Multi-decadal patterns and drivers of coral reef resilience and fish assemblages throughout American Samoa: implications for management

Technical report prepared for the Coral Reef Advisory Group, Pago Pago, American Samoa by
Alison L. Green[1], Alice Lawrence[2], Georgia Coward[2], Charles Birkeland[3],
Douglas Fenner[4], Motusaga Vaeoso[2], and Ivor Williams[5].
September 2022

[1] Alison Green Marine, Coombabah, Gold Coast, Australia aligreenfish9@gmail.com; [2] Previously Coral Reef Advisory Group, Department of Marine and Wildlife Resources, Pago Pago, American Samoa; [3] Department of Biology, University of Hawaii at Manoa, Honolulu, Hawaii, U.S.A.; [4] Coral Reef Consulting, Pago Pago, American Samoa; and [5] 6/25 Portland Gardens, Edinburgh, Scotland, United Kingdom.

Image 1 (Front Cover) *Coral reef on Ofu in the Manu'a Islands © Valentine Vaeoso.*

Citation: Green AL, Lawrence A, Coward G, Birkeland C, Fenner D, Vaeoso M, Williams I 2022 Multi-decadal patterns and drivers of coral reef resilience and fish assemblages throughout American Samoa: implications for management. Technical report prepared for Coral Reef Advisory Group, Pago Pago, American Samoa, 66 pp.

Acknowledgements

We thank the American Samoa Department of Marine and Wildlife Resources, Coral Reef Advisory Group, National Marine Sanctuary of American Samoa, Rose Atoll National Wildlife Refuge, U.S. Fish and Wildlife Service, and NOAA Coral Reef Conservation Program for funding and logistic support.

Image 2 *Survey team in 2018 from left to right: Alice Lawrence, Georgia Coward, Alison Green, Charles Birkeland. Doug Fenner and Motu Vaeoso.*

American Samoa
Historical Coral Reef Surveys
1994-2018

Table of Contents

List of Figures

List of Tables

List of Images

Executive Summary

Patterns and drivers of coral reef resilience and fish assemblages are described based on monitoring >30 sites spanning hundreds of kilometers throughout American Samoa over 24 years. Benthic communities (corals, other invertebrates and algae) have been resilient to large-scale disturbances at most sites due to the presence of natural resilience factors (good water quality, the prevalence of CCA and abundant herbivorous reef fishes), with coral cover increasing at the majority of islands and exposures over time. Some benthic communities on the main island of Tutuila have been less resilient, probably due to chronic impacts from land-based runoff.

Reef fishes closely associated with corals (e.g., some damsel and butterflyfishes) are thriving in response to resilient coral communities. Populations of fisheries species are lower (with fewer individuals ≥ 35 cm in size) on Tutuila compared to the Manu'a Islands and remote atolls, probably due to fishing pressure. Large species that are highly vulnerable to overfishing (i.e., sharks, large-bodied groupers and parrotfishes and humphead wrasses) are rare or uncommon throughout the Territory and encountered more frequently on remote atolls and in the Manu'a Islands than on Tutuila. Populations of some small to medium sized parrotfish species have increased over time, likely due to decreasing fishing pressure (and a ban on nighttime scuba spearfishing).

Coral communities are thriving in marine protected areas throughout the Territory due to the presence of natural resilience factors. However, biomass of fisheries species remains low in marine protected areas on Tutuila (including those designated as no take areas i.e., Fagatele Bay National Marine Sanctuary and Fagamalo Village MPA), which are not yet realizing their potential as effective fisheries management tools.

Rose Atoll National Wildlife Refuge is recovering from a phase shift following a ship grounding and associated fuel spill in 1993. Prior to the grounding, pink crustose coralline algae (CCA) dominated benthic communities. After the grounding, opportunistic turf algae and cyanobacteria dominated the substratum on two sides of the atoll for > 13 years, likely stimulated by iron leaching from the wreckage. Twenty-five years after the grounding, the United States Fish and Wildlife Service and the Department of Marine and Wildlife Resources have removed 95% of the wreckage, there has been a substantial decline in cover of opportunistic algae and pink CCA dominates most of the substratum on reef slopes again. However, a cyanobacteria bloom remains in the immediate vicinity of the grounding, possibly due to iron continuing to leach from the remaining wreckage.

Over the last few decades, there appears to have been a mass mortality of giant clams (*Tridacna* spp.) at Rose Atoll National Wildlife Refuge from an unknown cause. This is of great concern as the atoll was once an important refuge for giant clams that have been overfished throughout the rest of the archipelago.

Based on the results of this study, we recommend the following management actions to ensure the sustainability of coral reef resources throughout the Territory:

- Take a resilience-based approach to management to maintain or enhance coral reef resilience to local and global threats by improving watershed management (to reduce land-based runoff of sediments and other pollutants), improving management of functionally important species (e.g.., large parrotfishes), expanding monitoring programs to monitor ecological processes that influence reef resilience (e.g., coral recruitment, herbivory and water quality) and designing and implementing a resilient network of no take MPAs throughout the Territory.
- Improve fisheries management on Tutuila and Manu'a by enforcing existing and implementing new fisheries legislation and no take marine protected areas. In particular, there is an urgent need to protect species that are highly vulnerable to fishing pressure (sharks, large reef fishes and giant clams), which are rare or uncommon throughout the Territory.
- Conduct a comprehensive survey to confirm if the giant clam population has collapsed at Rose Atoll National Wildlife Refuge, determine the likely cause of the mass mortality, and explore management options to facilitate recovery of the population.
- Remove remaining wreckage from the ship grounding site at Rose Atoll National Wildlife Refuge. Repeat the detailed survey of reef flat algae conducted on the atoll in 1995 to document recovery. Compile a comprehensive report describing the recovery of the atoll from the ship grounding over the last 25 years, and the costs and benefits of the cleanup operation.
- Use the results of this study to develop report cards for local communities regarding the condition of their coral reef resources and recommendations for co- management.
- Continue long-term monitoring of coral reefs to support management in American Samoa. This includes repeating long-term monitoring throughout the archipelago (this study) every five years and repeating the more detailed long-term monitoring of Fagatele Bay National Marine Sanctuary and the Aua Transect in Pago Pago Harbor every three years.

Introduction

Local and global anthropogenic stressors are threatening the survival of coral reef ecosystems, and coral cover and associated fish assemblages have declined on many reefs worldwide (reviewed in Pratchett et al. 2008 and Souter et al. 2021). Several factors influence how coral reefs respond to natural and anthropogenic stressors, including drivers of coral reef resilience and other factors influencing associated fish assemblages.

Drivers of Coral Reef Resilience

Coral reefs vary in how they respond to stressors based on different internal (e.g., genetic) and external (e.g., environmental) factors (reviewed by McClanahan et al. 2012 and McLeod et al. 2019). Resilient reefs tend to have high coral and fish diversity, with heat-tolerant corals for resistance to stressors, and rapidly growing corals and high coral recruitment rates for recovery from disturbances (reviewed in McClanahan et al. 2012 and McLeod et al. 2019; Birkeland et al. 2021). Some functional groups (e.g., pink CCA and herbivorous reef fishes) can also play important roles in reef recovery by facilitating coral recruitment (reviewed by McLeod et al. 2019, Birkeland et al. 2021). Reefs with low resilience are often those with anthropogenic stressors (e.g., overfishing and land-based runoff of sediments and nutrients) that reduce coral resistance to other stressors and impede recovery (e.g., reviewed in McClanahan et al. 2012 and McLeod et al. 2019).

Some reefs recover from local and global stressors within years or decades, while others have not recovered many decades after a disturbance (e.g., Green et al. 1999; Birkeland et al. 2021). In some situations, reefs have experienced phase shifts from coral- to algal dominated systems (Jackson et al. 2014), with few documented examples of phase shift reversals (Bellwood et al. 2006). Consequently, coral reef resilience varies at a range of spatial (global, regional and local) and temporal (ecological and geological) scales (Birkeland et al. 2021; Souter et al. 2021).

Factors Influencing Coral Reef Fish Assemblages

Spatial and temporal patterns in coral reef fish assemblages vary in response to a variety of environmental drivers (e.g., reef type, geographic location, depth, wave energy, primary productivity, temperature and larval supply: e.g., Williams et al. 2015; Harborne et al. 2018). Habitat structure (particularly coral cover and topographic complexity) also plays a critical role in structuring reef fish assemblages, with significant declines in fish abundance, diversity and species composition following extensive coral loss and reduced topographic complexity associated with chronic and large-scale disturbances (reviewed in Pratchett et al. 2008 and Coker et al. 2014; Emslie et al. 2020). Highly specialized corallivores or small-bodied species (including many chaetodontids and pomacentrids) that rely on structurally complex corals (particularly branching, plate or digitate *Acropora* and *Pocillopora* spp.) for food and predator refuges are consistently among the worst affected following extensive coral loss. In contrast, dietary and habitat generalists (e.g., some herbivorous acanthurids and scarids) have increased in abundance following coral loss, and large predatory fishes (e.g., lutjanids, lethrinids and serranids) appear more resistant to most disturbances. However, there may still be longer-term negative consequences for any species that relies on live corals at settlement, for shelter or for coral dependent prey abundance.

Fishing pressure also leads to declines in density, biomass, and size composition of coral reef fisheries species, particularly heavily targeted, large-bodied and upper trophic level fishes such as apex predators (e.g., sharks and jacks) and excavating parrotfishes (reviewed in Sandin et al. 2008; Williams et al. 2015; Harborne et al. 2018). Consequently, several studies have demonstrated that reef fish biomass is typically several times higher (and dominated by apex predators) at remote reefs than in human-populated areas, while lower-trophic groups (e.g., small-bodied herbivores, planktivores and lower-level carnivores) dominate biomass on populated islands in the Pacific (reviewed in Williams et al. 2015).

Fishing pressure can also affect population size and structure of macroinvertebrates. For example, Green and Craig (1999) described how giant clams (*Tridacna* spp.) were overfished throughout the Samoan Archipelago, except at Rose Atoll National Wildlife Refuge that comprised the only viable population of giant clams in the archipelago.

Using Long-Term Monitoring to Examine Patterns and Drivers of Coral Reef Resilience and Fish Assemblages over Broad Spatial Scales in American Samoa

Many previous studies describing patterns and drivers of coral reef resilience and fish assemblages are either short-term or focused on a few locations (see reviews by Pratchett et al. 2008, McClanahan et al. 2012, Coker et al. 2014 and Williams et al. 2015), with few long-term (multi-decadal) studies over broad spatial scales (e.g., Emslie et al. 2020). In this study, we examine if the patterns and drivers of coral reef assemblages described above are consistent over broad temporal and spatial scales by monitoring benthic communities and fish assemblages on coral reefs over 24 years across hundreds of kilometers in American Samoa.

Coral Reefs and Associated Fisheries in American Samoa

American Samoa is a U.S. Territory comprising five volcanic islands with mostly narrow fringing coral reefs (Tutuila, Aunu'u, Ofu, Olosega and Ta'u) and two remote atolls (Rose and Swains: Fig. 1). Over the last four decades, American Samoa has experienced many large-scale disturbances and local anthropogenic stressors (Fig. 2) that have caused serious damage to coral reefs and associated fish assemblages (e.g., Green et al. 1999; Birkeland et al. 2021).

Samoans have relied on coral reef resources for food, livelihoods, and cultural practices for thousands of years, and coral reef fisheries are predominantly subsistence or small-scale artisanal (reviewed in Levine and Allen 2009). Over the last five decades, the human population has tripled on the main island of Tutuila, and fishing has become less prominent due to sociological changes associated with a shift from subsistence to a market economy. Consequently, coral reef fishing effort and catch have decreased substantially on Tutuila over the last 50 years (except from 1997 to 2000 when the catch increased dramatically due to nighttime scuba spearfishing, which was banned in 2001: reviewed in Levine and Allen 2009). In contrast, in the Manu'a Islands (Ofu, Olosega and Ta'u), the human population has declined, villagers continue to lead a more subsistence-based way of life, and fishing effort does not appear to have declined (reviewed in Levine and Allen 2009).

Over the last few decades, there have been different assessments regarding the status of coral reef resources and drivers of populations of fisheries species throughout the Territory (reviewed in Levine and Allen 2009). Several studies have reported that total reef fish and large fish biomass are lowest around Tutuila and in the Manu'a Islands and highest on the two uninhabited atolls, and there is a lack of large fishes and sharks throughout the Territory, primarily due to fishing pressure (e.g., Williams et al. 2015; Nadon et al. 2012). Others have suggested that decreasing catches on Tutuila are due to a combination of declining fishing pressure and habitat loss or degradation (e.g., from hurricanes), and that the fishery shows many characteristics of sustainability (e.g., stable or expanding fish populations: reviewed in Levine and Allen 2009).

This Study

In this study, we examine long term, broad scale patterns in the status of marine resources, drivers of coral reef resilience and other factors influencing coral reef fish assemblages, to inform conservation and management throughout American Samoa.

Fig. 1 Location of (a) each island in American Samoa (note the distance to Swains is not to scale) and (b-e) coral reefs, survey sites on reef slopes (10 m), topography and buildings on each island.

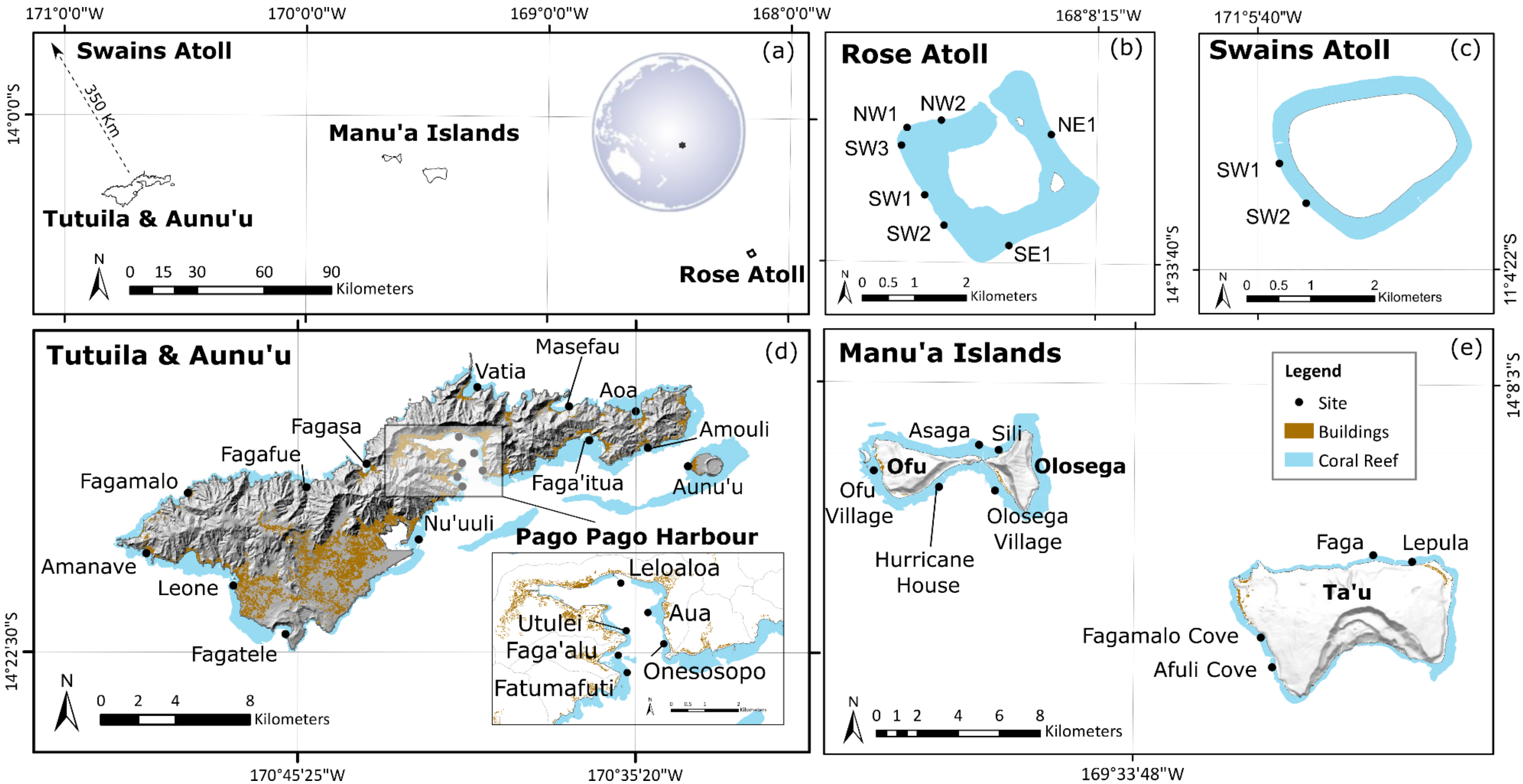
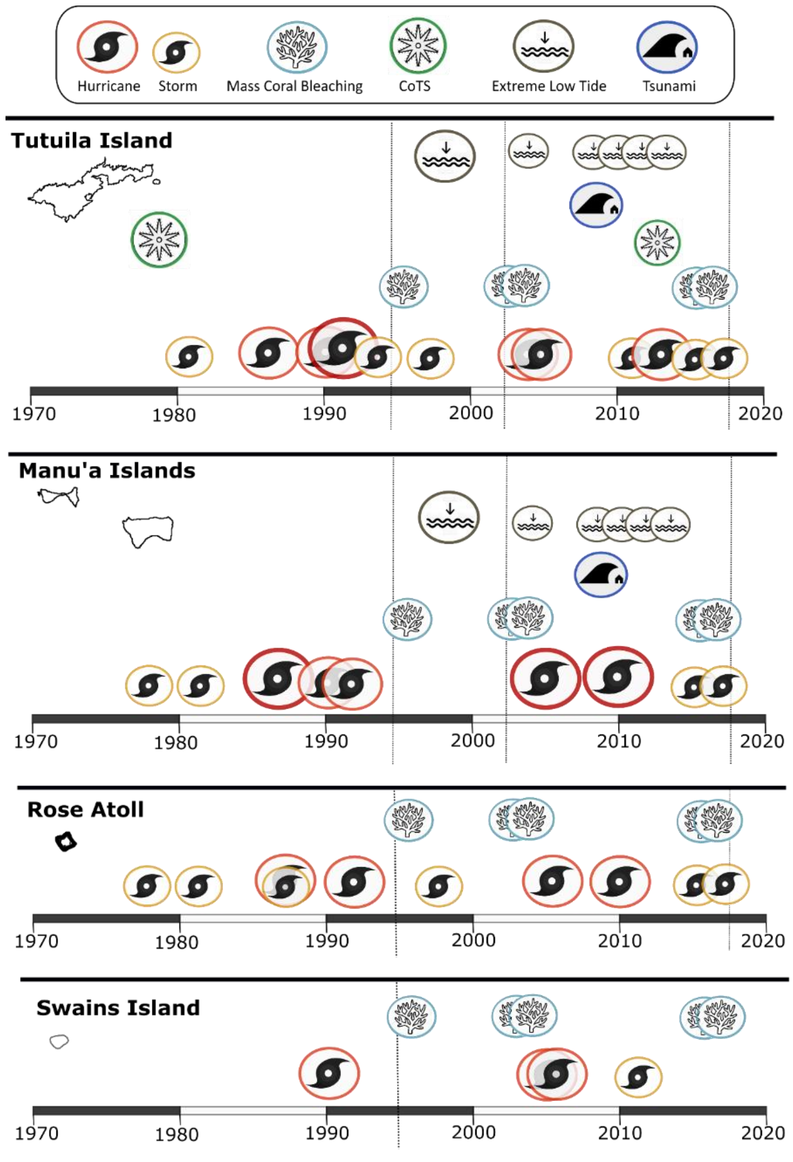


Fig. 2 Timing of acute large-scale disturbances that caused serious damage to coral reefs on each island in American Samoa over the last four decades. Dashed vertical lines indicate when we conducted surveys on each island in 1994/95, 2002 and 2018; and symbols indicate each type of disturbance.



