Chapter 42. Cold-Water Corals

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1. Inventory and Ecosystem Functions

Globally viewed, cold-water corals cover a wide range of depths (39 - 2000 m) and latitude (70°N – 60°S). In this Chapter, we will focus on the corals found below 200 m, the average depth below which photosynthesis does not occur, to avoid overlap with other chapters. The term "corals" refers to a diverse group of species in the Phylum Cnidaria, including the scleractinian hard corals, octocorals including the sea fans and soft corals, antipatharian black corals, and stylasterid lace corals. Although the majority of the species-level diversity of scleractinians is in the solitary corals (Cairns, 2007), some of the scleractinian corals may form extensive reef structures, occasionally accumulating into large carbonate mounds, or bioherms. Many of the ecological patterns discussed in this chapter are derived from the study of these structures, simply because they have been the focus of the most extensive research in this developing field. However, other types of cold-water corals can also form highly significant structural habitat and these are also discussed. The most representative cold-water, framework-building, scleractinian corals are *Enallopsammia rostrata*, *Goniocorella dumosa*, *Lophelia pertusa* (Figure 1) *Madrepora oculata*, *Oculina varicosa* and *Solenosmilia variabilis* (Roberts et al., 2006). The most common and widespread of the large, structure-forming octocorals are found in the genera *Corallium*, *Isidella*, *Paragorgia*, *Paramuricea*, and *Primnoa* (Watling et al., 2011) (Figure 2).

Cold-water corals (CWC) most commonly occur in continental slope settings, on deep shelves and along the flanks of oceanic banks and seamounts. The majority of CWC occur between the depths of 200 to 1000 m, with the bathymetric ranges becoming shallower towards the poles (Roberts et al., 2009). However, there are numerous, dense coral gardens (primarily octocorals and black corals) found on the slopes of seamounts and the base of the continental slope to over 3000 m, and some soft corals and sea pens are found on soft substrata down to abyssal depths (Yesson et al., 2012). The shallowest occurrences of typically deep-water species are in high latitudes associated with the rocky slopes and sills of fjords (*L. pertusa* off of Norway at 37 m depth, Wilson, 1979) or narrow passes between islands (the octocorals *Paragorgia arborea* and *Plumarella* spp. at 27 m depth in Alaska**, (**Stone, 2006)). Continental slopes exhibit a variety of specific topographic irregularities that provide suitable substrate for cold-water coral larvae to

settle. In many parts of the world ocean, the shelf edge is incised by gullies and submarine canyons (Harris and Whiteway, 2011; Harris et al., 2014). Some prominent examples are located at the canyon-rich slope of the Gulf of Lion off the coast of France (Fabri et al., 2014), the Bay of Biscay under the national jurisdiction of France and Spain (De Mol et al., 2011; Sánchez et al., 2014), the Gully off the coast of Nova Scotia (Mortensen and Buhl-Mortensen, 2005), and the canyons off the eastern United States (Watling and Auster, 2005; Brooke and Ross, 2014). Narrow straits between land-masses may also provide suitable substrate, such as the Straits of Florida (Correa et al., 2012), Gibraltar (De Mol et al., 2012), Sicily (Freiwald et al., 2009), and the Yucatan (Hebbeln et al., 2014). Open-slope CWC mounds are known from the large reefs off the Norwegian coast (Mortensen et al., 2001; Buhl-Mortensen et al., 2014), the Northeast Atlantic along the Rockall and Porcupine Banks (Van der Land et al., 2014), the Southeast coast of the United States (Stetson et al., 1962; Reed et al., 2006), the Gulf of Mexico (Reed et al., 2006; Cordes et al., 2008), Southwestern Atlantic Ocean (Viana et al., 1998; Sumida et al., 2004; Pires, 2007; Carranza et al., 2012), and off Mauritania (Colman et al., 2005). These mounds are not randomly distributed over the slope but show a strong affinity with distinct water mass boundaries passing along the slope (Mienis et al., 2007; Arantes et al, 2009; White and Dorschel, 2010). Open-slope coral gardens appear to be common along most of the continental margins of the world (Figure 3, Yesson et al., 2012). Oceanic seamounts represent another important cold-water coral-rich environment (see Chapter 51), such as the Tasmanian seamounts off South Australia (Thresher et al., 2011), the seamount speckled Chatham Rise off the coast of New Zealand (Tracey et al., 2011), seamounts of the central Pacific (Rogers et al., 2007), and seamounts of the Mid-Atlantic Ridge system (Mortensen et al., 2008). A compilation of framework-forming cold-water coral occurrences is displayed in Figure 4 based on the UNEP-WCMC database (Freiwald et al., 2005) and more recent findings. The current information on deep-water octocorals suggests that they are ubiquitous along continental margins and seamounts on hard substrata, as well as occasionally on soft-bottom in the case of the sea pens and a few species of bamboo corals. A combination of octocorals collections and observations along with a predictive habitat suitability model is displayed in Figure 3 (Yesson et al., 2012).

Cold-water corals have been known since the first descriptions in the 18th century and the first deep-water research expeditions of the 19th century (Roberts et al., 2006). The presence of large reef structures in deep water was not broadly appreciated by the scientific community until the first submersibles were available in the late 20th century (Cairns, 2007). Using these new tools, a more complete set of distribution records and characterization of the habitat requirements of CWC were developed. Based on these recent data, the use of habitat modelling has led to the discovery of numerous cold-water coral sites and habitats. As an example, scleractinians were discovered on steep submarine cliffs after modelling (Huvenne et al., 2011) and field observation in the Mediterranean (Naumann et al., 2013) and the Bay of Biscay (De Mol et al., 2011; Reveillaud et al., 2008). Similarly, an extensive screening of newly available mapping and visualization technology in the Mediterranean revealed additional and more extensive

coral formations than anticipated hitherto (Freiwald et al., 2009). Habitat modelling has thus far mostly been applied to a few of the most common species at a global and regional scale (Rengstorf et al., 2013; Yesson et al., 2012) at a coarse spatial resolution (Ross and Howell, 2013). However, models are now being applied at finer resolution levels in order to guide surveys with the visual tools of remotely-operated and manned submersibles (Georgian et al., 2014). Additional fine-grained and broad-scale habitat modelling, specifically incorporating the best available taxonomic identifications (Henry and Roberts, 2014) is still needed to discover additional habitats, and to forecast the fate of CWC facing both direct (fisheries) and indirect (environmental) impacts (Guinotte et al., 2006; Clark and Tittensor, 2010).

