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RESEARCH ARTICLE

Recovery and restoration potential of cold-water corals: experience from a deep-sea marine protected area

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Cold-water corals (CWCs) are important species that provide habitat for other taxa but are sensitive to mechanical damage from bottom trawling. CWC conservation has been implemented in the form of marine protected areas (MPAs), but recovery from impact may be particularly slow in the deep-sea environment; consequently, the use of restoration techniques has been considered. To gain some insight into CWC recruitment and growth, in 2011 we deployed small seabed moorings in the Darwin Mounds MPA (~1,000 m water depth). This site hosts hundreds of CWC mounds, that had previously (until 2003) been impacted by deep-water trawling. In 2019, we carried out in situ visual surveys of these moorings and the surrounding seabed environment, then recovered two of the moorings. The mooring buoys, glass floats with plastic covers, were extensively colonized by a diverse epifauna that included the CWCs *Desmophyllum pertusum* and *D. dianthus*. The presence of coral recruits indicated that environmental conditions, and larval supply, remained favorable for the settlement and growth of CWCs within the MPA. Based on our observations, we consider four possible restoration methods, together with a "do-nothing" option, for the Darwin Mounds CWCs that have shown little, if any, natural recovery despite 16 years of protection. We conclude that seabed emplacement of high-relief artificial substrata is likely to be the most efficient and cost-efficient means of promoting enhanced recovery of the CWCs.

Key words: artificial reefs, cold-water coral, coral recruitment, Darwin mounds, *Desmophyllum pertusum*, habitat restoration

Implications for Practice

- Environmental and ecological characteristics of the deep sea, including the high seas areas beyond national jurisdiction that may be exploited in the years ahead, suggest that ecosystem recovery from human impacts may be a greatly prolonged process.
- Structural habitat loss, modification, or degradation may be one key cause of such prolonged recovery, particularly where the structural habitat is biogenic, as in the case of cold-water coral reefs.
- In the parallel UN decades of Ocean Science for Sustainable Development and of Ecosystem Restoration it may be particularly timely to tackle the challenges and opportunities of deep-sea restoration.

Introduction

Cold-water corals (CWCs), azooxanthellate species of scleractinian, antipatharian, alcyonacean, and stylasterid cnidarians, are important habitat-forming organisms in the deep sea (Roberts et al. 2009). In the NE Atlantic, the key species include *Desmophyllum pertusum* (Linnaeus 1758), *Madrepora oculata* (Linnaeus 1758), and *Solenosmilia variabilis* (Duncan 1873), as they can form extensive and dense biogenic frameworks (Teichert 1958). Although often comprising of a mix of CWC species, OSPAR terms these areas as "*Lophelia pertusa* Reefs" (or more correctly CWC reefs) when they cover at least 25 m^2 (noting that this threshold applies to the total area of a patchy reef, rather than the minimum size for a patch), and that some minimum elevation above the surrounding seafloor is required (>64 mm or > 26 cm; see e.g. Irving 2009). Where CWCs occur in sedimentary environments, they may promote the development of seabed mounds that may be referred to as "Coral Carbonate Mounds" (OSPAR 2010). These vary greatly in size, from "micro-mounds" of order 5 m diameter and 20 cm topographic height (Thornton et al. 2021), to features 2 km in diameter and 350 m in elevation (OSPAR 2010).

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These coral frameworks can increase the provision of hard substratum and overall habitat heterogeneity, promote local species richness (Henry & Roberts 2007; Bongiorni et al. 2010), and provide habitat for commercial fish species (Costello et al. 2005; Söffker et al. 2011; Baillon et al. 2012). However, bottom contact fishing is particularly destructive for CWCs because of their fragility and slow growth (Hall-Spencer et al. 2002; Wheeler et al. 2005; Huvenne et al. 2016). In addition to the physical damage associated with trawling, indirect effects include biodiversity loss, community change (Althaus et al. 2009), and coral smothering by resuspended sediment (Larsson & Purser 2011). Fosså et al. (2002) estimated that 30–50% of *D. pertusum* reefs offshore Norway had been impacted by bottom trawling. Worldwide, extensive reviews on the effects of deep-sea trawling on benthic organisms (Puig et al. 2012; Pusceddu et al. 2014; Clark et al. 2016) have emphasized that even a small number of events can have long-lasting effects (15+ years to recovery; see Clark et al. 2019).

Habitat restoration is routinely used to support the recovery of both terrestrial and marine habitats (Coen & Luckenbach 2000; Miller 2002; Orth et al. 2020). Restoration techniques such as substratum enhancement (i.e. placement of artificial or additional natural substrata to support settlement), stock enhancement (i.e. enhancement of the population via hatchery-produced individuals or predator removal), and transplantation (i.e. movement of adult material from a healthy donor site to a recipient restoration site) have proven effective for coral, seagrass, mangrove and saltmarsh restoration (Bayraktarov et al. 2016). Restoration techniques are not widely practiced in the deep sea because of the current projected costs and uncertainty over success. The potential use of active restoration has been suggested in the deep sea (Da Ros et al. 2019) and the techniques and challenges explored (Montseny et al. 2021). Van Dover et al. (2014) costed a conceptual deep-sea restoration project for CWCs, suggesting that, although costly, it would be highly valuable for facilitating the recovery of these ecosystems and the services they deliver. Brooke et al. (2006) summarized their experiences implementing a restoration project for *Oculina varicosa* (Le Sueur 1820), in an area off the Atlantic coast of Florida (50–180 m water depth), that is, transplanted coral exhibited moderately good survival rates and some of the older structures were supported several new coral colonies. In the Mediterranean, Montseny et al. (2020) returned net-caught soft corals (Octocorallia) back to the continental shelf (5 or 30 m) to save these colonies and promote recovery. Boch et al. (2019) also translocated fragments from multiple coral species to a site off central California (800–1,300 m depth). Unlike other translocation studies, survival was monitored for the first year and fragments were found to have a mean survivorship (across all species) of ~52%. The same fragments were monitored for a further 2 years and survival was found to differ between species: zero for two species, *Paragorgia arborea* (Linnaeus 1758) and *Sibogagorgia cauliflora* (Herrera et al. 2010); below 50% for two species, *Keratoisis* sp. and *Isidella tentaculum* (Etnoyer 2008); above 50% for two species, *Swiftia kofoidi*, now *Callistephanus kofoidi* (Nutting 1909), and *Corallium* sp.; and 100% for one species, *Lillipathes* sp. (Boch et al. 2020).

The first deep-water marine protected area (MPA) to be established in the United Kingdom, the Darwin Mounds, was put in place to protect deep-sea CWCs and enable their recovery from evidenced impacts by bottom trawling (Wheeler et al. 2005; De Santo & Jones 2007). Trawling damage was apparent in the east and west of the Darwin Mounds, with both areas showing high abundances of dead coral and coral rubble in trawled versus non-trawled areas (Wheeler et al. 2005). Before the closure, tracking of fishing activity, via vessel monitoring system data, indicated higher levels of fishing effort in the eastern field of the mounds (Davies et al. 2007), denoting that a substantial fishing impact may have occurred within the short period between the announcement of the closure and its enforcement (Wheeler et al. 2005). In 2000, CWC occurrence was found to be approximately equal between the east and west mounds (Huvenne 2011). However, in 2011, observations suggested that live coral occurrence on mounds had reduced to almost zero in the eastern field, with erect coral frameworks effectively absent (Huvenne 2011). Furthermore, observations by Waller and Tyler (2005) found that *D. pertusum* was non-reproductive at the Darwin Mounds.

Subsequent monitoring of the Darwin Mounds CWCs has suggested little if any indication of recovery following 16 years of effective protection, with scleractinian colony density at $0.07/m^2$ on eastern mounds and $0.38/m^2$ on western mounds (N. Piechard 2023, Institute of Marine Research, Bergen, Norway, personal communication). The CWCs of the Darwin Mounds may therefore represent a system that would particularly benefit from restoration measures. The use of restoration at the Darwin Mounds was considered by Van Dover et al. (2014) who suggested the use of shore-based cultivation of CWCs. In this article, we assess feasibility based on (i) new observations on the settlement of CWCs on settlement panels and seabed moorings; (ii) what those observations suggest for possible restoration scenarios; and (iii) finally assess the likely efficacy, impact, cost, and timescale of a CWC restoration program in the Darwin Mounds MPA, and by extension, similar CWC sites.

