

# Ecology and geology of pockmarks

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## **Preface**

This work was carried out jointly at the Physics of Geological Processes (PGP) and the Department of Biology, University of Oslo. The project was funded by a young researcher of excellence grant from the Norwegian Research Council awarded to Dr. Øyvind Hammer.

First of all, I wish to dedicate this thesis to the memory of my late supervisor Professor John Gray without whom none of this would have been possible. I am eternally grateful, not only for his support and encouragement as my supervisor but also for all the opportunities he gave me. His enthusiasm and knowledge were an inspiration and I feel honoured to have been able to work with such an outstanding scientist. My time in Norway was made all the more enjoyable for not only being embraced as a member of his marine biodiversity group, but also within his home. John and Anita made me feel incredibly welcome, and well fed (Anita is an amazing cook, and I became particularly fond of her pavlova!). John encouraged me to try all things Norwegian, such as cross country skiing (which does not come naturally to most Brits!) and cabin life in both Sweden and Rondane.

Special thanks to Dr David Barnes, who has been truly amazing, I cannot say enough about how grateful I am for all his help and how he always finds time for me. Not only has he encouraged and supported me constantly throughout this project, but also joined me on small boat sailing around Svalbard fraught with drama, all in the name of science!

My thanks also go to Øyvind Hammer for giving me the opportunity to undertake this PhD and for his support throughout. His motivation and enthusiasm to discover what is forming the Oslofjord pockmarks has driven on the geological aspects of this research.

I would like to thank Professor Ketil Hylland for stepping in as my supervisor, this support has been enormously helpful and much appreciated. Having his encouragement and advice has enabled me to reach the finishing line.

Thanks to Sverre Planke for giving me the opportunity to work on the Troll Shallow Gas project. Additionally, Tor Inger Tjelta and StatoilHydro for allowing me to bring a biological aspect to the project and publish the data within my PhD. I thoroughly enjoyed working within their project; I learnt a lot and was able to add new dimensions to this thesis.

I am grateful for the technical support by Rita Amundsen and Mufak Naoroz. I also wish to thank Henrik Svensen and Adriano Mazzini for their valuable discussions and sound advice on geological aspects and the PGP admin staff for sorting so many things.

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Papers I-V



## **Abstract**

Pockmarks have now been recognised for nearly four decades, and are one of the most obvious and abundant structural features of the seafloor in some areas, yet there is still little knowledge of their influence on fauna or their exact ages and modes of formation. This thesis investigates mechanisms of pockmark formation in the recently discovered pockmarks in the Oslofjord and aspects of the benthic ecology of these ubiquitous topographic features in the North Sea and the Oslofjord. Piston cores collected from a pockmark in the Oslofjord indicated that their formation was probably initiated between 10.7 and 9.5 kyr BP. Thus, pockmarks may have initially formed in an ice-marginal marine setting, where mechanisms such as submarine melt water outflux, ice rafting and rapid isostatic uplift may be of strong relevance. The biostratigraphic and radiocarbon data collected indicate continuously low sedimentation rates inside the pockmark since its formation and that it has been actively seeping artesian ground water since this time.

The influence of the pockmarks on the faunal communities in the Oslofjord was subtle. However, the abundances of key species inside pockmarks were significantly different to the surrounding seabed and as such I argue that the abundance of pockmarks in the Oslofjord has a considerable cumulative influence on overall faunal densities and populations.

The megafaunal communities inside and outside of pockmarks in the North Sea were studied using remotely operated vehicles. The abundance, species richness and diversity increased from outside (background seabed) towards the centre of the pockmarks, probably due to habitat enrichment and morphological protection provided by the pockmark environment. The numbers of taxa present in the centre of pockmarks were approximately double those of the surrounding areas, and the centres had almost an order of magnitude more individuals than outside. Carbonate rocks provided alternative habitat for fauna: a complex hard substrate for colonisation and shelter in an otherwise homogeneous soft sediment environment. Despite fishing data showing the wider area to be intensively disturbed, large slow growing and vulnerable species, such as gorgonian corals, were found in the centre of the pockmarks indicating that they may offer important refuges from trawling activity.

This thesis suggests that pockmarks are important structural features influencing biological abundance and richness, and highlights the need for more research investigating their effects on faunal communities at a range of scales (regional and global) and in different environmental settings.

## List of papers

This thesis is a summary of the following papers:

- Paper I** Webb K.E., Hammer Ø., Lepland A. and Gray J.S. (2009). Pockmarks in the Inner Oslofjord, Norway. *Marine Geology* 29(2): 111-124.
- Paper II** Webb K.E., Barnes D.K.A. and Gray J.S. (*In press*). Benthic ecology of pockmarks and the Inner Oslofjord, Norway. *Marine Ecology Progress Series*.
- Paper III** Webb K.E., Barnes D.K.A. and Planke S. (*In press*). Pockmarks: refuges for marine benthic biodiversity. *Limnology and Oceanography*.
- Paper IV** Borgersen G., Webb K.E., Hylland K. and Gray J.S. (*Submitted*). Benthic communities of elongated pockmarks in the Inner Oslofjord, Norway. *Marine Biology*.
- Paper V** Hammer Ø. and Webb K.E. (*Submitted*). Piston coring of Inner Oslofjord pockmarks: constraints on age and mechanism. *Norwegian Journal of Geology*.



## Introduction

Pockmarks are ubiquitous topographic features of the seafloor and lake bottoms. They were first described as concave, crater-like depressions that occur in profusion on mud bottoms of the Scotian Shelf (King & MacLean 1970). Since this time pockmarks have been the subject of numerous studies around the world (see Table 1 and reviews by Hovland & Judd 1988, Judd & Hovland 2007). They are found globally in a variety of settings from the deep sea to continental slopes and shelves, as well as estuaries, fjords and lacustrine environments (Fig. 1). Pockmarks occur in a variety of shapes, with circular and elliptical as the most common types. The orientation of elliptical and elongated pockmarks is often correlated with the dominant bottom current direction (Hovland et al. 1984, Gontz et al. 2002). They do not exhibit raised rims and range from cone shaped to flat-bottomed with internal slopes of  $2^{\circ}$  –  $35^{\circ}$ . They have diameters from less than 1 m to in excess of 1500 m, and can be over 150 m in depth. Although pockmark sizes range over four orders of magnitude, the majority are between 10 - 250 m in diameter and 1 - 25 m in depth (Pilcher & Argent 2007). Pockmarks can form in strings of aligned circular pockmarks or composites where several pockmarks merged together. Pockmark complexes form where large (possibly composite) pockmarks are surrounded by numerous small unit pockmarks (~1 m in diameter, Hovland & Judd 1988) and intermediate sized satellite pockmarks (10 – 20 m diameter, Paper III). Relict sub-surface buried pockmarks up to 4 km in diameter have been discovered in Palaeogene age strata and interpreted to be composite pockmarks made up of several smaller (100-200) pockmarks (Cole et al. 2000).

A number of theories for pockmark formation have been suggested. The widely accepted explanation is that of expulsion of fluids or gases through the seabed, i.e. biogenic or thermogenic gas (Scanlon & Knebel 1989), pore water expelled by compaction (Harrington 1985) or meteoric (artesian) groundwater (Khandriche & Werner 1995). However, as active fluid flux is rarely observed in pockmarks, the driving mechanism can be difficult to identify.

