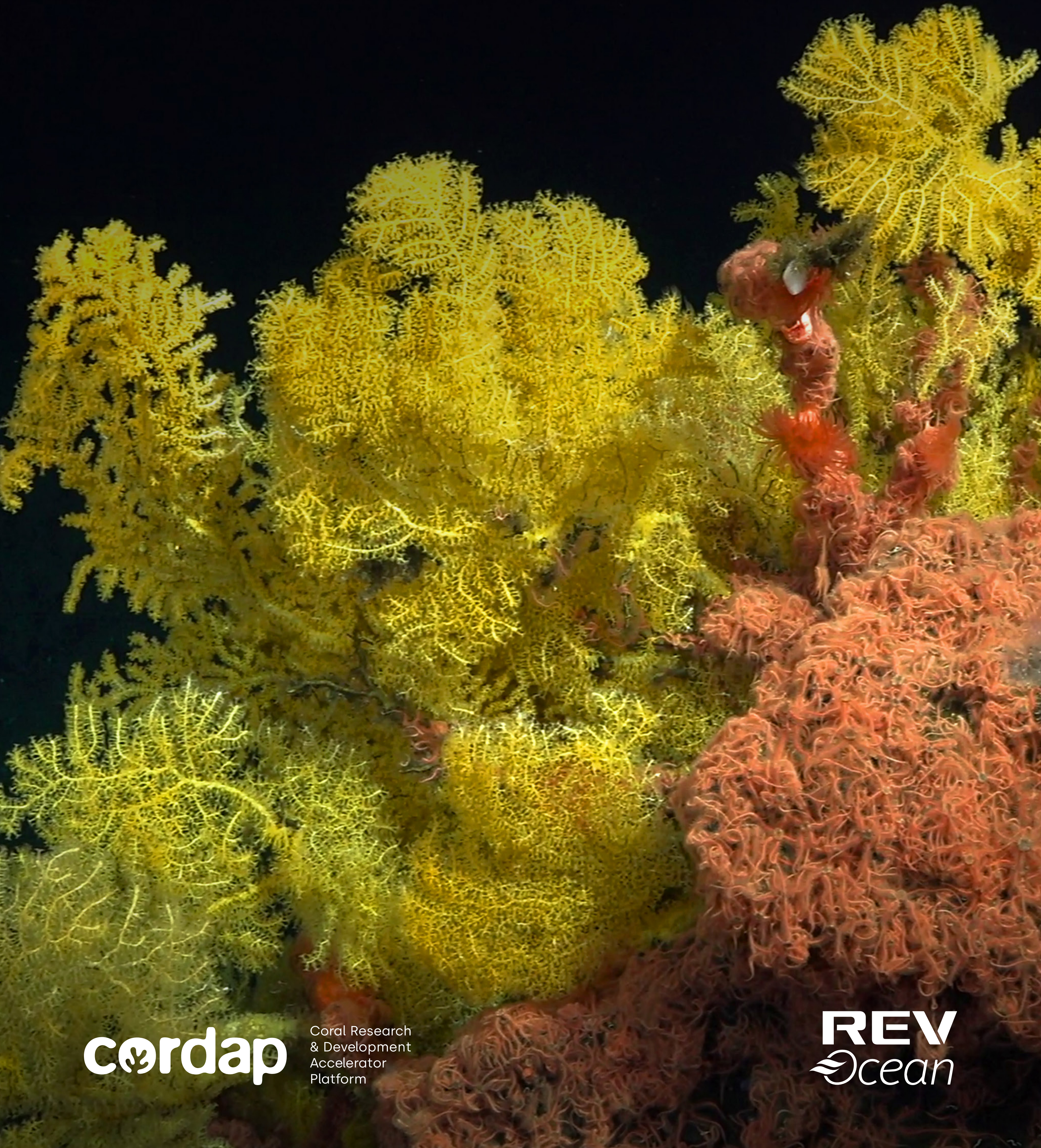
# Conservation and Restoration of Cold-Water Corals

## CORDAP R&D Technology Roadmap



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# Authors

- **Liu,** Q. State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China; University of Bristol, Bristol, UK
- **Rogers,** A.D., REV Ocean, Norway; The Nippon Foundation-Nekton Ocean Census, UK
- **Roch,** C. King Abdullah University of Science and Technology (KAUST), Saudi Arabia
- **Gordon,** J. University of Essex, UK
- **Duarte,** C.M., CORDAP, King Abdullah University of Science and Technology (KAUST), Saudi Arabia
- **Robinson,** L.F. University of Bristol, University of York, UK
- **Waller,** R.G. Gothenburg University, Gothenburg Global Biodiversity Centre, Sweden
- **Ferrier-Pagès,** C. Centre Scientifique de Monaco, France
- **Brooke,** S. Florida State University Coastal and Marine Lab, USA
- **Carreiro-Silva,** M. Institute of Marine Sciences - Okeanos, University of the Azores, Portugal
- **Benson,** K. NOAA Fisheries, USA
- **De Carvalho Ferreira,** M.L. University of Bristol, UK. University of Chicago, USA
- **Du Preez,** C. Fisheries and Oceans Canada (DFO), Canada
- **Banks,** S. Charles Darwin Research Station, Galapagos Ecuador
- **Barry,** J.P. Monterey Bay Aquarium Research Institute (MBARI), USA
- **Cordeiro,** R.T.S. Universidade Federal Rural de Pernambuco, Brazil
- **Cordes,** E. Temple University, USA
- **Hennige,** S. University of Edinburgh, UK
- **Hourigan,** T.F. National Oceanic and Atmospheric Administration, USA (Retired)
- **Kitahara,** M.V. University of São Paulo, Brazil
- **Kutti,** T., Institute of Marine Research, Norway
- **Larsson,** A.I. University of Gothenburg, Sweden
- **Lauretta,** D.M. Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” Conicet. Argentina
- **Matsumoto**, A.K. Chiba Institute of Technology, Japan
- **Ross,** R.E., Institute of Marine Research, Norway
- **Ramirez-Llodra,** E., REV Ocean, Norway
- **Yánez Suárez,** A.B. Memorial University of Newfoundland, Canada
- **Edinger,** E. Memorial University of Newfoundland, Canada
- **Metaxas,** A. Dalhousie University, Canada
- **Filander,** Z.N.P. Biodiversity and Coastal Research, Oceans and Coasts, Department of Forestry, Fisheries, and Environment, Cape Town, South Africa
- **Taylor,** M.L. University of Essex, UK

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Credits: Fisheries and Oceans Canada

# 1. Executive Summary

Cold-water corals form globally significant, yet understudied and poorly understood, diverse productive ecosystems. In this study and roadmap, the term ‘cold-water coral’ (CWC) serves as a general definition for a multitude of coral species that occupy different habitats beyond the warm, sunlit waters inhabited by tropical corals, thus covering both deep-water and cold-water corals.

This roadmap reviews the background and current status of CWC knowledge, identifies and analyses the most significant gaps in our knowledge, and puts forward a number of recommendations to enhance CWC conservation and restoration over the next decade.

Cold-water corals have only become more widely studied in recent decades, despite early records dating back to the late eighteenth century. Unlike most shallow-water corals, CWCs do not rely on sunlight, and thus are not limited to living within shallow depths. Instead, CWCs are often found in cold, dark waters at depths, from approximately 3 m in temperate and polar areas to up to 6,400 m below the ocean surface and colonise continental margins, ridges, seamounts and plains across most of the world's ocean basins. Many are characterised by slow growth rates, long lifespans, and fragile structures.

Due to the slow growth rates and extreme longevity of most CWCs, in which maximum lifespans often exceed 100 years (with one found to be over 4200 years old), conservation and restoration strategies require careful consideration. Most CWCs provide significant ecosystem functions in the deep sea, such as habitat and nursery grounds for other species including commercially valuable fish and crustacean species.

Despite their ecological importance, CWCs are poorly understood and face numerous threats from various human activities, such as bottom fishing, oil pollution, deep-sea mining and climate change. Their vulnerability is aggravated by the fact that they are poorly mapped in most regions, and often only discovered when they have already sustained substantial damage. Consequently, several CWCs have been identified as indicator species for classifying vulnerable marine ecosystems and their role in the conservation of marine biodiversity in various regions is widely recognised.

Efforts have been made to protect and restore CWC ecosystems which focus on reducing or eliminating human activities that damage CWC habitats through marine protected areas (MPA) or other effective conservation measures. Although active restoration of damaged or degraded CWC habitats is still in its early stages, initial experiments show some degree of promise in assisting recovery. The primary obstacles to effective CWC conservation and restoration continue to be a lack of knowledge as well as insufficient action and resources.

Research on CWCs has significantly increased over the past two decades, primarily conducted in Europe and North America. Key focus areas include CWC ecology, environmental impacts, and human activities. Despite the growing body of research, gaps remain in their classification, genetic studies, restoration techniques, and long-term monitoring. The results emphasize the importance of international collaboration, increased funding, and expanding research efforts to underrepresented regions to address these gaps and advance the conservation and restoration of CWCs.

Building on a comprehensive review of the literature, a workshop on CWC conservation and restoration was held in Norway in May 2023, in which 26 leading international researchers participated. Discussions were directed around identifying key knowledge gaps, challenges faced by the coral community, and resulting recommendations to move the field forward and secure a future for cold water corals.

Key Knowledge gaps identified included poorly understood global and regional distribution of CWC's, with accurate mapping a challenging but essential part of effective conservation and management. Related to this are the geographical gaps in exploration, particularly in the waters of the Global South due to logistical challenges and limited resources. There exists a range of gaps in our scientific understanding of CWC's, from the composition of CWC communities, to their reproduction, growth, feeding dynamics, reef building processes and how global communities of CWC's are connected.

To address the significant lack of knowledge of, and to secure a future for, these vital global ecosystems, the following actions requiring the scientific community, national and international agencies, policy makers and governments working together are recommended:

1. **Capacity development for an equitable deep-sea and CWC research and management community:** Workshop participants emphasized the need to develop CWC information exchange and capacity in the Global South, addressing the deep-sea data bias favoring the Global North. No CWC restoration activities currently exist in the Global South due to access challenges. Nations with deep-sea infrastructure should support knowledge exchange and training with the Global South and provide access to their resources. Promoting affordable deep-sea initiatives like those by the Ocean Discovery League is essential for equitable access to deep sea.
2. **Work towards stopping bottom-trawl fishing in areas of CWC occurrence:** Bottom trawling has impacted 14% of the 7.8 million-km$^2$ study area of 24 continental shelves and slopes down to 1,000 meters, indicating some hope for CWC survival in the 86% untrawled areas. Trawled seabeds will not support CWC regrowth for decades to centuries to come. The multi-century recovery times mean the destruction of

impacted CWC habitats, which can be thousands of years old, may be considered irreversible within managerial time scales. Efforts should focus on identifying non-trawled locations for protection. Prioritizing prevention of further impacts over post-impact restoration is both an economic and ecological imperative.

3. **CWC research and management community coordination:** Better coordination of the CWC research, policy, management, conservation, and academic pursuit would support more collaboration, results dissemination, knowledge exchange, and data sharing. There are common global issues that the CWC community face and a united approach to these significant challenges would be better supported by a coordinated community.

4. **CWC sample rescue:** Biological samples from past and future deep-sea expeditions should be made widely available to support diverse research goals. Many thousands of specimens are stored locally and not in accessible and registered locations acknowledged by workshop participants. Hence "sample rescue" activities should be urgently deployed, such as those developed by Ocean Census.

5. **CWC occurrence data rescue and compilation:** It was acknowledged that vast amounts of CWC data (distribution, taxonomic, biological, video, etc.) are held in academia and industry but are not accessible in online databases. A global data rescue initiative would significantly enhance knowledge of CWC presence, essential for restoration, conservation, and management. Current data rescue efforts are operated in isolation. The Ocean Biodiversity Information System (OBIS) could potentially be a universal database for CWC data, but organizing and formatting this data requires a significant increase in resources.

6. **Increasing public knowledge of CWC:** Public awareness and understanding of the importance of CWCs and the threats they face are generally low, impacting the success of conservation initiatives. It is important that CWC specifically become a more widely known ecosystem to ensure public and political support for current and future protections. Active participation of the CWC scientific community in relevant policy forums, such as the United Nations Framework Convention on Climate Change (UNFCCC) and Convention on Biological Diversity (CBD), where CWCs are notoriously absent from events and discussions is important.

To secure a future for our deep-sea ecosystems and the incredible life they sustain, we must act now. Crucial for marine biodiversity and commercial fisheries, they face numerous threats and remain poorly understood. We urge the scientific community, national and international agencies, policymakers, and governments to join forces. Through sustained investment and collaborative efforts on the recommendations put forward in this report, we can advance the conservation and restoration of cold-water corals, ensuring their survival for future generations. Your support is crucial—let's make a difference today.

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# 2. Background and Status of CWC Knowledge

Deep/cold-water corals (CWCs) (Figure 1) have only become more widely studied in recent decades, despite early records dating back to the late eighteenth century (Rogers, 1999; Roberts *et al.*, 2009). Unlike most shallow-water corals, CWCs do not rely on symbiotic relationships with photosynthetic algae, and thus are not limited to living within the photic zone. Instead, CWCs are often found in cold, dark waters at depths, from the photic zone in temperate and polar areas (e.g. Cairns, 2000; Venkataraman, 2007; Santodomingo *et al.*, 2013; Movilla *et al.*, 2016; also deepwater emergence, reviewed in Häusserman *et al.*, 2021) to up to 6,400 m below the ocean surface (Cairns, 2016) and colonise continental margins, ridges, seamounts and even sedimentary plains across most of the world's ocean basins (OBIS, 2023).

Many are characterised by slow growth rates, long colonial lifespans, and fragile structures (Roberts *et al.*, 2009). Due to the slow growth rates and extreme longevity of most CWCs, which maximum lifespans often exceed 100 years (Prouty *et al.*, 2017; with one aged at over 4200 years; Roark *et al.*, 2009), conservation and restoration strategies require careful consideration. Most CWCs provide significant ecosystem functions in the deep sea, such as habitat and nursery grounds for other species (Rogers, 1999; Harter *et al.*, 2009; Henderson *et al.*, 2020), including commercially valuable fish and crustacean species (Rogers, 1999; Costello *et al.*, 2005; Husebø *et al.*, 2002; Söffker *et al.*, 2011). Despite their ecological importance, CWCs face threats from various human activities, such as bottom fishing (Clark *et al.*, 2016; Victorero *et al.*, 2018), oil pollution (e.g., Deepwater Horizon oil spill; Girard and Fisher, 2018), deep-sea mining (Gollner *et al.*, 2017; Vanreusel *et al.*, 2016), and climate change (Danovaro *et al.*, 2001; Hebbeln *et al.*, 2020).

Their vulnerability is aggravated by the fact that they are poorly mapped in most regions, and often discovered when they have already sustained substantial damage (Hall-Spencer *et al.*, 2022). Consequently, several CWC taxa have been identified as indicator species for classifying vulnerable marine ecosystems (VMEs; United Nations General Assembly [UNGA] Resolution 64/72), and the role of their conservation of marine benthic biodiversity in various regions is widely recognised (e.g. Long *et al.*, 2020). Efforts have been made to protect and restore CWC ecosystems (Chaniotis *et al.*, 2020; Da Ros *et al.*, 2019; Montseny *et al.*, 2021a; Van Dover *et al.*, 2014), which focus on reducing or eliminating human activities that damage CWC habitats through marine protected areas (MPA) or other effective conservation measures (Beazley *et al.*, 2021; Otero and Marin, 2019). Although active restoration of damaged or degraded CWC habitats is still in its early stages, initial experiments show some degree of promise in assisting recovery (Montseny *et al.*, 2021a). This roadmap seeks to comprehensively assess the present state of knowledge of CWC conservation and restoration, with a focus on identifying knowledge gaps and key scientific, technological, and economic challenges. Additionally, it aims to provide recommendations for prioritizing future research and specific areas for investment and development.

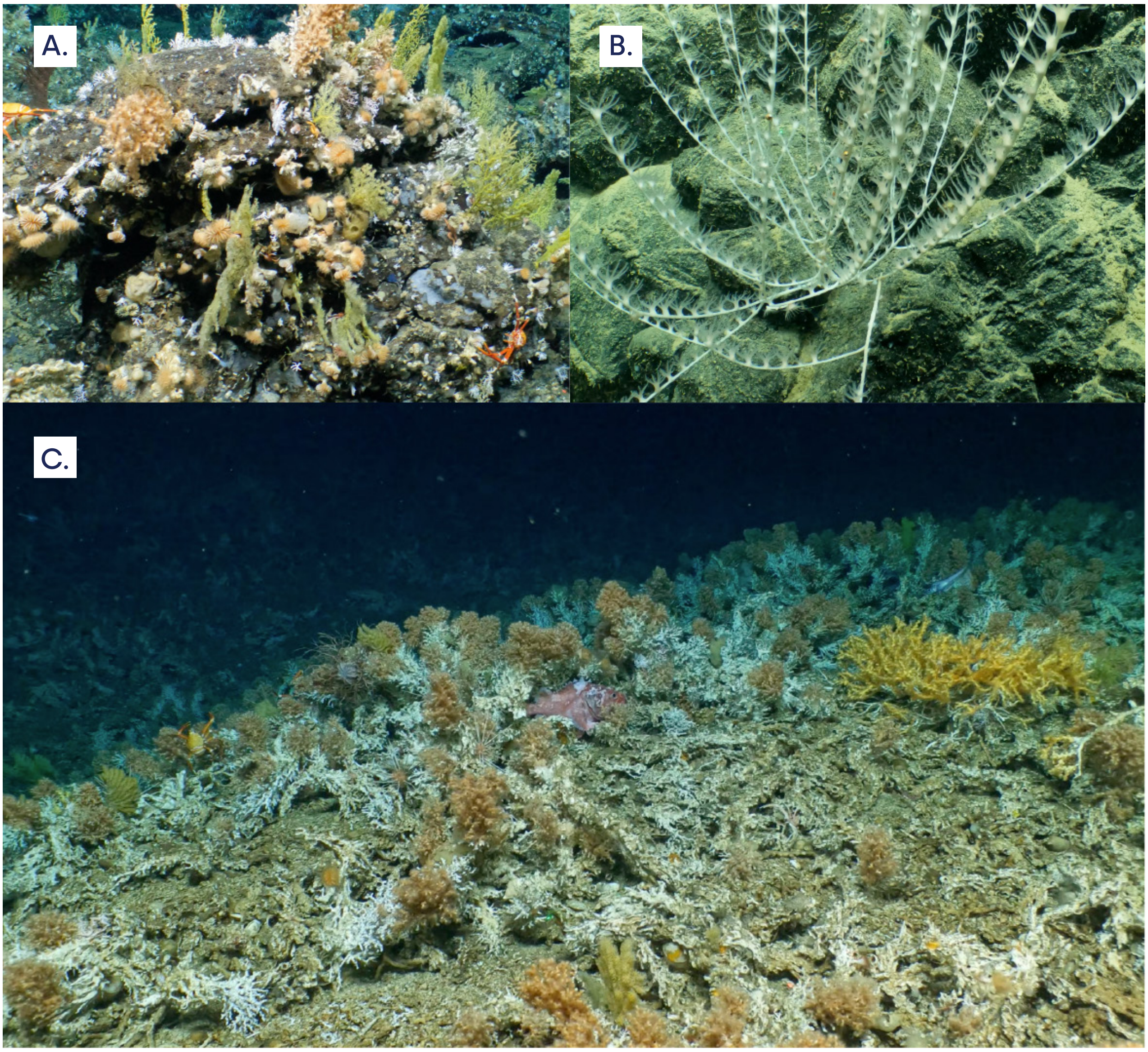

Figure 1. Cold-water corals reef and individual coral discovered in Galapagos. A. CWC garden; B. individual Keratoisididae; C. CWC reef (*Madrepora* sp.). Credits: UBristol/WHOI/UEssex/UBoise/NERC/NSF/National Park Galapagos.

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## 2.1 A Definition of "Cold-Water Corals"

The wide range of ocean conditions on our planet and the diverse adaptations that enable corals to survive in these environments present a significant challenge in providing a concise description that encompasses the various types of cold-water corals. Consequently, the term 'cold-water coral' (CWC) serves as a blanket term for a multitude of coral taxa that occupy different habitats beyond the warm, sunlit waters inhabited by tropical zooxanthellate corals. Conventionally this includes Octocorallia, some Hexacorallia, and at least one family of Hydrozoa, the Stylasteridae (lace corals). This terminology has been applied to 'deep-water corals', even though the same taxa can be found in shallow polar seas (a phenomenon called cold-water / deep-water emergence; Hessler, 1970; Grange and Singleton, 1988; Stone and Shotwell, 2007, Taylor and Rogers, 2015, Häussermann *et al.*, 2021). It has also been used to refer to any corals found in cold "deep" water. The threshold for the "deep sea" is often considered to be 200 m, but in some regions, "deep water" may not necessarily equate to cold water.

