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Monitoring deep-sea cold-water coral ecosystems: 16-years of protection but no recovery on the Darwin Mounds (Bathyal NE Atlantic)

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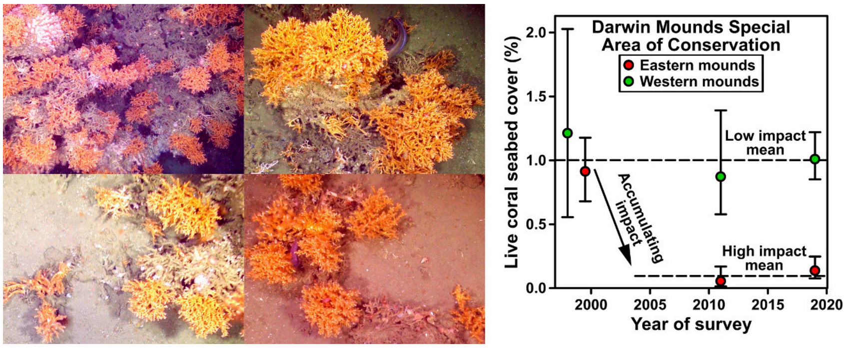
HIGHLIGHTS

- Cold-water corals in the UK Darwin Mounds Marine Protected Area (MPA) are assessed.
- Data are available for 5-years pre-MPA, 8-years post-MPA, and 16-years post-MPA.
- Trawling impact detected in 2000; no recovery detected to date (2011, 2019)
- Given slow growth rates, a multi-decadal recovery period should be expected.
- Monitoring will benefit from autonomous systems and computer vision techniques.

GRAPHICAL ABSTRACT



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ABSTRACT

The Darwin Mounds marine protected area has been afforded protection from bottom trawl fishing since August 2003, following the discovery of cold-water coral (CWC) communities in June 1998. Surveys of the area in 2000 provided evidence that deep-water trawling activities were impacting the corals, prompting the development of a conservation response. Here we report the most recent survey of these CWCs in 2019, contrasting those data with a prior survey in 2011, and the earliest observations in the area (1998–2000). Our assessment is focussed on the colonial scleractinian corals *Desmophyllum pertusum* and *Madrepora oculata*. The status of the CWCs was determined using seafloor visual imagery from a remotely operated vehicle (2011), off-bottom towed cameras (1998–2000, 2019) and additionally draws on images from an autonomous underwater vehicle seabed survey (2019). Considering the numerical density, seabed cover, and size distribution of living CWCs, no evidence was detected that the previously impacted corals had recovered. The order of magnitude reduction in live coral abundance in impacted areas remained evident in the 2019 survey after 16-years of protection. Given the likely growth rates of *D. pertusum* and *M. oculata*, we suggest that a multi-decadal recovery period should be expected. Our interpretation of long-term change was complicated by the evolving monitoring methodology employed, a common problem and tension in the development of long-term offshore ecosystem monitoring programmes. We further consider a prospectus for effective and efficient future monitoring, noting that autonomous systems and computer vision techniques are likely to play an increasingly important role.

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1. Introduction

The deep sea is increasingly exposed to human impacts through global environmental change, pollution, mining, and most notably, fishing (Levin et al., 2019). These pressures typically lead to a decline in standing stocks, biological diversity, and key ecosystem services (Thurber et al., 2014). Several international initiatives, such as resolution 61/105 of the United Nations General Assembly, and the Oslo-Paris Convention (Table S1), emphasise the need for states to reduce impacts and increase protection for seafloor ecosystems, particularly those considered to be fragile, unique, and of high ecological significance referred to as vulnerable marine ecosystems (VMEs; Table S1). Marine protected areas (MPAs) are designed to safeguard important marine features through various mechanisms including the ability to manage and reduce the prevalence of damaging pressures and thereby allow the recovery of impacted ecosystems (Vigo et al., 2023). MPAs can be effective at preventing further damage (Knowlton, 2020) and in some cases may even lead to economic benefits for local stakeholders (White and Costello, 2014). Effective and efficient conservation measures depend on a sound understanding of the sensitivity, resilience, and recovery potential of the target ecosystems (Borja et al., 2016). That understanding requires both a knowledge of pre-impact baseline conditions and the development of a monitoring programme that tracks any continuing impact and the various facets of ecosystem recovery.

Where management measures, such as MPAs, have prompted the cessation of impacts in deep-sea settings, the subsequent ecosystem recovery trajectories remain largely unknown, with few studies documenting recovery, particularly in the long term (Gollner et al., 2017). Deep-sea ecosystems are logistically challenging to monitor, making repeated observations and the assessment of temporal change difficult (Ramirez-Llodra et al., 2010). The few studies that have attempted to document the recovery of VMEs (Baco et al., 2020) suggest that the process could take decades or even centuries (Beazley et al., 2021). One of the deep-sea ecosystems most vulnerable to bottom-contact fishing impacts are those supported by cold-water corals (CWCs), particularly framework-building scleractinian corals such as *Desmophyllum pertusum* (Linnaeus, 1758) and *Madrepora oculata* Linnaeus, 1758. These communities of long-lived and slow-growing corals are found worldwide in the deep ocean. Their skeletal frameworks host a rich and diverse community of associated fauna (Buhl-Mortensen et al., 2010) and can act as a refugia for commercially important species (Costello et al., 2005). The negative impact of bottom trawling on CWCs has been observed and includes both direct mechanical destruction, as well as smothering by plumes of resuspended sediment, or secondary mortality because of cumulative stresses (Althaus et al., 2009). As a result, CWCs, particularly reef-building species, were among the first to receive protection via conservation measures such as the designation of MPAs. Species such as *D. pertusum* are listed in Annex I of the EU Habitats Directive (Table S1) and are considered VME indicators (Table S1). However, there remains a lack of knowledge on the recovery mechanisms and timescales for CWC communities, preventing the efficient implementation and monitoring of conservation strategies (Strong et al., 2023).

In this contribution we focus our attention on the CWCs of the Darwin Mounds, the UK's oldest offshore MPA. The primary conservation objective for this site is the protection/restoration of its colonial scleractinian coral populations (Table S1). Here we report the results of a new survey of the CWCs in the Darwin Mounds MPA, c. 1000 m water depth, offshore NW Scotland (Fig. 1). Our primary aims were (i) to assess the current (2019) status of those corals, (ii) to compare their condition with a similar prior survey (2011), and (iii) to attempt to extend that assessment to the earliest available observations (1998–2000). Drawing on those primary observations we then consider those results in the context of (iv) the conservation objectives set for the MPA, (v) the evolution of the Darwin Mounds CWC monitoring programme, and finally (vi) offer a prospectus for future monitoring efforts as may be applied to offshore VMEs and MPAs more widely. This work raises two themes likely to have broad relevance to offshore marine conservation and monitoring more generally – how best to deal with observation and monitoring schemes that have developed over time, and how best to embrace new autonomous field survey techniques and the potential for automated data generation through machine vision (Trotter et al., 2025).

