



# Active Ecological Restoration of Cold-Water Corals: Techniques, Challenges, Costs and Future Directions

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Cold-water coral (CWC) habitats dwell on continental shelves, slopes, seamounts, and ridge systems around the world's oceans from 50 to 4000 m depth, providing heterogeneous habitats which support a myriad of associated fauna. These highly diverse ecosystems are threatened by human stressors such as fishing activities, gas and oil exploitation, and climate change. Since their life-history traits such as long lifespan and slow growth rates make CWCs very vulnerable to potential threats, it is a foremost challenge to explore the viability of restoration actions to enhance and speed up their recovery. In contrast to terrestrial and shallow-water marine ecosystems, ecological restoration in deep marine environments has received minimal attention. This review, by means of a systematic literature search, aims to identify CWC restoration challenges, assess the most suitable techniques to restore them, and discuss future perspectives. Outcomes from the few restoration actions performed to date on CWCs, which have lasted between 1 to 4 years, provide evidence of the feasibility of coral transplantation and artificial reef deployments. Scientific efforts should focus on testing novel and creative restoration techniques, especially to scale up to the spatial and temporal scales of impacts. There is still a general lack of knowledge about the biological, ecological and habitat characteristics of CWC species exploration of which would aid the development of effective restoration measures.

To ensure the long-term viability and success of any restoration action it is essential to include holistic and long-term monitoring programs, and to ideally combine active restoration with natural spontaneous regeneration (i.e., passive restoration) strategies such as the implementation of deep-sea marine protected areas (MPAs). We conclude that a combination of passive and active restoration approaches with involvement of local society would be the best optimal option to achieve and ensure CWC restoration success.

**Keywords:** deep-sea, human impacts, coral reefs, marine protected area, coral husbandry, challenges, review

## INTRODUCTION

Over the past 50 years humans have changed ecosystems more rapidly and extensively than in any comparable historical period. This transformation of the planet has contributed to substantial net gains in human well-being and economic development, but at the same time has resulted in a substantial and largely irreversible loss in the diversity of life on Earth (Millennium Ecosystem Assessment, 2005; Cardinale et al., 2012; IPBES, 2019). Many ecosystems and their functioning have been impaired beyond critical points and are not able to return to their native states or previous developmental trajectories (Jackson et al., 1995; Jackson, 2001). Conservation measures are crucial for the preservation and recovery of natural and cultural heritage. However, the current pace and scale of global environmental degradation across a wide swath of ecosystems call for active ecological restoration measures, to aid the recovery of these ecosystems and the services they provide (Lotze et al., 2011; Gann et al., 2019; Duarte et al., 2020).

At present, the practice of ecological restoration – as part of a larger set of ecosystem management practices designed to conserve natural ecosystems – is receiving increasing attention worldwide. Ecological restoration has been recognized under different frameworks, and conventions (e.g., the UN Decade on Ecosystem Restoration, the UN Decade of Ocean Science for Sustainable Development and the Convention on Biological Diversity), as it offers the opportunity to counteract the anthropogenic damage that has already taken place (Falk et al., 2006). The Society for Ecological Restoration (SER), founded in 1983, established that ecological restoration actions aim to move a degraded ecosystem to a trajectory of recovery that allows the persistence of its component species, as well as the adaptation to local and global changes (Gann et al., 2018). Ecological restoration activities seek to accelerate the recovery of ecosystem structure and functioning relative to an appropriate reference model (the chosen endpoint of restoration).

However, the term “restoration” has always been surrounded by a certain ambiguity (Ounanian et al., 2018), and SER has re-evaluated and altered its definition several times in the last decade. The latest standard set by SER in 2019 established three different approaches to restoration that may be applied individually or in combination, as appropriate. We consider these approaches in this review: (1) Natural regeneration: this corresponds to so-called ‘passive restoration.’ It encompasses the removal of stressors through the creation of protected areas where the recovery of the biota arises from natural colonization,

dispersal and other *in situ* process. (2) Assisted regeneration: once the source of degradation has been removed, this type of ‘active restoration’ necessitates direct human interventions that actively trigger the natural population growth capacity of biota. Interventions include removal of non-native species, installation of resources to prompt colonization, etc. (3) Reconstruction: when ecosystems have been severely damaged, this type of ‘active restoration’ calls not only for the removal of sources of degradation but also the improvement of the biotic and abiotic ecosystem condition. Here, direct human intervention is needed to reintroduce all, or a major proportion of the biota, which otherwise would not be able to regenerate or recolonize the area within a reasonable time frame.

Complete recovery of ecosystems is difficult to achieve (Jones et al., 2018), since all identified ecosystem attributes (e.g., physical environment, desirable species) should be reintegrated into a self-organizing system that most resembles the reference model (Gann et al., 2019). Emerging formulations of restoration use historical knowledge as a guide, rather than a template, accepting multiple potential ecosystem trajectories, recognizing the major importance of ecological processes over ecosystem structure and composition, and promoting the establishment of pragmatic goals to reflect human livelihood needs (Higgs et al., 2014). The three approaches to ecological restoration are part of a continuum of restorative activities that strive toward recovery of an ecosystem (McDonald et al., 2016; Aronson et al., 2017). It is beneficial to consider that some restorative actions (such as reducing human impacts) may not have as an ultimate goal, full recovery of an ecosystem at the time of implementation, but will contribute toward a more sustainable use of the ecosystem and facilitate future decisions toward restoration. In order to encourage this difficult task, the active restoration efforts often target key foundation species such as trees, kelps, or corals. These taxa often facilitate the re-establishment of associated species and succession processes that are crucial to restore the functioning of the ecosystems (Bruno et al., 2003).

In the specific case of marine ecosystems, most active ecological restoration actions have been performed in shallow waters, mainly focused on the restoration of salt marshes (Bakker et al., 2002; Hughes and Paramor, 2004; Laegdsgaard, 2006), tropical coral reefs (Rinkevich, 2005; Precht and Robbart, 2006; Young et al., 2012), oyster reefs (Babcock et al., 1998; Brumbaugh et al., 2006; Baggett et al., 2015), mangroves (Proffitt and Devlin, 2005; Bosire et al., 2008; Primavera and Esteban, 2008), seagrass meadows (Paling et al., 2009; van Katwijk et al., 2009, 2016) macroalgal forests (Verdura et al., 2018; Layton et al., 2020;

Medrano et al., 2020) and temperate gorgonians (Weinberg, 1979; Linares et al., 2008; Fava et al., 2010). Recently, marine restoration reviews (Basconi et al., 2020; Duarte et al., 2020) reported high frequency of success, supporting the feasibility and potential of active restoration techniques, however, neglecting deeper habitats. Yet, primarily due to technical challenges and associated high cost in accessing the intermediate (from 50–70 to 200 m depth) and deep-sea environments (below 200 m depth), active ecological restoration efforts on these ecosystems still remain scarce (Van Dover et al., 2014; Da Ros et al., 2019). Cold-water corals (CWCs) are often key habitat-forming species in this part of the ocean, generating complex three-dimensional structures that create hotspots of biodiversity over large areas, including CWC reefs and coral gardens (Roberts et al., 2009). They are increasingly affected by multiple stressors including fisheries with bottom-contact gears, offshore oil and gas activities, and climate change (Althaus et al., 2009; White et al., 2012; Clark et al., 2016; Morato et al., 2020). In the near future many CWCs will also be on the frontline of exposure to impacts from deep-sea mining (Levin et al., 2016; Gollner et al., 2017).

The present study synthesizes the latest information on CWC active restoration with the aim of advancing beyond the challenges of restoring CWC ecosystems and to create a new understanding of opportunities now available to undertake these activities. We first summarize the main biological and ecological features of CWC species (Section 2), their main drivers of degradation (Section 3), and their protection (Section 4). We then compile and discuss techniques used for actively restoring CWC habitats, highlight current challenges facing their restoration, and examine restoration costs and collaboration with industry (Section 5). Finally, we conclude by highlighting lessons learned from shallow-water restoration to move forward in active CWC ecological restoration (Section 6).

## COLD-WATER CORAL ECOSYSTEMS

CWCs are cnidarians encompassing species from Scleractinia, Octocorallia, Antipatharia and Stylasteridae (ICES and Hall-Spencer, 2007; Roberts et al., 2009). Despite the high prevalence of tropical coral reefs at shallow depths, most coral species are found in the world's aphotic zone, in cold waters from 50 to 4000 m depth (Roberts et al., 2009; Bergmark and Jorgensen, 2014) on continental shelves, margins, seamounts, canyons and ridge systems (Freiwald and Roberts, 2005; Roberts et al., 2006, 2009; Cordes et al., 2016a). In those habitats, in addition to the six species of reef framework-forming scleractinian CWCs (Scleractinia), many other CWC species can form extensive coral gardens (Octocorallia, Antipatharia and Stylasterida) often mixed with solitary and/or reef framework-forming corals, under suitable conditions (e.g., appropriate substrate, water current and food supply). These CWC ecosystems increase habitat heterogeneity and support enhanced biological diversity and ecosystem functioning (Roberts et al., 2006, 2009; Cordes et al., 2008; Armstrong et al., 2014). The structures they create can alter current flow, food availability, and sediment resuspension, which provides niches, shelter and nursery grounds for an

abundant and diverse associated fauna including economically valuable species, both within and in the immediate vicinity of their habitats (Costello et al., 2005; Henry and Roberts, 2007; Demopoulos et al., 2014). CWC ecosystems support unique species, providing benefits to adjacent fisheries through the spill-over effect of eggs, larvae, juveniles and adults (D'Onghia et al., 2010; Corbera et al., 2019).

