SAMOA COASTAL MARINE EXPEDITION REPORT

2022









Photo Credit: Andy Estep

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01

Executive SUMMARY

In September 2022, an expedition was carried out along the northwestern and southwestern forereefs of the main islands of Samoa, with the goal of providing a systematic, national snapshot of the state of coral reefs across the country. In total, 36 sites were surveyed, returning standardized data on benthic composition, reef fish communities, macroinvertebrate communities, coral recruitment, reef rugosity (structural complexity), and water quality. Of these sites, 13 were resurveys of sites previously surveyed in 2017 and 2019 using identical methods. The data collected during this expedition serves to support the research and marine spatial planning goals of the Samoa Ocean Strategy (Government of Samoa 2020).

Overall, mean coral cover was 20.9%, and coral cover was higher on Upolu than Savai'i. Time series data from resurveyed sites show a consistent increase in coral cover on Upolu since 2017, likely indicating recovery from a 2015 coral bleaching event. However, despite higher coral cover on Upolu, reefs on this island were dominated by a few coral genera, while reefs on Savai'i had higher coral diversity. Rugosity, or structural complexity, of reefs on Upolu was higher than on Savai'i, potentially providing more habitat for mobile organisms such as fish and invertebrates. Finally, the mean density of juvenile corals was similar on both islands, with an overall mean of 5.7 individuals m⁻².

In total, 244 fish species were recorded during the survey. Reef fish density was similar across both islands, but biomass was higher on Upolu, indicating the presence of larger fish on this island. While fish density and biomass declined on Savai'i between 2017 and 2022 at resurveyed sites, these values stayed somewhat consistent on Upolu, with a peak in 2019. Macroinvertebrates, particularly edible and commercially viable taxa such as giant clams, sea cucumbers, and trochus, were found only in low densities. In particular, only two individuals of one sea cucumber species were recorded in surveys, and were only present on Savai'i. The results of the fish and invertebrate surveys indicate that heavy fishing and harvesting pressure may be leading to overexploitation of certain reef resources in some cases.

Finally, water quality surveys showed mixed results. Although there was some indication that there may be sources of land-based pollution on some of the surveyed reefs, the signal was likely diluted by the time it reached the forereef, so no strong conclusions can be drawn. δ^{15} N, which is higher when human sewage is present, varied significantly with latitude on Upolu, suggesting that pollution may be more prevalent on the north shore, near the capital city of Apia. However, additional water quality surveys within the lagoons are needed to draw any concrete conclusions regarding sources of land-based pollution on Samoa's reefs.

INTRODUCTION

Samoa is an independent nation in the Southwest Pacific, comprised of two main islands, Savai'i and Upolu, and seven small islets. Over 98% of Samoa's territory is ocean (Government of Samoa 2020), with an approximate land area of 2,935 km² and an approximate ocean area of 120,000 km² (Pinca et al. 2010). Despite the high proportion of ocean to land, Samoa has some of the smallest coral reef area in the West Pacific, with the nation's mostly fringing reefs covering an area of approximately 490 km² (Samuelu & Sapatu 2007). Reefs are disproportionately distributed across the two main islands, with only ~57 km² of reef on Savai'i (Zann 1999, Government of Samoa 2013). While reefs are limited, they are separated from land by large shallow lagoons up to 2 km wide (Green 1996); however, lagoons are wider and clearer off of the south coasts of both islands (Skelton et al. 2000).



oto Credit: Andy Estep



Due in part to the higher proportion of reefs on Upolu, the majority of the country's population resides on this island (Mollica 1999), with fewer inhabitants on Savai'i, and small settlements on the islets of Manono and Apolima. The steep volcanic terrain of the main islands causes most of the population to live near the sea, with >70% of the population living within 1 km of the coast (Lovell et al. 2004; Chrichton & Esteban 2018; Government of Samoa 2020) and 97% of the population living within 5 km of the coast (Shedrawi et al. 2019). Fishing is an important part of daily life for many villagers, and reef fish and invertebrates provide a large proportion of protein for the people of Samoa. However, the low ratio of reef area per capita leads to high pressure on reef resources to sustain the nutritional needs of the country (Holbrook et al. 2022). Paired with an increase in population of 5-6 fold in the past 150 years (Zann 1999), this reliance on reef fish and invertebrates has put a strain on the coastal marine resources of Samoa.

Samoans consume between 57-87 kg of seafood per person per year (Passfield et al. 2001; Lovell et al. 2004; Samuelu & Sapatu 2007; Pinca et al. 2010; South et al. 2010; Government of Samoa 2020) - one of the highest rates of fish consumption in the region (Critchton & Esteban 2018). Of this, 44% is derived from subsistence fishing, while 56% is purchased (Government of Samoa 2020). Historically, most Samoans relied on subsistence fishing, with fishers either keeping the majority of their catch to eat or sharing with the rest of the village (Mollica 1999). However, with the advent of cash economies, there has been a shift from subsistence to artisanal fishing as a source of income (Horsman & Mulipola 1995; Mulipola et al. 1995; Mollica 1999; Samuelu & Sapatu 2007; South et al. 2012; Crichton & Esteban 2018). While previously subsistence fishers had only harvested enough food to feed themselves and their families, the shift towards artisanal fishing has led some fishers to try to catch as much as possible in order to maximize their income (Mulipola et al. 1995; Mollica 1999; Skelton et al. 2000; Olson 2001; Samuelu & Sapatu 2007). This has resulted in the adoption of fishing practices that maximize catch, which in some cases include destructive methods such as dynamite or poison fishing (Green 1996; Olson 2001; Samuelu & Sapatu 2007; Zeigler et al. 2018). While these methods have been banned under the Fisheries Regulations since 2005, it is believed that some fishers continue to employ them to increase their catch (Samuelu & Sapatu 2007).



In addition to reef fish, reef invertebrates constitute a sizable proportion of the Samoan diet. Studies estimate that invertebrates make up between 11-22% of the seafood consumed in Samoa (Passfield et al. 2001; Pinca et al. 2010). They are also important for livelihoods; although women make up only 18% of the fishers and are responsible for only 10% of the total fishing effort, it is estimated that they harvest approximately 23% of the total weight of seafood consumed, as they tend to harvest most of the invertebrates for each village (Passfield et al. 2001). However, this reliance on reef invertebrates, along with the sedentary and easy-to-harvest nature of most edible species, has led to documented overfishing of several key species. For example, giant clam harvests declined 100-fold, from 10 tons to 0.1 tons, from 1986-1989 while the fishery was open (Zann 1999), leading to the extinction or functional extinction of several giant clam species on Samoan reefs (Skelton et al. 2000, Pinca et al. 2010, Government of Samoa 2013). Similarly, although the export of sea cucumbers has been banned since 1997 (Samuelu & Sapatu 2007), they remain an important part of the subsistence fishery, and densities across the country have been found to be below regional reference densities for healthy populations (Samuelu & Sapatu 2007; Government of Samoa 2013; Shedrawi et al. 2019). In an effort to supplement invertebrate fisheries and diversify livelihoods, several invertebrate species have been introduced or reintroduced to Samoan reefs. Giant clams have been reintroduced several times with broodstock from American Samoa, Fiji and Tonga (Skelton et al. 2000: Crichton & Esteban 2018). While densities have not recovered enough to support an export fishery, these reintroductions have been considered successful in some cases due to the cultural and societal benefits associated with giant clam mariculture (Quimby et al. 2023). Similarly, the non-native gastropod snail Rochia nilotica, commonly known as trochus, was introduced to Samoa between 2003-2006 with the goal of creating a new fishery (Purcell et al. 2019; Senior et al. 2020). Recent surveys have identified established populations of trochus on both Upolu and Savai'i, and have found no negative impacts on native gastropod species (Senior et al. 2020; Purcell & Ceccarelli 2021). Currently, over 1000 fishers harvest trochus, and the benefits of the fishery have been found to be inclusive and gender equitable (Purcell et al. 2019). However, it should be noted that trochus densities were found to be highly variable, with only a few sites supporting densities suitable for

harvesting (Purcell et al. 2019), and sites known to have trochus populations were quickly overfished in some cases (Pinca et al. 2010).

In Samoa, as in many other Pacific Island nations, coastal villages have historically retained customary ownership of their adjacent reef area, with the responsibility of reef management falling to each village's fono ("village council"; Fairbairn 1991; Olson 2001). However, with the colonization of Samoa and other Pacific islands came a shift towards centralized, national governments, which disrupted traditional management frameworks. In Samoa, lack of resources within the central government complicates the enforcement of national laws for fisheries management (Mollica 1999; Crichton & Esteban 2018). So in 1995, the Community-Based Fisheries Management Program (CBFMP; also called the Village Fisheries Management Program) was launched in collaboration with AusAID, with the goal of restoring traditional village management rights within the framework of the national government (Fa'asili & Taua 2001; Quimby et al. 2023).

Photo Credit: Joe Lepore

The CBFMP is one of the oldest and most well-established co-management programs in the Pacific, with 89 participating villages across Samoa (Samuelu & Sapatu 2007). Under the structure of the CBFMP, communities develop coastal management plans for their traditional reef tenure areas with the support of technical and legal expertise from the Fisheries Division (Mollica 1999; Fa'asili & Taua 2001; Quimby et al. 2023). In addition, under the program, villages have the power to create and implement legally recognized by-laws to govern the use of marine resources within their tenure area (Fa'asili & Taua 2001; South et al. 2012; Quimby et al. 2023). By-laws are created in consultation between the Fisheries Department and the village leaders (matai) and are submitted to the office of the Attorney General, where they are put into legal context and published, making them legally binding (South et al. 2012). Some examples of by-laws implemented by participating villages include: prohibiting dynamite or poison fishing; size limits on certain species; controls on the use of overly effective fishing techniques such as the use of torches at night; limits on the number and size of fish fences; and seasonal closures of certain reef areas (Mollica 1999; Zann 1999; Kendall & Poti 2011). Punishments for violating the village by-laws are at the discretion of the village council as well, and can range from warnings, fines of pigs or money, or banishment from the village (Mollica 1999; Zann 1999; South et al. 2012).

