



**NOAA
FISHERIES**

Spatiotemporal Trends of Benthic and Reef Fish Communities in the Mariana Archipelago

Laura Gajdzik, Kurt Ingeman, Tye L. Kindinger, and Thomas Oliver

NOAA Technical Memorandum NMFS-PIFSC-152
Pacific Islands Fisheries Science Center
National Oceanographic and Atmospheric Administration
U.S. Department of Commerce
December 18, 2023

Spatiotemporal Trends of Benthic and Reef Fish Communities in the Mariana Archipelago

Laura Gajdzik^{1,2}, Ingeman Kurt^{1,2}, Tye L. Kindinger¹, and Thomas Oliver¹

¹ Pacific Islands Fisheries Science Center
National Marine Fisheries Service
1845 Wasp Boulevard
Honolulu, HI 96818

² Cooperative Institute for Marine and Atmospheric Research
University of Hawaii
1000 Pope Road
Honolulu, Hawaii 96822

NOAA Technical Memorandum NMFS-PIFSC-152

December 2023



U.S. Department of Commerce

Gina Raimondo, Secretary

National Oceanic and Atmospheric Administration

Richard W. Spinrad, Ph.D., NOAA Administrator

National Marine Fisheries Service

Janet Coit, Assistant Administrator for Fisheries

About this report

The Pacific Islands Fisheries Science Center of NOAA's National Marine Fisheries Service uses the NOAA Technical Memorandum NMFS-PIFSC series to disseminate scientific and technical information that has been scientifically reviewed and edited. Documents within this series reflect sound professional work and may be referenced in the formal scientific and technical literature.

Cover photo: A large aggregation of jacks (Carangidae) surround a diver conducting reef-fish surveys for the NOAA National Coral Reef Monitoring Program (NCRMP) in June 2022.

Recommended citation

Gajdzik L, Ingeman K, Kindinger TL, Oliver T. 2023. Spatiotemporal trends in benthic and reef fish communities in the Mariana Archipelago. U.S. Dept. of Commerce, NOAA Technical Memorandum NMFS-PIFSC-152, 45p. 45. doi:10.25923/7efh-qt23

Copies of this report are available from

Pacific Islands Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
1845 Wasp Boulevard, Building #176
Honolulu, Hawaii 96818

Or online at

<https://repository.library.noaa.gov/>

Table of Contents

List of Figures	iii
List of Tables	v
Executive Summary	vi
Introduction	1
Methods	3
Data Compilation	3
Benthic data	3
Fish data	4
Defining Reporting Downscaled Sectors	5
Producing Data Summaries	6
Region-scale	6
Island-scale	6
Sector-scale	7
Metadata	7
Statistical Analysis for the Island- and Sector-Scales	7
Results	8
Data Summary	8
Benthic Cover	8
Regional-scale	8
Island-scale	10
Sector-scale	12
Fish Community	17
Regional-scale	17
Island-scale	18
Sector-scale	20
Discussion	25
Declines in Coral Cover and Shifting Benthic Communities	26
Variation in Fish Biomass	26
Spatial Variation and Correspondence to Potential Reef Resilience	27
The Influence of Depth	30
Limitations and Future Research Directions	30

Take Home Messages	31
Acknowledgments	32
Literature Cited	33

List of Figures

Figure 1. Location map of the populated (inhabited) islands in the Mariana Archipelago.	2
Figure 2. Functional groups of benthic cover through time for populated islands (A, C) and remote islands (B, D).	9
Figure 3. Trajectories of benthic community (calcified and non-calcified living covers) for (A) populated and (B) remote islands.	10
Figure 4. Percent coral cover (only scleractinian corals) for each island in the Mariana Archipelago across all years combined.	11
Figure 5. Benthic functional group percent cover trends for each of the populated islands	11
Figure 6. Trends in coral cover (mean \pm standard error) over time for populated islands.	12
Figure 7. Reporting sectors for Guam with sector-scale trends in coral cover for (A) each sector and (B) per depth bin per sector. Lines show the smoothed trends over time.	13
Figure 8. Reporting sectors for Saipan with sector-scale trends in coral cover for each sector. Lines show the smoothed trends over time.	14
Figure 9. Reporting sectors for Tinian with sector-scale trends in coral cover for each sector. Lines show the smoothed trends over time.	15
Figure 10. Reporting sectors for Rota with sector-scale trends in coral cover for each sector. Lines show the smoothed trends over time.	16
Figure 11. Mean fish biomass across all years combined (A) for the populated (yellow) and remote (green) islands and (B) over time, and (C) mean species richness.	17
Figure 12. Mean fish biomass of trophic groups over time for the populated (A) and remote (B) islands in the Mariana Archipelago.	18
Figure 13. Mean fish biomass (A) and species richness (B) across all years combined for each island in the Mariana Archipelago, colored by human presence: populated (yellow) and remote (green).	19
Figure 14. Fish biomass for each populated (yellow) island in the Mariana Archipelago. Mean and standard errors are shown as well as the smoothed curves. Asterisk indicates significant trend over time (GAMM).	19
Figure 15. Mean biomass of fish trophic groups over time for each populated island in the Mariana Archipelago.	20
Figure 16. Mean fish biomass and standard errors per sector in Guam. The lines represent loess regressions. Asterisks indicate significant trend over time (GAMs).	22
Figure 17. Mean fish biomass and standard errors per sector in Saipan. The lines represent loess regressions. Asterisks indicate significant trend over time (GAMs).	23
Figure 18. Mean fish biomass and standard errors per sector in Tinian. The lines represent loess regressions. Asterisks indicate significant trend over time (GAMs).	24

Figure 19. Mean fish biomass and standard errors per sector in Rota. The lines represent loess regressions. Asterisks indicate significant trend over time (GAMs)..... 25

List of Tables

Table 1. Sectors that showed significant trends in total fish biomass over time (p-value from GAMs)	21
Table 2. Sectors from the four populated islands of the Mariana Archipelago assigned to different categories of resilience based on coral % cover relative to 2015 estimates of relative resilience potential	29

Executive Summary

Long-term, large-scale monitoring programs are critical for assessing the resilience of coral reefs to global climate change. Resilience is defined as the ability of reefs to maintain key functions by either resisting the environmental changes or recovering from them (McLeod et al. 2019; Shaver et al. 2022). However, to enable coral reef managers to support resilience through effective management interventions, monitoring programs need to be able to capture the ecological processes that underpin resilience at management-relevant scales and over a long period of time. The National Coral Reef Monitoring Program (NCRMP) was explicitly designed to summarize coral reef site-level data at the regional and island scales. While the results are geographically comprehensive, this sampling design limits the utility of the NCRMP dataset to inform local resource management decisions at sub-island scales. Accordingly, managers typically rely on smaller-scale efforts that trade spatial comprehensiveness for finer spatiotemporal resolution. To reconcile managers' scale of interest and better leverage NCRMP data, we present an effort to integrate NCRMP with local coral reef monitoring data to assess the temporal variation in fish and benthic communities over the last couple decades, during which heat stress events and acute disturbances (e.g., typhoons, crown-of-thorns outbreaks) have occurred. We identified common community metrics from all monitoring programs, compared these metrics between populated and remote islands, and analyzed their trends at the island- and downscaled sector-scales (sub-island spatial units that are homogeneous in benthic cover).

Our integrated benthic data set (from NCRMP and our jurisdictional monitoring programs) resulted in 2,298 observations from 1,800 unique locations across the Marianas and spanned two decades. From these data, we observed a general decline in hard coral cover which was accompanied by a substantial increase in turf algae across the archipelago. These trends were present at smaller spatial scales (islands and sectors). Specifically, coral cover significantly declined at three of the four populated islands and in 50% of the sectors. Unlike benthic data, we were unable to combine NCRMP fish data with our jurisdictional partners' programs due to differences in methodology, impeding the estimation of reliable biomass estimates. Thus, only using NCRMP fish data (representing 9,090 observations from 1,338 unique sites), our results revealed that populated islands supported, on average, half the biomass of remote islands, especially for piscivores that include large mobile predators. Fish biomass trends varied across the populated islands and either decreased by 2022 or, in contrast, slightly increased over time. Such variability was also observed at the sector level and across depths, emphasizing the complex response of fish communities at various spatial scales. When combining both coral and fish trends to gauge resilience, our results revealed evidence of reef resistance and recovery in fish biomass for some sectors which represent potential good candidates for resilience-based spatial management. Overall, this project combined different data streams, covered a wide spatiotemporal scale, and employed a spatial downscaling approach to unveil patterns of resilience at management-relevant scales which were otherwise masked or undetected when investigating trends at island or regional scale.

Introduction

As ocean conditions shift in response to global climate change, marine heatwaves are increasing which directly threatens coral reefs' functioning and compounds the effects of local stressors (Hughes et al. 2018). Widespread loss of coral reefs following mass bleaching events has emphasized the role of resilience-based management (RBM) to support natural processes of resistance and recovery (McLeod et al. 2019) and even inform restoration efforts (Shaver et al. 2022). Resilient reefs are those that are less likely to be transformed into a noncalcified, algal-dominated state by either (i) resisting changes (i.e., less affected by changes, such as maintaining high coral cover and/or being less impacted by bleaching) or (ii) recovering (i.e., returning to a pre-disturbance state by rapid coral growth or high coral recruitment) (Shaver et al. 2022).

Large-scale, long-term monitoring programs play a key role in quantifying the resilience of coral reefs to environmental stressors through time and across gradients of environmental conditions and human impacts. These large-scale efforts can inform RBM by identifying locations with differential levels of resistance to stressors and document the processes of loss and recovery. Yet most local monitoring efforts are either temporally-comprehensive but localized (e.g., one site surveyed for a decade) or spatially-widespread but explicitly temporal in nature (e.g., dozens of sites surveyed only once). While extremely valuable, such efforts only capture a snapshot of resilience (e.g., McClanahan et al. 2012), which may not adequately capture the realized histories of resistance and recovery from warming events or other disturbances (Oliver et al. 2020).

In contrast, geographically comprehensive long-term monitoring programs mainly provide information at large regional or island scales. For example, the National Coral Reef Monitoring Program (NCRMP) was explicitly designed to allow inference at large spatial scales with a “wide-but-thin,” spatially randomized sampling design. While NCRMP provides data across broad gradients of environmental conditions (Brainard et al. 2015), the utility of the NCRMP data set for informing local-scale resource management decisions is limited. Thus, there is a mismatch between jurisdictions' monitoring (i.e., site-specific, temporally-restricted, or question-specific, such as gauging the effects of bleaching) and NCRMP scales (across the U.S. Pacific).

One approach to reconcile these different survey programs is to define *sectors* at a sub-island scale, which is the most relevant scale for RBM. Oliver and colleagues (2020) document the statistical methods to spatially downscale the NCRMP Pacific Reef Assessment and Monitoring Program data, which uses hierarchical methods to define clusters of monitoring sites based on similar benthic metrics (e.g., coral cover, algae cover). Such downscaling methods can be extended to incorporate data from several monitoring programs into a single analysis, spanning decades of environmental disturbances.

Guam and the Commonwealth of the Northern Mariana Islands (CNMI)—hereafter referred to as “Marianas”—are candidate regions for RBM (Figure 1). The Marianas experienced back-to-back environmental disturbances, particularly in the past decade. Massive bleaching events occurred yearly from 2013 to 2017 and were exacerbated in 2015 by extreme low tides caused by an El Niño event (Raymundo et al. 2019).

Likewise, crown-

of-thorns (COTS) outbreaks and super typhoons have also been causing significant damages since the 2010s. Additionally, the Marianas are composed of remote (unpopulated) and highly populated islands, whereby local stressors (such as land-based pollution) can act additively or synergistically to global warming.

Thus, the Ecosystem Sciences Division at the NOAA Pacific Islands Fisheries Science Center proposed a project to integrate NCRMP and local coral reef monitoring to assess the temporal variation in fish and benthic communities over the last decades during which the Marianas have been subjected to successive acute disturbances. Combining NCRMP's wide-but-thin information with local monitoring data can illuminate patterns of resilience of reef communities over a long period of time and over broader spatial scales. This approach is particularly insightful when comparing trends in fish and benthic cover between remote and populated, urbanized islands to determine the generality of patterns corresponding with the presence of local human populations. We will first explore whether data from NCRMP sampling and jurisdictional partners' monitoring programs can be integrated into a single data set by identifying common community metrics. Additionally, to further enhance management decision-making, we will investigate trends in reef communities and patterns of resilience at relevant spatial units by employing a downscaling approach to define *sub-island scale* reporting sectors, which are ecologically informed (similar in benthic cover) instead of being *a priori* defined by cardinal points, protection status, and/or general wind direction (i.e., windward vs. leeward).

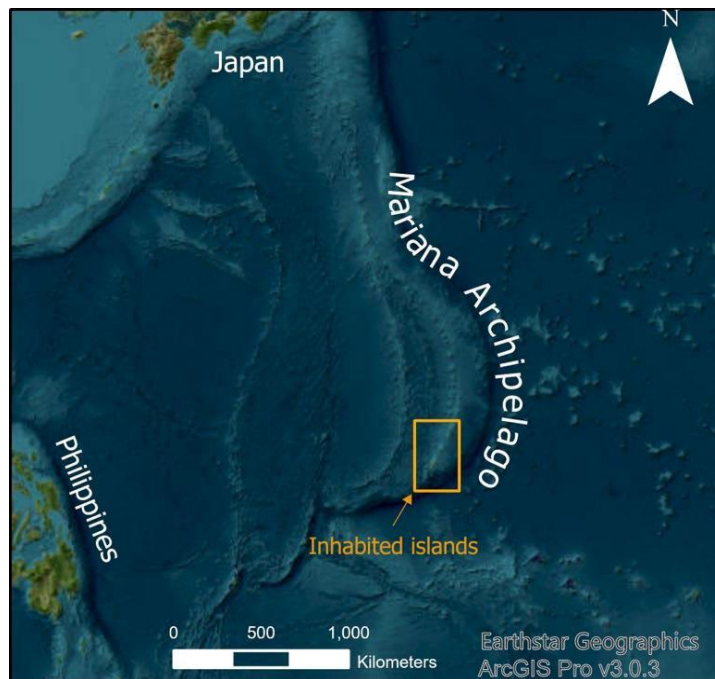


Figure 1. Location map of the populated (inhabited) islands in the Mariana Archipelago.

