Report for CRAG on the 2018 Survey of the Coral Communities of the American Samoan Archipelago and the 2024 Survey of the Corals, Fishes, and Benthos in Fagatele Bay

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Fagatele Bay National Marine Sanctuary (Photo by Wendy Cover)

Abstract – The coral communities in Fagatele Bay National Marine Sanctuary (FBNMS) were found in 2018 and 2024 to be in the best condition and most fully developed since 1979. Although the coral communities were seriously damaged by an outbreak of *Acanthaster planci* in 1978-1979 and Cyclone Val in 1991, the populations of corals in the genus *Acropora* have significantly increased in abundance and size-distribution in FBNMS since 1979 while *Acropora* surveyed around the rest of Tutuila have significantly decreased in abundance. Despite ups and downs in population densities of coral colonies from disturbances, the overall regression of coral population densities on years from 1985 to 2024 show the coral communities at FBNMS have been sustaining themselves well. The slope of the regression of coral population density per year is not significantly different from zero (anova on slope, p> 0.79, df 1,158). *Porites rus* and *Montipora grisea* have also become significantly more abundant in FBNMS as well as on the rest of the outer coasts of Tutuila. Since the overall population densities of coral colonies has not significantly decreased, while *Acropora* spp., and *Montipora grisea* have substantially increased, some other species must have decreased. The endemic *Porites randalli* was once the most abundant species of coral in FBNMS, but now appears to be gone from FBNMS, the decline starting around 2002. *Pocillopora* and *Porites* species have been decreasing significantly on the outer coasts of Tutuila since 1982, but there has been no overall change in *Pocillopora* spp. population densities in Fagatele Bay since 1985 ($p > 0.492$). *Montipora verrilli* was one of the more predominant species of *Montipora* through 1998, but it crashed to very few in 2002 and has not been recorded on our transects for the last 22 years. In contrast, *Montipora grisea* was not recorded at all on our transects before 1995. When it abruptly appeared in 1995, it was immediately the most abundant coral with 3379 *M. grisea* recorded, or 23% of the total number of colonies of about 160 other species and has been the most abundant species around Tutuila since that initial arrival. Strangely, *Pavona varians* s.l. and *P. chiriquiensis* (part of *P. varians* s.l.) together are generally second or third most abundant species around Tutuila, but are almost nonexistent in FBNMS. The most remarkable finding is that although the waters in FBNMS have a significantly lower carbonate ion availability (measured by aragonite saturation state) than the waters of Rose Atoll, and therefore the corals at Rose Atoll should be growing faster, the living coral cover and size distributions of coral communities are substantially greater in FBNMS. A hypothetical explanation is that the corals at Rose Atoll are growing as fast or faster than in FBNMS because of the availability of carbonate ions, but the crustose coralline algae *Porolithon* spp., in combination with consistent wave energy, may respond to high levels of carbonate ion availability more than the corals do and are thereby overgrowing the coral colonies before the corals can grow to large sizes. *Porolithon* spp. probably plays major roles in the good performance of coral reefs in American Samoa by serving as a good substratum for successful recruitment of coral larvae and binding loose or weak substrata for survival of the coral colony as it grows. Coral colonies of most species have been found to be increasing in the larger size classes and increasing in population density since Cyclone Val in 1991.

Introduction

The Fagatele Bay National Marine Sanctuary of American Samoa was established in 1986 by the NOAA National Marine Sanctuary System in cooperation with the Government of American Samoa's Division of Marine and Wildlife Resources. Although at 0.25 square miles (0.65 km^2), FBNMS is the smallest of all NOAA National Marine Sanctuaries, it nevertheless preserves a treasure of at least 158 species of reef-building corals (Green et al. 1999; D. Fenner unpublished data) which is well over twice the number found in the entire Atlantic Ocean. There are at least 297 species of reef fishes in FBNMS (Green et al. 1999).

A year in advance (1985) of the establishment of FBNMS (1986), a baseline survey was done of the corals, fishes, macroinvertebrates, and algae. Six permanent location transects perpendicular to shore, running from 3 m to 18 m (where possible), were set up at approximately even intervals to provide information representing the entire bay (Fig. 1). Perpendicular to the permanent location transects, survey transects along which the data were collected were set up at depths of 3 m, 6 m, 9 m, and 12 m where possible (Fig. 1). The baseline survey in 1985 found the coral communities to be recovering from the especially massive *Acanthaster planci* outbreak of 1978-

1979. Surveys were also done in 1988, 1995, 1996, 1998, 2001, 2002, 2007, and 2018. This report is on the tenth survey in February 2024.

Although the past four decades have been demanding on the coral communities, the corals of Fagatele Bay have been remarkably resilient. In the past four decades there have been two outbreaks of corallivorous crown-of-thorns seastars, four mass bleaching events, ten cyclones, six extreme low tides, and a tsunami. Furthermore, the island of Tutuila has been sinking five times the normal rate since 2010 (Han et al. 2019). Yet the coral communities in FBNMS have consistently performed better than those in numerous other sites around Tutuila with greater mean living coral cover, greater mean colony sizes, greater species richness in corals, and greater mean colony abundance (Green et al. 1999). (This report tells that FBNMS no longer has greater mean colony abundances, but the living coral cover is still greater because of the substantially greater proportion of colonies in the exponentially greater colony sizes.) The fishes in FBNMS have shown greater abundance and species richness per transect in FBNMS than at other locations on Tutuila (Green et al. 1999).

From the nine previous surveys, it had been concluded that the coral communities in the 2018 survey of Fagatele Bay were in the best condition and development since the coral communities were first observed in 1979. When coming to do the surveys in 2024, we were looking forward to see if the coral communities in FBNMS were still in such outstanding condition.

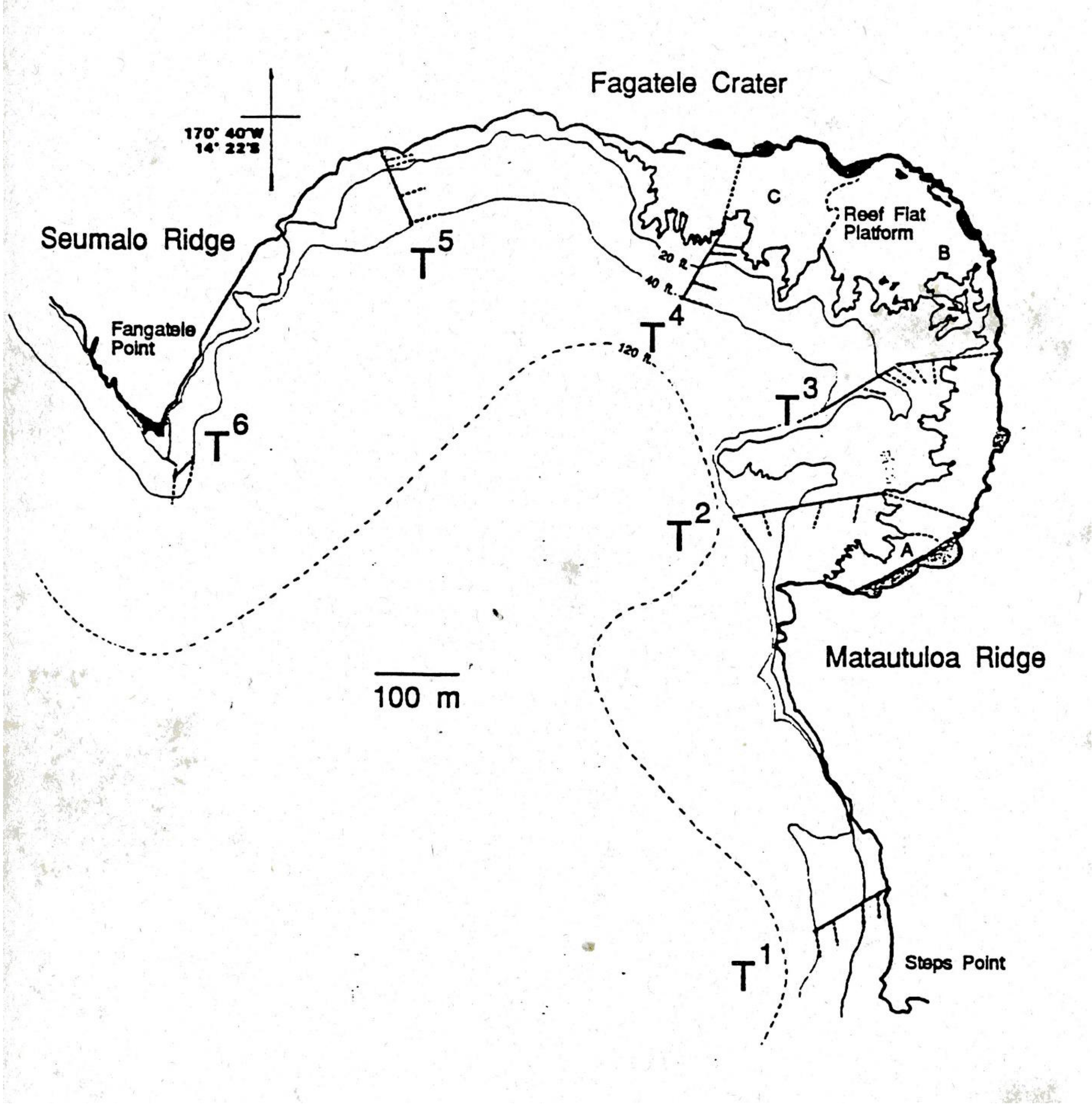


Fig. 1. Positions of the permanent location transects (T1 – T6, solid lines) in FBNMS and the 30-m survey transects (dotted lines).

Methods

Survey transects 30 X 1 m were laid perpendicular to the permanent location transects at 3 m depth intervals (3, 6, 9, 12 m) where feasible (Fig. 1). Diameters of all coral colonies whose center occurred within the 30 x 1 m were recorded. Fenner usually recorded diameters and identifications of corals within 50 cm to the right of the transect and Birkeland usually recorded diameters and species to the left 50 cm for the total of 1 m. For each transect, the diameters and species were then sorted into seven size classes based on the maximum diameter of the colony; < 5 cm, 5-10 cm, 10-20 cm, 20-40 cm, 40-80 cm, 80-160 cm, and >160cm.

Since 1917, the surveys in American Samoa have usually focused on population densities and size distributions of coral colonies rather than surface cover in order to better assess what is happening. For example, we will show that at least 100 species have been doing well because of their abundant recruitment, but we have found only large colonies of three species of *Goniopora*, with no sign of recruitment of *Goniopora* spp. in our surveys for four decades. This report will emphasize the dynamics of the coral communities with population densities and size distributions.

From 1917 through 1973, surveys were done counting coral colonies in quadrats along the transects. From 1982 to 1988, we used the point-quarter method, which was precise and super-informative, but very slow. In 1995, Craig Mundy brought from Australia the method of rapidly sorting coral diameters into seven size classes that has been used since. (Birkeland and Fenner find it faster to measure diameters and sort them into size classes in the evening after dives. This is because Birkeland, at least, finds it too hard and too prone to error to try to remember which class is which when rapidly measuring. Nevertheless, it is still much faster than the point-quarter method.)

The reason binning into size classes is better than precise measures is because the extreme range of sizes of coral colonies demands as many data as possible. We record colonies from 2 cm to 22.4 m (Coward et al. 2020), a 1120-fold range of diameters with everything in between. With each colony bringing such extreme variance, we need many data, maintaining accuracy, but compromising precision. When diameters are translated into surface areas, the 2-cm disk is 3.14 cm^2 while the massive hemisphere is 7,881,627.65 cm^2, a 2,510,072.5-fold difference in living area. Surveys of most animals do not need to handle such a range of sizes.

Sorting into seven size categories is a good procedure because it allows us to collect coral survey data more rapidly. We found that the coral colonies in Fagatele Bay grew into larger size categories more frequently than at Rose Atoll or on the outer coast of Tutuila. This is much more substantial than is indicated by the size-class categories. The size-class categories double at each step, but that greatly underrepresents what this means in size (surface area), because surface area involves the radius squared. Each stage increases by the square of a doubled number. The surface area increases with the size category from (in cm^2): 4.9 44.2 177 707 2,827 11,310 (180,956).

Our calculations involve a gross assumption that all colonies are circular, but this is a reasonable method to illustrate the pattern, because the random variations resulting from shape probably have smaller effects than the large scale of fixed variation resulting from the squared increase of doubled radius. It also involves a gross assumption that the median diameter is a reasonable representative of the category size. The colony surface area in Category 7 is in parenthesis because it was calculated like the earlier categories, but it actually has no upper boundaries. Therefore, I plan to empirically calculate the areas of actual colonies in category 7 individually from the raw data.

Because the difference in coral colony population densities between Fagatele and Rose are insignificant, I assumed they are the same. In calculations to illustrate the influence of a few corals in the larger size classes towards total living coral cover, I multiplied the percent of the corals in each size class times the representative area of each size class.

In this report, we are combining *Pavona varians* s.l. with *P. chiriquiensis* data because *P. chiriquiensis* was only recently described (Appendix 1, Taxonomic Notes) and data were not distinquished between them in earlier years. They appear to have very similar ecological roles and preferred environmental conditions. We will combine them under the name *Pavona varians* s.l. The "s.l." stands for "sensu lato" which means *Pavona varians* "in the broad sense".

Results

Population densities of coral colonies

It is surprising that overall, despite the severe cyclones, bleaching, crown-of-thorns outbreaks, and other events that have caused major damages to many coral communities on time-scales of years approaching decades, the abundances or population densities of all coral colonies has not changed significantly overall (Fig. 2A) during the years between 1982 and 2024 (42 years) for all the sites around Tutuila and Aunu'u (19 sites after excluding Pago Pago Harbor and FBNMS). The same can be said for the coral communities along the six sets of permanent transects in Fagatele Bay (Fig. 2B). Although the total abundance or population density of all species of coral colonies for all sites has not changed, the changes in size distributions and the reassortment of relative abundances of coral genera and species have produced important changes in community structure of corals over these 42 years.

It was also a surprise to find the average population densities of coral colonies on the open coast of Tutuila (12.8 ± 8.28 colonies m^{-2}) to be significantly greater ($p < 0.05$, t-test df 351) than the population densities of coral colonies in FBNMS (11.0 colonies ± 7.42 m^{-2}). The coral colony population densities on Rose Atoll (12.5 ± 8.35 colonies m^{-2}) were also larger than in FBNMS (11.0 colonies m^{-2}), but not significantly ($p = 0.13$, t-test df 199). The mean densities and standard deviations of outer coast Tutuila and Rose Atoll are so similar, that it is unbelievable that one was significantly different from Fagatele Bay and the other was not. We carefully repeated the analysis, but the same results continue to be found. Calculations of living coral cover based on proportions of colonies among size distributions (explained in Methods section) at Fagatele Bay, Rose Atoll, and the open coast Tutuila indicate that living coral cover is greater in FBNMS because of the size distributions of coral colonies, even though the population densities are greater at Tutuila and Rose.

