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Effects of ocean acidification on macroalgal communities

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ABSTRACT

There are high levels of uncertainty about how coastal ecosystems will be affected by rapid ocean acidification caused by anthropogenic CO₂, due to a lack of data. The few experiments to date have been short-term (<1 year) and reveal mixed responses depending on the species examined and the culture conditions used. It is difficult to carry out long-term manipulations of CO₂ levels, therefore areas with naturally high CO₂ levels are being used to help understand which species, habitats and processes are resilient to the effects of ocean acidification, and which are adversely affected. Here we describe the effects of increasing CO₂ levels on macroalgal communities along a pH gradient caused by volcanic vents.

Macroalgal habitat differed at taxonomic and morphological group levels along a pH gradient. The vast majority of the 101 macroalgal species studied were able to grow with only a 5% decrease in species richness as the mean pH fell from 8.1 to 7.8. However, this small fall in species richness was associated with shifts in community structure as the cover of turf algae decreased disproportionately. Calcitic species were significantly reduced in cover and species richness whereas a few non-calcified species became dominant. At mean pH 6.7, where carbonate saturation levels were < 1, calcareous species were absent and there was a 72% fall in species richness. Under these extremely high CO₂ conditions a few species dominated the simplified macroalgal assemblage and a very few exhibited enhanced reproduction, although high CO₂ levels seemed to inhibit reproduction in others.

Our data show that many macroalgal species are tolerant of long-term elevations in CO₂ levels but that macroalgal habitats are altered significantly as pH drops, contributing to a scant but growing body of evidence concerning the long-term effects of CO₂ emissions in vegetated marine systems. Further study is now needed to investigate whether the observed response of macroalgal communities can be replicated in different seasons and from a range of geographical regions for incorporation into global modelling studies to predict effects of CO₂ emissions on Earth's ecosystems.

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1. Introduction

The oceans currently absorb over 25 million tonnes of anthropogenically produced CO₂ every day, causing unprecedented changes to ocean chemistry (IPCC, 2007). Observations and models indicate that the average pH of the surface ocean has declined from 8.2 by 0.1 units since pre-industrial times due to CO₂ emissions, and is projected to be around mean pH 7.8 by the end of the century (The Royal Society, 2005). In addition to lowering pH, increasing CO₂ levels are lowering calcium carbonate saturation states but increasing the amounts of bicarbonate ions (HCO³⁻). Laboratory and mesocosm experiments have shown that these changes in carbonate chemistry can significantly affect carbon fixation by photoautotrophs, which may cause global ecological disturbances over the coming decades

(Kroeker et al., 2010) although there are still too few data to confirm whether this is the case (Hendricks and Duarte, 2010).

Benthic photoautotrophs exhibit mixed responses to ocean acidification, indicating that there will be changes in their settlement, competition and dominance that will have knock-on effects on coastal ecosystems (Connell and Russell, 2010). However, it is very difficult to scale up the observations undertaken to date to predict the effects of increasing CO₂ emissions at the ecosystem level since most studies have been short-term (<1 year) on single or small groups of species. Some cyanobacteria grow well with CO₂ enrichment and their increased N₂ fixation may alter ocean biogeochemistry (Fu et al., 2008; Kranz et al., 2009). Some marine algae also benefit from higher CO₂ levels, enhancing their growth (Gao et al., 1999; Kübler et al., 1999; Riebesell et al., 2007) and calcification (Iglesias-Rodriguez et al., 2008), although the effects can vary between closely related species and even between strains of the same species (Langer et al., 2009). In general, seagrasses seem able to thrive under high CO₂ conditions (Palacios and Zimmerman, 2007; Hall-Spencer et al., 2008), although the associated epiphytic algal cover falls as CO₂ levels increase (Martin

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et al., 2008). Coralline algae appear to be amongst the most sensitive photoautotrophs as they have a skeletal mineralogy that dissolves easily at predicted levels of calcium carbonate saturation (Gao et al., 1993; Martin and Gattuso, 2009) and this is a particular concern as these algae are of fundamental ecological importance in a range of coastal habitats worldwide (Nelson, 2009).

Macroalgal communities perform a range of ecosystem services in shallow coastal systems such as providing food, forming substrata for settlement, offering protection from predators and shelter from disturbances. Macroalgal communities are sensitive to anthropogenic disturbances and so are used to assess the status of coastal ecosystems, for example, under the European Water Framework Directive (Orfanidis et al., 2001; Ballesteros et al., 2007). The sensitivity of Mediterranean macroalgal communities is well documented; Ulvales can become dominant in nutrient enriched areas (Pergent, 1991), habitat-forming *Cystoseira* spp. are lost from large stretches of polluted coastlines (Rodríguez-Prieto and Polo, 1996; Thibaut et al., 2005; Mangialajo et al., 2008) and ecosystems have been degraded by the invasive behaviour of introduced organisms such as *Caulerpa* spp. (Balata et al., 2004).

Differences in the susceptibility of macroalgae to ocean acidification may completely alter coastal ecosystems as changes in algal communities lead to changes in herbivore diversity and abundance (Benedetti-Cecchi et al., 2001; Darcy-Hall and Hall, 2008). Such changes in species distributions and abundances are expected to propagate up through the trophic levels of marine food webs (Fabry et al., 2008; Guinotte and Fabry, 2008) but little research has been carried out on the effects of ocean acidification at the ecosystem level (Wootton et al., 2008).

To improve knowledge regarding the responses of marine ecosystems to ocean acidification we assess macroalgal community changes at a site described by Hall-Spencer et al. (2008), where increasing CO₂ levels cause a natural pH gradient at ambient temperature and salinity. We examine changes in seaweed species diversity and abundance along a pH gradient and also examine changes in morphological groups to help link changes in community structure to ecosystem functioning (Micheli and Halpern, 2005).

2. Materials and methods

2.1. Sampling

Sampling was conducted in autumn 2007 along a 300 m stretch of rocky coast of Castello Aragonese (Fig. 1) off Ischia Island in the Gulf of

Naples, Italy. In this subtidal area, volcanic CO₂ vents acidify the seawater causing a pH gradient varying from 8.20 to 6.07. Water chemistry analyses (e.g., pH, pCO₂ and saturation states of calcite and aragonite) are described by Hall-Spencer et al. (2008) and the data are available at <http://doi.pangaea.de/10.1594/PANGAEA.728715>.

