Benthic macrofauna of elongated, shallow-water pockmarks in the Inner Oslofjord, Norway

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Preface

Først vil jeg takke min opprinnelige veileder John S. Gray. Jeg satte veldig pris hvordan du inkluderte alle i gruppa, og to-kaffen på kontoret ditt er sterkt savnet. Du holdt motet oppe og var sterk og positiv gjennom hele den vanskelige sykdomsperioden, og var en inspirasjon for oss alle.

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Abstract

A large number of round and elongated pockmarks were recently discovered in the Oslofjord, Norway. Pockmarks are formed by expulsion of fluid, most commonly methane or ground water. The elongated shape is a believed to be a result of either strong bottom currents, linear sub-surface weakness zones, the merging of circular pockmarks, or a combination of these factors. The seeping of methane may generate high microbial production, providing a stable nutrient supply to the benthic fauna. Some specialized 'seep' species are also known to contain endosymbiotic chemosynthetic bacteria.

The benthic macrofauna of five elongated pockmarks were investigated by quantitative sampling and multivariate statistical techniques. The results showed that the faunal composition inside the pockmarks was significantly different compared to the outside, although with a high degree of overlap. The faunal diversity was not higher inside the pockmarks, and no species known to obtain energy by chemosynthetic symbionts were identified. This indicates that methane does not provide an additional nutrient source for the benthic community.

Other aspects of the pockmarks are discussed as possible explanations for the different species composition. Eruptive rather than continuous fluid escape may act as a disturbance and remove resident macrofauna inside the pockmarks. Another possible explanation is that the pockmarks act as traps for organic material due to reduced bottom current flow. This could lead to increased organic deposition inside the pockmarks, and in combination with low oxygen content lead to anoxic conditions in the sediment surface layer. Higher abundances inside the pockmarks of opportunistic polychaete taxa ('indicator species'), such as *Capitelle capitata* and *Polydora* sp. were found, indicating that the pockmark sediments might be disturbed. However, the high overall abundance of such opportunists suggests that the study area in general is environmentally stressed. The environmental variables were on the whole similar inside and outside the pockmarks, and correlated only weakly with the species patterns observed.

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1. Introduction

1.1 Occurence of pockmarks

Pockmarks are circular or elongate depressions in the sea floor believed to be formed by expulsion of fluid through the seabed (Hovland *et al.* 1984). King and MacLean (1970) were the first to discover and recognize pockmarks, and described them as “concave, crater-like depressions that occur in profusion on mud bottoms across the Scotian Shelf”. At first they were considered just a geological curiosity, but interest increased with the discovery of an association between pockmarks and nearby hydrocarbon deposits (Fader 1991). Since 1970 a growing number of marine seismic surveys by the petroleum industry have made numerous reports on pockmark-related structures. By improved technology, such as side scan sonar, submersibles, remotely operated vehicles and new coring and grabbing techniques, more insight has been gained on both the geology and the ecology of pockmarks (Fader 1991).

Today, pockmarks are recognized as a common topographical feature, and have been found in most oceans and also in some lakes (Hovland *et al.* 2002a). Pockmarks have been described from all parts of the world, among others the Gulf of Maine, North America (Kelley *et al.* 1994; Rogers *et al.* 2006), the Scotian Shelf and the Norwegian Trench of the North Sea (Hovland *et al.* 1984), Patras and Corinth gulfs, Greece (Christodoulou *et al.* 2003), North-Norwegian fjords (Plassen & Vorren 2003), Canada’s Atlantic coast (Fader 1991), the Bering Shelf of Alaska (Nelson *et al.* 1979) and the equatorial African margin (Ondréas *et al.* 2005). Densities of up to 1000 pockmarks per km^2 have been reported in some areas (Hovland & Judd 1988). They occur mainly in soft silt-clay sediment and are found in a variety of marine environments, such as continental shelves and slopes, fjords, estuaries and deeper oceanic basins (Hovland & Judd 1988). The depressions may take on a variety of shapes, from nearly perfectly circular to asymmetrical or elongated (Hovland *et al.* 2002a). A wide range of pockmark diameters have been reported, but most fall within the range from 10 to 250 m. Recently, mega-pockmarks with diameters of 1500 m and depths of 150 m have been described from the West African continental margin as the largest pockmarks known (Pilcher & Argent 2007). Pockmarks occur in water depths ranging from 6-4800 m (Fader 1991).

1.2 Morphology of pockmarks

The morphology of pockmarks varies, and the subdivision into six morphological classes has been suggested (Fig. 1) (Hovland *et al.* 2002a): 'Normal' pockmarks are the classic ones described by King and MacLean (1970) as circular depressions, either regular (Fig. 1a) or asymmetric (Fig. 1b). Complex pockmarks are clusters of normal pockmarks. Unit pockmarks (Fig. 1c) are small depressions, 1-10 m across and up to 0.5 m deep, and are common inside and around normal pockmarks (Fig. 1d). Many unit pockmarks may occur together in strings or chains up to several kilometres in length. 'Eyed' pockmarks (Fig. 1e) have central bottom areas of very strong acoustic reflection, indicating the presence of gas pockets in the sediment. Elongated pockmarks (Fig. 1f) are depressions with one axis that is much longer than the other.

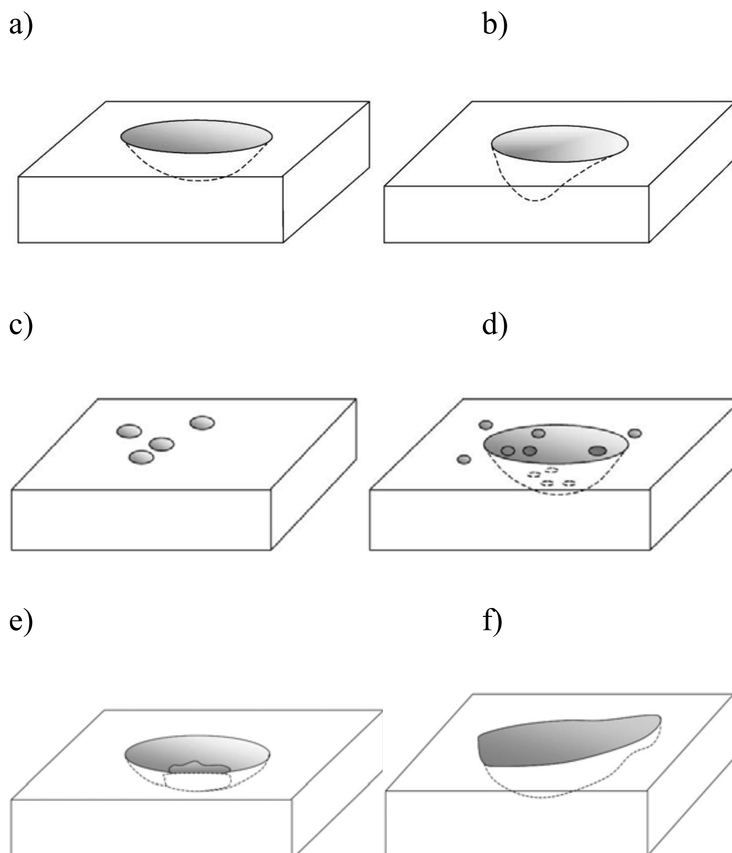


Fig. 1: Illustration of the six main morphological classes of pockmarks: normal pockmarks, either regular (a) or asymmetric (b), unit pockmarks, either independent (c) or in profusion with normal pockmark (d), eyed pockmark (e) and elongated pockmark (f). From Hovland *et al.* (2002a).

1.3 Formation of pockmarks

A variety of mechanisms for pockmark formation have been proposed. Most theories include seepage or eruption of fluid, either gas or water. The most common source of gas is methane of thermogenic (Solheim & Elverhøi 1985) or microbial (Nelson *et al.* 1979) origin.

Thermogenic methane is formed through thermochemical reactions, whereas microbial methane (also denoted bacterial or biogenic methane by some authors) is derived from bacterial methanogenesis of organic material (Nelson *et al.* 1979; Schoell 1988; Hill *et al.* 2004). Other sources of fluid such as porewater (Harrington 1985) or ground water (Whiticar & Werner 1981) also form pockmarks.

Pockmark formation by ascending gas or water was first suggested by King and MacLean (1970). As more evidence has accumulated, the following scenario has been outlined by Hovland and Judd (1988): When gas or porewater accumulates, pressure will build up in sediment near the seabed. Excess pressure is relieved by deformation and doming of the seabed and the fluid will eventually be released to the overlying waters through fractures in the seabed. Fine-grained sediments become suspended in the water, transported by currents and deposited elsewhere, depending on grain size and current speed. Coarser material will fall back into or near the newly formed pockmark.

Some high latitude pockmarks are proposed to be formed by freshwater ice formation at the sediment-water interface that binds and floats sediment off the seafloor (Paull *et al.* 1999). Freshwater seeping upward through the sediments freezes when bottom water temperatures are below 0°C. The buoyant ice is capable of lifting small amounts of sediment off the sea floor, and over time a pockmark depression could be excavated, even at very low fluid flow rates.

Elongated pockmarks generally occur on areas of the seafloor influenced by strong bottom currents (Hovland *et al.* 2002a). Hovland (1983) recognized elongated depressions on the Western slope of the Norwegian trench to be closely related to the formation of other round pockmarks in the region. He concluded that these depressions were caused by shallow gas seepage and less compact sediments around the gas escape route, in combination with bottom currents. Elongated pockmarks seem to have a preferred orientation, which is often coincident with the dominant bottom current direction (Hovland *et al.* 1984; Harrington 1985), indicating that water movements may affect the shape of pockmarks during their formation. Exceptionally deep and elongate pockmarks were discovered at the southern slope of the Norwegian Trench (Skagerrak), with depths up to 45 m, widths up to 400 m and lengths up to 2 km (Bøe *et al.* 1998). The elongated shape was again interpreted as a result of ocean bottom current activity. More recently, elongated pockmarks have been described from the Turkish Shelf, Eastern Black Sea (Çifçi *et al.* 2003) and the US mid-Atlantic shelf

break (Newman *et al.* 2008). These elongated pockmarks are believed to be formed by merging of smaller circular pockmarks, possibly in combination with bottom currents and subsurface linear weakness zones.

Considering the diverse occurrence, morphology and size of pockmarks, they are probably formed by different mechanisms in different areas and geological settings. For example, two pockmark fields located only 30 km apart along the coast of Greece were found to be formed by different mechanisms; one as a result of methane seepage and the other of ground water seepage (Christodoulou *et al.* 2003). Emanating gas bubbles have been observed from some pockmarks, indicating continuous activity, but many seem dormant or extinct, possibly with periodic activity (Hovland *et al.* 2002a). However, it is believed that the pockmarks must be maintained by active processes; otherwise they will be obliterated by seafloor sediment deposition or redistribution (Paull *et al.* 1999). The level of activity necessary for maintaining the pockmark after formation is not known, and will depend on local sedimentation rates and bottom currents. No pockmarks have been monitored over long periods of time, and it has therefore been difficult to determine their normal or typical activity level (Hovland *et al.* 2002a).

The Oslofjord pockmarks were discovered in 2005 (Webb *et al.* unpublished manuscript). Due to the recent discovery, very little is known about these pockmarks. It is not known when or how they were formed or the source of fluid responsible for the formation, or if the pockmarks are actively seeping, dormant or extinct. However, the sedimentation rate in the Oslofjord is relatively high, about 1-2 mm/year (Pederstad *et al.* 1993), suggesting that the pockmarks should 'fill up' over time unless periodic or continuous fluid flow took place.

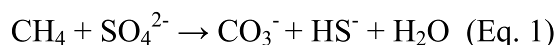
1.4 Fluid flow and biogeochemical processes in sediments

The most common mechanisms for pockmark formation involve upward fluid flow through the seafloor and pockmarks are therefore concidered indicators of some form of seafloor fluid escape (Paull *et al.* 1999). The gas most frequently associated with seabed seeps is methane (CH_4) (Fader 1991), which is a small molecular size hydrocarbon gas. Hovland and Judd (1988) and Hovland and Thomsen (1989) have suggested that methane seeping from pockmarks in the North Sea increases the local benthic production through a bacteria based food web. This suggestion was based on ROV (Remotely Operated Vehicles) video

recordings of pockmarks, observing a richer fauna inside the pockmarks compared to the surrounding seabed.

Active methane-seeping pockmarks bring the gas from deeper reservoirs up to, or close to, the seabed sediment where it is oxidized both anaerobically within the sediment and aerobically close to the sediment surface. Anaerobic oxidation of methane (AOM) is a widely occurring process in marine anoxic sediment, and acts a sink for upwardly diffusing methane (Valentine & Reeburgh 2000). Most of the methane produced in the deeper sediment layers will be oxidized by microbial processes before reaching the overlying waters. AOM is, therefore, geochemically and biologically important since it decreases the flux of methane from marine sediments to the atmosphere (Hinrichs & Boetius 2002; Valentine 2002). At methane seep sites, the AOM rate is at least an order of magnitude higher than in non-seeping sediments (Hinrichs & Boetius 2002), thus high concentrations of methane and focused fluid flow, such as along faults or fractures in the seabed, are necessary for methane to escape as bubbles and for natural seeps and pockmarks to occur (Judd 2003).

AOM is closely linked to sulphate reduction, and is believed to be carried out by a consortium of both methanotrophic archea and sulphate reducing bacteria (Hoehler *et al.* 1994; Hinrichs *et al.* 1999; Boetius *et al.* 2000; Orphan *et al.* 2001; Knittel *et al.* 2005). The chemical reaction associated with AOM involves oxidation of methane with sulphate as the terminal electron acceptor:



$$CH_4 + SO_4^{2-} \rightarrow CO_3^{-} + HS^{-} + H_2O \quad \text{(Eq. 1)}$$

Products of the reaction are carbonate and sulphide (Valentine 2002). The sulphide may be utilized by symbiotic sulphur oxidizing bacteria (Dubilier *et al.* 2001) or free-living sulphur bacteria such as *Beggiatoa* (Nelson & Jannasch 1983). High rates of anaerobic oxidation of methane coupled to sulphate reduction generates high microbial biomass, and may provide a significant supply of methane-derived carbon to the sediment microbial community (Levin 2005).

1.5 Possible impacts of fluid flow on benthic fauna

Food webs at actively seeping pockmarks may rely partly on chemosynthetically derived energy. Chemosynthesis, or more correctly chemoautotrophy, is the fixation of inorganic carbon (e.g. CO_2) into organic carbon, using energy derived from the chemical oxidation of

inorganic compounds (Jannasch 1985). Sulphur oxidizing bacteria fix CO_2 using energy from the oxidation of reduced sulphur compounds such as H_2S, HS^-, S^{-2} or $S_2O_3^{2-}$ (Dubilier *et al.* 2001) and methane oxidizing bacteria use methane as the sole carbon and energy source (Hanson & Hanson 1996).

Sites where reduced sulphur and/or methane emerge from the sea floor at ambient temperature are collectively termed cold seeps (Levin 2005). A number of specialized mega- and macrofauna containing chemosynthetic symbionts have been identified from cold seeps, including the annelid *Siboglinum* sp. (Southward *et al.* 1981), the seep mussel *Bathymodiolus* sp. (Duperron *et al.* 2005) and vesicomyid clams (*Calyptogena* sp. and *Vesicomya* sp.) (Olu-Le Roy *et al.* 2007). Also smaller and less conspicuous species such as infaunal clams of the families Thyasiridae (Schmaljohann *et al.* 1990) and Lucinidae (Schweimanns & Felbeck 1985) have been found to contain endosymbiotic sulphur oxidizing bacteria. However, only a few cold seep communities have been reported from pockmarks. MacDonald *et al*. (1990) described a large bed of the mussel *Bathymodiolus* sp. around a brine-filled pockmark in the Northern Gulf of Mexico. Faunal assemblages dominated by *Bathymodiolus* sp., vesicomyid clams or *Siboglinum* sp. were discovered in a pockmark off West Africa (Olu-Le Roy *et al.* 2007).

Methane seeping from pockmarks may also promote increased faunal abundances by providing hard substrate habitats in an otherwise soft sediment environment. The carbonate produced by AOM precipitates as calcium carbonate (Eq. 1), resulting in authigentic carbonate deposits frequently found in association with seeps (Aloisi *et al.* 2002). Such carbonate structures provide habitat for a diverse ecosystem including hard substrate fauna, such as sponges, hydrozoans and bryozoans (Jensen *et al.* 1992). Deep-water corals (most commonly *Lophelia* sp.) have been found to occur in close association with pockmarks and seepages, often situated at the edge of pockmarks (Sumida *et al.* 2004; Hovland 2005). It has been suggested that chemoautotrophic bacteria stimulate coral growth by providing a stable nutrient supply (Hovland *et al.* 2002b; Hovland & Risk 2003). High abundances of fish have also been observed inside North Sea pockmarks (Hovland & Thomsen 1988), possibly attracted by nutrient enrichment in the bottom of pockmarks or by local current effects caused by the pockmark depressions (Fader 1991).

Groundwater is another fluid commonly known to be involved in pockmark formation (Hovland & Judd 1988). Freshwater is suspected to have a detrimental effect on most marine

fauna, as lowered salinity in the sediment will increase osmotic stress on the organisms (Bussmann *et al.* 1999). Most marine fauna are, therefore, not able to tolerate freshwater for long periods. A reduction in the number of species is a common characteristic of marine environments influenced by freshwater, such as estuaries which are characterized by abundant faunal populations, but with relatively few species (McLusky & Elliott 2004 pp. 19-33). Fluctuations in salinity and episodic freshwater flushing may cause reduction in the abundance of benthic fauna (Cyrus 1988; Montague & Ley 1993). Both continuous seeping and episodic escape of freshwater may lead to lower diversity of benthic fauna inside the pockmarks.

