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A REVIEW OF POCKMARKS IN THE UK PART OF THE NORTH SEA, WITH PARTICULAR RESPECT TO THEIR BIOLOGY

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A REVIEW OF POCKMARKS IN THE UK PART OF THE NORTH SEA, WITH PARTICULAR RESPECT TO THEIR BIOLOGY

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1. POCKMARKS, THEIR TYPES AND SIZES IN THE NORTH SEA

Pockmarks are depressions or craters in the seabed. In the North Sea they range from less than 0.5 m to approximately 20 m in depth and from 1 m to more than 1 km long (Hovland & Judd, 1988). In the Gulf of Mexico a pockmark as deep as 58 m has been described (Prior et al., 1989). The North Sea pockmarks are typically roughly circular or ellipsoidal at the top and cone-shaped in cross-section, although they may also be irregular in cross-section, with the long axis being typically parallel to the bottom current direction (Hovland & Judd, 1988). Asymmetrical pockmarks are particularly common in the Witch Ground Basin (Hovland & Judd, 1988; Stoker, 1981). Small depressions, typically 3 m across and 0.5 m or more deep have been called “unit pockmarks” (Hovland et al., 1984) or “pits” (Harrington, 1985) and are very common in some areas of the North Sea. Large pockmarks are often composites of several smaller pockmarks leading to irregular shapes. The “eyed” pockmarks described from small pockmarks in the Norwegian sector (Hovland & Judd, 1988; Hovland & Thomsen, 1989) consist of an aggregation of biological material in the centre, possibly based on a carbonate concretion. These appear to be rare in small pockmarks in the UK sector.

Pockmarks are generally confined to north of 56° in the North Sea with the highest densities being found west of the Norwegian Trench within the North Sea Plateau and the Witch Ground Basin of the central North Sea. Up to 20 pockmarks km^{-2} were reported from a basin in the plateau area (Long, 1988). In the Fladen area the pockmarks reach high densities of >30 km^{-2}, where they are typically 50-100 m in diameter and 2-3 m deep (Long, 1986), with lower densities, 10-15 km^{-2}, but larger pockmarks, being present in the mud of the deepest parts of the Witch Ground Basin.

It is generally believed that pockmarks are formed by the expulsion of fluid, either gas (Hovland, et al., 1984; King & Maclean, 1970) or water (Harrington, 1985; Whiticar & Werner, 1981) through seafloor sediments. Pockmarks may be formed by a one-off explosive release of fluid, especially following the dissociation of methane hydrates as a result of falling sea levels or elevated temperatures, or by the release of gas trapped under hydrate layers which had become destabilised. Pockmarks such as those 10-30 m deep in the mudstone deposits below the shallow post-glacial sediments of the Barents Sea (Linke & Dando, 1994; Solheim & Elverhøi, 1993) were clearly formed by explosive release of fluid. Most of these pockmarks are currently inactive.

Some pockmarks may have remained active, with continual seepage from the date of formation to the present. An example of the latter are the pockmarks in Eckernförde Bucht in the Baltic, where there is active submarine ground water release from aquifers (Bussmann et al., 1999; Bussmann & Suess, 1998; Werner, 1978). This type of pockmark, due to groundwater flow, almost certainly exists in the UK sector, although none have been described to date. Pockmark formation appears to be continuing at the present time since large sediment plumes have been reported during surveys (McQuillin et al., 1979).

Large deep pockmarks are unusual in the UK sector of the North Sea although 3, named the ‘Scanner’, ‘Scotia’ and ‘Challenger’ pockmarks, are present in UK block 15/25 (Figure 1) near the centre of the Witch Ground Basin (Judd et al., 1994). The ‘Scanner’ and ‘Challenger’ pockmarks are approximately 20 m deep at their deepest part while the ‘Scotia’ pockmark, which is a double pockmark, is approximately 15 m deep. All 3 pockmarks are active with an escape of methane (Dando, 1990; Dando, 1991; Dando et al., 1991; Hovland & Sommerville, 1985; Judd, et al., 1994). The ‘Scanner’ pockmark has been studied using both a ROV and the submersible *Jago*. It was found to have large rocks of carbonate-cemented sediment in the centre (Dando, 1990; Dando, et al., 1991; Hovland & Judd, 1988). The other two large pockmarks have not been surveyed visually.

