



Recovery of deep-water megafaunal assemblages from hydrocarbon drilling disturbance in the Faroe–Shetland Channel

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ABSTRACT: Recovery of megabenthic assemblages from physical disturbance at the Laggan deep-water hydrocarbon drilling site in the Faroe–Shetland Channel was assessed using remotely operated vehicle quantitative video survey. Twelve undisturbed control sites and 2 well sites (A and C, disturbed 3 and 10 yr prior to this work, respectively) were analysed and compared with a previous survey immediately following disturbance at A. The megabenthic epifauna at Laggan was dominated by sponges (69.6% total fauna) represented by 20 taxa. Cnidarians (12.8%; 9 taxa) and echinoderms (7.1%; 11 taxa) were also common. Diversity was generally high and typical for the cold waters of the Faroe–Shetland Channel. Two distinct assemblages were found: one in the deeper area of the study site (also incorporating Site C), and one in the other areas (incorporating Site A). Motile faunal densities and richness were significantly elevated immediately after drilling in an area with intermediate disturbance, presumably attracted to available carcasses of organisms killed by drilling disturbance. After 3 and 10 yr, densities of motile organisms were less variable with distance, except very close to drilling where densities and richness were still reduced. Sessile faunal densities and richness increased significantly with increasing distance from drilling in all years, although both metrics were significantly higher close to drilling after 3 and 10 yr when compared to immediately after drilling. These data suggest partial megabenthic recovery between 3 and 10 yr post-disturbance. Despite this, in the area remaining completely covered by drill cuttings there were few megafauna observed even after 10 yr.

KEY WORDS: Recovery · Megafauna · Disturbance · Benthic · Deep-sea · Hydrocarbon drilling · Remotely operated vehicle video · ROV video

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INTRODUCTION

Disturbance from typical best-practice hydrocarbon drilling generally causes sedimentation and some chemical stress to benthic communities, rarely measurable beyond 250 m of the drilled area (Jones et al. 2007b, Santos et al. 2009). With increasing drilling activity in deeper waters (Radler 2006), and in environmentally sensitive areas, disturbance from drilling is an increasing threat to benthic ecosystems across the globe. The UK continental shelf and slope

has around 0.3% of the world's proven hydrocarbon reserves (Radler 2006), much of which is in the Faroe–Shetland Channel. With studies highlighting the effects of declining biodiversity on ecosystem functioning in the deep sea (Danovaro et al. 2008), it is important to understand the losses being experienced and the potential for recovery.

The megabenthos play a key role in the functioning of deep-sea ecosystems (Smith & Hamilton 1983), and they are important to include in environmental studies. Megabenthic organisms are difficult to study

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using conventional sampling methods because of their low density. In addition, in rocky areas, such as the Faroe–Shetland Channel, trawled gear and their catch are typically badly damaged when retrieved (Thomson 1873). Recovery in epibenthic megafaunal assemblages after anthropogenic disturbance is rarely investigated as it requires multi-year assessment over large areas at high-resolution.

The impact of hydrocarbon exploration drilling at the Laggan field in the Faroe–Shetland Channel includes complete smothering of the seabed with drill cuttings (composed of sediments and drill mud; see Schaanning et al. 2008) up to 120 m from the well and a subsequent significant reduction in megafaunal abundance and diversity (Jones et al. 2006). In addition to disturbance from smothering, potential ecotoxicological effects of components of the drilling muds (Terzaghi et al. 1998, Schaanning et al. 2008, Trannum et al. 2010) and changes in sediment grain size from coarse to fine may have reduced recovery rates (Trannum et al. 2010). Hydrocarbon drilling, as a known and quantifiable disturbance, provides a useful model for studying the effects of anthropogenic disturbance in the deep sea.

Recovery typically implies a return of an ecosystem to pre-disturbance conditions as a result of the operation of homeostatic ecological control mechanisms (O'Neill 1998). Recovery is a complex phenomenon involving spatially and temporally dynamic biotic and abiotic changes. The recovered ecosystem may have altered in some way from its original state, for example in ecosystem function, structure, species complement or diversity (O'Neill 1998). Although disturbance to megafaunal assemblages from drilling has been reported (Jones et al. 2006, 2007b, Hughes et al. 2010), there have been few assessments of recovery associated with deep-water drilling impacts.

Study area

The Faroe–Shetland Channel is a deep channel separating the Faroe Plateau from the Scottish continental shelf (Fig. 1). It has a complex hydrographic regime, with warm North Atlantic waters overlying the cold water flowing from the Norwegian Sea (Turrell et al. 1999, Bett 2001). At 600 m depth, the Laggan oil field (Fig. 1) is located at the transition between warmer and colder water masses: Arctic Intermediate Water (400 to 600 m; 2 to 5.5°C) and Norwegian Sea Arctic Intermediate Water (–0.5 to 0.5°C in 600 to 800 m) (Turrell et al. 1999). The deep-water thermocline, at approximately 550 m depth in

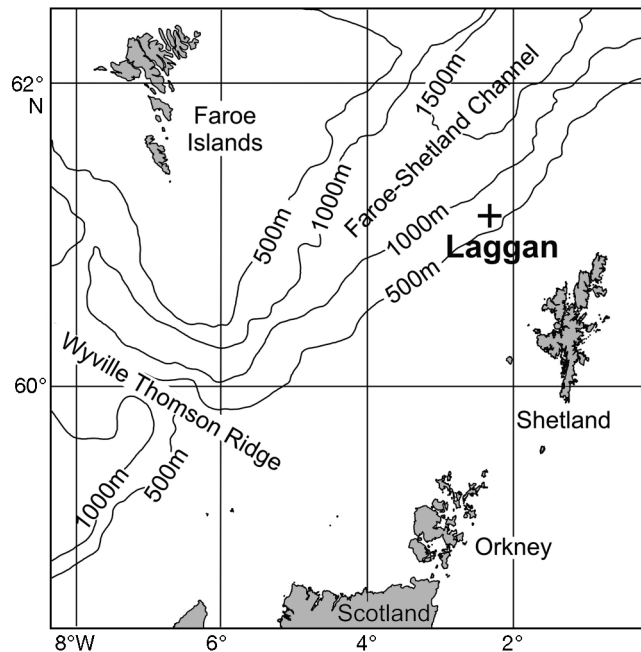


Fig. 1. Location of the Laggan study site in the Faroe–Shetland Channel

the Laggan area, can vary in depth by more than 40 m during a tidal cycle (Sherwin 1995).