Methods

Study Area

The Darwin Mounds are located in the NE Rockall Trough, approximately 190 km northwest of Scotland and were discovered in 1998 (Bett 2001; Fig. S1). There are hundreds of small CWC mounds, c. 75 m across and 5 m high, in water depths of 950–1,050 m (Masson et al. 2003). They occur in two main groups, an eastern field and a western field, the former having suffered extensive impact by bottom trawling, the latter only modest impact (Huvenne et al. 2016). Mounds in the east are more elongated but with diffuse edges (the East being characterized by stronger currents and coarser sediments), whereas the western mounds are more clearly delineated (Huvenne et al. 2016). Bottom contact fishing within the Darwin Mounds MPA has been banned since August 2003, with subsequent fishing vessel monitoring and seabed observations suggesting that the closure to fishing has been well respected (Davies et al. 2007; Huvenne et al. 2016; Huvenne & Thornton 2020).

Seabed Settlement Panel Moorings. In May 2011, four short seabed moorings (Fig. S2) were deployed during RRS *James Cook* cruise 060 to serve as recruitment experiments (Huvenne 2011). Two moorings were deployed in the western and two in the eastern Darwin Mound fields (Fig. S1). Each mooring comprised a steel plate anchor (35 kg) and a single glass sphere with a polyethylene cover (as typically employed in deep-sea mooring designs), having a nominal buoyancy of 25 kg (Teledyne Benthos Ribbed 204HR-17; Fig. S2), connected by a mooring line of 25 mm diameter polypropylene rope. The moorings deployed in the western field were approximately 4.5 m in length and 6 m in the eastern field, mooring length was kept short (c. 5 m) to avoid any interference with future research operations while remaining detectable to scanning sonar on vehicles operating close to the seafloor. The variation in mooring length and panel number was unintentional. The original purpose for the moorings was to mark the start point of ROV transects. Moorings for this purpose were deployed in the western field. However, at the eastern field, the opportunity to augment the mooring was ceased and the length of the mooring rope was increased to accommodate two settlement panels (concrete roof tiles), located at 0.5 and 1 m above the sea bed (Table S1; Fig. S2). To make sure the moorings had correctly landed on the seabed, a SeaEye Lynx remotely operated vehicle fitted with a Kongsberg OE14-208 digital stills camera was used to visually inspect them shortly after their deployments (Fig. S3).

In 2019, during the RRS *Discovery* cruise 108/9 (Huvenne & Thornton 2020), the Hydraulic Benthic Interactive Sampler (HyBIS; Murton et al. 2012) was used to record in situ videos of the fauna growing on all four moorings (Table S1; Huvenne & Thornton 2020). HyBIS carried two camera systems: (a) an Insite Pacific Inc. Super Scorpio camera providing 1920 × 1,080 pixel video and 4,672 × 2,628 pixel still images; and (b) a Teledyne Bowtech DIVECAM-720 providing 1,280 × 720 pixel video. The HyBIS vehicle was then used to recover two of the four moorings; one mooring from each area was chosen randomly; the remaining two moorings were left in place to continue the settlement experiment.

Processing of Epifauna on Moorings. Upon recovery, all colonized surfaces were photographed before the scleractinian corals on the settlement panels were carefully removed, photographed, and preserved in 96% ethanol. The recovered settlement panel (lower panel) from the JC060-050 (eastern area) mooring was also preserved in ethanol. The upper panel had been lost upon recovery. Because the mooring at JC060-030 did not include any settlement panels, all fauna from an area of 659 cm^2 of the surface of the buoy (matching the area of one side of the settlement panel) was preserved by freezing. One-eighth subsample of the fouling community of both moorings was removed and preserved in ethanol. Given the homogeneity and high density of the encrustation (Fig. 1), this proportion was considered sufficient to provide a representative sub-sample of the majority community on each buoy. All remaining fouling was weighed (wet). All taxa from the representative mooring surface area were identified directly from specimens (i.e. not from photographs) to species level (where possible), counted, and the wet mass of the larger and most abundant taxa was measured. Specimens have been retained in the Discovery Collections at the National Oceanography Centre, United Kingdom (http://grscicoll.org/institution/national-oceanography-centre-southampton).

Assessment of CWC Restoration Strategies. In addition to the Darwin Mounds restoration strategy proposed by Van Dover et al. (2014), that is, harvesting wild parent stock, laboratory propagation, and transplantation of coral recruits to the seafloor attached to anchor substrata (taken to be weighted, plate-like “reefdisks” similar to those used by Brooke et al. (2006))—we considered four other options. These strategies mirror those thought to be most effective in tropical coral restoration: brood-stock enhancement, substrata enrichment, artificial reef units, and translocated adult material (Bayraktarov et al. 2016). In summary, we considered options (see detail in Table 1) as follows:

(1) Wild harvest of parent stock, laboratory propagation, attachment to substrata, and transplant to the seafloor (Van Dover et al. 2014).

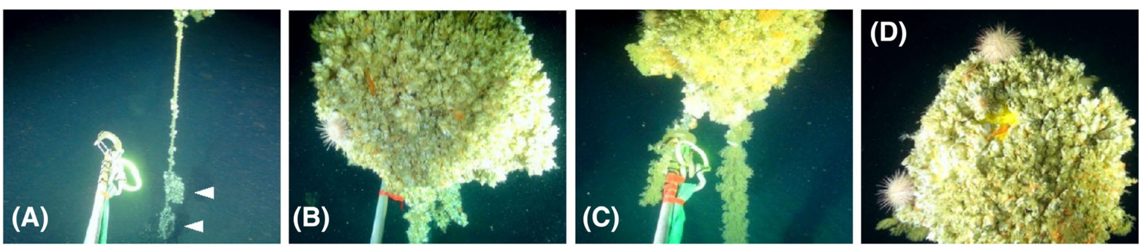

Figure 1. Moorings in situ as recovered; (A,B) eastern field mooring JC060-050, note recovery snap hook and settlement panels, arrowed, in (A); (C,B) western field mooring JC060-030. Note also hydroid “turf” fouling of the mooring line in (C) and the presence of regular urchins on the buoy, and barnacle encrustations in (B) and (D).

Table 1. Description of each restoration scenario (Scren) and the "do-nothing" option.

Scenario	*Description*
Scen1	*Wild harvest of parent stock, laboratory propagation, attachment to substrata, transplant to the seafloor.* This restoration option would use a laboratory propagation and transplant protocol within an adaptive management framework to test the efficacy of coral transplants at two densities. Coral fragments would be harvested sustainably by collecting short fragments of coral tips. These fragments would be propagated in the laboratory, attached to anchor substrata, positioned on the seafloor, and monitored for coral growth and biodiversity of associated fauna. Three adjacent coral rubble patches would serve as reference areas. Measures of success would include the demonstration that transplanted corals grow and propagate through sexual and asexual reproduction and an increase in associated biodiversity via high-resolution AUV and ROV imagery.
Scen2	*High-relief artificial substrata emplaced on the seafloor.* This restoration option relies on deploying 3D artificial reef units throughout the restoration site. Artificial reef units would be of sufficient size to allow for the settlement of the units in softer sediments and yet maintain 1 m of elevation above the seabed. Substratum surfaces, such as rugged concrete surfaces (e.g. roofing tiles) would be angled to reduce siltation and rugose to provide differing settlement opportunities. Adjacent mounds of coral rubble would serve as reference areas for natural recruitment onto existing substrata. Artificial reef units would be winched to the seabed in batches and relocated on the seabed by a work-class ROV. Monitoring of colony formation would be provided by an in-situ time-lapse camera, AUV photomosaics and imagery obtained by a ROV.
Scen3	*Low-relief artificial substrata spread on the seafloor.* As above but the artificial substratum is a loose, coarse material designed to simulate dense, fresh coral rubble. Adjacent mounds of coral rubble would serve as reference areas for natural recruitment onto existing substrata. Loose rubble substratum would be winched to the seabed in bulk bags and opened either on the seabed by a work-class ROV or near the seabed using a release mechanism on the winch wire. Monitoring of colony formation would be provided by an in-situ time-lapse camera, AUV photomosaics and imagery obtained by a ROV.
Scen4	*Translocation from other sites.* Living cold-water coral biomass is collected from a suitable donor site (e.g. site with abundant cold-water coral with a similar depth, temperature, and genetic profile). Translocated material will be collected using a work-class ROV. Harvested material will need to be maintained in cooled holding tanks on surface until the ship has relocated to the restoration site. Translocated material is deployed by ROV at the recipient site. Adjacent mounds of coral rubble would serve as reference areas for natural recruitment onto existing substrata. Monitoring of colony formation would be provided by in situ time-lapse camera, AUV photomosaics and imagery obtained by a ROV.
Scen5	*Do-nothing.* No biological or substrata are placed at the site: recruitment rates are determined by the availability of larvae and colonizable natural substrata. Multiple mounds of natural substrata would be monitored for natural recruitment. Monitoring of colony formation would be provided by in situ time-lapse camera, AUV photomosaics and imagery obtained by a ROV.

