PERSPECTIVE

Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems?

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Scleractinian cold-water corals, sometimes referred to as deep-water or deep-sea corals, form perhaps the most vulnerable marine ecosystems to the human dependence on burning fossil fuels (Guinotte et al. 2006). While cold-water corals were discovered two centuries ago, their significance in habitat formation is only just emerging with the deployment of manned and unmanned submersibles and the development of advanced acoustics to map their distribution (Hovland et al. 2002; Roberts et al. 2005; Grasmueck et al. 2006; Fig. 1a). They are found throughout the world oceans, usually between approximately 200–1,000+ m depth, and unlike many warm-water corals do not contain photosynthetic symbiotic algae (Freiwald 2002 and see papers within Freiwald and Roberts 2005). They are long-lived (several 100 s of years old), form reef frameworks that persist for millennia and are thought to

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experience relatively little environmental variability (reviewed by Roberts et al. 2006). Reef-like structures can be sizable (e.g., the Røst *Lophelia* Reef off northern Norway is 100 km^2 with some parts reaching 30 m off the seabed) and may cover a similar or even greater proportion of the oceans as warm-water coral reefs (Mortensen et al. 2001; Freiwald and Roberts 2005; Guinotte et al. 2006; Fig. 1c). Whilst only around 6 out of the 700 known species act as reef framework-forming species in deep waters, these deep-water reef structures are biodiversity hotspots and play an important role as a refuge, feeding ground and nursery for deep-sea organisms, including commercial fish (Rogers 1999; Fosså et al. 2002; Husebø et al. 2002). Little is known about the feeding behaviour of cold-water corals, but they are thought to depend on zooplankton and organic matter that sinks from the productive euphotic zone or organic matter laterally transported by currents for their nutritional requirements (Duineveld et al. 2004; Kiriakoulakis et al. 2004). They are therefore sensitive to changes in currents, surface ocean productivity and the strength of the biological pump of particles to deeper waters. Their slow growth and limited ability to recover make them particularly vulnerable to anthropogenic activities such as bottom trawling, seabed mining, cable and pipe laying, and oil and gas exploration. Some NE Atlantic deep-water reefs have now been severely damaged by bottom trawling (Rogers 1999; Roberts et al. 2000; Fosså et al. 2002; Hall-Spencer et al. 2002; Reed 2002; Freiwald et al. 2004; Wheeler et al. 2005).