The Faroe–Shetland Channel harbours a wide variety of megafaunal species (Bett 2001). The abundance of hard substratum (iceberg rafted drop stones) generally leads to a well-developed encrusting epifauna of poriferans, cnidarians and bryozoans. On softer substrata, echinoderms are abundant (Bett 2001, Jones et al. 2007a). There is a distinct community separation between the different temperature regimes in the channel in all faunal groups investigated (Bett 2001, Narayanaswamy et al. 2005, Witbaard et al. 2005, Jones et al. 2007a).

The Laggan area (Well 206/1a-4-az; here Well A) was subject to a detailed investigation of the initial effects of drilling disturbance in 2004 on the benthic megafaunal assemblage (Jones et al. 2006). Two wells studied in the warmer shallower waters of the Faroe–Shetland Channel revealed different species but similar disturbance regimes and responses of megafauna to disturbance (Jones et al. 2007b).

Aims

The objectives of this study are to determine the recovery of deep-water megafaunal density and diversity after physical anthropogenic disturbance in the Faroe–Shetland Channel.

MATERIALS AND METHODS

Survey design

The study was undertaken in April 2007 and had 3 study targets:

(1) Drill Site A—drilled in March 2004; i.e. studied 3 yr after drilling (also surveyed previously, in April 2004, by Jones et al. 2006)

(2) Drill Site C—drilled in 1997; i.e. studied 10 yr after drilling (not surveyed previously; drilled using a similar method to A)

(3) Background environment—randomly selected locations at least 500 m from the drilling sites and presumed to be beyond the influence of acute drilling impacts (see e.g. Jones et al. 2006). These locations were divided equally between 2 depth strata, based on the approximate transition depth (600 m) between the shallower Arctic Intermediate Water and the deeper Faroe–Shetland Channel Bottom Water (Turrell et al. 1999) and associated changes in biology (Bett 2001).

The background environment samples at Laggan (Fig. 2) were constrained to a 6 × 6 km square (corners: NW 6759873 N, 502888 E; NE 6759873 N, 508888 E; SE 6753873 N, 508888 E; SW 6753873 N, 502888 E; Fig. 2). All positional information was recorded in Universal Transverse Mercator (UTM) zone 30 N, based on the World Geodetic Society 1984 datum. The 2 well sites were located as follows: A at 6756872.9 N, 505887.6 E (drilling commenced on 25 March 2004) and C at 6758191.0 N, 503849.5 E (drilled in 1997).

Data collection

Data were collected using a Seaeye Tiger remotely operated vehicle (ROV) equipped with a colour video camera, digital still camera (Kongsberg OE14-208), sonar (Tritech) and ultra-short baseline navigation transponder. Before each transect, the camera was centred, fully zoomed out and tilted to its most vertical angle (47° below horizontal) to optimise scaling of oblique images.

Well site surveys were radiating video transects, 500 m in length (Fig. 2, Table S1 in the supplement at

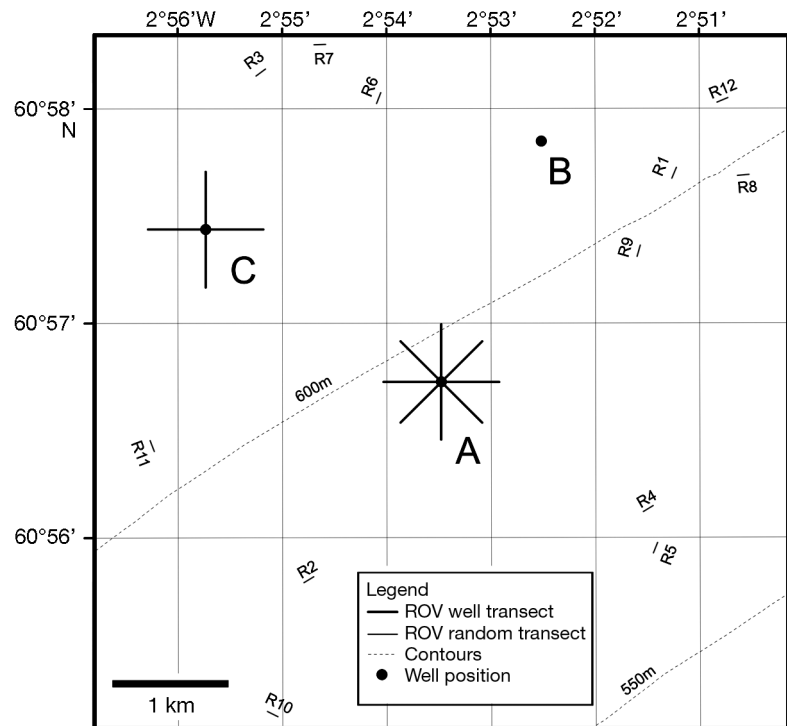


Fig. 2. Laggan site (6 × 6 km) showing sampling locations. R = random 100 m background remotely operated vehicle (ROV) transects. The position of Wells A, B and C is shown. At Site A and C, 500 m ROV transects radiate from the drilling location. Well B was not investigated in this study. The 550 and 600 m contours are shown as dotted lines. Scale bar = 1 km

www.int-res.com/articles/suppl/m461p071_supp.pdf; Site A: n = 8, Site C: n = 4). Each transect was split into 100 m sections by distance from the well (5 distance zones: 0–100 m, 100–200 m, 200–300 m, 300–400 m and 400–500 m; Site A: n = 40, Site C: n = 20). The seabed water depth along transects was 595 to 601 m for Site A and 631 to 640 m for Site C.

Video transects designed to characterise the natural seabed conditions (prefix R; Table S1 in the supplement; n = 12; length = 100 m) commenced from pre-defined random positions on random headings within the 2 depth strata (6 transects in 550 to 600 m and 6 in 600 to 650 m water depth). Transect 5 was subsequently excluded from the analysis as a fault with the ROV caused loss of video quality. Although the survey design initially separated random transects into 2 strata based on the 600 m contour, random transects shallower than 611 m and deeper than 633 m were found to be distinctly different (see 'Results'). Random transects were subsequently divided by depth into 2 groups, R_{shallow} and R_{deep} (see 'Results'). Sampling units for all analysis consisted of segments of video repre-

senting 100 m² of seabed (n = 71 for the 2007 study). Faunal counts are total counts for this 100 m² area. The 2004 dataset (Jones et al. 2006) provided an additional 18 sampling units in both the 0–100 m and 100–200 m zones (n = 36 for the 2004 study). There were insufficient data in the 2004 dataset to assess changes beyond 200 m from the well. Control sites were not assessed in 2004. Unfortunately, this precludes estimation of natural temporal variation in the background fauna and prevented a full BACI (Before After Control Impact) design being followed (Underwood 1994).