Macroalgal samples were collected from 0.70–1.0 m below mean sea level along the pH gradient using a hierarchical experimental design. Three 30 m wide sectors were chosen as follows: sector 1 (S1) was at normal pH ($8.14 \pm SE 0.01$, $n = 7$); S2 had mean pH 7.83 ($\pm SE 0.06$, $n = 18$) and S3 had mean pH 6.72 ($\pm SE 0.06$, $n = 30$). In each sector, three 5 m wide zones were chosen at least 6 m apart (A–I, Fig. 1). In each zone, all organisms were removed from the bedrock using a hammer and a chisel from three randomly placed 20*20 cm quadrats, following macroalgal sampling techniques developed for this type of Mediterranean rocky shore habitat (Ballesteros, 1986). A sector was a fixed factor with three levels, each zone (A–I) was a fixed factor with three levels nested in each sector whereas quadrats were random replicates (Fig. 1). Samples were preserved in 4% formalin: seawater and subsequently sorted in the laboratory. Algae were identified to species and quantified in terms of coverage (percentage of horizontal surface measured after spreading the algal thalli in a laboratory tray (Ballesteros, 1986). Species with negligible abundance were assigned coverage of 0.01%. Light microscopy was used to detect the presence of reproductive structures: their occurrence was compared only in those species recorded at the three pH conditions. Macroalgal species were grouped into three morphological categories, i.e., ‘crustose,’ ‘turf’ and ‘erect’. Algal turfs consist mostly of tiny filaments with canopy height of less than 10 mm; erect algae are larger canopy formers (>10 mm in height) and can be either fleshy or calcareous; and crustose algae are prostrate forms, both calcareous and non-calcareous (Diaz-Pulido and McCook, 2008).

2.2. Community data analyses

Differences among sectors were determined by calculating the species number, percent cover of each species, species diversity (estimated as log_e based Shannon–Weaver diversity Index H'), and percent cover of the crustose, turf and erect groups. K-dominance curves of species coverage data were plotted and principal component analysis (PCA) was performed on these data using Syn-tax software (Podani, 2001). Species with <0.03 percentage cover were excluded from this analysis. ANOVA and the *post hoc* Tukey test (GraphPad Prism package) were applied to data from the 27 quadrats to test for differences among the three sectors. The normality and homogeneity of variances were

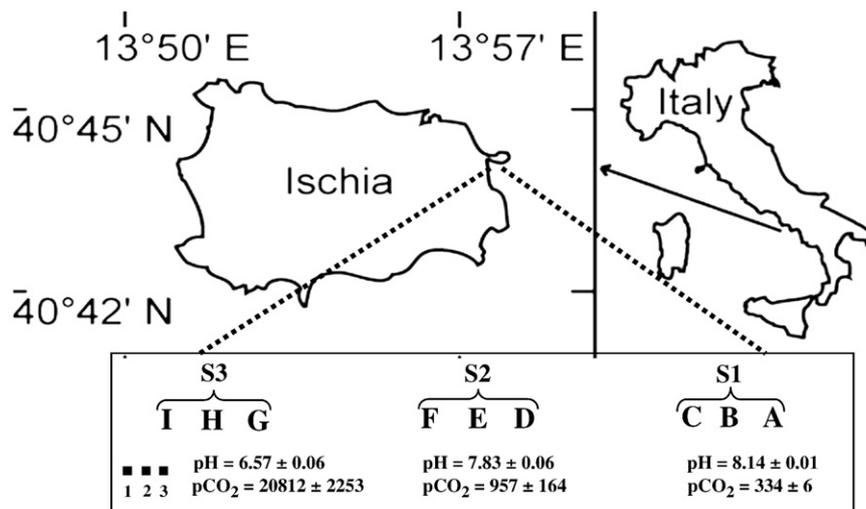


Fig. 1. Location of gas vents off Castello Aragonese on Ischia Island, Italy, showing three sectors (S1–S3), each split into three zones (A–I), each sampled for macroalgae with three quadrats in autumn 2007 along a gradient in mean pH (±SD) and increasing mean pCO₂ levels (±SD, see Hall-Spencer et al., 2008).

Table 1

Total number of Rhodophyta, Ochrophyta and Chlorophyta species and the total number of erect, crustose and turf species collected from nine 20*20 cm quadrats placed in three sectors along a rocky shore pH gradient.

	S1 pH = 8.1	S2 pH = 7.8	S3 pH = 6.7
Rhodophyta	50	48	10
Ochrophyta	12	11	6
Chlorophyta	12	11	3
Erect	17	14	7
Crustose	19	20	2
Turf	38	36	10
Total	74	70	19

always tested; when not met, data were log-transformed. Differences in community composition among sectors were evaluated by means of similarity analysis (ANOSIM). For samples found to be significantly

different using ANOSIM, SIMPER was used to determine which species contributed most to the differences between samples. This program calculates the average similarity between all pairings of each replicate within a treatment to the replicates in another treatment and tabulates the average percent contribution of each species to the dissimilarity observed between the treatments. Community structure based on algal categories was examined by multivariate analysis (nMDS). K-dominance, ANOSIM, SIMPER and nMDS analyses were performed with PRIMER 5 (Clarke and Warwick, 2001).

3. Results

A total of 101 macroalgal taxa were recorded in the 27 20*20 cm quadrats, including 71 Rhodophyta, 16 Ochrophyta and 15 Chlorophyta (Table 1). The highest species richness (Table 2) was sampled at S1 (pH=8.1); 5% fewer species were sampled at S2 (pH=7.8) and 72% fewer species were sampled at S3 (pH=6.7). ANOVA and a *post hoc*

Table 2

List of species and their mean percentage cover from nine 20*20 cm quadrats placed in three sectors along a rocky shore pH gradient (nc = negligible cover; numbers correspond to the analysis shown in Fig. 5).

