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Herbivore diversity improves benthic community resilience to ocean acidification

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Herbivore diversity improves benthic community resilience to ocean acidification

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ABSTRACT

Ocean acidification is expected to alter a wide range of marine systems, but there is great uncertainty about the outcome because indirect effects are often crucial in ecology. Work at volcanic seeps has shown that major ecological shifts occur due to chronic exposure to acidified seawater. Changes in herbivore densities are often seen and this may interact with direct CO_2 effects to determine benthic community structure. Here, an exclusion experiment was used to test effects of herbivory in benthic communities along a pCO_2 gradient off Methana (Greece). A manipulative experiment was used to examine how large herbivores affected sublittoral algal communities as seawater carbon dioxide levels increased. Sea urchins and herbivorous fish dramatically reduced macroalgal biomass at background carbon dioxide levels; this effect was not hampered by increased pCO_2 despite lower sea urchin densities near the seeps, since herbivorous fish abundances increased concurrently. We found that carbon dioxide levels up to about 2000 μatm are unlikely to reduce the role of herbivory in structuring benthic communities if tolerant species are able to replace those that are vulnerable. A shift from sea urchins to fish as main grazers highlights that ocean acidification may cause unexpected responses at the community level, and that maintaining high functional redundancy in marine ecosystems is key to improving their resilience.

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1. Introduction

Increasing anthropogenic atmospheric CO_2 is altering the chemistry of surface seawater worldwide, resulting in ocean acidification (Caldeira and Wickett, 2003). Mean surface ocean pH has already decreased by 0.1 units (a 30% increase in H^+ concentration) compared to pre-industrial times, and is falling rapidly (Doney et al., 2009). Studies at volcanic seeps have shown that chronic exposure to increased CO_2 reduces diversity and causes changes in benthic macroalgal and invertebrate communities (Fabricius et al., 2014; Kroeker et al., 2011; Porzio et al., 2011). These changes could be caused by direct physiological effects of CO_2 or indirect effects, such as altered competitive interactions between species (Arnold et al., 2012; Kroeker et al., 2013). Grazers often determine the structure of shallow water communities (Poore et al., 2012); some are expected to become more abundant as CO_2 increases (e.g., amphipods, Cigliano et al., 2010; Kroeker et al., 2011), whereas others are expected to decrease in abundance (e.g., sea urchins, Hall-Spencer et al., 2008; Johnson et al., 2012). The contribution of grazers to community changes along pCO_2 gradients has not been previously tested experimentally.

If sea urchin densities do decrease due to ocean acidification this may leave marine ecosystems vulnerable to phase shifts; for example, tropical coral reefs may be overgrown by macroalgae if grazing pressure is removed and the algae are competitively advantaged over corals (Diaz-Pulido et al., 2011; Hughes et al., 2007).

In Mediterranean sublittoral environments, high densities of the sea urchins *Paracentrotus lividus* (Lamarck, 1816) and *Arbacia lixula* (Linnaeus, 1758) can reduce fleshy algae biomass creating assemblages dominated by encrusting algae (Guidetti and Dulcic, 2007). Sea urchin grazing often reduces seaweed standing crop in temperate rocky reefs worldwide; encrusting algal communities are considered an alternative stable state to kelp beds (Filbee-Dexter and Scheibling, 2014) since, once established, they can be maintained by relatively low sea urchin densities (Chiantore et al., 2008). Herbivorous fish typically exert weaker grazing pressure on temperate macroalgal communities than sea urchins (Floeter et al., 2005), but in the Mediterranean they can limit the distribution of many macroalgae (Vergés et al., 2009) and maintain habitats with very low macroalgal biomass (Sala et al., 2011). The main herbivorous fish are the sparid *Sarpa salpa* (Linnaeus, 1758) and the scarid *Sparisoma cretense* (Linnaeus, 1758), as well as the lessepsian migrant *Siganus luridus* (Rüppell, 1829) and *Siganus rivulatus* (Forsskål and Niebuhr, 1775); the latter two species can account for over 90% of herbivorous fish biomass in Greek southern seas (Kalogirou et al., 2012).

Here we examine the interplay between herbivorous fish and sea urchins. Ocean acidification is detrimental to many sea urchin species and their densities often decrease as seawater pCO_2 increases (Bray et al., 2014; Calosi et al., 2013). Although increasing CO_2 can affect fish behaviour, making them less alert to predators (McCormick et al., 2013; Munday et al., 2014), many fish seem to tolerate carbon dioxide levels predicted for the end of this century (Melzner et al., 2009). Herbivorous fish could benefit from ocean acidification because of increased food availability following increasing primary productivity and decreased competition with more susceptible herbivores, such as sea urchins (Johnson et al., 2012; Pinnegar and Polunin, 2004).

Our understanding of ecosystem shifts due to elevated CO_2 has evolved through a series of studies at volcanic seeps. Initial work led researchers to conclude that a shift from coralline to fleshy algal dominated communities was driven by dissolution effects on calcified algae (Hall-Spencer et al., 2008; Martin et al., 2008). Subsequent work showed that certain coralline algae were able to withstand dissolution at CO_2 levels predicted for the end of this century, but that fleshy algae outcompeted them at elevated CO_2 levels (Kroeker et al., 2013). In a comparison of tropical and temperate CO_2 seep systems, Johnson et al. (2012) found that *Padina* spp. thrived at high CO_2 levels despite dissolution of their carbonate layer and postulated that this was possible because their main grazers (sea urchins) were unable to tolerate high CO_2 conditions. There is now a growing realisation that major ecological effects of ocean acidification are likely to be indirect and mediated through changes in trophic interactions, and that functional redundancy may have a role in ecosystem resilience to increased CO_2 (Alsterberg et al., 2013; Gaylord et al., in press). Here we test the indirect and direct effects of ocean acidification on rocky Mediterranean shores with and without grazers present.