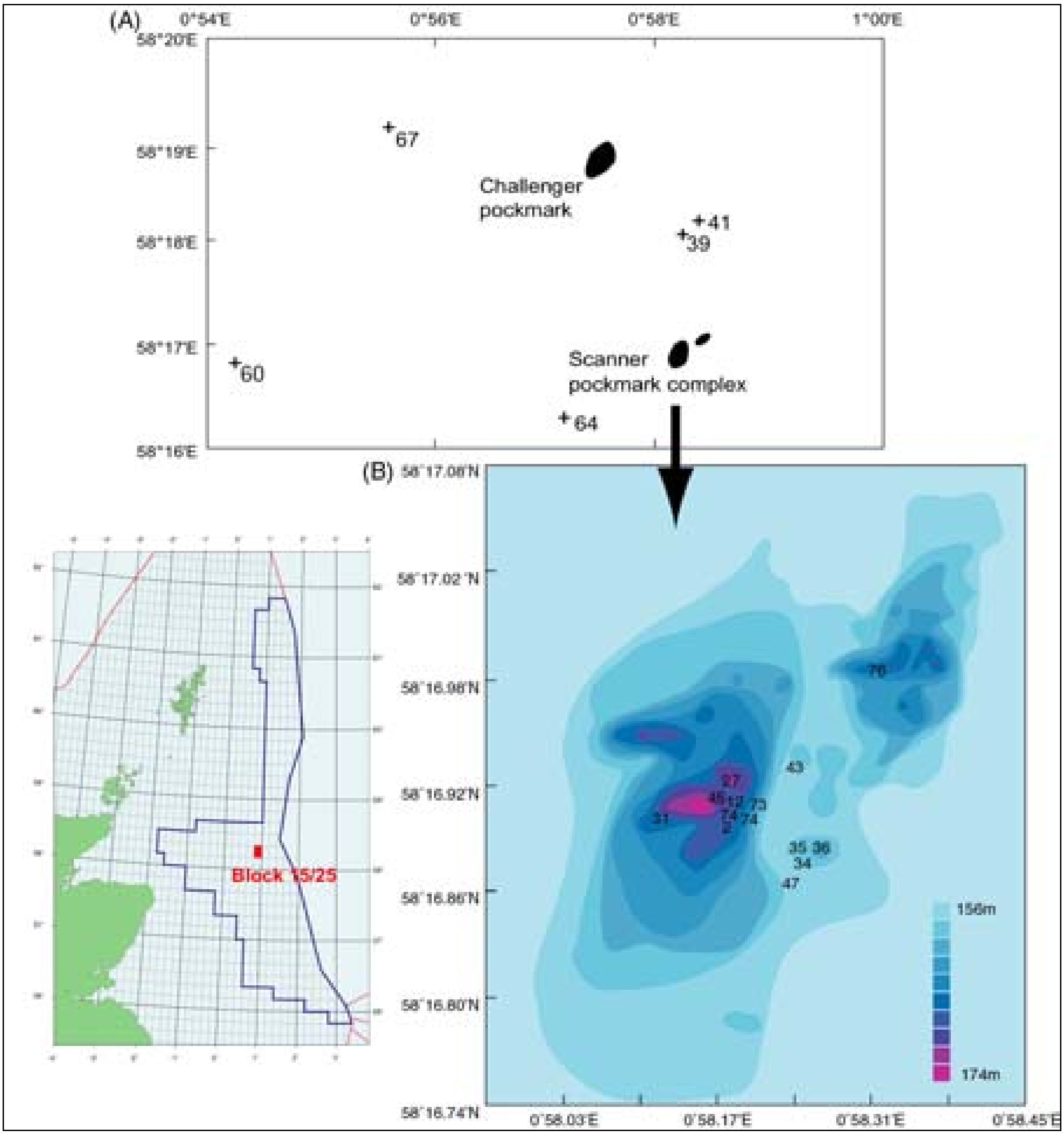

Figure 1 Location of stations samples during RRS Challenger Cruise 70 to the Scanner and Challenger pockmarks in block 15/25. Note that the initial digit 7 has been omitted for clarity, e.g. 34 is Station 734.

2. BIOLOGY OF POCKMARKS IN THE NORTH SEA

The species composition of pockmarks, compared with that of the surrounding seafloor, might be expected to be determined by two sets of factors:

1. that pockmarks are depressions in the seabed, resulting in reduced bottom current flow within the pockmark and enhanced sedimentation.

2. factors related to past or current fluid seepage, such as sediment sorting, cementation of part of the sediment, channels of fluid flow and altered geochemistry including increased concentrations of reduced compounds such as sulphide and methane.

Factor one is found to hold for the Scanner pockmark which often retains colder more saline water than the surrounding seabed. Enhanced fill in the pockmark has been noted in deep-tow boomer records (Judd et al., 1994). The second set of factors is common in many seepage situations (Dando & Hovland, 1992) and all were observed during the RRS Challenger cruises 70 and 82 to study the Scanner and Challenger pockmarks. Most North Sea pockmarks are shallow and currently inactive and would be expected to have a biology more similar to that of the surrounding seafloor than pockmarks which are currently, or have recently been, active.

Since the only pockmark in the UK sector whose biology has been studied in detail is the 'Scanner' pockmark (Dando, 1990; Dando, 1990; Dando, 1991; Dando, et al, 1991; Jones, 1993; Jones, 1996), references will be made to observations on other pockmarks in the North Sea and in the North-east Atlantic area in order to estimate the likely variation in biology between pockmarks.

2.1 Inactive pockmarks

These are the most common type of pockmarks in the North Sea. Although there has been no detailed study on the biological aspects of such pockmarks it is possible to speculate from related studies the possible biological consequence of such depressions in areas of low bottom current velocity. A survey (DTI 2001) has recently been completed of such pockmarks but the results were not available at the time of writing.

Even small depressions in the seabed in areas of soft sediment, i.e. of low current flow, will act as sediment traps, accumulating finer-grained sediment and organic flocs preferentially over the surrounding seafloor due to the reduced bottom current flow (Yager et al., 1993). Depressions left by seabed mining operations have been observed to fill fairly rapidly (Jewett et al., 1999). Surficial sediments within pockmarks have been found, as expected, to have a higher organic carbon content than the sediments outside (P. Dando and R. Corner, unpublished studies). Sediment erosion and deposition is dependent on the bottom current velocity (Perkins, 1974) as is benthic production (Olafsson et al., 1994, Hall, 1994). The shallower parts of the North Sea with a sandy, or coarser, seabed, are, however, unlikely to show such effects due to high bottom current velocity. Pockmarks acting as sediment traps are most likely to be found in deeper basins such as the Witch Ground Basin in the Central North Sea. Even in the latter situation differences are only likely to be found at the base of the pockmarks and remotely operated vehicles or camera-directed samplers would be needed to sample at the required resolution to show a marked effect.

The reduction in bottom currents below a critical minimum means that depressions can be areas of increased larval settlement (Snelgrove, 1994). The funnel shape of pockmarks will concentrate settling particles in the base, a strategy used by some burrowing organisms (Yager et al., 1993). Pockmark bases might therefore be expected to show an increase in the abundance of deposit feeding organisms compared with the surrounding sediment, unless they are in areas of high bottom current velocity, more than a mean of 30 cm s^{-1}.(Wildish and Kristmanson, 1993). Conversely, many suspension feeding organisms grow faster at higher current velocities up to a maximum, e.g. 3 cms^{-1} in the case *of Mytilus edulis* (Wildish and Kristmanson, 1985). Depending on the size and shape, the bottom of the pockmarks would be likely to be less damaged by trawling activity, which is well-known to reduce the biomass of the benthos. As a consequence of the combined effects of reduced bottom current velocity and reduced disturbance in inactive pockmarks in areas of low current flow, it would be expected that there would be a change in the composition of the benthos compared to the surrounding seabed. Such changes would be dependent on the change in bottom current velocity inside the pockmark compared with outside (Olafsson et al., 1994, Hall, 1994). This would be quite unrelated to any factors due to recent or current seepage. Measurements on bottom current velocity in pockmarks are, however, lacking.