In every transect, the ROV was run in a straight line, on a set bearing, at a constant speed (~0.3 m s⁻¹) and set altitude (0.2 m). Transect width (mean of 1.0 m; maximum variation ± 0.2 m) was calculated from the camera acceptance angles and verified following Jones et al. (2006). The optical resolution of the cameras permitted all organisms larger than 50 mm to be reliably distinguished. In addition to the transects, previous ROV suction sampling, detailed inspection and still photography of selected individual organisms aided species identifications (Jones & Gates 2010).

Prior to this survey, quantitative video transects were conducted at Laggan Site A in 2004 using an industry-operated work-class Clansman ROV (Jones 2009). Other than the ROV and camera system being different models, an identical methodology was used in that study (Jones et al. 2006), enabling direct comparison of the data obtained from both surveys.

Data analysis

Fauna were enumerated from video following the methods of Jones et al. (2006). It was frequently not possible to identify organisms to known species, and fauna were classified into separate morphologically distinguishable entities (referred to as taxa). Numbers of organisms were quoted as abundances (numbers in each sampling unit) or as densities (no. m⁻²). In addition, observations were made describing the horizontal extent of the drill cuttings and the natural state of the seabed. These were categorised as complete coverage (where more than 90% of the sea bed was covered) and partial coverage (where there was some visual evidence of drill cuttings on the sea bed). Estimates of area disturbed were made by analysing maps in Image J software (v1.41, National Institutes of Health).

Univariate diversity indices were calculated to assess the dominance (Pielou's evenness) and species

richness (the number of species) aspects of diversity (Magurran 2003). The common Shannon-Wiener index was also presented for comparison with other studies. Shannon-Wiener and Pielou's evenness were calculated using PRIMER (v6).

Four generalized linear (GLM) statistical models were independently developed (Dobson & Barnett 2008) to examine whether the density (no. m⁻²) and taxon richness (number of species in a sample unit) of both sessile and motile megafauna at Laggan could be explained using the explanatory variables distance, depth group and year. Random sites were coded with a distance of >1000 m from drilling and included in all analysis. An additional GLM was developed for overall assemblage evenness with the same explanatory variables as above. All 3 explanatory variables were treated as categorical data. The residual deviance (1652.5 for sessile; 473.6 for motile) was greater than the residual degrees of freedom (91 for both), indicating overdispersion. The model was, therefore, fitted with quasi-Poisson errors using the R function `glm` and the ANOVA function of the R package `CAR` (companion to applied regression) (Fox & Weisberg 2011) in the R programming environment (R Development Core Team 2010).

Assessment of recovery

Recovery is indicated by a reduction in magnitude of the gradient in disturbance that occurs with distance from drilling. In the shallow samples (Drill Site A and R_{shallow}), evidence for recovery was provided by the significance and direction of the statistical interaction between time since disturbance (year) and distance from drilling (distance). Recovery was suggested by a reduction in the variation in the response variable (e.g. sessile faunal density) with distance from 2004 to 2007. Further evidence of recovery at Laggan was provided by the significance and direction of the statistical interaction between the distance from drilling (drilling) and the well site (depth zone). Recovery was suggested by a reduction in the variation in the response variable with distance in the samples from the deeper zone (sampled 10 yr after drilling) compared to the shallower zone (sampled 3 yr after drilling). It should be noted that changes in response variables between the shallow and deep zones at Laggan should be treated with caution, as specific responses across distance zones may have differing drivers with disparity in the assemblage composition.

RESULTS

The background environment at Laggan

Benthic megafaunal density was variable in background areas (Table 1), and their fine-scale (<100 m²) distribution appeared to be primarily governed by substratum type and the availability of suitable microhabitats. Most sessile filter feeders were

attached to hard substrata. Echinoderms generally were found on finer sediments, being common in gravel and sand areas. The megabenthic epifauna at Laggan (in 2007; Tables 1 & 2) was dominated by sponges (20 taxa). Echinoderms (11 taxa) and cnidarians (9 taxa) were also important.

The total density of fauna varied over nearly an order of magnitude (Table 1) between the background samples (6.41 [R7] to 0.9 m⁻² [R8]). Three

Table 1. Taxon abundances (per 100 m² sampling unit; averaged for groups) from the present survey and that of Jones et al. (2006); R_{shallow} = background samples <615 m depth; R_{deep} = background samples >615 m depth. Distance zones, i.e. distance from well: 0–100, 100–200, 200–300, 300–400 and 400–500 m. Indet = Indeterminate. Taxonomic precision given where applicable: ^aidentified from specimens; ^bconfident identification from high-resolution photograph (Jones & Gates 2010); ^clow confidence identification; ^dmotile megafauna. A,C: sites

