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## 8 Ocean acidification locks algal communities in a species-poor early

- 9 successional stage
- 10
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## 19 ABSTRACT

Long-term exposure to CO<sub>2</sub>-enriched waters can considerably alter marine biological 20 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>  $8.137 \pm 0.056$  SD) and CO<sub>2</sub>-enriched conditions 26  $(pH_T 7.788 \pm 0.105 \text{ SD})$  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 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 and had a lower biomass, diversity and complexity than tiles from the reference conditions. 34 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  $pCO_2$  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  $pCO_2$  will enable the recovery of algal communities. By understanding the ecological processes responsible for driving shifts 46 47 in community composition, we can better assess how communities are likely to be altered by 48 ocean acidification.



## **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 of marine organisms (Harvey et al., 2013; Kroeker, Kordas, et al., 2013), and this affects 53 54 ecosystem functioning and the goods and services that people derive from marine resources (Gattuso et al., 2015; Hall-Spencer & Harvey, 2019). To better understand the effects of ocean 55 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 long-term exposure to ocean acidification conditions projected for the end of the century 61 62 fundamentally alters the composition of marine biological communities, usually resulting in simplified systems with reduced biodiversity and less ecological complexity (Agostini et al., 63 2018; Sunday et al., 2017; Vizzini et al., 2017). Many of these studies have been observation-64 65 based, and so an understanding of the underlying processes responsible for driving these patterns in community development remains limited. To help assess the future effects of ocean 66 acidification, it would be useful to better understand how community development processes 67 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.

Ecological theory suggests that the successional trajectories of 'disturbed' marine subtidal communities will be primarily driven by physical stresses, competition for resources through the mechanisms of 'facilitation' and 'inhibition' (J. H. Connell & Slatyer, 1977), and the strength of associated bottom-up and top-down interactions. One of the difficulties in 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 production being pervasive, top-down control by consumers has a stronger influence on the 93 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 resulting in 'urchin barrens' dominated by crustose coralline algae (Ling et al. 2015; Kelly et 96 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 temperate and warm temperate ecosystems experience large seasonal changes in environmental 112 113 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 substantial physical disturbance that affects benthic community structure and habitat 118 119 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).

Observations at natural CO<sub>2</sub> seeps worldwide provide a good understanding of how long-term
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  $\mu$  atm pCO<sub>2</sub>) and acidified (~900  $\mu$  atm pCO<sub>2</sub>) conditions (using a natural CO<sub>2</sub> seep area) to 128 129 assess the early to mid-successional trajectories of algal communities in two different seasons (cooler months - January to July, and warmer months - July to January) to end of the century 130 131 pCO<sub>2</sub> 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

To investigate our core question of how ocean acidification influences early community succession of algal communities, experiments using recruitment tiles were carried out using an acidified area of the Shikine Island CO<sub>2</sub> seep, Japan ( $34^{\circ}19'9''$  N,  $139^{\circ}12'18''$  E), and a nearby reference *p*CO<sub>2</sub> area in an adjacent bay (~ 600 m away by the shortest route). Both the reference and acidified locations (hereafter '350 µatm' and '900 µatm', respectively) have had their carbonate chemistry and biology well characterised previously (Agostini et al., 2015, 2018; 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<sub>T</sub> (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  $\mu$ atm' site had a mean pH<sub>T</sub> of 8.137 ± 0.056 (SD) and the '900  $\mu$ atm' site had a mean pH<sub>T</sub> of 7.781 ± 0.105 (SD), and the mean 155 156 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 pCO<sub>2</sub> 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 Power Tools, CA, USA). The tiles at each site were deployed haphazardly across a ca. 400 m<sup>2</sup> 165 166 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 $\mu$ atm and 900 $\mu$ atm locations. The pH <sub>T</sub> (350 $\mu$ atm, n = 1964; 900 $\mu$ atm, n = 10,818),
168	salinity (350 $\mu$ atm, n = 1964; 900 $\mu$ atm, n = 10,818), and total alkalinity (A <sub>T</sub> ; 350 $\mu$ atm, n = 56; 900 $\mu$ atm, n = 47) are measured values. All other
169	values were calculated using the carbonate chemistry system analysis program CO2SYS: Seawater $pCO_2$ , dissolved inorganic carbon (DIC),
170	bicarbonate (HCO <sub>3</sub> <sup>-</sup> ), carbonate (CO <sub>3</sub> <sup>2-</sup> ), carbon dioxide (CO <sub>2</sub> ), saturation states for calcite ( $\Omega$ calcite), and aragonite ( $\Omega$ 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	$\mathbf{p}\mathbf{H}_{\mathrm{T}}$	Salinity	A <sub>T</sub>	pCO <sub>2</sub>	DIC	HCO <sub>3</sub> -	CO <sub>3</sub> <sup>2-</sup>	$\Omega$ calcite	Ωaragonite
		(psu)	(µmol kg <sup>-1</sup> )	(µatm)	(µmol kg <sup>-1</sup> )	(µmol kg <sup>-1</sup> )	(µmol kg <sup>-1</sup> )		
(250 ··· a 4ma )	8.137	34.504	2264.29	316.057	1962.694	1740.629	211.979	5.087	3.301
350 µatm	0.056	0.427	15.34	47.466	34.376	55.084	22.221	0.534	0.348
(000 ··· a 4ma ?	7.788	34.351	2268.33	841.148	2125.785	1984.889	115.150	2.771	1.805
'900 µatm'	0.106	0.484	19.45	291.762	39.381	52.510	21.308	0.512	0.336