CWCs are mainly sustained by feeding on particulate organic matter and zooplankton, which they capture from the water (Kiriakoulakis et al., 2005; Dodds et al., 2009; Mueller et al., 2013a), although more recently, chemosynthesis has been suggested to provide an additional source of energy (Middelburg et al., 2015). Significantly higher levels of biogeochemical cycling, respiration and benthic-pelagic coupling processes take place in CWC ecosystems in comparison to the surrounding seafloor, enhancing the ecosystem functioning of the deep-sea biome (Wild et al., 2009; Burdett et al., 2014; Cathalot et al., 2015; Rovelli et al., 2015). CWC species are often slow-growing, with potentially long lifespans (Andrews et al., 2002; Roark et al., 2009; De Moura Neves, 2016), delayed sexual maturity and limited recruitment success (Roberts et al., 2009; Watling et al., 2011; Lacharité and Metaxas, 2013); thus, many species are expected to recover slowly after any disturbance. Two separate studies have shown that over a period of 8 to 10 years following the cessation of fishing activities with bottom-contact gears there was no natural recovery of impacted CWC communities, even at depths shallower than 1000 m (Althaus et al., 2009; Williams et al., 2010; Huvenne et al., 2016). It has been estimated that CWCs heavily impacted by the *Deepwater Horizon* oil spill (Gulf of Mexico, April 2010) could take up to three decades to visibly recover, and likely hundreds of years to grow back to their original size (Girard et al., 2018). According to their fragility, structural complexity, functional significance, and low recovery capability from impacts, many CWC ecosystems meet the criteria for Vulnerable Marine Ecosystems (VME; FAO, 2009a) and are listed in the OSPAR List of Threatened and/or Declining Species and Habitats (OSPAR, 2009, 2010). Thus, their conservation is internationally recognized as a high priority for the maintenance of marine biodiversity and the ecosystem services provided (Thurber et al., 2014; Cordes et al., 2016a).

## DRIVERS OF DEGRADATION

The main threats for CWC ecosystems come from human maritime activities, such as fishing, hydrocarbon exploitation and the incipient mining activity, which have direct contact with the seabed causing an immediate impact on CWC communities (Ragnarsson et al., 2017; Miller et al., 2018). Fishing is one of the most extensive activities that interacts with the seabed and has gradually encroached into deeper waters (Roberts, 2002; Gross, 2015). Worldwide fishing impacts down to 1000 m depth are widespread, with almost all shelf and slopes areas being fished to some extent (Puig et al., 2012; Pham et al., 2014). Whilst the majority of trawling occurs on soft flat sediments, impacted areas also include CWC habitats (Hall-Spencer et al., 2002; Pham et al., 2014; Boavida et al., 2016; Huvenne et al., 2016;

Ragnarsson et al., 2017; Buhl-Mortensen and Buhl-Mortensen, 2018) because of their role as important faunal nursery grounds for the surrounding fisheries (Baillon et al., 2012). Bottom trawling causes direct habitat degradation (Pusceddu et al., 2014; Rijnsdorp et al., 2016) as well as indirect effects including the resuspension of sediment plumes from the trawl track that can smother corals as they precipitate over the reefs (Ramirez-Llodra et al., 2011; Martín et al., 2014). Other bottom-contact fishing gears such as traps, longlines and trammel nets may also impact through the damage and removal of corals, as they are easily entangled in nets, overall contributing to the degradation of CWC communities (Wareham and Edinger, 2007; Durán Muñoz et al., 2011; Sampaio et al., 2012). Impacts from the fishing industry also include those caused by lost fishing gears and fishing related litter in which corals can get entangled (Bo et al., 2014; Buhl-Mortensen and Buhl-Mortensen, 2018). Operations in offshore oil and gas industries also produce large contaminated cuttings piles and sediment plumes that can impact CWCs in a variety of ways (Cordes et al., 2016b). While adult colonies of the CWC *Lophelia pertusa* can generally withstand a degree of discharged cuttings without significant ecophysiological impacts (Larsson et al., 2013; Baussant et al., 2018) the dispersive larval phase of this CWC is highly susceptible to mortality from sediment loads (Järnegren et al., 2017). Moreover, accidental oil spills can profoundly affect CWCs, with impacts from the molecular to the ecosystem scale (White et al., 2012; Fisher et al., 2014; DeLeo et al., 2016; Joye et al., 2016; Weinnig et al., 2020). Additionally, CWC ecosystems are expected also to be exposed to the future impacts of deep-sea mining activities (Christiansen et al., 2019).

Global change will exacerbate these stressors (e.g., ocean acidification and increase in temperature, Weinnig et al., 2020) and will, within the coming century, significantly reduce suitable habitats for CWCs (Sweetman et al., 2017; Morato et al., 2020; Puerta et al., 2020). By the year 2100, projections indicate that about 70% of current CWC reef locations will become undersaturated with respect to aragonite, thus exposing the majority of presently existing reefs to an environment that favors carbonate dissolution, likely altering their global distribution and abundance (Guinotte et al., 2006). Although existing evidence suggests that some scleractinian corals can persist in undersaturated waters (Thresher et al., 2011; Movilla et al., 2014; Baco et al., 2017; Gómez et al., 2018), the metabolic rates of CWC species could be altered due to reallocation of energy reserves, reducing their fitness (Hennige et al., 2015; Georgian et al., 2016; Gori et al., 2016). Additionally, rise of seawater temperature, even in deep-sea environments (Purkey and Johnson, 2010), and decline in O<sub>2</sub> concentrations together with reduced flux of organic matter to seafloor (Danovaro et al., 2017; Sweetman et al., 2017) can significantly impact CWCs by directly affecting food supply, growth, survival and recruitment rates (Danovaro et al., 2017).

## PROTECTING CWC ECOSYSTEMS

International agreements and directives supporting the protection of CWC ecosystems are increasing worldwide

(Armstrong et al., 2014). Fishing closures and protected areas are the main instruments for the current conservation of deep-sea ecosystems (Harter et al., 2009; Huvenne et al., 2016), while Marine Spatial Planning with ecosystem-based approach (EB-MSP) and Other Effective Conservation Measures (OEC) have been recently highlighted as key tools for balancing socio-economic and environmental objectives in a comprehensive marine conservation approach (Shabtay et al., 2019; Manea et al., 2020). To date, a number of countries have created specific Marine Protected Areas (MPAs) for CWC ecosystems: the Darwin Mounds and Hatton Bank (United Kingdom), the Oculina Bank Marine Protected Area, the Davidson Seamount and Aleutian Gorgonian Gardens (United States), the Northeast Channel Coral Conservation Area (Canada), and the Commonwealth Marine Reserve (Australia), amongst others (DeVogelaere et al., 2005; George et al., 2007; Durán Muñoz et al., 2009; Harter et al., 2009; Huvenne et al., 2016; Althaus et al., 2017; Bennecke and Metaxas, 2017). Harter et al. (2009) were the first to quantify positive effects of a deep-sea MPA (Oculina Bank Marine Protected Area). Moreover, high coral abundances and the presence of some large colonies and recruits pointed to a coral population recovery after 12 years following the closure of the Northeast Channel Coral Conservation Area to fishing (Bennecke and Metaxas, 2017). Likewise, after being a traditional fishery area, the North-western Hawaiian Ridge and Emperor Seamounts have been protected for 30 years. After this period, evidence for coral re-growth and greater abundances of benthic megafauna were detected (Baco et al., 2019). In some cases, protection alone is however not always successful. For instance, in the Eastern Darwin Mounds (United Kingdom), very little re-growth and no coral re-colonization have been detected after 8 years of fishing closure (Huvenne et al., 2016). Similarly, CWC communities in New Zealand seamounts did not recover after 15 years from cessation of trawling (Clark et al., 2019). Both examples highlighted the low resilience and slow natural recovery capability of CWC ecosystems.

## ACTIVE ECOLOGICAL RESTORATION OF CWC ECOSYSTEMS

To initiate or expedite recovery, it is highly desirable to actively improve the natural recovery (Dayton, 2003) by means of ecological restoration actions (Rinkevich, 2005). Ecological restoration is an attempt to return a damaged system to an ecological state that is within some acceptable limits relative to a less disturbed system, to recover a natural range of ecosystem structure and dynamics (Falk et al., 2006). Today, the practice of ecological restoration is receiving immense attention because it offers the hope of recovery from much of the environmental damage inflicted by misuse or mismanagement of natural resources (Falk et al., 2006).