For instance, in the Red Sea, corals can be found in 22 °C water down to 100 m depth (Roder *et al.*, 2013, Qurban *et al.*, 2014). It is, therefore, beneficial to have a unified definition that encapsulates this complexity. We propose the following definition: Acknowledging that exceptions are common in biology, we propose that the term "cold-water coral" (CWC) describes all corals that do not harvest light (azooxanthellate) or are facultatively zooxanthellate (e.g. *Oculina varicosa*), indicating the absence of symbiotic dinoflagellates that are, in contrast, commonly found in "shallow" (less than 200 m) and "warm" (above 12 °C) water corals.

This definition would typically include deep/cold water corals and exclude the majority of warm-water corals found shallower than 30 m depth, while acknowledging the possibility of exceptions in biology to this general classification. We believe this operational description covers most species that researchers refer to as deep/cold water corals and we hope, therefore, that it will be adopted by the scientific community. A single description is after all important in terms of public outreach and informing policy, as it makes this ecosystem more accessible to non-specialists. It is important to note that this does/should not replace secondary descriptors (i.e. deep-sea; deep-water emerged; etc.) in the peer reviewed literature where needed to describe specific habitats/species.

## 2.2 Bibliometric Analysis

CWC research is a rapidly growing field, with an increasing number of publications each year.

Despite the increasing number of published articles, there is a lack of scientometric study that explores the global research landscape of CWCs. The lack of a coherent lens through which to examine and analyse the field from various perspectives and levels of detail results in an incomplete or fragmented comprehension of the field and its development. To fill this gap, this study aims to perform a bibliometric analysis of publication metadata to provide a comprehensive overview of the publication landscape, which is invaluable for identifying key research priorities and collaboration opportunities. Specifically, we aim to examine:

1. Publication growth trends,
2. Authorship patterns,
3. Research collaboration networks among countries and institutions.

### 2.2.1 Methods

The Web of Science (WoS) Core Collection was used to collect bibliographic data using the following search terms: ("deep sea" OR "cold water" OR "deep water") NEAR/5 (coral$ OR gorgonia* OR anthozoa*) in the title, keywords, and abstract up until the year 2022. Bibliographic data, including the full record and cited references, were extracted and imported into VOSviewer for visualising co-authorship patterns and keyword co-occurrence, while InCites was used for descriptive analysis. Keyword co-occurrence analysis, conducted using author keywords, assumes that words that frequently occur together have a thematic relationship with each other and can thus provide meaningful insights into thematic clusters and research topic hotspots (Donthu *et al.*, 2021). Co-authorship patterns can be an informative method to analyse the connectedness of research and intellectual collaboration (Donthu *et al.*, 2021).

### 2.2.2 Global Publication and Collaboration Patterns

Our search identified 1,649 articles in the field of CWC research, with the first article published in 1964. In its nascent phase, publication frequency was low, with around three new articles published per year up until 2000. In the early 2000's-2010 the field experienced a significant increase in CWC publications, with an average of 34 new publications annually. This growth accelerated further, reaching an average of 97 new publications per year between 2010 and 2022. Overall, publication rate followed an exponential growth trend ($R^2$=0.86) with an average annual growth rate of 10.46% (Figure 2B).

Overall, researchers from 76 countries have contributed to the academic literature of CWC research, which represents approximately 50% of all countries with coastlines. Our analysis highlights significant disparities in research output between countries, where scientists from the global north published the majority of articles (Figure 2A). Authors of US institutions showed the highest research output, contributing to approximately one third (35%) of all publications in CWC research, followed by the UK which contributed to 29% of publications. Germany, France, and Spain were also actively involved, contributing to 18%, 12% and 10% of all publications, respectively.

To examine publication trends according to leadership positions, we analysed authorship patterns focusing on first authors. High-income nations dominated first authorship, accounting for 93% of all articles, while upper-middle-income countries contributed 6%, and lower-middle-income countries less than 1%. Notably, no articles were led by researchers from low-income countries. Leading the publication authorship were researchers from US institutions, which led nearly a quarter (22%) of all articles, followed by authors from the UK and Germany, who led 13% and 10% of articles respectively.

According to the collaborative networks observed in CWC research (Figure 2C), the United States and Germany appear as central nodes. They have the most extensive collaborative engagements, collaborating with 54 and 51 other countries respectively. The network also indicates strong intercontinental links between North America and Europe, with the most frequent collaborations occurring between the US and the UK, the US and Canada, and the US and Germany, highlighting a pattern where high income-nations tend to collaborate among each other. Lower income nations are positioned at the extremity of the network and tend to collaborate with higher income nations.

### 2.2.3 CWC Research Themes and Keyword Co-Occurrence

The keyword co-occurrence network provides a visualization of key research themes and their interconnectivity within the body of CWC literature. Our analysis indicates that CWC research focusses on the biology of CWCs, their habitats and environmental influences. For instance, certain regions such as the Mediterranean (n =81) and Northeast Atlantic (n = 50), along with coral species like Desmophyllum pertusum (n = 158; originally called Lophelia pertusa), are frequent keywords in the literature, signifying concentrated research in these areas. The research directions of CWC-related publications were divided into four distinct clusters of concepts that frequently appeared alongside each other (Figure 3). The yellow cluster represents the central focus on the biological and taxonomic aspects of CWC research, where a substantial body of research is dedicated to studying coral biodiversity, phylogenetic relationships, and species-specific traits as evidenced keywords such as "phylogeny", "taxonomy", and "new species". The blue cluster represents

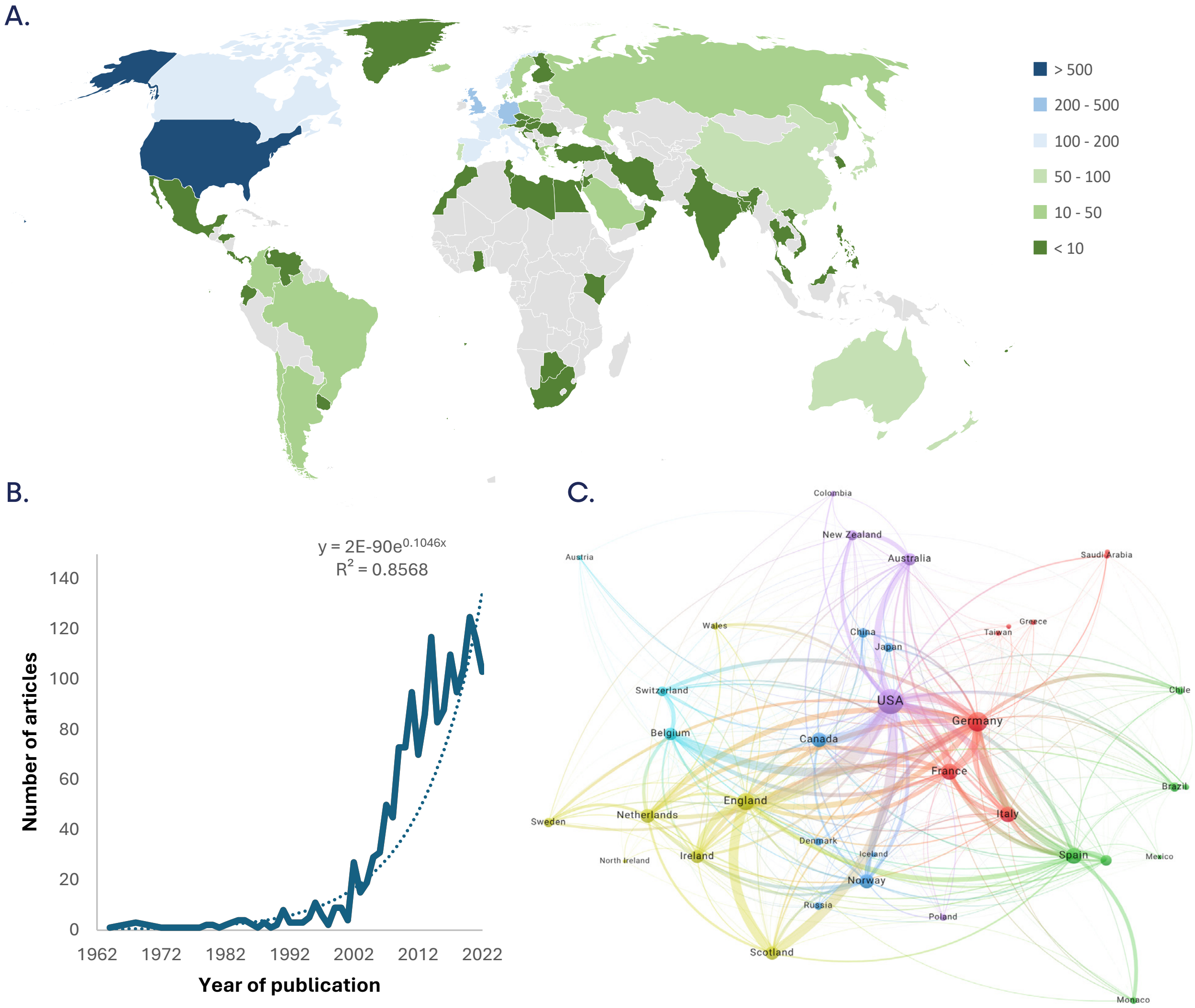


Figure 2. Global trends in CWC research output and collaborations. A. Geographic distribution of authors contributing to CWC research. B. Annual publication trends illustrating the new articles published each year. C. Collaboration network between countries, where node size represents the number of articles per country and line thickness the strength of collaboration, representing the frequency of co-authorship between countries. The colour coding corresponds to a PCoA analysis, clustering countries with similar collaboration patterns.

investigation into the environmental dynamics impacting CWC ecosystems, encompasses the physical characteristics and environmental factors affecting CWC growth and development. Important terms in this cluster include “ocean acidification,” “climate change,” “biomineralization,” and “calcification,” suggesting an emphasis on the physiological responses of CWCs to changing ocean conditions. The green cluster includes terms such as “management”, “vulnerable marine ecosystems”, “conservation” and “biodiversity”. The red cluster refers to themes related to geomorphology with terms such as “habitat mapping”, “carbonate mounds”, “bottom currents” etc.

### 2.2.4 Discussion on the Bibliometric Analysis

In recent years, there has been a growing interest in studying cold-water corals (CWC), with the number of articles published on this topic experiencing exponential growth. CWC research started to gain momentum in the 2000s and has been on a rapid rise ever since, particularly as new organizations and initiatives focused on deep-sea ecosystems, like the International Symposium on Deep-Sea Corals in 2000, came into existence. Although CWC research is rapidly growing, it represents only a small fraction of coral research compared to their shallow water counterparts (18,311 publications; WOS accessed on 01/05/2023).

The growing interest in CWC is likely driven by technological advances such as remote-operated vehicles (ROVs), advanced imaging techniques, and the huge strides made in acoustic seabed mapping with multibeam echosounder allowing to investigate ever deeper waters (Brandt *et al.,* 2016; Robison, 1999). Additionally, concerns about the impact of human activities in these areas has increased. Activities like offshore oil exploration and deep-sea fishing have expanded into deeper waters, raising the need for conservation measures (Ragnarsson *et al.,* 2017; Roberts and Cairns, 2014). However, despite this increasing interest and concern, keyword clustering analysis reveals that topics related to interventions like conservation and management have yet to receive widespread attention in the research community so far. For instance, the keyword "restoration" only occurred five times in the dataset. Additionally, publications addressing conservation and management tend to cluster together but are not strongly connected to other research topics (Figure 3), underscoring the need to better integrate these aspects into the broader research field.

Although recent technological advances have made deep sea research more accessible in terms of broadening our capacity to explore more remote and deep regions of the ocean, the issue on unequal access to participate in CWC research across nations is pronounced. This inequality is particularly visible in terms of geographic distribution of authors and institutions, with the highest contributions coming from a select few high-income nations (Figure 2C). In fact, more than 93% of all research was led by economically

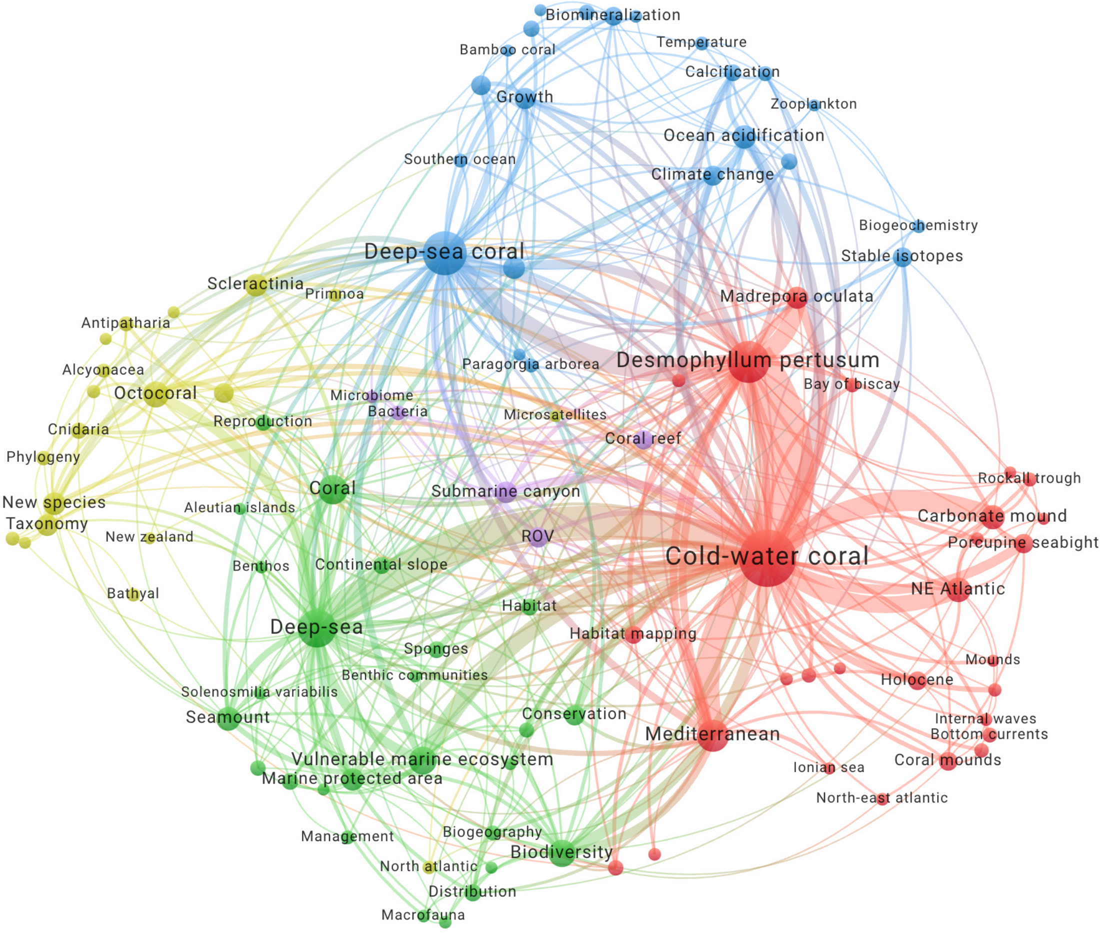


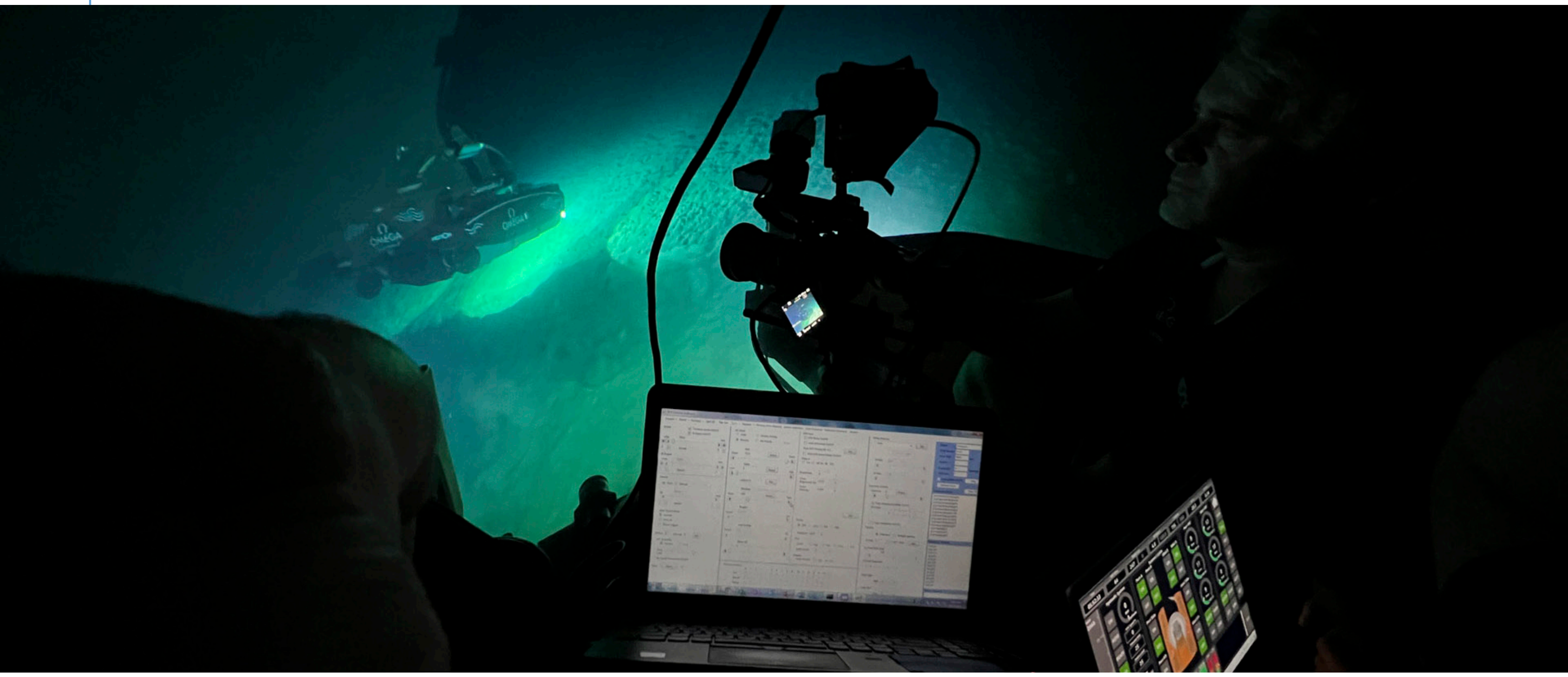
Figure 3. Network of CWC research themes. Author keyword co-occurrence network, where nodes the node size is proportional to the term's frequency, and the link thickness indicates the strength of co-occurrence between terms. The distance between nodes displays the relatedness of the link connections and nodes with common attributes are assigned to a colour-coded cluster following Principal Coordinates Analysis (PCoA). (Note: only author keywords with n > 10 are displayed).

developed nations and there was a significant underrepresentation of scientists from lower income nations, such as for example African countries and Small Island Nations. The high costs associated with deep-sea exploration and the limited access to suitable infrastructure are likely the most significant barriers, effectively limiting the participation of many developing nations in CWC research (Harden-Davies *et al.,* 2022). Additionally, the lack of available research funding in less economically developed countries often results in a lack of local expertise to support deep-sea research, resulting in unequal research capacity across the globe (Miloslavich *et al.,* 2019). The underrepresentation of scientists from developing nations in deep-sea research can result in limited scientific progress, hindered conservation efforts, and potentially negative impacts on the environment and local communities in these regions. It highlights the importance of promoting inclusivity and diversity in scientific research to address these challenges effectively.

The network analysis illustrates strong collaborations and interconnectedness among researchers from wealthy nations, such as the US, the UK, Germany, Italy, and France, all of which demonstrate high publication output in CWC research. Simultaneously, it highlights the scarcity of collaborations between developed and developing nations (Figure 2C). Moving forward in the Decade of Ocean Science for Sustainable Development, this presents an opportunity to develop strong and long-lasting collaborative relationships with developing nations to co-develop and co-produce transregional research (Howell *et al.,* 2020). Inclusive and equitable collaborations that span the whole research process are essential for transferring skills and knowledge. This is particularly important for strengthening local expertise in developing countries where national research capacity and funding are often limited. Additionally, such collaborative efforts would ensure that diverse perspectives and approaches to deep-sea research are considered. Recognizing that greater diversity, equity, and inclusion within deep-sea research and conservation communities are not just ethical imperatives but also drivers of scientific progress and the success of conservation efforts (Freeman and Huang, 2015; Tulloch, 2020).

