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## 8 **Ocean acidification locks algal communities in a species-poor early** 9 **successional stage**

10

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17 **Keywords:** Global change ecology, CO<sub>2</sub> seeps, Ecosystem function, Community dynamics,  
18 Inhibition, Competition, Turf algae

### 19 **ABSTRACT**

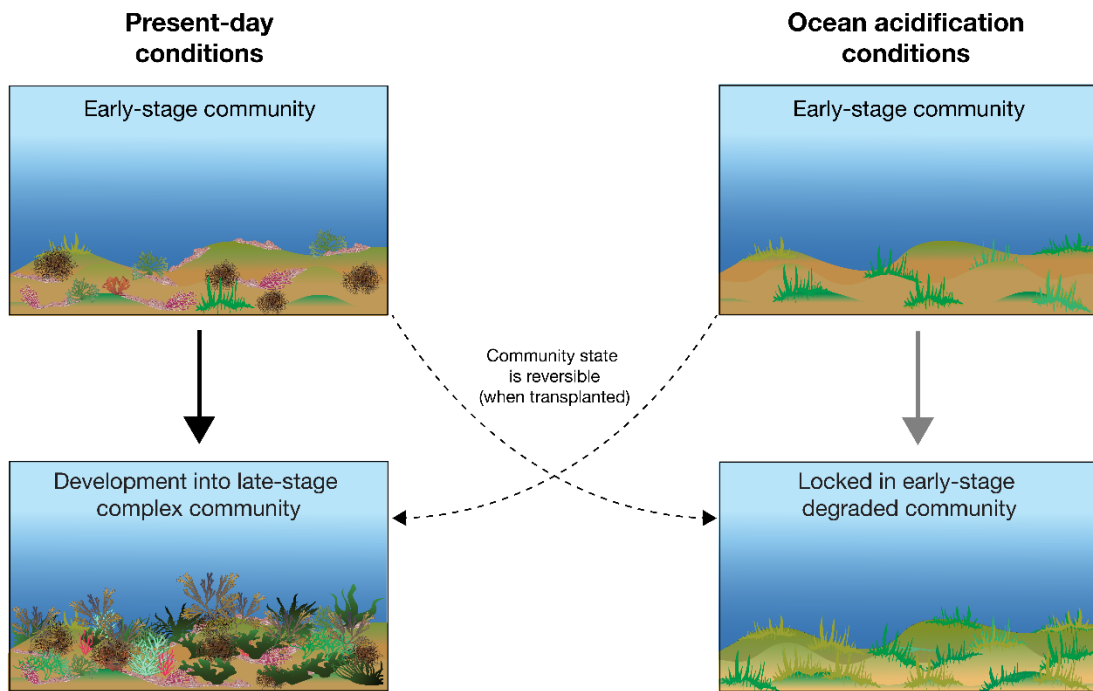
20 Long-term exposure to CO<sub>2</sub>-enriched waters can considerably alter marine biological  
21 community development, often resulting in simplified systems dominated by turf algae that  
22 possess reduced biodiversity and low ecological complexity. Current understanding of the  
23 underlying processes by which ocean acidification alters biological community development  
24 and stability remains limited, making the management of such shifts problematic. Here, we  
25 deployed recruitment tiles in reference (pH<sub>T</sub> 8.137 ± 0.056 SD) and CO<sub>2</sub>-enriched conditions  
26 (pH<sub>T</sub> 7.788 ± 0.105 SD) at a volcanic CO<sub>2</sub> seep in Japan in order to assess the underlying  
27 processes and patterns of algal community development. We assessed (i) algal community

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28 succession over six months in two different seasons (Cooler months: January–July, and warmer  
29 months: July–January), (ii) the effects of initial community composition on subsequent  
30 community succession (by reciprocally transplanting pre-established communities for a further  
31 six months), and (iii) the community net production of the resulting communities, in order to  
32 assess how any changes in community composition will alter their functioning (following 12  
33 months recruitment). Settlement tiles became dominated by turf algae under CO<sub>2</sub>-enrichment  
34 and had a lower biomass, diversity and complexity than tiles from the reference conditions.  
35 The enriched-CO<sub>2</sub> conditions enabled opportunistic *r*-selected species to competitively exclude  
36 others and lock the community in a species-poor early successional stage. This pattern was  
37 consistent across seasons, and when considering both new- and pre-established algal  
38 communities. In terms of community functioning, the elevated *p*CO<sub>2</sub> community exhibited  
39 greater net community production, and yet this apparent boost to the community did not result  
40 in benefits for the ecosystem such as increased community cover, biomass, biodiversity or  
41 structural complexity. Taken together, this shows that both new and established communities  
42 become simplified with rising CO<sub>2</sub> levels. Our transplant of pre-established communities from  
43 enriched-CO<sub>2</sub> to reference conditions showed the high resilience of the algal communities, with  
44 these transplanted communities indistinguishable from communities maintained entirely in  
45 reference conditions. This shows that meaningful reductions in *p*CO<sub>2</sub> will enable the recovery  
46 of algal communities. By understanding the ecological processes responsible for driving shifts  
47 in community composition, we can better assess how communities are likely to be altered by  
48 ocean acidification.

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## Community development and succession



50 **1 INTRODUCTION**

51 The oceanic uptake of anthropogenic carbon dioxide emissions is a global environmental issue  
52 termed ocean acidification. The effects of ocean acidification are detrimental to a wide range  
53 of marine organisms (Harvey et al., 2013; Kroeker, Kordas, et al., 2013), and this affects  
54 ecosystem functioning and the goods and services that people derive from marine resources  
55 (Gattuso et al., 2015; Hall-Spencer & Harvey, 2019). To better understand the effects of ocean  
56 acidification, there has been an effort in recent years to move beyond aquarium-based  
57 experiments on single species towards *in-situ* experiments (e.g. Albright et al., 2016, 2018;  
58 Brown et al., 2016), long-term mesocosm observations (e.g. Algueró-Muñiz et al., 2017;  
59 Moulin et al., 2015), and studies using natural CO<sub>2</sub> seeps (e.g. Agostini et al., 2018; Fabricius  
60 et al., 2011; Hall-Spencer et al., 2008; Milazzo et al., 2014). These approaches have shown that  
61 long-term exposure to ocean acidification conditions projected for the end of the century  
62 fundamentally alters the composition of marine biological communities, usually resulting in  
63 simplified systems with reduced biodiversity and less ecological complexity (Agostini et al.,  
64 2018; Sunday et al., 2017; Vizzini et al., 2017). Many of these studies have been observation-  
65 based, and so an understanding of the underlying processes responsible for driving these  
66 patterns in community development remains limited. To help assess the future effects of ocean  
67 acidification, it would be useful to better understand how community development processes  
68 are affected by rising levels of seawater CO<sub>2</sub> (Gaylord et al., 2015), and how such changes will  
69 influence their associated ecosystem functioning.

70 Ecological theory suggests that the successional trajectories of ‘disturbed’ marine subtidal  
71 communities will be primarily driven by physical stresses, competition for resources through  
72 the mechanisms of ‘facilitation’ and ‘inhibition’ (J. H. Connell & Slatyer, 1977), and the  
73 strength of associated bottom-up and top-down interactions. One of the difficulties in  
74 predicting how community development will be affected by ocean acidification is that the

75 changes in carbonate chemistry can simultaneously act as both resource and stressor (S. D.  
76 Connell et al., 2013, 2018; Milazzo et al., 2019). It provides a bottom-up resource to primary  
77 producers by enhancing the availability of bicarbonate and CO<sub>2</sub> (S. D. Connell et al., 2013;  
78 Koch et al., 2013), but also acts as a physical stressor to many organisms (including calcified  
79 primary producers) via negative effects on their physiology (Harvey et al., 2013; Kroeker,  
80 Kordas, et al., 2013). Subsequently, marine communities are expected to be re-organised by  
81 the effects of ocean acidification. Ocean acidification alters the initial successional trajectories  
82 of algal communities, which lead to dominance by fleshy algae over calcified algae in acidified  
83 conditions projected for the end of the century in both temperate and tropical settings (Crook  
84 et al., 2016; Kroeker et al., 2012). Enriched CO<sub>2</sub> alters competitive interactions, acting as a  
85 physical stressor to calcified macroalgae whereas turf algae can use the additional carbon to  
86 boost growth, which allows turf algae to attain dominance (also see S. D. Connell et al., 2018).  
87 Fast-growing opportunistic (*r*-selected) turf algal species are usually suppressed beneath  
88 macroalgal canopies on temperate reefs (C. R. Johnson & Mann, 1988) and by top-down  
89 control of grazers in coral reefs (Hughes et al., 2007). In the absence of strong competition or  
90 compensatory processes (e.g. S. D. Connell et al., 2018; Ghedini et al., 2015; Ghedini &  
91 Connell, 2016), turf species can become dominant thereby changing the ecosystem state.

92 Under present-day conditions, it has been suggested that despite bottom-up control of primary  
93 production being pervasive, top-down control by consumers has a stronger influence on the  
94 trajectories of algal community succession (Gruner et al., 2008; Hillebrand et al., 2007). For  
95 example, intense grazing by sea urchins and herbivorous fish can prevent kelp forest growth  
96 resulting in ‘urchin barrens’ dominated by crustose coralline algae (Ling et al. 2015; Kelly et  
97 al., 2016). Ocean acidification is expected to reduce bottom-up control on those species which  
98 are carbon-limited, as long as sufficient nutrients are available (Celis-Plá et al., 2015; Gordillo  
99 et al., 2003; Li et al., 2012). Top-down control by benthic invertebrates in acidified conditions

100 may also diminish, given that at CO<sub>2</sub> seeps the abundance and size of many marine fauna are  
101 reduced (Garilli et al., 2015; Harvey et al., 2016, 2018), with such examples as the observed  
102 number of sea urchin feeding halos being reduced in a CO<sub>2</sub> seep (Kroeker, Gambi, et al., 2013).  
103 Fish communities include a greater proportion of herbivorous fish within acidified conditions  
104 (during the period of peak macroalgae biomass; Cattano et al., 2020), and so it may be possible  
105 in some systems for fish to maintain top-down control (Baggini et al., 2015). Taken together,  
106 any strong reductions in bottom-up and/or top-down control are likely to alter community  
107 successional trajectories and allow *r*-selected opportunistic species to outcompete other species  
108 and dominate under ocean acidification.

109 Seasonality is an important aspect of shallow-water ecosystems, and yet the consequences of  
110 seasonally-induced environmental fluctuations have rarely been considered in ocean  
111 acidification studies (Baggini et al., 2014; Godbold & Solan, 2013). Algal communities in  
112 temperate and warm temperate ecosystems experience large seasonal changes in environmental  
113 conditions (Fig. 1), which result in considerable temporal shifts with a period of high  
114 recruitment and peak biomass typically occurring in late spring. Thus the responses of algal  
115 communities to ocean acidification will likely be strongly influenced by seasonality (Baggini  
116 et al., 2014). In the Northern Pacific Ocean, this is further complicated by the occurrence of  
117 typhoons, which typically occur between July and October in Japan. Typhoons act as a  
118 substantial physical disturbance that affects benthic community structure and habitat  
119 complexity, such as the removal of corals (Done, 1992), macroalgae (Cattano et al., 2020) and  
120 seagrass cover (Wilson et al., 2020), and can indirectly change the community function of  
121 associated species (e.g. fish; Cattano et al., 2020).