Descriptions of visual observations by ROV, bottom camera or submersible (Hovland & Judd, 1988; Hovland & Thomsen, 1989; King & Maclean, 1970; Linke & Dando, 1994) support the predictions of biomass and/or species differences inside and outside the large pockmarks that were studied. Visibility is often greatly reduced in the base of deep pockmarks due to high concentrations of suspended particles which attract swarms of shrimps and euphausids (King & Maclean, 1970; Linke & Dando, 1994). Such swarms were not seen on the surrounding seabed although they may occur elsewhere in the area. Concentrations of anthozoans and sponges have been observed (Hovland & Thomsen, 1989; Linke & Dando, 1994). In the very shallow, relatively wide pockmarks, which are the most common type in the North Sea, there may be no changes in bottom current velocity and consequent faunal differences from the surrounding seabed. Measurements of bottom current velocity are lacking for all pockmarks. Fish, especially ling (*Molva* sp.) have been observed to shelter in even shallow pockmarks (Hovland & Thomsen, 1989). This does not mean that they are especially attracted to pockmarks since they will take advantage of any relief on the seafloor including pipelines, wrecks and debris.

In active pockmarks, seepage, due to factors including sediment removal, sulphide toxicity, reduced oxygen concentrations or reduced salinity may cause reductions in the infauna and cause changes in the species composition of both infauna and epifauna.

2.2 Active pockmarks

2.2.1 Prokaryotes

Active pockmarks have channels through which methane is brought up to, or close to, the surface of the sediment. The methane can originate either in biogenic or thermogenic reservoirs of gas. In pockmarks flushed with submarine ground water the methane is flushed out of the overlying sediments (Bussmann, et al., 1999). Methane is oxidised both anaerobically within the sediment and aerobically, by methanotrophic bacteria, close to the sediment surface (Bussmann, et al., 1999; Dando et al., 1994). Anaerobic methane oxidation is closely linked to sulphate reduction and is now believed to be carried out by a consortium of methanogenic archaea and sulphate reducing bacteria (Boetius et al., 2000). Such aggregates of prokaryotes have yet to be looked for in pockmarks although they are probably responsible for the excess carbonate within the sediment and the formation of carbonate cement. Erosion of the surface sediment by water currents or seepage (Dando et al., 1994; Jensen et al., 1992; Jørgensen, 1989; Jørgensen, 1992) exposes the carbonate-cemented sediment. These carbonates are confined to pockmarks that have, or have had, long term seeps.

Sulphide seeping out of the sediment in active pockmarks can support mats of sulphur-oxidising bacteria. Such mats are a good visual guide to the presence of active seepage (Dando & Hovland, 1992) and were observed in video data from the Scanner pockmark. Although such mats are normally described as *Beggiatoa* sp. (Hovland & Judd, 1988) no positive identification have been made of the mats in North Sea pockmarks. *Beggiatoa* were identified from 1-2 cm thick mats in pockmarks in the Baltic (Bussmann, et al., 1999).

Seepage areas can provide 'windows' into the deep biosphere. This is an area of particular interest at present because of the biotechnological potential of prokaryotes which can survive in extreme environments. No detailed microbiological study has yet been made of a seeping pockmark, in contrast to the numerous studies conducted at, for example, hydrothermal venting sites on the seafloor.

Only one study of bacterioplankton in a pockmark has been reported. In a seeping pockmark on the Oregon shelf there was an approximately two-fold increase in heterotrophic bacteria both in the bottom water and again at the surface (Juhl & Taghon, 1993). However, since the control and pockmark samples were taken 12 h apart, the difference may not be significant.

2.2.2 Infauna

A preliminary investigation into the fauna of the Scanner and Scotia pockmarks was made in June-July 1989 (Dando, et al., 1991). The macro-infauna in the pockmarks was similar to that of the surrounding area with the infauna being dominated by four spp. of polychaetes *Paramphinome jeffreysii*, *Levinsenia gracilis*, *Heteromastus filiformis* and *Spiophanes kroyeri*, the bivalve *Thyasira equalis* and juvenile echinoderms, *Echinocardium* sp. These 6 species accounted for 65% of the total number of individuals. Only one species was found only in the pockmark sediments, the bivalve *Thyasira sarsi* (Dando, et al., 1991). *T. sarsi* is a species which obtains most of its nutrition from endosymbiotic sulphur-oxidising bacteria located in its gills and is confined to sulphide-rich sediments (Dando & Southward, 1986). It occurs around methane seeps in the Skagerrak (Dando, et al., 1994) but otherwise, outside fjord habitats, it has only been reported in the North Sea around oil platforms where oil-based drilling muds have stimulated sulphate reduction.

During the Jago dives a piece of carbonate cemented sediment was recovered with a dead shell of the lucinid bivalve *Lucinoma borealis* attached. *L. borealis* is a large (35 mm) bivalve which derives its nutrition, like, *T. sarsi*, from endosymbiotic sulphur-oxidising bacteria (Dando, Southward & Southward, 1986). Since *L. borealis* inhabits sediments of sand or sandy mud, it is not found elsewhere in the Witch Ground Basin and is almost certainly confined to such pockmarks.

The meiofauna was dominated by nematodes and, in particular, by a previously undescribed species of gutless nematode, *Astononema southwardorum* (Austen et al., 1993), also containing endosymbiotic bacteria. This nematode was found in the pockmark sediments just above the main sulphate reduction zone in the cores (Dando, et al., 1991). At the time of writing this report, the Scanner pockmark is still the only known locality for this unusual species.

A further, more detailed, study of the benthos was undertaken during two cruises (CH70 and CH82) by R.R.S. Challenger, in August 1990 and July 1991 to investigate the infauna of the Scanner and the Challenger pockmarks (Dando, 1990; Dando, 1991). During the first cruise the manned submersible *Jago* was deployed for dives into the Scanner pockmark. The following results are taken from an unpublished report by Y. Leahy, P. R. Dando, J. A. Hughes, I. Akoumianaki and A. Eleftheriou. A total of 38 stations were sampled using box-cores, 18 being located in the Scanner pockmark and 7 in the Challenger pockmark; the remaining 13 stations were sampled in the general area and designated as controls (Figures 1 & 2). A total of 282 taxa were recorded from both surveys. As in the preliminary study, polychaetes dominated the fauna, accounting for 45% (127 species) of the total, while molluscs and crustaceans contributed 24.5% (69 species) and 19.5% (55 species), respectively. The minor phyla (16 species) and the echinoderms (15 species) accounted for 5.7% and 5.3%, respectively. This pattern of dominance occurred within both pockmarks and also at the control stations.

