Cold-Water Corals in an Era of Rapid Global Change: Are These the Deep Ocean's Most Vulnerable Ecosystems?

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Abstract

Cold-water corals create highly complex biogenic habitats that promote and sustain high biological diversity in the deep sea and play critical roles in deep-water ecosystem functioning across the globe. However, these often out of sight and out of mind ecosystems are increasingly under pressure both from human activities in the deep sea such as fishing and mineral extraction, and from a rapidly changing climate. This chapter gives an overview of the importance of cold-water coral habitats, the threats they face and how recent advances in understanding of both past and present cold-water coral ecosystems helps us to understand how well they may be able to adapt to current and future climate change. We address key knowledge gaps and the ongoing efforts at national and international scales to promote and protect these important yet vulnerable ecosystems.

Keywords

Cold-water coral • Ocean acidification • Aragonite saturation horizon • *Lophelia pertusa* • Conservation

36.1 Introduction

Corals are a highly diverse and evolutionarily adaptable group, with more than 5000 species described to date. Of these around 65 % are found in waters greater than 50 m deep (Cairns 2007; Roberts et al. 2009) and among this hidden coral diversity are the habitat forming cold-water corals.

Given suitable substrate and food supply conditions cold-water corals can develop elaborate framework reefs (primarily corals from the order Scleractinia) or extensive coral gardens (primarily corals from the orders Octocorallia and Stylasteridae) which provide highly complex biogenic habitats for other species and thus play critical roles in deep-water ecosystem functioning across the globe.

Targeted research on cold-water corals began to grow exponentially in the late 1990s, as technological developments brought their deep-sea habitats within the range of underwater remotely operated vehicles (ROVs). This revealed physically complex cold-water coral ecosystems that promote and sustain a biological richness in the deep sea unrivalled by many other ecosystems, and produced a step change in scientific understanding and public awareness of these remote areas (Fig. 36.1). Cold-water corals support a rich variety of lifeforms. At a microbial level bacterial and fungal biofilm communities encrust coral surfaces. Grazers, deposit feeders and small benthic predators forage among the polyps and branches of corals. Larger coral surfaces are colonized by sessile active and passive suspension feeding
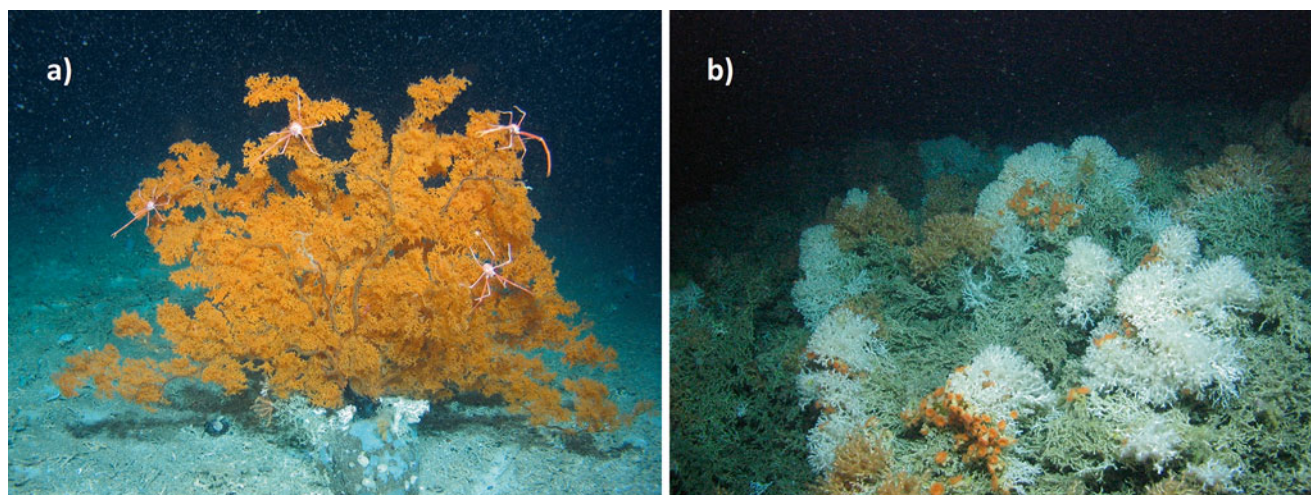
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Fig. 36.1 Examples of (**a**) anomuran crustaceans on a *Leiopathes* sp. (Order Antipatharia) in a coral garden and (**b**) a *Lophelia pertusa* reef both at the Logachev mounds West of the UK and Ireland (Photographs taken during the 2012 Changing Oceans Expedition, RRS *James Cook* cruise 073 (Roberts and shipboard party 2013))

epifauna and a variety of teleost and elasmobranch fishes use cold-water coral habitats to forage, to seek refuge and to breed. Many species have mutualistic or commensal symbiotic relationships with the corals or other associated fauna, such as the well-known mutualistic relationship between the scleractinian cold-water coral *Lophelia pertusa*, the dominant framework building coral in the North Atlantic and the eunicid polychaete *Eunice norvegica* (Roberts 2005). Actinarians live on the glass sponge *Aphrocallistes* sp. in a commensal relationship in cold-water coral reef habitats constructed by *Lophelia pertusa* and *Enallopsammia profunda* in the Campeche Bank area in the southern Gulf of Mexico (Hebbeln et al. 2014), and further research may identify a mutual benefit to the hard corals themselves such as protection of coral surfaces from grazers. Just over half of symbioses with cold-water corals tend to be obligate parasites, a relationship most strongly pronounced with gorgonian hosts (Buhl-Mortensen and Mortensen 2004).

The biodiversity hotspots provided by cold-water corals are in part explained by the close interactions between seafloor topography and impinging water currents that drive enhanced food flux (Davies et al. 2009). This biophysical coupling supplies high quality food to deep-sea organisms that is otherwise scarce or erratic in supply. Critically, the combined persistence of this physical complexity, stability, and the flow of carbon and nutrients through these habitats is vital to maintaining such high levels of biodiversity. The significantly higher levels of biogeochemical cycling and respiration taking place in these habitats (Cathalot et al. 2015; Rovelli et al. 2015) in comparison to the surrounding seafloor contributes to the wider ecosystem functioning of the deep-sea biome and global carbon budgets, highlighting the importance of these largely unseen ecosystems. However,

whilst studies have provided glimpses into this incredible world, they have also revealed the extensive damage they have suffered from deep-sea bottom trawling and the vulnerability of cold-water corals and the biodiversity they support to climate change, in turn prompting international efforts towards their management and conservation (Roberts et al. 2009).