122 Observations at natural CO<sub>2</sub> seeps worldwide provide a good understanding of how long-term  
123 ocean acidification simplifies the composition of climax communities (Foo et al., 2018;

124 González-Delgado & Hernández, 2018; Hall-Spencer & Harvey, 2019), yet it remains unclear  
125 whether these simplified communities develop due to altered successional trajectory, stunted  
126 community development (*via* successional inhibition), or driven by reduced bottom-up and/or  
127 top-down control. To address these gaps, we deployed recruitment tiles in reference (~350  
128  $\mu\text{atm } p\text{CO}_2$ ) and acidified (~900  $\mu\text{atm } p\text{CO}_2$ ) conditions (using a natural  $\text{CO}_2$  seep area) to  
129 assess the early to mid-successional trajectories of algal communities in two different seasons  
130 (cooler months - January to July, and warmer months - July to January) to end of the century  
131  $p\text{CO}_2$  conditions (the RCP 8.5 scenario, 851 to 1370  $\mu\text{atm}$ ; IPCC, 2013). The study was carried  
132 out over these two time periods to investigate whether the effects of ocean acidification on  
133 community development are temporally consistent. Following this we carried out a reciprocal  
134 transplant of some of those established communities, in order to assess the effects of initial  
135 community composition on subsequent community succession in the reference and acidified  
136 conditions. Finally, we assessed the community production of these reciprocally transplanted  
137 communities (including the associated sessile invertebrate communities which contribute in  
138 terms of respiration), in order to assess how any changes in community composition will alter  
139 their ecosystem functioning.

## 140 **2 MATERIALS AND METHODS**

### 141 **2.1 *Experimental Design***

142 To investigate our core question of how ocean acidification influences early community  
143 succession of algal communities, experiments using recruitment tiles were carried out using an  
144 acidified area of the Shikine Island  $\text{CO}_2$  seep, Japan (34°19'9" N, 139° 12'18" E), and a nearby  
145 reference  $p\text{CO}_2$  area in an adjacent bay (~ 600 m away by the shortest route). Both the reference  
146 and acidified locations (hereafter '350  $\mu\text{atm}$ ' and '900  $\mu\text{atm}$ ', respectively) have had their  
147 carbonate chemistry and biology well characterised previously (Agostini et al., 2015, 2018;  
148 Cattano et al., 2020; Harvey et al., 2018, 2019; Kerfahi et al., 2020; Witkowski et al., 2019),



149 and we present two-months of additional original  $\text{pH}_T$  (Fig. S1) and temperature data collected  
 150 with a Durafet sensor (SeaFET, Sea-Bird Scientific, Halifax, Canada) using the same approach  
 151 as Agostini et al. (2018). Salinity was measured concurrently using Hobo conductivity loggers  
 152 (U24-002-C, Onset, MA, USA), and discrete samples for total alkalinity were collected  
 153 throughout the study period, with total alkalinity measured using an auto-titrator (916 Ti-  
 154 Touch, Metrohm, Switzerland). In summary, the ‘350  $\mu\text{atm}$ ’ site had a mean  $\text{pH}_T$  of  $8.137 \pm$   
 155  $0.056$  (SD) and the ‘900  $\mu\text{atm}$ ’ site had a mean  $\text{pH}_T$  of  $7.781 \pm 0.105$  (SD), and the mean  
 156 carbonate chemistry of the two locations is presented in Table 1. Long-term temperature data  
 157 were recorded over a one-year period by deploying a temperature logger (HOBO Pendant  
 158 Temperature/Light 64K Data Logger, Onset, MA, USA) at ~6 m depth in each site. The ‘900  
 159  $\mu\text{atm}$ ’ elevated  $p\text{CO}_2$  location represents an end-of-the-century projection for reductions in pH  
 160 (the RCP 8.5 scenario; IPCC, 2013), and was not confounded by differences in temperature,  
 161 salinity, dissolved oxygen, total alkalinity, nutrients or depth relative to reference sites used for  
 162 comparison (Agostini et al., 2015, 2018; Harvey et al., 2019). Our basalt recruitment tiles were  
 163 130 x 130 x 15 mm and were secured using individual anchor bolts (8.5 mm width, 70 mm  
 164 length) drilled into rock by SCUBA divers at ~6 m depth (Nemo Underwater Drill, Nemo  
 165 Power Tools, CA, USA). The tiles at each site were deployed haphazardly across a *ca.* 400  $\text{m}^2$   
 166 area (with at least 5 m between individual tiles), fixed to upward-facing substrata.

167 Table 1. Summary of the carbonate chemistry for the 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$  locations. The  $\text{pH}_T$  (350  $\mu\text{atm}$ ,  $n = 1964$ ; 900  $\mu\text{atm}$ ,  $n = 10,818$ ),  
 168 salinity (350  $\mu\text{atm}$ ,  $n = 1964$ ; 900  $\mu\text{atm}$ ,  $n = 10,818$ ), and total alkalinity ( $A_T$ ; 350  $\mu\text{atm}$ ,  $n = 56$ ; 900  $\mu\text{atm}$ ,  $n = 47$ ) are measured values. All other  
 169 values were calculated using the carbonate chemistry system analysis program CO2SYS: Seawater  $p\text{CO}_2$ , dissolved inorganic carbon (DIC),  
 170 bicarbonate ( $\text{HCO}_3^-$ ), carbonate ( $\text{CO}_3^{2-}$ ), carbon dioxide ( $\text{CO}_2$ ), saturation states for calcite ( $\Omega_{\text{calcite}}$ ), and aragonite ( $\Omega_{\text{aragonite}}$ ). Values are  
 171 presented as mean, with standard deviation below. NOTE: ‘350  $\mu\text{atm}$ ’ carbonate chemistry data is sourced from Agostini et al. 2018, ‘900  $\mu\text{atm}$ ’  
 172 carbonate chemistry data is averaged across Agostini et al. 2018 and original data collected between 2017/05/31 and 2017/08/08.

Location	$\text{pH}_T$	Salinity (psu)	$A_T$ ( $\mu\text{mol kg}^{-1}$ )	$p\text{CO}_2$ ( $\mu\text{atm}$ )	DIC ( $\mu\text{mol kg}^{-1}$ )	$\text{HCO}_3^-$ ( $\mu\text{mol kg}^{-1}$ )	$\text{CO}_3^{2-}$ ( $\mu\text{mol kg}^{-1}$ )	$\Omega_{\text{calcite}}$	$\Omega_{\text{aragonite}}$
‘350 $\mu\text{atm}$ ’	8.137	34.504	2264.29	316.057	1962.694	1740.629	211.979	5.087	3.301
	0.056	0.427	15.34	47.466	34.376	55.084	22.221	0.534	0.348
‘900 $\mu\text{atm}$ ’	7.788	34.351	2268.33	841.148	2125.785	1984.889	115.150	2.771	1.805
	0.106	0.484	19.45	291.762	39.381	52.510	21.308	0.512	0.336

173

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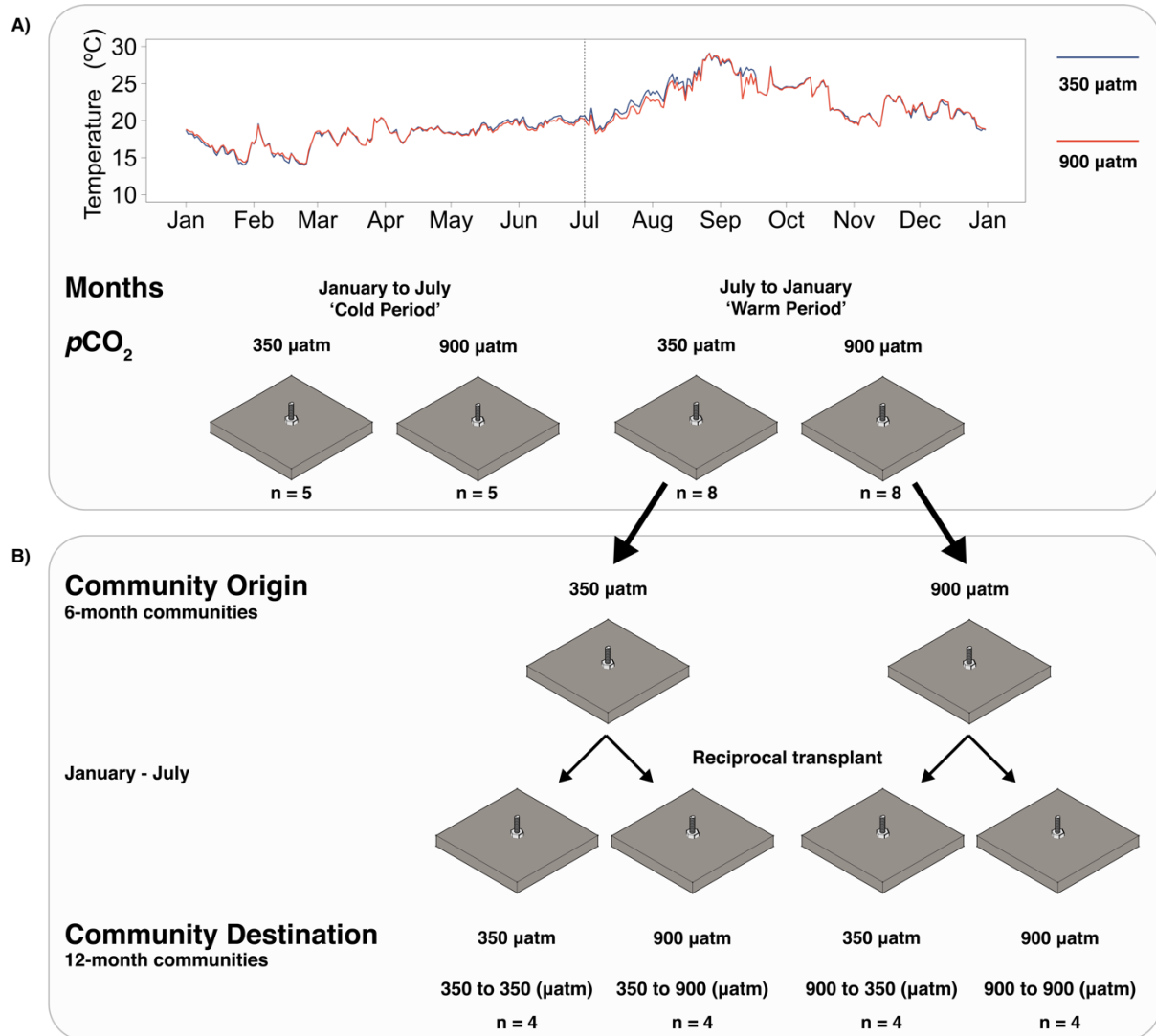
175 *2.1.1 Seasonal experiment*

176 For the first experiment, five recruitment tiles were individually deployed in each location (350  
177 and 900  $\mu\text{atm}$ ) during the cooler months of January 2017 – July 2017 (hereafter termed ‘Cold  
178 Period’), with eight recruitment tiles deployed in each location (350 and 900  $\mu\text{atm}$ ) during the  
179 warmer months of July 2017 – January 2018 (hereafter termed ‘Warm Period’). Mean seawater  
180 temperature ( $\pm$  SD) during the ‘Cold Period’ was  $18.14 \pm 1.81$  °C at 350  $\mu\text{atm}$  and  $18.07 \pm 1.63$   
181 °C at 900  $\mu\text{atm}$ , and during the ‘Warm Period’ was  $22.86 \pm 2.97$  °C at 350  $\mu\text{atm}$  and  $22.67 \pm$   
182  $2.83$  °C at 900  $\mu\text{atm}$ . See Fig. 1A for a conceptual overview of the experimental design.

183 *2.1.2 Reciprocal experiment*

184 For the second experiment, tiles from the ‘Warm Period’ of the seasonal experiment were used  
185 (each tile had an algal community following 6-months recruitment). Sixteen tiles from the  
186 seasonal experiment were reciprocally transplanted into the 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$  locations  
187 for a further six months to assess the effects of initial community composition on subsequent  
188 community succession in reference and acidified conditions (four tiles in each combination,  
189 see Fig. 1B).

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**Figure 1. Conceptual representation of the recruitment tile treatments. A)** Tiles were deployed for six-months during the ‘Cold Period’ or ‘Warm Period’ in either reference  $p\text{CO}_2$  (350  $\mu\text{atm}$ ; black line) or acidified conditions (900  $\mu\text{atm}$ ; grey line). **B)** Tiles from the ‘Warm Period’ were then used as part of a reciprocal transplant either being transplanted into 350  $\mu\text{atm}$  or 900  $\mu\text{atm}$  conditions for a further six-months.

