat stress was most common in the Ratak (Western) Chain (NOAA Coral Reef Watch, 2019).*

Methods

Data Collection

Data were collected by the Marshall Islands Conservation Society (MICS) in October 2020 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. Sites surveyed in Likiep Atoll. Benthic data were collected at all sites except L-OS-3, where only fish surveys were done due to dangerous diving conditions.

Island	SiteID	Ocean/ Lagoon	Windward/ Leeward	Latitude	Longitude
Likiep	L-OS-1	Ocean	Leeward	9.821897	169.30804
Likiep	L-LS-2	Lagoon	Leeward	9.824764	169.291319
Jebal	*L-OS-3*	*Ocean*	*Windward*	*9.901389*	*169.2753*
Jebal	L-LS-4	Lagoon	Windward	9.889149	169.269459
Jeltonet	L-OS-5	Ocean	Windward	9.993056	169.1208
Liklal	L-OS-7	Ocean	Windward	10.03056	169.0022
Ronglap	L-OS-9	Ocean	Leeward	9.97025	169.0173
Ronglap	L-LS-10	Lagoon	Leeward	9.970833	169.0253
Anil	L-OS-12	Ocean	Leeward	9.82977	169.24014
Anil	L-LS-11	Lagoon	Leeward	9.83231	169.2298
Lukonor	L-OS-13	Ocean	Leeward	9.798889	169.1444
Pinnacle 1	L-LS-14	Lagoon	Windward	9.87561	169.18686
Pinnacle 2	L-LS-8	Lagoon	Windward	9.962099	169.09426
MPA	MPA	Lagoon	Windward	9.849228	169.297326

Data Analysis

Photo Identification

Staff from MICS processed the photos from the transects to calculate the benthic percent cover using Coral Point Count with Excel Extensions (CPCe) research software (Kohler and Gill, 2006), which overlaid 5 random points per photo for 200-250 photos per site total (between 30 - 50 photos per transect for 5 transects), which equates to 1,000-1,250 random points per site. Each point was manually identified to the genus level for hard coral (including the octocorals *Heliopora* and *Millepora*, because they are common in the region) and macroalgae, and to the functional group for sponges, soft corals, turf algae, crustose coralline algae, invertebrates, and cyanobacteria. MICS staff would normally also identify corals that were bleached to the genus level, but in this case, no bleaching was observed.

The categories and codes for benthic analyses were provided by Martin Romain, R2R Chief Technical Advisor. These codes have been used by MICS and MIMRA for previous analyses of coral reefs at different locations throughout the Marshall Islands (they are included in the supplementary materials, S1). Using consistent codes across sites in the Marshall Islands will allow local resource users to compare the results from these analyses to those from other atolls and/or time periods. The results from the analyses presented here have consolidated some of these codes for ease of interpretation, but in the future, higher resolution codes may allow more detailed analyses without requiring repeating the photo identification.

To allow comparisons to other data that used 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 (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 updates 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 4.0.3 (R Core Team, 2020) and R Studio for Desktop version 9.0.351 (RStudio Team, 2020). Plots were created using the R packages ggplot2 (Wickham, 2016, p. 201) and ggbiplot (Vu, 2011).

Descriptive statistics of the coral reefs at each site and for each of the key taxa were calculated, along with the Genera Richness (number of distinct genera) for hard coral at each site, as a way to estimate the diversity of hard corals; diversity metrics may be useful for estimating resilience to stressors, as more diverse reefs are broadly considered more resilient (Richards *et al.*, 2008).

Similarity Percentages (SIMPER) analysis is useful in that it calculates the contribution of each genera (by percent) to differences between two groups. Here, SIMPER (999 permutations) was used to analyze drivers of benthic community differences across the sites using the R vegan package (Oksanen *et al.*, 2019). There was no bleaching observed in these surveys.

The results from previous surveys were reported by pooling sites together (Pinca *et al.*, 2001) and comparing (1) lagoon vs. ocean sites, and (2) into four groups representing different exposure regimes: lagoon-leeward (LL), lagoon-windward (LW), ocean-leeward (OL), and ocean-windward (OW). We have preserved those groupings here to estimate changes in coral and algae cover over time as compared to the past report. The raw data from these past surveys were not available, so comparisons were done using percent cover values that were estimated visually from plots included in Pinca et al. (2001).

Results and Discussion

Overview

Collectively, sites in Likiep were dominated by turf algae, sand, and to a lesser extent, macroalgae and live coral (Table 2), although the overall cover of both of these groups varied across sites, especially in the case of sand (which ranged from <1% cover to almost 80% cover). The percent cover of sand in 2020 is consistent with what was reported in 2001, when the authors found that sand accounted for 30.42 ∓ 27.35% of benthic cover across all sites. Photos of the most common substrate types are shown in Fig. 4.

In 2001, the average live coral cover across all sites was 32.33 ∓ 20.58%, which, when compared to more recent surveys, suggests that coral cover has declined by more than 50% over the last decade. The standard deviation in past surveys was larger than from recent surveys, which could indicate that coral cover has become slightly more uniform across sites than it was previously.

Table 2. Percent cover of functional groups (including all sites) from 2020 surveys, sorted from the highest to lowest overall percent cover. Photos of the functional groups are in Fig. 3.

Functional Group	Mean Percent Cover	Median	Minimum	Maximum	Standard Deviation
Turf	30.28	26.43	11.33	48.37	16.03
Sand	25.29	18.99	0.08	78.45	27.35
Macroalgae	19.97	21.79	5.71	48.25	11.46
Live Coral	14.72	8.26	1.85	44.67	12.78
CCA	8.39	6.39	0.00	35.67	10.24
Other invertebrates	0.84	0.49	0.00	4.34	1.22
Other non-living/ unidentifiable	0.25	0.08	0.00	1.27	0.39
Branching coralline algae	0.02	0.00	0.00	0.16	0.05
Chrysophytes	0.01	0.00	0.00	0.08	0.02

