Anthropogenic disturbance of deep-sea megabenthic assemblages: a study with Remotely-Operated Vehicles in the Faroe-Shetland Chanel, NE Atlantic

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ABSTRACT

The effects of local-scale anthropogenic disturbance from active drilling platforms on epibenthic megafaunal abundance, diversity and assemblage pattern were examined in two West of Shetland hydrocarbon fields at 420 m and 508 m water depth. These areas were selected to include a range of disturbance regimes and contrasting faunal assemblages associated with different temperature regimes. Remotely Operated Vehicle (ROV) video provided high-resolution megafaunal abundance and diversity data, which were related to the extent of visible disturbance from drilling spoil. These data, in conjunction with a study deeper in the Faroe-Shetland Channel, have allowed comparison of the effects of disturbance on megabenthos across a range of sites. Disturbance to megafaunal assemblages was found to be high within 50 m of the source of drill spoil and in areas where spoil was clearly visible on the seabed, with depressed abundances (Foinaven 1900 individuals ha^{-1}; Schiehallion 2178 individuals ha^{-1}) and diversity (H´ = 1.75 Foinaven; 1.12 Schiehallion) as a result of smothering effects. These effects extended to around 100 m from the source of disturbance, although this was variable, particularly with current regime and nature of drilling activity. Further from the source of disturbance, megafaunal assemblages became more typical of the background area with increased diversity (H´ = 2.02 Foinaven; 1.77 Schiehallion) and abundance (Foinaven 16484 individuals ha^{-1}; Schiehallion 5477 individuals ha^{-1}). Visible effects on megafaunal assemblages as a result of seabed drilling were limited in extent although assemblage responses were complex, being controlled by differing effects to individual species often based on their motility.

INTRODUCTION

Disturbance is an important source of temporal and spatial heterogeneity in natural communities (e.g. Sousa 1984). The importance of disturbance has been highlighted (e.g. Connell 1978) in maintaining species diversity by preventing competitive exclusion by dominant species in an assemblage. Physical disturbance is a key factor in controlling spatial and temporal composition of shallow-water benthic communities. Like shallow waters, deeper waters are now increasingly subject to a range of anthropogenic perturbations that include commercial trawling (Kaiser 1998), mining (Radziejewska and Stoyanova 2000) and increasingly oil exploration (Jones et al. 2006). Oil exploration activities are becoming more important in the Faroe-Shetland Channel with the majority of fields located on the upper slope (Figure 1). This area supports a high diversity of deep-water fauna primarily controlled by its unusual temperature regime (Turrell et al. 1999; Bett 2001). This study will compare the effects of disturbance from drilling on megafaunal assemblages in the three major thermal regimes encountered in the Faroe-Shetland Channel between 200 and 1000 m water depth. This study extends that of Jones et al. (2006) to include new megafaunal data from contrasting thermal regimes.

Human induced disturbance in the deep sea typically has a large impact on benthic communities (Bluhm 2001). Deep-sea environments are typically stable in comparison with often more dynamic shallow-water habitats (Gage and Tyler 1991). Physical habitat characteristics are important in controlling benthic community structure (Levin et al. 2001). Anthropogenic disturbance from a variety of sources can alter these characteristics very rapidly by smothering the existing seabed with sediments from elsewhere (Stronkhorst et al. 2003; Jones et al. 2006). In addition, large-scale disturbance can also occur naturally in deeper waters from turbidity currents, debris flows and benthic storms (Gage and Tyler 1991). In communities with limited food supply and with invertebrate assemblages depauperate in both abundance and biomass, disturbance effects are likely to be greater and recovery times longer (Bluhm 2001). The greatest change in communities may be expected to occur in areas where disturbance alters habitat type most radically. The upper slope of the Faroe-Shetland Channel harbours an unusual deep-sea habitat consisting of a heterogeneous mix of sediments with a preponderance of hard substratum (cobble, boulder). Introduction of drill spoil acts to reduce hard substratum availability and homogenise the habitat, which can directly influence the abundance, diversity, species composition and distribution of the local benthic fauna (Jones et al. 2006).

The effects of anthropogenic disturbance, such as oil drilling activity, on the benthic environment is conventionally assessed by sampling (typically by grab) a range of chemical parameters and occasionally macrofauna from the source of effect at geometrically increasing distances along four radiating transects (Gray et al. 1990; Kingston 1992). The effects on macrofauna are usually recorded as changes in diversity indices (Davies et al. 1989; Kingston 1992), although multivariate approaches may be more effective (Olsgard and Gray 1995). The effects of physical disturbance on whole assemblages is less well known, with shallow-water studies suggesting a range of responses depending on the severity of disturbance and nature of the assemblage (Airoldi 2003; Dernie et al. 2003).

Typical environmental assessments do not specifically address the larger epibenthic megafauna, yet these organisms play an important role in benthic processes (Piepenburg and Schmid 1997). Monitoring of megafauna has been shown to be effective in evaluating the impacts of disturbance on the seafloor (Bluhm 2001).

Photographic studies allow fine scale survey of megabenthic abundance, diversity and distribution (Piepenburg and Schmid 1997) and can have a much larger spatial extent than is usually possible with conventional macrofaunal sampling techniques. Remotely Operated Vehicles (ROV) are ideal tools for such surveys, capable of high resolution, systematic video and photographic investigation of epibenthic megafaunal assemblages (e.g. Jones et al. 2006).

The main objectives of this study are to: 1) describe the composition, diversity and distribution of megafaunal assemblages on the Faroe-Shetland Channel slope, 2) determine the effect and extent of physical disturbance from drilling operations on benthic megafauna, 3) determine the differences between benthic megafaunal assemblages and their responses to disturbance at two contrasting study sites and 4) compare results from these with existing data collected in an identical manner at a deeper Faroe-Shetland Channel site (Jones et al. 2006).

MATERIALS AND METHODS

Study background:

Investigations for this study were carried out aboard the semi-submersible oil drilling platforms Paul B Loyd Junior (PBLJ, 14-28/5/2003) and Transocean Leader (TOL, 27/9-3/10/2003). The PBLJ was operating in the Foinaven field (507-509 m depth, 60°18.68´ N 4°20.33´ W) and TOL in the Schiehallion field (420-421 m depth, 60°22.95´ N 04°05.95´ W). The Foinaven and Schiehallion oil reservoirs were discovered in 1992 and 1993 respectively. Drilling activities began in the Foinaven region in 1997 and in the Schiehallion region in 1998.

