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Precision and cost-effectiveness of bioindicators to estimate nutrient regimes on coral reefs

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Highlights

- Multiple bioindicators and stable isotopes provide comprehensive, spatio-temporal assessments of nutrient regimes on coral reefs.
- N- and C-based nutrient signatures were assessed across eight bioindicators both within and among reefs as well as between degraded reef states, the most precise being brown macroalgae, green macroalgae, and zoanthids.
- There was low congruency between signatures of these three indicators due to differences in internal nutrient processing.
- Turf algae and sediment were more widespread, but their signatures were variable and did not reflect their local environment.

Abstract

Bioindicators are useful for determining nutrient regimes in marine environments, but their ability to evaluate corals reefs in different ecological states is poorly understood. The precision, availability and congruency of eight potential bioindicators (brown macroalgae, green macroalgae, turf algae, cyanobacteria, soft corals, zoanthids, sponges, and sediment) and their stable isotopic and elemental signatures ($\delta^{15}N$, $\delta^{13}C$, %N, %C, and C:N Ratio) were assessed across 21 reefs in the Inner Seychelles. The coefficient of variation (CoV) for $\delta^{15}N$ showed that green and brown macroalgae were highly precise (2.47 ± 0.95, n=11; 4.68 ± 1.33, n=16, respectively), though were less common on recently-bleached reefs relative to macroalgal-dominated ones. Zoanthids were also highly precise for $\delta^{15}N$ (2.98 ± 1.20), but were more readily available regardless of reef state (n=18). Congruency was low among these indicators, suggesting that different physiological mechanisms for nutrient processing have a stronger influence on a bioindicator's effectiveness than reef state.

Keywords: *Pollution; stable isotopes; macroalgae; environmental monitoring; regime shifts*

1. Introduction

Coral reefs are facing global declines in live coral cover due to climate change (Hughes et al., 2018), and local-scale degradation from overfishing and pollution (Burkepile & Hay, 2006; Littler et al., 2006; Zaneveld et al., 2016; MacNeil et al., 2019). Increased anthropogenic nutrient loads and reduced herbivory can cause the proliferation of opportunistic species such as fleshy macroalgae, which may lead to a regime shift from a coral-dominated to an algal-dominated reef (Littler et al., 2006; Hughes et al., 2007; Fulton et al., 2019). Monitoring the state of coral reefs relative to anthropogenic stressors provides insights into causes of decline in reef condition, potentially instigating management actions. Two particularly widespread

local stressors are fishing and eutrophication (Fabricius et al., 2005; Burkepile & Hay, 2006; Littler et al., 2006; Zaneveld et al., 2016). While there has been significant progress in understanding the effects of fishing (e.g. Cinner et al. 2018), it has been more difficult to detect and quantify nutrient loads that cause eutrophication in the marine environment, due to high spatio-temporal variability in the water column (Fabricius et al., 2005; Wyatt et al., 2013; D'Angelo & Wiedenmann, 2014; Briand et al., 2015; Lowe & Falter, 2015; Clausing & Fong, 2016; MacNeil et al., 2019. It is therefore critical to identify more cost-effective methods of capturing nutrient enrichment to improve assessments of coral reef health over different spatial scales as part of routine environmental monitoring strategies (Fabricius et al., 2012; Bal et al., 2020).

Bioindicators are used widely to capture nutrient regimes in tropical marine systems, as they provide an ecologically relevant response to bioavailable nutrients in the surrounding water column (Fichez et al., 2005; Cooper et al., 2009; Fabricius et al., 2012). As such, bioindicators are cost-effective alternatives to direct measures of seawater nutrients, which can be highly variable and require frequent sampling that do not always capture fine-scale temporal variation or wider ecological impacts(Fabricius et al., 2012). Suitable bioindicators are defined in Cooper et al. (2009) as those with biological responses that are a) specific towards a driver of change or stressor, b) reflective of the magnitude of any changes, c) consistent across different scales, d) cost-effective, and e) ecologically relevant. Non-biological indicators, conversely, are those which can still reflect drivers of change, but not through biological responses (i.e. nutrients stored in reef sediments) (Linton & Warner, 2003; Fichez et al., 2005).

Previous studies have measured the presence: absence ratio of selected bioindicators to investigate water quality (Fichez et al., 2005; Cooper et al., 2009), however, using this type of methodology alone does not take into account other biophysical factors that may influence their abundance (Linton & Warner, 2003). Therefore, measuring stable isotope signatures ($\delta^{15}N$ and $\delta^{13}C$) and concentration levels (%N, %C and C:N ratio) in the tissues of a selected bioindicator allows scientists and environmental managers to assess both the source(s) and concentration of nutrient regimes, respectively, better determine the spatio-temporal variability of nutrient regimes and detect and map the spatial ecological impacts (Costanzo et al., 2001)Fleshy macroalgae are widely used for such a purpose, because they respond rapidly to high nutrient concentrations by assimilating bioavailable nutrients from their local environment into their tissues over their active growth periods, thereby capturing temporal variation in nutrients (Costanzo et al., 2001). They are also easy to collect and survey in the field, especially in nutrient-rich coastal areas (Fichez et al., 2005; García-Seoane et al., 2018a&b; Zubia et al., 2018).

One of the main limitations of using only a single species of macroalgae, even with stable isotopic analyses, are the spatio-temporal gaps in their distribution, which are driven by a number of abiotic factors such as wave exposure, irradiance, temperature, rainfall and seasonality (Linton & Warner, 2003; Williams et al., 2013; Clausing & Fong, 2016; Duran et al., 2016; Fulton et al. 2019), and biotic factors such as herbivory and competition (Burkepile & Hay, 2006; Duran et al., 2016). These limiting factors may also affect the ability of macroalgae to proliferate on some reefs that have experienced significant disturbances (Littler et al., 1991; Graham et al., 2015). These distributional gaps can also lead to inconclusive or even misleading findings in any studies or monitoring programs, particularly if they are quantifying the abundance of a particular species across a range of target sites

(Linton & Warner, 2003). As such, the utility of alternative bioindicators to capture nutrient regimes is of importance to monitoring programmes.

A range of other marine organisms have been used as bioindicators in water quality or nutrient enrichment studies, such as scleractinian corals (Hoegh-Guldberg et al., 2004), soft corals (Fleury et al., 2000; Risk, 2014), and sponges (Ward-Paige et al., 2005). In addition, multiple candidate bioindicators have been used to assess water quality depending upon their response time to a change in their local nutrient environment (Cooper et al., 2009), or on the extent of their abundance and distribution, which also allows the spatial extent of nutrient runoff to be assessed (Fabricius et al., 2012). Some bioindicators may take longer to find or process than others, particularly in areas where they are relatively uncommon or rare. Selection of bioindicators should therefore also consider the cost-effectiveness of the collection and subsequent processing of samples (Risk et al., 2001; Drummond & Connell, 2008; Bal et al., 2020). This will be especially important for researchers and managers tasked with monitoring water quality over large spatial and temporal scales, such as entire reef systems (De'ath & Fabricius, 2010; Graham et al., 2015).

Few studies have tested whether patterns in nutrient signatures of different bioindicators are congruent (i.e. they are able to show the same relative trends in isotopic values between indicators) across different spatio-temporal scales or gradients (Tucker et al., 1999; Gartner et al., 2002; Pitt et al., 2009), and this multi-taxa approach is even less common in coral reef studies,(Connolly et al., 2013; Kürten et al., 2014; Graham et al., 2018). Untested variability in isotopic composition within and between different reefs , bioindicators, and even studies could therefore reduce the reproducibility, or else the comparability of large-scale and long-term monitoring assessments (Pitt et al., 2009; Connolly et al., 2013).

If multiple bioindicators can demonstrate similarly precise and congruent spatial patterns of nutrients over a large-scale gradient, then other taxa, particularly as those from multiple trophic positions, may become useful proxies in areas where macroalgae are scarce, such as on reefs that are dominated by reef-building corals or turf algae (den Haan et al., 2014; Fulton et al, 2019). However, some of these bioindicators may not be directly comparable with others due to the way they take up and process nutrients internally or how other biophysical drivers could potentially influence their signatures (Raimonet et al., 2013; Viana & Bode, 2013; Clausing & Fong, 2016). In addition, species at different trophic levels have different $\delta^{15}N$ signatures due to isotopic fractionation (Boecklen et al., 2011). This may therefore impact the overall effectiveness of a suite of bioindicators, so additional measures are needed to directly compare their compatibility before they can be used for monitoring programs.

In this study, we investigated the precision and cost-effectiveness of a suite of eight potential bioindicators collected from coral reefs across the Inner Seychelles Islands for measuring nutrient regimes. The specific objectives of the study were to (1) quantify the precision of different bioindicators for measuring stable isotopic and elemental signatures of nitrogen and carbon, (2) determine how much variation exists within bioindicators across different coral reef sites which vary in ecological condition, (3) consider whether there is congruency between selected precise bioindicators based on their nitrogen (N)- and carbon (C)-based measurements, and (4) assess cost-effectiveness of using different bioindicators and the tasks involved.

2. Methods

2.1 Study Sites and Sample Collections

The inner Seychelles islands (43°S, 55°30'E) are comprised of high granitic islands with well-developed carbonate fringing reefs (Littler et al., 1991; Dajka et al., 2019). Bioindicator samples were collected from 21 coral reef sites around the populated islands of Mahé and Praslin, between 11th – 22nd April 2017. These sites have been used as part of a 23-year long-term coral reef monitoring survey, of the reefs of the Inner Seychelles Islands (Suppl. Table 1; Graham et al., 2015; Wilson et al., 2019). The 21 reefs in this study were formed on habitats of either granite, contiguous carbonate or patches that are surrounded by sand or rubble. Twelve of these reefs were defined as "recovering" live coral from a mass bleaching event in 1998, and nine as "regime-shifted" where macroalgae had proliferated (Wilson et al., 2019). However, another mass bleaching event in 2016 caused mass coral mortality on the recovering reefs (Wilson et al., 2019), and so here we define them as "coral-mortality" reefs. Using nitrogen content of brown macroalgae collected from these sites, Graham et al. (2015) also found that nutrient regimes are one of the key determinants of whether a reef can recover or experience a regime shift after a major disturbance like bleaching.

To assess the availability of potential bioindicators, eight replicate 7-m radius point counts were surveyed along the reef slope at each site, and within each point count area, the percent cover of benthic groups such as hard coral, soft coral, macroalgae, sand, rubble, and rock was quantified using eight replicate 10m line-intercept transects (Wilson et al., 2019). Along each transect, the distance of tape occupied by different benthic organisms and substrates was recorded, including live hard coral, soft coral, macroalgae, sponge, cyanobacteria, zoanthids, sand, rubble and rock. For the purpose of this study, the percent cover of dead hard coral and rubble was pooled for an estimate of turf algae per site. Up to ten replicate samples of eight

different bioindicators (i.e. each replicate was a separate individual or sample) were collected haphazardly using SCUBA from within the same area used for the benthic surveys on each reef . However, there were not always ten available replicate samples at all sites, and some reefs had none of some types at all. Bioindicators were selected based on their presence in long-term benthic composition data and their use in previous nutrient enrichment and bioindicator studies (Risk et al., 2001; Fichez et al., 2005; Cooper et al., 2009; Fabricius et al., 2012). Bioindicators included whole fronds of mature foliose brown macroalgae with the apical tips (*Sargassum* sp., Littler et al., 1991; Schaffelke, 1999), filamentous green macroalgae (*Chlorodesmis* sp., Schaffelke, 1999), cyanobacteria (Ford et al., 2018), soft corals (*Sarcophyton* sp., Fleury et al., 2000), turf algal matrix (Graham et al., 2018), sponges (Demospongaie: Ward-Paige et al., 2005; Lamb et al., 2012), and zoanthids (*Palythoa* sp., Leal et al., 2017). For turf algae, branches of dead *Acropora* spp. coral densely covered in turf algal assemblages were broken off and scraped with a scalpel to collect enough material to make up ten replicate samples. Marine sediment (< 4 cm depth; Fichez et al., 2005; Umezawa et al., 2008) which was considered as a non-biological indicator in this study, was also collected to determine nutrient signatures as an important store of nutrients on coral reefs. All samples were frozen at -20°C for up to one month.

2.2 Stable Isotopic and Elemental Analyses

Sample processing and preparation for isotopic analyses were conducted between the Seychelles Fishing Authority laboratory, Victoria, Mahé, Seychelles and Lancaster Environment Centre, Lancaster University, UK. All frozen samples were defrosted, rinsed thoroughly with distilled water and replicate samples were placed in a drying oven for ~48 hr at 60°C.. Once dried, samples were each ground into a fine powder using a ball mill and stored in individual airtight containers at SFA. All dried samples were weighed, alongside the

relevant standards (IAEA 600, cornflour, wheatflour and LEC flour), for stable isotopic analyses at LEC. For bioindicators which contained inorganic carbon material (i.e. calcifying organisms such as soft corals, sponges, and zoanthids), additional acidification was required to remove the inorganic carbonate which can affect carbon-based signatures (Schlacher & Connolly, 2014). ~10g of material was digested in 10% v/v hydrochloric acid (HCl) at room temperature until all constituent carbonate had been removed. Samples were then centrifuged, repeatedly washed until all traces of acidity had been removed, and left to dry prior to analysis for carbon stable isotope composition. The carbon stable isotopic and elemental signatures could not be measured in sediments in this study, because the samples were almost entirely composed of inorganic carbon material, so almost all of the test sediment material dissolved during initial runs of the acidification process. In addition, a subset of all calcified samples were not acidified so that they could be used for nitrogen-based stable isotopic signatures, as acidification can alter $\delta^{15}N$ signatures in some organisms (Schlacher & Connolly, 2014).

Stable isotopic and elemental analyses for nitrogen stable isotopes ($\delta^{15}N$), carbon stable isotopes ($\delta^{13}C$), nitrogen content (%N), carbon content (%C), and C:N Ratio (calculated from dividing the values of %C over %N) were undertaken within the Lancaster Environment Centre stable isotope facility, using an Isoprime100 Isotope Ratio Mass Spectrometer (IRMS) linked to an Elementar VARIO MICROcube Elemental Analyser. Combustion of samples within tin capsules at 950°C yielded N_2 and CO_2 for determination of $\delta^{15}N$ and $\delta^{13}C$ respectively. Analyses were standardised to AIR (for $\delta^{15}N$) and VPDB (for $\delta^{13}C$) using internal reference materials calibrated to international standards. Within-run replication (1 σ) was <0.3 ‰ for $\delta^{15}N$ and <0.1 ‰ for $\delta^{13}C$ for both standards and samples.

2.3 Cost-Effectiveness Analyses

To evaluate the cost-effectiveness of each of the techniques used to quantify the nutrient signatures in the eight different bioindicators, the time taken for collection, processing and analysis was calculated as follows. Collection time involved the time taken to search for and retrieve samples from up to 21 sites, where the average time recorded for each dive was ~1 h. Processing time included sample drying, crushing, weighing, and/or acidifying. Drying time represented the time taken to completely dry each sample in the drying oven, while crushing time was the time taken to crush each dried sample into a fine power. For weighing, the average time weighing standards for each mass spectrometric analysis was added to the time taken to weigh each individual sample, and stable isotope analysis time represented the time per analysis. The time taken to acidify each sample of the four calcified bioindicators was also included, though these samples had to be run twice to obtain results for both N and C signatures, with the first subset of samples unacidified, and the second subset acidified. All recorded and calculated times were then standardised to hours (h). The time taken per unit sample was used as a measure of "cost" instead of monetary value in this study, because the methods used to collect, process and analyse them were the same, except for the carbonate-containing samples which needed to be weighed and analysed twice.

