

## Nitrogen enrichment in macroalgae following mass coral mortality

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# Nitrogen enrichment in macroalgae following mass coral mortality

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## 16 Abstract

Scleractinian corals are engineers on coral reefs that provide both structural complexity as 17 habitat and sustenance for other reef-associated organisms via the release of organic and 18 inorganic matter. However, coral reefs are facing multiple pressures from climate change and 19 20 other stressors, which can result in mass coral bleaching and mortality events. Mass mortality of corals results in enhanced release of organic matter, which can cause significant alterations 21 22 to reef biochemical and recycling processes. There is little known about how long these nutrients are retained within the system, for instance within the tissues of other benthic 23 organisms. We investigated changes in nitrogen isotopic signatures ( $\delta^{15}N$ ) of macroalgal 24 tissues a) ~1 year after a bleaching event in the Seychelles and b) ~3 months after the peak of 25

26	a bleaching event in Mo'orea, French Polynesia. In the Seychelles, there was a strong
27	association between absolute loss in both total coral cover and branching coral cover and
28	absolute increase in macroalgal $\delta^{15}N$ between 2014 and 2017 (adjusted $r^2 = 0.79$ , $p = 0.004$
29	and adjusted $r^2 = 0.86$ , $p = 0.002$ , respectively). In Mo'orea, a short-term transplant
30	experiment found a significant increase in $\delta^{15}$ N in <i>Sargassum mangarevense</i> after specimens
31	were deployed on a reef with high coral mortality for $\sim 3$ weeks (p < 0.05). We suggest that
32	coral-derived nutrients can be retained within reef nutrient cycles, and that this can affect
33	other reef-associated organisms over both short- and long-term periods, especially
34	opportunistic species such as macroalgae. These species could therefore proliferate on reefs
35	that have experienced mass mortality events, because they have been provided with both
36	space and nutrient subsidies by the death and decay of corals.

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38 Key words: Climate change; macroalgal bioindicators; coral bleaching; stable isotopes;
39 biogeochemical cycles; coral reef ecology

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# 41 Introduction

Tropical coral reefs are highly productive ecosystems, but as they are typically surrounded by 42 43 oligotrophic waters, they require constant recycling and retention of water-borne nutrients and organic matter (Galloway et al., 2004). There are a wide range of physical and biological 44 45 processes on coral reefs which can retain these essential energetic resources within local 46 biogeochemical cycles for extended periods of time. Thus, these processes can sustain rapid rates of biological activity such as primary productivity, as well as many other key ecosystem 47 functions (Wyatt et al., 2013). For instance, coral-derived particulate organic matter (POM) 48 in the form of mucus can act as an energy carrier and particle trap, so these nutrients may be 49

recycled by benthic and planktonic communities over longer timescales (Ferrier-Pagès et al., 50 1998; Wild et al., 2004a,b). However, even in a coral-dominated ecosystem, they are not the 51 52 only natural, or autochthonous, source of bioavailable nutrients (Davey et al., 2008; Wyatt et al., 2013). Microbes, for instance, are capable of nitrogen fixation (Moulton et al., 2016), and 53 other primary producers, such as phytoplankton and macroalgae, readily take up and store 54 nutrients and dissolved organic matter (DOM) in their tissues (Fong et al., 1994). This DOM 55 56 is then recycled either through tissue breakdown or through consumption by higher trophic level organisms such as herbivorous fishes, which in turn recycle significant amounts of 57 58 nutrients through excretion (Burkepile et al., 2013).

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Healthy coral reefs typically persist in suboptimal nutrient concentrations, although nutrient 60 61 pulses can disrupt the balance of natural biogeochemical dynamics jeopardising reef health. Disturbances such as marine heat waves that cause coral bleaching have a direct negative 62 impact on corals, but can also have indirect consequences for reefs by altering nutrient 63 dynamics (D'Angelo & Wiedenmann, 2014). Branching scleractinian corals are often 64 dominant on a reef, providing structural complexity and micro-habitats for a variety of reef-65 associated organisms, but they are also particularly vulnerable to heat stress (Hughes et al., 66 2019). The loss of these vital foundation species therefore has huge implications for the entire 67 ecosystem (Graham et al., 2015; Wilson et al., 2019). Where coral bleaching causes extensive 68 69 mortality, the metabolic exchange between corals and associated organisms on a reef is reduced, along with the capacity of corals to trap organic matter. This can subsequently 70 trigger the dysfunction of major biogeochemical processes (Glynn, 1993; Wild et al., 2011). 71 72

