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Community-level sensitivity of a calcifying ecosystem to acute *in situ* CO_2 enrichment

Heidi L. Burdett[1,2,*], Gabriela Perna[3,4], Lucy McKay[5,6], Gemma Broomhead[5], Nicholas A. Kamenos[4]

[1]Lyell Centre for Earth and Marine Science and Technology, Edinburgh EH14 4AP, UK
[2]School of Energy, Geoscience, Infrastructure and Society, Heriot-Watt University, Edinburgh EH14 4AS, UK
[3]School of Geographical and Earth Science, University of Glasgow, Glasgow G12 8QQ, UK
[4]King Abdullah University for Science and Technology, Thuwal 23955, Saudi Arabia
[5]School of Earth & Environmental Sciences, University of St Andrews, St Andrews KY16 9AL, UK
[6]School of Civil and Environmental Engineering, University of Strathclyde, Glasgow G1 1XJ, UK

ABSTRACT: The rate of change in ocean carbonate chemistry is a vital determinant in the magnitude of effects observed. Benthic marine ecosystems are facing an increasing risk of acute CO_2 exposure that may be natural or anthropogenically derived (e.g. engineering and industrial activities). However, our understanding of how acute CO_2 events impact marine life is restricted to individual organisms, with little understanding for how this manifests at the community level. Here, we investigated *in situ* the effect of acute CO_2 enrichment on the coralline algal ecosystem — a globally ubiquitous, ecologically and economically important habitat, but one which is likely to be sensitive to CO_2 enrichment due to its highly calcified reef-like structures engineered by coralline algae. Most notably, we observed a rapid community-level shift to favour net dissolution rather than net calcification. Smaller changes from net respiration to net photosynthesis were also observed. There was no effect on the net flux of DMS/DMSP (algal secondary metabolites), nor on the nutrients nitrate and phosphate. Following return to ambient CO_2 levels, only a partial recovery was seen within the monitoring timeframe. This study highlights the sensitivity of biogenic carbonate marine communities to acute CO_2 enrichment and raises concerns over the capacity for the system to 'bounce back' if subjected to repeated acute high-CO_2 events.

KEY WORDS: Calcification · Photosynthesis · Community · Ecosystem · Maerl bed · Carbon dioxide · Acidification

INTRODUCTION

Long-term environmental change as a result of rising atmospheric CO_2 levels are projected to have significant impacts on marine organisms, especially those with calcified body parts (Kroeker et al. 2010). Simultaneously, the risk of exposure to acute periods of high-CO_2 conditions is also increasing, due to the cumulative effects of coastal/marine processes (e.g. tidal flushing, Abril et al. 2004; upwelling Lachkar 2014), land runoff (Strong et al. 2014) and the development of engineering activities such as carbon capture and storage (Blackford et al. 2015). Research has shown that the rate of environmental change is critical in determining the extent of organismal damage, and that acute high-CO_2 exposures can have long-lasting effects (Burdett et al. 2012, Kamenos et al. 2013). However, our understanding of how marine ecosystems (rather than individuals) impact, and are impacted by, acute changes in ocean carbon chemistry is poorly understood (Pfister et al. 2014). This is despite the known importance of key biological processes such as calcification, photosynthesis, respiration and nutrient uptake in driving marine ecosystem variability.

In the natural environment, an organism's response to environmental change is mediated by community dynamics within the ecosystem. Failure to take these

*Corresponding author: h.burdett@hw.ac.uk

community-level interactions into account prevents macro-scale predictions of future ecosystem change (Queirós et al. 2015). To date, the majority of acute or chronic environmental change experiments have focused on 1, or maybe 2, environmental factors (e.g. increased CO_2/temperature) and consider organisms in isolation (Riebesell & Gattuso 2015). However, whilst informing our mechanistic understanding of physiological responses, these types of experiments are not representative of real-world impacts, due to laboratory artefacts and the lack of appreciation for community-wide interactions (Cornwall & Hurd 2015, Riebesell & Gattuso 2015). Consequently, efforts in developing methods for *in situ* experimentation have recently increased.