Caveat --- It may also be the case that we record lower population densities of coral colonies in Fagatele Bay because it is impractical to try to count individual colonies in larger stands of branching corals such as *Acropora intermedia* (Fig.16) so we recorded large continuous stands as a s a single colony, whereas smaller digitate colonies typical of outer Tutuila and Rose Atoll are easily recorded separately. Nevertheless, there is substantially more living coral cover in Fagatele, which needs to be explained.

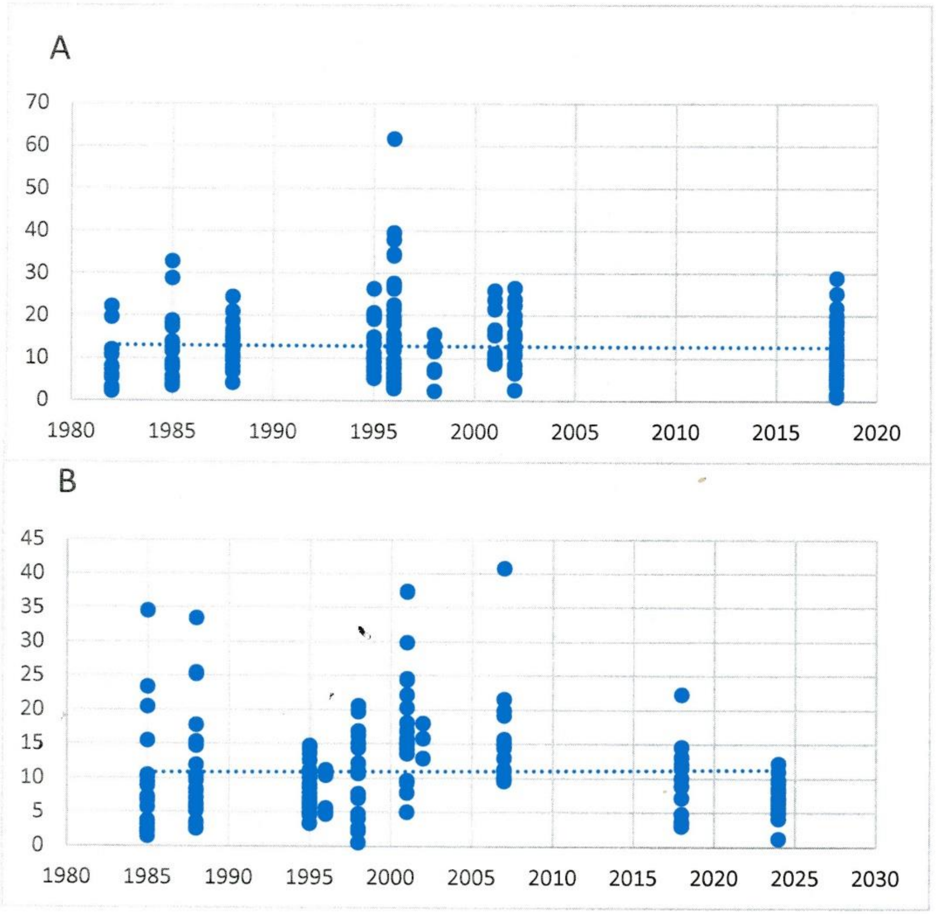


Fig. 2. The population densities of coral colonies in American Samoa through four decades, combining all coral species. A --- Open coast of Tutuila and Aunu'u, excluding Pago Pago Harbor and Fagatele Bay. The probability that the slope of the regression of population density of all species of coral colonies over the years 1982 – 2018 (anova on the slopes) does not differ from zero is p > 0.80 (df 1, 191). B --- Fagatele Bay National Marine Sanctuary. The probability that the slope of the regression of population density of all species of coral colonies over the years 1985 – 2024 does not differ from zero is p > 0.79 (df 1,158). Each of the dots represents data from a transect, not just a coral colony.

Prevalence of coral recruits

One aspect of coral population dynamics that may be a key factor in the success of American Samoan corals during the Anthropocene is the prevalence and continuity of coral recruitment. About a hundred of the species found in our transects on the forereefs of the American Samoan Archipelago have recruits (defined as corals < 5 cm diameter) representing a substantial portion of their size distributions (Appendix 2). Combining the diameters of all species on all transects at all sites for all years, the recruits made up 23.60% of the combined size distributions (Fig. 3).

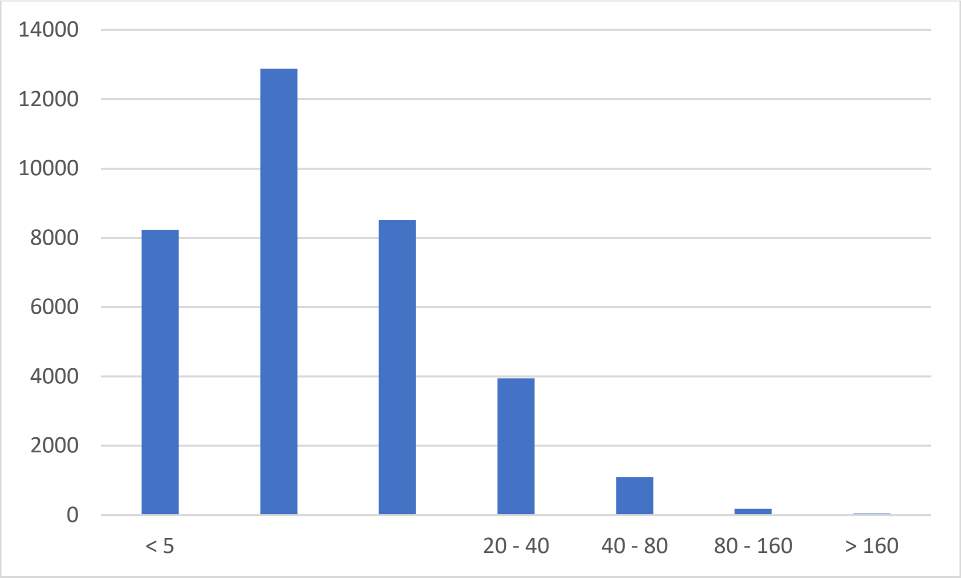


Fig. 3. The size distribution of all species at all sites (except Swains not surveyed), on all years, n = 34,883 diameters (Appendix 2) in American Samoa

Reassortment of coral species and genera over four decades

Acropora is probably the genus of reef-building coral most influential to the topographic complexity of the reef which provides shelter for reef fishes. From 1985 to 2024, the population density of *Acropora* spp. increased significantly in FBNMS (Fig. 4A), while the population densities of *Acropora* at other sites on the open coast of Tutuila and Aunu'u (not including Pago Pago Harbor and FBNMS) from 1982 to 1985 decreased significantly (Fig. 4B). Although neither FBNMS and the outer coast of Tutuila and Aunu'u have changed overall in coral population density during the past four decades, the increased prevalence of large, branching *Acropora* (especially *A. intermedia*) has made FBNMS appear to have changed for the better in coral community structure while a large part of the rest of the open coast of Tutuila and Aunu'u may seem to have declined.

More important than increasing population density, *Acropora* grew into the larger size-class colonies which increased their living-coral cover exponentially (see Methods and Discussion) in contrast to *Acropora* on the outer coast of Tutuila, Rose, and Ta'u (Fig. 5). This raises the question about why *Acropora* does much better at FBNMS than on Rose Atoll, Ta'u, and the rest of Tutuila.

We had a strong impression that the corals in Fagatele Bay, especially *Acropora*, were in the greatest state ever in 2024, but the data actually show that the increase in population density and size distribution of *Acropora* may have reached an asymptote just before 2018. If we compare

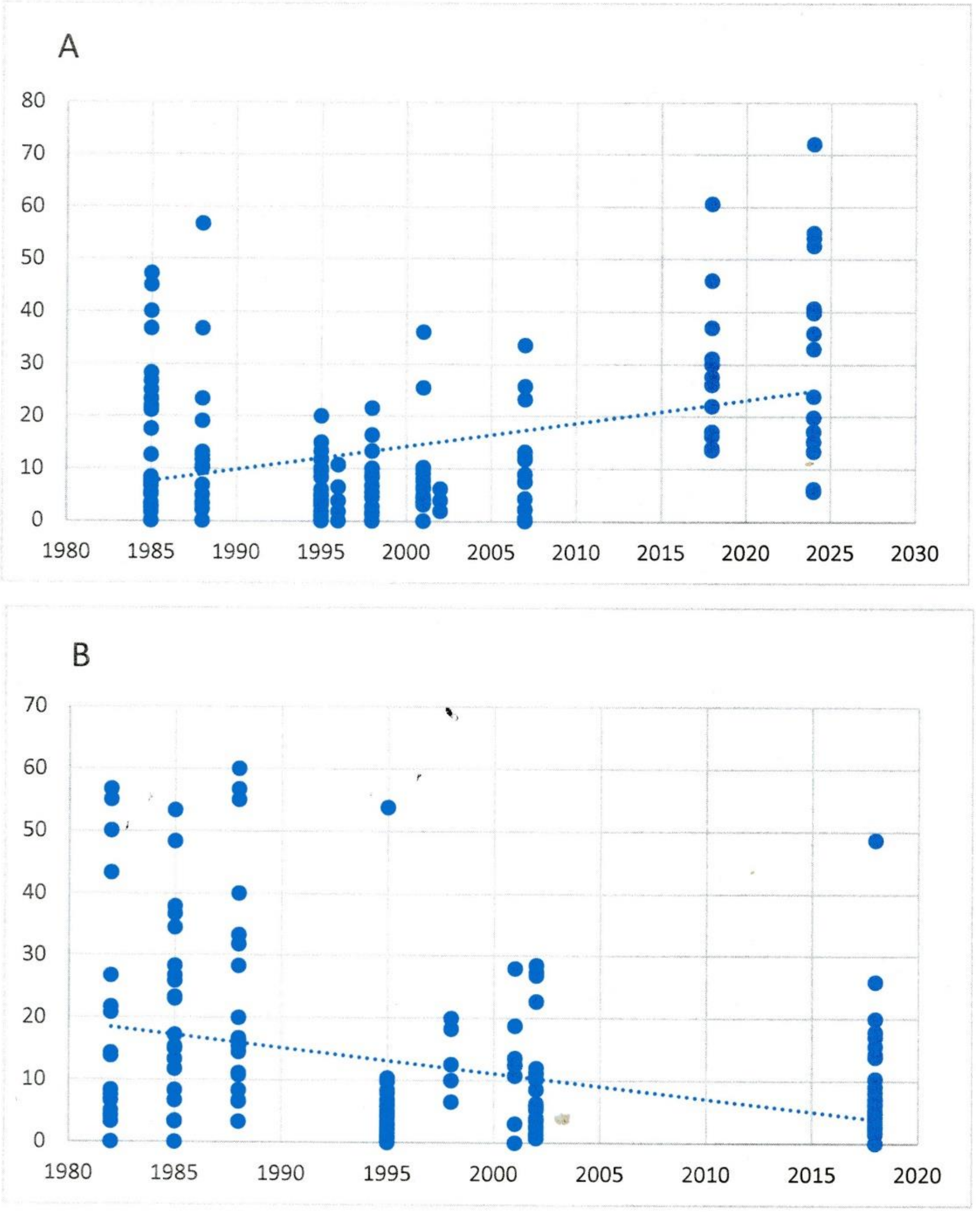


Fig. 4. The population densities of *Acropora* spp. in American Samoa through four decades. A --- Fagatele Bay National Marine Sanctuary. The probability that the slope of the regression of population density of *Acropora* spp. over the years 1985 – 2024 is zero and not positive (anova on the slope) is $p < 0.001$ (df 1,154). B --- Open coast of Tutuila and Aunu'u, excluding Pago Pago Harbor and Fagatele Bay. The probability that the slope of the regression of population density of *Acropora* spp. over the years 1982 – 2018 is zero and not negative is $p < 0.001$ (df 1, 194). Each dot is a total from a transect, not an individual colony.

the size distributions of *Acropora* in in 2018 and 2024 (Appendix 3), we find they are remarkably similar. Likewise, although the regression of population density of *Acropora* colonies significantly increases as the years continue, the final two years look as though they could be

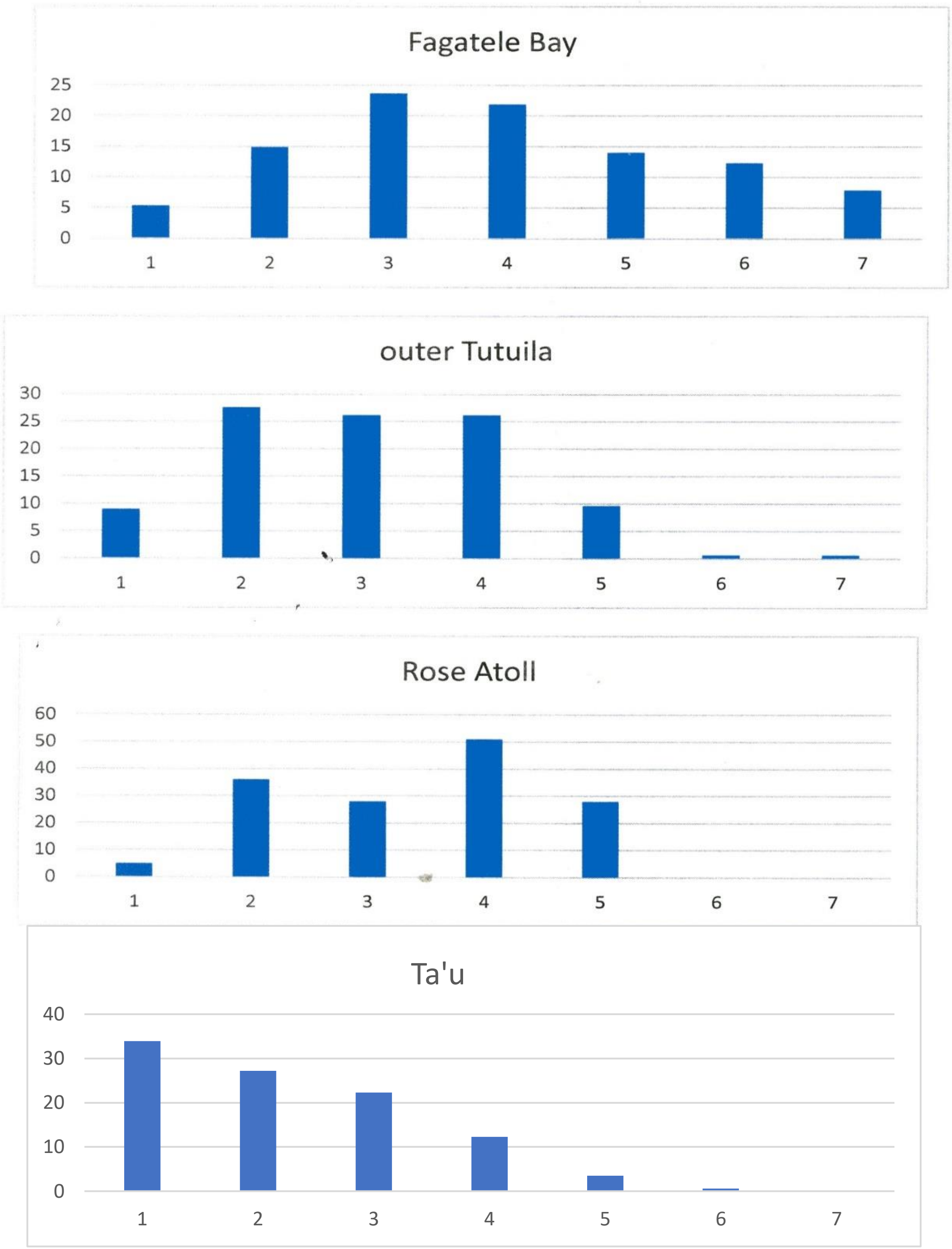


Fig. 5. Size distributions of *Acropora* in Fagatele Bay, the rest of outer coast of Tutuila and Aunu'u, Rose Atoll, and Ta'u. This raises the question as to why *Acropora* is doing better at skeletal growth in Fagatele Bay. *Acropora* grows into larger size classes than in most other places in American Samoa. At Ta'u and at Rose Atoll, *Acropora* recruits well and apparently does well while still small colonies, but generally fails to grow to larger colony sizes. There may

be some larger *Acropora* on Ta'u, but they did not show up in our surveys at Afuli, Faga, Fagamalo Cove, and Lepula.

