**The palaeoecology of the latest Jurassic–earliest Cretaceous hydrocarbon seep carbonates from Spitsbergen, Svalbard**

Running header: Jurassic–Cretaceous seep palaeoecology

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Latest Jurassic–earliest Cretaceous hydrocarbon seeps from Spitsbergen, Svalbard, are known to contain unusual fauna, lacking most of the species characteristic for roughly coeval seep deposits. This paper summarizes and analyzes the fauna from 16 seep carbonate bodies from Spitsbergen in order to explain its composition. The seeps formed in a shallow epicontinental sea with widespread deposition of fine-grained, organic-rich sediments. They are spread over a relatively large area and are positioned roughly in the same interval, indicating seepage on the extensive areas of the palaeo-Barents Sea. The seep fauna is very species-rich and with low dominance, counting 54 species, with a composition similar to that known from Jurassic–Cretaceous normal-marine environments of other Boreal seas. Seep-restricted fauna is not abundant and represented by four species only. Hokkaidoconchids and possible siboglinid worm tubes characteristic for high sulphide fluxes are rare. Apart from seep-restricted sulphide-mining lucinid and thyasirid bivalves, chemosymbiosis was also a source of nourishment for background solemyid and nucinellid bivalves, all of which take sulphide from infaunal sources. This all suggests a relatively weak sulphide flux. The high diversity and low dominance of the fauna and significant richness and abundance of background species, is typical for shallow water seeps.

Key words: palaeoecology, flux strength, chemosymbiosis, Jurassic, Cretaceous, Boreal, background fauna, shallow water.

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Hydrocarbon seeps are submarine sites where fluids charged with reduced organic compounds are leaking from the subsurface (Sibuet & Olu 1998; Levin 2005). The methane released in such sites is oxidized in the shallow subsurface by a process of anaerobic oxidation of methane (AOM). The process rises alkalinity and facilitates the precipitation of methane-derived authigenic carbonates (MDAC) on one hand, and elevates the sulphide content within the sediment on the other (Peckmann & Thiel 2004). As such, seeps differ significantly from hydrothermal vents where most of the sulphide dissolved in the hot fluids is released directly into the water column (Van Dover 2000). The sediment sulphide becomes an important factor attracting chemosymbiotic fauna, which derive their nutrition from bacterial symbionts (e.g. Dufour 2005; Dupperon 2010; Taylor & Glover 2010). Among the chemosymbiotic fauna inhabiting seeps, the important adaptation is the ability to utilize the redox layer located at varying depths within, or at the surface of the sediment (Levin 2005). The most common chemosymbiotic groups in seeps and vents are solemyid, thyasirid, lucinid and vesicomyid clams, and bathymodiolin mussels (some of which are also able to utilize methane) (e.g. Taylor & Glover 2000; 2010), provannid gastropods (Warén & Bouchet 1993; Sasaki *et al*. 2010) and ‘vestimentiferan’ siboglinid tubeworms (Bright & Lallier 2010; Hilário *et al.* 2011). These groups show a certain degree of dependence on the seep and vent environments at various taxonomic levels (Sibuet & Olu 1998; Levin 2005). All have their own preferences regarding sulphide depth and content and can show complex spatial and temporal distribution patterns depending on flux intensity in space and time (e.g. Sahling *et al*. 2002). The species which tend to be restricted to vent and seep environments preferentially occur in deep-water sites (Sibuet & Olu 1998). Shallow-water seeps are home to few seep-restricted fauna, instead being dominated by species-rich and abundant background fauna from the surrounding normal marine environment (Levin *et al*. 2000; Sahling *et al*. 2003; Dando 2010).

Mesozoic seep faunas differed from their Cenozoic and modern equivalents. Vesicomyid clams and bathymodiolin mussels are unknown from sites older than the Mid–Eocene (Squires & Goedert 1991; Amano & Kiel 2007) and the epifaunal/semi-infaunal niche in the latest Jurassic–Late Cretaceous seep-restricted bivalves was occupied by the extinct modiomorphid *Caspiconcha* (Jenkins *et al*. 2013). Many Jurassic and older seeps were inhabited by brachiopods, which are largely absent from seeps today (Kaim *et al*. 2010). Brachiopods from the extinct superfamily Dimerelloidea show a particular affiliation with seep environments and often appear in monospecific accumulations (Sandy 2010). Jurassic and Early Cretaceous seep-restricted gastropods were largely represented by provannoid hokkaidoconchids, known from the Late Jurassic to Oligocene (Kiel 2010a) and by other genera, like the supposed neomphalid ?*Retiskenea*, together with *Paskentana* and *Atresius*, which are of uncertain taxonomic affinity (Kiel *et al*. 2008a). The infauna was largely represented by the same bivalve families as in Cenozoic and Recent seep settings, although the generic composition of some families differed significantly from that of the Recent seeps (e.g. Kiel 2013; Hryniewicz *et al*. in press). In addition, the protobranch *Nucinella* was also present in some Triassic to Oligocene seep sites (e.g. Amano *et al*. 2007; Peckmann *et al*. 2011; Amano *et al*. 2013; Kiel *et al*. 2013). The fauna associated with individual Mesozoic seep sites may differ considerably for reasons which are not yet fully understood, although palaeobathymetry (Kiel 2010b), palaeobiogeography (e.g. Campbell & Bottjer 1995; Sandy & Blodgett 1996) and flux strength (Jenkins *et al*. 2007a) have been mentioned as some factors controlling their faunal composition.

The latest Jurassic–earliest Cretaceous seeps in Spitsbergen were previously known to be highly diverse macrofaunistically, with up to 18 species at one single site and 31 species in total recorded to date (Hammer *et al*. 2011). The purpose of this paper is to summarize and extend the data published previously on the sedimentology and fauna of these seeps (Wierzbowski *et al*. 2011; Hjálmarsdóttir *et al*. 2012; Holmer & Nakrem 2012; Hryniewicz *et al*. 2012; Hammer *et al*. 2013; Hryniewicz *et al*. in press; Sandy *et al*. in press; Vinn *et al*. in press), to characterize the environment of these seeps and to explain the qualitative and quantitative composition of the fauna.

Geological setting

All but one of the latest Jurassic–earliest Cretaceous seeps of Spitsbergen are located along the ca. 20 km long outcrop belt in the Sassenfjorden area, stretching from the Janusfjellet (west) to Knorringfjellet (east) (Fig. 1). The seep carbonates are hosted by the Slottsmøya Member of the upper Agardhfjellet Formation in a thin interval below the top of the unit (Fig. 2). In the area of study the Slottsmøya Member is a ca. 75 m thick, organic-rich, fine-grained succession, deposited on a low-energy middle to outer Boreal continental shelf (Nagy *et al*. 1988; Dypvik *et al*. 1991a, b; Collignon & Hammer 2012). The uppermost ten to 15 metres of the section are silty to sandy and highly condensed, recording a possible shallowing episode in the area (Dypvik *et al*. 1991b; Hryniewicz *et al*. 2012). Some bedding planes in the Slottsmøya Member are accentuated by layers of concretionary siderite and dolomite. The unit belongs to the Volgian–Ryazanian (Nagy & Basov 1998; Rogov 2010), which are local Boreal stages roughly correlative to the Tithonian and Berriasian standards (for details, see Houša *et al*. 2007; Zakharov & Rogov 2008; Rogov & Zakharov 2009).

All but one of the seep carbonates are preserved *ex situ* and have been discovered as short-distance slumped scree composed of loose, heavily weathered carbonate blocks. The only larger seep, seep 9, has slumped *en masse* within a gully from its original position and is preserved as large blocks surrounded by loose scree (Hammer *et al*. 2011; fig. 3). Due to intense landsliding on the northeastern slopes of Knorringfjellet in 2012, seeps 10–14 have been eroded away since the studied fossils were collected. Seep 8 is preserved partially *in situ* as a small carbonate lens with a siderite cap.