(2) High-relief artificial substrata emplaced on the seafloor.
(3) Low-relief artificial substrata spread on the seafloor.
(4) Translocation from other sites (harvest, attachment to substrata, transplant to seafloor).
(5) Do nothing (background rates of recruitment on existing natural substrata).

To assess the potential of each restoration strategy, expert judgment was used to estimate:

(1) Potential restoration success; assessed against two hypothetical strategies: (A) a modest objective seeking to restore 20% of the coral cover within a restoration area (600 m^2); and (B) a high objective seeking to restore 80% of the coral cover within a restoration area (600 m^2).
(2) Timescale required to generate an established, adult population.
(3) Environmental impact in terms of local footprint and carbon emissions.
(4) The estimated cost for establishing the restoration project and implementing an operational monitoring program to gauge success.

The probability of success for both outcomes (A and B) was estimated, collectively amongst the authors (various ecologists, taxonomists, biologists, and those with experience in restoration programs), using the following criteria: (1) overall complexity of the method (i.e. the number of failure points); (2) the number of steps requiring the handling of biological material (i.e. steps likely to induce mortalities); (3) susceptibility to stochastic events; (4) the use of tested or established techniques; (5) reliance on natural processes outside the control of the restoration program; and (6) potential for passive restoration to continue once the restoration program had ceased.

The likely timescale for reaching restoration objectives was estimated using the following criteria: (1) the timescale required to establish the infrastructure or hardware required to deliver the restoration program; (2) the life history stage used at the start of the program (e.g. larval or adult material); and (3) the reliability of any natural processes required (e.g. spawning and settlement events). The impact of restoration programs considered both the footprint of collection, processing and deployment operations, as well as a broad consideration for the need for energy-intensive processes, which might inflate the carbon footprint of the program. Specific impact criteria included: (1) the necessity of the harvesting of existing coral; (2) modification of the natural habitat with artificial structures; and (3) reliance on energy-intensive processes (e.g. pumping and water cooling for shore-based facilities) or logistics (e.g. regular or lengthy use of ships).

Costs were directly estimated by the authors or were based on the values given by Van Dover et al. (2014) corrected for inflation from 2013 to 2022.

Results

In Situ Observations

In situ observations of the moorings indicated that the buoys in the western area had accumulated a full coverage of epifaunal growth, consisting predominantly of barnacles (~90%). The buoys had acted as effective settlement surfaces for the scleractinian corals *Desmophyllum pertusum* and *D. dianthus* (Figs. 1 & 2). The moorings located in the eastern area had substantial amounts of epifaunal growth present, but very few scleractinian corals were observed. None of the ballast weights were visibly colonized by scleractinian corals (>1 cm). The mooring ropes were covered in a dense hydroid turf and barnacles.

Further in situ observation of the seabed revealed two additional points regarding the colonization of scleractinian corals and barnacles (Figs. S4 & S5). Boulders were present at the seabed in both the western and eastern fields, though were generally more frequent in the latter, reaching c. 1 m in maximum dimension and having an elevation up to 0.5 m above the seabed. Although barnacles were observed growing on some of the boulders, none had barnacles present to the same degree as on the moorings. Colonial scleractinian corals were observed to be associated with approximately a quarter of the boulders seen (Fig. S4d, *Madrepora oculata*). Items of large litter were also observed and found to be colonized by anemones (Fig. S5a & S5b), barnacles (Fig. S5b & S5c), and potentially scleractinian polyps (Fig. S5c & S5e).

Observations of Recovered Material

In total, 36 nominal taxa were identified on the moorings; faunal abundance and taxon richness were greater on the western than the eastern buoy (Table S2). Small pectinid bivalves *Delectopecten vitreus* (Gmelin 1791), the large balanomorph barnacles *Bathylasma hirsutum* (Hoek 1883), and the urchin *Gracilechinus* sp. being the most abundant species found on both moorings (Table S2). In terms of wet weight, *B. hirtusum* (82.4%) and the corals *D. dianthus* (5.7%) and *D. pertusum* (4.6%) contributed the most to the total mass on the western mooring. On the eastern mooring, *B. hirtusum* (92.1%), *D. vitreus* (5.0%), and the ophiuriod *Ophiactis abyssicola* (Sars 1861) (2.3%) contributed the most to total mass. The contribution of the more mobile species to the wet weight should be taken as an approximation as it is possible that individuals were lost during the ascent.

The western mooring was inhabited by a variety of mobile epifaunal species, including urchins, hermit crabs, gastropods, brittlestars, and shrimps (Table S2); much of the mobile fauna was lost during recovery to the surface. Small soft coral colonies were also present, including a single large specimen of *Gersemia fruticosa* (Sars 1860) (Fig. 3D). Four *D. pertusum* colonies of 25–95 mm in maximum dimension were recorded, all attached directly to barnacle wall plates, and typically located on the upper surface of the buoy (Table 2; Figs. 3A & 3B & 4A & 4B). Assuming that the buoy was colonized immediately, which seems unlikely as the colonies *of D. pertusum* were attached to barnacle plates, the minimum colony extension rate would be 11.4 mm/yr. Seven individual *D. dianthus* (Esper 1794) polyps were recorded, interspersed between barnacles, and attached to both barnacle plates and the plastic surface of the buoy (Figs. 3A–C & 4C–E). The mooring rope for both moorings was also colonized, although sparsely, with *B. hirsutum*, individual *D. dianthus* polyps and hydroids, *Stegopoma plicatile* (Sars 1863). The steel plate anchors used for both moorings were coated in oxide and devoid of any fouling.

The eastern mooring buoy was inhabited by one small colony (maximum dimension 20 mm) of *D. pertusum* and the settlement panel located 0.5 m above the seafloor was inhabited by one small colony (maximum dimension 15 mm) of *D. pertusum*; in both cases attached to barnacle plates

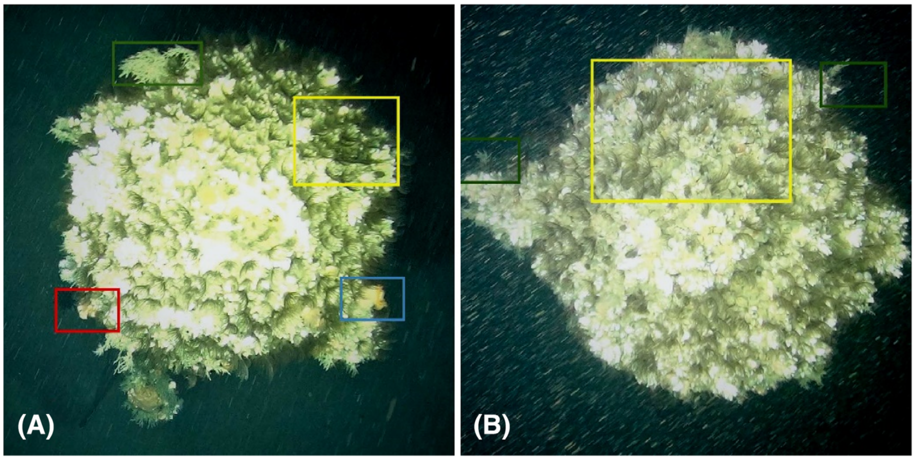

Figure 2. Overhead views of moorings left in place, (A) western field JC060-029, and (B) eastern field JC060-049 buoys, illustrating extensive overgrowth by feeding barnacles.

