Effectiveness of a deep-sea cold-water coral Marine Protected Area, following eight years of fisheries closure

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ABSTRACT

Pressure on deep-sea ecosystems continues to increase as anthropogenic activities move into ever deeper waters. To mitigate impacts on vulnerable habitats, various conservation measures exist, such as the designation of Marine Protected Areas (MPAs). So far, however, little evidence is available about their effectiveness. This paper presents a unique follow-up study assessing the status and recovery of a deep-sea fisheries closure and MPA at ~1000 m water depth in the NE Atlantic, eight years after designation. The Darwin Mounds cold-water coral ecosystem was discovered in 1998, and closed to all bottom contact fisheries, especially trawling, in 2003. Our repeat survey in 2011 used both high-resolution sidescan sonar data collected by Autonomous Underwater Vehicle (AUV) and video footage from a Remotely Operated Vehicle (ROV) to evaluate recovery. The results demonstrate that (1) protection was successful and fishing impact was largely avoided in the Western Darwin Mounds, which contained similar proportions of live cold-water coral occurrence in 2011 as observed in 1998–2000; however (2) the Eastern Darwin Mounds suffered severe damage pre-closure, and by 2011 showed no coral recolonisation and very little regrowth. These results are further evidence for the low resilience and slow recovery potential of deep-sea ecosystems, and underline once again the importance of the precautionary principle in deep-sea conservation.

1. Introduction

1.1. Context: cold-water corals, bottom trawling and the effectiveness of conservation measures

Over the last decade, increasing evidence of the environmental impacts of deep-water demersal fisheries, especially bottom trawling (e.g. Benn et al., 2010; Puig et al., 2012; Pusceddu et al., 2014), has resulted in the development of several national and international policies to protect deep-sea vulnerable marine ecosystems (VMEs). The process is largely driven by international agreements and directives, such as the United Nations General Assembly resolutions 61/105 and 64/72 on sustainable fisheries (UNGA, 2006, 2009), or the EC Habitats Directive, which as a result of the so-called 'Greenpeace judgement' was explicitly deemed applicable not only to coastal waters, but also to Member States' 200 nm Exclusive Economic Zones (De Santo, 2013). To implement the conservation policies, increasing numbers of fisheries closures, deep-water Marine Protected Areas (MPAs), MPA networks, and Special Areas of Conservation (SACs) are being designated, also in offshore waters. So far, however, limited evidence exists about their effectiveness, especially on the longer term. It remains a question how well deep-

sea ecosystems recover, and to what extent conservation strategies for shallow-water settings need to be adapted for deep-water application.

Cold-water corals, the azooxanthellate species of scleractinian, antipatharian, gorgonian and stylasterid coral that are not restricted to the photic zone, are important habitat-forming organisms in the deep sea (e.g. Rogers, 1999; Roberts et al., 2009). They are among the VMEs that require protection (UNGA, 2006; FAO, 2009), while reef habitats, including deep-water reefs, are protected under Annex I of the EC Habitats Directive. They create habitat complexity in otherwise (apparently) homogeneous, sedimented environments, resulting in an increased biodiversity (Henry and Roberts, 2007; Bongiorni et al., 2010). In addition, cold-water coral reefs may act as nursery grounds and adult habitat for commercial fish species (e.g. Costello et al., 2005; Söffker et al., 2011; Baillon et al., 2012).

However, deep-water bottom trawling is particularly destructive for cold-water coral reefs, which are relatively fragile and slow-growing (Hall-Spencer et al., 2002). The technique has been compared to forest clear-cutting (Watling and Norse, 1998), and the effects on cold-water corals have been reported from several locations (e.g. coral gardens along the Aleutian Islands (Shester and Ayers, 2005; Heifetz et al., 2009); *Oculina* reefs offshore Florida (Reed et al., 2007); stony coral habitat on seamounts offshore New Zealand and Australia (Williams et al., 2010)). Fosså et al. (2002) estimated that between 30 and 50% of *Lophelia* reefs offshore Norway were impacted by bottom trawling.

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In addition to the physical damage, the indirect effects include biodiversity loss, community changes (Althaus et al., 2009) and coral smothering by resuspended sediment (Larsson and Purser, 2011).

In several cases, these observations have triggered conservation measures, often based on temporary or permanent area closures. The restrictions may apply to either bottom trawling only, or to all bottom contact gear. Although in general these closures seem fairly well respected (e.g. Armstrong and van den Hove, 2008), and in some cases are even developed by the fishing industry itself (e.g. Benthic Protection Areas offshore New Zealand; Helson et al. (2010)), so far there is little information about recovery rates of the coral ecosystems. In the few cases where follow-up surveys have been carried out, trawling impacts seem to persist for over a decade, and recovery is slow (e.g. in the *Oculina* reefs offshore Florida, protected for 15 years (Reed et al., 2007); in the *Solenosmilia* reefs offshore Australia and New Zealand, protected for 5–10 years (Althaus et al., 2009; Williams et al., 2010); or based on modelling studies for a wide range of sponge and coral species around the Aleutian Islands, Alaska (Rooper et al., 2011)). In order to support further policy development and the continued sustainable management of the deep ocean, there is an urgent need for more information on the effectiveness of conservation measures in the deep sea, and the recovery rates of deep-sea habitats. So far no long-term studies (~10 years) have been published from the NE Atlantic, where *Lophelia pertusa* and *Madrepora oculata* are the main reef framework building species. This paper describes the situation in the Darwin Mounds, an area of small cold-water coral mounds protected from bottom trawling since 2003. A repeat survey in 2011 provided the unique opportunity to evaluate the status of the cold-water coral habitat after eight years of protection, and gave insight in the recovery potential of a deep-water VME.