Cold-water coral reefs, mounds, and gardens support a highly diverse community, comprising faunal biomass that is orders of magnitude above that of the surrounding seafloor (Mortensen et al., 1995; Henry and Roberts, 2007; Cordes et al., 2008; Roberts et al., 2008; Rowden et al., 2010). In addition to this tightly-associated community, cold-water corals may also serve as important spawning, nursery, breeding and feeding areas for a multitude of fishes and invertebrates (Koslow et al., 2001; Fossa et al., 2002; Husebo et al., 2002; Colman et al., 2005; Stone, 2006; Ross and Quattrini, 2009; Baillon et al., 2012; Henry et al., 2013), and habitat for transient diel vertical migrators (Davies et al., 2010). The ability to construct massive calcium carbonate frameworks, which makes both shallow and deep-water coral reefs unique, provides an important biogeochemical function in both the carbonate system (Doney et al., 2009) and in calcium balance (Moberg and Folke, 1999). CWC skeletons also provide an information function (*sensu* de Groot et al., 2002) through their archiving of paleoclimate signals (Adkins et al., 1998; Williams et al., 2006). Besides this, CWC ecosystems possess an inherent aesthetic value (*sensu* de Groot et al., 2002) demonstrated through countless films, photographs, and paintings of reefs or reef organisms.

Cold-water corals and the communities they support rely on surface productivity as their primary source of nutrition; either through the slow, relatively steady deposition of particulate organic carbon (POC) in the form of marine snow, which may be enhanced by hydrographic mechanisms (e.g. Davies et al., 2009; Kiriakoulakis et al., 2007), or through more active transport of carbon provided by vertical migrators (Mienis et al., 2012). However, *L. pertusa* has been shown to incorporate everything from dissolved organic carbon (DOC) to POC to algal biomass to small zooplankton (van Oevelen et al., 2009). As in shallow-water systems, corals and sponges of the deep reefs recycle these nutrients and form both the structural and trophic foundation of the ecosystem. In addition to these ties from shallow to deep water, the transport of nutrients from deep to shallow water is accomplished both by the diel vertical migrations of plankton and small fishes (Davies et al., 2010) as well as by periodic down- and upwelling that can occur near some of the reefs (Mienis et al., 2007; Davies et al., 2009). Although the mechanisms for deep-to-shallow water transport are well established, the input of deep-water secondary productivity to shallow ecosystems remains unquantified.

2. Features and Trends

All geological structures mentioned share some environmental factors that facilitate coral settlement and subsequent growth: provision of current-swept hard substrate, and often topographically-guided hydrodynamic settings. It has been suggested that corals are preferably confined to narrow seawater density (Sigma-theta) envelopes (Dullo et al., 2008) in which along-slope larval dispersal propagation may be facilitated. Survival and growth may be most closely associated with specific hydrodynamic settings including tidal-driven internal-wave fronts hitting continental slopes and seamounts (Mienis et al., 2007; Henry et al., 2014), specific up- and downwelling currents affecting the summits of shallow-water seamounts (Ramirez-Llodra et al., 2010), and tidal-driven downwelling phenomena on inner shelf settings (Davies et al., 2009; Findlay et al., 2013). These hydrographic transfer processes tend to concentrate or prolong the retention time of nutrients and food that sustain the metabolic demands of the suspension-feeding community.

Another perspective on the occurrence of coral habitat is a combined biogeophysical and hydrochemical analysis of the ambient seawater, a very recent endeavour in the still young research history of cold-water coral systems (e.g., Findlay et al., 2014; Flögel et al., 2014; Henry et al., 2014; Lunden et al., 2013). These forms of data along with species presence data were incorporated into global habitat suitability study by Davies and Guinotte (2011) that was conducted on the six major cold-water framework-building corals (*Enallopsammia rostrata, Goniocorella dumosa, Lophelia pertusa, Madrepora oculata, Oculina varicosa* and *Solenosmilia variabilis*) using the Maximum Entropy modelling approach (MAXENT). This approach uses species-presence data, global bathymetry 30-arc second grids (1 km^2 resolution) and incorporates environmental data from several global databases. Viewed on such a global scale, these corals generally thrive in waters that: (1) are supersaturated with respect to aragonite, (2) occur shallower than 1500 m water depth, (3) contain dissolved oxygen concentrations of >4 ml l^{-1}, (4) have a salinity range between 34 and 37 ppt, and (5) show a temperature range between 5 and 10°C. Laboratory experiments have confirmed many of these ranges, with *L. pertusa* being the most commonly studied species. Mediterranean *L. pertusa* and *M. oculata* colonies survived and grew at 12°C for three weeks, with *M. oculata* showing a greater sensitivity to high temperature (Naumann et al., 2014). Gulf of Mexico *L. pertusa* colonies survived and grew at up to 12°C, but died when exposed to 14°C for 8 days (Lunden et al., 2014). Studies of *L. pertusa* from west of Scotland, United Kingdom of Great Britain and Northern Ireland, demonstrated that this species can maintain respiratory independence and even survive periods of reduced oxygen (Dodds et al., 2007).

