Benthic ecology of pockmarks in the Inner Oslofjord, Norway

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ABSTRACT: Despite pockmarks being one of the most widespread small-scale topographic features of the seabed, almost nothing is known of their influence on fauna. Here we present the first ecological study of fjordic pockmarks, focusing on the contrast between macrofauna inside and outside of these craters. We report an analysis of macrofauna from 27 pockmarks of the Inner Oslofjord, Norway. Five replicate grab samples were collected from each of 3 pockmarks at 3 sites plus a further control (non-pockmark) sample at each site. A single grab sample was collected from an additional 3 pockmarks at 6 sites and 6 control locations. We compared macrofaunal assemblages inside and outside of pockmarks and found important but subtle differences to those on non-pockmarked substrata. The fauna of pockmarks were typical of a disturbed fjord environment with a dominance of small opportunistic taxa, such as pioneer bivalves and polychaetes. The position of sites in the fjord gradient drove the most obvious faunal differences, but contrary to expectations, we could find no influence of pockmarks on the composition of the fauna at any taxonomic level. This makes them very unusual amongst marine topographic features, which usually have considerable influence on the nature of benthic communities. However, we found that pockmarks do significantly alter the abundances of key species and, as such, we suggest that the presence of pockmarks in the Oslofjord has a considerable cumulative influence on densities and populations of benthic organisms.

KEY WORDS: Benthic community · Pockmarks · Oslofjord · Environmental factors

INTRODUCTION

Heterogeneity of the seabed can be very important in the generation and maintenance of biodiversity due to creation of more varied gradients of hydrography and grain size and the provision of refuge from predation and trawling (Thrush et al. 2006). Bioconstructors, particularly hermatypic corals in tropic shallows, provide strong benthic heterogeneity. In the polar regions ice impacting the bottom in shallow waters creates scours that can shape the seabed considerably. King & Maclean (1970) described a more geographically and bathymetrically ubiquitous seabed topographic feature, pockmarks. These crater-like depressions in soft-sediments are now recognised as a common feature across oceans, including the Barents Sea (Harrington 1985), the equatorial West African continental slope (Pilcher & Argent 2007), the Bering Sea (Nelson et al. 1979) and the North Sea (Hovland 1984). They range in size from less than 1 m to over 4 km in diameter, with depression depths of 1 m to over 200 m, and occur in densities of up to 1340 km^{-2} (Nelson et al. 1979). They do not exhibit strongly raised rims, and their internal slopes range from 2 to 35° with conical to flat centres. To date, pockmarks have been found in clay, silt and sand at water depths from 6 to 4800 m (Fader 1991) in a variety of environments including the deep ocean, continental shelves, slopes, estuaries, fjords and even some lakes (Hovland & Judd 1988). Despite their recent discovery it seems they may be one of the most widespread small-scale structural features on the seabed.

A number of mechanisms may be responsible for pockmark formation (Paull et al. 1999), but the majority of studies consider that fluid or gas expulsion from sediments is the most likely. Proposed and observed agents include biogenic or thermogenic methane (Scanlon & Knebel 1989), sulphides, meteoric (artesian) groundwater from land (Khandriche & Werner 1995) and pore water driven out as a result of compaction (Harrington 1985). The maintenance of pockmarks is thought to be caused by sporadic or continuous seeping of gas or fluids, or by local currents. Research into pockmarks has mainly concentrated on their geological and geophysical aspects. They have been considered geohazards by offshore construction industries (Hovland 1989) and possible indicators of hydrocarbon sources for prospecting (Whiticar & Werner 1981). The few studies on the ecology associated with pockmarks have mainly described observations made using remotely operated vehicles (ROV) during geological surveys. However, the importance of pockmarks may be more than merely increasing heterogeneity, biodiversity and refuges for biota; they may help explain the paradox of why an apparently uniform seafloor contains so many species.

Support for higher biodiversity associated with pockmarks does exist. Hovland & Judd (1988) found that North Sea pockmarks had spectacularly higher biological productivity compared with surrounding sediment. The large complex 'Regab' pockmark on the Gabon continental margin seems to contain a novel and important fauna, chemosynthetic communities and carbonate concretions (Ondréas et al. 2005, Gay et al. 2006, Olu-Le Roy et al. 2007). Three pockmarks farther north of the 'Regab' pockmark also seem to contain a high abundance of typical seep fauna (vesicomyid clams and vestimentiferan worms) (Sahling et al. 2008). Pockmarks have also been linked to reefs of cold-water corals in the North Sea by Hovland (2005) and off the coast of Brazil by Sumida et al. (2004). The observed co-occurrence between corals and pockmarks may be linked to gas and pore water from the pockmark stimulating coral growth by providing nutrients from bacteria and micro-organisms or protection from disturbance (Webb et al. in press).

Although pockmarks are ubiquitous (at least in the Atlantic Ocean) and they have putatively been linked to increased biodiversity, only 2 papers have examined the biology and ecology of pockmark macrofauna in any detail (Dando et al. 1991, Wildish et al. 2008). Dando et al. (1991) reported that the fauna of a North Sea pockmark was characterised by 2 species not previously reported from the area, the bivalve *Thyasira sarsi* and the nematode *Astomonema* sp., both of which contain endosymbiotic bacteria. The flat centre of the pockmarks had impoverished macrofauna and nema-

todes, which the authors ascribed to the consolidated clay in the surface layers. Wildish et al. (2008) is the only study to investigate variability in biodiversity and ecology across pockmarks. These investigators concluded that of 14 pockmarks studied in detail 5 (their 'upper habitat A') were at a pre-equilibrium succession, whilst 9 (their 'lower habitat A') were at or near equilibrium.