Species	S1 pH = 8.1	S2 pH = 7.8	S3 pH = 6.7	see Fig. 5	Species	S1 pH = 8.1	S2 pH = 7.8	S3 pH = 6.7	see Fig. 5
<i>Jania rubens</i>	69.22	10.09	–	18	<i>Spermothamnion strictum</i>	0.04	0.01	–	nc
<i>Valonia utricularis</i>	28.5	2.57	0.12	45	<i>Corallinaceae</i>	0.04	0.14	–	nc
<i>Flabellia petiolata</i>	20.33	66.22	–	42	<i>Polysiphonia denudata</i>	0.04	–	–	nc
<i>Amphiroa rigida</i>	10.28	3.56	–	2	<i>Ceramium codii</i>	0.03	0.01	–	4
<i>Phymatolithon</i> cfr <i>lenormandii</i>	7.79	2.94	–	26	<i>Crouania attenuata</i>	0.03	–	–	nc
<i>Dictyota dichotoma</i>	6.09	1.34	44.17	31	<i>Gelidium minusculum</i>	0.03	0	–	nc
<i>Laurencia obtusa</i>	5.69	–	–	nc	<i>Cladophora dalmatica</i>	0.03	0.02	–	39
<i>Peyssonnelia polymorpha</i>	4.22	1.5	–	23	<i>Cladophora sericea</i>	0.03	–	–	nc
<i>Peyssonnelia squamaria</i>	3.87	8.86	–	24	<i>Dasya baillouviana</i>	0.03	–	–	nc
<i>Sphacelaria tribuloides</i>	3.67	0.9	–	35	<i>Anotrichium tenue</i>	0.02	0.05	–	nc
<i>Lobophora variegata</i>	3.6	8.39	–	nc	<i>Ceramium diaphanum</i>	0.02	–	0.02	nc
<i>Stypocaulon scoparium</i>	3.56	1	0.14	36	<i>Monosporus pedicellatus</i>	0.02	–	–	nc
<i>Hildenbrandia rubra</i>	3.18	4.44	26.28	15	<i>Meredithia microphylla</i>	0.02	–	–	nc
<i>Phyllophora crispa</i>	3.07	–	–	25	<i>Halopteris filicina</i>	0.02	–	–	nc
<i>Neogoniolithon brassica-florida</i>	2.9	0.22	–	nc	<i>Chaetomorpha linum</i>	0.02	0.01	0.3	38
<i>Lithophyllum</i> sp.	2.69	–	–	19	<i>Cladophora flexuosa</i>	0.02	–	–	nc
<i>Hydrolithon cruciatum</i>	2.53	18.53	–	17	<i>Titanoderma pustulatum</i>	0.02	0.16	–	nc
<i>Bryopsis plumosa</i>	2.33	0.37	–	37	<i>Cladostephus spongiosus</i>	0.02	–	2.57	30
<i>Dictyota spiralis</i>	2.31	1.67	–	32	<i>Sphacelaria cirrosa</i>	0.02	0.18	0.09	nc
<i>Corallina elongata</i>	1.87	0.44	–	7	<i>Antithamnion cruciatum</i>	0.01	0.02	0.42	3
<i>Mesophyllum</i> sp.	1.83	4.61	–	20	<i>Centroceras clavulatum</i>	0.01	–	–	nc
<i>Padina pavonica</i>	1.67	0.92	–	33	<i>Cladophora socialis</i>	0.01	–	–	nc
<i>Cystoseira amentacea</i> var. <i>stricta</i>	1.61	–	–	nc	<i>Acrothamnion preissii</i>	–	–	0.01	nc
<i>Griffithsia phyllamphora</i>	1.11	1.27	–	nc	<i>Aglaothamnion bipinnatum</i>	–	0.03	–	1
<i>Pseudochlorodesmis furcellata</i>	1.01	1.14	–	44	<i>Aglaothamnion diaphanum</i>	–	0.03	–	nc
<i>Polysiphonia scopulorum</i>	0.91	0.42	0.03	28	<i>Antithamnion</i> sp.	–	0.02	–	nc
<i>Gelidiella pannosa</i>	0.7	0.31	–	11	<i>Ptilothamnion sphaericum</i>	–	0.01	–	nc
<i>Herposiphonia secunda</i> f. <i>tenella</i>	0.6	0.06	–	13	<i>Spermothamnion repens</i>	–	–	0.01	nc
<i>Lophosiphonia cristata</i>	0.59	0.57	–	nc	<i>Amphiroa criptarthroidea</i>	–	0.33	–	nc
<i>Heterosiphonia crispella</i>	0.57	0.14	–	14	<i>Pterocladia capillacea</i>	–	–	0.5	29
<i>Corallina officinalis</i>	0.56	–	–	nc	<i>Chondracanthus acicularis</i>	–	–	4.96	6
<i>Nitophyllum punctatum</i>	0.48	0.16	–	21	<i>Peyssonnelia armorica</i>	–	–	0.17	nc
<i>Cladophora rupestris</i>	0.44	–	–	41	<i>Peyssonnelia bornetii</i>	–	0.33	–	nc
<i>Herposiphonia secunda</i>	0.42	–	–	nc	<i>Peyssonnelia</i> cfr <i>rubra</i>	–	0.02	–	nc
<i>Halimeda tuna</i>	0.38	0.19	–	nc	<i>Phyllophora sicula</i>	–	0.01	–	nc
<i>Gelidium bipectinatum</i>	0.29	0.18	–	12	<i>Contarinia squamariae</i>	–	0.03	–	nc
<i>Ceramium flaccidum</i>	0.28	0.1	–	5	<i>Herposiphonia</i> sp.	–	0.01	–	nc
<i>Ceramium circinatum</i>	0.26	–	–	nc	<i>Cladophora laetevirens</i>	–	0.01	–	nc
<i>Cladophora prolifera</i>	0.24	0.64	–	nc	<i>Cladophora pellucida</i>	–	0.12	0.37	40
<i>Osmundea truncata</i>	0.22	0.07	4.7	22	<i>Choreonema thuretii</i>	–	0.01	–	nc
<i>Champia parvula</i>	0.2	0.21	–	nc	<i>Lithophyllum incrustans</i>	–	1.22	–	nc
<i>Peyssonnelia dubyi</i>	0.2	–	–	nc	<i>Phymatolithon lenormandii</i>	–	0.36	–	nc
<i>Pneophyllum fragile</i>	0.18	0.06	–	27	<i>Dasya hutchinsiae</i>	–	0.01	–	nc
<i>Falkenbergia</i> sp.	0.16	0.04	–	10	<i>Polysiphonia fibrata</i>	–	0.02	–	nc
<i>Parvocaulis parvulum</i>	0.12	0.06	–	43	<i>Feldmannia irregularis</i>	–	0.01	–	nc
<i>Dasya rigidula</i>	0.12	–	–	9	<i>Dictyopteris polypodioides</i>	–	0.01	–	nc
<i>Hydrolithon boreale</i>	0.11	0.04	–	16	<i>Dictyota dichotoma</i> var. <i>intricata</i>	–	–	0.26	nc
<i>Chondrophycus papillosus</i>	0.07	–	–	nc	<i>Sargassum vulgare</i>	–	–	22.17	34
<i>Hydrolithon farinosum</i>	0.06	0.03	–	nc	<i>Sphacelaria rigidula</i>	–	0.01	–	nc
<i>Titanoderma</i> sp.	0.06	0.11	–	nc	<i>Sphacelaria</i> sp.	–	0.01	–	nc

Tukey test showed highly significant reductions in species diversity (H') as CO_2 levels increased ($H'_{S1} = 2.29 \pm 0.07$; $H'_{S2} = 1.88 \pm 0.07$ and $H'_{S3} = 1.18 \pm 0.05$, respectively) ($F = 25.62$; $p < 0.0001$, and $S1 > S2 > S3$).

