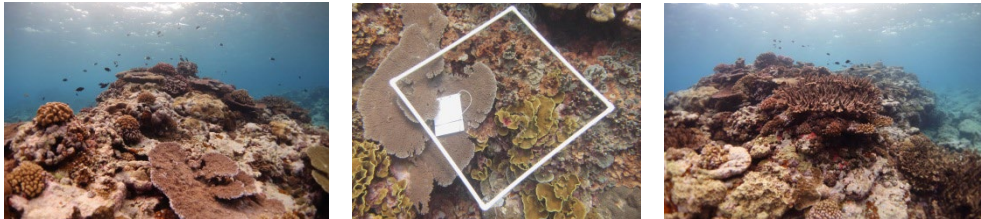


Watershed-based coral reef monitoring across Tutuila, American Samoa: Summary of decadal trends and 2013 assessment



Monitoring program partnership between the American Samoa Environmental Protection Agency, Pacific Marine Resources Institute, and the University of Guam Marine Laboratory



Authors:

Peter Houk^{1,2*}, David Benavente^{1,3}, and Steven Johnson³

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^{*1} Marine Laboratory, University of Guam, Mangilao Guam; ² Pacific Marine Resources Institute, Saipan, MP; ³ CNMI Marine Monitoring Program, Saipan, MP.

*Correspondence email: houkp@uguam.uog.edu

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Executive Summary

Introduction

The goals of the American Samoa Environmental Protection Agency (ASEPA) coral-reef monitoring program are to conduct long-term monitoring activities to characterize the present condition and temporal dynamics of coral-reef assemblages adjacent to several village-based watersheds around Tutuila. This effort started in 2003 when six watershed-based monitoring sites were first established, and has expanded over the years to include 15 sites with temporal trends developed.

The design, spatial scale, and methodology of this monitoring program were selected to match management programs that are focused at the village level, and account for inherent natural variation that exists on Tutuila's reefs. On Tutuila, coral-reef assemblages on the northern shoreline are distinguishable from the south (*furthered within*). While both have well-developed reefs within the embayments, they differ in taxonomic composition, as many of the most common benthic substrates, corals, and fish differ between the north and south. This is likely an artifact of natural settings, geology of the underlying watershed bedrock, or some combination of both. While these findings are of interest for further study in themselves, the existing monitoring effort deals with the inherent variation by stratifying survey designs. Representative sites have been established within each reef type (north and south), along gradients of watershed size, land use, and human population density. In addition, sites associated with uninhabited watersheds are used to provide ecological endpoints from comparatively undisturbed watersheds; Tafeu in the north and Fagatele in the south.

At each monitoring site standardized, transect-based protocols were used to gather data depicting the benthic substrates, coral, and fish assemblages with appropriate statistical confidence to detect change through time. Through this monitoring approach, trends in coral-reef status indicators are being detected at time scales relevant to management (1 – 5 years). The present report highlights decadal trends since the inception of monitoring in 2003, which includes a timeframe where a major disturbance (cyclone Heta in 2004) impacted Tutuila's reefs, and recovery occurred. We analyzed metrics of coral-reef recovery and present reef condition with respect to proxies of watershed pollution, grazing potential of herbivorous fishes, and wave exposure. Prior studies have shown that these variables represent the localized stressors and natural regimes of greatest significance to the condition of corals and benthic substrates.

Decadal Trends

The most significant change to Tutuila's reefs since ASEPA monitoring began has been the sharp decline (~15%) in coral cover following cyclone Heta, and subsequent recovery over the past decade. The decadal trends hypothesize a nearly full recovery of coral growth since the damage from cyclone Heta in 2004, however, these trends must be understood alongside the baseline that our monitoring efforts are founded upon. Previous studies

suggested that island wide coral cover estimates may have been higher in the past (as high as 62% in 1982), substantially higher than the 2003 baseline we have noted. Thus, while we note successful recovery, the overall trends were disproportionately driven by a few of the monitoring sites that had the greatest coral loss and regrowth (such as Fagaitua, Fagatele, Tafu, and Aoa), while sites with less coral remained more static or had a slow, steady decline through time (such as Fagaalu, Laulii, Fagasa, and Masefau). Therefore, successful recovery indicated that sites classified by high and low condition indices remained that way since 2003 when monitoring began. In support of these findings, EPA-based aquatic life use support rankings (i.e., the classification system used to assess reef condition) found that most (10 of 15 sites) of the aquatic life use support rankings did not change through time.

Causes of impairment to Tutuila's reefs

More detailed insight into the causes of impairment to Tutuila's coral reefs was generated through examining the rate of recovery at each site using regression models and correlation analyses. Following the 2008 monitoring event, early stages of recovery from cyclone Heta were already noted based upon two ecological indicators, benthic substrate ratios and coral evenness. Benthic substrate ratios describe the ratio of calcifying versus non-calcifying substrate on the reef, and provide an overall indication of reef growth capacity. Coral evenness describes the extent to which the total coral coverage at each sites was distributed across many species. These initial results suggested that recovery rates were dependent upon both water quality and herbivore biomass, both in conjunction with wave exposure. Interestingly, the relative influence of water quality and herbivore biomass was equal for reefs along the southern shoreline, while herbivore biomass had a disproportionate influence for the reefs along Tutuila's northern shoreline.

The present monitoring effort used enhanced datasets to expand upon these findings. Regression models highlighted a similar magnitude of influence from pollution proxies and mean herbivore size for the reefs along Tutuila's southern shoreline, yet proxies to land-based pollution were components of more of the significant models examined. Similar to past reports, wave exposure was a required component for all models. For reefs along Tutuila's north shoreline, fewer sites were investigated and only exploratory correlation analyses were performed. Correlations also indicated that both herbivore size and proxies to pollution were associated with the recovery process and current reef condition. Examinations with coral evenness were strongest with mean herbivore size, while benthic substrates had greatest associations with pollution proxies and wave exposure. Notably, the influence of wave exposure differed between the north and south. In the south wave exposure had a negative relationship with recovery indices, while in the north the relationship was positive. This was attributed to the predominant weather patterns and wind directions around Tutuila (*furthered within*).

ALUS rankings

The present condition assessment determined that 8 of the monitoring sites were considered either full or partially supportive for aquatic life use support, while 7 were considered not

supportive. Sites that have consistently been described with non-supportive ALUS rankings since the inception of monitoring include Fagaalu, Fagasa, Laulii, Alofau, Aoa. While their rankings are similar, the perceived causes behind the rankings differ based upon the decadal trend data. Alofau and Fagaalu had the lowest mean herbivore sizes, moderate to high proxies to land-based pollution, and relatively low wave exposure. In contrast, Fagasa and Aoa had highest proxies to land-based pollution, with moderate to low herbivore sizes and wave exposure. Last, Laulii had equal influence from high wave exposure, moderate to low herbivore sizes, and high proxies to land-based pollution.

Among the four sites with partially supportive ALUS rankings, three have remained in this category since monitoring began (Fagaitua, Leone, and Vaitogi), while Matuu has improved from a 2008 non-supportive ranking based upon trend data suggesting wave exposure is the most limiting environmental parameter for improved benthic substrate ratios, and a general improvement in the coral assemblage.

In addition to Fagatele and Tafeu that have been ranked as fully supportive since monitoring efforts began, both Masausi and Alega now also considered to be fully supportive based upon recovery trends that depicted wave exposure as the limiting factor for non-significant improvements to the benthic and coral assemblages noted.

Conclusions and future directions

The present study summarized decadal disturbance and recovery trends across Tutuila initiated by cyclone Heta in 2004. Over the past decade we report that coral cover appears to have rebounded to pre-disturbance levels, but we caution that pre-disturbance levels were based upon a snapshot of the reefs in 2003, and do not take into account changes that have occurred over longer periods of time (i.e., several decades). So, while overall recovery trends were encouraging, sites in good ecological condition (i.e., fully and partially supportive ALUS) were drivers of the trends. In contrast, sites with poor condition rankings remained more static. While high proxies to land-based pollution and small mean herbivore sizes both limited the recovery process, recovery along the south shore of Tutuila appeared to have more consistent ties with pollution proxies. One hypothesized driver of these findings is that the nature of freshwater input from the watershed to the nearshore reefs differs between the north and south shores, but spatial and temporal salinity profiles would be needed to further this hypothesis.

Continued efforts to better understand the influence of localized stressor upon Tutuila's nearshore reefs and to assess management regimes are long-term goals for ASEPA's monitoring effort. Reports in the past indicated that pig densities per km², alone or in combination with other pollution proxies, had significant ties with the ecological metrics used here. Over the years since the ASEPA piggery program has started, pig densities have become less influential predictors of reef condition, and the present analyses found no significant ties evident with pig densities. Clearly linkages such as these are speculative, but these findings can support further study directed at understanding the contribution of piggery waste to overall watershed pollution levels, and are useful in generating funding to perform such a study. Similarly, the Fagaalu watershed and nearby sewage treatment

plant are the current (or proposed) topic for more descriptive study that can benefit from long-term ecological datasets. Cumulatively, the ALUS rankings generated here are currently being used to establish a watershed priority list that assists with maximizing the effectiveness of limited management budgets, and fulfills federal grant requirements.

