

1   **Coral thermal stress and bleaching enrich and restructure reef  
2   microbial communities via altered organic matter exudation**

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21   **ABSTRACT**

23       Coral bleaching is a well-documented and increasingly widespread phenomenon in reefs  
24   across the globe, yet there has been relatively little research on the implications for reef water  
25   column microbiology and biogeochemistry. A mesocosm heating experiment and bottle  
26   incubation compared how unbleached and bleached corals alter dissolved organic matter  
27   (DOM) exudation in response to thermal stress and subsequent effects on microbial growth and  
28   community structure in the water column. Thermal stress of healthy corals tripled DOM flux  
29   relative to ambient corals and DOM exudates from stressed corals (heated and/or previously  
30   bleached) were compositionally distinct from healthy corals. These exudates significantly  
31   increased bacterioplankton densities up to twice that of (3E6 cells/mL) of bacterioplankton  
32   grown on healthy coral exudates and engendered a consistent, significant shift in  
33   bacterioplankton communities towards increased proportions of copiotrophic  
34   Alteromonadaceae, Flavobacteriaceae, and Saprospiraceae families as well as putative

35 pathogens in the Pseudoalteromonadaceae and Colwellieaceae families. Together these results  
36 demonstrate how the impacts of both short-term thermal stress and long-term bleaching may  
37 extend into the water column, with altered coral DOM exudation driving microbial feedbacks that  
38 influence how coral reefs respond to and recover from mass bleaching events.

39 **INTRODUCTION**

40 Coral reef ecosystems are engineered by benthic primary producers via interactions with  
41 the water column, and unraveling these interactions is a critical step in understanding how  
42 healthy reefs function and how to prevent their degradation. Corals and algae influence the  
43 surrounding water column biogeochemistry (Atkinson, 1987; Lewis, 1977; Moberg & Folke,  
44 1999; Odum & Odum, 1955; Smith et al., 2013) by providing fixed carbon substrates to primary  
45 consumers through dissolved organic matter (DOM) exudation (Crossland, 1987; Ferrier-Pages  
46 et al., 1998; Ferrier-Pagès et al., 2000; van Duyl & Gast, 2001). Reef benthic primary producers  
47 can release upwards of 30% of their daily photosynthate into the water column in the form of  
48 DOM, which can serve as a carbon and nutrient source for bacterioplankton (Ducklow, 1990;  
49 Haas et al., 2011). Coral DOM exudates have unique fluorescent DOM signatures (fDOM),  
50 dissolved combined neutral sugars (DCNS) compositions, and organic compound mass  
51 spectrometry profiles compared to DOM exudates from the surrounding seawater and other  
52 benthic primary producers (Nelson et al., 2013; Quinlan et al., 2018; Wegley Kelly et al., 2022).  
53 Beyond DOM serving as an energy and nutrient source for bacterioplankton, the unique quality  
54 of different DOM exudates may elicit distinct physiological changes in bacterioplankton  
55 communities as they respond to the chemical cues exuded by different benthic primary  
56 producers.

57 Coral DOM exudation facilitates the interaction between the coral holobiont and the  
58 surrounding bacterioplankton. Coral reef bacterioplankton exhibit chemotactic responses to a  
59 variety of DOM released by corals, including dimethylsulfoniopropionate (DMSP) (Tout et al.,  
60 2015). DOM exudates from coral also support the growth and activity of distinct heterotrophic  
61 bacterioplankton communities (Haas et al., 2011, 2013; Nakajima et al., 2018; Nelson et al.,  
62 2013; Silveira et al., 2017). *In situ* studies have identified unique metabolites and microbial  
63 communities adjacent to corals compared to the surrounding seawater (Silveira et al., 2017;  
64 Tout et al., 2014; Walsh et al., 2017; Weber et al., 2019). These microbial communities are

enriched in genes related to chemotaxis, motility, and signal transduction, suggesting that these regions surrounding corals contain bacterioplankton with the metabolic capacity to directly interact with corals (Ochsenkühn et al., 2018; Silveira et al., 2017; Tout et al., 2014; Walsh et al., 2017). This zone of interaction is an essential area for feedback loops between the benthos and the water column in the coral reef ecosystem, as changes in bacterioplankton may influence coral physiology. Despite the burgeoning knowledge of how healthy corals influence bacterioplankton via DOM exudation, relatively little is known about if and how this relationship changes when corals are stressed.

One major stressor corals experience is ocean warming, with marine heatwaves occurring more frequently due to global climate change (Arias et al., 2021; Cooley et al., 2022; Levitus et al., 2012). Thermal stress harms corals via bleaching, a well-documented and widespread phenomenon in which the symbiosis between corals and Symbiodinaceae breaks down as corals are exposed to elevated temperatures for an extended period of time (Brown, 1997). Mass coral bleaching has been recorded since 1979 and has increased in frequency, with a 3-fold increase in bleaching events in 2006-2012 compared to 1985-1991, restricting the time for coral reefs to recover between bleaching events (Cooley et al., 2022; Heron et al., 2016; van Hooidonk et al., 2016). Although corals can recover from bleaching, they will die if thermal stress persists (Hoegh-Guldberg, 1999). Even at sub-lethal levels, coral bleaching alters the coral holobiont's metabolism (Innis et al., 2021), its chemistry (Roach et al., 2021), and microbiota (Bourne et al., 2016; Liang et al., 2022; Littman et al., 2011; McDevitt-Irwin et al., 2017; Oppen & Blackall, 2019; Thurber et al., 2009).

Recent research suggests that coral-water column interactions are altered during periods of elevated temperatures (Garren et al., 2014; Niggl et al., 2009; Tremblay et al., 2012). Niggl et al. (2009) found that bleaching corals released elevated levels of particulate nitrogen (PN) and particulate organic carbon (POC) into the water column. In another study, heated *Stylophora pistillata* corals showed a change in total organic carbon (TOC) flux direction,

91 transitioning from negative flux in healthy corals (uptake) to positive flux in heated/bleached  
92 corals (release) (Tremblay et al., 2012). These alterations to water column chemistry likely shift  
93 the bacterioplankton community composition as specific taxa respond to metabolites released  
94 by stressed corals. In one study, the bacterial pathogen *Vibrio coralliilyticus* responded to DMSP  
95 as a chemotactic cue when it was released at elevated concentrations by heat stressed coral  
96 (Garren et al., 2014). Even under ambient conditions, coral mucus elicits a rapid chemokinetic  
97 and transcriptional response in *Vibrio coralliilyticus*, further suggesting that this pathogen uses  
98 coral chemical cues to trace and target its host (Gao et al., 2021). Given that healthy corals  
99 exude DOM into the surrounding seawater and influence subsequent bacterioplankton  
100 dynamics, we hypothesized that 1) thermal stress and bleaching can dramatically alter DOC  
101 exudation rates and DOM composition with cascading effects on bacterioplankton growth and  
102 community structure and 2) short-term thermal stress and long-term bleaching will have different  
103 effects. These different effects will help elucidate how the succession of bleaching, from onset  
104 to recovery or death, influences the succession of DOM and bacterioplankton *in situ*.

105 **RESULTS**106 **Experimental Design**

107 We tested these hypotheses during a mass bleaching event on Mo'orea, French  
108 Polynesia. In April 2019, the reefs of Mo'orea bleached after a prolonged period of high water  
109 temperatures (Leinbach et al., 2021; Speare et al., 2021) (Figure 1). In May 2019, immediately  
110 following this thermal stress event, we leveraged the natural distributions of recently bleached  
111 and unbleached corals to elucidate the independent and combined impacts of experimentally-  
112 induced thermal stress and recent bleaching on coral DOM exudation and subsequent  
113 bacterioplankton remineralization and growth. In brief, coral nubbins from three different species  
114 (*Pocillopora verrucosa*, *Acropora pulchra*, and *Porites rus*) assigned to both bleached and  
115 unbleached phenotypes were collected and exposed to seven days of either ambient (28.6 °C)  
116 or elevated water temperatures (32 °C +/- 0.2 °C) and ambient light levels in flow through  
117 aquaria (n=3 per treatment) (Fig 1A.I). The combination of bleaching level and temperature  
118 yielded four treatments representing a factorial cross of prior bleaching phenotype and  
119 temperature: "Control", "Heated", "Bleached", and "Bleached + Heated" (Fig 1 A.II). Additionally,  
120 two water-only control aquaria, one for each temperature treatment, were included ("Negative  
121 Control" and "Negative Control + Heated"). After seven days of pretreatment, DOM exudates  
122 from each of the aquaria were collected (Fig 1.A.III) and used as growth media for dark  
123 incubation dilution cultures (Fig 1 A.IV). Unfiltered back-reef seawater was used as an inoculum  
124 representative of ambient back-reef bacterioplankton communities (Nelson et al., 2013). Dilution  
125 cultures were conducted in 1 L 10% acid-washed, triple milliQ rinsed (hereafter termed "acid  
126 washed") polycarbonate bottles in the dark at ambient temperatures for 36 hours and sampled  
127 at the beginning (n=3 per treatment) and end (n=3 per treatment) of the incubation. We used a  
128 combination of bulk DOC measurements, flow cytometry, 16S amplicon sequencing, and  
129 untargeted metabolomics to assess differences in the composition of DOM exudates and how  
130 these exudates altered microbial growth and community structure (Fig 1 A.V).

131

132 **Symbiodiniaceae Densities**

133 Symbiodiniaceae cell densities were used to assess individual and aquaria-wide

134 bleaching levels of corals collected in the field and after the seven day pre-treatment,

135 respectively. At collection, bleached corals had significantly lower Symbiodiniaceae cell

136 densities (two-way ANOVA,  $F=45.552$ ,  $p=2.67e-08$ ). Coral species also had a significant effect

137 on Symbiodiniaceae densities (two-way ANOVA,  $F=4.738$ ,  $p=0.0137$ ), as well as the interaction

138 between coral species and bleaching (two-way ANOVA,  $F=4.287$ ,  $p=0.0199$ ) (Figure 1C).

139 After seven days of incubation at ambient and elevated temperatures, the average

140 Symbiodinaceae densities showed that the four coral treatments had varying degrees of

141 bleaching (Figure 1D). Bleached corals had significantly lower Symbiodinaceae densities (two-

142 way ANOVA,  $F=6.584$ ,  $p=0.0333$ ). Heating did not have a significant effect on Symbiodiniaceae

143 cell densities ( $F=0.001$ ,  $p=0.9727$ ), and neither did the interaction between heating and

144 bleaching (two-way ANOVA,  $F=1.284$ ,  $p=0.2901$ ). Therefore the Control treatment had the

145 highest Symbiodiniaceae densities during the exudation experiment. Heated aquaria exhibited

146 slightly lower Symbiodiniaceae cell densities consistent with some paling, yet still had higher cell

147 densities than their Bleached and Bleached + Heated counterparts.

148

149 **Dissolved Organic Carbon**

150 Control corals exuded roughly  $5 \mu\text{M C} \cdot (\text{dm}^2)^{-1} \cdot \text{h}^{-1}$  while Heated corals and Bleached

151 corals exhibited roughly 289% (mean  $13.22 \mu\text{M C} \cdot (\text{dm}^2)^{-1} \cdot \text{h}^{-1}$ ) and 177% (mean  $8.10 \mu\text{M}$

152  $\text{C} \cdot (\text{dm}^2)^{-1} \cdot \text{h}^{-1}$ ) higher DOC fluxes. Bleached + Heated corals exhibited undetectable DOC flux.

153 Although DOC exudation appeared to be affected by treatment, we were unable to elucidate

154 significant differences in areal DOC flux rates possibly due to small sample size and short

155 exudation times (Kruskal-Wallis chi-squared=4.1667,  $p=0.244$ ) (Figure 2A). Coral treatments

156 generally had higher raw DOC concentrations than the water controls, although this effect was  
157 not significant (Kruskal-Wallis chi-squared=9.3187, p=.09) (Figure S2).

158

159 **Microbial Growth**

160 Flow cytometry revealed distinct microbial growth patterns between the DOM  
161 treatments. Two-way ANOVAs were used to test the effect of both timepoint and treatment on  
162 bacterioplankton cell concentrations. We found that bacterioplankton concentrations significantly  
163 increased through time in the dark bottle incubations (two-way ANOVA,  $F=104.372$ ,  $p<2.2E-16$ )  
164 and differed significantly between treatments (two-way ANOVA,  $F=53.685$ ,  $p<2.2E-16$ ) (Figure  
165 2B). All coral treatments had significantly higher cell concentrations than both the Negative  
166 Control and the Negative Control + Heated (Tukey post-hoc test,  $p<0.05$ ). Within the coral DOM  
167 treatments, Heated exudates yielded significantly higher bacterioplankton concentrations than  
168 the Control (Tukey post-hoc test,  $p<0.05$ ), with bacterioplankton grown on Heated DOM  
169 reaching concentrations of 3,160,000 cells/mL ( $\pm 790,000$ ), nearly double that of the Control  
170 (1,562,000 cells/mL  $\pm 137,000$ ) (Figure 2B). Bacterioplankton specific growth rate also differed  
171 significantly between the treatments (one-way ANOVA,  $F=6.363$ ,  $p=0.005$ ) (Figure S3).

172

173 **Microbial Community Structure**

174 The DOM derived from the six treatments yielded distinct microbial communities after 36  
175 hours of growth. There was a significant change in microbial communities from the start to the  
176 end of the bottle incubations, indicating that communities changed through the bottle incubation  
177 and were not simply reflective of the starting communities (PERMANOVA,  $F=72.033$ ,  $R^2=0.71$ ,  
178  $p\leq.001$ , Figure S4). After 36h, bacterioplankton grown on coral exudates were significantly  
179 different from those grown on water negative controls (PERMANOVA  $F=8.679$ ,  $R^2=0.40$ ,  
180  $p\leq.001$ ) (Figure 3A). Within the coral treatments, Controls maintained distinct community  
181 structure from the Heated, Bleached, and Bleached + Heated communities, hereafter

182 collectively referred to as “stressed” (PERMANOVA  $F=2.822$ ,  $R^2=0.59$ ,  $p=0.009$ ). There was  
183 overlap within the stressed communities and a consistent shift in ordination space away from  
184 the Controls, indicating a potentially conserved change that occurs in microbial communities in  
185 response to stressed coral exudates.

186 Many eutrophic coastal-associated bacterial families were overrepresented in the  
187 negative controls including Nitrincolaceae and Methylophagaceae (Francis et al., 2021), as well  
188 as the common coral reef associated family Rhodobacteraceae (Apprill et al., 2021; Comstock  
189 et al., 2022; Haas et al., 2016; Kelly et al., 2019; Nelson et al., 2011). Coral DOM microbial  
190 communities were dominated by the families Alteromonadaceae and Rhodobacteraceae,  
191 although there was substantial variation between the four treatments (Figure 3B, Table S1).  
192 Control corals maintained distinct microbial communities from both negative controls and  
193 stressed corals, overrepresented in the families Cryomorphaceae, Litoricolaceae, and  
194 Halieaceae. Alteromonadaceae, a common marine copiotrophic family (Baumann et al., 1972),  
195 was lowest in communities grown on Control exudates (28.3%) and substantially higher in the  
196 communities growing on the stressed coral exudates (46.6%-38.6%). Pseudoalteromonadaceae  
197 also increased in abundance from Control communities to stressed communities (3.3% in  
198 Control, and a mean of 9.1% in stressed). The common coral reef-associated family  
199 Rhodobacteraceae was higher in the Control (21.3%) and lower in the three stressed treatments  
200 (13.7%-19.4%). Another common coral reef associated family, Cryomorphaceae, was abundant  
201 in the Control treatment (13.0%) and then reduced in abundance in the stressed treatments  
202 (5.6%-7.2%). Microbial community alpha diversity metrics (observed sequences, Chao diversity,  
203 Shannon diversity, and Shannon’s Evenness) were assessed after 36 hours of growth (Figure  
204 S5), with none of these indices being significantly affected by treatment (one-way ANOVA,  
205  $p\geq.05$ ).

206

207 **Bacterial Taxa Differential Abundance Analysis**

208 Multivariate analysis demonstrated that stressed corals enriched distinct  
209 bacterioplankton communities compared to their Control counterparts. In order to directly  
210 elucidate which specific bacterial taxa were driving these differences, we performed DESeq2,  
211 (see supplementary methods) on a subset of the data that only included the four coral DOM  
212 treatments (Love et al., 2014), yielding a final count of 159 OTUs to be run through DESeq2.  
213 The log<sub>2</sub> fold-change of OTU abundances was calculated between the three coral stress  
214 treatments and the coral controls to elucidate OTUs that were differentially abundant when  
215 corals were bleached and/or heated (Table S2) (Figures 3C and S6).

216 A total of 31 significantly differentially abundant bacterial OTUs (19.5%) were identified  
217 by DESeq2 (DESeq2, log<sub>2</sub> fold-change>0, p≤.05 after FDR adjustment, Table 1, Figures 3C,  
218 S6, and S7). These OTUs belonged to four bacterial and one archaeal class:  
219 Alphaproteobacteria, Gammaproteobacteria, Bacteroidia, Deltaproteobacteria, and  
220 Thermoplasmata, with the majority (64.5%) of differentially abundant OTUs belonging to  
221 Gammaproteobacteria. Within Gammaproteobacteria, there was a significant enrichment of  
222 numerous abundant Alteromonadaceae and Pseudoalteromonadaceae OTUs in at least one of  
223 the three treatments (75% of all differentially abundant Gammaproteobacteria OTUs).

224 In all three stress treatments there was a significant enrichment of two  
225 *Pseudoalteromonas* OTUs (1224 and 1296), one *Alteromonas* OTU (734), and one unclassified  
226 Saprospiraceae OTU (322). All three stress treatments also showed an enrichment of a highly  
227 abundant *Alteromonas* OTU (2), although this was only statistically significant in the Bleached  
228 and Heated treatments. There were 12 differentially abundant OTUs found only to be significant  
229 in the Bleached treatment including significant enrichment in members of the genus  
230 *Psuedoalteromonas* (OTUs 75 and 85), unclassified Saprospiraceae (OTU 101), and  
231 *Phaeocystidibacter* (OTU 480), and significant reductions in members of the genus *Litoricola*  
232 (OTUs 27 and 419) and unclassified Alteromonadaceae (OTUs 368, 1012, and 1023). The two  
233 heated treatments had significant enrichment in OTUs of the genus *Psuedoalteromonas* (OTU

234 853), *Aestuariibacter* (OTU 48), and an unclassified Flavobacteriaceae (OTU 277). The two  
235 bleached treatments showed significant enrichment of OTUs in the genera *Pseudoalteromonas*  
236 (OTU 823) and *Thalassotalea* (OTU 649).