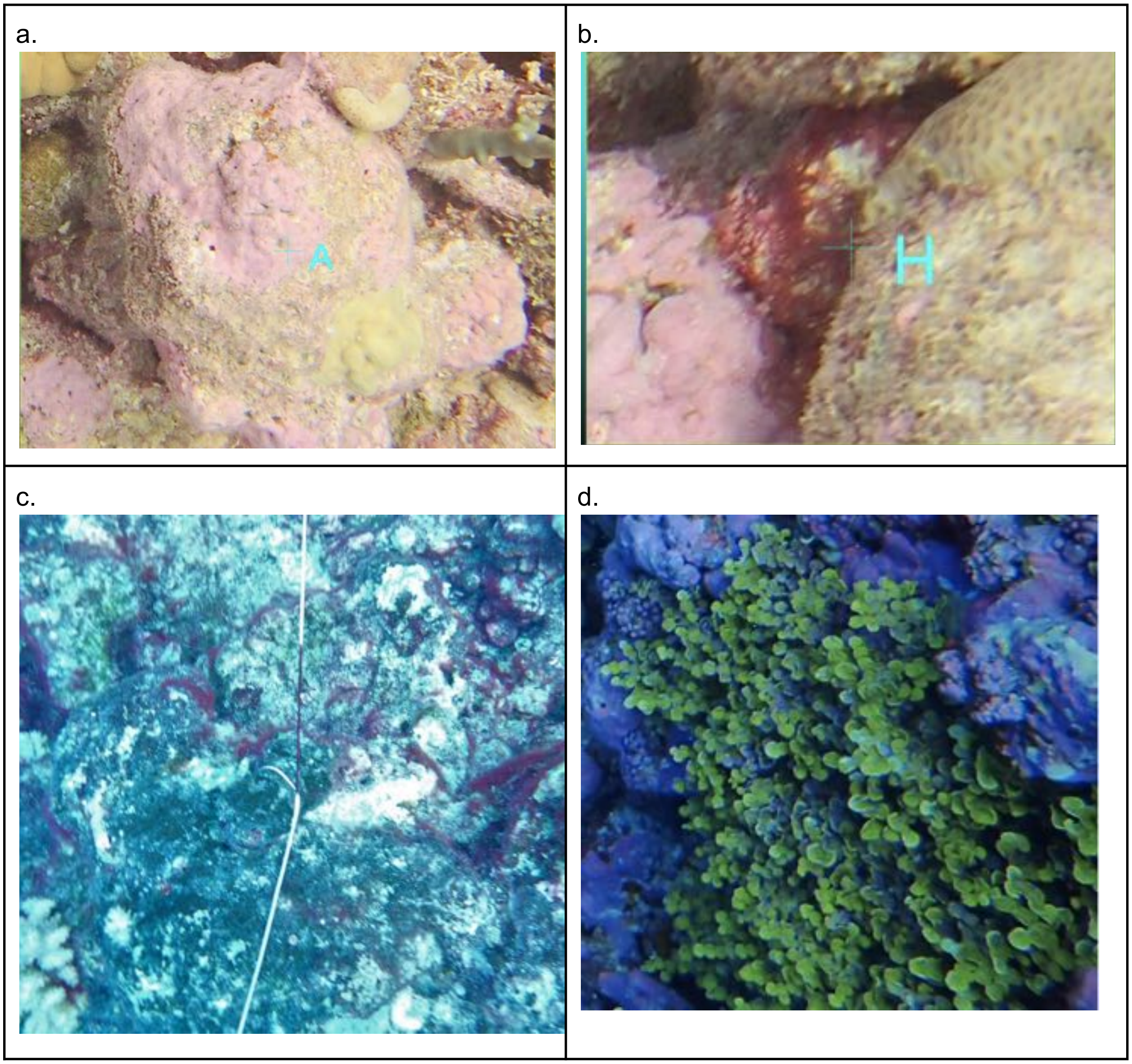

Fig. 4: *Most common benthic categories, including (a) CCA surrounded by turf algae, (b) fleshy coralline algae surrounded by CCA (left) and turf algae(right), (c) cyanobacteria (included in the category Macroalgae, Supplementary Materials S1), and (d) Halimeda, a genus of macroalgae that is associated with less human disturbance, surrounded by CCA.*

Benthic Communities by Site

The community compositions varied across sites (Fig. 5, table in S2). In general, the lagoon sites had lower coral cover and more macroalgae and sand than those on the ocean side. Four sites had coral cover that was over 20%, all of which were on the ocean side. Seven sites had hard coral cover below 10% (over half of the 13 sites surveyed); scientists have estimated that coral cover must remain above 10% for a reef to produce enough carbonate to withstand erosion and keep up with sea level rise (Perry *et al.*, 2015). All but one of the sites with coral cover below 10% were in the lagoon (Table 3).

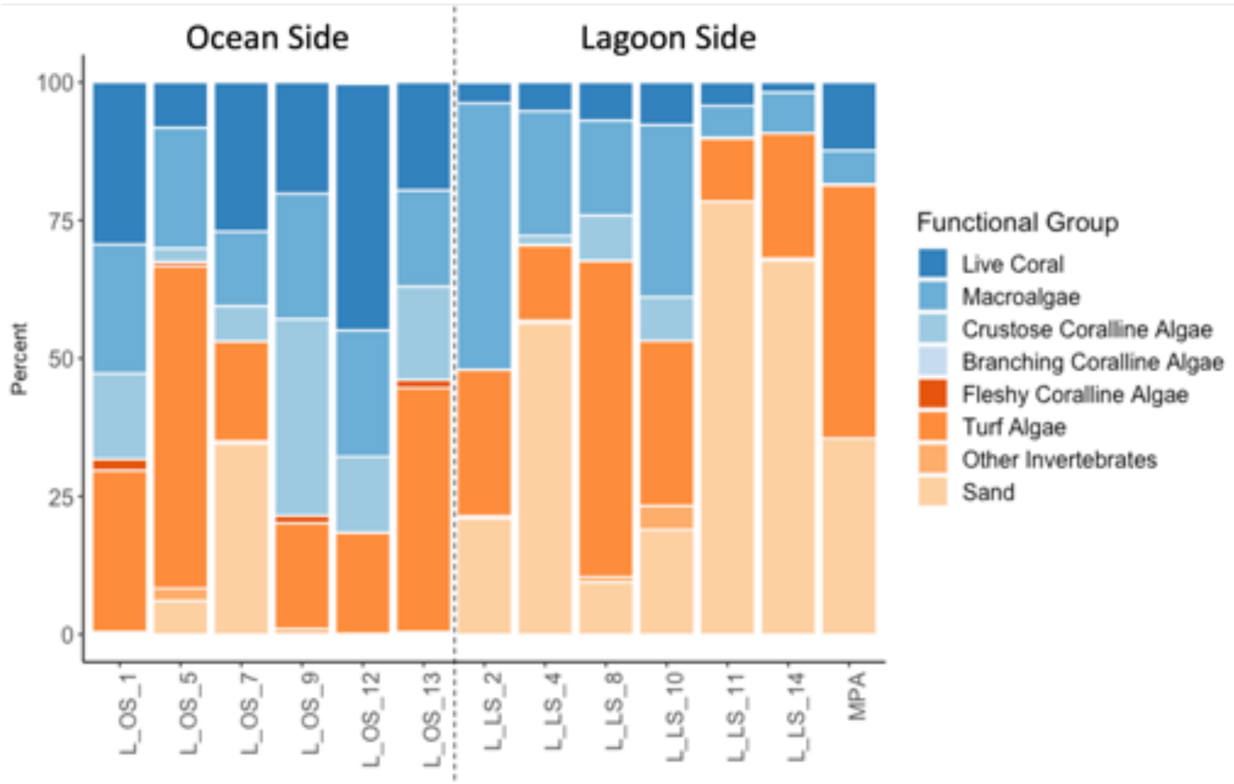

Fig. 5. Percent cover of key functional groups by site.

Three sites on the ocean side had the highest genera richness (L_OS_1, L_OS_9, and L_OS_12, Table 3), which were also among the sites with the highest coral cover. In general, sites with higher coral cover also tended to have higher diversity of coral genera, indicating that they may also be more resilient to different stressors (although this resilience depends on the community composition and the type of stressor, because some taxa are more sensitive to heat stress than others).

Table 3. Genera richness by site and reef type.

Site	Lagoon/Ocean	Leeward/Windward	Hard Coral Genera Richness
L_LS_2	Lagoon	Windward	6
L_LS_4	Lagoon	Windward	7
L_LS_8	Lagoon	Windward	10
L_LS_10	Lagoon	Leeward	10
L_LS_11	Lagoon	Leeward	7
L_LS_14	Lagoon	Windward	3
L_OS_1	Ocean	Leeward	17
L_OS_5	Ocean	Windward	12
L_OS_7	Ocean	Windward	13
L_OS_9	Ocean	Leeward	17
L_OS_12	Ocean	Leeward	17
L_OS_13	Ocean	Leeward	12
MPA	Lagoon	Windward	4

The community composition at each site also differed within functional groups. For example, the hard coral communities differed across sites and reef types (Fig. 6). The MPA, a lagoon site, was almost entirely covered by *Acropora*, a sensitive genus of coral that was more common at lagoon sites in general, but the other lagoon sites had higher genera richness, with the exception of L_LS_14 where coral cover was composed of two types of coral, the genus *Acropora* and the massive morphology of the genus *Porites*. Most other sites had more even distributions of coral community composition, but *Stylophora* was only present on outer reefs. The most common coral taxa are shown in Fig. 7.