The future goal of the ASEPA coral monitoring effort is to conduct surveys on a bi-annual basis, tracking changes over time and drawing linkages with human disturbances. The existing program would benefit from increasing the number of sites visited along both the north and south shore to improve the (statistical) foundation for assessing the trends presented, or focusing the existing resources on either the south or north shore.

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1. Introduction

The goals of the American Samoa Environmental Protection Agency (ASEPA) coral-reef monitoring program are to conduct standardized, long-term monitoring to characterize the present condition and temporal dynamics of coral-reef assemblages adjacent to several watersheds around Tutuila. This effort started in 2003 when six watershed-based monitoring sites were established (Houk et al. 2005), and has currently expanded to include 15 sites that have developed temporal trends (Figure 1). Initially, the results were used for spatial assessments of Tutuila's nearshore reefs, whereby relationships between watershed characterizations (i.e., size, disturbed land, human population) and coral reef metrics (i.e., percent coral cover, coral species richness, and algal substrate abundances) were established. These relationships served as a basis for assessing 'condition' at individual sites, drawing upon the body of known resilience indicators to serve as indices of condition (McClanahan et al. 2012; Mumby et al. 2013). However, continued monitoring over the years has facilitated more desirable comparisons over time, allowing for investigations into why some coral-reef assemblages began to recover faster following a major disturbance in 2004 (cyclone Heta; Houk et al. 2010). Within this report, we expand upon this foundation and provide new datasets that improve our characterization of change over the past decade. In addition, we provide a current assessment of the watershed-based monitoring sites to meet grant reporting requirements set forth by ASEPA.

Extensive ecological work has been undertaken throughout American Samoa over the past 15 – 20 years (*a subset includes*: Birkeland et al. 2003, Green et al. 1999, Mundy 1996, Fisk and Birkeland 2002, Green et al. 2005; Sabater and Tofaeono 2007; Fenner 2009), with different questions being posed explicitly, and implicitly as suggested by varying survey designs. Houk et al. (2005) compared and contrasted the goals and survey techniques employed in several studies that have focused upon coral and benthic assemblages as primary ecological measures of interest. In summary, the present monitoring effort differs because it is targeted upon the reefs situated within defined embayments that are in closest proximity to village populations. Thus, the present monitoring assesses the impacts of watershed pollution, in conjunction with other localized stressors (i.e., herbivory) and natural regimes (i.e., wave exposure), that are influential to reef communities around Tutuila.

Studies and monitoring programs relating human disturbances to various aspects of corals and coral-reef assemblages have a long history (Fishelson 1977; Tomascik and Sander 1985; Fabricius 2005; Smith et al. 2005; Dikou and van Woesik 2006). Many studies drawing causality between pollution and corals (or reef assemblages) have focused upon manipulative experiments that expose individual organisms (corals), or plots of reef, to enhanced nutrient levels (Tomascik and Sander 1985; Smith et al. 2001; Lapointe et al. 2004). While insightful, the results gained are spatially dependent, as relationships that exist for individual coral colonies (~1 m² scale of investigation) often may not be consistent with those found for coral assemblages (~100 m² scale of investigation) because other driving forces and indirect interactions often take precedence (Levin 1992). In contrast, other studies take a much larger spatial and temporal approach, examining coral declines that are a suspected result of human influences at the regional scale over decades (Gardner

et al. 2005; Bruno and Selig 2007). Examining decadal trends over large spatial scales (thousands of square kilometers) provides less opportunity to develop insight into causes and mechanisms. In addition, very small or very large spatial and temporal scales are often not consistent with management and policy needs. In reconciliation, the ASEPA monitoring effort examines the dynamics associated with localized reef assemblages across moderate spatial scales (i.e., hundreds of square meters of reef). This design was selected to match watershed management programs that are focused at the village level, and to improve our understanding of the dynamics of coral, benthic substrate, and fish assemblages that shift at time scales appropriate to assess management (1 – 5 years).

Before attempting to draw relationships between anthropogenic disturbances and coral assemblages it is desirable to account for the inherent variation that is associated with the physical setting of reefs (i.e., environmental regime) (Goreau 1959; Sheppard 1982; Grigg 1998; Houk and van Woelk 2010). Through geological time, different reef settings emerge because coral assemblages have distinct reef-building capacities in accordance with environmental regimes such as wave exposure and the nature of watershed discharge. On Tutuila, two visually distinct reef types categorized by previous studies are most relevant: 1) primary framework with interstitial spaces common throughout the reef matrix, found mainly on the south side of Tutuila, and 2) primary framework with a well-cemented, underlying basement, lacking significant interstitial spaces, mainly found on the northern side of the island (*furthered in methods*). Monitoring was designed to sample representative sites within each major reef type, along gradients of watershed size, land use, and human population density. Here, we first describe the inherent differences between benthic substrates, coral, and fish assemblages associated with varying reef types. We then stratify examinations by reef types to isolate upon trends that are best explained by watershed characteristics, proxies to grazing potential, and wave exposure.

2. Methods

2.1. Study Design

Monitoring was conducted to support the American Samoa Environmental Protection Agency NPS pollution control program. In culmination, 15 locations around Tutuila, the main and most populated island, have been surveyed over the past 10 years (Figure 1). Initial site visits to most locations (12 sites) were conducted in 2003 and 2005. Sites visited in 2003 were re-visited in 2007, and sites visited in 2005 were re-visited in 2008 (Table 1 describes all site visits). Three additional sites were established in 2007. During each annual survey event, sites were selected across reef types, watershed sizes, and human population densities. In 2013 all monitoring sites were re-visited to provide an anchor point to help assess trends through time developed within this report. Notably, the timeframe for this monitoring effort coincided with significant impacts from cyclone Heta (2004, Tutuila), limited impacts from cyclone Olaf (2005, Manu'a), and unknown impacts from a devastating tsunami (2010).

Three reef types have been identified during the course of ASEPA monitoring efforts: 1) primary framework with interstitial spaces common throughout the reef matrix, found

mainly on the south side of Tutuila, and 2) primary framework with a well-cemented, underlying basement, lacking significant interstitial spaces, mainly found on the northern side of the island, and 3) intermixed sand and primary-framework reef patches. Primary coral framework (Holocene) were defined by a consolidated reef matrix created mainly by large coral skeletons cemented together with coralline algae, and interstitial spaces refer to the presence of cavities within the primary reef framework (Insalaco 1998). Present monitoring designs are mainly focused on the first two reef types because they are the most predominant, and classified by geography (i.e., reef types 1 and 2 represents reefs along the south and north shore of Tutuila, respectively). For the present study, reef type 3 (intermixed sand and reef patches) was only represented by one site, Vatia, where modern growth was limited and dominated by *Porites cylindrica*. Within each of the two major reef types, representative sites were selected for investigation in accordance with watershed sizes, several proxies of watershed pollution, and along a gradient of wave exposure (Table 2).

2.2. Ecological Data

Monitoring sites were established on the nearshore reef slopes (8–10 m) adjacent to selected watersheds, approximately 250 m away from stream discharge. During each survey event, a hand held global positioning system unit was used to identify the location of transects that were placed at a uniform depth of 9 – 11 m, with a known geographic heading. Benthic cover was evaluated using video and photo quadrat protocols along a series of transect lines (Houk and van Woesik 2006). During the 2013 surveys, transect lines were separated into 6 x 25 m long replicates, and benthic substrate abundances were estimated from photographs of 0.5 x 0.5 m quadrats taken at 1 m intervals. Prior to 2013, benthic substrates were estimated from still frames captured from video transects along 3 x 50 m long replicates, also at 1 m intervals. In both instances cameras were calibrated so that each photograph (or screen shot) represented a 0.5 x 0.5 m section of the reef. Methods were shifted in 2013 to improve statistical confidence while keeping the same overall sampling area. The shift in methods provides for enhanced confidence intervals (i.e., lower standard deviations) while having less influence on the mean abundances being estimated (Houk and van Woesik 2006). Photographs were analyzed by projecting five random dots on the screen and noting the life form under each of the dots. The benthic categories chosen for analysis were corals (to genus level), turf algae (less than 2 cm), macroalgae (greater than 2 cm, to genus level if abundant), fleshy coralline algae known to overgrow coral (*Peyssonnelia*, *Pneophyllum*) (Keats et al. 1997; Antonius 1999,2001; O'Leary et al. 2012), calcifying crustose coralline algae, sand, and other invertebrates (genus level if abundant). From these categories, a benthic substrate ratio was classified as the percent cover of calcifying corals and crustose coralline algae divided by the percent cover of turf, macroalgae, and fleshy coralline algae substrate. High benthic substrate ratios indicate favorable reef condition, and dominance of calcifying substrates that accrete through time.

At each location coral communities were examined using a point quadrat technique. Ten replicate 1 x 1 m quadrats were haphazardly tossed at equal distances along the transect lines. Every colony whose center point lay inside the quadrat was recorded to species level, and the maximum diameter and diameter perpendicular to the maximum were measured.

These measurements were used to estimate percent coverage, relative abundance, population density, and geometric diameter, with the mathematical assumption that colonies are circular. Margalef's d-statistic was calculated as a measure of the number of corals present, making some allowance for the abundance of individuals, or community evenness (Washington 1984). This describes how evenly coral coverage was distributed at each site, but does not take overall percent cover into account. A low d-statistic suggests that coral coverage was not dominated by one, or a few, species.