In addition, villages participating in the CBFMP have the option to establish fisheries reserves and to request support for mariculture and other alternative livelihood projects. The boundaries and rules governing established fish reserves are determined by the village council; some ban all or some fishing within the reserve, while other reserves can be fished only on special occasions (Skelton et al. 2000). Communities can also request broodstock for invertebrates such as giant clams to reintroduce to their fish reserves at no cost to the village (Mollica 1999; Zann 1999; Fa'asili & Taua 2001; Quimby et al. 2023). Giant clam broodstock is the most common support requested by villages participating in the CBFMP (Fa'asili & Taua 2001), and while clams have not become a profitable export, these mariculture programs have been found to provide numerous social and cultural benefits, such as supporting women's livelihoods (Quimby et al. 2023). To date, 73 villages have active fish or giant clam reserves (Quimby et al. 2023). While data on the ecological impacts of the CBFMP are sparse, participating villages have reported increased catch per unit effort (CPUE), higher fishing incomes, and higher frequencies of fish consumption (Passfield et al 2001; Samuelu & Sapatu 2007).

Despite innovative efforts to manage fisheries, Samoan reefs have been subject to a number of local and global stressors in recent decades. In the early 1990s, Samoa was hit by two consecutive cyclones, Ofa and Val, which caused extensive damage to its reefs (Rearic 1990; Zann 1991; Green 1996, Zann 1999; Skelton et al. 2000, Government of Samoa 2013; Zeigler et al. 2018). Cyclone Ofa in particular dramatically altered reefs, reducing coral cover to <1% on the northern reefs of Upolu (Zann 1991) and creating exposed coral rubble banks up to 2-3 m high and 2 km long (Rearic 1990; Zann 1999; Skelton et al. 2000). However, recovery from these disturbances was swift, with some reefs showing high coral cover and diversity within five years (Skelton et al. 2000). Palolo Deep, off of the capital city of Apia on the north coast of Upolu, showed a dramatic increase in coral cover from 0% in 1994 to 91% in 1999 (Sulu et al. 2002). However, in 2004, another cyclone, Heta, hit Samoa, this time damaging up to 13% of live coral (Lovell et al. 2004, South et al. 2012). Again, reefs rebounded, with monitored sites showing evidence of coral cover recovery between 2005-2007 (Samuelu & Sapatu 2007).





Disturbances, however, have continued to affect Samoan reefs in recent years. In 2009, a tsunami triggered by an 8.3 magnitude earthquake hit the south coast of the country, causing particular damage to the reefs on the south coast of Upolu (South et al. 2012). While reef damage was variable (McAdoo et al. 2011; South et al. 2012), communities affected by the tsunami suffered the loss of important food and income sources as fisheries, agriculture, and tourism (South et al. 2012; Quimby et al 2023). More recently, in 2012, Cyclone Evan passed through Samoa, causing flooding and sediment runoff onto coastal reefs (Crichton & Esteban 2018; Zeigler et al. 2018). Additionally, periodic outbreaks of the corallivorous crown of thorns starfish (COTs; Acanthaster planci) have been documented in Samoa since the 1960s, with known outbreaks as recently as 2015 (Zann 1991; Green 1996; Wabnitz & Nahacky 2015; Berthe et al. 2016; Zeigler et al. 2018).

In addition to natural disasters such as cyclones and tsunamis, coral bleaching has been identified as a major threat to Samoan coral reefs (Kendall & Poti 2011). While Samoa, along with other islands in the Central South Pacific, escaped the brunt of the 1998 global bleaching event (Skelton et al. 2000; Sulu et al. 2002), there have been several documented cases of bleaching in recent years. Extensive bleaching was noted in 2002-2003, with up to 26.4% of corals affected (Lovell et al. 2004; South et al. 2012; Holbrook et al. 2022). Another bleaching event, affecting 15.5% of corals, occurred in 2005-2007 (Samuelu & Sapatu 2007; South et al. 2012). Most notable, however, was the 2015 bleaching event, which coincided with strong El Niño conditions (Crichton & Esteban 2018; Holbrook et al. 2022). While quantitative data on this bleaching event in Samoa are sparse, qualitative reports note severe bleaching, mostly affecting corals in the genus Acropora (Wabnitz & Nahacky 2015). Indeed, Samoan reefs saw up to 16 degree heating weeks (DHW) of heat stress during this year, indicating that severe bleaching and mortality were likely (Zeigler et al. 2016). Looking forward, it is likely that Samoa will experience more frequent and severe heating events likely to lead to coral bleaching, as the frequency of marine heatwaves across the Pacific has increased at a rate of one additional heatwave per decade (Holbrook et al. 2022).

While climate change-induced coral bleaching and increased cyclone activity are global stressors with no immediate local solution, water quality on Samoa's reefs has also been identified as an important threat to reef health. In Samoa, the lack of a well-defined sewage and waste disposal system, paired with heavy rains during the wet season, lead to influxes of nutrients, pesticides and raw sewage onto nearshore reefs (Gangaiya & Wele 1994; Skelton et al. 2000; Samuelu & Sapatu 2007; South et al. 2012). While few quantitative water quality surveys have been undertaken, a recent study found that 33 out of 34 seawater samples collected on Upolu at 10m depth had coliform bacteria concentrations of >1 cell/100ml; the only sample free of coliform bacteria was collected 20 km offshore (Ochsenkühn et al. 2021). In some extreme cases, nearshore seawater samples have been shown to have coliform bacteria counts of up to 300 cells/100ml (Gangaiya & Wele 1994). In addition, qualitative reports of sedimentation from various rivers across the country have been noted and, in some cases, linked to reef degradation (Gangaiya & Wele 1994; Green 1996; Skelton et al. 2000; South et al. 2012). While some efforts have been made to regulate the use of pesticides and to control waste disposal, the effects have been variable, with mangrove swamps, drains, and riversides continuing to be used for waste disposal in some areas (Samuelu & Sapatu 2007). To this end, the Government of Samoa has identified a need to introduce new pollution reduction technologies and to build capacity for effective pollution monitoring as part of the national strategy for marine health (Government of Samoa 2020).



In an effort to combat threats to reef health, Samoa has been a regional leader in marine protection. In 1974, it became the first Pacific country to create a marine reserve when it protected Palolo Deep, off of Apia Harbor (Skelton et al. 2000; Sulu et al. 2002; Ward et al. 2007; South et al. 2012). In Aleipata and Safata districts, MPAs were established in 20 villages starting in 1999 (Sulu et al. 2002; Lovell et al. 2004; Samuelu & Sapatu 2007). In addition, the CBFMP program has allowed for the designation of 73 fish reserves within participating communities' traditional tenure areas; however, these reserves are typically small and, combined, cover less than 1% of Samoa's total reef area (Kendall & Poti 2011). In an effort to continue the tradition of marine protection and strengthen Samoa's protected area networks, the region is undertaking a comprehensive marine spatial planning (MSP) process that has to-date resulted in a final draft map and a draft legislative framework.

To date, robust data on reef conditions are lacking, and systematic studies of benthic and fish populations have been identified as a scientific need (Kendall & Poti 2011). Coral reef assessments over the past few decades have been sporadic and typically focused on a few sites not representative of the entire country, such as Palolo Deep and other marine reserves (Lovell et al. 2004). Study sites are often focused on Upolu, while few descriptions of Savai'i's reefs exist. While some time series exist (e.g., Samuelu & Sapatu 2007; Berthe et al. 2016; Zeigler et al. 2018), these are limited in scope and in some cases focus only on sites within marine reserves. Knowledge of benthic biodiversity in Samoa is limited (Skelton et al. 2000; South et al. 2012), and though fish biodiversity has been cataloged (Jordan & Seale 1906; Wass 1984), few recent studies have documented the current composition of fish communities with high taxonomic resolution.



This study aims to provide a comprehensive overview of forereef communities across Samoa, with the goal of supporting the research and MSP goals outlined in the Government's Samoa Ocean Strategy (Government of Samoa 2020). This research fits into the Strategy's Strategic Priority C: Research and Data Collection, supporting Integrated Management Solutions 4) Improve scientific research, data collection, and monitoring within Samoa's ocean and 5) complete a marine spatial plan for Samoa's ocean. The expedition was led by the Ministry of Natural Resources and Environment (MNRE) and the Ministry of Agriculture and Fisheries (MAF), in partnership with the Waitt Institute and Conservation International, and supported by the Scripps Institution of Oceanography and CRIOBE. Data on fish, benthic, and invertebrate communities as well as water quality were collected at 36 sites along the northwest, west, and southwest coasts of Savai'i and Upolu in September 2022. In addition, time series data from 2017, 2019, and 2022 are presented for 13 of the sites, allowing for the analysis of trends over time.

APPROACH

The data presented in this report were collected during a field expedition undertaken in September 2022. During the expedition, researchers conducted surveys of reef fish populations, benthic coral reef communities, marine macroinvertebrates, and water quality parameters. 36 sites were surveyed across the islands of Savai'i, Upolu and Manono (Figure 1). A detailed summary of survey methods can be found in Appendix 1, and a summary of the sites surveyed as well as the corresponding metadata can be found in Appendix 2.



Sites were selected with three goals in mind: surveying priority sites identified by the Ministry of Agriculture and Fisheries, resurveying established sites, and prioritizing safe diving conditions. 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. These sites were surveyed in 2017 as well as 2019. However, due to rough weather and sea conditions during the time of the survey, some priority locations and established sites had to be skipped in order to find safe diving conditions. Two sites were surveyed off of Manono island, but due to the proximity of these sites to the main island and the continuity of the reef between Manono and Upolu, these sites have been grouped with the survey sites on Upolu. All sites were located on the forereef; no surveys were undertaken in the lagoon.

All resurveyed sites are on the north-west coasts of the main islands, while sites on the western and southern coasts were newly established. In total, five sites on Savai'i and eight sites on Upolu were resurveyed, for a total of 13 resurveys. (While the existing photomosaic plot at UPO_04 was not located, this site is included as a resurvey as the same GPS coordinates were used to locate the site as had been used previously.) Efforts were made to ensure that sites were at least 2 km apart from each other to avoid pseudoreplication (exceptions are sites UPO_21 & UPO_22, SAV_34 & SAV_35, and SAV_18 & SAV_19, which are all 1.8 km apart. UPO_17 & UPO_CRIOBE are approximately 1 km apart; however, UPO_CRIOBE was surveyed with different methods than the rest of the sites, so only rugosity and coral recruits are reported from this site). 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 10 m, 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.