The seeping of freshwater may also stimulate shallow microbial methane production, because methane will form preferentially in freshwater rather than saline environments (Paull *et al.* 1999) Methanogenesis is, in the presence of sulphate, often inhibited by sulphate reducing bacteria (Abram & Nedwell 1978) and generally limited to below the sulphate reduction zone (Reeburgh & Heggie 1977; Paull *et al.* 1985). However, slow upward seeping of freshwater can flush the interstitial pore spaces free of seawater sulphate, and promote the microbial generation of a shallow methane reservoir (Paull *et al.* 1999). Thus, seeping freshwater may lead to increased concentrations of methane within the pockmark sediments.

1.6 Previous studies of pockmark fauna

Most studies of pockmarks have been undertaken for geological purposes where faunal sampling is not a priority (Sibuet & Olu 1998; Ondréas *et al.* 2005). Biological studies have mainly focused on large, symbiont-bearing megafauna observed by ROV (Ondréas *et al.* 2005; Olu-Le Roy *et al.* 2007) or on microbial processes (Levin 2005), or sampled only for pelagic and epibenthic fauna (Juhl & Taghon 1993). Hovland and Thomsen’s (1988) hypothesis of enriched faunal communities inside pockmarks due to the seeping of methane is based on ROV video recordings. Detailed understanding of how fluid flow will affect the mid-size infauna (e.g. macro- and meiofauna) is at present lacking. Only three previous studies have sampled pockmarks for benthic infauna: Dando *et al*. (1991) investigated a single pockmark in the North Sea, and Bussmann *et al*. (1999) sampled a pockmark formed by freshwater in the Western Baltic Sea, but neither reported of increased infaunal abundances inside the pockmarks. In fact, Dando (1991) found lower faunal abundances in the pockmarks, and suggested that the fluid escape prevented establishment of a stable community by removing the surface sediment. However, neither Dando *et al*. (1991) nor

Bussmann *et al*. (1999) performed any multivariate statistics on their data. Recently, a more extensive investigation of the ecology of 17 pockmarks in Passamaquoddy Bay, Canada, indicated that some of the pockmark communities were at different successional stages following a disturbance that initially resulted in a reduction of the fauna (Wildish *et al.* in press). The biology of elongated pockmarks has never been investigated.

1.7 Objective of this study

The purpose of this study was to investigate the species composition and diversity of benthic macrofauna inside elongated pockmarks in the Oslofjord, by quantitative sampling and multivariate statistics. The aim was to investigate whether the faunal composition inside the pockmarks was different than the outside. Multivariate analysis has proved particularly sensitive to detecting even small changes in faunal communities (Gray *et al.* 1990). Environmental variables related to sediment characteristics were measured in order to give a general description of the study area and investigate their influence on the patterns of species composition observed. The ecological question addressed was: Do the pockmarks support macrofaunal assemblages distinct from sediments outside with respect to composition and diversity? The null hypothesis tested was that there was no difference in community structure of benthic macrofauna between the inside and outside of the pockmarks.

2. Methods

2.1 Study site

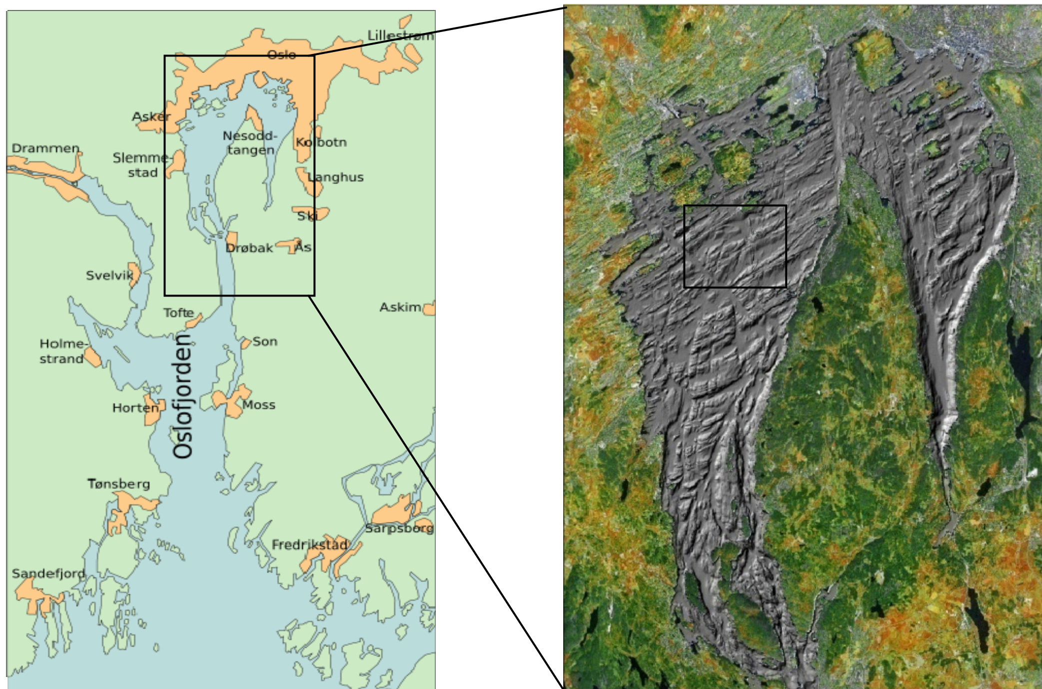
The study was conducted south of Ostøya in the inner Oslofjord, southern Norway (59.92°N, 10.75°E) (Fig. 2). The fjord is 110 km long, extending in a north-south direction from the city of Oslo to the open Skagerrak coast. The inner fjord is separated from the outer part by the shallow Drøbak Sill, with a maximum depth of 19.5 m. The sill restricts water exchange between the outer and inner part of the fjord and strongly influences the hydrology of the entire inner fjord (Gade 1970; 1973). The inner Oslofjord consists of two main basins, Vestfjorden with a maximum depth of 173 m and Bunnefjorden with a maximum depth of 155 m. The basins are separated by the peninsular Nesodden and a 50 m deep sill. Ostøya is situated in the northern part of Vestfjorden and, together with adjacent islands, isolates the smaller basin Bærumsbassenget from Vestfjorden.

Deep water exchange within the inner and outer part of the fjord depends upon strong northerly winds and a weak thermocline (Gade 1968). During such conditions, more saline waters from the outer Oslofjord can cross the Drøbak Sill and flow into the deeper parts of the inner fjord. In Vestfjorden, this process causes the renewal of bottom water every winter, increasing the oxygen content of the deeper layers (Gade 1968). The surface salinity is coupled to variation in local run-off and precipitation. In the summer, the salinity goes down to 15-20‰, mainly due to freshwater discharge from the Drammen River into the outer fjord. In the winter, the brackish layer is practically absent because of snow accumulation and low rate of precipitation (Gade 1968). Below the pycnocline the water mass is almost homogenous with salinity >30‰ (Baalsrud & Magnusson 2002 pp. 33-34). The inner fjord is affected by eutrophication and organic enrichment (NIVA 2005), causing periodic anoxic conditions in the deepest parts of Vestfjorden and Bunnefjorden. (Mirza & Gray 1981) found that the diversity of benthic communities was lowest in the innermost parts of the fjord and gradually increased to high diversity outside the Drøbak Sill.

A total of 537 pockmarks were discovered in the inner Oslofjord after analysis of multibeam data (Webb *et al.* unpublished manuscript). The data originated from an NGU (Geological Survey of Norway) multibeam survey (NGU 2005, unpublished data) aimed at mapping the topography of the fjord. Most of them are normal round pockmarks (470), the remaining are

either strings of unit pockmarks (31) or channel-shaped structures referred to as elongated pockmarks (36) (Webb *et al.* unpublished manuscript). Multibeam data from the NGU survey were used to create images of the topography of the inner Oslofjord (Fig. 2). Based on these images, five elongated pockmarks were selected for further investigation (Fig. 3 and 4). The pockmarks are orientated either in a NE-SW or N-S direction (Fig. 3 and 4), corresponding to subsurface fault lines in the fjord (NE-SW) or to the folding related to formation of the Norwegian mountains about 400 million years ago (N-S) (Webb *et al.* unpublished manuscript).

Fig. 2: Map of Norway (top), the entire Oslofjord extending 110 km in a north-south direction (bottom left), and multibeam image (bottom right) of the topography of the inner Oslofjord (gray area). The study area is located inside the square. The data used to create this and the following multibeam images are from a 2005 NGU survey (unpublished data). Map of Norway is taken from 1Hhttp://www.gate-norway.com/map.php and map of the Oslofjord from 2Hhttp://commons.wikimedia.org/wiki/Image:Oslofjord_Slemmestad.png.



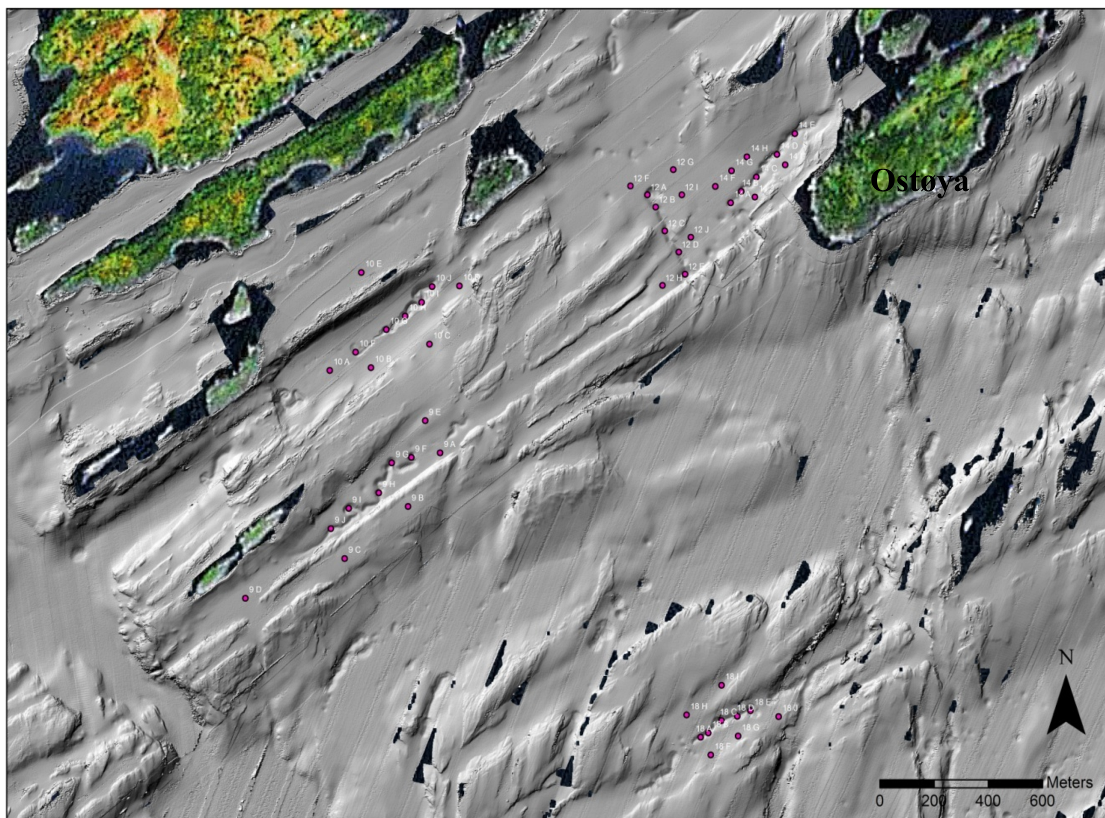
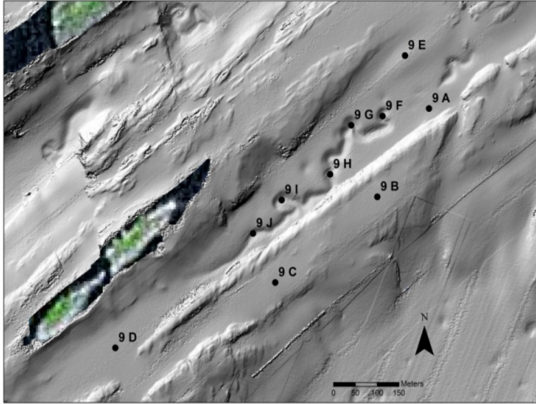


Fig. 3: Multibeam image of the study area and the five elongated pockmarks. The positions of the grab samples are indicated by pink dots. Pockmark number 12 and 14 are situated to the north close to Ostøya, pockmark 9 and 10 are to the west and station 18 lies to the south.

a)



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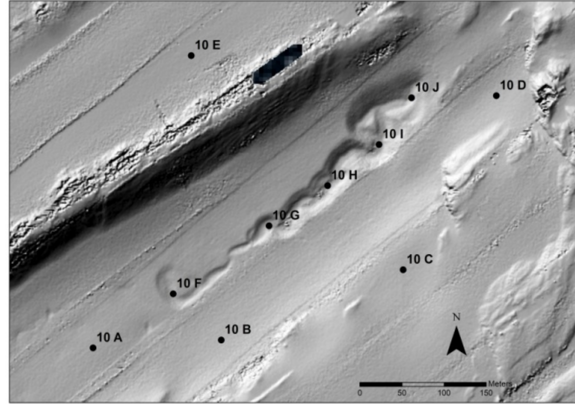

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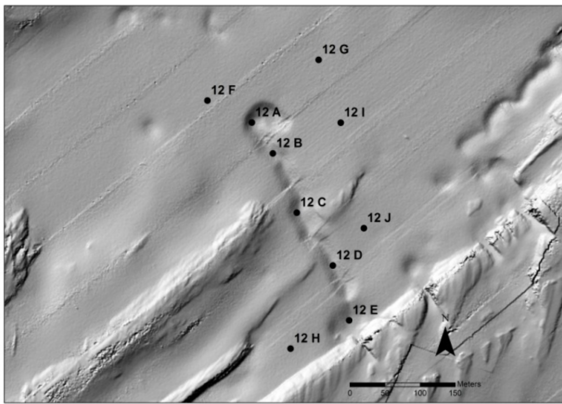

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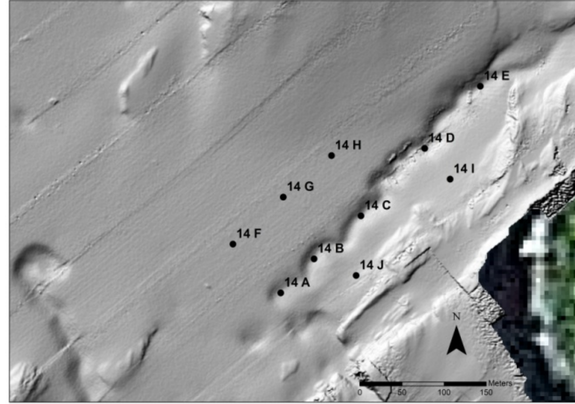

e)

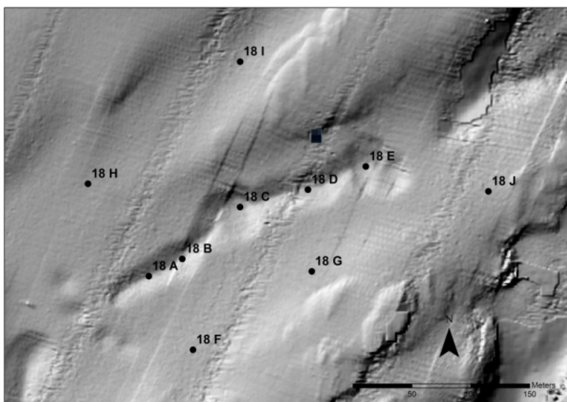

Fig. 4: Close-up multibeam image of pockmark 9 (a), 10 (b), 12 (c), 14 (d) and 18 (e). Ten grab samples were taken from each pockmark; five from inside the pockmarks and five from the surrounding bottom outside. Grab sample positions are indicated by dot and sample number.

2.2 Field sampling

Field sampling took place from 28th to 31st of August 2006 from the University of Oslo research vessel F/F *Trygve Braarud*. Within each elongated pockmark, five replicate grab samples were taken in order to sample the full length of the pockmark, in addition to five reference grab samples from the flattened seabed outside, giving a total of 50 grab samples. Sampling depths ranged from 35 – 56 m (Table 1). The depths of the pockmarks ranged from 2 to 8 m below the surrounding seafloor.

Samples were collected with a Van Veen grab (0.1 m^2). pH, redox potential (Eh) and temperature (°C) of the sediment were measured *in situ* through the top flap of the grab with a pH/mV meter (ph 340i/ set) (Bale & Kenny 2005). Sub samples of approximately 0.5 L of sediment were taken from the grab samples for sediment analysis and stored in double plastic bags in a freezer (-18°C). The grab samples were sieved through a 0.5 mm mesh (round hole) and the animals retained on the sieve were fixed with 4% formalin to prevent deterioration and stained with Rose Bengal (Eleftheriou & Moore 2005). Temperature and salinity measurements of the overlying water column were made by a mini CTD (MINI SRD/CTD SD 204) at two sites inside and two sites outside each pockmark.

