Cold-water corals in a changing ocean ☆

J Murray Roberts[1,2,3] and Stephen D Cairns[4]

Although known since Antiquity, corals in deep, cold waters remained largely unappreciated and overlooked by the scientific community until the 1990s. The last two decades have seen a dramatic increase in our understanding of these diverse ecosystems alongside growing realisation that many cold-water coral habitats had been degraded by bottom trawling and are threatened by ocean warming and acidification. This paper discusses recent improvements in our understanding of cold-water coral ecology, taxonomy and biodiversity following a variety of advances from the application of predictive mapping to the use of molecular phylogenetic approaches. Since many cold-water coral ecosystems occur in deep-waters beyond national jurisdiction, conservation management measures are being developed through the United Nations and related conventions. All such management measures require not only international agreement but also monitoring and enforcement to ensure their success.

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Introduction

There are more coral species in waters over 50 m deep than there are on shallow, tropical coral reefs [1]. Set apart from tropical corals by the cooler waters they inhabit, cold-water corals are amongst the most significant ecosystem engineers on continental shelves, slopes, canyons, seamounts and ridge systems across the globe [2]. The habitats engineered by cold-water corals vary from 'coral gardens', frequently structured by bamboo or gorgonian corals, to the large deep-water framework reefs usually constructed by one or two of a small group of scleractinian corals (*Oculina varicosa*, *Madrepora oculata*, *Lophelia pertusa*, *Solenosmilia variabilis*, *Goniocorella dumosa*, *Enallopsammia profunda* and *Bathelia candida*). In all cases the coral skeletons provide complex three-dimensional structural habitat used by many other species as refuge or as a place from which to feed.

Research on cold-water corals grew rapidly from the mid-1990s onwards with international symposia beginning in 2000. This was first driven by technological advances coupled with a growing need to understand ecosystems on deep continental margin and slope settings as offshore hydrocarbon exploration and deep-water fisheries expanded into these areas. The huge strides made in acoustic seabed mapping using multibeam echosounders have revealed a previously unknown density of cold-water coral reefs and coral carbonate mounds [3,4]. Both support extensive long-lived biogenic reefs that, through the dynamic processes of growth and (bio)erosion, can accumulate tens of metres above the surrounding seafloor, locally alter sedimentary patterns and provide niches for a diverse community [5]. In the NE Atlantic, cold-water coral reef frameworks structured by *Lophelia pertusa* developed during interglacials, but were absent during glacial climate periods indicating a very close coupling with global climate [6••]. The substantial structures produced by coral carbonate mounds are formed by sequences of interglacial coral reef framework overlain with glacial deposits (Figure 1). In other regions, cold-water coral research is growing rapidly with examples including studies of the solitary scleractinian *Desmophyllum dianthus* in Chilean fjords [7] and of colonial scleractinians in Mediterranean canyons [8].

In parallel with the work to map and characterise cold-water coral habitats has been a growing understanding of the environmental factors that control their distribution. Cold-water corals are frequently associated with certain temperatures and salinities, with evidence that *L. pertusa* in the NE Atlantic is found in a particular density layer (sigma-theta 27.35–27.65 kg m^{-3}) perhaps because larvae disperse laterally along this horizon [9]. However, at local scales cold-water corals occurrence is closely associated to