237

238 **Metabolomes**

239 Another potential driver of bacterioplankton enrichment in this study, beyond DOC  
240 concentration, was compositional differences in the DOM exudates. Untargeted metabolomics  
241 was performed to assess the impact of DOM quality on microbial community structure. The exo-  
242 metabolomes consisting of the extracted ion-chromatograms (XIC values) of each metabolite  
243 were used to generate a Bray-Curtis dissimilarity matrix to test multivariate differences between  
244 the six treatments at time point T= 0. The exo-metabolomes indicated that different treatments  
245 produced compositionally distinct DOM exudates following the three hour DOM exudation  
246 (PERMANOVA, F=1.7847, R<sup>2</sup>=0.44788, p≤.001) (Figure 4A). Consistent with the  
247 bacterioplankton data, coral samples clustered separately from the water negative controls and  
248 within the coral treatments, coral Controls maintained distinct metabolomes compared to the  
249 three stress treatments (one-way PERMANOVA F=1.3799, R<sup>2</sup>=0.37162, p=0.005). Multivariate  
250 comparisons between the 16S rDNA and metabolomics distance matrices confirmed that DOM  
251 composition significantly correlated with bacterioplankton community structure (Procrustes  
252 correlation=0.8612, significance=0.001; Mantel R=0.5993, significance=0.001) (Figure 4B),  
253 indicating that bacterioplankton community changes may be a response to shifts in DOM  
254 exudate quality as well as quantity.

255 **DISCUSSION**

256 This study presents a comprehensive assessment of how short-term thermal stress and  
257 long-term bleaching, separately and in combination, influence reef bacterioplankton via DOM  
258 exudation. Our results indicate that thermally-induced bleaching events both increase and alter  
259 coral DOM exudation with cascading impacts on reef bacterioplankton dynamics that potentially  
260 hamper coral resistance to and recovery from bleaching.

261

262 **Thermally stressed and bleaching corals release DOM that increases microbial load**

263 Heated corals had the highest DOC fluxes of roughly  $15 \mu\text{M C} \cdot (\text{dm}^2)^{-1} \cdot \text{h}^{-1}$ , marking a  
264 substantial contribution to reef DOC that is between 8.4 and 13.6 times higher than previously  
265 documented coral DOC release rates in Mo'orea (Haas et al., 2011, 2013). Photosynthesis  
266 reactions, which contribute to a portion of the DOC released by corals, are sensitive to  
267 increases in temperature (Oakley et al., 2014; Ros et al., 2020) and elevated temperatures are  
268 known to speed up enzymatic reaction rates. It is possible that maintenance of intact coral-algal  
269 symbiosis in the face of elevated temperatures may lead to higher rates of carbon fixation and  
270 higher DOC release (Oakley et al., 2014). This is supported by Hillyer et al., 2017 who found  
271 that glucose, a major product of dinoflagellate-cnidarian symbiosis (Burriesci et al., 2012;  
272 Streamer et al., 1993; Whitehead & Douglas, 2003), appears to increase in thermally stressed  
273 corals.

274 Both Bleached and Bleached + Heated corals had lower DOC release rates that were  
275 generally similar to DOC release rates of coral Controls. Without their endosymbionts, corals  
276 are known to catabolize internal carbon stores, especially lipids, to meet their energetic  
277 demands that are no longer satisfied by photoautotrophy (Grottoli et al., 2004, 2006; Grottoli &  
278 Rodrigues, 2011; Imbs & Yakovleva, 2012; Rodrigues & Grottoli, 2007; Schoepf et al., 2021).

279 DOM mobilization from internal stores could yield similar DOC release compared to healthy  
280 corals, despite reduced densities of Symbiodiniaceae.

281 DOM exudates from Heated, Bleached, and Bleached + Heated corals appear to be  
282 labile, i.e. readily mobilized by bacterioplankton into metabolic pathways (Carlson & Hansell,  
283 2015). In general, DOM derived from coral treatments grew more concentrated microbial  
284 communities with faster growth rates than the Negative Controls. Heated coral DOM produced  
285 higher microbial growth rates resulting in double the bacterioplankton concentrations compared  
286 to the coral Control treatment (3,000,000 cells/mL). This rapid growth of microbes on heated  
287 coral DOM could have negative impacts on corals *in situ*, where already stressed individuals are  
288 further stressed through the generation of hypoxic zones from high levels of bacterial respiration  
289 (Barott et al., 2012; Barott & Rohwer, 2012; Jorissen et al., 2016; Roach et al., 2017; Silveira et  
290 al., 2017; Smith et al., 2006). Despite the lower DOC release rates than Heated corals, both  
291 Bleached and Bleached + Heated DOM increased bacterioplankton concentrations compared to  
292 coral Controls. This suggests that changes in the composition DOM released by stressed corals  
293 may generally increase microbial growth, regardless of concentration.

294

295 **DOM from stressed corals yields a conserved enrichment of copiotrophic**  
296 **bacterioplankton and putative pathogens**

297 Bacterioplankton communities fed stressed coral DOM show a conserved, directional  
298 shift of microbial community structure away from bacterioplankton associated with healthy coral  
299 DOM, indicating a potential universal response of bacterioplankton to coral stress, whether that be  
300 heating, bleaching, or both. Differential abundance analysis of OTUs using DESeq2 revealed  
301 that this universal stress response in bacterioplankton communities was largely driven by an  
302 enrichment of copiotrophs and putative pathogens.

303 The three stressed treatments were highly enriched in bacteria commonly associated  
304 with large inputs of labile organic matter, including three *Alteromonas* OTUs (OTUs 2, 195, and

305 734, although OTUs 2 and 195 were only significantly enriched in Bleached and Heated), one  
306 Saprospiraceae OTU (OTU 322, significantly enriched in all three treatments), and two  
307 *Pseudoalteromonas* OTUs (OTUs 1224 and 1296, significantly enriched in all three treatments).  
308 These three taxa are common copiotrophs associated with large inputs of organic matter  
309 including from algal blooms (Baumann et al., 1972; McCarren et al., 2010; Romera-Castillo et  
310 al., 2011; Shi et al., 2012; Tada et al., 2011), in controlled incubations (James et al., 2019;  
311 Nelson & Carlson, 2012; Pontiller et al., 2022), and in response to pulses of POM on coral reefs  
312 during coral spawning (Guillemette et al., 2018). The enrichment of these OTUs in all coral  
313 stress treatments suggests a universal response of corals to heating and/or bleaching that  
314 induces the release of labile organic matter which then rapidly enriches heterotrophic bacteria in  
315 the plankton.

316 The universal stress response in bacterioplankton communities was also driven by an  
317 enrichment of putative pathogens, specifically in the families Colwellieaceae and  
318 *Pseudoalteromonadaceae*. OTU 649, belonging to the genus *Thalassotalea*, was enriched in all  
319 three treatments (only significantly so in Bleached + Heated and Bleached) and shared a 100%  
320 16S rDNA sequence identity with a *Thalassomonas* bacteria that induced severe bleaching in  
321 corals after only 24 hours (Vieira et al., 2016). *Pseudoalteromonas* OTU 823 was also highly  
322 enriched in all three stressed coral treatments (again only significantly so in Bleached + Heated  
323 and Heated) and was closely related (100% 16S rRNA identity) to *Pseudoalteromonas piratica*,  
324 which has been identified as the causative agent of the coral disease “acute *Montipora* White  
325 Syndrome” (Beurmann et al., 2017). Enrichment of putative pathogens in the stress treatments  
326 could be driven by a positive association with coral stress metabolites (Garren et al., 2014) or  
327 because stressed corals lack the production of defense molecules; in either case, the  
328 enrichment of these pathogenic taxa could be detrimental to coral health.

329 Although we are not aware of any studies that have examined how coral DOM alters  
330 bacterioplankton in bottle incubations, Sun et al., 2022 examined the impact of coral bleaching

331 on bacterioplankton in a flow through aquaria setting and corroborate many of the observations  
332 found here: copiotrophic taxa (in this case Flavobacteriaceae) increased in heated coral  
333 treatments and there is an uptick in pathogenic gene functions after seven days of heating.

334

335 **Stressed corals exude compositionally distinct DOM that correlates with conserved**  
336 **shifts in bacterioplankton communities**

337 One potential driver of microbial changes in this study beyond bulk DOC differences `  
338 is qualitative differences in the DOM exudates. The composition of DOM has been  
339 shown to shape microbial communities in numerous systems including coral reefs (Nelson et al.,  
340 2013), the open ocean (Azam & Malfatti, 2007), and synthetic microbial consortia (Fu et al.,  
341 2020). The same patterns hold in this study; different DOM treatments yielded different  
342 microbial communities, with DOM metabolomic composition significantly correlated with  
343 microbial community structure. This suggests that changes in the quality of coral DOM  
344 exudates, not just quantity, shapes bacterioplankton communities during thermally-induced  
345 bleaching.

346 The four coral treatments clustered away from the two negative water controls, aligning  
347 with previous observations that corals alter water column DOM composition (Nelson et al.,  
348 2013; Quinlan et al., 2018; Wegley Kelly, et al., 2022). Importantly, there was no distinction  
349 between two negative controls, suggesting that temperature alters DOM quality indirectly via  
350 coral exudation rather than by directly acting on the water column. Within the coral treatments,  
351 the three stressed treatments clustered away from the Control corals, suggesting that stressed  
352 corals altered the quality of their DOM exudates. The consistent clustering of stressed coral  
353 treatments away from healthy coral treatments in both the microbial and metabolomics data  
354 hints at the potential release of universal stress metabolites by corals experiencing a variety of  
355 heating/bleaching regimes, leading to conserved shifts in the DOM pool and in turn conserved  
356 shifts in bacterioplankton communities. These metabolites would be present regardless of the

357 specific stress regime and, once exuded into the water column, would fuel the consistent growth  
358 of opportunistic families and putative pathogens. Further studies should aim to directly assess  
359 this possibility.

360

361 **Bacterioplankton response to stressed coral DOM may accelerate coral decline**

362 Our data suggest a novel, positive feedback mechanism in which thermally stressed  
363 and/or bleached corals release DOM that enriches high abundances of rapidly growing  
364 copiotrophs and putative pathogens, which can then potentially harm the coral via hypoxia due  
365 to microbial respiration or through coral disease. A similar mechanism has been observed on  
366 algae dominated reefs; high algal benthic cover quantitatively increases and qualitatively  
367 changes DOM release, which in turn fosters a more copiotrophic microbial community with  
368 higher microbial biomass and energy use (Haas et al., 2016). This process, termed  
369 “microbialization”, is part of the broader DDAM (DOM, Disease, Algae, and Microbes) negative  
370 feedback loop in which microbialization harms coral through disease (pathogens) and hypoxia  
371 (copiotrophs), further promoting algal dominance on the reef (Barott et al., 2012; Haas et al.,  
372 2016; McDole et al., 2012). In much the same mechanism as the DDAM model, corals may  
373 negatively impact their own resistance to/recovery from thermally-induced bleaching via DOM  
374 exudation and subsequent bacterioplankton enrichment.

375 This study did not take into account increased temperatures during microbial growth,  
376 only the impacts of DOM. Elevated temperatures could further amplify this feedback loop by  
377 increasing microbial metabolic rates, which could be an additional factor for a rapid switch to  
378 copiotrophic communities and higher microbial abundances that wasn't observed at ambient  
379 incubations. The combination of elevated temperatures and increased DOM could also rapidly  
380 accelerate microbial respiration, resulting in more severe hypoxia than under ambient  
381 temperatures.

382       The ecological implications of this study can be understood by situating the four coral  
383 treatments within the context of an *in situ* reef experiencing elevated water temperatures (Figure  
384 5). The four experimental treatments can represent four phases of thermally-induced bleaching  
385 on a coral reef, from ambient (Control) to thermally-stressed (Heated) to actively bleaching  
386 (Bleached + Heated) to recovering (Bleached). In all three of the stressed coral DOM treatments  
387 there was a marked change in DOM exudation that drove an enrichment of copiotrophs and  
388 putative pathogens in the bacterioplankton. In the above ecological interpretation of the  
389 treatments, this indicates that the aforementioned positive feedback mechanism will be present  
390 throughout various stages of a thermal anomaly, hampering both coral resistance to and  
391 recovery from bleaching via disease and hypoxia at both the onset and termination of marine  
392 heatwaves.

393       Importantly, the highest concentration of DOC exudate and greatest growth of  
394 bacterioplankton was in the Heated treatment. This indicates the feedback mechanism is most  
395 pronounced at the onset of coral thermal stress. Water column pathogens and copiotrophs,  
396 sniffing out and gorging on thermally stressed coral DOM exudate, may push individual corals  
397 towards more severe bleaching. If a single coral bleaches, this mechanism may have minimal  
398 impact on the water column biogeochemistry, but if an entire reef experiences elevated  
399 temperatures, the large flux of labile DOM into the water column could propagate a reef-wide  
400 shift in microbial communities that may prevent coral recovery. Additionally, coral mortality as a  
401 result of bleaching and the aforementioned mechanisms could lead to a further pulse of organic  
402 matter fuel into the water column, exacerbating the already adverse situation and turning  
403 bleaching reefs into a dead zone.

404

405 **Conclusion**

406       Assessing the effect of thermally-induced coral bleaching on water column dynamics  
407 reveals that stressed corals enrich a glut of copiotrophic, putatively pathogenic bacteria in the

408 plankton via DOM exudation. At the coral colony level these effects may reduce a corals' ability  
409 to resist and recover from thermally-induced bleaching. Translated to a reef-wide scale, thermal  
410 anomalies and mass bleaching events could sharply alter biogeochemistry, carbon flux,  
411 microbial communities, and ecosystem health. In this dramatic positive feedback loop, DOM is  
412 the herald of the change, translating shifts in coral physiology to shifts in water column  
413 dynamics. At the moment, this dynamic remains unrecognized and the effects understudied. To  
414 fully understand how complex coral reef ecosystems respond to marine heatwaves, producer-  
415 DOM and microbe-DOM dynamics must be taken into account.

416 **METHODS**

417 **Experimental Design**

418 ***Field Collection***

419 Coral nubbins from three different species (*Pocillopora verrucosa*, *Acropora pulchra*, and  
420 *Porites rus*) were collected in Mo'orea, French Polynesia on May 8th, 2019 immediately  
421 following a bleaching event (Figure 1B). For more on this bleaching event, temperatures of  
422 Figure 1B, and sample collection, see supplementary methods. Coral nubbins from the three  
423 species were visually inspected at the time of collection and assigned as either "unbleached" or  
424 "bleached" phenotypes. Coral bleaching status was again validated prior to the experiment with  
425 a visual inspection and assessment of Symbiodiniaceae cell densities via flow cytometry (Figure  
426 1C).

427

428 **Pre-Treatment in Flow-Through Aquaria**

429 To mimic reef-wide bleaching/thermal stress signals, two nubbins from each of the three  
430 coral species at a given bleaching phenotype were combined with unfiltered water in individual  
431 aquaria for a total of six coral fragments in each of the 12 aquaria. Aquaria (n=3 per treatment)  
432 were exposed to seven days of either ambient (28.6 °C) or elevated water temperatures (32 °C  
433 +/- 0.2 °C) and ambient light levels. For specifications of the pumps and heaters, see  
434 supplementary methods. The combination of bleaching level and temperature yielded four  
435 treatments: "Control", "Heated", "Bleached", and "Bleached + Heated" (Fig A.I and A.II).  
436 Additionally, two water-only control aquaria, one for each temperature treatment, were included  
437 ("Negative Control" and "Negative Control + Heated").

438

439 **DOM Exudation Experiment**

440 On the day of the experiment, after seven days of pretreatment, the flow through of  
441 unfiltered water and the recirculation of water within the aquaria was stopped. Water was

442 removed from each aquaria until 400 mL remained (roughly  $\frac{1}{3}$  of the aquaria volume).  
443 Subsequently, 800 mL 0.22  $\mu\text{m}$ -filtered offshore water was then added to yield a final volume of  
444 1200 mL. Corals were left in the aquaria to exude DOM for three hours (15:00 h - 18:00 h) while  
445 heat treatments were maintained (Fig 1.A.III). After three hours DOM exudates were collected  
446 by filtering the 1200 mL of aquaria water through a 0.22  $\mu\text{m}$  PES Sterivex (Millipore) filter into  
447 acid-washed 2 L polycarbonate bottles. One of the triplicates of the “Heated” treatment was lost  
448 during this step resulting in n=2. To minimize DOM contamination from the filter matrix, all filters  
449 were previously flushed with 50-100 mL of 0.22  $\mu\text{m}$  filtered offshore water. Following exudation  
450 corals were removed from the aquaria and airbrushed to collect tissue slurry for downstream  
451 Symbiodiniaceae quantification.

452

453 Dilution Cultures

454 Filtered DOM exudates were used as growth media for dark incubation dilution cultures.  
455 Unfiltered back-reef seawater collected from the LTER 1 was used as an inoculum. From each  
456 replicate aquaria 1200 mL of DOM media was mixed with 400 mL bacterioplankton inoculum  
457 (3:1 volumetric ratio) via inversion in acid washed 2 L polycarbonate bottles (Figure 1.A.IV).  
458 Dilution cultures were then split equally into two 1 L acid washed polycarbonate bottles (800 mL  
459 culture per bottle). Half of the bottles were immediately destructively sampled at the beginning  
460 of culturing (T0, n=3 per treatment), while the remaining bottles (n=3 per treatment) were  
461 incubated in the dark at ambient temperatures for 36 hours.

462

463 Sample Collection and Processing

464 Symbiodiniaceae Quantification

465 To assess bleaching status of the corals during collection and at the end of the seven  
466 day incubation and exudation experiment, coral nubbins were flash-frozen and airbrushed using

467 0.22 µm filtered seawater. Tissue slurries were analyzed using flow cytometry following the  
468 protocol outlined in Fox et al., 2021. For details, please see supplementary methods.

469

470 Bacterioplankton Abundance

471 Samples for bacterioplankton abundance measurement via flow cytometry were taken  
472 throughout the dilution cultures at 0, 2, 8, 16, 20, 24, 32, and 36 hours. At every time point, 1 mL  
473 of each sample was fixed with 16 µL of 32% paraformaldehyde PFA. Samples were run on an  
474 Attune Acoustic Focusing Cytometer (Applied Biosystems, Part No. 4445280ASR) at University  
475 of Hawai'i at Mānoa to enumerate bacterial cell counts (Nelson et al., 2015). For sample  
476 collection details and flow cytometer settings, see the supplementary methods (Figure S1).

477

478 Water Collection for Bacterial Community Composition, Dissolved Organic Carbon and  
479 Metabolite Solid Phase Extraction

480 At 0 and 36 h timepoints water (800 mL) was sampled for microbial communities, DOC,  
481 and solid phase extraction of DOM using a peristaltic pump connected to acid washed and  
482 seawater leached silicon tubing. Sample water (800 mL) was passed through a 0.22 µm  
483 Sterivex to collect bacterioplankton for downstream DNA analysis.

484 DOC samples were taken by collecting 35 mL of 0.22µm sterivex filtrate in acid washed,  
485 combusted, triple sample-rinsed clear glass vials. Care was made to flush each Sterivex with  
486 ~50 mL of sample water prior to collecting DOC to avoid contamination from the filter. DOC  
487 samples were then acidified with 50 µL of 4N hydrochloric acid to yield a pH of less than 3. The  
488 DOC samples were processed and analyzed via high-temperature combustion on slightly  
489 modified Shimadzu TOC-V analyzers at UCSB according to the protocol outlined in Carlson et  
490 al., 2010.