To better understand the current state of the art in CWC active ecological restoration, a systematic literature search was conducted using the biographic database Web of Science in August 2020. Specifically, an advanced search was confined by the combination of the terms “restore\*,” “transplant\*,” “protect\*,” “conserve\*,” and “marine protected area” with a second term



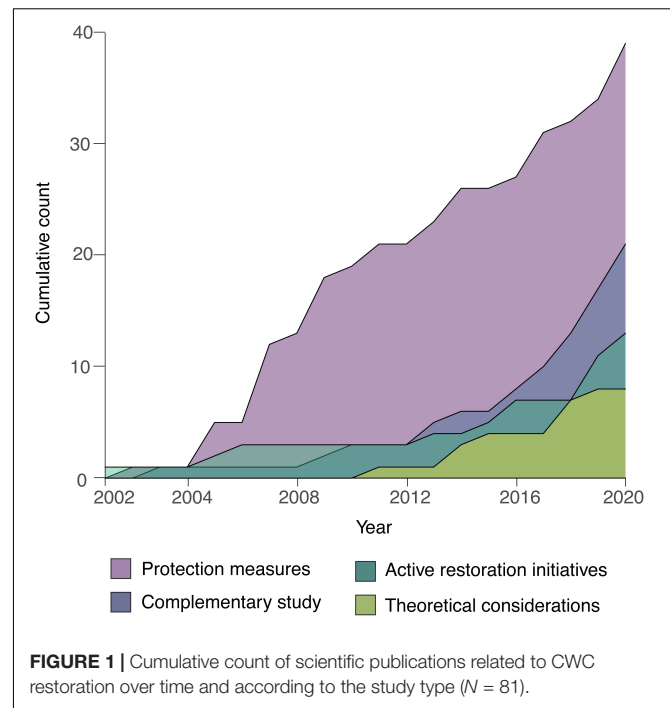
related to the coral taxa, habitats and target of restoration: “deep sea,” “cold-water coral,” “deep sea coral\*,” “deep sea octocoral\*,” “deep sea scleractinian\*,” and “deep sea gorgonian\*.” Published articles up to August 2020, including scientific papers, book chapters, reports and technical summaries were screened and included in the analysis if they contained information regarding restoration of CWC communities and ecosystems. Reference lists of articles, including reviews identified in the literature search, were checked for additional studies.

A total of 81 scientific publications contained data related to CWC restoration, including passive and active restoration approaches. The first studies focusing on the protection and restoration of CWCs were published at the beginning of the 20th century and have been gradually increasing to date (Figure 1). Given the international concern for the conservation of deep-sea ecosystems (Davies et al., 2007) and the establishment of deep-sea MPAs, passive restoration studies focused on the protection and management of CWCs constitute most of the published papers (48.2%). In contrast, studies on active restoration initiatives (16.0%), complementary studies with implications for active restoration (25.9%) and reviews with theoretical considerations (9.9%) have been less frequently published, appearing mainly in the last decade, and providing evidence that little work has been done so far and that CWC restoration is a very recent research line (Figure 1). Only 13 publications focus on CWC active restoration initiatives (Table 1) since 2001, contrasting with the 221 scientific publications for the case of active restoration of coral ecosystems in shallower waters since 1980 (Boström-Einarsson et al., 2020). Complementary studies encompassed scientific publications exploring natural recovery of CWCs, larval dispersion and recruitment, deep-sea connectivity and *in situ* coral growth monitoring, with implications for actively restoring CWC ecosystems. All of these, together with theoretical consideration studies, are crucial for adding scientific and technical knowledge to support active restoration actions and improve their success.

Following previous experience in shallow-water ecosystems, scientific efforts to restore CWCs (including protection measures and active restoration) were more focused on scleractinian species and CWC reefs (45.7%) rather than on octocoral species and CWC gardens (17.2%) (Figure 2). There were also publications encompassing both taxa (11.1%) or CWCs in general, without specifying the taxon involved (25.9%). The CWC scleractinian *L. pertusa* stands out as the most commonly studied coral species appearing in 29.6% of CWC restoration publications (Figure 2).

## Techniques for Actively Restoring CWC Ecosystems

There are currently only a few active restoration actions carried out worldwide, all of them located in the northern hemisphere (13 scientific publications for 7 case studies in 6 different countries): the Säcken Reef in Sweden, the Sur Ridge in California, CWC Reefs in the Gulf of Mexico and south eastern off Florida, and CWC gardens in the Western Mediterranean and Azores (Figure 3 and Table 1). Learning



**FIGURE 1** | Cumulative count of scientific publications related to CWC restoration over time and according to the study type (N = 81).

from experience in shallow coral restoration, the most used techniques for active CWC restoration are transplantation techniques (52%) and the use of artificial structures (44%) (Figure 4). Transplantation studies were focused on testing methods to attach CWC fragments to natural or artificial substrates. Studies with artificial structures encompassed the deployment or the decommissioning of artificial structures such as obsolete offshore oil and gas structures and collectors, for CWC larval recruitment. Mineral accretion through electrolysis (Biorock™), another restoration technique first developed for restoring shallow coral reefs, was tested in laboratory conditions with promising results as a suitable method for CWCs (Strömberg et al., 2010).

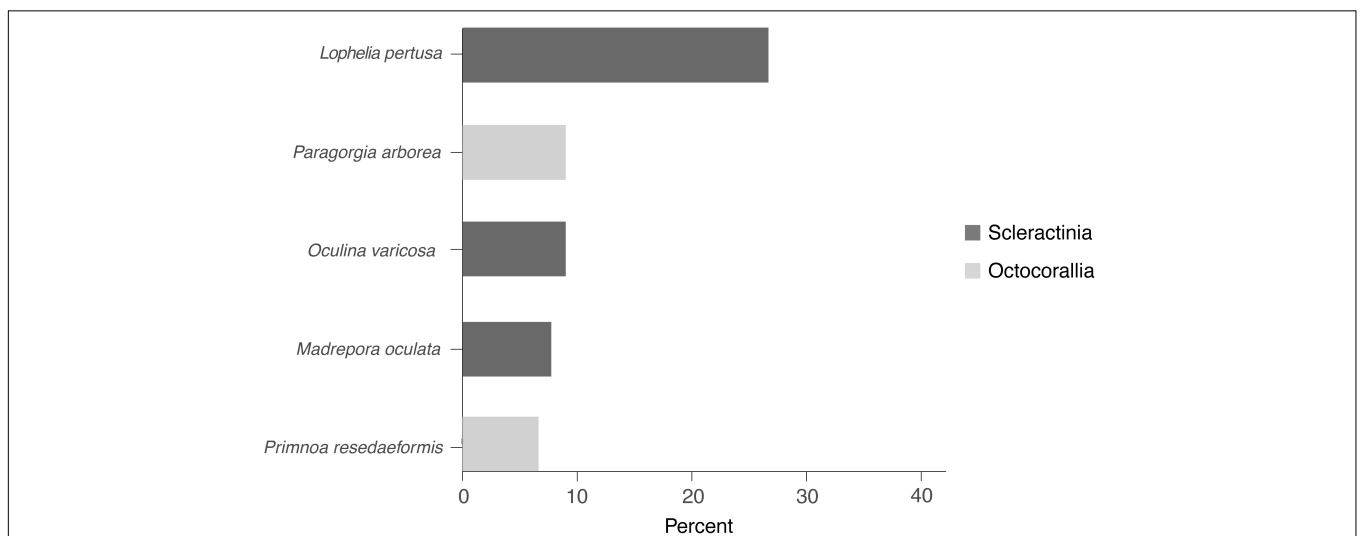
## Fragment Transplantation

First attempts of active CWC restoration emerged in the early 21st century, targeted on the CWC reef forming species *Oculina varicosa* (United States, Florida; Koenig, 2001; Brooke et al., 2006) and *L. pertusa* (Sweden; Dahl et al., 2012; Jonsson et al., 2015; Strömberg, 2016). These actions were based on transplantation of coral fragments from a healthy donor reef to a degraded one, using ROVs. Because of the difficulties associated with the *in situ* manipulation of coral fragments using ROVs, transplants were attached to artificial structures (concrete modules or racks), and then deployed at 70–100 m depth in impaired areas. After more than 2 years, transplanted coral fragments showed high survival (> 76%) and growth, with associated fauna being re-established, but there was little evidence of new larval settlement or coral recruitment (Brooke et al., 2006; Dahl et al., 2012; Jonsson et al., 2015).