2. Methods

2.1. Study site and environmental parameters monitoring

Volcanic seeps off Methana influence carbonate chemistry along a wide stretch of rocky shore, and can be used to study the effects of elevated CO_2 on biological communities as there are no confounding gradients in temperature, salinity, total alkalinity, nutrients, hydrogen sulphide and total and bioavailable heavy metals (Baggini et al., 2014). In addition, the study sites had similar substratum type (sparse large boulders) and degree of urbanisation, with only small villages and hotels in the area (Baggini et al., 2014). Macroalgal communities change consistently between pCO_2 levels but not with any of the other factors analysed, so carbon dioxide is the main determinant of benthic community structure (Baggini et al., 2014). For the present study, a site with high and variable pCO_2 (SEEP) and a reference site (REF) were used

(Fig. 1). Environmental variables were measured in September 2012 and June 2013. Seawater pH, temperature and salinity were measured using a multiprobe (YSI 63) from the shore. The probe was calibrated before use with pH 4.01, 7.01 and 10.01 NBS standards. Since variations of up to 1 pH unit were detected over a few hours at the low pH site, the lack of precision in using the NBS scale for seawater measurements (approximately 0.05 pH, Riebesell et al., 2010) was considered acceptable for this study. For pH, medians and interquartile ranges (IQ) were calculated from hydrogen ion concentrations before re-converting back to pH values following seep monitoring methods provided by Kerrison et al. (2011). Seawater samples for total alkalinity determination were collected in 125 ml borosilicate glass bottles with Teflon caps. Three independent samples per site were collected twice per visit, immediately poisoned with $HgCl_2$ and stored in the dark until analysis. Samples were analysed by Gran titration (AS-ALK 2, Apollo SciTech) and the reliability of the measurements was checked against standard seawater samples provided by A. Dickson (batches 112 and 121). The average total alkalinity value per site and individual pH measurements were used to calculate pCO_2, HCO_3^-, CO_3^{2-}, Ω_{Ar} and Ω_{Ca} using CO2Sys software (Lewis and Wallace, 1998).

2.2. Herbivore surveys

Herbivore densities were determined at both sites. Densities of *P. lividus* and *A. lixula* were determined separately using transects: individuals present between 1 and 2 m depth were counted by snorkelers along five transects (5 m long and 1 m wide) per site per species in September 2012 and June 2013. Fish community composition and biomass were quantified in September 2013 using a standard visual census technique (while SCUBA diving) within belt transects of 25 m length and 5 m width placed at 3 m depth (three replicates, 125 m^2 surface each). The observer conducting the fish survey moved at constant speed identifying, counting and attributing all individuals to 5 cm size classes within 2.5 m on either side of the 25 m transect line (La Mesa and Vacchi, 1999; Giakoumi et al., 2012). Length estimates of fish from the visual surveys were converted to wet weight by using the allometric length–weight conversion: $W = aL^b$, where W is weight in g and L is total length in cm. The constant parameters a and b corresponding to the closest geographical area were obtained from Morey et al. (2003).

2.3. Herbivore exclusions

Four sterile 10×10 cm ceramic tiles were attached to rocks using epoxy putty and deployed at the two Methana study sites by snorkelers as controls; four tiles per site were enclosed in a 1 cm mesh cage to exclude herbivores, and four additional tiles per site were enclosed in a three-sided cage acting as procedural controls (Fig. S1). The cages
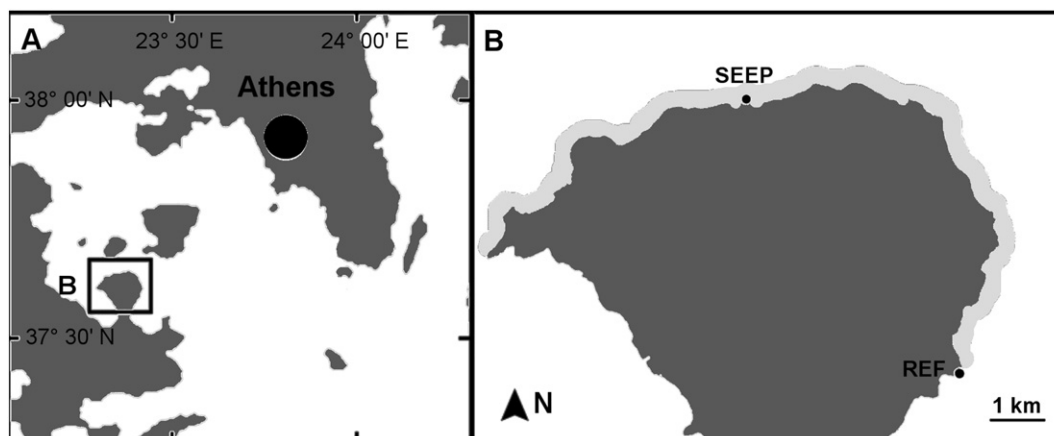

Fig. 1. Study sites (points) and area where pH was more variable than at reference site (light grey).

were painted using non-toxic antifouling paint (EP-2000, ePaint, Florida) to prevent epiphytes from growing and shading the tiles. Tiles were deployed in September 2012 and recovered in June 2013, when Mediterranean seaweed biomass reaches its annual peak. All tiles were recovered, except for one procedural control at both sites and one exclusion tile at the high CO_2 site.

