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

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17 **Keywords:** Global change ecology, CO₂ seeps, Ecosystem function, Community dynamics,
18 Inhibition, Competition, Turf algae

19 **ABSTRACT**

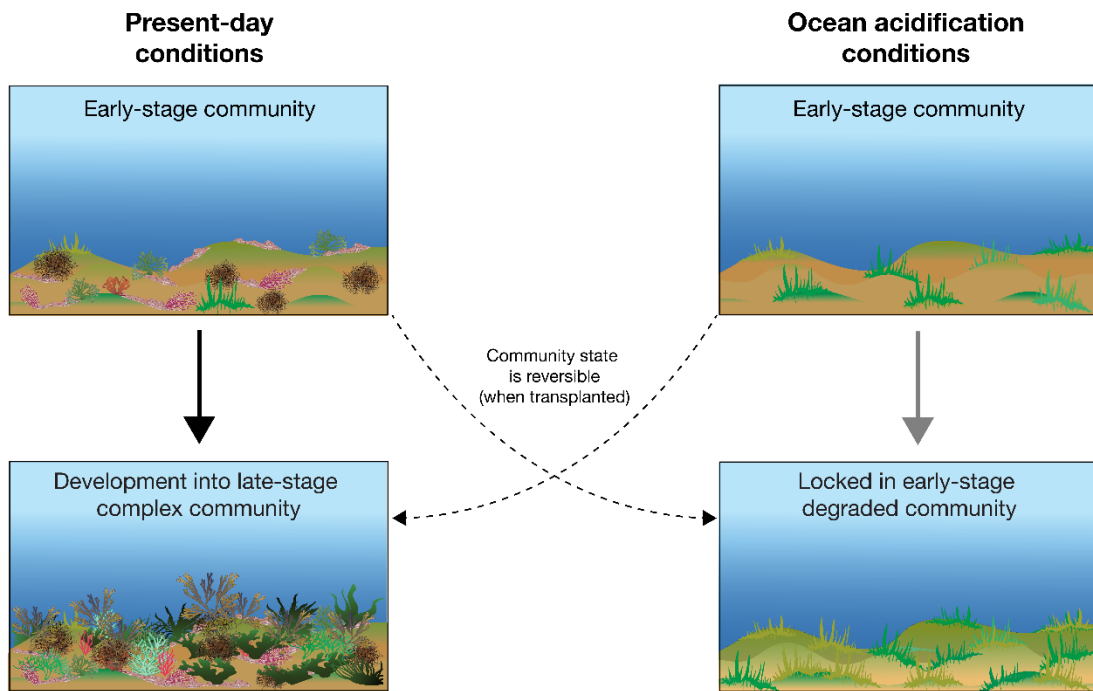
20 Long-term exposure to CO₂-enriched waters can considerably alter marine biological
21 community development, often resulting in simplified systems dominated by turf algae that
22 possess reduced biodiversity and low ecological complexity. Current understanding of the
23 underlying processes by which 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_T 8.137 ± 0.056 SD) and CO₂-enriched conditions
26 (pH_T 7.788 ± 0.105 SD) at a volcanic CO₂ 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 CO₂-enrichment
34 and had a lower biomass, diversity and complexity than tiles from the reference conditions.
35 The enriched-CO₂ 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*CO₂ 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 CO₂ levels. Our transplant of pre-established communities from
43 enriched-CO₂ 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*CO₂ 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 CO₂ 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 CO₂ (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 CO₂ (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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 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 μatm ; 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 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 μatm ' and '900 μatm ', 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 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 μatm ’ site had a mean pH_T of $8.137 \pm$
 155 0.056 (SD) and the ‘900 μatm ’ site had a mean pH_T of 7.781 ± 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 μatm ’ 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 m²
 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 μatm and 900 μatm locations. The pH_T (350 μatm , $n = 1964$; 900 μatm , $n = 10,818$),
 168 salinity (350 μatm , $n = 1964$; 900 μatm , $n = 10,818$), and total alkalinity (A_T ; 350 μatm , $n = 56$; 900 μatm , $n = 47$) 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 (HCO_3^-), carbonate (CO_3^{2-}), carbon dioxide (CO_2), saturation states for calcite (Ω_{calcite}), and aragonite ($\Omega_{\text{aragonite}}$). Values are
 171 presented as mean, with standard deviation below. NOTE: ‘350 μatm ’ carbonate chemistry data is sourced from Agostini et al. 2018, ‘900 μatm ’
 172 carbonate chemistry data is averaged across Agostini et al. 2018 and original data collected between 2017/05/31 and 2017/08/08.