Active restoration of CWC gardens has been attempted only recently by evaluating the feasibility of coral transplantation

**TABLE 1** | Active restoration initiatives carried out to date focused on CWC habitats.

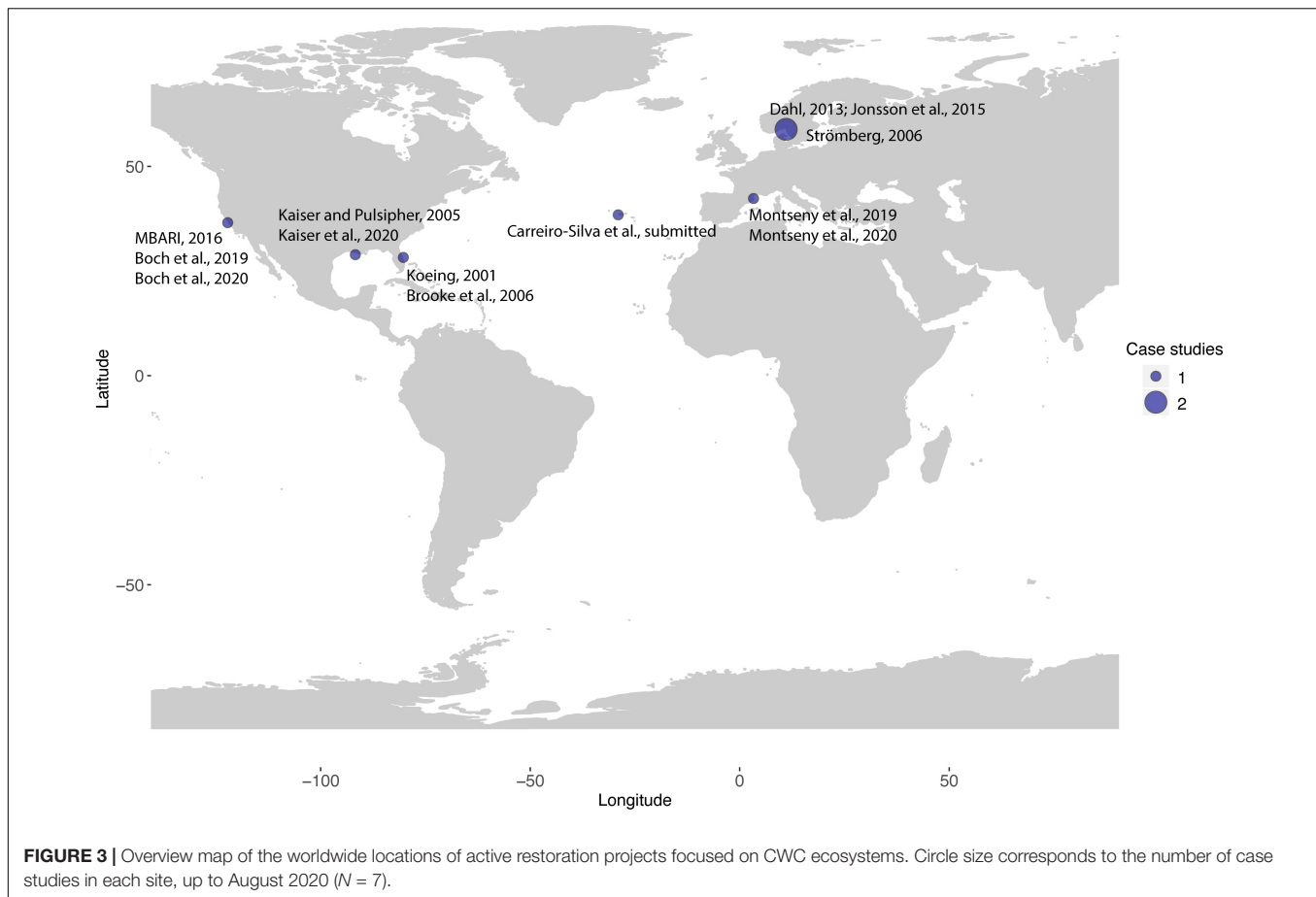
Locality	Restoration technique	Restored Taxa	Depth (m)	Duration time (years)	Results	References
SE Florida	Transplantations on artificial structures	<i>Oculina varicosa</i>	70 - 100	4 - 8	Mean survival rate 50–60%, Larval recruitment episodic Fish abundance enhanced	Koenig, 2001; Brooke et al., 2006
Gulf of Mexico	Deployment of artificial structures	Coral species	21 - 400	30 - 34	Attachment of corals and other sessile invertebrates	Kaiser and Pulsipher, 2005; Kaiser et al., 2020
Sweden	Transplantation on artificial structures	<i>Lophelia pertusa</i>	82 - 87	3 - 4	Mean survival rate of 76% Mean size increase of 39%	Dahl et al., 2012; Jonsson et al., 2015
Sweden	Transplantation on artificial structures	<i>Lophelia pertusa</i>	75 - 90	Not specified	Still not recorded	Strömberg, 2016
California	Transplantation	<i>Corallium</i> sp., <i>Lillipathes</i> sp., <i>Swiftia kofoidi</i> , <i>Keratoisis</i> sp., <i>Isidella tentaculum</i> , <i>Paragorgia arborea</i> , and <i>Sibogorgia cauliflora</i>	800 - 1300	1	Mean survival rate of 52% After 3 years coral survival differed among species (0% - 100%)	MBARI, 2016; Boch et al., 2019; Boch et al., 2020
NW Mediterranean	Transplantataion on artificial structures	<i>Eunicella cavolini</i>	85	1	Mean survival rate of 87.5%. Feasibility of large-scale and low-cost active restoration method	Montseny et al., 2019; Montseny et al., 2020
Azores	Transplantation on artificial structures	<i>Dentomuricea aff. Meteor</i> , <i>Viminella flagellum</i> , <i>Callogorgia verticillata</i> , <i>Paracalyptrophora josephinae</i>	230	1	Coral survival differed among species (15–100% survival rates)	Carreiro-Silva et al., submitted



**FIGURE 2** | Five most studied coral species in CWC restoration publications (N = 81).

techniques previously developed for tropical (Yap, 2000; Lindahl, 2003; Forrester et al., 2011) and temperate gorgonians (Weinberg, 1979; Linares et al., 2008; Fava et al., 2010). Pilot restoration actions focused on CWC gardens were tested at 200 m depth on the Condor Seamount (Azores Archipelago, **Supplementary Box 1**) and at 85 m depth in the Cap de Creus continental shelf (Western Mediterranean, **Supplementary Box 2**). During the same period, Boch et al. (2019) carried out a multiple species translocation study with seven different CWCs, including gorgonians, at 800–1300 m depth on the Sur Ridge within the Monterey Bay National Marine Sanctuary (United States) (**Supplementary Box 3**).

Transplantation of coral fragments may not be easily applicable to all CWC species. Handling, collecting, transporting and maintaining some CWCs in aquaria facilities before returning them to their natural habitat can be an issue. The stress suffered by corals during collection, such as thermal changes, and the complexity of replicating their natural environment in the laboratory, can compromise the survival of corals in aquaria (Orejas et al., 2019). In a first attempt to restore CWC gardens at the Sur Ridge, none of five coral fragments (*Keratoisis* sp., *Paragorgia arborea*) that were maintained overnight in aquaria prior to transplantation, or five fragments transplanted *in situ* (i.e., not brought to the surface) were found alive after 1 year



from their reintroduction (MBARI, 2016). This was overcome, in part by avoiding long-term maintenance of corals in aquaria and by also improving the attachment of coral fragments to transplantation structures on board the ship at sea, resulting in a mean coral survival of 52% after 1 year (Boch et al., 2019). The main advantage of transplanting coral fragments (usually with branching forms) is the faster recovery of the three-dimensional structure of coral populations, facilitating the recovery of their habitat-forming functions for a large number of associated species (Horoszowski-Fridman et al., 2015; Geist and Hawkins, 2016). Conversely, the main disadvantage of fragment translocation is the requirement for coral fragment collections that usually impact healthy coral assemblages. Moreover, by using large transplants (which suffer less natural mortality after transplantation, Brooke et al., 2006), more material is required from the donor site.

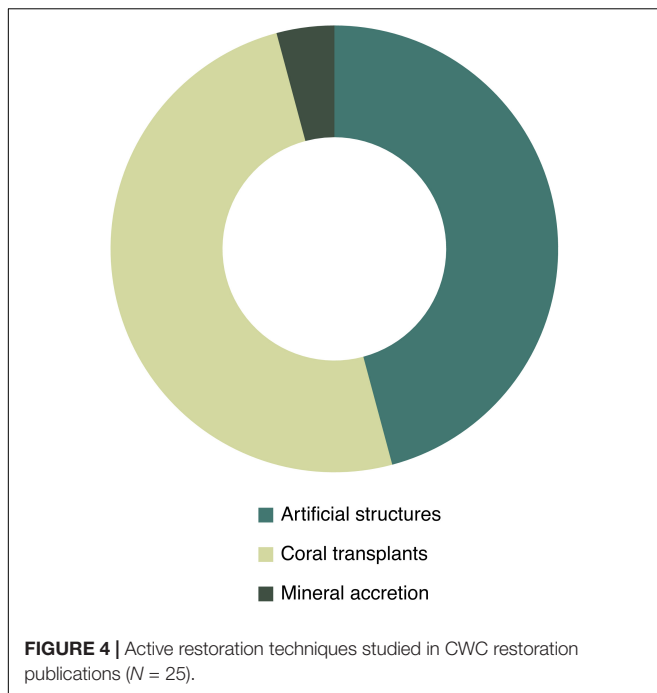
One partial solution developed in both the Mediterranean Sea and Azores was to work with local fishers using bycatch corals (**Supplementary Boxes 1, 2**). These pilot studies showed that not all CWC corals are able to survive and recover from the impacts of being accidentally fished, however some species do and easily recover if they are kept in appropriate aquaria conditions before restoration (Montseny et al., 2019). By using bycatch corals, the fishing impact on the natural populations is also mitigated, as bycatch corals are being returned to the

environment and at least a small part of this loss is reversed. The overall cost of the restoration action is also reduced, with no need for expensive technology for coral collection. Furthermore, since fishing activity generally covers a wide spatial extent, it could favor an increase in the genetic diversity of transplanted coral fragments, which would provide more potential for habitat shelf-support. However, this requires active, deep-water fishing activity near or around the area designated for restoration and fishers willing to collaborate, which is not always the case.

