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Christoffer Schander^{ab}; Hans Tore Rapp^{ab}; Jon Anders Kongsrud^c; Torkild Bakken^d; Jørgen Berge^e; Sabine Cochrane^f; Eivind Oug^g; Ingvar Byrkjedal^c; Christiane Todt^b; Tomas Cedhagen^h; Audun Fosshagen^b; Andrey Gebrukⁱ; Kim Larsen^j; Lisa Levin^k; Matthias Obst^l; Fredrik Pleijel^m; Sabine Stöhrⁿ; Anders Warén^o; Nina Therese Mikkelsen^{bc}; Silje Hadler-Jacobsen^b; Rozemarijn Keuning^b; Kristin Heggøy Petersen^b; Ingunn H. Thorseth^{ao}; Rolf B. Pedersen^{ao}

^a Centre for Geobiology, University of Bergen, Bergen, Norway ^b Department of Biology, University of Bergen, Bergen, Norway ^c University of Bergen, Bergen, Norway ^d Museum of Natural History and Archaeology, Norwegian University of Science and Technology (NTNU), Trondheim, Norway ^e UNIS, The University Centre in Svalbard, Longyearbyen, Norway ^f Akvaplan-niva AS, Tromsø, Norway ^g Norwegian Institute for Water Research (NIVA), Grimstad, Norway ^h Department of Marine Ecology, Institute of Biological Sciences, University of Aarhus, Aarhus, Denmark ⁱ P.P.Shirshov Institute of Oceanology of Russian Academy of Sciences (IORAS), Moscow, Russia ^j Department of Natural History, Kitakyushu Museum of Natural History & Human History, Kitakyushu, Japan ^k Integrative Oceanography Division, Scripps Institution of Oceanography, La Jolla, California, USA ^l Kristineberg Marine Biological Laboratory, Fiskebäckskil, Sweden ^m Tjärnö Marine Biological Laboratory, Strömstad, Sweden ⁿ Department of Invertebrate Zoology, Swedish Museum of Natural History, Stockholm, Sweden ^o Department of Earth Science, University of Bergen, Bergen, Norway

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ORIGINAL ARTICLE

The fauna of hydrothermal vents on the Mohn Ridge (North Atlantic)

CHRISTOFFER SCHANDER^{1,2*}, HANS TORE RAPP^{1,2}, JON ANDERS KONGSRUD³,
TORKILD BAKKEN⁴, JØRGEN BERGE⁵, SABINE COCHRANE⁶, EIVIND OUG⁷,
INGVAR BYRKJEDAL³, CHRISTIANE TODT², TOMAS CEDHAGEN⁸, AUDUN
FOSSHAGEN², ANDREY GEBRUK⁹, KIM LARSEN¹⁰, LISA LEVIN¹¹,
MATTHIAS OBST¹², FREDRIK PLEIJEL¹³, SABINE STÖHR¹⁴, ANDERS WARÉN¹⁴,
NINA THERESE MIKKELSEN^{2,3}, SILJE HADLER-JACOBSEN², ROZEMARIJN
KEUNING², KRISTIN HEGGØY PETERSEN², INGUNN H. THORSETH^{1,15} &
ROLF B. PEDERSEN^{1,15}

¹Centre for Geobiology, University of Bergen, Bergen, Norway; ²Department of Biology, University of Bergen, Bergen, Norway; ³University of Bergen, Bergen, Norway; ⁴Museum of Natural History and Archaeology, Norwegian University of Science and Technology (NTNU), Trondheim, Norway; ⁵UNIS, The University Centre in Svalbard, Longyearbyen, Norway; ⁶Akvaplan-niva AS, 9005 Tromsø, Norway; ⁷Norwegian Institute for Water Research (NIVA), Grimstad Norway; ⁸Department of Marine Ecology, Institute of Biological Sciences, University of Aarhus, Aarhus, Denmark; ⁹P.P. Shirshov Institute of Oceanology of Russian Academy of Sciences (IORAS), Moscow, Russia; ¹⁰Department of Natural History, Kitakyushu Museum of Natural History & Human History, Kitakyushu, Japan; ¹¹Integrative Oceanography Division, Scripps Institution of Oceanography, La Jolla, California, USA; ¹²Kristineberg Marine Biological Laboratory, Fiskebäckskil, Sweden; ¹³Tjärnö Marine Biological Laboratory, Strömstad, Sweden; ¹⁴Department of Invertebrate Zoology, Swedish Museum of Natural History, Stockholm, Sweden; ¹⁵Department of Earth Science, University of Bergen, Bergen, Norway

Abstract

The macrofauna of the newly discovered hydrothermal vent field on the Mohn Ridge at 71°N was investigated. Samples were collected during the cruise BIODEEP 2006 using the ROV 'Bathysaurus'. A total of 180 species-level taxa were identified. The region contains very few vent-endemic species, but some species of Porifera, Crustacea and Mollusca may be vent-associated. Dense aggregations of motile non-vent species such as *Heliogeton glacialis* and *Gorgonocephalus eucnemis* surrounded the vent area, but the area in general only held small numbers of sedentary animals. Calcareous sponges comprised an unusually high portion of the sponge species found and they constitute one of the first pioneers among the sessile invertebrates settling on these vents. Possible explanations for the structure of the fauna in the region are discussed.

Key words: Arctic fauna, bacterial mats, Beggiatoa, hydrothermal vents, Mohn Ridge, vent fauna, white smoker

Introduction

Deep-sea hydrothermal vents are usually associated with a highly specialized fauna and since their discovery in 1977 more than 400 species of animals have been described (Van Dover et al. 2002; Desbruyères et al. 2006). A specialized vent fauna includes most animal phyla, but the most conspicuous and well known are annelids, molluscs and

crustaceans. All previously investigated vent regions have had some specific fauna unique to them, and vent communities are usually distinct from the surrounding waters. Only a few species inhabit both vent and non-vent areas. Some vent fauna can also be found associated with hydrocarbon seeps and whale and wood falls (e.g. Black et al. 1997; Feldman et al. 2001; Smith & Baco 2003; Levin & Mendoza 2007).

*Correspondence: Christoffer Schander, University of Bergen, Biology, P.O. Box 7800, Bergen, 5020 Norway. E-mail: Christoffer.Schander@bio.uib.no

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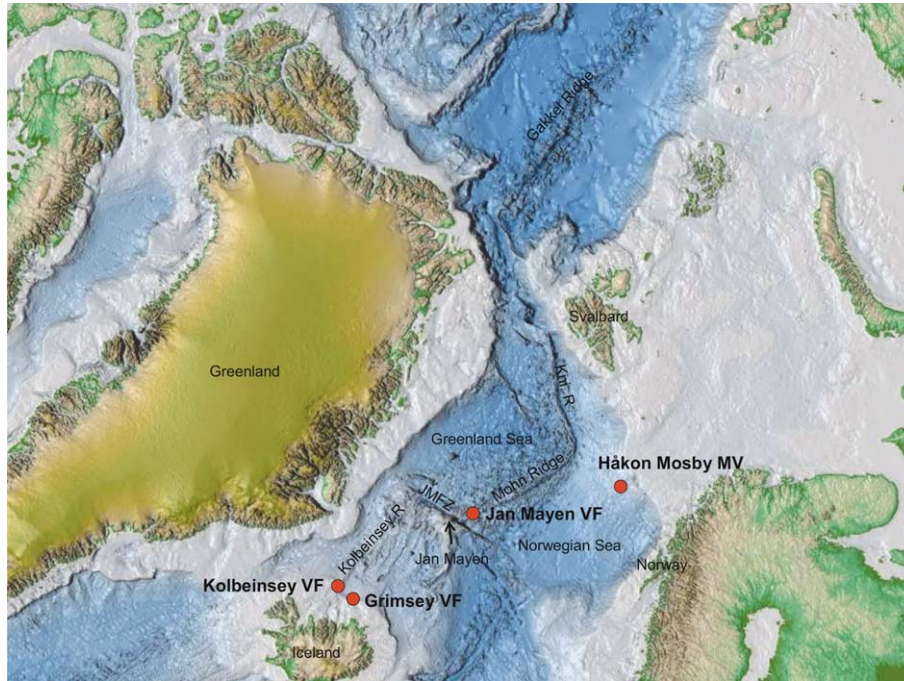