This chapter will give a brief overview of our understanding of cold-water coral biology and ecology in a changing environment (with a primary focus on the Scleractinia), and how the longevity of the corals and the structures they produce opens windows into the environments they experienced in the past. With research 20 years ago largely focused upon geological mapping and habitat characterization we are now entering an era when sound biological and ecological understanding of these habitats must underpin management across local, regional and global scales. With an ever expanding human population, the pressures on global resources are leading to increased fishing, mining and hydrocarbon extraction in the deep sea. Alongside the unprecedented threat of climate change, cold-water corals will be exposed to multiple stresses from anthropogenic activities and may be amongst the most vulnerable of marine ecosystems.

36.2 Cold-Water Corals in an Era of Rapid Global Change: Present-Day

It is now well established that anthropogenic carbon emissions are driving an unprecedented rise in global temperatures (IPCC 2013). For marine life this is coupled with ocean acidification, raising concerns for the future of calcifying species, such as corals. Much of the research to date has

focused on tropical corals and implies that rising seawater temperatures are the more immediate threat to shallow reefs, leading to wide scale bleaching events (Frieler et al. 2013). For deeper dwelling cold-water corals however, the effects of elevated CO_2 on seawater carbonate chemistry are likely to have more impacts in the immediate future than for their shallow water counterparts (Hennige et al. 2014a). This is because the distribution of the coral reefs of the deep sea is highly dependent, at the global scale, on seawater carbonate chemistry (Guinotte et al. 2006), as corals require aragonite and calcite, polymorphs of calcium carbonate, to build their skeletons. Both these compounds are supersaturated in surface waters but become less saturated with depth largely due to the effect of pressure on the $CaCO_3$ solubility constant. Variations in in situ CO_3^{2-} concentration result in the saturation horizon for $CaCO_3$ being found at different depths in different ocean basins, and due to the different solubility of $CaCO_3$ polymorphs, seawater becomes undersaturated firstly for aragonite (termed the aragonite saturation horizon, ASH) and then for calcite (the calcite saturation horizon) as depth increases (Cairns 2011). In ocean basins with higher calcium carbonate saturation states the depths to which aragonitic corals can persist are far greater, helping in part to explain the proliferation of scleractinian reef framework forming corals in the Atlantic (Guinotte et al. 2006; Roberts et al. 2006). Areas of the global ocean with naturally lower CO_3^{2-} and hence calcium carbonate saturation states, such as the north Pacific, support far fewer aragonitic corals, but corals which build their skeletons from calcite can persist and also provide important structural habitats (Stone 2014). As atmospheric CO_2 levels rise, the oceans absorb more CO_2 and become more acidic (Zeebe and Wolf-Gladrow 2005). As a result, ocean pH has already fallen by 0.1 pH units and will likely fall another ~0.3 units by the end of the century (Caldeira and Wickett 2003). Such a pH decline shifts the distribution of dissolved carbon species away from CO_3^{2-} and hence directly impacts $CaCO_3$ saturation states (Feely et al. 2004; Orr et al. 2005). By 2100 the ASH will become sufficiently shallow to expose approximately 70 % of known aragonitic cold-water corals to corrosive waters undersaturated with respect to aragonite (Guinotte et al. 2006). Eventually the calcite saturation horizon will also shallow, exposing calcitic corals to corrosive conditions, but aragonitic corals face the more immediate threat. Given the importance of seawater carbonate chemistry for cold-water coral reef frameworks, and the direct relationship between aragonite saturation and atmospheric CO_2, they appear to be one of the most vulnerable marine ecosystems to present-day anthropogenic climate change.

Concerns about global CO_2 emissions were first raised in the 1950s and the Intergovernmental Panel on Climate Change (IPCC) was established in 1988. Whilst it was first identified in the late 1950s that changes in atmospheric CO_2 alters seawater carbonate chemistry (Revelle and Suess 1957), ocean acidification research only gathered momentum from 2000 onwards. There is now a large body of research examining how ocean acidification will impact tropical corals but there has been far less effort focused on understanding its effects on cold-water corals (Wicks and Roberts 2012), even though they are arguably more at risk than tropical corals, due to their depth range and thus proximity to corrosive waters. It remains unclear how coral calcification rates and other metabolic processes (e.g. feeding, respiration, reproduction) may be affected by ocean acidification, but several cold-water coral species are already periodically exposed to waters undersaturated with respect to aragonite (Langdon et al. 2000; Guinotte et al. 2006; Thresher et al. 2011; Henry et al. 2014a) and these populations are characterized by slow growth rates and therefore may have a limited ability to withstand the harsher environmental conditions that will become prevalent in a warmer and acidified future ocean.

Furthermore, whilst scleractinian corals can up-regulate their internal pH at the sites of calcification through energy intensive processes (Venn et al. 2009; Anagnostou et al. 2012; McCulloch et al. 2012a, b), the regulation only applies for coral skeleton that is covered by living coral tissue. Cold-water coral framework reefs are typically composed of a significant amount of bare, dead skeleton beneath the living material (Fig. 36.2) and this exposed dead skeleton will start to dissolve in undersaturated conditions, a process hastened by the increased efficiency of bio-eroding sponges in acidified seawater (Wisshak et al. 2012). Net reef accretion in aragonite-undersaturated conditions will thus only occur if coral calcification exceeds dissolution and bioerosion of exposed dead skeleton. This is critical to understand since the coral's skeletal framework provides important ecosystem functions and can persist for millennia after the coral has
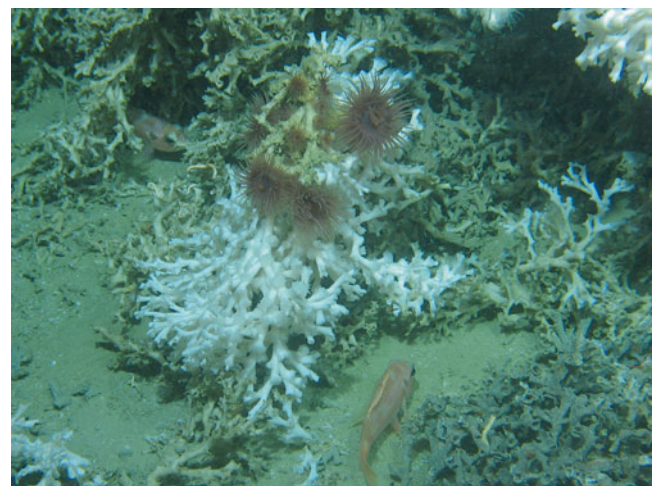