## 175 2.1.1 Seasonal experiment

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

## 183 2.1.2 Reciprocal experiment

For the second experiment, tiles from the 'Warm Period' of the seasonal experiment were used (each tile had an algal community following 6-months recruitment). Sixteen tiles from the seasonal experiment were reciprocally transplanted into the 350 µatm and 900 µatm locations for a further six months to assess the effects of initial community composition on subsequent community succession in reference and acidified conditions (four tiles in each combination, see Fig. 1B).



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  $pCO_2$  (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 = 4 and crustose algae = 3. The habitat complexity score was then normalised to between 0 and 207 208 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  $(pH_{NBS} 8.05 \pm 0.01 \text{ SD vs. } pH_{NBS} 7.83 \pm 0.01 \text{ SD})$  was collected from the same location offshore (oceanic pH<sub>NBS</sub> 8.05) and treatments of pH<sub>NBS</sub>  $7.83 \pm 0.01$  SD were acquired by bubbling 217 218 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 production (60-minute light period, ca. 200 µmol m<sup>-2</sup> s<sup>-1</sup>), and after a 30-minute dark period, 220 221 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 measurements are presented as mol O<sub>2</sub> hr<sup>-1</sup> m<sup>-2</sup>. To assess whether any changes in respiration 224 225 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 percent cover of the sessile faunal species). 228

#### 229 2.4 Statistical analysis

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

For the seasonal experiment, differences in community composition (based on percentage cover) between  $pCO_2$  (two levels: 350 µatm and 900 µatm) and Season (two levels: 'Cold Period' and 'Warm Period') were assessed using an nMDS (vegan::*metaMDS*) and a permutational analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity (vegan::*vegdist* and vegan::*adonis*). To test for differences in the percentage cover of the

specific algal functional groups, we employed a two-way GLM (Family: Binomial (Link = Logit)), with  $pCO_2$  (two levels: 350 µatm and 900 µatm) and Season (two levels: 'Cold Period' and 'Warm Period') as fixed factors (stats::*glm*).

243 For the reciprocal transplant experiment, differences in community composition (based on percentage cover) between Community Origin (two levels: 350 µatm and 900 µatm), 244 245 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: Binomial (Link = Logit)), with Community Origin (two levels: 350 µatm and 900 µatm) and 252 253 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 using a two-way GLM (Family: Gaussian (Link = Identity)), with Community Origin (two 255 256 levels: 350 µatm and 900 µatm) and Community Destination (two levels: 350 µatm and 900 µatm) as fixed factors (stats::*glm*). To assess whether changes in respiration were driven by an 257 altered sessile invertebrate community for the 12-month communities, we assessed for 258 259 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

## OA locks algal succession to early stage

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

Post-hoc comparisons for all PERMANOVAs were achieved using a Bonferroni-corrected 267 268 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 combinations of Community Origin (two levels: 350 µatm and 900 µatm) and Community 270 271 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 pCO<sub>2</sub> and Season on Community Composition