491 For analysis of metabolites, exactly 700 mL of the remaining 0.22 µm Sterivex filtrate  
492 was collected in acid washed 1 L polycarbonate bottles and acidified with HCl to pH < 2. A small

493 volume (50 mL) of the acidified sample water was used to flush the lines prior to the solid phase  
494 extraction resulting in 650 mL of sample for solid phase extraction. Two bottles had less than  
495 650 mL acidified sample water and were equalized to 500 mL solid phase extractions. The  
496 difference in volume was later corrected by the resuspension step prior to LC-MS/MS analysis.  
497 Metabolites were extracted using a 200 mg mass Bond Elut-PPL (Agilent) cartridges following  
498 Dittmar et al., 2008 and Petras et al., 2017. Detailed metabolite extraction methods and all  
499 sample handling and storage can be found in the supplementary methods.

500

501 *Microbial Community DNA Extraction, Library Prep, and Sequencing*

502 Sample DNA extraction protocols followed those outlined in Bullington et al., 2022. For  
503 details, please see supplementary methods. Library preparation of the V4 16S rRNA gene  
504 region for amplicon sequencing was conducted at the University of Hawai'i at Mānoa Microbial  
505 Genomics and Analytical Laboratory using a single barcode library preparation approach with  
506 Golay barcoded forward primers and non-barcoded reverse primers. For an overview of primers  
507 and settings used, see the supplementary methods. Amplicons were pooled and sequenced  
508 using an Illumina MiSeq V3 600 paired-end cycle run at the University of Hawai'i at Mānoa  
509 Advanced Studies in Genomics, Proteomics and Bioinformatics facility. All samples were  
510 amplified and sequenced in duplicate technical replicates. Method blanks had substantially  
511 lower sequence read depth (mean = 1,590 reads/sample) than samples (mean = 88,681), with  
512 samples ranging from 12,609 reads/sample to 155,685 reads/sample.

513

514 *Dissolved Organic Matter Composition*

515 PPL cartridges were eluted with 2 mL methanol. Extracts were dried down with a  
516 vacuum centrifuge and redissolved with 70 µL 80% methanol:water with 1% formic acid. The  
517 two samples that had less volume were redissolved to 50 µL so that all concentrations were  
518 normalized to filtrate volume. Samples were transferred into a combusted glass insert. A 10 µL

519 aliquot of each sample was analyzed by injection into a Vanquish ultra-high performance liquid  
520 chromatography system (UHPLC) coupled to a Q-Exactive Orbitrap Mass Spectrometer  
521 (Thermo Fisher Scientific, Bremen, Germany). Chromatographic separation was performed with  
522 a C18 core-shell column (Kinetex, 150 × 2 mm, 1.8 µm particle size, 100 Å pore size,  
523 Phenomenex, Torrance, USA) all using the settings and protocol described in Petras et al.,  
524 2017 and Wegley Kelly et al., 2022.

525

526 **Data Processing and Analysis**

527 **16S Amplicon Bioinformatics**

528 16S rRNA gene amplicon sequences were processed using the nextflow bioinformatic  
529 pipeline (version 19.10.0) outlined in Arisdakessian et al., 2020 and Jani et al., 2021. Detailed  
530 bioinformatic methods can be found in the supplementary methods. In brief, raw paired fastq  
531 reads were preprocessed using the DADA2 R package (Callahan et al., 2016a). We used  
532 mothur (Schloss et al., 2009) with the Silva (release 132) database (Quast et al., 2013) to align  
533 and annotate the sequences, respectively. Per-sample read depth was normalized to 12,000  
534 sequences per sample. OTUs were defined as unique “amplicon sequence variants” (100%  
535 clustering OTUs) by DADA2 (Callahan et al., 2016). Lastly, we used the lulu R package to  
536 remove artefactual OTUs (Frøslev et al., 2017) and discarded OTUs represented by two or less  
537 reads across the 243 samples included in this library. UniFrac distance matrices were  
538 constructed from the OTU data and used to assess multivariate differences between microbial  
539 communities (Lozupone & Knight, 2005). At the final time point, two outlier samples were  
540 identified and removed from downstream 16S analysis (outliers were defined as samples whose  
541 log10 distance from the centroid of a treatment  $\geq$  1.5 SD above the mean log10 distance from  
542 the centroid for a given treatment).

543

544 **Metabolomics Chemoinformatics**

545           RAW files were converted to .mzML files using MSConvert (Chambers et al., 2012).  
546           MZmine3 (version 3.2.8) (Pluskal et al., 2010) was used for alignment between samples and  
547           feature extraction. In order to yield higher consensus alignment quality of MS2 spectra to  
548           improve database matching and molecular networking, the 35 samples from this experiment  
549           were combined in MzMine with 756 coral reef environmental and experimental DOM samples  
550           belonging to tandem studies conducted during the same fieldwork period at Gump Station.  
551           Detailed chemoinformatic parameters can be found in the supplemental methods. Metabolite  
552           cheminformatics generated 54,040 total metabolite ion-features (hereafter referred to as  
553           features). Ten procedural blanks (LC/MS grade water run in parallel with samples) were  
554           included in the run. These procedural blanks were used to identify background features and  
555           transient features in the 35 samples from this experiment. Background features were defined as  
556           features with an average intensity across all samples which is less than double the maximum  
557           intensity of that feature in the procedural blanks. Transient features are defined as features that  
558           do not exceed  $5 \times 10^4$  extracted ion chromatogram values (XIC) in more than 2 samples. Blank  
559           correction and transient feature removal removed 29,286 and 6,483 features, respectively. This  
560           resulted in 18,271 features with XIC-values (Extracted-ion chromatogram values or peak areas)  
561           which composes what we consider the exo-metabolome (mixture of ambient and exudate  
562           features) which was used in downstream analysis.

563

564           Statistics

565           Data analysis and statistics were done using R (version 4.2.1). Main packages used are  
566           the core packages within tidyverse (Wickham et al., 2019), vegan (Oksanen, 2013),  
567           BiodiversityR (Kindt & Coe, 2005), pairwiseAdonis (Martinez P., 2020), and stats (R Core Team,  
568           2013). R scripts and additional packages are available through <https://github.com/NIOZ-DOM-Analysis/ABCDom>.

570 Symbiodiniaceae cell densities and bacterioplankton cell concentrations had Gaussian  
571 distributions after log10 transformation and square root transformation, respectively, and  
572 treatment effects were tested using ANOVAs. Surface area normalized DOC flux for the coral  
573 treatments was determined by calculating the difference in DOC concentration between each  
574 treatment and their respective negative controls, normalizing this value to coral surface area  
575 and dividing it by the duration of the DOC exudation period (three hours). DOC areal flux data  
576 had a non-Gaussian distribution and thus treatment was tested using non-parametric Kruskal-  
577 Wallis tests. PERMANOVA tests were run on weighted Unifrac dissimilarity matrices derived  
578 from 16S amplicon sequencing data to test the effect of treatment on microbial community  
579 structure. To assess multivariate shifts in the exo-metabolomes, the metabolite feature table  
580 containing XIC data was converted to relative abundance data and used to generate a Bray-  
581 Curtis dissimilarity matrix, which was then used in downstream PERMANOVA testing.

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603

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618 WJS, MGIA, LWK, ZQ, AFH, CEN designed the study, CC, PCD, LIA, CEN, AFH, LWK

619 provided reagents and analytical tools. WJS, MGIA, ZQ, JAB performed the experiment.

620 Samples were processed by WJS, ZQ, IK, JAB, and data analysis and curation was performed

621 by WJS, MGIA, ZQ, IK. WJS, MGIA performed the formal analysis, visualization and wrote the

622 original draft. All co-authors reviewed and edited the manuscript at various stages. CEN and

623 AFH supervised the project. WJS and MGIA contributed equally.

624

## 625 **COMPETING INTERESTS**

626 The authors declare no competing interests.

627

## 628 **DATA AVAILABILITY**

629 Sequencing reads from the demultiplexed samples analyzed in this study have been deposited

630 in the NCBI Sequence Read Archive (SRA) under the BioProject accession xxxxxx (submission

631 to SRA to be finalized and made public upon acceptance). All LC-MS/MS data are publicly

632 available and deposited in the MassIVE data repository (<http://massive.ucsd.edu>) under the  
633 accession number MSV000088021 (MassIVE repository made public upon acceptance).

634

635 **CODE AVAILABILITY**

636 Scripts used to analyze the data in R have been deposited in GitHub at  
637 <https://github.com/NIOZ-DOM-Analysis/ABCDom> (repository made public with DOI via Zenodo  
638 upon acceptance).

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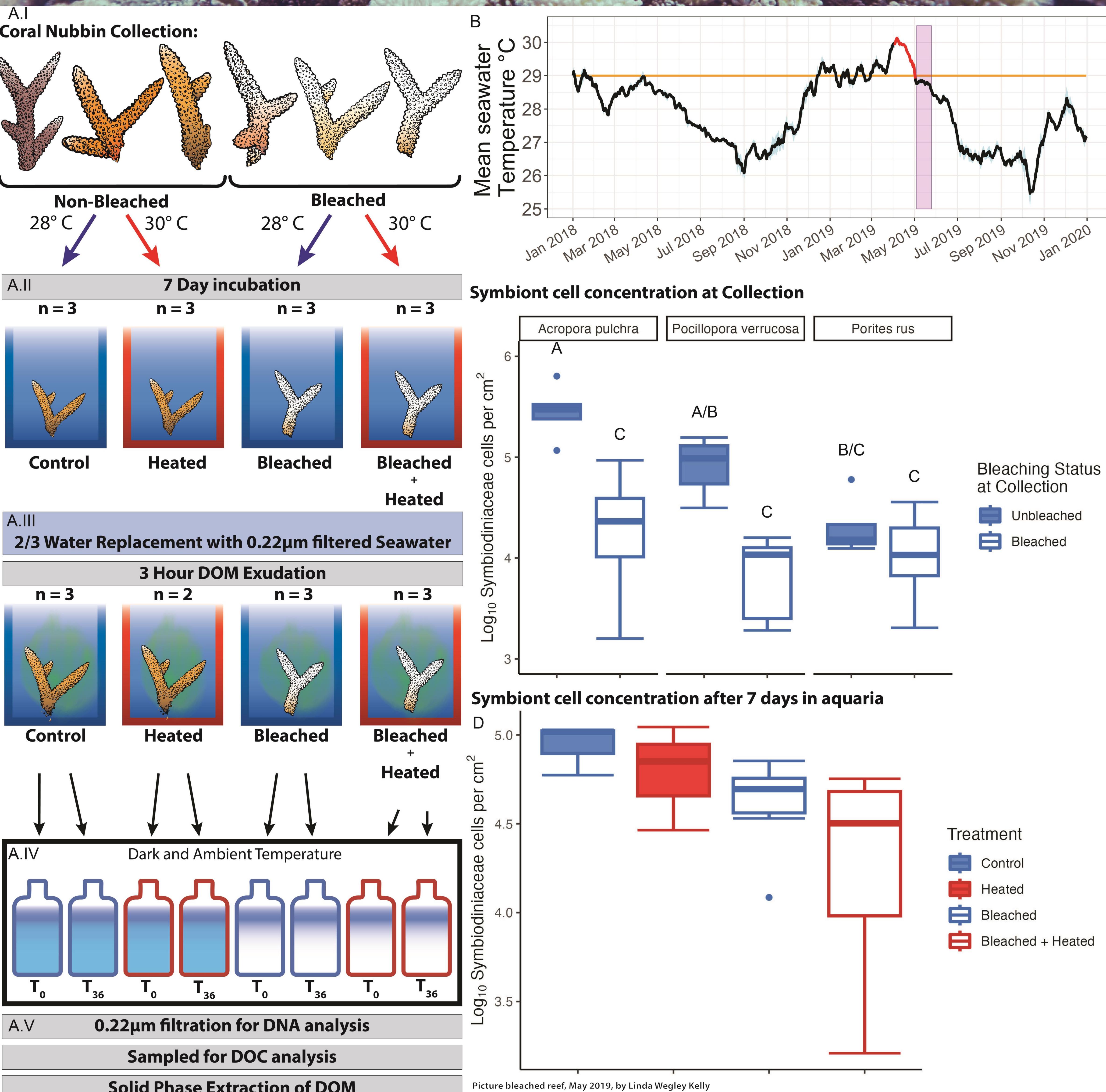
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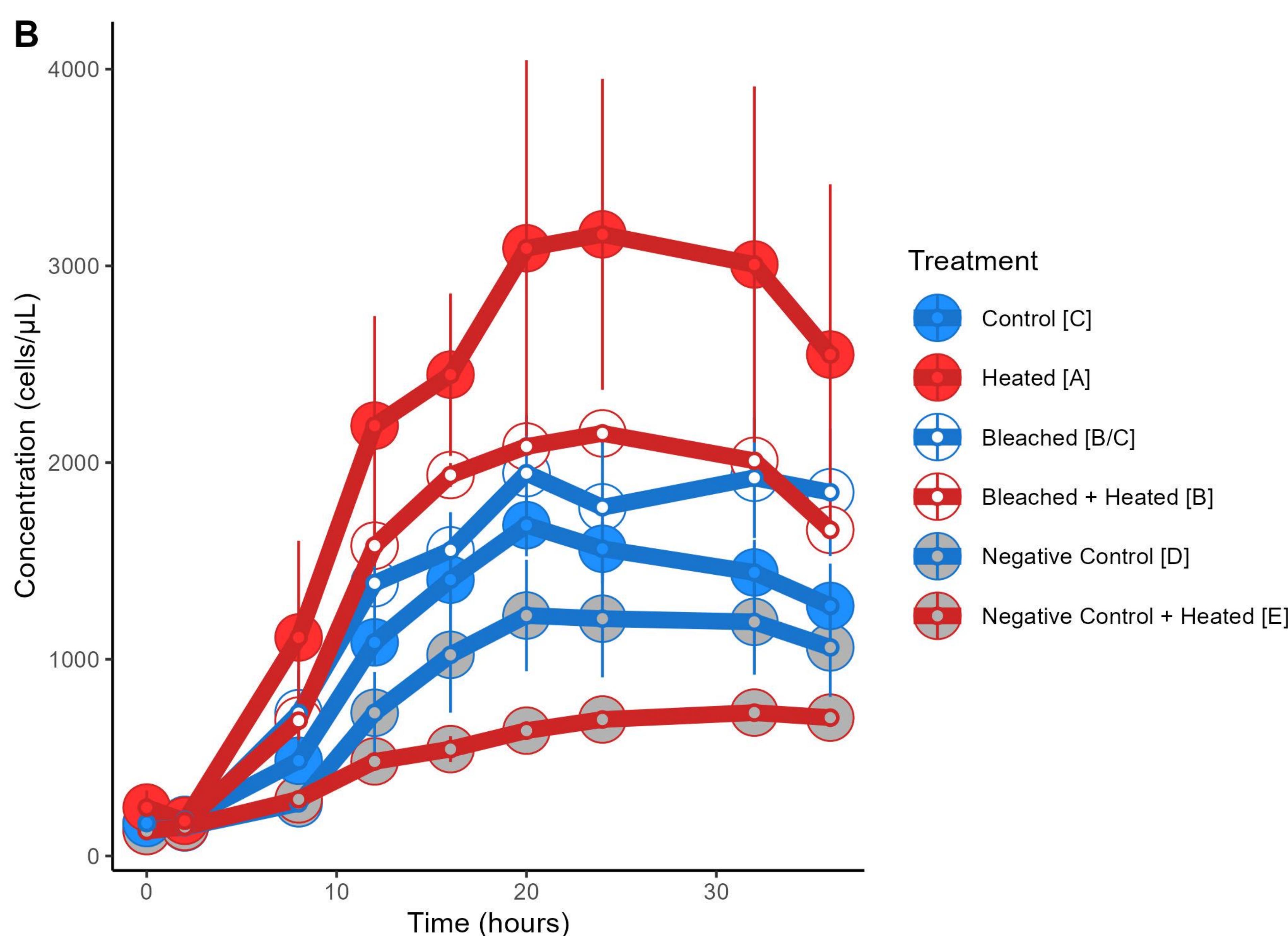
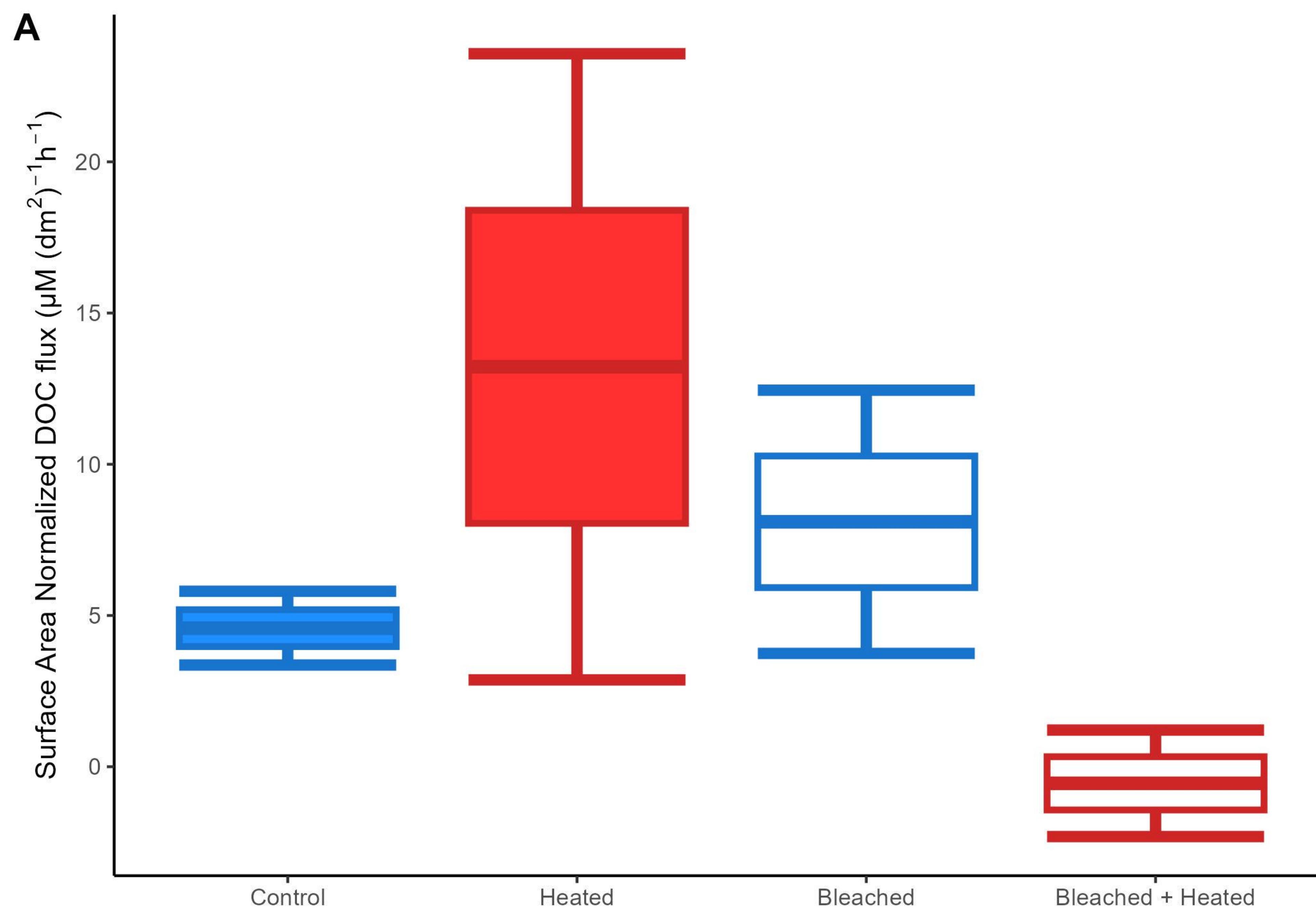
# Bleaching Event 2019