However, some remarkable outliers to these trends exist in the Red Sea and the Gulf of Mexico. The Red Sea represents the warmest and most saline deep-sea basin on Earth, with temperatures >20°C throughout the water column and salinity in excess of 40 ppt.

Recent findings of typically deep-dwelling corals in these habitats shed new light on the persistence of corals in deep waters (Roder et al., 2013; Qurban et al., 2014). Although none of the coral species found in the Red Sea are among the most common globally (see above for list), limited framework growth is recorded mainly by *Eguchipsammia fistula* under food- and oxygen deprived conditions (1.02 – 2.04 ml l^{-1}). Coral survival under such extreme environmental conditions may follow the strategy of metabolic depression (*sensu* Guppy and Withers, 1999), including depressed aerobic respiration and calcification rates. However, the high temperatures in combination with high aragonite saturation values of 3.44-3.61 in the Red Sea may facilitate calcification under these otherwise adverse conditions (Roder et al., 2013). The cold-water coral communities in the northern Gulf of Mexico belong to the most intensively studied sites in waters of the United States (e.g., Cordes et al., 2008). The major framework-constructor is *L. pertusa* and most environmental variables (i.e., temperature, salinity and aragonite saturation state) reflect the ranges known from Atlantic *Lophelia* sites (Davies et al., 2010; Lunden et al., 2013). However, dissolved oxygen values appear to be low, 2.7–2.8 ml l^{-1} are typically observed (Davies et al., 2010) and values as low as 1.5 ml l^{-1} have been recorded adjacent to coral mounds (Georgian et al., 2014). Coral nubbins from these Gulf of Mexico populations survived and grew in the lab at oxygen levels as low as 2.9 ml l^{-1}, but eight-day incubations at lower oxygen concentrations (1.5 ml l^{-1}) caused complete mortality, suggesting that these conditions are short-lived *in situ* (Lunden et al., 2014). Similarly, low oxygenation levels were found in the newly discovered *Lophelia-Enallopsammia* coral mounds in the Campeche Bank coral mound province, in the southern Gulf of Mexico (Hebbeln et al., 2014). It is possible that the low oxygen concentrations of the Gulf of Mexico result in lower growth rates observed for *L. pertusa* on natural (Brooke and Young, 2009) and man-made substrata (Larcom et al., 2014), although this remains to be examined empirically.

There have been numerous recent advances in our knowledge of the oceanographic variables describing coral habitat in the deep sea. However, knowledge gaps still remain when up-scaling from local to regional to global scales. Furthermore, limited capacity to carry out long-term *in situ* measurements with benthic landers and cabled observatories persists. This knowledge is of utmost importance to understand the consequences of already perceptible environmental change, such as ocean acidification, spread of oxygen minimum zones, and rising temperatures, on deep-sea ecosystems.

3. **Major Pressures Linked to the Trends**

Numerous anthropogenic threats to cold-water coral communities exist, the most significant of which include fisheries, hydrocarbon exploration and extraction, and mining, as well as global ocean change including warming and acidification. An improved understanding of the function of cold-water corals as habitat, feeding grounds and nurseries for many fishes including certain deep-sea fisheries targets has emerged along with concerns as to the impact of fisheries on these ecosystems (Costello et al., 2005;

Grehan et al., 2005; Stone, 2006; Hourigan, 2009; Maynou and Cartes, 2012). Physical impacts from both trawl fisheries and long-lining, now being conducted as deep as 1500-2000 m, are likely to be significant anywhere deep-water fisheries are active, but have been well-demonstrated in the North Atlantic and Norwegian Seas (Roberts et al., 2000; Fossa et al., 2002; Hall-Spencer et al., 2002, Reed, 2002), on the Australian seamounts (Koslow et al., 2001), off the coast of New Zealand (Probert et al., 1997, Clark and Rowden, 2009), and Southwestern Atlantic slope (Kitahara, 2009). Trawl fisheries have the most severe impacts, by removal of large volumes of organisms and of cold-water coral framework from the seafloor and the concomitant destruction of the habitat, but long-lining impacts have also been observed (Heifetz et al., 2009). Recovery times from these types of disturbance are likely to require settlement and regrowth of the corals, which based on radiometric dating of cold-water coral species, can require decades to centuries (Andrews et al., 2002; Prouty et al., 2014) or in the case of the black corals, could require millennia (Roark et al., 2009). Direct evidence of recovery times is consistent with these estimates, indicating that there was no apparent recovery 5-10 years after the closure of seamount fisheries on the Tasmanian seamounts (Althaus et al., 2009). These impacts have also been the most recognized in terms of management efforts, thus far (see below).

Installation of oil and gas offshore facilities and drilling activities (see Chapter 21) have a great potential to impact cold-water coral communities. The potential impact should be higher in areas where much of the available substrate is from authigenic carbonates related to natural oil and gas seepage, such as the Gulf of Mexico (Cordes et al., 2008), some locations on the Norwegian margin (Hovland, 2005), and the New Zealand margin (Baco et al., 2010). Most of the typical impacts would be from infrastructure installation and the deposition of drill tailings that can include high concentrations in barium, among other potential toxins (Continental Shelf Associates, 2006). These impacts are typically confined to a few hundred metres, but can have been shown to extend over 2 kilometres in some cases (Continental Shelf Associates, 2006). The most glaring example of oil and gas industry impacts in the deep sea is the Deepwater Horizon disaster in 2010 in the Gulf of Mexico. Material conclusively linked to the spill was discovered on octocoral colonies (primarily *Paramuricea biscaya*) approximately 11 km away from the site of the drilling rig (White et al., 2012a). These colonies suffered tissue loss and many have continued to decline in health since the spill (Hsing et al., 2013). Subsequent surveys detected at least two additional sites, extending the impacts to 26 km from the site of the well, and from 1,370 m to 1,950 m water depth (Fisher et al., 2014). One of the primary lessons learned from this tragic incident is that there is an urgent need for improved baseline surveys in deep waters prior to industrial activity. Offshore energy industry activity in the form of wind and wave energy is also increasing (see Chapter 22), and physical structure placed on the seafloor, including pipelines and cables, could have an impact on cold-water corals if the appropriate surveys are not completed prior to installation.