After recovery, tiles were detached from the rock, put in individual zip-lock bags and stored frozen. In the laboratory, their cover was visually assessed and quantified as percent cover of functional groups. The functional groups used were: fucoid algae (mostly *Cystoseira* sp.; C. Agardh, 1820), erect brown algae, fleshy brown algae (mostly *Dictyota* sp.; J.V. Lamouroux, 1809), calcifying brown algae (mostly *Padina pavonica*; (Linnaeus) Thivy, 1960), turf algae (mat-forming algae shorter than 2 cm, mostly juvenile *Halopteris scoparia*; (Linnaeus) Sauvageau, 1904), encrusting black sponge, encrusting green algae, filamentous green algae, articulated coralline algae, coralline crustose algae (CCA), serpulid worms, biofilm, and bare substratum. The biomass of turf and erect algae was measured by scraping the algae from the tiles, drying them at 60 °C for 72 h and weighing them to obtain dry weight (DW).

2.4. Statistical analyses

Sea urchin data were analysed with a three-way ANOVA (fixed factors: species, sampling month and site) after transforming them (fourth root) to comply with the normality and variance homogeneity requirements of ANOVA. Log-transformed biomass of the three recorded herbivorous fish was also analysed using an ANOVA with site and species as fixed factors. All the analyses above were performed using SPSS v19 (IBM, USA).

Structure of communities grown on tiles quantified using visual census was tested using a two-factor PERMANOVA with "site" and "treatment" as fixed factors. A square-root transformation was used to reduce the influence of abundant taxa in the community and a Bray–Curtis dissimilarity matrix was used. Type III sum of squares with 9999 unrestricted permutations of the raw data was used to account for small sample sizes. Pairwise tests were performed when a factor with more than two levels was significant. A nMDS plot was used to visually inspect the similarities among samples. The same procedure was used to analyse biomass of communities grown on tiles.

Percent cover or biomass changes in key groups of macroalgae were analysed using a two-factor permutational ANOVA with "site" and "treatment" as fixed factors. Percent cover was used for those functional groups that could not be reliably scraped from the tile (i.e., CCA, encrusting green algae, encrusting black sponge, biofilm and bare substratum). All analyses above were performed using PRIMER 6 with PERMANOVA + extension (Plymouth Routines in Multivariate Ecological Research, version 6).

3. Results

3.1. Environmental parameters

Measured and calculated carbonate chemistry parameters are shown in Table 1. The mean pH near the seeps was approximately 7.7, more than 0.3 points lower than the reference site. Temperature and salinity were not significantly different between the two sites. At the high CO_2 site, seawater pCO_2 was double that of the reference site,

even though on average seawater was still saturated with respect to both calcite and aragonite.

3.2. Herbivore surveys

Sea urchin densities significantly differed both between sites and between species (Table S1). No effect of sampling month was detected, and the lack of significant interactions indicates that both *A. lixula* and *P. lividus* densities changed consistently between sites. As no significant effect of sampling month was detected, sea urchin densities were pooled between sampling months for easier representation. Densities of *A. lixula* were consistently higher than those of *P. lividus* (Fig. 2A), with average densities of the former species ranging from 1.9 to 7.5 individuals in a five-metre transect. *P. lividus* densities ranged from 0.2 to 1.6 individuals. There was also a clear reduction in the densities of both species near the seeps, with *P. lividus* being almost absent at the high CO_2 site.

Three herbivorous fish species were recorded at the study sites: *S. salpa*, *S. luridus* and *S. cretense*. Similarly to sea urchins, both site and species had a significant effect on fish biomass (Table S2). No significant interactions were found, meaning that changes in each of the species biomass followed a similar pattern between sites. All species increased in biomass near the seeps (Fig. 2B), but the magnitude of the change was very different among species: while *S. cretense* had a low biomass that changed very little between sites, the two other species had very marked changes in biomass between sites. *S. luridus* was present at both sites and its mean biomass increased from 65 to 1565 g from REF to SEEP. *S. salpa* was absent from REF, while at SEEP it was the dominant species in terms of biomass.

3.3. Herbivore exclusion

Structure and composition of assemblages growing on the experimental units changed significantly between sites and treatments, but there was no interaction between the two factors (Table 2). Since the factor 'treatment' was significant, pairwise comparisons were performed among treatment levels to detect which pairs were significantly different. Exclusions were significantly different from both control ($t_{2,11} = 2.7397$, $p = 0.0001$) and procedural control ($t_{2,9} = 2.3722$, $p = 0.0009$), which did not differ between each other ($t_{2,10} = 1.2182$, $p > 0.05$).

Fig. 3 shows that SEEP and REF were clearly different for all treatments. Controls and procedural controls were closely grouped whereas exclusion tiles were very different. At the SEEP site, where a different group of algae (erect brown algae, fleshy brown algae, calcifying brown algae) was dominant in each exclusion tile, whereas in the reference site there was mostly an increase in calcifying brown algal cover when herbivores were excluded.

Statistical analysis of the fleshy and erect algal biomass produced results analogous to the percent cover data, so only the latter are reported as they are more comprehensive (i.e., they also include encrusting forms). Total biomass significantly increased in the exclusion treatment (Table S3), ranging from about 0.1 g in the control to approximately 3 g in the exclosures (Fig. 4). However, at the reference site procedural controls had values intermediate between controls and exclusions.

The eight most abundant functional groups accounted for more than 95% of total abundance or percent cover and were analysed for significant effects of site and treatment (statistical analyses reported

Table 1

Mean ($\pm$SD, n = 11–24) environmental parameters: pH, temperature and salinity were measured at Methana in September 2012 and June 2013 and pCO_2, bicarbonate ions, carbonate ions, seawater saturation with respect to calcite and aragonite were calculated using CO2Sys.

