NOO RAAJJE

MALDIVES
Coral Reef Assessment

The expedition research crew brought together local Maldivians, scientists, and partners from six countries.

CONTENTS

Acknowledgments

A Maldives clown fish (*Amphibian nigripes*) in an anemone.

EXECUTIVE SUMMARY

English

In January and February of 2020, the Waitt Institute, Scripps Institution of Oceanography, and the Maldives Marine Research Institute partnered together to survey 127 forereef sites across 15 atolls in the Northern and Central Maldives, in order to increase understanding of the health of the Maldivian ocean and support future marine spatial planning efforts across the nation.

Sites were classified as **inhabited, resort, or uninhabited** based on the island use designation of the closest emergent land and were surveyed for:

- fish abundance, diversity, and biomass,
- benthic community composition,
- juvenile coral abundance and diversity,
- reef rugosity,
- and macroinvertebrate abundance and diversity.

Fish survey data showed a high density of small-bodied planktivores, moderate densities of large-bodied herbivores, and low densities of top predators and sharks across the sites surveyed, but found no significant differences in fish biomass between different island use types.

Coral cover was shown to have recovered somewhat from the 2016 bleaching event, with the current mean percent cover (19.4%) approximately half of what it was prior to 2016, and dominated by *Porites* species rather than *Acropora*.

This apparent recovery may be due in part to the high levels of recruitment recorded at the sites surveyed (an average of over 14 individual recruits per square meter), likely facilitated by high herbivory rates. Island use type affected benthic and, to an extent, invertebrate communities, but did not significantly drive patterns in fish communities. The results from this study suggest that Maldivian reefs overall have the capacity for recovery following disturbance, but that local stressors may impact reef health at the local scale.

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INTRODUCTION

As an island nation composed entirely of coral reefs and low-lying coral islands, the Republic of the Maldives possesses a large territorial sea and covers an extensive latitudinal gradient, spanning approximately 650 km north to south and containing 25 distinct atolls (Naseer and Hatcher 2004).

Consequently, the Maldivians depend heavily on marine resources not just to support the nation's economy—particularly its two largest industries: fishing and tourism (Domroes 2001, Athukorala 2004, National Bureau of Statistics 2019)—but also to support the livelihoods of locals and to provide important ecosystem services.

Therefore, understanding and promoting the health of the nation's coral reefs is of the utmost importance for maintaining the prosperity of the Maldives and its citizens (Hosterman and Smith 2012, Shareef et al. 2012).

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Reefs

The reefs of the Maldives are subject to a number of natural and anthropogenic impacts that affect the health of their coral reef communities (Zahir et al. 2009, McClanahan and Muthiga 2014, Morri et al. 2015, Montefalcone et al. 2020).

Rising sea surface temperatures associated with climate change have led to an increased incidence of coral bleaching. The most severe bleaching in the Maldives coincided with global coral bleaching events in 1998 and 2016, both of which decimated local coral reef communities (Ateweberhan et al. 2011, Morri et al. 2015, Ibrahim et al. 2017, Pisapia et al. 2016).

His Excellency President Solih participates in the underwater research at Keylakunu.

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Prior to the 1998 coral bleaching event, branching corals (*Acroporidae*, *Pocilloporidae*) were the dominant taxa (Ciarapica and Passeri 1993). Though coral cover was known to range between 50-80% (Scheer 1972, 1974), the mean coral cover in the Maldives was estimated at 40.08% (Pisapia et al. 2016).

Following the 1998 bleaching event, mean coral cover was reduced to approximately 1.69%, and the dominant taxa shifted from branching corals to massive corals from the families *Poritidae*, *Faviidae*, and *Agariciidae*, as branching corals were the most affected (Edwards et al. 2001, Loch et al. 2002).

Similarly, the 2016 bleaching event found that while branching acroporids were highly susceptible to bleaching, massive poritids, faviids, and agaraciids were less so (Ibrahim et al. 2017).

Coral populations gradually recovered following 1998. However, the mass bleaching event in 2016 along with periodic disturbances from subsequent "minor" bleaching events (i.e. 2003, 2006, 2010), tsunamis (2004), and outbreaks of crown of thorns and cushion starfish (*Acanthaster planci* and *Culcita schmedeliana*, respectively; 2015) have slowed recovery and have further contributed to shifts in coral diversity across the archipelago (Goffredo et al. 2007, Lasagna et al. 2008, 2010, Morri et al. 2015, Pisapia et al. 2016, Pisapia et al. 2019).

Despite national strategies to minimize environmental impacts associated with coastal development, there is a limited capacity to mitigate and monitor development impacts and enforce national guidelines.

Coastal Development

Further affecting the recovery of the reefs are coastal developments—often unavoidable and necessary, as many projects are implemented to ensure the development of basic infrastructure, shelter growing populations, meet various needs and wants of expanding local communities, and meet the demands of an ever-growing tourism industry.

These coastal developments, which can include harbor construction, airport development, waste management systems, beach enrichment, coastal protection, and housing projects, often, though not always, require some amount of land reclamation and dredging.

With an area of only 227 km^2 (Ministry of Environment and Energy [MEE] 2015), dry land is one of the scarcest and most limited resources of the nation and one that often has to be artificially procured through these processes.

Sedimentation and siltation associated with these activities can smother and kill coral and hinder recovery and resilience of local reefs (Jaleel 2013, Pancrazi et al. 2020). While coral mining was once a common method of procuring building materials in the Maldives, removing hundreds of thousands of cubic meters of coral over the years (Brown and Dunne 1998), pioneering regulations introduced in the 1990s banned this practice, relieving mining pressure from Maldivian reefs (Jaleel 2013).

Sewage and/or grey water runoff can impact adjacent reefs, with instances of nitrogen loading (Heikoop et al. 2000) where waste is not properly managed.

Despite national strategies to minimize environmental impacts associated with coastal development, there is a limited capacity to mitigate and monitor development impacts and enforce national guidelines.

Tourism

The tourism industry in the Maldives has been growing since its establishment in 1972, and is now the nation's current major contributor to its Gross Domestic Product (National Bureau of Statistics 2019).

The industry has begun to expand beyond the traditional "one island, one resort" concept, a concept of developing uninhabited islands into resorts, to include hotels and guest houses on inhabited islands as well as safari boats (Ministry of Tourism 2019).

Currently, there are 162 registered resort islands (Ministry of Tourism 2020) within the Maldives, and many of the coastal developments that take place within the nation are either resort island developments or developments within established resort islands (e.g., beach nourishment, construction of bungalows, harbor expansions, seagrass removal).

While some studies have suggested that tourist resorts can offer a protective respite for reefs (e.g., Moritz et al. 2017), others have suggested the opposite (e.g., Domroes 2001, Scheyven 2011, Cowburn et al. 2018), indicating that the effect of tourist resorts on coral reefs may differ on a case-by-case basis.

Fisheries

Fishing, especially for tuna, was historically the backbone of the local economy, providing employment, sustenance, and foreign exchange until the establishment and development of the tourism industry. Despite the current prominence of the tourism sector, fishing and fishing-related activities remain the primary means of employment and income for many of the local island populations.

Fishing provides employment to about 74% of the workforce within the primary (fishing and agriculture) industries (National Bureau of Statistics 2018). The Maldives has a long history of being a tuna fishing nation despite having easy access to large areas of reef with an abundance of reef associated fin fishes (Adam et al. 1997; Yadav et al. 2019).

The Maldives pole-and-line skipjack tuna fishery has been recognized for its sustainability through Marine Stewardship Council (MSC) certification since 2012 (MSC 2020), and has been recognized among small island and coastal nations in regional fisheries management bodies when advocating for the sustainable harvest of tuna.

Reef Fisheries

The growth of the tourism industry, however, has led to the development of a growing reef fish fishery in the Maldives over the past few decades (Sattar et al. 2014). The tourism sector engages in recreational fishing activities and is a major contributor to reef fish consumption. It is therefore a large contributor to total reef fish harvests.

Reef fish have also gained popularity with locals, many of whom now consume reef fish on a weekly basis (Sattar et al. 2014). Despite the diverse abundance of species, Maldivians consume a limited variety of reef fishes. The most commonly caught reef fish are lutjanids (snappers), lethrinids (emperors), carangids (jacks), and serranids (groupers) (Sattar et al. 2014).

In addition to the reef fish fishery, an export-based fishery specifically targeting groupers began operating out of the Maldives beginning in 1994, with over 600 tons of fresh, chilled, and live grouper exported to countries such as Thailand, Taiwan, and Hong Kong in 2010 (Sattar et al. 2011).

Other reef-based fisheries operating in the Maldives are an export-based aquarium fishery, a sea cucumber fishery, and a small lobster fishery to supply the local markets. Invertebrates such as sea cucumbers are not consumed locally, and other invertebrates such as bivalves and molluscs are not harvested commercially.

While an export-oriented giant clam fishery operated in the early 1990s, harvesting of giant clams was quickly prohibited due to concerns of overexploitation of clam stocks (Basker 1991, Ahmed et al. 1997).

The aquarium and sea cucumber fisheries, though minor compared to the other fisheries in the Maldives, have been operating as export-oriented fisheries since 1979 (Adam 1996) and 1985 (Adam et al 1997), respectively.

Fishing provides employment to about 74% of the workforce within the primary (fishing and agriculture) industries (National Bureau of Statistics 2018).

A school of Powder-blue surgeonfish (*Acanthurus leucosternon*) mixed with Dusky surgeonfish (*Acanthurus tristis*) in the forefront with Shabby parrotfish (*Chlorurus sordidus*) in the background.

Photo Credit // © Emanuel Gonçalves

Shark Fisheries

Prior to 2010, an export-based shark fishery also operated in the Maldives (Sinan et al. 2011). Beginning in the 1980s, the government of the Maldives began regulating shark fishing, until finally declaring a complete ban on shark fishing throughout the nation's entire Exclusive Economic Zone (EEZ) in 2010, followed by a complete trade ban in 2011 (Sinan et al. 2011).

While the shark fishery was very minor compared with the tuna fishery, it was a prominent livelihood activity on some islands. While there is some anecdotal evidence of increasing shark populations negatively impacting tuna catch, the presence of some shark species, such as the silky shark (*Carcharhinus falciformis*), are believed by fishermen to actually increase tuna catch (Ali and Sinan 2015).

In addition, healthy shark populations have been shown to be an important asset to the dive-tourism industry in the Maldives (Anderson and Waheed 2001, Zimmerhackel et al. 2018).

One estimate suggests that increasing shark populations in the Maldives could increase dive trip demand by tourists by up to 15%, leading to annual economic benefits of >US $6 million per annum (Zimmerhackel et al. 2018).
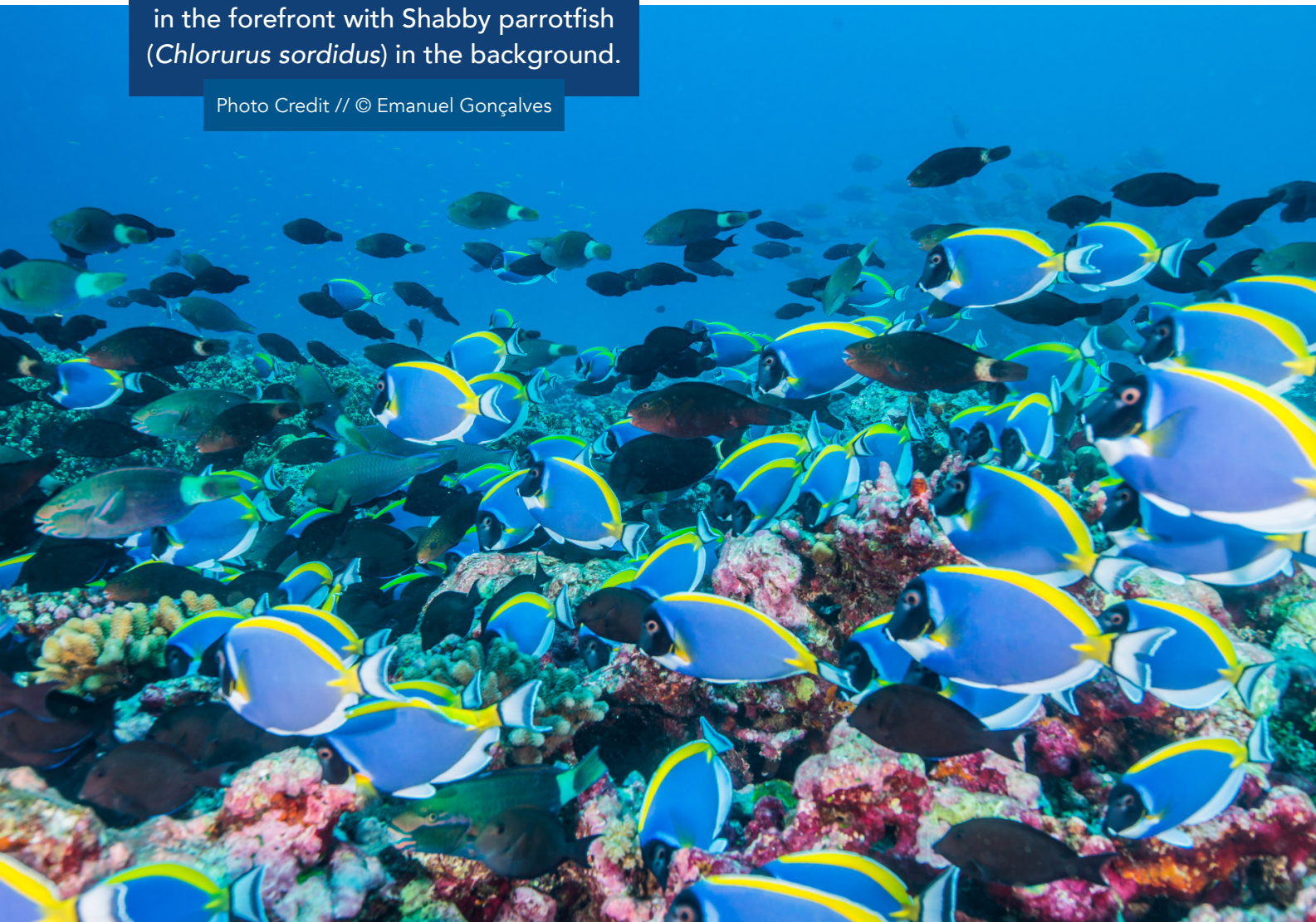
Management Partnerships

In 2019, the Waitt Institute, as the organizing body of the Blue Prosperity Coalition, partnered with the Government of the Maldives to develop a plan for effective marine management, aiming to protect and value the ocean and its resources to build a bright future for communities, the economy, and the environment. This partnership, named Noo Raajje or "Blue Maldives", will accomplish these goals through the work pillars of marine spatial planning, blue economy, sustainable fisheries, and marine protection.

The Noo Raajje team is based in the Maldives with international support from the Blue Prosperity Coalition and Waitt Institute. The program is led by the Government of the Maldives, including the President's Office, the Ministry of Fisheries, Marine Resources and Agriculture, and the Maldives Marine Research Institute. The program is collaborative and will work closely with local and international organizations, ocean stakeholders, and the public to make a comprehensive plan for future ocean health.

The goals of the program include, but are not limited to, the following:

- to develop a comprehensive marine spatial plan based on the best available science, which designates at least 20% of Maldivian waters as marine protected areas using sound scientific data;
- develop a joint research program focused on coral reefs, fisheries, and biodiversity;
- and to ensure sustainable ocean management to support local livelihoods, the national economy, and long-term sustainability of Maldivian marine resources (Government of the Maldives and Blue Prosperity Coalition, 2019).

This report serves to inform the marine spatial planning efforts identified in this partnership, and the research priorities for this study have been determined in consultation with the Maldives Marine Research Institute (MMRI) in order to inform the specific management goals in the Maldives.

Here, we focus on six important elements of coral reef ecosystems:

1. coral reef fishes;
2. reef-building corals;
3. benthic community structure;
4. coral recruitment;
5. macroinvertebrates; and
6. water quality.

This survey aims to present a baseline assessment of coral reefs across the Northern and Central Maldives archipelago to provide actionable data to the marine spatial planning process, by addressing the following key research objectives.

The goal for this assessment was to conduct a spatially expansive assessment across the Maldives, focusing on a single habitat type (forereef), depth (10m), and exposure (western side of each atoll) during a single season (North East Monsoon).

While all efforts were made to ensure the data collected as part of this assessment are representative of the entire archipelago, logistics related to weather, dive safety, and the global COVID-19 pandemic restricted the geographic extent, depths, and site locations available for survey.
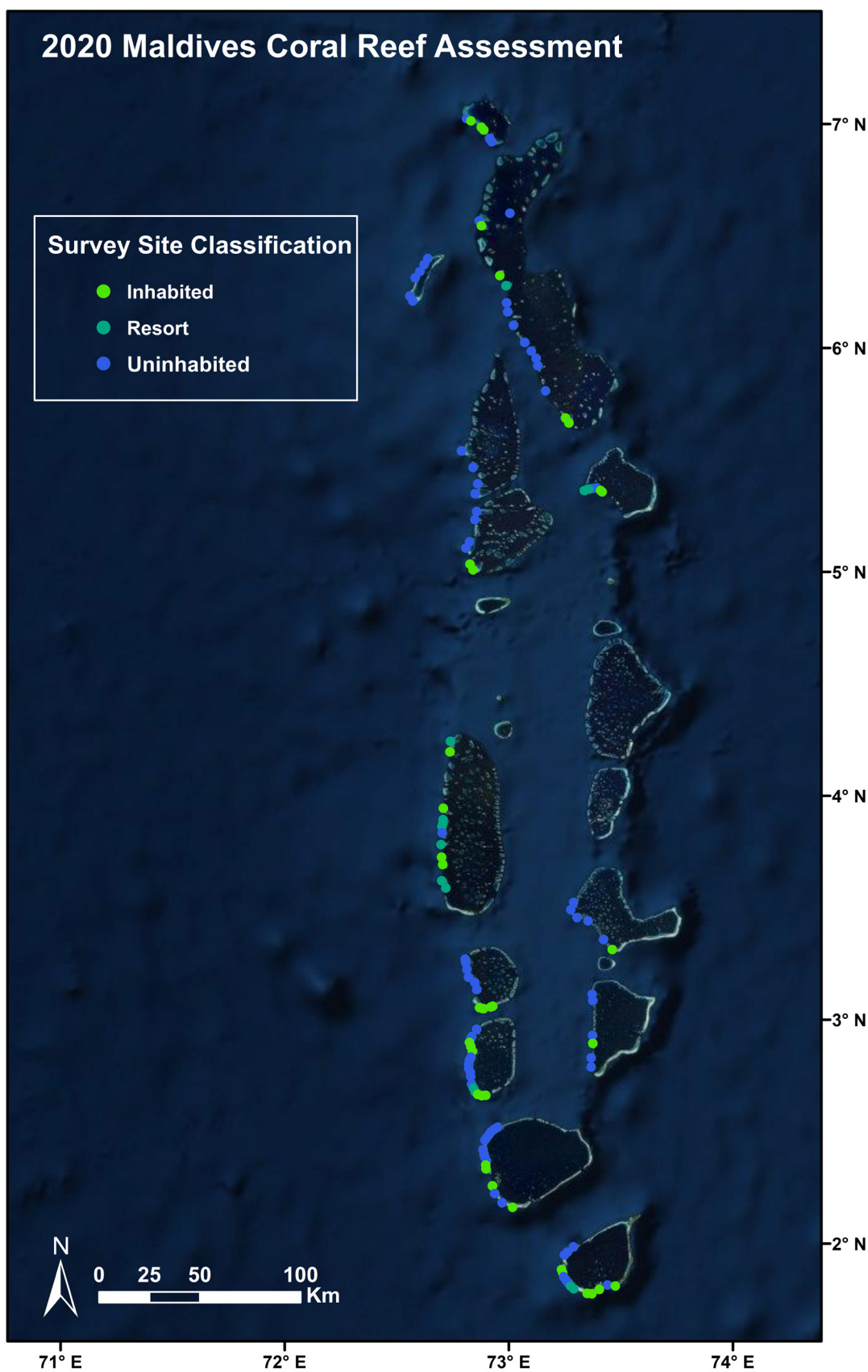
APPROACH

An ornate ghost pipefish (*Solenostomus paradoxus*) camouflaged on the reef.

The Survey

In January and February of 2020, the Waitt Institute partnered with researchers from Scripps Institution of Oceanography (USA), the University of Western Australia (Australia), MMRI (Maldives), and the Small Island Research Group (Maldives) who were partnered with MMRI, to conduct surveys of reef fish populations, benthic coral reef communities, marine macroinvertebrates, and water quality parameters at 127 sites in the Northern and Central Maldives **(Figure 1)**.

Support Team

The survey efforts were aided by personnel from Oceano Azul Foundation (Portugal), IUCN Maldives (Maldives), Maldives Coral Institute (Maldives), the Environmental Protection Agency (Maldives), Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE) (French Polynesia), Vava'u Environmental Protection Association (VEPA) (Tonga), University of California Santa Barbara (USA), NEKTON (UK), and University of Hawai'i (USA).

A summary of the sites surveyed, as well as the corresponding metadata can be found in Appendix 2.

Due to travel restrictions put in place as a response to the COVID-19 global pandemic, field operations were suspended before any sites surrounding North and South Malé Atolls or the Southern atolls (Huvadhoo Atoll, Addu Atoll, and Fuvahmulah) could be surveyed.

Therefore, this report focuses on the reefs of the Northern and Central Maldives; additional expeditions to survey the remaining sites will be conducted in 2021.

The uninhabited island of Keylakunu, which became a protected area in 2019.

Photo Credit // © Nizam Ibrahim

Site Selection

Sites were selected with the goal of providing a systematic snapshot of coral reef communities across the Northern and Central Maldives. Islands in the Maldives are officially designated by the government into various island use types based on the dominant human activities undertaken on each island.

Island Use Types

Based on these island use designations, sites included in this study were classified into three island use types:

- uninhabited,
- inhabited,
- and resort islands.

Uninhabited islands do not have any permanent human settlement, while inhabited islands have permanent settlements of varying sizes. Resort islands are designated specifically for tourism-related activities and follow a one-island, one-resort model, where each island is occupied by a single resort.

While designated resort islands do not have non-tourism-related community settlements, some inhabited islands now support tourism-related activities through guesthouses or hotel-based tourism.

Site Distribution

Sites were distributed randomly along forereef habitats at each atoll with a minimum of 2 km spacing between each site. Because the survey took place during the North East monsoon season, sites on the western sides of atolls were preferentially selected in order to ensure safe diving conditions.

Sites that were within 2 km of an island designated as a resort or inhabited island (as reported by the Ministry of Fisheries, Marine Resources, and Agriculture) were classified with the island use type of the closest island; sites that were within 2 km of an uninhabited island, or >2 km from any emergent land were designated as uninhabited. Therefore, some uninhabited sites are not associated with an emergent island, which may affect oceanographic dynamics at these sites. Overall, 74 uninhabited, 39 inhabited, and 14 resort islands were surveyed.

In addition, large-area imagery data was collected at a site within a marine protected area in the far north (HAD-PRES), and these data were included in the coral recruit and rugosity analyses. No fish, invertebrate, photoquadrat, or water quality data were collected at this site.

A list of the site designations and the protocols for selecting and designating sites can be found in Appendices 1 and 2.

Results are presented at the atoll and island use type level. While atolls in the Maldives are officially designated both geographically and administratively, the results presented here separate atolls using a mix of geographic and administrative atoll designations in order to understand the ecology associated with each reef structure.

For example, Makunudhoo is presented separately to Haa Dhaalu, despite the two being in the same administrative atoll.

(It should also be noted that although Makunudhoo is technically a faro (Naseer and Hatcher 2004), it is categorized as an atoll in this report.)

Survey effort varied from atoll to atoll, from two sites at Haa Dhaalu to 18 sites at Dhaalu.

Indicators

At each site, the following indicators of reef health were surveyed:

1. reef fish, reef shark, and large bodied fish abundance, diversity, and biomass;
2. benthic community composition, including percent cover and diversity of benthic taxa;
3. the abundance of juvenile corals;
4. reef rugosity;
5. the abundance and diversity of benthic macroinvertebrates;
6. and water quality parameters.

Unfortunately, due to laboratory closures as a result of the COVID-19 pandemic and other logistical constraints, the water quality and reef shark and large bodied fish abundance data were not available at the time of reporting and will be reported at a later date.

Survey methods were designed to provide comprehensive summaries of each indicator and in some cases to give specific information regarding species of ecological and/or economic significance.

A brief summary of the survey methods used can be found in Table 1, and full methods can be found in Appendix 1.