Fish numerical abundance and biomass have been estimated since 2008 using a modified stationary point count (SPC) protocol (Bohnsack JA 1986). During 2008, five replicate SPC's were conducted. In each instance, an observer counted and estimated the size of all food fish that resided within a 7.5 m radius for a period of 5-minutes. During 2013, an observer took similar measurements within 12 replicate SPCs using a 7.5 m radius, but a shorter time of 3-minutes. Food fish were defined by acanthurids, scarids, serranids, carangids, labrids, lethrinids, lutjanids, balistids, kyphosids, mullids, and holocentrids that are known to be harvested. Fish biomass estimates were calculated using the length assessments recorded during the SPCs. The biomass was calculated by using the formula $W=A*L^B$ where W =weight, L = length, and A & B = growth parameters obtained from www.fishbase.org. When growth parameters were not known for a given species, values from a closely related species were used.

In order to account for varying SPC observation times, fish abundances were estimated for individual SPCs by dividing the biomass by the amount of time spent observing the fish. Given the potential bias associated with longer, 5-minute SPC's conducted in 2008, only the complete 2013 datasets were used in the statistical analyses described below (i.e., multivariate PCO plots, regression modeling, and correlation examination). However, estimated abundances for the most abundant fishes were explored between the two time frames by examining data from the same set of sites (2008 and 2013).

Macroinvertebrates have been counted along the transect lines used for benthic assessments since the inception of ASEPA monitoring efforts. However, we have continually found macroinvertebrate populations to be extremely scarce at all monitoring locations, and consistently have standard deviations that are over double the mean values. Therefore, macroinvertebrate data are not further discussed in the present report.

2.3. Environmental Data

Wave exposure data were gathered from NOAA Wave Watch III model predictions, summarized for American Samoa (Brainard et al. 2008). For each monitoring site, mean wave heights were recorded with respect to their angle of exposure, using the wave-rose data, and the sum of wave intensity for all angles of exposure was calculated for each site (Table 3). Watersheds adjacent to each site were quantified using existing American Samoa Department of Commerce GIS layers pertaining to land use and boundaries. Disturbed land included all regions that no longer have tropical rainforest as the dominant tree cover, based upon United States Forest Service vegetation maps

(<http://www.fs.usda.gov/r5>). Human population estimates were derived from the most recent census report.

2.4. Data Analysis

Reef Types and Geography –

Examinations were first conducted to describe the inherent differences between coral, fish, and benthic assemblages along the south shore of Tutuila compared with the north (i.e., framework reefs with interstitial spaces in the south versus predominately consolidated reef in the north). For all assemblages, data were aggregated at the site level, and species-by-site matrices were generated and used to create Bray-Curtis similarity matrices (Anderson et al. 2008). Bray-Curtis similarity matrices were calculated by:

$$S_{(j, k)} = 1 - (\sum |Y_{ij} - Y_{ik}| / \sum (Y_{ij} + Y_{ik})) \quad (1)$$

where S represents the ecological similarity between two sites (j and k), \sum (numerator) represents the summation of the absolute differences in the abundance of each species (Y_i) at the two sites, and \sum (denominator) represents the sum of the abundances of species (Y_i) at the two sites. Bray-Curtis similarities define how consistent species abundance patterns were between each pair of sites. Similarity matrices were graphically interpreted using principle components ordination plots that depict the site-based distances into two-dimensional space (Anderson et al. 2008). Significance between reef types is calculated from PERMANOVA tests that are similar to standard ANOVA tests that calculate significance based upon Bray-Curtis variation within and across reef types. These tests provide a pseudo-F statistic that is analogous to a standard ANOVA test result, and a P-value based upon permutation, or repeating the process until a probability distribution is generated.

Trends -

We first summarized general trends in coral cover and fish biomass at the island scale with respect to disturbance regimes and time. Shortly after monitoring efforts were initiated in 2003, a category 5 cyclone (Heta) impacted Tutuila, with wave heights reaching as high as 13 m reported offshore. In 2005, cyclone Olaf hit the nearby (150 km) Manu'a Islands, but wave intensities were less influential to Tutuila. Last, in 2010 a devastating tsunami impacted many low-lying areas around Tutuila, but significant impacts to the coral reef assemblages, particularly the reef slopes, have not been documented.

The general trends suggested that cyclone Heta was the largest, most ubiquitous acute disturbance to impact Tutuila since the inception of monitoring. We therefore sought to examine recovery trajectories for each site with respect to proxies of land pollution, herbivory, and wave exposure. For the south shore of Tutuila sufficient monitoring sites existed to perform regression analyses between ecological indicators of recovery and present status with respect to stressors and wave exposure. Three ecological indicators of recovery were generated. We calculated: 1) the change in mean coral colony size between 2013 and 2007/8 to provide an indication of coral growth capacity, 2) the change in the

benthic substrate ratio over the same time period to provide an indication of calcification, and 3) the change in coral assemblage evenness to provide an indication of the distribution of coral species abundance patterns. Prior to regression analyses, correlations were examined between the three noted ecological indicators of change to assess their association during the recovery time period. In addition, two ecological indicators of present status were generated: 1) 2013 benthic substrate ratio, and 2) 2013 coral assemblage evenness.

Regression modeling was performed using the freely available R software (R Development Core Team 2008). Dependent variables were listed above. Independent variables included wave exposure, disturbed land per km², human population per km², a combined pollution proxy that represented the sum of disturbed land and human population, and mean herbivore size excluding new recruits that resided within size class bins below 10 cm. All variables were standardized to provide equal weighting for assessing their relative contributions, and a constant value was added to make all numbers positive (required for regression modeling). Only single term models were considered due to small sample sizes and to aid the relative assessment of individual stressors. Residual normality was inspected using the Shapiro-Wilk tests. Best-fit models were described in association with their Akaike's Information Criterion (AIC), whereby lower AIC scores indicated a better fit based upon R² values as well as the residual distributions.

Due to limited sites being established on the north shore of Tutuila compared to the south for logistical reasons, standard correlation testing was used to explore associations between the noted ecological indicators and environmental variables.

Two sites represented extreme outliers and were not considered in the existing regression modeling or correlation analysis. These were Leone (south) and Vatia (north). Leone has a disproportionately large and complex watershed, coupled with the most extensive human population density among sites in the present study. Further, watershed topography differs substantially at Leone, whereby watershed runoff runs through an extensive, flat drainage system prior to discharge to marine waters. Vatia represents the only site surveyed from a different reef type (type 3 noted in methods). As in previous reports, initial inspection of regression models and correlation analyses found that both sites represented outliers for the present analyses.

2013 ASEPA ALUS Assessments -

Site-based, aquatic-life-use-support (ALUS) rankings were made following established United States Environmental Protection Agency (USEPA) guidance material (USEPA 1997, 2002). Three categories were used for condition rankings: fully, partially, and not supportive for aquatic life use support. Previous monitoring reports have provided assessments based upon data available in the past (Houk and Musburger 2007, 2008). Given the emergence of improved temporal data, the present ALUS assessments were based upon past rankings, in addition to recovery indicators pertaining to the benthic substrates (benthic substrate ratio recovery) and coral assemblages (combined coral colony-size and evenness recovery). Noted above, recovery indicators were standardized

to have a mean value of 0 and standard deviation of 1, and rankings were made following guidance criteria (Figure 2).

3.0 Results

3.1. Reef types – north versus south shore species assemblages

Pairwise ANOSIM tests showed strong separation of the benthic, coral, and fish assemblages between sites on the north and south shores (Figure 3, pseudo-F Statistics = 7.5, 3.9, and 2.2, respectively, P-values <0.006 for all). R-statistics quantified that benthic and coral assemblages had the greatest degree of separation (Figure 3). However, trends were also perpetuated through the fish assemblages, suggesting interdependences between mobile and sessile trophic guilds may exist. Reefs along the south shore of Tutuila (i.e., framework reefs with interstitial spaces common) supported distinctively higher abundances of all coralline algae and soft corals, while more consolidated framework reefs on the northshore had less coralline algae and more turf algae and sand in comparison (Figure 3, vectors lengths depict weightings). With regards to the coral assemblages, reefs in the south supported more table, corymbose, and arborescent *Acropora* corals, as well as more plate-like *Echinopora* and *Merulina*. In contrast, several massive and encrusting corals were most affiliated with the northern reefs: *Leptastrea*, encrusting *Psammocora*, massive *Porites*, *Porites rus*, and encrusting *Leptoseris*.

Fish assemblages associated with reefs along the north shore had higher abundances of the browser (*Naso unicornis*), common scraper (*Chlorurus japanensis*), common goatfish (*Parupeneus cyclostomus*), and two other detritivore surgeonfish. In contrast, the reefs along the south shore had larger populations of different small-bodied detritivores and scrapers (*Ctenochaetus striatus* and *Scarus psittacus*), as well different secondary consumers and small piscivores (*Cheilinus fasciatus* and *Cephalopholis argus*). Interestingly, the shift in species composition appeared to be attributed more to taxonomy within functional groups, as compared with functional group differences. In support, mean fish size, but not overall biomass, was larger on the north compared to the south for both herbivores and all fish grouped (P<0.05, t-test for both, Figure 4), suggesting assemblage distinctions. While not approached further within, the distinctions between coral and fish species assemblages on the northern and southern reefs deserves more attention to discern the influences of geographic isolation versus environmental selection.