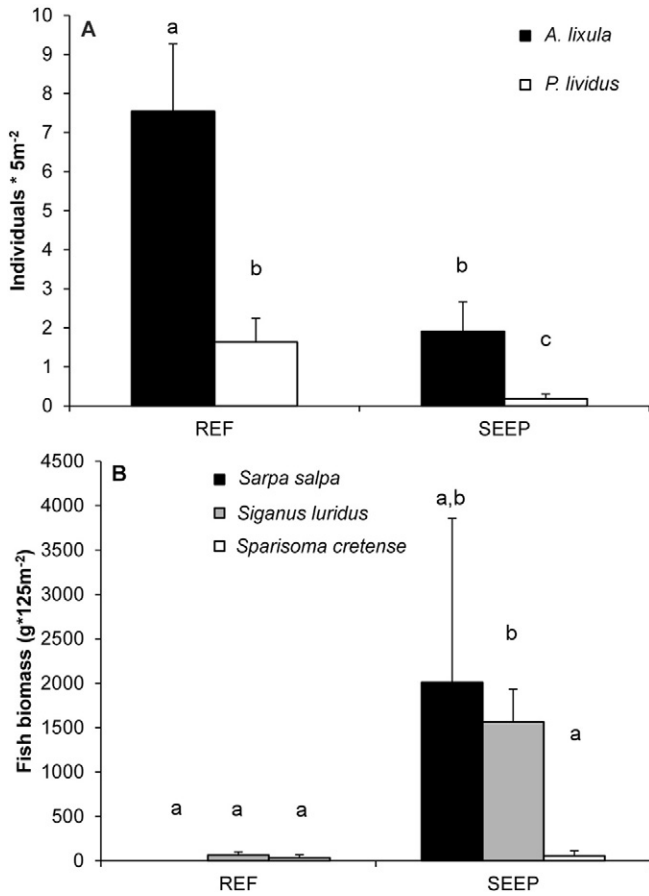|	pH_{NBS}	T (°C)	S (PSU)	pCO_2 (μatm)	HCO_3^- (mmol/kg SW)	CO_3^{2-} (mmol/kg SW)	Ω_{Ca}	Ω_{Ar}
SEEP	7.70 ± 0.16	25.34 ± 0.85	38.77 ± 0.93	1676.8 ± 643.5	2485.4 ± 112.4	125.0 ± 46.5	2.91 ± 1.06	1.93 ± 0.71
REF	8.09 ± 0.06	25.01 ± 1.05	38.94 ± 0.87	586.9 ± 106.7	2140.5 ± 63.3	232.1 ± 25.9	5.40 ± 0.59	3.57 ± 0.39

Fig. 2. Herbivores abundance. (A) Average number ($\pm$SE, n = 11) of sea urchins along 5 m transects at Methana study sites pooling data from September 2012 and June 2013. (B) Average biomass ($\pm$SE, n = 3) of herbivorous fish per 25 m transect at REF and SEEP in September 2013. Different letters represent significantly different groups.
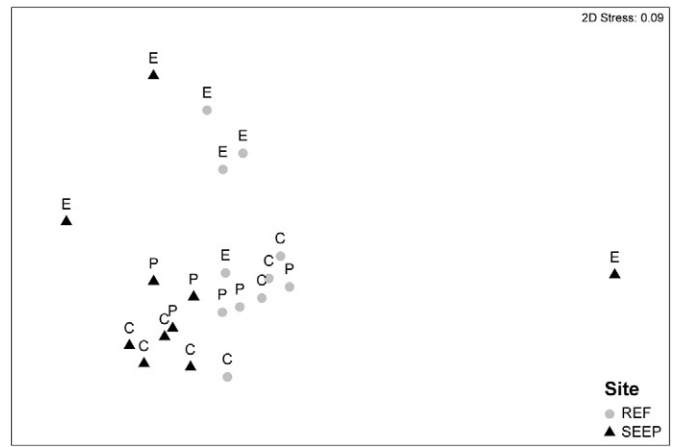

Fig. 3. MDS plot of the results of an herbivore exclusion experiment performed at Methana from September 2012 to June 2013; circles represent tiles placed at REF, triangles were tiles placed at SEEP. Letters above the symbols represent the treatments: C is control, P is procedural control, and E is exclusion.

4. Discussion

Coastal assemblages often have low functional redundancy, so the loss of a few species can negatively affect ecosystem functioning (Micheli and Halpern, 2005). Although taxonomic diversity is known to improve marine community resilience to increased temperatures (Allison, 2004), there was so far no evidence that this applies to ocean acidification. Here, we found that taxonomic diversity improved marine community resilience to ocean acidification: herbivorous fish kept seaweed biomass low at elevated CO_2 even though sea urchin densities decreased.

We should bear in mind that sublittoral rocky shore communities off present day Greece are not 'natural' in that overfishing of apex predators has led to higher abundances of Mediterranean sea urchins and herbivorous fish, as these are usually not targeted by commercial fisheries (Guidetti and Dulčić, 2007; Sala et al., 2012). We found that grazer diversity enabled present day community structure to remain the same along a pCO$_2$ gradient. At a global level, herbivorous fish abundance has been strongly reduced by overfishing (Micheli and Halpern, 2005), and where this is combined with other herbivores disappearing (e.g., sea urchin mass mortality in Jamaica) benthic habitats can experience dramatic phase shifts (Hughes, 1994). Given that increased CO_2 levels appear to benefit fleshy seaweeds but negatively affect scleractinian corals, maintaining herbivore diversity may help increase coral reef resilience to ocean acidification.
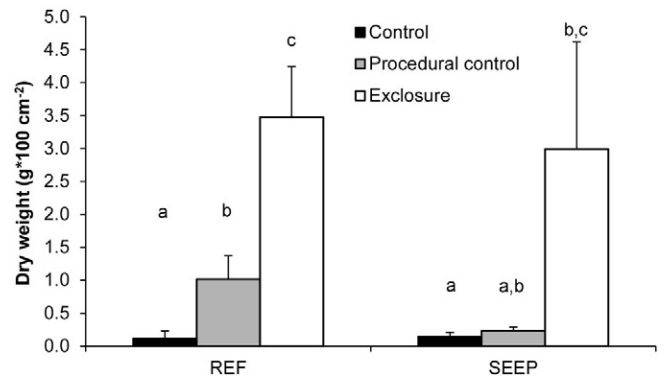
in Table S4), and percent cover or biomass of the four most abundant functional groups are reported in Fig. 5. Overall, turf and erect algae increased in herbivore exclusions, whereas encrusting forms showed the opposite trend (Table S5). Biofilm percent cover did not show any clear effect of herbivore exclusion, but it significantly increased at the high CO_2 site (Table S5). The effect of herbivore exclusion was always clear at SEEP, while at REF some functional groups (turf algae and bare substratum) had biomass or cover values similar between exclusion and procedural control (Fig. 5). There were significant differences between sites as well, with turf algae, calcifying brown algae and CCA decreasing as CO_2 increased and fucoid algae, fleshy brown algae, biofilm and bare substratum showing the opposite trend (Fig. 5; Table S5).

