



Coral reef community recovery trajectories vary by depth following a moderate heat stress event at Swains Island, American Samoa

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Received: 16 April 2024 / Accepted: 1 October 2024

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Abstract

The 2014–2017 global coral bleaching event caused mass coral mortality and reshaped benthic communities across the Pacific. Swains Island (11.0° S, 171.1° W), a remote and uninhabited island within American Samoa, was exposed to moderate heat stress (6 °C-weeks) during this event. Temporal patterns in benthic cover and coral demography were monitored across 13 years straddling this heat stress event to assess the impacts across depth and the recovery trajectory. While Swains's reefs retain some of the highest calcifier cover in the US Pacific Islands, successional trajectories across depth following the 2016 heat stress suggest that these reefs are experiencing a more nuanced pattern of resilience to disturbance, with early signs of recovery in shallow reefs (3–6 m), a shift to non-calcifier dominance at mid depth (6–18 m), and stability on deep reefs (18–30 m). Shallow reefs experienced the largest changes with a relative 50% decline in coral cover, which was replaced by CCA between 2015 and 2018. Shifts in shallow coral community composition were strongly driven by the loss of *Pocillopora* and early recovery seven years after the event evidenced by an increase in small colonies. Mid-depth reefs experienced a 33% loss in coral cover between 2015 and 2023, and corresponding increase in upright macroalgae. The degree to which increasing macroalgae represents a temporary shift or gradual decline in calcifiers remains to be seen. While Swains's recovery bodes well for persistence of shallow reefs, its remoteness from broodstock and dominance of thermally sensitive taxa pose a threat to future climate resilience.

Keywords Coral bleaching · *Pocillopora* · Resilience · Depth · Benthic cover · Colony density · Colony size · Uninhabited island

Introduction

Heat stress and mass coral bleaching events are affecting coral reefs with increasing intensity and reshaping benthic community composition. Bleaching-related coral mortality can result in a range of benthic community-level responses. Newly available substrate from dead corals is colonized by early successional taxa such as encrusting macroalgae and turf algae, followed by crustose coralline algae (CCA) and coral spat (e.g. Littler and Littler 1984; Adam et al. 2011; Holbrook et al. 2018; Huntington et al. 2022a), which may be a decisive step in reef recovery (Holbrook et al. 2018). However, in the absence of herbivores and/or in combination with eutrophication, fleshy macroalgae can proliferate thus preventing coral settlement (Wittenberg and Hunte 1992; Burkepile and Hay 2006; Robinson et al. 2018).

Beyond shifts in the broader benthic community, coral communities experience shifts in the distribution of coral

Communicated by R. Alderdice.

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taxa and size classes due to differential susceptibility to heat stress. For instance, fast growing, branching morphologies are typically more susceptible to bleaching-induced mortality, while slower growing, massive morphologies have higher survivorship (Loya et al. 2001; Darling et al. 2012; Guest et al. 2012; Burn et al. 2023). Heat stress may result in shifts in size frequency distributions that are difficult to predict. Higher bleaching-induced mortality in juvenile corals can drive size distributions towards larger colonies (Lachs et al. 2021). Conversely, partial mortality of large colonies (McClanahan 2008) or high coral recruitment (Koester et al. 2021) can shift size distributions towards smaller colonies. Therefore, shifts in size distributions can be ambiguously indicative of recovery through recruitment of new corals or decline through recruitment failure and/or fragmentation of large colonies—providing a valuable tool for elucidating demographic mechanisms of recovery.

In addition to coral taxonomic composition, environmental factors such as depth can influence the severity of bleaching events on coral populations (e.g. Jokiel and Brown 2004; Sully et al. 2019). Deeper reefs are often exposed to cooler water and lower UV irradiance – another trigger of coral bleaching, are hypothesized to provide a refuge from thermal (Glynn 1996; Riegl and Piller 2003) and light stress (Gleason and Wellington 1993). However, several studies have found a lack of thermal stress mitigation and/or differential bleaching tolerance on deeper reefs (Penin et al. 2007; Smith et al. 2016; Venegas et al. 2019). Alternatively, deep-water refugia may be linked to strong patterns of species zonation across depths — a fundamental principle of coral community ecology (Done 1983) — as species with differential responses to thermal stress may occupy different locations on a reef (e.g. Marshall and Baird 2000; Darling et al. 2012; Frade et al. 2018).