Drill spoil was deposited on the seabed during the initial phases of drilling (tophole drilling) as sediment is displaced directly. Once this phase is completed all subsequent rock cuttings were recirculated with drilling mud back to the rig where they were cleaned and depending on potential contamination, discharged at the surface or shipped back to land. With the high current regime in the Faroe-Shetland Channel the rock cuttings disposed at the surface were spread widely and very little was deposited on the seabed close to the rig (Aurora 2004). In this environment, the majority of spoil deposited on the seabed close to the drill site was produced for less than a day per well during tophole drilling. In the area investigated at Foinaven, 14 wells were present at the time of investigation within 50 m of each other. These wells had been drilled over a 5 year period with the most recent still being drilled during this investigation. Seabed spoil resulting from this drilling operation was produced 14 days prior to the start of the investigation (1/5/2003), over a period of approximately 24 hours. In the area investigated at Schiehallion there was only one well, which was also being drilled during this investigation. Seabed disturbance from tophole drilling occurred twice owing to operational problems, 12 and 14 days before this investigation began (on 13 and 15/9/2003; both for approximately 24 hours).

For survey purposes the seabed around the drilling activity was divided into 50 m zones radiating from the outer limit of all seabed installations (Figure 2). The area to the southeast of the Foinaven well could not be surveyed owing to operational constraints. The distance of the ROV from the rig was calculated from transect duration and the length of the ROV tether released from the Tether Management System with an approximate error of ±1 m. Data were collected using an industry-operated work-class Pioneer HD ROV, following the methodology of Jones et al. (2006).

Data analysis

Abundances were standardised to numbers per hectare. Each transect was partitioned into 50 m zones and analysis was carried out on data from each zone. There were 5 zones at Foinaven (0 – 250 m) and 4 at Schiehallion (0 – 200 m, owing to limited data in the 250 m zone at Schiehallion). Counts for each individual transect 50 m zone formed the sampling unit.

A range of univariate diversity indices were calculated to assess both the dominance and species richness aspects of diversity (Magurran 2003). Confidence intervals (95%) for abundance and diversity were calculated using a bootstrapping technique (Manly 1998). As implemented here, 1000 bootstrap samples were calculated and a 95% confidence interval determined from the resultant data.

Variations in taxon composition were assessed by multivariate analysis (hierarchical group-average clustering and non-metric multi-dimensional scaling, MDS) following a square root transformation and calculation of Bray-Curtis similarity coefficients (Clarke and Warwick 2001). The difference in assemblage composition between distance zones was assessed using analysis of similarities (ANOSIM). Multivariate dispersion (MVDISP) was used to measure within-zone multivariate assemblage dispersion (Clarke & Warwick 2001). Data analysis was performed using the computer programmes PRIMER (Clarke and Warwick 2001), Biodiversity Pro (Natural History Museum, London and Scottish Association for Marine Sciences, Oban), MATLAB (MathWorks Inc.) and MINITAB (Minitab Inc.).

RESULTS

Foinaven

General observations

At Foinaven 1075 megabenthic organisms from 33 nominal taxa were recorded in a total area of 1519 m^2 (Table 1; Figure 3 & 4). Crustaceans were the dominant megafaunal group (47% megafauna; 5253 ha^{-1}), predominantly represented by the ubiquitous squat lobster *Munida sarsii*, but also included hermit crabs, natant decapods and *Siphonocetes* tube dwelling amphipods. Porifera (27% megafauna, 3382 ha^{-1}) were abundant. Echinoderms (22% megafauna, 2046 ha^{-1}) were dominated by *Echinus acutus* and the holothurian *Stichopus tremulus*. Asteroids (*Porania pulvillus pulvillus*, *Ceramaster granularis* and *Henricia pertusa*), comatulid crinoids and ophiuroids were also present. The remainder (4%) of the megabenthos was made up of molluscs, polychaetes, cnidarians and demersal fish. Seabed structures at Foinaven attracted large numbers of fish (predominantly *Sebastes viviparus*, *Brosme brosme* and *Pollachius virens*) but in disturbed areas benthic megafauna were relatively sparse, being largely represented by motile deposit feeders principally echinothurid urchins and *Munida sarsii*.

Despite the large number of drilling sites in the Foinaven study area, drill spoil was constrained to a ~ 50 m zone around the drill sites. Outside the disturbed area the seabed consisted of a heterogeneous mix of sand, gravel and occasionally larger cobbles and boulders characteristic of the “iceberg ploughmark zone” (Bett 2001; Masson 2001).

Abundance

Megafaunal abundance (Figure 3A) was significantly different between zones (Kruskal-Wallis $H = 22.81$, $df = 4$, $p < 0.001$) increasing with distance from drilling activity at Foinaven (Spearman's rank correlation $r' = 0.9$, $p < 0.05$). Large changes in abundance with distance from disturbance were observed particularly for dominant phyla, with Porifera and Crustacea displaying changes in abundance by almost an order of magnitude. A marked increase in abundance between 0 and 100 m from drilling activity was noted for major faunal groups with post-hoc non-parametric multiple comparisons of total faunal abundance (after Miller 1981) revealing significant differences ($p < 0.05$) between the 0-50 m zone and all other zones, but no significant differences between zones > 50 m from the drilling disturbance. Both motile and sessile taxa abundances were significantly different between zones (Kruskal-Wallis: motile: $H = 20.80$, $df = 4$, $p < 0.001$; sessile: $H = 23.87$, $df = 4$, $p < 0.05$). Sessile taxa increased continuously in abundance from very low values close to the source of disturbance. Motile taxa had low abundances close to disturbance but increased beyond 50 m. Beyond 50 m from the source of disturbance there was no significant differences in motile megafaunal abundance ($p > 0.5$ in post-hoc non-parametric multiple comparisons).

Diversity

Univariate diversity measures (Figure 4A) revealed significant changes in diversity with distance from the disturbance. Species richness was lowest close to the source of disturbance, increased to peak values at intermediate distances and dropped slightly in the least disturbed 250 m zone. Heterogeneity diversity (H') changed significantly between zones (Kruskal-Wallis H = 22.31, df = 4, $p < 0.001$), revealing lowest diversity in the area of drill spoil disturbance, particularly that within structures. This was primarily driven by lack of rarer species, revealed in type I indices (those that emphasis the rarer component of the assemblage). Heterogeneity diversity followed similar trends to species richness, increasing at intermediate distances and dropping slightly further away.

Composition

Multivariate analyses showed significant differences in megafaunal assemblages with distance from disturbance (ANOSIM R = 0.56, $p < 0.01$). Transects between structures were highly scattered in the MDS ordination and cluster diagram (Figure 5&6, respectively) with very low similarity to other zones (37% similarity). Fauna in the 50 m zone on transects away from structures had higher, but still generally low similarity compared to other zones (55%). Areas close to the disturbance displayed high dispersion of sample similarities (PRIMER MVDISP = 1.07). Outside the zone of drill spoil there was a faunal transition zone, which occurred between 50 and 100 m from the nearest disturbed area. Beyond this, multivariate similarities were much more similar between samples (MVDISP decreases from 0.425 in 100 m zone to 0.179 for 250 m zone).