Note: Hurricanes (64 to 145 knots) and storms (> 50 knots) are those that had maximum sustained wind speeds above 50 knots that may have caused severe damage to reef structure (see Done, 1992; Puotinen et al. 2007; Fabricius et al. 2008). The size of the hurricane symbols denotes the likely scale of the impact on each island based on hurricane tracks and maximum sustained wind speeds derived from NOAA NCDC International Best Track Archive for Climate Stewardship (IBTrACS) website (https://www.ncdc.noaa.gov/ibtracs/index.php?name=ib-v4-access). The large symbol denotes hurricanes that passed directly over or within 20 nm of the island, and the small hurricane symbol denotes hurricanes that passed ≥20 nm or more from the island. Storms are those with wind speeds above 50 knots that passed within 200 nm of the islands. Other sources of information include: for crown-of-thorns starfish (CoTS: Birkeland 1979; Clark, 2015); for mass coral bleaching (observations by AG and DF); for extreme low tides (Birkeland et al. 2004; and observations by AG and DF); for the tsunami (Fenner 2011).

Materials and Methods

Study Area

American Samoa comprises seven islands, six in the Samoan Archipelago and one (Swains) in the Tokelau group (350 km north: Fig. 1). Tutuila is the largest island with 98% of the population (approximately 49,710 people: USCB 2020), and Aunu'u is a small island off Tutuila. The Manu'a Islands (Ofu, Olosega, and Ta'u) are small and comprise 2% of the population. The two remote atolls (Rose and Swains) are uninhabited.

Large-scale disturbances have caused serious damage to coral reefs on different islands at different times over the last four decades (Fig. 2). There have been five major hurricanes, numerous storms, five mass coral bleaching events, two crown-of-thorns starfish (CoTS) outbreaks, an extreme low tide event, and a tsunami.

Reefs on the southern sides of the islands are exposed to southeast trade winds (although Pago Pago Harbor is more sheltered), while those on the northern sides are protected from trade winds but tend to be more affected by hurricanes and storms (Image 3).

Image 3 *Coral reefs with different exposures: northern and southern sides of Ofu-Olosega (left) and Pago Harbor on Tutuila (right) © Valentine Vaeoso.*

Some reefs on Tutuila appear to have experienced habitat loss or degradation from ship groundings, watershed development and poor land use practices (leading to runoff of pollution, sediments and nutrients: Table 1). These stressors are generally lower in Manu'a and on the atolls (Table 1).

American Samoa manages their coral reefs through Local Action Strategies addressing land-based sources of pollution, fisheries and climate change (Levin and Allen 2009). The Territory also has a goal to protect 20% of reefs in no-take marine protected areas (MPAs: Raynal et al.

2016). Currently, there are 27 MPAs encompassing 25% of the reef area, with 7% designated as no-take areas (NTAs: Raynal et al. 2016). Federal, territorial governments and/or villages manage the MPAs. However, many village based MPAs are inactive.

In 1993, a fishing vessel ran aground on the southwest side of Rose Atoll National Wildlife Refuge (SW1 in Fig. 1), spilling 100,000 gallons of pollutants and 300 tons of metal onto the reef (Green et al. 1997). The pollutants flowed over the reef into the lagoon on the southwest side and exited via the channel and adjacent reef flat on the northwest side (Green et al. 1997, Image 4).

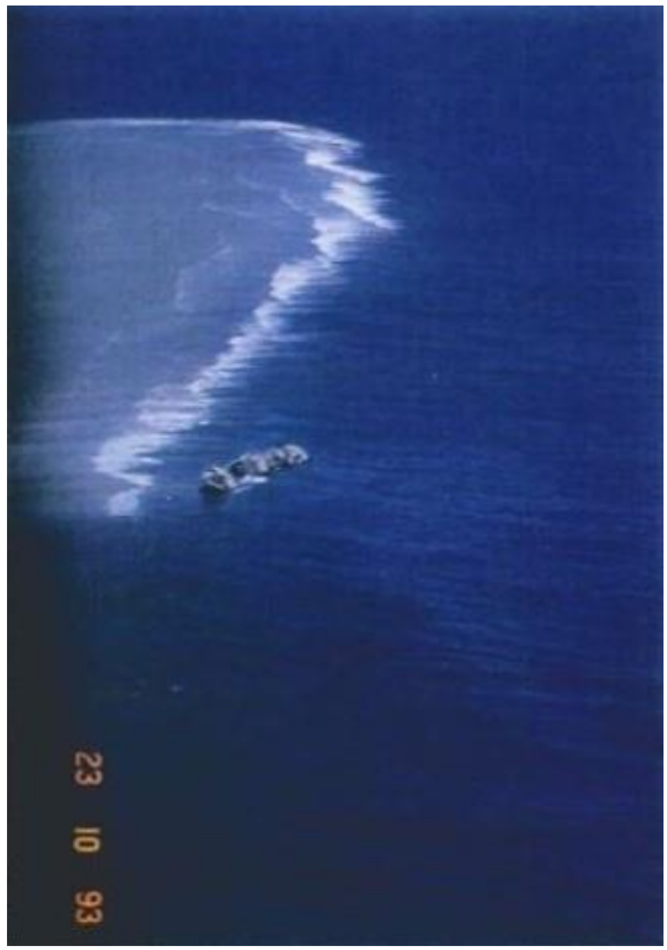


Image 4 *Ship grounding at Rose Atoll (right), showing the contaminant spill flowing over the reef north of the vessel (from Green et al. 1997).*

Prior to the grounding, reef-building CCA dominated benthic communities at Rose. The grounding and associated contaminants caused a rapid die-off of CCA on the southwest and northwest sides of the atoll, which was replaced by opportunistic turf algae and cyanobacteria, likely stimulated by dissolved iron from the wreckage (Green et al. 1997). Over the last 18 years, the U.S. Fish and Wildlife Service and American Samoa Department of Marine and Wildlife Resources have removed 95% of the wreckage costing approximately 1.3 million USD (B. Peck, USFWS *pers. comm.*).

Survey Sites, Times and Methods

We surveyed benthic communities and coral reef fish assemblages at 26 to 35 sites on different exposures on five to seven islands in American Samoa in 1994/95, 2002 and 2018 (Fig. 1, Appendix 1). Sites varied in environmental characteristics (e.g., wave exposure), chronic stresses (watershed development and fishing pressure) and MPA status (Table 1).

At each site, we surveyed reef slopes (10 m) where fish species richness, density and biomass tend to be highest (Green 1996) and coral reef fisheries are focused (Levine and Allen, 2009). One observer (ALG) used underwater visual census (UVC) methods to monitor abundance, size (total length in cm) and species richness of fishes amenable to UVC (see Appendix 2 Electronic Supporting Information 1) along three to five 50 m x 3 m belt transects at each site surveyed each year (Appendix 1). We surveyed different species on three passes of the transects: large, highly mobile species (e.g., scarids, lutjanids and lethrinids) on the first pass; medium sized mobile species (e.g., most acanthurids, chaetodontids and labrids) on the second pass; and small, site attached species (mostly pomacentrids) on the third pass (Image 5).

Image 5 *Reef fishes surveyed on the first (left), second (middle) and third (right) pass of the transect.*

We surveyed benthic communities on the fish transects by recording substratum type at three points (under the tape, and 1 m either side) at 25 2-m intervals along each transect (75 points per transect). At each point, we recorded the substratum as belonging to different non-living (reef matrix, sand, rubble or crevice/hole) or lifeform categories (plate, massive, digitate, branching, encrusting, mushroom or foliaceous coral; pink CCA, turf algae, cyanobacteria and other macroalgae; and other: sensu English et al. 1997, Image 6).

Image 6 *Corals categories include branching (left), plate, foliaceus and digitate (middle), massive and encrusting (right) lifeforms.*

We surveyed the abundance and size of giant clams (*Tridacna* spp.: Image 7) along the 50 m fish transects on reef slopes (10 m) in 1994/95, 2002 and 2018 (Appendix 1), using a transect width of 2 m. We also surveyed giant clams on 14 (in 1994/95) and six (in 2018) of the 15 flat topped, steep sided lagoon pinnacles (Fig. 3) at Rose Atoll where Green and Craig (1999) recorded the highest densities of giant clams in the Samoan Archipelago. We surveyed each pinnacle using a single transect (50 m x 2 m where possible) at each of three depths: along the top (exposed at low tide), around the side at 3 m and around the base at 10 m. On each transect, we counted and recorded maximum shell length of live clams in each survey. In 2018, we also recorded recently dead (still intact *in situ*) and long dead (shells that were old, eroded, or laying loose on the substratum) clams at Rose. Minimum size of clams reliably detected was 2 cm.

Image 7 *Faisua (Tridacna spp.).*

Fig. 3 A lagoon pinnacle (below) and the location of the lagoon pinnacles surveyed for giant clams at Rose Atoll in 1994/95 and 2018 (right).

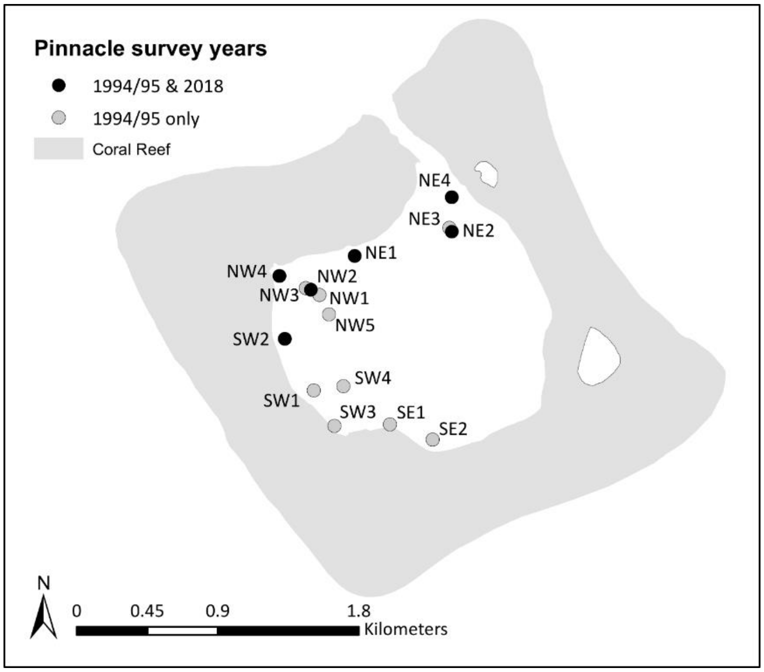


Table 1 Environmental characteristics (wave exposure and slope), chronic stressors (watershed development and relative fishing pressure) and marine protected area (MPA) type, management agency[1] and fishing restrictions (if applicable) of each survey site. Relative fishing pressure[2] is calculated based on the size of the resident human population[3] divided by reef area <30 m deep[4] on each island.

Island	Exposure	Site	MPA type, management agency and fisheries restrictions	Environmental Characteristics		Chronic Stressors	
				Wave Exposure	Slope	Watershed Development	Relative Fishing Pressure
Tutuila	NE	Aoa	VMPA subsistence fishing only	Semi exposed	Moderate	High	High
		Masefau		Wave sheltered	Moderate	Medium	High
		Vatia	VMPA subsistence fishing only	Semi exposed	Moderate	Medium	High
	NW	Fagafue		Wave sheltered	Moderate	Medium	High
		Fagamalo	VMPA no take	Semi exposed	Moderate	Low	High
		Fagasa		Wave sheltered	Moderate	Medium	High
	Harbour	Aua		Wave sheltered	Steep	High	High
		Fagaalu		Semi exposed	Moderate	High	High
		Leloaloa		Wave sheltered	Gradual	High	High
		Onesosopo		Wave sheltered	Steep	High	High
		Utulei		Wave sheltered	Steep	High	High
	SE	Amouli		Exposed	Moderate	High	High
		Fagaitua		Semi exposed	Gradual	High	High
		Fatumafuti		Exposed	Steep	High	High
		Nuuuli		Exposed	Steep	High	High
	Aunu'u	Aunu'u		Semi exposed	Steep	Low	High
	SW	Amanave	VMPA subsistence fishing only	Semi exposed	Moderate	Medium	High

[1] NMSAS = National Marine Sanctuary of American Samoa; NPAS =National Park of American Samoa; NMFS = National Marine Fisheries Service; USFWS = United States Fish and Wildlife Service; and VMPA = Village MPAs (co-managed by the territorial government and local communities).
[2] High is 10.0 residents/ha, moderate is 0.3 to 0.6 residents/ha, and low is 0 residents/ha.
[3] Tutuila is 48,878, Ofu and Olosega is 279, Ta'u is 553, and Rose and Swains are 0 (USCB 2020).
[4] Tutuila = 4,888 ha, Ofu and Olosega = 1,055 ha, Ta'u = 1,003 ha, Rose = 110 ha and Swains = 281 ha (Williams *et al.* 2015).

Island	Exposure	Site	MPA type, management agency and fisheries restrictions	Environmental Characteristics		Chronic Stressors	
				Wave Exposure	Slope	Watershed Development	Relative Fishing Pressure
		Fagatele	NMSAS no take	Semi exposed	Gradual	Low	High
		Leone		Semi exposed	Gradual	High	High
Ofu-Olosega	NE	Asaga		Semi exposed	Gradual	Low	Moderate
		Sili		Semi exposed	Moderate	Low	Moderate
	SW	Hurricane House	NPAS subsistence fishing only	Exposed	Moderate	Low	Moderate
		Ofu Village		Semi exposed	Gradual	Low	Moderate
		Olosega Village		Semi exposed	Moderate	Low	Moderate
Ta'u	NE	Faga		Semi exposed	Moderate	Low	Moderate
		Lepula		Semi exposed	Moderate	Low	Moderate
	SW	Afuli Cove		Semi exposed	Moderate	Low	Moderate
		Fagamalo Cove	NMSAS open to fishing	Semi exposed	Gradual	Low	Moderate
Rose	NE	NE1	NMFS/USFWS no take	Exposed	Moderate	Low	Low
	NW	NW1	NMFS/USFWS no take	Semi exposed	Moderate	Low	Low
		NW2	NMFS/USFWS no take	Semi exposed	Moderate	Low	Low
	SE	SE1	NMFS/USFWS no take	Exposed	Moderate	Low	Low
	SW	SW1	NMFS/USFWS no take	Semi exposed	Moderate	Low	Low
		SW2	NMFS/USFWS no take	Semi exposed	Moderate	Low	Low
		SW3	NMFS/USFWS no take	Semi exposed	Moderate	Low	Low
Swains	SW	SW1	NMSAS open to fishing	semi exposed	Moderate	Low	Low
		SW2	NMSAS open to fishing	semi exposed	Moderate	Low	Low

Communications

After we completed our most recent survey in 2018, we provided preliminary results of our long-term, broad scale monitoring and key messages for management to government agencies, local communities, and other stakeholders in an information sheet entitled *How are American Samoa's Coral Reefs Doing? Results from long-term monitoring conducted over the last 25 to 40 years* (Appendix 3). In this technical report, we examine our results in more detail (see below).

Electronic Databases

We compiled the results from our long term, broad scale monitoring throughout American Samoa into three electronic databases for data analysis, one each for benthic communities, coral reef fishes, and giant clams (Appendix 2). These databases are an important resource for science, conservation, and management in American Samoa, and are available as supplementary information for this report upon request (Appendix 2).

Data Analyses

We focused our analysis of spatial and temporal patterns in benthic communities on cover of lifeform categories (i.e., all corals, coral by lifeform, CCA, turf and macroalgae). For fish assemblages, we focused on total species richness (number of species observed per survey transect), total density (number of individuals ha^{-1}) and total biomass (kg ha^{-1}); as well as on biomass of targeted fishes, one of the most abundant targeted fish families (Scaridae), and a relatively common targeted grouper (*Cephalopholis argus*). Targeted fishes included coral reef fish families harvested in the Territory (WPRFMC 2009), which were relatively abundant on the transects: Acanthuridae, Carangidae, Lutjanidae, Lethrinidae, Mullidae, Scaridae and Serranidae (Epinephelinae).

We derived fish biomass from survey data using the allometric length-weight conversion formulae: weight(g)=a*((length(cm)^{b}) where a and b are length-weight conversion parameters for each species (see Appendix 2 Electronic Supporting Information 1). As we conducted surveys throughout the year (Appendix 1), we removed fishes that we nominally considered 'young-of-year' (individuals <30% of their species` maximum length: Electronic Supporting Information 1) from the analyses to avoid effects caused by ephemeral mass recruitment events e.g., by *pala'ia* (*Ctenochaetus striatus*: see Green 2002).

We also used the cover of corals that provide most of the topographic complexity (branching, digitate, plate and foliaceous lifeforms: BDPF; Image 6) to investigate the influence of changes in habitat characteristics on two coral reef fish families: chaetodontids and pomacentrids.

We used bootstrapping to assess changes in benthic communities and fish assemblages over time, specifically between the first (1994/5) and most recent (2018) sampling periods, using only sites surveyed in both surveys (Appendix 1). We grouped sites by island and exposure (e.g., 'Tutuila SE') and used these as the base spatial units for analysis, excluding two spatial units ('Rose SE' and 'Tutuila Aunu'u') with only one site surveyed in both sampling periods. We calculated the mean and confidence intervals of the difference in fish density, biomass, or richness, and cover of lifeforms, between time-periods using the *boot* package in R (Canty and Ripley 2019) and used 5,000 bootstrap iterations to estimate the mean and quantile ranges of the difference between the two sampling periods for each metric. For fish metrics, we converted those to proportional changes over the 1994/5-2018 period (e.g., a change equivalent to a doubling of biomass would take the value 2). Quantile ranges are equivalent to confidence intervals, and we considered changes between sampling periods to be significant (i.e., we have 95% confidence that the metric had changed over time) if 95% confidence intervals do not overlap 1 in the case of fishes (being proportional metrics) and 0 for benthic metrics (being absolute measures).

We also compared size distributions (biomass per size bin [e.g., 10-20 cm]) of some fisheries species (Scaridae and *Cephalopholis argus*) among islands and times, and calculated encounter rates (percentage of transects on which a species was observed) for species highly vulnerable to fishing pressure (sharks and large-bodied groupers, wrasse, parrotfishes and snapper: Abesamis et al. 2014).

We compared the density and size structure of giant clams among locations and years using three size bins (recruits $\leq$ 5 cm, immature 6-11 cm, and mature $\geq$12 cm) based on a growth and maturity study of *Tridacna maxima* Rose Atoll (Radtke 1985, Green and Craig 1999).