3.2. Temporal trends

The most significant ecological change since monitoring began has been the sharp decline in coral cover following cyclone Heta, and subsequent recovery over the past decade (Figure 5). These trends were evidenced by aggregating coral cover data across Tutuila during each survey year to provide representative estimates. While sites visited during 2003, 2005, 2007, and 2008 were not identical (*see methods*), each annual survey event was designed to include sites from both the north and south shores of Tutuila, across watersheds that ranged in size, human population density, and wave exposure. The present (2013) dataset provided an anchor point that is based upon data from all 15 monitoring

sites. The decadal trends in coral cover hypothesize a nearly full recovery of coral growth since the damage from cyclone Heta in 2003, however the nature and rates of recovery were the subject of further investigation described below. The lack of significant impact observed from cyclone Olaf could be due to the large distance between Tutuila and Manu'a (~140 km) where the typhoon track passed. More remarkable is the lack of substantial impact observed on coral cover from the 2010 Tsunami that had devastating impacts to Tutuila's coastline and society.

Temporal comparisons between the 2008 and 2013 fish biomass datasets suggested that non-significant declines may have occurred within four functional groups (large-bodied snappers, trevallies, small-bodied snappers, and large-bodied emperors) (Figure 6; large and small body-size refers to species with estimated size-at-maturity above or below 30 cm, respectively, as reported by fishbase). Most other functional group comparisons showed little change, while small-bodied surgeonfishes and parrotfishes appeared to increase. These data are considered exploratory due to shifting times used in the SPC data collection protocols between the two years, but serve to provide one indication of fish assemblage dynamics for the coral reefs most accessible to village populations.

3.2. Patterns and causes of ecological change

The temporal dynamics in coral cover provided a foundation for deeper investigations into the recovery process. While there was a general indication that reefs have had positive recovery since cyclone Heta, assessments of the rates of change for three ecological metrics provided improved details: annual change in mean coral colony-size, coral assemblage evenness, and benthic substrate ratios since 2007/8.

Reefs along Tutuila's south shoreline -

Ecological metrics used to assess ecological recovery were weakly, but non-significantly, correlated in most instances. For the reefs along Tutuila's southern shoreline, the rate of change in mean coral colony-size since 2007/8 was negatively related to the change in coral evenness ($r = -0.4$, Figure 7). However, the relational fit was log-linear in nature, suggesting that the increase in species richness was highest where small coral colony-sizes existed, and smallest where larger coral colonies existed. Thus, the presence of large coral colonies and rapid coral growth served to decrease evenness. Benthic substrate ratios also had a weak, negative, log-linear relationship with mean coral colony-size (Figure 7). Benthic substrate ratios, or the ratio of calcifying versus non-calcifying substrates, increased most where small coral colonies existed, and least where larger colonies were found. Both relationships suggested a saturation in the recovery process along Tutuila's southern shores, and that differential drivers may be responsible for various attributes of coral-reef recovery. Last, correlations between the rate of recovery in benthic substrate ratios and coral evenness were highly significant ($r = 0.7$), suggesting that predictive models for both would be redundant.

The array of regression models consistently highlighted that herbivore size and the pollution proxy both served as primary predictors of recovery, and when combined with

wave exposure significant regression models were evident in both cases (Table 3, Figure 8). The rate of colony-size growth since 2007/8 was largest for Alega, where high wave exposure and small proxies to pollution were noted. While high wave exposure limits the total amount of coral growth at Alega (e.g., high wave exposure and low percent coral cover exist at Alega, Table 1 and 2), the corals that can survive high wave exposure regimes appeared to grow back fastest. Fagatele and Fagaitua also had high rates of coral colony size change, but were associated with less wave exposure and greater overall coral coverage. The smallest change in coral colony size was noted for Vaitogi, where large stands of *Merulina* corals have represented one dominant component of the coral assemblage since monitoring began there.

In contrast, benthic substrate ratio recovery and the highly correlated coral evenness recovery were best predicted by independent models that included either wave exposure or human population density. Increases in calcifying substrate and coral evenness were inversely related to wave exposure, as high wave exposure diminished both metrics (Figure 8, Table 3). These results resonate with the above findings that high wave exposure limits overall coral coverage, which represents a primary calcifying substrate on the reefs. In addition, high wave exposure constrained the diversity of coral that could persist. Both substrate recovery and coral evenness were also diminished (inversely) with human population density. As a result of the collective findings, Fagatele and Vaitogi, two sites with limited human population density and relative low wave exposure had the highest recovery rates for benthic substrates and coral evenness.

Regression models using two dependent variables that depicted the current status of reefs on the southern shoreline were consistent with those describing recovery rates. The 2013 benthic substrate ratios were well predicted by an interactive model with human population density and wave exposure, depicting negative relationships with both variables (Figure 8, Table 3). Coral coverage and colony-size were both highly correlated ($r > 0.7$ for both) with benthic substrate ratios, suggesting that similar relationships exist between human population density, wave exposure, and these two metrics. Present coral assemblage evenness, however, was well predicted by two models that included either herbivore size or the amount of disturbed land per km², both in conjunction with wave exposure.

Overall, we report nearly identical slopes for regression models between recovery/status, herbivore size, and the pollution proxy (e.g., slopes of standardized variables depict their relative contribution to change), but more of the significant models contained pollution proxies as predictors, potentially suggesting a stronger influence (Table 3). In addition, wave exposure was a required component of most significant models.

Reefs along Tutuila's north shoreline -

Due to limited sample sizes only exploratory correlation examinations were conducted for the reefs along Tutuila's northern coast. In contrast to the south, both the present 2013 benthic substrate ratio and its recovery rate were strongly and positively associated with wave exposure, and negatively associated with several proxies to land-based pollution ($r > 0.7$, Table 4). These trends were exemplified by high abundances of calcifying substrates

(and recovery rates) at Tafeu, and low abundances and recovery at Masefau since 2007/8. Uniquely, Aoa had a high 2013 substrate ratio due to extremely high cover of encrusting *Montipora*, yet a relative low rate of change over the years. The varying role of wave exposure between the north and south may be due to the predominant weather patterns in American Samoa. Southeast tradewinds provide wind-generated swells to the southern shoreline for the majority of the year, while the northern reefs examined are subjected to lower wave intensities throughout the year (Table 1). Thus, moderate wave exposure may be beneficial for benthic substrates, while high exposure, characteristic of many of the south shore reefs examined, may not be (i.e., unimodal, humped relationship).

Associations with coral assemblage metrics were also different from the reefs along Tutuila's southern shoreline. In the north, coral colony-size recovery and 2013 evenness both had strongest associations with the herbivorous fish assemblage (Table 4). Colony-size recovery had positive ties with herbivore size, and no secondary ties with wave exposure, being highest at Tafeu and lowest at Masefau (Table 2). Colony-size recovery was negatively correlated with coral evenness recovery ($r = -0.67$), suggesting that high evenness can persist with or without colony-size recovery. In support, 2013 evenness was disproportionately high at Masefau where limited coral regrowth occurred, but was also high for Tafeu where maximal coral regrowth occurred. Evenness had negative ties with wave exposure, suggested that extremely low wave exposure sites sampled along the north shore had a reduced diversity of corals compared with areas where moderate exposure existed.

Given the limited sample sizes for northern reefs the results are more exploratory as compared with the south, yet the findings hypothesize a diminished role of wave exposure for the north shore, and a slightly increased role of herbivory compared to land-based pollution.

3.3. Aquatic life use support rankings (ALUS)

Out of the 15 sites where sufficient data were available to determine aquatic life use support (ALUS) rankings, 8 were either full or partially supportive, while 7 were not supportive (Table 5). Based on coral and benthic assemblage recovery trends, the primary causes attributed to ALUS rankings for each site were also described. Sites that have consistently been described with non-supportive ALUS rankings since the inception of monitoring included Fagaalu, Fagasa, Laulii, Alofau, Aoa. While their rankings are similar, their perceived causes differ based upon the decadal trend data. Alofau and Fagaalu had the lowest mean herbivore sizes, moderate to high proxies to land-based pollution, and relatively low wave exposure. In contrast, Fagasa and Aoa had highest proxies to land-based pollution, with moderate to low herbivore sizes and wave exposure. Last, Laulii had equal influence from high wave exposure, moderate to low herbivore sizes, and high proxies to land-based pollution.

Among the four sites with partially supportive ALUS rankings, three have remained in this category since monitoring began (Fagaitua, Leone, and Vaitogi), while Matuu has improved from a 2008 non-supportive ranking based upon trend data suggesting wave exposure is the most limiting environmental parameter for improved benthic substrate

ratios, and a general improvement in the coral assemblage (i.e., the integrated measure of mean colony-size and evenness).

In addition to Fagatele and Tafeu that have been ranked as fully supportive since monitoring efforts began, both Masausi and Alega now also considered to be fully supportive based upon recovery trends that depicted wave exposure as the limiting factor for non-significant improvements to the benthic and coral assemblages noted.