### Artificial Structures

Colonization of artificial structures is determined by the arrival of larvae and propagules and the subsequent local survival of adults (Dannheim et al., 2018). New recruits that will settle on artificial structures will be probably better adapted to the new conditions at the site. The capability of *L. pertusa* larvae to disperse over long distances and to potentially survive for a long time confirms the potential of this CWC to colonize artificial structures (Strömberg and Larsson, 2017; Henry et al., 2018). The type of structure, age, and depth of artificial reefs used all influence colony density and growth as observed in *L. pertusa* on 10 artificial structures in the Northern Gulf of Mexico (Larcom et al., 2014).

Finding the best larval settlement surface is a first key step for the use of artificial structures. Complex substrates have been shown to promote higher colonization by deep-sea



benthic invertebrates than simple substrates (Girard et al., 2016). Likewise, new larval recruitment of *L. pertusa* observed close to some restored sites has mainly been on dead coral skeleton with a remaining elevated 3D structural complexity, while no recruitment has been observed on other former CWC reef sites in the area where only unconsolidated coral rubble remains (authors unpublished data).

However, *in situ* larval settlement experiments targeting CWCs have had mixed results. While a study found high recruitment rates for *Primnoa resedaeformis* on artificial substrate deployed for 4 years in the Northeast Channel Coral Conservation area off eastern Canada, very few *Paragorgia arborea* recruits were recovered on these same substrates (Lacharité and Metaxas, 2013). Differences in the number of recruits of the two species could be due to differences in the reproductive strategies (broadcast spawning vs brooding). Recent work with larvae of *L. pertusa* has shown that they probably prefer cryptic spaces when settling (Strömberg et al., 2019), indicating that settling substrates must be specific to target species. Moreover, very little or no coral recruitment was observed for *O. varicosa* after 5 years from the deployment of concrete modules in south eastern off Florida (Brooke et al., 2006). The varying recruitment successes of these studies highlight the importance of increasing the knowledge on CWC larval ecology, especially about factors affecting dispersal, settlement and recruitment success. The more that is known for larvae of a species, the better the artificial substrates can be modeled to promote its settlement and recruitment. This approach is being used in the recently started CWC restoration project LIFE Lophelia (coral reef habitat restoration in Kosterhavet, Sweden) (**Supplementary Box 4**). Obsolete oil and gas industry platforms represent *de facto* artificial substrate for natural and active

recolonization of corals and other epifaunal species (Macreadie et al., 2011; Bergmark and Jorgensen, 2014; Larcom et al., 2014). Part of these structures may be left *in situ* as part of the decommissioning process, e.g., as in the North Sea (Henry et al., 2018) where platforms have been in place for > 40 years, toppled *in situ* or transported to locations where coral restoration is required and where their disposal makes ecological sense (Macreadie et al., 2011). Through the Louisiana and Texas Rigs-to-Reef Programs, established respectively in 1986 and 1991, a total of 97 artificial platforms had been transported to deep locations (> 120 m) in the Gulf of Mexico as of 2008 (Kaiser et al., 2020). Shortly after offshore structures were installed, corals and others sessile invertebrates such as oysters, sponges, hydroids, mussels and barnacles attached to the structures, attracting a number of mobile invertebrates and fish species, forming highly complex communities (Kaiser and Pulsipher, 2005; Kaiser et al., 2020). However, it should be noted that the potential use of decommissioned structures of the offshore oil and gas industry as artificial structures to prompt CWC reef formation is still controversial. There are scenarios where unexpected recolonization of man-made structures may assist in restoring ecosystems at a faster rate than would occur through natural recolonization events (**Supplementary Box 5**), but at the same time, a range of factors need to be considered including health and safety, technology readiness, social factors, and the spread of invasive species (Fowler et al., 2018). Indeed, invasive species of *Tubastrea* have long since colonized rigs-to-reefs structures in Gulf of Mexico (Sammarco et al., 2010) and operational platforms in Brazil.

### Mineral Accretion Through Electrolysis

Mineral accretion through electrolysis techniques was developed by Hilbertz and Goreau (1996) and has been widely used in tropical shallow coral reefs active restoration actions to enhance the growth of coral transplants. During the active phase of the mineral accretion, when the cathode is getting a trickle current and accretion of aragonite is ongoing, coral transplants bud and branch more frequently. The accreted material has the same composition of minerals as the coral skeleton itself (i.e., calcium carbonate in the form of aragonite). Moreover, when the electricity is turned off the accreted material attracts coral larval recruits (Kihara et al., 2013). Applied to the CWC *L. pertusa*, mineral accretion through electrolysis significantly increased polyp budding frequency and growth rates. However, the optimal current density level was found to be considerably lower than levels used in previous studies with shallow coral species. This highlighted the method to be suitable for at least some CWC, after the assessment of the optimal current density level to be used (Strömberg et al., 2010).

## Challenges in Actively Restoring CWC Ecosystems

### Performing Active Restoration

The main technical constraints in CWC restoration are the difficulties and associated costs in accessing remote deep-sea ecosystems (Van Dover et al., 2014). Technical diving with mixed gases can allow divers to access only relatively shallow



depths (50–150 m) (Pyle and Copus, 2019) across the CWC bathymetric distribution (50–4000 m depth) (Freiwald and Roberts, 2005; Roberts et al., 2006, 2009). In theory, divers could easily transplant coral fragments on natural substrate following the same techniques used for shallow coral reefs (Rinkevich, 1995; Edwards and Gomez, 2007; Edwards et al., 2010). However, the working-time for deep technical diving is extremely limited, and the risks associated with the activity are high (Fock and Millar, 2008; Sayer et al., 2008; Pyle and Copus, 2019). As a consequence, a long overall operational time will be needed to perform a restoration action by means of technical diving, and advanced safety measures (continuous access to decompression chambers and medical personnel) would be necessary to support the activity at all times, thereby increasing costs. In contrast, ROVs are the main and most widespread alternative for access to the deep sea (Van Dover et al., 2014). ROVs allow for long bottom-working time and significantly reduce risks to human life. However, technological hurdles involved in manipulating corals in the deep sea are still significant (Thresher et al., 2015). In particular, the main technical challenge is the dexterity of an ROV's manipulator arms to attach fragile coral fragments to rocky substrates using reattachment materials such as epoxy resins. This is a difficult task to be performed with fragments of stony corals, but even more so with gorgonians or black corals, whose flexible axial skeletons may be moved by seabed currents while the reattachment material hardens, compromising the stability of the transplanted fragments (Collier et al., 2007). Thus, gorgonian and black coral fragments need to be first fixed with epoxy resin to a small sturdy base in aquaria with no water flow and subsequently be transplanted in the field once the resin has dried (Clark and Edwards, 1995; Jaap, 2000; Young et al., 2012). In this sense, as for shallower waters, if the gorgonian or the black coral remains attached to a piece of dislodged substrate, it can be more easily reattached using the same methods as for stony corals (Collier et al., 2007). The employment of Autonomous Underwater Vehicles (AUVs) to autonomously transplant coral fragments to natural substrata in the deep sea is still in the distant future and will require substantial technological development. The possibility for an AUV to move and automatically locate and place small structures or modules supporting transplanted coral fragments on the seabed, could be a first step in this direction. Promising advances are being made on the capability of AUVs to autonomously locate and manipulate objects (Galloway et al., 2016; Mura et al., 2018; Sahoo et al., 2019). In addition, machine-learning approaches are helping to advance the automated detection of suitable sites for CWC active restoration actions (Henry et al., 2016).

### Selecting Donor Sites

The selection of donor populations, from where to collect fragments to be used in any active restoration action, is also of increased difficulty for CWCs compared to shallow coral species, owing to still quite limited knowledge of CWC distribution and connectivity in the deep sea. Even less information is available on CWC population structure and dynamics, which is basic information required to select donor populations and to evaluate potential collection impacts (Edwards et al., 2010). In the absence

of this knowledge, donor sites should be selected as close to the restored sites as possible since these would have a higher probability of containing colonies adapted to the environmental and ecological conditions of the area.