Fig. 36.2 Live *Lophelia pertusa* (*white*) growing on dead skeletons (*grey*) (Photograph taken during the 2012 Changing Oceans Expedition, RRS *James Cook* cruise 073 (Roberts and shipboard party 2013))

died. The ability and long-term sustainability of cold-water corals to survive and thrive below the ASH is currently a topic of active research.

36.2.1 Impacts of Climate Change on *Lophelia pertusa*

Lophelia pertusa is the most widespread and dominant reef framework building coral of the North Atlantic, and as such has been the focus of many of the cold-water coral studies to date. It is arguably the best understood cold-water coral species, but there are still significant gaps in the literature regarding the physiology and biology of this species. The general consensus from studies examining the response of *L. pertusa* to single stressors of ocean acidification or warming, and to a combined increased temperature and CO_2 treatment, is that considerable variability exists between individuals, but *L. pertusa* has the ability to acclimatize (Dodds et al. 2007; Form and Riebesell 2012; Hennige et al. 2014a, 2015; Lunden et al. 2014; Maier et al. 2009, 2013a, b; Movilla et al. 2014).

However, time scales are important when considering whether corals can acclimatize or not, as short-term experiments may produce results (including a detrimental impact of ocean acidification upon key processes) which may not appear in long-term studies, as organisms have undergone alterations in key regulatory processes to acclimatize (Widdicombe and Spicer 2008). This makes it very useful to compare both short and long term research and, with regard to *L. pertusa*, Fig. 36.3 highlights that the most significant changes in respiration and calcification only occur in the short term, from 24-h experiments to 4 weeks. Beyond 4 weeks, decreases in calcification and respiration (with regard to ocean acidification) are not observed (Form and Riebesell 2012; Maier et al. 2013a, b; Movilla et al. 2014). Likewise, for temperature, *L. pertusa* respiration increases following a 24-h exposure (Dodds et al. 2007) but is either unaffected or even decreases in 3–12 month exposures (Hennige et al. 2014a). Given that *L. pertusa* has only been demonstrated to be significantly impacted by ocean acidification and temperature in short term exposures (Form and Riebesell 2012; Hennige et al. 2014a; Lunden et al. 2014; Maier et al. 2009), we can infer from non-significant differences in longer term studies that corals readily acclimatize to their new undersaturated conditions. It is likely that in the days to months following a perturbation, energetic pathways in this species may prioritize protective or acclimation pathways as recorded in tropical coral species (Gates and Edmunds 1999).

Even when acclimatization has been demonstrated, it may come at a cost to other processes and may therefore not be sustainable in the long-term, in particular with regards to maintaining growth under ocean acidification. With this in mind, recent research has demonstrated that although growth rates continue as normal under low pH conditions, skeletal biomineralization, molecular-scale bonding, and skeletal structure all change (Hennige et al. 2015). The breakdown in the recognized positive linear correlation between respiration and calcification (Maier et al. 2013a) at the end of long term experiments (Hennige et al. 2015) may also indicate that 'normal' energetic strategies no longer apply in the long-term, possibly due to other processes using energetic reserves, and highlights that many processes may be occurring of which we have poor understanding, and/or cannot easily measure.

In addition to potential energetic implications for the live coral, the dead, exposed skeletal framework which supports the reef itself and provides habitat for a range of associated species (Roberts et al. 2009) may be at risk from ocean acidification. Exposed skeleton cannot acclimatize or adapt to future conditions, and its dissolution is a purely biogeochemical process (Eyre et al. 2014; Fig. 36.4). The dissolution and weakening of the exposed skeleton observed after long term ocean acidification exposure (Hennige et al. 2015) when combined with bio-erosion (Silbiger and Donahue 2015; Wisshak et al. 2012), may mean that reefs of the future may be smaller than they are currently, and consequently unable to support the rich biodiversity present today. While the ecologically significant ability of adult *L. pertusa* to skeletally fuse (Hennige et al. 2014b) helps strengthen the framework as a whole, the fact that over 95 % of cold-water coral reefs are found above the ASH depth (Guinotte et al. 2006) infers that, in the long-term, net reef growth cannot normally be maintained in undersaturated water.

