

## Recent Changes (2018-2022) in Benthic Cover in Tubbataha Reefs Natural Park, Sulu Sea, the Philippines

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**Tubbataha Reefs Natural Park is a benchmark for reef condition in the Philippines. However, there has been a notable decline in hard coral cover from 2018–2022, coinciding with an increase in sponges and cyanobacteria – changes that were earlier posited to be due to eutrophication. Over the five-year time series used in this study, changes in the studied benthic components (hard coral, soft coral, sponges, macroalgae, turf algae, and cyanobacteria) did not all align with expected changes for a reef system experiencing nutrient enrichment. Moreover, these changes were not statistically significant at most spatial scales, and only turf algae and cyanobacteria exhibited significant changes with adequate statistical power at any given spatial scale. At present, nutrient enrichment cannot be confirmed nor completely ruled out as the main driver of the changes seen. Other drivers of change such as typhoon impacts must also be considered. The shortage of statistically powerful results indicates the need for a more robust dataset before a conclusive cause for the changes in the cover of benthic components can be drawn.**

Keywords: benthic cover, coral reefs, eutrophication, monitoring, power analysis

### INTRODUCTION

Tubbataha Reefs Natural Park (TRNP), located in the Sulu Sea, is a UNESCO World Heritage Site (Tubbataha Management Office 2020). It is the largest and best-managed no-take marine protected area in the Philippines (Dygico *et al.* 2013). The reefs of TRNP may also serve as a benchmark for hard coral cover and diversity in the Philippines (Licuanan *et al.* 2017). However, according to Feliciano *et al.* (2022), hard coral cover in TRNP has been declining at several spatial scales, particularly from 2017–2022. These declines, specifically in the South Atoll

(see Figure 1), have coincided with observed increases in the cover of cyanobacteria and sponges. Additionally, Licuanan and Bahinting (2021) identified an increase in algal assemblage cover (separated into the categories of turf algae and cyanobacteria in this study). This has led to the hypothesis that TRNP, and specifically the South Atoll, is experiencing eutrophication (Licuanan and Bahinting 2021).

The impact of eutrophication on water quality may cause changes in reef benthos – particularly declines in the cover of hard and soft corals, as well as increases in the cover of sponges, turf algae, macroalgae, and cyanobacteria (Fabricius 2011; Flower *et al.* 2017). These changes may

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only be evident after several years of persistent eutrophic conditions but may be seen within the spatial scale of hundreds of meters (Reyes *et al.* 2022).

TRNP is well-protected against direct human impacts such as fishing. It is also located very far from human settlements and is therefore minimally impacted by land-based disturbances and stressors. Identifying the drivers of coral reef decline in this reef may reveal threats that are not immediately apparent.

Thus, this research examines changes in reef benthos in TRNP from 2018–2022 to evaluate the veracity of the hypothesis presented by Licuanan and Bahinting (2021) and to determine if the changes in reef benthos are consistent with expected changes due to nutrient enrichment.

## MATERIALS AND METHODS

### Survey Methods

The reefs of TRNP were sampled using a hierarchical design. The park is composed of two atolls (the North and the South Atolls) and one cay (Jessie Beazley Reef). Each atoll is sampled with two sites, with two stations nested in each site. Jessie Beazley has only one site with two stations nested within it, denoted as JBA and JBB. The sampling stations may be seen in Figure 1. Each station measures 75 m long (following the reef's depth contour) and 25 m wide (from shallow to deep) and is 2–5 m in depth. Five 50-m transects were deployed at random intervals within each station, with a distance of at least one meter between each transect. A series of 50 1 m x 1 m photographs were taken on the shallow side of each transect.

The reefs of TRNP are monitored annually from late April to early May. This analysis makes use of data collected by the Tubbataha Management Office and the De La Salle University Br. Alfred Shields FSC Ocean Research Center from 2018–2022.

### Data Processing Methods

Photographs from the 2018–2022 monitoring periods were imported into the program Coral Point Count with Excel extensions (CPCe) (Kohler and Gill 2006). In the program, a 1 m x 1 m frame was placed over each image, and 10 points were randomly scattered within the frame. The benthos under each point were identified as one of the following categories: hard coral (HC), soft coral (SFT), sponges (SP), macroalgae (MA), turf algae (TURF), and cyanobacteria (CYANO). Each transect, with 50 subsamples, was considered a replicate (five replicates per station, 10 replicates per site, *etc.*)

### Data Analysis Methods

Raw data from the CPCe data processing was imported into the program R v.4.3.1 (R Core Team 2023). The base function `shapiro.test()` was used to determine normality. However, despite the data being non-normal at all spatial scales, for the sake of using a more powerful statistical test, the base `aov()` function was used to run repeated measures analysis of variance (ANOVA) to determine significant differences in the cover of benthos over the years. These analyses were run at all spatial scales (location-level, atoll-level, site-level, and station-level). All figures were generated using the package `ggplot2` (Wickham 2016).

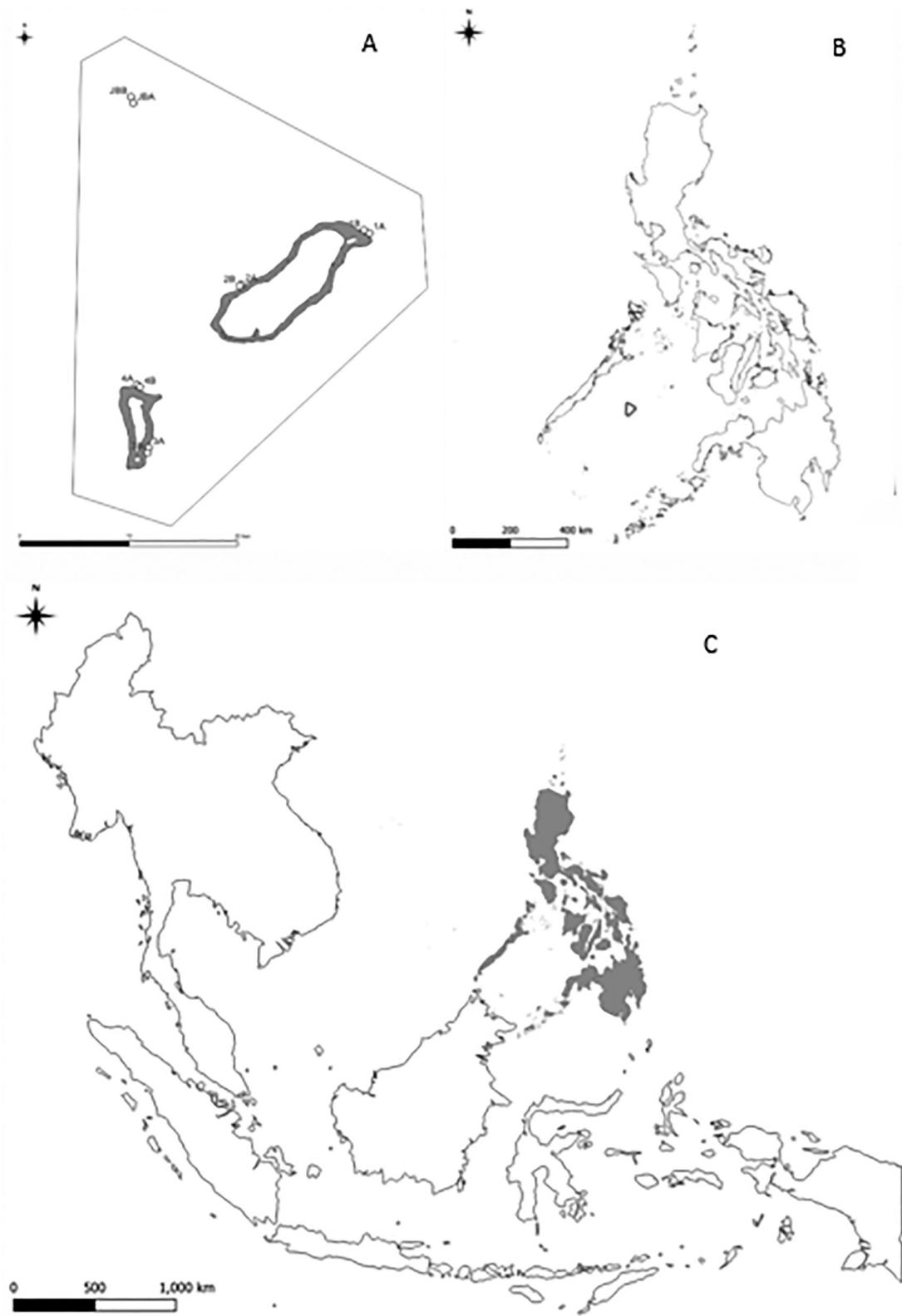
The power analysis provides further insight into the validity of the statistical results. Statistical power gives the likelihood of making a Type II error, or failing to reject the null hypothesis when the null hypothesis should be rejected (Serdar *et al.* 2021). In this case, the null hypothesis would be that there is no significant difference in the cover of the benthic components over the years. A statistically powerful result would have a power of at least 0.8 or 80%, indicating an 80% probability that a Type II error has not been made (Serdar *et al.* 2021). Given this, the statistical power of the ANOVA test was also determined. To determine statistical power, Cohen's *f* value was first calculated using the `cohens_f()` function in the `effectsize` package (Ben-Shachar, Lüdtke, and Makowski 2020). Statistical power was then calculated using the `wp.rmanova()` function in the `WebPower` package (Zhang and Yuan 2018).

## RESULTS

### Initial Trends in Benthic Components

Across the whole of TRNP, the only statistically significant changes from 2018–2022 were declines in both CYANO and TURF. This was true for datasets that included and excluded data from Jessie Beazley. There was no significant change in HC at this spatial scale. Similarly, the only significant changes at each atoll (North and South) and Jessie Beazley were declines in both CYANO and TURF. Although there was an apparent decline in HC at the South Atoll, this decline was not statistically significant based on the repeated measures ANOVA.