There are few studies assessing how climate-derived disturbances affect mucus release by
live corals, and associated processes. Davey et al. (2008) found that in the weeks that follow

coral bleaching, a 30-fold higher production of new nitrogen occurred on coral reefs 75 compared to those that did not experience bleaching. Such nitrogen productivity has also 76 been shown in an experimental setting (Niggl et al., 2009). While release rates of mucus-77 derived POM from corals increase during the early stages of bleaching, providing a burst of 78 nutrients to coral reefs (Coffroth, 1990), these rates can decrease after the initial bleaching 79 response (Fitt et al., 2009; Wooldridge et al., 2009). If corals recover from bleaching, which 80 81 can take many weeks to occur (Gates, 1990), there may only be short- to medium-term effects on biogeochemical processes. However, if corals die, the subsequent mass release of 82 83 coral tissue into reef environments may also alter biogeochemical processes, and over longer time scales. In addition, colonisation of the exposed coral skeleton by microbial biofilms, turf 84 algae, macroalgae, sponges, cyanobacteria or other invertebrates may not only reduce coral 85 recruitment success, but can also change biogeochemical processes such as nitrogen fixation 86 (Diaz-Pulido & McCook 2002; Davey et al. 2008; Haas et al., 2010). 87

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In order to identify changes in nutrient regimes due to mass coral mortality, nitrogen stable 89 isotopes ( $\delta^{15}N$ ) and nitrogen content (%N) can be analysed from macroalgal tissues to capture 90 temporally-extensive records of nutrient loads (Costanzo et al., 2001). Stable isotopes of 91 92 nitrogen have been used in nutrient studies for several decades, helping to identify the origins of nitrogen (Heaton, 1986; Kolasinski et al., 2011). In addition, certain types of marine algae 93 are commonly used in biomonitoring studies due to their widespread distribution and 94 responsiveness to bioavailable pollutants. Sargassum, for example, is a genus used worldwide 95 as it has been found to be responsive to nutrient enrichment (Schaffelke & Klumpp, 1998; 96 97 Schaffelke, 2002; García-Seoane et al., 2018). However, marine algae are not the only functional group that can be used to measure isotopic signatures as a proxy of nutrient 98 regimes on reefs. Organisms at higher trophic levels also assimilate nutrients from lower 99

100 trophic levels, resulting in increasing isotopic enrichment up the food chain (Bierwagen et al., 2018). For instance, corals are at a higher trophic level than primary producers such as 101 macroalgae, and thus have enriched isotopic signatures (Graham et al., 2018). As corals 102 release organic matter into the water column after the death and subsequent decay of tissue 103 following marine heatwave-driven mortality events (Leggat et al., 2019), opportunistic 104 benthic species such as macroalgae may capitalise on this new nutrient source, assimilate it 105 106 into tissues for growth and storage, and consequently become more enriched (Pawlik et al., 2016). 107

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In the current study, the temporal effect of coral mass mortality on macroalgal stable isotopic 109 signatures is investigated in two different coral reef systems, over two different time periods. 110 111 As such, it offers new understanding on whether macroalgae can indicate longer-term effects of coral mortality events on reef nutrient dynamics and biogeochemical cycles. Specifically 112 this study assesses: (1) changes in Sargassum sp. nutrient signatures over three years in the 113 inner Seychelles Islands, western Indian Ocean, spanning a mass coral bleaching event, and 114 (2) shorter-term changes in Sargassum mangarevense nutrient signatures ~3 months after the 115 peak of a severe bleaching event in Mo'orea, French Polynesia, using an *in-situ* three-week 116 transplant experiment. 117

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123	Methods
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124 **Study Site 1: Seychelles** 125 126 The inner Seychelles islands experienced two severe coral bleaching events, in 1998 and 127 2016. In 1998, coral cover dropped by 90%, and though hard coral cover steadily recovered 128 on some study sites (average coral cover of 27% by 2014) (Graham et al., 2015), another 129 130 global bleaching event in 2016 (Hughes et al., 2018) led to live coral cover declining by 70% on these same sites (Wilson et al., 2019). Around the Inner Seychelles, heat stress reached 131 4°C-weeks in January 2016, rapidly increased in April and peaked at 11.4°C-weeks in May 132 (Wilson et al., 2019; http://coralreefwatch.noaa.gov/vs/index.php). 133 134 135 Eighteen reefs were surveyed in April 2014, before the mass bleaching event caused extensive coral mortality in 2016 and again in April 2017, a year after the event occurred 136 137 (Wilson et al., 2019). These reefs form part of a 25-year coral reef monitoring survey around 138 the inner Seychelles, with roughly half the reefs having been defined as "recovering" from a previous mass bleaching event in 1998, and the other half as transitioning to a "regime-139 shifted" macroalgae-dominated state (Graham et al. 2015). Eight replicate 7-m radius point 140 counts were surveyed along the reef slope on each reef for both survey years. Within each 141 142 point count area, the percent cover of benthic categories including live hard coral, soft coral, macroalgae, sand, rubble, and rock was quantified using 10m long line-intercept transects 143 144 (Wilson et al. 2019).