Clear shifts were evident in species distribution along the CO_2 gradient (Fig. 2). Twenty species of calcareous algae were sampled at normal pH, but only 15 at mean pH 7.8 and none at mean pH 6.7, where both calcite and aragonite saturation states were < 1 (Fig. 3). ANOVA results (Table 3) show a significant decrease in calcitic species number at mean pH 7.8, where the overall cover of calcareous algae was much lower than at mean pH 8.1. Most calcitic (e.g., *Jania rubens*, *Amphiroa rigida*, *Phymatolithon* cf. *lenormandii*) and aragonitic species (e.g., *Peyssonnelia* spp., *Padina pavonica* and *Halimeda tuna*) were more abundant at mean pH 8.1 (S1) although the thin calcitic crust *Hydrolithon cruciatum* and the lightly calcified aragonitic crust *Peyssonnelia squamaria* were more abundant at mean pH 7.8 (S2).

The diversity and abundance of non-calcareous algae also shifted along the CO_2 gradient. For example, the Ochrophyte *Dictyota dichotoma* and the Rhodophyte *Hildenbrandia rubra* were present along the whole pH gradient with their highest percentage cover at mean pH 6.7 (S3). In contrast, *Sargassum vulgare*, *Cladostephus spongiosus*, *Osmundaea truncata* and *Chondracanthus acicularis* were confined to the most acidified zone. These differences in species

richness and abundance affected the structure of the community, as shown in Fig. 4, where the cumulative percentage dominance of species is ranked on a logarithmic scale. The highest algal community complexity was evident at S1, whereas at S2 there was a shift towards greater dominance by fewer species and at S3 the simplified community was dominated by very few species.

The PCA biplot (Fig. 5) displays both sample (triangles) and species (numbers with vectors) distribution between the two principal components. The first component explains 26.8% of the species distribution, and with the second component this reaches 38.8%. The biplot displays a typical horseshoe shape because of non-linear relationships among species, for example, due to competition for space and light.

Samples A–C group together on the right side of the diagram and were from mean pH 8.1 (S1) with many calcified species present (circled), samples D–F (from mean pH 7.8) group at the centre with fewer calcifiers and samples G–I from the most acidified area (S3) show a sharp discontinuity from the others. This differentiation is due both to species composition and their abundance differences among the three sites. Statistical differences in community composition among sectors are highlighted by ANOSIM results (Table 4). The SIMPER analysis of percentage species cover (Table 5) shows that

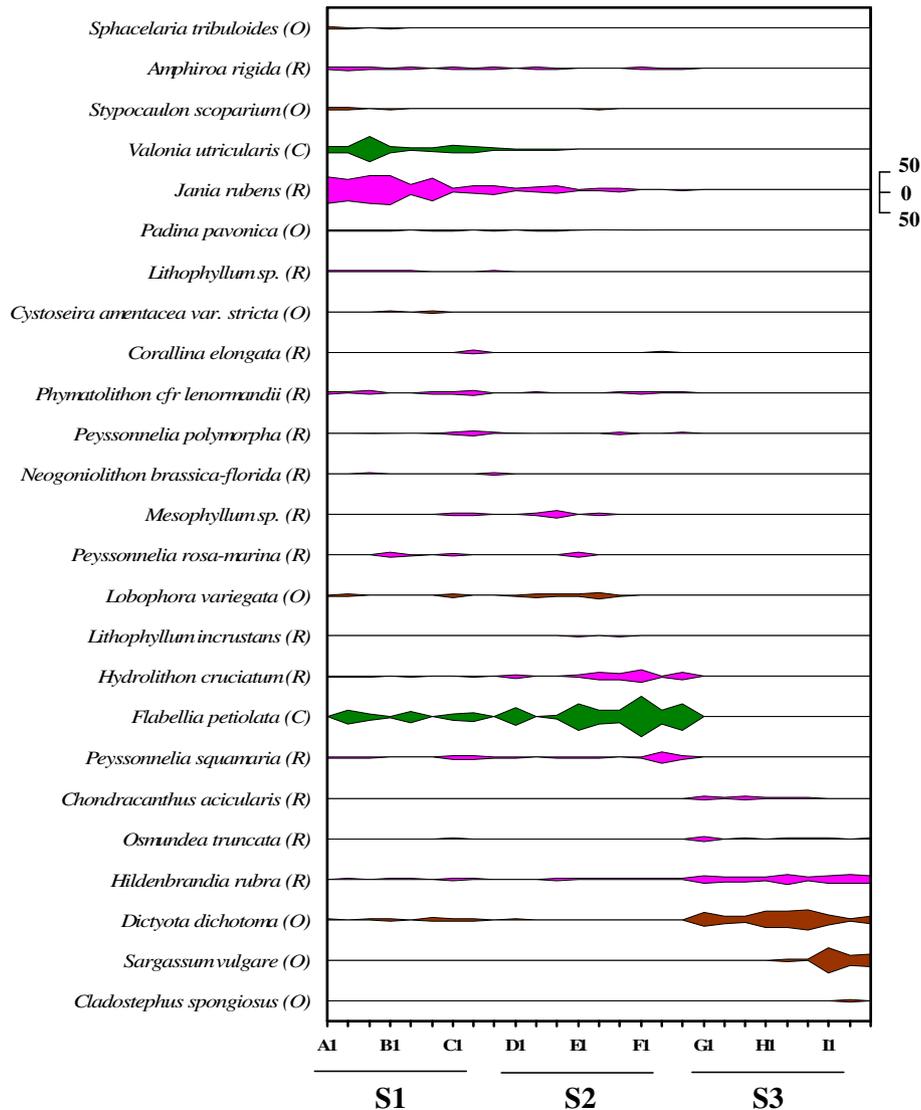


Fig. 2. Kite diagram showing the distribution of the most abundant macroalgal species (>3% coverage) in 27 20*20 cm quadrats taken along a pH gradient from S1 (pH = 8.1), S2 (pH = 7.8) and S3 (pH = 6.7). R = Rhodophyta, O = Ochrophyta, and C = Chlorophyta.

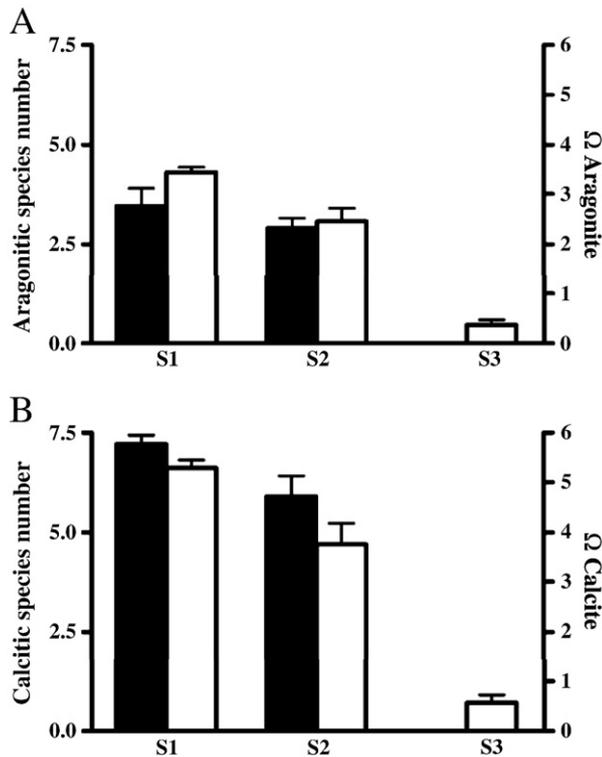


Fig. 3. Mean number of A) aragonitic and B) calcitic macroalgal species (black bars, $n=9$) along a pH gradient from S1 (pH=8.1), S2 (pH=7.8) and S3 (pH=6.7). Corresponding Ω values (white bars) are reported. Error bars = SEM.