It seems intuitively reasonable that fauna in a depression such as a pockmark will be protected to some degree from physical disturbance (e.g. trawling), but leakage of methane or fluids may also influence species in various ways, e.g. by increasing food availability for chemotrophic organisms or by physical disturbance. The aim of the present study was to investigate whether the newly discovered pockmarks in the Inner Oslofjord, Norway, have characteristic fauna and, if so, how they differ from fauna in non-pockmarked areas of seabed. Due to the lack of conclusive evidence of biodiversity enhancement, deduced from previous remotely operated vehicle (ROV) surveys (Webb et al. 2009), we hypothesised that the fauna would not significantly differ within and outside pockmarks in terms of abundance, richness or composition. In contrast to any previous pockmark study, we investigated the influence of various environmental factors on species composition and, importantly, our comparisons were made at a range of spatial scales within the fjord. This also represents the first description of the ecology of pockmarks in a postglacial fjord.

MATERIALS AND METHODS

Study site. Pockmarks were sampled in the Inner Oslofjord, Norway (59° 50' N, 10° 34' E). Over 500 pockmarks have recently been discovered in this area (Webb et al. 2009). The Oslofjord extends over 100 km northwards from the Skagerrak and 30 km north from Drøbak, where a sill at a depth of 19 m separates the inner from the outer fjord (Fig. 1). This sill restricts water circulation and exchange, and the renewal of deep waters in the inner fjord (Gade 1968). The inner fjord consists of 2 natural basins, Vestfjorden and Bunnefjorden, separated by a 50 m plateau. The Vestfjorden and Bunnefjorden have maximum depths of 173 and 155 m, respectively. The surface area of the inner fjord is 195 km^2 and the total volume of water is about 9.4×10^9 m^3 (Mirza & Gray 1981). Pockmarks have been found between 14 and 71 m depth, and their distribution appears to be correlated with the underlying bedrock faults (Webb et al. 2009). These pockmarks range in diameter from 16 to 100 m (mean diameter 20 m) with depths ranging from 1 to 12 m below the surrounding seabed (mean depth 3.8 m).

Fig. 1. The Inner Oslofjord, showing the distribution of circular pockmarks (•)

The tidal influence on the Inner Oslofjord is low, with mean ranges between 52 and 80 cm. A pycnocline is normally present from April to September and most water exchange takes place in winter months, initiated by northerly winds. Brackish water in the upper few metres of the water column flows out of the fjord driven by surface currents, and more saline bottom water flows in. Deep water in the fjord has salinities of 33 to 34. The Oslofjord is characterised by both stagnation and eutrophication effects (Mirza & Gray 1981). The substratum consists of glacial and postglacial sediments, which fill the trenches and valleys of the glacially eroded bedrock.

Sampling protocol. Sampling took place in summer 2006 using the RV 'Trygve Braarud.' Sampling locations were selected using high resolution bathymetric data previously collected by the Geological Survey of Norway (NGU). ArcGIS (Environmental Systems Research Institute [ESRI]) was used to generate bathymetric maps and georeference pockmark locations in the Inner Oslofjord.

This showed the number and location of all pockmarks. A total of 27 pockmarks were sampled in the present study. These were selected so that their spatial distribution was representative of conditions throughout the entire inner fjord. Three pockmarks were investigated at each of 9 sites. Using the bathymetric maps, 15 non-pockmarked reference locations were selected to be in a similar depositional setting as the sampled pockmarks but at least 100 m from the edge of any pockmark (Fig. 2). These reference locations were labelled C1 to C15, whilst the pockmarks had identification labels that related to previous geological studies (described by Webb et al. 2009). The pockmark depths, diameters and the surrounding water depths were recorded for each pockmark studied.

Grab samples were taken within each sampling location using a van Veen grab (0.1 m^2 sampling area). Positioning of the grab in the centre of the pockmark was based on positions taken from the bathymetric maps processed in ArcGIS and depth readings from the echosounder and grab winch system. Five grabs were taken at pockmark locations 58, 56, 54, 78, 73, 76, 89, 86 and 82 and reference locations C4, C5 and C6. The 5 replicate grabs were within 10 m of each other. These were taken from the deepest central parts of the pockmark to ensure they sampled equivalent areas. At all other locations, 1 grab was taken from the centre of each pockmark, giving a total of 63 pockmark grab samples and 27 non-pockmarked reference samples. The Oslofjord pockmarks do not exhibit discrete zones of slopes and bottoms, as defined in other pockmark studies (see Wildish et al. 2008). Their shape was more akin to rotated cosines, with a continuous gradation in slope, and it was not possible to define a line separating the bottom from the sloped sides. Redox and pH were measured immediately using a pH/Redox 340i probe (WTW) for every grab sample. Macrofaunal samples were washed through a 1 mm round-holed sieve and the retained fauna were fixed in 4% formalin and stained with rose bengal. In the laboratory, samples were washed, sorted and preserved in 70% ethanol. All macrofauna were identified to the lowest possible taxonomic level (typically species) and enumerated.