36.2.2 Impacts of Climate Change on Other Cold-Water Coral Species

In studies to date the cosmopolitan solitary cold-water coral *Desmophyllum dianthus* has generally shown the ability to acclimate to ocean acidification (McCulloch et al. 2012a; Rodolfo-Metalpa et al. 2015; Naumann et al. 2013). Unlike *L. pertusa*, the geographic and bathymetric distribution of *D. dianthus* includes corrosive waters, for example in upwelling regions where the pH can be as low as 7.4 (Thresher et al. 2011; Anagnostou et al. 2012; McCulloch et al. 2012a; Jantzen et al. 2013; Fillinger and Richter 2013). This suggests that *D. dianthus* may be better adapted to deal with ocean acidification than *L. pertusa* and for this species ocean warming may be the greater threat from rising atmospheric CO_2. Indeed, bulk growth and calcification did not significantly differ in corals incubated for 2–11 months in acidified seawater (Movilla et al. 2014; Rodolfo-Metalpa et al. 2015). However,
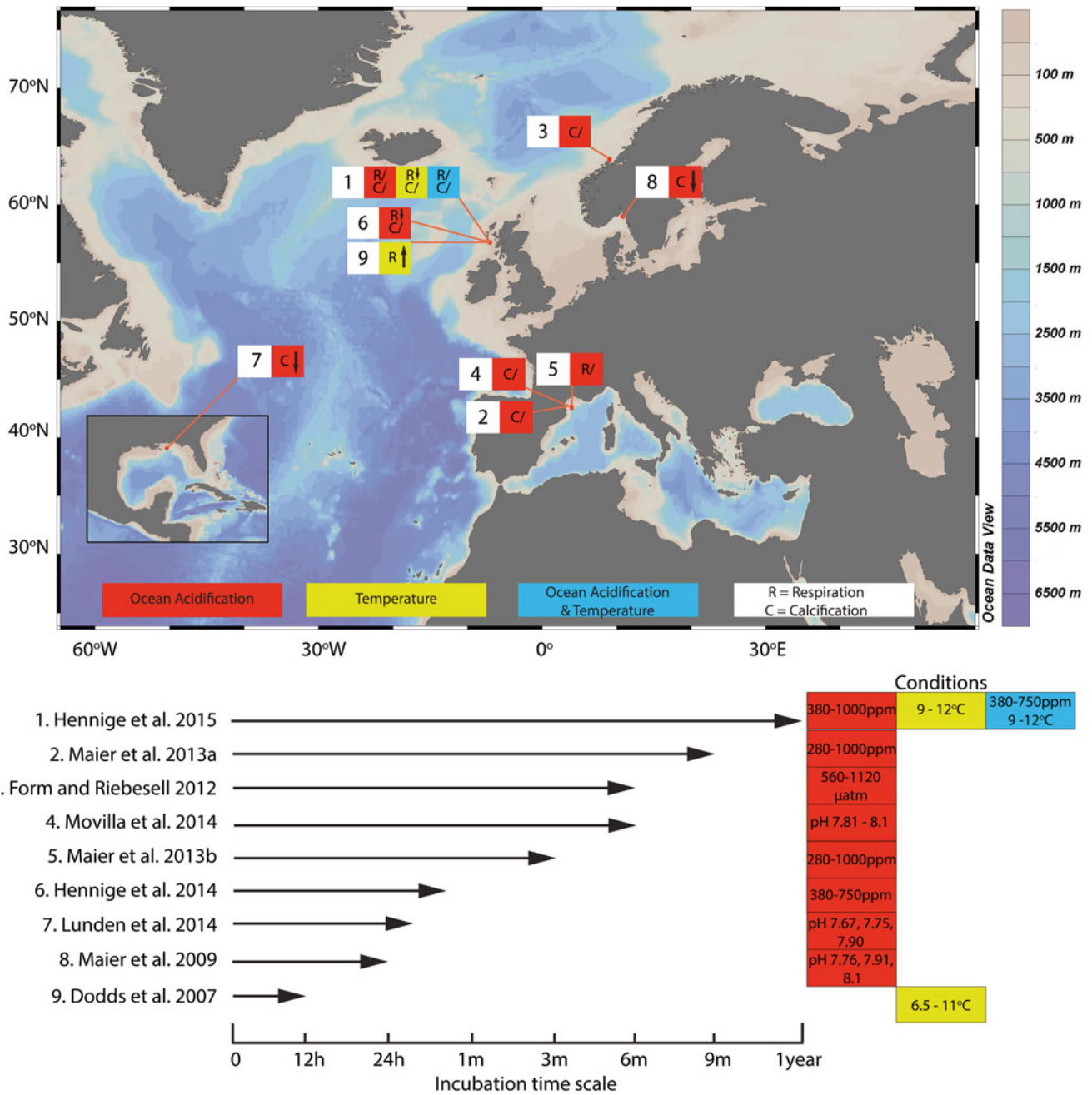
Fig. 36.3 Chart showing locations and summarizing physiological results from research on projected future impacts of temperature and ocean acidification on *Lophelia pertusa*. 'R', Respiration; 'C', calcification; '↑', an increase; '↓', a decrease; '/', no statistically significant change. *Symbols* represent experiment endpoint results, pH is recorded in the total scale (Adapted from Hennige et al. (2015))

these studies used mature polyps and younger, fast-growing polyps have been observed to reduce their growth rate after long incubations in acidified seawater (Movilla et al. 2014), possibly due to their energetic requirements for growth. In mature polyps, neither respiration nor ammonium excretion rates have been found to respond to seawater acidification (Carreiro-Silva et al. 2014), suggesting coral metabolism is unaffected. However the upregulation of genes involved in cellular calcification and energy metabolism in acidified seawater (Carreiro-Silva et al. 2014) imply that *D. dianthus* may maintain growth and metabolism by switching from a mixed use of protein and carbon-based substrates, to a carbohydrate or lipid-dominated metabolism. This highlights the need for more fully integrated assessments that consider the full implications of ocean warming and acidification on coral metabolism, energy budget and resource allocation.
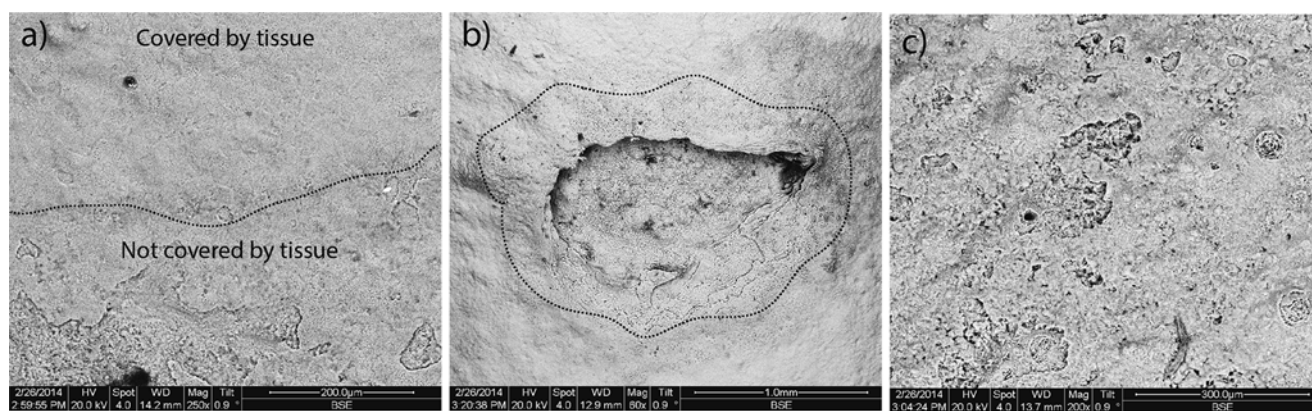
Fig. 36.4 Back Scattered Electron emission (BSE) of *Lophelia pertusa* skeleton fragments maintained in $\Omega_{Aragonite}$ <1. (**a**) The interface between tissue-protected skeleton (*top*) and exposed skeleton (*bottom*). The interface is highlighted with the *dashed line*. (**b**) A site of tissue damage on *L. pertusa*, and subsequent dissolution of skeleton in an otherwise protected area. *Dashed line* indicates the interface between tissue-protected and exposed skeleton. (**c**) Exposed section of skeleton (Adapted from Hennige et al. (2015))

