

# CONSERVATION & ACTIVE RESTORATION OF GUAM'S STAGHORN *ACROPORA* CORALS

L.J. Raymundo, M.D. Andersen, C. Moreland-Ochoa, A. Castro,  
C. Lock, N. Burns, F. Tajeron, D. Combosch, D. Burdick



UNIVERSITY OF GUAM MARINE LABORATORY  
TECHNICAL REPORT #168. March 2022





---

## Table of Contents

<b><i>Tables</i></b>	<b>3</b>
<b><i>Figures</i></b>	<b>3</b>
<b><i>Background and Objectives</i></b>	<b>4</b>
<b><i>Staghorn Acropora on Guam</i></b>	<b>6</b>
<b><i>Current Extent and Condition of Staghorn Populations on Guam</i></b>	<b>7</b>
Survey Methods	9
Current Staghorn Extent and Condition	9
<b><i>Guam’s Coral Ocean Nurseries</i></b>	<b>12</b>
Piti Bomb Holes Coral Nursery	13
Merizo Coral Nursery	17
<b><i>Outplanting Activities</i></b>	<b>18</b>
Outplanting on Hard Substrate	19
Outplanting on Soft Substrate	21
<b><i>Genetic Work to Inform Restoration Efforts</i></b>	<b>24</b>
Resolution of taxonomic questions of staghorn <i>Acropora</i>	24
Population genetics	25
Genotyping of all nursery populations	25
<b><i>Interagency Cooperation</i></b>	<b>26</b>
<b><i>Acknowledgements</i></b>	<b>27</b>
<b><i>References</i></b>	<b>28</b>
<b><i>Appendix One: Summaries of Current Staghorn Populations on Guam</i></b>	<b>30</b>

---

## Tables

- Table 1. Reported estimated extent of staghorn *Acropora* populations in Guam reef flats and lagoons
- Table 2. Current extant wild populations of staghorn morphospecies on Guam. Numbers presented at each site in parentheses refer to site locations on Figure 4
- Table 3. Source populations of the staghorn morphospecies in culture within the Piti Bomb Holes Coral Nursery
- Table 4. Mean growth rates of five suspended populations of staghorns monitored in the Piti Bomb Holes coral nursery for two years; MEV = monthly elliptical growth rate, after Kiel et al. (2012). *From:* Burns (2018) M.S. Thesis
- Table 5. Mean growth rates of monitored species in the Piti Ocean Coral Nursery
- Table 6. Mean growth rates for species grown in the Merizo Ocean Coral Nursery

## Figures

- Figure 1. Island-wide causes of mortality in staghorn *Acropora* from 2013 to 2017
- Figure 2. Diseases and overgrowths of staghorn *Acropora* on Guam
- Figure 3. Putative morphospecies of staghorn *Acropora* currently found on Guam
- Figure 4. Map of Guam showing the sites surveyed for extent and condition of staghorn populations
- Figure 5. Resheeting of new tissue over dead skeleton
- Figure 6. Coral species recruited onto staghorn skeleton and rubble
- Figure 7. Location of Guam's ocean coral nurseries
- Figure 8. Coral nursery structures deployed in Guam, to date
- Figure 9. Herbivory in the Piti Coral Ocean Nursery
- Figure 10. Silt impacts in the Merizo Coral Ocean Nursery
- Figure 11. Maps showing locations of current outplanting sites
- Figure 12. Outplanting on the Piti southwestern reef flat
- Figure 13. A nursery-reared fragment of *A. aspera*, outplanted to Cocos Lagoon pavement
- Figure 14. Use of C-frames to provide stable substrate for outplanting into unstable sand or rubble substrates
- Figure 15: Rope nursery use
- Figure 16. Creating and managing the curated coral collection
- Figure 17: Sampling for genotyping and population genetics
- Figure 18. Interagency personnel efforts

---

## Background and Objectives

Following an unprecedented decline in global coral populations in response to climate change and local stressors, efforts by local governments and institutions to mitigate further loss of reef biodiversity have gained traction. This has largely been enacted through reef restoration and conservation, with increasing financial incentives to protect local marine resources and tourism industries.

In the 1960s, Guam's island-wide live coral cover was estimated at 50% (Randall 1971); by the 1990s, it had decreased to less than 25% (Birkeland 1997). A NOAA Rapid Ecological Assessment conducted in 2005 confirmed this with a mean value of 26% cover for Guam's reefs (Burdick et al. 2008). Coral communities have continued to decline in response to multiple and simultaneous local anthropogenic impacts: siltation, eutrophication, and road runoff combine to lower water quality; overfishing removes herbivores and, thus, the control on macroalgae; and Crown-of-Thorns sea star outbreaks wipe out entire reef slope communities (Burdick et al. 2008). These combined local stressors have resulted in a chronic degradation of the structure and productivity of Guam's reefs.

From 2013 to 2017, Guam further experienced a series of coral mortality events initiated by warming sea surface temperatures that induced mass bleaching and subsequent island-wide staghorn mortality estimated at 53% across this three-year time period (Raymundo et al. 2017). The first event began in July 2013 and extended into October, causing 85% of Guam's coral taxa to bleach (Reynolds et al. 2014). Subsequent island-wide bleaching events occurred in 2014, 2016, and 2017. In addition, extreme low tide events, associated with the ongoing ENSO that triggered 2014 bleaching, caused additional mortality to shallow water reef flat coral communities beginning in 2014 and extending into 2015 (Heron et al. 2020). Localized White Syndrome disease outbreaks in Guam's staghorn corals further exacerbated extensive mortality in 2016 and 2017. These events are also summarized in Raymundo et al. (2019); an estimated 37% of coral on shallow reef flats was lost within this five-year period (Figure 1).



**Figure 1.** Island-wide causes of mortality in staghorn *Acropora* from 2013 to 2017: A. Severe bleaching, 2017, Apra Harbor; B. Subaerial exposure from ENSO-related extreme low tides, 2014-2015, Togcha reef flat; C. White Syndrome disease outbreak, 2016 and 2017, Tumon Bay. Photos: D. Burdick, V. Lapacek, L. Raymundo.

In response to the 2013 mass bleaching, Guam's marine management entities (University of Guam Marine Lab, Bureau of Statistics and Plans, Guam Environmental Protection Agency, Department of Aquatic and Wildlife Resources) recognized the need for developing a new strategy that would

---

guide science and management in an era of rapid environmental change. Activities included the implementation of pilot studies to develop ecological restoration techniques suitable to Guam's typhoon-controlled reef communities, and these studies continued through subsequent events. Mitigation, nursery culture, and active restoration were recognized as essential to managing Guam's remaining corals, while the protection of Guam's five Marine Preserves alone was deemed no longer sufficient to ensure the sustainability of its coral reefs and their essential functions. By 2017, Guam had developed a Bleaching Response Plan (Hoot and Burdick 2017) and a Crown-of-Thorns Response Plan (Hoot 2017), and by 2018, a Coral Reef Resilience Strategy was completed (Hoot 2018). Through 2020 and 2021, a Reef Restoration Working Group was formed, led by W. Hoot and composed of representatives of the Bureau of Statistics and Plans, Department of Agriculture, Guam EPA, NOAA, and UOG. This group created an action plan for reef restoration under the guidance of a program initiated by The Nature Conservancy (Hoot et al. 2021).

Active coral restoration on Guam began in 2013, with a coral ocean nursery established within the Piti Bomb Holes Marine Preserve to grow out newly settled corals spawned and settled onto tiles in the UOG Marine Lab *ex situ* facility during a workshop held by SECORE International. In 2015, the nursery was co-opted to house fragments of staghorn *Acropora* corals from populations that had survived the 2013 and 2014 bleaching events, on the premise that these populations represented potentially resilient stock. Since that time, efforts have expanded to include more populations, species, and experimental nursery structures to house them.

The science of ecological restoration is relatively new and its development is ongoing and responsive to recent world-wide catastrophic declines in many of the world's ecosystems (Young et al. 2005). The Society for Ecological Restoration defines ecological restoration as "*the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed*" (<https://www.ser-rrc.org/what-is-ecological-restoration/>); a definition that accurately encompasses the approach and process undergone to address the problems of reef decline in Guam. Coral reef restoration has borrowed heavily from forest restoration concepts due, in part, to similarities in life history strategies and ecological function between trees and corals (Epstein et al. 2003). Both are habitat structuring species and both exhibit clonality and indeterminate growth. Similarly, coral restoration has frequently employed the use of ocean nurseries as grow-out facilities for both sexual and asexual colony sourcing. Ocean nurseries provide a refuge culture environment that can increase both survival and growth of coral fragments (Rinkevich 2005), which translates into less impacts on wild populations as smaller fragments can be collected and grown out to transplantable size.

The principle objectives of Guam's coral ocean nurseries were identified through in-depth discussion among local experts and representatives of management agencies, in response to mass mortality documented during the successive events of 2013-2017. In addition, community information meetings were held for the Merizo nursery, located in Cocos Lagoon, to achieve community support. The following nursery objectives were developed as a result of these discussions:

- *to provide refugia for species at risk of extirpation, particularly those that are currently very rare due to recent mortality events;*

- 
- to provide a cultured stock of corals from surviving populations that can be pruned and outplanted for replenishment of degraded populations; and
  - to preserve material for genetic research related to population structure, diversity, endemism, and population-level responses to environmental change.

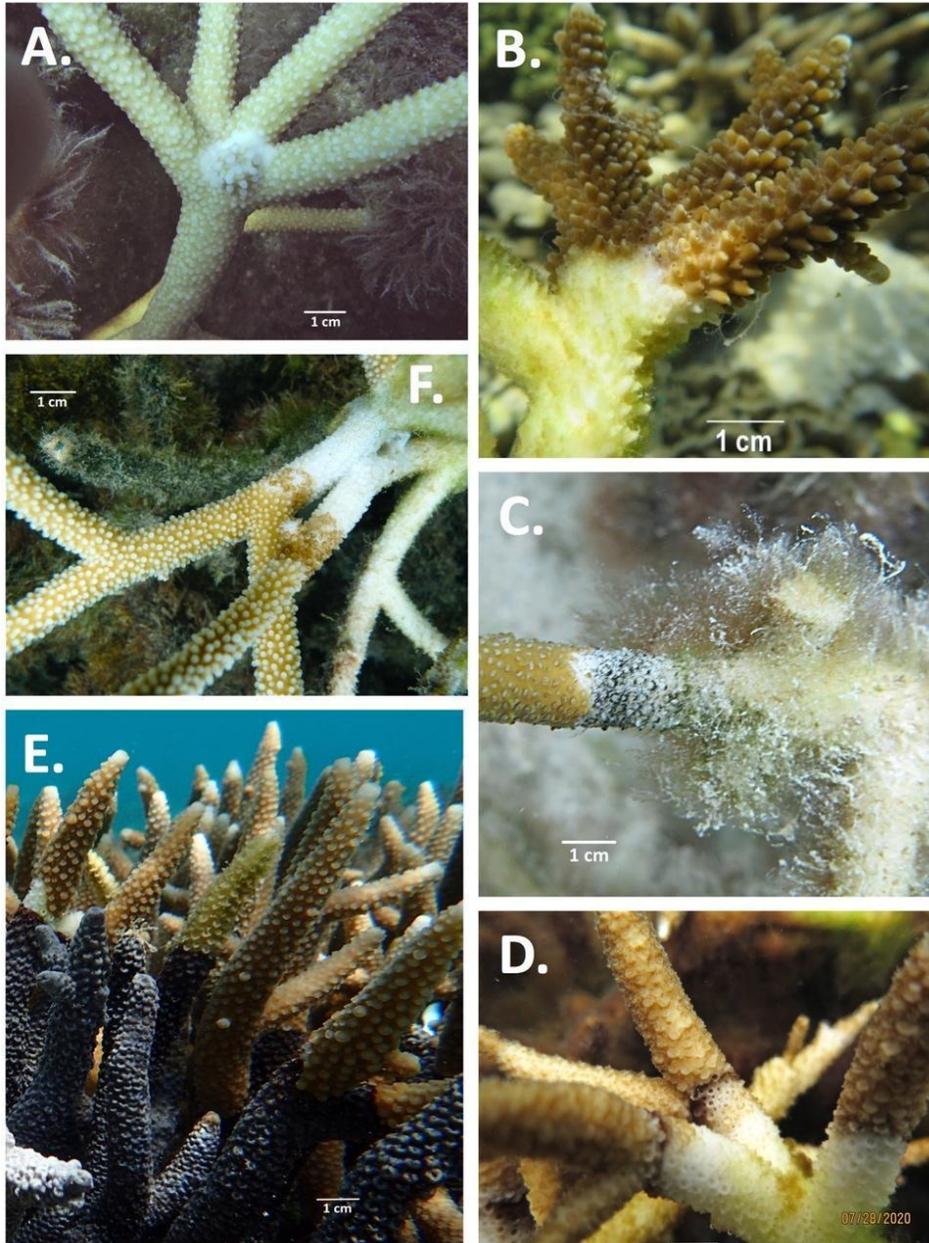
This report summarizes the current state of these nurseries and restoration efforts on Guam.

## Staghorn *Acropora* on Guam

The current focus of restoration efforts on Guam is on vulnerable populations of staghorn *Acropora*, known for their rapid growth rates that facilitate their recovery after stress events (Boyett et al. 2007; Herlan and Lirman 2008). In addition, they are ecologically important as architects of complex habitats (Johnson et al. 2011) and as coastal wave buffers (Kuffner and Toth 2016). On Guam, they are generally located in accessible areas; principally on wide, shallow reef flats where they form extensive and locally charismatic communities favored by snorkelers. As fragmentation is part of their life history as an asexual means of reproduction (Tunncliffe 1981; Smith and Hughes 1999), this facilitates their collection and rearing. Many of these characters, however, make them highly vulnerable to heat stress (Loya et al. 2001; Raymundo et al. 2019), predation (Miller 2001), and infectious disease (Palmer et al. 2008; Joyner et al. 2015). Staghorn species are a favored host of the corallivorous gastropod *Drupella* spp. (Moyer et al. 1982; Tsang & Ang 2015), as well as farming *Stegastes* damselfish, and are threatened by Crown-of-Thorns seastar *Acanthaster planci* (De'ath & Moran 1998; Pratchett 2007; Caballes 2009). They are susceptible to the following coral diseases: *Acropora* White Syndrome (Myers and Raymundo 2009), Black Band Disease (this report), growth anomalies, Skeletal Eroding Band (Myers and Raymundo 2009), Brown Band Disease (Nicolet et al. 2013), as well as overgrowth by the aggressive, coral-killing sponge *Terpios hoshionota* (this report; Figure 2). Extensive nearshore thickets were decimated in the 1960s and 1970s by coastal development projects and typhoons (M. Gawel, pers. comm.) and failed thereafter to recover, creating rubble-dominated substrates in many nearshore reef flat zones along the western coast. Despite these chronic and acute stressors, extensive populations continued to thrive in certain areas, covering a total estimated area of 33.3 ha prior to 2013. That area was reduced to an estimated 17.8 ha by 2015 (Raymundo et al. 2017). The most recent estimate of extent and condition is presented in the next section.

All things considered, Guam staghorns represented a tractable group for developing an island-wide restoration strategy and testing protocols that can later be adopted for other species and community types. Guam's staghorn populations have shown differential responses to stress, with some populations recovering quickly and others showing increasing decline to 100% mortality (Raymundo et al. 2017). This suggests that studies to better understand the nature and cause of these differences, hypothesized to be the result of species level, within-species genotypic, and environmental factors, would be of use in developing a management strategy for this critically important group of reef-building species.

At present, there are eight recorded putative species of staghorn on Guam (Figure 3): *Acropora* cf. *pulchra*, *A. muricata*, *A. acuminata*, *A. aspera*, *A. teres*, *A. vaughani*, *A. austera*, and *A. virgata*. However, current taxonomic identification is based on morphological characters which may not



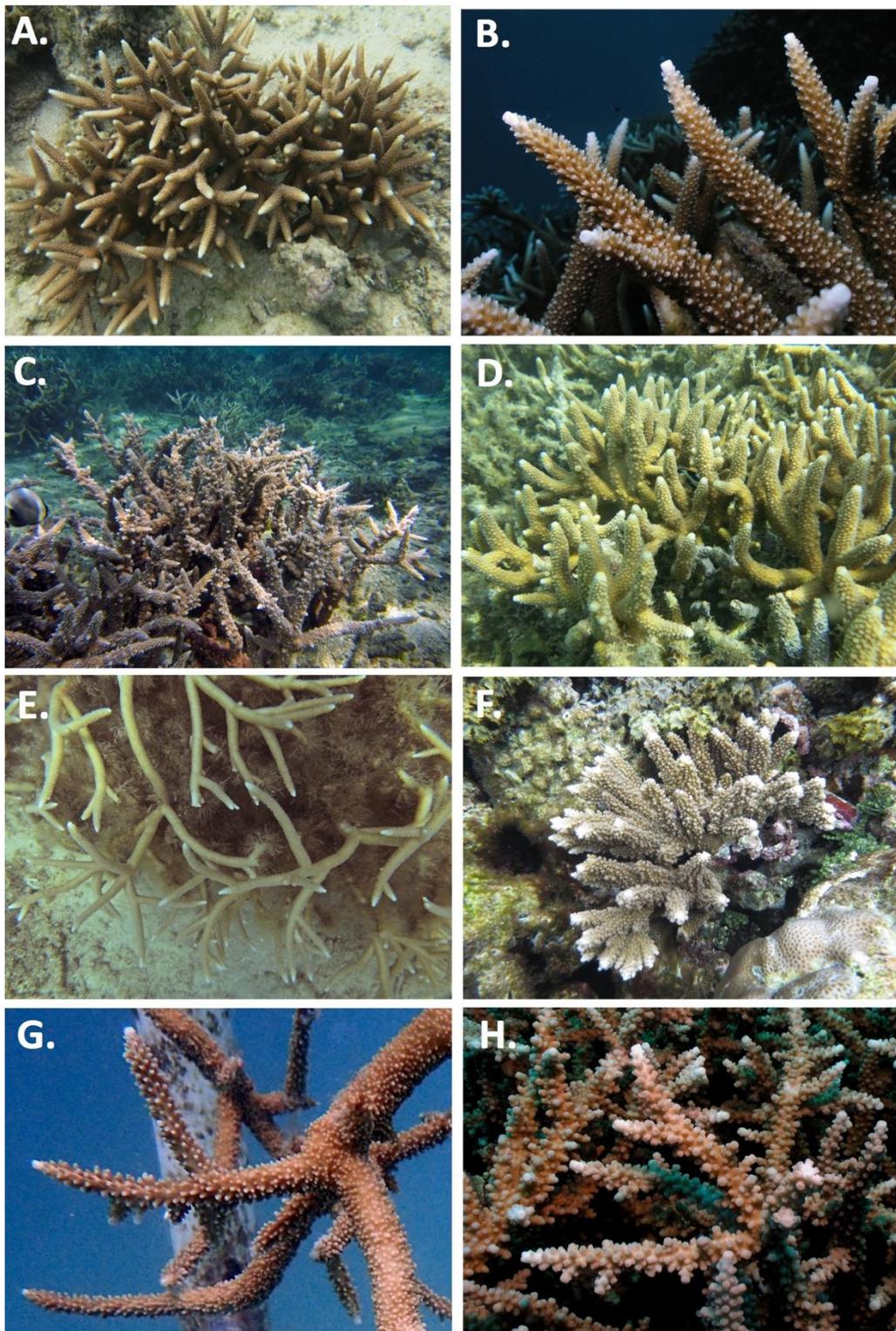
**Figure 2.** Diseases and overgrowths of staghorn *Acropora* on Guam: A: growth anomaly; B: *Acropora* White Syndrome; C: Skeletal Eroding Band found on a colony that is also affected by the farming damselfish *Stegastes nigricans*; D: Black Band Disease; E: *Terpios* overgrowth; F: Brown Band Disease. Photos: L. Raymundo

known staghorn populations in Guam; results are summarized in Raymundo et al. (2017, 2019). However, in an attempt to establish a more current reference against which to measure success of restoration work, a third set of surveys was conducted in 2020-21. Methods and results are presented here.

match descriptions of these species known from other areas. Original descriptions provided in Randall and Myers (1983) have been updated and certain names changed to adhere to these updated descriptions. The need to resolve these identifications using molecular tools is clear; for instance it is unknown if any of these species are endemic to Guam. We discuss these challenges further in the section on *Genetic Work to Inform Restoration*, below.