4. Discussion

Cyclone Heta represented the largest natural disturbance since ASEPA coral-reef monitoring efforts began in 2003, and impacted reefs on both the north and south shore of Tutuila. The suspected drivers of the ubiquitous decline in coral cover surrounding this time frame are the direct impacts of the cyclone, major upwelling of cool nutrient rich waters that accompanies tropical storms (Walker et al. 2005), or time integrated responses of both (Guillemot 2010). It is encouraging that island wide coral cover trends highlighted a recovery to pre-disturbance states, and that recovery trajectories were similar to those reported in the past (Craig et al. 2005). Crustose coralline algae first colonized bare substrates following disturbances, followed by coral growth. However, recovery trends must be understood alongside the baseline that 2003 data provided (Knowlton and Jackson 2008). Previous studies suggest that island wide coral cover estimates were higher in the past (as high as 62% in 1982, Fenner et al. 2008 and Wass 1982 cited within), substantially higher than the 2003 baseline we have noted. Thus, while we documented successful recovery at expected time frames for healthy coral reefs (i.e., 10-year recovery cycles; Golbuu et al. 2007), the overall trends were disproportionately driven by a few of the monitoring sites that had the greatest coral loss and growth potential (such as Fagaitua, Fagatele, Tafeu, and Aoa), while sites with less coral remained more static or had a slow, steady decline through time (such as Fagaalu, Laulii, Fagasa, and Masefau). Cumulatively then, successful recovery indicated that sites classified by high and low condition indices remained that way since 2003 when monitoring began. In support of these findings, most (10 of 15) of the aquatic life use support rankings (ALUS) found did not change through time. More detailed insight into the drivers of coral-reef condition across Tutuila was offered through regression and correlation analyses.

4.1. Environmental drivers of reef condition across Tutuila

After collecting data during the 2008 survey event, Houk et al. (2010) reported that early stages of recovery from cyclone Heta were observed based upon two ecological metrics, benthic substrate ratios and coral evenness. The 2010 study further summarized that recovery was dependent upon water quality and herbivore biomass, both in conjunction with wave exposure. Interestingly, the relative influence of water quality and herbivore biomass was equal for reefs along the southern shoreline, while herbivore biomass had a disproportionate influence for the reefs along Tutuila's northern shoreline. The present study agrees and expands upon these findings. Regression models highlighted a similar influence (i.e., standardized slopes of similar magnitude) from both herbivore size and several pollution proxies for the reefs along the southern shoreline, yet more of the

significant models contained terms describing proxies to pollution. Similarly, wave exposure was a required component for all models.

For reefs along Tutuila's north shoreline, exploratory correlation analyses similarly indicated that both herbivore size and proxies to pollution were associated with the recovery process and current reef condition, yet given limited sample sizes, assessments of their relative magnitude of influence (i.e., assessments of the slopes describing relationships) were not appropriate. Independent correlations were strongest for a paired, association between coral colony-size recovery and herbivore size, hypothesizing a larger contribution of grazing population in the north compared to the south.

4.2. Integration of findings with existing studies

Relatively few studies have used longer-term datasets to attribute cause, proportionally, to individual stressors, despite a pressing need to prioritize management and policy (Hughes et al. 2010). While many acute disturbances negatively impact coral reefs (Hughes et al. 2007; Baker et al. 2008; Graham et al. 2011), insight into the recovery process is an ideal means towards assessing the contribution of chronic, localized stressors. For instance, two stressors that are of primary concern for coral reefs (globally) are reductions in grazing fish populations and degraded water quality that may act independently or in combination with disturbance cycles to inhibit the growth of calcifying organisms such as corals (Fabricius 2005; Mumby et al. 2006).

In the Caribbean, (Mumby and Harborne 2010) reported significantly higher recovery of coral coverage and colony sizes inside of a fishery closure over a 2.5 year period. Similarly, the recovery of coral colony sizes (McClanahan 2008), but not recruitment (McClanahan et al. 2005), was found to be most heavily dependent upon fishing pressure in Kenya. In contrast, a meta-analysis of coral reef recovery dynamics across all major oceanic basins provided some evidence for unintuitive, reduced recovery rates within fisheries closures following disturbance events (Graham et al. 2011). These findings were a perceived artifact of higher pre-disturbance coral coverage within no-take closures, and not attributed to management status. Further, the causes behind recovery trajectories were not consistent across major geographic regions. In sum, it seems most probable that recovery is context dependent with respect to physical settings as well as management regimes, as context-dependent roles have been summarized for both manipulative and field studies (Burkepile and Hay 2006; Banse 2007; Mork et al. 2009; Sjoo et al. 2011; Wilson et al. 2012). Considering that predicting reef futures is becoming more of a priority for both local and global research, further study of the recovery process is ideal to support management.

4.2. Conclusions and future directions

The present study summarized decadal disturbance and recovery trends across Tutuila initiated by cyclone Heta in 2004. Over the past decade we report that coral cover appears to have rebounded to pre-disturbance levels, but we caution that pre-disturbance levels were based upon a snapshot of the reefs in 2003, and do not take into account changes that

have occurred over longer time periods (i.e., several decades). So, while overall recovery trends were encouraging, sites in good ecological condition (i.e., fully and partially supportive ALUS) were drivers of the trends. In contrast, sites with poor condition rankings remained more static or declined. While high proxies to land-based pollution and small mean herbivore sizes limited the recovery process, recovery along the south shore of Tutuila appeared to have more consistent ties with pollution proxies. One hypothesized driver of these findings is that the nature of freshwater input from the watershed to the nearshore reefs differs between the north and south shores, but spatial and temporal salinity profiles would be needed to further this hypothesis.

Continued efforts to better understand the influence of localized stressor upon Tutuila's nearshore reefs and to assess management regimes are long-term goals for ASEPA's monitoring effort. For instance, reports in the past indicated that pig densities per km², alone or in combination with other pollution proxies, had significant ties with the ecological metrics used here. Over the years since the ASEPA piggery program has started, pig densities have become less influential in prediction models, and the present analyses found no evidence for their independent or combined contribution (thus were not reported on). Clearly linkages are speculative, but these findings can support further study directed at understanding the current contribution of piggery waste to overall watershed pollution levels, and perhaps be useful in generating funding to perform such a study. Similarly, the Fagaalu watershed and nearby sewage treatment plant are the current (or proposed) topics for further study that can benefit from monitoring datasets. Cumulatively, the ALUS rankings generated here are being used, in part, to establish a watershed priority list that assists with maximizing the effectiveness of limited management budgets, and fulfills federal grant requirements.

The future goal of the ASEPA coral monitoring effort is to conduct surveys on a bi-annual basis, tracking changes over time and drawing linkages with human disturbances. The existing program would benefit from increasing the number of sites visited along both the north and south shore to improve the (statistical) foundation for assessing the trends presented, or focusing the existing resources on either the south or north shore.

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Figures

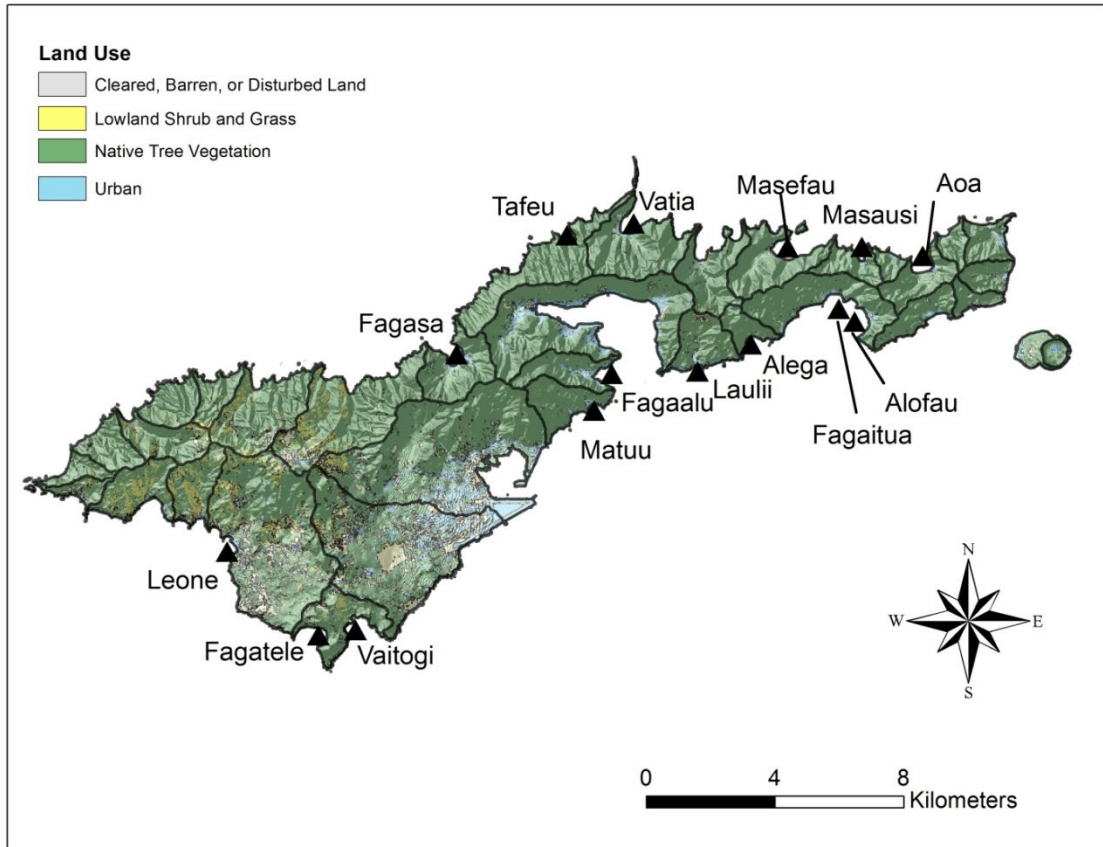


Figure 1. ASEPA coral-reef monitoring locations, watershed boundaries (black lines), and land use.