2.4 Statistical Analyses

Availability of the bioindicators was assessed in two ways. Firstly, the abundance of the selected groups from the benthic composition data across the 21 sites was averaged and pooled for the two different types of reef state. Secondly, the number of sites that the different bioindicator types were collected from were totalled and categorised according to reef state (i.e. coral-mortality or regime-shifted). The percentage of sites from which each bioindicator was collected, relative to each reef state (i.e. out of 12 for coral-mortality reefs,

and out of 9 for regime-shifted reefs), was calculated, as there were different numbers in each category. The mean and standard deviation of the five nutrient signatures ($\delta^{15}N$, $\delta^{13}C$, %N, %C and C:N Ratio) from samples of each bioindicator, collected from up to 21 sites, were then analysed in R (R-Core-Team 2018).

The spatial variation for nutrient signatures of each bioindicator was assessed across all available sites using generalized linear models (GLM). All model fits were inspected for normality using visual plots, and GLMs were used on those with non-normal distributions. A GLM was used to determine the impact of the bioindicator, reef state and individual site on the five nutrient signatures (i.e. the response variables), using the following model for each individual signature:

Model 1: Nutrient Signature ~ Bioindicator + Reef State + Site

Where the nutrient signature was either $\delta^{15}N$, $\delta^{13}C$, %N, %C and C:N Ratio, and bioindicator (eight levels), reef state (two levels) and site (up to 21 levels) as fixed factors for each of the five response variables, (C-based signatures in sediment were omitted, as there was no data available). A total of 37 models were therefore run for the overall analysis (alpha = 0.05).

The coefficient of variation (CoV) was used to calculate the overall precision of each bioindicator across all available sites. CoV is the ratio of the sample standard deviation to the same mean, for a given set number of data points, and was used in this study because it is a unitless measure of variation, which is useful when testing the statistical effectiveness (i.e. precision) of the signatures across the different bioindicators. High precision is defined in this study as a small standard deviation compared to the mean, which increases the ability to detect statistical significance, both between the replicate samples of each bioindicator collected at each site, and over all the sites from which each bioindicator was collected. Low

precision, conversely, is a large standard deviation compared to the mean (Conquest, 1983). Though there is not one set standard in the literature, it is generally assumed that values of CoV < 10 can be regarded as "precise". CoV was calculated from the raw measurements detected in the replicate samples of each bioindicator collected from individual sites. Following this, the CoV of the N- and C-based signatures were compared across all the sites from which each bioindicator was collected with five linear models (Model 2), which were run separately for each nutrient signature:

Model 2: CoV ~ Bioindicator + Reef State + Site

Where CoV was the CoV value for $\delta^{15}N$, $\delta^{13}C$, %N, %C and C:N Ratio, and Bioindicator (eight levels), reef state (two levels) and site (up to 21 levels) were the fixed factors. The overall mean and standard deviation for the CoV each bioindicator were also summarised in box-plots.

A principal components analysis (PCA) (PRIMER-E Ltd, V.6.1.5, Plymouth, UK) based on a Bray–Curtis similarity matrix was used to visualise the similarities between averaged values of the five different nutrient measurements and the different bioindicators as a way of assessing the level of congruency of the bioindicators (Clarke & Warwick, 2001). The selection of a subset of bioindicators for this analysis (brown macroalgae, green macroalgae and zoanthids) was based on their level of precision, and the number of sites used, out of 21, depended upon the availability of each of these three indicators. Therefore nine sites were selected, as they had sufficient replicates of all three bioindicators to compare across sites (n=4), and the nutrient measurements were averaged at site level to compensate for the varying numbers of replicate samples available at each site. However, for C-based signatures, zoanthid samples from one site could not be acidified due to limited material so for these, eight sites were used. A correlation matrix was also constructed to assess the different

correlation values between the three selected indicators, where a p-value < 0.05 was considered significant.

To statistically assess the cost-effectiveness of each bioindicator, another GLM was used (as the data was not normally distributed) to compare the average times taken (per sample per bioindicator) for (a) collecting from the field, (b) drying and crushing of samples, (c) weighing and preparing samples (i.e. acidification) for isotopic analyses, and (d) running isotopic analyses. In this model, "Time" was the response variable, and "Bioindicator" and "Task" were the fixed factors (eight and two levels in each factor, respectively):

Model 3: Time ~ Bioindicator * Task

The interaction between these two fixed factors in Model 3 was also analysed to determine whether the "Bioindicator" (eight levels), "Task" (4-5 levels, depending on whether or not the bioindicator was acidified), or the interaction between them affects the time per unit sample. Reef State was also used as a fixed factor (with two levels) during initial statistical analyses, but was not included in this study as it showed no significant effect.

3. Results

3.1 Sample Collection and Benthic Cover

Across the 21 sites, a total of 150 samples of brown macroalgae (*Sargassum* sp.), 91 green macroalgae (*Chlorodesmis* sp.), 103 cyanobacteria, 59 soft corals, 112 sponges, 134 zoanthids (*Palythoa* sp.), 171 turf algal assemblages, and 204 sediment samples were collected. Availability of bioindicator varied between regime-shifted and coral-mortality reefs, as did the percentage of sites within these two categories where they were present (*Table 1*). Average cover of *Sargassum* sp. was significantly higher at the regime-shifted sites where it was an order of magnitude greater than on the coral-mortality sites. As such, there were specimens available at 100% of the regime-shifted sites, whereas they were only found at 58% of regime-shifted reefs. There was a similar percent cover of sediment across sites (along the line-intersect transect) regardless of reef state, and sediment samples were collected from all 21 sites. Percent cover of turf algae on coral-mortality reefs was 32.8 ± 23.8 %, compared to 12.2 ± 8.11 % on regime-shifted reefs, but still had 100% availability in both reef states. Cyanobacteria, soft coral and sponge all had higher percent cover and were also present on a higher percentage of coral-mortality sites than on regime-shifted ones.

Table 1. Summary table for percent cover (% cover) of candidate bioindicators (BM = brown macroalgae; CYB = Cyanobacteria; GM = Green Macroalgae; SED = Sediment; SC = Soft Coral; TA = Turf Algae; ZO = Zoanthid) from the line-intercept transect surveys at 21 coral reefs around the Inner Seychelles Islands. Percentage of Sites represents the percentage of sites relative to the total number in each reef state (out of n=12 for "coral-mortality" reefs versus n=9 "regime-shifted" reefs). Mean ± S.D for percent cover.

	Regime-Shifted Reefs (n=9)		**Coral-Mortality Reefs (n=12)**	
Bioindicator	**Mean ± S.D. (%)**	**Percentage of Sites (%)**	**Mean ± S.D. (%)**	**Percentage of Sites (%)**
Sargassum (BM)	36.9 ± 20.3	100	2.7 ± 8.47	58
Cyanobacteria (CYB)	1.2±2.8	44	2.5 ± 5.0	75
Chlorodesmis (GM)	0.2 ± 0.3	89	0.3 ± 0.4	25
Soft Coral (SC)	0.1 ± 0.8	11	1.2 ± 2.5	67
Sediment (SED)	6.7± 3.4	100	9.52 ± 11.5	100
Sponge (SP)	0.00*	56	1.4 ± 2.1	75
Turf Algae (TA)	12.2 ± 8.1	100	32.8 ± 23.8	100
Palythoa (ZO)	0.2 ± 0.4	67	1.3 ± 1.0	100

3.2 Spatial Variation of Nutrient Signatures in Bioindicators

The type of bioindicator had variable effects on each of the five nutrient signatures. Overall, brown and green macroalgae (BM and GM, respectively) not only had lower average $\delta^{15}N$ signatures than the other indicators, but they also had the smallest variations in signatures across all of their sites (5.58 ± 0.82 and 5.33 ± 0.45‰, respectively. *Fig. 1a*). Bioindicators representing higher trophic levels, such as sponges (SP), soft corals (SC), and zoanthids (ZO) (7.51 ± 0.67; 7.61 ± 1.27, and 9.08 ± 0.88‰, respectively) had more enriched average $\delta^{15}N$ signatures, as did sediment (SED) (9.61 ± 1.41 ‰). After acidification, the four bioindicators that contained inorganic carbon (soft corals, sponges, and turf algae (TA)) showed similar signatures of $\delta^{13}C$ on average (-16.3 ±1.29; -17.4 ± 0.38; and -18.5 ± 3.16, ‰, respectively), though it was less negative in zoanthids (-13.7 ± 0.88 ‰). The two types of macroalgae also differed (BM: -16.2 ± 1.58, and GM: -21.3 ± 0.96 ‰) whereas cyanobacteria (CYB) (-21.3 ± 3.36 ‰) was similar to green macroalgae (*Fig. 1b*).

Turf algae had a similar average signature for %N (1.53 ± 0.45‰) relative to brown macroalgae (1.10 ± 0.18 %) but green macroalgae had a much higher value (4.32 ± 0.48 %), which was even higher than cyanobacteria (3.31 ± 1.25 %). The N content of brown macroalgae was also most similar to zoanthids (1.06 ± 0.22 %). N content was also much lower in sediment (0.05 ± 0.11 %) (*Fig. 1c*). There was much higher C content in green macroalgae than in the other bioindicators (42.2 ± 2.40 %), followed by brown macroalgae (31.0 ± 1.41 %), and cyanobacteria (28.7 ± 5.52 %). Zoanthids had the lowest %C (11.2 ± 2.74) (*Fig. 1d*). Brown macroalgae had higher C:N Ratio signatures with a large range due to high %C content and low %N content (28.8 ± 4.99). The other five groups were quite similar to one another, with the exception of sponge (0.85 ± 0.11) (*Fig. 1e*).

The GLMs showed that the type of bioindicator had a strong influence on the variability of nutrient signatures, with significance evident across almost all signatures. However, both types of macroalgae were statistically similar for $\delta^{15}N$, as were brown macroalgae, turf algae and zoanthid for %N (Suppl. Table 2). However, the effect of reef state varied among both bioindicators and nutrient signatures. For instance, differences in $\delta^{15}N$ signatures in BM ($p=0.0002$), CYB ($p=0.002$), GM ($p<0.0001$), SED ($p=0.01$), TA ($p=0.02$) and ZO ($p<0.0001$) were significant, whereas the difference in %N for GM between reef states was not ($p=0.93$). Reef state was also significantly different for $\delta^{13}C$ in cyanobacteria ($p=0.002$), green macroalgae ($p < 0.0001$), sediment ($p=0.01$), turf algae ($p=0.02$) and zoanthids ($p<0.0001$). For %N, reef state also significantly differed in BM ($p <0.0001$), CYB ($p<0.0001$) and ZO ($p=0.04$). For %C, reef state differed significantly for CYB ($p<0.0001$) and ZO ($p=0.01$), and for C:N Ratio, only BM ($p=0.04$) and TA ($p=0.0002$) differed significantly.