Mining activities have increased in the deep sea in recent years. This activity has mainly focused on massive seafloor sulphide deposits near hydrothermal vents, cobalt-rich

crusts on seamounts, and also on polymetallic nodules on the abyssal plain (Ramirez-Llodra et al., 2011). These forms of mining would involve removal of a large area of the seafloor surface, and complete removal of any associated communities, along with the generation of large sediment and tailing plumes that may impact filter feeding communities at a distance from the mining activity (Ramirez-Llodra et al., 2011). On the seamounts of the Kermadec Arc, some which have already been leased for mining, cold-water coral communities consisted of scleractinian, schizopathid, stylasterid, primnoid, and isidid corals primarily associated with inactive areas away from hydrothermal venting (Boschen et al., 2015). Deep-sea corals are often found on the hard substrata in inactive vent fields, and may be subject to significant impacts from their removal due to their long life spans and low recruitment rates.

Global climate change is affecting every community type on Earth, and its effects are already being felt in the deep sea. Ocean warming has been recorded in numerous deep-water habitats, but is particularly significant in marginal seas, which are home to many of the world's cold-water coral reefs. In particular, there is evidence that the Mediterranean has warmed by at least 0.1°C between 1950 and 2000 (Rixen et al., 2005), and this change has been shown to impact the deep-sea communities there (Danovaro et al., 2004). Cold-water corals are highly sensitive to warming waters because of their upper thermal limits, and the temperature excursions around this general upward trend are likely to be much higher.

Ocean acidification is another pervasive threat (see Chapter 5). Continued additions of CO_2 into the atmosphere exacerbate the problem as the oceans absorb approximately 26 per cent of the CO_2 from the atmosphere (Le Quere et al., 2009). Because the carbonate saturation state in seawater is temperature-dependent, it is much lower in cold waters and therefore cold-water corals lie much closer to the saturation horizon (the depth below which the saturation state is below 1 and carbonate minerals will dissolve) than shallow-water corals. As ocean acidification proceeds, the saturation horizon will become shallower, thus exposing more cold-water corals to undersaturated conditions (Guinotte et al., 2006). Solitary corals of the South Pacific are already facing saturation states below 1 (Thresher et al., 2011), and small reef frameworks constructed by *Solenosmilia variabilis* grow in periodically undersaturated waters on Northeast Atlantic (Henry and Roberts 2014; Henry et al., 2014) and New Zealand seamounts (Bostock et al., 2015). The *Lophelia* reefs of the Gulf of Mexico lie very close to the saturation horizon, at a minimum saturation state of approximately 1.2 (Lunden et al., 2013). Since these recent studies represent the baseline for the deep-water carbonate system, the extent to which anthropogenic CO_2 contributes to these low values remains unclear.

Other possible effects of global climate change include deoxygenation and changes in sea-surface productivity. Declines in oxygen availability are primarily linked to increasing water temperature, but also to synergistic effects of pollution and agricultural runoff, which are most significant in shallow water. However, because some cold-water corals live at oxygen-minimum zone depths (Davies et al., 2010; Georgian et al., 2014), even small changes in oxygen concentration could be significant. Because cold-water corals

live below the photic zone and rely for their nutrition on primary productivity transferred from the surface waters to depth, changes in surface productivity could have significant negative impacts. In particular, the increased stratification of surface waters above the thermocline will lead to decreased productivity in high latitude spring-bloom and upwelling ecosystems (Falkowski et al., 1998). This includes the North Atlantic, where the most extensive examples of the known cold-water coral reefs exist.

Through *in situ* habitat characterization as well as by experimental approaches, it has become clear that acidification and the expansion of oxygen minimum zones, together with rising temperatures, will affect the average metabolism and physiology of most scleractinians (Gori et al., 2013; Lartaud et al., 2014; McCulloch et al., 2012; Naumann et al., 2013). However, whether such changes will result in range shifts, massive extinctions (as suggested by Tittensor et al., 2010), or if species possess the resources to cope with variations through phenotypic plasticity or adaptive genetic changes, is still largely unknown. The solitary coral *Desmophyllum dianthus* and colonial scleractinian *Dendrophyllia cornigera* have shown resistance to high temperature in aquaria (Naumann et al., 2013). The *L. pertusa* colonies from the North Atlantic and Mediterranean have shown the ability to acclimatize to ocean acidification in long-term experiments (Form and Riebesell, 2012; Maier et al., 2012). In other experiments, certain genotypes of *L. pertusa* from the Gulf of Mexico were able to calcify at saturation states as low as 1.0, suggesting a possible genetic basis to their sensitivity to ocean acidification (Lunden et al., 2014). However, to date no long-term studies combining acidification with temperature stress have been produced and long-term effects on bare skeletal structure are unknown. In addition, some cold-water coral species seem to be resilient to some of these processes, and may hold some of the answers for coral survival in future global climate-change scenarios. Regardless, the projected shoaling of the aragonite saturation horizon (Orr et al., 2005) threatens the future integrity of deep-water scleractinian reef structures world-wide (Guinotte et al., 2006).