Additional samples were collected by a multicorer, with single cores of 10 cm internal diameter from 9 of the selected pockmarks (58, 56, 54, 78, 73, 76, 89, 86 and 82) and 3 reference locations (C4, C5 and C6) (Fig. 2). Dissolved oxygen (DO) and salinity were measured immediately on board using a DO 200 probe (VWR) and
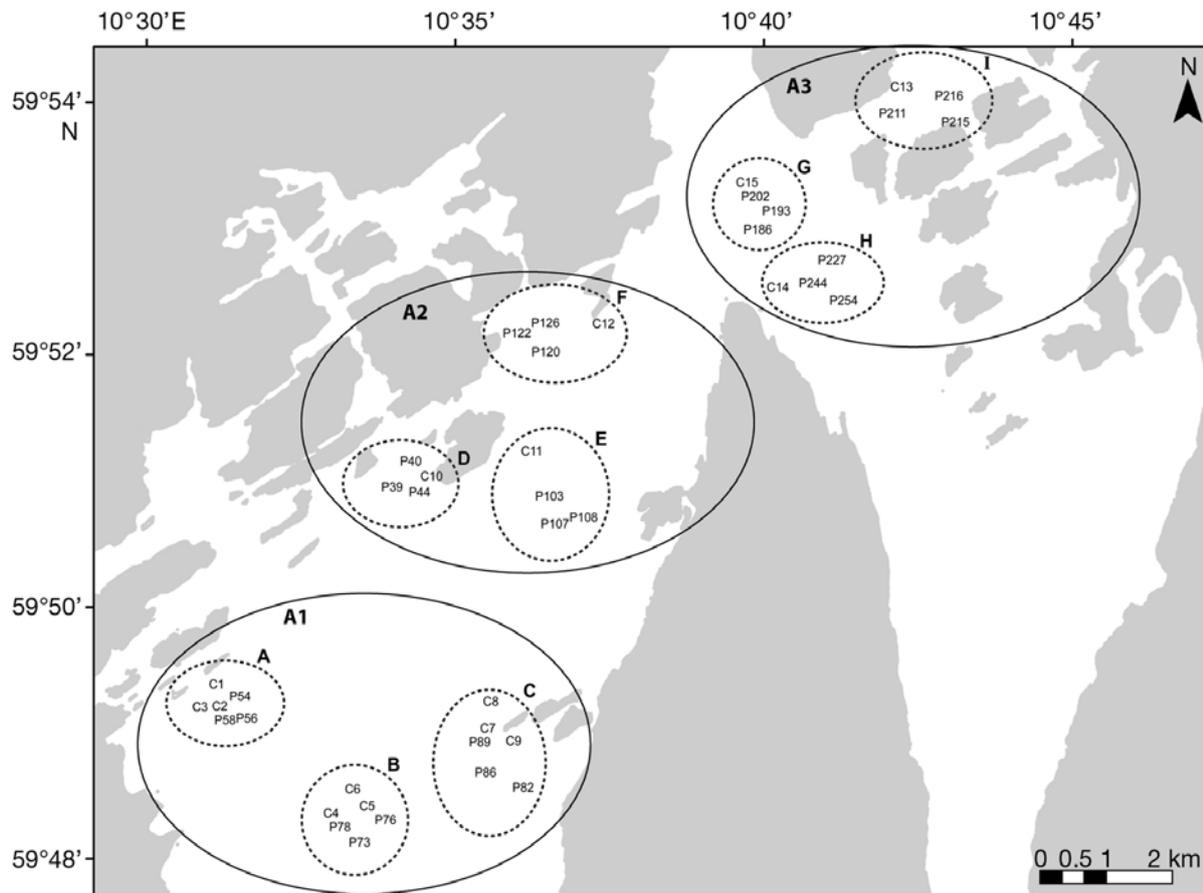
Fig. 2. Sampling structure across 3 spatial scales. The samples were divided into 3 areas (A1, A2, A3) and 9 sites (A to I) shown by the ellipses. Each location has a unique identifier: P indicates pockmark locations; C indicates reference locations outside of pockmarks

EC300 (VWR). The top 4 cm of each core was stored and frozen at –20°C for analysis of sediment and grain size and measurement of total organic carbon (TOC) and N. Grain size was determined by a combined method involving wet sieving for coarse fractions (>63 µm) and SediGraph for the fine fractions (<63 µm). The percentage of mud and the mean geometric grain size were calculated using the Gradistat software (Blott & Pye 2001). The analyses of TOC and total inorganic carbon (TIC) were carried out at the Department of Geosciences, University of Oslo. Pre-acidified samples (1 M HCl) were analysed using a C-412 carbon analyser (LECO). Samples were heated in a pure oxygen atmosphere to 1350°C where the oxidised carbon (CO_2) was measured with an infrared CO_2 detector. The inorganic carbon was calculated as the difference between the acid-treated sample (TOC) and the bulk sample.

Statistical analysis. The two taxonomic groups, Nematoda and Calanoida (Copepoda), were excluded from the data analysis as they are not properly sampled by the methods used. Species abundance data for 63 pockmark grabs and 27 grabs from non-pockmarked

locations were used in the analysis. Macrofaunal taxa were compared inside and outside of the pockmarks (inside/outside) using reference and pockmark locations. Further groupings were structured by site (A, B, C, D, E, F, G, H and I) and area (A1, A2 and A3) (Fig. 2). Species data were summarised by the following diversity indices: species richness (*S*), number of individuals (N), Shannon-Wiener diversity (*H'* [$\log_e$]) and Pielou's coefficient of evenness (*J'*). The comparison of these indices, inside and outside the pockmarks, was made by estimating variance components at the different scales. We used a general linear mixed effects model (GLMM), which incorporated random variation at different scales to allow for the nested structure of our sampling design. Area and inside/outside were included as fixed effects with sites, locations within sites and grabs within locations as random effects. We further tested the effects of site by fitting the model with site effects as fixed. Numbers of individuals (N) were not normally distributed and so these data were log transformed to comply with assumptions for GLMM analysis.

Multivariate statistics were applied using PRIMER v. 6 (Clarke & Warwick 2001) to determine underlying patterns of community structure. To reduce the influence of highly abundant species, species abundance values were square root transformed before calculating a similarity matrix based on the Bray-Curtis similarity measure. The relatedness of inside and outside pockmark samples was assessed using non-metric multidimensional scaling ordination (nMDS). Two-way analysis of similarities (ANOSIM) was carried out to determine whether site, or inside and outside of the pockmarks were significant predictors of faunal composition. Taxa that contributed most to the observed differences between samples from inside and outside of pockmarks, taking site into account, were determined by means of 2-way similarity percentage analyses (SIMPER).