None of the sites exhibited statistically significant changes in HC. However, all sites exhibited significant changes in spatial competitors of hard coral (Table 1). For the North Atoll sites, Site 1 had a significant increase in TURF and a significant decline in CYANO, whereas Site 2 had significant increases in TURF and CYANO and a significant decline in SP. For the South Atoll sites, Site



**Figure 1.** Map showing [a] the sampling stations Tubbataha Reefs Natural Park, [b] the location of the park within the Philippines, and [c] the Philippines within Southeast Asia.

**Table 1.** Summary of observed changes across different spatial scales, from 2018–2022, compared to expected changes for a reef undergoing eutrophication. Cover values per year may be seen in Appendix I. Figures showing changes per benthic component may be seen in Appendix II. Observed changes marked in red or green are in line with expected changes. Observed changes marked in gray do not align with expected changes. [ns] not significant.

Benthic component	Expected change	Observed change																	
		Whole of TRNP		Atolls and shoals			Sites				Stations								
		With data from Jessie Beazley	Without data from Jessie Beazley	North Atoll	South Atoll	Jessie Beazley Reef	1	2	3	4	1A	1B	2A	2B	3A	3B	4A	4B	Jessie Beazley A
HC	↓	ns	ns	ns	ns	ns	ns	ns	ns	↑	↑	ns	ns	↓	ns	ns	ns	ns	↓
SFT	↓	ns	ns	ns	ns	ns	ns	↓	ns	ns	↑	ns	ns	↓	ns	ns	ns	ns	↓
SP	↑	ns	ns	ns	ns	ns	ns	ns	ns	ns	↑	↑	ns	ns	ns	↑	ns	ns	ns
MA	↑	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
TURF	↑	↓	↓	↓	↓	↓	↑	↑	↓	↓	↓	↓	↓	↓	↓	↓	↑	↓	↑
CYANO	↑	↓	ns	↓	↓	↓	↓	↑	↑	↓	↑	↑	↓	↓	↑	↓	↓	↓	↑

**Table 2.** Results of power analysis of statistically powerful results at the site spatial scale and higher. Result marked as n/a is not statistically powerful.

Benthic component	% power						
	Whole of TRNP		Atolls and shoals		Sites		
	With data from Jessie Beazley	Without data from Jessie Beazley	North Atoll	South Atoll	1	2	3
TURF	99.9	99.9	99.9	96.3	98.6	99.9	96.7
CYANO	99.9	99.7	99.2	81.9	98.8	95.5	n/a

3 had a significant decline in TURF and a significant increase in CYANO, whereas Site 4 had a significant decline in both TURF and CYANO. It should be noted that an increase in spatial competitors is not always accompanied by a decrease in HC, depending on the habitable space available on the substrate.

Significant changes in HC only occurred at the station level for Stations 1A and 1B, with both exhibiting an increase in HC for the five-year period. Other significant changes included an increase in SFT in Station 1A, an increase in SP in Station 1B, and declines in TURF and increases in CYANO for both stations (Table 1).

**Power Analysis**

Power was below 80% for most of the statistical tests performed in this study, indicating a high probability that the null hypothesis (that there is no significant change in cover over the years) could not be rejected even if it is false (Serdar *et al.* 2021). This means that the non-significant results of the statistical test are due more to high variability over time and insufficient levels of replication rather than the absence of differences in cover of particular benthic components over the years. For HC, SFT, and SP at all spatial scales and at all sampling points, the sample size was too small for the statistical tests to have high (≥ 80%) statistical power at the 95% confidence level. At the location level (with and without Jessie Beazley

data) and the atoll level (both North and South Atolls), statistical tests were only statistically powerful for TURF and CYANO.

At the site level, statistical tests were only statistically powerful for TURF and CYANO for Site 1; MA, TURF, and CYANO for Site 2; and TURF for Site 3. No statistical tests were statistically powerful for Site 4 nor for Jessie Beazley. This was also reflected at the station level, where none of the statistical tests for Stations 4A, 4B, JBA, nor JBB were statistically powerful.

At the station level, change could only be detected for TURF and CYANO for Station 1A and only CYANO for Station 1B. For Station 2A, the change could only be detected for TURF, as opposed to both TURF and CYANO for Station 2B. For Station 3A, the change was only detectable for MA, and for Station 3B, the change was only detectable for TURF. The results of the power analysis are summarized in Table 2.

**DISCUSSION**

**Evidence for Eutrophication**

If eutrophication is the main driver of benthic change, a reef is expected to exhibit a decline in hard coral and

soft coral (Fabricius 2011), and a simultaneous increase in the cover of sponges, macroalgae, turf algae, and cyanobacteria (Fabricius 2011; Flower *et al.* 2017). According to Reyes *et al.* (2022), the changes should be observable at the spatial scale of hundreds of meters, which would correspond to the site level or larger spatial scale in the sampling hierarchy.

At the larger spatial scales, the only significant changes were in TURF and CYANO, following downward trends across the whole of TRNP, and at each atoll and Jessie Beazley. This is in contrast with expected trends. Moreover, the changes in TURF and CYANO were also the only statistically powerful results (Table 2).

At the site level, Site 2 exhibited the most significant changes in line with expected trends: increases in TURF and CYANO, and a decline in SFT. Site 2 is located near a channel through which water drains from the atoll (Feliciano *et al.* 2022). This would support the hypothesis of Licuanan and Bahinting (2021) that observed changes may be driven by nutrient-rich waters draining from the lagoon. However, only the results for TURF and CYANO were statistically powerful for Site 2 (Table 2). Sites 1 and 3 also had significant changes in line with expected trends. Specifically, there was an increase in TURF at Site 1 and an increase in CYANO at Site 3. However, the latter was not a statistically powerful result (Table 2).

It must be noted that this study did not examine water quality data. According to the 2022 Tubbataha Ecosystem Research and Monitoring report, concentrations of nitrates in TRNP are well within the recommended levels for protected areas, but the concentration of phosphates exceeded these recommended levels (Alaba *et al.* 2022). This indicates that if nutrient enrichment is occurring in TRNP, it is being driven by an increase in phosphates rather than nitrates. Further studies in TRNP may benefit from additional water quality assessment and monitoring to better understand the relationship between nutrient levels and changes in benthic components.

### Changes in Hard Coral Cover

Although changes at the station level alone may not be indicative of nutrient enrichment, based on the spatial scale proposed by Reyes *et al.* (2022), there were significant changes in HC at four stations: Stations 1A, 1B, 3A, and JBA. In Stations 1A and 1B, HC increased, in contrast with expected trends. However, the power of the statistical tests used to examine changes in Stations 1A and 1B were both below 80% (37 and 13%, respectively), indicating that these apparent changes may be artifacts of random sampling.

Station 3A showed a fluctuation in HC with an ultimately declining trend, whereas Station JBA had a marked

increase in HC from 2018–2019 but declined from 2019–2022. Neither of the stations exhibited HC trends consistent with what could be expected if an increase in nutrient concentrations was driving these changes. The driver of eutrophication proposed by Licuanan and Bahinting (2021) is an influx of nutrients from seabird guano, with these nutrients reaching the reef slope via the tidal discharge of lagoon waters. However, neither of these explanations can apply to Jessie Beazley, as there is no substantial seabird aggregation at this site, nor a lagoon from which nutrient-rich waters would drain.

Examination of the most abundant hard coral at these stations reveals that the station-wide changes are driven by changes in the most abundant coral – *Isopora brueggemanni* (16.5 to 11.7% absolute cover) at Station 3A, and foliose and encrusting *Montipora* (64.4 to 20.6% absolute cover) at Station Jessie Beazley A. At both stations, the second most abundant corals do not surpass 10% absolute cover at any given year. Both *I. brueggemanni* and foliose and encrusting *Montipora* exhibit competitive life history strategies, which makes them fast-growing but susceptible to mechanical damage (Darling *et al.* 2012).

For Station 3A specifically, “payao” (fish aggregating devices) floats struck the station in 2016, which may have created the *I. brueggemanni* rubble fields at this station (Bahinting *et al.* 2020).

Two major storms hit TRNP during the time series, specifically Tropical Storm Vicky (international name Krovanh) in December 2020 and Typhoon Odette (international name Rai) in December 2021, which may account for the decline in HC the following year. Several other storms may have impacted the reefs of Tubbataha. Before Tropical Storm Vicky, Category Three Typhoon Ursula (international name Phanfone) passed through the Visayas and Southern Tagalog regions in December 2019, and Supertyphoon Rolly (international name Goni) passed through the Southern Tagalog region in October 2020 (<https://www.pagasa.dost.gov.ph/climate/tropical-cyclone-associated-rainfall>). From 2019–2022 specifically, there is an apparent decline in HC across TRNP (see Appendix II), although this decline is non-significant and not consistent across all spatial scales. The difference in the possible impacts of these typhoons may be attributed to the different life-history strategies of the corals across TRNP (Darling *et al.* 2012).

Additionally, the statistical power of the tests used to determine the significance of the changes of HC for both stations was below 80% – 27% for Station 3A, and 67% for Station Jessie Beazley A. Therefore, despite the significant result, there is still a need for more replication or a longer time series.

**Table 3.** Differences in hard coral cover reported in this study and that of Licuanan and Bahinting (2021) and compared with the minimum detectable change (delta) reported by Licuanan *et al.* (2017).

Site	Year	% hard coral cover ( $\pm$ SE)		Delta (%) (Licuanan <i>et al.</i> 2017)
		Licuanan and Bahinting (2021)	This study	
Site 1	2018	30.6 ( $\pm$ 1.1)	30.9 ( $\pm$ 2.7)	5
	2019	32.9 ( $\pm$ 1.5)	33.6 ( $\pm$ 4.0)	
Site 2	2018	19.7 ( $\pm$ 1.5)	20.8 ( $\pm$ 1.6)	9
	2019	19.1 ( $\pm$ 1.7)	19.3 ( $\pm$ 1.7)	
Site 3	2018	30.2 ( $\pm$ 2.7)	30.5 ( $\pm$ 1.5)	7
	2019	35.0 ( $\pm$ 3.7)	36.5 ( $\pm$ 2.5)	
Site 4	2018	23.4 ( $\pm$ 2.6)	24.1 ( $\pm$ 2.0)	6
	2019	22.5 ( $\pm$ 3.5)	23.7 ( $\pm$ 2.5)	

It should also be noted that the two years in common between this study and that of Licuanan and Bahinting (2021), *i.e.* 2018 and 2019, report different values for HC at the site level. As seen in Table 3, this study reports 1% higher HC at five of the overlapping year-site data points. However, the standard error range of the HC values between the two studies overlaps, and 1% is below the minimum detectable difference (delta) reported by Licuanan *et al.* (2017) for these sites (Table 3). This indicates that the difference in HC is likely an artifact of the re-randomization of points in CPCe when the photos were reprocessed for this study.