Table 1. Summary of the main published research on pockmarks categorised by location.

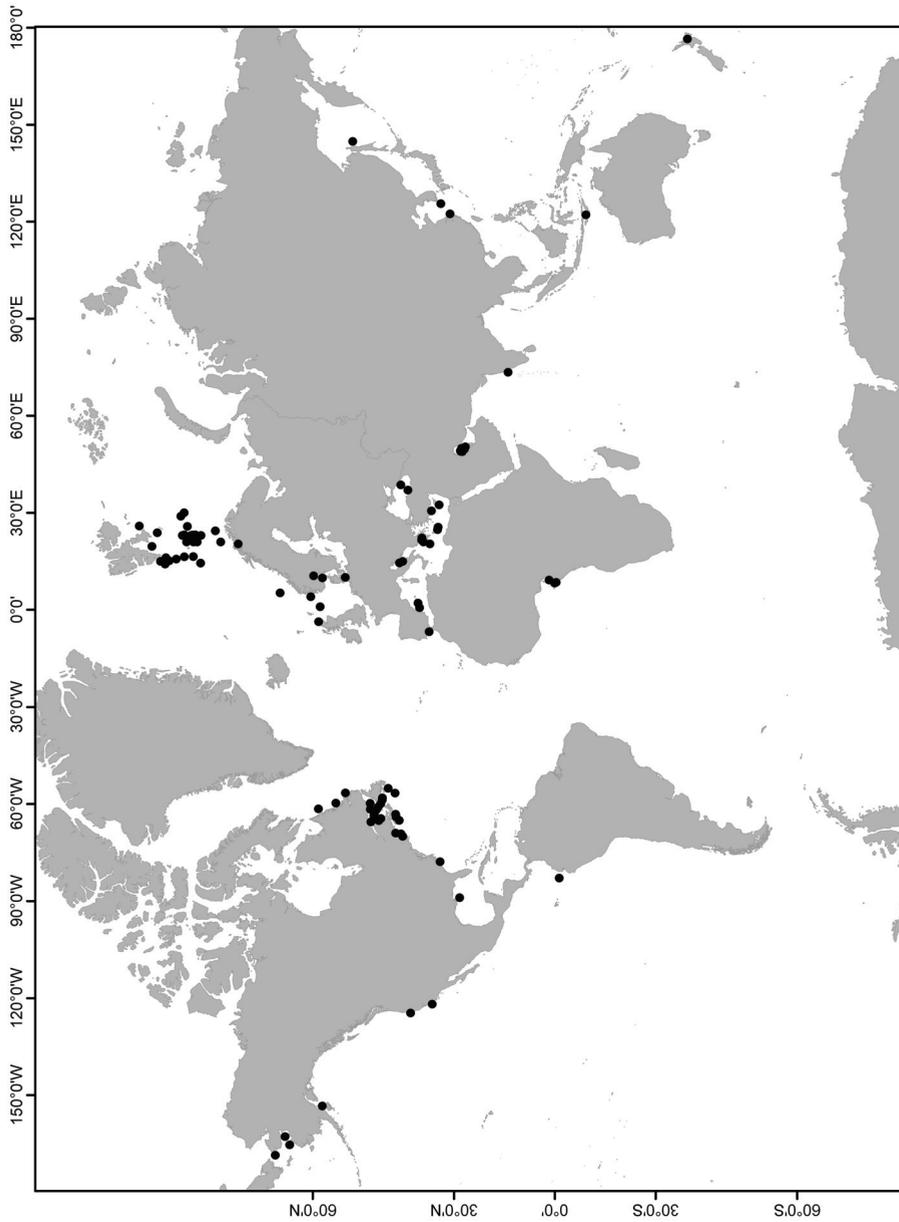
<b>Continent</b>	<b>Ocean, Sea or Country</b>	<b>Location</b>	<b>Reference</b>
Africa	South Atlantic	Gulf of Guinea	Sahling et al. (2008) Gay et al. (2007) Gay et al. (2006) Olu-Le Roy et al. (2007) Pilcher & Argent (2007) Ondréas et al. (2005)
Asia	South China Sea	South China Sea	Platt (1977)
	Arabian Sea	Arabian Sea	Karisiddaiah & Veerayya (2002)
Australasia	New Zealand	Lake Rototiti	Pickrill (1993)
Europe	Baltic Sea	Eckernfoerde Bay Baltic Sea	Khandriche & Werner (1995) Werner (1978)
	Barents Sea	Barents Sea	Solheim & Elverhøi (1993)
	Black Sea	Turkish Shelf	Çifçi et al. (2003)
	Greenland Sea	Fram Strait	Vogt et al. (1994)
	Mediterranean	Killini peninsula Patras Gulf Patras & Corinth Gulfs Ibiza Channel Coast of Greece	Hasiotis et al. (2002) Hasiotis et al. (1996) Christodoulou et al. (2003) Acosta et al. (2001) Dimitrov & Woodside (2003)
	North Atlantic	Gulf of Cadiz Scotian Shelf	Baraza & Ercilla (1996) King & MacLean (1970)
	North Sea	North Sea	Hovland & Judd (1988) Harrington (1985) Long (1992) Forsberg et al. (2007) Dando et al. (1991) Cole et al. (2000) Rise et al. (1999)
		Skagerrak	
	Norwegian Sea	Ullsfjorden Norwegian Sea	Plassen & Vorren (2003) Mazzini et al. (2006)
North America	North Atlantic	Passamaquoddy Bay Belfast Bay	Wildish et al. (2008) Rogers et al. (2006) Ussler et al. (2003) Kelley et al. (1994)
		Penobscot Bay	Scanlon & Knebel (1989)
		Bering Shelf	Nelson et al. (1979)
	North Pacific	California – Big Sur	Paull et al. (2002)
South America	South Atlantic	Brazil Santos Basin	Figueiredo et al. (1996) Sumida et al. (2004)

Pockmarks form in soft, fine-grained, clay-rich sediments and occur at water depths ranging from 6 – 4800 m (Fader 1991) and can reach densities of greater than 1300 km<sup>-2</sup> (Nelson et al. 1979). Their distribution is sometimes observed as non random, with some patterns being linked to underlying geological structures, whereby faults act as conduits for the migration of fluids to the surface. Examples of this are seen in the Oslofjord (Paper I) where both circular and elongated pockmarks align to the faults and folds of the bedrock; the Norwegian trench (Bøe et al. 1998) where strings of pockmarks coincide with the sub-crop strike pattern of the underlying Jurassic-Cretaceous strata; and the Killini Peninsula, Greece (Hasiotis et al. 2002) where the linear distribution of large pockmarks has possibly evolved along the trace of a small fault created by a Triassic salt diapir deep in the sedimentary column. Pockmark strings have also been observed above faults and weakness zones in soft sediments (Hovland et al. 1996).