36.3 Cold-Water Corals in an Era of Rapid Global Change: Looking to the Past to Predict the Future

Scleractinian corals arose in the Triassic 237 million years ago (Stanley 2003) with examples of today's characteristic cold-water coral fauna emerging from the Cretaceous onwards (Fig. 36.5). However, the coral fossil record is punctuated by several mass extinction events related to major perturbations in the global carbon cycle (Knoll et al. 1996; Veron 2008). Recent work is attempting to understand coral resilience to past and present climate change using an array of geochemical tools and proxies of seawater acidification, temperature and nutrient regimes as the geochemistry of the skeletons of cold-water corals may provide unique insights into the effect of ocean acidification and other stressors on coral survival. Scleractinian corals can be used as archives of seawater chemistry, as they deposit carbonate skeletons from a semi-isolated pool created and controlled by the coral, yet influenced by the external seawater environment (Tambutté et al. 2011; Comeau et al. 2013; Gagnon 2013). The isolation of the coral's calcifying space is made possible by the presence of cellular membranes, modifying seawater chemistry at the site of calcification (McConnaughey 1989; Adkins et al. 2003; Cohen and McConnaughey 2003) and also presenting a physical barrier to less saturated ambient conditions (Cohen et al. 2009). By looking to the past it may be possible to predict how cold-water corals will respond to the rapidly changing climate of today.

Boron isotopes ($\delta^{11}B$) are one such geochemical tool which have recently been used to study cold-water coral resilience to ocean acidification. As a tracer, boron is directly linked to seawater pH because its speciation (borate ion and boric acid) and the isotopic composition of the aqueous species are pH dependent (Zeebe and Wolf-Gladrow 2005; Klochko et al. 2006; Nir et al. 2015). There are a number of studies in cold-water corals that have used this proxy to study past ocean acidification events, coral calcification mechanisms and resilience (Blamart et al. 2007; Rollion-Bard and Erez 2010; Anagnostou et al. 2012; McCulloch et al. 2012b). Coral $\delta^{11}B$ composition is a recorder of calcifying fluid pH, as verified by microelectrode measurements (Al-Horani et al. 2003) and the use of a pH sensitive fluorescent indicator (Venn et al. 2011), and it has been suggested that cold-water corals record elevated pH to that of ambient seawater (Anagnostou et al. 2012; McCulloch et al. 2012b). This upregulation is not perfect because corals are unable to completely control their internal pH (if they were their $\delta^{11}B$ composition would have to be constant and independent of ambient seawater pH), however corals have been shown to elevate their calcifying fluid pH more when external pH is lower (Fig. 36.6). This ability is vital in allowing calcification to continue in conditions where carbonate ion concentrations are extremely low (aragonite saturation <1).

Although disentangling the mechanism of coral biomineralization is currently an active research area, using the available models (McConnaughey 1989; Zoccola et al. 2004) first approximations can be made to identify the energetic thresholds for maintaining the required calcifying fluid pH such that calcification can take place (Cohen et al. 2009; McCulloch et al. 2012a; Venn et al. 2013). Further development and expanding application of biological and geochemical tools to probe the pH of calcification may be key to understanding the chemical response of coral resilience to ocean acidification (Gagnon 2013). Further, the energetically demanding process of calcification could be assisted by elevated food availability counteracting the cost of ocean

Fig. 36.5 Temporal evolution of cold-water corals. Age indications derived from Gradstein et al. (2004). The bold line at 65 Ma marks the position of the end-Cretaceous mass extinction event (Adapted from Roberts et al. (2009))

Era	Period	Epoch	Stage		Million years before present
Cenozoic	Palaeogene	Eocene	Priabonian	Oldest *Enallopsammia, Goniocorella* and *Corallium*	34 / 37
		Palaeocene	Danian	Oldest *Lophelia*	61 / 65
Mesozoic	Cretaceous		Maastrichtian	Oldest *Madrepora*	
			Coniacian	Oldest deep-water hexactinellid (*Aphrocallistes*)	
			Cenomanian	Oldest deeper water coral thickets	99
			Albian	Oldest colonial dendophyliid coral (*Blastozopsammia*)	112
			Aptian	Oldest *Oculina*	121
			Barremian	Oldest dendrophyliid coral (*Palaeopsammia*)	125

acidification. Coral survival likely depends on a complex array of factors including the interaction of deep-water currents with surface primary productivity and seafloor topography to supply organic rich particles (Duineveld et al. 2004, 2007; Kiriakoulakis et al. 2004; Davies et al. 2009; Dodds et al. 2009), seawater oxygen concentrations (Thiagarajan et al. 2013), and temperature (e.g. McCulloch et al. 2012b). Therefore, to produce robust conclusions on the sensitivity of cold-water corals to ocean acidification, the roles of not only pH, but also nutrients, temperature, and oxygen all need to be considered in combination.