### Necessity of Power Analysis

Based solely on the results of the repeated measures ANOVA, the changes (or lack thereof) in benthic components may have led to the premature elimination of eutrophication as a possible driver of change. For example, Stations 1A and 1B both displayed a significant increase in HC, in contrast with expected results for a reef experiencing eutrophication. Similarly, the changes in spatial competitors are not totally aligned with a reef experiencing eutrophication. However, the power of the statistical tests for most of the benthic components is below 80%.

### Need for a Longer Time Series

Overall, results show that powerful, significant changes are only occurring in TURF and CYANO, regardless of spatial scale. Upon looking at the linear trends of these two spatial competitors, a “boomerang” type pattern is apparent at most spatial scales, wherein there is relatively high cover in 2018, relatively low cover from 2019–2021, then a relative increase in cover in 2022. If seabird guano is the source of nutrient inputs [as suggested by Licuanan and Bahinting (2021)], it would be expected that TURF and CYANO abundances would follow a similar trend to seabird population abundances. Although the seabird population

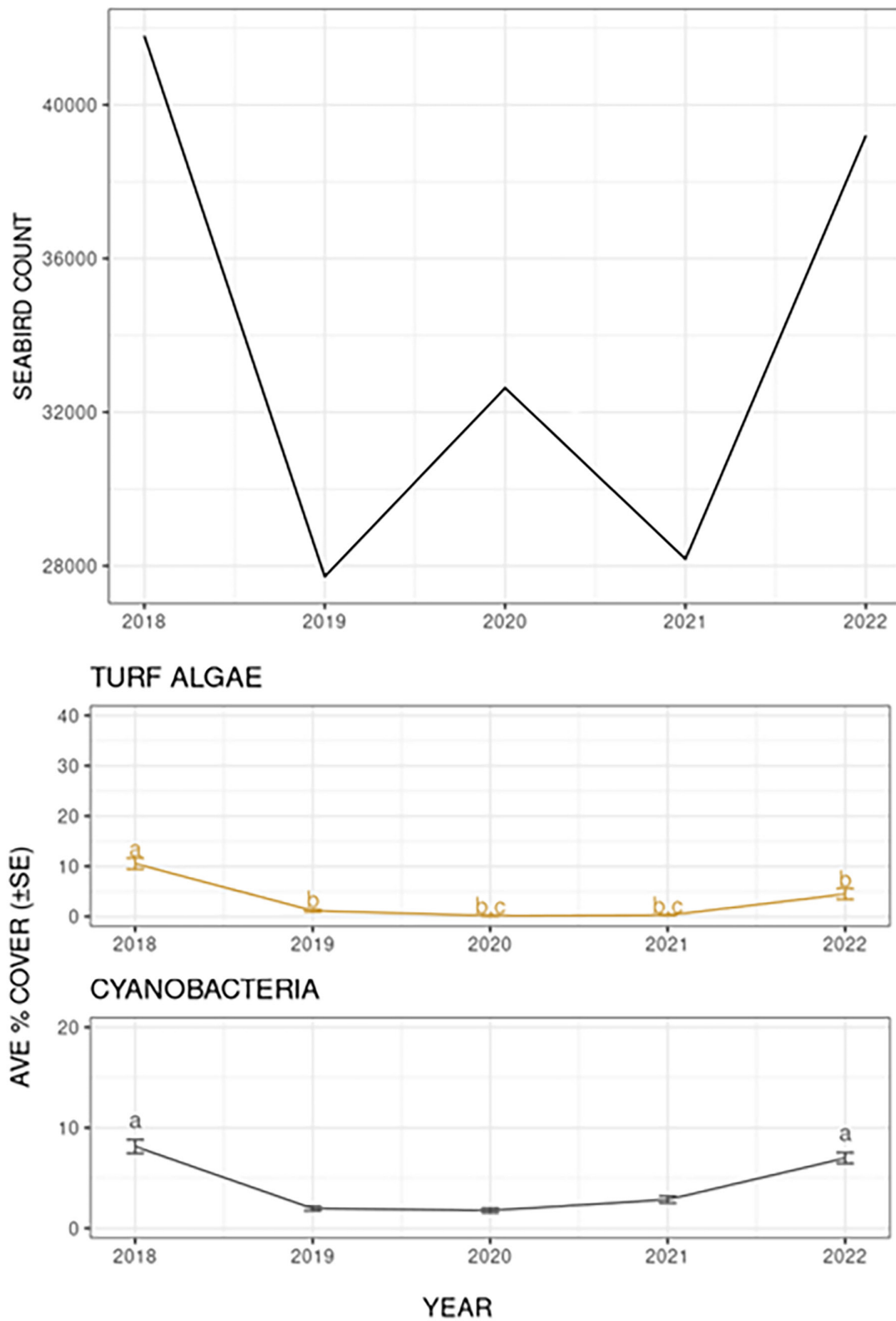
abundances do follow a similar “boomerang” trend (Figure 2), this is not enough to conclude that the changes in benthic spatial competitors are driven by increased nutrient input from seabird guano in years with higher seabird abundance. A longer-term time series for hard coral and spatial competitors, as well as seabird populations, may provide further insight.

Additionally, the significant changes in some benthic components, specifically in HC, TURF, and CYANO, have low statistical power, indicating that a more extensive dataset with a larger sample size is necessary to understand how the benthos of TRNP is changing. In line with this goal, a longer time series is currently being examined by the Br. Alfred Shields FSC Ocean Research Center.

## CONCLUSIONS

Nutrient enrichment cannot be definitively ruled out, nor confirmed, as the main driver for the changes occurring in the benthos of TRNP. Statistically significant and powerful changes in cyanobacteria and turf algae at the site level were in line with changes expected of a reef experiencing nutrient enrichment. Additionally, seabird guano as the mechanism for nutrient input may not be completely discarded, as there appears to be a correlation between seabird abundance and the abundance of turf algae and cyanobacteria. However, changes in other benthic components were nonsignificant, not statistically powerful, or in contrast with expected changes. Significant changes in hard coral were limited to the station spatial scale and may be attributed to factors other than nutrient enrichment, specifically typhoon impacts.

Due to the low statistical power of most of the results in this study, it is recommended that a longer time series be analyzed. Additionally, it may be beneficial to examine in detail the changes in hard coral composition at all spatial scales.



**Figure 2.** Seabird population in Tubbataha Reefs Natural Park based on data presented in the Tubbataha Reefs Ecosystem Research and Monitoring Report 2022, Appendix 9 (Jensen *et al.* 2022), compared to turf algae cover and cyanobacteria cover ( $\pm$  standard error) of the whole of TRNP, including data from Jessie Beazley Reef. Changes in all benthic components may be seen in Appendix II, Figure A2.1.

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## APPENDICES

### Appendix I. Benthic composition data.

**Table A1.1.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – across Tubbataha Reefs Natural Park, including data from Jessie Beazley Reef, during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	30.7 $\pm$ 2.0	5.9 $\pm$ 1.1	3.8 $\pm$ 0.4	0.3 $\pm$ 0.2	10.5 $\pm$ 1.1	8.1 $\pm$ 0.7
2019	33.6 $\pm$ 2.5	6.3 $\pm$ 1.2	4.1 $\pm$ 0.4	0.6 $\pm$ 0.1	1.2 $\pm$ 0.23	2.0 $\pm$ 0.2
2020	33.1 $\pm$ 2.1	5.1 $\pm$ 1.0	4.1 $\pm$ 0.5	0.1 $\pm$ 0.0	0.2 $\pm$ 0.0	1.8 $\pm$ 0.2
2021	32.3 $\pm$ 2.1	2.7 $\pm$ 0.6	3.1 $\pm$ 0.4	0.1 $\pm$ 0.0	0.3 $\pm$ 0.01	2.9 $\pm$ 0.3
2022	29.7 $\pm$ 1.7	3.5 $\pm$ 0.8	4.2 $\pm$ 0.4	0.1 $\pm$ 0.0	4.5 $\pm$ 1.1	7.0 $\pm$ 0.5

**Table A1.2.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – across Tubbataha Reefs Natural Park, excluding data from Jessie Beazley Reef, during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	26.6 $\pm$ 1.5	5.4 $\pm$ 1.2	4.4 $\pm$ 0.4	0.4 $\pm$ 0.3	11.9 $\pm$ 1.3	8.7 $\pm$ 0.8
2019	33.6 $\pm$ 2.8	6.3 $\pm$ 1.3	4.1 $\pm$ 0.4	0.6 $\pm$ 0.1	1.2 $\pm$ 0.3	2.0 $\pm$ 0.3
2020	33.1 $\pm$ 2.4	5.1 $\pm$ 1.1	4.1 $\pm$ 0.5	0.1 $\pm$ 0.0	0.2 $\pm$ 0.0	1.8 $\pm$ 0.3
2021	32.3 $\pm$ 2.4	2.7 $\pm$ 0.7	3.1 $\pm$ 0.4	0.1 $\pm$ 0.0	0.3 $\pm$ 0.1	2.9 $\pm$ 0.4
2022	29.7 $\pm$ 1.9	3.5 $\pm$ 0.9	4.2 $\pm$ 0.4	0.1 $\pm$ 0.0	4.5 $\pm$ 1.2	7.0 $\pm$ 0.6