Results

Benthic Communities

Following two devastating hurricanes (Fig. 2), coral cover was low to moderate (<20 to <40%) and predominantly encrusting and massive lifeforms, at most islands and exposures throughout the Territory in 1994/5, and reefs were dominated by CCA, other algae and non-living substratum (Figs. 4 to 7, Electronic Supporting Information 2). The exception was at Swains (which was less affected by the hurricanes), where very high cover (83 to 100%) of CCA, branching (predominantly *Pocillopora*) and foliaceous corals dominated the substratum.

Coral cover was significantly higher on most islands and exposures in 2018 than in 1994/95 (Figs. 4 to 7, Electronic Supporting Information 2 and 3), generally replacing algae and non-living substratum. Exceptions were the northeast and southeast exposures of Tutuila, likely due to variations among sites associated with different environmental characteristics and chronic stressors (Table 1, Figs. 4 to 7).

On Tutuila's northeast exposure, total coral cover was already high (mostly encrusting coral) at Vatia (a semi-exposed reef with medium watershed development) in 1994/95 and did not increase over time, although there was a significant increase in BDPF coral cover (Figs. 4 and 5). In contrast, coral cover increased at another semi-exposed site with high watershed development (Aoa) and decreased at a wave-sheltered site with medium watershed development that experienced recent mass coral bleaching and a CoTS outbreak (Masefau).

On Tutuila's southeast exposure, coral cover increased at two sites in semi-exposed or exposed bays (Fagaitua and Amouli) but remained about the same at two sites most exposed to wave action during storms (Nu'uuli and Fatumafuti).

Elsewhere on Tutuila, increases in coral cover were moderate to high from 1994/5 to 2018 at some semi-exposed sites with low to medium watershed development (e.g., Fagatele and Amanave on the southwest side), predominantly due to an increase in BDPF corals (Fig. 5). At other sites in sheltered bays with medium to high watershed development and high sediment loads (e.g., Fagafue and Fagasa in the northwest, and Aua and Utulei in the Harbor), increases in coral cover were relatively low and cover remained dominated by encrusting and massive corals.

In the Manu'a Islands, coral cover was significantly higher in 2018 than 1994/95 due to a significant increase in most lifeforms (Figs. 4 and 6).

At Rose Atoll in 1994/95, benthic communities on the northwest side comprised a moderate to high cover of pink CCA, other algae and reef matrix, and very low coral cover (Figs. 4, 7 and 8). In contrast, benthic communities on the southwest side were dominated by a very high cover of turf/bare matrix, and a low to moderate cover of CCA and coral. At the ship-grounding site (SW1), CCA cover was very low and 16% of the area was covered by cyanobacteria (Fig. 8). Cyanobacteria was also present at the other two southwest sites.

By 2018, coral cover (mostly branching, massive and encrusting lifeforms) had increased significantly to moderate to high levels (21 to 48%) on both the northwest and southwest sides of Rose (Figs. 4, 7 and 8). On the southwest side, turf/bare matrix had decreased significantly and CCA and macroalgae cover had increased significantly (Figs. 4, 7 and 8). There was no significant change in cover of CCA and turf/bare matrix on the northwest side (Figs. 4, 7 and 8), although macroalgae cover declined at NW1 and cyanobacteria increased (especially at NW2: Fig. 8). Cyanobacteria still comprised 16% of the cover at the ship-grounding site, although it had declined to no or very low cover at other southwest sites (Fig. 8).

Satellite and aerial images show that prior to the ship grounding, the reef flat at Rose was dominated by a uniform cover of pink CCA (Fig. 9a, see also Green et al. 1997). One year after the grounding, large areas of the reef flat on the southwest and northwest sides were covered in black opportunistic turf algae and cyanobacteria (Fig. 9b: see also Green et al. 1997), particularly at the grounding site (Fig. 9c). Eighteen years after the grounding, black opportunistic turf algae and cyanobacteria is mosty limited to the immediate vicinity of the grounding site (Fig. 9d).

Fig. 4 Left: Cover of (a-d) corals (total, and major lifeforms), (e) pink crustose coralline algae, (f) turf/bare matrix and (g) macroalgae at sites surveyed on each island and exposure in all three surveys in 1994/5, 2002 and 2018 in American Samoa (colors denote different sites). Right: Values for bootstrap analysis showing mean change from 1994/5 to 2018 and 95% confidence intervals for each lifeform. Confidence intervals that do not overlap zero (shown as red or green) are taken as evidence of significant change.

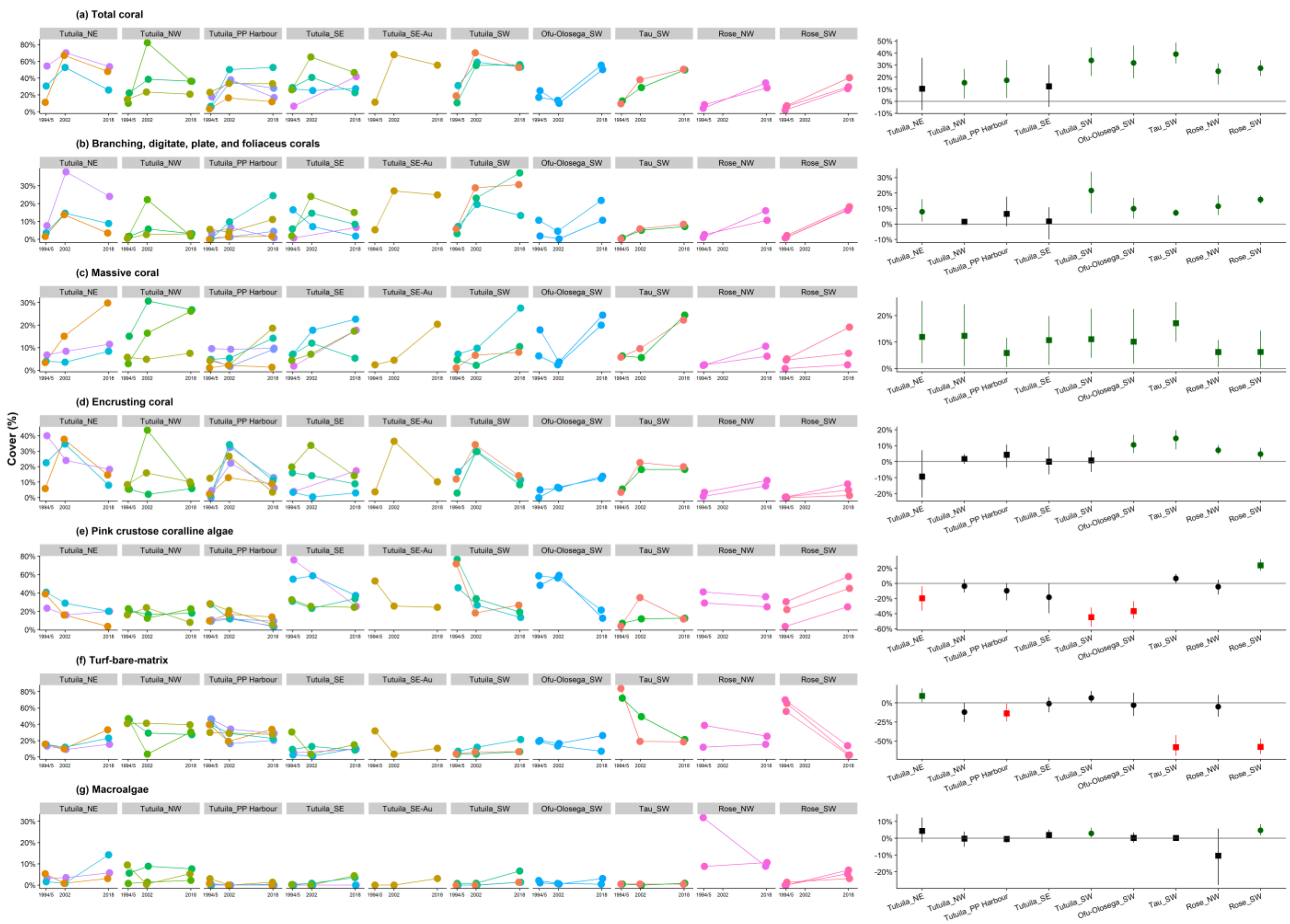


Fig. 5 Spatial and temporal patterns of benthic lifeforms and fish assemblages surveyed at each site on Tutuila and Aunu'u in 1994/1995, 2002 and 2018 including: a) percent cover of benthic lifeforms; b) percent cover of coral lifeforms; c) total fish species richness (number per transect); d) total fish density (number of individuals per ha) and e) total fish biomass (kg per ha:). Note: Young of the year (YOY) removed from fish dataset.

.

Fig. 6 Spatial and temporal patterns of benthic lifeforms and fish assemblages surveyed at each site in the Manu'a Islands (Ofu-Olosega and Ta'u) in 1994/1995, 2002 and 2018 including: a) percent cover of benthic lifeforms; b) percent cover of coral lifeforms; c) total fish species richness (number per transect); d) total fish density (number of individuals per ha) and e) total fish biomass (kg per ha:). Note: Young of the year (YOY) removed from fish dataset.

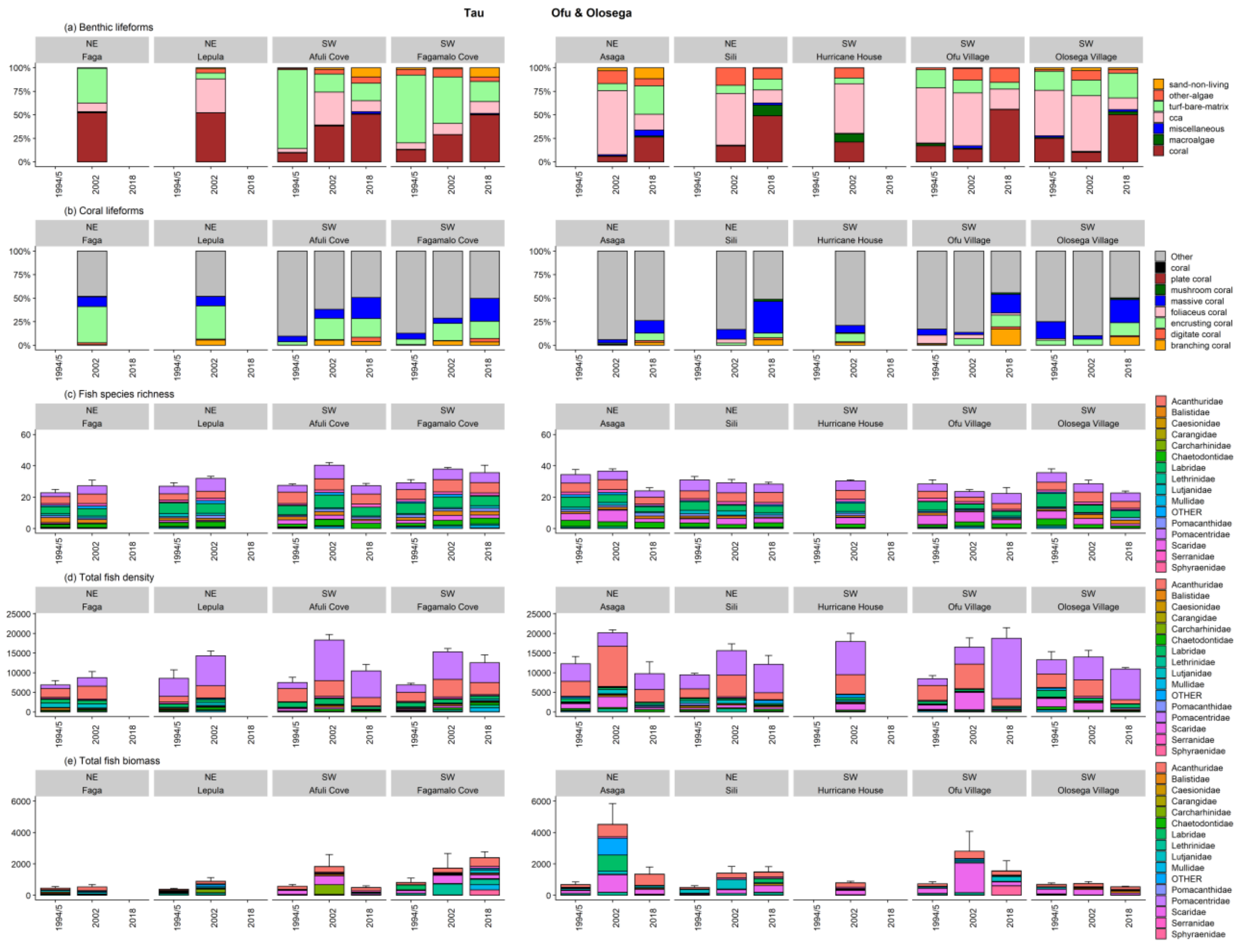


Fig. 7 Spatial and temporal patterns of benthic lifeforms and fish assemblages surveyed at each site on Rose and Swains Atolls in 1994/1995, 2002 and 2018 including: a) percent cover of benthic lifeforms; b) percent cover of coral lifeforms; c) total fish species richness (number per transect); d) total fish density (number of individuals per ha) and e) total fish biomass (kg per ha:). Note: Young of the year (YOY) removed from fish dataset.

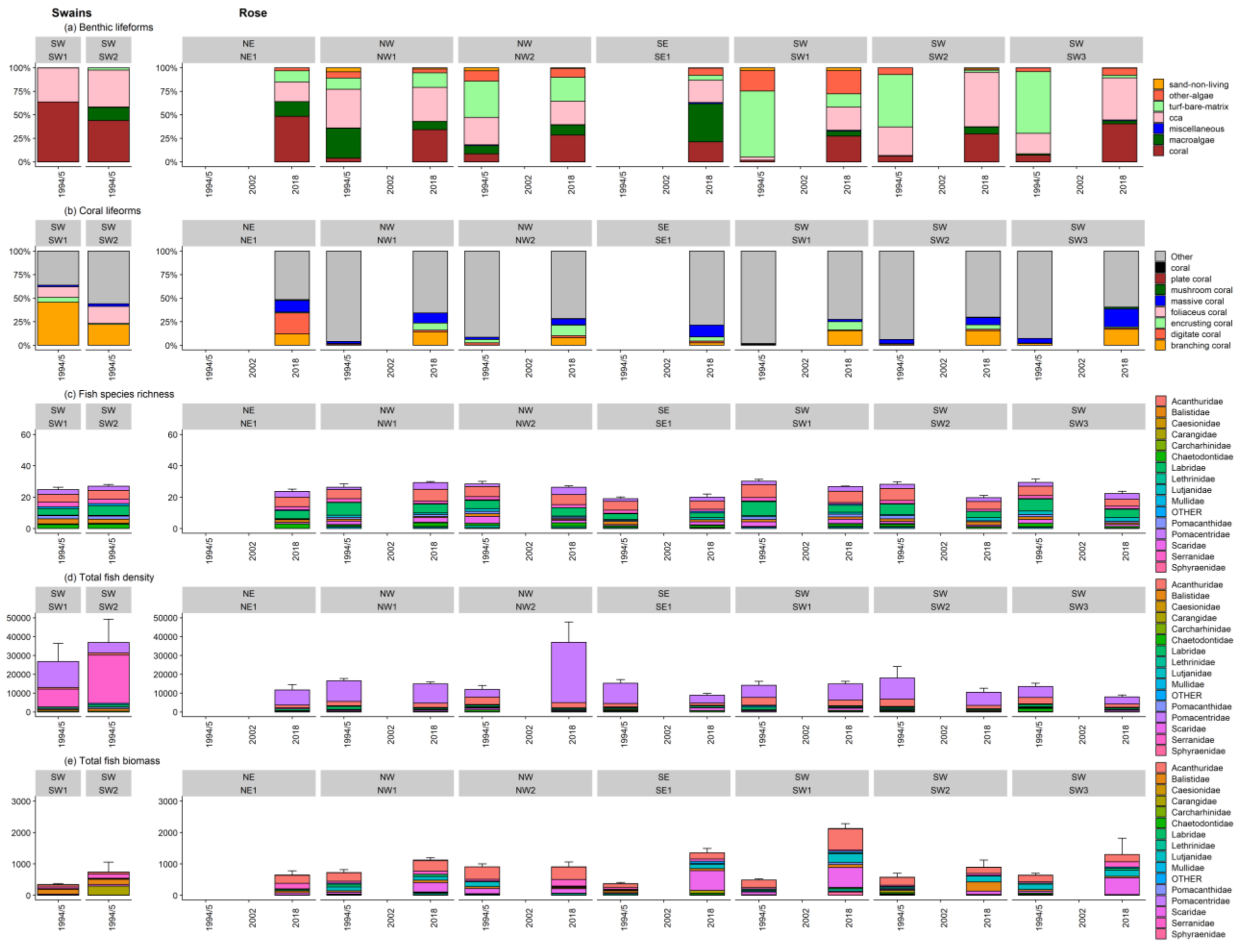


Fig. 8 Cover of (a) benthic lifeforms and (b) coral lifeforms, and (c) biomass of herbivorous scarids and acanthurids at sites surveyed in both 1994/95 and 2018 at Rose Atoll. SW1 is the ship-grounding site.