## Experiment May 2019

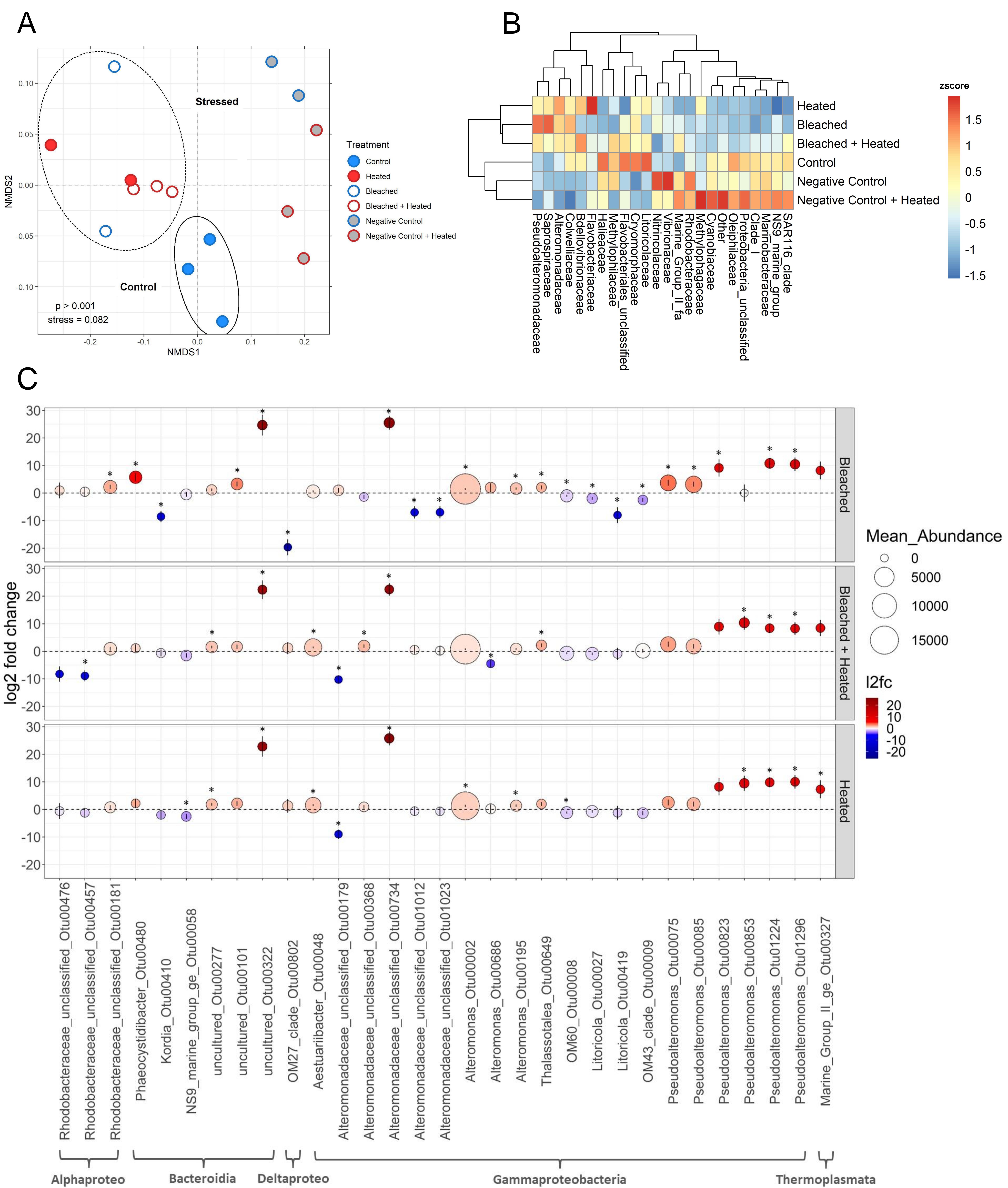


Picture bleached reef, May 2019, by Linda Wegley Kelly  
Coral art adjusted from Jeneses Imre, dreamstime.com

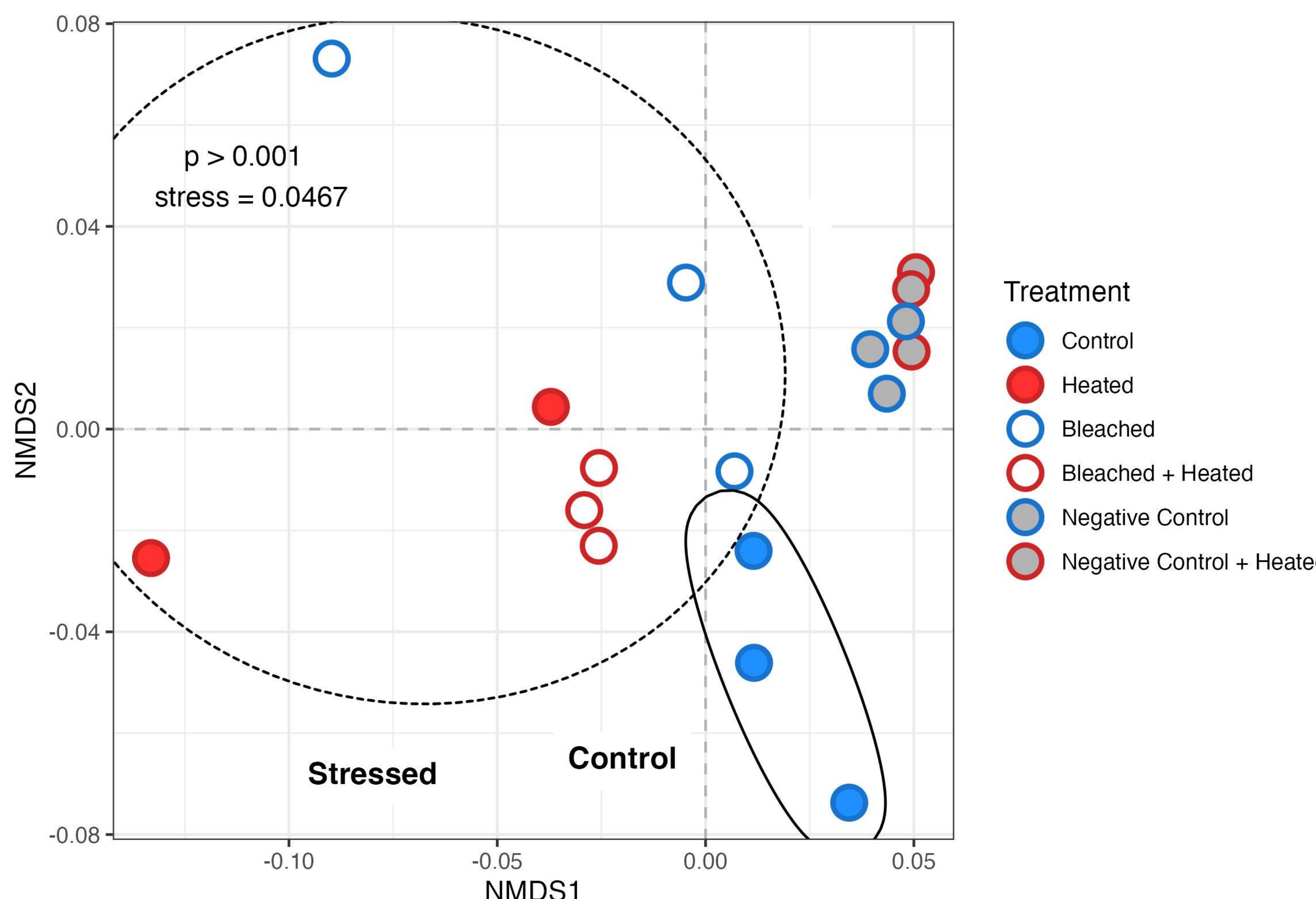
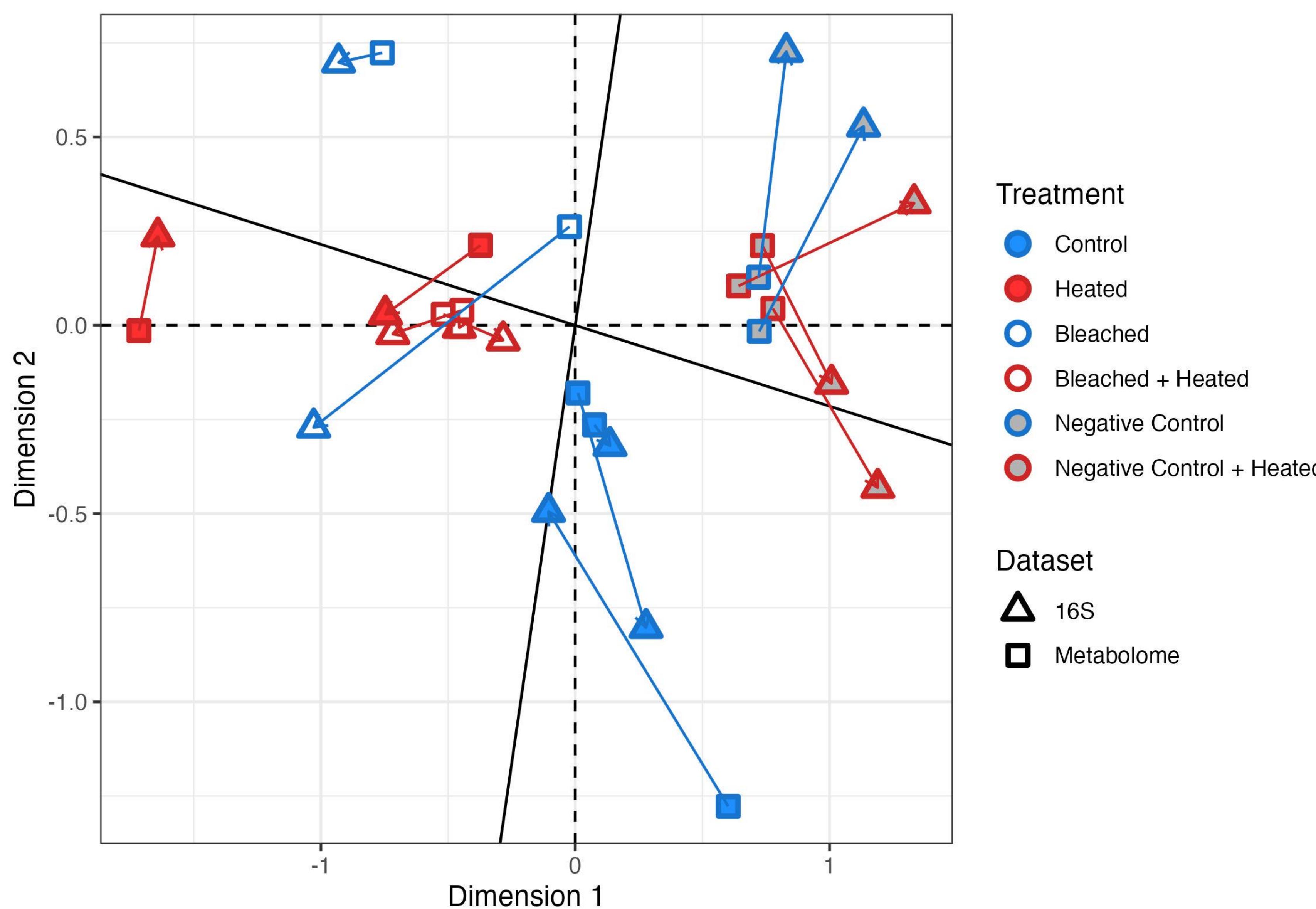
**Figure 1:** Field collections and experimental design. Unbleached and bleached corals were collected from a reef in Mo'orea, French Polynesia immediately following a bleaching event. Picture on top: the LTER1 fore reef in Mo'orea, French Polynesia representative of the status of the reef where both bleached and unbleached corals were present. **A.I-A.V)** Overview of the experimental design. In addition to the four treatments two negative controls of ambient and heated water were run in parallel but are not shown in the overview. **A.I)** Coral nubbin collection of non-bleached and bleached corals. **A.II)** 7 day pretreatment in flow through aquaria at ambient or heated water temperatures. **A.III)** DOM exudation, **A.IV)** 36 hour dark bottle incubation, **A.V)** and sampling of DNA (16S), DOC, and DOM. **B)** Mean seawater temperatures over the period from January 1st 2018 until December 31<sup>st</sup> 2019 from three fore reef LTER sites. Standard deviation depicted in blue. The orange line indicates the thermal stress accumulation threshold level of 29°C (Leinbach et al., 2021; Pratchett et al., 2013; Speare et al., 2021). Bleaching was first observed in April 2019 (Leinbach et al., 2021), indicated by the start of the red line, which continued until the temperature levels dropped under the thermal stress accumulation threshold. The experiment, indicated by the purple block, was started immediately after temperatures dipped below the thermal stress accumulation threshold. **C)** A subset of collected nubbins of the three coral species (*Acropora pulchra*, *Pocillopora verrucosa*, *Porites rus*) were sacrificed after the three day acclimatization period for symbiont cell concentration analysis to validate the observed bleaching status at collection **D)** Symbiont cell concentrations of the coral nubbins from the different treatments after seven days in the aquaria.



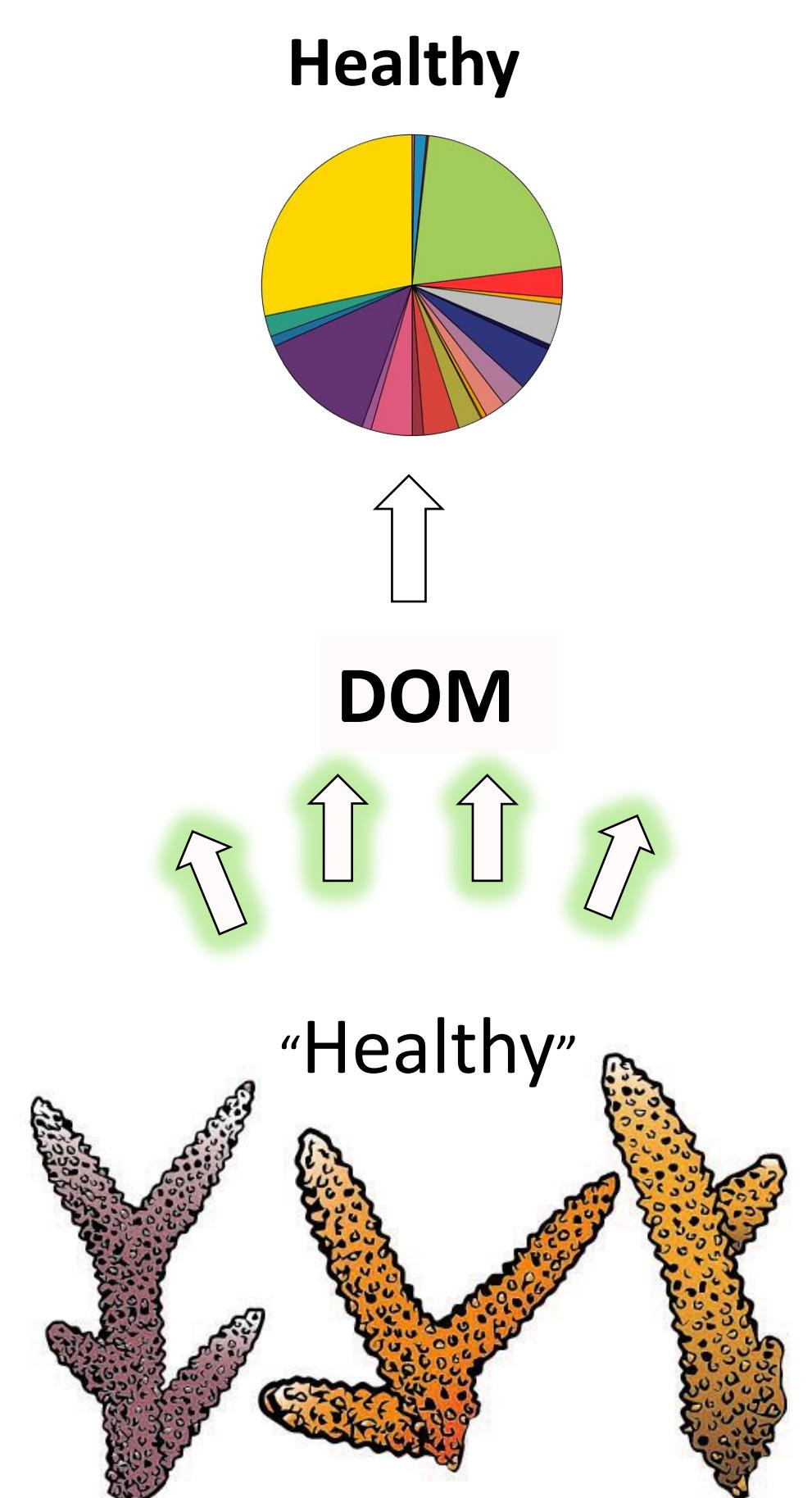
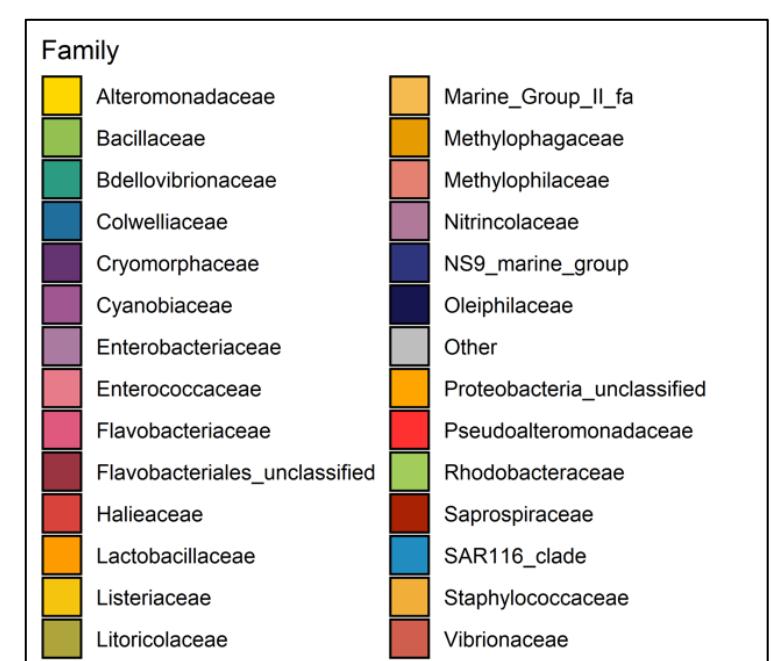
**Figure 2:** **A)** Box and whisker plots of surface area normalized DOC concentrations for the four coral treatments. **B)** Bacterial growth curves for the six treatments in the 36 hour bottle incubation, error bars indicate standard error of the mean. Significant differences between treatments at T=24 (Tukey post-hoc test, p<0.05) are denoted by the square brackets after each treatment name in the legend.