KEY METRIC	SIGNIFICANCE TO REEF HEALTH	METHOD	UNITS
Reef fish abundance, diversity, biomass	Healthy reefs are able to support diverse, abundant fish communities, as well as higher fish biomass. Overfished reefs will tend to have lower biomass and diversity. Important trophic groups, such as herbivores, promote reef health by removing macroalgae and creating space for coral recruitment	Belt transect surveys	Biomass: g/m ² Abundance: Individuals/m ²
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 10cm 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.	Transect surveys	Individuals/site (300m ²)
Water quality	Poor water quality can stress reefs by causing macroalgal blooms, promoting coral disease, increasing bioerosion, etc.	Stable isotope (δ13C–δ15N) approaches	Stable isotope ratio (‰) and total N (µg)



RESULTS

Photo Credit: Andy Estep

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.

In total, 244 fish species from 38 families were recorded in the belt transect surveys (Appendix 3). *Acanthurus nigrofuscus* was the most commonly recorded fish, appearing in the transects at 33 of the 35 sites where fish surveys were conducted. Labridae (wrasses) was the most diverse family, with 45 species recorded. *Pycnochromis margaritifer* had the highest mean density of any fish species (0.2 individuals m⁻²), while *Ctenochaetus striatus* had the highest mean biomass (14.1 g m⁻²).

The total mean fish biomass across all sites surveyed was 88.8 g m⁻², while mean fish density across all sites was 2.2 individuals m⁻². Fish communities in Samoa were characterized by moderate numbers of large herbivores, smaller planktivores, and medium to small lower carnivores (Figures 2-6). Top predators and sharks were rare across the sites surveyed. Despite similar overall densities of fish on both islands, biomass was higher on Upolu than on Savai'i, indicating that fish were generally larger on this island. Herbivores, mainly scarids (parrotfish) and acanthurids (surgeonfish) made up the largest proportion of the biomass across the country.

While planktivores and lower carnivores made up similar or larger proportions of the overall fish density when compared to herbivores, these were generally small fishes from the families Pomacentridae (damselfish), Caesionidae (fusiliers) and Labridae (wrasses), and as such did not contribute a sizable portion of the overall biomass (Figure 7).

Fish densities across trophic groups were generally similar across islands. The largest difference was seen in the planktivores, with a higher mean density on Upolu than Savai'i (1.1 individuals $m^{-2} \pm 0.2$ SE and 0.8 individuals $m^{-2} \pm 0.1$ SE, respectively). Lower carnivore and top predator densities were slightly higher on Savai'i (0.7 individuals $m^{-2} \pm 0.1$ SE and 0.05 individuals $m^{-2} \pm 0.01$ SE, respectively) than on Upolu (0.5 individuals $m^{-2} \pm 0.1$ SE and 0.03 individuals $m^{-2} \pm 0.01$ SE, respectively). Notably, no sharks were recorded in any transects on Savai'i, while one shark was recorded on Upolu, for a mean density of 0.0001 individuals $m^{-2} \pm 0.0001$ SE. However, it should be noted that belt transect surveys have been found to undersample large, mobile organisms such as sharks (Richards et al. 2011), so true shark densities may be slightly higher than reported here.

Biomass, on the other hand, was noticeably higher on Upolu across all trophic categories, indicating that fish tended to be larger on this island.

The largest differences were seen in the herbivores and planktivores. On Upolu, mean herbivore biomass was 60.9 g m⁻² ± 16.5 SE, compared to 43.4 g m⁻² ± 7.6 SE on Savai'i. Planktivore biomass showed a similar difference between islands, with a mean of 25.9 g m⁻² ± 10.1 SE on Upolu and 8.8 g m⁻² ± 1.7 SE on Savai'i. Differences in biomass of lower carnivores and top predators between islands were less pronounced, but in both cases, values were higher on Upolu (lower carnivores: 20.0 g m⁻² ± 4.1 SE on Upolu vs. 13.8 g m⁻² ± 1.7 SE on Savai'i; top predators: 9.4 g m⁻² ± 5.4 SE on Upolu vs. 6.7 g m⁻² ± 2.4 SE on Savai'i).





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



FIGURE 3:

Samoa fish density.





FIGURE 4:

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



FIGURE 5:

Samoa biomass map.



FIGURE 6:

Samoa fish biomass map.





This pattern held true for most fish families of interest, except for Balistidae (triggerfish), which had higher biomass on Savai'i (6.7 g m⁻² \pm 0.7 SE) than on Upolu (2.6 g m⁻² \pm 0.8 SE). For all other families of interest, biomass was either similar between islands (e.g., Labridae (wrasses), Lethrinidae (emperors), and Serranidae (groupers)) or higher on Upolu (e.g., Acanthuridae (surgeonfish), Caesionidae (fusiliers), Lutjanidae (snappers), Pomacentridae (damselfish), and Scaridae (parrotfish)). The family with the greatest difference between islands was Caesionidae, with a mean biomass of 13.3 g m⁻² \pm 9.4 SE on Upolu, compared to only 0.4 g m⁻² \pm 0.4 SE on Savai'i. Large differences were also seen for acanthurids (33.6 g m-2 \pm 5.0 SE on Upolu, 23.9 g m⁻² \pm 4.4 SE on Savai'i), scarids (26.4 g m⁻² \pm 11.6 SE on Upolu, 18.1 g m^{-2} \pm 3.4 SE on Savai'i), and pomacentrids (9.0 g m^{-2} \pm 1.2 SE on Upolu, 2.6 g m⁻² \pm 0.4 SE on Savai'i).

When compared to the surveys from past years, distinct patterns emerge on each island. On Savai'i, both mean fish density and biomass have declined consistently since 2017 (Figures 8 & 9). Conversely, on Upolu, both fish density and biomass were highest in 2019. However, despite similar fish densities in 2017 and 2022 on Upolu, biomass was higher in 2022, indicating that fish were larger on average during that survey. On both islands, herbivore density was the lowest in 2022 of the three survey periods. However, although this corresponded to lower herbivore biomass on Savai'i in 2022, herbivore biomass on Upolu was higher in 2022 than in 2017, indicating that herbivores were larger during the most recent survey period. While sharks were scarce in the surveys across all time points, they were present more often on Upolu than Savai'i.





FIGURE 8:

Mean fish density at each island in 2017, 2019 and 2022. Only the data from resurveyed sites are included.





FIGURE 9:

Mean fish biomass at each island in 2017, 2019 and 2022. Only the data from resurveyed sites are included.



BENTHIC COVER

Benthic communities in Samoa are characterized by an almost equal cover of calcifying organisms (e.g., hard corals, crustose coralline algae (CCA), and calcified macroalgae) and non-calcifying organisms (e.g., turf algae, fleshy macroalgae, invertebrates and soft corals). Overall, mean hard coral cover was 20.9% \pm 0.5 SE. Mean CCA cover was similar at 23.1% \pm 0.5 SE. Turf algae represented the highest proportion of benthic cover, with a mean cover of 39.3% \pm 0.7 SE across all sites. Cover of fleshy macroalgae was generally low, with a mean value of 2.6% \pm 0.2 SE.

Mean coral cover was slightly higher on Upolu (25.3% \pm 0.9 SE) than on Savai'i (18.4% \pm 0.6 SE; Figures 10-12). CCA cover was roughly equal to coral cover on Upolu (25.8% \pm 0.7 SE), while on Savai'i, CCA cover slightly exceeded coral cover (21.6% \pm 0.7 SE). Turf cover was highest on Savai'i, where mean cover was 44.4% \pm 0.9 SE; on Upolu, turf cover was 30.4% \pm 1.0 SE. However, Upolu had higher macroalgal cover (4.7% \pm 0.4 SE) compared to Savai'i (1.4% \pm 0.1 SE).

Thirteen of the permanent monitoring sites established in 2017 were resurveyed in 2019 and 2022; five on Savai'i and eight on Upolu. Over the three survey periods, hard coral cover at these sites has almost doubled, increasing from 10.6% \pm 0.7 SE in 2017, to 13.1% \pm 0.6 SE in 2019, and 20.9% \pm 0.9 SE in 2022. At the same time, fleshy macroalgae cover has decreased, from 9.1% \pm 0.8 SE in 2017, to 7.6% \pm 0.4 SE in 2019, and 4.8% \pm 0.4 SE in 2022. Turf was the dominant benthic cover at all three time points and has remained relatively stable over the years, ranging between 46.4% \pm 1.1 SE in 2022 and 55.1% \pm 1.0 SE in 2019. Similarly, CCA cover was similar between timepoints, ranging from a high of 21.2% \pm 0.8 SE in 2017 to a low of 16.1% \pm 0.6 SE in 2019.





When grouped by island, however, data from the resurveyed sites show opposing trends between Savai'i and Upolu (Figure 13). While coral cover on Savai'i declined slightly over the three time points (from $19.8\% \pm 1.5$ SE in 2017 to $13.4\% \pm 1.2$ SE in 2022), coral cover on Upolu increased five-fold, from $4.8\% \pm 0.5$ SE in 2017 to $25.9\% \pm 1.2$ SE in 2022. This trend toward increasing coral cover is present in all resurveyed sites on Upolu, while coral cover trajectories on Savai'i were more variable from site to site (Figure 14). There was a concurrent decline in fleshy macroalgae on Upolu throughout the time series, decreasing from $13.9\% \pm 1.1$ SE in 2017 to $6.9\% \pm 0.6$ SE in 2022.

In 2022, coral communities on both islands were dominated by corals in the genus *Montipora* (Figure 15). The remaining coral cover was more evenly spread across several genera on Savai'i, whereas cover on Upolu was dominated by corals from fewer genera. With the exception of *Acropora* and *Pocillopora*, all of the most common coral genera on both islands are dominated by encrusting or mounding morphologies. In total, 30 coral genera were recorded in the benthic photoquadrats (Appendix 4).



FIGURE 11:

Samoa cover map.



FIGURE 12:

Samoa hard coral.





FIGURE 13:

Mean percent cover of main benthic functional groups at resurveyed sites in Savai'i and Upolu in 2017, 2019 and 2022, grouped by island.





2017 2019 2022

0.25 0.00

FIGURE 14:

Mean percent cover of main benthic functional groups at resurveyed sites in Savai'i and Upolu in 2017, 2019 and 2022, grouped by site.



FIGURE 15:

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".