Site B. Position within the fjord is known to play an important role in structuring the benthic assemblages. Therefore, one site in the fjord, Site B, was selected for a more detailed analysis including 8 environmental variables, removing the influence of location. The species abundance data for this site were ordinated using nMDS. A suite of environmental variables were chosen: redox (Eh), pH, TOC, geometric mean grain size (µm) (Folk & Ward 1957), percent mud, dissolved oxygen, C:N ratio and depth, which were all normalised before analysis. A principal component analysis (PCA), based on the correlation matrix between samples was used to analyse the environmental data from Site B (PRIMER). Environmental variables inside and outside of pockmarks were compared using ANOSIM (PRIMER). The relationships between the abundance of macrofauna and the environmental variables from Site B were investigated using the BIOENV procedure (PRIMER). The Spearman rank correlation coefficient (ρ^s) between the ranked biotic and environmental similarity matrices provided the basis for this procedure.

RESULTS

Combined analysis of all sites

The sampled locations had a mean water depth of 53 ± 7.5 m (mean ± SD) and the pockmarks had an average depth below the surrounding seabed of 5.0 ± 2.6 m, with the deepest pockmark sampled being 8.8 m in depth (Table 1).

A total of 144 taxa and 16 382 ind. were identified from 90 grabs, 63 grabs taken from inside pockmarks and 27 grabs from non-pockmarked locations. Infaunal polychaetes and bivalves dominated the samples, forming 64 and 29 %, respectively, of all the individuals sampled. The remaining 7 % comprised Crustacea, Echinodermata, Priapulida, Cnidaria, Sipunculida, Gastropoda and Aplacophora.

There were no significant differences in the biodiversity measures, S, N, H' and J', between the inside and outside of pockmarks. Position within the fjord had a significant effect on all biodiversity indices measured. H' ranged between 0.26 (grab P215) and 3.05 (grab P58E), indicating a low to moderate faunal diversity. Pielou's J' ranged from 0.24 (grab P215) to 0.94 (grab P58D), showing a low faunal dominance. Sites I and D had the lowest mean (±SD) diversities (0.82 ± 0.45 and 1.4 ± 0.58, respectively). The highest sample diversity was observed for P58E and P89D, with 3.05 and 3.03, respectively, and Sites A, B and C had the largest H' values, ranging from 2.2 ± 0.27 to 2.5 ± 0.35. The pockmark sample P215 from Site I only had 3 species and 81 ind. per 0.1 m^2 and the reference sample from this location, C13, had 3 species and 106 ind. per 0.1 m^2, indicating that these low diversity sites had high dominance of a few species. The lowest densities

Table 1. Morphology and location of sampled pockmarks. dd: decimal degrees

Site	Location	Water depth (m)	Pockmark depth (m)	Diameter (m)	Latitude (N) (dd)	Longitude (E) (dd)
P73	A	64.78	8.73	36.98	59.850266	10.563557
P76	A	52.77	4.85	23.21	59.853618	10.568678
P78	A	54.09	2.73	18.14	59.849553	10.570700
P54	B	46.23	2.28	19.42	59.823101	10.521260
P56	B	49.81	1.91	18.13	59.820215	10.522252
P58	B	46.81	2.54	18.86	59.820005	10.517106
P82	C	63.31	8.75	47.86	59.803424	10.552682
P86	C	52.10	7.07	31.98	59.806304	10.559787
P89	C	63.77	5.90	56.51	59.805463	10.547358
P39	D	39.10	3.33	20.28	59.810076	10.597155
P40	D	37.81	2.71	18.28	59.812266	10.586865
P44	D	43.31	4.07	21.86	59.816235	10.585484
P103	E	53.55	3.59	18.64	59.848500	10.605833
P107	E	61.63	7.60	49.90	59.844978	10.607412
P108	E	61.05	9.32	41.99	59.845624	10.613316
P120	F	44.82	4.52	23.71	59.867632	10.605684
P122	F	30.63	4.21	20.81	59.868854	10.601206
P126	F	32.86	3.71	21.54	59.871401	10.605901
P186	G	62.02	5.84	23.45	59.883076	10.663752
P193	G	53.73	2.26	20.79	59.885527	10.668789
P202	G	65.63	7.78	46.60	59.887392	10.663414
P227	H	50.33	4.90	22.98	59.898046	10.701203
P244	H	70.48	8.17	41.82	59.896572	10.717842
P254	H	71.15	8.84	52.62	59.900097	10.716165
P211	I	31.79	4.91	43.18	59.878690	10.683776
P215	I	26.56	2.70	23.18	59.875794	10.678467
P216	I	25.76	2.70	23.10	59.873446	10.686494

were recorded at locations P211 and P89A (26 to 32 ind. per $0.1\ m^2$) and the highest at locations P244, C14 and P202 (763 to 785 ind. per $0.1\ m^2$).

In the GLMM none of the responses showed a significant effect of the inside/outside criterion, although the results were suggestive of higher levels inside pockmarks of *H'* (Table 2). Site had the largest effect on *S* and log N, but the estimated components of variance had large standard errors. Area showed a significant difference in *J'* (Wald statistic = 15.51, p < 0.001). Running the model with site as a fixed effect showed highly significant differences between sites for all responses except *J'* (p < 0.001). Fixing site effects did not change the observed differences between in and out (Table 2).