Schiehallion

General observations

At the Schiehallion site a total of 1133 megabenthic organisms from 17 nominal taxa were recorded from a total area of 2715 m^2 (Table 1). Porifera were the dominant group (62% megafauna, 2819 ha^{-1}) followed by Echinodermata (26% megafauna, 1170 ha^{-1}) which were dominated by *Cidaris cidaris* urchins, the holothurian *Stichopus tremulus* and various asteroids (*Porania pulvillus pulvillus, Ceramaster granularis, Asterias rubens* and *Henricia pertusa*). Crustaceans (11% total megafauna, 495 ha^{-1}) were predominantly represented by *Munida sarsii* but also included hermit crabs, *Geryon* sp. and *Cancer pagarus*. The remainder (1%) of the megabenthos comprised molluscs and polychaetes. In the area of drill spoil fish were present (predominantly *Gadus morhua*, *Helicolenus dactylopterus dactylopterus* and *Molva molva*), and were most abundant around drilling structures although in lesser numbers than at Foinaven.

At Schiehallion, despite there being only one drill site, the extent of spoil was greater than at Foinaven, extending to over 155 m in places. Outside the disturbed area the seabed consisted of a heterogeneous mix of sand, gravel and occasionally larger cobbles and boulders.

Abundance

Large changes in abundance with distance from drilling activity were observed, particularly for dominant phyla. Megafaunal abundance (Figure 3B) was significantly different between zones (Kruskal-Wallis H = 15.45, df = 3, $p < 0.001$); increasing with distance from drilling activity (r´ = 0.982, $p < 0.001$). A large increase in abundance between 0-50 and 50-100 m from drilling activity was noted for major faunal groups with post-hoc non-parametric multiple comparisons of total faunal abundance (after Miller 1981) revealing significant differences ($p < 0.05$) between the 0-50 m zone and all other zones but no significant differences between zones > 50 m from the drilling disturbance. Both motile and sessile taxa abundances were significantly different between zones (Kruskal-Wallis: motile: $H = 26.96$, $df = 3$, $p < 0.001$; sessile: $H = 8.11$, $df = 3$, $p < 0.05$). Sessile taxa abundance increased continuously with distance from disturbance while motile faunal abundances peaked at intermediate distances before declining again between 150-200 m.

Diversity

Species richness was low close to the source of disturbance, increased to a maximum in the 150 m zone and dropped slightly in the zone furthest from disturbance (Figure 4B). Significant differences in heterogeneity diversity were observed between zones in H´ (Kruskal-Wallis $H = 17.63$, $df = 3$, $p < 0.001$; Figure 4B), owing to depressed megafaunal diversity in the 50 m zone (particularly in indices weighted towards rarer species). Outside this zone there was no significant difference in H´ (post-hoc non-parametric multiple comparisons $p > 0.05$).

Composition

Multivariate analyses (Figure 5&6) showed significant differences in megafaunal assemblages with distance from disturbance (ANOSIM $R = 0.26$, $p < 0.05$). The fauna in the 50 m zone were highly scattered in the MDS ordination (65.86% similarity). While distinct from other stations, the 50 m zone samples had high within zone dispersion of samples (MVDISP = 1.24). Beyond this transition zone diversity was high and distance from the source of drilling did not appreciably affect the assemblage, all of these outer zones formed a grouping on the MDS plot and showed high similarity with cluster analysis (> 85%; Figure 5&6). There was relatively low dispersion of within zone samples (mean MVDISP = 0.93).

Comparison between sites

Total megafaunal abundance was higher in Foinaven except in the areas less than 50 m from the source of disturbance. Motile faunal abundance followed similar patterns at both sites but was typically around 4 times greater in Foinaven. Sessile faunal abundances were considerably lower close to disturbance in Foinaven but were approximately equal outside this area.

Megafaunal species richness and heterogeneity diversity were significantly lower at Schiehallion when compared to Foinaven (based on grand site totals: Schiehallion S = 18, H´ = 1.66; Foinaven S = 33, H´ = 2.05) despite the larger survey extent at Schiehallion. Notable differences in megabenthic assemblage composition were observed between Schiehallion and Foinaven (ANOSIM R = 1.00, $p < 0.01$; Figure 6). Although 15 of the observed taxa were common to both areas, there were some notable differences in important taxa. For example *Cidaris cidaris* was the only echinoid observed at Schiehallion, however at Foinaven no cidarids were recorded and large numbers of *Echinus acutus* and other *Echinus* sp. urchins dominated instead. There were also differences amongst megafaunal scavengers: at Schiehallion crabs appeared to be predominant (particularly *Geryon* sp.), whereas at Foinaven these were not present and natant decapods and whelks were more common.

DISCUSSION

Changes in megabenthic assemblages with disturbance

The extent of disturbance was shown to drive changes in megafaunal abundance; low megafaunal numbers were associated with drill spoil and close to sites of recent drilling impact. Physical smothering and burial of organisms was likely to be the most important cause for reduction in megafaunal numbers (Stronkhorst et al. 2003). Highly motile organisms responded by moving away from the disturbance, as has been found in other studies (e.g. Bluhm 2001; Jones et al. 2006). For less motile taxa, reduced motility led to increased mortality. Where disturbance was partial, the megafaunal response to disturbance in this study was based not only on motility but also on feeding mode, particle removal rate and degree of disturbance.

Sessile megafauna increased in abundance with a reduction in disturbance. Impact of drilling disturbance on sessile forms was related directly to their ability to clear particles from their feeding and respiratory surfaces as shown in many sessile shallow-water organisms (Rogers 1990). Sessile megafauna were less disturbed at Schiehallion where abundance was significantly greater than Foinaven (particularly in the area close to disturbance) as a result of reduced overall disturbance. At the deep-water (600 m) Laggan site sessile fauna showed a similar response to Foinaven. The Laggan site is also situated in the Faroe-Shetland Channel (60°57´N, 02°53´W) in an area with similar substratum but colder seabed temperatures (-1 to 2° C) than those investigated here (Jones et al. 2006).

Megafaunal species diversity generally increased with distance from the point of disturbance as reduced levels of sedimentation increased survival of sessile and other less resilient organisms. Some diversity indices showed a small decrease in diversity at maximal distance and minimal disturbance. Diversity was depressed by high disturbance, but intermediate levels may have increased diversity levels through influx of vagrant scavenging animals or motile fauna taking advantage of decreased competition as a result of reduced numbers of dominant species (Connell 1978) as was also found to occur at Laggan (Jones et al. 2006). Multivariate measurements for the whole assemblage revealed an increased similarity of megabenthic assemblages with decreased disturbance. This trend has been commonly observed in community measures in many marine disturbance settings (Clarke and Warwick 2001) and also found at the Laggan site deeper in the Faroe-Shetland Channel (Jones et al. 2006).

Timing and extent of disturbance appears to have been an important factor in this study with the least disturbed Schiehallion site having less discernable changes in assemblage structure than the repeatedly disturbed Foinaven site. The Laggan site (Jones et al. 2006) had two drilling events similar to Schiehallion but relatively higher disturbance (greater coverage of drill spoil) and greater changes in assemblage structure were observed. Frequent disturbance has been shown to have dramatic and long lasting effects on shallow-water communities of the North Sea (Stronkhorst et al. 2003) and a similar effect would be expected in deeper water. It was apparent, however, that there was some immigration of selected mobile megafaunal taxa into disturbed zones, this also occurred at Laggan (Jones et al. 2006) and has been found in studies of fishing disturbance (Ramsay et al. 1998). With disturbance from drilling leading to reductions in suspension feeder abundance and an increase in availability of fine particles of high organic matter content it is likely that deposit feeding forms such as echinoids and holothurians may preferentially colonise drill spoil as individual animals can select and retain fine particles without the need to sort through more heterogeneous sediment complexes (Hudson et al. 2004). Although this study was based on two distinct points in time the first phases of recovery were already apparent.