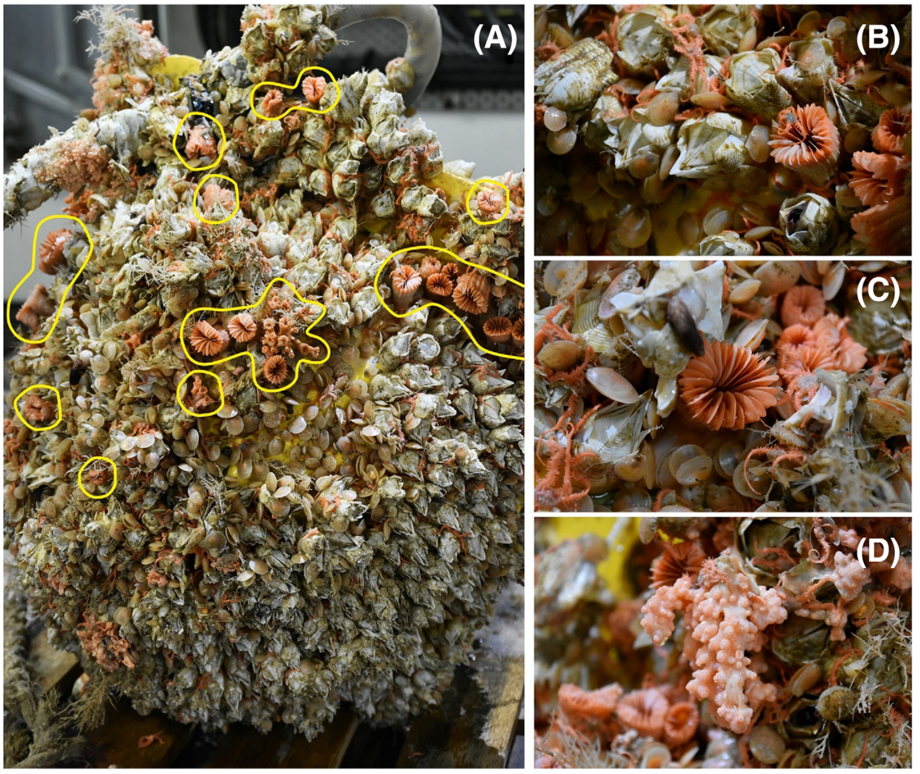

Figure 3. Western field mooring, JC060-030 buoy as recovered to deck; (A) composite image with scleractinian polyps immediately visible outlined in yellow; (B,C) closer views of example scleractinian polyps; and (D) the soft coral, *Gersemia fruticose*, attached to a barnacle plate.

(Fig. 5A & 5B). Assuming immediate colonization, the minimum colony extension rate would be 2.4 mm/yr. In addition, c. 50 smaller *D. dianthus* polyps were found, interspersed throughout the barnacle cover on the buoy.

Potential Mechanisms of CWC Restoration

Our assessments of restoration scenarios are summarized in Tables 3 and S3, with the basis of each scenario having been described in Table 2. We judged scenario 1 (Scen1; Van Dover et al. 2014) to have the least localized environmental impact of the active restoration techniques (Scen1–4) in that brood stock harvesting is kept to a minimum (although sufficient to maintain genetic diversity within laboratory cultures) and artificial substratum is limited to anchor substrata only. As such, we considered Scen1 to have a low overall impact, although it is associated with the second highest number of ship operation days, and therefore carbon footprint. Use of artificial substrata, Scen2 and Scen3, have the lowest allocation of ship time of the active restoration techniques but their need to place high (Scen2) and low (Scen3) relief substrata on the seabed means their impact was estimated to be high and moderate, respectively. With the high number of days at sea (and resulting carbon footprint), and the need to harvest large quantities of *D. pertusum* biomass

Table 2. *Desmophyllum* spp. specimens recovered from the Darwin Mounds moorings (dim., dimension; na, not applicable).

Observation	*Descriptor*	*Western Field*	*Eastern Field*
Desmophyllum pertusum from buoy	Colonies and (density)	4 (5.5 colonies/m^2)	1 (1.4 colonies/m^2)
	Longest dim. in mm and (number of polyps)	25 (5), 32 (14), 62 (22) 95 (36)	20 (4)
	Substrata	*Bathylasma hirsutum* wall plates	*B. hirsutum* wall plates
D. pertusum from panel	Colonies and (density)	na	1 (7.6 colonies/m^2)
	Longest dim. in mm and number of polyps	na	15 (4)
	Substrata	na	Panel
D. dianthus from buoy	Individuals and (density)	5 (6.8 ind/m^2)	7 (9.5 ind/m^2)
	Substrata	*B. hirsutum* wall plates and buoy surface	*B. hirsutum* wall plates and buoy surface

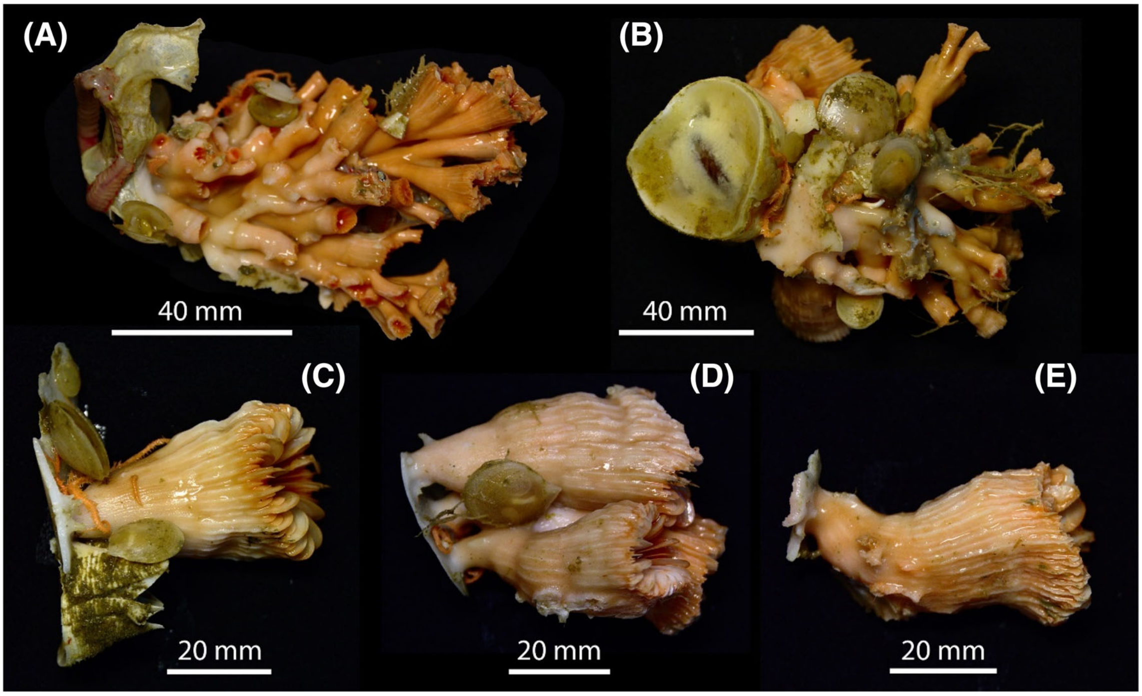

Figure 4. Example images of (A,B) *Desmophyllum pertusum*, and (C–E) *Desmophyllum dianthus*, recovered from the western field mooring, JC060-030.

from donor sites, Scen4 was estimated to generate the greatest impact when compared with other scenarios.

Financially, it is the ship time that drives costs (Table S3), with the transplantation technique (Scen4), estimated to be the most expensive. The onshore hatchery costs and relatively large ship time requirement make Scen1 the second most expensive approach. Reliance on the placement of artificial substrata, namely Scen2 and Scen3, offered the cheapest of the active approaches. The "do nothing" option (Scen5) is inevitably the cheapest, although it is not costless as the monitoring package, common to all scenarios, has been included so that the rate of natural recruitment can be tracked over time.

Figure 5. Eastern field mooring, JC060-050; (A) buoy, and (B) settlement panel from 0.5 m above seabed as recovered to the deck. Scleractinian polyps immediately visible are ringed in yellow.

Table 3. Potential restoration scenarios (Scen) for *Desmophyllum pertusum* in the Darwin Mounds marine protected area. Restoration objectives: A = potential for an 20% increase, B = potential for an 80% increase (M USD, millions of US dollars).