In 2011, a seep carbonate body was discovered on Myklegardfjellet on East Spitsbergen by Snorre Olaussen, The University Centre in Svalbard (UNIS). This carbonate body is preserved *in situ* ca. 40–50 m below the top of the Agardhfjellet Formation as a series of stacked carbonate lenses up to a half a metre in thickness and two–three metres in horizontal extent. The ammonite fauna suggests it is probably of Mid–Late Volgian age (M. Rogov, personal communication) and probably has the same initial shape as the weathered and eroded seeps from the Sassenfjorden area in Central Spitsbergen. Due to the short time available for fieldwork, this site has not yet been sampled in detail and only a single serpulid and a single solemyid fossil collected there are included in the current analysis (e.g. Vinn *et al.* in press).

Materials and methods

The stratigraphic subdivision of the Central Spitsbergen seeps follows that of Wierzbowski *et al*. (2011). The types of substrates available in the seep carbonates have been described by Hryniewicz *et al*. (2012). The larger part of the fossil material used in this paper has already been systematically described and identified to the species level by Wierzbowski *et al*. (2011) (ammonites), Holmer & Nakrem (2012) (lingulate brachiopod), Hammer *et al*. (2013) (cephalopod arm hooks), Hryniewicz *et al*. (in press) (bivalves), Sandy *et al*. (in press) (rhynchonellate brachiopods) and Vinn *et al*. (in press) (serpulid tubes) and the nomenclature of the fauna follows that used in the papers. The reader is referred to these papers for any additional information regarding taxonomy. Additional systematic work on Spitsbergen seep gastropods is underway. The remaining groups, such as belemnoids, crustaceans, echinoderms (both crinoids and echinoids), scaphopods, sponges and non-serpulid worm tubes, have not received a separate taxonomic treatment, and for the purpose of this study they have been identified to the lowest taxonomic level possible. The specimens belonging to each major faunal group have been counted, and the number of species or higher taxa in each major group was determined. As the species richness of ammonites (Wierzbowski *et al*. 2011) and buchiids (Hryniewicz *et al*. in press) is caused by short evolutionary ranges of species rather than by ecological heterogeneity, both ammonites and buchiids have been treated as a single taxon each.

Most of the fossils are articulated and semi-articulated, so each single fossil was counted as a single individual. There were a few exceptions, however. Among the bivalves, the large number of valves (left valves) of the inequivalved bivalve *Oxytoma* *octavia* was considered as individuals. The disarticulated valves of *Pseudolimea* *arctica* were counted and divided by two, rounding up, and the resulting number was taken as the number of individuals. ‘Spp.’ is used for specimens belonging to more than one species which have not been determined to species level. As such, *Camptonectes*, ‘spp.’ refers to poorly preserved specimens probably belonging to the two species identified. The disarticulated valves of the brachiopod *Lingularia similis*?, the number of specimens designated by Holmer & Nakrem (2012) was added to half of the number of valves found after the publication of the material. Fragments of cephalopods, such as ammonite aptychi, were considered parts of the individuals already preserved in the assemblage, and were not counted separately. Belemnoid arm megahooks were counted separately only when they did not co-occur with belemnoid guards. Only well preserved sponges have been counted; disarticulated masses of loose spicules and tuberoids have not been included. Only two separated skeletal plates of echinoids have been found; each each of them wascounted as a single individual. Crinoids were preserved as compact accumulations of disarticulated trochites. Aware of the difficulties in quantifying crinoids based on trochites only, we applied a semi-quantitative approach and refer to crinoids as present/absent only.

Fossils from all seep bodies of the latest Jurassic˗earliest Cretaceous of Spitsbergen have been summed up for the purpose of this paper. Several factors contributed to this approach. First of all, only seep 8 is preserved relatively *in situ*, whereas the remaining 14 seep carbonates are slumped and preserved *ex situ*. Because of that, only one of the seep carbonates is investigated as a larger entirety. All other seep carbonates found represent blocks of carbonate that are separated from the rest of their main seep body (e.g. Hryniewicz *et al*. 2012). Treating each seep separately would therefore introduce bias which potentially could be attributed to incomplete seep preservation only, and would therefore be difficult to discuss. Second, the sampling of the seep sites was very uneven both in terms of time spent at a particular locality and in terms of methods applied for fossil material from various sites. Therefore, qualitative and quantitative differences encountered in different seep sites could very well be applied merely to uneven sampling of the material or different methods used during the study (such as acid residue picking for the lingulids from some seep sites only, for example), further adding to the confusion. The material can not therefore be considered a true bulk sampling and possible taxonomic bias in the counting procedure should be kept in mind. To average these biases between the particular seep sites, all counted fossils from all the seep localities have been treated as a single assemblage. This is justified by the stratigraphic record from 10 seep carbonates, showing relatively continuous seepage during 9 Ma and stratigraphic continuity between seep sites (Wierzbowski *et al*. 2011) and by a relatively stable middle to outer shelf depositional environment of the upper Slottsmøya Member (Dypvik *et al*. 1991b; Collignon & Hammer 2012; Hryniewicz *et al*. 2012). However, the discussion of some qualitative differences between particular seep sites has been presented when such differences appeared. The seeps and the surrounding succession have also been sampled for microfauna and non-faunistic elements that are important for the palaeoecological analysis.

Diversity indices, rarefaction curve and rank abundance (Whittaker) plot were calculated using Past, version 3.01 (Hammer *et al*. 2001). The version of the Simpson index (Simpson 1949) used is



where *N* is the total number of specimens and *ni* is the number of specimens of species *i*. In this form, it is a measure of evenness ranging from 0 to 1. The Shannon index (Shannon 1948) uses the natural logarithm according to the formula

where *N* is the total number of specimens and *ni* is the number of specimens of species *i*.

The bias-corrected Chao-1 species richness estimator (Chao 1984) provides an estimate of total species richness based on the sample:

Chao1 = *S* + *F*1(*F*1 - 1) / (2 (*F*2 +1)),

where *S* is the number of observed species, *F*1 is the number of singleton species and *F*2 the number of doubleton species.

Results

*Abundance of species*

The quantitative abundance of each species and higher taxon is given in Table 1. In total, 1932 individuals have been analyzed. The most abundant fossil in the assemblage is the arcticid bivalve *Pseudotrapezium* aff. *groenlandicum* (820 individuals, 42.4% of the assemblage). It forms monospecific accumulations composed of hundreds of specimens in seep 9, but it is fairly uncommon in the other sites. Other species are less common. Among them, the most abundant is the bivalve *Buchia* spp. (159; 8.2% ) followed by ammonoids (153; 7.9%), the pectinid bivalves *Camptonectes* spp. (including *C*. (*Co*.) aff. *milnelandensis* and *C*. (*Cc*.) *clathratus*) (123; 6.4%) and the nucinellid *Nucinella svalbardensis* (98; 5.1%). The chemosymbiotic bivalve *Solemya* (*Petrasma*) cf. *woodwardiana* is even less abundant (27; 1.4%). Gastropods are uncommon. Among them, the most abundant is a species of a genus *Ambercyclus* (20, 1.0%). Other gastropods are less abundant and, apart from a rissoid *Hudlestoniella* sp. (17, 0.9%), only a few specimens of each species have been found. The most abundant species of brachiopod is a lingulid *Lingularia similis*? (21; 1.1%), followed by rhynchonellide *Ptilorhynchia mclachlani* (15; 0.8%). Other brachiopods are less numerous with species typically represented by several to single specimens only. Seep restricted bivalves are much less abundant than other bivalve species and are present only in small clusters or in scatter. They are represented by the lucinid *Tehamatea rasmusseni* (60; 3.1%) and a thyasirid *Cretaxinus hurumi* (56; 2.9%), which have been found in seep 9 only. Tubes of non-serpulid worm have been found in limited numbers (30; 1.6%). Seep-restricted hokkaidoconchid gastropods are rare (5; 0.3%).

Calculated diversity indices are given in Table 2. The Simpson diversity index for the pool of all seep samples is *D*=0.79 (95% bootstrapped confidence interval: 0.77 to 0.81). The Shannon index is *H*=2.37 (95% CI: 2.28 to 2.42). The observed species richness is *S*=54, while the Chao-1 species richness estimator is Chao1=70 (95% CI: 45 to 86). A rank abundance plot is shown in Figure 3 and the rarefaction curve in Figure 4.