Table 1: Descriptions of the pockmarks sampled including sample identification names for inside and outside samples, position of the pockmarks (latitude and longitude), length of the longitudinal axis, width range (from the narrowest to the widest part of the pockmark), depth of the depression and depth of the overlying water column.

Pockmark number	Inside samples	Outside samples	Latitude, longitude	Length (m)	Width (m)	Depth of depression (m)	Water column depth (m)
9	F,G,H,I,J	A,B,C,D,E	59° 50’ N 10° 33’ E	560	16 – 30	5	35 - 40
10	F,G,H,I,J	A,B,C,D,E	59° 51’ N 10° 33’ E	400	25 – 75	6	35 - 50
12	A,B,C,D,E	F,G,H,I,J	59° 51’ N 10° 34’ E	350	20 – 50	7-8	36 - 47
14	A,B,C,D,E	F,G,H,I,J	59° 51’ N 10° 34’ E	460	16 – 20	2-8	30 - 38
18	A,B,C,D,E	F,G,H,I,J	59° 50’ N 10° 34’ E	266	25-50	6	50-56

2.3 Species identification

In the laboratory the samples were washed and the fauna sorted into 5 groups: Annelida, Crustacea, Mollusca, Echinodermata and “Varia”. The animals were then identified to lowest taxonomic level possible and preserved with 70% ethanol. Faunal groups not properly sampled by the method used, such as meiofaunal nematodes and hard substrate fauna (e.g. bryozoans and cirripeds) were not included. Faunal abundances were enumerated for each sample.

2.4 Grain size analysis

Sediment samples were defrosted overnight before grain size analysis. Grain size distribution of the sediment was determined by wet sieving through 2000 µm, 1000 µm, 500µm, 250 µm, 125 µm, and 63 µm meshes (Wentworth 1922). Each fraction was dried and weighed, and calculated as a proportion of total sediment dry weight (Bale & Kenny 2005).

2.5 Determination of organic matter in the sediment

Total organic carbon (TOC) content was determined in dried and acidified sediments using a LECO CR 12 Carbon Analyser (King *et al.* 1998). A small portion from each sediment sample was collected in a glass bottle and dried at room temperature (18-20°C). The dried samples were ground to a fine mass using a mortar and pestle, and stored in air-tight glass bottles. Approximately 0.350 g of dried and homogenized sediment was transferred to a small ceramic crucible and 1M HCl added to remove inorganic carbonate. Finally, the samples were washed, dried and re-weighed The carbon analyser was calibrated prior to carbon analysis by combustion of a calcium carbonate standard with known carbon content of 12 %. The samples were then combusted at 1350 °C in an oxygen atmosphere so that any carbon present was converted to CO_2. Nitrogen content was analysed using a CHN Analyser (Thermo Finnigan Flash EA 1112 series) by combustion of the samples at 930°C to convert the sample nitrogen to simple gases (N_2). The mass of the gases (CO_2 for carbon and N_2 for nitrogen) was converted to weight percentages of total organic carbon (TOC) and total nitrogen based on the dry sample weight (Hedges & Stern 1984).

2.6 Data analysis

The data were analysed using both univariate and multivariate techniques. Macrofaunal diversity was examined by faunal abundance data, species (taxa) richness, Shannon's diversity (exp(H')) (Shannon & Weaver 1963), the expected number of species in a sample of 50 individuals using rarefaction curves ($E(S_{50})$) (Hurlbert 1971), Simpson's diversity (1/D) (Simpson 1949) and Pielou's evenness index (J') (Pielou 1966) The data were checked for normality using the Anderson-Darling test (Anderson & Darling 1952) and for homogeneity of variances by Levene's test (Levene 1960). All data except Pielou's evenness index were then root-transformed to obtain a normal distribution. Potential differences between inside and outside the pockmarks and between the different pockmarks were examined with two-way ANOVA.

Multivariate analyses were carried out on the faunal data to assess differences (dissimilarities) in the faunal composition between inside and outside the pockmarks. Prior to the multivariate analysis, the species abundance data were root-transformed to down-weight the influence of highly abundant species (Field *et al.* 1982). Non-metric Multidimensional Scaling analysis (NMDS ordination) was performed on a similarity matrix based on Bray-Curtis similarity coefficient (Bray & Curtis 1957). NMDS ordination reduces high-dimensional data by placing the samples in a two dimensional space so that the distances between pairs of samples reflect their relative similarity of faunal composition (using rank order, not absolute values) (Clarke & Warwick 2001). The 'goodness-of-fit' in the NMDS ordination plot is measured as stress with Kruskal's stress formula 1 (Kruskal 1964), which reflects the agreement between the similarity ranking and the corresponding distance ranking (Clarke & Warwick 2001). Classification was performed using hierarchical agglomerative clustering with group-average linking of the Bray-Curtis similarities in combination with similarity profiles (SIMPROF). SIMPROF determines the statistical significance of each individual split in a dendrogram with no pre-defined grouping, using a permutation technique (Clarke & Warwick 2001; Potter *et al.* 2001).

Analysis of similarities (ANOSIM) was conducted to determine whether the faunal composition inside the pockmarks were significantly different from that of the surrounding seafloor outside the pockmarks. ANOSIM is a distribution-free, multivariate analogue of ANOVA, testing for difference between groups defined *a priori* (Clarke 1993). A two-way

ANOSIM was carried out in order to separate the area effect (differences between the pockmarks) from differences in faunal composition between the inside and outside of the pockmarks (Warwick *et al.* 1990; Clarke 1993). A two-way ANOSIM tests the null hypothesis of no difference in the faunal composition between inside and outside pockmarks, while accounting for the natural spatial heterogeneity by allowing for differences between pockmarks. An ANOSIM R statistic designed to measure the degree of separation among the two groups (inside and outside) is calculated for each pockmark and averaged to give the global R. The R statistic is a standardized number and will always be between 0 and 1; if $R = 1$, all replicates within a group are more similar to each other than any replicates from other groups, if $R = 0$ will similarities between and within groups be the same (Clarke 1993). As for NMDS, ANOSIM measure differences based on average ranks and not on the actual similarities themselves. The significance level for group differences is given by a permutation test, generating a permutation distribution under the null hypothesis of no difference between groups and comparing this distribution with the observed global R. The same procedure is performed to test for differences between stations, this time allowing for the differences between inside and outside the pockmarks. Pair wise tests for all pockmarks are also obtained by the procedure (Clarke 1993).

Compositional differences between the inside and outside of pockmarks were also visualized by a constrained analysis using Canonical Analysis of Principal Coordinates (CAP) (Anderson 2004). CAP is a kind of constrained version of NMDS. Constrained methods are designed to view the data so that *any* differences in the species composition that might be apparent in multivariate, high-dimensional space can be viewed in a lower-dimensional space (e.g. 2-D) (Anderson & Robinson 2003; Anderson & Willis 2003). The ordination is constrained because it uses the *a priori* hypothesis (that the macrofaunal assemblages inside the pockmarks differ from the outside) as part of the criterion for finding the ordination axis (Willis *et al.* 2004). CAP is a two-step procedure that involves calculation of principal coordinates from Bray-Curtis dissimilarities, followed by Canonical Discriminant Analysis (CDA) on these principal coordinates. The first canonical variable (CV1) is an axis drawn through the data points that best separates the groups, i.e. finds the linear combination of original variables that maximizes the variation between the groups. This axis is then plotted against the first principal coordinate axis (PCO1), providing a constrained ordination plot. The allocation success is a measure of group distinctness, and gives the probability that a new observation will be placed into its correct group when placed into the ordination plot. A

squared canonical correlation value (δ^2) between 0 and 1 is given for the canonical axis, and this is the correlation between the group structure and the species data. The closer the value is to 1, the greater is the strength of the group effect. The statistical significance of δ^2 is calculated by permutation test (Anderson & Robinson 2003; Anderson & Willis 2003; Willis *et al.* 2004). The CAP ordination is based on root-transformed species abundance data and Bray-Curtis dissimilarity.

Similarity percentages (SIMPER) analysis was performed on the root-transformed species abundance data to examine the contribution of individual species to any differences between the groups. Each species' contribution is listed as percentage of average dissimilarity between the groups. The dissimilarity contribution of each species divided with the standard deviation gives a measure of how consistently the species contribute to the dissimilarity (i.e. the best discriminator species) (Clarke 1993).

The abiotic dataset consisted of eight variables: pH, redox potential (Eh), depth of the overlying water column (m), TOC (%), % nitrogen, temperature of the sediment (°C), mean grain size (µm) and % silt-clay sediment (<63 µm). To obtain approximate multivariate normality and avoid skewness, all variables were log-transformed (log (x+1)) prior to analysis (Clarke & Gorley 2006), except for the percentage data (TOC, % nitrogen and silt-clay fraction) which were arcsine-transformed (Dytham 1999 pp. 41-42). Each environmental variable was normalized by subtracting the mean and dividing by the standard deviation for each variable, in order to account for the different scales in the environmental measurements (Clarke & Gorley 2006). The transformed and normalized variables were subjected to Principal Component Analysis (PCA). The first principal component axis (PC1) is a linear combination of the original variables that minimizes the sum of squared deviations of points to the new axis, i.e. in the direction of maximum variation in the data. The second axis (PC2) is perpendicular to PC1 (Clarke & Warwick 2001). The two groups (inside and outside) and the environmental variables' eigenvector coefficients were superimposed on the PCA plot.

The BIO-ENV procedure in PRIMER was performed in order to extract the environmental variables most important for structuring the biotic dataset. This procedure measures how closely related the two sets of multivariate data (biotic and environmental) are by calculating a rank correlation coefficient (Spearman's ρ) between all the elements of the two similarity

matrices. Input data were the Bray-Curtis similarity matrix based on root-transformed species abundance data and a Euclidian distance matrix of transformed, normalized environmental variables. The variable or combination of variables that gives the highest correlation coefficient is assumed to be the most important explanatory variable and reflects the degree to which the environmental data explains the community structure. A permutation test was performed to test the null hypothesis of ρ=zero (the environmental combination is not better than any random combination of variables) (Clarke & Ainsworth 1993).

All univariate statistics were performed using Minitab version 15, and multivariate analyses were conducted using PRIMER (Plymouth Routines In Multivariate Ecological Research) version 6 (Clarke 1993; Clarke & Warwick 2001; Clarke & Gorley 2006), except for the constrained ordination and discriminant analysis which was done using the CAP computer program (Anderson & Robinson 2003; Anderson & Willis 2003; Anderson 2004). The initial statistical analysis of grain size was performed using the Microsoft Excel spreadsheet Gradistat (Blott & Pye 2001).

3. Results

The raw data (species abundances and environmental variable measurements) are given in the Appendices A and B.

3.1 Environmental variables

The grab samples (n=50) consisted most frequently of silt-clay sediment with dark grey to grey-brownish colour. Mean values and standard deviations of all environmental variables measured are listed in Table 2. The mean silt-clay content was 93.1% (± 10.2 SD) and mean grain size was 20.8 µm (± 12.1 SD) (textural group: mud). The mean organic carbon content of the sediment was 3.30% (± 1.12 SD) dry weight, and the mean C:N ratio was 11.1 (± 1.4 SD). The redox potentials were negative for all grab samples; mean = - 40.3 Eh (± 7.9 SD) Hydrogen sulphide odour was detected in some grab samples from all pockmarks, except pockmark 18 where none of the samples smelled of H_2S. Surface temperatures ranged from 17.5-19°C and bottom temperature was 8°C. Surface salinities were 24-25‰ and increased to 32-33‰ near the seafloor. The pycnocline was at approximately 10 m below the surface. No temperature or salinity anomalies were detected (see Appendix C for salinity and temperature curves).

The environmental variables were on the whole similar inside and outside the pockmarks; depth of the overlying water column was the only environmental variable significantly different between the two groups (Table 2). Redox potential and organic carbon content were close to significant ($p = 0.06$ and 0.09, respectively), with sediments from inside the pockmarks having a higher TOC value and lower (more negative) redox potential. By removing one TOC value (10F), the difference between inside and outside becomes highly significant ($p = 0.02$). There was large variation between the pockmarks and among replicate samples for many of the variables (Fig. 5). The boxplots of grain size show that pockmark 10 had coarser sediments than the other four pockmarks (textural group: sandy mud) and lower redox potential.

Table 2: Mean values and standard deviation for all samples (n=50) and for inside and outside each pockmark (n=25) for the eight environmental variables and for the C:N ratio. Significance level (p) for difference between the groups is given by two-sample t-test or the non-parametric Mann-Whitney U-test (*) for variables that were not normally or log-normally distributed. The percentage data (TOC, % total nitrogen and % mud) were arcsine transformed prior to the test.

Variable	All samples	Inside	Outside	p
pH	7.73 (± 0.16)	7.76 (± 0.17)	7.7 (± 0.14)	0.14
TOC (%)	3.30 (± 1.12)	3.61 (± 1.23)	2.99 (± 0.93)	0.09
% N	0.39 (± 0.15)	0.43 (± 0.17)	0.35 (± 0.13)	0.11
Redox (Eh)	-40.3 (± 7.9)	-42.4 (±7.9)	-38.2 (± 7.5)	0.06
Grain size (µm)	20.8 (± 12.1)	22.4 (± 15.4)	19.3 (± 7.4)	0.42*
% mud	93.1 (± 10.2)	93 (± 11.2)	93.1 (± 9.4)	0.39*
Depth (m)	41.3 (± 9.5)	46.3 (± 6.4)	36.3 (± 9.6)	<0.01
Temperature (°C)	10.7 (± 1.5)	10.7 (± 0.2)	10.6 (± 0.1)	0.93*
C:N	11.1 (± 1.4)	11 (± 1.6)	11 (± 1.1)	0.96

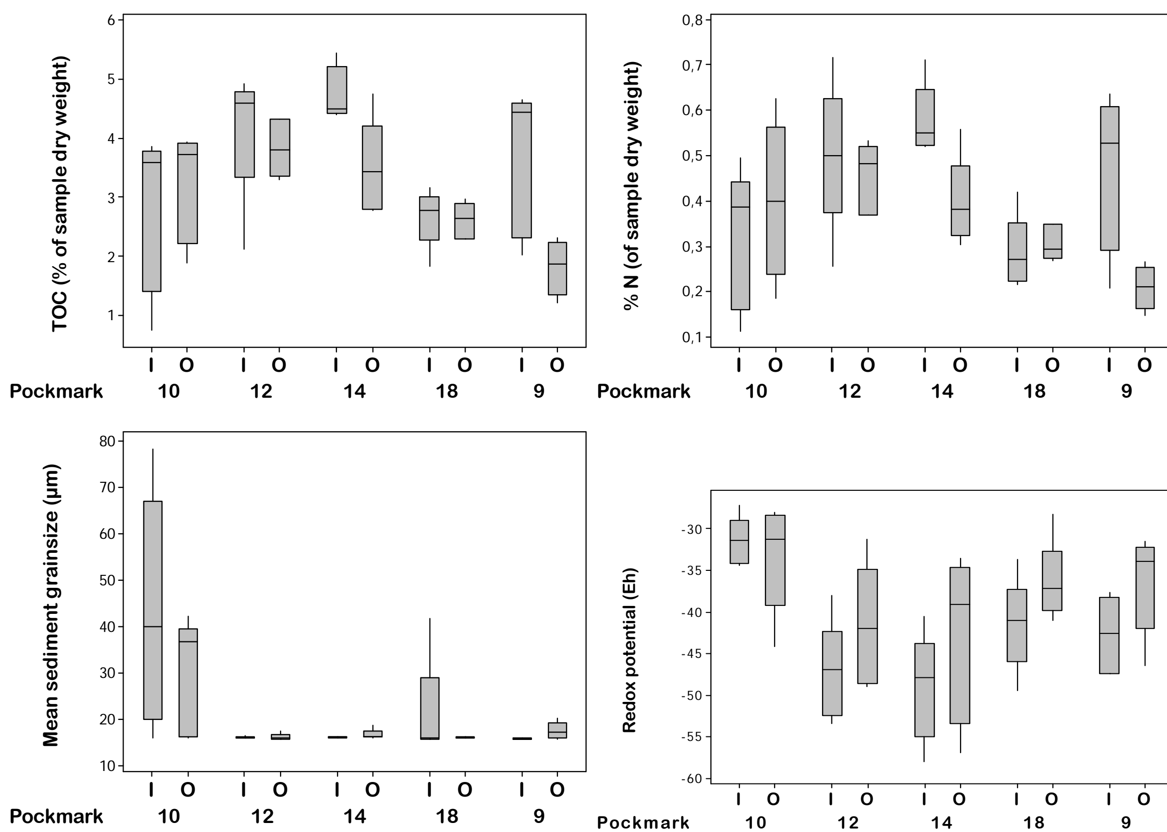

Fig. 5: Boxplots with median and upper and lower quartiles for the inside and outside of each pockmark for four sediment variables: organic carbon content (TOC), nitrogen content (%N), mean grain size and redox potential of the sediment. Lines extending from the boxes are the full range.

The PCA ordination plot of eight environmental variables is shown in Fig. 6. The first principal component, PC1, explains 45% of the variation in the data set and PC2 accounts for 19%. The two axes combined explain 64% of the variability in the data. Vector length and direction reflects the importance of that variable's contribution to the PC axes. Their eigenvectors are given in Table 2. PC1 is a roughly equally weighted combination of the organic variables (pH, redox, TOC and %N, eigenvector coefficients ranging from -0.39 to -0.42), decreasing in the positive PC direction. PC2 reflects a grain size gradient, with grain size decreasing and % mud increasing in the positive PC2 direction (eigenvector coefficients for grain size and % mud are -0.52 and 0.48, respectively). However, also the grain size variables contribute to PC1 and no clear environmental gradients are readily discernible from the plot. Depth is not strongly related to either axis (Table 3).