1.2. Darwin Mounds

The Darwin Mounds are a field of small cold-water coral mounds, each up to 75 m across and 5 m high, found at about 1000 m water depth in the northern Rockall Trough, west of Scotland (Fig. 1). They were discovered in 1998 (Masson and Jacobs, 1999; Bett, 2001). Subsequent ground-truthing with high-resolution sidescan sonar and video confirmed the mounds were covered with cold-water corals, while recently recovered piston cores demonstrated that a dense framework of fossil coral fragments could also be found within the mounds (Victorero et al., 2015). The main framework-forming species are *Lophelia pertusa* L. and *Madrepora oculata* L. (Masson et al., 2003), occurring together with, among others, soft corals, sponges, tube-forming polychaetes, squat lobsters and echiuran worms (Kiriakoulakis et al., 2004; Howell et al., 2014). In the surrounding areas, and especially in the scoured 'tail' features (Masson et al., 2003), high numbers of the giant single-celled organism *Syringammina fragilissima* have been reported (Xenophyophores: Gooday and Tendal, 2000; Hughes and Gooday, 2004).

The high-resolution sidescan sonar and video data also illustrated heavy impacts from bottom trawling (Wheeler et al., 2005). These observations, together with the fact that at the time of discovery, the Darwin Mounds were the only example of *Lophelia* growing on sandy rather than rocky substrata, were the main drivers behind the development of a conservation policy. This started with an emergency closure under the EU Common Fisheries Policy (CFP) in August 2003, that was made permanent in March 2004 (De Santo and Jones, 2007). The Darwin Mounds became the first offshore MPA for the UK (De Santo, 2013), and were also designated as Special Area of Conservation under the EC Habitats Directive in December 2015 (JNCC, 2015). The implementation of these protection measures is being managed by the UK's Joint Nature Conservation Committee (JNCC) and Marine Scotland.

Since the initial discovery and surveys in 1998–2000, no further scientific surveys had been carried out in this area until May 2011, and the status of the mound province and the effect of the protection measures were unknown. A study by Davies et al. (2007) based on Vessel Monitoring System (VMS) data indicated an increase in vessel activity in the area just before the closure was put in place. This could have been
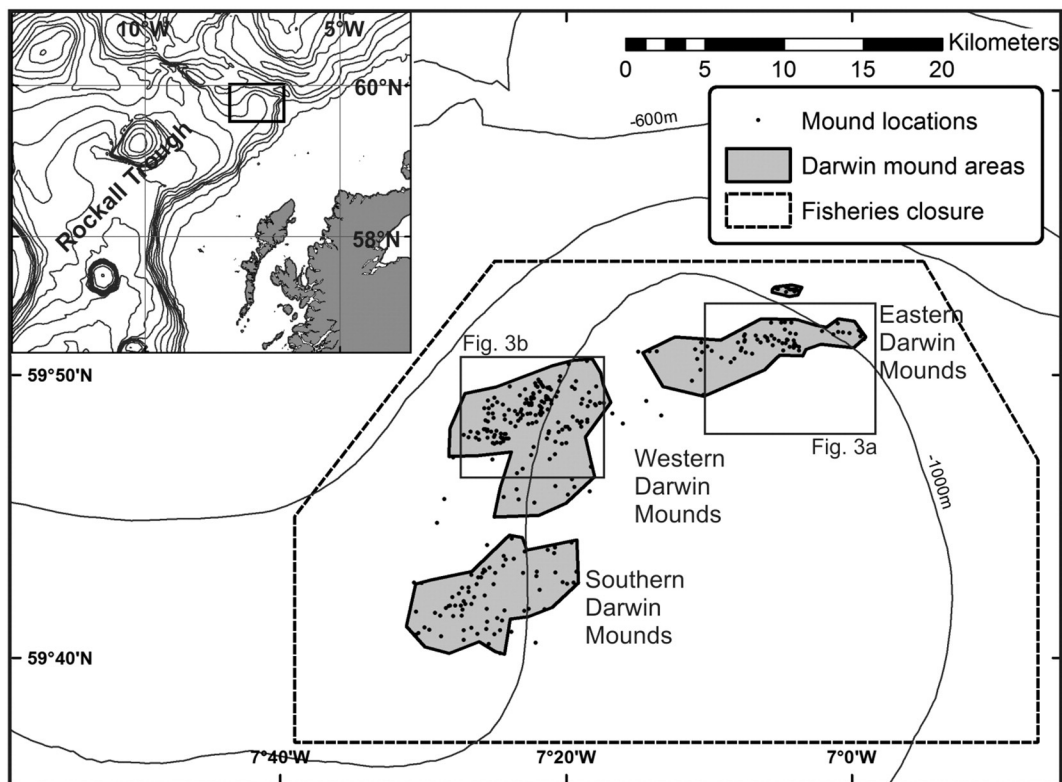

Fig. 1. Location map of the Darwin Mound fisheries closure and Marine Protected Area in the Northern Rockall Trough. Locations of all Darwin Mounds in the area (solid dots) were digitised from ancillary sidescan sonar data (after Huvenne et al., 2009a). Grey boxes outline the locations of Fig. 3.

part of the seasonal fishing effort in the general area, but may have had a detrimental effect on the ecosystem just prior to its protection. Hence a new survey was carried out in 2011, with the aim of comparing the situation with the conditions reported in 1998–2000 in terms of coral cover and trawling intensity.

2. Data collection and analyses

2.1. Datasets

The comparative exercise presented here is based on data collected during cruises RRS Charles Darwin 112, 119 and 123 in 1998–2000 (video data, Bett, 1999; Bett, 2007; Bett and Jacobs, 2007), RRS Discovery 248 in 2000 (high-resolution sidescan sonar data, Bett et al., 2001; Wheeler et al., 2005), and RRS James Cook 60 in 2011 (high-resolution sidescan data, video and stills imagery, Huvenne, 2011). During JC060, the Autonomous Underwater Vehicle (AUV) Autosub6000 (Huvenne et al., 2009a) was deployed to collect high-resolution geophysical data close to the seabed. Based on the 1998–2000 data, three main clusters of Darwin Mounds were identified (Huvenne et al., 2009b), of which the eastern and western clusters formed the main focus for the survey in 2011 (Fig. 1). All data and spatial information were combined within a Geographical Information System (GIS), using ArcGIS v10.