### Life-History Traits of CWCs

Longevity is strongly and positively correlated with maximum depth of occurrence in marine sessile species (Montero-Serra et al., 2018). Hence, it is not surprising that some CWC species live for hundreds to thousands of years (Roark et al., 2009; Bennecke et al., 2016). Slow growth rates have been reported for both stony corals (Reed, 1981; Rogers, 1999; Freiwald et al., 2004; Orejas et al., 2008, 2011; Lartaud et al., 2014) and gorgonians (Andrews et al., 2002; Risk et al., 2002; Sherwood and Edinger, 2009; Watling et al., 2011; Bennecke et al., 2016). Growth rates in stony corals ranges from 0.3–1.8 cm yr<sup>-1</sup> in *Madrepora oculata*, 0.4–1.1 cm yr<sup>-1</sup> in *L. pertusa*, and 1.1–1.6 cm yr<sup>-1</sup> in *O. varicosa* (Orejas et al., 2008, 2011; Lartaud et al., 2014). Slightly higher growth rates were measured in cold-water gorgonians, ranging from 1.5–4.1 cm yr<sup>-1</sup> in *P. resedaeformis*, 1.6–4.0 cm yr<sup>-1</sup> in *P. arborea* and 0.14 to 2.5 cm yr<sup>-1</sup> in *Paramuricea* spp. (Andrews et al., 2002; Buhl-Mortensen and Buhl-Mortensen, 2005; Sherwood and Edinger, 2009; Bennecke et al., 2016; Girard et al., 2019), with a general trend of exponentially decreasing growth rates with increasing colony size (Bennecke et al., 2016), and no increase in size for the largest colonies (Buhl-Mortensen et al., 2005; Watanabe et al., 2009; Bennecke et al., 2016). Overall, the range of such growth rates are a magnitude lower than observed for tropical shallow-water corals (Buddemeier and Kinzie, 1976; Bongiorno et al., 2003; De'ath et al., 2009). For this reason, CWC habitats are generally considered to have low recovery potential, which does not offer an effective short-term restoration solution (Bekkby et al., 2020). Long time spans (tens of years) will be required for transplanted CWC fragments to grow up to medium sized colonies, and even longer to grow up to fully functioning reef habitats.

Little is known about the reproductive biology of most CWCs, with some information available for the stony corals *L. pertusa*, *M. oculata*, *O. varicosa*, *Enallopsammia rostrata*, *Solenosmilia variabilis* and *Goniocorella dumosa* (Brooke and Young, 2003; Burgess and Babcock, 2005; Waller, 2005), and a number of cold-water gorgonians (Cordes et al., 2001; Orejas et al., 2007; Mercier and Hamel, 2011; Watling et al., 2011). While the knowledge is quite extensive considering fecundity, our understanding of dispersal processes and population connectivity is still hampered by the lack of knowledge about other reproductive traits (Watling et al., 2011). Factors such, as sexual condition (gonochorism or hermaphroditism), reproductive mode (broadcast spawning, internal or surface brooding), reproductive timing (continuous, periodic or seasonal reproduction) as well as larval ecology strongly affect dispersal potential (Waller, 2005; Trembl et al., 2015; Reynaud and Ferrier-Pagès, 2019). When information on larval ecology and behavior becomes available, it can be of profound value to improve the predictions of larval dispersal (Fox et al., 2016; Strömberg and Larsson, 2017; Henry et al., 2018). Likewise, information on genetic population structure in CWCs is limited (Watling et al., 2011). This limited available knowledge

on both CWC reproductive ecology and genetic connectivity significantly precludes or hinders proper spatial planning for CWC conservation (Cudney-Bueno et al., 2009), as well as the identification of priority locations for restoration actions.

### Limited Knowledge on Species Interactions

As habitat-forming ecosystem engineers (Jones et al., 1994), CWCs create physical structures that enhance space, resources, and refuges for hundreds of associated species across trophic levels (Henry and Roberts, 2007; Buhl-Mortensen et al., 2010), facilitating the coexistence of species in highly diverse communities (Bruno and Bertness, 2001; Stachowicz, 2001). Consequently, transplanting coral fragments into impacted environments will provide habitats for other species, facilitate their return and re-establishment, and ultimately aid ecosystem recovery (Abelson, 2006; Halpern et al., 2007). However, very limited information is available on intra- and interspecies interactions, including predation, competition, symbiosis and facilitation processes in CWC ecosystems (Buhl-Mortensen and Buhl-Mortensen, 2004). These interactions may significantly impact the success of CWC active restoration actions. One example of the importance of species interactions is the four-fold enhanced calcification rates measured in *L. pertusa* when living in association with the polychete *Eunice norvegica* (Mueller et al., 2013b).

Density dependence in population dynamics may act as a negative force (inducing density-dependent mortality), but minimum densities are also necessary for population persistence or growth (Halpern et al., 2007). Positive population-level interactions include minimum population sizes (avoiding Allee effects) and conspecific cues that enhance recruitment and survival of juveniles (Halpern et al., 2007). This is extremely important for corals, as density may control reproductive success and feeding efficiency (Levitan, 1991; Wildish and Kristmanson, 1997). Moreover, interspecific interactions may result in indirect facilitation processes through trophic cascades (Halpern et al., 2007). In the case of CWCs, recent research has highlighted a key role of sponges in transferring energy and nutrients to higher trophic levels in the community by transforming dissolved organic matter into particulate organic matter (DOM to POM) (Rix et al., 2016). The presence of a trophic 'sponge loop' contributes to high levels of biogeochemical cycling enabling CWC reefs to develop in deep-sea energy-limited environments (Burdett et al., 2014; Cathalot et al., 2015; Rix et al., 2016). Overall, positive interactions have been recognized as important factors shaping population and community structure (Stachowicz, 2001; Bruno et al., 2003), and should be considered in ecological restoration actions to achieve the most effective results, accelerating recovery while reducing restoration times (Bruno and Bertness, 2001; Halpern et al., 2007). In this sense, multispecific restoration actions (e.g., including corals and sponges) may be a significant step forward for the successful recovery of functional CWC communities.

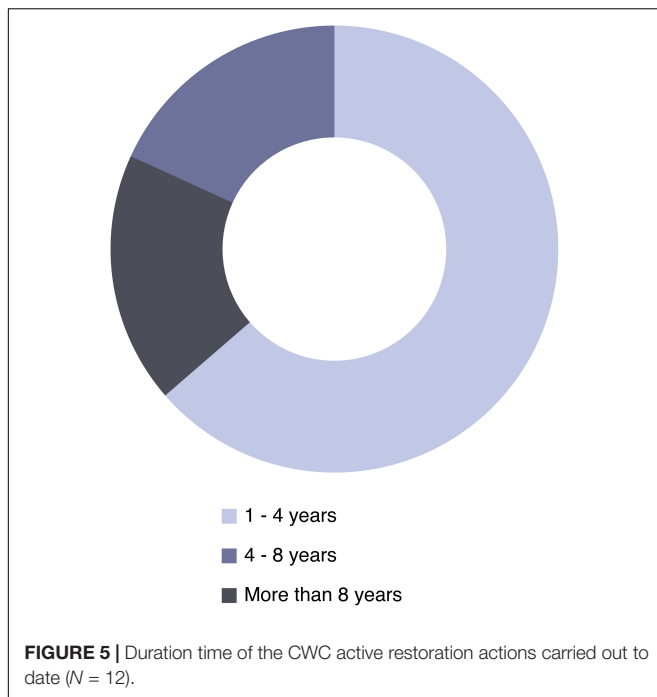
### Monitoring the Restoration Actions

The success of most active coral restoration actions is mainly evaluated in terms of transplant survival. In tropical shallow coral

reefs, highly successful restoration entails survival of more than 85% of restored corals, while failure occurs if less than 10% of restored corals survived after 5 years (Bayraktarov et al., 2016). However, beyond survival of restored organisms, there is active discussion to define appropriate metrics to properly evaluate restoration success (Fonesca et al., 2002; Elliott et al., 2007). Indeed, success of ecological restoration should be measured in terms of recovery of ecosystem function after the restoration effort, monitoring recovery trajectories and comparing with reference control sites (Kaly and Jones, 1998; Ruiz-Jaen and Mitchell Aide, 2005; Bayraktarov et al., 2016). Monitoring must be standardized, holistic, and linked to the objectives/goals set at the beginning of the restoration project. Thus, biological, ecological and physical assessments should measure not only the survival of transplanted organisms, but also changes in overall population and community structure, ecosystem functioning and changes in key abiotic factors. It is crucial to establish realistic restoration objectives in order to not fail in the evaluation of success, which could reduce public, academic, charitable and industrial support (Ferse et al., 2010; Boström-Einarsson et al., 2020) and lead to inaction (McAfee et al., 2019). Monitoring allows for the improvement of transplantation techniques and provides guidance for future restoration efforts (Collier et al., 2007). Most active restoration projects, including coral reefs, seagrasses, mangroves, saltmarshes, and oyster reefs, are generally short-term projects, limited to 1 or 2 years of duration (Bayraktarov et al., 2016). Of 362 case studies on shallow coral restoration, 60% reported less than 18 months of monitoring of restored sites (Boström-Einarsson et al., 2020). Contrarily, it should be noted that long-term monitoring (15–20 years) has been considered as a paramount factor in properly evaluating the success of tropical, shallow coral restoration actions (Bayraktarov et al., 2016). Minimum time spans of 30–40 years should be considered for a proper monitoring of restored CWC populations, due to their commonly slow growth rates and population dynamics (Bennecke et al., 2016). However, this is usually at odds with funding timeframes. Indeed, most active CWC restoration case studies performed to date lasted between 1 to 4 years (Figure 5). Longer actions (longer than 8 years) are associated with the initiation of the Louisiana Rigs-to-Reefs program in 1986 (Kaiser and Pulsipher, 2005; Kaiser et al., 2020).