Methods

We describe the methods in five sections in parallel with the general project approach: (1) data compilation, (2) defining reporting downscaled sectors, (3) producing summaries, (4) metadata, and (5) statistical analyses.

Data Compilation

Beginning in 2018, PIFSC ESD worked with our jurisdictional partners in Guam and the CNMI to compile a list of candidate benthic and fish community data sets. Data were compiled from a variety of academic (e.g., the University of Guam Marine Lab), territorial government (e.g., CNMI Bureau of Environmental and Coastal Quality [CNMI BECQ], Department of Agriculture), and federal government (NOAA NCRMP) sources. These different data sets were screened for applicability to project goals and potential to be integrated into a single data set.

Benthic data

Considerations included reef location (i.e., forereef vs. lagoon), sampling methods (e.g., fixed-site vs. stratified-random, photo-quadrats vs. timed-swims or line point intercept), and response metrics (e.g., benthic invertebrates cover vs. demographics) collected. Two monitoring programs that collected information on individual coral colonies and demographics rather than benthic percent cover were not retained based on the rationale that data from those programs were created for targeted questions (e.g., counts of bleached coral colonies and diversity-based metrics for resilience) and time- and island-specific (e.g., Guam, only in 2016–2017), and thus outside the scope of this study.

Of the six candidate sources of data for benthic cover, four were included in the combined data set:

- NOAA NCRMP Pacific reef-monitoring surveys: Stratified random sampling of benthic transects in three depth bins spanning nearly two decades (2005, 2007, 2009, 2011, 2014, 2017, and 2022)
- University of Guam Long-term Monitoring Program: Stratified random (2013) and quasi-permanent sites (2015–2021)
- CNMI BECQ Long-term Marine Monitoring Program: Fixed sites with multiple transects-within-site spanning 2000–2018 (annual surveys), and
- CNMI BECQ / University of Queensland Saipan Surveys: Non-repeated survey effort from a single site in 2016 and multiple sites in 2020

Estimates of benthic cover were primarily generated from benthic substrate photographs (hereafter referred to as “photoquadrats”) and using the line-point intercept methodology. Photoquadrats are commonly taken along a 30-m transect at every meter

at each site. The benthic photoquadrat imagery is then analyzed using the web-based annotation tool such as CoralNet (Beijbom et al. 2015); generally 10 random points are selected per photo. The line-point-intercept methodology consists of consecutively placing 25-m line transects (with a usually 5-m inter-transect distance) to determine the benthic composition at pre-determined intervals along the transect line. All living benthic elements (e.g., coral, algae, and other sessile invertebrates) are identified to the lowest taxonomic level possible, often substituting functional group categories for turf algae and crustose coralline algae.

The resulting list of data sets was then screened for common response metrics that could be calculated from the raw data. Given the diversity of response metrics collected across the different data sets, a tradeoff emerged between the taxonomic resolution of the responses and the number of data sets represented. In accordance with one of the aims of the study—to synthesize NOAA and partner data—we chose to focus on relatively coarse metrics of benthic functional groups (i.e., benthic % cover) that allowed us to retain the maximum number of data sets. Benthic diversity measures were not explored in downstream analyses because they are sensitive to the survey effort and area of subsamples within each site, and by the skill of the observer in distinguishing among cryptic taxa, all of which drastically varied among datasets.

Where raw data included sub-samples within sites (e.g., multiple, non-independent transects at a single study site), site-level means were calculated to ensure comparability among data sets. Individual data sets were then compiled into a common format with site-level percent cover of (i) *hard coral* (strictly scleractinian live corals), (ii) *macroalgae* (excluding turf), (iii) *turf*, and (iv) *crustose coralline algae* (CCA). In addition to these functional groupings, we also investigated trajectories and trends over time between *calcified cover* (i.e., corals, CCA, and other calcifiers such as *Halimeda* algae) and *non-calcified cover* (non-calcifying algae, sponges, and other non-calcified living substrates, excluding pavement, rock, sand, and other non-living substrates).

Fish data

We attempted to integrate fish data from NCRMP and our jurisdictional partners in Guam and the CNMI. Seven different data sets were shared with us from different groups at the NOAA PIFSC, the University of Guam, and the Department of Agriculture. However, the nature of fish monitoring surveys creates several challenges that preclude the integration of data—namely the derivation of common abundance, biomass, or diversity metrics—when survey efforts do not conform to a common spatial scale, sampling design, and survey methodology.

Specifically, partners' data could not be integrated with archipelago-wide NCRMP surveys when their survey methods greatly differed (e.g., stationary point count [SPC] vs. line transects or timed-swims) and/or they targeted a different subset of fish species and sizes (i.e., all species and sizes from blennies to sharks vs. fish species over 40 cm, mainly including large and/or elusive species). These differences impact estimates in species richness, area covered, and depth surveyed, which ultimately affect abundance and biomass estimates, making it unreliable to integrate data from distinct

methodologies into a single dataset. For example, timed-swims such as roving surveys usually result in a higher species richness compared to other survey methods with the caveat that a higher number of surveys is required (e.g., Rassweiler et al. 2020). In contrast, belt surveys often under-estimate piscivore biomass but overestimate herbivore biomass (Williams et al. 2015). Finally, the focus of SPC survey design is estimation of composite groups of species rather than individual species (Heenan et al. 2017). Other data transformations, such as presence/absence or abundance ratio, were deemed out of scope for this report, which was to retain a focus on gauging spatiotemporal trends in fish and coral communities following recurring disturbance events. While our jurisdictional partners' data sets remain valuable for a variety of other targeted analyses, only SPC surveys from NOAA NCRMP sampling were retained for the purposes of this study.

In brief, SPC surveys consist of a pair of scuba divers who identify, count, and size all fishes to the nearest centimeter (total length) within cylindrical survey areas with a 7.5-meter radius. In the first five minutes, divers enumerate all fish species within the cylinder; after that, divers begin the tallying portion of the count in which they systematically work through their species list and record the number and visually estimate the size of each individual. The tallying portion is conducted as a series of rapid visual sweeps of the plot, with one species-grouping counted per sweep. Surveys are conducted between 1 and 30 meters depth, and in the Mariana Archipelago, almost exclusively on forereef habitats. Additional details regarding the SPC method and underlying NCRMP survey design can be found in Ayotte et al. (2015) and Heenan et al. (2017).

Response variables for fish data are computed as follows. Species count and size between the pair of SPC divers are pooled and averaged per survey. From this, we calculated the fish biomass for each species using the allometric length-weight conversion: $W = a \times L^b$, where parameters a and b are species-specific constants, L is the fish length, and W is weight in grams. *Biomass* estimates are then summarized for each particular spatial scale (island, sector, site levels; additional details provided in the data summaries and statistical analysis section) and for each trophic group: herbivores, invertivores, piscivores, and planktivores.

Defining Reporting Downscaled Sectors

We followed the method developed by Oliver et al. (2020) to statistically downscale the data and define sub-island reporting sectors. The goals of downscaling are to (1) identify spatial sectors that are smaller than the initial survey design scale while retaining statistically robust sampling, (2) to define ecologically homogeneous sectors (rather than using *a priori* boundaries), and (3) to synthesize data from disparate sources and methodologies to extend spatiotemporal coverage.

Briefly, after compiling and integrating data spanning the last two decades (2000–2018), the downscaling method generates hierarchical, spatial “clusters” for each island by first converting survey points into individual polygons to identify groups of homogeneous, contiguous polygons through a neighbor-joining network. These networks connect

clusters to one another using ecological distance across four benthic categories (i.e., hard coral cover, CCA, sand/sediment, and total algal cover). The neighbor network is then pruned into a minimum spanning tree that retains only a single path joining all neighboring polygons which represents the minimum ecological distance among polygons, thereby grouping ecologically similar polygons together and leaving these groups separated by longer, between-group branches. By “cutting” this minimum spanning tree at its longest branch lengths, one can successively return cluster groupings that are spatially contiguous and maximally ecologically homogeneous. The optimal number of spatial clusters for each island is then determined by first setting a minimum cluster size (in this case, 15 points) and then balancing the number and size of the clusters against the statistical performance of the cluster set, as defined by AICc of models of benthic cover as a function of cluster ID and date (and the interaction between these variables). The total number of clusters per island varied between one for small and ecologically homogeneous islands and ten for larger and ecologically diverse islands. Finally, where the boundaries of the resulting spatial clusters closely approximated existing management units (e.g., marine reserves boundaries) or geographic breaks, we adopted the existing boundary in order to maximize the utility of the final reporting sectors to managers. Further details regarding the downscaling method are provided in Oliver et al. (2020).

Producing Data Summaries

We generated summaries of fish and benthic metrics at three main levels: (i) regional-, (ii) island-, and (iii) downscaled sector-scale (i.e., not the sectors that NCRMP commonly uses and refer to cardinal points and wind direction). To do so, raw data (survey-level data) were temporally averaged within a given year (regardless of sampling date) and then further averaged at the different spatial scales (see details below).

Region-scale

To illuminate broad-scale temporal trends, response metrics were first aggregated to the archipelago-wide scale and mean values were plotted over the study period. While this scale necessarily obscures much of the variation attributable to finer-scale location and depth, it provides a large-scale baseline against which to measure the performance of individual islands and sectors. For that particular scale, only descriptive trends were provided. Our benthic cover time series across the Marianas was also smoothed with a moving average of three years to account for NCRMP survey cycles.

Island-scale

Response metrics were then summarized at the island-scale to illuminate inter-island variability and facilitate comparisons among populated and remote islands. Again, such summaries compress observations with important distinctions but temporal trends that are robust to the merging of disparate data provide useful island-scale patterns from which to evaluate individual sectors.

Sector-scale

Finally, we analyzed trends for both coral and fish communities in each individual sector, which were generated by the spatial downscaling method described above. Site-level data were allocated to the appropriate reporting sector by merging the geospatial data produced by the downscaling process (sector polygons) with the response data using location coordinates for each survey (latitude and longitude).

Metadata

The list of all metadata variables for both benthic and fish data is as follows.

- *source*: the origin of the raw data (e.g., NOAA NCRMP)
- *island*: the official geographic name of the island where the survey occurred
- *method*: only for benthic cover: "photoquad" = points from photo quadrats annotated. "LPI" = field annotation using Line-Point Intercept method
- *site*: site identifier. For data sources that use only numeric, a string that identifies source was added
- *lat/long*: spatial data. Following the NCRMP convention, location data converted to degree decimal
- *year*: year in which surveys were conducted
- *date*: survey day. Following NCRMP convention, timing data in dd/mm/yyyy
- *depth* (meters): Following NCRMP convention, depth bins include shallow (0–6 m), mid (6–18 m), and deep (18–30 m).
- *sector*: spatial units resulting from the downscaling method (described above).

Statistical Analysis for the Island- and Sector-Scales

We ran analyses at the island- and sector-levels only for populated islands because managers indicated that they were a priority.

To investigate temporal trends in percent coral cover for each island, we first used generalized linear mixed models (GLMMs) with random intercepts for sectors and depth bins. The "method" design was dropped from our models because of little to no crossover between years and survey design methods and/or between survey designs and depth bins, resulting in variance-covariance matrices close to zero. GLMMs were fitted with a gamma distribution error and a log-link function. We also scaled the time variable by subtracting the mean and dividing it by the standard deviation to obtain continuous, standardized values for times. After that, we ran our analysis at the sector scale. For each individual sector, we used generalized linear models (GLMs) with coral cover as the response variables, time (scaled years) as explanatory variables, and depth bins as fixed variables. The goal is to determine whether coral cover increased or decreased over time and whether this trend varied over time per depth bin. The fit of all models was determined using the AIC, and we selected the optimal model when AIC values did not differ by more than 2. We further validated the optimal model by plotting the residuals against the fitted values. All models were computed with the package *lme4*.

To determine whether there was an increase or decrease in total fish biomass at the island and sector levels, we used generalized additive models (GAMs) and mixed models (GAMMs) instead of GLMMs/GLMs. While all of those models share similarities, GAMMs/GAMs allow us to explore nonlinear relationships between years and biomass response variables using smoothers with no *a priori* assumptions regarding the shape of the relationship. In the present study, our raw fish biomass data display such a nonlinear relationship with time (years), which further reinforced the use of GAMMs/GAMs. Similar to the GLMMs, we first investigated whether there was a significant change over time in fish biomass at the island scale and added the depth bin and sector as random effects. After that, at the sector level, we applied GAMs to determine whether depth had an effect on the fish biomass over time. All GAMs were fitted with an optimal number of knots [k] (varying between two and five), which was determined by comparing the estimated degree of freedom (EDF) to k. The EDF is a summary statistic specific to GAMs, which relates to the degree of non-linearity of a curve with the following corollary: the closer to 1, the more linear relationship, whereas values above 1 and over two suggest a highly non-linear relationship (Wood, 2006). We used a Gaussian distributed error term after log-transforming fish biomass data to normalize the residuals. Model assumptions were checked by plotting model residuals against fitted values using the package *gratia*.

All statistics and modeling were conducted in R (version 4.3.0).

Results

Data Summary

Together, the four sources we used for benthic cover provided 2,298 observations from 1,800 unique locations across the archipelago, spanning 2000 through 2022. It is important to note that more than 90% of surveys occurred after 2008, so inference about trends is most robust in the most recent decade of the data set.

