# 2022 TONGA
## Expedition Report

VEPA

WAITT INSTITUTE

SCRIPPS INSTITUTION OF OCEANOGRAPHY
UC San Diego
100 ISLAND CHALLENGE

CRIOBE

SNO CORAIL

# TABLE OF CONTENTS

# ACKNOWLEDGEMENTS

*Expedition Team*
*August 2022*

PHOTO CREDIT // Joe Lepore

*Expedition diver conducting transect surveys along the reef.*

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# EXECUTIVE SUMMARY

In January 2022, the Hunga Tonga-Hunga Ha'apai (HTHH) volcano erupted violently, creating a series of destructive tsunamis which traveled across Tonga and spread across several ocean basins. While terrestrial impacts were quantified soon after the eruption, logistical issues related to the recovery efforts and the COVID-19 pandemic prevented an immediate assessment of the impacts to coral reefs. In August of 2022, a field expedition led by the Ministry of Fisheries, Ministry for Environment (MEIDECC), Ministry of Lands and Natural Resources and Waitt Institute, in partnership with VEPA and Scripps Institution of Oceanography, was undertaken to assess the impact of the eruption and tsunami on Tonga's nearshore marine resources. The expedition surveyed several measures of reef health, including reef fish biomass, abundance, and diversity; macroinvertebrate abundance and diversity; coral recruitment and diversity; benthic percent cover; reef rugosity; and water quality parameters at sites across Tongatapu & 'Eua, Ha'apai, and Vava'u. Qualitative assessments and observations of tsunami impacts were also recorded to support the quantitative surveys. Sites were selected to prioritize reefs within Special Management Areas (SMAs), as well as those potentially impacted by the tsunami. Efforts were also made to resurvey sites established during a previous expedition in 2017, in order to draw direct comparisons prior to and following the eruption and tsunami.

The surveys conducted during this expedition were designed to efficiently provide a comprehensive assessment of reef health across three island districts. Healthy reefs tend to have higher cover of coral and crustose coralline algae (CCA), and lower cover of turf and fleshy macroalgae. While the absolute amount of coral that constitutes a "healthy reef" varies from location to location, changes in coral and algae cover can indicate whether reef health is increasing or decreasing over time. Rates of coral recruitment can help predict this trajectory in cases where time series data are not available, by indicating the capacity for new corals to colonize a reef in the future. Similarly, water quality data can indicate whether excess nutrients from land are present on a given reef, potentially leading to increases in fleshy algae cover. Higher coral cover tends to lead to higher structural complexity (rugosity), and more complex reefs provide more habitat for organisms such as fish and invertebrates to live. By combining data on benthic community composition and complexity with data on the number and size of fish and macroinvertebrates, it is possible to begin to determine how habitat quality and anthropogenic impacts, such as fishing and harvesting, drive patterns in fish and invertebrate populations. Understanding the composition of fish and invertebrate communities can also provide insight into future reef health trajectories, as healthy populations of these organisms support healthy reefs through ecological functions such as herbivory.

The data from this expedition indicate that the HTHH eruption and tsunami caused noticeable damage to the benthic communities of reefs in Tonga; however, these impacts were localized and likely related to the severity of the tsunami at each location. Coral cover in Ha'apai decreased from 2017 to 2022, and exposed sites in Tongatapu & 'Eua supported little live coral. However, in Vava'u, coral cover increased since 2017, and islands in Ha'apai and Tongatapu & 'Eua that were sheltered from the full force of the tsunami showed healthier benthic communities than those that were in the direct path. Coral recruitment was generally low across all islands and districts, with the exception of 'Eueiki (Tongatapu), which supported a mean density of 24.4 juvenile corals per $m^2$. Patterns in juvenile and adult coral diversity did not follow any obvious geographic patterns, and no one genus dominated across the country. However, mounding and encrusting species, which are better able to withstand high wave energy, dominated coral communities, indicating that more fragile branching and tabular species may have suffered greater damage from the tsunami.

Fish communities, however, do not seem to have been noticeably affected by the eruption or tsunami, and showed similar patterns to previous surveys. While overall diversity declined slightly since 2017, patterns in diversity stayed similar, with damselfish (pomacentrids) and wrasses (labrids) showing the highest diversity. Fish from these families were also the most abundant, while herbivores such as parrotfish (scarids) and surgeonfish (acanthurids) contributed the highest proportion of overall biomass. Predatory fish, such as snappers (lutjanids) and groupers (serranids) were rare at all sites except Fonualei, suggesting that in some cases these taxa may be overfished. Overall patterns and values of fish biomass, diversity and density were

similar to previous surveys undertaken in 2014 and 2017, indicating that fishing pressure and geography are likely driving patterns in fish populations, rather than impacts from the HTHH eruption.

Conversely, macroinvertebrate densities and diversity have declined since 2017. Overall, 27 species of macroinvertebrates were recorded in 2022- a significant decrease from the 56 species recorded during the 2017 expedition. In particular, sea cucumber populations saw a distinct decrease in diversity, from 19 species recorded in 2017 to only 9 in 2022. Sea cucumber densities were low across all islands surveyed, with a maximum mean density of 3 individuals per site ($300m^2$). It is possible that this decline is due in part to the HTHH eruption, which may have exacerbated stresses on invertebrate stocks created by the periodic reopening of the sea cucumber fishery, although a full stock assessment may be needed to support these claims.

*Close up of a macroinvertebrate, giant clam, Tridacna maxima.*

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# INTRODUCTION

On January 15, 2022, the Hunga Tonga- Hunga Ha'apai (HTHH) volcano, located in southwestern Tonga, erupted violently. This eruption, which lasted approximately 11 hours (Borrero et al., 2022b) was explosive, creating a giant plume of ash reaching heights of 30km, sonic booms that could be heard up to 10,000 km away, and a series of destructive tsunamis which traveled across several ocean basins (Borrero et al., 2022a). The tsunami caused widespread destruction across the Tongan archipelago, destroying seafront communities, severing internet connectivity cables, and in some cases washing completely across small islands (Borrero et al., 2022a, b). Despite the magnitude of the eruption and resulting tsunami, as well as the difficulty in delivering aid during the COVID-19 border closure, only three lives were lost in the disaster–a testament to Tonga's effective tsunami warning system and education campaigns (Borrero et al., 2022a). However, due to the recovery time required, as well as continued pandemic travel restrictions, the impacts of the tsunami on Tonga's marine resources were unknown for several months following the eruption. The data presented in this report represent the first post-eruption surveys from August 2022 of coastal coral reef systems across the Kingdom of Tonga following the HTHH eruption.

The Tongan archipelago is located in the Central South Pacific, in an area of high tectonic and volcanic activity between the Pacific and Australian tectonic plates. Islands within Tonga are a mix of volcanic and uplifted reef structures. The Exclusive Economic Zone of the Kingdom of Tonga covers approximately 700,000 $km^2$, and hosts 1,500 $km^2$ of coral reef habitat, across which over 190 species of coral can be found (Purkis et al., 2020). The archipelago is divided into four main island districts: Tongatapu and 'Eua, in the south, is home to the island's capital and is the largest population center in the country; Ha'apai, in the center of the country, contains the largest reef area; Vava'u, in the north, is comprised of several tightly-packed limestone islands; and the Niuas (Niuatoputapu and Niuafo'ou) in the far north, which is the most remote and least populated island district in the country. In addition, a number of offshore volcanic islands exist to the west of the main island groups.

The 2022 HTHH eruption is considered the most violent recorded since the eruption of Krakatau in 1883 (Borrero et al., 2022a). The resulting tsunami reached peak heights of ~20 m throughout several locations in Tonga and wave surges overtopped entire low-lying islands as well as ridges of up to 15 m in Tongatapu (Borrero et al. 2022b). On land, the tsunami caused catastrophic damage, with inundation distances between 20-1000 m depending on the topography of the coastline. The western portion of Tongatapu was particularly hard hit, as well as the islands of Southern Ha'apai–particularly, Nomuka Iki, Mango, and Tonumea, where low-lying areas were completely overtopped and vegetation almost completely stripped away (Borrero et al. 2022a). Other low-lying areas, such as the peninsula at the south of 'Atata, were also completely overtopped, leading to severe damage to structures and

vegetation. While the terrestrial impacts of the tsunami were immediately apparent and quantified shortly following the eruption, the impacts to Tonga's important marine resources were not immediately assessed.

## Effects of Volcanic Eruptions on Coral Reef Communities

Prior to the volcanic eruption, mean live coral cover across Tonga was reported between 16-31% (Purkis et al., 2017, Stone et al. 2017, Smallhorn-West et al., 2020). Coral cover tended to increase towards the south of the country, with Tongatapu hosting a mean cover of 24.9% while Vava'u, in the north, had a mean cover of 10.4%. Similarly, fish diversity and density were higher in Tongatapu and Ha'apai than in Vava'u, with means of approximately 35 species/transect and 2500 fish km$^{-2}$ in Tongatapu and Ha'apai, and approximately 24 species/transect and 1700 fish km$^{-2}$ in Vava'u. Biomass of target reef fish was highest in Ha'apai, at 820 kg ha$^{-2}$ and lowest in Vava'u at 340 kg ha$^{-2}$ (Smallhorn-West et al., 2020d). Based on these findings, fisheries in Tonga were determined to be moderately to heavily exploited, with most sites surveyed supporting less than 500 kg ha$^{-2}$ of target fish biomass (Smallhorn-West et al., 2020d) and fish communities tending to be dominated by small-bodied fish (Purkis et al., 2020).

*A healthy leather coral structure and associated reef fish.*

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Few studies examining the effect of volcanic eruptions on coral reef communities exist; however, results from these studies indicate that impacts can vary widely in space. One study, conducted around the volcanic island of Antahan in the Northern Marianas Islands, showed that reefs on one side of the island were completely smothered by a thick layer of volcanic ash, whereas reefs on the opposite side had coral cover of up to 35% (Vroom and Zgliczynski 2011). At Pagan, another volcanic island in the Marianas Islands, volcanic ash triggered localized outbreaks of cyanobacteria and the coral-killing cyanobacteriosponge *Terpois hoshinota* (Schils 2012). Indeed, following the 2015 eruption of the HTHH volcano in Tonga, reefs on the northern flank of the island appeared to have been sheltered from many of the impacts, and showed thriving coral communities shortly following the eruption, whereas reefs on the west and central portions of the island showed stronger signs of disturbance (Smallhorn-West et al. 2020c). Similarly, fish communities have been shown to vary across different intensities of lava flows following volcanic eruptions at Reunion Island in the Indian Ocean (Pinault et al., 2013).

Likewise, the impacts of tsunamis on coral reefs have been found to be variable, and the factors leading to the degree of impact are complex and poorly understood. For example, reefs within 300 km of the epicenter of the Sumatra-Andaman tsunami of 2004 were found to be largely unaffected by the disturbance and showed more variability by management regime than by exposure to the tsunami (Campbell et al., 2007). Conversely, reefs in the Seychelles, approximately 5000 km away from the epicenter, saw up to 100% mortality on some reefs, although the extent of the damage varied widely with substrate type and location within the archipelago (Obura and Abdulla 2005). Interestingly, nearby in the Maldives, located ~3000 km from the epicenter, destruction from the same tsunami was comparatively minimal (Goffredo et al., 2007). This variability in impact indicates that the effect of tsunamis on coral reefs is complex and is likely based on a number of factors, including location, exposure, bathymetry, and substrate, as well as the health and composition of the reef communities prior to the event.

While disturbances such as cyclones and volcanic activity have the clear potential to decimate reef ecosystems, studies have suggested that reefs in Tonga have the potential to recover. Recent investigations have shown that genetic diversity of *Pocillopora damicornis* and *Seriatopora hsytrix* have recovered following the total devastation caused by the 1883 Krakatau eruption in Indonesia (Starger et al., 2010). In a more local example, one study conducted following the 2015 eruption of the HTHH volcano, which created an emergent landmass connecting the previously separated islands of Hunga Tonga and Hunga Ha'apai, indicated that affected reefs showed high recruitment only four years later (Smallhorn-West et al. 2020c). The authors hypothesize that this recovery may have been possible due to the existence of refuge populations of corals that were able to reproduce after the eruption, and the remoteness of the HTHH volcano from human impacts; therefore, it remains to be seen if reefs in central Tonga will have a similar recovery trajectory after the more recent, more powerful eruption and tsunami.

## Coral Reef Management in Tonga

Prior to the 1830's-60's, reefs in Tonga were managed through traditional chiefs and communities; however, in 1875, ownership of fisheries resources moved to the Monarchy, and marine resources became open access throughout the country (Sun et al. 2011). In 2002 the Government of Tonga introduced the Special Management Areas (SMA) program, under the Fisheries Management Act 2002 (Smallhorn-West et al., 2020e). The goal of the SMA program is to enable communities to manage their fishery resources in order to promote sustainable fishing practices and reduce overfishing on nearshore reefs of Tonga. Under the program, communities can apply to the Ministry of Fisheries to have their reef designated as an SMA. Once the application is accepted, the community is granted exclusive access from the high water mark to the area offshore of their community reaching to the 50m depth contour or 2500m offshore. Once the SMA is established, only registered members of the community are allowed to fish within its boundaries. However, in exchange for this exclusive access, each SMA must also have at least one area within its boundary designated as a Fish Habitat Reserve (FHR), where fishing is prohibited (Stone et al., 2017, Smallhorn-West et al., 2020a, MoF and VEPA, 2022). The goals and potential benefits of this design are multifold. By allowing the community to manage their own reefs, they are given the responsibility to ensure they are not overfished, which requires that community members and youth are educated on sustainable fishing practices. Additionally, granting exclusive fishing rights to community members may relieve fishing pressure on reefs that were previously accessed by multiple parties, and the requirement for an FHR ensures complete protection for certain reef areas across the country (Smallhorn-West et al., 2020a).

Since the first SMA was designated at O'ua in Ha'apai in 2006, the program has grown quickly, with 54 SMAs across the country as of 2022 (MoF & VEPA, 2022). Studies of the effectiveness of the SMA program have shown FHRs to have positive ecological impacts, with 5.6 times higher fish biomass, 3.6 times higher fish density, and 15% higher fish diversity than control sites (Smallhorn-West et al., 2020b, Smallhorn-West et al., 2020e). However, areas within the SMAs but outside of the FHRs did not tend to differ significantly from control sites, except for a small increase in the average size of scarids (parrotfish) and lethrinids (emperors). However, given the positive ecological impacts of the FHRs, along with the socioeconomic benefits that come with the community management structure of the SMAs (raising community awareness, promoting sustainable fishing practices, improving standards of living, and establishing customary tenure), the outcomes of the SMA program are seen as a net positive for Tonga and the participating communities (Smallhorn-West et al. 2020b). Community members actively engaged in the SMA program overwhelmingly support it, with 89% of households indicating that they believe it will help provide fish and seafood for future generations (MoF and VEPA, 2022).

In addition to SMAs, a number of marine protected areas (MPAs), have been established to manage and protect biodiversity hotspots across the country. These

MPAs are designated under the Parks and Reserve Act 1988. Based on previous reef surveys, five island areas of Vava'u have been designated as MPAs based on their high biodiversity (Stone et al., 2017). In 2015, the Government of Tonga initiated marine spatial planning (Tonga's Ocean Management Plan) to sustainably manage 100% of their EEZ including 30% no-take areas inshore and offshore, which was approved by Cabinet in 2021.

While the eruption of the HTHH volcano was the most recent and dramatic disturbance to Tonga's reef ecosystems, it is not the only stressor these reefs have faced. Ha'apai and Tongatapu, for example, have experienced multiple large cyclones (category 4 and above) in the past decade, which have resulted in storm surges across these regions, and coral bleaching events were reported in 2012, 2014 and 2016 (Purkis et al., 2020, Smallhorn-West et al., 2020d, MoF and VEPA, 2022). The SMA program has delivered actual and perceived benefits to the adjacent communities; however, when surveyed prior to the volcanic eruption, community members reported feeling like they had little to no ability to cope with natural disasters (e.g., cyclones) or climate change-related stressors (e.g., coral bleaching) due to the livelihood options available (MoF and VEPA, 2022). Based on these findings, it is imperative to understand the effects of this most recent disturbance on reef resources, as it has the potential to strongly affect coastal communities across the country.
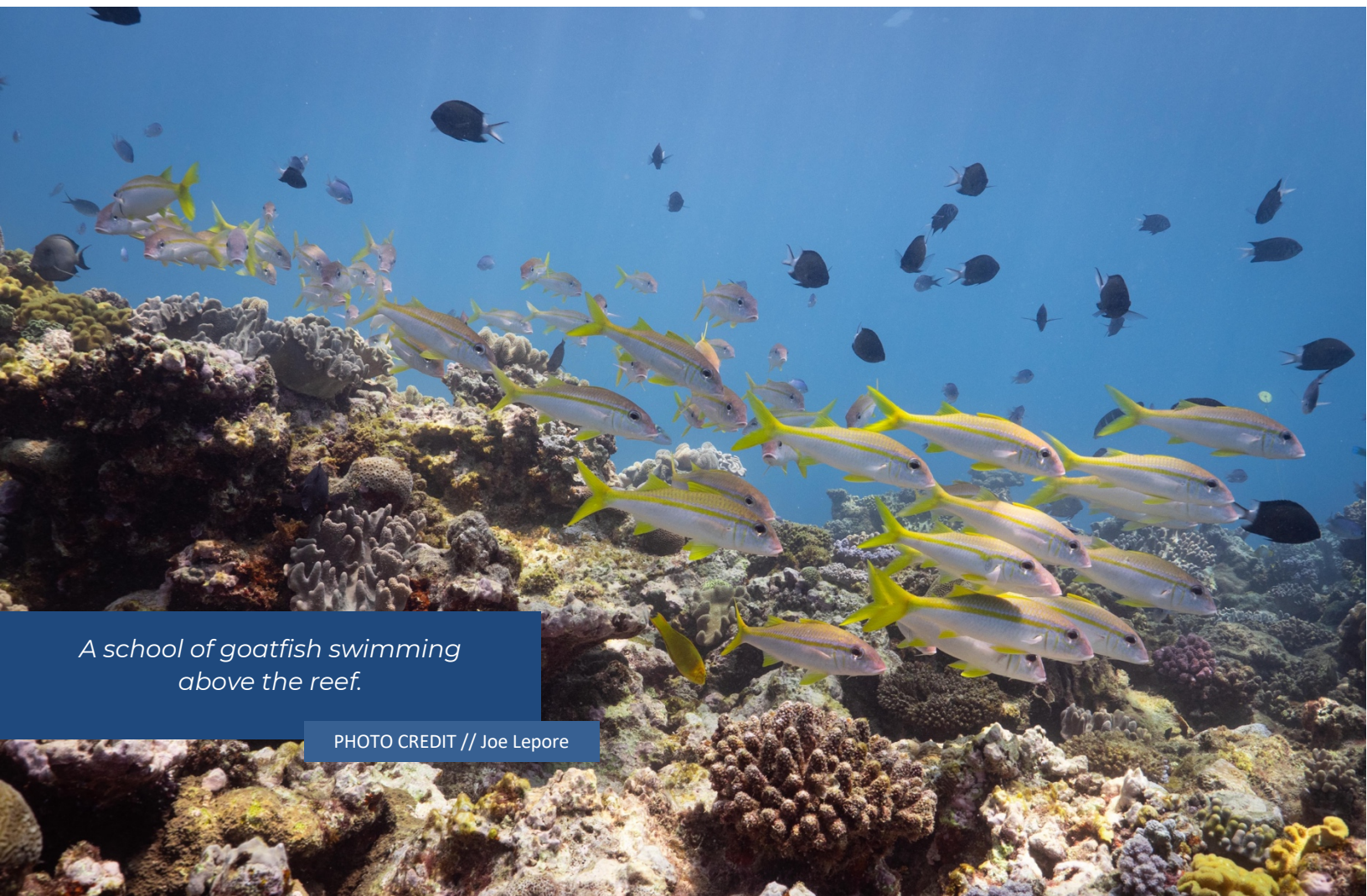


*A school of goatfish swimming above the reef.*

PHOTO CREDIT // Joe Lepore

# EXPEDITION GOALS

Following the eruption of the HTHH volcano, the Waitt Institute partnered with the Government of Tonga, the Vava'u Environmental Protection Association (VEPA), and the Scripps Institution of Oceanography to organize an expedition in August and September 2022 to assess the impact of the disturbance on nearshore reefs across the country. Due to the continued border closures in Tonga from the COVID-19 pandemic, this expedition marked the first arrival of a private international research vessel and research team into the country since the pandemic began in 2020. The sites surveyed during this expedition were selected with the goals of assessing the impact of the volcanic eruption and tsunami across priority locations within and outside of management areas (SMAs, MPAs) across the main island districts. In addition, the availability of a large research vessel (*M/Y Plan b*) afforded the opportunity to survey the offshore volcanic islands of Late and Fonualei.

While the main goal of the expedition was to assess priority sites for volcanic and tsunami impacts, efforts were made, where possible, to prioritize resurveys of established sites surveyed during a previous expedition conducted in 2017. That expedition, supported by the Government of Tonga and conducted by the Waitt Institute, VEPA, and the Scripps Institution of Oceanography,  collected baseline data across a number of islands in Ha'apai and Vava'u, and established permanent plots at each site. By revisiting these locations in 2022, pre- and post-eruption comparisons could be made to help quantify the impact of the HTHH eruption on Tonga's coral reef communities.

## APPROACH

The data presented in this report were collected during a field expedition undertaken in August 2022. During the expedition, researchers conducted surveys of reef fish populations, benthic coral reef communities, marine macroinvertebrates, and water quality parameters. In August-September 2022, 49 sites were surveyed across the island groups of Vava'u, Ha'apai, and Tongatapu & Eua (Figure 1). A detailed summary of survey methods can be found in Appendix 1, and a summary of the sites surveyed with the corresponding metadata can be found in Appendix 2.



*A diver conducting a visual survey of the reef.*

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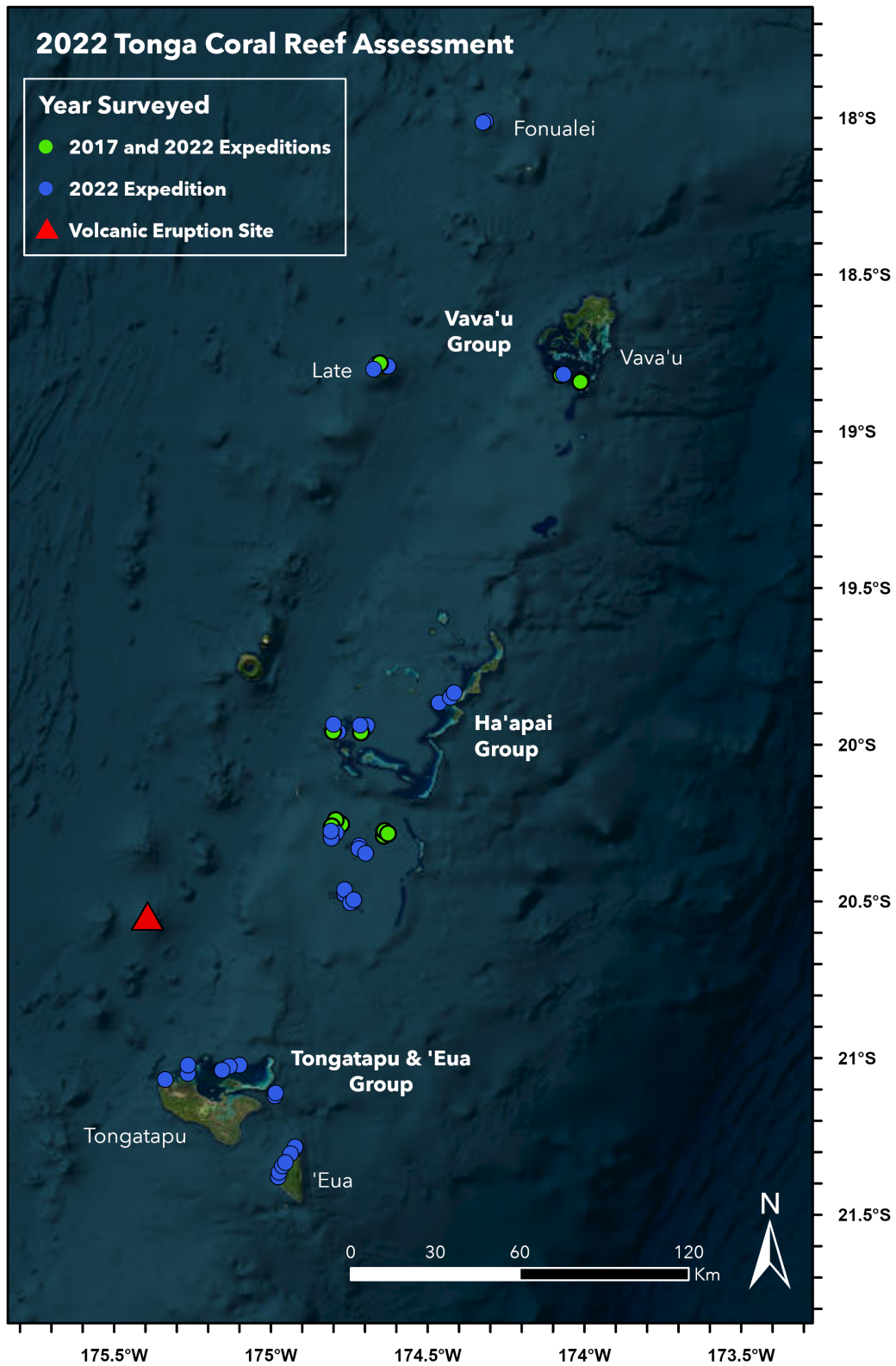
**FIGURE 1.** *Map of survey sites.*

Sites were selected with three goals in mind: assessing damage from the HTTH eruption and tsunami, surveying reefs inside and outside of established SMAs, and resurveying sites previously visited in 2017 using the same methods (summarized in Stone et al., 2017). Permanent photomosaic plots were established using GPS coordinates and stainless steel stakes installed on the benthos, so that the exact same area could be imaged for subsequent surveys. While fish and photoquadrat surveys were undertaken at two depths in 2017 (5m and 10m), only the 10m data from this expedition was used to compare with the 2022 data to minimize variation in community structure between depth strata.

Because Ha'apai saw the greatest impact from the tsunami, and because Ha'apai and the outer islands are more reliant on their marine resources for food, the majority of sites were located within this island group. In addition, the offshore volcanic islands of Late and Fonualei were prioritized due to the availability of a vessel suitable for working at these locations. Sites were distributed randomly around surveyed islands with a minimum of 1 km spacing between each site (except for sites MPAL1 and MPAT2 at Lualoli & Taula, which were <1 km apart but were located on reefs adjacent to separate islands). In total, 13 sites from the 2017 expedition were located and resurveyed, while the remaining 36 sites were either established at new locations or near existing sites when permanent site markers from 2017 could not be found. Only the 13 sites that were successfully located and resurveyed were used in time series comparisons between 2017 and 2022.

Results are presented at the island and island group (district/region) level. In some cases, when sites from two islands were part of the same SMA (for example, Nomuka and Nomuka Iki) or no-take area (for example, Lualoli and Taula), these sites were grouped together as a single "island". Effort varied between islands, from one to six sites per island based on the size of the island, accessibility, and diving conditions.

At each site, the following indicators of reef health were surveyed: 1) reef fish abundance, diversity, and biomass; 2) benthic community composition, including percent cover and diversity of benthic taxa; 3) the abundance of juvenile corals (coral recruitment); 4) reef rugosity; and 5) the abundance and diversity of benthic macroinvertebrates. Algal samples were collected at each site to be utilized for stable isotope analysis, which provides information on the concentration and origin of nutrients at the collection sites. Survey methods were designed to collect comprehensive data for each indicator, and in some cases to gather specific information regarding species of ecological and/or economic significance. All surveys were undertaken at a depth of 10m, and sites with continuous or nearly continuous hard bottom were prioritized where possible in order to minimize variability in community composition between sites. A brief summary of the survey methods used can be found in Table 1, and full methods can be found in Appendix 1. While algal samples were collected to provide information on water quality, the analysis of these samples is ongoing, and these results will be presented in a subsequent report, expected in 2024.