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The objectives of this component of the study were to assess the relationship betweenchanges in percent cover of corals between the study years of 2014 and 2017 with differences

in  $\delta^{15}$ N and %N signatures in tissues of *Sargassum* sp. that were collected from the same sites during the same surveys. Low availability of macroalgae at some reefs meant that macroalgae for stable isotope analyses were not collected from all reefs in both years. A minimum of four replicate *Sargassum* sp. samples were collected from each of the seven "coral mortality" reefs (a subset of the previously termed "recovery reefs", named as such following the impacts of the 2016 bleaching event) and from the six "regime-shifted" reefs in both 2014 and 2017.

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### 156 Study Site 2: Mo'orea

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Mo'orea, an island which is part of the Society Archipelago in French Polynesia, has 158 demonstrated rapid coral recovery from previous disturbances (Vercelloni et al., 2019; 159 Hédouin et al., 2020). For example, following an outbreak of Acanthaster spp. from 2006 to 160 2009 and a cyclone in 2010, mean coral cover on the outer reefs was reduced to 2% at 10 m 161 depth from a high of 39% in 2005, before recovering to 27% in just four years. The branching 162 coral genus *Pocillopora* spp. was found to be a significant driver in that recovery, as it made 163 up 53% of the re-established coral community (18% cover) (Tsounis & Edmunds, 2016). 164 There were no recorded episodes of abnormally high sea surface temperature (SST) in 1998 165 in Mo'orea, but it was impacted by the global coral bleaching event in 2016, with heat-166 sensitive branching corals being the worst affected (Hughes et al., 2019). Donovan et al. 167 (2020) reported that 37% of Acropora and 28% of Pocillopora colonies exhibited bleaching 168 across all sites, with up to 100% bleaching of Acropora on north shore sites. Coral mortality 169 was rare (~1%), as heat stress did not exceed 1.1°C weeks (Hédouin et al., 2020). 170 171

Annual surveys of 13 marine areas around Mo'orea were established in 2004 (Service 172 National d'Observation CORAIL). For the purpose of this study, data for the reef slope at the 173 174 four areas along the north coast of the island, where bleaching was highest and our study site was located, was used (Suppl. Fig. 1). This includes the site Tiahura which is closest to our 175 study site. The benthic cover of each sample area was quantified at a similar depth to the 176 transplant site (~10 m) using 3 replicate non-permanent 25 m transects (Horta e Costa et al., 177 178 2016). The percentage cover of benthic components was sampled every 50 cm using the Point Intercept Transect (PIT) method. Macroalgae was categorised as all the non-coralline 179 180 algae of large enough size to identify with the naked eye.

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Sea surface temperature (SST) was measured hourly using an SBE-56 sensor (Sea Bird 182 Scientific) on the Tiahura forereef at 3m depth from 1998 to 2005. The time series was 183 interrupted for 5 years before being collected continuously again from 2010. In order to 184 characterise the temperature trend in 2019, relative to that of other years, we calculated 185 weekly means for 2019 and compared this with the average temperature time series and 95% 186 confidence intervals for the entire period. In addition, following Donovan et al. (2020), we 187 calculated cumulative heat stress (in °C weeks) as a 12-wk running sum for all temperatures 188 exceeding 29 °C, a threshold that is considered a good predictor of bleaching in Mo'orea 189 based on previous studies (Pratchett et al., 2013; Donovan et al., 2020; Hédouin et al., 2020). 190 191 The maximum water temperature during 2019 exceeded 29 °C in March and peaked at  $\sim$ 30°C in April. Patterns of cumulative heat stress peaked at  $\sim$ 6 °C weeks. As the duration of 192 193 heat stress was much longer in 2019 than in the previous bleaching event (Donovan et al., 2020; Hédouin et al., 2020), the extent of coral mortality was much higher (Suppl. Fig.2). 194