Figure 1. Location of the hydrothermal vents on the Mohn Ridge.

We have investigated the fauna collected around newly discovered hydrothermal vents on the Mohn Ridge north of Jan Mayen (Figures 1 and 2).

The vent fields are located at 71°N and the venting takes place within two main areas separated by 5 km (Pedersen et al. 2005). The shallowest vent area is at 500–550 m water depth and is located at the base of a normal fault. This vent field stretches approximately 1 km along the strike of the fault, and is composed of 10–20 vent sites each with multiple chimney constructions discharging up to 260°C hot fluids. A large area of diffuse, low-temperature venting surrounds the high-temperature field (Pedersen et al. 2005; Pedersen et al. in press). Here, partly microbially mediated iron oxide-hydroxide deposits occur in abundance (Thorseth et al. 2005, 2007; Øvreås et al. 2007; Schander et al. 2007; Steinsbu et al. 2007).

The second area is located at a rifted volcanic ridge at 700–750 m depth, where venting takes place at two fields, each ~100–200 m across. At both fields white smoker fluids with temperatures up to 260–270°C discharge from numerous chimneys, whereas lower temperature fluids slowly emanate from up to 10 m tall, irregular sulphate and sulphide formations (Pedersen et al. 2005, Pedersen et al. in press) (Figure 2).

The vent fluids have up to 6 mmol/kg H₂S (Pedersen et al. 2007) and both vent sites host a rich flora of sulphide and methane oxidizing bacteria (Øvreås et al. 2007; Steinsbu et al. 2007).

The only other vent area north of Iceland previously investigated is the very shallow Kolbeinsey

field (Fricke et al. 1989). The Kolbeinsey field was discovered in 1974 a few kilometres south of the volcanic island of Kolbeinsey off North Iceland. Two venting areas are located at approximately 90 m water depth (Olafsson et al. 1989). The vent area was first visited and sampled in 1988 when venting was documented from fissures, small chimneys, and large, crater-like dips in the volcanic seafloor. The highest temperature of fissure effluents was ~89°C (Fricke et al. 1989). The hydrothermal fluids were either crystal clear or very turbid, loaded with large pieces of bacterial mats. There were no significant amounts of hydrothermal deposits at the vent sites, but the venting areas were distinguished from the non-vent bottom by their whitish overgrowth of thick, filamentous mats of *Beggiatoaceae* (Fricke et al. 1989). The macrofauna at Kolbeinsey was dominated by the sponges *Sycon quadrangulatum* and *Tethya aurantium* (Fricke et al. 1989). Shallow vents are also known from the Grimsey region north of Iceland (Hannington et al. 2001), but the fauna of the Grimsey vent field has not been investigated yet. Venting has also been reported from the Gakkel Ridge, but no specialized vent fauna have been recorded (Ramirez-Llodra et al. 2007), while the fauna from the hydrocarbon seeps of the Hakon Mosby Mud Volcano was described by Gebruk et al. (2003).

This study aims to present the first comprehensive investigation on fauna found at high- and low-temperature shallow hydrothermal vents in the northernmost Atlantic Ocean.

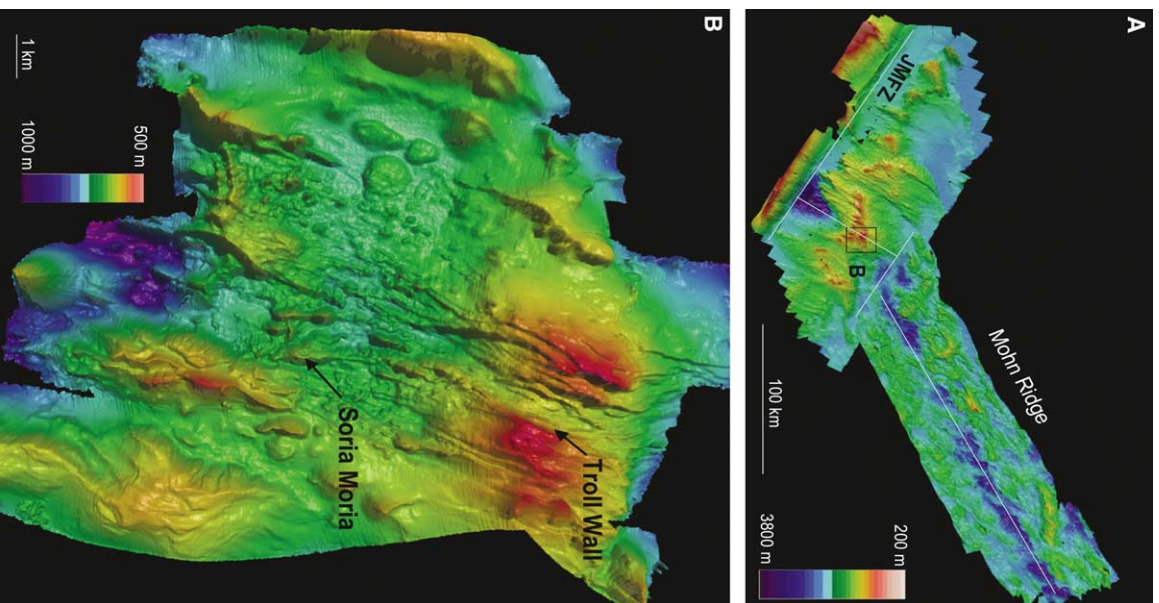


Figure 2. A. Location of the two major vent sites at the southernmost segment of the Mohn Ridge. B. Detail showing the Soria Moria and Troll Wall vent sites.

Materials and methods

Material was collected during the cruise BIODEEP 2006 around the vent sites in June 2006 using the ROV ‘Bathysaurus’ equipped with a horizontal boxcorer (to be described elsewhere) and a suction sampler with a single collection container. Material was obtained in the direct vicinity of the vents and at the actual venting sites (Figures 1 and 2). A list of the sampling stations is found in Table I. Also, observations from video and still photos are included. Due to the sampling gear employed and since the samples were split to be used also for microbiological and geological analyses, the samples must be regarded as purely qualitative.

Table I. Dive and sampling locations during the 2006 cruise.