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

| Key metric | Significance to reef health | Data Collection 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: $g/m^2$ <br><br> 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, and size frequency distribution | Macroinvertebrates such as herbivorous urchins can clear reefs of macroalgae. Other invertebrates, such as sea cucumbers, crustaceans, and bivalves are important food/fisheries resources. | Belt transect surveys | Individuals/site |
| Water quality* | Poor water quality can stress reefs by causing macroalgal blooms, promoting coral disease, increasing bioerosion, etc. | Algal samples | Stable isotope ratio |

# RESULTS

## Qualitative Observations

In addition to quantitative surveys, observers recorded qualitative evidence of tsunami damage at survey sites. Visible evidence of damage varied from site to site, and was most severe at sites directly in the path of the tsunami. For example, entire coconut trees, as well as garbage and other terrestrial debris were found on the reef at Tonumea, Malinoa, Atata and Nomuka (Figure 2).
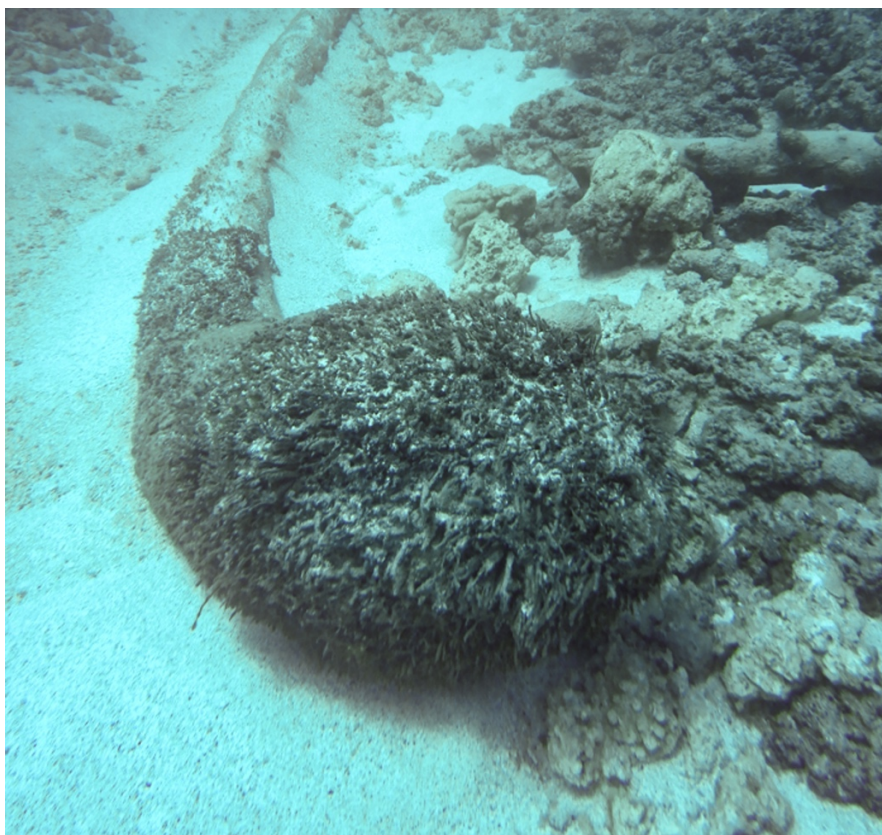


**FIGURE 2.** Image of a coconut tree on the reef at a survey site in Tonumea at 15 meters depth.

These islands were noted as having some of the highest terrestrial impacts from the tsunami, with some islands such as Nomuka Iki being completely overtopped by the surge (Borrero et al., 2022a&b). Indeed, many of the reefs adjacent to Nomuka and Nomuka Iki were reduced almost entirely to rubble, and sedimentation at these and other impacted reefs was high (Figures 3 and 4).
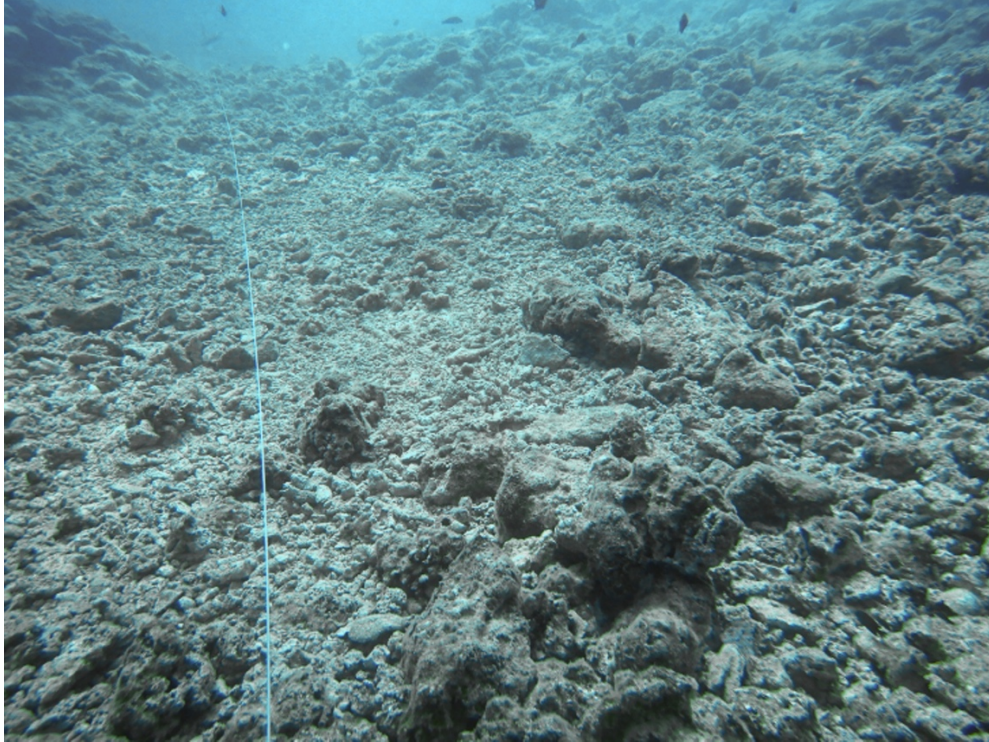
**FIGURE 3.** *Image of a survey site at Nomuka (Nomuka Iki) showing a large area of coral habitat reduced to rubble.*



**FIGURE 4.** *Heavy sedimentation on the reef at Nomuka (Nomuka Iki).*

Comparisons of photomosaic imagery between 2017 and 2022 illustrates the complete devastation of these exposed reefs, with the most extreme example being site NOS1, located directly off of Nomuka village (Figure 5).
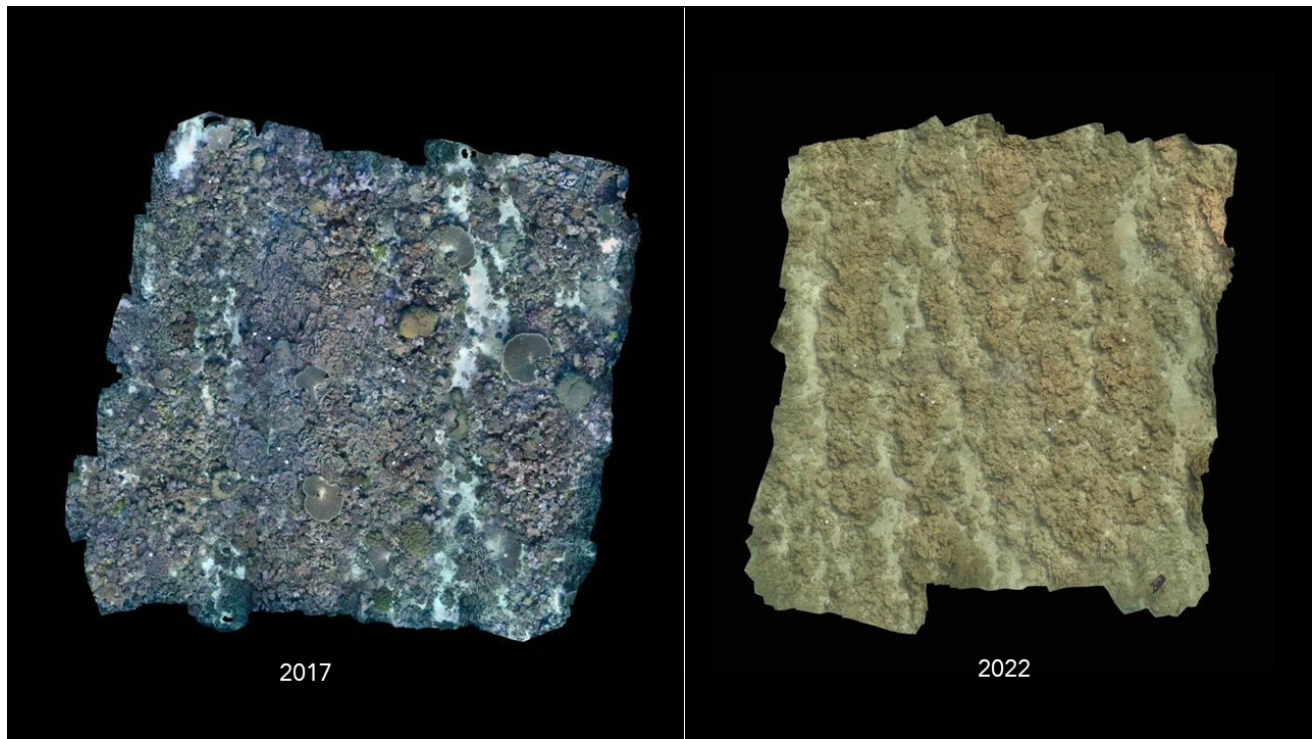


**FIGURE 5.** *Orthoprojections of 3D mosaics from site NOS1, directly in front of Nomuka village, in 2017 (left) and 2022 (right) showing the complete devastation of the hard coral community following the eruption and tsunami.*

While delicate corals such as those with branching or tabular morphologies would be expected to experience high amounts of physical damage during a strong wave event, mounding corals such as those in the genus *Porites* tend to be more resilient to high wave energy. Nevertheless, the force of the tsunami was strong enough in many locations to completely overturn large colonies (Figure 6). However, tsunami impacts were patchy, even within locations; for example, at Mango, large, overturned coral colonies were observed near to healthy patches of reef (Figures 7 & 8). In addition, islands that were shielded from the full force of the tsunami, such and 'Eueiki, did not show any obvious signs of tsunami damage, and supported diverse coral communities including more fragile branching and tabular species (Figure 9).

**FIGURE 6.** *A large* Porites *coral colony overturned due to the force of the tsunami.*



**FIGURE 7.** *A large overturned coral colony at a survey site at Mango Island. This colony was found nearby to the comparatively undamaged reef pictured in Figure 8.*
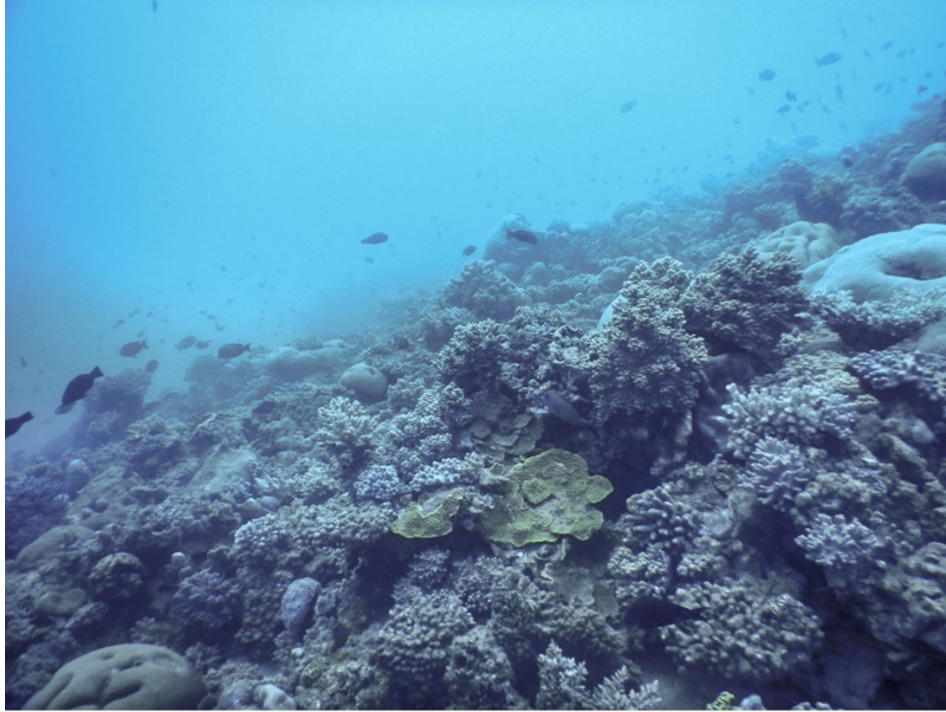
**FIGURE 8.** *In contrast to the overturned coral present at Mango (Figure 7), other portions of the reef at this island had comparatively healthy reef communities.*
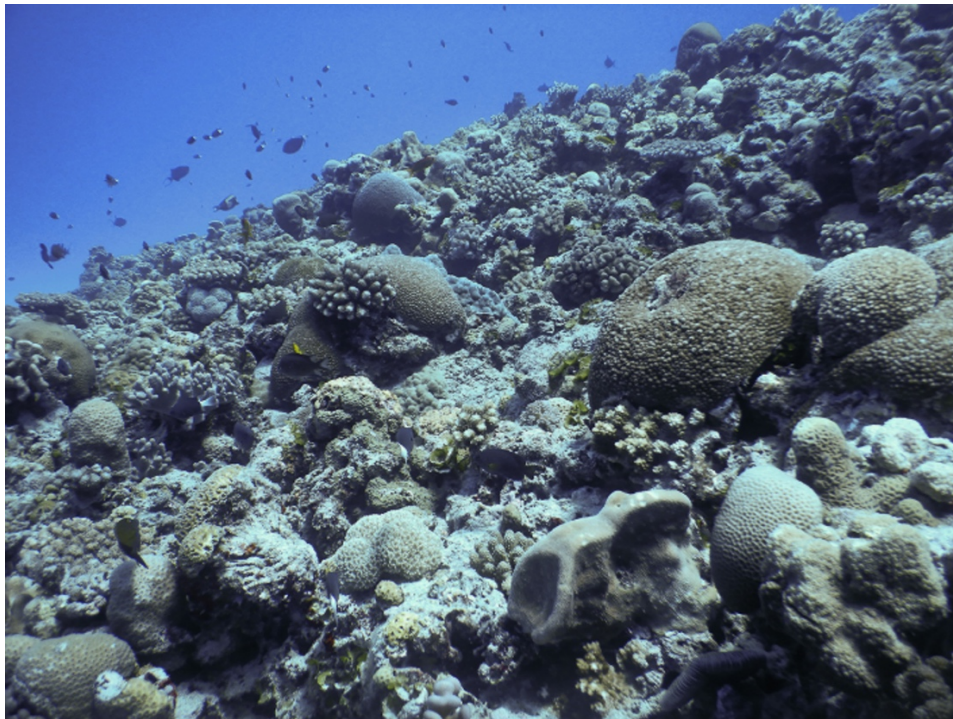


**FIGURE 9.** *Diverse and comparatively healthy reef at 'Eueiki, where little to no visible tsunami damage was observed.*

## Reef Fish

Data from three of the four observers were available to be included in this report, and the number of observers at each site is shown in Appendix 2. The results presented here have been normalized with respect to effort to account for any imbalance in the number of observers.

Across the country, total mean fish biomass was 115.4 g m$^{-2}$, while mean fish density was 1.9 individuals m$^{-2}$. Fish communities in Tonga were characterized by moderate to high densities of small planktivores (mostly damselfish) and lower carnivores (mainly wrasses), low to moderate densities of large herbivores, and low densities of top predators (Figures 10, 11, and 12).
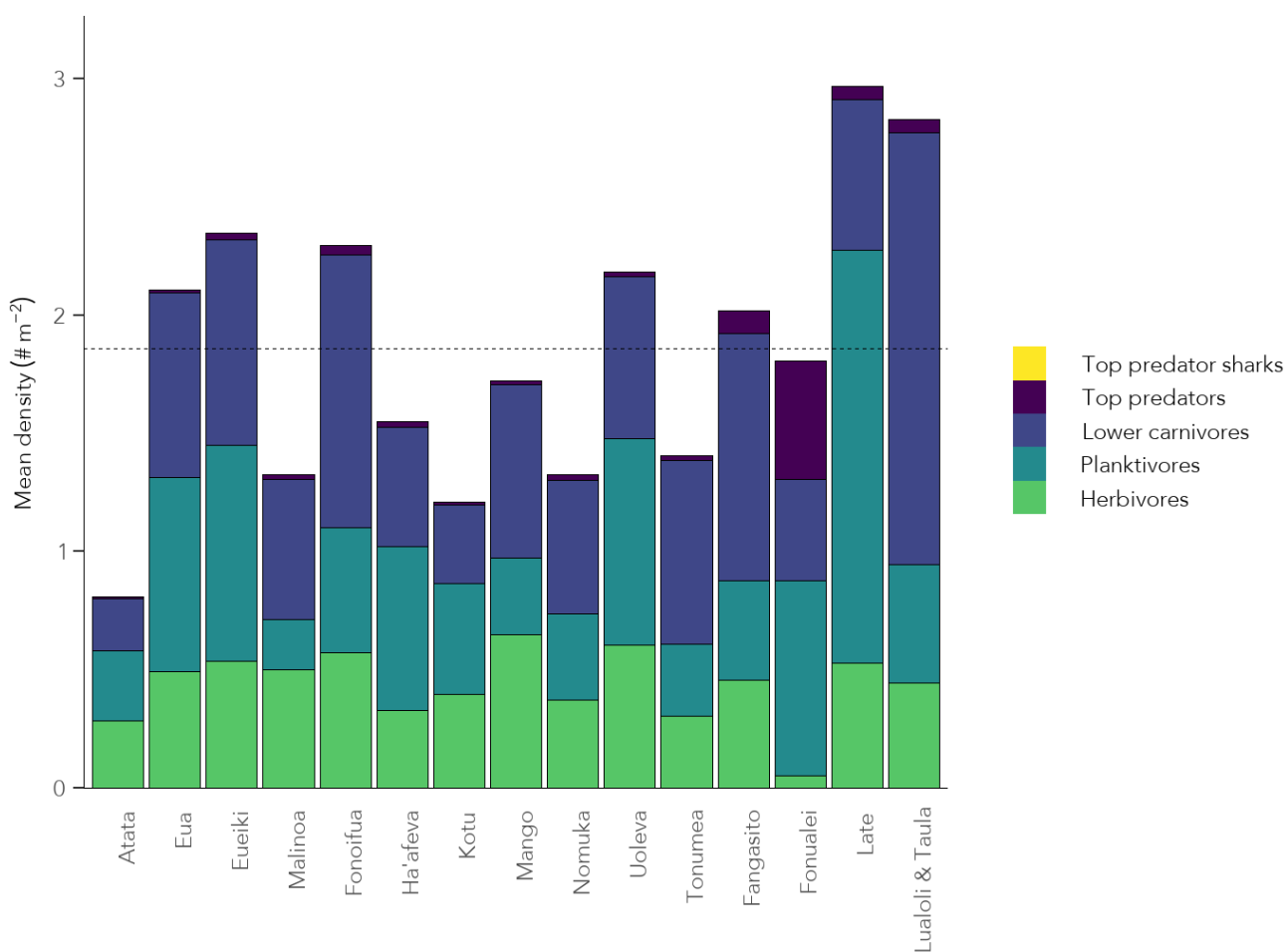


**FIGURE 10.** *Mean fish density at each island surveyed, by trophic group. The horizontal dashed line represents the overall mean fish density across islands.*
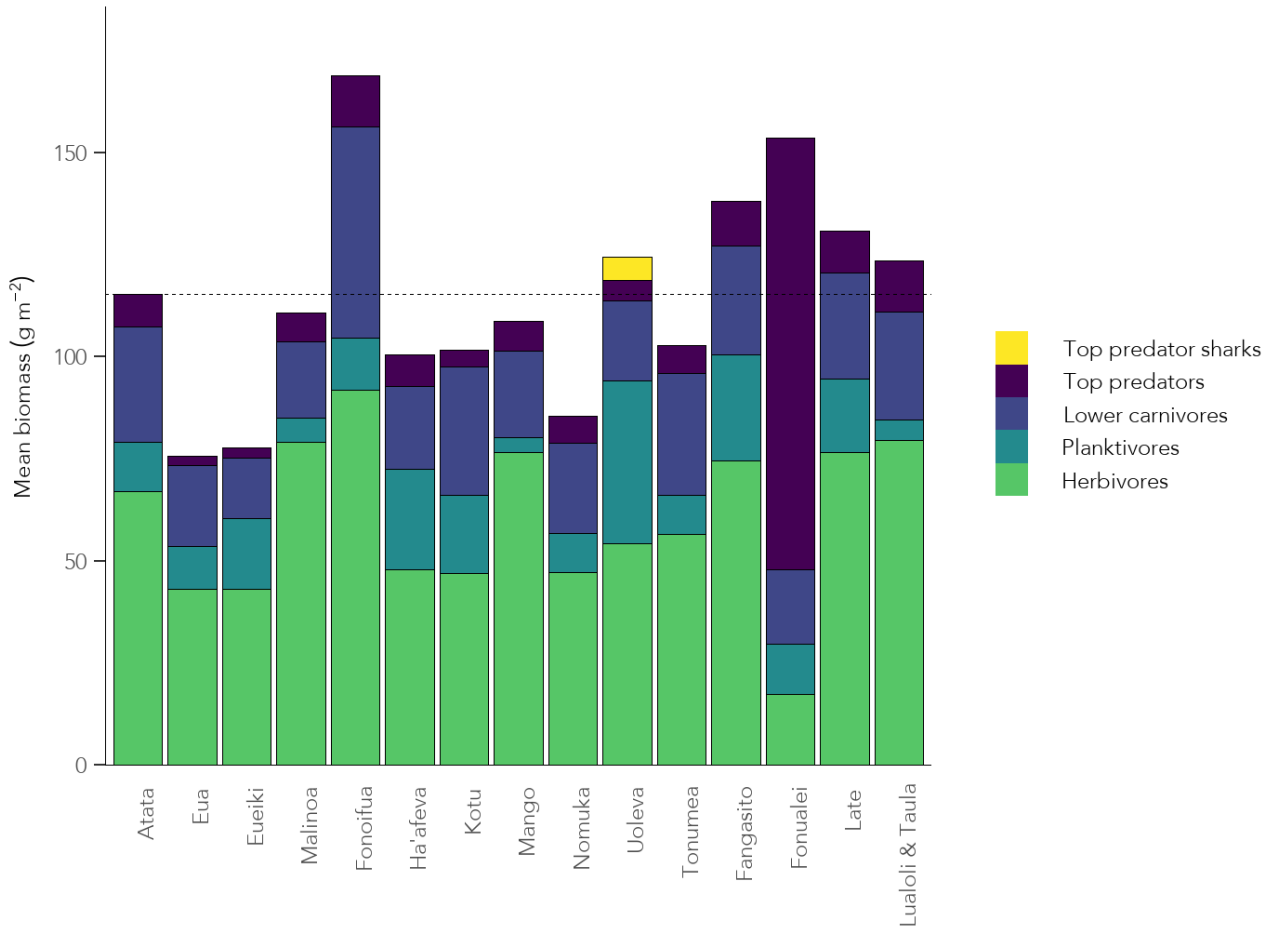
**FIGURE 11.** *Mean fish biomass at each island surveyed, by trophic group. The horizontal dashed line represents the overall mean fish biomass across islands.*



*A white tip reef shark, Triaenodon obesus*, in ʻUoleva.

PHOTO CREDIT // Joe Lepore
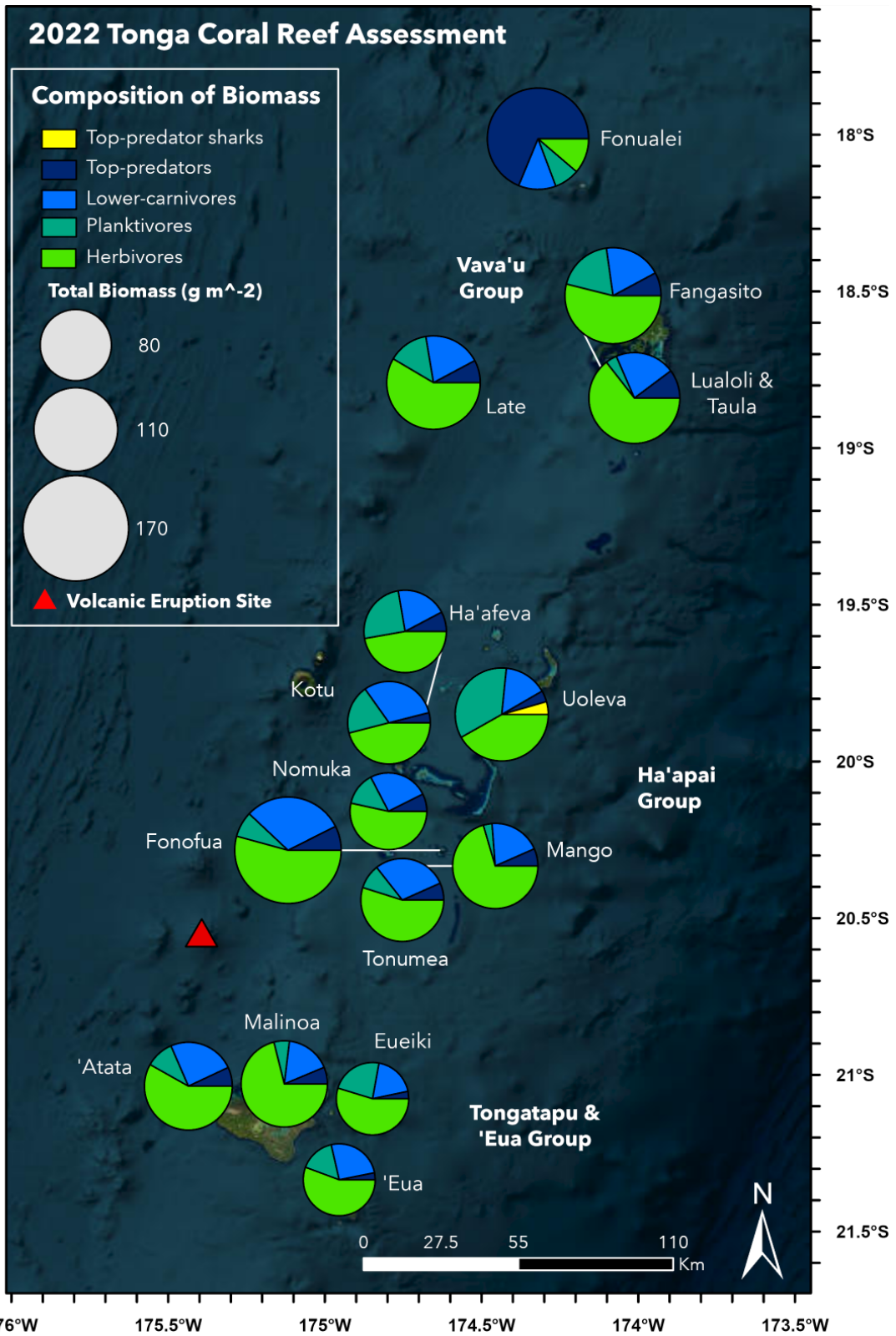
**FIGURE 12.** *Map of mean fish biomass by trophic group at each of the islands surveyed. The size of each circle represents the overall mean biomass at each island.*

Fish biomass increased from south to north, with the highest biomass found in Vava'u (135.4 g m$^{-2}$± 22.2 SE) and the lowest in Tongatapu & 'Eua ( 91.3 g m$^{-2}$ ± 8.7 SE; Figure 14). Herbivores, mainly scarids (parrotfish) and acanthurids (surgeonfish) made up the majority of the biomass across the country. While planktivores and lower carnivores made up the largest proportion of the overall abundance, these were generally small fishes from the families Pomacentridae (damselfish) and Labridae (wrasses), and as such did not contribute a sizable portion of the overall biomass (Figure 13).
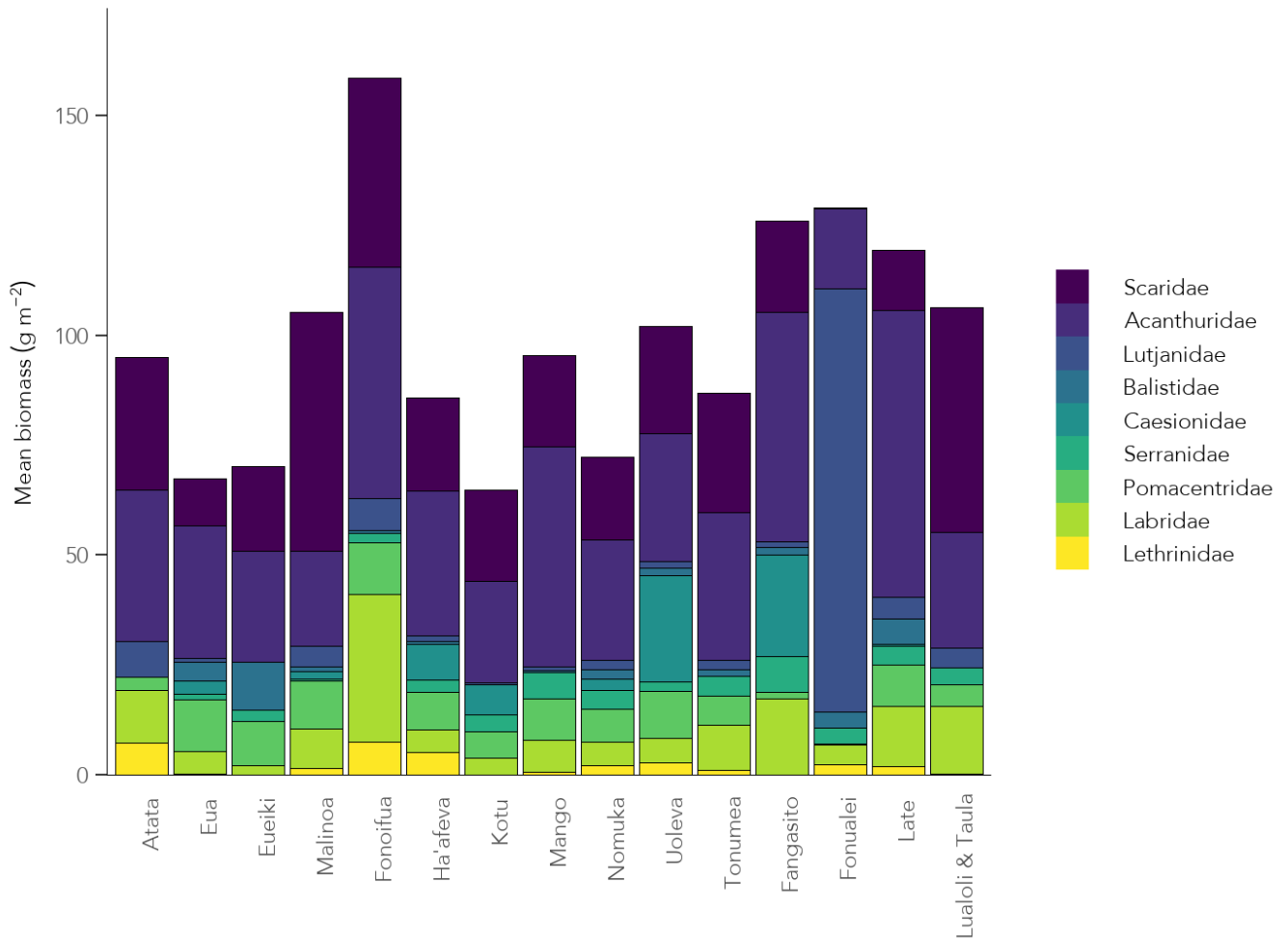


**FIGURE 13.** *Mean biomass of key fish families at each island surveyed.*
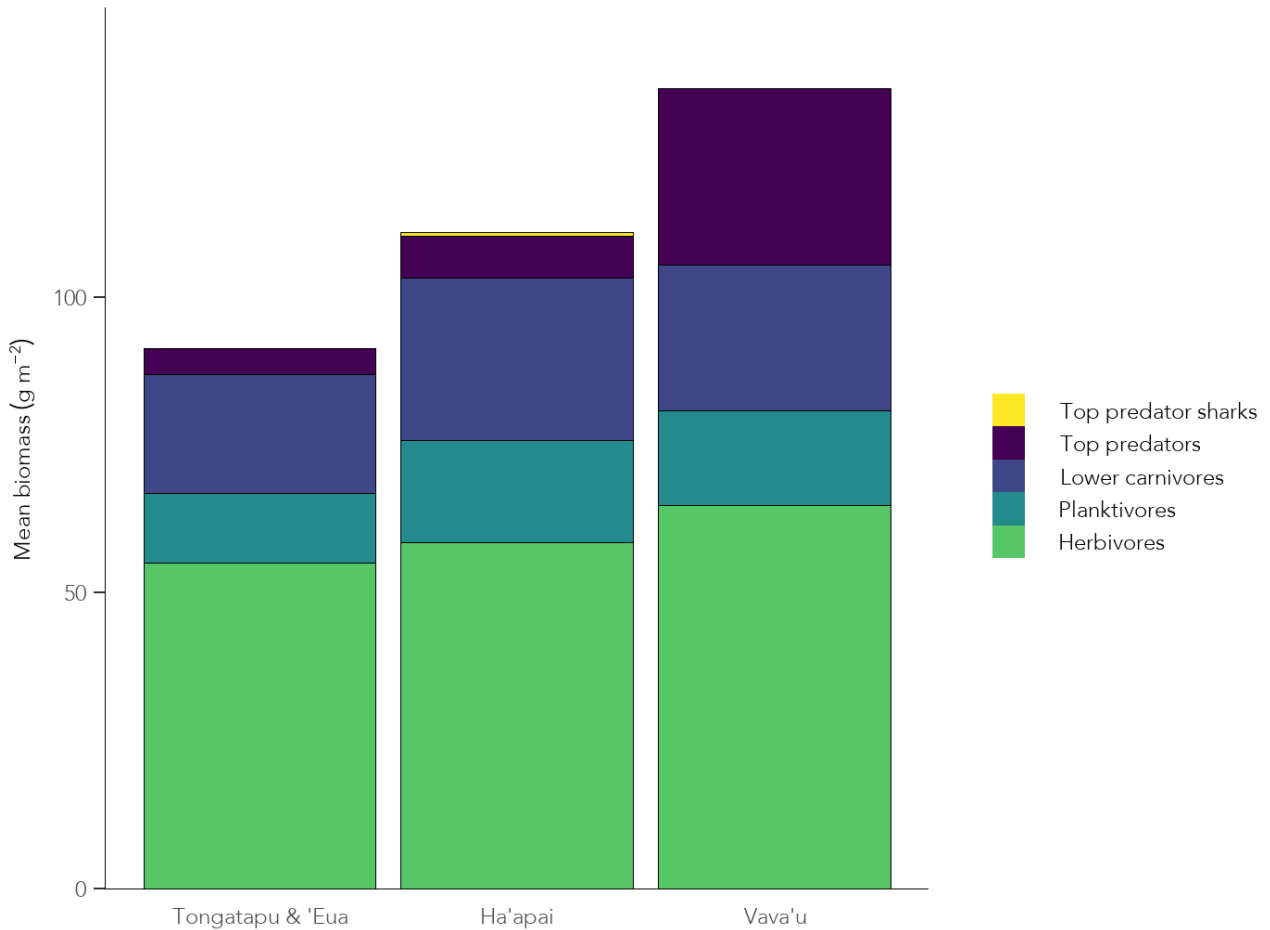
**FIGURE 14.** *Mean fish biomass by trophic group, by island district.*

Patterns in fish abundance versus fish size varied widely between islands. For example, although 'Atata had the lowest fish abundance of any island (0.81 individuals m$^{-2}$ ± 0.1 SE), the mean biomass was about average (115.4 g m$^{-2}$ ± 11.1 SE), indicating the presence of larger fish at this island. Conversely, 'Eua and 'Eueiki (Tongatapu) had relatively high overall fish densities (2.1 individuals m$^{-2}$ ± 0.2 SE and 2.3 individuals m$^{-2}$ ± 0.2 SE, respectively), but had the two lowest mean biomass values (77.5 g m$^{-2}$ ± 9.7 SE and 78.6 g m$^{-2}$ ± 24.2 SE, respectively), suggesting that though more abundant, fish are smaller at these islands.