The majority of pockmark research has been driven by the oil and gas industry, in terms of their usefulness as an exploration tool (Fader 1991) or as indicators of hydrocarbon sources for prospecting (Whiticar & Werner 1981). Thus, previous research on pockmarks has been dominated by geological and geophysical aspects. Yet, pockmarks also affect the ecology of the seabed. Soft sediment environments have previously been considered as relatively homogeneous, but pockmarks are now being recognised as important features in structuring topography. Highly structured habitats are important in the generation and maintenance of biodiversity. For example, in soft sediment environments, much of this structure is created by inhabiting organisms in a number of ways. These fauna burrow into and bioturbate sediments, provide hard substrates such as shells, form biogenic reefs, and modify surface topography (Thrush and Dayton 2002; Thrush et al. 2006). Soft sediment environments are particularly vulnerable to habitat homogenization by anthropogenic disturbances such as the physical destruction caused by trawling and the removal of selective habitat forming species (Thrush et al. 2006). Pockmarks not only increase habitat structure and complexity, they may also provide refuges from trawling activity and other anthropogenic disturbances (Paper III).

Early ecological investigations reported unexpected increases in biological productivity inside pockmarks in the North Sea (Hovland & Judd 1988). Despite this, and the fact that pockmarks are one of the most widespread small-scale topographic features of the seabed, only a few biological studies have been conducted. ROV observations of the large complex 'REGAB' pockmark on the Gabon continental margin confirmed reports of increased biological productivity, observing novel and important fauna, and chemosynthetic communities (Ondréas et al. 2005, Olu-Le Roy et al. 2007). The structure of these chemosynthetic communities was characterised by high spatial variability with different assemblages dominated by three key symbiotic taxa (Mytilidae, Vesicomidae and Sibloglinidae). Other pockmarks in this region have also been reported to contain a high abundance of typical chemosynthetic seep fauna, including vesicomid clams and vestimentiferan worms (Sahling et al. 2008). Prior to this thesis only two other studies have examined the biology and ecology of infaunal communities in pockmarks (Dando et al. 1991, Wildish et al. 2008), but neither of these studies supported the theory of enhanced communities. Wildish et al. (2008) found reduced faunal abundance in one group of pockmarks and concluded that these pockmarks were at a pre-equilibrium stage of successional development. Although infaunal pockmark communities in the North Sea were characterised by two chemosynthetic species not previously recorded from the area, the nematode *Astomonema* sp. and the bivalve *Thyasira sarsi*, the centre of the pockmark studied showed an overall reduced faunal abundance (Dando et al. 1991). Thus, the influence of pockmarks on the fauna inhabiting them is not yet clearly understood. Therefore pockmark research should be pursued in greater depth to determine how these ubiquitous features structure benthic communities.

Figure 1. Location of pockmark fields worldwide (data from the literature, see appendix 1)



## **Objectives of investigation**

This study investigated the biology and geology of temperate pockmarks, in the Oslofjord, Norway and around the Troll Platform in the North Sea.

In order to achieve this, the following objectives were addressed:

1. To examine any effects of pockmarks on infaunal communities
2. To examine any effects of pockmarks on epifaunal communities
3. To determine the formation mechanism of recently discovered pockmarks in the Oslofjord.

## **Methods**

### **Study sites**

The papers I, II, IV and V were carried out in the Oslofjord, Norway (59°50'N, 10°34'E) and Paper III was conducted in the Troll area of the North Sea off the west coast of Norway (61° N, 4° E).

### **Coring**

Papers I and V aimed to determine origin of pockmarks in the Oslofjord by investigating their geology. Seafloor sediment cores are a fundamental data source for information on seabed properties, depositional history and environmental change (Rothwell & Rack 2006). Initial short core samples were collected using a Bowers and Connelly multicorer. This device allowed four core tubes to be collected simultaneously. The sampler is lowered into the sediment using a damping system on a supportive frame, which reduces the production of a bow wave enabling minimum disturbance during sampling. The cores sampled were 10 cm in diameter and 30 - 40 cm long. These cores were analysed with a range of techniques in order to detect any direct or indirect evidence for active or recent seepage of freshwater or gas.

Piston core samples were collected using a deepwater sampler (DWS) developed by the Norwegian Geotechnical Institute (NGI). This system overcomes the difficulties of investigating the very soft sediments of the seabed. These sediments are easily disturbed, making it hard to recover samples without disturbance or loss of the sample. Within this system a piston seals off the upper side of the sampler from surrounding pressure, thus minimising the forces exerted on the sample and preserving its condition. The 8 m long core samples collected with the piston corer were analysed using a multi-sensor core logger. This instrument produces high quality incremental measurements of gamma-ray attenuation bulk density, P-wave velocity, and magnetic susceptibility and is capable of resolving subtle changes in sediment properties that are of geological significance (Rothwell & Rack 2006). Cores are passed by a computer-controlled conveyor belt through a sensor platform allowing automatic incremental measurements to be taken.

These data can then be related to the sediment character. Magnetic susceptibility is used as a relative proxy indicator of changes in composition that can be linked to palaeoclimate-controlled depositional processes. The high precision and sensitivity of susceptibility loggers makes this measurement extremely useful for core to core correlation. Gamma ray attenuation data provides a precise and densely sampled record of bulk density: an indicator of lithology and porosity changes. P-wave velocity varies with lithology, porosity and bulk density of the material. In marine sediments, velocity values are controlled by the degree of consolidation and lithification, fracturing, occurrence and abundance of free gas and gas hydrates. Detailed pictures of the core's composition can also be obtained by X-ray tomography with a CT scanner. Core samples were tested using standard techniques for dating, porewater and gas analysis to determine the age and possible mechanisms of pockmark formation (Paper I & V).

### **Grab**

Infaunal samples were collected using a 0.1 m<sup>2</sup> van Veen grab. Positioning of the grab in the centre of the pockmark was based on positions taken from the bathymetric maps processed in ArcGIS and depth readings from the echosounder and grab winch system. Grab samples were emptied into the top of a set of washing tables and washed through a round holed sieve with 1 mm mesh size. The retained fauna were placed in containers and fixed in 4 % formalin stained with rose bengal. Macrofaunal samples were washed, sorted and preserved in 70 % ethanol in the laboratory. All macrofauna were identified to the lowest possible taxonomic level (typically species) and enumerated.

### **ROV**

Traditional grab sampling significantly underestimates the abundance of large bodied organisms (Kendall and Widdicombe 1999) and is unsuitable on hard, coarse substrates. Remotely operated vehicles (ROV) are the ideal tool for surveying such megafaunal epibenthic communities, easily covering large areas and allowing repeated monitoring with preservation of the fauna. They permit non-destructive sampling of the seabed using video and stills photography. For this thesis megafauna were defined as animals large enough to be identified on video transects (> 5 cm). The remote quantification of community

parameters such as diversity and abundance can be determined with accuracy over relatively wide areas. These surveys also provide a visual record of seabed topography, rugosity, sediment characteristics and any indication of seeping gas or fluids. Biological and geological samples can be taken using a manipulator arm with scoop attachment, corers and collection boxes attached to the ROV. When working inside pockmarks the ROV is usually set to be neutrally, to slightly positively, buoyant to avoid downward thrusting that would disturb the sediments and reduce visibility.

Videos taken using ROV are often digitised and analysed using specialist reviewing software (Paper III used VisualReview software (VisualSoft)). Lasers can be used to define an area for counting abundances of mega- and larger macro-biota. Additional, cameras with side views of the central cameras view can also be used to aid identification of fauna by providing alternative perspectives. Playback software allows the recordings to be replayed at half speed and so that all the visible fauna can be identified to the lowest possible taxonomic level and counted. Colonial organisms should be recorded as single 'individuals' and only benthic fish species included. Additionally descriptions of sediment type (categorised into mud, fine sand and gravel) and seabed morphology can be recorded for each transect.