*Abundance of major faunal groups*

The quantitative abundance of major groups is given in Table 3. The most abundant group is bivalves, with 1520 individuals representing almost 79% of the assemblage (Fig. 5A). The second most abundant group, the cephalopods, is much less abundant with 162 individuals (8.4%). Rhynchonellate brachiopods (comprising rhynchonellides, terebratulidines and terebratellidines) are the third most abundant (112; 5.6%), followed by gastropods (57; 2.9 %), non-serpulid worm tubes (30; 1.5%) and lingulid brachiopods (21; 1.1%). The other groups, like serpulids, sponges, scaphopods, echinoids, crustaceans and vertebrates each constitute less than 1% of the assemblage.

*Species richness of major faunal groups*

The species richness of all major groups is given in Table 4. The seep fauna is very diverse, with 54 species or higher taxa. The most diverse groups are bivalves and rhynchonellate brachiopods with 15 species (27.8%) each (Fig. 5B). Among the latter, 11 species belong to terebratulidines (20.4 %), three to rhynchonellides (5.6%), and one to terebratellidines (1.9%). Other diverse groups are gastropods (10 species; 18.5%) and serpulids (4 species; 7.4%). Cephalopods are represented by two higher taxa (3.7%), the ammonoids and belemnoids. Echinoderms are represented by both crinoids and echinoids (3.7%). Other fossil groups are represented by a single taxon only, crustaceans, scaphopods, sponges, vertebrates and non-serpulid worm tubes, representing 1.9% of species richness each.

*Seep-restricted vs. background taxa.*

The quantitative data on seep-restricted and background fauna are given in Table 5. Of 1940 individuals recorded, only 151, representing 7.8% of total abundance have been classified as seep restricted. (Fig. 6A). They belong to three or possibly four species, representing only 7.4% of the Spitsbergen seep species richness (Fig. 6B). These are: the lucinid *Tehamatea rasmusseni* sp. nov (60 individuals; 3.1%), *Cretaxinus hurumi* (56; 2.9%), hokkaidoconchid gastropods (5; 0.3%) and possibly the non-serpulid worm tubes (30; 1.5%) and (Tab. 1).

In spite of being chemosymbiotic, the solemyid bivalve *Solemya* (*Petrasma*) cf. *woodwardiana* was not included in the group of seep-restricted taxa as it occurs in normal-marine Jurassic sediments of Europe (e.g. Duff 1978). The same applies to *Nucinella svalbardensis*, as small species of *Nucinella* occasionally occur in normal-marine Mesozoic and Cenozoic sediments (e.g. Clausen & Wignall 1990) and large species of *Nucinella* are known from normal deep-water settings in Recent oceans (La Perna 2005; Hryniewicz *et al*. in press and references therein).

*Other elements*

All seeps and surrounding black shales contain chert and quartz pebbles, which are rounded and up to 3 cm in diameter (Fig. 7A). Chert lithology is common in the Upper Permian rocks of the Kapp Starostin Formation cropping out about 1300 m lower in the section (Dallmann 1999). The origin of the quartz pebbles is unknown. Both seep carbonates and the surrounding shale succession contain sunken driftwood (Fig. 7A), varying in size from fragments of a couple of millimetres to well-preserved logs more than a metre in length. Wood from the seeps is heavily mineralized with carbonate and pyrite, and from the black shales it is preserved as lignite. Some wood fragments in seep 8 are associated with the common pectinid *Camptonecte*s spp. No fauna has been found around the driftwood outside the seeps. In the immediate vicinity of seeps 2, 3, 5 and 8 some tubular carbonate concretions occur, here interpreted as possible fluid conduits (Fig. 7B).

Discussion

*General environment*

The Kimmeridgian–Berriasian was a time of a relative fall of global sea level, which due to lack of significant polar ice-caps was 100 to 150 metres higher than today (Haq *et al*. 1988). This allowed the persistence of latest Jurassic–earliest Cretaceous shallow epicontinental seas covering large areas of Europe, Russia and Greenland (Fig. 8; Ziegler 1988). The Boreal Jurassic seas of Northwestern Europe flooded a shelf, which was dissected by the Late Jurassic rifting phase into islands, separated by grabens with restricted water circulation (e.g. Ziegler 1988, 1992; Doré 1992; Kjennerud *et al.* 2001). The seas lay in an arid and warm Late Jurassic climatic zone, which by the latest Jurassic–earliest Cretaceous shifted towards more humid and tropical in the south, and temperate towards the north (e.g. Abbink *et al*. 2001; Price & Mutterlose 2004; Lindström & Erlström 2011; Dera *et al*. 2011). During the Late Jurassic, the semi-isolated Boreal seas were a locus of wide-spread deposition of fine-grained, organic-rich sediments of the Kimmeridge Clay and coeval formations (e.g. Smelror 1994; Hvoslef *et al*. 1985; Knudsen *et al*. 1988; Ineson *et al*. 2003). The organic matter of mixed algal-terrestrial origin reflects phytoplankton productivity and seaward transport of land-derived plant material (e.g. Langrock *et al*. 2003). The increased preservation of organic matter supplied to the seabed was facilitated by reduced oxygenation of bottom waters (Mutterlose *et al*. 2003); in extreme cases rocks reach up to 50% TOC (e.g. Wignall 1990a). However, the diverse benthic fauna shows that few bottom environments of the Boreal seas were truly anoxic and oxygen-depletion must have been a seasonal rather than a permanent phenomenon and was predominantly associated with sediment pore fluids (e.g. Wignall 1990a; Oschmann 1991; Wignall & Pickering 1993). As such, the Boreal seas differ significantly from the Black Sea of today, which is heavily stratified and anoxic below 150 metres (Özsoy & Ünlüata 1997).

The Palaeo-Barents Sea was a semi-enclosed epicontinental sea, belonging to the Mesozoic Arctic oceanic domain partially isolated from the Northern Atlantic and Tethyan Oceans (Fig. 8; Zakharov *et al*. 2002). Spitsbergen lay in the Palaeo-Barents Sea, north of the deep and narrow Norwegian-Greenland Seaway and west of the shallower Timan-Petchora Sea (Fig. 8; Doré 1992; Ziegler 1988; Dypvik *et al.* 2002). Also, there was a link to Siberia to the northeast and Russian Seaway towards the southeast (Fig. 8) and possibly to the Palaeo-Pacific towards the northwest (Fig. 8; Ziegler 1988; Zakharov *et al*. 2002). Episodes of higher energy deposition in the area were infrequent and were mostly associated with migration of shelf sand ridges, possibly caused by tidal currents (Dypvik *et al*. 1991b; cf. Wierzbowski *et al*. 2011). The sedimentary environment permitted rhythmic, low-energy deposition of muds with high total organic carbon (TOC), up to 14% (Dypvik *et al.* 1991b; Hammer *et al*. 2012). The Jurassic–Cretaceous Palaeo-Barents Sea supported a diverse assemblage of invertebrates (Rogov 2010; Sokolov & Bodylevsky 1931; Rousseau & Nakrem 2012; Birkenmajer *et al*. 1982; Wierzbowski *et al*. 2011; Hjálmarsdóttir *et al*. 2012; Hammer *et al*. 2013; Hryniewicz *et al*. in press; Sandy *et al*. in press; Vinn *et al*. in press) and vertebrates (Druckenmiller *et al*. 2012; Hurum *et al.* 2012; Knutsen *et al.* 2012a, b, c). The large amount of well-preserved fossil wood (Fig. 7A) indicates that the sea was supplied with abundant land-derived plant material. Rounded chert pebbles dispersed in the shale and seep carbonate (Fig.7A) probably came from roots of drifting trees or from drifting algal holdfasts. Abundant supply of plant detritus is also supported by the presence of *Epistomina* sp., a supposed algal-grazing foraminifera (Hjálmarsdóttir *et al*. 2012).

Hydrocarbon seep carbonates are fairly abundant in the uppermost Jurassic–lowermost Cretaceous in the Janusfjellet-Knorringfjellet area (15 seep carbonates along the ca. 20 km transect, Fig. 1). Similar seep carbonates were also discovered in roughly equivalent strata in eastern Spitsbergen 80 km away (Fig. 1). All of the above suggests that during the latest Jurassic–earliest Cretaceous large areas of the organic-rich sea bottom of the palaeo-Barents Sea were affected by fluid and gas seepage.