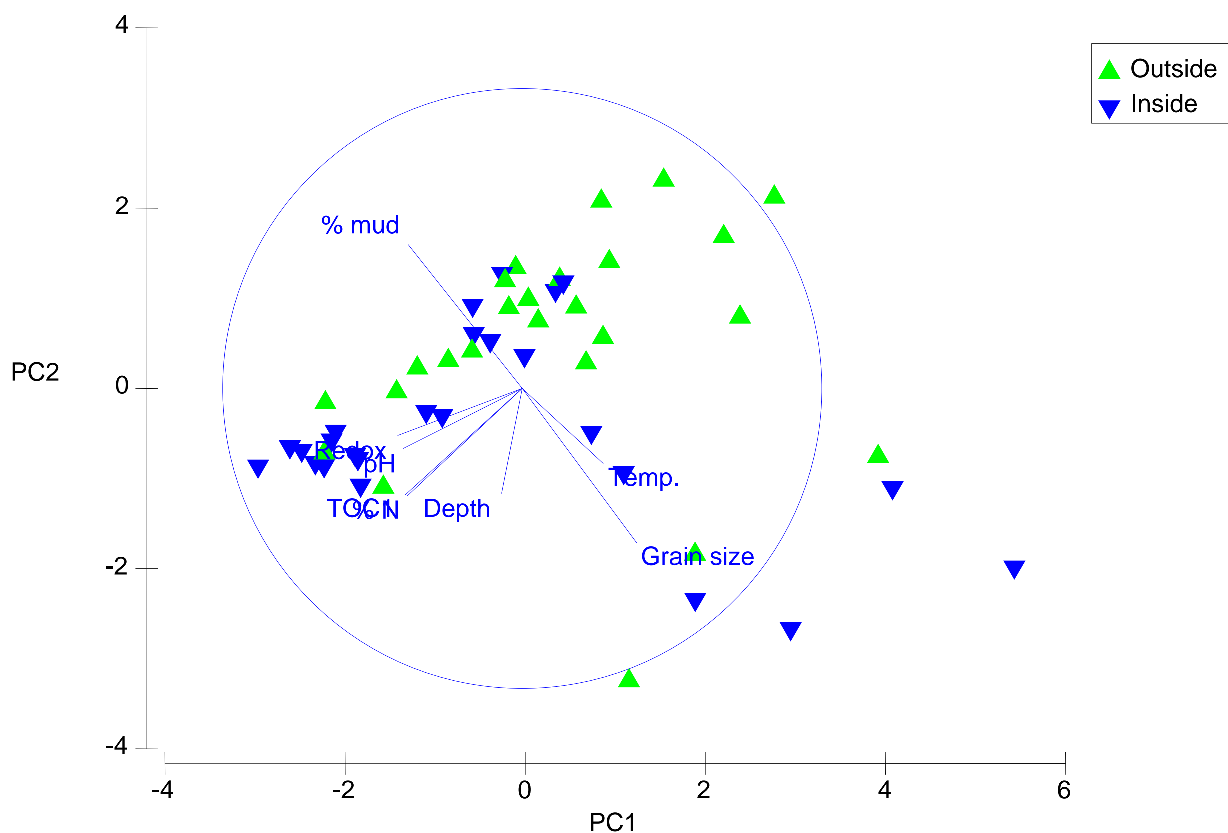

Fig. 6*:* PCA of the 8 environmental variables for 50 grab samples from the five pockmarks. TOC=total organic carbon (% of sample dry weight), %N = percentage nitrogen of sample dry weight), Depth = depth of water column (m), pH = pH of sediment, Grain size = mean grain size (µm), % mud = % silt-clay fraction of sediment (<63 µm) and Temp = temperature of sediment (°C). All variables were log-transformed, except % mud, %N and TOC which were arcsine-transformed. Variable vectors are superimposed on the plot as blue circle and lines.

Table 3: Eigenvectors for the 8 environmental variables.

Variable	**PC1**	**PC2**
pH	-0.398	-0.201
Temperature	0.270	-0.250
Depth	-0.069	-0.350
% mud	-0.381	0.479
Grain size	0.382	-0.515
% N	-0.385	-0.359
Redox	-0.415	-0.157
TOC	-0.391	-0.355

3.2 Faunal diversity

A total of 11,510 individuals, representing 104 taxa, were identified from 50 grab samples. Aproximately 2/3 of the taxa (69 out of 104) were identified to the species level. Annelida (Polychaeta) was the dominant group, comprising 59 % of the taxa and 69 % of the individuals. Crustaceans, molluscs and echinoderms made up the remainder of the samples, in addition to the group 'Varia' which included the phyla Cephalorhyncha (Priapulida), Cnidaria, Sipuncula and Phoronida (Table 4).

Table 4: The total number of individuals and taxa within each phylum, and the percentage of individuals and taxa that each phylum made up. The group 'Varia' includes the following phyla: Cephalorhyncha, Cnidaria, Sipuncula and Phoronida. Both abundance and number of taxa are absolute values.

	Annelida	**Crustacea**	**Mollusca**	**Echinodermata**	**Varia**
Total no. of individuals	7920	2354	1021	92	123
Total no. of taxa	61	17	12	8	6
% of the individuals	69	20	9	1	1
% of the taxa	59	16	12	8	6

The total number of individuals found inside and outside the pockmarks were 4360 and 7145, respectively. The total abundance outside was thus 63% higher than inside the pockmarks. Also the total number of taxa found outside (91) was higher than inside (73). There was, however, large variation in the faunal abundances and taxa richness within each site-group, due to large differences between the different pockmarks (Table 5, Fig. 7). Pockmark 18 was the most diverse, and contained nearly three times as many individuals as pockmark 10 and 12. At pockmark 10, 8 out of ten grab samples contained less than 100 individuals, and only three samples had more than 10 taxa. The number of taxa was highest at pockmark 18, followed by pockmark 9.

Shannon's diversity ranged from 2.0 to 16.2. Estimated numbers of taxa in a sample of 50 individuals ($E(S_{50})$) were between 5.2 and 16.8. Simpson's diversity ranged from 1.75 to 8.72 and Pielou's evenness from 0.470 to o.751 (Table 5). Faunal abundance, number of taxa and the diversity and evenness measures differed significantly between the pockmarks ($p < 0.01$, see Appendix D for complete two-way ANOVA tables). In contrast, no statistically significant differences were found between the inside and outside (pooled across all pockmarks), except for number of individuals ($p < 0.05$, two-way ANOVA), which were much higher outside (Table 5). The pattern of lower faunal abundances inside the pockmarks

was fairly consistent, but with large variation among replicate samples (Table 5, Fig. 7). The number of taxa found was also lower inside the pockmarks, although not statistically significant ($p = 0.08$, two-way ANOVA). An exception to this pattern was pockmark 12, which had more taxa inside than outside. No consistent pattern was detectable among the diversity and evenness measures; while Shannon's diversity (per 0.5 m^2) was lower inside than outside, Simpson's diversity showed the opposite (Table 5, Fig. 7).

Table 5: Total number of taxa (S), total number of individuals, Shannon's diversity exp(H'), Simpson's diversity (1/D), Hurlbert's rarefaction index $E(S_{50})$ and Pielou's evenness index per 0.5 m^2 for inside and outside each pockmark.

Inside	S	N	Exp(H')	$E(S_{50})$	1/D	J'
9	22	880	7.0	10.2	3.47	0.611
10	9	174	2.0	5.2	1.75	0.478
12	29	657	9.8	12.2	5.11	0.712
14	16	418	7.65	9.8	4.55	0.751
18	61	2239	16.2	16.8	8.72	0.743
Mean (0.5 m^2)	27.4	874	6.7	10.8	4.72	0.659

Outside	S	N	Exp(H')	$E(S_{50})$		J'
9	49	1247	13.1	15.2	5.67	0.704
10	29	1170	6.4	10.1	2.69	0.470
12	22	725	6.0	9.7	3.68	0.676
14	32	1905	5.8	8.7	2.92	0.596
18	63	2098	13.4	15.6	4.99	0.637
Mean (0.5 m^2)	39	1429	8.2	11.9	3.99	0.617

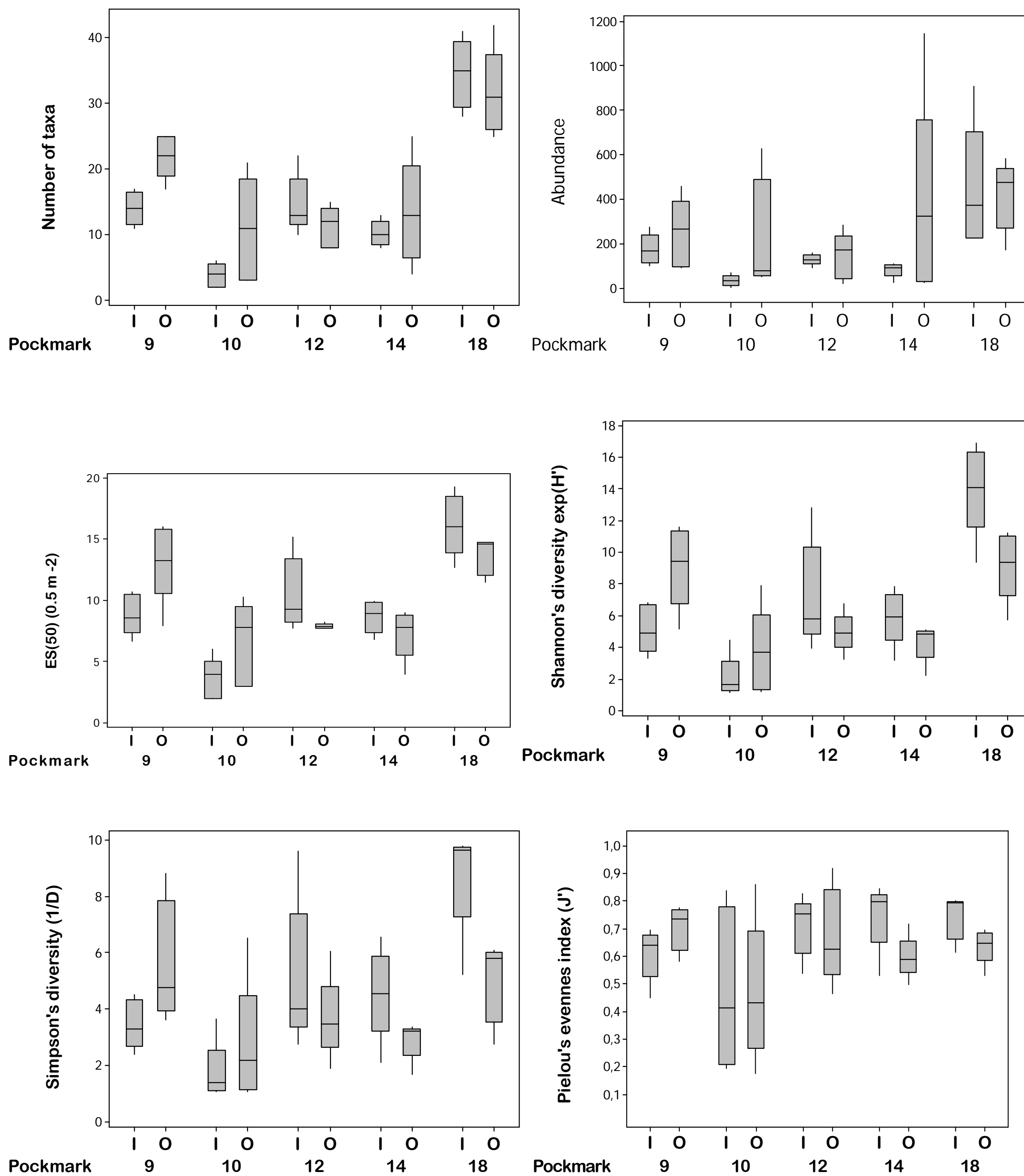

Fig. 7: Boxplots with median and upper and lower quartiles for the number of taxa (S), faunal abundance (N), Hurlbert's E (S_{50}) and Shannon's diversity exp(H'), Simpson's diversity (1/D) and Pielou's evenness index (J') inside (I) and outside (O) each pockmark. The lines extending from the box are the full range of values.

3.3 Faunal composition

NMDS ordination did not provide any clear clustering of inside and outside samples (Fig. 8). The stress value is 0.13. As this is below the generally accepted value of 0.2, the ordination gives a reasonable representation of the overall faunal pattern (Clarke 1993). Consistent differences in the faunal assemblages between the inside and outside would be indicated by two more or less distinct groups of samples in the plot. Although there is a tendency towards such a clustering (inside samples on the left and outside samples on the right), many samples 'fall out' of their designated group. In contrast, it seems that samples from the same pockmarks cluster together in three distinct groups. The fauna in the three groups are significantly different as determined by SIMPROF, and are visible in the dendrogram (Fig. 9) at a 34 % similarity level. One cluster consists mainly of samples from pockmark 10 (top left), one of samples from pockmark 9 and 18 (top right), while the bottom cluster consists of samples from pockmark 12 and 14 (Fig. 8).

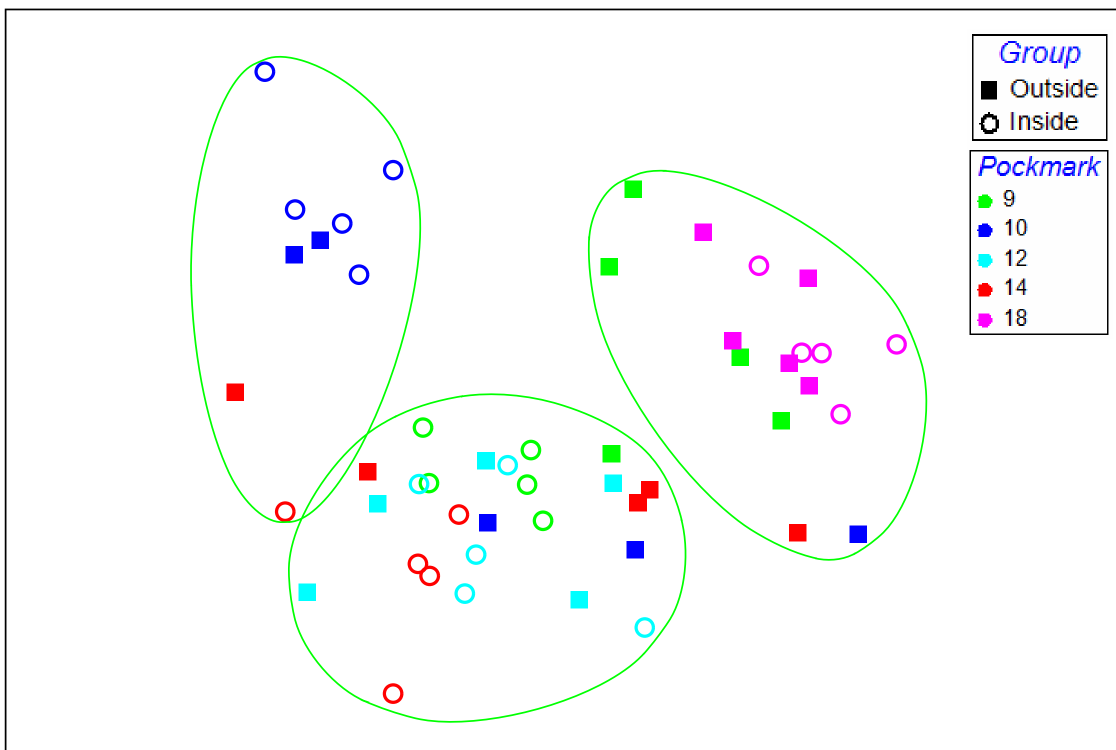

Fig. 8: Nonmetric multidimensional scaling (NMDS) ordination of 50 grab samples from five pockmarks, using Bray-Curtis similarities on root-transformed species abundances (NMDS stress = 0.13) SIMPROF groupings from the cluster analysis in Fig. 10 are superimposed. Filled square = outside and open circle = inside the pockmarks.

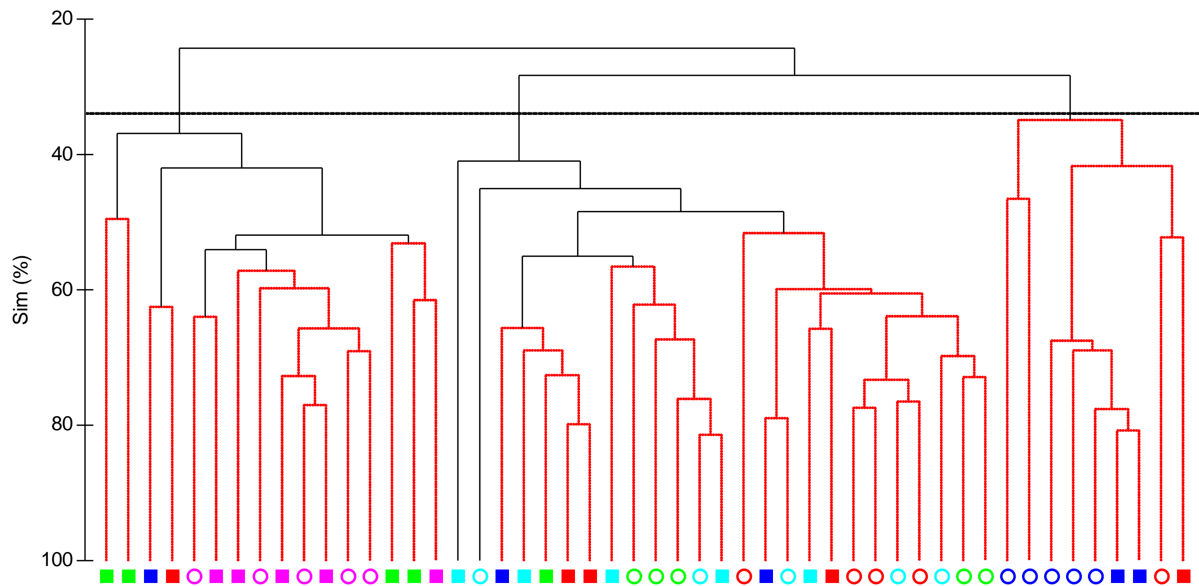

Fig. 9: Hierarchical agglomerative clustering with group-average linking of the 50 grab samples from five pockmarks, using Bray Curtis similarities on root-transformed species abundances. The 34% similarity threshold (horizontal line) separates three clusters with significant different species composition, as suggested by SIMPROF. Red split = not statistically different species composition. Symbol keys are the same as Fig. 9.

