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1 pH variability at volcanic CO₂ seeps regulates coral calcifying fluid chemistry

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3 running title: Coral calcifying fluid chemistry at CO₂ seeps

4

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7

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23

24 **Abstract**

25

26 Coral reefs are iconic ecosystems having immense ecological, economic and cultural
27 value, but globally their carbonate-based skeletal construction is threatened by ocean
28 acidification. Identifying coral species that have specialised mechanisms to maintain
29 high rates of calcification in the face of declining seawater pH is of paramount
30 importance to predicting future species composition, and growth of coral reefs. Here,
31 we studied multiple coral species from two distinct volcanic CO₂ seeps in Papua New
32 Guinea to assess their capacity to control their calcifying fluid chemistry. Several
33 coral species living under conditions of low mean seawater pH but with either low or
34 high variability in seawater pH were examined and compared with those living under
35 ‘normal’ (non-seep) ambient seawater pH. We show that when mean seawater pH is
36 low but highly variable, corals have a greater ability to maintain constant pH_{cf} in their
37 calcifying fluid, but this characteristic was not linked with changes in abundance.
38 Under less variable low seawater pH, corals with limited reductions in pH_{cf} at the seep
39 sites compared to controls tended to be more abundant at the seeps site than at the
40 control site. However, this finding was strongly influenced by a single species
41 (*Montipora foliosa*), able to maintain complete pH_{cf} homeostasis. Overall, while our
42 findings indicate that there might be an association between ecological success and
43 greater pH_{cf} homeostasis, further research with more species and at more sites with
44 differing seawater pH regimes is required to solidify inferences regarding coral
45 ecological success under future ocean acidification.

46

47 **Keywords**

48

49 Calcifying fluid, ocean acidification, abundance, coral, Dissolved inorganic carbon,
50 Coral reefs, Papua New Guinea, Calcification

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57 **Introduction**

58

59 Ocean acidification (OA) is caused by a shift in ocean carbonate chemistry resulting
60 from increased atmospheric CO₂ concentrations, and is one of the major threats to the
61 future of coral reefs (Hoegh-Guldberg et al., 2017). Declining seawater pH and altered
62 relative concentrations of the different forms of dissolved inorganic carbon are
63 expected to reduce the capacity of corals, the main reef-building taxon, to precipitate
64 calcium carbonate (Kleypas & Yates, 2009). Indeed, laboratory experiments
65 demonstrate that decreases in pH expected by the end of the century will cause an
66 average ~ 15-20% decrease in coral calcification (Chan & Connolly, 2013; Cornwall
67 et al., 2021). However, coral responses are highly species-specific, with some species
68 being more resistant to OA, while others are highly sensitive (Comeau, Cornwall,
69 DeCarlo, et al., 2019; Comeau et al., 2014a; Kornder et al., 2018). Lack of
70 understanding of why certain species are resistant to OA, while others are not, limits
71 reliable projections of how the species composition and ecological functioning of
72 reefs is likely to change in the future.

73 The physiological mechanisms that control species' capacity to tolerate OA
74 are still unclear. Coral calcification is a key physiological and ecological process that
75 enable corals to form large three-dimensional structures. New coral skeleton made of
76 aragonite is formed via biomineralization of the calcifying fluid (CF) that lies between
77 aboral coral tissues layers and the existing calcium carbonate skeleton (Tambutté et
78 al., 2011). To form their skeleton, corals have the ability to modify the chemical
79 conditions of the calcifying fluid to facilitate the mineralization process. In the CF, pH
80 is maintained at values well above that in seawater (pH_{cf} ~ 8.2–8.9, McCulloch et al.,
81 2012; Venn et al., 2019), and the dissolved inorganic carbon (DIC) is increased to
82 values about 1.5–2 times higher than in ambient seawater (Sevilgen et al., 2019). As a
83 result, the saturation state of calcium carbonate in the CF is elevated to values that
84 thermodynamically favor its precipitation (i.e., $\Omega_{cf} \sim 12$, DeCarlo et al., 2017), which
85 is being catalyzed by a set of organic molecules (e.g., CARPs, Drake et al., 2018;
86 Mass et al., 2013). Decreasing seawater pH under OA generally decreases pH_{cf}
87 (Comeau et al., 2017; Holcomb et al., 2014; Venn et al., 2013). Similarly, increasing
88 seawater DIC under OA elevates DIC_{cf} (Comeau et al., 2018). While this increase in
89 DIC_{cf} could partially alleviate the negative effects of decreasing pH_{cf} (Cornwall et al.,
90 2018; Schoepf et al., 2017) large uncertainties exist in the magnitude and

91 physiological controls of these effects. Physiological compensating mechanisms under
92 OA, which are being used to maintain optimal conditions within the CF (i.e., pH
93 homeostasis vs DIC upregulation vs calcium upregulation), are species-specific and
94 can be modulated by environmental conditions (Comeau, Cornwall, Pupier, et al.,
95 2019). In this study we quantify the capacity of different coral species to control their
96 pH_{cf} , and assess whether and how this capacity changes among locations subject to
97 either stable or variable seawater pH.

98 Both the average pH of seawater, and the magnitude of pH variability, have
99 been suggested to modulate the response of marine organisms to OA on coral reefs
100 (Rivest et al., 2017). However, a large range of coral responses to treatments with
101 different levels of pH variability has been reported in laboratory experiments, ranging
102 from no measurable impacts (Camp et al., 2016) to positive offsets against OA
103 (Comeau et al., 2014b). This range of impacts could arise due to species-specific
104 responses to pH variability, but also because of differences among studies in the
105 frequency and magnitude of pH fluctuations used in the experiments. To date, only
106 one laboratory study has specifically addressed the effect of a regular diel pH
107 variability on the CF of corals and coralline algae, where mean seawater pH was the
108 main driver of the CF chemistry (Cornwall et al., 2018). However, resolving these
109 apparently conflicting results requires an understanding of the physiological
110 mechanisms involved in regulating the composition of the CF, and the factors that
111 constrain those mechanisms.

112 Field observations at naturally acidified sites such as volcanic CO₂ seeps,
113 semi-enclosed lagoons, and upwelling regions provide unique opportunities to
114 investigate the effects of ocean acidification and pH variability on time scales that
115 cannot be matched by laboratory experiments (i.e., years to decades). At most of these
116 sites, the pH level, alongside other abiotic parameters, fluctuate around mean pH
117 values similar to those predicted for the global ocean by the end of this century (pH ~
118 7.7-7.8, Fabricius et al., 2011; Teixidó et al., 2020). So far, contradictory results
119 describing the effects of OA on benthic marine calcifying taxa have emerged from
120 these naturally acidified sites. For instance, in a semi-enclosed lagoon in New
121 Caledonia with persistent low pH (mean pH ~ 7.6), coral communities are diverse and
122 some species can maintain calcification rates as high as the ones from control sites
123 (Camp et al., 2017). In contrast, deleterious effects of decreasing pH on the
124 physiology, abundance, and diversity of calcareous organisms were reported at seep

125 sites in Papua New Guinea (Fabricius et al., 2011, 2017). Specifically, at the CO₂
126 seeps in Normanby, naturally acidified reef areas have reduced species diversity and
127 evenness compared to control sites, and were reported to be mostly dominated by
128 resistant species such as massive *Porites* (Fabricius et al., 2011). This dominance of
129 *Porites* spp. could be due to its capacity to maintain elevated pH_{cf} under a large range
130 of seawater pH, as demonstrated both *in situ* (Wall et al., 2016; Wall et al., 2019a) and
131 *ex situ* (Comeau, Cornwall, DeCarlo, et al., 2019). Furthermore, the ability to elevate
132 DIC_{cf} under low pH could be an additional mechanism that favours the presence of
133 certain coral species in naturally acidified sites (Wall et al., 2019a; Wall et al., 2019b).
134 Both mechanisms lead to constant Ω_{cf} in corals from low pH conditions.

135 Some locations with naturally-occurring low pH conditions host abundant and
136 diverse hard-coral assemblages, such as in Palau (Barkley et al., 2017; Golbuu et al.,
137 2016; Shamberger et al., 2018), Papua New Guinea (Pichler et al., 2019), West
138 Australia (Dandan et al., 2015; Schoepf et al., 2015), New Caledonia (Camp et al.,
139 2017), and the Virgin Islands (Yates et al., 2014). At one of the CO₂ seep sites in
140 Papua New Guinea (Upa-Upasina, Normanby), more than 100 coral species were
141 observed near the seep during our expeditions (Hoogenboom M. and Rodolfo-Metalpa
142 R., Pers. Obs.) coexisting with the dominant mound-shaped massive *Porites* colonies.
143 This high species richness under OA conditions was confirmed also at the CO₂ seeps
144 of Ambitle Island, where around 100 species were found in a large, acidified bay in
145 addition to massive *Porites* spp. (Shlesinger T. and Rodolfo-Metalpa R., Pers. Obs.).
146 Previous studies have shown that corals cannot acclimatise within one year to low pH
147 conditions, and that the ability to resist changes in pH_{cf} under low seawater pH (i.e.,
148 pH homeostasis) is a species-specific inherent trait (Comeau, Cornwall, DeCarlo, et
149 al., 2019). Therefore, environments with regular high pH could promote species that
150 calcify at enhanced rates during periods of elevated pH. Accordingly, we hypothesize
151 that corals living in consistently low pH their entire lifetime will show stronger
152 control over their calcifying fluid chemistry than corals living under variable or
153 different pH regimes.