High atmospheric carbon dioxide concentrations caused by emissions from fossil fuel burning are now recognised to be the major cause of global warming, but these emissions are also acidifying our oceans (IPCC 2007). The oceans are a massive reservoir for CO_2 and there is a flux
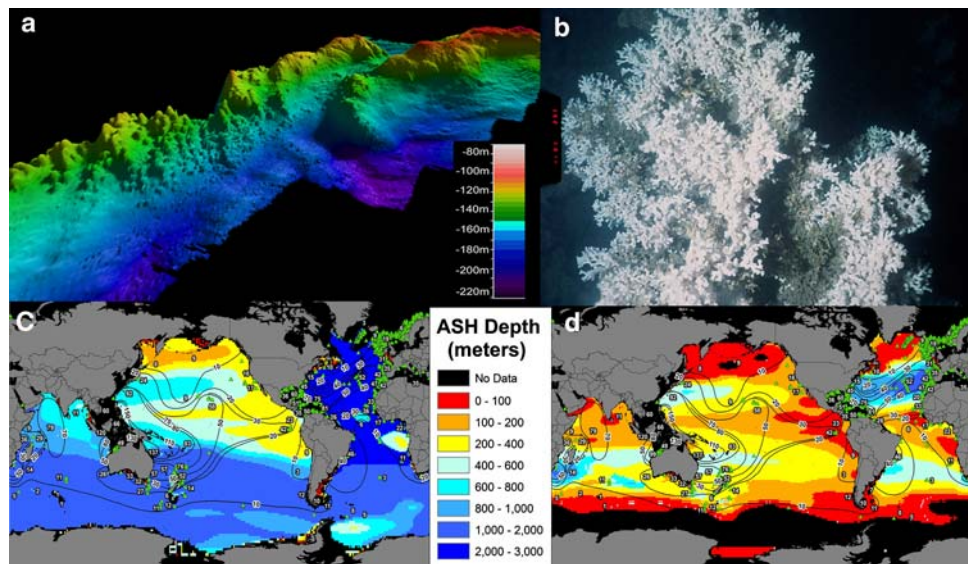
Fig. 1 a Multibeam echosounders can be used to identify and characterise cold-water coral reefs. Three-dimensional bathymetry, exaggerated sixfold in the vertical, showing the many seabed mounds formed by *Lophelia pertusa* reefs of the Mingulay Reef Complex, north east Atlantic (Roberts et al. 2005). **b** Photograph of a *L. pertusa* colony from these mounds. **c** Projected aragonite saturation horizon (*ASH*) depth for year 1765, $pCO_2 = 278$ ppmv and **d** projected ASH depth for year 2099, $pCO_2 = 788$ ppmv. *Green triangles* are locations of six deep-sea bioherm-forming coral species (*L. pertusa*, *Madrepora oculata*, *Goniocorella dumosa*, *Oculina varicosa*, *Enallopsammia profunda*, *Solensomilia variabilis*). *Black areas* appearing in the Southern Ocean and North Pacific in **d** indicate areas where ASH depth has reached the surface. *Contour lines* show species diversity for all azooxanthellate corals. *Numerals* not falling on diversity contours indicate number of azooxanthellate coral species. Figures 1c, d are from Guinotte et al. (2006)

of CO_2 across the interface between the ocean surface and atmosphere (Royal Society 2005). The oceans are a sink for anthropogenic CO_2 and have already taken up nearly half of the atmospheric CO_2 that humans have produced over the last 200 years and will continue to do so as CO_2 emissions increase (Caldeira and Wickett 2003; Sabine et al. 2004). While ocean CO_2 uptake is essentially buffering climate change, ocean chemistry is changing (Wolf-Gladrow et al. 1999) through the following simple chemical reactions:

$$CO_2 + H_2O \leftrightarrow HCO_3^- + H^+ \leftrightarrow CO_3^{2-} + 2H^+$$
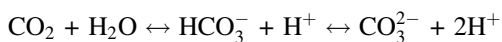
Ocean pH has already fallen by 0.1 unit and is set to fall another 0.3–0.4 units by the year 2100 and 0.67 by 2300 if we continue to burn fossil fuels at current rates (Calderia and Wickett 2003). Fifty-five million years ago, at the Paleocene–Eocene thermal maximum (PETM), an acidification event on the scale of the projected future changes resulted in the extinction of a large proportion of benthic calcifiers (Zachos 2005). However, the rate of change of the current event (decades to centuries) is far more rapid than the PETM event (several thousands of years); so much so that ocean pH by 2050 will be lower than for around 20 million years (Turley et al. 2006). Along with the decline in surface ocean pH a substantial change to carbonate chemistry will occur, including a decline in

carbonate ion concentration (Kleypas et al. 1999; Feely et al. 2004; Royal Society 2005). Aragonite and calcite are the main calcium carbonate crystal structures formed by marine calcifying organisms to make their shells, liths and skeletons. The impact of future decreases in aragonite and calcite saturation (Feely et al. 2004; Orr et al. 2005) on marine calcifiers has concerned many scientists and has the potential to alter marine food webs (Royal Society 2005; Haugen et al. 2006; Kleypas et al. 2006; Turley et al. 2006). Aragonite is more soluble than calcite and therefore aragonitic organisms such as scleractinian corals are most vulnerable and will be among the first organisms to be impacted by lower saturation state. A number of independent experiments on warm-water zooxanthellate corals have shown them to be sensitive to lower aragonite saturations with 9–66% and 13–83% reduction in their ability to calcify in high CO_2 waters of 2× pre-industrial and 3× pre-industrial levels, respectively (reviewed in Kleypas et al. 2006). A direct relationship between calcification and carbonate ion concentration is now emerging as results from these different studies are combined.