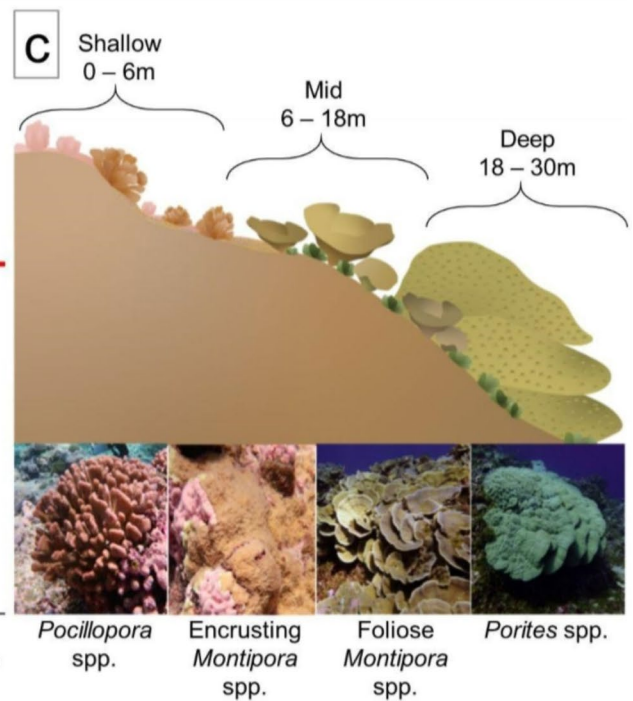
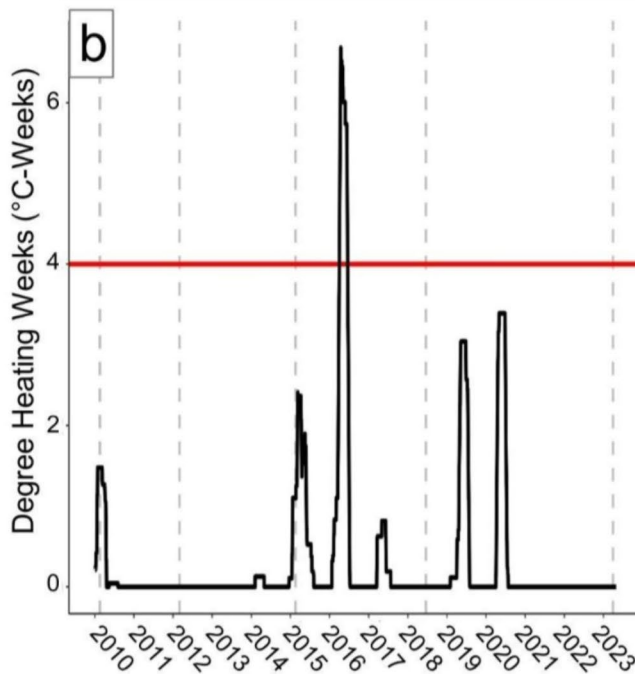
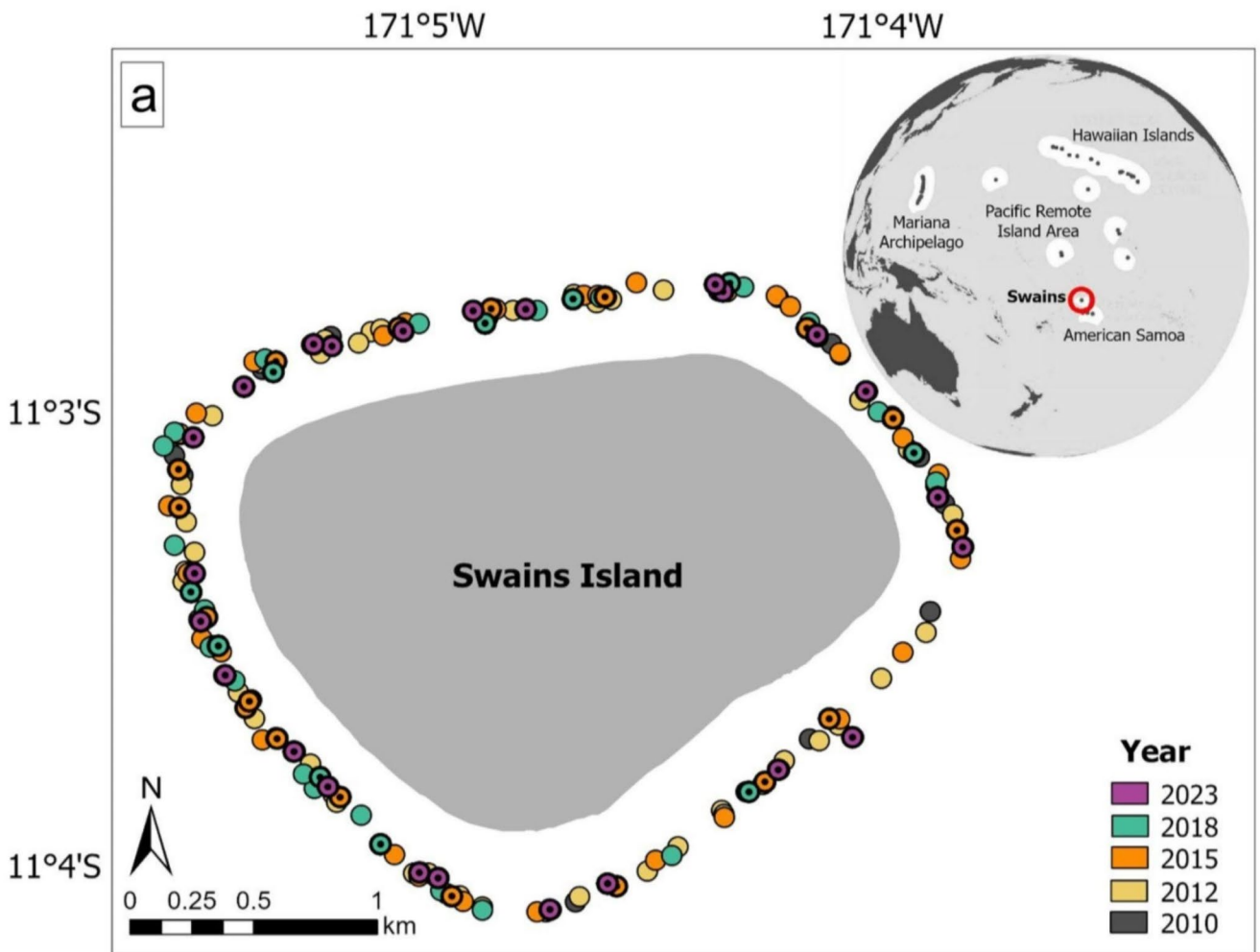
In 2014–2017, the formation of a strong El Niño resulted in the most severe global coral bleaching event on record (Eakin et al. 2019). In the central tropical Pacific, heat stress peaked in late 2015 and early 2016 and varied widely across latitudes, with prolonged exposure near the equator (Barkley et al. 2018; Brainard et al. 2019). Some islands in this region such as Jarvis Island, located at 0.37° S, experienced > 20 °C-weeks (degree heating weeks) of accumulated heat stress, which resulted in catastrophic mortality and shifts in benthic community structure (Barkley et al. 2018; Vargas-Ángel et al. 2019; Huntington et al. 2022a). Alternatively, islands at higher latitudes such as Palmyra (5.8° N) and French Polynesia (16–18° S) experienced less heat stress, bleaching, and coral mortality (Fox et al. 2019; Hédouin et al. 2020). Situated at 11.0–14.5° S, American Samoa was exposed to low to moderate heat stress and several qualitative observations of ‘severe’ bleaching in Tutuila (Office of National Marine Sanctuaries 2022). However, the

Fig. 1 (a) Location of benthic sites at Swains Island from 2010–2023, colored by survey year. Sites with co-located coral demographic and benthic cover surveys indicated with dots. (b) Satellite-derived thermal stress represented by daily Degree Heating Weeks (°C-weeks) (NOAA Coral Reef Watch 2019) at Swains Island from 2010–2023 where the gray dashed lines indicate benthic survey dates and the red line indicates the 4 °C-weeks threshold above which reef-wide bleaching is likely; (c) Historical foreereef zonation pattern in benthic communities at Swains Island with photographs of the dominant coral taxa present in each depth stratum

impacts of this heat stress and recovery of the coral reef communities within American Samoa is largely unknown.