Figure 1
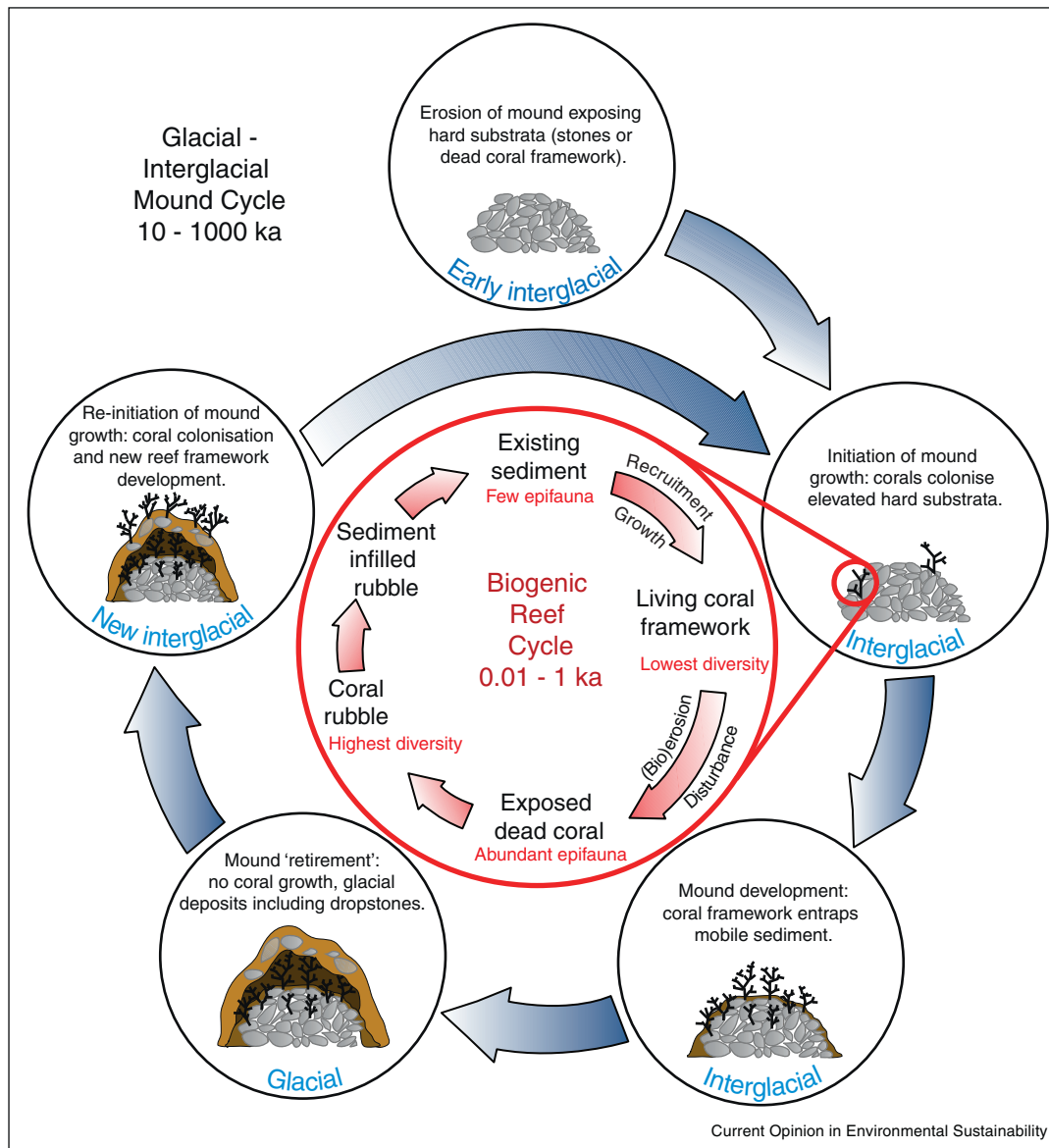
Schematic illustration showing: (1) outer circle; cyclic stages of carbonate mound growth from initiation, development, 'retirement' and re-colonisation; (2) inner circle; smaller scale cycle of reef microhabitats, succession and faunal diversity. Figure redrawn from [5].

sites where fresh labile food material is transported rapidly from the surface [10], often in settings where seabed topography and water flow interact to promote enhanced food supply [11]. However, without a suitable hard surface for larval attachment it is unlikely that cold-water corals will be able to settle and flourish.

With the development of predictive habitat modelling approaches and greater availability of regional and global datasets of key environmental parameters (e.g. temperature, dissolved O_2, and nutrients) work to develop predictive models of cold-water coral occurrence has begun. Following the first studies published in 2005 [12] using

Ecological Niche Factor Analysis [13] a number of studies have been carried out both at regional and global scales. The most recent work uses the Maximum Entropy approach with examples including scleractinian corals on seamounts [14] and deep-water octocorals [15•]. Interestingly oceanic carbonate chemistry emerges as an important explanatory variable for both groups with the aragonitic scleractinian corals and calcitic octocorals related closely to aragonite and calcite saturation states respectively. As the progressive acidification of the oceans continues there is great concern that large areas of the global ocean will become undersaturated as the calcium carbonate saturation horizons shallow [16,17].