A widespread major change in the coral communities of American Samoa since the early 1980s is the significant increase in *Porites rus*, both in Fagatele Bay and on the outer coasts of Tutuila (Fig. 6). This year (2024), *P. rus* made 324/2380, or 13.6 % of the corals in Fagatele Bay. As with *Acropora, P. rus* increased in upper size classes in Fagatele Bay, but *P. rus* also increased in upper size classes on the outer coast of Tutuila (Fig. 7). Combining increases in abundances with increases in size distributions, *Porites rus* is making the most substantial increases over the years in many places.

Porites rus and *Pavona varians* s.l. are among the most abundant species around Tutuila and they have been increasing further in recent years (Appendix 4 – Ranking of species by abundance in 1995, 2002, and 2018). In 2018, after *Montipora grisea* (nearly always the most abundant coral since it first appeared in 1995), the second most common was *Pavona varians* s.l. and third was *Porites rus* (Appendix 4).

However, Fagatele Bay is an exception for *Pavona varians* s.l. *Pavona varians* s.l. did the opposite of *Acropora* species. *Pavona varians* s.l. has been significantly increasing in relative abundance on the outer coast of Tutuila since 1982 (Fig. 8B), but *P. varians* s.l. has been perpetually so rare in Fagatele that Excel would not do a regression (Fig. 8A). This year in Fagatele, *P. varians* (11) and *P. chiriquiensis* (17) together made 28/2380, or 1.2 % of the coral in Fagatele Bay. Since most species do better in Fagatele than elsewhere, why does *P. varians* s.l. do so well everywhere except Fagatele? Why was it the second most common among hundreds of species around Tutuila in 2018, but nearly absent from Fagatele?

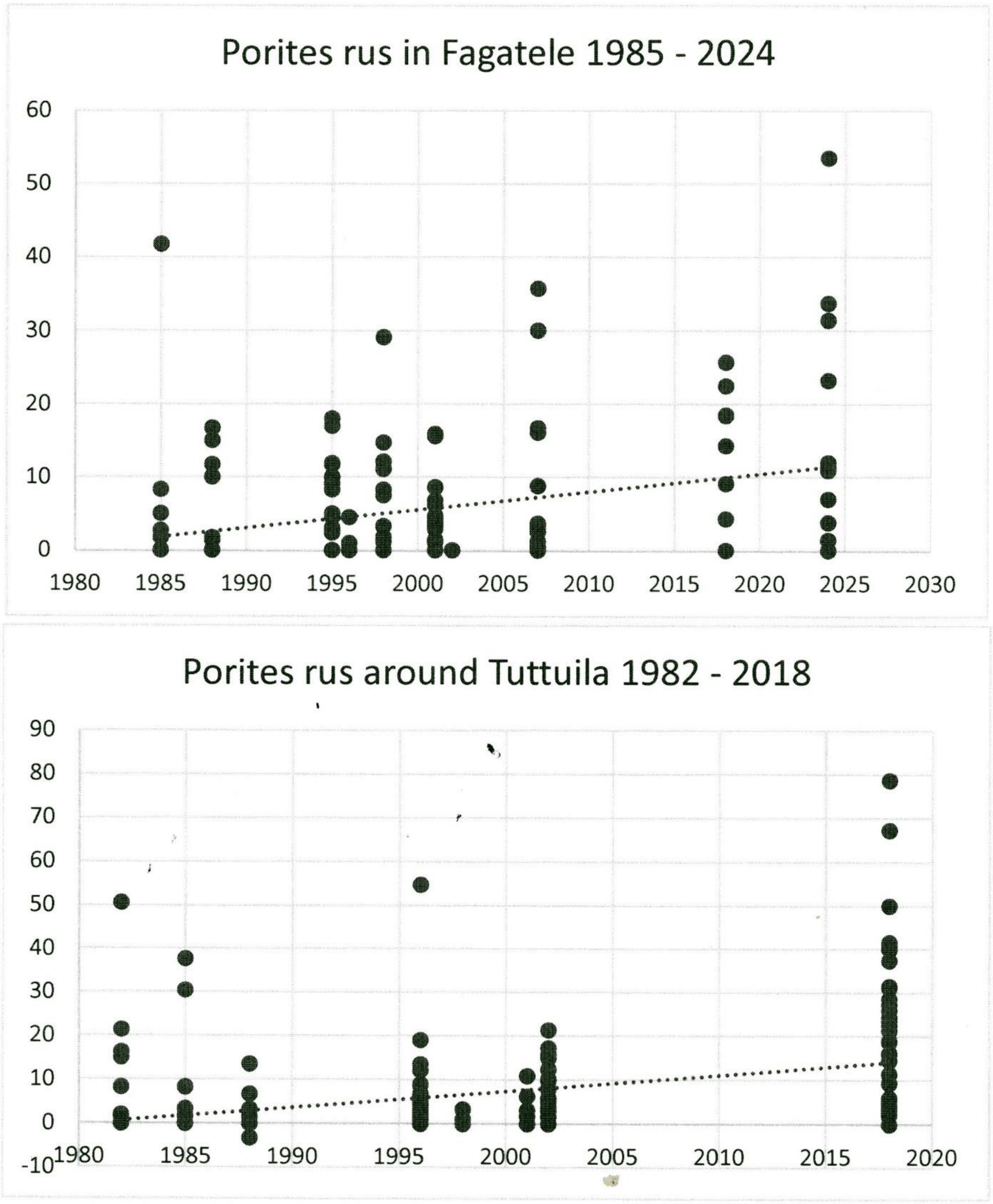


Fig. 6. *Porites rus* has significantly increased in population densities since the 1980s, both in Fagatele Bay (Fig. 6A, $p < 0.001$ df 1,154) and other sites on the open coast of Tutuila and Aunu'u (Fig. 6B, $p < 0.001$ df 1,188). Each of the dots represents data from a transect, not just a coral colony.

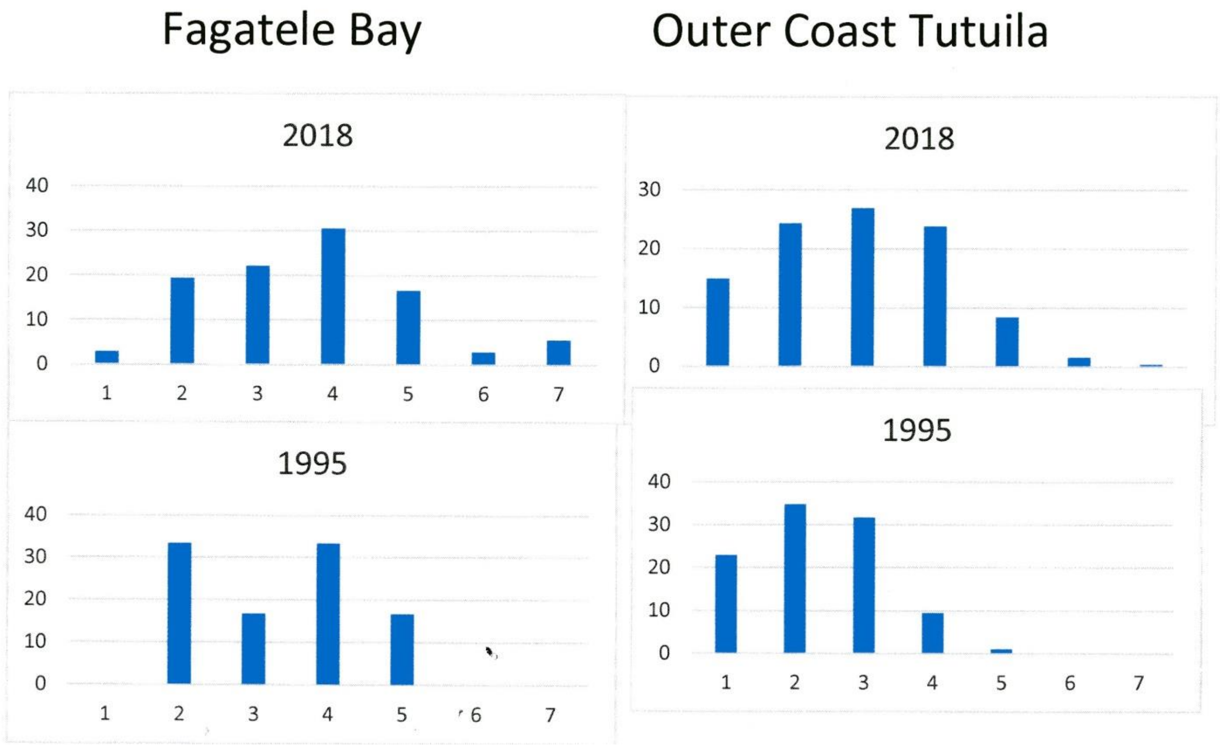


Fig. 7. *Porites rus* has grown into the upper classes of size distribution after Cyclone Val in 1991. *Porites rus* is doing as well on the outer coast of Tutuila and Aunu'u as in Fagatele Bay.

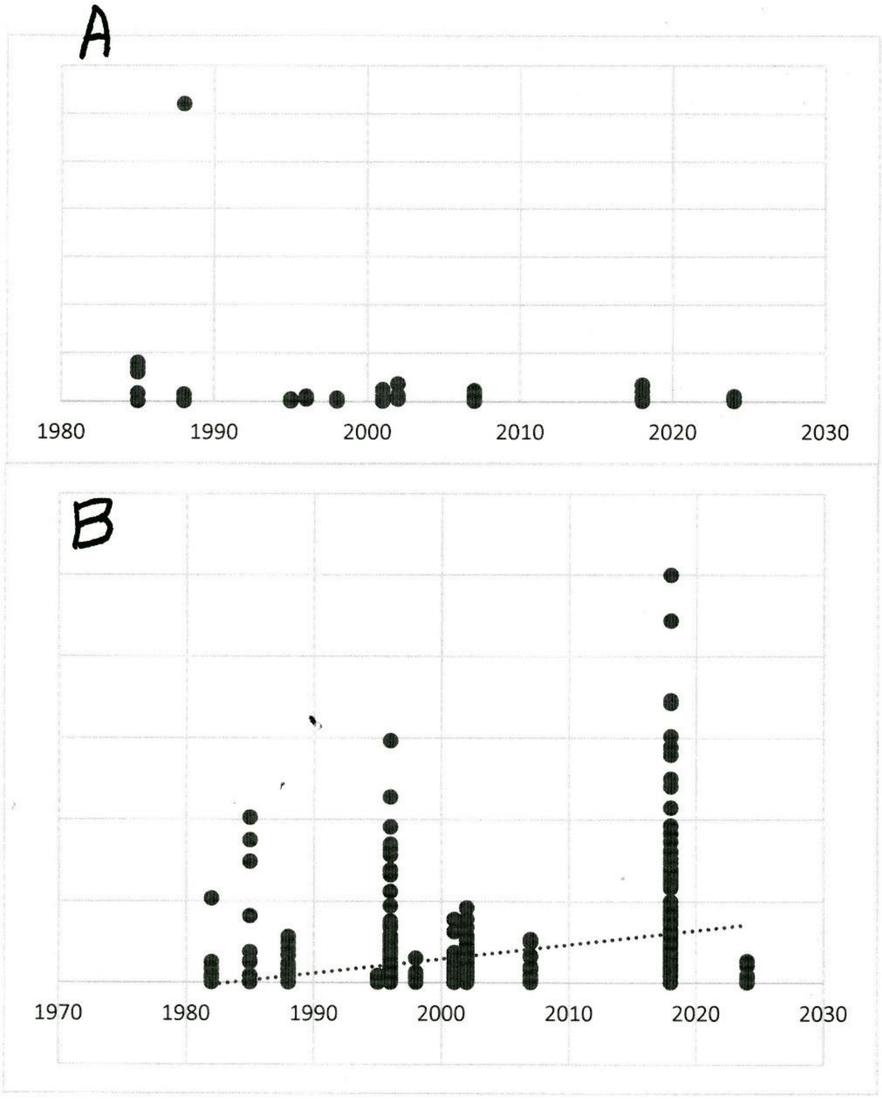


Fig. 8. *Pavona varians* s.l. significantly increased everywhere ($p < 0.001$, df 1,551) except in Fagatele Bay where it has been consistently very rare (Fig. 8A). Fig. 8 B shows an abrupt drop in 2024, but of course that is because we only surveyed Fagatele this year. Each of the dots represents data from a transect, not just a coral colony.

Two more striking changes in coral communities on Tutuila over the past 44 years involve *Montipora* species. *Montipora verrilli* was one of the more prevalent *Montipora* through 1998, but it crashed to very few in 2002 and has not been recorded on our transects for the last 22 years (Fig. 9). In contrast, *Montipora grisea* was not recorded at all on our transects before 1995. Of the 6,416 corals recorded in 1982, 1985, and 1988, none were *M. grisea*. When it abruptly appeared in 1995, it was immediately the most abundant coral with 3379 *M. grisea* recorded, or 23% of the total number of colonies of about 160 other species (Fig. 9). Questions as to the taxonomy of these two species of Montipora are explained in Taxonomic Notes, Appendix 1.