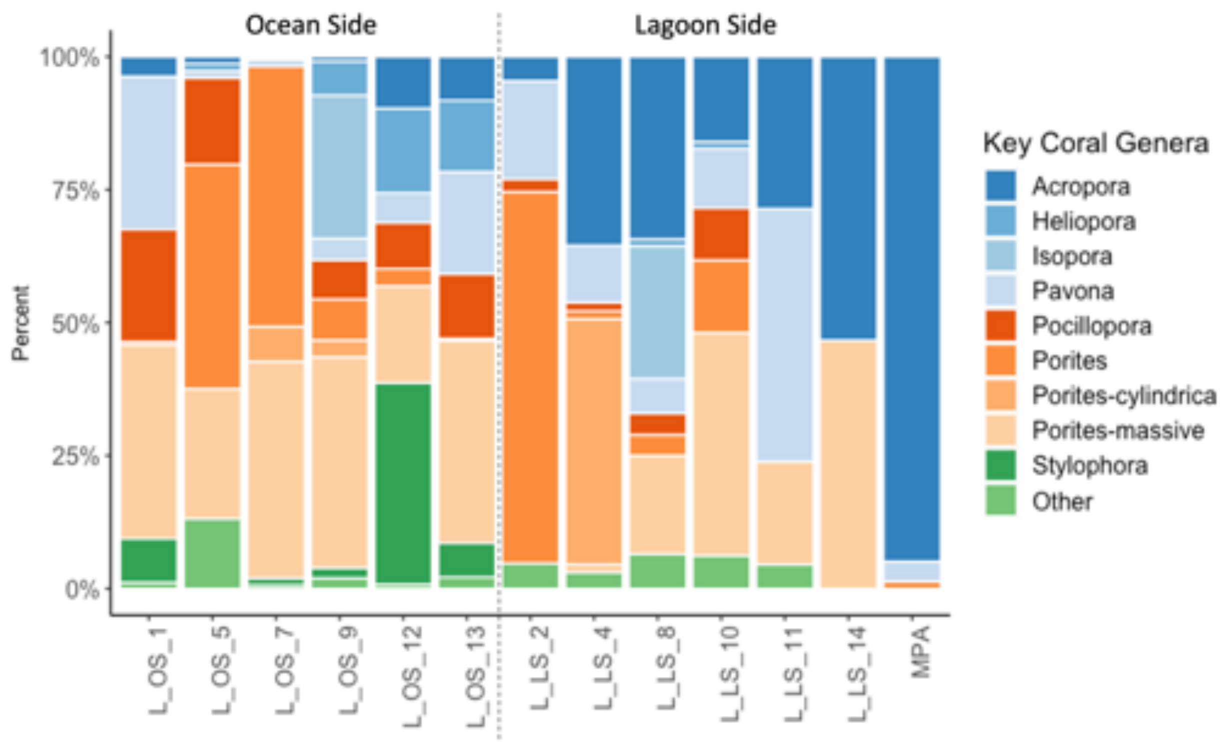

Fig. 6. Percent cover of key coral genera by site.

Fig. 7. Most common coral found in Likiep Atoll: (a) *Acropora*, (b) *Heliopora*, (c) *Isopora*, (d) *Pavona*, (e) *Pocillopora*, (f) *Porites cylindrica*, (g) massive *Porites,* and (h) *Stylophora*.

The macroalgae cover also varied across sites and reef types. Bluegreen algae (also called cyanobacteria) was more common on lagoon reef sites and was almost 100% of the macroalgae cover at site L_LS_2 (Fig. 8), which also had high (almost 50%) macroalgae cover overall (Table 2). The genus *Halimeda* was common across all sites but was more prevalent on oceanic sites, while the genus *Microdictyon* was also common at all sites but was more prevalent on lagoon sites. The most common macroalgae types from Likiep are shown in Fig. 9.

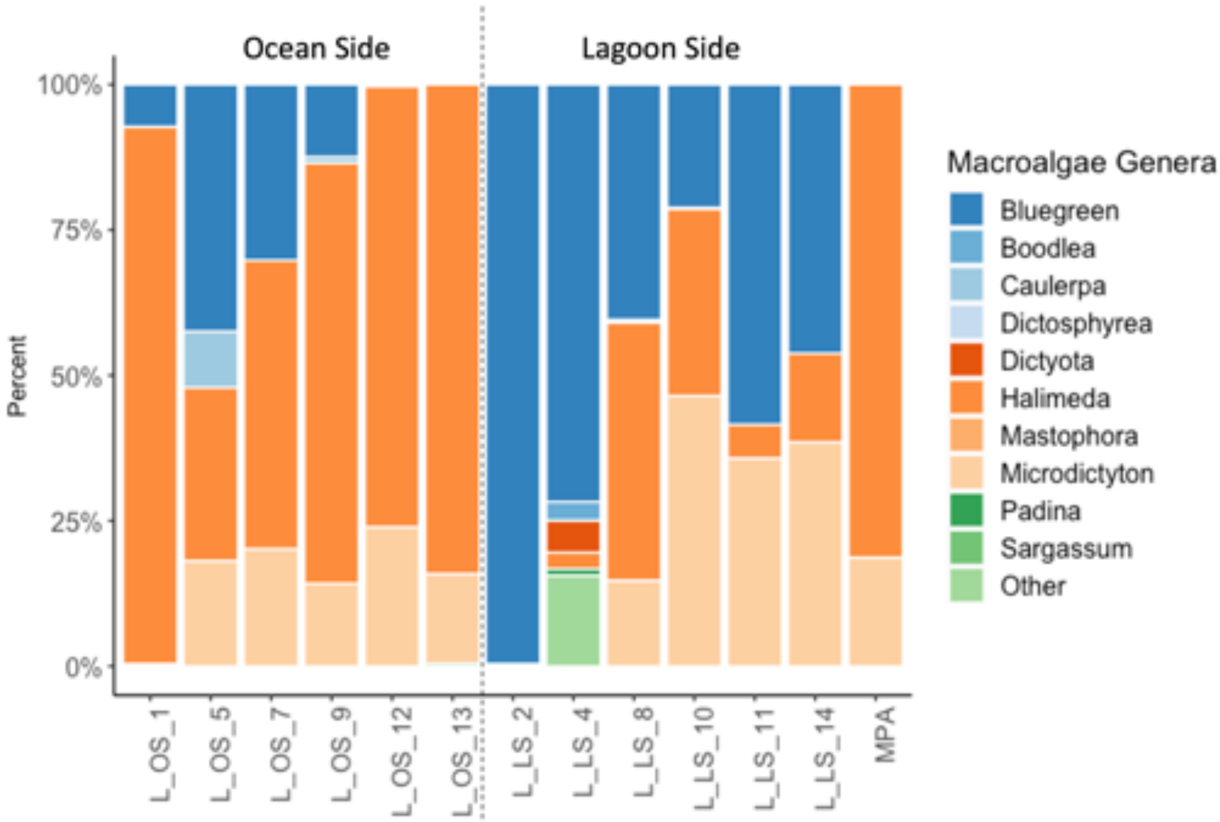

Fig 8. Percent cover of key macroalgae genera across sites.