There is a long history of developing temperature proxies from scleractinian cold-water corals. Two emerging proxies with great promise are the Li/Mg ratio and clumped oxygen isotopic composition of coral skeletons. The Li/Mg proxy (Case et al. 2010; Montagna et al. 2014) is based on systematic patterns observed between Mg/Ca and Li/Ca in the various microstructural components of scleractinian cold-water corals. The combination of the two ratios, in the form of the Li/Mg ratio, seems to produce a relatively pure environmental signal, which in this case is principally temperature. Nevertheless, paleo-temperature reconstructions carry large uncertainties on
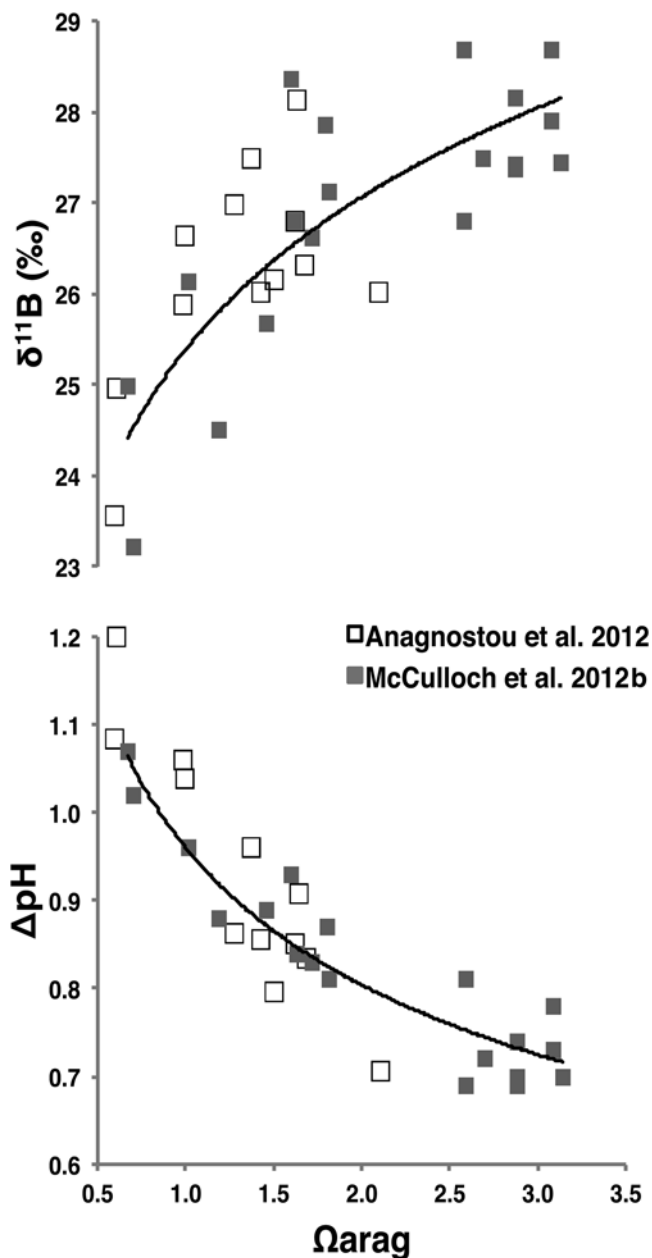
Fig. 36.6 pH upregulation as a function of aragonite saturation in scleractinian cold-water corals. *Top* panel shows the $\delta^{11}B$ measurements and *bottom* panel the pH elevation (=pH recorded – pH seawater)

the scale of ±1.6–1.8 °C and the current uncertainty regarding the exact nature of the relationship between Li/Mg and temperature (i.e. either linear (Case et al. 2010) or exponential (Montagna et al. 2014)) could lead to even larger errors. An alternative temperature proxy is the Δ_{47} (clumped isotopes of C and O in the carbonate skeleton (Thiagarajan et al. 2011)). This approach exploits the degree of disorder in the isotopologues of the C-O bonds of carbonates, and has been calibrated over a wide range of temperatures, although it is currently characterized by poor precision (up to ±2.8 °C equivalent).

In addition to these temperature proxies, the skeletons of *D. dianthus* have been proposed as a reliable recorder of seawater phosphate, a key nutrient. Coral carbonate P/Ca ratio is the only direct nutrient proxy described to date, and as such it holds great promise. An earlier study on this proxy (Montagna et al. 2006) was revised to obtain reliable deep-water nutrient compositions with an uncertainty of ±0.4 μmol kg^{-1} for the majority of intermediate oceanic waters (Anagnostou et al. 2011). Despite good field calibrations, the mechanism of phosphorus incorporation is still debated with NMR studies suggesting that the majority of phosphorus in corals is in the form of the inorganic phosphate in aragonite crystal defects (Mason et al. 2011). Application of the proxy requires fine scale sampling and thorough data filtering to account for the presence of different structural features and phosphate contaminants (Anagnostou et al. 2011; Mason et al. 2011), but novel sampling strategies offer high precision. Nonetheless, further work is needed to study the validity of the proxy in waters undersaturated for aragonite and in controlled incubation experiments.

Past environments hold a plethora of information on the effect of climate change on coral proliferation and demise. The skeletons of fossil scleractinian corals can be accurately dated using radiometric techniques (Lomitschka and Mangini 1999; Cheng et al. 2000; Douville et al. 2010; McIntyre et al. 2011; Longworth et al. 2013), and a number of proxies have been developed to reconstruct the corals' paleo-environment. When geochemical reconstructions are combined with records of coral density and distribution, insights into the synergistic effects among ocean acidification, nutrients and temperature on coral survival and growth can be revealed (Thiagarajan et al. 2013), assisted by genetic connectivity data providing further insights into cold-water coral dispersal and extinction at ocean basin scales (Henry et al. 2014b).

36.4   Knowledge Gaps

Despite the recent research advances, there are still major knowledge gaps to be explored before any certain inferences can be made as to the long-term survival and ecological role of cold-water coral reefs (Rodolfo-Metalpa et al. 2015).

36.4.1 Acclimatization Versus Adaptation

Whilst the ability of *L. pertusa* to acclimatize to ocean acidification conditions in laboratory mesocosms, albeit with subsequent impacts on its physiology, has been established; its ability to evolve and adapt to future conditions has not been addressed. *Lophelia pertusa*, like many long lived species has high levels of phenotypic plasticity which allow it to

thrive over a wide geographic distribution (Roberts et al. 2009) and research to date has focused on this species' ability to cope with ocean acidification within this existing plasticity. This acclimatization is important because although adaptation to changing conditions can occur over subsequent generations, the slow growth of cold-water corals coupled with the projected rapid change in ocean acidification and warming (CBD 2014a), means that reef survival will depend heavily on the acclimatization capacity of currently living cold-water corals. There is, however, a disconnect between laboratory observations where *L. pertusa* can survive and grow in acidified seawater and field observations as *L. pertusa* reefs have not been observed below the ASH (Guinotte et al. 2006), raising further questions over the ability of *L. pertusa* to acclimate or adapt to ocean acidification. Furthermore there is some debate as to whether the plasticity of long lived species like *L. pertusa* aids adaptation by extending the persistence of populations long enough to allow time for local adaptation (Jump and Penuelas 2005) and possibly by supplying an initial step in the evolutionary process (Pfennig et al. 2010; Reed et al. 2011) or if it impedes long-term adaptation to environmental change by delaying the onset of evolutionary responses (Ghalambor et al. 2007). Since the most likely future climate scenario involves changes in both temperature and CO_2 (IPCC 2013), it is vital to understand whether cold-water corals can acclimatize to multiple stressors simultaneously, what the cost is to other processes (Gates and Edmunds 1999), and whether they have the potential to adapt in the longer term. To assess the acclimatization and adaptation abilities of organisms, it is vital to conduct long-term experiments.