154 While laboratory research has enabled us to understand more of the
155 physiological mechanisms responsible for resistance to low pH, they are unable to
156 provide information regarding how or if this translates to ecological success under
157 OA. Here, we aimed firstly to understand whether changes in mean seawater pH and
158 in the magnitude of variability in seawater pH affects the control of coral calcifying

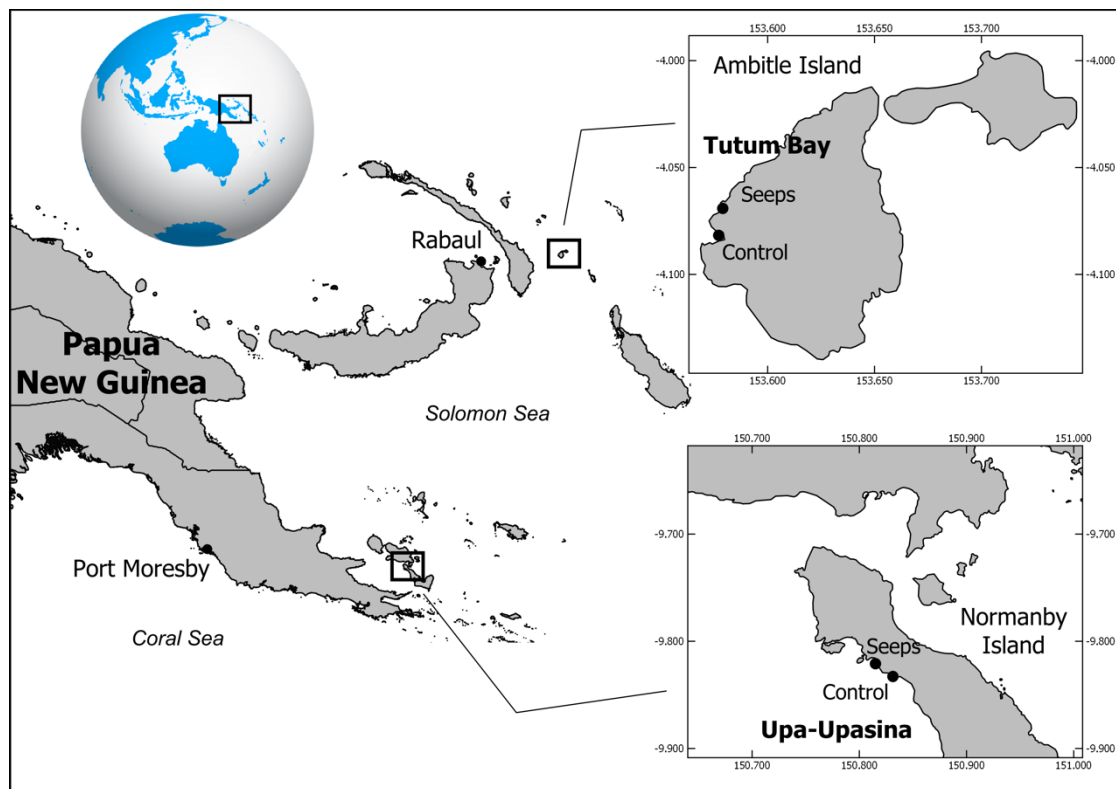
159 fluid in the field for multiple species. Secondly, we aimed to explore whether the
160 capacity of species to better regulate CF chemistry is correlated to species relative
161 abundances at sites with different pH and DIC conditions. To that end, we utilised two
162 natural CO₂ seeps locations with distinct pH characteristics. Using physiological
163 measurements and field observations of coral species abundances, we tested three
164 complementary hypotheses: 1) corals growing in acidified sites have the capacity to
165 maintain chemical conditions optimal for calcification in their calcifying fluid (i.e.,
166 pH_{cf} homeostasis), 2) the most abundant corals in acidified sites are the ones with the
167 best control on their calcifying fluid, and 3) seawater pH variability will alter both
168 ecological outcomes and corals' CF chemistry.

169

170 **Materials and Methods**

171 *Study sites, surveys, and sample collections*

172 Two reefs surrounding CO₂ seeps and adjacent control reefs (i.e., sites with ambient
173 conditions) in Papua New Guinea were repeatedly visited between September 2016
174 and October 2019: Upa-Upasina Reef (Normanby Island, Milne Bay Province) and
175 Tutum Bay (Ambitle Island, New Ireland Province) (Fig. 1).



176

177 **Figure 1.** Maps showing the sampling and surveyed sites. Corals were collected from
178 Ambitle Island and Normanby Island at both control sites and seeps sites in Tutum

179 Bay in Ambitle and Upa-Upasina Reef in Normanby (map redrawn from Biscéré et al.
180 2019).

181

182 The seawater carbonate chemistry of the seep areas, and of the adjacent
183 control reefs, at both locations was characterized continuously during each of the
184 seven 10-day trips performed between 2016 and 2019 (i.e., 4 trips to Ambitle and 3
185 trips to Normanby). Most of the seawater carbonate chemistry data from Normanby
186 has been already reported (Fabricius et al., 2011; Fabricius et al., 2014), and several
187 subsequent studies (e.g., Fabricius et al., 2017). Most of these studies were conducted
188 on the same reef areas as visited during this study, and where hundreds of discrete
189 water samplings verified that the median pH was close to 7.8 pH_T units as projected
190 for 2100. However, only a limited number of studies to date have logged pH at high
191 frequency to characterise pH variability at the Normanby study site (Fabricius et al.,
192 2014; Smith et al., 2017; Uthicke et al., 2016). The seeps site in Ambitle Island was
193 only recently studied and an exhaustive dataset of seawater physical and chemical
194 conditions have been published (Biscéré et al., 2019; Pichler et al., 2019).

195 During our seven field works at the Normanby and Ambitle seeps, we
196 measured the extent to which pH fluctuated at the study sites because of its potential
197 importance in affecting the coral ability to control their calcifying fluid chemistry. At
198 both Normanby and Ambitle seeps, and at the reference (control) sites at each
199 location, we used three pH loggers (SeaFET V2, Sea-Bird Scientific, Bellevue, WA
200 98005, USA) recording every 10 minutes (i.e., Tutum Bay in Ambitle; Fig. 1 in
201 Pichler et al., 2019; see all Supplementary Data, [https://ars.els-](https://ars.els-cdn.com/content/image/1-s2.0-S0025326X1830780X-mmc1.pdf)
202 [cdn.com/content/image/1-s2.0-S0025326X1830780X-mmc1.pdf](https://ars.els-cdn.com/content/image/1-s2.0-S0025326X1830780X-mmc1.pdf)). At each seeps site,
203 we collected continuous pH data for a duration of 10 days at each of 4 fixed stations
204 located in the area where the coral samples were collected, and an additional 20 24-h
205 measurements all around the seeps area. Seawater samples were filtered through 0.45-
206 μm Whatman filters using a Nalgene vacuum system and stored at 4 °C in the dark for
207 further testing at the Institut de Recherche pour le Développement (IRD) in New
208 Caledonia. Total alkalinity (A_T) was determined using an auto titrator (TIM865
209 Titralab, Radiometer). Three replicate 20 mL sub-samples were analysed at 25 °C
210 using an open cell potentiometric method. Total alkalinity was calculated from the
211 Gran function applied to pH from 4.2 to 3.0, as mEq L^{-1} from the slope of the pH vs
212 HCl curve. Results were corrected against A_T standards provided by A.G. Dickson

213 (batch #155). Parameters of the carbonate system were calculated from pH_T (median,
214 5th and 95th percentile); median A_T , temperature and salinity (34) using the R package
215 seacarb. A full description of the carbonate chemistry at the two locations and sites is
216 presented in the Table S1.

217 During the expedition of 2016, we collected fragments of 14 and 8 coral
218 species at Normanby Island and Ambitle Island, respectively, from both the seeps and
219 control sites (CITES collection permits n. 016132 and 017027). The 14 species
220 sampled in Normanby Island were: *Acropora cytherea*, *Acropora millepora*, *Acropora*
221 *samoensis*, *Acropora tenuis*, *Favites halicora*, *Favites pentagona*, *Galaxea*
222 *fascicularis*, *Merulina ampliata*, *Pachyseris speciosa*, *Pocillopora verrucosa*, *Porites*
223 *rus*, *Seriatopora caliendrum*, *Tubastraea* sp., and *Turbinaria reniformis*. The 8
224 species sampled in Ambitle Island were: *Acropora nana*, *Acropora tenuis*,
225 *Echinopora lamellosa*, *Galaxea fascicularis*, *Montipora foliosa*, *Pocillopora*
226 *damicornis*, *Porites lutea*, *Psammocora contigua*. For each species, one branch tip or
227 a piece of skeleton (3–7 cm long) was collected from three spatially separated
228 colonies (5–20 m distant) using a bone cutter or a hammer and chisel for branching or
229 massive and foliose species, respectively. Coral tissues were removed using high
230 pressure water and they were dried in air over 48 h before being carefully preserved in
231 individual bags.