279 Overall community composition following six months settlement were highly separated by 280 nMDS, being significantly affected by both 'pCO<sub>2</sub>' and 'Season' (PERMANOVA: pCO<sub>2</sub> \* Season,  $F_{1,25} = 4.351$ , p = 0.012; Fig. 2A; Table 2). Community composition was similar 281 282 between seasons at 350  $\mu$ atm (*post-hoc* Bonferroni-adjusted, p = 0.102), but greatly differed 283 between seasons at 900  $\mu$ atm (*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* (Harvey) Hommersand, 1993) and crustose coralline algae (Fig. 2D, including Lithophyllum 287

*sp.* Philippi, 1837). The community at 350 µatm during the 'Cold Period' was similar, the only
difference being a significantly lower cover (approximately half) of corticated macrophytes
relative to the 'Warm Period' (Fig. 2C).



Figure 2 – (A) nMDS of community composition based on algal functional groups. Treatments are displayed by  $pCO_2$  ('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  $pCO_2$  ('Warm Period' – darker blue, 'Cold Period' – lighter blue) or 900 µatm  $pCO_2$  ('Warm Period' – darker red, 'Cold Period' – lighter red). Two-way GLM ( $pCO_2$  \* Season) results are presented in the top-right of B-D. See Table S1 for more detailed statistics.

Table 2. PERMANOVA summary of  $pCO_2$  (350 vs. 900 µatm) and Season ('Cold Period' vs. 'Warm Period') for the algal communities.

Term	Df	Sum Sq.	Mean Sq.	F	р	
pCO <sub>2</sub>	1	1.995	1.995	32.58	0.001	***
Season	1	0.378	0.378	6.18	0.003	**
$pCO_2 * Season$	1	0.266	0.266	4.35	0.014	*
Residuals	22	1.347	0.061			
Total	25	3.986				

292	Relative to 350 µatm CO <sub>2</sub> , 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 CO2.

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

Term	Df	Sum Sq.	Mean Sq.	F	р	
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				

## 304 3.2 Effects of early-stage composition and pCO<sub>2</sub> on subsequent community succession

After performing a reciprocal transplant of the established six-month communities for a further six-months, it was found that regardless of the conditions under which the communities were established (i.e. 'Community Origin'), the communities converged to form similar communities based on the  $pCO_2$  conditions they were currently residing in (i.e. 'Community Destination') (Fig. 3; Table 3).

At 12 months the 350 µatm CO<sub>2</sub> recruitment tiles typically had a corticated macrophyte upperstory (Fig. 4B, including *Codium coactum* Okamura, 1930 and *Chondracanthus 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  $\mu$ atm throughout (darker blue), transplanted from 900  $\mu$ atm to 350  $\mu$ atm (lighter blue), transplanted from 350  $\mu$ atm to 900  $\mu$ atm (lighter red), and exposed to 900  $\mu$ 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.

coralline algae (Fig. 4C, including *Lithophyllum* sp.). Both the '350 to 350 µatm' and the '900 to 350 µatm' communities had a higher total cover than at 6-months (significant increase by ~40 % cover for both). This was due to an increased cover of understory microalgae and turf algae in the '350 to 350 µatm' community (Fig. 4A), and increased corticated macrophytes (Fig. 4B; both as understory and canopy) for both communities. Overall the '350 to 350 µatm' complex, followed by the '900 to 350 µatm' community (Fig. 4D).

319 At 900 µatm CO<sub>2</sub>, 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 uatm ('350 to 900 uatm') 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 corticated macrophytes and crustose coralline algae (Figs 4B and 4C). The community that was 325 326 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 6-months and ~120 % cover at 12-months) and complexity (Fig. 4D) relative to the initial 6-328 329 month community.



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.

#### Effects of early-stage composition and pCO<sub>2</sub> on community production 330 3.3

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

levels of gross community production (Fig. 5C). 336



Figure 5. (A) Net community production (mol  $O_2 hr^{-1} m^{-2}$ ), (B) Community respiration (mol  $O_2 hr^{-1} m^{-2}$ ), and (C) Gross community production (mol  $O_2 hr^{-1} m^{-2}$ ). 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.

