Benthic communities at high-Arctic cold seeps

Faunal response to methane seepage in Svalbard

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Emmelie K.L. Åström
A dissertation for the degree of Philosophiae Doctor – April 2018

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Illustration iii: cc *www.blacklamb.net/2011/09/line-drawing-tree.html*

Där under trädet, bakom stängslet
finns en stig för dig

Fortsätt...

Jag tror att när vi går igenom livet
att det bästa inte hänt än

- H. Hellström

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Starting a PhD-project is a challenge, finishing a PhD degree is an even bigger one and it would not be possible without many helpful and encouraging people.

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SUMMARY

Cold seeps are chemosynthetic habitats found in both deep sea and shallow ocean-shelves worldwide, including the polar regions. At seeps, hydrocarbons, sulfide, and other reduced compounds emerge from the seafloor, providing energy to fuel chemoautotrophic production. Microbial assemblages, supported by the oxidation and reduction of gases and fluids, form the base of a food web composing unique and specialized cold-seep ecosystems.

Several methane cold seeps have been documented in the high-Arctic, offshore Svalbard and in the Barents Sea, within the depth range of 85-1200 m. The widespread seabed gas seepage in these areas can be a strong environmental driver, influencing the local seafloor conditions and biosphere, including benthic community structure and ecosystem function.

The primary aim of this doctoral thesis has been to describe the current seep-associated communities and habitats located on the shelf of western Svalbard and in the Barents Sea. This included determining the ecological structure, diversity and food web interactions of macrofaunal assemblages at high-Arctic cold seeps, describing how they compare with conventional non-seep communities, and examining the interaction between seep and non-seep communities where they co-occur.

Key findings from the study are:

1) Cold seeps have a strong, localized effect over small spatial scales, supporting dense communities of small chemosymbiotic worms that play a fundamental role in structuring the seabed animal community

2) Cold seeps are identified as focal areas for the biosphere, providing heterogeneous substrates and additional food resources independent of photosynthetic sources from the surface ocean, resulting in animal aggregations at these habitats.

3) Methane-derived carbon is incorporated into the food web of the Barents Sea ecosystem.

4) The discovery of two new species of methane-associated bivalves at Svalbard cold seeps.

Cold seeps in the Arctic are of high ecological importance and methane is a key environmental driver of the biological system. Characteristic seep features, such as methane derived carbonate rocks and chemosymbiotic worm tufts, add complexity and 3D structure to the otherwise relatively flat and barren seafloor. Cold seeps provide shelter and substrate to both infauna and sessile organisms at seafloor, and to larger motile animals. Furthermore, cold seeps and seabed methane emissions add a supplementary energy source into the Arctic ecosystem. By combining results of analyses from different benthic habitats, this doctoral research project provides new insights into Arctic faunal community patterns at high-latitude cold seeps.

The beginning of knowledge is the
discovery of something we do not understand

- Frank Herbert

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PREFACE

This doctoral thesis was carried out at the Department of Geosciences and UiT - The Arctic University of Norway, Tromsø, from April 2014 to April 2018. Funding was provided from the Research Council of Norway; funding scheme # 223259 for its Centre of Excellence CAGE – Centre for Arctic Gas Hydrate, Environment and Climate. The scientific content of this doctoral thesis has been supervised by Professor JoLynn Carroll (Akvaplan-niva and the Department of Geosciences, UiT - The Arctic University of Norway, Tromsø), Dr. Michael L. Carroll (Akvaplan-niva and CAGE) and Professor William G. Ambrose Jr (Department of Biology, Bates College).

Findings and conclusions from this doctoral project have been presented in poster and oral presentations in various international conferences and meetings within the field of bio-geosciences, marine ecology and Arctic biology such as Arctic Frontiers, Benthic Ecology Meeting (BEM), Gordon Research Conference (GRC) on natural gas hydrate systems, Gas In Marine Sediments (GIMS), and Chemosynthetic Based Ecosystems (CBE6). At the European Geological Union (EGU) 2016 general assembly, I was invited as a panelist at a press conference on methane release in the Arctic and biological impacts for the session: *"Giant seafloor craters and thriving fauna: methane seepage in the Arctic"* as one of eight sessions at the overall conference.