2.2. Sidescan sonar mapping

High-resolution sidescan sonar surveys were carried out in 2000 (100 and 410 kHz; Wheeler et al., 2005) by towing a Geo-Acoustics dual frequency system at ~25 to ~10 m above the seabed. For the repeat surveys, a dual frequency (120 and 410 kHz) EdgeTech FS2200 sidescan sonar was integrated into Autosub6000, and operated at ~15 m (for the 410 kHz) above the seabed. All high-resolution sidescan data were processed with the NOC in-house software package PRISM (Le Bas and Huvenne, 2009) to a pixel size of 0.5 m × 0.5 m (Geo-Acoustics) or 0.2 m × 0.2 m (EdgeTech). The AUV, using an inertial navigation system, a Doppler Velocity Log and a unique 'range-only' method for the determination of its initial position (Huvenne et al., 2009a), had a significantly higher positional accuracy than the towed GeoAcoustics system, whose navigation was based on lay-back calculations using the ship's position and the length of cable deployed. Hence the 2000 sidescan data were repositioned with regard to the 2011 data, using common features as tie-points in a georeferencing exercise within ArcGIS.

2.3. Video and photography of the seabed

Initial video data were collected in 1998–2000 with the WASP vehicle ('Wide-Angle Seafoor Photography') of the National Oceanography Centre (Bett et al., 2001). The system was towed behind the ship and had limited navigation accuracy, which was based on the ship's position. It was equipped with a downward-looking digital colour video camera. Transects covered ca. 3950 m in total in the Western Darwin Mounds, and 3580 m in the Eastern Darwin Mounds. The field of view was variable as a result of heave (vertical motions of the WASP vehicle); sections where seabed visibility was poor (due to turbidity or high altitude) were excluded from the analysis.

During the repeat survey in 2011, a commercial inspection-class ROV was used (SeaEye Lynx Remotely Operated Vehicle), equipped with a Kongsberg OE14-366 colour zoom and a Kongsberg OE14-208 digital stills camera, the latter carrying parallel lasers for scale (0.1 m apart). The ROV was positioned by USBL technology (Ultra Short Base Line). Four dives were carried out in the Eastern Darwin Mounds (total length: 6800 m), and three in the Western Darwin Mounds (6750 m). The field of view was kept constant as much as possible, with an average width of 1.5 m. Photographs were taken at 30 s intervals.

Given the large uncertainty in navigational positioning of the WASP vehicle (relative to the physical scale of individual mounds), it was impossible to definitively repeat the original 1998–2000 video transects. Instead, entirely new transects were chosen in 2011, within the boundary of the AUV sidescan sonar surveys. They consisted of a series of randomly positioned and oriented 100 m sections, connected into a number of transects which each could be completed within a 12-hour ROV dive. In effect, both in 1998–2000 and in 2011, a number of mounds were randomly surveyed, with randomisation formally achieved in the 2011 survey, and effectively achieved in the 1998–2000 surveys (as the uncertainty in location of both the mounds and the WASP vehicle exceeded the physical scale of a mound, while the camera tow direction was determined by variable wind, sea, and current conditions).

The video data were classified into six seabed facies, allowing calculation of the distance travelled over each. The ROV-based video data from 2011 are of sufficient quality to be analysed for epibenthic megafauna species composition (Howell et al., 2014), but this level of detail could not be obtained from the old 1998–2000 video data, hence the analysis was limited to facies. The facies represent the main seabed types with relevance for sidescan sonar interpretation (acoustic reflectivity) and for conservation issues. They include (Fig. 2): (1) sand, (2) sand with pebbles, (3) sand with xenophyophores, (4) widely scattered coral fragments, (5) (sediment clogged) coral rubble, (6) live *Lophelia* or *Madrepora*. Facies 6 was attributed as soon as some live polyps were visible. As a result of video quality and the constantly changing field of view for the 1998–2000 data (due to the vertical motions of the WASP vehicle), no attempt to quantify the percentage of live coral was made. Erect but dead coral framework was not encountered, except for a short section (11 m) in transect WASP55254, which was classified under facies 5.

2.4. Pre- vs. post-closure comparison

Trawl door scars could be clearly identified on 410 kHz sidescan sonar data, and were digitised on both the 2000 and 2011 maps. Where the marks of both trawl doors could be identified as a pair (based on an average distance of 100–150 m and on the net marks found in between), the event was counted as the passage of one trawl (Supp. Fig. 1). Trawl marks were quantified both in number and length per unit area of sidescan sonar data.

The CFP emergency closure, MPA and later SAC were specifically designed to protect the cold-water corals and their reef-forming potential. To evaluate the coral status before and after, the two video datasets were used to quantify the proportion of distance travelled over live coral versus the distance travelled over all framework coral (live and rubble, but not thinly scattered coral fragments). This approach compensates for variations in survey speed and for the different fractal dimension and resolution of the navigation in the 1998–2000 vs. 2011 data. The analysis was limited to video transects that were approximately straight, i.e. sections where the ROV was used to circle around features of interest were omitted.