	R _{shallow}	R _{deep}	2004 A		2007 A					2007 C				
			0–100	100–200	0–100	100–200	200–300	300–400	400–500	0–100	100–200	200–300	300–400	400–500
Sponge A	0.3	0.0	0	0	0	0.1	0	0.1	0	0	0	0	0	0
Sponge B	0.3	4.7	0	0	3.5	8.4	9.6	8.3	4.5	1.5	1.0	2.0	0.3	0.8
Spherical sponge	16.8	56.0	0.1	0.9	19.1	40.4	44.8	43.0	35.3	87.3	82.0	48.8	61.5	58.9
Sponge F	7.9	10.7	0	0	3.9	11.5	13.8	11.1	10.3	20.5	16.8	12.5	18.3	23.6
Sponge H	5.3	24.0	0	0	10.8	24.5	27.8	23.5	15.9	10.0	13.5	9.3	13.3	15.8
Sponge I	1.5	1.7	0	0	0.1	0	0	0.5	0.3	0	0	0	0	0
Sponge J	5.3	11.0	0	0	8.5	22.3	20.3	18.0	14.9	7.5	8.0	8.3	7.3	8.5
Sponge K	2.0	3.3	0	0	2.1	3.1	3.1	2.1	2.4	0.3	0	0	1.5	0.3
Sponge L	1.1	1.7	0.1	0.3	13.5	18.1	11.3	6.5	8.9	2.0	0.5	2.0	3.0	2.4
Sponge M	7.3	1.7	0	0.1	4.3	9.1	8.8	8.8	6.4	1.3	2.0	0.8	0.8	0.5
Sponge N	9.4	22.3	0	0	1.0	1.1	1.5	0.9	2.3	0.3	0.5	0	0	0.8
Indet. white encrusting sponge	15.9	10.7	1.3	13.4	7.6	23.4	29.5	28.3	27.1	19.5	19.0	20.5	15.0	11.3
Indet. yellow encrusting sponge	3.0	6.0	0.1	1.1	1.3	6.0	7.9	7.0	6.1	1.3	1.0	2.5	0	1.4
Indet. red encrusting sponge	1.5	0	0	0	0.5	0.4	0.1	0.3	0	0	0.5	0	0.3	0.3
Indet. tall cylindrical sponge	11.3	6.7	0	0	0.8	2.6	8.1	4.3	3.6	8.8	4.0	5.0	7.5	10.4
<i>Stylocordyla borealis</i> ^a	0.9	2.0	0	0.1	0	0.3	0.4	0.1	0.4	1.0	1.0	1.5	1.0	2.4
<i>Geodia</i> sp.	0.8	13.3	0	0	0	0.1	0.3	0	0	0	0	0	0	0.3
Indet. brown digitate sponge	0	2.3	0	0	1.0	1.0	1.0	1.4	1.4	0.8	1.5	0.8	0.5	0.6
<i>Chondrocladia gigantea</i> ^a	0	0	0	0	0	0	0	0.1	0	0.3	0.5	0	0	0.3
Indet. white small sponges	4.9	6.0	0.8	15.4	0	1.9	7.1	9.6	11.0	29.5	12.3	19.3	13.8	16.3
<i>Tubularia regalis</i> ^c	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0
<i>Corymorpha gronlandica</i> ^a	0.1	0.3	0	0	0	0	0	0	0	0	0	0.3	0.3	0
<i>Drifa glomerata</i> ^c A (white)	1.8	14.3	0	0	0.9	0.1	0.4	0.1	0.1	3.0	3.8	1.5	0.5	1.6
<i>Gersemia</i> sp. ^c B (blue)	0	6.0	0	0.4	0.1	0.3	0.4	0.1	0.4	46.3	27.0	29.5	34.8	37.8
<i>Gersemia</i> sp. ^c C (pink)	0	5.7	0	0	0	0	0	0	0	3.3	0.3	2.8	2.8	2.4
<i>Gersemia</i> sp. ^c D (red)	0.1	22.3	0	0	0	0	0	0	0	53.8	36.0	32.5	38.8	32.9
Indet. actinarian	0.8	0	0	0	0.3	0	0	0	0	0	0.3	0	0	0
<i>Bolocera</i> sp. ^c	4.5	4.3	0.2	1.4	2.6	1.9	1.9	3.8	2.4	0.8	3.0	2.0	1.8	1.6
<i>Halcompa arctica</i> ^a	0.5	3.0	0	0	0	0	0	0.5	0.9	1.8	6.0	5.3	5.5	8.1
Sabellid	1.9	190.3	0	0	0.4	0.4	1.1	1.3	0.6	0.3	1.3	0.5	1.8	5.3
<i>Colus</i> sp. ^{b,d}	1.5	0.7	0	0.3	0.9	0.5	0.1	0.4	0.6	1.0	1.3	0.8	1.0	0

Table 1 (continued)

	R _{shallow}	R _{deep}	2004 A		2007 A					2007 C				
			0–100	100–200	0–100	100–200	200–300	300–400	400–500	0–100	100–200	200–300	300–400	400–500
<i>Colossendeis proboscidea</i> ^{a,d}	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3
<i>Boreonymphon</i> sp. ^d	0.1	0	0.1	0.1	0	0	0	0	0	0	0	0	0	0.5
<i>Atlantopandalus propinquus</i> ^{c,d}	1.3	2.3	1.9	37.7	2.0	0.8	1.1	0.4	0.8	0	0.3	0	0	0
<i>Pagurus</i> sp. ^d	0	0	0.1	1.1	0.3	0.1	0	0	0.1	0	0	0	0	0
<i>Reteporella</i> sp. ^b	0.1	1.0	0	0	0.1	0	0	0	0.1	0	0	0	0	0
Indet. bryozoan	0.1	1.0	0	0	0	0	0	0.1	0	0	0	1.3	1.5	0.8
Indet. asteroid ^d	1.0	0.3	0	0	1.4	1.1	2.0	1.4	0.6	0	0	0.3	0.3	0.3
<i>Henricia</i> sp. ^{a,d}	0	0	0.6	4.9	0	0.3	0.3	0.5	0.1	0	0	0	0	0
Asteropectinidae ^d	0.1	0	0	0.1	0	0	0	0	0	0	0	0	0	0.5
<i>Pteraster militaris</i> ^{a,d}	0	0.3	0.1	1.2	0	0	0	0	0	0.3	0.3	0.3	0.3	0
<i>Ceramaster granularis</i> ^{a,d}	1.5	0	1.1	4.6	0.6	2.9	2.4	2.4	1.9	0.3	0	0	0.3	0
<i>Crossaster papposus</i> ^{a,d}	0.3	0	0	0	0.3	0.3	0.1	0	0.1	0.5	0.8	0.8	0.5	0.8
<i>Porania pulvillus pulvillus</i> ^{b,d}	0	0	0	0	0	0.3	0.1	0.1	0	1.3	0	1.0	0.3	0.6
<i>Tremaster mirabilis</i> ^{a,d}	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0
Indet. ophiuroid ^d	1.0	1.3	0	0	0	0.9	0.3	0.4	1.4	0.8	0	1.0	3.8	1.0
<i>Poliometra proluxa</i> ^{a,d}	0	0.3	0.3	0.8	0	0	0	0	0	0	0	0.8	0.3	1.3
<i>Echinus</i> spp. (<i>E. alexandri</i> and <i>E. elegans</i>) ^{a,d}	5.9	0.3	1.4	8.3	7.1	10.5	10.3	11.5	8.8	0	0.5	0	0.5	0.3
<i>Myxine glutinosa</i> ^{a,d}	0.3	2.0	0	0	0	0	0.1	0.1	0.1	2.3	0.5	1.0	1.8	1.3
<i>Lycodes esmarkii</i> ^{b,d}	0.1	0	0.2	0.9	0.1	0	0.4	0.5	0.3	1.5	1.0	0.5	0.3	0.5
<i>Lycodon mirabilis</i> ^d	0.5	0.3	0	0	0.3	0.8	0.3	0.1	0.4	0	0	0	0	0
<i>Cottunculus microps</i> ^{b,d}	0	0	0	0.1	0	0	0	0	0	0	0.3	0.3	0	0.3
<i>Rajella fyllae</i> ^{b,d}	0	0	0	0.1	0	0	0.1	0.1	0.1	0	0	0	0.3	0.3
<i>Amblyraja hyperborea</i> ^{b,d}	0	0	0	0	0.3	0.6	0.1	0.5	0.3	0.5	0	0.3	0.5	3.5
Indet. juvenile fish ^d	0.1	0	0.2	0.4	0	0	0	0	0	0	0	0	0	0
Indet. flat fish ^d	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0
Indet. organisms	0.5	1.3	0	0	5.5	7.6	3.3	2.5	2.4	0	0	0	0.3	0