averaged species abundances allow discrimination of one sector from another. This differentiation is quantified by a dissimilarity percentage. SIMPER attributed the highest average similarity among quadrats of sector S3 dominated by *D. dichotoma* and the highest dissimilarity (>89%) among S3 and the other two sectors (Table 5). The highest percentage contributions to the dissimilarities were due to the erect calcareous Rhodophyta *J. rubens*, which was dominant at mean pH 8.1 (S1), the erect Chlorophyta *Flabellia petiolata*, which was dominant at mean pH 7.8 (S2), and the erect Ochrophyta *D. dichotoma*, which was dominant at mean pH 6.7 (S3). Of the turf-forming species, the loss of *Valonia utricularis* and replacement by *Osmundea truncata* drove much of the community shift as the pH decreased (Table 6).

Of the 101 macroalgal species recorded, 51% were turf-forming species, 25% were crustose and 24% were erect forms. There was little change in the numbers of species in each morphological category from mean pH 8.1 to mean pH 7.8 although there was a large reduction in morphological category diversity at mean pH 6.7 (Table 1).

A bubble plot (Fig. 6) on an nMDS graph (Stress value = 0.07) of the percentage cover for each algal morphology highlighted little change in the area covered by erect algae along the pH gradient. Each bubble represents the mean cover percentage distribution along the gradient of a morphological category in the pH zones, showing the abundances of each algal group. Crustose algae remained abundant at

Table 3

ANOVA results for carbonate saturation states (Ω_{calcite} and $\Omega_{\text{aragonite}}$) and the species richness of aragonitic and calcitic calcareous species from nine 20*20 cm quadrats placed along a rocky shore pH gradient from S1 (pH=8.1), S2 (pH=7.8) and S3 (pH=6.7). Both Ω_{calcite} and $\Omega_{\text{aragonite}}$ values had to be \log_{10} transformed to run ANOVA.

	d.f.	F	P	Tukey's test
Calcitic species	2	130.5	<0.0001	S1>S2>S3
Ω_{calcite}	2	92.95	<0.0001	S1 = S2>S3
Aragonitic species	2	38.65	<0.0001	S1 = S2>S3
$\Omega_{\text{aragonite}}$	2	93.31	<0.0001	S1 = S2>S3

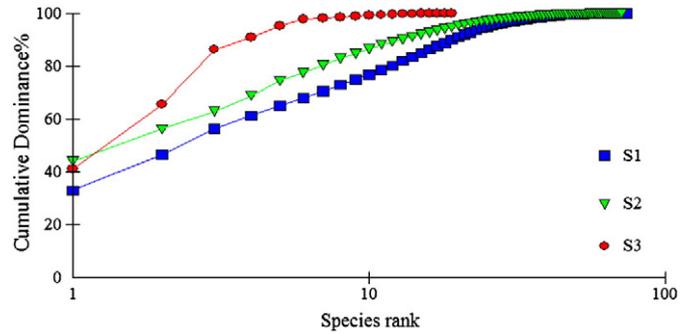


Fig. 4. K-dominance curves for mean rocky shore macroalgal coverage along a pH gradient from S1 (pH=8.1), S2 (pH=7.8) and S3 (pH=6.7).

mean pH 7.8 (S2) but were reduced in abundance in the area with highest CO_2 levels (S3). The SIMPER analysis shows that turf algae had a reduction and shift in species composition and area covered at mean pH 7.8 and that they were particularly scarce in the most acidified sector as also shown by the high values of average dissimilarity (91.8 and 93.2) between this sector and S2 and S1, respectively (Table 6).

Only seven genera were contemporaneously found with reproductive structures at different pH values (Fig. 7); among them, *Polysiphonia scopulorum*, *O. truncata* and *D. dichotoma* were able to reproduce at very high levels of CO_2 . There was even an increase in reproductive frequency recorded in the high CO_2 areas for *D. dichotoma* and *O. truncata*, whereas reproduction in calcareous species appeared to be negatively affected (Fig. 7).

4. Discussion

Research into the effects of ocean acidification on benthic marine habitats has been largely restricted to tropical reefs (Hoegh-Guldberg et al., 2007; Anthony et al., 2008; Kuffner et al., 2008; De'ath et al., 2009; Manzello et al., 2009) while in temperate benthic systems research focus has centred on individual species or small species groups (e.g., Dupont et al., 2008; Parker et al., 2009; Thomsen et al., 2010; Crim et al., 2011–this issue; Yu et al., 2011–this issue). The present study is the first to detail how the changes in marine carbonate chemistry that result from increasing CO_2 levels can result in complex effects in macroalgal habitats, affecting the structure of rocky shore communities. Naturally acidified areas are useful as they encompass the life histories of interacting organisms and include the feedbacks and indirect effects that occur within natural marine systems but which are difficult to replicate in mesocosm and laboratory conditions (Thomsen et al., 2010). Our paper adds to similar field studies on the effects of ocean acidification on seagrass algal epiphytes (Martin et al., 2008), foraminiferan community structure (Dias et al., 2010) invertebrate settlement (Cigliano et al., 2010), and bryozoan calcification (Rodolfo-Metalpa et al., 2010), all of which indicate major ecological shifts as CO_2 levels rise.