## 2.3 Challenges of Cold-Water Coral Research

Cold-water coral research poses challenges to marine scientists which are less relevant in terrestrial and/or shallow-water marine science. These ecosystems are typically found in the deep-sea, which requires ocean-going research vessels capable of deploying observing systems to depths of 100s to 1000s of metres. Dredges and trawls were historically



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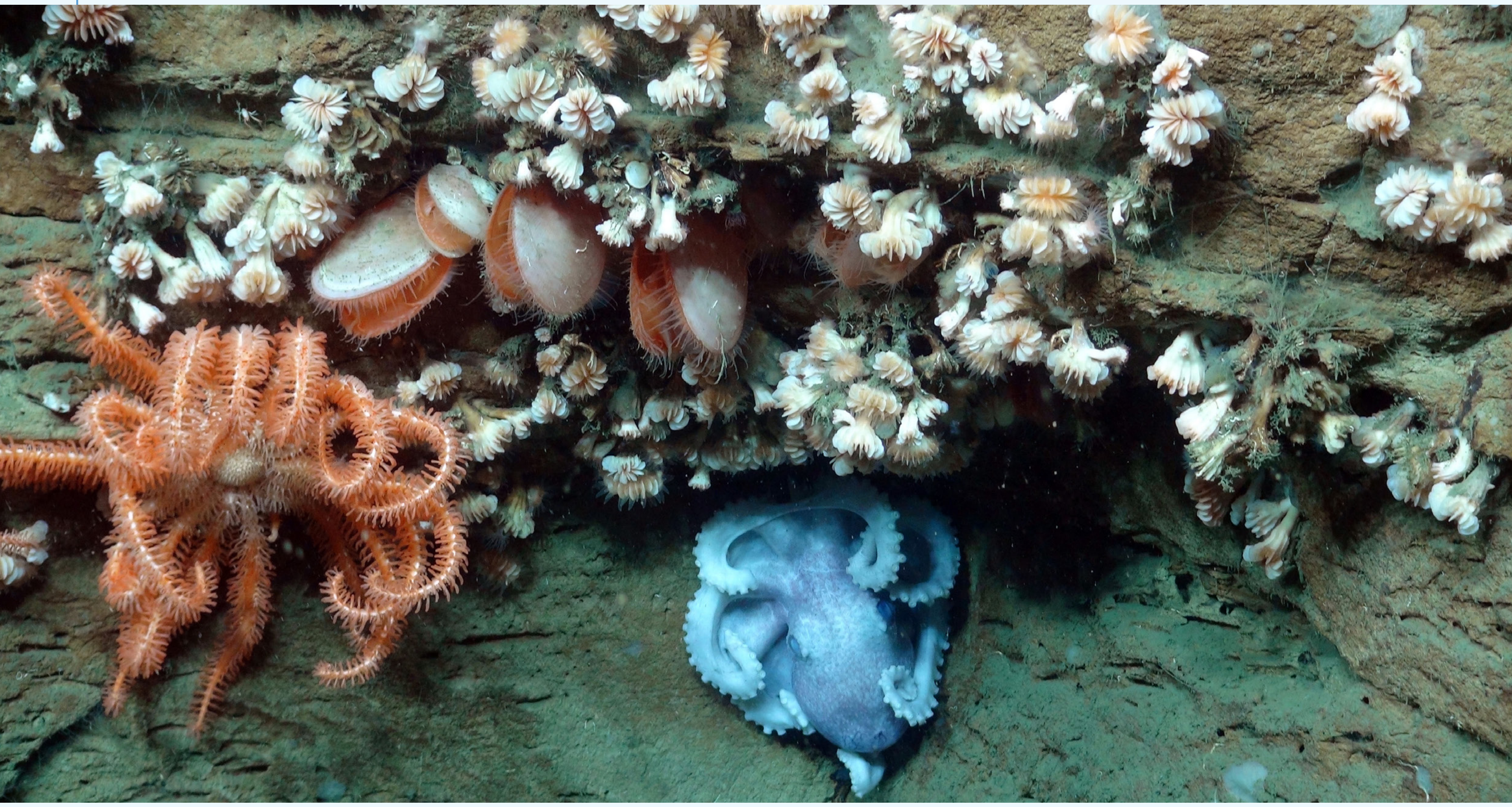
the common “tools of the trade” (for example the Challenger, Siboga and Albatross expeditions), however remotely operated vehicles (ROV), autonomous underwater vehicles (AUV), and human-occupied vehicles (HOV), are becoming the sampling gold standard given that they have lower impacts on the environment, aid more targeted research, and produce high quality biological samples and imagery. However, suitable research platforms are often out of reach financially to many researchers (Rogers *et al.,* 2021). These expensive technological entrance requirements (Howell *et al.,* 2020; Sink *et al.,* 2021; Bell *et al.,* 2023), render deep-sea science largely a privilege of the Global North. Equity in deep-sea sciences is essential to ensure equal and balanced international collaboration (de Vos *et al.,* 2023; Spalding *et al.,* 2023) while avoiding negative impacts on locally-led efforts, or undermining local expertise which can hinder the potential for conservation success (Bennet *et al.,* 2021; de Vos *et al.,* 2023). The unevenly distributed footprint of deep-sea research is also one reason why only 25% of Earth's Ocean seafloor has been mapped in high resolution to date (as of 2nd May 2023 – Seabed 2030; General Bathymetric Chart of the Oceans Compilation Group, 2023). The high costs of the infrastructure required to study deep-growing CWC explains why an estimate of the global extent of this habitat is lacking, even though it is likely to exceed, by at least an order of magnitude, that of tropical water corals (Van Dover *et al.,* 2014).

The high costs of deep-sea research also explains why active conservation, and ecological and physiological research *in situ*, including restoration, are still very rare endeavours in the deep sea. CWC research is thus lagging behind that of shallow-water coral reefs; yet human impacts in the deep sea are wide-ranging and increasing in scope. Additionally, because CWCs function over long time scales, there have been few observations of recovery of coral assemblages from the impacts of bottom trawling, even over multi-decadal time scales (e.g., Waller *et al.,* 2007, Clark and Rowden, 2009). One exception being communities on some once-trawled Hawaiian seamounts where certain CWC species showed signs of recovery after 30-40 years (Baco-Taylor *et al.,* 2019). So, although this review aims to prioritise research topics for the next 10 years, CWC restoration and monitoring are inherently multi-decadal-/ century-scale efforts that need longer term, innovative, and ambitious future investment.



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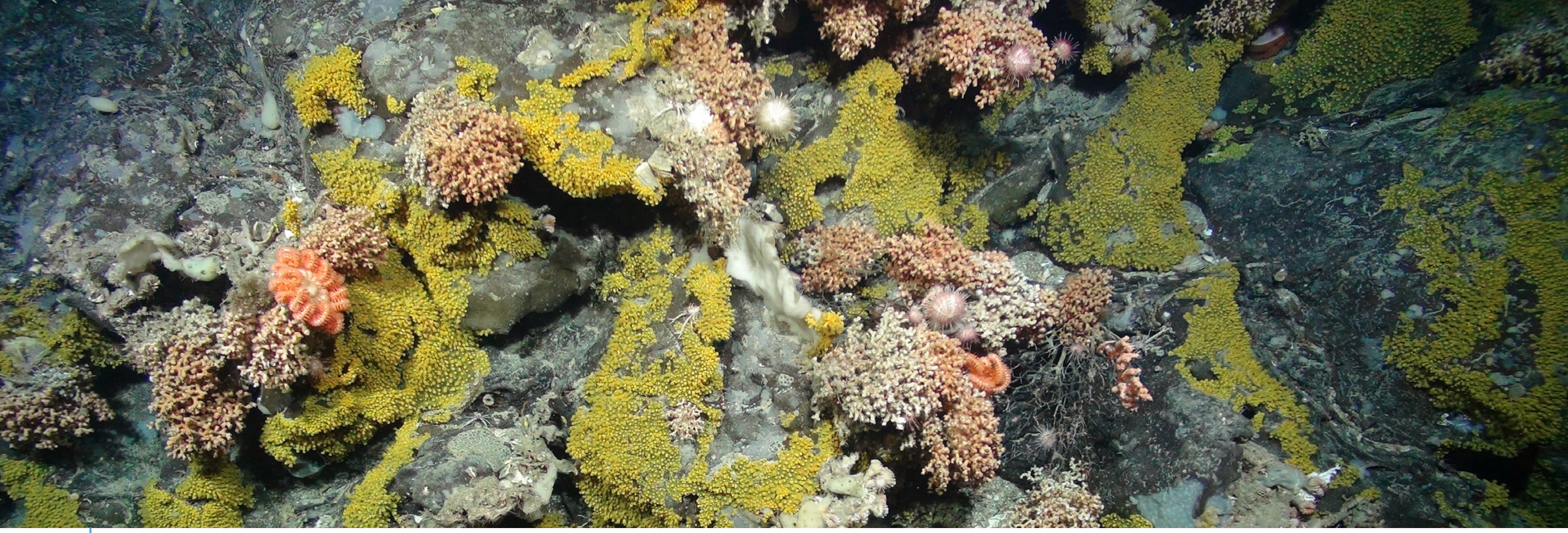

Credits: University of Plymouth

## 2.4 Ecological Functions of CWCs

CWCs form significant marine benthic ecosystems and as "ecosystem engineers" maintain and enhance biodiversity (Freiwald *et al.*, 2004; Morgan, 2006; Rogers, 1999, 2004, Baillon *et al.*, 2012; Hennige *et al.*, 2014a; Wild *et al.*, 2011), which in turn promotes greater resilience of ecosystems to disturbance (Armstrong *et al.*, 2014; Hughes *et al.*, 2005; Steneck *et al.*, 2002). Various CWCs, including branching scleractinians, octocorals, black corals, and stylasterids, create intricate three-dimensional structures that offer shelter, feeding areas, breeding and nursery grounds for many marine organisms (Rogers *et al.*, 1999; Söffker *et al.*, 2011; Stone, 2006; Tissot *et al.*, 2006; Edinger *et al.*, 2007; Husebø *et al.*, 2002; Maynou and Cartes, 2012), especially fish species (Henderson *et al.* 2020; Kutti *et al.*, 2014; Baillon *et al.*, 2012, D'Onghia, 2019 and references therein). In addition, CWC habitats have been shown to host and shelter distinct fish assemblages from surrounding non-coral areas (Fosså *et al.*, 2002).

The specific ecological functions of CWCs are not studied adequately to quantitatively measure their influence on marine biodiversity maintenance and fisheries production for human consumption as yet. Only a few studies have shown the potential benefits of CWCs to commercial fish species; for example, Costello *et al.* (2005) found that 92% of commercial fish species and 80% of individual fishes were associated with *Desmophyllum pertusum* (formerly *Lophelia pertusa*) reef habitat in the North Atlantic. Sea-pen beds in Eastern Canada act as larvae shelters for the commercial fish *Sebastes* spp (Baillon *et al.*, 2012). In addition, Hebbeln *et al.* (2009) observed shark eggs on black coral colonies at 452 and 647 m on El Idrissi Bank (Alborán Sea), a sighting that has been reported in many other CWC surveys globally (D'Onghia, 2019; Henry *et al.*, 2013; Henry and Roberts, 2017), meaning these habitats may play a role in shark fishery maintenance too.

Beyond providing habitat, particularly critical for recruitment, for fishes and sharks, CWCs also serve as substrates for other organisms to settle and grow, such as sponges, sea anemones, and hydroids, further enhancing the overall biodiversity of the ecosystem (Buhl-Mortensen *et al.*, 2010; Longo *et al.*, 2005; Rogers, 1999; Henry *et al.*, 2013). The complex structure of CWCs provides microhabitat diversity (e.g., Krieger and Wing, 2002; Marchese *et al.*, 2021). As a consequence, CWCs and associated organisms contribute to marine carbon cycling and carbon sequestration (Alexander, 2022). Recent studies have shown that CWCs and sponges together form a carbon recycling loop, providing an additional organic-matter-recycling pathway to the established microbial loop (Bart *et al.*, 2021; Maier *et al.*, 2020a, 2021; Rix *et al.*, 2016).

CWCs also serve as a food source for other benthic organisms. Sea stars, in particular, are considered main predators of CWCs (Bo *et al.*, 2019; Mah, 2020). Krieger and Wing (2002) observed sea stars consuming 34 – 45% of the polyps of *Primnoa* spp. at two study sites in the Gulf of Alaska. Matsumoto (2005) reported the nudibranch *Tritonia* feeding on *Primnoa pacifica* in the Northwest Pacific Ocean (Sea of Japan). Furthermore, some filter-feeding organisms utilise CWCs as feeding platforms to sit upon to elevate themselves into higher-current zones above the seafloor, where the rate of food supply is enhanced relative to the seabed (e.g., Buhl-Mortensen and Mortensen, 2005). However, the ecological functions underlying the ecosystem service of food provision to associates is poorly understood (La Bianca *et al.*, 2023). Other potential ecological services are just being discovered; for example, symbiotic nitrogen fixation has been found in CWCs (Middelburg *et al.*, 2015).

La Bianca *et al.* (2023) reviewed current research of deep-sea ecological services that CWCs provide to humans and proposed three regulating services and three cultural services of the deep-sea ecological services framework. The regulating services included i) mediation of wastes or toxic substances of anthropogenic origin by living processes, ii) pest and disease control, iii) regulation of chemical composition of atmosphere and oceans, atmospheric composition, and conditions; and the cultural services included i) intellectual and representative interactions with natural environment, ii) spiritual, symbolic, and iii) other interactions with natural environment, other biotic characteristics that have a non-use value. Understanding of these supporting services lags far behind that of provisioning services and requires further, comprehensive, study.

## 2.5 Anthropogenic Impacts on CWCs

Their slow growth rates (Liu *et al.*, 2023; Neves *et al.*, 2015; Prouty *et al.*, 2011) and long lifespan (Hitt *et al.*, 2020; Robinson *et al.*, 2014; Roark *et al.*, 2009) make CWC populations vulnerable to human activities that damage the seafloor or alter the deep-ocean environment (Freiwald *et al.*, 2004; Morgan, 2006; Roberts *et al.*, 2009; Rogers, 1999). The likelihood of recovery on human time scales is very low, with little evidence for recovery at sites studied for over 30 years post-impact (Clark *et al.*, 2019; Clark and Rowden, 2009; Waller *et al.*, 2007), although such study sites are few and far between. Currently, CWCs are facing various threats from human activities. These activities include direct impacts like fishing, especially bottom trawling, oil and gas exploration and extraction, and mineral extraction as well as impacts from non-point source pressures, like climate change (Clark *et al.*, 2016; Cordes *et al.*, 2016; Järnegren *et al.*, 2017; Levin *et al.*, 2023; Ragnarsson*et al.*, 2017; Ross *et al.*, 2020) and plastic pollution (Pinheiro *et al.*, 2023).

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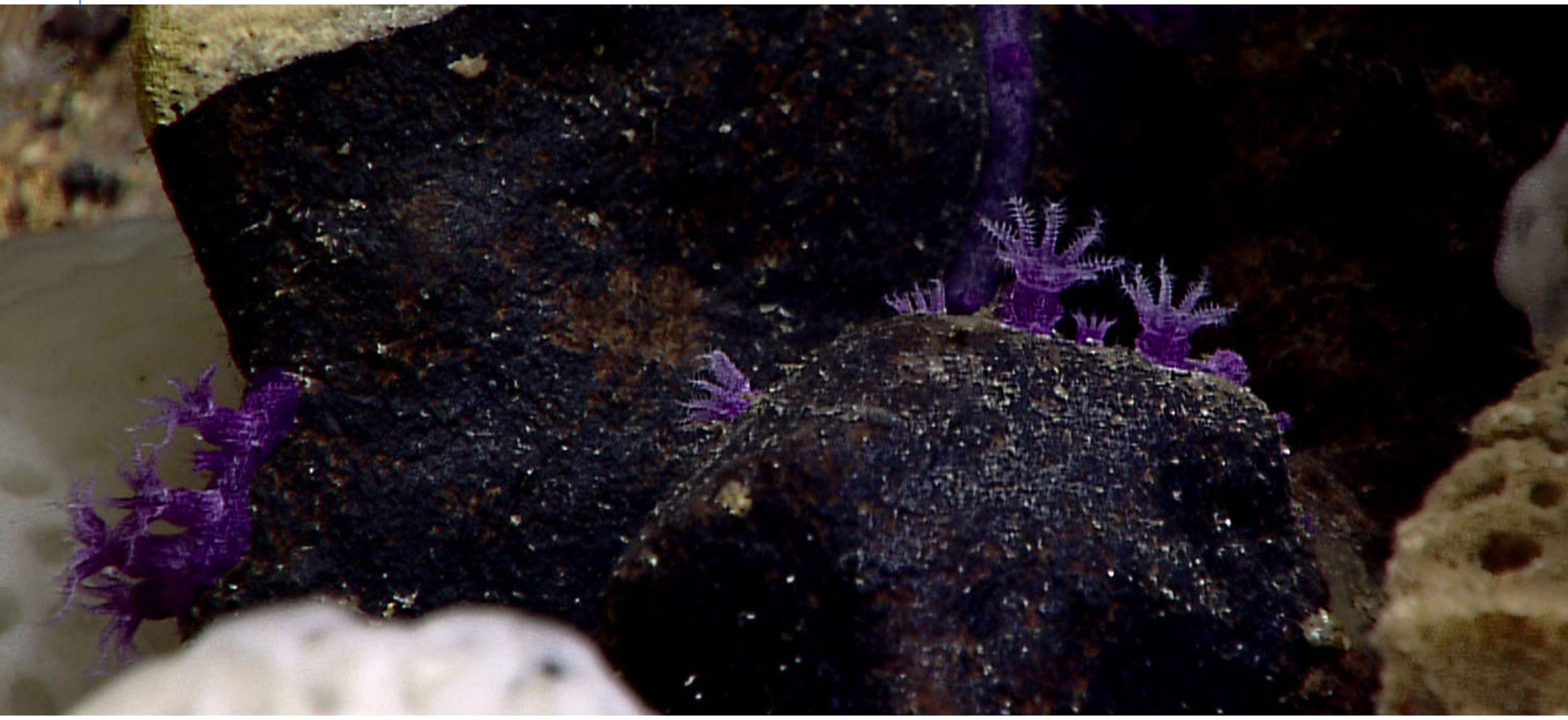

### 2.5.1 Bottom-Contact Fishing

The overexploitation of shallow-water fisheries, coupled with the rapid and subsidised development of fishing techniques and capacity, has facilitated the expansion of the deep-water fishing industry since the 1950s and 1960s (Morato *et al.*, 2006; Roberts, 2002). Bottom-contact fishing, including bottom trawl fishing, bottom longlines, and traps, is one of the most common methods used in the deep-water fishing industry and is considered the greatest threat to CWC communities (Clark *et al.*, 2016; Ragnarsson *et al.*, 2017). The direct impact of bottom-contact fishing is the physical structural damage and removal of CWCs (Figure 4). The heavy gear used in bottom trawl fishing can cause significant damage to coral colonies, or their entire removal, and even physically alter the surrounding seafloor (Clark and Rowden, 2009; D'Onghia *et al.*, 2017; Maynou and Cartes, 2012), leading to substantial reductions in coral cover, and the associated benefits supplied by these complex habitats. Clark *et al.* (2016) summarise the types of observed impacts caused by bottom-contact fishing practices on deep-sea fauna, including removal of habitat-formers (i.e. CWCs), decline in diversity, change in abundance and biomass, reduction in abundance and distribution, and change in community structure. The area of seafloor impacted by a bottom trawl, the severity of its effects on CWC and other epibenthic benthic communities, and the worldwide geographic extent of its use are all much greater than for other bottom-contact gears (Benn, 2010; Ragnarsson *et al.*, 2017; Rooper *et al.*, 2017). Fosså *et al.* (2002) found that 30 – 50% of pre-existing *Desmophyllum pertusum* reefs had been impacted or destroyed by trawling in Norway. Nearly 100% of live coral cover in the six coral reef sites within the boundaries of the Oculina Habitat Area of Particular Concern, in Florida, had been damaged by bottom trawling between 1977 and 2001 (Reed *et al.*, 2007). Video and image studies on seamounts off Tasmania suggest that bottom cover of the reef-forming scleractinian *Solenosmilia variabilis* was reduced by 2 orders of magnitude because of bottom trawling; this loss of CWC habitat caused 3-fold declines in richness, diversity, and density of other megabenthos (Althaus *et al.*, 2009). Although longlines and traps such as static gears are considered to have lower impacts than trawling gears (Pham *et al.*, 2014), they may move laterally across the seabed during their retrieval, resulting in damage of CWCs and other benthic habitats (Waller *et al.*, 2007, Mytilineou *et al.*, 2014; Sampaio *et al.*, 2012).