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Samples of Sargassum mangarevense (n=10) were collected from Papetoai lagoon, a low-196 nutrient reef in the northwest region of Mo'orea on 6th July 2019 (Suppl. Fig.1). These 197 waters were found to typically have low  $\delta^{15}$ N and %N values, shown in nutrient heat maps in 198 Leichter et al. (2013) and Donovan et al. (2020). Specimens were placed in shaded coolers 199 filled with seawater before they were transported back to the CRIOBE research station, 200 Mo'orea. After all visible, larger epiphytes were carefully removed from the fronds using a 201 202 scalpel, initial tissue samples were taken and frozen at -20°C for later stable isotopic analyses. Algal specimens were then placed in pre-transplant holding tanks for seven days, 203 204 with water changes every two days. Water changes in the tanks involved surface water collected from the forereef, as it was found to typically be low in  $\delta^{15}N$  (< 3.0 ‰, Lin & Fong, 205 2008, Donovan et al., 2020). This was done to ensure that internal nutrient stores in S. 206 207 mangarevense were depleted before specimens were transplanted on the forereef where there were high levels of coral mortality. Following this seven-day acclimation period, further 208 tissue samples were taken for stable isotopic analyses. For the in situ macroalgal bioassay, a 209 cage was made out of chicken-wire mesh and attached to a cinder block that was already 210 placed on the forereef at ~12 m depth. At the time of the transplant experiment in July 2019, 211 while some corals were still bleached, ~40% had already died (S.J.H., 2020, pers. obs.). It 212 was not possible to have a control bioassay, due to restrictions on deploying additional cinder 213 blocks and the lack of non-bleached reefs at that time. The ten macroalgal specimens were 214 deployed on the reef for ~3 weeks from 15<sup>th</sup> July to 4<sup>th</sup> August 2019 before they were 215 collected and returned to CRIOBE. Final tissue samples were taken and frozen before stable 216 isotopic analyses were performed. 217

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#### 220 Stable Isotopic Analyses

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222 All frozen samples from both studies were individually defrosted, rinsed thoroughly with 223 fresh or distilled water, and placed in a drying oven for 48 h at 60°C. Once dried, samples were each ground into a fine powder using a ball mill and stored in individual airtight 224 containers. All dried samples were weighed, alongside the relevant standards, for stable 225 226 isotopic analyses. Samples were then run on an IsoPrime Dual Analyser to determine 227 signatures of stable isotopes and elemental content. The stable isotopic ( $\delta^{15}N$ ) and elemental analyses (%N) for both the 2017 samples from the Seychelles study and the 2019 Mo'orea 228 229 samples were run on an Isoprime100 Isotope Ratio Mass Spectrometer (IRMS) linked to an Elementar VARIO MICROcube Elemental Analyser at Lancaster Environment Centre, 230 Lancaster University. The samples collected in 2014 from the Seychelles were analysed using 231 a Costech Elemental Analyzer fitted with a zero-blank auto-sampler at James Cook 232 University's Advanced Analytical Centre, Cairns. Analyses from both years were 233 standardised using internal reference materials calibrated to international standards. 234

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#### 236 Statistical Analyses

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For the Seychelles data, four separate two-way analysis of variance (ANOVAs) were used to 238 assess the effect of time period (two levels: 2014 and 2017), reef state (two levels: coral 239 240 mortality and regime shift) and their interaction on a) total coral cover, b) branching coral cover, c),  $\delta^{15}$ N, and d) %N across all 13 reefs where *Sargassum* were consistently collected. 241 Based on this analysis and subsequent post-hoc Tukey tests, we found that predominant 242 changes in these response variables were observed on "coral mortality" reefs, with little 243 response on "regime-shifted" reefs. We therefore include the seven reefs with high levels of 244 coral mortality to investigate the relationship between changes in nutrient signatures against 245

a) absolute and b) branching coral cover loss, using linear regression models. This decision was further supported by coral cover changes on "regime-shifted" reefs, where starting absolute values in 2014 were already very low at  $6.69 \pm 1.8$  % before dropping by ~5% in 2017, and macroalgal cover was very high in both years. Therefore, any influence of coral cover on nutrient signatures in the system would be negligible (Suppl. Fig. 3; Wilson et al., 2019). 

For the Mo'orea data, differences between a) average  $\delta^{15}N$  and b) %N signatures in the *Sargassum* specimens in the three treatments (initial, pre-transplanted, and post-transplanted) from the transplant experiment were analysed using a repeated measures ANOVA. Repeated measures were incorporated into this ANOVA as tissue samples were taken from the same experimental specimens placed under the three different treatments. A time series analysis was conducted to compare the average mean monthly SST in 2019, relative to SST in previous years. Normality of data was assessed visually, and homogeneity of variance for all ANOVAs conducted for both studies was assumed with a Levene's test. All statistical analyses were conducted in R (R-Core-Team 2018), and the time series analyses for Moorea were performed using 'zoo' and 'xts' packages to produce Supplementary Figure 2 (Zeileis & Grothendieck. 2005; Ryan & Ulrich, 2020). 