Cluster analysis of the data suggested that there were five station groups (Figure 3, Tables 1 & 2). The majority of the stations of the study area were grouped together (> 40% similarity) in one large station group, Group A. This included all but one of the control stations, 9 of the 13 Scanner and 3 of the 7 Challenger stations. Within this group, three distinct sub-groupings, A1, A2 and A3, could be distinguished. The groups B, C and D were composed of only a few stations (2, 1 and 2 stations, respectively) and, with the exception of one station, were all found within the pockmarks. The final station group, Group E, consisted of those stations from the base of the Scanner pockmark. Although this group consisted of a greater number of stations than groups B, C and D, it displayed a higher degree of within group dissimilarity and suggests that these stations were grouped together on the basis of their dissimilarity with the stations of the study area rather than their similarity to one another.

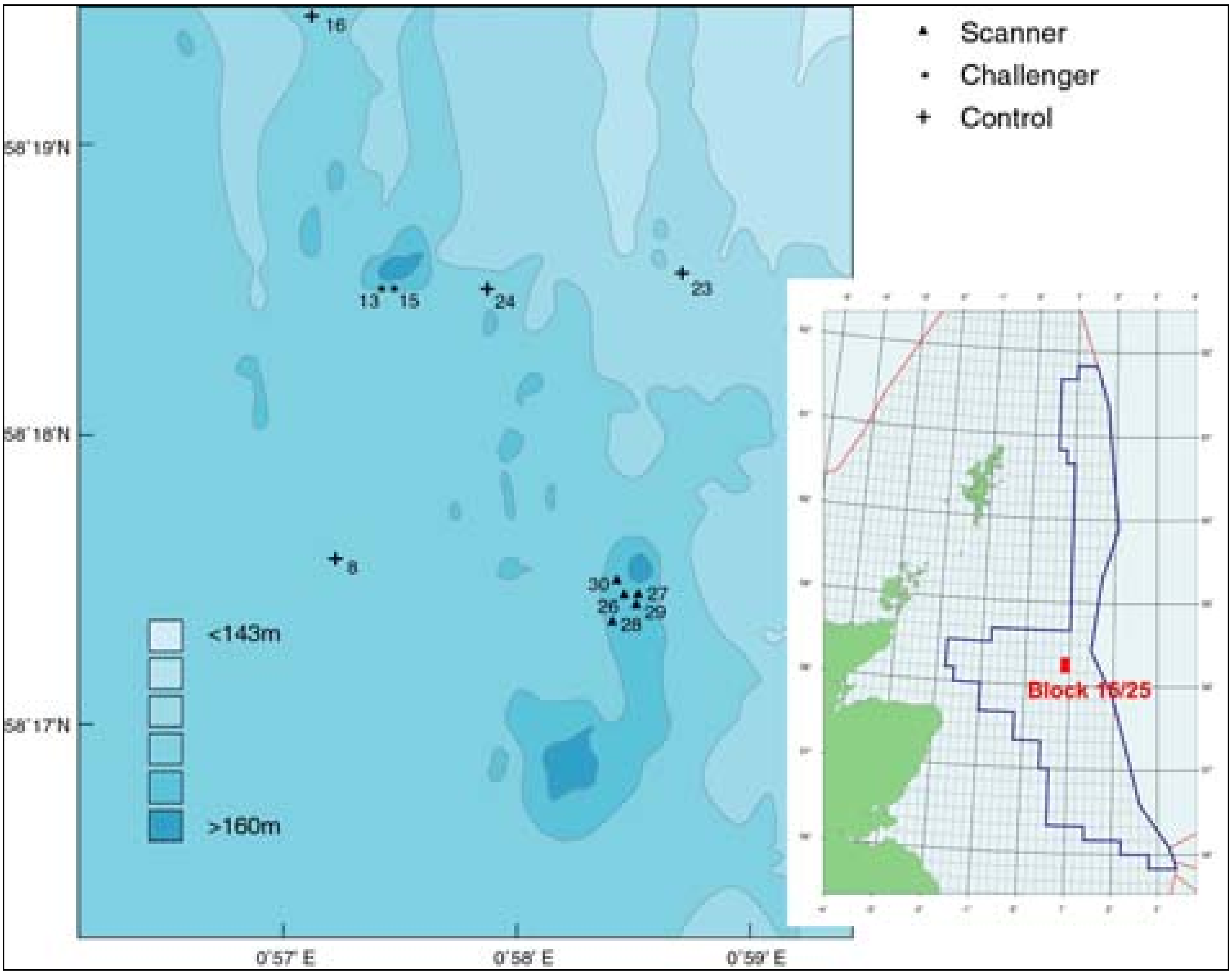

Figure 2 ***Location of stations sampled during RRS Challenger Cruise 82 to Block 18/25 in July 1991. Note that the initial digit 8 has been omitted for clarity, e.g. 30 is Station 830.***