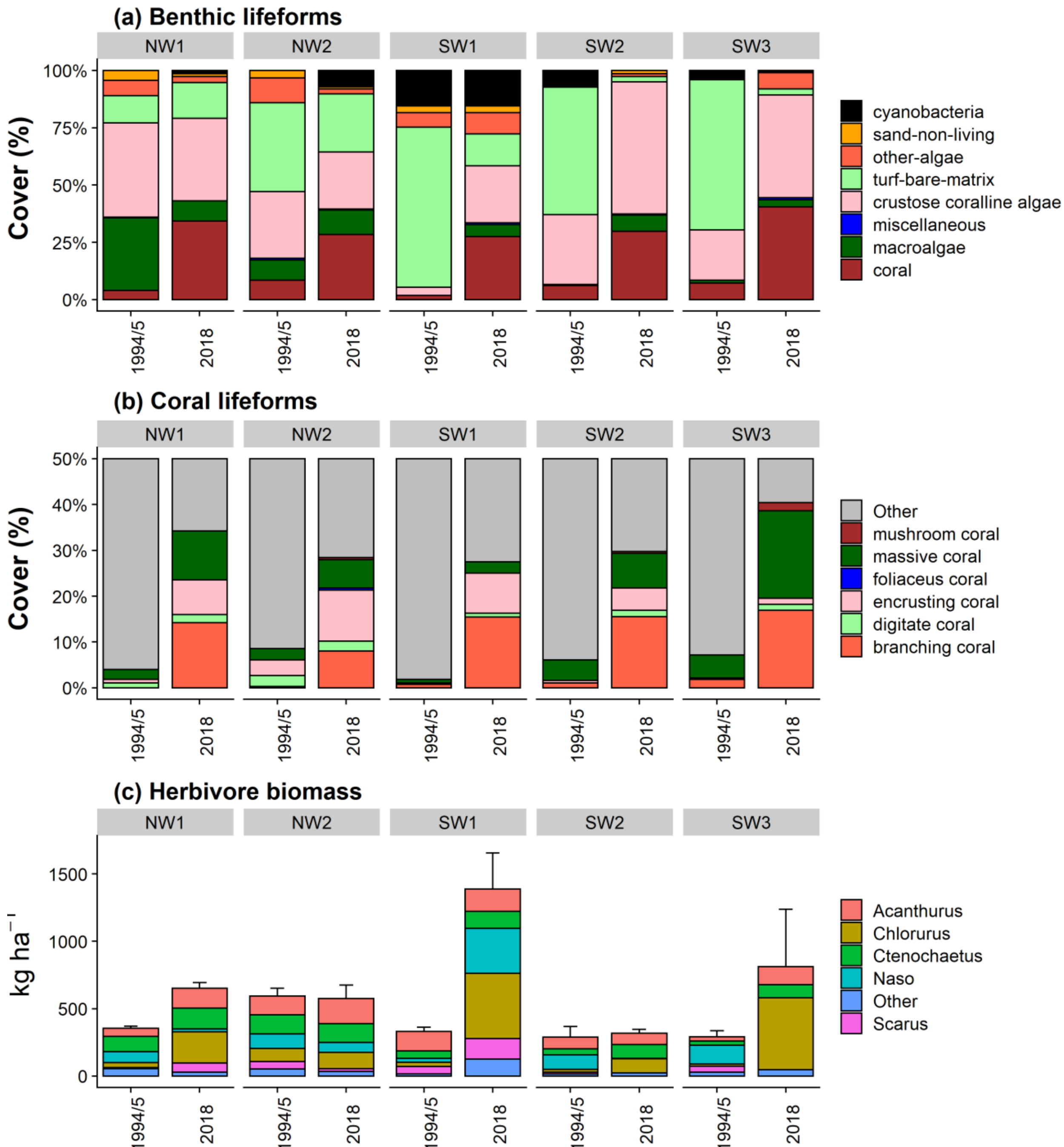
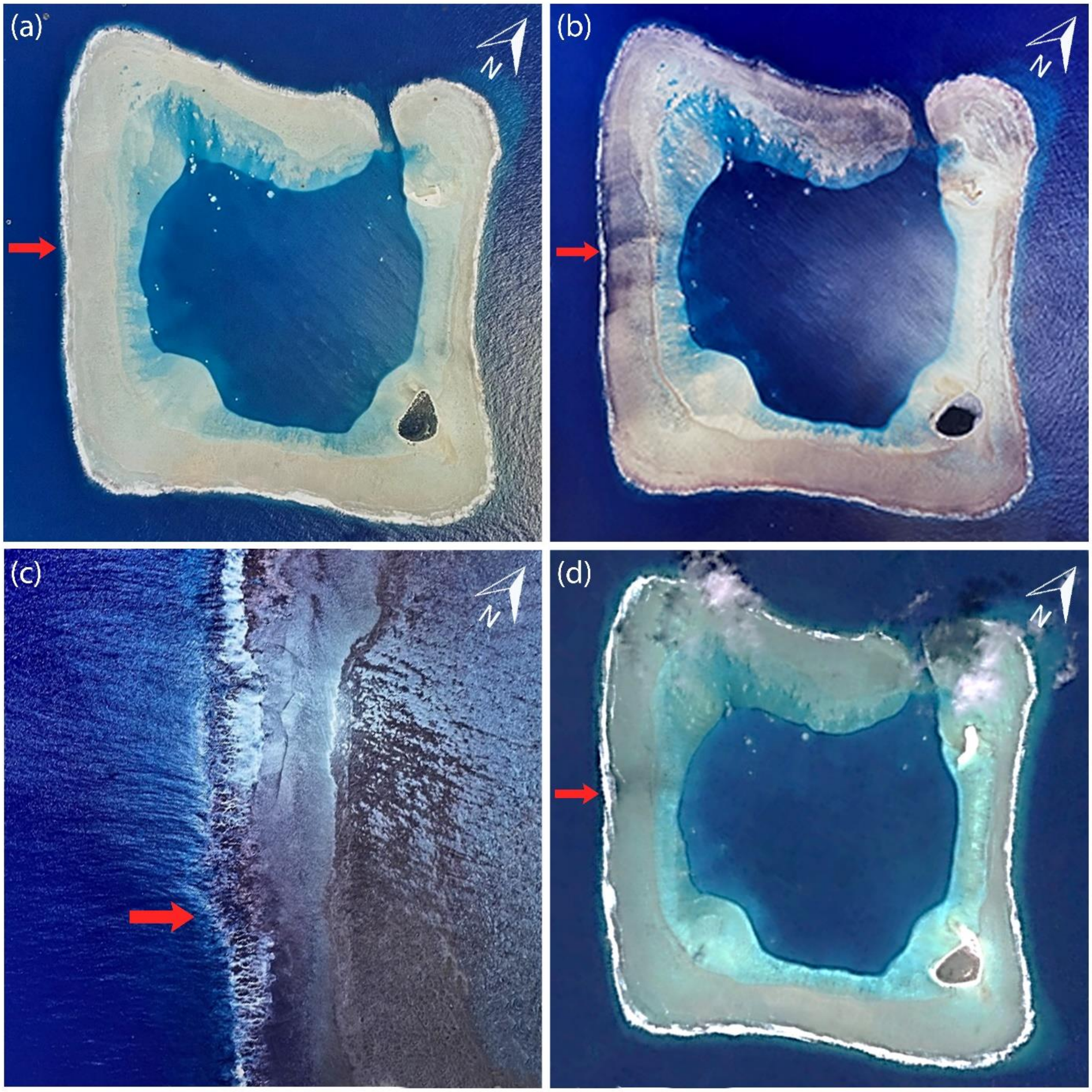


Fig. 9 Satellite and aerial images of Rose Atoll: (a) prior to the ship grounding in 1993 (October 1990); (b-c) one year after the grounding including in the immediate vicintiy of the grounding site (red arrow: October 1994); and (d) 18 years after the grounding (Google Earth NOAA 2021).



Coral Reef Fish Assemblages

We surveyed 122,830 individuals from 285 fish species in 36 families on 372 transects (distance = 18.6 km) throughout American Samoa over 24 years (Appendix 1 and Electronic Supporting Information 1) during > 550 hours of UVC.

Species Composition

Species composition varied among islands (see Electronic Supporting Information 1). Several species abundant on Swains were only recorded there (*Luzonichthys whitleyi*, *Ctenochaetus hawaiiensis, Zebrasoma rostratum* and *Pseudocheilinus tetrataenia*), and were replaced by other species on the volcanic islands and Rose (e.g., *Pseudanthias pascalus*, *Ctenochaetus striatus*, *Zebrasoma veliferum* and *Pseudocheilinus hexataenia*). Some species were also more abundant or only present on the two atolls (*Centropyge loricula* and *Chromis acares*), Rose (*Acanthurus achilles, Ctenochaetus cyanocheilus* and *Hemitaurichthys thompsoni*), or the volcanic islands (e.g., *Ctenochaetus striatus, Hemitaurichthys polylepis*, *Chromis xanthura*, *Chrysiptera taupou*, *Pomacentrus brachialis* and *Pomacentrus vaiuli).*

Species Richness

Species richness tended to be moderate to high (20 to >30 species per transect) at most sites, irrespective of whether coral cover (including BDPF) was high or low (e.g., Vatia, Aunu'u and Aua: Figs. 5 to 7 and 10). Although species richness was lowest at sites with high sediment loads and low cover of mostly massive and encrusting corals (Fagafue and Faga'alu: Table 1) or at exposed sites where coral cover is low (e.g., Rose SE1).

Species richness did not change significantly from 1994/5 to 2018 on most islands and exposures, despite significant increases in coral cover (Figs. 4 to 7 and 10, Electronic Supporting Information 1 and 3). Exceptions were an increase in species richness on northwest Tutuila along with increased coral cover and decreases on southwest Rose and Ofu-Olosega despite increases in coral cover. In some situations, the lack of a significant difference in species richness over time was because patterns varied among sites e.g., despite an increase in coral (including BDPF) cover on southwest Tutuila, species richness increased or was similar at two sites (Amanave and Leone) and declined at the third (Fagatele).

Density

Total density was lowest on islands and exposures in 1994/95, and significantly higher at four of five exposures on Tutuila (all except the northwest) and at southwest Ta'u in 2018 (Figs. 5 to 7 and 10, Electronic Supporting Information 1 and 3). Pomacentrids were the most abundant family and contributed most to changes in density, although other families also contributed to higher abundances at some sites and times e.g., roving acanthurids at Asaga on Ofu (Image 5, middle photo), and anthiids at Swains.

The abundance of some families and species varied with changes in benthic communities (Fig. 11). For example, some chaetodontid species showed a generally positive relationship with increasing cover of BDPF corals from 1994/5 to 2018 (e.g., *Chaetodon ornatissimus,* and to a lesser extent *Chaetodon trifascialis*), while others did not (e.g., *Chaetodon unimaculatus*). Similarly, some pomacentrid species (particularly *Plectroglyphidodon dickii*) showed a strong positive relationship with increasing cover of BDPF corals, while others did not (e.g., *Chysiptera taupou* and *Pomacentrus vaiuli*).

We recorded the highest densities at sites with different habitat characteristics, due to high densities of different pomacentrid species (Electronic Supporting Information 1). For example, some of the highest densities we recorded were at sites where BDPF coral cover was moderate to high (e.g., Vatia and Amanave), primarily due to the abundance of *Chromis xanthura* and *Plectroglyphidodon dickii*. Density was also high at some sites with low to moderate coral cover due to the abundance of *Pomacentrus brachialis* and *Pomacentrus vaiuli* (e.g., at Aua or Fatumafuti) and *Chromis acares* (on Rose and Swains). The lowest densities we recorded were at sheltered sites with medium to high watershed development, high sediment loads and low coral cover (e.g., Fagafue).

Biomass

Total biomass, targeted fishes biomass and scarid biomass significantly increased between 1994/5 and 2018 at most exposures on Tutuila, and at southwest Rose and northeast Ofu-Olosega (for targeted fishes only) (Fig. 10, Electronic Supporting Information 1 and 3). There were no significant differences in biomass at most exposures in Manu'a between 1994/95 and 2018 (Fig. 10).

We recorded the highest total biomass at Nu'uuli, Aua, Masefau and Fagaitua on Tutuila, Asaga, Ofu Village and Fagamalo Cove in Manu'a, and the ship-grounding site (SW1) at Rose, most of which comprised targeted fisheries families (Figs 5 to 7).

Scarids comprised a large proportion of the biomass at many islands, exposures and times, although other families comprised more of the biomass at some sites and times e.g., acanthurids, lethrinids, lutjanids, serranids, scombrids, labrids, carcharhinids and ginglymostomatids (Figs 5 to 7).

Surgeonfishes (particularly *Ctenochaetus* species and *Naso lituratus*) and/or parrotfishes (particularly *Chlorurus spilurus*) comprised 33 to 68% of the biomass at all sites at Rose in both surveys, particularly at the ship-grounding site where they comprised >60% of the biomass (Figs 7 and 8).

Biomass of *Cephalopholis argus* was lower at most exposures, sites and times on Tutuila compared to Manu'a or Rose (Fig. 10). This species was significantly more abundant on the southwest exposure of Ta'u in 2018 than in 1994/5, with no significant difference detected between time periods at other exposures in Manu'a or on Tutuila or Rose (Fig. 10).

Size Distribution of Fisheries Species

Size distribution of fisheries taxa varied among islands and years. For example, biomass of *Cephalopholis argus* (especially in larger size categories) was highest on Rose, followed by Manu'a and then Tutuila (Fig. 12). Biomass of *Cephalopholis argus* increased on Rose and in Manu'a between 1994/5 and 2018 (especially for medium to larger size categories), but not on Tutuila.

In contrast, scarid biomass was low on all islands in 1994/5, and had increased on Tutuila and Manu'a by 2002 (Fig. 12). Scarid biomass (particularly medium and larger size categories) was highest on Tutuila and Rose in 2018 but decreased in Manu'a from 2002 to 2018.

Encounter Rates of Vulnerable Species

Reef fishes highly vulnerable to fishing pressure (particularly sharks, large-bodied groupers and *Cheilinus undulatus:* Image 8) were rare or uncommon (Fig. 13) or not encountered on the transects (*Bolbometopon muricatum*) throughout American Samoa. We encountered large individuals of most of these species in Manu'a or at Rose (Image 8) more frequently than on Tutuila. The encounter rate of some species (particularly large *Cephalopholis argus* and large-bodied parrotfishes) increased over time.

Image 8 *Large reef fishes highly vulnerable to fishing pressure (e.g., sharks and large groupers: top) are rare or uncommon throughout American Samoa and encountered more often on Rose and in Manu'a than on Tutuila. Larger individuals of fisheries species (e.g., Caranx melampygus and Cephalopholis argus: bottom) are also encountered more often on Rose and in Manu'a than on Tutuila.*

Fig. 10 Left: (a-c) Mean total species richness, density and biomass of coral reef fishes, and (d-f) biomass of selected fisheries taxa, at sites surveyed on each island and exposure in all three surveys in 1994/5, 2002 and 2018 in American Samoa (colors denote different sites). Right: Proportional change between 1994/5 and 2018. Values shown are biomass, density or richness in 2018 relative to 1994/5 and 95% confidence intervals for those. Confidence intervals that do not overlap one (shown as red or green) are taken as evidence of significant change.

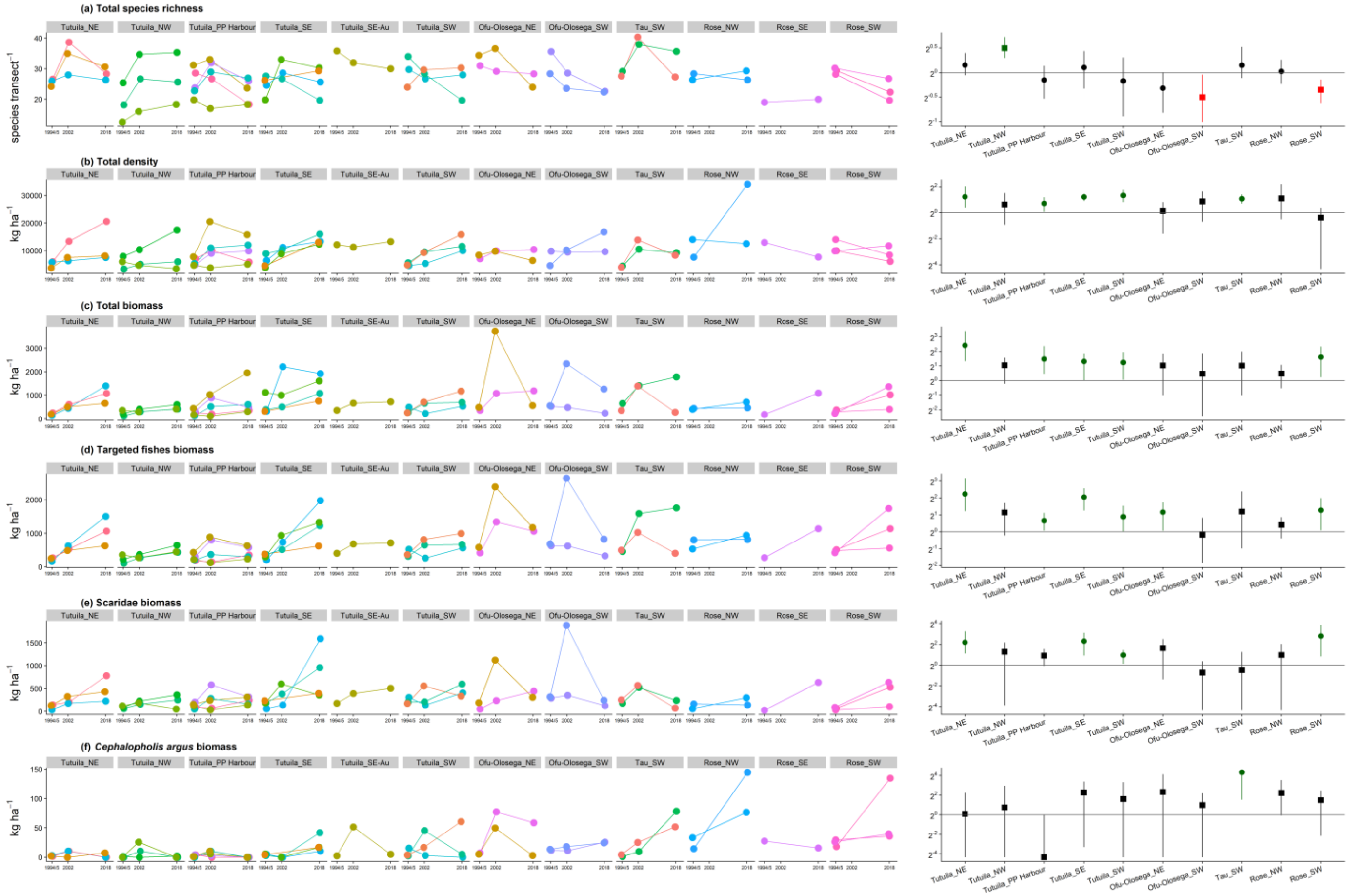


Fig. 11 Changes in abundance of chaetodontids (top) and pomacentrids (bottom) associated with change in cover of branching, digitate, plate and foliaceous corals (BDPF) between 1994/5 and 2018. The gray shaded area represents the 95% confidence intervals of the line of best fit generated by a linear regression.

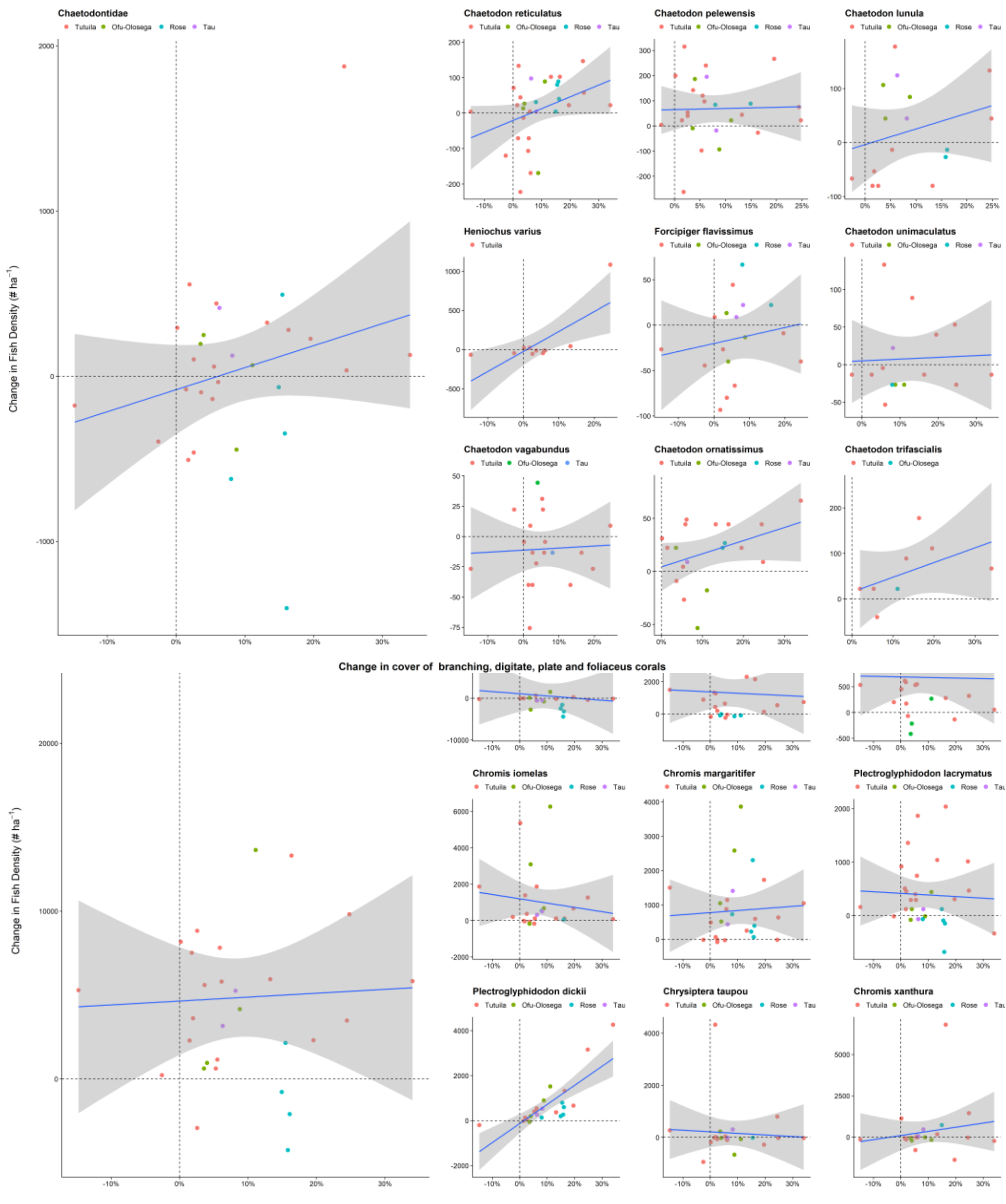


Fig. 12 Mean biomass (kg ha^{-1}) of (a) a grouper (*Cephalopholis argus*) and (b) all Scaridae, in each size bin on Tutuila, Manu'a and Rose in American Samoa in 1994/5, 2002 and 2018.