**Table A1.3.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at the North Atoll during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	25.9 $\pm$ 2.5	9.8 $\pm$ 1.8	4.5 $\pm$ 0.4	0.2 $\pm$ 0.1	8.4 $\pm$ 1.1	7.5 $\pm$ 0.7
2019	33.6 $\pm$ 4.0	6.3 $\pm$ 1.8	4.1 $\pm$ 0.6	0.6 $\pm$ 0.1	1.2 $\pm$ 0.4	2.0 $\pm$ 0.4
2020	33.1 $\pm$ 3.3	5.1 $\pm$ 1.6	4.1 $\pm$ 0.7	0.1 $\pm$ 0.0	0.2 $\pm$ 0.1	1.8 $\pm$ 0.4
2021	32.3 $\pm$ 3.4	2.7 $\pm$ 1.0	3.1 $\pm$ 0.6	0.1 $\pm$ 0.0	0.3 $\pm$ 0.1	2.9 $\pm$ 0.5
2022	29.7 $\pm$ 2.7	3.5 $\pm$ 1.2	4.2 $\pm$ 0.6	0.1 $\pm$ 0.0	4.5 $\pm$ 1.7	7.0 $\pm$ 0.9

**Table A1.4.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at the South Atoll during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	27.3 $\pm$ 1.3	4.4 $\pm$ 0.4	0.6 $\pm$ 0.3	1.0 $\pm$ 0.1	15.4 $\pm$ 1.4	9.9 $\pm$ 1.0
2019	30.1 $\pm$ 2.0	4.5 $\pm$ 0.4	0.7 $\pm$ 0.1	1.0 $\pm$ 0.2	2.0 $\pm$ 0.4	2.2 $\pm$ 0.3
2020	28.4 $\pm$ 1.7	5.5 $\pm$ 0.6	0.0 $\pm$ 0.0	1.0 $\pm$ 0.1	0.3 $\pm$ 0.1	1.9 $\pm$ 0.4
2021	30.4 $\pm$ 2.6	3.5 $\pm$ 0.5	0.0 $\pm$ 0.0	0.6 $\pm$ 0.1	0.2 $\pm$ 0.1	3.5 $\pm$ 0.5
2022	24.4 $\pm$ 1.9	5.0 $\pm$ 0.5	0.2 $\pm$ 0.0	0.9 $\pm$ 0.2	4.2 $\pm$ 1.3	7.9 $\pm$ 0.7

**Table A1.5.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Jessie Beazley Reef during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	47.3 $\pm$ 5.8	7.9 $\pm$ 2.6	1.3 $\pm$ 0.7	0.0 $\pm$ 0.0	5.0 $\pm$ 1.4	6.0 $\pm$ 1.2
2019	55.1 $\pm$ 6.5	10.0 $\pm$ 3.3	1.1 $\pm$ 0.2	0.4 $\pm$ 0.1	0.7 $\pm$ 0.3	1.7 $\pm$ 0.5
2020	47.8 $\pm$ 5.2	7.9 $\pm$ 3.3	1.4 $\pm$ 0.5	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	2.1 $\pm$ 0.5
2021	40.6 $\pm$ 2.7	5.3 $\pm$ 2.1	1.2 $\pm$ 0.4	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	3.0 $\pm$ 0.6
2022	32.8 $\pm$ 3.3	7.1 $\pm$ 2.6	1.9 $\pm$ 0.6	0.1 $\pm$ 0.1	7.3 $\pm$ 2.1	7.4 $\pm$ 0.1

**Table A1.6.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Site 1 during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	30.9 $\pm$ 2.7	11.0 $\pm$ 2.1	3.5 $\pm$ 0.3	0.1 $\pm$ 0.0	5.3 $\pm$ 0.6	6.6 $\pm$ 0.6
2019	33.6 $\pm$ 4.0	6.3 $\pm$ 1.8	4.1 $\pm$ 0.6	0.6 $\pm$ 0.1	1.2 $\pm$ 0.4	2.0 $\pm$ 0.4
2020	33.1 $\pm$ 3.3	5.1 $\pm$ 1.6	4.1 $\pm$ 0.7	0.1 $\pm$ 0.0	0.2 $\pm$ 0.1	1.8 $\pm$ 0.4
2021	32.3 $\pm$ 3.4	2.7 $\pm$ 1.0	3.1 $\pm$ 0.6	0.1 $\pm$ 0.0	0.3 $\pm$ 0.1	2.9 $\pm$ 0.5
2022	29.7 $\pm$ 2.7	3.5 $\pm$ 1.2	4.2 $\pm$ 0.6	0.1 $\pm$ 0.0	4.5 $\pm$ 1.7	7.0 $\pm$ 0.9

**Table A1.7.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Site 2 during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	20.8 $\pm$ 1.6	8.7 $\pm$ 1.6	5.4 $\pm$ 0.5	0.3 $\pm$ 0.1	11.4 $\pm$ 1.1	8.4 $\pm$ 0.7
2019	19.3 $\pm$ 1.7	6.0 $\pm$ 1.5	6.2 $\pm$ 0.4	1.2 $\pm$ 0.1	0.7 $\pm$ 0.1	1.3 $\pm$ 0.2
2020	21.2 $\pm$ 1.8	5.9 $\pm$ 1.7	4.6 $\pm$ 0.4	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	1.3 $\pm$ 0.2
2021	22.5 $\pm$ 1.6	2.4 $\pm$ 0.8	3.5 $\pm$ 0.4	0.0 $\pm$ 0.0	0.1 $\pm$ 0.0	1.7 $\pm$ 0.3
2022	23.0 $\pm$ 2.1	2.2 $\pm$ 0.6	4.9 $\pm$ 0.7	0.1 $\pm$ 0.3	1.2 $\pm$ 0.3	3.8 $\pm$ 0.5

**Table A1.8.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Site 3 during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	30.5 $\pm$ 1.5	0.2 $\pm$ 0.1	4.0 $\pm$ 0.3	0.3 $\pm$ 0.0	16.5 $\pm$ 2.1	10.8 $\pm$ 1.7
2019	36.5 $\pm$ 2.5	0.2 $\pm$ 0.1	3.7 $\pm$ 0.3	0.8 $\pm$ 0.1	1.6 $\pm$ 0.4	3.0 $\pm$ 0.6
2020	32.7 $\pm$ 1.7	0.5 $\pm$ 0.2	4.4 $\pm$ 0.6	0.0 $\pm$ 0.0	0.3 $\pm$ 0.1	2.9 $\pm$ 0.7
2021	33.7 $\pm$ 4.9	0.1 $\pm$ 0.0	1.9 $\pm$ 0.3	0.1 $\pm$ 0.0	0.3 $\pm$ 0.1	4.4 $\pm$ 0.8
2022	22.9 $\pm$ 3.4	0.4 $\pm$ 0.1	3.3 $\pm$ 0.4	0.2 $\pm$ 0.1	0.8 $\pm$ 0.2	11.1 $\pm$ 1.0

**Table A1.9.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Site 4 during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	24.1 $\pm$ 2.0	1.7 $\pm$ 0.2	4.9 $\pm$ 0.8	1.0 $\pm$ 0.1	14.4 $\pm$ 2.0	8.9 $\pm$ 1.1
2019	23.7 $\pm$ 2.5	1.8 $\pm$ 0.3	5.7 $\pm$ 0.7	0.5 $\pm$ 0.1	2.4 $\pm$ 0.8	1.5 $\pm$ 0.2
2020	24.2 $\pm$ 2.6	1.6 $\pm$ 0.1	6.7 $\pm$ 1.1	0.0 $\pm$ 0.0	0.2 $\pm$ 0.1	1.0 $\pm$ 0.1
2021	27.1 $\pm$ 2.1	1.1 $\pm$ 0.2	5.2 $\pm$ 0.7	0.0 $\pm$ 0.0	0.1 $\pm$ 0.0	2.6 $\pm$ 0.7
2022	25.9 $\pm$ 2.0	1.4 $\pm$ 0.5	6.7 $\pm$ 0.6	0.2 $\pm$ 0.1	7.7 $\pm$ 2.5	4.6 $\pm$ 0.2

**Table A1.10.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Station 1A during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	19.7 $\pm$ 1.4	2.6 $\pm$ 0.9	3.4 $\pm$ 0.8	0.2 $\pm$ 0.1	6.2 $\pm$ 1.4	8.3 $\pm$ 1.0
2019	23.6 $\pm$ 1.4	5.5 $\pm$ 1.1	3.4 $\pm$ 0.5	0.3 $\pm$ 0.1	0.5 $\pm$ 0.1	2.9 $\pm$ 0.4
2020	28.8 $\pm$ 2.2	3.9 $\pm$ 0.9	3.0 $\pm$ 0.8	0.2 $\pm$ 0.1	0.0 $\pm$ 0.0	2.0 $\pm$ 0.4
2021	18.5 $\pm$ 1.3	1.9 $\pm$ 0.1	5.8 $\pm$ 0.9	0.0 $\pm$ 0.0	0.4 $\pm$ 0.2	2.4 $\pm$ 0.6
2022	22.8 $\pm$ 1.6	3.9 $\pm$ 0.4	5.7 $\pm$ 0.7	0.1 $\pm$ 0.0	0.8 $\pm$ 0.2	9.5 $\pm$ 1.0

**Table A1.11.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Station 1B during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	42.1 $\pm$ 1.1	19.3 $\pm$ 1.9	3.7 $\pm$ 0.5	0.1 $\pm$ 0.1	4.5 $\pm$ 1.1	4.9 $\pm$ 0.9
2019	43.6 $\pm$ 2.2	20.9 $\pm$ 2.1	4.1 $\pm$ 0.5	0.2 $\pm$ 0.1	0.4 $\pm$ 0.1	2.0 $\pm$ 0.5
2020	50.1 $\pm$ 2.4	25.6 $\pm$ 1.2	3.9 $\pm$ 0.7	0.0 $\pm$ 0.0	0.1 $\pm$ 0.1	1.3 $\pm$ 0.1
2021	35.7 $\pm$ 7.5	10.2 $\pm$ 2.7	3.4 $\pm$ 0.8	0.0 $\pm$ 0.0	0.5 $\pm$ 0.2	2.2 $\pm$ 0.5
2022	44.4 $\pm$ 0.7	14.9 $\pm$ 1.9	4.9 $\pm$ 0.8	0.1 $\pm$ 0.1	1.0 $\pm$ 0.3	7.9 $\pm$ 1.0