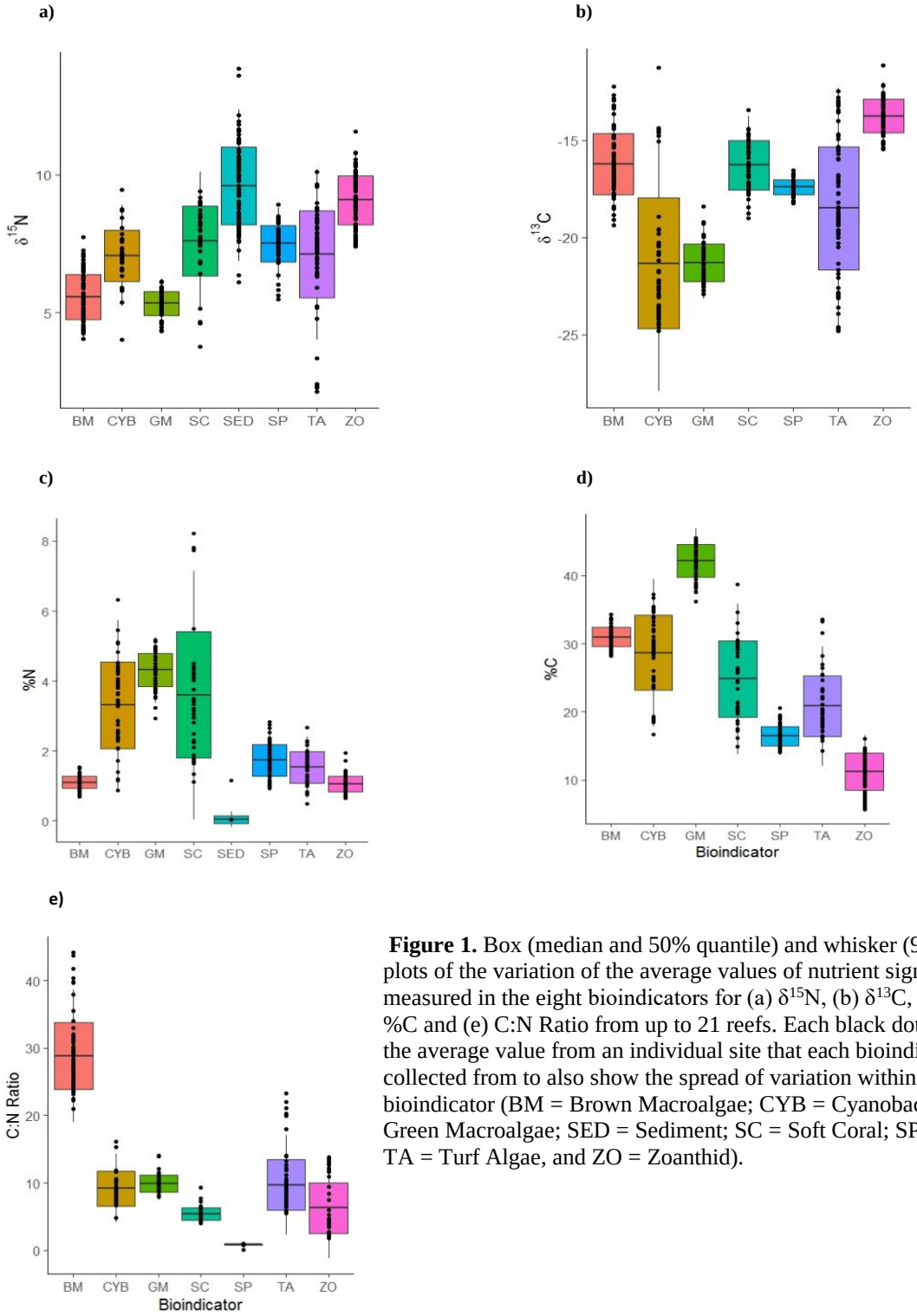


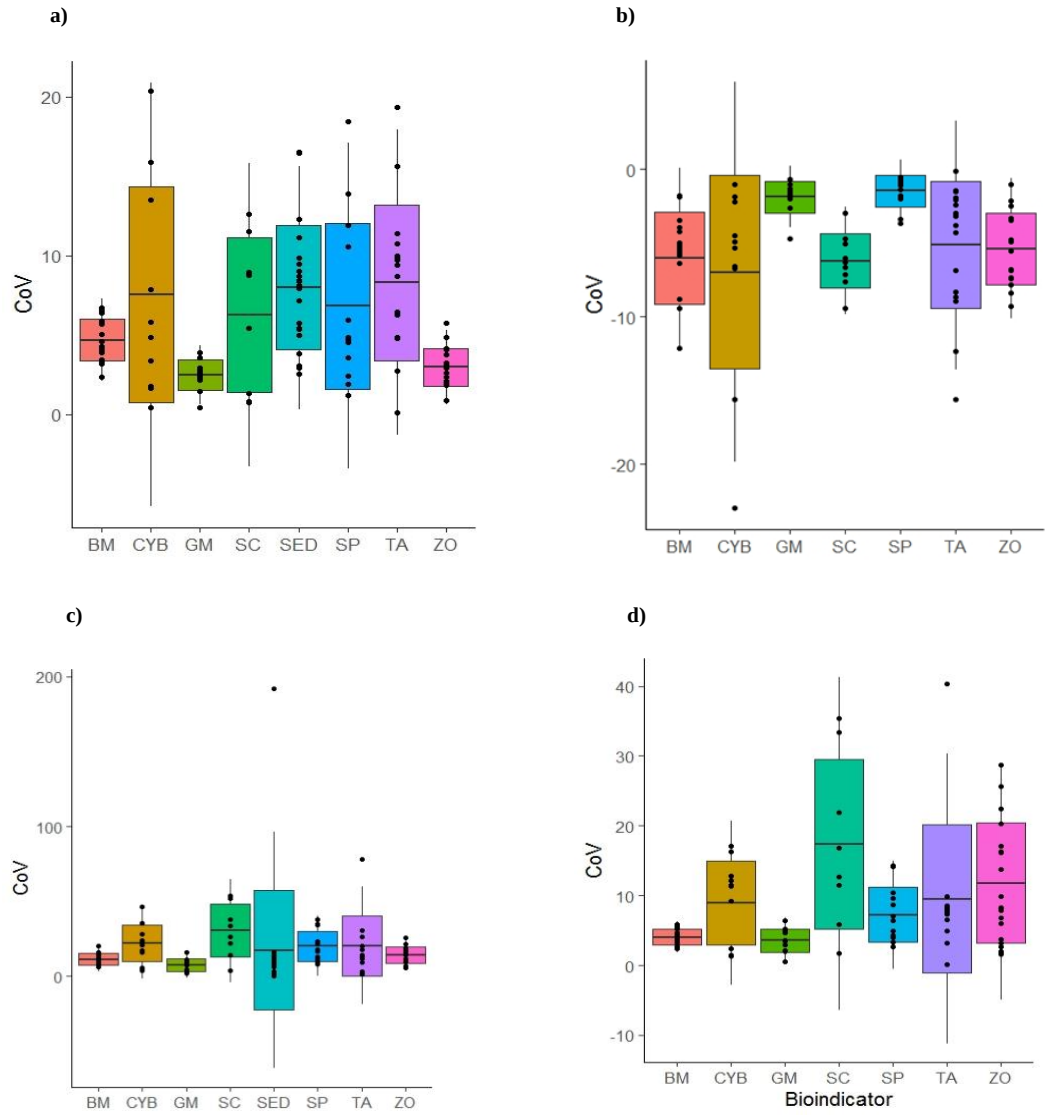
Figure 1. Box (median and 50% quantile) and whisker (95% quantile) plots of the variation of the average values of nutrient signatures measured in the eight bioindicators for (a) $\delta^{15}N$, (b) $\delta^{13}C$, (c) %N, (d) %C and (e) C:N Ratio from up to 21 reefs. Each black dot represents the average value from an individual site that each bioindicator was collected from to also show the spread of variation within each bioindicator (BM = Brown Macroalgae; CYB = Cyanobacteria; GM = Green Macroalgae; SED = Sediment; SC = Soft Coral; SP = Sponge; TA = Turf Algae, and ZO = Zoanthid).

3.3 Precision of Bioindicators

The precision of the bioindicators was assessed using CoV, as this standardised the nutrient signatures between bioindicators (including the non-biological indicator sediment) and controlled for differences in isotopic fractionation in measurements, particularly between trophic levels. Green macroalgae had the lowest and most consistent CoV within and across reefs, and therefore the highest precision for all N-based nutrient measurements (δ^{15}N: 2.47 ± 0.95; %N: 7.53 ± 4.29; C:N Ratio: 5.76 ± 5.39), however this pattern was not as distinct for C-only signatures (δ^{13}C: -1.87 ± 1.06 and %C: 3.60 ± 1.67) (*Fig. 2)*. This was closely followed by brown macroalgae (δ^{15}N: 4.68 ± 1.33 ‰; δ^{13}C: -6.03 ± 3.12; %N: 11.3 ± 4.07; %C: 4.07 ± 1.12, and C:N Ratio: 9.92 ± 3.75). Turf algal assemblages had much more variable average signatures for all five measures, especially those that were N-based (δ^{15}N: 8.30 ± 4.90 ; δ^{13}C: -5.14 ± ; %N: 20.5 ± 20.1; %C: 9.54 ± 10.6, and C:N Ratio: 10.6 ± 10.3).

Zoanthids had lower average CoV values for N-based signatures than higher trophic organisms and were more similar to the two macroalgal types ($\delta^{15}N$: 2.98 ± 1.20, and *%N*: 14.3 ± 5.52), as well as for δ^{13}C (-5.14 ± 2.43), though the CoV values for both %C and C:N Ratio were much higher than for any of the other bioindicators (11.8 ± 8.57 and 20.0 ± 24.1, respectively). The other higher trophic level organisms, such as soft corals (δ^{15}N: 6.26 ±4.87; δ^{13}C:-6.20 ± 1.86; %N: 30.4 ± 17.6; %C: 17.4 ± 12.2, and C:N Ratio:11.6 ± 8.68*)* and sponges (δ^{15}N: 6.82 ±5.24; δ^{13}C: -1.44 ± 1.08; %N: 20.0 ± 10.3; C%: 7.24 ± 3.94, and C:N Ratio: 7.58 ± 12.1) showed inconsistent levels of precision across the five signatures. Though sediment had similar precision for δ^{15}N to the other candidates (7.97 ± 3.90), it had the highest range of CoV values for %N (17.4 ± 40.2) (*Fig. 2a*).

Overall, the CoV analyses showed that both brown and green macroalgae had low average CoV values for N-based signatures, as well as small variations in CoV across the sites. In addition, while the C-based signatures were more variable for zoanthids, the N-based results were more precise compared to the other higher-trophic bioindicators. There was also no overall significant effect of reef state or site-level variation on CoV for any of the five nutrient signatures, suggesting that precision did not vary over different spatial scales or between the coral-mortality and regime-shifted reefs. The statistical models showed variable patterns for each nutrient signature type across the eight bioindicators, however for %C and C:N Ratio, zoanthids were the only bioindicator that significantly differed from brown macroalgae due to its high variation (Suppl. Table 3).



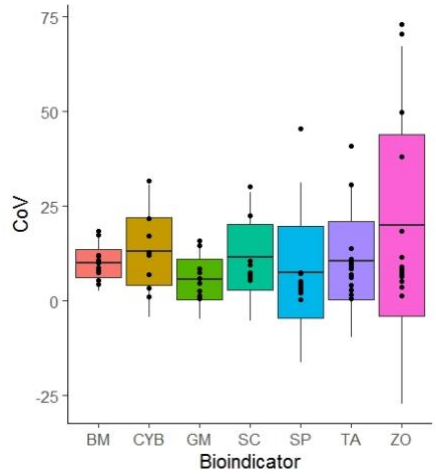


Figure 2. Box (median and 50% quantile) and whisker (95% quantile) plots of the spread of the coefficient of variation (CoV) of the eight bioindicators for (a) $\delta^{15}N$, (b) $\delta^{13}C$, (c) %N, (d) %C and (e) C:N Ratio up to 21 reefs (mean ± S.D.). Each black dot represents the average CoV from the individual sites from which each bioindicator was collected to also show the spread of variation within- and among sites (BM = Brown Macroalgae; CYB = Cyanobacteria; GM = Green Macroalgae; SED = Sediment; SC = Soft Coral; SP = Sponge; TA = Turf Algae, and ZO = Zoanthid). CoV for each nutrient measurement in each bioindicator collected from each site was calculated by the ratio of standard deviation to the mean of a given number of replicate data points (i.e. up to 5 samples per indicator per site).

3.4. Congruency of Bioindicators

A principal components analysis (PCA) was used to assess congruency between the three selected bioindicators. Brown and green macroalgae had low correlation, especially for signatures of N, while zoanthids had no significant relationships with either macroalgae. There were weak positive relationships between N-based signatures of green and brown macroalgae (Table 2), but these explain <40% of the variance and are not significant at alpha =0.05 (*Fig. 3*). This was also shown by Pearson's correlation analyses between the different combinations of bioindicators (Table 2). The two types that showed the highest similarity for N-based signatures were between brown and green macroalgae for C:N Ratio measurements (r^2 = 0.61), closely followed for those of %N (r^2 = 0.60) and $\delta^{15}N$ (r^2 = 0.55) signatures, though none of these were significantly correlated. However, the highest similarity for C-only signatures was between %C of brown and green macroalgae (r^2 = 0.81), but was very low for $\delta^{13}C$ (r^2 = 0.041) (Table 2).

Table 2. Pearson's correlation analyses between the three selected bioindicators (brown macroalgae versus green macroalgae; brown macroalgae versus zoanthids; green macroalgae versus zoanthids) to determine amount of correlation between them (correlation coefficient) The significance level for the p-values is alpha = 0.05.

Bioindicator	**$\delta^{15}N$**	**$\delta^{13}C$**	**%N**	**%C**	**C:N Ratio**
BM vs. GM	0.55	0.041	0.60	0.81	0.61
	(p=0.12)	(p=0.92)	(p=0.09)	(p=0.02)	(p=0.08)
BM vs. ZO	0.10	0.11	0.18	-0.005	0.07
	(p=0.79)	(p=0.80)	(p=0.64)	(p=0.99)	(p=0.68)
GM vs. ZO	0.28	0.64	0.23	-0.23	-0.36
	(p=0.47)	(p=0.09)	(p=0.55)	(p=0.58)	(p=0.34)

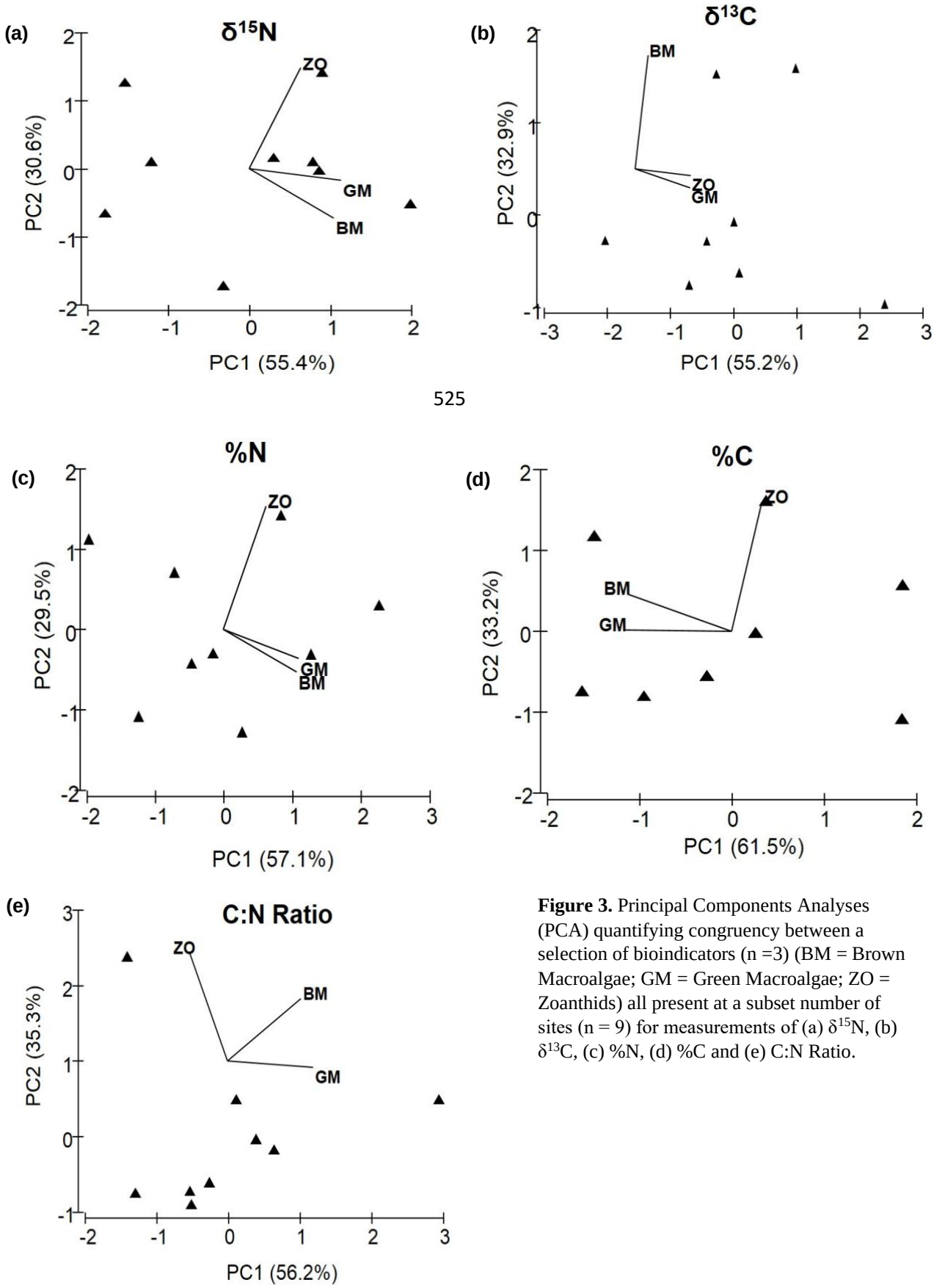


Figure 3. Principal Components Analyses (PCA) quantifying congruency between a selection of bioindicators (n =3) (BM = Brown Macroalgae; GM = Green Macroalgae; ZO = Zoanthids) all present at a subset number of sites (n = 9) for measurements of (a) $\delta^{15}N$, (b) $\delta^{13}C$, (c) %N, (d) %C and (e) C:N Ratio.

3.5 Cost-Effectiveness of Bioindicators

The time taken for the whole process, from collection to stable isotopic analyses, per unit sample, differed among the eight bioindicators (Table 3; Suppl. Table 4). The GLMs suggested that both bioindicator and task can have a significant effect on the time taken, per sample, to use each bioindicator for capturing measure nutrient regimes, but reef state does not. Overall, it took a similar amount of time to collect the two macroalgae and cyanobacteria, whereas soft corals, sponges, turf algae and zoanthids took significantly longer to find. Sediment, in contrast, took the least time overall to find and collect (Table 3). Each task differed significantly as well, with “Drying and Crushing” taking the most time to complete and “Field Collection” took the least time, but significance varied between the bioindicators. The time taken to process the four calcified bioindicators was much greater, because each sample of these indicators required the additional step of “Acidification”.

Table 3. Summary of the mean time taken (per unit sample, per hour) for each task undertaken to process each bioindicator for the cost-effectiveness. *Acidifying only includes the four bioindicators that were acidified, and thus weighed and analysed in the mass spectrometer. Significance Level is $p < 0.05$. Normality inspected using visual plots. Mean ± S.D.