232 To quantify the abundance of the focal species mentioned above, field surveys
233 were performed in May 2017 in Normanby Island and in June 2018 in Ambitle Island.
234 We used 10 x 1 m belt transects haphazardly positioned at a depth range of ~2–10 m
235 at both seeps and control sites in each location. Every colony identified as one of the
236 studied species (except for massive or encrusting *Porites* that were grouped as *Porites*
237 spp.) was counted along 15 belt transects at each site in Normanby Island, and along
238 18 belt transects at each site in Ambitle Island, and the species abundances are
239 presented as the number of colonies per transect.

240

241 *Analyses of calcifying fluid pH and DIC*

242 Calcifying fluid pH (pH_{cf}) and dissolved inorganic carbon (DIC_{cf}) were estimated
243 respectively using the $\delta^{11}\text{B}$ proxy method (Trotter et al., 2011) and the $\delta^{11}\text{B}$ and B/Ca
244 method (Holcomb et al., 2016; M. T. McCulloch et al., 2017). Fragments of coral
245 colonies were collected from 3 to 4 colonies per species, and the tissues were removed
246 by water pressure before being sun dried. The skeletons were then shipped to the

247 University of Western Australia, where they were cleaned with mQ water, bleached
248 for 24 hours in 6.25 % NaClO to remove any tissue left at the surface of the samples,
249 and dried in a drying oven for 48 h at 50 °C.

250 For branching corals (e.g., *Acropora*, *Seriatopora*, *Pocillopora*), geochemical
251 analyses were performed on a ~ 1 cm long piece of skeleton from the tip of each of
252 three branches per colony. The three tips were then crushed together to smooth
253 potential differences in calcifying fluid chemistry within colonies and were
254 considered as one sample (for a total of three samples per species and condition). For
255 massive corals (e.g., *Favites*, *Galaxea*), a fragment of 0.5 cm³ located ~ 0.5 cm below
256 the surface was selected using a dental drill to avoid the area of the skeleton where
257 tissues were present (first mm of the skeleton). For the foliose corals (e.g.,
258 *Echinopora*, *Pachyseris*, *Turbinaria*), a section of the skeleton close to the growing
259 edge of laminae of the colonies was sampled using cutting pliers. The selected
260 portions of skeletons were bleached for an additional 24 hours in 6.25 % NaClO and
261 then rinsed three times with mQ water to remove any residual traces of organic matter
262 and bleach. Bleached samples were dried for 48h at 50°C. Skeleton samples from all
263 colonies were then crushed in a mortar with a pestle to powder prior to analysis.

264 In the clean laboratory of the Advanced Geochemical Facility for Indian
265 Ocean Research (AGFIOR, University of Western Australia), 10 mg of powdered
266 skeleton from each coral sample was prepared for dissolution and dilution to 10-ppm
267 Ca solutions. The 10 mg samples were dissolved in 0.51 N HNO₃, and the boron was
268 quantitatively separated on ion exchange columns. δ¹¹B was measured on a
269 multicollector inductively coupled plasma mass spectrometer (NU II). Measurements
270 of the international carbonate standard JCP-1 yielded a mean value of 24.43 ± 0.08 ‰
271 (mean ± SE, n = 10), which was similar to the 24.33 ± 0.11 ‰ (SE) reported
272 previously. pH_{cf} was estimated from δ¹¹B using the calculations described by Trotter
273 et al. (2011), as:

$$274 \quad \text{pH}_{\text{cf}} = \text{pK}_{\text{B}} - \log \left[\frac{(\delta^{11}\text{B}_{\text{sw}} - \delta^{11}\text{B}_{\text{carb}})}{(\alpha_{(\text{B}_3-\text{B}_4)} \delta^{11}\text{B}_{\text{carb}} - \delta^{11}\text{B}_{\text{sw}} + 1000 (\alpha_{(\text{B}_3-\text{B}_4)} - 1))} \right] \quad (1),$$

275 where pK_B is the dissociation constant dependent on temperature and salinity as
276 measured at the site of coral collection, δ¹¹B_{sw} = 39.61 (Foster et al., 2010), and α_(B₃-B₄)
277 is the boron isotopic fractionation factor for the pH dependent equilibrium of the
278 borate (B(OH)₄⁻) relative to the boric acid (B(OH)₃) species in the calcifying fluid,
279 with a value of 1.0272 (Klochko et al., 2006).

280 B/Ca ratios were determined on the same aliquot of the solution used for $\delta^{11}\text{B}$.
281 Both B/Ca and $\delta^{11}\text{B}$ were utilized to determine $[\text{CO}_3^{2-}]$ and then [DIC] at the site of
282 calcification $[\text{DIC}]_{\text{cf}}$ following (McCulloch et al., 2017). Estimates of carbonate ion
283 concentrations in the calcifying fluid were calculated using the following equation:

$$284 \quad [\text{CO}_3^{2-}]_{\text{cf}} = K_{\text{D}}[\text{B}(\text{OH})_4^-]_{\text{cf}} / \left(\frac{\text{B}}{\text{Ca}}\right)_{\text{CaCO}_3} \quad (2),$$

285 where $K_{\text{D}} = K_{\text{D},0} \exp(-k_{\text{KD}}[\text{H}^+]_{\text{T}})$ with $K_{\text{D},0} = 2.97 \pm 0.17 \times 10^{-3}$ ($\pm 95\%$ CI) and $k_{\text{KD}} =$
286 0.0202 ± 0.042 . The concentration of DIC_{cf} was then calculated from estimates of
287 pH_{cf} and $[\text{CO}_3^{2-}]_{\text{cf}}$.

288 T-tests were used to assess differences in the estimates of pH_{cf} and DIC_{cf} between the
289 seeps and the control samples at both locations, with locations analysed separately. T-
290 tests were used separately for each species because we were interested in whether
291 there is a CO_2 effect for each species rather than an effect between species. All of the
292 analyses and visualizations were done in R v4.0.2. All data are presented as mean \pm
293 SE. The data that support the findings of this study are archived in the Pangaea
294 database (<https://doi.pangaea.de/10.1594/PANGAEA.939651>).

295

296 *Relationship between coral abundance and carbonate chemistry*

297 We used two complementary approaches to determine if the most abundant coral
298 species at the seeps sites were the species with the best control on their calcifying
299 fluid. First, we investigated the relationships between coral abundance at the seeps
300 sites and corals pH_{cf} or DIC_{cf} . Second, to consider the differences in species
301 abundance between the seeps and control sites, we calculated the proportional change
302 in their abundance at the seeps relative to the control at each location. We then
303 examined the relationship between the differences in the corals' abundance among
304 sites and their calcifying fluid carbonate chemistry using a linear regression.

305 Differences for each species in mean abundance between the sites were calculated as
306 the relative change in mean abundance as follows:

$$307 \quad \text{Relative change} = (\text{mean abundance in the seeps} - \text{mean abundance in the control}) /$$
$$308 \quad \text{mean abundance in the control}$$

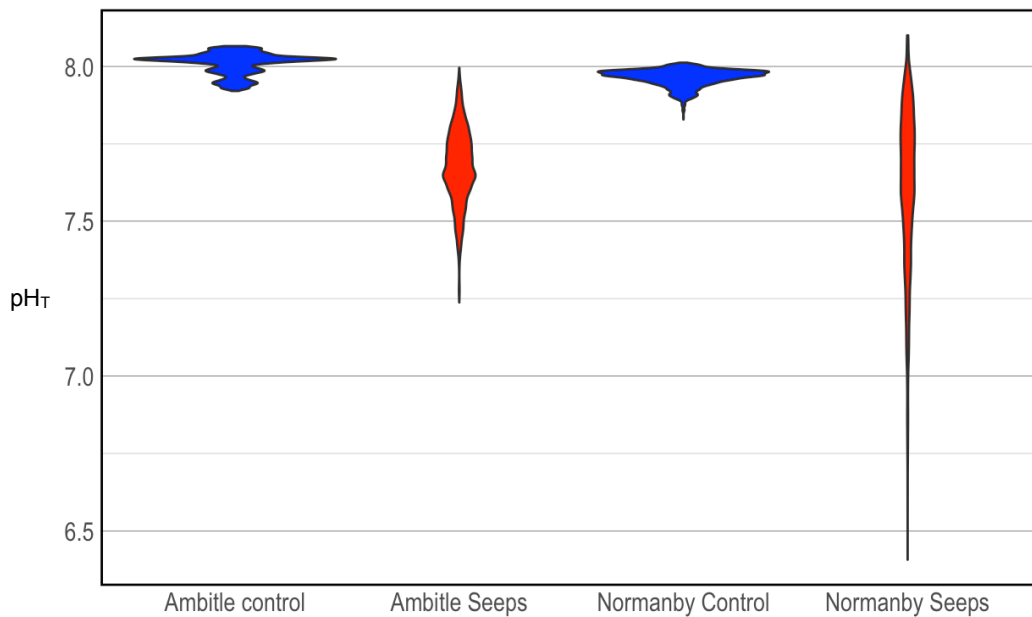
309 Principal Component Analyses were used to evaluate how relative change in mean
310 abundance, vent pH_{cf} and DIC_{cf} , delta pH_{cf} ($\text{pH}_{\text{cf}} \text{ vent} - \text{pH}_{\text{cf}} \text{ control}$) and delta DIC_{cf}
311 ($\text{pH}_{\text{cf}} \text{ vent} - \text{pH}_{\text{cf}} \text{ control}$) were correlated.