Location	pH_T	Salinity (psu)	A_T ($\mu\text{mol kg}^{-1}$)	$p\text{CO}_2$ (μatm)	DIC ($\mu\text{mol kg}^{-1}$)	HCO_3^- ($\mu\text{mol kg}^{-1}$)	CO_3^{2-} ($\mu\text{mol kg}^{-1}$)	Ω_{calcite}	$\Omega_{\text{aragonite}}$
‘350 μatm ’	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 μatm ’	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

174

175 *2.1.1 Seasonal experiment*

176 For the first experiment, five recruitment tiles were individually deployed in each location (350
177 and 900 μatm) 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 μatm) 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 ± 1.81 °C at 350 μatm and 18.07 ± 1.63
181 °C at 900 μatm , and during the ‘Warm Period’ was 22.86 ± 2.97 °C at 350 μatm and $22.67 \pm$
182 2.83 °C at 900 μatm . 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 μatm and 900 μatm 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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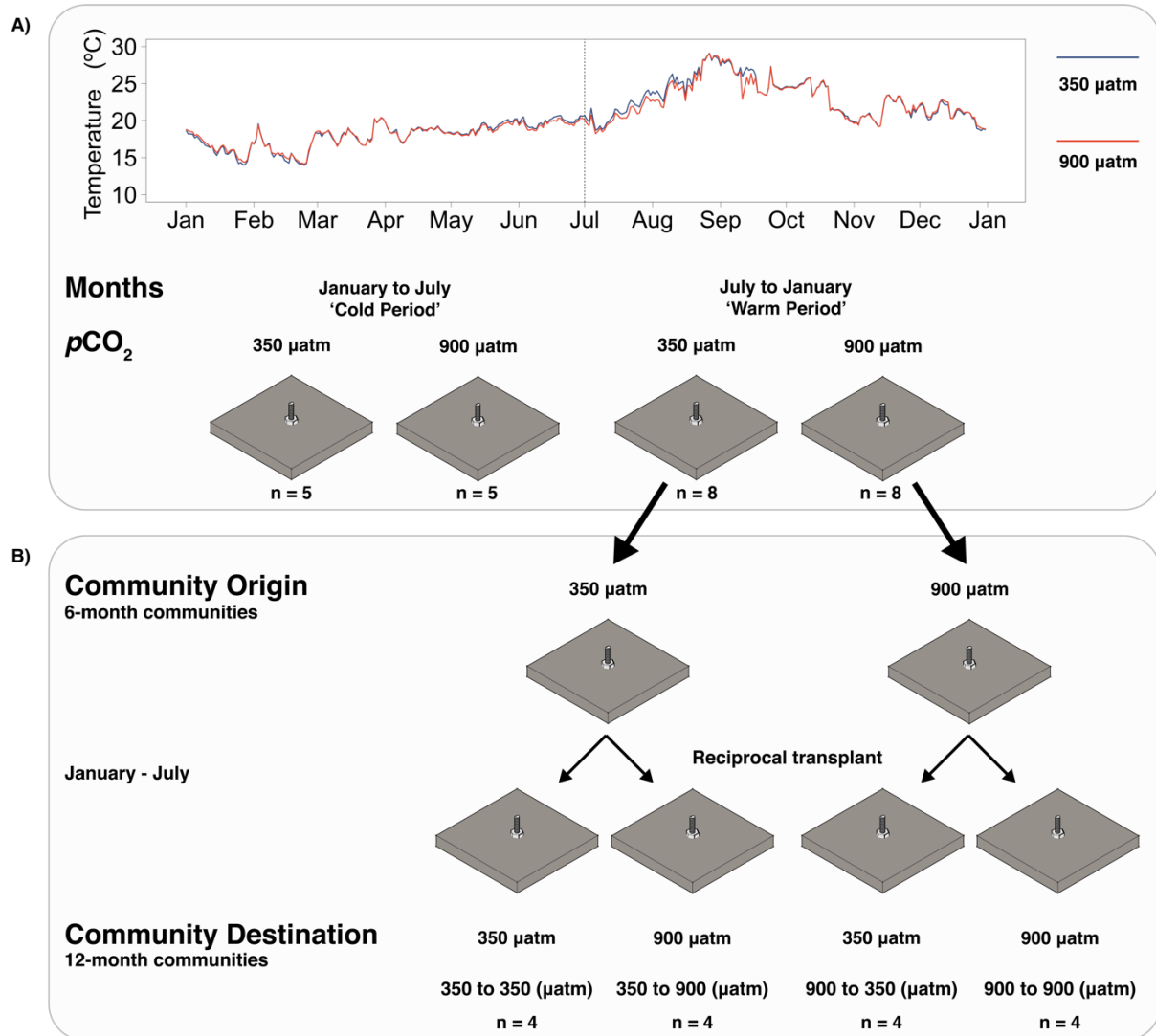