 Fonoifua had the highest overall biomass (169.4 g m$^{-2}$ ± 55.6 SE), mostly due to the presence of particularly large herbivores compared to other islands. Fonualei had unusually high numbers of large top predators (particularly snappers from the family Lutjanidae, 0.5 individuals m$^{-2}$) compared to other islands, contributing approximately ⅔ of the biomass at this island (105.6 g m$^{-2}$ of a total of 153.6 g m$^{-2}$). Sharks were almost absent from the fish surveys, except for one white tip reef shark (*Triaenodon obesus*) in 'Uoleva at site HAP_UOL2. Sharks were rare in 2017 as well,

with only three sharks (two *T. obesu*s and one grey reef shark, *Carcharhinus amblyrhynchos*, recorded during the surveys (Stone et al. 2017).

Vava'u had the highest biomass of the three island districts, driven primarily by the high biomass of top predators at Fonualei, with a mean value in this trophic group of 29.9 g m$^{-2}$ (± 17.4 SE), compared to 7.1 g m$^{-2}$ (± 1.5 SE)in Ha'apai and 4.4 g m$^{-2}$ (± 1.2 SE) in Tongatapu & 'Eua. Herbivore biomass was also highest in Vava'u, although the difference between island districts was less for this trophic group (maximum of 64.9 g m$^{-2}$ ± 12.7 SE in Vava'u, minimum of 55.2 g m$^{-2}$ ± 7.1 SE in Tongatapu & 'Eua). Ha'apai had the highest biomass of lower carnivores and planktivores (27.4 g m$^{-2}$ ± 4.6 SE and 17.3 g m$^{-2}$ ± 4.1 SE, respectively), while Tongatapu & 'Eua had the lowest biomass values across all trophic groups.

In total, 342 species of fish were observed across all sites (Appendix 3). This is a reduction from 2017, when 403 species were recorded across Ha'apai and Vava'u (Stone et al. 2017). However, similar to 2017, fish from the families Labridae and Pomacentridae had the highest species diversity across the country, with 65 labrid (wrasse) species identified and 49 pomacentrid (damselfish) species noted in 2022. The families Acanthuridae (surgeonfish) and Chaetodontidae (butterflyfish) were also diverse, with 26 species recorded from each. The damselfish *Pomacentrus vaiuli* was the most common species, appearing in surveys at 46 of the 48 sites where fish surveys were conducted, and having the maximum mean density of any species (0.28 individuals m$^{-2}$). The surgeonfish *Ctenochaetus striatus* was the next most abundant, appearing in surveys at 43 sites. *C. striatus* also had the highest mean biomass of any fish species surveyed (12.7 g m$^{-2}$). It should be noted that the diversity estimates listed in this report may underestimate the distribution of some species due to the unavailability of data from one of the observers; however, tests in which data from one of the remaining observers was excluded from the analysis did not significantly affect the distribution and number of species surveyed, so the data presented here represent a reasonable estimate of the overall diversity and distribution patterns of fish in Tonga.
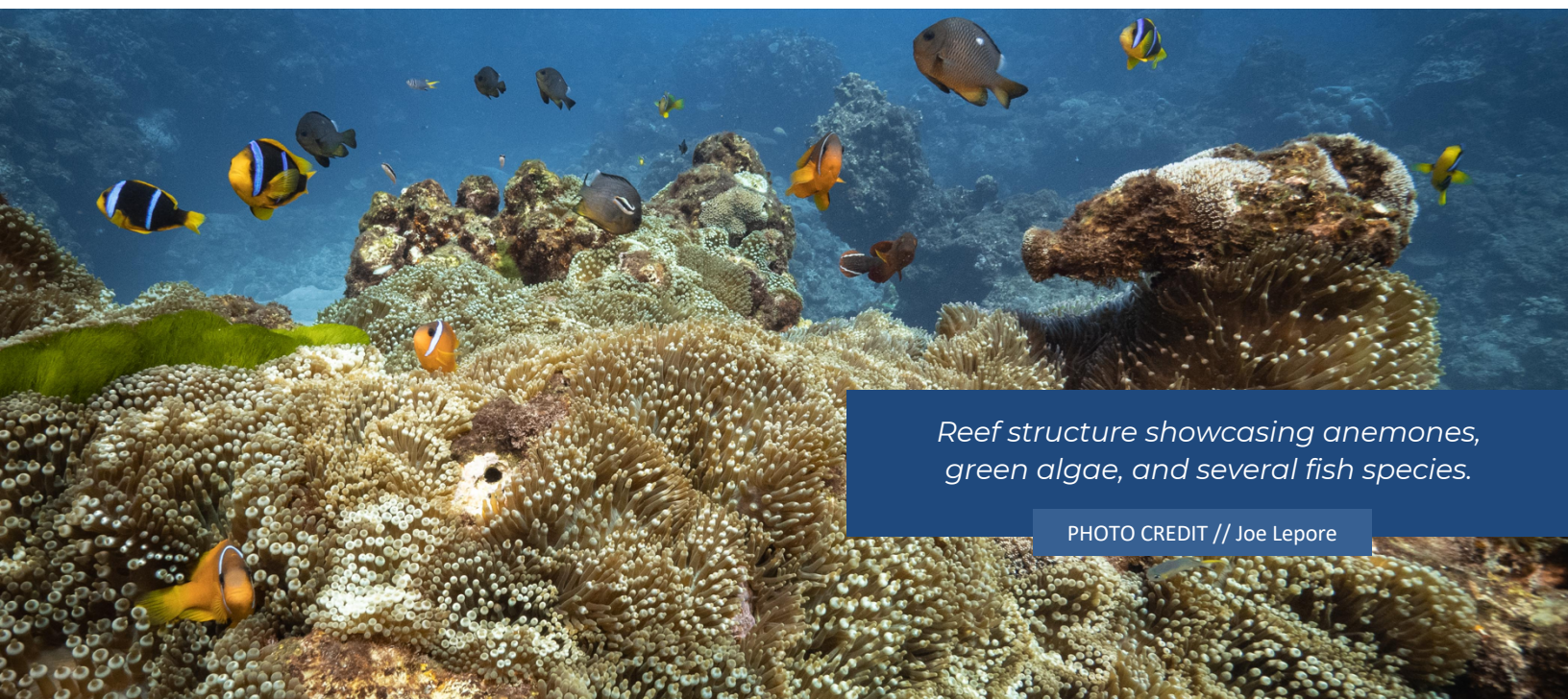


*Reef structure showcasing anemones, green algae, and several fish species.*

PHOTO CREDIT // Joe Lepore

## Benthic Cover

Benthic communities across Tonga in 2022 were characterized by high mean cover of turf algae (60.3% ± 0.6 SE), moderate to low cover of calcifiers such as hard coral (7.7% ± 0.3 SE) and CCA (8.3% ± 0.3 SE) and low levels of fleshy (1.9% ± 0.1 SE) and calcified (4.3% ± 0.2 SE) macroalgae (Figures 15 and 16).
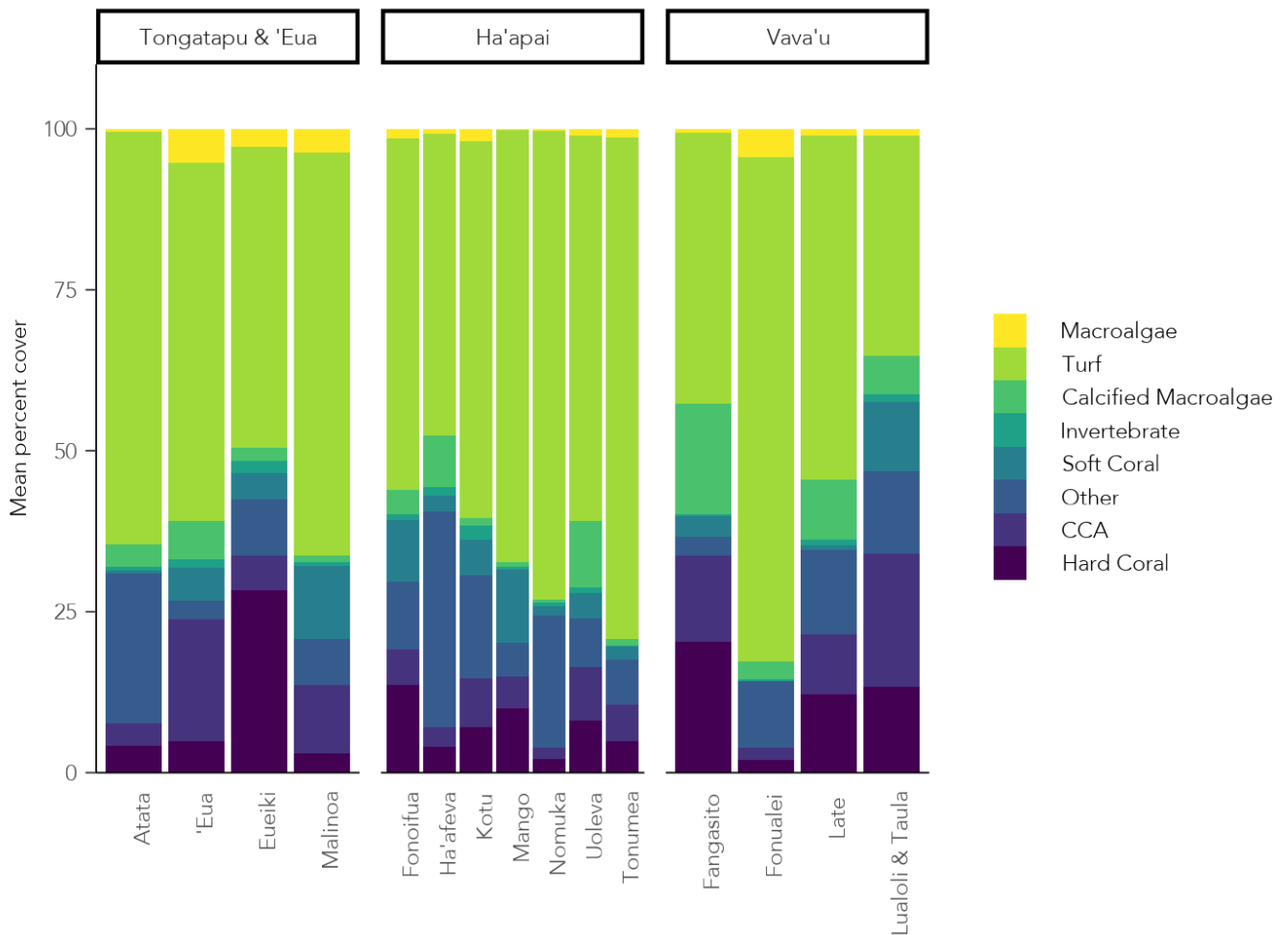


**FIGURE 15.** *Mean percent cover of main benthic functional groups at each island surveyed.*

Despite the disturbance caused by the volcanic eruption, along with the bias towards selecting sites which may have seen stronger impacts from the resulting tsunami in 2022, overall mean coral cover only dropped by about 1% from 2017 to 2022, from 8.6% to 7.7%. However, during this period, turf cover increased from 32.2% to 60.3%, while CCA decreased from 13.6% to 8.3%.
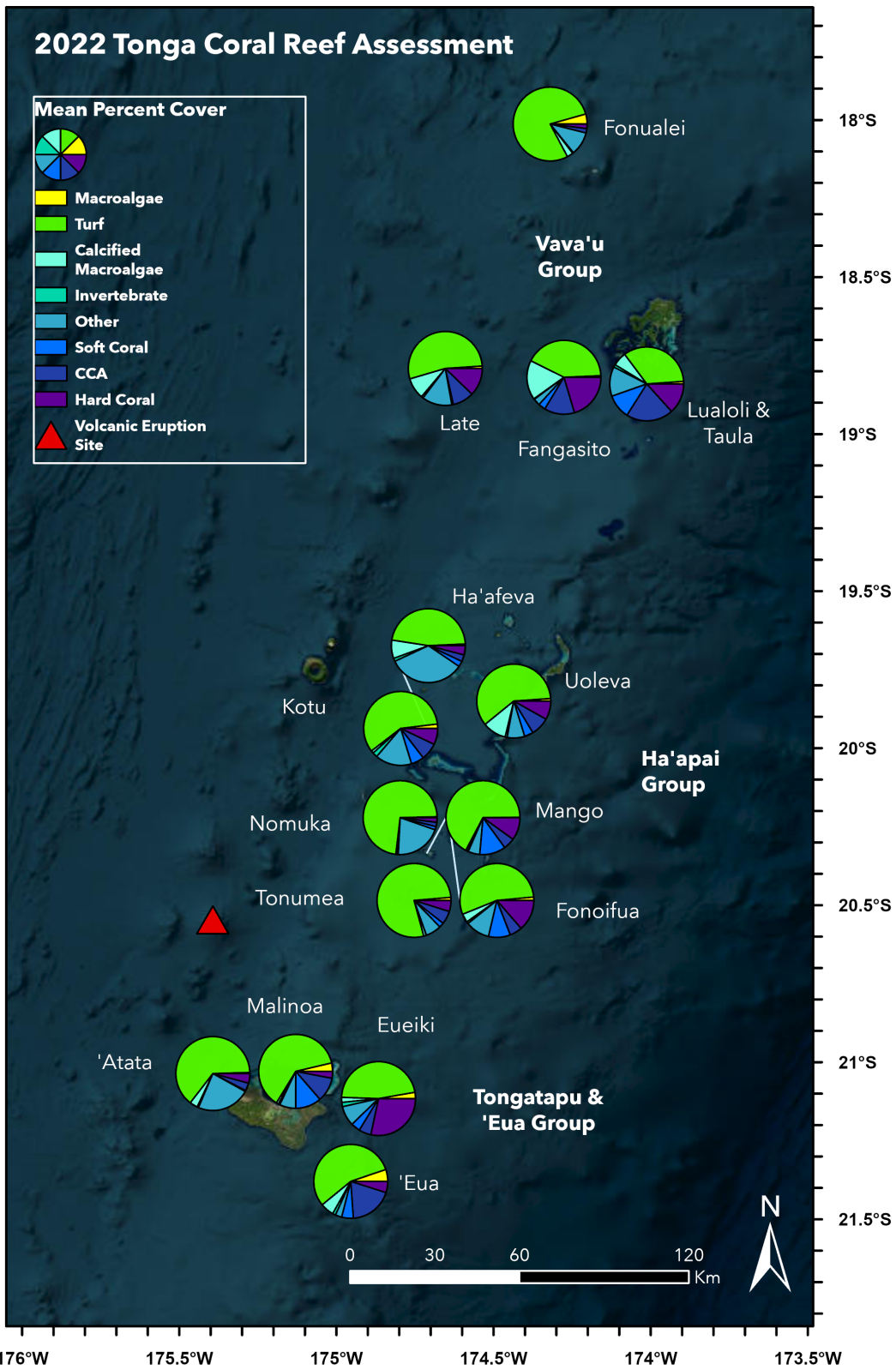
**FIGURE 16.** *Map of mean percent cover of main benthic functional groups at each island surveyed.*

'Eueiki had the highest mean coral cover in 2022, at 28.4% (± 1.4 SE). However, this island stood out within the Tongatapu & 'Eua island group, as the other three islands in this region had coral cover ranging from only 3.0% (± 0.4 SE) at Malinoa to 4.9% (± 0.7 SE) at 'Eua. In Ha'apai, coral cover ranged from 2.1% (± 0.3 SE) at Nomuka to 13.6% (± 1.3 SE) at Fonoifua, and in Vava'u it ranged from 2.0% (± 0.4 SE) at Fonualei to 20.4% (± 2.0 SE) at Fangasito. Overall, turf was highest at Fonualei (78.4% ± 2.3 SE) and lowest at Lualoli & Taula (34.1% ± 1.6 SE). Conversely, Lualoli & Taula had the highest cover of CCA (20.6% ± 1.5 SE), while Nomuka and Fonualei had the lowest (both 1.9% ± 0.3 SE). Cover of fleshy macroalgae was generally low, with a minimum cover of 0.2% (± 0.1 SE) at Mango to a maximum of 5.2% (± 0.5 SE) at 'Eua. Calcified macroalgae was highest at Fangasito (17.3% ± 2.2 SE) and lowest at Nomuka (0.5% ± 0.1 SE).

Of the three island districts, Vava'u had the highest mean coral cover (11.2% ± 0.7 SE) and Ha'apai had the lowest (6.5% ± 0.3 SE; Figure 17). Cover of other calcifying organisms, including CCA and calcified macroalgae, followed the same pattern, with maximum values in Vava'u (10.7% ± 0.7 SE and 8.0% ± 0.5 SE, respectively), and minima in Ha'apai (4.9% ± 0.2 SE and 3.2% ± 0.2 SE, respectively). Calcifier cover varied inversely with turf, with the highest turf algae cover at Ha'apai (64.4% ± 0.8 SE) and the lowest at Vava'u (53.1 ± 1.4 SE). Tongatapu had the highest mean cover of fleshy macroalgae (3.8% ± 0.3 SE), while Ha'apai had the lowest (0.9% ± 0.1 SE).
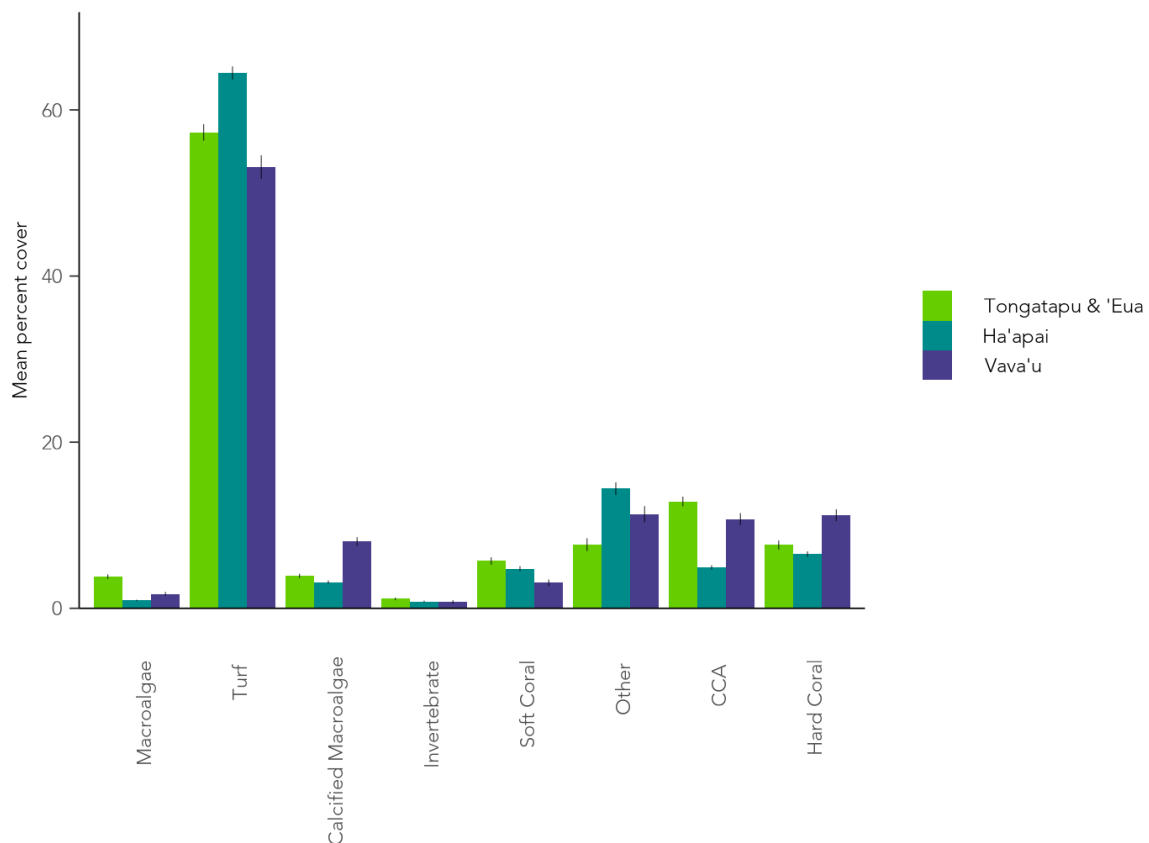


**FIGURE 17.** *Mean percent cover of main benthic functional groups in different island districts.*

From 2017 to 2022, coral cover at resurveyed sites in Ha'apai decreased from a mean of 17.1% (± 0.6 SE) to 6.9% (± 0.4 SE; Figure 18), while resurveyed sites in Vava'u saw an increase from 7.1% (± 0.8 SE) to 13.8% (± 1.0 SE; Figure 19). Resurveyed reefs in Ha'apai saw a large increase in mean turf cover, from 24.8% (± 0.8 SE) to 61.9% (± 1.0 SE), and a concurrent decrease in the cover of CCA, from 12.0% (± 0.6 SE) to 4.1% (± 0.3 SE). Resurveyed sites in Vava'u showed the opposite pattern, but the changes were less dramatic; turf cover decreased slightly from 48.2% (± 1.7 SE) to 42.5% (± 1.5 SE), while CCA increased from 8.3% (± 0.7 SE) to 15.0% (± 1.1 SE).
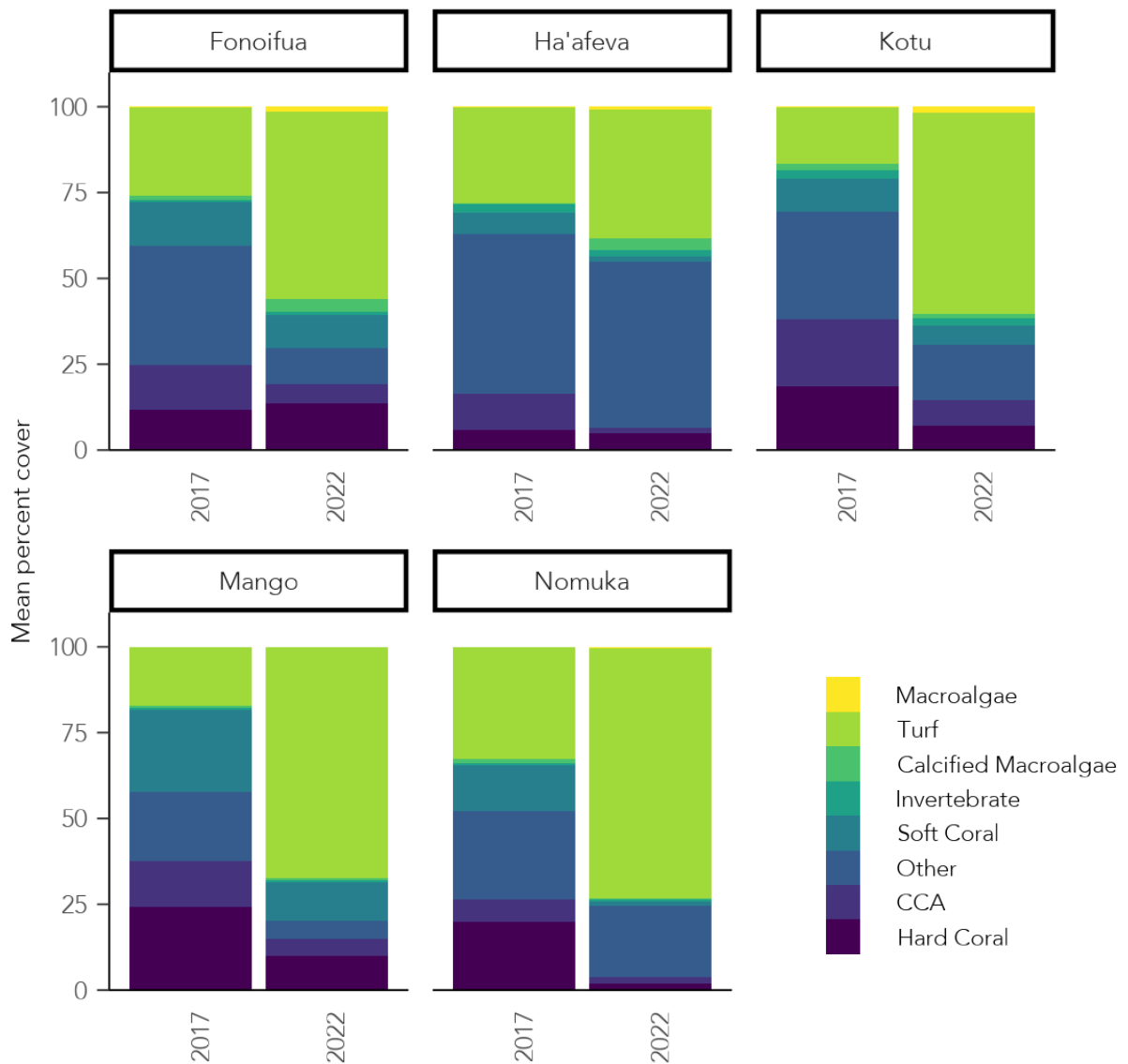


**FIGURE 18.** *Mean percent cover of main benthic functional groups at resurveyed sites in Ha'apai in 2017 and 2022.*
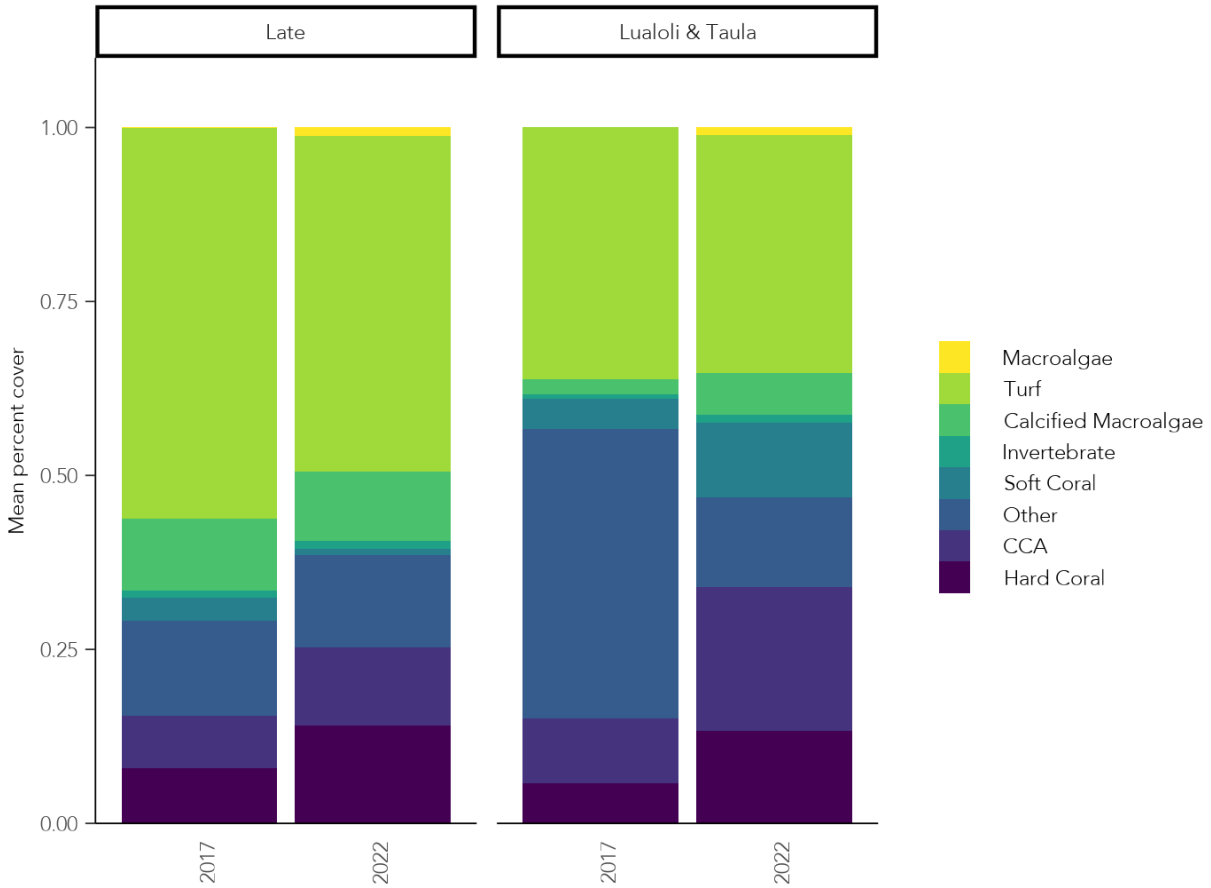
**FIGURE 19.** *Mean percent cover of main benthic functional groups at resurveyed sites in Vava'u in 2017 and 2022.*

Coral cover decreased between 2017 and 2022 at all resurveyed sites in Ha'apai except for Fonoifua, which saw an increase from 11.7% (± 1.1 SE) to 13.6% (± 1.3 SE). Nomuka had the greatest decrease in coral cover of any of the resurveyed sites, dropping from 19.8% (± 1.1 SE) in 2017 to only 2.1% (± 0.3 SE) in 2022. Conversely, coral cover increased at both resurveyed sites in Vava'u, with the greatest increase at Lualoli & Taula, from 5.8% (± 1.5 SE) in 2017 to 13.3% (± 1.5 SE) in 2022. Mean cover of CCA decreased across all resurveyed sites in Ha'apai, and increased at both resurveyed sites in Vava'u. Turf cover followed the opposite pattern, increasing across all resurveyed sites in Ha'apai and decreasing at resurveyed sites in Vava'u. Fleshy macroalgae cover was low at all sites across both time points but did increase slightly at all resurveyed sites between 2017 and 2022.