Natural CO_2 vents, where the water column is enriched with CO_2 due to benthic bubbling of volcanic gases, have proven useful for understanding the impacts of long-term exposure to a high-CO_2 environment on marine ecosystem structure (Hall-Spencer et al. 2008, Fabricius et al. 2011, Kamenos et al. 2016). However, these study areas are typically characterised by conditions more extreme or more variable than those predicted for the future, due to variation in physical factors such as water currents and venting rates (Hall-Spencer et al. 2008). 'Free Ocean CO_2 Enrichment' (FOCE) experimental setups attempt to bridge the gap between the precise control of laboratory experiments and the natural setting of CO_2 vents (Gattuso et al. 2014) by artificially exposing organisms or communities to a high-CO_2 environment. This also allows the effects of both chronic and acute CO_2 enrichment to be tested. Partially artificial designs (where organisms are manually placed in the chambers, rather than the natural system being examined) have been conducted on tropical reefs (Kline et al. 2012) and in the deep sea (Barry et al. 2014), whilst smaller chambers deployed on tropical seagrass beds have investigated the community-level response of this vegetated habitat to short-term CO_2 enrichment (e.g. Campbell & Fourqurean 2014).

One of the potentially most susceptible groups of organisms to both long and short-term CO_2 enrichment are the red coralline algae (Kroeker et al. 2010), which are key ecosystem engineers in the coastal zone (Riosmena-Rodríguez 2017). Coralline algal beds — supported by a free-living coralline algal framework — are globally distributed (van der Heijden & Kamenos 2015), highly diverse (BIOMAERL Team 1999, Barbera et al. 2003) and biogeochemically active (Burdett et al. 2015b, van der Heijden & Kamenos 2015). However, the community susceptibility of coralline algal habitats is currently unknown, despite the real-world relevance of this matter compared to results from laboratory-based single organism studies (Gattuso et al. 2014). Coralline algal beds are listed as 'Vulnerable' or 'Endangered' by the IUCN (Gubbay et al. 2016), a status driven by the sensitivity of coralline algae to environmental change, but also due to the paucity of data available on the functioning of these habitats at the community level.

Our understanding of coralline algal community functioning remains limited, even under ambient conditions. Despite substantial gross primary production, coralline algal communities exhibit net heterotrophy (i.e. O_2 uptake; Attard et al. 2015), acting as both a CO_2 source (Martin et al. 2007a) and organic carbon sink (Attard et al. 2015). While nutrient availability is not thought to limit the growth of coralline algal ecosystems (Steller et al. 2009), there is evidence that coralline algal communities act as a nutrient source, at least in the Mediterranean (Martin et al. 2007b). Coralline algae also represent a globally significant stock of dimethylsulphoniopropionate (DMSP) (Burdett et al. 2015a) — an algal secondary metabolite that is the major precursor to the climate gas dimethylsulphide (DMS). DMSP and DMS (DMS/P) drive a range of community interactions (e.g. grazing behaviour; Lyons et al. 2007) and seabed DMS/P flux dynamics may influence the biogeochemistry of the overlying water column under ambient conditions (Burdett 2017). At an individual level, we know that CO_2 enrichment can affect the photosynthesis, calcification and DMSP production of coralline algae (Burdett et al. 2012, Kamenos et al. 2013), but it is not currently understood how this is manifest at a community level, despite the significant implications for ecosystem functioning.

Here, we investigated the effect of acute *in situ* CO_2 enrichment on key community-level, biologically driven processes in a temperate coralline algal bed. Periodic CO_2 enrichment is a risk to marine habitats in this region due to the prevalence of human activities such as aquaculture, a rapidly expanding industry in Scotland and also globally (OECD-FAO 2014). Diel-scale pulsed release of CO_2 can occur from aquaculture infrastructures due to periodicity in fish metabolism, e.g. after feeding (Forsberg 1997, Zakęś et al. 2003). In addition, the development of carbon capture and storage facilities may further accentuate the risk of periodic acute CO_2 release in the future (Blackford et al. 2015). *Lithothamnion glaciale*, the coralline algal ecosystem engineer of this system, is known to be highly sensitive to acute CO_2 exposure (Burdett et al. 2012,

Kamenos et al. 2013), but sensitivity at a community level remains unclear. Here, we investigated the integrated community-level response of a coralline algal habitat to short-term CO_2 enrichment via *in situ* experimentation.