Dive NO	Location (start G.O. Sars)	Location samples	Depth (m)	Sampling/substrate	Comments
01	71°17.893N–5°47.048W	71°17.99N–5°46.82W	616	Horizontal box chore – Fe mound	‘Gallionella Garden’ low-temperature hydrothermal vent field
03	71°15.578N–5°48.974W	71°15.55N–5°48.86W 71°15.55N–5°48.85W	711–713	Suction sampler – sediment	High-temperature vent field ‘Soria Moria II’, located southeast of the vent field ‘Soria Moria I’. Only a couple of m from the chimneys Lilleputt/Storestå
04	71°15.547N–5°48.936W	71°15.56N–5°48.88W	711	Horizontal box chore – white bacterial mat	High-temperature vent field ‘Soria Moria II’, located southeast of the vent field ‘Soria Moria I’. Only a couple of m from the chimneys Lilleputt/Storestå
07	71°17.992N–5°46.824W	71°17.99N–5°46.8W	616	Horizontal box chore – sediment	‘Gallionella Garden’ low-temperature hydrothermal vent field
09	71°17.875N–5°46.322W	71°17.869N– 5°46.29W	556	White bacterial mat and sediment	‘Trollveggen’ high-temperature venting area east of Gallionella Garden low-temperature area
11	71°17.988N–5°46.839W	71°17.99N–5°46.8W	616	Suction sampler	‘Gallionella Garden’ low-temperature hydrothermal vent field
12	71°17.990N–5°46.845W	71°17.98N–5°46.92W	616	Horizontal box chore – sediment	‘Gallionella Garden’ low-temperature hydrothermal vent field
13	71°15.687N–5°48.812W	71°15.59N–5°48.82W	667	+	Soria Moria I – Sfinxen. Part of dead smoker covered with bacterial mats
16	71°17.878N–5°46.331W	71°17.86N–5°46.29W	557	Suction sampler – on smoker	‘Trollveggen’ high-temperature venting area east of Gallionella Garden low-temperature area. Sample from active smoker
18	71°15.535N–5°48.870W	71°15.54N–5°48.86W 71°15.59N–5°48.87W	724	Suction sampler – sediment	High-temperature vent field ‘Soria Moria II’, located southeast of the vent field ‘Soria Moria I’. Sample directly on smoker

The samples were sorted on board ship under a stereo-microscope directly after coming up on deck and then fixed in 96% alcohol and/or 5% formaldehyde. Most of the material has been deposited in Bergen Museum, University of Bergen.

Results

General notes about the fauna

A total of 180 taxa have been identified from the two investigated vent fields (Table II). Of these, only a handful of species of sponges, crustaceans and molluscs are potential vent specialists. The absence of large long-living sessile invertebrates (with the exception of actinians, cladorhizid sponges, and the soft coral *Gersemia*, mainly on vertical surfaces at some distance from the vents), even though there does not seem to be any shortage of hard bottom substrate, is noteworthy. Dense aggregations of the motile crinoid *Heliometra glacialis* dominate large areas surrounding the vent fields. *Gorgonocephalus eucnemis* is also very common in the area. *In situ* observations show that anthozoans near to the venting feed on amphipods stunned by hot plumes of water.

Large clouds of planktonic organisms were observed above the vents. Such clouds have also been observed over other venting areas (Wiebe et al. 1988; Thomson et al. 1992; Burd & Thomson 1994, 1995; Burd et al. 2002), but little is known about the trophic interactions. During the cruise in 2006, preliminary studies and sampling of the hydrothermal cloud were carried out using acoustic equipment and MOCNESS trawls. From this material it was concluded that the plankton clouds were comprised mainly of crustaceans, and 18 species were identified (Aarbakke 2007).

The trophic interactions remain to be studied, but few of the species appear to be able to feed directly on bacteria. One of these is the gastropod *Rissoa* cf. *griegi*. It is found in high densities on the bacterial mats covering the chimneys, and is the dominating macroorganism inhabiting this part of the system.

Selected representatives of the fauna are shown in Figure 3 and a list of all identified species is found in Table II.

Foraminifera

The foraminiferans found in the area are well known from many areas of the Northeast Atlantic region. Some of the species, for example *Tholosina* spp., *Cibicides* spp. and *Rupertia stabilis*, are firmly attached or cemented to the substrate. Other species such as *Miliolinella* cf. *enoplostoma* and *Rosalina globularis* are loosely attached. None of the species here reported can be classified as typical vent fauna

or are known to host any symbiotic microorganisms. A previously undescribed monothalamous foraminiferan (Allogromiidae) is recorded here, but this is not surprising since these foraminifera are poorly known in this region (Gooday et al. 2005).

Porifera

The sponge fauna found in the vent area is characterized by very small sponges of the classes Demospongiae and Calcarea. The fauna is dominated by species also found outside the area of hydrothermal activity. However, the three cladorhizid sponges *Asbestopluma pennatula*, Cladorhizidae sp. 1 and Cladorhizidae sp. 2 were found in a high-temperature venting area directly associated with smokers. They are also found on substrates completely covered by dense bacterial mats. Some cladorhizid sponges are known to harbour symbiotic methane-oxidizing bacteria and to utilize the enriched water surrounding the vents (Vacelet et al. 1996; Vacelet & Boury-Esnault 2002). In addition, these sponges are carnivorous, feeding on the highly abundant small crustaceans in the vent area (Vacelet & Duport 2004; Vacelet 2006). Calcareous sponges have not previously been reported from high-temperature vents, but *Sycon quadrangulatum* was reported to be the dominant macroorganism on shallower and colder seeps on the Jan Mayen Ridge (Fricke et al. 1989). Calcareous sponges normally represent only a minor fraction of the sponge fauna and it was therefore surprising that 8 out of a total of 13 species reported here are calcareans. They mainly represent species well-known from bathyal and abyssal depths in the Nordic Seas (Janussen et al. 2003; Rapp 2006; Rapp unpublished data). Calcareous sponges of the genus *Guancha* are found on bare surfaces and seem to be among the first invertebrates settling in this harsh environment. The same species are also in number dominating among the very scarce fauna found on recently formed pillow lavas in deep waters along the Mohn and Knipovich Ridges, indicating that calcareous sponges may be pioneers also in deep waters (Rapp unpublished data).

Some thinly encrusting sponges (probably Hymedesmidae) were observed at some distance from the smokers, but no larger erect or massive demosponges or hexactinellids characteristic of rocky bottoms in this part of the north Atlantic were found.

Cnidaria

The hydroid *Corymorpha groenlandica* was mainly found scattered around the base of the chimneys. However, some specimens were also found directly

Table II. Fauna found at the hydrothermal vents on the Mohn Ridge. Taxa identified from the Kolbeinsey shallow vents (Fricke et al. 1989) and the Håkon Mosby mud volcano (Gebruk et al. 2003) are included for comparison. Numbers 1–18 refer to station data found in Table I.