2. Materials & methods

2.1. Study site

The Darwin Mounds Special Area of Conservation (SAC; Fig. 1), a class of UK MPA, was closed to all bottom-contact fisheries in August 2003, under an emergency measure of the EU Common Fisheries Policy (De Santo and Jones, 2007). This followed the initial discovery of CWCs on small seabed mounds, c. 5 m high and 75 m across, in 1998 (Bett, 2001) and subsequent evidence of extensive trawling damage detected in 2000 (Wheeler et al., 2005; Table S1). The status of the CWCs in the Darwin Mounds MPA was assessed in 2011 (Huvenne et al., 2016) and re-examined in 2019 (Table S1). A comparison of the CWCs observed

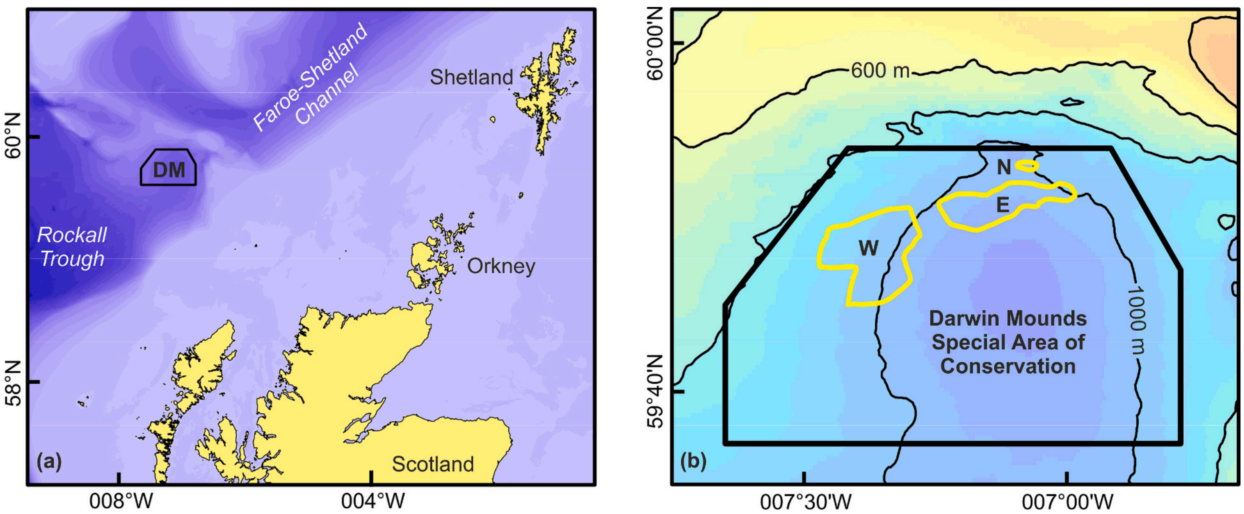

Fig. 1. General location of the Darwin Mounds marine protected area (DM). (b) Detail of the marine protected area indicating the general bathymetry and the locations of the northern (N), eastern (E), and western (W) mounds. Bathymetry derived from GEBCO Compilation Group (2024).

during these two surveys forms the basis of this study. The CWCs primarily occur in three areas of tailed mounds known as the eastern, western, and northern mounds (Fig. 1b; Masson et al., 2003; Huvenne et al., 2009). The tails referred to are acoustically distinct oval to elongate features that lead in a down-current direction from the mounds and appear to represent regions of seabed current scour (Masson et al., 2003; Huvenne et al., 2016). The extent of bottom-contact trawling is thought to have been substantially greater on the eastern mounds, based on fishing vessel activity and the visual and acoustic detection of seabed trawl marks (Davies et al., 2007).

2.2. *Field surveys*

Seafloor photographs were acquired during RRS *James Cook* cruise 060, May–June 2011 (Table S1) and RRS *Discovery* IV cruise 108, September–October 2019 (Table S1). In 2011, seven dives were conducted with a Saab SeaEye Lynx inspection-class remotely operated vehicle (ROV; Fig. S1c), three in the western mounds and four in the eastern mounds. The dive tracks were designed to connect 100-m transect segments, across randomly chosen mounds on randomly selected headings (Table S1). The 2019 survey was carried out using an off-bottom towed camera platform (HyBIS; Table S1; Fig. S1e) and attempted to broadly reproduce the 2011 dive tracks by reference to ultra-short baseline (USBL) navigation data available from both survey vehicles. The ROV photographs were shot every 30 s using a Kongsberg OE14–366 camera positioned at a low-oblique angle (c. 45°). The HyBIS photographs were shot every 10 s using a Super Scorpio (Sony Handycam HDR-CX560) camera positioned vertically (c. 90°). In both cases (a) image geolocation was provided by a Sonardyne USBL system, (b) image scale was estimated by reference to 10 cm separation parallel laser illumination points, and (c) the vehicle's speed over ground was c. 0.3 knots (0.15 ms^{-1}).

2.3. *Seabed image selection and annotation*

As the mounds represent the predominant location for CWCs in the area, only photographs from mound locations were included in this study. This was achieved by digitising mound outlines from sidescan sonar maps produced in 2011 (Table S1; Huvenne et al., 2016) and processing images falling within these mound outlines. The 2011 ROV images were cropped to a rectangular region of best illumination (Fig. S2b), filtered to minimum time interval separation of 60 s to limit potential overlap, resulting in 192 images for analysis, on average each representing 1.3 m^2 of seabed area. The 2019 HyBIS images were cropped to a circular region of best illumination (Fig. S2d), filtered to minimum horizontal distance separation of 3 m to limit potential overlap, resulting in 1107 images for analysis, on average each representing 4.1 m^2 of seabed area. The occurrence and maximum linear dimension of three dominant coral taxa were recorded, the colonial scleractinians *D. pertusum* and *M. oculata*, and an erect soft coral identified as Octocorallia stet. All the images were annotated using BIIGLE 2.0 (Table S1). Colonies partially inside the cropped image were retained for numerical density estimation, and, where possible, measured to their greatest dimension in the corresponding uncropped image.

2.4. *Estimation of seabed cover*

In addition to the HyBIS vehicle, RRS *Discovery* IV cruise 108 also deployed a second photographic system known as BioCam (Thornton et al., 2021), fitted to the autonomous underwater vehicle Autosub6000 (Table S1). This system acquired over 20,000 seafloor photographs, covering a seabed area of c. 29 ha in the western mounds (Table S1). Of those images, 96 were randomly selected for a detailed assessment of scleractinian colony morphometrics. These vertically oriented images had been colour, illumination, and optical distortion corrected, and scaled by reference to camera altitude. Each of these images was examined by 11 analysts who drew a polygon around the extent of any living scleractinian coral colony, i.e., *D. pertusum* and *M. oculata* were not distinguished and dead coral framework was discounted (full details are provided in Curtis et al., 2024). The polygon coordinates were then processed to estimate the maximum Feret diameter (*mFd*) and areal extent (*A*) of each live colony, where Feret diameter is the distance between any two parallel lines that are tangent to the polygon boundary. A simple linear regression of $\log_{10}(A\ \mathrm{m}^2)$ on $\log_{10}(mFd\ \mathrm{m})$ was implemented in Minitab 20.2 (Minitab LLC, 2021) and yielded the following equation, $\log_{10}(A\ \mathrm{m}^2) = -0.536 + 1.702\log_{10}(mFd\ \mathrm{m})$. The relationship was significant ($F_{[11316]} = 7721$, $p < .001$) and of good predictive power (adjusted $R^2 = 85\ \%$, predicted $R^2 = 85\ \%$; Fig. S3, in the Supplementary material). This relationship was used to estimate live colonial scleractinian areal extent and referenced to total imaged area to derive seabed cover (Table S1; Levin et al., 2019).