To account for the area effect caused by large differences in abundance and taxa richness between the pockmarks, a two-way ANOSIM was carried out. The test indicated that the faunal composition inside the pockmarks was significantly different from the outside ($p < 0.01$, $R = 0.296$). There was also a significant difference between the pockmarks ($p < 0.01$, global $R = 0.547$). The larger R statistic suggests that the differences between the pockmarks are greater than the differences between the two groups. The significance level is the same ($p < 0.01$), but is not directly comparable between the tests as they are based on different numbers of replicates (Clarke & Gorley 2006). The relatively low R of 0.296 suggests that the faunal composition overlap between the inside and outside of pockmarks.

The pair wise tests (Table 6) give an R statistic for comparison between every pockmark. All comparisons were significant ($p < 0.1$, but not adjusted for multiple comparisons). The test indicates that pockmark 18 has a quite different faunal composition compared to the other pockmarks (R from 0.706 to 0.96). Pockmark 12 and 18 had very different faunal compositions ($R = 0.960$), while the pockmark 12 and 14 were most similar ($R = 0.184$).

Table 6: ANOSIM pair wise test, giving R statistics for comparison of faunal composition for each pair of pockmarks (global R=0.547, p<0.01). All pair wise comparisons were significant ($p < 0.01$).

Pockmark	9	10	12	14
9				
10	0.542			
12	0.386	0.534		
14	0.340	0.423	0.184	
18	0.706	0.722	0.960	0.8

The constrained ordination (Fig. 10) reveals the differences in faunal composition found by ANOSIM between the inside and outside of the pockmarks. The two groups were well separated with the inside samples on the left side and the outside samples on the right. The allocation success was 72%. This is the probability that any new observation will be placed in its correct group when placed into the ordination plot. The squared canonical correlation coefficient $\delta^2 = 0.63$, thus the correlation between the group structure and the species data is fairly good. The correlation value of 0.63 was as for ANOSIM highly significant ($p < 0.01$). The results of ANOSIM and discriminant analysis combined strongly indicate that the species composition inside the pockmarks is significantly different than outside.

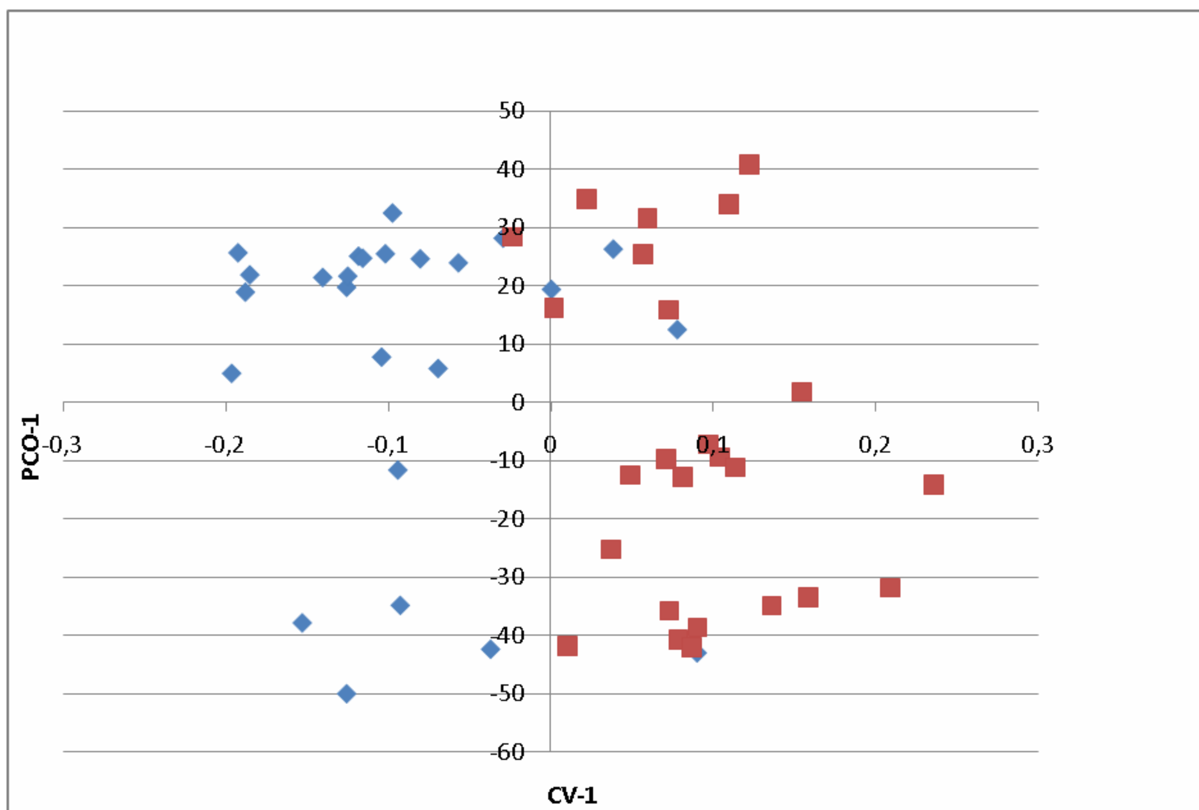

Fig. 10: Canonical analysis of principal coordinates (CAP) of 50 grab samples from five pockmarks, using Bray Curtis similarities on root-transformed species abundances. Axis 1 is the first canonical axis (CV-1) (constrained) and axis 2 is the first principal coordinate axis (PCO-1) (unconstrained). Blue squares = inside, red square = outside.

3.4 Taxa: most abundant and best discriminators

The ten most numerically abundant taxa are listed in Table 7. The majority are polychaetes, in addition to small crustaceans (copepods) and two bivalve taxa (*Nuculoma tenuis* and *Thyasira* sp.). The polychaete *Pseudopolydora* sp. was the most abundant taxon, comprising 26 % of the total faunal abundance, followed by copepods, and the polychaete *Heteromastus filiformis*. Of the 104 taxa identified, 60 were present both inside and outside the pockmarks. 13 species were found exclusively inside and 31 species exclusively outside the pockmarks.

Table 7: The ten most numerically abundant taxa, given as total abundance for all samples, mean abundance (per 0.5 m^2) and percentage of total abundance.

Taxa	Total abundance	Mean (per 0.5 m^2)	% of total abundance
Pseudopolydora sp.	3003	601	26.1
Copepoda	2036	407	17.7
Heteromastus filiformis	1828	366	15.9
Thyasira sp.	535	107	4.6
Polydora sp.	531	106	4.6
Chaetozone setosa	377	75	3.3
Nuculoma tenuis	356	71	3.1
Capitella capitata	302	60	2.6
Pholoe minuta	260	52	2.3
Prionospio cirrifera	175	35	1.5

The average Bray-Curtis dissimilarity in faunal composition between the inside and outside of the pockmarks was 56, and the taxa that contributed most to this dissimilarity are listed in Table 8. With a cut-off point of 50% of cumulative percentage contribution of each taxon, the list includes seven taxa. Five of the seven taxa are polychaetes, with *Pseudopolydora* sp. and *Heteromastus filiformis* contributing most to the dissimilarity. The two non-polychaete species included in this list are copepods and the bivalve *Thyasira* sp. The dissimilarity contribution of each taxon divided with the standard deviation is a measure of how consistently the taxon contributes to dissimilarity (i.e. the best discriminator taxon). *Pseudopolydora* spp. and *Chaetozone setosa* contributed most consistently to the differences in faunal composition between the two groups.

Table 8: List of taxa contributing to the differences in faunal composition between inside and outside the pockmark, determined by two-way crossed SIMPER analysis. The table lists the average abundance of each taxon and the average dissimilarity of each taxon for inside and outside groups. Each taxon's contribution to the total dissimilarity between the groups is given as a percentage, and the cumulative contribution of each taxon is set to a cut-off point of 50 %. Column 4 gives the ratio of average contribution divided by standard deviation (SD) of those contributions across all pairs of samples making up this average, and is a measure of how consistently the taxa contribute to the group differences.

Taxa	Average abundance inside	Average abundance outside	Average dissimilar.	Average dissimilar. /SD	Contri-bution (%)	Cumulative contribution (%)
Pseudopolydora sp.	4	7.62	7.23	1.2	13	13
Heteromastus filiformis	2.02	4.87	5.12	0.86	9	22
Copepoda	5.26	6.07	4.61	0.74	8	30
Polydora sp.	3.08	1.11	3.23	0.94	6	36
Capitella capitata	2.04	0.95	3.03	0.83	5	42
Thyasira sp.	2.15	2.43	2.72	0.94	5	47
Chaetozone setosa	1.01	2.25	2.46	1.09	4	51

3.5 Linking biota and environmental variables

The results of the BIOENV procedure are listed in Table 9 as Spearman's rank correlation ρ between biotic and environmental similarity matrices. The single environmental variable that best structured all the samples, in a manner consistent with the faunal patterns, was the total organic carbon content (ρ = 0.32), followed by depth of the water column, % nitrogen, redox potential, pH and grain size. The variable combination that gave maximum correlation included the five variables pH, depth, mean grain size, TOC and redox potential (ρ = 0.42). Organic carbon was also the single variable with the highest correlation with the faunal pattern outside the pockmarks (ρ = 0.37). The 'best' variable combination for the outside samples included pH, grain size and nitrogen and organic carbon content (ρ = 0.55). For the inside samples, depth of the overlying water column was the single variable with highest correlation with the biotic pattern (ρ = 0.61). In fact, depth alone gave a higher correlation than any combination of environmental variables.

Table 9: Relationship between environmental variables and faunal pattern, given as Spearman's rank correlation *ρ* between environmental data and biotic similarity matrix, using BIOENV in PRIMER. *ρ* is given for each environmental variable and for the combination of variables giving the highest overall correlation. All variables are log-transformed, except % mud, % nitrogen and TOC which are arcsine-transformed.

Inside		**Outside**		**Overall**	
Variable	**ρ**	**Variable**	**ρ**	**Variable**	**ρ**
Depth	0.61	TOC	0.37	TOC	0.32
Redox	0.32	% N	0.36	Depth	0.29
pH	0.32	Redox	0.32	% N	0.28
Temp.	0.31	pH	0.30	Redox	0.23
TOC	0.30	Depth	0.24	pH	0.21
% mud	0.26	Grain size	0.22	Grain size	0.20
Grain size	0.24	% mud	0.20	% mud	0.19
% N	0.21	Temp.	-0.01	Temp.	0.11
Max. corr.: Depth	0.61	Max. corr.: pH, grain size, % N, TOC	0.55	Max. corr.: pH, grain size, depth, TOC, redox	0.42

4. Discussion

Multivariate analysis of the species abundance data showed that the faunal composition inside the pockmarks differs significantly from the outside, as determined both by ANOSIM and the discriminant analysis. The ANOSIM R statistic gives an absolute measure between 0 and 1 of how separated the groups are: a value of $R > 0.5$ means the faunal compositions are overlapping but clearly different and $R < 0.25$ means they are barely separable (Clarke & Gorley 2001). The R statistic of 0.296 indicates that the faunal composition differs but with a high degree of overlap. In fact, 60 of the 104 taxa identified in this study were found both inside and outside the pockmarks.

The differences in faunal composition between the inside and outside of pockmarks, although statistically significant, are not obvious on the NMDS plot (Fig. 8). The NMDS plot confirms the overlap among the two groups, but does not reveal the group differences. The purpose of an NMDS plot is to view the data and infer possible patterns without the use of an *a priori* hypothesis (let the data 'tell their own story'- Clarke & Ainsworth 1993). It has proven to be a robust tool for the exploration of ecological data, but may be inadequate in studies with an *a priori* hypothesis concerning differences between groups (Clarke 1993). NMDS ordination may also, in some cases, mask real patterns in multivariate location among groups due to a conflicting overall dispersion pattern (Anderson & Willis 2003). The constrained ordination, on the other hand, will find the axis that maximizes differences between groups. In the present study, it is clear that the constrained method (Fig. 10) uncovered the differences in faunal composition between the inside and outside of pockmarks that were not visible on the unconstrained NMDS plot (but suggested by ANOSIM).

There were also significant differences in faunal composition between the pockmarks. The global R for differences between pockmarks was 0.547, indicating that the faunal compositions are overlapping but clearly different (Clarke & Gorley 2001). Since the R statistic is an absolute measure of distance between groups, this value is directly comparable to the R of 0.296 for differences between inside and outside, despite different numbers of replicates (Clarke & Gorley 2006). Thus, there are larger differences in the faunal composition between the pockmarks than between the inside and outside of pockmarks, reflecting the large spatial heterogeneity characteristic of all natural environments (Levin

1992). Morrisey *et al*. (1992) showed that the abundance of infauna in soft sediments are patchy at a range of spatial scales, from a meter up to several kilometers. Archambault and Bourget (1996) found that scale smaller than 20 cm influenced abundance of benthic intertidal macrofauna- and flora. The patchiness has implications for all studies concerning the distribution of benthic fauna; scales of variation smaller than the spacing of replicate samples will be incorporated into estimates of variation among locations and may lead to loss of power when testing for differences (Morrisey *et al.* 1992). The distance between replicate samples is large in the present study (50-150 m and 100-200 m for inside and outside samples, respectively), giving raise to large variation among replicate samples. For example, the faunal abundance ranged from 25 to 1147 individuals per 0.1 m^2 for samples taken outside pockmark 14. The distance between every pair of pockmarks influenced their pair-wise similarity of faunal composition. Pockmark 18 is situated 1.5 to 2 km from the other pockmarks, and has very different faunal composition. Pockmarks 12 and 14 are located less than 500 m apart, and have very similar faunal composition (Table 6). The large variation among replicate samples and between the pockmarks may have confounded the differences between the inside and outside groups. A two-way ANOSIM will account for between-pockmark differences but not for the among-replicate variation.

The faunal abundance inside the pockmarks was significantly lower than outside (Table 5). The taxa richness was also lower inside, although not significantly. One might notice that the different diversity measures did not provide any consistent differences between inside and outside the pockmarks. Shannon's diversity and Hurlbert's rarefaction index were both lower inside, while Simpson's diversity and Pielou's evenness index were lower outside (Table 5). The diversity measures differ in their relative weighing of rare and common species (Peet 1974). Shannon's diversity is more sensitive to changes in the importance of rare species than Simpson's diversity. Simpson's index is highly influenced by the most common species in the sample, and is considered a measure of dominance (diversity is the reciprocal of D), while Pielou's index is a measure of evenness. The results of the univariate measures indicate more even faunal communities inside the pockmarks. However, the differences are small and not statistically significant.

The lower faunal abundances found inside the pockmarks are in contrast to the observations of enriched faunal communities in pockmarks made by e.g. Hovland and Thomsen (1988). They are, on the other hand, consistent with previous (Dando *et al.* 1991) and recent (Wildish *et al.* in press) studies on pockmark benthic infauna. It seems plausible to conclude

that the seeping of methane does not lead to elevated faunal abundances inside the Oslofjord pockmarks. This implies that a) the methane does not provide an additional nutrient source to the benthic fauna, b) the seeping fluid is fresh water and not methane, c) the fluid escape is eruptive rather than continuous seeping, or d) the pockmarks are extinct, i.e. relict features of past fluid escape. Some of these scenarios are discussed further in the following as possible explanations for the different faunal composition found inside the pockmarks.

4.1 Physical disturbance by eruptive fluid escape

Long-term measurements of fluid flux rates in cold seeps have demonstrated that flow patterns are complex, and that small-scale temporal variation in flux rates affects the benthic community (Tryon & Brown 2001). Episodic fluid escape rather than continuous micro-seepage is a common feature for pockmarks (Hovland *et al.* 2002a). Thus, the Oslofjord pockmarks could be in a 'dormant state' in between more active periods. External events, such as extreme low pressure, extreme low tides, storm surges or earthquakes, influence fluid flow and can possibly trigger an eruptive fluid escape (Hovland *et al.* 2002a). An eruptive fluid escape would be a major physical disturbance of the sediment, and could prevent stable communities from being established in the pockmarks, as proposed by Dando *et al*. (1991). Such a sudden displacement of a large volume of sediment would also result in loss of resident macrofauna inside the pockmarks. Recovery of a disturbed area has occurred 'when the disturbed community has attained a state that is no longer significantly different to the composition of an adjacent undisturbed area' (definition by Dernie *et al.* 2003). The different species composition found inside the Oslofjord pockmarks could indicate that the community has not yet recovered from a possible disturbance.