All encrusting *Montipora* other than M. verrilli and *M. grisea* taken together have not shown an overall change from 1985 to 2024 in Fagatele Bay (Fig. 10A), but there has been a significant increase in abundance from 1982 to 2018 on the outer coast of Tutuila and Aunu'u (Fig. 10 B).

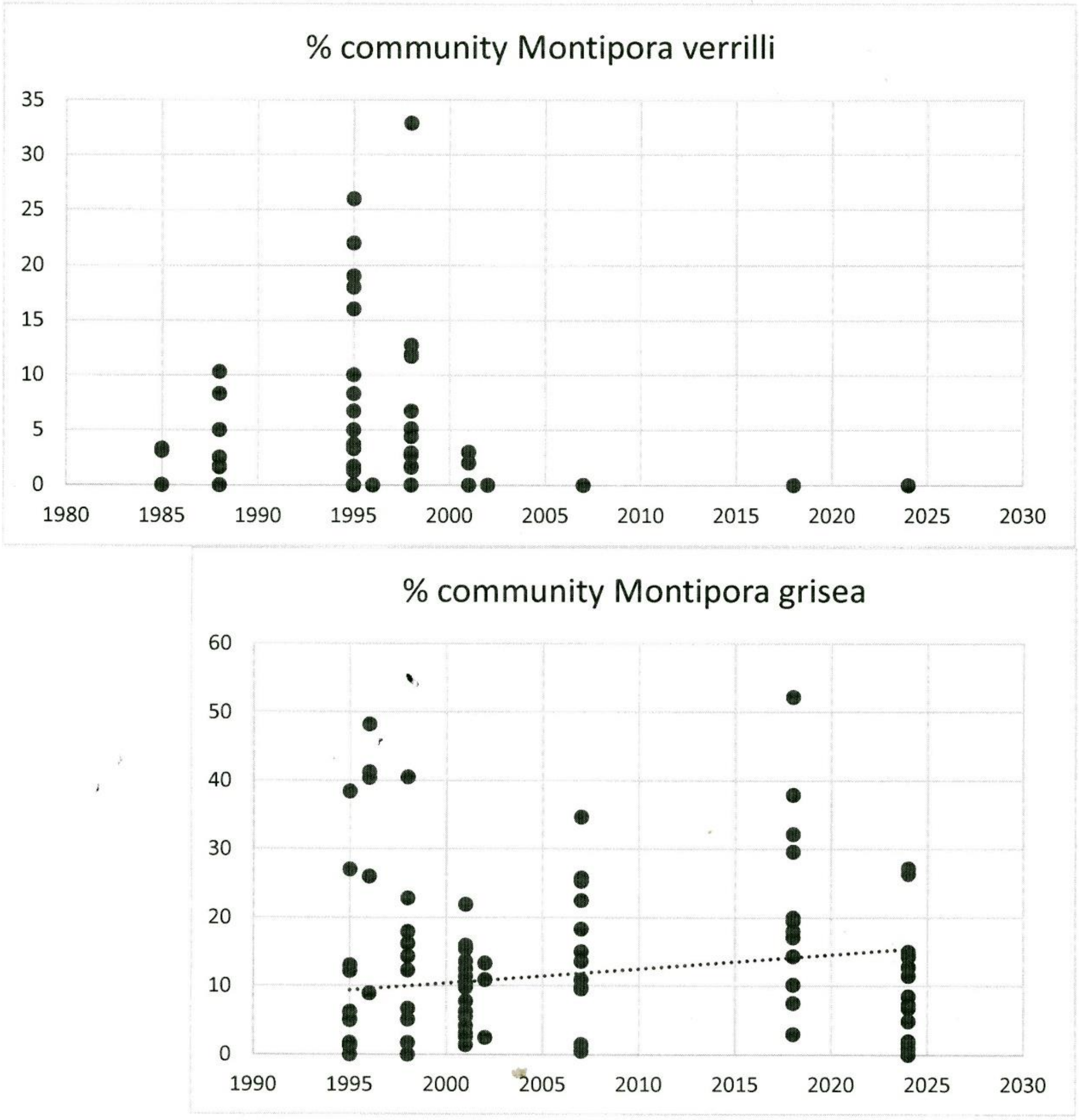


Fig. 9. *Montipora verrilli* was an abundant species until 2002, after which it was never seen. *Montipora grisea* was not seen until 1995 when it was instantly most abundant species. It has remained the most abundant species since 1995. Although the regression appears to have an increasing slope through the years, but it was not significant ($p = 0.059$, df 1,107). Each of the dots represents data from a transect, not just a coral colony.

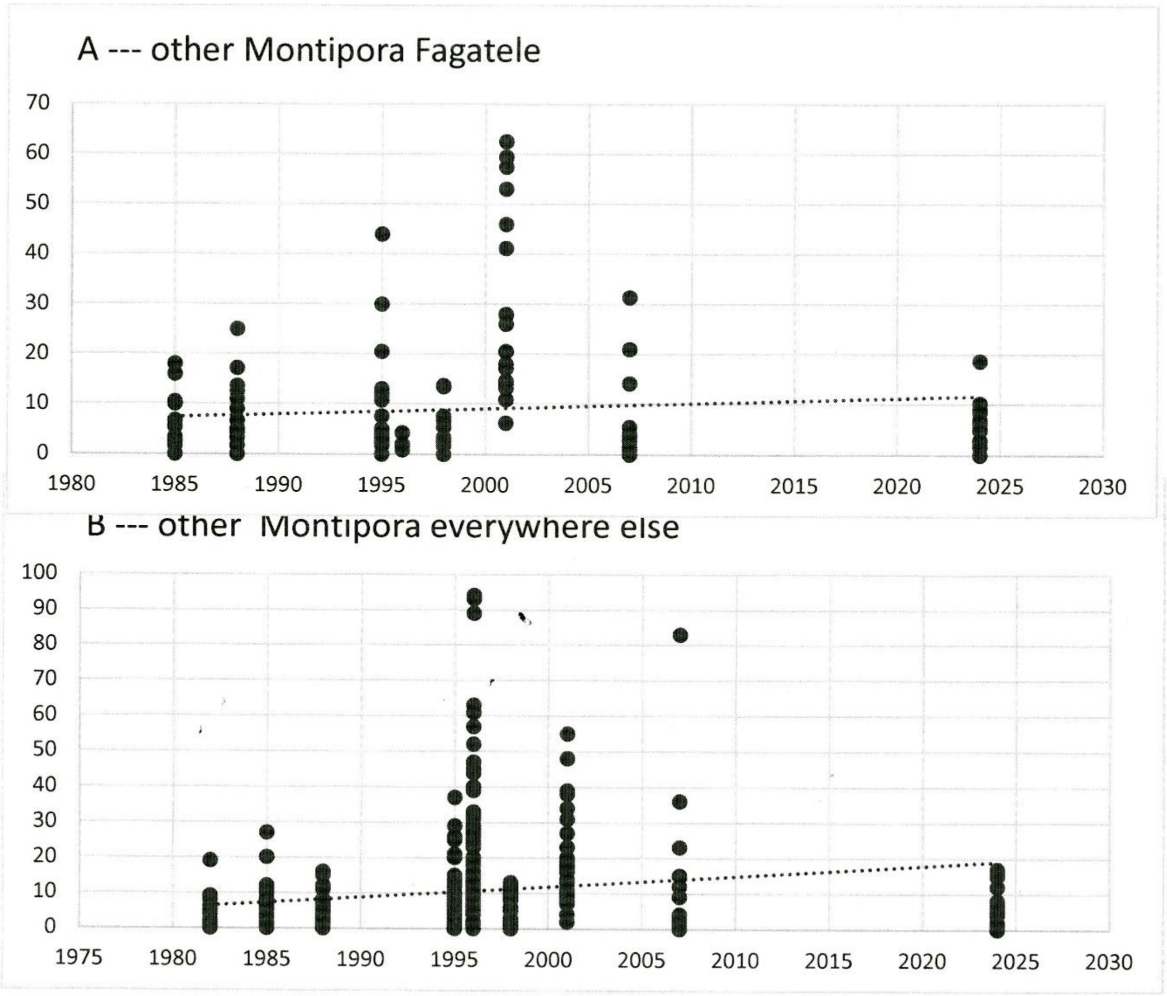


Fig. 10. All species of encrusting *Montipora* other than *M. verrilli* and *M. grisea*. In Fagatele Bay (Fig. 10A), there was no overall change in population density between 1985 and 1024 ($p = 0.232$, df 1,143), but there has been a significant increase in population density of encrusting *Montipora* on the outer coast of Tutuila and Aunu'u between 1982 and 2018 (p , 0.001, df 1,367). Each of the dots represents data from a transect, not just a coral colony.

Pocillopora species have also been decreasing significantly on the outer coasts of Tutuila since 1982 (Fig. 11, $p < 0.001$, df 1, 551), but there has been no overall change in *Pocillopora* spp. population densities in Fagatele Bay since 1985 (Fig. 11 $p > 0.492$ df 1, 154). No change is actually another positive score for Fagatele Bay because it is in contrast to the significant declines elsewhere.

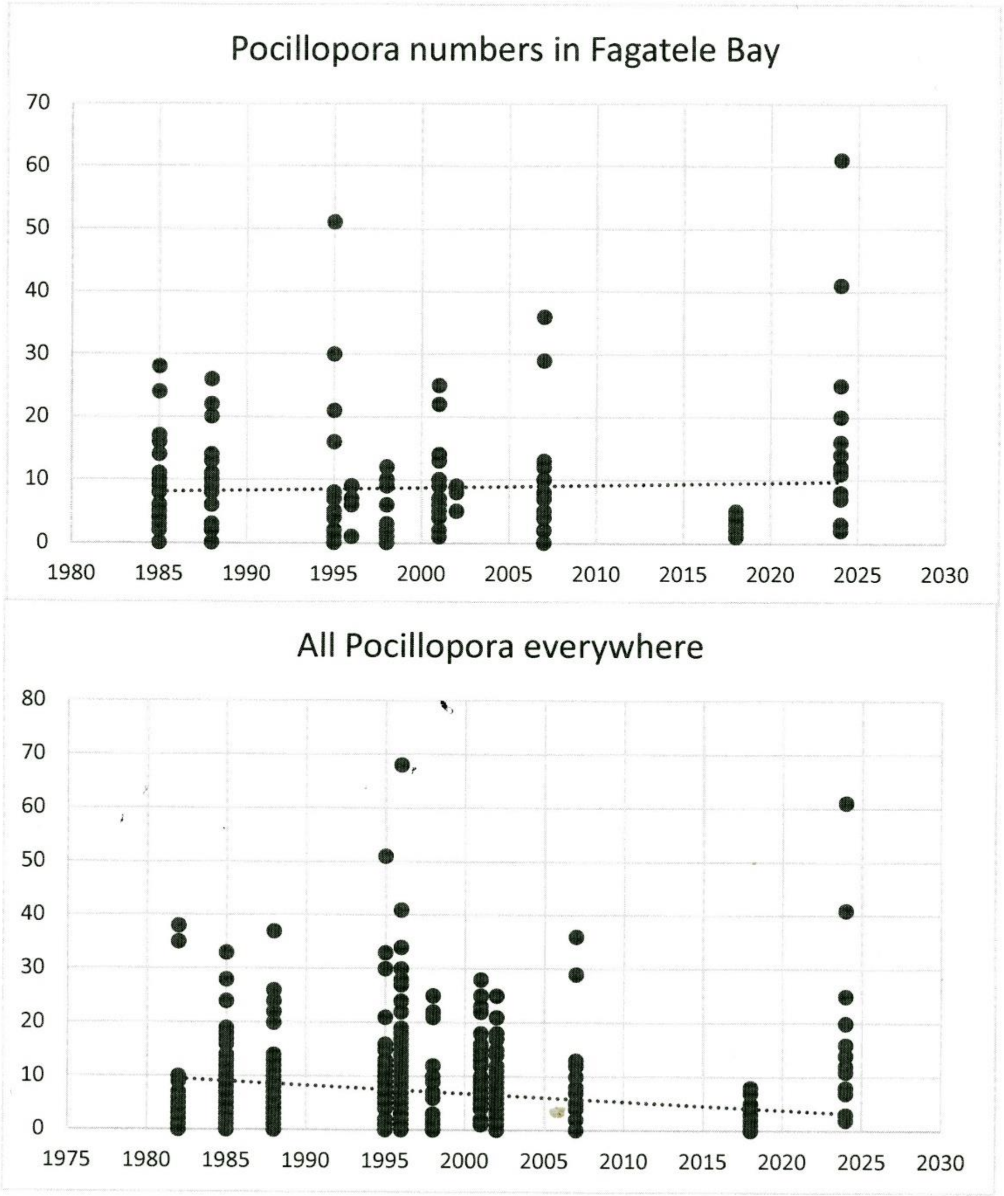


Fig. 11. *Pocillopora* spp. declined significantly in population density from 1982 to 2018. However, there was no significant change in abundance of *Pocillopora* spp. in Fagatele Bay from 1985 to 2024. Each of the dots represents data from a transect, not just a coral colony.

Large colonies of massive *Porites* have been maintaining themselves over the decades (Coward et al. 2020), but the more common colonies in the smaller size classes have been significantly declining in abundance, both in Fagatele Bay (Fig. 12A) and on the outer coast of Tutuila and Aunu'u (Fig. 12 B, not including Pago Pago Harbor and Fagatele Bay). Mound-shaped *Porites* species recruit better on Tutuila (including Fagatele Bay), Aunu'u, and Ofu-Olosenga, than at Ta'u, but tend to survive longer and reach the larger size classes on Ta'u (this paper Fig. 13; Coward et al. 2020).