American Samoa supports the most diverse coral reef ecosystems in the U.S. Pacific, with the highest abundance of calcifying organisms (coral and crustose coralline algae – CCA) observed at Swains Island (Huntington et al. 2022b). Swains (11.0° S, 171.1° W) is a small, isolated, and uninhabited island within American Samoa located 365 km north of Tutuila, the nearest populated island (Fig. 1a). Unlike the other reefs of American Samoa, Swains’s reefs are more similar to the isolated islands in the central Pacific, with low coral diversity dominated by *Montipora*, *Pocillopora*, and *Porites* (Bellwood et al. 2005; Venegas et al. 2019) and distinct zonation across depths (Fig. 1c). However, unlike other remote Pacific Islands such as Jarvis Island, Swains is not exposed to upwelling suggesting that there is minimal variation in temperature across depths (Brainard et al. 2008; Venegas et al. 2019). In early 2015, Swains was exposed to mild heat stress (2.5 °C-weeks; degree heating weeks) (Fig. 1b) with low bleaching (6%) observed at peak heat stress (NOAA National Coral Reef Monitoring Program 2023). In April 2016, heat stress reached 6 °C-weeks (Fig. 1b), exceeding the 4 °C-weeks threshold above which reef-wide bleaching typically occurs (Liu et al. 2014). While bleaching observations were not made during the peak of the 2016 heat stress given the challenges of accessing this remote island, widespread *Pocillopora* mortality was observed in May 2017 (Fig. S1). This mortality was most likely associated with the 2016 heat stress given the widespread mortality of a thermally sensitive taxon rather than crown-of-thorns starfish predation which is historically spatially aggregated (Brainard et al. 2008). Swains was not impacted by cyclones during this time period. Given Swains’s relative isolation and historically coral-dominated state, understanding the impacts of thermal stress and recovery trajectory of these benthic communities can shed light on the resilience of reefs that are protected from local anthropogenic stressors under the continued threat of climate change.

Here, we describe patterns in heat stress from in situ temperature data, as well as temporal trends in the benthic community to evaluate patterns in mortality and recovery after the 2014–2017 heat stress event. We hypothesize that changes in benthic cover will be distinct across depth given



gradients in temperature and irradiance as well as the pronounced zonation in coral communities and abundance of thermally sensitive taxa on shallow reefs. Further, we hypothesize that thermally sensitive taxa such as *Pocillopora* experienced the largest changes in colony density, partial mortality and size structure relative to more stress-tolerant taxa such as *Porites*.

Methods

Swains Island, also known as Olosega, has a history of human habitation dating back to early Polynesian voyagers and was later established as a copra plantation (Van Tilburg et al. 2013), but was evacuated in 2008 following severe damage from Cyclone Heta. In 2012, a majority of the coastal waters around Swains were incorporated into the National Marine Sanctuary of American Samoa. This low-lying island contains a fully enclosed brackish lagoon and is surrounded by a reef flat, crest, and steep reef slope. Swains's benthic communities display pronounced zonation across the forereef habitats (Fig. 1c). Historically, the reefs shallower than 3 m have been dominated by crustose coralline algae with sparse coral and exposed to heavy wave energy. Shallow reefs between 3 and 6 m have been dominated by CCA, *Pocillopora*, and encrusting *Montipora*. Mid depth reefs between 6 and 18 m have been dominated by foliose *Montipora*. Deep reefs between 18 and 30 m have been dominated by large mounding *Porites*, foliose *Montipora*, and the upright macroalga *Microdictyon*.

Benthic surveys

Surveys were conducted on forereef habitats as part of the NOAA Coral Reef Conservation Program's National Coral Reef Monitoring Program (NCRMP) (Fig. 1a). Benthic cover surveys were conducted in 2010, 2012, 2015 (prior to the bleaching-level heat stress), 2018, and 2023 using a stratified random sampling design ($n = 178$ across all survey years). During each survey, sites were randomly selected from within hard bottom habitats from three depth strata (shallow: 0–6 m, mid: > 6–18 m, and deep: > 18–30 m). Sample size within each stratum was proportional to the amount of hard bottom area in a given depth strata and the variance of coral density (Smith et al. 2011). Sites shallower than 3 m were excluded from the analyses given challenges of consistent access due to wave exposure. A subset of 50 sites were randomly selected for coral colony-level demographic information during the 2015, 2018, and 2023 surveys.

At each site, benthic and coral demographic surveys were conducted along one 30 m transect line deployed

along the depth contour (Winston et al. 2019). To assess benthic cover, digital images (3–10 MB and $0.7\text{--}1\text{ m}^{-2}$ per image) were taken with a Canon PowerShot SD1200IS (2010–2014), Canon PowerShot S110 (2015–2017), and Canon PowerShot G9x (2018–2023). Thirty images were collected along the transect at 1 m increments 1 m above the benthos. Benthic cover data were extracted from images using the web-based image annotation tool, CoralNet (Beijbom et al. 2015). For each image, the benthic feature under ten, randomly overlaid points was identified to the lowest taxonomic level possible and assigned to one of five functional groups: coral, crustose coralline algae (CCA), upright macroalgae (UPMA; 95% of which was *Microdictyon* sp.), encrusting macroalgae (EMA), turf/bare substrate, and other (0.33% of points which were excluded from analyses). Points were pooled across all imagery to generate site-level percent cover of benthic functional groups (300 points/site) (Lamirand et al. 2022).

Demographic surveys of colony density, size, and partial mortality were conducted on the same transects within three to four, 1×2.5 m segments spaced evenly along the first 18-m of each transect and were pooled due to the lack of spatial independence. For each coral ≥ 5 cm in max diameter, divers recorded the identity to the lowest taxonomic level possible (species, species complex, or genus), maximum diameter, morphology, and percent of the colony area that had experienced partial mortality (identified by denuded skeleton colonized by turf algae or other organisms). Juvenile colonies (1–5 cm max diameter) were also recorded within the first 1×1 m portion of the first 3 segments and were identified to the genus-level.

In-situ temperature measurements

In-situ temperature was measured using subsurface temperature recorders (STRs) made by Sea-Bird Electronics (SBE-56 Temperature Sensor). These high accuracy temperature loggers were deployed at two to three fixed stations at cardinal directions around the island at depths of 5, 15, and 25 m, corresponding to the shallow, mid, and deep strata. Temperature was collected hourly with STR download and redeployment occurring every three years between 2013 and 2018.

Data analysis

To account for the complex NCRMP survey design, all response variables were weighted by the inverse of their selection probability for a given depth stratum and survey year using the 'survey' package in R (Lumley 2022). All response variables were tested for homogeneity of variance. To identify differences in mean temperature between depths

across time, we used the STR data to calculate and plot monthly mean temperature for each depth from 2014, prior to the heat stress, until 2017.