The nMDS ordination of macrofaunal assemblages showed that position of sites within the fjord had an effect on sample groupings, with Sites D and I grouping separately (Fig. 3), but there was no obvious separation between pockmarks and non-pockmarked samples. Sites D and I had a low diversity and high

dominance of a few species. The species found to be typical in Site D were *Thyasira* sp., *Corbula gibba* and *Polydora* sp. and those typical in Site I were *Capitella capitata*, *Polydora* sp. and *Heteromastus filiformis*. However, ANOSIM indicated an overall significant difference in macrofaunal assemblages (Global R = 0.343, p = 0.01) inside and outside of the pockmarks. Position within the fjord had a significant effect on the species composition of samples (Global R = 0.596, p = 0.01). Pairwise comparisons were only considered between Sites A, B and C due to low sample sizes at the other sites, and these were all significantly different (p < 0.05).

The average Bray-Curtis similarity between all pairs of locations outside pockmarks was 44.69. Seven taxa made up about 50 % of the cumulative contribution for this similarity in locations outside of pockmarks, i.e. the bivalves *Nuculoma tenuis* and *Thyasira* sp. and the polychaetes *Chaetozone setosa*, *Pseudopolydora* sp., *Goniada maculata*, *Heteromastus filiformis* and *Pista cristata*. The average Bray-Curtis similarity
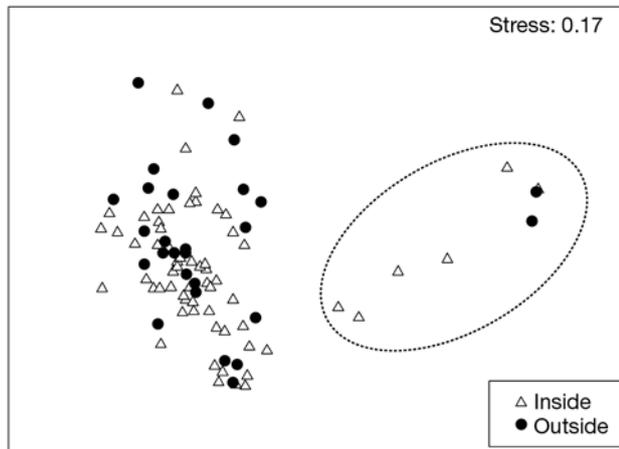

Fig. 3. Non-metric multidimensional scaling ordination (nMDS) of all species abundance data for inside and outside of the pockmarks. The dotted ellipse indicates grabs from locations at Sites D and I. (△) represents grabs from inside and (●) from outside of pockmarks

Table 3. Dominant taxa inside and outside of pockmarks in the Inner Oslofjord. The groups inside and outside of pockmarks had average similarities of 52.94 and 44.69, respectively

Dominant taxa	%	Cumulative %
Inside		
Nuculoma tenuis	13.41	13.41
Heteromastus filiformis	10.30	23.71
Goniada maculata	8.46	32.17
Thyasira sp.	7.97	40.14
Chaetozone setosa	5.39	45.52
Glycera alba	5.22	50.74
Outside		
Nuculoma tenuis	13.79	13.79
Chaetozone setosa	8.70	22.49
Thyasira sp.	6.62	29.11
Pseudopolydora sp.	5.87	34.97
Goniada maculata	5.68	40.65
Heteromastus filiformis	5.36	46.01
Pista cristata	5.30	51.30

Table 2. Summary of results of fitted mixed model to test for effects of inside as opposed to outside (inside/outside) of pockmarks, and estimate variance components at different spatial scales. Wald statistic (*W*) tests for differences amongst areas. *S*: species richness; *J'*: Pielou's coefficient of evenness; *H'* (log_e): Shannon-Wiener diversity index; *z*: estimated variance component

Response variable	Inside/outside (SE)	*z*	p	Sites	Locations (within sites)	Grabs (within locations)	Total	*W*	p
S	0.82 (1.13)	0.73	0.46	79 (82)	2 (2)	16 (16)	97	0.60	0.30
log N	−0.16 (0.17)	0.91	0.36	0.55 (63)	0.20 (23)	0.12 (14)	0.88	1.32	0.52
J'	0.047 (0.036)	1.29	0.20	0 (0)	0.0078 (57)	0.0059 (43)	0.014	15.51	<0.001
H' (log_e)	0.20 (0.12)	1.72	0.085	0.18 (56)	0.07 (22)	0.07 (22)	0.33	4.01	0.13

between all pairs of locations inside pockmarks was 52.94, with 6 species contributing to 50% of this similarity, i.e. the bivalves *N. tenuis* and *Thyasira* sp. and the polychaetes *H. filiformis*, *G. maculata*, *C. setosa* and *Glycera alba* (Table 3). The species with the largest differences in their abundances between the locations inside and outside of the pockmarks, as calculated by SIMPER, is shown in Table 4. The species contributing the most to the differences were *N. tenuis*, *Pseudopolydora* sp. and *H. filiformis*, with the first two having a higher abundance outside and the latter having a higher abundance inside of pockmarks. High values for the ratio of average dissimilarity contribution to standard deviation denote species that are likely to be good discriminators between inside and outside of pockmarks. This expresses how consistently a species contributes to the dissimilarity between the 2 groups. Three main discriminating species with a higher abundance inside pockmarks were the polychaetes *H. filiformis*, *Terebellides stroemi* and *Syllis cornuta*, whilst species with a higher abundance outside were the polychaetes *C. setosa* and *Diplocirrus glaucus*.