	Video	1	3	4	7	9	11	12	13	16	18	Kolbeinsey	Håkon Mosby
FORAMINIFERA													
<i>Anomalina balthica</i> (Schröter, 1783)							+						
<i>Cibicides lobatulus</i> (Walker & Jacob, 1798)							+	+					
<i>Cibicides cf. lobatulus</i> (Walker & Jacob, 1798)							+						
<i>Cibicides refulgens</i> Montfort, 1808							+	+					
<i>Hanzawaia</i> sp.							+						
<i>Miliolinella cf. enoplostoma</i> (Reuss, 1851)								+					
<i>Rosalina globularis</i> d'Orbigny, 1826							+						
<i>Rupertia stabilis</i> Wallich, 1877								+					
<i>Sagenina</i> sp. ?								+					
<i>Tholosina vesicularis</i> (Brady, 1879)							+	+					
<i>Tholosina</i> sp.								+					
Allogromiidae sp. nov.					+								
PORIFERA													
<i>Artemisina arcigera</i> (Schmidt, 1870)								+					
<i>Asbestopluma pennatula</i> (Schmidt, 1875)	+										+		
Baeridae indet.								+					
<i>Breitfussia</i> sp.								+					
Cladorhizidae sp. 1	+							+			+		
Cladorhizidae sp. 2	+				+			+			+		
<i>Guancha</i> sp. nov.								+					
<i>Guancha pellucida</i> Rapp, 2006								+					
Hymedesmiidae indet.							+						
<i>Leucandra</i> sp. 1								+			+		
<i>Leucandra</i> sp. 2								+			+		
<i>Leucandra</i> sp. 3					+								
<i>Sycon quadrangulatum</i> (Schmidt, 1868)												+	
<i>Sycon abyssale</i> Borojevic & Graat-Kleeton, 1965					+								
<i>Tethya aurantium</i> (Pallas, 1766)													+
CNIDARIA													
<i>Corymorpha groenlandica</i> (Allman, 1876)	+												+
<i>Gersemia rubiformis</i> (Ehrenberg, 1834)	+						+	+					
<i>Hormathia</i> sp.	+										+		
<i>Urticina felina</i> (Linnaeus, 1761)													+
<i>Umbellula ecrinus</i> Linnaeus, 1758	+												
BRYOZOA													
<i>Celleporina</i> sp.								+					
<i>Crisia</i> sp.								+					
<i>Disporella hispida</i> (Fleming, 1828)								+					
<i>Hemicyclopora microstoma</i> (Norman, 1864)							+						

Table II (Continued)

	Video	1	3	4	7	9	11	12	13	16	18	Kolbeinsey	Håkon Mosby
<i>Hornea lichenoides</i> (Linnaeus, 1758)					+			+					
<i>Palmiskenea skenei</i> (Ellis & Solander, 1786)								+					
<i>Smittoidea reticulata</i> (MacGillivray, 1842)								+					
<i>Stomatopora</i> sp. ?							+						
Unidentified cheliostome								+					
Unidentified bryozoan								+					
NEMERTEA													
<i>Procephalotrix</i> aff. <i>spiralis</i> (Coe, 1930)												+	
<i>Micrura</i> aff. <i>varicolor</i> Punnett, 1903												+	
Nemertea indet.										+			
ANNELIDA: Polychaeta													
<i>Abyssoninoe</i> cf. <i>scopa</i> (Fauchald, 1974)								+					
<i>Ampharete</i> sp.											+		
Amphinomidae indet.													+
Amphitritinae indet. juv.											+		
<i>Baldia johnstoni</i> Garwood & Bamber, 1988					+								
<i>Brada villosa</i> (Rathke, 1843)								+					
<i>Brada</i> sp.													+
<i>Capitella capitata</i> (Fabricius, 1780)												+	
<i>Capitella</i> sp.			+	+	+			+	+				
Capitellidae indet.													+
<i>Chaetozone</i> cf. <i>jubata</i> Chambers & Woodham, 2003					+			+					
<i>Chaetozone</i> sp.					+			+					
<i>Chone paucibranchiata</i> (Krøyer, 1856)											+		
<i>Chone</i> sp.								+		+			
Chaetopteridae indet.					+								
<i>Diplocirrus longisetosus</i> (Marenzeller, 1890)					+			+					
<i>Eclysippe</i> sp.											+		
<i>Ephesiella abyssorum</i> (Hansen, 1879)					+			+					
<i>Euchone papillosa</i> (M. Sars, 1851)					+								
<i>Euchone</i> ('Chiade') indet.								+			+		
<i>Euphrosine</i> sp.								+					
<i>Galathowenia oculata</i> (Zachs, 1923)					+								+
<i>Glyphanostomum pallescens</i> (Théel, 1879)									+				+
<i>Grubianella klugei</i> (Pergament & Chlebovitch in Chlebovitch, 1964)													+
<i>Harmothoe fragilis</i> Moore, 1910											+		
<i>Lanassa nordenskiöldi</i> Malmgren, 1866								+					
Lacydoniidae indet.				+									
<i>Laonice cirrata</i> (M. Sars, 1851)								+					
<i>Leaena ebranchiata</i> (M. Sars, 1865)								+					
<i>Lumbrineris</i> sp.												+	+
<i>Macrochaeta polyonyx</i> Eliason, 1962					+								
<i>Macroclymene</i> sp. A					+			+			+		

Table II (Continued)

	Video	1	3	4	7	9	11	12	13	16	18	Kolbeinsey	Håkon Mosby
<i>Melythasides laubieri</i> (Desbruyères, 1978)								+			+		+
<i>Myriochele heeri</i> Malmgren, 1867													+
<i>Myriochele olgae</i> Blake in Blake, Hilbig & Scott, 2000								+					
<i>Nereimyra punctata</i> (O.F. Müller, 1776)												+	
<i>Nerilla</i> sp.												+	
<i>Nicomache quadrispinata</i> Arwidsson, 1907					+			+					
<i>Nothria conchylega</i> (M. Sars, 1835)					+			+			+		
<i>Notomastus latericeus</i> M. Sars, 1851					+			+					
<i>Notoproctus oculatus arctica</i> Arwidsson, 1907					+			+			+		
<i>Oligobrachia haakonmosbiensis</i> Smirnov, 2000													+
<i>Ophelia</i> sp.													+
<i>Ophelina</i> sp.					+			+			+		
Orbiniidae indet.													+
Oweniidae indet. (fragment)											+		
<i>Petaloproctus tenuis</i> (Théel, 1879)					+			+					
<i>Pterocirrus slastnikovi</i> Annenkova, 1946									+				
<i>Pholoe assimilis</i> (Ørsted, 1844)					+			+					
<i>Polycirrus medusa</i> Grube, 1850			+							+	+		
<i>Polycirrus</i> sp.								+					
Polynoidae indet.													+
<i>Praxillura longissima</i> Arwidsson, 1907					+								+
<i>Prionospio cirrifera</i> Wirén, 1883								+			+		
<i>Prionospio</i> (not <i>cirrifera</i>) sp.					+								
<i>Proclea graffi</i> (Langerhans, 1884)								+			+		
<i>Pseudoscalibregma parvum</i> (Hansen, 1879)					+			+					
<i>Scolelepis foliosa</i> (Audouin & Milne-Edwards, 1833)					+								
<i>Scoletoma</i> sp.					+			+			+		
<i>Sclerolinum contortum</i> Smirnov, 2000													+
Serpulidae indet.													+
<i>Sphaerodoropsis philippi</i> (Fauvel, 1911)					+						+		
Spionidae indet.													+
<i>Spiophanes kroyeri</i> Grube, 1860					+								
<i>Spiochaetopterus typicus</i> M. Sars, 1856													+
Spirorbidae indet.												+	
Syllidae indet. epitok								+					
<i>Thelepus cincinmatus</i> (O. Fabricius, 1780)											+		+
Terebellidae indet.			+		+								
<i>Terebellides</i> sp.								+					
Trichobranchidae indet.								+					
SIPUNCULIDA													
<i>Ochmesoma</i> sp.													+
MOLLUSCA													
<i>Alvania</i> sp. 1													+