Table 2. Proportional abundance of each megafaunal phylum observed at Laggan (%). See Table 1 for definitions

	R _{shallow}	R _{deep}	2004 A		2007 A					2007 C				
			0–100	100–200	0–100	100–200	200–300	300–400	400–500	0–100	100–200	200–300	300–400	400–500
Porifera	79.6	41.7	21.0	33.9	79.2	86.1	88.1	83.4	84.6	63.0	65.6	64.0	62.8	62.1
Cnidaria	6.5	12.7	3.5	1.9	4.1	1.2	1.3	2.9	2.2	34.2	31.6	32.1	31.7	30.0
Mollusca	1.3	0.2	0.0	0.2	0.7	0.2	0.1	0.1	0.4	0.4	0.7	0.3	0.4	0.0
Annelida	1.6	43.1	0.0	0.0	0.2	0.2	0.4	0.6	0.3	0.1	0.4	0.3	0.8	1.8
Arthropoda	1.2	0.5	14.1	39.8	2.2	0.5	0.6	0.1	0.5	0.0	0.1	0.0	0.0	0.3
Echinodermata	8.5	0.6	35.5	22.4	9.1	7.8	7.2	10.0	9.2	0.8	0.7	1.8	2.6	1.8
Bryozoa	0.2	0.5	0.0	0.0	0.1	0.0	0.0	0.0	0.2	0.0	0.0	0.5	0.5	0.3
Vertebrata: Pisces	1.3	0.8	3.7	1.8	0.6	0.7	0.6	0.8	0.6	1.6	0.9	1.0	1.2	2.1

samples had high total densities (4.21 [R3], 2.63 [R6], 6.41 [R7] m⁻²). The other samples had similar densities (mean 1.2 m⁻² ± 0.19 m⁻² SD). Sabellids were almost exclusive to 2 samples (R3 = 2.17 m⁻², R7 = 3.54 m⁻²; other samples < 0.06 m⁻²) and only found in fine sediment. The samples with the highest total number of taxa (*S*) were R7 (31), R3 (28) and R6 (27);

R1 had the lowest *S* (19). Evenness was clearly reduced in samples R7 (*J'* = 0.56) and R3 (*J'* = 0.59) compared to the other samples (*J'* = 0.82 to 0.89), owing to high sabellid densities.

There was a clear separation in assemblage composition of background sites, with 2 distinct groups. Ten taxa were unique to R_{shallow} and 5 were only

found in R_{deep} (Table 1). One group (R1, 2, 4, 8, 9, 10, 11, 12) was sampled in shallower water (562 to 610 m) and the other (R3, 6, 7) in deeper water (634 to 637 m). All background images show a heterogeneous seabed composed of fine sediments, gravel and occasionally cobbles and boulders, but the proportion of these visible grain sizes varied between samples. Most samples had a predominance of sandy gravel, with cobbles and occasional boulders. Samples R3 and R7 had a visible reduction in dominant sediment grain size, confirmed in concurrent sediment samples (see Table S2 in the supplement at www.int-res.com/articles/suppl/m461p071_supp.pdf).

The survey of background sites was designed to have 2 depth strata, with a division at 600 m water depth. The preceding analysis suggests that the faunal division was located a little deeper than predicted, between 610 and 634 m. This was important in subsequent analysis of recovery at the well sites. Site A (595 to 601 m) transects were in the shallower zone and Site C (631 to 640 m) transects were in the deeper zone. As a result, in subsequent analysis, Samples R1, 2, 4, 8, 9, 10, 11 and 12 (collectively referred to as R_{shallow} ; $n = 8$) were considered to represent background samples for Site A and Samples R3, 6 and 7 (collectively referred to as R_{deep} ; $n = 3$) were considered to represent background samples for Site C. Sediment properties (Table S2 in the supplement) were generally similar between the R_{shallow} and R_{deep} zones. The exception to this was the percentage of fine grains in the sediment, which was significantly lower in R_{shallow} than in R_{deep} (t -test: $t = -2.286$, $df = 10$, $p < 0.05$). The R_{shallow} and R_{deep} zones had similar levels of organic matter as well as hydrocarbon and heavy metal contamination (Table S2 in the supplement).

Environmental variation resulting from disturbance

In 2007, the environment beyond 100 m from the well was visually similar to typical undisturbed areas. Within 100 m of previous drilling, disturbance was visible (Fig. 3) as obvious cuttings piles with fine sediments of a lighter colour than background and, close to the drilling location, cement from the ‘plug-and-abandon’ phase of the drilling operations (Fig. 4, Fig. S1 in the supplement at www.int-res.com/

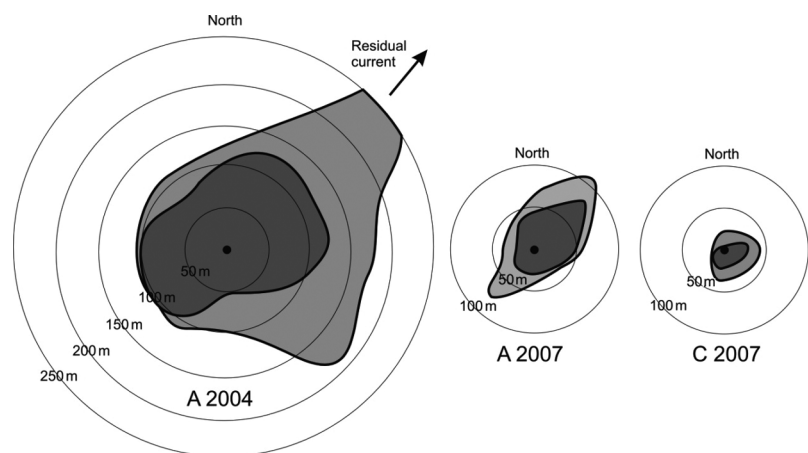


Fig. 3. Extent of complete (central dark grey area) and partial (light grey area) physical disturbance of the seabed at Laggan. Circles represent 50 m zones radiating from the disturbance source. Filled circles represent final drilling locations (point source of disturbance). A, C: sites

[articles/suppl/m461p071_supp.pdf](http://www.int-res.com/articles/suppl/m461p071_supp.pdf)). At Site A in 2004, there was an often gradual transition between complete cuttings coverage and natural seabed (area of complete cuttings 30 700 m²; area of complete and partial cuttings >70 890 m²), with an extended area of partial cuttings (Jones et al. 2006). In this survey, the boundary between thick cuttings and typical seabed was much more distinct at both sites. The area impacted by complete cuttings at A (area of complete cuttings 5570 m²; area of complete and partial cuttings 10 980 m²) had reduced from 2004 levels. In terms of distance, the extent of complete cuttings at A reduced to an average of 40 m from the drilling location, compared with 90 m in 2004. Conditions at Site C were similar to those found at A, with complete cuttings extending from the drill location to 18 m on average (area of complete cuttings 920 m²; area of complete and partial cuttings 2700 m²). The seabed was smothered by cuttings to a maximum depth of 1.5 m, although typically of a lesser thickness.