Table 2
PERMANOVA analyses of percentage cover of uncaged and caged tiles (square-root transformed) deployed at Methana from September 2012 to June 2013. Main factors and their interactions and degrees of freedom (df), sum of squares (SS), mean square (MS), pseudo-F and permutational p for each of them are reported. Significant p values (<0.05) are in bold.

Source	df	SS	MS	Pseudo-F	p (perm)
Site	1	5380.7	5380.7	5.3584	**0.0003**
Treatment	2	11,675	5837.4	5.8133	**0.0001**
Site $\times$ Treatment	2	2318.5	1159.2	1.1544	0.3204
Residual	15	15,062	1004.2		
Total	20	34,487			

Fig. 4. Average biomass ($\pm$SE; n = 3–4) of fleshy and erect algae grown on tiles for all three treatments of the herbivore exclusion experiment conducted at Methana from September 2012 to June 2013. Different letters represent significantly different groups.
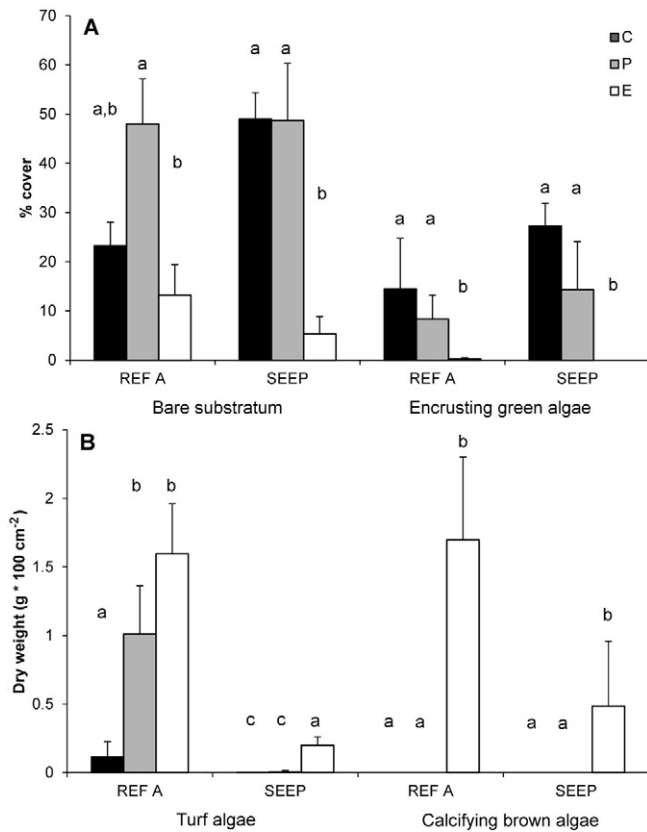
Fig. 5. Mean (± SE, n = 3–4) percent cover (A) or biomass (B) of most abundant functional groups at the study sites (REF A and SEEP); all treatments are shown (C = controls; P = procedural controls; E = herbivore exclusions). Different letters indicate significantly different sub-groups within a functional group.

calcifying turf algae such as those growing off Methana can be palatable to grazers (Falkenberg et al., 2014), and therefore may be removed if their grazers are resilient to ocean acidification. Conversely, biofilm percent cover increased near the seeps, in accord with findings at CO_2 seeps off Vulcano (Italy), where benthic diatoms and biofilm production increase at elevated CO_2 (Johnson et al., 2013; Lidbury et al., 2012).

Herbivore exclusion at Methana dramatically changed macroalgal communities grown on tiles, with an increase in algal biomass regardless of site. At the reference site the calcifying brown algae *P. pavonica* colonised all caged tiles, whereas at the high CO_2 site caged tiles were colonised by a variety of taxa (*P. pavonica*, *Dictyota* sp. and erect brown algae). This confirms that non-calcifying algae increase in abundance as pCO_2 increases, likely because they can outcompete calcifying species at elevated CO_2 levels (Kroeker et al., 2013; Porzio et al., 2011).

Herbivory alters outcomes of macroalgal competition, favouring less palatable macroalgal species or extremely fast-growing opportunistic algae (Hereu et al., 2008). At Methana, herbivore-resistant encrusting algae became more abundant at both CO_2 levels when herbivores were present. Benthic communities at Methana had smaller differences between CO_2 levels when herbivores were present (Fig. 4). This adds to a growing body of evidence that grazers dampen the effects of climate change on primary producers, both in terrestrial and marine ecosystems (Anthony et al., 2011; Falkenberg et al., 2014; Post and Pedersen, 2008).