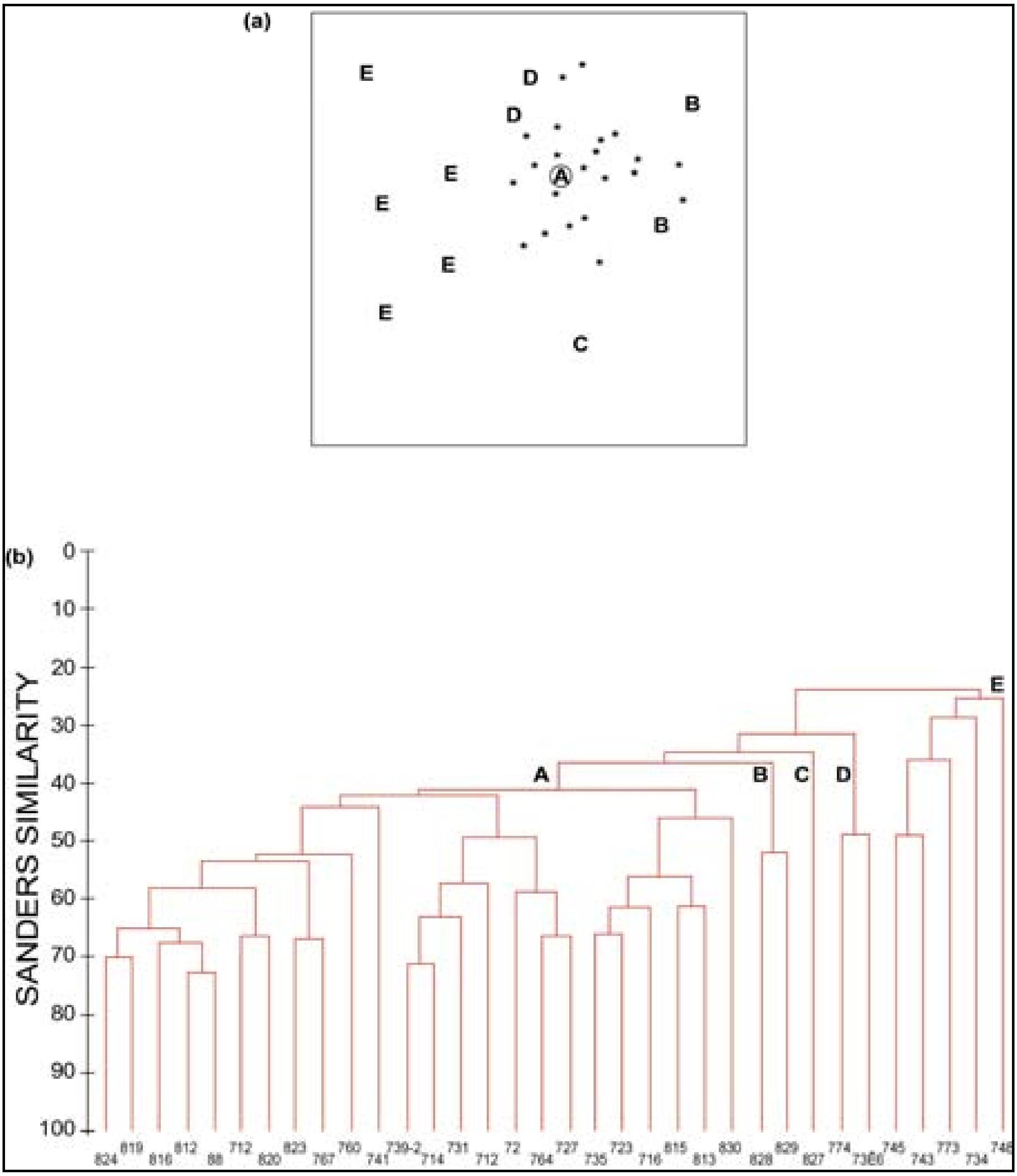

***Figure 3.** (a) MDS plot of the stations from the CH70 and CH82 cruises.*
(b) Cluster analysis, using the Sanders sorting coefficient of the stations from the CH70 and CH82 cruises.

Table 1 Rank analysis of the station groups identified by Cluster analysis, groups A-D

Taxon	**Score**	**Feeding type**	**% occurrence**	**Mean density ± S.D. (m^{-2})**
Group A1				
Levinseniagracilis (Tauber)	50.5	Deposit(SB)	100	360±160
Heteromastusfiliformis (Claparede)	32	Deposit(SB/SF)	100	114±160
Paramphinomejeffreysii (McIntosh)	23	Omnivore	90.9	241±244
Thyasiracroulinensis (Jeffreys)	11	Suspension	72.7	66±34
	Maximum score = 55			
Group A2				
Heteromastus filiformis (Claparede)	35	Deposit (SB/SF)	100	1019 ± 1103
Levinsenia gracilis (Tauber)	19	Deposit (SB)	100	349 ± 247
Paramphinome jeffreysii (McIntosh)	23	Omnivore	90.9	275 ± 425
Thyasira croulinensis (Jeffreys)	11	Suspension	72.7	151 ± 116
	Maximum score =35			
Group A3				
Thyasira croulinensis (Jeffreys)	19	Suspension	100	198 ± 187
Levinsenia gracilis (Tauber)	13	Deposit (SB)	100	72 ±86
	Maximum score = 30			
Group B				
Retusa truncatula (Bruruiere)	10	Carnivore	100	312 ± 241
Heteromastus filiformis (Claparede)	6	Deposit (SB/SF)	100	94 ±50
	Maximum score = 10			
Group C				
Thyasira equalis (Verril & Bush)	5	Deposit (SB)	100	71
	Maximum score = 5			
Group D				
Amphiura chiajei Forbes	5	Deposit (SF)	50	230 ± 325
Lysilla sp.	5	Deposit (SF)	50	171 ± 241
Retusa truncatula (Bruguiere)	4	Carnivore	100	241 ± 158
	Maximum score = 10			

SB: Subsurface deposit feeder
SF: Surface deposit feeder

Table 2 Top five most abundant species at each station of group E, and their densities (per m2) in each station of this group

Taxon	**Feeding type**	**Density/m²**				
Group E		Stn 774	Stn 736	Stn 745	Stn 743	Stn 748
Thyasira sp. indet.	Other	200	12			
Pholoe sp.	Carnivore	71	35	12	188	
Spiophanes kröyeri Grube	Deposit (SF)	143	47	24	35	
Thyasira croulinensis(Jeffreys)	Suspension	71	94			129
Thyasira equalis (Verril & Bush)	Deposit (SB)/ Suspension	129		12		56
Flabelligera affinis Sars	Deposit (SF)			118		
Myriochele sp.	Deposit (SF)	14	12		12	100
Onuphis conchylega Sars	Omnivore					71
Natica montagui Forbes	Carnivore	14		35	59	29
Retusa truncatula (Bruguiere)	Carnivore	57		35	12	
Nephtys incisa Malmgren	Carnivore	29	47	35	35	

SB: Subsurface deposit feeder
SF: Surface deposit feeder

Over the study area in general, the mean number of individuals was 1919 individuals/m^2 ± 1680 ranging from a minimum of 1 to a maximum of 8765 individuals/m^2 for two stations in the Scanner pockmark. One polychaete species, *Heteromastus filiformis* (3306 individuals/m^2) accounted for the high number of individuals at the latter station. At the Challenger pockmark, the number of individuals ranged from 776 to 3859 individuals/m^2 (station 813), while at the control stations the number of individuals ranged from 718 to 3229 individuals/m^2.