BIOINDICATOR	***FIELD COLLECTION***	***DRYING & CRUSHING***	***ACIDIFICATION***	***WEIGHING***	***STABLE ISOTOPIC ANALYSES***
Brown Macroalgae (BM)	0.038 ± 0.04 (p<0.0001)	24.8 ± 0.5 (p < 0.0001)	-	1.5 ± 0.01 (N/A)	0.18 ± 0.03 (p<0.0001)
Cyanobacteria (CYB)	0.35 ± 0.4 (p=0.52)	23.2 ± 1.4 (p < 0.0001)	-	1.5 ± 0.03 (N/A)	0.21 ± 0.1 (p=0.93)
Green Macroalgae (GM)	0.078 ± 0.08 (p=0.86)	24.1 ± 0.005 (p=0.26)	-	1.5 ± 0.01 (N/A)	0.17 ± 0.05 (p=0.98)
Soft Coral (SC)	0.25 ± 0.3 (p=0.001)	22.2 ± 1.2 (p < 0.0001)	0.17 ± 0.001 (p < 0.0001)	3.1 ± 0.06 (p=0.95)	0.48 ± 0.2 (p=0.004)
Sediment (SED)	0.015 ± 0.003 (p=0.0002)	22.7 ± 1.2 (p=0.05)	-	0.14 ± 0.02 (N/A)	0.25 ± 0.1 (p<0.0001)
Sponge (SP)	0.24 ± 0.3 (p=0.0006)	22.6 ± 1.3 (p < 0.0001)	0.17 ± 0.0 (p < 0.0001)	3.1 ± 0.00 (p=0.89)	0.37 ± 0.07 (p=0.002)
Turf Algae (TA)	0.03 ± 0.04 (p=0.0002)	24.6 ± 0.5 (p=0.0003)	0.17 ± 0.002 (p < 0.0001)	3.0 ± 0.02 (p=0.98)	0.34 ± 0.08 (p=0.0005)
Zoanthids	0.18 ± 0.2 (p<0.0001)	23.0 ± 1.5 (p<0.0001)	0.17 ± 0.0 (p < 0.0001)	3.0 ± 0.00 (N/A)	0.41 ± 0.03 (p=0.0004)

Although the time taken per sample to collect each bioindicator from the field did not differ between reef states, the availability of samples on the different reef did (*Table 1*). There was a strong negative correlation between average time taken per sample to collect and the percentage of sites from which each indicator was available on regime-shifted reefs (relative to the total number of sites, i.e. n=9) ($r^2 = 0.94$), whereas there was a very weak negative relationship between average time taken and sample availability on coral-mortality sites ($r^2 = 0.15$; n=12) (*Fig. 4*). This suggests that although the time taken varied more among bioindicators on regime-shifted reefs (i.e. it took over an hour, on average, to find one sample of soft coral), it is a better predictor for finding specific bioindicator(s) on sites dominated by macroalgae. For coral-mortality reefs, in contrast, the times among bioindicators were more similar, but sample availability was more variable. Brown macroalgae had similar collections times between reef states (regime-shifted: 0.01 ± 0.01; coral-mortality: 0.07 ± 0.05 h), but

there was 100% availability on regime-shifted sites relative to 58% on coral-mortality sites. Turf algae and sediment, in contrast, not only had 100% availability on both reef states, but they took the least time to collect .

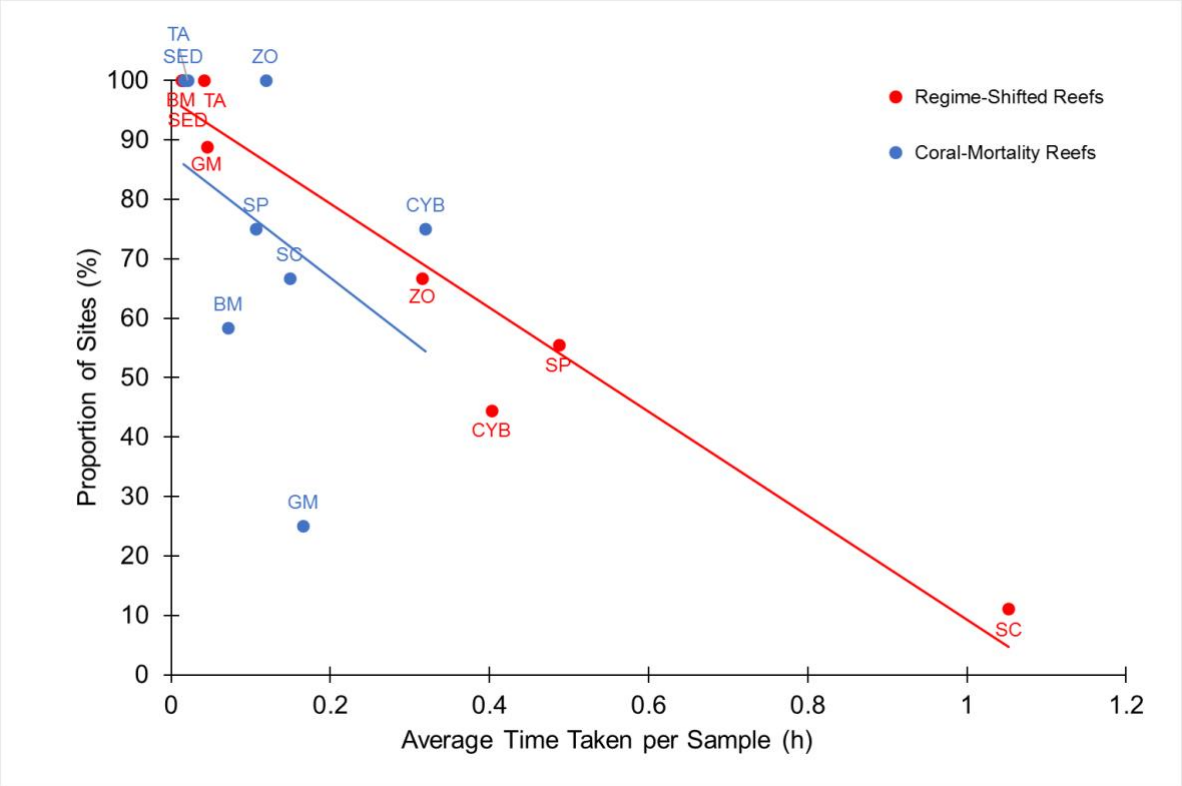


Figure 4. The relationships between the average time taken, per unit sample (h) and the availability of samples on both reef states. Each individual point in red represent the total average time, per sample, for the eight bioindicators collected from regime-shifted sites versus the percentage of sites they were available to collect at (n=12), and the individual point in blue represented each indicator from coral-mortality sites. $r^2 = 0.94$ on regime-shifted reefs, and $r^2 = 0.15$ on coral-mortality reefs. BM = Brown Macroalgae; CYB = Cyanobacteria; GM = Green Macroalgae; SED = Sediment; SC = Soft Coral; SP = Sponge; TA = Turf Algae, and ZO = Zoanthid.

4. Discussion

The principal aims of this study were to identify precise, cost-effective, and congruent bioindicators for capturing nutrient regimes on coral reefs, particularly over those in different ecological conditions. Overall, nutrient signatures of brown macroalgae, green macroalgae and zoanthids were considered to meet these criteria, relative to the other candidates. While the macroalgae were more consistent indicators for reefs that have undergone a regime shift, zoanthids were more common on both types of reef state. Turf algae and sediment took the least time to collect and were also the most abundant and available samples across the 21 reefs studied, regardless of reef state, but their utility as indicators is limited by their highly variable CoV values. There was low congruency between the three most precise indicators (brown macroalgae, green macroalgae and zoanthids), which suggested that physiological processing of nutrients within each bioindicator has a greater influence on N- and C-based signatures than its local environment. Congruency between multiple taxa could be improved by either choosing a suite of indicators from the same functional group, such as macroalgae with comparable nutrient uptake mechanisms, or by tracing the accumulation of nutrient signatures across different trophic levels from the same food chain.

4.1 Spatial Variation, Precision and Congruency of Nutrient Signatures in Bioindicators

The N- and C-based nutrient signatures of the bioindicators in the current study appear typical of measurements reported in the literature (Atkinson & Smith, 1983; Smit, 2001). For instance, the range of absolute values of $\delta^{15}N$ signatures in all of the bioindicators are quite consistent (5 – 10 ‰), though they are slightly high relative to other marine systems (Sigman & Casciotti, 2001). In addition, the $\delta^{13}C$ signatures reflect that of a carbonate-dominated system, which for instance lies within the range of -10 to -30‰ for most marine macrophytes (Smit, 2001; Raven et al., 2002). The N-based signatures also follow trophic status whereby

those organisms at higher trophic levels are relatively more enriched than those of primary producer status (Boecklen et al., 2011; Lamb et al., 2012)..

Spatial variation of the different nutrient signatures, both within- and among-reefs, varied widely across the inner Seychelles. The N-based signatures also showed a significant difference between coral-mortality and regime-shifted reefs for a number of the bioindicators, including $\delta^{15}N$ in the two macroalgae and zoanthids, whereas signatures tended to be more similar across sites for the C-based signatures. Being able to capture variability in nutrient regimes, especially across different spatial scales or even different reef states, is another important aspect of a good bioindicator (Cooper et al., 2009), so this study provides supporting evidence that $\delta^{15}N$ and %N are particularly effective proxies of nutrient regimes (Lin & Fong, 2008)**.** For instance, Littler et al., (1991) found that nutrient concentrations in a number of algal species were generally higher on reefs around the high granitic, populated islands like Mahe and Praslin, relative to the low, remote carbonate atolls in the wider Seychelles Archipelago. In a related study in Vaughan et al. (2021), the use of macroalgal $\delta^{15}N$ helped to determine that the dead coral tissue released into the water column after the 2016 coral bleaching event in the Seychelles may have been subsequently taken up and retained by *Sargassum* on the coral-mortality reefs. However, the high variability shown across nutrient signatures in the current study, particularly in $\delta^{15}N$, may not be solely due to differences in local sources of nutrients. Other studies, for example, have found that differences in signatures are not always consistent with distinct sources of nutrient loads (i.e. in areas with known anthropogenic run-off), which implied that external inputs are not always the cause of variations in nutrient regimes captured in bioindicators (Raimonet et al., 2013; Viana & Bode, 2013).

There were discrepancies found in some of the signatures even between different primary producers in this study, such as between brown (*Sargassum sp.)* and green macroalgae (*Chlorodesmis* sp.). For instance, although they had similar $\delta^{15}N$ values across the sites, the other four signatures varied on average between these two bioindicators, particularly for %N, which was much higher in green macroalgae, although it was similar between reef states (*Fig. 2a&c)*. This could be because nitrogen content in *Chlorodesmis* is affected by both biological nutrient uptake mechanisms and environmental factors (Fong et al., 2001; Raimonet et al., 2013; Viana & Bode, 2013; Clausing & Fong, 2016), and therefore do not reflect either inorganic concentrations or the $\delta^{15}N$ of their surrounding environment (Viana & Bode, 2013). Slower-growing algal species like *Chlorodesmis* have a greater capacity for internal nutrient storage so are not as nutrient-limited, and therefore are less responsive to fluctuations in nutrients as other, more opportunistic species like *Sargassum* (Schaffelke., 1999; García-Seoane et al., 2018a&b).

Zoanthids are positioned at a higher trophic level than benthic algae so their nutrient signatures tend to fractionate and become more enriched (*Fig. 1a;* Zanden & Rasmussen, 2001; Fox et al., 2018). There has been little research into zoanthids as potential indicators of nutrient runoff (Leal et al., 2017), but Costa Jr. et al. (2008) found that phosphorus and silica water concentrations had positive effects on both algal and zoanthid growth, and negative effects on coral cover. However, unlike primary producers, zoanthids have to balance auto- and heterotrophic processes for acquiring sources of C and N (Smit, 2001; Leal et al., 2017) because, like scleractinian corals, they have photosynthetic symbionts in their tissues (Hoegh-Guldberg et al., 2004; Fox et al., 2018). This could explain the large variations in %C and C:N Ratio, both within- and among-reefs in this study (*Fig. 2d &e*; Suppl. Table 2), as they represent the combined signatures from both host and symbiont (Leal et al., 2017).

Even though the three most precise bioindicators (brown macroalgae, green macroalgae and zoanthids) all showed significant differences in $\delta^{15}N$ between the two reef states for the spatial variation analyses, their CoV values did not. This suggests that these bioindicators are not only consistently precise among reefs and reef states, but are also able to detect differences in nutrient regimes across the same areas, which is why $\delta^{15}N$ is such a versatile tool for monitoring water quality (Costanzo et al., 2001; Lin & Fong, 2008). However, when compared directly, the congruency among these three bioindicators was relatively low. This could be due to the differences in nutrient processing between the different bioindicators. Congruency is important, as a single-species approach may result in an underestimation of spatial patterns in nutrient regimes (Linton & Warner, 2003), and it has been shown across multiple taxa in previous studies (Connolly et al., 2013), but these studies were also conducted along strong nutrient gradients (i.e. with increasing distance from a sewage outfall) (Fernandes et al., 2012). This suggests that in the current study, the biological mechanisms of individual species may have outweighed the effect of environmental factors on their isotopic and elemental signatures.

The other (bio)indicators included in this study were found to have variable and inconsistent nutrient signatures across sites and the two reef states, which was why they were not included in the congruency analyses. Like macroalgae, turf algal assemblages and cyanobacteria are primary producers that not only take up and utilise bioavailable nutrients but are becoming more prevalent on reefs across a range of reef states, particularly following a disturbance (den Haan et al., 2016; Zaneveld et al., 2016, Ford et al., 2018). However, this study showed that both bioindicators had variable precision among the five nutrient signatures with no clear spatial patterns between reefs, which implied they were also more influenced by biological

factors (i.e. multiple species within the turf assemblage) than their local environment (Steneck & Dethier, 1994; Raimonet et al., 2013). Similarly to zoanthids, soft corals can also harbour symbionts (Fleury et al., 2000; Risk, 2014; Williams et al., 2018), and while sponges are not photosynthetic, they do have symbiotic relationships with cyanobacteria, which is reflected in their $\delta^{13}C$ signatures (Smit, 2001; Lamb et al., 2012). Sediments can also capture a range of nutrients within a reef, which can be resuspended within local biogeochemical cycles through various biophysical factors and thus provide an additional source (Fabricius, 2005; Umezawa et al., 2008). However, some studies have found sediments to be an overall poor indicator (Fichez et al., 2005). In the current study, for instance, very little N was detected in the subsamples of sediment analysed even before acidification, so the low precision calculated for it was more likely due to random error than environmental factors, and so was not comparable for either N- or C-based signatures.

4.2 Cost-Effectiveness of Bioindicators

Cost-effectiveness is often mentioned as an important criteria in previous bioindicator studies (Fichez et al. 2005; Cooper et al., 2009; Risk et al., 2001). However, analyses are rarely conducted to quantify these in ecological studies (Drummond & Connell, 2008; Bal et al., 2020) even though the “cost” of any particular indicator can be affected by various different factors. For instance, the average time taken to collect an individual sample from a study site depended upon its availability and/ or abundance, which is why there was a significant difference in collection time with reef state. While it only took ~1 to 2 minutes on average to collect samples of turf algae and sediments from each site, regardless of ecological condition, it took significantly less time to collect brown macroalgae from regime-shifted reefs than it did on coral-mortality reefs. Differences in availability on those reefs could be influenced by

nutrient loads, abundance of herbivores, depth, structural complexity, and juvenile coral cover (Graham et al., 2015; Dajka et al., 2019). The findings of both the sample collection and the line-intercept survey of benthic cover at the 21 sites illustrated the importance of considering the local abundance of a bioindicator when assessing nutrient regimes (Cooper et al., 2009; Fabricius et al., 2012). For instance, turf algae and sediments were ubiquitous at all sites, so could be considered as more "cost-effective" in terms of sampling availability and abundance. However, as turf algae are composed of an assemblage of varying functional groups, and there was very little N detected in sediment, it is difficult to interpret results for nutrient signatures from either bioindicator, and therefore to rely on them for capturing nutrient regimes precisely, despite their widespread abundance.

4.3 Future Directions in Bioindicator Research

This study investigated novel ways of assessing potential bioindicators for monitoring programs across coral reefs under different ecological states. However precision and effectiveness of bioindicators used in this study could be improved, even if these improvements will increase costs. For instance, to reduce the CoV of turf algal assemblages, cyanobacteria, and symbiotic organisms, future studies could isolate and individually measure the different functional groups within assemblages (Steneck & Dethier, 1985), individual strains of cyanobacteria (Thacker & Paul, 2001), or the host and symbiont fractions in zoanthids and soft corals (Hoegh-Guldberg et al., 2004; Leal et al., 2017) so that the nutrient signatures of each group can be measured and interpreted separately. Conversely, such techniques will increase the time taken to process and analyse samples, and thus will increase their "costs" as a bioindicator.