Table II (Continued)

	Video	1	3	4	7	9	11	12	13	16	18	Kolbeinsey	Håkon Mosby
<i>Alexandromenia</i> sp.								+					
<i>Anatoma crispata</i> (Fleming, 1828)								+		+			
<i>Astarte acuticostata</i> Friele, 1877					+								
<i>Bathyarca</i> sp.					+								
<i>Bathyarca frielei</i> (Friele, 1877)					+								
<i>Buccinum</i> sp.			+										
<i>Cuspidaria glacialis</i> (G.O. Sars, 1878)													+
<i>Cyclopecten imbrifer</i> (Lovén, 1846)								+					
<i>Dacrydium</i> sp.													+
Diaphanidae indet.					+			+					
<i>Heteronomia squamula</i> (Linnaeus, 1758)												+	
<i>Limacina retroversa</i> (Fleming, 1823)				+				+					
<i>Limatula hyperborea</i> Jensen, 1905								+					
<i>Lionsiella abyssicola</i> G.O. Sars, 1878													+
<i>Mohnia mohni</i> (Friele, 1877)													+
<i>Oenopota</i> sp.				+									
<i>Onoba semicostata</i> (Montagu, 1803)			+										
<i>Thyasira (Parathyasira) dunbari</i> Lubinsky, 1976													+
<i>Thyasira</i> sp.								+					+
<i>Rissoa</i> cf. <i>griegi</i> Friele, 1879			+				+		+	+	+		
<i>Rugulina fragilis</i> (G.O. Sars, 1878)								+					
<i>Simrothiella margaritacea</i> (Koren & Danielssen, 1877)								+					
<i>Skenea</i> sp. juv.			+										
<i>Skenea basistriata</i> (Jeffreys, 1877)										+			+
<i>Toledonia limmaeoides</i> (Odhner, 1913)										+			
<i>Velutina undata</i> J. Smith, 1839								+					
<i>Yoldiella propinqua</i> (Leche, 1878)													+
CRUSTACEA: Amphipoda													
<i>Amphilocheopsis hamatus</i> Stephensen, 1925					+								
<i>Amphilocheus</i> sp.								+					
Amphipoda indet.				+									
<i>Amphitoe</i> sp.			+										
<i>Amphitoe</i> cf. <i>rubricata</i> Montagu, 1808								+					
<i>Andaniexis lupus</i> Berge & Vader, 1997								+					
<i>Anonyx nugax</i> (Phipps, 1774)													+
<i>Aristias</i> sp.											+		
<i>Bouvirella</i> sp.							+						
<i>Byblis minuticornis</i> G.O. Sars, 1879													+
<i>Cleippides quadricuspis</i> Heller, 1875													+
<i>Erichthonius difformis</i> Milne-Edwards, 1830										+			
<i>Gammaropsis</i> sp.													+
<i>Harpina abyssi</i> G.O. Sars, 1879													+
<i>Harpiniopsis similis</i> Stephensen, 1925													+
<i>Hyperia galba</i> (Montagu, 1815)			+										

Table II (Continued)

	Video	1	3	4	7	9	11	12	13	16	18	Kolbeinsey	Håkon Mosby
<i>Leptamphopus sarsi</i> Vanhoffen, 1897													+
<i>Leptamphopus</i> sp.												+	
<i>Liljeborgia fissicornis</i> (G.O. Sars, 1858)													+
Lysianssoidea indet.				+									
<i>Metacaprella horrida</i> (G.O. Sars, 1877)													+
<i>Metopa boeckii</i> G.O. Sars, 1892													+
<i>Metopa</i> sp.											+		
<i>Monoculodes latissimanus</i> Stephensen, 1931													+
<i>Onisimus</i> sp.					+			+					
<i>Parapleustes</i> aff. <i>gracilis</i> (Buchholz, 1874)													+
<i>Pardalisca tenuipes</i> G.O. Sars, 1893					+			+					
<i>Paroedicerus propinquus</i> (Goes, 1866)			+			+	+		+	+	+		
<i>Paroedicerus</i> sp.								+					+
<i>Pleusymtes</i> sp.								+	+	+	+		
Pleustidae indet.								+					
<i>Stenopleustes eldingi</i> Gurjanova, 1929													+
<i>Stenopleustes malmgreni</i> (Boeck, 1871)			+				+	+					
CRUSTACEA: Copepoda													
Aetididae indet.					+		+	+					
<i>Amphiascopsis</i> sp.												+	
<i>Amphiascus</i> sp.												+	
<i>Calanus hyperboreus</i> (Krøyer, 1838)			+	+	+	+	+	+					
<i>Calanus</i> sp.			+	+	+	+	+	+				+	
<i>Conchoecia</i> sp.							+						
Harpacoidea indet.			+		+			+				+	
<i>Heterolaophonte</i> sp.													+
<i>Idyella</i> (?) sp.													+
<i>Metridia longa</i> (Lubbock, 1854)				+	+								
<i>Neoscolecithrix</i> sp.					+								
<i>Parastenhelia</i> sp.													+
<i>Schizopera</i> sp.													+
CRUSTACEA: Cirripedia													
Fragments													+
CRUSTACEA: Isopoda													
<i>Astacilla</i> sp.					+			+					
<i>Eurycope producta</i> G.O. Sars, 1868 ?							+	+		+			
<i>Eurycope</i> sp.					+								
<i>Gnathia</i> sp.				+	+		+	+					
<i>Idothea</i> cf. <i>emarginata</i> (Fabricius, 1793)					+			+				+	
<i>Ilyaracna</i> sp.			+							+		+	
<i>Janthe</i> sp.								+				+	
<i>Munna</i> sp.					+		+	+				+	

Table II (Continued)

	Video	1	3	4	7	9	11	12	13	16	18	Kolbeinsey	Hákon Mosby
CRUSTACEA: Tanaidacea													
<i>Akanthophoreus gracilis</i> (Krøyer, 1842)													+
<i>Leptognathia</i> sp.								+		+			
<i>Pseudotanais</i> sp.			+					+			+		
<i>Sphyrapus</i> sp.					+								
CRUSTACEA: Ostracoda													
<i>Paracytherois</i> aff. <i>arcuata</i> (Brady, 1868)												+	
Ostracoda spp.							+			+	+		
CRUSTACEA: Decapoda													
<i>Hyas</i> sp.												+	
<i>Lebbeus polaris</i> (Sabine, 1824)							+						
HALACARIDA													
<i>Halacarellus</i> sp.												+	
<i>Lohmanella</i> sp.												+	
Indet.								+					
PYCNOGONIDA													
<i>Colossendeis proboscidea</i> (Sabine, 1824)	+												+
<i>Nymphon</i> sp.	+		+							+			
NEMATODA													
<i>Linhomoeus</i> aff. <i>hirsutus</i> Bastian, 1865												+	
<i>Desmodora scaldensis</i> de Man, 1889												+	
<i>Desmodora communis</i> (Bütschli, 1874)												+	
<i>Anticoma acuminata</i> (Eberth, 1863)												+	
<i>Enoplus communis</i> Bastian, 1865												+	
<i>Neochromadora poecilosoma</i> (de Man, 1893)												+	
ECHINODERMATA													
<i>Amphioplus daleus</i> (Lyman, 1879)								+					
<i>Crossaster papposus</i> (Linnaeus, 1767)			+										
<i>Gorgonocephalus eucnemis</i> (Müller & Troschel, 1842)	+						+				+		
<i>Heliopecten glacialis</i> (Owen, 1833 ex Leach MS)	+	+											
<i>Lophaster furcifer</i> (Düben & Koren, 1846)							+						
<i>Ophiacantha bidentata</i> (Retzius, 1805)		+						+					
<i>Ophiopleura borealis</i> Daniellssen & Koren, 1877													+
<i>Ophiocten gracilis</i> (G.O. Sars, 1871)		+			+			+			+		+
<i>Ophiopus arcticus</i> Ljungman, 1867								+					
<i>Ophiura sarsii</i> Lütken, 1858					+			+					
<i>Strongylocentrotus droebachiensis</i> (O.F. Müller, 1776)	+						+			+			