### **Statistical Methods**

Databases of species occurrence and supporting environmental data were constructed in MS Excel. The species lists were standardised to the currently agreed scientific taxonomic names using the European Register of Marine Species (ERMS) as an authoritative taxonomic list of species occurring in the European marine environment. These community ecology data were then assessed using PRIMER v.6 (Plymouth Routines In Multivariate Ecological Research, Clarke & Warwick 2001). PRIMER is an ideal statistical package for analysing multivariate ecological and environmental data. It is commonly used by benthic ecologists providing standardised methods of analysis that are comparable amongst studies. This software was used to summarise the species data by the following diversity indices: species richness ( $S$ ), and number of individuals ( $N$ ), Shannon-Wiener diversity ( $H'$  (log base  $e$ )) and Pielou's evenness ( $J'$ ). Multivariate statistics were applied to both the faunal and abiotic data to determine underlying patterns of community structure and their relationship to the surrounding environment. Species abundance values

were square root transformed, to down-weight the influence of highly abundant species, before a similarity matrix based on the Bray-Curtis similarity measure was calculated. The relatedness of samples was assessed using non-metric multidimensional scaling ordination (nMDS). Two-way analysis of similarities (ANOSIM) was carried out to determine whether site, or inside and outside of the pockmarks were significant predictors of faunal composition. Taxa that contributed the most to the observed differences between samples from inside and outside of pockmarks, taking into account site, were determined by means of two-way similarity percentage analyses (SIMPER). The relationships between the abundance of macrofauna and the environmental variables were investigated using the BIOENV procedure (PRIMER) with the Spearman rank correlation coefficient ( $\rho^s$ ), between the ranked biotic and environmental similarity matrices, providing the basis for this procedure.

A general linear mixed effects model (GLMM) was used to test for differences in benthic community structure inside and outside of pockmarks in the Oslofjord. This model incorporated random variation at different scales to allow for the nested structure of the sampling design (Paper I). Area and in/out were included as fixed effects with sites, locations within sites, and grabs within locations as random effects. Further tests were performed on the effects of site by fitting the model with site effects as fixed. Numbers of individuals (N) were not normally distributed and so these data were log transformed to comply with assumptions of GLMM analysis.

The compositional differences between inside and outside of the elongated trenches (Paper IV) were visualized using constrained ordination, Canonical Analysis of Principal Coordinates (CAP) (Anderson 2004). This method uses a traditional canonical discriminant analysis based on distances to uncover patterns that may be masked in an unconstrained MDS ordination. The ordination axes were drawn so as to maximise the differences between inside and outside of the pockmarks. The analysis 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, by finding 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 ( $\delta^2$ ) 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  $\delta^2$  is calculated by a permutation test (Anderson & Robinson 2003, Anderson & Willis 2003).

## **Discussion**

### **Formation of pockmarks**

Eye-witness accounts of the formation of pockmarks have never been reported, but theories about how they are formed have been widely discussed. One of the first reports (King & Maclean 1970) suggested they were created by fluid expulsion from the sediment, a theory that is still favoured today. However, various other more unusual suggestions have been made such as, pits made by feeding whales, by bombs or iceberg grounding. On reviewing the literature and Papers I-V, I conclude that pockmark formation based on fluid flow from the sediments seems the most plausible. Two modes of formation through fluid flow have been proposed, either an eruption of gas from over-pressured shallow gas pockets or continuous fluid discharge, which hinders sediment deposition and causes winnowing of fine sediments from around the seep. The nature of the seeping fluid has been suggested to vary in different settings around the world. Many researchers have sought to determine the origin and types of fluid seepage in pockmarks through their investigations.

Geophysical methods such as seismic profiling have been used to search for evidence of gas within the seafloor below pockmarks. Seismic manifestations of migrating gas can be indicated by various acoustic anomalies. In small concentrations gas bubbles scatter acoustic energy and enhance seismic reflections. Increasing concentrations of gas leads to acoustic absorption or scattering. This results in acoustic turbidity or blanking on seismic profiles when the acoustic energy is so scattered by gas bubbles that other reflectors are masked (Schubel 1974). Such acoustic turbidity has been observed in many pockmarked areas (Hovland & Judd 1988, Scanlon & Knebel 1989, Hasiotis et al. 1996, Karisiddaiah & Veerayya 2002). For example, in the Gulf of Patras acoustic turbidity has been observed underneath pockmarks suggesting there is a continuous supply of gas towards the pockmarks from below and that the sediments within the migration path are gas-charged. Some pockmarks have chimney-like structures beneath them indicative of fluid venting (Paull et al. 2008). Seismic profiles taken within the Oslofjord (Paper I) showed no clear acoustic blanking or signs of gas within the sediments. Active and present day seepage was observed over a pockmark field in the North Sea, interpreted from seismic profiles

showing seepage plumes in the water column and shallow gas enhanced reflectors in the sediments. However, these features were also observed in areas with no pockmarks so cannot necessarily be linked to their formation (Schroot et al. 2005).

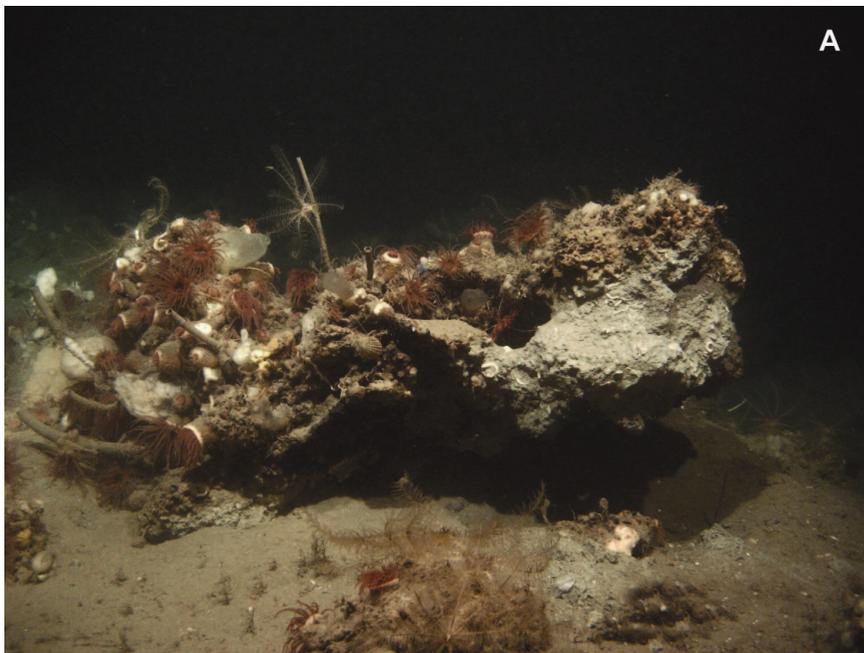
For gas generated deep within the seafloor to be expressed at shallow depths, upward migration pathways must exist. Vertical faults and tilted permeable sedimentary layers are two common examples of such migration paths (Karisiddaiah & Veerayya 2002). The distribution of pockmarks has commonly been linked to the underlying geological structure. Faults can provide active conduits for gas and fluid to migrate to the seabed surface and create a fracture permeability allowing gas and fluid to flow to the surface. For example, pockmarks in the Black Sea are elongated and tend to follow a linear trend in a direction sub-parallel to the underlying Archangelsky Ridge axis in E–SE/W–NW direction (Çifçi et al. 2003). In the Norwegian Trench, Bøe et al. (1998) reported that the orientation of linear rows of pockmarks coincides with the subcrop strike pattern of underlying Jurassic–Cretaceous strata. In the same region, Hovland et al. (1996) observed pockmark strings above faults and weakness zones in soft sediments, providing vertical pathways for migrating fluid. Hasiotis et al. (2002) also reported the linear distribution of large pockmarks in the Killini Peninsula, Greece, where a pockmark string had evolved along the trace of a weak surface (fault or joint), facilitating gas migration. The elongated and elliptical pockmarks of the Oslofjord are also non-randomly distributed and work reported in this thesis correlated their positions to topography of the underlying bedrock - consistent with formation by release of underlying fluids (Paper I).