It was also difficult to determine the accuracy of the bioindicator nutrient signatures, as there is little reference data for nutrient levels around the inner Seychelles Islands, even from seawater samples, and especially at the spatio-temporal scales required for this study. Further research should therefore also investigate the accuracy of cost-effective bioindicators such as macroalgae for capturing either natural or anthropogenic sources by additionally measuring stable isotopic signatures of potential point sources (Costanzo et al., 2001; Dailer et al., 2010; Fernandes et al., 2012; den Haan et al., 2012).. Another approach could entail building up a suite of relatively similar bioindicators by focusing on specific functional group(s), appropriately matched to the scale of the ecological process being investigated (Fong & Fong, 2014). If this option is not possible, for instance, when a group of congruent bioindicators (i.e. fleshy macroalgae) is only found on reefs in a certain ecological state, then nutrient signatures could be compared across a suite of bioindicators to see the accumulation of this energy source across different trophic levels within the same food chain (Smit, 2001; Pitt et al., 2009; Connolly et al., 2013; Kürten et al., 2014; Graham et al., 2018).

5. Conclusion

In conclusion, the stable isotopic and elemental signatures of fleshy macroalgae were found to be precise and cost-effective bioindicators across coral reefs in the inner Seychelles, as primary producers with widespread distribution and consistent measurements within their tissues. If the precision of bioindicators can be increased, it would provide additional opportunities to determine differences in bioavailable nutrient regimes between reefs. This could be particularly useful in remote coastal areas where environmental monitoring efforts to assess the local anthropogenic impacts of coastal run-off and excessive nutrient loads on coral reefs are currently limited, but would be highly beneficial to assessing overall ecosystem health. If remote reefs have been subjected to any large disturbance, such as a

mass bleaching event, having precise and cost-effective bioindicators to detect whether any areas have excessive nutrient loads, could enable better-informed efforts to improve water quality and mediate coral recovery potential.

6. Author Contributions

Eleanor Vaughan: Conceptualisation, Data curation, Formal analysis, Investigation, Methodology, Visualisation, Writing – original draft, Writing – review and editing. **Nicholas Graham:** Conceptualisation, Funding acquisition, Project administration, Resources, Supervision, Writing – review and editing. **Shaun Wilson:** Funding acquisition, Investigation, Writing – review & editing. **Peter Wynn:** Methodology, Resources, Supervision. **Gareth Williams:** Supervision, Writing – review and editing. **Phillip Barker:** Supervision, Writing – review & editing.

7. Declaration of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary Figures

Supplementary Table 1. Summary of the 21 coral reefs surveyed around the inner Seychelles islands, including latitude, longitude, habitat type and reef state as categorised in 2017 (CM= coral-mortality reef; RS – regime-shifted reef). * denotes the sites added to the 2017 survey in place of the three sites around Cousin Island that were not surveyed that year (Graham et al., 2015).

Site	Lat	Long	Habitat Type	Reef State
Mahe West patch reef	-4.684675	55.43472	Patch	CM
Mahe West carbonate	-4.669121	55.40025	Carbonate	CM
Mahe West granitic reef	-4.659828	55.36099	Granitic	CM
Mahe North West carbonate	-4.634994	55.37612	Carbonate	CM
Mahe North West patch reef	-4.614482	55.41627	Patch	CM
Mahe North West granitic	-4.562673	55.43691	Granitic	CM
Ste. Anne granitic reef	-4.605095	55.51353	Granitic	CM
Ste. Anne patch reef	-4.618086	55.5094	Patch	CM
Ste Anne carbonate	-4.609864	55.49636	Carbonate	RS
Mahe East granitic reef	-4.734961	55.52896	Granitic	RS
Mahe East carbonate	-4.710589	55.52704	Carbonate	RS
Mahe East patch reef	-4.703574	55.5282	Patch	CM
Praslin North East patch reef	-4.303653	55.74655	Patch	CM
Praslin North East carbonate	-4.315847	55.75669	Carbonate	RS
Praslin NE granitic reef	-4.290079	55.7075	Granitic	CM
Praslin SW granitic reef	-4.313662	55.67872	Granitic	CM
Praslin SW patch reef	-4.333943	55.69204	Patch	RS
Praslin SW carbonate	-4.350873	55.70152	Carbonate	RS
Curieuse South West carbonate*	-4.28007	55.71199	Carbonate	RS
Curieuse North East granitic reef*	-4.27987	55.74425	Granitic	RS
Baie Ste Anne patch reef*	-4.34278	55.76919	Patch	RS

Supp. Table 2. Model (1) for each nutrient measurement and for each bioindicator: Nutrient Signature ~ Bioindicator + Reef State + Site. Model type was selected for each individual model based on normality of distribution. Sediment (SED) values were not available and so were not included for C-based signatures. Significance is noted as: '***' p < 0.001; '**' p < 0.01; '*' p < 0.05; and ',' p < 0.1.

Bioindicator	Model Type (Family)	Intercept	Lower C.I. (5%)	Upper C.I. (95%)	p-value
$\delta^{15}N$					
Brown Macroalgae					
BSAP_Coral Mortality (Intercept)	GLM	0.15	0.14	0.16	**< 0.0001*** **
Reef State: Regime Shift	GLM	0.020	0.010	0.029	**0.0002 *** **
CNEG	GLM	0.020	0.0095	0.031	**0.0005 *** **
CSWC	GLM	0.013	0.0029	0.024	**0.16 * **
MEC	GLM	0.0090	-0.0014	0.019	0.095.
MEG	GLM	0.046	0.034	0.057	**<0.0001*** **
MEP	GLM	0.0028	-0.0063	0.012	0.55
MNWP	GLM	-0.012	-0.021	-0.0032	**0.010 * **
PNEC	GLM	0.064	0.052	0.076	**<0.0001*** **
PNEG	GLM	0.028	0.018	0.037	**<0.0001*** **
PNEP	GLM	0.033	0.023	0.043	**<0.0001*** **
PSWC	GLM	0.039	0.028	0.050	**<0.0001*** **
PSWG	GLM	0.033	0.023	0.044	**<0.0001*** **
PSWP	GLM	0.047	0.035	0.059	**<0.0001*** **
SAC	GLM	0.017	0.0062	0.028	**0.003 ** **
SAG	GLM	0.0091	-0.00012	0.018	0.058.
SAP	GLM	N/A	N/A	N/A	N/A
Cyanobacteria					
Intercept (BSAP_Coral Mortality)	GLM	0.12	0.10	0.13	**<0.0001*** **
Reef State: Regime Shift	GLM	0.039	0.017	0.062	**0.002** **
MEC	GLM	-0.013	-0.038	0.013	0.35
MEG	GLM	0.0055	-0.019	0.030	0.66
MEP	GLM	0.019	0.00051	0.038	0.054.
MNWC	GLM	0.015	-0.0023	0.033	0.10.
MNWG	GLM	0.020	0.0029	0.039	**0.03* **
MWC	GLM	0.037	0.018	0.056	**0.0006*** **
MWG	GLM	0.031	0.0097	0.053	**0.009** **
PNEC	GLM	0.017	-0.022	0.060	0.42
PSWG	GLM	0.033	0.015	0.052	**0.0014** **
SAG	GLM	0.026	-0.0046	0.061	0.12
SAP	GLM	N/A	N/A	N/A	N/A

Green Macroalgae					
Intercept (BSAP_Coral Mortality)	GLM	0.17	0.16	0.17	**<0.0001*** **
Reef State: Regime Shift	GLM	0.030	0.023	0.036	**<0.0001*** **
CNEG	GLM	-0.029	-0.035	-0.023	**<0.0001*** **
CSWC	GLM	-0.014	-0.021	-0.0078	**<0.0001*** **
MEC	GLM	-0.021	-0.027	-0.015	**<0.0001*** **
PNEC	GLM	-0.010	-0.017	-0.0037	**0.004** **
PNEG	GLM	0.013	0.0072	0.020	**0.0001*** **
PSWC	GLM	0.15	0.0067	0.023	**0.0009*** **
PSWG	GLM	0.020	0.013	0.026	**<0.0001*** **
PSWP	GLM	0.026	0.019	0.033	**<0.0001*** **
SAC	GLM	-0.014	-0.021	-0.0077	**<0.0001*** **
SAG	GLM	N/A	N/A	N/A	N/A
Soft Coral	GLM				
Intercept (MEC_Coral Mortality)	GLM	0.12	0.11	0.13	**<0.0001*** **
Reef State: Regime Shift	GLM	0.016	-0.004	0.038	0.14
MEP	GLM	0.026	0.012	0.041	**0.001** **
MNWC	GLM	0.012	0.00097	0.024	**0.042* **
MNWP	GLM	0.10	0.084	0.12	**<0.0001*** **
MWC	GLM	0.0060	-0.0052	0.017	0.31
MWG	GLM	0.015	0.0035	0.027	**0.017* **
MWP	GLM	0.0058	-0.0054	0.017	0.32
PNEG	GLM	-0.0039	-0.015	0.0068	0.48
PSWG	GLM	N/A	N/A	N/A	N/A
Sediment					
Intercept (BSAP_Coral Mortality)	LM	9.4	8.7	10.2	**<0.0001*** **
Reef State: Regime Shift	LM	1.4	0.35	2.5	**0.010* **
CNEG	LM	0.076	-0.99	1.1	0.89
CSWC	LM	0.90	-0.17	2.0	0.10
MEC	LM	-1.3	-2.3	-0.18	**0.022* **
MEG	LM	-1.1	-2.3	0.15	0.085.
MEP	LM	-1.0	-2.1	0.051	0.062.
MNWC	LM	-1.1	-2.1	0.0018	0.050.
MNWG	LM	0.52	-0.55	1.6	0.34
MNWP	LM	-0.95	-2.0	0.12	0.081.
MWC	LM	-1.2	-2.3	-0.13	**0.029* **
MWG	LM	1.2	0.021	2.3	**0.046* **
MWP	LM	1.5	0.43	2.6	**0.0064** **
PNEC	LM	-2.6	-3.7	-1.5	**<0.0001*** **
PNEG	LM	1.2	0.09	2.2	**0.034* **
PNEP	LM	-0.12	-1.2	0.95	0.83

PSWC	LM	-1.2	-2.2	-0.080	**0.035***
PSWG	LM	1.3	0.25	2.4	**0.012***
PSWP	LM	-3.7	-4.8	-2.6	**<0.0001*** **
SAC	LM	-2.1	-3.2	-1.0	**0.0002*** **
SAG	LM	0.95	-0.12	2.0	0.082.
SAP	LM	N/A	N/A	N/A	N/A
Sponge					
Intercept (CNEG_Coral Mortality)	GLM	0.13	0.12	0.14	**<0.0001*** **
Reef State: Regime Shift	GLM	0.0013	-0.016	0.019	0.89
CSWC	GLM	0.0026	0.0062	0.046	**0.013***
MEG	GLM	-0.0034	-0.029	0.023	0.80
MEP	GLM	0.0043	-0.010	0.020	0.56
MNWG	GLM	-0.0024	-0.016	0.011	0.72
MWC	GLM	0.0098	-0.0041	0.024	0.17
MWG	GLM	0.01	-0.0038	0.024	0.16
MWP	GLM	0.0011	-0.012	0.015	0.87
PNEC	GLM	0.0067	-0.012	0.025	0.47
PNEG	GLM	0.0064	-0.0073	0.020	0.37
PSWC	GLM	0.0097	-0.017	0.038	0.49
PSWG	GLM	0.0062	-0.0075	0.020	0.38
PSWP	GLM	0.0017	-0.017	0.020	0.86
SAG	GLM	-0.0036	-0.017	0.0095	0.59
SAP	GLM	N/A	N/A	N/A	N/A
Turf Algae					
Intercept (BSAP_Coral Mortality)	GLM	0.13	0.12	0.15	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.029	-0.052	-0.0044	**0.020***
CNEG	GLM	0.0066	-0.017	0.028	0.57
CSWC	GLM	0.041	0.016	0.065	**0.001** **
MEC	GLM	0.026	0.0012	0.048	**0.036***
MNWC	GLM	-0.0044	-0.021	0.012	0.60
MNWG	GLM	0.0055	-0.011	0.022	0.53
MNWP	GLM	0.0037	-0.014	0.022	0.69
MWC	GLM	0.018	-0.0027	0.039	0.10
MWG	GLM	0.0015	-0.015	0.018	0.86
PNEC	GLM	0.30	0.26	0.34	<0.0001***
PNEG	GLM	-0.0064	-0.023	0.0098	0.44
PNEP	GLM	-0.00036	-0.017	0.016	0.97
PSWC	GLM	0.054	0.018	0.093	**0.006** **
PSWG	GLM	-0.0043	-0.021	0.012	0.61
PSWP	GLM	0.093	0.062	0.12	**<0.0001*** **
SAC	GLM	0.028	0.0029	0.05	**0.026***

SAG	GLM	0.019	-0.0050	0.043	0.14
SAP	GLM	N/A	N/A	N/A	N/A
Zoanthids					
Intercept (BSAP_Coral Mortality)	GLM	0.12	0.11	0.12	**<0.0001*** **
Reef State: Regime Shift	GLM	0.017	0.012	0.022	**<0.0001*** **
CNEG	GLM	0.017	-0.024	-0.014	**<0.0001*** **
MEG	GLM	-0.019	-0.031	-0.16	**<0.0001*** **
MEP	GLM	-0.024	0.0069	0.020	**<0.0001*** **
MNWC	GLM	0.013	-0.011	-0.0018	**0.0001*** **
MNWG	GLM	-0.011	-0.016	-0.0071	**0.008** **
MNWP	GLM	-0.018	-0.022	-0.014	**<0.0001*** **
MWC	GLM	-0.013	-0.018	-0.0091	**<0.0001*** **
MWG	GLM	-0.012	-0.017	-0.0082	**<0.0001*** **
MWP	GLM	-0.022	-0.026	-0.018	**<0.0001*** **
PNEC	GLM	-0.011	-0.016	-0.0058	**<0.0001*** **
PNEG	GLM	-0.0044	-0.0088	-0.000024	0.056.
PNEP	GLM	-0.0014	-0.0058	0.0031	0.55
PSWC	GLM	-0.0037	-0.0087	0.0014	0.16
PSWG	GLM	-0.0039	-0.0083	0.00053	0.089.
PSWP	GLM	-0.025	-0.030	-0.020	**<0.0001*** **
SAC	GLM	-0.033	-0.038	-0.028	**<0.0001*** **
SAG	GLM	-0.0043	-0.0090	0.00031	0.072.
SAP	GLM	N/A	N/A	N/A	N/A
		$\delta^{13}C$			
Brown Macroalgae	GLM				
Intercept (BSAP_Coral Mortality)	GLM	-17.0	-17.9	-16.1	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.25	-1.6	1.1	0.72
CNEG	GLM	-0.42	-1.7	0.91	0.54
CSWC	GLM	1.2	-0.079	2.6	0.070.
MEC	GLM	0.44	-0.89	1.8	0.52
MEG	GLM	0.16	-1.2	1.5	0.82
MEP	GLM	0.20	-1.1	1.5	0.77
MNWP	GLM	4.1	2.8	5.4	**<0.0001*** **
PNEC	GLM	1.9	0.54	3.2	**0.008** **
PNEG	GLM	2.5	1.2	3.8	**0.0005*** **
PNEP	GLM	1.6	0.31	3.0	**0.02* **
PSWC	GLM	-0.18	-1.5	1.1	0.79
PSWG	GLM	-0.60	-2.0	0.81	0.41
PSWP	GLM	1.2	-0.17	2.5	0.093.
SAC	GLM	2.0	0.70	3.4	**0.004** **
SAG	GLM	0.36	-0.96	1.7	0.59