Scenario	*Advantages*	*Disadvantages*	*Potential to increase colonization*	*Environmental impact*	*Timescale and Cost*
Scen1	Consistent production of recruits. Targeted placement of recruits in favorable habitat (attached to "anchor substrata"). Effort scalable with budget.	Degradation of donor reefs. No existing suitable hatcheries. Mortalities during transportation and handling. Very high costs. Modification of genetic identity of recipient population. Low retention of larvae locally.	A: High based on the probability of establishing a successful hatchery and the benefit of direct placement of live material on the seabed. B: Moderate based on the difficulty and cost of scaling up hatchery operations and transportation.	Low due to the use of captive brood stock for supplying recruits; other than "anchor substrata," no extensive use of artificial structures on the seabed but high energy consumption from hatchery and transportation.	Costed for 5 years by Van dover et al. (2014). 6.3 M USD 55 ship days
Scen2	Hatchery facilities are not required. Uses established reef creation practices. Immediate structure and biodiversity increase.	Reliant on natural colonization. Potential for surfaces to be dominated by other encrusting species. Reliance on artificial structures within an MPA.	A: Very high based on observed colonization of artificial surfaces within this study. B: Low based on an assumed limitation of larval supply/local brood stock	High due to the placement of artificial structures near mounds within an MPA. Moderate energy uses due to construction and transportation.	Observed to be 8 years based on this study. 4.6 M USD 36 Ship days
Scen3	Logistically simple. Hatchery not required. Immediate substratum for colonization. Substratum enhancement common to bivalve restoration projects.	Reliant on natural colonization. Uncertainty in suitability of artificial substrata. Alters the composition of surficial sediments. Uncertainty about the longevity of artificial mounds.	A: Low based on the low rates of recruitment and uncertainty about the suitability of substratum toppings. B: Very low based on the low rates of recruitment and uncertainty about the suitability of substratum toppings.	Moderate due to the addition of surficial toppings changing the fundamental substrata and topography of the seabed.	Estimated to be >8 years based on higher predation, disturbance, and lower growth nearer the seabed. 5.7 M USD 36 ship days
Scen4	Immediate increase in abundance. Not immediately dependent on settlement and recruit processes.	Degradation of donor reefs. Mortalities during translocation and initial re-establishment. Modification of genetic identity of recipient population. Low retention of larvae locally.	A: Very high based on the ability to harvest a moderate amount of coral from a donor site and that larvae are retained locally. B: Moderate based on the ability to harvest sufficient coral to support the higher rate of colonization.	High due to the need to harvest and translocate coral from healthy sites.	Estimated to be 2- year-based observations of Maier (2008). 7.0 M USD 69 ship days
Scen5	No risks of damaging existing coral populations or modifying the seabed at Darwin Mounds.	Reliant on natural rates of colonization and the presence of existing settlement surfaces	A: Not known baseline colonization without restoration intervention B: Not known baseline colonization without restoration intervention	None based on the absence of artificial structures, substrata, or translocated biomass	No observed natural recovery (present study) 2.9 M USD 21 ship days

The full suite of activities originally proposed by Van Dover et al. (2014) would now cost 6.0 million U.S. dollars. However, their proposal incorporated the implementation of a major, replicated field experiment, with three subsequent monitoring visits to the experimental treatments. The costing included: (1) 0.6×10^6 USD for parent stock collection, (2) 2.2×10^6 USD for transplant to seabed, and (3) 2.7×10^6 USD for monitoring equipment and monitoring surveys. Removing the need for nursery techniques but including costs for artificial surfaces (scaled to cover 600 m^2) and deployment costs, the cost of implementing Scen2 and Scen3 would be in the order of 4.5×10^6 USD to 5.7×10^6 USD, respectively (Table S3). This revised costing provides a more useful basis on which to compare alternative scenarios.

Estimated timescales vary between scenarios; we judged that the shortest timescale was likely associated with Scen4 as it involves the transplantation of live colonies directly to the recipient site (depending on mortality and growth rates). Van Dover et al. (2014) originally costed Scen1 for 5 years on the basis of the rapid growth of colonies in laboratory conditions (Rogers 1999). However, what is not certain is the time needed to optimize the ex situ spawning, settlement, and rearing processes, although these processes have been documented under laboratory conditions (Larsson et al. 2013, 2014). The use of artificial substrata, as per Scen2 and Scen3, was estimated to be occupied within 8 years, based on our observations reported here. At present our best estimation for natural recovery can only be greater than 16 years, which is the limit of our current observations (Huvenne & Thornton 2020).

In terms of the likelihood of success, we judged that for the lower colonization rate objective (20% over natural rates), Scen2 and Scen4 were the most effective methods (very high), followed by Scen1 (high) (Table 3). The use of low-relief artificial substrata (Scen3) was judged likely to be of moderate success based on the observations of colonized boulders at the site. For the higher colonization rate objective (80% over natural rates), Scen1 and Scen4 were judged to be the most effective techniques (moderate probability of success), followed by Scen2 (low), Scen3 (very low), and Scen5 (very low) (Table 3).

Discussion

Our observations of settled and seemingly healthy framework-forming *Desmophyllum pertusum* and solitary *D. dianthus* corals on the artificial surfaces provide evidence that recruitment, a critical mechanism of population recovery, had occurred within the Darwin Mounds MPA between 2011 and 2019. This suggests that local environmental conditions generally remain favorable for settlement. However, we note that the dominant species of scleractinian coral on the Darwin Mounds (Howell et al. 2013), *Madrepora oculata*, was not detected in our settlement study. In addition, we were unable to detect any clear evidence of natural recruitment or growth of any scleractinians during our 2019 survey (Huvenne & Thornton 2020). In the following we consider three potential factors influencing differential recruitment: (1) local environmental conditions; (2) biological interactions; and (3) availability of settlement substrata.

Concerning the suitability of environmental conditions, the apparently increased recruitment to our moorings over the seabed environment may be linked to local hydrodynamics. Reduced current speeds close to the seabed, induced by increasing seafloor drag through the benthic boundary logarithmic layer (Wildish 2001), will reduce food supply and encounter rates with proximity to the seabed. Conversely, at greater elevation above the seabed, current speeds rapidly increase, and the localized turbulence around the moorings, may promote settlement as well as food supply and survival rates (Young 1989; Hennige et al. 2021). In part, this increased elevation may mimic the hydrodynamic environment of natural CWC mounds in the Darwin Mound fields and at other locations (De Clippele et al. 2018).

The influence of predators and/or epistrate grazers on the mortality of early coral recruits is well-studied in tropical corals (Rice et al. 2019) but less is known about CWC predation. Survival rates of the corals on the moorings may be greater because mobile grazers/predators, such as starfish and sea urchins, are partially excluded from the moorings. Conversely, a reduction in mobile predators could hamper the recruitment of scleractinians if competitive species, such as barnacles and bivalves, rapidly occupy the available substratum. Indeed, the dense aggregations of filter-feeding organisms observed on the buoys may have led to the consumption of coral larvae, as noted in other studies (Fabricius & Metzner 2004).

The apparent exclusive settlement of *D. pertusum* onto barnacle plates may be a product of selective settlement or simply reflect that barnacles were the dominant first colonists. Although of a different crystalline form, the calcium carbonate plates of barnacles are similar in composition to coral rubble and may be favored for settlement as well as releasing inorganic cues (Levenstein et al. 2022). The filtering currents of barnacles may also have acted to sweep larvae into the interstitial spaces between barnacles and further increased the probability of corals settling onto these surfaces. Barnes et al. (2010) observed that oyster larvae often became entrained in small-scale eddies created by feeding barnacles and that these larvae were often expelled, unharmed, during this process. Regardless of the process, it is apparent that the wall plates of live barnacles are, at least in the short term, a viable settlement surface for *D. pertusum*. In the longer term, it is not clear whether the wall plates of barnacles could support larger coral colonies.

Direct attachment of *D. pertusum* to plastic surfaces was not recorded here, though *D. dianthus* was observed, directly attached to both the polyethylene buoys and the polypropylene mooring lines. Battaglia et al. (2019) reported colonization of expanded PVC fishing floats by *D. pertusum*, and Bergami et al. (2021) reported *D. dianthus* attachment to a low-density polyethylene bottle, likely employed as a sub-surface float. Our seabed surveys of the Darwin Mounds MPA encountered numerous occurrences of plastic debris, notably including lost and/or discarded fishing gear. Although image resolution precluded definitive identifications, cnidarian colonists were apparent, with coral polyps present in at least one case. Barnacles were also common colonists of this debris.

We recorded the settlement of *D. pertusum* onto barnacle plates and the concrete settlement panel but observed none on mooring anchors. The absence of any obvious epifaunal colonization of anchors may be related to their occasional burial and/or scouring by mobile sediment as well as the friable nature of the oxidized surface of the anchors. The ability of *D. pertusum* to settle and grow extensively on steel structures is well documented from oil and gas installations in the North Sea (Bell &

Smith 1999; Gass & Roberts 2006) and the Gulf of Mexico (Larcom et al. 2014). Indeed, these observations of extensive coral growth prompted the "rigs-to-reefs" concept as a means to facilitate conservation/restoration in the deep sea (Macreadie et al. 2011), and further consideration of the resultant enhanced larval supply to natural deep-sea environments (Henry et al. 2018). Natural hard substrata, potentially available for colonization, were present in the Darwin Mounds MPA, in the form of glacial erratic boulders (Belderson et al. 1973), and coral rubble (Huvenne et al. 2016). The boulders observed were not as densely colonized as the mooring buoys, potentially suggesting a settlement advantage for the buoys from their elevated position and the presence of abundant barnacles plates.