The wet weight biomass for the study area varied from 0.83 g m^{-2} (Scanner sample 745) to 61.75 g m^{-2} (Challenger sample, 813). The mean weight for the Scanner pockmark samples was 8.82 ± 11.78 g m^{-2}(n=18) and for the control stations it was 6.87g ± 4.04 g (range 1.13 to 15.54 g m^{-2}, n=12). Although there was no significant difference in overall mean values, the highest and lowest biomass values occurred in samples collected from the highly variable environments in the base of the pockmarks.

Over the total study area, the greatest variability in diversity values, as calculated by the Hurlbert equation (Hurlbert, 1971), was found among those stations located in, or near, the base of the Scanner pockmark. The diversity values, expressed as the expected number of species for 50 individuals, ranged from 10.6 species at station 773 to 27.9 species at station 775.

The sediment chemistry of both the control stations and those within the pockmarks were on the whole similar. The exceptions to this occurred at two cores taken at the base of the Scanner pockmark and also a scoop sediment sample taken from there by the submersible. High methane values were recorded from these pockmark stations and very high sulphate reduction rates were also recorded in the case of the scoop sample. From observations made from the seeps in the gas-charged sediments of the Skagerrak, it appears that chemical changes in the sediment as a result of seepage are very localised (Dando, et al., 1994) and hence fauna depending on chemosynthetic bacteria for their nutrition are equally localised. It therefore appears that the observed distribution of the infauna at the base of the pockmark, with the exception of *Thyasira sarsi* and *Astononema southwardorum,* is more strongly limited by the scarcity of suitable substrate rather than by the physical disturbance by gas vents or the resultant chemical conditions. A similar conclusion was reached in a study of the biota at shallow methane seeps in the Kattegat (Dando, et al., 1994). The infauna of the sites chosen as controls and of some of the pockmark stations was dominated by four species, *Levinsenia gracilis*, *Heteromastus filiformis*, *Paramphinome jeffreysii* and *Thyasira croulinensis*, although at the base of the pockmark the infauna was highly variable. The effect of gassing on the sediment geochemistry is very localised and the observation that the infauna of the area was severely limited in its distribution within the pockmark is probably due to the lack of substrate rather than to the geochemical conditions.

The foraminifera from the *Challenger* cruise 70 samples from the Scanner and Challenger pockmarks were described by Jones (Jones, 1993; Jones, 1996). The distribution of the benthic foraminifera within the pockmark was statistically distinguishable from those in that surrounding sediment. As with the macro-infauna a lot of the differences could be accounted for by the presence of hard ground in the base of the pockmark, resulting in higher relative abundances of epifaunal and surficial as opposed to infaunal types. The pockmark samples had a lower abundance and diversity of foraminifera compared to the controls. Higher relative abundances of the species *Uvigerina angulosa, Cassidulina laevigata, Hyalina balthica* and *Elphidium* ex. gr. *clavatum* were found in the pockmark samples (Jones, 1993).

2.2.3 Epifauna

Pockmarks with bioherms and/or carbonate cementation are conspicuous by the large number of epifaunal species found compared with the surrounding soft-bottom sediments (Hovland & Thomsen, 1989). It was found at the spectacular “Bubbling Reef” methane seeps in the Kattegat that the difference is largely due to the presence of a fouling fauna which, in the absence of man-made structures or ice-rafted boulders, do not occur elsewhere on soft-bottomed sediments (Jensen, et al., 1992). Hard grounds around natural seepage areas may well be a source of propagules for the colonisation of industry structures such as pipelines and rigs. Historic records of epifaunal density are sparse and we are therefore unable to ascertain the effect of debris, wrecks and offshore structures on the distribution of epifauna across the North Sea.

In the UK sector our knowledge of the epifauna in pockmarks is largely confined to the Jago observations within the Scanner pockmark. Most conspicuous were the Anthozoa including *Pennatula phosphorea, Virgularia mirabilis, Cerianthus lloydii* and the sea anemones *Bolocera tuediae, Urticina felina* and *Metridium senile*. Among other species the whelk, *Buccinium undatum*, and an egg mass were observed, hermit crabs. *Pagurus* sp. were present and large echinoderms, *Astropecten irregularis*, were seen. Most of these species are known from this area of the North Sea at low densities (Basford, Eleftheriou & Raffelli, 1989). Video tapes of the bottom show conspicuous differences in the density of such infauna in the bases of the pockmarks compared with their sides and the surrounding seafloor, where such epi-fauna is only occasionally seen unless projecting structures, such as pipelines, are present. The major feature of the Scanner pockmark was the conspicuously high densities of Anthozoa, a situation also found in the Norwegian pockmarks (Hovland & Thomsen, 1989).

The observed gas flow rates from individual seeps were insufficient to keep the gravel pockets in the base of the pockmark free of sediment. It is probable that periodic explosive releases of gas from the base of the pockmark keep the exposed areas free of sediment. Winnowing of the displaced sediment in the water column removes the fine particles, also allowing the fish otoliths to fall back into the depression. The carbonate rocks in the pockmark base were covered with sediment to sufficient depth to allow *Nephrops norvegicus* to form burrows in the sedimentary pile. Episodic release may be a major factor in determining methane loss from sub-bottom reservoirs and in maintaining the exposed lag deposit at the base of the pockmark, which in turn determines the small-scale differences in the fauna.