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# 272 **Results**

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274 Seychelles

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There was a significant effect of year, reef state and interaction on total coral cover across the 276 thirteen reefs (interaction:  $F_{1,204} = 37.3$ , p < 0.0001). The post-hoc Tukey test revealed that 277 278 there was no significant difference between the pre- and post-bleaching years for the "regime-shifted" reefs (p = 0.32; Suppl. Fig. 2). In contrast, the seven "coral mortality" reefs 279 declined significantly from  $27.0 \pm 1.5$  to  $8.01 \pm 0.5$  % between 2014 and 2017 (p < 0.0001; 280 *Fig. 1a*). This was mainly due to a loss in branching coral cover on these reefs from  $16.0 \pm$ 281 1.5 to  $0.30 \pm 0.05$  % (p < 0.0001; Fig. 1a). Percent cover of massive corals remained similar 282 283 between 2014 and 2017 on "coral mortality" reefs, whereas table coral cover declined from 1.27% to 0%. There was also a 0.8 % increase in total macroalgal cover on the seven study 284 285 reefs between the years.

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The  $\delta^{15}$ N signature in *Sargassum* tissues differed significantly between 2014 and 2017 across 287 all thirteen reefs (interaction between year and reef state,  $F_{1,124} = 11.4$ , p = 0.001), but only 288 289 showed a significant difference for the seven "coral mortality" reefs between survey years (p < 0.0001, Fig. 1b; p = 0.15 for regime-shifted reefs). Similarly, %N in Sargassum tissues 290 was higher in samples collected from "coral morality" reefs in 2017 than in 2014 (p < 0.0001, 291 *Fig 1c*; significant interaction between year and state  $F_{1,124} = 5.0$ , p = 0.03), although there 292 was no temporal difference in N content in samples collected from "regime-shifted" reefs (p 293 294 = 0.20). For the seven "coral mortality" reefs selected for the purpose of this study, there was a significant positive relationship between increase in  $\delta^{15}$ N in *Sargassum* tissue and (a) loss 295

of total coral (adjusted  $r^2 = 0.79$ ; p = 0.004; *Fig.* 2) and (b) branching coral cover (adjusted  $r^2 = 0.86$ ; p = 0.002). There was no significant relationship between changes in %N and total coral cover ( $r^2 = 0.04$ ; p = 0.67) or branching coral cover ( $r^2 = 0.04$ ; p = 0.66).

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300 Moorea

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Before the bleaching event peaked in April 2019 (Suppl. Fig. 2), the benthic cover survey 302 conducted across the outer slopes of the four northern sites of Moorea in March 2019 showed 303 an average of  $73.7 \pm 2.8\%$  live coral cover, with a significant decline to an average of  $36.2 \pm$ 304 2.9 % in 2020, a year after the event (p < 0.0001; Mean ± SE). The closest site to the 305 transplant experiment, Tiahura, had  $73.3 \pm 5.5\%$  and  $36.0 \pm 2.0\%$  in live coral cover in 2019 306 and 2020, respectively. The high coral cover across the four sites in 2019 was primarily due 307 to the abundance of branching coral Pocillopora on the forereefs in Mo'orea (Tsounis & 308 309 Edmunds, 2016). For instance, at Tiahura, there was  $60.7 \pm 5.7\%$  cover of *Pocillopora* and an average of 55.5  $\pm$  3.3% cover across the four sites in 2019. When the survey was repeated in 310 March 2020, there was a significant decrease in *Pocillopora* to  $24.5 \pm 1.7\%$  across all four 311 sites (p < 0.0001), and a similar pattern was shown at Tiahura (p < 0.0001). Other than this 312 predominant branching coral, no significant differences were found between the years for the 313 314 other reef-associated organisms, including other coral genera.

