



Indirect effects may buffer negative responses of seagrass invertebrate communities to ocean acidification



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ABSTRACT

Ocean acidification has been shown to have highly variable effects, with many negative and some positive responses from individual species, while community level effects are largely unknown. Although an overall loss of biodiversity is expected, predicting the effects of ocean acidification on whole assemblages can be problematic as both direct and indirect effects of acidification must be taken into consideration. This study demonstrates how invertebrate assemblages associated with the highly productive seagrass, *Posidonia oceanica*, respond to natural acidification that occurs at CO₂ vents off the coast of Italy. We examined seasonal differences in invertebrate community structure between two distinct pH zones: control (pH 8.1) and acidified (pH 7.8) and show that many groups of invertebrate taxa were robust to acidification effects. Differences in community structure appeared to be driven by the indirect effects of acidification, such as changes to canopy structure and food availability, rather than physiological intolerance to low pH. The number of invertebrates collected in acidified stations was almost double that of control stations during the study and many heavily calcified species appeared to thrive. These results highlight how positive indirect effects may buffer the ecological impacts of acidification, and provide evidence that this highly productive, nearshore habitat may provide refuge to its associated communities from future ocean acidification.

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1. Introduction

The pH of ocean surface waters is decreasing, as a result of rising concentrations of atmospheric CO₂ (Brewer, 2013). A large quantity of anthropogenic CO₂ has been absorbed by the oceans, leading to changes in ocean carbonate chemistry. Dissolved inorganic carbon (DIC) can exist in three forms; aqueous carbon dioxide (CO_{2(aq)}), bicarbonate (HCO₃⁻) and carbonate (CO₃²⁻). This increase in DIC leads to a subsequent reduction in carbonate ions (CO₃²⁻) and the calcite (Ω_{cal}) and aragonite (Ω_{arg}) saturation states of the water (Fabry et al., 2008). Secondly this shift in carbonate chemistry leads to an increasing concentration of protons (H⁺) and a subsequent decrease in pH. Increased concentration of DIC has pushed the pH of ocean surface waters from approximately 8.2 in pre-industrial times down to current values of 8.1 (Raven et al., 2005). A further drop of 0.2–0.4 units is expected by the end of this century (Caldeira and Wickett, 2005; IPCC, 2007). These changes to

carbonate chemistry and pH have been collectively termed “ocean acidification” (OA) (Doney et al., 2009).

Invertebrate communities are highly susceptible to the effects of OA (Fabricius et al., 2014; Kroeker et al., 2011). Calcifying organisms are important components of benthic marine communities, and appear to be most affected by OA. In response to a decrease in calcite and aragonite saturation states, a reduction in calcification and an increase in carbonate dissolution rates has been observed in different calcifying invertebrate taxa such as echinoderms (Dupont et al., 2008), and molluscs (Gazeau et al., 2007; Ries et al., 2009). This decline in calcification is not uniform across taxa and some species have shown no response to OA (Comeau et al., 2013b; Ries et al., 2009; Rodolfo-Metalpa et al., 2011), whilst others have been shown to increase their calcification rates (Ries et al., 2009). This variation in response is now recognised and experiments show some species may be able to actively control extracellular pH through ion transport, actively converting HCO₃⁻ to CO₃²⁻ at the site of calcification (Calosi et al., 2013; Melzner et al., 2009; Ries et al., 2009). Further evidence suggests that some marine calcifiers may be able to tolerate low pH by utilising HCO₃⁻ for calcification, and therefore compensate for the decrease in CO₃²⁻ caused by OA (Comeau et al., 2013a; Iglesias-Rodriguez et al., 2008). Organisms that have a protective external organic layer may be more tolerant to low

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pH (Lombardi et al., 2011; Ries et al., 2009; Rodolfo-Metalpa et al., 2011). However, some forms of tolerance to OA may come at a cost. For example the brittlestar, *Amphiura filiformis*, was demonstrated to up-regulate metabolism and calcification in response to OA but this response led to muscle loss, reducing fitness and making long-term tolerance unsustainable (Wood et al., 2008).

OA will not only affect calcification but can have negative effects on the survival, growth, reproduction, metabolic function and respiration of many marine organisms (reviewed in Kroeker et al., 2010; Widdicombe and Spicer, 2008). Again, responses can be extremely varied. For example growth and reproduction were depressed in the shrimp, *Palaemon pacificus*, in response to long-term acidification (Kurihara et al., 2008), whilst no response in terms of growth and reproduction were observed in the barnacle, *Amphibalanus amphitrite* (McDonald et al., 2009). Metabolic depression was observed in the mussel, *Mytilus chilensis* (Navarro et al., 2013), whilst increased metabolism was observed in Antarctic krill, *Euphausia superba* (Saba et al., 2012). These metabolic responses may be caused by stress: the mussel's decreased metabolic rate may be due to extracellular acidosis (Michaelidis et al., 2005), whilst the krill may increase metabolic function to cope with increased physiological costs of maintaining homeostasis (Saba et al., 2012).

Whilst direct effects of changes in carbonate chemistry will be important in structuring marine communities, indirect effects will also play an important role (Russell et al., 2012). These indirect effects may include changes to the attributes of habitat-forming species (such as seagrasses) and other associated communities (epiphytes), thus affecting food and shelter availability for mesograzers (Gartner et al., 2013). Other indirect effects may occur through changes in biotic relationships (competition, grazing, predation etc), due to changes in species distribution and abundance (Hofmann et al., 2010; Kroeker et al., 2011, 2013a). This variation in species 'tolerance' or 'sensitivity' to low pH, coupled with uncertainties in how species interactions will change, makes it difficult to predict the outcome for invertebrates at the community level (Garrard et al., 2013).