MATERIALS AND METHODS

Study site and experimental set-up

The experiment was performed on a coralline algal bed in Loch Sween, located on the west coast of Scotland, UK, at a depth of 6 m. The ecosystem framework is dominated by the free-living non-geniculate red coralline alga *Lithothamnion glaciale*, supporting a highly diverse community across multiple trophic levels. This includes both calcified and non-calcified macroalgae (including Laminariale) and invertebrates, being particularly rich in Mollusca (e.g. queen scallops *Aequipecten opercularis* [~4 per 20 m^2]) and particularly abundant in Ophiuroidea (sea stars & brittle stars, e.g. *Ophiocomina nigra* [up to 10 000 per m^2] and *Asterias rubens* [~11 per 20 m^2]) (BIOMAERL Team 1999, Barbera et al. 2003, Kamenos 2004). Community biodiversity was not further quantified in this study. Four benthic chambers (28 l volume, diameter = 38 cm) were deployed within the coralline algal bed by SCUBA divers pushing them into the seabed. Chambers were left open for 24 h to allow the water within the chambers to equilibrate with the surrounding environment. Following equilibration, lids were fitted and the experiment begun, which consisted of 3 phases: (1) before CO_2 enrichment at ambient (control) conditions (15 h), (2) during CO_2 enrichment (28 h) and (3) post-enrichment recovery (37 h).

Chambers were individually connected to the surface via a flow-through system, which continually pumped water through the chamber via the surface at a rate of 120 l h^{-1} (Swell Filter Pump 5000). Pumps were located perpendicular from the chambers in relation to the tidal current to prevent the re-pumping of water through the system. CO_2 enrichment was achieved by bubbling pure CO_2 directly into a mixing chamber on the surface, prior to the water being directed to the main *in situ* chambers. pH (total scale) of water in the mixing chamber was monitored using a pH probe (VitalSINE, daily 3 point calibration following the manufacturer's instructions) and the rate of CO_2 bubbling was adjusted as required to maintain a stable ~0.2 pH unit offset from the incoming water supply. Actual pH change in the chambers (reflecting both the CO_2 addition and biogeochemical community processes) was determined by sampling the in-chamber water during the experimental periods and analysing for total alkalinity (A_T) and dissolved inorganic carbon (C_T), from which pH is calculated (details below). Flow-through circulation was maintained for the duration of the experiment, except during 2 h incubation periods when the water flow was stopped, but within-chamber circulation was maintained by stirring paddles (Attard et al. 2015). Water samples were taken for determination of dissolved oxygen, carbonate chemistry, nutrients and dimethylated sulphur at the beginning and end of a 2 h incubation period, which was carried out every ~12 h during the experiment (i.e. around midday and midnight during the 3 experimental phases). Measurements from the beginning and end of the incubation were used for the determination of seabed flux measurements of each parameter to gain understanding of the community response to CO_2 enrichment. All water samples were collected in borosilicate glass syringes using SCUBA. Immediately after collection, water samples were returned to the shore and prepared for various water chemistry parameters, as detailed below.

Net photosynthesis/respiration (dissolved oxygen)

Winkler reagents (200 µl of 3M $MnSO_4 \cdot H_2O$ solution and 200 µl of 8M NaOH+ 4M NaI) were added to 12 ml unfiltered water samples for subsequent dissolved oxygen (DO) determination, and stored in the dark at 4°C until analysis. DO concentrations were determined using the Winkler titration method (Grasshoff et al. 2007): the sample was acidified with 200 µl 5M sulphuric acid and titrated against 0.05M sodium thiosulphate solution with potassium iodate as a standard.