CWC taxonomy and associated biodiversity

Cold-water corals are members of the Orders Scleractinia, Zoanthidea, the Subclass Octocorallia and the Family Stylasteridae (Table 1). Understanding their global distribution remains very limited by the lack of information from many deep-sea areas of the world. Where sufficient information exists it has only recently become possible to produce summaries of global species diversity. For example, the azooxanthellate Scleractinia show three high diversity centres (Figure 2), although recent unpublished work by Kitahara and Cairns suggest that the New Caledonian region and adjacent northern Norfolk Ridge may be the overall centre of deep-sea coral biodiversity. In parallel with work on other taxa, molecular approaches to phylogeny are now starting to help unravel patterns in the relationships between cold-water corals. For example, Lindner *et al.* [18] produced a phylogeny for stylasterid corals including 100 species that showed strong evidence for evolution and diversification in deep waters (>50 m). These findings supported earlier interpretation of the fossil record [19] and implied this group evolved protective lids and opercula in the deep sea and invaded shallow waters at least three times. Herrera *et al.* [20••] recently analysed genetic variation in the cosmopolitan gorgonian cold-water coral *Paragorgia arborea* discovering that this species originated in the N Pacific and colonised the Southern Hemisphere before it spread into the N Atlantic, a model consistent with inferred Miocene ocean

circulation patterns [21]. McFadden *et al.* [22,23••] have reviewed the status of molecular phylogenetic analysis among the deep octocorals, acknowledging that mitochondrial gene sequences have limited value in this group, advocating the use of sequencing selected nuclear genes, complete transcriptomes, and using secondary structure, and gene order. The basic issue of identification based on morphology of deep-water corals has been aided by the publication of a colour-illustrated key (with glossary) to the 120 deep-water scleractinian coral genera [24•], and an illustrated glossary to all scanning electron microscopy characters used in the identification of the Stylasteridae [25•]. Finally, Stolarski *et al.* [26••] have presented the latest phylogeny of the higher taxa of Scleractinia, with heavy emphasis on deep-water taxa, showing a third major clade of scleractinians, originating at the base of the scleractinian lineage.

Like their shallow tropical counterparts, cold-water corals engineer habitats that support many other species. A European margin census in 2003 listed over 1300 species recorded with *Lophelia pertusa* habitats in the NE Atlantic [5], a figure that has risen over the decade since then to 1804 in the NE Atlantic and 2704 worldwide species (Roberts *et al.*, unpublished data). The dominant taxa found with cold-water corals include a diverse mix of suspension feeders with many sponges, hydroids and bryozoans that settle and grow on exposed dead coral


Table 1

Classification of the seven different coral groups (in bold) with some common names, the total number of species (as of March 2007) and number of deep-water (>50 m) species. Table adapted from [2], after [1]

Taxon	Common names	Number species	Number species deeper than 50 m
Phylum Cnidaria (=Coelenterata)			
Class Anthozoa			
Subclass Hexacorallia (=Zoantharia)			
Order **Scleractinia** (=Madreporaria)	Hard corals, stony corals, true corals, cup corals, star corals, solitary corals, zooxanthellate corals, azooxanthellate corals	1488	622
Order **Zoanthidea** (in part)	Zoanthids, gold coral (*Gerardia* spp.)	3	3
Order **Antipatharia**	Black corals, whip corals, wire corals, thorny corals	241[a]	182[a]
Subclass **Octocorallia** (=Alcyonaria)	Soft corals, gorgonians, sea fans, sea whips, sea feathers, precious corals, pink coral, red coral, golden corals, bamboo corals, leather corals, horny corals, sea pens	3159[a]	2325[a]
Class Hydrozoa			
Subclass Hydroidolina			
Order Anthoathecata (=Athecata)	Athecate hydroids		
Suborder Filifera			
Family **Stylasteridae**	'Hydrocorals', lace corals, stylasterids	249	223
Family **Hydractiniidae** (in part)	Longhorn hydrozoans (*Janaria, Hydrocorella*)	3	1
Suborder Capitata			
Family **Milleporidae**	'Hydrocorals', fire corals, millepores	17	0
Total		5160[a]	3356[a]

[a] Implies an estimate.