191 **2.2 Community analysis**

192 For both the seasonal experiment and the reciprocal experiment, following the six-months  
193 experimental period each tile was brought into the laboratory and photographed (Nikon D7200,  
194 Nikon, Japan). For each twelve-month tile, two photos were taken to image the upper story  
195 community, and (after removal of the upper-story community by hand) the under-story  
196 community. These data were then combined for analysis. Community composition was  
197 assessed using ImageJ (Abràmoff et al., 2004) by overlaying 64 points on a grid, and recording  
198 the abundance of each algal functional group underlying that point. Functional groups used  
199 followed Steneck & Dethier (1994), with algal grouping being based on their morphology,  
200 thallus size and complexity (microalgae, filamentous algae, foliose algae, corticated foliose  
201 algae, corticated macrophytes, leathery macrophytes, articulated calcareous algae and crustose  
202 algae). The habitat complexity of each tile was determined by combining the abundance of  
203 each algal functional group with a rank (0 to 5) based on the biogenic habitat complexity  
204 provided by that functional group. The ranking was based on categories assigned by Steneck  
205 & Dethier (1994): microalgae = 1, filamentous algae = 2, foliose algae = 3, corticated foliose  
206 algae = 3.5, corticated macrophytes = 4, leathery macrophytes = 5, articulated calcareous algae  
207 = 4 and crustose algae = 3. The habitat complexity score was then normalised to between 0 and  
208 1.

209 **2.3 Community production**

210 Community production and respiration of individual tiles was assessed by measuring, with an  
211 Orion 4-Star pH and dissolved oxygen meter (Thermo Scientific, USA), the changes in  
212 dissolved oxygen concentrations during an incubation within a 2.5 L seawater container (15  
213 cm wide x 20 cm length x 10 cm height) in a temperature-controlled water bath. Magnetic  
214 stirrers (M-1 Controller and MS101A Stirrer, AS-One, Japan) were used to continuously mix  
215 the seawater within each container throughout measurements. Seawater for each treatment

216 (pH<sub>NBS</sub> 8.05 ± 0.01 SD vs. pH<sub>NBS</sub> 7.83 ± 0.01 SD) was collected from the same location off-  
 217 shore (oceanic pH<sub>NBS</sub> 8.05) and treatments of pH<sub>NBS</sub> 7.83 ± 0.01 SD were acquired by bubbling  
 218 with pure CO<sub>2</sub> (Fukurow pH Controller; Aqua Geek, Kawaguchi, Japan). Community  
 219 production and respiration were measured over a 150-minute period; first determining oxygen  
 220 production (60-minute light period, *ca.* 200 μmol m<sup>-2</sup> s<sup>-1</sup>), and after a 30-minute dark period,  
 221 oxygen consumption (60-minute dark period). Net community production and community  
 222 respiration are measured during the light and dark periods, respectively, with gross primary  
 223 production calculated as the net community production minus community respiration. All three  
 224 measurements are presented as mol O<sub>2</sub> hr<sup>-1</sup> m<sup>-2</sup>. To assess whether any changes in respiration  
 225 rates were driven by an altered sessile invertebrate community for the 12-month communities,  
 226 the community composition and total cover of the sessile fauna (located on the underside of  
 227 the tile) was assessed, following the same procedure as the community analysis (based on the  
 228 percent cover of the sessile faunal species).

#### 229 **2.4 Statistical analysis**

230 Statistical analyses were conducted using R (version 3.6.0; Team & R Development Core  
 231 Team, 2019), with the ‘vegan’ (Oksanen et al., 2019), ‘mvabund’ (Wang et al., 2012) and base  
 232 ‘stats’ package used for statistical analysis, and the ‘ggplot2’ (Wickham, 2016) and ‘ggpubr’  
 233 (Kassambara, 2019) packages used for figure production. For each of the analyses performed,  
 234 the package and specific function used in R are listed below as ‘package::*function*’.

235 For the seasonal experiment, differences in community composition (based on percentage  
 236 cover) between pCO<sub>2</sub> (two levels: 350 μatm and 900 μatm) and Season (two levels: ‘Cold  
 237 Period’ and ‘Warm Period’) were assessed using an nMDS (vegan::*metaMDS*) and a  
 238 permutational analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity  
 239 (vegan::*vegdist* and vegan::*adonis*). To test for differences in the percentage cover of the

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240 specific algal functional groups, we employed a two-way GLM (Family: Binomial (Link =  
241 Logit)), with  $p\text{CO}_2$  (two levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ) and Season (two levels: ‘Cold Period’  
242 and ‘Warm Period’) as fixed factors (stats::glm).

243 For the reciprocal transplant experiment, differences in community composition (based on  
244 percentage cover) between Community Origin (two levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ),  
245 Community Destination (two levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ) and Time (two levels: 6-months  
246 and 12-months) as fixed factors were assessed using an nMDS (vegan::metaMDS) and a  
247 PERMANOVA based on Bray-Curtis dissimilarity (vegan::vegdist and vegan::adonis). As the  
248 starting communities at 6-months could influence the resulting communities at 12-months on  
249 a particular tile, we accounted for this repeated measure in the PERMANOVA by using the  
250 ‘strata’ argument within vegan::adonis. To test for differences in the percentage cover of the  
251 specific algal functional groups at 12-months, we employed a two-way GLM (Family:  
252 Binomial (Link = Logit)), with Community Origin (two levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ) and  
253 Community Destination (two levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ) as fixed factors (stats::glm).

254 Differences in community production and respiration of the 12-month communities were tested  
255 using a two-way GLM (Family: Gaussian (Link = Identity)), with Community Origin (two  
256 levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ) and Community Destination (two levels: 350  $\mu\text{atm}$  and 900  
257  $\mu\text{atm}$ ) as fixed factors (stats::glm). To assess whether changes in respiration were driven by an  
258 altered sessile invertebrate community for the 12-month communities, we assessed for  
259 differences in the community composition (based on percentage cover) and total percentage  
260 cover of the sessile fauna. Differences in the community composition of the sessile fauna, with  
261 Community Origin (two levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ), and Community Destination (two  
262 levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ) as fixed factors, were assessed using a PERMANOVA based  
263 on Bray-Curtis dissimilarity (vegan::vegdist and vegan::adonis). Differences in the total

264 percentage cover of the sessile fauna were tested using a two-way GLM (Family: Gaussian  
265 (Link = Identity)), with Community Origin (two levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ) and  
266 Community Destination (two levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ) as fixed factors (stats::glm).

267 Post-hoc comparisons for all PERMANOVAs were achieved using a Bonferroni-corrected  
268 pairwise PERMANOVA. For the reciprocal transplant, only comparisons chosen *a priori* were  
269 tested; these were between Time (two levels: 6-months and 12-months) for each of the four  
270 combinations of Community Origin (two levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ) and Community  
271 Destination (two levels: 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$ ). The assumptions of the generalised linear  
272 models (GLMs) were met, with the response variable independent, the mean-variance  
273 relationship suitable (assessed by plotting the residuals vs. fits; mvabund::manyglm), and  
274 dispersion parameters not being under- or over-dispersed (assessed using quasibinomial error  
275 distributions in R; stats::glm).

276

### 277 3 RESULTS

#### 278 3.1 Effects of $p\text{CO}_2$ and Season on Community Composition

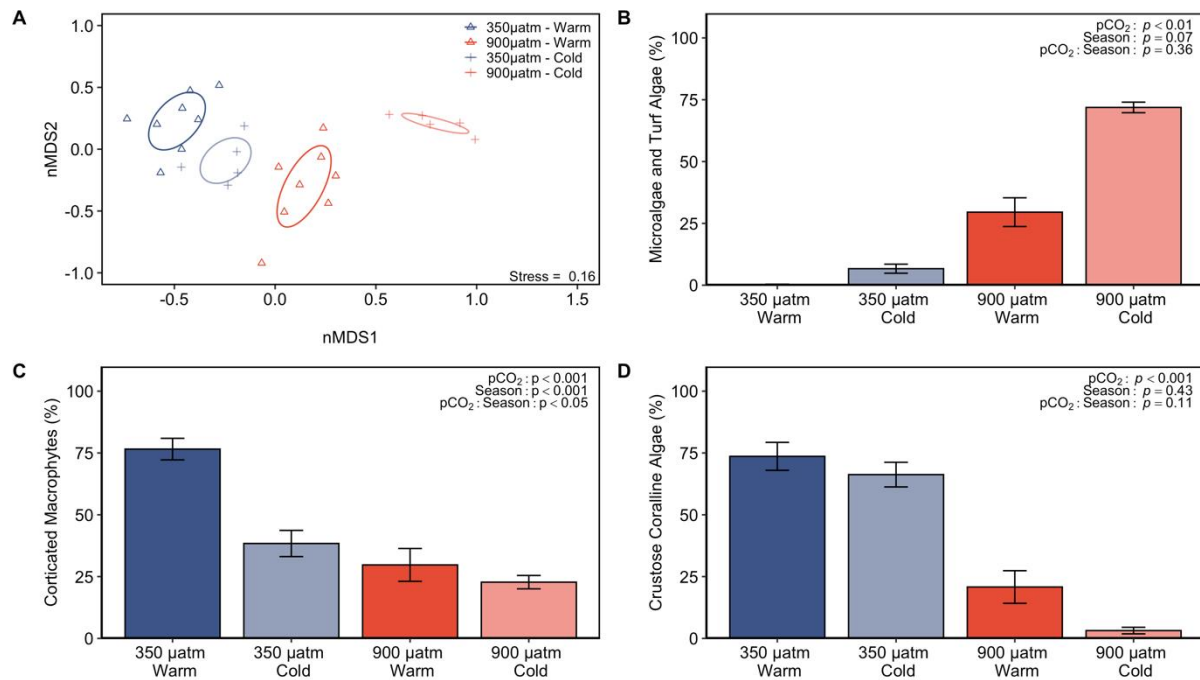
279 Overall community composition following six months settlement were highly separated by  
280 nMDS, being significantly affected by both ‘ $p\text{CO}_2$ ’ and ‘Season’ (PERMANOVA:  $p\text{CO}_2$  \*  
281 Season,  $F_{1,25} = 4.351$ ,  $p = 0.012$ ; Fig. 2A; Table 2). Community composition was similar  
282 between seasons at 350  $\mu\text{atm}$  (*post-hoc* Bonferroni-adjusted,  $p = 0.102$ ), but greatly differed  
283 between seasons at 900  $\mu\text{atm}$  (*post-hoc* Bonferroni-adjusted,  $p = 0.018$ ). The typical newly  
284 settled community at 350  $\mu\text{atm}$  during the ‘Warm Period’ largely comprised of a low coverage  
285 (< 10 %) of microalgae and turf algae (Fig. 2B) as well as corticated foliose algae, and a high  
286 coverage (~ 75 %) of both corticated macrophytes (Fig. 2C, including *Chondracanthus tenellus*  
287 (Harvey) Hommersand, 1993) and crustose coralline algae (Fig. 2D, including *Lithophyllum*



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288 *sp. Philippi, 1837*). The community at 350  $\mu\text{atm}$  during the ‘Cold Period’ was similar, the only  
 289 difference being a significantly lower cover (approximately half) of corticated macrophytes  
 290 relative to the ‘Warm Period’ (Fig. 2C).