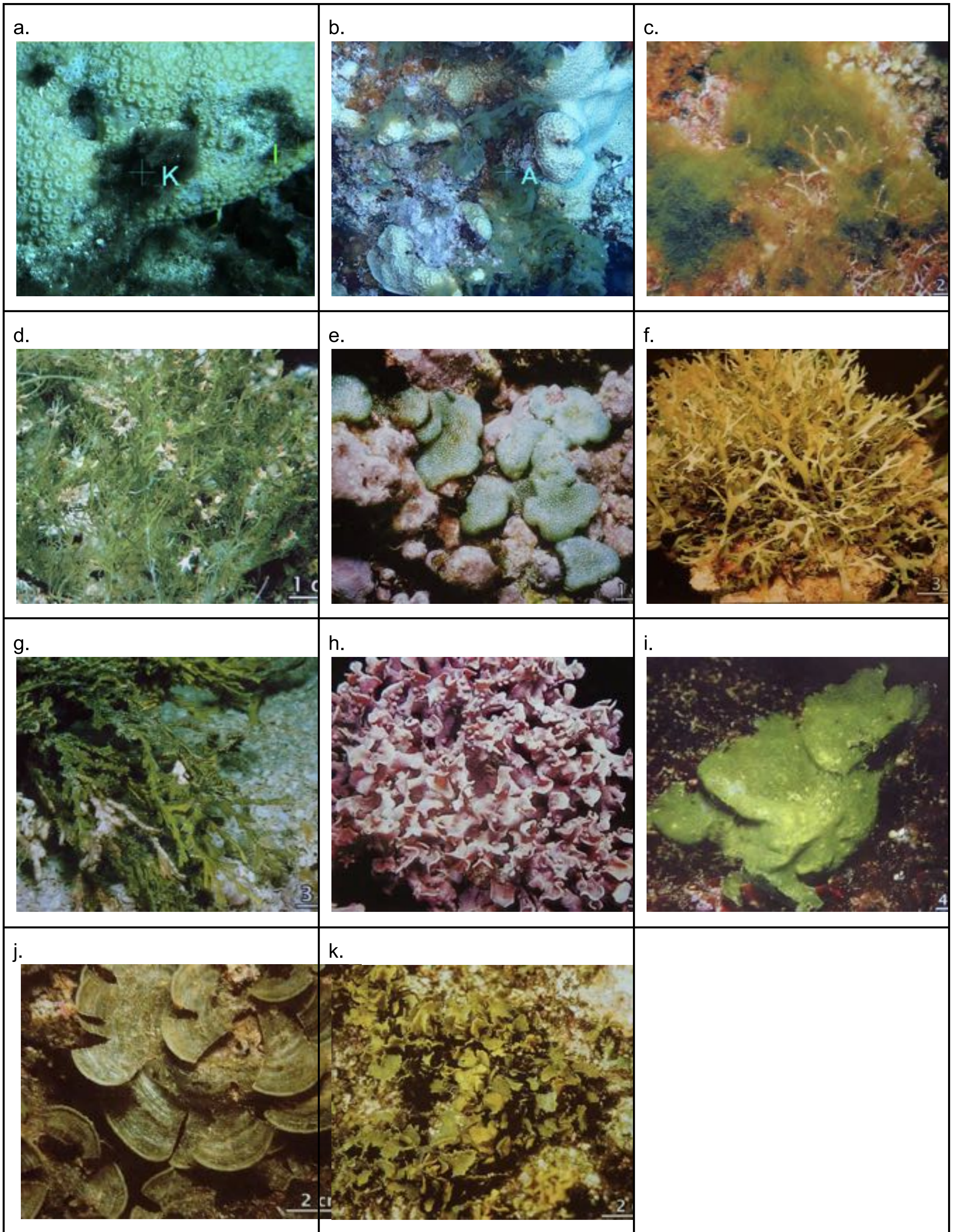

Fig. 9. Most common macroalgae found on Likiep: (a, b) Cyanobacteria/blue-green algae, (c) *Boodlea*, (d) *Caulerpa*, (e) *Dictyosphaeria*, (f) *Dictyota*, (g) *Halimeda*, (h) *Mastophora*, (i) *Microdictyon*, (j) *Padina*, (k) *Sargassum*.

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. I therefore investigated the different community compositions of the reefs in Likiep Atoll by their location either in the lagoon or on the ocean side, following the methods used in Pinca et al. (2001). Overall, ocean sites had high coral cover and CCA when compared to lagoon sites, which had higher percent cover of sand (Table 4). Ocean and lagoon sites had similar macroalgae and turf algae percent cover overall, although the type of macroalgae also differed by reef type; for example, *Halimeda* was more common on ocean sites while cyanobacteria/blue-green algae was more common on lagoon sites (Fig. 9).

Table 4. Percent cover of main benthic categories by reef type.

Category	Average Percent Cover	Average Percent Cover (Ocean)	Average Percent Cover (Lagoon)
Live Coral	14.72	24.86	6.02
CCA	8.39	15.14	2.61
Macroalgae	19.97	20.24	19.73
Sand	25.29	6.89	41.05
Turf	30.28	31.16	29.53

We found that the lagoon sites had lower genera richness (6.71) than ocean sites (14.33), and the PCA shows that reef type had a clear influence on the community composition at each site (Fig. 10). PCA is a statistical analysis that seeks to reduce 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 as shown in Fig. 10 only shows the first two PCs, and when these two PCs (representing each of the axes on Fig 10) sum to greater than 50%, the PCA is considered statistically significant (Jolliffe, 2002). Here, the first two Principal Components (PCs) sum to 68.80%, indicating that the majority of the difference in benthic communities across sites (almost 70%) was captured in the first two PCs. Therefore, the difference in benthic communities by reef types is statistically significant.

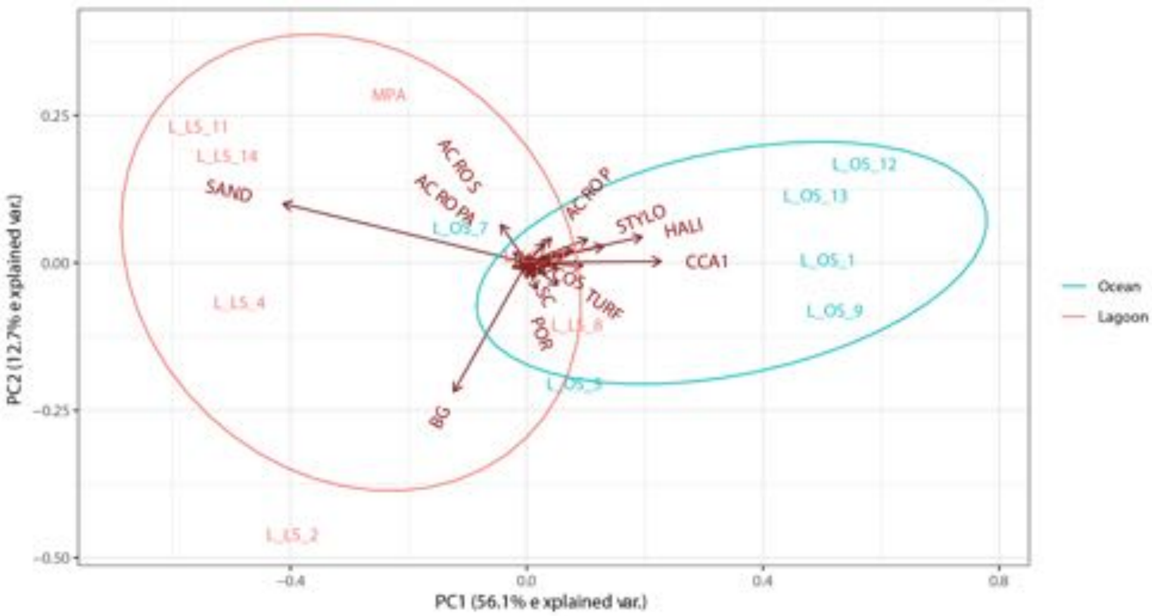

Fig. 10. Principal Component Analysis of benthic percent cover data, by reef type. Each point represents a site, and the arrows represent the taxa. The length of each arrow indicates how much of the difference across the sites is explained by that variable (with longer arrows having greater explanatory power). The closer the points are to each other, the more similar those sites are.