Potential CWC Restoration in the Darwin Mounds MPA

Given the potential efficacy of restoration techniques, Van Dover et al. (2014) examined the cost of a restoration program in the Darwin Mounds (Scen1). They suggested the use of shore-based coral cultivation to provide small colonies for transplantation to the seabed. This approach comes with difficulties as the cultivation of these corals in artificial conditions is extremely challenging with a high level of uncertainty of the success (Orejas et al. 2019). Furthermore, although CWC larvae have been successfully kept for up to 1 year in laboratory cultures (Strömberg & Larsson 2017), settlement of the larvae has never been observed. The evidence presented here that natural settlement continues in the Darwin Mounds expands the restoration strategies available.

The potential efficacy of each scenario depends on which aspects of the recruitment and growth processes are limiting the expansion of the population (Török & Helm 2017). If the availability of a hard substratum, suitable for settlement, is the limiting factor, then options employing the addition of artificial substrata are likely to be needed. A shortage of suitable settlement surfaces is known to limit the expansion of oyster reefs and therefore the artificial placement of suitable surfaces, typically dead, clean shell, or rock, is a common restoration practice in such cases (La Peyre et al. 2014). We observed recruitment and growth of *D. pertusum* on artificial substrata, and that it occurred despite the absence of established colonies in the immediate vicinity. An elevated position above the seabed appeared to be advantageous. The ability to exploit the recruitment of larvae from natural in-situ sources would represent a significant reduction in the complexity and cost, and greatly improve the feasibility of, the restoration process when compared with a strategy using onshore nursery techniques (i.e. Scen1). This would also remove the need to harvest wild parent stock (Scen1 and Scen4), an activity that may be seen as counterproductive in conservation terms. Similarly, potential mortalities associated with the wild harvest, onshore culture, transport offshore, and transplantation to depth would be avoided.

If larval supply is the key limiting factor, then stock enhancement via Scen1 or direct transplants from other populations (Scen4) may be the most effective approaches. Hydrodynamic modeling of the connectivity of the Darwin Mounds MPA with other protected areas supporting *D. pertusum* suggested that the area is a net larval sink within the region and that larval retention was very high (Fox et al. 2016; Ross et al. 2017). Although competent larvae were predicted to be present at the Darwin Mounds, if the settlement cues needed are diminished at the site, recruitment and hence recovery, may still not be possible without restoration intervention. Equally, the settlement observed, and the variation in the size of these recruits, does not guarantee a consistent supply of larvae at the site: additional panels have been deployed at the Darwin Mounds so that the consistency of settlement can be determined (V. Huvenne 2022, National Oceanograhy Centre, United Kingdom, personal communication).

The lack of detailed information on the factors that constrain the rate of population increase of CWCs in the Darwin Mounds makes it difficult to be certain which restoration approach would be most successful. Nevertheless, given the common association of CWCs with both natural and artificial topographic elevations, our observations of successful recruitment and growth on buoys c. 5 m above the seabed, and the likely benefit of three-dimensional (3D) habitat framework to the broader seafloor community, we concluded that the use of high-relief artificial substrata (Scen2) had the greatest potential for long-term success in the Darwin Mounds. As evident from our own observations, we acknowledge the epifaunal assemblage colonizing artificial substrata may be distinct from that of natural surfaces. However, given the high retention of larvae locally (Fox et al. 2016; Ross et al. 2017), colonized structures are likely to enlarge the brood stock locally, thereby supplying more larvae for the re-colonization of local natural substrata.

Finally, we would note that this approach need not be particularly costly as artificial reef structures are frequently formed from concrete (Baine 2001), a cheap and readily available material easily fabricated into a 3D structure. Alternative substances such as a pozzolans, can be 3D printed to also form suitable reef units (Yoris-Nobile et al. 2023). Similarly, such structures can simply be lowered to the seabed without the need to use remotely operated vehicles, as envisioned in the original Van Dover et al. (2014) proposal (Scen1). It was also considered that the likelihood of long-term success would be greater for restoration scenarios benefiting from the products of sexual reproduction (Scen1–3), from a genetically diverse brood stock (Scen2–3), as colonizing progeny will have greater genetic diversity. This diversity may enhance the probability that some of the young recruits will be better adapted to higher ambient temperatures and more resilient to climate change (Crow 1992; Waxman & Peck 1999).

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LITERATURE CITED

Althaus F, Williams A, Schlacher TA, Kloser RJ, Green MA, Barker BA, Bax NJ, Brodie P, Schlacher-Hoenlinger MA (2009) Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. Marine Ecology Progress Series 397:279–294

Baillon S, Hamel JF, Wareham VE, Mercier A (2012) Deep cold-water corals as nurseries for fish larvae. Frontiers in Ecology and the Environment 10:351–356. https://doi.org/10.1890/120022

Baine M (2001) Artificial reefs: a review of their design, application, management and performance. Ocean & Coastal Management 44:241–259. https://doi.org/10.1016/S0964-5691(01)00048-5

Barnes BB, Luckenbach MW, Kingsley-Smith PR (2010) Oyster reef community interactions: The effect of resident fauna on oyster (Crassostrea spp.) larval recruitment. Journal of Experimental Marine Biology and Ecology 391: 169–177

Battaglia P, Consoli P, Ammendolia G, D'Alessandro M, Bo M, Vicchio TM, Pedà C, Cavallaro M, Andaloro F, Romeo T (2019) Colonization of floats from submerged derelict fishing gears by four protected species of deep-sea corals and barnacles in the Strait of Messina (central Mediterranean Sea). Marine Pollution Bulletin 148:61–65. https://doi.org/10.1016/j.marpolbul.2019.07.073

Bayraktarov E, Saunders MI, Abdullah S, Mills M, Beher J, Possingham HP, Mumby PJ, Lovelock CE (2016) The cost and feasibility of marine coastal restoration. Ecological Applications 26:1055–1074. https://doi.org/10.1890/15-1077

Belderson RH, Kenyon NH, Wilson JB (1973) Iceberg plough marks in the northeast Atlantic. Palaeogeography, Palaeoclimatology, Palaeoecology 13: 215–224. https://doi.org/10.1016/0031-0182(73)90020-5

Bell N, Smith J (1999) Coral growing on North Sea oil rigs. Nature 402:601. https://doi.org/10.1038/45127

Bergami E, Caroselli E, Vaccari L, Corsi I, Semenov A, Macali A (2021) Pioneer settlement of the cold-water coral *Desmophyllum dianthus* (Esper, 1794) on plastic. Coral Reefs 40:1355–1360. https://doi.org/10.1007/s00338-021-02131-9

Bett BJ (2001) UK-Atlantic margin environmental survey: introduction and overview of bathyal ecology. Continental Shelf Research 21:917–956. https://doi.org/10.1016/S0278-4343(00)00119-9

Boch CA, DeVogelaere A, Burton E, King C, Lord J, Lovera C, Litvin SY, Kuhnz L, Barry JP (2019) Coral translocation as a method to restore impacted deep-sea coral communities. Frontiers in Marine Science 6:540. https://doi.org/10.3389/fmars.2019.00540

Boch CA, DeVogelaere A, Burton EJ, King C, Lovera C, Buck K, et al. (2020) Guide to translocating coral fragments for deep-sea restoration. Pages 25. In: National Marine Sanctuaries Conservation Series ONMS-20-10. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries, Silver Spring, MD. https://repository.library.noaa.gov/view/noaa/25571

Bongiorni L, Mea M, Gambi C, Pusceddu A, Taviani M, Danovaro R (2010) Deep-sea scleractinian corals promote higher biodiversity in deep-sea meiofaunal assemblages along continental margins. Biological Conservation 143:1687–1700. https://doi.org/10.1016/j.biocon.2010.04.009

Brooke S, Koenig CC, Shepard AN (2006) *Oculina* banks restoration project: description and preliminary assessment. Proceedings of the Gulf and Caribbean Fisheries Institute 57:607–620. http://aquaticcommons.org/id/eprint/13900

Clark MR, Althaus F, Schlacher TA, Williams A, Bowden DA, Rowden AA (2016) The impacts of deep-sea fisheries on benthic communities: a review. ICES Journal of Marine Science 73:i51–i69. https://doi.org/10.1093/icesjms/fsv123

Clark MR, Bowden DA, Rowden AA, Stewart R (2019) Little evidence of benthic community resilience to bottom trawling on seamounts after 15 years. Frontiers in Marine Science 6:63. https://doi.org/10.3389/fmars.2019.00063