The benthic infaunal communities inside the Oslofjord pockmarks may be in different successional stages, reflecting the time and intensity of the disturbance. Dernie *et al*. (2003) showed that the recovery rate differ with the intensity of the disturbance; recovery from more intense disturbance may take at least twice as long as from less intense disturbance. Wildish *et al*. (in press) discussed the impact of a physical disturbance inside pockmarks in more detail. They recognized two different pockmark habitats with respect to species composition: one had significantly lower species number and faunal density compared to the outside while the other showed small but varying differences. The authors suggest that the two habitats are at different successional stages following disturbance. The time since the disturbance was estimated to be 5 to 15 years before sampling for the pockmark habitat with

reduced faunal abundances. Assuming similar rates of re-establishment in the Oslofjord pockmarks, the results of the present study would imply a relatively recent fluid expulsion.

Measurements of size and biomass of individuals to verify a potentially higher proportion of juveniles inside the pockmarks were not done in the present study, due to time constraints. However, re-colonization of disturbed areas may occur gradually through adult migration or passive advection from surrounding sediment rather than by recruitment of juveniles (Savidge & Taghon 1988; Thrush *et al.* 1992; Dernie *et al.* 2003).

4.2 Increased deposition of organic matter inside pockmarks: environmental disturbance

An alternative explanation for the different faunal composition inside the pockmarks, that has not been previously documented, is environmental disturbance in the form of increased deposition of organic material into the pockmarks. This scenario is related to the topographic structures themselves rather than disturbance by or effects of fluid escape, and would be relevant for extinct or long-term dormant pockmarks. Depressions in the seabed, such as pockmarks, can act as sediment traps and accumulate organic material due to reduced bottom current flow (Yager *et al.* 1993). Increased sedimentation of organic matter into the pockmarks and subsequent bacterial degradation may make the pockmarks more susceptible to anoxic conditions in the sediment surface layer.

Dissolved oxygen penetration depth by molecular diffusion is typically just a few mm for clay sediment to 1 cm for sandy sediment (Revsbech *et al.* 1980a; Revsbech *et al.* 1980b; Cai & Sayles 1996). Bioturbation by macrofauna, however, is important for transporting oxygen into deeper layers and provide oxidized conditions 5-10 cm below the sediment surface (Revsbech *et al*. 1980b). The oxygenated surface layer is followed by a transition zone between the oxygenated and reduced conditions. This is a layer of rapid change of redox potential called the redox potential discontinuity (RPD) layer. The depth of the RPD layer will decrease as a response to increased organic input (Pearson & Stanley 1979; Rosenberg *et al.* 2001). Below the RPD layer, the reducing conditions are found as a black sulphide layer. For many benthic species, this layer represents an effective ecological barrier and is the lower limit of depth distribution, because sulphide is toxic to most aerobic organisms (Gray 1981 pp. 17-18). Thus, the depth of the RPD layer is an important factor structuring the benthic infauna.

The deep water exchange in the inner Oslofjord was considered good in the winter of 2006 (NIVA 2007). However, the oxygen conditions in Bærumsbassenget were considered very bad, and hydrogen sulphide was detected in the water from April to December. The northern part of Vestfjorden also had low oxygen content in 2006 (about 2-3 mL/L in August) (NIVA 2007). My study area was located north in Vestfjorden, adjacent to Bærumsbassenget, and the oxygen conditions were, therefore, suspected to be bad at the time of sampling. Oxygen measurements were not taken to confirm this, however. Low oxygen concentrations coupled with increased deposition of organic material inside the pockmarks due to reduced bottom currents may lead to decreased depth of the RPD layer and anoxic conditions in the sediment surface layer. Additionally, the anaerobic degradation of organic matter produces sulphate, and the sulphate is reduced to sulphide by anaerobic sulphate reducing bacteria (Jørgensen 1977).

The majority of the taxa that contributed most to the differences in faunal composition between inside and outside the pockmarks (Table 8) were small opportunistic polychaetes commonly known to indicate ecologically unbalanced situations (Borja et al. 2000). *Capitella capitata* is a cosmopolitan complex of several sibling species (Grassle & Grassle 1976) and classified as opportunistic deposit-feeders that proliferate in reduced sediments (Borja *et al.* 2000). Whereas most animal taxa will avoid H_2S concentrations >1 mM (Levin *et al.* 2003), *C. capitata* is tolerant to anoxia and high sulfide concentrations (Gamenick *et al.* 1998). Sulfide may, in fact, promote larval settlement of this species (Cuomo 1985; but see Dubilier 1988). There is an overall trend of more individuals of *C. capitata* inside the pockmarks. This may be suggestive of higher sulphide concentrations in the pockmark sediments. In a similar study of methane seeps on the California shelf and slope, Levin *et al*. (2000) reported that *Capitella* sp. was found exclusively in seep sediment and absent from nearby non-seep sediment.

The dominance of opportunistic species under conditions of organic enrichment is, however, usually a result of life-history traits such as dynamics of dispersal and recruitment, rather than tolerance (Gray *et al.* 1979). Polychaetes of the genus *Polydora* are opportunistic surface deposit-feeders that may form dense populations as a result of increased organic enrichment and ecologically unbalanced situations (Pearson 1975; Ramberg & Schram 1983; Borja *et al.* 2000). The overall pattern of higher abundances of *Polydora* sp. inside pockmarks (Table 8) observed in this study may indicate increased organic deposition in the

Oslofjord pockmarks. Elevated abundances of *Polydora* were also observed in Baltic Sea pockmarks (Bussmann *et al.* 1999).

The degree to which the Oslofjord pockmarks act as traps for organic matter, and hence are more susceptible to organic enrichment and anoxic conditions, remains speculation. Numerous studies have showed that the benthic faunal abundance and biomass initially rise under organic enrichment, followed by reduction in the number of species and diversity and increased dominance of opportunistic species (e.g. Pearson 1975; Gray *et al.* 1979; reviewed by Gray *et al.* 2002). Significantly lower faunal diversity was not detected in the present study, possibly due to the large variation among replicates and between pockmarks. In contrast, small but significant differences in the faunal composition were found using multivariate techniques such as ANOSIM, discriminant analysis and constrained ordination. Multivariate statistics have proven more powerful at detecting differences between communities with different degrees of anthropogenic disturbances than univariate measures (Hewitt *et al.* 2005). Perhaps a prolonged period of increased organic deposition has led to a slightly unbalanced situation, hence the subtle compositional differences reported here. No previous studies have looked at this aspect of pockmarks. A more thorough analysis of the benthic fauna and the sediment would be necessary in order to verify (or falsify) this hypothesis.

One might argue (quite rightfully) that the seafloor surrounding the pockmarks does not represent undisturbed sites. The mean sedimentary C:N ratio of 11 indicates a significant terrestrial component of the organic matter (Ruttenberg & Goni 1997), and the organic carbon content is relatively high both inside and outside the pockmarks (Table 3). The dominance of small, opportunistic deposit-feeding polychaetes implies that the study area in general is environmentally stressed. The numerically dominating taxa in the present study are *Pseudopolydora* sp., *Polydora* sp., *Heteromastus filiformis*, *Chaetozone setosa*, *Capitella capitata* and *Pholoe minuta* (Table 7). Mirza and Gray (1981) found the same taxa to dominate in moderately organically enriched areas in the Oslofjord, and these species seem to reflect the general background fauna in the Inner Oslofjord (the fjord is still subjected to organic enrichment, although the conditions have improved since 1981 (NIVA 2005)). One should also note that the two species discriminating most consistently between inside and outside the pockmarks, *Pseudopolydora* sp. and *Chaetozone setosa*, both had higher abundances outside the pockmarks (Table 8).

4.3 Environmental variables

The combination of environmental variables that 'best' explained the overall community structure was organic carbon content, pH, redox potential and grain size of the sediment and depth of the overlying water column (Table 9). The correlation value ($\rho = 0.32$) was relatively low, implying that the environmental variables measured were not adequate for explaining the observed faunal patterns. Because of the close physical association between benthic fauna and the surrounding sediment, sediment characteristics such as redox potential, pH and organic content are regarded as important factors structuring benthic infaunal communities. However, the relationships between benthic fauna and sediments are complex and highly variable between different habitats (Chapman & Tolhurst 2007). Additionally, many benthic species are mobile and capable of dispersion in response to changing conditions. Sediment conditions may also vary on much smaller scale than 0.1 m^2; hence the measurements presented here may be crude.

The sediment characteristics, such as grain size, pH, organic content and redox, are generally inter-correlated. The grain size and organic content will affect the redox potential profile (Pearson & Stanley 1979; Gray 1981). Positive Eh values are associated with well-oxygenated coarse-grained sediment, whereas negative values are characteristic of fine-grained sediments rich in organic matter. High abundance of available decomposable organic matter also promotes reducing conditions (Pearson & Stanley 1979). The negative redox values reported here are therefore to be expected in coastal soft-bottom sediment with high silt-clay content. Sediment sampled by grab is, however, not optimal for redox potential measurements, as the sediment becomes highly disturbed during the process and redox conditions may be distorted. More important than the redox values alone is, perhaps, the depth of the RPD layer, which has been shown to correlate with biomass and diversity of benthic fauna (Pearson & Stanley 1979; Nilsson & Rosenberg 2000). The depth of the RPD layer could not determined by the methods used in the present study.

This study would have benefited from more extensive analyses of sediment geochemistry such as pore water analysis of methane, sulphide and oxygen levels. Increased knowledge of the biogeochemical processes in the sediments may have answered the question of why the species composition inside the pockmarks differs from the outside. As with all analysis involving correlation, it is also important to keep in mind that correlation does not

necessarily imply causation; the measured environmental variables may simply be collinear with unmeasured characteristics.

4.4 Chemosynthetically based communities in pockmarks

In the pockmarks investigated here, no macrofauna known to host chemosynthetic symbionts were identified. One possible exception is *Thyasira* sp., a small deep-burrowing bivalve genus where several species, e.g. *Thyasira sarsi* and *T. equalis,* are known to contain endosymbiotic sulphur oxidizing bacteria (Dando & Southward 1986). Unfortunately, individuals from this genus could not be identified to species level in the present study because of their small size. However, *Thyasira* is found in a variety of reduced environments, e.g. very organic-rich fjord sediments and is, thus, not necessarily indicative of seeping fluid (Dando *et al.* 2004). *T. sarsi* and *T. equalis* obtain a varying fraction of their nutrition from their symbionts, depending on the concentration of reduced sulphur in the sediment and may, under some conditions, rely solely on heterotrophic nutrition (Dando & Spiro 1993). Additionally, the abundance of *Thyasira* spp. was higher outside the Oslofjord pockmarks than inside. The absence of species known to host endosymbiotic chemosynthetic bacteria indicates that chemosynthesis does not constitute a major part of the nutritional basis for the benthic fauna. However, the possibility of indirect utilization of chemosynthetically derived carbon by heterotrophic organisms, through ingestion of either free-living chemosynthetic bacteria or heterotrophic bacteria, cannot be ruled out. Stable isotope analysis could have determined whether the higher trophic level carbon comes from chemosynthetic or photosynthetic primary production, and provided insight into the nutrition of the benthic fauna. Chemoautotrophy results in cell carbon with depleted $\delta^{13}C$ (Southward *et al.* 1981). Because the $^{13}C/^{12}C$ ratio of an animal is usually close to that of its food source (+1‰), depleted $\delta^{13}C$ in invertebrate tissue is indicative of nutritional dependence on chemosynthetic bacteria.

The impact of potential fluid escape may, however, be less in shallow waters such as the study area (<60 m), because energy supplies are dominated by photosynthetically derived carbon from the overlying water column. Bussmann *et al.* (1999) found high methane oxidation and sulphate reduction rates, and high densities of sulphur oxidizing bacteria inside shallow pockmarks (25 m depth) in the western Baltic Sea. This did, however, not lead to higher densities of macrofauna or symbiotic associations inside the pockmarks. Similarly, isotope analysis revealed that methane did not contribute to the carbon of

pockmark infauna of an active North Sea pockmark at 150 m water depth (Dando *et al.* 1991) and only a minor contribution at an Oregon pockmark (132 m depth) (Juhl & Taghon 1993). In contrast, chemosynthetic assemblages consisting of the symbiotic taxa *Mytilidae, Vesicomyidae* and *Siboglinidae* were observed during a ROV study of a giant pockmark off West Africa at 3000 m water depth (Ondréas *et al.* 2005). Isotopic analysis confirmed that methane and sulphide formed the nutritional base for this community (Olu-Le Roy *et al.* 2007).

Depth seems to be the major factor structuring the broad-scale distribution of chemosynthetically-based communities. Most assemblages of the large chemosynthetic 'seep species' are found in deep waters (below 400 meters but usually deeper), even though the required methane and sulphide are more characteristic of shallower continental shelf depth (Carney 1994). Sahling *et al*. (2003) investigated cold-seep sites in four depth zones and confirmed that the number of chemoautotrophic species decreases with depth. No chemoautotrophic macrofauna, only bacterial mats, were found at the 160 m seep, and typical seep-endemic fauna with chemosynthetic symbionts were only found below 370 m. Elevated faunal abundances at shallow sites were primarily caused by available hard substrate (carbonate) and not nutrient enrichment. No such carbonate structures were detected in the Oslofjord pockmarks. Most studies on pockmarks and cold seeps have focused on large epifauna, hence the elevated faunal abundances reported by some authors (Hovland & Judd 1988; Hovland & Thomsen 1988) could be a result of hard substrates in an otherwise soft bottom environment, rather than nutrient enrichment by seeping of fluid.

The approach taken in the present study is quantitative sampling of infaunal macrobenthos, which has previously only been done by Dando *et al*. (1991) and Bussmann *et al*. (1999), and recently by Wildish *et al*. (in press). Chemosynthetic communities may have a very patchy distribution, reflecting the localized nature of seafloor fluid escape (Newman *et al.* 2008). Thus, local chemosynthetic communities may be overlooked by the design of random sampling conducted in the present study. On the other hand, the importance of such typical 'seep communities' may be overestimated because they are so easily observed by ROV cameras and submersibles. Smaller infaunal bivalves containing endosymbiotic chemoautotrophic bacteria, such as Thysiridae and Lucinidae, may be an equally important community component in many seep ecosystems.

5. Conclusion

Despite large variation in faunal composition between the pockmarks and among replicate samples, multivariate statistics were able to demonstrate that the species composition inside the pockmarks was significantly different from the outside. There was, however, a large degree of compositional overlap.The faunal abundance was signifcantly lower inside the pockmarks, but none of the other univariate diversity measures differed signifcantly. The results gave no indication of an enriched benthic fauna inside the pockmarks, and no species known to rely on chemosynthetic energy were identified. Thus, methane does not seem to provide an additional nutrient source for the benthic fauna. Other possible explanations for why the species composition differs are physical disturbance by an eruptive fluid escape followed by re-colonisation and increased organic deposition inside the pockmarks due to reduced bottom currents. None of these hypotheses could be confirmed and, thus, they remain speculations. The environmental variables measured were only weakly correlated with the biotic data, and did not seem adequate to explain the faunal patterns.