### Current Extent and Condition of Staghorn Populations on Guam

Two surveys were conducted in 2015 and 2017 during mass mortality events, to track mortality and change in condition of



**Figure 3.** Putative morphospecies of staghorn *Acropora* currently found on Guam: A: *Acropora* cf. *pulchra*; B: *A. acuminata*; C: *A. muricata*; D: *A. aspera*; E: *A. teres*; F: *A. austera*; G: *A. virgata*; H: *A. vaughani*. Photos: L. Raymundo and D. Burdick.

---

## Survey Methods

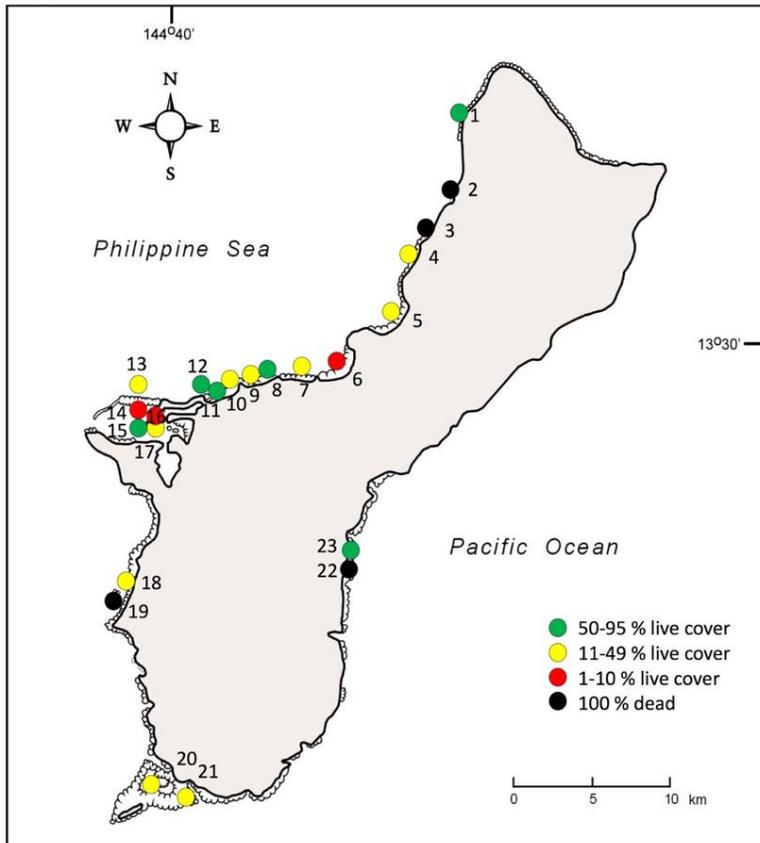
A total of 23 sites were surveyed, encompassing all known areas that either currently support staghorns or had existing populations prior to 2013-2017 mortality events (Figure 4). At each site with contiguous staghorn beds, a snorkeler with a hand-held GPS unit swam around the periphery of the staghorn community, tracking the path to create a polygon of the spatial extent within which staghorns were found. To determine the area within each polygon was inhabited exclusively by staghorns, replicate Point Intercept Transects (PITs) were laid perpendicular to shore, bisecting the polygon at 5m - 10m intervals, depending on the size of the polygon. Transects were read and computed for percent cover of each for the following benthic categories: Staghorn Coral (live and dead), Other Live Coral, Dead Coral, Rubble, Pavement, and Sand. Simultaneously, replicate 0.25 m<sup>2</sup> quadrats (n=16 points/quadrat) were read along transects within each staghorn thicket at 1 m - 2 m distances for Species Composition and Percentage Live vs. Dead Staghorn. Notes on cause of mortality were also taken if it could be ascertained. To further characterize each population, colony sizes were binned into *scattered colonies* (0.25 m-4 m diameter), *thickets* (contiguous growth 4 m-20 m diameter); and *super thickets* (contiguous growth >20 m diameter). Estimated mean extent of staghorn was determined by multiplying the traced polygon size by the percentage cover of staghorns (live and dead) within the polygon. At sites where staghorn colonies were scattered among other species, a systematic search pattern was used to locate all colonies, which were then measured and processed using quadrats and the method described above. Spatial coverage of staghorns was then computed by adding all estimated colony sizes.

## Current Staghorn Extent and Condition

Figure 4 presents our estimates of percent live cover of each population (obtained from quadrat sampling), binned into four percent-cover categories. Summaries of the estimated size, species composition, percentage cover and condition of these beds are presented as one-page descriptions in Appendices at the end of this report. The total spatial extent of staghorns within Guam's shallow reef flats and lagoon was estimated at 134,702.25 m<sup>2</sup>, or 13.5 ha, with a mean live staghorn cover across all sites at 33.9% ± 21.4%. Our surveys were considerably more detailed than those previously undertaken during our rapid assessments (Raymundo et al. 2017) and included additional sites and areas not previously surveyed. Two sites in particular, Urunao and Agat Cemetery (Fig. 4), merit mention. Urunao, the northernmost staghorn site, was a previously unknown population and had not been included in past surveys. The Agat Cemetery site was much more extensive than we had previously observed; both of these sites added to our estimation of current coral cover. Nonetheless, our estimates show a marked decline between 2013 and 2021, with continued loss beyond 2017 (Raymundo et al. 2019) (Table 1). The increase in estimated extent from 2015 to 2017 surveys was likely a combination of more refined methods that increased our accuracy beyond the very rapid 2015 surveys, as well as limited recovery. However, our most recent 2021 survey has documented additional loss after the 2017 bleaching season; two populations that we surveyed in 2017, Double Reef and Shark's Hole, were completely devoid of staghorns that were present in 2017. Extensive dead areas of large thickets, such as those in Achang, West Agaña, and Tumon, have also failed to recover.

**Table 1.** Reported estimated extent of staghorn *Acropora* populations in Guam reef flats and lagoons

Survey Year	Estimated Extent	Source
pre-2013	33.3 ha	Burdick, 2005-2010 unpubl. surveys
2015	15.8 ha	Raymundo et al. 2017
2017	21.3 ha	Raymundo et al. 2019
2020-21	13.5 ha	<i>This report</i>



**Figure 4.** Map of Guam showing the sites surveyed for extent and condition of staghorn populations. See Table 2, below, for site names. Percent live cover refers to the amount of live staghorn relative to the total amount of staghorn present within a mapped polygon.

the persistence of these large thickets may be in question, particularly in the shallowest reef flat areas. In contrast, dead skeleton and rubble patches acted as recruitment surfaces for *Pavona* spp., *Pocillopora damicornis*, *Porites rus*, and *Leptastraea purpurea* (Figure 6). As these species are currently very common on many reef flat communities, it is possible that their spatial dominance is due to past community shifts from former staghorn-dominated communities during previous mortality events.

Table 2 lists locations of current populations of the morphospecies (i.e., species identified by morphological characteristics) currently extant on Guam. We also include records of known past locations. Sources of mortality that could be ascertained include probable bleaching mortality, damage by farming damselfish territories (*Stegastes* spp.), extreme low tide exposure, bleaching, *Drupella* predation, Brown Band Disease, and *Acropora* White Syndrome.

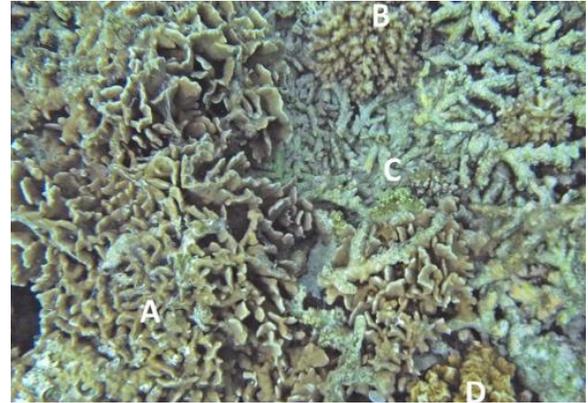
Finally, our surveys revealed interesting patterns of recovery. In extensive thickets, large areas of dead standing skeleton persisted in the thicket centers, with healthy tissue limited to the thicket periphery. Resheeting of tissue over this skeleton was common (Fig. 5), but in thickets seasonally exposed to extreme low tides, this tissue also repeatedly died back during the summer months. This strongly suggests that the

**Table 2.** Current extant wild populations of staghorn morphospecies on Guam. Numbers presented at each site in parentheses refer to site locations on Figure 4. Data are based on observations as of 2022.

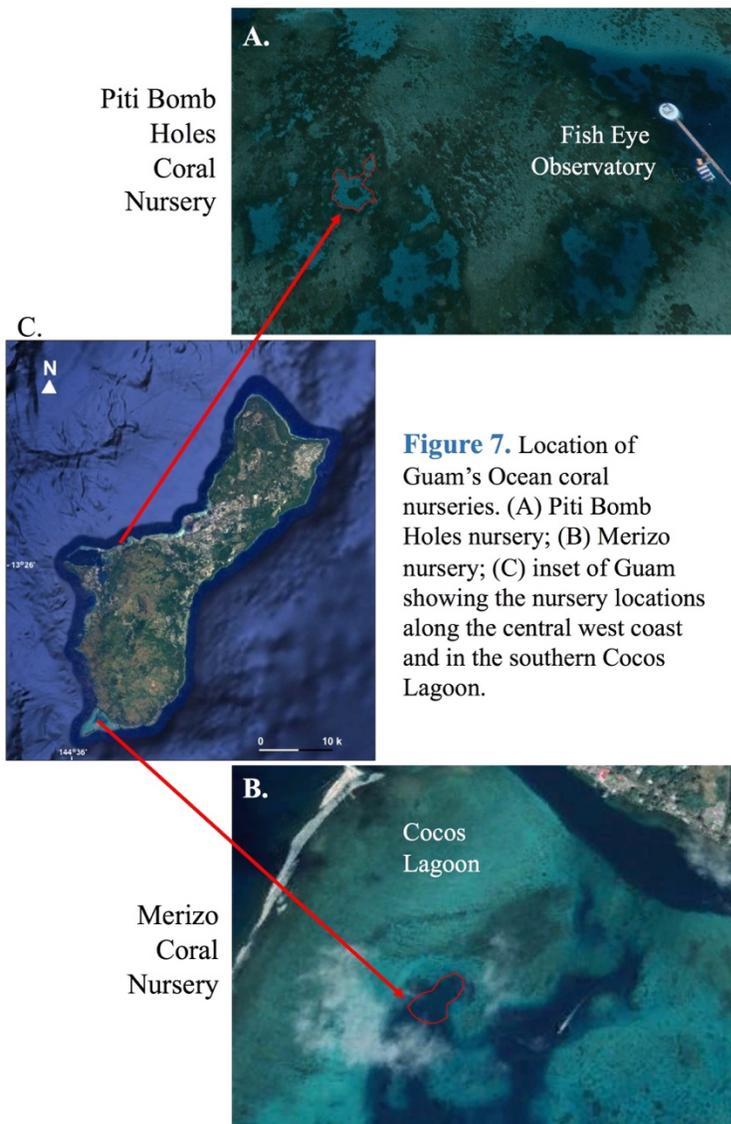
Staghorn Morphospecies	Locations of Current Populations	Additional Pre-2013 Previous Populations
<i>Acropora cf. pulchra</i>	Urunao (1), Tanguisson (4), Tumon Bay (5), East Agaña (6), West Agaña (7), Adelup Governors (8), Adelup NPS (9), Piti Bomb Holes (10-12), Luminao (13), Agat Cemetary (18), Achang (21), Togcha (23)	Alutom Is., Calvo Beach (D. Burdick pers. obs.)
<i>Acropora teres</i>	Piti Bomb Holes (10), Achang (21), West Agaña (7)	Tumon Bay, Cocos Lagoon (Randall & Sherwood 1982; D. Burdick pers. obs.)
<i>Acropora muricata</i>	Luminao (13), Agat Cemetary (18), Apra Harbor (16,17; Western Shoals, Big Blue), East Agaña (6)	Tumon Bay, Piti Bomb Holes, Sharks Hole, Cocos Lagoon (Randall & Sherwood 1982; D. Burdick pers. obs.)
<i>Acropora virgata</i>	Apra Harbor (adjacent to 14; Polaris Point), Cocos Lagoon (20)	Apra Harbor (Dogleg Reef), Piti Bomb Holes (D. Burdick pers. obs.; Randall & Sherwood 1982)
<i>Acropora austera</i>	Apra Harbor (15-17) (Western Shoals, Big Blue, Gabgab)	Double Reef, Haputo Bay, Sharks Hole, Tumon Bay, Anae Island (D. Burdick & L. Raymundo, pers. obs.)
<i>Acropora acuminata</i>	Tumon Bay (5)	Piti Bomb Holes, Double Reef, Sharks Hole, Agat Cemetery/Ga'an Pt., Apra Harbor (Western Shoals), East and West Agaña (USACE, 1989), Cocos Lagoon (Randall and Sherwood, 1982)
<i>Acropora aspera</i>	Achang (21)	Alutom Island (D. Burdick pers. obs.)
<i>Acropora vauhani</i>	Apra Harbor (15,17) (Gabgab Two, Big Blue)	Apra Harbor (Western Shoals) (D. Burdick pers. obs.)



**Figure 5.** Resheeting of new tissue (red arrows) over dead, weathered skeleton in 2017, after previous bleaching mortality. Photo: L. Raymundo



**Figure 6.** Coral species recruited onto staghorn skeleton and rubble: A: *Pavona decussata*; B: *Pocillopora damicornis*; C: *Porites rus*; D: *Pavona divaricata*. Photo: L. Raymundo.



**Figure 7.** Location of Guam's Ocean coral nurseries. (A) Piti Bomb Holes nursery; (B) Merizo nursery; (C) inset of Guam showing the nursery locations along the central west coast and in the southern Cocos Lagoon.

## Guam's Coral Ocean Nurseries

Selection of sites for the nurseries was made via in-depth consultation and discussion among reef managers and scientists from the University of Guam Marine Laboratory, Guam Bureau of Statistics and Plans, Underwater World, NOAA, Guam EPA, and SECORE International. Sites that provided refuge from Guam's history of major typhoons, *Acanthaster planci* outbreaks, water quality, and potential human interference with nursery structures were considered top priority, despite the collective awareness that such sites would differ in depth, water motion, and temperature regime from source and recipient reef sites. Ease of access to the site was also considered essential to facilitate maintenance and fragment collection, and reduce overall costs. Two nurseries have been established on Guam: the Piti Bomb Holes Coral Nursery and the Merizo Coral

Nursery (Figure 7) (USACE permits 2013-00149.20200320 for the Piti nursery and 2017-00049.20200320 for the Merizo nursery).

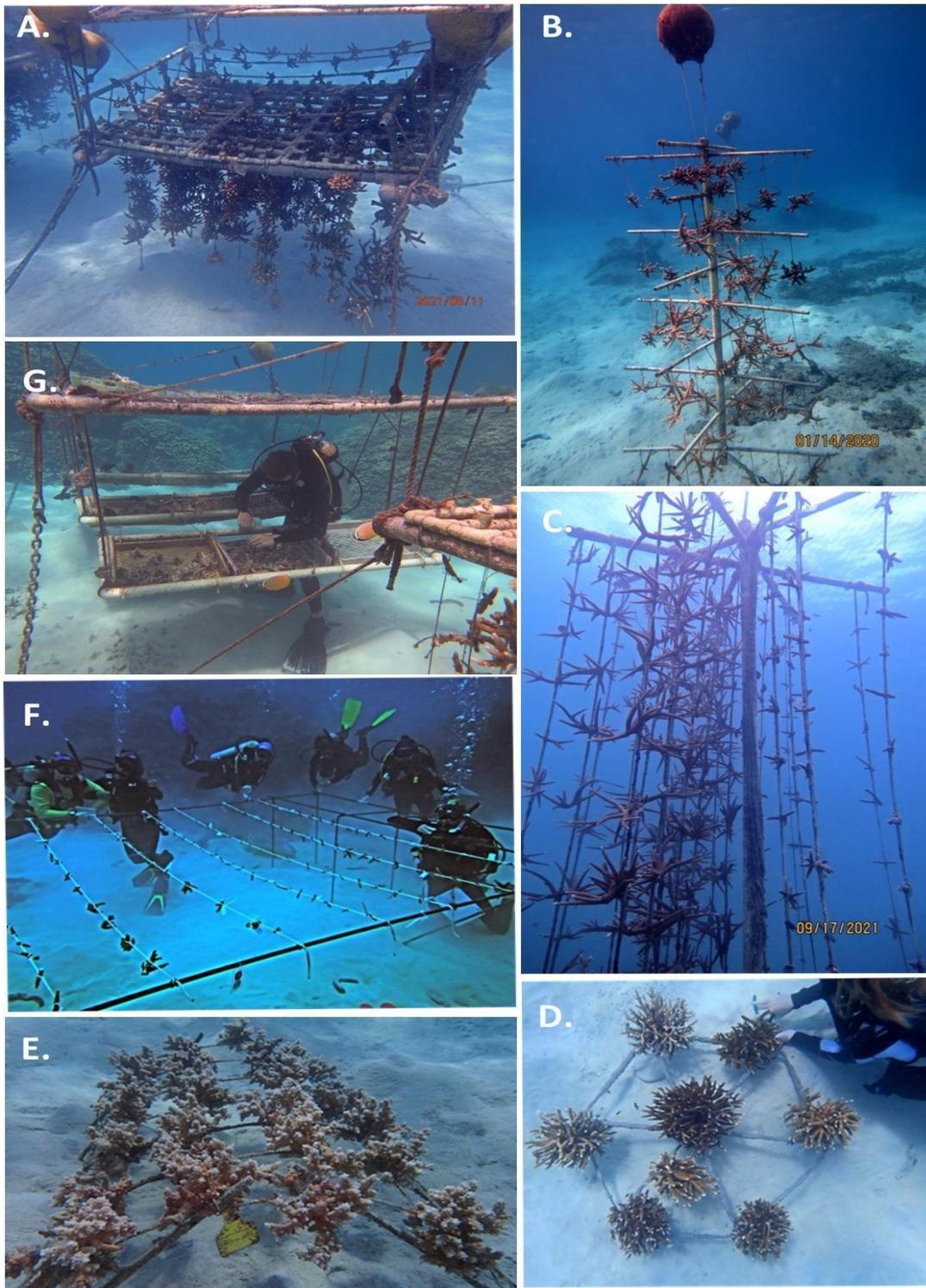
### Piti Bomb Holes Coral Nursery

Piti Bomb Holes was the top choice for the first nursery, as the karst sinkholes provide sufficient depth (4 -7 m), refugia from *A. planci*, sufficient water circulation, low sedimentation, and Marine Preserve status. The Piti Bomb Holes Coral Nursery was established in 2014, permitted under US Army Corps of Engineers and Guam Dept. of Aquatic and Wildlife Resources. The nursery is situated within a sinkhole at 4m depth (Figure 7a) and consists of nursery grow-out structures and prototype substrate provisioning structures. Structures for fragment grow-out and pruning include four tables, nine trees, and one rope nursery (Figure 8 A,G,B,F). Structures that provide an attachment and stability for corals growing in sand or rubble (i.e., substrate provision) are populated with fragments that are not pruned and are allowed to grow into reproductive colonies. These structures include nine A- and C-frames anchored in sand and four spiders (Figure 8 D,E). And, while the numbers of fragments housed in the nursery changes over time, together, these structures currently support approximately 1,700 fragments sourced from wild populations listed in Table 3.