2.5. *Statistical treatment*

To account for variation in the sampled area within individual seafloor photographs, both within and between surveys, area-weighted mean numerical densities and seabed cover of CWC taxa were calculated together with corresponding 95 % confidence intervals. The latter were estimated by a bootstrapping procedure implemented in R (version 4.0.1; Table S1) using the 'boot' package, in all cases based on 10,000 randomisations and using the adjusted bootstrap percentile method (BCa; Table S1). Note that *D. pertusum* was not recorded in the 2011 assessment of the eastern mounds but was noted in off-mound photographs from the eastern mounds (Section 4.1). Consequently, to enable meaningful and conservative statistical comparisons, the corresponding dataset was 'spiked' with an additional single colony of *D. pertusum* in a seabed area equivalent to the average area of the annotated photographs (1.245 m^2) – results involving these spiked data are highlighted and flagged in the subsequent results tables and graphics. Direct statistical comparisons between mounds (eastern, western) and years (2011, 2019) were carried out by a randomisation test of the difference between two means, implemented in Minitab 20.2 (Minitab LLC, 2021) using 10,000 randomisations in each case.

2.6. *Adequacy of survey extent*

Given the substantial mismatches in the total number of images (73 to 731) and total seabed area observed (91 to 3057 m^2) across the four elements of our assessment (eastern vs. western, 2011 vs. 2019), the different camera orientations employed (low vs. high oblique) and the variance in the median seabed footprints of individual images annotated (1.1 to 3.7 m^2), we attempted to assess the adequacy of individual survey elements in terms of the number of images assessed and the total area examined in determining the numerical density and seabed cover of live CWCs. This was implemented by random resampling of the field data with replacement in the R environment (version 4.2.2; Table S1) using the base function 'sample' and 9999 resamples at each image count level, i.e., from 1 to the maximum number of images available for a given mound group and year of survey. The resampling results were summarised as median value and standardised to a fraction of the corresponding value for the full seafloor extent surveyed. To assess the minimum extent of seafloor survey required to achieve a reasonable estimate of live CWC colony numerical density or seabed cover an arbitrary 90 % level of the corresponding value from the full extent surveyed was adopted. Comparable approaches to the assessment of minimum survey requirements are examined by Benoist et al. (2019).

2.7. *Intercalibration with prior surveys (1998–2000)*

In the previous assessment of the status of CWCs on the Darwin Mounds, Huvenne et al. (2016) used a live coral cover statistic (LCCS).

To enable an approximate conversion of LCCS to seabed cover, mean and 95 % confidence interval end points of LCCS, as determined by Huvenne et al. (2016), and seabed cover, as determined in the present study, were scatter plotted for the eastern and western mounds from the 2011 survey. The relationship between these variables was estimated as a quadratic regression line fit, as implemented in Minitab 22.1 (Minitab LLC, 2021).

3. Results

3.1. Cold-water coral abundance

A total of 534 colonies of *D. pertusum*, 1195 colonies of *M. oculata*, and 219 colonies of Octocorallia stet. were recorded in the 1299 still images examined from the 2011 and 2019 surveys. *Madrepora oculata* dominated both fields in both years in terms of numerical density (Fig. 2b). *Desmophyllum pertusum*, *M. oculata*, and when assessed jointly as Scleractinia spp. (numerical density and seabed cover) exhibited the same temporal and spatial patterns. All comparisons between eastern and western mounds were statistically significantly different, and all comparisons within mound groups between years were not statistically significantly different (Table 1, Figs. 2 and 3). Temporal and spatial comparisons of Octocorallia stet. indicated statistically significantly differences in numerical density between 2011 and 2019 in the western mounds and between the eastern and western mounds in 2019 (Table 1, Fig. 2). There was no statistically significant difference in scleractinian density or seabed cover between years in either mound group. All comparisons of scleractinian density or seabed cover between mound groups within years were statistically significant, with values uniformly lower in the eastern mounds. Octocorallia stet. exhibited significant temporal variation in the western field (lower 2019) and significant spatial variation in 2019 (lower western mounds).

Table 1
Statistical comparisons of cold-water coral numerical density and seabed cover on the eastern (E) and western (W) mounds surveyed in 2011 and 2019, as *p*-values of differences in the mean values of Comparator-1 and Comparator-2, *p*-values <.05 are highlighted in bold.

Comparator 1	E2011	E2011	E2011	W2011	W2011	E2019
Comparator 2	W2011	E2019	W2019	E2019	W2019	W2019
Desmophyllum pertusum numerical density	**.012**[a]	.551[a]	**.014**[a]	**<.001**	.301	**<.001**
Madrepora oculata numerical density	**.002**	.975	**.004**	**<.001**	.560	**<.001**
Scleractinia spp. numerical density	**<.001**	.558	**.002**	**<.001**	.379	**<.001**
Scleractinia spp. seabed cover	**.001**	.474	**.003**	**<.001**	.310	**<.001**
Octocorallia stet. numerical density	.522	.714	.372	.394	**.007**	**.006**

[a] Includes spiked data (Section 2.5).

3.2. Cold-water coral colony size distributions

Given the methodological difference between surveys, i.e., the use of low-oblique images of median pixel resolution 0.55 mm px^{-1} in 2011 and high-oblique images of median pixel resolution 0.76 mm px^{-1} in