291



**Figure 2 – (A) nMDS of community composition based on algal functional groups. Treatments are displayed by pCO<sub>2</sub> (‘350  $\mu\text{atm}$ ’ – blue; ‘900  $\mu\text{atm}$ ’ - red) and season (‘Warm Period’ – triangles; ‘Cold Period’ – crosses). (B-D) Percentage cover (%) of (B) microalgae and turf algae, (C) corticated macrophytes, and (D) crustose coralline algae following 6-months settlement at either 350  $\mu\text{atm}$  pCO<sub>2</sub> (‘Warm Period’ – darker blue, ‘Cold Period’ – lighter blue) or 900  $\mu\text{atm}$  pCO<sub>2</sub> (‘Warm Period’ – darker red, ‘Cold Period’ – lighter red). Two-way GLM (pCO<sub>2</sub> \* Season) results are presented in the top-right of B-D. See Table S1 for more detailed statistics.**

**Table 2. PERMANOVA summary of pCO<sub>2</sub> (350 vs. 900  $\mu\text{atm}$ ) and Season (‘Cold Period’ vs. ‘Warm Period’) for the algal communities.**

Term	Df	Sum Sq.	Mean Sq.	F	p	
pCO <sub>2</sub>	1	1.995	1.995	32.58	0.001	***
Season	1	0.378	0.378	6.18	0.003	**
pCO <sub>2</sub> * Season	1	0.266	0.266	4.35	0.014	*
Residuals	22	1.347	0.061			
Total	25	3.986				

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292 Relative to 350  $\mu\text{atm}$   $\text{CO}_2$ , at 900  $\mu\text{atm}$  the newly settled community during the ‘Warm Period’  
 293 showed increased coverage by microalgae and turf (from almost zero to ~30 % coverage; Fig.  
 294 2B), as well as increased corticated foliose algae (ten-fold increase; including the species  
 295 *Zonaria diesingiana* J. Agardh, 1841), but a three-fold decrease in corticated macrophytes (Fig.  
 296 2C) and a four-fold decrease in crustose coralline algae (Fig. 2D). This resulted in a community  
 297 with roughly similar coverage of the microalgae and turf, corticated macrophytes and crustose  
 298 coralline algae. During the ‘Cold Period’, the 900  $\mu\text{atm}$  communities showed a high coverage  
 299 of microalgae and turf algae (~72 %; Fig. 2B), but an absence of corticated foliose algae. Both  
 300 the corticated macrophytes (Fig. 2C) and crustose coralline algae (Fig. 2D) were similar in  
 301 coverage between the ‘Warm Period’ and ‘Cold Period’ at 900  $\mu\text{atm}$   $\text{CO}_2$ .

302

**Table 3. PERMANOVA summary of Community Origin (‘Origin’: 350 vs. 900  $\mu\text{atm}$ ), Community Destination (‘Destination’: 350 vs. 900  $\mu\text{atm}$ ), and Time (‘6-months’ vs. ‘12-months’) for algal communities grown on settlement tiles off Shikine Island, Japan.**

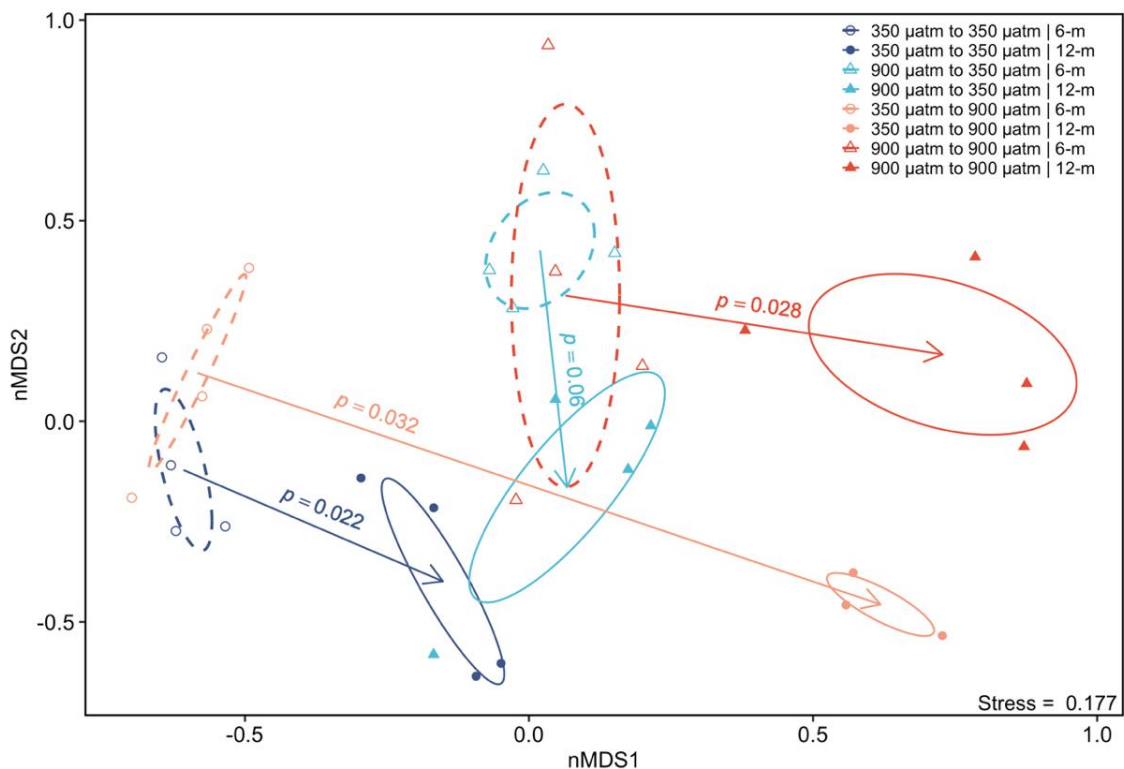
<b>Term</b>	<b><i>Df</i></b>	<b>Sum Sq.</b>	<b>Mean Sq.</b>	<b><i>F</i></b>	<b><i>p</i></b>	
Origin	1	0.910	0.910	13.05	0.001	***
Destination	1	0.669	0.669	9.59	0.002	**
Time	1	1.267	1.267	18.17	0.001	***
Origin * Destination	1	0.141	0.141	2.03	0.085	
Origin * Time	1	0.490	0.490	7.03	0.003	**
Destination * Time	1	1.16	1.16	16.66	0.001	***
Origin * Destination * Time	1	0.074	0.074	1.06	0.356	
Residuals	23	1.604	0.070			
Total	30	6.136				

303

304 **3.2 Effects of early-stage composition and  $p\text{CO}_2$  on subsequent community succession**

305 After performing a reciprocal transplant of the established six-month communities for a further  
 306 six-months, it was found that regardless of the conditions under which the communities were  
 307 established (i.e. ‘Community Origin’), the communities converged to form similar  
 308 communities based on the  $p\text{CO}_2$  conditions they were currently residing in (i.e. ‘Community  
 309 Destination’) (Fig. 3; Table 3).

310 At 12 months the 350  $\mu\text{atm}$   $\text{CO}_2$  recruitment tiles typically had a corticated macrophyte  
 311 upperstory (Fig. 4B, including *Codium coactum* Okamura, 1930 and *Chondracanthus*  
 312 *tenellus*), with an understory of microalgae and turf algae (Fig. 4A), as well as crustose



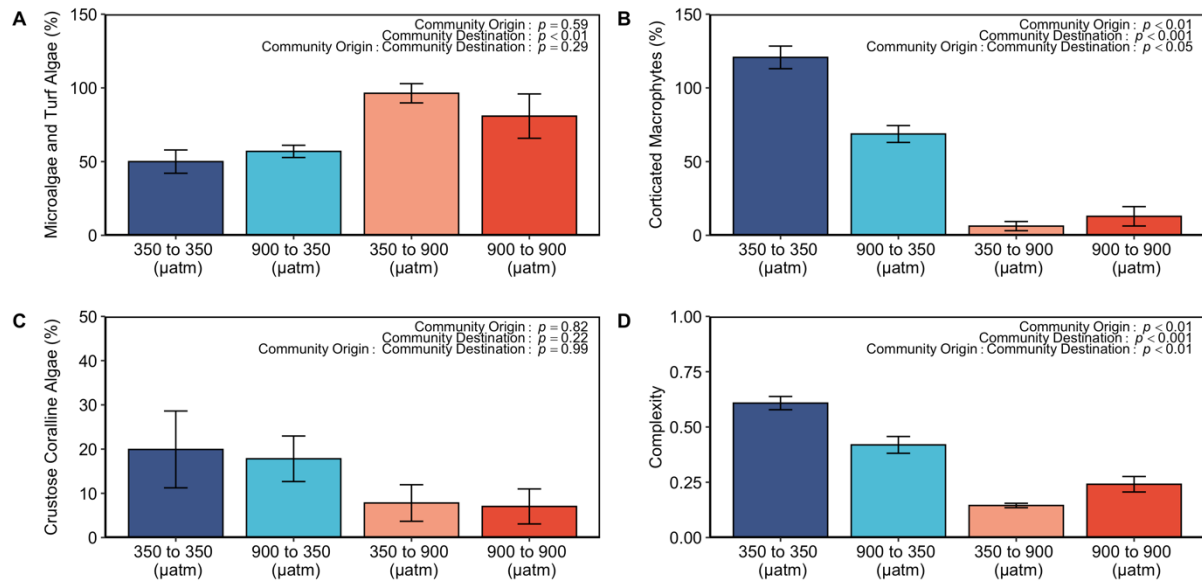
**Figure 3 – nMDS of community composition based on algal functional groups. Communities are grouped as those exposed to 350  $\mu\text{atm}$  throughout (darker blue), transplanted from 900  $\mu\text{atm}$  to 350  $\mu\text{atm}$  (lighter blue), transplanted from 350  $\mu\text{atm}$  to 900  $\mu\text{atm}$  (lighter red), and exposed to 900  $\mu\text{atm}$  throughout (darker red). The initial starting 6-month communities are displayed with open symbols and dashed lines, and the 12-month communities following the transplant are displayed with solid symbols and lines.**

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313 coralline algae (Fig. 4C, including *Lithophyllum* sp.). Both the ‘350 to 350  $\mu\text{atm}$ ’ and the ‘900  
314 to 350  $\mu\text{atm}$ ’ communities had a higher total cover than at 6-months (significant increase by  
315 ~40 % cover for both). This was due to an increased cover of understory microalgae and turf  
316 algae in the ‘350 to 350  $\mu\text{atm}$ ’ community (Fig. 4A), and increased corticated macrophytes  
317 (Fig. 4B; both as understory and canopy) for both communities. Overall the ‘350 to 350  $\mu\text{atm}$ ’  
318 community was most complex, followed by the ‘900 to 350  $\mu\text{atm}$ ’ community (Fig. 4D).

319 At 900  $\mu\text{atm}$   $\text{CO}_2$ , a typical community after 12 months lacked canopy algae and was  
320 predominantly comprised of turf algae (Fig. 4A, including *Biddulphia biddulphiana*) with  
321 some corticated foliose algae (including *Zonaria diesingiana*), and minimal cover of corticated  
322 macrophytes (Fig. 4B) and crustose coralline algae (Fig. 4C). The community that was  
323 transplanted into 900  $\mu\text{atm}$  (‘350 to 900  $\mu\text{atm}$ ’) showed a decline in total cover (significant  
324 decrease by ~45% cover), and a large reduction in complexity (Fig. 4D) due to the loss of  
325 corticated macrophytes and crustose coralline algae (Figs 4B and 4C). The community that was  
326 consistently maintained at 900  $\mu\text{atm}$  (‘900 to 900  $\mu\text{atm}$ ’) showed an increased coverage by turf  
327 and microalgae (Fig. 4A), but overall displayed similar levels of total cover (~100 % cover at  
328 6-months and ~120 % cover at 12-months) and complexity (Fig. 4D) relative to the initial 6-  
329 month community.