Net calcification/dissolution (carbonate chemistry)

Samples for A_T and C_T were stored in borosilicate glass vials (Labco) and poisoned with mercuric chloride, following Dickson et al. (2007). A_T was measured on a Metrohm 848 Titrino Plus using the 2-stage open-cell potentiometric titration method on 10 ml sample volumes with 0.01 M HCl (Dickson et al. 2007). All A_T samples were analysed at 25 ± 0.1°C with temperature regulation using a water bath (Julabo 19). C_T was determined by infra-red detection of CO_2 from acidified samples on a dissolved

inorganic carbon analyser (Marianda Airica). Additional carbonate chemistry parameters (pH_{NBS}, pCO_2, [HOC_3^-], [CO_3^{2-}], aragonite saturation state [Ω_{Arg}]) were calculated from A_T and C_T using CO2SYS (Pierrot et al. 2006) with dissociation constants from Mehrbach et al. (1973) refit by Dickson & Millero (1987) and [KSO_4] using Dickson (1990). *In situ* water temperature (°C), salinity and pH were measured hourly throughout the experimental period using an Exo2 multiparameter sonde (YSI). Nitrate and phosphate concentrations were calculated throughout the experimental period (see below) and included in carbonate chemistry calculations. Net community calcification rates were calculated using the alkalinity anomaly technique (Chisholm & Gattuso 1991) based on the change in seawater A_T during the incubation period. For each mole of $CaCO_3$ precipitated (i.e. calcification), A_T is lowered by 2 molar equivalents. Therefore, the change in alkalinity can be converted to the mass of $CaCO_3$ precipitated. Certified seawater reference materials for oceanic CO_2 (Scripps Institution of Oceanography, University of California, San Diego) were used as A_T and C_T standards, following Dickson et al. (2007).

Net DMS+DMSP (DMS/P_T) flux

Samples for total (dissolved+particulate) DMS+DMSP (DMS/P_T) were stored in 50 ml crimp-top serum vials (Wheaton) fitted with Pharma-Fix lids. NaOH was added to a final concentration of 0.03 M to hydrolyse DMSP into DMS. Samples were analysed by purge-and-trap gas chromatography (Turner et al. 1990) using an SRI 8610C GC fitted with a flame photometric detector (nitrogen carrier gas @ 8 psi). Sample concentrations were quantified via comparison to a DMSP standard (Research Plus); sample detection limit was <1 nmol l^{-1}, precision and accuracy for standards and samples was within 1%.

Net nitrate and phosphate flux

Unfiltered samples for nitrate and phosphate were stored in HDPE bottles (Fisher Scientific) and frozen within 1 h of collection. 10 ml samples were analysed for nitrate following the cadmium reduction spectrophotometric method (Grasshoff et al. 2007); absorbance was measured at 400 nm, with sodium nitrate used as a standard. 10 ml samples were analysed for phosphate using the ammonium molybdate/ascorbic acid method (Grasshoff et al. 2007); absorbance was measured at 885 nm, with potassium phosphate used as a standard.

Statistical analyses

Where parametric assumptions for normality and homogeneity of variance were met, parametric tests were used to interrogate the data. One-way ANOVAs were used to test for differences between ambient, CO_2 enrichment and recovery experimental phases in terms of carbonate chemistry and net fluxes of DO, calcification rate, DMS/P_T, nitrate and phosphate (i.e. experimental phase included as a factor; no data transformation was required). Correlation tests were used to test correlation significance between fluxes of dissolved oxygen, calcification, DMS/P_T, nitrate and phosphate. Kruskall-Wallis tests were used to test for differences in DO fluxes (parametric assumptions could not be met). Analyses were conducted using Minitab V14.1.

RESULTS

Environmental conditions

Water temperature was 15.3 ± 0.32°C and salinity was 33.0 ± 0.38 throughout the experimental period (mean ± SD, n = 80 for both temperature and salinity). No significant difference in T_A was observed between the 3 experimental phases ($F_{2,20}$ = 0.11, p = 0.89; Table 1). In contrast, C_T was significantly higher during the CO_2 enrichment compared to the ambient/recovery phases ($F_{2,20}$ = 31.6, p < 0.001; Table 1), resulting in a significant increase in HCO_3^- ($F_{2,20}$ = 10.45, p = 0.001) and pCO_2 ($F_{2,20}$ = 4.24, p = 0.03). Mean aragonite saturation state and pH were reduced during CO_2 enrichment compared to the ambient/recovery phases, but not to the extent that significant differences were observed (ΩAr: $F_{2,20}$ = 1.47, p = 0.26; pH: $F_{2,20}$ = 2.76, p = 0.09; Table 1). Average *in situ* pH at the site in the 38 d before and during the experiment was 8.04 ± 0.04 (mean ± SD) (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m587p073_supp.pdf).