To test how the cover of different benthic functional groups changed in each depth zone following the 2016 heat stress event, we used survey-weighted generalized linear models (GLMs) using the *svyglm* function followed by post hoc tests using the ‘emmeans’ package for each depth strata separately. Due to strong zonation in benthic communities across depth (Fig. 1c) and the a priori hypothesis regarding heat stress-related bleaching across depths, we ran separate models for each depth stratum rather than including depth as a fixed effect in a single model, which would have led to over-parameterization. For percent cover, we used quasibinomial *svyglm* models with a logit link with year (categorical) and functional group as interacting fixed effects. We adjusted the survey design using `survey.lonely.psu = “adjust”` to account for single site in the deep stratum in 2010. To test for differences between years for each taxon and depth strata, we ran pairwise comparisons to contrast changes through time within each taxonomic group and applied Benjamini-Hochberg multiple test corrections as an alternative to the highly conservative Bonferroni-based correction (Waite and Campbell 2006).

To test for shifts in adult coral communities across the three years where detailed demographic data were collected, we used one-way permutational multivariate analyses of variance (PERMANOVAs). Bray-Curtis distances were calculated from square-root transformed colony density after rare taxa (present at only 1 site) were excluded. We ran separate models for each depth stratum followed by pairwise post-hoc tests to identify between year differences in R using the packages ‘vegan’ and ‘pairwiseAdonis’ (Oksanen et al. 2008). The PERMANOVA assumption of multivariate homogeneity of dispersion among years was evaluated and confirmed for each model (PERMDISP2 procedure; Anderson et al. 2006). Coral community composition among years was visualized using non-metric multidimensional scaling (nMDS).

For depth strata that experienced significant shifts in community composition, we followed up with univariate analyses of adult density and partial mortality for the three most abundant coral taxa (*Porites* spp., *Montipora* spp., and *Pocillopora* spp.) at the species complex or genus/morphology-level to test for differences among survey years. Given the challenges of species level identification of juvenile corals, we also tested for changes in juvenile density for the dominant taxa at the genus-level. For density metrics, we used *svyglm* models with a quasipoisson distribution or tweedie distribution for the zero-inflated taxa (*Porites* in shallow and *Pocillopora* in deep). Average percent partial mortality was analyzed using a gaussian

distribution or nonparametric *svyranktest* for each taxon (note, *P.meandrina/verrucosa* complex was square root transformed). When significant differences were detected, we used pairwise tests in ‘emmeans’ to test for differences between years.

Lastly, for the top three dominant genera (*Porites*, *Montipora*, and *Pocillopora*), we explored changes in size structure between 2015 and 2023. The NCRMP sampling design surveys juvenile corals over a different sampling domain (3m² per site) than adult corals (10m² per site), preventing us from merging adult and juvenile size data into a single size frequency distribution at the site level. Rather, for each genera, we first pooled all log₁₀-transformed adult colony diameter data (regardless of site), and identified the 10th and 90th percentiles to bin corals as ‘small’, ‘medium’, and ‘large’ sized colonies (Dietzel et al. 2020). For each site, we then calculated the density per size class bin, as well as colony density of juveniles. We then converted these densities into relative proportions as we were interested in the proportion of corals in different size classes over time, irrespective of differences in absolute density. For each of these three genera, the proportion of colonies in each of the four size classes was used as the response variable in a gaussian *svyglm* model for each of the three depth strata with size class and year included as interacting fixed effects.

Results

Heat stress

Between December 2015 and April 2016, Swains Island experienced moderate heat stress, culminating in 6 °C-weeks above the regional coral bleaching threshold (Fig. 1b). Reefs experienced similar temporal patterns in mean monthly seawater temperatures across depth during the heat stress event, displaying minimal vertical structure in temperature (Fig. S2). Temperatures in shallow habitats warmed slightly earlier and at a faster rate starting in December 2015 and were 0.07–0.2 °C warmer than mid and deep habitats in March 2016, just before the peak of the heat stress event in April 2016.

Benthic cover

Overall, benthic cover of the functional groups was generally stable up to 2015 and predominantly coral-dominated at all three depth strata (Fig. 2). However, after the 2015 thermal stress event, percent cover of functional groups varied across years most notably in the shallow and mid depth reefs, while deep reefs remained mostly stable.