**Table 3.** Source populations of the staghorn morphospecies in culture within the Piti Bomb Holes Coral Nursery.

Source Population	Species
Tanguisson	<i>Acropora</i> cf. <i>pulchra</i>
Agat Cemetary	<i>Acropora</i> cf. <i>pulchra</i> , <i>A. muricata</i>
West Agaña	<i>Acropora</i> cf. <i>pulchra</i>
Babi Is. reef flat (Achang)	<i>Acropora aspera</i> , <i>A. cf. pulchra</i>
Shimizu Beach (Togcha)	<i>Acropora</i> cf. <i>pulchra</i>
Piti Bomb Holes	<i>Acropora teres</i>
Tumon Bay	<i>Acropora</i> cf. <i>pulchra</i> , <i>A. acuminata</i>
Apra Harbor	<i>Acropora austera</i> , <i>A. virgata</i> , <i>A. vauhani</i>
Luminao	<i>Acropora muricata</i>
Urunao	<i>Acropora</i> cf. <i>pulchra</i>

Tables accommodate hanging and upright fixed fragments where additional species may be added, such as massive, digitate, or corymbose species. One table houses settlement tiles held in suspended trays; the top of this table is set aside for quarantine of fragments or short-term experimental trays. Over time, crustose coralline algae have recruited to all PVC<sup>®</sup> structures and a resident herbivorous fish population controls algal growth (Figure 9), eliminating the need for cleaning. During bleaching season, shade cloths are installed, which has greatly reduced or prevented bleaching in nursery fragments relative to bleaching in the surrounding reef. A nursery bleaching census of the shaded tables conducted during the mass bleaching event of 2017 showed that 65% of fragments were fully pigmented, 31.6% were slightly pale, and only 0.3% were completely bleached with partial mortality (Raymundo & Combosch, unpubl. census).



**Figure 8.** Coral nursery structures deployed in Guam, to date. A: coral table with prototype rope nursery and shade cloth; B: coral tree; C: chandelier; D: spider; E: C frame; F: rope nursery; G: coral table with recruitment tile rearing tables. Photos: L. Raymundo, F. Tajeron, C. Moreland-Ochoa, M. Andersen.

Burns (2018) examined growth rates among initial nursery populations. In general, survival of fragments in the nursery was high (90.5%); the highest source of mortality was detachment from the structure and subsequent burial by sand (71% of mortality). White Syndrome coral disease also accounted for 24% of the mortality observed and an additional 4.5% died from fish predation. Fragments suspended on lines below the tables grew significantly faster than those affixed upright on the top of the tables. Growth differences between species and between populations of *A. cf. pulchra* were observed using an ellipsoid volume (EV) measurement (Kiel et al. 2012), a non-destructive method of assessing three-dimensional volume of a branching morphology:

$$EV = (4/3) \times \pi \times H/2 \times L/2 \times W/2$$

Through this, she established mean growth rates of the following populations of hanging (suspended) fragments on the tables (Table 4). Based on low growth rates exhibited by fragments affixed upright (<10 cm<sup>3</sup>/mo; all populations; Burns 2018), they were subsequently be grown suspended on nylon line.

**Table 4.** Mean growth rates of five suspended populations of staghorns monitored in the Piti Bomb Holes coral nursery for two years; MEV = monthly elliptical growth rate, after Kiel et al. (2012). *From:* Burns (2018) M.S. Thesis.

Source Population	Species	Mean ± SD MEV, cm <sup>3</sup> /mo
West Agaña	<i>Acropora cf. pulchra</i>	64.7 ± 28.6
Agat Cemetary	<i>Acropora cf. pulchra</i>	79.1 ± 37.9
	<i>Acropora muricata</i>	49.6 ± 29.7
Shimizu (Togcha)	<i>Acropora cf. pulchra</i>	94.5 ± 30.7
Babi Is (Achang)	<i>Acropora aspera</i>	65.3 ± 29.5

To continue our work to determine growth rates among cultured species growing on different structures and between the two nurseries, branch length and diameter were measured monthly on n=10 tagged fragments of each species. Growth measurements began when a finger-sized, unbranched fragment was collected from a source population for nursery growth and were taken monthly for one year. When fragments are small with few branches, Total Linear Extent (TLE) (Kiel et al. 2012) is used to assess rate:

$$TLE = \Sigma (\text{Length}_{Br1} + \text{Length}_{Br2} + \dots + \text{Length}_{BrN}), \quad \text{where}$$

$$\text{Growth} = TLE_{\text{Time T+1}} - TLE_{\text{Time T}}$$

---

However, once juvenile colonies reach 20 cm in diameter, EV is used (Kiel et al. 2012). Our summary growth data, to date, is presented in Table 5:

**Table 5.** Mean growth rates of monitored species in the Piti Ocean Coral Nursery

Species	4-mo Mean Total Growth $\pm$ SD, cm
<i>Acropora acuminata</i>	2.67 $\pm$ 1.36
<i>Acropora aspera</i>	4.51 $\pm$ 1.09
<i>Acropora virgata</i>	6.18 $\pm$ 4.34

At present, all structures that are permitted have been added to the nursery. Future plans include expanding the number of populations and species in culture; species of interest include *Acropora abrottenoides*, *Heliopora coerulea*, and shallow forereef Pocilloporidae. Selection of species to include in restoration will be guided by consultation with other managers and resource agency personnel. We will continue to monitor the unpruned colonies attached to A- and C-frames for reproductive maturity. Lastly, we will outplant staghorn clusters in the vicinity of the nursery bomb holes to replenish populations decimated by bleaching; *Acropora muricata* and *A. teres*, once common within the Bomb Holes area, suffered almost complete mortality and most thickets have been reduced to rubble patches.



**Figure 9.** Herbivory within the Piti Coral Nursery. Over time, nursery structures have attracted resident fish populations and as herbivory increased, cleaning and maintenance efforts by restoration technicians have decreased.

---

## Merizo Coral Nursery

With the initial success and lessons learned from the Piti Bomb Holes Coral Nursery, local managers desired to establish a second nursery, both for risk reduction should the Piti nursery encounter storm damage, and for expansion of species and populations for outplanting. Given the previously discussed limitations in selecting potential locations, Cocos Lagoon and Apra Harbor were identified as other potential sites. Apra Harbor, as a commercial and military port, presented potential access issues, as well as water quality and high traffic challenges. Therefore, Cocos Lagoon was explored as a second site. Consultation with the Merizo community, as part of the Manell-Geus Habitat Focus Area project, allowed a period of time to introduce the concept, achieve consensus regarding the location of the nursery structures, and develop support for the project among the community. The Merizo Coral Nursery was deployed in June 2019, to culture species from reefs in the southern and southwestern half of the island to provide fragments for outplanting projects in this region. The selected site is at 10m depth and is on sand substrate, sheltered near a reef community (Figure 7B). Twelve coral trees, one prototype chandelier (Figure 8C), and one rope nursery have been deployed to date, and are populated with fragments of *Acropora aspera*, *A. virgata*, *A. cf. pulchra*, and *A. teres* from Cocos Lagoon, and *A. muricata*, *A. austera*, *A. vaughani*, and *A. virgata* from Apra Harbor. In addition, eight C-frames have been deployed in sand substrate to house fragments that will be allowed to grow out to adult size, creating small thickets that it is hoped will eventually be reproductive. At present, this nursery houses approximately 1,645 colonies.

Growth rates have been monitored in this nursery as well. Table 6 presents mean growth for monitored fragments, to date:

**Table 6.** Mean growth rates for species grown in the Merizo Ocean Coral Nursery

Species	4-mo Mean Total Growth $\pm$ SD, cm
<i>Acropora acuminata</i>	4.56 $\pm$ 1.93
<i>Acropora austera</i>	0.33 $\pm$ 1.36
<i>Acropora vaughani</i>	0.78 $\pm$ 1.38
<i>Acropora muricata</i>	0.73 $\pm$ 1.18

Poor water quality continues to challenge to this nursery. The lagoon is considerably more silty and turbid than that of Piti Bay. It is also not a Marine Preserve and fish herbivores are rare. Thus, the Merizo nursery requires cleaning every three weeks. Silt and fouling arborescent algae build up on all structures and appear to cause partial mortality on fragments at the point of contact between tissue and nylon; the coral disease *Acropora* white syndrome is sometimes associated with silt and algal fouling (Figure 10). Fragments on branches higher in the trees are more silty

---

than those on lower branches, though lower branches are obviously more shaded. The silt and lack of herbivores prevent crustose coralline algae from recruiting on PVC<sup>®</sup> surfaces.



**Figure 10.** Silt impacts in the Merizo Coral Ocean Nursery. (A): A. Williams, of the National Parks Service, cleans silt off a nursery tree; (B): silt smothering and the coral disease *Acropora* White Syndrome cause partial mortality in a colony of *Acropora teres*. Photo credits: M. Andersen and L. Raymundo

## Outplanting Activities

Outplanting activities are ongoing and are currently focused on two areas: Piti Marine Preserve and Cocos Lagoon, identified in consultation with the Guam Restoration Strategy Working Group. These areas were selected due to their close proximity to the coral nurseries, the presence of suitable substrate and depth, water flow, familiarity of divers with the sites, and knowledge of previous existence of staghorn species within the site. In selecting specific outplanting sites, we ensured that depth at low tide was sufficient to prevent subaerial exposure of upper branches and avoided backreef/nearshore areas where water flow was minimal during summer bleaching seasons, and where human activity (trampling, gill net fishing, gleaning) was minimal. As a general protocol, no outplanting takes place between July and October (Guam’s bleaching season) to minimize stress and mortality.

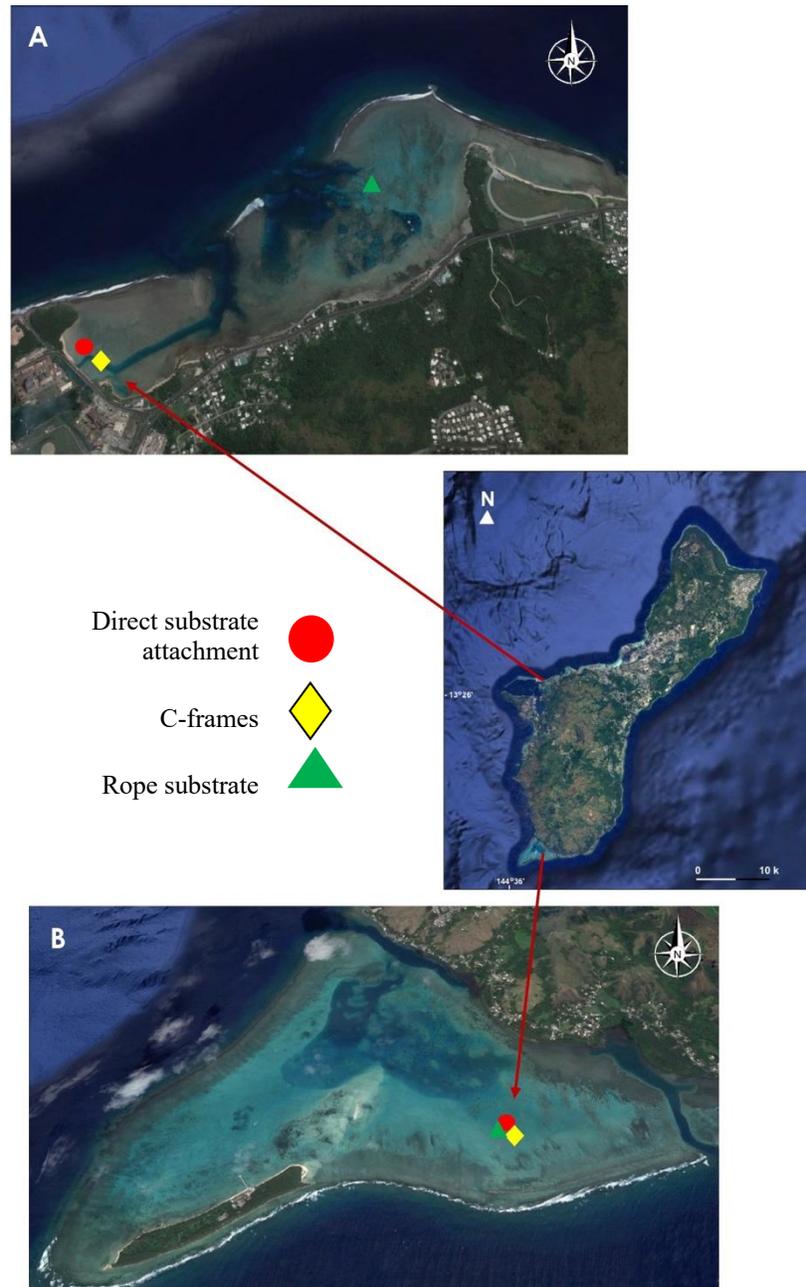
Here we provide examples of the approaches we have developed for use on hard vs. soft substrates. The southwestern border of the Piti Marine Preserve offered contrasting environments for staghorn outplants, both of which currently support viable and healthy populations of *A. cf. pulchra* (Fig. 11A). The shallow reef flat is characterized by mixed pavement and sand substrate and clear, well-flushed water, ranging in depth from 1.25m to 2m. Water flow is perpetually high, as a longshore current originating on the northeastern tip flows across the bay, ending at the southwestern shore (Fig. 11A, red dot). Adjacent to the reef flat is the human-constructed Tepungan Channel, originating at the Cabras Power Station. The channel bottom is 7m deep, with a mixed sand-rubble substrate. Water current is influenced by tidal patterns, but there is a constant flow seaward, pushing water from the power station (Fig. 11A, yellow diamond). A large, semi-protected sand pit seaward of the nursery offered an additional area which was well-flushed, 3m deep, and surrounded by healthy hard and soft corals (Fig. 11A, green triangle). An extensive area

within Cocos Lagoon offered a combination of pavement patches and sand, with a depth of 3m-4m and some exposure to flushing from the south (Fig. 11B).

Interestingly, both of these sites contain numerous healthy *A. cf. pulchra* colonies that were not significantly affected by the 2013-2017 mortality events. In both of these sites, staghorns form large ovoid colonies, up to 4m in diameter, but the extensive thickets seen in other sites were not present. Thus, water flow around the colonies did not stagnate during the hot bleaching season and mortality within the center of colonies was not observed, and contrasts with our numerous observations of extensive mortality within the centers of larger thickets (Raymundo et al. 2017). Due to the continued health and low bleaching prevalence of *A. cf. pulchra*, we are attempting to develop this site as a refuge for all of Guam's staghorn species by outplanting our other species in nursery culture to these sites.

#### Outplanting on Hard Substrate

On Guam reef flats, the most abundant hard substrate is weathered calcium carbonate pavement. With preparation, this provides a highly effective surface on which to attach fragments. Area A in Fig. 11 contains large patches of weathered pavement nearshore to a large staghorn zone (Figure 12); substrate is first prepared by removing loose rocks and other debris, and scrubbing to remove turf algae and sediment. Fragmented colonies are then positioned and affixed with a cement mixture designed to be used in saltwater (cement and Plaster of Paris in a 5:1 ratio, mixed with beach sand at a 1:1



**Figure 11.** Maps showing locations of current outplanting sites. A: Piti Marine Preserve; B: Cocos Lagoon.

---

ratio; saltwater is then added on site and mixed to form firm balls that can be handled underwater). Fragments are planted in monospecific 4m x 4m plots at an average density of 12 colonies/m<sup>2</sup>; larger colonies are planted at lower densities. Fragments pruned from nursery colonies for outplanting range in size from 10cm to 30cm diameter, depending on the species and branching pattern. Colonies are visited within one week post-outplant, to re-affix any that have loosened and to census for post-outplant stress responses.

During the first year of the upscaled restoration project, five plots (182 colonies) have been established in Piti Southwest and six in Cocos Lagoon (210 colonies), using this method. Four staghorn species: *Acropora acuminata* (Piti), *A. teres*, *A. virgata* (Cocos), and *A. aspera* (both sites) have been introduced. An additional 117 juvenile massive *Porites* spp and 151 fragments of



**Figure 12.** Outplanting on the Piti southwestern reef flat. A: a plot of nursery-reared *Acropora aspera* cemented to pavement, with a large *A. cf. pulchra* colony in the background; B: Restoration technician A. Castro preparing substrate prior to cementing a nursery-reared colony of *A. acuminata*. Photos: L. Raymundo.

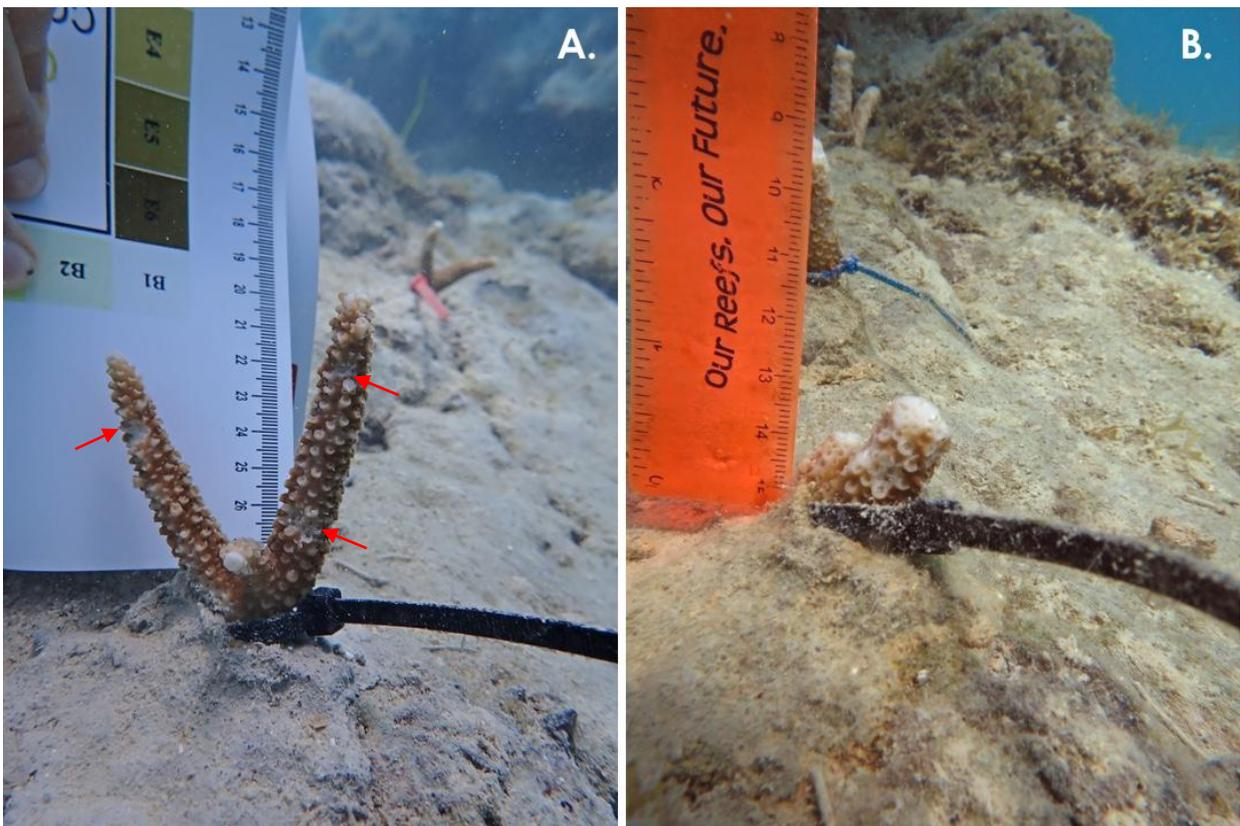
the blue coral *Heliopora coerulea* were also planted within this site, as part of a collaboration with the US Navy. In addition, four plots of 157 nursery-grown microfragments of the non-scleractinian blue coral *Heliopora coerulea* were outplanted onto pavement within the Tumon Bay Marine Preserve, as a first effort to test its performance as a restoration target species.

Outplant stress responses are generally limited to mild bleaching on the reef flat sites, as the light regime differs from that of the nurseries. Partial mortality of tissue around the base where attachment to substrate occurs is frequent but is followed by resheeting of new tissue within one month. A massive predation event was observed among *A. aspera* outplants in two plots within Cocos Lagoon, within two weeks of outplanting (Figure 13). Interestingly, fragments recovered within three months, with the appearance of new apical corallites, as predation did not continue. This suggests that fish may have been attracted to stress responses, such as excess mucous production, from the corals (Seguin et al. 2008). To date, mortality among outplants is very low; <1% of outplants have completely died, though we will be monitoring closely during the upcoming bleaching season.