36.4.2 Reproduction

No experiments to date on cold-water corals have considered the impacts of climate change on reproductive fitness or connectivity. Early life stages are particularly vulnerable in a number of species (CBD 2014a), and this needs to be investigated in cold-water corals as a matter of urgency. However, there are serious logistical constraints with regard to this, as it is not feasible to collect fresh reproductive material at the time of spawning due to the often-unsuitable weather, and reliably harvesting gametes from aquaria-kept cold-water coral specimens has only recently been achieved (Larsson et al. 2014, Sect. 36.4.3). In the tropical coral *Acropora tenuis*, it has been demonstrated that fertilization success was negatively impacted by increased CO_2 (Albright and Mason 2013). It is therefore feasible to assume that similar effects may occur in cold-water corals, and acclimatization may not ensure the long-term survival of corals if reproductive fitness decreases.

36.4.3 Connectivity Between Populations

The only mechanism available for gene flow between geographically separate cold-water coral populations and for provision of new recruits to colonize new sites or recolonize damaged sites is the production of pelagic larvae. This connectivity, an important part of coral ecosystem function and resilience, is poorly understood, but the use of emerging genetic techniques integrated with geochemistry has provided some information on current and historical connectivity (Henry et al. 2014b). Gene flow between large ocean regions, Gulf of Mexico, coastal southern US, New England Seamounts and NE Atlantic, is restricted in North Atlantic *L. pertusa* populations (Morrison et al. 2011). Within regions however, connectivity has been shown across large distances, suggesting some larvae are widely dispersed. While there is evidence of long-range gene flow between some *L. pertusa* populations (Flot et al. 2013), there can be poor connectivity between reefs that are relatively close together, for example within the Norwegian fjords and the Skagerrak (Dahl 2013). To understand the fine detail of the connectivity suggested by genetic data, and predict how this connectivity might change under climate change we need to understand both the behavior of the larvae and the local hydrography. To date larval behavior remains the largest knowledge gap in attempts to understand cold-water coral population connectivity.

Lophelia pertusa larvae have not been observed in ocean plankton samples, possibly due to their small size and fragile nature, so knowledge of the larval behavior is restricted to laboratory studies. Successful fertilization of *L. pertusa* gametes and subsequent description of embryogenesis and larval development has recently been achieved in the laboratory (Larsson et al. 2014). The larvae survived for several weeks and showed a negative geotactic behavior, accumulating exclusively in the upper half or one third of experimental aquaria, even when kept in the dark. Measurements of swimming speed suggest the ability to move vertically in the water column sufficiently fast to reach the surface waters, even from deep cold-water coral reefs. If larvae can reach the surface they have the potential to travel hundreds of km before settling and models of larval dispersal in other species (e.g. Corell et al. 2012; Coscia et al. 2012) show dispersal, and hence connectivity, to be crucially dependent on larval depth distribution and vertical movement. Genetic connectivity studies of *D. dianthus* populations revealed that the genetic differentiation with depth is consistent with the stratification of water masses, suggesting that, for some coral species, larvae will be retained within, and rarely migrate between, different water masses (Miller et al. 2011). This implies that as the aragonite saturation horizon shallows, deep populations may be unable to colonize shallow water. Likewise, deep populations are unlikely to be able to act as refuges for

shallower populations impacted by fishing or mining activities. Furthermore, in addition to temperature rises and ocean acidification, changes in ocean and atmospheric circulation patterns are expected. Numerical model projections suggest that the Atlantic Meridional Overturning Circulation (AMOC) is likely to weaken over the twenty-first century (e.g. Cheng et al. 2013) while, in the northern hemisphere extratropics, models indicate changes to atmospheric circulation including a poleward shift and strengthening of the Atlantic storm tracks (Pinto et al. 2007; Gillett et al. 2013; IPCC 2013), although there is a great deal of uncertainty in these predictions (IPCC 2013). Any changes in ocean circulation are likely to impact on cold-water coral larval dispersal, and thus connectivity, and it remains unclear what the implications of this may be for the resilience of these species in a changing ocean.

36.5   Conservation and Policy

Conserving cold-water coral habitats is challenging, in part because of the nature of the threats they face, from deep sea trawling to climate change, and in part because many of the known reefs and coral gardens occur beyond the limits of national jurisdictions and thus require international legal frameworks and efforts to manage and protect these ecosystems. Furthermore, deep-sea habitats are often out of sight and out of mind and therefore "invisible" to the public and policy makers alike who are not readily aware of the goods and services they supply.

Cold-water coral reef frameworks can attract and concentrate commercially valuable fish species but are highly susceptible to damage from heavy fishing gear and very slow to recover (Ramirez-Llodra et al. 2011). The extent of the damage caused by fishing activities has not been widely quantified, however trawling on seamounts off Tasmania (Australia) has resulted in a reduction in cold-water coral reef cover (*Solenosmilia variabilis*) by two orders of magnitude resulting in threefold declines in the richness, diversity and density of other benthic fauna (Althaus et al. 2009), with no sign of recovery 5 years after the area was closed to trawling. Even where heavy fishing gear has not directly come into contact with corals, fishing activity can cause high mortalities. In the northwestern Mediterranean, intensive trawling between 400 and 700 m has caused substantial sediment erosion leading to sediment gravity flows down to 1200 m which can suffocate cold-water corals in submarine canyons far from the immediate reach of the trawling fleet (Palanques et al. 2006). Consequently, closing cold-water coral habitats to fishing may not be enough to protect them from the impacts of trawlers.