Physical disturbance observed at the study sites resulted in complete coverage with sediment (presumed mortality) and potentially non-lethal effects from physical smothering. These effects have also been observed in studies on disposal grounds for dredged material (Stronkhorst et al. 2003), however the associated chemical changes were not investigated in this study. Increase in drilling derived particulates as a result of disturbance may have lead to non-lethal effects such as clogging of filter feeding apparatus of some organisms (Sharma et al. 2001). Although redistribution of nutrient rich subsurface layers could lead to an increase in population size over time (Raghukumar et al. 2001; Sharma et al. 2001), it is likely that the initial impacts of changes in seabed habitat will have had the dominant effect on the benthic communities.

The composition of seabed sediments changed as a result of drilling activity, from a heterogeneous substratum with extensive exposed hard surfaces to a homogeneous soft substratum. This change further reduced diversity and although changes are difficult to separate from those directly related to disturbance, reduction in habitat heterogeneity has been shown to reduce diversity in the deep sea (Levin et al. 2001). Smothering of existing sediment with that of a different composition resulted in conditions unfavourable to existing communities and would therefore reduce rates of re-colonisation and larval settlement, potentially prolonging recovery (Snelgrove et al. 1999). Changes in substratum may also have favoured particular faunal elements in the existing communities, increasing dominance and altering community composition.

Outside of the area impacted by drill spoil there was a highly heterogeneous distribution of benthic megafauna. Distribution of megafauna in these ‘natural’ seabed areas seems primarily driven by availability of suitable microhabitats as has been found elsewhere in the Faroe-Shetland Channel (Fautin et al. 2005; Tyler et al. 2005; Jones et al. 2006). The stochastic arrangement of ice rafted larger stones may have gone some way to structuring the distribution of megabenthos. Most sessile filter feeders lived attached to hard substrata; whereas many echinoderms preferred softer sediments, being more common on gravel and sandy areas of seabed. Many species, particularly *Munida sarsii* were cryptic, preferring to live under rocks. Strong currents (up to 0.5 ms^{-1}) observed at both sites may have had an important effect on the distribution of megafauna as have been observed by Rosenberg (1995) and Flach et al. (1998).

Comparison of the undisturbed assemblages of Schiehallion and Foinaven

Megafaunal abundance at both sites was variable (from 1,900 to 16,483 individuals ha^{-1} at Foinaven and from 2,178 to 5,626 individuals ha^{-1} at Schiehallion). Megabenthic abundance has generally been found to decrease with depth (Thurston et al. 1994; Piepenburg et al. 2001); however in the Faroe-Shetland Channel the situation is more complex, with warm Atlantic waters overlaying cold Arctic water (Turrell et al. 1999) with some indication of higher macrofaunal abundances in the deeper cold water compared with the shallower warmer waters (Bett 2001). Results from this study and Jones et al. (2006) suggest this may extend to megafauna. At Foinaven megafaunal abundances were higher than that of Schiehallion. The fauna at Foinaven were at a depth where they must experience wide temperature variations (of around 5°C: from -0.5 to 4.5°C), with abundances similar to those found at deeper sites (e.g. Laggan) characterised by Arctic water masses with temperatures between -1 and 2°C (Jones et al. 2006), however few representatives of the typical Arctic faunas found at greater depths in the Faroe-Shetland Channel extend into the present study sites (Jones et al. 2006). Comparison with the Atlantic fauna of the Rockall Trough, south of the Wyville-Thomson Ridge, revealed similar assemblages, particularly to those at Schiehallion (Gage 1986) although comparable megafaunal abundance values are not quoted. These comparisons suggest stronger affinities between the shallow Faroe-Shetland Channel and the northeast Atlantic rather than with the Norwegian Basin and other northern waters.

Megafaunal species richness values were recalculated as $ES_{(70)}$ for comparison with other literature (10.8 to 15.1 for Foinaven; 9.3 to 10.7 for Schiehallion). Species richness at Laggan ($ES_{(70)}$ for Laggan between 11.7 and 12.2) was comparable with Foinaven but higher than Schiehallion. This supports the hypothesis that megafaunal richness patterns are similar to those found in macrofauna, with increased diversity at intermediate depths in the Faroe-Shetland Channel (Bett 2001; Narayanaswamy et al. 2005). Richness in this study was high in comparison with the Arctic stations investigated by Starmans and Gutt (2002) although these were within the confidence limits for the more diverse shallow Greenland station (Starmans and Gutt 2002). In comparison with the Atlantic, although direct megafaunal diversity measures are unavailable, from species tables and figures it appears that megafaunal diversity in the two areas was similar, with a similar species complement (Gage 1986; Gage et al. 2000).

There was a clear difference in megafaunal species composition between Foinaven and Schiehallion; this is likely to be predominantly driven by temperature. The fauna at the Schiehallion and Foinaven sites are in an area of natural transition between those organisms more typical of the Atlantic in the warmer shallower waters of the Faroe-Shetland Channel, and those more typical of the Arctic deep Norwegian Sea (Bett 2001). The boundary between warm and cold waters in the Faroe-Shetland Channel oscillates between 400-600 m (Turrell et al. 1999). The fauna of Schiehallion therefore predominantly live in comparatively warm Atlantic waters. The fauna of Foinaven on the other hand is subject to extreme changes in temperature over very short time scales. The fauna at Laggan, living in constantly cold temperatures, was different again from Foinaven, with only 5 taxa common to both areas (Jones et al. 2006). Hydrographic regimes are important in structuring benthic communities (Gage et al. 1995), and environmental temperature is a major contributing factor governing the range of species found in marine communities (Gage and Tyler 1991) particularly in the Faroe-Shetland Channel (Bett 2001; Narayanaswamy et al. 2005). It is also likely that differences in specific taxa may be related to bathymetric gradients in faunal distribution (Gage and Tyler 1982; Rex et al. 1997).

This study represents an important step forward in quantifying the effects of anthropogenic disturbance across a number of sites in deep waters, being especially relevant in the context of increasing hydrocarbon drilling at deep-water sites. The use of ROVs for monitoring has been shown to be highly effective in studies of this nature, which, as this technology is routinely used in these developments, may increase industry and science collaboration initiatives in monitoring disturbance and the subsequent recovery of benthic assemblages. Disturbance was shown to have important effects on benthic assemblages particularly through smothering and resultant habitat changes. These changes were difficult to predict, based on individual species ecology but the study of assemblage parameters such as abundance, diversity and faunal distribution reveals the ecosystem level effects of disturbance. This work also provides the foundation for future studies monitoring faunal recovery in these areas. It also helps to identify targets for future directed *in situ* ROV experimental studies of individual species responses to anthropogenic disturbance.