Table II (Continued)

	Video	1	3	4	7	9	11	12	13	16	18	Kolbeinsey	Hákon Mosby
CHORDATA													
<i>Amblyraja hypertorea</i> (Collett, 1879)	+												
<i>Amblyraja</i> sp.	+												
<i>Anarhichas</i> sp.	+												
<i>Careproctus</i> sp.	+												
<i>Ciliata septentrionalis</i> (Collett, 1875)	+												
<i>Gaidropsarus argentatus</i> (Reinhardt, 1837)	+												
<i>Leptogonus decagonus</i> (Bloch & Schneider, 1801)	+												
<i>Lycodes reticulatus</i> Reinhardt, 1835	+												
Macrouridae indet.	+												
<i>Macrourus berglax</i> Lacepède, 1801	+												

attached to black smokers. At vertical surfaces some meters away from the smokers there were dense aggregations of *Hormathia* sp. and several unidentified anthozoans. These anthozoans are also found at the base of the chimneys, completely embedded in microbial mats. The cold water octocoral *Gersemia rubiformis* was found at some metres distant from the chimneys.

Crustacea

One of the largest groups collected in the vent areas of Jan Mayen, both in terms of number of specimens and species, was the Crustacea. An array of surveys of other vent areas around the world (e.g. Vinogradov 1995; Bellan-Santini & Thurston 1996; Desbruyères et al. 2001; Martin 2003; Martin & Haney 2005; Larsen 2006) have revealed a large number of species that apparently are specially adapted to this unique environment. However, in the samples from the Jan Mayen vents, the vast majority of identified species are commonly reported from the surrounding waters. Among the few exceptions are a new tanaid species (one ovigerous female belonging to a new taxon closely related to *Portarattrum*) and a pleustid species (Amphipoda) that appear to be new to science. Of the crustacean taxa, the Amphipoda had the highest number of both species and individuals with approximately 280 specimens allocated to 19 different species (15 genera). Apart from the new pleustid species (above), the most striking feature of the fauna around the vents is the relatively low number of scavenging lysianassid taxa that are very common elsewhere in the North Atlantic (Palerud et al. 2004). From investigations of vent fauna in other areas, this group appears to have the highest potential for colonization of such chemically reduced environments (Vinogradov 1995) representing more than 99% of all collected species in the Pacific. Most of the amphipod species identified belong to taxa dominated by either opportunistic predators (Dauby et al. 2001) or micropredators on other marine invertebrates, such as sea anemones and other cnidarians (Moore et al. 1994; Berge unpublished data).

Annelida

A relatively diverse fauna of annelids was recorded from the two vent areas, and a total of 53 taxa (23 families) were recorded. Several taxa are only represented by fragments, making exact identification difficult, and this partly explains why only about 60% of the recorded taxa were identified to species level. The material also contains species (e.g. *Macro-*