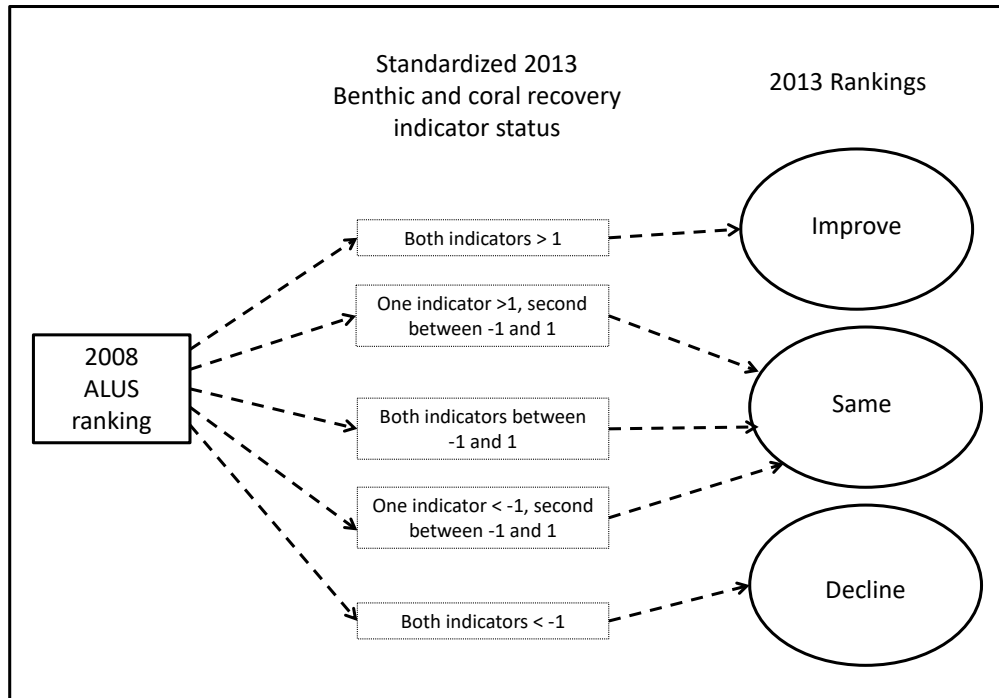


Figure 2. Decision making criteria used for determining aquatic life use support rankings. Benthic and coral recovery indicators were the rate of change in the benthic substrate ratio (a ratio of calcifying versus non-calcifying growth), and an integrated measure of coral colony size and evenness recovery, since 2007/8. Both indicators were standardized to have a mean value of 0 and a standard deviation of 1, forming the basis for the decision criteria.

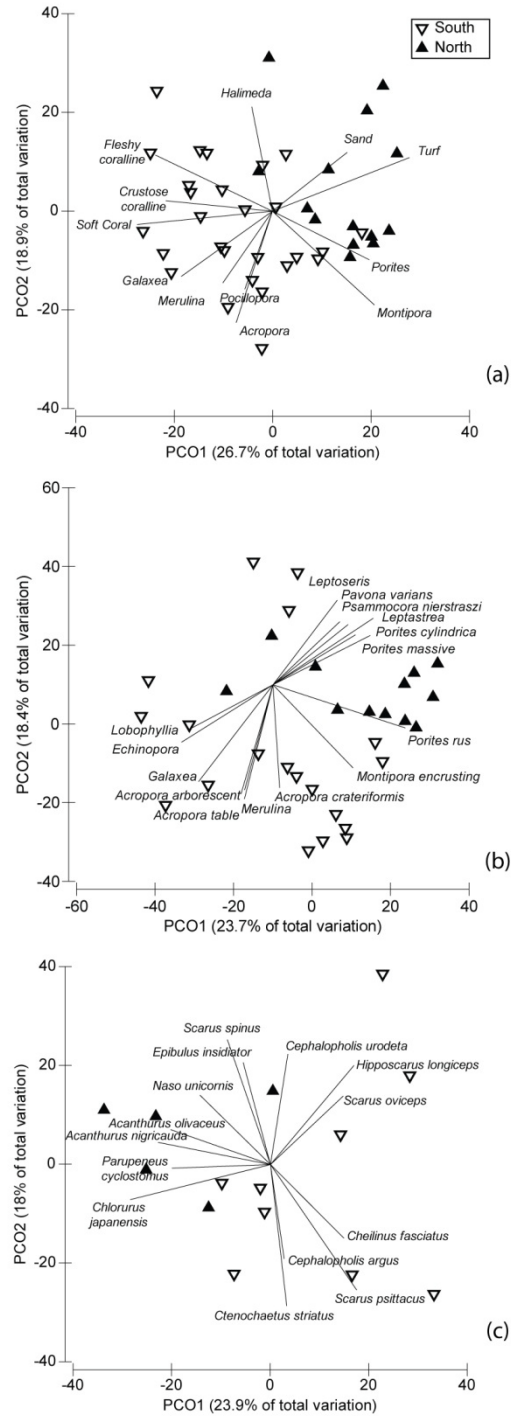


Figure 3. Principle components ordination plots of the benthic substrate, coral assemblage, and fish assemblage data collected in 2013. Plots highlight taxonomic difference between reefs along Tutuila’s northern and southern shoreline. Species and functional groups noted on the plots indicate the taxa that were strongest contributors to the observed trends, while vector lengths provide a relative assessment of their strength.

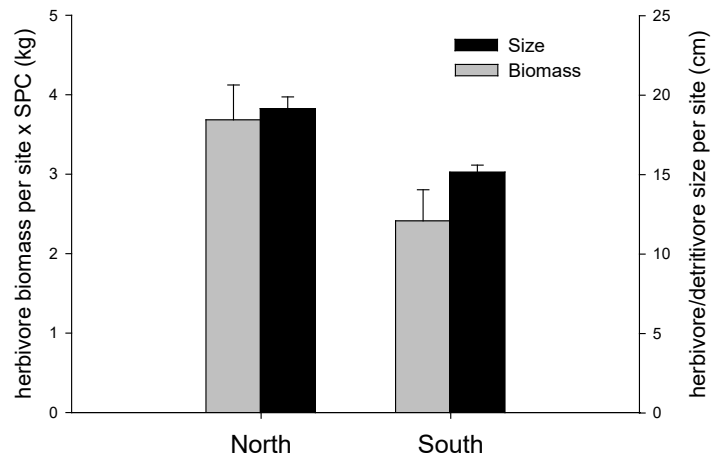


Figure 4. Mean biomass and size of herbivore/detritivore fish assemblages from the reefs on the north and south of Tutuila.

