Marine Pollution Bulletin xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Tropical CO_2 seeps reveal the impact of ocean acidification on coral reef invertebrate recruitment

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ARTICLE INFO

Article history:
Received 23 August 2016
Received in revised form 30 November 2016
Accepted 11 December 2016
Available online xxxx

Keywords:
Marine invertebrates
Marine communities
Coastal habitats
Settlement
CO_2 seeps
Pacific Ocean

ABSTRACT

Rising atmospheric CO_2 concentrations are causing ocean acidification by reducing seawater pH and carbonate saturation levels. Laboratory studies have demonstrated that many larval and juvenile marine invertebrates are vulnerable to these changes in surface ocean chemistry, but challenges remain in predicting effects at community and ecosystem levels. We investigated the effect of ocean acidification on invertebrate recruitment at two coral reef CO_2 seeps in Papua New Guinea. Invertebrate communities differed significantly between 'reference' (median pH 7.97, 8.00), 'high CO_2' (median pH 7.77, 7.79), and 'extreme CO_2' (median pH 7.32, 7.68) conditions at each reef. There were also significant reductions in calcifying taxa, copepods and amphipods as CO_2 levels increased. The observed shifts in recruitment were comparable to those previously described in the Mediterranean, revealing an ecological mechanism by which shallow coastal systems are affected by near-future levels of ocean acidification.

1. Introduction

Atmospheric carbon dioxide concentrations increased from preindustrial levels of 280 ppm to 400 ppm in 2016, increasing oceanic uptake of CO_2 and lowering both the pH and the carbonate saturation level of surface waters (Gattuso et al., 2015). Concentrations of corrosive H^+ ions are now 30% higher than in the preindustrial age and are expected to be 150% higher by 2100 (Williamson and Turley, 2012). Seawater saturation states of aragonite and calcite are falling rapidly, making it more difficult for some organisms to maintain shells and exoskeletons and causing the expansion of areas that are corrosive to carbonates (Rodolfo-Metalpa et al., 2011; Chan and Connolly, 2013; Jackson et al., 2014).

Laboratory experiments have shown that the early life-history stages of a wide range of marine invertebrates are acutely vulnerable to elevated pCO_2 (Kurihara, 2008; Kroeker et al., 2013; Parker et al., 2013). Furthermore, key settlement processes of larval attachment and metamorphosis are affected to elevated pCO_2 (Ko et al., 2014; Dineshram et al., 2016). This has raised concerns that benthic recruitment from the meroplankton may be severely affected (Ross et al., 2011; Byrne, 2012; Weatherdon et al., 2015). To assess the likely effects of ongoing ocean acidification on larval success we need to factor in altered larval-substratum interactions (Doropoulos et al., 2012; Uthicke et al., 2013) and changes in organism interactions (Gaylord et al., 2015).

To date, the effects of ocean acidification on marine invertebrate recruitment remain poorly documented, although work at upwelling areas and at volcanic CO_2 seeps show that recruitment success at high seawater pCO_2 depends on a range of environmental factors (Thomsen et al., 2010). These acidified environments can be useful for investigations into the ecosystem effects of ocean acidification since they have gradients in seawater pCO_2 and carbonate saturation that provide 'space for time' analogs in environmentally realistic settings (Wernberg et al., 2012; Andersson et al., 2015). Coral reefs in waters with low carbonate saturation erode easily (Jackson et al., 2014) and surveys of reefs affected by CO_2 seeps have major declines in macrobenthic species richness in acidified waters (Fabricius et al., 2011, 2014; Enochs et al., 2015). We do not yet know how ocean acidification might affect invertebrate recruitment to coral reefs.

Here, we assessed the effects of elevated CO_2 on invertebrate recruitment and community development using artificial recruitment substrata to standardize habitat characteristics at CO_2 seeps on two coral reefs in Papua New Guinea. We compare our findings to data collected using similar methods at CO_2 seeps in Italy (Cigliano et al., 2010) to assess the

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http://dx.doi.org/10.1016/j.marpolbul.2016.12.031
0025-326X/

likely effects of ocean acidification on benthic invertebrate recruitment. Based on previous laboratory and field data on the effects of ocean acidification on early life-history stages and key settlement processes in marine invertebrates, we hypothesize that elevated CO_2 conditions will affect species composition and community structure, with the strongest effects observed in the recruitment of calcifying invertebrates.

2. Materials and methods

2.1. Study area and seawater chemistry

Invertebrate recruitment was investigated at 2–4 m depth on two coral reefs in Papua New Guinea (Fig. 1) where gas comprising 99% CO_2 was bubbling up through the sea bed into the water column (see Fabricius et al., 2015 for further details). The seeps have been active for at least 70 years and may be significantly older (Fabricius et al., 2011). Adjacent reference sites had ambient levels of CO_2 but were otherwise similar in terms of topography, geomorphology, wave exposure, temperature, alkalinity and salinity.