The elongated pockmarks in the Oslofjord (Paper I and IV) were parallel with either the NE–SW strike of bedrock folds and thrust faults, or the N–S direction of extensional faults, indicating migration of gas or fluids along weakness zones. The elliptical pockmarks (Paper I) also follow an ENE–WSW direction paralleling that of the bedrock folds and thrust faults. But other studies have suggested that pockmarks may be elongated through scouring and current action (Josenhans et al. 1978, Bøe et al. 1998). Elongated depressions in the Norwegian Trench with widths of up to 400 m and lengths of up to 2 km are interpreted as current-modified pockmarks (Bøe et al. 1998). Several studies have reported that elliptical pockmarks are frequently elongated in the direction of prevailing currents (King & MacLean 1970, Nelson et al. 1979, Fader 1991), but currents in the Inner Oslofjord do not follow an ENE–WSW direction.

Pockmarks tend to occur in fine-grained sediments and some studies have linked sediment texture to variations in pockmark size; the finer the sediment, the larger the size of the pockmark. Pockmarks tend to be smaller in compacted, fine sediments and are poorly developed in coarse sediments. Their number decreases with decreasing grain size, presumably as a result of diminishing permeability (Uchupi et al. 1996).

Venting of gases or fluids removes the fine-grained sediments by suspending them so that they may be transported away. This explains why pockmarks do not have ejecta rims like those seen associated with impact craters. This also potentially explains why many seismic profiles of pockmarks show dark reflectors in, or slightly below, their centres. Such pockmarks have been termed ‘eyed’ pockmarks (Hovland et al. 2002). These ‘eyes’ are likely to represent coarse material remaining after the winnowing of fine sediment during pockmark formation (Paper I). Eyed pockmarks may also be due to the presence of authigenic carbonates that commonly occur at fluid seepage sites and are evidence of past or present methane seepage. Such carbonate rock is created by the activity of a consortium of Archaea and sulphate reducing bacteria mediating the oxidation of methane (Boetius et al. 2000). Several pockmarks in the North Sea (Paper III, Hovland et al. 1987) and Norwegian Sea (Mazzini et al. 2006) have been found to contain carbonate rocks. The discovery of carbonates within all four pockmarks studied in the Troll region of the North Sea (Paper III) suggests a history of active methane seepage and that seep carbonates are a common feature of pockmark complexes in this region. Carbonate rocks tend to have a complex structure with numerous cavities and protrusions (Fig. 2).

Figure 2. (A) Heavily encrusted carbonate rocks in the centre of a North Sea pockmark. (B) Carbonate rock showing the surface complexity. (Courtesy of the Troll Shallow Gas Project, StatoilHydro)



The nature of the seeping gases or fluids can be identified by geochemical analysis of seafloor sediments. For example, pore water concentration gradients of chloride, methane and sulphate are sensitive indicators of fluid advection within shallow seafloor sediments (Ussler et al. 2003). The most common gas found seeping from the seafloor is methane. This methane may either be biogenic, derived from bacterial activity in shallow sediments, or thermogenic, produced at high pressure and temperatures. Thermogenically derived methane is consequently formed at depths greater than 1000 m, within sedimentary rocks. Biogenic gas is the most commonly reported vehicle for sediment resuspension in pockmark fields (Nelson et al. 1979, Scanlon & Knebel 1989, Kelley et al. 1994).

The pockmarks in the Oslofjord are unlikely to have been formed by thermogenic gas, as there is no obvious gas source within the crystalline bedrock areas of the Oslofjord (Paper I). The Lower Palaeozoic succession does contain hydrocarbon traces (Pedersen et al. 2007) but appreciable amounts of gas have never been documented in the study region. Hovland and Judd (1988) documented how pockmarks diminish in size and frequency towards coastal areas where bedrock is crystalline. Yet in the Swedish Baltic Sea, pockmarks are interpreted to be sourced by thermogenic gas occurring in an area of crystalline bedrock (Söderberg & Floden 1992). Paper V confirmed that methane concentrations measured from cores sampled in the Oslofjord were too low to suggest free gas in the sediments. The profiles from paper V show that methane was produced near the seafloor, and gradually depleted at depth by microbial degradation. It seems likely that the methane is biogenic, produced by an input of anthropogenic organic material. Sulphate concentrations are often used as a proxy for methane in porewater (Borowski et al. 1997). Lower sulphate in the pockmark cores could indicate the presence of methane seepage, as sulphate reduction to sulphide is induced by methane oxidation. Interestingly, Paper V showed that sulphate curves differed significantly between inside and outside of the pockmark. Outside of the pockmark there was a steady reduction in sulphate concentration with depth, yet inside the pockmark concentrations were almost constant with depth. Steeper sulphate gradients may indicate higher methane flux as a sulphate-methane transition is forced upwards, yet the source of any methane is unclear. However, similar trends of steeper sulphate gradients outside compared to inside pockmarks have also been observed in the Storegga Slide area, offshore from Norway (Paull et al. 2008). This was suggested to be due to reduced permeability under the pockmark.

Pockmark formation by trapped porewater escaping from soft cohesive (silt or clay) sediments was proposed by Harrington (1985). Such a mechanism can create a winnowing effect so that grain size increases locally with a corresponding increase in permeability. Under such circumstances, water draining laterally into a sink, especially along the more porous layers, would concentrate the area of water expulsion forming a pit. Continued expulsion of water may lead to slight compaction in a circular zone around the pit, forming the observed pockmark morphology. This method of formation is the hardest to document because of the lack of corroborative chemical signature, but it remains a possible explanation for the formation of the Oslofjord pockmarks (Paper I).