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316 In the short-term transplant experiment shortly after the peak of the bleaching event in

317 Mo'orea, treatment had a significant effect on macroalgal  $\delta^{15}$ N signatures (repeated-measures

ANOVA:  $F_{2,27} = 31.71$ , p <0.0001; *Fig. 3*). Post hoc tests indicated that there were significant

- differences in  $\delta^{15}$ N between all three treatments (initial, pre-transplant, and post-transplant,
- n=10), which suggested that  $\delta^{15}N$  declined in the pre-transplant holding tanks, and then

321	increased substantially on the transplant reef (initial and pre-transplant: $p = 0.003$ ; initial and
322	post-transplant: $p < 0.0001$ ; pre-transplant and post-transplant: $p < 0.0001$ ). However, there
323	was no significant effect of treatment on macroalgal %N (repeated-measures ANOVA: $F_{2,23} =$
324	0.6, $p = 0.58$ ; <i>Suppl. Fig. 4</i> ). Although it was not possible to include either control sites or
325	reefs with varying levels of bleaching due to permit restrictions, the benthic data shows that
326	the extent of mortality across the outer slopes on the northern region of Mo'orea was quite
327	similar.
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# 345 **Discussion**

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The current study suggests that mass coral mortality events can be detected through nitrogen 347 isotopic signatures in macroalgal tissues, a proxy for nutrient sources, up to a year after a 348 severe bleaching event. Although the exact source of the enrichment could not be traced in 349 this study, a significant increase in  $\delta^{15}$ N was shown in both reef systems over different 350 timescales after two separate coral mortality events. For instance, in the Seychelles, there was 351 352 a strong positive correlation between a decline in total coral cover and an increase in  $\delta^{15}$ N. This suggested that the N present in algal tissues could be coral-derived. These findings may 353 help improve understanding of how mass disturbances such as coral bleaching impact 354 multiple ecosystem processes on climate-impacted reefs. For instance, the loss of live coral 355 cover, especially branching corals, provides a large amount of new substrate for opportunistic 356 357 species such as macroalgae and other primary producers to colonise and prevent coral recovery, and may also provide an additional source of nutrients which become locked in the 358 359 system. Consequently, this could enhance macroalgal proliferation on this colonised space, 360 reinforcing alternative regimes.

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The isotopic signature of fleshy macroalgae changed significantly over both short and long 362 363 timeframes following bleaching events on two different reef systems. The positive relationship between  $\delta^{15}$ N and the declines in coral cover suggest that nutrients from dead 364 and decaying corals have contributed to this change of isotopic signatures in macroalgae. 365 While this might be an important natural source of nutrients (Coffroth, 1990; Brown & 366 Bythell, 2005; Bythell & Wild, 2011), any substantial increase could affect or disrupt natural 367 metabolic exchanges between corals and other organisms, not only with their endosymbiotic 368 zooxanthellae, but with sponge, seaweed and microbial communities (de Goeij et al., 2013; 369

Rix et al., 2016, 2017; Pawlik et al., 2016; Mumby & Steneck, 2018; Leggat et al., 2019). 370 Much of the literature focuses on the mucus released from live corals and how it is recycled 371 within the system (Davey et al., 2008; Naumann et al., 2009; Wild et al., 2004a,b, 2010, 372 2011), as well as the short term effects of changes in organic matter release after a bleaching 373 event (Niggl et al., 2009; Wooldridge, 2009). Other work such as Radice et al., (2020) 374 supports this by showing that isotopic signatures of particulate organic nitrogen in the water 375 376 column decreased eight months after a bleaching event. However, there is still little understanding of changes in reef biogeochemical cycles. 377

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Excess nutrients are one of the key factors that can drive a bleached reef towards a regime 379 shift (Graham et al 2015). If the increased release of organic matter through mass coral 380 mortality provides more nutrients to opportunistic species, this may encourage fast-growing 381 macroalgae to proliferate on the exposed coral skeletons. This negative feedback loop can 382 inhibit coral recovery and foster regime shifts to macroalgal-dominated states (Diaz-Pulido & 383 McCook, 2002; Haas et al., 2010; Wild et al., 2011). For instance, the lack of available 384 substrata may reduce the ability for any coral larvae to colonise this space and repopulate 385 reefs, but increases in algal-derived DOM and POM can subsequently increase pathogenic 386 microbial activity through what has been termed the DDAM positive feedback loop 387 (dissolved organic carbon, disease, algae, microorganisms) (Haas et al., 2016). Macroalgae 388 389 release labile organic matter which benefit pathogenic microbes and together they create unfavourable conditions for corals. For example, they collectively disrupt the function of the 390 coral holobiont, thereby exacerbating death of coral recruits, and maintaining competitive 391 dominance in algae (Wild et al., 2010; Barott & Rohwer, 2012; Pawlik et al., 2016; Mumby 392 & Steneck, 2018). 393

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While mass mortality has the potential to release a substantial source of new nutrients, this 395 type of organic matter is still considered to be internal, or autochthonous (Briand et al., 396 397 2015). Excessive nutrient enrichment from external anthropogenic nutrient loads, particularly certain types of nitrogen such as nitrates found in coastal runoff, can further exacerbate 398 changes in biogeochemical cycles on reefs (Burkepile et al., 2020; Donovan et al., 2020). 399 400 This could accelerate the proliferation of macroalgae and other opportunistic organisms, and 401 further decrease the chance of scleractinian corals re-establishing themselves. In addition, declines in water quality can develop and cause the formation of algal blooms (Fabricius, 402 403 2005; Tanaka et al., 2010).