Coen LD, Luckenbach MW (2000) Developing success criteria and goals for evaluating oyster reef restoration: ecological function or resource exploitation? Ecological Engineering 15:323–343. https://doi.org/10.1016/S0925-8574(00)00084-7

Costello MJ, McCrea M, Freiwald A, Lundälv T, Jonsson L, Bett BJ, van Weering TC, Haas HD, Roberts JM, Allen D (2005) Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. Pages 771–805. In: Cold-water corals and ecosystems. Springer, Berlin, Heidelberg. https://doi.org/10.1007/3-540-27673-4_41

Crow JF (1992) An advantage of sexual reproduction in a rapidly changing environment. Journal of Heredity 83:169–173. https://doi.org/10.1093/oxfordjournals.jhered.a111187

Da Ros Z, Dell'Anno A, Morato T, Sweetman AK, Carreiro-Silva M, Smith CJ, et al. (2019) The deep-sea: the new frontier for ecological restoration. Marine Policy 108:103642. https://doi.org/10.1016/j.marpol.2019.103642

Davies AJ, Roberts JM, Hall-Spencer J (2007) Preserving deep-sea natural heritage: emerging issues in offshore conservation and management. Biological Conservation 138:299–312. https://doi.org/10.1016/j.biocon.2007.05.011

De Clippele LH, Huvenne VA, Orejas C, Lundälv T, Fox A, Hennige SJ, Roberts JM (2018) The effect of local hydrodynamics on the spatial extent and morphology of cold-water coral habitats at Tisler Reef, Norway. Coral Reefs 37:253–266. https://doi.org/10.1007/s00338-017-1653-y

De Santo EM, Jones PJ (2007) The Darwin Mounds: from undiscovered coral to the development of an offshore marine protected area regime. Bulletin of Marine Science 81:147–156

Duncan PM (1873) A description of the Madreporaria dredged up during the Expeditions of H.M.S. "Porcupine" in 1869 and 1870. Transactions of the Zoological Society of London 8:303–344. https://doi.org/10.1111/j.1096-3642.1873.tb00560.x

Esper EJC (1794) Fortsetzungen der Pflanzenthiere. Nürnberg 1:1–64

Etnoyer PJ (2008) A new species of *Isidella* bamboo coral (Octocorallia: Alcyonacea: Isididae) from northeast Pacific seamounts. Proceedings of the Zoological Society of Washington 121:541–553. https://doi.org/10.2988/08-16.1

Fabricius KE, Metzner J (2004) Scleractinian walls of mouths: predation on coral larvae by corals. Coral Reefs 23:245–248

Fosså JH, Mortensen PB, Furevik DM (2002) The deep-water coral Lophelia pertusa in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471:1–12

Fox AD, Henry LA, Corne DW, Roberts JM (2016) Sensitivity of marine protected area network connectivity to atmospheric variability. Royal Society Open Science 3:160494

Gass SE, Roberts JM (2006) The occurrence of the cold-water coral *Lophelia pertusa* (Scleractinia) on oil and gas platforms in the North Sea: colony growth, recruitment and environmental controls on distribution. Marine Pollution Bulletin 52:549–559. https://doi.org/10.1016/j.marpolbul.2005.10.002

Gmelin JF (1791) Vermes. In: Gmelin JF (ed) Caroli a Linnaei systema naturae per regna tria naturae Ed. 13. Tome 1(6). G. E. Beer, *Lipsiae* [Leipzig]. pp. 3021–3910. Systema Naturae. Linneaeus (ed.). Ed. 13. 1: pars. 6.

Hall-Spencer J, Allain V, Fosså JH (2002) Trawling damage to Northeast Atlantic ancient coral reefs. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:507–511

Hennige SJ, Larsson AI, Orejas C, Gori A, De Clippele LH, Lee YC, Jimeno G, Georgoulas K, Kamenos NA, Roberts JM (2021) Using the Goldilocks Principle to model coral ecosystem engineering. Proceedings of the Royal Society B 288:20211260. https://doi.org/10.1098/rspb.2021.1260

Henry LA, Mayorga-Adame CG, Fox AD, Polton JA, Ferris JS, McLellan F, McCabe C, Kutti T, Roberts JM (2018) Ocean sprawl facilitates dispersal and connectivity of protected species. Scientific Reports 8:11346. https://doi.org/10.1038/s41598-018-29575-4

Henry LA, Roberts JM (2007) Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. Deep-Sea Research Part I: Oceanographic Research Papers 54:654–672. https://doi.org/10.1016/j.dsr.2007.01.005

Herrera S, Baco A, Sánchez JA (2010) Molecular systematics of the bubblegum coral genera (Paragorgiidae, Octocorallia) and description of a new deep-sea species. Molecular Phylogenetics and Evolution 55:123–135. https://doi.org/10.1016/j.ympev.2009.12.007

Hoek PPC (1883) Report on the Cirripedia collected by H.M.S. Challenger during the years 1873–76. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 8:1-169. https://doi.org/10.5962/bhl.title.12873.

Howell KL, Huvenne V, Piechaud N, Robert K, Ross RE (2013) Analysis of biological data from the JC060 survey of areas of conservation interest in deep waters off north and West Scotland. JNCC Report No. 528. https://data.jncc.gov.uk/data/c0b8843a-f731-4c16-9af8-f9980f87da9a/JNCC-Report-528-FINAL-WEB.pdf

Huvenne VAI (2011) RRS James Cook Cruise 60, 09 May–12 June 2011. Benthic habitats and the impact of human activities in Rockall Trough, on Rockall Bank and in Hatton Basin. National Oceanography Centre Southampton (National Oceanography Centre Cruise Report 04), Southampton, UK. http://nora.nerc.ac.uk/id/eprint/293835/

Huvenne VAI, Bett BJ, Masson DG, Le Bas TP, Wheeler AJ (2016) Effectiveness of a deep-sea cold-water coral marine protected area, following eight years of fisheries closure. Biological Conservation 200:60–69. https://doi.org/10.1016/j.biocon.2016.05.030

Huvenne VAI, Thornton B (2020) RRS Discovery Cruise DY108-109, 6 Sept–2 Oct 2019. CLASS—Climate-linked Atlantic system science Darwin Mounds marine protected area habitat monitoring, BioCAM—first equipment trials. BLT-recipes: pilot study. Pages 224 (National Oceanography Centre Cruise Report, 66). National Oceanography Centre, Southampton. http://nora.nerc.ac.uk/id/eprint/526682/

Irving R (2009) The identification of the main characteristics of stony reef habitats under the Habitats Directive. Summary report of an inter-agency workshop 26–27 March 2008. JNCC Report No. 432. Joint Nature Conservation Committee, Peterborough. https://data.jncc.gov.uk/data/21693da5-7f59-47ec-b0c1-a3a5ce5e3139/JNCC-Report-432-FINAL-WEB.pdf

La Peyre M, Furlong J, Brown LA, Piazza BP, Brown K (2014) Oyster reef restoration in the northern Gulf of Mexico: extent, methods and outcomes. Ocean & Coastal Management 89:20–28. https://doi.org/10.1016/j.ocecoaman.2013.12.002

Larcom EA, McKean DL, Brooks JM, Fisher CR (2014) Growth rates, densities, and distribution of *Lophelia pertusa* on artificial structures in the Gulf of Mexico. Deep-sea Research Part I: Oceanographic Research Papers 85: 101–109. https://doi.org/10.1016/j.dsr.2013.12.005

Larsson AI, Järnegren J, Strömberg SM, Dahl MP, Lundälv T, Brooke S (2014) Embryogenesis and larval biology of the cold-water coral *Lophelia pertusa*. PLoS One 9:e102222. https://doi.org/10.1371/journal.pone.0102222

Larsson AI, Lundälv T, van Oevelen D (2013) Skeletal growth, respiration rate and fatty acid composition in the cold-water coral *Lophelia pertusa* under varying food conditions. Marine Ecology Progress Series 483:169–184. https://doi.org/10.3354/meps10284

Larsson AI, Purser A (2011) Sedimentation on the cold-water coral Lophelia pertusa: cleaning efficiency from natural sediments and drill cuttings. Marine Pollution Bulletin 62:1159–1168

Le Sueur CA (1820) Description de plusiers animaux appartenant aux polypiers lamellifères de M. le Chev Lamarck. Mémoires du Muséum d'Histoire Naturelle 7:271–298