Pockmarks in the western Baltic Sea are thought to be formed by freshwater discharge. This is indicated by a strong decrease in chloride concentration with increasing depth within the pockmark sediments (Whiticar & Werner 1981, Khandriche & Werner 1995). Freshwater fluid flow was confirmed by radionuclide enrichment in the water column. Groundwater discharge can be estimated based on the distribution of  $^{222}\text{Rn}$  and  $^{226}\text{Ra}$  in the water column. The decay of  $^{226}\text{Ra}$  to  $^{222}\text{Rn}$  occurs at higher levels in sediments than in seawater, thus groundwater samples will be enriched in  $^{222}\text{Rn}$  compared to seawater (Schluter et al. 2004). High latitude areas of pockmarks with groundwater seepage have been suggested to be formed by ice rafting (Paull et al. 1999). Freshwater seeping into shallow seafloor sediments is said to periodically freeze binding sediments, which then float off the seafloor. The porewater profiles of the Oslofjord pockmarks showed reduced salinity in the upper 2.6 m of the core (Paper V). This may indicate that freshwater seepage is responsible for the formation of these pockmarks. Although other studies have found reduced chloride concentrations at depth (Whiticar & Werner 1981, Khandriche & Werner 1995), this was not seen in the Oslofjord cores. This maybe due to the core not hitting the conduit inside the pockmark so that the freshwater at the top of the cores could represent lateral transport of freshwater away from the conduit near the surface. Interestingly low salinities were not observed in the initial study of Oslofjord pockmarks (Paper I). This may be due to the seepage being sporadic and the samples only representing the topmost 30 cm of sediment.

Biostratigraphic and radiocarbon data from Paper V indicate an initial age of the Oslofjord pockmarks as close to the base of Holocene, suggesting they formed after the glacial retreat. The pockmarks may have initially formed in an ice-marginal marine setting, where

the out-of-equilibrium conditions at that time, such as high meltwater fluxes, high sedimentation rates and pressure drop, offer several possible mechanisms for their initiation. The continuous but low sedimentation rates inside the pockmarks since this time indicates that they have been active through the Holocene by mechanisms such as outflux of artesian ground water or the action of water currents.

## **Ecology**

The geochemical nature of the seabed, and associated structures such as pockmarks, can have a profound influence on the identity, quantity and profusion of life at local and perhaps regional scales. Many sediment parameters are linked and follow from the hydrodynamic regime. Examples of this are the sediment properties grain size and sorting that affect porosity and permeability, which in turn influence oxygen content, salinity and sediment chemistry (e.g. redox potential). For example coarse intertidal sediments are inhospitable environments due to limited retention of water or organic matter, therefore only species which can tolerate these conditions will survive. In contrast areas of fine clay sediments, where grains pack tightly together, may preclude the presence of meiofauna, which would normally inhabit the pore spaces between the grains. It is therefore important to understand the geology of an area as physical, chemical and biological sedimentary variables are all interlinked.

## **Infaunal macrobenthic communities in pockmarks**

Soft sediments cover most of the ocean seabed and the benthic species that reside within this habitat form one of the richest species pools in oceans (Snelgrove 1999). Pockmarks are one of the most widespread small-scale topographic features within these sediments. Despite this almost nothing is known of their influence on the ecology of the marine environment. As macrobenthic fauna play important roles in ecosystem processes such as nutrient cycling, pollutant metabolism, dispersion and burial, and in secondary production (Snelgrove 1999) it is important to improve our understanding of the effects of these features.

Biodiversity in the marine environment is often positively correlated with the complexity and heterogeneity of habitats (Tokeshi 1999, Thrush & Dayton 2002). In soft sediment environments much of this structure is created by the inhabiting organisms; providing hard substrates such as shells, burrowing and bioturbating sediments, forming biogenic reefs, and modifying surface topography (Thrush & Dayton 2002, Thrush et al. 2006). However, these habitats are increasingly being homogenized by wholesale physical destruction or the selective removal of habitat forming species (Thrush et al. 2006).

Previously soft sediments have been considered to have little topographic structure but now, features such as pockmarks should be considered as important in structuring these environments. Faunal communities are influenced by the physical and chemical properties of the seafloor sediments they inhabit. Changes to these properties can exert a strong influence on the infaunal communities (Levin et al. 2000). One such change is the formation and presence of pockmarks. It seems intuitively reasonable that fauna in depressions such as pockmarks will be protected to some degree from physical disturbance (e.g., trawling), but seepage or altered current patterns may also influence the fauna in various ways, e.g. by increasing food availability for chemotrophic organisms or by physical disturbance.

This thesis represents only the third study to quantitatively examine the ecology of infauna in pockmarks. Paper II and IV report on the ecology of benthic communities within newly discovered pockmarks in the Oslofjord. Paper II investigates the distribution of infaunal communities in circular pockmarks. This paper shows that pockmarks significantly alter the abundances of key infaunal species and, as such, the abundance of pockmarks in the Oslofjord (4 pockmarks km<sup>-2</sup>) will have a considerable cumulative influence on densities and populations. The fauna of pockmarks were typical of a disturbed fjord environment with a dominance of small opportunistic taxa, such as pioneer bivalves and polychaetes. I found that the position of sites in the fjord drove the most obvious faunal differences which potentially masked the full effect of pockmarks on infaunal communities. Paper IV investigating the ecology of elongated pockmarks in the Oslofjord also showed subtle differences in species composition inside the elongated pockmarks when compared to background samples. The differences were due to different abundances of small opportunistic polychaetes however, no species were obviously characteristic of pockmark communities. There were both similarities and differences between findings in this thesis

and the other two reports of pockmark ecology. Dando et al. (1991) reported that the fauna of a North Sea pockmark was characterised by two species not previously reported from the area, the bivalve *Thyasira sarsi* and the nematode *Astomonema* sp., both of which contain endosymbiotic bacteria. The flat centre of their pockmarks had impoverished macrofauna and nematodes that they ascribed to the consolidated clay in the surface layers. Wildish et al. (2008) is the only previous study to investigate variability in biodiversity and ecology across pockmarks. They concluded that of 14 pockmarks studied in detail, five (upper habitat A) were at a pre-equilibrium succession, whilst nine (lower habitat A) were at or near equilibrium.

### **Comparison between elongated and circular pockmarks**

There are no previous studies on the ecology of elongated pockmarks and no comparisons of the influences of pockmark morphology on the fauna within them. Elongated pockmarks had lower redox potentials and higher organic contents than the circular pockmarks within the inner Oslofjord (Paper II & IV). Interestingly, unlike the circular pockmarks (Paper II), no differences were observed in the sediment grain size between inside and outside of the elongated pockmarks. The most likely explanation is that the location of these pockmarks in the fjord, and their proximity to land, increased the influence of terrigenous runoff. Such terrestrial sediment runoff and the effects of eutrophication can lead to dead zones that cause the removal of habitat structuring organisms (Karlson et al. 2002). Large numbers of pockmark studies, including Paper II and Paper III, report coarser sediments in the centre of the pockmarks, due to the removal of fine grains during the pockmark formation and any subsequent seepage.

Both elongated and circular pockmarks showed subtle differences in faunal composition when comparing the inside of pockmarks to non pockmarked areas. The data sets from Paper II and IV cannot be compared statistically due to differences in the sampling, the former having sampled fauna to 1 mm and the later 0.5 mm. Interestingly, the elongated pockmarks had a variable effect on the abundance and richness of fauna when comparing species composition inside and outside of pockmarks. In two elongated pockmarks species richness and abundance were both lower inside, however, this pattern was reversed in two other sites. Due to the lack of effect of location on species richness and abundance,

observed differences were suggested to be related to differing successional stages or hydrodynamic regimes of the pockmarks.