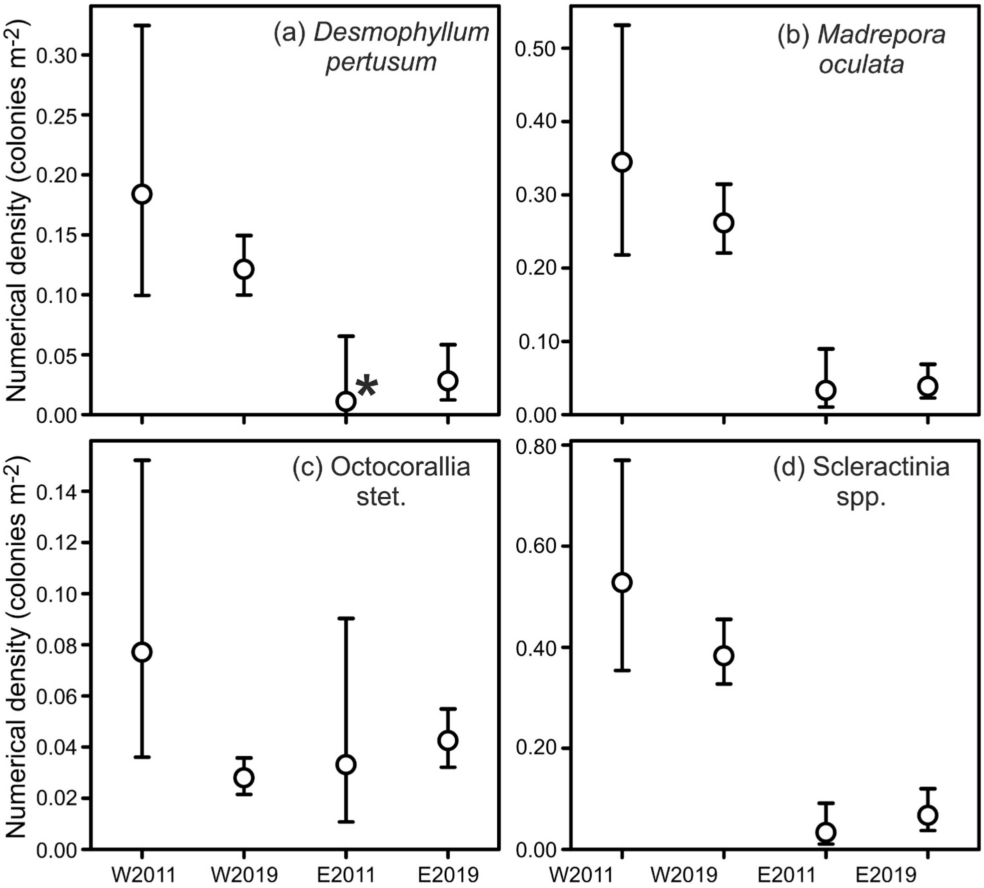

Fig. 2. Numerical density of cold-water coral taxa on the eastern (E) and western (W) mounds surveyed in 2011 and 2019, shown as area-weighted means with corresponding 95 % confidence intervals (* includes spiked data; Section 2.5).

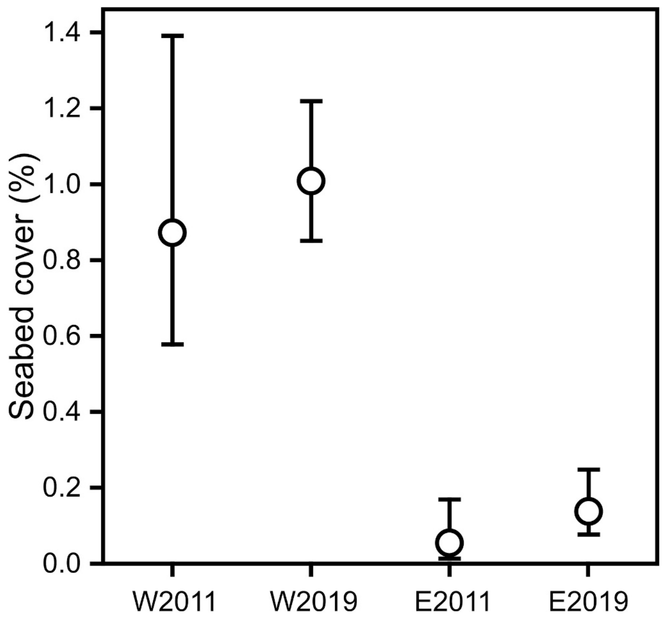

Fig. 3. Seabed cover of Scleractinia spp. (*Desmophyllum pertusum* and *Madrepora oculata*) in the eastern (E) and western (W) mounds as surveyed in 2011 and 2019, shown as area-weighted means with corresponding 95 % confidence intervals.

2019, potential apparent temporal variations in colony size structure must be viewed with some caution. A joint consideration of scleractinian numerical density and colony size suggested little if any change in time in either the eastern or western mounds and a broadly consistent difference between the mound groups (Fig. 4a). In the case of Octocorallia stet., accepting the rather limited observations in 2011, there was little indication of variation between mound groups or years (Fig. 4b). More robust comparisons were possible between mound groups from the 2019 survey data. For scleractinians, there was a very close correspondence in colony size structure (Fig. S5a), with no significant difference in median maximum dimension (Mood's median test, $\chi^2 = 2.83$, $p = .092$). Although a much greater range in colony size was recorded in the western (2.7–94.6 cm) than eastern (4.9–44.1 cm) mounds, this was likely driven by the much greater number of observations in the western ($n = 1168$) than eastern ($n = 98$) mounds. In the case of Octocorallia stet., there was a statistically significant difference in median dimension (Mood's median test, $\chi^2 = 15.51$, $p < .001$) between the eastern (9.6 cm) and western (14.0 cm) mounds. That difference was clearly driven by the markedly increased abundance of smaller specimens on the eastern mounds (Fig. S5b).

3.3. *Adequacy of survey extent*

The impact of number of images assessed on the apparent numerical density and seabed cover of live scleractinian colonies on Darwin Mounds is illustrated in Fig. S6. Using an arbitrary 90 % level of the corresponding value from the full extent surveyed to set the minimum survey extent required, that value was translated into the corresponding seafloor area and number of images required (Table S2). That level was readily obtained for the W2011, E2019, and W2019 surveys given their asymptotic responses. In the case of the E2011 survey, the sparse nature of the data, four positive observations in 73 images, resulted in a dampening oscillation response where we selected the first value of the final oscillation that remained within the bounds 90–110 %.

3.3.1. *Numerical density*

An adequate sample for numerical density was estimated to be 68 images for the eastern mounds in 2011 and 66 images in 2019. For the western mounds the 2011 estimate was 11 images and the 2019 estimate was 15 images. There was an apparent disparity in the estimated minimum extent of seafloor survey required between years within mound groups, 78 versus 246 m^2 for the western mounds, and 15 versus 56 m^2 for the eastern mounds. This appeared largely to reflect the difference in the areal coverage of individual photographs between the 2011 ROV operations, having an average image extent of 1.35 m^2, and the 2019 HyBIS operations, having an average image extent of 4.08 m^2. This c. ×3 factor of change in individual image extent between years approximately matched the corresponding factor of change in the estimated minimum extent of seafloor survey required. The consistency in the estimated minimum number of images required in each mound group was reflected by their comparable coefficients of variation in the colony count data, eastern mounds 419 % and 543 %, western mounds 212 % and 236 %, for the 2011 and 2019 surveys respectively.