Additionally, to achieve the more general recovery of ecosystem functioning, small-scale active restoration actions and tests already carried out with CWCs need to be properly scaled up (Elliott et al., 2007). In fact, there is a mismatch between the scale at which deep-sea ecological restoration can currently be performed and the scale at which major impacts act, as also highlighted for tropical shallow coral reefs (Edwards and Gomez, 2007; Montoya-Maya et al., 2016; Pollock et al., 2017). This is of particular concern for CWCs, because of the logistical challenges and limitations in performing and monitoring restoration actions over wide areas in the deep sea.

A combination of AUV and ROV inspection can allow for repeated monitoring of large restored areas over time (Armstrong et al., 2010; Morris et al., 2014; Benoist et al., 2019). The possibility for an AUV to autonomously acquire high-resolution images would allow scientists to generate a reference map for relocating



transplanted corals. These reference maps are imperative and should occur concurrently with restoration actions (Collier et al., 2007). Indeed, several studies have already efficiently applied photomosaic techniques for surveys of coral ecosystems (Pedersen et al., 2019), including CWC reefs (Bohlukos et al., 2019). Recent advances in automated classification of CWCs from ROV images including live *versus* dead coral cover (Henry et al., 2016) combined with sonar imaging point to the possible future use of automatic classification of data acquired by AUVs to regularly monitor CWC populations, including restored ones (Williams et al., 2010; Huvette et al., 2011; Henry et al., 2016; Sture et al., 2018).

Extensive monitoring performed with AUVs can be complemented with intensive survey performed with ROVs to acquire images of all, or a subsample of, the restored coral fragments, to monitor survival and growth through time. High-resolution images of the same individual coral fragment taken at different times, allows for the detection of small changes in the health of coral colonies as well as the measurement of *in situ* growth rates (Hsing et al., 2013; Girard and Fisher, 2018; Girard et al., 2019). For this purpose, the recent development in 3D photogrammetry for quantitative measurements and its application to ROV-acquired images of deep-sea fauna, including CWCs, is highly promising (Bennecke et al., 2016; Thornton et al., 2016; Prado et al., 2019). Additionally, staining techniques for assessing *in situ* growth rates of CWCs have been developed, offering another methodological basis to monitor transplant growth, although they require destructive sampling (Brooke and Young, 2009; Lartaud et al., 2013).

Finally, fixed-point deep-sea seafloor observatories with *in situ* cameras and instruments are now functioning in several areas of the world's oceans (Favali et al., 2010), allowing for continuous

monitoring and observation of deep-sea fauna, including CWCs (Doya et al., 2014; Van Engeland et al., 2019) and also could be applied to the monitoring of restored CWC populations. Even so, their employment for monitoring CWC restoration actions is probably unnecessarily complex and expensive (for installation, maintenance and the analysis of the large amount of data they produce) compared to a wider periodic monitoring by combining AUVs and ROVs (Armstrong et al., 2008).

### Protecting the Restoration Effort

Actively restored CWC ecosystems might continue to be exposed to further impacts from anthropogenic activities and ongoing global change (Ramirez-Llodra et al., 2011; Thresher et al., 2015). Consequently, appropriate selection of locations targeted for CWC active restoration actions should prioritize refugia areas forecasted to be sheltered from future impacts and extreme changes in environmental features driven by global change (Thresher et al., 2015; Sweetman et al., 2017; Morato et al., 2020). Active restoration may assist CWC habitat recovery once management is in place, but it will certainly fail without effective protection (Edwards et al., 2010). Conservation measures should precede active restoration to avoid any direct impacts that may compromise the restoration effort (Davies et al., 2007). However, effective management of deep-sea protected areas can be a challenge, particularly since most sites are located far offshore and in the High Seas (Davies et al., 2007). To this aim, global positioning surveillance of fishing vessels (Marrs and Hall-Spencer, 2002; Deng et al., 2005) and remote-imaging with large spatial coverage (Kourti et al., 2001, 2005) may become more cost effective for the monitoring of deep-sea MPAs (Davies et al., 2007).

### Costs for Actively Restoring CWC Ecosystems

CWCs face many risks from the business activities of fisheries, oil and gas extraction, and mineral exploitation. These risks occur throughout the lifetime of an industrial project, from the initial exploration activities to the decommissioning and closure of operations. In order to deal with the continued impacts over the life of a project, economic sectors and industries are encouraged to adopt a "mitigation hierarchy" to first try to avoid, then to minimize, any significant adverse impacts, and finally, where these steps cannot eliminate environmental effects, to consider the potential for ecosystem restoration assuming the corresponding costs (Arlidge et al., 2018; Billett et al., 2019).

### Regulatory Mechanisms Aiding the Engagement of Industries in CWC Restoration

In the case of fisheries, there has been good development of regulations to reduce impacts from bottom trawling. Deep-water fisheries are widespread and governed by regulations that depend on national jurisdiction, exclusive economic zones, regional sea authorities, and pan-international bodies (e.g., EU). The FAO has played a fundamental role in guiding states and Regional Fisheries Management Organizations (RFMOs) toward the conservation of species and habitats impacted by High Seas



fishing operations (FAO, 2008, 2009a,b). In relation to CWCs, the most important outcomes have been the recommendations to identify, map, monitor and introduce measures to protect VMEs, to refrain from expanding fishing effort and its spatial extent, and reduce fishing effort in specific fisheries. Specific fisheries closures have been, and are being, put into effect under a number of schemes and authorities. “Move-on” rules are being adopted by various RFMOs requiring fishing vessels to stop fishing when a threshold of VME indicator is reached during fishing operations. VMEs are characterized by the presence of particular sensitive species, and the thresholds that constitute their “level of catch” and “minimum distance” are different in different RFMOs. In some cases, the designation of VMEs is contentious because they may continue to be targeted when present even if the weight of the catch falls slightly below the threshold level (Auster et al., 2011). Regulations have restricted access to sensitive areas and there may be recourses in the way of compensation and fines should vessels operate illegally in these areas. Liability or litigation payments have been made for accidental damage to sensitive coastal habitats from vessel grounding, but this is unlikely to occur for CWCs. However, there are additional and more direct ways that fishers can help in restoration. They have a good knowledge of the environments in which they are working and some degree of access to these sites through their fishing vessels. Coral bycatch from artisanal fishers is being used in collaborative projects as donor material for fragmentation in coral restoration experiments in the Atlantic (Azores), and Western Mediterranean (Cap de Creus) (**Supplementary Boxes 1, 2**). Society at large can also play a role in restoration by encouraging and pressing governments to develop and promote conservation policies and laws. For example, the general public in Ireland would be willing to pay a personal tax of 1€ annually to protect VME from trawling (Wattage et al., 2011). It is important to foster awareness about the importance of CWC ecosystems in order to increase society’s interest and public support for their protection.

In the case of hydrocarbons and mineral industries, if the project cannot be moved to a different location in order to avoid impacts to CWCs, measures to minimize impacts may be introduced through engineering innovations and management actions. Industry operators then may explore potential options for ecosystem restoration once the impacts have ceased, such as rigs-to-reefs programs, as long as it makes ecological sense. Using subsea structures as potential artificial coral reef for natural colonization could offer considerable cost savings for the industry, government bodies and tax payers. From 2004 to 2018, in the framework of Louisiana Artificial Reef Program (Gulf of Mexico), industry paid an average \$392,000 per structure to the state for the decommissioning and subsequent use of obsolete structures as artificial reefs. In exchange, the state assumed the ownership and liability for the platforms (Kaiser et al., 2020). However, as mentioned above, there is a current debate about the implementation of rigs-to-reefs programs.

Financing for fossil fuel and mineral extraction projects may also need to comply with the environmental and social

safeguarding policies of International Finance Institutions (IFIs), such as the World Bank. Safeguards associated with loans and investments mean operators need to demonstrate how they will conform to the mitigation hierarchy, as indicators for how their projects will achieve good environmental performance (Hayes et al., 2015). At the project level, oil and gas operators should estimate the cost of each step of the hierarchy with respect to the biodiversity gains and losses incurred. In areas with CWCs that are costly to access and operate in, early costing and risk evaluation could result in the developers adopting options higher up the mitigation hierarchy. This might include avoiding sensitive sites, thereby reducing long-term costs by not having to restore them or offset damage (Arlidge et al., 2018). Notably, failure to adequately consider avoidance could cost operators more in the long run, not only through delays in operations caused by unintentional environmental impacts, but also relating to damage to their corporate reputation when accidents occur in sensitive environments (Hayes et al., 2015). These considerations are key parts of assessing and reducing risks to businesses.