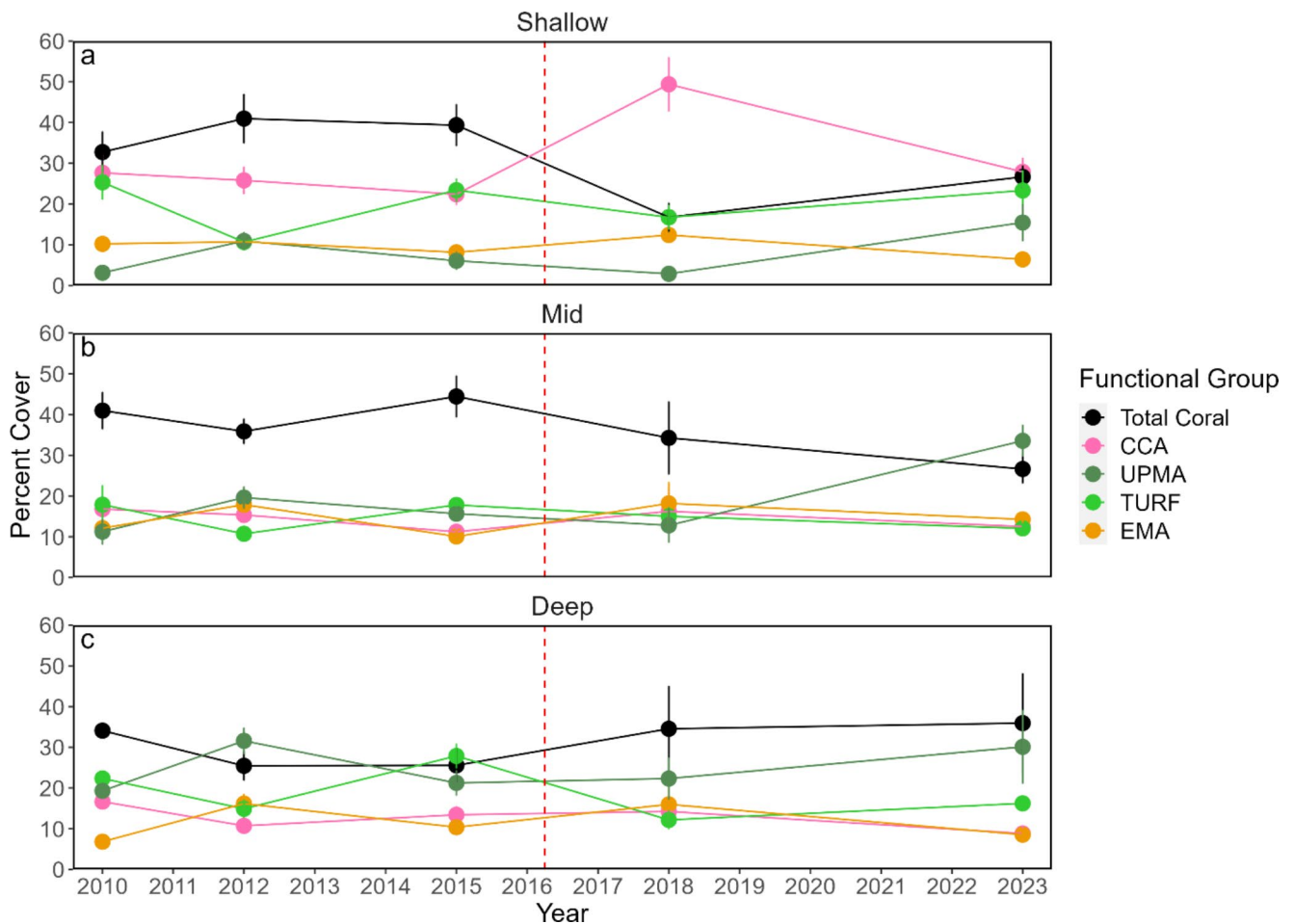


Fig. 2 Time series of percent cover (mean \pm SE) of functional groups (coral, crustose coralline algae [CCA], upright macroalgae [UPMA], turf algae, and encrusting macroalgae [EMA]) across (a) shallow (3–6 m), (b) mid (6–18 m), and (c) deep (18–30 m) depth strata. Site

counts for the depth strata, listed in order of Shallow/Mid/Deep were: 2010–8/8/1; 2012–17/28/10; 2015–20/25/11; 2018–10/11/6; 2023–11/10/3. Vertical dashed line represents the peak of El Niño heat stress event at Swains

Prior to the thermal stress event, benthic cover on shallow reefs was stable for every functional group except turf algae, which dropped by $\sim 15\%$ from 2010 to 2012 (post hoc $p < 0.001$), but rebounded by 2015 ($p < 0.001$; Fig. 2a). Roughly two years after the 2015 thermal stress event, coral cover on the shallow forereef at Swains had dropped from between 30 and 40% to $16.7 \pm 3.5\%$ in 2018 ($p = 0.003$). The reduction in coral cover between 2015 and 2018 was accompanied by a 27% increase in CCA ($p < 0.001$), which was the only other functional group that changed significantly over this time period. Between 2018 and 2023, the percent cover of CCA has dropped significantly by 21.5% ($p = 0.011$) and EMA by 6% ($p = 0.031$) to pre-heat stress levels and appear to have been displaced by upright macroalgae and coral. Upright macroalgae, primarily *Microdictyon*, never exceeded 11% in previous surveys but increased by 12.6% from 2018 to 2023 ($p = 0.005$). Coral cover increased by 9.9% between 2018 and 2023 and although this increase

was not significant ($p = 0.072$), is now similar to 2010 levels ($p = 0.366$) with 26.6% cover.

Benthic cover on mid depth reefs was less variable than on shallow reefs (Fig. 2b). Prior to the heat stress, coral cover was stable between 2010 and 2015 ($p = 0.68$), but showed a gradual and significant decline of 17.8% from 2015 to 2023 ($p = 0.037$). While CCA cover remained low and unchanged across years, other early successional taxa such as turf algae showed small significant changes in cover across years, but no general trend (EMA: 2010–2012, $p = 0.047$; 2012 to 2015, $p = 0.01$; Turf: 2012–2015, $p = 0.039$, 2018–2023, $p = 0.039$). In contrast, upright macroalgae cover was stable until 2018, but increased by 20.8% by 2023 and is now the dominant functional group ($p = 0.007$).

On deep reefs, percent cover of all functional groups except turf and encrusting macroalgae remained stable across years ($p > 0.05$ for all pairwise comparisons; Fig. 2c). Coral cover remained between 25.4 ± 4.2 to $35.9 \pm 12.2\%$ cover across all years. Similar to shallow and mid-depth

reefs, turf algae was variable across the time series, with a 13.0% increase from 2012 to 2015 followed by a 15.7% decline from 2015 to 2018 ($p < 0.001$), and no changes between 2018 and 2023 ($p = 0.281$). Upright macroalgae cover increased by 12.2% ($p = 0.001$) between 2010 and 2012 then declined to 2010 levels and has remained stable across the remainder of the time series ($p > 0.05$ for all pairwise comparisons). EMA cover was generally stable at deep depths, but cover gradually declined by 7.6% from 2012 to 2023 ($p = 0.036$).

Coral community demography

Between 2015 and 2023 the community composition of adult colonies only changed in the shallow depth stratum (PERMANOVA: shallow, $F_{1,22} = 2.35$, $p = 0.03$; mid depth, $F_{1,17} = 1.21$, $p = 0.31$; deep, $F_{1,7} = 1.89$, $p = 0.08$), with each year significantly different from the others (Fig. 3; $p < 0.005$ for all pairwise adonis comparisons). Comparisons of the dominant taxa across years on shallow reefs revealed that adult coral densities of *P. meandrina/verrucosa* complex, *P. grandis/woodjonesi* complex, and mounding *Porites* declined significantly between 2015 and 2018 (Fig. 4), with the largest decline in *P. meandrina/verrucosa* complex. By 2023, mounding *Porites* rebounded to 2015 density levels. In contrast, both *Pocillopora* complexes increased from

2018 to 2023, but remained approximately 40% lower than pre-2015 bleaching densities (Fig. 4). Despite changes in the shallow coral community composition, the overall zonation patterns of these communities persist with shallow reefs dominated by *Pocillopora*, mid depths by foliose *Montipora*, and deep reefs a mix of foliose *Montipora* and mounding *Porites* (Table S1).

The extent of partial mortality remained relatively stable across years in each depth strata for all the dominant coral taxa except the *P. meandrina/verrucosa* complex (Fig. S4). Partial mortality in *P. meandrina/verrucosa* varied significantly across years on shallow reefs ($p < 0.001$), with a 5-fold increase from $5.6 \pm 1.2\%$ in 2015 to $30.1 \pm 4.2\%$ in 2018. By 2023, *P. meandrina/verrucosa* complex partial mortality dropped back to levels similar to those recorded in 2015 (2023: $6.54\% \pm 0.75$; $p = 0.487$).