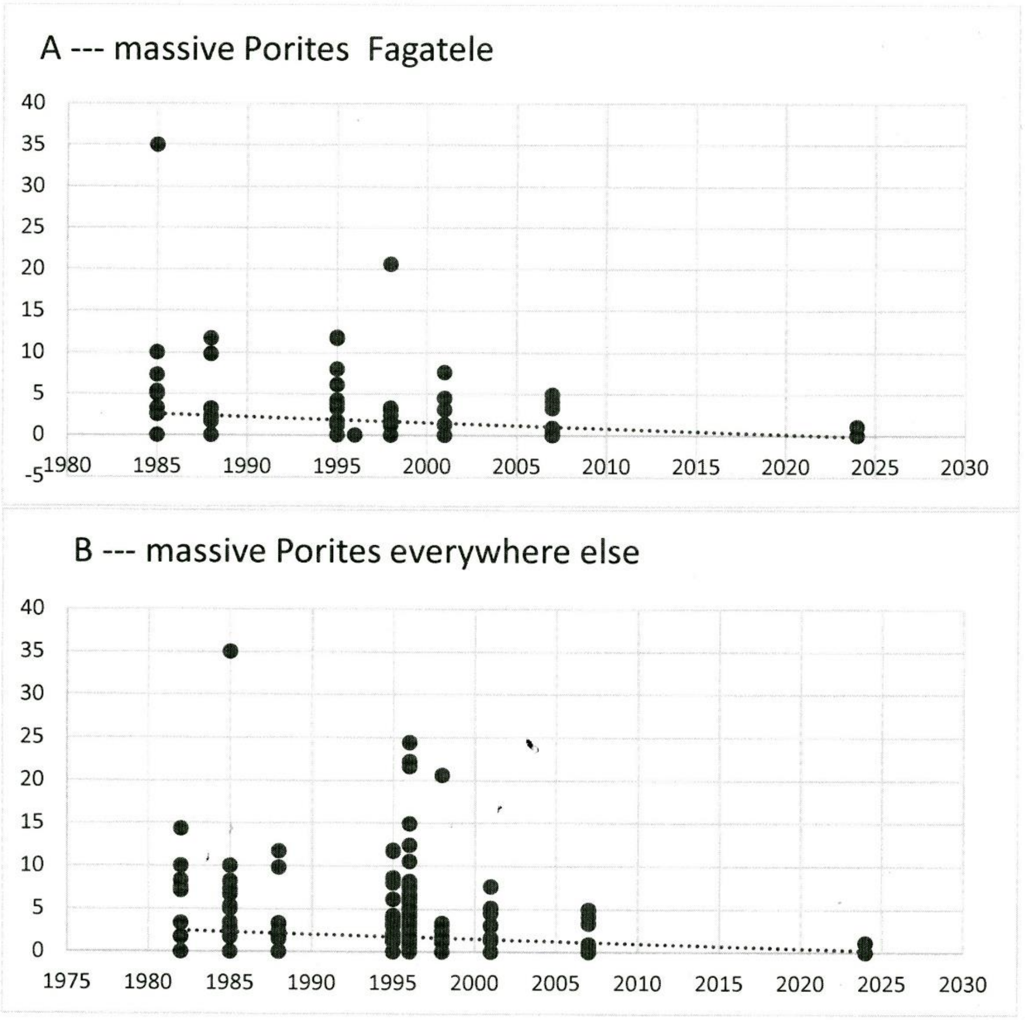


Fig. 12. Massive Porites have been significantly declining in abundance since 1982 on the outer coast of Tutuila and Aunu'u (not including Fagatele Bay and Pago Pago Harbor, $p < 0.05$ df 1, 367) and in Fagatele Bay ($p < 0.05$ df 143). Each of the dots represents data from a transect, not just a coral colony.

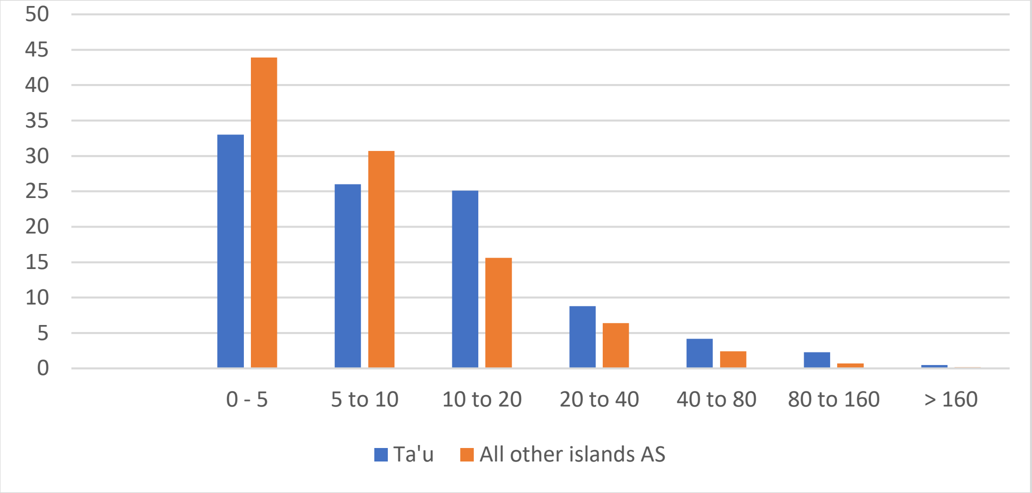


Fig. 13. Size distributions of mound *Porites.* On Ta’u, *Porites* mound-species do not recruit better than on other islands, but they tend to last longer and grow to larger sizes. This corroborates Coward et al. 2020.

The most spectacular long-term change in the coral communities in American Samoa 1982 – 2024 has been the history of the endemic *Porites randalli*. In the 1980s and 1990s, the survey reports showed it sometimes to be the most abundant coral in Fagatele Bay, Fatumafuti, Faga’alu, Fagaitua, and Masefau, and a close second to *Montipora grisea* at Vatia and Aunu’u. McArdle, in his 2003 review of American Samoa coral surveys, called it the most ubiquitous species, uniformly distributed among the depths surveyed (1 m – 12 m). The regression in Fig. 14 shows the extreme drop in *P. randalli* abundance starting about the year 2000. Note that the regression has its abundance below zero in 2024 and, indeed, we saw no *P. randalli* in the February 2024 survey. However, we saw 12 *P. randalli*-like encrusing colonies for the first time in 2024.The small dots over the zero line in 2024 represent the *P. randalli*-like encrusting colonies in Fagatele Bay.

Another measure of the drastic decline in endemic *P. randalli* over the decades is the ranking of coral species abundances through the years (Appendix 4). In 1995, *Montipora grisea* was in top place with 3379 recorded colonies. (*Montipora grisea* has remained the most prevalent ever since.) In 1995, *P. randalli* was second place with 2635 recorded colonies. *Pavona varians* s.l. was a distant third place with 745 colonies. Then in 2002, *P. randalli* was 56th place with 33 colonies and in 2018 52nd place with 21 colonies recorded. Then in 2024, it was not ranked because we recorded zero colonies *P. randalli*. It is probably still doing fine in the Ofu pools and other shallow places, but it is no longer ubiquitous at all sites at all depths (to at least 12 m).

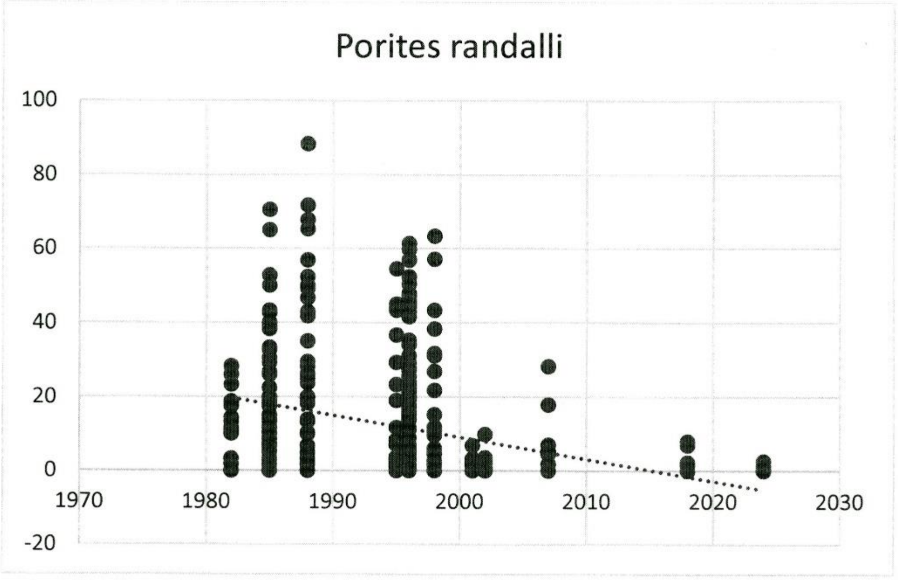


Fig. 14. *Porites randalli* for all sites and years. The probability that the negative slope of the regression equals zero is p < 0.001 df 1, 551. Each of the dots represents data from a transect, not just a coral colony.

DISCUSSION

Abundances of coral colonies

If it is indeed the case that since the 1950s, the global coverage of living coral cover has declined by about 50% and the global capacity of coral reefs to provide ecosystem services has also declined by 50% (Eddy et al. 2021), the coral reefs of American Samoa, especially in Fagatele Bay National Marine Sanctuary, are showing outstanding performances. Despite the major mortalities of coral colonies from crown-of-thorns seastar outbreaks, severe widespread destruction of coral colonies by cyclones, and the stress brought by bleaching events, the recoveries have been consistent and there has been no overall significant change in average population densities between 1982 and 2018 on the outer coast of Tutuila and Aunu'u (19 sites, not including Pago Pago Harbor and Fagatele Bay) and between 1985 and 2024 in the FBNMS.

Full recovery of coral communities in Fagatele Bay

The two main events affecting the coral reefs of Tutuila and Aunu'u in the past four decades have been the 1978-1979 outbreak of crown-of-thorns seastars and the 1991 Cyclone Val. *Acropora* spp. in FBNMS, *Pavona varians* s.l., *Pavona chiriquiensis,* and *Montipora* spp. (not including *M. verrilli* and *M. grisea*) everywhere except in FBNMS, and *Porites rus* and *Montipora grisea* everywhere including FBNMS significantly increased in population densities from low in population densities found in surveys in1995. Further, the size distributions of the majority of coral species in 1995 surveys were in lower size classes, but the species grew into the larger size class from 1995 to sometime between 2002 and 2018.

Cyclone Val was a direct hit on NW Tutuila and sat on Tutuila for 5 days with winds up to 240 km/hr (150 mi/hr) and with some waves 15 m (50 ft) tall. There was also a major bleaching in 1994. We speculate that the increases in population densities and growths into higher size classes from 1995 through 2018 – 2024 were recoveries from low points caused by Cyclone Val, with effects perhaps enhanced by the major bleaching in 1994. American Samoan reefs have been hit in the past four decades by a second crown-of-thorns outbreak, nine additional cyclones, four mass bleaching events, six extreme low tides, and a tsunami which have caused local damages to coral communities, but our data have not clearly shown these events to have caused such large-scale declines and recoveries in population densities and larger size classes as those shown by between 1995 and 2018-2024 resulting from Cyclone Val.

Both coral colony population densities and growth into the larger size classes seem to have reached an asymptote of full community recovery in 2018 and 2024 (Figs. 15, 16). Full recovery was achieved between our 2002 and 2018 surveys. This means the full recovery of FBNMS corals from a serious disturbance takes between 11 and 17 years, i.e., between Cyclone Val in 1991 and full recovery sometime between 2002 and 2018.

Fig. 15. Alice Lawrence surveys a fully recovered coral community dominated by *Acropora* species in February 2024. (Photo by Alison Green)

Consistent recruitment

Steady recruitment may be an important factor explaining the outstanding resilience of American Samoan coral communities. At least a hundred coral species on the forereef slopes of American

Samoan reefs have good recruitment (Appendix 2). Of all coral colony diameters we have measured (34,883), 23.60 % were < 5 cm. Good recruitment is a sign that the species is not seriously affected by Allee effects. It also is a sign that the species population is not seriously stressed by temperature or other factors because when stressed, most corals divert energy from reproduction to survival (Birkeland 2015). When recovering from bleaching, some corals can go for four years before spawning (Levitan et al. 2014). Corals in the same area that did not bleach can also go for four years before spawning because they also endured the stress even though they were able to avoid bleaching (Levitan et a. 2014). Recruitment is a sign that at least some of the species population was in areas where it was not stressed. While species at the top of the recruitment list are shown to be doing well, this does not imply that those lower in the list are affected by Allee effects or are stressed. We only surveyed the forereef slopes. Those lower on the recruitment list may be doing well in other habitats.

Trajectories over four decades

Although the total coral colony population density of all species combined over all sites and all years has not changed when considering the entire four decades (Fig. 2), there have been major changes in species composition during this time. Although corals of individual species or genera have had their ups and downs, perhaps several times each, there are a number of these species that have had a significant increase or decrease over the entire four decades. This is what we are calling "trajectories". According to the Merriam-Webster Dictionary, a "trajectory" is a straight line or path, or a line or path with a constant angle. The antonym of "trajectory" is "deviation". Deviations in coral colony abundances over shorter time intervals within our four decades may be called "decreases" and "disturbances" or "increases" and "recoveries". Trajectories are a rather abstract concept of an overall significant change (or significant lack of change) over decades.

Coral-reef scientists who started their careers after the 1970s grew up familiar with climate change and long-term broad-scale changes in coral-reef systems and so they are familiar with trajectories, but those starting their careers in the 1970s and earlier perceived events and changes in coral-reef systems as cyclic, e.g., disturbance and recovery, El Niño – La Niña, seasons, etc. Those starting by the 1970s understand trajectories, but are uncomfortable with them, feeling the systems should be fluctuating about some "normal" state, rather than continuing long-term changes to a new state for decades, perhaps permanently in our scale of reference.

The average population densities of coral colonies were about 12-13 per m^2 from 1982 – 2018 on the outer coast of Tutuila and 11 per m^2 from 1985 – 2024 in FBNMS. Within this general population density over these four decades, there have been some trajectories, or overall changes over these four decades.

Acropora spp. increased over these four decades in FBNMS, but decreased on the outer coasts of Tutuila and Aunu'u. This is probably the change that leads people to believe the coral communities in FBNMS from 2018 to 2024 have been in the best condition since 1979. *Porites rus* and *Montipora grisea* have increased on both the outer coast of Tutuila and FBNMS.

Observations by one of us on Guam and Maui and conversations with colleagues from around the tropical Pacific suggest that *Porites rus* is increasing in many sites in the tropical Pacific.

The encrusting *Montipora* spp. (other than *M. verrilli* and *M. grisea*) and *Pocillopora* spp. did not change significantly over the four decades in Fagatele Bay. This is another kudo for FBNMS, because *Pocillopora* has significantly declined in areas other than Fagatele Bay.

On the other hand, *Pavona varians* s.l. has been increasing significantly ($p < 0.001$ df 1,551) on most sites outside Fagalete Bay, but *P. varians* s.l. has been almost nonexistent in Fagatele Bay since 1985.

Since the total coral colony population density at FBNMS has remained the same across the four decades, then the significant increases in *Acropora* spp., *Porites rus*, and *Montipora grisea* suggests there must have been substantially decreased population densities of some other species. Although the larger colonies of massive *Porites* are persisting, the population density of mound-shaped *Porites* spp. have bee significantly decreasing both on the outer coast of Tutuila and in FBNMS. The endemic *Porites randalli* has showed the most drastic decrease since 1996 (Fig. 14). Up until 1996, it was first or second (to *M. grisea*) most abundant and ubiquitous (McArdle 2003) of all coral species in American Samoa. Although it has practically disappeared from the forereef slope, it still seems to be doing fine in other habitats such as reef-flat pools.