312

313 **Results**

314 *Seawater pH variability*

315 All seawater carbonate chemistry and seawater pH variability measured at fixed
316 stations are in Supplementary Table S1. Ambient mean pH values were 8.01 and 7.96
317 in the control sites, and 7.64 and 7.51 in the seeps sites in Ambitle and Normanby,
318 respectively (Fig. 2). pH variability was considerably larger at the Normanby seep site
319 where the pH dropped down as low as 6.64 pH units. During the entire time frame of
320 pH logging, corals were exposed to low pH conditions (i.e., pH ranging between 7.6–
321 7.8) for 60% of the time at Ambitle, and for 31% of the time at Normanby. Very low
322 pH values (i.e., pH < 7.6) were less frequent in Ambitle than in Normanby (24% and
323 43% of the time, respectively). Similarly, high pH values (> 7.8) were less frequent in
324 Ambitle than in Normanby (16% and 26% of the time, respectively).



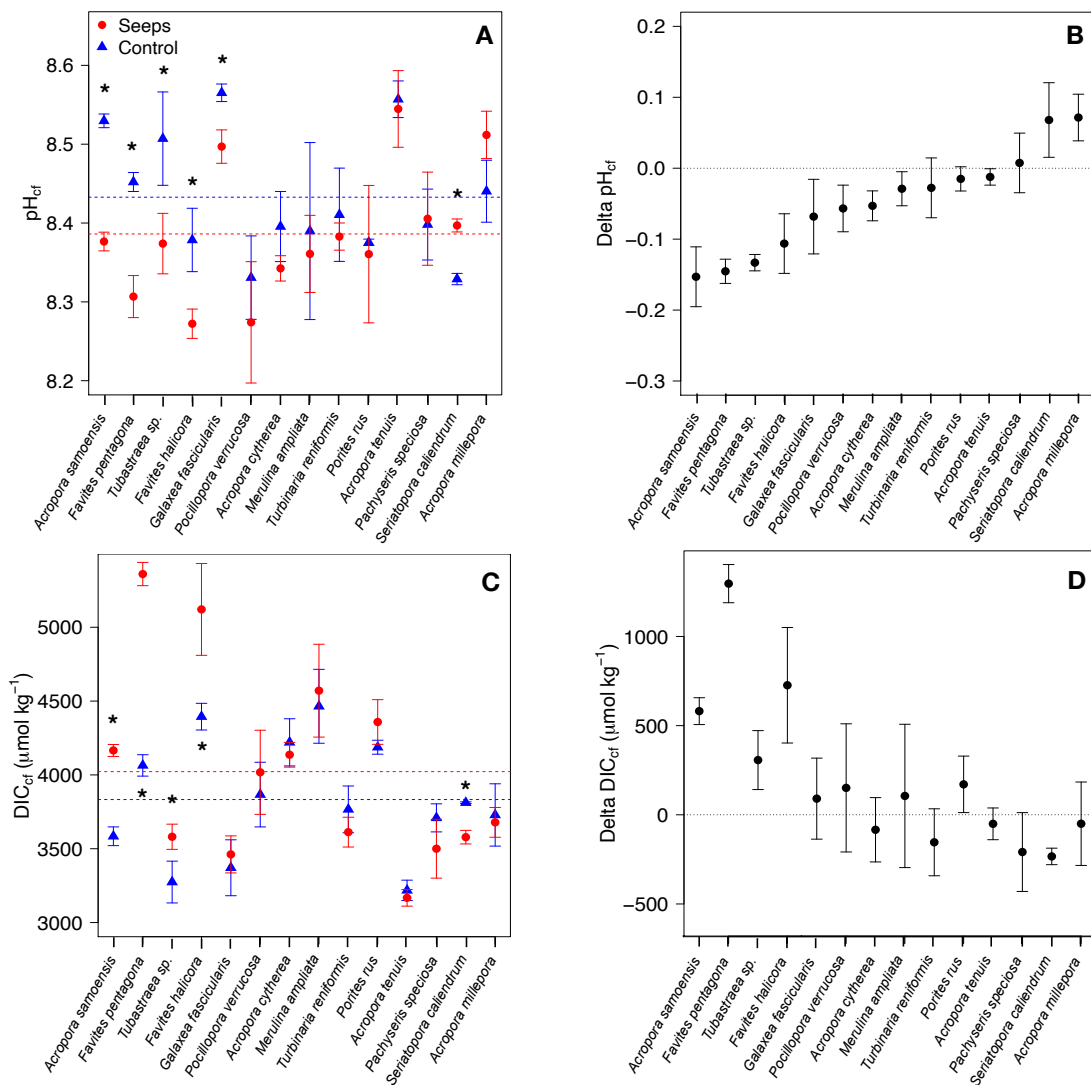
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326 **Figure 2.** Violin plot showing the *in situ* pH (n > 15,000 for each site) measured using
327 autonomous pH sensors SeaFET at both Ambitle and Normanby seeps and respective
328 control sites during fieldwork in September 2016 and May 2017.

329

330 *pH of coral calcifying fluid*

331 Across the 14 coral species studied in Normanby average pH_{cf} was higher in the
 332 control site (8.43 ± 0.02 , mean \pm SE, $n = 42$) than in the seeps site (8.39 ± 0.02 , mean
 333 \pm SE, $n = 42$, t-test, $p < 0.05$). The highest pH_{cf} was observed in *Galaxea fascicularis*
 334 at the control site (8.57 ± 0.01 , $n = 3$), while the lowest was measured in *Favites*
 335 *halicora* at the seeps site (8.27 ± 0.01). pH_{cf} was significantly lower at the seeps site
 336 compared with the control site in five species (Fig. 3A; t-test, $p < 0.05$ for all five),
 337 with delta pH_{cf} the lowest in *Acropora samoensis* (-0.15, Fig. 3B). There was no
 338 difference in pH_{cf} between sites for eight species, while pH_{cf} was higher at the seeps
 339 site in *Seriatopora caliendrum* (Fig. 3A; t-test, $p < 0.001$), with a positive delta pH_{cf}
 340 of 0.07 (Fig. 3B).

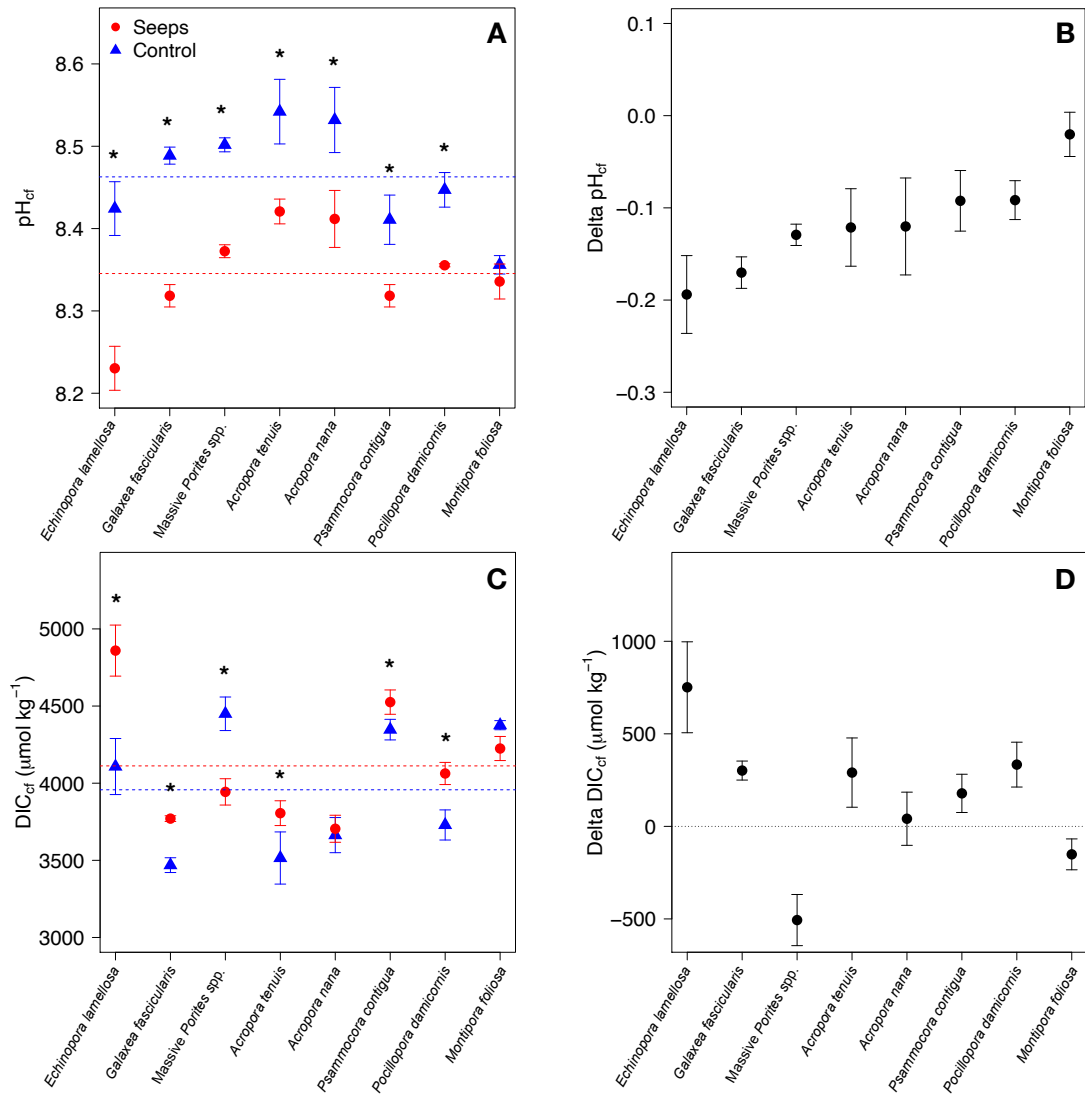


341
 342 **Figure 3.** Calcifying fluid carbonate chemistry estimates of 14 coral species from the
 343 control and seeps sites in Normanby Island. A) pH of the calcifying fluid (pH_{cf}); B)
 344 Difference in mean pH_{cf} between control and seeps sites; C) Dissolved inorganic

345 carbon at the site of calcification (DIC_{cf}); and D) Difference in mean DIC_{cf} . Blue and
346 red colours indicating the control and seeps data, respectively. Dashed lines in (A) and
347 (C) represent the pooled pH_{cf} and DIC_{cf} mean across all species in each site. Asterisks
348 indicating species in which significant differences were found. All data presented as
349 mean \pm SE, with $n = 3$.