Patterns of coral diversity were highly variable, with no consistent patterns emerging across islands or island districts (Figures 20 & 21). While *Monitpora* was the most common genus overall, there were several islands where it was not the dominant, or even second most dominant, genus. Some islands were dominated by a single

genus, such as Fonualei, where the majority of coral was *Pocillopora,* Mango, where *Goniastrea* dominated, or 'Atata and 'Uoleva, which were dominated by *Montipora*. Other islands, such as 'Eueiki, Tonumea, and Lualoli & Taula had a more even spread of genera, regardless of overall coral cover. This variability in coral diversity between islands, particularly between islands of the same island group, indicates that something other than geography is driving patterns of coral diversity in Tonga. When aggregated by island group, overall patterns become slightly clearer; however, there is still a high level of variability in the abundance of common genera between island groups.
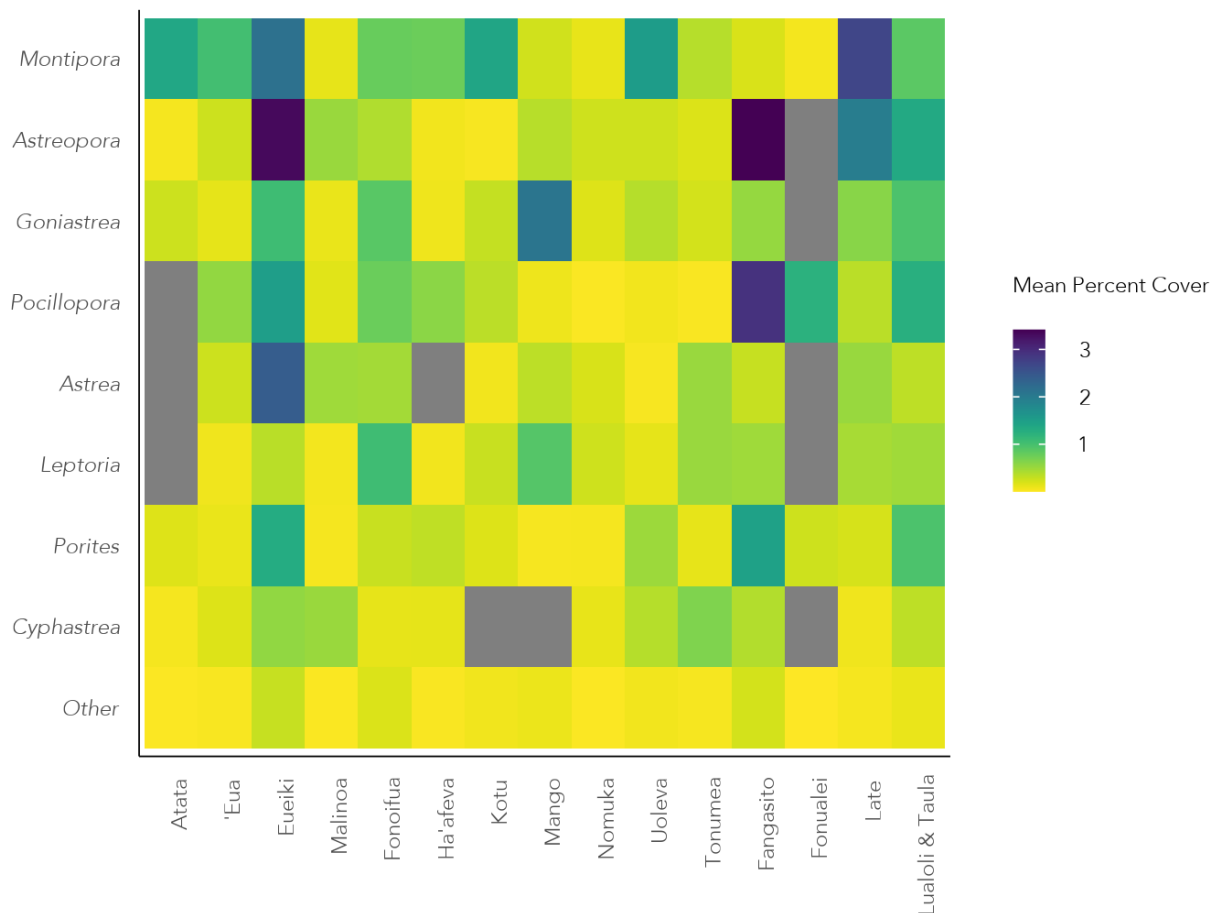


**FIGURE 20.** *Heatmap of the mean percent cover of most abundant coral genera at each island. Grey cells represent instances where the genus was not present at the corresponding island. Coral genera are ranked in order of overall abundance. All coral genera with an overall mean percent cover <0.2% were grouped into "Other".*
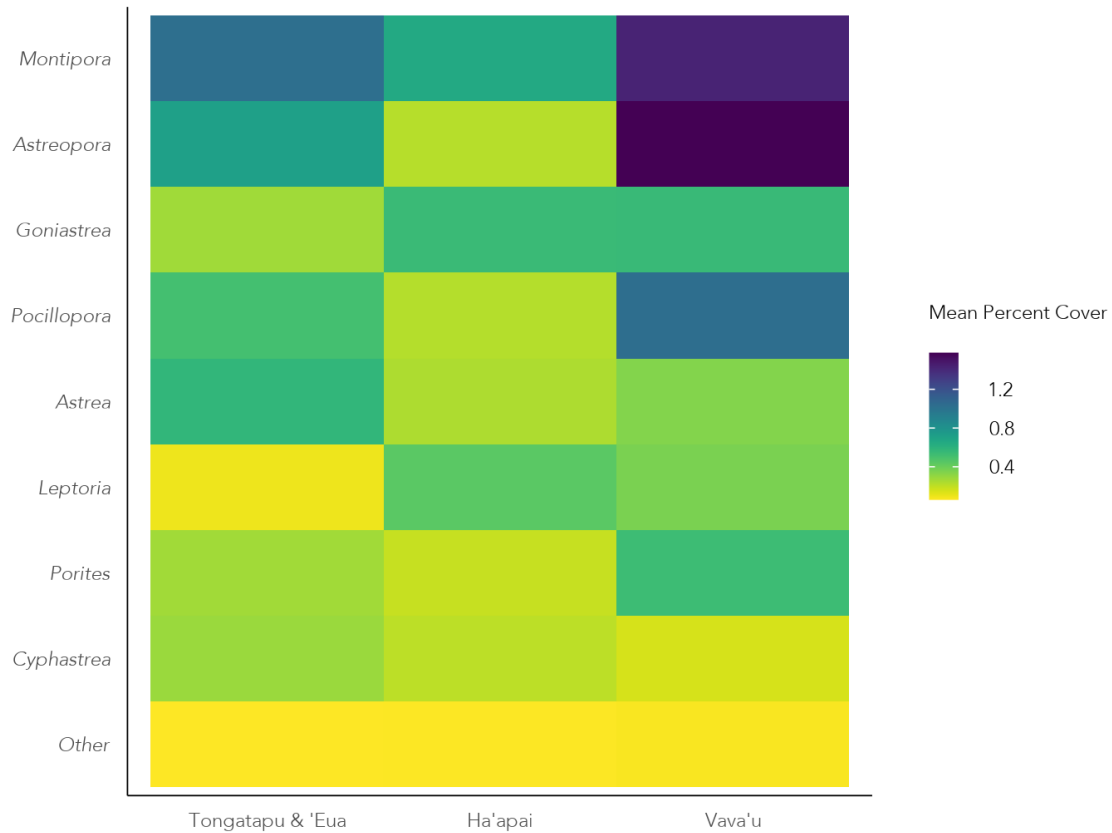
**FIGURE 21.** *Heatmap of the mean percent cover of most abundant coral genera at each island district. Coral genera are ranked in order of overall abundance. All coral genera with an overall mean percent cover <0.2% were grouped into "Other".*



*A diver surveying a large, healthy Porites coral colony.*

PHOTO CREDIT // Joe Lepore

## Coral Recruitment

Overall mean density of coral juveniles across all sites was 6.2 individuals $m^{-2}$ (± 0.8 SE). Mean density of coral juveniles at each island typically ranged between 2-10 individuals $m^{-2}$; however, 'Eueiki stood out from all other islands surveyed with a mean density of 24.4 individuals $m^{-2}$ (± 4.4 SE; Figure 22). Of the remaining islands, Lualoli & Taula had the highest mean juvenile density (10.5 individuals $m^{-2}$ ± 5.5 SE), and Tonumea had the lowest (2.2 individuals $m^{-2}$ ± 0.8 SE).
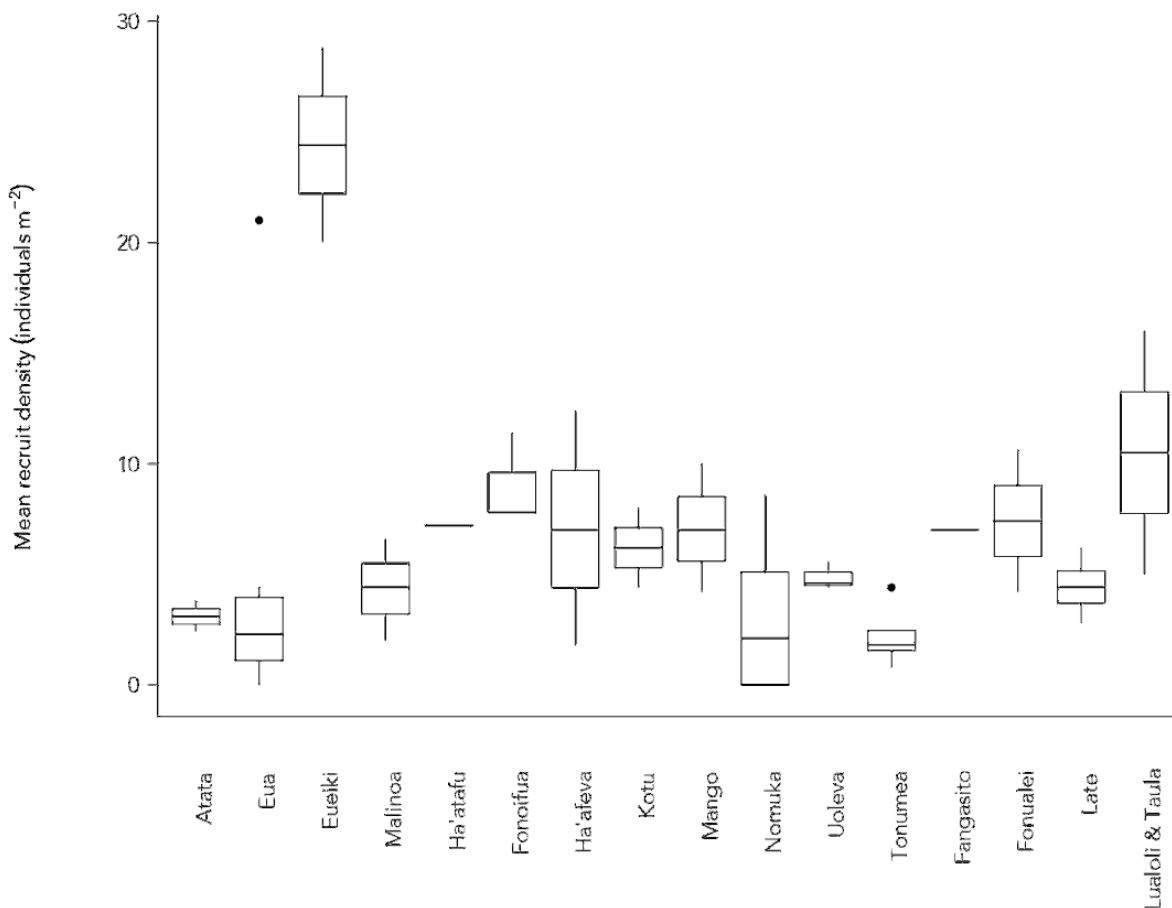


**FIGURE 22.** *Mean coral recruit density at each island surveyed. Bold horizontal lines represent the median value for each island.*

Of the three island districts, Tongatapu & 'Eua had the highest mean juvenile coral density (7.6 individuals $m^{-2}$ ± 2.4 SE; Figure 23); however, this distinction is largely due to the extremely high densities found on 'Eueiki, as other islands in this island group had relatively low densities (between 3.1 individuals $m^{-2}$ ± 0.7 SE at 'Atata to 5.1 individuals $m^{-2}$ ± 3.2 SE at 'Eua). Ha'apai had the lowest mean density of juvenile corals at 5.1 individuals $m^{-2}$ ± 0.7 SE.
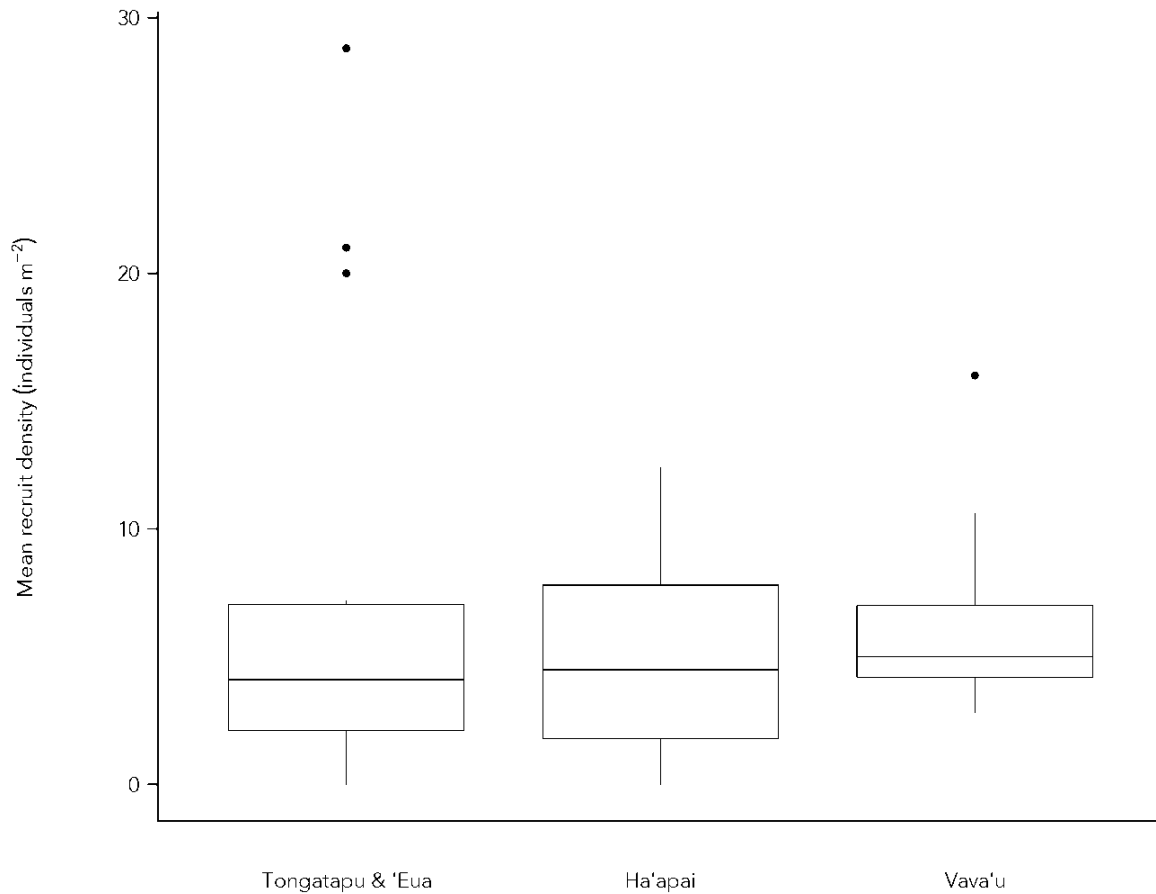
**FIGURE 23.** *Mean coral recruit density at each island district. Bold horizontal lines represent the median value for each island group.*

The most abundant genus among coral juveniles across all sites was *Astrea* (9.3 individuals m$^{-2}$ ± 0.2 SE), closely followed by massive *Porites* (9.2 individuals m$^{-2}$ ± 0.1 SE; Figure 24). Juvenile *Astrea* were particularly abundant at 'Eueiki (6.8 individuals m$^{-2}$ ± 2.8 SE) and Ha'atafu (3.6 individuals m$^{-2}$), while juvenile *Porites* were more evenly distributed across the country, ranging from 0.3 individuals m$^{-2}$ (± 0.2 SE) at 'Eua to 2.0 individuals m$^{-2}$ (± 0.8 SE) at 'Eueiki. 'Eueiki and Malinoa had the highest density of juvenile *Acropora* (2.7 individuals m$^{-2}$ ± 0.7 and 0.5 SE, respectively), while Fonualei had particularly high densities of juvenile *Pocillopora* (5.0 individuals m$^{-2}$ ± 3.4 SE). However, in general, juvenile coral diversity varied widely between islands and showed few, if any, geographic patterns.
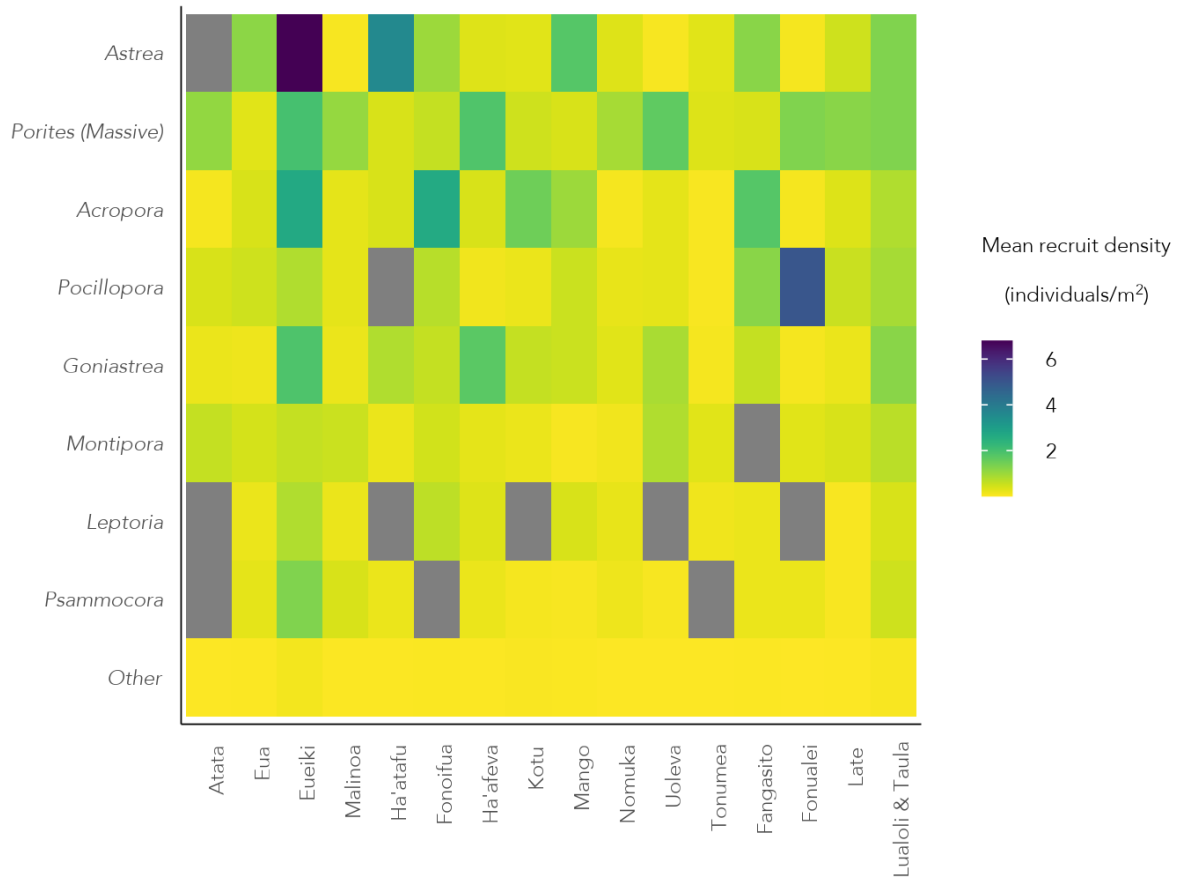
**FIGURE 24.** *Heatmap of the mean recruit density of the most abundant coral genera at each island. Grey cells represent instances where the genus was not present at the corresponding island. Coral genera are ranked in order of overall abundance, and where possible, further broken down by morphology. All coral genera with an overall mean recruit density <0.2 individuals m-² were grouped into "Other".*

Patterns in the data when grouped by island district reflect this variability, as outliers such as the high densities of *Astrea* at 'Eueiki and *Pocillopora* at Fonualei drive regional spikes in the mean densities of these genera (Figure 25). The ubiquity of massive *Porites* across all island groups is evident, with densities ranging from 0.83 individuals m$^{-2}$ (± 0.2 SE) in Tongatapu & 'Eua to 1.2 individuals m$^{-2}$ (± 0.3 SE) in Vava'u.

**FIGURE 25.** *Heatmap of the mean recruit density of the most abundant coral genera at each island district. Grey cells represent instances where the genus was not present at the corresponding island group. 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 <0.2 individuals m-² were grouped into "Other".*
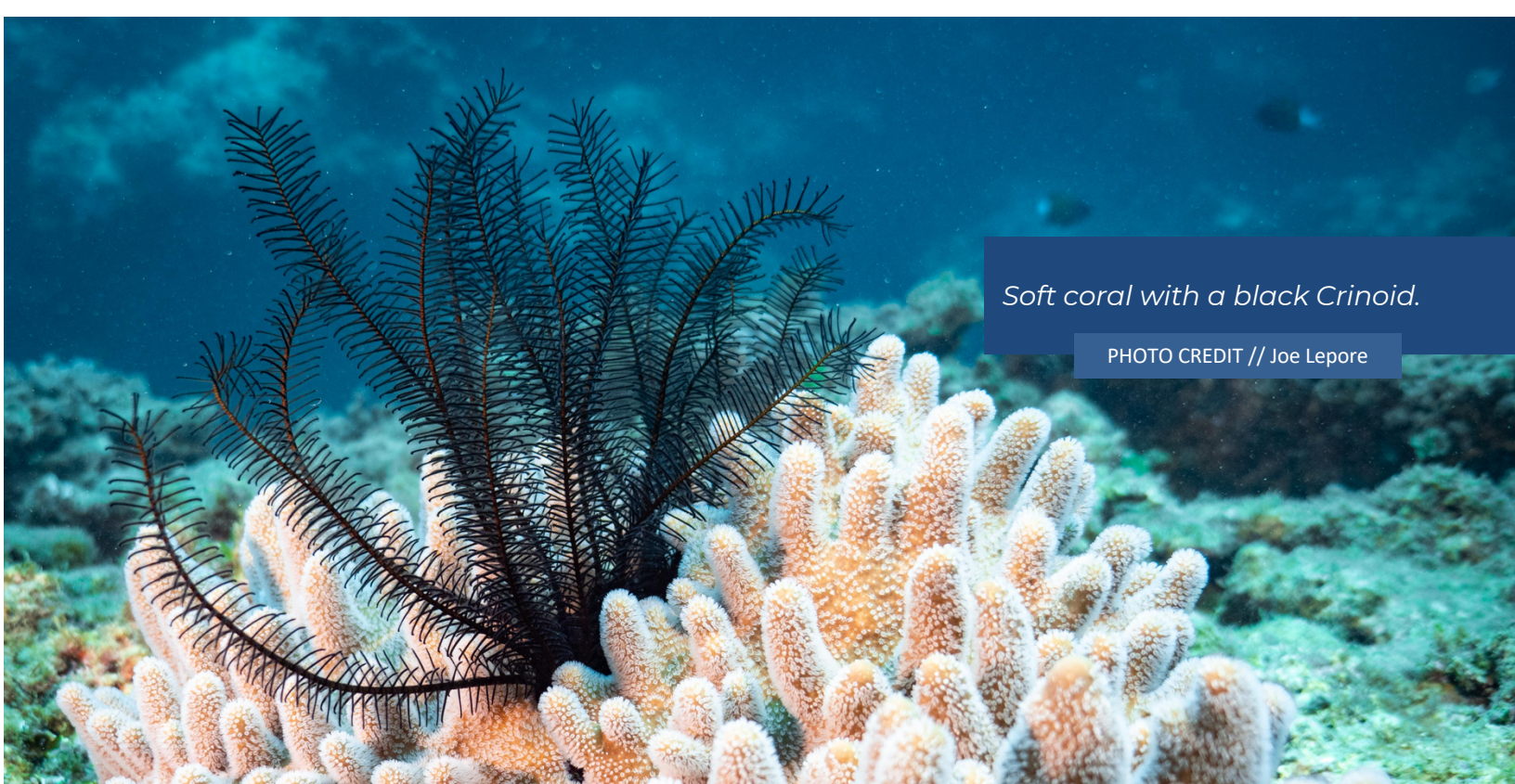


*Soft coral with a black Crinoid.*

PHOTO CREDIT // Joe Lepore

Rugosity was highest at Kotu, with a mean rugosity ratio of 1.4 (± 0.8 SE; Figure 26). The two sites at Kotu where mosaics were collected were located along a steep drop off. This certainly contributed to Kotu's high rugosity values relative to other sites, which typically covered a more consistent depth. Rugosity was lowest at Ha'atafu (1.1) and Tonumea (1.1 ± 0.01 SE), although it should be noted that only one site was surveyed at Ha'atafu. With the exceptions of Kotu and Lualoli & Taula, all islands had a mean rugosity ratio between 1.1 and 1.2.