Future projections of global aragonite saturation state indicate that while warm-water corals will experience lower saturation levels and may suffer from reduced calcification it is the cold-water corals that are likely to experience under-saturated conditions with respect to aragonite (Orr et al. 2005; Guinotte et al. 2006). The shoaling

of the aragonite saturation horizon (ASH), the depth between saturated and under-saturated waters, is predicted to occur in polar waters within the century (Orr et al. 2005). Guinotte et al. (2006) has estimated that 70% of known scleractinian cold-water coral ecosystems will be in under-saturated water by 2100 (Fig. 1c, d) although some will experience aragonite under-saturation as early as 2020. It would seem unlikely that scleractinian cold-water corals would be able to calcify under these conditions, it would be more likely that aragonitic structures would experience dissolution. Indeed, if cold-water corals respond in the same way as warm-water coral species where a substantial decrease in calcification occurred with relatively small reductions in aragonite saturation state (reviewed in Kleypas et al. 2006), then their calcification rates may decrease well before aragonite under-saturation occurs. Unlike warm-water corals, there have been no published experimental results on the impact of higher seawater CO_2 concentrations on cold-water corals. This is partly due to their relative inaccessibility but also because few researchers are working on these deep-water ecosystems.

Carbonate chemistry and the depth of the ASH vary by ocean basin and could be limiting the distribution of cold-water scleractinian corals in certain regions of the world's oceans (Guinotte et al. 2006). The ASH in the North Atlantic is deep (>2,000 m) and numerous well-developed cold-water scleractinian ecosystems have been discovered in the region. Few records of cold-water frame-work forming corals exist from the North Pacific where the ASH is shallow (50–600 m) (see Feely et al. 2004). Large, reef-like structures similar to those found in the North Atlantic are curiously absent in the North Pacific, a region dominated by soft coral ecosystems, which suggests that aragonite saturation state is limiting scleractinian distribution and calcification rates (Guinotte et al. 2006). Ancient giant carbonate mounds, structures formed by successive periods of reef development, sedimentation and erosion, are impressive storehouses of coral skeletal remains that provide proxy records of temperature and ocean ventilation history. Their usefulness for the reconstruction of paleo-climate history is now emerging (Roberts et al. 2006).

Researchers studying cold-water and warm-water corals can benefit from information exchange and collaboration, as there remain significant unanswered questions on cold-water coral ecosystems and a dearth of scientists work on them. Direct laboratory and field experiments on the major scleractinian cold-water corals reef builders are urgently needed to see whether the relationship of decreasing coral calcification and increasing pCO_2 is similar to that seen for the warm-water corals (Kleypas et al. 2006). The extensive knowledge of fish-coral association in warm-waters might be able to help formulate testable hypotheses for cold-water coral-fish associations. While there is evidence that

Lophelia reefs and giant carbonate mounds support a characteristic fauna several times as diverse as that found on the surrounding seabed (Rogers 1999; Husebø et al. 2002; Henry and Roberts 2007) we know very little about the functional relationships between these animals, nor what the impact of ocean acidification will mean for cold-water coral-associated fish and other species.

Increased greenhouse gases are causing the oceans to warm and become more acidic at unprecedented rates (IPCC 2007). The paleo record tells us that scleractinians have survived several mass extinction events, but in all cases took several millions of years to recover (Stanley and Fautin 2001; Stanley 2003; Veron 2007). It now seems likely that perturbations in the carbon cycle, most likely resulting in ocean acidification, has played a fundamental role in all major mass extinctions of the Scleractinia (Veron 2007). However, the extremely rapid release of anthropogenic CO_2 from fossil fuel deposits is unprecedented in geological history and risks fundamentally perturbing deep-water coral ecosystems before the scientific community has begun to map and understand them.

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