Figure 2
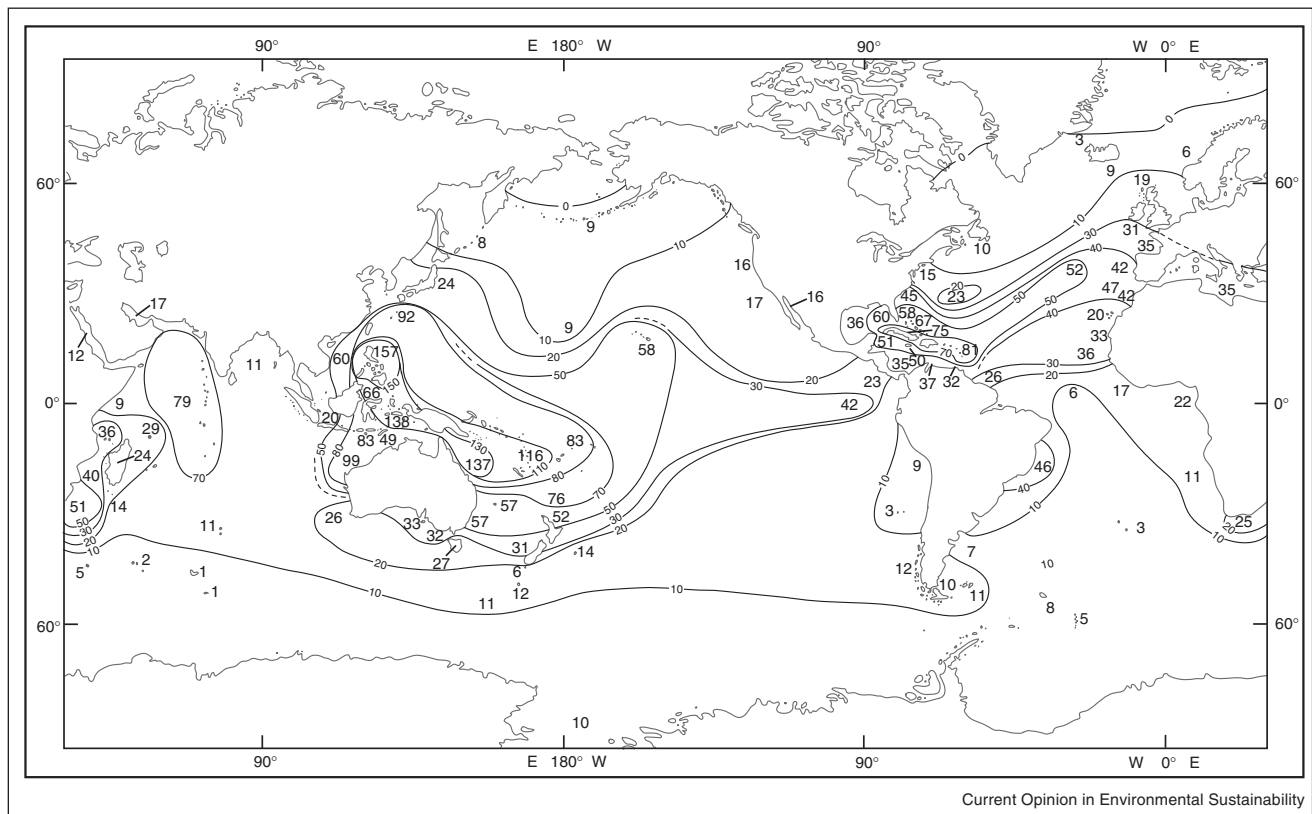
Global species diversity of the 706 azooxanthellate Scleractinia showing three high diversity centres: (1) the region bordered by the Philippines to the north, by New Caledonia to the southeast, including New Guinea and the northeast coast of Australia, (2) the region of the Caribbean from Cuba to the Lesser Antilles and (3) the northwest Indian Ocean. Two other isolated diversity centres can be seen in the southwestern Indian Ocean and off Brazil. Figure redrawn from [1].

framework. However, our understanding of the entire community is greatly limited by two factors: the technical difficulties of getting intact, quantitative samples from cold-water coral habitats and the taxonomic resolution and expertise in any subsequent analysis. However, despite these difficulties, and the geographic biases in studies to date, some important trends are becoming apparent. For example, cold-water coral habitats frequently host intimate symbiotic associations ranging from parasites, such as the lamippid copepod *Gorgonophilus canadensis* on the gorgonian *Paragorgia arborea* in Atlantic Canada [27] to the ubiquitous mutualistic association between the polychaete *Eunice norvegica* and scleractinian reef framework forming corals including *Lophelia pertusa* [28,29•]. In some cases the association becomes very tight such as that between seamount-dwelling corals and ophiuroids. Indeed, ophiuroids like *Asteroschema clavigera* and *Ophiocreas oedipus* showed particularly strong associations with their coral hosts on NW Atlantic seamounts with *O. oedipus* restricted to just one host species, the chrysogorgiid octocoral *Metallogorgia melanotrichos* [30,31] (Figure 3).