Response of megafaunal density

Motile faunal density (Fig. 5) was generally a small percentage of total density (mean 11.1 % at R_{shallow}), but, taken alone, the densities of motile fauna were highly variable between samples. There was a significant influence of time since disturbance (year) on motile megafaunal densities in the shallow samples (L -ratio = 25.226, $df = 1$, $p < 0.001$), with both lower (0–100 m zone) and higher (100–200 m zone) densities in 2004 compared to 2007 surveys. The GLM

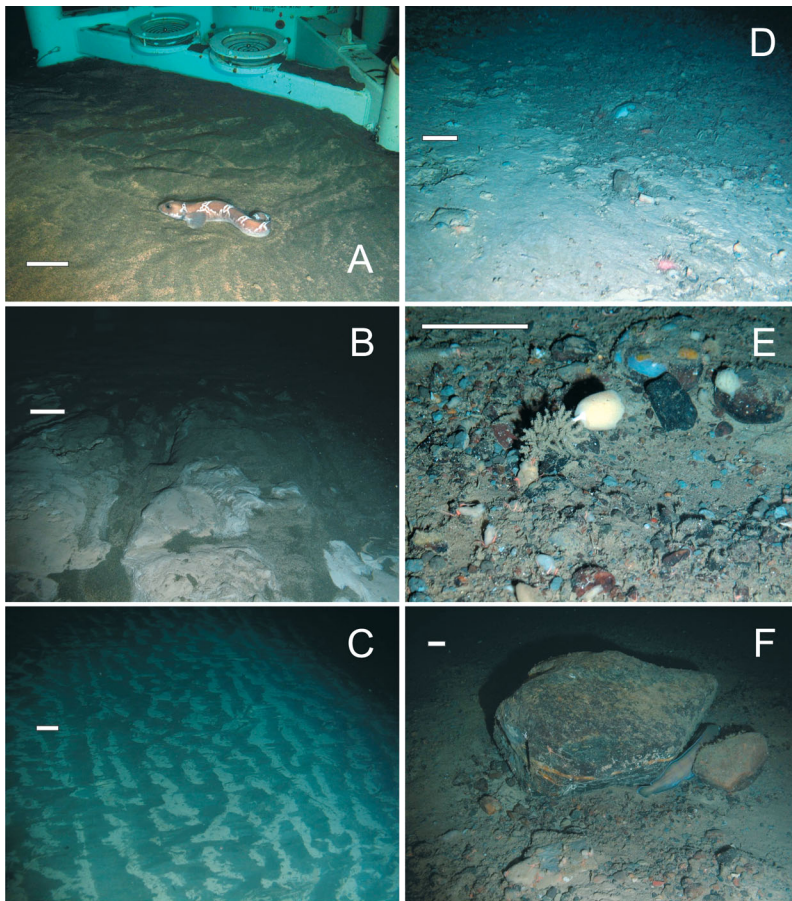


Fig. 4. Example images of disturbance regime at Laggan. (A) Seabed next to the blow-out preventer showing cuttings and *Lycodes esmarkii*, (B) area of complete cuttings and exposed cement, (C) complete cuttings area with ripples, (D) edge of cuttings, (E) normal seabed with gravel and pebbles, encrusting sponges and *Stylocordyla borealis*, (F) large iceberg-raftered boulder on normal seabed with *Brosme brosme* (species not seen on transect video). Scale bar = approximately 100 mm on the seafloor at its location

revealed an interaction of time since disturbance and distance in the shallow samples (L -ratio = 29.981, $df = 1$, $p < 0.001$). In the shallow sites, motile organism densities were much more consistent in 2007 than in 2004, when density was very different between distance zones. This is taken to provide evidence of partial recovery between 2004 and 2007 in motile organism densities. Despite this, there was an influence of the distance (significant main effect) in both years (L -ratio = 151.361, $df = 5$, $p < 0.001$), with a general increase in density of motile fauna with increased distance (Fig. 5). There was a difference in motile megafaunal density between the shallow and deep water samples (L -ratio = 17.470, $df = 1$, $p < 0.001$), with generally greater densities of motile megafauna in the shallow samples. There was no significant interaction between the distance from drilling and

the depth zone (L -ratio = 3.067, $df = 5$, not significant [ns]).

Sessile fauna made up the majority of organisms found at Laggan (Fig. 5). There was a significant influence of time since disturbance on shallow sessile megafaunal densities (L -ratio = 140.803, $df = 1$, $p < 0.001$), with increases in density in 2007 compared with 2004 surveys in the shallow samples. The GLM revealed an interaction of time since disturbance and distance in the shallow samples (L -ratio = 11.373, $df = 1$, $p < 0.001$). An increased time since drilling in the shallow samples led to greater densities of sessile organisms closer to the site of drilling, suggesting partial recovery between 2004 and 2007 in the densities of sessile megafauna. There was a weak influence of distance (model with 2004 and 2007 data) (L -ratio = 14.973, $df = 5$, $p < 0.05$), revealing that densities of sessile organisms increased with increased distance from drilling in all samples investigated. There was a significant interaction between distance and depth zone (L -ratio = 49.349, $df = 5$, $p < 0.001$), and the density of sessile benthic megafauna increased with increasing distance to a greater extent in shallow water than deep. This provides some evidence that there had been higher recovery in sessile benthic megafaunal densities after 10 yr than after 3. The model suggests that there

were significantly higher sessile megafaunal densities in the deeper samples compared with those from shallower water (L -ratio = 58.189, $df = 1$, $p < 0.001$).