The ability of these organisms to keep up with the pace of ocean change and disperse into a new environment or to recolonize depleted areas depends on the capacity for mid- or long-distance dispersal. This capacity has been demonstrated for *L. pertusa* by isotope reconstruction and genetic analysis (Henry et al., 2014), supporting the hypothesis of a post-glacial recolonization of the Atlantic by refugees in the Mediterranean (De Mol et al., 2002; De Mol et al., 2005; Frank et al., 2009).

Overall, *L. pertusa* shows a pattern of relative homogeneity within regions (e.g. the North Atlantic), and modest but significant differentiation among regions, both for the Western Atlantic (e.g. Gulf of Mexico vs. Southeast United States vs. North Atlantic; Morrison et al., 2011), as well as along Eastern Atlantic margins from the Bay of Biscay to Iceland for both *L. pertusa* and *M. oculata* (Becheler, 2013). Previous studies on the Eastern Atlantic margin had shown less extensive connectivity, possibly reflecting the peculiar position of fjord populations in Sweden and Norway (Le Goff-Vitry et al., 2004). Preliminary studies on *D. dianthus* suggest a lack of barrier to large-scale dispersal (Addamo et al., 2012), although bathymetric barriers to gene flow are evident (Miller et

al., 2011). Bathymetric barriers to dispersal are also apparent in the phylogenetic community structure of deep-water octocoral assemblages in the Gulf of Mexico (Quattrini et al., 2014).

Finally, the distribution of genetic polymorphism among populations of octocorallians and antipatharians across seamounts of the Pacific spanning 1700 km also showed no evidence for strong endemism, supporting the ability for large scale dispersal of the species studied (Thoma et al., 2009). It is only recently that the embryonic and larval biology of *Lophelia pertusa* has been described (Brooke and Järnegren, 2013). The settlement and benthic juvenile stages have not been observed. Knowledge on the possible effects of ocean acidification on coral reproduction so far comes from tropical corals but it is reasonable to believe that there are many similarities (Albright, 2011).

Altogether, the present state of knowledge of genetic connectivity of deep-water corals suggests that the potential exists for some species to disperse and colonize across large distances in response to major environmental changes, and some species have a more limited dispersal capacity. However, more studies need to be conducted at a finer spatial scale using specific genetic markers (e.g. Dahl et al., 2012) to improve the understanding of the impact of environmental changes on connectivity and persistence at the local scale. These different degrees of differentiation among and within ocean basins indicate the need for regional-scale conservation strategies.

4. Implications for Services to Ecosystems and Humanity

Impacts on cold-water corals and the structures they form would have significant implications for the functioning of the surrounding deep sea and wider oceanic ecosystems. The linkages from shallow to deep water, and back again, implicate cold-water corals as key components of the broader oceanic ecosystem. The physical structures created by cold-water corals support fisheries through the direct provision of habitat, refuge, or nursery grounds, which is likely to lead to increases in commercially significant fish populations. These effects are most pronounced where cold-water corals are known to be highly abundant, such as on the North Atlantic, North Pacific, and Australian and New Zealand seamounts.

The ecosystem services provided go beyond the direct provision of substrate and shelter (see review by Foley et al., 2010). The complex habitat formed by cold-water corals increases the heterogeneity of the continental margin, promoting higher diversity (Cordes et al., 2010). As in other ecosystems (e.g. Tilman et al., 1997), increased diversity mostly promotes higher levels of ecosystem function, including carbon cycling. This specific ecosystem service may be important in relatively oligotrophic regions such as the Gulf of Mexico and the Mediterranean where cold-water corals-enhanced nutrient cycling and remineralization would generate nutrients that may be transported back to the surface. Recent findings from reefs off Norway demonstrated their

significant role in carbon cycling, raising additional concerns as to the impact of their disappearance on global biochemical cycles (White et al., 2012b).

Cold-water corals also hold genetic resources that may provide services to humanity, either directly or through their function as biodiversity hotspots in the deep sea (Arrieta et al., 2010). Taxa such as cnidarians, sponges, and molluscs have been shown to harbour the highest abundance of natural marine products of interest for biotechnology development (Molinski et al., 2009; Rocha et al., 2011). As an example, the anti-AIDS drug AZT was developed from an extract of a sponge from a shallow Caribbean reef (de la Calle, 2009). At least half, and likely far more, of the diversity of corals and sponges lies in deep, cold waters (Cairns, 2007; Hogg et al., 2010), and therefore, these understudied and often unknown species have the highest potential for new discoveries. With this potential comes a management concern, especially as some of the potential genetic resources (see also chapter 29) harboured within the genomes of cold-water corals and sponges lie in areas beyond national jurisdiction (Bruckner, 2002; de la Calle, 2009).

5. Conservation Responses

Raised awareness of the susceptibility of cold-water coral communities to impacts of human activities in recent decades has resulted in national and international actions to protect cold-water corals and facilitate recovery of coral areas adversely affected in the past. In some areas where significant damage was documented, e.g. along the continental shelf off Norway (Fossa et al., 2002) and on seamounts in Australia and New Zealand (Koslow et al., 2001), national legislation was introduced and specific management measures were implemented. A growing number of protected areas and fisheries closures in areas within national jurisdiction in the Atlantic and North Pacific have followed, and in some countries, e.g. Norway, it is illegal to deliberately fish in coral areas even if the area is not formally closed as a protected area.

Since the mid-2000s a series of United Nations General Assembly (UNGA) resolutions (e.g. 61/105, 64/72, 66/68) on sustainable fisheries have called for a number of measures, including the implementation of the International Guidelines for the Management of Deep-Sea Fisheries in the High Seas (FAO, 2009), and action to avoid significant adverse impacts of fisheries on vulnerable marine ecosystems,[1] including e.g. cold water corals.[2] These resolutions focus in particular on areas beyond national

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[1] The International Guidelines for the Management of Deep-Sea Fisheries in the High Seas describe vulnerable marine ecosystems and list characteristics to be used as criteria in the identification of such ecosystems.