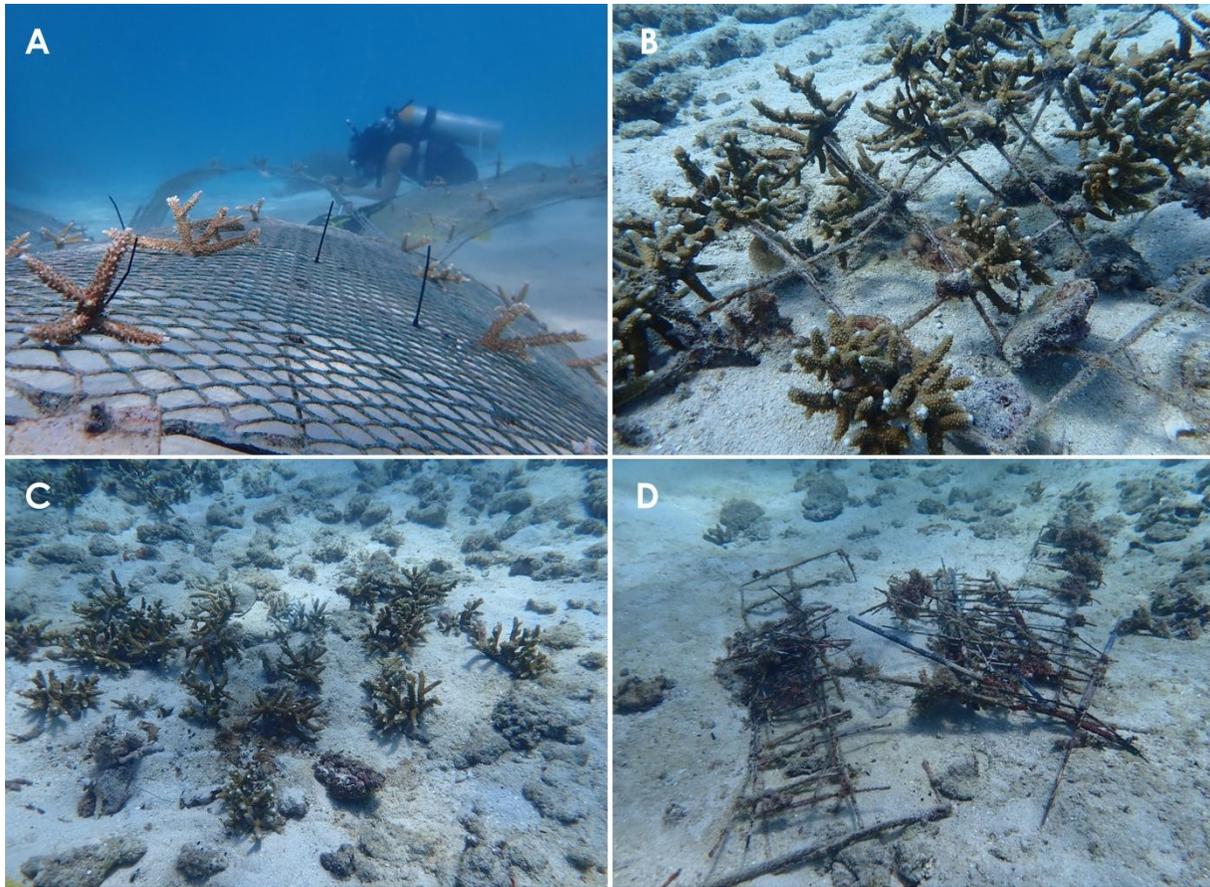
---

## Outplanting on Soft Substrate

Although staghorn *Acropora* can—and do—become established on unstable substrates such as sand and rubble, they do so by anchoring their lowest branches into sand. As this results in mortality of the lower branches, restoration efforts may be more successful on unstable substrates if such mortality can be reduced or eliminated. We are testing two methods of establishing outplants onto such substrates: substrate provisioning using C-frames and rope nurseries (Figure 14). C-frames are low-relief structures composed of wire and plastic mesh which are anchored in sand or rubble, using rebar stakes (Fig. 14A). Small nursery fragments are attached to the upper surfaces of the frames using zip ties and are allowed to grow over the mesh, encapsulating the material in coral skeleton. Over time, the frame itself deteriorates (Fig. 14B), sinking under the weight of growing colonies. The frame is then sunk into the substrate and excess material is removed (Fig. 14C, D). Remaining supportive mesh is covered with sand, and the attached coral is firmly anchored to substrate. To date,  $n=16$   $1\text{m}^2$  frames have been introduced in Tepungan Channel, Piti, and eight frames in Cocos Lagoon, each housing approximately 20 fragments. Six-month mortality has been  $<1\%$  on frames.

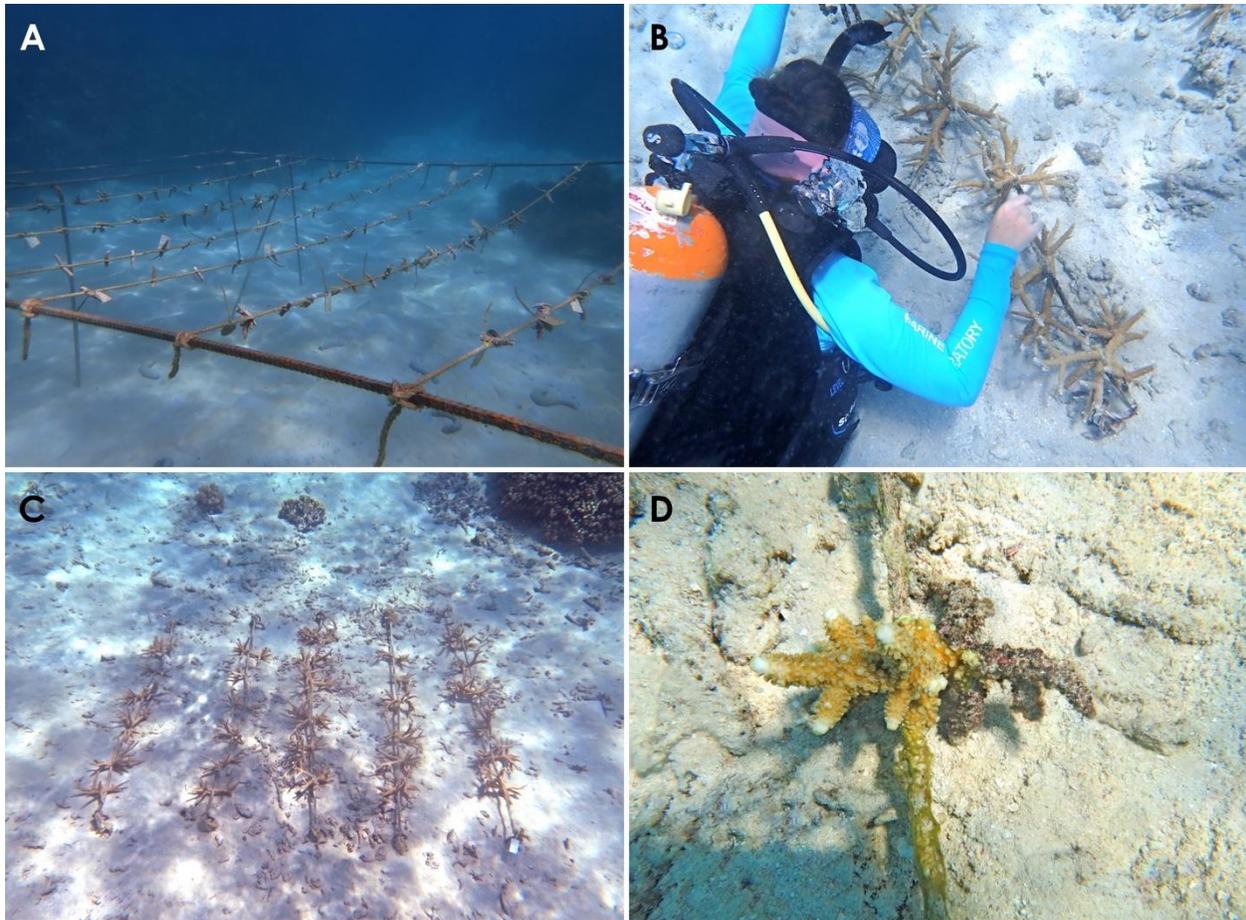


**Figure 13.** A nursery-reared fragment of *A. aspera*, outplanted to Cocos Lagoon pavement. A: two days after outplanting; three fish predation scars are present (arrows); B: two weeks post-outplant; 80% of the fragment was consumed. Photo: R. Crisostomo.



**Figure 14.** Use of C-frames to provide stable substrate for outplanting into unstable sand or rubble substrates. A: Attaching nursery fragments to C-frames in Tepungan Channel, Piti; B: and old C-frame prototype in Tepungan Channel that has collapsed; C: the same frame sunk and positioned into a mixed sand-rubble substrate; D: excess debris from the collapsed frame removed from site after the corals and attached frame are sunk and stabilized in sand (C). Photos: L. Raymundo

Rope nurseries are a modification of the C-frame in an attempt to reduce the use of introduced material on which corals will grow (Figure 15). A rebar frame housing numerous ropes is set up in the nursery and coral fragments are inserted into the ropes and allowed to sheet over the rope material (Figure 15A). The ropes are then removed when corals grow to a minimum of 15cm and outplanted directly onto sand with corals intact (Figure 15B, C). Lower branches are immediately immersed along with the rope, resulting in some mortality of the lower anchoring branches (Figure 15D). Initial results of this method indicate that faster-growing species (such as *A. acuminata*) respond more favorably to this method, as upward growth is greater than the loss of lower branches (Figure 15B), while slower-growing species (such as *A. aspera*) may benefit more from the C-frame method (Figure 15D).



**Figure 15.** Rope nursery use. A: the rope nursery in the Piti coral ocean nursery, newly populated with fragments from the coral trees; B: a rope with 18-mo-old *Acropora acuminata* colonies from the prototype nursery; C: lay-out of five ropes, each housing six colonies; D: Close-up of an 18-mo-old *A. aspera* colony showing 50% mortality from sand burial post-outplant. Photos: L. Raymundo.

To date, a total of 15 ropes housing 90 colonies have been planted in the sand pit at the outer edge of the Piti Marine Preserve (Figure 11A), and another 15 ropes, housing 90 colonies have been outplanted within the Cocos restoration area (Figure 11B). Mortality is 3.3% at both sites, with sand burial the most probable cause. Partial mortality from burial of lower branches has occurred on most colonies, but this was expected as part of the stabilization process.

For all outplants, a hierarchical monitoring schedule was designed to allow both rapid health surveys and more labor-intensive growth measurements. Health and sources of partial mortality (bleaching, disease, predation, competitive overgrowth, tissue loss from unknown causes) is visually assessed within one week of outplanting, then at monthly intervals till six months, then at six-month intervals. Growth is assessed annually, via image analysis (ImageJ<sup>®</sup> software; NIH) of still photos. In addition, Line Intercept Transects are accomplished annually within plots and in adjacent non-restored plots, to examine temporal changes in coral cover in response to restoration.

---

## Genetic Work to Inform Restoration Efforts

The genetic component of Guam's restoration efforts has three goals: resolve taxonomic uncertainties, perform populations genetics analyses of remaining species, and genotype nursery corals. These are discussed below:

### Resolution of taxonomic questions of staghorn *Acropora*

Guam occupies a unique biogeographical position within the Indo-Pacific and forms the base of the Mariana Archipelago. While we have a history of sound taxonomic work via the seminal efforts of Richard Randall and ongoing efforts by David Burdick (creator of <https://guamreeflife.com>), unresolved taxonomic questions remain, particularly in light of enhanced taxonomic resolution due to novel molecular methods. These issues represent a significant conservation challenge. Without clear knowledge of species boundaries and correct nomenclature, we do not know their geographic range and relationship to similar species elsewhere, nor can we fully understand their local abundance and potential extirpation risk. At present, all of Guam's staghorn *Acropora* have been identified based on published morphological characters, using the original species descriptions provided in Randall and Myers (1983) and updates to that publication, Wallace (1999), and Veron (2000) (D. Burdick, pers. comm.). However, a number of these morphospecies do not closely adhere to the type specimen descriptions and the possibility of cryptic, potentially endemic species remains largely unexplored.

A recent effort entitled Project Phoenix (<https://coralprojectphoenix.org/>) is molecularly evaluating *Acropora* nomenclature in the Indo-Pacific and Guam has submitted specimens of all of our known staghorn *Acropora* to be included in this assessment (D. Burdick, pers. comm.). Additional support for this effort is provided by the UOG Biorepository, currently supported by the National Science Foundation's EPSCoR program to the Guam Ecosystems Collaboratorium for Corals and Oceans (GECCO), which now contains curated skeletal and DNA samples of our nursery corals (Fig. 16). It is hoped that some of our questions of our species identification will be resolved via this effort, which will allow us to better manage remaining populations. In addition, a current effort is investigating species boundaries among staghorn *Acropora* corals on Guam, using molecular and morphological approaches to identify characters suitable for verified species identification.



**Figure 16:** Creating and managing the curated coral collection housed in the UOG Biorepository; an effort of D. Burdick. Photo: EPSCOR file photo.

---

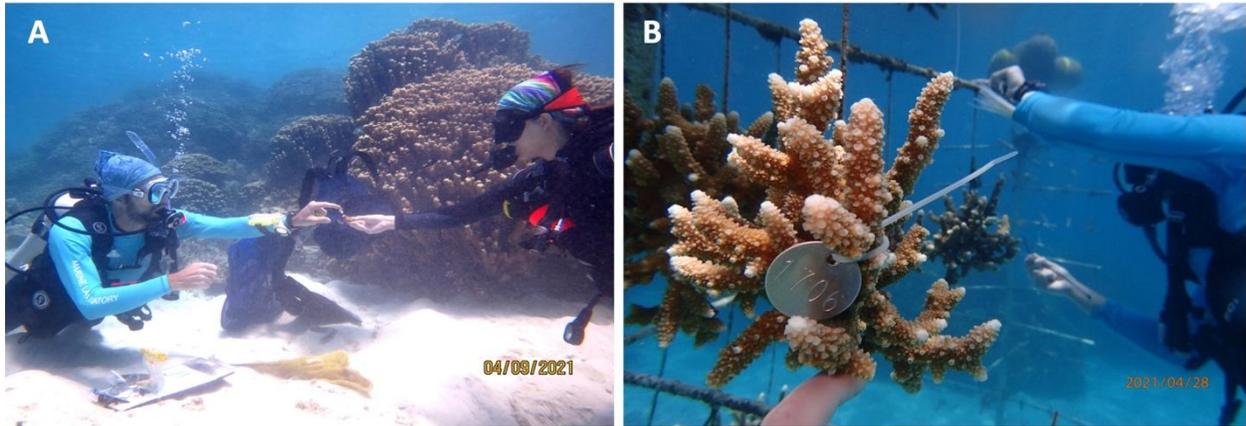
## Population genetics

As stated previously, staghorn *Acropora* are susceptible to a number of biotic and abiotic threats and this knowledge has guided our restoration efforts. They are highly vulnerable to bleaching (Raymundo et al. 2019), yet vulnerability appears to vary within and between populations. *Acropora* cf. *pulchra* is, at present, the only widespread species on Guam (14 sites; Table 2) and population genetics work has, thus, focused on this species. Rios (2020) analyzed five physically discrete populations of *A. cf. pulchra* around Guam and noted that populations composed of ~60% clones, indicating that both asexual fragmentation and sexual reproduction was important for population sustenance. A significant result of her analysis was the determination that the southern population of Cocos-Achang (Fig. 4, site 21) was genetically distinct from those to the North--West Agaña (Fig. 4, site 6) and Urunao (Fig. 4, site 1)--and the Agat (Fig. 4, site 18) population showed links with both, suggesting it connects northern and southern populations. Interestingly, the recently discovered Urunao population proved the most genetically diverse and was predominantly affiliated with heat tolerant symbionts, that were virtually absent in other populations. Thus, this population genetic analysis indicated that Agat should be protected and Urunao should be sampled more extensively to increase the diversity and resilience of our nursery and restored populations.

One restoration proposal that has been put forth, for instance, is to exchange fragments of specific species between Saipan and Guam to increase genetic diversity on both islands. This is a novel restoration approach which could be highly beneficial but requires knowledge of taxonomic status, careful consideration of potential impacts, and consistent post-introduction monitoring. Preliminary population genetic analyses of a small number of Saipan samples indicate only minor genetic differences, especially with Guam's northernmost Urunao populations. Additional investigations with additional samples from Saipan (and Rota) are scheduled for later on this year.

## Genotyping of all nursery populations

The greatly reduced extent of Guam's remaining staghorns, summarized in Figure 4 and Table 2, strongly suggests quantification of genetic diversity as a priority. Determining the number of genotypes present in culture will address these main questions: 1) how genetically diverse are the colonies in culture? 2) how can we best increase the genetic diversity of our nursery and outplanted populations, e.g. by additional sampling of specific populations? 3) how can we generate genetically diverse restored populations to increase populations resilience? 4) how can we best outplant different genotypes in close proximity to increase chances for sexual reproduction and outbreeding; and 5) is there evidence for genotype-based differential responses to outplanting, bleaching, and disease? To facilitate answers to these questions, a minimum of 20 fragments of all nursery species-populations have been sampled for genotyping by the Combosch Genetics Lab (Figure 17).



**Figure 17.** Sampling for genotyping and population genetics. A: Population geneticist D. Combosch receives a nursery fragment from graduate student R. Crisostomo for genotyping; B: a nursery colony of *A. aspera* tagged for genotyping. Photos: M. Andersen.

As genotyping work progresses, we are simultaneously tracking the performance of outplants of the sampled fragments. Specifically, we monitor the length of post-outplant stress, manifested in bleaching, disease susceptibility, partial mortality, and predation susceptibility. Other metrics, such as length of time to cement to underlying substrate, growth, and bleaching during the hot summer season, are also tracked. Once genotyping is complete, we will be able to trace these performance metrics to specific genotypes, and follow their performance over time. The combination of genotyping efforts and population genetics will further allow us to outplant genotypes in specific combinations to maximize fertilization success during spawning and to potentially cross specific genotypes that are manifesting phenotypic traits associated with higher resilience.

## Interagency Cooperation

Guam reef restoration work has benefitted from the creation of an interagency cooperative group, the Guam Reef Restoration and Intervention Partnership (GRRIP). Memoranda of Understanding (MoUs) have been created between the University of Guam Marine Laboratory, Dept. of Aquatic and Wildlife Resources, Guam Bureau of Statistics and Plans, Guam Environmental Protection Agency, Underwater World, Inc. and informal agreements exist with the National Parks Service and The Nature Conservancy. These agencies have pledged personnel and resources support for restoration work, and several projects have been undertaken involving interagency personnel (Figure 18).

One result of this effort has been the drafting of two documents that provide guidance to Guam’s management agencies, the Guam Coral Reef Resilience Strategy (Hoot 2018) and the Guam Reef Restoration Strategy (Hoot et al. 2021). The goal of the Reef Resilience Strategy is to “enhance

---

*the resilience of Guam’s coral reef ecosystems and human communities to the impacts of climate change by 2025.”* The document provides mechanisms for engaging the local community in reef conservation, identifies management needs and strategies, and provides guidance for funding and sustainability. The process by which local managers and scientists conceived of and created this document strengthened the goals of these practitioners and led to the most recent cooperative contribution, the Restoration Strategy.



**Figure 18.** Interagency cooperation in restoration efforts. Five agencies assisted in the collection and populating of the Merizo Ocean Coral Nursery in 2019: University of Guam Marine Laboratory, Guam Environmental Protection Agency, Bureau of Statistics and Plans, Division of Aquatic and Wildlife Resources, and Underwater World, Inc., and. Photo: L. Raymundo.

## Acknowledgements

The authors would like to acknowledge a number of people who were instrumental in the establishment and early maintenance of the Piti nursery: M. McCue, SECORE International, V. Lapacek, J. Fifer, A. Williams. W. Hoot led the establishment of the working group to write Guam’s Restoration Strategy; we acknowledge input from working group members J. Cruz, M. Auyong, and F. Roberto as well. W. Hoot also assisted in the establishment of both nurseries and the staghorn surveys. Members of GRRIP, particularly Guam EPA, have supported restoration activities since the initiation of the nurseries.