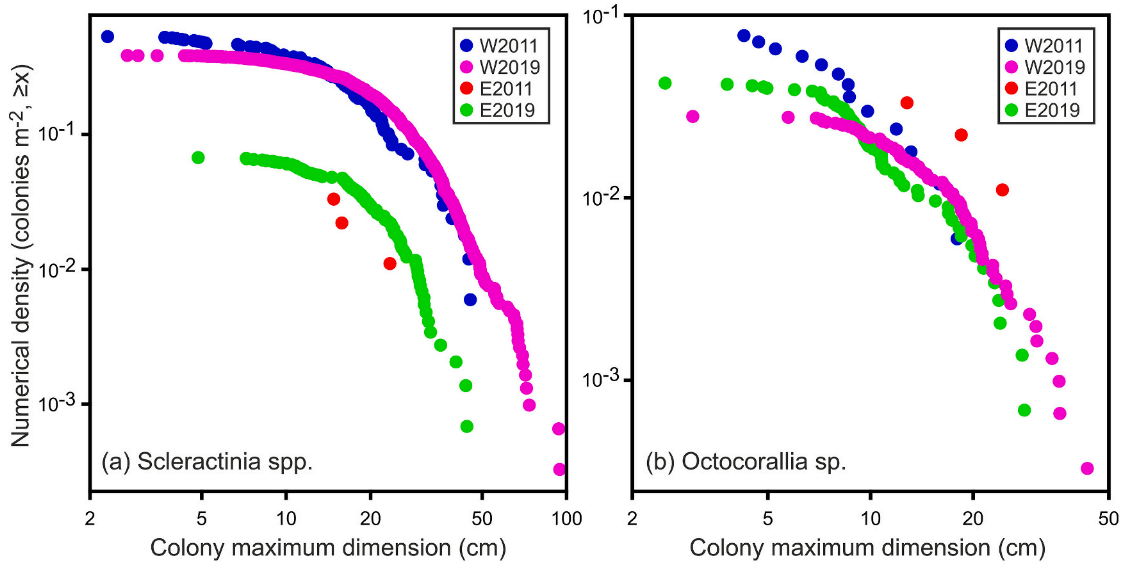

Fig. 4. Complementary cumulative colony size spectra of (a) Scleractinia spp. (*Desmophyllum pertusum* and *Madrepora oculata*) and (b) Octocorallia stet. in the eastern (E) and western (W) mounds surveyed in 2011 and 2019 (note log-log scaling).

3.3.2. *Seabed cover*

To provide an adequate assessment of seabed cover on the eastern mounds, a sample of 50 images was estimated for 2011 and 80 images for 2019. For the western mounds 17 images were deemed the minimum needed in 2011 and 20 images for 2019. A disparity in minimum extent of seafloor, 24 versus 83 m^2 for the western mounds, and 62 versus 312 m^2 for the eastern mounds was apparent, again primarily relating to the difference in the areal coverage of individual photographs between the ROV and HyBIS operations. The relative consistency in the estimated minimum number of images required in each field was again reflected in their coefficients of variation, eastern mounds 592 % and 544 %, western mounds 238 % and 259 %, for the 2011 and 2019 surveys respectively.

3.4. *Intercalibration with prior surveys (1998–2000)*

The apparent relationship between the live coral cover statistic (LCCS) employed by Huvenne et al. (2016) and live colonial scleractinian seabed cover as reported in the present study is illustrated in Fig. S4. The approximate conversion of LCCS to seabed cover was established as a quadratic polynomial line fit, seabed cover (%) = $-0.00671 + 0.01471$ LCCS(%) $+ 0.000124$ LCCS(%)^2.

4. Discussion

4.1. *Current status of CWCs on the Darwin Mounds*

Live colonies of *D. pertusum*, *M. oculata*, and Octocorallia stet. were frequently observed on both eastern and western mounds during the 2019 survey. While there were significant differences in the abundance and size structure of coral populations between mound groups, live and seemingly healthy corals were observed on most of the mounds surveyed. Sixteen years after bottom-contact trawling was banned a clear difference in colony density and seabed cover of scleractinians between the western (low prior impact) and the eastern (high prior impact) mounds, as observed in 2011 (Huvenne et al., 2016), remained evident. Accepting the limitations of our observations to date (Section 4.3), there appeared to be no signs that CWC communities on the eastern mounds had measurably recovered after 16-years of protection. Although we recorded no live colonies of *D. pertusum* on the eastern mounds in 2011 (Section 2.5), four live colonies were noted in off-mound areas of the eastern mounds. In addition, the 2019 survey of the eastern mounds recorded live colonies up to 44 cm in maximum dimension, i.e., too large to have been recruits since the 2011 survey (Strong et al., 2023).

Given the difference in camera geometry between the 2011 and 2019 surveys, detailed scrutiny of apparent temporal variation in colony size distributions were not warranted. Nevertheless, spatial comparisons within the more extensive 2019 dataset, i.e. having consistent camera geometry, were justified. In the case of scleractinians, the distributions of maximum colony dimensions were very similar between the eastern and western mounds (Fig. S5a). This might suggest that the original impact of bottom-contact trawling may have been broadly uniform with respect to colony size and that any potential subsequent recovery has similarly been broadly uniform with respect to colony size, i.e., that any recruitment, growth, and natural fragmentation has not impacted the overall colony size distribution. Between the 2011 and 2019 surveys the recruitment and growth of *D. pertusum* and its solitary congener *D. dianthus* (Esper, 1794) on artificial substrata was recorded in the eastern and western mounds by Strong et al. (2023). They recovered six *D. pertusum* colonies that ranged 1.5–9.5 cm in maximum dimension and comprised 4–36 polyps. In the present study, combining all observations of *D. pertusum*, 22.4 % of colonies had a maximum recorded dimension of ≤9.5 cm, suggesting that our approach had the potential to detect recruitment had it occurred. However, our assessments of the natural populations indicated no significant change in *D. pertusum*, *M. oculata*, or scleractinian numerical density, nor in scleractinian seabed cover (Table 1) or colony size structure within either the western or eastern mounds between 2011 and 2019.

In contrast, the Octocorallia stet. colony size distributions recorded from the 2019 survey suggested a substantive difference between the eastern and western mounds. There was also a statistically significant difference in the numerical density of Octocorallia stet. with a greater abundance on the eastern mounds (Table 1). That increased numerical density appeared to be entirely driven by smaller colonies (maximum dimension < 10 cm; Fig. S5b) potentially suggesting population growth. It is conceivable that the great reduction in colonial scleractinian corals on the eastern mounds, presumed to have resulted from bottom-contact trawling (Huvenne et al., 2016), had benefited the Octocorallia stet. by reducing competition for a potentially common resource, i.e., seston (Maier et al., 2023).

4.2. *Recovery potential of CWCs on the Darwin Mounds*

Our failure to detect measurable change in the eastern mounds scleractinian population was not unexpected. The few studies that have examined recovery in deep-sea communities report that it may take decades to centuries (Gollner et al., 2017). Seamount associated CWCs have been the focus of most of the existing studies, comparisons of surveys separated by 5 to 15 years tend to show no evidence of recovery (Williams et al., 2010). Longer-term studies and models suggest that recovery may require longer periods (30–40 years; Baco et al., 2020). Deep-water sponge communities have also been impacted by bottom-contact trawling (Vieira et al., 2020), and signs of disturbance may remain visible for 10–30+ years (Malecha and Heifetz, 2017). Similarly, studies of simulated or test mining of polymetallic nodule fields in the abyssal Pacific suggest detectable impacts to 40+ years (Jones et al., 2025), with signs of scientific trawling in the NE Atlantic abyss apparent to 30+ years (Table S1). For scleractinians, a simplistic assessment based on the minimum colony extension rate observed in the Darwin Mounds, *D. pertusum* c. 1 cm yr^{-1} (Strong et al., 2023), and the median (20 cm) and maximum (95 cm) colony dimensions we have recorded suggests that regrowth could require decades to a century. In controlled long-term aquarium studies at 12 °C, the linear growth rate of *D. pertusum* was estimated at 0.9 cm yr^{-1} and *M. oculata* at 0.5 cm yr^{-1}, with both species exhibiting order of magnitude variations between colonies, respectively 0.3–2.1 and 0.1–1.0 cm yr^{-1} (Orejas et al., 2011).