[2] The Annex to the Guidelines refers to "certain coldwater corals" as part of examples of species groups, communities and habitat forming species that are documented or considered sensitive and potentially vulnerable to deep-sea fisheries in the high seas, and which may contribute to forming vulnerable marine ecosystems.

jurisdiction. Some of the protective efforts, including fisheries closures, within EEZs predate the UNGA resolutions, but the resolutions stimulated further action. Such actions run in parallel with efforts to create networks of marine protected areas in areas within national jurisdiction, partly motivated by the need to protect corals.

In response to the measures called for by the General Assembly, seamounts and continental slope habitats with a documented or assumed coral presence have now been set aside as marine reserves or fisheries closures by competent authorities. These areas are protected partly through area-based management tools (for example, by Australia, New Zealand and the United States within areas under their respective national jurisdictions) and partly by regional fisheries management organizations and arrangements (RFMO/As) in the high seas of the North and South-eastern Atlantic. In the north-eastern Atlantic, substantial areas have been protected within national jurisdictions of European Union Member States, as well as of Iceland and Norway. Beyond areas of national jurisdiction, RFMOs/As with competence to regulate bottom fisheries (for example, the Northwest Atlantic Fisheries Organization (www.nafo.int) and the North East Atlantic Fisheries Commission (www.neafc.org)) have closed a range of seamounts and seabed areas to bottom fishing. Within their regulatory areas, these RFMOs have also restricted fishing to a limited agreed set of sub-areas outside the "existing fishing areas", and have created strict rules and impact assessment requirements for these sub-areas. These measures are intended not only to protect known areas with significant concentrations of cold-water coral, but also essentially to reduce the incentive for exploratory bottom fishing outside existing fishing areas. Similar rules apply in the southeast Atlantic high seas implemented by the South East Atlantic Fisheries Organization (SEAFO, www.seafo.org) which closed selected ridge sections and seamounts to fishing, and restricted fisheries to certain subareas. In the Mediterranean, the General Fisheries Commission for the Mediterranean (GFCM, www.gfcm.org) implemented fisheries restriction zones in specific coral sites.

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR, http://www.ccamlr.org/) banned bottom trawl fishing within the CCAMLR Convention area. Bottom fishing regulations and area closures aim to facilitate responsible fisheries and to prevent adverse impacts on bottom-associated vulnerable marine communities as defined by FAO (2009). Marine protected areas in this area are being considered but only one MPA has been established thus far.

Currently little information exists to assess the impacts on target or by-catch species by deep-sea fishing on seamounts in the Indian Ocean. The Southern Indian Ocean Deepsea Fishers Association declared a number of seamounts in the Southern Indian Ocean as voluntary areas closed to fishing. The entry into force in 2012 of the Southern Indian Ocean Fisheries Agreement[3] (SIOFA), a new regional fisheries management arrangement for the region, may lead to better documentation and regulation of seamount fisheries.

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[3] United Nations, *Treaty Series*, vol. 2835, No. 49647.

In the North Pacific, the United States designated Habitat Areas of Particular Concern (HAPCs) that contain Essential Fish Habitat (EFH) and closed subareas of the shelf and upper slope from California to the Aleutian Islands to bottom trawling. Additional areas of *L. pertusa* habitat have recently been designated as HAPCs off the southeast coast of the United States. Canada also has a strategy to develop and implement further measures. In areas beyond national jurisdiction in the North and South Pacific, respectively, States which participated in the negotiations to establish the North Pacific Fisheries Commission (NPFC) and the South Pacific Fisheries Management Organization (SPRFMO) introduced measures similar to those adopted by the Atlantic RFMOs.

Within areas under national jurisdiction of the United States in the Gulf of Mexico, mitigation areas are established around mapped seafloor seismic anomalies that often coincide with hardgrounds that may support cold-water coral communities. Although these measures may prevent most direct impacts from infrastructure, the persistent threat of deep-water fishing, accidental loss of gear, and catastrophic oil spills remains a concern.