Analysis of Site B

Additional information about environmental variables, which were analysed separately, was available for locations within Site B. Ordination in a nMDS of the species abundance data from each site showed that samples from reference location C5 grouped separately from all other samples and the difference
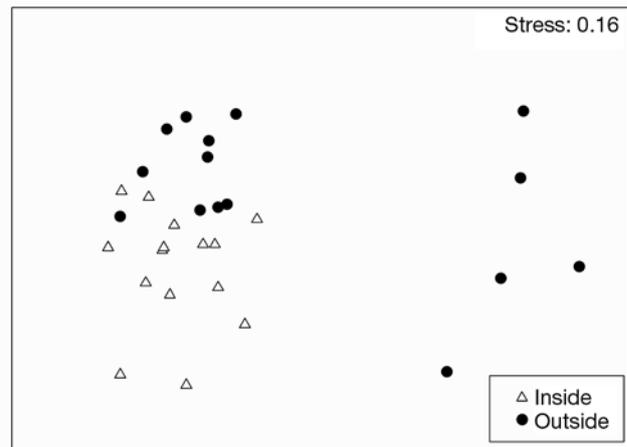

Fig. 4. Non-metric multidimensional scaling ordination (nMDS) of species abundance data from 30 grab samples taken inside and outside of the pockmarks from Site B. △: grabs from inside of pockmarks. ●: grabs from outside of pockmarks; data to the right of the panel are control location C5

between inside pockmark samples and those from outside could be clearly seen (Fig. 4). The environmental data (Table 5) showed that there was a significant difference in the environmental variables, water depth, redox, pH, TOC, mean grain size, percent mud, pH and DO, between inside and outside of pockmarks (ANOSIM, Global R = 0.562, p = 0.001). Eight abiotic factors were combined in a PCA ordination with the first PCA axis, which accounted for 56.4% of the overall variance and PC2 for 27.5% (Fig. 5). The inside and outside pockmark samples were distinguished most clearly along the axis of the first principal component (PC1). The environmental factors that had the strongest influence on this component were water depth (positive) and percent mud (positive). In addition, large contributions to the variability along PC1 also came from mean grain size (negative), TOC (positive) and the ratio of C:N (negative). The second principal component (PC2) was influenced by the correlating factors pH (positive) and redox (negative). The BIOENV procedure indicated moderate correlation of biotic patterns with the environmental variables of water depth, dissolved oxygen, percent mud and grain size (Global ρ = 0.624, p = 0.001, Table 6). The highest correlation coefficient for an individual variable was observed for water depth (ρ^s = 0.624), which was also the best

Table 4. Taxa responsible for differences between inside and outside of pockmarks based on similarity percentage analysis (SIMPER) of square-root transformed abundance data. The best discriminating species shown in **bold** text are indicated by high average dissimilarity/standard deviation (δ_i/SD). Inside/outside indicates whether the abundance is higher inside or outside of the pockmarks

Taxon	Class	δ_i/SD	%	Cumulative %	Inside/ outside
Nuculoma tenuis	Bivalve	1.12	6.83	6.83	Outside
Pseudopolydora sp.	Polychaete	1.07	6.43	13.27	Outside
Heteromastus filiformis	Polychaete	**1.29**	6.14	19.41	Inside
Thyasira sp.	Bivalve	1.17	3.99	23.40	Inside
Chaetozone setosa	Polychaete	**1.23**	3.74	27.14	Outside
Amphiura filiformis	Polychaete	0.80	3.52	30.65	Outside
Philomedes globosus	Crustacean	1.04	3.37	34.03	Inside
Diplocirrus glaucus	Polychaete	**1.20**	2.76	36.78	Outside
Goniada maculata	Polychaete	0.97	2.75	39.54	Inside
Ampelisca sp.	Crustacean	1.05	2.38	41.92	Outside
Terebellides stroemi	Polychaete	**1.19**	2.30	44.21	Inside
Syllis cornuta	Polychaete	**1.20**	2.25	46.47	Inside
Glycera alba	Polychaete	1.00	2.16	48.62	Inside
Polycirrus sp.	Polychaete	**1.25**	1.95	50.57	Outside

Table 5. Environmental data for Area B. Means ± SE are given for the variables redox, pH and water depth, measured for the 5 grabs in each location. The other variables were taken from a single representative core in each location. TOC: total organic carbon (%); DO: dissolved oxygen (% saturation)

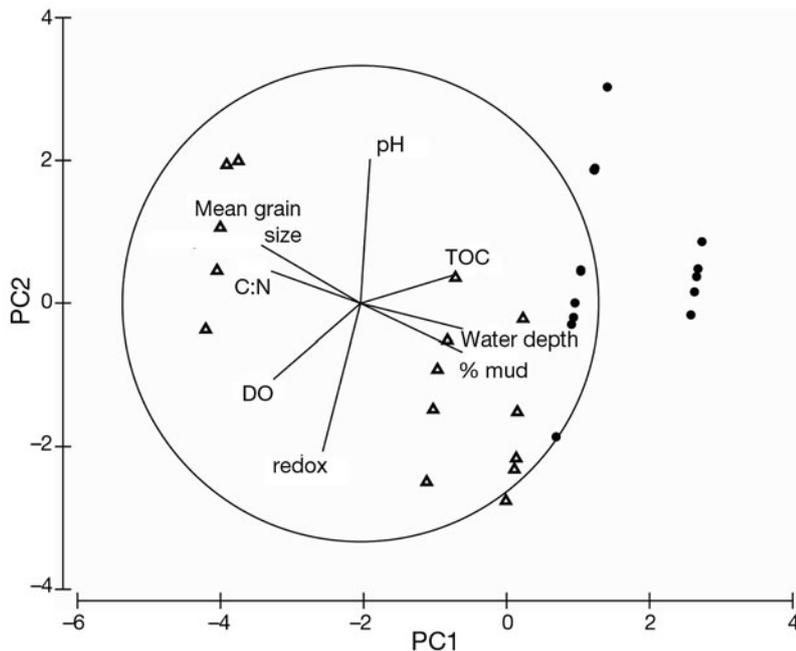| Location	Redox (Eh)	pH	Water depth (m)	TOC (%)	Mean grain size (µm)	Mud (%)	DO (%)	C:N
76	−28.4 ± 1.11	7.7 ± 0.06	52 ± 0.30	2.33	9.76	76	62	5.83
73	−36.8 ± 2.27	7.8 ± 0.04	64 ± 0.45	1.60	36.57	47	61	19.91
78	−31.6 ± 2.52	7.7 ± 0.04	53 ± 0.25	2.12	10.44	74	59	18.18
C4	−37.7 ± 2.17	7.7 ±0.04	49 ± 0.06	2.65	9.19	73	50	8.65
C5	−41.4 ± 0.85	7.8 ±0.02	39 ± 0.01	2.52	5.20	89	35	8.57
C6	−44.6 ± 2.53	7.8 ± 0.05	53 ± 0.06	3.07	14.18	71	38	10.03