Colony size structure was stable for all three dominant coral genera across survey years and depths. Significant interactions were found between year and size class for *Montipora* and *Pocillopora* in the shallow depth strata only. For these two genera, the proportion of small adult colonies (10th percentile) increased significantly from 2015 to 2023 ($p < 0.015$ for both genera). This increase represents more than a doubling of the proportion of small adult *Pocillopora* colonies in the population (2015 mean = $8.7\% \pm 1.8$ SE, 2023 mean = $20.8\% \pm 3.3$ SE), and a three-fold increase in

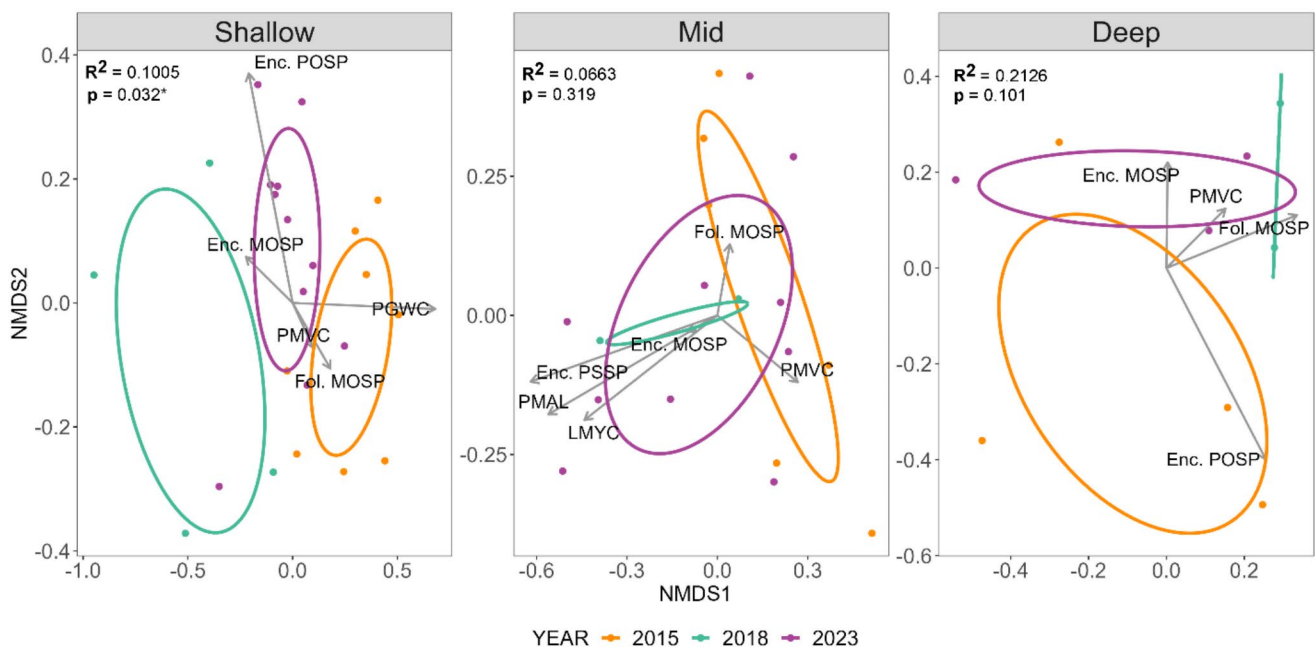


Fig. 3 Nonmetric multidimensional scaling (nMDS) plot for sites across the shallow, mid, and deep strata (Stress value shallow (3–6 m)=0.10; mid (6–18 m)=0.09; deep (18–30 m)=0.02). Only vectors for the dominant coral taxa are shown. Ellipses represent 95% confidence intervals around the community centroid for each survey year. PGWC: *Pocillopora grandis/woodjonesi* complex; PMVC:

Pocillopora meandrina/verrucosa complex; Enc. POSP: encrusting *Porites* spp.; Enc. MOSP: encrusting *Montipora* spp.; Fol. MOSP: foliose *Montipora* spp.; Mound POSP: mounding *Porites* spp. PERMANOVA results are reported in the corner of each depth stratum plot, * indicates significant effect of year ($p < 0.05$)

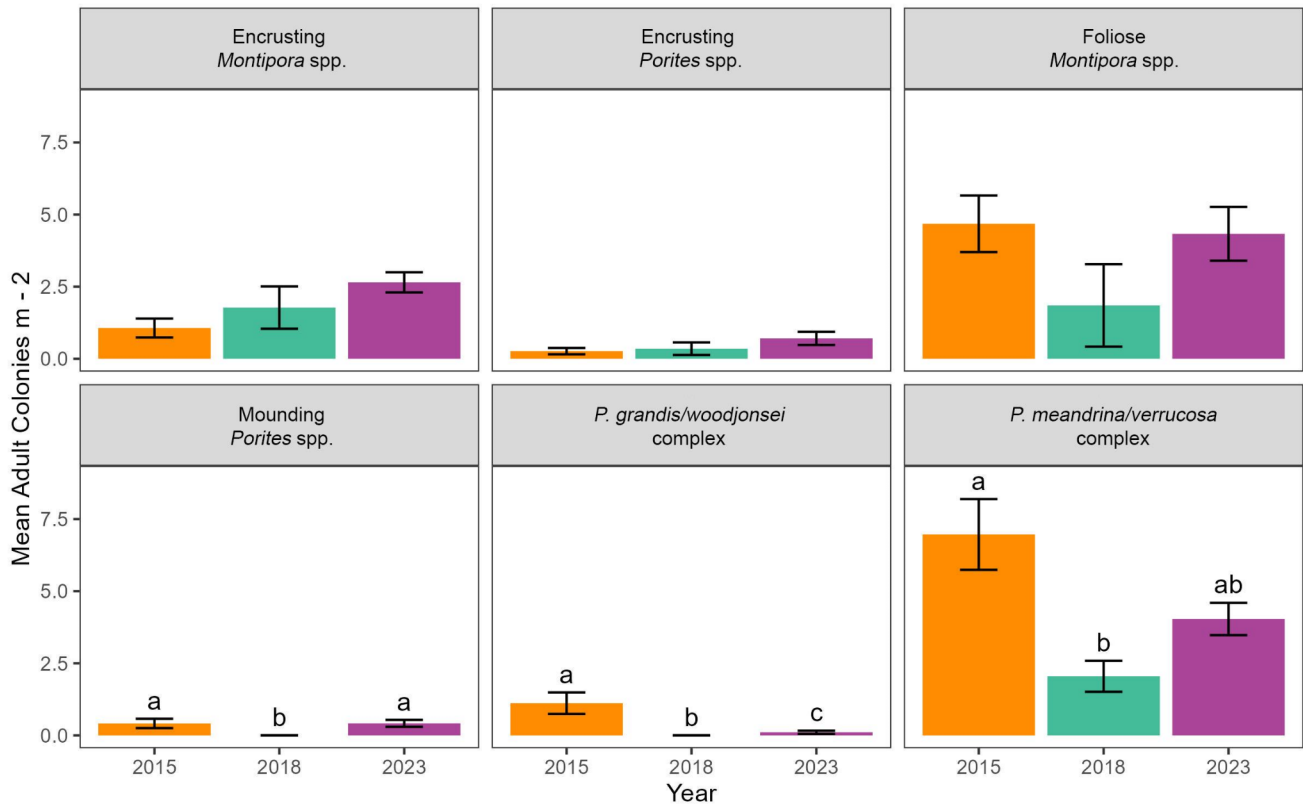


Fig. 4 Mean adult colony density of coral taxa (\pm SE) within the shallow (3–6 m) depth strata that contributed to changes in community structure. Letters are used to indicate significant ($p < 0.05$) differences

in colony density between years. $N = 8$ sites in 2015, 4 sites in 2018, and 11 sites in 2023

the proportion of *Montipora* (2015 mean = $4.5\% \pm 1.3$ SE, 2023 mean = $13.7\% \pm 1.6$ SE). No other significant differences in size classes were observed in any strata (Table S2).