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FIGURES

Figure 1: Bathymetry of the West of Shetland area, north of Scotland, UK, showing the position of the sampling sites at the Schiehallion and Foinaven fields (cross symbol). Laggan site also identified (star symbol) for comparison with Jones et al. (2006).

Figure 2: ROV video transects conducted at Foinaven and Schiehallion fields, West of Shetland, showing the extent of the visible drill spoil, subsea structures and 50m zones radiating from sources of disturbance.

Figure 3: Abundances of motile and sessile megafauna in Foinaven (A) and Schiehallion (B) fields, West of Shetland. Error bars represent 95% confidence intervals derived from bootstrapping.

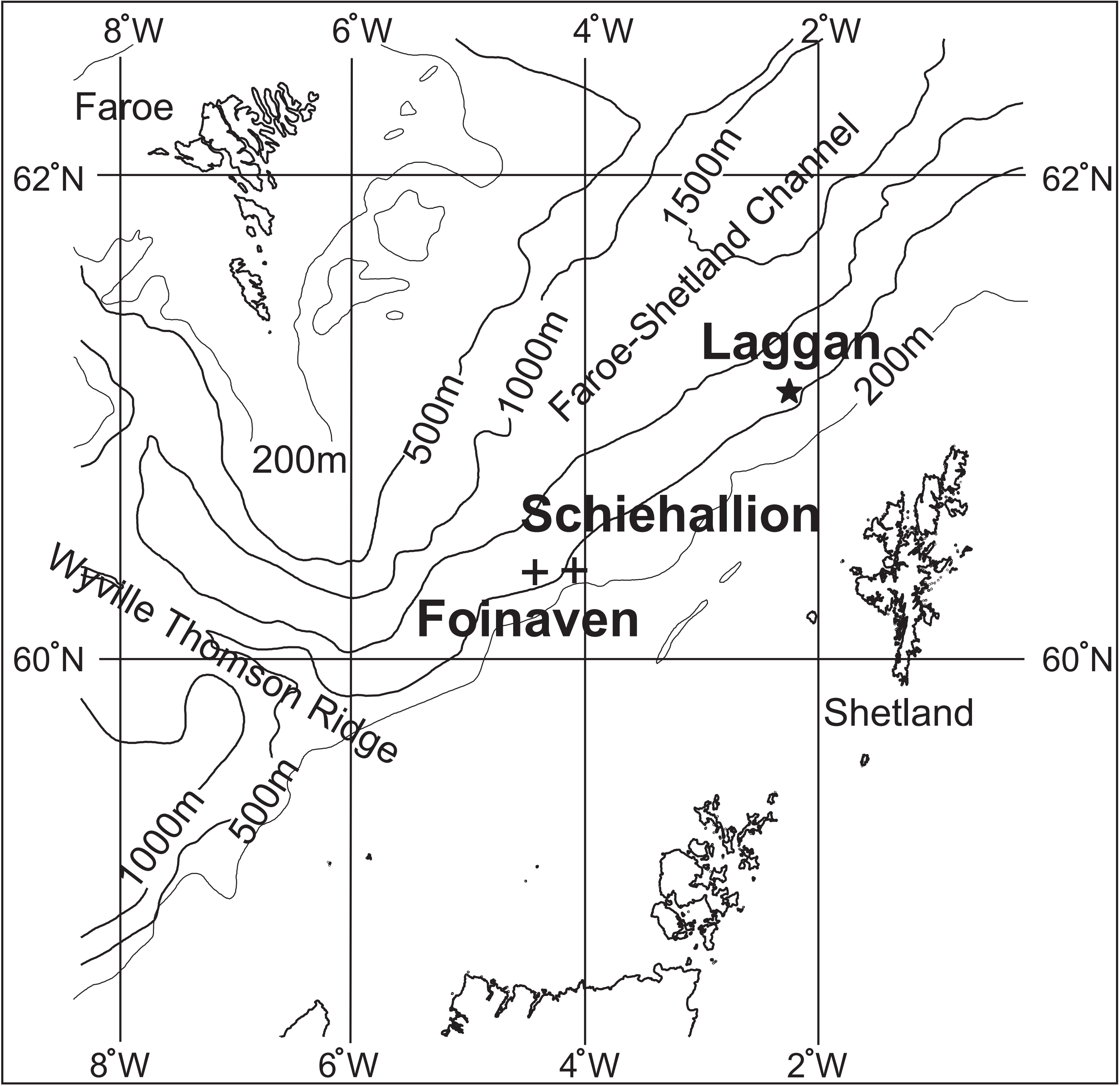
Figure 4: Alpha species diversity from ROV video survey of megabenthos in Foinaven (A) and Schiehallion (B) fields, West of Shetland. Shannon-Wiener Index, (H´ log e), Total number of taxa observed (S), plotted with distance zones from source of disturbance.