350

351 In Ambitle, for the 8 species pooled together, pH_{cf} was on average
352 significantly higher (t-test, $p < 0.05$) in the control site (8.46 ± 0.02 , $n = 24$) than in
353 the seeps site (8.35 ± 0.02 , $n = 24$). The highest pH_{cf} was measured in *Acropora tenuis*
354 at the control site (8.54 ± 0.04), while the lowest was found in *Echinopora lamellosa*
355 at the seeps site (8.23 ± 0.03). pH_{cf} was higher in the control site compared with the
356 seeps site in all species (t-test, $p < 0.05$ for all) but one, *Montipora foliosa*, which
357 showed no differences (Fig. 4A). As a result, delta pH_{cf} which is equal to $\text{pH}_{\text{cf seeps}} -$
358 $\text{pH}_{\text{cf ambient}}$ varied between -0.19 in *Echinopora lamellosa* and -0.02 in *Montipora*
359 *foliosa* (Fig. 4B).



360

361 **Figure 4.** Calcifying fluid carbonate chemistry estimates of 8 coral species from the
 362 control and seeps sites in Ambitle Island. A) pH of the calcifying fluid (pH_{cf}); B)
 363 Difference in mean pH_{cf} between control and seeps sites; C) Dissolved inorganic
 364 carbon at the site of calcification (DIC_{cf}); and, D) Difference in mean DIC_{cf}. Blue and
 365 red colours indicating the control and seeps data, respectively. Dashed lines in (A) and
 366 (C) represent the pooled pH_{cf} and DIC_{cf} mean across all species in each site. Asterisks
 367 indicating species in which significant differences were found. All data presented as
 368 mean ± SE, with n = 3.

369

370 *Dissolved inorganic carbon in coral calcifying fluid*

371 In Normanby, for the 14 species pooled together, mean DIC_{cf} was 3833 ± 105 μmol
 372 kg⁻¹ and 4022 ± 173 μmol kg⁻¹ at the control and seeps site (n = 42 for both),
 373 respectively, with no statistical differences (t-test, p = 0.268). DIC_{cf} was more

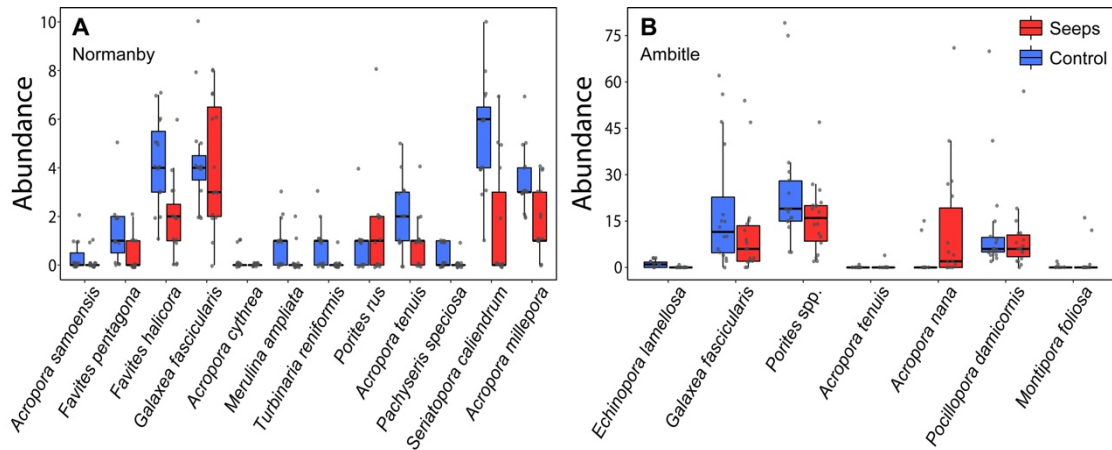
374 elevated at the seeps site compared with the control site in four species (*A. samoensis*,
375 *F. pentagona*, *Tubastraea* sp., and *F. halicora*; t-test, $p < 0.05$ for all), while it was
376 more elevated in the control site for *S. caliendrum* (t-test, $p < 0.05$). There was no
377 difference in DIC_{cf} between sites in the nine other species (Fig. 3C). There was a large
378 range of species-specific delta $DIC_{cf} = DIC_{cf\ seeps} - DIC_{cf\ ambient}$ with the maximal
379 increase in delta DIC_{cf} at the seeps found in *Favites pentagona* ($1200\ \mu\text{mol kg}^{-1}$, Fig.
380 3D). In contrast, delta DIC_{cf} $233\ \mu\text{mol kg}^{-1}$ at the seeps site in *Seriatopora caliendrum*
381 (Fig. 3D), which was also one of the only species with higher pH_{cf} at the seeps.

382 Across the 8 coral species studied in Ambitle, mean DIC_{cf} was 3957 ± 144
383 $\mu\text{mol kg}^{-1}$ and $4112 \pm 143\ \mu\text{mol kg}^{-1}$ at the control and seeps site ($n = 24$ for both),
384 respectively, with no statistical differences (t-test, $p = 0.206$). DIC_{cf} was more
385 elevated at the seeps site compared with the control sites in five species (*E. lamellosa*,
386 *G. fascicularis*, *A. tenuis*, *Psammocora* sp., and *P. damicornis*; t-test, $p < 0.05$ for all),
387 while it was lower at the seeps sites for only massive *Porites* spp. (t-test, $p < 0.05$)
388 despite lower pH_{cf} also found at the seeps. There was no difference between sites in
389 DIC_{cf} for *Acropora nana* and *Montipora foliosa* (Fig. 4C). The delta DIC_{cf} ranged
390 from $-506\ \mu\text{mol kg}^{-1}$ in massive *Porites* spp. to $751\ \mu\text{mol kg}^{-1}$ in *Echinopora*
391 *lamellosa* (Fig. 4D).

392

393 *Coral abundance and calcifying fluid chemistry*

394 In Normanby, most of the studied species were either similarly abundant (absolute
395 abundance) in both sites or more abundant at the control site than at the seeps site
396 (Fig. 5A). By contrast, this pattern was not observed in Ambitle (Fig 5B), where three
397 species were more abundant at the control site than at the seeps site (*G. fascicularis*,
398 *P. damicornis*, and massive *Porites* spp.) but two other species were more abundant at
399 the seeps site than at the control site (*A. nana* and *M. foliosa*). Although being
400 relatively rare in Ambitle, two more species had opposing abundances: *A. tenuis* was
401 more abundant at the seeps site than at the control site (0.22 ± 0.9 and 0.06 ± 0.2
402 mean abundance per transect, respectively) while *E. lamellosa* was more abundant at
403 the control site than at the seeps site (1 ± 1.1 and 0.05 ± 0.2 mean abundance per
404 transect, respectively).

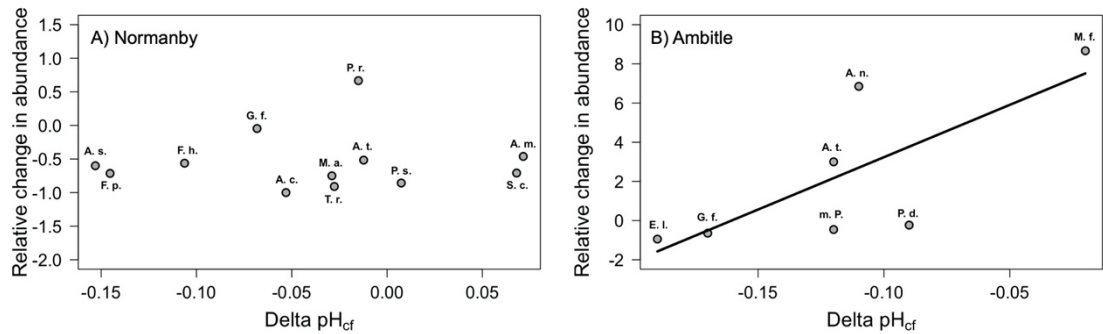


405

406 **Figure 5.** Abundance of the studied species in A) Normanby Island; and, B) Ambitle
 407 Island. The abundance is presented as the number of colonies per belt transect with
 408 points indicating individual belt transect data (n = 15 at each site in Normanby, and n
 409 = 18 at each site in Ambitle). To aid the visualization of panel B, three outlying data
 410 points were excluded. Two of these points were values > 100 for *G. fascicularis* in the
 411 control and the third was a value > 80 for *Porites* spp. in the control. Blue and red
 412 colours indicating the control and seeps data, respectively. Center lines of the box
 413 plots indicate the medians, boxes indicate the lower and upper quartiles, and whiskers
 414 indicate 1.5x interquartile range.