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Fleshy macroalgae are important indicators of changes in nutrient cycles because the 405 406 bioavailable nutrients which are taken up from the water column and assimilated into their tissues can be easily measured over both short and long periods of time (Costanzo et al., 407 2001). Macroalgae have been used as proxies to study the effects of nutrient enrichment in 408 both laboratory and *in situ* experiments, but these mostly tend to be for investigating 409 anthropogenic sources, such as from coastal run-off (Fong et al., 1994; García-Seoane et al., 410 2018; Burkepile et al., 2020) and less commonly for natural nutrient inputs, such as seabird 411 guano, deep-water upwelling events or coral-derived organic matter (Schaffelke, 2002; 412 Graham et al. 2018; Williams et al., 2018). 413

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The kind of nutrient signature used as a bioindicator is also an important factor to consider. Lin & Fong (2008) found  $\delta^{15}$ N to be a more sensitive indicator to changes in nutrients in transplanted macroalgae than %N. Nitrogen content is typically diluted during rapid growth of specimens, suggesting that nutrients are only stored in macroalgal tissues over the long term when nutrient supply exceeds growth rate, as they first must assimilate excess nitrogen

420 into growth. This likely explains why we found no patterns in %N in neither the Seychelles421 regression analysis, nor the Mo'orea transplant experiment.

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Although the duration of transplant experiments in the literature vary considerably, from 423 hours to ~1 year, García-Seoane et al. (2018) recommended an exposure time of < 1 month, 424 as the uptake kinetics of algal transplants can vary based on the species used or local 425 426 environmental conditions. The current study suggests that these changes in nutrients may be detected in Sargassum tissues up to 12 months after an event, implying that nutrients have 427 428 been trapped and retained in the system for at least a year. It is also known that Sargassum undergoes major seasonal fluctuations in production and biomass that may supplement 429 adjoining ecosystems within the broader seascape (Fulton et al., 2019). This study supports 430 previous literature suggesting macroalgae can easily be deployed in target areas to investigate 431 changes in nutrient loads (Costanzo et al., 2001; García-Seoane et al., 2018), but also applies 432 this common technique to capturing energetic resources. Therefore, macroalgal assays have 433 the potential to provide insight into changes in nutrient sources from both natural and 434 anthropogenic events, such as widespread coral bleaching. 435

436

There are a number of potential sources of nitrogen that could have influenced our results 437 other than coral-derived nutrients. A strong nutrient gradient from the land-end of Opunohu 438 439 Bay in Mo'orea to its ocean-end (Lin & Fong, 2008) suggests that the nutrient enrichment from the shrimp farm effluent entering the bottom of the bay was unlikely to affect the 440 isotopic signatures of our specimens. However, storms and heavy rainfall can influence both 441 the spatial extent of run-off and nutrient uptake in reef macroalgae (Clausing & Fong, 2016; 442 Adam et al., 2020). Local upwelling could have provided nutrients and influenced our results, 443 but Lin & Fong (2008) suggest that the  $\delta^{15}$ N of tropical ocean seawater is typically ~3 ‰, 444

which is lower than the signatures found in both the post-transplant and pre-transplant tissue 445 samples. In addition, no *Sargassum* specimens were found at the depth where the bleaching 446 447 occurred in Mo'orea (~12m), so samples had to be taken from the nearby nutrient-limited lagoon (~1 m). Although this lagoon typically has low nutrient levels (Donovan et al., 2020) 448 and the algal specimens collected from there had low tissue nutrient history, some bleaching 449 was observed in the lagoon at the time of collection, but not in the specific area where the 450 451 specimens were collected. Even if some coral-derived nutrients were captured by the initial specimens, we accounted for this by depleting tissue nutrient stores in the holding tanks. This 452 453 resulted in a significant decline in  $\delta^{15}$ N, followed by a significantly higher signature in the post-treatment algae after they were transplanted at the site where extensive coral bleaching 454 and mortality had occurred. Other factors such as light intensity can also affect algal 455 condition and isotopic signatures (Marconi et al., 2011; García-Seoane et al., 2018), so may 456 have also influenced results in Mo'orea. 457