On the basis that framework corals are largely restricted to 'mound' features (identifiable and defined by acoustic mapping), 'mounds' were chosen as a practical sampling unit, and the video transects were divided into segments, each containing one mound. Sampling units (video segments) were divided into four groups based on time (pre-closure vs. 2011 post-closure observations) and geographic location (Western Darwin Mounds vs. Eastern Darwin Mounds). The Eastern and Western Mounds are spatially distinct, distinct in terms of water depth (approx. 950 vs. 1050 m), and appear to be distinct in general character (e.g. Wheeler et al., 2008). We have limited our statistical analyses to one-way non-parametric assessments, to acknowledge the ad hoc unbalanced nature of the experimental design and the likely non-normality and heteroscedasticity of the test statistic. All statistical manipulations were carried out as standard features in the software package Minitab (16.2.4; Minitab Inc.).
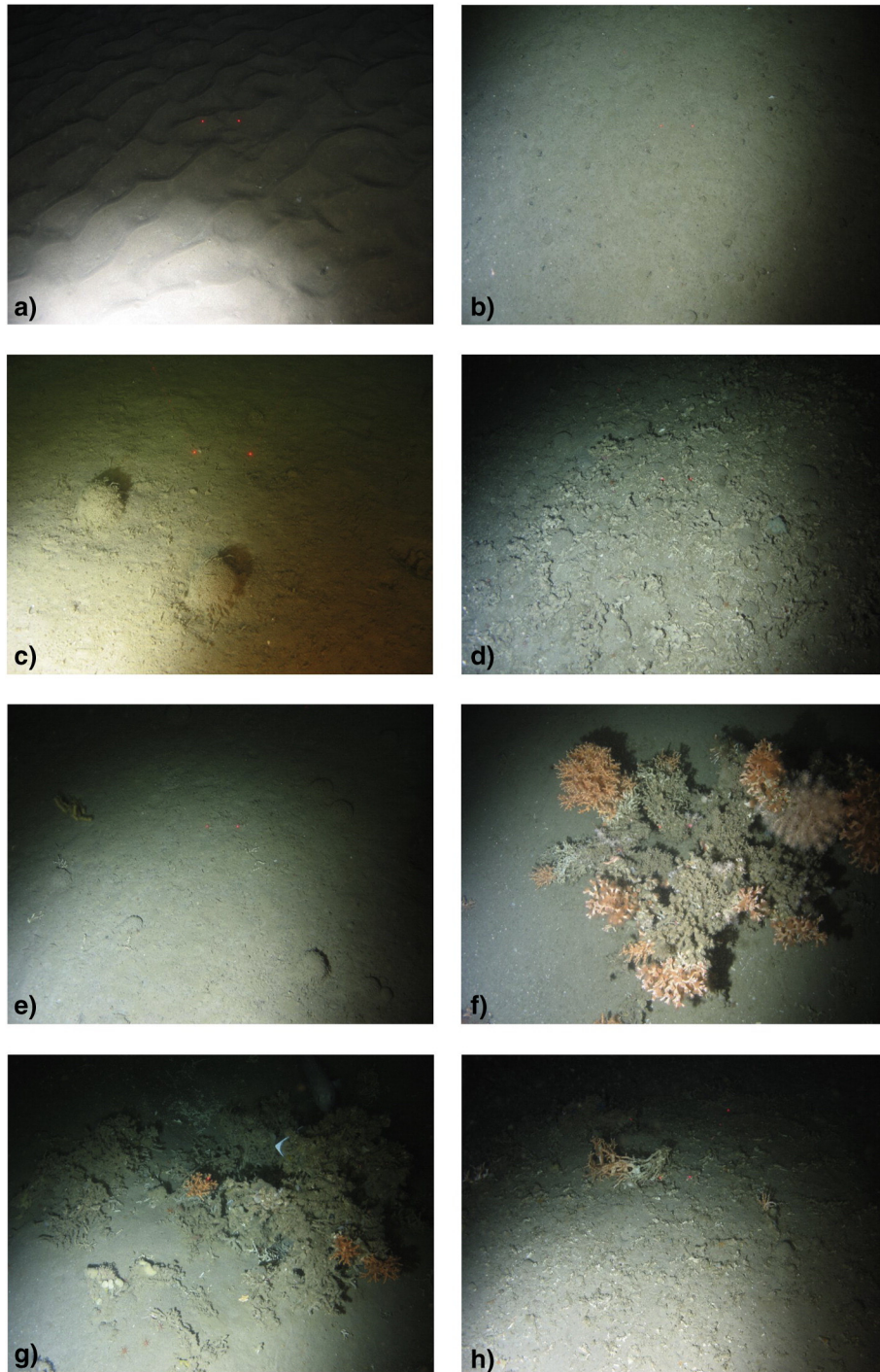
Fig. 2. Example photographs of the six seabed facies identified throughout the 1998–2000 and 2011 video data: (a) sand, (b) sand with pebbles, (c) sand with xenophyophores, (d) coral rubble, (e) scattered coral fragments, (f) live coral — as found in the Western Darwin Mounds, including both *Lophelia pertusa* and *Madrepora oculata*, (g) live coral — as found in the Eastern Darwin Mounds (note plastic litter between dead coral frameworks). In addition: (h) example of coral regrowth in the Eastern Darwin Mounds (coral colony that was disturbed but remained alive). Red laser marks are 0.1 m apart.

3. Results

3.1. Pre- and post-closure trawl mark density

The analysis of the high-resolution sidescan sonar data indicated that a significant reduction in trawling intensity took place between 2000 and 2011 (Fig. 3, Table 1). The reduction was particularly marked in the Eastern Darwin Mounds, the area most heavily impacted in 2000. None of the trawl marks identified in the 2000 dataset could be identified in the maps from 2011 (Fig. 3, Suppl. Fig. 1). The two pairs of scars

recorded in the 2011 data of the Western Darwin Mounds, however, suggest that some violation of the fisheries closure had occurred (Fig. 3).