Less well understood are the potential impacts of subsea cabling, mineral and fossil fuel exploration and extraction,

bioprospecting and indeed scientific sampling and survey activities for cold-water coral ecosystems. However, the depletion of terrestrial resources combined with technological advances making the deep sea more accessible means that anthropogenic pressures on cold-water coral habitats are likely to increase. These activities can be highly profitable and difficult to regulate in international waters. Combined with unfavorable conditions brought by the rising ASH (Sect. 36.2), which is predicted to shallow to depths above which 70 % of present day aragonitic cold-water coral reefs live by 2100 (Guinotte et al. 2006), cold-water corals face an uncertain future.

Nevertheless, progress has been made towards safeguarding these vulnerable ecosystems, most notably in the north Atlantic. The value of cold-water coral habitats, in particular reefs and gardens, is well known and has been recognized in conservation legislation since the 1990s. The Earth Summit held by the UN in Rio de Janeiro in 1992 was the first conference of its kind and the legally binding Convention on Biological Diversity (CBD) with 168 signatories was one of its major outputs (CBD 2015). The CBD explicitly categorizes cold-water coral reef and coral garden habitats as ecologically and biologically significant areas (EBSA). Countries which have ratified the CBD are obligated to take measures to protect cold-water coral habitats. The EU made steps towards fulfilling its obligations with the Habitats Directive (also from 1992) that lists cold-water corals as priority habitats (EC 1992).

The most recent international efforts by the CBD to protect cold-water corals fall under the Nagoya Protocol (2010) where cold-water corals fall under three Aichi targets: Target 5 "By 2020, the rate of loss of all natural habitats, including forests, is at least halved and where feasible brought close to zero, and degradation and fragmentation is significantly reduced"; Target 6: "By 2020 all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably, legally and applying ecosystem based approaches, so that overfishing is avoided, recovery plans and measures are in place for all depleted species, fisheries have no significant adverse impacts on threatened species and vulnerable ecosystems and the impacts of fisheries on stocks, species and ecosystems are within safe ecological limits"; and Target 10: "By 2015, the multiple anthropogenic pressures on coral reefs, and other vulnerable ecosystems impacted by climate change or ocean acidification are minimized, so as to maintain their integrity and functioning". However at the halfway point none of these Aichi targets are on track to be achieved by 2020. Some progress has been made towards Targets 5 and 6, but anthropogenic pressures on coral reefs have continued to increase (CBD 2014b).

Nevertheless, at national levels protection for cold-water coral ecosystems is coming into effect. Norway was the first country in Europe to take measures to protect their cold-

water coral reefs when they closed an area of about 978 km^2 in 1999 to protect *L. pertusa* reefs (CBD 2008). This banned bottom trawls but did not affect fishers using static gear (Armstrong and van den Hove 2008). Subsequently the USA, Canada and New Zealand have closed areas to bottom trawling to protect cold-water coral habitats on seamounts (CBD 2008). The EU closed the Darwin Mounds (Northwest of Scotland) to bottom fishing in 2003 in the first example of a conservation area for cold-water corals in an area fished by several nations, namely the UK, France and Spain (Roberts et al. 2009).

Outside of national jurisdictions, protection measures are more difficult to instigate and enforce. Globally a number of structures and mechanisms have been developed at international levels to support the implementation of global conservation policies including United Nations Convention on the Law of the Sea (UNCLOS), and efforts from the Food and Agriculture Organization of the United Nations (FAO) and the CBD at national and international levels. Of particular importance for protecting cold-water corals is their designation as Vulnerable Marine Ecosystems (VMEs) with respect to fishing by the FAO (FAO 2009), which gained momentum after UN Resolution 61/105 (Sustainable Fisheries) was passed in 2006. In 2009 the FAO published guidelines on the management of deep-sea fisheries aimed at ensuring sustainable fisheries and long term conservation of deep-sea habitats which includes measures to "prevent significant adverse impacts on VMEs". These guidelines apply both to individual states and to regional fisheries management organizations and arrangements (RFMO/As) and require contributions to compiling the FAO global database on VMEs through the identification of known and likely locations of VMEs. They recommend that such areas should be closed to fishing activity until suitable management and conservation structures can be established which could include closures or the introduction of gear specifications, catch limits and measures to limit both bycatch and ghost fishing through lost equipment (FAO 2009). They also require states to establish policies and legal frameworks which would enable them to control the fishing efforts of any vessel flying their flag in the high seas and stop their vessels fishing in VMEs.

Whilst these guidelines are voluntary, there have been international efforts made to protect VMEs outside of national jurisdictions, such as the establishment of six MPAs, a network covering 286,200 km^2, in the international waters of the North Atlantic under the OSPAR convention (O'Leary et al. 2012). The countries that surround the North Atlantic are all developed nations and it may be more difficult to establish such networks in other parts of the world, nevertheless it provides a precedent that could be implemented elsewhere.

36.6 Conclusions

Cold-water corals remain relatively poorly understood ecosystems and key questions about their biology and ecology are yet to be answered. It is clear however, that they are increasingly at risk from growing anthropogenic pressures and their slow growth and stable environments may render them exceptionally vulnerable. Headway has been made and is continuing towards protecting cold-water coral habitats although the global distribution of efforts is highly skewed and much more is required to safeguard these ecosystems. The CBD has had some success both in the number of countries which have signed and ratified the convention, and in progress made towards the Aichi targets (if not as substantial as hoped for). The FAO too has had successes in embedding VMEs into management regimes for deep-sea fisheries in areas beyond national jurisdiction. However, the UN Framework Convention on Climate Change (UNFCCC), which also emerged from the 1992 Earth Summit has been less successful. The Kyoto Protocol (1997) largely failed as major polluters refused to sign up. The subsequent Copenhagen Agreement (2009) did not seek to be legally binding in the same way and was not ambitious enough even in its aims to limit global warming to 2 °C above pre industrial levels (Stern and Taylor 2010). At the time of writing, the outcomes of the Paris 2015 climate talks may prove critical in determining future carbon emissions. Whilst protecting cold-water corals from trawling and other physical impacts is important, without similar advances in curbing carbon emissions, the future of cold-water coral habitats remains uncertain.

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