*Chemosymbiosis at latest Jurassic–earliest Cretaceous Spitsbergen seeps*

The most abundant chemosymbiotic species in Spitsbergen seeps is *Nucinella*, which together with the solemyid *Solemya* (*Petrasma*) cf. *woodwardiana* is also the most widespread chemosymbiotic bivalve in the seeps, found in 9 and 7 out of 16 seep sites, respectively (Tab. 1). *Nucinella* species are shallow burrowers which are capable of particulate feeding, but symbiosis with chemosynthetic bacteria has been suggested as obligate for the genus (Oliver & Taylor 2012). The large size and longitudinal striation on the inner shell surface of *N*. *svalbardensis* of the Spitsbergen seep nucinellid suggest that it derived at least part of its nutrition from chemosymbiotic bacteria and possibly were actively using the reduced compounds available within the seep environment (e.g. Amano *et al*. 2007; Oliver & Taylor 2012; Oliver & Taylor 2012). . *Solemya* (*Petrasma*) cf. *woodwardiana*, as in extant solemyids, was probably a burrower, forming U toY-shaped burrows used to pump sulphide from a depth of 5 cm or greater (Stanley 1970; Reid 1980; Seike *et al*. 2012). In Recent seeps solemyids are usually associated with zones of low sulphide content (0.1 – 0.3 mM; Sahling *et al*. 2002) and similar sulphidic conditions are confirmed for some of them in non-seep, reducing sediments (Conway *et al*. 1992). *Nucinella* co-occurs with the solemyid *Acharax* in lateral zones that have possibly the weakest seepage in some fossil seep sites (Jenkins *et al*. 2007a). It is therefore likely that seeps with chemosymbiotic fauna represented only by *Nucinella* and *Solemya*, or both, are environments with fairly weak flux, displacing the redox boundary to a depth of a few centimetres below the sediment-water interface.

The deep-burrowing chemosymbiotic bivalves *Tehamatea rasmusseni* (lucinid) and *Cretaxinus hurumi* (thyasirid) have been found in seep 9 only (Hryniewicz *et al*. in press). They form small, mixed clusters of a few specimens or occur dispersed within the bioclastic grainstone (Hryniewicz *et al*. in press). Seep 9 was the only long-lasting seep on Spitsbergen (Wierzbowski *et a*l. 2011; Ogg & Hinnov 2012). Such conditions facilitated accumulation of bioeroded and current-winnowed shell grainstone, not observed in other seeps (Hryniewicz *et al*. 2012). This particular substrate may have been more suitable for colonization by large chemosymbiotic lucinids and thyasirids. Both lucinids and large thyasirids mine sulphide from the deeper interstitial layers and supply it to the bacterial symbionts within their gills: thyasirids construct a network of elaborate ventral tunnels reaching as deep as 50 cm below the sediment-water interface (Dando & Southward 1986; Dando *et al*. 1994; Oliver & Killeen 2002; Taylor & Glover 2010). They require fairly low concentrations of sulphide within the pore fluids as compared to other chemosymbiotic biota populating seep sites (e.g. Fisher & Hand 1984; Dando *et al*. 1985, 1986) and in comparison to solemyids they are able to utilize similar or lower sulphide contents (cf. Sahling *et al*. 2002). Their presence in Spitsbergen seeps suggests weak sulphide flux and deep penetration of marine waters into the coarse-grained sediment. Chemosymbiotic thyasirids are also fairly low-sulphide substrate dwellers (Dando & Spiro 1993; Dando *et al*. 2004) and, as lucinids, indicate low, diffusive flux at seep 9 (Dando *et al*. 1986). The possible explanation of the co-occurrence of a lucinid and thyasirid with *S.* (*P.*) cf. *woodwardiana* and *Nucinella* *svalbardensis* is either lateral flux zonation or temporal changes in flux intensity. As *S.* (*P.*) cf. *woodwardiana* and *Nucinella* *svalbardensis* both occur in the same facies as the *Tehamatea* *rasmusseni* and *Cretaxinus hurumi*, sometimes in close proximity, possible temporal changes and time-superimposition of both chemosymbiotic faunas is more likely. We suggest that as flux started waning, *Nucinella svalbardenis* and *S*. (*P*.) cf. *woodwardiana* were gradually replaced by the lucinid *Tehamatea* *rasmusseni* and the thyasirid *Cretaxinus hurumi*, relying on sulphides from deeper sediment layers. A collapse of communities relying on shallower and stronger sulphide sources with waning flux and lowering of the redox boundary down to 50 cm below the sediment surface or greater, has been described from a Recent seep in the Weddell Sea (Domack *et al*. 2005; Niemann *et al*. 2009).

Non-serpulid worm tubes are present in seven out of 15 seeps (Hammer *et al*. 2011, fig. 5c˗d). These tubes have similar carbonate laminated tube walls to siboglinid ‘vestimentiferans’ from modern seep sites that have been replaced by carbonate minerals (Haas *et al*. 2009). On this basis we suggest that the fossils probably belong to this group, with the proviso that other groups of polychaete worms which produce rather similar tubes have been found in chemosymbiotic environments (e.g. chaetopterids; Kiel & Dando 2009; Fabri *et al*. 2011) and the molecular age estimate for the origin of the siboglinids is younger than the Spitsbergen fossils (Halanych *et al*. 1998). ‘Vestimentiferan’ siboglinids are sedentary, gutless, organic-tube dwelling polychaetes which pump sulphide-rich fluids by their root-like lower shafts (Dattagupta *et al*. 2008). ‘Vestimentiferan’ larvae require a carbonate substrate to settle and initially high sulphide levels at the surface or in the very shallow subsurface; adults can utilize deeper sulphide levels as they extend their roots down into the sediment and mine for sulphide (Bright & Lallier 2010). This means that ‘vestimentiferans’ (if correctly identified as such) are latecomers in Spitsbergen seeps with exposed carbonate substrates. Their presence also shows that some sites had initially high sulphide at the surface or immediately below it, although never in significant amounts able to maintain large vestimentiferan “bushes”, as at modern seep sites, because only 30 isolated tubes have been found in total. In one of the Spitsbergen seep sites the non-serpulid worm tubes co-occur with poorly preserved hokkaidoconchid gastropods. Hokkaidoconchids were a Mesozoic seep-restricted gastropod family possibly related to provannids (Kaim *et al*. 2008, 2009; Kiel *et al*. 2008a). Large provannid gastropods derive their nutrition directly from chemosymbionts (Suzuki *et al*. 2006), while smaller ones graze on surface films of apparently toxic bacteria (Warén & Bouchet 1993), developing in zones of high sulphide flux (e.g. Sahling *et al*. 2002; Knittel *et al*. 2003, 2005). The mass-occurrence of fossil hokkaidoconchids in some Mesozoic seep sites (Kaim & Kelly 2009), together with possible fossilized bacterial mats (Kelly *et al*. 1995) makes it likely that at least some fossil hokkaidoconchid gastropods were feeding on bacterial mats developed in high-flux zones. Whether Spitsbergen fossil hokkaidoconchids were taking their nourishment directly from chemosynthetic bacteria or by grazing is unclear. Nonetheless, they are rare in Spitsbergen seeps (Tab. 1). There is no clear sedimentological evidence for bacterial mats (Hryniewicz *et al*. 2012), and only few tubular conduits have been found (Fig. 7B). Petrographic evidence for weak flux, such as rare and dispersed cavities filled with botryoidal cements (Peckmann *et al*. 2009), is also in accordance with dominance of weak flux at Svalbard seeps (Hammer *et al*. 2011, Hryniewicz *et al*. 2012).