We found that both sea urchin species had reduced densities near CO_2 seeps regardless of sampling month, which is in accord with their predicted sensitivity to ocean acidification resulting from laboratory experiments (Dupont et al., 2010). Sea urchins were replaced by herbivorous fish at the high CO_2 site; functional redundancy of herbivores can maintain top-down control on macroalgal biomass and reduce the effects of multiple stressors on benthic communities (Blake and Duffy, 2010; Eriksson et al., 2011). It should be noted, however, that fish are highly mobile and could swim in and out of the high CO_2 area (Riebesell, 2008), masking potential negative effects of ocean acidification such as those on neuroreception (Shaw et al., 2013).

Our herbivore exclusion experiment was only performed at one reference and one high CO_2 site; with more resources, performing the experiment at more than one reference site would have been preferable. However, at Methana we consider that pCO_2 was the main driver of change, since other environmental factors (temperature, salinity, heavy metals, hydrogen sulphide) did not vary significantly between study sites (Baggini et al., 2014). Moreover, the consistent presence of *Cystoseira corniculata* at both sites may well reflect similar hydrodynamic regimes, as this species is known to characterize Mediterranean rocky shores of high to moderate-high wave energy (Huvé, 1972; Montesanto and Panayotidis, 2001). Between-sites differences reported here are therefore likely to be caused by changes in pCO_2 levels, but repeating these experiments in more than one reference site would improve their statistical power. In particular, replicating herbivore fish surveys in more sites and combining them with laboratory experiments would be extremely useful, as they have more variable distribution patterns than macroalgae or sea urchins, and they can usually swim in and out of high pCO_2 areas (Riebesell, 2008).

Recent research has shown that indirect effects can be as important as the direct effects of CO_2 in shaping community responses to ocean acidification (Kroeker et al., 2013). Here we show that carbon dioxide affects the composition of macroalgal communities in sublittoral habitats, but that grazers can maintain similar habitats despite increases in CO_2. The most striking finding of this study is that herbivore functional redundancy can offset indirect effects of ocean acidification; this is only possible in diverse ecosystems, highlighting the necessity of managing local stressors to maintain high diversity and increase ecosystem resilience to environmental change (Ghedini et al., 2013).

The relative role of bottom-up and top-down processes in shaping marine ecosystems has long been a critical issue in marine ecology research. The relative importance of these two types of processes is highly context-dependant (Burkepile and Hay, 2006). Our study adds to several others that show 'bottom-up' CO_2 effects can have significant effects on benthic communities (Fabricius et al., 2014; Hall-Spencer et al., 2008). Here we found that herbivory strongly controlled seaweed biomass and community structure regardless of pCO_2 levels, even though herbivore community composition changed dramatically.

Even though herbivores kept macroalgal biomass low at both pCO_2 levels, the encrusting algal community changed since crustose coralline algal cover significantly decreased at high CO_2. There is now widespread evidence that this group is sensitive to ocean acidification, and even tolerant species can be outcompeted by non-calcifying algae at elevated CO_2 levels (Brodie et al., 2014; Kroeker et al., 2013). Brown algae significantly increased near the seeps, which aligns with observations at other CO_2 seeps (Porzio et al., 2011). Johnson et al. (2012) reported increasing densities of the calcifying brown alga *Padina* spp. as CO_2 increased at temperate and tropical seeps, possibly because of lower consumption by sea urchins. In the present study, calcifying brown algae (mostly *P. pavonica*) decreased in biomass with increasing CO_2 when herbivores were excluded due to increased competition with the fleshy brown alga *Dictyota* sp.

Biomass of turf algae (i.e., brown mat-forming algae shorter than 2 cm) decreased near the Methana seeps, in line with surveys off Ischia (Porzio et al., 2011). This is in contrast to many laboratory experiments, where turf algae can be advantaged by increased CO_2 due to fast growth rates and carbon limitation (Connell et al., 2013). However, some non-

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2015.04.019.

References

Allison, G., 2004. The influence of species diversity and stress intensity on community resistance and resilience. Ecol. Monogr. 74 (1), 117–134.

Alsterberg, C., Eklof, J.S., Gamfeldt, L., Havenhand, J.N., Sundback, K., 2013. Consumers mediate the effects of experimental ocean acidification and warming on primary producers. Proc. Natl. Acad. Sci. 110 (21), 8603–8608.

Anthony, K.R.N., Maynard, J.A., Diaz-Pulido, G., Mumby, P.J., Marshall, P.A., Cao, L., Hoegh-Guldberg, O.V.E., 2011. Ocean acidification and warming will lower coral reef resilience. Glob. Chang. Biol. 17 (5), 1798–1808.

Arnold, T., Mealey, C., Leahey, H., Miller, A.W., Hall-Spencer, J.M., Milazzo, M., Maers, K., 2012. Ocean acidification and the loss of phenolic substances in marine plants. PLoS One 7 (4), e35107.

Baggini, C., Salomidi, M., Voutsinas, E., Bray, L., Krasakopoulou, E., Hall-Spencer, J.M., 2014. Seasonality affects macroalgal community response to increases in pCO2. PLoS One 9 (9), e106520.

Blake, R.E., Duffy, J.E., 2010. Grazer diversity affects resistance to multiple stressors in an experimental seagrass ecosystem. Oikos 119 (10), 1625–1635.

Bray, L., Pancucci-Papadopoulou, M.A., Hall-Spencer, J.M., 2014. Sea urchin response to rising pCO2 shows ocean acidification may fundamentally alter the chemistry of marine skeletons. Mediterr. Mar. Sci. http://dx.doi.org/10.12681/mms.579.

Brodie, J., Williamson, C.J., Smale, D.A., Kamenos, N.A., Mieszkowska, N., Santos, R., Cunliffe, M., Steinke, M., Yesson, C., Anderson, K.M., Asnaghi, V., Brownlee, C., Burdett, H.L., Burrows, M.T., Collins, S., Donohue, P.J.C., Harvey, B., Foggo, A., Noisette, F., Nunes, J., Ragazzola, F., Raven, J.A., Schmidt, D.N., Suggett, D., Teichberg, M., Hall-Spencer, J.M., 2014. The future of the northeast Atlantic benthic flora in a high CO2 world. Ecol. Evol. http://dx.doi.org/10.1002/ece1003.1105.