Recent work is revealing that cold-water corals are not only significant in local species richness (α-diversity) but, thanks to their macro-habitat heterogeneity, are also significant centres of spatial turnover in diversity (β-diversity) [32,33]. Beyond these observations it is now possible to conduct analyses that combine environmental data on seabed structure (often derived from multibeam echosounder data) with hydrographic data and an understanding of species ecology to develop a more explanatory and predictive understanding of spatial patterns in cold-water coral biodiversity [34•]. Such an understanding is key to appreciating the full implications of ecosystem damage from anthropogenic activities, including the wider ramifications of ocean warming and acidification.

Threats

Although still largely unknown to the wider public, cold-water corals have been damaged by human activity and face an uncertain future in a global ocean forecast to rise in temperature and increase in acidity. From the 1970s onwards the trawl fishing industry has progressively

Figure 3

Current Opinion in Environmental Sustainability
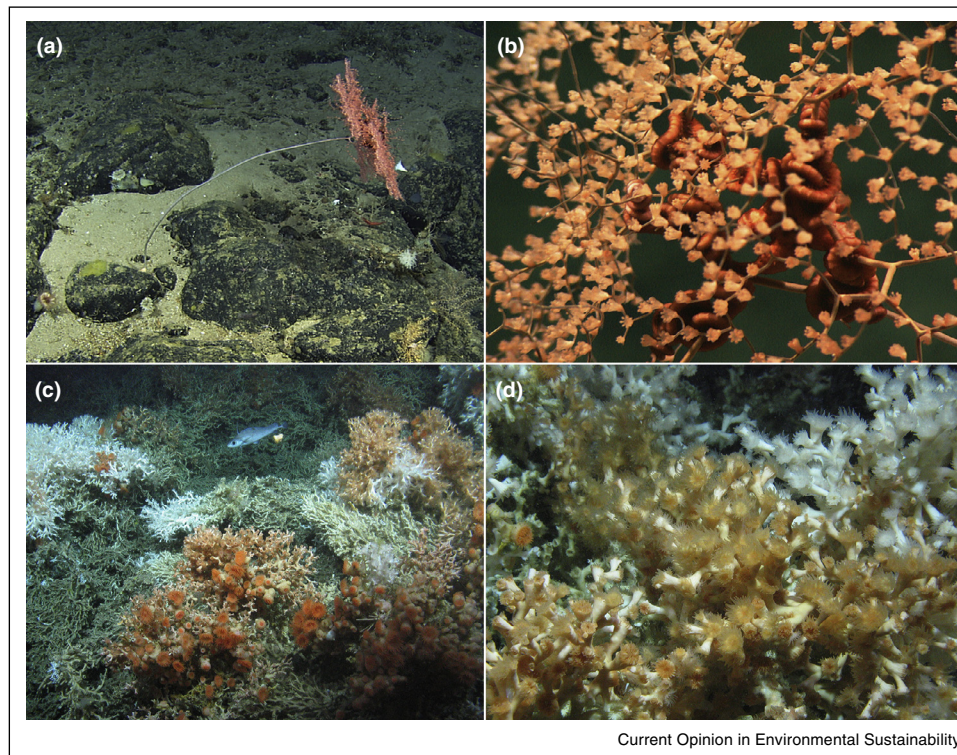
The chrysogorgiid octocoral *Metallogorgia melanotrichos* **(a)** shows a close association with the ophiuroid *Ophiocreas oedipus* **(b)** at >2000 m depth on New England and Corner Rise seamounts (NW Atlantic) [30]. Deep-water reef frameworks **(c)** from the Logachev coral carbonate mound province (NE Atlantic) are constructed at 600–800 m depth by the scleractinian coral *Lophelia pertusa* **(d)**. Images a and b courtesy of Les Watling. Images c and d taken during the 2012 *Changing Oceans Expedition*, RRS *James Cook* cruise 073 [63].

moved to deeper waters as shallower stocks became depleted and vessel size, range and technology improved. As deep-water trawls were strengthened and rock-hopper gears developed to allow trawling on rougher grounds, deep-water fisheries began to come into increasing contact with cold-water coral habitats. Mounting evidence of physical damage from visual surveys in the 1990s onwards led to conservation efforts first at national and latterly at international High Seas levels [35].