Fig. 5. Principal component plot of environmental variables for Site B showing their direction and influence on the component scores. Grab samples inside (△) and outside (●) of the pockmarks

Table 6. BIOENV results for Area B showing the Spearman rank correlation coefficient (ρ) for correlations between individual environmental variables and the best combination of variables with the species abundance data

Variable	ρ
Water depth (m)	0.624
Dissolved oxygen (DO, % saturation)	0.478
% mud	0.419
Mean grain size (µm)	0.360
C:N	0.031
% TOC	0.008
Redox (Eh)	−0.039
pH	−0.063
Best combinations	
DO, water depth	0.564
% mud, DO, water depth	0.547

overall correlation. Dissolved oxygen and water depth had the highest combined correlation ($\rho^s = 0.564$).

DISCUSSION

The Oslofjord is one of the best studied marine areas at high northern latitudes, and pockmarks are arguably the major surface feature of its seabed. Despite this and the fact that seabed topography typically has a pronounced, and often dominant influence on adjacent life, the present study is the first to report the benthic fauna of pockmarks in any fjord environment. Although pockmarks are abundant in Oslofjord, scientific studies on the structuring of faunal communities have focussed on the obvious and more accessible fjordic gradient (terminus to open sea). We considered pockmarks to be of great potential importance in structuring biodiversity by increasing habitat heterogeneity and acting as refuges from anthropogenic disturbance such as trawling. We undertook a spatial study that encompassed a large part of the inner end of the fjord to map distributions and a detailed study of the benthos associated with selected pockmark areas. Our analysis showed that whilst there were differences in the infaunal assemblages inside and outside of Oslofjord pockmarks, the largest differences were driven by the strong gradient of the fjord environment itself. The community structure within the pockmarks showed subtle differences to the 'background' communities, yet the fauna were typical of the Oslofjord in general, which is known to be a disturbed fjord environment and thus dominated by disturbance-tolerant species (Mirza & Gray 1981). In some respects, ice scours and pockmarks are both small-scale structures that at high latitude dominate

seabed topography, but whilst the former drive regional scale diversity patterns (Gutt 2001), it appears that in fjordic pockmarks these patterns are driven by the fjord environment.

Position within the Oslofjord, as in other fjords (Pearson 1980), is clearly important in structuring benthic communities. Our study shows that this is so important that it overrides the influence of the most apparent structural features. The key positional features tend to be proximity to land and restriction of water exchange and circulation within the basins. Mirza & Gray (1981) reported that the diversity of macrofauna increased from Bunnefjorden towards the sill at Drøbak. This was supported by the results of our ANOSIM test for all study locations. Sample Sites I and D of the present study had a high dominance and low diversity of fauna typical of organic enrichment (Pearson & Rosenberg 1978). Site I was near the harbour, which has a substantial pollution load (Trannum et al. 2004), and Site D was amongst inhabited islands and likely to be affected by runoff and inputs from the Sandvika river. *Capitella* and *Polydora* (polychaete) species found at these sites often dominate in such organically enriched areas due to their opportunist life history traits and tolerance of low oxygen stress (Gray 1979). Our other study sites were characterised by higher diversity and evenness, with fauna typical of a polluted fjord environment (Pearson & Rosenberg 1978, Mirza & Gray 1981).

Bivalves and polychaetes were the dominant taxonomic groups both inside and outside of the pockmarks in the Inner Oslofjord, as suggested previously (Mirza & Gray 1981). The most prevalent species across samples seem to have remained consistent for decades; in our study they were the bivalves *Nuculoma tenuis* and *Thyasira* spp. and the polychaetes *Heteromastus filiformis*, *Chaetozone setosa* and *Pseudopolydora* sp., as found by the baseline study of Mirza & Gray (1981). Pollution seems to be a strong driver of patterns in the benthos of Oslofjord (Trannum et al. 2004, Olsen et al. 2007). The majority of the dominant species found in this study were opportunist pioneers, e.g. *C. setosa* (Rygg 1985) and *H. filiformis* (Pearson & Rosenberg 1978). In contrast, a North Sea pockmark was characterised by 2 species, a thyasirid bivalve, known to contain endosymbiotic sulphur oxidising bacteria, and a mouthless and gutless nematode, *Astomonema* sp., also associated with endosymbiotic bacteria (Dando et al. 1991). Thyasirid bivalves also occurred in Oslofjord pockmarks and were found at higher abundances than our 'reference' locations. They are known to be associated with organic rich sediments and are common in several Norwegian fjords (Dando et al. 2004). Wildish et al. (2008) similarly reported 2 bivalve species, *T. flexuosa* and *Solemya* sp.