Oceanic sites on the outside of the atolls tended to be categorized by higher cover of the macroalgae *Halimeda*, massive *Porites*, CCA, and *Stylophora* (Fig. 10). Crustose coralline algae (CCA) is an important structural component of coral reefs (it is an encrusting algae that cements reefs together), and it also provides substrate that allows coral larvae to settle and grow. Therefore, it is often considered an important indicator of healthy reefs. The lagoon sites were more categorized by 'sand', cyanobacteria/blue-green algae, and to a lesser extent, staghorn *Acropora* (Fig. 10).

We used SIMPER analysis to identify the taxa that were most important when explaining the difference across reef sites (Table 5, full results in supplementary materials). The results of the SIMPER analysis support the results of the PCA, in that they indicate that the same key taxon drove the differences across reef types (for example, sand drove about 36% of the difference in community compositions between oceanic reefs and lagoon reefs). As shown in Fig. 10, lagoon sites were more categorized by sand and blue-green algae, while outer reefs were characterized by higher percentages of CCA and the macroalgae *Halimeda*.

Table 5. Results of SIMPER analysis, with the percentage of key taxon contributing the most to differences across outer and back reefs. Only the taxon accounting for up to 95% of the difference across site types are listed here; please see the supplementary materials for full results.

Category	Average	Average (Lagoon)	Average (Ocean)	Contribution	Cumulative Sum
Sand	17.00	41.05	6.89	0.36	0.36
CCA	6.00	2.61	15.14	0.13	0.50
Halimeda	5.00	3.51	13.83	0.11	0.61
Blue-green	5.00	12.07	2.99	0.10	0.70
Massive *Porites*	3.00	0.72	7.15	0.07	0.77
Stylopora	2.00	0.00	3.28	0.04	0.81
Porites (other)	1.00	0.54	3.05	0.03	0.84
Pocillopora	1.00	0.15	2.24	0.02	0.86
Pavona	1.00	0.55	2.39	0.02	0.88
Heliopora	1.00	0.02	1.71	0.02	0.90
Turf algae	1.00	29.53	31.16	0.02	0.91
Acropora (staghorn)	1.00	1.46	0.00	0.02	0.93
Fleshy coralline algae (FCA)	0.45	0.07	0.97	0.01	0.94
Sponges	0.30	0.68	0.08	0.01	0.94

Change in Benthic Cover Over Time

We compared the results from these recent surveys in 2020 to previous surveys conducted by Pinca et al. (2001), by pooling the percent cover measurements of key coral taxa into lagoon and ocean sites (Table 6). The results show that there was an overall decline in hard coral cover on lagoon sites (from 20% cover in 2001 to 11% cover in 2020). In particular, on lagoon sites, *Acropora* declined from 42% to 27% of hard coral cover, and branching *Acropora* specifically declined from 35% cover to 18% between 2001 and 2020, while non-*Acropora* coral cover increased from 45% of the percent cover of hard corals to 82%. Total coral cover also declined on the ocean side (from 43% to 25%), with *Acropora* also declining steeply, from 21% to 2% of the total coral cover. This drove an increase in the proportion of non-*Acropora* from 67% of the hard coral cover to 98%. Collectively, these results show that coral cover overall has declined atoll-wide, with *Acropora* in particular declining steeply, which may correspond with declining coral diversity through increasing percent cover of non-Acroporid corals.

Table 6. Comparison of survey results for percent cover of key hard coral taxa, from 2001 to 2020.

Mean Total Coral Cover	2001		2020	
	Lagoon	Ocean	Lagoon	Ocean
	20%	**43%**	**6%**	**25%**
Percent of all coral cover:				
Acropora	42%	21%	27%	2%
Acropora (Branching)	35%	15%	18%	0%
Non-*Acropora*	45%	67%	82%	98%
Millepora	0%	4%	0%	0%
Heliopora	1%	11%	0%	8%

Unfortunately, we were only able to compare some of the key functional groups over time because the data were not in compatible units (for example, in 2001, the results were grouped by coral morphology, while in 2020, results were grouped by genus). Still, we were able to see that in addition to changes in the percent cover of live coral over time, other categories also changed. Specifically, the percent of sand declined from 59% to 41% in the lagoon and increased from 2% to 7% in the ocean, while turf algae increased across all sites (Table 7). However, here we assumed that what the previous surveys considered “dead coral” would be comparable to what we identified as “turf algae” (because dead coral is almost always very quickly colonized), which may not be accurate; for example, it is possible that Pinca et al. included taxa we identified separately (such as CCA or turf algae).

Table 7. Comparison of survey results by substrate type from 2001 to 2021.

	2001			2021		
	Sand	**Dead coral / Turf algae**	**Live coral**	**Sand**	**Dead coral / Turf algae**	**Live coral**
Lagoon	59%	8%	20%	41%	29%	6%
Ocean	2%	11%	43%	7%	31%	25%

The previous surveys by Pinca et al. (2001) also grouped the sites into four clusters: lagoon-leeward (LL), lagoon-windward (LW), ocean-leeward (OL), and ocean-windward (OW). However, the authors found that the site communities were most explained by their position on the ocean or lagoon sides, and so we did not repeat the full analyses for these four groups and instead chose to focus on comparing sites across the ocean and lagoon.

For comparative purposes, we have included the percent cover statistics of key benthic taxa for these four groups from the 2020 surveys in the supplementary materials (S4), and our results are similar to those reported from the 2001 surveys. We found that the differences were most pronounced across lagoon versus ocean sites, although the percent cover of key taxa did differ slightly on the ocean side; leeward sites had higher percent cover of hard coral and CCA than windward sites, while windward sites had higher percent cover of sand, turf algae, and macroalgae. This is unlikely to be any indication of reef health, and is likely driven by increased exposure to wind and waves on the windward side of the atolls (Pinca *et al.*, 2001).

Conclusions

While coral reefs on the ocean side of Likiep appear healthy, it is concerning that there was an overall decline in hard coral cover across reef types. In 2020, all sites on the ocean side of Likiep except one exceeded the 10% threshold of coral cover required for reefs to keep up with future sea level rise (Perry *et al.*, 2015). The oceanic reefs also had higher coral genera richness on average (14.33) than sites in the lagoon (6.71) and were most commonly home to massive *Porites* and *Stylophora* (hard corals), the macroalgae *Halimeda*, and crustose coralline algae (CCA). Both *Halimeda* and CCA are commonly associated with healthy reefs and *Halimeda* has been shown to be most correlated with sites that had low human disturbance in other parts of the Marshall Islands (Cannon *et al.*, 2019). CCA in particular is often considered an indicator of a healthy reef, because it plays an important part in successful coral recruitment by providing settlement substrate for coral larvae, and is also important in reef structure (Björk *et al.*, 1995; Littler and Littler, 2013).

In the lagoon, sites had lower coral and CCA cover (6.02%) and greater percent cover of sand (41.05%). While turf algae and macroalgae were similar across reef types, the composition of macroalgae communities differed; for example, bluegreen algae/cyanobacteria was more common in the lagoon than on ocean sites. While it is common for lagoon sites to have lower coral cover than outer reefs, all of the sites within the lagoon had less than 10% total hard coral cover (with the exception of the MPA site, where hard coral accounted for 12.41% of the total benthic cover), the threshold required for keeping up with sea level rise (S2, supplementary materials), although this threshold may be too conservative for lagoon sites as they do not experience as much wave energy as sites on the ocean. Still, the higher percent cover of cyanobacteria combined with low coral and CCA cover may indicate that the lagoon sites have been negatively affected by poor water quality, which could be the result of pollution from land, low circulation between the lagoon and ocean, unsustainable harvesting of ecologically important species, or some combination of these factors. This is consistent with the results of previous surveys from Pinca et al. (2001) who found that the lagoon sites were also less productive than ocean sites, and hypothesized that the higher sedimentation in the lagoon may be in part due to the lagoon being partially enclosed. This limits coral recruitment because of the restricted flow of larvae and also because higher turbidity environments are less favorable for settlement, and may make sites in the lagoon less resilient than sites on the ocean side to future stressors. Identifying the causes of stress to reefs in the lagoon will allow managers to make informed decisions about how to stop them at the source. For example, water quality analysis (in particular for nutrients like nitrogen and phosphorus) would confirm the drivers of this turbidity in lagoon sites (and whether land-based pollution is a concern), which would help to target interventions that could improve water quality in the lagoon.