---

## References

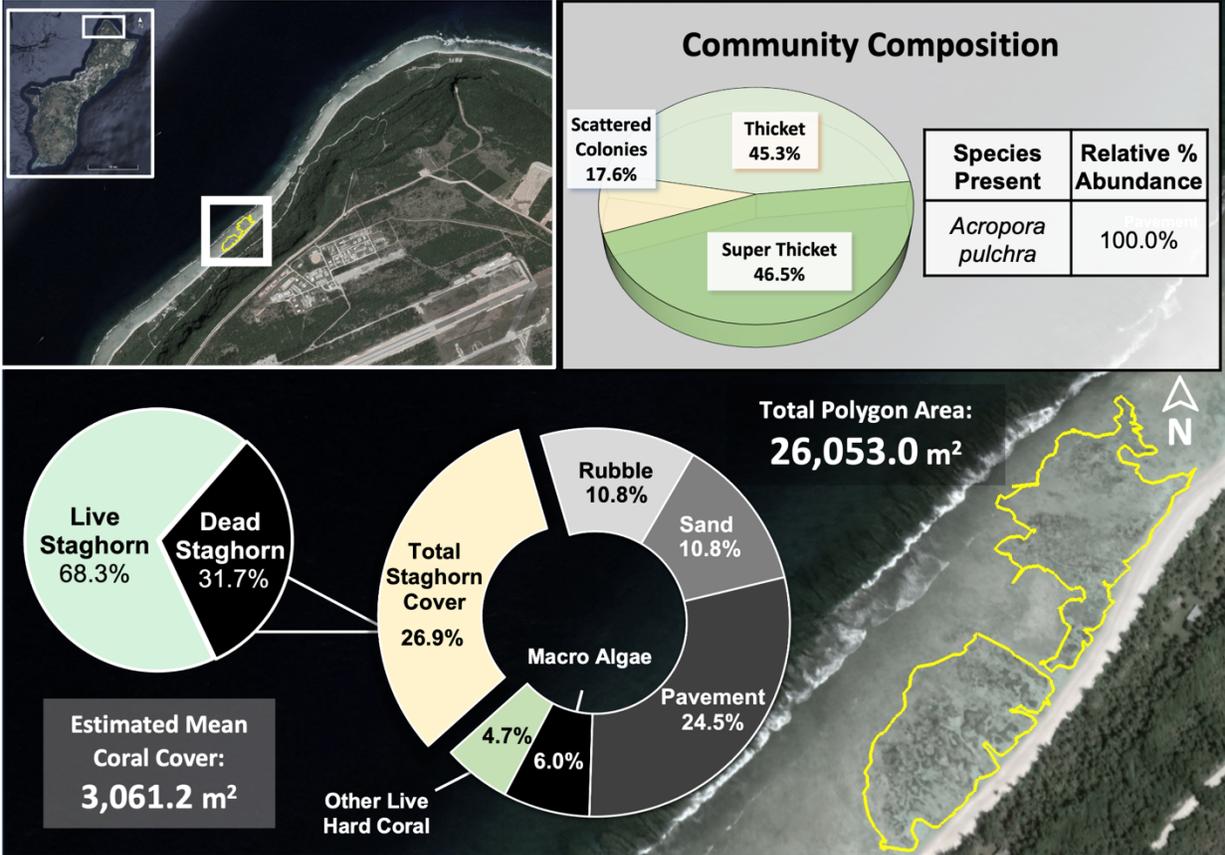
- Birkeland C (ed) (1997) Life and Death in Coral Reefs. Chapman & Hall, NY 536 pp.
- Boyett H V, Bourne DG, Willis BL, Boyette H, Bourne DG, Willis BL, Boyett H V, Bourne DG, Willis BL (2007) Elevated temperature and light enhance progression and spread of black band disease on staghorn corals of the Great Barrier Reef. *Mar. Biol.* 151:1711–1720
- Burdick D, Brown V, Asher J, Gawel M, Goldman L, Hall A, Kenyon J, Leberer T, Lundblad E, McIlwain J, Miller J, Minton D, Nadon M, Pioppi N, Raymundo L, Richards B, Schroeder R, Schupp P, Smith E, Zgliczynski B (2008) The State of Coral Reef Ecosystems of Guam. In: Waddell J.E., Clarke A.M. (eds) The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2008. NOAA/NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team, Silver Spring, MD, pp 465–510
- Caballes CF (2009) The role of chemical signals on the feeding behavior of the crown-of-thorns seastar, *Acanthaster planci* (Linnaeus, 1758). M.S. Thesis, University of Guam. 164 pp.
- De'ath G, Moran P (1998) Factors affecting the behaviour of crown-of-thorns starfish (*Acanthaster planci* L.) on the Great Barrier Reef: 2: Feeding Preferences. *J. Exp. Mar. Biol. Ecol.* 220:107–126
- Epstein N, Bak RPM, Rinkevich B (2003) Applying forest restoration principles to coral reef rehabilitation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 13:387–395
- Herlan J, Lirman D (2008) Development of a coral nursery program for the threatened coral *Acropora cervicornis* in Florida. *Proc. 11th Int. Coral Reef Symp.* 24:1244–1247
- Heron S, Raymundo L, Sweet W, Papa A, Moreland-Ochoa C, Burdick D (2020) Predicting extreme tide events to inform shallow reef community restoration and management in Guam. NOAA Tech. Memo. CRCP 38; UOGML Tech. Rep. 167. 29 pp.
- Hoot W (2017) Guam Crown-of-Thorns Outbreak Response Plan. Guam Bureau of Statistics and Plans. 48 pp.
- Hoot W, Burdick D (2017) Guam Coral Bleaching Response Plan. Guam Bureau of Statistics and Plans. 53 pp.
- Hoot W (2018) Guam Coral Reef Resilience Strategy. Guam Bureau of Statistics and Plans. 69 pp.
- Hoot W, Raymundo L, Auyong M, Burdick D, Roberto F, Cruz J. (2021) Guam Coral Reef Restoration Action Plan. Part 1. The Nature Conservancy. 19 pp.
- Johnson ME, Lustic E, Bartels E, Baums I, Gilliam DS, Learson L, Lirman D, Miller MW, Nedinmayer K, Schopmeyer S, Lustic C, Bartels E, Baums I, Gilliam DS, Larson L, Lirman D, Miller MW, Nedimyer K, Schopmeyer S (2011) Caribbean *Acropora* Restoration Guide: Best Practices for Propagation and Population Enhancement. The Nature Conservancy. 54 pp.
- Joyner JL, Sutherland KP, Kemp DW, Berry B, Griffin A, Porter JW, Amador MHB, Noren HKG, Lipp EK (2015) Systematic analysis of White Pox Disease in *Acropora palmata* of the Florida Keys and role of *Serratia marcescens*. *Appl. Environ. Microbiol.* 81:4451–7
- Kiel C, Huntington BE, Miller MW (2012) Tractable field metrics for restoration and recovery monitoring of staghorn coral *Acropora cervicornis*. *Endanger. Species Res.* 19:171–176
- Kuffner IB, Toth LT (2016) A geological perspective on the degradation and conservation of western Atlantic coral reefs. *Conserv. Biol.* 30:706–715
- Loya K, Sakai, K. Yamazato, Y. Nakano, H. Sambali, R. van Woeski Y, Loya K. Sakai, K. Yamazato, Y. Nakano, H. Sambali, R. van Woeski Y, Loya Y, Sakai K, Nakano Y, Woesik R Van, Loya K. Sakai, K. Yamazato, Y. Nakano, H. Sambali, R. van Woeski Y (2001) Coral bleaching: the winners and the losers. *Ecol. Lett.* 4:122–131
- Miller MW (2001) Corallivorous snail removal: evaluation of impact on *Acropora palmata*. *Coral Reefs* 19:293–295
- Moyer JT, Emerson WK, Ross M (1982) Massive destruction of scleractinian corals by the muricid gastropod, *Drupella*, in Japan and the Philippines. *Nautilus (Philadelphia)*. 96(2):69–82

- 
- Myers RL, Raymundo LJ (2009) Coral disease in Micronesian reefs: a link between disease prevalence and host abundance. *Dis. Aquat. Organ.* 87:97–104
- Nicolet KJ, Chong-Seng KM, Pratchett MS, Willis BL, Hoogenboom MO (2018) Predation scars may influence host susceptibility to pathogens: Evaluating the role of corallivores as vectors of coral disease. *Sci. Rep.* 8:1–10
- Palmer C V, Mydlarz LD, Willis BL (2008) Evidence of an inflammatory-like response in non-normally pigmented tissues of two scleractinian corals. *Proc. R. Soc. B* 275:2687–2693
- Pratchett M (2007) Feeding preferences of *Acanthaster planci* (Echinodermata: Asteroidea) under controlled conditions of food availability. *Pacific Sci.* 61:113–120
- Randall R (1971) Tanguisson-Tumon, Guam reef corals before, during and after the crown-of-thorns starfish (*Acanthaster planci*) predation. M.S. Thesis. University of Guam. 119 pp.
- Randall RH, Sherwood TS (1982) Resurvey of Cocos Lagoon, Guam, Territory of Guam. UOGML Tech. Rep. 103 pp.
- Randall RH, Myers RF (1983) Guide to the Coastal Resources of Guam Volume II. The Corals. University of Guam Press, Mangilao, Guam
- Raymundo LJ, Burdick D, Lapacek VA, Miller R, Brown V (2017) Anomalous temperatures and extreme tides: Guam staghorn *Acropora* succumb to a double threat. *Mar. Ecol. Prog. Ser.* 564:47–55
- Raymundo LJ, Burdick D, Hoot WC, Miller RM, Brown V, Reynolds T, Gault J, Idechong J, Fifer J, Williams A (2019) Successive bleaching events cause mass coral mortality in Guam, Micronesia. *Coral Reefs* 38:
- Reynolds T, Burdick D, Houk P, Raymundo L, Johnson S (2014) Unprecedented coral bleaching across the Marianas Archipelago. *Coral Reefs* 33:499
- Rinkevich B (2005) Conservation of coral reefs through active restoration measures: Recent approaches and last decade progress. *Environ. Sci. Technol.* 39:4333–4342
- Rios D (2020) The Population Genetic Structure of *Acropora pulchra* in Guam. M.S. Thesis. University of Guam. 85 pp.
- Seguin F, Brun OL, Hirst R, Al-Thary I, Dutrieux E (2008) Large coral transplantation in Bal Haf (Yemen ): An opportunity to save corals during the construction of a liquefied natural gas plant using innovative techniques. *Proc. 11th Int. Coral Reef Symp.* 1267–1270
- Smith LD, Hughes TP (1999) An experimental assessment of survival, re-attachment and fecundity of coral fragments. *J. Exp. Mar. Bio. Ecol.* 235:147–164
- Tsang RHL, Ang P (2015) Cold temperature stress and predation effects on corals: their possible roles in structuring a nonreefal coral community. *Coral Reefs* 2015:97–108
- Tunncliffe VJ (1981) Breakage and propagation of the stony coral *Acropora cervicornis*. *Proc. Natl. Acad. Sci.* 78:2427–2431
- U.S. Army Corps of Engineers (1989) Agaña Bayfront Area Typhoon and Storm Surge Protection Study, Agaña, U.S. Territory of Guam. Technical Report.
- Veron JEN (2000) Corals of the World. Australian Institute of Marine Science, Townsville, Australia
- Wallace C (1999) Staghorn Corals of the World. CSIRO Publishing, Collingwood, Australia
- Young TP, Petersen DA, Clary JJ (2005) The ecology of restoration: Historical links, emerging issues and unexplored realms. *Ecol. Lett.* 8:662–673

---

## Appendix One: Summaries of Current Staghorn Populations on Guam

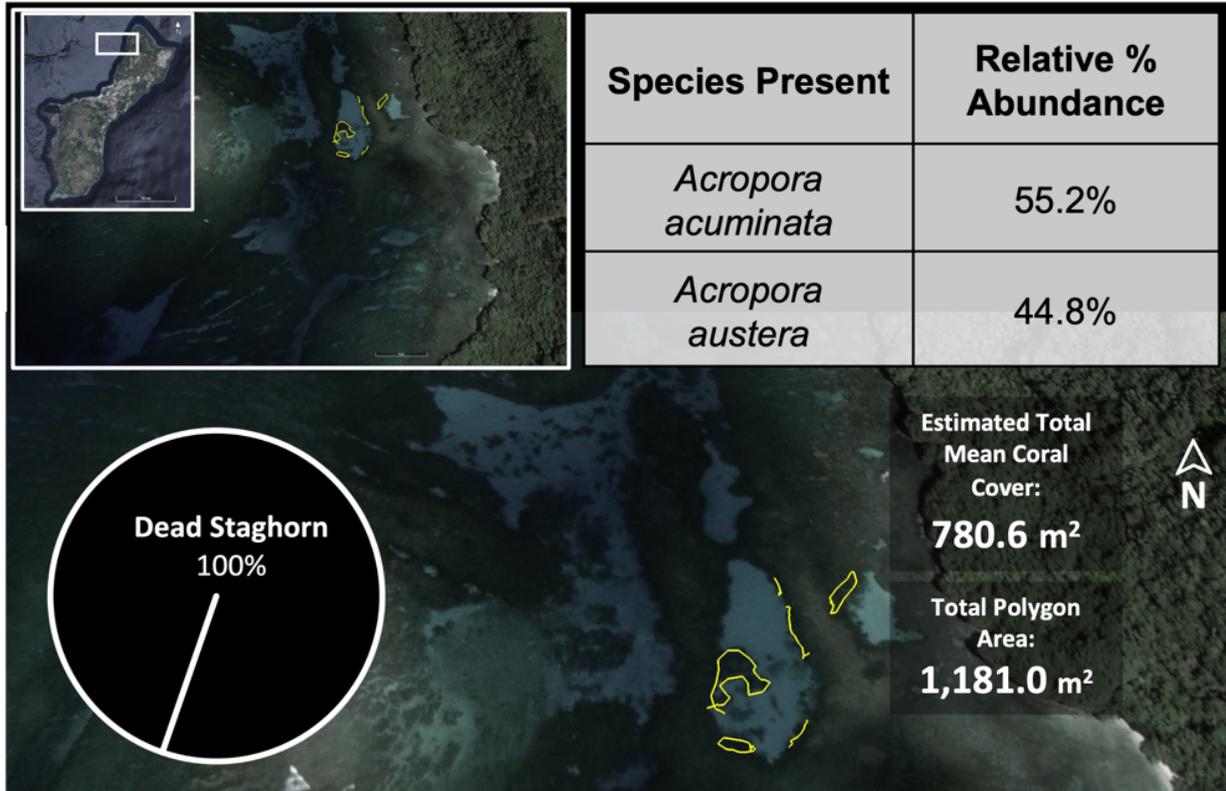
# URUNAO (Site 1, Fig.4)



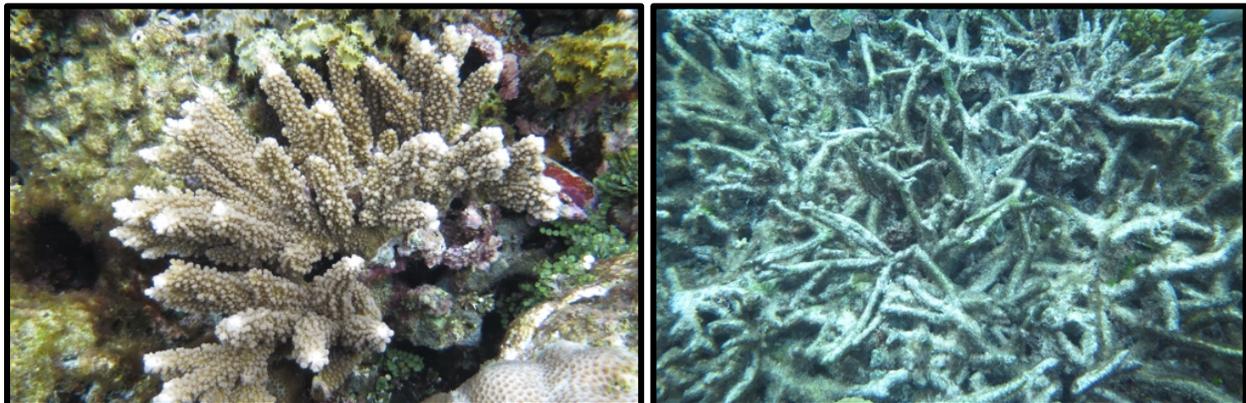
This northwestern reef was first surveyed in 2021, as its existence had not been previously known by the authors (Rios 2019). It constitutes the northernmost staghorn population on Guam, and is characterized by large pavement platforms and extensive staghorn thickets within a shallow reef. Relatively high water movement and flushing combined with extremely shallow depth makes this site especially susceptible to typhoons and low tide exposure events. Bleached and dead branch tips of colonies of *A. pulchra* in both individual colonies (upper photo) and large thickets appeared largely caused by low tide exposure. Extensive mortality was also visible within the centers of large thickets, possibly from stress events in previous years. However, healthy colonies were in abundance, and live cover was one of the highest observed during these surveys (lower photo).



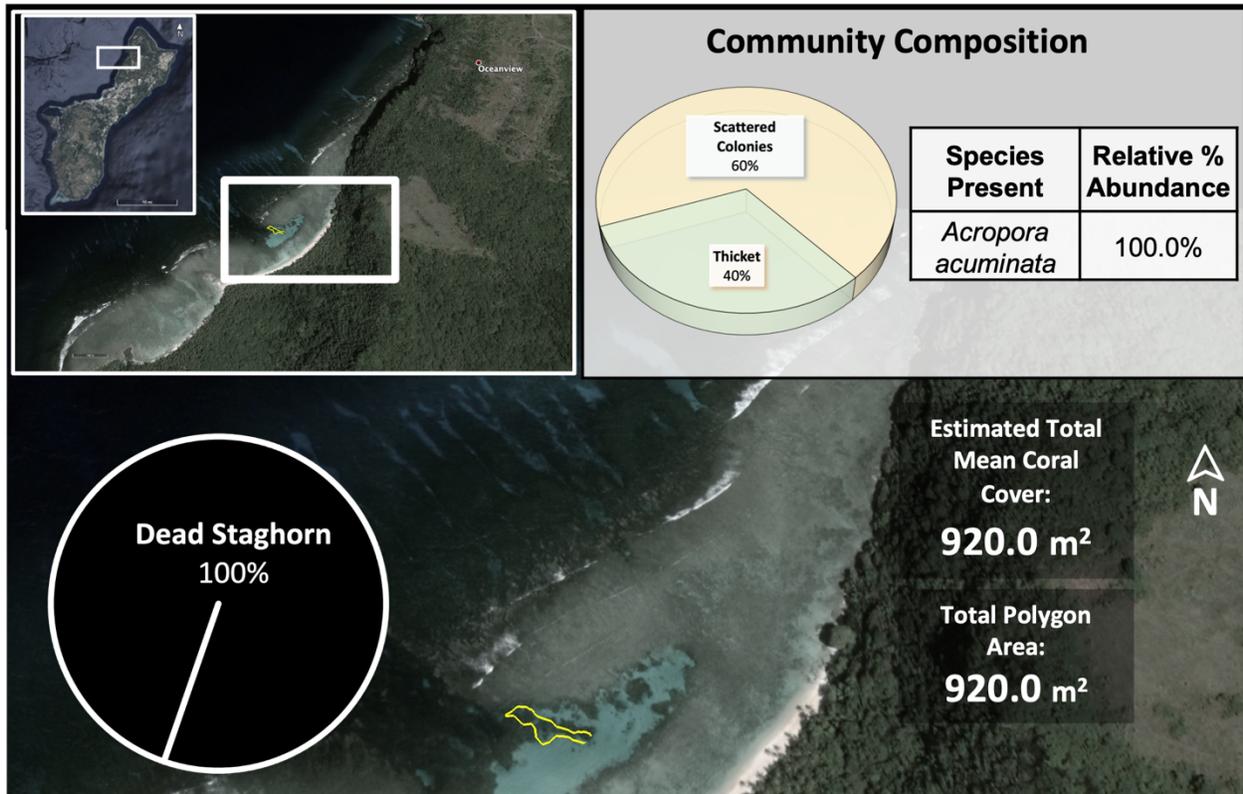
# DOUBLE REEF (Site 2, Fig.4)



Double Reef is located to the south of Urunao, along Guam’s northwest coast. As the name suggests, it consists of two small barrier reefs parallel to the coastline. This site is characterized by seasonally high wave action, high water quality, and structurally complex substrate. While Double Reef had remaining healthy colonies of *A. austra* along the shallow inner reef crest and in shallow pools when surveyed in 2017 (left lower photo), it had experienced 100% mortality of staghorns by 2021; no living colonies were observed. It is unknown what caused this additional mortality, as widespread bleaching did not occur between 2017 and 2021. Staghorn skeletons and extensive rubble patches were further identified as previous communities of *A. acuminata* and *A. austra* (right lower photo).