Burkepile, D.E., Hay, M.E., 2006. Herbivore vs nutrient control of marine primary producers: context-dependent effects. Ecology 87 (12), 3128–3139.

Caldeira, K., Wickett, M.E., 2003. Oceanography: anthropogenic carbon and ocean pH. Nature 425 (6956), 365.

Calosi, P., Rastrick, S.P.S., Graziano, M., Thomas, S.C., Baggini, C., Carter, H.A., Hall-Spencer, J.M., Milazzo, M., Spicer, J.I., 2013. Distribution of sea urchins living near shallow water CO2 vents is dependent upon species acid–base and ion-regulatory abilities. Mar. Pollut. Bull. 73 (2), 470–484.

Chiantore, M., Vielmini, I., Privitera, D., Mangialajo, L., Cattaneo-Vietti, R., 2008. Habitat effects on the population structure of Paracentrotus lividus and Arbacia lixula. Chem. Ecol. 24, 145–157.

Cigliano, M., Gambi, M.C., Rodolfo-Metalpa, R., Patti, F.P., Hall-Spencer, J.M., 2010. Effects of ocean acidification on invertebrate settlement at volcanic CO2 vents. Mar. Biol. 157 (11), 2489–2502.

Connell, S.D., Kroeker, K.J., Fabricius, K.E., Kline, D.I., Russell, B.D., 2013. The other ocean acidification problem: CO2 as a resource among competitors for ecosystem dominance. Phil. Trans. R. Soc. B Biol. Sci. 368 (1627), 20120442.

Diaz-Pulido, G., Gouezo, M., Tilbrook, B., Dove, S., Anthony, K.R.N., 2011. High CO2 enhances the competitive strength of seaweeds over corals. Ecol. Lett. 14 (2), 156–162.

Doney, S.C., Fabry, V.J., Feely, R.A., Kleypas, J.A., 2009. Ocean acidification: the other CO2 problem. Ann. Rev. Mar. Sci. 1, 169–192.

Dupont, S., Dorey, N., Thorndyke, M., 2010. What meta-analysis can tell us about vulnerability of marine biodiversity to ocean acidification? Estuarine Coast. Shelf Sci. 89 (2), 182–185.

Eriksson, B.K., van Sluis, C., Sieben, K., Kautsky, L., Raberg, S., 2011. Omnivory and grazer functional composition moderate cascading trophic effects in experimental Fucus vesiculosus habitats. Mar. Biol. 158 (4), 747–756.

Fabricius, K.E., De'ath, G., Noonan, S., Uthicke, S., 2014. Ecological effects of ocean acidification and habitat complexity on reef-associated macroinvertebrate communities. Proc. R. Soc. B Biol. Sci. 281 (1775), 20132479.

Falkenberg, L.J., Connell, S.D., Russell, B.D., 2014. Herbivory mediates the expansion of an algal habitat under nutrient and CO2 enrichment. Mar. Ecol. Prog. Ser. 497, 87–92.

Filbee-Dexter, K., Scheibling, R.E., 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Mar. Ecol. Prog. Ser. 495, 1–25.

Floeter, S.R., Behrens, M.D., Ferreira, C.E.L., Paddack, M.J., Horn, M.H., 2005. Geographical gradients of marine herbivorous fishes: patterns and processes. Mar. Biol. 147 (6), 1435–1447.

Gaylord, B., Kroeker, K.J., Sunday, J.M., Anderson, K.M., Barry, J.P., Brown, N.E., Connell, S.D., Dupont, S., Fabricius, K.E., Hall-Spencer, J.M., Klinger, T., Milazzo, M., Munday, P.L., Russell, B.D., Sanford, E., Schreiber, S.J., Thiyagarajan, V., Vaughan, H., Widdicombe, S., Harley, C.D.G., 2015. Ocean acidification through the lens of ecological theory. Ecology http://dx.doi.org/10.1890/14-0802.1 (in press).

Ghedini, G., Russell, B., Connell, S., 2013. Managing local coastal stressors to reduce the ecological effects of ocean acidification and warming. Water 5 (4), 1653–1661.

Giakoumi, S., Cebrian, E., Kokkoris, G.D., Ballesteros, E., Sala, E., 2012. Relationships between fish, sea urchins and macroalgae: the structure of shallow rocky sublittoral communities in the Cyclades, Eastern Mediterranean. Estuar. Coast. Shelf Sci. 109, 1–10.

Guidetti, P., Dulčić, J., 2007. Relationships among predatory fish, sea urchins and barrens in Mediterranean rocky reefs across a latitudinal gradient. Mar. Environ. Res. 63 (2), 168–184.

Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M., Rowley, S.J., Tedesco, D., Buia, M.-C., 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. Nature 454 (7200), 96–99.

Hereu, B., Zabala, M., Sala, E., 2008. Multiple controls of community structure and dynamics in a sublittoral marine environment. Ecology 89 (12), 3423–3435.

Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265 (5178), 1547–1551.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr. Biol. 17 (4), 360–365.

Huvé, E., 1972. Aperçu sur la distribution en mer Égée de quelques espèces du genre Cystoseira (Pheophycees, Fucales). Soc. Phycol. Fr. 17, 22–37.

Johnson, V.R., Russell, B.D., Fabricius, K.E., Brownlee, C., Hall-Spencer, J.M., 2012. Temperate and tropical brown macroalgae thrive, despite decalcification, along natural CO2 gradients. Glob. Chang. Biol. 18 (9), 2792–2803.