Mean Percent Cover





CORAL RECRUITMENT

Average juvenile coral density across all sites was 5.7 individuals $m^{-2} \pm 0.5$ SE. Mean densities were similar across islands, with an average of 5.5 individuals $m^{-2} \pm 0.7$ SE at Savai'i and 6.0 individuals $m^{-2} \pm 0.9$ SE (Figure 16). While the majority of sites had values between 0-10 individuals m^{-2} , two sites (SAV_31 and UPO_23) had mean juvenile coral densities of greater than 15 individuals m^{-2} (15.6 individuals $m^{-2} \pm 3.4$ SE at SAV_31 and 15.4 individuals $m^{-2} \pm 3.1$ SE at UPO_23). The lowest juvenile coral density was found at SAV_15, with a mean value of only 0.8 individuals $m^{-2} \pm 0.6$ SE.

The juvenile coral communities at both islands were dominated by corals in the genus *Porites* (Figure 17). *Acropora, Montipora,* and *Pocillopora* juveniles were also relatively abundant on both islands. In total, 17 genera of juvenile corals were recorded in the surveys (Appendix 4).

FIGURE 16:

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



Mean recruit density (individuals m^{-2})

FIGURE 17:

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 <0.1 individuals m-² were grouped into "Other".

Mean recruit density







RUGOSITY

Mean rugosity, or structural complexity, was higher at Upolu (1.32 ± 0.04 SE) than at Savai'i (1.16 ± 0.02 SE; Figure 18). Several sites on Savai'i had rugosity values close to 1, indicating a completely flat reef (mean value of 1.03 at site SAV_36, mean value of 1.04 at sites SAV_25, SAV_30 and SAV_37), while the highest rugosity value on this island was 1.37 ± 0.09 SE at SAV_42. On Upolu, the lowest rugosity value was 1.14 ± 0.03 SE at site UPO_13, while the highest value was 1.54 ± 0.10 SE at UPO_22.

FIGURE 18:

Mean rugosity at each island surveyed. Bold horizontal lines represent the median value at each island, and diamonds represent the mean.





Upolu

Mean rugosity



MACROINVERTEBRATES

For ease of interpretation, all invertebrate densities are reported in individuals per site, with a site representing 300m².

Two species of giant clam, *Tridacna maxima* and *Tridacna squamosa*, were recorded in the surveys (Figure 19). T. *squamosa* was recorded on both islands, whereas *T. maxima* was only present on Savai'i. Giant clam densities were higher on Savai'i, with a mean *T. maxima* density of 1.3 individuals per site \pm 0.5 SE and mean *T. squamosa* density of 1.5 individuals per site \pm 0.5 SE. In contrast, *T. maxima* was absent on Upolu, and *T. squamosa* densities were only 0.1 individuals per site \pm 0.1 SE. By far the most abundant bivalve was the jewel box clam *Chama sp.*, which was present only on Savai'i in densities of 25.0 individuals per site \pm 17.7 SE. Interestingly, this clam was absent on Upolu.

Gastropod densities were generally low across the sites surveyed. The introduced gastropod *Rochia nilotica* (commonly referred to as trochus) was found in higher densities on Upolu, with a mean of 1.2 individuals per site \pm 0.7 SE. In some cases, observers were not able to distinguish between introduced and native trochus- these observations have been reported here as *Trochus sp.* While it is possible that this category includes some introduced trochus, densities of this group were low as well, with a mean value of 1.0 individuals per site \pm 0.6 SE on Savai'i and 0.3 individuals per site \pm 0.1 SE on Upolu. Three additional gastropod species, *Charonia tritonis*, *Lambis lambis*, and *Lambis scorpius*, were found only on Savai'i in low densities.

Only one species of sea cucumber, *Actinopyga mauritiana*, was recorded in the belt transects. This species was present only on Savai'i, where it appeared in densities of 0.1 individuals per site \pm 0.1 SE. No sea cucumbers were recorded on Upolu.

In total, four species of sea star were recorded. The cushion star *Culcita novaguinae* was the only sea star species found on both islands, with densities of 0.3 individuals per site \pm 0.1 SE on Savai'i and 0.1 individuals per site \pm 0.1 SE on Upolu. On Savai'i, *Linckia guildingi* were found in densities of 0.3 individuals per site \pm 0.3 SE. On Upolu, *Linckia leavigata* and the corallivorous crown of thorns sea star *Acanthaster planci* were both recorded in densities of 0.1 individuals per site (\pm 0.1 SE for both).

The burrowing urchin *Echinostrephus aciculatus* was the most abundant invertebrate recorded in the surveys, with mean densities orders of magnitude higher than any other species (Figure 20). Densities were highest on Savai'i, with a mean of 2184.8 individuals per site \pm 946.8 SE. On Upolu, *E. aciculatus* was found in densities of 133.1 individuals per site \pm 46.0 SE. A different species of burrowing urchin, *Echinometra mathaei*, was found in much lower densities, with a mean of 0.1 individuals per site \pm 0.1 SE on Savai'i and 0.4 individuals per site \pm 0.2 SE on Upolu. Finally, *Echinothrix calamaris* was the least abundant urchin species, with densities of 0.1 individuals per site \pm 0.1 SE on both islands.

One crustacean, the crab *Carpilus maculatus*, was recorded at site SAV_19; no other crustaceans were found in the belt transect surveys.



FIGURE 19:

Mean density of bivalves, gastropods, sea cucumbers and sea stars at each island. Note differing y-axes for each panel.

> Tridacna maxima Tridacna squamosa Chama sp. Charonia tritonis Lambis lambis Lambis scorpius Rochia nilotica Trochus sp. Actinopyga mauritiana Acanthaster planci Culcita novaguinae Linckia guildingi Linckia laevigata



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WATER QUALITY

Stable isotope and total N data were extracted from dried samples of *Halimeda spp.*, a widely distributed calcified green alga. *Halimeda* was not present at all sites surveyed, so data from the 21 sites where samples were collected are presented here. See Appendix 2 for a list of sites where algal samples were collected.

Mean $\boldsymbol{\delta}^{15}$ N was similar on both islands, with an average value of 4.6‰ ± 0.1 SE on Savai'i and 4.4‰ ± 0.1 SE on Upolu (Figures 21 & 22). $\boldsymbol{\delta}^{15}$ N varied significantly with latitude on Upolu (p=0.001),

with higher values in the north and lower values further south (Figure 23). However, this pattern was not present on Savai'i, where δ^{15} N did not vary significantly with latitude. δ^{15} N did not vary significantly with longitude on either island (Figure 24).

Total N was also similar on both islands, with a slightly higher mean value on Upolu (120.9 μ g ± 5.2 SE) than on Savai'i (113.3 μ g ± 4.3 SE; Figure 25).

FIGURE 21:

Mean δ 15N at each island surveyed. Bold horizontal lines represent the median value at each island, and diamonds represent the mean.



Mean §15N

FIGURE 22:

Mean d 15N



FIGURE 23:

Scatterplot of δ^{15} N vs latitude at each island. Green triangles show values for Upolu, and teal circles show values for Savai'i. Regression lines show the best fit for the linear model for each island, along with 95% confidence intervals.



FIGURE 24:

Scatterplot of $\delta^{15}N$ vs longitude at each island. Green triangles show values for Upolu, and teal circles show values for Savai'i. Regression lines show the best fit for the linear model for each island, along with 95% confidence intervals.







KEY FINDINGS

The data collected during this survey demonstrate distinct differences between the forereef communities on Savai'i and Upolu. Reefs on Upolu had higher coral cover and higher rugosity than those on Savai'i. Additionally, time series data showed a positive trend in coral cover on Upolu since 2017, while coral cover on Savai'i has declined slightly. However, Upolu also had higher macroalgal cover and less diverse coral communities than Savai'i, and there was no difference in coral recruitment between the two islands. While fish abundance was similar on both islands, biomass was much higher on Upolu, indicating larger fish on average when compared to Savai'i. Indeed, time series data shows a decline in fish biomass on Savai'i since 2017, while biomass on Upolu has remained relatively stable. Invertebrate density and diversity tended to be higher on Savai'i across most taxa. While mean δ^{15} N and total N were similar on both islands, δ^{15} N varied significantly with latitude on Upolu but not Savai'i.

Despite having a larger human population on land, Upolu's forereefs have higher coral cover, rugosity, and fish biomass than those on Savai'i. Some of this difference may be explained by the fact that reefs on Upolu are generally more extensive and well developed than those on Savai'i (Mollica 1999; Zann 1999; Government of Samoa 2013). Indeed, the reef off northwest Upolu, which extends to Manono Island and was the location of several survey sites in this study, is the largest in the nation (Government of Samoa 2013). In addition, qualitative observations from this study indicated that several reefs on Savai'i, particularly in the southwest, consisted of flat, turf-covered pavement with few corals until approximately 10m depth, after which more complex reef communities were observed (Lubarsky, personal observation). As all surveys in this study were conducted at 10m depth, it is possible that in many cases, the flat pavement terrace was captured, obscuring the presence of higher coral cover just below. However, when only resurveyed sites are considered, time series data indicate opposite trends in coral cover since 2017, with a marked increase in coral cover on Upolu, and a less pronounced, but consistent, decline on Savai'i. When presented by site, all resurveyed sites on Upolu showed an increase in coral cover over this period, while results in Savai'i were mixed.



The increase in coral cover on Upolu appears to be a pattern of recovery following the 2015 coral bleaching; although this time series does not include any pre-bleaching data, previous studies on Upolu showed low coral cover (0-10%) in 2015 and 2016, compared to an estimated 40-80% prior to the bleaching event (Berthe et al. 2016; Ziegler et al. 2018). Coral cover from the resurveyed sites on Upolu in this study has doubled since 2017, from 10.6% to 20.9%, and the overall mean coral cover for all sites on Upolu in 2022 is 25.3%. This apparent recovery from the 2015 bleaching is consistent with previous studies showing that reefs on Upolu have recovered relatively quickly from past disturbances, such as cyclones, bleaching events and tsunamis (Skelton et al. 2000; Sulu et al. 2002; Samuelu & Sapatu 2007; Government of Samoa 2013; Wabnitz & Nahacky 2015).