For the fish data set, only NOAA NCRMP surveys were used, and these represented 9,090 observations from 1,338 unique sites across 13 islands in the Mariana Archipelago spanning over a decade (2011–2022).

Benthic Cover

Regional-scale

Across the Marianas, cover of scleractinian corals (hereafter, “coral cover”) declined steadily through time ([Figure 2, A&B](#)), with mean values decreasing by half over two decades (from 25% to 10% for populated islands and from 45% to 18% for remote islands). This temporal decline in coral cover was accompanied by a decrease in CCA and an increase in both algae functional groups, particularly turf algae. Furthermore, when percent cover of coral, CCA, and other calcified substrates are combined (collectively referred to as “calcifiers”), declining trends through time are further evident ([Figure 2, C&D](#)). Taken together, these changes in benthic cover at the regional-scale

show little indication of resilience and a benthos increasingly composed of non-calcifying organisms.

When investigating trajectories of calcified and non-calcified cover over time, the benthic community for both populated and remote islands progressed from a relatively high calcified cover (50–60%) to a high non-calcified cover (> 60%; [Figure 2](#)). It is worth noting that this striking pattern in shifting benthic cover composition between calcified and non-calcified organisms is partly due to the fact that that inverse relationships are common with proportional data falling into exclusive groups.

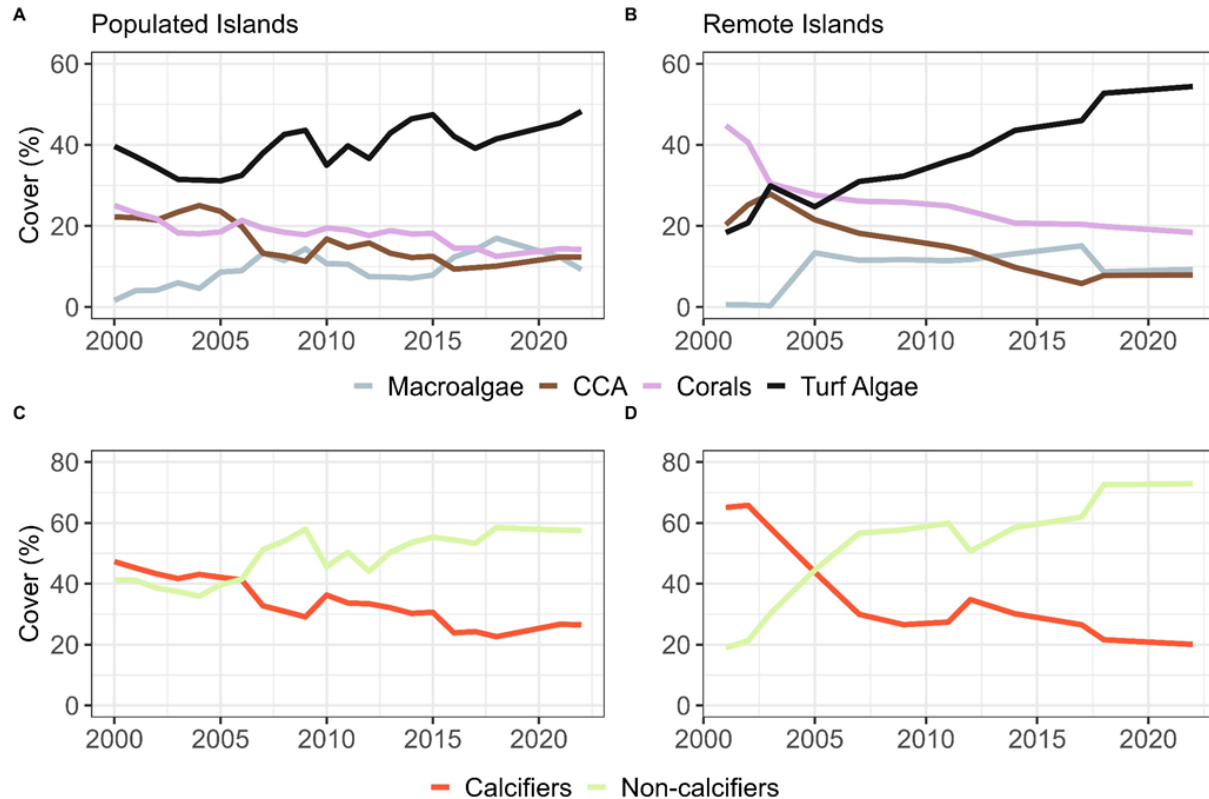


Figure 2. Functional groups of benthic cover through time for populated islands (A, C) and remote islands (B, D).

Benthic cover at populated islands was equally composed of both calcified and non-calcified cover types in early 2000s but after that, percent of non-calcified cover types progressively increased while calcified cover decreased. However, there is evidence of partial recovery with a slight rebound in calcified cover type in 2021 and 2022 ([Figure 3A](#)). In contrast, remote islands had a high calcified and low non-calcified benthos (60%, and 19%, respectively) in the early 2000s, but only two islands (Aguijan and Santa Rosa) were represented at that time. The calcified state of the benthos rapidly dropped over time, reaching the lowest point in 2022 of ~20% based on data from six remote islands ([Figure 3B](#)). Surprisingly, mean calcifier cover at remote islands is approximately the same at the populated islands.

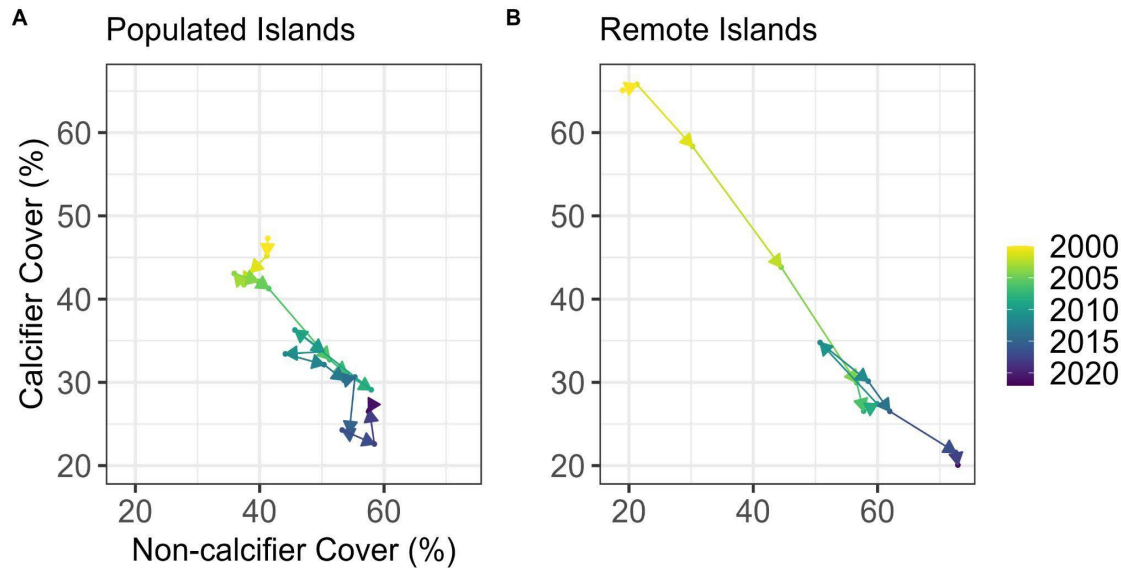


Figure 3. Trajectories of benthic community (calcified and non-calcified living covers) for (A) populated and (B) remote islands.

Island-scale

Collapsing the temporal data into a single mean per island reveals that coral cover for each island ranged between 6% and 22%, with two remote islands having the lowest and highest values (i.e., Farallon de Pajaros and Maug, respectively). Coral cover at the populated islands varied between 10% and 20%, with Rota having the lowest values and Saipan the highest (Figure 4). These values represent the average coral cover value over the last two decades.

When investigating changes only for the populated islands, patterns roughly followed those across the entire region (Figure 5). Over the past decades, there was an increase in turf algae concurrent with declines in coral cover and CCA, whereas trends for macroalgae were more ambiguous.

Out of the four populated islands, only Guam and Tinian experienced a significant decline in coral cover over time (Figure 6; GLMMs, $p < 0.05$). There was no significant decrease over time for Saipan and Rota (GLMMs, $p = 0.07$), although the overall pattern of Saipan's coral cover tends to decline when looking at the trends in mean values across years. These differences in significance of time at the island scale could be attributed to variation in coral cover at a smaller spatial scale such as at the sector scale and/or depth bin. Such differences are explored in the next section.

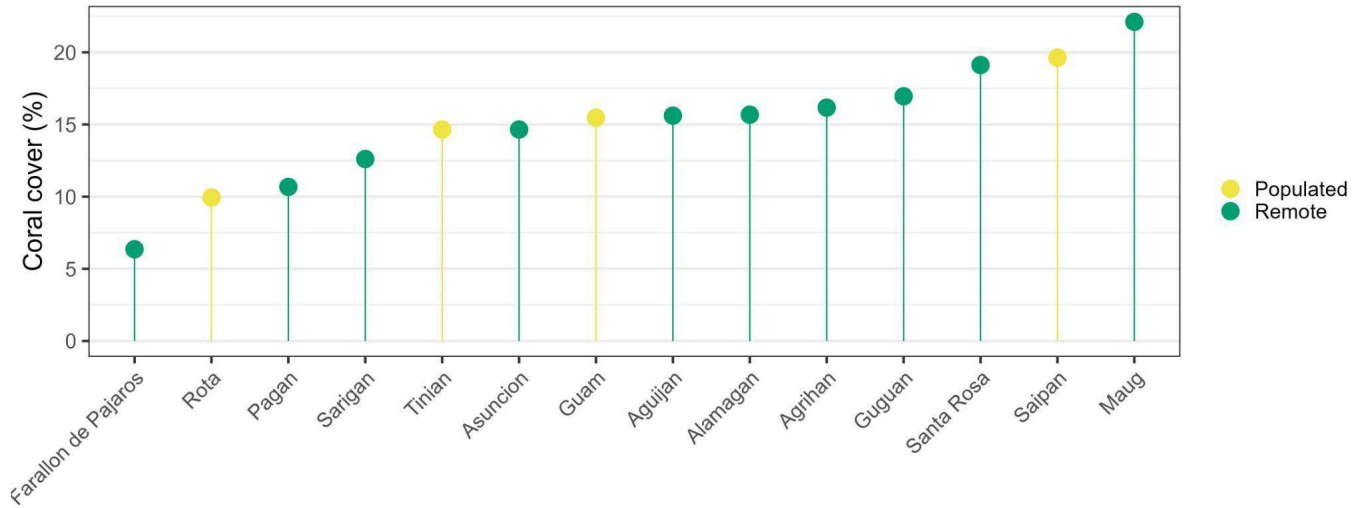


Figure 4. Percent coral cover (only scleractinian corals) for each island in the Mariana Archipelago across all years combined.

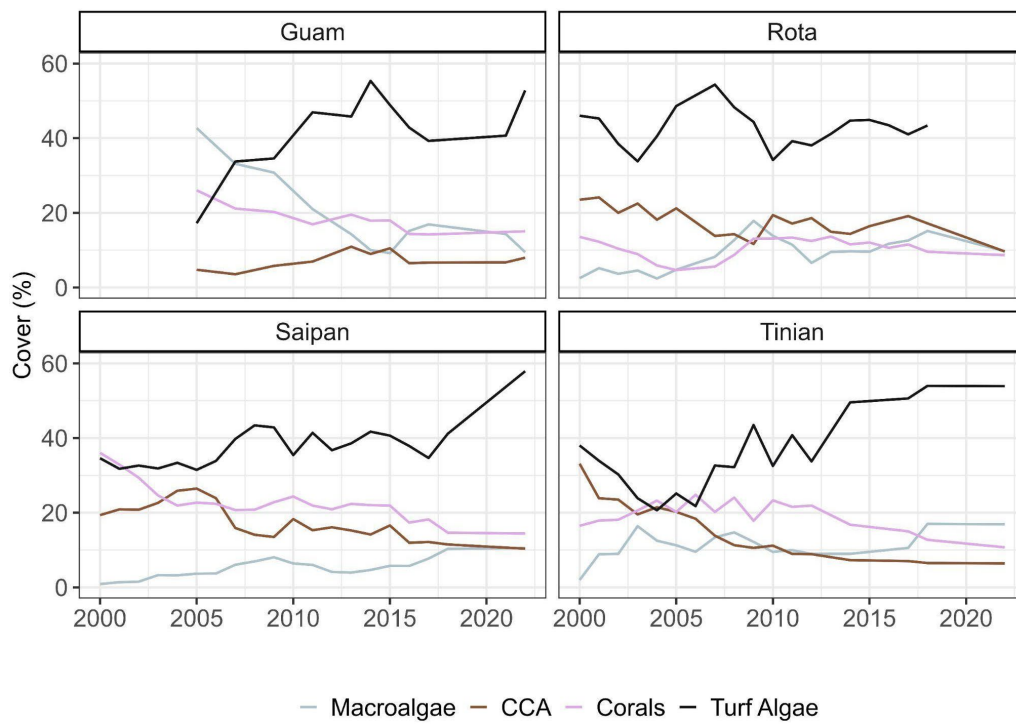


Figure 5. Benthic functional group percent cover trends for each of the populated islands

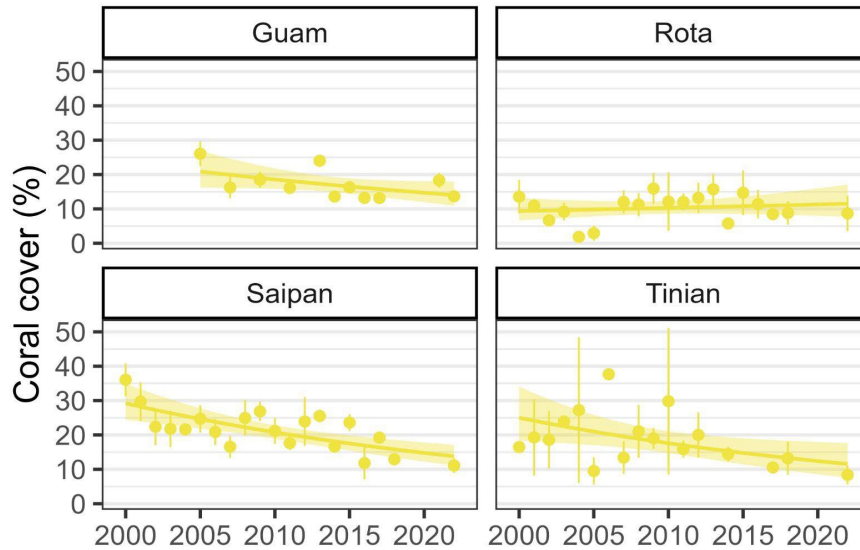


Figure 6. Trends in coral cover (mean \pm standard error) over time for populated islands.