Johnson, V., Brownlee, C., Rickaby, R., Graziano, M., Milazzo, M., Hall-Spencer, J., 2013. Responses of marine benthic microalgae to elevated CO2. Mar. Biol. 160, 1813–1824.

Kalogirou, S., Wennhage, H., Pihl, L., 2012. Non-indigenous species in Mediterranean fish assemblages: contrasting feeding guilds of Posidonia oceanica meadows and sandy habitats. Estuar. Coast. Shelf Sci. 96, 209–218.

Kerrison, P., Hall-Spencer, J.M., Suggett, D.J., Hepburn, L.J., Steinke, M., 2011. Assessment of pH variability at a coastal CO2 vent for ocean acidification studies. Estuar. Coast. Shelf Sci. 94 (2), 129–137.

Kroeker, K.J., Micheli, F., Gambi, M.C., Martz, T.R., 2011. Divergent ecosystem responses within a benthic marine community to ocean acidification. Proc. Natl. Acad. Sci. 108 (35), 14515–14520.

Kroeker, K.J., Micheli, F., Gambi, M.C., 2013. Ocean acidification causes ecosystem shifts via altered competitive interactions. Nat. Clim. Chang. 3, 156–159.

La Mesa, G., Vacchi, M., 1999. An Analysis of the Coastal Fish Assemblage of the Ustica Island Marine Reserve (Mediterranean Sea). Mar. Ecol. 20 (2), 147–165.

Lewis, E., Wallace, W.R., 1998. Program Developed for CO2 System Calculations. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge.

Lidbury, I., Johnson, V., Hall-Spencer, J.M., Munn, C.B., Cunliffe, M., 2012. Community-level response of coastal microbial biofilms to ocean acidification in a natural carbon dioxide vent ecosystem. Mar. Pollut. Bull. 64 (5), 1063–1066.

Martin, S., Rodolfo-Metalpa, R., Ransome, E., Rowley, S., Buia, M.C., Gattuso, J.P., Hall-Spencer, J., 2008. Effects of naturally acidified seawater on seagrass calcareous epibionts. Biol. Lett. 4 (6), 689–692.

McCormick, M.I., Watson, S.A., Munday, P.L., 2013. Ocean acidification reverses competition for space as habitats degrade. Sci. Rep. 3, 3280.

Melzner, F., Gutowska, M.A., Langenbuch, M., Dupont, S., Lucassen, M., Thorndyke, M.C., Bleich, M., Portner, H.O., 2009. Physiological basis for high CO2 tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? Biogeosciences 6 (10), 2313–2331.

Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. Ecol. Lett. 8 (4), 391–400.

Montesanto, B., Panayotidis, P., 2001. The Cystoseira spp. communities from the Aegean Sea. Mediterr. Mar. Sci. 2 (1), 57–67.

Morey, G., Moranta, J., Massutí, E., Grau, A., Linde, M., Riera, F., Morales-Nin, B., 2003. Weight–length relationships of littoral to lower slope fishes from the Western Mediterranean. Fish. Res. 62 (1), 89–96.

Munday, P.L., Cheal, A.J., Dixson, D.L., Rummer, J.L., Fabricius, K.E., 2014. Behavioural impairment in reef fishes caused by ocean acidification at CO2 seeps. Nat. Clim. Chang. 4 (6), 487–492.

Pinnegar, J.K., Polunin, N.V.C., 2004. Predicting indirect effects of fishing in Mediterranean rocky littoral communities using a dynamic simulation model. Ecol. Model. 172 (2–4), 249–267.

Poore, A.G.B., Campbell, A.H., Coleman, R.A., Edgar, G.J., Jormalainen, V., Reynolds, P.L., Sotka, E.E., Stachowicz, J.J., Taylor, R.B., Vanderklift, M.A., Emmett Duffy, J., 2012. Global patterns in the impact of marine herbivores on benthic primary producers. Ecol. Lett. 15 (8), 912–922.

Porzio, L., Buia, M.C., Hall-Spencer, J.M., 2011. Effects of ocean acidification on macroalgal communities. J. Exp. Mar. Biol. Ecol. 400 (1–2), 278–287.

Post, E., Pedersen, C., 2008. Opposing plant community responses to warming with and without herbivores. Proc. Natl. Acad. Sci. 105 (34), 12353–12358.

Riebesell, U., 2008. Climate change: acid test for marine biodiversity. Nature 454 (7200), 46–47.

Riebesell, U., Fabry, V.J., Hansson, L., Gattuso, J.-P. (Eds.), 2010. Guide to Best Practices for Ocean Acidification Research and Data Reporting. Publications Office of the European Union, Luxembourg.

Sala, E., Kizilkaya, Z., Yildirim, D., Ballesteros, E., 2011. Alien marine fishes deplete algal biomass in the Eastern Mediterranean. PLoS One 6 (2), e17356.

Sala, E., Ballesteros, E., Dendrinos, P., Di Franco, A., Ferretti, F., Foley, D., Fraschetti, S., Friedlander, A., Garrabou, J., Güçlüsoy, H., Guidetti, P., Halpern, B.S., Hereu, B., Karamanlidis, A.A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S., Micheli, F., Pais, A., Riser, K., Rosenberg, A.A., Sales, M., Selkoe, K.A., Starr, R., Tomas, F., Zabala, M., 2012. The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. PLoS One 7 (2), e32742.

Shaw, E.C., Munday, P.L., McNeil, B.I., 2013. The role of CO_2 variability and exposure time for biological impacts of ocean acidification. Geophys. Res. Lett. 40 (17), 4685–4688.

Vergés, A., Alcoverro, T., Ballesteros, E., 2009. Role of fish herbivory in structuring the vertical distribution of canopy algae *Cystoseira* spp. in the Mediterranean Sea. Mar. Ecol. Prog. Ser. 375, 1–11.