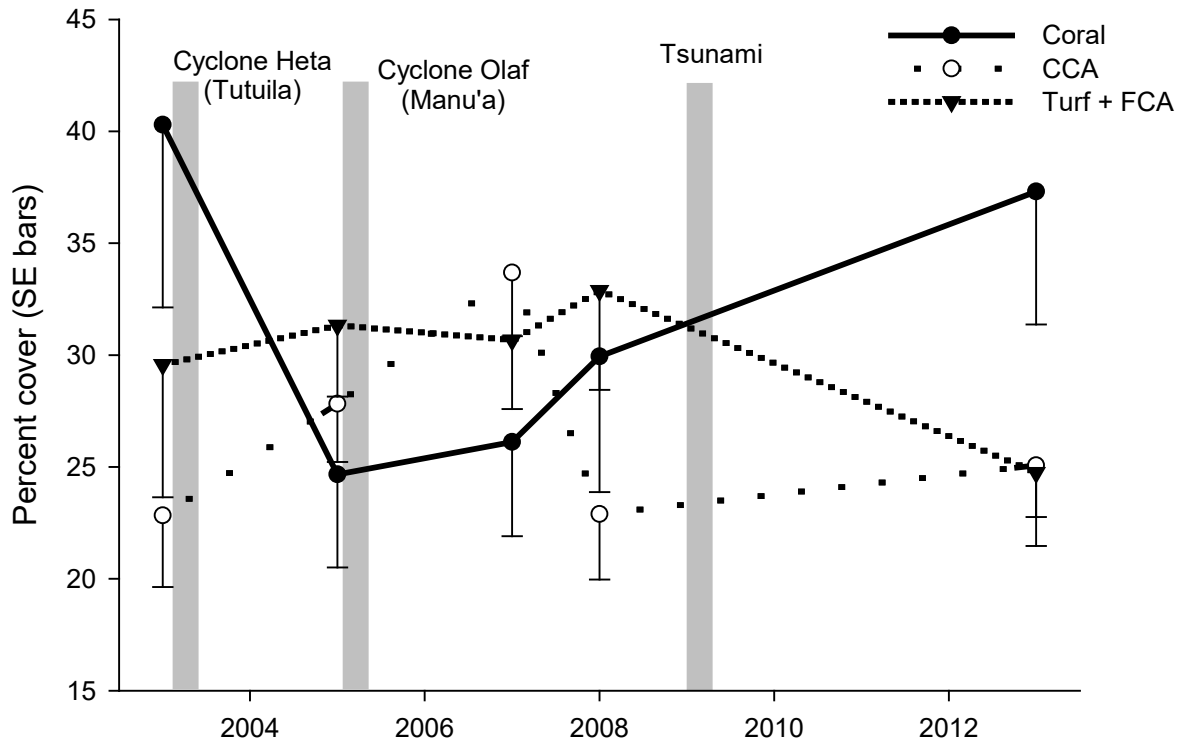


Figure 5. Trends in coral cover, crustose coralline algae (CCA), and combined turf and fleshy-corralline algae (Turf + FCA) since the inception of ASEPA monitoring efforts in 2003. Disturbances are noted by grey rectangular bars.

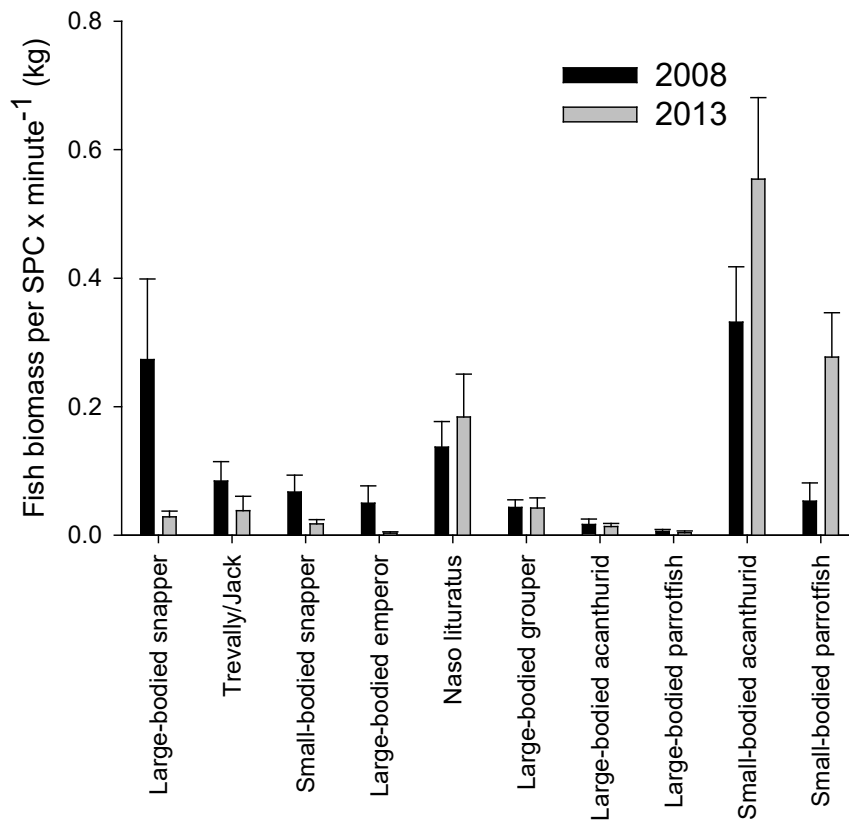


Figure 6. Temporal trends in the most abundant fish observed during ASEPA monitoring efforts. Fish were grouped based upon taxonomy and estimated size at maturity. Large-bodied species were defined by mean reproductive sizes greater than 30 cm, while small-bodied species were less than 30 cm (www.fishbase.org, *see methods*). Differing time intervals were used for stationary point count (SPC) surveys in 2008 (5-minutes per SPC) and 2013 (3-minutes per SPC), so data were reported per minute of investigation time (*see results*).

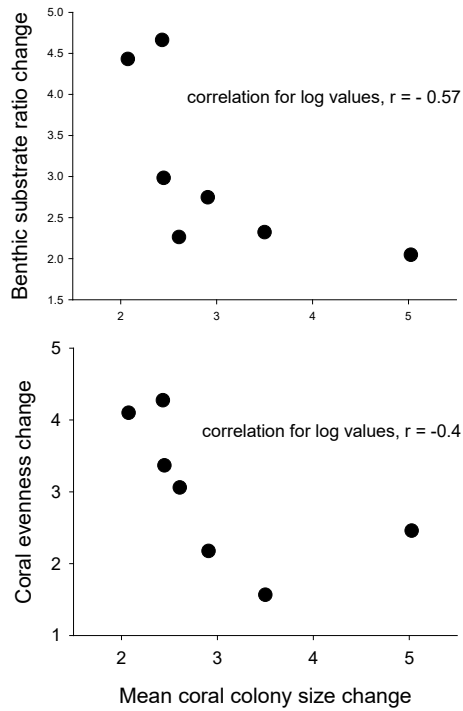


Figure 7. Correlations between three indicators of coral-reef recovery used to assess reefs along Tutuila's southern shoreline prior to conducting regression analyses. Change refers to the mean rate of change per year since 2007/8. Sites used in the correlation analyses included Alofau, Fagaitua, Alega, Fagaalu, Matuu, Fagatele, and Vaitogi. Data from Leone were not used because the site represented an outlier for regression analyses due to the disproportional size of the watershed and human population density (*see methods*).

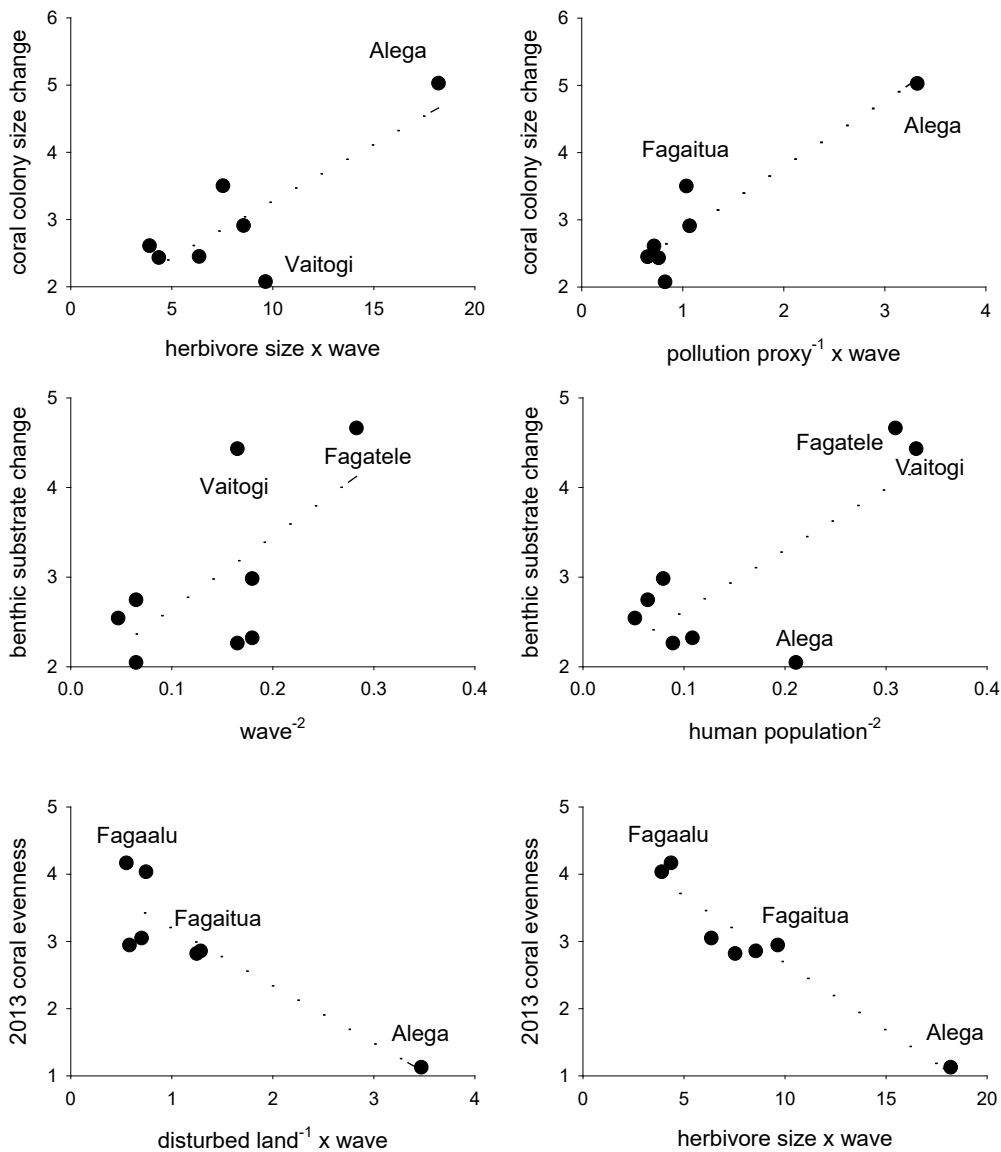


Figure 8. Regressions between ecological indicators of recovery/current status and independent predictor variables (*see Table 3 for model descriptions*). Change refers to the mean rate of change per year since 2007/8 (*Table 2*). Disturbed land and human population represent were calculated with respect to watershed size (per km²), and the pollution proxy represents their combination (*Table 1*). Wave represents wave exposure (*Table 1*). Sites used in the regression analyses included Alofa, Fagaitua, Alega, Fagaalu, Matuu, Fagatele, and Vaitogi. Sites were noted on the graphs to help understand the trends (*see results*). Data from Leone were not used because the site represented an outlier due to the disproportional size of the watershed and human population density (*see methods*). One of the regression models had a greater reliance on an influential data point at Alega compared with others (top right plate), however residuals were not significantly different from a normal distribution ($P = 0.07$, Shapiro-Wilk test).