Sector-scale

Our downscaling effort resulted in 10 reporting sectors in Guam, 9 in Saipan, 5 in Tinian, and 4 in Rota (Figures 7, 8, 9, 10).

Similar to trends across the Mariana Archipelago or at the island scale, most sectors had cover coral close to or below 10% by 2021 to 2022 and many displayed significant trends over time (Figures 7 & 9). In Guam and Tinian, nearly half of the sectors showed a significant negative relationship between coral cover and time, which was consistent across all three depth bins for Guam (GLMs, $p < 0.05$). Of notable importance, coral cover appeared to be depth-stratified, with generally less cover in deep reefs in Guam compared to mid and shallow depths (Figure 9). Similar trends exist for the sectors in Rota (figure not shown) but were not detected for Saipan and Tinian.

However, there remains a high degree of temporal variability across many sectors. Some exhibited coral cover that greatly fluctuated every year, most likely illustrating local variation in environmental factors (e.g., Sasanhaya Marine Reserve (MR) in Tinian, Southeast in Saipan) and/or lower survey effort (e.g., Harbor in Guam, West in Tinian). Coral cover in other sectors remained relatively similar over the years (e.g., North in Guam or West in Rota) and some seemed to have recovered, such as Piti and Northwest in Guam.

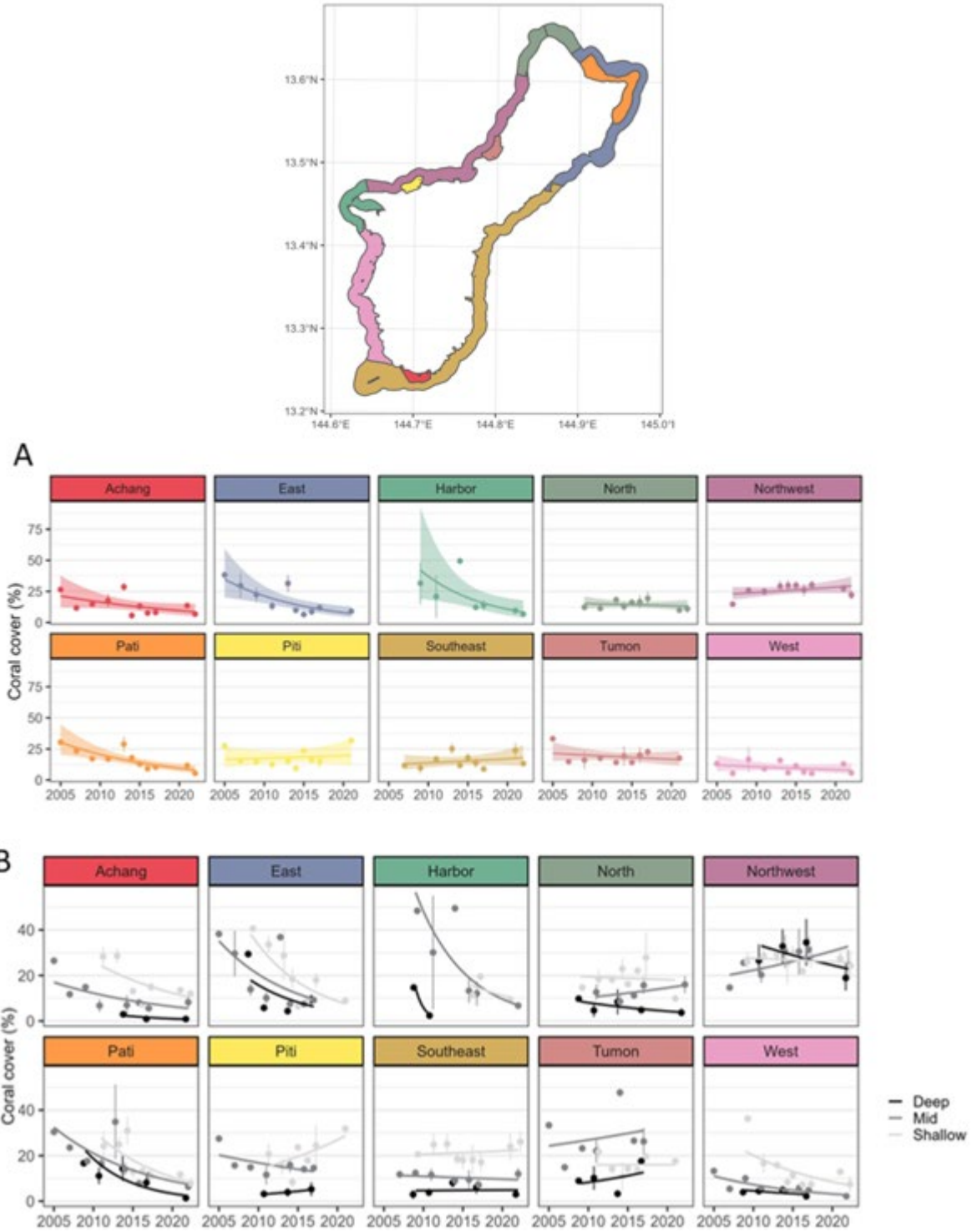


Figure 7. Reporting sectors for Guam with sector-scale trends in coral cover for (A) each sector and (B) per depth bin per sector. Lines show the smoothed trends over time.

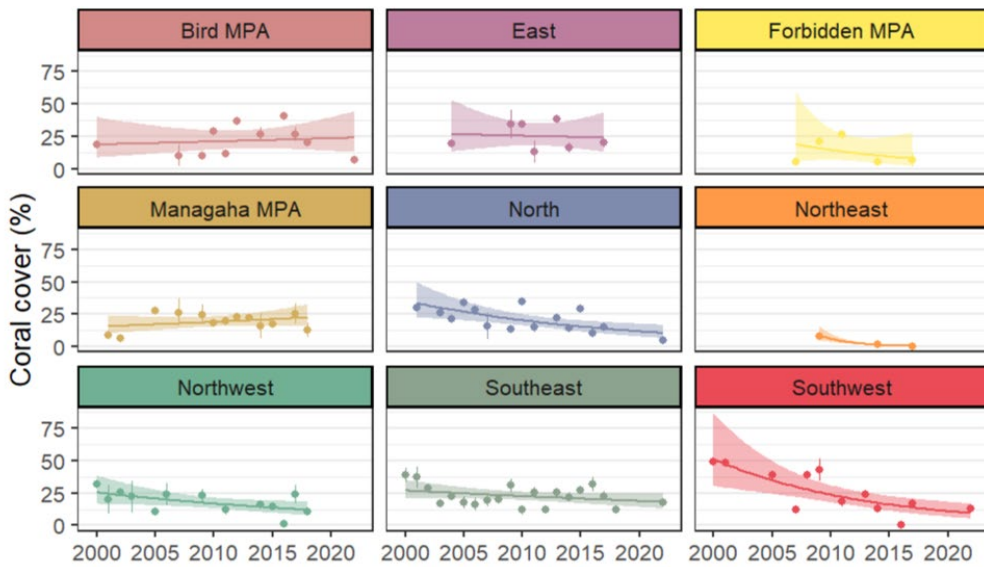
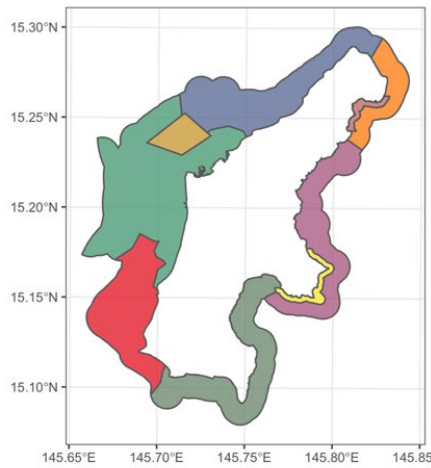


Figure 8. Reporting sectors for Saipan with sector-scale trends in coral cover for each sector. Lines show the smoothed trends over time.

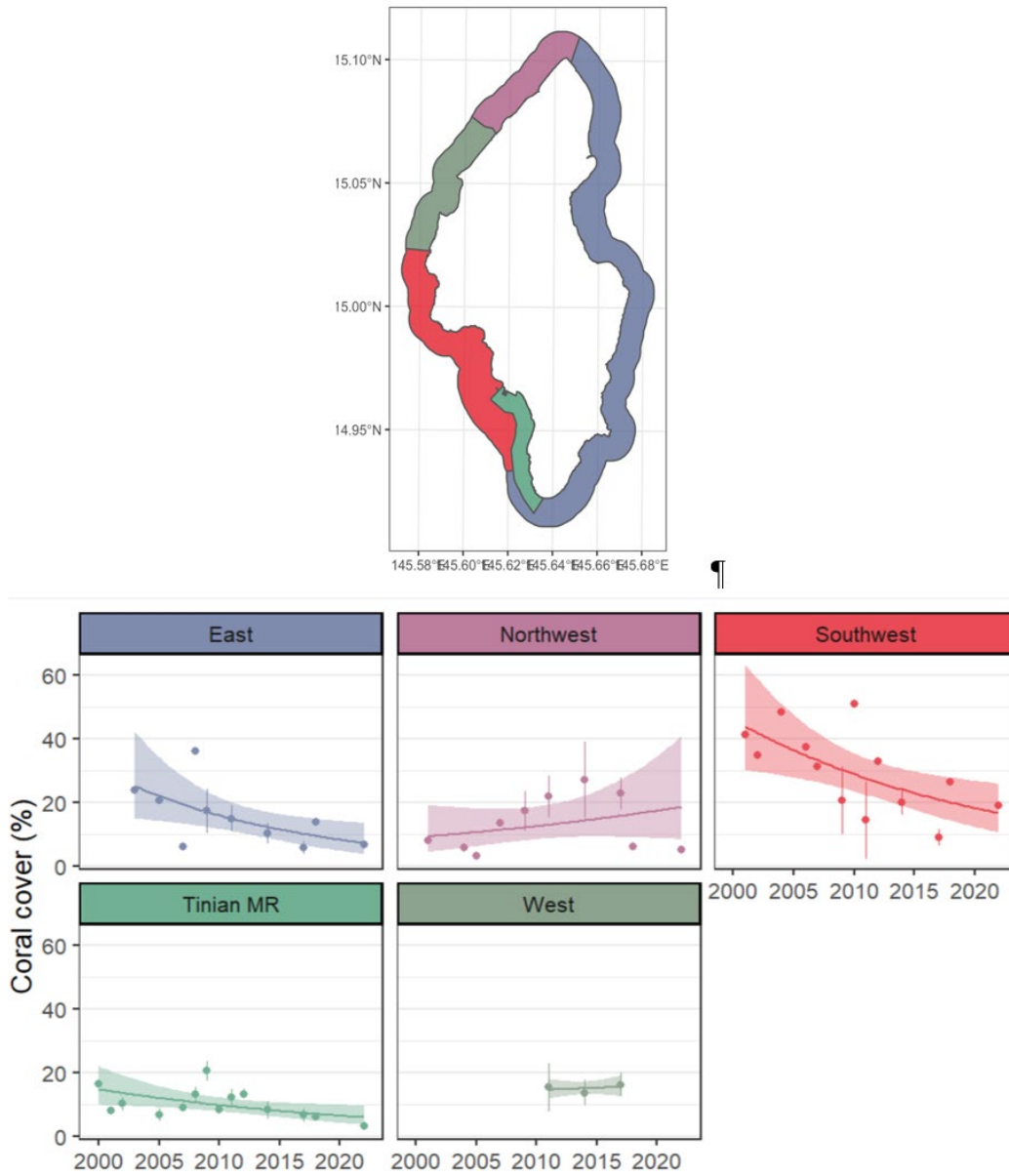


Figure 9. Reporting sectors for Tinian with sector-scale trends in coral cover for each sector. Lines show the smoothed trends over time.