Table 1: Survey Methods

Key metric	Significance to reef health	Method	Units
Reef fish abundance, diversity, biomass	Healthy reefs are able to support diverse, abundant fish communities, as well as higher fish biomass. Overfished reefs will tend to have lower biomass and diversity. Important trophic groups, such as herbivores, promote reef health by removing macroalgae and creating space for coral recruitment.	Belt transect surveys	Biomass: g/m^2
			Abundance: individuals/m^2
		IUCN presence/absence surveys	Presence/absence
Reef sharks and large-bodied fish abundance, diversity, biomass*	Large-bodied predators, such as sharks, play an important role in reef ecosystems, but are often underestimated using traditional survey techniques such as belt-transects.	Baited Remote Underwater Video (BRUV)	Biomass: g/m^2
			Abundance: individuals/m^2
Benthic community composition	Corals are the building blocks of coral reefs, so higher coral cover is indicative of healthier reefs. Competitors such as macroalgae can outcompete corals for space, reducing reef health.	Photoquadrats	Percent cover
Juvenile coral abundance	Coral recruits are the incoming generation of coral colonies, and higher numbers likely represent greater resilience of the coral community to rebound following a mortality event.	Large-area imagery	Individuals/m^2
Reef rugosity	More complex (higher rugosity) reefs provide more habitat for important coral reef species, such as fish and invertebrates.	Large-area imagery	Rugosity ratio (ratio of surface distance [measured at 10 cm intervals]/linear distance)
Macroinvertebrate abundance & diversity	Macroinvertebrates such as herbivorous urchins can clear reefs of macroalgae. Other invertebrates, such as sea cucumbers, crustaceans, and bivalves are important food/fisheries resources.	Transect surveys	Individuals/site
Water quality*	Poor water quality can stress reefs by causing macroalgal blooms, promoting coral disease, increasing bioerosion, etc.	Stable isotope (δ13C–δ15N) approaches	Stable isotope ratio

Table 1: Summary of methods used to survey the key indicators of reef health. Parameters with an asterisk (*) are not included in this report and will be reported at a later date.

RESULTS

Andy Estep and Aya Naseem survey coral cover and benthic life along a transect line.

Photo Credit // © Emanuel Gonçalves

OVERVIEW

This section provides results from the fish, benthic, and invertebrate surveys undertaken in the Northern and Central Maldives. In order to understand patterns both geographically and based on a gradient of human impacts, the results of these surveys are grouped by atoll as well as by island use type.

Fish

In total, 415 fish species were recorded during fish belt transect surveys (see Appendix 3 for a full species list), and an additional 26 species were noted in the IUCN presence/absence surveys. Four species were present in belt transects at all 127 survey sites: *Melichthys indicus*, *Labroides dimidiatus*, Centropyge multispinnis, and *Chromis dimidiata.*

The IUCN Red Listed (endangered) humphead wrasse (*Cheilinus undulatus*) contributed to the greatest proportion of total fish biomass of any fish species surveyed, with a mean biomass of 3.0 g/m² (± 1.8 SE; **Appendix 3**).

The fish communities in the Maldives are characterized by a high density of small-bodied planktivores, moderate densities of large-bodied herbivores, and low densities of top predators and sharks (**Figures 2, 3**).

Fish trophic groupings were determined using diet information from FishBase and the published literature. At five atolls (Baa, Laamu, Lhaviyani, Makunudhoo, and Raa), herbivores made up over half of the total fish biomass (**Figure 3**), despite comprising, on average, only 18% of the overall numeric density.

This pattern was most obvious at Makunudhoo, where the mean density of herbivores was only 1.4 individuals/m² (± 0.2 SE), yet the mean herbivore biomass was 241.0 g/m² (± 44.1 SE). Herbivore biomass at this atoll was split approximately evenly between acanthurids and scarids (**Figure 4**).

FIGURE 2: Mean fish density at each atoll surveyed, broken down by trophic group. The horizontal dashed line represents the overall mean fish density for the archipelago.
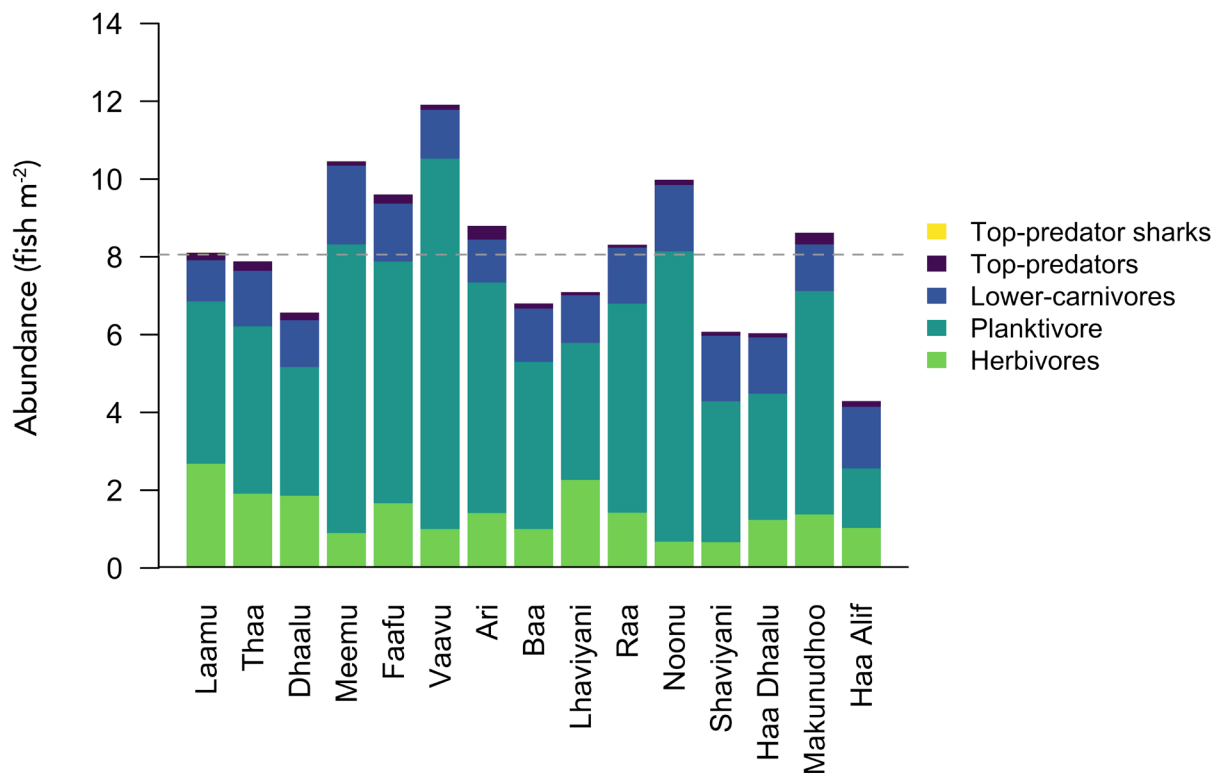
FIGURE 3: Mean fish biomass at each atoll surveyed, broken down by trophic group. The horizontal dashed line represents the overall mean fish biomass for the archipelago.
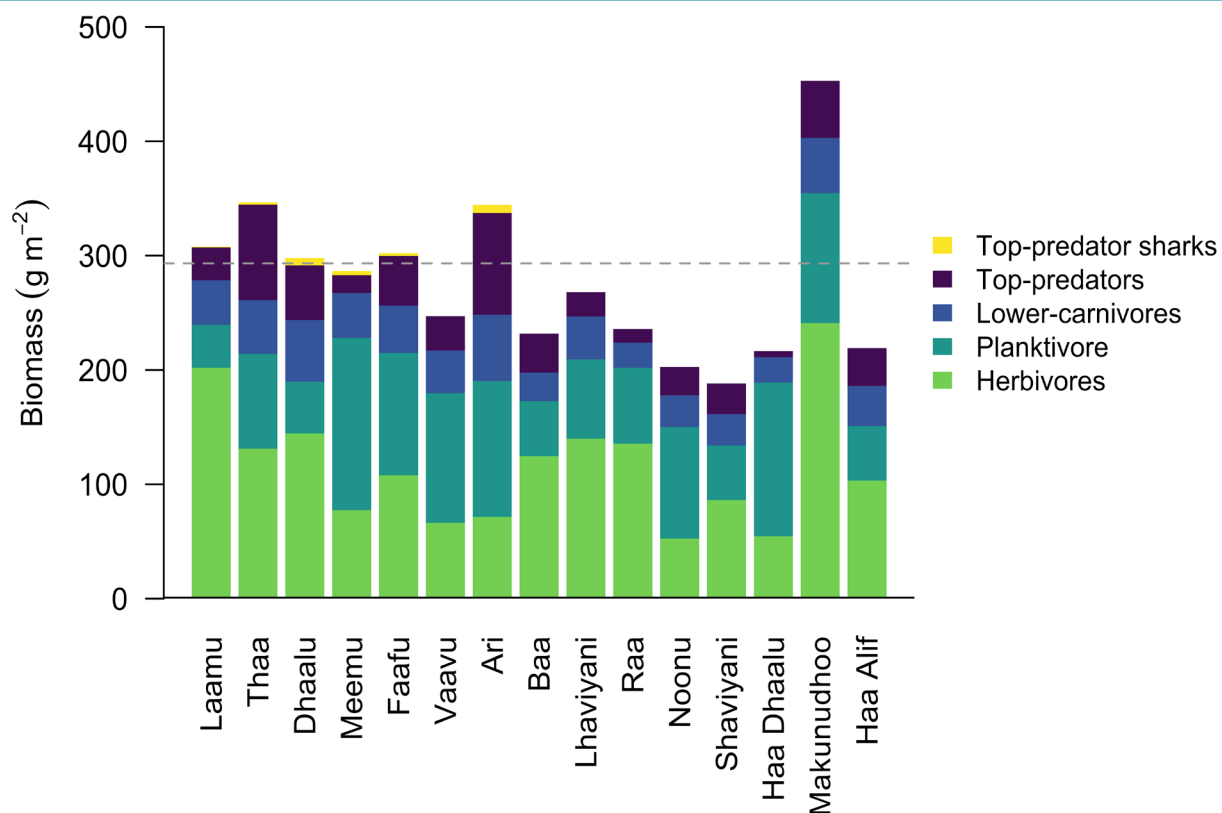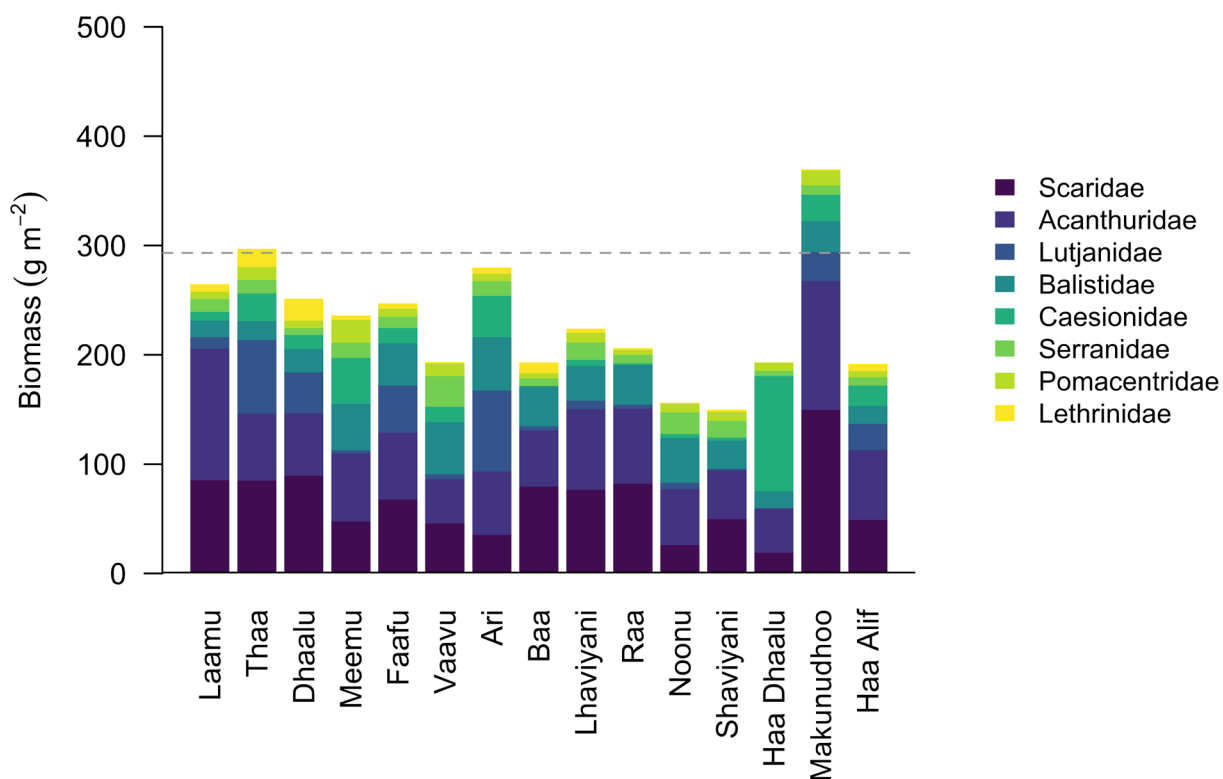

FIGURE 4: Mean biomass of key fish families at each atoll surveyed. The horizontal dashed line represents the overall mean biomass for the archipelago.

Indeed, scarid species such as *Cetoscarus bicolor*, *Chlorurus strongylocephalus* and *Scarus prasiognathos*, as well as acanthurid species such as *Naso brachycentron*, *Naso hexacanthus*, and *Naso unicornis* had among the highest overall biomass of any species surveyed during this study (**Appendix 3**).

Overall, there were no significant differences in fish populations between the three island use types **(Figure 5)**.

Analysis of variance (ANOVA) results showed no differences between fish biomass in any trophic categories between different island use types ($p=0.36$ for herbivores, $p=0.56$ for planktivores, $p=0.93$ for lower carnivores, $p=0.73$ for top predators, and $p=0.98$ for sharks).

Fish biomass did not vary latitudinally, either; an ANOVA showed no significant difference between biomass in the North and Central Atolls ($p=0.98$; **Figure 6**).

Although the numeric density of top predators was fairly consistent across the sites surveyed (**Figure 3**), top predator biomass tended to be higher in the Central Atolls. In particular, Ari and Thaa atolls had high levels of top predator biomass compared to other atolls, which was largely driven by the higher biomass of lutjanids at these locations.

Sharks were only observed in the belt transect surveys from Ari Atoll southward (**Figures 3, 6**). While belt transect surveys can sometimes underestimate the abundance and biomass of larger species such as sharks (Richards et al. 2010), this pattern is consistent with the results of the IUCN presence/absence surveys, which found higher incidences of sharks in the Central Atolls (**Figure 7**).

Conversely, rays were more commonly sighted in the Northern Atolls, with several species only present from Baa Atoll northward. On average, sites in the Central Atolls had a higher incidence of, and a higher diversity of, large-bodied species than those in the Northern Atolls.

The IUCN presence/absence surveys showed a higher diversity of Red Listed species in the Central Atolls (**Figure 7**). Similarly, each site in the Central Atolls tended to have more Red Listed species present on average than sites in the Northern Atolls.

FIGURE 5: Mean fish biomass by trophic group, broken down by island use type.
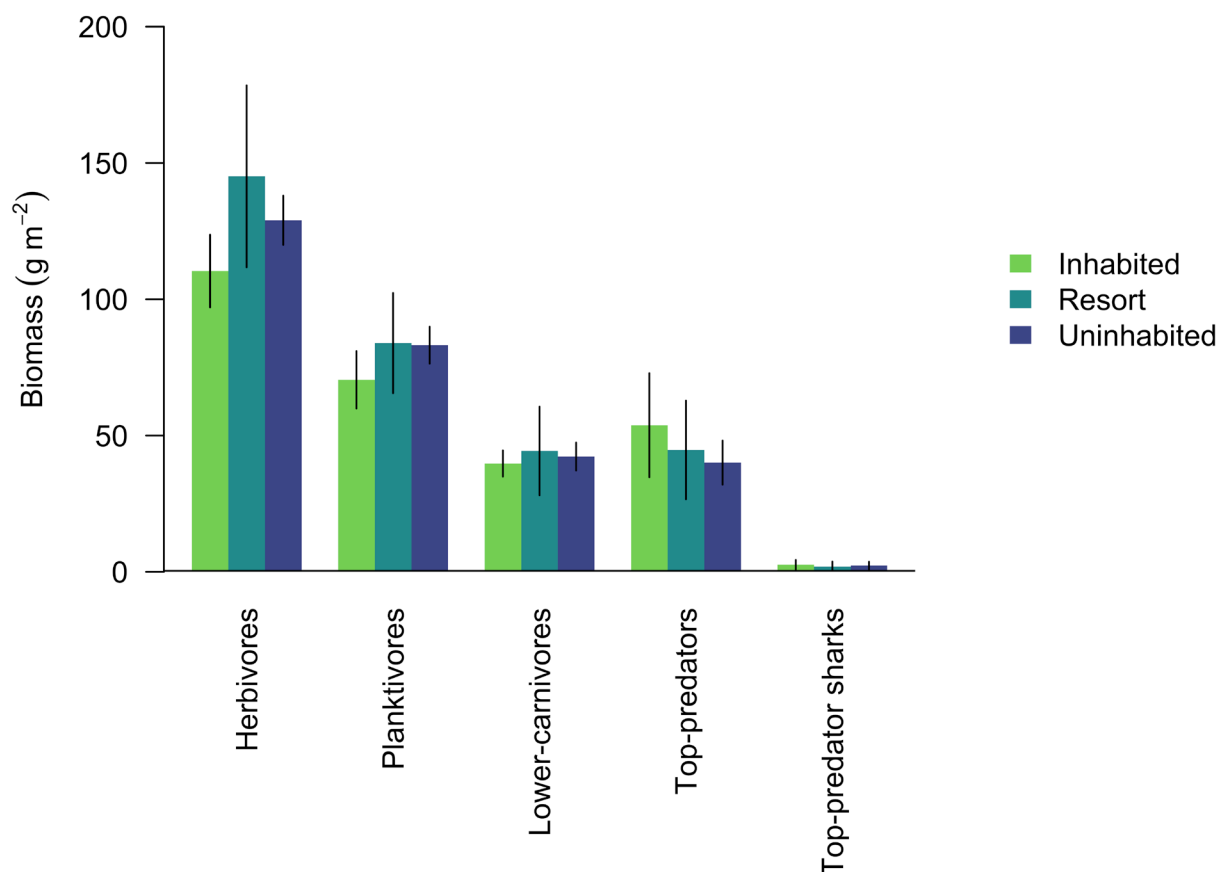
FIGURE 6: Map of mean fish biomass by trophic group at each of the atolls surveyed. The size of each circle represents the overall mean biomass at each atoll.
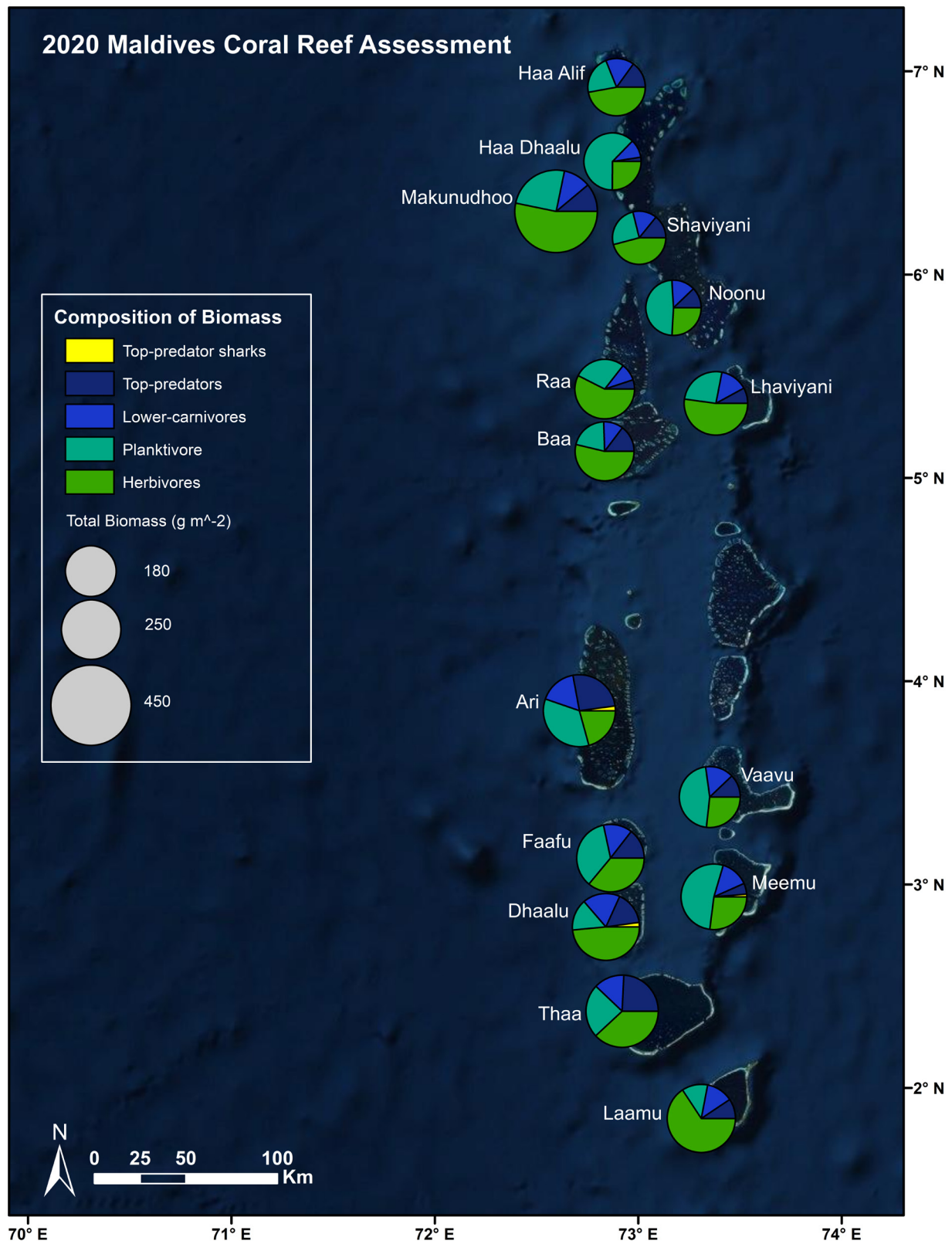
FIGURE 7: Geographic distribution of IUCN Red Listed species surveyed in the presence/absence surveys. Species are categorized by IUCN threat level: DD=data deficient, NT=near threatened, V=vulnerable, EN=endangered. The size of each circle represents the average number of Red Listed species present at each site surveyed.
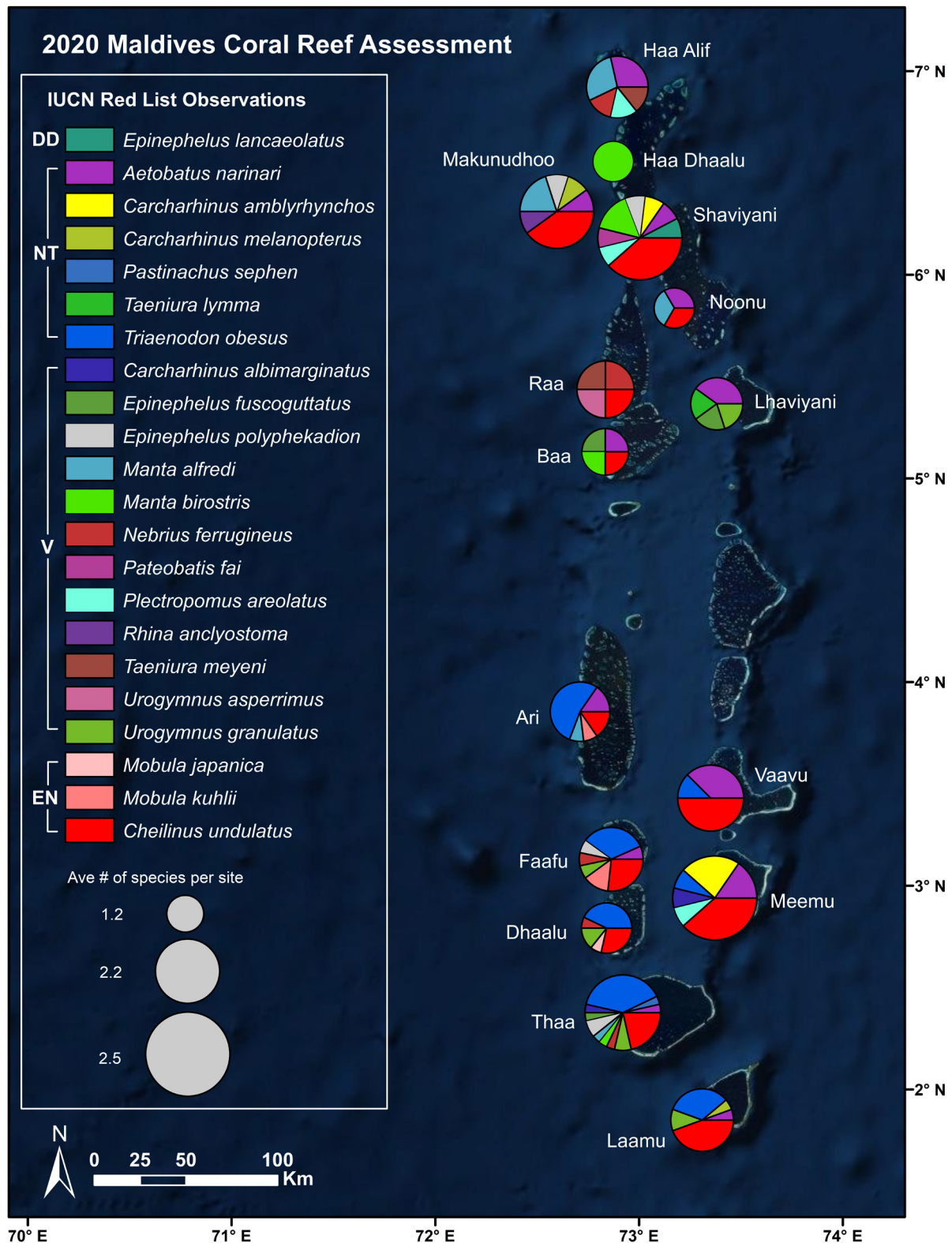
Benthic Cover

Across the sites surveyed, reefs were characterized by a high mean percent cover of turf (55.4% ± 0.33 SE), moderate mean cover of hard coral (19.4% ± 0.22 SE) and crustose coralline algae (CCA; 16.9% ± 0.22 SE), and extremely low mean cover of fleshy macroalgae (0.284% ± 0.02 SE).