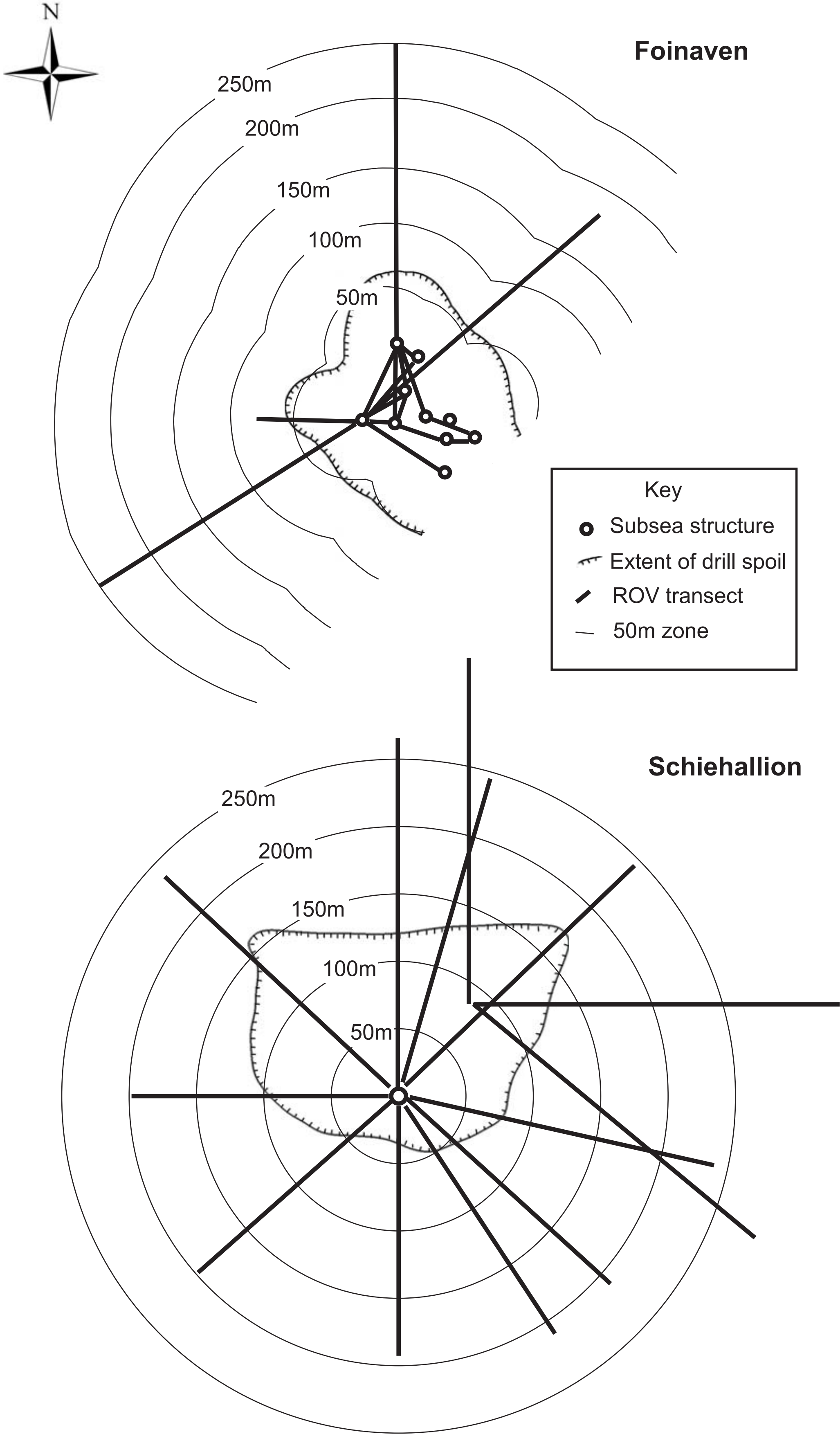
Figure 5: Multidimensional scaling ordination (based on Bray-Curtis similarities computed from root transformed abundances) of megafauna from ROV video footage in 50m zones from drilling disturbance at Foinaven and Schiehallion fields, West of Shetland.

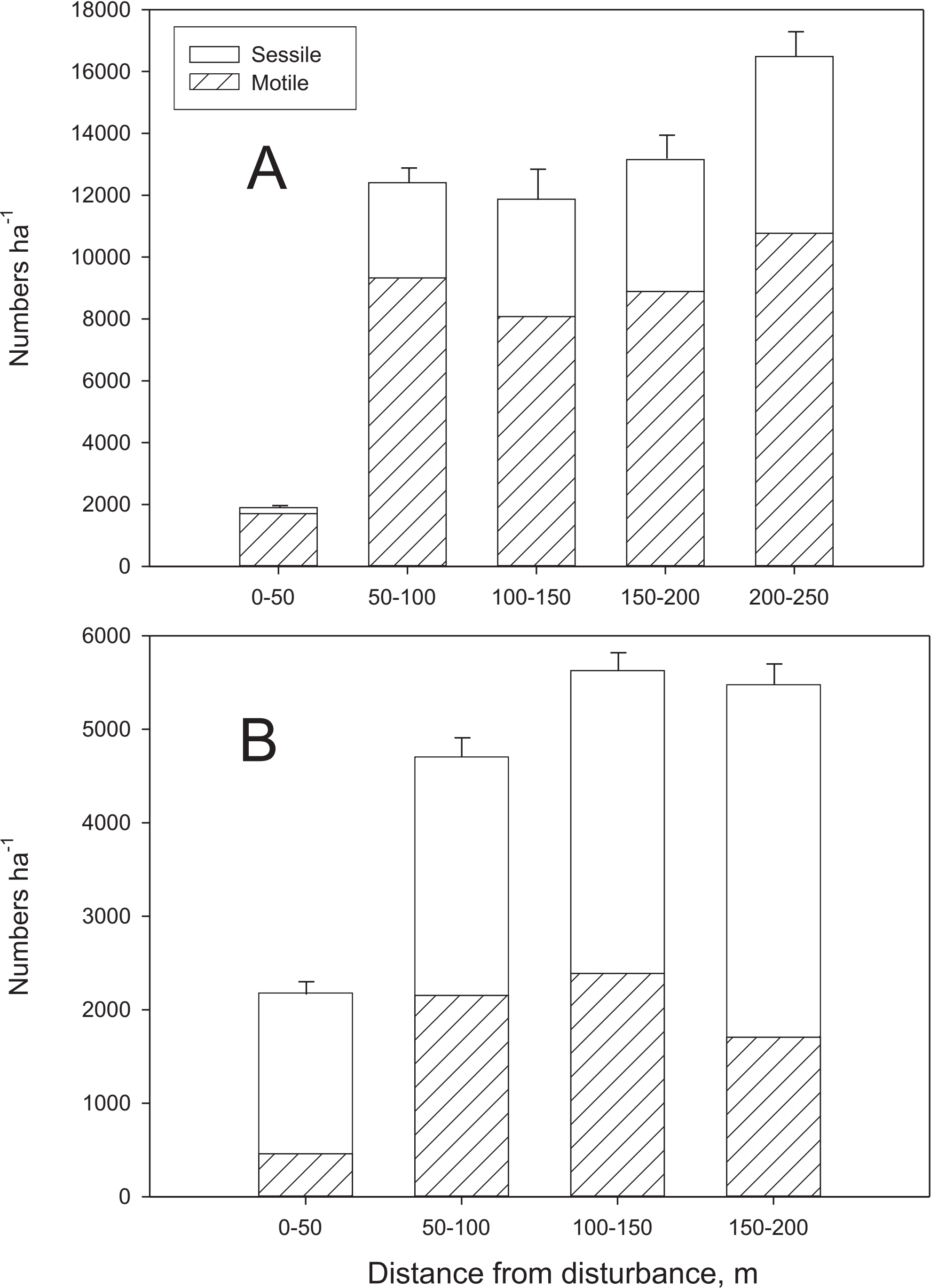
Figure 6: Percentage similarity of ROV megafaunal video transects based on Hierarchical cluster analysis (based on Bray-Curtis similarities of root transformed abundances) of megafauna from ROV video footage in 50m zones radiating from drilling disturbance at Foinaven and Schiehallion fields, West of Shetland.