The recovery of coral communities on Upolu since the 2015 bleaching can be observed visually by comparing 2D projections of 3D photomosaics collected at the same sites over time. For example, site UPO_CRIOBE is part of a longer time series program (Polynesia Mana; CRIOBE 2023) and has been surveyed since at least 2013 using standardized methods. Photoquadrat data from this site showed a rapid decline in coral cover, from 42% in 2013 to 0% in 2015 (Berthe et al. 2016). Since then, repeated 3D imaging of the plot has shown a noticeable increase in coral cover over time (Figure 26).

FIGURE 26:

2D orthophotomosaics of site UPO_CRIOBE in A) 2017, B) 2019, and C) 2022, showing an increase in coral cover over time.



In addition to higher coral cover, reefs on Upolu had higher fish biomass, despite having similar fish density to Savai'i. The disparity between fish density and biomass indicates that fish are larger on average on Upolu than on Savai'i. This result is somewhat counterintuitive, considering this higher population density, and therefore, higher assumed fishing pressure, on Upolu. However, it is possible that this can in part be attributed to the availability of habitat capable of supporting populations of larger fish on Upolu. In addition to having higher coral cover, reefs on Upolu had higher mean rugosity, meaning they are more structurally complex than those on Savai'i. High structural complexity is often associated with increased habitat for fish and other reef organisms, and reefs with higher rugosity may be capable of supporting populations of larger fish (Nemeth & Appeldoorn 2009; Harborne et al. 2012). While it is possible that management measures, such as participation of local villages in the CBFMP, may have an effect on fish populations as well, this study did not include data on specific management actions with relation to the sites surveyed.

While coral cover and rugosity were highest on Upolu, density of juvenile corals was similar on both islands. Average juvenile coral density across all sites was 5.7 individuals m⁻². This value falls within the range of other inhabited Pacific reefs. For example, reefs in Tonga, surveyed using the same methods during the same year, had an average of 6.2 juvenile corals m⁻² (Vava'u Ocean Initiative 2023). On Heron Island in Australia, juvenile coral density was 3.8 individuals m⁻² (Doropolus et al. 2015), while reefs in Palau were found to have an average of 6.3 juveniles m⁻² at 10m depth (Gouzeo et al. 2020). However, more remote locations have been found to have much higher rates of recruitment; for example, reefs at Palmyra Atoll had an average of 59.5 juvenile corals m⁻² (Roth & Knowlton 2009).

Despite having average juvenile coral density for the region, diversity of both juvenile and adult corals was lower than neighboring nations. In this study, 30 genera of adult corals were recorded, while only 17 genera were recorded in juvenile coral surveys. By comparison, in nearby Tonga, the adult coral population was made up of 38 genera, and juvenile corals from 31 genera were recorded (Vava'u Ocean Initiative 2023). Of the 30 genera recorded in Samoa, Montipora was by far the most dominant taxon, and only 10 genera had mean percent cover estimates >0.2%. While reefs in Upolu tended to be dominated by only a few taxa (e.g., Montipora, Pocillopora, and Acropora), coral diversity on Savai'i was more evenly distributed among several genera. Porites dominated the juvenile coral communities, and only 6 genera had densities of higher than 0.1 individuals m⁻². Again, juvenile coral communities on Upolu were dominated by fewer taxa than on Savai'i.





Similarly, fish diversity in Samoa was relatively low. In total, 244 of the estimated 890 shallow water reef fish species found in Samoa (Skelton et al. 2000; Government of Samoa 2013) were recorded in this survey. By comparison, 342 fish species were recorded in Tonga in 2022 (Vava'u Ocean Initiative 2023). Dominant species found in this study were Acanthurus nigrofuscus, and Ctenochaetus striatus (Acanthuridae): Paracirrhites arcatus (Cirrhitidae): Halichores hortulanus and Pseudocheilinus hexataenia (Labridae); Melicthys vidua (Monacanthidae); Centropyge flavissima (Pomacanthidae); Chromis ternatensis, Pycnochromis margaritifer, Plectroglyphidodon lacrymatus, and Pomacentrus vaiuli (Pomacentridae); Chlolorus spilirus (Scaridae); and Cephalopholis urodeta (Serranidae; Appendix 3). While some of these species, including acanthurids such as C. striatus and scarids such as C. spilirus, are known to be commonly caught and consumed in Samoa (Lovell et al. 2004), the majority are small species that are typically not considered food fish.

Several previous studies have found evidence of overfishing of Samoa's coral reef fish and invertebrates (Horsman & Mulipola 1995; Mollica 1999; Skelton et al. 2000; Samuelu & Sapatu 2007; Pinca et al. 2010; Government of Samoa 2013; Zeigler et al. 2018). Several explanations for this pattern exist. First. Samoa has both a small reef area and minimal land suitable for agriculture, meaning that limited reef resources are an important part of food security for most Samoans (Zann 199; Samuelu & Sapatu 2007; Government of Samoa 2013; Quimby et al. 2023). At the same time, the country's population has increased in recent decades, meaning that Samoa has a low ratio of coral reef habitat per capita, leading to a gap between sustainable harvest of reef fish and the recommended annual fish consumption of 35 kg per person per year required to meet nutritional needs (Holbrook et al. 2022). In addition, the advent of cash economies in Samoa in recent decades has led to a shift from subsistence fishing, in which fishers typically only harvest what they need for themselves and their family, towards artisanal fishing, in which there is an incentive to catch as much as possible to increase profits (Horsman & Mulipola 1995; Mulipola 1995; Mollica 1999; Skelton et al. 2000; Samuelu & Sapatu 2007; South et al. 2012; Zeller et al. 2015; Crichton & Esteban 2018). This shift has led to reports of destructive fishing practices, such as the use of dynamite or poisonous derris root, being used to increase catch, despite a ban on these types of fishing methods (Fairbairn 1991; Green 1996; Olson 2001; Samuelu & Sapatu 2007; Zeigler et al. 2018).

The values of fish biomass and density found in this study are on par with past studies that have found evidence of overexploitation of reef fish in Samoa. Pinca et al. (2010) reported that the average biomass for the Pacific region was 118 t km⁻², and that the biomass in Samoa at the time was 77-197 t km⁻². The mean biomass in this study (88.8 t km-2) falls near the low end of this range, and is well below the regional mean. Conversely, the mean fish density from the present study (2.2 individuals m⁻²) was slightly higher than the estimates of 0.6-1.88 individuals m⁻² reported by Pinca et al. This indicates that there may have been a shift towards smaller fish in the time between the two studies, which may be indicative of excess fishing pressure on larger, more desirable fish. Indeed, certain fish species (Acanthurus triostegus and Zanclus cornutus) were found to be 10% smaller on Upolu than in the neighboring islands of Mo'orea (French Polynesia), Aitutaki (Cook Islands), and Niue (Zeigler et al. 2018). The study also noted that fish in Samoa exhibited distinct "shy" behavior and traveled in smaller schools than on other islands, indicating degraded habitat and heavy fishing pressure.

The results of the invertebrate surveys from the present study indicate that harvesting pressure on edible macroinvertebrates may be high, as well. Commercially or nutritionally important invertebrate taxa, such as giant clams, trochus, and sea cucumbers, were found in low abundance across the survey sites. Only one species of sea cucumber, A. mauritiana, was recorded in low densities on Savai'i only. These findings support those from a recent report which concluded that sea cucumber stocks are below regional reference densities and have not recovered sufficiently to reopen an export fishery in Samoa (Shedrawi et al. 2019). Giant clams, though present on both islands, were also found in very low densities, also suggesting that fishing pressure has exceeded the abilities of the stocks to recover to sustainable levels. While giant clam restocking is an option for villages participating in the CBFMP (Mollica 1999; Zann 1999; Fa'asili & Taua 2001; Quimby et al. 2023), it appears that densities on the forereef are generally low across much of the coast. The introduced gastropod R. nilotica (trochus) had maximum densities of 40 individuals ha⁻¹, well below the suggested sustainable harvesting density of 500 individuals ha-1 (Pinca et al. 2010). However, previous studies have indicated that trochus densities are patchy across the country (Purcell et al. 2019; Purcell & Ceccarelli 2021), and it is possible that the surveys conducted during this study were not located in prime habitat for trochus (Senior et al. 2020).

Mean δ^{15} N in this study ranged from 4.4‰ on Upolu to 4.6‰ on Savai'i. The stable isotope ratio of nitrogen (¹⁵N:¹⁴N, expressed as δ^{15} N), can be used to trace the source of nutrients on a reef (Dailer et al. 2010; Dailer et al. 2012; Page et al. 2023). Typically, natural (atmospheric/oceanic) sources of nitrogen, as well as nitrogen from synthetic fertilizers, have low $\boldsymbol{\delta}^{15}$ N values ranging from 0-4‰, while sewage tends to have higher values greater than 7‰ (Dailer et al. 2010; Dailer et al. 2012). Therefore, the values recorded in this study likely represent a mix of nitrogen sources, with some of the nitrogen originating from atmospheric or oceanic sources, and some originating from terrestrial sources, potentially including pollution. It is possible that any signal of terrestrially-derived pollution may have been diluted due to the location of the sites at 10m depth on the forereef; it is likely that if pollution is present, the signal would be stronger within the lagoons, which are closer to potential pollution sources and have restricted water flow. In this study, $\delta^{15}N$ varied significantly with latitude on Upolu, with higher values in the north than in the south. This may indicate that land-based pollution is more prevalent in the north, near the capital city of Apia. However, despite the proximity of several sites to Apia, none of the samples showed a strong pollution signal.