Paradox of Rose Atoll corals compared to corals in Fagatele Bay

We have been confronted with the question as to why *Acropora* grow into the substantially larger size classes in Fagatele Bay, but not at Ta'u and Rose Atoll (Fig. 5). It has been suggested that wave energy may affect coral colonies that have a lot of branches or wave-resistant surface area attached to the substratum by a smaller stalk or trunk. Both Ta'u and Rose Atoll drop off steeply from shore and are frequently exposed directly to strong surf. The stronger trade winds come from the east-southeast (PIFSC-CRED data provided in Aeby et al. 2008). Brian Peck suggested that heavy wave action on the open coasts of Rose Atoll prevent branching genera such as *Acropora* from getting large. This same suggestion was previously given independently by Alice Lawrence for the *Acropora* colonies staying small at Ta'u. Tutuila has a broader, shallower shelf than do Ta'u and Rose and also has offshore banks such as Taema that help reduce the energy of oceanic waves. Fagatele Bay is an exception on Tutuila because the shelf drops steeply off Fagatele. However, Fagatele is relatively protected from waves from the southeast by Larsen Bay and Steps Point. Ironically, our February 2024 survey has hindered by strong swells from the west; but these were swells, not surf, which tossed the scientists around, but did not break corals..

It is possible that frequent strong waves limit the sizes of branching corals (Figs. 5, 17), but the massive or mound-shaped *Porites* tend to grow into the larger size classes (Fig. 13 and 18 this paper; Coward et al. 2020). It may be that massive coral colonies with a broad attachment at their bases and with rounded hemispherical morphologies are less vulnerable to waves than branching corals. Therefore, wave action may be a plausible explanation of Ta'u where *Acropora* are

Fig. 16. Alison Green is surveying little fishes (Where are they?) near or within the large colonies in the fully recovered reef community in FBNMS. Note the size distribution into large branching colonies of *Acropora intermedia*. (Photo by Alice Lawrence)

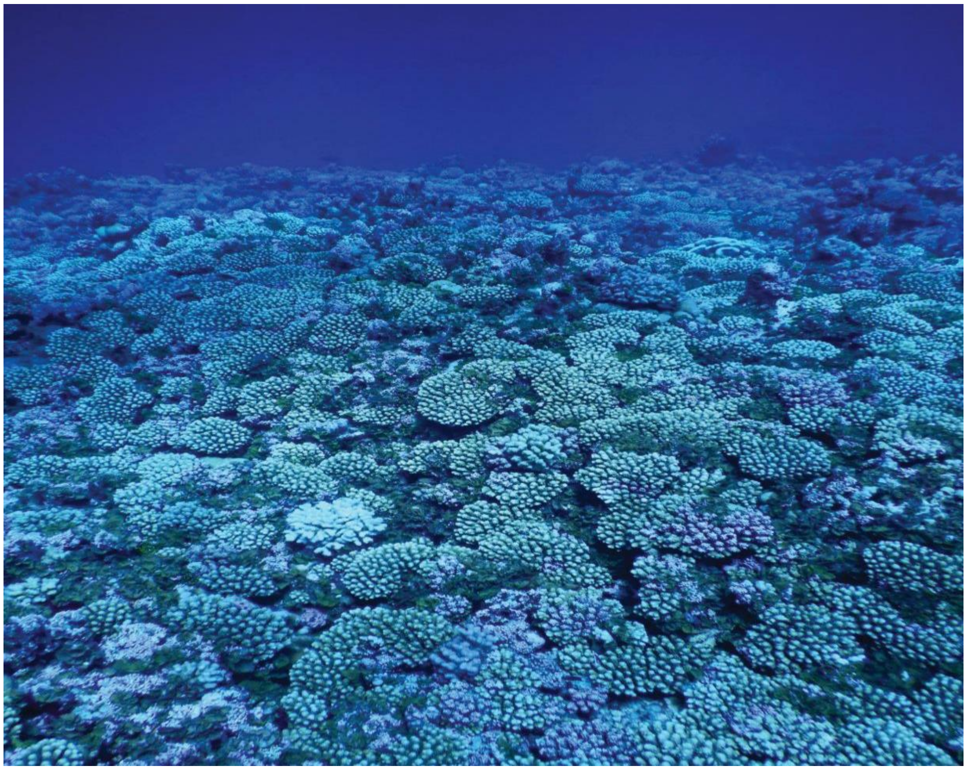
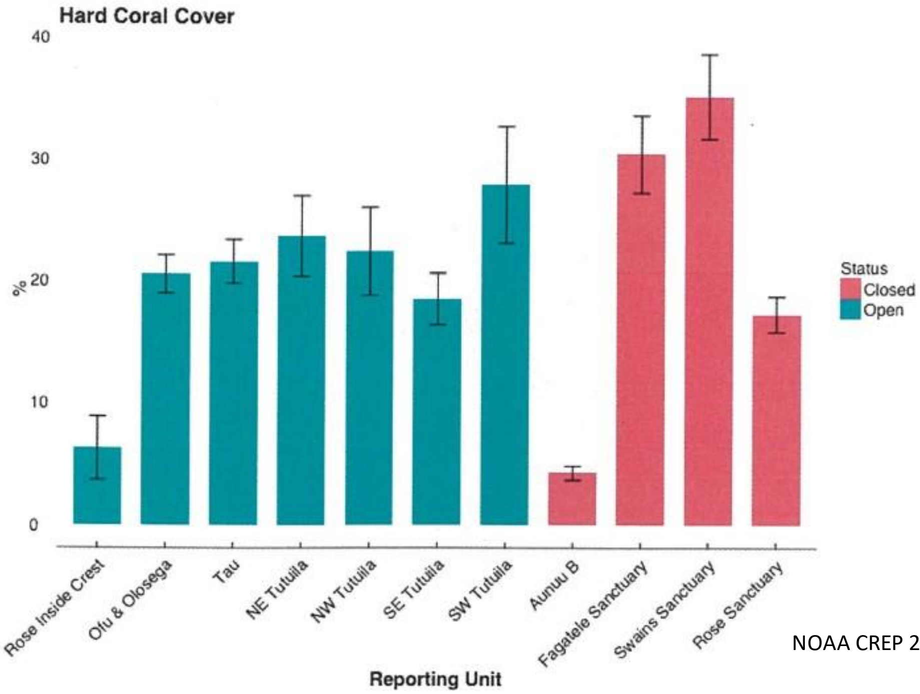


Fig. 17. Digitate *Acropora* are numerous on the open coast of Rose Atoll, but colonies rarely get as large as in FBNM

Fig. 18. Alice Lawrence expresses approval that despite the significant declines in population densities of mound-shaped species of *Porites* in Fagatele Bay (Fig. 12A) and around the open coast of Tutuila and Aunu'u (Fig. 12B), the massive *Porites* in Fagatele Bay, including one that was dynamited by fishers decades ago, are still doing fine. However, note the background dominance of *Acropora*. (Photo by Alison Green)

restricted in size while massive *Porites* can grow large. But how do we explain the open coast of Rose Atoll where *Porites* and other massive hemispherical corals also do not grow large?

This question is exacerbated by the fact that local seawater chemistry suggests we should expect the corals to actually grow larger and produce more living coral cover on Rose Atoll than in Fagatele Bay. Waters around Rose Atoll may have the highest aragonite saturation state in US territories (NOAA CRED 2016), which is a measure of the availability of carbonate ion, which in turn determines that carbonate accretion rate should be highest at Rose Atoll. Carbonate accretion rate is indeed greatest in American Samoa at Rose Atoll and much less at Tutuila (NOAA CRED 2016), yet corals appear to grow less at Rose and much better at Fagatele (Fig. 5) and produce significantly more living coral cover at Fagatele Bay (Fig. 19). The greater carbonate accretion at Rose Atoll may be by organisms other than corals, perhaps by CCA. It is also possible that corals are accreting carbonate skeletons as fast or faster than at Fagatele Bay, but mortality from wave action and/or overgrowth by CCA increases turnover so although the corals are growing more rapidly, their size distribution stays concentrated in the smaller size classes.



NOAA CREP 2016

Fig. 19. The 2016 survey by NOAA CRED found that despite substantially greater rates of carbonate accretion (from greater carbonate ion availability as measured by aragonite saturation state 4.034 ±0.014) and therefore potential for reef-building, the living coral cover on the forereef slope at Rose Atoll (far right bar) was significantly less than living coral cover at Fagatele Bay (third bar from right) which had significantly less (anova p< 0.001, df 1,54) aragonite saturation state (3.818 ±0.022) or potential for reef-building. (Data on aragonite saturation state and anova from Vargas – Ángel et al. 2019).

Since the aragonite saturation state ($CaCO_3$ accretion or reef-building potential) is significantly greater on Rose Atoll than at Tutuila, the recruitment of corals is good and lower size classes are doing well and population densities are as good as anywhere in our surveys (Fig. 5). It seems like the population is robust, with rapid turnover. The high levels of aragonite saturation state are good for coral growth, but perhaps even better for CCA. Although CCA sometimes overgrows *Acropora* in Fagatele, corals are still dominant in Fagatele. What makes Rose Atoll almost unique in the dominance of CCA over corals (Fig. 20)? Perhaps Rose Atoll has a special combination of carbonic ion availability (as indicated by aragonite saturation state) and strong wave action.

Field observations suggest that the increased carbonate accretion is done more by CCA and with a greater reaction to carbonate ion availability than by corals. Therefore, the corals are losing in competition (Fig. 20), even though the aragonite saturation state, and perhaps their growth rates, are especially high.

Fig. 20. Field observations suggest that CCA (mostly *Porolithon craspedium* and *Porolithon onkodes* s.l.) react more strongly than corals to increased available carbonate ions (as measured by aragonite saturation state) and are thereby overgrowing corals, reducing the chances of corals to grow into the larger size classes.

It could be that the carbonate accretion on the forereef slopes at Rose is mostly CCA rather than corals. In areas of strong wave action, CCA thrives. Note the robust coralline algal ridge in the surf zone of the Aua transect, but the meagre CCA on unconsolidated rubble on the protected reef flat of the Aua transect. Note the prevalence of CCA to greater depths on the windward south coast of Tutuila, but the relatively meagre CCA on the north coast. Note corals are often being overgrown before they get big on the open coast forereef slopes of Rose, but corals are allowed to get big in the lagoon of Rose protected from waves in which CCA is mediocre. The strong wave action in combination with the high aragonite saturation state (abundantly available carbonate) may allow CCA to usurp the otherwise best of all growth conditions from the corals.

CCA is probably an important positive factor in the extraordinary success of coral communities in American Samoa, especially at FBNMS, because CCA enhances successful coral recruitment. In American Samoa, coral successful recruits were found on CCA 94% of the time (Birkeland et al. 2021).

What evidence shows FBNMS coral communities to have outstanding performance?

In contrast to most of the reef-building coral communities around the world (Eddy et al. 2021), the coral colony population densities in FBNMS over the past four decades have remained at the same level, despite major mortalities of corals from crown-of-thorns outbreaks, major cyclones, and the stress brought about by bleaching events.

The coral communities in FBNMS fully recovered from Cyclone Val within 11 – 17 years.

The Coralline Lethal Orange Disease (CLOD) has been seen on CCA nearly every dive in Fagatele Bay for over 20 years, but the CCA has kept it under control. This may change if seawater temperatures increase, but the CCA in Fagatele Bay are not succumbing yet.

Acropora spp. significantly increased in population density and grew into larger size categories in FBNMS, but significantly decreased in population density and showed almost no growth into larger size categories on the outer coat of Tutuila and Aunu'u.

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APPENDIX 1 – Taxonomic Notes

Pavona varians are combined with *P. chiriquiensis* in this report because they were not usually distinguished in the early surveys and so we cannot reliably sort them out among data from earlier years. Dick Randall always recognized them as different species. He called *P. chiriquiensis “Pavona* collines*”*. “Collines” are little hills. The species was not officially described until 2001 when it was described from Panamá by Glynn, Maté. And Stemann (2001). We have no worries when combining their analysis because they seem to have the same ecological roles and they are both common.

That *Montipora verrilli* was abundant, but completely disappeared after 2002, while M. grisea suddenly appeared in full abundance in 1995 might suggest that since encrusting *Montipora* species are usually hard to tell apart, this may all be a result of confused identification. However, both Dick Randall and Craig Mundy independently distinguished and recoded both *M. verrilli* and *M. grisea* between 1995 and 2002. Both species are common on Guam, and Dick Randall includes them both on his publications on corals of the Marianas. I believe the late Dick Randall knew these species well, and if he did not see *M. grisea* before 1995, then it was not there or it was too rare to be recorded before 1995. From my less expert view, the surface of *M. verrilli* is largely relatively orderly cobblestones while the surface of *M. grisea* is more chaotic and rough.

APPENDIX 2 – Size distributions based on diameters of colonies on our transects. Species are listed from the greatest to least number of colonies less than 5 cm, considered "recruits". The endemic *Porites randalli* is a small coral, but < 5 cm still indicates healthy recruitment even if mixed with adults.