The highest mean hard coral cover was found at Ari Atoll (33.2% ± 0.88 SE), while Makunudhoo had the lowest (11.2% ± 0.64 SE; **Figures 8, 9**).

Notably, fleshy macroalgae cover was found to be extremely low across all atolls with a maximum mean cover of only 1.7% (± 0.24 SE) at Vaavu Atoll (**Figures 8, 9**). This is likely due to the high abundance of large herbivores noted on reefs across the archipelago (**Figure 3**).

Benthic cover did not vary as obviously between the different island use types (**Figure 10**). For example, mean coral cover ranged from a low of 17.4% (± 0.37 SE) at inhabited island sites to a high of 22.0% (± 0.88 SE) at resort islands.

However, a Kruskal-Wallis test with a subsequent Dunn's procedure for pairwise comparisons showed significant differences in coral cover between inhabited and resort islands (Dunn's p=0.029) and between inhabited and uninhabited islands (Dunn's p<0.001).

In both cases, inhabited islands had significantly lower coral cover. However, coral cover did not differ significantly between resort and uninhabited islands. CCA followed the opposite pattern, with significantly more CCA at inhabited versus resort islands (Dunn's p=0.007) and at inhabited versus uninhabited islands (Dunn's p<0.001).

Percent cover of turf only differed significantly between inhabited and uninhabited islands (Dunn's p<0.001). Macroalgae (including both fleshy and calcified macroalgae) differed significantly across all island types.

FIGURE 8: Mean percent cover of main benthic functional groups at each atoll surveyed.
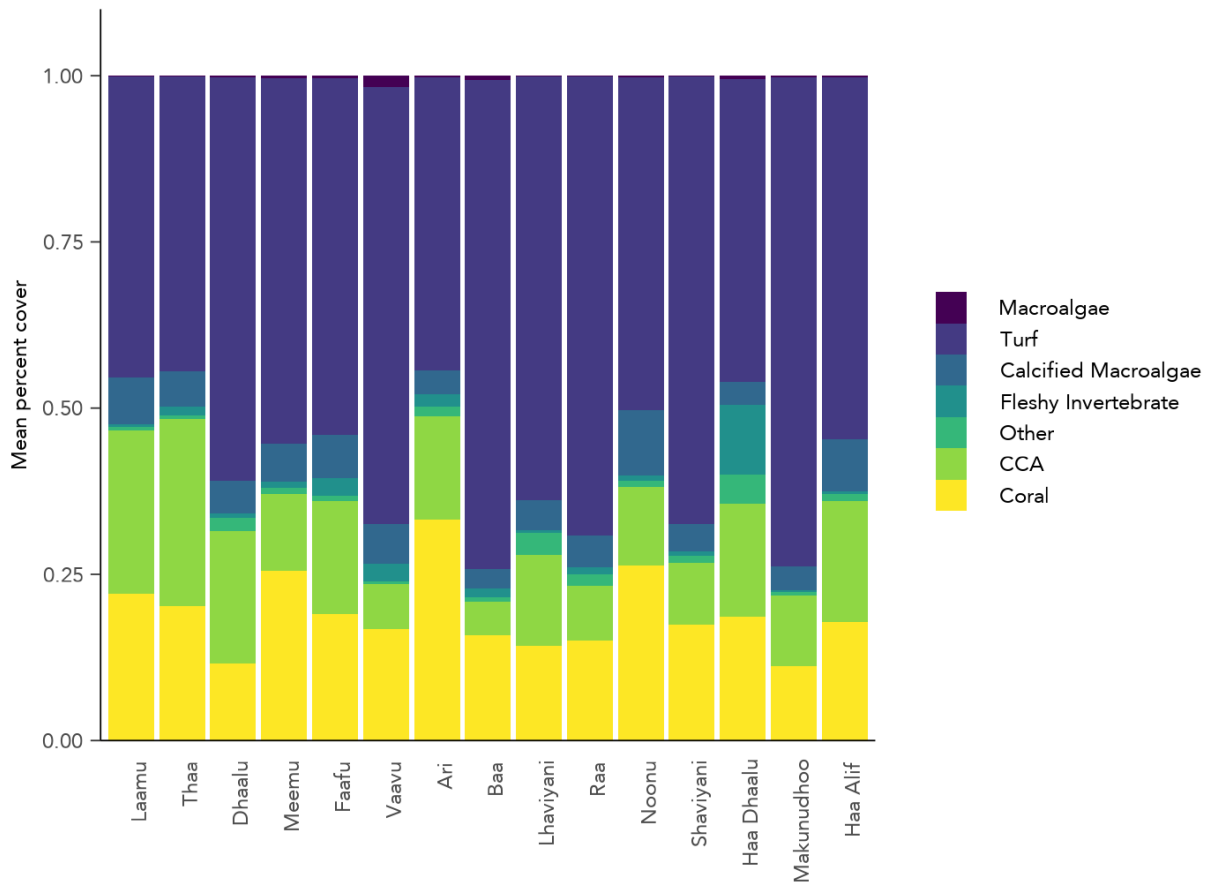
FIGURE 9: Mean percent cover of main benthic functional groups at each atoll surveyed.
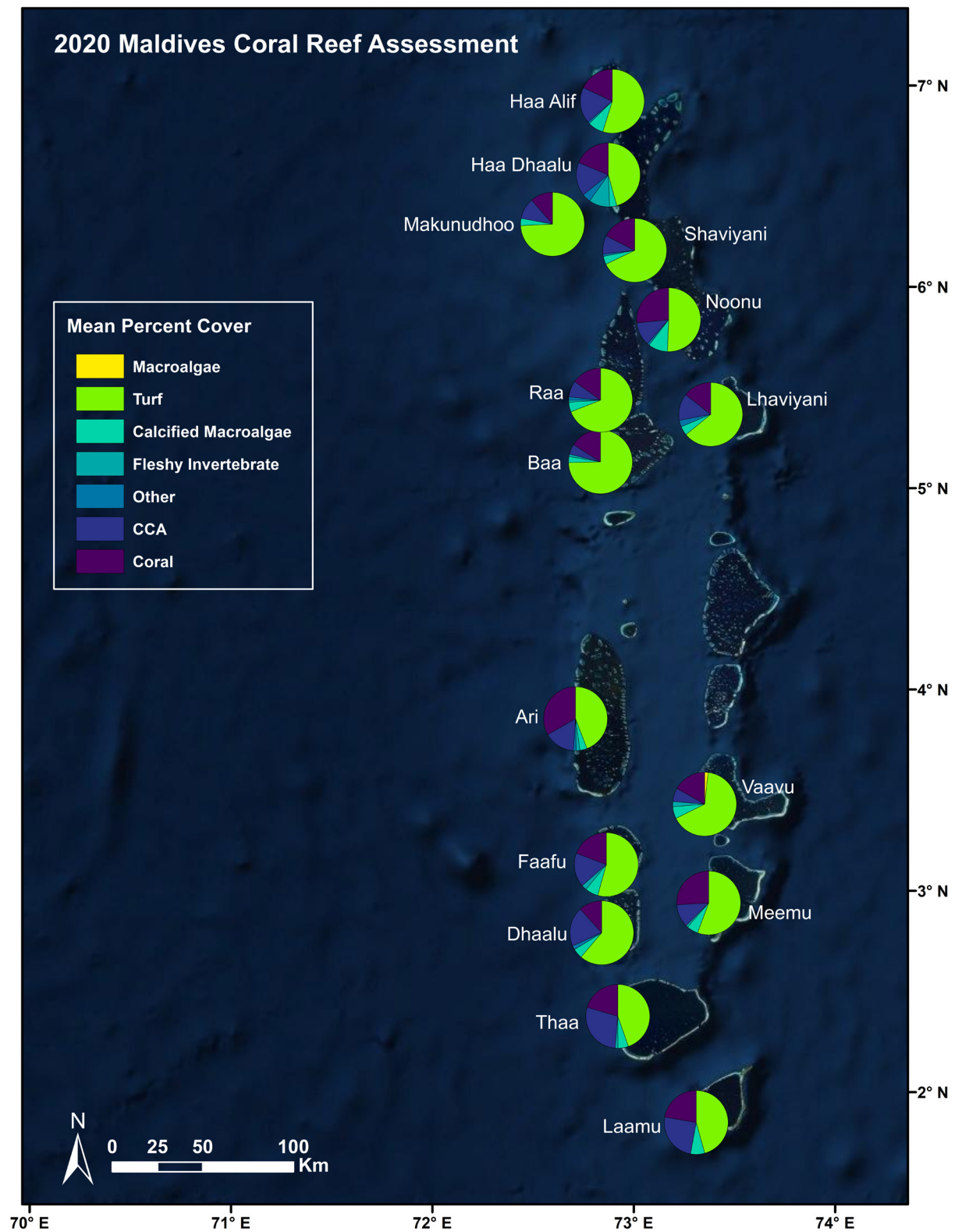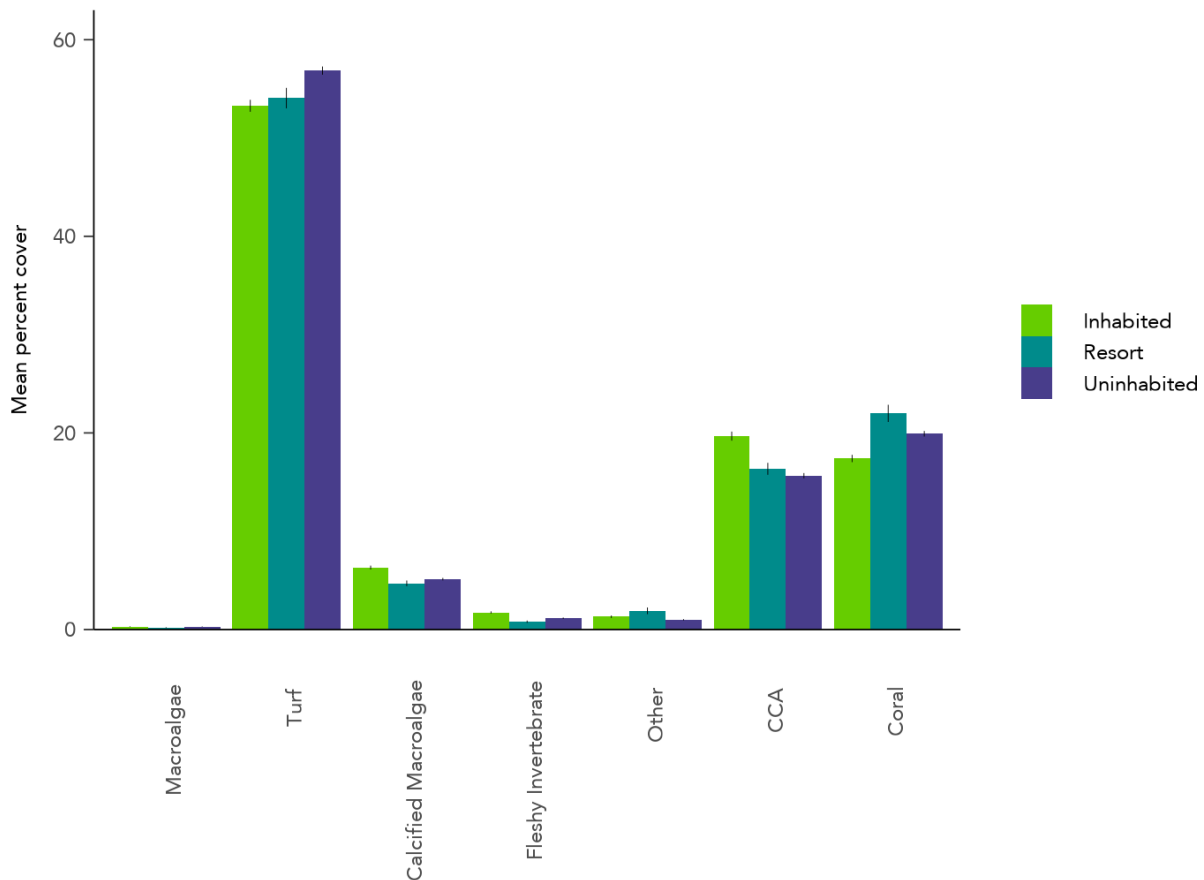
Overall patterns of coral diversity were similar across the sites surveyed, with a few notable exceptions (**Figure 11**). At all atolls except for Ari, *Porites* was the dominant coral genus, with mean percent cover ranging from 5.9% (± 0.44 SE) at Makunudhoo to 17.3% (± 0.98 SE) at Noonu, and an overall mean percent cover of 9.9% ± (0.16 SE).

While *Acropora* ranked second in overall mean cover across the archipelago (2.4% ± 0.11 SE), this was driven mostly by particularly high *Acropora* cover at Ari, where this genus accounted for 14.3% (± 0.77 SE) cover on average.

At all other atolls, mean *Acropora* cover was approximately 2.5% or less. *Pocillopora* and *Montipora* were also relatively abundant across all atolls, averaging 2.3% (± 0.06 SE) and 1.1% (± 0.04 SE) cover, respectively. While 37 genera of hard coral were recorded as part of the benthic surveys, the 33 least-abundant genera each made up less than 1% of the overall benthic cover across the archipelago (see **Appendix 4** for a full list of coral genera).

Porites was the dominant genus at inhabited and uninhabited islands (mean cover=8.5% ± 0.25 SE and 11.6% ± 0.23 SE, respectively), while *Acropora* dominated at resort islands (mean cover=9.5% ± 0.68 SE; **Figure 12**). However, the latter pattern is likely driven by high *Acropora* cover at resort islands in Ari Atoll, and is not necessarily representative of all resort islands across the archipelago.

Nevertheless, mean cover of *Porites* and *Acropora* differed significantly across all island use types (Kruskall-Wallis test, p<0.001 for both genera). *Pocillopora* cover differed significantly between inhabited and resort islands (Dunn's p=0.02) and between resort and uninhabited islands (Dunn's p=0.009), but not between inhabited and uninhabited islands. *Montipora* cover did not differ significantly between island types.

FIGURE 11: Heatmap of the mean percent cover of most abundant coral genera at each atoll. Grey cells represent instances where the genus was not present at the corresponding atoll. Coral genera are ranked in order of overall abundance.

FIGURE 12: Heatmap of the mean percent cover of most abundant coral genera at each island use type. Coral genera are ranked in order of overall abundance.
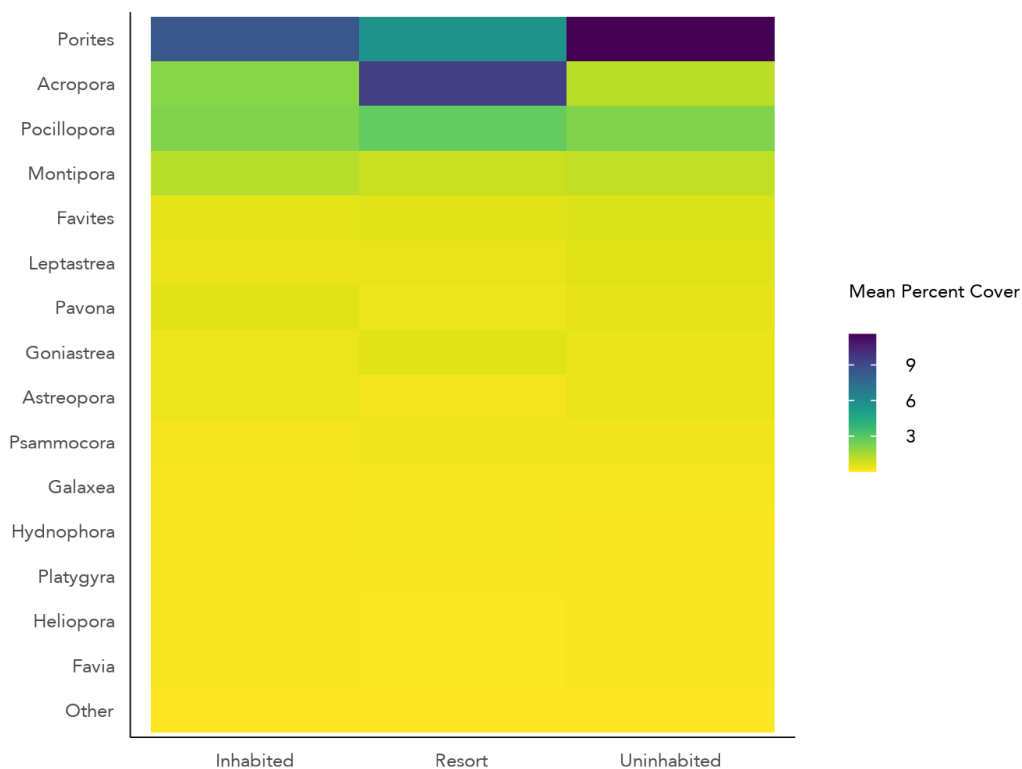
Coral Recruitment

Coral juveniles were defined as individual corals of with a diameter of 5 cm or less. Juvenile coral density varied widely across the sites surveyed, but was generally relatively high, with an overall mean value of 14.3 individuals/m². The highest mean juvenile density was found at Vaavu, which had on average 23.3 individuals/m² (± 3.7 SE; **Figure 13**).

In contrast, Laamu and Haa Dhaalu had the lowest mean juvenile densities (10.1 individuals/m² ± 1.0 SE and 10.1 individuals/m² ± 4.8 SE, respectively). All but four atolls (Meemu, Noonu, Raa, and Vaavu) had mean juvenile densities between 10 and 15 individuals/m². Site NOO_039 at Noonu had the highest mean juvenile coral density of all the sites surveyed, with an average of 55.6 individuals/m² (± 5.9 SE).

Recruitment was highest at uninhabited islands, where mean juvenile density was 15.8 individuals/m² (± 1.0 SE), and lowest at inhabited islands, where mean density was 12.2 individuals/m² (± 0.8 SE; **Figure 14**).

It should be noted that juvenile coral analysis was not possible at 13 sites due to problems with image quality (n=2 sites at Dhaalu, 2 sites at Raa, 1 site at Baa, 5 sites at Thaa, and 3 sites at Laamu; n=1 inhabited island site, 1 resort island site, and 11 uninhabited island sites).

Juvenile coral density varied widely across the sites surveyed, but was generally relatively high, with an overall mean value of 14.3 individuals/m².

A well-developed colony of *Echinopora spp.*

FIGURE 13: Mean coral recruit density at each atoll surveyed. Bold horizontal lines represent the median value for each atoll.

FIGURE 14: Mean coral recruit density at each island use type. Bold horizontal lines represent the median value for each island type.
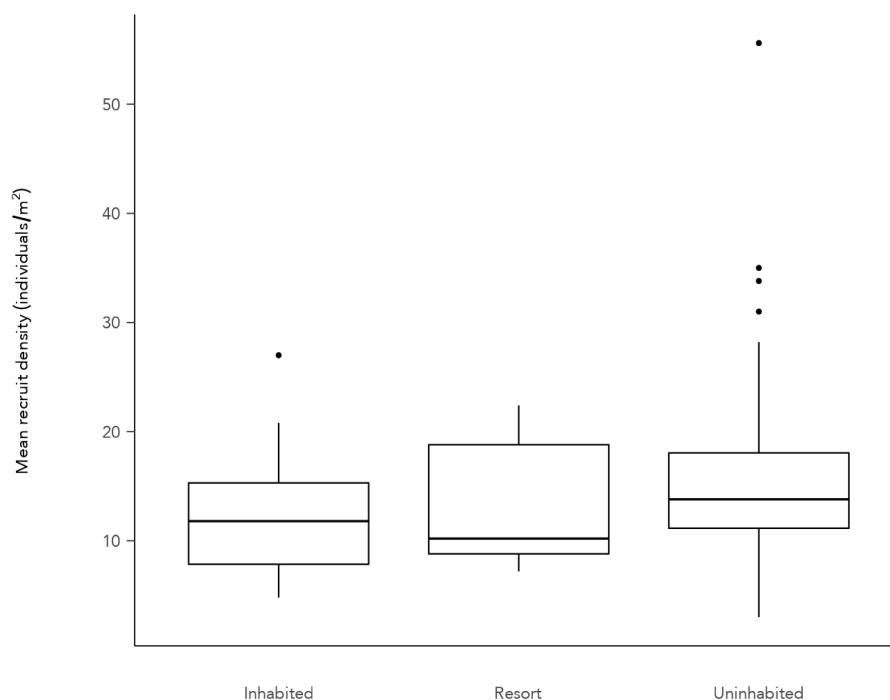
Encrusting *Pavona* made up the highest proportion of juvenile coral diversity, with an average density of 3.16 individuals/m² (± 0.20 SE) across all sites surveyed. *Pocillopora*, massive *Porites*, and *Psammocora* were the next most abundant juveniles, with average densities of 3.15 (± 0.17 SE), 2.3 (± 0.16 SE), and 1.8 (± 0.13 SE) individuals/m², respectively. All other genera had average densities of <1 individual/m² (see **Appendix 4** for a full list of juvenile coral genera).

In general, patterns of juvenile coral diversity were more or less consistent across atolls (**Figure 15**). *Pocillopora* juveniles were particularly abundant at Vaavu, with an average of 6.2 individuals/m² (± 1.2 SE), and encrusting *Pavona* juveniles were particularly abundant at Noonu, with an average of 6.3 individuals/m² (± 2.2 SE).