There was very little variability in mean rugosity ratio when summarized by island district (Figure 27). Vava'u had the highest mean rugosity (1.21 ± 0.02 SE); however, the lowest mean rugosity, in Ha'apai, was very similar at 1.18 (± 0.02 SE).
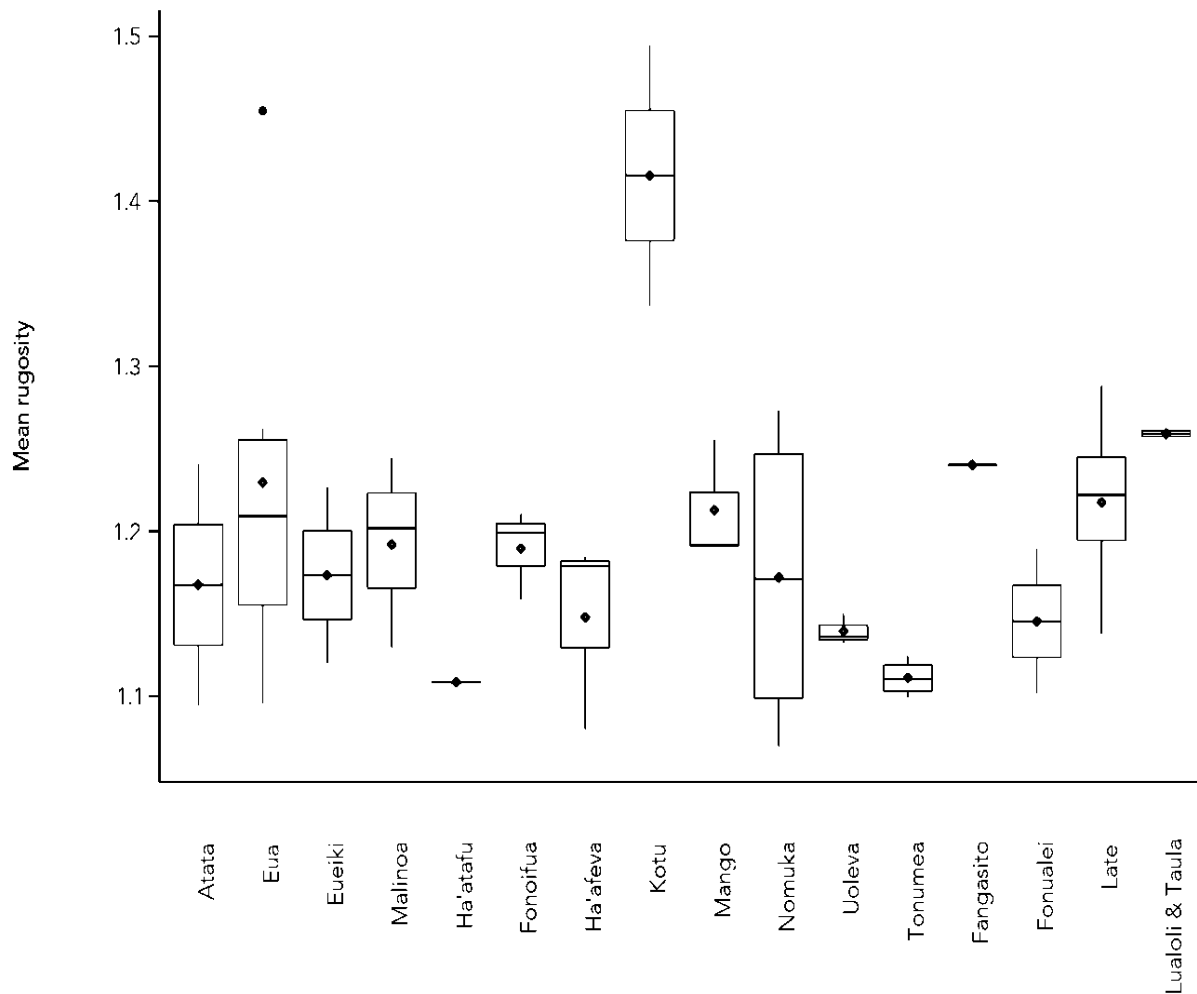


**FIGURE 26.** *Mean rugosity at each island surveyed. Bold horizontal lines represent the median value at each island, and diamonds represent the mean.*
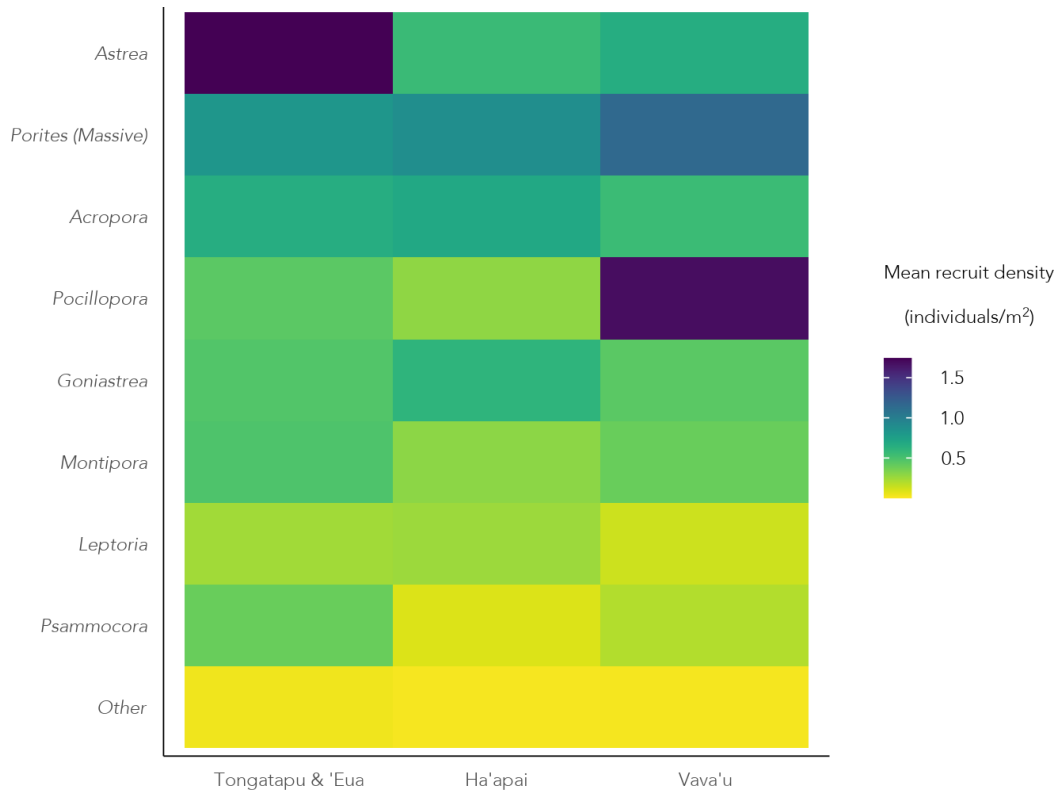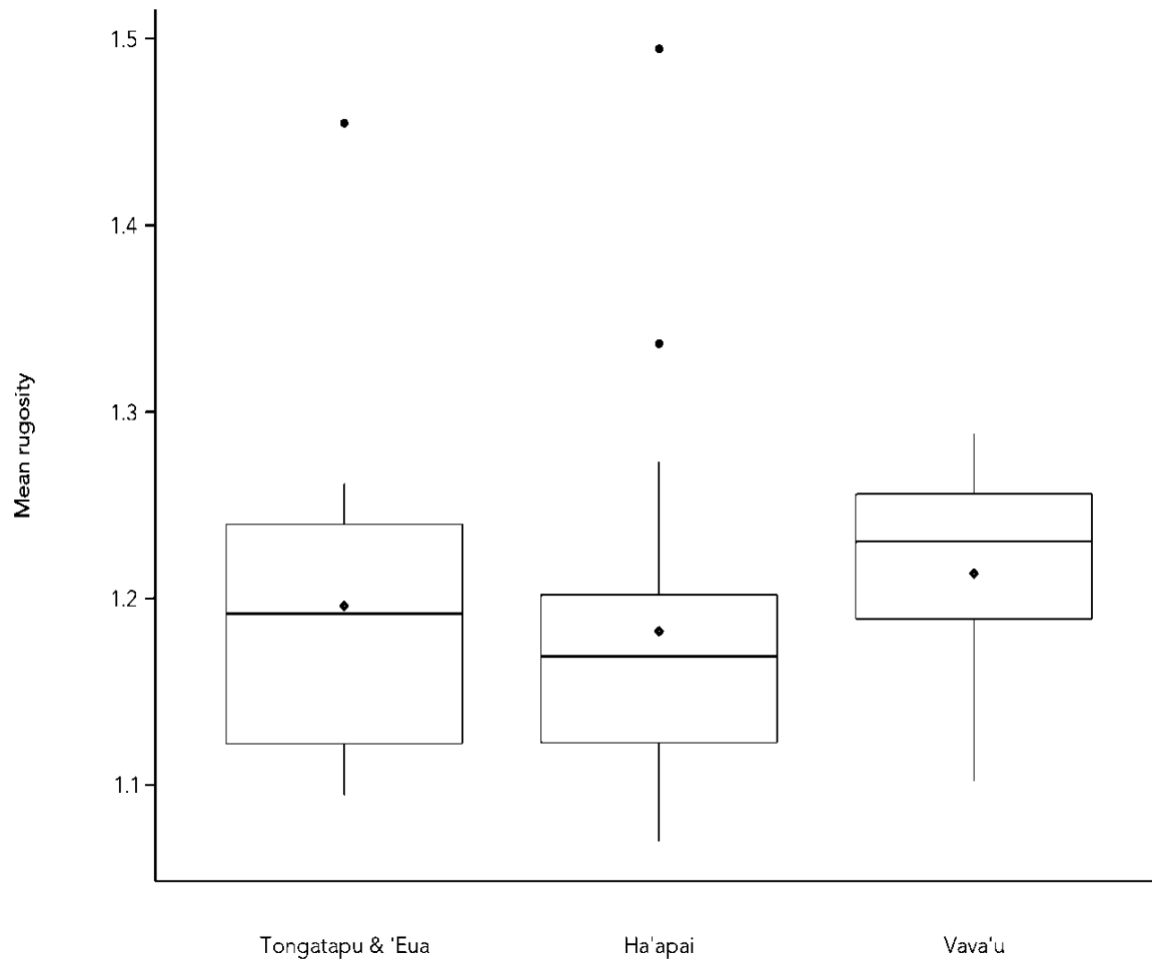
**FIGURE 27.** *Mean rugosity at each island district. Bold horizontal lines represent the median value for each island group, and diamonds represent the mean.*

## Macroinvertebrates

In total, nine species of sea cucumber were observed in the belt transects. Sea cucumber densities were generally low, with a maximum of three individuals per site (300 m$^2$) at 'Eueiki and Mango (Figure 28). At the two volcanic islands, Fonualei and Late, no sea cucumbers were recorded in any of the transects. In general, most species were present in densities of ≤1 individual per site; however, *Stichopus chloronatus* was particularly abundant at Tonumea (2 individuals per site ± 2.0 SE) and *Holothuria atra* was abundant at Mango (1.5 individuals per site ± 0.5 SE). *Bodiaschia argus* and *S. chloronatus* were the most widely distributed species, with both appearing at 6 islands; however, their distribution did not follow any latitudinal or obvious geographic patterns. Sea cucumber diversity was highest in Ha'apai, with eight out of the nine recorded species present in this district, while Vava'u had the lowest diversity with only three species present (Figure 29).



Legend:
- *Bohadschia argus*
- *Holothuria atra*
- *Holothuria edulis*
- *Holothuria fuscopunclata*
- *Holothuria leucospilata*
- *Holothuria whitamei*
- *Stichopus chloronatus*
- *Thelenota ananas*
- *Thelenota anax*
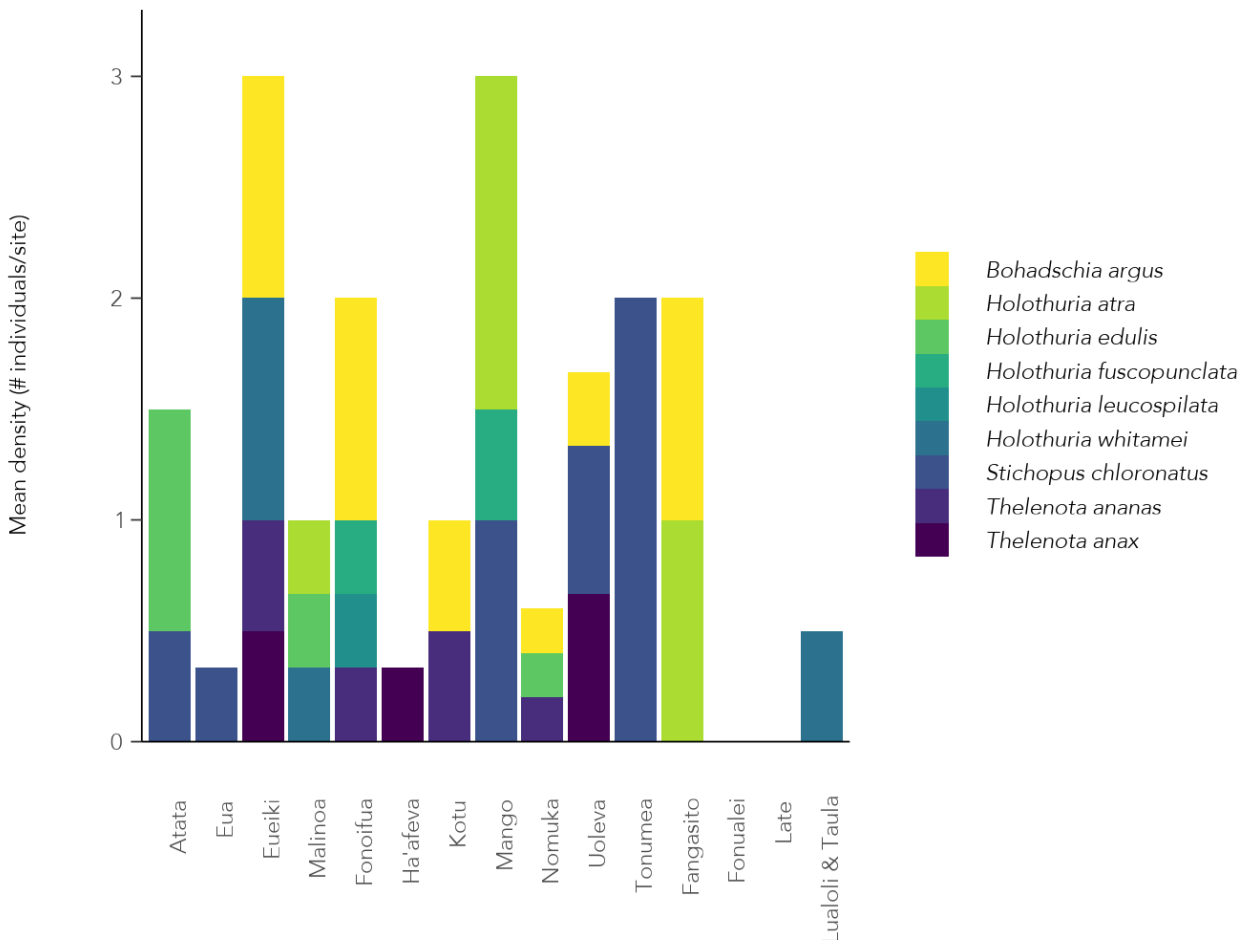
**FIGURE 28.** *Mean density of sea cucumbers at each island.*
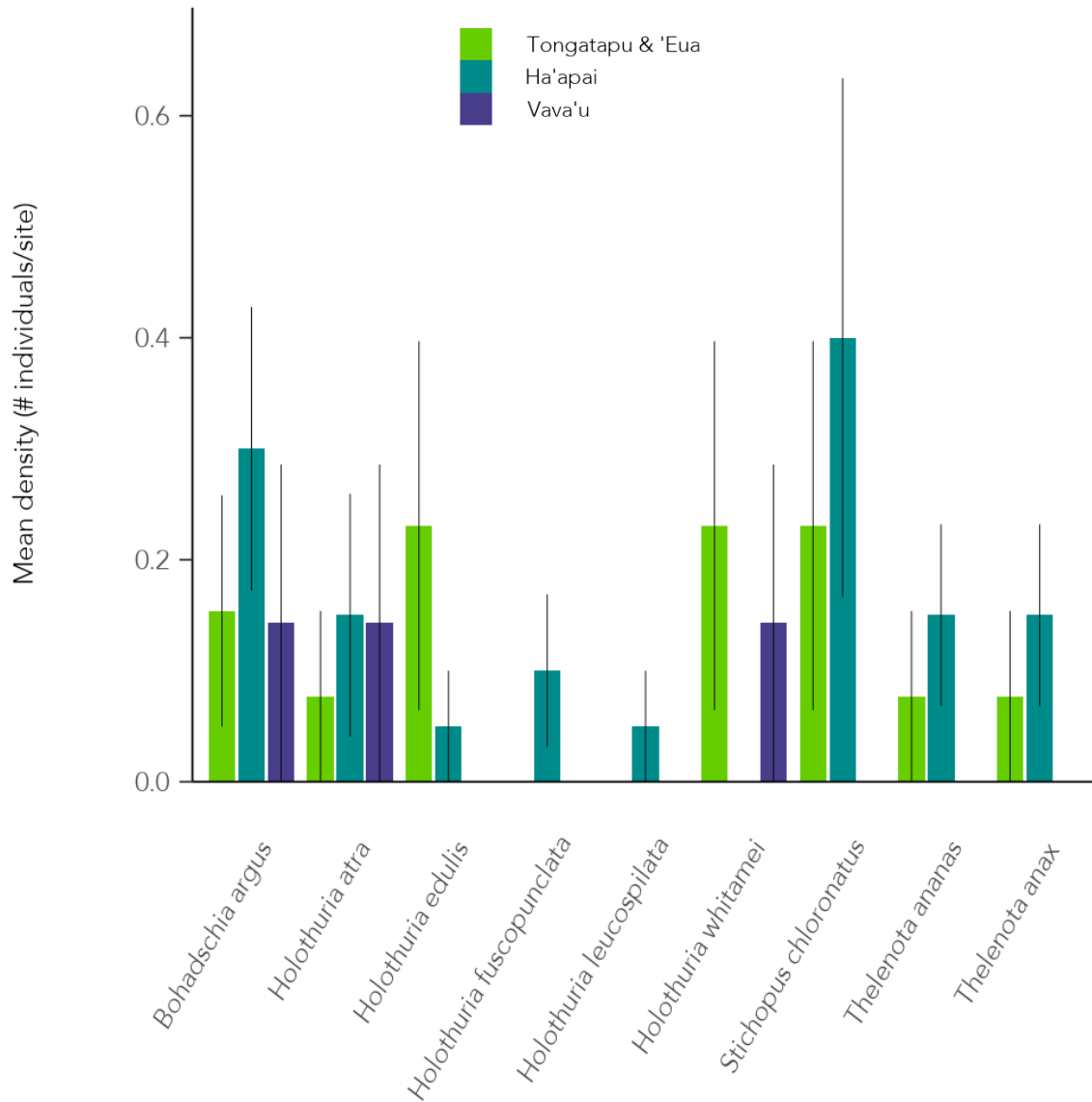
**FIGURE 29.** *Mean density of sea cucumbers at each island district.*

Three species of giant clam (*Tridacna gigas, Tridacna maxima,* and *Tridacna squamosa*) were recorded in the belt transects. *T. maxima* was by far the most abundant, occurring at all islands except 'Atata and Fonualei (Figure 30). *T. maxima* were particularly abundant at Ha'afeva, where they occurred at a mean density of 31 individuals per site (± 17.9 SE); at all other islands, *T. maxima* occurred in densities ≤4 individuals per site. *T. squamosa* was absent in Vava'u and only found in low densities in Tongatapu & 'Eua and Ha'apai (0.4 individuals per site ± 0.2 SE and 0.6 individuals per site ± 0.2 SE, respectively; Figure 31). *T. gigas* was only recorded at Tonumea (0.5 individuals per site ± 0.5 SE). The oyster *Hyotissa hyotis* was found only at Mango (0.5 individuals per site ± 0.5 SE), and the octopus *Octopus cyanea* was

recorded only at Nomuka (0.2 individuals per site ± 0.2 SE). Ha'apai had the greatest diversity of bivalves and cephalopods, with all five recorded species present in this district. Conversely, only *T. maxima* was recorded in Vava'u.
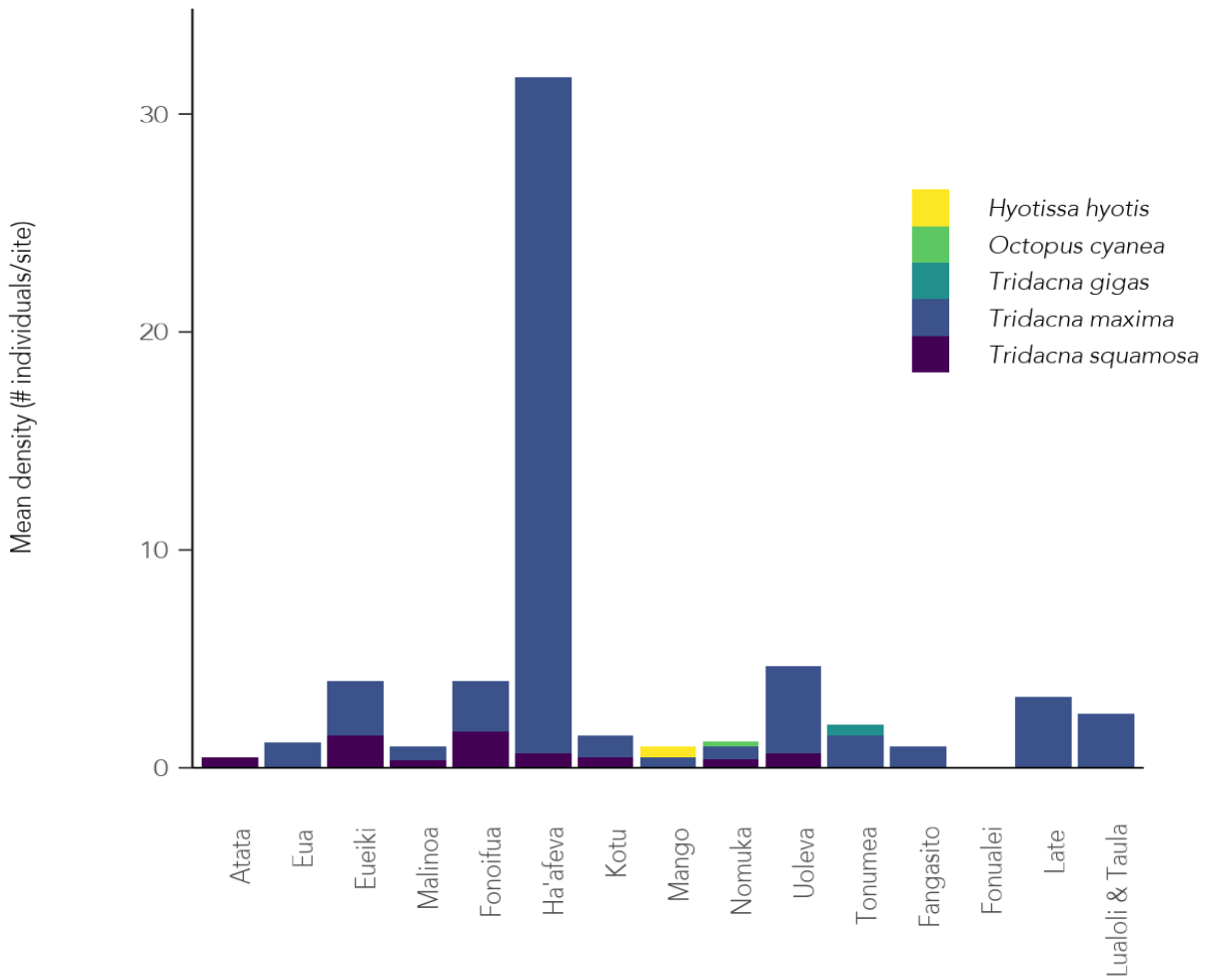


**FIGURE 30.** *Mean densities of bivalves and cephalopods at each island.*
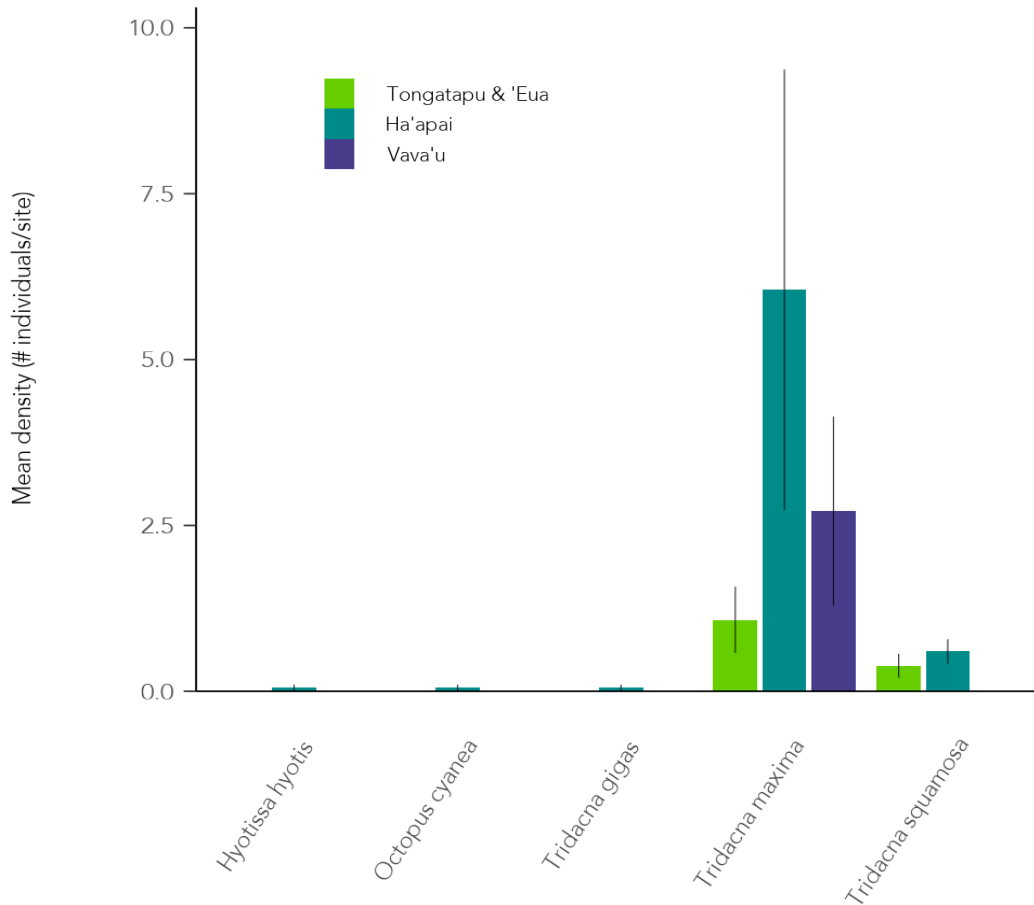
**FIGURE 31.** *Mean densities of bivalves and cephalopods at each island district.*

Gastropods were recorded at all islands except for Fangasito and Fonualei (Figure 32). With the exception of 'Eua, 'Eueiki and Fonoifua, all islands where gastropods were recorded only had one species present; however, the dominant species varied from island to island. *Lambis lambis* was most widespread, occurring at seven of the 15 islands. This species was particularly abundant at Lualoli & Taula and 'Eueiki, with mean densities of 2.5 (± 0.5 SE) and 2.0 (± 0.0 SE) individuals per site, respectively. *Rochia nilotica* was found at six islands and was particularly abundant at Ha'afeva with a mean density of 3.7 individuals per site (± 1.9 SE). Two species were only found at one island each: *Turbo marmolatus* at 'Eua, and *Chicoreus ramosus* at 'Eueiki. Tongatapu & 'Eua had the highest diversity of gastropods, with all six species recorded present in this region. Vava'u had the lowest diversity, with only two species present (Figure 33).
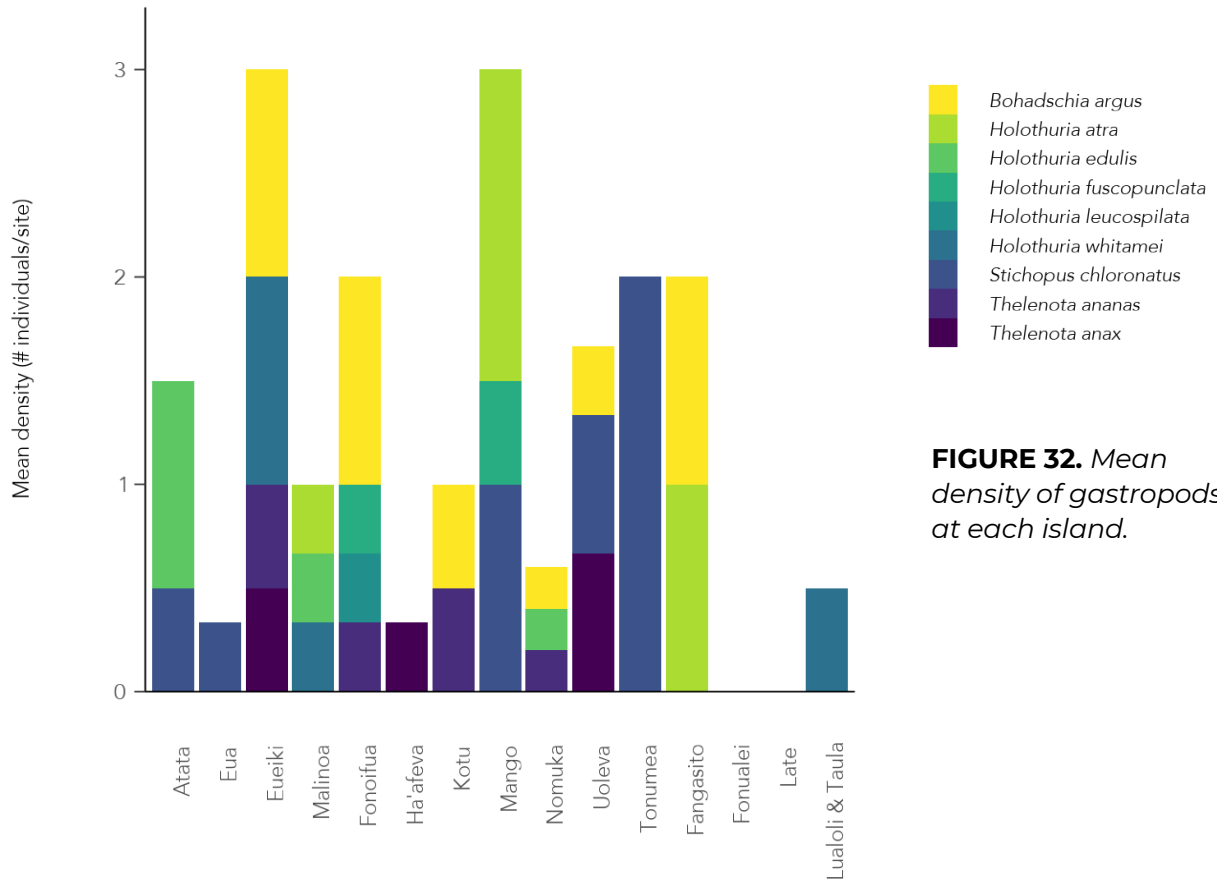
**FIGURE 32.** *Mean density of gastropods at each island.*