A few studies have addressed the response of multispecies assemblages to OA, one of which was conducted using the natural CO₂ gradient at Ischia, Italy. This study highlighted that at very low pH levels (lower than those predicted for 2100) an abrupt ecosystem shift to an invertebrate community dominated by a few species occurs (mainly amphipods and polychaetes), with a loss of many calcifying species, reduced community biomass, and a simplified trophic structure (Kroeker et al., 2011). A similar study on the response of invertebrates to natural acidification at coral reefs in Papua New Guinea revealed a decrease in invertebrate density, although taxa such as echinoids and molluscs appeared tolerant (Fabricius et al., 2014). A decrease in calcifying species in response to acidification has been noted in a number of multi-species studies (Hale et al., 2011; Wootton et al., 2008).

Posidonia oceanica meadows host one of the most diverse benthic assemblages in the Mediterranean (Mazzella et al., 1992), and the majority of taxa are represented by calcifying organisms; molluscs, crustaceans, serpulid polychaetes and echinoderms. For this reason *P. oceanica* assemblages are expected to be sensitive to OA. Epiphytic cover of crustose coralline algae on *P. oceanica* has been shown to be extremely susceptible to vent induced acidification, (Martin et al., 2008). Natural CO₂ vents offer a model system to investigate the possible effects of OA on a complex community and important and widespread habitat. CO₂ vents at the Castello Aragonese, off Ischia (Tyrrhenian Sea, Italy) are not confounded by factors such as the discharge of heat or toxic substances (Hall-Spencer et al., 2008), and can be useful for providing information on changes in multispecies assemblages in response to OA (Kroeker et al., 2011).

In this paper we present an investigation that compares invertebrate community structure in control (pH 8.1) and acidified (pH 7.8) stations in *P. oceanica* beds at the Castello Aragonese, Ischia. Incorporating seasonality into understanding the effects of OA has been highlighted

as a key requirement of future OA studies (Godbold and Solan, 2013). This study was conducted over a year, using a systematic design and sampling at three time points to incorporate cold (March), warm (July) and intermediate (November) seawater temperatures, taking into account different morphological features of *P. oceanica* canopy, from its maximum development (July), in term of leaf area index and epiphytic cover, to the minimum cover (March). Our aim was to understand how acidification will affect invertebrate community structure and characterize any changes among different taxonomic groups, to gain further insight into the ecological effects of OA.

2. Methods

The CO₂ vents at the north and south of the Castello Aragonese allowed us to take a systematic approach to evaluating the effect of acidification on invertebrate communities. Studies were conducted at each of the CO₂ vents and control stations located within the same seagrass meadow but separated by at least 70 m and unaffected by the vents (see Table 1, Fig. 1). These CO₂ vents are the only ones known to vent into *P. oceanica* meadow, and this research represents a novel approach to assessing how seagrass-associated communities may respond to future acidification. Each station was approximately 60 m², an area chosen as preliminary investigation indicated that stations were sufficiently affected by the vents (pH <8.0) over this local area. Depth variation was not a confounding factor as all stations occurred a depth of 2.5–3.5 m. Ten water samples were collected bi-monthly between March and November 2011. Water samples were collected just above the canopy, as the high productivity of *P. oceanica* can alter pH conditions within the canopy (Hendriks et al., 2013). pH of samples was analysed within 4 h of collection at ambient seawater temperature (Millero, 1995). Measurements were made using a Mettler Toledo SG2 pH meter which measures to 0.01 units equipped with an InLab 413 electrode and calibrated regularly using NIST-traceable buffers. Although this approach does not measure the total hydrogen ion concentration, it measures the relative change in pH between sites (precision within 0.05 pH units: Zeebe and Sanyal, 2002). Temperature was continuously monitored using a HOBO data logger which was positioned between the northern control and acidified station throughout the year. Temperature varied between 14 – 29 °C, with warmest water occurring in August and coldest water temperatures in March and April. Temperature is not expected to differ between stations. The salinity regime around Ischia is typical for Tyrrhenian coastal waters and varies generally between 37.0 and 38.5 psu (Lorenti et al., 2005). For analysis of total alkalinity (TA) 10 samples were collected from each site on the 04/11/11. This was deemed sufficient as other studies have shown that TA shows little temporal variation at these sites (Cigliano et al., 2010; Rodolfo-Metalpa et al., 2010). Samples were filtered through GF/F Whatman filter paper and 0.02% mercuric chloride was added. They were then stored in the dark and later analysed using the Apollo SciTech Alkalinity Titrator Model AS-ALK2 and Batch 100 certified reference materials (Dickson et al., 2007). Other carbonate parameters were calculated using CO₂ SYS software (Lewis and Wallace, 1998).

To investigate benthic invertebrate assemblages, four randomly selected plots were sampled at each station in March, July and November 2011. All samples were collected within a four day sampling window to ensure that results were not influenced by longer term temporal variation. Plots were marked with buoys and different areas were sampled during each sampling period to prevent pseudoreplication. Samples were collected with an airlift sampler, as this is a non-destructive, quantitative and reproducible method which uses the discharged air from a scuba tank to dislodge and lift the macrofauna from around the seagrass blades, rhizomes and sediment surface into the net (400 µm) for collection. During sampling, the quadrat was framed by a 1 mm net to prevent escape of more motile invertebrates (e.g., crustaceans). Invertebrates were collected from a 40 x 40 cm plot, as this the optimal size for investigating invertebrate populations within a seagrass system (Buia et al.,

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