Again, it is a concern that coral cover has declined across both the lagoon and ocean sites. Comparisons with the 2001 surveys suggest that the coral declines happened across the different morphologies of the genus *Acropora*, as well as non-*Acroporid* corals. We are unable to say for certain what caused this decline, although it is possible that these sites experienced heat-driven coral bleaching during the prolonged El Niño event between 2014 and 2017 (Fellenius, 2014; Coral Reef Watch, 2017). While to our knowledge there have been no reports of bleaching from Likiep specifically, sites in Likiep did experience intermittent bleaching watches and warnings throughout this time period (e.g. Fig. 3). Also, in locations where heat stress is less common and corals do not have a history of bleaching, corals may be more sensitive to heat stress (and therefore could bleach at lower temperature thresholds than corals in other places where heat stress is more common), which could make reefs in places like Likiep more vulnerable. This, combined with *Acropora*'s reputation as one of the regular 'losers' after bleaching events (Loya *et al.*, 2001; Van Woesik *et al.*, 2011), support the hypothesis that declines in coral cover between 2001 and 2020 may have been driven at least in part by heat stress.

Because the previous surveys grouped the non-*Acroporid* corals by morphology, we cannot compare the most recent surveys by taxa with the exception of *Acropora*, which is an important reef-growing coral and a potential indicator of a healthy reef, because it is a competitive, fast-growing species that provides integral structural complexity and essential fish habitat. However, this fast-growing life history means that *Acropora* is also sensitive to heat stress and local stressors such as sedimentation and nutrients (Darling *et al.*, 2012). Once *Acropora* cover declines past a certain level, it may be difficult for populations to recover because they are broadcast spawners, making them density-dependent (meaning that in order to recover, there must be enough *Acropora* in close enough proximity to each other for the gametes to find each other in the water column during spawning events) (Teo and Todd, 2018). The good news is that the fast-growing, competitive life-history strategy of *Acropora* makes corals of this genus good candidates for restoration projects, because they can be easily grown as a part of coral gardening projects. However, it is important to recognize that restoration efforts will not succeed if the underlying drivers of coral decline are not addressed (for example, planting *Acropora* at sites with high turbidity is unlikely to be successful, and the corals may still be vulnerable to any future bleaching events).

We are also unable to evaluate the effectiveness of the protected area despite surveying that site, as we do not have data from before it was designated a protected area. MICS staff also conducted fish surveys at the same time as the October 2020 benthic surveys. The results showed that fish biomass was low at the MPA site, even when compared to other sites in the lagoon (which had lower biomass overall compared to ocean sites). The presentation concluded that the MPA is currently not successful although it is not clear if this is because it is currently not being enforced (Marshall Islands Conservation Society, 2021).

The reefs at the MPA site appear to be healthier than other sites in the lagoon, although given the results from the fish surveys, this is likely not the result of reduced fishing pressure. Not only does this site have the highest percent cover of hard coral of all the lagoon sites (12.41%, more than double the lagoon-wide average of 6.02%), but macroalgae taxa at the MPA site was also limited to genera associated with less degraded reefs, such as *Halimeda*. The MPA site also had no cyanobacteria/blue-green algae (Fig. 7, S2 Supplementary materials), which was common at other sites within the lagoon and is often associated with poor water quality (12.07% on average, Table 5). Still, despite appearing healthier than other lagoon sites overall, the MPA site had low hard coral genera richness (4), even when compared to other sites in the lagoon (for which the genera richness averaged 6.71). Because the MPA site was dominated by one taxa of coral in particular, it may be especially vulnerable to 'ecological surprises', meaning that any stressor affecting this one coral taxa will have a disproportionate effect on the ecosystem as a whole, because of the outsized role played by that taxa in the overall ecological community (Paine, Tegner and Johnson, 1998). That said, the MPA site may be a good place for a coral gardening project, given that it is already home to higher percentages of *Acropora* than other sites across the atoll. Eventually, offspring from the coral gardening project could then be transported to leeward oceanside sites, where they hopefully would be able to contribute to *Acropora* recovery on those reefs and in the long term, could provide a source of *Acropora* larvae that would boost recovery on other sites around the atoll. Including this site in the MPA network is therefore important for restocking neighboring reefs.

In addition, the MPA site and a potential coral gardening project might offer an opportunity for furthering the work by the MICS and Woods Hole Oceanographic Institution (WHOI) (e.i., Super Reef Project) and establishing new partnerships with researchers such as Dr. Guest from the Coral Assist Laboratory at Newcastle University, who are working to understand the local drivers of coral colonies' resistance to heat stress. Sites in Likiep's lagoon are likely warmer than sites on the ocean side because they are shallow and have lower water circulation. Similar to the ongoing work on Majuro Atoll, the MICS could place temperature loggers at sites on the ocean and lagoon sides to determine which experiences the highest sea surface temperatures, if those temperatures change throughout the year, and the range of temperature fluctuations. If the MPA site is warmer than others and/or experiences more temperature variation, it could mean that the *Acropora* found there will be more resistant to future heat stress. Gardening and transplanting coral offspring from these colonies to other sites might therefore enhance their resilience as well. This would benefit coral reefs in Likiep through greater resistance to heat stress as the climate continues to warm, and may also contribute to the scientific literature on coral reef resilience by testing and/or demonstrating how understanding local environmental variation can improve restoration efforts.

Summary of findings

- Overall hard coral cover has declined for all reef types between 2001 and 2020, and the declines were particularly pronounced for *Acropora*. In 2001, *Acropora* accounted for 42% of all coral cover in the lagoon and 21% of all coral cover on the ocean, but by 2021, these numbers had dropped to 27% in the lagoon and only 2% on the ocean. We are unaware of any major stressors that may have driven this change, although it is possible that reefs in Likiep experienced bleaching during the 2014-2017 global mass bleaching event. The genus *Acropora* is known to be sensitive to heat stress and is often considered one of the ‘losing’ taxa after bleaching events (Loya *et al.*, 2001; Van Woesik *et al.*, 2011).

- Sites on the ocean side were healthy, with a higher percent cover of hard coral (24.86%) and greater diversity (as measured by coral genera richness, 14.33) on average than sites in the lagoon. Ocean sites were categorized by high percent cover of massive *Porites* and *Stylophora*, CCA, and *Halimeda*.

- Lagoon sites had low coral cover overall (6.02%) and low genera richness on average (6.71) when compared to ocean sites. Lagoon sites were characterized by high percentages of blue-green algae/cyanobacteria and sand.

- Scientists have estimated that coral reefs must have at least 10% cover of hard corals in order to keep up with future sea level rise (Perry *et al.*, 2015). All but one of the sites on the ocean side met this threshold, while only one of the sites in the lagoon (the MPA site) had more than 10% total coral cover.

- The low diversity of corals at lagoon sites, coupled with the lower percent cover of hard coral overall, may mean that sites within the lagoon are less resilient to future stressors than sites on the ocean.

- The MPA site had the highest prevalence of hard coral of all the lagoon sites (12.41%), almost all of which was *Acropora* (Fig. 6). This site also had low genera diversity (4), which may make it vulnerable to future disturbances. However, this site could be a good source of *Acropora* for a potential future coral gardening project, which may help to restore *Acropora* populations on other sites across the atoll. Because *Acropora* is density dependent, populations may not recover on their own without a nearby source of larvae.

