



# 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<sub>2</sub> effects to determine benthic community structure. Here, an exclusion experiment was used to test effects of herbivory in benthic communities along a pCO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sup>+</sup> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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).

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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  $p\text{CO}_2$  increases (Bray et al., 2014; Calosi et al., 2013). Although increasing  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$  levels predicted for the end of this century, but that fleshy algae outcompeted them at elevated  $\text{CO}_2$  levels (Kroeker et al., 2013). In a comparison of tropical and temperate  $\text{CO}_2$  seep systems, Johnson et al. (2012) found that *Padina* spp. thrived at high  $\text{CO}_2$  levels despite dissolution of their carbonate layer and postulated that this was possible because their main grazers (sea urchins) were unable to tolerate high  $\text{CO}_2$  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  $\text{CO}_2$  (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  $\text{CO}_2$  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  $p\text{CO}_2$  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  $p\text{CO}_2$  (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  $\text{HgCl}_2$  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  $p\text{CO}_2$ ,  $\text{HCO}_3^-$ ,  $\text{CO}_3^{2-}$ ,  $\Omega_{\text{Ar}}$  and  $\Omega_{\text{Ca}}$  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<sup>2</sup> 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

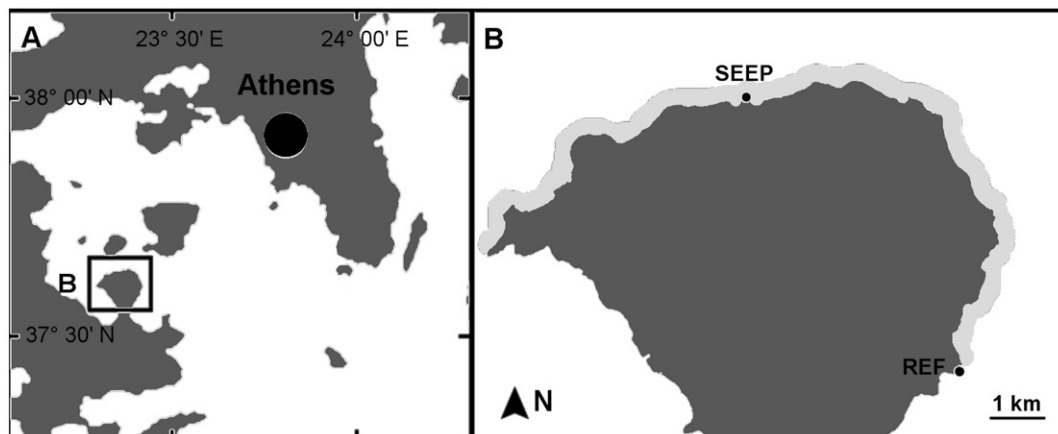


Fig. 1. Study sites (points) and area where pH was more variable than at reference site (light grey).

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