*Ecology of background fauna*

The Spitsbergen seep assemblage is significantly dominated by bivalves, which constitute nearly 80% of the whole fauna and are represented by 15 species (Tab. 1; Fig. 5A, B). The dominant species is the arcticid *Pseudotrapezium* aff. *groenlandicum*, which forms nearly half (42.4%) of the assemblage. Arcticids are common in shallow-water Middle Jurassic to Early Cretaceous clastic sediments of Europe (e.g. *Anisocardia*, *Pronoella* and *Pseudotrapezium*; Cox 1944). Mesozoic arcticids were probably shallow burrowers populating low sedimentation rate environments, as does their extant relative *Arctica islandica* (Morton 2011). *P*. aff. *groenlandicum* is present in large numbers in seep 9 only (Hryniewicz *et al*. in press). The depositional environment of this particular seep was characterized by seabed omission and formation of winnowed bioclastic grainstones (Hryniewicz *et al*. 2012) and, therefore, was favorable for arcticids. The second most common bivalve in the Spitsbergen seeps is the buchiid *Buchia* spp. (Tab. 1). Buchiids are very common inhabitants of the late Jurassic–early Cretaceous high-latitude and deep seas (e.g. Zakharov 1981; Grey *et al*. 2008) and are often the most common fossil in Boreal organic-rich shales (Wignall 1990a). They have been reported from some cold seeps (e.g. Kiel *et al*. 2008a). As byssally attached epifauna (Wignall & Pickering 1993), buchiids probably took advantage of the hard substrate available within the seep environment. At least two species of the byssally-attached pectinid *Camptonectes* are common, which are typical members of the latest Jurassic–earliest Cretaceous shelf faunas of the Boreal realm (Johnson 1984; Hryniewicz *et al*. in press). *Camptonectes* is more frequent in seeps with a large content of sunken driftwood. Some specimens may have possibly been delivered to the seep site with sinking wood and were pseudoplanktonic (Wignall & Simms 1990). Pectinids occur in some Mesozoic sites in California (Kiel *et al*. 2008a) and Hokkaido (Yasukawa site, Campanian; Jenkins *et al*. 2007a), and some Cenozoic sites in Oregon-Washington states (Oligocene-Miocene; Kiel 2006; Kiel 2010a). They have also been occasionally reported from Recent seep sites (e.g. Vaughn-Barrie *et al*. 2011). Cephalopods are a very common group in Spitsbergen seeps and are predominantly ammonoids, with a much smaller number of belemnoids (Fig. 5A, B). Ammonoid life habits and feeding strategies are not fully resolved and were probably complex (e.g. Westermann 1996). However, it is agreed that adults were predators (e.g. Jacobs & Landman 1993). Ammonoids are associated with many Mesozoic seeps (e.g. Beauchamp & Savard 1992; Kelly *et al*. 2000; Landman *et al*. 2012; Kiel *et al*. 2013) and it has been suggested that they may have been attracted to seep carbonates by the rich food source and shelter, provided by seep carbonates. Belemnoids are represented as guards, while others as arm megahooks (Hammer *et al*. 2013), and it is more difficult to envisage any relationship between them and the seep environment; probably they represent water column predators.

Another common bivalve is the shallow burrowing malletiid *Mesosaccella* (Tab. 1). It is represented by two species (Hryniewicz *et al*. in press), *M*. *rogovi* and *M*. *toddi*. The more common elongated *M*. *rogovi* has a similar shape to *Mesosaccella* species found in fine, organic-rich sediments in the Jurassic of Europe (e.g. Duff 1978; Hodges 2000). The shorter and stouter *M*. *toddi* was presumably better adapted to coarser substrates and is present only in those sites where such substrates have been identified (Hryniewicz *et al*. in press). Malletiids are accompanied by rare specimens of the shallow-water nuculid bivalve *Dacromya chetaensis* (Hryniewicz *et al*. in press). All protobranch bivalves are shallow-burrowing deposit feeders (Zardus 2002). They are fairly common in fossil seep sites (e.g. Kiel 2006; Kiel *et al*. 2008b) and present in Recent seep sites, although rarely mentioned, probably due to their small size and infaunal mode of life (A. Kaim, personal observation). It has been suggested that some protobranchs living in chemosynthetic environments benefit from chemosynthetically-produced organic matter (e.g. Allen 1993). A deep infaunal niche was also occupied by the deep-burrowing anomalodesmatan bivalve *Goniomya literata*, which is rare, possibly due to exclusion by unfavorable substrate conditions (Dando 2010).

Somewhat less common byssally attached bivalves are the oxytomiid *Oxytoma octavia* and the limid *Pseudolimea arctica*. *Oxytoma* is present in small numbers in most of the seep sites (Tab. 1). As all of the specimens are disarticulated, it is likely that *O*. *octavia* was living at some distance above the sediment-water interface and valves were reaching the seep substrate separately. Oxytomiids have similar morphology to pteriids, which usually attach to kelp, corals or other erect benthic organisms (Stanley 1970). *Oxytoma* species may have been partially pseudoplanktonic, as has been suggested for *O*. *inequivalve* (Duff 1975; Wignall & Simms 1990), but not exclusively, as it was also a bottom-dweller in low energy depositional environments (Kaim 2001). The right valves found represent only ca. 10% of the total number of valves found within the Spitsbergen seeps (Hryniewicz *et al*. in press), which is much less than that found in normal-marine fossil settings (≈ 35%; Wignall 1990b), so the smaller right valves may have dissolved. Limids, apart from the parasitic species *Acesta oophaga*, which feeds on the eggs of the siboglinid polychaete *Lamellibrachia luymesi* (Järnegren *et al*. 2005), have been occasionally reported as background fauna in some recent seep sites (e.g. Taviani *et al*. 2013). *Pseudolimea arctica* was an element of normal marine, shallow water faunas of the Boreal seas (Hryniewicz *et al*. in press) and was an epibenthic, byssally attached filter feeder, exploiting available hard substrates.

A few cementing bivalves identified as possible anomiids or dimyids have been found in the Spitsbergen seep fauna (Hryniewicz *et al*. in press). Recent anomiids are frequently associated with mangroves (e.g. Yonge 1977) and the abundance of driftwood in the Slottsmøya Member suggests they may have been delivered to the seep site with the wood. As most of the cementing biota, they require large hard surfaces for attachment (Stanley 1970). The single seep site where possible anomiids have been found also yields tubes of the serpulid polychaete *Propomatoceros* sp. (Vinn *et al*. in press), which also require larger hard surfaces for attachment. Other Spitsbergen seeps contain rare and dispersed tubes of the serpulids *Pyrgopolon*? and *Nogrobs*, which have only the juvenile stage cemented and thus are able to exploit small hard elements such as e.g. broken shells. *Pyrgopolon*? *nodulosum* form current-winnowed mass accumulations in the silty Echinoderm bed 45 metres lower in the Spitsbergen succession (Fig. 2; Vinn *et al*. in press), and is likely a member of a local background fauna. Spitsbergen seep serpulid taxa are present in Jurassic shallow marine sediments (Parsch 1956) and they probably represent colonists to the seep environment. *Propomatoceros* and possibly *Nogrobs* have been reported from some younger (Cretaceous) hydrocarbon seep carbonates of North America and Japan (Vinn *et al*. 2013).

Another element of hard substrate fauna are rhynchonellate brachiopods, which are very species-rich (up to 15 species), but not abundant (112 individuals; 5.6%) (Sandy *et al*. in press). The rhynchonellate brachiopod fauna is dominated by terebratulides, specifically terebratulidines (Fig. 5A, B). Among them, loboidothyridoids with long flanges on the brachidium dominate over short-flanged terebratuloids; terebratellidines are represented by three individuals only, and rhynchonellides are subordinate (Fig. 5A). As such, the composition of the latest Jurassic–earliest Cretaceous Spitsbergen brachiopod seep fauna is similar to coeval shelf brachiopod faunas of the Boreal Realm (Dagys 1968; Smirnova 1997). There is no similarity with other Jurassic–Early Cretaceous seep brachiopod faunas, which are characterized by monospecific mass-accumulation of dimerelloid rhynchonellids (Sandy 2010). There is also little similarity with younger Early Cretaceous (Sandy 1990) and Late Cretaceous (Kaim *et al*. 2010) brachiopod seep faunas, which are composed of single species only. Pedunculate brachiopods prefer carbonate for substrate, as their attachment is facilitated by chemical etching (Bromley & Surlyk 1972) and exposed carbonate as well as accumulation of shells were much more favorable for attachment than surrounding siliciclastic sediment. The single species of lingulid brachiopod *Lingularia similis*? (Fig. 5A; Holmer & Nakrem 2012) was, unlike rhynchonellate brachiopods, an infaunal filter feeder (Savazzi 1991). Extant lingulids are gregarious and populate subtidal to intertidal environments in tropical and subtropical seas (Craig 1952); they were possibly occupying comparable environments in the fossil record. *Lingularia* *similis*? has been noted from the Middle Jurassic (Bathonian) of Spitsbergen (Biernat & Emig 1993); lingulids were probably fairly common in the latest Jurassic–earliest Cretaceous shallow Boreal seas (e.g. Fürsich 1984) and were colonists of the seep environment.