458

Future research could build on this study, and on other studies in the literature (García-459 Seoane et al., 2018) by applying the above methods to test the degree of influence of coral-460 461 derived organic matter on macroalgal nutrient signatures, relative to anthropogenic sources, either in laboratory- or field-based experiments. For instance, macroalgal bioassays could be 462 deployed on bleached reefs with low levels of coastal run-off, such as those in other regions 463 around Mo'orea, and compared to those with significantly higher levels, to test if these 464 effects are synergistic. Clearly assessment of macroalgal isotope signatures across different 465 nutrient loads and levels of coral mortality are required to fully understand nutrient sources 466 before attribution of nitrogen enrichment in macroalgae to nutrients released from dead and 467 decaying corals can be definitively determined. 468

469

While this study compared the  $\delta^{15}$ N signatures in tissues of *Sargassum* from pre- and post-470 bleaching years in the Seychelles, no macroalgal samples were collected during the bleaching 471 472 and the subsequent mortality event in 2016 itself, so it was not possible to compare the stable isotopic results when this mass tissue release was occurring. The short-term experiment in 473 Mo'orea was conducted in part to understand these shorter-term dynamics and to further 474 support these findings. Though the results from the two different reef systems are not directly 475 comparable, this study suggests that macroalgal tissue  $\delta^{15}$ N signatures can be affected by 476 mass morality events. However, as the current study only implies that the mass release of 477 dead coral tissue enriched the macroalgal  $\delta^{15}$ N signatures, future research could expand on 478 this work by determining the exact source(s) of enrichment (Briand et al., 2015). For 479 instance, enriched stable isotope tracers (<sup>15</sup>N and <sup>13</sup>C) (Naumann et al., 2010) or compound-480 specific stable isotopes (McMahon et al., 2016) could be used to quantify the flow of organic 481 matter from dead corals to macroalgae in an experimental setting, or seawater from reefs with 482 varying levels of coral mortality could be collected and used to test the responses of 483 macroalgae. 484

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In conclusion, this study highlights how mass coral mortality events, trigged by marine heat 486 waves, may add additional sources of nutrients into coral reef biogeochemical cycles, which 487 are available to opportunistic macroalgae. These changes in nutrient dynamics could have 488 489 significant impacts on coral reefs, particularly if those sources are specifically becoming more available because key ecosystem engineers such as scleractinian corals are in decline 490 (Wild et al., 2011). It also suggests that these nutrients can be retained within reefs and can 491 have both short-term and long-term impacts on their biogeochemical cycles. Although it is 492 not yet known how long these nutrients remain in the system, if other environmental 493 conditions are favourable enough, then corals might still be able to recover (Graham et al., 494

495	2015). However, if these same reefs are also facing other local anthropogenic stressors, such
496	as nutrient runoff or overfishing of herbivores, then large coral mortality events may result in
497	competitive advantages to benthic organisms such as macroalgae, leading to a benthic regime
498	shift (Ainsworth et al., 2020). This emphasises the critical need to manage local stressors by
499	detecting and reducing nutrient runoff and other drivers, especially on reefs that do still have
500	high abundance of corals, and/ or have recently bleached.
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Figure 1. Box and whisker plots of the median a) total and branching coral cover in both pre-

bleaching and post-bleaching years (2014 and 2017, respectively) on "coral mortality" reefs (n=7), b) the average  $\delta^{15}N$  signatures in *Sargassum* sp. tissues in both years, and c) the average percent N (%N) in both years,. The pale blue boxes represent the pre-bleaching year and pale pink boxes represent the post-bleaching year, both showing the third quartile (Q3) and first quartile (Q1) range of the data, the whiskers (95% quartile) and data outliers.





**Figure 2.** Change in absolute total coral cover and the corresponding changes in  $\delta^{15}$ N in *Sargassum* tissues across seven coral mortality reefs in the Seychelles between 2014 and 2017. The regression

lines and confidence intervals were obtained using linear regression coefficient of determination  $(r^2)$ ;

773 95% confidence intervals.

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**Figure 3.** Box and whisker plots of the median  $\delta^{15}$ N in *Sargassum mangarevense* tissue across three treatments from a short-term transplant experiment, showing the third quartile (Q3) and first quartile (Q1) range of the data, the whiskers (95% quartile) and data outliers. Connecting letters indicate significance between treatments. Stable isotopic signatures were measured in subset samples of the same specimens that were collected from a low-nutrient reef (Initial), placed in laboratory aquaria to deplete internal nutrient stores for ~7 days (Pre-Transplant), before they were deployed on the

784 bleached reef for 3 weeks (Post-Transplant) (n=10).