A continued challenge is to assess the effectiveness of current and new protective measures and to develop management in areas that need greater attention, such as those for which no RFMOs exist. The fisheries sector is often perceived as representing the major threat to cold-water corals, but a growing challenge is to avoid adverse impacts from other industries moving into areas containing known coral habitats, e.g. mining, oil and gas industries, and renewable energy industries operating under different management regimes.
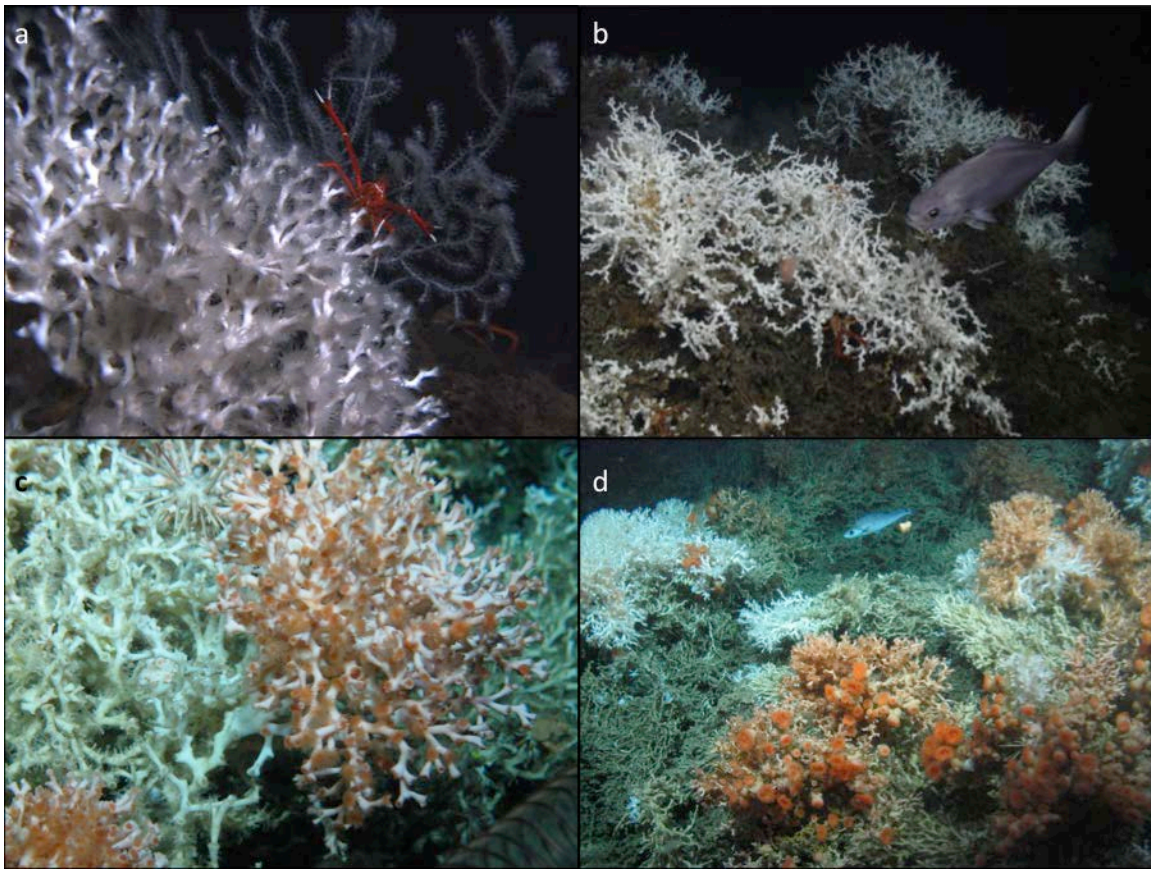
Figure 1. Examples of dense cold-water *Lophelia pertusa* reef frameworks, including provision of fish habitat. (a) and (b) from 400-500 m depth in the Viosca Knolls region of the Gulf of Mexico. (c) and (d) from 600 to 800 m depth on the Logachev coral carbonate mounds on the Rockall Bank in the Northeast Atlantic.

All photos are property of the contributors to this chapter and should also be attributed to:

(a) and (b): Ecosystem Impacts of Oil and Gas Inputs to the Gulf (ECOGIG), a consortium funded by the Gulf of Mexico Research Initiative (GoMRI), and the Ocean Exploration Trust; (c) and (d): Roberts, J.M., Changing Oceans Expedition 2012, funded by UK Ocean Acidification programme (NERC, DECC, Defra).
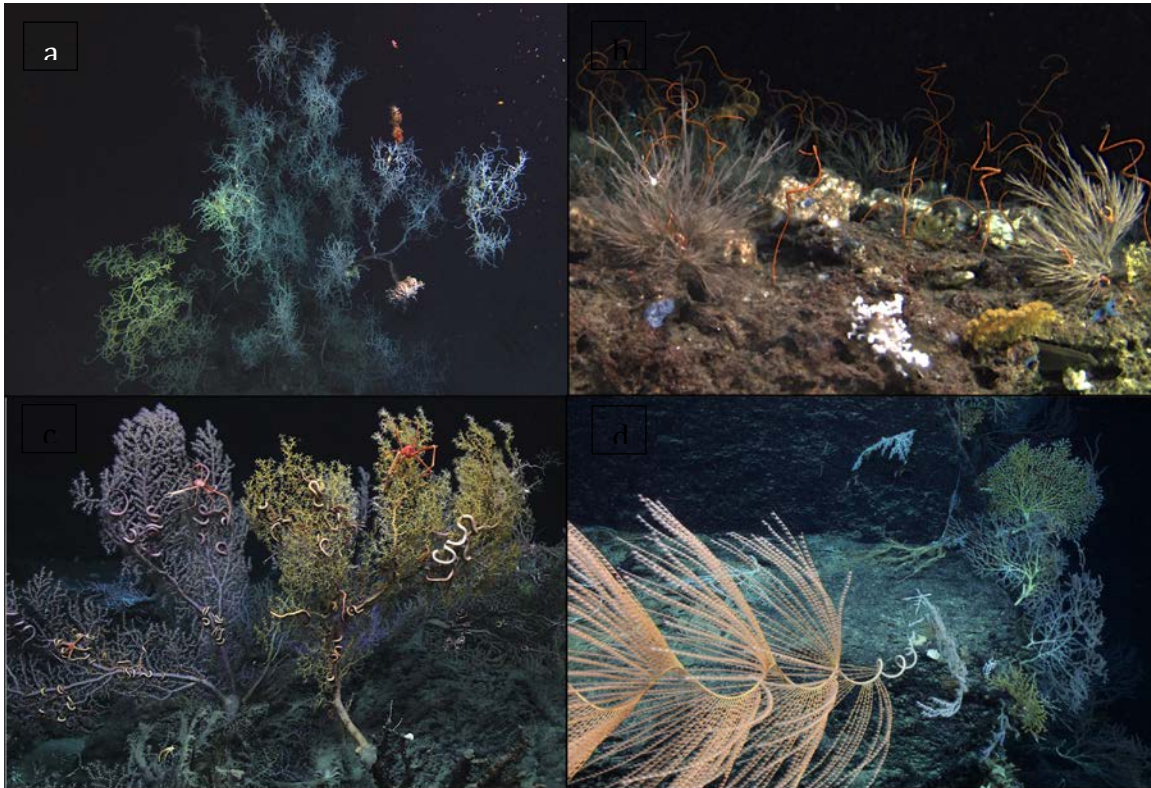
Figure 2. Octocoral gardens from different depths within the Gulf of Mexico. (a): A 2m tall Leiopathes glaberrima black coral colony from 200 m depth. (b): A diverse community of Stichopathes sp. black corals, keratoisid bamboo corals, and other octocorals from 500 m depth. (c): Large, habitat-forming Paramuricea sp. colonies from 1000 m depth. (d): A diverse community of octocorals including Iridogorgia sp., keratoisid bamboo corals, Paramuricea biscaya, and Corallium sp. from 2000 m depth.