RECOMMENDATIONS

Implement standardized, long-term monitoring program for reef fish, benthic, and invertebrate communities.	Despite the importance of reef health for the well-being of the people of Samoa, few recent surveys exist, and even fewer time series. Robust data on Samoa's reef biodiversity and ecology have been cited as lacking (Kendall & Poti 2011), but also as an important need for appropriate reef management (Government of Samoa 2020). Indeed, as part of the Samoa Ocean Strategy, "improv[ing] scientific research, data collection and monitoring within Samoa's ocean" was identified as an integrated management solution (Government of Samoa 2020). In order to gain a stronger understanding of reef health, responses to disturbance, and recovery trajectories, it is recommended that an ongoing monitoring program be established at permanent sites using standardized methods. The sites established and resurveyed in this study may serve as a starting point; however, this survey only covered the north-west, west, and south-west shores of Savai'i and Upolu and therefore leaves gaps in the understanding of reef health on the eastern shores. It is recommended that, if possible, any future monitoring include representative sites from all regions in the country which can be resurveyed periodically to track trends over time.
Encourage offshore fishing and alternative livelihoods to relieve pressure on reef fish.	While Samoa has pioneered a unique and well-established reef management strategy with the CBFMP, evidence of overexploitation of reef fish and invertebrates was detected in this survey. In an effort to combat this, several villages enrolled in the CBFMP have created initiatives to relieve reef fishing and harvesting pressure by encouraging fishers to fish offshore, where fish stocks are more resilient (Mollica 1999; Fa'asili & Taua 2001; Shawahid & McNally 2001). Similarly, participating villages can request assistance to help establish alternative livelihoods, such as tilapia aquaculture or giant clam mariculture, to minimize fishing impacts on their reefs (Mollica 1999; Zann 1999; Pinca et al. 2010; Quimby 2023). The findings from this study support the development and adoption of these and other initiatives aimed at reducing fishing pressure on reef fish and invertebrates, while still meeting the nutritional needs of the country.
Continue export bans on sea cucumbers and giant clams.	The surveys in this study support recent reports of low density of commercially desirable marine macroinvertebrates such as sea cucumbers and giant clams (e.g, Shedrawi et al. 2019), despite bans on their export and mariculture programs aimed at boosting stocks (Quimby et al. 2023). While the export of these organisms has been banned for decades, both are consumed locally; sea cucumbers and their viscera are collected, usually by women, and sold on the roadside (Government of Samoa 2013), and giant clams are harvested for subsistence in villages where they are present (Quimby et al. 2023). Villages participating in the CBFMP can request giant clam broodstock for restocking of their reefs (Mollica 1999; Fa'asili & Taua 2001; Quimby 2023); while no data exists on the effects of this program on clam abundance, it has been shown to provide cultural benefits such as women's livelihoods (Quimby et al. 2023). The low densities recorded in this study support the continuation of the export bans on both taxa, as well as mariculture programs to increase stocks. In some cases, additional management of harvests for local consumption may be considered to allow for stocks to recover to sustainable levels.
Conduct water quality surveys at nearshore sites.	The water quality surveys in this study indicated the potential for some terrestrial pollution, but due to the sites' locations on the forereef, it is likely that any signal may have been diluted. Conducting similar surveys closer to shore may shed more light on reef areas affected by pollution and may aid in the identification of pollution sources on land. Understanding patterns of terrestrial input onto nearshore reefs can help prioritize locations in need of management and support any management measures aimed at improving water quality.
Finalize marine spatial planning to identify priority areas for management.	As part of the Samoa Ocean Strategy, the Government of Samoa has identified the completion of a marine spatial plan as an integrated management solution to support research and data collection in Samoa's ocean areas (Government of Samoa 2020). Marine spatial planning can help identify priority areas for protection or management. While the offshore MSP process in Samoa is near completion, work still remains for developing a nearshore marine spatial plan. Strategic application of marine management or protection measures can help improve reef health at the identified locations as well as on the surrounding reefs. The results from this survey, along with other ecological and social data regarding ocean use, can be used to support the development of a

nearshore marine spatial plan aimed at improving reef health across Samoa.

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Photo Credit: Kyle Roepke

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This report was compiled by Katie Lubarsky (Scripps Institution of Oceanography) in collaboration with Danita Strickland (Conservation International) and Ute Zischka (Waitt Institute).



APPENDIX

Photo Credit: Joe Lepore

Appendix 1 METHODOLOGY

SITE SELECTION

Sites were selected with three goals in mind: surveying priority sites identified by the Ministry of Fisheries, resurveying established sites, and prioritizing safe diving conditions. 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. These sites were surveyed in 2017 as well as 2019. However, due to rough weather and sea conditions during the time of the survey, some priority locations and established sites had to be skipped in order to find safe diving conditions.

All resurveyed sites are on the north-west coasts of the main islands, while sites on the western and southern coasts were newly established. Efforts were made to ensure that sites were at least 2km apart from each other to avoid pseudoreplication (exceptions are sites UPO_21 & UPO_22, SAV_34 & SAV_35, and SAV_18 & SAV_19, which are all 1.8km apart. UPO_17 & UPO_CRIOBE are approximately 1km apart; however, UPO_CRIOBE was surveyed with different methods than the rest of the sites, so only rugosity and coral recruits are reported from this site).



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 25m 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 25m transect: on the outward swim, the divers surveyed an 8m width (200m² area) for individuals >20cm total length (TL), and on the return swim, a 4m width (100m² area) was surveyed for species ≤20cm 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 0.72m² 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 10m x 10m 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 27) approximately 1.5m above the reef at each site. As the diver slowly swam the plot, the cameras took 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 27:

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 28).

For the juvenile coral analysis, a 10m x 10m area was defined on each photomosaic, and 1m x 1m 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 5cm in maximum diameter were identified to the lowest taxonomic level possible.



FIGURE 28:

Schematic showing the different scales of resolution afforded by the large-area imagery methodology.

RUGOSITY

Rugosity data were collected from the 3D models described above using a simulated point gauge approach (McCormick 1994). In Viscore, a 10m x 10m 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 10cm apart were sampled in an alongshore direction across the model. Along each transect, depths were sampled every 10cm 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 25m transects used for fish and photoquadrat surveys. For each survey, a 4m wide swath was inspected for invertebrates, yielding a 100m² survey area for each transect. Results from macroinvertebrate surveys are reported in individuals per site (300 m²) rather than individuals per m² due to the low densities of most invertebrate species at each site.





WATER QUALITY

Stable isotope (δ^{13} C– δ^{15} N) approaches were used to assess water quality across Samoa. These water quality assessments were made by collecting five samples of the calcified macroalga *Halimeda spp*. along the three transects at each site. In some cases, where algal cover was low or if *Halimeda* was not present at a site, fewer samples were collected. For each site, three replicate samples (where available) were randomly selected for stable isotope analysis. See Appendix 2 for a list of sites where algae was collected.

Samples were first rinsed with fresh water, dried in a salad spinner to remove excess water, and dried overnight in a food dehydrator for storage and transport in sealed plastic bags. Once in the lab, samples were rinsed with deionized water and decalcified for 24 hours in a 5% HCl solution. Samples were then rinsed with deionized water and placed in a food dehydrator to dry for 48 hours. Dried samples were then ground into a fine powder using a Wig-L-Bug amalgamator, and 2.5mg (\pm 0.5mg) of each sample was packed into foil for analysis. Samples were analyzed using mass spectrometry at the UC Davis Stable Isotope Facility for δ^{15} N, total N, δ^{13} C and total C.

Appendix 2 SITE METADATA

TABLE 2: Site metadata for all sites surveyed.

*Surveys at site UPO_04 were conducted at approximately the same coordinates as a previously surveyed site (UPO_02). While the existing photomosaic plot from UPO_02 could not be located for resurvey, the location is considered sufficiently close to the original site to compare benthic photoquadrat and fish survey data between survey periods.

STATION ID	ISLAND	LATITUDE (DD)	LONGITUDE (DD)	RESURVEY	ALGAE SAMPLES	NUMBER OF OBSERVERS (FISH SURVEYS)
SAV_13	Savai'i	-13.48404	-172.56863	Y	Y	1
SAV_15	Savai'i	-13.49168	-172.60287	Y	Ν	1
SAV_18	Savai'i	-13.49934	-172.66071	Y	Ν	2
SAV_19	Savai'i	-13.50533	-172.67613	N	N	1
SAV_21	Savai'i	-13.51234	-172.71886	Y	Ν	2
SAV_23	Savai'i	-13.49158	-172.76183	Y	N	1
SAV_25	Savai'i	-13.51751	-172.80508	N	Ν	1
SAV_26	Savai'i	-13.53924	-172.78931	N	N	1
SAV_27	Savai'i	-13.57334	-172.74861	N	Y	1
SAV_30	Savai'i	-13.49711	-172.79114	N	N	1
SAV_31	Savai'i	-13.59721	-172.72527	N	Y	2
SAV_32	Savai'i	-13.61589	-172.70164	N	Y	1
SAV_33	Savai'i	-13.64003	-172.6739	N	Y	2
SAV_34	Savai'i	-13.66504	-172.64804	N	N	1
SAV_35	Savai'i	-13.67921	-172.63953	N	Y	2
SAV_36	Savai'i	-13.69694	-172.62178	N	Y	1
SAV_37	Savai'i	-13.72181	-172.6001	N	Y	1
SAV_38	Savai'i	-13.78572	-172.55299	N	Y	2
SAV_39	Savai'i	-13.79509	-172.47346	N	Y	1
SAV_40	Savai'i	-13.78048	-172.37938	N	Y	2
SAV_41	Savai'i	-13.78363	-172.30331	N	Y	1
SAV_42	Savai'i	-13.79833	-172.25195	N	Y	2
UPO_04	Upolu	-13.79401	-171.79646	Y*	Ν	2
UPO_05	Upolu	-13.77171	-171.83777	Y	Y	1
UPO_06	Upolu	-13.77416	-171.85651	N	Ν	2
UPO_07	Upolu	-13.76846	-171.87349	Y	Y	1
UPO_13	Upolu	-13.80449	-171.9752	Y	N	1
UPO_14	Upolu	-13.80336	-171.99669	Y	N	2
UPO_17	Upolu	-13.81162	-172.03905	Y	N	2
UPO_19	Upolu	-13.8461	-172.08818	Y	Ν	2
UPO_20	Upolu	-13.85013	-172.13235	Ν	Y	2
UPO_21	Upolu	-13.94622	-171.97397	Ν	Y	1
UPO_22	Upolu	-13.95886	-171.96455	N	Y	2
UPO_23	Upolu	-13.97908	-171.95264	Ν	Y	1
UPO_25	Upolu	-14.01959	-171.8419	N	Y	1
UPO_CRIOBE	Upolu	-13.80583	-172.03200	N	Y	NA

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 \ge 75% of sites
- **A** = observed at 50-74% of sites
- **C** =observed at 25-49% of sites
- **O** = observed at 10-24% of sites
- **R** = observed at <10% of sites