SPECIES	**< 5**	**6 to 10**	**11 to 20**	**21-40**	**41-80**	**81-160**	**>160**
Porites randalli	1042	1345	290	12	0	0	0
Montipora grisea	893	1422	2209	1010	266	23	0
Astrea curta	551	457	265	56	3	0	0
Pavona varians s.l.	315	632	566	278	39	4	1
Leptastrea purpurea	238	202	127	23	0	0	0
Montipora turgescens	233	187	172	85	21	2	0
Porites rus	225	321	316	207	98	39	12
Porites cf horizontalata	225	130	41	5	1	1	0
Goniastrea edwardsi	186	100	69	31	7	0	0
Montipora venosa	169	106	41	7	2	1	0
Leptoria phrygia	161	82	76	32	6	0	0
Goniastrea retiformis	182	145	85	39	15	0	0
Psammocora profundacella	147	133	46	4	2	0	0
Dipsastraea matthaii	144	114	51	19	4	0	0
Montipora caliculata	140	82	32	4	2	0	0
Montipora efflorescens	134	97	134	50	17	0	0
Galaxea fascicularis	130	419	377	9	0	0	0
Psammocora haimeana	115	73	24	2	4	0	0
Dipsastraea stelligera	102	116	76	87	20	1	0
Pocillopora verrucosa	99	162	186	111	2	0	0
Montipora danae	86	81	38	7	1	0	0
Montipora informis	83	243	319	208	30	7	0
Porites mound	131	101	35	17	4	1	0
Astreopora listeri	74	72	65	39	10	6	0
Montipora monasteriata	72	153	164	55	9	0	0
Isopora crateriformis	71	92	86	61	14	0	0
Pocillopora spp	123	1	2	0	0	0	0
Goniastrea pectinata	67	48	50	7	0	0	0
Montipora spp	136	46	46	49	27	1	1
Montipora hoffmeisteri	61	63	80	37	13	0	0
Montipora corbettensis	60	52	91	144	111	7	1
Acropora spp	112	65	45	30	11	2	1
Pocillopora damicornis	48	50	33	2	0	0	0

Porites lichen	48	38	14	1	0	0	0
Montipora effusa	45	65	78	41	21	3	0
Montipora tuberculosa	51	50	66	39	12	0	0
Echinopora lamellosa	41	18	9	6	2	1	1
Dipsastraea pallida	41	35	6	2	0	0	0
Pavona venosa	41	66	82	40	3	0	0
Galaxea astreata	40	42	24	1	0	0	0
Montipora calcarea	40	18	5	2	0	0	0
Oxypora lacera	45	31	28	23	8	1	0
Pavona maldivensis	39	10	7	9	4	0	0
Stylocoeniella armata	38	10	7	2	0	0	0
Montipora foveolata	36	46	30	22	1	1	0
Acropora valida	34	38	36	2	2	0	0
Pocillopora meandrina	33	122	260	122	10	0	0
Platygyra pini	33	25	14	7	2	0	0
Astreopora myriopthalma	53	78	45	20	15	6	0
Echinopora hirsutissima	33	46	26	10	5	1	0
Leptastrea transversa	31	943	44	20	2	1	0
Montipora verrucosa	29	13	7	3	0	0	0
Platygyra daedalea	28	27	35	14	7	1	0
Merulina ampliata	26	1758	19	18	7	1	1
Fungia spp	42	14	7	2	0	0	0
Leptoseris mycetoseroides	25	53	31	9	0	0	0
Favites russelli	23	17	14	8	0	0	0
Alveopora spp	22	9	0	0	0	0	0
Goniastrea favulus	21	21	4	0	1	0	0
Phymastrea valenciennesi	29	15	9	2	0	0	0
Alveopora tizardi	20	10	0	1	0	0	0
Porites stephansoni	40	33	31	9	0	0	0
Montipora aequituberculata	19	19	26	19	2	0	0
Tubastraea coccinea	19	0	0	0	0	0	0
Acanthastrea echinata	19	15	11	2	1	0	0
Favites halicora	19	24	24	10	5	0	0
Alveopora allingi	17	4	5	0	0	0	0
Fungia concinna	17	17	17	1	0	0	0
Coscinaraea columna	16	30	25	26	10	3	0
Fungia fungites	15	690	46	18	0	0	0
Hydnophora exesa	15	5	9	8	6	0	0
Alveopora spongiosa	16	2	1	0	0	0	0
Montipora mollis	14	8	1	2	0	0	0
Pavona chiriquiensis	28	41	51	29	4	0	0
Psammocora contigua	14	13	9	4	2	0	0

Favites abdita	13	13	5	4	2	0	0
Millepora exaesa	13	15	11	6	8	0	0
Montipora millepora	12	9	6	4	0	0	0
Astreopora gracilis	21	57	56	22	5	0	0
Dipsastraea speciosa	11	5	11	2	0	0	0
Porites cylindrica	11	15	10	12	7	4	0
Montipora floweri	11	14	26	18	2	0	0
Dipsastraea favus	10	13	5	2	0	0	0
Fungia scutaria	10	15	13	1	0	0	0
Acropora samoensis	10	43	45	9	3	0	0
Acropora nasuta	10	45	47	14	1	0	0
Diploastrea heliopora	9	7	6	11	7	7	6
Goniastrea aspera	9	9	9	1	0	0	0
Leptastrea bewickensis	9	7	8	3	1	0	0
Lobophyllia hemprichii	9	15	27	25	10	1	0
Cladiella spp	16	18	8	0	0	0	0
Cyphastrea chalcidicum	10	21	12	3	0	0	0
Cyphastrea serailia	7	5	7	6	0	0	0
Pocillopora eydouxi	7	133	262	161	52	0	0
Dipsastraea laxa	7	6	3	6	1	0	0
Echinophyllia aspera	6	1	3	7	4	0	0
Favites flexuosa	6	5	6	1	1	0	0
Leptastrea spp	7	7	3	0	0	0	0
Acropora digitifera	9	18	6	4	3	0	0
Lobophyllia corymbosa	5	5	3	6	0	1	0
Acropora hyacinthus	5	20	17	4	7	4	0
Millepora platyphylla	5	24	9	5	6	3	1
Acropora humilis	4	10	9	9	2	0	0
Astrea annuligera	4	17	12	6	1	0	0
Dipsastraea sp.	7	4	2	4	0	0	0
Goniastrea australensis	4	7	6	2	1	0	0
Pavona duerdeni	4	12	15	5	7	2	0
Platygyra sinensis	4	10	5	2	0	0	0
Psammocora superficialis	4	7	6	6	1	0	0
Stylocoeniella guentheri	4	8	3	1	0	0	0
Turbinaria reniformis	4	15	8	8	1	1	0
Acropora danai	4	18	25	1	1	0	0
Acropora gemmifera	4	20	29	17	3	0	0
Acropora abrotanoides	3	4	6	2	5	9	5
Acropora austera	3	13	6	5	7	5	2
Acanthastrea spp	4	0	0	0	0	0	0
Acropora glauca	4	27	48	38	3	1	0
Acropora hemprichii	3	0	0	0	0	0	0

Astreopora cucullata	3	7	14	11	1	2	0
Astreopora ocellata	3	1	1	0	0	0	0
Cyphastrea sp.	3	6	11	5	2	0	0
Distichopora spp	3	0	0	0	0	0	0
Montipora orientalis	3	3	1	0	0	1	0
Montipora peltiformis	3	3	1	0	0	0	0
Porites annae	3	4	1	0	0	0	0
Stylophora pistillata	3	1	4	0	0	0	0
Acropora latistella	2	7	8	4	7	1	0
Acropora retusa	4	4	2	17	1	0	0
Acropora secale	2	3	4	5	1	0	0
Astreopora spp	4	0	0	2	0	1	0
Coeloseris mayeri	2	3	3	1	0	0	0
faviid	2	1	9	8	1	0	0
Favites spp	7	10	7	6	5	0	0
Fungia danai	2	2	0	0	0	0	0
Montipora capitata	2	0	6	0	0	0	0
Pavona clavus	2	1	2	2	1	0	0
Porites napopora	2	0	0	0	0	0	0
Acropora cytherea	1	2	1	4	2	1	2
Acropora intermedia	1	3	8	4	1	4	2
Acropora nobilis	1	2	6	2	3	3	2
Acropora aculeus	1	5	18	12	0	0	0
Acropora akajimensis	1	0	5	5	0	1	0
Acropora nana	1	10	10	2	0	0	0
Acropora cophodactyla	1	4	3	1	0	0	0
Acropora divaricata	1	5	5	4	4	0	0
Acropora globiceps	1	2	2	3	1	0	0
Acropora pagoensis	1	13	7	7	2	0	0
Acropora rosaria	1	1	1	0	1	0	0
Acropora surculosa	1	4	2	0	0	0	0
Astrea spp	3	5	1	2	0	0	0
Astreopora expansa	1	2	2	1	0	0	0
Cantharellus sp.	1	0	0	0	0	0	0
coralliomorph sp.	1	0	0	0	0	0	0
Cyphastrea microphthalma	1	0	1	1	0	0	0
Dipsastraea helianthoides	1	0	0	0	0	0	0
Echinopora horrida	1	6	5	3	3	2	0
Fungia klunzingeri	1	5	1	0	0	0	0
Goniastrea minuta	1	0	0	1	0	0	0
Goniastrea spp	1	0	2	1	0	0	0
Hydnophora microconos	1	0	4	2	0	0	0
Isopora palifera	1	2	2	1	0	0	0

Leptoseris explanata	1	1	2	0	0	0	0
Lithophyllon undulatum	1	0	0	0	0	0	0
Pavona divaricata	1	8	11	1	0	0	0
Pavona explanulata	1	3	2	1	0	0	0
Pavona frondifera	2	4	3	0	1	0	0
Pavona verrucosa	1	2	1	1	0	0	0
Plesiastrea versipora	1	2	4	3	0	0	0
Pocillopora danae	1	0	0	0	0	0	0
Pocillopora setchelli	1	8	12	6	0	0	0
Porites nigrescens	1	1	10	7	0	0	0
Sandalolitha robusta	1	3	1	0	0	0	0
Scapophyllia cylindrica	1	3	2	1	0	0	0
Stylaster sp.	1	0	0	0	0	0	0
Stylophora mordax	1	1	0	0	0	0	0
Turbinaria mesenterina	1	1	1	0	1	0	0
Turbinaria sp	1	0	0	0	0	0	0
Acropora tenuis	1	12	14	2	0	0	0
Goniopora somaliensis	0	0	0	1	1	0	1
Acanthastrea brevis	0	0	1	0	0	0	0
Acanthastrea hillae	0	0	3	1	0	0	0
Acropora acuminata	0	0	0	0	1	0	0
Acropora azurea	0	1	3	5	0	0	0
Acropora cerealis	0	6	8	7	1	0	0
Acropora clathrata	0	0	1	7	5	6	0
Acropora cytharea	0	1	2	1	1	0	0
Acropora dendrum	0	0	0	1	0	0	0
Acropora lutkeni	0	1	1	2	0	1	0
Acropora microclados	0	0	0	0	1	0	0
Acropora microphthalma	0	0	0	0	2	1	0
Acropora monticulosa	0	2	3	1	0	0	0
Acropora muricata	0	0	1	1	1	0	0
Acropora paniculata	0	2	1	2	1	0	0
Acropora pulchra	0	0	1	0	0	0	0
Acropora selago	0	0	1	0	0	0	0
Acropora striata	0	2	0	1	0	0	0
Acropora subulata	0	1	4	1	0	0	0
Acropora verweyi	1	6	2	7	1	0	0
Caulastrea furcata	0	3	1	1	0	0	0
Echinopora pacificus	0	1	1	0	0	0	0
Euphyllia aspera	0	0	3	7	1	2	0
Euphyllia cristata	0	2	0	1	0	0	0
Mycedium spp	0	2	1	1	4	0	0
Favites complanata	0	0	0	1	0	0	0

Fungia granulosa	0	1	1	0	0	0	0
Fungia horrida	0	3	1	0	0	0	0
Fungia molluccensis	0	0	2	0	0	0	0
Fungia scruposa	0	5	1	0	0	0	0
Fungia seychellensis	0	1	0	0	0	0	0
Psammocora nierstraszi	2	10	7	7	0	0	0
Gardineroseris planulata	0	0	0	1	0	0	0
Goniopora djiboutiensis	0	0	0	0	0	1	0
Goniopora fruticosa	0	0	1	1	1	0	0
Goniopora sp.	0	0	2	0	0	0	0
Halomitra pileus	0	0	1	0	0	0	0
Isopora brueggemanni	0	0	0	0	1	0	0
Leptastrea pruinosa	0	2	0	0	0	0	0
Leptoseris foliosa	0	0	1	0	0	0	0
Lobophyllia robusta	0	0	1	0	0	0	0
Merulina scabricula	0	2	0	1	0	0	0
Millepora tenella	0	1	0	0	0	0	0
Montipora incrassata	0	1	0	0	0	0	0
Montipora lobulata	0	2	0	0	0	0	0
Montipora vaughani	0	0	4	3	0	0	0
Mycedium elephantotus	0	2	3	3	3	0	0
Mycedium robokaki	0	0	0	1	2	1	0
Oulophyllia bennettae	0	1	4	0	0	0	0
Oulophyllia crispa	0	1	2	0	0	0	0
Oulophyllia sp	0	2	0	1	0	0	0
Pavona sp	0	0	0	1	0	0	0
Pavona decussata	0	1	1	0	0	0	0
Pavona gigantea	0	0	1	0	1	0	0
Pavona minuta	0	2	1	1	0	0	0
Platygyra sp	0	0	1	0	2	0	0
Platygyra contorta	0	1	1	0	0	0	0
Caulastrea echinulata	0	1	0	0	1	0	0
Pocillopora ligulata	0	0	0	2	0	0	0
Pocillopora woodjonesi	0	0	0	5	2	0	0
Porites arnaudi	0	0	0	0	1	0	0
Sarcophyton sp.	0	1	1	0	0	0	0
Sinularia sp.	0	1	2	2	1	0	0
Symphyllia agaricia	0	0	1	0	0	0	0
Symphyllia recta	0	0	2	0	0	0	0
Tubastrea mesenteriensis	0	0	0	1	0	0	0
Pachyseris speciosa	0	1	3	0	2	1	0
Fungia repanda	0	2	1	0	0	0	0

Total	34,883	8234	12878	8511	3942	1098	181	39
Percent	100	23.60%	36.92%	24.40%	11.30%	3.15%	0.52%	0.11%

APPENDIX 4 – Ranking abundances of coral species 1995, 2002, 2018

Row Labels		Row Labels	Sum of N	Row Labels
1995	**14744**	**2002**	**10983**	**2018**
Montipora grisea	3379	Montipora grisea	1439	Montipora grisea
Porites randalli	2635	Montipora nodosa	546	Pavona varians s.l.
Pavona varians s.l.	745 = 5 %	Astrea curta	479	Porites rus
Montipora informis	714	Montipora corbettensis	462	Astrea curta
Galaxea fascicularis	482	Pavona varians s.l.	444 = 4 %	Pocillopora verrucosa
Montipora monasteriata	365	Porites cf horizontalata	401	Pocillopora meandrin
Astrea curta	317	Porites rus	372 = 3%	Pocillopora eydouxi
Pocillopora meandrina	312	Goniastrea retiformis	349	Galaxea fascicularis
Pocillopora eydouxi	301	Montipora venosa	322	Porites massive
Psammocora profundacella	300	Montipora efflorescens	310	Acropora cf glauca
Porites rus	288 = 2%	Galaxea fascicularis	296	Dipsastraea stelligera
Goniastrea edwardsi	279	Leptastrea purpurea	283	Porites deep corallite
Leptastrea purpurea	238	Montipora effusa	253	Montipora informis
Leptoria phrygia	199	Montipora caliculata	250	Pavona chiriquiensis
Dipsastraea stelligera	191	Psammocora haimeana	189	
Astreopora listeri	183	Pocillopora eydouxi	142	Acropora sp.
Isopora crateriformis	169	Leptoria phrygia	138	Porites stephensoni
Porites enc	157	Porites cf lutea	138	Leptastrea transversa
Dipsastraea matthaii	156	Dipsastraea matthaii	134	Lobophyllia hemprich
Montipora hoffmeisteri	154	Pavona venosa	125	Leptastrea purpurea
Montipora efflorescens	122	Pocillopora verrucosa	123	Porites sp. 4
Goniastrea pectinata	120	Isopora crateriformis	120	Porites lutea
Pocillopora verrucosa	120	Montipora danae	114	Porites sp. 1
Astreopora cf. gracilis	102	Acropora valida	111	Merulina ampliata
Acropora samoensis	101	Montipora informis	100	Montipora sp. 4
Montipora tuberculosa	101	Porites lichen	99	Cladiella sp.
Montipora danae	99	Montipora tuberculosa	98	Oxypora lacera
Pavona venosa	99	Montipora hoffmeisteri	97	Pavona maldivensis
Goniastrea retiformis	96	Montipora sp. 1	94	Porites stephansoni
Acropora nasuta	85	Goniastrea edwardsi	89	Coscinaraea columna
Acropora spp	78	Montipora monasteriata	88	Leptoseris mycetoser