415

416 There was no relationship between delta pH_{cf} or delta DIC_{cf} and the abundance
 417 of corals at the seeps sites of both Normanby and Ambitle (Fig. S1) (Table S2).
 418 Similarly, there was also no significant relationship between delta pH_{cf} and the
 419 relative change in species abundance between the seeps site and the control site in
 420 Normanby (Fig. 6A). By contrast, a relationship between delta pH_{cf} and the relative
 421 change in abundance was found in Ambitle (Fig. 6B; linear regression, p-value of the
 422 slope = 0.05, p-value of the intercept = 0.02, R² = 0.55), although it appears to be
 423 largely driven by one species, *M. Foliosa*. The delta DIC_{cf} had no significant
 424 relationship with the relative change in abundance at both Normanby and Ambitle
 425 (Fig. S2).



426

427 **Figure 6.** Relationship between the difference in mean pH_{cf} between the control and
 428 seeps sites (i.e., Delta pH_{cf}) and the mean relative change in coral abundance between
 429 the control and the seeps sites. Positive values indicate an increase in relative
 430 abundance between the seeps and the control. There was no relationship in Normanby
 431 (A), while there was a linear relationship in Ambitle (B) (p-value of the slope = 0.05,
 432 p-value of the intercept = 0.02, R² = 0.56). Species names are indicated as initials on
 433 the figure.

434

435 These results were confirmed by the PCA, which demonstrated no association
 436 between proportional abundance and the calcifying chemistry parameters in
 437 Normanby (Fig. S3A). In contrast, the PCA for Ambitle showed a clear negative
 438 association between delta pH_{cf} at the seep site and relative change in abundance there
 439 (Fig. S3B).

440

441 **Discussion**

442 We observed major site-specific differences in the responses of corals'
 443 calcifying fluid chemistry. At the consistently low pH seeps site (i.e., at Ambitle
 444 Island) most coral species had lower pH_{cf} at the CO₂ seeps compared to the control
 445 site. This mirrors observations made on laboratory grown corals under well-controlled
 446 and consistently low pH (McCulloch et al., 2012). Conversely, this pattern was less
 447 clear at the inconsistently low pH seeps site (i.e., at Normanby Island) when
 448 compared to the control site. Additionally, at Ambitle, coral species with limited
 449 reductions in pH_{cf} at the seep sites compared to controls (i.e. greater pH homeostasis)
 450 also tended to be more abundant at the seeps site than at the control site. This
 451 association was influenced heavily by the species with complete pH_{cf} homeostasis,
 452 which also increased in abundance more than any other species between the control
 453 and seep site at Ambitle. However, three out of four of the species that increased in

454 abundance also had the highest pH homeostasis. Three of the four species with the
455 least pH_{cf} homeostasis also had the greatest declines in abundance between the control
456 and seeps. Such trends were not observed at Normanby. We suggest that the disparity
457 between responses of pH_{cf} in the different locations is most likely due to the larger
458 range and variability in pH at Normanby. Nonetheless, we cannot rule out other
459 factors such as differences in light, temperature, and flow that can affect the calcifying
460 fluid chemistry (Comeau, Cornwall, Pupier, et al., 2019). As correlation does not
461 imply causation, further assessments at additional sites with consistently low pH are
462 warranted to assess the logical association between coral pH_{cf} homeostasis and
463 directionality of abundance change under consistently low pH that our study suggests.

464
465 Controlling pH in the calcifying fluid well above external seawater pH is one
466 of the key mechanisms that corals have developed to favour the precipitation of
467 calcium carbonate. pH homeostasis, where pH in the calcifying fluid remains constant
468 independent of changes in external seawater pH, has therefore been suggested as a
469 mechanism for corals to cope with ocean acidification (Georgiou et al., 2015;
470 McCulloch et al., 2017). To date, pH homeostasis in corals has been demonstrated
471 only in a handful of species: On fragments of *Porites cylindrica* during an *in situ*
472 experiment (Georgiou et al., 2015), on massive *Porites* during a flume experiment
473 (Comeau, Cornwall, DeCarlo, et al., 2019), and on massive *Porites*, *Porites*
474 *astreoides*, and *Balanophyllia europaea* at naturally low pH sites (Wall et al., 2016,
475 2019a, 2019b). Using a large range of taxa and morphologies, our study confirms the
476 difficulties associated with determining the resistance to ocean acidification based on
477 coral phylogeny and/or morphology (Comeau et al., 2014a; Okazaki et al., 2017).

478
479 While it has been suggested that certain coral genera, such as *Porites*, are
480 particularly resistant to OA, we found that some species of other coral genera that are
481 largely regarded as highly susceptible to OA (Kavousi et al., 2016; Kornder et al.,
482 2018), such as *Acropora* and *Montipora*, can also exert strong control over their
483 calcifying fluid chemistry. However, a large range of species-specific responses
484 within a genus was found. For example, *Acropora millepora* was one of the species
485 with the best apparent control over its pH_{cf} at Normanby while *Acropora samoensis*
486 was the species exhibiting the largest decline in pH_{cf} at this location. Similarly, coral
487 morphology was not correlated with pH homeostasis in the calcifying fluid. Although

488 massive species have been suggested to be more resistant to OA, we found that many
489 of the species that are able to maintain homeostasis were branching (e.g., *Acropora*
490 *cytherea*, *Acropora millepora*, *Pocillopora verrucosa*) and foliose (e.g., *Merulina*
491 *ampliata*, *Montipora foliosa*, *Pachyseris speciosa*, *Turbinaria reniformis*) while some
492 of the species with massive growth morphologies had poor control over their
493 calcifying fluid chemistry (e.g., *Favites pentagona*, *Galaxea fascicularis*). However,
494 these trends might be confounded by the differences in seawater pH variability at the
495 two locations.

496

497 The trends in pH control may only be physiologically meaningful for sites
498 where seawater pH was consistently low. Apparent pH homeostasis was much more
499 common in Normanby, where eight out of 14 taxa experienced pH_{cf} homeostasis (and
500 one coral had higher pH_{cf} at the seeps than in the control site). In Ambitle,
501 homeostasis was found only for *Montipora foliosa*, while pH_{cf} was lower at the CO_2
502 seep site in the other seven species investigated. *Montipora foliosa* was also the
503 species with the highest proportional increase in abundance between the control and
504 the seeps site. This suggests that the capacity of this species to control its pH_{cf} could
505 represent an ecological advantage. However, it is important to note that this species
506 was relatively rare in Ambitle with a total of three colonies recorded in the surveys at
507 the control site and 29 colonies at the seeps site. Therefore, even small increases in
508 abundance equate to large relative increases. Additionally, three of the four species
509 with the least control over their pH_{cf} also had the greatest declines in relative
510 abundance. Together, these results explain the clear association between pH_{cf}
511 homeostasis and relative change in abundance found with the PCA. They also show
512 that rather than the absolute value of pH_{cf} at the vents, it is a greater control over pH_{cf}
513 that could give some ecological advantage in a future high CO_2 ocean. However,
514 further assessment at additional sites where seawater pH is low and not highly
515 variable is now needed to confirm these results.

516

517 In contrast, a relationship between pH_{cf} control and proportional change in
518 abundance was not found in Normanby. While different species were studied at both
519 sites, this difference between locations was unlikely to be solely because of taxonomic
520 composition as the two species studied at both locations (*Acropora tenuis* and
521 *Galaxea fascicularis*) also exhibited lower pH_{cf} in Ambitle's seeps site compared to

522 Normanby's seep site. Furthermore, these results are based on a large range of coral
523 genera and morphologies representative of the local diversity. Thus, variability in
524 seawater pH and time spent by corals in different pH levels can likely explain the
525 discrepancies between locations. Despite similar mean pH at both CO₂ seeps, corals in
526 Normanby experienced much larger variations in seawater pH. This includes frequent
527 records of pH as low as 6.6, but also values close to ambient conditions (pH 8.0) very
528 frequently. pH in Normanby occasionally varied by as much as one pH unit in less
529 than one hour. This large variability in pH is likely driven by the shallow topography
530 of the Upa-Upasina reef, where depth varies between ~1–4 m, which makes seawater
531 pH extremely dependent on water mixing caused by local wind conditions (Fabricius
532 et al., 2011). In contrast, Pichler et al. (2019) showed that in Tutum Bay (Ambitle
533 Island) the main seep and other associated sparse seeps change the seawater carbonate
534 chemistry of the whole bay (1-8 m deep). In Tutum Bay, pH variability is mostly
535 driven by tides, with lower pH associated with low tides. Apparent pH_{cf} homeostasis
536 in Normanby in most coral species studied could therefore result from the high
537 variability in pH at this location. Moreover, it is likely that this apparent pH
538 homeostasis in Normanby might represent calcification occurring predominantly
539 during these high pH events associated with high tide. Other environmental
540 parameters such as temperature, light, and flow are known to affect the composition
541 of the calcifying fluid chemistry (Comeau, Cornwall, Pupier, et al., 2019; Guo, 2019).
542 However, they did not impact the present results, as all environmental parameters
543 other than seawater pH were similar between control and seeps sites (Table S1).
544 Therefore, the different responses observed in Normanby and Ambitle can likely be
545 attributed to differing seawater pH (and DIC) variability.