The time scales of recovery in deep-sea environments may vary with ecosystem type, the species involved, the nature of the impact, and the action of multiple stressors (Williams et al., 2010). The extent of the original trawling impact and the potentially slow growth rates of CWCs may not be the only causes of limited recovery on the Darwin Mounds. Other broadscale stressors such as global warming, ocean acidification (Portilho-Ramos et al., 2022), or the accumulation of plastic debris (Table S1) could also potentially limit recruitment and growth (Jones and Schmitz, 2009). Pham et al. (2014) document litter within the Darwin Mounds MPA using the images from the 2011 survey, and we noted the presence of macroplastic plastic litter associated with the CWCs during the 2019 survey (Fig, S1d). The relative connectivity of local CWC populations may also influence their viability (Strömberg and Larsson, 2017). Genetic analysis of *D. pertusum* from the Darwin Mounds indicated a greater prevalence of rare haplotypes and asexual reproduction than in other northeast Atlantic populations, potentially indicating a reduced connectivity (Le Goff-Vitry et al., 2004).

Multidecadal datasets for the deep-sea benthos are rare but have revealed unanticipated levels of temporal variability in ecological attributes (Levin, 2021). Consequently, many if not all studies of deep-sea impacts have an incomplete knowledge of their true baseline conditions and little if any knowledge of natural variation through time (Da Ros et al., 2019). In the present case, the assumption that recovery of CWCs on the eastern mounds would be represented by a return to their former state and broadly similar to the condition of the western mounds is a useful working hypothesis but is an assumption none-the-less. The environment, and consequently the ecology and biology, of the eastern and western mounds is not identical (Masson et al., 2003; Huvenne et al., 2009). On a geological timescale, the CWCs of the Darwin Mounds experienced their fastest growth 8800 years ago (Victorero et al., 2016), this may suggest that the contemporary environment is suboptimal for CWC growth. Given these various uncertainties, it is impossible to predict whether and how the CWCs of the Darwin Mounds might recover/develop into the future. A clearer picture may only emerge after decades of biological and environmental monitoring.

4.3. The evolution of CWC monitoring on the Darwin Mounds

The Darwin Mounds MPA was designated for the presence of biogenic reefs under the EU Habitats Directive 1992 as transposed into UK law by The Conservation of Offshore Marine Habitats and Species Regulations 2017. The formal conservation objectives for this MPA are to restore, subject to natural change, the (i) extent and distribution, (ii) structure and function, and (iii) supporting processes of the colonial scleractinian populations (Table S1). While no specific objectives are set for these three attributes, their stated scopes provide a useful envelope for the development of a comprehensive ecosystem monitoring programme (Table S1). The potential monitoring targets can be divided into three groups (a) structural biological, (b) functional biological, and (c) environmental features (Table 2). The present study and the prior study of Huvenne et al. (2016) focussed on structural biological properties that are tractable to remote sensing surveys, i.e., sidescan sonar and seabed photography. Although in situ determination of CWC rate processes is possible (Cathalot et al., 2015), to a greater or lesser degree functional biological characteristics are most likely to be inferred or estimated from structural condition (Greiffenhagen et al., 2024). Monitoring of broad-scale environmental conditions within the MPA was initiated in 2019 by means of a complete swathe bathymetric survey of the mound areas and the deployment of a long-term seabed mooring carrying hydrodynamic and oceanographic sensors, a sediment trap, and colonisation substrata (Table S1).

The monitoring of colonial scleractinian populations in the Darwin Mounds MPA has been an evolving process to date. The earliest observations were undertaken in an exploratory mode to establish the nature of the seabed features then only known from broadscale low frequency sidescan sonar mapping (Masson et al., 2003). Colonial scleractinians were first observed on the western mounds in 1998 (Bett, 2001; Table S1), on the eastern mounds in 1999 (Table S1), and on the northern mounds in 2000 (Table S1). In all three cases, these observations were made using a vertically mounted camera on an off-bottom towed camera platform (WASP; Table S1; Fig. S1a). Those early observations were combined and assessed by Huvenne et al. (2016) to establish the notional baseline conditions of colonial scleractinans on the eastern and northern (1999, 2000) and western mounds (1998). Video observations of *D. pertusum* and *M. oculata* on mounds were classified to 'live', 'dead', and 'rubble' and a live coral cover statistic (LCCS) derived as the relative frequency of live to all coral observations. These early observations were limited in extent because of the maximum video recording time (63 min) available on the WASP platform. This also restricted the number of mounds assessed, being six in the western and seven in the jointly assessed eastern and northern mounds. The later surveys, video and still imagery in 2011 and still imagery in 2019, assessed 18+ mounds in each instance.

During the 2011 surveys, observations were made using both video and digital still cameras mounted on a ROV in a low oblique orientation (Table S1). The video imagery was used by Huvenne et al. (2016) to derive LCCS values and the digital still images were used in the present study to derive colonial scleractinian seabed cover estimates. Combining those two datasets provided a means to approximately convert the LCCS values from the earlier observations (1998–2000) to seabed cover as employed in the present study (Section 3.4; Fig. 5). The presumed low trawling impact cases, eastern mounds in 1999–2000 and western mounds in 1998, 2011, and 2019, had a broadly consistent colonial scleractinian seabed cover of 1.0 %, while the presumed high trawling impact cases, eastern mounds in 2011 and 2019, had order of magnitude lower seabed cover values (0.1 %).

The impact of bottom-contact trawling on Darwin Mounds was first detected in 2000 using high frequency sidescan sonar mapping (Wheeler et al., 2005; Table S1). Subsequent analysis of vessel monitoring system (VMS) satellite tracking data indicated potential bottom-contact trawling within the Darwin Mounds MPA throughout 2002, that continued until August 2003, with the emergency closure of the area to bottom-contact fisheries coming in to force on 21 August 2003 (Davies et al., 2007). Note that the VMS data for August 2003 appeared to show extensive trawling around the eastern mounds. In the Rockall Trough, a trawl fishery exploiting spawning aggregations of Blue Ling, *Molva dypterygia*, developed in the early 1970s and increased through the 1980s, with further expansion as a multi-species trawl fishery through the 1990s with the landing of other deep-water species, particularly the Roundnose Grenadier, *Coryphaenoides rupestris* and the Black Scabbardfish, *Aphanopus carbo* (Gordon, 2001). Consequently, it is conceivable that seabed areas within the Darwin Mounds MPA were impacted

Table 2
Summary of potential monitoring targets for the Darwin Mounds marine protected area as identified from the formal conservation objectives of the marine protected area (Table S1).