- Fish surveys conducted at the same time as the benthic surveys (October 2020) found that sites in the lagoon had lower fish biomass than sites on the ocean, and recommended that management focus on lagoon fisheries.

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 greenhouse gas emissions locally, will be integral to ensuring a future for coral reefs as the climate warms, in the Marshall Islands and elsewhere.

- Establishing or improving current protected areas with the goal of limiting fishing in the lagoon may help fish populations to rebound. Importantly, as noted by Pinca et al. (2001)**,** effective management must be led by the communities in Likiep, and they should also be responsible for enforcement. Rotated closures could be a way to ensure that the citizens of Likiep are able to access fishing grounds while giving reef fish populations a chance to recover. Gear restrictions may also be effective (for example, limiting the use of throw nets that target small herbivorous fish).

- Coral gardening for *Acropora* may be possible at the MPA site, where *Acropora* cover was comparatively high and the benthic communities appeared healthier than other lagoon sites. This would provide juvenile *Acropora* that could be transplanted at other sites around the atoll, potentially facilitating the recovery of *Acropora* populations atoll-wide (although their long-term survival may depend on future stressors, such as bleaching events).

- Water quality tests would help to say with certainty whether water quality within the lagoon is degraded by pollution from land. In the meantime, communities in Likiep could take steps to limit pollutants from entering the water, including solid waste and wastewater from households and agriculture. This is important on both the lagoon and ocean sides, but may be especially integral on the lagoon side of the islands, because flushing rates in the lagoon are lower than in the ocean and nutrients and pollutants may accumulate over time.

- Communities in Likiep can also collect their own data to guide future decision making about how best to conserve local reefs and ensure that they still provide ecosystem services in the future. The Likiep Fisheries Management Advisory Committee recommended this as a part of the Fisheries Management Plan for Likiep (Likiep Atoll Local Government, 2006), but it is unclear whether the data were ever collected. 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, for example, this could be a place that might need to be temporarily closed for fishing.

- Communities in Likiep 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, when conditions allow), and estimating the percent-cover of certain taxa or coral morphologies. These data would 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 the percent cover of *Acropora* over time).

- Protecting the physical integrity of reefs in Likiep will be important to ensure that they continue to grow fast enough to keep up with rising sea levels, particularly in the lagoon where coral cover is low. Educational programs that describe the harms of damaging live coral colonies and rubble through acts like mining or anchoring will help to limit these activities and to keep coral reefs intact, while also possibly providing more substrate where corals 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 contribute to preserving the physical structure of coral reefs on Likiep.

- Finally, repeating these surveys of reefs in Likiep (every 3-5 years) will be important for further untangling the patterns observed here and the changes occurring over time, including the key drivers of the patterns documented in this report (for example, the low cover of *Acropora*).

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Supplementary Materials

S1. Identification codes used by MICS to identify benthic taxa.

Code_short	Code_long	Category
ACAN	Acanthastrea	Coral
ACROP	Acropora	Coral
ACROPARB	Acropora-arborescent	Coral
ACROST	Acropora-stag	Coral
ACROTBL	Acropora-table	Coral
ASTRP	Astreopora	Coral
CAUL	Caulastrea	Coral
COSC	Coscinaraea	Coral
CTEN	Ctenactis	Coral
CYPH	Cyphastrea	Coral
DIPLO	Diplioastrea	Coral
ECHPO	Echinopora	Coral
ECHPHY	Echinphyllia	Coral
EUPH	Euphyllia	Coral
FAV	Favia	Coral
FAVT	Favites	Coral
FUNG	Fungia	Coral
GAL	Galaxea	Coral
GARD	Gardineroseris	Coral
GON	Goniastrea	Coral
GONIO	Goniopora	Coral
HELIO	Heliopora	Coral
HERP	Herpolitha	Coral

HYD	Hydnophora	Coral
ISOP	Isopora	Coral
LEPT	Leptastrea	Coral
LEPTOR	Leptoria	Coral
LEPTOS	Leptoseris	Coral
LOBOPH	Lobophyllia	Coral
MERU	Merulina	Coral
MILL	Millepora	Coral
MONT	Montastrea	Coral
MONTI	Montipora	Coral
MYCED	Mycedium	Coral
OULO	Oulophyllia	Coral
OXYP	Oxypora	Coral
PLSIA	PLeisastrea	Coral
PACHY	Pachyseris	Coral
PAV	Pavona	Coral
PECT	Pectinia	Coral
PHYSO	Physogyra	Coral
PLAT	Platygyra	Coral
PLERO	Plerogyra	Coral
POC	Pocillopora	Coral
POR	Porites	Coral
PORCYL	Porites-cylindrica	Coral
PORMAS	Porites-massive	Coral
PORRUS	Porites-rus	Coral
PSAM	Psammocora	Coral
SANDO	Sandalolitha	Coral

SCAP	Scapophyllia	Coral
SERIA	Seriatopora	Coral
STYLC	Stylocoeniella	Coral
STYLO	Stylohpora	Coral
SYMP	Symphyllia	Coral
TURBIN	Turbinaraea	Coral
ANEM	Anenome	Other Invertebrates
ASC	Ascidian	Other Invertebrates
CUPS	Cup Sponge	Other Invertebrates
DISCO	Discosoma	Other Invertebrates
DYS	Dysidea Sponge	Other Invertebrates
G	Gorgonians	Other Invertebrates
NOIDINV	Not Identified Invertebrate	Other Invertebrates
OLV	Olive Sponge	Other Invertebrates
SC	Soft Coral	Other Invertebrates
S	Sponges	Other Invertebrates
TERPS	Terpios Sponge	Other Invertebrates
Z	Zoanthids	Other Invertebrates
ASP	Asparagopsis	Macroalgae
BG	Bluegreen	Macroalgae
BOOD	Boodlea	Macroalgae
BRYP	Bryopsis	Macroalgae
CLP	Caulerpa	Macroalgae
CHLDES	Chlorodesmis	Macroalgae
DYCTY	Dictosphyrea	Macroalgae
DICT	Dictyota	Macroalgae
GLXU	Galaxura	Macroalgae

HALI	Halimeda	Macroalgae
LIAG	Liagora	Macroalgae
LOBO	Lobophora	Macroalgae
MAST	Mastophora	Macroalgae
MICDTY	Microdictyton	Macroalgae
NEOM	Neomeris	Macroalgae
NOIDMAC	Not ID Macroalgae	Macroalgae
PAD	Padina	Macroalgae
SARG	Sargassum	Macroalgae
SCHIZ	Schizothrix	Macroalgae
TURB	Turbinaria	Macroalgae
TYDM	Tydemania	Macroalgae
AMP	Amphiroa	Branching Coralline algae
BCA1	Branching Coralline general	Branching Coralline algae
JAN	Jania	Branching Coralline algae
CCA1	Crustose Coralline	Crustose Coralline Algae
SAND	Sand	Sand
FCA1	Fleshy-Coralline	Fleshy Coralline Algae
CHRYOBRN	Brown Chysophyte	Chrystophytes
TURF	Turf	Turf
SHADOW	Shadow	Tape-Wand-Shadow
TAPE	Tape	Tape-Wand-Shadow
WAND	Wand	Tape-Wand-Shadow

S2. Percent cover of key functional groups by site.