Figure 1. Conceptual representation of the recruitment tile treatments. A) Tiles were deployed for six-months during the ‘Cold Period’ or ‘Warm Period’ in either reference $p\text{CO}_2$ (350 μatm ; black line) or acidified conditions (900 μatm ; grey line). **B)** Tiles from the ‘Warm Period’ were then used as part of a reciprocal transplant either being transplanted into 350 μatm or 900 μatm 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_{NBS} 8.05 ± 0.01 SD vs. pH_{NBS} 7.83 ± 0.01 SD) was collected from the same location off-
217 shore (oceanic pH_{NBS} 8.05) and treatments of pH_{NBS} 7.83 ± 0.01 SD were acquired by bubbling
218 with pure CO₂ (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⁻² s⁻¹), 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 O₂ hr⁻¹ m⁻². 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 pCO₂ (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 μatm and 900 μatm) 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 μatm and 900 μatm),
245 Community Destination (two levels: 350 μatm and 900 μatm) 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 μatm and 900 μatm) and
253 Community Destination (two levels: 350 μatm and 900 μatm) 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 μatm and 900 μatm) and Community Destination (two levels: 350 μatm and 900
257 μatm) 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 μatm and 900 μatm), and Community Destination (two
262 levels: 350 μatm and 900 μatm) 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 μatm and 900 μatm) and
266 Community Destination (two levels: 350 μatm and 900 μatm) 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 μatm and 900 μatm) and Community
271 Destination (two levels: 350 μatm and 900 μatm). 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 μatm (*post-hoc* Bonferroni-adjusted, $p = 0.102$), but greatly differed
283 between seasons at 900 μatm (*post-hoc* Bonferroni-adjusted, $p = 0.018$). The typical newly
284 settled community at 350 μatm 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 μatm 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