Response of megafaunal diversity

There were fewer motile taxa than sessile taxa at Laggan and the richness of motile taxa was less variable between sites (Table 3). The richness of motile organisms was not significantly different between the shallow and deep sites (L -ratio = 0.028, $df = 1$, ns). Taxon richness in the shallow samples was virtually identical between 2004 and 2007 within a distance zone (Table 3). There was a significant main effect of distance on richness of motile organisms (L -ratio = 39.067, $df = 5$, $p < 0.001$), and richness increased with

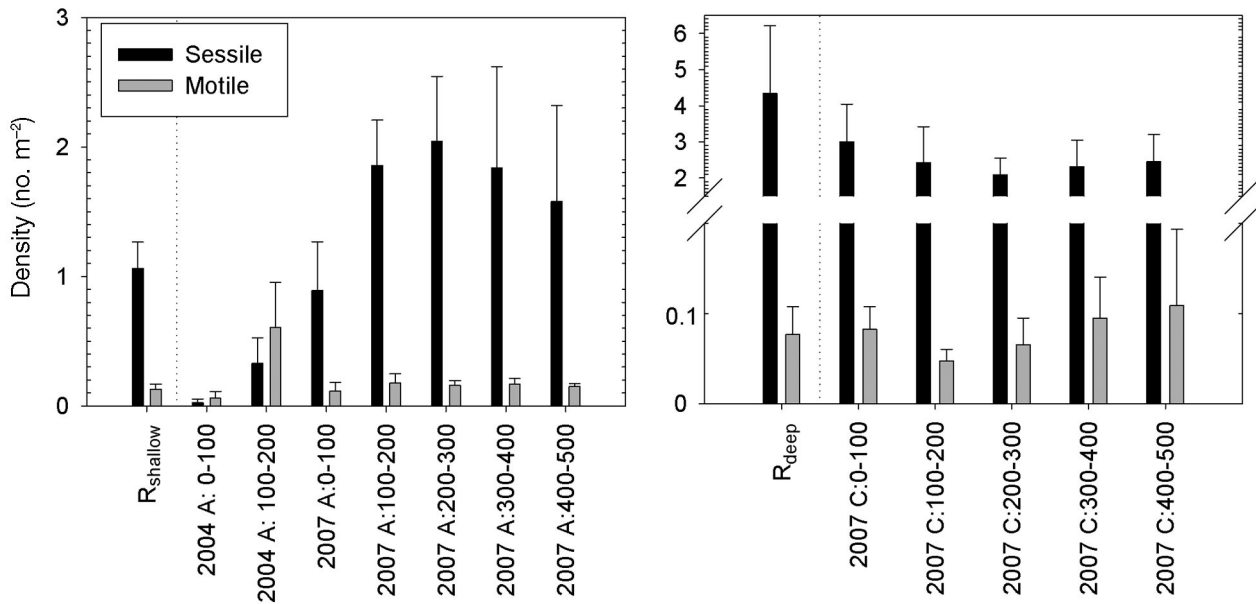


Fig. 5. Densities (no. m^{-2}) of sessile and motile fauna under different disturbance regimes at Laggan. Error bars represent standard deviations. See Table 1 for definitions

Table 3. Variations in megafaunal species density and diversity measures around the Laggan site: density: no. m^{-2} , mean \pm SD; total taxa observed: S_{sessile} = total number of unique sessile taxa in sample, S_{motile} = total number of unique motile taxa in sample; H' = Shannon-Wiener index [\log_e]; J' = Pielou's evenness. H' included to provide comparison with other literature. All diversity indices were calculated from total numbers of each taxon for each station (i.e. several sampling units). S is not adjusted for sampling effort. See Table 1 for other definitions

	n	Density (no. m^{-2})	S_{sessile}	S_{motile}	H'	J'
R_{shallow}	8	1.19 \pm 0.02	28	14	2.97	0.79
R_{deep}	3	4.41 \pm 0.63	28	9	2.30	0.63
2004 A: 0–100	18	0.09 \pm 0.08	6	10	2.23	0.81
2004 A: 100–200	18	0.94 \pm 0.43	10	12	1.93	0.62
2007 A: 0–100	8	1.01 \pm 0.43	22	10	2.71	0.78
2007 A: 100–200	8	2.03 \pm 0.40	22	13	2.63	0.74
2007 A: 200–300	8	2.20 \pm 0.50	22	15	2.64	0.73
2007 A: 300–400	8	2.01 \pm 0.76	25	13	2.64	0.72
2007 A: 400–500	8	1.73 \pm 0.73	23	14	2.68	0.74
2007 C: 0–100	4	3.09 \pm 1.05	24	9	2.27	0.66
2007 C: 100–200	4	2.47 \pm 1.00	26	9	2.31	0.66
2007 C: 200–300	4	2.15 \pm 0.49	24	11	2.52	0.72
2007 C: 300–400	4	2.41 \pm 0.74	24	13	2.46	0.68
2007 C: 400–500	4	2.56 \pm 0.82	26	16	2.59	0.70

distance from drilling in all samples. There was a significant interaction of distance zone and year in the richness of motile fauna in the shallow samples (L -ratio = 5.77, df = 1, p < 0.001). Although richness of motile taxa was lower on average in samples from the 0–100 m zone in 2004 ($S_{\text{mean motile}}$ = 2.8) than in 2007 ($S_{\text{mean motile}}$ = 3.8), sample richness in

the 100–200 m zone was higher in 2004 ($S_{\text{mean motile}}$ = 7.0) than in 2007 ($S_{\text{mean motile}}$ = 5.3). There was no significant interaction of distance and depth group (L -ratio = 3.185, df = 5, ns), suggesting that motile organisms did not recolonise the disturbed areas any more after 3 yr than after 10 yr of recovery time.

Taxon richness of sessile taxa varied between 6 and 28 (Table 3). There was a significant main effect of time since drilling on richness of sessile taxa (L -ratio = 156.084, df = 1, p < 0.001), and taxon richness in the shallow samples was significantly lower in 2004 than in 2007. Richness of sessile organisms was lowest close to the well immediately after drilling (2004 A 0–100 m S_{sessile} = 6). Richness of sessile organisms increased with distance from drilling in all samples (L -ratio = 19.716, df = 5, p < 0.01).

Both distance zones in 2004 had lower richness of sessile megafauna than R_{shallow} and any of the 2007 A zones (Table 3), supporting major reduction in sessile taxon richness as a result of drilling. In the zone closest to the well (0–100 m) in 2007, richness of sessile organisms (S_{sessile}) had increased nearly 4 times from 2004 levels. This area still had significantly lower

richness than either R_{shallow} or the areas further from disturbance in 2007 (Table 3), indicating incomplete recovery. None of the sessile taxa missing from the 2007 A 0–100 m zone but present in R_{shallow} were common in R_{shallow} (Table 1). There was a significant interaction of distance and year (L -ratio = 23.212, $df = 1$, $p < 0.001$), and in the shallow samples, increased time since drilling led to greater richness of sessile organisms closer to the site of drilling. There was no significant interaction of distance and depth group (L -ratio = 2.021, $df = 5$, ns).

Evenness (measured by J') was similar between samples taken in 2007 (Table 3). The 2004 samples at 0–100 m from drilling had the highest evenness ($J' = 0.81$). This was higher than the 2004 A 100–200 m samples, which had the lowest evenness ($J' = 0.62$). Evenness was higher at R_{shallow} ($J' = 0.79$) than at R_{deep} ($J' = 0.63$). There were no significant differences in evenness with any of the explanatory variables investigated.