Biological structure	Biological function	Environmental condition
Areal extent Spatial distribution Taxon composition Colony morphology/size Physical structure of coral framework Key and influential taxa Presence of characteristic communities	Nutrition Climate regulation Provision of recruits Provision of biochemical products	Hydrodynamic regime Physical topography Supporting habitat Water and sediment quality

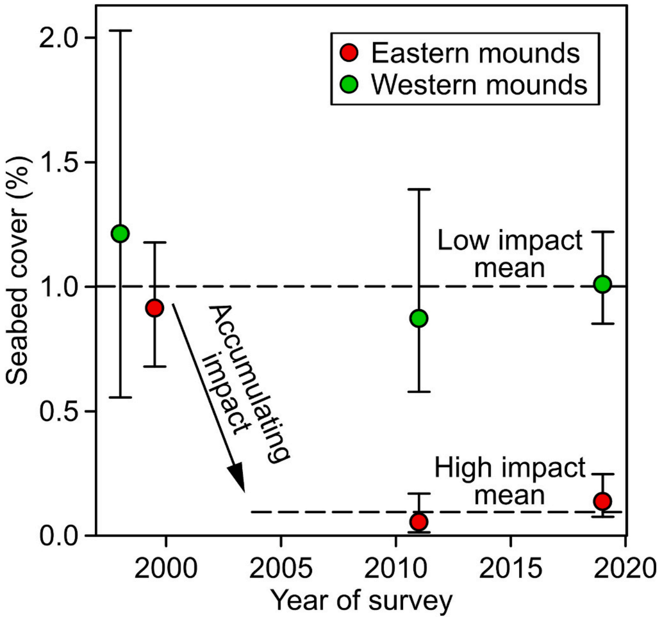

Fig. 5. Temporal variation in approximated and estimated means and 95 % confidence intervals of colonial scleractinian seabed cover on eastern (E) and western (W) mounds. Illustrated with low impact mean (1.00 %; E1999–2000, W1998, W2011, W2019) and high impact mean (0.09 %; E2010, E2019) levels, together with suggested impact trajectory from first detection in July 2000 to closure to bottom-contact trawling in August 2003.

by trawling prior to 2000.

The VMS data presented by Davies et al. (2007) indicated an average trawl fishing effort within the MPA of 3285 h mo^{-1} for January 2002 to August 2003. That figure reduced to an average of 169 h mo^{-1} in the last four months of 2003 post-closure, suggesting that the protected area was being respected. Using the online mapping and analysis tools available directly on the Global Fishing Watch website (https://globalfishingwatch.org/; Kroodsma et al., 2018) we obtained automatic identification system (AIS) satellite tracking data, c. 645 h of apparent trawl fishing effort were detected within the Darwin Mounds MPA in the period 1 January 2014 to 1 January 2024 corresponding to an average of 5 h mo^{-1}, again suggestive that the protected area was being respected. We can perhaps conclude that trawling impact to the CWCs of the Darwin Mounds began in or before the year 2000 and that since September 2003 the impact of bottom-contact fisheries has been reduced to near-zero. The latter point is additionally supported by an apparent lack of 'fresh' trawl marks in the sidescan sonar data acquired during the 2011 and 2019 surveys (Huvenne et al., 2016; Table S1).

Our ability to detect impact was clearly limited in the early studies (1998–2000) by the low number of mounds assessed (6 and 7) and the need to amalgamate data from the northern and eastern mounds in assessing the mounds on the eastern side of the MPA (Huvenne et al., 2016). There was nonetheless no indication of difference in the LCCS values for the eastern and northern mounds when assessed separately, with median and 95 % confidence intervals of respectively 40.1 % (25.0–66.7 %) and 46.9 % (33.6–53.6 %). Our ability to detect change was substantially improved in the 2011 surveys through the increased number of mounds assessed (≥18 mounds), that was increased further still in the 2019 surveys (≥30 mounds). Detection of change between the 2011 and 2019 surveys was complicated by the switch in observing system from low-oblique ROV to high-oblique HyBIS imagery with concomitant change in the typical seabed area of an image and the seabed pixel resolution achieved (Sections 2.6 and 3.2). However, our assessment of minimum survey extent requirement suggested consistency between years within mound groups, with 50–80 images required for numerical density or seabed cover in the eastern mounds, and 11–20 images required in the western mounds (Table S2). This difference between mound groups is driven by the approximately order of magnitude difference in numerical density and seabed cover between the two mound groups, i.e. the accuracy and precision of assessments will ultimately be determined by the number of colonies observed. This difference in precision between mound groups is similarly reflected in the coefficients of variation recorded for numerical density and seabed cover, eastern mounds 419–592 %, western mounds 212–259 %. The seabed footprint of images, both their areal extent and their shape (ROV 1.33 m^2 trapezoidal; HyBIS 3.74 m^2 circular), may have had some additional impact on precision but were unlikely to have influenced the accuracy of CWC abundance estimates.

4.4. Monitoring prospectus

As detailed by Levin (2021), time-series data on the deep-sea benthos are rare and limit the scientific community's ability to appropriately assess both human impacts and the recovery potential of vulnerable marine ecosystems in the deep sea. Consequently, there is a clear need to (i) maintain existing longitudinal studies, (ii) establish new monitoring programmes in a range of ecosystem types, and (iii) to refine such investigations to ensure they are both efficient and effective in detecting and understanding change in deep-sea ecosystems. The long-term study of colonial scleractinian populations within the Darwin Mounds MPA poses some site-specific challenges together with several difficulties that are common to other deep-water ecosystem monitoring programmes.

The spatial distribution of *D. pertusum* and *M. oculata* colonies imposes constraints on the development of an effective and efficient monitoring strategy given that they are preferentially but not exclusively encountered on mounds (Bett, 2001), and that on individual mounds they may occur predominantly on the peripheries (Thornton et al., 2021). The mounds themselves are distributed in four somewhat distinct groups (western, eastern, northern, southern; Huvenne et al., 2009) with research and survey efforts focussed primarily on the topographically distinct mounds with acoustic tails (Masson et al., 2003) of the eastern and western mounds, with similar mounds also present in the small northern field (Fig. 1). These tailed mounds are subcircular with dimensions in the range 50–100 m with an edge-to-edge nearest neighbour spacing of order 10–500 m within a given field. To deal with these spatial constraints, Huvenne et al. (2016) adopted a stratified random sampling survey design in the eastern and western mounds, selecting mounds at random, for each of which a 100 m long mound-crossing transect was established on a randomly selected heading. That methodology was effectively repeated in the 2019 survey as reported in the present study. As noted by Huvenne et al. (2016), the earlier observations (1998–2000) were broadly of a similar character, with mounds haphazardly selected, given the navigational uncertainty of both the mound positions and the survey platform at that time, and with mound-crossing direction being determined by the prevailing wind, sea, and current conditions.