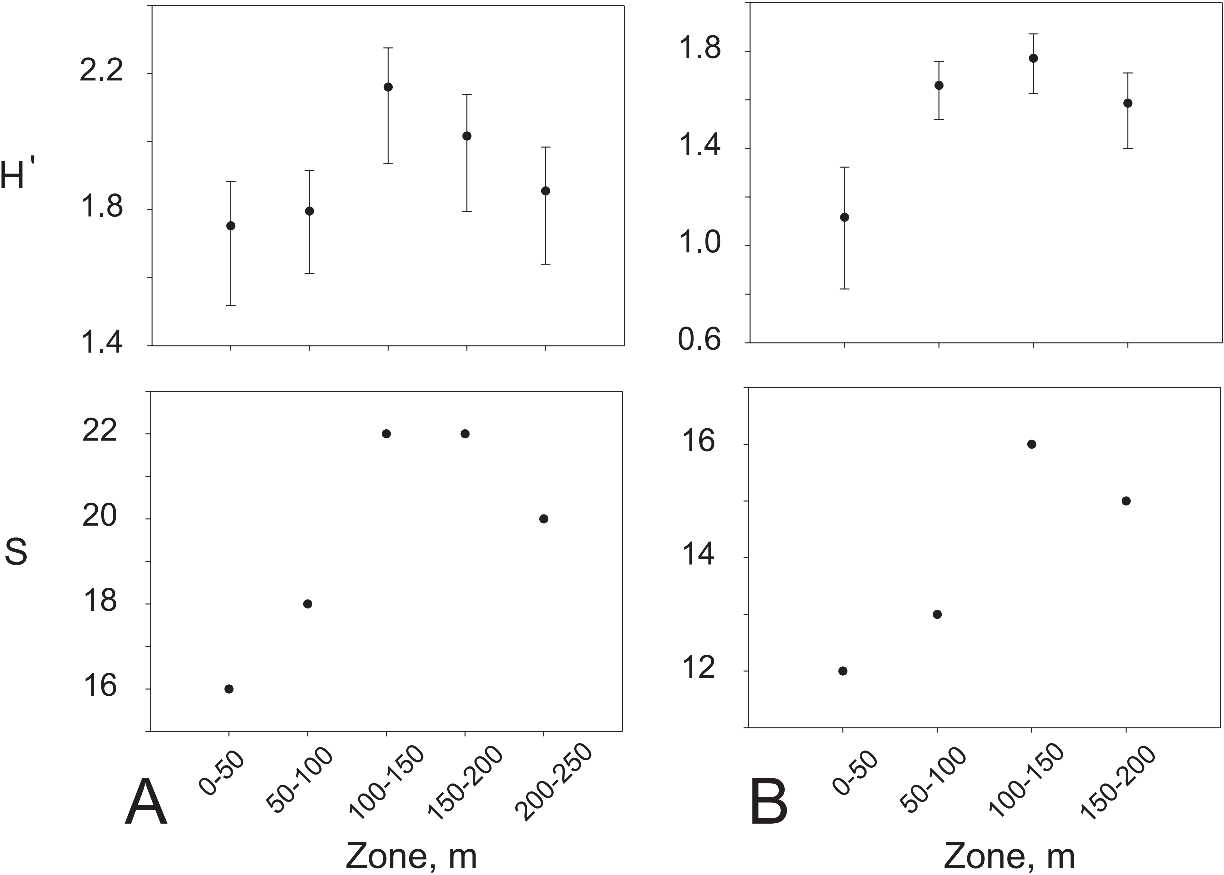
TABLES

Table 1: Densities of megafaunal taxa within concentric 50 m zones around two oil drilling sites, Foinaven and Schiehallion, West of Shetland. Species densities (no ha^{-1}) tabulated by distance from source of disturbance (50 meter distance zones).

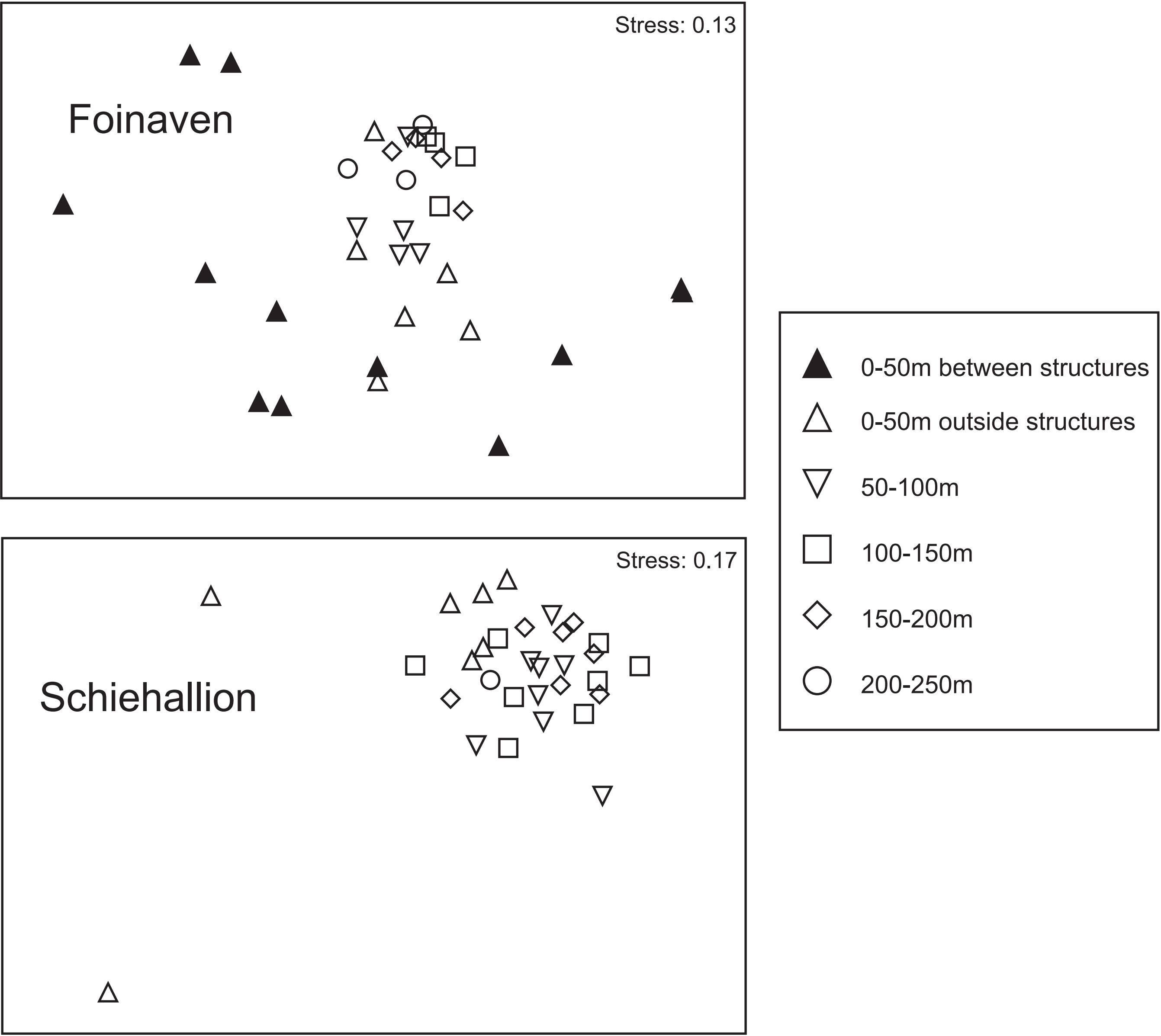

8°W
6°W
4°W
2°W
Faroe
62°N
62°N
1500m
Faroe-Shetland Channel
1000m
500m
200m
Laggan
200m
Schiehallion
Foinaven
Wyville Thomson Ridge
60°N
60°N
Shetland
1000m
500m
8°W
6°W
4°W
2°W