Bottom-contact fishing also has indirect consequences such as the resuspension of sediment caused by trawl gear (Brooke *et al.*, 2009). An experimental assessment of the sediment tolerance of two morphotypes of *Desmophyllum pertusum*, by using sediment collected from the northern Gulf of Mexico slope; showed that while both morphotypes can tolerate relatively heavy sediment conditions, mortality rates rise significantly with prolonged burial or higher sediment loads (Brooke *et al.*, 2009). For the same species in Skagerrak (Sweden), Larsson and Purser (2011) and Larsson *et al.* (2013) also found high tolerance to benthic sediment exposure but higher sediment loads resulted in coenosarc loss and decreased polyp activity. The impacts of bottom-contact fishing on CWC can thus be significant and long-lasting (Althaus *et al.*, 2009), especially given the centurial time scales for potential recovery.

Bottom-trawling has destroyed many CWC habitats before they were even mapped (Fosså *et al.*, 2002), although, beyond a few case studies, such as those cited above, a comprehensive assessment of the global loss of CWC is lacking as are both historical and contemporary baselines. CWC therefore stand among the least known of the marine habitats of biodiversity significance, which hinders conservation and restoration efforts.

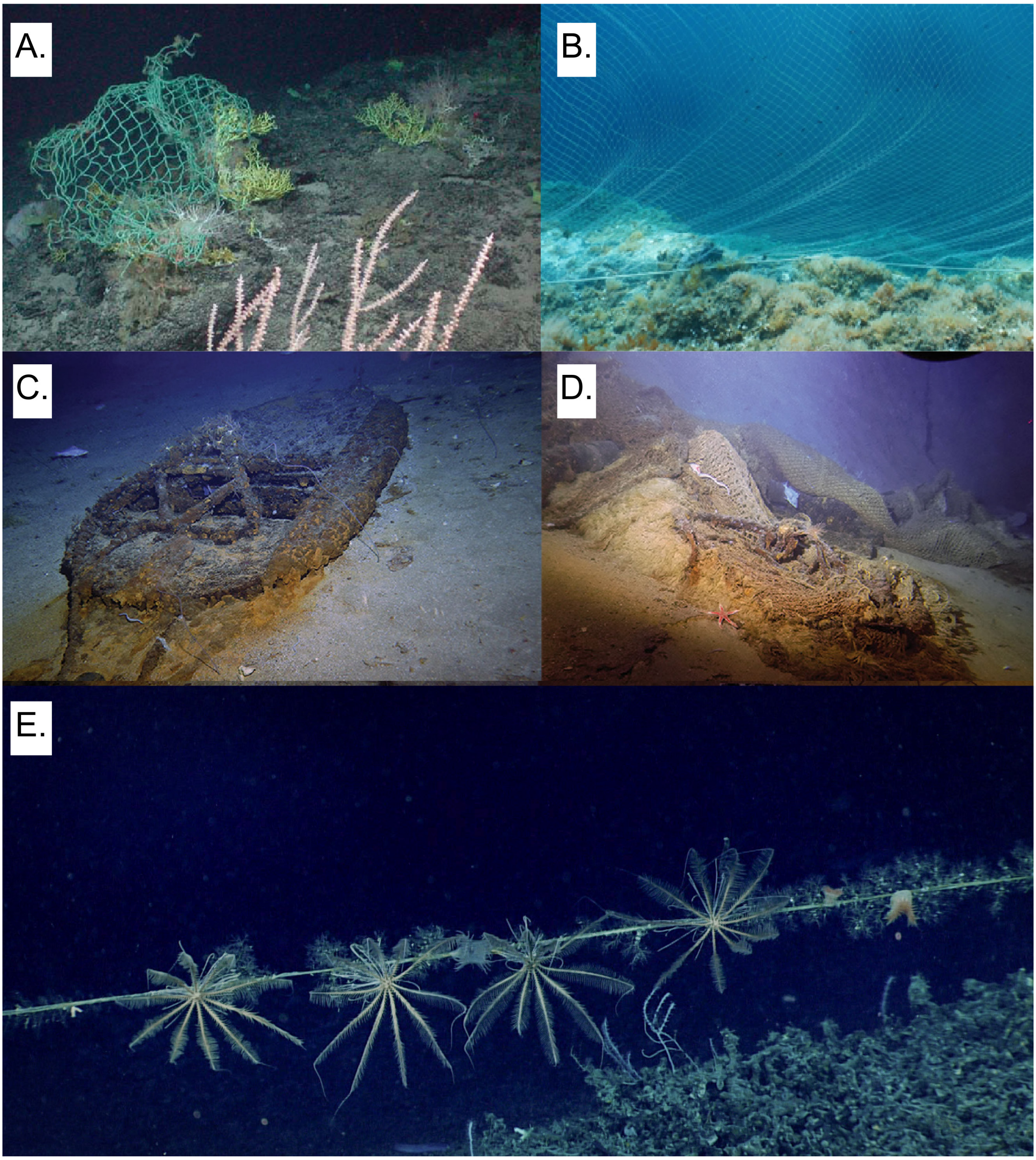

Figure 4. Bottom-contact fishing impacts on CWCs. A. Discarded fishing gear caught on scleractinian corals on Manning Seamount—part of the New England Seamount Chain. B. Lost bottom trawl. C. Lost trawl door on NW Hancock at 300 m. D. Lost trawl net from a second location on NW Hancock at 400 m. E. Crinoids on the rope leading from the lost net. Photo credits: A. DSV Alvin, Medusa Cruise on Manning Seamount, 2003; B. https://www.1ocean.org/ocean-tales/bottom-trawling-and-the-impacts-on-the-ocean; C-D. A. Baco-Taylor (FSU) and E. B. Roark (TAMU), NSF, with HURL pilots T. Kerby and M. Cremer; E. the NOAA Office of Ocean Exploration and Research, 2019 Southeastern U.S. Deep-sea Exploration.

## 2.5.2 Oil and Gas Exploration and Extraction

Oil and gas exploration and extraction are another concern to CWC communities (Cordes *et al.*, 2016), because these activities often involve the use of heavy equipment and machinery, which can cause physical damage to CWC habitats. In addition to direct impacts, drilling can produce excessive sediment and drill cuttings which can smother / bury CWC, causing asphyxiation and ultimately mortality. For example, in laboratory studies the scleractinian *Desmophyllum pertusum* had significant polyp mortality following burial by 6.5 mm of drill cuttings, the maximum permissible under environmental risk assessments in Norway (Larsson and Purser, 2011). High particle concentrations over longer periods resulted in reduced skeletal growth and reduced larval survival, indicating early life stages may be particularly vulnerable to drill cutting exposure (Larsson *et al.*, 2013a). The Deep-Water Horizon blowout in 2010 led to impacts on deep-sea communities of megabenthos, including corals (e.g., Etnoyer *et al.*, 2016; Girard and Fisher, 2018). Seven years after the accidental release of oil and use of dispersants in the deep sea, CWCs showed persistent damage which may, over the long-term, lead to further mortality (Girard and Fisher, 2018). Such *in situ* observations of potential impacts remain exceedingly rare. One such study undertaken 2 years after drilling on the Norwegian Margin showed neither observed degradation of reef structure over time, nor reductions of associated fauna abundance (Purser, 2015). However, the impacts on energy stores, changes in reproductive behaviour, or the behaviour/ abundance of coral larvae are among many aspects of coral reef biology, physiology, and ecology not well studied *in situ* or *ex situ*, yet are aspects of life history which will impact the sustained existence of CWC communities.

Oil rigs themselves have been found to be ideal substrates for some species of CWC (Bell and Smith, 1999; see Figure 5). The utility of decommissioned rigs as "reefs" has been investigated since the 1980s (Kaiser *et al.*, 2020) and remains controversial (discussed in Montseny *et al.*, 2021), although it is clear communities of CWC, and associated fauna, do thrive in these environments thus providing a useful avenue to improve wider understanding about CWC growth and survivorship.

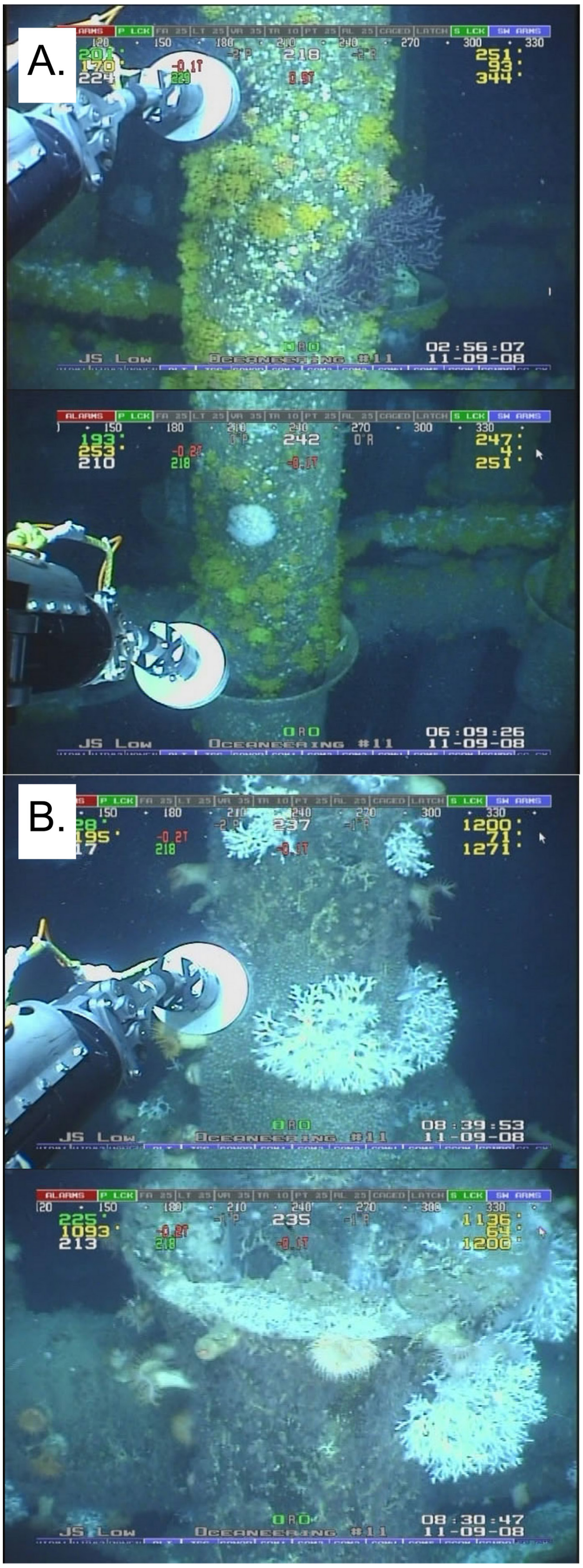

Figure 5. Images of CWC A. Octocorallia, B. Scleractinia *Desmophyllum pertusum* on rig structures in the Gulf of Mexico. Images care of Oceaneering Inc. / Cordes Lab / Temple University.

### 2.5.3 Deep-Sea Mining

Mining for diamonds is already taking place in continental shelf sediments off Namibia (Rogers and Li, 2002; Schneider, 2020) and South Africa (Moller *et al.*, 2003; Penney and Pulfrich, 2004; Majiedt *et al.*, 2019), but most deep-sea mining remains experimental and is yet to move into exploitation phase (Ashford *et al.*, 2023). Several different ecosystems are potential locations for mineral extraction in the ocean, including abyssal depths in large areas of the ocean covered with polymetallic nodules; deep-sea active and inactive hydrothermal vents, and sites where hydrothermal vents form seabed massive sulphides; and seamounts for cobalt and manganese crusts (Christiansen *et al.*, 2020).

The targeting of inactive hydrothermal vents for seabed massive sulphides may pose moderate direct and indirect threats to CWCs. The inactive vents act like rock pinnacles and provide habitat for CWCs; with the whole inactive vent chimney potentially being removed during mining, this poses a clear threat to such CWC colonies (Boschen *et al.*, 2016). Meanwhile, recent mining impact studies have predicted some degree of overlap between the dispersal of polymetallic sulphide (PMS) plumes and the distribution of CWCs on surrounding ridge habitats and seamounts around the Azores, suggesting a wider impact may be likely (Morato *et al.*, 2022). Mining of cobalt and manganese crusts on seamounts are a significant concern in terms of potential damage to CWC communities (Jones *et al.*, 2019; Schlacher *et al.*, 2014). Impacts of mining cobalt crusts on seamounts are likely to be extremely severe with removal of fauna, and the surface layers of rock. Indirect impacts of increased sedimentation will also influence CWC habitats in a wide footprint around these activities (Rogers, 2019). Given the life-history characteristics of CWC taxa, recovery will take a long time and may be in the order of hundreds or thousands of years (Rogers, 2019). Studies on the Hawaiian Ridge comparing the benthic fauna of areas with and without cobalt crusts demonstrated that community structure was different between the two types of seamounts (Schlacher *et al.*, 2014). As with other studies on seamounts, depth was a significant driver of differences in communities, while distance between seamounts was a poor predictor of community composition (Schlacher *et al.*, 2014).

Experiments testing the physiological tolerance of octocorals to deep-sea mining sediment demonstrated that PMS exposure could lead to a progressive loss in tissue condition, necrosis, bioaccumulation of copper in tissues and skeletons, and ultimately the death of all coral fragments (Carreiro-Silva *et al.*, 2022). The effects from copper exposure were similar in the whip coral *Viminella flagellum*, where mortality was high, but delayed (Martins *et al.*, 2022). However, information on the transport and affected area of PMS, along with sensitivity of CWCs to PMS exposure, is very limited. Future studies focusing on PMS impact area modelling and the potential impacts on the health of CWCs are needed.

In addition, understanding the interplay of depth and community structure, especially on seamounts with cobalt crusts, should be an important research target if deep-sea mining progresses from exploration to production. Indeed, lack of knowledge on the present distribution of CWCs, the vulnerability of these habitats to direct mechanical damage and pollutants from the plumes generated by mining activities (Carreiro-Silva *et al.*, 2022; Martins *et al.*, 2022), along with the currently limited capacity to conserve and restore them are components of the call for a moratorium on deep-sea mining.

### 2.5.4 Climate Change

CWCs are sensitive to their physical environment and research on their distribution suggests that temperature and biogeochemistry (e.g., oxygen, aragonite, or calcite concentrations) play a role in their ability to exist and/or thrive (Anderson *et al.*, 2016; Cordes and Mienis, 2023; Davies and Guinotte, 2011; Morato *et al.*, 2020; Tittensor *et al.*, 2009; Yesson *et al.*, 2012). Climate change may therefore influence the survival, and ultimately the distribution of CWCs, if it drives changes in the physicochemical properties of seawater. Tittensor *et al.* (2010) used habitat suitability models to investigate the effects of ocean chemistry changes on CWC distribution under various climate change scenarios. This research suggested that future changes of ocean chemistry, particularly ocean acidification from increased ocean uptake of anthropogenic $CO_2$, may significantly reduce the distribution of CWCs by the end of the century (Tittensor *et al.*, 2010).

The most concerning problems include ocean acidification, temperature increase, deoxygenation, and pollution, and the extent to which CWCs can tolerate these changes remains uncertain. There has been an increase in multi-stressor response tests on CWC in the last decade (Gómez *et al.*, 2018; Hennige *et al.*, 2014b; 2015; Lunden *et al.*, 2014; Ross *et al.*, 2020) but with varying responses depending on experimental timescales. Fragments of *Desmophyllum pertusum* collected from the California margin demonstrated net dissolution of –0.010 0.014% $d^{-1}$ under unfavourable acidification conditions (Gómez *et al.*, 2018), and *in situ* and laboratory observations suggest ocean acidification can cause ecosystem-scale habitat loss for most CWC reefs (Hennige *et al.*, 2020). Of note is that Stylasteridae can survive in undersaturated waters despite also maintaining aragonite skeletons (Stewart *et al.*, 2022), and along with other groups of CWCs, such as Antipatharia (black corals), and Octocorallia, have been largely understudied with regard to impacts of multiple stressors.

The effects of warming and deoxygenation on the survivorship of CWCs are larger than those found for acidification. *Desmophyllum pertusum* collected from the Gulf of Mexico, showed up to 100% mortality at temperatures above 14 °C and oxygen concentrations of approximately 1.5 $ml \cdot l^{-1}$ (Lunden *et al.*, 2014). An *in situ* study suggests bamboo coral (Isididae) gardens, which are generally tolerant of hypoxia (Etnoyer, 2008), may experience one or more episodic mortality events due to low oxygen (Ross *et al.*, 2020). However, Mediterranean CWCs have demonstrated high temperature tolerance over short term exposure, suggesting that the thermal history is important (Naumann *et al.*, 2013, 2014; Gori *et al.*, 2014), although long-term experiments suggest CWCs collapse after one-year exposure to high temperatures (Reynaud *et al.*, 2021). *Desmophyllum pertusum* can thrive in hypoxic and rather warm waters under high surface ocean productivity (Hebbeln *et al.*, 2020; Hughes *et al.*, 2020). Thus, high food supply may help CWCs build their capacity to adapt to extreme conditions (Naumann *et al.*, 2011), holding potential significance for the development of restoration strategies, e.g. "safe" donor or future locations for translocation.

In addition, early life (i.e. gametogenesis, larval) responses to climate change are largely unknown. One study on Antarctic *Flabellum impensum* larvae suggests some tolerance to end-of-century ocean warming (Johnstone *et al.*, 2022), whereas temperature changes have been shown to affect embryogenesis in a deep octocoral from the Azores (Rakka *et al.*, 2021). And acidification had detrimental effects on gametogenesis in Alaskan *Primnoa pacifica* (Rossin *et al.*, 2017). In addition to direct impacts, climate change-related multiple stressors also affect recovery from short-term pollution exposure (Weinnig *et al.*, 2020), making restoration even more challenging. Current evidence on the response of CWCs to climate change is mostly focussed on Scleractinia, more specifically, *Desmophyllum pertusum*. This is likely because of the challenges of maintaining other CWC species in aquaria – another area of research and experimentation that requires urgent attention.

When considering CWC ecosystem response to climate change, dead CWCs should also be considered as their complex structures are an important habitat (Barnhill *et al.*, 2023). While live corals may be able to use their energy to adjust to a changing environment, dead CWCs cannot. Thus, as pH decreases, the mainly aragonite skeletons of scleractinians will dissolve without the protection of living coral tissue (Büscher *et al.*, 2022; Wolfram *et al.*, 2022; Hennige *et al.*, 2020). CWC reefs and coral carbonate mounds are often built upon a matrix of dead coral framework, the integrity of which, and thus complexity and role as a habitat, could be impacted by dissolution (Hennige *et al.*, 2020). Therefore, both live coral and the framework of dead CWCs should be considered in future studies and conservation measures (Barnhill *et al.*, 2023; Büscher *et al.*, 2019, 2022).

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## 2.6 CWC Conservation

### 2.6.1 The historical and Status of CWC Conservation

CWCs and the human-induced challenges they face were only recognised as a significant conservation issue in the 1980s. The Oculina Bank Habitat Area of Particular Concern was the first CWC area protected from trawling, instigated by the South Atlantic Fishery Management Council in 1984, after 90% of the coral reef had been destroyed by deep trawling in the 1970s and 1980s (Pugliese *et al.*, 1998). In Norway, in the early 1990s, fishermen approached the Institute of Marine Research (IMR) in Bergen because of concerns that bottom trawling was destroying *Desmophyllum pertusum* reefs and, as a result, having negative impacts on associated commercially valuable fish populations. This initiated investigations into the distribution of *Desmophyllum pertusum* reefs in Norway using a combination of approaches including ROV surveys, drop cameras, side scan sonar and, when it became available, multibeam sonar. Initial results from surveys suggested that 30-50% of Norwegian *Desmophyllum* reefs had been damaged or destroyed by trawling (Fosså *et al.*, 2002). As early as 1999, the Norwegian Government enacted regulation to prevent activities likely to damage CWC reefs and gave special protection to five reefs where no bottom fishing using towed gears was allowed (Armstrong and van den Hove, 2008; Fosså and Skjoldal, 2010). Later, the regulations were extended to include a wider range of human activities likely to damage CWC reefs and a larger network of marine protected areas was developed (Fosså and Skjoldal, 2010).

Since the mid-1990s in the UK, oil and gas exploration in deep water to the west of Scotland raised concerns regarding damage to CWC reefs in the vicinity of the continental slope and Rockall Bank. A court case determined that the European Habitats Directive (EHD) applied to the deep seas of the exclusive economic zone (EEZ) and extended continental shelf of the UK (Bett, 2003). This led to the first deep-water marine protected areas in the UK, The Darwin Mounds, established in 2003 (Huvenne *et al.*, 2016), and established case law for the designation of deep-sea habitats under the EHD (Chaniotis *et al.*, 2020).