Our macroalgal data offer some cause for relief as they show that many seaweeds can clearly continue to photosynthesise even at extremely high CO_2 levels. Various Rhodophyta (e.g., *C. acicularis*), Ochrophyta (e.g., *S. vulgare*) and Chlorophyta (*Chaetomorpha linum*) are able to grow at CO_2 levels that far exceed those predicted due to human emissions. A cautionary note is, however, needed when interpreting these results, as one of the problems with using CO_2 vents to predict the effects of ocean acidification is that they only affect localised areas. It is possible that some of the species present at the vents are not able to complete their life history in high CO_2 conditions but recruit into the acidified areas from populations outside. The filamentous Rhodophyta *P. scopulorum*, for example, decreased in reproductive capacity as CO_2 levels increased, even though it was present in the most acidified area. Surprisingly, we found that some of the Ochrophyta (*D. dichotoma* and *O. truncata*) appeared to grow and

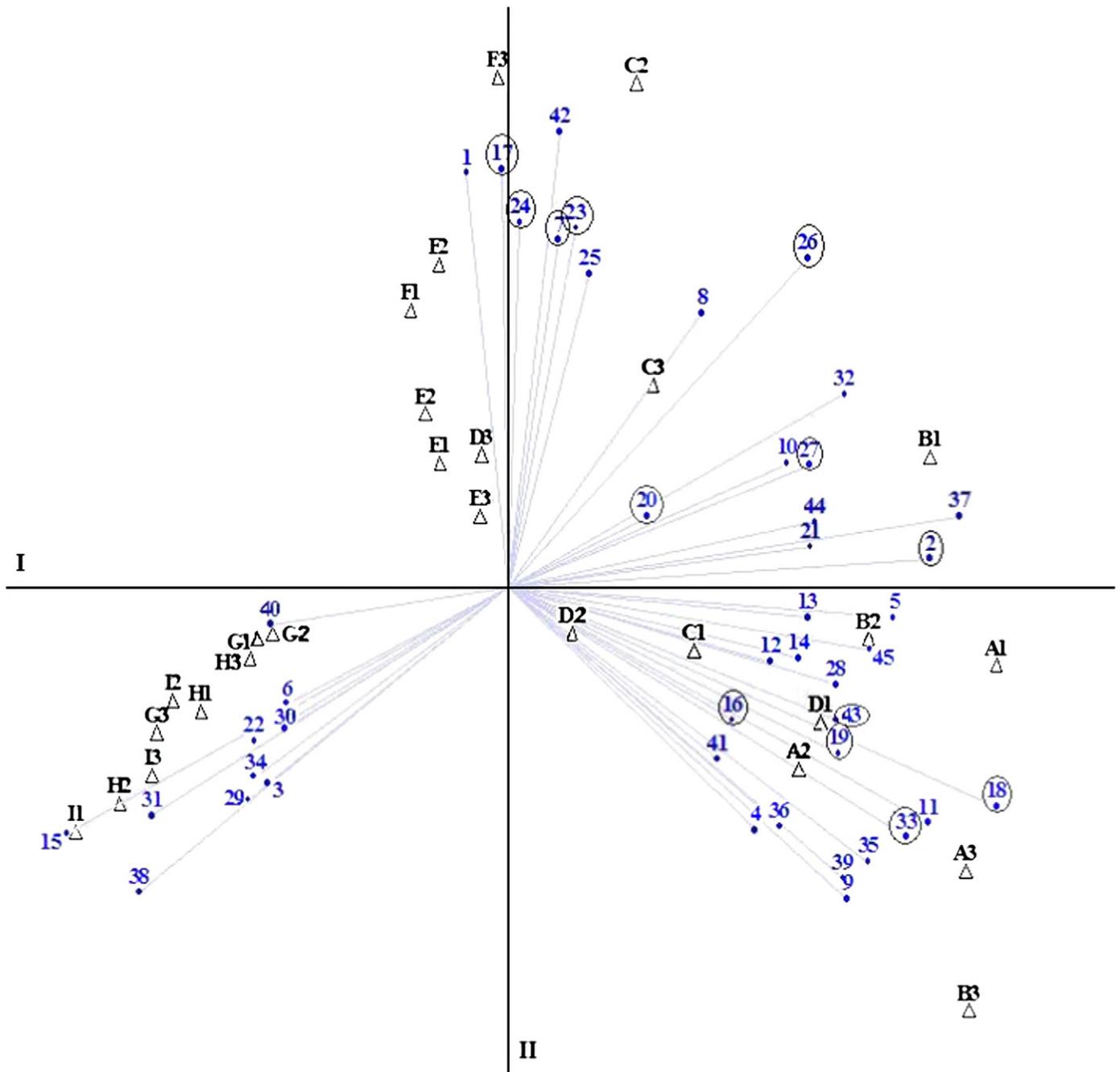


Fig. 5. Principal component analysis (PCA) ordination for macroalgal cover data collected along a pH gradient. Triangles represent sampling locations, labelled with letters corresponding to Fig. 1. Dots represent individual species (calcified species circled) and numbers correspond to species listed in Table 2.

reproduce best at the highest CO₂ levels found within the vents. Comparison with data obtained from sampling already performed in different seasons (Porzio, unpublished data) will allow us to confirm

Table 4

ANOSIM Global Test for species. Sample statistic (Global R): 0.886. Significance level of sample statistic: 0.1%. Number of permutations: 999 (random samples from a large number). Number of permuted statistics greater than or equal to Global R: 0.

Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number ρ Observed
S3–S2	1	0.1	24310	999	0
S3–S1	1	0.1	24310	999	0
S2–S1	0.559	0.2	24310	999	1

or reject these preliminary results. The resilience of a diverse range of Ochrophyta to high CO₂ conditions offers hope that kelp forests of the world may survive the ongoing acidification of the coming decades. However, preliminary experimental work suggests that increased CO₂ levels may be detrimental to kelp forest habitats as they encourage the growth of algal competitors (Connell and Russell, 2010).

The examination of macroalgal communities living near CO₂ vents at mean pH 7.8 provides us with insights as to what to expect as the global oceans acidify due to anthropogenic CO₂ emissions. Fortunately, 95% of the macroalgal species present in our study were able to tolerate mean pH 7.8, even though diel fluctuations in pH at these volcanic vents was greater and more rapid than would be expected due to ocean acidification (Hall-Spencer et al., 2008; Riebesell, 2008). Given the widespread concerns over the fate of calcified algae in the coming

Table 5
SIMPER similarity analysis of macroalgal species coverage within sectors along a pH gradient. SIMPER dissimilarity analysis of macroalgal species coverage between pairs of sectors.