Net photosynthesis/respiration (dissolved oxygen)

At ambient conditions, an average net uptake of O_2 (i.e. net respiration) was observed, characterised by a small net release of O_2 during the day (i.e. net photo-

Table 1. System parameters under ambient, CO_2-enrichment and recovery phase conditions in benthic chambers deployed on a coralline algal bed in Loch Sween, Scotland. Water temperature, salinity, photosynthetically active radiation (PAR), total alkalinity (A_T) and dissolved inorganic carbon (C_T) were directly measured; all other carbonate parameters were calculated as detailed in the 'Materials and methods' (pH is on NBS scale; Ω_{Arg} = aragonite saturation state). Data presented as mean ± SD (n = 18, except for temperature and salinity, where n = 80). **Bold** text denotes parameters that were significantly different during the CO_2 enrichment phase ($p < 0.05$)

	Ambient conditions	CO_2 enrichment	Recovery period
Temperature (°C)	15.3 ± 0.32	15.3 ± 0.32	15.3 ± 0.32
Salinity	33.0 ± 0.38	33.0 ± 0.38	33.0 ± 0.38
Max PAR (µmol photons m^{-2} s^{-1})	158	158	158
A_T (µmol kg^{-1})	2190.7 ± 87.2	2202.0 ± 123.28	2210.8 ± 68.2
C_T (µmol kg^{-1})	**2084.8 ± 12.8**	**2168.9 ± 31.20**	**2066.2 ± 23.2**
pH_{NBS}	7.9 ± 0.2	7.7 ± 0.39	8.0 ± 0.2
***p*CO_2 (µatm)**	**821.6 ± 343.4**	**1747.7 ± 1403.33**	**646.7 ± 320.6**
HCO_3^- (µmol kg^{-1})	**1961.1 ± 27.5**	**2033.5 ± 20.35**	**1927.6 ± 49.2**
CO_3^{2-} (µmol kg^{-1})	92.0 ± 45.9	67.8 ± 50.77	113.5 ± 45.5
Ω_{Arg}	1.4 ± 0.7	1.0 ± 0.78	1.7 ± 0.7

synthesis) to net respiration during the night (Fig. 1). During the CO_2 enrichment, average net O_2 release increased compared to the ambient/recovery phases, reducing the difference between day (higher net O_2 release) and night (lower net O_2 release/net uptake) measurements ($F_{2,27}$ = 2.98, p = 0.07). During the recovery phase, net O_2 uptake decreased towards initial levels, but did not quite reach the magnitude of net photosynthesis originally observed. When compared separately, net oxygen flux was significantly higher in CO_2-enriched conditions than ambient or recovery periods during the night (H_1 = 4.20, p = 0.040), but not during the day (H_1 = 1.70, p = 0.192), reflecting the observed overall trend towards increased O_2 flux under CO_2 enrichment (Fig. 1).

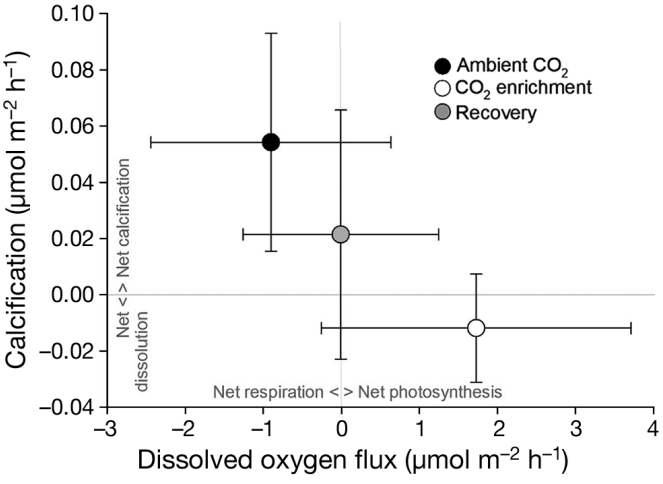

Fig. 1. Community response of acute *in situ* CO_2 enrichment in terms of net dissolved oxygen flux and net calcification rate under initial ambient CO_2 conditions, during CO_2 enrichment or during the recovery phase at ambient CO_2. Data presented as mean ± SD