Gastropods are rare in comparison to bivalves, but are also fairly diverse (Fig. 5A, B). The most common is *Ambercyclus* (Tab. 1; Ferrari *et al*. in press), cosmopolitan in Jurassic–Cretaceous normal-marine shelf settings (Huddleston 1892; Ferrari *et al*. in press). Closely related taxa are also known from Jurassic–Cretaceous seeps of California (Stanton 1895; Kiel *et al*. 2008a). Extant relatives of the family are widespread in deep oceanic fine-grained substrates and are selective deposit-feeders (Hickman 1981). It is notable that in Spitsbergen the seep eucyclids are most common in seeps developed in fine-grained sediments (Hryniewicz *et al*. 2012). The second most common gastropod in the seep sites is the rissoid *Hudlestoniella* (Tab. 1). This genus is also fairly common in Jurassic–Cretaceous shelf environments (Huddleston 1892; Beisel 1983; Kaim *et al*. 2004). Rissoids are in general very common in Jurassic–Cretaceous shallow water environments (e.g. Kaim 2001, 2004, 2008). In recent settings they are often associated with algae and cryptic environments beneath rocks, where they graze on surface films or feed on foraminifera (Warén 1996, Ponder & Keyzer 1998). Some rissoids have been occasionally found in recent chemosymbiosis-based ecosystems (Desbruyères *et al*. 2006; Sasaki *et al*. 2010), but it is not clear whether there is any trophic relation between them and the chemosymbiotic environment. Among rarer gastropods, hyalogyrinids (Tab. 1) have been reported in association with seeps, vents and other chemosymbiosis-based environments on several occasions (e.g. Warén & Bouchet 1993, 2009; Hasegawa 1997; Desbruyères *et al*. 2006). However, the family has also been reported from non-chemosymbiotic environments from both shallow (e.g. Haszprunar *et al*. 2011) and deep (e.g. Warén *et al*. 1996) settings in modern oceans; therefore, a link between them and the seep environment is unclear. The turbinid *Cantrainea* has been found in one of the seep sites (Tab. 1). This genus has been reported from Cretaceous (Kaim *et al*. 2009) and Miocene (Gill *et al*. 2005) fossil seep sites, and occurs in some recent seeps (e.g. Warén & Bouchet 1993) and vents (e.g. Okutani 2001, Okutani & Fujikura 1990). It has also been found in normal-marine, deep water sites (Warén & Bouchet 1993). The stomach contents of some species suggest they may be deposit-feeders (Warén & Bouchet 1993). Rare acmaeids have been noted in seep 9 (Tab. 1). Acmaeids have been previously recorded from hard substrates in some Late Cretaceous seeps (Jenkins *et al*. 2007b; Kaim *et al*. 2009) and a similar association has been noted from recent chemosymbiotic settings (e.g. Hashimoto *et al*. 1995). However, the family is not exclusive to chemosymbiotic settings as it is common also in normal-marine littoral environments and is a typical hard-substrate dweller (e.g. Tanaka *et al*. 2002). They were using hard substrates in the latest Jurassic–earliest Cretaceous seeps of Spitsbergen as one of the limpets was found attached to the posterior of a lucinid shell. A single gastropod identified as a possible member of the problematic family Maturifusidae has been found (Tab. 1; Kaim 2004; Bandel 2006). Maturifusids occur rarely in normal marine fine-grained shelf settings (e.g. Kaim 2008) and are very common around sunken driftwood (Kaim 2011). The feeding strategy of this group of gastropods remains unknown; they may have been either grazers or predator-scavengers, depending on which systematic affiliation is assumed (Kaim 2011).

Galatheid crustaceans occur in seep and vent environments (e.g. Sibuet & Olu 1998; Levin 2005), but they are not exclusive to them, occurring in shallow to deep water settings worldwide (e.g. Macpherson & Segonzac 2005). Galatheids can apply diverse feeding strategies, among which deposit-feeding and scavenging/predating are dominant and which can change seasonally (Nicol 1932; Romero *et al*. 2004). Crustacean body and trace fossils are not abundant in fossil seeps, but have been noted on several occasions from Late Jurassic and younger seep carbonates (Bishop & Williams 2000; Peckmann *et al*. 2007; Senowobari-Daryan *et al*. 2007). Galatheid crustaceans in seeps are known from the Eocene of Washington state, where mass accumulation of the apparently vent and seep-restricted genus *Shinkaia* suggests that at that time some members of the family were already adapted to the chemosymbiotic environment (Schweitzer & Feldmann 2008). Only a single, poorly preserved fragment of an appendage has been found in the Spitsbergen seeps (Fig. 9A), and it is difficult to say whether Spitsbergen galatheids had any direct relationship with the seep environment, as do some other galatheids (e.g. Baba & Williams 1998), or if they were members of the background fauna. The scarcity of this group on Spitsbergen seeps, and the absence of mass-accumulations of crustacean coprolites (Hryniewicz *et al*. 2012) suggest the latter.

Other fauna is rare. The few scaphopods (Fig. 9B) were possibly micropredators feeding on foraminifera (Dinamani 1964). Regular echinoids are represented by a single skeletal plate; a pedinoid *Hemipedina* sp. has been previously found in the echinoderm assemblage of the silty Echinoderm bed of the Slottsmøya Member, together with asteroids and ophiuroids (Rousseau & Nakrem 2012). It is likely that the plate found in the seeps also belongs to this genus. Pedinoids have weak teeth (Smith 1984) useful for picking food from the substrate rather than for grazing and rasping. Crinoids have also been found in the surrounding sediments (Rousseau & Nakrem 2012); the Spitsbergen seep findings represent stalked, benthic filter-feeders (e.g. Ausich *et al*. 1999). An ichthyosaur tooth (Fig. 9C) represents a fragment of pelagic-dwelling marine reptiles common in the Slottsmøya Member (e.g. Druckenmiller *et al*. 2012). A single aptychus (Fig. 9D) is a fragment of an ammonite feeding apparatus.

Based on the above, a composite interpretation of the latest Jurassic–earliest Cretaceous seep assemblage from Spitsbergen is shown on Figure 10.

*”Background” vs. ”seep-restricted” species*

Increased diversity and abundance of background species with respect to seep-restricted species is characteristic for shallow-water seeps and is believed to be caused by the increased delivery of photosynthetically-produced organic matter towards the seabed and more intense predation in shallow-water sites (Dando 2010). Studies on recent seeps in the Sea of Okhotsk show that shelf and upper slope seeps contain only background fauna, some of which may, or may not be, chemosymbiotic (Levin *et al*. 2000; Sahling *et al*. 2003). Where tested in other areas of the world, shallower seep sites in general do not have seep-restricted fauna, but instead very diverse background fauna (e.g. Dando 2010 and references therein). The background fauna populating the seep sites can be more diverse than that in the surrounding environment due to increased availability of hard substrate (Dando *et al*. 1991, 1994).

The contribution of the seep-restricted species to the overall fauna of the latest Jurassic–earliest Cretaceous Spitsbergen seeps is limited, as three or possibly four seep species represent only 7.4% of the species richness and 7.8% of the abundance (Fig. 6A, B). Three or possibly four species of seep-restricted fauna is less than in some deeper-water Mesozoic seep sites (11 in Omagari and 6 in Yasukawa sites). However, this value is still not significantly less than in most of the other Mesozoic deep-water seep sites (Kiel 2010b). The presence of a seep-restricted fauna in all except the shallowest Mesozoic shelf seep sites has been explained by the generally higher Mesozoic sea level limiting the delivery of photosynthetically-produced organic matter to deeper shelves, thus inhibiting the development of background fauna and enabling development of a seep-restricted fauna (Kiel 2010b). The background fauna in the Spitsbergen seeps is very abundant, comprising more than 92% of the total seep fauna (Tab. 5, Fig. 6A) and is very diverse, comprising more than 92% of all the species identified (Fig. 6B) and can therefore be explained by the shallow-water setting. The only other Mesozoic seep sites with similar background faunal diversity are the very shallow water (<100 m) Late Cretaceous Tepee Buttes from the Mid-Continent Seaway, USA (Kauffman *et al*. 1996), which have more than 150 recorded species of background fauna (Howe 1987; Kauffman *et al*. 1996; Kiel *et al*. 2012). Interestingly, other Mesozoic shelf sites, for example the middle to outer shelf Barremian Kuhnpasset seeps, contain only 3 species of background fauna (Kelly *et al*. 2000; Kiel 2010b).