2.2.4 Fish

Pockmarks frequently contain unusual densities of fish (Hovland & Judd, 1988; Hovland & Thomsen, 1989). The high density of fish otoliths observed in one North Sea pockmark, 1550 m^{-2} (Dando, et al., 1991), could be taken as evidence for long-term evidence of fish accumulation and death in the crater (Judd, et al., 1994). A more extensive survey among the Challenger cruise 70 and cruise 82 samples revealed densities up to 42,188 m^{-2} in the bottom of the pockmarks, with a maximum of 82 otoliths m^{-2} being found in the surrounding bottom sediment (Figure 4). The otoliths mainly belonged to cod, *Gadus morhua*. Analysis of videos taken during the Jago submersible dive in the pockmark in UK sector 15/25 showed that only a few small demersal fish were present on the seafloor outside the pockmark. In the base of the crater shoals of large cod and ling, *Molva molva*, were present, together with occasional Norway Haddock, *Sebastes viviparus*, and wolf-fish, *Anarhychus lupus*. The latter species was observed under rock overhangs in the base of the pockmarks (*Jago* observations and Hovland & Judd, 1988). Two hagfish, *Myxine glutinosa*, were observed, one was burrowing into mud in the bottom of the pockmark. One dying cod was observed, an unusual occurrence but an illustration of how the otolith accumulations may have arisen. The otoliths were so dense in the base of the pockmark that some polychaete worms had formed their tubes out of fish otoliths instead of the usual sand grains.

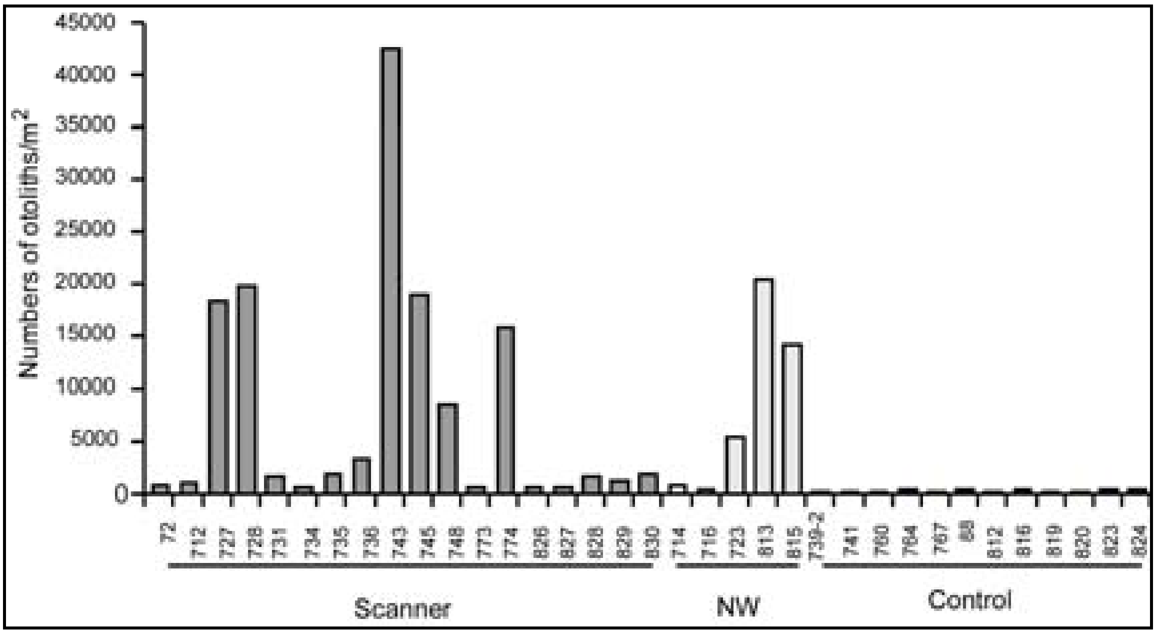

Figure 4 Numbers of fish otoliths m^{-2} present in the macrofaunal samples from cruises CH70 and CH82

Comparative video transects through pockmarks are lacking and need to be undertaken to quantify the effect of pockmarks in 'attracting' fish. Similarly it is not known whether individual pockmarks are inhabited long-term by a sub-set set of the fish population , i.e. do the pockmarks form a part of a small home range of individual fish or do many fish occupy them for a few days each.

A list of the fish species observed in North Sea pockmarks is given in Table 3. Large cod concentrations were also observed in large pockmarks in the Barents Sea (Linke & Dando, 1994)

Table 3 Fish species found in North Sea Pockmarks

Species	Location	Reference
Myxine glutinosa (hagfish)	Scanner (UK 15/25)	*Jago* observations
Gadus morhua (cod)	Scanner (UK 15/25) Holene (N 24/9)	*Jago* observations (Hovland & Judd, 1988)
Molva molva (ling)	Gullfaks (N 34/10) Holene (N 24/9) Scanner (UK 15/25)	(Hovland & Thomsen, 1989) (Hovland & Thomsen, 1989) *Jago* observations
Brosme brosme (torsk)	Gullfaks (N 34/10) Holene (N 24/9) N 25/7	(Hovland & |Thomsen, 1989) (Hovland & |Thomsen, 1989) (Hovland & Judd, 1988)
Sebastes viviparus (Norway haddock)	Gullfaks (N 34/10) Scanner(UK 15/25)	(Hovland & Thomsen, 1989) *Jago* observations
Anarhychus lupus	Scanner (UK 15/25) Holene (N 24/9)	*Jago* observations (Hovland & Thomsen, 1989)

Surrounding the pockmarks the common fish species may change. Haddock (*Melanogrammus aeglefinus*) were seen both around the pockmarks in Norwegian block 25/7 in ROV surveys (Hovland & Judd, 1988) and were caught in trawls around the Challenger pockmark (Dando, et al., 1991), although none have been observed sheltering within a pockmark. Other fish caught around the Challenger pockmark were hagfish (*Myxine glutinosa*), rockling (*Rhinonema cimbrius*), Norway haddock (*Sebastes viviparus*) and rough dab (*Hippoglossoides platessoides*), while Argentines (*Argentina silus*) were observed around the N block 25/7 pockmarks. Only Norway haddock and the hagfish were common to both data sets. One of the reasons for this is that smaller species within the pockmarks would be liable to be eaten by the large gadoids