Two water chemistry data sets were collected. The first was pH logging data (from SBE 18 pH Sensors (Sea-Bird Scientific, Halifax) and SeaFET (Satlantic) sensors) deployed at reference, high CO_2, and extreme CO_2 stations at both reefs between April 2012 and November 2014. The second data set was from 863 individual seawater samples collected at reference, high CO_2, and extreme CO_2 stations at both reefs between 2011 and 2013. Each seawater sample from reference and high CO_2 stations at each reef was collected next to nylon scouring pads that we deployed as standard recruitment substrata (see below). Individual seawater samples collected from extreme CO_2 stations did not correspond to specific scouring pads. We took pH measurements of each seawater sample at the time of collection using a Mettler Toledo InLab Expert Pro pH electrode and a SG78 pH/Temperature meter (see Fabricius et al., 2014). A subset of 541 seawater samples from Dobu (reference: 64, high CO_2: 96, extreme CO_2: 22) and Upa Upasina (reference: 184, high CO_2: 148, extreme CO_2: 99) reefs were preserved in mercuric chloride for subsequent laboratory processing (see Fabricius et al., 2015). Total alkalinity (TA) and dissolved inorganic carbon (DIC) for 509 samples were determined with a Vindta 3C meter (Marianda, Kiel). In the remaining 32 samples total alkalinity was determined using a Metrohm 855 automated open cell potentiometric titrator (Metrohm AG, Herisau, Fangue et al., 2010). Using established chemical relationships, variables describing seawater carbonate chemistry (pCO_2, $\Omega_{aragonite}$ and $\Omega_{calcite}$) were calculated using the Seacarb v2.4.8 package in R (Lavigne and Gattuso, 2013).

2.2. Invertebrate sampling

We collected invertebrates using the same type of standardized recruitment substrata as Cigliano et al. (2010), i.e. 8 cm diameter scouring pads made of tightly rolled 0.25 cm^2 nylon mesh. The scouring pads were fixed at haphazard locations ~2 cm above the benthos at 2–4 m water depth along 50 m stretches of reef slope (Dobu reference: 11, high CO_2: 24, extreme CO_2: 11, Upa Upasina reference: 12, high CO_2: 23, extreme CO_2: 11) in January 2013. After 116–127 days they were removed and preserved. In the laboratory, the nylon netting was unrolled and rinsed on a 500 μm sieve. Material retained by the sieve was stored in 70% industrial methylated spirit before examination under a ×40 stereomicroscope. A total of 75,889 invertebrates were removed and sorted into 30 taxa. Identification to a greater taxonomic resolution was not possible as the region is exceptionally species-rich with many species undescribed, and comprehensive identification keys were unavailable. A subsample of 4644 invertebrates from 15 randomly selected artificial recruitment substrata from Dobu reef (5 per station) were

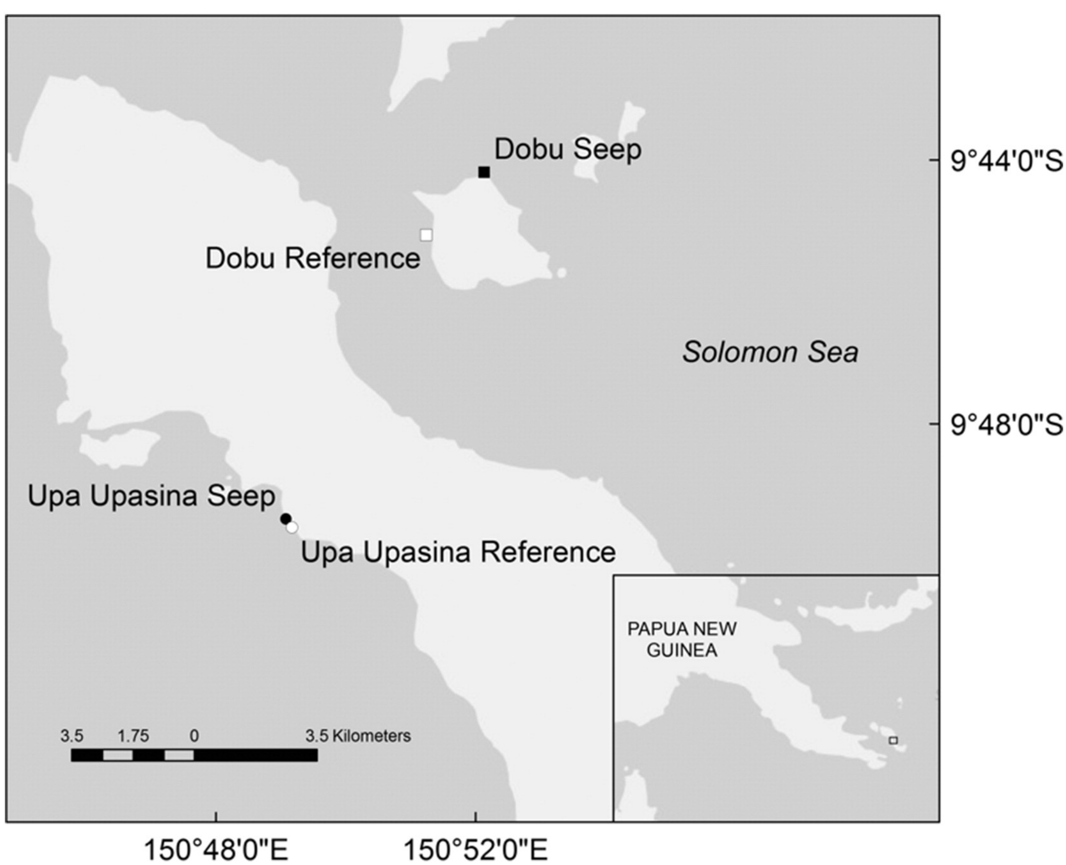

Fig. 1. Milne Bay Province in eastern Papua New Guinea showing two sets of reference sites (white filled) plus high CO_2 and extreme CO_2 stations (black filled).