546

547 Greater pH variability could elicit at least three distinct responses. 1) Periods
548 of elevated seawater pH could allow calcification to occur unabated as pH_{cf} is
549 elevated during these time periods, but pH_{cf} is then decreased when seawater pH is
550 reduced. Since calcification rates are higher when pH_{cf} is higher, a greater proportion
551 of boron would be incorporated during the periods of time when pH_{cf} is elevated,
552 which would be reflected by elevated pH_{cf} at CO₂ seeps, as in our data. This might
553 further explain the absence of a relationship between relative change in abundance of
554 species and their ability to maintain constant pH_{cf} at the CO₂ seeps in Normanby,
555 where the reef might be dominated by species that are able to rapidly calcify in brief

556 periods when seawater pH is high. This hypothesis is also supported by the two co-
557 occurring species at Ambitle/Normanby possessing lower pH_{cf} at Ambitle, indicative
558 of calcification occurring more rapidly in higher seawater pH. However, this cannot
559 be tested with the present data, as boron isotopes only provide indication on the mean
560 pH_{cf} during the precipitation of calcium carbonate over several weeks and other
561 methods, such as dyes and microelectrodes, cannot be used *in situ* presently. 2)
562 Periods of extremely low pH could cause physiological stress and even dissolution of
563 resident organisms, especially for any individuals where skeletal CaCO_3 material
564 becomes exposed. For example, the low pH values found in Upa-Upasina reef
565 (Normanby Island) could also explain the deleterious effects of seawater pH on coral
566 skeletal characteristics reported at this site (Prada et al. preprint). In this scenario,
567 dissolution-resistant species would be favoured at Normanby. 3) Greater pH
568 variability itself could cause deleterious effects, such as reduction of calcification as
569 observed in the coralline alga *Arthrocardia corymbosa* (Cornwall et al. 2013). The
570 only study on the effect of pH variability on coral CF chemistry has shown that pH_{cf}
571 of the coral *Goniopora* sp. was driven by the mean seawater pH and was not affected
572 by diurnal variability in seawater pH (Cornwall et al., 2018). However, this supports a
573 null hypothesis 4) that responses at Normanby are equivalent to those that will occur
574 under future ocean acidification. While this contradicts what is found here, it is
575 important to note that this study was restricted to only one species exposed to a
576 regular diurnal variability in pH (low pH at night and high pH during the day), which
577 could elicit much different responses than those occurring at our sites. Collectively,
578 the effects of differences in pH variability on calcification physiology is also highly
579 species-specific (Rivest et al., 2017), and thus extremely high pH, low pH and
580 differences in pH variability itself could have altered both the pH_{cf} and the ecological
581 outcomes at Normanby (and even Ambitle to a lesser extent) in ways that are difficult
582 to predict from our available data.

583

584 DIC_{cf} is another important parameter of the calcifying physiology of corals
585 (McCulloch et al., 2017; Ross et al., 2018; Wall et al., 2019) and is generally
586 inversely correlated with pH_{cf} , whereby DIC_{cf} is elevated when pH_{cf} decreases. This
587 trend also persists when corals are grown under low pH in the laboratory (Cornwall et
588 al., 2018; Schoepf et al., 2017; Sevilgen et al., 2019) and occurs on seasonal cycles *in*
589 *situ* (McCulloch et al., 2017; Ross et al., 2017). Here, the average DIC_{cf} across all

590 coral species in each site was similar between the control and seeps sites at both
591 locations, and only 4 species out of 14 in Normanby and 5 out 8 in Ambitle had
592 higher DIC_{cf} at the seeps compared to the control. As for pH_{cf} , the lack of differences
593 in DIC_{cf} at the seeps compared to the control at Normanby in most corals could have
594 resulted from the high variability in seawater DIC, because seawater DIC and pH are
595 highly correlated in most conditions, i.e. where total alkalinity is similar. The present
596 results also showed that the relative change in abundance was not associated with
597 either DIC_{cf} or ΔDIC_{cf} . This is not surprising, as previous studies have shown that
598 while increasing DIC_{cf} can help to partially mitigate the negative effects of ocean
599 acidification on corals calcification, seawater pH and its impact on pH_{cf} is the main
600 driver of the calcifying fluid chemistry (Comeau et al. 2018). Nevertheless, there was
601 a significant relationship between pH_{cf} and DIC_{cf} at both locations when all the
602 samples were assessed (Fig. S4). Elevation of DIC_{cf} by some species has been
603 invoked as one potential mechanism whereby Ω_{cf} could be increased under OA,
604 thereby reducing the negative effects of OA on calcification (Cornwall et al., 2018;
605 Schoepf et al., 2017; Wall et al., 2019). However, we did not find a significant
606 relationship between DIC_{cf} elevation and coral abundance or relative change in
607 abundance at either locations. This result therefore suggests that while the control of
608 DIC_{cf} could help corals to sustain calcification in low pH under specific
609 circumstances, this mechanism likely plays a minor role compared to the control of
610 pH_{cf} .

611 Overall, our results support the idea that species-specific coral physiology
612 controls responses to OA *in situ* (as observed with seaweed inorganic carbon use
613 previously; Cornwall et al., 2017) with no or minor relations to coral phylogeny and
614 morphological traits. Moreover, our findings suggest that coral control of carbonate
615 chemistry in the calcifying fluid might influence their ecological success under OA.
616 This manifested in Ambitle, where pH variability is low and where corals with the
617 highest control on their calcifying fluid pH generally had a higher change in relative
618 abundance between the CO₂ seeps and control sites. However, these traits only
619 provide partial information and further research at a more extensive set of sites is now
620 required. In contrast, our study also shows that large pH variability, such as the one
621 found in Normanby, could mask the link between species physiological traits and
622 ecological success, highlighting the importance of characterizing environmental
623 conditions *in situ* at high temporal resolution. By combining geochemical, ecological,

624 and chemical approaches, our study demonstrates that even under seawater pH lower
625 than that predicted by the end of the century because of climate change, a variety of
626 corals that exert strong control on their calcifying fluid might still be able to calcify,
627 grow, and persist.

628

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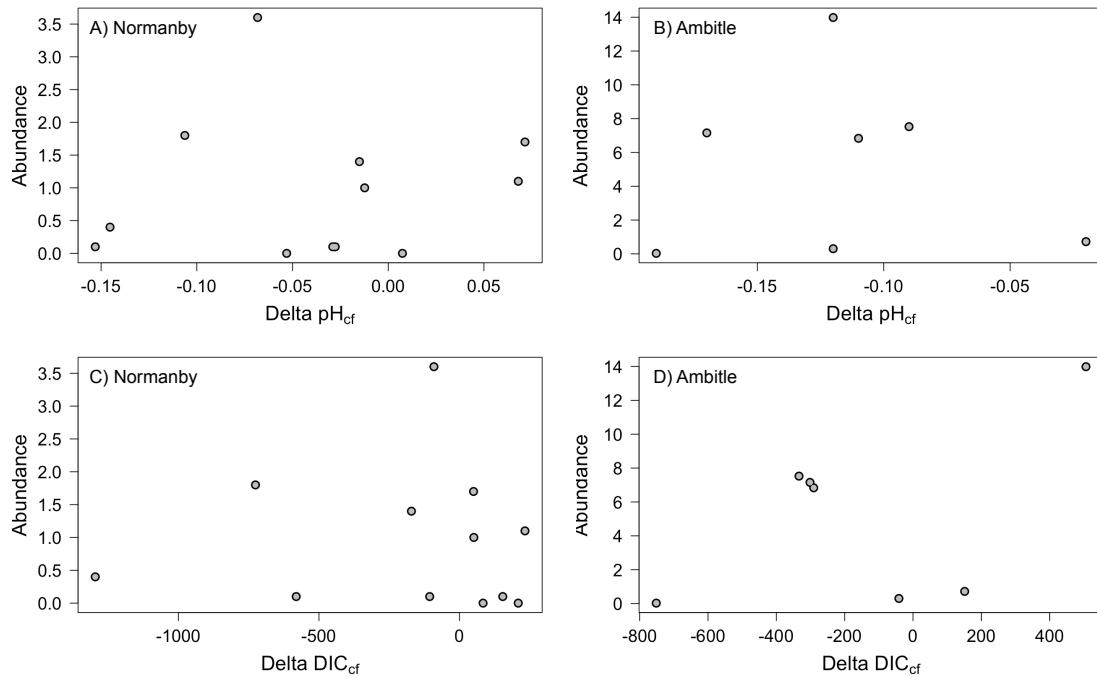
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872 **Supplementary materials**

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877 **Figure S1.** Relationship between the difference in pH_{cf} and DIC_{cf} between the control

878 and seeps sites (i.e., Delta pH_{cf} and Delta DIC_{cf}) and the abundance of corals at the

879 seeps sites. There was no relationship with pH_{cf} in Normanby (A) and Ambitle (B).