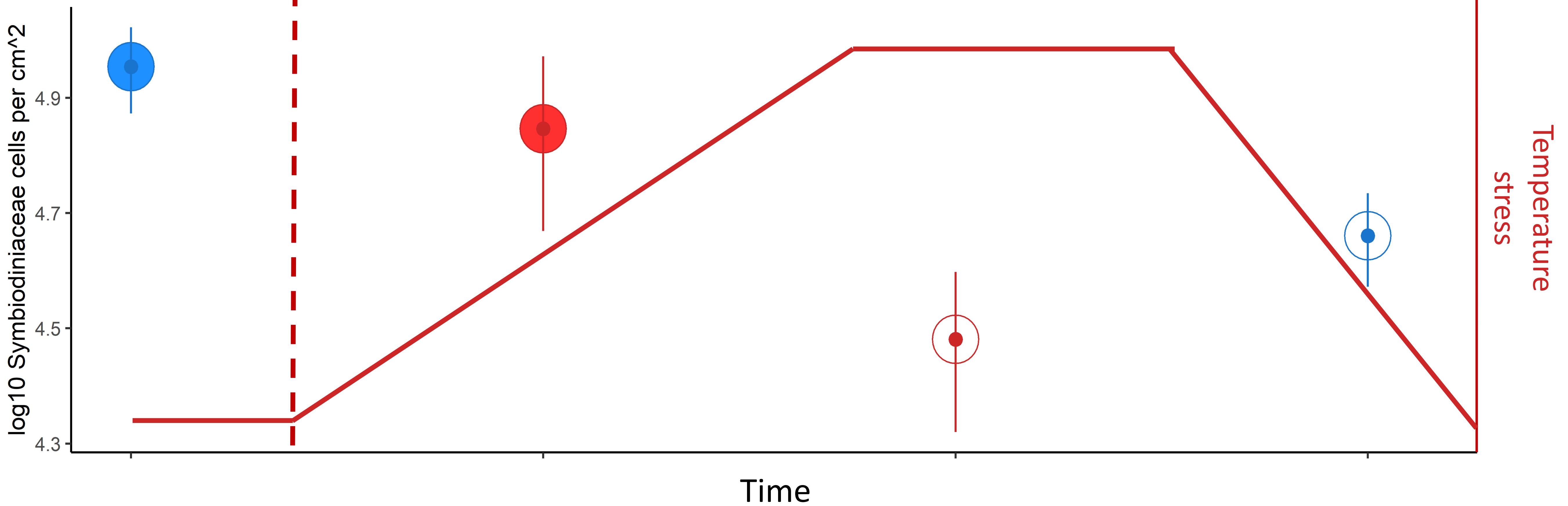
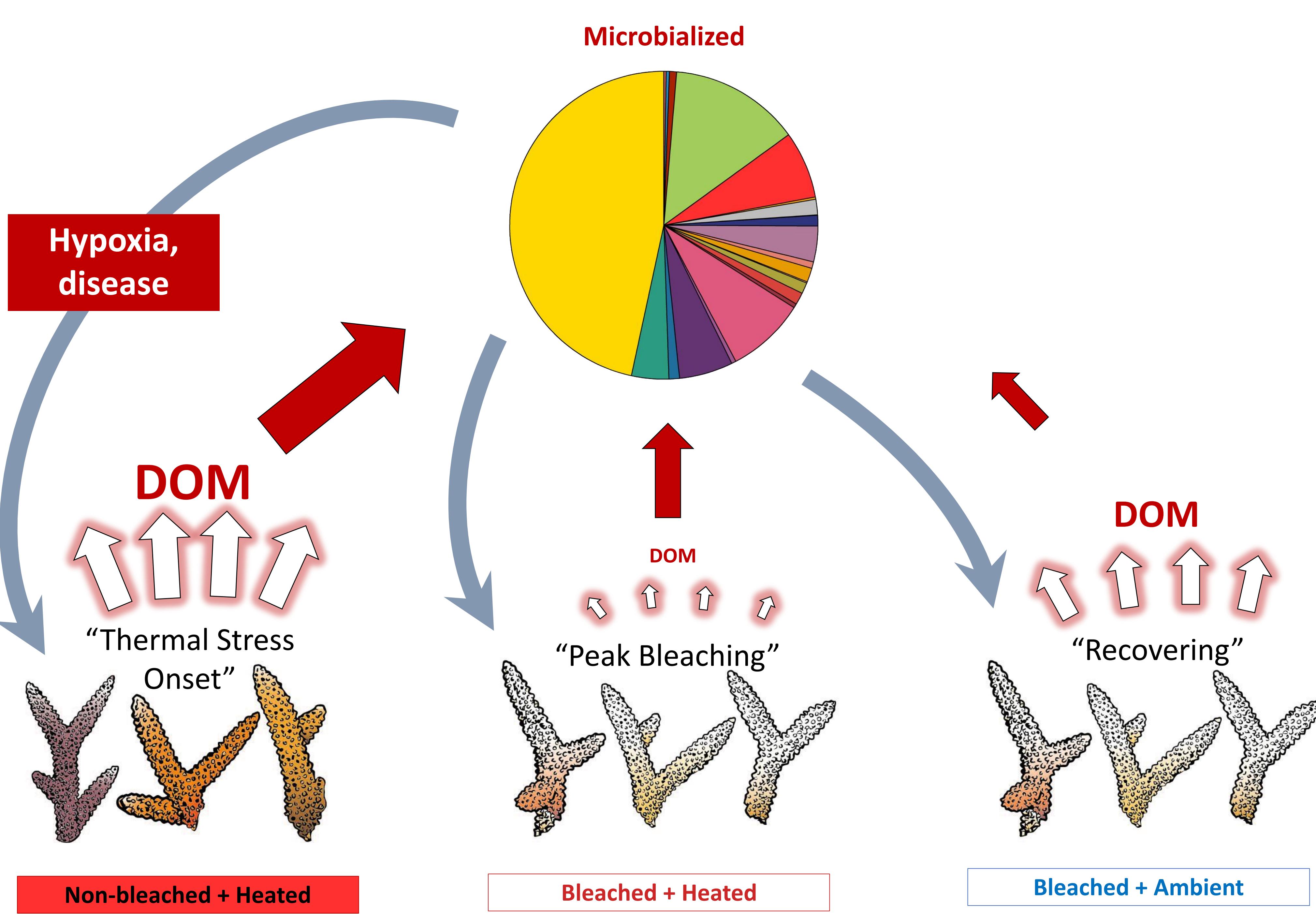
**Figure 3:** **A)** Non-metric multidimensional scaling of microbial community samples using Unifrac distances derived from 16S amplicon data. A dashed ellipse denotes the 3 coral stress treatments while a solid ellipse denotes the coral Control treatment. **B)** Two-way heatmap of the most abundant bacterial families in each treatment. Abundant families were defined as: relative abundance  $\geq .005$  in samples  $\geq 3$  or a relative abundance  $\geq .1$  in samples  $\geq 1$ . Each cell represents the z-scored mean relative abundance of a given family in a treatment. Cells are colored according to z-score, with warmer colors indicating enrichment and cooler colors indicating depletion. Clustering was performed using Euclidian distances. **C)** Visualization of the 31 OTUs determined to be significantly differentially abundant (DA) in at least one of the three stress treatments compared to Control samples by DESeq2. Dotplot of the log2 fold-change values for the 31 significantly DA OTUs in the three coral stress treatments. Each dot represents a given OTU in a given treatment. Dot height on the y-axis and color correspond to log2 fold-change values. Error bars depict the standard error of each log2 fold-change value calculated by DESeq2. Dot size corresponds to mean raw abundance. Each OTU is labeled according to its class, family, and Genus\_OTUNumber on the x-axis. Asterisks denote a significantly DA ASV in a treatment.

**A****B**

**Figure 4:** **A)** Non-metric multidimensional scaling plot of t0 metabolomic samples using bray curtis dissimilarity. A dashed ellipse denotes the 3 coral stress treatments while a solid ellipse denotes the coral Control treatment. **B)** Procrustes visualization of multivariate metabolomic and microbial samples. Arrows point from microbial samples to corresponding metabolomic samples.



Non-bleached + Ambient

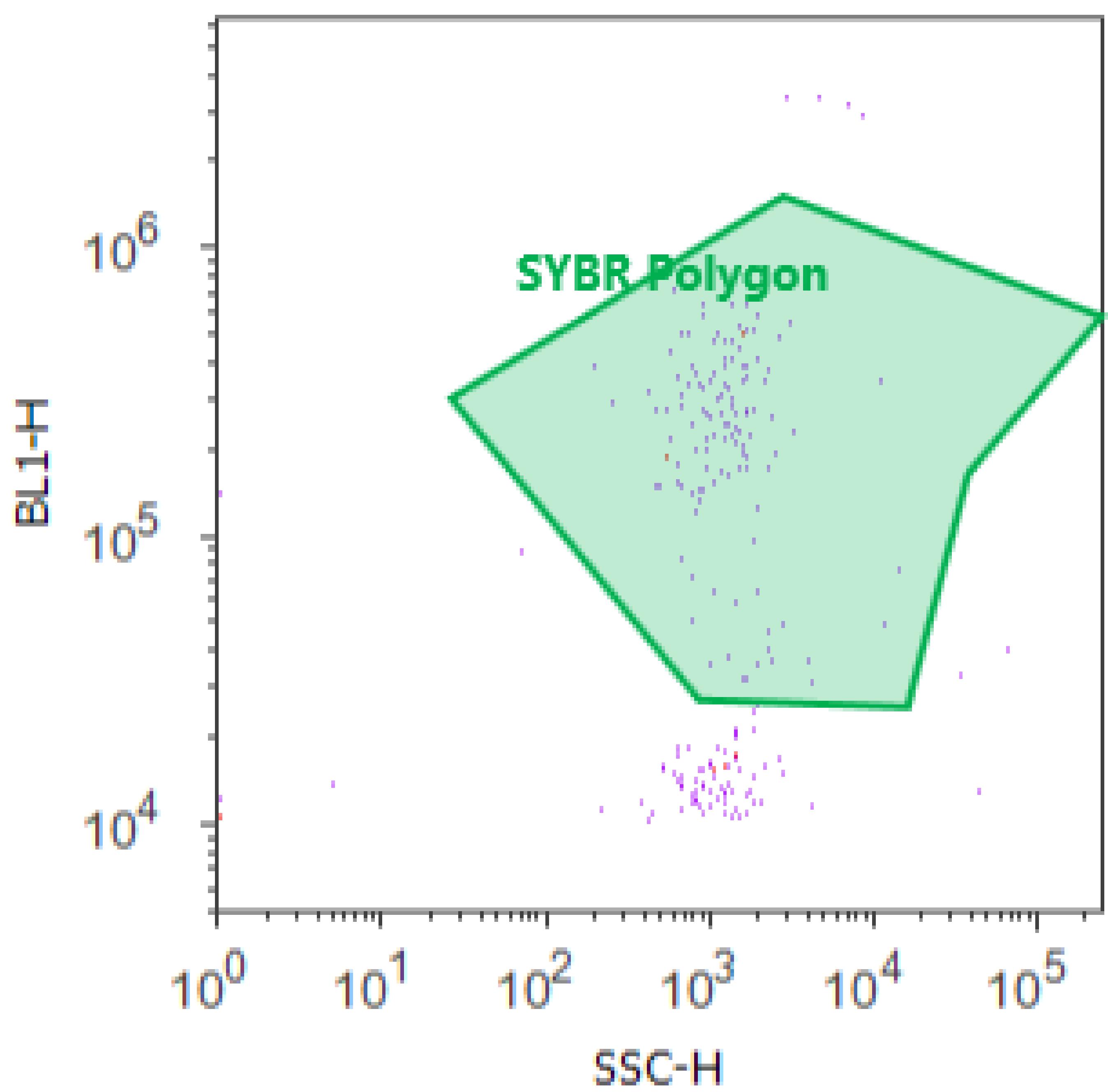


**Figure 5:** Conceptual representation of biogeochemical changes during a coral bleaching event. Bleaching progresses from left to right, with SST values increasing until their peak and then return to ambient values. Corals experience a change in physiological state and symbiont densities through the thermal anomaly, going from "Healthy" to "Thermal Stress Onset" to "Peak Bleaching" and lastly, "Recovering". The associated treatment names from our experiment are written below the corals. Symbiont densities for each treatment are plotted with temperature, with densities decreasing through "Peak Bleaching" and then increasing slightly in "Recovering." Densities were derived from data presented in Figure 1D. DOM flux is highest at "Thermal Stress Onset", indicated by the size of the arrows pointing from corals to "DOM". In all 3 of the stressed treatments, bacterioplankton communities shift towards a "microbialized" state marked by increased cell counts (indicated by the size of the arrow pointing towards the pie chart) and a greater relative abundance of copiotrophs and pathogens, namely in the Alteromonadaceae, Pseudoalteromonadaceae, and Flavobacteriaceae families. We propose that these microbialized communities derived from stressed coral DOM exudates further harm the corals via hypoxia from increased bacterial loads and disease from the uptick in bacterial pathogens. The state of microbialization is most pronounced at the onset of thermal stress, may push corals towards more severe bleaching and ultimately, mortality.

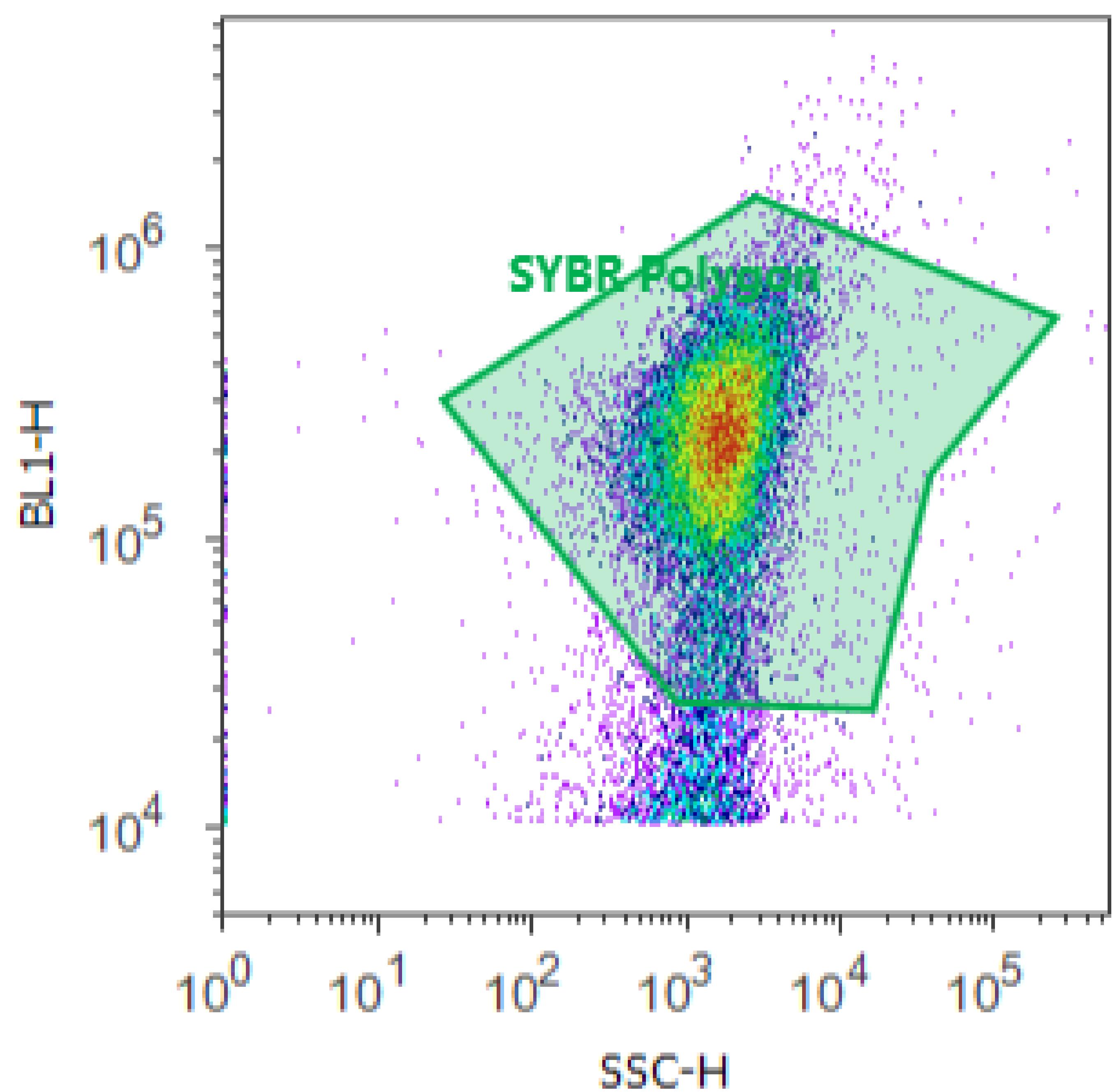
OTU	Heated adjusted pvalue	Bleached adjusted pvalue	Bleached + Heated adjusted pvalue	Heated I2fc	Bleached I2fc	Bleached + Heated I2fc	Phylum	Class	Order	Family	Genus
Otu01224	1.57E-06	6.00E-08	2.71E-05	9.847232822	10.79266169	8.36232019	Proteobacteria	Gammapro teobacteria	Alteromonadales	Pseudoalterom onadaceae	Pseudoalteromas
Otu01296	0.000856922	0.000561011	0.005141682	10.04404043	10.45934919	8.232520837	Proteobacteria	Gammapro teobacteria	Alteromonadales	Pseudoalterom onadaceae	Pseudoalteromas
Otu00322	6.42E-08	2.29E-09	2.21E-09	22.86585664	24.67060057	22.36474822	Bacteroidetes	Bacteroidia	Chitinophagales	Saprosiraceae	uncultured
Otu00734	8.50E-23	3.11E-22	2.80E-20	25.79903195	25.54192061	22.46096177	Proteobacteria	Gammapro teobacteria	Alteromonadales	Alteromonadac eae	Alteromonadaceae_u nclassified
Otu00195	0.013386864	0.00193969	0.163719978	1.369049784	1.622337073	0.845563362	Proteobacteria	Gammapro teobacteria	Alteromonadales	Alteromonadac eae	Alteromonas
Otu00002	0.004336786	0.000715469	0.120200566	1.292770944	1.468968919	0.775714091	Proteobacteria	Gammapro teobacteria	Alteromonadales	Alteromonadac eae	Alteromonas
Otu00008	0.012939139	0.035693556	0.153825239	-1.15038439	-0.99083639	-0.723915892	Proteobacteria	Gammapro teobacteria	Cellvibrionales	Haliaceae	OM60
Otu00179	3.03E-06	0.717552218	3.63E-11	-8.977840531	1.002252708	-10.22923634	Proteobacteria	Gammapro teobacteria	Alteromonadales	Alteromonadac eae	Alteromonadaceae_u nclassified
Otu00277	0.005073071	0.110479945	0.010219414	1.820452043	1.183562608	1.550819102	Bacteroidetes	Bacteroidia	Flavobacteriales	Flavobacteriac eae	uncultured
Otu00048	0.00042511	0.386129529	0.000257098	1.560964377	0.591538296	1.434128075	Proteobacteria	Gammapro teobacteria	Alteromonadales	Alteromonadac eae	Aestuariibacter
Otu00853	0.006798514	1	0.000765194	9.519537909	0	10.36647892	Proteobacteria	Gammapro teobacteria	Alteromonadales	Pseudoalterom onadaceae	Pseudoalteromas
Otu00058	0.048883543	0.931163267	0.302512595	-2.52361206	-0.482066258	-1.518716588	Bacteroidetes	Bacteroidia	Flavobacteriales	NS9_marine_g roup	NS9_marine_group_ge
Otu00823	NA	0.031179732	0.023655739	8.24000674	9.123083651	8.911697244	Proteobacteria	Gammapro teobacteria	Alteromonadales	Pseudoalterom onadaceae	Pseudoalteromas
Otu01012	NA	0.015381298	0.997343993	-0.587243215	-6.975738423	0.518289667	Proteobacteria	Gammapro teobacteria	Alteromonadales	Alteromonadac eae	Alteromonadaceae_u nclassified
Otu01023	NA	0.015381298	0.997343993	-0.687454186	-6.963518469	0.238381381	Proteobacteria	Gammapro teobacteria	Alteromonadales	Alteromonadac eae	Alteromonadaceae_u nclassified
Otu00419	NA	0.035693556	0.997343993	-1.158221028	-7.988865898	-0.928714273	Proteobacteria	Gammapro teobacteria	Oceanospirillales	Litoricolaceae	Litoricola
Otu00327	NA	0.075398398	0.038471134	7.309356596	8.193753569	8.464131894	Euryarchaeota	Thermopla smata	Marine_Group_II	Marine_Group_II_ta	Marine_Group_II_ge
Otu00476	NA	0.931163267	0.036816121	-0.575524572	0.963578486	-8.258405214	Proteobacteria	Alphaprote obacteria	Rhodobacterales	Rhodobacterac eae	Rhodobacteraceae_u nclassified
Otu00649	0.065233476	0.034948803	0.011581861	1.985756711	2.101911452	2.205220625	Proteobacteria	Gammapro teobacteria	Alteromonadales	Colwelliaceae	Thalassotalea
Otu00101	0.099973871	0.002285941	0.234525577	2.185078263	3.294200193	1.633946032	Bacteroidetes	Bacteroidia	Chitinophagales	Saprosiraceae	uncultured
Otu00181	0.69627657	0.035693556	0.825289484	0.777679188	2.221388853	0.908460509	Proteobacteria	Alphaprote obacteria	Rhodobacterales	Rhodobacterac eae	Rhodobacteraceae_u nclassified
Otu00027	0.502997039	0.001748299	0.245692049	-0.714321143	-1.943918868	-0.898704378	Proteobacteria	Gammapro teobacteria	Oceanospirillales	Litoricolaceae	Litoricola
Otu00410	0.520079901	0.000561011	0.997343993	-1.991835073	-8.511628793	-0.632952773	Bacteroidetes	Bacteroidia	Flavobacteriales	Flavobacteriac eae	Kordia
Otu00480	0.495008674	0.002075657	0.997343993	2.222815497	5.766700401	1.107160047	Bacteroidetes	Bacteroidia	Flavobacteriales	Cryomorphacea ae	Phaeocystidibacter
Otu00075	0.116575213	0.005535059	0.068099299	2.552530067	3.699294535	2.545924273	Proteobacteria	Gammapro teobacteria	Alteromonadales	Pseudoalterom onadaceae	Pseudoalteromas
Otu00085	0.168430135	0.004035638	0.163719978	1.965130057	3.203074746	1.797279721	Proteobacteria	Gammapro teobacteria	Alteromonadales	Pseudoalterom onadaceae	Pseudoalteromas
Otu00802	0.825080317	5.56E-10	0.997343993	1.328142611	-19.63555197	1.188804472	Proteobacteria	Deltaprote obacteria	Bdellovibrionales	Bdellovibrionac eae	OM27_clade
Otu00009	0.394038388	0.007270622	0.997343993	-1.293968348	-2.496030483	0.162912968	Proteobacteria	Gammapro teobacteria	Betaproteobacter iales	Methylophilacea eae	OM43_clade
Otu00368	0.529884931	0.231526274	0.029464859	0.927913394	-1.38182967	1.855013862	Proteobacteria	Gammapro teobacteria	Alteromonadales	Alteromonadac eae	Alteromonadaceae_u nclassified
Otu00457	0.805201058	0.941906395	0.000151366	-1.195502441	0.494594853	-8.927337169	Proteobacteria	Alphaprote obacteria	Rhodobacterales	Rhodobacterac eae	Rhodobacteraceae_u nclassified
Otu00686	0.964756238	0.663330615	0.02552918	0.234359488	1.952445776	-4.511709297	Proteobacteria	Gammapro teobacteria	Alteromonadales	Alteromonadac eae	Alteromonas