Documentation of damage to CWC ecosystems from around the world rapidly accumulated in the early 2000s giving rise to international concerns regarding the impacts of fishing on vulnerable marine ecosystems (VMEs, e.g. sponges, coral, hydrothermal vent) including those formed by CWCs. The UNGA adopted Resolutions 59/25 and 61/105 in 2004 and 2006, respectively, to address international concerns regarding the adverse impacts of deep-sea fisheries on VMEs and individual species, including targeted and non-targeted fish in the deep sea (UNGA, 2004, 2007). Subsequent to the adoption of the UNGA resolution, the UN FAO hosted a series of consultations and negotiations to draft a set of guidelines for the implementation of UNGA Resolution 61/105. The UN FAO International Guidelines for the Management of Deep-Sea Fisheries in the High Seas (FAO Guidelines), adopted by member countries of the UN FAO in 2008, sought to elaborate science-based criteria to identify VMEs, conduct impact assessments of bottom fisheries on the High seas, and determine whether "significant adverse impacts" to such ecosystems would occur (Rogers and Gianni, 2011). In the event of VMEs being identified during impact assessments or encountered during fisheries operations, measures were required to protect the ecosystems from significant harmful impacts. Usually this meant establishing areas closed to bottom trawl fisheries around the identified location (Rogers and Gianni, 2011).

The response to both the UNGA Resolutions and the FAO Guidelines was the establishment by regional fisheries management organizations (RFMOs) of areas closed to bottom trawling where CWC ecosystems and other VMEs were known to be present in areas beyond national jurisdiction (ABNJ). Established deep-sea fisheries footprints were also mapped and environmental impact assessments required for deep-sea fisheries in ABNJ. Furthermore, "move-on rules" were established for situations where fishing vessels using bottom-contact fishing gear encountered species indicating the possible presence of VMEs on the seafloor (Rogers and Gianni, 2011). The implementation of the FAO Guidelines has continued to evolve to the present day but is widely believed to be poorly applied (e.g., few compliant impact assessments for VMEs; Kaikkonen *et al.*, 2022).

Outside of specific measures to prevent significant impacts on VMEs by bottom fisheries in ABNJ there has been no legal framework for the establishment of protected areas or other conservation measures in ABNJ. The agreement of the Biodiversity Beyond National Jurisdiction (BBNJ) Treaty in March 2023 will allow the establishment of such a framework and should enable a more proactive approach to the protection of CWC ecosystems in ABNJ. The treaty will require ratification by at least 40 countries before it comes into force as international law (to date 83 countries have signed the treaty as of 22nd November 2023).

## 2.6.2 The Effectiveness of Conservation Measures

Implementation and effectiveness of conservation measures for CWC ecosystems have been mixed and enacted mostly in relation to fisheries activities. In Norway, fishing vessels have largely been compliant with closed areas (Armstrong and van den Hove, 2008). In the UK, although there is evidence of compliance with The Darwin Mounds MPA, the eastern portion of the area was heavily impacted prior to establishment and has not subsequently recovered (Huvenne *et al.*, 2016). In contrast, a conservation area established to protect *Desmophyllum pertusum* reefs off the coast of Canada does appear to have shown signs of recovery, with higher abundance of epibenthic megafauna than a nearby unprotected area, and some recruitment of *Desmophyllum pertusum* over a period of 12 years (Beazley *et al.*, 2021).

However, another fisheries closure to protect CWC in the Northeast Channel Coral Conservation Area in the northwest Atlantic, showed spatially variable recruitment and change in abundance of CWC 13 years after closure, indicating the slow recovery of these organisms (Bennecke and Metaxas 2017). A review of implementation of the FAO Guidelines indicated that implementation was slow, and effectiveness of specific measures undertaken by some RFMOs questionable (Rogers and Gianni, 2011).

In particular, development of lists of VME indicator species and threshold values for activation of "move-on" measures has been an area of particular contention (Auster *et al.*, 2011; Rogers and Gianni, 2011). RFMOs can be slow to establish MPAs to protect CWC ecosystems where they reduce opportunities to fish (Rogers and Gianni, 2011). Within an EEZ, monitoring and enforcement of fisheries regulations can be achieved using vessel monitoring systems (VMS e.g., Armstrong and van den Hove, 2008). This becomes more difficult in ABNJ as fishing vessels may turn such equipment off (i.e., go dark) and surveillance of their activities is usually only possible using satellite radar (synthetic aperture radar) which is expensive and time-consuming to access (Haines, 2019).

A well planned and executed national management plan that included CWC protections at its core was the recent 20 MPAs established in South African waters (Sink *et al.*, 2023). A barrier to such activities is identification of the location of CWC and VME structures. Recent CWC research community efforts are tackling this challenge by creating a consensus on VME identification from imagery (Baco *et al.*, 2023).

Implementation of the BBNJ Treaty to protect CWC ecosystems in ABNJ using MPAs or other effective conservation measures will require cooperation with RFMOs. Given these are dominated by fisheries interests and many have limited scientific capacity on marine

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biodiversity, this will inevitably lead to conflict and require support for scientists to engage and provide independent data to these processes. Incomplete mapping is a major obstacle for CWC conservation, as MPAs to protect them can only be considered where the presence of these habitats is documented. The repeated case of finding evidence for extensive CWCs only after they have been damaged, following the first such reports in the 1980's (Fosså *et al.*, 2002), is an unacceptable status that can only be reversed by an international program to map these ecosystems before 2030, so they can be included, as needed, in the 30% ocean areas to be protected under the Kunming-Montreal Global Biodiversity Framework, for areas within national jurisdiction, and the BBNJ treatise.

## 2.7 CWC Restoration

At present, restoration of CWC is rare. However, it is predictable that, similarly to shallow-water reefs, restoration measures will start being considered to restore damaged and degraded CWC communities, to comply with the commitment to restore, or be on the way to restore, 30% of damaged habitats by 2030 under the Kunming-Montreal Global Biodiversity Framework. Understanding the challenges and opportunities of CWC restoration, therefore, is crucial for the successful implementation of this framework.

Restoration methods can currently be categorised into two types: passive and active restoration. Passive restoration generally refers to natural regeneration which mainly includes the removal or reduction of disturbances or stressors to facilitate the spontaneous recovery of the ecosystem (Beazley *et al.*, 2021; Gann *et al.*, 2019). Passive restoration typically requires minimal or no active human intervention once the initial restoration actions have been taken. For CWC communities, passive restoration could be making an area restricted to bottom contact fishing gear, leaving CWC communities to recovery naturally (Beazley *et al.*, 2021; Da Ros *et al.*, 2019; Young *et al.*, 2012); one commonly known example is through the designation of Marine Protected Areas (MPAs), or zones within MPAs (e.g., Beazley *et al.*, 2021). Active restoration normally refers to interventions and techniques that involve direct assistance, post-impact activities, to enhance the recovery of an ecosystem (Clewell and Aronson, 2012).

In the context of CWC communities, active restoration can include activities such as coral transplanting, introducing artificial substrates, or assisting larval settlement (Montseny *et al.*, 2021a). Despite the awareness of CWC restoration, there have only been a few attempts to conduct and monitor CWC restoration experiments (Montseny *et al.*, 2021a; Van Dover et al., 2014). The vast majority of actions performed in the marine environment have been heavily skewed towards shallow tropical coral restorations (e.g., McLeod *et al.*, 2019; Raymundo *et al.*, 2007; Williams *et al.*, 2019). For the subset that includes active restoration, there are even fewer studies and activities (Boch *et al.*, 2019; Montseny *et al.*, 2021b, 2019; Shester *et al.*, 2021). As a result, the success of these efforts is also poorly evaluated.

## 2.7.1 Passive Restoration

Passive restoration has been used in terrestrial ecosystems for several decades, but its application in deep-sea ecosystems is relatively new (Da Ros *et al.*, 2019). A direct and effective protection and restoration approach for CWC is to remove or reduce the key stressors (e.g., closing areas to damaging fishing practices). The first passive restoration efforts for CWC began in the 1980s, with the implementation of marine protected areas (MPAs), Oculina Bank Habitat Area of Particular Concern (HAPC), and the establishment of fishing regulations to limit the impacts of bottom trawling (South Atlantic Fishery Management Council, 1982). Many countries have designated and created MPAs for CWC ecosystem protection and restoration by exerting strong control over human activities (Davies *et al.*, 2007). For example, the European Union, Canada, New Zealand, Australia, and USA have all taken steps to prohibit bottom trawling in certain CWC areas. An increasing number of MPAs or other spatial conservation measures for CWC ecosystems have been designated and created by each country in the recent two decades, e.g., the Darwin Mounds and Hatton Bank, the East Mingulay Marine Protected Area (UK), the Northeast Channel Coral Conservation Area, Davidson Seamount, Northeast Canyons and Seamounts (US), reefs and banks of the northern Gulf of Mexico, Tasmanian Seamount Reserve (Australia), Tisler Reef (Norway), Browns Bank and Port Elizabeth Coral MPAs (South Africa) (Althaus *et al.*, 2017; Bennecke and Metaxas, 2017; Harter *et al.*, 2009; Huvenne *et al.*, 2016; La Beur *et al.*, 2019; NOAA, 2016; Sink *et al.*, 2023).

Despite these spatial conservation measures being designated and established, monitoring and evaluation of their effectiveness is rare. Table 1 summarises passive restoration projects for the recovery of deep-sea CWCs. For the 14 restoration areas that have been evaluated, observations indicate that 5 areas show signs of recovery, but none of them are considered completely recovered. The first observed evidence of recovery was in the Oculina Bank deep-sea MPA (Harter *et al.*, 2009). After 2 years of fisheries closure, Harter *et al.* (2009) found the protected area showed a higher percentage of intact coral than outside the protected area, resulting in higher biodiversity and grouper densities in the MPA. A longer protection time in some places also resulted in signs of recovery. For example, although not at all sites, there was a higher coral abundance in the fisheries closure in the Northeast Channel Coral Conservation Area with the presence of some larger colonies after 13 years of fisheries closure (Bennecke and Metaxas, 2017). Similarly, after 30 years of protection in the Northwestern Hawaiian Ridge and Emperor Seamounts evidence of coral regrowth and greater abundances of benthic megafauna has been observed (Baco *et al.*, 2019). The successful protected areas tend to be shallower than the unsuccessful areas (Table 1), potentially indicating that the effectiveness of passive restoration largely depends on environmental conditions, although with such small numbers it's impossible to analyse this further.

Table 1. Passive restoration initiatives carried out to date focused on cold-water coral (CWC) habitats.

| Case Study | Locality | Type of Action | Organisms | Depth (m) | Duration Time | Results | Reference |
|---|---|---|---|---|---|---|---|
| 1 | Georges Bank, USA | Fisheries closure | Macrofauna | 1760 | 26 months | No significant recovery | Grassle, 1977 |
| 2 | Sisters seamounts off southern Tasmania, Australia | Fisheries closure | *Solenosmilia* | 1100-1350 | 5 years | No evidence of recovery or regrowth | Althaus *et al.*, 2009 |
| 3 | Oculina Bank, USA | Fisheries closure | *Oculina varicosa* | 70-100 | 19-21 years | Higher biodiversity and grouper densities than outside the protected area | Harter *et al.*, 2009 |
| 4 | Chatham Rise, New Zealand | Fisheries closure | Scleractinia | 750-1600 | 20 years | No recovery of community composition | Clark and Rowden, 2009 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 5 | Seamounts off New Zealand, New Zea-land | Fisheries closure | Megafauna including CWCs | 750-1600 | 5-10 years | No complete recovery | Williams *et al.*, 2010 |
| 6 | Western Darwin Mounds, UK | Fisheries closure | Scleractinia, soft corals | 1000 | 8 years | Successful recovery with similar proportions of live CWCs in 2011 as observed in 1998-2000 | Huvenne *et al.*, 2016 |
| 7 | Eastern Darwin Mounds, UK | Fisheries closure | Scleractinia, soft corals | 1000 | 8 years | No coral recolonisation and very little regrowth | Huvenne *et al.*, 2016 |
| 8 | Darwin Mounds, UK | Fisheries closure | Scleractinia, soft corals | 1000 | 16 years | No coral recolonisation and very little regrowth | Strong *et al.*, 2023 |
| 9 | The Northeast Chan-nel Coral Conserva-tion Area in the Gulf of Maine, USA | Fisheries closure | *Primnoa resedaeformis* and *Paragorgia arborea* | 400-700 | 13 years | Higher coral abundance and the presence of some very large colonies as well as recruits in 2014 compared to 2001, but not found at all sites | Grassle, 1977 |
| 10 | Gulf of Mexico, USA | Passive recovery from oil exposure | *Paramuricea* spp. colonies | 1050 | 14 years | Pollution impacts were still ongoing, and no complete recovery observed | Girard and Fisher, 2018; Girard, 2024 |
| 11 | The Northwestern Hawaiian Ridge and Emperor Seamounts | Fisheries closure | Octocorallia, Scleractinia | 300-600 | >30 years | Higher number of total megafaunal individuals, corals and mean number of taxa observed on the recovering seamounts than still trawling seamounts | Baco *et al.*, 2019 |
| 12 | Chatham Rise, New Zealand | Fisheries closure | Thicket-forming scleractinian corals | 748-987 | 15 years | No recovery | Clark *et al.*, 2019 |
| 13 | Scotian Shelf, Canada | Fisheries closure | *Desmophyllum pertusum* (*Lophelia pertusa*) reef | 300-400 | 12 years | Megafaunal increase in density and abundance | Beazley *et al.*,2021 |
| 14 | Gulf of Mexico | Fisheries closure | Octocorallia, Scleractinia | 50-2000 | 4 years | Insufficient time elapsed since enactment of protections for adequate documentation of recovery | OOTIG, 2019 |

In addition, the effectiveness of the passive restoration also largely depends on the levels of damage within the protected area. For example, after 8 years of fisheries closure, similar proportions of live Scleractinia and soft corals were observed in 2011 in the Western Darwin Mounds as observed in 1998 – 2000 (Huvenne *et al.*, 2016). However, the authors also found no coral recolonisation and very little regrowth in a nearby place, the Eastern Darwin Mounds, where a much higher trawl mark density was observed (Huvenne *et al.*, 2016).

As well as environmental conditions and the severity of the damage, the effectiveness of passive restoration also depends on the enforcement of the protective implementation, which can be difficult in remote and deep-sea areas (see above). Another challenge is the lack of knowledge about the biology and ecology of CWC which makes it challenging to assess the effectiveness of passive restoration and to determine the most appropriate locations for the designation of MPAs. The high cost of deep-sea research also limits the amount of monitoring that can be conducted on CWC ecosystems to determine appropriate baselines and to understand recovery trajectories.

## 2.7.2 Active Restoration

Active restoration involves direct intervention to enhance or accelerate the recovery of an ecosystem. Active restoration for CWC communities has started in trial experiments only in the last few decades (Brooke *et al.*, 2006; Koenig, 2001), but many challenges remain.

The principal challenge is the lack of understanding of the biology and ecology of CWC, including their reproductive and growth patterns (Da Ros *et al.*, 2019; Montseny *et al.*, 2021a; Van Dover *et al.*, 2014), the cues that initiate settlement, larval behaviour, and many aspects of coral physiology and resilience.

Table 2: Active restoration activities on cold water coral habitats to date.

| Case Study | Locality | Type of Action | Organisms | Depth (m) | Duration Time | Results | Reference |
|---|---|---|---|---|---|---|---|
| 1 | SE Florida, USA | Transplantations on artificial structures | *Oculina varicosa* | 70 – 100 | 2 – 5 years | Coral transplants alive and growing, new coral recruits observed | Koenig, 2001 |
| 2 | SE Florida, USA | Transplantations on artificial structures | *Oculina varicosa* | 70 – 100 | 1 year; 8 years | 75% reef balls still had attached coral fragments and 25% of these were alive; Reef balls observed on 2 dives of total 7 dives, none showed coral colonization or enhanced fish abundance | Brooke *et al.*, 2006; Koenig, 2009 |
| 3 | Viosca Knoll, USA | Coral transplants | *Desmophyllum pertusum* | 450-520 | 1 year | >90% polyp survival for all transplant units, average growth rate fell at the lower end of published data | Brooke and Young, 2009 |
| 4 | Gulf of Mexico, USA | Artificial structures | Various coral species | 21-400 | 30 – 34 | Unaided natural recruitment of corals and other sessile invertebrates | Kaiser *et al.*, 2020; Kaiser and Pulsipher, 2005 |
| 5 | Sweden | Transplantations on artificial structures | *Desmophyllum pertusum* | 82 – 87 | 3 – 4 | Mean survival rate of 76%, mean size increase of 39% | Dahl *et al.*, 2012 |
| 6 | Sweden | Transplantations on artificial structures | *Desmophyllum pertusum* | 75 – 90 | Not specified | Not yet recorded | Strömberg, 2016 |
| 7 | California, USA | Transplantations on artificial structures | Seven species of gorgonian CWCs | 800 – 1300 | 3 | Mean survival rate of 52%After 3 years, coral survival differed among species with 0 – 100% survival. | Boch *et al.*, 2020, 2019 |
| 8 | NW Mediterranean, Spain | Transplantations on artificial structures | *Eunicella cavolini* | 85 | 1 | Mean survival rate of 87.5% | Montseny *et al.*, 2020, 2019 |
| 9 | NW Mediterranean, Spain | Involving fishers | *Eunicella cavolini* | 80-90 | | 77% survival rate with low cost | Montseny *et al.*, 2021b |
| 10 | Azores, Spain | Coral transplantation | *Desmophyllum pertusum* | 230 | 8 – 13 months or 3 years | Maximal 85% survival rate after 8 – 13 months, 50% survival rate after 3 years | Linares *et al.*, 2019 |
| 11 | Azores, Spain | Coral transplantation | Several species of octocorals | 230 | 10 – 21 months | Survival rate decreased significantly between 10 and 21 months for most species except Acanthogorgia sp., which had 100% survival rate. 15 – 100% survival rate after 21 months | Linares *et al.*, 2019 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 12 | Koster-Väderö Fjord, Sweden | Deployment of artificial reef structures to facilitate larval settlemen | *Desmophyllum pertusum* | | Ongoing | | https://www.gu.se/forskning/life-lophelia |
| 13 | Off the coast of the provinces of Girona and Barcelona, Spain | Transplantation on artificial reef structures | *Soft corals* | 90 – 140 | Ongoing | | https://www.life-ecorest.eu/the-project/#acciones |
| 14 | Mediterranean Sea, EU | Deploying artificial structures | Scleractinians, black corals, etc | | Ongoing | | https://www.life-dream.eu/project/ |
| 15 | the northern Mid-Atlantic (nMAR) and Arctic (AMOR) ridges, EU | the northern Mid-Atlantic (nMAR) and Arctic (AMOR) ridges, EU | *Desmophyllum pertusum (Lophelia pertusa)* reef | | Ongoing | | https://deep-rest.ifremer.fr/ |
| 16 | Gulf of Mexico, USA | Various propagation techniques | 12 species of octocorals | 50-3000 | Ongoing | Recent *in situ* fragment deployments show high survival (<90%); lab-based sexual and asexual propagation trials also promising | https://www.fisheries.noaa.gov/southeast/habitat-conservation/mesophotic-and-deep-benthic-communities-restoration |

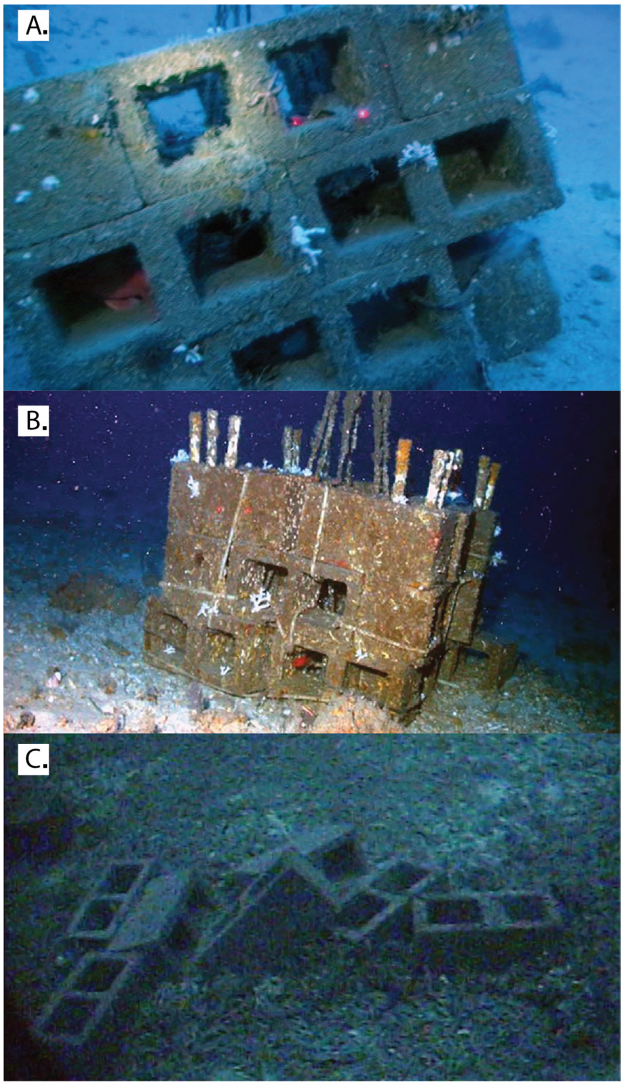


Figure 6. Survey results of a cold-water coral restoration project (Koening, 2001, 2009). A. ROV survey of 3 blocks per site in 1998 (1-2 years after deployed) with coral transplants alive; B. Submersible survey in 1999 showing coral transplants alive and growing with new coral recruits observed; C. Technical diver survey in 2008 showing coral recruitment and growth with destroyed blocks.