Montipora nodosa	77	Dipsastraea stelligera	85	Pavona duerdeni
Montipora turgescens	73	Astreopora listeri	81	Astrea annuligera
Pocillopora damicornis	73	Astreopora myriopthalma	80	Isopora crateriformis
Montipora spp	70	Galaxea astreata	80	Fungia fungites
Favites halicora	65	Acropora sp	76	Millepora platyphylla
Oxypora lacera	64	Montipora foveolata	74	Psammocora contigua
Fungia fungites	63	Pocillopora sp	73	Alveopora tizardi
Montipora foveolata	62	Astreopora myriophthalma	71	Fungia scutaria
Platygyra daedalea	59	Echinopora hirsutissima	70	Acropora aculeus
Porites lutea	58	Platygyra pini	70	Acropora pagoensis
Favites russelli	50	Echinopora lamellosa	67	Dipsastraea matthaii
Acropora danai	49	Montipora calcarea	65	Porites cylindrica
Acropora gemmifera	49	Porites cf solida	61	Pocillopora damicorn
Leptoseris mycetoseroides	49	Astreopora gracilis	59	Hydnophora exesa
Astreopora myriophthalma	46	Leptastrea transversa	57	Fungia concinna
Coscinaraea columna	46	Montipora aequituberculata	55	Goniastrea edwardsi
Pocillopora spp	45	Montipora sp	53	Acropora nasuta
Millepora exaesa	43	Pocillopora meandrina	51	Pocillopora setchelli
Montipora floweri	43	Montipora verrucosa	49	Astreopora cucullata
Cyphastrea chalcidicum	38	Goniastrea favulus	47	Acropora hyacinthus
Dipsastraea pallida	38	Dipsastraea pallida	46	Porites randalli
Echinopora hirsutissima	31	Goniastrea pectinata	45	Astreopora myriophth
Montipora aequituberculata	30	Fungia sp	43	Leptoria phrygia
Stylocoeniella armata	30	Platygyra daedalea	43	Acropora big bulbous
Turbinaria reniformis	29	Porites cf lobata	37	Echinopora hirsutissim
Alveopora spp	28	Porites randalli	33	Tubastraea coccinea
Acropora tenuis	26	Favites abdita	32	Acropora latistella
Alveopora allingi	26	Porites sp	32	Psammocora haimean
Diploastrea heliopora	25	Porites vaughani	32	Acropora digitate sha
Acanthastrea echinata	22	Porites cylindrica	29	Diploastrea heliopora
Acropora hyacinthus	22	Dipsastrea speciosa	28	unknown guentheri
Montipora millepora	22	Goniastrea aspera	28	Cladiella sp.
Merulina ampliata	21	Psammocora profundacella	27	Psammocora nierstras
Phymastrea valenciennesi	21	Leptoseris mycetoseroides	26	Echinophyllia aspera
Psammocora superficialis	21	Stylocoeniella armata	26	Euphyllia aspera
Echinopora horrida	20	Acanthastrea echinata	25	Goniastrea retiformis

Porites nigrescens	19	Merulina ampliata	25	Mycedium sp.
Acropora nana	18	Montipora mollis	25	Acropora cytherea
Dipsastraea favus	18	Pocillopora damicornis	25	Porites monticulosa
Fungia concinna	18	Acropora abrotanoides	22	Acropora abrotanoide
Leptastrea transversa	18	Acropora austera	22	Acropora austera
Galaxea astreata	17	Acropora intermedia	22	green tuberosa
Hydnophora rigida	17	Cyphastrea sp.	22	Pocilloopora verrucos
Acropora cerialis	16	Phymastrea valenciennesi	22	Porites sp. 3
Acropora divaricata	16	Coscinaraea columna	21	Galaxea astreata
Fungia spp	16	Dipsastrea laxa	20	Montipora sp. 5
Cyphastrea serailia	15	Leptastrea bewickensis	20	Acropora cophodacty
Porites densa	15	Lobophyllia corymbosa	20	Acropora gemmifera
Pavona divaricata	14	Lobophyllia hemprichii	20	Acropora retusa
Pavona maldivensis	14	Platygyra sinensis	20	Acropora austera 100
Porites massive	13	Montipora floweri	19	Acropora nobilis
Acropora nobilis	11	Oxypora lacera	18	Favites sp.
Echinopora lamellosa	11	Favites halicora	17	Leptastrea bewickens
Psammocora haimeana	11	Acropora digitifera	16	Montipora capitata
Acropora humilis	10	Acropora humilis	16	Pavona venosa
Lobophyllia hemprichii	10	Alveopora spongiosa	16	Acropora digitifera
Acropora azurea	9	Porites sp. 3	16	Cladiella sp.
Coeloseris mayeri	9	Acropora gemmifera	15	Cyphastrea sp.
Goniastrea australensis	8	Acropora secale	15	Goniastrea pectinata
Pavona clavus	8	Astreopora cucullata	15	Montipora caliculata
Porites annae	8	Acropora hyacinthus	14	Montipora floweri ?
Stylophora pistillata	8	Favites flexuosa	14	Montipora vaughani
Acropora clathrata	7	Porites cf australiensis	14	Oxypora lacera cups
Fungia klunzingeri	7	Acropora latistella	13	Pavona nierstraszi
Hydnophora exesa	7	Acropora akajimensis	12	Platygyra daedalea
Mycedium elephantotus	7	Diploastrea heliopora	12	Platygyra pini
Acropora monticulosa	6	Favites russelli	12	Acropora cerealis
Acropora subulata	6	Goniastrea australensis	12	Acropora globiceps
Goniastrea retiformis	6	Leptastrea sp	12	Acropora humilis
Pavona explanulata	6	Phymastia valenciennesi	12	Acropora sp. 2
Psammocora contigua	6	Acropora verweyi	11	Acropora surculosa
Scapophyllia cylindrica	6	Dipsastraea favus	11	Favites 1010728 101
Acropora aculeus	5	Hydnophora exesa	11	Favites 1010730 101
Acropora cytharea	5	Pavona maldivensis	11	Leptastrea cf purpure
Favites flexuosa	5	Cyphastrea serailia	10	Pachyseris speciosa
Acanthastrea hillae	4	Fungia concinna	10	Pocillopora sp.
Dipsastraea sp.	4	Millepora exaesa	10	Astrea curta/annulige
Fungia danai	4	Acropora samoensis	9	Dipsastraea sp.
Leptoseris explanata	4	Montipora millepora	9	Fungia sp.

Montipora corbettensis	4	Cyphastrea chalcidium	8	Montipora blue
Pavona minuta	4	Montipora cf orientalis	8	Montipora sp. 3
Acropora cf. verweyi	3	Acropora clathrata	7	Montipora tuberculos
Alveopora cf. spongiosa	3	Acropora nasuta	7	Pavona verrucosa
Dipsastraea laxa	3	Acropora retusa	7	Psammocora profund
Distichopora spp	3	Fungia scutaria	7	(blank)
Favites abdita	3	Montipora peltiformis	7	20026 20017
Fungia repanda	3	Pavona divaricata	7	Dipsastraea pallida 1
Goniopora somaliensis	3	Pocillopora woodjonesi	7	faviid .5-.6 60060
Montipora verrucosa	3	Acropora glauca	6	Letastrea purpurea
Oulophyllia crispa	3	Astreopora expansa	6	Montipora thick plate
Sandalolitha robusta	3	Echinophyllia aspera	6	Pavona frondifera
Astreopora spp	2	Turbinaria reniformis	6	Sinularia
Cyphastrea microphthalma	2	Acropora lutkeni	5	Turbinaria mesenteri
Diosastraea stelligera	2	Astrea	5	Acanthastrea sp.
Dipsastaea stelligera	2	Astreopora ocellata	5	Acropora cf retusa
Dipsastraea spp.	2	Oulophyllia bennettae	5	Acropora clathrata
Echinophyllia aspera	2	Acropora paniculata	4	Acropora fused
Favites spp	2	Acropora rosaria	4	Acropora nana
Fungia horrida	2	Fungia scruposa	4	Acropora verweyi
Pavona decussata	2	Hydnophora microconos	4	Astreopora SMOOT
Porites cylindrica	2	Mycedium robokaki	4	Cyphastrea 8090048
Porites lichen	2	Pavona frondifera	4	Dipsastraea sp. 1
Acropora paniculata	1	Porites sp. 4	4	Dipsastraea stelligera
Acropora valida	1	Acropora cf hemprichii	3	Goniopora fruticosa
Astrea annuligera	1	Acropora divaricata	3	Hydnophora microco
Caulastrea furcata	1	Acropora globiceps	3	Isopora palifera
Corallomorph spp	1	Acropora microphthalma	3	Leptastrea pupurea
Diopsastraea stelligera	1	Acropora muricata	3	Merulina scabricula
Dipsastraea speciosa	1	Acropora prolifera	3	Montiora turgescens
Dipsastraeasp.	1	Acropora striata	3	Montipora hoffmeiste
Favites complanata	1	Acropora tenuis	3	Montipora turgescens
Fungia scutaria	1	Alveopora sp	3	Pavona duerdoni
Gardineroseris planulata	1	Euphyllia cristata	3	Plesiastrea versipora
Goniastrea spp	1	Fungia fungites	3	Plesiastrea versipora
Goniopora djiboutiensis	1	Hydnophora rigida	3	Pocillpora setchelli (
Halomitra pileus	1	Millepora cf platyphyllia	3	Pocillpora verrucose
Leptoseris foliosa	1	Mycedium elephantotus	3	Porites blue bumpy
Millepora tenella	1	Porites sp. 1	3	Porites evermanni
n/a	1	Psammocora contigua	3	Porites sm lumpy
Pachyseris speciosa	1	Psammocora superficialis	3	Acropora cf nana
Platygyra pini	1	Astreopora juv	2	Acropora cf nasuta

Platygyra sinensis	1	Caulastrea furcata	2	Acropora clathrata 10
Porites spp	1	Echinopora pacificus	2	Acropora digitate
		faviid	2	Astreopora listeri
		Fungia molluccensis	2	Caulastrea echinulata
		Montipora lobulata	2	Caulastrea furcata
		Oulophyllia sp	2	Dipsastraea 10 mm
		Pavona duerdeni	2	Dipsastraea matthaii 8
		Platygyra contorta	2	Dipsastraea stelligera
		Plesiastrea versipora	2	Dipsastrea matthaii
		Porites napopora	2	faviid 1.0 PB070001
		Psammocora nierstraszi	2	faviid green bottom o
		Symphyllia recta	2	faviid sp. 1
		Acropora aculeus	1	Favites
		Acropora acuminata	1	Favites 1010716 1010
		Acropora cytherea	1	Favites abdita
		Acropora dendrum	1	Fungia granulosa
		Acropora microclados	1	Fungia scruposa
		Acropora pulchra	1	Goniastrea minuta
		Acropora selago	1	Goniastrea sp.
		Astrea annuligera	1	Leptastrea pruinosa
		Astrea sp.	1	Leptoseris ??
		Cyphastrea micropthalma	1	Montipora floweri
		Favites (spinosa?)	1	Montipora grosea sp.
		Fungia horrida	1	Montipora sp. 1
		Goniopora sp.	1	Montipora sp. 1 1012
		Lithophyllon undulatum	1	Montipora venosa
		Montipora incrassata	1	Montopira cf. tubercu
		Pocillopora danae	1	Pavona cf frondifera
		Pocillopora eydouxi	1	Pavona gigantea
		Stylocoeniella guentheri	1	Pavona haimeana
		Stylophora mordax	1	Platygyra pini 101072
		Turbinaria sp	1	Playgyra daedalea
				Plesiastrea versipora
				Pocillopora
				Pocillopora brevicorn
				Pocillopora breviseria
				Pocillopora cf verruco
				Pocillopora ligulata
				Porites densa 8090039
				Porites horizontallata
				Porites rus
				Porites rus ?
				Sandalolitha robusta

Sarcophyton sp.
Sinularia sp.
Turbinaria reniformis
80900010 8090011 8
Acanthasrea brevis
Acanthasrea sp.
Acanthastrea echinata
Acropora glauca
Acropora humilis 600
Acropora humilis 600
Acropora intermedia
Acropora not rosette
Acropora paniculata
Acropora photo
Acropora photo 1
Acropora photo 2
Acropora photo 3
Acropora setchelli
Acropora sp. 1
Acropora sp. 7
Acropora surculosa
Cantharellus sp.
Cyphastrea
Cyphastrea 8090043
Dipsastraea annuliger
Dipsastraea favus
Dipsastraea heliantho
Dipsastraea mathaii
Dipsastraea matthaii
Dipsastraea stelligera
Echinopora lamellosa
faviid .6-1.0 300219
faviid 0.3 60087
faviid 0.5 cm deep ga
faviid 1.0 290073
faviid 1.0-1.5 290074
faviid 60054 deep cai
0.7 cm
faviid 60087
faviid brown 0.5 8080
faviid PB070006 = 00
Favites 8080029
Favites .3-.4 290048

Favites .7-1.0 290073
Favites 1,1-1.6 3103
Favites 1.0 8080027
Favites 1.0-1.5 30021
Favites 1.5 cm 60068
Favites sp
Fungia 1010732
Fungia horrida
Fungia seychellensis
Galaxea
Galaxea sp.
Goniastre retiformis
Goniastrea sp
Goniopora sp.
Isopora brueggemann
Leptastrea
Leptastrea
Leptastrea purpurata
Leptastrea sp.
Leptoseris transversa
Lobophyllia robusta
Montipora 290075
Montipora 60086
Montipora caliculata
Montipora caliculata
Montipora cf tubercu
Montipora cf venosa
Montipora even tufts
Montipora nierstraszi
Montipora sp.
Montipora sp. 4
Montipora sp. 5 8090
Montipora venosa P
Montipors sp. 4
Montopora caliculata
Mycedium elephanto
Oulophyllia 1010717
Pammocora nierstras
Pavona 8090005 809
Pavona chiriquiensis
Pavona chiriquiensis
Pavona contigua
Pavona duerdeni

Pavona explanulata
photo Acropora (whic
Platygyra PB070008
Platygyra daedalea
Platygyra pini-like
Platygyra sp. 80800
Platygyra sp. 808003
Pocillopora eydouxi?
Porites arnaudi
Porites bumpy deep
Porites cf. evermanni
Porites lutea
Porites sm rough
Porites sp
Porites yellow moun
Psammocora nierstas
Scapophyllia cylindri
Stylaster sp.
Stylophora mordax
Symphyllia agaricia
thick thumb bulbous
Tubastrea mesenterie