In a similar vein the hydrocarbon industry has progressively moved to deeper waters raising the concern that cold-water corals could become smothered by discharged cuttings [36]. Subsequent studies have shown that, while corals such as *Lophelia pertusa* seem relatively well-adapted to an environment with active near-bed sediment fluxes, exposure to fine sediments and drill cuttings can slow skeletal growth [37,38]. Following the Deep-water Horizon oil spill in the Gulf of Mexico, visual surveys showed that cold-water corals 11 km SW of the Macondo well were exposed to the oil plume leading to tissue loss and other signs of stress [39] but the wider long-term significance of this accident to the Gulf's cold-water coral populations remain unclear.

At the time of writing several mining companies had succeeded in raising venture capital to exploit deep-sea mineral resources, notably the seafloor massive sulphide deposits associated with extinct hydrothermal vent systems. These proposals have led to concerns that the destructive process of pit mining in the deep sea will destroy habitats and potentially create plumes of sediment and/or toxic metals that would spread the impact across a far wider area [40]. Vent sites may support cold-water corals [41] and contain unique species that would be vulnerable to local extirpation or even extinction if significant areas were mined.

Beyond the collateral damage reported from trawling or hydrocarbon exploration and the potential damage from deep-water mining, some important cold-water coral groups are collected for jewellery. These coral fisheries began many thousands of years ago but with increasing scale and demand have shown the boom and bust patterns characteristics of over-exploited stocks. The Pacific beds of *Corallium secundum* discovered by Japanese fishers in 1965 on the Milwaukee Banks in the Emperor Seamount chain were over-exploited within 5 years. This pattern was repeated with deeper coral beds that were discovered

in the late 1970s. This led to a rapid increase in landings during the 1980s but the fishery was abandoned in 1989 [42]. For a detailed discussion of the ecology, exploitation, socio-economics and conservation of precious corals see Tsounis *et al.* [43].

However, the most insidious, least understood and most societally challenging threats to cold-water corals come from global climate change brought about by the inexorable rise of atmospheric carbon dioxide concentrations. It is estimated that >80% of global heating processes over the last 40 years have gone into warming the oceans [44] and that this warming signal has penetrated to at least 700 m depth [45]. Increased Mediterranean summer temperatures from 1999 to 2003 led to mass mortality of the precious coral *Corallium rubrum* [46]. Studies have begun to examine the sensitivity of cold-water corals including *Lophelia pertusa* [47,48] and *Dendrophyllia cornigera* [49] to temperature change.

But anthropogenic carbon dioxide does not only cause global atmospheric and ocean warming. Approximately a third of the CO_2 released since the Industrial Revolution has dissolved in the oceans of the world. While this has mitigated global warming it is causing the oceans to gradually acidify. While the chemistry of 'ocean acidification' is well understood its implications for marine ecosystems are far less certain [50].

The global trend of rising oceanic pCO_2 and declining pH has far reaching implications. In terms of deep-water organisms it is necessary to understand how these changes alter the chemistry of seawater at depth. To date, there has been no long-term continuous monitoring of deep-sea carbonate chemistry and our understanding of potential changes relies on sparse measurements and modelled predictions. Evidence of anthropogenic CO_2 has been detected at depths of up to 2500 m and is thought to have penetrated to at least 5000 m [51]. In 2005, Orr *et al.* [16] presented a modelled simulation of the effects of CO_2 release on the carbonate saturation state of the oceans. This model showed that, under the Intergovernmental Panel on Climate Change (IPCC) 'business as usual' scenario (IS92a) where little is done to mitigate CO_2 emissions, the depth of the aragonite saturation horizon (ASH) would rapidly shoal in the 21st Century. This meant that virtually all of the Atlantic's cold-water corals would become exposed to undersaturated seawater [17], and exposed dead coral skeletons would therefore begin to dissolve potentially destroying deep-water reef structure [5,52].