In addition, there is a lack of long-term data on the success of CWC restoration projects, making it difficult to assess the effectiveness of different methods and make informed decisions about future restoration efforts. Compounding these issues, difficulty in accessing CWC habitats and the major expenses related to the required technology, technically and economically limit the spatial scale of current restoration actions (Montseny *et al.*, 2021a). To date, there are only a few active restoration actions carried out around the world, all located in the northern hemisphere (Table 2). Restoration actions have been mostly successful at least in the short term, with more than 50% of reintroduced corals alive after more than one year (Table 2).

The first active restoration experiment for CWC was conducted in the Oculina Banks Habitat Area of Particular Concern (OHAPC) from 1996 to 1999 and demonstrated promising survival of transplanted coral (Figure 6; Koenig, 2001). This was followed by the first large-scale coral transplanting on Sebastian Pinnacles in 2000 with two different types of transplant structures (Figure 7; Brooke *et al.*, 2006; Koenig, 2001). After 1 year, there were still 75% of the reef balls with their coral fragments attached and 25% of the fragments were alive (Brooke *et al.*, 2006). However, a subsequent survey suggested reefballs observed in only 2 dives of total 7 dives with none showing coral colonization or enhanced fish abundance, even within this protected area, indicating a failure of restoration (Koenig, 2009).

A few more projects were undertaken in the following decade. The technique used in most active restorations is coral transplantation, with or without artificial structures (Boch *et al.*, 2020, 2019; Brooke and Young, 2009; Dahl *et al.*, 2012; Jonsson *et al.*, 2015; Montseny *et al.*, 2020, 2019). Coral transplantation can accelerate the recovery of damaged coral populations by introducing new, healthy coral fragments to degraded areas. Transplanting coral by this technique can also increase the genetic diversity of coral populations in a given area, potentially enhancing their resilience to future environmental stressors (Montseny *et al.*, 2021a). In addition, coral transplantation can be relatively low-tech and cost-effective compared to other restoration methods, especially in shallow (deep)-water areas. However, there are also limitations in terms of coral transplantation. For example, transplanting corals can be logistically challenging and potentially damaging to both the donor and recipient sites. An innovative exception is if procured fragment transplants are sourced from the by-catch of fishermen (Montseny *et al.*, 2021b). Especially in deep-sea environments it may even be difficult to identify the suitable donor coral populations/ habitat and appropriate recipient sites, let alone specific suitable colonies. Also, transplanted corals may be more vulnerable to stressors, such as predation, disease, or environmental changes, as they may not be adapted to the new site (Montseny *et al.*, 2021a). And with climate change, new sites may also not be suitable environments long term; an important factor considering the aged nature of of many CWC species.

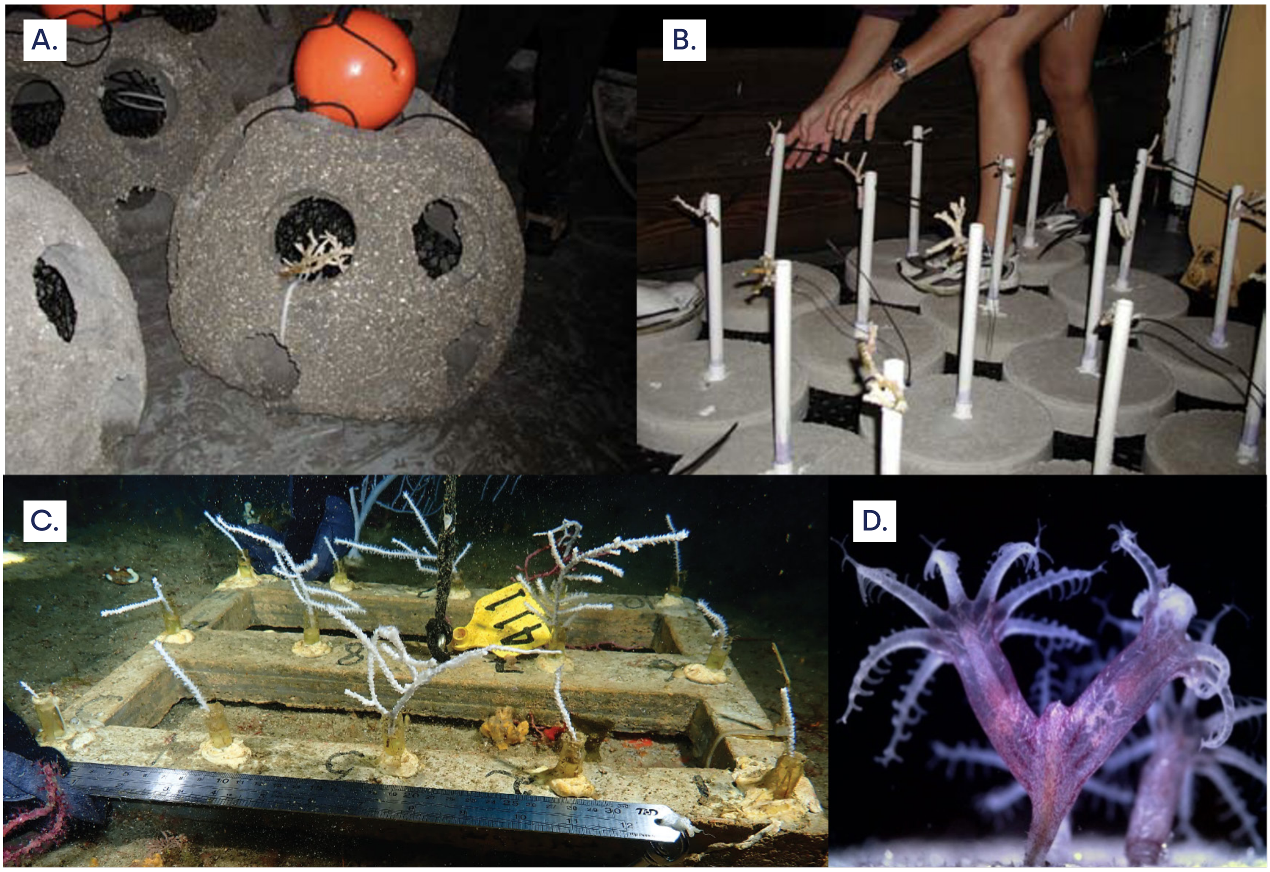
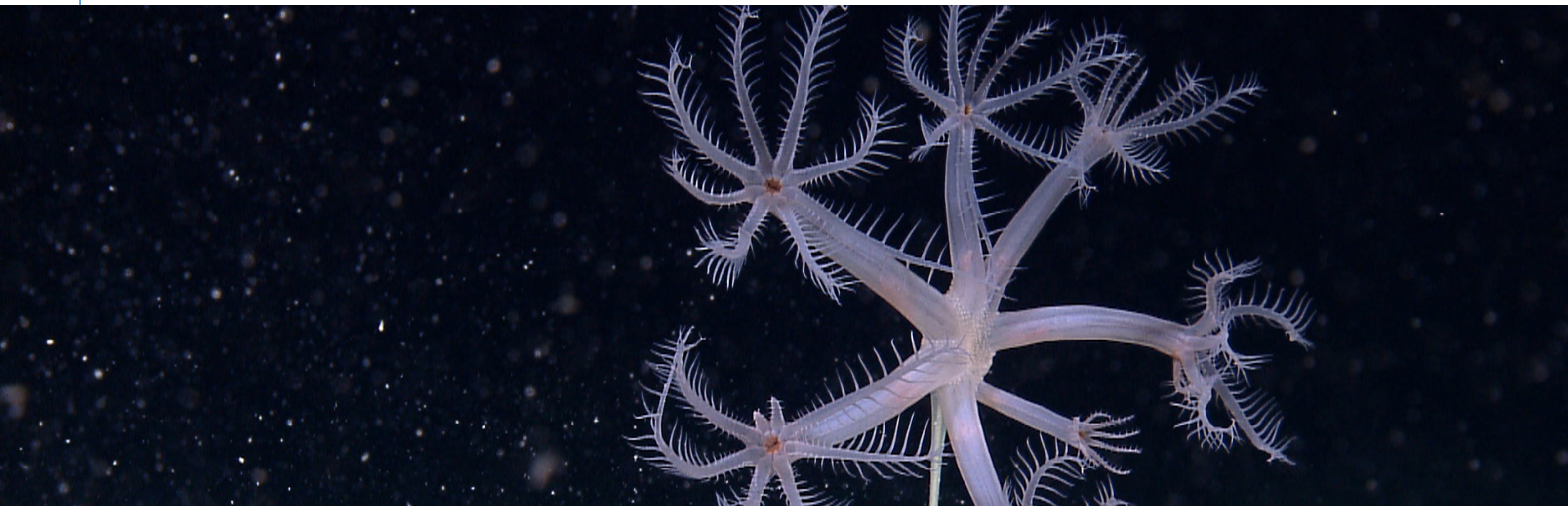


Figure 7. Different types of transplant structures used in Brooke *et al.* (2006) and Koenig (2001), Prada (2024), and Jenkins (2024). A. Reefball with attached *Oculina*; B. Reefdisks with attached *Oculina* fragments; C. fragmentation rack with *Swiftia* and *Muricea*; D. sexually reproduced *Swiftia* colonies at 5 months after recruitment to settlement tiles in a lab setting.

In addition to coral transplantation, there are other methods that vary in technological sophistication. They include the use of reef balls with coral transplants, direct transplantation of coral, and the use of cobbles to which transplants are attached (Montseny *et al.*, 2021b, 2020). In addition, the use of 3D-printed artificial materials as substrata placed on the seafloor has been investigated which could reduce the cost of restoration by using cheaper materials (Yoris-Nobile *et al.*, 2023). Recently initiated restoration efforts responding to the Deepwater Horizon oil spill in the northern Gulf of Mexico incorporate tests of propagation for twelve species of mesophotic and deep-sea corals, including *in situ* and lab-based techniques involving both sexual reproduction and asexual fragmentation, as well as recruitment to artificial substrates (OOTIG, 2019; Johnstone, 2024; Jenkins, 2024; Prada 2024). Whilst these experiments show promising results, all were either recently begun or of a short duration; thus, the long-term effectiveness of these restoration approaches cannot yet be assessed, and longer-term and larger-scale experimental approaches are required.

Based on previous restoration projects and *in situ* observation, Strong *et al.* (2023) summarised the potential restoration scenarios for *Desmophyllum pertusum* in the Darwin Mounds MPA. Five restoration scenarios including one "do-nothing" option were described: 1) wild harvest parent stock, laboratory propagation, attachment to substrata, and transplant to the seafloor; 2) high-relief artificial substrata placed on the seafloor; 3) low-relief artificial substrata spread on the seafloor; 4) translocation from other sites; 5) do-nothing (passive restoration). Among the five scenarios, high-relief artificial substrata placed on the seafloor was judged to have the greatest potential for long-term success in The Darwin Mounds; the suggested estimated costs for this activity were 4.6 million USD to restore an area of 600 $m^2$ (Strong *et al.*, 2023). The estimated cost of 7.67 thousand USD $m^{-2}$ is 200-500 fold higher than the median cost for shallow, tropical coral restoration (Bayraktarov *et al.*, 2016), and the area damaged is potentially much larger.

In conclusion, active restoration of CWC ecosystems is a complex and challenging practice, but one that holds significant promise for promoting the recovery of damaged or depleted CWC ecosystems. While there are several approaches that have shown success, such as coral transplantation (Montseny *et al.*, 2021a), significant challenges remain, including limited knowledge of deep-sea coral biology and ecology, logistical challenges associated with working in the deep-sea environment, high costs of restoration compared to that of shallower marine habitats, and conflicts with other human activities. The largest active restoration effort initiated globally to date was only made possible due to the substantial settlement reached for natural resource damages from the Deepwater Horizon oil spill, and major components of that effort are focused on science to inform restoration in recognition of those knowledge gaps (OOTIG, 2019). Addressing these challenges will require collaboration between scientists, policymakers, and stakeholders, as well as continued research to improve our understanding of CWC ecosystems and their responses to different restoration strategies.



Credits: NOAA Ocean Exploration

# 3. Methods

## 3.1 Expert Identification of Key Knowledge Gaps

With the above data and review as background knowledge, the CORDAP Workshop on CWC ecosystems was held on the 10th - 12th May 2023 at the Engineerium Centre (https://www.engineerium.no/) in Fornebu, Lysaker, Norway. It was attended by 26 researchers and members of CORDAP representing 12 countries. Attendees included early- to senior-career through researchers and included expertise on CWC ecology, conservation, restoration, reproduction, taxonomy, phylogenetics, microbiomes, and geochemistry.

The workshop was preceded by a summary report on current knowledge of CWC ecology, conservation and restoration practices including a bibliometric analysis. The 2.5-day workshop was anchored by presentations on different aspects of the status of CWC knowledge, conservation, their ecology, reproduction, and restoration by some of the experts present. Discussions were directed around the CORDAP request to collate knowledge gaps across this field of science. Small breakout teams discussed topics, lists of ideas were then voted on to aid priority selection.

Credits: GEBCO Seabed 2030

Credits: MBARI

# 4. Results

## 4.1 Overarching Priorities and Challenges for CWC Research and Conservation

Knowledge gaps and priorities for future research discussed at the workshop were very broad and here we cluster them into themes. Starting with some overarching priorities for CWC research and conservation.

### 4.1.1 Capacity Development for an Equitable Deep-Sea and CWC Research and Management Community

One aspect of CWC science that was unanimously supported by workshop participants was to develop CWC information exchange and capacity through the Global South. There is a clear deep-sea data bias to the Global North, as shown in bibliometric analysis and the known distribution of CWC (Cordes and Mienis, 2023), with a singular exception being South Africa who have significant deep-sea capabilities and a relatively stronger deep-sea research field (Filander *et al.*, 2022a, b; Sink *et al.*, 2021). There have been no CWC restoration activities in the Global South. Accessing deep-sea areas is a huge obstacle for any nation and, therefore, nations with such infrastructure should develop plans to support knowledge exchange and training with collaborators in the Global South along with making infrastructure available. Affordable deep-sea initiatives, such as those created by the Ocean Discovery League, require promotion and expansion. The vast majority of Earth's deep-sea is a global common and it is only right that it is equitably accessible.

### 4.1.2 Work Towards Stopping Bottom-Trawl Fishing in Areas of CWC Occurrence

A second universally supported action was to cease bottom-trawl fishing in areas of CWC occurrence. Understanding what exactly has been trawled is a challenging academic endeavour, with one recent paper providing the most comprehensive overview to date (Amoroso *et al.*, 2018). Data from the Food and Agriculture Organization of the United Nations (FAO) estimated that bottom trawling contributes around a quarter of global fish and invertebrate wild marine landings annually. Overall, Amoroso *et al.* (2018) estimated that 14% of the 7.8 million-km$^2$ study area of 24 continental shelves and slopes down to 1,000m has been trawled, and 86% was not trawled, which gives some hope of pockets of CWC survival. With CWC VMEs occurring on both soft and hard substrata there is likely a wide overlap with this trawling footprint, although the specific proportions and geography of such overlap remains unstudied as the specifics of CWC distribution are unknown. Some effort should be focused on identifying non-trawled locations as priorities for protective measures.

An area of seabed that has been trawled, particularly hard substrata, will not support CWC regrowth for decades (Clark *et al.*, 2019), to centuries, noting that CWC recovery in soft substrates post-trawling have not been adequately studied. The multi-century recovery times expected for these ecosystems means that the destruction of unimpacted CWC habitats, which can be thousands of years old (Roark *et al.*, 2009), may be considered irreversible within managerial time scales. Hence, CWCs are referred to as vulnerable marine ecosystems (VMEs) by the UNGA. Therefore, prioritising the prevention of further impact rather than relying on post-impact restoration is a far more economically and ecologically sensible precautionary approach, thus this priority suggestion.

### 4.1.3 CWC Research and Management Community Coordination

Better coordination of the CWC research, policy, management, conservation, and academic pursuit would support more collaboration, results dissemination, knowledge exchange, and data sharing. There are common global issues that the CWC community face and a united approach to these great challenges would be better supported by a coordinated community.

### 4.1.4 CWC Sample Rescue

Biological samples collected during past and future deep-sea expeditions should be made available as broadly as possible to support a breadth of research goals. The costly expeditions that collect and preserve deep-sea specimens are often funded with narrow ideas and aims. The cataloguing and long-term preservation of incidental, non-target collections are, thus, not financed. In fact, many times the core collected items do not have a designated home post-project either as this is not a requirement for many funding agencies, so the necessary finance is not added to grants. Just within the small group of workshop participants many 1000s of specimens were stored locally and not in accessible and registered locations, such as institute collections and/or museums. An assessment across the wider CWC community would probably unearth many 10s of 1000s of rare “dark materials”, hidden from community awareness and access (Matsumoto and Ofwegen, 2015). Hence “sample rescue” activities should be urgently deployed, such as those developed by Ocean Census, amongst others. A CWC effort to catalogue these “dark coral materials” into museums, would mean a wealth of specimens, taxonomic, and distribution data would be released for wider use.

### 4.1.5 CWC Occurrence Data Rescue and Compilation

It was widely acknowledged at the workshop that there are large amounts of CWC data (distribution, taxonomic, biological, video, etc) held in academia and industry that is not openly available in online databases. Activities such as data rescue (from museums, video / images, expeditions, etc) are key and are currently undertaken in silos. The Ocean Biodiversity Information System (OBIS), the largest system for ocean biodiversity information, can potentially become a universal online database for CWC data. The biggest hurdle to sharing such data is time, i.e. human capacity, to organise and format data, especially for internationally useful portals such as OBIS. Although some international efforts such as Fathomnet (Katija *et al.*, 2022) are emerging, they require more global coordination, especially for standardisation of data and data sharing. Active promotion and support from funding bodies are necessary to facilitate the uploading of occurrence data. Currently, there is no comprehensive inventory of existing and historic CWC habitats, and even the modelling of CWC habitats relies mainly on representative and sufficient available CWC occurrence data. Therefore, as a global data rescue activity would be transformative in improving knowledge of CWC presence globally. We have to know where the CWC are in order to restore, conserve, and better manage these critical habitats.

### 4.1.6 Increasing Public Knowledge of CWC

As has been eloquently discussed in a recent paper (Jamieson *et al.*, 2021), the deep-sea is a "hard sell" to most of the public. It is far away from people's everyday lives, it can conjure up deeply held fears of the dark, of scary animals therein, amongst many other complex emotions and stances, most of which are not positive. Unpacking this is difficult but it is clear that it leads to a public apathy that, to secure the future of CWC, needs expert and targeted community outreach and education. The CWC community perhaps has an easier task than many deep-sea academic fields. Corals are after all at least a term that is publicly, and positively, appreciated. However, it is important that CWC specifically become a more widely known ecosystem to ensure public and political support for current and future protections, especially given the decadal to century time scales required in protection measures.

## 4.2 CWC Research Knowledge Gaps

The workshop was wide-ranging and from the intense discussions and the background research it was clear that there are many academic knowledge gaps in this field. Here we present the 10 prioritised research knowledge gaps that the workshop felt required urgent attention and action; they are by no means a comprehensive list of CWC knowledge gaps.

### 4.2.1 CWC Status and Distribution

#### 4.2.1.1 Prioritised Knowledge Gap 1: The Global and Regional Distribution Patterns of CWCs

CWCs exhibit a global distribution, ranging from the shelf break to abyssal depths (Figure 8). However, the global and regional distribution patterns of CWCs have not been studied comprehensively. The distribution patterns of CWCs depend largely on the species and different types of CWC assemblages or communities, such as CWC reefs, CWC garden habitats and sea pen field etc (Cordes and Mienis, 2023).

Reef-forming cold-water scleractinian corals are primarily concentrated on the shelf break and bathyal zone, extending to approximately 1,500 metres deep (Roberts *et al.*, 2009), along continental margins, offshore banks, ridges, and seamounts. These coral reefs are typically constructed by a dominant framework-building species (e.g., *Desmophyllum pertusum*) with contributions from other secondary framework-forming corals (e.g., M*adrepora oculata*; Rogers, 1999). Remarkably, CWC reefs are known to occur across a vast range of environments, from sub-Arctic to sub-Antarctic

Credits: CORDAP

regions, although there are no complete global maps specifically for 'reef' distribution (rather than 'coral' distribution).