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Appendices

Appendix A: Taxa abundance data

Taxa/Sample number	**9A**	**9B**	**9C**	**9D**	**9E**	**9F**	**9G**	**9H**	**9I**	**9J**
Abra sp.		12	2	7	6					
Ampelisca sp.				1						
Ampharete sp.				1						
Amphipoda species A			1							
Amphiura filiformis		20	7		8					
Anobothrus gracilis		21	2	6	15					
Aphrodita aculeata				1						
Bosmina coregoni maritima			4							
Bosminidae				1		1			1	
Capitella capitata	2						9	5	3	5
Cauleriella sp.										
Ceriantharia	1				1	1	3	10	2	1
Chaetozone setosa	2	2	6	2	50		1			
Chone duneri	1									
Copepoda	70	38	43	13	83	26	63	42	91	48
Corbula gibba	2	3					7	8		1
Cytheridae		1								
Diplocirrus glaucus		1			6					
Echinocardium cordatum		4	1	3						
Eriopisa elongata				2						
Glycera alba	2	1	1		7	3		6	2	3
Goniada maculata	1	3			2			1	1	
Harmothoe spp.					1	1	1	3	1	1
Heteromastus filiformis	28	24	1	1	67		1	1	1	
Holothurioidea						1		1		
Lipobranchus jeffreysii			4		7	17	9	5		
Mysida	1		3				1		1	1
Nephtys ciliata				1						
Nereimyra punctata	2		1					1		
Nuculoma tenuis		8	7	28	58					
Ophiocten affinis	1	5	4	2	1					
Ophiura albida				2	2					
Pectinaria koreni	17						3	3		
Pholoe minuta		6			9					
Phoronida					2					
Phyllodoce groenlandica		2		1		3	9			
Phyllodoce sp.									1	
Pista cristata			1							
Podon sp.		1					2	1	3	
Polycirrus medusa					1					
Polydora sp.	1					2	15	118	61	34
Prionospio cirrifera		9		1						
Prionospio fallax		1								
Prionospio sp.					65					
Pseudopolydora sp.	115	149	4	14	37	64	66	45	1	4
Scalibregma inflatum	1		1	3	2	5	3	8		1

Scoletoma fragilis		9	1	1	2					
Scoloplos armiger		1		2	11					
Sipuncula					1					
Spiophanes kroyeri		3								
Syllis variegata			1							
Thyasira sp.	19	5	5	1	13	6	8	18	1	4
Trichobranchus roseus		2								

Taxa/sample number	**10A**	**10B**	**10C**	**10D**	**10E**	**10F**	**10G**	**10H**	**10I**	**10J**
Abra sp.					9					
Amphipode species D				1						
Anobothrus gracilis					1					
Arctica islandica					2					
Bosmina coregoni maritima										1
Bosminidae juv.		3				1				
Capitella capitata			12	34						
Ceriantharia				3	1					
Chaetozone setosa	1		2	4	36					
Copepoda	49	54	17	7		64	32	40	4	5
Diastylis cornuta					4					
Eriopisa elongata								1		
Eteone sp.					1					
Glycera alba			11	12	3					
Goniada maculata					1					
Heteromastus filiformis			2	43	409	2	1		1	2
Maldanidae indet.					1					
Mysida										2
Nephtys caeca					1					
Nuculoma tenuis				2	12					
Ophelina modesta						1				
Ophiocten affinis					3					
Ophiodromus flexuosus			1							
Pectinaria koreni			6	5						
Pherusa plumosa										
Pholoe minuta				1	12					
Phyllodoce groenlandica				3						
Podon sp.	1	3		2		1		1		1
Polycirrus medusa					1					
Polydora sp.			4	3						
Pseudopolydora sp.			18	220	104			6		8
Scalibregma inflatum			3	5	7					
Terrebellides stroemii					14					
Thyasira sp.			3	9	6					
Virgularia mirabilis					1					

Taxa/Sample number	**12A**	**12B**	**12C**	**12D**	**12E**	**12F**	**12G**	**12H**	**12I**	**12J**
Abra sp.					9					
Arctica islandica					2					
Bosminidae		3				1				
Capitella capitata	6	20	18	10	25	18	3		3	2
Cauleriella sp.				1						
Ceriantharia	2	2	3	5	17	4	5	2		2

Chaetozone setosa	1		2		1			13		2
Copepoda	49	54	17	7		64	32	40	4	5
Diastylis cornuta					4					
Diplocirrus glaucus					1					
Euchone sp.				1						
Eulalia bilineata								1		
Glycera alba	1	3	4	1	3			3		4
Goniada maculata	1	1		1	1					1
Harmothoe sp.	1			1	1	2			1	
Heteromastus filiformis	2				2	1		52		
Lipobranchus jeffreysii					3	3				4
Mysida										2
Nereimyra punctata		1								
Nuculoma tenuis				2	12					
Nudibranchia species A							1			1
Nudibranchia species B									1	
Ophiocten affinis					3					
Ophiodromus flexuosus								1		
Pectinaria koreni	3		4	1	4	7	2	5	1	
Pholoe minuta					1					
Phyllodoce sp.		1			1			2		3
Podon sp.	1	3		2		1		1		
Polydora sp.	8	27	55	36	13	7	8	30	2	10
Pseudopolydora sp.	81	4	18	5	27	64	5	131	5	133
Scalibregma inflatum	2	10	3	13	10	1	9	1	4	16
Sige fusigera								1		
Spiophanes kroyeri								2		
Tharyx sp.		1								
Thyasira sp.			3	9	6					
Virgularia mirabilis					1					

Taxa/Sample number	**14A**	**14B**	**14C**	**14D**	**14E**	**14F**	**14G**	**14H**	**14I**	**14J**
Abra sp.									3	
Anobothrus gracilis									6	
Bosminidae	1				1	1				
Brada villosa									2	
Capitella capitata	13	9	21	9	68	3	5			
Ceriantharia	2	2	3	3	2		3		6	5
Chaetozone setosa								5	83	4
Chone duneri										1
Copepoda	28	12	10		16	18	20	26	21	33
Corbula gibba	1	4	3		1			1		3
Diplocirrus glaucus								1		
Eulalia bilineata									1	
Glycera alba	2		3	1			1	2	7	
Goniada maculata									1	1
Harmothoe sp.	1									
Heteromastus filiformis				1				79	516	47
Lipobranchus jeffreysii									2	
Mysida		1								3
Nereis sp									1	
Nuculoma tenuis									11	

Ophiodromus flexuosus					1			1	1	
Pectinaria koreni	1		1	1				10	5	9
Pholoe minuta									9	2
Phyllodoce sp.								1	5	1
Podon sp.	2	2	4		9		2	2	5	6
Polydora sp.	17	18	26	6	3	2	2	5		6
Prionospio fallax									10	
Pseudopolydora sp.	12	4	2	2			2	154	320	190
Scalibregma inflatum	16	4	1				1		2	3
Syllis armarillis									3	
Terrebellides stroemii									1	
Thyasira sp.	15	38	11	2	2		1	36	125	60
Trochochaeta multisetosa									1	

Taxa/Sample number	**18A**	**18B**	**18C**	**18D**	**18E**	**18F**	**18G**	**18H**	**18I**	**18J**
Abra sp.			2			8		2		8
Ampelisca sp.										1
Ampharete sp.					3	1			3	1
Amphipoda species A	4	3				1				
Amphipoda species B	3	1						4	5	
Amphipoda species C	1									
Amphiura filiformis									1	1
Anobothrus gracilis	1		2		1	2	1		1	
Aphelochaeta serrata										2
Astarte sp	1	2	2	4	3					3
Asychis biceps										1
Bathymedon obtusifrons						2				
Bosminidae			1							
Brada villosa			1				2	1	3	1
Brissopsis lyrifera						1		1		
Buccinum undatum				1				1		
Ceriantharia	1		2							
Chaetozone setosa	70	19	19	5	2	6	1	13	22	4
Chlamys septemradiatus						1				
Chone duneri									1	
Copepoda	123	33	98		57	54	77	139	92	118
Corbula gibba	2	1							1	
Cucumariidae	2				2					
Diastylis boecki									2	
Diastylis cornuta					1					
Diplocirrus glaucus	10	2	1			4		3	5	7
Eriopisa elongata			1		4		4	3	1	5
Glycera alba	5	3	5	3	2	2	3	4	4	8
Golfingia vulgaris			1							
Goniada maculata	12	12	16	10	5	11	5	8	3	11
Harmothoe sp.		1	1		1		7	1	3	
Heteromastus filiformis	100	94	69	49	14	7		105	87	19
Lipobranchus jeffreysii	4	12	3	2	8	3	4	1	7	
Macoma calcarea					1	1	1		4	
Maldane sarsi	66	43	4	1				1	8	
Melinna cristata	1	5	2	1			1			
Mysida		1					1			

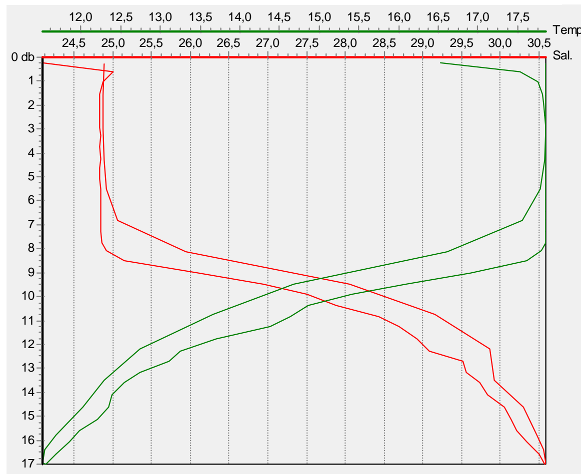
Nereimyra punctata	6	9	3	2	2		3	2		2
Nuculoma tenuis	16	20	45	10	30	13	20	20	24	18
Nudibranchia species B									1	
Ophiocten affinis	2	2	1	1	2		2	1	2	4
Ophiura ophiura						1				
Orbiniidae indet					1					
Pectinaria koreni									1	
Pherusa plumosa			1						1	
Philomedes sp										149
Pholoe minuta	42	18	47	17	6	4		39	35	12
Phoronida	1	1	5		3			1	4	3
Phyllodoce sp.	1							2		
Pista cristata	4	5	4	5	4	7	5	2	4	7
Pistella lornensis									1	
Podon sp.			2		3	1		2	6	
Polycirrus medusa		2			1		1	4	3	
Polycirrus norvegicus	1			1	1	2	3			
Polycirrus sp.					1				9	
Polydora sp.	2	10								
Polyphysia crassa	1									
Priapulida			1							
Prionospio cirrifera		19	39	28	20	3	3	13	4	36
Prionospio sp.	16		1	1	3					
Pseudopolydora sp.	346	4	77	30	10	216	18	79	195	14
Sabella pavonina			1					1		
Sabellidae indet.	1		1	1		1				1
Scalibregma inflatum									1	1
Scoletoma fragilis	4	3	9	7	13	4	1	3	8	6
Scoloplos armiger				1						
Sige fusigera							1			2
Sipuncula	1		1				1		1	
Spiophanes bombyx				1	3		2			
Spiophanes kroyeri	4	8	14	9	4			1	13	6
Syllis cornuta	5	10	7	17	6	3	6	6	6	13
Syllis sp.	14	9	1		6					
Terrebellides stroemii	5	4	2	5	1			2	2	
Tharyx sp.			1							
Thyasira sp.	30	16	9	14	3	15		7	5	30
Trichobranchus roseus	1		1	1				4	2	
Venerupis pullastra									1	
Westwoodilla sp.				1						

Appendix B: Raw data for the environmental variables: Depth (m), redox potential (Eh), pH, temperature (°C), TOC, % nitrogen, C:N ratio, mean grain size (µm and Φ) and % mud).

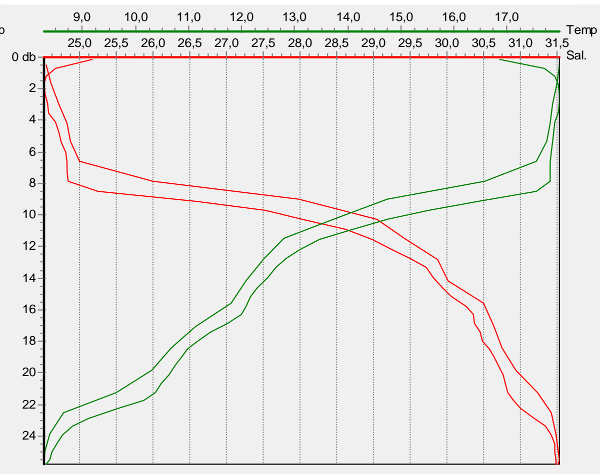
Sample	Depth	Redox	pH	Temp	TOC	% N	C:N	Mean (µm)	Mean (Φ)	% mud
9A	33.0	-31.5	7.56	9.5	2.32	0.267	10.29	15.78	5.99	99.4
9B	18.3	-37.6	7.68	12.3	1.49	0.181	9.89	18.34	5.77	89.7
9C	30.4	-46.4	7.85	9.9	1.88	0.241	9.24	16.31	5.94	97.1
9D	20.2	-33.9	7.61	13.0	1.23	0.147	10.00	17.34	5.85	93.1
9E	28.0	-33.0	7.58	11.5	2.15	0.211	12.68	20.29	5.62	84.2
9F	36.3	-37.6	7.68	9.3	2.59	0.374	8.80	15.85	5.98	99.1
9G	41.0	-42.6	7.78	10.9	2.03	0.208	12.04	16.08	5.96	98.1
9H	41.9	-38.8	7.71	11.1	4.44	0.528	11.33	16.03	5.96	98.3
9I	43.1	-47.3	7.86	12.8	4.65	0.636	10.42	15.81	5.98	99.3
9J	40.8	-47.4	7.87	11.6	4.55	0.581	10.97	15.84	5.98	99.1
10A	46.5	-28.8	7.53	10.0	3.91	0.501	9.75	36.77	4.77	74.3
10B	45.9	-28.0	7.51	10.5	1.89	0.187	12.52	42.31	4.56	70.1
10C	31.1	-44.1	7.79	14.7	3.94	0.627	8.19	36.64	4.77	66.8
10D	29.9	-34.2	7.62	13.3	3.73	0.400	12.36	16.39	5.93	96.8
10E	14.2	-31.3	7.57	12.2	2.56	0.292	10.94	16.03	5.96	98.3
10F	50.8	-34.4	7.62	13.3	0.75	0.114	8.06	78.18	3.68	60.4
10G	50.9	-27.2	7.49	12.9	2.06	0.209	12.42	40.06	4.64	76.2
10H	47.5	-30.7	7.56	12.8	3.59	0.392	12.67	55.73	4.17	75.0
10I	487.5	-31.4	7.57	14.7	3.85	0.495	11.10	16.11	5.96	97.9
10J	43.5	-33.8	7.62	10.2	3.70	0.388	10.25	24.02	5.38	80.7
12A	44.3	-46.9	7.86	9.7	2.13	0.256	9.64	15.95	5.97	98.6
12B	44.8	-53.4	7.98	9.8	4.65	0.494	12.85	15.89	5.98	98.9
12C	44,2	-46.6	7.85	10.0	4.53	0.717	8.04	15.95	5.97	98.6
12D	45.2	-38.0	7.69	10.2	4.91	0.501	13.35	16.02	5.96	98.3
12E	40.3	-51.5	7.95	9.9	4.59	0.535	11.13	16.55	5.92	96.1
12F	37.6	-48.2	7.88	10.7	3.31	0.369	11.82	15.92	5.97	98.7
12G	39.1	-49.0	7.90	9.6	4.33	0.507	11.83	15.82	5.98	99.2
12H	35.3	-31.2	7.56	10.1	3.40	0.37	11.93	17.48	5.84	92.6
12I	39.3	-42.0	7.76	10.6	4.31	0.533	11.24	15.75	5.99	99.5
12J	38.7	-38.6	7.71	10.2	3.81	0.483	10.67	15.90	5.98	98.9
14A	42.8	-40.5	7.71	9.6	5.43	0.711	9.83	16.26	5.94	97.3
14B	43.2	-47.9	7.89	9.4	4.43	0.520	11.24	16.16	5.95	97.7
14C	42.7	-58.0	8.07	9.2	4.40	0.527	11.13	16.29	5.94	97.2
14D	41.5	-51.8	7.97	10.1	4.49	0.550	10.98	15.96	5.97	98.6
14E	39.4	-47.1	7.84	9.7	4.99	0.579	11.79	16.12	5.96	97.9
14F	39.0	-56.9	8.04	10.1	3.68	0.396	12.34	18.75	5.74	88.5
14G	37.7	-50.0	7.92	10.0	4.75	0.559	11.71	16.31	5.94	97.1
14H	35.7	-39.1	7.72	9.4	2.80	0.304	11.77	16.0	5.97	98.4
14I	31.2	-35.7	7.65	10.6	3.43	0.381	11.32	16.34	5.94	97.0
14J	36.4	-33.5	7.61	9.4	2.79	0.343	10.42	16.26	5.94	97.3
18A	55.3	-33.7	7.62	10.9	3.16	0.421	9.26	15.77	5.99	99.4
18B	56.6	-40.8	7.75	10.0	2.85	0.281	12.73	15.89	5.98	98.9
18C	59.4	-42.4	7.78	10.9	279	0.233	14.57	41.71	2.36	68.2
18D	57.3	-41.0	7.04	9.2	2.73	0.271	13.00	15.92	5.97	98.8
18E	57.2	-49.4	7.91	9.3	1.84	0.216	11.00	16.34	5.94	97.0
18F	48.5	-28.3	7.53	9.3	2.64	0.294	11.29	16.01	5.97	98.4
18G	48.5	-38.6	7.70	9.1	2.84	0.278	12.58	16.12	5.96	97.9
18H	47.6	-37.1	7.67	11.0	2.29	0.268	10.83	16.0	5.97	98.4
18I	45.7	-37.2	7.68	9.6	2.29	0.349	11.12	16.01	5.97	98.4
18J	49.9	-41.0	7.75	9.2	2.97	0.349	11.31	16.31	5.94	97.1