### **Megafaunal communities in pockmarks**

Megabenthic organisms have been defined as species large enough to be determined on photographs (Grassle et al. 1975). Monitoring epibenthic megafauna has been shown to be effective in evaluating some impacts of disturbance on the seafloor (Bluhm 2001). Epibenthic communities are important because they are good indicators of fishing effects, sometimes sensitive to pollution, a food source for commercial fisheries (Jennings et al. 1999), and they have a key function in benthic habitats (Piepenburg & Schmid 1997). In the study of pockmark ecology, megafaunal communities have received the most attention, due to the majority of investigations employing ROVs for surveying. These provide video and photographs that naturally focus on the observation and identification of these conspicuous fauna. Additionally reports of novel and specialised fauna have attracted interest as seep ecosystems remain at the forefront of scientific discovery.

The active seepage of methane, hydrogen sulphide or other hydrocarbons are described as cold seeps. Only two regions have pockmarks containing obvious cold seep communities, the Congo Fan off the west coast of Africa (Gay et al. 2006, Sahling et al. 2008) and the North Gulf of Mexico (Macdonald et al. 1990). The most unusual of these are the findings in the Gulf of Mexico, where a brine filled pockmark was discovered ringed by a bed of *Bathymodiolus* sp.. The anoxic brine contained high concentrations of methane, which nourish the methanotrophic symbionts in the mussels (Macdonald et al. 1990). In the Congo Fan area the 'Kouilou pockmarks', and the 'REGAB' pockmark were also discovered to contain a high abundance of chemosynthetic seep fauna. The REGAB is a large 800 m wide complex pockmark in 3160 m water depth, formed from about 20 smaller depressions with depths up to 15 m. Inside the pockmark, the faunal assemblages were dominated by bivalves of the families Mytilidae (*Bathymodiolus* sp.) or Vesicomidae (*Calyptogena* sp., '*Vesicomya*' aff. *chuni*), or by Siboglinidae polychaetes (*Escarpia southwardae*) (Ondréas et al. 2005, Olu-Le Roy et al. 2007). The Kouilou pockmarks are three large pockmarks, up to 1000 m in diameter and 15 m in depth, in water depths of around 3100 m. All three of these pockmarks have comparable faunal

compositions of vestimentiferan tubeworms and vesicomid clams similar to the fauna of the REGAB pockmark (Sahling et al. 2008).

The occurrence of seep communities within pockmarks is not only related to the type or activity of the pockmarks but also by the depth of water in which they occur. From examining cold seeps at four depth zones from 160 m to 1600 m in the Sea of Okhotsk, Sahling et al. (2003) concluded that the number of chemosynthetic fauna decreased dramatically with decreasing water depth and that seep-endemic fauna were confined to seep sites at depths below 370 m. They suggested this was due to higher predation pressure at shallower depths, but it may also be an effect of other depth related factors such as bottom-water currents, sedimentary regimes, oxygen concentrations or the supply of suitable substrates.

Paper III represents one of only two quantitative studies of megafaunal communities within shallow water (less than 400 m) pockmarks. This paper examined megafaunal communities of four large pockmarks in the North Sea using video analysis to calculate densities of fauna inside and outside of pockmarks. It revealed that megafauna increased in abundance, species richness and diversity from outside (background seabed) towards the centre of the pockmarks. The numbers of taxa present in the centre of pockmarks were approximately double that of similar surrounding areas, and the centres had almost an order of magnitude more individuals than outside. The main reasons for this increased faunal abundance and species richness were suggested to be habitat enrichment and refuge from disturbance. The other study of the megabenthos in pockmarks was carried out using a towed underwater camera across pockmarks in Passamaquoddy Bay, east coast Canada (Wildish et al. 2008). They calculated the density of three species of megabenthos; *Asterias rubens*, *Cucumaria frondosa* and an unidentified bryozoan or hydrozoan, inside and outside of pockmarks. *A. rubens* occurred in higher densities outside pockmarks and although *C. frondosa* occurred both inside and outside of the pockmarks, aggregated populations were only observed inside. They proposed that this was linked to special hydrodynamic conditions, which cause turbulent re-suspension of material.

Carbonate rocks in the centre of pockmarks have been observed in fossil and active pockmarks, and seep sites (Levin 2005, Mazzini et al. 2006, Sahling et al. 2008). This carbonate represents a hard substrate in an otherwise soft sediment environment providing

habitat to encrusting organisms and shelter for others. Pockmarks studied in the North Sea (Paper III) showed increases in megafaunal abundance associated with carbonate rocks in their centres. This is similar to findings at other cold seep sites, where carbonates are common. A study in the Sea of Okhotsk found the abundances of the megafaunal groups (classes) Gastropoda, Asteroidea and Echinoidea were positively correlated with the presence of hard substrates (e.g. carbonates) at seep sites (Sahling et al. 2008). The distribution of characteristic seep fauna, siboglionids and mytilid bivalves, is limited by the nature of the geological substratum, both needing hard substratum for larval settlement. In contrast, vesicomysids require soft sediments as they are usually observed partially buried in the sediment (Ondréas et al. 2005). Whilst epifauna attached to carbonates have been investigated, there have been no community descriptions of carbonate-associated or carbonate-burrowing seep taxa, either epifauna or endolithofauna (Levin 2005).

### **Pockmarks as refuges**

The complex morphology of carbonates not only provides a large surface area for the settlement of fauna, it also offers protection against predation and some environmental disturbances. Natural habitat complexity, such as that associated with carbonate rocks, can provide spatial refuges within which juvenile fish species can avoid predation (Tupper & Boutilier 1995, Scharf et al. 2006). This may be vitally important with increasing homogenisation of habitats by physical disturbance (Thrush et al. 2006). Some fauna are known to associate with depressions in the seafloor, where they either seek refuge from predators or lie in wait optimizing ambush predation tactics (Auster et al. 1995). Deep pockmarks in the North Sea have been shown to act as refuges for several fish species; cod (*Gadus morhua*), torsk (*Brosme brosme*) and ling (*Molva molva*) (Hovland & Judd 1988). Fish have been observed seeking refuge in burrows on the east slopes of large pockmarks (Fig. 3A) and in unit pockmarks (Fig. 3B) in the North Sea (Paper III).

The recessed morphology of pockmarks offers protection from disturbances such as trawling (Paper III). The observations, in Paper III, of large abundances of fragile sponges, cnidarians and corals are unusual in the North Sea. Benthic communities in the North Sea are known to be affected by fishing disturbance causing decreases in biomass, abundance and production (Thrush & Dayton 2002). The pockmarks studied had trawl scars running across the top of them yet they had a high abundance of epifauna in their centres, including

large 2 m high colonies of the Gorgonian coral, *Paragorgia arborea*. Although trawls may pass over pockmarks it appears that the diameter and depth of the pockmarks, compared to the size of nets, means that the recessed centres of the pockmarks remain undisturbed. It has been estimated that, on average, any seabed area of the North Sea is trawled over at least twice per year by increasingly heavy gear (Sydow 1990). Any protection offered by pockmarks is of key importance because, with bottom fishing gear causing mortality and injury to surface dwelling and shallow burying fauna on the seafloor (Tuck et al. 1998), (over)fishing is considered the biggest current anthropogenic impact (Dayton et al. 1995, Jackson et al. 2001).