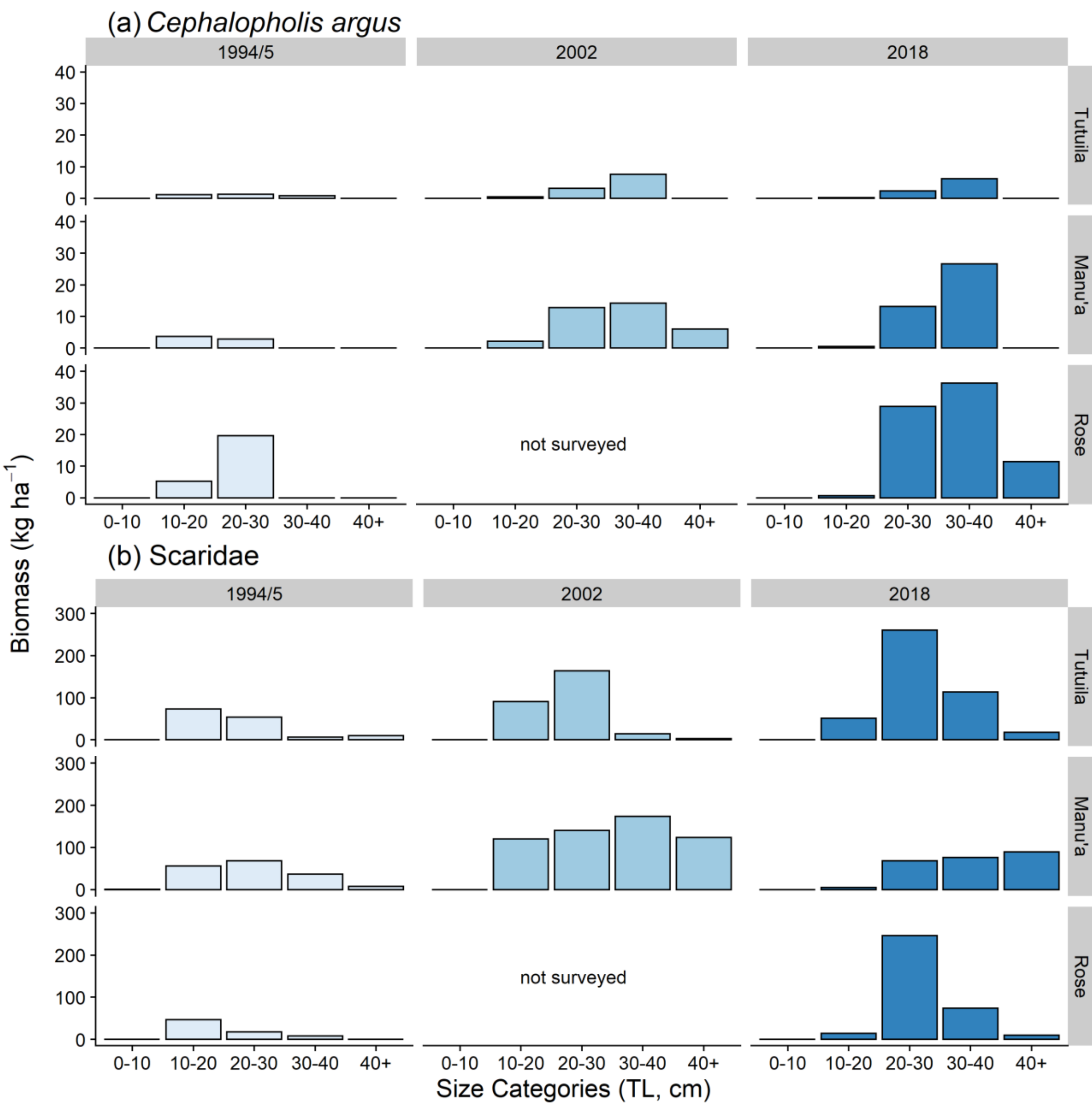
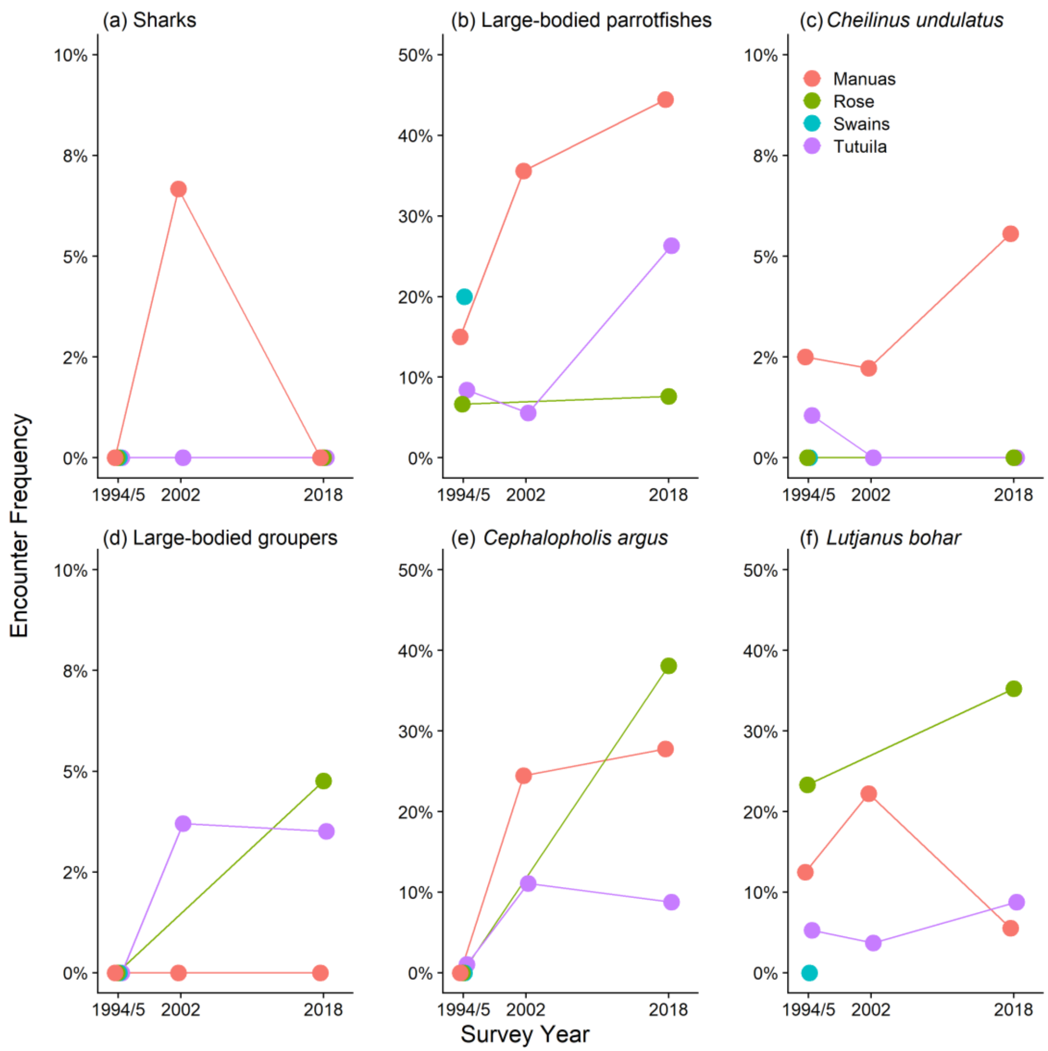


Fig. 13 Encounter rates (percentage of transects on which the species was recorded) of large individuals ($\geq$ 35 cm) of reef fishes highly vulnerable to fishing pressure on Tutuila, Manu'a and Rose Atoll in 1994/5, 2002 and 2018. Species include (a) all sharks, (b) large-bodied parrotfishes (*Cetoscarus ocellatus*, *Chlorurus microrhinos* and *Scarus rubroviolaceus*), (c) humphead wrasse (*Cheilinus undulatus*), (d) large-bodied groupers (*Epinephelus* and *Plectropomus* species), (e) a moderately-sized grouper (*Cephalopholis argus*), and (f) a large-bodied snapper (*Lutjanus bohar*).



Giant Clams

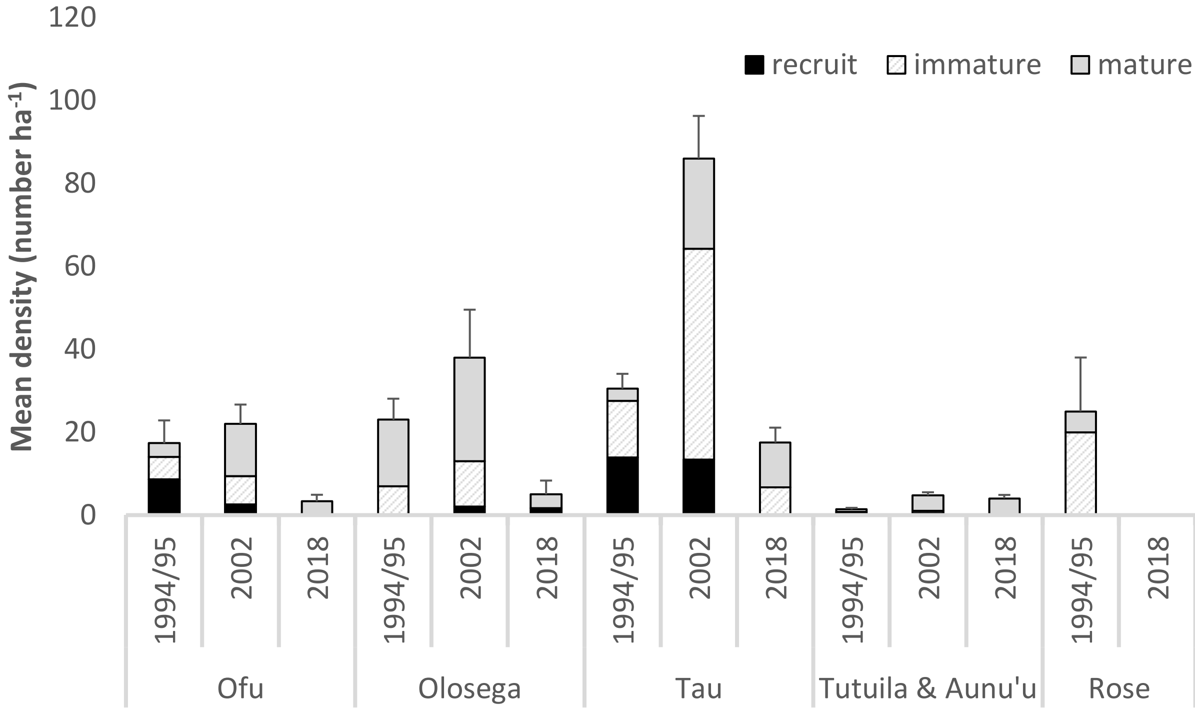
Mean density of giant clams on reef slopes (10 m) varied among islands and years throughout the Territory (Fig. 14a, Table 2). Clam density was very low on Tutuila and Aunu'u in all three surveys and tended to be higher in the Manu'a islands and on Rose Atoll on most surveys (except in 2018). We recorded the highest density on the reef slopes in Ta'u in 2002, which was comprised primarily of immature clams. In 2018, giant clam density was lower than in 1994/95 and 2002 on each of the islands in Manu'a and on Rose. In contrast to previous years, recruits were rare in 2018 with only two recorded at Olosega (Table 2).

The giant clam population on the lagoon pinnacles at Rose declined dramatically between 1994/95 and 2018 (Fig. 14b, Table 3). In 1994/95, mean clam density on the pinnacles was very high (ranging from 951 to 8,871 clams ha^{-1}), while in 2018 mean density was very low (ranging from 7 to 23 clams ha^{-1}). The size structure of the population had also changed. In 1994/95, most the clams recorded on the pinnacles were recruits (43.6%), followed by mature (29.6%) and immature (26.8%) individuals. In 2018, most of the clams were mature (81.3%), with only a few immature individuals (11.3%) or recruits (7.3%) recorded (Table 3).

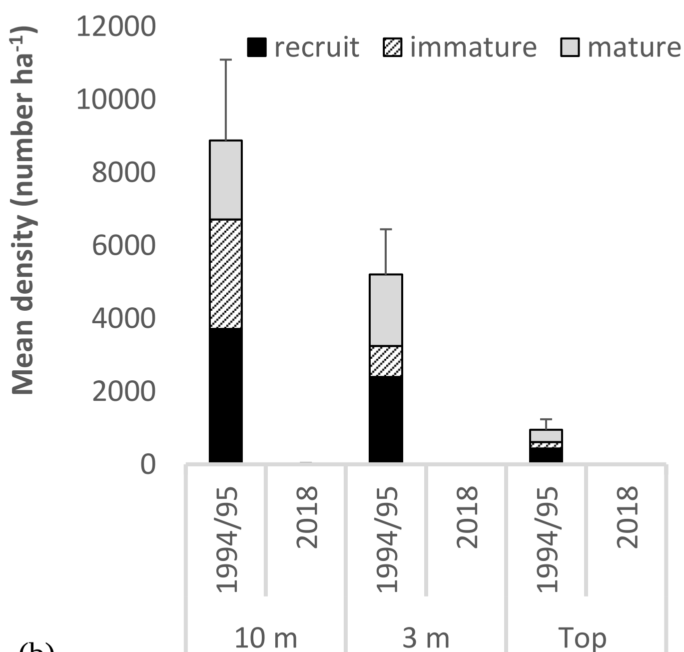
In 2018, we only recorded 226 clams on the transects on the lagoon pinnacles at Rose, most of which were dead (199, or 88%: Table 3). In fact, we only observed live clams on four of the six pinnacles surveyed in 2018, most of which were on two pinnacles (NE1 and NW2: Fig. 15). The density of live clams on each pinnacle surveyed in 2018 (Figs. 3 and 15) was much lower than the mean density of live clams surveyed on pinnacles in same exposures in 1994/95 (Fig. 16).

Most of the dead clams that we observed on the transects in 2018 were on Pinnacles NW4 (62) and SW2 (126: Figs. 3 and 15). Many of the dead clams on SW2 were heavily calcified, indicating that they had been dead for a long time. We also observed a very large number (100s) of heavily calcified and eroded dead clams on the sand flat adjacent to NW4 (Image 9).

Fig. 14 Mean density (+ SE) and size structure of live giant clams a) on reef slopes (10 m) on each island in 1994/95, 2002 and 2018; and b) at three depths (top, 3 m and 10 m) on lagoon pinnacles at Rose Atoll in 1994/95 and 2018.



(a)



(b)

Table 2 Mean density (number of individual ha^{-1}) of live giant clams in each size category surveyed on reef slopes (10 m) on six islands in American Samoa in 1994/95, 2002 and 2018.

Island	Year	Recruit (≤ 5 cm)	Immature (6 - 11 cm)	Mature (≥ 12 cm)	Total (+/-SE)
Ofu	1994/95	8.7	5.3	3.3	17.3 (5.5)
	2002	2.5	6.9	12.6	22.0 (4.7)
	2018	0.0	0.0	3.3	3.3 (1.6)
Olosega	1994/95	0.0	7.0	16.0	23.0 (5.1)
	2002	2.0	11.0	25.0	38.0 (11.5)
	2018	1.7	0.0	3.3	5.0 (3.3)
Ta'u	1994/95	13.9	13.6	3.0	30.5 (3.6)
	2002	13.4	50.8	21.8	86.0 (10.3)
	2018	0.0	6.7	10.8	17.5 (3.6)
Tutuila & Aunu'u	1994/95	0.4	0.4	0.6	1.4 (0.4)
	2002	0.5	0.5	3.7	4.7 (0.8)
	2018	0.0	0.2	3.9	4.0 (0.8)
Rose	1994/95	0.0	20.0	5.0	25.0 (13.0)
	2018	0	0	0	0 (0)

Table 3 Mean density (number of individuals ha^{-1}) of live clams and total number of live (dead) clams in each size class surveyed at three depths on 14 lagoon pinnacles in 1994/95 and six of the same pinnacles in 2018 at Rose Atoll. Dead clams were only recorded in 2018.

Depth (m)	Year	Total number of live (dead) clams	Mean density of live clams (+/- SE)	Mean density of live clams		
				Recruit	**Immature**	**Mature**
Top (< 1 m)	**1994/95**	380	951 (284)	440.3	176.1	334.6
	2018	13 (58)	15 (11.1)	1.7	1.7	11.7
Side (3 m)	**1994/95**	2079	5198 (1,245)	2395.3	854.7	1948.0
	2018	7 (29)	7 (2.1)	0.0	1.8	5.3
Bottom (10 m)	**1994/95**	6210	8,871 (2,222)	3710.8	2996.7	2163.5
	2018	7 (112)	23 (12.2)	1.6	1.6	19.7
Total clams	**1994/95**	8669				
	2018	27 (199)				

Fig. 15 Density of giant clams (live and dead) at three depths (top, 3 m, and 10 m) on each of six lagoon pinnacles at Rose Atoll in 2018.