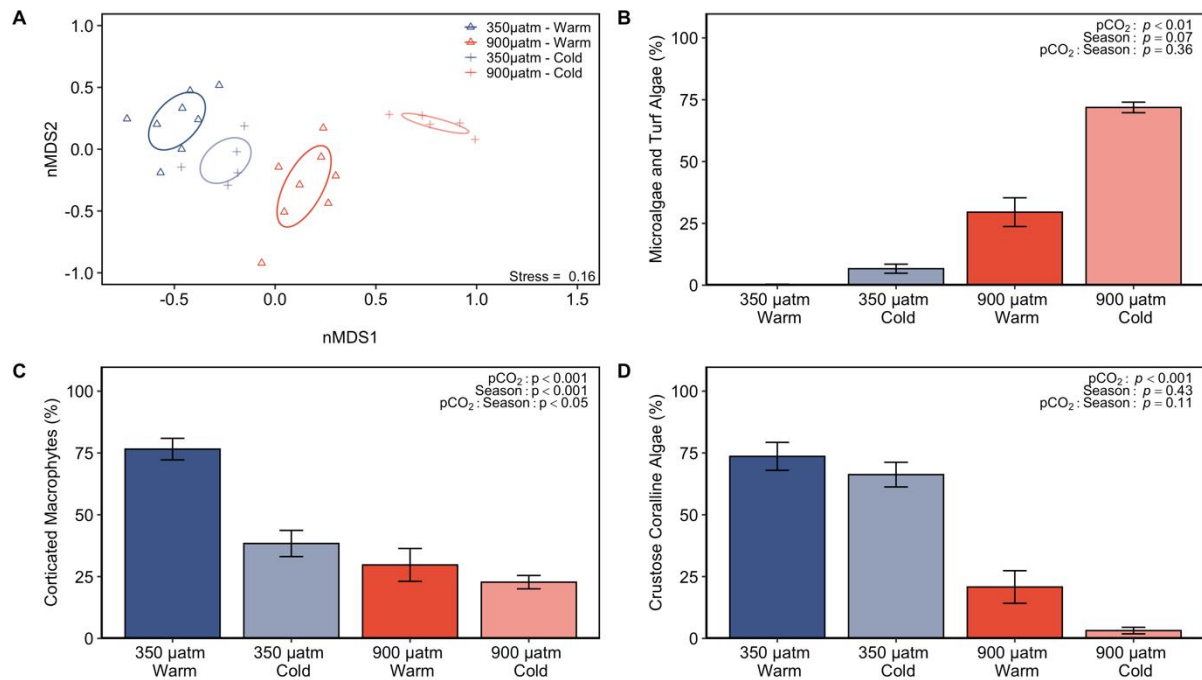


Figure 2 – (A) nMDS of community composition based on algal functional groups. Treatments are displayed by $p\text{CO}_2$ (‘350 μatm ’ – blue; ‘900 μatm ’ - red) and season (‘Warm Period’ – triangles; ‘Cold Period’ – crosses). (B-D) Percentage cover (%) of (B) microalgae and turf algae, (C) corticated macrophytes, and (D) crustose coralline algae following 6-months settlement at either 350 μatm $p\text{CO}_2$ (‘Warm Period’ – darker blue, ‘Cold Period’ – lighter blue) or 900 μatm $p\text{CO}_2$ (‘Warm Period’ – darker red, ‘Cold Period’ – lighter red). Two-way GLM ($p\text{CO}_2$ * Season) results are presented in the top-right of B-D. See Table S1 for more detailed statistics.

Table 2. PERMANOVA summary of $p\text{CO}_2$ (350 vs. 900 μatm) and Season (‘Cold Period’ vs. ‘Warm Period’) for the algal communities.

Term	Df	Sum Sq.	Mean Sq.	F	p	
$p\text{CO}_2$	1	1.995	1.995	32.58	0.001	***
Season	1	0.378	0.378	6.18	0.003	**
$p\text{CO}_2$ * 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 μatm CO_2 , at 900 μatm 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 μatm 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 μatm CO_2 .

302

Table 3. PERMANOVA summary of Community Origin (‘Origin’: 350 vs. 900 μatm), Community Destination (‘Destination’: 350 vs. 900 μatm), and Time (‘6-months’ vs. ‘12-months’) for algal communities grown on settlement tiles off Shikine Island, Japan.

Term	Df	Sum Sq.	Mean Sq.	F	p	
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 μatm 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