For cable deployed seafloor observing systems, e.g. the WASP, ROV, and HyBIS vehicles (Fig. S1), a stratified random sampling scheme focussed on individual mounds as the primary observational units, seems likely to deliver the most effective and efficient monitoring approach. However, if the seabed survey were to be carried out by an autonomous underwater vehicle (AUV; Morris et al., 2014), independently of a surface vessel, then alternative designs may be possible or desirable (Benoist et al., 2019). The AUV Autosub6000 (Table S1) was employed to acquire high frequency sidescan sonar mapping of the eastern and western mounds in both 2011 and 2019 (Huvenne et al., 2016; Table S1). These mapping efforts provided direct information on conservation objective monitoring targets (i.e., spatial distribution, physical structure of coral framework, physical topography; Table 2) and on compliance with the ban on bottom-contact fisheries through the identification of trawl marks (Wheeler et al., 2005; Huvenne et al., 2016). In addition to the sidescan sonar system, Autosub6000 also carried an innovative seafloor imaging system during the 2019 survey (Section 2.4; BioCam; Table S1). That system, comprising a stereo pair of digital still cameras and a pair of microtopography line lasers, was successfully deployed in the western mounds returning a near-100 % coverage survey of 29 ha comprising over 20,000 images (Thornton et al., 2021; Curtis et al., 2024).

4.4.1. Future ship-based surveys

Our experiences to date would suggest that for cable deployed seafloor observing systems an off-bottom towed platform equipped with a vertically mounted digital still camera is likely to be the preferred option (e.g., HyBIS; Table S1). Operated in a similar manner to our 2019 survey, i.e., a stratified random sampling design, targeting multiple mounds (30+) in each field, with the vertical views of the seafloor offering the simplest means to assess colony size and seabed cover. One obvious lesson from our work to date is the level of survey effort that should be directed towards the low impact (western mounds) and high impact (eastern mounds) areas. As noted in Section 4.3, the order of magnitude lower colonial scleractinian abundance in the eastern mounds results in a substantially greater relative variability, coefficient of variation order 500 % on eastern mounds versus c. 200 % on western mounds. This would tend to suggest survey resources should be split 1/3 western and 2/3 eastern to improve the ability to detect change/recovery in the eastern mounds.

A key capability of ship-based surveys is the additional ability to recover physical samples and to deploy other ecosystem monitoring equipment. We noted in Section 4.2 the potential significance of assessing the genetic diversity of Darwin Mounds CWCs as a contribution to the biological function monitoring target of provision of recruits (Table 2). An attribute that can also be addressed with the deployment of recolonisation experiments (Strong et al., 2023) that may also indicate whether active restoration measures would be feasible within the Darwin Mounds MPA (Da Ros et al., 2019). Such recolonisation experiments have now been combined with hydrodynamic and oceanographic sensors on a long-term mooring designed to assess the environmental condition monitoring targets (Table 2; Section 4.3; Table S1).

4.4.2. *Future AUV-based surveys*

The switch from a low-tech solution, e.g., the use of the WASP vehicle in the 1998–2000 surveys, to the prospect of a fully autonomous underwater vehicle survey illustrates a common problem and tension in long-term monitoring programmes – to maintain an old, low efficiency, high cost, methodology to ensure consistency in the derived data or to adopt a contemporary, high efficiency, reduced cost approach and interpret the resultant data with due caution. Given the pressure for marine science to address net-zero carbon emissions targets (Turrell, 2019), the increased use of autonomous systems seems inevitable. Visual surveys of deep-water benthic ecosystems from AUVs are now a relatively well-established technique in ecological research (Durden et al., 2020), environmental impact assessment (Jones et al., 2019), and marine conservation (Benoist et al., 2019).

It would certainly be possible to implement an AUV-based stratified random sampling design, targeting multiple mounds (30+) in each field, as suggested for cable deployed seafloor observing systems (Section 4.4.1). However, that would be a cost-inefficient option because of having to dedicate a significant amount to surface vessel time to navigational aiding. Instead, it is now possible to conduct a fully autonomous survey of even distant offshore vulnerable marine ecosystems using a shore-launched AUV with no requirement for a surface support vessel (Supplementary Information). A fully autonomous mission, adopting a sparse lawnmower survey design (Table S1), expected to survey 30+ mounds in both the western and eastern mounds is within the current capabilities of the UK National Oceanography Centre's Autosub Long Range vehicles, having a range of 1000–2000 km and a multi-week endurance (Table S1). Consideration of this capability should, perhaps, now be incorporated in the development of ecosystem monitoring targets, e.g., with a bias towards those that can be addressed by autonomous survey and automated data generation from seafloor imagery via computer vision techniques (Trotter et al., 2025).

4.4.3. *Expansion to other taxa*

In the present contribution we have focussed on CWCs, particularly the colonial scleractinians *D. pertusum* and *M. oculata*, as their generation of biogenic reef structures is the primary basis of the protection afforded to the site. The conservation objectives monitoring targets for the marine protected area also refer to taxonomic composition, key and influential taxa, and characteristic communities (Table 2), suggesting the need for and value in expanding the assessment to other taxa. For example, we have included observations on the status of Octocorallia stet. that might suggest recruitment and population growth in the eastern mounds (Section 4.1). Similarly, the visual monitoring of other taxa may provide additional insights into ecosystem health and change. In addition to the CWCs, aggregations of xenophyophores (Xenophyophoroidea) associated with Darwin Mounds and their tails (Bett, 2001) are also regarded as a vulnerable marine ecosystem habitat (Table S1), that has already proved amenable to automated computer vision identification (Fig. 4 in Thornton et al., 2021). Other taxa of potential significance include the echiuran worms (Polychaeta, Echiuroidea), they are frequently observed and locally very abundant on western mounds (Kiriakoulakis et al., 2004), with up to 16 individuals recorded on a single image during our 2019 survey (4.3 ind m^{-2}). It is not immediately clear why they are very infrequently recorded on the eastern mounds; this may relate to the general change in environmental conditions between the fields (Section 4.2) or may reflect a close dependence of the echiurans on the presence of erect coral frameworks to baffle and draw down suspended organic matter (e.g., phytodetritus; Bett, 2001).

5. Conclusion

Live and seemingly healthy colonies of *D. pertusum* and *M. oculata* were frequently observed on both eastern and western mounds during the 2019 survey. However, we detected no signs that the previously impacted colonial scleractians on the eastern mounds had recovered in terms of numerical density, seabed cover, or colony size structure. Although recruitment and growth of *D. pertusum* has been recorded in the eastern and western mounds through experimental studies, it is not yet detectable in the field populations. Given the growth rates of *D. pertusum* and *M. oculata*, a multi-decadal recovery period should be expected. The 16-years of protection afforded to the Darwin Mounds area has been effective in eliminating the physical impacts from bottom contact trawling and in maintaining the status of the CWC populations through that period. However, achieving the conservation objective of restoring the biogenic reefs of the eastern mounds has not been advanced, such that suggestions for active restoration should potentially be considered. The means of monitoring offshore vulnerable marine ecosystems have rapidly advanced in the 26-years since the initial discovery of the Darwin Mounds, it seems clear that autonomous systems and computer vision techniques will play an increasingly important role into the future.

CRediT authorship contribution statement

Brian J. Bett: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Nils Piechaud:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **James A. Strong:** Writing – review & editing, Data curation. **Emma J. Curtis:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Veerle A.I. Huvenne:** Writing – review & editing, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.180118.

Data availability

Data will be made available on request.

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