SAP	GLM	N/A	N/A	N/A	N/A
Cyanobacteria					
Intercept (BSAP_Coral Mortality)	GLM	-14.6	-16.5	-12.7	**<0.0001*** **
Reef State: Regime Shift	GLM	-9.3	-12.2	-6.4	**<0.0001*** **
MEC	GLM	-2.4	-3.3	2.8	0.88
MEG	GLM	0.40	-2.4	3.2	0.78
MEP	GLM	-8.8	-11.5	-6.1	**<0.0001*** **
MNWC	GLM	-2.4	-5.0	0.11	0.069.
MNWG	GLM	-7.9	-10.4	-5.3	**<0.0001*** **
MNWP	GLM	-7.2	-9.7	-4.6	**<0.0001*** **
MWC	GLM	-5.0	-7.5	-2.5	**0.0004*** **
MWG	GLM	-9.2	-12.1	-6.4	**<0.0001*** **
PNEC	GLM	3.1	-1.2	7.5	0.17
PSWG	GLM	-7.8	-10.4	-5.3	**<0.0001*** **
SAG	GLM	-8.5	-12.7	-4.3	**0.0004*** **
SAP	GLM	N/A	N/A	N/A	N/A
Green Macroalgae					
Intercept (BSAP_Coral Mortality)	GLM	-21.0	-21.4	-20.5	**<0.0001*** **
Reef State: Regime Shift	GLM	1.2	0.64	1.8	**0.0002*** **
CNEG	GLM	-2.6	-3.2	-2.0	**<0.0001*** **
CSWC	GLM	-1.1	-1.6	-0.52	**0.0005*** **
MEC	GLM	-1.4	-2.0	-0.83	**<0.0001*** **
PNEC	GLM	-2.7	-3.2	-2.1	**<0.0001*** **
PNEG	GLM	0.89	0.29	1.5	**0.006** **
PSWC	GLM	-1.8	-2.5	-1.2	**<0.0001*** **
PSWG	GLM	-0.98	-1.6	-0.39	**0.002** **
PSWP	GLM	-1.6	-2.2	-1.1	**<0.0001*** **
SAC	GLM	-2.3	-2.9	-1.8	**<0.0001*** **
SAG	GLM	N/A	N/A	N/A	N/A
Soft Coral					
Intercept (MEC_Coral Mortality)	GLM	-17.7	-18.6	16.7	**<0.0001*** **
Reef State: Regime Shift	GLM	0.93	-1.3	3.2	0.42
MEP	GLM	3.0	1.6	4.5	**0.0003*** **
MNWC	GLM	2.3	1.0	3.6	**0.001** **
MNWG	GLM	1.1	-0.19	2.4	-0.10
MNWP	GLM	1.3	0.028	2.6	0.053.
MWC	GLM	2.2	0.89	3.5	**0.002** **
MWG	GLM	0.41	-0.88	1.7	0.54
MWP	GLM	2.1	0.76	3.3	**0.004** **
PNEG	GLM	0.81	-0.48	2.1	0.23
PSWG	GLM	N/A	N/A	N/A	N/A

Sponge					
Intercept (CNEG_Coral Mortality?)	GLM	-17.2	-17.5	-16.9	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.034	-0.53	0.47	0.89
CSWC	GLM	-0.023	-0.52	0.48	0.93
MEG	GLM	0.13	-0.60	0.86	0.73
MEP	GLM	0.15	-0.22	0.53	0.43
MNWG	GLM	-0.53	-0.91	-0.15	**0.008** **
MWC	GLM	-0.12	-0.49	0.26	0.55
MWG	GLM	-0.60	-0.98	-0.22	**0.003** **
MWP	GLM	-0.44	-0.81	-0.059	**0.028* **
PNEC	GLM	0.31	-0.19	0.81	0.24
PNEG	GLM	-0.30	-0.68	0.079	0.13
PSWC	GLM	-0.42	-1.1	0.31	0.27
PSWG	GLM	-0.44	-0.82	-0.064	**0.027* **
SAG	GLM	-0.21	-0.58	0.17	0.29
SAP	GLM	N/A	N/A	N/A	N/A
Turf Algae					
Intercept (BSAP_Coral Mortality)	GLM	-14.3	-15.4	-13.2	**<0.0001*** **
Reef State: Regime Shift	GLM	-1.6	-4.3	0.97	0.22
CNEG	GLM	-1.8	-4.4	0.85	0.19
CSWC	GLM	0.74	-1.9	3.4	0.58
MEC	GLM	-0.98	-3.6	1.6	0.46
MNWC	GLM	-6.6	-8.1	-5.1	**<0.0001*** **
MNWG	GLM	-3.0	-4.5	-1.5	**0.0002*** **
MNWP	GLM	-6.4	-8.0	-4.8	**<0.0001*** **
MWC	GLM	-8.2	-10.0	-6.5	**<0.0001*** **
MWG	GLM	-10.1	-11.6	-8.6	**<0.0001*** **
PNEC	GLM	2.7	0.078	5.3	**0.048* **
PNEG	GLM	-5.1	-6.6	-3.5	**<0.0001*** **
PNEP	GLM	-4.5	-6.0	-3.0	**<0.0001*** **
PSWC	GLM	-0.60	-3.3	2.1	0.65
PSWG	GLM	-5.2	-6.7	-3.7	**<0.0001*** **
PSWP	GLM	-6.9	-9.5	-4.2	**<0.0001*** **
SAC	GLM	-2.4	-5.0	0.24	0.080.
SAG	GLM	-4.9	-6.9	-2.9	**<0.0001*** **
SAP	GLM	N/A	N/A	N/A	N/A
Zoanthids					
Intercept (BSAP_Coral Mortality)	GLM	-13.8	-14.6	13.1	**<0.0001*** **
Reef State: Regime Shift	GLM	1.1	0.14	2.2	**0.031* **
CNEG	GLM	-2.2	-3.4	-1.1	**0.0002*** **
MEG	GLM	-1.5	-3.2	0.14	0.079.

MEP	GLM	0.33	-0.97	1.6	0.62
MNWC	GLM	0.60	-0.47	1.7	0.27
MNWG	GLM	-0.12	-1.1	0.90	0.82
MNWP	GLM	0.10	-0.91	1.1	0.84
MWC	GLM	0.56	-0.45	1.6	0.29
MWG	GLM	-0.23	-1.2	0.78	0.66
MWP	GLM	0.57	-0.44	1.6	0.28
PNEC	GLM	-0.84	-1.9	0.17	0.11
PNEG	GLM	0.044	-1.6	1.7	0.96
PNEP	GLM	-0.55	-1.9	0.75	0.41
PSWC	GLM	-1.3	-2.3	-2.5	**0.018***
PSWG	GLM	-0.0030	-1.3	1.3	0.99
PSWP	GLM	-1.0	-2.0	0.0065	0.057.
SAG	GLM	-0.97	-2.0	0.039	0.066.
SAP	GLM	N/A	N/A	N/A	N/A
%N					
Brown Macroalgae					
Intercept (BSAP_Coral Mortality)	LM	1.07	0.96	1.2	**<0.0001*** **
Reef State: Regime Shift	LM	0.18	0.053	0.31	**0.040***
CNEG	LM	-0.41	-0.57	-0.25	**<0.0001*** **
CSWC	LM	-0.16	-0.32	0.0052	0.058.
MEC	LM	0.13	-0.033	0.29	0.12
MEG	LM	-0.072	-0.23	0.091	0.38
MEP	LM	0.19	0.025	0.35	**0.024***
MNWP	LM	0.053	-0.11	0.22	0.52
PNEC	LM	-0.20	-0.36	-0.034	**0.019***
PNEG	LM	0.16	-0.0028	0.32	0.054.
PNEP	LM	-0.088	-0.25	0.075	0.28
PSWC	LM	0.037	-0.13	0.20	0.65
PSWG	LM	-0.0072	-0.18	0.17	0.93
PSWP	LM	-0.26	-0.42	-0.096	**0.002** **
SAC	LM	-0.11	-0.27	0.053	0.18
SAG	LM	0.037	-0.13	0.2	0.65
SAP	LM	N/A	N/A	N/A	N/A
Cyanobacteria					
Intercept (BSAP_Coral Mortality)	GLM	0.65	0.50	0.83	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.41	-0.60	-0.24	**<0.0001*** **
MEC	GLM	-0.024	-0.12	0.07	0.62
MEG	GLM	-0.023	-0.11	0.060	0.60
MEP	GLM	-0.44	-0.62	-0.28	**<0.0001*** **
MNWC	GLM	-0.063	-0.28	0.14	0.56

MNWG	GLM	-0.32	-0.51	-0.16	**0.0007*** **
MWC	GLM	-0.22	-0.42	-0.035	**0.030***
MWG	GLM	-0.41	-0.60	-0.24	**<0.0001*** **
PNEC	GLM	-0.017	-0.14	0.13	0.80
PSWG	GLM	-0.37	-0.56	-0.21	**0.0002*** **
SAG	GLM	-0.41	-0.62	-0.20	**0.0004*** **
SAP	GLM	N/A	N/A	N/A	N/A
Green Macroalgae					
Intercept (BSAP_Coral Mortality)	GLM	0.23	0.21	0.25	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.0012	-0.028	0.026	0.93
CNEG	GLM	0.030	0.0033	0.057	**0.034***
CSWC	GLM	0.0023	-0.023	0.028	0.86
MEC	GLM	-0.026	-0.050	-0.0019	**0.041***
PNEC	GLM	0.015	-0.011	0.041	0.28
PNEG	GLM	-0.012	-0.039	0.014	0.37
PSWC	GLM	-0.026	-0.053	0.0014	0.069.
PSWG	GLM	0.029	0.0012	0.058	**0.047***
PSWP	GLM	-0.013	-0.038	0.011	0.30
SAC	GLM	0.014	-0.013	0.040	0.32
SAG	GLM	N/A	N/A	N/A	N/A
Soft Coral					
Intercept (MEC_Coral Mortality)	GLM	0.43	0.32	0.57	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.14	-0.35	0.12	0.24
MEP	GLM	0.023	-0.18	0.25	0.83
MNWC	GLM	-0.20	-0.35	-0.064	**0.0098** **
MNWP	GLM	-0.29	-0.43	-0.17	**0.0002*** **
MWC	GLM	0.0010	-0.18	-0.18	0.99
MWG	GLM	-0.16	-0.32	-0.020	**0.41***
MWP	GLM	-0.12	-0.28	0.033	0.14
PNEG	GLM	-0.12	-0.28	0.031	0.14
PSWG	GLM	N/A	N/A	N/A	N/A
Sediment					
Intercept (BSAP_Coral Mortality)	GLM	27.5	18.3	39.4	**<0.0001*** **
Reef State: Regime Shift	GLM	-5.1	-19.3	8.3	0.46
CNEG	GLM	1.3	-11.3	14.1	0.84
CSWC	GLM	1.9	-10.8	15.0	0.76
MEC	GLM	10.3	-4.4	26.4	0.19
MEG	GLM	10.4	-6.4	30.9	0.27
MEP	GLM	1.1	-14.3	16.6	0.89
MNWC	GLM	8.6	-8.48	26.8	0.34
MNWG	GLM	5.8	-10.6	23.1	0.49

MNWP	GLM	0.81	-14.5	16.3	0.92
MWC	GLM	5.1	-11.2	22.1	0.54
MWG	GLM	0.10	-15.7	16.6	0.99
MWP	GLM	0.84	-14.5	16.3	0.91
PNEC	GLM	7.2	-6.7	22.2	0.32
PNEG	GLM	-3.7	-18.1	10.2	0.61
PNEP	GLM	2.3	-13.4	18.2	0.78
PSWC	GLM	9.9	-4.7	25.8	0.20
PSWG	GLM	-23.7	-35.7	-14.3	**<0.0001*** **
PSWP	GLM	-2.6	-14.4	8.8	0.65
SAC	GLM	5.9	-7.7	20.3	0.41
SAG	GLM	-4.6	-18.9	9.0	0.51
SAP	GLM	N/A	N/A	N/A	N/A
Sponge					
Intercept (CNEG_Coral Mortality)	GLM	0.53	0.44	0.64	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.055	-0.22	0.12	0.53
CSWC	GLM	0.15	-0.044	0.34	0.13
MEG	GLM	0.41	0.058	0.86	**0.046***
MEP	GLM	0.25	0.068	0.45	**0.012***
MNWG	GLM	-0.061	-0.19	0.07	0.37
MWC	GLM	0.064	-0.08	0.21	0.40
MWG	GLM	0.029	-0.11	0.17	0.69
MWP	GLM	0.24	0.076	0.43	**0.008** **
PNEC	GLM	-0.0010	-0.18	0.16	0.99
PNEG	GLM	0.16	-0.0034	0.32	0.064.
PSWC	GLM	-0.027	-0.25	0.22	0.82
PSWG	GLM	-0.079	-0.21	0.050	0.24
PSWP	GLM	0.052	0.133	0.23	0.57
SAG	GLM	0.16	-0.018	0.33	0.056.
SAP	GLM	N/A	N/A	N/A	N/A
Turf Algae					
Intercept (BSAP_Coral Mortality)	GLM	0.64	0.41	0.96	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.058	-0.39	0.21	0.70
CSWC	GLM	0.031	-0.13	0.20	0.71
MNWC	GLM	-0.16	-0.49	0.10	0.30
MNWG	GLM	-0.0069	-0.35	0.28	0.97
MWG	GLM	-0.063	-0.42	0.24	0.71
PNEC	GLM	0.42	0.20	0.65	**0.0007*** **
PNEG	GLM	-0.059	-0.39	0.21	0.70
PNEP	GLM	-0.074	-0.27	0.36	0.64
PSWC	GLM	0.052	-0.11	0.22	0.54

PSWG	GLM	-0.053	-0.40	0.24	0.74
SAC	GLM	0.11	-0.065	0.28	0.23
SAG	GLM	1.4	0.74	2.1	**0.0003*** **
SAP	GLM	N/A	N/A	N/A	N/A
Zoanthids					
Intercept (BSAP_Coral Mortality)	GLM	0.94	0.82	1.1	**<0.0001*** **
Reef State: Regime Shift	GLM	0.22	0.021	0.42	**0.036***
CNEG	GLM	-0.30	-0.49	-0.11	**0.0037****
MEG	GLM	-0.29	-0.58	0.027	0.62
MEP	GLM	0.33	0.044	0.64	**0.034***
MNWC	GLM	0.12	-0.079	0.33	0.25
MNWG	GLM	-0.010	-0.19	0.17	0.91
MNWP	GLM	0.064	-0.12	0.25	0.50
MWC	GLM	-0.085	-0.26	0.085	0.33
MWG	GLM	-0.040	-0.21	0.13	0.66
MWP	GLM	0.025	-0.15	0.21	0.79
PNEC	GLM	0.14	-0.10	0.40	0.26
PNEG	GLM	-0.07	-0.24	0.10	0.42
PNEP	GLM	0.14	-0.050	0.33	0.15
PSWC	GLM	-0.42	-0.61	-0.24	**<0.0001*** **
PSWG	GLM	-0.11	-0.28	0.058	0.21
PSWP	GLM	-0.16	-0.38	-0.52	0.14
SAC	GLM	-0.14	-0.37	0.10	0.26
SAG	GLM	0.26	-0.43	-0.90	**0.004*** **
SAP	GLM	N/A	N/A	N/A	N/A
%C					
Brown Macroalgae					
Intercept (BSAP_Coral Mortality)	GLM	0.031	0.030	0.032	**<0.0001*** **
Reef State: Regime Shift	GLM	0.0010	-0.00060	0.0027	0.22
CNEG	GLM	-0.00012	-0.0018	0.0015	0.89
CSWC	GLM	0.00033	-0.0013	0.0020	0.70
MEC	GLM	-0.00074	-0.0024	0.00091	0.38
MEG	GLM	0.0018	0.00013	0.0036	**0.039***
MEP	GLM	0.0025	0.00080	0.0042	**0.0052*** **
MNWP	GLM	0.0011	-0.00056	0.0028	0.20
PNEC	GLM	-0.00038	-0.0020	0.0013	0.65
PNEG	GLM	0.0012	-0.00042	0.0029	0.15
PNEP	GLM	0.00041	-0.0012	0.0020	0.62
PSWC	GLM	0.00019	-0.0015	0.0019	0.82
PSWG	GLM	0.0022	0.00044	0.0040	**0.017***
PSWP	GLM	0.00087	-0.00082	0.0026	0.32