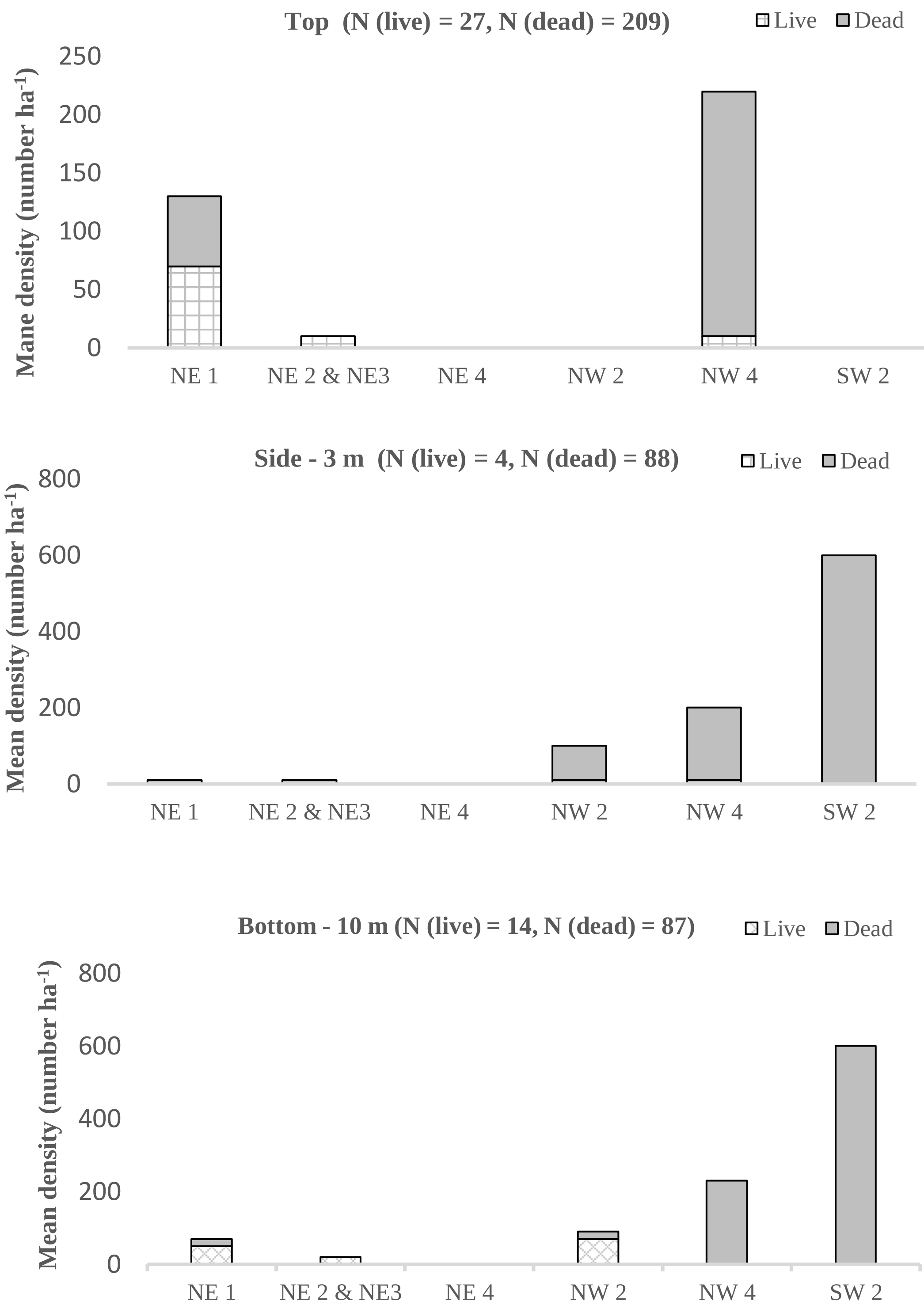
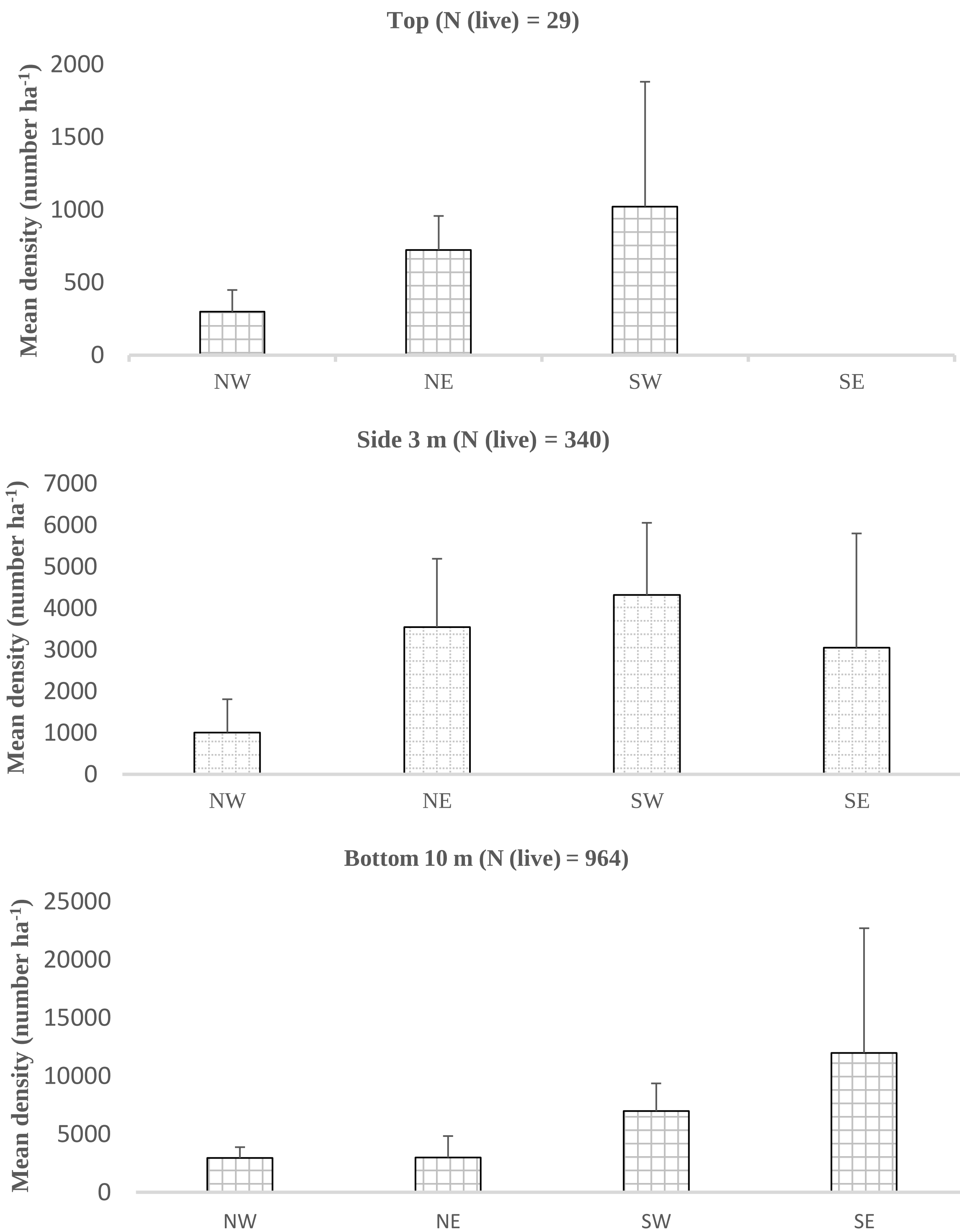


Fig. 16 Mean density (+ SE) of live giant clams at three depths (top, 3 m and 10 m) on 14 lagoon pinnacles in four exposures at Rose Atoll in 1994/1995.



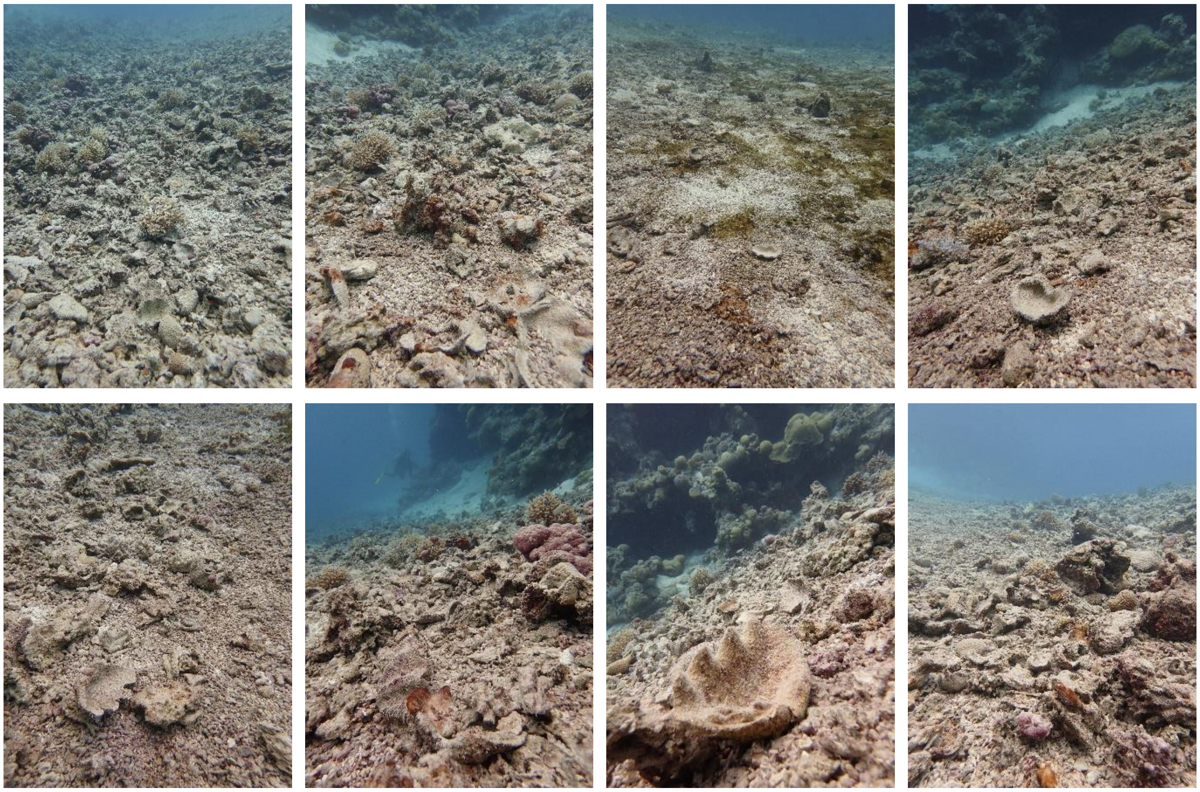


Image 9 *Large numbers of dead giant clams adjacent to Pinnacle NW4 at Rose Atoll*.

DISCUSSION

Globally, few long-term studies empirically measure changes in coral reef ecosystems that can be used to examine factors important in structuring coral reef ecosystems over wide spatial scales (e.g., Emslie et al. 2020). In this study, we use long term (multi-decadal) monitoring to examine patterns and drivers of coral reef resilience and factors influencing reef fish assemblages across hundreds of kilometers to inform conservation and management in American Samoa.

Coral Reef Resilience

Consistent with previous studies, benthic communities varied in response to environmental characteristics (e.g., wave exposure), the history of acute and chronic disturbances, and factors influencing reef resilience (e.g., McLeod et al. 2019) in American Samoa.

Benthic communities on many reefs demonstrated remarkable resilience to large-scale disturbances. This is in stark contrast to many reefs of the world, where coral communities have been declining for decades (Jackson et al. 2014; Birkeland et al. 2021; Souter et al. 2021).

Several hurricanes devastated the reefs of American Samoa in the 1980s and early 1990s, and most reefs were in early stages of recovery (with low to moderate cover of predominately encrusting and massive corals) in 1994/5. Since then, coral communities on most islands and exposures have recovered well, with coral cover (particularly of BDPF lifeforms: Image 6) increasing significantly over the last few decades (Fig. 4). Recovery was strong in areas where there are factors that appear to promote reef resilience, including a lush growth of pink CCA (see also Birkeland et al. 2021) and moderate to high biomass of parrotfishes (e.g., at Rose Atoll and SW Ofu-Olosega: Image 10).

On Tutuila, recovery also appeared strongest (with high BDPF coral cover) on semi-exposed reefs with low or medium watershed development, which did not appear to be suffering from chronic effects of land-based runoff of sediments (e.g., Vatia and Fagatele: Image 11). In contrast, less resilient reefs (where coral cover has not increased since the hurricanes and remains dominated by encrusting and massive corals) tend to be in areas with moderate to high watershed development and high sediment loads (e.g., Fagafue or Aua: Image 11), or where there have been frequent disturbances (e.g., from mass coral bleaching, CoTS or storms: e.g., Masefau and Nu’uuli).

Image 10 *Pink crustose coralline algae (right), parrotfishes and good water quality (left) play important roles in promoting coral reef resilience in American Samoa.*

Image 11 *Coral communities with high resilience in Fagatele Bay (left) and low resilience at Aua (right) in 2018.*

Influence of Habitat Characteristics on Coral Reef Fishes

As in previous studies (e.g., Pratchett et al. 2008; Coker et al. 2014; Williams et al. 2015; Harborne et al. 2018), reef fish assemblages varied with a range of environmental and habitat characteristics in American Samoa. Species composition varied among geographic locations (e.g., Swains Atoll vs the other islands) and reef types (volcanic islands and atolls). Changes in abundance of some species also appeared associated with the recovery of coral communities following the hurricanes that reduced both live coral cover and associated topographic complexity.

As expected from the literature, the direction and strength of the relationship between the abundance of some fish species and coral cover tended to vary in relation to their habitat and dietary preferences (reviewed in Pratchett et al. 2008 and Coker et al. 2014). For example, the abundance of an obligate corallivore (*Chaetodon ornatissimus*) and a small-bodied species (*Plectroglyphidodon dickii*) that rely on live coral for food and shelter increased with increasing live coral cover (particularly of BDPF corals: Fig. 11, Image 12). Conversely, some species that feed primarily on hard or soft corals (*Chaetodon unimaculatus:* Pratchett 2005) or are omnivores that tend to be associated with mixed coral-algae areas and/or non-living substrate species (e.g., *Chrysiptera taupou* and *Pomacentrus vaiuli*: Myers 1991) did not show a positive relationship with BDPF coral cover (Image 12).

***Image 12** Fish species that tend to be associated with live coral cover (Plectroglyphidodon dickii left, and Chaetodon trifascialis: middle) or mixed coral algal areas or nonliving substrate (Chrysiptera taupou: right).*

One of the most specialized species (*Chaetodon trifascialis*: Image 12) that feeds almost exclusively on the plate coral *Acropora hyacinthus* (Pratchett 2005) did not show a strong positive relationship with BDPF coral cover over broad spatial and temporal scales in our study. This may be because there were not enough records for this species in our surveys since plate corals were not abundant at many sites (particularly following the hurricanes). This relationship seems clearer when we examine individual sites where plate coral cover has increased over the last few decades. For example, in Fagatele Bay, plate coral cover increased from <1% in 1994/95 and 2002 to 9% in 2018, and the density of *Chaetodon trifascialis* increased from 0 to 66.7 per hectare over the same time period.

Populations of some reef fishes closely associated with live corals recovered quickly following increases in coral cover. For example, BDPF coral cover increased from 3% to 23% and 37% from 1994/95 to 2002 and 2018 respectively in Fagatele Bay, with an associated increase in

Plectroglyphidodon dickii density from 8,840 to 12,533 and 14,577 ha^{-1}. This is consistent with previous studies demonstrating that reef fish assemblages can take as little as five years to rebound following major habitat perturbations provided there are refuge adult populations and recovery of critical aspects of their habitat structure (Pratchett et al. 2008).

Contrary to previous studies (reviewed in Pratchett et al. 2008), no clear pattern existed for species richness in American Samoa, which either increased or decreased with increasing coral cover and associated topographic complexity at different locations. For example, in Fagatele Bay, species richness declined from 1994/5 to 2018 despite coral cover (including BDPF corals) increasing from 11 to 56% over the same time period. This is consistent with previous studies that determined that species richness may be higher in areas with moderate coral cover (consistent with intermediate disturbance hypotheses: reviewed in Sandin et al. 2008).

Influence of Fishing Pressure on Coral Reef Fishes

Our results support previous studies indicating that relative fishing pressure is a primary driver of biomass (and size structure) of targeted fisheries species in American Samoa (e.g., Williams et al. 2015), since both metrics show an inverse relationship with relative fishing pressure among islands. Tutuila has high relative fishing pressure, and the lowest biomass (and sizes) of fisheries species at most sites. The Manu'a Islands and Rose have moderate and low relative fishing pressure respectively, and a higher biomass (and larger sizes) of most fisheries species than at most sites on Tutuila.

Consistent with previous studies (reviewed in Levine and Allen 2009), we also found that large-bodied species highly vulnerable to fishing pressure were rare, uncommon or not recorded throughout the archipelago. When present, we encountered these species more often in Manu'a or at Rose Atoll than on Tutuila (Image 8).

Even though fishing pressure is low relative to some other Pacific Islands (Williams et al. 2015), the reef area is small (Table 1) so continuous, low-scale exploitation appears to have impacted populations of fisheries species in American Samoa (reviewed in Levine and Allen 2009, this study). This observation is consistent with previous studies that demonstrated dramatic declines in reef fish biomass in the Pacific Islands (including American Samoa), even when fishing pressure was low (e.g., Nadon et al. 2012; Williams et al. 2015).

Our study does not support the hypothesis that declining catches on Tutuila may be due to habitat degradation (reviewed in Levine and Allen 2009), because most fisheries species tend to be affected less by changes in habitat than other species (Emslie et al. 2020) and populations of fisheries species have not recovered along with coral communities at many sites on Tutuila. Thus, while the devastating hurricanes may have contributed to a temporary decline in some fisheries species, they are unlikely to be the cause of the relatively low biomass of these species on Tutuila now where there are healthy coral communities (e.g., in Fagatele Bay: Image 11).

The perception of overfishing (or not) on American Samoa's reefs is influenced by the taxa examined. Examining this issue using all fisheries taxa is problematic because of the high degree of variability in abundance of schooling species (e.g., some lutjanids and lethrinids).

The medium size grouper *Cephalopholis argus* (Image 8) is a good indicator of fishing pressure because it has a small home range (Green et al. 2014), can be abundant and is moderately to highly vulnerable to fishing pressure (Abesamis et al. 2014). This species shows a strong inverse relationship between their population size and structure and relative fishing pressure among islands in American Samoa. However, while the biomass of this species has not changed over time, the size structure has, and there are more larger individuals on Rose and in Manu'a now, which may indicate lower fishing pressure for this species on these islands over the last few decades.

Parrotfishes tell a different story. This family comprises much of the targeted fish biomass in American Samoa. Most parrotfish species have a low or moderate vulnerability to most types of fishing pressure, except large species that are highly vulnerable to fishing (e.g., *B. muricatum* or *Cetoscarus ocellatus*: Abesamis et al. 2014). This may explain why there is not a strong inverse relation between relative fishing pressure and total parrotfish biomass and size structure among islands, because less vulnerable species are abundant (e.g., *Chlorurus spilurus* and *Chlorurus japanensis*: Image 10). However, all parrotfishes are very vulnerable to nighttime scuba fishing, so the increase in biomass and size of targeted fishes (mostly parrotfishes) on Tutuila from 2002 to 2018 (this study) may be due to American Samoa banning this fishery in 2001 (Green 2002). The decline in parrotfish biomass and size on Manu'a from 2002 to 2018 also coincides with an increase in spearfishing on these islands over the last five years (A. Lawrence *pers. obs.*). In contrast, there has been an increase in parrotfish biomass and size on southwest Rose from 1994/95 to 2018, possibly due to enhanced food resources or juvenile habitat provided by opportunistic algae associated with the shipwreck.