**Table A1.12.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Station 2A during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	$\pm$	$\pm$	$\pm$	$\pm$	$\pm$	$\pm$
2019	$\pm$	$\pm$	$\pm$	$\pm$	$\pm$	$\pm$
2020	$\pm$	$\pm$	$\pm$	$\pm$	$\pm$	$\pm$
2021	$\pm$	$\pm$	$\pm$	$\pm$	$\pm$	$\pm$
2022	$\pm$	$\pm$	$\pm$	$\pm$	$\pm$	$\pm$

**Table A1.13.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Station 2B during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	26.6 $\pm$ 1.4	2.7 $\pm$ 0.4	3.1 $\pm$ 0.6	0.4 $\pm$ 0.3	12.7 $\pm$ 2.5	7.7 $\pm$ 0.8
2019	25.5 $\pm$ 1.9	3.0 $\pm$ 0.6	3.4 $\pm$ 0.6	1.5 $\pm$ 0.3	0.5 $\pm$ 0.2	0.8 $\pm$ 0.2
2020	25.0 $\pm$ 4.2	3.0 $\pm$ 0.8	2.4 $\pm$ 1.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	1.0 $\pm$ 0.2
2021	28.3 $\pm$ 1.6	0.6 $\pm$ 0.3	2.2 $\pm$ 0.7	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	1.0 $\pm$ 0.3
2022	31.0 $\pm$ 2.4	1.2 $\pm$ 0.4	2.9 $\pm$ 1.5	0.1 $\pm$ 0.1	0.7 $\pm$ 0.2	4.9 $\pm$ 1.4

**Table A1.14.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Station 3A during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	34.4 $\pm$ 1.2	0.3 $\pm$ 1.9	4.1 $\pm$ 0.6	0.2 $\pm$ 0.1	10.9 $\pm$ 4.9	7.7 $\pm$ 2.9
2019	43.3 $\pm$ 5.0	0.3 $\pm$ 1.2	2.8 $\pm$ 0.1	1.2 $\pm$ 0.2	2.0 $\pm$ 0.9	1.4 $\pm$ 0.5
2020	32.4 $\pm$ 3.0	0.8 $\pm$ 1.9	4.2 $\pm$ 1.5	0.0 $\pm$ 0.0	0.5 $\pm$ 0.2	3.3 $\pm$ 1.9
2021	49.4 $\pm$ 3.2	0.2 $\pm$ 0.1	2.1 $\pm$ 0.6	0.0 $\pm$ 0.0	0.7 $\pm$ 0.3	2.9 $\pm$ 1.2
2022	30.6 $\pm$ 5.0	0.3 $\pm$ 1.6	3.5 $\pm$ 0.5	0.0 $\pm$ 0.0	1.1 $\pm$ 0.5	12.3 $\pm$ 2.4

**Table A1.15.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Station 3B during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	26.6 $\pm$ 3.5	1.7 $\pm$ 0.2	3.8 $\pm$ 0.5	0.3 $\pm$ 0.1	9.0 $\pm$ 4.0	13.9 $\pm$ 3.3
2019	29.8 $\pm$ 2.6	2.1 $\pm$ 0.1	4.6 $\pm$ 0.8	0.4 $\pm$ 0.2	1.4 $\pm$ 0.6	4.6 $\pm$ 1.4
2020	32.9 $\pm$ 4.1	2.0 $\pm$ 0.2	4.5 $\pm$ 1.1	0.1 $\pm$ 0.1	0.4 $\pm$ 0.2	2.4 $\pm$ 0.9
2021	18.0 $\pm$ 9.0	0.8 $\pm$ 0.0	1.7 $\pm$ 0.5	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	5.8 $\pm$ 2.0
2022	15.2 $\pm$ 6.9	1.4 $\pm$ 0.4	3.0 $\pm$ 1.0	0.3 $\pm$ 0.1	0.6 $\pm$ 0.3	10.0 $\pm$ 1.5

**Table A1.16.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Station 4A during the study period.

	HC	SFT	SP	MA	TURF	CYANO
2018	18.0 $\pm$ 3.1	1.1 $\pm$ 1.1	2.4 $\pm$ 0.5	1.9 $\pm$ 1.9	7.4 $\pm$ 3.3	10.8 $\pm$ 2.8
2019	16.2 $\pm$ 3.5	1.4 $\pm$ 1.2	3.0 $\pm$ 0.6	0.4 $\pm$ 0.1	4.5 $\pm$ 2.0	1.4 $\pm$ 0.3
2020	14.8 $\pm$ 2.4	1.1 $\pm$ 1.1	2.4 $\pm$ 0.3	0.0 $\pm$ 0.0	0.5 $\pm$ 2.3	0.7 $\pm$ 0.2
2021	19.5 $\pm$ 2.5	1.1 $\pm$ 0.6	2.4 $\pm$ 0.1	0.0 $\pm$ 0.0	0.4 $\pm$ 0.2	3.5 $\pm$ 1.7
2022	18.5 $\pm$ 2.1	2.1 $\pm$ 0.7	4.6 $\pm$ 0.7	0.2 $\pm$ 0.1	14.3 $\pm$ 6.4	4.7 $\pm$ 0.7

**Table A1.17.** Percent cover ( $\pm$  standard error) of benthic – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Station 4B during the study period.

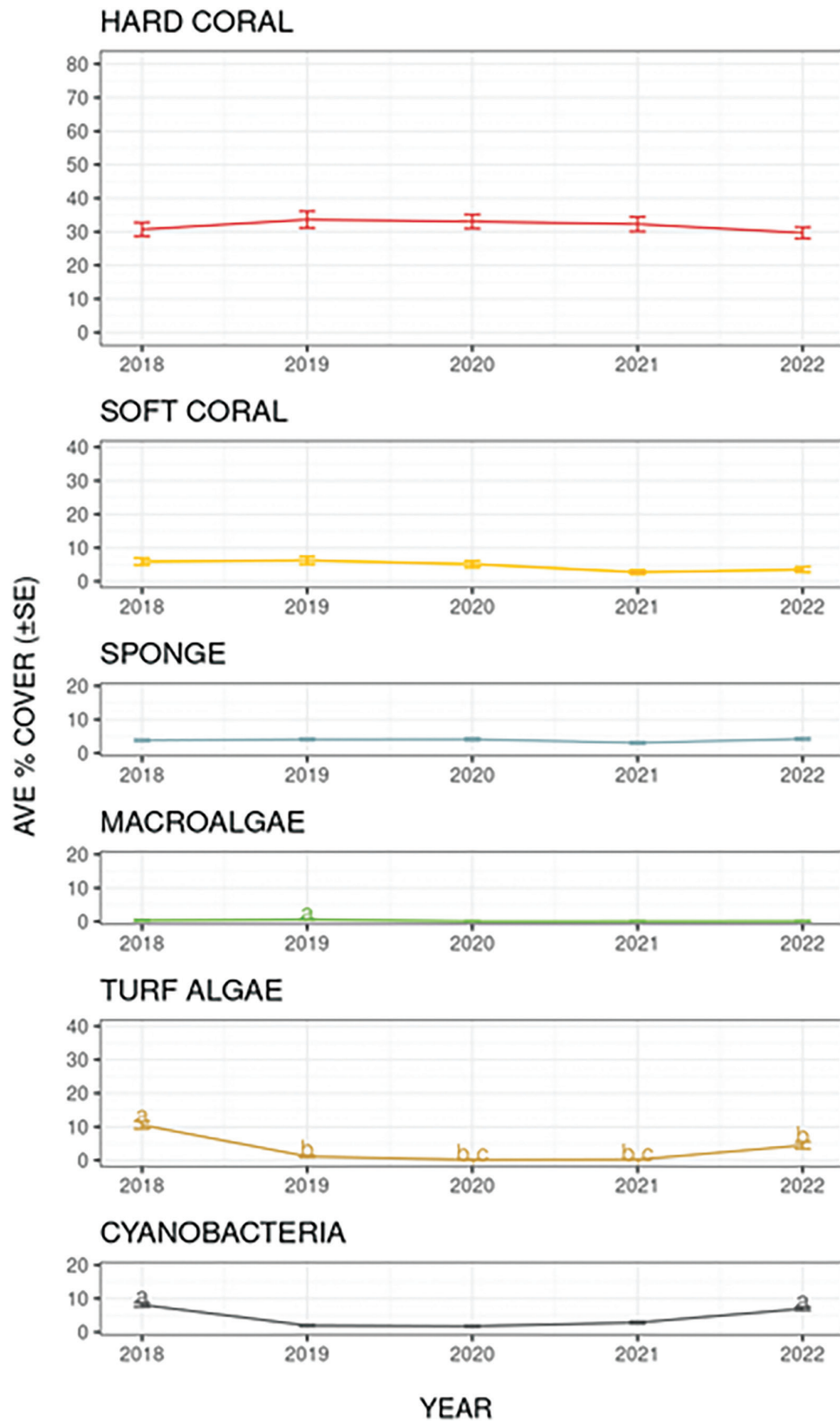
	HC	SFT	SP	MA	TURF	CYANO
2018	30.1 $\pm$ 3.1	3.3 $\pm$ 2.4	7.4 $\pm$ 1.4	0.1 $\pm$ 0.1	5.7 $\pm$ 2.4	7.1 $\pm$ 0.1
2019	31.1 $\pm$ 4.2	3.7 $\pm$ 2.5	8.3 $\pm$ 1.0	0.7 $\pm$ 0.2	0.8 $\pm$ 0.4	1.5 $\pm$ 0.1
2020	33.6 $\pm$ 3.1	5.0 $\pm$ 2.0	11.1 $\pm$ 0.8	0.0 $\pm$ 0.0	0.1 $\pm$ 0.0	1.3 $\pm$ 0.4
2021	34.6 $\pm$ 2.2	3.6 $\pm$ 1.6	8.0 $\pm$ 1.1	0.0 $\pm$ 0.0	0.1 $\pm$ 0.1	1.8 $\pm$ 0.9
2022	33.3 $\pm$ 1.9	3.9 $\pm$ 2.1	8.8 $\pm$ 1.0	0.2 $\pm$ 0.1	2.9 $\pm$ 1.3	4.5 $\pm$ 0.3