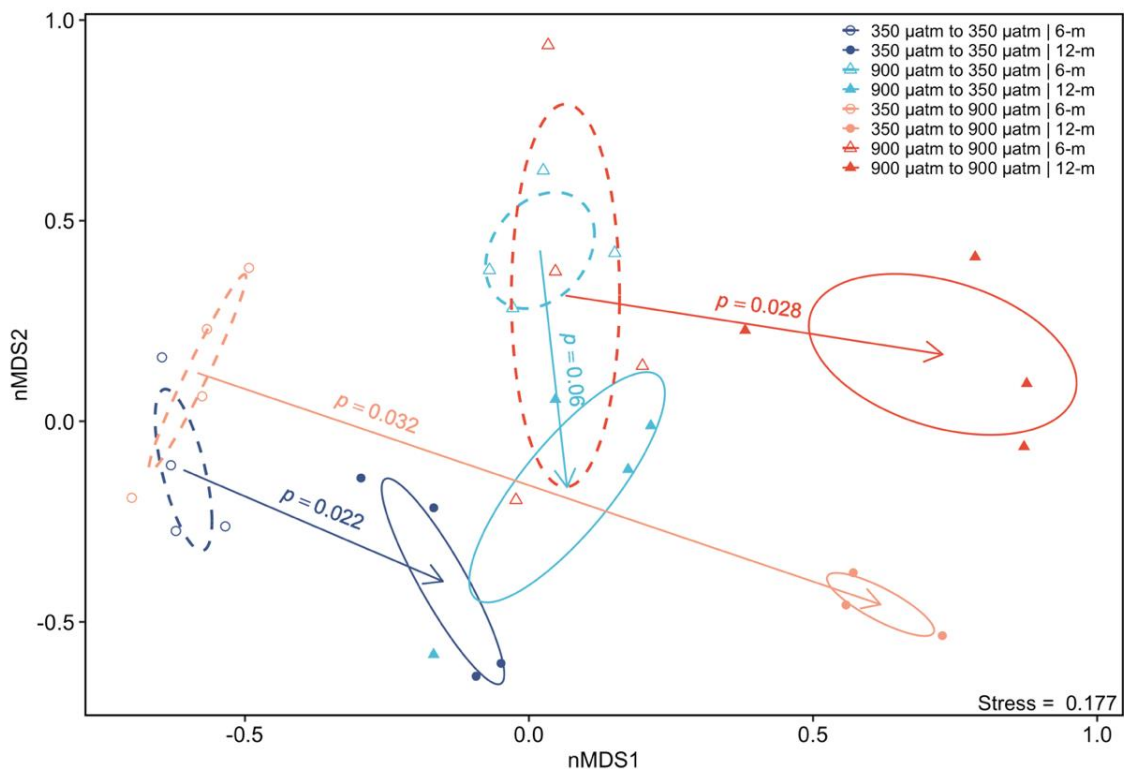


Figure 3 – nMDS of community composition based on algal functional groups. Communities are grouped as those exposed to 350 μatm throughout (darker blue), transplanted from 900 μatm to 350 μatm (lighter blue), transplanted from 350 μatm to 900 μatm (lighter red), and exposed to 900 μatm throughout (darker 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 μatm ’ and the ‘900
314 to 350 μatm ’ 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 μatm ’ community (Fig. 4A), and increased corticated macrophytes
317 (Fig. 4B; both as understory and canopy) for both communities. Overall the ‘350 to 350 μatm ’
318 community was most complex, followed by the ‘900 to 350 μatm ’ community (Fig. 4D).

319 At 900 μatm 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 μatm (‘350 to 900 μatm ’) 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 μatm (‘900 to 900 μatm ’) 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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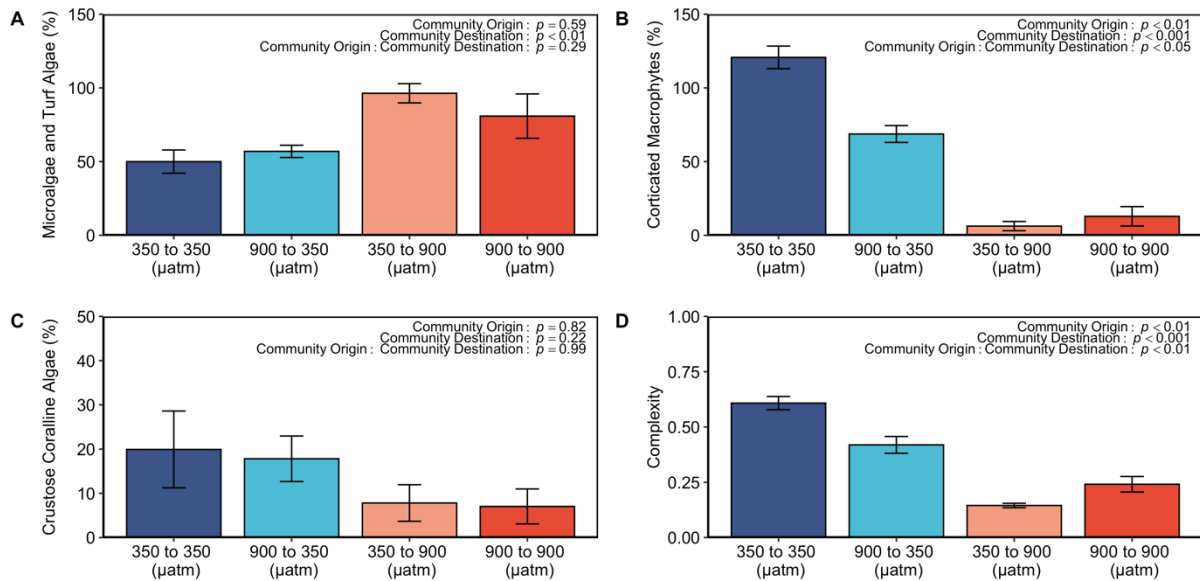