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

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

elevated  $pCO_2$  conditions ('350 – 900 µatm' and '900 – 900 µatm') and a greater coverage of polychaetes (Serpulidae) in the reference  $pCO_2$  conditions ('350 – 350 µatm' and '900 – 350 µatm') (see Fig. S3). However, the overall coverage of sessile fauna did not significantly differ between the treatments (GLM: 'Community Origin' t = 1.17, p = 0.27 and 'Community Destination' t = -0.18, p = 0.86), with no interaction (GLM: 'Community Origin' \* 'Community Destination' t = -0.07, p = 0.95).

## 352 4 DISCUSSION

353 Ocean acidification alters the competitive abilities of algae and so is expected to change the structure, composition and functioning of both coastal and open ocean marine habitats 354 355 (Cornwall et al., 2017; Hall-Spencer & Harvey, 2019). Observations at volcanic CO<sub>2</sub> 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 complexity (Agostini et al., 2018; S. D. Connell et al., 2018; Foo et al., 2018; González-358 359 Delgado & Hernández, 2018; Kroeker, Gambi, et al., 2013). The underlying processes by which ocean acidification affects the structure of shallow-water marine communities are not 360 361 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 al., 2013; Teixidó et al., 2018; Vizzini et al., 2017). We found that an enriched CO<sub>2</sub> 363 364 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<sub>2</sub> 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  $pCO_2$  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 limited recruitment or a physiological intolerance to the acidified conditions, but was driven 387 388 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  $pCO_2$  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<sub>2</sub> seeps (Kroeker, Gambi, 397 et al., 2013). Fish communities also play a key role in top-down control and, in our site, communities included more herbivorous fishes than the surrounding non-acidified areas 398 399 (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  $pCO_2$  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  $pCO_2$  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<sub>2</sub> 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  $pCO_2$  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; Kroeker, Gambi, et al., 2013; Vizzini et al., 2017), with such changes leading to a functional-417 418 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 chemistry and reduces the survival of other recruits (Airoldi, 2003; Gorman & Connell, 2009). 423 424 Such dominance by short-lived species, which then locks the system in place, can lead to decreased stability in the system (Stachowicz et al., 2007), with implications for the functioning 425 426 of the system under future ocean acidification (Teixidó et al., 2018).

427 In terms of community dynamics, both the reference and elevated  $pCO_2$  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  $pCO_2$  conditions converging (in terms of community composition) to 431 almost match the community formed under elevated  $pCO_2$  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; Falkenberg et al., 2013). In contrast, the convergence of the communities transplanted from 437 438 elevated  $pCO_2$  conditions to the reference  $pCO_2$  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  $pCO_2$  location, and/or the turf algae losing its competitive edge in the absence of 441 elevated  $pCO_2$ . Therefore, a combination of conservation strategy and meaningful reductions in atmospheric CO<sub>2</sub> emissions could achieve substantial recovery of the abundance, structure 442 443 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  $pCO_2$ 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, but will be lacking in terms of biomass and species diversity (Cooke, 1967). This further 450 451 supports the concept that the algal community developing under elevated  $pCO_2$  is arrested into 452 a typical early stage community dominated by *r*-selected species. Previous studies in CO<sub>2</sub> 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  $pCO_2$  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<sub>2</sub> seeps can be highly variable (S. P. S. 468 Rastrick et al., 2018), and areas in close proximity to CO<sub>2</sub> 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  $98 \pm 3$  % CO<sub>2</sub>, and although concentrations of hydrogen sulfide are detected at the main vent, they are 473 474 below detection limits ~ 50 m away from the main vents (Agostini et al., 2015) and the study site used in this study is more than 300 m away from the main vent. An additional consideration 475 476 for  $CO_2$  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 exclude other species and lock the community in a species-poor early successional stage. The 487 488 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 communities. This highlights that without reducing atmospheric  $CO_2$  emissions we may 490 491 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

- 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.

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507 Some of the images used within the graphical abstract are courtesy of the Integration and 508 Application Network, University of Maryland Center for Environmental Science 509 (ian.umces.edu/symbols/).

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.

## 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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