Levenstein MA, Marhaver KL, Quinlan ZA, Tholen HM, Tichy L, Yus J, et al. (2022) Composite substrates reveal inorganic material cues for coral larval settlement. American Chemical Society Sustainable Chemistry & Engineering 10:3960–3971. https://doi.org/10.1021/acssuschemeng.1c08313

Linnaeus C (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. 10th revised edition. Vol 1. Pages 824. Holmiae, Laurentius Salvius. https://doi.org/10.5962/bhl.title.542

Macreadie PI, Fowler AM, Booth DJ (2011) Rigs-to-reefs: will the deep-sea benefit from artificial habitat? Frontiers in Ecology and the Environment 9: 455–461. https://doi.org/10.1890/100112

Maier C (2008) High recovery potential of the cold-water coral Lophelia pertusa. Coral Reefs 27:821–821

Masson D, Bett B, Billett D, Jacobs C, Wheeler A, Wynn R (2003) The origin of deep-sea, coral-topped mounds in the northern Rockall Trough, Northeast Atlantic. Marine Geology 194:159–180. https://doi.org/10.1016/S0025-3227(02)00704-1

Miller MW (2002) Using ecological processes to advance artificial reef goals. International Council for the Exploration of the Sea Journal of Marine Science 59:S27–S31. https://doi.org/10.1006/jmsc.2001.1162

Montseny M, Linares C, Carreiro-Silva M, Henry LA, Billett D, Cordes EE, et al. (2021) Active ecological restoration of cold-water corals: techniques, challenges, costs and future directions. Frontiers in Marine Science 8:621151. https://doi.org/10.3389/fmars.2021.621151

Montseny M, Linares C, Viladrich N, Capdevila P, Ambroso S, Díaz D, Gili JM, Gori A (2020) A new large-scale and cost-effective restoration method for cold-water coral gardens. Aquatic Conservation: Marine and Freshwater Ecosystems 30:977–987. https://doi.org/10.1002/aqc.3303

Murton BJ, Huhnerbach V, Garrard J (2012) HyBIS: a new concept in versatile, 6000-m rated robotic underwater vehicles. Pages 77. In: Roberts GN, Sutton R (eds) Further advances in unmanned marine vehicles. The Institution of Engineering and Technology (Control Engineering Series), Stevenage

Nutting CC (1909) Alcyonaria of the Californian coast. Proceedings of the United States National Museum 35:681–727. https://doi.org/10.5479/si.00963801.35-1658.681

Orejas C, Taviani M, Ambroso S, Andreou V, Bilan M, Bo M, et al. (2019) 38 Cold-water coral in aquaria: advances and challenges. A focus on the Mediterranean. Pages 435–471. In: Mediterranean cold-water corals: past, present and future: understanding the deep-sea realms of coral. Coral Reefs of the World, vol 9. Springer, Cham. https://10.1007/978-3-319-91608-8_38

Orth RJ, Lefcheck JS, McGlathery KS, Aoki L, Luckenbach MW, Moore KA, Oreska MPJ, Snyder R, Wilcox DJ, Lusk B (2020) Restoration of seagrass habitat leads to rapid recovery of coastal ecosystem services. Science Advances 6:eabc6434. https://doi.org/10.1126/sciadv.abc6434

OSPAR Commission (2010) Background document for carbonate mounds. https://www.ospar.org/documents?d=7219 (accessed 2 June 2023)

Puig P, Canals M, Martín J, Amblas D, Lastras G, Palanques A, Calafat AM (2012) Ploughing the deep-sea floor. Nature 489:286–289. https://doi.org/10.1038/nature11410

Pusceddu A, Bianchelli S, Martín J, Puig P, Palanques A, Masqué P, Danovaro R (2014) Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. Proceedings of the National Academy of Sciences 111:8861–8866. https://doi.org/10.1073/pnas.1405454111

Rice MM, Ezzat L, Burkepile DE (2019) Corallivory in the Anthropocene: interactive effects of anthropogenic stressors and corallivory on coral reefs. Frontiers in Marine Science 5:525. https://doi.org/10.3389/fmars.2018.00525

Roberts JM, Wheeler A, Freiwald A, Cairns S (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511581588

Rogers AD (1999) The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. International Review of Hydrobiology 84:315–406. https://doi.org/10.1002/iroh.199900032

Ross RE, Nimmo-Smith WAM, Howell KL (2017) Towards "ecological coherence": assessing larval dispersal within a network of existing marine protected areas. Deep-sea Research I: Oceanographic Research Papers 126: 128–138. https://doi.org/10.1016/j.dsr.2017.06.004

Sars M (1860) Bemaerkninger, over følgende norske Coelenterater. Forhandlinger i Videnskabs-selskabet i Christiania 1860:140–151

Sars M (1861) Oversigt af Norges echinodermer. Udgiven af Videnskabsselskabet i Christiania. Med 16 lithographerede Plancher. Trykt i Brøgger & Christie's bogtrykkerie, i commission hos J. Dybwad.

Sars M (1863) Bemaerkninger over fire norske Hydroider. Forhandlinger i Videnskabs-selskabet i Christiania 1862:25–39

Söffker M, Sloman KA, Hall-Spencer JM (2011) In situ observations of fish associated with coral reefs off Ireland. Deep-sea Research Part I: Oceanographic Research Papers 58:818–825. https://doi.org/10.1016/j.dsr.2011.06.002

Strömberg SM, Larsson AI (2017) Larval behavior and longevity in the cold-water coral Lophelia pertusa indicate potential for long distance dispersal. Frontiers in Marine Science 4:00411. https://doi.org/10.3389/fmars.2017.00411

Teichert C (1958) Cold-and deep-sea coral banks. Bulletin of the American Association of Petrolium Geoscientists 42:1064–1082

Thornton B, Bodenmann A, Yamada T, Stanley D, Massot-Campos M, Huvenne V, Durden J, Bett B, Ruhl H, Newborough D (2021) Visualising multi-hectare seafloor habitats with BioCam. Oceanography 34:92–93. https://doi.org/10.5670/oceanog.2021.supplement.02-34

Török P, Helm A (2017) Ecological theory provides strong support for habitat restoration. Biological Conservation 206:85–91. https://doi.org/10.1016/j.biocon.2016.12.024

Van Dover CL, Aronson J, Pendleton L, Smith S, Arnaud-Haond S, Moreno-Mateos D, et al. (2014) Ecological restoration in the deep-sea: Desiderata. Marine Policy 44:98–106. https://doi.org/10.1016/j.marpol.2013.07.006

Waller RG, Tyler PA (2005) The reproductive biology of two deep-sea, reef-building scleractinians from the NE Atlantic Ocean. Coral Reefs 24:514–522. https://doi.org/10.1007/s00338-005-0501-7

Waxman D, Peck JR (1999) Sex and adaptation in a changing environment. Genetics 153:1041–1053. https://doi.org/10.1093/genetics/153.2.1041

Wheeler A, Bett B, Billett D, Masson D, Mayor DJ (2005) The impact of demersal trawling on northeast Atlantic deepwater coral habitats: the case of the Darwin Mounds, United Kingdom. American Fisheries Society Symposium 41:807–817. https://fisheries.org/docs/books/x54041xm/59.pdf

Wildish DJ (2001) Benthic boundary layer effects. Pages 267–274. In: Steele JH (ed) Encyclopedia of ocean sciences. Academic Press, Cambridge, MA. https://doi.org/10.1006/rwos.2001.0215

Yoris-Nobile AI, Slebi-Acevedo CJ, Lizasoain-Arteaga E, Indacoechea-Vega I, Blanco-Fernandez E, Castro-Fresno D, et al. (2023) Artificial reefs built by 3D printing: systematisation in the design, material selection and fabrication. Construction and Building Materials 362:129766. https://doi.org/10.1016/j.conbuildmat.2022.129766

Young CM (1989) Larval depletion by ascidians has little effect on settlement of epifauna. Marine Biology 102:481–489. https://doi.org/10.1007/BF00438349

Supporting Information

The following information may be found in the online version of this article:

Table S1. Details of the moorings in the western and eastern fields.
Table S2. Taxon list for the material removed as subsamples from the buoys.
Table S3. Hypothetical project costs for deep-sea restoration scenarios for 600 m^2 of cold-water coral reef.
Figure S1. The location of Darwin Mounds MPA and the settlement panel buoys.
Figure S2. Mooring designs as deployed in the western and eastern fields.
Figure S3. Moorings in situ as deployed.
Figure S4. Example HyBIS seafloor images of glacial erratic boulders.
Figure S5. Example HyBIS seafloor images of human debris with colonizing fauna.

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