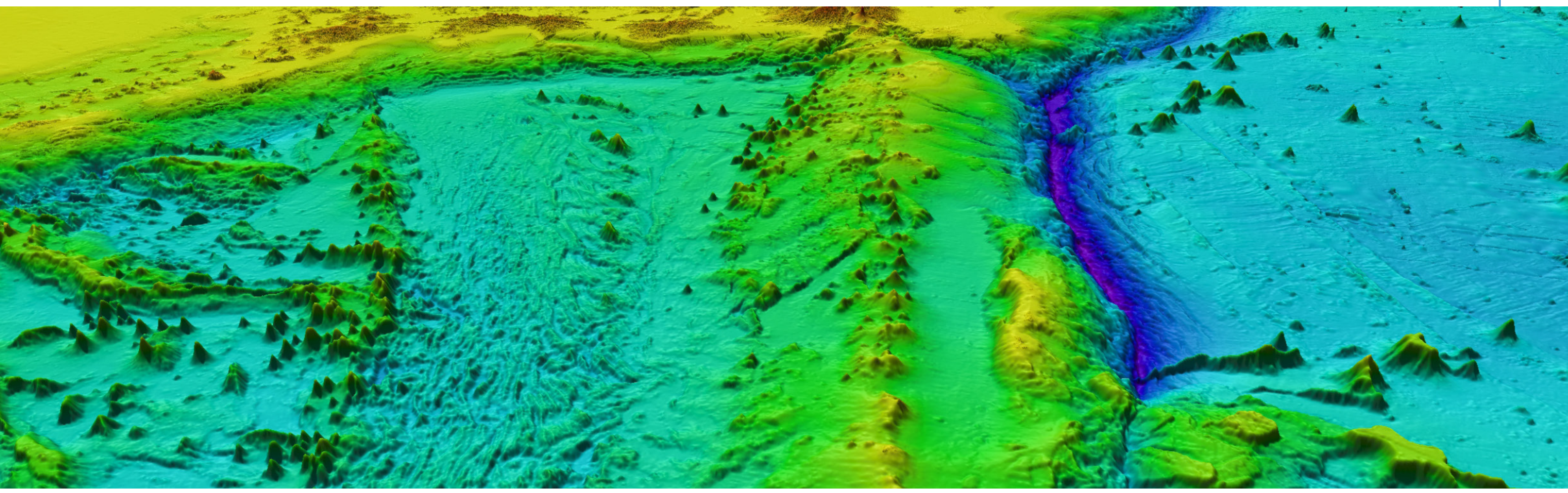
CWC garden habitats are formed by a wider range of coral taxa including octocorals, scleractinian corals, antipatharians, and stylasterids. Therefore, the distribution of CWC garden habitats is likely more extensive than that of CWC reefs; known distribution is over a wider range of depths (from mesophotic to abyssal; Roberts *et al.*, 2009) and from Arctic to Antarctic waters (e.g., Auscavitch and Waller, 2017; Long *et al.*, 2020; Stone, 2006; Figure 8). Again, no maps of CWC garden habitats (rather than individual colony occurrence) distributions exist, making understanding the drivers of existence hard to decipher.

Due to limited occurrence data, the biogeography of CWCs is not fully understood. Based on these limited data, some environmental factors that influence the distribution of CWC taxa include bathymetry and hydrography (Gori *et al.*, 2013; Buhl-Mortensen *et al.*, 2015); bottom temperature and the slope of the seafloor (Cordes and Mienis, 2023); food supply and oxygen concentration (Portilho-Ramos *et al.*, 2022).

Over large geographical scales, the distribution of cold-water Scleractinia appears to be driven partially by ocean biogeochemistry and food supply (Chaabani *et al.*, 2019). The global distributions of most Scleractinian reef-forming taxa are primarily controlled by average bottom temperature and seafloor slope (Cordes and Mienis, 2023). Aragonite saturation and oxygen concentration are also important control factors of coral occurrence at depth (Cordes and Mienis, 2023; Tittensor *et al.*, 2009). For octocorals, temperature, salinity, broad scale slope, productivity, oxygen and calcite saturation state have been identified as important factors for determining habitat suitability (Yesson *et al.*, 2012). For Antipatharia temperature and depth appear to have a strong influence on colony distribution (Yesson *et al.*, 2015).

At smaller scales, reef-forming cold-water Scleractinia generally require hard substrata and are commonly found in areas exposed to strong current flow. Typically, these corals inhabit slopes or topographic highs, such as banks or seamounts (Davies *et al.*, 2009). These locations may coincide with depths where internal wave formation occurs, providing a consistent influx of suspended particulate food or zooplankton to sustain the corals (e.g., Frederiksen *et al.*, 1992). In certain regions, these habitat-forming corals can also be found on shallower sills and banks, where their distribution may be influenced by local hydrographic phenomena that enhance access to food (e.g., localized downwelling of food-rich shallow water; Davies *et al.*, 2009). Additionally, some habitat-forming corals show a preference for steep terrain, or areas associated with local topographic highs (e.g., Taylor *et al.*, 2013).

Given the identified importance of dead CWC as habitats, it is also important to document the historical distribution of CWC during times of climate change and oceanographic rearrangement (e.g. Robinson *et al.*, 2014). These data will inform our understanding of current coral distributions and allow us to test drivers of local extinctions and growth. Clearly there is still research to be undertaken to understand the drivers of CWC occurrence across different scales. The drivers behind the envelope of existence for CWC are crucial to


Credits: GEBCO Seabed 2030

understand as this knowledge will underpin current and future restoration efforts by informing suitable areas for translocations and/or restorations and/or conservation (preserving havens that will be suitable in our future climate).

### 4.2.1.2 Prioritised Knowledge Gap 2: The Geographical Gaps of CWC Exploration

CWCs have been found globally, but there are still large geographical gaps. This is not an isolated issue, as only approximately 25% of the seafloor has been mapped in any detail (General Bathymetric Chart of the Oceans Compilation Group, 2023). Cordes and Mienis (2023) predicted that the distribution of CWC reefs is wider than currently observed as existing CWC occurrence data reflects the extent of ocean exploration efforts. For example, the most abundant CWC occurrence records occur in the Northeast Atlantic, United States continental margins, and the Southwest Pacific (Figure 8), which are the most frequently explored regions, indicating a bias in the distribution data due to geographic bias in exploration efforts. Such bias could significantly influence predictions of suitable CWC habitats. Based on the current occurrence compilation and model predictions (Cordes and Mienis, 2023), potential future regions for investigating CWC habitats include the west coast of Africa, parts of the western Indian Ocean (e.g., North of Madagascar, around the Seychelles, off the Horn of Africa), the southern shore of the Arabian Peninsula and the Bay of Bengal, the Andaman Sea, western South America and central America, and large parts of the Pacific, particularly the Southern Pacific Ocean (e.g., East and South China Seas, the Macquarie Ridge off New Zealand, Antarctic Peninsula, and the Weddell Sea). Understanding the global occurrence and diversity of CWC in these areas will improve our understanding of CWC evolution, biogeography, and the drivers of their occurrence, all facets that will support successful restoration and conservation efforts.

## 4.2.2 CWC Community Composition

### 4.2.2.1 Prioritised Knowledge Gap 3: Taxonomy and Community Composition

CWCs exhibit extraordinary diversity and have, in many cases, complex taxonomy due to the great plasticity seen in morphological characters and the few consistent characters across families (McFadden *et al.*, 2022). Understanding the taxonomy of CWCs is essential for conducting biodiversity and species-specific studies alike, particularly when, for example, developing restoration

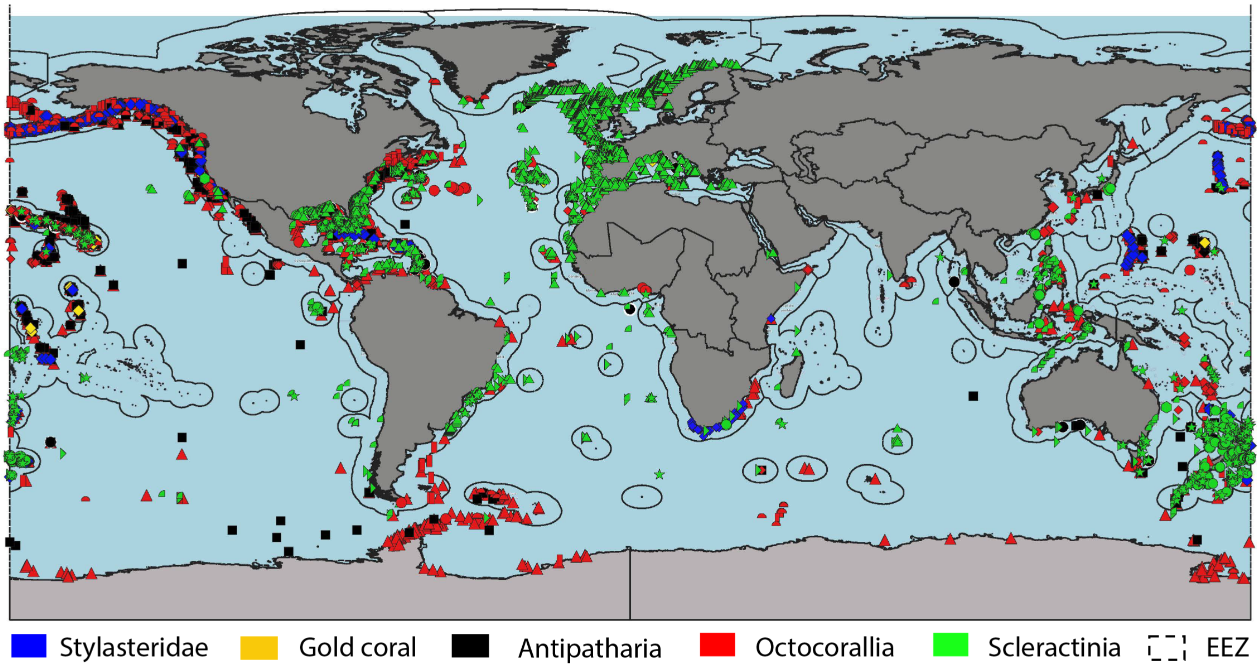


Figure 8. The distribution of CWCs from NOAA, UNEP-WCMC (Freiwald *et al.*, 2021; Deep Sea Coral Research and Technology Program (DSCRTP), 2016), Filander *et al.*, 2022b, Cairns and Zibrowius, 2013, with edits to remove erroneous points.

methods, which may be species specific. However, significant knowledge gaps and challenges persist in CWC taxonomy. Novel genomic techniques in combination with morphological taxonomic studies ("integrative taxonomy"; Padial *et al.*, 2010) are challenging previous morphology-based taxonomies (McFadden *et al.*, 2022; Hoeksema and Cairns, 2023; Morrissey *et al.*, 2023). The taxonomy of the Class Octocorallia, Family Stylasteridae, and Order Antipatharia remain poorly studied and insufficiently understood (Saucier *et al.*, 2017; Bax and Cairns, 2014). There have been major revisions in the systematics of Octocorallia in recent years (e.g., Saucier *et al.*, 2021, 2017; Watling *et al.*, 2022), with McFadden *et al.* (2022) increasing the number of recognised families from 63 to 79. Similarly, the taxonomy of the family Stylasteridae has also undergone substantial revisions (Cairns, 1984; Cairns and Lindner, 2011), albeit none so far with genome-wide next generation sequencing data. And of course, the slow but steady discoveries of new species, e.g., under family Stylasteridae (Cairns and Pica, 2019; Lizcano-Sandoval and Cairns, 2018; Pica *et al.*, 2015) and within Octocorallia (Taylor *et al.*, 2013; Bayer *et al.*, 2015; Samimi-Namin and van Ofwegen, 2016; Watling, 2015), contributes to the complexity of CWC taxonomy.

The limited understanding of CWC taxonomy and the vast number of undescribed species, with just a small but dedicated community of morphological taxonomists globally significantly hinders other crucial studies. Advancing our understanding of taxon distribution patterns (biogeography), CWC ecosystem biodiversity, rarity and endemism depends in part on clearly described taxonomy. Similarly, CWC taxonomy is important in understanding species interactions such as symbioses, growth rates and biomineralisation of different CWCs species, resilience to environmental change, and species-specific conservation status. Ultimately, lack of adequate taxonomic information impedes the development of effective conservation restoration methods as well, given some species are challenging to tell apart and thus "species" studies are sometimes confounded. CWC taxonomy is the bedrock for a lot of research, and it is of utmost priority to advance knowledge within this field to support meaningful assessments of the conservation status of CWCs.

### 4.2.3 CWC Reproduction

Reproduction constitutes a fundamental ecological process inherent to the life cycle of all species, essential for sustaining population growth and expansion (Burgess and Babcock, 2005; Strömberg and Larsson, 2017; Waller *et al.*, 2023). Understanding the intricate reproductive processes of CWCs is a crucial aspect of the development and implementation of effective restoration strategies. Although the number of CWC reproduction studies is increasing, the studied species represent generally less than 4% of known CWC species (Waller *et al.*, 2023). Scleractinia and Octocorallia (or Alcyonacea) dominate CWC reproduction research, with only two studies devoted to Stylasteridae (Waller *et al.*, 2023). Substantial knowledge gaps persist within the field of CWC reproduction, obscuring our understanding of their potential for recovery and posing significant challenges to CWC conservation and restoration efforts. Drawing upon the limited available data, Waller *et al.* (2023) synthesised a simplified general model of CWC life cycles (Figure 9) and discussed four distinct sections of CWC reproduction as the primary knowledge gaps requiring attention. The workshop participants agreed these were significant knowledge gaps to CWC restoration and conservation.

#### 4.2.3.1 Prioritised Knowledge Gap 4: Sexuality and Gametogenesis

The sexuality patterns and gametogenesis processes of CWCs also remain poorly understood. While gonochorism (the occurrence of separate sexes) is the predominant sexual strategy across examined taxa, instances of hermaphroditism (both sexes within a single individual) have been observed in CWC Scleractinia and Octocorallia (reviewed in Waller *et al.*, 2023). Some groups, like Stylasteridae, are vastly understudied (Brooke and Stone, 2007), making definitive conclusions regarding the sexual strategies of this particular taxa impossible. Waller *et al.* (2023) summarises the general gametogenesis patterns across all taxa studied. Gametogenesis in Stylasteridae remains insufficiently documented and even within the relatively well-studied Scleractinia, knowledge is still poor compared to shallow water counterparts, in particular, asexual fragmentation and reproduction as a means to build reefs and communities, something that is commonly reported for shallow water corals, is an aspect that is virtually unstudied in CWC. There are just single studies reporting 1) direct observation of asexual budding (Waller *et al.*, 2002), 2) polyp bailout (Rakka *et al.*, 2019), and 3) inferred reef building by fragmentation in *Desmophyllum pertusum* (Dahl *et al.*, 2012). This highlights the need for further investigations as clonal growth may become a dominant vector of restoration approaches, as is the case for shallow-water, tropical corals.

#### 4.2.3.2 Prioritised Knowledge Gap 5: Sexual Maturity and Fecundity

Sexual maturity and fecundity play pivotal roles in the population dynamics of CWCs and, consequently, their capacity to recover from disturbance. However, similarly to other aspects of CWC reproduction, very little is known about their sexual maturity and fecundity (Waller *et al.*, 2023). Current research underscores the challenges of establishing generalised maturity criteria and fecundity assessments for CWCs, largely due to inconsistencies in measurement methodologies. Moreover, research efforts have predominantly concentrated on well-documented taxa, such as Scleractinia and Octocorallia; sexual maturity studies have been done on only two species of Antipatharia and none on Stylasteridae. Generally, Scleractinia exhibit the highest fecundity, while brooding Octocorallia exhibit the lowest (Fig. 7 in Waller *et al.*, 2023). Enhanced insights into CWC sexual maturity and fecundity hold the potential to inform the development of more efficient and successful restoration strategies.

#### 4.2.3.3 Prioritised Knowledge Gap 6: Reproductive Mode and Seasonality

To know the reproductive mode of CWCs direct observation of actual reproductive spawning or offspring release events is required (Waller *et al.*, 2023). One crucial knowledge gap revolves around the precise timing of reproductive events in CWCs. More commonly, researchers rely on assessing stages of gamete development to infer the timing of maturation and release relying mostly on being able to understand gametogenic patterns, which, however, is also a key knowledge gap. CWCs demonstrate either seasonal (reproductive activities happen during specific seasons or times of the year) or periodic (reproductive activities at regular intervals which may not necessarily align with specific seasons) reproductive modes. In Scleractinia, about half of the examined species exhibited periodicity (Waller, 2005; Waller *et al.*, 2023). In Octocorallia most of the examined species display periodicity

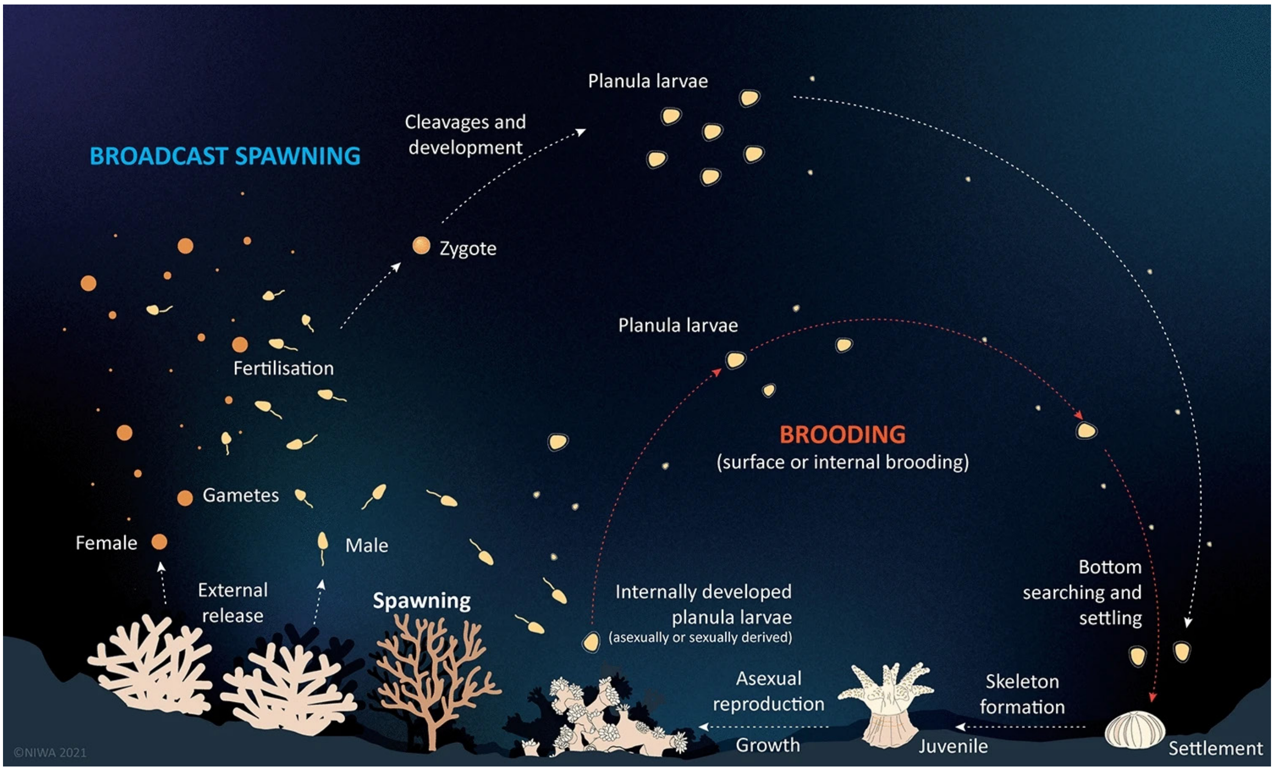


Figure 9. Simplified general model of the life cycles of cold-water corals (reproduced with permission from Waller *et al.*, 2023).

while seasonality is also seen in some species (Waller *et al.*, 2023). Remarkably, within the same family and similar environments, species may exhibit different reproductive modes (Beazley and Kenchington, 2012; Mercier and Hamel, 2011). Observations of Antipatharia and Stylasteridae are again very limited, precluding the formulation of clear patterns. Addressing this knowledge gap through further research on these underexplored groups is imperative. Comprehensive understanding of these reproductive patterns empowers conservationists to synchronise restoration initiatives with natural reproductive events, thereby enhancing the prospects of successful larval settlement and colony establishment for restoration.