Net calcification/dissolution (carbonate chemistry)

A significant reduction in net calcification was observed during the CO_2 enrichment compared to the ambient/recovery phases ($F_{2,25}$ = 5.49, p = 0.01; Fig. 1). Under ambient CO_2 conditions, the coralline algal community consistently exhibited a net calcification. During CO_2 enrichment, a significant shift towards net dissolution was observed. The recovery phase was characterised by an intermediate rate of net calcification. A significant negative correlation between DO flux and net calcification rate was observed (r = –0.40, p = 0.05; Fig. 1).

Net DMS/P_T flux

Under ambient CO_2 conditions, there was a net uptake of DMS/P_T by the coralline algal community of between 11–24 µmol m^{-2} h^{-1} (Table 2). During CO_2 enrichment, there was a small reduction in net uptake rates, manifest as a shift towards the occasional net release of DMS/P_T, but this change was not significant between experimental phases ($F_{2,27}$ = 0.62, p = 0.54; Table 2). DMS/P_T flux was not significantly correlated with any of the other biogeochemical parameters, at $p < 0.05$.

Net nitrate and phosphate flux

Average net nutrient release and uptake rates were balanced (i.e. flux of ~zero), and no significant change was observed during CO_2 enrichment compared to the ambient/recovery phases (nitrate: $F_{2,25}$ = 0.80, p = 0.46; phosphate: $F_{2,25}$ = 0.01, p = 0.99; Table 2). Net benthic flux of phosphate, but not nitrate, was significantly correlated with benthic oxygen flux (r = 0.46, p = 0.02). No other significant correlations between net O_2, nitrate, phosphate and DMS/P_T flux and net calcification rate (at $p < 0.05$) were observed.

Table 2. Community response of acute *in situ* CO_2 enrichment in terms of net DMS/P_T, nitrate and phosphate flux under initial ambient CO_2 conditions, during CO_2 enrichment and during the recovery phase at ambient CO_2. Data presented as mean ± SD

	Ambient conditions	CO_2 enrichment	Recovery period
Net DMS/P_T flux ($\mu mol\ m^{-2}\ h^{-1}$)	−23.13 ± 27.12	−13.46 ± 28.12	−11.47 ± 11.39
Net nitrate flux ($mg\ m^{-2}\ h^{-1}$)	−11.40 ± 36.11	−0.55 ± 19.90	7.71 ± 27.37
Net phosphate flux ($mg\ m^{-2}\ h^{-1}$)	0.04 ± 0.44	0.02 ± 0.24	0.05 ± 0.29

DISCUSSION

Despite the known issues with investigating the effect of elevated CO_2 in a laboratory setting, only a handful of *in situ* CO_2 enrichment experiments have been conducted, and even less on the whole natural community. This is the first community-level *in situ* acute CO_2 enrichment study in mid/high latitudes and the first to consider the rate of recovery following acute CO_2 perturbation. In this study, there was a rapid community-level response to acute CO_2 enrichment. This was particularly evident for net calcification, demonstrating the sensitivity of the whole community to acute CO_2 exposure, not just individual species.