(with symbiotic bacteria) within their pockmarks, but the former occurred in relatively low mean densities and the latter in only 1 pockmark. Thus, apart from these few reports of chemosynthetic species, few species characterise the Oslofjord pockmarks or those elsewhere (Wildish et al. 2008, Dando et al. 1991). This is not surprising, as all 3 of these geographic sites (Oslofjord, Passamaquoddy Bay, Canada, and the North Sea) are non- or intermittently active and postglacial in origin; thus, it could be argued there has been insufficient time (5000 to 12 000 yr at most) for speciation events to occur.

The community structure inside the pockmarks was significantly different from outside despite a high degree of overlap of the species present (and the strong influence of position within the fjord). As far as we could detect, pockmarks do not seem to influence which species are present but instead alter their relative abundances. The more abundant taxa inside the pockmarks appeared to be those less tolerant of disturbed environments. The large overlap in species and the subtle nature of any observed differences meant that using coarse indices such as total abundance or number of species did not detect differences at the pockmark level. Although the inside of pockmarks showed a significantly more even distribution of species than the outside, these differences were again overshadowed by the differences caused by the strong gradient of the fjord environment itself. We found that the best discriminating species for locations outside pockmarks were *Diplocirrus glaucus*, *Chaetozone setosa* and *Polycirrus* sp., all species typically found in organically enriched conditions (Hily 1987, Feder & Jewett 1988). The best discriminating species for inside of pockmarks were *Terebellides stroemi*, *Heteromastus filiformis* and *Syllis cornuta*. *T. stroemi* and *S. cornuta* are thought to be less tolerant to disturbance than the discriminating species for the outside of pockmarks (Rygg 1985).

However, in some cases differences between pockmark and background faunas can even be detected using coarse indices, such as alpha richness. In Passamaquoddy Bay, Wildish at al. (2008) found both lower species richness and density inside rather than outside pockmarks. In one area, referred to as upper habitat A (5 pockmarks), they found significant differences with lower species richness (number of species per grab) and density inside the pockmarks compared with reference locations. Likewise, Dando et al. (1991) found that the centre of a North Sea pockmark had fewer fauna compared with the normal surrounding seabed and suggested this was due to fluid leakage from the pockmark removing silty sediments and preventing the establishment of a stable community. The second difference found by Wildish et al. (2008) was

only detectable by the use of multivariate statistics. This is comparable with our findings where only subtle community differences were indicated by the results of the ANOSIM and SIMPER with similar taxa, but some at lower and some higher abundance, compared with the reference locations. The formation of pockmarks is likely to cause significant disturbance to benthic infauna whether this occurs through an explosive event or gradual seepage. Therefore, we might expect there to be differences in the density or abundance of taxa if pockmark communities are in differential succession compared with the surrounding seabed (see Wildish et al. 2008). However, for our study the polluted fjord environment itself represents a disturbed environment, typified by opportunist species and low diversity, so that such differences will at best be subtle and small. Differences in density and abundance of taxa may also be related to specific environmental conditions in pockmarks.

The present study and that by Webb et al. (2009) showed that there are differences in environmental conditions inside and outside of the pockmarks. The subtleties of faunistic differences make implications for biodiversity within adjacent areas hard to interpret. The structure of soft-bottom communities is often linked to sediment grain size (Jones 1950), and sediments within pockmarks were coarser than background (Webb et al. 2009). This corresponds with the coarse, poorly sorted sediments known to be the habitat of the discriminating species *Terebellides stroemi* and *Syllis cornuta* found inside pockmarks (Hughes et al. 1972, Kirkegaard 1992). The environmental factors showing the best correlation with the biotic factors were water depth and DO. Depth influences other environmental variables, especially the amount and wavelengths of light. DO was higher inside the pockmarks compared with the reference locations, which was unexpected as deeper waters would be expected to have lower oxygen concentrations; however, these differences could possibly be due to different hydrodynamics or seeping fluids (e.g. groundwater) within the centre of the pockmarks. Overall, though, the concentrations are low and differ from those in the North Sea and Passamaquoddy Bay, the latter of which is tidally flushed with well oxygenated water above the sediment–water interface. These low oxygen conditions in the Oslofjord are likely to drive a large-scale effect on the macro-infauna.

Overall, pockmarks could have several effects on the benthos of an area for a number of reasons. Increased surface area and altered current patterns change sedimentation, food supply and larval dispersal. Seeping fluids may provide nutrients, cause disturbance, affect sedimentation and potentially alter the composition of the seabed sediments; methane seeps often cause the precipitation of carbonate, providing a hard surface area for colonisation in an otherwise soft sediment environment. Perhaps one of the most important roles pockmarks play in the ecology of the seabed is increasing the sediment–water interface. The increased surface area can nearly double the secondary benthic production (Wildish et al. 2008). Therefore, the large number of pockmarks in the Oslofjord will have a significant cumulative effect.

The subtle differences between the inside and outside of pockmarks highlight both the need for spatial scale to be taken into account during such studies and the strength of multivariate techniques over simple univariate proxies such as diversity indices. The subtlety of the differences in faunal composition of dominant taxa inside and outside of the pockmarks is surprising, as topographical features in the seabed, e.g. seamounts, iceberg scours, whale feeding pits and dropstones, usually influence the species present. Craters in the seafloor alter current patterns (Hammer et al. in press), provide refuge (Webb et al. in press) and increase the seafloor's surface area (Wildish et al. 2008). The changes to current patterns would be expected to influence larval settlement, silt deposition and the supply of food, as well as nutrients and dissolved gasses, and so also affect fauna (Hiscock 1983). Given the widespread distribution of pockmarks we recommend further research and biological surveys which should include the mapping of such topological features, as the presence of pockmarks may have implications for seabed biodiversity and species distribution.

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