N
Foinaven
250m
200m
150m
100m
50m
Key
Subsea structure
Extent of drill spoil
ROV transect
50m zone
Schiehallion
250m
200m
150m
100m
50m


A
Sessile
Motile
Numbers ha^{-1}
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
0-50
50-100
100-150
150-200
200-250
B
6000
5000
4000
3000
2000
1000
0
0-50
50-100
100-150
150-200
Distance from disturbance, m



H'
2.2
1.8
1.4
1.8
1.4
1.0
0.6
S
22
20
18
16
16
14
12
0-50
50-100
100-150
150-200
200-250
A
0-50
50-100
100-150
150-200
B
Zone, m
Zone, m


Stress: 0.13
Foinaven
Stress: 0.17
Schiehallion
0-50m between structures
0-50m outside structures
50-100m
100-150m
150-200m
200-250m

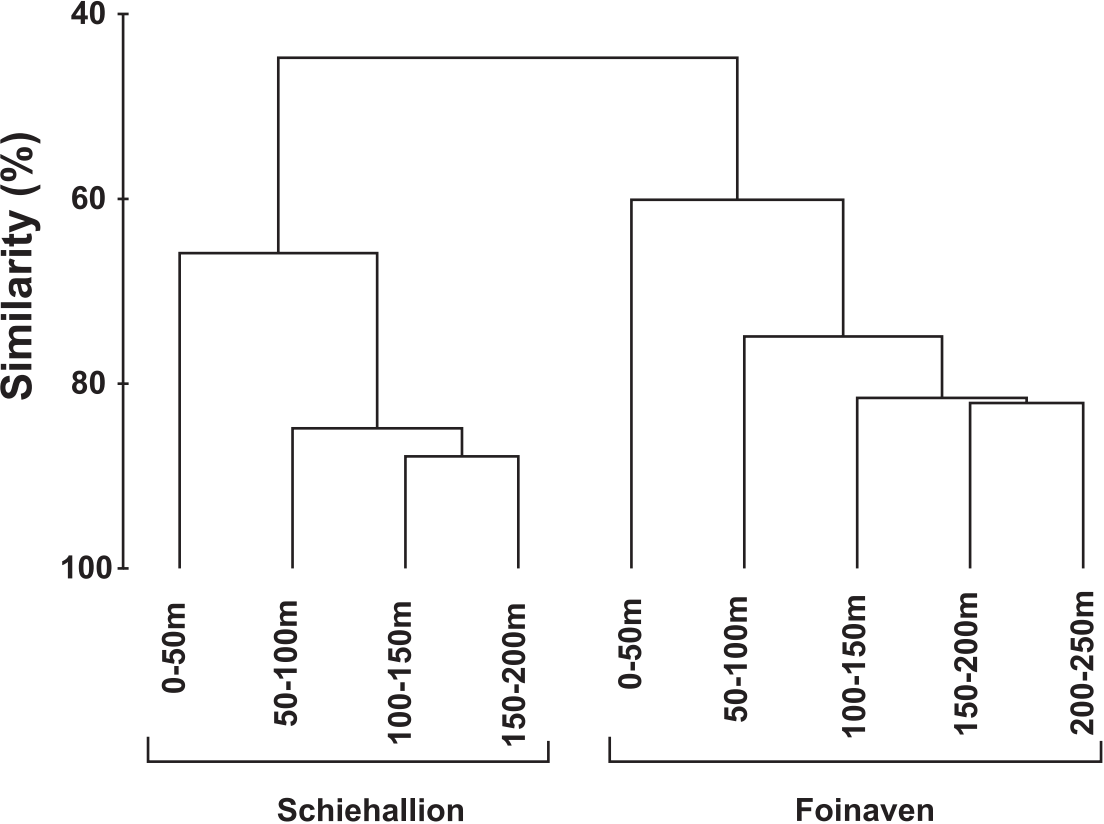

Similarity (%)
40
60
80
100
0-50m
50-100m
100-150m
150-200m
0-50m
50-100m
100-150m
150-200m
200-250m
Schiehallion
Foinaven

Table 1:

Phylum	Class	Species	Foinaven 0-50	Foinaven 50-100	Foinaven 100-150	Foinaven 150-200	Foinaven 200-250	Schiehallion 0-50	Schiehallion 50-100	Schiehallion 100-150	Schiehallion 150-200
Porifera	demospongia	Indet. sponge 1				12		18	44	29	18
		Indet. sponge 2		192	824	3	22				
		Indet. sponge 3				6					
		Indet. sponge 4	12	192	165	24	44	35	117	352	233
		Indet. sponge 5	169	1779	1319	212	4176	1611	2168	255	3142
		Hymedesmia paupertas?		48		12	73			44	9
		Indet. encrusting sponge 1			22	12					
		Indet. encrusting sponge 2			55						
		Indet. encrusting sponge 3		336	495	24	293	18	13	59	9
		Aplysilla sulphurea?		529	659	91	513	35	117	249	198
Cnidaria	actiniaria	Indet. actinarian 1			55						
		Indet. actinarian 2	12			6					
Annelida	polychaeta - errantia	Indet. errant polychaete	12	96	549	3	73		15		
Mollusca	gastropoda	Indet. buccinid	12	48	22	12	513				
	bivalvia	Indet. pectenid		48	55					15	18
	cephalopoda	*Sepiola atlantica*			55						
Arthropoda	decapoda	*Pandalus borealis*	61		165						
		Geryon sp.						18	15	29	72
		Pagarus sp.	36	192	385	18	147			15	
		Cancer pagarus									18
		Munida sarsii	666	69	555	65	733	89	791	63	35
	amphipoda	*Siphonocetes* sp.	12	144	55	12					
Echinodermata	crinoidea	Indet. comatulid				12	147				
	ophiuroidea	Indet. ophiuroid	19	144		12	147				
	asteroidea	*Ceramaster granularis*		48	55	6	73	35	44	132	18
		Asterias rubens	12						29	29	36
		Henricia pertusa			55	6	147	53	132	161	18
		Porania pulvillus pulvillus			55			18		15	
	echinoidea	Indet. echinothurid	641	1634	824	121	1538				
		Echinus acutus		48			73				
		Echinus sp.	12	144	165	48	293				
		Cidaris cidaris						177	835	1143	88
	holothuria	*Stichopus tremulus*	19	769	385	3	44	71	293	22	233
Chordata	chondrichthyes	*Chimaera monstrosa*	12				73				
	osteichthyes	*Lophius piscatorius*	12								
		Paraliparis sp.					73				
Total		Abundance	1900	12402	11868	13151	16484	2178	4703	5626	5477
		Number of taxa	16	18	22	22	20	12	13	16	15