#### 4.2.3.4 Prioritised Knowledge Gap 7: Fertilisation, Larval Development and Settlement

Currently data on CWC fertilisation, larval development (including dispersal) and settlement are predominantly available for Scleractinia (Altieri, 2003; Larsson *et al.*, 2014, Strömberg and Larsson, 2017; Tracey *et al.*, 2021; Beaumont *et al.*, 2024) and Octocorallia (Cordes *et al.*, 2001; Rakka *et al.*, 2021; Sun *et al.*, 2011). For Pennatulacea, limited data are available (Chia and Crawford, 1973). These data reveal significant variability in fertilisation modes and larval settlement patterns, with the latter occurring anywhere from hours to weeks post-fertilization (Waller *et al.*, 2023). Investigating the underlying mechanisms governing larval dispersal and settlement (which clearly links with population connectivity), including sensory cues and influential environmental factors, holds paramount importance for CWC restoration and conservation.

## 4.2.4 CWC Metapopulation dynamics and connectivity

#### Prioritised Knowledge Gap 8: Connectivity of CWC Populations and Population Structure

Ecological spatial connectivity refers to the flow of genes, propagules and individuals among spatially distinct populations. To ensure recruitment to restored sites and resilience of restored populations, it is essential to study CWC population connectivity. Well-connected populations are more resilient to anthropogenic disturbance, and larvae from source populations can help passively restore areas that have been damaged by recruiting in suitable habitats (Oleksiak, 2019; Jenkins and Stevens, 2018). The difficulty of obtaining CWCs has contributed to a critical knowledge gap in the understanding of the connectivity of CWC populations with only a few studies being completed (Taylor and Roterman, 2017). Additionally, the samples that have been collected historically have been preserved in formalin- a chemical which preserves tissue well for histology but destroys DNA that could be used for future genetic studies.

Previously, studies examining genetic connectivity in CWCs used 10-20 microsatellite markers to determine gene flow within populations requiring twenty to thirty individuals per site (Ballesteros-Contreras *et al.*, 2022; Herrera *et al.*, 2012; Miller and Gunasekera, 2017; Miller *et al.*, 2011; Quattrini *et al.*, 2015). However recently, the availability of cheaper next generation sequencing has allowed researchers to use fewer available samples and higher sequencing power to complete more extensive in-depth genetic connectivity studies using hundreds to thousands of DNA markers (Erickson *et al.*, 2021; Everett *et al.*, 2016; Herrera and Shank, 2016). These studies are few in number, focus on local/ regional connectivity, and do not cover extensive ocean-wide connectivity patterns. More broad scale studies of this kind are needed to understand connections across ocean basins and global connectivity of CWC.

Another option is to estimate potential connectivity using ocean circulation models in combination with particle tracking. One such study in the North Atlantic found the potential for larvae to disperse great distances based on different larval behaviours and durations (Gary *et al.*, 2020). Coral connectivity is reliant on currents that will carry larvae to a suitable location to settle; however, very little is known about CWC reproduction and larval behaviour - see section on reproduction- and only estimates are available at this time. Several obstacles to distribution exist in the marine environment such as differences in water temperature, salinity, oxygenation, nutrient availability, and barrier currents (Benestan *et al.*, 2016). The understanding of these barriers to connectivity and gene flow between populations of CWC can better inform the management of these vulnerable marine ecosystems and ensure that there will be recruits with which to repopulate areas that have been disturbed (Cowen and Sponaugle, 2009; Jenkins and Stevens, 2018; Leiva *et al.*, 2023; Palumbi, 2003; Taboada *et al.*, 2022).

## 4.2.5 CWC Growth

### 4.2.5.1 Prioritised Knowledge Gap 9: Growth Rates and Biomineralization of CWCs and Potential Impact Factors

The biomineralization strategies and growth rate of CWCs comprise a critical knowledge gap for the development of CWC restoration approaches. The growth rate of CWCs exhibit considerable variation among different species. Currently, two primary methodologies are employed for determining CWC growth rates: *in situ* or in aquaria observation and geochemical dating. However, both types of methods raise challenges. Firstly, *in situ* observation demands a prolonged duration for accurate determination due to the generally slow growth rates exhibited by CWCs, even in cases of species considered to be relatively fast growing (Orejas *et al.*, 2008). Additionally, *in situ* observations face the challenge of precise growth measurement. Although studies have utilised *in situ* 3D photogrammetry to quantify CWC growth (Bennecke *et al.*, 2016; Lartaud *et al.*, 2014), available growth data remain limited and predominantly focus on fast-growing species. Geochemical dating offers an alternative way for generating growth rates by measuring a set of ages of the coral skeleton (Sabatier *et al.*, 2012). However, growth rates derived from geochemical dating represent long-term (decadal) averages and may not capture variations in CWC growth attributable to short-term environmental fluctuations. These challenges underscore the complexity of assessing CWC growth rates, especially in light of species-specific differences (Reynaud *et al.*, 2019; Tracey and Hjorvarsdottir, 2019).

The skeleton of CWCs provides support for the coral polyps and contributes to the formation of complex three-dimensional habitats (Edinger *et al.*, 2007; Husebø *et al.*, 2002; Maynou and Cartes, 2012; Söffker *et al.*, 2011). However, the mechanism through which CWC build their skeletons remains largely unknown (Chen *et al.*, 2023; Roberts *et al.*, 2016; Stewart *et al.*, 2022; Stolarski *et al.*, 2016). Depending on species, the main component of CWC skeleton is calcium carbonate (Scleractinia, Octocorallia and Stylasteridae) where calcium carbonate is deposited in crystalline forms known as aragonite and calcite (Roberts *et al.*, 2009; Robinson *et al.*, 2014) or organic matter (Antipatharia and gold coral). Formation of inorganic aragonite and calcite demands carbonate supersaturation, however, CWCs are able to build their skeleton even in the undersaturated seawater (Carreiro-Silva *et al.*, 2014; Stewart *et al.*, 2022). Some CWCs are able to use energy to operate ion pumps modulating their internal calcifying fluid, a potentially important strategy for their survival under the future ocean acidification (Adkins *et al.* 2003; Gagnon *et al.* 2012; McCulloch *et al.*, 2012). Other CWCs may use alternative strategies such as protective organic templates and / or coatings given the evidence that Stylasteridae build skeleton without modulating internal building fluid even in the undersaturation condition (Stewart *et al.*, 2022). The complicated biological modulation of skeletal growth in different species of CWCs impedes our understanding of the controls on CWC growth, and therefore the development of effective active restoration strategies.

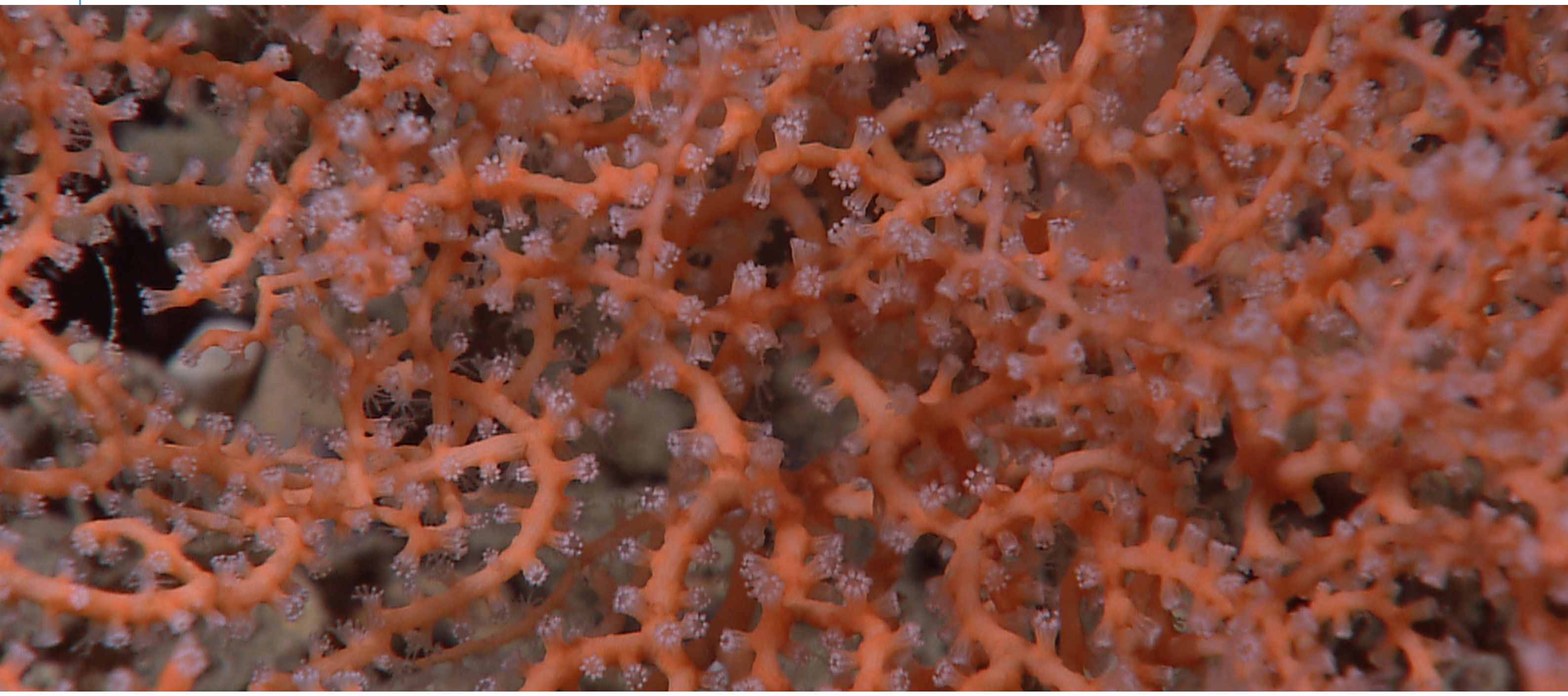
Comprehensive insights into the growth patterns and key determinants governing the morphological development of CWCs, particularly during their juvenile stages, remain notably lacking (Corbera *et al.*, 2022; Hennige *et al.*, 2021). It is recognized that growth of CWCs is a complex process influenced by various environmental and ecological factors (Corbera *et al.*, 2022; Dullo *et al.*, 2008; Eisele *et al.*, 2011; Mienis *et al.*, 2007, 2014). Understanding these factors is crucial for assessing CWC health, distribution, and responses to environmental changes that can then inform restoration efforts.

The controlling factors of CWCs growth include the hydrodynamics of the region (Corbera *et al.*, 2022; Davies *et al.*, 2009; Juva *et al.*, 2020; Mienis *et al.*, 2007; Mohn *et al.*, 2014; Mortensen *et al.*, 2001), food availability (Larsson *et al.*, 2013a; Maier *et al.*, 2019), biomineralization of CWC skeletons (Stewart *et al.*, 2022), seawater chemistry (e.g. oxygen and carbonate saturation), and temperature (Chapron *et al.*, 2018; Davies *et al.*, 2009; Eisele *et al.*, 2011; Fink *et al.*, 2013; Maier *et al.*, 2020a; Portilho-Ramos *et al.*, 2022; Gori *et al.*, 2014). However, despite our overarching understanding of these controlling factors, limited data are available to elucidate the precise mechanisms through which these factors influence CWC growth

(Corbera *et al.*, 2022; Hennige *et al.*, 2015). Consequently, there is an imperative for forthcoming research to delve into the controlling factors governing CWC growth patterns and rates, with particular attention directed towards underexplored taxa, such as Stylasteridae.

### 4.2.5.2 Prioritised Knowledge Gap 10: The Food Dynamics of CWCs

A comprehensive understanding of food dynamics is needed to identify optimal conditions for CWC restoration. Specific topics that need to be further investigated, including feeding mechanisms, preferred food sources, and seasonal variability, CWCs are believed to rely on carbon input from the ocean surface (Goldberg, 2018; Maier *et al.*, 2023). Their food sources may include zooplankton, bacteria, particular organic matter (POM), dissolved organic matter (DOM) (Dodds *et al.*, 2009; Mueller *et al.*, 2014; Orejas *et al.*, 2016). *Desmophyllum pertusum* is the most studied species and it does feed readily on zooplankton in low-flow conditions (Larsson *et al.*, 2013b; Naumann *et al.*, 2011; Purser, 2015), however lipid profiles, stable isotope signatures, and observations of localized mucus secretion in response to the presence of food particles, suggest POM is the main food source (Duineveld *et al.*, 2012; Zetsche *et al.*, 2016). By contrast, *Desmophyllum dianthus* and *Madrepora oculata* in the Mediterranean Sea consume mainly living zooplankton (Gori *et al.*, 2018; Naumann *et al.*, 2015). In addition to Scleractinia, studies suggest zooplankton might also be the main food source of Octocorallia (Liu *et al.*, 2023; Orejas *et al.*, 2003; Sherwood *et al.*, 2008). However, there are also studies suggesting DOM or bacterioplankton are dominant diet contributors of Octocorallia (Schlichter, 1982). A sufficient understanding of the food sources of Octocorallia is lacking, as well as for the food source of other groups of CWCs. There is little information on CWC feeding mechanisms (Goldberg, 2018). Scleractinia employ mostly tentacle capture likely involving mucociliary activity or extracoelenteric digestion, but the relative contribution of each process has not been evaluated (Goldberg, 2018). For Octocorallia, tentacular filtration of weakly swimming mesozooplankton, particulates, DOM, and picoplankton are thought to be their main feeding mechanisms (Lewis, 1982). They are also thought to be opportunistic feeders and shift their diet according to season from phyto- and nanoplankton in summer to primarily POM in winter (Ribes *et al.*, 1999). Time-lapse imagery studies of *Paragorgia arborea* off California have shown that *P. arborea* feeding, based on polyp opening/closing varies seasonally with food availability, and tidally according to current speed and direction (Girard *et al.*, 2022). Generally, the feeding mechanism is not clear for most of the CWCs.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# 5. Recommendations

The above priorities aim to bridge the critical gaps in knowledge required for transformative leaps forward in effective conservation and restoration of CWC in the next 10 years. Some overarching recommendations to researchers, managers, and donors are highlighted below:

- Deep-sea research is skewed to the Global North and lacks diversity. We encourage all actors in the CWC field to focus on widening participation in CWC research, conservation, and management to ensure its equitable future and to collaborate to fill in the evident geographical gaps in CWC knowledge.
- Encourage CWC community coordination and engagement as this is crucial to exchange ideas, results, and methods faster than allowed by the timelines of academic publication.
- Increasing understanding of CWC in the global consciousness is crucial to garner public, private and political support for conservation and restoration. We recommend the active participation of the CWC scientific community in relevant policy forums, such as the Convention of Parties of UNFCC and CBD, where CWCs are notoriously absent from events and discussions. We also recommend the exploration of innovative endeavours that bring together science, policy, and the arts as this breadth of experience and knowledge is required to approach this challenging task.
- Existing CWC location data should be made freely available and integrated in existing platforms, such as the Ocean Biodiversity Information System (https://obis.org/), thereby supporting global understanding of biogeography, ranges, diversity and conservation status. This knowledge is a necessary underpinning of conservation and restoration efforts.

Credits: Marcelo Kitahara

- If locations exist that are currently untrawled and likely have CWC they should be protected from the clear damage this fishing gear causes. These areas represent the hope spots whilst we expand the science of CWC conservation and restoration, providing our best bets for future healthy CWCs that should be left as potential refugia and sources of larvae for those areas already impacted. As our understanding of the factors important for maintaining healthy CWC through future centuries and millennia crystallises we can reassess these protections in an informed manner.

- CWC conservation and restoration can be advanced by focusing efforts on understanding CWC taxonomy, reproduction, growth and feeding. This basic understanding of CWC biology is required to formulate successful conservation and restoration efforts.

- The above recommendations require dedicated funding, and longer-term funding than is currently common for deep-sea research. We urge donors to think innovatively about how longer-term funding could be supported, as some aspects of CWC research, conservation and restoration require timescales that do not easily fit into current short term (~3yr) grant rounds.

The above recommendations address a wide-ranging collective that covers many fields of research, management, and politics. The whole community of CWC practitioners will be called upon to action these recommendations to ensure the knowledge gaps to secure successful current and future CWC conservation and restoration activities are filled. With the many threats CWC faces and the current dearth of knowledge in this field these activities are considered urgent to ensure the long-term survival of the essential ocean habitats CWCs are.

# 6. Conclusions

CWCs form globally relevant, diverse, and productive ecosystems that are severely understudied. The above priorities are a short list of the very wide and varied gaps in knowledge that the workshop and the CWC community highlighted. Other gaps include:

oceanographic models, standard monitoring protocols, CWC ecosystem functioning, microscale studies, microbial ecology, and disease; role of associations like microbes, parasites and their interactions, physiological studies; and fit-for-purpose conservation strategies, MPA management and regulations, as well as low-cost technology development supporting monitoring efforts.

Selecting priorities in a data-poor realm is challenging and any priority list is likely to miss knowledge gaps in need of attention. We, therefore, identify the key knowledge gaps above on the belief that, with appropriate funding and research attention by the CWC scientific community, these can be bridged in the coming decade.

Credits: NOAA Ocean Exploration

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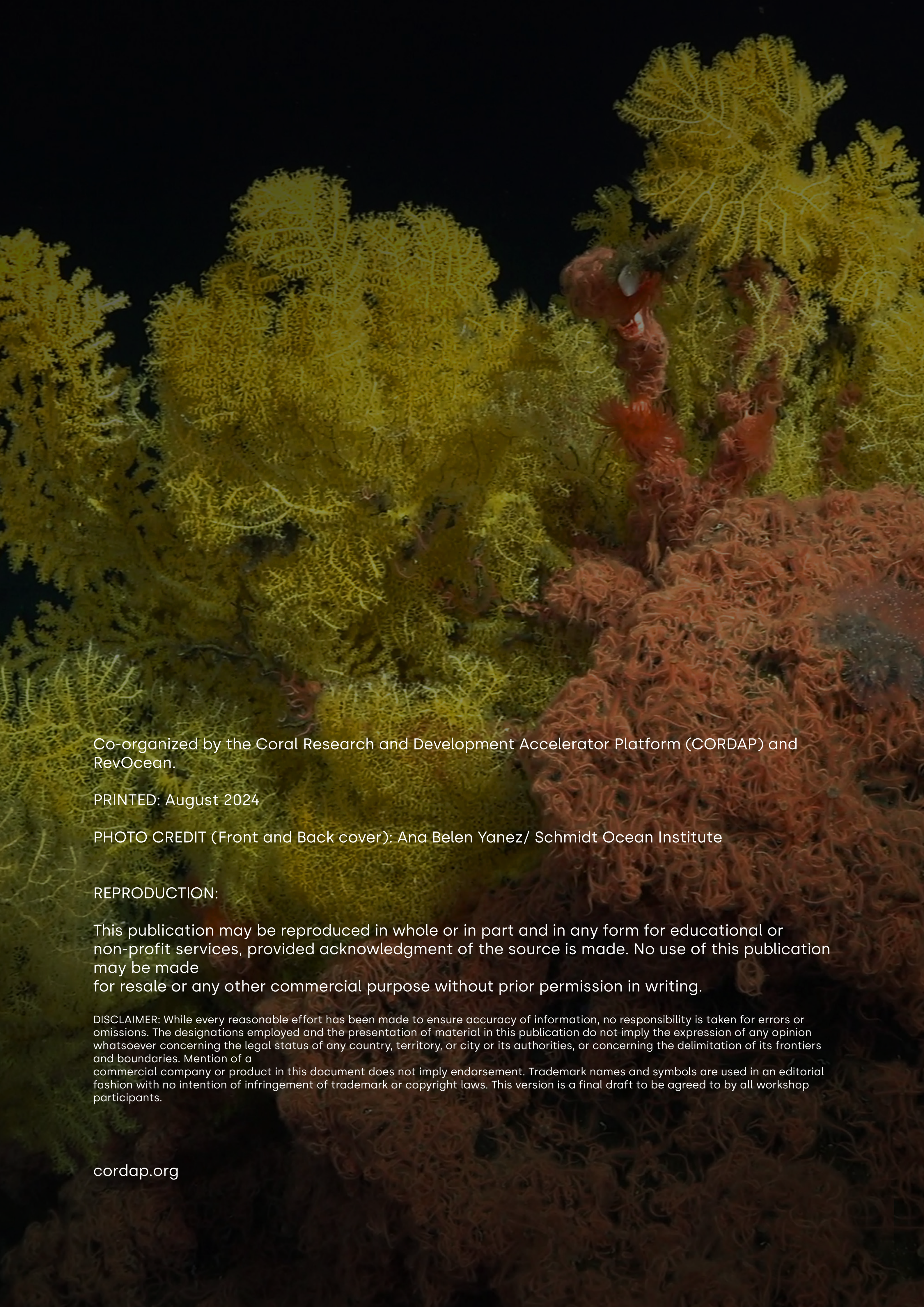

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