Family	Species	Mean density (individuals m^-2)	Mean biomass (g m^-2)	Number of sites	DACOR
Aetobatidae	Aetobatus narinari	0.00009523809524	0.6853201108	1	R
	Acanthurus blochii	0.0005714285714	0.225915223	4	0
	Acanthurus guttatus	0.0001904761905	0.03387195483	1	R
	Acanthurus lineatus	0.009571428571	2.440386259	13	С
	Acanthurus nigricans	0.02052380952	1.849737843	22	А
	Acanthurus nigricauda	0.0004761904762	0.08952789407	6	0
	Acanthurus nigrofuscus	0.05152380952	2.16655892	33	D
	Acanthurus nigroris	0.005428571429	0.6802576959	2	R
	Acanthurus olivaceus	0.003952380952	0.9115142098	12	С
	Acanthurus pyroferus	0.001333333333	0.0844822933	8	0
Acanthuridae	Ctenochaetus binotatus	0.007047619048	0.3546072527	9	С
	Ctenochaetus cyanocheilus	0.02438095238	1.963219215	16	С
	Ctenochaetus flavicauda	0.0002857142857	0.002203106669	2	R
	Ctenochaetus striatus	0.1002380952	14.10736142	29	D
	Naso brevirostris	0.00004761904762	0.01328152228	1	R
	Naso lituratus	0.006333333333	1.289409288	22	А
	Naso unicornis	0.0002857142857	0.3401584791	1	R
	Paracanthurus hepatus	0.0006666666666	0.1817652249	3	R
	Zebrasoma scopas	0.01133333333	0.6275348629	19	А
	Zebrasoma veliferum	0.0003333333333	0.1219989464	4	0
A	Ostorhinchus angustatus	0.0007619047619	0.0001940665235	3	R
Apogonidae	Ostorhinchus nigrofasciatus	0.0008571428571	0.0002712282875	1	R
Aulostomidae	Aulostomus chinensis	0.00009523809524	0.007298576617	1	R

Family	Species	Mean density (individuals m^-2)	Mean biomass (g m^-2)	Number of sites	DACOR
	Balistapus undulatus	0.008047619048	0.9856287319	25	А
Palistidae	Balistoides viridescens	0.0002380952381	0.1166274912	2	R
Dalisticae	Sufflamen bursa	0.004619047619	0.278323872	12	С
	Sufflamen chrysopterum	0.009142857143	0.5151120046	12	С
	Blenniella chrysospilos	0.002285714286	0.001922514286	3	R
	Cirripectes quagga	0.0001904761905	0.0000788344426	1	R
	Cirripectes stigmaticus	0.0066666666667	0.04743925691	14	С
Blenniidae	Cirripectes variolosus	0.02742857143	0.0496840637	27	А
	Ecsenius bicolor	0.02133333333	0.01143406292	24	А
	Meiacanthus atrodorsalis	0.006857142857	0.01239314851	7	0
	Plagiotremus tapeinosoma	0.003619047619	0.0004576779468	7	0
	Caesio caerulaurea	0.04138095238	3.506778252	4	0
	Caesio teres	0.00880952381	1.002814378	3	R
Caesionidae	Pterocaesio marri	0.002	0.1827975226	1	R
Caesionidae	Pterocaesio pisang	0.001428571429	0.03426197024	1	R
	Pterocaesio tile	0.002428571429	0.3788498746	3	R
	Pterocaesio trilineata	0.008666666667	0.2597562807	3	R
	Carangoides sp.	0.0001904761905	0.05856605769	1	R
Carangidae	Caranx melampygus	0.00009523809524	0.09608603713	1	R
	Scomberoides lysan	0.0002857142857	0.04218307094	1	R
Carcharhinidae	Triaenodon obesus	0.00004761904762	0.05998740338	1	R
	Chaetodon auriga	0.00004761904762	0.01369273233	1	R
	Chaetodon citrinellus	0.006095238095	0.09529435823	12	С
	Chaetodon ephippium	0.001857142857	0.238263082	7	0
	Chaetodon lineolatus	0.00009523809524	0.01288257303	1	R
	Chaetodon lunula	0.001714285714	0.1647967749	5	0
	Chaetodon lunulatus	0.001714285714	0.08041515953	5	0
	Chaetodon ornatissimus	0.001047619048	0.04960243295	4	0
Chaetodontidae	Chaetodon pelewensis	0.002952380952	0.0376151822	7	0
	Chaetodon reticulatus	0.006952380952	0.3614963401	14	С
	Chaetodon semeion	0.0007619047619	0.1275937945	2	R
	Chaetodon trifascialis	0.001428571429	0.06713505649	6	0
	Chaetodon ulietensis	0.0006666666667	0.0478353886	2	R
	Chaetodon vagabundus	0.002285714286	0.2021873372	10	С
	Forcipiger flavissimus	0.0007619047619	0.02264614598	1	R
	Forcipiger longirostris	0.000380952381	0.03176711105	1	R
	Heniochus acuminatus	0.00009523809524	0.01863734545	1	R

Family	Species	Mean density (individuals m^-2)	Mean biomass (g m^-2)	Number of sites	DACOR
	Heniochus chrysostomus	0.001428571429	0.224201255	5	0
Chaetodontidae (cont.)	Heniochus monoceros	0.0001904761905	0.07624752899	1	R
	Heniochus singularius	0.0001904761905	0.0334368	1	R
	Heniochus varius	0.0005714285714	0.09839761905	4	0
Cirrhitidaa	Cirrhitichthys falco	0.0001904761905	0.0008555576317	2	R
Cirrinudae	Paracirrhites arcatus	0.04066666667	0.2937088399	30	D
	Paracirrhites forsteri	0.002285714286	0.1031809476	12	С
Ephippidae	Platax orbicularis	0.0001428571429	0.1741598393	2	R
	Amblyeleotris steinitzi	0.00009523809524	0.00003317142857	1	R
	Eviota infulata	0.01161904762	0.004835338783	9	С
	Nemateleotris magnifica	0.002	0.0004914	6	0
	Paragobiodon sp.	0.0001904761905	0.00008965282436	1	R
Gobiidae	Ptereleotris evides	0.01047619048	0.009046977083	7	0
	Ptereleotris heteroptera	0.001047619048	0.003218350941	4	0
	Ptereleotris magnifica	0.00066666666667	0.004734254122	1	R
	Ptereleotris zebra	0.01228571429	0.4149622601	4	0
	Valenciennea strigata	0.005047619048	0.033054701	10	С
Haemulidae	Plectorhinchus vittatus	0.0007619047619	0.3795752979	7	0
	Myripristis adusta	0.0004761904762	0.1127029592	2	R
	Myripristis amaena	0.0001904761905	0.02899014081	1	R
	Myripristis berndti	0.002380952381	0.3070967868	6	0
	Myripristis kuntee	0.006857142857	0.8325422183	4	0
Holocentridae	Myripristis violacea	0.004619047619	0.6635870574	11	С
Theree and the second se	Neoniphon opercularis	0.00004761904762	0.00813030328	1	R
	Neoniphon sammara	0.002333333333	0.170495975	7	0
	Sargocentron caudimaculatum	0.005666666667	0.4704207774	9	С
	Sargocentron spiniferum	0.0004285714286	0.159057033	4	0
	Sargocentron tiere	0.002761904762	0.2555954073	4	0
Kyphosidae	Kyphosus cinerascens	0.0008571428571	0.4788330801	2	R
	Anampses caeruleopunctatus	0.000380952381	0.03321850728	3	R
	Anampses geographicus	0.00009523809524	0.0007165549059	1	R
	Anampses meleagrides	0.0005714285714	0.02491567723	1	R
Labridae	Anampses twistii	0.00009523809524	0.002779918109	1	R
	Bodianus axillaris	0.001428571429	0.07568544968	6	0
	Bodianus loxozonus	0.0001904761905	0.0746397251	2	R
	Bodianus mesothorax	0.0003333333333	0.02098899659	2	R
	Cheilinus chlorourus	0.0002857142857	0.03047384944	3	R

Family	Species	Mean density (individuals m^-2)	Mean biomass (g m^-2)	Number of sites	DACOR
	Cheilinus oxycephalus	0.0006666666666	0.02053150897	3	R
	Cheilinus trilobatus	0.0005238095238	0.08821268563	6	0
	Cheilinus undulatus	0.00009523809524	0.09791919832	1	R
	Cirrhilabrus scottorum	0.001333333333	0.007146604156	1	R
	Coris aygula	0.0001904761905	0.1055140308	2	R
	Coris gaimard	0.005380952381	0.3172980039	14	С
	Epibulus insidiator	0.004047619048	0.5342530374	18	С
	Gomphosus varius	0.01085714286	0.1297509091	18	С
	Halichoeres biocellatus	0.0005714285714	0.01383024762	2	R
	Halichoeres claudia	0.0005714285714	0.003219957231	3	R
	Halichoeres hortulanus	0.01828571429	0.5081678308	27	D
	Halichoeres margaritaceus	0.006380952381	0.0165148	8	0
	Halichoeres marginatus	0.000380952381	0.01417010213	3	R
	Halichoeres ornatissimus	0.0008571428571	0.005330907131	2	R
	Halichoeres prosopeion	0.0008571428571	0.01229595168	5	0
	Hemigymnus fasciatus	0.001142857143	0.09119491793	3	R
	Hemigymnus melapterus	0.0001904761905	0.0611713758	3	R
	Hologymnosus annulatus	0.0001904761905	0.04844683876	2	R
	Hologymnosus doliatus	0.0001428571429	0.03258550767	2	R
Labridae (cont.)	Labrichthys unilineatus	0.001142857143	0.004948571429	3	R
	Labroides bicolor	0.0008571428571	0.003266414488	5	0
	Labroides dimidiatus	0.01352380952	0.01325136332	25	А
	Labroides rubrolabiatus	0.0001904761905	0.00003877411894	1	R
	Labropsis australis	0.001142857143	0.01363563833	3	R
	Labropsis xanthonota	0.001619047619	0.006248734171	5	0
	Macropharyngodon meleagris	0.01247619048	0.02146810093	18	С
	Novaculichthys taeniourus	0.0005714285714	0.01899290133	4	0
	Oxycheilinus digramma	0.001	0.03174549555	7	0
	Oxycheilinus unifasciatus	0.00009523809524	0.00401517859	1	R
	Pseudocheilinus evanidus	0.0005714285714	0.0001323895285	1	R
	Pseudocheilinus hexataenia	0.02666666667	0.01819504762	27	D
	Pseudodax moluccanus	0.00009523809524	0.01783425634	1	R
	Stethojulis bandanensis	0.0004761904762	0.007742407793	4	0
	Stethojulis strigiventer	0.0001904761905	0.00143933162	1	R
	Thalassoma amblycephalum	0.0219047619	0.07858423936	8	0
	Thalassoma hardwicke	0.003	0.06908977546	10	С
	Thalassoma lutescens	0.002380952381	0.02668819776	8	0
	Thalassoma quinquevittatum	0.094	0.6152173557	22	А