**Table 1:** DESeq2 results for the 31 OTUs that were significantly differentially abundant in at least one coral stress treatment relative to coral Controls.

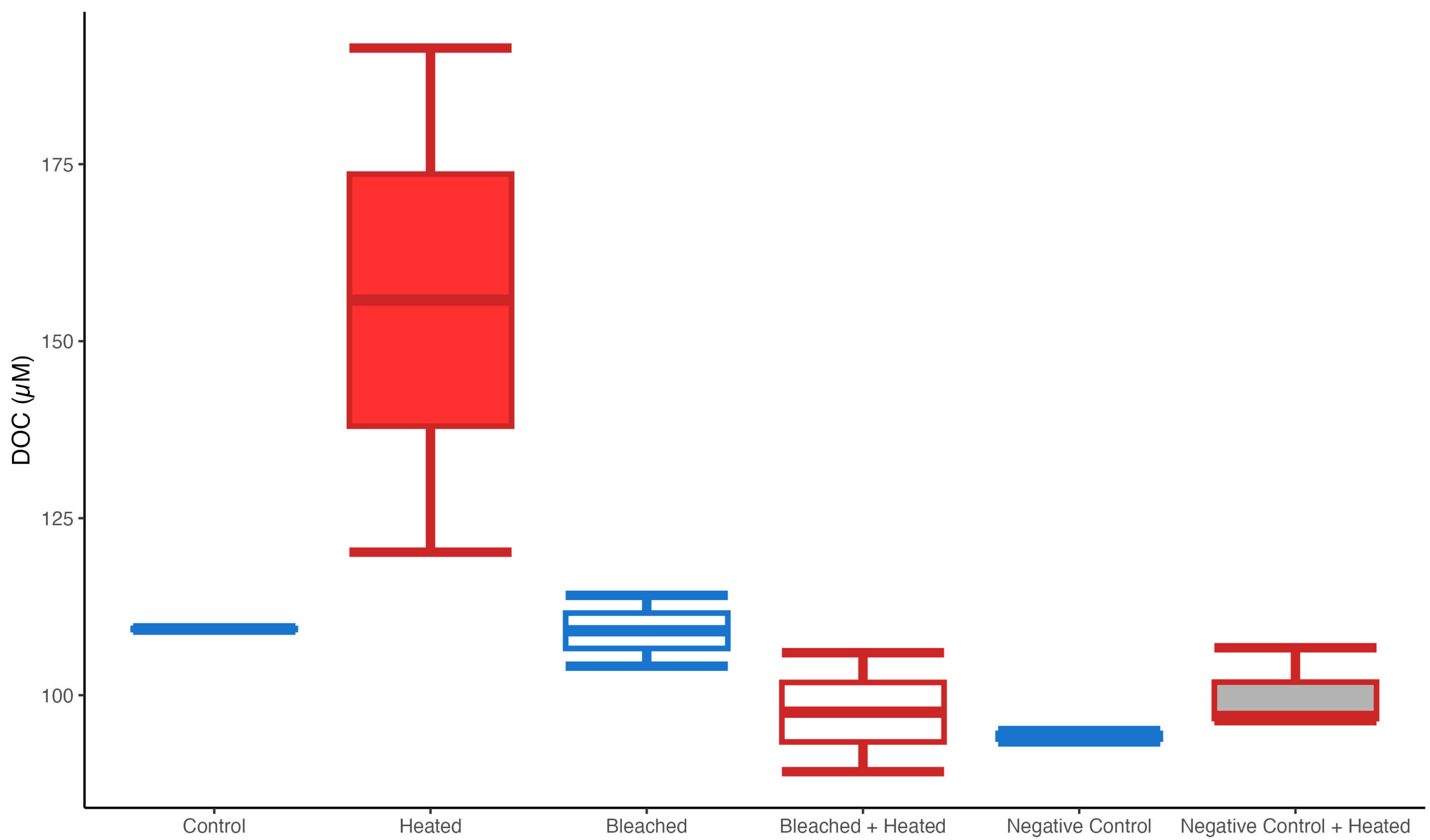
Control



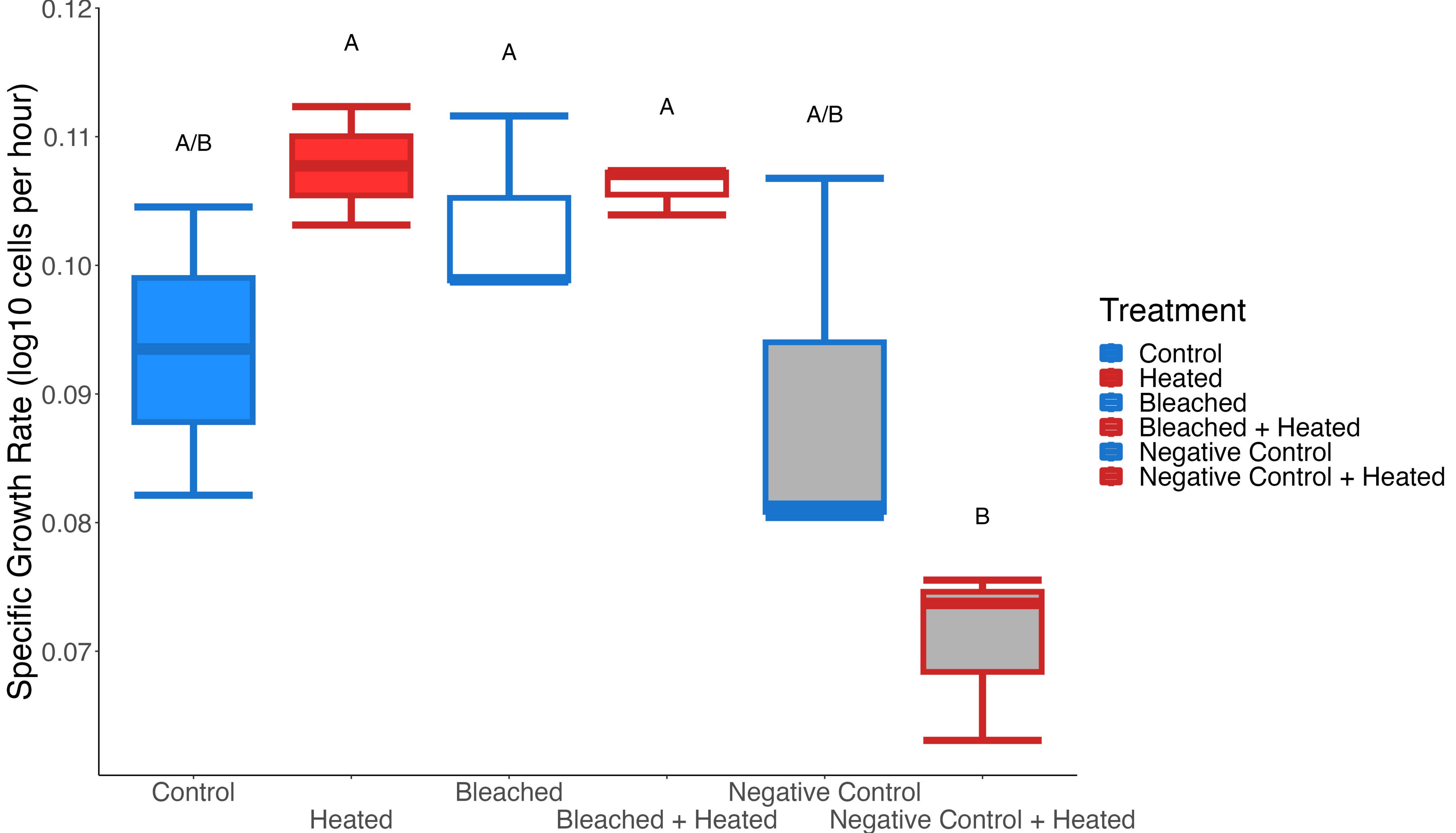
Sample



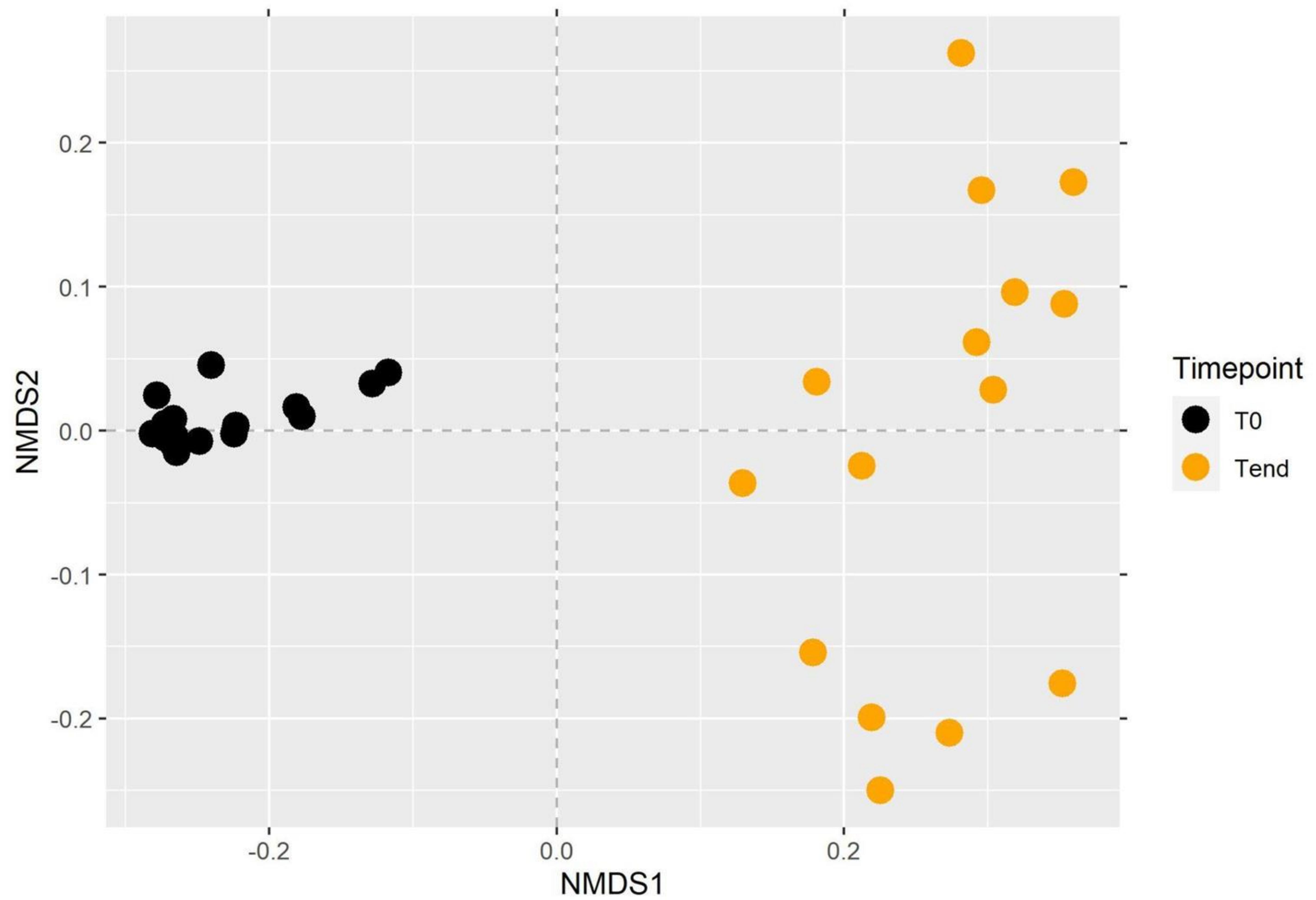
**Figure S1:** Representative density plots of gated SYBR polygon derived bacterial counts for a SYBR stained  $.2\mu\text{m}$  filtered milliq control and a SYBR stained sample.



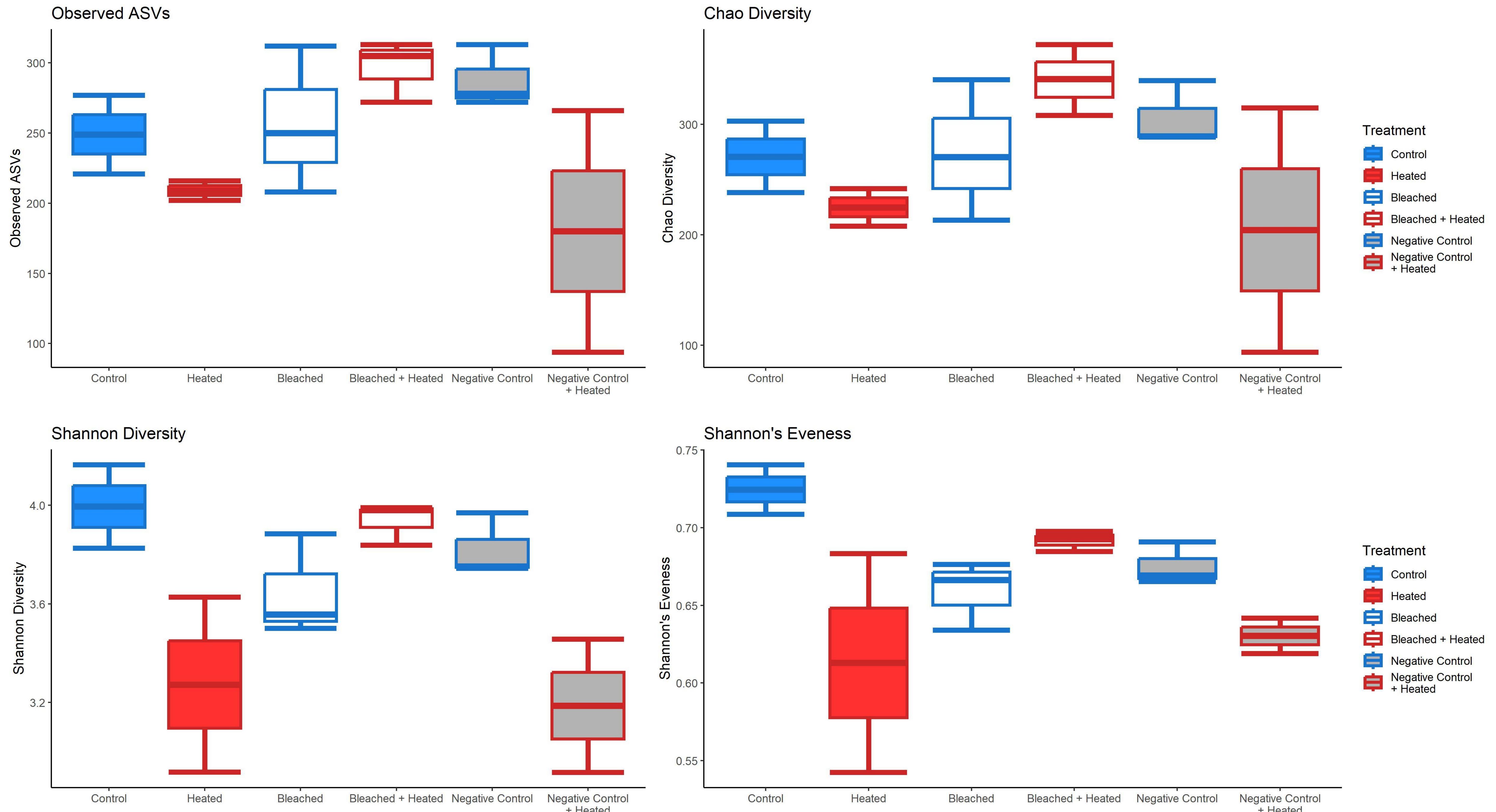
**Figure S2:** Box and whisker plots of raw DOC exudate concentrations ( $\mu\text{M}$ ) for the 6 treatments.