The availability of hard substrate had a significant influence on the background fauna at the latest Jurassic–earliest Cretaceous Spitsbergen seeps, as many species found within the seep sites were hard-substrate dwellers. Some deficiency of hard substrate can still be noticed, as cementing species (possible anomiid bivalve and the serpulid *Propomatoceros* sp.) have been found in a single site only (Tab. 1), and other sites had mostly fauna attaching to smaller hard substrates such as broken or dead shells. The Simpson and Shannon diversity indices (*D*=0.79 and *H*=2.37) are fairly high, and the rank abundance plot (Fig. 3) also illustrates the low dominance in the seep fauna. The large number of rare taxa represented by a single specimen implies that the full species richness may be considerably higher than observed (*S*=54), as illustrated by the total richness estimator (Chao1=70) and the rarefaction curve (Fig. 4). Because of the difference in preservation potential between the seep carbonate and the background shale, a quantitative comparison of seep and non-seep faunal diversity has not been carried out. In addition, both species richness and evenness may be inflated by the pooling of seep collections spanning a long time interval. Nevertheless, it is clear that the seep fauna is highly species rich and with high evenness, indicating a late-successional, stable community. Ritt *et al*. (2011) reported similar macrofaunal diversities in a Recent soft-bottom, deep-water (1150 m)seep area of the Amon Mud Volcano, Nile Delta (*S*=15, *D*=0.78, *H*=1.93), and also at a non-seep reference site (*S*=8, *D*=0.83, *H*=1.92). A similar situation was observed at clam beds in bathyal seepage sites in the East Pacific by Levin *et al*. (2003, 2010), where macrofaunal diversity was similar or higher than at non-seep sites (Levin *et al*. 2003, 2010). However, lower diversity at seep sites than at reference sites is also frequently observed (Sahling *et al*. 2002; Levin *et al*. 2010; Menot *et al*. 2010). Lower diversity at seep sites may partly be caused by episodic seepage favoring early-successional species, or very high hydrocarbon fluxes leading to toxic conditions (e.g. Ritt *et al*. 2011). Consequently, the high diversity in the Spitsbergen seeps is in accordance with a relatively weak flux hypothesis.

Conclusion

The latest Jurassic–earliest Cretaceous hydrocarbon seeps from Spitsbergen formed in a restricted, epicontinental sea supporting a diverse assemblage of metazoans. Organic matter produced within the water column and transported from the land was largely preserved within the sediment and may have contributed to the fluid seepage, affecting large areas of the palaeo-Barents Sea. At most of the seep sites, flux was weak and probably not able to lift the sulphide layer towards the seabed to an extent large enough to support tube worm bushes or extensive bacterial mats supporting significant numbers of hokkaidoconchid gastropods. Most of the chemosymbiotic fauna had to rely on infaunal sulphide sources. The youngest seep 9 was probably a very low and diffuse flux site, containing deep-burrowing lucinid and thyasirid bivalves mining for sulphide down to depths of dozens of centimetres. The Spitsbergen seeps supported a diverse and rich background faunal assemblage, represented predominantly by many species known from normal marine environments of the Boreal realm. This, together with a small diversity and low abundance of seep-restricted fauna of the Spitsbergen seeps is typical for shallow water conditions, probably slightly deeper that that of the Late Cretaceous Western Interior Sea seeps, which formed in less than 100 m of water.

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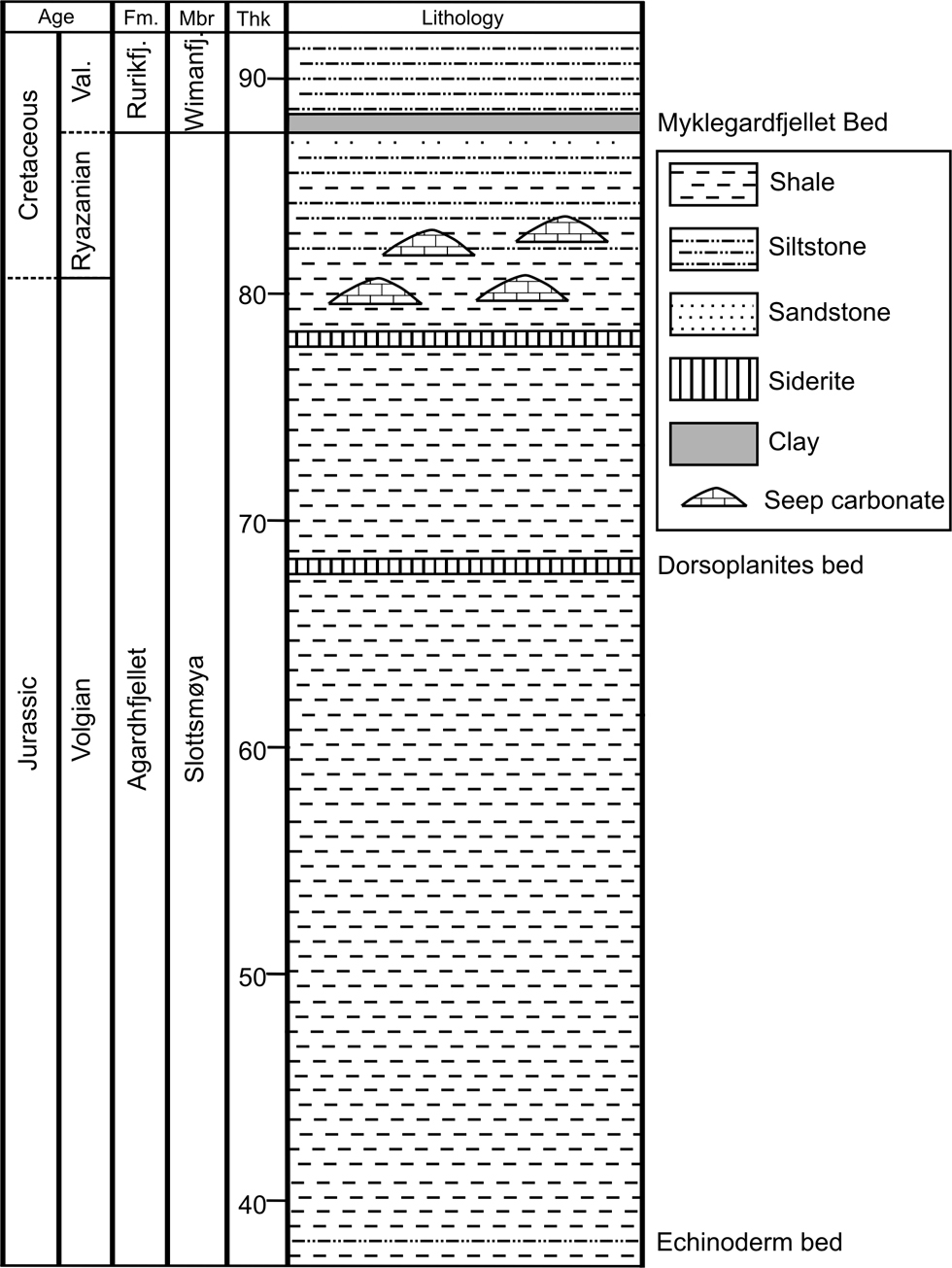
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*Figure captions and tables*

**

*Fig. 1*. Map showing location of the hydrocarbon seep carbonates on Spitsbergen, Svalbard. Modified from Dallmann *et al.* (2001). ‘Eb’ marks the outcrop of Echinoderm bed with mass accumulation of serpulid tubes.



*Fig. 2*. Simplified profile of the upper part of the Slottsmøya Member, Agardhfjellet Formation at the Janusfjellet section, Spitsbergen. ‘Echinoderm bed’ marks the position of most of the echinoderms described by Rousseau & Nakrem (2012). Modified from Wierzbowski *et al.* (2011).