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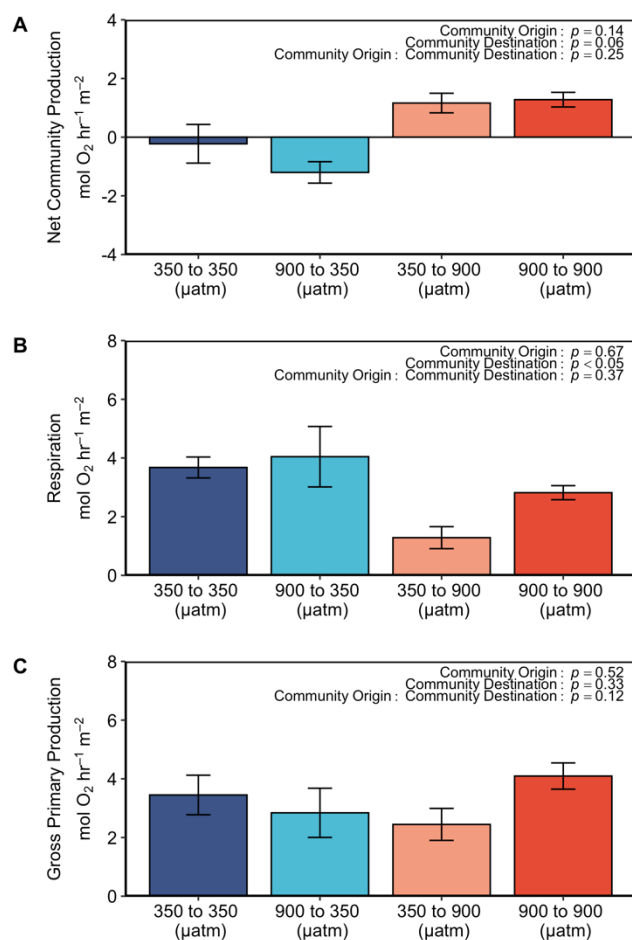


**Figure 4. Percentage cover (%) of functional groups following a further 6-months settlement: (A) microalgae and turf algae, (B) corticated macrophytes, (C) and crustose coralline algae. (D) structural complexity of the communities. Communities are grouped as those exposed to 350  $\mu\text{atm}$  throughout (darker blue), transplanted from 900 to 350  $\mu\text{atm}$  (lighter blue) or 350 to 900  $\mu\text{atm}$  (lighter red), and exposed to 900  $\mu\text{atm}$  throughout (darker red). Two-way GLM results are presented in the top-right of each. See Table S2 for more detailed statistics.**

### 330 3.3 Effects of early-stage composition and $p\text{CO}_2$ on community production

331 Net community production was reduced for the 350  $\mu\text{atm}$  communities compared to the 900  
332  $\mu\text{atm}$  communities (Fig. 5A). This is due to greatly increased community respiration rates for  
333 those communities at 350  $\mu\text{atm}$  (Fig. 5B), which resulted in the ‘350 – 350  $\mu\text{atm}$ ’ communities  
334 showing no net community production, and the ‘900 – 350  $\mu\text{atm}$ ’ communities having a  
335 negative net community production (Fig. 5A). Overall, the resulting communities had similar  
336 levels of gross community production (Fig. 5C).

## OA locks algal succession to early stage



**Figure 5. (A) Net community production (mol O<sub>2</sub> hr<sup>-1</sup> m<sup>-2</sup>), (B) Community respiration (mol O<sub>2</sub> hr<sup>-1</sup> m<sup>-2</sup>), and (C) Gross community production (mol O<sub>2</sub> hr<sup>-1</sup> m<sup>-2</sup>). Communities are grouped as those exposed to 350 μatm throughout (darker blue), transplanted between locations (900 to 350 μatm, lighter blue; and 350 to 900 μatm, lighter red), and exposed to 900 μatm throughout (darker red). See Table S3 for more detailed statistics.**

337

### 338 **3.4 Effects of early-stage composition and pCO<sub>2</sub> on sessile invertebrate community**

339 To assess whether increased respiration was driven by an altered sessile invertebrate  
340 community for the 12-month communities, the community composition and total cover of the  
341 sessile fauna was assessed. The sessile invertebrate community composition of the 12-month  
342 communities was altered by both ‘Community Origin’ and ‘Community Destination’  
343 (PERMANOVA:  $F_{1,14} = 15.07$ ,  $p < 0.001$  and  $F_{1,14} = 3.68$ ,  $p = 0.042$ , respectively; Fig. S2),  
344 with a greater coverage of ascidians (Didemnidae) and hydrozoans (Leptomedusae) in the

345 elevated  $p\text{CO}_2$  conditions ('350 – 900  $\mu\text{atm}$ ' and '900 – 900  $\mu\text{atm}$ ') and a greater coverage of  
346 polychaetes (Serpulidae) in the reference  $p\text{CO}_2$  conditions ('350 – 350  $\mu\text{atm}$ ' and '900 – 350  
347  $\mu\text{atm}$ ') (see Fig. S3). However, the overall coverage of sessile fauna did not significantly differ  
348 between the treatments (GLM: 'Community Origin'  $t = 1.17$ ,  $p = 0.27$  and 'Community  
349 Destination'  $t = -0.18$ ,  $p = 0.86$ ), with no interaction (GLM: 'Community Origin' \*  
350 'Community Destination'  $t = -0.07$ ,  $p = 0.95$ ).

351

#### 352 **4 DISCUSSION**

353 Ocean acidification alters the competitive abilities of algae and so is expected to change the  
354 structure, composition and functioning of both coastal and open ocean marine habitats  
355 (Cornwall et al., 2017; Hall-Spencer & Harvey, 2019). Observations at volcanic  $\text{CO}_2$  seeps in  
356 the photic zone have shown profound ecosystem shifts towards simplified non-calcareous  
357 communities that are often algal dominated with lower biodiversity and reduced ecological  
358 complexity (Agostini et al., 2018; S. D. Connell et al., 2018; Foo et al., 2018; González-  
359 Delgado & Hernández, 2018; Kroeker, Gambi, et al., 2013). The underlying processes by  
360 which ocean acidification affects the structure of shallow-water marine communities are not  
361 clearly established and require additional investigation, although significant progress has been  
362 made in recent years (see Kroeker et al., 2011, 2012; Kroeker, Gambi, et al., 2013; Porzio et  
363 al., 2013; Teixidó et al., 2018; Vizzini et al., 2017). We found that an enriched  $\text{CO}_2$   
364 environment had a positive effect on  $r$ -selected, fast-growing microalgae and turf algal species  
365 in the early stages of community development. This species-poor, low complexity, early-  
366 successional stage was then locked-in as it inhibited the settlement and growth of corticated  
367 macrophytes. We highlight the potential ecological processes responsible for this change in a  
368 temperate rocky reef community exposed to enriched  $\text{CO}_2$  conditions.

369 Ocean acidification altered competitive dominance after 6 months with substrata in the  
 370 acidified conditions being dominated by microalgae and turf algae, rather than the corticated  
 371 macrophytes and crustose coralline algae that dominated in reference  $p\text{CO}_2$  conditions. This  
 372 pattern was temporally consistent, showing that regardless of the growing season ocean  
 373 acidification truncates the normal successional trajectories of communities (Baggini et al.,  
 374 2014; Kroeker et al., 2012). The benefits of seawater acidification to opportunistic species,  
 375 such as turf algae, over others (including calcareous species) is well established (S. D. Connell  
 376 et al., 2013, 2018; Cornwall et al., 2017). Lowered carbonate saturation is a stressor to calcified  
 377 macroalgae (Brinkman & Smith, 2015; Enochs et al., 2015; Fabricius et al., 2011; Kamenos et  
 378 al., 2016) whilst turf algae and other fast-growing opportunistic species can use the additional  
 379 carbon from ocean acidification to grow and compete for resources (Harvey et al., 2019;  
 380 Kroeker et al., 2012; Porzio et al., 2013), thereby attaining dominance (S. D. Connell et al.,  
 381 2018). The shift from typical coastal habitat-forming species (such as corals and kelp forests)  
 382 to turf algal dominance causes a loss of structural complexity and associated ecosystem  
 383 services (O'Brien & Scheibling, 2018; Rogers et al., 2014).

384 Before turf algae overgrew the recruitment tiles in acidified conditions (between 6 and 12  
 385 months, see Fig. 3B), both crustose coralline algae and corticated macrophytes recruited onto  
 386 the substrata. This suggests that the divergence in community composition was not due to  
 387 limited recruitment or a physiological intolerance to the acidified conditions, but was driven  
 388 by altered competitive interactions (Crook et al., 2016; Kroeker et al., 2012) and/or loss of  
 389 compensatory processes (S. D. Connell et al., 2018; Ghedini et al., 2015). Although bottom-up  
 390 control helps stimulate algal growth on coral and rocky reefs, grazing pressure determines  
 391 whether turf algae dominate (Mumby et al., 2006). The grazing pressure of large benthic  
 392 invertebrates in acidified sites is thought to be lowered due to physiological impacts (Calosi et  
 393 al., 2013; O'Donnell et al., 2010) which cause their size and abundance to be reduced compared



394 to the reference  $p\text{CO}_2$  areas (Harvey et al. unpublished, this site and Vulcano, Italy; Connell et  
 395 al. 2018, White Island, New Zealand). Similarly, the observed number of sea urchin feeding  
 396 halos has also previously been found to be reduced in the Ischia  $\text{CO}_2$  seeps (Kroeker, Gambi,  
 397 et al., 2013). Fish communities also play a key role in top-down control and, in our site,  
 398 communities included more herbivorous fishes than the surrounding non-acidified areas  
 399 (Cattano et al., 2020). Clearly, the increased turf algae supported a greater herbivorous fish  
 400 population than in the reference conditions, but those same herbivores alone are not able to  
 401 control the increased growth of the boosted turf algae (also see Baggini et al., 2015; S. D.  
 402 Connell et al., 2018). Although outside the scope of this study, this may support the notion that  
 403 the fish are preferentially consuming different algae other than the turfs and further reinforcing  
 404 the ecological shift.

405 After 12 months, assemblages in reference  $p\text{CO}_2$  conditions continued to gain species through  
 406 time and had developed more structurally complex communities with clearly defined  
 407 understory and canopy species. The assemblages in the elevated  $p\text{CO}_2$  became arrested in terms  
 408 of their successional development due to competition for space by the turf algae. A similar  
 409 overgrowth and dominance by turf algae was observed on recruitment tiles in the Ischia  $\text{CO}_2$   
 410 seep (Kroeker et al., 2012; Porzio et al., 2013). This community development in our study  
 411 resulted in a similar community composition at 6 months and 12 months with only the  
 412 abundance of the turf algae being increased. At 12 months, communities on the tiles were  
 413 visually indistinguishable from the surrounding rocky substrata (Fig. S3). Similar declines in  
 414 macroalgal diversity with increasing  $p\text{CO}_2$  have also been demonstrated in Methana, Greece  
 415 (Baggini et al., 2014). The simplification of marine ecosystems has been observed across  $\text{CO}_2$   
 416 seeps (Agostini et al., 2018; Brown et al., 2018; Cigliano et al., 2010; Fabricius et al., 2011;  
 417 Kroeker, Gambi, et al., 2013; Vizzini et al., 2017), with such changes leading to a functional-  
 418 biodiversity loss in the system (Teixidó et al., 2018). It is likely that such simple systems are

419 maintained by reinforcing feedback loops (sediment trapping, changes in physicochemical  
420 environment, and recruitment inhibition) that facilitate turf algal dominance. Turf algae can  
421 inhibit successional development through reducing primary substratum availability (Airoldi,  
422 1998; S. D. Connell & Russell, 2010) and by trapping sediment which alters settlement surface  
423 chemistry and reduces the survival of other recruits (Airoldi, 2003; Gorman & Connell, 2009).  
424 Such dominance by short-lived species, which then locks the system in place, can lead to  
425 decreased stability in the system (Stachowicz et al., 2007), with implications for the functioning  
426 of the system under future ocean acidification (Teixidó et al., 2018).

427 In terms of community dynamics, both the reference and elevated  $p\text{CO}_2$  conditions appeared  
428 to overwhelm any ecological resistance that would have otherwise resisted ecosystem change.  
429 This was demonstrated by the established algal communities that were transplanted from  
430 reference to elevated  $p\text{CO}_2$  conditions converging (in terms of community composition) to  
431 almost match the community formed under elevated  $p\text{CO}_2$  conditions (and vice-versa). This  
432 suggests that acidification-driven ecological shifts to simplified turf algae communities will  
433 occur regardless of the state that the community is in, and means that the community  
434 successional trajectory is not fixed from the initial bare substratum during primary or secondary  
435 succession. The prevention of such shifts by ecosystem management will require resilience  
436 building in order to mitigate the future degradation of ecosystems (Billé et al., 2013;  
437 Falkenberg et al., 2013). In contrast, the convergence of the communities transplanted from  
438 elevated  $p\text{CO}_2$  conditions to the reference  $p\text{CO}_2$  conditions could mean that recovery from a  
439 degraded state is possible. This would likely be due to sufficient compensatory processes at  
440 our reference  $p\text{CO}_2$  location, and/or the turf algae losing its competitive edge in the absence of  
441 elevated  $p\text{CO}_2$ . Therefore, a combination of conservation strategy and meaningful reductions  
442 in atmospheric  $\text{CO}_2$  emissions could achieve substantial recovery of the abundance, structure  
443 and function of shallow coastal marine ecosystems (Duarte et al., 2020).