All photos are property of the contributors to this chapter, and should also be attributed to: (a) and (b): The *Lophelia* II project, funded by the United States Bureau of Ocean Energy Management (US BOEM) and the National Oceanic and Atmospheric Administration, Office of Ocean Exploration and Research (NOAA OER); (c) and (d): Ecosystem Impacts of Oil and Gas Inputs to the Gulf (ECOGIG), a consortium funded by the Gulf of Mexico Research Initiative (GoMRI), and the Ocean Exploration Trust.
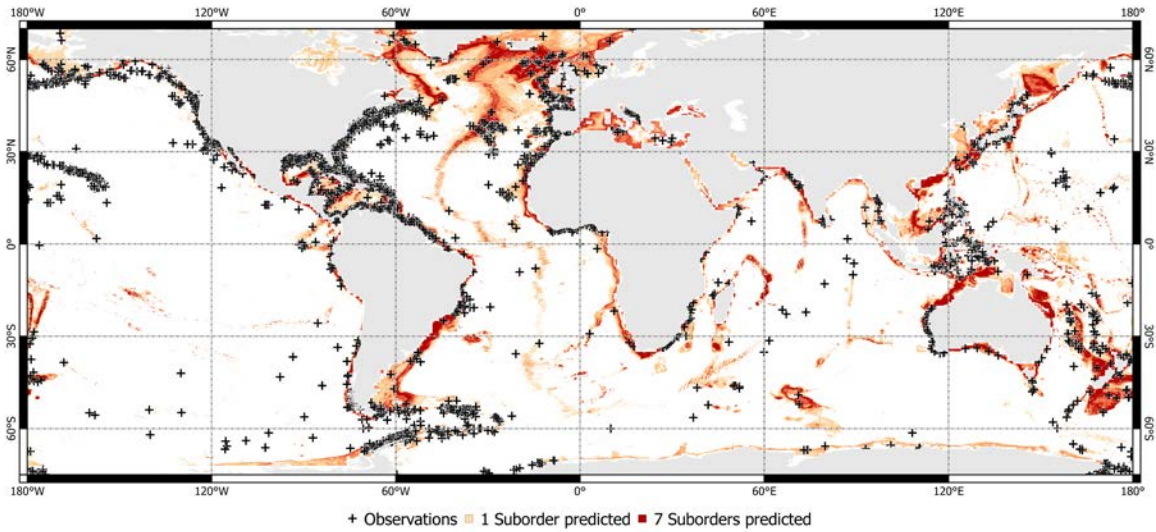
Figure 3. Global octocoral distribution. Direct observations and collections are noted by "x" while the shading represents the habitat suitability probability for the presence of one order (lighter orange) or all nine orders (darker orange) Adapted from Yesson et al., 2012.
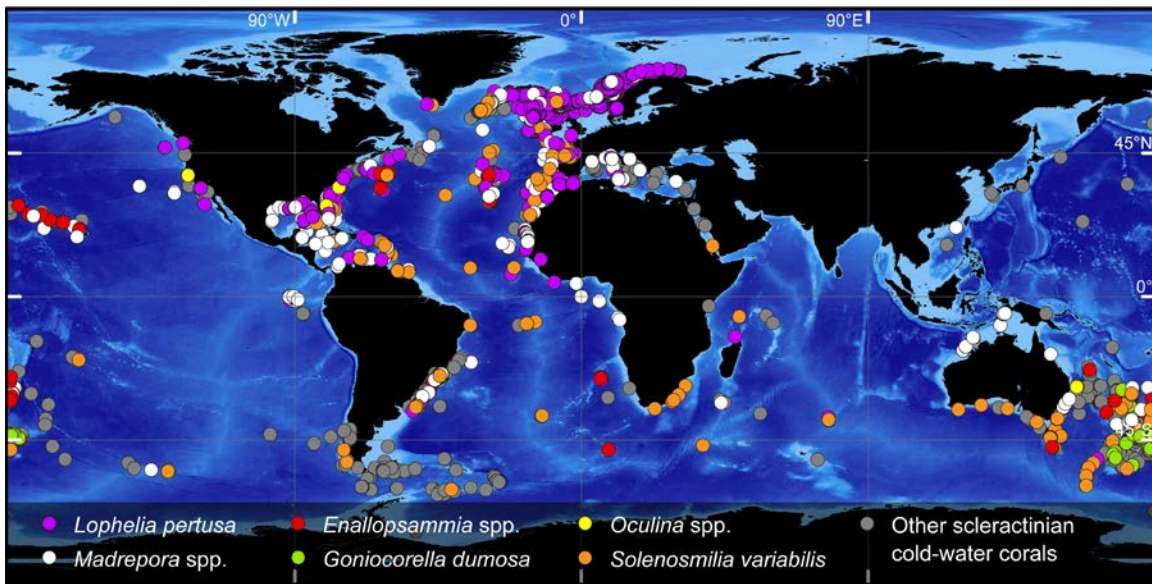
Figure 4. Global distribution of the major framework-forming cold-water corals. Source: Freiwald et al., 2005, and more recent published data, n = 7213 entries.

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