Family	Species	Mean density (individuals m^-2)	Mean biomass (g m^-2)	Number of sites	DACOR
	Gnathodentex aureolineatus	0.002714285714	0.3607602939	4	0
	Lethrinus harak	0.0001904761905	0.07958759723	1	R
Lathrinidaa	Lethrinus obsoletus	0.0004761904762	0.272825384	3	R
Letinindae	Lethrinus olivaceus	0.00009523809524	0.1709087396	1	R
	Monotaxis grandoculis	0.005904761905	0.9748865615	12	С
	Monotaxis heterodon	0.00009523809524	0.01243221722	1	R
	Aphareus furca	0.002952380952	0.6595774472	18	А
	Aprion virescens	0.00009523809524	0.3208329484	1	R
	Lutjanus bohar	0.001619047619	1.574028778	7	0
	Lutjanus fulvus	0.0003333333333	0.09803574845	2	R
Lutjanidae	Lutjanus gibbus	0.001714285714	0.5516710445	8	0
	Lutjanus kasmira	0.003619047619	0.2331695227	4	0
	Lutjanus monostigma	0.0004761904762	0.1946496008	3	R
	Macolor macularis	0.001	0.4859426742	5	0
	Macolor niger	0.0007619047619	0.2435047143	3	R
Malacanthidae	Malacanthus latovittatus	0.00004761904762	0.0236174339	1	R
	Cantherhines dumerilii	0.0005238095238	0.1428807878	4	0
	Cantherhines pardalis	0.0001904761905	0.01089891065	1	R
	Melichthys niger	0.00009523809524	0.04713219968	1	R
Monacanthidae	Melichthys vidua	0.008571428571	3.18594102	26	D
	Odonus niger	0.000380952381	0.005420713861	1	R
	Oxymonacanthus longirostris	0.001523809524	0.009079085714	3	R
	Pervagor janthinosoma	0.0001904761905	0.000002944647307	1	R
	Mulloidichthys vanicolensis	0.002333333333	0.3779289619	5	0
	Parupeneus barberinus	0.000380952381	0.05241338352	3	R
Mullidae	Parupeneus crassilabris	0.00004761904762	0.01180102034	1	R
manado	Parupeneus cyclostomus	0.002	0.2394838264	11	С
	Parupeneus insularis	0.0004761904762	0.06450328024	3	R
	Parupeneus multifasciatus	0.002857142857	0.1222504234	9	С
Muraeninae	Gymnothorax meleagris	0.00009523809524	0.03836390085	1	R
Ostraciidae	Ostracion meleagris	0.002	0.1095272278	10	С
Pempheridae	Pempheris oualensis	0.003	0.2118071462	6	0
Pinguipedidae	Parapercis clathrata	0.0005714285714	0.01070866542	3	R
- mgaipealate	Parapercis millepunctata	0.0001904761905	0.003786637252	1	R
	Apolemichthys trimaculatus	0.00009523809524	0.01673397526	1	R
Pomacanthidae	Centropyge bicolor	0.0002857142857	0.00647267619	2	R
	Centropyge bispinosa	0.001619047619	0.02540255694	5	0

Family	Species	Mean density (individuals m^-2)	Mean biomass (g m^-2)	Number of sites	DACOR
	Centropyge flavissima	0.0200952381	0.3954259271	26	D
Pomacanthidae (cont.)	Pomacanthus imperator	0.0001904761905	0.06448990325	2	R
	Pygoplites diacanthus	0.006	1.052278914	21	А
	Abudefduf sexfasciatus	0.003619047619	0.1573494467	3	R
	Amphiprion clarkii	0.0001904761905	0.0001051391682	1	R
	Amphiprion melanopus	0.003619047619	0.04689043723	1	R
	Amphiprion perideraion	0.0001904761905	0.0001197620726	1	R
	Chromis agilis	0.00009523809524	0.00160474247	1	R
	Chromis atripectoralis	0.0002857142857	0.002733711514	1	R
	Chromis ternatensis	0.01838095238	0.03862109801	1	R
	Chromis viridis	0.006476190476	0.01351910771	2	R
	Chromis weberi	0.001714285714	0.009327894718	3	R
	Chromis xanthura	0.03552380952	0.3082212767	17	А
	Chrysiptera leucopoma	0.07628571429	0.05979400361	13	С
	Chrysiptera taupou	0.07428571429	0.0389588842	14	С
	Dascyllus flavicaudus	0.01047619048	0.04155762526	4	0
	Dascyllus reticulatus	0.000380952381	0.0003152535804	1	R
Pomacentridae	Dascyllus trimaculatus	0.0007619047619	0.008339187984	2	R
	Neopomacentrus metallicus	0.03895238095	0.2436542814	3	R
	Plectroglyphidodon dickii	0.02895238095	0.1721635747	20	А
	Plectroglyphidodon johnstonianus	0.004	0.02767568088	14	С
	Plectroglyphidodon lacrymatus	0.07419047619	1.099882399	27	D
	Pomacentrus coelestis	0.1153333333	0.05462179117	20	А
	Pomacentrus nigriradiatus	0.1894285714	1.567190154	20	А
	Pomacentrus vaiuli	0.1574285714	0.5482305713	31	D
	Pomachromis richardsoni	0.04466666667	0.0260673822	13	С
	Pycnochromis acares	0.01333333333	0.007790154602	9	С
	Pycnochromis iomelas	0.02885714286	0.01405571094	10	С
	Pycnochromis leucurus	0.006095238095	0.003385653912	3	R
	Pycnochromis margaritifer	0.2076190476	0.1010176846	29	D
	Pycnochromis vanderbilti	0.004666666667	0.002726554111	4	0
	Stegastes fasciolatus	0.03657142857	0.3053049035	9	С
Priacanthidae	Heteropriacanthus cruentatus	0.00004761904762	0.008621834629	1	R
	Calotomus carolinus	0.0005714285714	0.2246275014	2	R
Scaridae	Cetoscarus ocellatus	0.0001904761905	0.07192693333	2	R
	Chlorurus japanensis	0.002333333333	0.8456454894	10	С
	Chlorurus microrhinos	0.000380952381	0.1133938751	2	R

Family	Species	Mean density (individuals m^-2)	Mean biomass (g m^-2)	Number of sites	DACOR
	Chlorurus spilurus	0.05085714286	7.835411849	31	D
	Hipposcarus longiceps	0.00009523809524	0.07888657482	2	R
	Scarus altipinnis	0.001142857143	1.161163779	3	R
	Scarus dimidiatus	0.00009523809524	0.01923503734	1	R
	Scarus forsteni	0.001523809524	0.6778973424	6	0
	Scarus frenatus	0.00004761904762	0.0090974396	1	R
	Scarus ghobban	0.0005238095238	0.2740538935	4	0
Scaridae	Scarus globiceps	0.00219047619	0.6732922486	17	А
(cont.)	Scarus niger	0.0001904761905	0.07961975627	2	R
	Scarus oviceps	0.008238095238	2.948138678	21	А
	Scarus prasiognathos	0.00004761904762	0.02159845436	1	R
	Scarus psittacus	0.01357142857	1.31841684	20	А
	Scarus rubroviolaceus	0.007904761905	3.329527467	19	А
	Scarus schlegeli	0.0005714285714	0.1319475659	5	0
	Scarus sp	0.002380952381	0.2553134983	6	0
	Scarus spinus	0.004952380952	1.101101295	20	А
Scombridae	Gymnosarda unicolor	0.00004761904762	0.119423585	1	R
	Caracanthus maculatus	0.007047619048	0.006412628571	2	R
Scorpaenidae	Caracanthus unipinna	0.0007619047619	0.0006932571429	8	0
	Cephalopholis argus	0.002333333333	0.3944722374	11	С
	Cephalopholis leopardus	0.00009523809524	0.002662155211	1	R
	Cephalopholis urodeta	0.02180952381	1.459086888	31	D
Forranidae	Epinephelus polyphekadion	0.00009523809524	0.1176589045	1	R
Jerranidae	Plectropomus laevis	0.0001428571429	0.2569702215	2	R
	Pseudanthias dispar	0.01333333333	0.003429130816	1	R
	Variola albimarginata	0.00009523809524	0.02584690103	2	R
	Variola louti	0.0001428571429	0.07879162143	2	R
Siganidae	Siganus spinus	0.00009523809524	0.02138523217	1	R
Sphyraenidae	Sphyraena barracuda	0.00009523809524	1.040571949	1	R
Synodontidae	Synodus variegatus	0.00009523809524	0.001555005527	1	R
	Arothron meleagris	0.00004761904762	0.02934125577	1	R
Tetraodontidae	Arothron nigropunctatus	0.000380952381	0.06850893333	4	0
ier acconticate	Canthigaster papua	0.000380952381	0.0003204759877	1	R
	Canthigaster solandri	0.002380952381	0.04581333348	8	0
Zanclidae	Zanclus cornutus	0.002523809524	0.5147573852	15	С

Appendix 4

CORAL DIVERSITY

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

Genus	Photoquadrats	Recruits
Acanthastrea	х	x
Acropora	x	x
Astrea	x	x
Astreopora	x	x
Coscinaraea	x	
Cyphastrea	×	×
Diploastrea	×	
Dipsastrea	x	×
Echinophyllia	х	
Echinopora	х	
Favites	х	х
Fungia	x	x
Galaxea	x	x
Gardineroseris	x	x
Goniastrea	x	x
Hydnophora	x	
Leptastrea	x	x
Leptoria	x	x
Lobophyllia	x	
Merulina	x	
Montipora	x	x
Pavona	x	x
Platygyra	x	
Pocillopora	x	x
Porites	x	
Psammocora	x	x
Sandalolithia	x	
Stylophora	x	
Symphyllia	x	
Turbinaria	х	

Appendix 5 SURVEY SITES MAP

FIGURE 29: Map of survey sites with labels.



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