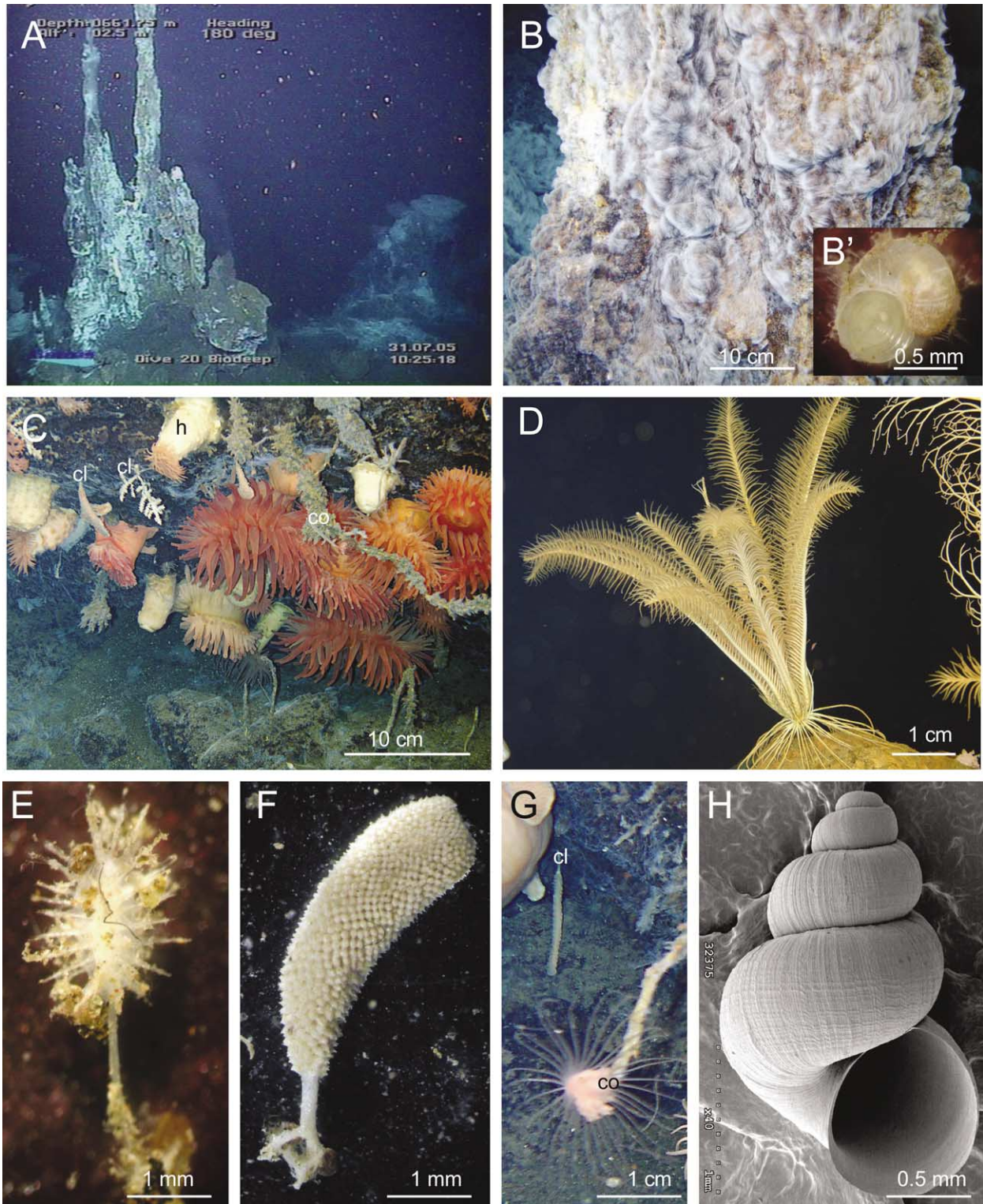


Figure 3. A. White smokers on the Soria Moria vent field. B. Chimneys covered by a dense mat of *Beggiatoa*-like bacteria. B'. A juvenile of *Skenea* sp. from the bacterial mats. Note the filamentous bacteria growing on the shell. C. Typical vertical rocky surface just some meters away from the chimneys. These surfaces are covered by large anthozoans (*Hormathia* sp. (h) and others), several species of cladorhizid sponges (cl) and the hydroid *Corymorpha groenlandica* (co). D. The crinoid *Heliometra glacialis* form dense aggregations surrounding the vent fields. E. Unidentified cladorhizid sponge found growing directly on a smoker. F. *Sycon abyssale*, one of the calcareous sponges common in the area. G. *Corymorpha groenlandica* (co) and a cladorhizid sponge (cl) hanging on a vertical surface. H. *Rissoa* cf. *griegi* without bacterial filaments (SEM photo).

clymene sp. A and *Euchone* sp.) which are believed to be undescribed.

The list of species shows strong similarities to the polychaete fauna known from Jan Mayen (Bakken et al. in press). Most of the species are also known from other deep-sea and shelf areas in the Nordic seas. No typical vent species were identified.

Mollusca

The molluscan fauna found in the vent area is an assortment of bathyal species known in the area. *Rissoa* cf. *griegi* is by far the most abundant species, and was found on smokers, in the bacterial mats and on the ferric deposits. The shell of this species was commonly covered by threads of *Beggiatoa*-like bacteria, indicating a close association with the bacterial mats in the area. This or a similar species has also been identified from woodfalls and seeps in the North Atlantic (Warén unpublished).

Eight of the species collected around the vents have not previously been recorded from the vicinity of Jan Mayen (Friele 1878; Ockelmann 1958; Gulliksen 1974a) (*Alexandromenia* sp., *Anatoma crispata*, *Onoba semicostata* (probably drifted with algae), *Rugulina fragilis*, *Simrothiella margaritacea*, *Skenea basistriata*, *Toledonia limnaeoides*, *Velutina undata*), while *Anatoma crispata*, *Rissoa* cf. *griegi*, *Skenea basistriata*, *Toledonia limnaeoides* and *Velutina undata* have been recorded from the Jan Mayen area (Friele 1879; Sneli & Steinnes 1975; Sneli 1977; Warén 1996; Brattegard 2000; Gulliksen et al. 1999, 2004; Palerud et al. 2004).

Echinodermata

The echinoderm fauna at the vent areas consists of species common to the North Atlantic at similar depths. None of the species seem to be related to the vent environment or are known to harbor symbiotic bacteria. Two ophiuroid species have not previously been found at Jan Mayen: *Ophiocten gracilis*, a boreal species, which otherwise has its northernmost distribution south of Greenland (Paterson et al. 1982), and *Amphioplus daleus*, a widespread abyssal species. The former is also by far the most numerous and common echinoderm species at these vents. Outside of the venting areas dense aggregations of *Heliometra glacialis* and *Gorgonocephalus eucnemis* were found. The echinoderms from Jan Mayen have previously been studied by Skjæveland (1973).

Vertebrata

The fish species observed in the area seem to be more or less typical cold-water northern species (Byrkjedal & Høines 2007) such as *Amblyraja hyperborea*, *Lycodes*

reticulatus, *Leptagonus decagonus* and to some degree also *Macrourus berglax*. *Gaidropsarus argentatus* is more of a continental slope species known from a zone around Norwegian Sea and Greenland Sea area (Pethon 2005). Somewhat unexpected was a specimen of *Ciliata septentrionalis*, but this species is poorly known both when it comes to biology and distribution. The closest record found in the literature is from the east coast of Iceland (Cohen et al. 1990).

Discussion

Unlike other deep-sea vent fields, the Jan Mayen fields do not support a high biomass of vent-endemic fauna. No mussel beds or alvinocarid shrimps characteristic for vent sites further south on the Mid Atlantic Ridge (MAR) were found.

This distinguishes these fields from the vent fields found south of the Azores. This difference may be related to the fact that the Jan Mayen fields occur in relatively shallow waters. At these depths penetration of bathyal species may lead to impoverishment of hydrothermal species, as has been observed when going from the Lucky Strike field at 1700 m to the Menez Gwen field at 850 m at the Azore platform (Desbruyères et al. 2001). However, at Menes Gwen – which is only 150 m deeper than the deepest of the Jan Mayen vent fields – there is still a high biomass of chemosynthetic organisms. Furthermore, at newly discovered Western Pacific vent sites, vent organisms thrive in much shallower waters, and 200 m seems to be a critical depth above which ‘vent-obligate’ animals do not exist (Tarasov et al. 2005).

Vent fluids discharging at relatively shallow depths may, as a result of subsurface mineral precipitation, have lost more of their reduced chemical species vital for chemosynthetic life than their deeper-water counterparts. Analyses of hydrothermal waters sampled from the chimney orifices at the Jan Mayen vent fields yielded H₂S content up to 6 mmol/kg (Pedersen et al. 2007). This is above the values reported from Menez Gwen (Charlou et al. 2000), and in the range observed at sites with a thriving vent endemic fauna. Therefore, the vent fluids seem not to lack the chemical energy needed to sustain a high biomass of chemosynthetic fauna. This conclusion is supported by the presence of a very visible microbial biomass at the Jan Mayen vent fields. Dense microbial mats with a diverse flora of sulfur and methane oxidizing bacteria cover chimneys and large areas of diffuse venting (Pedersen et al. 2005; Øvreås et al. 2007; Steinsbu et al. 2007). Specialized members of diverse animal taxa are known to feed on this type of bacterial mats (e.g. Bennett et al. 1994; Heptner & Ivanenko 2002; Tarasov et al. 2005; Dahlgren et al. 2006). Thus, the low number of such specialized

fauna at the Mohn Ridge vents is unexpected and requires further explanation.

It is obvious that there is little difference in faunal composition between the surrounding waters and the actual vent fields on the Mohn Ridge. All of the studied animal groups show an assemblage very similar to what is usually found at comparable depths in the surrounding waters. The same is true for the Kolbeinsey vents that were investigated by Fricke et al. (1989). This clearly indicates that depth may be a more important factor in this region than the actual venting. However, a striking pattern is that there are almost no faunal elements in common between the Mohn Ridge vents and the Kolbeinsey vents. The only hitherto reported species common to both Kolbeinsey and Mohn vent areas is the hydroid *Corymorpha groenlandica* (see Fricke et al. 1989), which is not an exclusive vent species, but among the most prominent species in both regions. As neither of the vent areas is fully investigated yet it is likely, however, that additional faunal elements common to both regions will be discovered.