Unlike single-organism laboratory experiments, this study integrated the response of the whole community. Whilst this means we are unable to assign individual species to specific biogeochemical changes, the results obtained are relevant to real-world challenges such as the designation of marine management strategies, which by necessity incorporate whole communities (even if a particular species is the target focus). At the level of CO_2 enrichment used in this study, the skeleton and epithelial cell surface of *Lithothamnion glaciale* is compromised (Burdett et al. 2012, Kamenos et al. 2013), allowing for skeletal dissolution (Langdon et al. 2000) — supporting the observed shift towards net community dissolution. This may have also been facilitated by dissolution of carbonate sediment and dead sections of coralline algae, which cannot exert biological control and buffering against changes in carbonate chemistry (Kamenos et al. 2013). Like other reef-based marine ecosystems, this coralline algal community is highly diverse across multiple trophic levels (BIOMAERL Team 1999, Barbera et al. 2003, Kamenos 2004). Calcifying invertebrates are especially abundant (e.g. *Ophiocomina nigra*, which can make up 47% of total faunal biomass; BIOMAERL Team 1999), and CO_2 enrichment is known to lead to a reduction in calcification rate/increase in dissolution rate of these organisms (Kroeker et al. 2010). Thus, these organisms are likely to have also contributed to the observed shift towards net dissolution, impacting their contribution to coastal CO_2 flux (Davoult et al. 2009). Due to the high heterotrophic diversity of coralline algal beds (Barbera et al. 2003), only a small net photosynthesis during the day was observed, supporting previous measurements using the Eddy correlation technique (Attard et al. 2015) and providing confidence that results recorded do not represent treatment artefacts. CO_2 enrichment led to a small increase in net O_2 release, suggesting an increased capacity for net photosynthesis — supporting the likely benefits of elevated CO_2 conditions for aquatic photosynthetic organisms (Kroeker et al. 2010). Photosynthetic use of CO_2 can also provide a potential refuge for calcifying species by buffering against the damaging effects of CO_2 enrichment (e.g. crustose coralline algae; Cornwall et al. 2014, Short et al. 2014, Kamenos et al. 2016), although this was not observed in this study. Increased photosynthetic capacity may also increase the carbon sequestration potential of these ecosystems (a key process in blue carbon storage; van der Heijden & Kamenos 2015), but a shift towards net dissolution may impact the stability of coralline algal carbonate deposits. The balance and interaction of photosynthesis and calcification/dissolution, and subsequent impact on carbon sequestration/storage is exemplified by the observed correlation between net O_2 flux and net calcification.

Change in the community-level flux of dimethylated sulphur compounds appears to be robust to acute CO_2 enrichment, despite the known sensitivity of coralline algal DMSP dynamics to acute CO_2 exposure (Burdett et al. 2012). Thus, it may be hypothesised that, although DMS/P_T concentrations did not change, the proportion of the molecular species (e.g. dissolved vs particulate, DMSP vs DMS) may have been altered, but this was not calculable by the approach employed. Nutrient fluxes were also insensitive to acute CO_2 enrichment, at least at the CO_2 level used in this study. However, the correlation between phosphate and DO suggests that a larger CO_2 perturbation (in duration and/or magnitude) may impact phosphorus cycling processes.

Acute CO_2 enrichment is just one aspect of carbon-chemistry pressures on marine habitats. In addition, the combined effects of acute CO_2 enrichment and chronic, long-term changes in carbonate chemistry may exacerbate biological responses. This has yet to be tested at the community scale, despite the known importance of both acute and chronic CO_2 enrichment in driving responses in marine organisms. Surprisingly, even after a recovery phase almost 1.5 times the length of the CO_2 enrichment, a full recovery (i.e. complete return of all parameters to the initial measured rates) was not seen, at least in terms of the parameters measured here, suggesting that, at best, there is considerable lag in community recovery response times. This calls into question the capacity for the system to 'bounce back' following repeated exposure to acute CO_2 inputs, which would be likely given the sources of short-term CO_2 enrichment (e.g. aquaculture, CCS). Previous studies have shown that damage to the coralline algal skeletal structure under CO_2-enriched conditions can rapidly occur (Burdett et al. 2012, Kamenos et al. 2013). *In situ*, this effect may manifest through to the community level. Results from this study and others (e.g. Hall-Spencer et al. 2008, Fabricius et al. 2011) collectively suggest that CO_2 enrichment may cause change across biological scales, from the individual to community levels. If these changes persist in the long-term, we may observe permanent transitions in community composition, perhaps one that favours net photosynthesis, thereby tipping the balance in terms of biodiversity and/or net dissolution. Such transitions would not favour the growth of carbonate-depositing ecosystem engineers such as coralline algae.

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