The sidescan sonar signatures of the Eastern and Western areas were appreciably different. The Western Mounds were more sharply delineated against the more homogeneous, low-backscatter background, in which the scouring tails were clearly developed (Fig. 4a). In several cases the same individual coral colonies appeared to be present in both 1998–2000 and 2011 datasets, suggesting temporal stability of the mounds and their coral populations (Supp. Fig. 2). Areas with high backscatter intensity and heterogeneity were interpreted as live coral
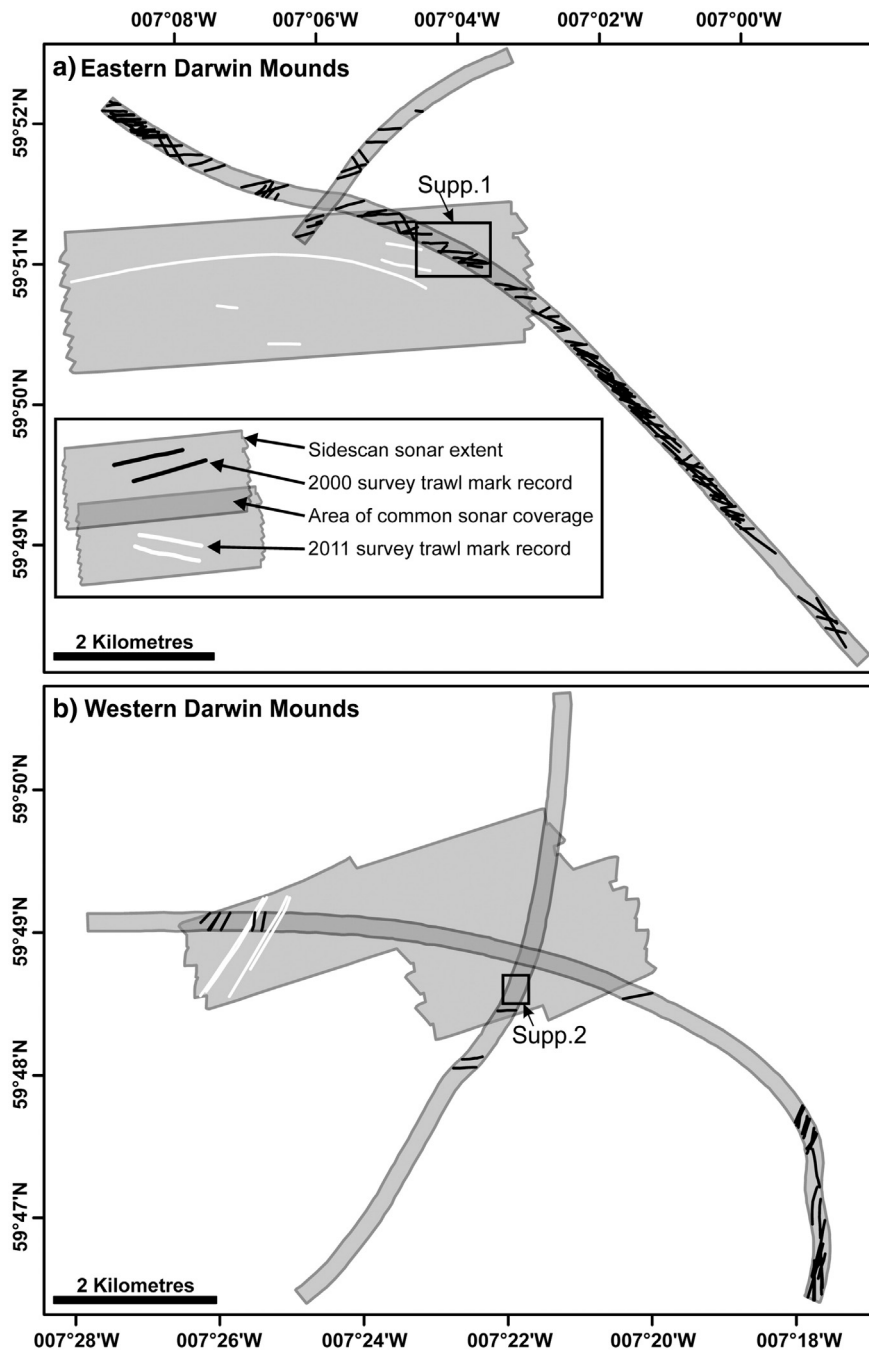
Fig. 3. Outlines of the pre- and post-closure sidescan sonar acoustic surveys and digitised trawl marks in the Eastern (a) and Western (b) Darwin Mound fields. Locations of Suppl. Figs. 1 and 2 are also indicated.

or erect coral framework (as per Hühnerbach et al. (2008)). They largely covered the same areas of the mounds in both 2000 and 2011 maps. This would indicate that additional trawling damage in the period 2000–2011 was limited, but also that no significant spatial expansion of live coral cover had occurred.

The Eastern Darwin Mounds were more elongated, with less well defined outlines (Fig. 4b). The background sediment had a higher backscatter strength, and its image texture was more grainy (Wheeler et al., 2008). This could be attributed to an overall difference in sediment composition, and therefore presumed current regime, between the two areas, with the Eastern Darwin Mounds characterised by stronger currents and coarser sediments (Masson et al., 2003; Huvenne et al., 2009b).

3.2. Mound character: the difference between the Eastern and Western Darwin Mounds

The facies classification of the video data suggested a clear difference between the Eastern and Western Darwin Mounds in terms of facies spatial distribution (Fig. 4). As observed on the sidescan sonar maps, mounds in the Western field were more clearly delineated, with sharper boundaries between coral framework and background sands. Most of the live coral observed seemed to occur on the edges of the mounds, while the centres were mainly covered in coral rubble (Supp. Fig. 2).

Xenophyophores were much more wide-spread in the Eastern Darwin Mound area than in the Western part, where they only occurred in the scoured tails. Again, these observations may be related to the

Table 1

Trawl mark occurrence assessed from sidescan sonar surveys conducted in the Eastern and Western Darwin Mounds. Data are presented for the total areas surveyed in 2000 and 2011 respectively, and separately for the seafloor area common to the surveys in both years. An apparent reduction in trawl mark observations is calculated based on the combined assessment of both fields.

	Abundance (marks/km^2)				Density (m/km^2)			
	Total survey		Common area		Total survey		Common area	
	2000	2011	2000	2011	2000	2011	2000	2011
Eastern field	19	0.4	21.1	0	5994	543	5789	0
Western field	3.8	0.2	2.2	1.1	1277	294	511	300
Both fields	10.3	0.3	7.2	0.8	3294	426	1899	221
Apparent reduction 2000–2011	97%		89%		87%		88%	

difference in current regime and resulting sediment composition between the two areas.