Legend:
- *Bohadschia argus*
- *Holothuria atra*
- *Holothuria edulis*
- *Holothuria fuscopunclata*
- *Holothuria leucospilata*
- *Holothuria whitamei*
- *Stichopus chloronatus*
- *Thelenota ananas*
- *Thelenota anax*
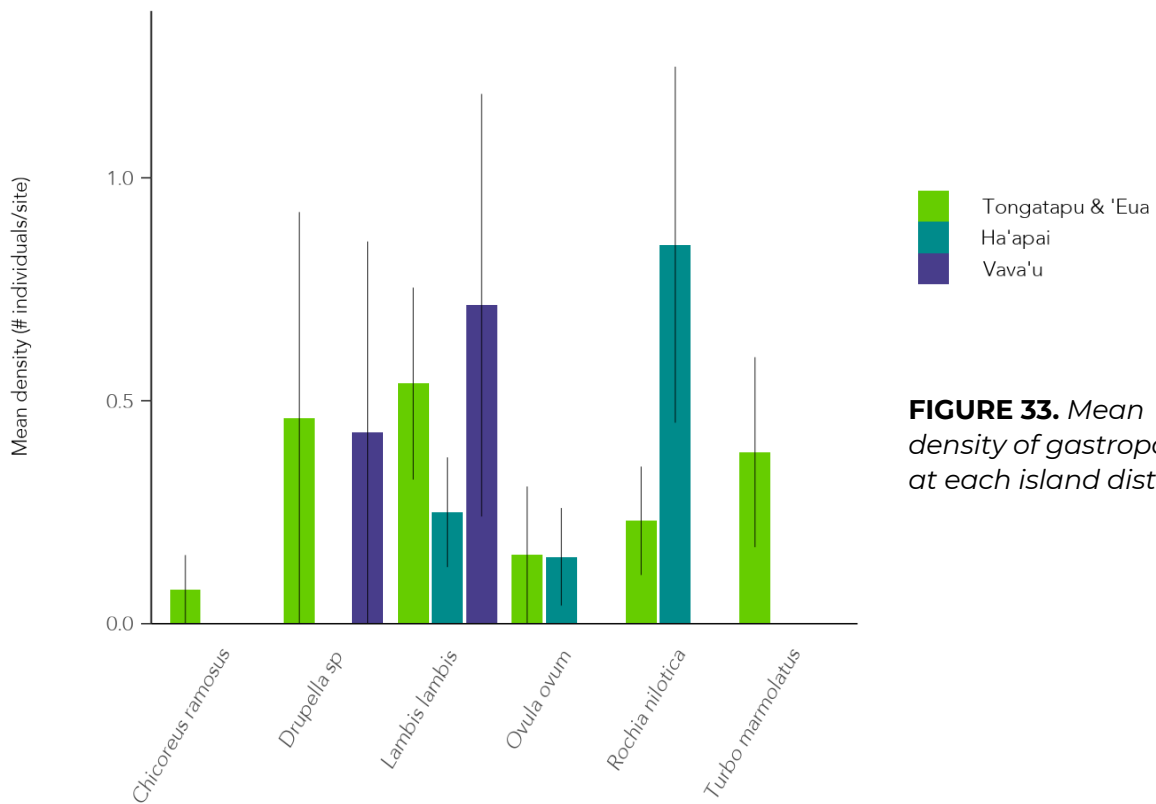


**FIGURE 33.** *Mean density of gastropods at each island district.*

Legend:
- Tongatapu & 'Eua
- Ha'apai
- Vava'u

Burrowing urchins from the genus *Echinostrephus* were the most abundant urchins, with particularly high densities at 'Atata and Late, where mean densities were 125.0 (± 122.0 SE) and 88.3 (± 27.8 SE) individuals per site, respectively (Figure 34). However, this species was patchily distributed, and was only present at seven islands. *Diadema setosum* was the most widely distributed urchin, appearing at eight islands, and dominating at Lualoli & Taula, where it was the only urchin species present and appeared in mean densities of 13.0 individuals per site (± 13.0 SE). *Acanthaster planci* was the most widely distributed sea star (starfish) species appearing at seven islands in densities of up to 3.7 individuals per site (± 2.4 SE) at 'Eua. However, *A. planci* was only found in Tongatapu & 'Eua and Ha'apai. No urchins or sea stars were recorded at Tonumea, Fangasito, or Fonualei. Ha'apai had the highest diversity of urchins and sea stars, with all seven species present, while only three species of urchin and no sea stars were found in Vava'u (Figure 35).
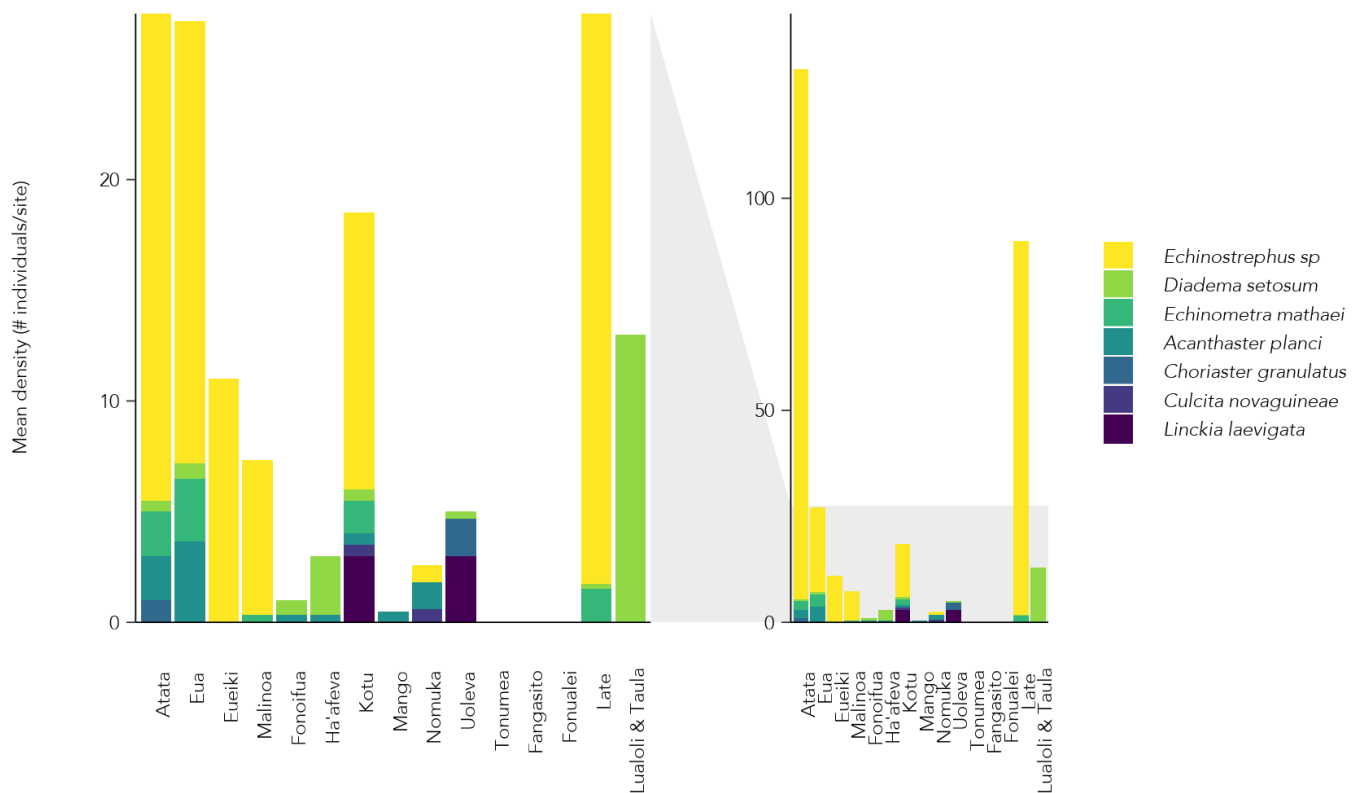


**FIGURE 34.** *Mean density of echinoderms (urchins and sea stars) at each island. The right-hand panel shows the full dataset, and the left-hand panel shows detail of the less abundant species.*
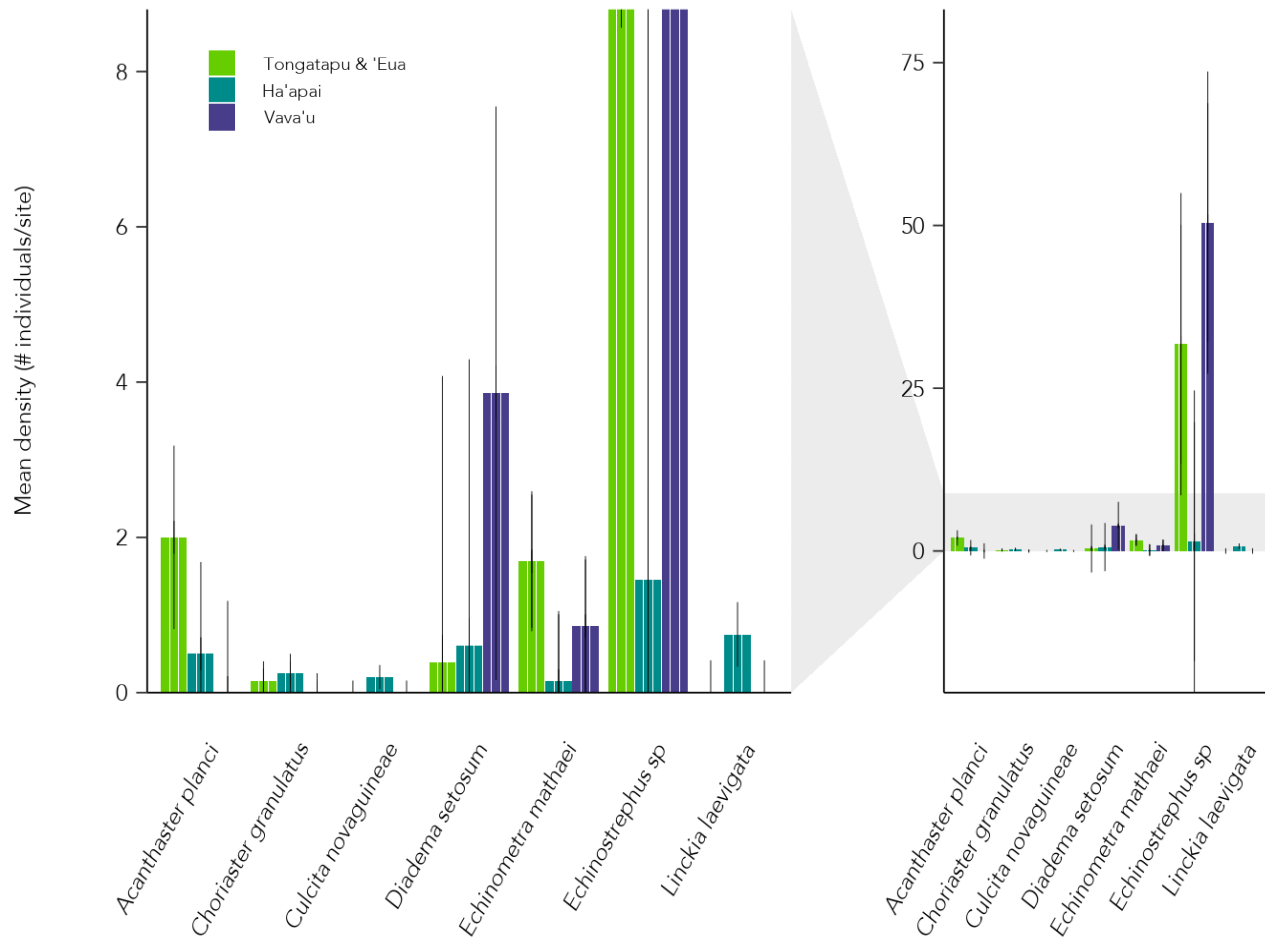
**FIGURE 35.** *Mean density of echinoderms (urchins and sea stars) at each island district. The right-hand panel shows the full dataset, and the left-hand panel shows detail of the less abundant species.*

Commercially important sea cucumbers, bivalves, and gastropods encountered within the transects were measured to the nearest centimeter. The smallest sea cucumber recorded was 10cm (*Holothuria edulis*) and the largest was 60cm (*Thelenota anax;* Figure 36). *H. edulis*, *S. chloronatus* and *Holothuria whitamei* were typically small, *B. argus, H. atra, Holothuria fuscopunclata* and *Holothuria leucospilata* were medium sized, while *Thelenota ananas* and *T. anax* were typically larger. *T. maxima*, the most abundant of the three giant clam species recorded, had a bimodal size distribution, with many small individuals (<10cm) and many medium sized individuals (between ~15-20 cm; Figure 37). The largest *T. maxima* recorded reached 30 cm. Similarly, *T. squamosa* tended to either be small (<10cm) or large (≥30cm). *L. lambis* exhibited a wide range of sizes, from a minimum of 15cm to a maximum of 45cm; however, the majority of individuals were medium sized, around 20cm. *R. nilotica* ranged from 5cm to 15cm (Figure 38).
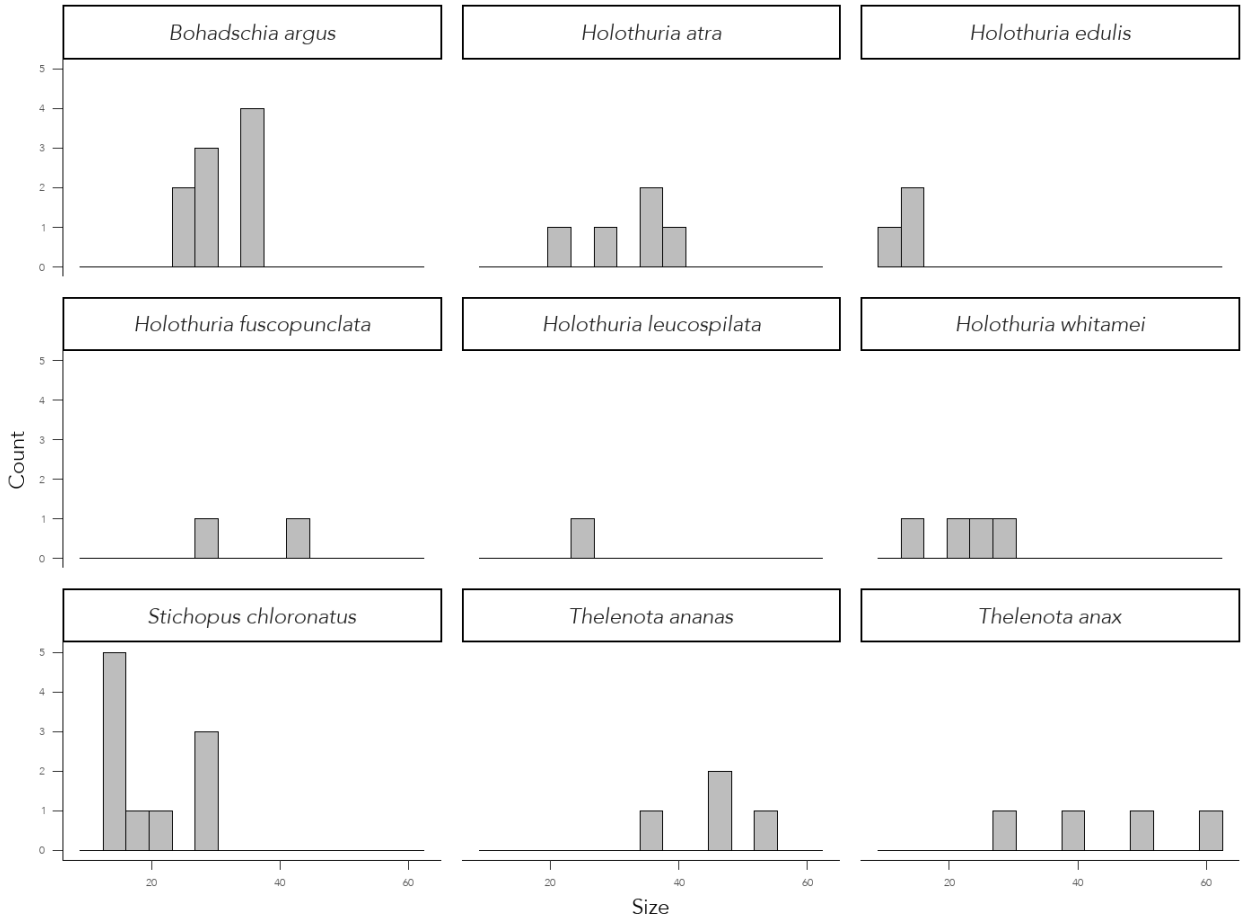
**FIGURE 36.** *Size frequency distributions of sea cucumbers across all sites.*
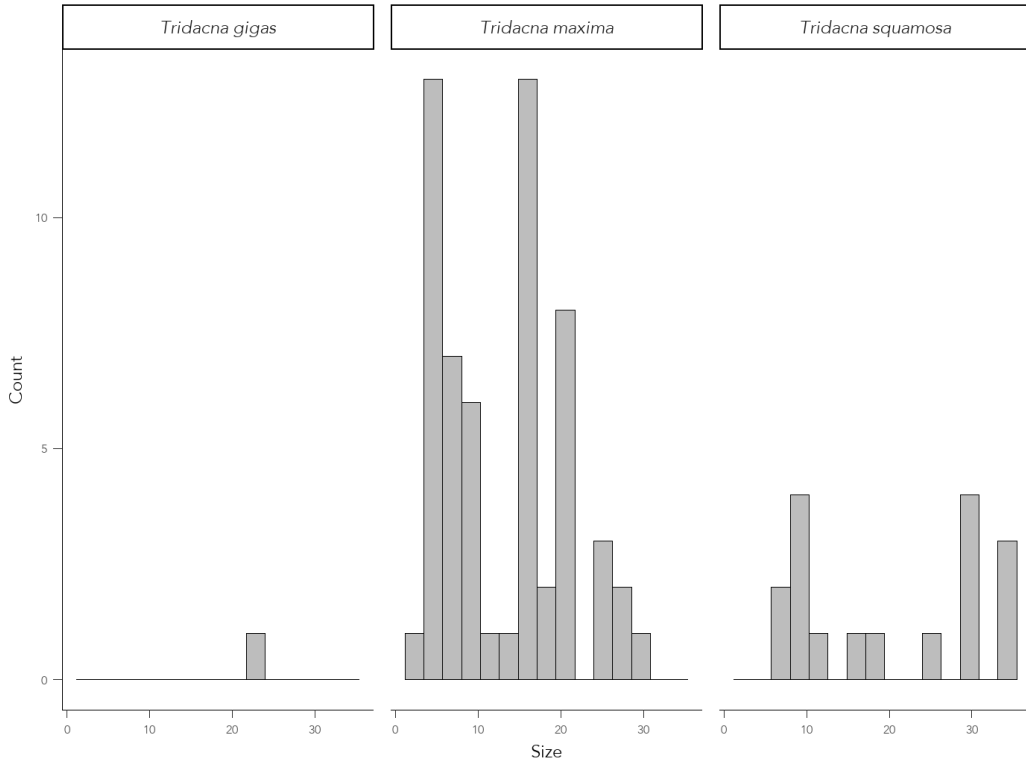
**FIGURE 37.** *Size frequency distributions of giant clams across all sites.*
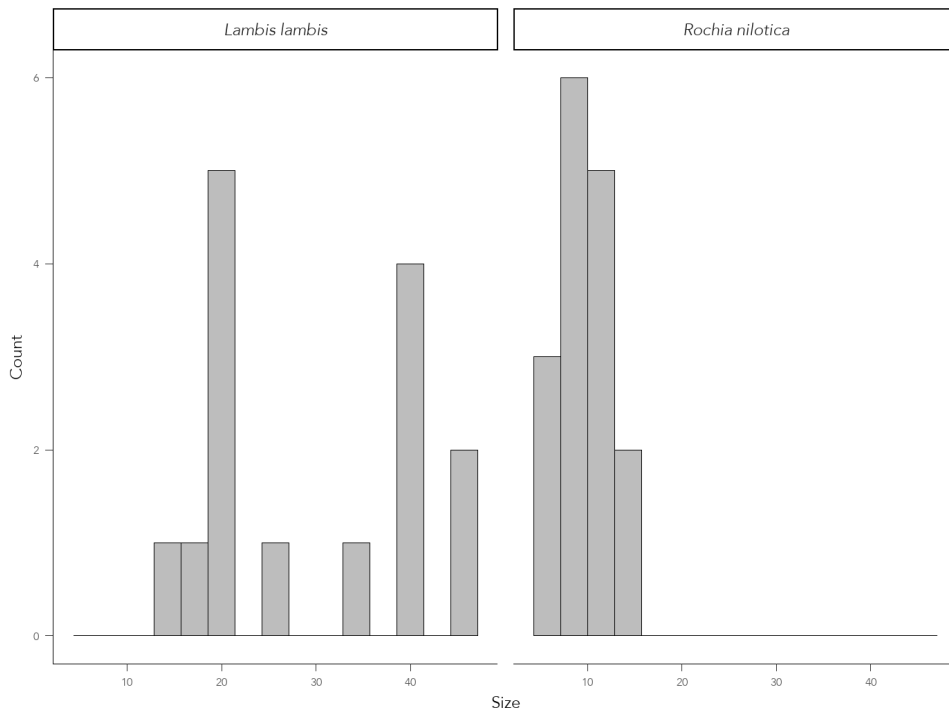


**FIGURE 38.** *Size frequency distributions of commercially important gastropod species across all sites.*

Encrusting Montipora on volcanic substrate.

PHOTO CREDIT // Joe Lepore

# DISCUSSION

## Key Findings

The data from this expedition indicate that the HTHH eruption and tsunami caused noticeable damage to the benthic communities of reefs in Tonga; however, the impacts were localized and likely related to the severity of tsunami impacts at each location. Reefs that were directly exposed to the tsunami, such as many of the reefs in Ha'apai and Tongatapu & 'Eua, tended to have lower coral cover, and, when time series comparisons could be made, showed decreases in coral cover since 2017. Conversely, reefs that were sheltered from the direct impact of the tsunami, such as 'Eueiki and reefs in Vava'u, had higher coral cover.  Fish communities, however, do not seem to have been noticeably affected by the eruption or tsunami, and instead mirror patterns from previous surveys. Fish abundance and biomass did not appear to correlate with coral cover or reef complexity, perhaps indicating a lag in impact on fish communities following the immediate impacts to the benthos. Conversely, macroinvertebrate densities and diversity have declined since 2017; it is possible that this decline is due in part to the HTHH eruption, which may have exacerbated stresses on invertebrate stocks created by the periodic reopening of the sea cucumber fishery.

Reefs in Ha'apai appear to have sustained the highest amount of damage from the eruption, while reefs in Vava'u were mostly spared. While surveys conducted prior to the eruption consistently showed the lowest coral cover in Vava'u and the highest in Ha'apai (Purkis et al., 2017, Stone et al. 2017, Smallhorn-West et al., 2020d), this pattern has been reversed, with Vava'u now boasting the highest coral cover of the

three island districts surveyed, and Ha'apai with the lowest. Indeed, visual assessments of reefs in Ha'apai during this expedition noted large amounts of debris from land (e.g., palm trees, garbage, vegetation) at survey sites, suggesting that the coral loss noted in this region was likely due to the tsunami rather than other environmental or anthropogenic stressors. While reefs in Tongatapu & 'Eua were found to have slightly higher coral cover than those in Ha'apai, it appears likely that several of the reefs in this region sustained some damage from the tsunami as well. For example, monitoring instrumentation previously deployed at the one site located in Ha'atafu had disappeared by the time of survey despite being anchored sturdily to the reef, suggesting strong tsunami impacts at this location. Despite these general trends, however, reef health was variable within each island district, and reefs on a number of islands within each region seem to have been spared from major destruction. In addition, patterns in fish abundance and biomass did not correlate directly with patterns in reef health, suggesting that forces beyond the HTHH eruption may be driving distributions of reef fish.

The most striking example of this intra-island group variability can be seen in Tongatapu & 'Eua, where, in contrast to the generally low coral cover at 'Atata, 'Eua and Malinoa, 'Eueiki had the highest coral cover of the islands surveyed on this expedition. This island also had the highest coral diversity as well as the highest density of coral recruits of any of the surveyed islands. 'Eueiki is located to the east of the island of Tongatapu, and as such was likely sheltered from the full force of the tsunami, which originated north-west of this island group. Conversely, 'Atata, Malinoa, and 'Eua were all more exposed and likely suffered much more damage. The existence of such a healthy reef in this region may aid in the recovery of the surrounding islands, as the coral community at 'Eueiki may serve as a refuge population to help seed future coral recruitment in the region.

While no sites in Tongatapu & 'Eua were surveyed in 2017, direct pre- and post-eruption comparisons could be made for several islands in Ha'apai and Vava'u. At both resurveyed sites in Vava'u, coral cover increased, nearly doubling at Late (7.9% in 2017, 14.1% in 2022) and more than doubling at Lualoli & Taula (5.9% in 2017, 13.3% in 2022). Vava'u experienced a coral bleaching event in 2014-2015 (Atherton et. al. 2015), and the results from this time series indicate that reefs in this district are on a trajectory towards recovery. Lualoli & Taula, along with the nearby island of Maninita, became an MPA following BioRAP surveys in 2014 (Stone et al., 2017). The increase in coral cover at these islands indicates that the protection afforded by this designation may be working to increase overall reef community health. Similarly, Late, while not a formal MPA, is geographically isolated from population centers in Tonga, and this isolation likely reduces the fishing pressure and other anthropogenic impacts around this island. These results indicate that, barring unforeseen disturbances such as those caused by the HTHH eruption in Ha'apai and Tongatapu & 'Eua, protection from human influence has the potential to increase the health of Tonga's coral reefs.

In contrast, of the five resurveyed islands in Ha'apai, only one (Fonoifua) saw an increase in coral cover, the magnitude of which was modest in comparison (11.3% in

2017, 13.6% in 2022). Coral cover at Ha'afeva did not change significantly between time points, but large decreases in coral cover were observed at Kotu, Mango, and Nomuka. In particular, Nomuka (which includes sites at both the islands of Nomuka and Nomuka Iki), saw a dramatic decrease in coral cover, from 19.8% in 2017 to only 2.1% in 2022. Tsunami damage was clearly evident at this location: terrestrial debris such as coconut trees and garbage were abundant, and large reductions in coral cover (and associated increases in turf and sediment cover) were obvious. One of the most dramatic examples can be seen from site NOS1, immediately in front of the village of Nomuka, where a once flourishing coral community was completely destroyed, leaving only sediment and turf in its place (Figure 5). As in Tongatapu & 'Eua, the islands in Ha'apai that were in the direct path of the tsunami (Kotu, Mango, and Nomuka) saw greater damage than those that were sheltered by islands to the west.

Fonualei had the lowest coral cover of any island surveyed, with a mean of only 2%, despite being the most distant site from the HTHH volcano and epicenter of tsunami. However, this is consistent with previous surveys that have found low coral cover on volcanic islands in Tonga, including Fonualei (Atherton et al. 2015). Indeed, it is possible that this pattern is due to volcanic activity at Fonualei itself, rather than from impacts of the HTHH eruption. At the time of survey, volcanic activity was



*Broken coral structure.*

PHOTO CREDIT // Joe Lepore

evident at Fonualei, with large plumes of sulfur emanating from vents along the coast (Latu 2022). The reefs at this island were comprised of basalt boulders that were largely devoid of adult corals, but that hosted a high density of juvenile *Pocillopora* colonies. Therefore, it is likely that the sites surveyed at this island were either the site of a recent volcanic eruption or are subject to continual volcanic activity, and that the corals present in 2022 are early colonizers following this disturbance.

Patterns of coral diversity did not follow any clear geographic patterns, and variability was high between islands. However, with the exception of *Pocillopora,* the most abundant genera across the archipelago were all typically made up of encrusting or mounding species, rather than those with typically branching, tabular, or corymbose morphologies. This pattern may reflect the impact of the tsunami, as encrusting and mounding species are typically more resistant to disturbance by wave action or storm surges. While many of the most abundant adult coral genera were also common as juveniles, there was still high inter-island variability in community composition of juvenile corals, as well as a lack of clear geographic patterning. The density of juvenile corals tended to correlate somewhat with overall coral cover at each island with the exception of Fonualei, which had low coral cover but relatively high juvenile coral density. This is likely a result of further tsunami damage at impacted sites, which had not yet had a chance to start recovering at the time of survey.

Reef rugosity was generally consistent across most of the archipelago, except for Kotu, which had significantly higher rugosity than any other island surveyed. This is likely due to the existence of a steep drop off around 10m at the sites surveyed on this island. As all surveys were conducted along the 10m depth contour, the photomosaic plots at Kotu encompassed this drop off, leading to higher complexity values at these sites.

Despite the disturbance caused by the HTHH eruption, patterns in fish abundance, diversity, and biomass were found to be comparable to those found in previous studies of Tonga's fish populations. As in this study, previous surveys have found fish abundance to be dominated by small pomacentrids (damselfish) and labrids (wrasses), with a distinct lack of larger, predatory species (SPREP 2014, Atherton et al. 2015, Purkis 2017, Stone et al. 2017, Smallhorn-West et al., 2020b). Indeed, the damselfish *P. vaiuli* was found to be the most widely distributed species in both this study and a 2014 BioRap survey of Vava'u, where it was found at 100% of the sites surveyed (Atherton et al. 2015). Both studies, as well as the 2017 survey, also found a low abundance of sharks (Atherton et al. 2015, Stone et al. 2017). While belt transects, like those used in this and the 2017 study, have been found to undersample larger mobile species (Richards et al. 2010), the BioRap study used roving diver surveys, which are better suited for capturing these taxa. This suggests that the low abundance of sharks found in this study is representative of their true distribution and is not an artifact of the survey design.

Patterns in the mean values of fish biomass have also stayed remarkably consistent since the BioRap surveys in 2014. Herbivores from the families Acanthuridae (surgeonfish) and Scaridae (parrotfish) made up the largest proportion of biomass both in 2014 and 2022 (Atherton et al. 2015), as well as in a similar study conducted by the Khaled bin Sultan Living Oceans Foundation (KSLOF) in 2017 (Purkis et al. 2017). While the total mean biomass for each family was slightly higher in 2014 (Acanthuridae: 48.7 g m$^{-2}$ in 2014 vs 34.8 g m$^{-2}$ in 2022; Scaridae: 38.0 g m$^{-2}$ in 2014 vs. 25.1 g m$^{-2}$ in 2022), the overall proportion of the total mean biomass was strikingly similar for each family between years (Acanthuridae: 27.8% of total mean biomass in 2014 vs. 30.2% in 2022; Scaridae: 21.7% of total mean biomass in both years). Despite differences in geographic extent and survey methods between the BioRap, KSLOF and current studies, the consistency of results indicate that patterns in reef fish biomass have not changed significantly over time.