Species	Average abundance	Average similitude	Similitude/SD	Contribution %	Cumulative %
Sector S1					
Average similarity: 57.02					
<i>Jania rubens</i>	69.22	11.1	3.04	19.46	19.46
<i>Valonia utricularis</i>	28.5	6.69	6.3	11.73	31.19
<i>Amphiroa rigida</i>	10.28	4.53	2.96	7.95	39.14
<i>Flabellia petiolata</i>	20.33	2.67	0.7	4.68	43.82
<i>Dictyota dichotoma</i>	6.09	2.48	1.92	4.35	48.17
Sector S2					
Average similarity: 49.58					
<i>Flabellia petiolata</i>	66.22	12.73	1.54	25.68	25.68
<i>Hydrolithon cruciatum</i>	18.53	5.69	1.19	11.48	37.15
<i>Jania rubens</i>	10.09	3.83	1.16	7.73	44.89
<i>Hildenbrandia rubra</i>	4.44	3.78	2.42	7.63	52.52
<i>Lobophora variegata</i>	8.39	2.8	0.8	5.64	58.17
Sector S3					
Average similarity: 64.35					
<i>Dictyota dichotoma</i>	44.17	25.12	3.12	39.03	39.03
<i>Hildenbrandia rubra</i>	26.28	21.07	6.37	32.75	71.78
<i>Osmundea truncata</i>	4.7	5.11	1.8	7.94	79.71
<i>Chondracanthus acicularis</i>	4.96	4.05	0.83	6.29	86.01
<i>Sargassum vulgare</i>	22.17	3.85	0.54	5.99	91.99
Species	Average abundance	Average abundance	Average dissimilarity	Contribution %	
Sectors S1 and S2					
Average dissimilarity: 58.22					
	Sector S1	Sector S2			
<i>Jania rubens</i>	69.22	10.09	5.39	9.25	
<i>Flabellia petiolata</i>	20.33	66.22	5.05	8.67	
<i>Valonia utricularis</i>	28.5	2.57	3.61	6.2	
<i>Hydrolithon cruciatum</i>	2.53	18.53	2.85	4.9	
<i>Peyssonnelia squamaria</i>	3.87	8.86	1.95	3.34	
Sectors S1 and S3					
Average dissimilarity: 89.61					
	Sector S1	Sector S3			
<i>Jania rubens</i>	69.22	0	9.97	11.12	
<i>Valonia utricularis</i>	28.5	0.12	5.97	6.66	
<i>Dictyota dichotoma</i>	6.09	44.17	5.36	5.98	
<i>Hildenbrandia rubra</i>	3.18	26.28	4.44	4.95	
<i>Flabellia petiolata</i>	20.33	0	4.14	4.62	
Sectors S2 and S3					
Average dissimilarity: 89.37					
	Sector S2	Sector S3			
<i>Flabellia petiolata</i>	66.22	0	11.74	13.13	
<i>Dictyota dichotoma</i>	1.34	44.17	8.94	10.01	
<i>Hydrolithon cruciatum</i>	18.53	0	5.96	6.67	
<i>Hildenbrandia rubra</i>	4.44	26.28	4.9	5.48	
<i>Sargassum vulgare</i>	0	22.17	4.63	5.18	

decades (Kuffner et al., 2008; Nelson, 2009) it is noteworthy that several calcitic and aragonitic species of algae were able to settle and grow at the high CO₂ levels found near the vents. *P. squamaria* and *H. cruciatum* increased in abundance at mean pH 7.8, replacing other calcified species that were lost from the system. The fact that algae with high Mg–calcite skeletons, the most soluble form, can survive high CO₂ conditions near the vents offers hope that this vulnerable group will not disappear, as some predict, but that calcareous species that are more tolerant of high CO₂ levels will replace those species that are lost. However, there are caveats; the mean pH 7.8 data show a 25% loss in biodiversity of calcareous algae and a major reduction in cover of all the erect articulated genera (the calcitic *J. rubens*, *Corallina officinalis*, *Corallina elongata*, *A. rigida*, *Amphiroa criptarthrodia* and the aragonitic *H. tuna*). Low abundances and bleached

C. elongata have also been recorded at acidified volcanic vents in the Azores (Couto et al., 2010). Erect calcareous algae are often important for calcareous sediment production and typically host a high biodiversity of associated fauna and flora (Nelson, 2009). Erect calcareous species may be more sensitive to corrosive short-term drops in pH caused by spikes in CO₂ levels at the vents than the crustose calcareous forms, which may benefit from chemical buffering in the benthic boundary layer. As a group, the calcareous algae exhibited a decrease in abundance and a decrease in reproductive capacity from normal pH conditions to mean pH 7.8. Our data on the selective effects of high CO₂ levels on seaweed reproduction are preliminary and worthy of further investigation given that some parts of an organism's life history can be more vulnerable to the effects of ocean acidification than others (e.g., Ellis et al., 2009).

Table 6
SIMPER dissimilarity analysis of turf algal group between pairs of sectors.

Species	Average abundance	Average abundance	Average dissimilarity	Contribution %
Sectors S1 and S2				
Average dissimilarity: 49.34				
	Sector S1	Sector S2		
<i>Valonia utricularis</i>	17.5	2.57	3.11	6.3
<i>Laurencia obtusa</i>	1.74	0	3.04	6.15
<i>Sphacelaria tribuloides</i>	3.67	0.9	2.69	5.45
<i>Herposiphonia tenella</i>	0.6	0.06	1.93	3.91
<i>Polysiphonia scopulorum</i>	0.96	0.52	1.9	3.85
Sectors S1 and S3				
Average dissimilarity: 93.17				
	Sector S1	Sector S3		
<i>Valonia utricularis</i>	17.5	0.17	8.21	8.82
<i>Sphacelaria tribuloides</i>	3.67	0	5.79	6.21
<i>Bryopsis plumosa</i>	2.33	0	5.67	6.09
<i>Osmundea truncata</i>	0.22	2.7	5	5.37
<i>Pseudochlorodesmis furcellata</i>	1.01	0	4.44	4.76
Sectors S2 and S3				
Average dissimilarity: 91.76				
	Sector S2	Sector S3		
<i>Osmundea truncata</i>	0.12	2.7	6.25	6.81
<i>Valonia utricularis</i>	2.57	0.17	5.59	6.09
<i>Griffithsia phyllamphora</i>	1.23	0	5.07	5.52
<i>Dasya corymbifera</i>	0.054	0	5.05	5.51
<i>Pseudochlorodesmis furcellata</i>	1.14	0	4.66	5.07

Whilst our observations show that the vast majority of algal species can tolerate the levels of CO₂ predicted to occur this century, and that even calcified species continue to grow, we recorded a simplification of the macroalgal community and increased dominance by a few species at mean pH 7.8. Both erect and crustose calcified species were largely replaced by non-calcified algae (e.g., *H. rubra*, *D. dichotoma* and *O. truncata*) that are presumably better adapted to the changes in carbonate chemistry that result from elevated CO₂ levels. Ochrophyta remained the dominant, high-biomass, canopy-forming species throughout the CO₂ gradient but *Cystoseira amentacea* var. *stricta* was present only in the mean pH 8.1 sector whereas *S. vulgare* was confined to the most acidified sector. These two genera often dominate Mediterranean phytobenthic assemblages but have steadily declined in abundance since the 1940s (Thibaut et al., 2005). In the Gulf of Naples, where our study took place, the loss of canopy-forming brown algae has been correlated with increased pollution levels, increased water turbidity, and increased temperature (Buia et al., 2007). The unique occurrence of *S. vulgare* in the most acidified zone (Buia, unpublished data) might relate to a lack of grazing by sea urchins, which are highly susceptible to ocean acidification (Miles et al., 2007) and completely absent from the Ischia CO₂ vents (Hall-Spencer et al., 2008).