Figure 4. Percentage cover (%) of functional groups following a further 6-months settlement: (A) microalgae and turf algae, (B) corticated macrophytes, (C) and crustose coralline algae. (D) structural complexity of the communities. Communities are grouped as those exposed to 350 μatm throughout (darker blue), transplanted from 900 to 350 μatm (lighter blue) or 350 to 900 μatm (lighter red), and exposed to 900 μatm 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 μatm communities compared to the 900
332 μatm communities (Fig. 5A). This is due to greatly increased community respiration rates for
333 those communities at 350 μatm (Fig. 5B), which resulted in the ‘350 – 350 μatm ’ communities
334 showing no net community production, and the ‘900 – 350 μatm ’ communities having a
335 negative net community production (Fig. 5A). Overall, the resulting communities had similar
336 levels of gross community production (Fig. 5C).

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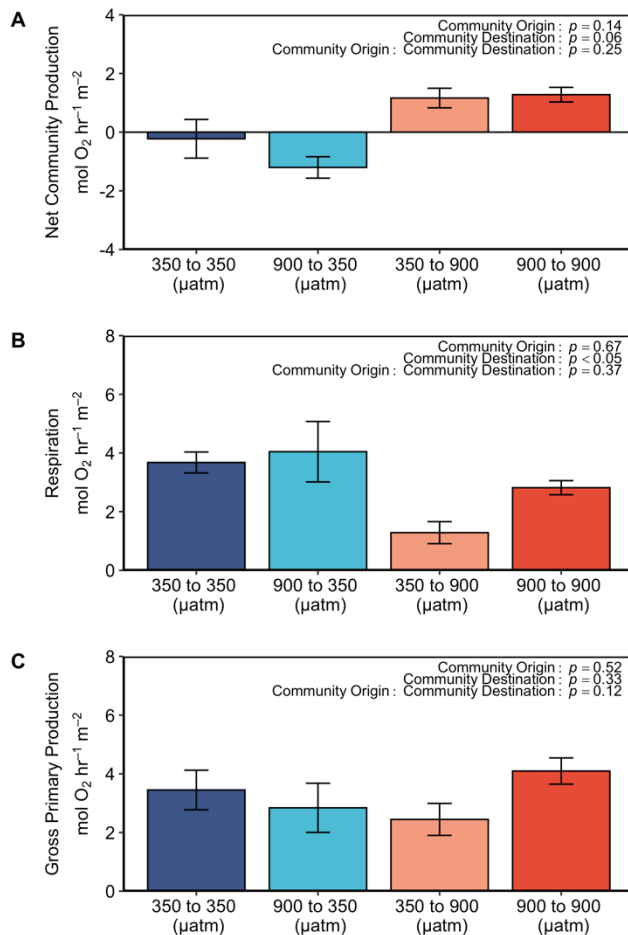


Figure 5. (A) Net community production (mol O₂ hr⁻¹ m⁻²), (B) Community respiration (mol O₂ hr⁻¹ m⁻²), and (C) Gross community production (mol O₂ hr⁻¹ m⁻²). Communities are grouped as those exposed to 350 μatm throughout (darker blue), transplanted between locations (900 to 350 μatm, lighter blue; and 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 pCO₂ 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 μatm ' and '900 – 900 μatm ') and a greater coverage of
 346 polychaetes (Serpulidae) in the reference $p\text{CO}_2$ conditions ('350 – 350 μatm ' and '900 – 350
 347 μatm ') (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 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 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 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 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 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 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 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 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 CO_2 seeps can be highly variable (S. P. S.
468 Rastrick et al., 2018), and areas in close proximity to 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 ± 3 %
473 CO₂, 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 CO₂ 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 CO₂ 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 CO₂ gradients (Alessi et al., 2019). Despite these caveats, the use of CO₂ 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 CO₂ 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 CO₂ 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

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