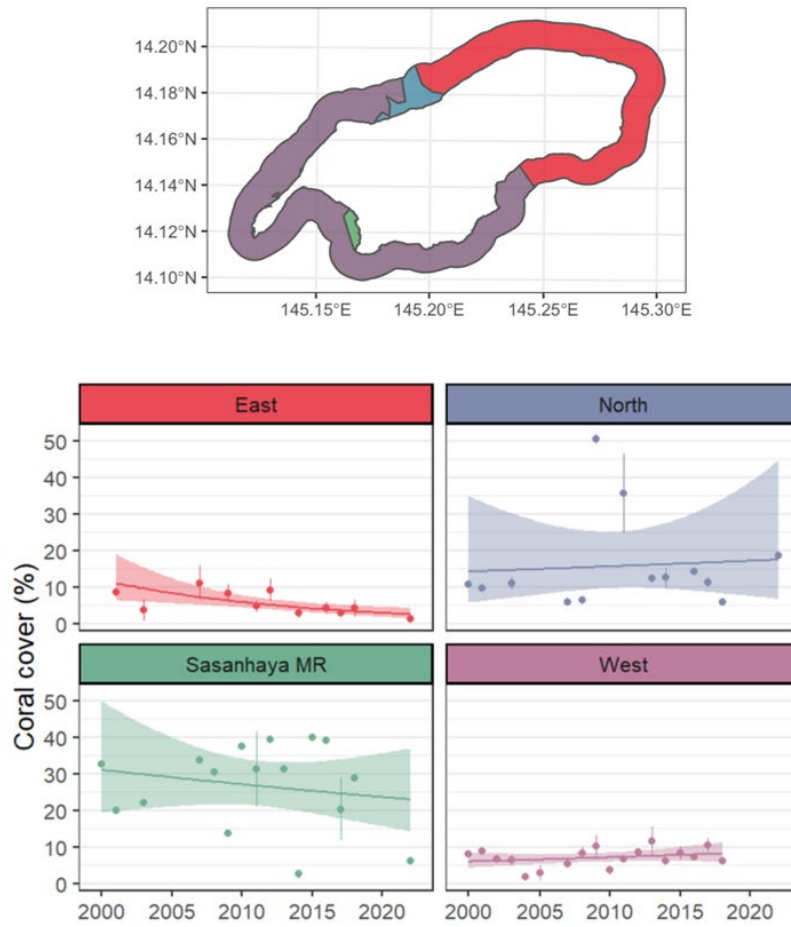


Figure 10. Reporting sectors for Rota with sector-scale trends in coral cover for each sector. Lines show the smoothed trends over time.

Fish Community

Regional-scale

Collapsing the data across our survey period (2011–2022), fish biomass estimates drastically varied between the populated and remote groups of islands; remote islands harbored, on average, between two to three times more biomass ([Figure 11A](#)). This trend persisted through time; mean fish biomass at the remote islands started close to 60 g m^{-2} in 2011 and has remained higher over the last decade. In contrast, the mean value for the populated islands started at 30 g m^{-2} and dropped nearly as low as 20 g m^{-2} in 2014 and remained around that level ([Figure 12B](#)). This stark difference between the groups of islands is further evidenced when investigating variation in biomass estimates for trophic groups. Remote islands have an average of 2–2.5 times more herbivores and piscivores than populated islands ([Figure 12 B&C](#)).

Similar trends were observed for species richness ([Figure 13B](#)), although differences were less pronounced. The number of species varied between 26.38 ± 0.38 and 37.2 ± 1.83 with less variation at populated areas.

Similar trends were observed for species richness ([Figure 11C](#)), although differences between populated and remote islands were less pronounced. The number of species, on average, varied between 25 and 37, with lower species richness for the populated islands which did not harbor more than an average of 30 species during any survey period.

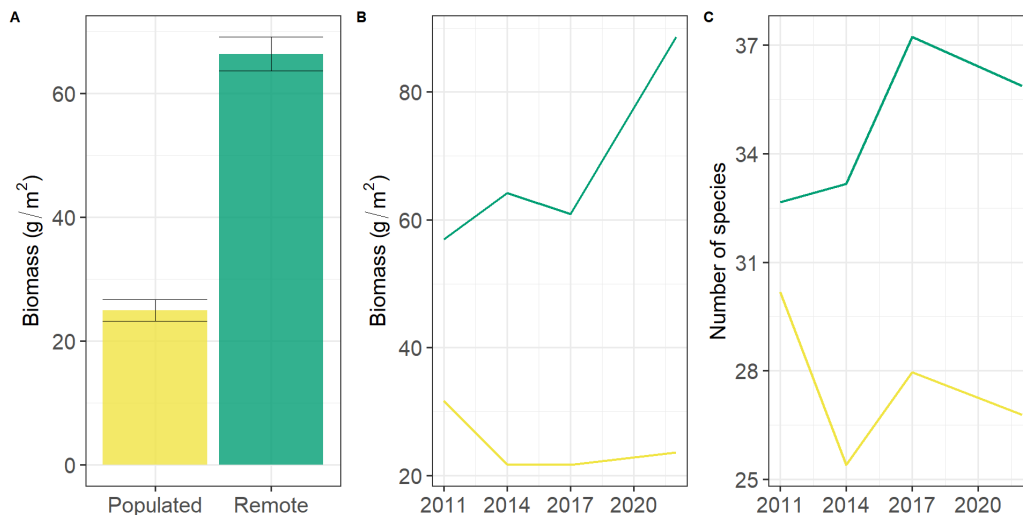


Figure 11. Mean fish biomass across all years combined (A) for the populated (yellow) and remote (green) islands and (B) over time, and (C) mean species richness.

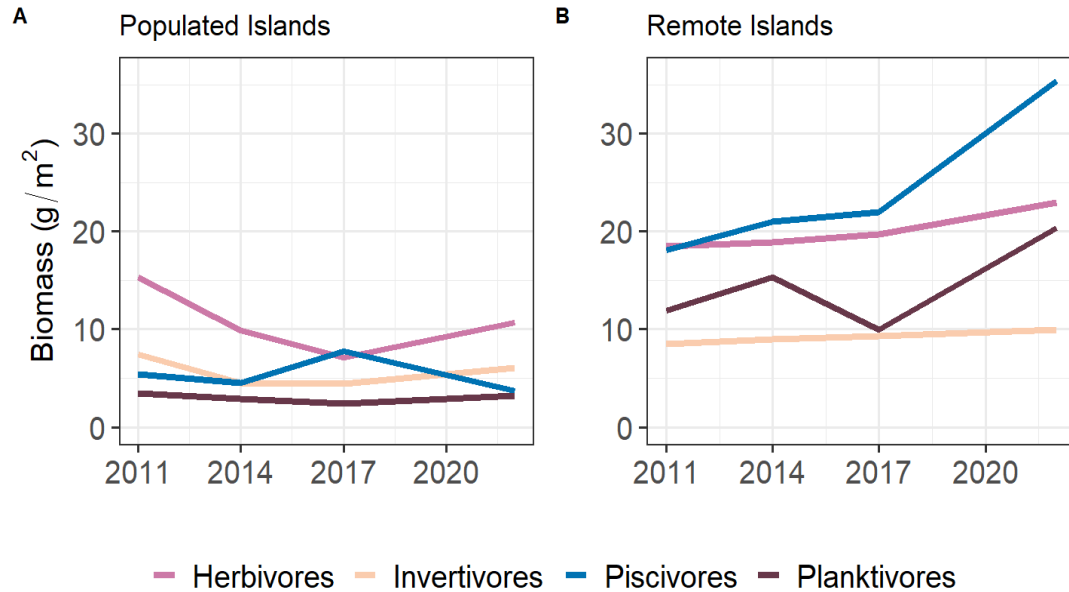


Figure 12. Mean fish biomass of trophic groups over time for the populated (A) and remote (B) islands in the Mariana Archipelago.

Island-scale

Across all years combined, the lowest fish biomass was observed at Tinian (mean \pm s.e.; 17.14 ± 1.43 g m⁻²) and the highest at Farallon de Pajaros (104.34 ± 16.79 g m⁻²; [Figure 13](#)). When investigating temporal trends, our modeling effort revealed similar trends in fish biomass among the populated islands. Guam had a significant non-linear trend in fish biomass over time (EDF = 2.38, $p = 2 \times 10^{-16}$), revealing a decrease in fish biomass until 2014. This was followed by a slight rebound in 2017 and by a decline in 2022 while holding sector and depth factors as random effects ($p = 2 \times 10^{-16}$; [Figure 14](#)). Unlike Guam, we did not find any evidence of a significant non-linear trend over time for the fish biomass in Saipan, Tinian, or Rota when depth and sector were assigned as random effects ($p > 0.05$). Rota's trend in fish biomass remained stable over time except in 2017, while Tinian's biomass seemed to decline and Saipan to increase through time ([Figure 14](#)).

These trends at the island-scale level could also be influenced by trophic groups (no statistical or modeling effort; [Figure 15](#)). Biomass estimates of trophic groups between Guam and Saipan are almost mirrored images for herbivore biomass, with Guam's mean biomass decreasing over time and Saipan's showing the opposite trend with the highest herbivore biomass in 2022. Such a trend is also present when comparing Tinian's and Saipan's fish biomass. Herbivorous fish contributed the most biomass in Rota almost every year followed by invertivores and piscivores ([Figure 15](#)). Notably, Guam had the highest mean piscivore biomass in 2017 among all populated islands which was driven by one site in the Pati Point Marine Reserve (MR).

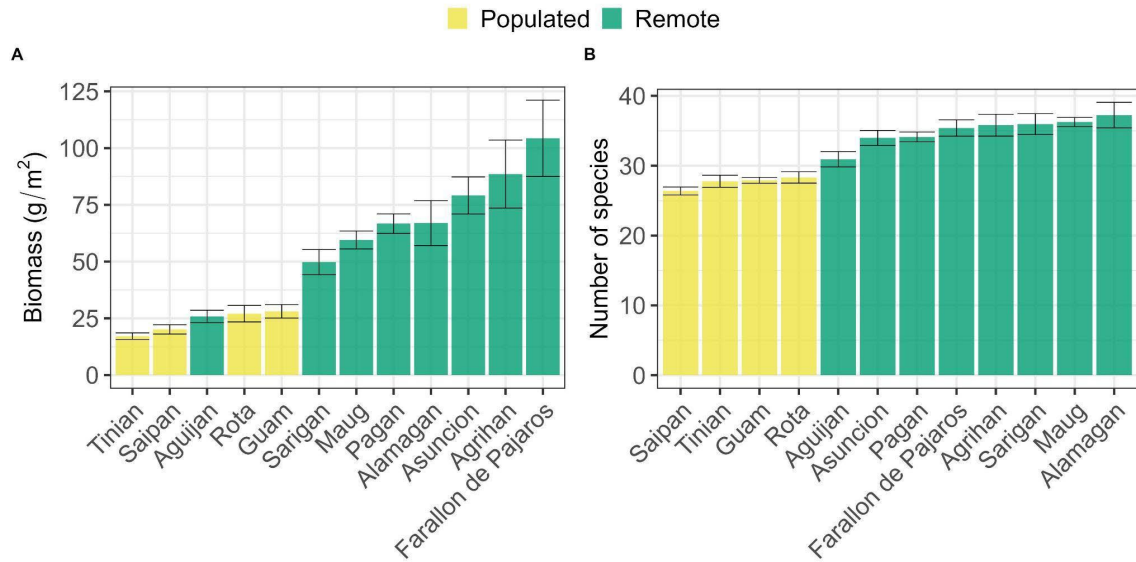


Figure 13. Mean fish biomass (A) and species richness (B) across all years combined for each island in the Mariana Archipelago, colored by human presence: populated (yellow) and remote (green).

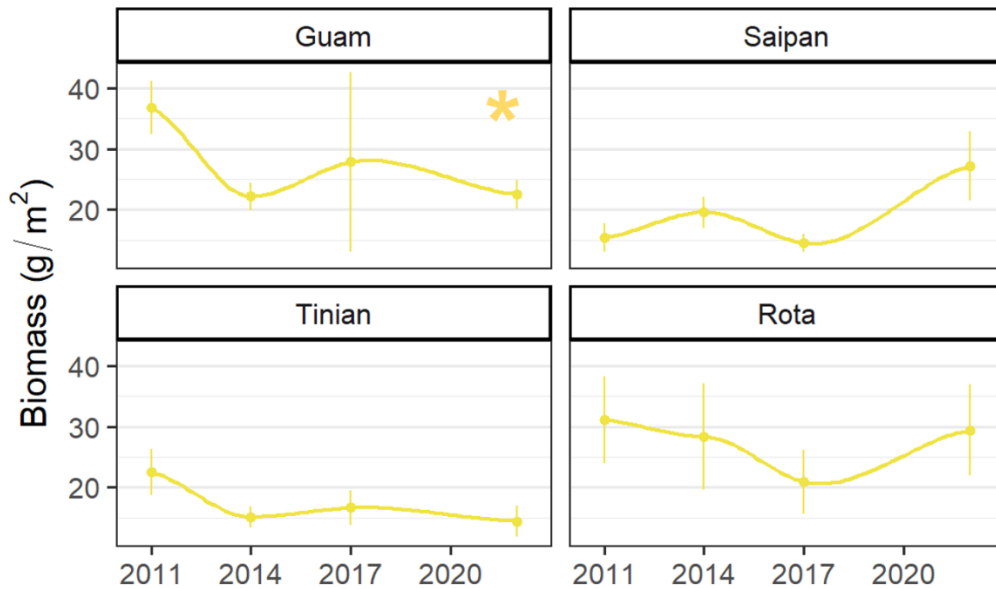


Figure 14. Fish biomass for each populated (yellow) island in the Mariana Archipelago. Mean and standard errors are shown as well as the smoothed curves. Asterisk indicates significant trend over time (GAMM).