FIGURE 15: Heatmap of the mean recruit density of the most abundant coral genera at each atoll. Grey cells represent instances where the genus was not present at the corresponding 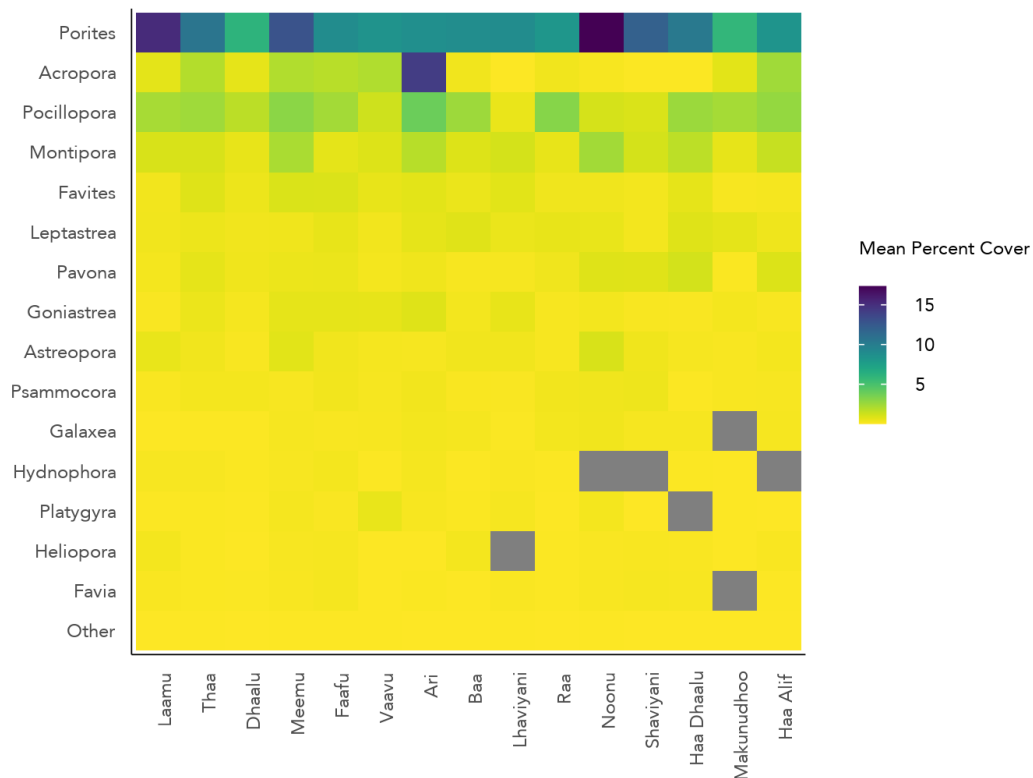atoll. Coral genera are ranked in order of overall abundance, and where possible, further broken down by morphology. All coral genera with an overall mean recruit density <0.1 individuals/m² were grouped into "Other".
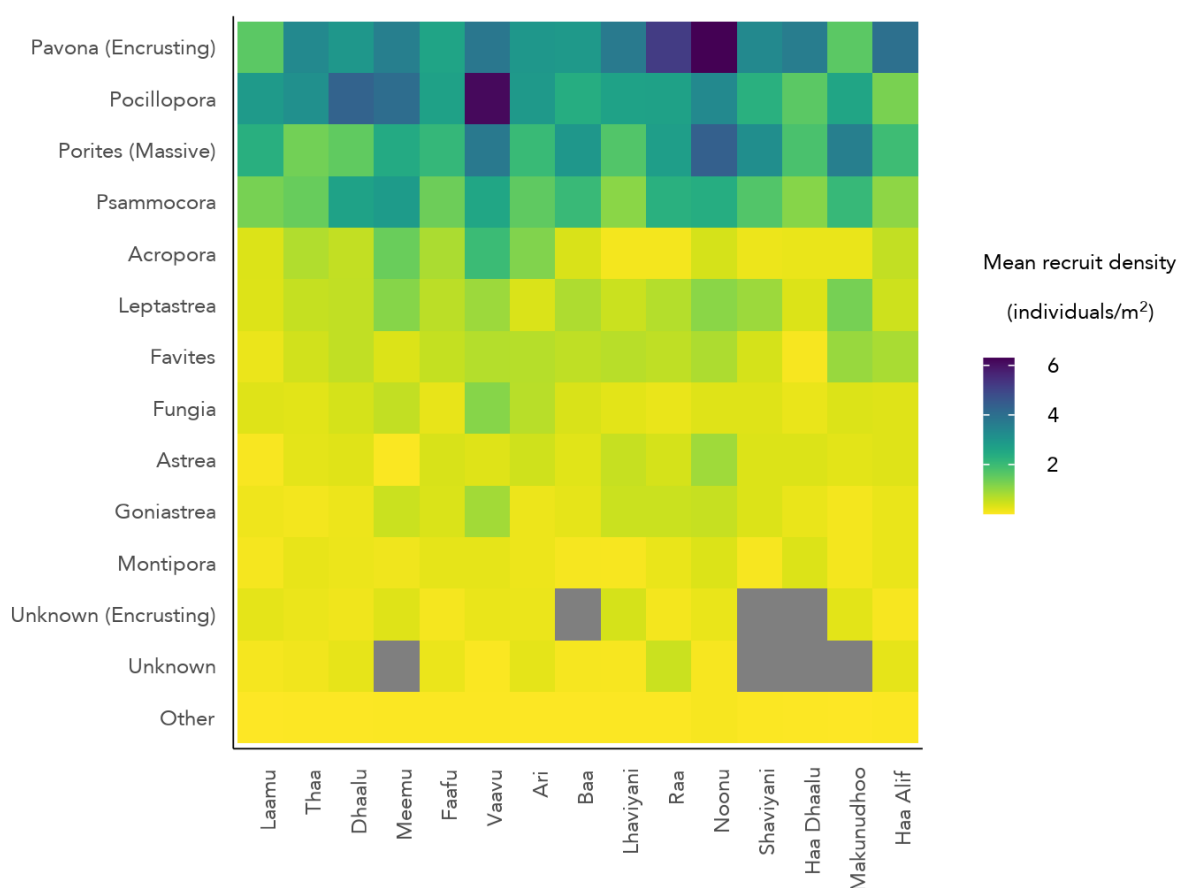
Similarly, patterns of juvenile coral diversity were similar across island use type (**Figure 16**). However, resort islands tended to have fewer juveniles, on average, from three of the top four most abundant genera (*Pocillopora*, encrusting *Pavona*, and *Psammocora*), but had slightly higher densities of *Favites* and Astrea than at inhabited or uninhabited islands.

FIGURE 16: Heatmap of the mean recruit density of the most abundant coral genera at each island use type. Grey cells represent instances where the genus was not present at the corresponding island type. Coral genera are ranked in order of overall abundance, and where possible, further broken down by morphology. All coral genera with an overall mean recruit density <0.1 individuals/m² were grouped into "Other".
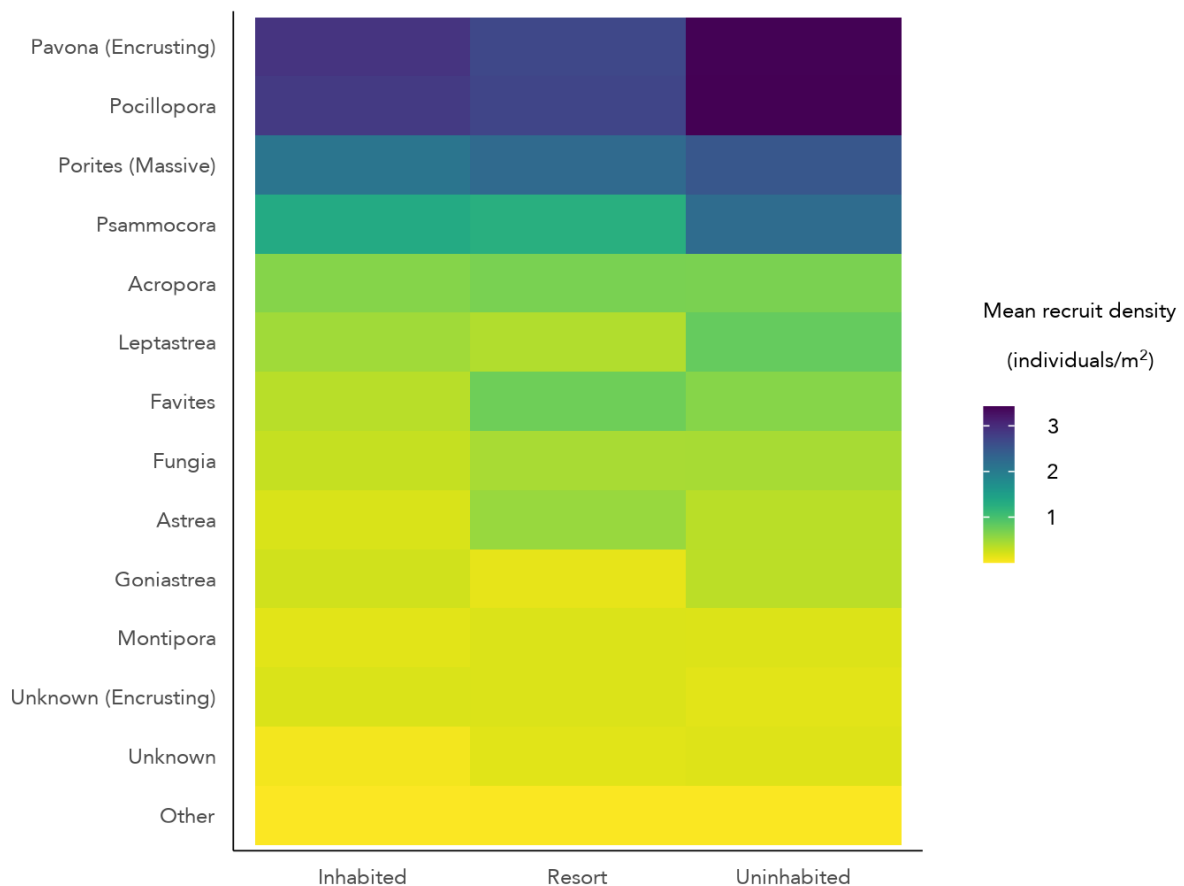
Rugosity

Rugosity, or the structural complexity of the reef, was fairly similar on average across atolls except for Meemu, which had the highest mean rugosity of all atolls surveyed (1.4± 0.03 SE; **Figure 17**).

While a few sites stood out as particularly complex (for example, site MAL_021 at Shaviyani, where mean rugosity=1.65), the great majority of sites surveyed across the archipelago had mean rugosity values between 1.1 and 1.3.
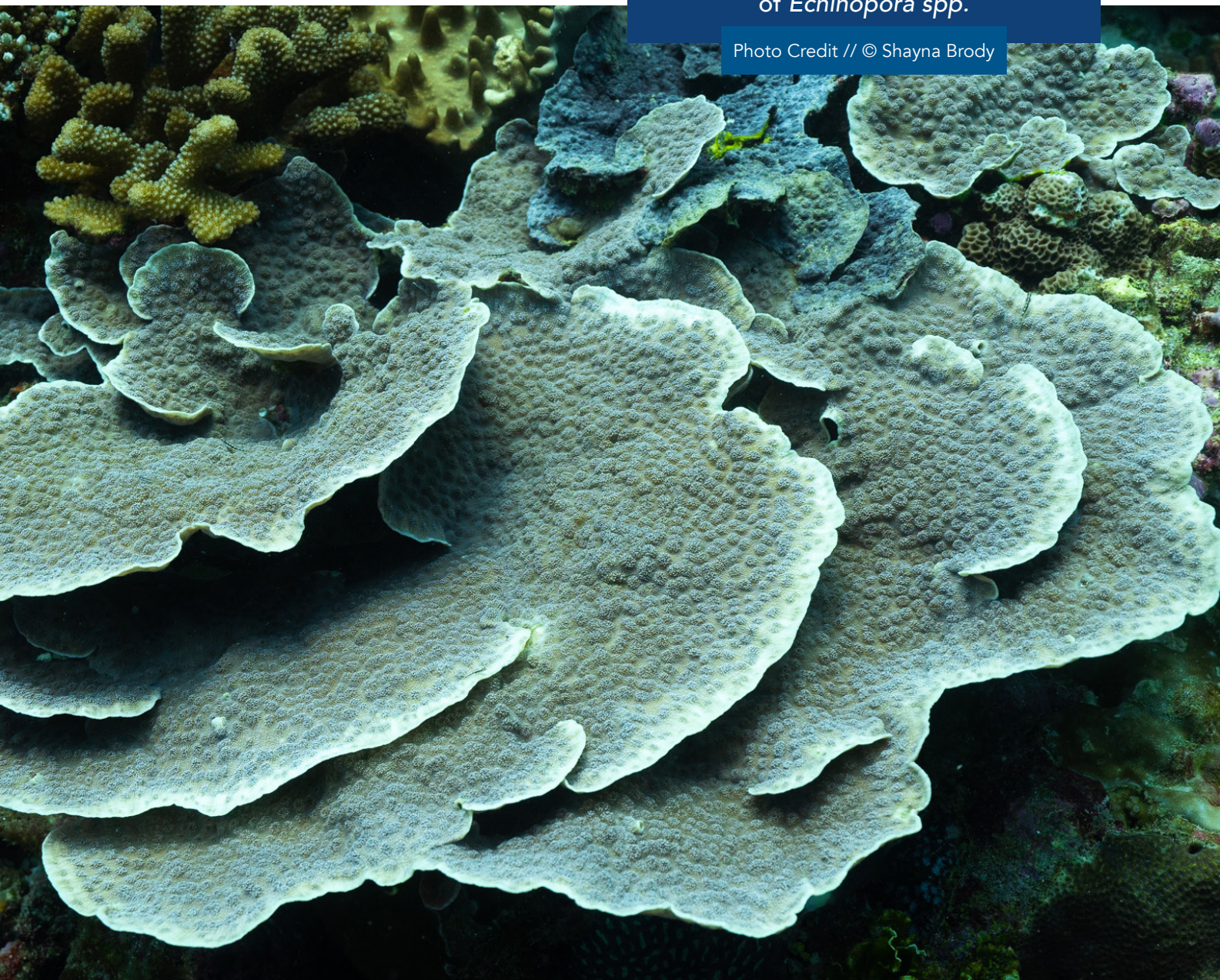
FIGURE 17: Mean rugosity at each atoll surveyed. Bold horizontal lines represent the median value at each atoll, and diamonds represent the mean.
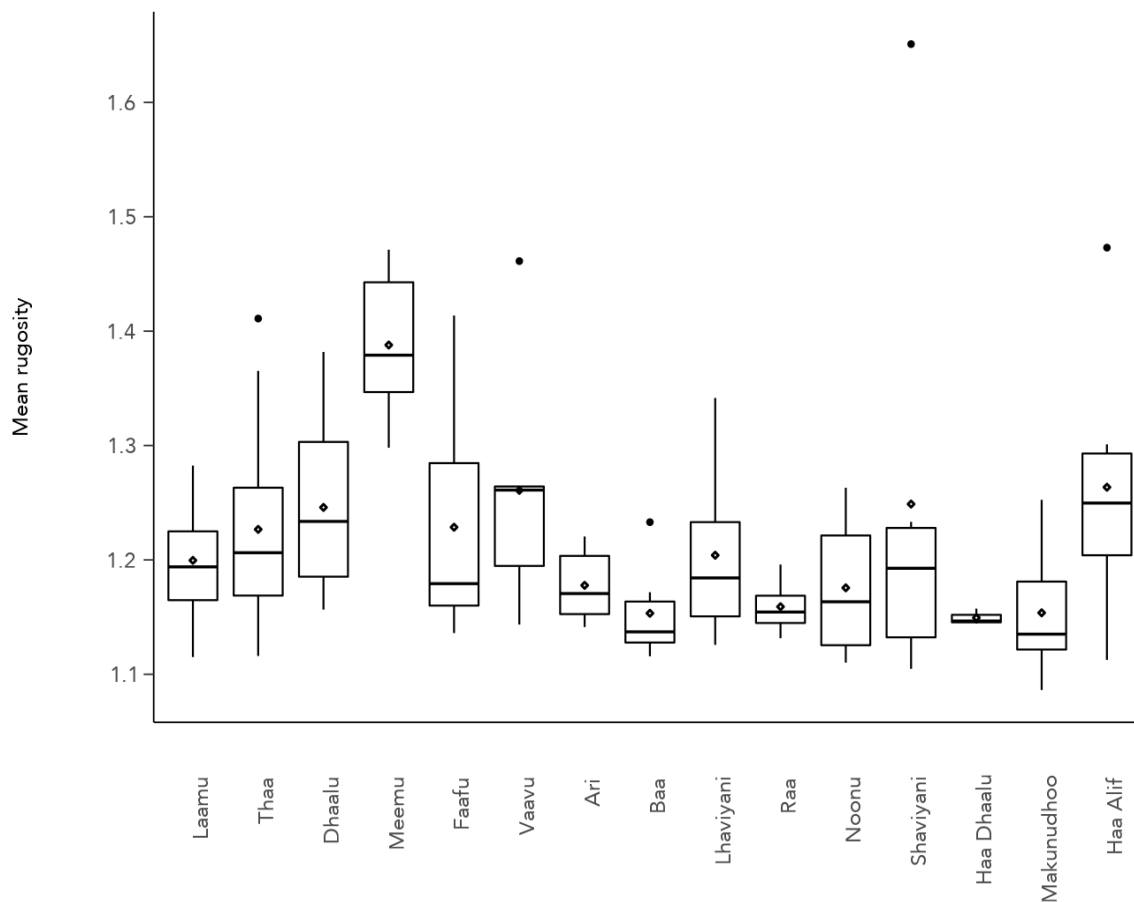
The reefs at Baa, Raa, and Haa Dhaalu were the least complex and, in general, were the least variable atolls surveyed in this study, with mean rugosity values of 1.15 (± 0.02 SE), 1.16 (± 0.01 SE), and 1.15 (± 0.004 SE), respectively.

Rugosity was consistent across island types, with mean values of 1.24 (± 0.02 SE) at inhabited islands, 1.20 (± 0.02 SE) at resort islands, and 1.21 (± 0.01 SE) at uninhabited islands (**Figure 18**).

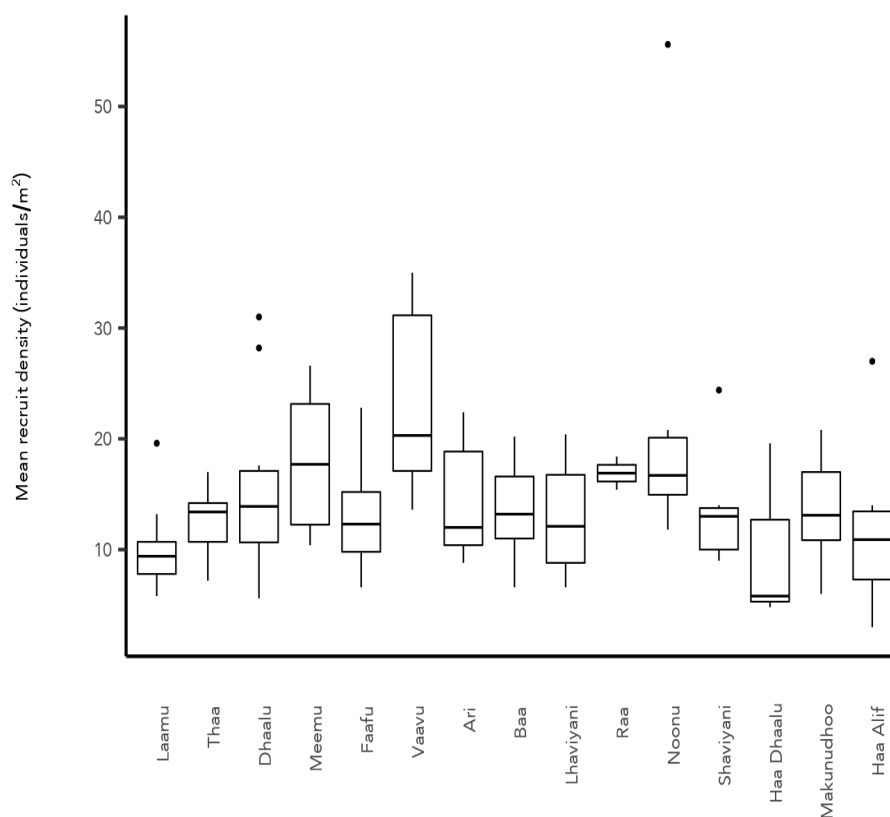**FIGURE 18**: Mean rugosity at each island use type. Bold horizontal lines represent the median value for each island type, and diamonds represent the mean.
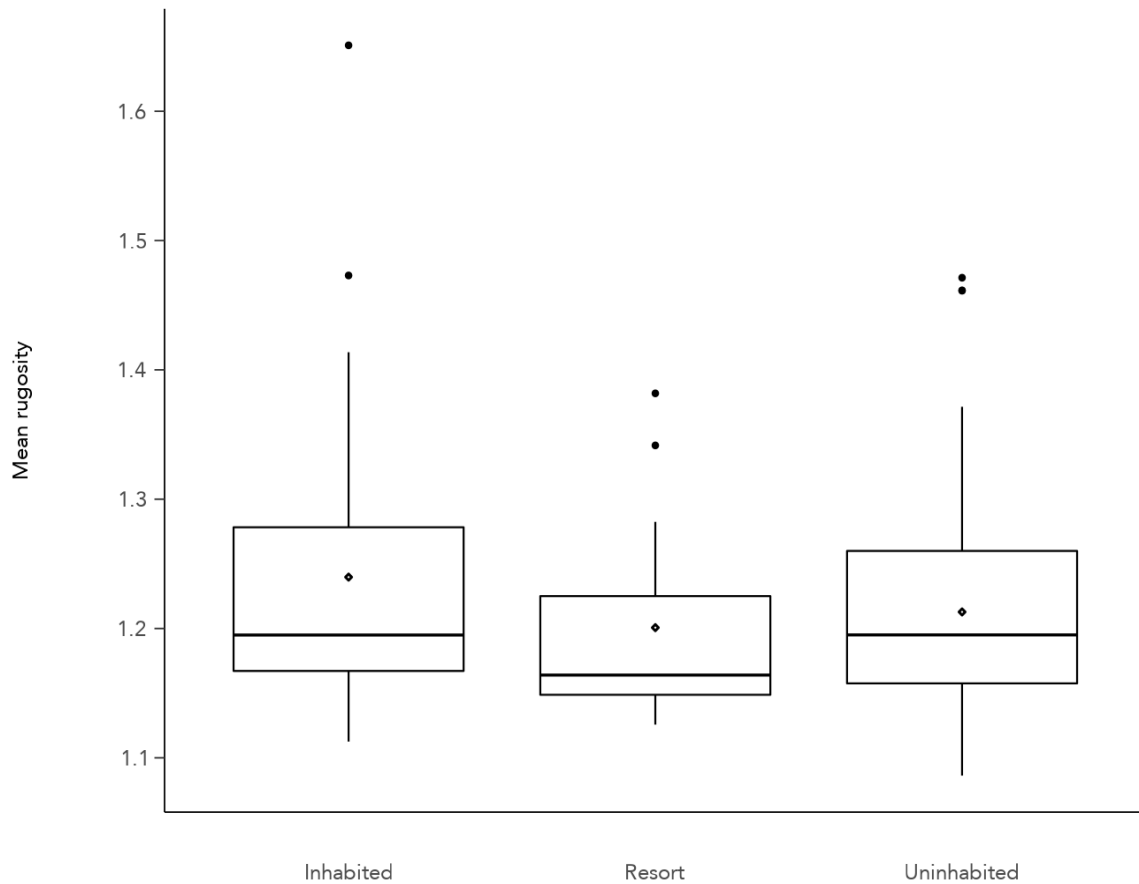
Invertebrates

Sea cucumbers

Nine species of sea cucumbers were identified across the archipelago, although densities and diversity varied widely between atolls (**Figure 19**). The edible sea cucumber (*Holothuria edulis*) and Graeffe's sea cucumber (*Pearsonothuria graeffei*) were the most abundant and most widely distributed, appearing at 10 and 11 of the 15 atolls surveyed, respectively.

FIGURE 19: Mean density of sea cucumbers at each atoll.
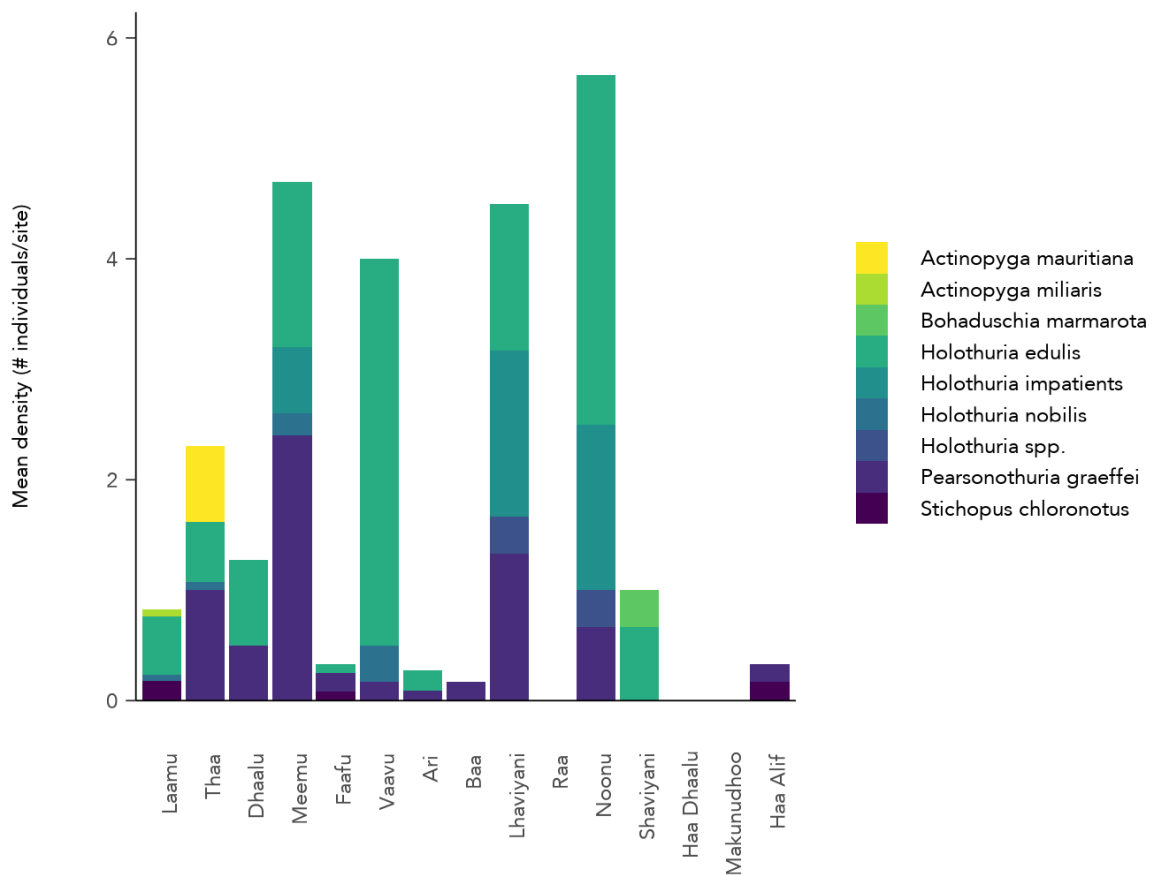
Importantly, the noble sea cucumber (*Holothuria nobilis*), an endangered species as recognized by the IUCN Red List and CITES (Conand et al. 2013, CITES Appendix II), was recorded at four of the 15 atolls. Notably, at three atolls in the North (Raa, Haa Dhaalu and Makunudhoo), no sea cucumbers were noted in the transects.