880 Similarly, there was no relationship with DIC_{cf} in Normanby (C) and Ambitle (C).

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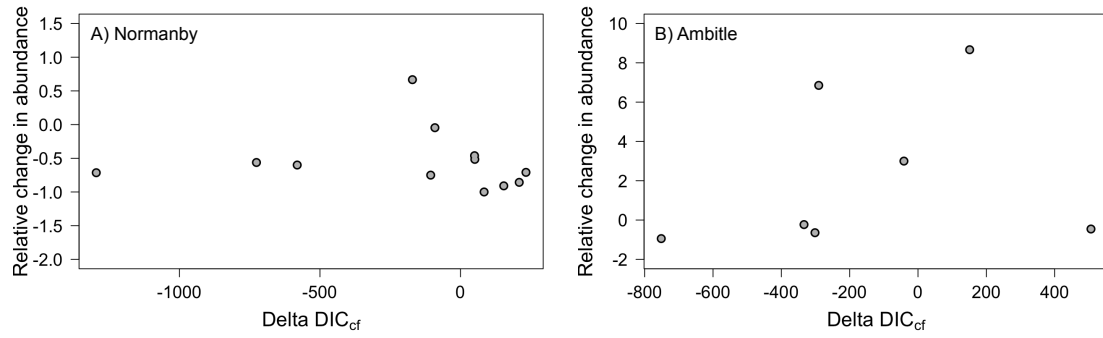
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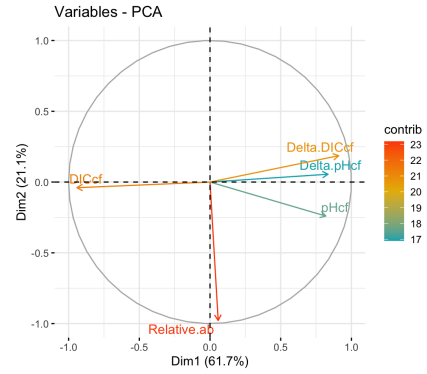
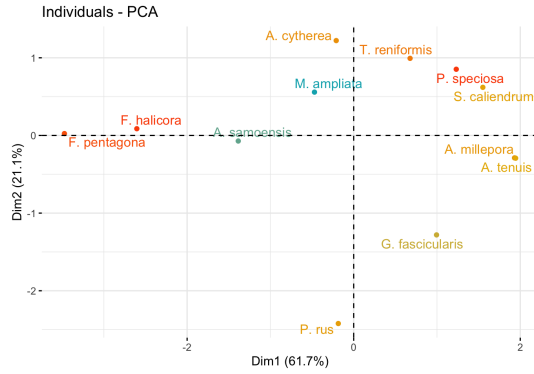
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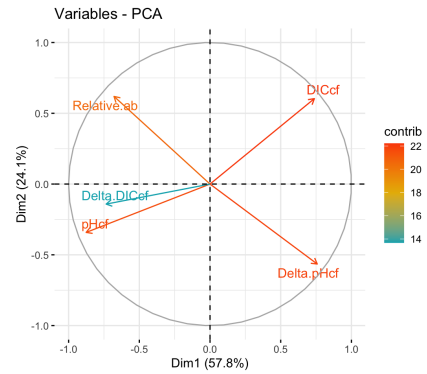
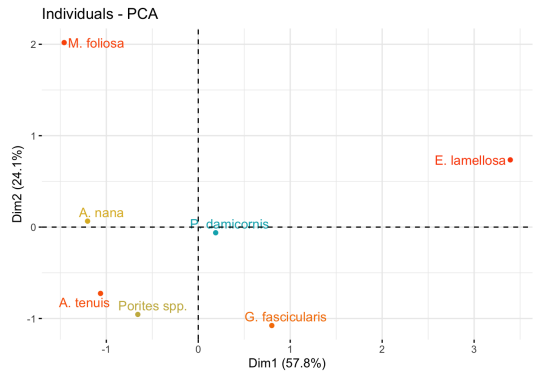
891 **Figure S2.** Relationship between the difference in DIC_{cf} between the control and
 892 seeps sites (i.e., Delta DIC_{cf}) and the relative change in coral abundance between the
 893 control and the seeps sites. There was no relationship in Normanby (A) and Ambitle
 894 (B).

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A) Normanby



B) Ambitle



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898 **Figure S3.** Principal Component Analyses showing the correlation between change in

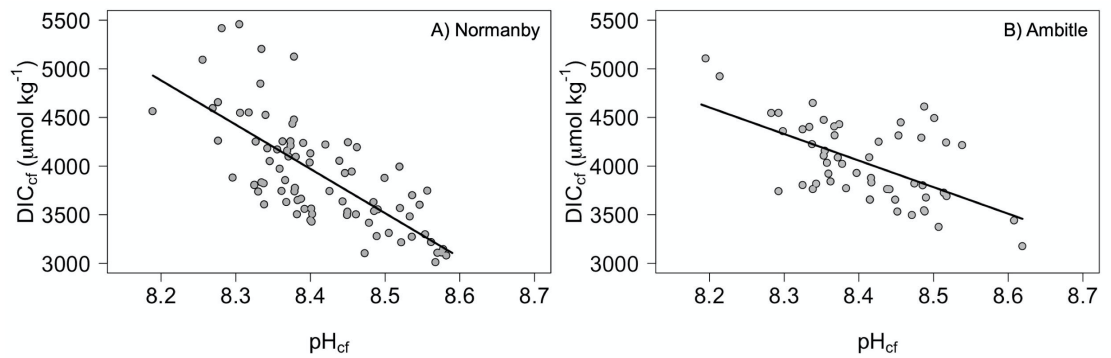
899 relative mean abundance (Prop_ab), vent pH_{cf} and DIC_{cf}, delta pH_{cf} (pH_{cf} vent – pH_{cf}

900 control; delta pH on the figure) and delta DIC_{cf} (pH_{cf} vent – pH_{cf} control; delta DIC on

901 the figure) were correlated.

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Figure S4. Relationship between pH_{cf} and DIC_{cf} in corals from Normanby and Ambitle. Corals from the control and the seeps sites were pooled together. A) relationship in Normanby Island (Linear regression: p-value of the slope < 0.001, R² = 0.50). B) relationship in Ambitle Island (Linear regression: p-value of the slope < 0.001, R² = 0.36).

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915 **Table S1.** Seawater carbonate chemistry in Ambitle and Normanby at the control and
 916 the seeps sites. Medians, 5th and 95th percentile (between parentheses) of the measured
 917 pH_T, total alkalinity (*A_T*) and temperature (T) are shown. pCO₂, *C_T*, and Ω_{arag} were
 918 calculated using the median values of *A_T* and T and the median, 5th and 95th percentile
 919 of pH_T.

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Site	pH _T	<i>A_T</i> (μmol kg ⁻¹)	T	pCO ₂ (μatm)	<i>C_T</i> (μmol kg ⁻¹)	Ω _{arag}
Ambitle	8.02	2315	30.3	422	1980	3.88
Control	(7.94 – 8.06)	(2149-2349)	(30.3-30.6)	(376-530)	(1955-2029)	(3.37-4.15)
Ambitle	7.65	2349	30.5	1178	2204	2.95
Seeps	(7.47-7.80)	(2183-2382)	(30.2–30.7)	(793-1863)	(2135-2276)	(2.03-3.95)
Normanby	7.97	2163	30.5	454	1872	3.33
Control	(7.91-8.00)	(2107-2192)	(30.1-30.8)	(416-537)	(1855-1905)	(2.99-3.51)
Normanby	7.66	2221	30.2	1084	2080	1.89
Seeps	(7.19-7.92)	(2184-2276)	(26.9-30.9)	(538-3495)	(1956-2246)	(0.70-3.10)

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923 **Table S2.** Summary of the mean changes in delta pH_{cf} (pH_{cf} seeps – pH_{cf} ambient),
 924 delta DIC_{cf} (DIC_{cf} seeps – DIC_{cf} ambient) and relative change in abundance at the two
 925 locations.
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Location	Species	Delta pH _{cf}	Delta DIC _{cf}	Change in relative abundance
Normanby	<i>Acropora samoensis</i>	-0.15	581	-0.6
	<i>Favites pentagona</i>	-0.14	1296	-0.71
	<i>Tubastrea sp.</i>	-0.13	306	NA
	<i>Favites halicora</i>	-0.10	726	-0.56
	<i>Galaxea fascicularis</i>	-0.07	90	-0.04
	<i>Pocillopora verrucosa</i>	-0.06	150	NA
	<i>Acropora cytherea</i>	-0.05	-83	-1
	<i>Merulina ampliata</i>	-0.03	106	-0.75
	<i>Turbinaria reniformis</i>	-0.03	-154	-0.91
	<i>Porites rus</i>	-0.02	170	0.66
	<i>Acropora tenuis</i>	-0.01	-50	-0.52
	<i>Pachyseris speciosa</i>	0.01	-208	-0.86
	<i>Seriatopora caliendrum</i>	0.07	-233	-0.70
	<i>Acropora millepora</i>	0.07	-50	-0.46
Ambitle	<i>Echinopora lamellosa</i>	-0.19	751	-0.94
	<i>Galaxea fascicularis</i>	-0.17	301	-0.64
	Massive <i>Porites sp.</i>	-0.13	-506	-0.45
	<i>Acropora tenuis</i>	-0.12	290	3
	<i>Acropora nana</i>	-0.10	28	6.85
	<i>Psammocora contigua</i>	-0.09	178	NA
	<i>Pocillopora damicornis</i>	-0.09	333	-0.23
	<i>Montipora foliosa</i>	-0.02	-151	8.67

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