*Fig. 3*. Rank abundance plot for the latest Jurassic–earliest Cretaceous Spitsbergen seep fauna. S=52 results from *Camptonectes* (*Camptochlamys*) *clathratus* and *Camptonectes* (*Costicamptonectes*) *milnelandensis* treated together with *Camptonectes* spp.



*Fig. 4*. Rarefaction curve for the latest Jurassic–earliest Cretaceous Spitsbergen seep fauna (red line) with 95% confidence intervals (blue lines).



*Fig. 5*. Pie charts showing A) abundance and B) species richness of the major groups in the latest Jurassic–earliest Cretaceous Spitsbergen seep fauna. The empty field on chart A) is a composite of crustaceans, echinoids, scaphopods, terebratellidinids and vertebrates (10 individuals altogether).



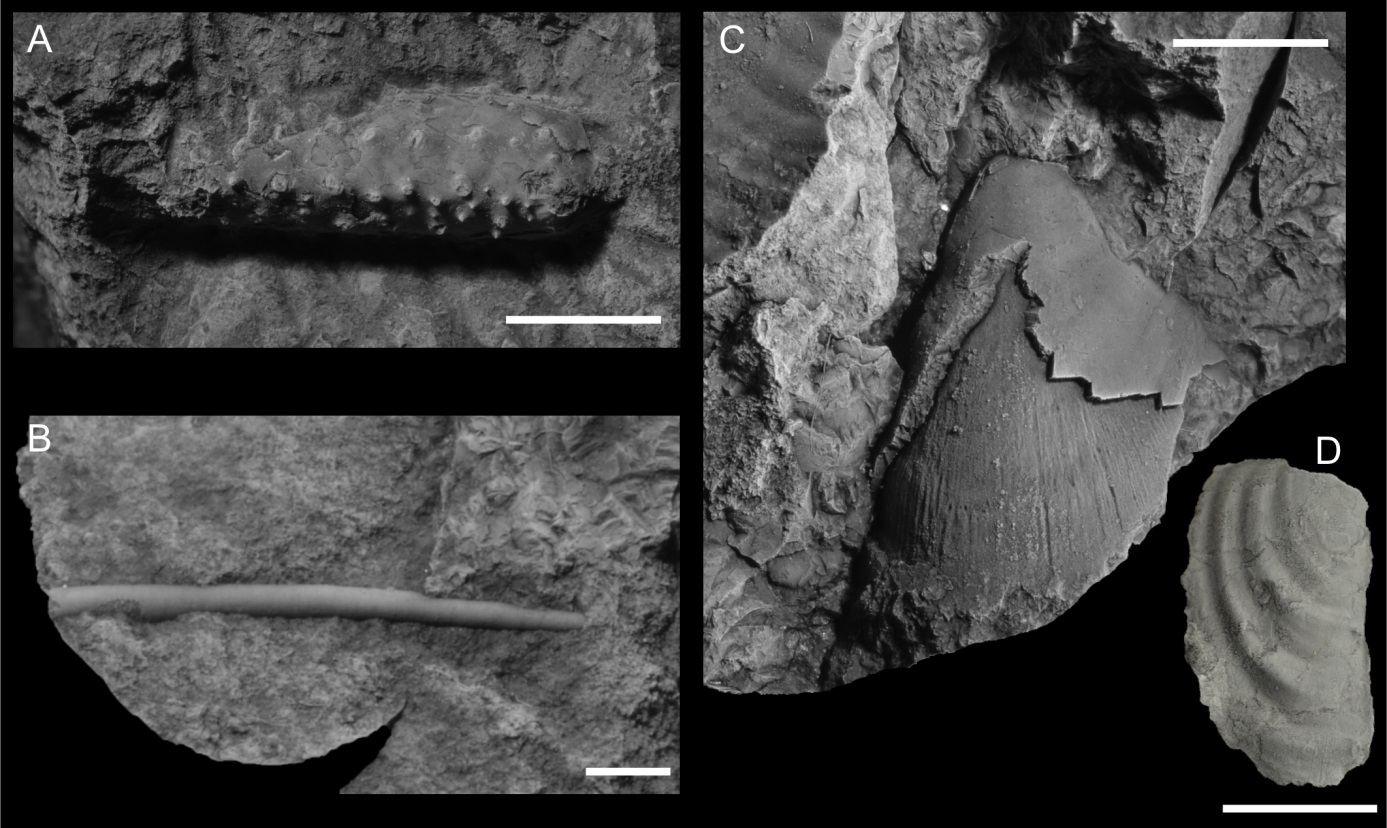
*Fig. 6*. Pie charts showing A) abundance of seep-restricted and background fauna and B) species richness of the latest Jurassic–earliest Cretaceous Spitsbergen seep-restricted and background faunas.



*Fig. 7.* A) Fragment of sunken driftwood (empty arrow) and white quartz pebble (white arrow) from seep 3. PMO 225.166. B) Tubular concretion representing a possible fluid conduit. Close (ca. 4 m) to seep 2, PMO 225.168. Scale bars 7 mm (A), 5 cm (B).



*Fig. 8*. Palaeogeographic map showing the position of the latest Jurassic–earliest Cretaceous Spitsbergen seeps (star). NA—North Atlantic, N-GS—Norwegian-Greenland Seaway, NSRS—North Sea Rift System, P-BS—Palaeo-Barents Sea, RS—Russian Seaway, T—Tethys, T-PS—Timan-Petchora Sea. Map by Ron Blakey, modified from <http://cpgeosystems.com/paleomaps.html>.



*Fig. 9*. Additional fossils from the latest Jurassic–earliest Cretaceous Spitsbergen seeps. A) Fragment of an appendage of a possible galatheid crustacean, seep 4, PMO 225.167. B) Scaphopod, seep 9, PMO 225.169. C) A tooth of a possible ichthyosaur, seep 8, PMO 217.564. D) Aptychus, seep 8, PMO 225.170. Scale bars 5 mm (A, C), 1 mm (B), 1 cm (D).



*Fig. 10*. Composite interpretation of the latest Jurassic–earliest Cretaceous Spitsbergen seep assemblage. Not to scale. 1) *Pseudotrapezium* aff. *groenlandicum*, 2) Pectinida gen. et. sp. indet. attached to a carbonate hardground, 3) *Propomatoceros* sp. attached to a carbonate hardground, 4) serpulids with erect tubes (*Pyrgopolon*? spp. & *Nogrobs* aff. *quadricarinata*, 5) current-winnowed mass accumulations of *Pyrgopolon*? aff. *nodulosum*, 6) drifting algal fronds, 7) tubular conduits, 8) *Goniomya literata*, 9) *Ambercyclus* sp. , 10) terebratulide brachiopods, 11) *Mesosaccella* *rogovi* A, 12) regular echinoid, 13) possible galatheid, 14) hexactinellid sponge, 15) Non-serpulid worm tubes, 16) Hokkaidoconchidae gen. et sp. indet., 17) *Oxytoma octavia*, 18) asteroids and ophiuroids, 19) sunken driftwood, 20) crinoids, 21) chert and quartz pebbles, 22) *Camptonectes* spp., 23) *Buchia* spp., 24) *Lingularia similis*?, 25) *Cantrainea* sp., 26) Hyalogyrinidae gen. et sp. indet. 27) *Hudlestoniella* sp., 28) Acmeidae? gen. et sp. indet. attached to the shell of a exposed dead lucinid *Tehamatea rasmusseni*, 29) *Pseudolimea arctica*, 30) sunken algal fronds with pebble in holdfast, 31) scaphopods, 32) *Cretaxinus hurumi* 33) *Mesosaccella* *toddi*B, 34) *Solemya* (*Petrasma*) cf. *woodwardiana*, 35) *Tehamatea* *rasmusseni*, 36) rhynchonellide brachiopods, 37) *Dacromya chetaensis*, 38) *Nucinella* *svalbardensis*, 39) mass accumulation of *Pseudotrapezium* aff. *groenlandicum*, 40) ammonoids, 41) belemnoids, 42) an ichthyosaur. Sparse stippling represents mud, dense stippling represents silt and sand.