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444 Despite possessing highly divergent communities, gross oxygen production was similar  
445 between all of the transplanted tiles. Net oxygen production, however, was positive in the  
446 acidified conditions, but balanced between productivity and respiration for the reference  $p\text{CO}_2$   
447 communities due to elevated respiration. Ecosystems that are more developed and stable will  
448 tend towards rates of oxygen production and respiration being equal, tending to not accumulate  
449 further biomass. Early stage ecosystems will tend to have a higher productivity per biomass,  
450 but will be lacking in terms of biomass and species diversity (Cooke, 1967). This further  
451 supports the concept that the algal community developing under elevated  $p\text{CO}_2$  is arrested into  
452 a typical early stage community dominated by *r*-selected species. Previous studies in  $\text{CO}_2$  seeps  
453 have generally focussed on the primary production or photophysiology of individual species  
454 of algae (e.g. Celis-Plá et al., 2015; Porzio et al., 2018, 2020) with the aim of assessing their  
455 physiological response to ocean acidification, rather than the effects on overall community net  
456 production (making comparisons difficult). The sessile invertebrate communities differed in  
457 community composition between the reference and elevated  $p\text{CO}_2$  sites, but not in percentage  
458 cover, suggesting that they were not a sizeable contributor toward such large changes in net  
459 oxygen production. Instead, the decreased net oxygen was likely driven by the greater algal  
460 biomass (as well as low surface to volume ratio) of the more highly structurally complex  
461 reference community compared to the high surface to biomass ratio of the turf algae. Taken  
462 together, this suggests that the greater net production stimulated by ocean acidification does  
463 not translate into enhanced ecosystem benefits, such as increased community cover, biomass,  
464 biodiversity or structural complexity, as well as an altered sessile invertebrate community.

465 Natural analogues provide a number of benefits for advancing our understanding about the  
466 responses of shallow water marine communities to ocean acidification conditions, but they are  
467 not perfect analogues. Carbonate chemistry at some  $\text{CO}_2$  seeps can be highly variable (S. P. S.  
468 Rastrick et al., 2018), and areas in close proximity to  $\text{CO}_2$  vents can be enriched in some metals

469 and toxins (Vizzini et al., 2013; Zitoun et al., 2020). It is possible to reduce such confounding  
470 factors by avoiding toxic areas and only selecting sites a suitable distance away, since  
471 contamination from hydrothermal fluids can be quickly diluted by mixing with seawater  
472 (Agostini et al., 2015; Pichler et al., 2019). The gas being released at our study site is  $98 \pm 3$  %  
473 CO<sub>2</sub>, and although concentrations of hydrogen sulfide are detected at the main vent, they are  
474 below detection limits ~ 50 m away from the main vents (Agostini et al., 2015) and the study  
475 site used in this study is more than 300 m away from the main vent. An additional consideration  
476 for CO<sub>2</sub> seeps is that they demonstrate the consequences of future ocean acidification but in  
477 the absence of concurrent ocean warming (Hughes et al., 2017), and temperatures will mediate  
478 the response of organisms and communities to future ocean acidification. Such an issue can be  
479 addressed by comparing CO<sub>2</sub> seep systems under different thermal regimes and assess the  
480 consistency of responses (V. R. Johnson et al., 2012), or by manipulating temperature along  
481 CO<sub>2</sub> gradients (Alessi et al., 2019). Despite these caveats, the use of CO<sub>2</sub> seeps is still  
482 invaluable for providing a window into the future state of organisms, communities and  
483 ecosystems to future ocean acidification (S. P. S. Rastrick et al., 2018).

484 In conclusion, ocean acidification can set the course of successional development in algal  
485 communities that benefit turf algae, causing reduced algal biomass, diversity and complexity.  
486 Altered carbonate chemistry can enable opportunistic *r*-selected species to competitively  
487 exclude other species and lock the community in a species-poor early successional stage. The  
488 ecological process responsible for this shift in community composition was not simply altering  
489 community trajectory during primary succession, as the same shift occurred in pre-established  
490 communities. This highlights that without reducing atmospheric CO<sub>2</sub> emissions we may  
491 increasingly observe the loss of large algal habitats and the spread of fast-growing, small  
492 opportunistic species that can utilise additional inorganic carbon. By understanding the  
493 ecological processes responsible for driving shifts in community composition, we can begin to

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494 better assess how communities are likely to be altered by ocean acidification. Finally, our  
495 results show that the recovery of shallow water marine communities is possible if meaningful  
496 reductions in CO<sub>2</sub> emissions are implemented, as encouraged by the Paris Agreement.

497

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506

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510

511 **COMPETING INTERESTS**

512 The authors declare no conflicts of interest.

513

514 **AUTHOR CONTRIBUTIONS**

515 BH conceived the idea, designed the methodology, analysed the data, and led the writing of  
516 the manuscript. BH and KK carried out the image analysis. BH and SA performed the oxygen  
517 production measurements. All authors assisted with field work, contributed critically to the  
518 drafts and gave final approval for publication.

519

520 **DATA AVAILABILITY**

521 [Upon acceptance] Raw data used to create Figs 2-5 and Tables 1-3 will be supplied and stored  
522 in the Pangaea repository (<http://pangaea.de>).

523

524 **REFERENCES**

525 Abramoff, M. D., Magalhães, P. J., & Ram, S. J. (2004). Image processing with ImageJ.  
526 *Biophotonics International*, 11(7), 36–42.

527 Agostini, S., Harvey, B. P., Wada, S., Kon, K., Milazzo, M., Inaba, K., & Hall-Spencer, J. M.  
528 (2018). Ocean acidification drives community shifts towards simplified non-calcified  
529 habitats in a subtropical-temperate transition zone. *Scientific Reports*, 8, 11354.  
530 <https://doi.org/10.1038/s41598-018-29251-7>

531 Agostini, S., Wada, S., Kon, K., Omori, A., Kohtsuka, H., Fujimura, H., Tsuchiya, Y., Sato,  
532 T., Shinagawa, H., Yamada, Y., & Inaba, K. (2015). Geochemistry of two shallow CO<sub>2</sub>  
533 seeps in Shikine Island (Japan) and their potential for ocean acidification research.  
534 *Regional Studies in Marine Science*, 2, Supplement, 45–53.

535 Airoldi, L. (1998). Roles of disturbance, sediment stress, and substratum retention on spatial  
536 dominance in algal turf. *Ecology*, 79(8), 2759–2770. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(1998)079[2759:RODSSA]2.0.CO;2)  
537 [9658\(1998\)079\[2759:RODSSA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2759:RODSSA]2.0.CO;2)

538 Airoldi, L. (2003). The effects of sedimentation on rocky coast assemblages. *Oceanography*  
539 *and Marine Biology, An Annual Review*, 41, 169–171.

540 Albright, R., Caldeira, L., Hoffelt, J., Kwiatkowski, L., Maclaren, J. K., Mason, B. M.,  
541 Nebuchina, Y., Ninokawa, A., Pongratz, J., Ricke, K. L., Rivlin, T., Schneider, K.,

OA locks algal succession to early stage

- 542 Sesboüé, M., Shamberger, K., Silverman, J., Wolfe, K., Zhu, K., & Caldeira, K. (2016).  
543 Reversal of ocean acidification enhances net coral reef calcification. *Nature*,  
544 *531*(7594), 362–365.
- 545 Albright, R., Takeshita, Y., Koweek, D. A., Ninokawa, A., Wolfe, K., Rivlin, T., Nebuchina,  
546 Y., Young, J., & Caldeira, K. (2018). Carbon dioxide addition to coral reef waters  
547 suppresses net community calcification. *Nature*, *555*, 516.  
548 <https://doi.org/10.1038/nature25968>
- 549 Alessi, C., Giomi, F., Furnari, F., Sarà, G., Chemello, R., & Milazzo, M. (2019). Ocean  
550 acidification and elevated temperature negatively affect recruitment, oxygen  
551 consumption and calcification of the reef-building *Dendropoma cristatum* early life  
552 stages: Evidence from a manipulative field study. *Science of The Total Environment*,  
553 *693*, 133476.
- 554 Algueró-Muñiz, M., Alvarez-Fernandez, S., Thor, P., Bach, L. T., Esposito, M., Horn, H. G.,  
555 Ecker, U., Langer, J. A. F., Taucher, J., Malzahn, A. M., Riebesell, U., & Boersma, M.  
556 (2017). Ocean acidification effects on mesozooplankton community development:  
557 Results from a long-term mesocosm experiment. *PLOS ONE*, *12*(4), e0175851.  
558 <https://doi.org/10.1371/journal.pone.0175851>
- 559 Baggini, C., Issaris, Y., Salomidi, M., & Hall-Spencer, J. (2015). Herbivore diversity improves  
560 benthic community resilience to ocean acidification. *Journal of Experimental Marine*  
561 *Biology and Ecology*, *469*(0), 98–104. <https://doi.org/10.1016/j.jembe.2015.04.019>
- 562 Baggini, C., Salomidi, M., Voutsinas, E., Bray, L., Krasakopoulou, E., & Hall-Spencer, J. M.  
563 (2014). Seasonality affects macroalgal community response to increases in  $p\text{CO}_2$ . *PLoS*  
564 *One*, *9*(9), e106520.



- 565 Billé, R., Kelly, R., Biastoch, A., Harrould-Kolieb, E., Herr, D., Joos, F., Kroeker, K., Laffoley,  
566 D., Oschlies, A., & Gattuso, J.-P. (2013). Taking Action Against Ocean Acidification:  
567 A Review of Management and Policy Options. *Environmental Management*, 52(4),  
568 761–779. <https://doi.org/10.1007/s00267-013-0132-7>
- 569 Brinkman, T. J., & Smith, A. M. (2015). Effect of climate change on crustose coralline algae  
570 at a temperate vent site, White Island, New Zealand. *Mar. Freshwater Res.*, 66(4), 360–  
571 370.
- 572 Brown, N. E. M., Milazzo, M., Rastrick, S. P. S., Hall-Spencer, J. M., Therriault, T. W., &  
573 Harley, C. D. G. (2018). Natural acidification changes the timing and rate of succession,  
574 alters community structure, and increases homogeneity in marine biofouling  
575 communities. *Global Change Biology*, 24(1), e112–e127.  
576 <https://doi.org/10.1111/gcb.13856>
- 577 Brown, N. E. M., Therriault, T. W., & Harley, C. D. G. (2016). Field-based experimental  
578 acidification alters fouling community structure and reduces diversity. *Journal of*  
579 *Animal Ecology*, 85(5), 1328–1339. <https://doi.org/10.1111/1365-2656.12557>
- 580 Calosi, P., Rastrick, S. P. S., Graziano, M., Thomas, S. C., Baggini, C., Carter, H. A., Hall-  
581 Spencer, J. M., Milazzo, M., & Spicer, J. I. (2013). Distribution of sea urchins living  
582 near shallow water CO<sub>2</sub> vents is dependent upon species acid-base and ion-regulatory  
583 abilities. *Mar. Pollut. Bull.*, 73(2), 470–484.
- 584 Cattano, C., Agostini, S., Harvey, B. P., Wada, S., Quattrocchi, F., Turco, G., Inaba, K., Hall-  
585 Spencer, J. M., & Milazzo, M. (2020). Changes in fish communities due to benthic  
586 habitat shifts under ocean acidification conditions. *Science of The Total Environment*,  
587 725, 138501. <https://doi.org/10.1016/j.scitotenv.2020.138501>