In addition, subsea technologies involved in extractive industries (e.g., ROVs and AUVs) could also be used for environmental management tasks, making best use of standby time in operations (Cordes et al., 2016b). In future, regulations could also specifically require ecosystem restoration and build the resulting costs into Environmental Impact Statements at the time of submission, prior to the award of a contract for exploitation. The costs of CWC restoration and its subsequent monitoring following the end of extraction can be included in a Closure Plan.

## Restoration Costs

Cost estimations for various hypothetical active restoration actions in the deep sea can be two to three orders of magnitude greater per hectare than costs for restoration in shallow-water ecosystems (Van Dover et al., 2014). The cost of shallow-water restoration initiatives, usually, ranged from US\$ 13,000 to US\$ > 1M ha<sup>-1</sup> (Spurgeon and Lindahl, 2000; Edwards et al., 2010). In contrast, in the scenario presented by Van Dover et al., (2014) for the active restoration of CWCs following bottom trawling impacts in the Darwin Mounds, the direct costs of only implementing a laboratory propagation-transplant protocol were estimated to be about US\$ 75M ha<sup>-1</sup>. This estimate did not include the additional costs of geoengineering the seabed to reconstruct the mounds on which the corals were first found (Bett, 2001; Wheeler et al., 2004; Huvenne et al., 2016). When all of the costs are considered, including socio-economic, ecological and technological considerations, the conclusion was still that the overall balance would be moderately in favor of a (limited) active restoration with estimated cost in the order of US\$ 4.8 million (Van Dover et al., 2014).

However, not all active restoration actions in deep waters necessarily incur great costs. The restoration carried out in the Mediterranean continental using bycatch cold-water gorgonians (**Supplementary Box 2**) accounted for about \$US 170,000 ha<sup>-1</sup>; a significantly lower cost compared to what was estimated by Van Dover et al. (2014) and more in accordance with shallow-water restoration actions (Montseny et al., 2020). Thus, confirming the



possibility of developing cost-effective techniques, even targeting deep-sea environments.

## LEARNING FROM SHALLOW-WATER CORAL RESTORATION TO ADVANCE CWC ACTIVE RESTORATION

Overall, despite many challenges facing active CWC restoration, outcomes from the few assisted regeneration actions performed to date point to the feasibility of actively restoring CWC reefs and coral gardens under certain circumstances. As pointed out in this review, recent national and international research projects have started to address CWC restoration, and significant advances have been achieved. Ecological active restoration of CWCs is a field of study in an early stage of development, and the vast experience in shallow coral active restoration is a great opportunity to learn from their successes and failures to more successfully address the challenges of restoring CWC ecosystems.

Since the 1980s, different methodologies have been designed and widely implemented to actively restore tropical shallow coral reefs (Rinkevich, 1995, 2014; Young et al., 2012; Ng et al., 2015; Barton et al., 2017; Boström-Einarsson et al., 2020). In shallow waters, rearing of fragments of coral species in either *ex situ* or *in situ* nurseries and their subsequent transplantation to degraded areas has become the most common and successful approach for reef active restoration (Rinkevich, 2005; Edwards and Gomez, 2007; Edwards et al., 2010; Pizarro et al., 2014). For CWCs, slow growth rates, and the complex logistic and high costs for their maintenance in aquaria (Orejas et al., 2019), are the main constraints on *ex situ* rearing of fragments to be used in active restoration actions. Additionally, while some CWC species can be successfully maintained in aquaria, others cannot, showing high mortalities after only a few days or weeks (Orejas et al., 2019). Hence, additional research is needed to identify the best conditions for maintaining CWC species and foster their growth in aquaria. Specifically, we identify water flow, feeding frequency, and food quantity and composition as the main variables to be explored. The *in situ* rearing of CWC fragments entails difficulties and high costs for setting up appropriate structures in the deep sea by using underwater technologies (ROVs and manned submersibles), as well as for their monitoring through time. Additionally, difficulties in manipulation and cleaning of reared coral fragments do not allow for expected increase in survival or growth rates for *in situ* reared fragments.

Identification and selection of resilient coral phenotypes and/or genotypes to be used in active restoration actions of shallow coral reefs have recently been highlighted as a possible way to face the impacts driven by ongoing climate change (e.g., van Oppen et al., 2015; Morikawa and Palumbi, 2019). A similar approach is being explored for CWCs to identify resistant genotypes by means of experiments under controlled conditions (Kurman et al., 2017). We highlight the importance of additional investigation along these lines, particularly for the most frequent and abundant CWCs.

Promising results can be expected based on the high intra-specific variability commonly observed among coral fragments in their response to laboratory exposure to stress conditions (e.g., Hennige et al., 2015). Additionally, as for shallow coral reef restoration (Cabaitan et al., 2015; Ladd et al., 2018), we identify multi-specific restoration actions as a promising approach to foster positive interactions among species to speed-up ecosystem recovery.

Substrate enhancement methods are also widespread in active shallow coral restoration techniques, either by creating or adding new substratum (such as artificial reefs) or by enhancing and stabilizing damaged substratum (Boström-Einarsson et al., 2020). For CWCs, high recruitment on artificial structures (Larcom et al., 2014) has highlighted this approach as being viable for the deep-sea. We identify research on the best composition, rugosity and morphology of the artificial structure for larval setting, survival and growth as paramount to advance with this approach for actively restoring CWC ecosystems. Moreover, additional knowledge is needed on reproductive and larval ecology and dispersion in the main CWC species, to identify the best locations and time for the deployment of the artificial structures.

Related to coral reproduction, larval enhancement methods, focused on increasing rates of coral fertilization, larval survival and recruitment, are also being applied in shallow coral reefs (Boström-Einarsson et al., 2020). However, these methods are difficult to apply to CWCs, for which knowledge on reproductive ecology is extremely scarce, and sexual reproduction and larvae obtention in aquaria has been successfully achieved only for a very few species (Larsson et al., 2014; Strömberg and Larsson, 2017). Additional research on CWC maintenance can enhance the ability to successfully obtain larvae in aquaria, and we identify their settlement on artificial substrate and subsequent translocation to the field after metamorphosis as a possible way to increase larval survival and recruitment. However, growth rate and mortality after translocation need to be carefully monitored in the field to quantitatively assess the success of this method of larval enhancement for CWCs.

Recent reviews reported high survival rates of transplanted tropical shallow corals (60–70%), highlighting that project failure was more related to a poor project design (inadequate site selection and ill-stated objectives) than to the technique used (Bayraktarov et al., 2016; Boström-Einarsson et al., 2020). It is crucial in any restoration project to establish realistic and clear objectives. In shallow-water environments, Boström-Einarsson et al. (2020) determined that a key missing objective of many restoration actions is the re-establishment of self-sustaining populations that would enhance natural larval production and recruitment processes. Furthermore, despite the well-known mismatch of the temporal and spatial scales of restoration projects and habitat degradation, shallow restoration actions are still mainly applied at small spatial extent and over limited time frames. For this reason, scientists are working on improving restoration techniques, with a special focus on scaling up both spatially and temporally (Bayraktarov et al., 2016; Tamburello et al., 2019; Boström-Einarsson et al., 2020). As for shallow-water corals, active restoration actions of CWC

ecosystems need the establishment of clear and achievable objectives and the development of viable methods to scale-up the extent of restoration actions and as well as undertaking longer, standardized, and integrated monitoring programs. In this sense, we identify the improvement in underwater technologies and the ability of ROVs and AUVs to perform restoration actions and monitoring, as a key step forward for the ecological restoration of CWC ecosystems.

It is likely that the combination of well-designed passive and active restoration approaches will be the most effective, as currently employed in shallow-water marine ecosystems (Mitsch, 2014; Possingham et al., 2015). Wide-scale and long-term experiments combining a variety of methods and involving local actors should be tested to determine the ways in which simple interventions might enhance the rate of natural recolonization.

Ultimately, the benefits of involving local stakeholders (e.g., RFMOs, NGOs, statutory conservation bodies, oil and gas industry and future deep seabed mining, etc.) in the planning and implementation of restoration actions are well demonstrated in shallow coral restoration actions (Ferse, 2010; Bayraktarov et al., 2016; Hein et al., 2019; Boström-Einarsson et al., 2020), and are likely to be crucial for ensuring restoration success in CWC ecosystems, firstly, in order to ensure a suitable development of the restoration action, and then to preserve the restoration effort in the long term.

## AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.621151/full#supplementary-material>

**Supplementary Box 1** | Bycatch gorgonians transplanted onto artificial structures.

**Supplementary Box 2** | A cost-effective and large-scale method to transplant gorgonians.

**Supplementary Box 3** | ROV-based translocation of coral fragments.

**Supplementary Box 4** | Restoration of *Lophelia pertusa* reef habitats in Skagerrak: enhancement of larval settling.

**Supplementary Box 5** | Coral colonization of oil and gas platforms.

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