Status of Marine Protected Areas

MPAs, particularly NTAs, can be effective tools for protecting biodiversity and maintaining or enhancing populations of fisheries species, but only if they are well designed and managed effectively (Green et al. 2014). Our study allows us to examine the role of MPAs towards achieving these objectives in American Samoa.

Coral communities are thriving in many MPAs in American Samoa due to the presence of natural resilience factors (i.e., good water quality, the prevalence of CCA and abundant parrotfishes: Images 10 and 11). However, many MPAs have a low biomass of fisheries species, and species highly vulnerable to fishing pressure (sharks and large-bodied groupers, wrasse, parrotfishes, and snapper: Image 8) are rare or absent throughout the Territory including in most MPAs. Therefore, many MPAs in American Samoa are not yet realizing their potential as effective fisheries management tools (described below), possibly due to a lack of compliance and enforcement.

Village Marine Protected Areas

Village MPAs are co-managed by the territorial government and local communities, although many are inactive. In our study we monitor four Village MPAs (Table 1). Our results show that while Fagamalo (designated as a no take Village MPA) has healthy and resilient coral communities, biomass of fisheries families is low. Furthermore, three Village MPAs (designated as subsistence fishing only e.g., Aoa, Vatia and Amanave) do not have a higher biomass of fisheries species than areas open to fishing (e.g., Masefau and Nu'uuli).

National Marine Sanctuary of American Samoa

The Fagatele Bay section of the NMSAS comprises one of the most resilient coral communities in the Territory. The coral communities have experienced several serious disturbances in the last three decades but have recovered well and are the healthiest they have been since we started monitoring them in the late 1970s, likely because of low watershed development, good water quality and a lush growth of CCA (Green et al. 1999; Table 1, Fig. 5, Image 11). Fish density has increased over time, primarily due to an increase in damselfishes (particularly *Plectroglyphidodon dickii*: Image 12) associated with increased BDPF coral cover (Green et al. 1999; this study). However, despite its designation as a NTA, biomass of fisheries species in Fagatele Bay remains low compared with many other sites throughout the Territory, except for small parrotfishes (particularly *Chlorurus spilurus*).

During our 1994/95 survey, we discovered one of the world's largest and oldest coral colonies at our site at Afuli Cove on Ta'u, a massive *Porites* colony we named Fale Bommie (because the shape resembles a Samoan fale: Image 13). This colony (also known as Big Momma) is now within the Ta'u Management Area of the NMSAS and appears healthy and recovering well from coring studies to estimate its age and study climate records in the skeleton. A recent study has also described more, exceptionally large, massive *Porites* colonies on Ta'u (Coward et al. 2020).

Image 13 *Fale Bommie (also known as Big Momma) at Afuli Cove on Ta'u.*

Rose Atoll National Wildlife Refuge

Populations of some fisheries species (especially vulnerable reef fishes) are higher at Rose Atoll National Wildlife Refuge than on Tutuila (Image 8), which is most likely due to the atoll's remoteness. However, there appears to have been a mass mortality of giant clams in the refuge due to an unknown cause (see below). Fortunately, Rose is recovering well from the ship grounding in 1993 (see below) since managers have removed most of the wreckage from the atoll.

<u>Recovery from the Ship Grounding</u>

After the ship grounding in 1993, a phase shift occurred on the southwest and northwest sides of Rose Atoll where reef slopes and flats once dominated by CCA were overgrown by opportunistic turf algae and cyanobacteria (likely stimulated by iron leaching from the wreckage: Green et al. 1997). Herbivorous fishes were also more abundant at the grounding site, associated with the high cover of turf algae and cyanobacteria (Green et al. 1997). This phase shift persisted for over 13 years (Schroeder et al. 2008).

Twenty-five years after the grounding, USFWS and DMWR have removed most of the wreckage and there has been a phase shift reversal: the cover of turf algae and cyanobacteria has declined substantially and CCA or coral dominate most reef flats and slopes on the atoll again (Figs. 4, 7 and 8; Image 14). The exception is in the immediate vicinity of the ship-grounding site that is still dominated by turf algae and cyanobacteria (and a high biomass of herbivorous fishes: Image 14), possibly because iron is continuing to leach from the remaining wreckage.

Image 14 *Benthic communities are dominated by reef building pink crustose coralline algae at most sites on Rose Atoll (top). The exception is at the ship grounding site, where there is still a high cover of turf algae and cyanobacteria (bottom left) associated with a high biomass of herbivorous fishes (bottom right).*

Is Rose Atoll Still a Refuge for Giant Clams?

Giant clams, locally known as *faisua* (Image 7), are a favored food item in American Samoa, and their accessibility and life history characteristics make them particularly vulnerable to over-harvesting (Green and Craig 1999). Thus, overfishing probably accounts for the inverse relationship between the density of clams and the size of the human population on the islands throughout the archipelago (Green and Craig 1999, this study).

Based on our extensive survey in 1994/95, we reported that Rose Atoll was an important refuge for giant clams that were overfished throughout most of the Samoan Archipelago (Green and Craig 1999). Most (97%) of the 2,853 clams that we recorded on six islands in American Samoa were on Rose (which accounted for 42% of the area surveyed). Clam densities were highest in the atoll lagoon, especially around the bases of the pinnaces (mean density = 8,870 ha^{-1}: Fig. 3). Twenty-four percent of the clam population on Rose were mature, 70% of which occupied the lagoon pinnacles and shallow habitats.

Green and Craig (1999) estimated that the atoll supported about 28,000 clams, and morality (natural, fishing and total) was low. More than 20% were juveniles, which is a sign of a healthy population. Unfortunately, we could not repeat this population size estimate in 2018, because we were only able to survey four of the eight habitat types and six of the 14 lagoon pinnacles that we surveyed in 1994/95. Furthermore, we did not repeat the mortality estimates conducted by Green and Craig (1999), because of the low number of live clams (28) recorded in 2018.

However, our survey in 2018 indicates that giant clam densities remain low on Tutuila and in the Manu'a Islands, and that the population appears to have collapsed at Rose. We recorded much lower densities of live clams in the most important habitat for this species (lagoon pinnacles) at Rose compared to 1994/95 (Fig. 14b). We also observed very large numbers of dead clams surrounding the pinnacles (Image 9) indicating that many clams may have died since our last survey 25 years ago.

There also appears to have been a major change in the size structure of giant clams at Rose. On the lagoon pinnacles in 1994/95, approximately half of the individuals (44%) surveyed were recent recruits (Fig. 14b). While in 2018, we saw very few recent recruits on Rose (or the other islands). The dramatic reduction in the number of recruits raises concerns that the density of giant clams on the atoll now may be so low that reproductive success and subsequent recruitment may have been diminished or that recruits may not be surviving due to other factors. The apparent collapse of the clam population on Rose may also have important consequences for other islands if the atoll was providing larvae to support their clam populations (see Green and Craig 1999).

There are several possible explanations for the putative collapse of the giant clam population at Rose. One option is poaching, since the atoll is remote and uninhabited, so surveillance and enforcement are problematic. However, this seems unlikely because fishers mostly harvest adult clams and there were low numbers of clams in all size classes in 2018.

A second option is that the clam population may have collapsed as a delayed response to the ship grounding. At the time of the event, the ship grounding appeared to have had only a minor effect on the clam population at Rose (<1% died: Green and Craig 1999). However, the grounding may have had longer-term lethal or sub lethal effects on the clam population, due to toxic effects of the fuel spill or overgrowth by cyanobacteria (Green et al. 1997). This is consistent with our observation that the highest mortality of clams that we observed was on the pinnacles in the northwest corner of the lagoon close to the grounding site, where there was still 14 to 20% cover of cyanobacteria (on pinnacles NW2 and NW4 respectively) in 2018.

A third option is that the clams may have died due to rising sea temperatures in the lagoon, which may have been more pronounced in the northwest corner where water circulation is low. This is possible, since dramatic declines (>80%) in giant clam *(Tridacna maxima*) populations have been reported at Tatakoto Atoll in French Polynesia, which have been attributed to unusually high sea temperatures (Adessi 2001, Andrefouet et al. 2013).

Management Recommendations

In this study, we documented the recovery of benthic communities and several groups of reef fishes in many locations over the last few decades, indicating that some management actions appear to have resulted in positive outcomes in American Samoa, particularly banning the nighttime scuba fishery and removing most of the shipwreck at Rose. However, there is still a need for improved management to ensure the long-term sustainability of coral reef resources in the Territory.

Populations of some fisheries species (reef fishes and giant clams) appear depleted, and there is a need for improved management on Tutuila and in Manu'a, including enforcing existing and implementing new fisheries legislation and MPAs (particularly NTAs) to ensure the long-term sustainability of these species. In particular, there is an urgent need for improved management to protect species that are highly vulnerable to overfishing due to their life history characteristics

(Abesamis et al. 2014), which are rare or absent throughout the Territory (particularly sharks, bumphead parrotfishes, humphead wrasse and large bodied groupers and parrotfishes: Williams et al. 2015; Nadon et al. 2012, this study).

We also recommend that American Samoa takes a resilience-based approach to management to maintain or enhance coral reef resilience to local and global threats (see review by McLeod et al. 2019). This will require improving land use practices to reduce runoff that appears to be impeding the resilience of some reefs on Tutuila, improving management of functionally important species (e.g., large-bodied parrotfishes), and designing and enforcing a resilient network of NTAs throughout the Territory (see Green et al. 2014; McLeod et al. 2019).

Local communities can play an important role in improving the condition of their reefs and fish populations. We recommend that they continue to work with government agencies to enhance or maintain coral reef resilience and fish populations by improving fisheries management and addressing land-based sources of pollution by expanding and implementing the Village MPA network of NTAs, as well as implementing other fisheries and watershed management tools (Levin and Allen 2009). To help facilitate this process, the results of our long-term monitoring of individual sites (Figs. 5 and 6) can be used to develop village-based report cards to summarize the condition of coral reef resources and management recommendations for local communities.

Long-term monitoring of coral reefs should also continue to support management in American Samoa but be expanded to monitor ecological processes that influence reef resilience (e.g., coral recruitment, herbivory and water quality: McLeod et al. 2019). This includes repeating long-term monitoring throughout the archipelago (Green 1996, 2002; this study) every five years and repeating the more detailed long-term monitoring of Fagatele Bay National Marine Sanctuary (previously surveyed seven times from 1985 to 2007: e.g., see Birkeland et al. 1987; Green et al. 1999) and the Aua Transect (surveyed 11 times from 1917 to 2017: e.g., see Mayor 1924; Birkeland et al. 2021).

A more comprehensive resurvey of the giant clam population (in more exposures, habitats and depths) at Rose Atoll National Wildlife Refuge is also required to compare results to those from the 1994/95 survey (Green and Craig 1999) to determine if the giant clam population has collapsed. Detailed studies are also required to determine the likely cause of the putative mass mortality and explore management options for maintaining or facilitating the recovery of the clam population on the atoll.

More intensive surveys should also be conducted to document the recovery of the benthic communities from the ship grounding at Rose Atoll National Wildlife Refuge over the last 25 years, particularly repeating the detailed survey of reef flat algae conducted following the ship grounding in 1995 (Green et al. 1997). This would allow for a comprehensive report including all previous studies (e.g., Green et al. 1997, Schroder et al. 2008, this study and other USFWS reports) to be prepared to describe the recovery of the atoll and the cost/benefits of the cleanup operation.

References

Abesamis RA, Green AL, Russ GR, Jadloc CRL (2014) The intrinsic vulnerability to fishing of coral reef fishes and their differential recovery in fishery closures. Rev Fish Biol Fish 24:1033-063

Adessi L. (2001) Giant clam bleaching in the lagoon of Takapoto atoll (French Polunesia). Coral Reefs 19: 220

Andrefouet S. Van Wynsberge S, Gaertner-Mazouni N, Menkes C, Gilbert A, Remoissenet G. (2013) Climate variability and massive mortalities challenge giant clam conservation and management efforts in French Polynesia atolls. Biological Conservation 160: 190-199

Bellwood DR, Hughes TP, Hoey AS (2006) Sleeping functional group drives coral-reef recovery. Curr Biol 16: 2434–2439

Birkeland C, Randall RH (1979) Report on the *Acanthaster planci* (Alamea) studies on Tutuila, American Samoa.

Birkeland C, Green A, Lawrence A, Coward G, Vaeoso M, Fenner D (2021) Different resiliencies in coral communities over ecological and geological time scales in American Samoa. Mar Ecol Prog Ser 673: 55-68.

Birkeland C, Green A, Mundy C, Miller K (2004) Long-term monitoring of Fagatele Bay National Marine Sanctuary and Tutuila Island (American Samoa) 1985 to 2001: summary of surveys conducted in 1998 and 2001. Report to the National Oceanic and Atmospheric Administration, U.S. Department of Commerce.

Birkeland, C., Randall, R., Wass, R., Smith, B., Wilkins, S. (1987). Biological resource assessment of the Fagatele Bay National Marine Sanctuary. NOAA Technical Memorandum NOS MEMD 3. 232pp.

Canty A, Ripley BD (2019) boot: Bootstrap R (S-Plus) functions. R package version 1.3-24

Clark T (2015) Control of crown of thorns starfish at the National Park of American Samoa. Report to National Park of American Samoa, Pago Pago, American Samoa.

Coker DJ, Wilson SK, Pratchett MS (2014) Importance of live coral habitat for reef fishes. Rev Fish Biol Fish 24:89–126

Coward G, Lawrence A, Ripley N, Brown V, Sudek M, Brown E, Moffitt I, Fuiava B, Vargas-Angel B (2020) A new record for a massive *Porites* colony at Ta'u Island, American Samoa. Nat Res Sci Rep 10: 21359

Done T J (1992) Effects of tropical cyclone waves on ecological and geomorphological structures on the Great Barrier Reef. Cont Shelf Res 12: 859-872

Emslie MJ, Bray P, Cheal AJ, Johns KA, Osborne K, Sinclair-Taylor T, Thompson CA (2020) Decades of monitoring have informed the stewardship and ecological understanding of Australia's Great Barrier Reef. Biol Conserv 252: 108854

English S, Wilkinson C, Baker V (eds) (1997) Survey manual for tropical marine resources. 2nd Edition. Australian Institute of Marine Science, Townsville, Australia.

Fabricius KE, De'Ath G, Puotinen ML, Done T, Cooper TF, Burgess SC (2008) Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. Limnology and Oceanography, 53(2), 690-704

Fenner D (2011) Results of the Territorial Monitoring Program of American Samoa for 2009, Benthic Section, including information on the tsunami effects. Report to Dept. Marine and Wildlife Resources and Coral Reef Advisory Group (American Samoa), and NOAA.

Green AL (1996) Status of the coral reefs of the Samoan Archipelago. DMWR Biological Report Series, Pago Pago, American Samoa.

Green AL (2002) Status of coral reefs on the main volcanic islands of American Samoa: a resurvey of long term monitoring sites (benthic communities, fish communities, and key macroinvertebrates). A report prepared for the Department of Marine and Wildlife Resources, American Samoa.

Green AL, Craig P (1999) Population size and structure of giant clams at Rose Atoll, an important refuge in the Samoan Archipelago. Coral Reefs 18(3): 205-211

Green AL, Birkeland C, Randall R (1999) Twenty years of disturbance and change in Fagatele Bay National Marine Sanctuary, American Samoa. Pac Sci 53:376-400

Green AL, Burgett J, Molina M, Palawski D, Gabrielson P (1997) The impact of a ship grounding and associated fuel spill at Rose Atoll National Wildlife Refuge, American Samoa. US Fish and Wildlife Service, Hawaii.

Green AL, Fernandes L, Almany G, Abesamis R, McLeod E, Aliño P, White AT, Salm R, Tanzer J, Pressey RL (2014) Designing marine reserves for fisheries management, biodiversity conservation and climate change adaptation. Coast Manage 42:143–159

Harborne AR, Green AL, Peterson NA, Beger M, Golbuu Y, Houk P, Spalding MD, Taylor BM, Terk E, Treml EA, Victor S, Vigliola L, Williams ID, Wolff NH, ZuErmgassen P, Mumby PJ (2018) Modelling and mapping regional-scale patterns of fishing impact and fish stocks to support coral-reef management in Micronesia. Divers Distrib 24:1729-1743

Jackson JBC, Donovan MK, Cramer KL, Lam W (eds) (2014) Status and Trends of Caribbean coral reefs: 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland

Levine A, Allen S (2009) American Samoa as a fishing community. US Department of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-PIFSC-19

Mayor A (1924) Structure and ecology of Samoan reefs. Carnegie Institute Washington Publication 340: 1−25

McClanahan TR, Donner SD, Maynard JA, MacNeil MA, Graham NAJ, Maina J, Baker AC, Alemu JB, Beger M, Campbell SJ, Darling ES, Eakin CM, Heron SF, Jupiter SD, Lundquist CJ, McLeod E, Mumby PJ, Paddack MJ, Selig ER, van Woesik R (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. PLoS One 7:e42884

McLeod E, Anthony KN, Mumby PJ, Maynard J, Beeden R, Graham NAJ, Heron SF, Hoegh-Guldberg O, Jupiter S, MacGowan P, Mangubhai S, Marshall N, Marshall PA, McClanahan TR, McLeod K, Nystrom M, Obura O, Parker B, Possingham HP, Salm RV, Tamelander J (2019) The future of resilience-based management in coral reef ecosystems. J Environ Manage 233: 291-301

Myers RF (1999) Micronesian reef fishes: a comprehensive guide to the coral reef fishes of Micronesia. Coral Graphics Publications.

Nadon MO, Baum JK, Williams ID, McPherson JM, Zgliczynski BJ, Richards BL, Schroeder RE, Brainard RE (2012) Re-creating missing population baselines for Pacific reef sharks. Conserv Biol 26:493–503

Pratchett MS (2005) Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. Marine Biology 148:373–382

Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes – ecological and economic consequences. Oceanography and Marine Biology: An Annual Review 46:251-296

Puotinen ML (2007) Modelling the risk of cyclone wave damage to coral reefs using GIS: a case study of the Great Barrier Reef, 1969–2003. International Journal of Geographical Information Science 21: 97-120

Radtke R (1985) Population dynamics of the giant clam, *Tridacna maxima*, at Rose Atoll. Technical Report, Hawaii Institute of Marine Biology, University of Hawaii, pp 1-24

Raynal JM, Levine AS, Comeros-Raynal MT (2016) American Samoa’s Marine Protected Area System: Institutions, Governance and Scale. Journal of International Wildlife Law and Policy 19:301-316

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos, JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the northern Line Islands. PLoS One 3:e1548

Schroeder RE, Green AL, DeMartini ED, Kenyon JC (2008) Long-term effects of a ship grounding on coral reef fish assemblages at Rose Atoll, American Samoa. Bull Mar Sci 82:345–364

Souter D, Planes S, Wicquart J, Logan M, Obura D, Staub F (eds) (2021) Status of coral reefs of the world: 2020. Global Coral Reef Monitoring Network, IUCN, Switzerland.

United States Census Bureau (USCB 2020) Census American Samoa.