**Table A1.18.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Jessie Beazley A during the study period.

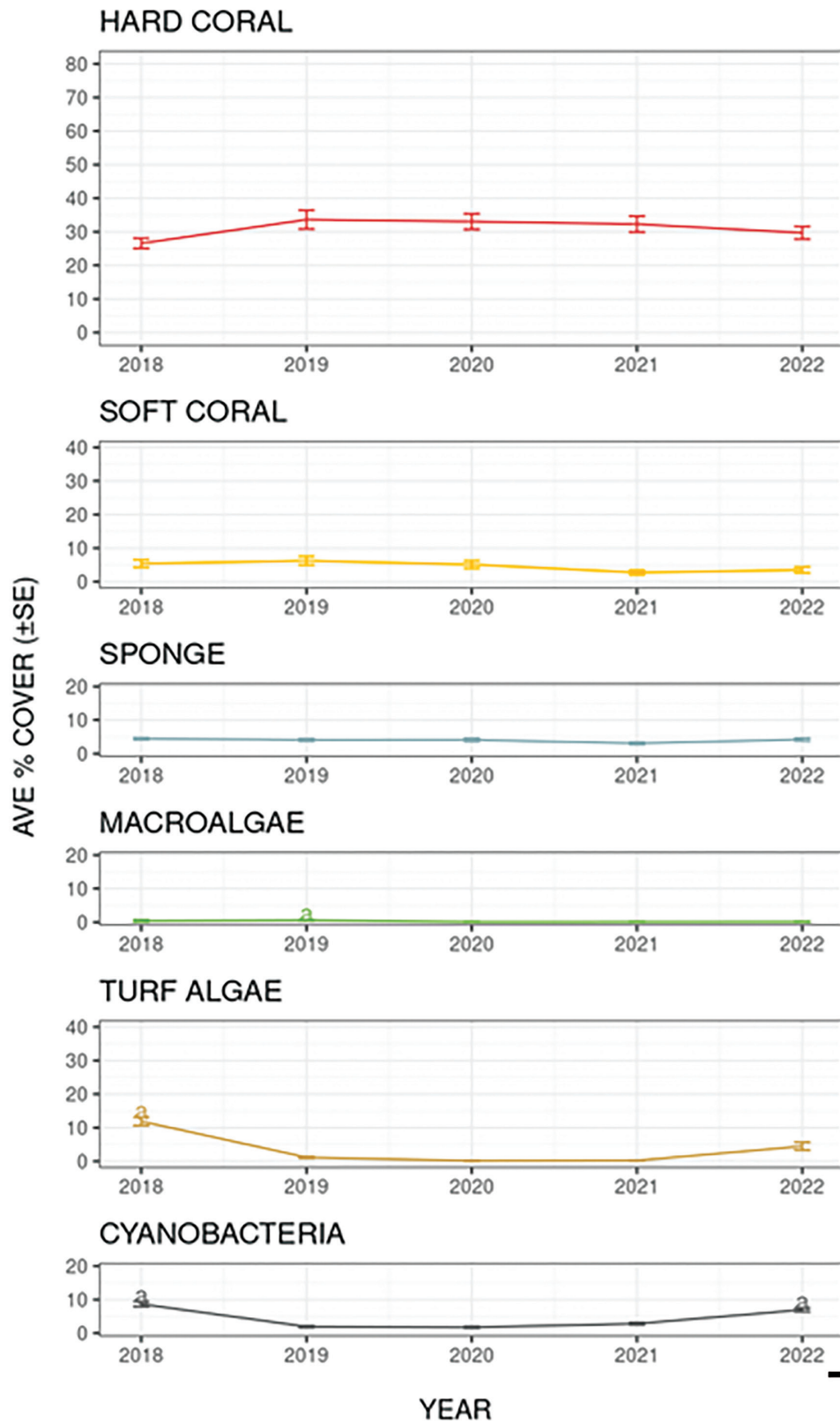
	HC	SFT	SP	MA	TURF	CYANO
2018	62.1 $\pm$ 4.3	2.3 $\pm$ 0.1	0.2 $\pm$ 0.1	0.0 $\pm$ 0.0	3.7 $\pm$ 1.5	3.9 $\pm$ 1.2
2019	72.0 $\pm$ 4.8	4.6 $\pm$ 0.3	0.8 $\pm$ 0.2	0.0 $\pm$ 0.0	0.2 $\pm$ 0.1	0.6 $\pm$ 0.2
2020	57.2 $\pm$ 8.3	1.9 $\pm$ 0.2	0.4 $\pm$ 0.2	0.3 $\pm$ 0.1	0.2 $\pm$ 0.1	0.8 $\pm$ 0.1
2021	42.9 $\pm$ 4.2	0.7 $\pm$ 0.1	0.2 $\pm$ 0.1	0.3 $\pm$ 0.1	0.4 $\pm$ 0.2	2.7 $\pm$ 1.0
2022	24.9 $\pm$ 3.5	1.1 $\pm$ 0.1	0.2 $\pm$ 0.1	0.0 $\pm$ 0.0	6.8 $\pm$ 3.0	8.4 $\pm$ 1.6

**Table A1.19.** Percent cover ( $\pm$  standard error) of benthic components – namely [HC] hard coral, [SFT] soft coral, [SP] sponges, [MA] macroalgae, [TURF] turf algae, and [CYANO] cyanobacteria – at Jessie Beazley B during the study period.

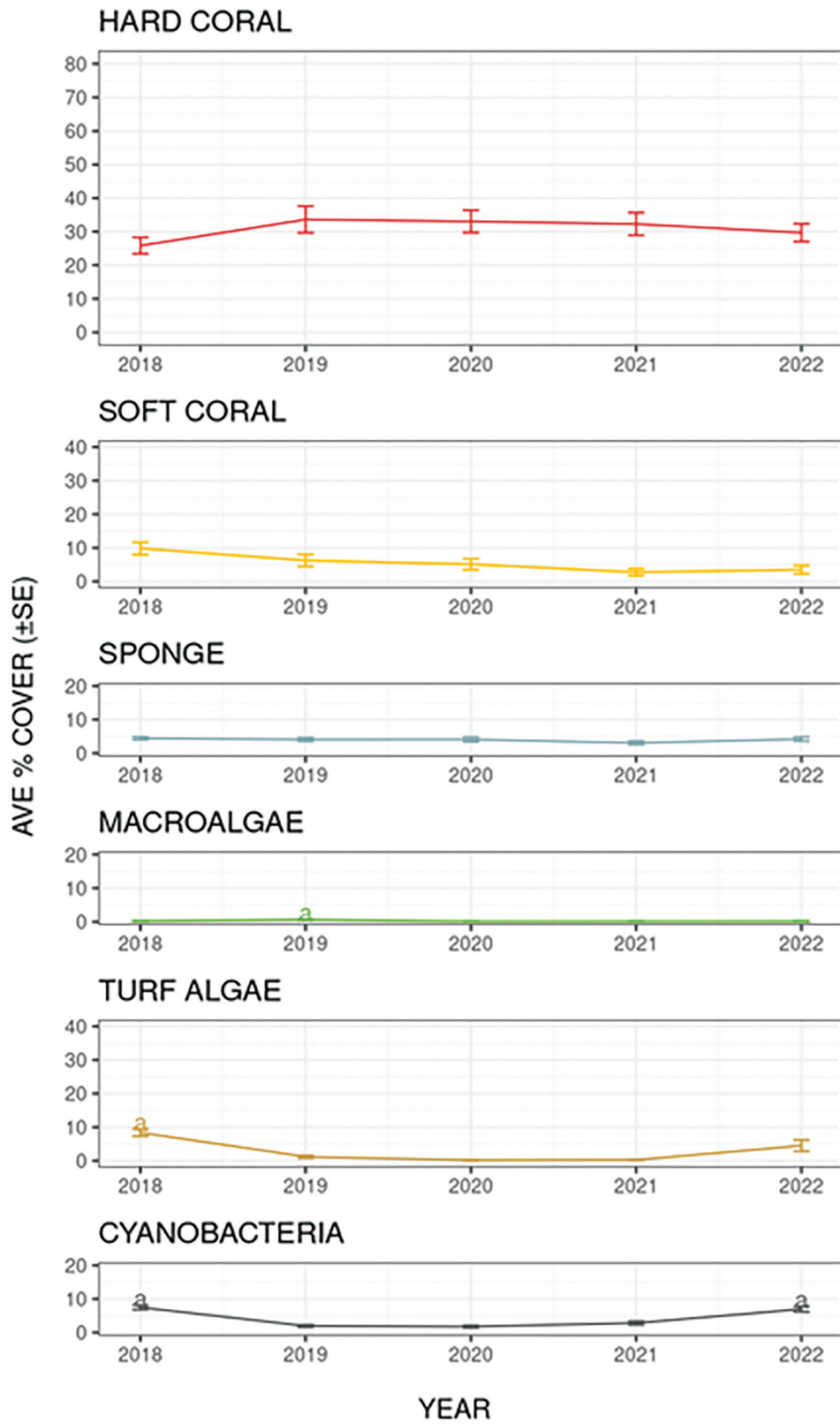
	HC	SFT	SP	MA	TURF	CYANO
2018	31.5 $\pm$ 2.6	13.5 $\pm$ 1.1	2.4 $\pm$ 1.1	0.0 $\pm$ 0.0	5.4 $\pm$ 2.4	8.1 $\pm$ 1.6
2019	38.2 $\pm$ 5.1	15.5 $\pm$ 0.7	1.5 $\pm$ 0.3	0.7 $\pm$ 0.2	1.1 $\pm$ 0.5	2.7 $\pm$ 0.8
2020	38.4 $\pm$ 3.1	14.0 $\pm$ 1.1	2.4 $\pm$ 0.7	0.2 $\pm$ 0.2	0.2 $\pm$ 0.1	3.4 $\pm$ 0.6
2021	38.3 $\pm$ 3.4	9.8 $\pm$ 1.0	2.1 $\pm$ 0.6	0.2 $\pm$ 0.0	0.3 $\pm$ 0.1	3.2 $\pm$ 0.6
2022	40.7 $\pm$ 2.5	13.1 $\pm$ 1.6	3.5 $\pm$ 0.6	0.3 $\pm$ 0.2	7.4 $\pm$ 3.3	6.4 $\pm$ 0.9



**Figure A2.1.** Comparison of cover of benthic components ( $\pm$  standard error) across the whole of Tubbataha Reefs Natural Park, including data from Jessie Beazley Reef. Years marked with different letters are significantly different.