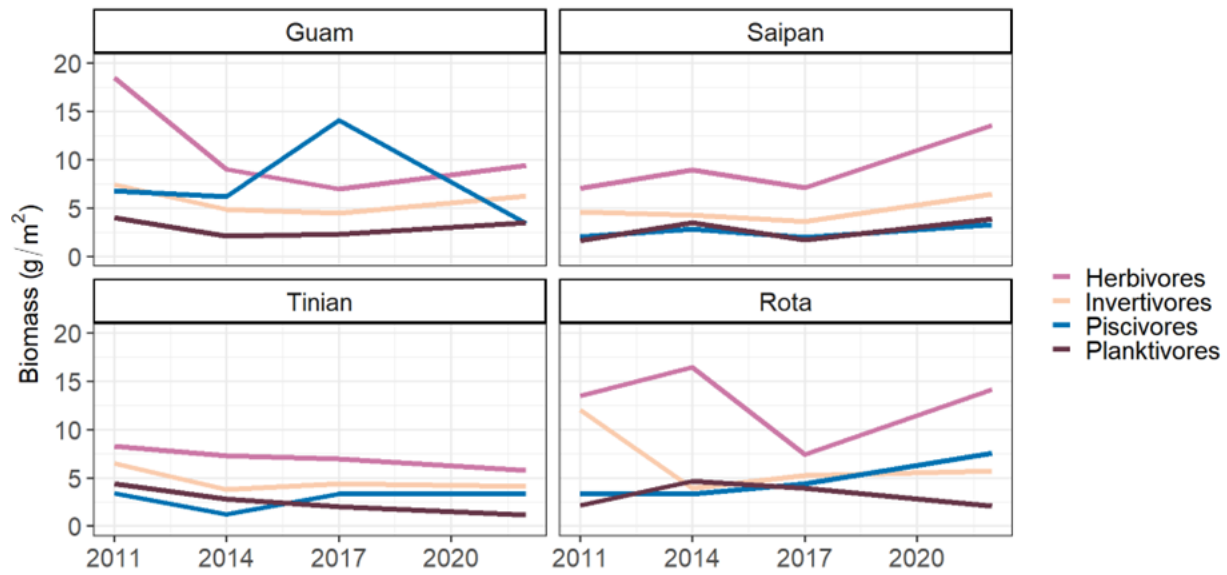


Figure 15. Mean biomass of fish trophic groups over time for each populated island in the Mariana Archipelago.

Sector-scale

The mean biomass per sector and the survey year effort varied on each island. Managaha marine protected area (MPA) and Harbor were only surveyed one year and two years, respectively. Considering the low sampling size, we thus removed these sectors from downstream analyses. Over the survey period (2011–2022) combined, 40–50% of Guam’s and Saipan’s sectors and 80% of Tinian’s sectors had a mean fish biomass below 20 g m⁻², whereas Rota’s sectors remained above that threshold (Figures [16A](#), [17A](#), [18A](#), and [19A](#))

Table 1. Sectors that showed significant trends in total fish biomass over time (p-value from GAMs).

Island	Sector	Significant trend	Depth bins and effect	P-value
Guam	North	Decline until 2017 but increase in 2022	Shallow	0.016
	Pati		No depth effect	0.012
	Northwest	Decline	Deep	0.010
	West		No depth effect	0.003
	East	Decline log-linearly	Not applicable	0.002
Saipan	East	Relatively flat and steep increase in 2022	Deep	0.002
	North	Increase log-linearly	Mid	0.050
Tinian	Northwest	Decrease	Deep	0.040
	Tinian MR	Increase log-linearly	Deep	0.020
			Mid	0.003
Rota	Sansahaya MR	Decrease until 2017 but increase by 2022	Mid	0.040

In Guam, four sectors showed significant non-linear trends over time. North's and Pati's biomass declined until 2017 but increased in 2022, whereas the Northwest and West sectors continued to decline over time ([Table 1](#)). Although we only have three years of data, the East sector's fish biomass also declined over time log-linearly (EDF = 1, [Table 1](#)). Similar patterns were observed for Saipan with an increase in fish biomass in the East and North sectors although trends differed (EDF = 2.12 and EDF = 1, respectively; [Table 1](#)). In Tinian, only the Northwest sector had a decrease in biomass over time (EDF = 1.8), while Tinian MR had a log-linear positive increase (EDF 1; [Table 1](#)). Lastly, in Rota, only one sector (Sansahaya MR) had a significant trend over time with a rebound in 2022 (EDF = 2.4; [Table 1](#)).

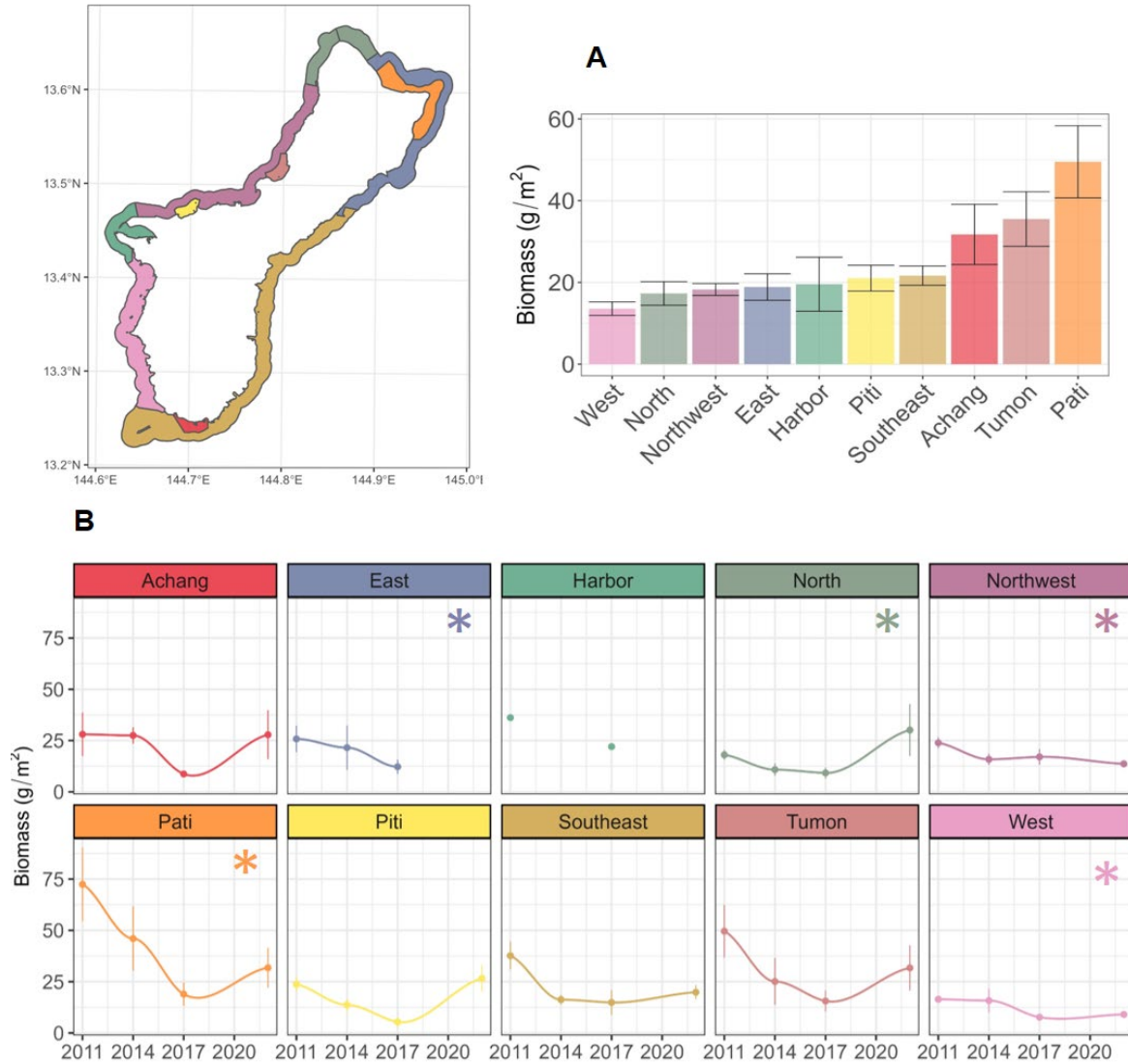


Figure 16. Mean fish biomass and standard errors per sector in Guam. The lines represent loess regressions. Asterisks indicate significant trend over time (GAMs).

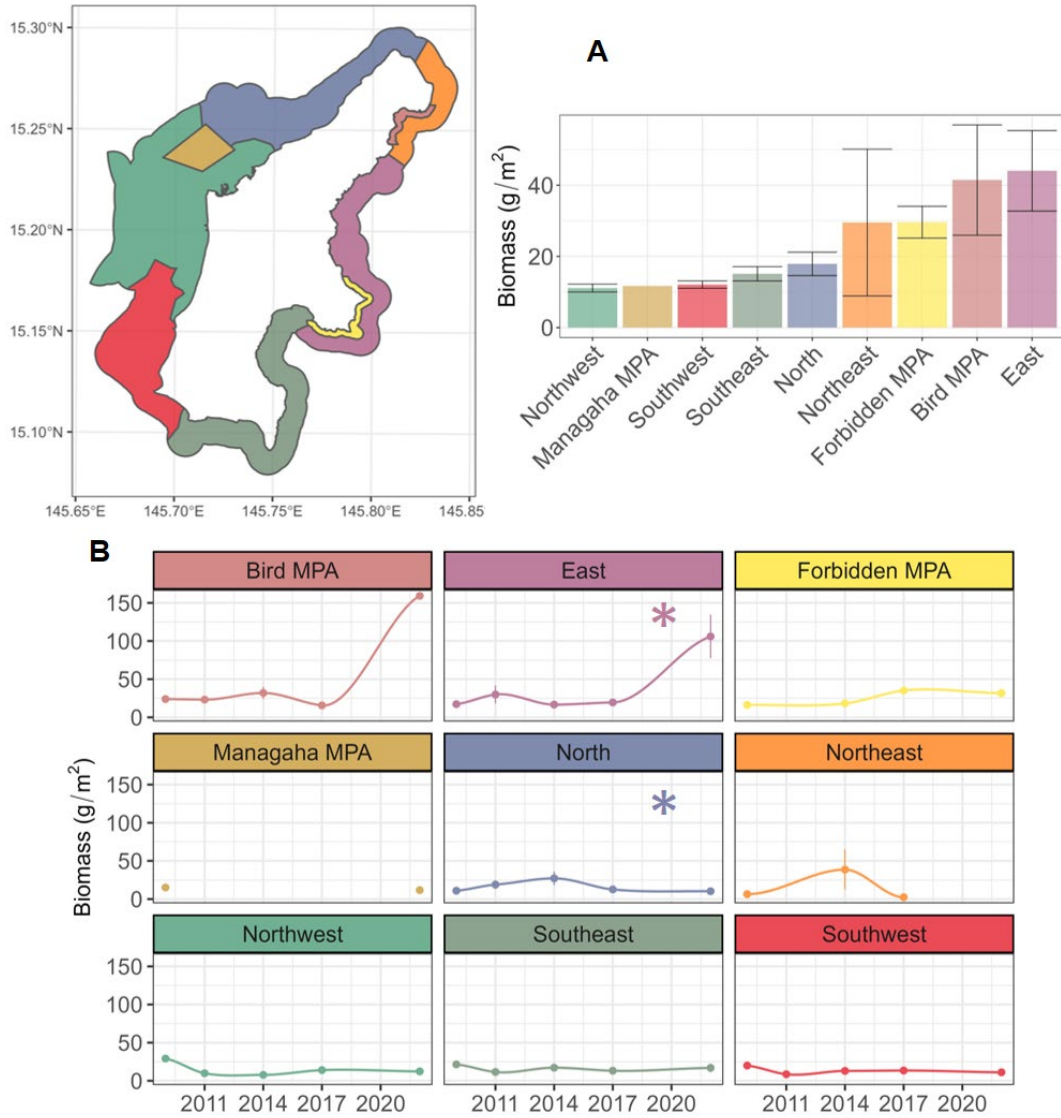


Figure 17. Mean fish biomass and standard errors per sector in Saipan. The lines represent loess regressions. Asterisks indicate significant trend over time (GAMs).

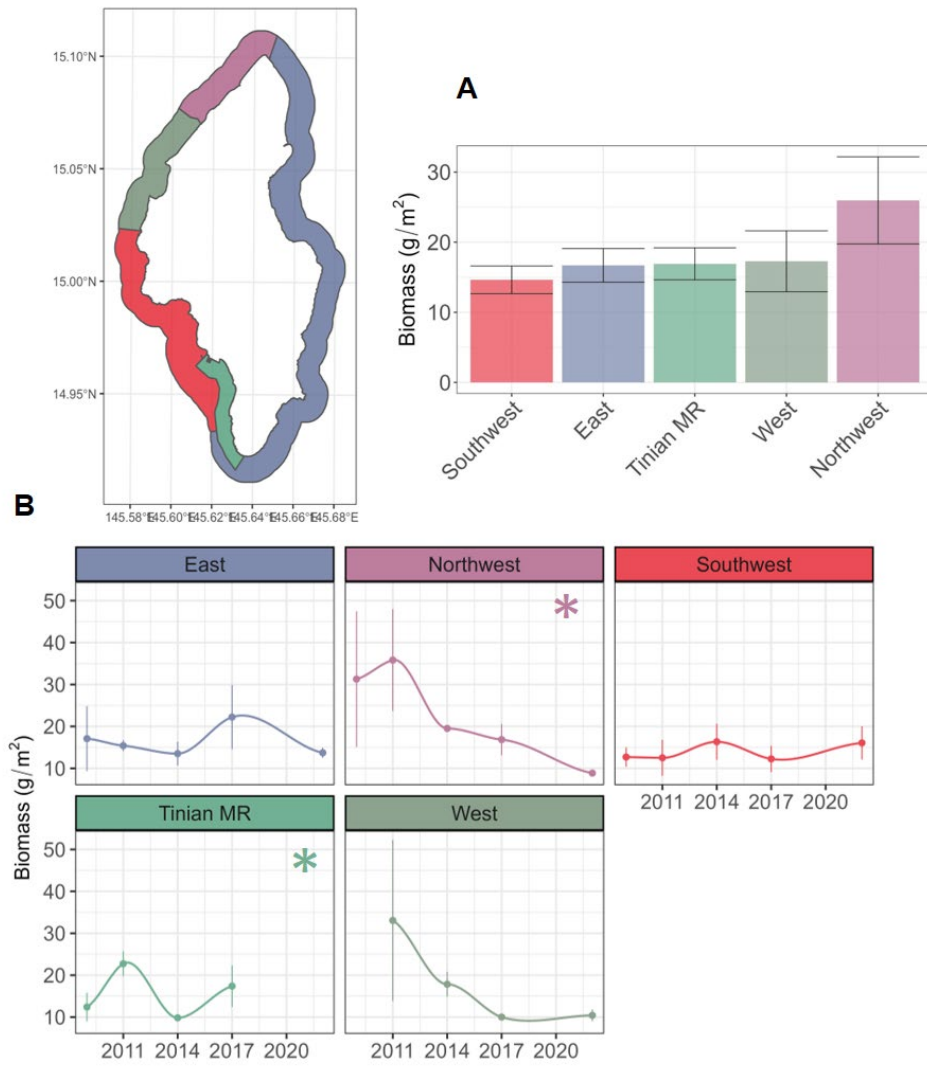


Figure 18. Mean fish biomass and standard errors per sector in Tinian. The lines represent loess regressions. Asterisks indicate significant trend over time (GAMs).