Uninhabited islands had higher density and diversity of sea cucumbers when compared with inhabited and resort islands (**Figure 20**). Four species (*Actinopyga mauritiana*, *Actinopyga miliaris*, *Bohadschia marmarota*, and *H. nobilis*) were only found at sites near uninhabited islands.

FIGURE 20: Mean density of sea cucumbers at each island use type.
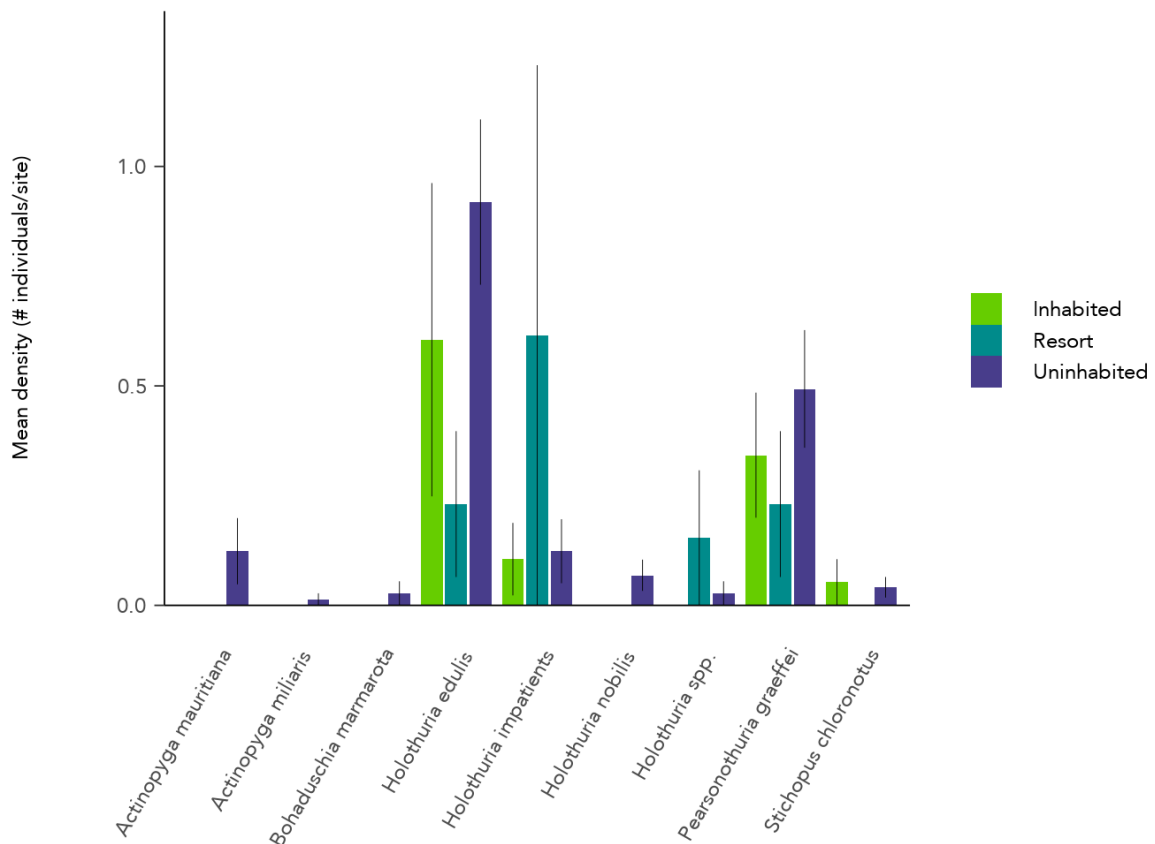
Gastropods

Shaviyani had the most abundant and diverse gastropod community on average compared to the other atolls (**Figure 21**). *Lambis spp.* and *Trochus spp.* were the most commonly seen gastropod species across the sites surveyed, with *Lambis spp.* present at all atolls except Meemu, and *Trochus spp.* present at all atolls except for Noonu and Haa Dhaalu.

While uninhabited islands had the highest diversity of gastropods, resort islands had the highest density, averaging approximately twice as many gastropods per site as either inhabited or uninhabited islands (**Figure 22**).

Bivalves, cephalopods, and crustaceans

Bivalve, cephalopod, and crustacean densities were generally higher in the Central Atolls than in the North (**Figure 23**). Dhaalu and Thaa had the highest density of these invertebrates, driven mostly by a particularly high abundance and diversity of *Tridacna* clams at each atoll. As with sea cucumbers, densities of bivalves and cephalopods were higher at uninhabited islands; however, resort islands had the highest densities of crustaceans, driven by high incidences of the large hermit crab *Dardanus spp.* (**Figure 24**).

Echinoderms

Echinoderm communities across the archipelago were dominated by extremely dense populations of the burrowing urchin *Echinostrephus molaris* at most atolls (**Figure 25**).

In particular, *E. molaris* densities at Dhaalu were very high, with over 2000 individuals surveyed per site, on average. However, while still the dominant echinoderm taxon, *E. molaris* densities at Meemu, Vaavu, and Noonu were two orders of magnitude lower, indicating that the presence of this species is patchy across atolls.

The collector urchin *Tripneustes gratilla* was also patchily distributed, with densities of up to 211 individuals per site at Baa, and moderate population densities at Raa and Shaviyani.

However, this species was found exclusively from Baa Atoll northward, and was not present in the Central Atolls. The cushion star *C. schmedeliana* was the most abundant sea star species and was present in low densities across the atolls surveyed.

Echinoderm density was spread fairly evenly across island types, with slightly lower densities overall at uninhabited islands (**Figure 26**).

While the echinoderm communities at all island types were dominated by *E. molaris*, resort islands had substantially fewer *T. gratilla* than inhabited and uninhabited islands. In addition, inhabited islands had higher densities of the urchin *Echinothrix diadema* when compared to the other two island types.

A snapshot of the benthic environment at South Malé Atoll.

Photo Credit // © Joe Lepore

FIGURE 21: Mean density of gastropods at each atoll.
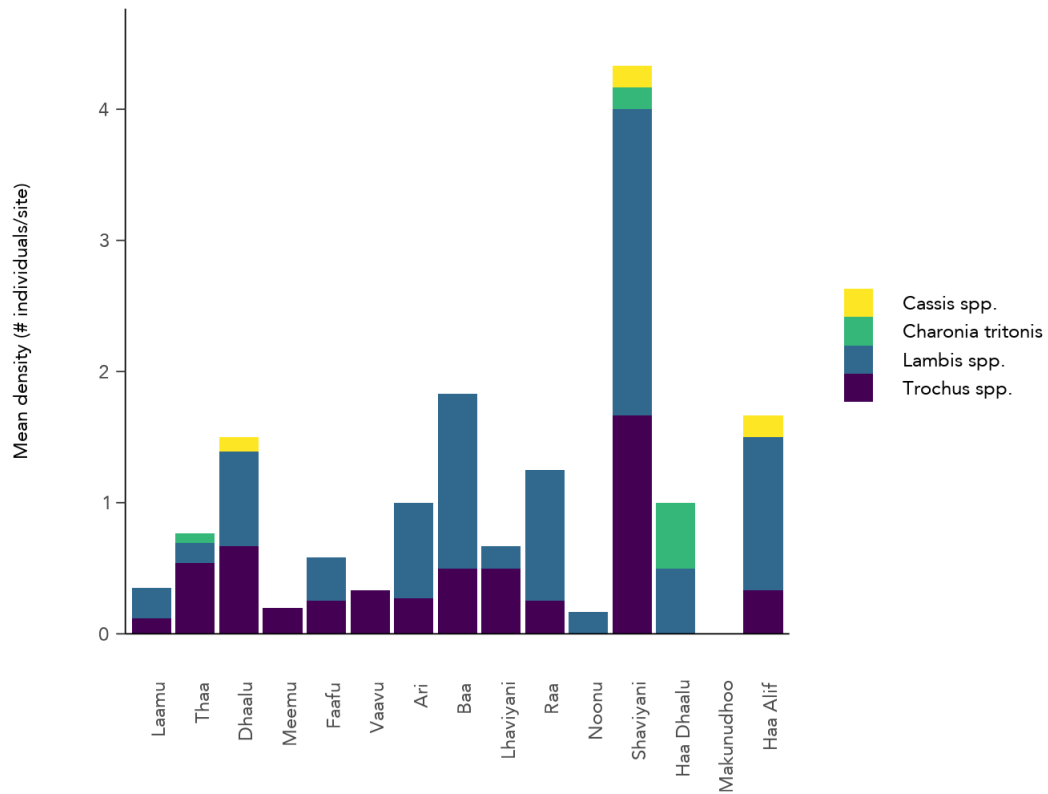
FIGURE 22: Mean density of gastropods at each island use type.
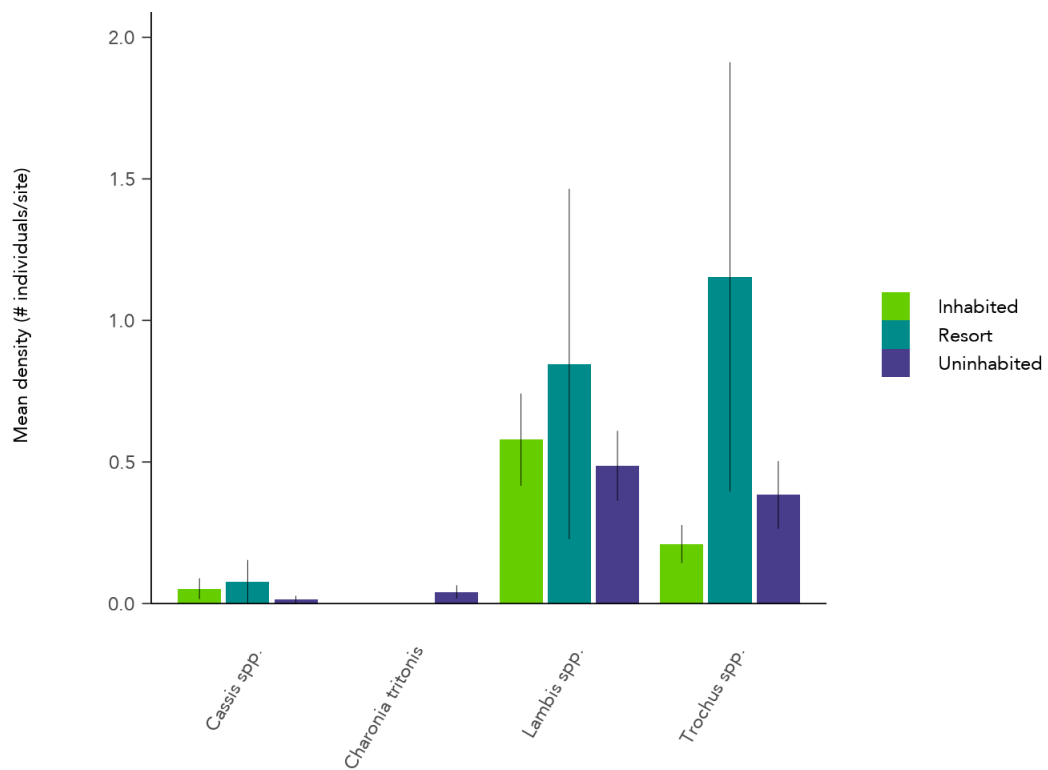
FIGURE 23: Mean densities of bivalves, cephalopods, and crustaceans at each atoll.
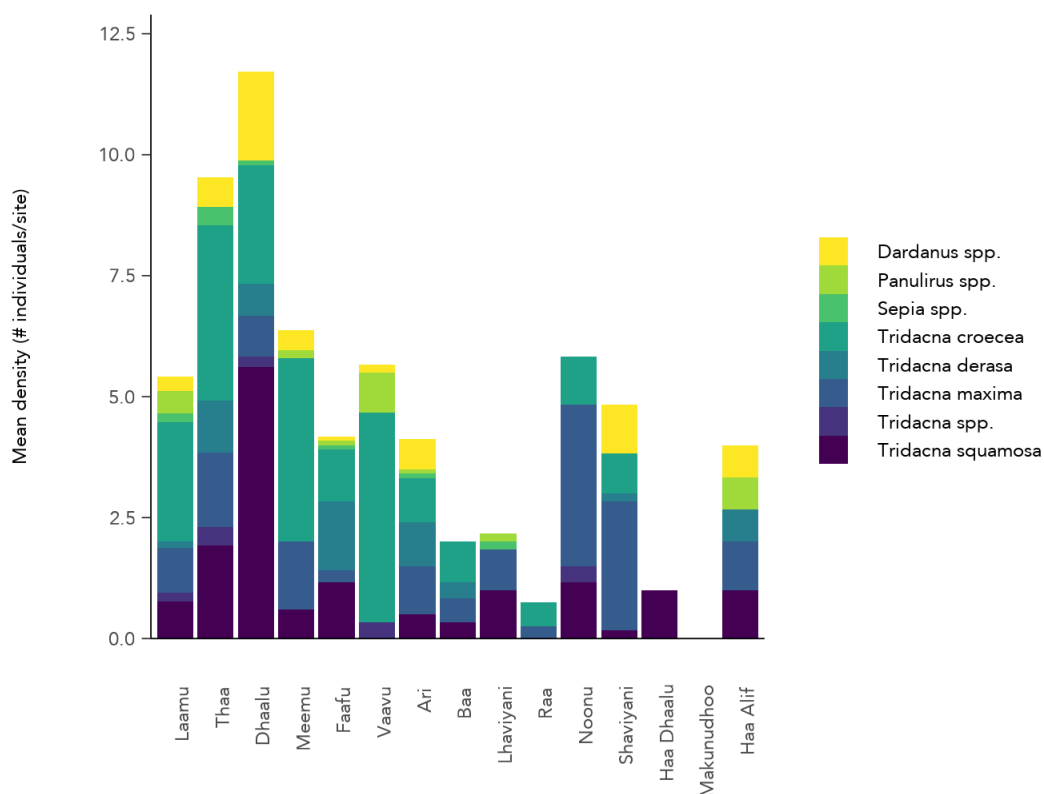
FIGURE 24: Mean densities of bivalves, cephalopods, and crustaceans at each island use type.
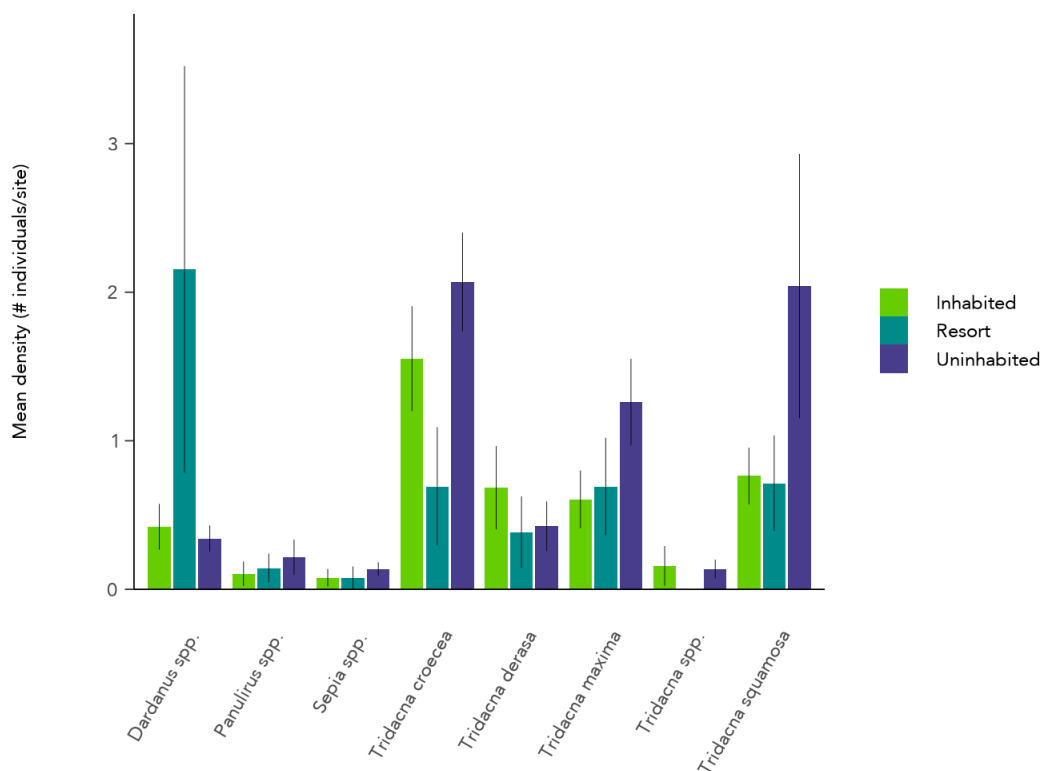
FIGURE 25: Mean density of echinoderms at each atoll. The left panel shows the full dataset, and the right panel shows detail of the less abundant species.
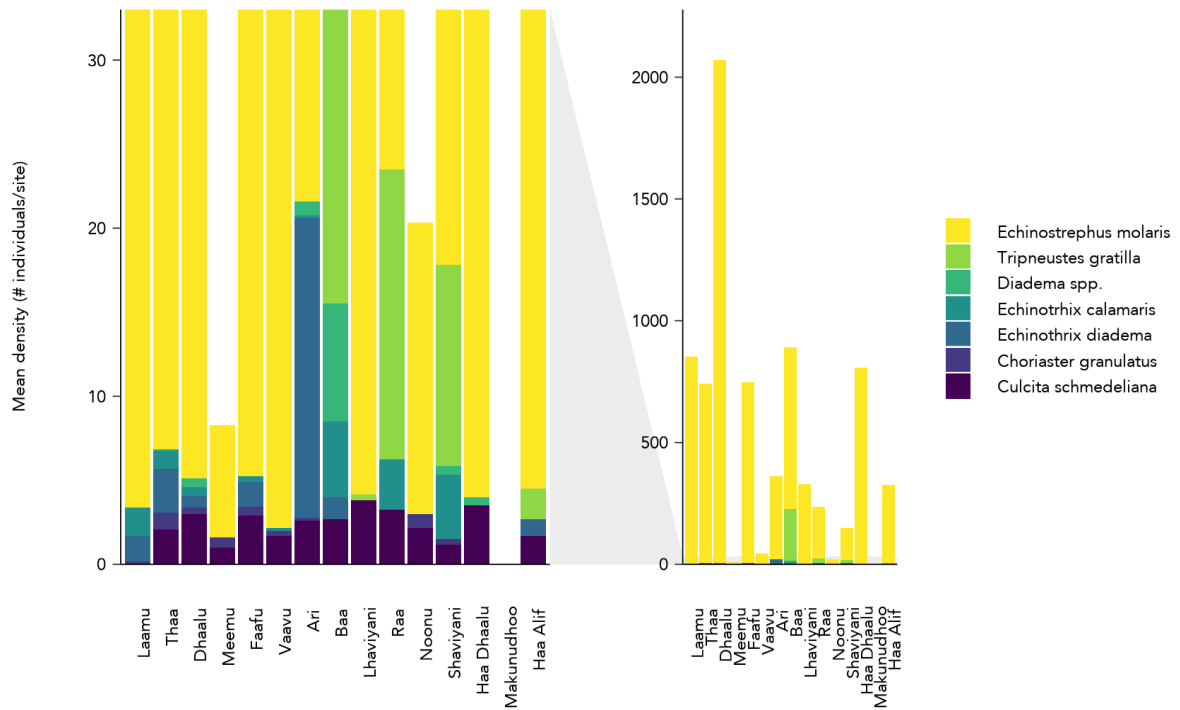
FIGURE 26: Mean density of echinoderms at each atoll. The left panel shows the full dataset, and the right panel shows detail of the less-abundant species.
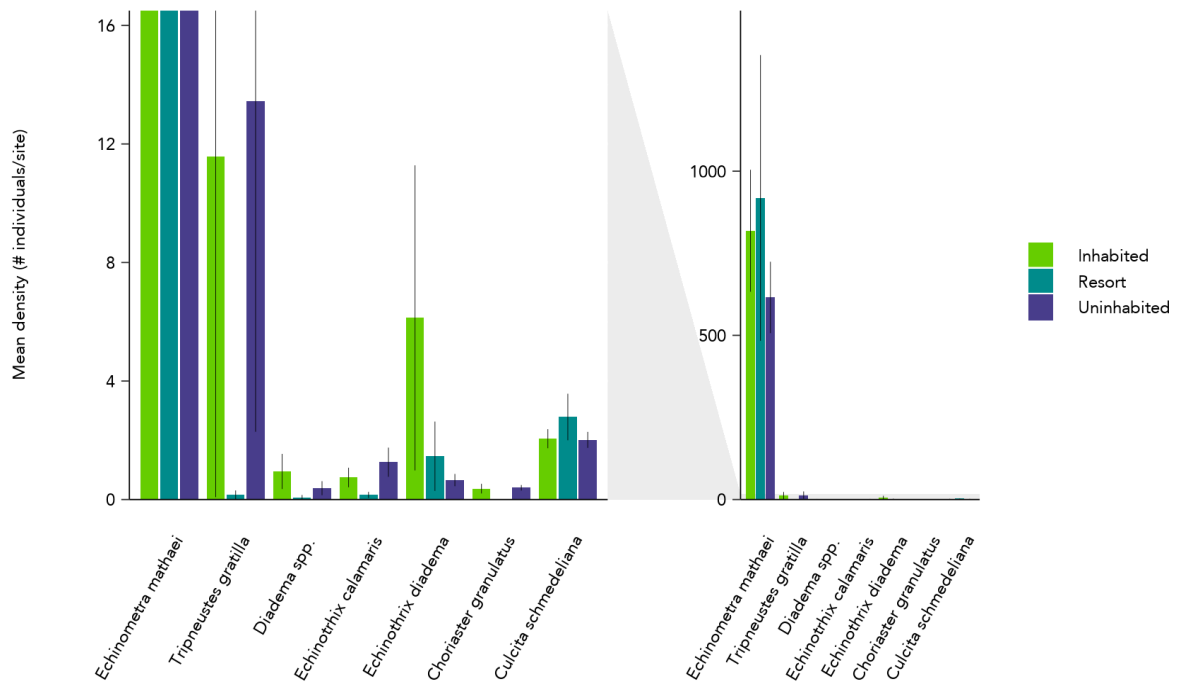
DISCUSSION

A feather star (*Colobometra perspinosa*) attached to a whip coral.

Photo Credit // © Shayna Brody

KEY FINDINGS

Coral cover in the Maldives has been slowly recovering following the coral bleaching events of 1998 and 2016. Prior to the 1998 hot water event, coral cover ranged between 50-80% nationwide (Scheer 1972, 1974), and despite dropping below 10% following the bleaching, had recovered to approximately pre-1998 values by 2013 (Morri et al. 2015). However, during 2016, 73% of corals across the archipelago bleached, leading to the death of over 80% of branching corals and about 10% of massive corals (Ibrahim et al. 2017).

The results from this survey indicate that reefs in the Northern and Central Maldives are in the process of recovering from both the 1998 and 2016 bleaching events and show signs of resilience. Overall mean coral cover in the Maldives is currently approximately half of what it was prior to the 1998 and 2016 bleaching events. However, while some reefs, such as those at Ari Atoll, are nearing pre-bleaching levels of coral cover, many of the reefs across the Northern and Central Maldives are still at less than half of pre-bleaching percent cover of hard corals.

The findings presented in this report support those from previous studies; for example, Pisapia et al. (2016) showed that following the 1998 bleaching event, coral cover increased at an average rate of 93.5% until 2012, and Morri et al. (2015) showed that coral cover had recovered to approximately pre-1998 levels prior to 2016.

Island Use Type

Coral cover was significantly higher at resort and uninhabited islands when compared with inhabited islands. This pattern is consistent with previous studies and suggests that human impacts, such as fishing, construction, and nutrient runoff associated with human settlements on inhabited islands, may negatively impact coral communities, however the *de facto* management practices on resort islands have a positive effect on corals in comparison to inhabited islands (Moritz et al. 2017).