Fricke et al. (1989) proposed that the barely specialized fauna found at the Kolbeinsey vent area represents a model for an early evolutionary step towards the formation of a genuinely specialized vent community. This is highly relevant to the Mohn vent fauna as well. Furthermore, it has been proposed that there is a general trend towards less specialized fauna in shallower vent areas (Sahling et al. 2003; Tarasov et al. 2005), which seems to be applicable for most groups, but is not clear for the molluscs (Sasaki et al. 2005). Absent or poorly developed vent fauna communities are commonly reported from many shallow vent areas (e.g. Kamenev et al. 1993; Cardigos et al. 2005), but there is a number of fully developed hydrothermal ecosystems that have been found in shallow waters (e.g. Pansini et al. 2000; Jeng et al. 2005; Sasaki et al. 2005). This indicates that depth is but one of many factors influencing hydrothermal vent communities.

Comparing the Mohn's Ridge vent sites with the MAR vent fields, little is found in common. The sponge *Asbestopluma pennatula* is one of the few species reported from both the Jan Mayen fields and from the Lucky Strike site on the MAR (Desbruyères et al. 2001). The most abundant echinoderm species at the MAR vents, in contrast, is lacking at the Mohn Ridge sites. The brittle star *Ophioctenella acies* is strongly related to reducing environments in the North Atlantic, has not been found shallower than 1600 m, reaches its greatest densities at depths below 3000 m (Stöhr & Segonzac 2005), and is usually associated with beds of *Bathymodiolus* spp. mussels, which are also absent on the Mohn Ridge. Both the shallower depth and the

absence of mussel beds may account for the absence of *O. acies*, but here the long distance between the two areas, which are also part of different biogeographical regions, may most likely explain the differences. It is also possible that geographic barriers, such as Iceland and the Greenland–Iceland–Faroe Ridge, prevent larvae from spreading from the MAR to the northern areas, but we still know very little about the amount of venting in the northern part of the MAR.

Most interestingly the fauna of the Mohn Ridge vent fields has more in common with the Haakon Mosby seep fauna reported by Gebruk et al. (2003) than with any of the other Atlantic vent field faunas. The polychaetes *Praxillura longissima*, *Glyphanostomum pallecens*, *Melythasides laubieri*, *Telephus cincinnatus* and the gastropod *Skenea basistriata* occur both at the Mohn Ridge and at the Haakon Mosby Mud Volcano (Gebruk et al. 2003). Among the echinoderms, the ophiuroid *O. gracilis* is as common at the mud volcano as at the Mohn Ridge vents. However, the fauna associated with the Haakon Mosby seep was dominated by two species of symbiotrophic pogonophorans, *Sclerolinum contortum* and *Oligobranchia haakonmosbiensis*, which are not found at the Mohn Ridge.

The fauna similarities and exchange of species may be explained by the small geographic distance between the Mohn Ridge and the Haakon Mosby mud volcano, the currents and the dominating water masses. Even with the difference in depth (500–700 m compared to 1250 m), both sites are under the influence of the same main water mass. The water surrounding the Haakon Mosby volcano is dominated by north-east Atlantic deep and intermediate waters flowing northwards along the Norwegian continental margin up to Svalbard. One branch of this current flow to the NW following the ridge between the Norwegian and Lofoten basins, and then flows to the NE along the southern side of the Mohns Ridge. In addition, some influence from arctic intermediate waters flowing over the Mohns Ridge from the Greenland Sea can be expected. The species identified from the Haakon Mosby Mud Volcano are included in Table II.

We can presently see several possible explanations for the low abundance of endemic vent fauna at the Mohn Ridge vent fields (Table III). It is obvious that it is not a single factor that affects the current composition of the fauna of the hydrothermal vent fields on the northernmost Atlantic/Arctic mid ocean ridge. During ROV dives in 2008 a number of experiments, including incubators and a range of different settling substrates, were placed at the vent site and recovery of these will hopefully give us additional information on which factors are most

Table III. Hypotheses with comments and possible explanations for the lack of an obligate vent fauna on the Mohn Ridge hydrothermal vents.

Hypothesis	Comment
● The hydrothermal activity is too infrequent, and no permanency is seen.	This is a possibility since the Mohn Ridge is an ultraslow spreading area (e.g. Engen et al. 2003). Cores are currently being investigated to study the frequency of the hydrothermal activities in the area.
● Migrational barriers hinder the influx of larvae from vent sites farther south on the MAR.	It has been suggested that vent species spread along the ridges in a stepping stone pattern (Tunncliffe & Fowler 1996). We find this assumption a likely explanation for the lack of specialized vent fauna in the area, as the Greenland–Iceland–Faroe ridge might act as a barrier effectively restricting any potential extensions of distributional ranges of more southern species. This, however, does not explain the lack of endemic species. The long distance to other vent areas may also prevent colonization from other vent areas. Those so far investigated are indeed distant from the currently investigated areas, but there are indications of vent areas just south of Iceland (O.R. Godø, personal communication). Even so, it does not explain the poor selection of endemic species.
● The benthic habitat is not suitable for settling of larger benthic organisms.	The iron-based crust surrounding in particular the low-temperature venting areas may not be stable enough to support long-living sessile organisms. This may in part explain the absence of larger demosponges in the area.
● The vents are too shallow and the competition with the regular (not geothermically driven) fauna is too great.	As discussed above, this may in part be an explanation, but shallow hydrothermal fauna are known from other parts of the world.
● The vent fields are too young and the surrounding fauna will not have had time to adapt to a chemosymbiotic lifestyle.	This explanation is unlikely since the Mohn Ridge system has existed for approximately 60 million years (Crane et al. 1988), which would be sufficient time for this type of adaptation.
● The surrounding bottom water is too cold (−0.7°C).	This would effectively exclude vent fauna having larvae that cannot withstand low temperatures. However, it should be noted that larvae of some species migrate up to surface, such as the gastropod <i>Bathynnerita</i> in the Pacific Ocean (van Gaest 2006; van Gaest et al. 2007), and may in this way overcome this obstacle.
● Toxic substances in the water prevent the fauna from adaptation.	The presence of toxic substances is not unique to the Mohn Ridge vent fields and would have to be overcome by organisms adapting to any vent field region. There are examples of vent fields where large numbers of dead metazoans have been found but that also held fauna that was specialized and persisting (e.g. Staudigel et al. 2006). This shows that vent environments can be detrimental to generalists, but that it is possible to adapt over a long time scale. There are no indications that the venting at the Mohn Ridge is different from other vent fields in this respect. It should also be noted that very few scavenging amphipods were found in the vicinity of the venting areas which may indicate that the fluids have little influence on the surrounding waters.
● There is not enough chemical energy in the fluids to support a hydrothermal vent community.	This is highly unlikely, since we observe a rich growth of associated bacteria and archaea. This is also not confirmed by measurements of the vent fluids (Pedersen et al. 2007).
● There are no/few taxa suitable for colonization of the vent areas.	It is clear that various biogeographic regions have contributed differently to different vent regions. We can however not see any reason why the Arctic Atlantic should host fewer potential immigrants than other areas. The gastropod <i>Rissoa</i> cf. <i>griegi</i> clearly has an advantage since it has been found associated with wood falls north and south of Iceland, but it is definitely not the only species ‘pre-adapted’ to life in reducing habitats

important in explaining the faunal composition at these vents.

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