DISCUSSION

Community heterogeneity at Laggan

The megafaunal assemblage at Laggan was spatially variable; at least 2 major assemblage types were identified. The high spatial variability of the Faroe–Shetland Channel makes assessment of the potential environmental impact of developments more difficult. Water depth and proportion of fine sediments were shown to be important for structuring assemblages in background sites here and in other studies in the Faroe–Shetland Channel (Bett 2001, Jones et al. 2007a) and elsewhere (Tecchio et al. 2011). The variable temperature gradient in the Faroe–Shetland Channel (Turrell et al. 1999) may have exposed the shallow sites to higher temperatures than the deeper sites. Extreme bottom water temperature variation appears to be limited to <600 m depth in this area (Turrell et al. 1999). Deeper than approximately 600 m, continually cold conditions, characteristic of Faroe–Shetland Channel bottom water, persist (Turrell et al. 1999). In the Laggan region this boundary was probably slightly deeper than suggested. Most identified taxa were Arctic forms, typical of the deep Faroe–Shetland Channel (Jones et al. 2007a), Norwegian Sea (Dahl et al. 1976) and higher latitude areas (Mayer & Piepenburg 1996, Piepenburg & Schmid 1996, Starmans et al. 1999, Piepenburg et al. 2001).

Effects of disturbance on megafauna

At Laggan, the initial disturbance by physical smothering and burial of organisms was severe within 100 m of drilling activity, as observed for other forms of physical smothering disturbance (Stronkhorst et al. 2003). Outside the area of complete disturbance, megafaunal taxa responded differently to disturbance, likely dependant on a complex interaction of factors including feeding mode, motility, particle removal rate and rate of sedimentation (Nichols et al. 1978). Mobile scavengers, such as *Atlantopandalus propinquus* and *Pagurus* sp., moved back into the area quickly to feed on moribund organisms. At this point, there was a relatively wide impacted area, where seabed disturbance was visible as fine sediment on the seafloor up to at least 250 m from the drilling activity.

Removal of cuttings at Laggan probably took place over time by lateral advection during high current events (velocities up to 1 m s^{-1} ; Masson et al. 2004) and from vertical redistribution in the sediments from bioturbation by abundant infaunal deposit feeders (Total E & P UK pers. comm.). After 3 yr, there was significant removal of cuttings from those initially deposited, particularly in the areas with relatively low initial deposition.

After 3 yr, faunal density within 100 m of the well had increased considerably and was no longer significantly different from conditions further away. Motile megafauna were no longer elevated close to drilling. This response occurs rapidly in shallow water megafauna after disturbance from fishing (Ramsay et al. 1998). Slow recovery of megafauna appears typical from the limited studies in both hard (Althaus et al. 2009) and soft substrata (Bluhm 2001) in the deep oceans. Deep-sea invertebrates are long-lived and slow growing (e.g. Gage 1991, Tracey et al. 2007), so sessile fauna may take a long time to reach megafaunal sizes after recolonisation. Only 2 species found at Laggan have published growth rates, both mobile animals from the nearby, but warmer, Rockall Trough. It took at least 10 yr for an echinoid found at Laggan, *Echinus elegans*, to reach 50 mm test diameter (Gage et al. 1986) and at least 5 yr for an ophiuroid, *Ophiecten gracilis*, common in samples at Laggan (and therefore probably included in the 'indeterminate ophiuroids' enumerated on video) to reach a disc diameter of 7 mm (Gage 2003), which equates to approximately 50 mm total diameter (including arms). More detailed studies are required to determine the source of recruits to areas disturbed by drilling activity.

The 2007 A 0–100 m samples showed that there were still megafaunal taxa that were displaced by disturbance, but the relative proportion of taxa was not clearly affected. As overall density of sessile organisms was low and only rarer taxa were absent from the more disturbed area in 2007, the reduced richness observed may have resulted from the reduced probability of sampling the rarer taxa (Magurran 2003). In 2007, the boulders that had harboured the majority of the organisms in the disturbed zones in 2004 (Jones et al. 2006) were observed again; however, they were no longer supporting an epilithic community, suggesting a chronic and ultimately lethal effect of either physical smothering from the initial sedimentation event (Nichols et al. 1978) or chemical influence from the drill cuttings (Terzaghi et al. 1998, Trannum et al. 2010).

After 10 yr at C, seabed disturbance was still visible close to the well and appeared similar to that found at A after 3 yr. This suggests a proportion of the deposited cuttings were resistant to erosion, probably owing to the presence of cement. There was still limited megafaunal recolonisation in this area. However, within 10 m of the disturbed area, there was an abundant, diverse megafaunal community, not readily distinguishable from that found over 100 m from the drilling location. A similar response occurred in the DISCOL deep-sea disturbance experiment (Bluhm 2001), where soft sediment megafaunal recovery was evident after 7 yr, although there were still small differences in the taxonomic and numerical composition of megafauna. There were probably also some species-specific responses to observed variable sediment levels and chemical concentrations found around the drilling location at Laggan (e.g. elevated barium was found in some samples near to Well A and C in 2007, Total E & P UK pers. comm.), but the heterogeneous seabed, irregular chemical distribution and naturally highly variable megafauna make these subtle effects difficult to distinguish.

Disturbance from drilling is known to affect the functioning of benthic communities (Schaanning et al. 2008, Trannum et al. 2010). Species diversity and density of the megafaunal assemblage likely correlate with the ecosystem functions they provide (Danovaro et al. 2008), suggesting little appreciable change in function beyond 100 m from the disturbance. It would be extremely valuable to evaluate functional changes beyond these generalisations. Some sessile taxa, particularly the sponges, may be suitable as species indicating functional recovery of a given area in space and time. The best specific example of this is the spherical sponge, which is conspicu-

ous and occurs at high densities in areas with low disturbance. Although their abundance decreased, they were not completely absent in disturbed areas. Further work is also required to understand potential functional change within smaller size fractions of the benthos (e.g. the bacteria, meio- and macrofauna), which may differ from the megafauna in their response to disturbance. Recovery potential from anthropogenic disturbance in the deep sea remains relatively unknown. Further study, using high-resolution methodologies, of community patterns and the ecology of key deep-water species is required at background sites as anthropogenic activity in the deep-sea realm continues to increase.

CONCLUSIONS

This study indicates that deep-water megafaunal density and diversity recovers partially from drilling disturbance after 3 yr. However, although there is increased recovery after 10 yr, drill cuttings and associated impacts on epibenthic megafaunal assemblages are still distinguishable after a decade. Megafauna may recover more slowly than the more commonly studied smaller infauna. Carefully designed, high-resolution and multi-year studies, such as this, are rare but essential to further our understanding of recovery from anthropogenic impact.

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