Tables

Table 1. Environmental characteristics associated with each site calculated from GIS layers and statistics derived from census data (*see methods*).

Site	Years surveyed	Geography	Watershed size (km ²)	Disturbed land (per km ²)	Human population (per km ²)	Wave exposure index
Alega	05 ² -08-13 ¹	South	0.96	0.03	115.6	8.8
Alofau	03 ² -07 ¹ -13 ¹	South	1.08	0.12	458.3	4.2
Aoa	03 ² -07 ¹ -13 ¹	North	2.15	0.04	235.8	3.6
Fagaalu	03 ² -05 ¹ -08 ¹ -13 ¹	South	2.46	0.12	408.9	4.5
Fagaitua	03 ² -07 ¹ -13 ¹	South	1.46	0.06	330.8	4.2
Fagasa	05 ² -08 ¹ -13 ¹	North	3.47	0.06	259.4	1.5
Fagatele	05 ² -08 ¹ -13 ¹	South	0.49	0.12	20.4	2.8
Laulii	05 ² -08 ¹ -13 ¹	South	1.76	0.13	673.9	10.8
Leone	03 ² -07 ¹ -13 ¹	South	4.75	0.19	463.2	6
Masausi	05 ² -13 ¹	North	0.8	0.05	240.0	2.4
Masefau	03 ² -07 ¹ -13 ¹	North	3.21	0.03	135.5	1.2
Matuu	07 ² -13 ¹	South	1.2	0.11	559.2	8.8
Tafeu	05 ² -08 ¹ -13 ¹	North	0.92	0.00	10.9	2.8
Vatia	07 ² -13 ¹	North	3.61	0.04	179.5	1.1
Vaitogi	07 ² -13 ¹	South	1.61	0.16	6.2	4.5

Table 2. Ecological statistics for each site (*see methods for descriptions*). Data represent absolute values that were subsequently standardized prior to regression analyses (*see methods*). ASEPA watershed identifier numbers follow the site names.

Site	Coral cover (%)	Coral evenness	Benthic substrate ratio	Colony-size change	Benthic ratio change	Coral evenness change
Alega (8)	14.7	6.74	1.41	0.58	0.00	-0.16
Alofau (10)	24.1	11.17	1.60	0.19	0.14	0.18
Aoa (11)	63.0	7.97	4.53	0.26	0.46	-0.19
Fagaalu (6)	7.8	13.44	0.93	0.21	0.03	0.06
Fagaitua (9)	36.5	10.63	2.14	0.35	0.04	-0.50
Fagasa (16)	30.0	10.68	0.78	0.77	0.02	0.25
Fagatele (4)	57.3	13.75	5.11	0.19	0.39	0.52
Laulii (7)	26.1	--	1.92	--	0.07	--
Leone (2)	69.7	8.17	8.58	0.28	0.81	0.00
Masausi (12)	37.4	11.66	2.61	0.44	0.10	0.24
Masefau (13)	2.0	19.56	0.49	-0.75	-0.12	1.20
Matuu (5)	32.6	10.72	2.01	0.26	0.10	-0.27
Tafeu (15)	71.4	10.19	7.76	1.22	1.08	-0.05
Vatia (14)	4.4	13.13	0.17	-1.26	-0.14	-0.16
Vaitogi (3)	49.5	10.93	5.68	0.13	0.36	0.46

Table 3. Summary of regression modeling that examined the predictors of recovery dynamics and present status of coral reefs along the south shore of Tutuila. Recovery in coral colony-size and benthic substrate refers to the rate of increase per year since surveys were last conducted (2007-2008). Independent variables were wave exposure, mean herbivore/detritivore size, human population density per km², disturbed land per km² (classified as non-forest vegetation), and a pollution proxy that combined standardized values of watershed pollution indicators (*see methods*). For each dependent variable, models are listed from top to bottom in accordance with their Akaike Information Criterion (AIC) values, or goodness of fit. Figure 8 depicts six of the models noted below, and provides a better understanding of individual sites that were influential to each model.

Coral colony-size recovery							
<i>Dependent variable</i>	<i>Independent variables</i>	<i>Slope</i>	<i>SE</i>	<i>Intercept</i>	<i>R²</i>	<i>P-Value</i>	<i>AIC</i>
Coral colony-size recovery	herb_size x wave	0.16	0.05	1.59	0.59	0.03	17.3
Coral colony-size recovery	poll_proxy ⁻¹ x wave	0.21	0.03	1.15	0.85	<0.001	9.9
Benthic substrate recovery							
Benthic substrate recovery	wave ⁻²	8.07	3.90	1.84	0.32	0.08	23.3
Benthic substrate recovery	hum_pop ⁻²	6.83	2.32	1.94	0.52	0.03	20.5
2013 benthic substrate ratio							
2013 benthic substrate	hum_pop ⁻² x wave ⁻²	29.6	6.81	2.22	0.72	0.004	16.2
2013 coral evenness							
2013 coral evenness	dist_land ⁻¹ x wave	-0.85	0.21	4.05	0.74	0.008	14.1
2013 coral evenness	herb_size x wave	-0.19	0.03	4.67	0.89	<0.001	7.1

Table 4. Summary of correlations examined the associations between recovery dynamics and present status of five coral reefs along the north shore of Tutuila. Recovery in coral colony-size and benthic substrate refers to the rate of increase per year since surveys were last conducted (2007-2008). Independent variables were wave exposure, mean herbivore/detritivore size, human population density per km², disturbed land per km² (classified as non-forest vegetation), and a pollution proxy that combined standardized values of watershed pollution indicators (*see methods*).

	<i>Benthic substrate ratio</i>	<i>Coral evenness</i>	<i>Benthic substrate recovery</i>	<i>Coral colony-size recovery</i>
Disturbed land	-0.82	--	-0.83	--
Human population density	-0.64	--	-0.69	--
Pollution proxy	-0.74	--	-0.77	--
Wave exposure	0.76	-0.77	0.67	--
Herbivore size (cm)	--	--	--	0.8

Table 5. ALUS Rankings for each site. 2008 rankings were taken from Houk and Musburger (2008), while 2013 rankings were calculated based upon the decision criteria noted in Figure 2 and results (*see results section*). ASEPA watershed numbers follow names in parentheses. Primary ranking attributes refer to the relative influence of each independent variable (exp-wave exposure, herb-mean herbivore/detrivore size, and lbsp-pollution proxies) in contributing to coral and benthic assemblage trends.

Site	Coral Assemblage Trend	Benthic Assemblage Trend	2008 ALUS Ranking	2013 ALUS Ranking	Primary ranking attribute
Alega (22)	non-significant improve	stasis	partially supportive	fully supportive	exp,herb, lbsp
Alofau (21)	Stasis	stasis	not supportive	not supportive	herb, lbsp, exp
Aoa (15)	non-significant improve	non-significant improve	not supportive	not supportive	lbsp, herb, exp
Fagaalu (25)	Stasis	non-significant decline	not supportive	not supportive	herb, lbsp, exp
Fagaitua (21)	Improve	non-significant decline	partially supportive	partially supportive	herb, lbsp, exp
Fagasa (8)	non-significant improve	non-significant decline	not supportive	not supportive	lbsp, exp, herb
Fagatele (29)	non-significant improve	non-significant improve	fully supportive	fully supportive	herb, exp, lbsp
Laulii (23)	--	non-significant decline	not supportive	not supportive	all equal influence
Leone (30)	non-significant improve	improve	partially supportive	partially supportive	lbsp, herb, exp
Masausi (13)	non-significant improve	stasis	partially supportive	fully supportive	exp,herb, lbsp
Masefau (12)	decline	decline	fully supportive	not supportive	herb, lbsp, exposure
Matuu (26)	non-significant improve	stasis	not supportive	partially supportive	exp, herb, lbsp
Tafeu (9)	improve	improve	fully supportive	fully supportive	exp, herb, lbsp
Vatia (14)	decline	non-significant improve	--	not supportive	lbsp, herb, exp
Vaitogi (29)	stasis	stasis	partially supportive	partially supportive	all equal influence