SAC	GLM	-0.00075	-0.0024	0.00090	0.38
SAG	GLM	0.0022	0.00051	0.0039	**0.013***
SAP	GLM	N/A	N/A	N/A	N/A
Cyanobacteria					
Intercept (BSAP_Coral Mortality)	GLM	0.053	0.047	0.059	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.024	-0.031	-0.017	**<0.0001*** **
MEC	GLM	-0.00033	-0.0055	0.0049	0.90
MEG	GLM	0.0042	-0.00078	0.0091	0.10
MEP	GLM	-0.023	-0.030	-0.017	**<0.0001*** **
MNWC	GLM	-0.0071	-0.015	0.00015	0.065.
MNWG	GLM	-0.021	-0.027	-0.014	**<0.0001*** **
MNWP	GLM	-0.017	-0.024	-0.011	**<0.0001*** **
MWC	GLM	-0.011	-0.019	-0.0045	**0.0030** **
MWG	GLM	-0.020	-0.027	-0.013	**<0.0001*** **
PNEC	GLM	0.00027	-0.0069	0.0080	0.94
PSWG	GLM	-0.020	-0.027	-0.013	**<0.0001*** **
SAG	GLM	-0.022	-0.031	-0.013	**<0.0001*** **
SAP	GLM	N/A	N/A	N/A	N/A
Green Macroalgae					
Intercept (BSAP_Coral Mortality)	GLM	0.024	0.023	0.025	**<0.0001*** **
Reef State: Regime Shift	GLM	0.00045	-0.0017	0.00082	0.49
CNEG	GLM	0.00073	-0.0019	0.00043	0.23
CSWC	GLM	0.0010	-0.0021	0.00016	0.098.
MEC	GLM	0.0019	0.0006	0.0031	**0.005** **
PNEC	GLM	0.0010	-0.0023	0.00021	0.11
PNEG	GLM	0.00095	-0.0022	0.00030	0.14
PSWC	GLM	0.000086	-0.0013	0.0015	0.90
PSWG	GLM	0.00043	-0.00084	0.0017	0.50
PSWP	GLM	0.00068	-0.0018	0.00048	0.26
SAC	GLM	0.0023	0.0011	0.0038	**0.0006*** **
SAG	GLM	N.A	N/A	N/A	N/A
Soft Coral					
Intercept (MEC_Coral Mortality)	GLM	51.5	49.8	53.1	**<0.0001*** **
Reef State: Regime Shift	GLM	2.5	-1.6	6.6	0.25
MEP	GLM	-0.13	-2.9	2.6	0.93
MNWC	GLM	1.6	-0.81	3.9	0.20
MNWG	GLM	-0.87	-3.2	1.5	0.48
MNWP	GLM	2.1	-0.21	4.5	0.084.
MWC	GLM	2.2	-0.21	4.5	0.084.
MWG	GLM	0.75	-1.6	3.1	0.54
MWP	GLM	0.43	-1.9	2.8	0.72

PNEG	GLM	0.56	-1.8	2.9	0.65
PSWG	GLM	N/A	N/A	N/A	N/A
Sponge					
Intercept (CNEG_Coral Mortality)	GLM	0.096	0.092	0.10	**<0.0001*** **
Reef State: Regime Shift	GLM	0.0011	-0.0066	0.0090	0.79
CSWC	GLM	-0.00032	-0.0082	0.0074	0.94
MEG	GLM	-0.0039	-0.015	0.0074	0.50
MEP	GLM	0.0032	-0.0028	0.0091	0.30
MNWG	GLM	0.011	0.0050	0.017	**0.00096*** **
MWC	GLM	0.0032	-0.0027	0.0092	0.29
MWG	GLM	0.0043	-0.0017	0.010	0.17
MWP	GLM	0.0016	-0.0043	0.0075	0.60
PNEC	GLM	0.0028	-0.0052	0.011	0.49
PNEG	GLM	0.0038	-0.0021	0.0098	0.21
PSWC	GLM	0.0083	-0.0036	0.021	0.19
PSWG	GLM	-0.0020	-0.0078	0.0038	0.51
SAG	GLM	0.0086	0.0025	0.015	**0.0084** **
SAP	GLM	N/A	N/A	N/A	N/A
Turf Algae					
Intercept (BSAP_Coral Mortality)	GLM	0.024	0.023	0.024	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.0013	-0.0026	0.00012	0.075.
CNEG	GLM	0.0017	0.00029	0.0031	**0.020* **
CSWC	GLM	0.00049	-0.00089	0.0018	0.49
MEC	GLM	0.00037	-0.0010	0.0071	0.60
MNWC	GLM	-0.0010	-0.0018	-0.000021	**0.016* **
MNWG	GLM	-0.0012	-0.0020	-0.00042	**0.004** **
MNWP	GLM	0.0029	0.0020	0.0039	**<0.0001*** **
MWC	GLM	0.00025	-0.00071	0.0012	0.61
MWG	GLM	0.000068	-0.00076	0.00089	0.87
PNEC	GLM	0.00067	-0.000070	0.0020	0.34
PNEG	GLM	-0.00026	-0.0011	0.00056	0.54
PNEP	GLM	0.00067	0.0016	-0.000030	**0.047* **
PSWC	GLM	-0.00084	-0.0011	0.0017	0.67
PSWG	GLM	-0.00078	-0.0016	0.000024	0.062.
SAC	GLM	0.0012	-0.00020	0.0025	0.094.
SAG	GLM	0.0033	0.0021	0.0044	**<0.0001*** **
		N/A	N/A	N/A	N/A
Zoanthids					
Intercept (BSAP_Coral Mortality)	GLM	0.038	0.026	0.053	**<0.0001*** **
Reef State: Regime Shift	GLM	0.056	0.026	0.091	**0.001** **
CNEG	GLM	0.040	-0.018	0.11	0.21

MEG	GLM	-0.071	-0.11	-0.038	**0.0001*** **
MEP	GLM	0.0052	-0.018	0.033	0.69
MNWC	GLM	0.14	0.081	0.21	**<0.0001*** **
MNWG	GLM	0.10	0.059	0.15	**<0.0001*** **
MNWP	GLM	0.11	0.063	0.16	**<0.0001*** **
MWC	GLM	0.0076	-0.012	0.027	0.44
MWG	GLM	0.025	0.0022	0.050	**0.042* **
MWP	GLM	0.0048	-0.014	0.024	0.62
PNEC	GLM	-0.055	-0.089	-0.024	**0.002** **
PNEG	GLM	0.11	0.026	0.23	**0.047* **
PNEP	GLM	-0.010	-0.029	0.0097	0.30
PSWC	GLM	-0.060	-0.10	-0.034	**0.0003*** **
PSWG	GLM	0.060	0.017	0.12	**0.023* **
PSWP	GLM	-0.040	-0.077	-0.0067	**0.027* **
SAG	GLM	0.036	0.011	0.064	**0.010* **
SAP	GLM	N/A	N/A	N/A	N/A
C:N Ratio					
Brown Macroalgae					
Intercept (BSAP_Coral Mortality)	GLM	0.033	0.030	0.036	**<0.0001*** **
Reef State: Regime Shift	GLM	0.0052	0.00049	0.0099	**0.035* **
CENG	GLM	-0.0134	-0.018	-0.0092	**<0.0001*** **
CSWC	GLM	-0.0046	-0.0093	0.00013	0.062.
MEC	GLM	0.0029	-0.0023	0.0081	0.28
MEG	GLM	-0.00027	-0.0053	0.0047	0.92
MEP	GLM	0.0088	0.0039	0.014	**0.0009*** **
MNWP	GLM	0.0028	-0.0017	0.0073	0.23
PNEC	GLM	-0.0072	-0.012	-0.0026	**0.003** **
PNEG	GLM	0.0063	0.0016	0.011	**0.012* **
PNEP	GLM	-0.0031	_-0.0073	0.0010	0.14
PSWC	GLM	0.0013	-0.0038	0.0064	0.61
PSWG	GLM	0.0017	-0.0030	0.0065	0.47
PSWP	GLM	-0.0073	-0.012	-0.0028	**0.002** **
SAC	GLM	-0.0043	-0.0090	0.00047	0.083.
SAG	GLM	0.0034	-0.0012	0.0079	0.15
SAP	GLM	N/A	N/A	N/A	N/A
Cyanobacteria					
Intercept (BSAP_Coral Mortality)	GLM	0.12	0.099	0.14	**<0.0001*** **
Reef State: Regime Shift	GLM	0.027	-0.0033	0.057	0.087.
MEC	GLM	-0.016	-0.047	0.016	0.34
MEG	GLM	N/A	N/A	N/A	N/A
MEP	GLM	0.016	-0.015	0.046	0.32

MNWC	GLM	-0.019	-0.046	0.0065	0.16
MNWG	GLM	-0.020	-0.046	0.0057	0.15
MWC	GLM	-0.029	-0.055	-0.0046	**0.031***
MWG	GLM	0.0094	-0.021	0.039	0.54
PNEC	GLM	0.010	-0.033	0.060	0.66
PSWG	GLM	-0.0014	0.031	0.027	0.92
SAP	GLM	-0.048	-0.073	-0.024	**0.0006*** **
Green Macroalgae					
Intercept (BSAP_Coral Mortality)	GLM	0.10	0.096	0.11	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.0015	-0.012	0.0093	0.78
CNEG	GLM	-0.016	-0.025	-0.0063	**0.002** **
CSWC	GLM	-0.0052	-0.015	0.0047	0.31
MEC	GLM	0.022	0.11	0.033	**0.0004*** **
PNEC	GLM	-0.012	-0.022	-0.0015	**0.031***
PNEG	GLM	0.00082	-0.010	0.012	0.88
PSWC	GLM	0.014	0.0010	0.026	**0.042***
PSWG	GLM	-0.010	-0.021	-0.00012	0.056.
PSWP	GLM	0.00067	-0.0095	0.011	0.90
SAC	GLM	0.0034	-0.0069	0.014	0.52
SAG	GLM	N/A	N/A	N/A	N/A
Soft Coral					
Intercept (MEC_Coral Mortality)	GLM	0.018	0.16	0.20	<**0.0001*** **
Reef State: Regime Shift	GLM	-0.00021	-0.053	0.060	0.99
MEP	GLM	0.021	-0.018	0.062	0.32
MNWC	GLM	0.0088	-0.024	0.042	0.61
MNWG	GLM	0.027	-0.0074	0.063	0.13
MNWP	GLM	-0.0046	-0.037	0.027	0.78
MWC	GLM	-0.027	-0.057	0.0031	0.090.
MWG	GLM	0.021	-0.014	0.055	0.25
MWP	GLM	0.016	-0.018	0.050	0.37
PNEG	GLM	0.00012	-0.032	0.033	0.99
PSWG	GLM	N/A	N/A	N/A	N/A
Sponge					
Intercept (CNEG_Coral Mortality)	GLM	1.2	1.0	1.3	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.041	-0.31	0.24	0.77
CSWC	GLM	0.030	-0.25	0.30	0.83
MEG	GLM	-0.041	-0.42	0.37	0.84
MEP	GLM	-0.026	-0.24	0.19	0.81
MNWG	GLM	0.022	-0.19	0.24	0.84
MWC	GLM	0.011	-0.20	0.23	0.92
MWG	GLM	-0.030	-0.24	0.18	0.78

MWP	GLM	-0.024	-0.24	0.19	0.83
PNEC	GLM	0.23	-0.09	0.51	0.13
PNEG	GLM	0.0041	-0.27	0.30	0.98
PSWC	GLM	0.12	-0.29	0.57	0.59
PSWG	GLM	-0.054	-0.26	0.15	0.61
SAG	GLM	-0.011	-0.22	0.20	0.92
SAP	GLM	N/A	N/A	N/A	N/A
Turf Algae					
Intercept (BSAP_Coral Mortality)	GLM	0.068	0.059	0.078	**<0.0001*** **
Reef State: Regime Shift	GLM	0.11	0.062	0.18	**0.0002*** **
CNEG	GLM	-0.060	-0.12	-0.0068	**0.048***
CSWC	GLM	-0.97	-0.16	-0.045	**0.0014** **
MEC	GLM	-0.78	-0.14	-0.026	**0.0098** **
MNWC	GLM	0.056	0.037	0.077	**<0.0001*** **
MNWG	GLM	0.053	0.034	0.072	**<0.0001*** **
MNWP	GLM	0.057	0.037	0.079	**<0.0001*** **
MWC	GLM	0.044	0.023	0.067	**0.0002*** **
MWG	GLM	0.039	0.021	0.056	**<0.0001*** **
PNEC	GLM	-0.084	-0.15	-0.031	**0.0059** **
PNEG	GLM	0.064	0.044	0.085	**<0.0001*** **
PNEP	GLM	0.068	0.046	0.092	**<0.0001*** **
PSWC	GLM	-0.13	-0.20	-0.084	**<0.0001*** **
PSWG	GLM	0.049	0.030	0.070	**<0.0001*** **
PSWP	GLM	-0.030	-0.095	0.026	0.33
SAC	GLM	-0.057	-0.12	-0.0039	0.059.
SAG	GLM	0.067	0.038	0.099	**<0.0001*** **
SAP	GLM	N/A	N/A	N/A	N/A
Zoanthids					
Intercept (BSAP_Coral Mortality)	GLM	0.25	0.19	0.32	**<0.0001*** **
Reef State: Regime Shift	GLM	-0.011	-0.095	0.071	0.80
CNEG	GLM	0.014	-0.074	0.11	0.76
MEG	GLM	0.0069	-0.11	0.16	0.92
MEP	GLM	-0.00023	-0.10	0.11	0.99
MNWC	GLM	-0.17	-0.24	-0.11	**<0.0001*** **
MNWG	GLM	-0.17	-0.24	-0.11	**<0.0001*** **
MNWP	GLM	-0.17	-0.24	-0.11	**<0.0001*** **
MWC	GLM	-0.072	-0.15	0.00014	0.065.
MWG	GLM	-0.050	-0.14	0.048	0.30
MWP	GLM	0.21	0.093	0.33	**0.0014** **
PNEC	GLM	0.012	-0.070	0.096	0.78
PNEG	GLM	-0.033	-0.15	0.11	0.61

PNEP	GLM	-0.0067	-0.11	0.11	0.90
PSWC	GLM	-0.0044	-0.084	0.077	0.91
PSWG	GLM	-0.13	-0.21	-0.059	**0.0012****
PSWP	GLM	-0.0077	-0.086	0.073	0.85
SAG	GLM	-0.095	-0.17	-0.026	**0.012***
SAP	GLM	N/A	N/A	N/A	N/A

Supp. Table 3. Model (2) for the CoV of each nutrient measurement in each bioindicator across all sites: CoV ~ Bioindicator + Reef State + Site. Model type selected for each individual model based on normality of distribution. Sediment (SED) values were not available and so were not included for C-based signatures. Significance is noted as: '***' p < 0.001; '**' p < 0.01; '*' p < 0.05; and '.' p < 0.1.