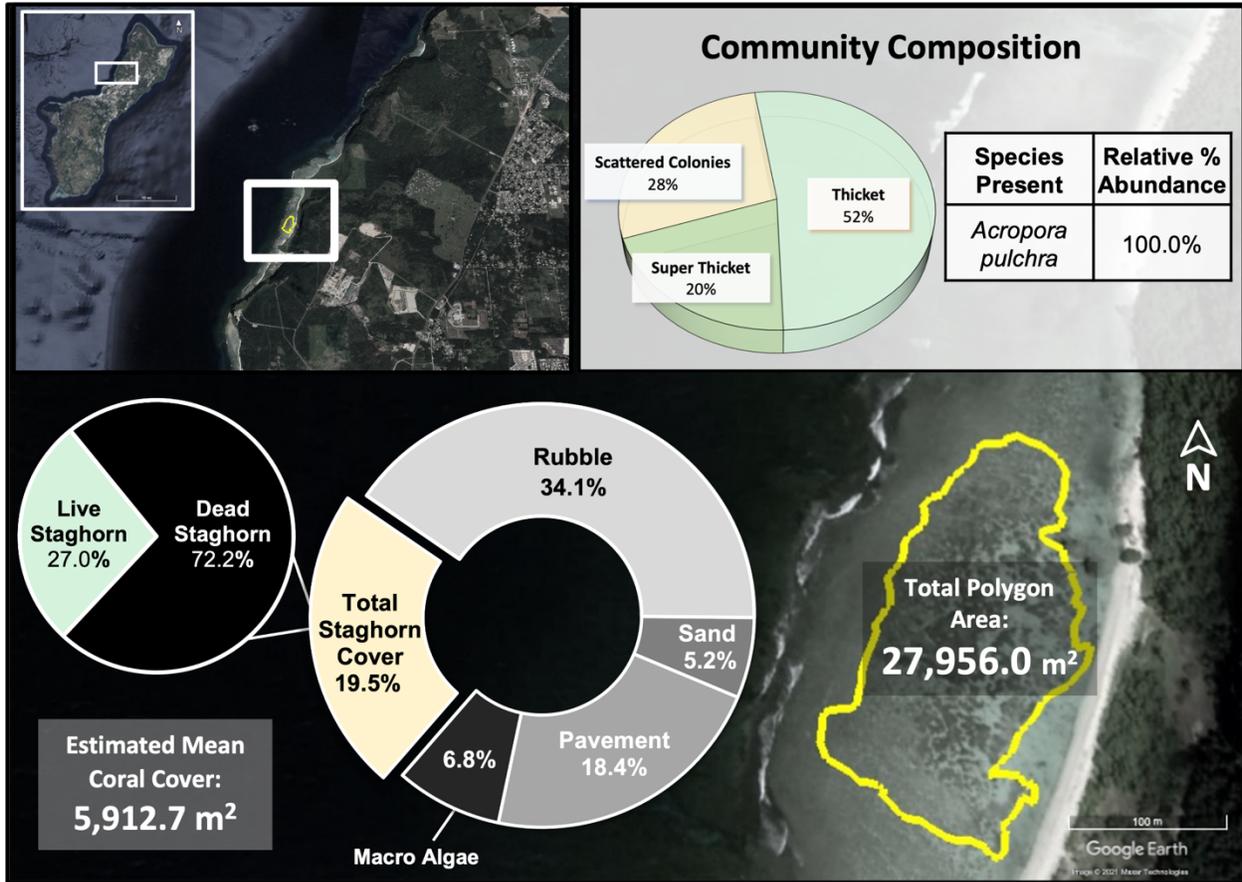
# SHARK’S HOLE (Site 3, Fig. 4)



Shark’s Hole is a complex reef community south of Double Reef. Seasonal heavy wave action, high water quality and high topographic complexity are features of this site. Healthy staghorn *Acropora* communities were recorded in the 2017 surveys, as large thickets of *A. acuminata* (left lower photo) and scattered clumps of *A. austra* (right lower photo) located in the bottom and margins of deeper sand pools between the forereef and reef flat. However, as with the Double reef communities, no living colonies were observed in the 2021 surveys. Dead skeleton and rubble patches were evident in areas where living colonies were previously present. The cause of this mortality is unknown, as mass bleaching events did not occur between 2018 and 2021.



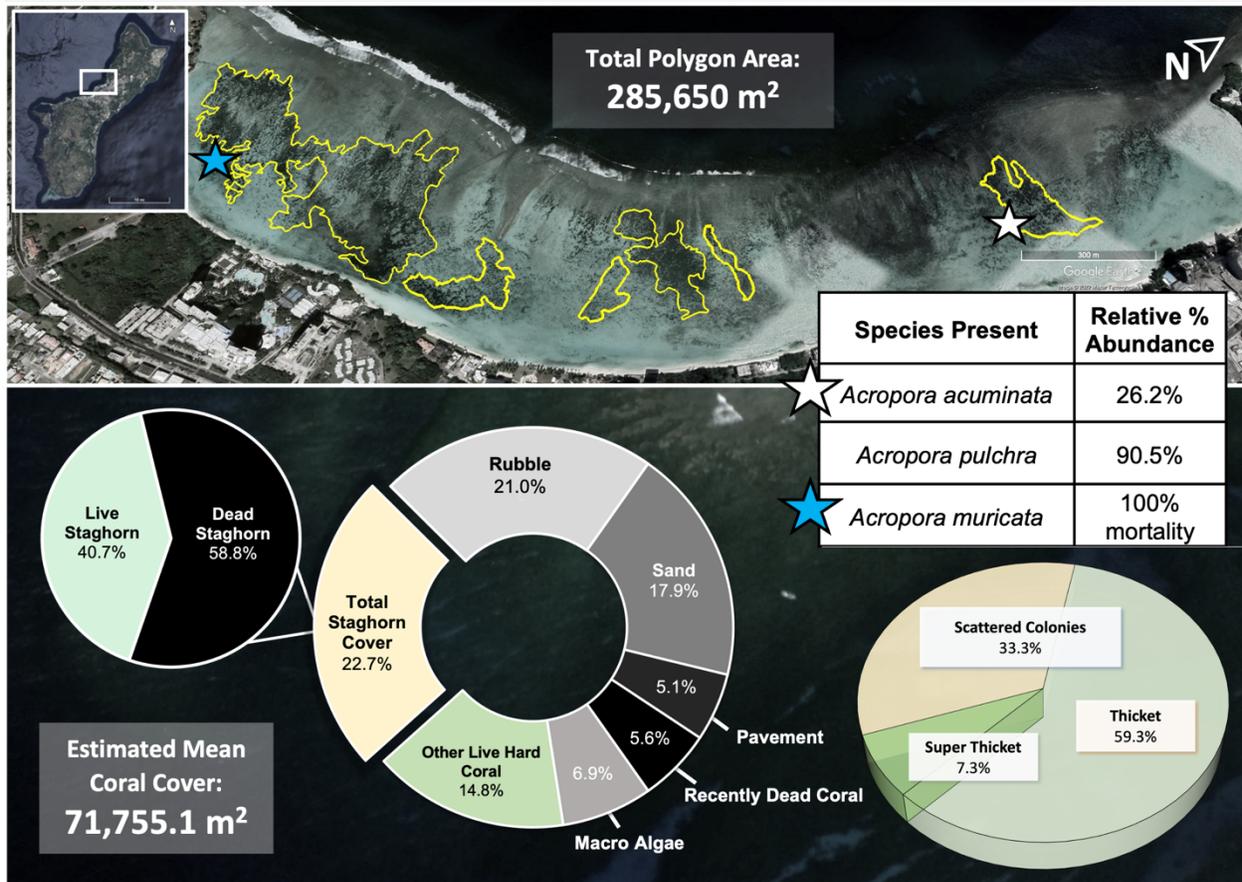
# TANGUISSON REEF (Site 4, Fig. 4)



Tanguisson is a shallow reef flat exposed to high wave energy and swell, located south of Shark's Hole. It was dominated by extensive thickets of *A. cf. pulchra* until 2013, when repeated mortality events resulted in accumulated decline of 80% of staghorns (Raymundo et al. 2017; Raymundo 2019). Currently, the reef flat has one remaining healthy thicket of *A. cf. pulchra*. Expansive fields of rubble patches and dead standing staghorn skeleton dominate (upper photo). *A. cf. pulchra* experienced bleaching, subaerial exposure, and White Syndrome across the 2013-2017 period. Recently dead colonies still maintained their structural integrity and contributed to the overall complexity of the reef (lower photo), but also increased algal stressors caused by accumulated turf and algae cover on branch tips. Low tide exposure events have been the most significant contributor to post-bleaching mortality and reduced recovery rates for this site.



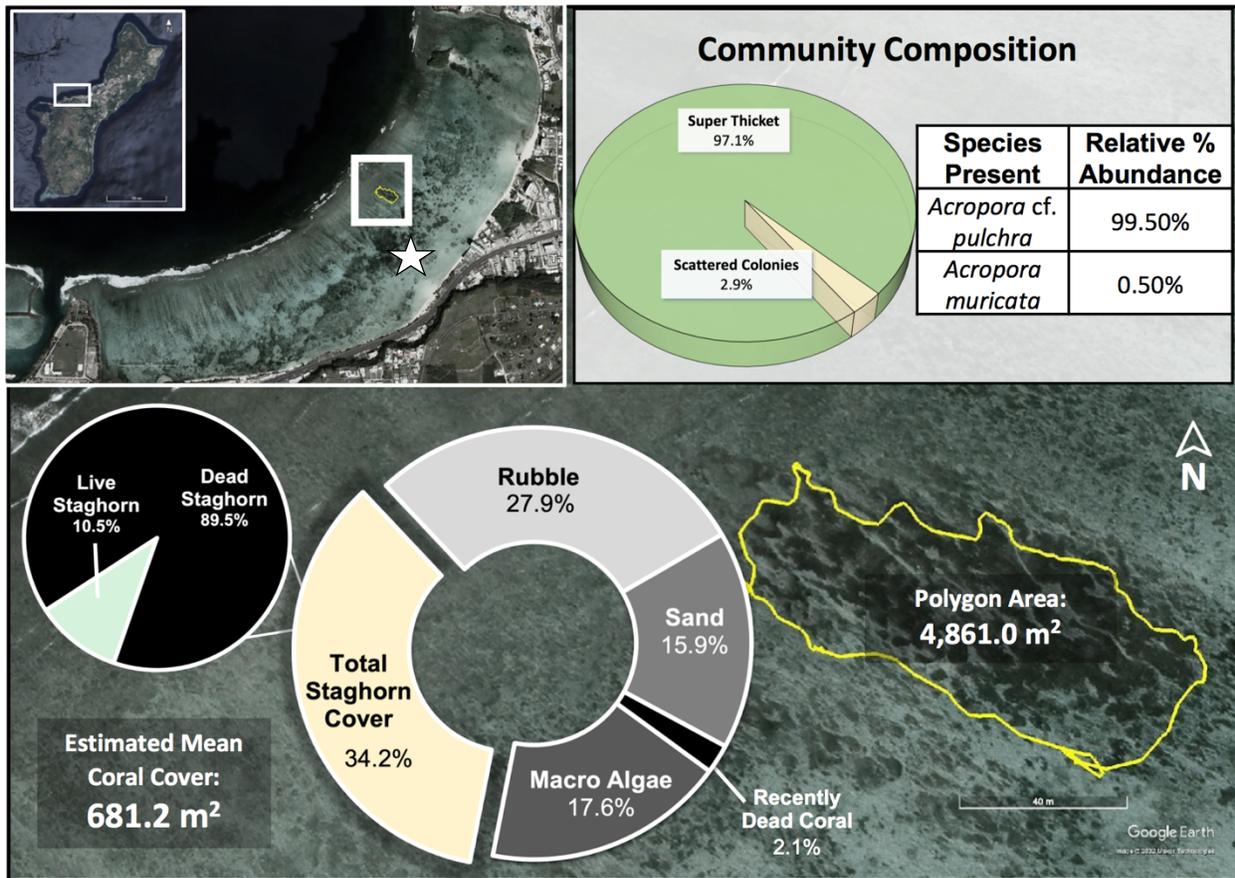
# TUMON BAY MARINE PRESERVE (Site 5, Fig. 4)



Located on the central-west coast of Guam, this Marine Preserve supports extensive fringing reefs in its expansive reef flat, as well as Guam’s main recreational water sport and tourist destination. Characterized by low turbidity, low wave energy and high water quality, this site is host to extensive thickets of *A. cf. pulchra* in shallow nearshore waters (upper photo), with scattered colonies of *A. acuminata*, (white star on map) and bommies of *A. muricata* nearshore (blue star on map). However, mortality from successive bleaching events showed cumulative mean coral loss of 49%, with *A. muricata* experiencing 100% mortality within the Bay. Overall stability of the community may be a direct reflection of an abundance of bleaching-resistant *Porites* spp. and *Pavona* spp. (lower photo), with some recovery of the community post 2013-2017 bleaching and disease outbreak events. However, continued mortality from annual low tide exposure results in slowed recovery rates, with more resistant corals recruiting onto staghorn skeleton. Thermal stress, disease, as well as storm water runoff caused by continued coastal development, may also contribute to slow recovery.



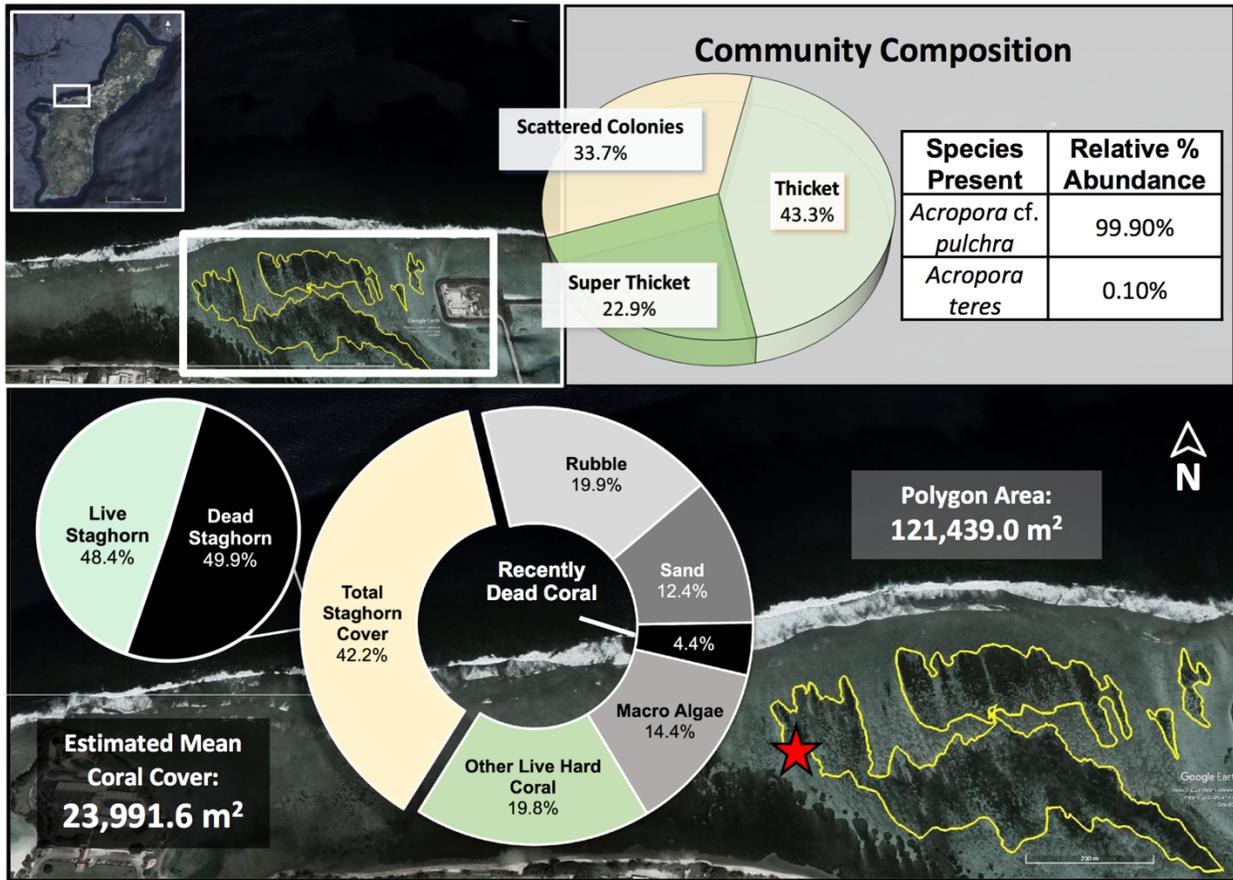
# EAST AGAÑA (Site 6, Fig. 4)



This wide, shallow reef flat is characterized by substrate alternating between pavement and sand with scattered seagrass patches, and is located northeast of the Guam Sewage Treatment Plant, nearshore to the highly developed Marine Corps Drive. Coral community diversity is low and dominated by stress-resilient massive *Porites* colonies. One large thicket of *A. cf. pulchra* was identified near the reef crest of this low wave energy and turbid reef site (upper photo). Exposed to high thermal stress levels during successive bleaching events, the staghorn community was estimated to have lost 20% cover between 2013 and 2014. Nearshore to the large contiguous patch are scattered individual colonies. In 2022, colonies of *A. muricata* (lower photo) were observed scattered among the *A. cf. pulchra* colonies (white star on map; R. Crisostomo, pers. obs.). Repeated low tide exposure, additional thermal stress, and algal farming by damselfish may continue to contribute to low recovery of the thicket at this site, though individual colonies appear to be healthier.