An analysis of shifts in algal morphological groups along the pH gradient revealed that among the crustose, erect and turf-forming algae the turfs declined the most in diversity and abundance along the pH gradient, despite the fact that these are usually considered opportunistic species that are resilient to ocean acidification (Kleypas et al., 2006). We were surprised to find that the turf algae were replaced by more morphologically complex erect species (e.g., leathery *S. vulgare* and corticated laminar and terete species such as

D. dichotoma and *O. truncata*) but perhaps a more structured thallus helps these species better regulate the effects of acidification on cellular homeostasis. Connell and Russell (2010) demonstrated in mesocosm experiments that increased CO₂ levels (550 ppm) had no effect on the cover of turf algae at ambient temperature (17 °C) but that turf cover increased considerably when increased CO₂ levels were combined with elevated temperatures. Our data suggest that in autumn, on a shallow Mediterranean rocky shore at a mean temperature of 21–22 °C, about 1000 ppm CO₂ (S2) causes a significant fall in the richness and cover of turf species that are present at background CO₂ levels. The nature of CO₂-induced shifts in macroalgal community structure are likely to vary with biogeographic region, but the fact that CO₂ enrichment can cause significant shifts in the abundance of whole morphological groups indicates that rising CO₂ levels will alter local ecosystems, including food web dynamics and the cycling of carbon and nutrients.

To conclude, our field observations show that a diverse range of macroalgal species are resilient to even greater changes in seawater carbonate chemistry than those predicted to occur due to anthropogenic CO₂ emissions over the coming century. However, our observations show that we need to plan for shifts in community structure and the loss of biodiversity because some algal species are intolerant of increased CO₂ levels whilst others thrive under these conditions. Many macroalgal species have reduced abundance at mean pH 7.8, and further work is required to determine the mechanisms that cause this. Changes in inorganic carbon chemistry

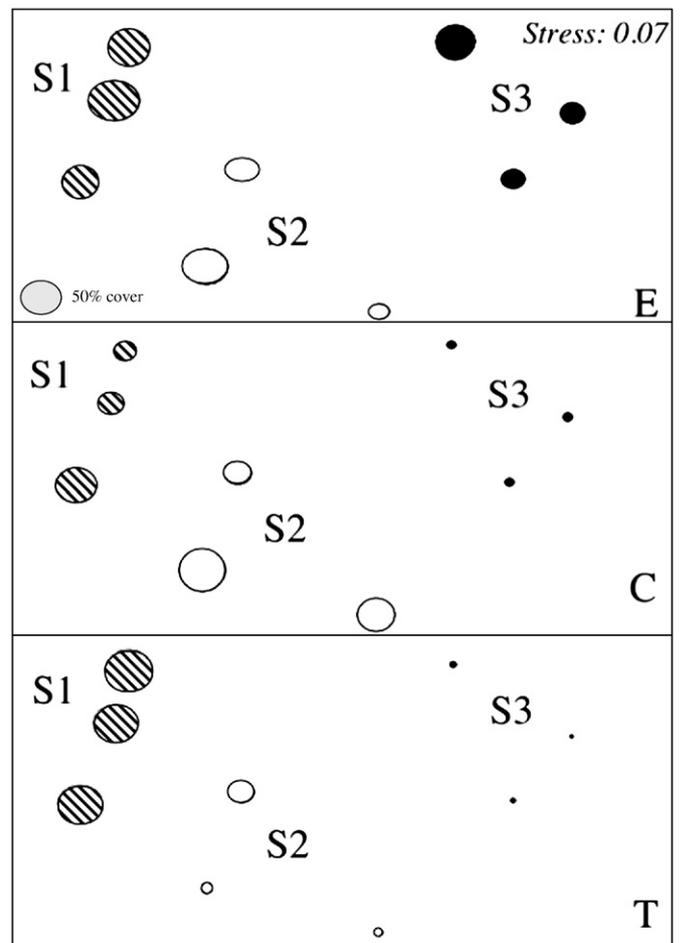


Fig. 6. nMDS of coverage of E) erect, C) crustose and T) turf macroalgal categories along a pH gradient from S1 (pH = 8.1), S2 (pH = 7.8) and S3 (pH = 6.7). Dot size corresponds to % coverage.

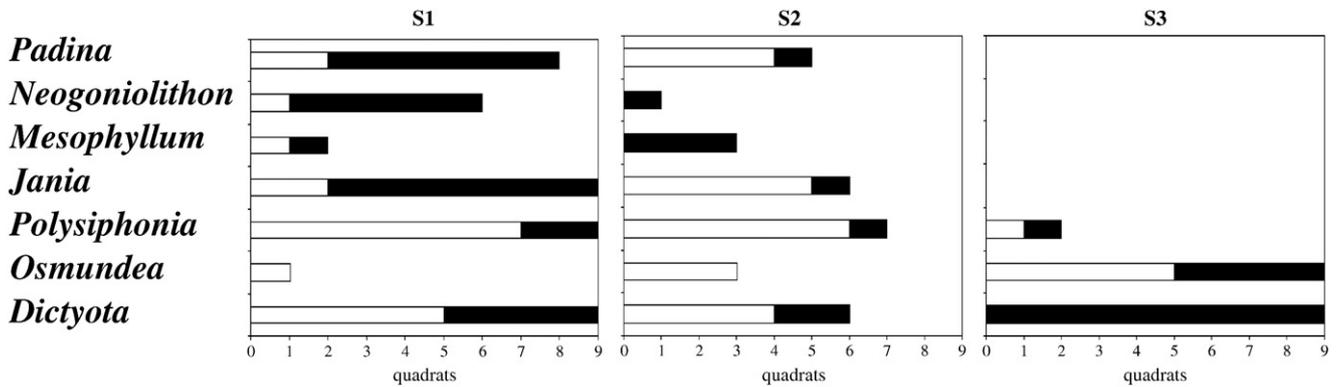


Fig. 7. Occurrence (black bars) and absence (white bars) of reproductive structures in species present in at least two sectors with different pH. S1 pH = 8.1, S2 pH = 7.8 and S3; pH = 6.7.

may disrupt a range of processes (e.g., calcification, reproduction, membrane transport and cellular physiology), putting some species at a competitive disadvantage. Research effort has been preoccupied with the detrimental effects of ocean acidification on marine organisms but we also need to better understand which marine organisms will proliferate as CO₂ levels increase. Volcanic vents show that some invasive macroalgae can tolerate persistent high CO₂ levels and also demonstrate what ecological shifts can be expected in vegetated marine ecosystems (Hall-Spencer et al., 2008). Ecophysiological studies are required to better understand why some species can live in a wide range of CO₂ conditions and what processes restrict others to the lowest or highest CO₂ concentration zones. As volcanic vents can persist for millennia it would also be interesting to investigate whether tolerant species have undergone genotype selection within high CO₂ environments.

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