Western Pacific Regional Fishery Management Council (WPRFMC 2009) Fishery Ecosystem Plan for the American Samoa Archipelago. WPRFMC, Hawaii, USA.

Williams ID, Baum JK, Heenan A, Hanson KM, Nadon MO, Brainard RE (2015). Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. PLoS One 10:e0120516

WoRMS Editorial Board (2021). World Register of Marine Species. https://www.marinespecies.org/

Appendix 1 GPS Co-ordinates and Transects Surveyed at Each Site in Each Year

GPS co-ordinates and number of transects surveyed at each site in each of three surveys in October 1994 to November 1995 (1994/95), March 2002 and October to November 2018. In 1994/95, we used hydrographic charts and natural features (e.g., the location of a reef channel or *ava*) to map and describe the location of each site (Green 1996). In 2002 and 2018, we used geographic co-ordinates (on WGS84 datum) for each site using a handheld GPS (Green 2002, this study). We surveyed fishes on all transects, and benthos and giant clams on all transects except at sites in northeast Manu'a (Ofu-Olosega and Ta'u) and southeast Rose in 1994/95.

Island	Exposure	Site	GPS Co-ordinates		Number of Transects		
			Latitude	Longitude	1994/95	2002	2018
Tutuila	NE	Aoa	-14.25783	-170.58892	5	3	3
		Masefau	-14.25550	-170.62217	5	3	3
		Vatia	-14.24625	-170.66780	5	3	3
	NW	Fagafue	-14.29493	-170.75263	5	3	3
		Fagamalo	-14.29772	-170.81153	5	3	3
		Fagasa	-14.28357	-170.72278	5	3	3
	Pago Pago Harbour	Aua	-14.27833	-170.66933	5	3	3
		Fagaalu	-14.28982	-170.67748	5	3	3
		Leloaloa	-14.27042	-170.67683	5	3	3
		Onesosopo	-14.28673	-170.66493	5	3	3
		Utulei	-14.28322	-170.67528	5	3	3
	SE	Amouli	-14.27563	-170.58288	5	-	3
		Fagaitua	-14.27200	-170.61213	5	3	3
		Fatumafuti	-14.29450	-170.67500	5	3	3
		Nuuuli	-14.32025	-170.69680	5	3	3
	SW	Amanave	-14.32708	-170.83222	5	3	3
		Fagatele	-14.36623	-170.76290	5	3	3
		Leone	-14.34263	-170.78897	5	3	3
Aunu'u	NW	Aunu'u	-14.28447	-170.56300	5	3	3
Ofu-Olosega	NE	Asaga	-14.16178	-169.63380	5	5	3
		Sili	-14.16397	-169.62493	5	5	3
	SW	Hurricane House	-14.18050	-169.65185	-	5	-
		Ofu Village	-14.17335	-169.68147	5	5	3
		Olosega Village	-14.16397	-169.62653	5	5	3
Ta'u	NE	Faga	-14.20955	-169.45502	5	5	-
		Lepula	-14.21233	-169.43742	5	5	-
	SW	Afuli Cove	-14.25937	-169.50048	5	5	3
		Fagamalo Cove	-14.24633	-169.50570	5	5	3
Swains	SW	SW1	-11.05775	-171.09138	5	-	-

Island	**Exposure**	**Site**	**GPS Co-ordinates**		**Number of Transects**		
			Latitude	**Longitude**	**1994/95**	**2002**	**2018**
		SW2	-11.06337	-171.08754	5	-	-
Rose	NE	NE1	-14.53873	-168.14571	-	-	3
	NW	NW1	-14.53780	-168.17140	5	-	3
		NW2	-14.53645	-168.16533	5	-	3
	SE	SE1	-14.55809	-168.15303	5	-	3
	SW	SW1	-14.54945	-168.16812	5	-	5
		SW2	-14.55467	-168.16463	5	-	3
		SW3	-14.54088	-168.17235	5	-	3

Appendix 2 Electronic Supporting Information

Four electronic databases (excel spreadsheets) used for data analysis are available as supporting information from Alison Green (aligreenfish9@gmail.com).

Electronic Supporting Information 1 Coral Reef Fishes

This database provides details of coral reef fish families and species surveyed in American Samoa including taxa, biomass conversion constants, length conversion factors and maximum length (LMAX); and mean biomass (and SE), mean density (and SE) and mean species richness (per transect) of each family and species at each site in 1994/95, 2002 and 2018. Species names are consistent with WoRMS (2021).

Electronic Supporting Information 2 Benthic Lifeforms

This database provides mean cover (and SE) of benthic lifeforms (supercategories i.e., all corals, CCA, turf and macroalgae) and coral lifeforms (CoralCats) surveyed at each site in 1994/95, 2002 and 2018. Benthic lifeforms are analyzed with (SuperCatIncCyano) and without (SuperCat) cyanobacteria analyzed separately

Electronic Supporting Information 3 Total Mean Values and Results of Statistical Analyses

This database provides:

- Mean (and SE) of cover per benthic lifeform per site per survey period. p-values are derived from t-tests between 1994/95 and 2018 data. Results significant at p=0.05 are highlighted in pink.
- Mean (and SE) of fish assemblage metrics (total biomass [kg ha^{-1}], density [number ha^{-1}] and species richness [number per transect]) per site per survey period. p-values are derived from t-tests between 1994/95 and 2018 data. Results significant at p=0.05 are highlighted in pink.

Electronic Supporting Information 4 Giant Clams

This database provides abundance and size (in cm) of giant clams (*Tridacna* spp.) surveyed in each habitat throughout American Samoa in 1994/95, 2002 and 2018.

Appendix 3 Key Messages for Managers, Communities and Other Stakeholders

How Are American Samoa's Coral Reefs Doing?

Results from long-term monitoring conducted over the last 25 to 40 years

American Samoa Coral Reef Historic Monitoring Project

American Samoa is very fortunate to have numerous long-term coral reef surveys that began in the 1970s and 1990s. Recently, the Coral Reef Advisory Group (CRAG) at the Department of Marine & Wildlife Resources (DMWR) invited two of the original scientists who have been monitoring our reefs for the last 25 – 40 years back to American Samoa to repeat these surveys. These scientists were also involved in resurveying the Aua Coral Transect on its 100 year anniversary in May, 2017.

The aim of this project was to repeat historic surveys conducted in American Samoa to evaluate the health of the coral reefs and fish communities, and to understand the changes that have taken place over the last 25-40 years. Baseline surveys were conducted throughout the Samoan Archipelago in 1994 and 1995 (including all of the main islands in American Samoa), and the sites around Tutuila and Manu'a were surveyed again in 2002. In 2018 we repeated these baseline surveys on Tutuila, in Manu'a, and Rose Atoll.

A total of 43 sites were surveyed on six islands between 15th October and 11th November 2018 by expert scientists Dr. Alison Green (reef fishes), Prof. Charles Birkeland and Dr. Douglas Fenner (corals), and CRAG ecologists Alice Lawrence, Georgia Coward, and Motusaga Vaeoso.

Survey Team: Alice, Georgia, Alison, Charles, Doug

Surveys of coral reef fishes (species, size and abundance), corals (species, abundance and colony size), benthic habitat (abundance of algae, corals and other invertebrates), juvenile corals and giant clams (abundance and size) were conducted on three 50 meter transects at each site. Approximately 16,000 individual reef fishes (199 species from 27 fish families), 6,741 coral colonies (113 species in 34 genera) and approximately 50 giant clams were recorded and measured, and over 8,233 observations were made of the benthic habitat.

Preliminary Observations indicate that the condition of American Samoa's coral reef ecosystem is highly variable both within and among islands. This is likely to be due to the varying oceanographic and geological conditions throughout the archipelago, in addition to the presence of villages, fishing activities, and sources of pollution. Further data analyses will be conducted over the next six months and this information will be collated in a final report by mid-2019. Village-based report cards will also be produced to summarize the condition of the coral reefs at each site based on key factors (such as coral cover, diversity and colony size, and fish abundance and biomass), along with management recommendations.

Bluefin trevally (***Caranx melampygus***) at Rose Atoll

Coral Reef Fishes

Dr. Alison Green has surveyed coral reef fish communities throughout American Samoa on three occasions over the last 24 years (1994/1995, 2002, and 2018). Dr Green's initial observations suggest that populations of fisheries species remain lower than expected at most of the sites surveyed. Reef fish larger than 30 cm in length are relatively uncommon on Tutuila and in Manu'a. Some vulnerable species (such as sharks and humphead wrasse) are rare while others (such as bumphead parrotfish and giant grouper) were not observed at all in 2018.

The exception is at Rose Atoll, where there are still healthy populations of fisheries species with more big fish and reef sharks, although diversity is naturally lower than on Tutuila and Manu'a. Less fishing around Rose Atoll has enabled reef fishes to grow larger and produce more offspring, providing a refuge for some of these species in American Samoa. But even at Rose the populations of the largest species such as sharks are less than on other remote reefs in the Pacific Islands.

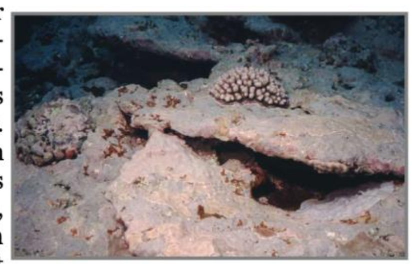
Coral Communities


Dr. Birkeland surveying coral at Fagatele Bay

- Prof. Charles Birkeland and Dr. Douglas Fenner have conducted surveys of coral communities in American Samoa on several occasions from the late 1970s to 2018.
- Initial observations from this survey suggest that coral communities are relatively healthy at the majority of sites (particularly at Fagatele and Vatia). However, there are some locations (e.g. Nu'uuli, Faga'alu and Fagafue) where the corals are not exhibiting the same rapid recovery rates following disturbances such as crown of thorns starfish outbreaks, coral bleaching, and hurricane damage. These could be priority sites for watershed and fishery management efforts.
- A site in Leloaloa, on the north side of Pago Pago Harbour is remarkable, with high coral cover of mainly plating species It is the best community of such corals Dr. Fenner has seen in the archipelago. It is remarkable that such a healthy looking coral community is inside the harbour.
- The survey site at Aunu'u looks like it has a few more dead corals than in the past, which may have been killed by recent coral bleaching events. The Leone site had terrestrial sediment in between corals, unlike the nearby DMWR monitoring site a few years ago. This could be a difference over space or time, and will be investigated further.
- Rose Atoll has a different coral community than any of the other islands in American Samoa. In fact it has two distinct communities, one on the outer slope, and one in the lagoon. The lagoon is a unique habitat in the entire archipelago, including Independent Samoa. The Lagoon has a high abundance of massive faviid corals, and some places are dominated by massive *Astreopora* unlike anywhere in American Samoa except western Ta'u. It also has a species (*Montipora capitata*) which is rare elsewhere in American Samoa, only being seen in the Ofu Pools by Fenner, and even there it is pretty rare. There appear to be some species in Rose that are not on the other islands.

Coral Reef Recovery and Resilience

- American Samoa is known for its strong, resilient coral reefs (particularly in Ofu Lagoon and Fagatele Bay), and researchers from around the world come to study the reefs to understand why.
- The coral reefs at some sites have recovered well from large-scale disturbances such as hurricanes, coral bleaching, and crown of thorns starfish outbreaks over the last 40 years (e.g. Fagatele and Vatia), while others have not recovered as well (e.g. Aua and Fagasa's outer bay).
- There are many factors that affect coral reef resilience (how well reefs recover from these disturbances). The survey scientists believe that some sites are healthier and more resilient than others because of better water quality conditions, which is the result of good watershed management practices and less damaging land-based activities nearby. Furthermore, the condition of the coral reefs in Pago Pago Harbour have improved since the cannery outfall pipe was moved from the inner to outer harbour in 1992. It is encouraging to know that we can make a difference to our reef ecosystems by ensuring better water quality in our villages. However, healthy populations of herbivorous reef fishes (e.g. parrotfishes) also play a critical role in coral reef resilience. Therefore good fisheries management is also important.
- One benefit that American Samoa has over perhaps most other reefs around the world is the prevalence of crustose coralline algae (CCA). CCA is a red alga that consists mostly of calcium carbonate that binds reef rubble and forms ideal settlement surfaces to facilitate the growth and recovery of coral reef communities. Recent surveys found rapid and abundant coral recruitment in areas where rubble from recent mortality of branching corals was bound by the CCA, *Porolithon onkodes*. On the reef flat at Aua, where *P. onkodes* is not prevalent and the rubble has not been bound (possibly since the 1930s), the reef community is still not showing signs of recovery after possibly as long as 85 years. Fortunately, *P. onkodes* was prevalent in most areas surveyed in Tutuila, Manu'a Islands and Rose Atoll and so the reef communities appeared either in good condition or on the way to recovery.


Crustose Coralline Algae cementing the reef structure

National Marine Sanctuary of American Samoa

Fale Bommie in Ta'u (with SCUBA diver for scale)

- The coral communities in Fagatele Bay section of the National Marine Sanctuary of American Samoa are healthy and thriving and are looking the best that the survey team have seen them in 40 years of monitoring (see photo top of page 2). Unfortunately, the fish populations are still low in the Sanctuary, and there are very few big fish.
- In 1994, DMWR staff (Fale Tuilagi and Alison Green) found one of the world's largest and oldest coral colonies, which they named Fale Bommie (the shape resembles a Samoan fale). It is now part of the Ta'u Management Area of the National Marine Sanctuary of American Samoa. The survey team were pleased to see that the bommie is still healthy and appears to be recovering well from coring studies to estimate its age and study the climate records in the skeleton.

Rose Atoll National Wildlife Refuge: 25 Years of Recovery from the Ship Grounding

- Rose Atoll is a special place. The reef is naturally dominated by a lush growth of pink CCA, which forms castle-like tower structures on the reef front.

Herbivorous reef fish at the ship grounding site

- On October 14, 1993, the Taiwanese longline fishing vessel Jin Shiang Fa ran aground on the SW side of the atoll, breaking up and spilling over 100,000 gallons of diesel fuel, 500 gallons of lube oil, and over 300 tons of metallic and other debris onto the reef. This caused a rapid deterioration of the reef ecosystem on the south-west and north-west sides of the atoll, including a large die-off of sea cucumbers, urchins, giant clams, and the important reef-building CCA. Iron from the wreckage stimulated the growth of cyanobacteria (a blue-green algae), which opportunistically took over the reef flat, reef crest, reef front, and some lagoon pinnacles on the affected sides of the atoll.
- The U.S. Fish and Wildlife Service (USFWS) and the American Samoa Department of Marine and Wildlife Resources (DMWR) worked together to remove the majority of the wreckage over the span of 15 years. However, some relatively small pieces remain on the reef at the grounding site and possibly more in deeper water.
- DMWR/CRAG and USFWS surveys from 1994/95 to 2018 indicate that Rose Atoll appears to be recovering well from the ship grounding. There appears to have been a substantial decrease in the area of opportunistic cyanobacteria, and recovery of the reef-building CCA, on the south-west and north-west sides of the atoll over the last few years. However, some physical damage to the reef and the cyanobacteria bloom remain at the grounding site, possibly due to iron continuing to leach from the remaining wreckage. Populations of herbivorous reef fishes also remain high at the grounding site, where they are feeding on the algae.
- The USFWS have existing plans to remove the remaining wreckage in 2019, which will hopefully further improve the health of the reef.
- Since it has now been 25 years since the ship grounding, we recommend: 1) repeating the detailed study of algae on the reef flat and iron enrichment to document the recovery on the south-west and north-west side of the atoll; and 2) compiling a comprehensive benchmark report (incorporating all previous studies) describing the recovery of the atoll from the ship grounding, and the cost/benefit of the clean-up operation.

Healthy pink crustose coralline algae at Rose Atoll

Rose Atoll National Wildlife Refuge: Giant Clams

- Giant clams (*Tridacna* sp.), known locally as *faisua*, are an important food item in American Samoa, but their accessibility and life history characteristics make them vulnerable to overharvesting.
- In the 1990s, DMWR (Dr. Alison Green and Dr. Peter Craig) conducted an extensive survey that found that Rose Atoll was an important refuge for giant clams that have been overfished throughout most of the Samoan Archipelago. They estimated that ~28,000 clams were present on the atoll, and more than 20% were juveniles (a sign of a healthy population).
- In our 2018 survey, we found that clam densities remain low on Tutuila and in Manu'a, with less than 30 individuals recorded. More importantly, we only recorded ~20 individuals on survey transects in the lagoon at Rose Atoll, which is a lot less than we recorded over a similar area in the 1990s. Furthermore, we saw very few juvenile clams at Rose Atoll this time, and large numbers of long-dead giant clam shells at the bottom of some of the pinnacles.


Giant clam or *faisua* within the coral reef structure

- This indicates that there appears to have been a mass mortality of giant clams on the atoll sometime over the last 25 years. Although, the likely reason(s) for the death of such a high number of clams remains unclear. This of great concern and we recommend that we repeat the full giant clam survey conducted by DMWR in the 1990s to confirm if the population on the atoll has collapsed, and invite giant clams experts to help investigate the possible causes of the collapse.

What Can You Do?

- Every place is different, and local communities can have a big role in improving the condition of their reefs and fish populations. We need to work together with local communities to implement fishery and watershed management tools to help enhance fish population recovery and keep coral reef ecosystems healthy.
- Examples of better watershed management practices include deterring deforestation and supporting protection of upland, lowland, and coastal forests, especially wetlands (mangrove habitats). Existing and new developments also need to be environmentally friendly, promoting vegetation growth and its many ecosystem functions, and allowing rain to soak into the ground to reduce runoff that reaches coral reefs. Septic systems and pig pens must remain at least 50 feet away from a stream, lagoon, or ocean.


Black tip reef shark inside Rose Atoll lagoon

- To ensure that the fish communities rebound on Tutuila and in Manu'a, Dr. Green recommends improved fisheries management and regulations, including enhancing our existing network of marine managed areas (MMAs). To help the fish populations recover, these MMAs need to be well managed and designed to be effective ecologically. For example, they will need to be in the right location, large enough and in place long enough to support the growth and successful reproduction of bigger and more vulnerable fish species. Existing regulations will also need to be fully enforced to protect rare and vulnerable species to ensure the health and recovery of the entire ecosystem.
- The lack of big, rare and threatened fish species recorded on this survey (see above), indicates that overfishing may be a concern for these species throughout most of American Samoa (less so at Rose Atoll). Improved fisheries management will be required to ensure that these species do not become locally extinct. In particular, the scientists recommend that the ban on fishing and possession of sharks in American Samoa should to be reinstated, because their life history characteristics make them particularly vulnerable to overfishing.

Project Support

The project was supported by DMWR and the Coral Reef Advisory Group (CRAG), with funding from the NOAA Coral Reef Conservation Program (CRCP). Dr. Alison Green and Prof. Charles Birkeland donated their time to the project, the US Fish & Wildlife Service (USFWS) funded the survey at Rose Atoll and the National Marine Sanctuary of American Samoa (NMSAS) funded the survey at Fagatele Bay.

For more information contact: Dr. Alison Green (agreen@tnc.org); Dr. Charles Birkeland (charlesb@hawaii.edu); Dr. Douglas Fenner (douglasfennertassi@gmail.com); DMWR Coral Reef Advisory Group (alice.lawrence@crag.as, georgia.coward@crag.as, motusaga.vaeoso@crag.as).