However, when broken down by island district, geographic patterns in fish biomass and density appear to have shifted over time. Aggregated fish survey data from 2016-2019 showed that during that time period, Vava'u had the lowest mean reef fish biomass and density of the three island districts (Smallhorn-West et al., 2020d, Smallhorn-West & Sheehan 2020e). However, in 2022, Vava'u had the highest overall biomass and islands in Vava'u tended to have higher fish density. It is possible that this change in pattern could be due to the concurrent increase in coral cover in Vava'u following the 2014-2015 coral bleaching event, creating more habitat to support reef fish populations. However, this apparent reversal may also be partly due to the sites in Vava'u selected for this survey. While previous studies focused more



*Reef with several species of coral and associated reef fishes.*

PHOTO CREDIT // Joe Lepore
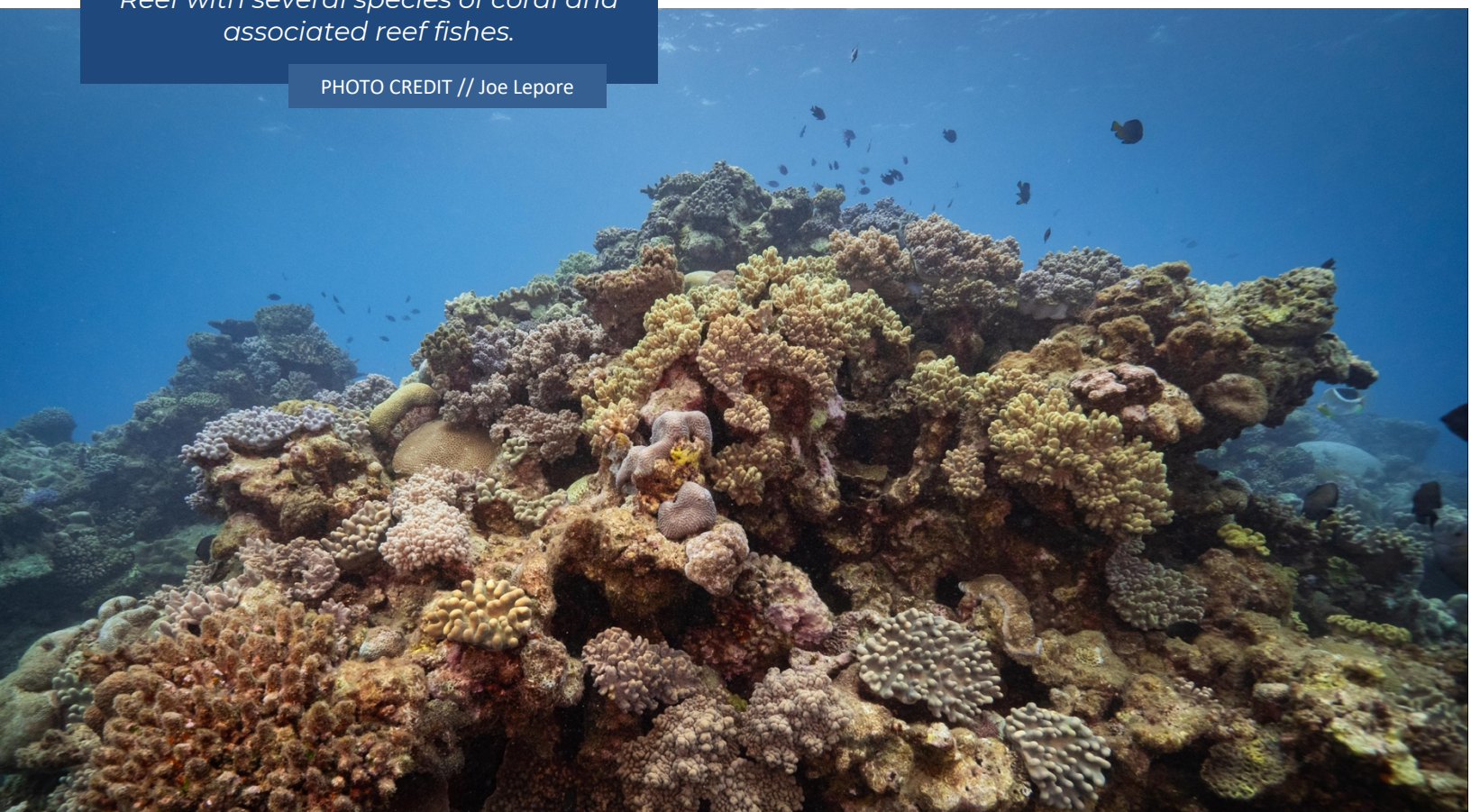
heavily on reefs near the main islands of Vava'u, this expedition took advantage of the opportunity to visit the more remote volcanic islands of Late and Fonualei, which are likely subject to less fishing pressure due to their distance from main population centers. Of those sites closer to the main islands, Lualoli & Taula are within an MPA. Therefore, a high proportion of the sites surveyed in Vava'u during this survey receive minimal fishing pressure, so results presented here may not be representative of fished reefs in this district.

The general lack of predatory fish such as snappers (lutjanids) and groupers (serranids) across the country appears to indicate widespread fishing pressure on these species. Tonga's reefs have been characterized as heavily to moderately exploited in some areas when compared to global baselines of fish biomass (Smallhorn-West et al. 2020d). Previous studies have found similar patterns, and have suggested that overfishing of these target taxa is likely given their high value and low abundance (Atherton et al. 2015, Purkis et al. 2017). One exception is Fonualei, which had the highest density and biomass of predatory fish, particularly snappers. This is consistent with the findings from the 2014 BioRap (Atherton et al. 2015), in which the authors suggest that Fonaualei's distance from the main island makes it inaccessible to most fishers, allowing for the proliferation of larger carnivorous species. This suggests that in the absence of heavy fishing pressure, reefs in Tonga would likely be able to support higher biomass of predatory fish species, perhaps indicating the need to evaluate fishing regulations in the main island districts to ensure sustainability of those stocks.

Interestingly, fish biomass and abundance did not correlate with coral cover or reef complexity. This is in contrast to previous studies that have found that reef complexity and coral cover were the main drivers of patterns in reef fish density and diversity in Tonga (Smallhorn-West et al. 2020d). Typically, reefs with higher coral cover and/or higher rugosity values are considered to be capable of supporting larger fish populations due to the increased availability of habitat at those sites. While it is not clear what is driving this mismatch, it is possible that there may be a lag in the impact of the HTHH eruption on fish populations, when compared to the immediate impacts on benthic communities. It is also possible that fishing dynamics at these sites may have a stronger influence on fish populations than habitat availability. In either case, continued monitoring of reef fish communities at these sites is needed to understand and disentangle the combined effects of fishing and the HTHH eruption.

Overall, 27 species of macroinvertebrates were recorded during this expedition- a significant decrease from the 56 species recorded during the 2017 expedition (Stone et al., 2017). While 19 species of sea cucumber were recorded in 2017, only 9 were recorded in 2022. The dominant species of sea cucumber also shifted during this time, from *H. atra* and *H. edulis* in 2017, to *B. argus* and *S. chloronatus* in 2022. While *T. maxima* remained the most abundant species of giant clam across both time points, *Tridacna derasa* was only recorded during 2017. However, in 2017 *T. derasa* was found in relatively low abundance only at islands that were not resurveyed in

2022, so it is not clear whether this equates to a drop in giant clam diversity or if this species simply has a localized distribution. The corallivorous sea star *A. planci* was found at seven islands in 2022 compared to five in 2017, and increased in density further south in the country. Notably, no *A. planci* were recorded in Vava'u in 2022.

The sea cucumber fishery in Tonga has experienced a number of boom and bust cycles in the past few decades, which have prompted two separate moratoria on their collection and export: the first was put in place between 1998 and 2007, and the second has been in place since 2015. Although stocks had recovered following the first moratorium, intense fishing pressure from 2008-2015 has led to slow recovery following the implementation of the second moratorium, and a 2019 survey found that stocks, particularly of high value species, showed little sign of recovery (Shedrawi et al., 2020). The results from the current study indicate that sea cucumber densities are still low, and potentially lower than to be expected due to disturbance caused by the HTHH eruption. Of the 26 species of sea cucumber known in Tonga (Shedrawi et al., 2020), only nine were recorded during the 2022 survey. Of those nine species, only one (*Holothuria whitmaei*) is considered high value for export (Shedrawi et al. 2020), and this species was only found at three islands. Three species recorded during this survey (*B. argus*, *S. chloronatus*, and *Theleonata ananas*) are considered medium value, while the rest represent economically low value species (Shedrawi et al., 2020).
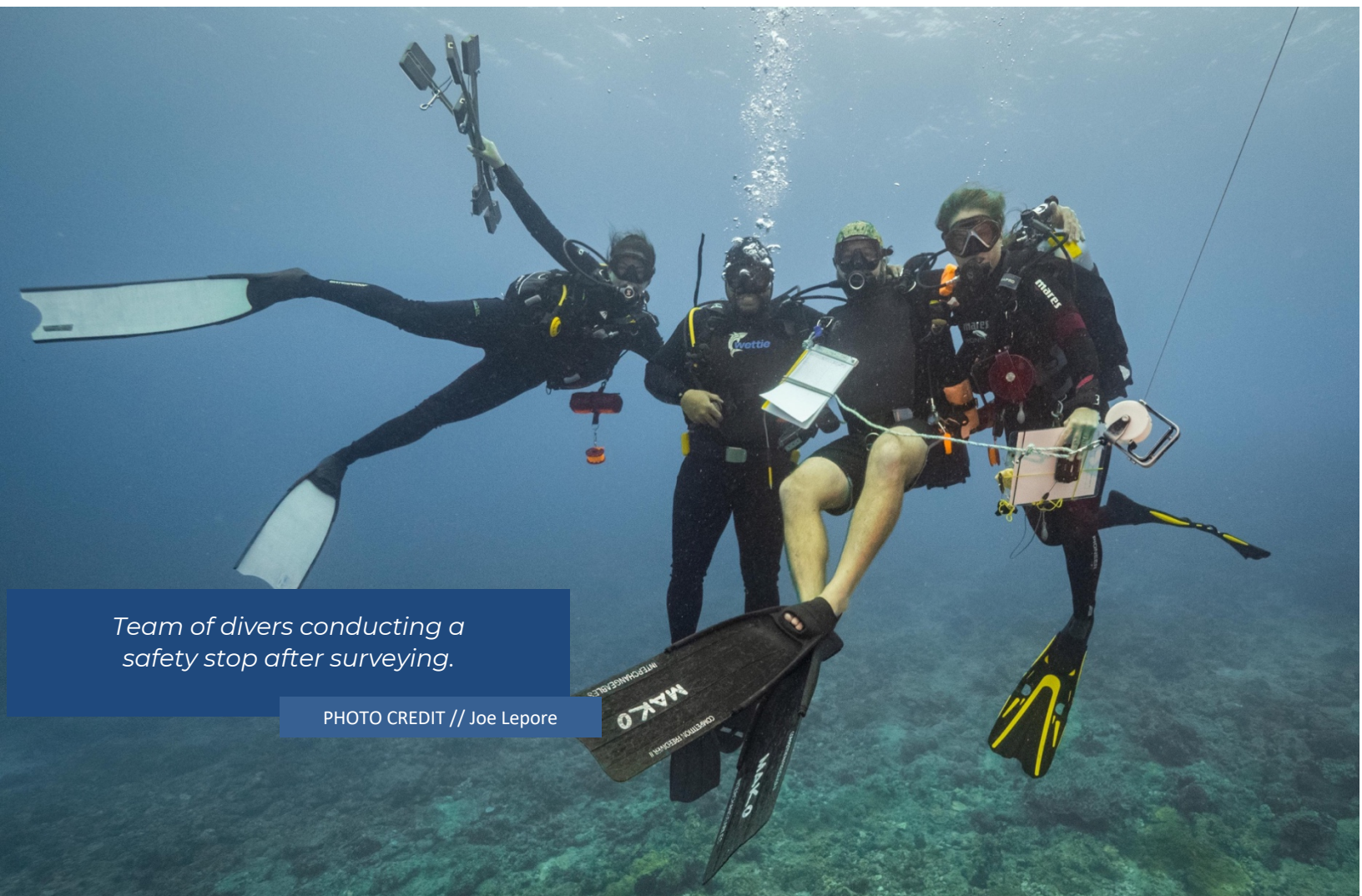


*Team of divers conducting a safety stop after surveying.*

PHOTO CREDIT // Joe Lepore

# RECOMMENDATIONS

**Implement a network of marine protected areas around Tonga under Tonga's Ocean Plan.** Tonga's Ocean Plan has identified ocean management areas including the Government's commitment of 30% no-take marine areas and was approved by Cabinet in 2021. The Plan is currently awaiting passage of the companion law and implementation planning is underway (Department of the Environment 2021).

Results from resurveyed sites in Vava'u indicate that when reefs are protected from human influence, coral cover is likely to increase over time. While of course these protections would not be sufficient to counteract the full force of an unforeseen event such as the HTHH eruption, having a network of MPAs throughout the country would increase the chances that in the event of a similar disturbance, a number of healthy reefs may be spared and could serve as refuge populations to assist in recovery.

Similarly, fish populations would likely benefit from reduced fishing pressure in certain locations. Fonualei, though not an official MPA, is geographically isolated from fishing pressure, and supports a high biomass of top predators and targeted food fish. This suggests that sites closer to the main island districts, which all had low biomass of predatory fish, are likely experiencing some amount of overfishing, and could benefit from a network of MPAs. Protecting key areas from fishing pressure would allow high value species safe spaces to reproduce and grow, and potentially spill over into areas open to fishing, helping to increase catches of targeted food fish. In addition, restoring the ecological balance of the fish populations in targeted areas may have positive effects on reef health, helping to assist in the recovery from the HTHH eruption.

**Strengthen reef monitoring networks within Tonga.** Consistent monitoring of reef health over time is crucial for understanding reef health trajectories and for effective management of reef resources, particularly following disturbances such as the HTHH eruption. While several reef monitoring efforts are currently in place in Tonga (for example, MoF, Department of Environment and VEPA each undertake annual monitoring surveys at localized sites), there remain opportunities to standardize and coordinate these programs to ensure data are comparable and transferable between projects. Establishing standardized methods for gathering data will allow for direct comparisons between different monitoring projects, so that reef health can be easily compared between regions. To support this goal, training sessions and workshops with both in-country and international partners may be beneficial in order to create an appropriate and approachable standardized methodology for capturing relevant reef health metrics. In addition, having the necessary tools to maintain this consistency (i.e., database access, sustainable funding, long-term monitoring plans, data standards, and field equipment) will help ensure the longevity of these programs.

**Extend the moratorium on sea cucumber harvesting and export until stocks recover.** A 2020 report by Shedrawi et al. found that in 2019, sea cucumber stocks had not recovered sufficiently to reopen the fishery, and recommended extending the 2015 moratorium to ensure recovery of stocks prior to resuming collection and exports. While the 2019 survey covered a larger area and included additional sea cucumber habitat such as seagrass meadows, the results from the current study indicate that sea cucumber densities and diversity are still low, and potentially lower than prior to the HTHH eruption. Furthermore, high- and medium-value species were found to be rare, in low abundance, or totally absent from the sites surveyed. Based on these findings the current data support the 2020 recommendation by Shedrawi et al. to maintain the moratorium on sea cucumber harvesting until surveys have shown stocks to have recovered sufficiently to support a fishery. Furthermore, in agreement with previous recommendations, once the fishery has been reopened, size limits should be placed on each species to ensure that enough sexually reproductive individuals remain to support a sustainable fishery.

**Support Special Management Areas, community livelihoods and domestic markets**. SMAs have been noted to have successful indicators for restoring fish stocks within the small FHR, however two years of COVID lockdowns (Marre and Imhof, 2021), low economic activities, and impacts from the HTHH eruption have directly impacted community and coastal livelihoods. Communities are at further risk for reducing SMA management when faced with food security and ongoing climate change impacts that likely increase fishing pressure.

The findings of this report showed that the HTHH eruption and tsunami caused extensive damage to some of the SMA reef communities in Tongatapu and Ha'apai, however critical reef areas such as 'Eueiki may benefit surrounding reefs and SMA communities in the ecological recovery.

Identifying niche and key support programs such as community-based ecotourism, aquaculture, agriculture and establishing stronger domestic markets through the availability of local produce to restaurant programs could be extremely beneficial to strengthen fishery management activities. These concepts are being further explored between MoF, Waitt Institute and VEPA to identify risks and benefits for community development within the SMA program.

# APPENDIX 1: Methodology

## Site Selection

Sites were selected with three goals in mind: assessing damage from the HTTH eruption and tsunami, surveying reefs inside and outside of established SMAs, and resurveying sites visited in 2017 using the same methods (results summarized in Stone et al., 2017). In 2017 permanent photomosaic plots were established using GPS coordinates and stainless steel stakes installed on the benthos, so that the exact same area could be imaged for subsequent surveys. While fish and photoquadrat surveys were undertaken at two depths in 2017 (5m and 10m), only the 10m data from this expedition was used to compare with the 2022 data to minimize variation in community composition between depth strata.

Because Ha'apai saw the greatest impact from the tsunami, the majority of sites were located within this island group. In addition, the offshore volcanic islands of Late and Fonualei were prioritized due to the availability of a vessel suitable for working at these locations. Sites were distributed randomly around surveyed islands with a minimum of 1 km spacing between each site (except for sites MPAL1 and MPAT2 at Lualoli & Taula, which were <1 km apart but were located on reefs adjacent to separate islands).

## Fish

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 25 m transect lines along the reef, identifying and estimating the length of all fishes to the nearest 5 cm size class along each transect. Fish abundance estimates were made by means of two passes for each 25 m transect: on the outward swim, the divers surveyed an 8 m width (200 m$^2$ area) for individuals >20 cm total length (TL), and on the return swim, a 4 m 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 cm, a is the species-specific scaling coefficient, and b is a species-specific shape parameter related to body shape.

## Benthic cover

Benthic cover was estimated using photoquadrats taken of the benthos at each site. Following the completion of each fish belt transect survey, divers collected photoquadrat images along the same transect line, taking photos every 2m, 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 from the expedition were analyzed using the image analysis software CoralNet, 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 D780 SLR cameras set to different focal lengths (24mm and 60mm) in a double lawnmower pattern (Figure 39) approximately 1.5m 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.
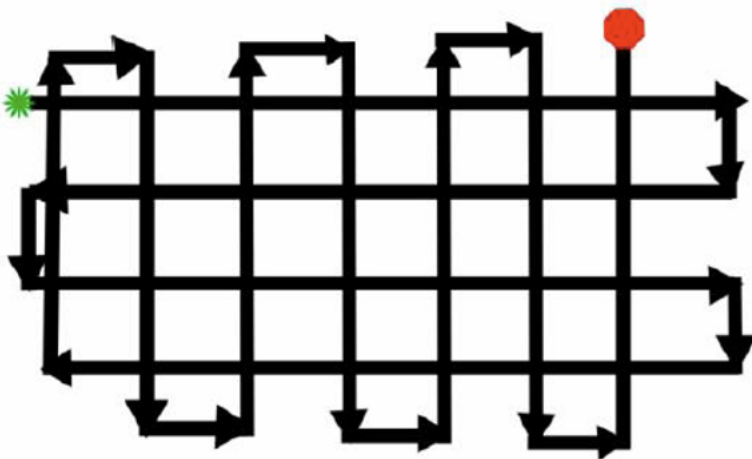


**FIGURE 39**. *Schematic of diver survey pattern to collect images of mosaic plot.*

3D models of each plot are reconstructed using the commercially available Structure from Motion (SfM) based software Agisoft Metashape, to fuse raw imagery from the 24mm camera to create 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 mm-scale resolution (Figure 40).

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.

**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 m$^2$ scale, sites are embedded within the island scale (10s − 100s km$^2$), and all are contained within the regional scale (1 − 10 million km$^2$).
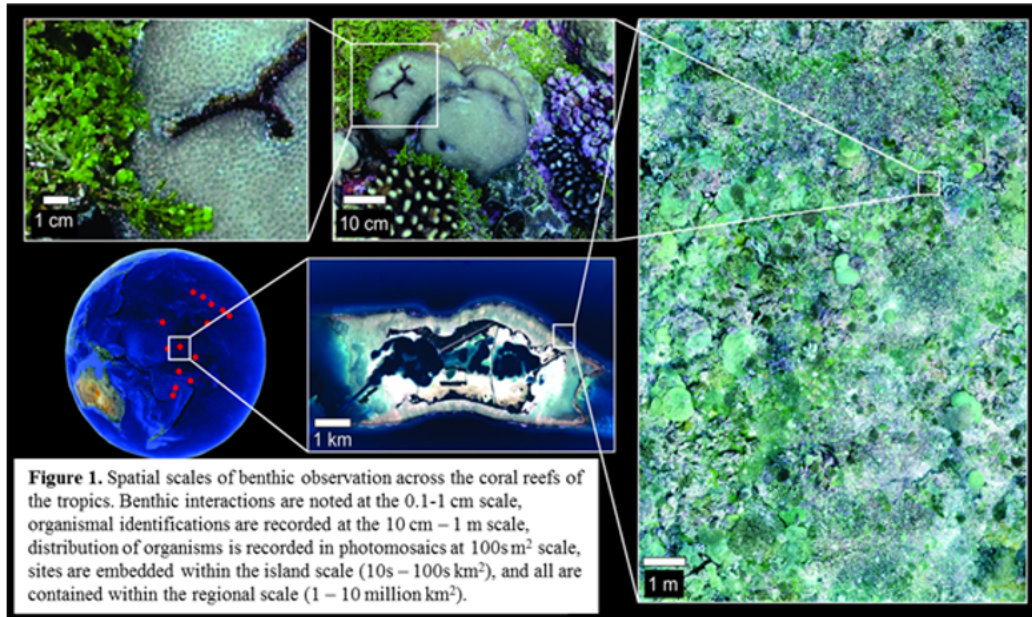
**FIGURE 40.** *Schematic showing the different scales of resolution afforded by the large-area imagery methodology.*

## 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. Point clouds that had noticeable noise (i.e. errant points floating above the reef surface) were cleaned up using *Viscore's* point confidence function prior to collecting rugosity measurements. 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, 10m) 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.

## Macroinvertebrates

Estimates of key macro-invertebrate 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 25-m transects used for fish and photoquadrat surveys. For each survey, a 4-m wide swath was inspected for invertebrates, yielding a 100m$^2$ survey area for each transect. Commercially important invertebrate groups (sea cucumbers and giant clams) that were found in the belt transects were measured to the nearest cm. Results from macroinvertebrate surveys are reported in individuals per site (300 m$^2$) rather than individuals per m$^2$ due to the low densities of most invertebrate species at each site.

# APPENDIX 2: Site metadata

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

| Station ID | Island Name | Island group | Latitude (dd) | Longitude (dd) | Number of observers (fish surveys) |
|---|---|---|---|---|---|
| TON_MAL_01 | Malinoa | Tongatapu & 'Eua | -21.0224 | -175.09981 | 2 |
| TON_MAL_02 | Malinoa | Tongatapu & 'Eua | -21.02567 | -175.13266 | 2 |
| TON_MAL_03 | Malinoa | Tongatapu & 'Eua | -21.03887 | -175.15581 | 2 |
| TON_ATA_01 | Atata | Tongatapu & 'Eua | -21.04945 | -175.26424 | 1 |
| TON_ATA_02 | Atata | Tongatapu & 'Eua | -21.022526 | -175.264 | 1 |
| TON_EUK_01 | 'Eueiki | Tongatapu & 'Eua | -21.11153 | -174.98489 | 2 |
| TON_EUK_02 | 'Eueiki | Tongatapu & 'Eua | -21.11983 | -174.98685 | 2 |
| TON_CRIOBE | Ha'atafu | Tongatapu & 'Eua | -21.067433 | -175.3376 | NA |
| TON_EUA_01 | 'Eua | Tongatapu & 'Eua | -21.28311 | -174.92221 | 1 |
| TON_EUA_02 | 'Eua | Tongatapu & 'Eua | -21.30458 | -174.93707 | 1 |
| TON_EUA_03 | 'Eua | Tongatapu & 'Eua | -21.33335 | -174.95374 | 1 |
| TON_EUA_04 | 'Eua | Tongatapu & 'Eua | -21.34445 | -174.96318 | 2 |
| TON_EUA_05 | 'Eua | Tongatapu & 'Eua | -21.36447 | -174.97324 | 2 |
| TON_EUA_06 | 'Eua | Tongatapu & 'Eua | -21.37908 | -174.97588 | 2 |
| HAP_NOS1 | Nomuka | Ha'apai | -20.26087 | -174.80539 | 2 |
| HAP_NOS2 | Nomuka | Ha'apai | -20.24048 | -174.79353 | 2 |
| HAP_NOS3 | Nomuka | Ha'apai | -20.25376 | -174.77603 | 2 |
| HAP_CS1 | Nomuka | Ha'apai | -20.27515 | -174.80894 | 1 |
| HAP_CS2 | Nomuka | Ha'apai | -20.29883 | -174.80638 | 1 |
| HAP_CS3 | Nomuka | Ha'apai | -20.28087 | -174.79263 | 1 |
| HAP_TON_01 | Tonumea | Ha'apai | -20.47629 | -174.7648 | 2 |
| HAP_TON_02 | Tonumea | Ha'apai | -20.46263 | -174.76555 | 2 |
| HAP_TON_03 | Tonumea | Ha'apai | -20.50452 | -174.7459 | 1 |
| HAP_TON_04 | Tonumea | Ha'apai | -20.49533 | -174.73547 | 1 |
| HAP_FS1 | Fonoifua | Ha'apai | -20.27597 | -174.63783 | 2 |

| HAP_FS2 | Fonoifua | Ha'apai | -20.28309 | -174.62596 | 2 |
| HAP_FS3 | Fonoifua | Ha'apai | -20.29071 | -174.64046 | 2 |
| HAP_MIS1 | Mango | Ha'apai | -20.32263 | -174.71866 | 1 |
| HAP_MIS2 | Mango | Ha'apai | -20.33138 | -174.71883 | 1 |
| HAP_MIS3 | Mango | Ha'apai | -20.3462 | -174.69731 | 1 |
| HAP_HFS2 | Ha'afeva | Ha'apai | -19.96036 | -174.71295 | 2 |
| HAP_HFS3 | Ha'afeva | Ha'apai | -19.93716 | -174.7148 | 2 |
| HAP_HFS4 | Ha'afeva | Ha'apai | -19.93896 | -174.69417 | 2 |
| HAP_KS1 | Kotu | Ha'apai | -19.93537 | -174.80008 | 1 |
| HAP_KS2 | Kotu | Ha'apai | -19.95802 | -174.80106 | 1 |
| HAP_KS3 | Kotu | Ha'apai | -19.95909 | -174.78506 | 1 |
| HAP_UOL1 | 'Uoleva | Ha'apai | -19.86644 | -174.46365 | 2 |
| HAP_UOL2 | 'Uoleva | Ha'apai | -19.84909 | -174.4278 | 2 |
| HAP_UOL3 | 'Uoleva | Ha'apai | -19.83438 | -174.41557 | 2 |
| VAV_LT1 | Late | Vava'u | -18.80224 | -174.67175 | 2 |
| VAV_LT2 | Late | Vava'u | -18.78308 | -174.6519 | 2 |
| VAV_LT3 | Late | Vava'u | -18.7925 | -174.62685 | 1 |
| VAV_LT5 | Late | Vava'u | -18.78596 | -174.66331 | 1 |
| VAV_FON_01 | Fonualei | Vava'u | -18.01051 | -174.31604 | 2 |
| VAV_FON_02 | Fonualei | Vava'u | -18.01482 | -174.32384 | 2 |
| VAV_MPAL1 | Lualoli | Vava'u | -18.83887 | -174.01187 | 2 |
| VAV_MPAT_2 | Taula | Vava'u | -18.84152 | -174.01309 | 2 |
| VAV_FS1 | Fangasito | Vava'u | -18.82049 | -174.07539 | 1 |
| VAV_FS2 | Fangasito | Vava'u | -18.81756 | -174.08588 | 1 |