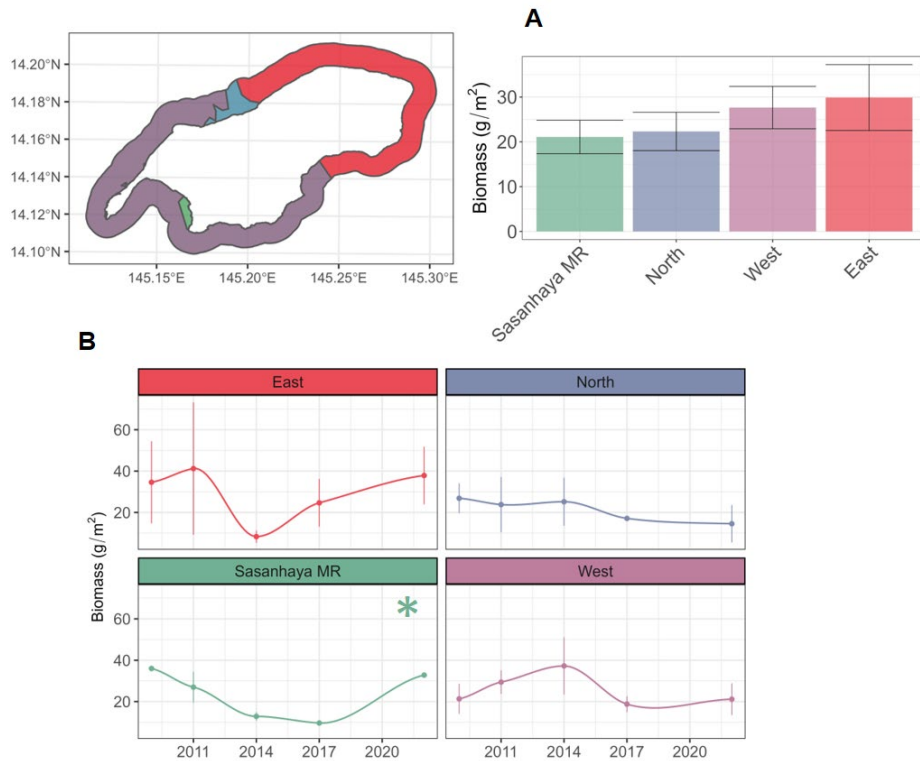


Figure 19. Mean fish biomass and standard errors per sector in Rota. The lines represent loess regressions. Asterisks indicate significant trend over time (GAMs).

Discussion

Coral reefs in the Mariana Archipelago have experienced recurring environmental disturbances, particularly within the past decade. Here, we integrated multiple data sources where possible to characterize trends in benthic and fish communities spanning a range of spatiotemporal resolutions (region-, island-, and sector-scale) and identified patterns of reef resilience. To further gauge human impacts, we compared benthic cover and fish biomass between populated and remote islands, where local human impacts are virtually absent.

This work also extends beyond previous efforts that have relied on snapshot estimates of resilience (based on the static environmental conditions at a single time point) and builds on statistical advances to provide inference at manager-relevant, sub-island (sector) scales. Investigating *realized* resilience (i.e., the ability for coral reefs to maintain key functions by either resisting the environmental changes or recovering from them) like this study can help better inform resilience-based management (RBM) efforts to buffer against the effects of global climate change and local disturbances. As a whole, coral reef ecosystems in the Marianas generate over \$104.5 million annually in economic value (Eastern Research Group 2019), constituting important sources of revenues for CNMI and Guam's economies and further highlighting the importance of RBM to improve prospects of reef recovery.

Declines in Coral Cover and Shifting Benthic Communities

Over the past 15 years, we observed a regional decline in hard coral cover in the Marianas accompanied by a substantial increase in turf algae. This decline, which was also present at the island scale and in many sectors, has been caused by the many environmental disturbances that affected both CNMI and Guam, including bleaching events, crown-of-thorns (COTS) eruptions, and typhoons. Before 1970, only two coral bleaching events had occurred in the Marianas Archipelago (NOAA 2005). After that, the frequency and severity of these events increased over time, especially in the last decades. Bleaching events occurred every year between 2013 and 2017, with two massive events in 2013 and 2014 (Reynolds et al. 2014; Heron et al. 2016). These back-to-back events were particularly detrimental to *Acropora* reefs (mainly staghorn corals) that previously dominated the reef flat and forereef (Burdick et al. 2019; Raymundo et al. 2019). Prior to the onset of bleaching events starting in 2013, reefs in the CNMI were impacted by (i) a concurrent COTS eruption and damages caused by several typhoons in 2003 through 2005, (ii) an additional COTS outbreak in 2010 to 2011 and more recently in 2022, (iii) three super typhoons in 2015, 2018, and 2023. This last typhoon damaged nearshore reefs with surge and debris by destroying or overturning coral colonies (Perez et al. 2021). Alarming, an increase in COTS density has been observed throughout CNMI's long-term forereef sites since 2018 (Perez et al. 2021) and high localized densities were observed in 2022 in Pagan. In addition to bleaching, typhoons, and COTS outbreaks, coral disease has also affected some reefs, such as in Guam in 2016 (Raymundo 2017). These recurring environmental disturbances left little to no respite for coral reefs to recover in the Marianas, which has lost between 30 and 60% of coral cover (or even more for certain genera such as *Acropora* and *Pocillopora* spp.) over the last decade (Burdick et al. 2019; Perez et al. 2021).

Considering the rapid pace at which these environmental disturbances have occurred, it is not surprising that our study revealed a dramatic reversal in the dominance of calcified and non-calcified benthic substrates for both populated and remote islands in the Marianas. This shift was previously documented by Huntington and colleagues (2022) who found that calcifiers no longer dominate remote island reefs but these reefs have calcifier cover (%) on par with populated islands. The replacement of live coral and calcified coralline algae with non-calcified substrates further highlights the ability of turf algae (typically composed of short filamentous and fleshy algae) to rapidly colonize dead coral skeletons, potentially reducing substrate availability for corals to settle (e.g., McCook et al. 2001). Overall, this shift toward turf dominance suggests an overall decrease in the resilience of Guam's and CNMI's reef to *future* disturbances.

Variation in Fish Biomass

Fish biomass varied dramatically among the islands of the Mariana Archipelago, with remote islands harboring between 2- and 10-fold more biomass than populated islands. This stark difference is largely a result of low piscivorous biomass in the populated islands. Our results further support Richards and colleagues' results (2012) which found that the biomass of large-bodied reef fish in the northern islands in the Mariana Archipelago was nearly twice that found in the southern islands. Although commercial

fishing has been permitted at some of the northern islands and poaching has been documented, most of the fishing pressure and anthropogenic activities occur off Saipan, Rota, and Tinian (Richards et al. 2012). For instance, reefs located in areas with low wave exposure in Saipan are also close to reef-based tourism (Houk et al. 2014) which could potentially contribute additional stresses to global changes, further compromising reef resilience.

Guam is also a fishery ground and hotspot for tourism, with reefs valued at \$127 million on a yearly basis (van Beukering et al. 2007; Conservation International 2008). Previous fishery-dependent and -independent studies revealed an overall depletion in large fish and reef fish from shallow waters (Richards et al. 2012; Weijerman et al. 2016; Williams et al., 2012, 2015). This is further illustrated in our study (except the increase in piscivore biomass in 2017 which was driven by one surveyed site). Alarmingly, a recent study indicated that the parrotfish biomass has decreased by almost 30% in the outer reef slopes in Guam over the last decade, which will most likely affect the resilience of coral reefs as their grazing activity—a key element in providing space for corals to recruit—has been reduced by almost a third (Taylor et al. 2022).

Yet when investigating biomass trends over time at a sub-island scale, spatiotemporal patterns were more complex for both CNMI and Guam. Although sectors differed in their levels of fish biomass (i.e., Tinian and Rota' sectors have, on average, twice less biomass than those in Guam or Saipan), we did not find any significant decrease over time for the majority of sectors, but rather relative stability over time. This mismatch between trends in coral cover and fish biomass (e.g., Pati in Guam, East in Rota) could be driven by habitat complexity remaining intact despite declines in live coral cover. Indeed, as long as the three-dimensional structure provided by corals remains in place, most fish species that do not have an obligate relationship with live corals will be unaffected (e.g., Friedlander et al. 2014). Yet there exists some concordance between coral cover and fish biomass trends for several sectors. Key examples are Piti and East in Guam and East and North sectors in Saipan.

Our results further highlight the complex and indirect effects that declining corals have on the fish community (Jones et al. 2004) which does not respond linearly to decreases in coral cover. Additionally, protection status might help in maintaining or increasing fish biomass, as potentially observed for the Sasanhaya marine reserve in Rota. A clear signature of effective protection in reefs around Guam has been found recently (Taylor et al. 2022) despite evidence of poaching in Tumon or Achang, for example.

Spatial Variation and Correspondence to Potential Reef Resilience

A major goal of this study was to incorporate previous statistical advancements (Oliver et al. 2020) to examine trends at manager-relevant scales despite the mismatch between this aim and the NCRMP monitoring design. We therefore used empirical data to define downscaled spatial reporting sectors and summarized benthic and fish responses at that scale. Accordingly, we observed the sub-island, sector-scale spatial variation in the resilience of reefs among the populated islands of the archipelago.

Comparing our observed spatial differences to previous efforts in the region, we found that spatial sectors for which we did not detect a significant decrease over time and

whose trends seemed to have “recovered” (reaching higher coral cover levels in last surveyed years) or “resisted” (no significant trends over time and coral cover remained above 20% during the last surveyed years) contained sites characterized as high to medium-high relative resilience potential by Maynard et al. (2015) ([Table 1](#)).

Table 2. Sectors from the four populated islands of the Mariana Archipelago assigned to different categories of resilience based on coral % cover relative to 2015 estimates of relative resilience potential (Maynard et al. 2015). Recovery means that sectors had higher coral cover values in last surveyed years compared to the early 2000s data. Resistance indicates that while sectors had no significant trends in coral cover over time, their values remained above 20% during the last surveyed years. The category “stable low” indicates that coral cover remained around 10% through time and no significant trend was detected.

Populated Island	Sector	Recovery	Resistance	“Stable low”	Relative resilience potential (Maynard et al. 2015)
Guam	Northwest	x	x		No data
	North		x		No data
	Piti Preserve		x		No data
	West			x	No data
Saipan	Bird MPA		x		High
	East		x		Medium-high
	Managaha MPA	x			Medium-high
	Southeast		x		High to low
Tinian	Northwest		x		Medium-high
	West			x	Medium-low
Rota	North		x		Medium-low
	West		x		Medium-high to low

These included four sectors in Saipan (East sector, Bird Island MPA, Mahagana MPA, and Southeast) and one in Tinian (Northwest). Yet for Bird Island, a localized outbreak of COTS was observed in 2019 to 2020 which might explain the slight decrease in coral cover post-2020. Interestingly, some sectors remained stable over time with coral cover barely varying over time but with low values ([Table 1](#)). This stability might indicate some ability to cope with fluctuating environmental conditions. Similarly, sectors showing the greatest declines were largely characterized as having low-to-medium and low resilience potential by Maynard et al. (2015) including sectors in southwest Tinian.

Yet not all of the areas predicted to be resilient by Maynard et al. (2015) maintained coral cover. A clear example is the Southwest sector in Saipan which was characterized by having medium-high resilience potential, yet we observed a significant decline in coral cover. It should be noted that the high potential resilience score for this area is attributable to high relative coral recruitment, one of the factors used to define resilience in Maynard et al. (2015). Thus, this sector may prove to have greater relative *recovery* potential, whereas the timing of our analysis is more suited to measure the *resistance* component of resilience. Further, clusters of individual sites in Maynard et al. (2015)

were not always directly comparable to our reporting sectors. For example, spatial downscaling resulted in a single large sector spanning much of southeast Saipan which showed moderate declines in coral cover. This sector covers sites in Maynard et al. (2015, 2018) spanning medium-low to high resilience potential.

Overall, while the Maynard et al.'s method (2015) and our temporal analysis inferring resilience are not directly comparable, there exists some overlap for certain sectors with sites previously designated as “high or moderate/high resilience”, which seemed to have fared better, such as Managaha MPA (also singled out by Maynard et al. 2018) and the East sector in Saipan. Surprisingly, some sectors with “low-moderate resilience” did not show a significant decrease in 2022. Together, this provides some hope for our reefs to maintain ecosystem structure in the face of ongoing disturbances.

The Influence of Depth

When investigating reef resilience, it is often hypothesized that reefs in deeper waters may fare better than shallower counterparts. The corollary is that reefs in deeper waters are posited to be less susceptible to heat stress. However, contrasting evidence has been found, which is probably driven by variation in coral susceptibility to bleaching (e.g., summarized in Glynn 1996). The present study only provides partial support for a high resilience or resistance to bleaching.