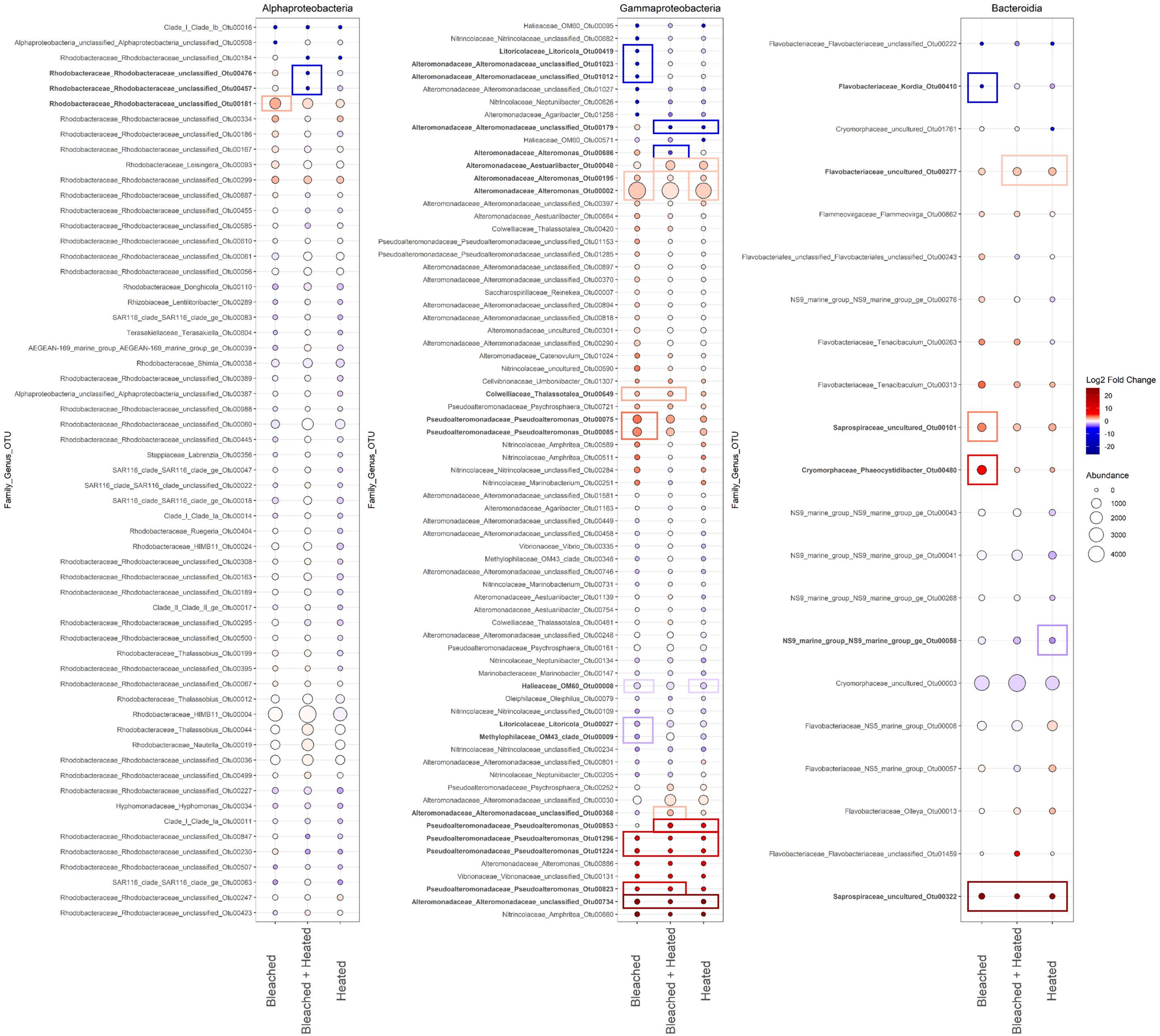
**Figure S3:** Box and whisker plots of bacterial specific growth rate, in  $\log_{10}$  cells per hour, for the 6 treatments. Significant differences between treatments (Tukey post-hoc test,  $p < 0.05$ ) are denoted by letters above each boxplot.



**Figure S4:** Non-metric multidimensional scaling plot of bacterial communities from start and end of bottle incubation using unifrac dissimilarity.



**Figure S5:** Box and whisker plots of the alpha diversity of the bacterial communities at the end of the incubation



**Figure S6:** Direct comparison of bacterial OTUs enriched and/or depleted in the three stressed coral treatments relative to the Control corals. The log2 fold change of the 159 most abundant/prevalent OTUs in the three coral stress treatments compared to the Control treatment. Points are colored by log2 fold change, with warmer colors indicating more enrichment and cooler colors indicating more depletion relative to the Controls. Point size indicates the mean abundance of a given OTU in a given treatment. OTUs are labeled according to their family, genus, and OTU Number on the y axis. OTUs labeled in bold were determined by DESeq2 to be significantly differentially abundant in at least one of the three treatments compared to Controls ( $p \leq .05$  after FDR). Boxes denote in which treatment there is a significant change and the color of the box indicates whether this was a significant enrichment (red) or depletion (blue).



**Figure S7:** Stacked barplots of the relative abundance of significant OTUs ( $p \leq .05$  after FDR) enriched or depleted in any of the 3 coral stress treatments relative to the Control treatment according to DESeq2. Column facets denote if a given OTU is enriched or depleted relative to the Control. Row facets denote which treatments a group of OTUs is either significantly enriched or depleted in. Relative abundance was derived from the non-subsampled, raw abundance data used in DESeq2. Bars are colored according to bacterial family.

Family	Ambient Water Control	Bleached	Bleached + Heated	Control	Negative Control	Negative Control + Heated
Alteromonadaceae	0.226792	0.425707	0.386279	0.283001	0.466167	0.203806
<b>Bdellovibrionaceae</b>	0.001584	0.002792	0.051251	0.022333	0.039083	0.001723
<b>Clade_I</b>	0.004751	0.001125	0.002584	0.004917	0.001375	0.006055
<b>Colwelliaceae</b>	0.001875	0.0175	0.012389	0.011139	0.011042	0.000472
<b>Cryomorphaceae</b>	0.007875	0.072083	0.057972	0.129278	0.056333	0.017111
<b>Cyanobiaceae</b>	0.010042	0.004958	0.004917	0.01	0.004751	0.017055
<b>Flavobacteriaceae</b>	0.039043	0.036251	0.044833	0.04436	0.082708	0.048277
<b>Flavobacteriales_unclassified</b>	0.005668	0.007458	0.009555	0.012027	0.004375	0.007223
<b>Halieaceae</b>	0.028792	0.013	0.0195	0.038306	0.012625	0.023194
<b>Litoricolaceae</b>	0.003833	0.003583	0.011528	0.025444	0.011625	0.002305
<b>Marine_Group_II_fa</b>	0.005834	0.002875	0.005083	0.001306	0.001333	0.008278
<b>Marinobacteraceae</b>	0.004542	0.000917	0.001917	0.003556	0.00075	0.005694
<b>Methylophagaceae</b>	0.006792	0.006125	0.004305	0.005306	0.01475	0.0455
<b>Methylophilaceae</b>	0.020417	0.002792	0.020583	0.022	0.006917	0.002861
<b>Nitrinolaceae</b>	0.111748	0.043625	0.01425	0.027361	0.037417	0.055972
<b>NS9_marine_group</b>	0.04225	0.028833	0.030028	0.047695	0.01125	0.06925
<b>Oleophilaceae</b>	0.002459	0.000292	5.00E-04	0.005528	0.000417	0.005695
<b>Proteobacteria_unclassified</b>	0.004042	0.002458	0.002972	0.006833	0.002375	0.0095
<b>Pseudoalteromonadaceae</b>	0.035792	0.122251	0.08125	0.033472	0.070583	0.022223
<b>Rhodobacteraceae</b>	0.380831	0.166	0.194276	0.212747	0.136707	0.333888
<b>Saprospiraceae</b>	0.002334	0.013083	0.005584	0.002055	0.007542	0.003832
<b>SAR116_clade</b>	0.008167	0.00425	0.009638	0.013028	0.003292	0.016917
<b>Vibronaceae</b>	0.011084	0.00325	0.002806	0.002445	0.002459	0.004944
<b>Other</b>	0.033459	0.018797		0.026	0.035864	0.014128
						0.088225

OTU	Heated adjusted pvalue	Bleached adjusted pvalue	Bleached + Heated adjusted pvalue	Heated I2fc	Bleached I2fc	Bleached + Heated I2fc	Phylum	Class	Order	Family	Genus
Otu01224	1.57E-06	6.00E-08	2.71E-05	9.847232822	10.79266169	8.36232019	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu01296	0.000856922	0.000561011	0.005141682	10.04404043	10.45934919	8.232520837	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu00322	6.42E-08	2.29E-09	2.21E-09	22.86585664	24.67060057	22.36474822	Bacteroides	Bacteroidia	Chitinophagales	Sapspiraceae	uncultured
Otu00734	8.50E-23	3.11E-22	2.80E-20	25.79903195	25.54192061	22.46096177	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u_nclassified
Otu00195	0.013386864	0.00193969	0.163719978	1.369049784	1.622337073	0.845563362	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonas
Otu00002	0.004336786	0.000715469	0.120200566	1.292770944	1.468968919	0.775714091	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonas
Otu00008	0.012939139	0.035693556	0.153825239	-1.15038439	-0.99083639	-0.723915892	Proteobacteria	Gammaproteobacteria	Cellvibrionales	Halieaceae	OM60
Otu00179	3.03E-06	0.717552218	3.63E-11	-8.977840531	1.002252708	-10.22923634	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u_nclassified
Otu00277	0.005073071	0.110479945	0.010219414	1.820452043	1.183562608	1.550819102	Bacteroides	Bacteroidia	Flavobacteriales	Flavobacteriaceae	uncultured
Otu00048	0.00042511	0.386129529	0.000257098	1.560964377	0.591538296	1.434128075	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Aestuaribacter
Otu00853	0.006798514	1	0.000765194	9.519537909	0	10.36647892	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu00058	0.048883543	0.931163267	0.302512595	-2.52361206	-0.482066258	-1.518716588	Bacteroides	Bacteroidia	Flavobacteriales	NS9_marine_group	NS9_marine_group_-
Otu00823	NA	0.031179732	0.023655739	8.24000674	9.123083651	8.911697244	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu01012	NA	0.015381298	0.997343993	-0.587243215	-6.975738423	-0.518289667	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae_u_nclassified	Alteromonadaceae_u_nclassified
Otu01023	NA	0.015381298	0.997343993	-0.687454186	-6.963518469	-0.238381381	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u_nclassified
Otu00419	NA	0.035693556	0.997343993	-1.158221028	-7.988865898	-0.928714273	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Litoricolaceae	Litoricola
Otu01027	NA	NA	NA	-1.88848212	-7.94023067	-2.034125724	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u_nclassified
Otu00251	NA	NA	NA	3.060033823	3.374630513	-1.262531859	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitrincolaceae	Marinobacterium
Otu00334	NA	NA	NA	1.747807596	2.125371669	-0.466164781	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Rhodobacteraceae_u_nclassified
Otu00590	NA	NA	NA	0.405261262	3.449498837	0.913961921	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitrincolaceae	uncultured
Otu00660	NA	NA	NA	24.67753244	25.18636193	20.43224732	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitrincolaceae	Amphritea
Otu00682	NA	NA	NA	-1.125497312	-7.505249022	-1.095319913	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitrincolaceae	Nitrinolac_ea_unclassified
Otu00886	NA	NA	NA	10.86560394	10.16269518	8.202090458	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonas
Otu00327	NA	0.075398398	0.038471134	7.309356596	8.193753569	8.464131894	Euryarchaeota	Thermoplasmata	Marine_Group_II_fa	Marine_Group_II_fa	Marine_Group_II_fa
Otu00476	NA	0.931163267	0.03681621	-0.575524572	0.963578486	-8.258405214	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Rhodobacteraceae_u_nclassified
Otu00988	NA	0.931163267	0.997343993	-0.635916566	-0.738271156	-0.164126611	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Rhodobacteraceae_u_nclassified
Otu01139	NA	0.941906395	0.997343993	-1.741397685	0.501820981	0.686723658	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Aestuaribacter
Otu01163	NA	0.959420103	0.997343993	-0.847291607	-0.476962989	-0.712268553	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Agaribacter
Otu01258	NA	0.090010579	0.853679818	-2.301468018	-8.253191608	-3.32275586	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Agaribacter
Otu01307	NA	0.546186871	0.536048968	1.720813377	2.670910972	2.734310686	Proteobacteria	Gammaproteobacteria	Cellvibrionales	Cellvibronaceae	Umbonibaeter
Otu00016	NA	0.26350177	0.161979995	-7.309673984	-7.885317528	-8.56105159	Proteobacteria	Alphaproteobacteria	SAR11_clade	Clade_I	Clade_lb
Otu01459	NA	1	0.085215831	0	0	9.115324903	Bacteroides	Bacteroidia	Flavobacteriales	Flavobacteriaceae	Flavobacteriaceae_unclassified
Otu00184	NA	0.999312469	0.245692049	-6.706807263	-0.307467432	-7.958212965	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Rhodobacteraceae_u_nclassified

Otu01581	NA	1	0.9973439 93	-0.193433094	0.040729 851	-0.485664221	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u nclassified
Otu01761	NA	1	0.9973439 93	-6.424341855	0.050024 234	-0.514027354	Bacteroidetes	Bacteroidia	Flavobacteriales	Cryomorphaceae	uncultured
Otu00022	NA	0.8431401	0.9973439 93	-1.110210692	0.829830 397	0.481767804	Proteobacteria	Alphaproteobacteria	Puniceispirillales	SAR116_clade	SAR116_c lade_unclassified
Otu00222	NA	0.145811281	0.9973439 93	-7.749039373	8.324643 028	-2.78043979	Bacteroidetes	Bacteroidia	Flavobacteriales	Flavobacteriaceae	Flavobacteriaceae_un classified
Otu00023	NA	0.837435504	0.9973439 93	-1.174800125	0.857240 258	-0.597667688	Actinobacteria	Acidimicrobia	Actinomarinales	Actinomarinae	Candidatus_Actinom arina
Otu00356	NA	0.931163267	0.9973439 93	-0.811495951	0.889485 134	0.217578411	Proteobacteria	Alphaproteobacteria	Rhizobiales	Stappiaceae	Labrenzia
Otu00395	NA	0.931163267	0.9973439 93	-1.062575938	0.670110 76	0.490079667	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacterac eae	Rhodobacteraceae_u nclassified
Otu00423	NA	0.931163267	0.9973439 93	0.115197523	0.898855 182	0.60341746	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacterac eae	Rhodobacteraceae_u nclassified
Otu00455	NA	0.996338958	0.9973439 93	-0.864357981	0.124267 665	-0.92669588	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacterac eae	Rhodobacteraceae_u nclassified
Otu00507	NA	0.816754226	0.9973439 93	-1.45997772	2.061429 117	-0.643812981	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacterac eae	Rhodobacteraceae_u nclassified
Otu00508	NA	0.23904069	0.9973439 93	-0.553377131	7.178294 271	-0.341839676	Proteobacteria	Alphaproteobacteria	Alphaproteobacteria_unclassifie d	Alphaproteobacteria_unclassifie d	AlphaproteobacteriaUnclassified
Otu00604	NA	0.816754226	0.9973439 93	-1.318872691	1.465148 706	0.040340127	Proteobacteria	Alphaproteobacteria	Rhodospirillales	Terasakiellacea e	Terasakiella a
Otu00610	NA	0.941906395	0.9973439 93	-0.140672059	0.539293 234	-0.013759769	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacterac eae	Rhodobacteraceae_u nclassified
Otu00626	NA	0.109618936	0.9973439 93	-2.067769953	8.279883 864	-2.542769707	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitricolaceae	Neptuniibacter
Otu00687	NA	0.931163267	0.9973439 93	-0.444666493	0.670576 067	-0.74704331	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacterac eae	Rhodobacteraceae_u nclassified
Otu00079	NA	0.931163267	0.9973439 93	-0.993641695	0.996162 738	-1.673393498	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Oleophilaceae	Oleophilus
Otu00731	NA	0.816754226	0.9973439 93	-0.798822042	1.233271 486	-0.453786534	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitricolaceae	Marinobacterium
Otu00746	NA	0.816754226	0.9973439 93	-1.399097676	1.428741 156	-0.754133632	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u nclassified
Otu00754	NA	0.999312469	0.9973439 93	-1.278808689	0.238943 64	-0.492098777	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Aestuariibacter
Otu00847	NA	0.999312469	0.9973439 93	-1.049063959	0.130324 896	-2.396139123	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacterac eae	Rhodobacteraceae_u nclassified
Otu00095	NA	0.187440685	0.9973439 93	-7.497171525	8.072758 528	-1.727314231	Proteobacteria	Gammaproteobacteria	Cellvibrionales	Haliaceae	OM60
Otu00649	0.065233476	0.034948803	0.0115818 61	1.985756711	2.101911 452	2.205220625	Proteobacteria	Gammaproteobacteria	Alteromonadales	Colwelliaceae	Thalassota lea
Otu00101	0.099973871	0.002285941	0.2345255 77	2.185078263	3.294200 193	1.633946032	Bacteroidetes	Bacteroidia	Chitinophagales	Saprospiraceae	uncultured
Otu00181	0.69627657	0.035693556	0.8252894 84	0.777679188	2.221388 853	0.908460509	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacterac eae	Rhodobacteraceae_u nclassified
Otu00027	0.502997039	0.001748299	0.2456920 49	-0.714321143	-1.943918 868	-0.898704378	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Litoricolaceae	Litoricola
Otu00410	0.520079901	0.000561011	0.9973439 93	-1.991835073	8.511628 793	-0.632952773	Bacteroidetes	Bacteroidia	Flavobacteriales	Flavobacteriaceae	Kordia
Otu00480	0.495008674	0.002075657	0.9973439 93	2.222815497	5.766700 401	1.107160047	Bacteroidetes	Bacteroidia	Flavobacteriales	Cryomorphaceae	Phaeocystidibacter
Otu00075	0.116575213	0.005535059	0.0680992 99	2.552530067	3.699294 535	2.545924273	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu00085	0.168430135	0.004035638	0.1637199 78	1.965130057	3.203074 746	1.797279721	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu00802	0.825080317	5.56E-10	0.9973439 93	1.328142611	-19.63555 197	1.188804472	Proteobacteria	Deltaproteobacteria	Bdellovibrionales	Bdellovibrionaceae	OM27_clade
Otu00009	0.394038388	0.007270622	0.9973439 93	-1.293968348	-2.496030 483	0.162912968	Proteobacteria	Gammaproteobacteria	Betaproteobacteriales	Methylophilaceae	OM43_clade