- 588 Celis-Plá, P. S. M., Hall-Spencer, J. M., Horta, P. A., Milazzo, M., Korbee, N., Cornwall, C.  
589 E., & Figueroa, F. L. (2015). Macroalgal responses to ocean acidification depend on  
590 nutrient and light levels. *Frontiers in Marine Science*, 2, 26.  
591 <https://doi.org/10.3389/fmars.2015.00026>
- 592 Cigliano, M., Gambi, M. C., Rodolfo-Metalpa, R., Patti, F. P., & Hall-Spencer, J. M. (2010).  
593 Effects of ocean acidification on invertebrate settlement at volcanic CO<sub>2</sub> vents. *Marine*  
594 *Biology*, 157(11), 2489–2502. <https://doi.org/10.1007/s00227-010-1513-6>
- 595 Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and  
596 their role in community stability and organization. *The American Naturalist*, 111(982),  
597 1119–1144. <https://doi.org/10.1086/283241>
- 598 Connell, S. D., Doubleday, Z. A., Foster, N. R., Hamlyn, S. B., Harley, C. D., Helmuth, B.,  
599 Kelaher, B. P., Nagelkerken, I., Rodgers, K. L., Sarà, G., & Russell, B. D. (2018). The  
600 duality of ocean acidification as a resource and a stressor. *Ecology*, 99(5), 1005–1010.  
601 <https://doi.org/10.1002/ecy.2209>
- 602 Connell, S. D., Kroeker, K. J., Fabricius, K. E., Kline, D. I., & Russell, B. D. (2013). The other  
603 ocean acidification problem: CO<sub>2</sub> as a resource among competitors for ecosystem  
604 dominance. *Philosophical Transactions of the Royal Society B: Biological Sciences*,  
605 368(1627), 20120442. <https://doi.org/10.1098/rstb.2012.0442>
- 606 Connell, S. D., & Russell, B. D. (2010). The direct effects of increasing CO<sub>2</sub> and temperature  
607 on non-calcifying organisms: Increasing the potential for phase shifts in kelp forests.  
608 *Proc. Biol. Sci.*, 277(1686), 1409–1415.
- 609 Cooke, G. D. (1967). The pattern of autotrophic succession in laboratory microcosms.  
610 *BioScience*, 17(10), 717–721. <https://doi.org/10.2307/1294089>

- 611 Cornwall, C. E., Revill, A. T., Hall-Spencer, J. M., Milazzo, M., Raven, J. A., & Hurd, C. L.  
612 (2017). Inorganic carbon physiology underpins macroalgal responses to elevated CO<sub>2</sub>.  
613 *Scientific Reports*, 7, 46297. <https://doi.org/10.1038/srep46297>
- 614 Crook, E. D., Kroeker, K. J., Potts, D. C., Rebolledo-Vieyra, M., Hernandez-Terrones, L. M.,  
615 & Paytan, A. (2016). Recruitment and succession in a tropical benthic community in  
616 response to in-situ ocean acidification. *PLOS ONE*, 11(1), e0146707.  
617 <https://doi.org/10.1371/journal.pone.0146707>
- 618 Done, T. (1992). Effects of tropical cyclone waves on ecological and geomorphological  
619 structures on the Great Barrier Reef. *Continental Shelf Research*, 12(7–8), 859–872.
- 620 Duarte, C. M., Agusti, S., Barbier, E., Britten, G. L., Castilla, J. C., Gattuso, J.-P., Fulweiler,  
621 R. W., Hughes, T. P., Knowlton, N., Lovelock, C. E., Lotze, H. K., Predragovic, M.,  
622 Poloczanska, E., Roberts, C., & Worm, B. (2020). Rebuilding marine life. *Nature*,  
623 580(7801), 39–51. <https://doi.org/10.1038/s41586-020-2146-7>
- 624 Enochs, I. C., Manzello, D. P., Donham, E. M., Kolodziej, G., Okano, R., Johnston, L., Young,  
625 C., Iguel, J., Edwards, C. B., Fox, M. D., Valentino, L., Johnson, S., Benavente, D.,  
626 Clark, S. J., Carlton, R., Burton, T., Eynaud, Y., & Price, N. N. (2015). Shift from coral  
627 to macroalgae dominance on a volcanically acidified reef. *Nature Climate Change*,  
628 5(12), 1083–1088. <https://doi.org/10.1038/nclimate2758>
- 629 Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki,  
630 R., Muehllehner, N., Glas, M. S., & Lough, J. M. (2011). Losers and winners in coral  
631 reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change*,  
632 1(3), 165–169. <https://doi.org/10.1038/nclimate1122>

- 633 Falkenberg, L. J., Connell, S. D., & Russell, B. D. (2013). Disrupting the effects of synergies  
634 between stressors: Improved water quality dampens the effects of future CO<sub>2</sub> on a  
635 marine habitat. *Journal of Applied Ecology*, 50(1), 51–58.  
636 <https://doi.org/10.1111/1365-2664.12019>
- 637 Foo, S. A., Byrne, M., Ricevuto, E., & Gambi, M. C. (2018). The carbon dioxide vents of  
638 Ischia, Italy, a natural system to assess impacts of ocean acidification on marine  
639 ecosystems: An overview of research and comparisons with other vent systems.  
640 *Oceanography and Marine Biology: An Annual Review*, 56, 237–310.  
641 <https://doi.org/10.1201/9780429454455-9>
- 642 Garilli, V., Rodolfo-Metalpa, R., Scuderi, D., Brusca, L., Parrinello, D., Rastrick, S. P. S.,  
643 Foggo, A., Twitchett, R. J., Hall-Spencer, J. M., & Milazzo, M. (2015). Physiological  
644 advantages of dwarfing in surviving extinctions in high-CO<sub>2</sub> oceans. *Nature Climate  
645 Change*, 5(7), 678–682. <https://doi.org/10.1038/nclimate2616>
- 646 Gattuso, J.-P., Magnan, A., Billé, R., Cheung, W. W. L., Howes, E. L., Joos, F., Allemand, D.,  
647 Bopp, L., Cooley, S. R., Eakin, C. M., Hoegh-Guldberg, O., Kelly, R. P., Pörtner, H.-  
648 O., Rogers, A. D., Baxter, J. M., Laffoley, D., Osborn, D., Rankovic, A., Rochette, J.,  
649 ... Turley, C. (2015). Contrasting futures for ocean and society from different  
650 anthropogenic CO<sub>2</sub> emissions scenarios. *Science*, 349(6243), aac4722.  
651 <https://doi.org/10.1126/science.aac4722>
- 652 Gaylord, B., Kroeker, K. J., Sunday, J. M., Anderson, K. M., Barry, J. P., Brown, N. E.,  
653 Connell, S. D., Dupont, S., Fabricius, K. E., Hall-Spencer, J. M., Klinger, T., Milazzo,  
654 M., Munday, P. L., Russell, B. D., Sanford, E., Schreiber, S. J., Thiyagarajan, V.,  
655 Vaughan, M. L. H., Widdicombe, S., & Harley, C. D. G. (2015). Ocean acidification  
656 through the lens of ecological theory. *Ecology*, 96(1), 3–15.

- 657 Ghedini, G., & Connell, S. D. (2016). Organismal homeostasis buffers the effects of abiotic  
658 change on community dynamics. *Ecology*, 97(10), 2671–2679.  
659 <https://doi.org/10.1002/ecy.1488>
- 660 Ghedini, G., Russell, B. D., & Connell, S. D. (2015). Trophic compensation reinforces  
661 resistance: Herbivory absorbs the increasing effects of multiple disturbances. *Ecology*  
662 *Letters*, 18(2), 182–187. <https://doi.org/10.1111/ele.12405>
- 663 Godbold, J. A., & Solan, M. (2013). Long-term effects of warming and ocean acidification are  
664 modified by seasonal variation in species responses and environmental conditions.  
665 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1627),  
666 20130186.
- 667 González-Delgado, S., & Hernández, J. C. (2018). The importance of natural acidified systems  
668 in the study of ocean acidification: What have we learned? *Advances in Marine Biology*,  
669 80, 57–99. <https://doi.org/10.1016/bs.amb.2018.08.001>
- 670 Gordillo, F. J., Figueroa, F. L., & Niell, F. X. (2003). Photon- and carbon-use efficiency in *Ulva*  
671 *rigida* at different CO<sub>2</sub> and N levels. *Planta*, 218(2), 315–322.
- 672 Gorman, D., & Connell, S. D. (2009). Recovering subtidal forests in human-dominated  
673 landscapes. *Journal of Applied Ecology*, 46(6), 1258–1265.  
674 <https://doi.org/10.1111/j.1365-2664.2009.01711.x>
- 675 Gruner, D. S., Smith, J. E., Seabloom, E. W., Sandin, S. A., Ngai, J. T., Hillebrand, H., Harpole,  
676 W. S., Elser, J. J., Cleland, E. E., Bracken, M. E. S., Borer, E. T., & Bolker, B. M.  
677 (2008). A cross-system synthesis of consumer and nutrient resource control on producer  
678 biomass. *Ecol. Lett.*, 11(7), 740–755.

- 679 Hall-Spencer, J. M., & Harvey, B. P. (2019). Ocean acidification impacts on coastal ecosystem  
680 services due to habitat degradation. *Emerging Topics in Life Sciences*.  
681 <https://doi.org/10.1042/ETLS20180117>
- 682 Hall-Spencer, J. M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S. M.,  
683 Rowley, S. J., Tedesco, D., & Buia, M.-C. (2008). Volcanic carbon dioxide vents show  
684 ecosystem effects of ocean acidification. *Nature*, *454*(7200), 96–99.  
685 <https://doi.org/10.1038/nature07051>
- 686 Harvey, B. P., Agostini, S., Kon, K., Wada, S., & Hall-Spencer, J. M. (2019). Diatoms  
687 dominate and alter marine food-webs when CO<sub>2</sub> rises. *Diversity*, *11*(12).  
688 <https://doi.org/10.3390/d11120242>
- 689 Harvey, B. P., Agostini, S., Wada, S., Inaba, K., & Hall-Spencer, J. M. (2018). Dissolution:  
690 The Achilles' heel of the triton shell in an acidifying ocean. *Frontiers in Marine*  
691 *Science*, *5*, 371. <https://doi.org/10.3389/fmars.2018.00371>
- 692 Harvey, B. P., Gwynn-Jones, D., & Moore, P. J. (2013). Meta-analysis reveals complex marine  
693 biological responses to the interactive effects of ocean acidification and warming.  
694 *Ecology and Evolution*, *3*(4), 1016–1030. <https://doi.org/10.1002/ece3.516>
- 695 Harvey, B. P., McKeown, N. J., Rastrick, S. P. S., Bertolini, C., Foggo, A., Graham, H., Hall-  
696 Spencer, J. M., Milazzo, M., Shaw, P. W., Small, D. P., & Moore, P. J. (2016).  
697 Individual and population-level responses to ocean acidification. *Scientific Reports*, *6*,  
698 20194. <https://doi.org/10.1038/srep20194>
- 699 Hillebrand, H., Gruner, D. S., Borer, E. T., Bracken, M. E. S., Cleland, E. E., Elser, J. J.,  
700 Harpole, W. S., Ngai, J. T., Seabloom, E. W., Shurin, J. B., & Smith, J. E. (2007).  
701 Consumer versus resource control of producer diversity depends on ecosystem type and

- 702 producer community structure. *Proceedings of the National Academy of Sciences*,  
703 104(26), 10904. <https://doi.org/10.1073/pnas.0701918104>
- 704 Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B.  
705 C., Kleypas, J., van de Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R.,  
706 van Nes, E. H., & Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*,  
707 546(7656), 82–90. <https://doi.org/10.1038/nature22901>
- 708 Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O.,  
709 McCook, L., Moltschaniwskyj, N., Pratchett, M. S., Steneck, R. S., & Willis, B. (2007).  
710 Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current*  
711 *Biology*, 17(4), 360–365. <https://doi.org/10.1016/j.cub.2006.12.049>
- 712 IPCC. (2013). *Climate Change 2013—The Physical Science Basis: Working Group I*  
713 *Contribution to the Fifth Assessment Report of the IPCC* (No. 0521880092; p. 1535).  
714 Cambridge University Press.
- 715 Johnson, C. R., & Mann, K. H. (1988). Diversity, patterns of adaptation, and stability of Nova  
716 Scotian kelp beds. *Ecological Monographs*, 58(2), 129–154.  
717 <https://doi.org/10.2307/1942464>
- 718 Johnson, V. R., Russell, B. D., Fabricius, K. E., Brownlee, C., & Hall-Spencer, J. M. (2012).  
719 Temperate and tropical brown macroalgae thrive, despite decalcification, along natural  
720 CO<sub>2</sub> gradients. *Glob. Chang. Biol.*, 18(9), 2792–2803.
- 721 Kamenos, N. A., Perna, G., Gambi, M. C., Micheli, F., & Kroeker, K. J. (2016). Coralline algae  
722 in a naturally acidified ecosystem persist by maintaining control of skeletal mineralogy  
723 and size. *Proceedings of the Royal Society B: Biological Sciences*, 283(1840),  
724 20161159. <https://doi.org/10.1098/rspb.2016.1159>