Juvenile density did not change significantly across years at each depth strata for the three dominant coral genera (Fig. S4).

Discussion

During the most recent global bleaching event, coral reefs surrounding Swains Island were exposed to ~ 6 °C-weeks of heat stress. This coincided with the relative loss of almost half of live coral cover on the shallow forereef, which was predominantly replaced by CCA between 2015 and 2018. While the mortality was less severe relative to other Pacific reefs that experienced prolonged heat stress (Le Nohaïc et al. 2017; Hughes et al. 2018; Vargas-Ángel et al. 2019; Raymundo et al. 2019; Bessell-Browne et al. 2021; Nakamura et al. 2022), coral mortality was surprisingly high given the moderate heat stress. Coral Reef Watch bleaching and mortality thresholds can be spatially variable and do not always predict reef-level responses with

thresholds sometimes under predicting bleaching responses (reviewed by McClanahan 2022). This mortality may also be explained by Swains's high abundance of thermally sensitive taxa and fairly stable climatology with only one minor heat stress event (~ 4 °C-weeks) occurring in 2003 (NOAA Coral Reef Watch 2019). Consistent with our hypothesis, these changes were not felt evenly across depth. Changes in benthic communities and coral demography were most pronounced on shallow reefs. On these reefs and consistent with our hypothesis, thermally sensitive *Pocillopora* spp. experienced a nearly 3-fold decline in colony density. Mid-depth reefs also lost a significant portion of live coral cover (albeit a smaller decline than the shallow reefs), which has largely been replaced by upright macroalgae. In contrast, benthic communities between 18 and 30 m remained stable, suggesting Swains deep reefs escaped damage from the 2015–16 global bleaching event.

While both shallow and mid-depth reefs experienced loss in coral cover in the years immediately following the heat stress event, the recovery trajectory of these benthic communities varied between depth strata. On shallow reefs (3–6 m), CCA colonized the substrate previously occupied by coral by 2018, preserving calcifier dominance. The

proliferation of CCA may have also laid the framework for the early coral recovery observed in this habitat as the preferred settlement substrate for coral larvae (Morse et al. 1988; Harrington et al. 2004). Rapid proliferation of CCA immediately following mass coral mortality is a common feature of many remote tropical reefs (Benkwitt et al. 2019; Huntington et al. 2022a). Unlike Swains, the remote Pacific Island of Jarvis Island experienced an increase in CCA abundance across depths < 30 m following catastrophic bleaching in 2016 (Huntington et al. 2022b). Although it is unclear why CCA did not respond on mid-depth reefs at Swains, one difference between the islands is that Jarvis experiences seasonal upwelling of nutrient rich water, which may have facilitated CCA growth across the larger depth range. Differences in herbivory between the islands may have contributed to the observed differences but unfortunately, fish data were not available for the full period following bleaching. Our study represents one of the few studies to assess the long-term patterns in CCA cover beyond two years after a major disturbance and highlights the ephemeral nature of this important taxon (Fox et al. 2019; Lange et al. 2023). In contrast, mid depth reefs (6–18 m) have transitioned to communities dominated by non-calcifying upright macroalgae following a steady decline in coral cover. Historical patterns in macroalgal communities at Swains indicate that this community is largely composed of the native *Microdictyon* (Brainard et al. 2008). This upright macroalgae is common on coral reefs, is often avoided by herbivorous fish, and consequently easily fills space (Dell et al. 2020). In the early 2000s, macroalgal cover increased 30% on mid depth reefs in the two years following the damage caused by Hurricane Heta in 2004 (Brainard et al. 2008), but declined to pre-disturbance levels by 2010 (Pacific Islands Fisheries Science Center 2018). We postulate that the low abundance of CCA, lower wave energy in the mid depths, combined with a historical and dynamic presence of *Microdictyon* has facilitated increasing growth of this macroalga, especially following disturbances.

Based on in situ temperature alone, we found no evidence of a depth refuge from heat stress at Swains. While numerous studies have documented reduced heat stress at depth (Glynn 1996; Riegl and Piller 2003), sub-surface temperature data at Swains suggests that heat stress was fairly similar across depths (Fig. S2). Venegas et al. (2019) also found that depth did not provide a consistent refuge from heat stress for coral communities in a study of 49 islands across the central and western Pacific. Thus, the absence of significant mortality on Swains's deeper reefs relative to shallow reefs is likely related to other factors rather than vertical patterns in temperature. The distribution of taxa and their corresponding thermal tolerance may partially explain differential patterns in mortality (e.g. Marshall and Baird

2000; Darling et al. 2012; Frade et al. 2018). At Swains, the deep reefs contained abundant mounding *Porites* which are more common on deeper and/or low wave energy systems (Done and Potts 1992) and more thermally-tolerant (Darling et al. 2012). In contrast, the thermally sensitive genus *Pocillopora* (Marshall and Baird 2000; Loya et al. 2001; Darling et al. 2012; Guest et al. 2012) were abundant on shallow reefs, but largely absent below 18 m. Interestingly, the thermally sensitive genus *Montipora* (Vargas-Ángel et al. 2019; Raymundo et al. 2019), remained stable and moderately abundant on deep reefs, suggesting the role of other environmental factors. Irradiance, another known trigger of coral bleaching, decreases with depth, which may have resulted in lower bleaching as seen in previous studies (Gleason and Wellington 1993), and lower mortality on deep reefs.