Nevertheless, despite the protective effects of resorts suggested by the results of this survey, only 14 resorts out of ~162 registered resorts were surveyed. With the studies showing variable success in relation to the *de facto* protection afforded to resort reefs (e.g., Domroes 2001, Scheyven 2011, Moritz et al. 2017, Cowburn et al. 2018), it is crucial that any future expedition properly samples resort reefs at a variety of atolls, depths, and exposures to ascertain their true potential and effect. In addition, it is important that data are collected on potential drivers of reef health, such as water quality.

Interestingly, island use type did not significantly impact fish communities at the sites surveyed. This contrasts with previous findings (e.g., Moritz et al. 2017) which found that island use type was a good predictor of fish abundance. It is possible that the lack of signal found in the present study may be due to the unbalanced nature of the survey sites: approximately five times as many uninhabited sites were surveyed than resort sites.

Alternatively, this result may suggest that fishers travel further than the 2 km buffer chosen in this study to a designated island type, which could result in sites classified as uninhabited in this study seeing comparable levels of fishing pressure as adjacent inhabited sites.

Coral Reef Resilience

This resilience to disturbance may be in part due to a shift in the dominant coral taxa, from *Acropora* and *Pocillopora* to the more stress-tolerant *Porites*. Prior to 1998, branching corals dominated Maldivian reefs (Edwards et al. 2001), but following widespread bleaching-related mortality among acroporids and pocilloporids, finger coral *Porites* became the dominant genus (McClananhan 2000). From 1998-2016, *Acropora* cover increased rapidly (Pisapia et al. 2016), but was again disproportionately affected by the 2016 bleaching event, which led to mortality of >80% of *Acropora* in North Malé Atoll (Ibrahim et al. 2017).

In contrast, less than 10% of *Porites* at the same location died in 2016. Currently, *Porites* dominates the majority of reefs surveyed, with the exception of Ari Atoll, where *Acropora* was the dominant taxon. While the abundance of *Acropora* at Ari Atoll may suggest that there is potential for this genus to recover relatively quickly following widespread mortality, it is also possible that this potential may differ based on the thermal regimes of individual atolls (Tkachenko 2014) and requires further investigation to establish a trend within the Maldives.

The shift towards *Porites* dominance indicates that the reefs of the Maldives may be shifting towards a more resilient community structure, which may be better equipped to endure future bleaching events.

Porites has been shown to exhibit high resistance and tolerance to thermal stress in the Maldives (Ibrahim et al. 2017) and elsewhere in the Indian Ocean, and reef communities dominated by corals with tolerance to bleaching may be more resilient (Obura 2005). These findings are generally consistent with previous studies which have indicated that wave-exposed reefs, like those surveyed during this expedition, are dominated by bleaching-resistant massive growth forms (Cowburn et al. 2019).

Therefore, this shift towards *Porites* dominance indicates that the reefs of the Maldives may be shifting towards a more resilient community structure, which may be better equipped to endure future bleaching events. However, while this study did account for island type, the study only surveyed wave-exposed reefs on the western side and only at 10 m depth.

Previous studies have indicated that exposure, anthropogenic influence, and depth (McClanahan and Muthiga 2014, Cowburn et al. 2019, Montefalcone et al. 2020) are key factors when assessing the resistivity and resilience of coral reefs within the Maldives, so it is important to note that this pattern may not hold true if the study were to be expanded to include these factors.

Recruitment Density

Coral recruitment was also shown to be high, averaging 14.3 individuals/m². This number far exceeds juvenile coral densities recorded on other Indo-Pacific reefs; for example, recruit density at Heron Island, Australia, was found to have a maximum mean value of 3.8 individuals/m² (Doropoulos et al. 2015), and reefs in Palk Bay, India were found to have a maximum of 6.2 recruits/m² (Manikandan et al. 2017).

Immediately following the 1998 bleaching event, recruitment rates in the Maldives, especially of massive and encrusting taxa, were extremely high, with estimates ranging from 23.2-28.9 individuals/m² (McClanahan 2000, Edwards et al. 2001). This pulse has been attributed to "emergency spawning" following catastrophic die off (Loch et al. 2002). However, after this initial pulse, recruitment rates varied widely over time, dropping as low as 0.7 individuals/m² (Loch et al. 2004) following the emergency spawning event, then increasing again approximately 6 years after the bleaching (Morri et al. 2015).

The relatively high level of recruitment observed in this study may indicate that Maldivian reefs are on a path towards recovery following the 2016 bleaching event.

A school of Indian Humbug (*Dascyllus carneus*) on *Acropora* coral.

Photo Credit // © Joe Lepore

Hussain Zahir surveys benthic populations.

Mean recruit density across the archipelago is presently about half of the 1998 emergency spawning densities; however, recruitment densities on atolls such as Vaavu neared those observed immediately following the 1998 bleaching event.

Indeed, the mean juvenile coral density found in this study is greater than twice the densities found to be necessary for reefs in the Seychelles to recover to a coral-dominated state following the 1998 bleaching (6.2 individuals/m²; Graham et al. 2015). Therefore, the relatively high level of recruitment observed in this study may indicate that Maldivian reefs are on a path towards recovery following the 2016 bleaching event.

Juvenile and Adult Coral Diversities

Interestingly, patterns of coral diversity did not align when comparing coral juveniles to coral cover. While *Porites* dominated in overall coral cover, encrusting *Pavona* species made up the highest number of coral recruits, followed closely by *Pocillopora*. These differences are reflective of the different life history strategies of the dominant taxa in response to disturbance: massive corals such as *Porites* are stress tolerant, allowing adult colonies to withstand stress events, while weedy species such as *Pocillopora* are adept at colonizing open space following mortality events.

These findings contrast with data from 2011-2012, which found that *Acropora* recruits were more abundant than *Pocillopora* (Tkachenko 2014), perhaps indicating that recruitment patterns in the Maldives change over time as succession progresses following disturbances. Agariciids such as *Pavona* were found to constitute a large fraction of the total recruits following the 1998 bleaching event (McClanahan 2000, Loch et al. 2002, Loch et al. 2004), and it appears this pattern is holding following the 2016 bleaching as well.

Herbivory Impact

High herbivory rates across the archipelago likely help facilitate the high rate of recruitment noted in this study by creating available space for recruits to settle (Smith et al. 2010). The data from this study indicate the presence of large-bodied herbivorous fish, particularly scarids and acanthurids, throughout the country, leading to extremely low levels of macroalgae at all atolls surveyed. Large parrotfish in particular have been found to facilitate coral recruitment by clearing available substrate of algae, allowing settlement to occur and recruits to survive to maturity (Mumby et al. 2007, Mumby 2009, Steneck et al. 2014).

A sea cucumber (*Pearsonothuria graffei*) hunts for food.

Photo Credit // © Emanuel Gonçalves

Predatory Fishes

Abundance and biomass of sharks and large-bodied predatory fishes, however, were very low across the sites surveyed. While it is possible that the lack of sharks and other predatory species noted in our surveys may be due in part to seasonality and/or limitations in belt transect surveys' ability to accurately enumerate large-bodied fish (Richards et al. 2011), the data presented here, including the IUCN presence/absence surveys, indicate that these large predatory species are extremely rare at these sites during the North East monsoon, particularly in the Northern Atolls.

> Abundance and biomass of sharks and large-bodied predatory fishes, however, were very low across the sites surveyed.

However, the shark biomass noted in this survey was on par with some atolls of the nearby Chagos archipelago (Graham et al. 2013), which was declared as a no-take zone in the same year as the Maldives' shark ban came into effect.

However, shark biomass in Chagos was shown to vary widely between atolls, and some sites, such as the Great Chagos Bank, were found to have much higher shark biomass than reported here. It must be noted, however, that reliable baseline data for both locations are lacking, so caution should be exercised when comparing shark populations between these regions.

Invertebrates

Sea Cucumbers

On the contrary, invertebrate taxa with a history of exploitation showed substantially higher densities at uninhabited islands. While sea cucumber harvesting from inhabited island reefs can occur sporadically, Maldivian sea cucumber harvesters generally go out for multi-day fishing trips, during which they visit several reefs. The results indicated that, despite potential use of uninhabited reefs for harvesting sea cucumbers, they can support abundant and diverse sea cucumber populations, while resort sites that are the least likely to be exposed to harvesting showed a similar trend to inhabited islands where sea cucumber harvesting can be common.

Even though island use types, as classified in this report, may not necessarily show a sea cucumber harvest intensity gradient, the results suggest uninhabited reefs as a key habitat for diverse and abundant sea cucumber populations. It is likely that habitat characteristics are an important determinant in structuring sea cucumber population across the Maldivian archipelago.

> It is likely that habitat characteristics are an important determinant in structuring sea cucumber population across the Maldivian archipelago.

Other Invertebrates

Clams showed a similar pattern to sea cucumbers across the sites surveyed. A non-traditional fishery for giant clams started in June 1990, primarily targeting *Tridacna squamosa* (Basker 1991, Manik 1998). Although the occasional *Tridacna maxima* was taken as part of this fishery, Basker 1991 notes that fishermen attempted to leave the species unexploited due to the belief that they were juvenile *T. squamosa* which would replenish the adult population over time.

Soon after the start of the fishery, noticeable overexploitation of the resource and concern over recovery of the giant clams led to an assessment which identified the fishery as unsustainable (Basker 1991, Ahmed et al. 1997). Consequently, after two years where over 20 metric tons of clams were exported (Ahmed et al. 1997), the fishery and export of giant clams was halted.

The results of this survey found that Raa Atoll had the lowest density of clams (**Figure 23**). Raa was the atoll where the major center of the fishery, Ugoofaru, was located when it operated (Ahmed et al. 1997). Hence, it is possible that this exploitation history is why clams show a similar pattern to sea cucumbers, though further targeted investigation would be required to draw meaningful conclusions.

Gastropods, on the other hand, were most abundant at resort islands, but uninhabited islands still had the most diverse gastropod populations. Echinoderms were abundant across island types, driven in large part by extremely high densities of *E. mathaei*., *E. mathaei* densities were patchy by atoll, however, ranging from an average of 6.7 individuals/site at Meemu to 2064.9 individuals/site at Dhaalu.

A Fluted Giant Clam (*Tridacna squamosa*).

Photo Credit // © Emanuel Gonçalves

RECOMMENDATIONS

The students of Hirilandhoo School on Thaa Atoll watch a presentation from the Noo Raajje expedition team.

Photo Credit // © Travis Matteson
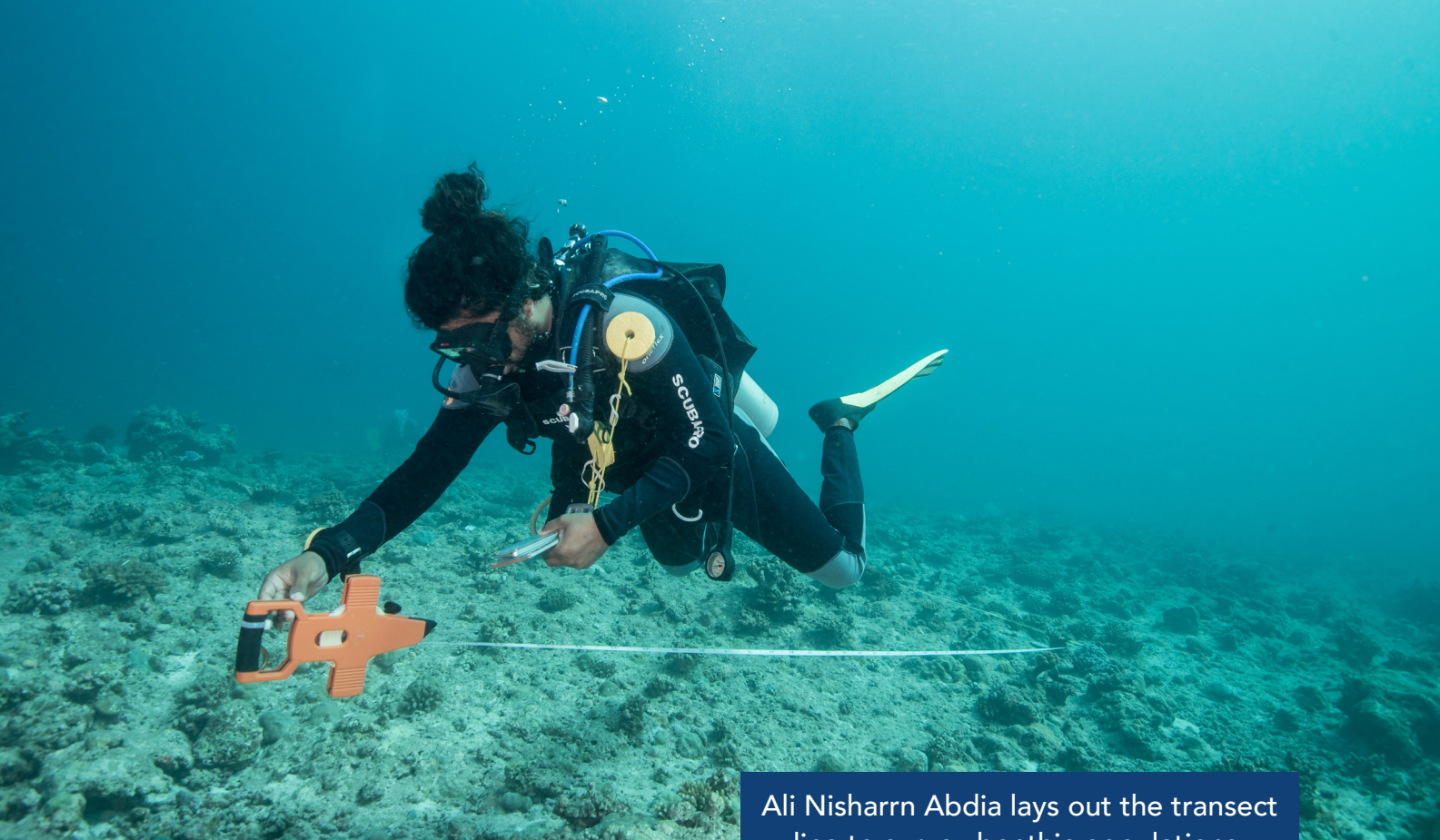
Ali Nisharrn Abdia lays out the transect line to survey benthic populations.

Photo Credit // © Emanuel Gonçalves

1 | Undertake additional, balanced surveys to account for differences in seasonality and location within atolls, reef habitats, and island use type.

While all efforts were made to ensure the data generated for this study were as representative as possible, due to logistical considerations, the location and depth of survey sites was constrained to western forereefs at 10m depth.

Additionally, the sites selected for this study resulted in unbalanced sampling of the three different island use types, with uninhabited islands being overrepresented in the data. Similarly, although the initial intention was to conduct surveys across the entire archipelago, the emergence of the COVID-19 global pandemic in February 2020 forced the suspension of field operations before the reefs around North and South Malé Atolls and the Southern Atolls could be surveyed.

Although additional expeditions to survey the remaining atolls will be conducted in 2021, the results generated from the present and future surveys will not account for seasonal differences, nor will they include the eastern or lagoonal reefs of any of the atolls. Seasonality may be particularly important for large, mobile species such as sharks or other predatory fishes.

Therefore, we recommend that additional surveys be undertaken during different seasons on different reef habitats in order to gain a comprehensive understanding of the state of Maldivian reefs as a whole. If possible, it would be ideal to select a balanced number of sites from different island use types for subsequent surveys. In addition, it is recommended that locations with the capacity to undertake regular coral reef assessments, such as resorts, implement a standardized monitoring strategy in order to contribute to a central national dataset.

2 | Monitor and assess reef fish and top predator/shark populations to support effective management efforts.

Herbivore and planktivore populations were found to be quite abundant across the atolls surveyed, but biomass of carnivores, top predators, and sharks was low at most locations. While anecdotal evidence from fishermen indicates that shark densities may be lower than average on leeward reefs during the North East monsoon, the data presented here suggest that continued management of shark populations in the Maldives is prudent.

Additionally, studies have shown that demand for reef species has increased as the tourism industry expands, with up to 83% of tourist seafood consumption coming from carnivorous reef species, primarily jacks (carangids), snappers (lutjanids), and emperors (lethrinids; Hemmings et al. 2014). As the reef fish and grouper fisheries continue to expand and pressure on predatory fish increases, it will be important to continue monitoring and assessing these resources and developing management measures as necessary to preserve fish stocks.

A whale shark (*Rhincodon typus*) spotted on the expedition.

Photo Credit // © Brian Zgliczynski

Aminath Angeela processes a water sample for eDNA.

3 | Implement local management efforts to mitigate effect of global-scale stressors.

Although coral cover in the Maldives has recovered to approximately half of pre-bleaching values, periodic disturbance events have prevented full recovery (Morri et al. 2015, Pisapia et al. 2016, Ibrahim et al. 2017). While most of these disturbance events are driven by global-scale drivers such as climate change, domestic management efforts can help put reef communities in the best position to endure and recover from future disturbances.

For example, the high coral recruitment rates seen in this study are likely possible in part due to the high number of large herbivorous fish present across the sites surveyed, which successfully maintain low levels of macroalgae and create bare substrate on which coral recruits can settle. Therefore, herbivore conservation (fishes and invertebrates) is one tool to promote healthy and resilient coral populations (Mumby et al. 2007, Mumby 2009).

It should be noted that at the time of writing, the Maldives has just announced the addition of parrotfish to the "Prohibited Species List" of the General Fisheries Regulation (2020/R-75), which should contribute positively to maintaining healthy herbivore populations, and subsequently, high coral recruitment densities. Similarly, the data in this study showed that the geographic and *de facto* protection afforded to reefs at uninhabited and resort islands resulted in higher coral cover than at inhabited islands, suggesting that management of or protection from human impacts where possible will likely result in healthier benthic communities.

4 | Research and support effective coral restoration initiatives and develop a national coral restoration strategy.

Coral restoration, though currently questionable in terms of scale, effectiveness, and success, is another tool which is currently being utilized to assist reef recovery in the Maldives. In particular, coral restoration techniques which focus on restoring resilient taxa may be effective in creating local coral populations which will be able to withstand future disturbance events.

This is already taking place to some extent in the Maldives; for example, one case study of a restoration project at a Maldivian resort indicated that the restoration group preferentially populate their coral frames with fragments from corals which have withstood previous bleaching events (Hein et al. 2020), although the efficacy of this strategy has not been formally tested. However, most efforts that take place within the country in the name of coral restoration are currently coral gardening efforts with minimal, if any, records of successful restoration of local reefs.

Most of these projects, which commonly take place in resorts, are often disjointed and somewhat ad hoc, often suffering from lack of continuity due to the high turnover of the resident marine biologists. This could be due to the fact that many "restoration" projects focus more on either perceived or real fiscal gain as opposed to any ecological or social gain. Therefore, the development of a national coral restoration strategy, along with research into restoration methods that promote thermally resilient coral populations, may improve the efficacy of these efforts.

A close-up of a soft coral, *Lobophyton*.

Photo Credit // © Shayna Brody
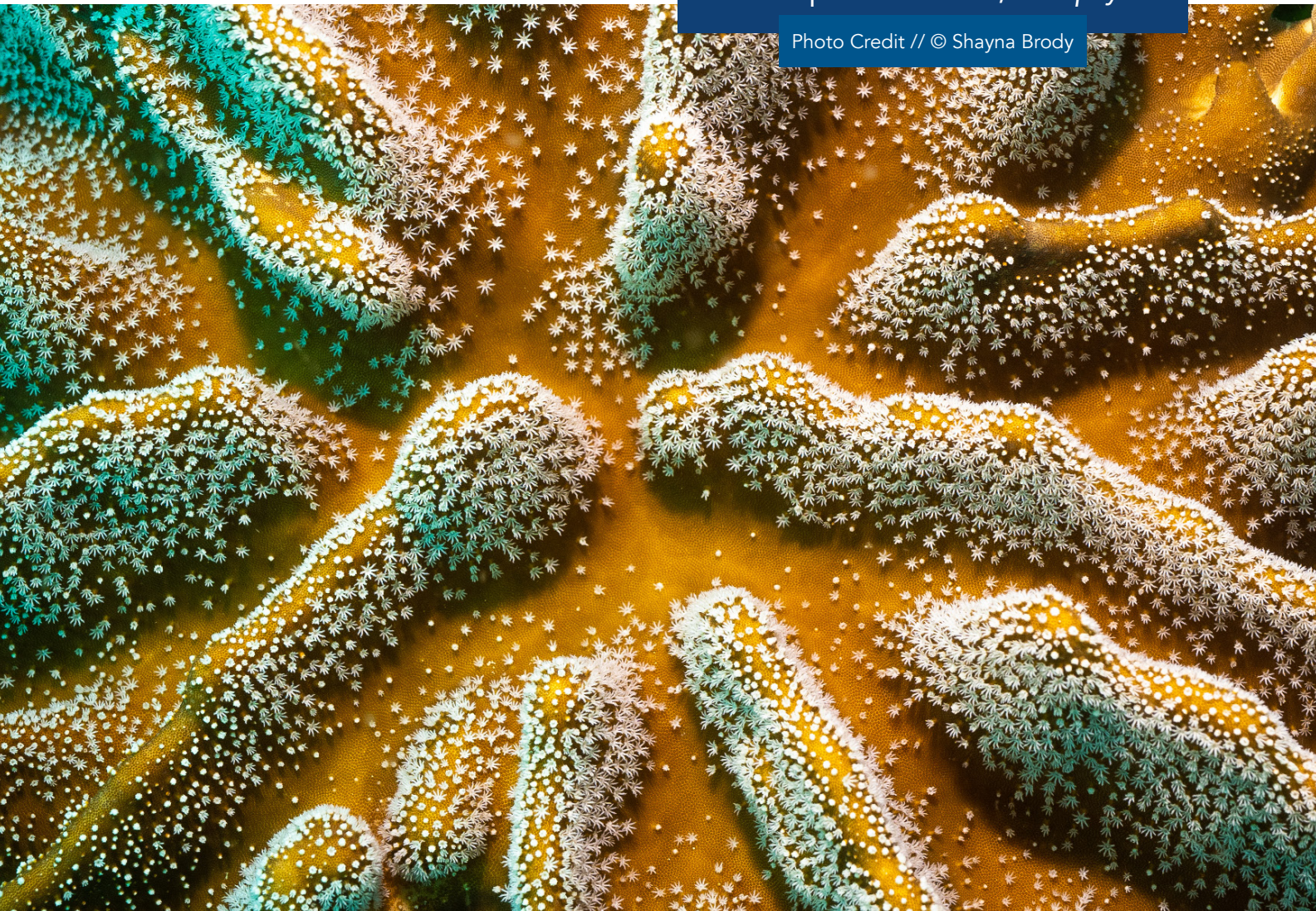
A pineapple sea cucumber (*Thelenota ananas*) with brittle stars.

Photo Credit // © Emanuel Gonçalves

5 | Consider further management measures for exploited sea cucumber species.

Although island use type had little effect on fish communities, certain invertebrate taxa—such as sea cucumbers and clams—were more abundant and diverse at uninhabited islands, indicating that harvesting pressure and/or environmental impacts related to development at inhabited and resort islands may negatively affect these taxa (Moritz et al. 2017). However, these results should be interpreted cautiously due to the imbalance of sites surveyed from each island use type.

Both the sea cucumber and giant clam fisheries in the Maldives have previously been identified as unsustainable, due to the life history characteristics and ease of collection of these species (Adam et al. 1997). While giant clam harvesting is no longer allowed in the Maldives as of 1995, due to the previous overexploitation and slow growth of the species, the patterns seen in this study may show the long-term effects of overharvesting at inhabited sites.

The sea cucumber fishery, in contrast, is still active in the Maldives, and harvesting has led to the decline of many of the most economically important species (Ducarme 2015). It should be noted that some recent management measures have been implemented to protect vulnerable species, such as the addition of two sea cucumber species (*Holothuria nobilis* and *Holothuria fuscogliva*) to CITES Appendix II.

However, it is recommended that increased management of the sea cucumber fishery be considered in order to allow for further recovery of overexploited species.

APPENDICES

His Excellency, President Ibrahim Mohamed Solih, and Speaker and former President Mohamed Nasheed visit an underwater survey site at Keylakunu.

Photo Credit // © Travis Matteson

APPENDIX 1 | METHODOLOGY

Site Selection

Sites were selected with the goal of providing a systematic snapshot of coral reef communities across the Maldives. Efforts were made to select sites that would complement long-term monitoring efforts or provide ecological information for less studied sections of reef. Sites were distributed randomly along forereef habitats at each atoll with a minimum of 2 kilometers spacing between each site. Sites which were within 2 kilometers of a resort or inhabited island were designated with the island use type of the closest island; sites that were within 2 kilometers of an uninhabited island, or less than2 kilometers from any emergent land were designated as uninhabited. Because the survey took place during the North-East monsoon season, sites on the western sides of atolls were preferentially selected in order to ensure safe diving conditions.