Bioindicator	Model Type	Estimate	Lower C.I. (%)	Upper C.I. (%)	p-value
		$\Delta^{15}N$			
Intercept (BM_BSAP_Coral Mortality)	GLM	0.26	0.17	0.37	**<0.0001*** **
CYB	GLM	-0.083	-0.16	-0.012	**0.027***
GM	GLM	0.17	0.042	0.33	**0.019***
SC	GLM	-0.059	-0.14	0.028	**0.17**
SED	GLM	-0.086	-0.15	-0.027	**0.008****
SP	GLM	-0.071	-0.14	-0.0011	0.053.
TA	GLM	-0.099	-0.17	-0.038	**0.003****
ZO	GLM	0.11	0.0077	0.21	**0.042***
Reef State: Regime Shift	GLM	-0.056	-0.18	0.066	0.36
CNEG	GLM	0.048	-0.077	0.18	0.45
CSWC	GLM	-0.045	-0.15	0.042	0.35
MEC	GLM	0.15	-0.0048	0.34	0.079.
MEG	GLM	-0.064	-0.17	0.018	0.16
MEP	GLM	-0.082	-0.19	0.015	0.12
MNWC	GLM	-0.051	-0.17	0.058	0.37
MNWG	GLM	-0.0048	-0.13	0.12	0.94
MNWP	GLM	-0.069	-0.18	0.037	0.21
MWC	GLM	-0.053	-0.17	0.048	0.32
MWG	GLM	0.16	-0.0079	0.36	0.083.
MWP	GLM	-0.047	-0.17	0.079	0.45
PNEC	GLM	-0.034	-0.14	0.057	0.49
PNEG	GLM	-0.051	-0.17	0.054	0.36
PNEP	GLM	-0.050	-0.17	0.074	0.42
PSWC	GLM	0.12	-0.056	0.34	0.24
PSWG	GLM	-0.0037	-0.13	0.11	0.95
PSWP	GLM	0.024	-0.095	0.14	0.68
SAC	GLM	0.017	-0.10	0.14	0.78
SAG	GLM	-0.019	-0.14	0.11	0.76
SAP	GLM	N/A	N/A	N/A	N/A
		$\Delta^{13}C$			
Intercept (BM_BSAP_Coral Mortality)	LM	-6.5	-10.0	-3.0	**0.0004*****
CYB	LM	-0.93	-3.8	1.9	0.52
GM	LM	4.2	1.4	7.0	**0.004****
SC	LM	0.61	-2.6	3.8	0.70
SP	LM	4.9	2.1	7.7	**0.0008*****
TA	LM	1.4	-1.1	3.9	0.26
ZO	LM	1.2	-1.4	3.7	0.37
Reef State: Regime Shift	LM	0.72	-4.0	5.4	0.76
CNEG	LM	-2.1	-6.8	2.5	0.36
CSWC	LM	-0.21	-5.2	4.7	0.93
MEC	LM	1.8	-3.1	6.7	0.46
MEG	LM	2.9	-3.2	8.9	0.35
MEP	LM	-0.48	-4.9	3.9	0.83
MNWC	LM	-3.3	-8.0	1.4	0.16
MNWG	LM	-1.1	-5.5	3.3	0.62
MNWP	LM	1.2	-3.2	5.6	0.58
MWC	LM	-1.0	5.4	3.4	0.64

MWG	LM	1.3	-3.1	5.7	0.56
MWP	LM	-0.61	-5.8	4.5	0.81
PNEC	LM	-0.73	-3.2	3.9	0.75
PNEG	LM	-0.41	-4.8	4.0	0.85
PNEP	LM	-.17	-6.8	3.4	0.50
PSWC	LM	-1.3	-6.2	3.6	0.59
PSWG	LM	1.6	-2.5	5.6	0.44
PSWP	LM	0.62	-4.3	5.5	0.80
SAC	LM	-3.6	-8.9	1.7	0.18
SAG	LM	3.3	-1.1	7.7	0.14
SAP	LM	N/A	N/A	N/A	N/A
%N					
Intercept (BM_BSAP_Coral Mortality)	GLM	14.8	-6.4	36.0	0.17
CYB	GLM	8.8	-8.8	26.4	0.33
GM	GLM	-3.7	-20.4	13.1	0.67
SC	GLM	14.6	-5.0	34.1	0.15
SED	GLM	5.2	-8.9	19.4	0.47
SP	GLM	5.0	-11.3	21.4	0.55
TA	GLM	7.2	-9.4	23.8	0.40
ZO	GLM	1.0	-13.8	15.8	0.89
Reef State: Regime Shift	GLM	-11.0	-37.7	15.8	0.42
CNEG	GLM	12.8	-12.9	38.5	0.33
CSWC	GLM	1.4	-25.6	28.2	0.92
MEC	GLM	0.050	-28.1	28.2	0.99
MEG	GLM	3.1	-27.8	34.0	0.85
MEP	GLM	0.18	-25.3	25.7	0.99
MNWC	GLM	-8.1	-35.1	18.9	0.56
MNWG	GLM	-2.0	-27.6	23.6	0.88
MNWP	GLM	-8.4	-37.0	20.2	0.57
MWC	GLM	-0.33	-27.1	26.4	0.98
MWG	GLM	7.3	-18.4	33.0	0.58
MWP	GLM	3.9	-24.7	32.5	0.79
PNEC	GLM	8.5	17.1	34.2	0.52
PNEG	GLM	-3.1	-28.1	21.8	0.81
PNEP	GLM	-1.1	-29.6	27.4	0.94
PSWC	GLM	5.8	-21.0	32.6	0.67
PSWG	GLM	16.5	-7.6	40.7	0.18
PSWP	GLM	8.2	-18.6	34.9	0.55
SAC	GLM	5.9	-20.9	32.7	0.67
SAG	GLM	-7.9	-33.7	17.8	0.55
SAP	GLM	N/A	N/A	N/A	N/A
%C					
Intercept (BM_BSAP_Coral Mortality)	GLM	0.34	0.053	0.84	0.075
CYB	GLM	-0.13	-0.22	-0.047	**0.004****
GM	GLM	0.023	-0.10	0.16	0.72
SC	GLM	0.081	-0.059	0.24	0.29
SP	GLM	-0.017	-0.12	0.093	0.76
TA	GLM	0.21	0.060	0.37	**0.011***
ZO	GLM	-0.19	-0.27	-0.12	**<0.0001*****
Reef State: Regime Shift	GLM	-0.046	-0.53	0.22	0.80
CNEG	GLM	-0.083	-0.22	0.0058	0.13
CSWC	GLM	0.038	-0.19	0.32	0.77
MEC	GLM	0.065	-0.14	0.33	0.58
MEG	GLM	0.055	-0.16	0.37	0.67
MEP	GLM	-0.13	-0.63	0.15	0.48
MNWC	GLM	-0.11	-0.61	0.18	0.56
MNWG	GLM	-0.12	-0.61	0.18	0.57
MNWP	GLM	-0.13	-0.62	0.17	0.54

MWC	GLM	-0.13	-0.63	0.15	0.48
MWG	GLM	-0.12	-0.62	0.17	0.54
MWP	GLM	-0.088	-0.59	0.21	0.65
PNEC	GLM	-0.091	-0.22	-0.0019	0.097.
PNEG	GLM	-0.065	-0.58	0.28	0.75
PNEP	GLM	-0.11	-0.61	0.18	0.56
PSWC	GLM	-0.080	-0.21	0.011	0.15
PSWG	GLM	-0.096	-0.59	0.20	0.62
PSWP	GLM	-0.097	-0.23	-0.018	0.072.
SAC	GLM	-0.091	-0.29	0.15	0.39
SAG	GLM	-0.075	-0.58	0.23	0.70
SAP	GLM	-0.13	-0.63	0.16	0.49
C:N Ratio					
Intercept (BM_BSAP_Coral Mortality)	GLM	2.6	-20.0	25.2	0.82
CYB	GLM	1.9	-9.7	13.5	0.75
GM	GLM	-4.9	-15.5	5.8	0.37
SC	GLM	0.14	-11.9	12.2	0.98
SP	GLM	-5.9	-16.6	4.7	0.28
TA	GLM	-0.87	-10.2	8.5	0.86
ZO	GLM	9.2	-0.46	18.9	0.066.
Reef State: Regime Shift	GLM	0.65	-21.2	22.5	0.95
CNEG	GLM	13.2	-5.2	31.6	0.17
CSWC	GLM	5.6	-13.9	25.0	0.58
MEC	GLM	4.1	-15.3	23.5	0.68
MEG	GLM	8.6	-15.0	32.2	0.48
MEP	GLM	1.6	-22.0	26.1	0.90
MNWC	GLM	4.0	-21.1	29.2	0.75
MNWG	GLM	5.2	-19.3	29.7	0.68
MNWP	GLM	1.2	-24.4	26.7	0.93
MWC	GLM	18.0	-6.6	42.5	0.16
MWG	GLM	17.8	-6.77	42.3	0.16
MWP	GLM	8.0	-18.9	34.9	0.56
PNEC	GLM	14.7	-3.0	32.5	0.11
PNEG	GLM	9.9	-14.7	34.5	0.43
PNEP	GLM	4.0	-22.7	30.7	0.77
PSWC	GLM	3.1	-16.2	22.4	0.75
PSWG	GLM	14.4	-9.1	37.9	0.23
PSWP	GLM	1.7	-17.6	21.0	0.86
SAC	GLM	8.6	-12.3	29.5	0.42
SAG	GLM	8.5	16.1	33.1	0.50
SAP	GLM	12.0	-12.5	36.4	0.34

Supp. Table 4. Generalised Linear Model (3) for the cost-effectiveness analyses to determine the effect of Bioindicator, Task, Reef State and the interaction between them on the time per unit sample (per hour): Time ~ Bioindicator * Task * Reef State. Normality inspected using visual plots. Significance is noted as: '***' p < 0.001; '**' p < 0.01; '*' p < 0.05; and ',' p < 0.1.

	Intercept	Lower C.I. (2.5%)	Upper C.I. (97.5%)	p-value
BM (Intercept)	-1.33	-1.89	-0.767	**<0.0001*** **
CYB	0.0109	-0.498	0.520	0.966
GM	0.00803	-0.689	0.704	0.982
SC	1.50	0.831	2.16	**<0.0001*** **
SED	-1.37	-1.85	-0.891	**<0.0001*** **
SP	1.49	0.838	2.15	**<0.0001*** **
TA	1.45	0.864	2.13	**<0.0001*** **
ZO	1.49	1.01	1.97	**<0.0001*** **
DRY-CRUSH	26.0	25.3	26.7	**<0.0001*** **
FIELD	1.40	0.719	2.08	**<0.0001*** **
SIA	1.51	0.830	2.19	**<0.0001*** **
WEIGH	2.84	2.43	3.25	**<0.0001*** **
REEF STATE- REGIME SHIFT	0.00376	-0.873	0.881	0.993
CYB-DRY	-1.91	-2.63	-1.19	**<0.0001*** **
GM-DRY	-0.562	-1.55	0.424	0.264
SC-DRY	-3.94	-4.79	-3.094	**<0.0001*** **
SED-DRY	-0.681	-1.36	-0.00183	**0.0500* **
SP-DRY	-3.83	-4.66	-3.00	**<0.0001*** **
TA-DRY	-1.48	-2.27	-0.684	**0.000293*** **
ZO-DRY	-3.10	-3.78	-2.42	**<0.0001*** **
CYB-FIELD	0.237	-0.483	0.957	0.519
GM-FIELD	0.0864	-0.899	1.072	0.864
SC-FIELD	-1.42	-2.27	-0.573	**0.00109** **
SED-FIELD	1.32	0.636	2.00	**0.000166*** **
SP-FIELD	-1.46	-2.29	-0.629	**<0.000620*** **
TA-FIELD	-1.55	-2.34	-0.753	**<0.000152*** **
ZO-FIELD	-1.45	-2.13	-0.767	**<0.0001*** **
CYB-SIA	0.0336	-0.686	0.753	0.927
GM-SIA	0.0158	-0.970	1.00	0.975
SC-SIA	-1.26	-2.12	-0.410	**0.00380** **
SED-SIA	1.40	0.720	2.08	**<0.0001*** **
SP-SIA	-1.29	-2.12	-0.459	**0.00246** **
TA-SIA	-1.43	-2.22	-0.635	**0.000461*** **
ZO-SIA	-1.25	-1.92	-0.566	**0.000361*** **
CYB-WEIGH	NA	NA	NA	NA
GM-WEIGH	NA	NA	NA	NA
SC-WEIGH	0.0198	-0.632	0.672	0.953
SED-WEIGH	NA	NA	NA	NA
SP-WEIGH	0.0476	-0.585	0.675	0.889
TA-WEIGH	0.00659	-0.576	0.590	0.982
ZO-WEIGH	NA	NA	NA	NA
CYB-REGIME	-0.00667	-0.799	0.785	0.987
GM-REGIME	-0.0157	-0.868	0.837	0.971
SC-REGIME	-0.00710	-1.39	1.38	0.992
SED-REGIME	0.0110	-0.665	0.687	0.975
SP-REGIME	-0.00376	-1.046	1.038	0.994
TA-REGIME	-0.00710	-0.991	0.976	0.989
ZO-REGIME	-0.00376	-0.721	0.713	0.992
DRY-REGIME	0.203	-0.811	1.22	0.695
FIELD-REGIME	-0.0627	-1.08	0.951	0.904
SIA-REGIME	-0.00429	-1.02	1.01	0.993
WEIGH-REGIME	<0.0001	-0.714	0.714	1.00
CYB-DRY-REGIME	1.13	0.0128	2.25	**0.0480* **
GM-DRY-REGIME	-0.194	-1.40	1.01	0.752
SC-DRY-REGIME	-0.313	-2.14	1.50	0.737
SED-DRY-REGIME	0.0877	-0.869	1.04	0.857

SP-DRY-REGIME	0.518	-0.771	1.81	0.431
TA-DRY-REGIME	-0.343	-1.54	0.850	0.573
ZO-DRY-REGIME	-0.176	-1.90	0.838	0.734
CYB-FIELD-REGIME	0.149	-0.972	1.27	0.795
GM-FIELD-REGIME	-0.0465	-1.25	1.16	0.940
SC-FIELD-REGIME	0.969	-0.854	2.79	0.298
SED-FIELD-REGIME	0.0462	-0.910	1.00	0.925
SP-FIELD-REGIME	0.443	-0.846	1.73	0.501
TA-FIELD-REGIME	0.0873	-1.11	1.28	0.886
ZO-FIELD-REGIME	0.259	-0.755	1.27	0.617
CYB-SIA-REGIME	-0.0562	-1.18	1.06	0.922
GM-SIA-REGIME	-0.0279	-1.23	1.18	0.964
SC-SIA-REGIME	0.520	-1.30	2.34	0.577
SED-SIA-REGIME	0.0742	-0.882	1.03	0.879
SP-SIA-REGIME	-0.0365	-1.33	1.25	0.956
TA-SIA-REGIME	0.233	-0.970	1.42	0.714
ZO-SIA-REGIME	0.0749	-1.09	0.939	0.885
CYB-WEIGH-REGIME	NA	NA	NA	NA
GM-WEIGH-REGIME	NA	NA	NA	NA
SC-WEIGH-REGIME	0.164	-1.51	1.84	0.848
SED-WEIGH-REGIME	NA	NA	NA	NA
SP-WEIGH-REGIME	- <0.0001	-1.07	1.07	1.00
TA-WEIGH-REGIME	0.0133	-0.939	0.965	0.978
ZO-WEIGH-REGIME	NA	NA	NA	NA