Fig. 3. (A) Torsk (*Brosme brosme*) in a hole on the east slope of a large pockmark in the North Sea. (B). Territorial torsk in unit pockmark, showing the coarse grain sediments and a ball sponge and anemone (*Bolocera tuediae*). (Courtesy of the Troll Shallow Gas Project, StatoilHydro)



### Seeping pockmarks

Deep-sea pockmarks have been shown to contain characteristic species associated with seepage. However, there are few reports of chemosynthetic organisms associated with pockmarks in shallower waters. Enhanced benthic fauna in pockmarks in the Holene and Gullfaks areas of the North Sea are suspected to be related to methane-, and carbon dioxide-, rich porewater seeping out of the seabed (Hovland & Thomsen 1989). The presence of such seepage was indicated by mats of sulphur oxidising bacteria. It is assumed that the benthic fauna are enhanced through a bacteria-based food web sustained by methane seepage (Hovland & Judd 1988). Paper III shows that pockmarks in the North Sea at around 300 m water depth have an increased abundance and diversity of fauna. However, the increased fauna observed is probably unrelated to any active seepage as these pockmarks are thought to be inactive or episodic in nature. They showed no active signs of seepage, such as bubbles and fluid flow, and no bacterial mats or specialised chemosynthetic fauna were observed during investigations.

The seepage of hydrocarbons has also been linked to other fauna around pockmarks. The 'hydraulic theory' was suggested to explain the paradoxical distribution of cold water coral reefs around the Norwegian coast. This theory states that coral growth is promoted by fluid flow, either through the seepage of groundwater under reefs in fjords, or hydrocarbon related fluids under the continental shelf reefs (Judd & Hovland 2007). An example of this is the occurrence of *Lophelia* coral reefs on the edge of pockmarks in the Kristin Field, which is suggested to be correlated with gas and porewater seepage stimulating growth through the provision of bacteria and micro-organisms (Hovland 2005). However, some studies have argued against the linkage between fluid seepage and corals reefs (Freiwald et al. 1999). Although some reefs are reported close to seeps and pockmarks, many, if not most, are not (Roberts & Hirshfield 2004). Isotope analysis of coral tissues from Galicia Bank on the North West Atlantic margin excludes the possibility that the coral community there is methane-supported, since the  $\delta^{13}\text{C}$  values expected from a methane seep were far outside the values found in coral tissue (Duineveld et al. 2004).

## **Currents**

The morphology of pockmarks could also play an important role in structuring benthic communities by altering current patterns. The physical energy above the seabed plays an important role in the settlement of larvae and the supply of food to the surface sediments as well as in the spatial distribution of different sediment types. Eroded seabeds and coarse sediments are associated with high-energy currents, compared to areas of low energy where accumulation of fine sands, muds and ooze is likely to prevail. Where bottom currents occur intermittently, episodic resuspension may take place. Advective processes also transport organic particles along the bottom, which may have an important impact on species composition and the feeding behaviour of benthic fauna (Rosenberg 1995). Wildish et al. (2008) proposed that aggregations of holothurians in the bottom of pockmarks were linked to hydrodynamic conditions that cause turbulent resuspension of material. Increased bottom flow may lead to more suspension feeders, or alternatively reduced water flow may increase larval settlement or lead to higher abundance of deposit feeders. Currents also help resuspend nutrients. Deposit feeders are found on all types of soft sediment but they reach their highest abundances where water movements are minimal, whereas suspension feeders require a higher rate of water movement (Wildish & Kristmanson 1997).

The current patterns within pockmarks are not fully understood, but observations of the fauna can give indications of the likely conditions. The pockmarks in the North Sea contained high abundances of suspension feeders (Paper III) which may indicate a rich source of food for these fauna either from increased water movement, or the resuspension of food particles from sediments by active seepage or turbulent current processes.

## **Comparisons of epifauna and infauna**

Epifaunal communities in the North Sea were enhanced within pockmarks (Paper III), whereas (from what little evidence is available) infaunal communities appeared to be negatively affected with reduced abundance and diversity (Paper IV, Dando et al. 1991). The same results of reduced infaunal populations have also been observed at methane seeps (Grassle 1985, Dando et al. 1991, Thiermann et al. 1997). It is well documented that pockmarks have coarser material in their centre (than surrounding sediments), thought to be caused during formation as fine sediments are removed by currents during eruption or

winning during gradual seepage. This coarser sediment within the centre of the pockmarks is correlated with the abundance and diversity of the benthic assemblages (Paper II & III). For example, coarser sediment composition had an effect on the species composition of the Oslofjord pockmarks (Paper II). Studies by Dando et al (1991) showed that the biomass of infauna on the pockmark slopes was similar to the surrounding seafloor. But the bottom of the pockmarks had a smaller number of species and lower biomass that they attributed to the disturbed sediments. Previous studies on the infauna and epifauna of the North Sea have shown that the strongest correlation with infaunal community composition was sediment granulometry, with the next-most strongly correlated factor being depth (Basford et al. 1990). For the epibenthos, depth was the major factor and the sediment composition was less significant. This may explain why increases in biodiversity and abundance were observed within pockmarks of epifauna (megabenthos) but not necessarily within the infaunal macrobenthic communities.

## **Concluding remarks**

The Oslofjord Pockmarks were probably initiated between 10.7 and 9.5 cal kyr BP and have experienced continuously low sedimentation rates since this time. Thus, these structures may have initially formed in an ice-marginal marine setting, where mechanisms such as submarine melt water outflux, ice rafting and rapid isostatic uplift may be of relevance. Reduced salinity in the upper sediments of the pockmark indicates they are actively seeping artesian ground water. Investigations in the North Sea and Oslofjord have shown that the influence of pockmarks is different between epifaunal and infaunal communities. The increase in some measures of epifaunal community presence within pockmarks was probably due to two main reasons. The presence of carbonate rocks providing a hard substrate for settling and development; and the protection offered by the morphology of the pockmark and carbonate rock. Infaunal communities showed both increases and decreases in species abundance and richness. This is presumed to be related to their location within the fjord, proximity to land and also possibly the successional stages of the pockmark. The abundances of key species inside pockmarks were significantly different to the surrounding seabed and as such the abundance of pockmarks in the Oslofjord has a considerable cumulative influence on overall faunal densities and

populations. This thesis highlights the need for more pockmark research, investigating their effects on the faunal communities globally, in different environmental settings.

## **Future perspectives**

Pockmarks have now been recognised for nearly four decades, yet there is still little detailed knowledge or understanding of the pockmark environments. More extensive surveying and long-term monitoring may help to gain stronger insights into pockmark processes and dynamics. Long term studies on pockmarks need to be undertaken to determine if they are dynamic, perturbed environments or if they are oases for epifauna. Monitoring of the hydrodynamics inside pockmarks may give explanations for the high epifaunal diversity. The effects of carbonate rocks as a substrate for larval settlement and refuge could be investigated in more detail by comparisons with glacial drop stones. This thesis has focused on the macrofaunal component of benthic biodiversity, but micro- and meiofauna must also be considered. This work also represents only the third investigation of infauna within pockmarks, so there is still limited knowledge of the biogeography of these communities on a global scale.

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## Appendix 1

Data used to compile figure 1.

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