Appendix C: Temperature and salinity graphs

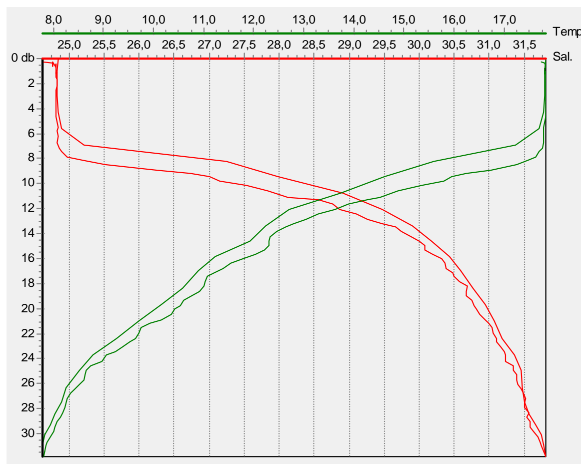
1) Sample (site) 9B



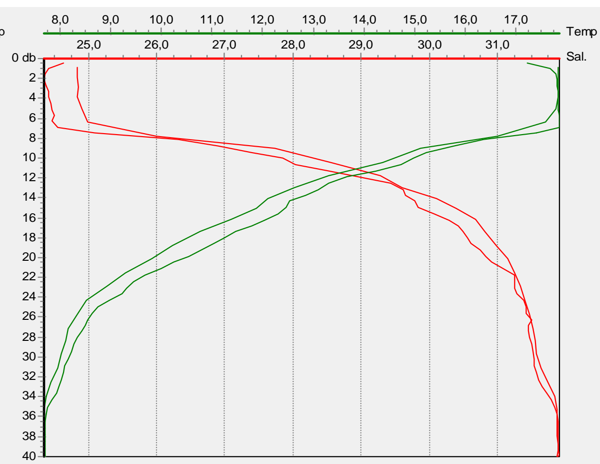
2) Sample (site) 9E



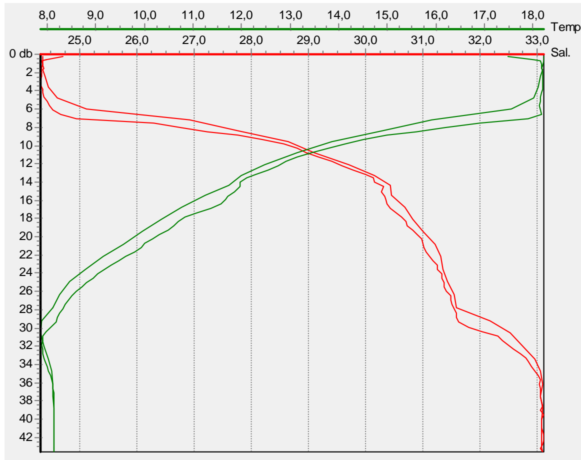
3) Sample (site) 9G



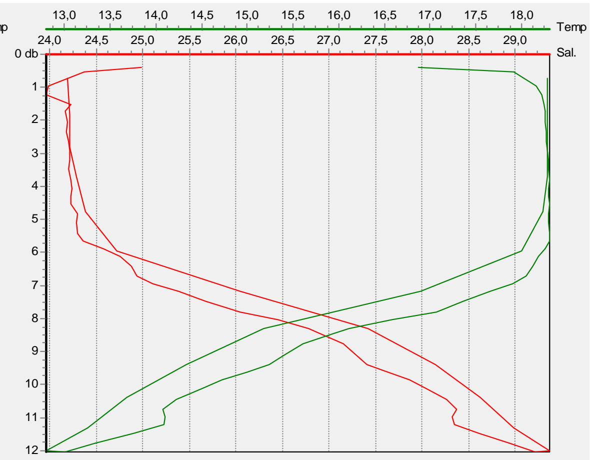
4) Sample (site) 9J



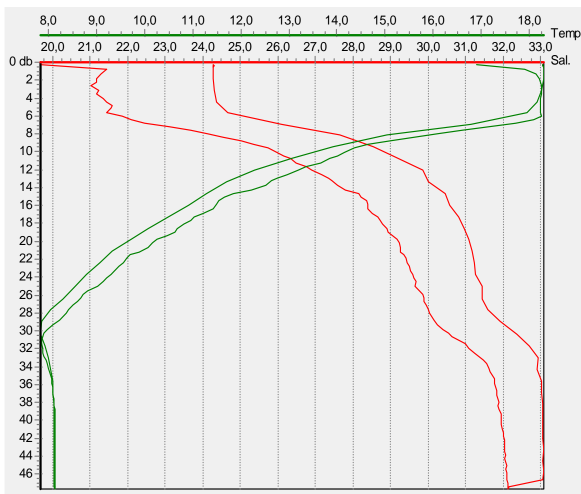
5) Sample (site) 10B



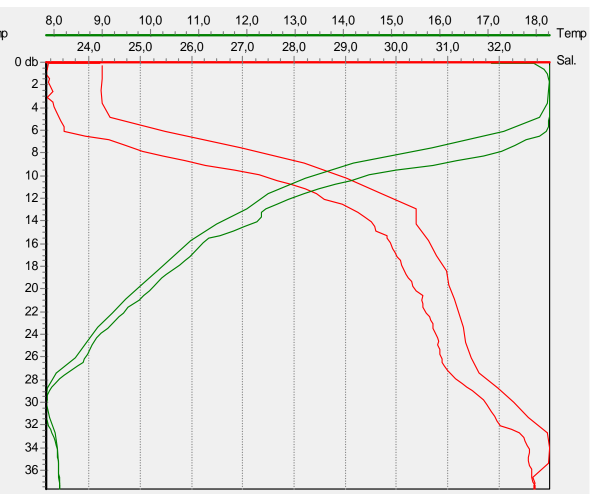
6) Sample (site) 10E



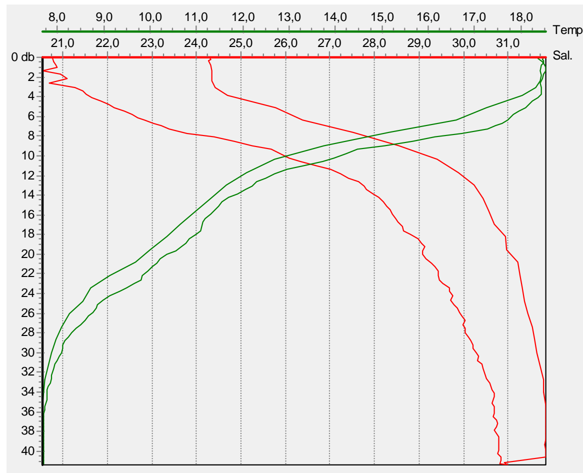
7) Sample (site) 10G



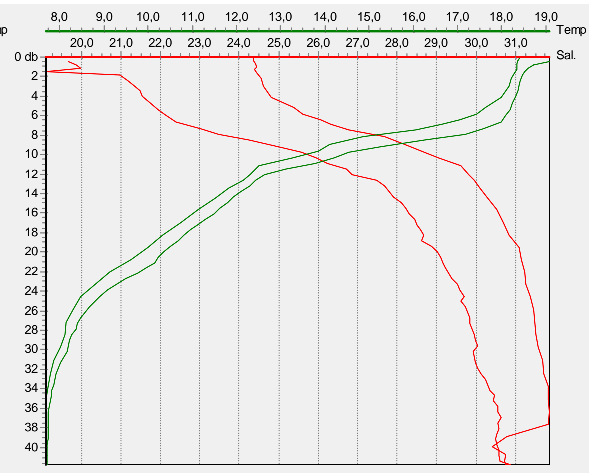
8) Sample (site) 10J



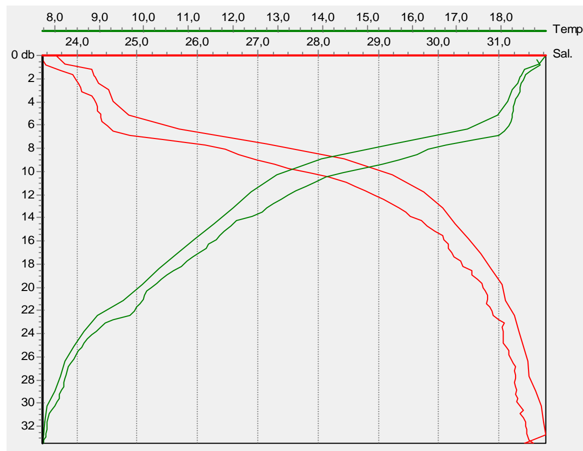
9) Sample (site) 12B



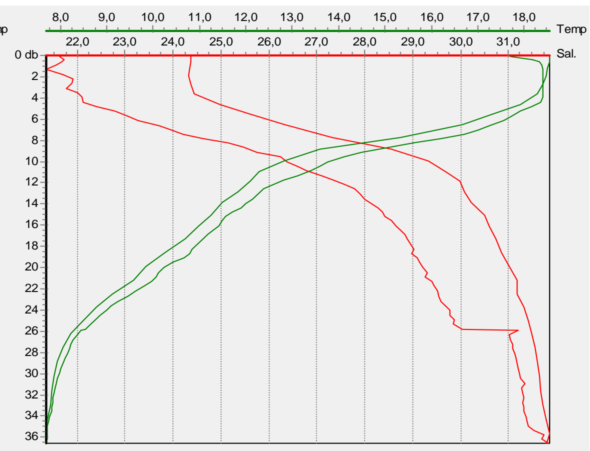
10) Sample (site) 12D



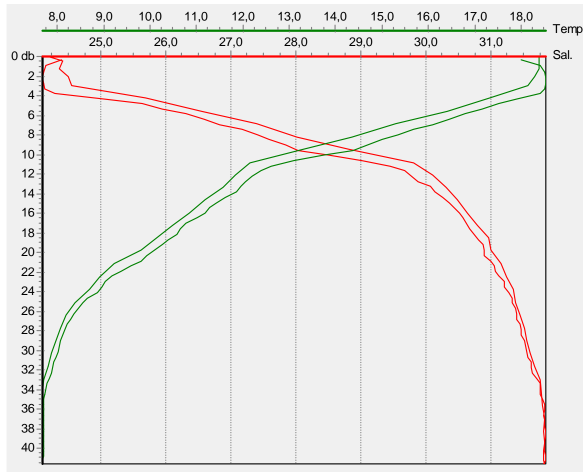
11) Sample (site) 12H



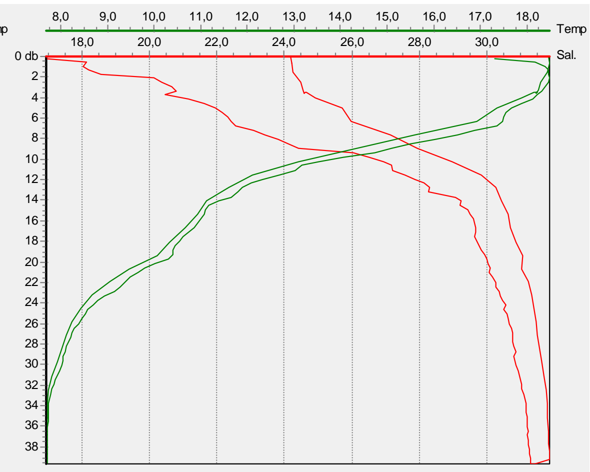
12) Sample (site) 12I



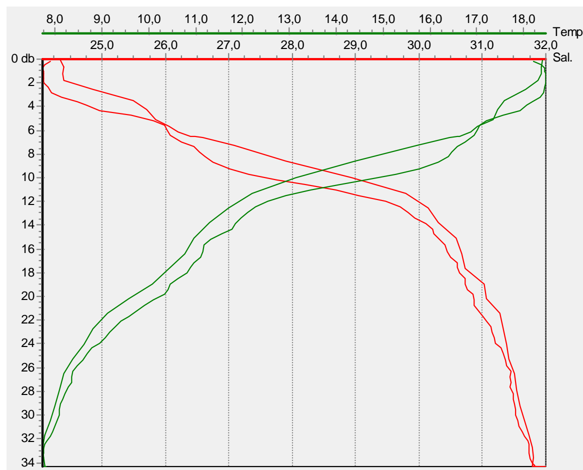
13) Sample (site) 14B



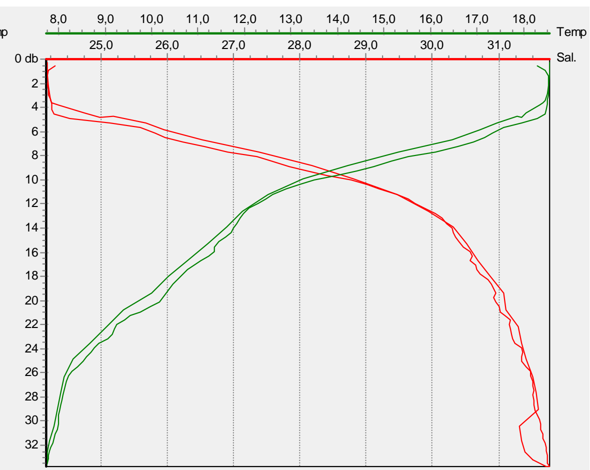
14) Sample (site) 14D



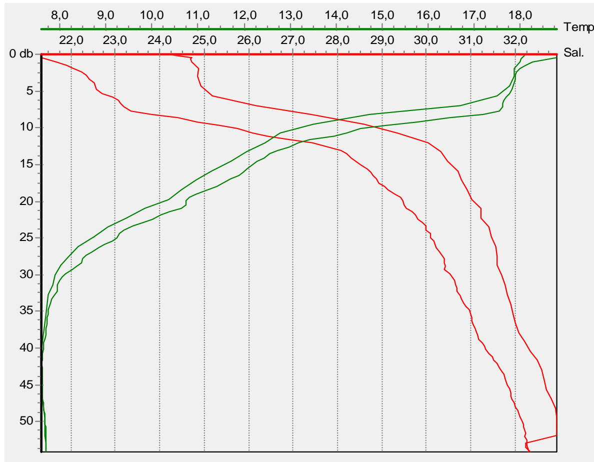
15) Sample (site) 14H



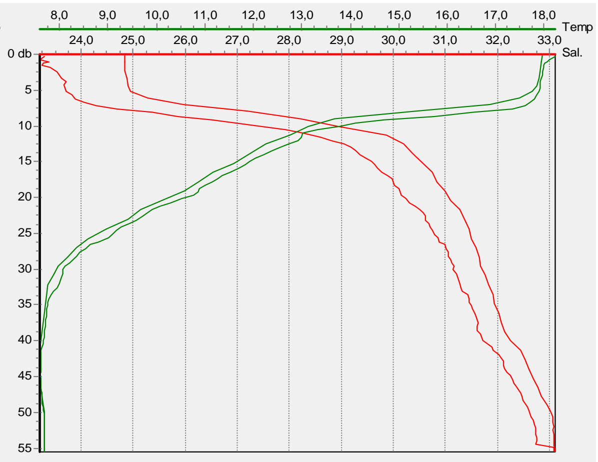
16) Sample (site) 14J



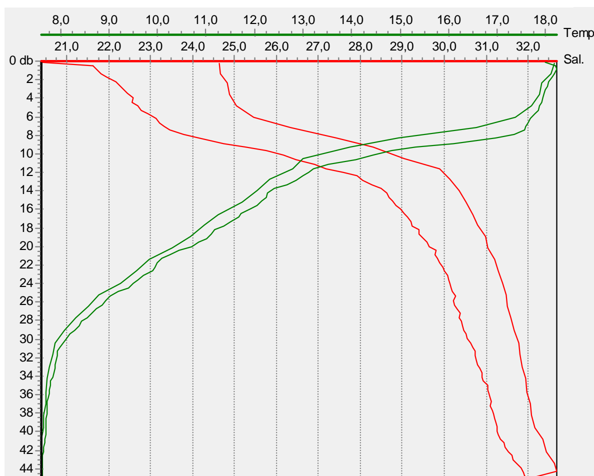
17) Sample (site) 18B



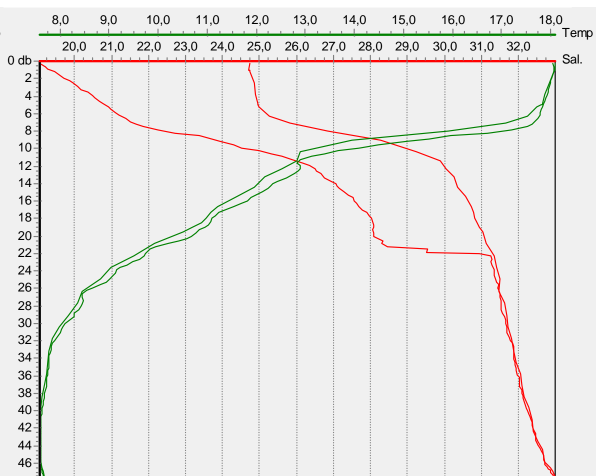
18) Sample (site) 18D



19) Sample (site) 18H



20) Sample (site) 18J



Appendix D: Two-way ANOVA testing for differences between inside and outside pockmarks and between pockmarks for the univariate community measures: faunal abundance (N), number of taxa (S), Shannon's diversity (expH'), Hurlbert's rarefaction index (E(S_{50}), Pielou's evenness index (J') and Simpson's diversity (1/D). All data except J' were root-transformed prior to analysis.

N	**DF**	**SS**	**MS**	**F**	**P**
Pockmark	4	672.95	168.24	5.12	0.002
Group	1	146.72	146.72	4.46	0.041
Interaction	4	165.78	41.45	1.26	0.301
Error	40	1314.52	32.86		
Total	49	2299.97			

S	**DF**	**SS**	**MS**	**F**	**P**
Pockmark	4	58.62	14.66	31.97	0.000
Group	1	1.48	1.48	3.23	0.080
Interaction	4	5.21	1.30	2.84	0.036
Error	40	18.34	0.46		
Total	49	83.66			

Exp(H')	**DF**	**SS**	**MS**	**F**	**P**
Pockmark	4	16.25	4.06	20.67	0.000
Group	1	0.05	0.05	0.24	0.627
Interaction	4	3.78	0.94	4.81	0.003
Error	40	7.86	0.20		
Total	49	27.92			

ES(50)	**DF**	**SS**	**MS**	**F**	**P**
Pockmark	4	15.27	2.82	24.74	0.000
Group	1	0.04	0.04	0.24	0.626
Interaction	4	2.80	0.70	4.53	0.004
Error	40	6.17	0.15		
Total	49	24.28			

J'	**DF**	**SS**	**MS**	**F**	**P**
Pockmark	4	0.34	0.09	3.62	0.013
Group	1	0.02	0.02	0.94	0.338
Interaction	4	0.09	0.02	0.95	0.446
Error	40	0.95	0.02		
Total	49	0.41			

1/D	**DF**	**SS**	**MS**	**F**	**P**
Pockmark	4	6.93	1.73	10.52	0.000
Group	1	0.23	0.23	1.42	0.241
Interaction	4	2.53	0.63	3.84	0.010
Error	40	6.59	0.16		
Total	49	16.29			