In Guam, where depth bins influenced the trends in coral cover over time at the sector level, shallow sites (> 6 m depth) usually showed the steepest declines compared to moderate-depth (6–15 m) and deep sites (15–30 m), which appeared more stable on average. At first glance, this result suggests a depth-refuge protecting live coral from the worst of heat-related stress, exacerbated by extreme low-tides in 2014–2015. However, it should be noted that the slope of decline as a measure of resistance to stressors does not consider the *initial* magnitude of percent cover, nor the community composition of coral species at different depths. To the first point, the steeper declines in coral cover at shallow sites compared to deeper sites are a result of shallow sites declining from higher initial percent cover. In fact, sites at varying depths in Guam ended with roughly the same level of live coral cover (at or below ~10%). Relatedly, the coral species composition at shallow sites tends toward a greater proportion of bleaching susceptible acroporids, with deeper sites dominated by more resistant *Porites* species. As repeated stressors shift coral communities toward more resistant compositions of species (Alvarez-Filip et al. 2009), the response of shallow, medium, and deep sites may converge, albeit at a low level of total coral cover and structural complexity (weeding out the vulnerable acroporids providing complex habitats). A recent study (Venegas et al. 2019) also did not find a depth refuge to heat stress in both Guam and CNMI.

Limitations and Future Research Directions

In the present study, our goal was to integrate and spatially downscale data from a variety of sources in order to better capture trends in the benthic and fish community responses. This methodology comes with limitations and tradeoffs. First, we relied primarily on partner data for the years prior to 2011 (when NCRMP standardized benthic data collection). This resulted in low spatial resolution, small sample sizes, and

few observations in Guam for the earliest years of the study period. Secondly, we combined two main methods for benthic cover (i.e., photo quadrats and line point intercept or LPI), which were not evenly distributed throughout the years, especially for the remote islands where LPI was only used until 2007. Thirdly, at a sector level, our investigation did not compare sectors' fish biomass that differed in protection status (i.e., across a range from no protection to designation as a marine reserve or marine protected area), which should be further explored by using a bootstrapping method to estimate relative quantile ranges (see Williams et al. 2011).

As with any investigation of community responses to stressors, it is difficult to adequately account for the prior history of disturbances and how such prior events mediate the response to disturbances within the study period. As natural and anthropogenic stressors have caused decline in total coral cover and a shift in community composition over the previous 125 years (Cybulski 2016), the patterns of differential resilience documented in this study were clearly shaped by a longer history and should be viewed in that context. Likewise, we only used coarse benthic metrics, which do not necessarily inform about specific processes that promote reef resilience. Demographic information alongside higher taxonomic resolution and reef complexity metrics could be additional avenues to explore.

Analogously, we used biomass as our main metric for fish communities and did not investigate any differences in community composition or in other metrics, such as trait-based diversity indices that can help gauge the ecosystem's vulnerability or resilience. Indeed, traits can assist in maintaining essential ecological function such as herbivory, nutrient uptake, and bioerosion (Brandl et al. 2019) by providing stability during disturbances when multiple species have analogous traits. In such a scenario, this trait redundancy means that losing one or few species will not jeopardize the ecosystem process and will help maintain the overall ability for ecosystems to resist environmental changes.

Take Home Messages

- Integrating NCRMP and Marianas partners' data sets into a single data set was possible for benthic data using coarse metrics (i.e., benthic cover) and functional groups (e.g., CCA, calcifying organisms).
- Data integration was not feasible for fish data sets because of drastic changes in methodologies, objectives, and scales among partners' monitoring programs.
- NCRMP contributed 80% of the benthic data and 100% of the fish data.
- There was a substantial decline in coral cover and increase in turf algae across the Marianas in concordance with environmental disturbances, including ocean heat stress events, typhoons, and COTS outbreaks.
- Significant decrease in coral cover was observed for Guam and Tinian, but not for Saipan (although the overall trend is declining).
- The downscaling effort resulted in populated islands being divided into several sectors (defined as sub-regional clusters of similar benthic cover values), which ranged from 10 to three, overlapped with marine reserve boundaries, and were less than 1 mile or over 10 miles in length.

- 50% of the sectors in Guam and Tinian had a cover coral near or below 10% by 2021 to 2022 and displayed significant decreasing trends over time.
- Yet other sectors resisted or showed resilience to warming and other environmental disturbances (e.g., northwest in Guam, Mahagana MPA in Saipan).
- Remote islands harbored between 2- and 10-fold more fish biomass than populated islands and up to three times more herbivores and piscivores.
- Although fish biomass at the island-scale for populated islands varied years to years, Guam's trend significantly decreased by 2022, and Rota showed a (not-significant) decrease as well. In contrast, Rota and Tinian displayed the opposite trend with an increase close to 30 g m⁻²; albeit not reaching values of remote islands.
- 50% of the sectors in Guam and in Rota had either a significant increase over time in fish biomass or seemed to experience a rebound in 2022; the picture is less clear for Saipan (except Bird MPA and East) and Tinian.
- There is only partial concordance between higher levels of coral cover and increased fish biomass, probably due the preservation of the three dimensionality of reefs years after bleaching events.

Acknowledgments

We thank all collaborators: the University of Guam, the University of Queensland Saipan surveys, the CNMI Bureau of Environmental and Coastal Quality (BECQ), and the Division of Fish and Wildlife. In particular, we are grateful to David Burdick, Lyza Johnston, Laurie Raymundo, and Denise Perez for sharing and curating benthic data from Guam and CNMI. Additionally, we thank the various crews and scientists involved in collecting the NCRMP benthic and fish data over the years. We also thank Courtney Couch for providing the latest NCRMP benthic data set. NOAA's Coral Reef Conservation Program funded this study through Project No. 31364, which collected the data as part of the National Coral Reef Monitoring Program (NCRMP).

Literature Cited

- Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc Royal Soc B*. 276:3019–3025.
- Anthony KRN, Marshall PA, Abdulla A, Beeden R, Bergh C, Black R, Eakin CM, Game ET, Gooch M, Graham NAJ, et al. 2015. Operationalizing resilience for adaptive coral reef management under global environmental change. *Glob Chang Biol*. 21:48–61.
- Ayotte PM, McCoy KS, Heenan A, Williams ID, Zamzow JP. 2015. Coral Reef Ecosystem Division standard operating procedures: data collection for rapid ecological assessment fish surveys. NMFS-PIFSC Administrative Report H-15-07.
- Brandl SJ, Rasher DB, Côté IM, Casey JM, Darling ES, Lefcheck JS, Duffy JE. 2019. Coral reef ecosystem functioning: eight core processes and the role of biodiversity. *Front Ecol Environ*. 17(8): 445– 454.
- Connell JH, Hughes TP, Wallace CC. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol Monogr*. 67:461–488.
- Conservation International. 2008. Economic values of coral reefs, mangroves, and seagrasses. Center for applied biodiversity science. Conservation International, Arlington, VA, USA.
- Cybulski JD. 2016. Push-core sampling in Micronesia: using paleoecological data to reconstruct Guam's coral reef community. American University.
- Eastern Research Group, Lexington, MA. 2019. Value of ecosystem services from coral reef and seagrass habitats in CNMI. Prepared for Bureau of Environmental and Coastal Quality's Division of Coastal Resources Management (BECQ-DCRM) Commonwealth of the Northern Mariana Islands (CNMI) Saipan.
- Friedlander AM, Obura D, Aumeeruddy R, Ballesteros E, Church J, Cebrian E, Sala E. 2014. Coexistence of low coral cover and high fish biomass at Farquhar Atoll, Seychelles. *PLOS ONE* 9(1): e87359.
- Glynn PW. 1996 Coral reef bleaching: facts, hypotheses and implications. *Glob Chang Biol*. 2:495–509.
- Heenan A, Williams ID, Acoba T, DesRochers A, Kosaki RK, Kanemura T, Nadon MO, Brainard RE. 2017. Long-term monitoring of coral reef fish assemblages in the Western central pacific. *Sci Data*. 4:170176.

- Heron SF, Johnston L, Liu G, Geiger EF, Maynard JA, De La Cour JL, S. Johnson S, Okano R, Benavente D, Burgess TFR, et al. 2016. Validation of reef-scale thermal stress satellite products for coral bleaching monitoring. *Remote Sensing*. 8(59):1–16.
- Houk P, Benavente D, Iguel J, Johnson S, Okano R. 2014. Coral reef disturbance and recovery dynamics differ across gradients of localized stressors in the Mariana Islands. *PLOS ONE* 9(8): e105731.
- Hughes TP. 1994. Catastrophes, phase shifts, and large-Scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, et al. 2018. *Nature* 556:492–496.
- Huntington B, Vargas-Ángel B, Couch CS, Barkley HC, Abecassis M. 2022. Oceanic productivity and high-frequency temperature variability—not human habitation—supports calcifier abundance on central Pacific coral reefs. *Front mar sci*. 9:1075972.
- Jones GP, McCormick MI, Srinivasan M, Eagle JV. 2004. Coral decline threatens fish biodiversity in marine reserves. *PNAS*. 101: 8251–8253.
- Maynard J, McKagan SC, Raymundo LJ, Johnson S, Ahmadi G, Houk P, Williams G, Kendall MS, Heron SF, Mcleod E. et al. 2015. Assessing relative resilience potential of coral reefs to inform management in the Commonwealth of the Northern Mariana Islands. *Biol Conserv*. 192: 109–119.
- Maynard J, McKagan S, Johnson S, Johnston L, Fenner D, Tracey D. 2018. Assessing resistance and recovery in CNMI during and following a bleaching and typhoon event to identify and prioritize resilience drivers and action options. Final Progress Report for NOAA CRCP Grant No. NA17NOS4820088. https://reefresilience.org/wp-content/uploads/CNMI_Saipan_2018_Demonstrated_Resilience_Final_Report.pdf
- McClanahan TR, Donner SD, Maynard JA, MacNeil MA, Graham NAJ, Maina J, Baker AC, Beger M, Campbell SJ, Darling ES, et al. 2012. Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLOS ONE* 7:e42884.
- McCoo L, Jompa J, Diaz-Pulido G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*. 19:400–417.
- Mcleod E, Anthony KRN, Mumby PJ, Maynard J, Beeden R, Graham NAJ, Heron SF, Hoegh-Guldberg O, Jupiter S, MacGowan P. et al. 2019. The future of resilience-based management in coral reef ecosystems. *J Environ Manage*. 233:291–301.

- NOAA (National Oceanic and Atmospheric Administration). 2005. The state of coral reef ecosystems of the United States and Pacific Freely Associated States. NOAA. Technical Memo NOS NCCOS 11.
- Perez DI, Camacho R, Hasegawa K, Suel IJ, David P. 2021. CNMI State of the Reef Report 2020-2021. Division of Coastal Resources Management, Bureau of Environmental and Coastal Quality, Commonwealth of the Northern Mariana Islands.
- R Cote Team .2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, URL <https://www.R-project.org/>.
- Rassweiler A, Dubel AK, Hernan G, Kushner DJ, Caselle JE, Sprague JL, Kui L, Lamy T, Lester SE, Miller RJ. 2020. Roving divers surveying fish in fixed areas capture similar patterns in biogeography but different estimates of density when compared with belt transects. *Front Mar Sci* 7:272
- 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* 38:677–700.
- Reynolds T, Burdick D, Houk P, Raymundo L, Johnson S. 2014. Unprecedented coral bleaching across the Marianas Archipelago. *Coral Reefs* 33, 499.
- Richards BL, Williams ID, Vetter OJ, Williams GJ. 2012. Environmental factors affecting large-bodied coral reef fish assemblages in the Mariana Archipelago. *PLOS ONE* 7(2): e31374.
- Shaver EC, McLeod E, Hein MY, Palumbi SR, Quigley K, Vardi T, Mumby PJ, Smith D, Montoya-Maya P, Muller EM, et al. 2022. A roadmap to integrating resilience into the practice of coral reef restoration. *Glob Change Bio* 28, 4751– 4764.
- Smith JE, Brainard R, Carter A, Grillo S, Edwards C, Harris J, Lewis L, Obura D, Rohwer F, Sala E, et al. 2016. Re-evaluating the health of coral reef communities: baselines and evidence for human impacts across the central Pacific. *Proc Royal Soc B.* 283:20151985
- Taylor BM, Duenas AEK, Lange ID. 2022. Decadal changes in parrotfish assemblages around reefs of Guam, Micronesia. *Coral Reefs.* 41:1693–1703.
- van Beukering P, Haider W, Longland M, Cesar H, Sablan J, Shjegstad S, Beardmore B, Liu Y, Garces GO. 2007. The economic value of Guam's coral reefs. University of Guam Marine Laboratory Technical Report 116, no. 116 (2007): 102.

- Venegas RM, Oliver T, Liu G, Heron SF, Clark SJ, Pomeroy N, Young C, Eakin CM, Brainard RE. 2019. The rarity of depth refugia from coral bleaching heat stress in the western and central Pacific islands. *Sci Rep* 9(1):19710.
- Weijerman M, Williams I, Gutierrez J, Grafeld S, Tibbatts B, Davis G. 2016. Trends in biomass of coral reef fishes, derived from shore-based creel surveys in Guam. *Fish Bull.* 114
- Williams ID, Baum JK, Heenan A, Hanson KM, Nadon MO, Brainard RE. 2015. Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLOS ONE* 10(4):e0120516.
- Williams ID, Richards BL, Sandin ASA, Baum JK, Schroeder RE, Nadon MO, Zgliczynski B, Craig P, McIlwain JL, Brainard RE. 2011. Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western Pacific. *J Mar Sci.* 14 (1687–9481).
- Williams ID, Zamzow JP, Lino K, Ferguson M, Donham E. 2012. Status of coral reef fish assemblages and benthic condition around Guam: a report based on underwater visual surveys in Guam and the Mariana Archipelago. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-PIFSC-33, 22 p. + Appendices.