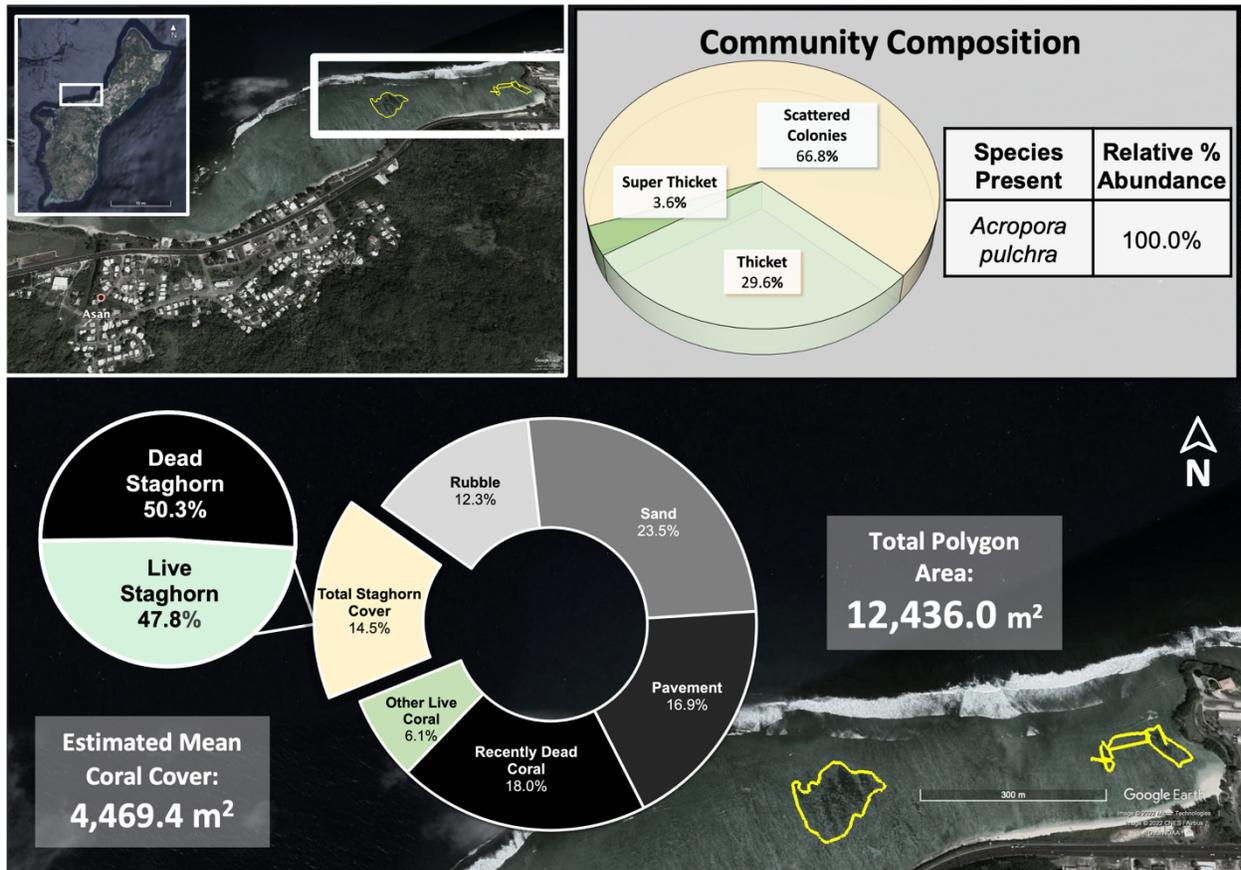
# WEST AGAÑA (Site 7, Fig. 4)



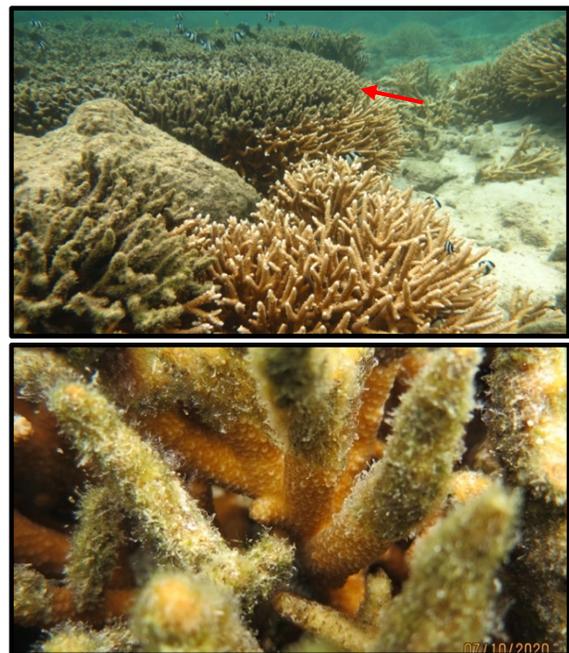
Characterized by a wide, shallow reef flat varying between 1.5 and 2 m depth, and extensive pavement substrate mixed with sand patches, this site is located west of the Guam Water Treatment Plant and nearshore to the sewage outfall pipe. In contrast to the East Aña site, this reef is dominated by extensive thickets of *A. cf. pulchra* (upper photo). In 2022, isolated colonies of *A. teres* were verified at the westernmost nearshore border (red star). A gradient of water flow and turbidity from nearshore to farshore resulted in differential mortality and subsequent recovery, with nearshore corals experiencing much higher mortality (Raymundo et al. 2019; Fifer et al. 2021). Staghorn rubble patches between live thickets are the product of mortality from previous bleaching events acted upon by heavy wave action during storms; cumulative bleaching-associated mortality was estimated at 55%. Brown and white band disease, as well as *Drupella* predation and *Stegastes* farming (lower photo), algal overgrowth, and siltation continue to compromise coral recovery. Dead branch tips within large thickets was also consistent with low tide exposure.



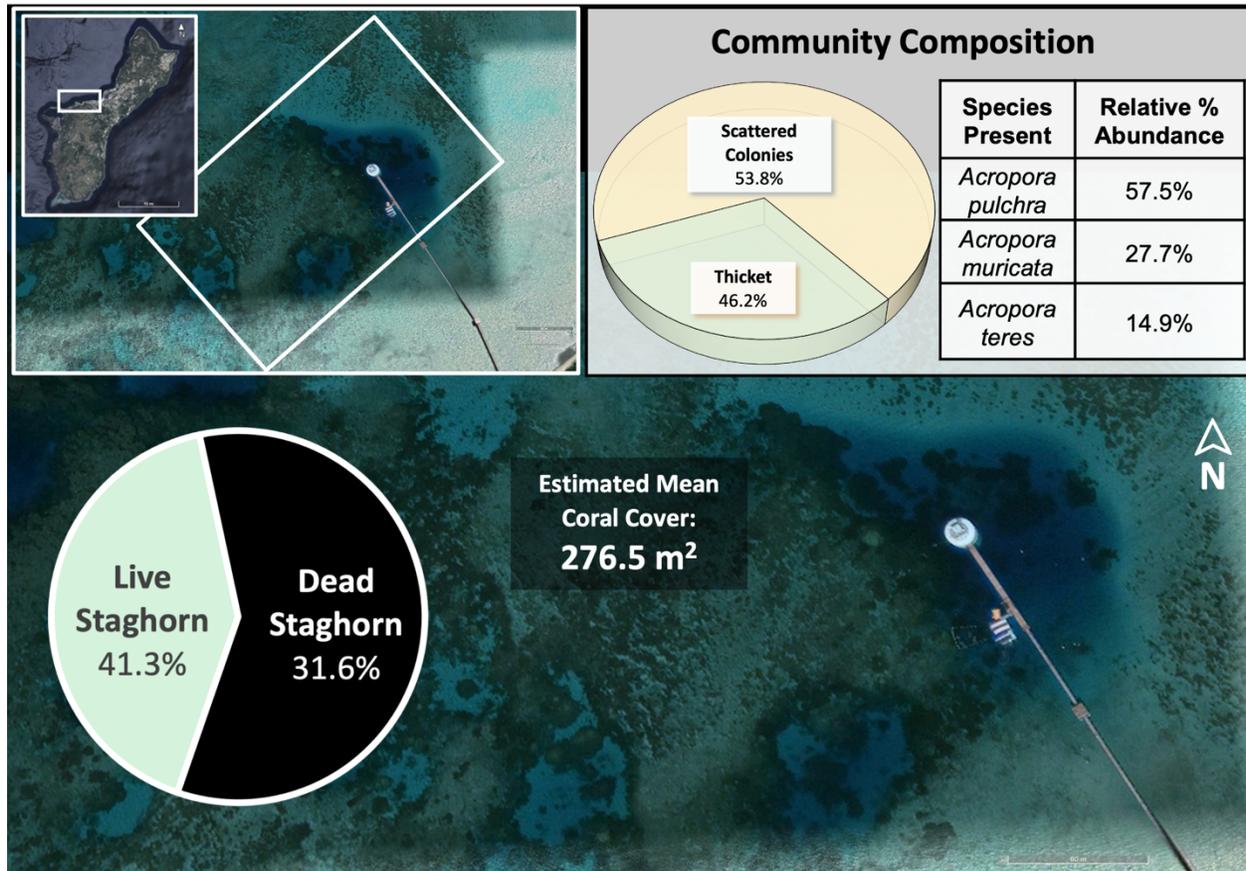
# ADELUP (Sites 8 & 9, Fig. 4)



Found within National Parks Service submerged lands, this site is characterized by high water quality, relatively high coral diversity and pavement substrate. Small, scattered colonies of *A. cf. pulchra* dominate the site closest to the Governor’s Complex, while larger thickets were found in the western polygon. Previous bleaching-related mortality and subaerial exposure caused an estimated 30% loss of the staghorn community at this site (upper photo, red arrow). Extreme low tide exposure events continue to be the dominant source of mortality to current coral communities recovering from the previous bleaching events. This mortality is characterized by loss of tissue on branch tips (lower photo), with some resheeting during periods of less extreme tides and cooler water, but mortality may recur during the next summer warm season.



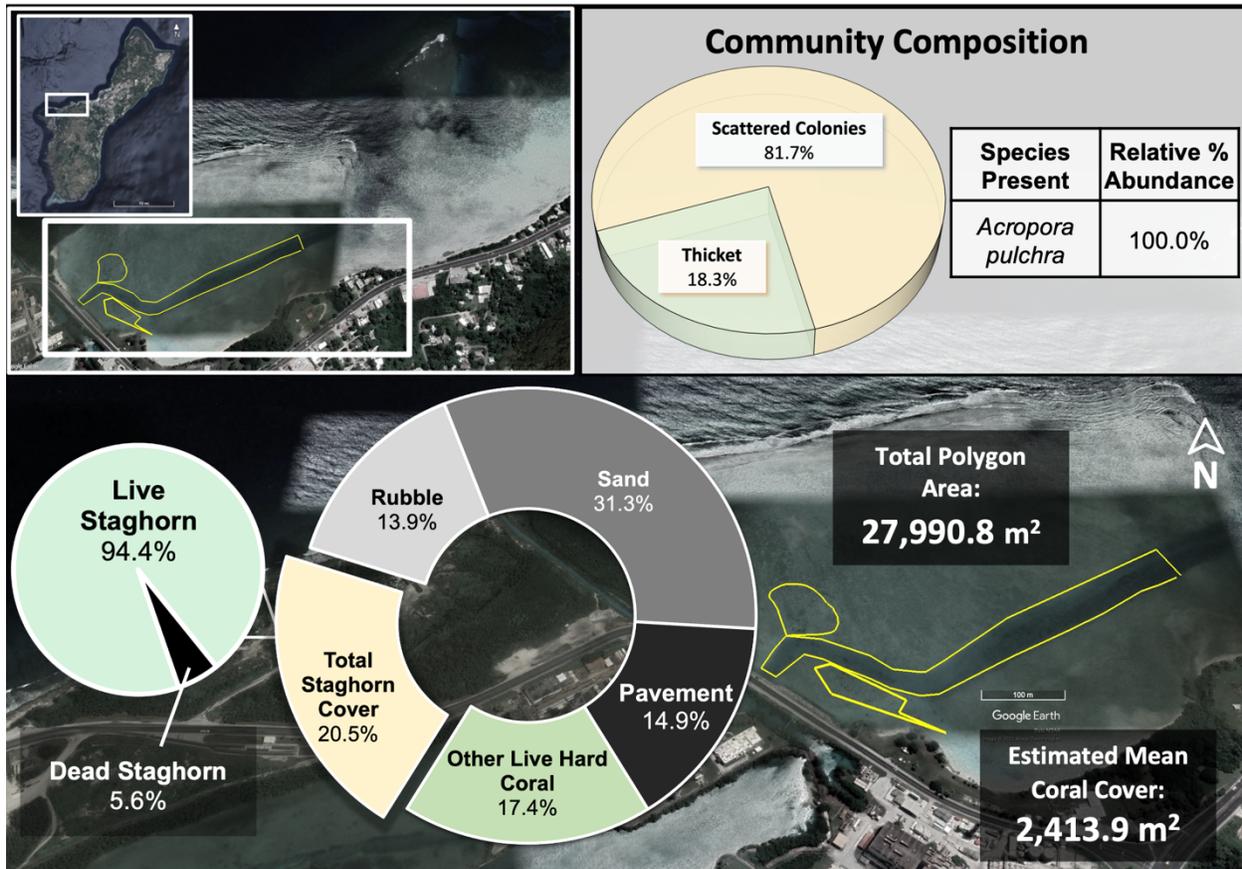
## PITI BOMB HOLE MARINE PRESERVE (Site 10, Fig. 4)



Located in the karst sinkhole area of the Tepungan Bay Marine Preserve, Piti Bomb Holes is a popular tourist destination hosting the Fish Eye Underwater Observatory. This region of the Bay is dominated by backreef seagrass beds and a reef flat community dominated the soft coral *Sinularia polydactyla* and *Porites cylindrica* (photo), and boasts a healthy fish biomass. Depths range between 1.5 m in pavement areas to 5 m within the sinkholes. Characterized by high water movement, low turbidity, and high water quality, coral populations remained stable during previous bleaching events, though staghorn populations declined by an estimated 31.6% in response to extreme thermal stress. Surviving populations of staghorns were scattered and rare, with small thickets of *A. cf. pulchra*, one remaining *A. muricata* thicket, and two thickets of *A. teres*. Thermal stress, a possible influence of tourism activity, and farming damsel fish continue to be stressors to these populations.



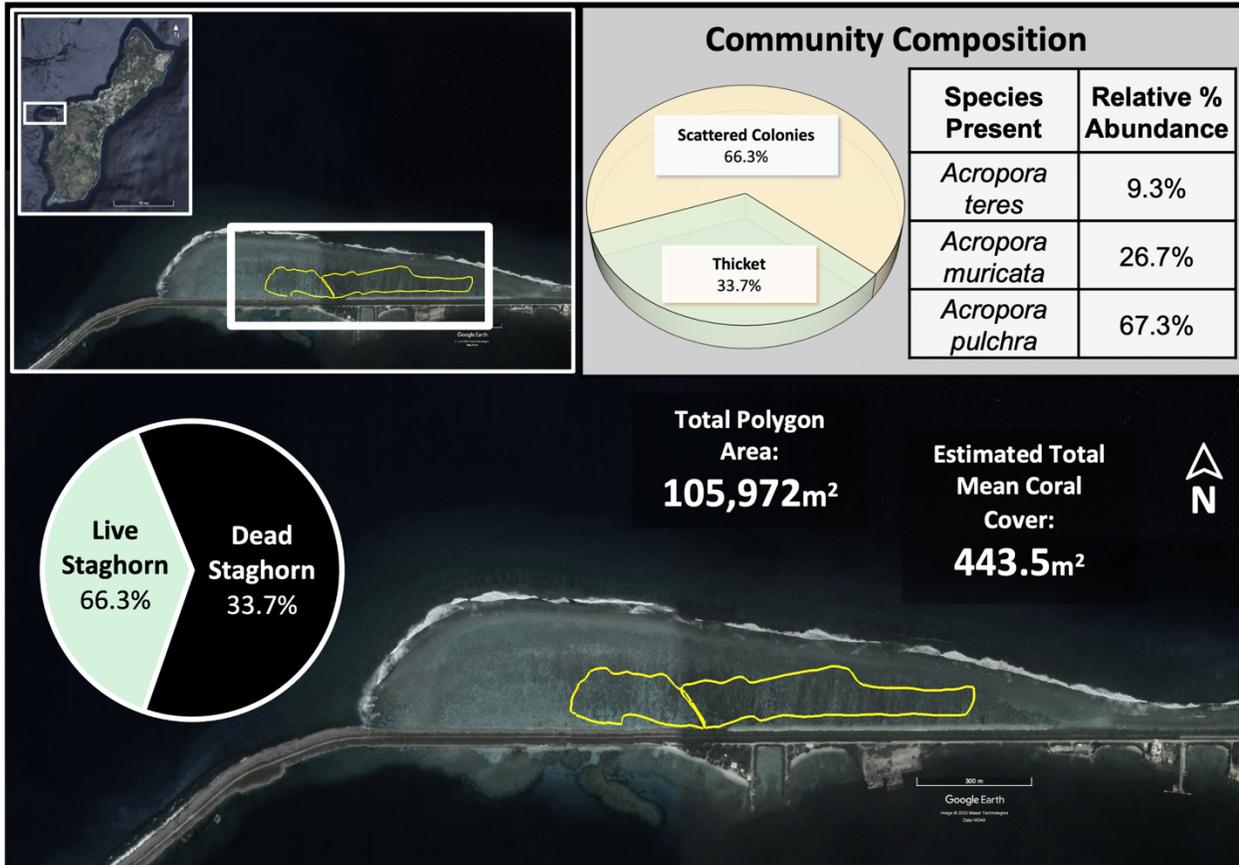
## TEPUNGAN CHANNEL & PITI WEST (Sites 11&12, Fig. 4)



These sites constitute the southwestern border of the Piti Bomb Holes Marine Preserve. They are characterized by high coral cover and community diversity. The coral community is dominated by massive *Porites* on the exposed reef flat border and *A. cf. pulchra* on the more protected inner reef flat and channel (upper photo). High wave energy, high water quality and a healthy associated biological community made this area a priority reef for restoration sites. Further, this area was the only site observed to be less impacted by 2013-2017 bleaching events, particularly for corals growing in the human-made Tepungan Channel; dead staghorn was estimated at 5.6%. Interestingly, several large colonies of an as-yet-undescribed staghorn *Acropora* were discovered at the bottom of the Tepungan Channel (lower photo). Occasional extreme low tide exposure, predation from *Drupella*, and high wave action resulting in occasional physical disturbance are the dominant stressors to these coral communities.



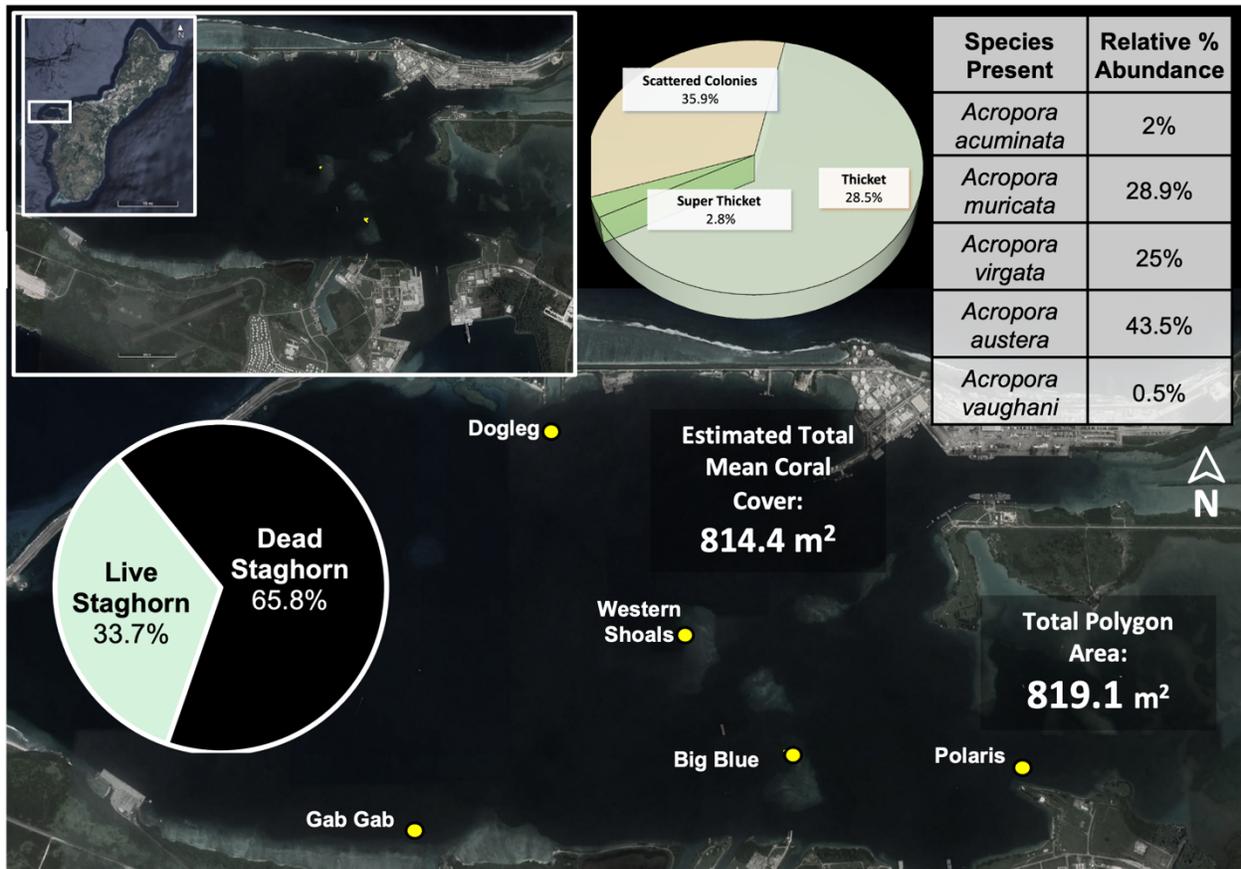
# LUMINAO (Site 13, Fig. 4)



This is a wide, shallow reef flat that developed on the seaward northern border of the Glass Breakwater, after it was built in WWII. The reef community is dominated by *Porites*, and characterized by high flushing, low sedimentation rates, and high coral cover (upper photo). It is host to non-contiguous, scattered small thickets of staghorn *Acropora*, many of which have suffered decline and mortality in recent decades, as observed in patches of dead skeleton and rubble piles. However, healthy thickets do remain and three species are found within this reef community (lower photo). Bleaching-related mortality, *Stegastes* farming, and White Syndrome and Brown Band Disease continue to be ongoing stressors for the scattered populations of *A. muricata*, *A. teres*, and *A. pulchra*.