**Figure A2.2.** Comparison of cover of benthic components ( $\pm$  standard error) across the whole of Tubbataha Reefs Natural Park, excluding data from Jessie Beazley Reef. Years marked with different letters are significantly different.



**Figure A2.3.** Comparison of cover of benthic components ( $\pm$  standard error) across the North Atoll. Years marked with different letters are significantly different.

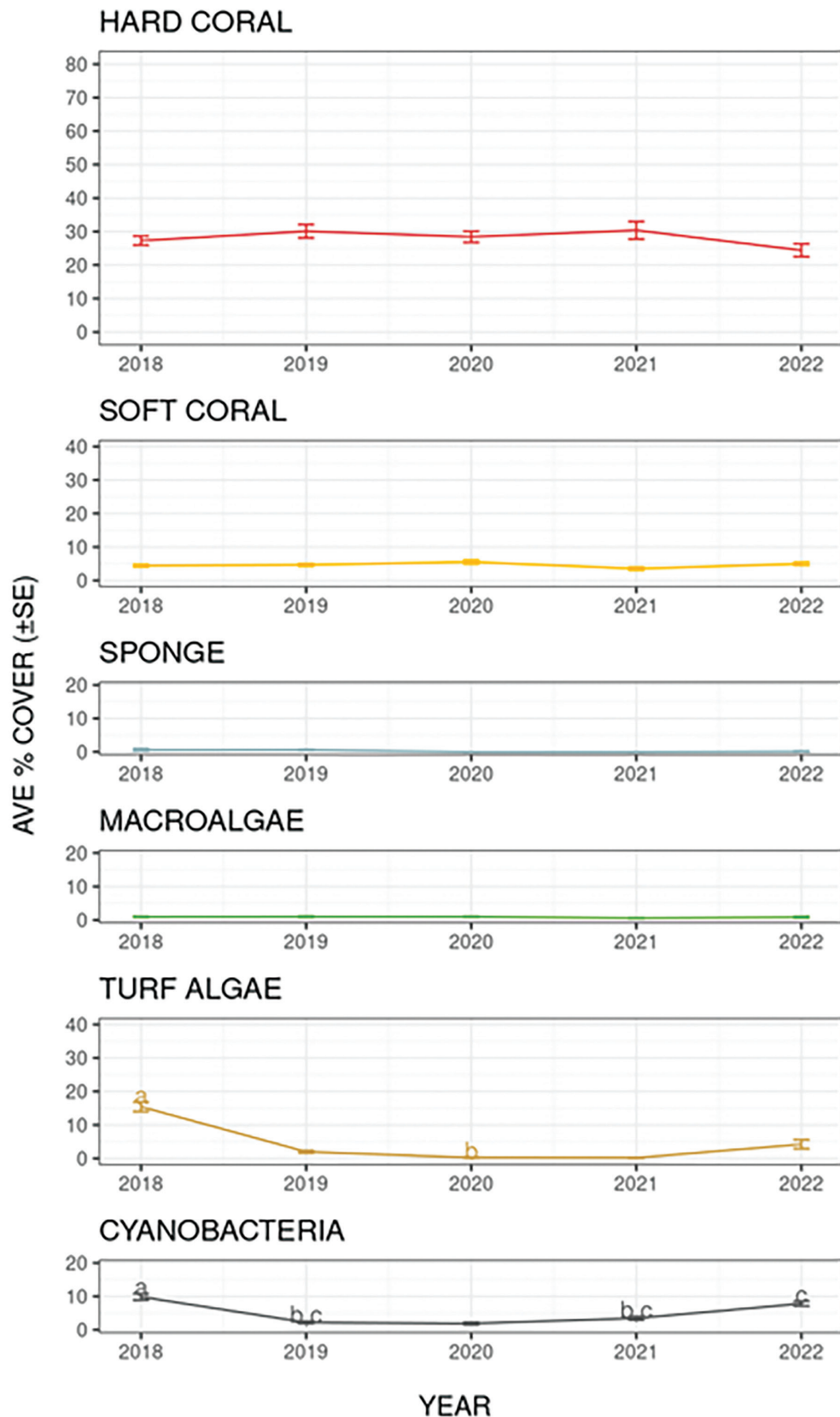
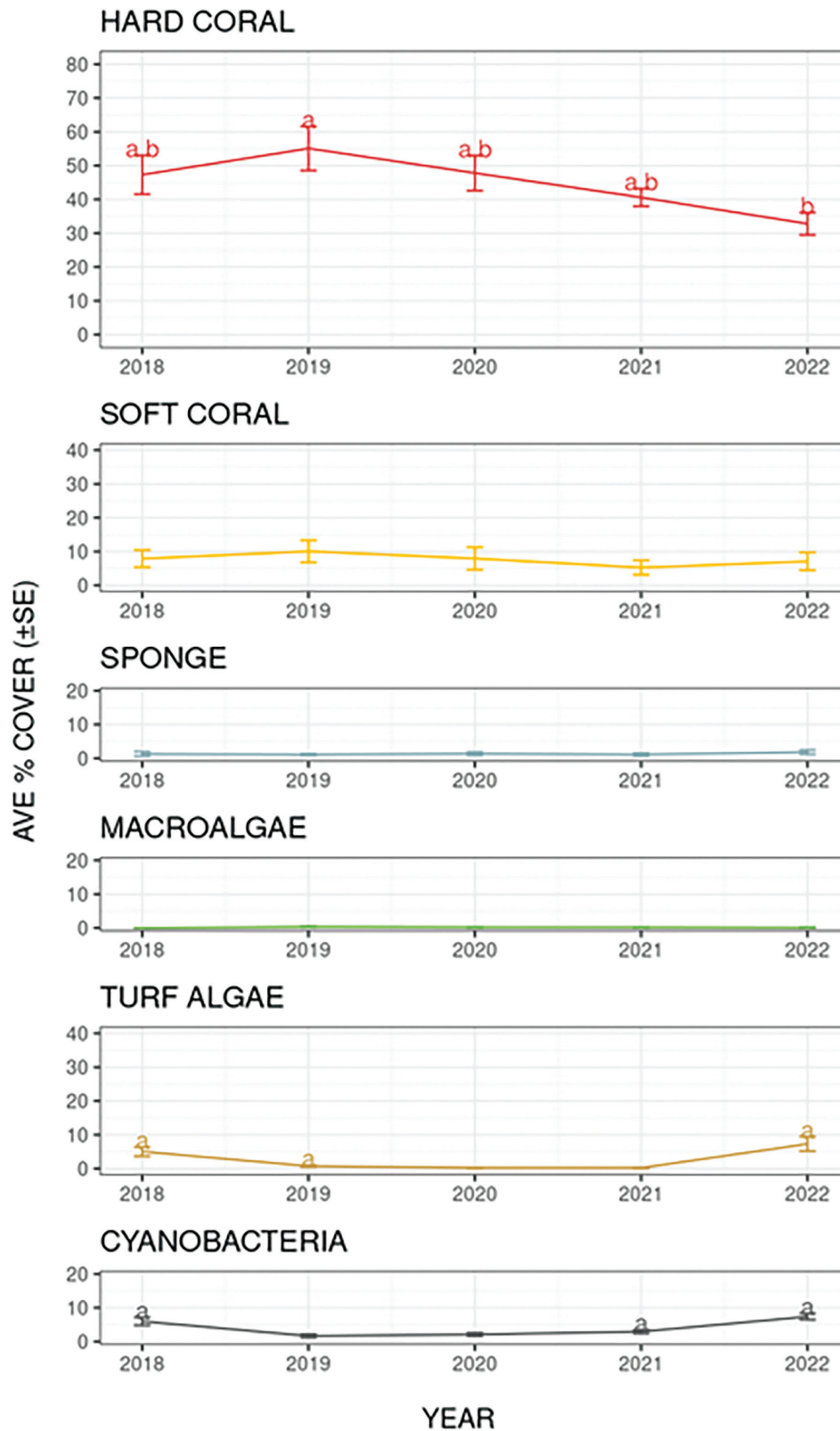
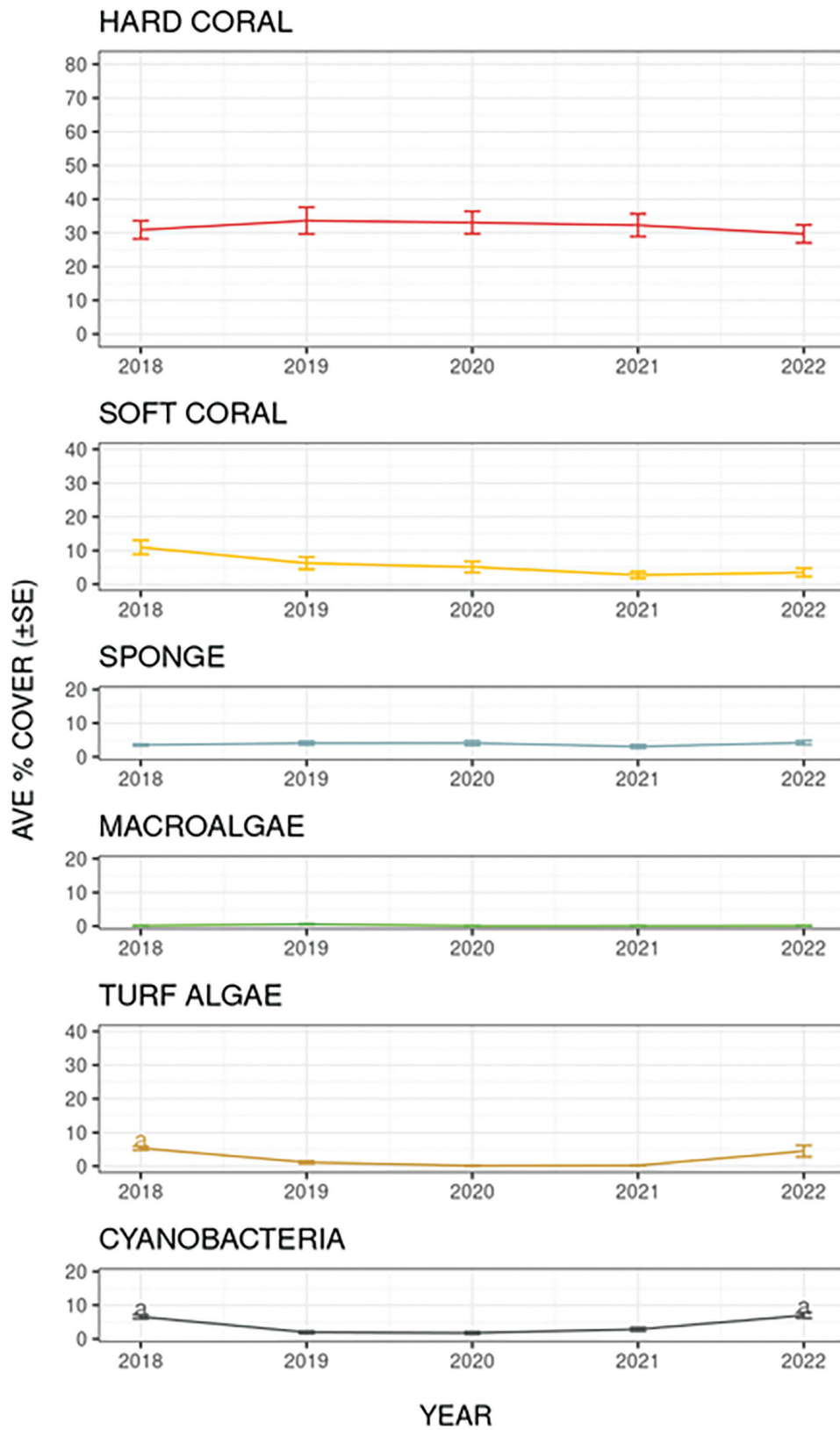