3.3. Pre- and post-closure live coral occurrence

In the 2011 video data of the Eastern Mounds, minimal live coral was observed. With the exception of a few small live colonies (Fig. 2g), the mounds were covered with coral rubble and dead coral fragments. In marked contrast, substantial live coral occurrence, including larger colonies (up to 50 cm tall), was recorded in the Western Darwin Mounds (Fig. 2f), reaching proportions comparable to those recorded in the 1998–2000 dataset for both areas. This impression was supported by our statistical analysis (Fig. 5). A global test of variation on the parameter 'proportion of live coral', was carried out using Mood's median test (as described in Siegel and Castellan, 1988). The result indicated a highly significant difference (p < 0.0005; $\chi^2 = 31.22$) in the proportion of live coral cover between the four groups tested (pre- and post-closure, both in the Eastern and Western Mounds). To identify which of the four groups were significantly different, pair-wise comparisons were carried out using the Mann-Whitney test (Siegel and Castellan, 1988). This provided highly significant differences (p < 0.0001) between the
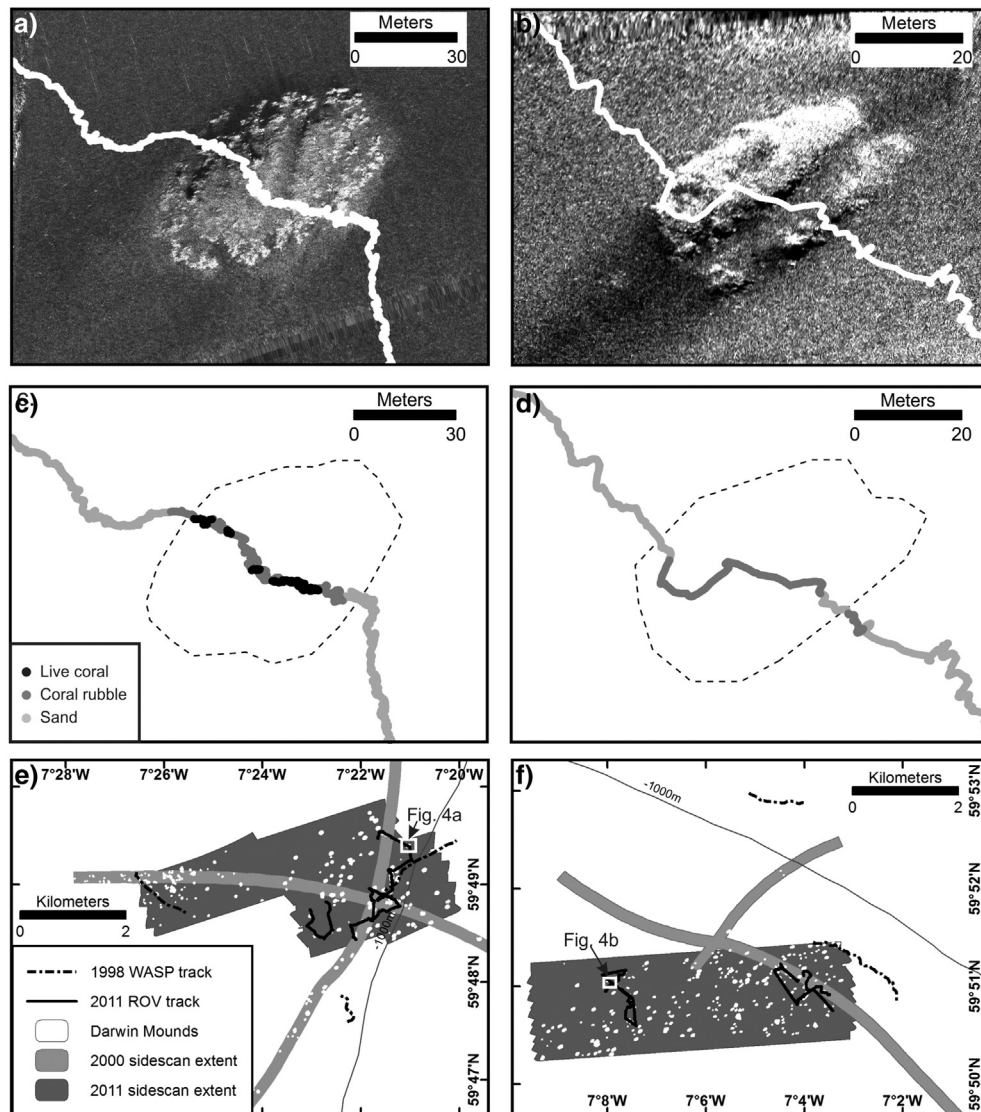

Fig. 4. Seabed facies identification in relation to sidescan sonar interpretation. (a) Example sidescan sonar image of a Western Darwin Mound, with indication of ROV video transect. Dark tones represent low backscatter (soft substrata), lighter tones correspond to high backscatter (hard materials). Mound location is indicated in panel (e); (b) example sidescan sonar image of an Eastern Darwin Mound, with indication of ROV video transect. Mound location is indicated in panel (f); (c) facies interpretation of ROV video transect presented in (a); (d) facies interpretation of ROV video transect presented in (b); (e) sidescan sonar interpretation of the Western Darwin Mound field, illustrating the outline of identified mounds and the position of the 1998–2000 WASP and the 2011 ROV video tracks; (f) sidescan sonar interpretation of the Eastern Darwin Mound field, illustrating the outline of identified mounds and the position of the 1998–2000 and the 2011 video tracks.
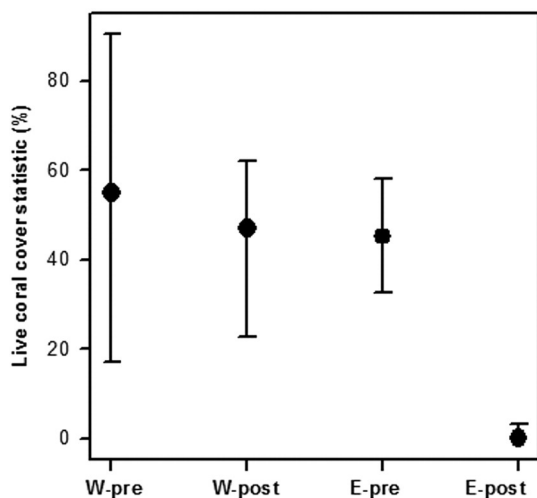
Fig. 5. Estimated median (pseudomedian) and approximate 95% confidence interval of the proportion live coral cover statistic. The confidence intervals (level achieved: 94.1–95.1%) were calculated using a Wilcoxon signed rank method (Bauer, 1972). All pair-wise comparisons (Mann-Whitney test; Siegel and Castellan, 1988) with E-post were significant (p < 0.001), all other pairs were non-significant (p > 0.05). (W, Western Darwin Mounds; E, Eastern Darwin Mounds; pre, 1998–2000 dataset; post, 2011 dataset.