Measurements now show that in the North Pacific the ASH has already shoaled by 50–100 m [53] and, given that the rates of anthropogenic CO_2 release are 8–15 times faster than seen in the last 60 million years [54], we can expect further significant shoaling in the years to come.

Under the IS92a scenario, it is predicted that atmospheric CO_2 will reach 780 ppm by the end of the 21st Century, with values ~2000 ppm being reached by the year 2300 [55]. These pCO_2 increases equate to pH drops of 0.3–0.5 by the end of the century, a rate of change not seen in over 20 million years [56].

In the years since these predictions, studies have begun to examine the vulnerability of cold-water corals to ocean acidification. As with all deep-water organisms, progress has been limited by the difficulties and expense of sampling and maintaining these corals in laboratory experiments. As a result, we know far less about the response of cold-water corals to ocean acidification than we do about shallow-water species.

The studies carried out so far have focused on those cold-water corals that engineer habitat, primarily the reef framework-forming scleractinian corals. In 2009, Maier *et al.* [57] presented the first information on calcification rates in *Lophelia pertusa* and showed that, over short incubations of 24 hours, reducing pH by 0.15–0.3 units caused a reduction in calcification of between 30 and 56%, but *L. pertusa* still maintained the ability to calcify at aragonite saturation states <1. Later work has provided more evidence that this species has some capacity to maintain calcification rates in reduced saturation states. Form and Riebesell [58] maintained *L. pertusa* for six months in seawater with CO_2 concentrations of up to ~1000 ppm and found evidence that the corals acclimated to these acidified conditions. Work is now developing to study the metabolic implications of any acclimation response. While no complete carbon and energy budgets yet exist there is emerging evidence that *L. pertusa* shows significantly lowered rates of respiration but unchanged calcification rates after 21 days exposure to elevated pCO_2 (750 ppm). This implies the corals are facing an energetic imbalance, forcing them to maintain calcification rates by using stored energy reserves [59]. However, none of these studies has examined the combined effects of ocean acidification and temperature increase. Evidence is now emerging that only when these two factors are combined, as they are in nature, do the real effects of ocean change become apparent.

Conservation

It is now recognised that cold-water corals are threatened at the levels of species (e.g. coral collection for jewellery), habitat (e.g. trawl damage) and ecosystem (e.g. ocean acidification). Efforts to promote their conservation have focussed upon creating marine protected areas (MPAs) within which activities such as bottom fishing with towed nets and dredges are restricted. However, as with any protective measure these are only effective if enforced. The first MPA for a cold-water coral habitat was established off Florida in 1984 as a 'Habitat Area of Particular Concern' to protect deep-water reefs of *Oculina varicosa*

but despite these efforts substantial fisheries damage took place between 1977 and 2001 [60]. Experiences such as the *Oculina* reserve bring home the importance of close monitoring and enforcement of MPAs to prevent them becoming 'paper parks'.

Effective monitoring approaches become particularly critical far from shore at the limits of national Exclusive Economic Zones and beyond in International Waters. Since the 1990s governments around the world have been using systems that either record vessel positions using an on board Vessel Monitoring System requiring the fisher's compliance or by using radar and satellite surveillance techniques that do not require compliance with the monitoring approach.

At the international level cold-water corals feature amongst the Vulnerable Marine Ecosystems (VMEs) listed by the United Nations in resolution 61/105 that called upon States to protect VMEs 'from destructive fishing practices, recognizing the immense importance and value of deep sea ecosystems and the biodiversity they contain' [61]. Cold-water corals also meet the criteria as Ecologically and Biologically Significant Marine Areas (EBSAs) laid down by the Conference of the Parties to the Convention on Biological Diversity [62] and work is presently on-going to define EBSAs across the global ocean.

In conclusion, the last 20 years have seen cold-water corals go from being relatively obscure components of deep-water ecosystems known only to a handful of deep-sea specialists and fishers to organisms under the spotlight of international conservation organisations and national governments across the world. The wider awareness of cold-water corals is growing but remains surprisingly low in the scientific community and is almost non-existent in the general public. There is still a great need for researchers, government agencies, NGOs and industry to work together to promote awareness of cold-water corals and other such vulnerable marine ecosystems.

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