# APRA HARBOR (Sites 14-17, Fig. 4)



Located in Western Guam, Apra Harbor is an active deep-water harbor sheltered by the Glass Breakwater and the fringing reef of Luminao in the north, and Point Udall in the south. The harbor is shared between U.S. Naval Base Guam and the Commercial Port of Guam, and is used by recreational boaters, snorkelers, and divers. Characterized by high turbidity, high sedimentation and relatively low wave action, this site has a narrow reef fringe dominated by *Porites rus*, bordered by steep walls that drop to a depth of 30m (right photo). The broad, sandy bottom is interrupted by scattered shoals concentrated in the eastern apex of the Harbor that are favored dive sites supporting dense and diverse coral communities. Staghorn *Acropora* are limited to small thickets on upper surfaces of shoals and along shallow reef community margins, with the exception of *A. vaughani*, which was observed at depth. The site hosts a unique assemblage of species found rarely in other parts of the island, but was badly impacted by the 2013-2017 bleaching events. Staghorns, in particular, were observed to be both severely bleached and impacted by localized White Syndrome and Brown Band Disease outbreaks in 2017 surveys.





**Big Blue Reef** is a shoal near the southeastern border of the Inner Harbor, named after the dry dock facility formerly installed at that site. *Acropora muricata* was previously abundant at this site, but was decimated by disease and bleaching by 2017. The photo shows 100% staghorn mortality observed in 2021.



**Gab Gab Reef** is a shallow shelf of high coral cover along the southern rim of the Harbor. While the coral community is dominated by *Porites* spp., healthy *A. austera* colonies are abundant (pictured here). A deeper reef, GabGab II, is a popular dive spot that supports the last known live population of *A. vaughani*.



**Western Shoals** is a large, shallow shoal near the apex of the Harbor. Coral cover around the fringe is high, and dominated by *Porites rus*, though physical damage from ship groundings and other human interactions has degraded the coral community on the upper surface. High bleaching mortality has eliminated a large thicket of *A. muricata*. Isolated colonies of *A. austera* remain (pictured here).

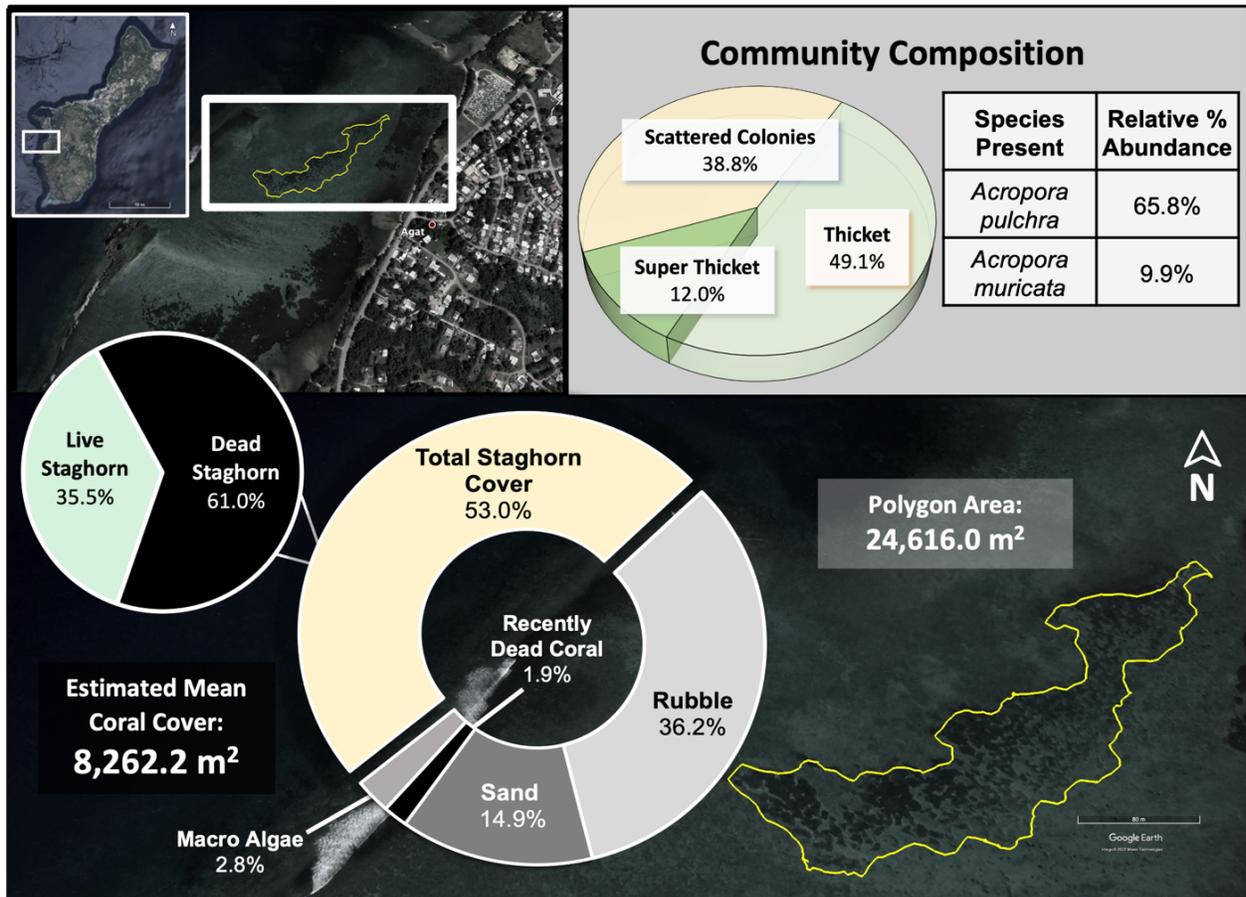


**Dogleg Reef** is a *Porites*-dominated mound inner to the Glass Breakwater, and is a popular snorkel site. A small patch of *A. virgata* (pictured here) within a larger dead thicket survived after 2017. Due to the high risk of total mortality, these living clusters were removed, fragmented, and transferred to the Merizo Nursery, where they are thriving and are being outplanted into Cocos Lagoon.



**Polaris Point** is a small, reef community near the northeaster entrance to the Inner Harbor. Water quality is poor but the site supports limited coral growth. Small thickets of *A. austera* and *A. virgata* (pictured here) survive.

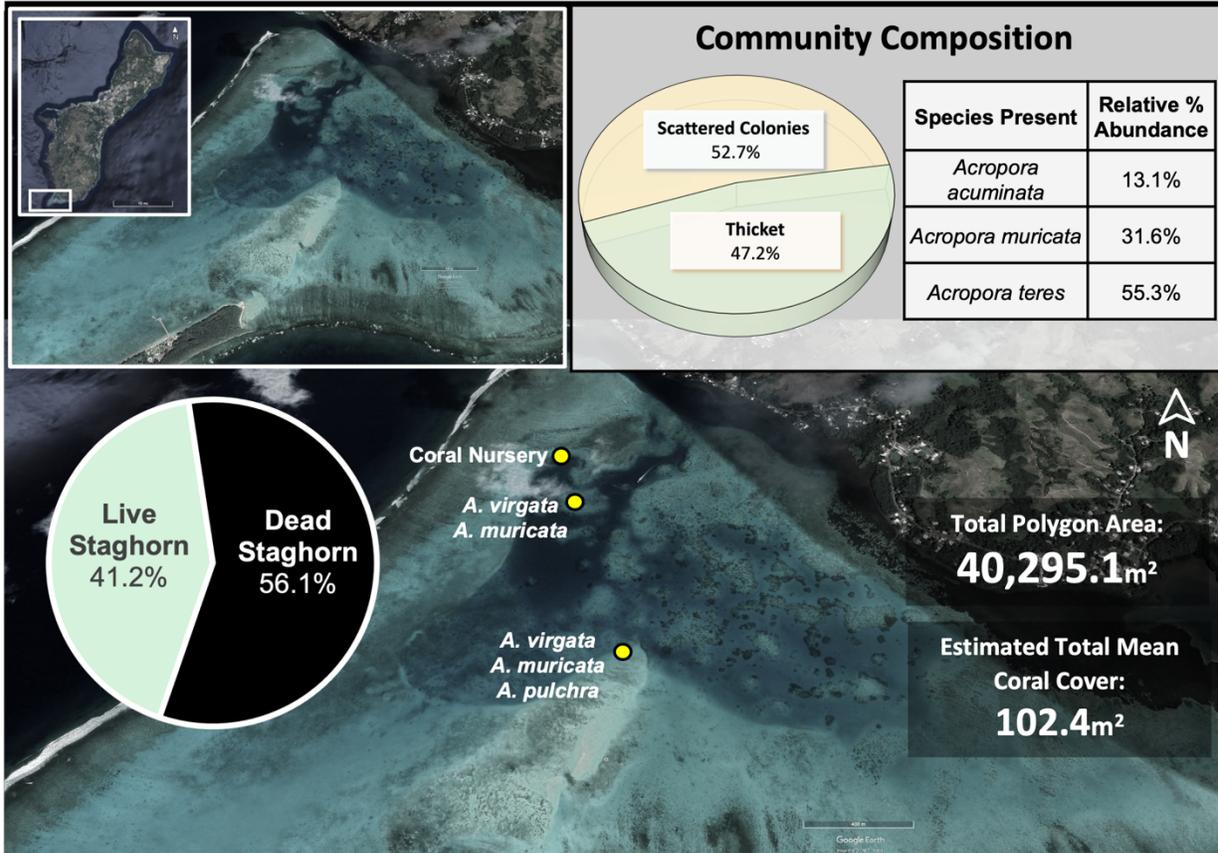
# AGAT CEMETARY (Site 18, Fig. 4)



Found on the southwestern coast of Guam, this site is characterized by a broad and shallow sand bottom, a coastal mangrove stand, and a depth range of 1-3 m. Water quality is poor and marked by high terrestrial runoff, low water flow, and high turbidity. Fishing pressure is high and storm damage in 2015 created a persistent rubble field which impinges on survival coral thickets (upper photo). Coral cover, condition, and diversity, are low. Scattered colonies and larger thickets of *A. cf. pulchra* and *A. muricata* were observed within an extensive polygon that also contained large rubble fields surrounding the thickets. Storm surge, possibly from Typhoon Dolphin (2015), repeated bleaching events, silt deposition, disease (Black Band Disease; lower photo), trampling, and an overharvested herbivore population have all contributed to ongoing mortalities at this site, with estimated decline of 25% in recent years.



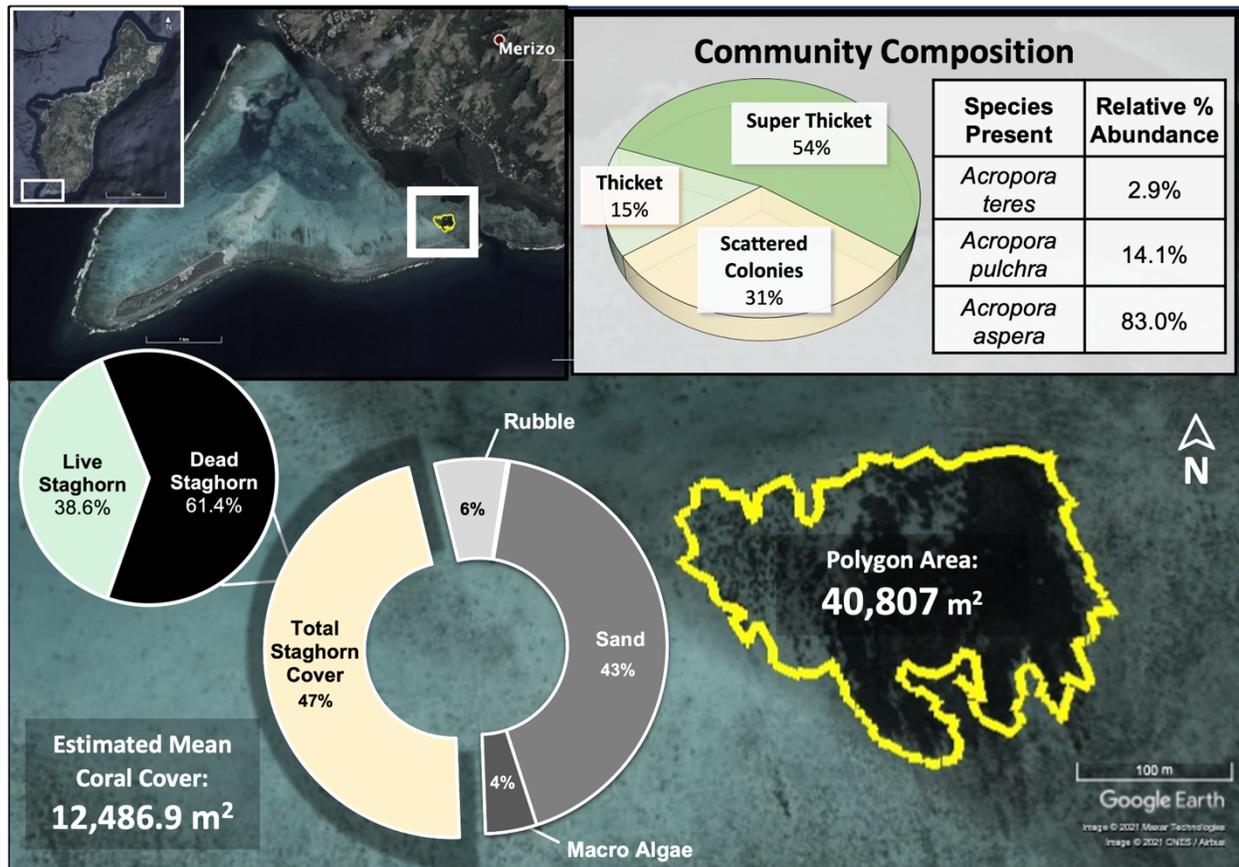
# COCOS LAGOON (Site 20, Fig. 4)



Situated at Guam’s southern tip and protected by Cocos Island and an extensive fringing reef, Cocos Lagoon features a sandy bottom mixed with pavement and coral mounts (left photo) and ranges from 3 m to 17 m. Low wave energy combined with high sedimentation from the Geus and Manell rivers make for a turbid, eutrophic environment with low water quality. Scattered patches of *A. acuminata*, *A. muricata* and *A. teres* within the lagoon have been noted on the above map, but overall populations of staghorn have been reduced to patches of rubble (middle photo) with an estimated decline of 55% caused by bleaching-related mortality. Continued stressors to these populations include predation, periods of extreme thermal stress and disease prevalence. One large thicket of *A. virgata* impacted by extensive *Stegastes* farming lies adjacent to the Merizo Coral Nursery (right photo).



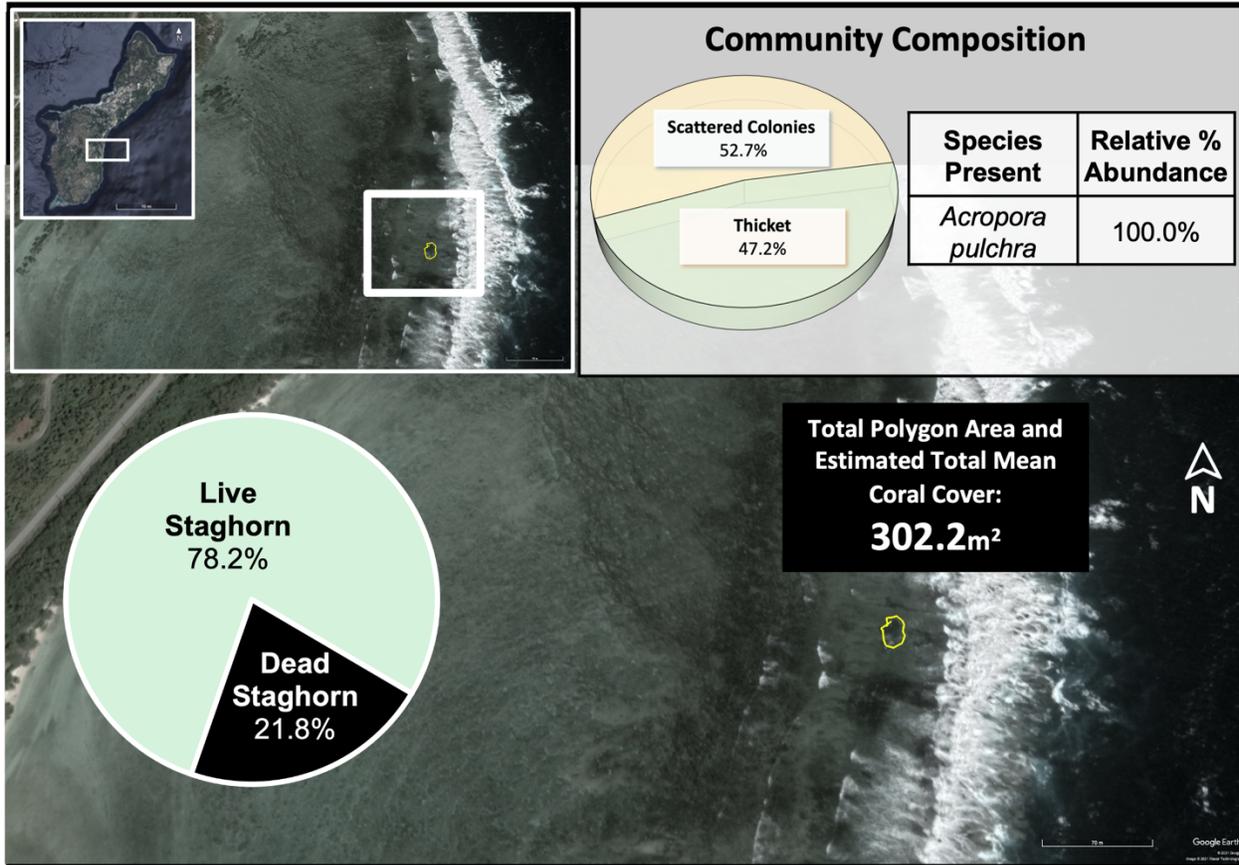
# ACHANG REEF FLAT (Site 21, Fig. 4)



Located in the easternmost margin of Cocos Lagoon, Achang reef flat is just outside the Achang Marine Preserve border, west of Manell Channel. It is characterized by mixed pavement, sand, and seagrass beds extending nearshore to Guam’s most developed mangrove forest. An extensive thicket of *A. aspera* represents the last remaining wild population of this species on Guam (upper photo). Scattered thickets of *A. cf. pulchra*, and *A. teres* are found along the western border of the thicket; depth ranges from 1.5 m to 3 m. While Achang is well flushed due to its position near the Manell Channel and the reef crest, low tide exposure, overgrowth by the coral-killing sponge *Terpios hoshionota* (lower photo), thermal stress, and *Stegastes* algal farming have impacted coral health, particularly within the center of the large thicket, resulting in an estimated 30% staghorn loss. While recovery in the center of the thicket is low, colony numbers are increasing to the west of the thicket, which will hopefully result in expansion of this thicket.



# TOGCHA REEF FLAT (Site 23, Fig. 4)



This site hosts the only eastern population of staghorn *Acropora* on Guam, and is the shallowest of all sites, with exception of Urunao. The reef flat is wide and dominated by pavement; the coral community is diverse and dense but limited to the fringe inner to the reef crest (upper photo). Thus, in contrast to the western-facing reefs, this site is characterized by very high wave action and flushing, and turbulent conditions from the direct exposure to northeastern swells brought in by the northeast trade winds. Small, scattered colonies of *A. cf. pulchra* were found closest to the reef crest (lower photo). Repeated 2015 low-tide exposure events resulted in mortality of 65%. However, recovery has been high and a small but thriving cluster of colonies remain. Extreme low tide exposure and inadequate depth are likely to prevent this population from expanding despite high water quality.