Eastern Darwin Mounds post-closure group (median = 0%) and each of the other groups (medians ranging from 45.2 to 55.0%), but no significant differences in all other comparisons (Fig. 5). A simple, conservative, Bonferroni correction would suggest that the significant results in these multiple comparisons could be relied upon at the 0.1% level (i.e. p < 0.001; see e.g. Rice, 1989).

In addition, the 2011 video data provided no evidence of coral recolonisation from larval settlement, and only a few cases of potential coral regrowth (i.e. where corals had been disturbed, but continued to grow, Fig. 2h).

4. Discussion

4.1. Compliance

The strong reduction in trawl mark density from 2000 to 2011 indicates that in general, the fishing community complies with the closure and the MPA designation. Similar compliance has been described from other areas, e.g. Norway (Armstrong and van den Hove, 2008). However, such positive results are not always achieved (e.g. offshore Florida (Reed et al., 2007)). Deep-water protected areas are difficult to enforce because of their remoteness and extent (Pala, 2013). Even in the Darwin Mounds, some violation of the closure did occur, as illustrated by the two pairs of trawl marks found in the 2011 data. Unfortunately, no VMS data were available for this study, which makes it difficult to determine how old those marks might be, and how often potential violations might have occurred. Information on the longevity of trawl scars in different sedimentary settings is scarce. Apart from bioturbation and sedimentation, sediment transport by bottom currents is the main process causing trawl marks to fade over time (Schwinghamer et al., 1998). Studies of sidescan sonar data in shallow-water environments have shown that most trawl scars fade after 6 to 18 months, with greater longevity in finer-grained sediments and low-energy environments (Schwinghamer et al., 1998; Tuck et al., 1998). Records of a benthic storm in the Eastern Darwin Mounds illustrated that currents of 30 cm s^{-1} or more, capable of completely remodelling the sandy bedform field, are not uncommon in the area (Masson et al., 2003; Huvenne et al., 2009b). While deep-water trawling gear may be heavier than shallow-water otter trawls, creating deeper trawl marks that may need more time to fade, we suspect that the trawl marks observed in the 2011 dataset were unlikely to be older than 1–2 years. The comparison

of high-resolution sidescan sonar records from 2000 and 2011 demonstrated that trawl marks were at least undetectable after 11 years, using these acoustic techniques.

4.2. Proportion of live coral

Despite the overall difference between the Eastern and Western Darwin Mound fields in terms of environmental characteristics (sediment grain size, current regime), the video analysis showed that the proportion of live coral was not significantly different between the two areas in 1998–2000. An estimated median of 45–55% could be considered as the 'normal' proportion of live coral occurrence for an average Darwin mound. This is comparable to area calculations reported by Mortensen et al. (1995) for Norwegian *Lophelia* reefs of similar diameter. This proportion was still evident in the Western Darwin Mounds in 2011, suggesting this area largely escaped trawling impacts post-2000. The situation in the Eastern area, however, had completely changed. Based on the VMS data published by Davies et al. (2007), and our own observations discussed above, we can assume that the initial fisheries closure and later MPA designation have been relatively well respected. Hence, it appears that between the initial video surveys in 1998–2000 and the emergency closure of the area in 2003, the Eastern Darwin Mounds were heavily impacted, resulting in a severe reduction in the amount of live coral occurrence. The VMS data for the months leading up to the closure (Davies et al., 2007) show that the Eastern Darwin Mounds were much more heavily trawled than the Western part. This is also reflected in the 2000 sidescan sonar dataset, where trawl mark density is much higher in the Eastern Darwin Mounds (Table 1). Given this latter observation, it is remarkable that the proportion of live coral occurrence in the 1998–2000 video data is similar in both areas, and as high as ~45–50%. However, some of the later coral loss may have been a result of delayed mortality following the physical disturbance and destruction of erect coral framework caused by the trawling. Studies in shallow-water reefs have shown that coral mortality can remain high or may even increase for an extended period of time (~years) after an event of mechanical damage (e.g. hurricane or cyclone, Knowlton et al., 1981; Guillemot et al., 2010). The fragmentation, to which especially branching coral types are susceptible, decreases the three-dimensionality of the reef, making the remaining coral fragments more sensitive to sediment smothering (Larsson and Purser, 2011), or predator attacks (Becker et al., 2009). It also puts the coral polyps under stress, causing vulnerability with regard to diseases. In high-energy environments, small coral fragments may experience higher levels of abrasion, or even mobility. This phenomenon has not yet been studied (in situ) in cold-water coral reefs, but a similar effect may have contributed to the very low amount of live coral in the Eastern Darwin Mounds as observed in 2011.

4.3. Low resilience and recovery potential

Although the fisheries closure and MPA were protecting the area from further mechanical impacts, our observations in 2011 seem to indicate that recovery was minimal in the Eastern Darwin Mounds. So far there were no signs of coral recolonisation, and regrowth was very limited. This is not entirely surprising, slow recovery of cold-water coral ecosystems has been reported from other locations, e.g. seamounts offshore of Tasmania and New Zealand (Althaus et al., 2009; Williams et al., 2010), and even shallow-water coral and sponge habitats may require more than 15 years to recover from trawling impacts (Sainsbury et al., 1997). Based on numerical modelling, Rooper et al. (2011) estimate that after a 67% reduction in cold-water coral biomass through trawling, 34 years would be required for the ecosystem around the Aleutian Islands to recover to ca 80% of its original biomass. Colonisation of suitable substrata by *Lophelia* larvae does happen in the wider Rockall area, and the resulting corals occasionally reach growth rates comparable to those of tropical species. Gass and Roberts (2006) reported coral