Otu00368	0.529884931	0.231526274	0.029464859	0.927913394	-1.38182967	1.855013862	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u_nclassified
Otu00457	0.805201058	0.941906395	0.000151366	-1.195502441	0.494594853	-8.927337169	Proteobacteria	Alphaproteobacteria	Rhodobacteraceae	Rhodobacteraceae_u_nclassified	Rhodobacteraceae_u_nclassified
Otu00686	0.964756238	0.663330615	0.02552918	0.234359488	1.952445776	-4.511709297	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonas
Otu00001	0.381036415	0.717552218	0.825289484	-0.876426519	0.533276725	-0.543701698	Cyanobacteria	Oxyphotobacteria	Synechococcales	Synechococcus_CC9902	Synechococcus_CC9902
Otu00894	0.994638893	0.816754226	0.997343993	0.045675774	1.440533454	-0.301027647	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u_nclassified
Otu00897	0.815004967	0.853542384	0.997343993	-0.710348136	0.821585187	-0.328295517	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u_nclassified
Otu00109	0.75423241	0.462106663	0.997343993	-1.236399236	2.214816925	-0.60771618	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitrinolaceae	Nitrinolaceae_unclassified
Otu00011	0.81361252	0.944210178	0.997343993	-1.509410359	0.599592267	-0.882937083	Proteobacteria	Alphaproteobacteria	SAR11_clade	Clade_I	Clade_la
Otu00110	0.406673715	0.155069283	0.997343993	-1.233260707	1.612787621	-0.625197991	Proteobacteria	Alphaproteobacteria	Rhodobacteraceae	Rhodobacteraceae	Donghicala
Otu01024	0.938466661	0.663330615	0.997343993	0.765633325	3.206446229	1.336305237	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Catenovulum
Otu00012	0.815004967	0.931163267	0.997343993	-0.340929343	0.250297106	-0.103322486	Proteobacteria	Alphaproteobacteria	Rhodobacteraceae	Rhodobacteraceae	Thalassobius
Otu00013	0.165533303	0.944210178	0.997343993	1.841073912	-0.181917587	0.746853599	Bacteroidetes	Bacteroidia	Flavobacteriales	Flavobacteriaceae	Olleya
Otu00131	0.121244671	0.110479945	0.153825239	9.602674377	9.473664791	8.488547811	Proteobacteria	Gammaproteobacteria	Vibrionales	Vibrionaceae	Vibrionaceae_unclassified
Otu01153	0.964756238	0.766136119	0.997343993	-0.387927792	2.498530463	0.015976332	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonadaceae_unclassified
Otu00134	0.394038388	0.682236431	0.997343993	-2.015201479	1.376780781	-0.891109576	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitrinolaceae	Neptuniibacter
Otu00014	0.805201058	0.931163267	0.997343993	-1.245800915	0.990982569	0.235889654	Proteobacteria	Alphaproteobacteria	SAR11_clade	Clade_I	Clade_la
Otu00147	0.520079901	0.816754226	0.997343993	-1.584622098	0.967474311	-0.78069344	Proteobacteria	Gammaproteobacteria	Alteromonadales	Marinobacteraceae	Marinobacter
Otu01285	0.962585859	0.816754226	0.997343993	-0.493401827	1.72892678	0.37437313	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonadaceae_unclassified
Otu00161	0.923626892	0.996338958	0.997343993	-0.480943156	0.153159643	0.178386507	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Psychrospira
Otu00163	0.75423241	0.941906395	0.997343993	-1.068220396	0.373861397	0.296938473	Proteobacteria	Alphaproteobacteria	Rhodobacteraceae	Rhodobacteraceae_u_nclassified	Rhodobacteraceae_u_nclassified
Otu00167	0.964756238	0.931163267	0.997343993	0.251435515	0.737706316	-0.460002935	Proteobacteria	Alphaproteobacteria	Rhodobacteraceae	Rhodobacteraceae_u_nclassified	Rhodobacteraceae_u_nclassified
Otu00017	0.630825576	0.931163267	0.997343993	-1.36454531	-0.578646568	-0.344813295	Proteobacteria	Alphaproteobacteria	SAR11_clade	Clade_II	Clade_II_ge
Otu00018	0.394038388	0.524952282	0.997343993	-1.092297532	0.910053687	0.058942676	Proteobacteria	Alphaproteobacteria	Puniceispirillales	SAR116_clade	SAR116_clade_ge
Otu00186	0.801717483	0.816754226	0.997343993	-0.893518902	1.01474532	-0.265631458	Proteobacteria	Alphaproteobacteria	Rhodobacteraceae	Rhodobacteraceae_u_nclassified	Rhodobacteraceae_u_nclassified
Otu00019	0.964756238	0.931163267	0.997343993	0.053604235	0.196817754	0.4406271	Proteobacteria	Alphaproteobacteria	Rhodobacteraceae	Rhodobacteraceae	Nautella
Otu00189	0.805201058	0.999312469	0.997343993	-0.975494472	-0.079057306	0.421765348	Proteobacteria	Alphaproteobacteria	Rhodobacteraceae	Rhodobacteraceae_u_nclassified	Rhodobacteraceae_u_nclassified
Otu00199	0.801717483	0.931163267	0.997343993	-0.874766739	0.431535534	0.219948377	Proteobacteria	Alphaproteobacteria	Rhodobacteraceae	Rhodobacteraceae	Thalassobius
Otu00205	0.964756238	0.816754226	0.997343993	0.319000179	2.008357797	-1.320957474	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitrinolaceae	Neptuniibacter
Otu00227	0.394038388	0.789470449	0.997343993	-2.035154969	1.104958069	-0.655289435	Proteobacteria	Alphaproteobacteria	Rhodobacteraceae	Rhodobacteraceae_u_nclassified	Rhodobacteraceae_u_nclassified
Otu00230	0.75423241	0.941906395	0.997343993	-2.020657589	0.700936588	-2.133421596	Proteobacteria	Alphaproteobacteria	Rhodobacteraceae	Rhodobacteraceae_u_nclassified	Rhodobacteraceae_u_nclassified
Otu00234	0.394038388	0.306223884	0.853679818	-2.31991559	-2.45837476	-1.490834101	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitrinolaceae	Nitrinolaceae_unclassified

Otu00024	0.679990349	0.999312469	0.9973439 93	-1.239855549	0.056074 764	0.094122335	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	HIMB11
Otu00243	0.964756238	0.655572657	0.9443192 18	-0.130906349	1.654220 562	-1.298336715	Bacteroidetes	Bacteroidia	Flavobacteriales	Flavobacteriales_unclassified	Flavobacteriales_unclassified
Otu00247	0.630825576	0.941906395	0.9973439 93	0.858487428	0.232038 828	-0.245931516	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Rhodobacteraceae_u_nclassified
Otu00248	0.81361252	0.964665376	0.9973439 93	-0.566283314	-0.160514 797	0.106085739	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae_u_nclassified	Alteromonadaceae_u_nclassified
Otu00252	0.831501556	0.941906395	0.8252894 84	0.515433071	-0.263647 114	1.155984062	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Psychospiraera
Otu00263	0.831501556	0.187331272	0.3025125 95	-0.746964218	3.038031 394	2.510263842	Bacteroidetes	Bacteroidia	Flavobacteriales	Flavobacteriaceae	Tenacibaculum
Otu00268	0.65402218	0.964665376	0.9973439 93	-1.349302009	0.200228 522	-0.439934141	Bacteroidetes	Bacteroidia	Flavobacteriales	NS9_marine_group	NS9_marine_group
Otu00276	0.75423241	0.766136119	0.9973439 93	-1.068205299	1.266319 314	0.218425104	Bacteroidetes	Bacteroidia	Flavobacteriales	NS9_marine_group	NS9_marine_group
Otu00284	0.520079901	0.314364579	0.9973439 93	2.592457695	3.222382 144	-0.691202236	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitrinolaceae	Nitrinolaceae_unclassified
Otu00289	0.801717483	0.835272942	0.9973439 93	-1.321766626	-1.334787 873	-0.413835505	Proteobacteria	Alphaproteobacteria	Rhizobiales	Rhizobiaceae	Lentilitoribacter
Otu00290	0.964756238	0.766136119	0.9973439 93	-0.21674809	1.279006 896	0.20764732	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae_u_nclassified	Alteromonadaceae_u_nclassified
Otu00003	0.449599418	0.584706139	0.3677849 46	-0.968663371	-0.838699 51	-0.997352693	Bacteroidetes	Bacteroidia	Flavobacteriales	Cryomorphacea	uncultured
Otu00030	0.679990349	0.959420103	0.6451133 09	0.581070215	0.104949 063	0.734842178	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae_u_nclassified	Alteromonadaceae_u_nclassified
Otu00295	0.75423241	0.944210178	0.9973439 93	-1.12687942	0.297503 728	-0.720288965	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Rhodobacteraceae_u_nclassified
Otu00299	0.394038388	0.145811281	0.3236578 3	1.518084509	1.984872 498	1.507955664	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Rhodobacteraceae_u_nclassified
Otu00301	0.964756238	0.816754226	0.9973439 93	-0.163685736	1.001653 407	0.244523496	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	uncultured
Otu00308	0.75423241	0.931163267	0.9973439 93	-1.03514458	-0.402579 327	0.366641346	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Rhodobacteraceae_u_nclassified
Otu00313	0.630825576	0.088612637	0.6451133 09	1.906177829	3.965959 836	2.113668814	Bacteroidetes	Bacteroidia	Flavobacteriales	Flavobacteriaceae	Tenacibaculum
Otu00034	0.529884931	0.734755148	0.9973439 93	-1.603847146	-1.247469 734	-0.817749941	Proteobacteria	Alphaproteobacteria	Caulobacteriales	Hyphomonadaceae	Hyphomonas
Otu00335	0.75423241	0.931163267	0.9973439 93	-1.566604152	-0.976816 387	-0.14995221	Proteobacteria	Gammaproteobacteria	Vibrionales	Vibrionaceae	Vibrio
Otu00348	0.694182914	0.816754226	0.9973439 93	-1.841965288	-1.352884 775	0.005397707	Proteobacteria	Gammaproteobacteria	Betaproteobacteriales	Methylophilaceae	OM43_clade
Otu00036	0.962585859	0.931163267	0.9973439 93	-0.127609963	0.171028 174	0.250027182	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Rhodobacteraceae_u_nclassified
Otu00038	0.630825576	0.816754226	0.9973439 93	-0.773462598	-0.529478 362	-0.4500489	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Shimia
Otu00370	0.831501556	0.722338482	0.9973439 93	-0.589667935	1.290928 206	-0.199134074	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u_nclassified
Otu00039	0.788219574	0.720371668	0.9973439 93	-0.976720266	-1.400927 857	0.248708184	Proteobacteria	Alphaproteobacteria	Rhodospirillales	AEGEAN-169_marine_group	AEGEAN-169_marine_group_g
Otu00004	0.768109682	0.931163267	0.9973439 93	-0.33004817	0.139657 231	0.191222716	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	HIMB11
Otu00387	0.801717483	0.931163267	0.9973439 93	-0.986606314	-0.481429 151	-0.007012365	Proteobacteria	Alphaproteobacteria	Alphaproteobacteria_unclassified	Alphaproteobacteria_unclassified	Alphaproteobacteria_unclassified
Otu00389	0.75423241	0.931163267	0.9973439 93	-0.986075742	-0.426452 163	-0.390521402	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Rhodobacteraceae_u_nclassified
Otu00041	0.218196094	0.941906395	0.9973439 93	-1.721748455	-0.211678 136	-0.402134726	Bacteroidetes	Bacteroidia	Flavobacteriales	NS9_marine_group	NS9_marine_group
Otu00397	0.75423241	0.777062029	0.9973439 93	1.34900832	1.462678 552	0.440782092	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u_nclassified
Otu00404	0.81361252	0.999312469	0.9973439 93	-1.186647081	-0.102376 509	0.121737876	Proteobacteria	Alphaproteobacteria	Rhodobacteriales	Rhodobacteraceae	Ruegeria

Otu00043	0.69627657	0.944210178	0.9973439 93	-1.181494427	0.265582 451	0.145403699	Bacteroides	Bacteroidia	Flavobacteriales	NS9_marine_group	NS9_marine_group
Otu00044	0.964756238	1	0.9973439 93	0.051805533	-0.009975 821	0.410578233	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Thalassobius
Otu00420	0.994359856	0.254205904	0.8252894 84	0.046377829	2.205291 664	1.334462423	Proteobacteria	Gammaproteobacteria	Alteromonadales	Colwelliaceae	Thalassota
Otu00047	0.65402218	0.931163267	0.9973439 93	-1.302601138	-0.564150 024	0.248810241	Proteobacteria	Alphaproteobacteria	Puniceispirillales	SAR116_clade	SAR116_clade
Otu00445	0.912352513	0.931163267	0.9973439 93	-0.704288439	-1.015562 507	0.061030694	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraeae_u
Otu00449	0.925139962	0.717552218	0.9973439 93	0.299262414	-1.002495 479	-0.528345619	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u
Otu00458	0.801717483	0.931163267	0.9973439 93	-1.297483893	-0.854455 863	-0.11245222	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u
Otu00005	0.630825576	0.931163267	0.6451133 09	-0.664200886	-0.263424 415	-0.739128364	Cyanobacteria	Oxyphotobacteria	Synechococcales	Cyanobiaceae	Prochlorococcus_MIT_9313
Otu00481	0.886836243	0.931163267	0.9973439 93	-0.39442347	0.397228 702	0.783870375	Proteobacteria	Gammaproteobacteria	Alteromonadales	Colwelliaceae	Thalassota
Otu00053	0.482047452	0.816754226	0.8874886 76	-1.463526698	0.730306 325	-1.000626189	Proteobacteria	Proteobacteri_a_unclassified	Proteobacteria	Proteobacteria	Proteobacteria
Otu00499	0.964756238	0.999312469	0.9973439 93	-0.278912882	-0.122559 524	0.594821806	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraeae_u
Otu00500	0.81361252	0.931163267	0.9973439 93	-0.744601537	0.414502 05	0.043516401	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraeae_u
Otu00511	0.495008674	0.309153198	0.9973439 93	3.283725883	3.940992 598	0.502795216	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitrinolaceae	Amphritea
Otu00055	0.964756238	0.931163267	0.8819346 93	0.337921255	1.432082 128	2.550123688	Euryarchaeota	Thermoplasmata	Marine_Group_II	Marine_Group_II	Marine_Group_II
Otu00056	0.994777655	0.931163267	0.9973439 93	-0.003071832	-0.188975 125	-0.150888952	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraeae_u
Otu00057	0.292687261	0.931163267	0.9973439 93	1.72636128	0.422569 663	-0.685064922	Bacteroides	Bacteroidia	Flavobacteriales	Flavobacteriaceae	NS5_marine_group
Otu00006	0.429532159	0.931163267	0.9973439 93	1.030547516	-0.216913 624	-0.30406563	Bacteroides	Bacteroidia	Flavobacteriales	Flavobacteriaceae	NS5_marine_group
Otu00060	0.805201058	0.78423847	0.9973439 93	-0.447017393	-0.640754 47	-0.07133124	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraeae_u
Otu00565	0.85390493	0.766136119	0.9973439 93	-0.955151837	-2.142812 125	0.008786852	Bacteria	Bacteria_unclassified	Bacteria	Bacteria	Bacteria_u
Otu00061	0.938466661	0.663330615	0.9973439 93	0.136766329	-0.574381 409	-0.034403425	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraeae_u
Otu00571	0.087919044	0.931163267	0.9973439 93	-8.752198579	-1.177065 438	-2.164500881	Proteobacteria	Gammaproteobacteria	Celvibrio	Haliaceae	OM60
Otu00063	0.596554528	0.682236431	0.9973439 93	-2.261509895	-2.156327 042	-0.372550617	Proteobacteria	Alphaproteobacteria	Puniceispirillales	SAR116_clade	SAR116_clade
Otu00585	0.964756238	0.999312469	0.9973439 93	-0.451292184	-0.220119 966	-1.149618959	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraeae_u
Otu00589	0.630825576	0.494392982	0.9973439 93	2.63041571	3.285944 344	0.383271309	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Nitrinolaceae	Amphritea
Otu00067	0.964756238	0.931163267	0.9973439 93	-0.358346019	0.709122 337	0.431167957	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraeae_u
Otu00007	0.994638893	0.717552218	0.9973439 93	-0.013377915	0.839190 484	-0.289178671	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Saccharospirillaceae	Reinekea
Otu00664	0.815004967	0.347373495	0.9973439 93	0.719394142	2.119640 156	0.878795505	Proteobacteria	Gammaproteobacteria	Alteromonadales	Aestuariibacter	Aestuariibacter
Otu00721	0.831501556	0.807260026	0.9973439 93	1.249011395	2.233049 307	2.006794233	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Psychrospira
Otu00083	0.577667459	0.722338482	0.9973439 93	-1.579899549	-1.309131 447	-0.448378004	Proteobacteria	Alphaproteobacteria	Puniceispirillales	SAR116_clade	SAR116_clade
Otu00801	0.815004967	0.816754226	0.9973439 93	1.13423132	-1.533110 403	-1.16460734	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u
Otu00818	0.992632864	0.816754226	0.9973439 93	0.067837716	1.089871 87	0.354811458	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_u
Otu00093	0.964756238	0.78423847	0.9973439 93	0.141511494	0.807787 887	0.13497413	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Leisingera
Otu00862	0.925139962	0.78423847	0.9973439 93	0.438494487	1.258206 435	1.192333004	Bacteroides	Bacteroidia	Cytophagales	Flammeovirgacae	Flammeovirgacae