Figure A2.4. Comparison of cover of benthic components ( $\pm$  standard error) across the South Atoll. Years marked with different letters are significantly different.

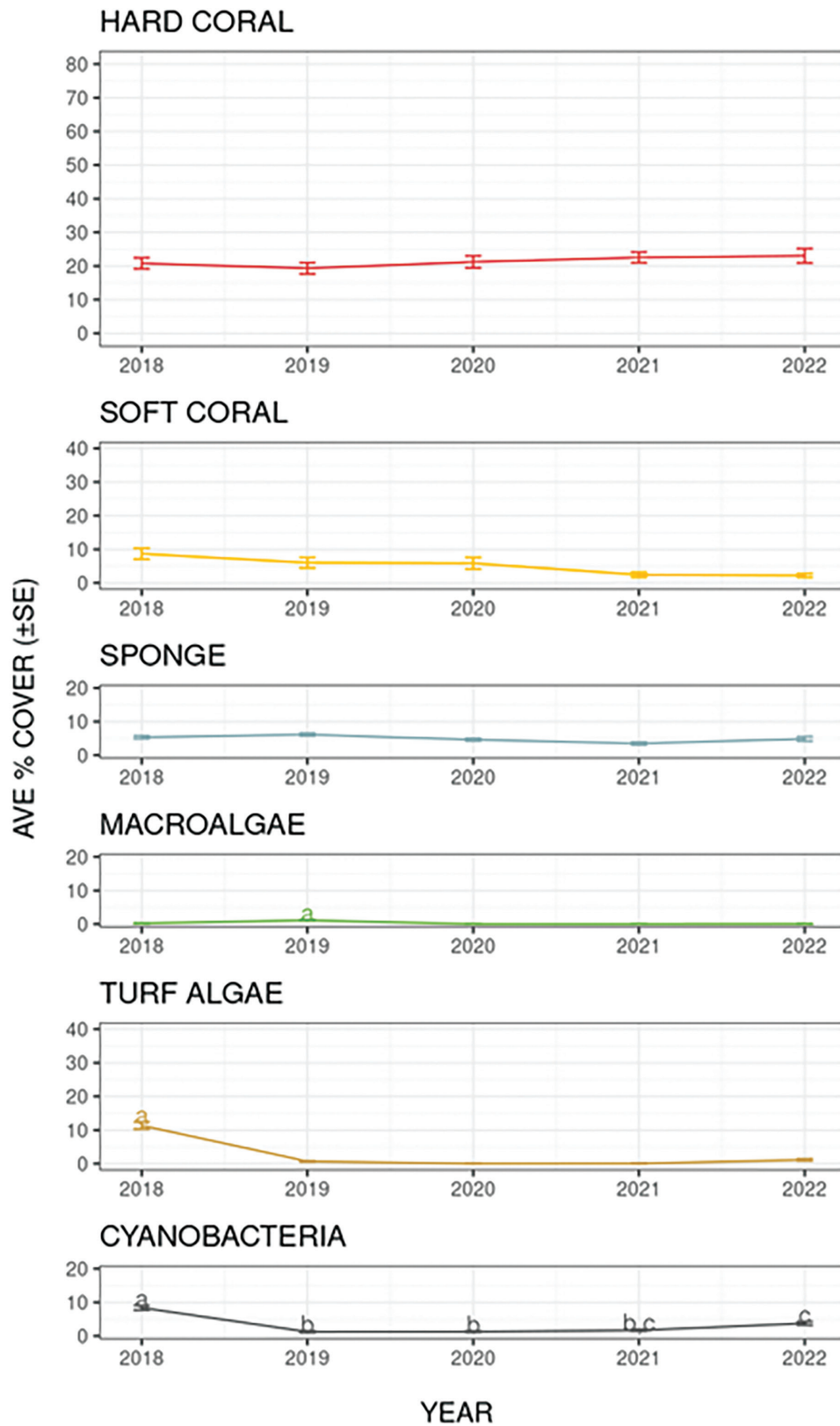




**Figure A2.5.** Comparison of cover of benthic components ( $\pm$  standard error) across Jessie Beazley Reef. Years marked with different letters are significantly different.



**Figure A2.6.** Comparison of cover of benthic components ( $\pm$  standard error) across Site 1, North Atoll. Years marked with different letters are significantly different.



**Figure A2.7.** Comparison of cover of benthic components ( $\pm$  standard error) across Site 2, North Atoll. Years marked with different letters are significantly different.

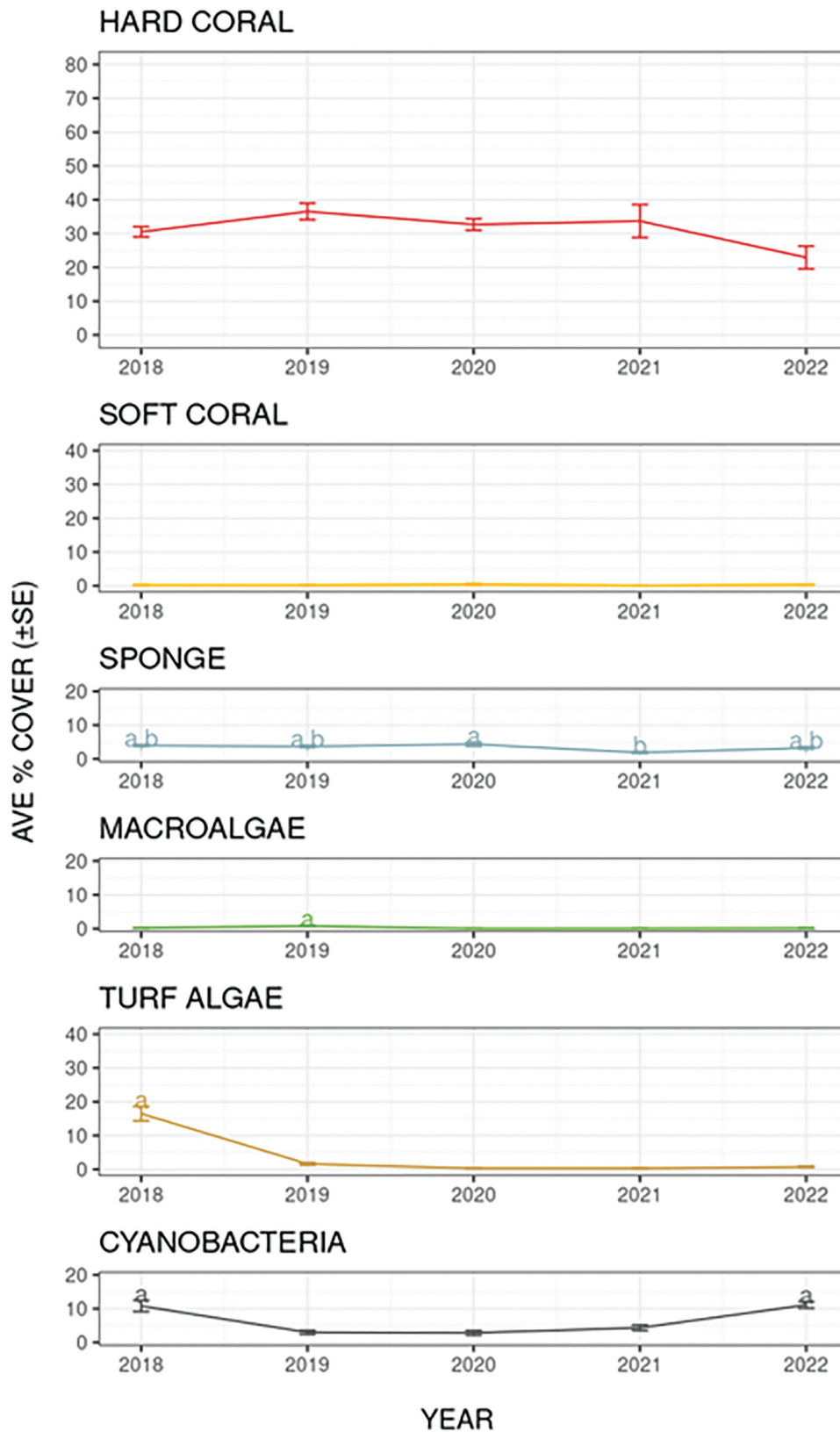


Figure A2.8. Comparison of cover of benthic components ( $\pm$  standard error) across Site 3, South Atoll. Years marked with different letters are significantly different.