colonisation on North Sea oil rigs with growth rates of 26 ± 5 mm yr^{-1}, while a benthic lander in the Logachev mound province (SW Rockall Trough) was covered in small polyps (<2 mm) after a one-year deployment (de Haas et al., 2002). However, such (re)colonisation does not appear to have taken place in the Eastern Darwin Mounds, and cold-water corals are more often than not reported as slow-growing (Roberts et al., 2009). It is also conceivable that, at the present day, the Darwin Mounds may be located near the limits of the environmental niche for *Lophelia* and *Madrepora*. The limited genetic variation reported by Le Goff-Vitry et al. (2004), compared to nine other sites along the European Atlantic Margin, indicated that most of the corals at the Darwin Mounds were clones. The authors suggested that this might reflect low recruitment of sexually produced larvae and local colonisation via asexual reproduction. In addition, Waller and Tyler (2005) noted *Lophelia* specimens from the Darwin Mounds were entirely non-reproductive, consistent with the suggested low production of larvae mentioned above. In contrast, radiocarbon dating of coral fragments from piston cores collected in 2011 in the Western Darwin Mounds demonstrated that cold-water coral growth was intense between 10,000 and 8500 years ago, although it reduced between 8500 and 4000 years ago, and was minimal thereafter (Victorero et al., 2015). Recent predictive habitat modelling that incorporated Darwin Mounds coral occurrence data, predicted a low likelihood of *Lophelia* presence in the area (Ross and Howell, 2013), suggesting that the present-day environmental conditions in the Darwin Mounds area might be considered unusual in supporting a *Lophelia* population. This may also play a part in the observed slow recovery of the Eastern Darwin Mounds, and may add to the vulnerability of the cold-water coral habitat in the area.

4.4. Deep-water MPA designation: the importance of the precautionary principle

Although the coral growths on the Darwin Mounds are no longer the only example world-wide of scleractinian coral reefs set within the mobile sediments of a sandy contourite – the Moira Mounds in the Porcupine Seabight being another example (Foubert et al., 2011) – they remain a rare example of their type, potentially hosting a benthic community distinct from other framework coral growths in the region, and controlled by a specific set of benthic processes (Henry and Roberts, 2007; Howell et al., 2014). As described above, the low fecundity, high susceptibility to fragmentation, associated delayed mortality, and the present-day environmental conditions which may be sub-optimal for the framework-building scleractinians *Lophelia pertusa* and *Madrepora oculata*, give this habitat a very low resilience, and make it particularly vulnerable to trawling impacts.

The Darwin Mounds illustrate the importance of the precautionary principle in marine conservation, especially for deep-water ecosystems. Following the initial discovery, a unique set of political circumstances caused the area to be protected within a few years (revision of the EU Common Fisheries Policy, the Greenpeace judgement, the Greenpeace and WWF campaigns on deep-sea conservation; De Santo, 2013). At that time, details of ecosystem functioning and benthic processes in the area were not known. Insights into the vulnerability of this habitat and its low resilience only came to light at a later stage. However, as a result of the relatively swift procedure, even if severe impacts to the Eastern Darwin Mounds could not be avoided, the Western Darwin Mounds escaped major trawling damage, and seem to have maintained a stable live coral population. We cannot predict how the Eastern Darwin Mounds will now evolve, if recovery will be possible, or which benthic communities will establish in the process. The current status of the scleractinians *Lophelia* and *Madrepora* of the Eastern Mounds does not look positive, but the reefs formed by the coral rubble still form an important hard-substratum habitat in a setting characterised by mobile sands. In addition, the high abundance of xenophyophores in the area forms a further incentive for protection. Increasingly, xenophyophores such as *Syringammina* are also recognised as autigenic ecosystem engineers, creating habitat structure for meio- and macrofauna, increasing deep-sea biological heterogeneity, faunal density and species richness (Levin and Gooday, 1992; Ashford et al., 2014). They are also listed as VME indicator species (NEAFC, 2014).

Taking the concept of deep-sea conservation one step further, Van Dover et al. (2014) recently opened the debate on the feasibility of deep-sea ecological restoration, using the Darwin Mounds as a possible example. Ecological restoration, defined as the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed, is much more common in the terrestrial environment than in the deep sea. Evaluating socio-economic, ecological and technological considerations, Van Dover et al. (2014) concluded that the overall balance would be moderately in favour of a (limited) restoration project in the Darwin Mounds, with estimated cost of US$4.8 million. Given our limited in situ observations of scleractinian regrowth or recolonisation in the Eastern Darwin Mounds, the outcome of such an experiment may be uncertain. Limiting the damage in the first place, by correctly applying the precautionary principle, may be the more sustainable and economical approach, as demonstrated by the success of the closure in the Western Darwin Mounds. A recent study by Aanesen et al. (2015) has shown that there is a willingness among the wider public to pay for such protection measures. The possibility that cold-water corals play an important role as fish habitat was quoted as the single most important reason for participants in the study to support protection measures.

By closing areas for fishing and other direct human impacts, effectively 'control' areas are created against which the ecosystem development of non-MPA areas can be compared in the future (Ballantine, 2014). VMS data, if available, can be used to monitor fishing intensity both inside (checking on compliance) and outside (evaluating fishing effort) the MPAs. The influence of fishing can then be tested and quantified in comparative studies of the benthic environment, based on a similar approach as illustrated here.

Although slowly gaining momentum, the designation of MPA networks in deep water is still in its infancy. As a result, very limited information is available about the effectiveness of conservation measures, and the potential recovery of deep-sea ecosystems. Deep-water habitats are difficult to access, while potential conservation areas are often much more extensive than shallow-water MPAs, making environmental surveys expensive and limited. Often no adequate pre-impact data are available, limiting the possibilities for a quantitative assessment of the status of the benthic community before and after closure. However, as our study has shown, in the case of habitats created by (single) ecosystem engineering species, a first-level assessment can be made, and may provide valuable information. In the longer term, there is a need for continued monitoring of MPAs, including those designated in deeper waters. It is likely that autonomous and robotic underwater systems, as used in this study, will play an important role in this respect (Wynn et al., 2014; Morris et al., 2014).

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