Fish

Belt Transects

Underwater visual census approaches in the form of belt transect methods were used to enumerate the density, size structure, biomass, and species composition of the reef fish assemblage at each reef. At each site divers laid out three 25m transect lines along the reef, identifying and estimating the length of all fishes to the nearest 5cm size class along each transect.

Fish abundance estimates were made by means of two passes for each 25m transect: on the outward swim, the divers surveyed an 8m width (200 m^2 area) for individuals >20 cm total length (TL), and on the return swim, a 4m width (100 m^2 area) was surveyed for species ≤20 cm TL. All fish were identified to the species level where possible.

Fish biomass estimation parameters and trophic groupings for each species surveyed were assigned using the best available information from FishBase and the published literature. Biomass was estimated using the length-weight equation $W = a \, L^b$, where W is the weight of the fish in grams, L is the total length of the fish in centimeters, a is the species-specific scaling coefficient, and b is a species-specific shape parameter related to body shape.

IUCN Presence/Absence Surveys

In addition to the belt transect surveys, divers conducted presence/absence surveys of IUCN Red Listed fish, shark, ray, and turtle species at each site. Divers recorded the presence of all IUCN species seen on each dive, regardless of whether the species was counted during a belt transect survey.

BRUVs

Mid-water baited remote underwater video systems (BRUVs) were deployed to quantify pelagic communities by providing information on abundance, diversity, size, and distribution of pelagic wildlife in the sampling area. BRUVs consist of a cross bar with two GoPro cameras fixed 0.8 m apart on an inward convergent angle of 8°. Five systems were deployed concurrently for a duration of 2 hours at a depth of 10 m, separated by 200 m in longline formation.

Rigs were baited with ~1 kg of crushed oily fish. Imagery collected was analyzed using the software program EventMeasure and all animals observed were identified to the lowest possible taxonomic resolution. Relative abundance was estimated as the maximum number of individuals of each taxon observed in any given video frame (MaxN) and lengths measurements were made for each species via 3D photogrammetry. Abundance and length estimates allow the estimation of biomass through established length-weight relationships.

Benthic Cover

Benthic cover was estimated using photoquadrats taken of the benthos at each site. Following the completion of each fish belt transect survey, a second team of divers collected photoquadrat images along the same transect line, taking photos every 2 m, for a total of 13-15 photos per transect. A monopod was attached to each camera to ensure that photos were taken from a fixed distance and covered the same area of the benthos (approximately 0.72 m^2 per photo).

Photoquadrat images were analyzed using the image analysis software PhotoGrid, which projects 25 points onto each image in a randomly stratified pattern. The taxon under each randomly generated point was identified to the lowest taxonomic level possible in order to determine percent cover of each taxon.

Coral Recruitment

Coral juveniles were identified using large-area imagery techniques. At each site, a 10 m x 10 m plot was selected to be surveyed using this method. To capture the imagery, a diver swam a specialized camera rig containing two Nikon D700 SLR cameras set to different focal lengths (18mm and 55mm) in a double lawnmower pattern (**Figure 27**) approximately 1.5 m above the reef at each site.

As the diver slowly swims the plot, the cameras take photographs of the benthos each second, creating a set of approximately 3000 photos of each plot, all with high overlap between adjacent images, which can be stitched together to form a 3D model.

3D models of each plot are reconstructed using the commercially available Structure from Motion (SfM) based software Agisoft Metashape, which fuses raw imagery from the 18mm camera and creates 3D point clouds. These point clouds can then be analyzed using a specially developed software, Viscore, allowing data to be extracted from the models. Viscore allows for the visualization of the 3D model and raw imagery, as well as the ability to measure reef features to millimeter-scale resolution (**Figure 28**).

For the juvenile coral analysis, a 10 m x 10 m area was defined on each photomosaic, and 1 m x 1 m quadrats were drawn inside this area. Five randomly selected quadrats were analyzed per model. Within each quadrat, the raw imagery used to build the mosaic was searched, and all coral juveniles less than 5 cm in maximum diameter were identified to the lowest taxonomic level possible.

Rugosity

Rugosity data are collected from the 3D models described above using a simulated point gauge approach (McCormick 1994). In Viscore, a 10 m x 10 m area was defined on each mosaic. Within this area, 100 parallel transects spaced 10 cm apart were sampled in an alongshore direction across the model.

Along each transect, depths were sampled every 10 cm following the contours of the reef from a top-down perspective. The length of each transect following the depth contours was divided by the linear length of the transect (in this case, 10 m) to calculate the rugosity ratio for each transect. The rugosity ratios for all 100 transects were then averaged to produce a mean rugosity value for each site. A ratio of 1 indicates a completely flat reef, with increasing values indicating more complex reefs.

Invertebrates

Estimates of key macroinvertebrate species were made using belt transect methodologies as outlined by the Global Coral Reef Monitoring Network (GCRMN). To summarize, at each site a diver estimated the number of macro-invertebrates found along the three 25m transects used for fish and photoquadrat surveys. For each survey, a 2m wide swath was inspected for invertebrates, yielding a 50m^2 survey area for each transect.

Water Quality

Stable isotope (δ13C–δ15N) approaches were used to assess water quality across the Maldives. These water quality assessments were made by collecting five samples of the most abundant macroalgae (e.g., Halimeda spp.) along the three transects at each site. These macroalgae samples will be dried, decalcified, and run through a mass-spectrometer upon reopening of the appropriate laboratory following the COVID-19 pandemic, in order to calculate stable isotope ratios.

FIGURE 27: Schematic of diver survey pattern to collect images of mosaic plot.
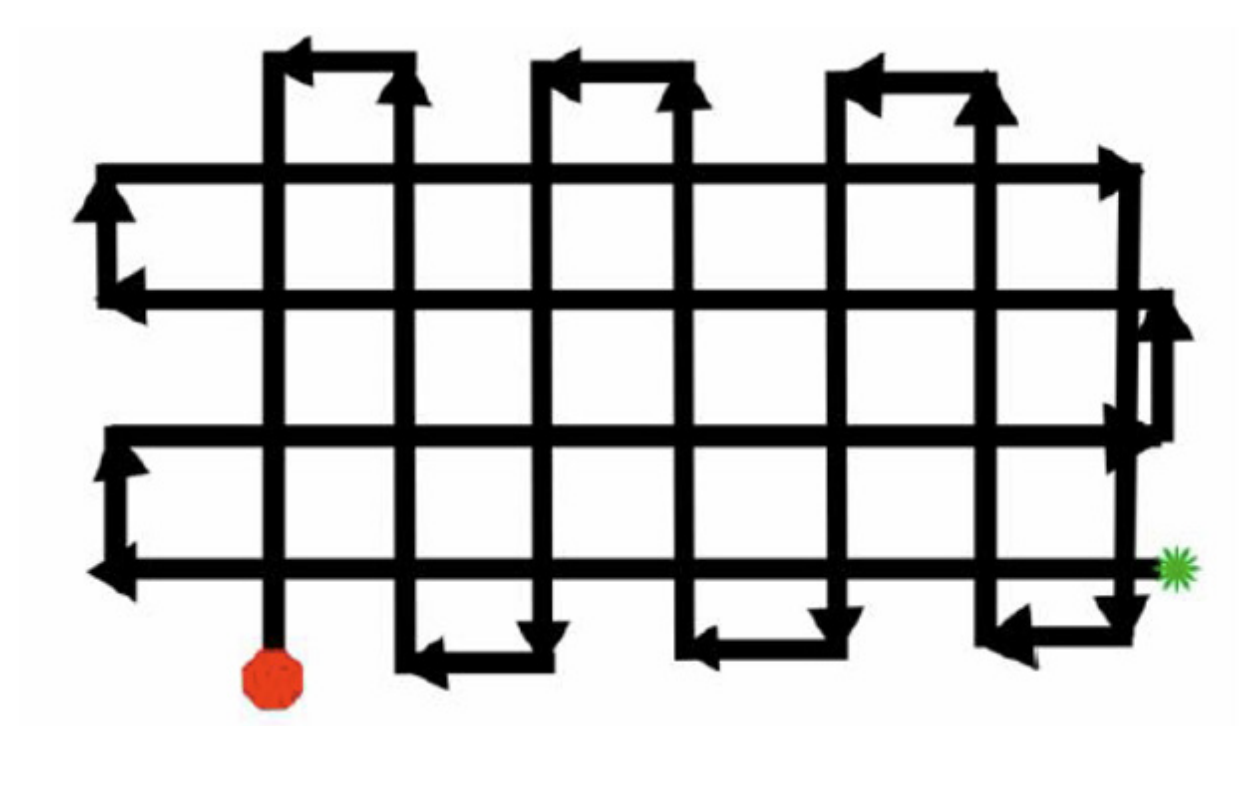
FIGURE 28: Schematic showing the different scales of resolution afforded by the large-area imagery methodology.

Figure 1. Spatial scales of benthic observation across the coral reefs of the tropics. Benthic interactions are noted at the 0.1-1 cm scale, organismal identifications are recorded at the 10 cm – 1 m scale, distribution of organisms is recorded in photomosaics at 100s m² scale, sites are embedded within the island scale (10s – 100s km²), and all are contained within the regional scale (1 – 10 million km²).

APPENDIX 2 | SITE METADATA

TABLE 2: *Site metadata for all sites surveyed.*

Station ID	Atoll Name	Administrative Division	Latitude (DD)	Longitude (DD)	Site Classification
MAL_001	Ari	North Central	3.86253	72.70189	Resort
MAL_002	Ari	North Central	3.89348	72.70696	Resort
MAL_003	Ari	North Central	3.87694	72.70611	Resort
MAL_004	Ari	North Central	3.94409	72.70818	Community
MAL_005	Ari	North Central	4.19583	72.7377	Community
MAL_006	Ari	North Central	4.24304	72.73992	Resort
MAL_007	Baa	North	5.00841	72.84043	Community
MAL_008	Baa	North	5.03456	72.82696	Community
MAL_009	Baa	North	5.10579	72.80859	Uninhabited
MAL_010	Baa	North	5.13436	72.82459	Uninhabited
MAL_011	Baa	North	5.23232	72.84914	Uninhabited
MAL_012	Baa	North	5.26891	72.85674	Uninhabited
MAL_013	Raa	North	5.3485	72.84949	Uninhabited
MAL_014	Raa	North	5.39264	72.86157	Uninhabited
MAL_015	Raa	North	5.53992	72.78889	Uninhabited
MAL_016	Raa	North	5.46613	72.84023	Uninhabited
MAL_017	Shaviyani	Upper North	6.10096	73.02132	Uninhabited
MAL_018	Shaviyani	Upper North	6.02424	73.07126	Uninhabited
MAL_019	Shaviyani	Upper North	6.20082	72.99064	Uninhabited
MAL_020	Shaviyani	Upper North	6.16079	72.99505	Uninhabited
MAL_021	Shaviyani	Upper North	6.32291	72.95978	Community
MAL_022	Shaviyani	Upper North	6.27726	72.98839	Resort
MAL_023	Haa Dhaalu	Upper North	6.54528	72.87829	Community
MAL_024	Haa Dhaalu	Upper North	6.56699	72.86826	Uninhabited
MAL_025	Haa Alif	Upper North	6.92054	72.92446	Uninhabited
MAL_026	Haa Alif	Upper North	6.93498	72.91491	Uninhabited
MAL_027	Haa Alif	Upper North	6.98519	72.8773	Community
MAL_028	Haa Alif	Upper North	6.97312	72.88859	Community
MAL_029	Haa Alif	Upper North	7.02314	72.8117	Uninhabited
MAL_030	Haa Alif	Upper North	7.01356	72.83073	Community
MAL_031	Makunudhoo	Upper North	6.39938	72.63877	Uninhabited
MAL_032	Makunudhoo	Upper North	6.37137	72.62236	Uninhabited
MAL_033	Makunudhoo	Upper North	6.34113	72.60352	Uninhabited
MAL_034	Makunudhoo	Upper North	6.31298	72.58212	Uninhabited
MAL_035	Makunudhoo	Upper North	6.23107	72.55811	Uninhabited

Station ID	Atoll Name	Administrative Division	Latitude (dd)	Longitude (dd)	Site Classification
MAL_036	Makunudhoo	Upper North	6.2097	72.57146	Uninhabited
MAL_037	Noonu	Upper North	5.98577	73.10034	Uninhabited
MAL_038	Noonu	Upper North	5.95369	73.12225	Uninhabited
MAL_039	Noonu	Upper North	5.80804	73.16443	Uninhabited
MAL_040	Noonu	Upper North	5.92037	73.12973	Uninhabited
MAL_041	Noonu	Upper North	5.66464	73.26814	Community
MAL_042	Noonu	Upper North	5.68655	73.25332	Community
MAL_043	Lhaviyani	North	5.36261	73.33754	Resort
MAL_044	Lhaviyani	North	5.36909	73.35722	Resort
MAL_045	Lhaviyani	North	5.37224	73.37579	Uninhabited
MAL_046	Lhaviyani	North	5.37459	73.39288	Uninhabited
MAL_047	Lhaviyani	North	5.35705	73.41684	Community
MAL_048	Lhaviyani	North	5.36308	73.40986	Community
MAL_049	Vaavu	North Central	3.52401	73.28937	Uninhabited
MAL_050	Vaavu	North Central	3.49112	73.27665	Uninhabited
MAL_051	Vaavu	North Central	3.45586	73.30456	Uninhabited
MAL_052	Vaavu	North Central	3.44077	73.35358	Uninhabited
MAL_053	Vaavu	North Central	3.35771	73.42272	Uninhabited
MAL_054	Vaavu	North Central	3.31324	73.46206	Community
MAL_055	Meemu	Central	3.11327	73.37189	Uninhabited
MAL_056	Meemu	Central	3.08515	73.37438	Uninhabited
MAL_057	Meemu	Central	2.92934	73.37369	Uninhabited
MAL_058	Meemu	Central	2.89397	73.37473	Community
MAL_059	Meemu	Central	2.78804	73.36782	Uninhabited
MAL_060	Meemu	Central	2.82906	73.36763	Uninhabited
MAL_061	Thaa	South Central	2.2575	72.92725	Community
MAL_062	Thaa	South Central	2.22352	72.93737	Uninhabited
MAL_063	Thaa	South Central	2.18235	72.96983	Uninhabited
MAL_064	Thaa	South Central	2.16184	73.01691	Community
MAL_065	Laamu	South Central	1.7978	73.29006	Resort
MAL_066	Laamu	South Central	1.77747	73.34977	Community
MAL_067	Laamu	South Central	1.81535	73.44044	Uninhabited
MAL_068	Laamu	South Central	1.79494	73.40432	Community
MAL_069	Laamu	South Central	1.81078	73.47569	Community
MAL_070	Laamu	South Central	1.77587	73.37118	Community
MAL_071	Laamu	South Central	1.88371	73.23505	Community
MAL_072	Laamu	South Central	1.86953	73.24029	Community
MAL_073	Laamu	South Central	1.85177	73.24471	Uninhabited
MAL_074	Laamu	South Central	1.83745	73.25482	Uninhabited

Station ID	Atoll Name	Administrative Division	Latitude (DD)	Longitude (DD)	Site Classification
MAL_075	Laamu	South Central	1.82344	73.26539	Uninhabited
MAL_076	Laamu	South Central	1.81006	73.27641	Resort
MAL_077	Laamu	South Central	1.94914	73.24849	Uninhabited
MAL_078	Laamu	South Central	1.98501	73.28856	Uninhabited
MAL_079	Thaa	South Central	2.39949	72.88975	Uninhabited
MAL_080	Laamu	South Central	1.96166	73.26178	Uninhabited
MAL_081	Thaa	South Central	2.36907	72.90089	Uninhabited
MAL_082	Thaa	South Central	2.41994	72.88557	Uninhabited
MAL_083	Thaa	South Central	2.38507	72.8942	Uninhabited
MAL_084	Thaa	South Central	2.35097	72.89671	Community
MAL_085	Thaa	South Central	2.3339	72.89793	Community
MAL_086	Thaa	South Central	2.47045	72.89969	Uninhabited
MAL_087	Thaa	South Central	2.46226	72.89379	Uninhabited
MAL_088	Thaa	South Central	2.49882	72.92063	Uninhabited
MAL_089	Thaa	South Central	2.48413	72.91068	Uninhabited
MAL_090	Thaa	South Central	2.5197	72.95078	Uninhabited
MAL_091	Thaa	South Central	2.51022	72.9352	Uninhabited
MAL_092	Dhaalu	Central	2.71234	72.83362	Uninhabited
MAL_093	Dhaalu	Central	2.69482	72.84218	Resort
MAL_094	Dhaalu	Central	2.67793	72.8499	Resort
MAL_095	Dhaalu	Central	2.66595	72.86166	Community
MAL_096	Dhaalu	Central	2.66031	72.87921	Community
MAL_097	Dhaalu	Central	2.66216	72.89733	Community
MAL_098	Dhaalu	Central	2.7471	72.82982	Uninhabited
MAL_099	Dhaalu	Central	2.76467	72.8287	Uninhabited
MAL_100	Dhaalu	Central	2.78183	72.82131	Uninhabited
MAL_101	Dhaalu	Central	2.80004	72.82085	Uninhabited
MAL_102	Dhaalu	Central	2.8177	72.82411	Uninhabited
MAL_103	Dhaalu	Central	2.83275	72.83117	Uninhabited
MAL_104	Dhaalu	Central	2.8591	72.83778	Community
MAL_105	Dhaalu	Central	2.87889	72.83057	Community
MAL_106	Dhaalu	Central	2.91594	72.83055	Uninhabited
MAL_107	Dhaalu	Central	2.89832	72.8245	Community
MAL_108	Dhaalu	Central	2.95724	72.85648	Uninhabited
MAL_109	Dhaalu	Central	2.92455	72.8354	Uninhabited
MAL_110	Faafu	Central	3.0602	72.92837	Community
MAL_111	Faafu	Central	3.0573	72.92135	Community
MAL_112	Faafu	Central	3.05686	72.92022	Community
MAL_113	Faafu	Central	3.04929	72.88781	Community

Station ID	Atoll Name	Administrative Division	Latitude (DD)	Longitude (DD)	Site Classification
MAL_114	Faafu	Central	3.04968	72.88129	Community
MAL_115	Faafu	Central	3.05293	72.86955	Community
MAL_116	Faafu	Central	3.16603	72.84771	Uninhabited
MAL_117	Faafu	Central	3.1343	72.85765	Uninhabited
MAL_118	Faafu	Central	3.22372	72.81377	Uninhabited
MAL_119	Faafu	Central	3.18931	72.8206	Uninhabited
MAL_120	Faafu	Central	3.25337	72.80838	Uninhabited
MAL_121	Faafu	Central	3.2702	72.8055	Uninhabited
MAL_122	Ari	North Central	3.62042	72.70043	Resort
MAL_123	Ari	North Central	3.58773	72.71944	Resort
MAL_124	Ari	North Central	3.72569	72.7002	Community
MAL_125	Ari	North Central	3.69253	72.70528	Community
MAL_126	Ari	North Central	3.83419	72.70254	Uninhabited
MAL_127	Ari	North Central	3.78217	72.69778	Resort
MAL_PRES*	Haa Dhaalu	Upper North	6.60159	73.00484	Uninhabited

* Large-area imagery data was collected at HAD-PRES, and these data were included in the coral recruit and rugosity analyses. No fish, invertebrate, photoquadrat, or water quality data were collected at this site.

APPENDIX 3 | BELT TRANSECT SUMMARY DATA

TABLE 3: Full list of species surveyed during the belt transect surveys.

DACOR (Dominant, Abundant, Common, Occasional, Rare) classifications are: D= observed at ≥ 75% of sites, A= observed at 50-74% of sites, C=observed at 25-49% of sites, O= observed at 10-24% of sites, and R= observed at <10% of sites.

Family	Species	DACOR	# Sites Observed	Mean density (# m-2)	Mean biomass (g m-2)
Acanthuridae	Acanthuridae species	R	1	0.00003	0.00004
	Acanthurus auranticavus	R	4	0.00009	0.04743
	Acanthurus bariene	R	1	0.00024	0.16477
	Acanthurus blochii	R	1	0.00003	0.01423
	Acanthurus dussumieri	R	4	0.00041	0.1058
	Acanthurus leucocheilus	A	58	0.00814	0.32638
	Acanthurus leucosternon	D	119	0.07299	0.56741
	Acanthurus lineatus	O	26	0.00646	0.1289
	Acanthurus maculiceps	R	6	0.00013	0.02796
	Acanthurus mata	O	19	0.00252	0.33368
	Acanthurus nigricans	R	1	0.00005	0.00073
	Acanthurus nigricauda	D	97	0.03207	1.09217
	Acanthurus nigrofuscus	D	118	0.08737	0.32538
	Acanthurus tennentii	C	42	0.00399	0.41823
	Acanthurus thompsoni	C	47	0.02607	0.17967
	Acanthurus tristis	O	18	0.00102	0.07008
	Acanthurus xanthopterus	R	4	0.00048	0.04127
	Ctenochaetus binotatus	A	91	0.01371	0.16526
	Ctenochaetus striatus	D	116	0.17607	0.71412
	Ctenochaetus truncatus	A	94	0.0659	0.21326
	Naso brachycentron	O	26	0.00357	1.80247
	Naso brevirostris	A	78	0.01397	1.49832
	Naso elegans	D	122	0.01265	0.94624
	Naso hexacanthus	A	55	0.00882	1.84603
	Naso mcdadei	R	2	0.00004	0.03498
	Naso thynnoides	O	13	0.00213	0.53096
	Naso tonganus	R	2	0.00016	0.19498
	Naso unicornis	O	20	0.00433	1.90133
	Naso vlamingii	A	51	0.00418	1.21197
	Paracanthurus hepatus	R	1	0.00008	0.00009
	Zebrasoma desjardinii	C	43	0.00268	0.18993
	Zebrasoma scopas	A	56	0.00993	0.09694
	Zebrasoma veliferum	R	4	0.0001	0.01796

DACOR (Dominant, Abundant, Common, Occasional, Rare) classifications are: D= observed at ≥ 75% of sites, A= observed at 50-74% of sites, C=observed at 25-49% of sites, O= observed at 10-24% of sites, and R= observed at <10% of sites.