- 725 Kassambara, A. (2019). Ggpubr:“ggplot2” based publication ready plots. *R Package Version*  
726 *0.2.4*. <https://CRAN.R-project.org/package=ggpubr>
- 727 Kerfahi, D., Harvey, B. P., Agostini, S., Kon, K., Huang, R., Adams, J. M., & Hall-Spencer, J.  
728 M. (2020). Responses of intertidal bacterial biofilm communities to increasing  $p\text{CO}_2$ .  
729 *Marine Biotechnology*. <https://doi.org/10.1007/s10126-020-09958-3>
- 730 Koch, M., Bowes, G., Ross, C., & Zhang, X.-H. (2013). Climate change and ocean acidification  
731 effects on seagrasses and marine macroalgae. *Global Change Biology*, *19*(1), 103–132.  
732 <https://doi.org/10.1111/j.1365-2486.2012.02791.x>
- 733 Kroeker, K. J., Gambi, M. C., & Micheli, F. (2013). Community dynamics and ecosystem  
734 simplification in a high- $\text{CO}_2$  ocean. *Proceedings of the National Academy of Sciences*  
735 *of the United States of America*, *110*(31), 12721–12726.  
736 <https://doi.org/10.1073/pnas.1216464110>
- 737 Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C.  
738 M., & Gattuso, J.-P. (2013). Impacts of ocean acidification on marine organisms:  
739 Quantifying sensitivities and interaction with warming. *Global Change Biology*, *19*(6),  
740 1884–1896. <https://doi.org/10.1111/gcb.12179>
- 741 Kroeker, K. J., Micheli, F., & Gambi, M. C. (2012). Ocean acidification causes ecosystem  
742 shifts via altered competitive interactions. *Nature Climate Change*, *3*(2), 156–159.
- 743 Kroeker, K. J., Micheli, F., Gambi, M. C., & Martz, T. R. (2011). Divergent ecosystem  
744 responses within a benthic marine community to ocean acidification. *Proceedings of*  
745 *the National Academy of Sciences of the United States of America*, *108*(35), 14515–  
746 14520. <https://doi.org/10.1073/pnas.1107789108>



- 747 Li, W., Gao, K., & Beardall, J. (2012). Interactive effects of ocean acidification and nitrogen-  
748 limitation on the diatom *Phaeodactylum tricornutum*. *PLoS One*, 7(12), e51590–e51590.  
749 PubMed. <https://doi.org/10.1371/journal.pone.0051590>
- 750 Milazzo, M., Alessi, C., Quattrocchi, F., Chemello, R., D'Agostaro, R., Gil, J., Vaccaro, A.  
751 M., Mirto, S., Gristina, M., & Badalamenti, F. (2019). Biogenic habitat shifts under  
752 long-term ocean acidification show nonlinear community responses and unbalanced  
753 functions of associated invertebrates. *Science of The Total Environment*, 667, 41–48.  
754 <https://doi.org/10.1016/j.scitotenv.2019.02.391>
- 755 Milazzo, M., Rodolfo-Metalpa, R., Chan, V. B. S., Fine, M., Alessi, C., Thiyagarajan, V., Hall-  
756 Spencer, J. M., & Chemello, R. (2014). Ocean acidification impairs vermetid reef  
757 recruitment. *Scientific Reports*, 4, 4189. <https://doi.org/10.1038/srep04189>
- 758 Moulin, L., Grosjean, P., Leblud, J., Batigny, A., Collard, M., & Dubois, P. (2015). Long-term  
759 mesocosms study of the effects of ocean acidification on growth and physiology of the  
760 sea urchin *Echinometra mathaei*. *Marine Environmental Research*, 103, 103–114.  
761 <https://doi.org/10.1016/j.marenvres.2014.11.009>
- 762 Mumby, P. J., Dahlgren, C. P., Harborne, A. R., Kappel, C. V., Micheli, F., Brumbaugh, D. R.,  
763 Holmes, K. E., Mendes, J. M., Broad, K., & Sanchirico, J. N. (2006). Fishing, trophic  
764 cascades, and the process of grazing on coral reefs. *Science*, 311(5757), 98–101.
- 765 O'Brien, J., & Scheibling, R. (2018). Turf wars: Competition between foundation and turf-  
766 forming species on temperate and tropical reefs and its role in regime shifts. *Marine*  
767 *Ecology Progress Series*, 590, 1–17.

- 768 O'Donnell, M. J., Todgham, A. E., Sewell, M. A., Hammond, L. M., Ruggiero, K., Fangué, N.  
769 A., Zippay, M. L., & Hofmann, G. E. (2010). Ocean acidification alters skeletogenesis  
770 and gene expression in larval sea urchins. *Mar. Ecol. Prog. Ser.*, 398, 157–171.
- 771 Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.  
772 R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., &  
773 Wagner, H. (2019). The vegan package. *Vegan: Community Ecology Package. R*  
774 *Package Version 2.5-5* [[https://Cran.r-Project.Org/Package=vegan](https://cran.r-project.org/package=vegan)].
- 775 Pichler, T., Biscéré, T., Kinch, J., Zampighi, M., Houlbrèque, F., & Rodolfo-Metalpa, R.  
776 (2019). Suitability of the shallow water hydrothermal system at Ambitle Island (Papua  
777 New Guinea) to study the effect of high  $p\text{CO}_2$  on coral reefs. *Marine Pollution Bulletin*,  
778 138, 148–158. <https://doi.org/10.1016/j.marpolbul.2018.11.003>
- 779 Porzio, L., Arena, C., Lorenti, M., De Maio, A., & Buia, M. C. (2020). Long-term response of  
780 *Dictyota dichotoma* var. *Intricata* (C. Agardh) Greville (Phaeophyceae) to ocean  
781 acidification: Insights from high  $p\text{CO}_2$  vents. *Science of The Total Environment*, 731,  
782 138896. <https://doi.org/10.1016/j.scitotenv.2020.138896>
- 783 Porzio, L., Buia, M. C., Ferretti, V., Lorenti, M., Rossi, M., Trifuoggi, M., Vergara, A., &  
784 Arena, C. (2018). Photosynthesis and mineralogy of *Jania rubens* at low pH/high  $p\text{CO}_2$ :  
785 A future perspective. *Science of The Total Environment*, 628–629, 375–383.  
786 <https://doi.org/10.1016/j.scitotenv.2018.02.065>
- 787 Porzio, L., Garrard, S. L., & Buia, M. C. (2013). The effect of ocean acidification on early algal  
788 colonization stages at natural  $\text{CO}_2$  vents. *Marine Biology*, 160(8), 2247–2259.  
789 <https://doi.org/10.1007/s00227-013-2251-3>

- 790 Rastrick, S. P. S., Graham, H., Azetsu-Scott, K., Calosi, P., Chierici, M., Fransson, A., Hop,  
791 H., Hall-Spencer, J., Milazzo, M., Thor, P., Kutti, T., & Handling editor: C. Brock  
792 Woodson. (2018). Using natural analogues to investigate the effects of climate change  
793 and ocean acidification on Northern ecosystems. *ICES Journal of Marine Science*,  
794 75(7), 2299–2311. <https://doi.org/10.1093/icesjms/fsy128>
- 795 Rogers, A., Blanchard, J. L., & Mumby, P. J. (2014). Vulnerability of Coral Reef Fisheries to  
796 a Loss of Structural Complexity. *Current Biology*, 24(9), 1000–1005.  
797 <https://doi.org/10.1016/j.cub.2014.03.026>
- 798 Stachowicz, J. J., Bruno, J. F., & Duffy, J. E. (2007). Understanding the effects of marine  
799 biodiversity on communities and ecosystems. *Annu. Rev. Ecol. Evol. Syst.*, 38, 739–  
800 766.
- 801 Steneck, R. S., & Dethier, M. N. (1994). A functional group approach to the structure of algal-  
802 dominated communities. *Oikos*, 69(3), 476–498.
- 803 Sunday, J. M., Fabricius, K. E., Kroeker, K. J., Anderson, K. M., E, B. N., Barry, J. P., Connell,  
804 S. D., Dupont, S., Gaylord, B., Hall-Spencer, J. M., Klinger, T., Milazzo, M., Munday,  
805 P. L., Russell, B. D., Sanford, E., Thiyagarajan, V., Vaughan, M. L. H., Widdicombe,  
806 S., & Harley, C. D. G. (2017). Ocean acidification can mediate biodiversity shifts by  
807 changing biogenic habitat. *Nature Climate Change*, 7, 81–85.  
808 <https://doi.org/10.1038/nclimate3161>
- 809 Team, R. D. C., & R Development Core Team, R. (2019). *R: A Language and Environment*  
810 *for Statistical Computing*.

- 811 Teixidó, N., Gambi, M. C., Parravacini, V., Kroeker, K., Micheli, F., Villéger, S., &  
812 Ballesteros, E. (2018). Functional biodiversity loss along natural CO<sub>2</sub> gradients. *Nature*  
813 *Communications*, 9(1), 5149. <https://doi.org/10.1038/s41467-018-07592-1>
- 814 Vizzini, S., Di Leonardo, R., Costa, V., Tramati, C. D., Luzzu, F., & Mazzola, A. (2013). Trace  
815 element bias in the use of CO<sub>2</sub> vents as analogues for low pH environments:  
816 Implications for contamination levels in acidified oceans. *Estuar. Coast. Shelf Sci.*, 134,  
817 19–30.
- 818 Vizzini, S., Martínez-Crego, B., Andolina, C., Massa-Gallucci, A., Connell, S. D., & Gambi,  
819 M. C. (2017). Ocean acidification as a driver of community simplification *via* the  
820 collapse of higher-order and rise of lower-order consumers. *Scientific Reports*, 7(1),  
821 4018. <https://doi.org/10.1038/s41598-017-03802-w>
- 822 Wang, Y., Naumann, U., Wright, S. T., & Warton, D. I. (2012). Mvabund—an R package for  
823 model-based analysis of multivariate abundance data. *Methods in Ecology and*  
824 *Evolution*, 3(3), 471–474.
- 825 Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.
- 826 Wilson, S. S., Furman, B. T., Hall, M. O., & Fourqurean, J. W. (2020). Assessment of  
827 Hurricane Irma Impacts on South Florida Seagrass Communities Using Long-Term  
828 Monitoring Programs. *Estuaries and Coasts*, 43(5), 1119–1132.  
829 <https://doi.org/10.1007/s12237-019-00623-0>
- 830 Witkowski, C. R., Agostini, S., Harvey, B. P., van der Meer, M. T. J., Sinninghe Damsté, J. S.,  
831 & Schouten, S. (2019). Validation of carbon isotope fractionation in algal lipids as a  
832  $\delta^{13}\text{C}_{\text{CO}_2}$  proxy using a natural CO<sub>2</sub> seep (Shikine Island, Japan). *Biogeosciences*,  
833 16(22), 4451–4461. <https://doi.org/10.5194/bg-16-4451-2019>

OA locks algal succession to early stage

834 Zitoun, R., Connell, S. D., Cornwall, C. E., Currie, K. I., Fabricius, K., Hoffmann, L. J.,  
835 Lamare, M. D., Murdoch, J., Noonan, S., Sander, S. G., Sewell, M. A., Shears, N. T.,  
836 van den Berg, C. M. G., & Smith, A. M. (2020). A unique temperate rocky coastal  
837 hydrothermal vent system (Whakaari–White Island, Bay of Plenty, New Zealand):  
838 Constraints for ocean acidification studies. *Marine and Freshwater Research*, *71*(3),  
839 321–344.

840