# 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 as follows: 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 | Mean density (individuals m^-2) | Mean biomass (g m^-2) | Number of sites | DACOR |
|---|---|---|---|---|---|
| Acanthuridae | Acanthurus albipectoralis | 0.001493056 | 0.448064207 | 6 | O |
| | Acanthurus blochii | 0.003784722 | 0.949162732 | 13 | C |
| | Acanthurus lineatus | 0.004513889 | 1.177631186 | 8 | O |
| | Acanthurus mata | 0.000173611 | 0.039984482 | 1 | R |
| | Acanthurus nigricans | 0.009131944 | 1.085822011 | 10 | O |
| | Acanthurus nigricauda | 0.002743056 | 0.777141112 | 17 | C |
| | Acanthurus nigrofuscus | 0.042361111 | 4.226656311 | 39 | D |
| | Acanthurus nigroris | 0.002708333 | 0.284847684 | 6 | O |
| | Acanthurus olivaceus | 0.004791667 | 1.443169592 | 14 | C |
| | Acanthurus pyroferus | 0.002604167 | 0.437756406 | 11 | O |
| | Acanthurus thompsoni | 0.002951389 | 0.403503088 | 7 | O |
| | Acanthurus xanthopterus | 0.000347222 | 0.110598405 | 4 | R |
| | Ctenochaetus binotatus | 0.017673611 | 1.061311158 | 25 | A |
| | Ctenochaetus cyanocheilus | 0.00625 | 0.417296091 | 12 | C |
| | Ctenochaetus flavicauda | 0.000208333 | 0.000861902 | 2 | R |
| | Ctenochaetus hawaiiensis | 0.000486111 | 0.121935847 | 4 | R |
| | Ctenochaetus striatus | 0.090243056 | 12.71374073 | 43 | D |
| | Naso brevirostris | 0.001979167 | 0.573070517 | 8 | O |
| | Naso hexacanthus | 0.002152778 | 0.777078584 | 5 | O |
| | Naso lituratus | 0.005694444 | 1.881566175 | 25 | A |
| | Naso thynnoides | 0.000173611 | 0.088408429 | 2 | R |
| | Naso tonganus | 0.000208333 | 0.529335975 | 4 | R |
| | Naso unicornis | 0.002083333 | 1.625756498 | 8 | O |
| | Naso vlamingii | 0.000381944 | 0.100480167 | 4 | R |
| | Zebrasoma scopas | 0.030972222 | 3.473088395 | 31 | D |
| | Zebrasoma veliferum | 0.001805556 | 0.304286935 | 13 | C |
| Apogonidae | Cheilodipterus artus | 0.000208333 | 0.004413576 | 2 | R |
| | Cheilodipterus isostigma | 0.000138889 | 0.001244625 | 2 | R |
| | Pristiapogon fraenatus | 0.000138889 | 0.005322676 | 1 | R |
| Aulostomidae | Aulostomus chinensis | 0.000520833 | 0.029788432 | 8 | O |

| Family | Species | | | | |
|---|---|---:|---:|---:|---|
| **Balistidae** | Balistapus undulatus | 0.0015625 | 0.502103517 | 15 | C |
| | Balistoides conspicillum | 0.000243056 | 0.212283577 | 4 | R |
| | Balistoides viridescens | 3.47E-05 | 0.049725872 | 1 | R |
| | Pseudobalistes fuscus | 3.47E-05 | 0.05893557 | 1 | R |
| | Rhinecanthus aculeatus | 0.000451389 | 0.052094952 | 3 | R |
| | Sufflamen bursa | 0.001840278 | 0.270287157 | 14 | C |
| | Sufflamen chrysopterum | 0.003854167 | 0.563971932 | 20 | C |
| | Sufflamen fraenatum | 6.94E-05 | 0.010857304 | 1 | R |
| **Blenniidae** | Aspidontus taeniatus | 0.000277778 | 0.003900149 | 2 | R |
| | Cirripectes polyzona | 0.001666667 | 0.003545646 | 6 | O |
| | Cirripectes stigmaticus | 0.002083333 | 0.021874993 | 10 | O |
| | Ecsenius bicolor | 0.000347222 | 0.001480884 | 2 | R |
| | Ecsenius midas | 0.000138889 | 3.96E-05 | 1 | R |
| | Exallias brevis | 0.000902778 | 0.012859601 | 4 | R |
| | Meiacanthus oualanensis | 0.000277778 | 3.28E-05 | 2 | R |
| | Meiacanthus tongaensis | 0.00125 | 0.014349403 | 10 | O |
| | Plagiotremus laudandus | 0.000729167 | 0.040716902 | 5 | O |
| | Plagiotremus tapeinosoma | 0.000138889 | 0.000160997 | 2 | R |
| **Caesionidae** | Caesio caerulaurea | 0.013506944 | 2.161278481 | 6 | O |
| | Caesio teres | 0.000555556 | 0.039726308 | 1 | R |
| | Pterocaesio digramma | 0.004652778 | 0.550543277 | 3 | R |
| | Pterocaesio marri | 0.00125 | 0.180750194 | 2 | R |
| | Pterocaesio tile | 0.004027778 | 1.209566291 | 2 | R |
| | Pterocaesio trilineata | 0.000833333 | 0.110223944 | 2 | R |
| **Carangidae** | Caranx melampygus | 0.000520833 | 0.41479484 | 4 | R |
| | Pseudocaranx dentex | 0.000486111 | 0.920185341 | 1 | R |
| **Carcharhinidae** | Triaenodon obesus | 3.47E-05 | 0.361545634 | 1 | R |
| **Chaetodontidae** | Chaetodon auriga | 0.000833333 | 0.038775589 | 4 | R |
| | Chaetodon citrinellus | 0.003194444 | 0.046154494 | 13 | C |
| | Chaetodon ephippium | 0.001111111 | 0.09291438 | 8 | O |
| | Chaetodon flavirostris | 0.000277778 | 0.012491704 | 2 | R |
| | Chaetodon kleinii | 6.94E-05 | 0.00098672 | 1 | R |
| | Chaetodon lineolatus | 0.000625 | 0.044117883 | 4 | R |
| | Chaetodon lunula | 0.002638889 | 0.041746695 | 4 | R |
| | Chaetodon lunulatus | 0.002638889 | 0.116854881 | 11 | O |
| | Chaetodon melannotus | 0.000277778 | 0.011325161 | 2 | R |
| | Chaetodon mertensii | 0.007986111 | 0.133773074 | 23 | C |
| | Chaetodon ornatissimus | 0.000208333 | 0.012458729 | 2 | R |
| | Chaetodon pelewensis | 0.014027778 | 0.21040151 | 33 | A |

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|---|---|---|---|---|---|
| | Chaetodon plebeius | 0.000902778 | 0.046291005 | 5 | O |
| | Chaetodon rafflesii | 6.94E-05 | 0.004396053 | 1 | R |
| | Chaetodon reticulatus | 0.000694444 | 0.039458457 | 4 | R |
| | Chaetodon trifascialis | 0.000625 | 0.010509683 | 3 | R |
| | Chaetodon ulietensis | 0.0025 | 0.087910625 | 10 | O |
| | Chaetodon unimaculatus | 0.001111111 | 0.091499174 | 6 | O |
| | Chaetodon vagabundus | 0.001875 | 0.191988934 | 6 | O |
| | Forcipiger flavissimus | 0.000555556 | 0.014891634 | 5 | O |
| | Forcipiger longirostris | 0.000555556 | 0.014239283 | 3 | R |
| | Hemitaurichthys polylepis | 0.001180556 | 0.037723854 | 3 | R |
| | Heniochus chrysostomus | 0.001458333 | 0.270964221 | 10 | O |
| | Heniochus monoceros | 0.000173611 | 0.0543522 | 3 | R |
| | Heniochus singularius | 0.000208333 | 0.04981341 | 1 | R |
| | Heniochus varius | 0.000347222 | 0.050625 | 3 | R |
| **Cirrhitidae** | Amblycirrhitus bimacula | 6.94E-05 | 0.000576702 | 1 | R |
| | Cirrhitichthys falco | 0.005486111 | 0.034474063 | 18 | C |
| | Neocirrhites armatus | 6.94E-05 | 3.55E-05 | 1 | R |
| | Paracirrhites arcatus | 0.005069444 | 0.073003607 | 15 | C |
| | Paracirrhites forsteri | 0.001388889 | 0.100342413 | 10 | O |
| **Fistulariidae** | Fistularia commersonii | 6.94E-05 | 0.027571418 | 1 | R |
| **Gobiidae** | Amblyeleotris fasciata | 0.000486111 | 0.000624877 | 4 | R |
| | Amblyeleotris steinitzi | 0.000763889 | 0.002003979 | 6 | O |
| | Amblygobius phalaena | 6.94E-05 | 0.00046233 | 1 | R |
| | Ctenogobiops aurocingulus | 6.94E-05 | 3.27E-05 | 1 | R |
| | Eviota albolineata | 0.000138889 | 5.78E-05 | 1 | R |
| | Eviota infulata | 0.000138889 | 5.78E-05 | 1 | R |
| | Eviota sp | 0.000208333 | 8.67E-05 | 1 | R |
| | Fusigobius neophytus | 6.94E-05 | 1.84E-05 | 1 | R |
| | Fusigobius signipinnis | 0.000416667 | 0.004156238 | 3 | R |
| | Istigobius decoratus | 6.94E-05 | 0.000205669 | 1 | R |
| | Nemateleotris magnifica | 0.00375 | 0.010116167 | 11 | O |
| | Ptereleotris evides | 0.008194444 | 0.070288131 | 13 | C |
| | Ptereleotris magnifica | 0.000555556 | 5.73E-05 | 2 | R |
| | Ptereleotris zebra | 0.000555556 | 0.001247144 | 1 | R |
| | Valenciennea strigata | 0.001736111 | 0.02043489 | 7 | O |
| **Grammistidae** | Grammistes sexlineatus | 0.000138889 | 0.006255347 | 2 | R |
| **Haemulidae** | Plectorhinchus picus | 0.000173611 | 0.075635919 | 4 | R |
| **Holocentridae** | Myripristis adusta | 0.000138889 | 0.01897334 | 1 | R |
| | Myripristis berndti | 0.003645833 | 0.730020403 | 12 | O |

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|---|---|---|---|---|---|
| | Myripristis kuntee | 0.002291667 | 0.304753328 | 4 | R |
| | Myripristis murdjan | 0.001180556 | 0.241387643 | 3 | R |
| | Myripristis violacea | 0.001597222 | 0.38966968 | 3 | R |
| | Neoniphon opercularis | 0.000243056 | 0.01998066 | 4 | R |
| | Neoniphon sammara | 0.001388889 | 0.178627357 | 8 | O |
| | Sargocentron caudimaculatum | 0.001840278 | 0.22355702 | 10 | O |
| | Sargocentron diadema | 0.000416667 | 0.062072002 | 4 | R |
| | Sargocentron ittodai | 6.94E-05 | 0.002998327 | 1 | R |
| | Sargocentron melanospilos | 6.94E-05 | 0.007233279 | 1 | R |
| | Sargocentron spiniferum | 0.003055556 | 1.009827624 | 24 | A |
| | Sargocentron tiere | 0.000520833 | 0.200566046 | 2 | R |
| | Sargocentron violaceum | 0.000138889 | 0.023758205 | 2 | R |
| **Kyphosidae** | Kyphosus cinerascens | 0.000208333 | 0.085611301 | 2 | R |
| | Kyphosus vaigiensis | 0.000416667 | 0.150100324 | 1 | R |
| **Labridae** | Anampses caeruleopunctatus | 0.001284722 | 0.051156545 | 7 | O |
| | Anampses geographicus | 0.000625 | 0.007223953 | 4 | R |
| | Anampses melanurus | 0.0003125 | 0.011583772 | 3 | R |
| | Anampses meleagrides | 0.000277778 | 0.008108094 | 3 | R |
| | Anampses neoguinaicus | 0.003333333 | 0.07622586 | 13 | C |
| | Anampses twistii | 0.002430556 | 0.048910204 | 14 | C |
| | Bodianus axillaris | 0.000902778 | 0.087635734 | 8 | O |
| | Bodianus loxozonus | 0.000347222 | 0.15110107 | 6 | O |
| | Bodianus mesothorax | 0.000277778 | 0.027425455 | 3 | R |
| | Cheilinus chlorourus | 0.004826389 | 0.308004502 | 14 | C |
| | Cheilinus fasciatus | 0.000763889 | 0.222869038 | 4 | R |
| | Cheilinus oxycephalus | 0.000347222 | 0.013726789 | 5 | O |
| | Cheilinus trilobatus | 0.002256944 | 0.525441552 | 24 | A |
| | Cheilinus undulatus | 0.000173611 | 2.152866018 | 4 | R |
| | Cheilio inermis | 6.94E-05 | 0.016585256 | 2 | R |
| | Cirrhilabrus exquisitus | 0.000833333 | 0.000409055 | 1 | R |
| | Cirrhilabrus punctatus | 0.042638889 | 0.307968868 | 24 | A |
| | Cirrhilabrus scottorum | 0.003125 | 0.00429536 | 3 | R |
| | Coris aygula | 0.001111111 | 0.379855822 | 11 | O |
| | Coris batuensis | 0.006493056 | 0.159503602 | 15 | C |
| | Coris dorsomacula | 0.000833333 | 0.024257542 | 3 | R |
| | Coris gaimard | 0.002395833 | 0.269137257 | 18 | C |
| | Epibulus insidiator | 0.000729167 | 0.193854715 | 12 | C |
| | Gomphosus varius | 0.006944444 | 0.134867199 | 24 | A |

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|---|---|---|---|---|
| Halichoeres argus | 0.000277778 | 0.005920293 | 2 | R |
| Halichoeres biocellatus | 0.006041667 | 0.059568972 | 17 | C |
| Halichoeres claudia | 0.000277778 | 0.00162373 | 3 | R |
| Halichoeres hortulanus | 0.007916667 | 0.646201642 | 25 | A |
| Halichoeres margaritaceus | 0.000486111 | 0.001567181 | 3 | R |
| Halichoeres marginatus | 0.002743056 | 0.087494735 | 16 | C |
| Halichoeres melanochir | 0.000138889 | 0.000891441 | 1 | R |
| Halichoeres melanurus | 0.000208333 | 0.006125944 | 1 | R |
| Halichoeres ornatissimus | 0.004722222 | 0.052043673 | 21 | C |
| Halichoeres prosopeion | 0.000694444 | 0.038686029 | 7 | O |
| Halichoeres sp | 6.94E-05 | 0.002365078 | 1 | R |
| Halichoeres trimaculatus | 0.001041667 | 0.035829691 | 3 | R |
| Hemigymnus fasciatus | 0.0015625 | 0.361732311 | 14 | C |
| Hemigymnus melapterus | 0.002291667 | 0.813375886 | 19 | C |
| Hologymnosus annulatus | 0.000243056 | 0.036624852 | 4 | R |
| Hologymnosus doliatus | 0.001319444 | 0.28265788 | 14 | C |
| Labrichthys unilineatus | 0.000625 | 0.01058125 | 4 | R |
| Labroides bicolor | 0.000763889 | 0.00273211 | 9 | O |
| Labroides dimidiatus | 0.006319444 | 0.020922402 | 23 | C |
| Labropsis australis | 0.001666667 | 0.012794821 | 10 | O |
| Labropsis xanthonota | 0.000138889 | 0.008338774 | 1 | R |
| Macropharyngodon kuiteri | 0.000138889 | 0.001675718 | 1 | R |
| Macropharyngodon meleagris | 0.009930556 | 0.090356041 | 23 | C |
| Macropharyngodon negrosensis | 0.00125 | 0.013808773 | 10 | O |
| Novaculichthys taeniourus | 0.001006944 | 0.047413618 | 6 | O |
| Oxycheilinus digramma | 0.004583333 | 0.304854444 | 17 | C |
| Oxycheilinus unifasciatus | 0.000868056 | 0.009087891 | 2 | R |
| Pseudocheilinus evanidus | 0.006944444 | 0.042001801 | 17 | C |
| Pseudocheilinus hexataenia | 0.012569444 | 0.059072771 | 30 | A |
| Pseudocheilinus octotaenia | 0.000208333 | 0.001509387 | 3 | R |
| Pseudojuloides cerasinus | 6.94E-05 | 0.002577112 | 1 | R |
| Pteragogus cryptus | 0.000208333 | 0.006614833 | 3 | R |

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|---|---|---|---|---|---|
| | Stethojulis bandanensis | 0.006666667 | 0.117941317 | 21 | C |
| | Thalassoma amblycephalum | 0.086041667 | 0.185536571 | 12 | C |
| | Thalassoma hardwicke | 0.001180556 | 0.053817009 | 9 | O |
| | Thalassoma lunare | 0.002777778 | 0.056969098 | 13 | C |
| | Thalassoma lutescens | 0.014444444 | 0.6156521 | 38 | D |
| | Thalassoma nigrofasciatum | 0.001215278 | 0.105388889 | 7 | O |
| | Thalassoma quinquevittatum | 0.019027778 | 0.073101775 | 8 | O |
| | Thalassoma trilobatum | 0.001701389 | 0.010884351 | 1 | R |
| **Lethrinidae** | Gnathodentex aureolineatus | 0.000972222 | 0.088754461 | 1 | R |
| | Lethrinus harak | 0.000173611 | 0.122620409 | 3 | R |
| | Lethrinus obsoletus | 0.000625 | 0.204427522 | 7 | O |
| | Lethrinus xanthochilus | 3.47E-05 | 0.094703434 | 1 | R |
| | Monotaxis grandoculis | 0.002118056 | 1.233998332 | 15 | C |
| | Monotaxis heterodon | 0.000416667 | 0.417170632 | 2 | R |
| **Liopropomatidae** | Belonoperca chabanaudi | 6.94E-05 | 0.002213628 | 1 | R |
| **Lutjanidae** | Aphareus furca | 0.000486111 | 0.091418194 | 4 | R |
| | Aprion virescens | 0.000138889 | 0.196979602 | 4 | R |
| | Lutjanus bohar | 0.002083333 | 1.709081113 | 17 | C |
| | Lutjanus fulvus | 0.001180556 | 0.249058132 | 8 | O |
| | Lutjanus gibbus | 0.008472222 | 2.403204981 | 13 | C |
| | Lutjanus kasmira | 0.011458333 | 1.578012223 | 3 | R |
| | Lutjanus monostigma | 0.000138889 | 0.081787935 | 2 | R |
| | Macolor macularis | 0.000277778 | 0.169232622 | 5 | O |
| | Macolor niger | 0.000416667 | 0.08336191 | 4 | R |
| **Monacanthidae** | Amanses scopas | 0.000208333 | 0.129922883 | 3 | R |
| | Cantherhines dumerilii | 0.000590278 | 0.176062081 | 6 | O |
| | Cantherhines fronticinctus | 0.000104167 | 0.012048391 | 2 | R |
| | Cantherhines pardalis | 0.000277778 | 0.015894245 | 3 | R |
| | Melichthys vidua | 0.001111111 | 0.415655926 | 10 | O |
| | Odonus niger | 0.003055556 | 0.212058 | 1 | R |
| | Oxymonacanthus longirostris | 0.000138889 | 0.000938667 | 1 | R |
| | Paraluteres prionurus | 6.94E-05 | 0.000429156 | 1 | R |
| | Pervagor alternans | 0.000277778 | 0.005040935 | 4 | R |
| | Pervagor janthinosoma | 0.000138889 | 0.000446659 | 2 | R |
| | Pervagor melanocephalus | 0.000208333 | 0.007436258 | 2 | R |

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|---|---|---|---|---|---|
| | Mulloidichthys flavolineatus | 0.002361111 | 0.456375157 | 3 | R |
| | Mulloidichthys vanicolensis | 0.000729167 | 0.113206597 | 4 | R |
| | Parupeneus barberinoides | 0.0003125 | 0.011881193 | 3 | R |
| **Mullidae** | Parupeneus barberinus | 0.000972222 | 0.355773997 | 10 | O |
| | Parupeneus ciliatus | 0.000347222 | 0.091125081 | 5 | O |
| | Parupeneus crassilabris | 0.001770833 | 0.679720676 | 14 | C |
| | Parupeneus cyclostomus | 0.001423611 | 0.332124833 | 11 | O |
| | Parupeneus indicus | 0.000590278 | 0.223528855 | 3 | R |
| | Parupeneus multifasciatus | 0.008020833 | 0.652112817 | 32 | A |
| | Parupeneus pleurostigma | 0.0003125 | 0.016847273 | 2 | R |
| **Muraeninae** | Gymnothorax flavimarginatus | 6.94E-05 | 0.112024966 | 2 | R |
| | Gymnothorax meleagris | 0.000104167 | 0.007874866 | 2 | R |
| **Nemipteridae** | Scolopsis bilineata | 0.0015625 | 0.20239091 | 12 | C |
| **Ostraciidae** | Ostracion meleagris | 0.000277778 | 0.048676411 | 3 | R |
| **Pempheridae** | Pempheris oualensis | 0.001979167 | 0.096128864 | 5 | O |
| **Pinguipedidae** | Parapercis clathrata | 0.002152778 | 0.065116721 | 12 | C |
| | Parapercis hexophtalma | 0.001076389 | 0.044268058 | 6 | O |
| | Centropyge bicolor | 0.001944444 | 0.0477915 | 7 | O |
| | Centropyge bispinosa | 0.024236111 | 0.135716561 | 31 | A |
| **Pomacanthidae** | Centropyge flavissima | 0.007569444 | 0.222107726 | 26 | A |
| | Centropyge woodheadi | 0.000694444 | 0.019572743 | 1 | R |
| | Pomacanthus imperator | 0.000208333 | 0.111494417 | 2 | R |
| | Pygoplites diacanthus | 0.000381944 | 0.141485458 | 6 | O |
| | Abudefduf sexfasciatus | 0.003402778 | 0.183877008 | 6 | O |
| | Amblyglyphidodon melanopterus | 0.002291667 | 0.036215814 | 5 | O |
| | Amphiprion chrysopterus | 0.000416667 | 0.003324931 | 3 | R |
| | Amphiprion clarkii | 0.000972222 | 0.005561416 | 3 | R |
| | Amphiprion melanopus | 0.000902778 | 0.043165276 | 5 | O |
| **Pomacentridae** | Amphiprion perideraion | 0.000555556 | 0.007026862 | 3 | R |
| | Chromis acares | 0.003819444 | 0.013772589 | 5 | O |
| | Chromis agilis | 0.004305556 | 0.066956917 | 4 | R |
| | Chromis amboinensis | 0.000347222 | 0.00284875 | 3 | R |
| | Chromis atripectoralis | 0.000625 | 0.003427574 | 3 | R |
| | Chromis atripes | 0.008055556 | 0.056919309 | 11 | O |
| | Chromis bami | 0.000138889 | 0.001054417 | 1 | R |

| | | | | |
|---|---|---|---|---|
| Chromis chrysura | 0.071805556 | 0.973765061 | 21 | C |
| Chromis fumea | 0.000138889 | 4.97E-05 | 1 | R |
| Chromis iomelas | 0.025 | 0.155751993 | 17 | C |
| Chromis lepidolepis | 0.000833333 | 0.003229594 | 3 | R |
| Chromis leucura | 0.000138889 | 7.71E-05 | 1 | R |
| Chromis margaritifer | 0.067847222 | 0.322874375 | 31 | A |
| Chromis retrofasciata | 0.000138889 | 0.002381124 | 1 | R |
| Chromis ternatensis | 0.002708333 | 0.072564025 | 7 | O |
| Chromis vanderbilti | 0.049166667 | 0.173710444 | 10 | O |
| Chromis weberi | 0.005625 | 0.054074937 | 13 | C |
| Chromis xanthura | 0.014930556 | 0.271603548 | 11 | O |
| Chrysiptera biocellata | 0.000972222 | 0.000627375 | 1 | R |
| Chrysiptera leucopoma | 0.003958333 | 0.043065411 | 3 | R |
| Chrysiptera rollandi | 0.001180556 | 0.000640507 | 7 | O |
| Chrysiptera species | 0.006111111 | 0.007381138 | 15 | C |
| Chrysiptera taupou | 0.030208333 | 0.044170852 | 32 | A |
| Dascyllus aruanus | 0.007291667 | 0.007145762 | 1 | R |
| Dascyllus reticulatus | 0.017291667 | 0.09709487 | 6 | O |
| Dascyllus trimaculatus | 0.011388889 | 0.477842692 | 19 | C |
| Neoglyphidodon carlsoni | 0.000277778 | 0.014645009 | 2 | R |
| Plectroglyphidodon dickii | 6.94E-05 | 0.001018664 | 1 | R |
| Plectroglyphidodon johnstonianus | 0.005763889 | 0.061945416 | 16 | C |
| Plectroglyphidodon lacrymatus | 0.080694444 | 1.256537351 | 30 | A |
| Pomacentrus adelus | 0.002847222 | 0.020415357 | 6 | O |
| Pomacentrus bankanensis | 0.005 | 0.011761606 | 3 | R |
| Pomacentrus callainus | 0.078263889 | 0.698658033 | 27 | A |
| Pomacentrus chrysurus | 0.000416667 | 0.00571401 | 2 | R |
| Pomacentrus coelestis | 0.032222222 | 0.24456165 | 13 | C |
| Pomacentrus flavioculus | 0.04125 | 0.44859121 | 30 | A |
| Pomacentrus maafu | 0.003402778 | 0.081876726 | 6 | O |
| Pomacentrus moluccensis | 0.002777778 | 0.029076968 | 1 | R |
| Pomacentrus spilotoceps | 0.037291667 | 0.349918171 | 25 | A |
| Pomacentrus vaiuli | 0.279861111 | 0.946536957 | 46 | D |
| Pomachromis richardsoni | 0.046875 | 0.156466443 | 10 | O |
| Pseudochromis sp | 0.000138889 | 6.23E-05 | 2 | R |

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|---|---|---|---|---|---|
| | Stegastes fasciolatus | 0.013541667 | 0.303438676 | 13 | C |
| | Stegastes nigricans | 0.009791667 | 0.286407881 | 9 | O |
| **Priacanthidae** | Priacanthus hamrur | 0.000625 | 0.147558376 | 7 | O |
| **Scaridae** | Calotomus carolinus | 0.0003125 | 0.101928731 | 6 | O |
| | Cetoscarus ocellatus | 0.000625 | 0.426609885 | 7 | O |
| | Chlorurus bleekeri | 0.002638889 | 1.197915924 | 13 | C |
| | Chlorurus frontalis | 0.000451389 | 0.073985604 | 4 | R |
| | Chlorurus microrhinos | 0.001041667 | 0.449048712 | 10 | O |
| | Chlorurus spilurus | 0.018680556 | 4.854575663 | 35 | A |
| | Hipposcarus longiceps | 0.002118056 | 0.648140958 | 10 | O |
| | Scarus altipinnis | 0.001388889 | 0.72512459 | 10 | O |
| | Scarus chameleon | 0.001805556 | 0.583962685 | 18 | C |
| | Scarus flavipectoralis | 0.000972222 | 0.303731821 | 2 | R |
| | Scarus forsteni | 0.001770833 | 0.942853953 | 17 | C |
| | Scarus frenatus | 0.002777778 | 1.137589568 | 15 | C |
| | Scarus ghobban | 0.001041667 | 0.553747092 | 8 | O |
| | Scarus globiceps | 0.002048611 | 0.786625194 | 15 | C |
| | Scarus longipinnis | 0.001180556 | 0.296710911 | 6 | O |
| | Scarus niger | 0.007673611 | 3.332275913 | 31 | A |
| | Scarus oviceps | 0.002083333 | 0.976739596 | 18 | C |
| | Scarus psittacus | 0.008229167 | 2.874040447 | 20 | C |
| | Scarus rivulatus | 6.94E-05 | 0.060710617 | 1 | R |
| | Scarus rubroviolaceus | 0.000520833 | 0.971441327 | 6 | O |
| | Scarus schlegeli | 0.005902778 | 2.050709656 | 27 | A |
| | Scarus sp | 0.001944444 | 0.118632284 | 10 | O |
| | Scarus spinus | 0.000729167 | 0.208477981 | 9 | O |
| **Scombridae** | Gymnosarda unicolor | 0.000104167 | 0.342675454 | 3 | R |
| **Scorpaenidae** | Caracanthus unipinna | 6.94E-05 | 6.32E-05 | 1 | R |
| | Pterois radiata | 3.47E-05 | 0.005842968 | 1 | R |
| **Serranidae** | Anyperodon leucogrammicus | 6.94E-05 | 0.023738485 | 2 | R |
| | Cephalopholis argus | 0.000902778 | 0.529112034 | 12 | C |
| | Cephalopholis miniata | 0.000138889 | 0.012007948 | 1 | R |
| | Cephalopholis spiloparaea | 0.000138889 | 0.009954283 | 2 | R |
| | Cephalopholis urodeta | 0.007604167 | 0.893128786 | 29 | A |
| | Epinephelus fasciatus | 0.000625 | 0.069105415 | 2 | R |
| | Epinephelus hexagonatus | 3.47E-05 | 0.006266445 | 1 | R |
| | Epinephelus macrospilos | 6.94E-05 | 0.005952852 | 1 | R |
| | Epinephelus malabaricus | 6.94E-05 | 0.113650443 | 1 | R |

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|---|---|---|---|---|---|
| | Epinephelus melanostigma | 3.47E-05 | 0.02879388 | 1 | R |
| | Epinephelus merra | 0.001909722 | 0.214613677 | 15 | C |
| | Epinephelus polyphekadion | 6.94E-05 | 0.089770428 | 1 | R |
| | Plectropomus laevis | 3.47E-05 | 0.124497944 | 1 | R |
| | Plectropomus leopardus | 0.000833333 | 0.439466439 | 6 | O |
| | Pseudanthias cooperi | 6.94E-05 | 0.000475946 | 1 | R |
| | Pseudanthias squamipinnis | 0.003680556 | 0.057639889 | 2 | R |
| | Variola louti | 0.001666667 | 0.642730618 | 19 | C |
| **Siganidae** | Siganus argenteus | 0.008402778 | 0.702221446 | 11 | O |
| | Siganus niger | 0.000277778 | 0.130912969 | 5 | O |
| | Siganus punctatus | 0.000208333 | 0.017486066 | 1 | R |
| **Synodontidae** | Saurida gracilis | 6.94E-05 | 1.21E-05 | 1 | R |
| | Synodus binotatus | 0.000486111 | 0.016563726 | 4 | R |
| **Tetraodontidae** | Arothron hispidus | 6.94E-05 | 0.144330457 | 1 | R |
| | Arothron nigropunctatus | 0.000729167 | 0.272841188 | 10 | O |
| | Canthigaster amboinensis | 6.94E-05 | 0.001939259 | 1 | R |
| | Canthigaster axiologus | 0.000138889 | 0.002318075 | 1 | R |
| | Canthigaster janthinoptera | 6.94E-05 | 0.001041174 | 1 | R |
| | Canthigaster solandri | 0.000208333 | 0.002088642 | 3 | R |
| | Canthigaster valentini | 0.000555556 | 0.00926838 | 5 | O |
| **Zanclidae** | Zanclus cornutus | 0.004826389 | 0.880514562 | 18 | C |
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# APPENDIX 4: Coral diversity

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

| Genus | Photoquadrats | Recruits |
|---|---|---|
| *Acanthastrea* | X | X |
| *Acropora* | X | X |
| *Astrea* | X | X |
| *Astreopora* | X | X |
| *Coscinaraea* | X | X |
| *Cyphastrea* | X | X |
| *Diploastrea* | X | |
| *Dipsastrea* | X | X |
| *Echinomorpha* | X | |
| *Echinophyllia* | X | |
| *Echinopora* | X | X |
| *Favites* | X | X |
| *Fungia* | X | X |
| *Galaxea* | X | X |
| *Gardineroseris* | X | X |
| *Goniastrea* | X | X |
| *Goniopora* | X | |
| *Halomitra* | X | X |
| *Herpolithia* | X | |
| *Hydnophora* | X | X |

| Genus | Photoquadrats | Recruits |
|---|---|---|
| *Isopora* | X | X |
| *Leptastrea* | X | X |
| *Leptoria* | X | X |
| *Leptoseris* | X | X |
| *Lobophyllia* | X | X |
| *Merulina* | X | X |
| *Montipora* | X | X |
| *Mycedium* | X | |
| *Pachyseris* | X | |
| *Pavona* | X | X |
| *Platygyra* | X | X |
| *Pocillopora* | X | X |
| *Porites* | X | X |
| *Psammocora* | X | X |
| *Sandolithia* | X | |
| *Stylophora* | X | X |
| *Symphyllia* | X | X |
| *Tubastrea* | | X |
| *Turbinaria* | X | X |
| | | |

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