Although Hovland *et al*. (Hovland, Judd & Masey, 1985 ; Hovland & Judd, 1988 ; Hovland & Thomsen, 1989) have argued that the abundance of fish in pockmarks is related to seepage and an increased productivity due to chemosynthesis there is little evidence to support the hypothesis. The fauna within the pockmarks is not sufficient to support the high density of fish observed and grab and box-corer sampling showed no evidence of increased infaunal biomass within a large pockmark in UK block 15/25 (Dando, et al., 1991). Stable isotope studies also gave no indication for carbon input through the food chain based on production by sulphur-oxidising or methane-oxidising bacteria. Since the methane released in the pockmark had a biogenic signature, with a $\delta^{13}C$ of $\leq$ -70‰ (C. J. Clayton, personal communication), a small input of methane carbon into the food chain should have been easily detectable. Even around a very active methane seep on the continental shelf only a very minor contribution from chemosynthesis to the food web could be detected (Juhl & Taghon, 1993).

Fish are attracted to artificial structures placed on the seabed which are similar to carbonate rocks, for example concrete hemispheres 1.3 m in diameter by 1 m high were shown to attract a variety of demersal fish species (Sherman, Gilliam & Spieler, 1999). The presence of holes in an artificial reef provide a further attraction to fish (Kellison & Sedberry, 1998). It is most likely that fish are using the pockmarks for shelter, leaving the pockmarks to forage for food. Ling, *Molva molva*, have been observed to lie in even small depressions (Hovland & Thomsen, 1989) and several species of fish are known to shelter alongside pipelines and wrecks in the North Sea. The pockmarks are probably marked as foul ground on fishing charts since trawl nets were observed on the rocks of the carbonate-cemented sediment within the pockmark base.

2.3 General comments on the biology of seeps

Pockmarks are but one physical manifestation of fluid seepage through the seafloor (Dando & Hovland, 1992). Only where the sediments are sufficiently soft and the fluid discharge sufficiently forceful are pockmarks likely to arise. Since the biological characteristics of other seepage areas may also apply to active pockmarks some comments on them are given in this section.

Pockmarks are not present, for example, at the active methane seeps on the Danish coast off Fredrikshavn in the Kattegat (Jensen et al., 1992) where subsurface carbonate cementation was later eroded to provide a reef-type landscape. The reefs are spectacular, since they occur, like most North Sea pockmarks, in areas of otherwise soft bottom where fouling type fauna are rare. The fauna living both on and within the carbonate-cemented sandstone around the gas seeps was not unique to the Danish coast and did not derive significant parts of their nutrition from chemoautotrophic bacteria. Similar active seeps with exposed reefs of carbonate-cemented sandstone are found in the low intertidal zone south of Frederikshavn, where the gas is ancient methane originating from interglacial deposits (Dando, et al., 1994). Sediment infauna was reduced, due to the shallow depth of soft sediment over cemented sediment, and there was no evidence for significant input of methane carbon into either filter-feeding mussels, *Mytilus edulis*, living directly of top of the gas outlets or into crabs, *Carcinus maenus*, at the same site (Dando, et al., 1994).

Deep water (>500 m water depth) cold seep sites are extremely productive, as productive as deep sea hydrothermal vents in many cases (Sibuet & Olu, 1998). The causes of the switch-over from ‘normal’ background fauna at shallow seeps to specialist endemic species at deep cold seeps is still controversial. Factors involved are the higher pressures, and hence greater gas solubilities, at deep sites and more predatory fauna at shallow sites. It is also uncertain at what depths this change in ecological relationships occurs. In the Skagerrak a gutless pogonophoran worm, endemic to methane seeps lives through symbiosis with methane-oxidising bacteria at 300 m water depth (Dando et al. 1994b). At these sites it is found together with *Thyasira sarsi*, which is also confined to seep situations in the Skagerrak. However, *T. sarsi* also occurs in organic rich sediments in fjords and cannot therefore be regarded as endemic to seeps. It is therefore likely that no pockmark endemic fauna may exist in the North Sea, although the status of *Astononema southwardorum* is uncertain.

3. CONCLUSIONS

Shallow inactive pockmarks, without hard grounds, in the UK sector of the North are unlikely to have a fauna that differs in species composition from that of the surrounding sediment. However, this needs to be confirmed by biological sampling. In deeper basins, with fine-grained sediment, the faunal composition, in terms of the dominance of feeding guilds, may differ from that of the surrounding sediment if the pockmark topography is such that it acts as a sediment trap.

Inactive pockmarks may be used by fish, especially ling, for shelter. Seabed structures, including oil pipelines, are commonly used by a variety of fish species in this way.

Shallow active pockmarks may differ in faunal composition from the surroundings and from each other, depending on the degree, and the effects, of the seepage. Any found in the North Sea should be studied biologically.

Deep pockmarks with cemented sediment in their base provide both a refuge for fish, especially large gadoids such as cod, torsk and ling, and as a site for colonisation by hard-bottom epifauna such as anthozoa spp. Such epifauna is much less common in the sedimentary basins where such pockmarks are found.

Deep active pockmarks, such as the three studied in UK block 15/25, additionally contain species dependent on high sulphide concentrations, originating from seepage or enhanced sedimentation. The bivalve species *Thyasira sars*i and *Lucinoma borealis* are not found elsewhere in the open North Sea, with the exception of recent colonisation of *T. sarsi* around some oil platforms. Natural scattered habitats such as seeping pockmarks are almost certainly responsible for the dispersal of species like these to man-modified habitats where they can play an important role in re-oxygenation of sediments (Dando & Spiro, 1993). Seeping pockmarks are likely to contain potentially interesting bacterial associations which have been little studied but which could have industrial potential for bioremediation.

The Scanner pockmark in UK block 15/25 is unique in that it is the only known habitat of the gutless nematode *Astononema southwardorum.* Further novel species may be discovered with more detailed investigations.

It is suggested that consideration be given to designating the best examples of seeping pockmarks, as Special Areas of Conservation (SACs), because of their biological interest, as well as for their roles as fish refugia and dispersal centres for otherwise less common species in the central North Sea.

Further research is required into the rates of seepage in active pockmarks, their episodicity and the effect of this on the biota.

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