Site	Live Coral	Crustose Coralline Algae (CCA)	Fleshy Coralline Algae (FCA)	Macro-algae	Other Invert-ebrates	Sand	Turf Algae
L_LS_2	3.70	0.00	0.08	48.25	0.50	20.96	26.43
L_LS_4	5.27	1.63	0.16	22.52	0.57	56.3	13.55
L_LS_8	6.94	8.28	0.08	17.12	0.96	9.44	57.18
L_LS_10	7.73	7.99	0.00	31.14	4.34	18.99	29.81
L_LS_11	4.27	0.24	0.00	5.71	0.00	78.45	11.33
L_LS_14	1.85	0.08	0.00	7.33	0.4	67.7	22.63
L_OS_1	29.39	15.61	2.01	23.33	0.32	0.16	29.17
L_OS_5	8.26	2.43	0.65	21.79	2.31	6.03	58.37
L_OS_7	27.07	6.39	0.08	13.44	0.49	34.53	18.01
L_OS_9	20.18	35.67	1.37	22.68	0.97	0.08	19.06
L_OS_12	44.67	13.74	0.00	22.83	0.08	0.08	18.21
L_OS_13	19.61	16.98	1.38	17.37	0.00	0.48	44.17
MPA	12.41	0.08	0.16	6.03	0.00	35.53	45.79

S3. SIMPER Analysis, showing the key drivers of differences between lagoon sites and ocean sites.

Category	Mean	Mean (Lagoon)	Mean (Ocean)	Contribution	Cumulative Sum
SAND	17.00	41.05	6.89	0.36	0.36
CCA1	6.00	2.61	15.14	0.13	0.50
HALI	5.00	3.51	13.83	0.11	0.61
BG	5.00	12.07	2.99	0.10	0.70
PORMAS	3.00	0.72	7.15	0.07	0.77
STYLO	2.00	0.00	3.28	0.04	0.81
POR	1.00	0.54	3.05	0.03	0.84
POC	1.00	0.15	2.24	0.02	0.86
PAV	1.00	0.55	2.39	0.02	0.88
HELIO	1.00	0.02	1.71	0.02	0.90
TURF	1.00	29.53	31.16	0.02	0.91
ACROST	1.00	1.46	0.00	0.02	0.93
FCA1	0.45	0.07	0.97	0.01	0.94
S	0.30	0.68	0.08	0.01	0.94
ISOP	0.29	0.22	0.81	0.01	0.95
ASTRP	0.00	0.17	0.73	0.01	0.96
FAV	0.00	0.01	0.53	0.01	0.96
NOIDMAC	0.00	0.50	0.00	0.01	0.97
CLP	0.00	0.01	0.39	0.00	0.97
PLAT	0.00	0.00	0.30	0.00	0.97
MICDTY	0.00	3.28	3.01	0.00	0.98
SC	0.00	0.13	0.37	0.00	0.98
ACROPARB	0.00	0.25	0.03	0.00	0.98

FAVT	0.00	0.12	0.32	0.00	0.98
DICT	0.00	0.17	0.00	0.00	0.99
G	0.00	0.00	0.12	0.00	0.99
MONTI	0.00	0.00	0.11	0.00	0.99
BOOD	0.00	0.11	0.00	0.00	0.99
SHADOW	0.00	0.13	0.23	0.00	0.99
GARD	0.00	0.00	0.08	0.00	0.99
WAND	0.00	0.08	0.00	0.00	0.99
TURBIN	0.00	0.06	0.14	0.00	0.99
LOBOPH	0.00	0.01	0.08	0.00	0.99
NOIDINV	0.00	0.16	0.12	0.00	0.99
GON	0.00	0.00	0.04	0.00	1.00
BCA1	0.00	0.00	0.04	0.00	1.00
CTEN	0.00	0.04	0.00	0.00	1.00
PAD	0.00	0.04	0.00	0.00	1.00
PORCYL	0.00	0.35	0.38	0.00	1.00
TAPE	0.00	0.05	0.01	0.00	1.00
FUNG	0.00	0.00	0.03	0.00	1.00
HERP	0.00	0.00	0.03	0.00	1.00
LEPT	0.00	0.00	0.03	0.00	1.00
MILL	0.00	0.00	0.03	0.00	1.00
MAST	0.00	0.02	0.00	0.00	1.00
PORRUS	0.00	0.02	0.00	0.00	1.00
CYPH	0.00	0.07	0.05	0.00	1.00
ECHPHY	0.00	0.00	0.01	0.00	1.00
PSAM	0.00	0.00	0.01	0.00	1.00
SARG	0.00	0.00	0.01	0.00	1.00

COSC	0.00	0.00	0.01	0.00	1.00
DYCTY	0.00	0.01	0.00	0.00	1.00
ACROP	0.00	1.27	1.28	0.00	1.00
CHRYOBRN	0.00	0.01	0.00	0.00	1.00
STYLC	0.00	0.01	0.01	0.00	1.00
ACAN	0.00	0.00	0.00	0.00	1.00
ACROTBL	0.00	0.00	0.00	0.00	1.00
AMP	0.00	0.00	0.00	0.00	1.00
ANEM	0.00	0.00	0.00	0.00	1.00
ASC	0.00	0.00	0.00	0.00	1.00
ASP	0.00	0.00	0.00	0.00	1.00
BRYP	0.00	0.00	0.00	0.00	1.00
CAUL	0.00	0.00	0.00	0.00	1.00
CHLDES	0.00	0.00	0.00	0.00	1.00
CUPS	0.00	0.00	0.00	0.00	1.00
DIPLO	0.00	0.00	0.00	0.00	1.00
DISCO	0.00	0.00	0.00	0.00	1.00
DYS	0.00	0.00	0.00	0.00	1.00
ECHPO	0.00	0.00	0.00	0.00	1.00
EUPH	0.00	0.00	0.00	0.00	1.00
GAL	0.00	0.00	0.00	0.00	1.00
GLXU	0.00	0.00	0.00	0.00	1.00
GONIO	0.00	0.00	0.00	0.00	1.00
HYD	0.00	0.00	0.00	0.00	1.00
JAN	0.00	0.00	0.00	0.00	1.00
LEPTOR	0.00	0.00	0.00	0.00	1.00
LEPTOS	0.00	0.00	0.00	0.00	1.00

LIAG	0.00	0.00	0.00	0.00	1.00
LOBO	0.00	0.00	0.00	0.00	1.00
MERU	0.00	0.00	0.00	0.00	1.00
MONT	0.00	0.00	0.00	0.00	1.00
MYCED	0.00	0.00	0.00	0.00	1.00
NEOM	0.00	0.00	0.00	0.00	1.00
OLV	0.00	0.00	0.00	0.00	1.00
OULO	0.00	0.00	0.00	0.00	1.00
OXYP	0.00	0.00	0.00	0.00	1.00
PACHY	0.00	0.00	0.00	0.00	1.00
PECT	0.00	0.00	0.00	0.00	1.00
PHYSO	0.00	0.00	0.00	0.00	1.00
PLERO	0.00	0.00	0.00	0.00	1.00
PLSIA	0.00	0.00	0.00	0.00	1.00
SANDO	0.00	0.00	0.00	0.00	1.00
SCAP	0.00	0.00	0.00	0.00	1.00
SCHIZ	0.00	0.00	0.00	0.00	1.00
SERIA	0.00	0.00	0.00	0.00	1.00
SYMP	0.00	0.00	0.00	0.00	1.00
TERPS	0.00	0.00	0.00	0.00	1.00
TURB	0.00	0.00	0.00	0.00	1.00
TYDM	0.00	0.00	0.00	0.00	1.00
Z	0.00	0.00	0.00	0.00	1.00

S4. Key benthic categories from surveys in 2020, by reef type.

Benthic Category	Lagoon		Ocean	
	Leeward	**Windward**	**Leeward**	**Windward**
Live coral	6.00	6.62	28.46	13.01
CCA	4.12	2.52	20.50	2.94
Macroalgae	18.42	13.25	21.55	27.83
Other Inverts	2.17	0.48	0.34	1.10
Sand	48.72	42.24	0.20	20.51
Turf Algae	20.57	34.79	27.65	34.27