Family	Species	DACOR	# Sites Observed	Mean density (# m-2)	Mean biomass (g m-2)
Apogonidae	*Apogon species*	O	26	0.00985	0.02304
	Cheilodipterus isostigma	R	1	0.00058	0.00065
	Cheilodipterus macrodon	R	4	0.00029	0.0026
	Cheilodipterus quinquelineatus	R	2	0.00026	0.00082
	Cheilodipterus species	R	1	0.00003	0.00003
	Ostorhinchus angustatus	O	21	0.00328	0.0158
	Ostorhinchus apogonides	R	1	0.00052	0.00075
	Ostorhinchus nigrofasciatus	C	43	0.0086	0.02882
	Ostorhinchus spp	R	1	0.0001	0.00015
	Pristiapogon fraenatus	R	3	0.00047	0.00098
	Pristiapogon kallopterus	R	5	0.00215	0.00258
	Rhabdamia gracilis	R	1	0.00052	0.00069
	Zapogon evermanni	R	1	0.00249	0.00271
Aulostomidae	*Aulostomus chinensis*	R	1	0.00003	0.0055
Balistidae	*Balistapus undulatus*	D	125	0.02694	0.27596
	Balistoides conspicillum	A	55	0.00197	0.5957
	Balistoides viridescens	C	45	0.00113	1.46339
	Canthidermis macrolepis	R	2	0.00063	0.46395
	Melichthys indicus	D	127	0.0333	0.91334
	Melichthys niger	O	19	0.00136	0.17768
	Odonus niger	D	100	0.56584	1.29465
	Pseudobalistes flavimarginatus	R	12	0.00031	0.17363
	Rhinecanthus rectangulus	R	1	0.00003	0.00122
	Sufflamen bursa	D	113	0.00997	0.21716
	Sufflamen chrysopterum	C	44	0.00518	0.06273
Blenniidae	*Aspidontus taeniatus*	O	16	0.00087	0.00414
	Blenniella chrysospilos	R	7	0.00055	0.00089
	Cirripectes auritus	O	15	0.00129	0.00245
	Cirripectes castaneus	A	51	0.00777	0.01203
	Cirripectes sp	R	8	0.00066	0.00132
	Ecsenius bicolor	C	38	0.00328	0.00442
	Ecsenius lineatus	O	13	0.0015	0.0028
	Ecsenius midas	R	11	0.00131	0.00211
	Ecsenius minutus	A	71	0.01782	0.0202
	Ecsenius species	O	15	0.00586	0.00709
	Exallias brevis	R	1	0.00003	0.00015
	Helcogramma maldivensis	C	46	0.01451	0.01623

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Blenniidae	*Meiacanthus smithi*	R	5	0.00018	0.00044
	Plagiotremus phenax	O	27	0.0022	0.0024
	Plagiotremus rhinorhynchos	A	79	0.0062	0.01467
	Plagiotremus tapeinosoma	D	110	0.01648	0.02261
Caesionidae	*Caesio caerulaurea*	R	1	0.00003	0.00714
	Caesio lunaris	C	33	0.02438	1.81476
	Caesio teres	R	3	0.00226	0.02478
	Caesio varilineata	O	27	0.04143	1.51039
	Caesio xanthonota	C	34	0.06455	0.45298
	Dipterygonotus balteatus	R	4	0.0111	0.0341
	Gymnocaesio gymnoptera	R	1	0.00003	0.00003
	Pterocaesio chrysozona	R	2	0.00207	0.022
	Pterocaesio lativittata	O	20	0.0298	1.18833
	Pterocaesio pisang	O	28	0.06677	0.28442
	Pterocaesio sp	R	2	0.00577	0.00895
	Pterocaesio tile	C	48	0.08581	1.88735
	Pterocaesio trilineata	R	3	0.00396	0.02972
Caracanthidae	*Caracanthus maculatus*	R	3	0.00037	0.00058
	Caracanthus unipinna	R	8	0.00081	0.00127
Carangidae	*Carangoides ferdau*	R	4	0.00008	0.05311
	Carangoides fulvoguttatus	R	4	0.00012	0.02705
	Carangoides orthogrammus	R	10	0.00025	0.15811
	Caranx ignobilis	R	2	0.00004	0.28495
	Caranx lugubris	R	2	0.00005	0.01071
	Caranx melampygus	A	77	0.0063	1.29379
	Caranx sexfasciatus	R	2	0.00035	0.05879
	Decapterus macarellus	R	5	0.00906	0.61927
	Elagatis bipinnulata	R	3	0.00026	0.04512
	Scomberoides lysan	R	2	0.00028	0.00661
Carcharhinidae	*Carcharhinus amblyrhynchos*	R	1	0.00001	0.1699
	Carcharhinus melanopterus	R	1	0.00001	0.03727
	Triaenodon obesus	R	7	0.00009	2.12333
Chaetodontidae	*Chaetodon auriga*	O	28	0.00151	0.07688
	Chaetodon bennetti	R	2	0.00013	0.01278
	Chaetodon citrinellus	C	42	0.00325	0.02526
	Chaetodon collare	C	35	0.00604	0.24365
	Chaetodon falcula	O	20	0.00127	0.06752

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Chaetodontidae	*Chaetodon flavocoronatus*	R	1	0.00005	0.00087
	Chaetodon guttatissimus	D	118	0.0293	0.12514
	Chaetodon kleinii	D	117	0.0198	0.10729
	Chaetodon lineolatus	R	1	0.00002	0.00581
	Chaetodon lunula	R	11	0.00052	0.04197
	Chaetodon lunulatus	R	9	0.00089	0.00643
	Chaetodon madagaskariensis	O	17	0.00117	0.01222
	Chaetodon melannotus	R	4	0.00012	0.00603
	Chaetodon meyeri	C	49	0.00263	0.11628
	Chaetodon ornatissimus	R	2	0.00008	0.00151
	Chaetodon triangulum	O	18	0.00138	0.02525
	Chaetodon trifascialis	C	32	0.00232	0.03033
	Chaetodon trifasciatus	A	52	0.00477	0.12708
	Chaetodon ulietensis	R	3	0.00018	0.00571
	Chaetodon xanthocephalus	O	19	0.00096	0.12289
	Forcipiger flavissimus	C	49	0.00395	0.04216
	Forcipiger longirostris	O	18	0.00139	0.02263
	Hemitaurichthys zoster	C	33	0.0294	0.31023
	Heniochus diphreutes	R	1	0.00079	0.05459
	Heniochus monoceros	O	21	0.00102	0.26187
	Heniochus pleurotaenia	A	55	0.00667	0.24789
	Heniochus singularius	R	7	0.00034	0.06976
Cirrhitidae	*Amblycirrhitus bimacula*	R	3	0.00013	0.00058
	Cirrhitichthys oxycephalus	D	95	0.03851	0.05786
	Paracirrhites arcatus	A	82	0.01557	0.04094
	Paracirrhites forsteri	D	122	0.02485	0.08324
Clupeidae	*Clupeidae species*	R	1	0.00525	0.01502
Dasyatidae	*Urogymnus granulatus*	R	3	0.00004	1.261
Diodontidae	*Diodon hystrix*	R	1	0.00001	0.02041
	Diodon liturosus	R	7	0.00013	0.09148
Ephippidae	*Platax orbicularis*	R	5	0.00007	0.10395
Fistularidae	*Fistularia commersonii*	R	9	0.00039	0.01954
Ginglymostomatidae	*Nebrius ferrugineus*	R	1	0.00001	0.04968
Gobiidae	*Amblyeleotris aurora*	R	3	0.00013	0.00018
	Amblyeleotris wheeleri	R	3	0.00013	0.00034
	Bryaninops yongei	R	1	0.00005	0.00007
	Eviota albolineata	O	30	0.0057	0.00655

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Gobiidae	*Eviota mikiae*	O	15	0.00948	0.01058
	Eviota sebreei	O	27	0.0099	0.01147
	Eviota sp	R	1	0.00005	0.00007
	Fusigobius neophytus	R	3	0.00021	0.00024
	Gnatholepis anjerensis	R	2	0.00005	0.00006
	Gnatholepis cauerensis	O	13	0.00144	0.00167
	Nemateleotris magnifica	D	115	0.07528	0.0882
	Paragobiodon species	R	1	0.00003	0.00004
	Pleurosicya micheli	R	6	0.00031	0.00043
	Ptereleotris evides	D	106	0.0909	0.14443
	Ptereleotris heteroptera	R	7	0.0152	0.01756
	Ptereleotris zebra	C	32	0.04692	0.09419
	Trimma naudei	R	1	0.0001	0.00015
	Trimma species	R	2	0.00005	0.00008
	Valenciennea strigata	A	50	0.01221	0.02266
Haemulidae	*Plectorhinchus albovittatus*	R	2	0.00004	0.09224
	Plectorhinchus chaetondonoides	R	2	0.00013	0.04881
	Plectorhinchus gibbosus	R	3	0.00007	0.08055
	Plectorhinchus vittatus	A	56	0.0038	0.83442
Holocentridae	*Myripristis adusta*	O	24	0.00244	0.21819
	Myripristis berndti	C	36	0.01023	0.29097
	Myripristis kuntee	O	20	0.00645	0.15974
	Myripristis murdjan	R	10	0.00163	0.08374
	Myripristis violacea	R	4	0.00029	0.01959
	Myripristis vittata	R	3	0.00113	0.0248
	Neoniphon argenteus	R	1	0.00005	0.00189
	Neoniphon opercularis	R	3	0.0001	0.00714
	Neoniphon sammara	R	5	0.0011	0.02209
	Sargocentron caudimaculatum	A	64	0.01572	0.19052
	Sargocentron diadema	O	17	0.00249	0.02382
	Sargocentron microstoma	R	8	0.00092	0.0335
	Sargocentron spiniferum	A	68	0.00333	0.92135
	Sargocentron violaceum	R	1	0.00001	0.00306
Kyphosidae	*Kyphosus cinerascens*	R	12	0.00081	0.14961
	Kyphosus species	R	1	0.00004	0.01422
	Kyphosus vaigiensis	R	2	0.00008	0.00879

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Labridae	*Anampses caeruleopunctatus*	O	19	0.00075	0.0242
	Anampses lineatus	R	4	0.00015	0.001
	Anampses meleagrides	A	61	0.00452	0.02988
	Bodianus axillaris	A	72	0.00551	0.04981
	Bodianus diana	A	58	0.00342	0.06351
	Cheilinus arenatus	R	2	0.00005	0.00034
	Cheilinus chlorourus	R	10	0.0005	0.00771
	Cheilinus fasciatus	R	3	0.00005	0.00948
	Cheilinus oxycephalus	C	32	0.00213	0.02648
	Cheilinus trilobatus	O	25	0.00059	0.06567
	Cheilinus undulatus	O	18	0.00035	3.04135
	Cheilio inermis	R	1	0.00003	0.00027
	Cirrhilabrus exquisitus	D	119	0.23853	0.34394
	Coris aygula	R	2	0.00005	0.01916
	Coris batuensis	R	4	0.00018	0.00063
	Coris cuvieri	C	43	0.00133	0.11802
	Coris formosa	R	10	0.00021	0.03278
	Epibulus insidiator	C	34	0.00174	0.05575
	Gomphosus caeruleus	D	124	0.04589	0.09127
	Gomphosus varius	R	1	0.00013	0.00018
	Halichoeres chrysotaenia	R	2	0.00005	0.00111
	Halichoeres chrysus	R	4	0.00021	0.00149
	Halichoeres cosmetus	D	122	0.03409	0.06232
	Halichoeres hortulanus	D	125	0.05572	0.10326
	Halichoeres leucoxanthus	R	5	0.00031	0.0012
	Halichoeres leucurus	R	4	0.0001	0.00078
	Halichoeres marginatus	R	9	0.00035	0.00309
	Halichoeres nebulosus	R	4	0.00021	0.00068
	Halichoeres scapularis	R	2	0.00017	0.00102
	Hemigymnus fasciatus	A	58	0.00249	0.07185
	Hemigymnus melapterus	C	40	0.00129	0.3233
	Hologymnosus annulatus	R	11	0.00034	0.03357
	Labrichthys unilineatus	O	20	0.00097	0.00871
	Labroides bicolor	C	49	0.00313	0.00986
	Labroides dimidiatus	D	127	0.06444	0.07972
	Labroides rubrolabiatus	R	2	0.00008	0.00009
	Labropsis xanthonota	R	4	0.0001	0.00037

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Labridae	*Macropharyngodon bipartitus*	A	86	0.00965	0.03613
	Macropharyngodon ornatus	R	2	0.00005	0.00039
	Novaculichthys taeniourus	R	9	0.00027	0.018
	Oxycheilinus digramma	O	21	0.00114	0.02737
	Oxycheilinus rhodochrous	O	22	0.00076	0.02303
	Oxycheilinus unifasciatus	R	1	0.00003	0.00027
	Pseudocheilinus evanidus	O	16	0.01582	0.03016
	Pseudocheilinus hexataenia	D	124	0.08949	0.09501
	Pseudocoris yamashiroi	R	6	0.00081	0.00281
	Pseudodax moluccanus	C	43	0.00218	0.08431
	Stethojulis albovittata	A	88	0.01058	0.03642
	Stethojulis strigiventer	R	2	0.00005	0.00045
	Stethojulis trilineata	R	1	0.00003	0.00019
	Thalassoma amblycephalum	D	126	0.96122	1.23787
	Thalassoma hardwicke	R	6	0.00034	0.00241
	Thalassoma jansenii	A	89	0.03892	0.2824
	Thalassoma lunare	D	115	0.03954	0.07079
	Thalassoma purpureum	R	1	0.00005	0.00009
	Thalassoma quinquevittatum	C	33	0.00922	0.02413
Lethrinidae	*Gnathodentex aureolineatus*	R	9	0.01597	0.13757
	Lethrinus erythracanthus	R	6	0.00008	0.11638
	Lethrinus obsoletus	R	3	0.00018	0.03902
	Lethrinus olivaceus	R	7	0.00034	0.44384
	Lethrinus rubrioperculatus	R	1	0.00001	0.00395
	Lethrinus xanthochilus	C	33	0.00229	0.7575
	Monotaxis grandoculis	A	62	0.00863	0.77862
	Monotaxis heterodon	R	4	0.00017	0.08132
Lutjanidae	*Aphareus furca*	C	41	0.00129	0.0856
	Aprion virescens	O	14	0.00054	0.17667
	Lutjanus biguttatus	R	3	0.00165	0.07539
	Lutjanus bohar	A	81	0.00698	0.64165
	Lutjanus decussatus	R	6	0.00028	0.035
	Lutjanus fulvus	R	4	0.00028	0.06708
	Lutjanus gibbus	C	38	0.05939	1.2434
	Lutjanus kasmira	R	11	0.01748	0.24377
	Lutjanus monostigma	O	22	0.00207	0.26721
	Macolor macularis	O	24	0.00149	0.34559

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	Macolor niger	O	14	0.00148	0.72318
Malacanthidae	*Malacanthus brevirostris*	R	3	0.00004	0.01221
	Malacanthus latovittatus	O	15	0.00052	0.06493
Microdesmidae	*Gunnellichthys curiosus*	R	1	0.00005	0.00018
Mobulidae	*Mobula kuhlii*	R	2	0.00003	0.05383
	Mobula species	R	1	0.00021	1.08298
Monacanthidae	*Aluterus scriptus*	R	3	0.00004	0.01206
	Amanses scopas	R	1	0.00003	0.00025
	Cantherhines dumerilii	O	16	0.00038	0.13939
	Cantherhines pardalis	O	19	0.00071	0.0456
	Pervagor janthinosoma	R	4	0.00016	0.00113
Mullidae	*Mulloidichthys vanicolensis*	R	1	0.00031	0.01516
	Parupeneus cyclostomus	A	85	0.00897	0.0807
	Parupeneus indicus	R	2	0.00016	0.00033
	Parupeneus macronemus	D	121	0.06045	0.12612
	Parupeneus multifasciatus	R	1	0.00004	0.00005
	Parupeneus pleurostigma	R	2	0.00013	0.00176
	Parupeneus trifasciatus	D	101	0.01794	0.20134
Muraenidae	*Echidna nebulosa*	R	4	0.00008	0.00838
	Gymnomuraena zebra	R	1	0.00001	0.00236
	Gymnothorax breedeni	R	7	0.0001	0.03723
	Gymnothorax fimbriatus	R	3	0.00007	0.01191
	Gymnothorax flavimarginatus	O	29	0.00052	0.15008
	Gymnothorax javanicus	O	31	0.00061	0.46419
	Gymnothorax meleagris	R	4	0.00005	0.01629
	Gymnothorax undulatus	R	1	0.00001	0.00729
Myliobatidae	*Aetobatos ocellatus*	R	1	0.00001	0.02562
	Aetobatus narinari	R	1	0.00003	0.18889
Nemipteridae	*Scolopsis bilineata*	C	35	0.00393	0.06483
Ostraciidae	*Ostracion cubicus*	R	10	0.00025	0.08162
	Ostracion meleagris	O	16	0.0005	0.02756
Pempheridae	*Parapriacanthus ransonneti*	R	1	0.00446	0.0048
	Pempheris vanicolensis	R	2	0.00031	0.00618
Pinguipedidae	*Parapercis hexophtalma*	R	1	0.00003	0.00061
	Parapercis millepunctata	A	68	0.00749	0.07363
	Parapercis pacifica	R	2	0.00008	0.00106
	Parapercis sp	O	17	0.00105	0.0123

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Pomacanthidae	*Apolemichthys trimaculatus*	O	23	0.001	0.07059
	Centropyge flavissima	R	1	0.00003	0.00044
	Centropyge multispinis	D	127	0.12336	0.20655
	Pomacanthus xanthometopon	R	8	0.00043	0.07924
	Pygoplites diacanthus	O	22	0.00176	0.09272
Pomacentridae	*Abudefduf vaigiensis*	R	3	0.00205	0.02986
	Amblyglyphidodon leucogaster	R	4	0.00087	0.00338
	Amphiprion clarkii	O	20	0.00185	0.00951
	Amphiprion nigripes	R	8	0.00207	0.00569
	Chromis atripectoralis	R	7	0.00819	0.00952
	Chromis dimidiata	D	127	0.93009	1.01339
	Chromis iomelas	R	1	0.00018	0.00026
	Chromis lepidolepis	R	1	0.00003	0.00006
	Chromis nigrura	C	42	0.01703	0.01818
	Chromis opercularis	A	71	0.058	0.09797
	Chromis ternatensis	C	40	0.12257	0.23215
	Chromis viridis	R	3	0.00072	0.002
	Chromis weberi	D	123	0.60058	0.84806
	Chromis xanthura	R	5	0.00018	0.00437
	Chromis xutha	R	10	0.00226	0.00384
	Chrysiptera brownriggii	R	5	0.00021	0.00033
	Chrysiptera chrysocephala	R	2	0.00014	0.0002
	Dascyllus aruanus	R	1	0.00005	0.00008
	Dascyllus carneus	A	72	0.11577	0.14184
	Dascyllus trimaculatus	A	69	0.01626	0.05135
	Lepidozygus tapeinosoma	R	1	0.00003	0.00003
	Plectroglyphidodon dickii	O	18	0.00236	0.00733
	Plectroglyphidodon lacrymatus	D	95	0.04735	0.09331
	Pomacanthus imperator	C	42	0.00095	0.30034
	Pomacentrus bankanensis	R	1	0.00002	0.00003
	Pomacentrus caeruleus	C	47	0.00701	0.01298
	Pomacentrus chrysurus	D	117	0.18229	0.25486
	Pomacentrus coelestis	R	2	0.00005	0.00008
	Pomacentrus indicus	D	108	0.13275	0.16891
	Pomacentrus nagasakiensis	R	9	0.00079	0.0026
	Pomacentrus pavo	R	2	0.00068	0.00081
	Pomacentrus philippinus	D	99	0.17267	0.26208

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Pomacentridae	Stegastes fasciolatus	O	15	0.00102	0.01097
Priacanthidae	Heteropriacanthus cruentatus	R	2	0.00008	0.00777
Priacanthidae	Priacanthus hamrur	R	9	0.00151	0.04202
Pseudochromidae	Chlidichthys inornatus	R	1	0.00003	0.00004
Scaridae	Calotomus carolinus	R	9	0.00026	0.02884
	Cetoscarus bicolor	A	70	0.00676	1.62482
	Cetoscarus ocellatus	R	1	0.00001	0.00742
	Chlorurus capistratoides	R	3	0.00005	0.02689
	Chlorurus enneacanthus	R	5	0.00018	0.08573
	Chlorurus sordidus	D	105	0.03605	0.52719
	Chlorurus strongylocephalus	D	109	0.02153	2.15954
	Hipposcarus harid	A	92	0.01004	1.13309
	Scarus caudofasciatus	R	3	0.00007	0.02851
	Scarus festivus	R	2	0.00004	0.02801
	Scarus forsteni	O	14	0.00037	0.11471
	Scarus frenatus	A	91	0.00623	1.01691
	Scarus ghobban	C	32	0.0018	0.42437
	Scarus globiceps	R	1	0.00001	0.00567
	Scarus niger	A	62	0.00473	0.57915
	Scarus oviceps	R	7	0.00018	0.03591
	Scarus prasiognathos	A	91	0.00977	2.2997
	Scarus psittacus	A	50	0.00345	0.20141
	Scarus rubroviolaceus	D	119	0.01977	1.91954
	Scarus russelii	O	13	0.00045	0.23711
	Scarus scaber	C	49	0.00198	0.32408
	Scarus sp	O	25	0.00458	0.05005
	Scarus spinus	R	1	0.00003	0.00249
	Scarus tricolor	D	99	0.0072	0.92697
	Scarus viridifucatus	R	8	0.00018	0.04342
Scombridae	Gymnosarda unicolor	O	21	0.00051	0.58908
Scorpaenidae	Pterois antennata	R	4	0.00018	0.00398
	Pterois radiata	R	2	0.0001	0.00789
	Pterois volitans	R	2	0.00005	0.00965
	Scorpaenopsis oxycephala	R	1	0.00001	0.00523
	Scorpaenopsis spp	R	1	0.00003	0.00291
	Sebastapistes cyanostigma	R	4	0.00026	0.00038
Serranidae	Aethaloperca rogaa	A	84	0.00484	0.2728

DACOR (Dominant, Abundant, Common, Occasional, Rare) classifications are: D= observed at ≥ 75% of sites, A= observed at 50-74% of sites, C=observed at 25-49% of sites, O= observed at 10-24% of sites, and R= observed at <10% of sites.

Family	Species	DACOR	# Sites Observed	Mean density (# m-2)	Mean biomass (g m-2)
Serranidae	*Anyperodon leucogrammicus*	R	10	0.0002	0.05214
	Cephalopholis argus	D	109	0.01635	0.5011
	Cephalopholis leopardus	C	45	0.00559	0.04981
	Cephalopholis miniata	O	31	0.00433	0.06813
	Cephalopholis nigripinnis	D	115	0.0252	0.20098
	Cephalopholis sexmaculata	R	4	0.00012	0.02024
	Cephalopholis spiloparaea	R	1	0.00001	0.00248
	Cephalopholis urodeta	R	1	0.00005	0.00007
	Epinephelus areolatus	R	1	0.00001	0.00387
	Epinephelus coeruleopunctatus	R	5	0.0001	0.0935
	Epinephelus fasciatus	C	40	0.00453	0.12682
	Epinephelus fuscoguttatus	R	2	0.00003	0.03023
	Epinephelus macrospilos	O	28	0.00058	0.17511
	Epinephelus melanostigma	R	1	0.00003	0.00086
	Epinephelus merra	R	5	0.00027	0.01162
	Epinephelus ongus	R	2	0.00003	0.01718
	Epinephelus polyphekadion	R	1	0.00008	0.00214
	Epinephelus spilotoceps	C	35	0.00192	0.09045
	Gracila albomarginata	R	5	0.0002	0.00776
	Nemanthias carberryi	O	20	0.19851	0.25653
	Plectropomus areolatus	R	2	0.00003	0.06054
	Plectropomus laevis	R	11	0.00018	0.43526
	Pseudanthias evansi	C	39	0.18029	0.22378
	Pseudanthias ignitus	O	22	0.08168	0.10091
	Pseudanthias squamipinnis	D	96	0.73765	0.87472
	Variola albimarginata	R	5	0.00007	0.06504
	Variola louti	A	72	0.00219	0.91692
Siganidae	*Siganus argenteus*	O	31	0.00546	0.28094
	Siganus corallinus	O	25	0.00108	0.26421
	Siganus stellatus	A	72	0.00387	0.45299
Sphyraenidae	*Sphyraena barracuda*	R	5	0.00017	0.17714
	Sphyraena helleri	R	1	0.00003	0.02499
Synodontidae	*Saurida nebulosa*	R	6	0.00031	0.00395
	Synodus binotatus	R	3	0.00008	0.0004
	Synodus jaculum	R	1	0.00003	0.00014
	Synodus species	R	4	0.00016	0.00165
	Synodus variegatus	O	22	0.00113	0.00717

DACOR (Dominant, Abundant, Common, Occasional, Rare) classifications are: D= observed at ≥ 75% of sites, A= observed at 50-74% of sites, C=observed at 25-49% of sites, O= observed at 10-24% of sites, and R= observed at <10% of sites.

Family	Species	DACOR	# Sites Observed	Mean density (# m-2)	Mean biomass (g m-2)
Tetraodontidae	*Arothron hispidus*	R	1	0.00001	0.00811
	Arothron mappa	R	2	0.00003	0.0236
	Arothron meleagris	R	8	0.00023	0.18973
	Arothron nigropunctatus	O	15	0.00038	0.0773
	Arothron stellatus	R	1	0.00001	0.06196
	Canthigaster amboinensis	R	1	0.00003	0.00011
	Canthigaster bennetti	R	1	0.00003	0.00005
	Canthigaster janthinoptera	C	40	0.0021	0.01086
	Canthigaster solandri	R	1	0.00003	0.00005
	Canthigaster spp	R	1	0.00003	0.00042
	Canthigaster tyleri	R	1	0.00003	0.00042
	Canthigaster valentini	O	23	0.00162	0.00612
Zanclidae	*Zanclus cornutus*	A	81	0.00732	0.44869

APPENDIX 4 | CORAL DIVERSITY

TABLE 4: Full list of coral genera recorded in the photoquadrat and coral recruit surveys.

Genus	Photoquadrats	Recruits	Genus	Photoquadrats	Recruits
Acanthastrea	Present	Present	*Leptoria*	Present	Absent
Acropora	Present	Present	*Leptoseris*	Present	Present
Astrea	Present	Present	*Lobophyllia*	Present	Absent
Astreopora	Present	Present	*Merulina*	Present	Absent
Caulastrea	Absent	Present	*Montipora*	Present	Absent
Coscinaraea	Present	Present	*Mycedium*	Absent	Present
Cyphastrea	Present	Present	*Other Coral*	Present	Present
Diploastrea	Present	Absent	*Oxypora*	Absent	Present
Echinophyllia	Present	Present	*Pachyseris*	Present	Present
Echinopora	Present	Present	*Pavona*	Present	Present
Favia	Present	Present	*Platygyra*	Present	Present
Favities	Present	Present	*Plesiastrea*	Absent	Present
Fungia	Present	Present	*Pocillopora*	Present	Present
Galaxea	Present	Present	*Porites*	Present	Present
Gardineroseris	Present	Absent	*Psammocora*	Present	Present
Goniastrea	Present	Present	*Sandolitha*	Present	Absent
Goniopora	Present	Absent	*Seriatopora*	Present	Absent
Halomitra	Present	Absent	*Stylophora*	Present	Absent
Herpolitha	Present	Absent	*Symphyllia*	Present	Present
Hydnophora	Present	Present	*Turbinaria*	Present	Present
Leptastrea	Present	Present			

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