Beyond the broader changes in the benthic community, heat stress resulted in shifts in shallow coral communities predominantly driven by changes in *Pocillopora* spp. More specifically, we observed a 100% loss of *P. grandis/woodjonesi* complex and 65% decline in the more abundant *P. meandrina/verrucosa* complex. Given the low abundance of other branching taxa such as *Acropora*, declines in *Pocilloporids* represent a substantial loss of this unique habitat with the potential to affect local reef fish communities (e.g. Wilson et al. 2008). However, contrary to our hypothesis, we did observe a small but significant decline in mounding *Porites* in the shallow reefs and the thermally sensitive and important reef-building taxon *Montipora* did not decline following heat stress (Fig. 4). This stands in stark contrast to the severe to catastrophic *Montipora* mortality recorded on other Pacific reefs during this global bleaching event (Vargas-Ángel et al. 2019; Raymundo et al. 2019), suggesting that at moderate levels of heat stress, *Montipora* may be able to withstand ocean warming. Patterns in partial mortality also set Swains apart from other reefs in the Pacific. A quarter of *Pocillopora* colonies experienced partial mortality in 2018, which is surprising given that this genus typically experiences whole colony mortality following heat stress (Loya et al. 2001; Burgess et al. 2021). Swains's more moderate community-level response to heat stress effects is likely influenced by the moderate nature of this heat stress event (6 °C-weeks) relative to other Pacific Islands that experienced severe heat stress exceeding > 8 °C-weeks.

Coupling patterns in benthic cover with those in coral demography suggest the shallow communities at Swains are on the road to recovery. Adult density has started to increase, especially in *Pocillopora*, and partial mortality has returned to pre-bleaching levels. Interestingly, the 2–3 fold increase in the abundance of small *Pocillopora* and *Montipora* colonies at Swains suggests recruitment succeeded post-heat stress, despite Swain's overall low juvenile density (2–4.5

colonies/m²) compared to other Pacific reefs (Couch et al. 2023) — which may be related to its geographic isolation and reliance on local recruitment pulses. This increase is evidence of post-disturbance local recruitment, survival, and growth into the early adult size class rather than fragmentation of larger colonies since partial mortality was accounted for in our surveys. Therefore, the *Pocillopora* recovery at Swains aligns with its role as an early successional taxon (Grigg and Maragos 1974; Darling et al. 2012; Adjeroud et al. 2018) and suggests that these reefs are not suffering from post-bleaching recruitment failure seen on other reefs (Hughes et al. 2019; Carlot et al. 2021). While Swains's *Pocillopora* recovery bodes well for reef accretion in the shallow reefs, the continued coral decline at mid depth reefs is concerning. The absence of a demographic signal amidst declining coral cover on mid depth reefs may be explained by our survey approach. As an upright, space-filling algae, *Microdictyon* readily takes up space and may obscure underlying coral colonies when viewed in the top-down imagery used for benthic cover assessments, resulting in a decline in coral cover. However, when we look at the 3D morphology, our demographic surveys often revealed living coral tissue under the algae, resulting in consistent density, size structure and partial mortality through time. Our spatially comprehensive and long-term dataset highlight the value of taking a more holistic approach to understanding the demographic mechanisms driving changes in coral cover past the first two years post bleaching, which is largely absent in the literature (Edmunds and Riegl 2020).

Remote reef communities provide insight into baselines of ecological functioning and resilience of coral reefs to the effects of climate change in the absence of local anthropogenic disturbances (Sandin et al. 2008; Smith et al. 2008; Halford and Caley 2009). Historically, Swains's coral reefs have been especially resilient with coral communities recovering within a decade following acute disturbance. During the late 1980s to early 2000s, Swains was exposed to severe storms which caused localized decline in coral cover of 50 to 80% (Itano 1997; Brainard et al. 2008), followed by outbreaks of *Acanthaster planci* and a native tunicate, resulting in further coral mortality (Brainard et al. 2008; Vargas-Ángel et al. 2009). In the subsequent years, coral cover returned to pre-disturbance levels (Page and Green 1998; Pacific Islands Fisheries Science Center 2018) and was largely stable between 2010 and 2015.

However, successional patterns following the 2016 heat stress event suggest that contemporary reefs are experiencing a more nuanced pattern of resilience to disturbance with early signs of coral recovery in shallow reefs, a shift to non-calcifier dominance at mid depth, and community stability on deep reefs. Despite a decline in coral cover island wide since 2015 and increasing non-calcifier abundance, Swains

still has among the highest calcifier abundance (51% cover) in the U.S. Pacific Islands (Huntington et al. 2022b). While the factors driving calcifier persistence at Swains are unclear, American Samoa's high aragonite saturation state combined with the high wave energy on shallow reefs creates an environment in which calcifiers such as CCA and corals have been able to thrive (Barkley et al. 2022; Office of National Marine Sanctuaries 2022). However, unlike other islands in American Samoa, Swains is showing a warming trend without reprieve between heat stress events suggesting that Swains is at risk of continued reef-wide bleaching (Smith and Barkley *in review*). In fact, at the time of writing, Swains is experiencing severe heat stress exceeding the 2016 event (> 8 °C-weeks) (NOAA Coral Reef Watch 2019). Swains's geographic isolation and the dominance of thermally sensitive taxa such as *Pocillopora* and *Montipora* may pose a threat to future climate resilience. However, the island's isolation also provides a reprieve from many local anthropogenic stressors. Accordingly, Swains and other remote islands and atolls provide a rare opportunity to understand potential "best case" scenarios for Anthropocene coral reefs if local stressors can be well managed or eliminated. Thus, the continued persistence of CCA and coral at Swains, and the degree to which increasing *Microdictyon* represents a temporary shift or gradual "ratcheting down" of coral and calcifier abundance (Birkeland 2004) may be a telling indicator for the future of coral reef communities.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-024-04533-z>.

Acknowledgements Institutional, logistic, and financial support was also provided by NOAA Pacific Islands Fisheries Science Center's Ecosystem Sciences Division (ESD). We would like to thank the many NCRMP scientists who helped collect the data used in this study and the crew of the NOAA Ships Hi'ialakai and Rainier for field support. We thank Hannah Barkley and two anonymous reviewers for insightful feedback on this manuscript.

Author contributions CSC, BH, JAC, CA, MA, IB, ML, DTP and AAS contributed to the study design. CSC, BH, JAC, CA, MA, IB, ML, and DTP collected data. CSC, BH, JAC, CA, ML, and AAS conducted data analysis. CSC, JAC, BH and AAS lead the writing of the manuscript. VB provided expert knowledge and a historical perspective on the study region. All authors reviewed and edited drafts, and approved the final manuscript.

Funding This work was supported by the NOAA Coral Reef Conservation Program's National Coral Reef Monitoring Program (NCRMP) (Project 743).

Data availability Data and scripts used to summarize and analyze data are available at <https://github.com/cscouch/swains>.

Declarations

Ethical approval All surveys were approved and permitted through the Department of Marine and Wildlife Resources American Samoa government.

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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