As a doctoral candidate at the department of Geosciences UiT - The Arctic University of Norway, Tromsø, I have been a member of two research schools:
AMGG - Arctic Marine Geology and Geophysics and ARCTOS - The Arctic Marine Ecosystem Research Network, in Tromsø. Furthermore, the position at the department of Geosciences has included assigned duty work, where I have been involved in teaching, cruises, seminars and other activities within the department.

This doctoral thesis is composed of an introduction and summary of the work conducted and three scientific peer reviewed and published articles and one manuscript in preparation. The articles provide new knowledge of previously poorly known Arctic cold seep ecology and how sub-seabed gas emissions influence benthic faunal communities offshore Svalbard and in the Barents Sea. During this PhD-project, I have also contributed to the work in Ambrose et al. (2015) and Sen et al. (2018).

LIST OF PAPERS

Article I:

Åström, E. K. L., Carroll, M. L., Ambrose, W. G., & Carroll, J. (2016).

Arctic cold seeps in marine methane hydrate environments : impacts on shelf macrobenthic community structure offshore Svalbard

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Article II:

Åström, E. K. L., Carroll, M. L., Ambrose, W. G., Sen, A., Silyakova, A., & Carroll, J. (2017).

Methane cold seeps as biological oases in the high-Arctic deep sea.

Limnology and Oceanography, 1–23. https://doi.org/10.1002/lno.10732

Article III:

Åström Hammenstig E. K. L., Carroll, M. L., Sen, A., Niemann, H., Ambrose, W. G., Lehman F.M., & Carroll, J.

Trophic interactions and community structure at Barents Sea cold seeps

(manuscript)

Article IV :

Åström, E. K. L., Oliver, P. G., & Carroll, M. L. (2017). **A new Genus and two new Species of Thyasiridae Associated with Methane Seeps off Svalbard, Arctic Ocean**.

Marine Biology Research, 13(4), 402–416. https://doi.org/10.1080/17451000.2016.1272699

INTRODUCTION

1.1 Background

Prior to the start of this doctoral thesis in 2014, Arctic cold seep biology was a poorly explored topic, with only a limited number of studies focusing on ecology, ecosystem functions and faunal communities at seeps in the Arctic. The most well documented location in the Arctic was Håkon Mosby Mud Volcano (HMMV) located in the southern Barents Sea at 72° N and 1200 m water depth. Since the discovery of HMMV, the site has been of focus for many biogeochemical studies documenting the system (e.g. Vogt et al. 1997; Niemann et al. 2006; Lösekann et al. 2007; Decker et al. 2012). The habitat around the circularl shaped mud volcano exhibit of different zones covered by large microbial mats and chemosymbiotic fauna, represented by siboglinid worms, (family Siboglinidae), *Oligobrachia haakonmosbiensis* and *Scleronlinum contortum,* (Gebruk et al. 2003). There was a high degree of mixing with conventional 'background' species at HMMV and moreover, it was confirmed that a few taxa associated with the tufts of chemosymbiotic tubeworms (e.g. caprellid shrimps) showed input of chemosynthesis-based nutrition, revealed by stable isotope analysis of carbon (δ^{13}C) (Gebruk et al. 2003; Decker and Olu 2012; Rybakova et al. 2013). Further north of the HMMV, several locations are known offshore Svalbard and in the Barents Sea where sub-seabed gas reservoirs have been located and where hydrocarbons (methane) emanate from the sea floor (Solheim and Elverhøi 1993; Vogt et al. 1994; Westbrook et al. 2009). At the time, it was known that Arctic seafloor and permafrost regions can store vast amounts of methane hydrates (clathrates) in the seabed provided that there is continuous high pressure and low temperatures (MacDonald 1990). Since methane is a potent greenhouse gas and with concerns about rapid Arctic warming, scientific attention was raised to elucidate the role of methane and climate change in the Arctic (MacDonald 1990; Lashof and Ahuja 1990; Hunter et al. 2013).

Large field campaigns were initiated through the framework by the Center for Arctic Gas Hydrate, Environment and Climate (CAGE), focused on Arctic sources and sinks of gas hydrates and methane and its impact in the environment and climate system, starting in November 2013. With an interdisciplinary approach and based on prior geophysical investigations, a few target areas were selected to form a basis of the cold seep ecology research that is the focus for this doctoral thesis (Figure 1). The areas of interest in this project have been widely distributed, covering cold seeps both in the deep sea and at the Svalbard shelves, including the Barents Sea, within the depth range of 85 m – 1200 m.
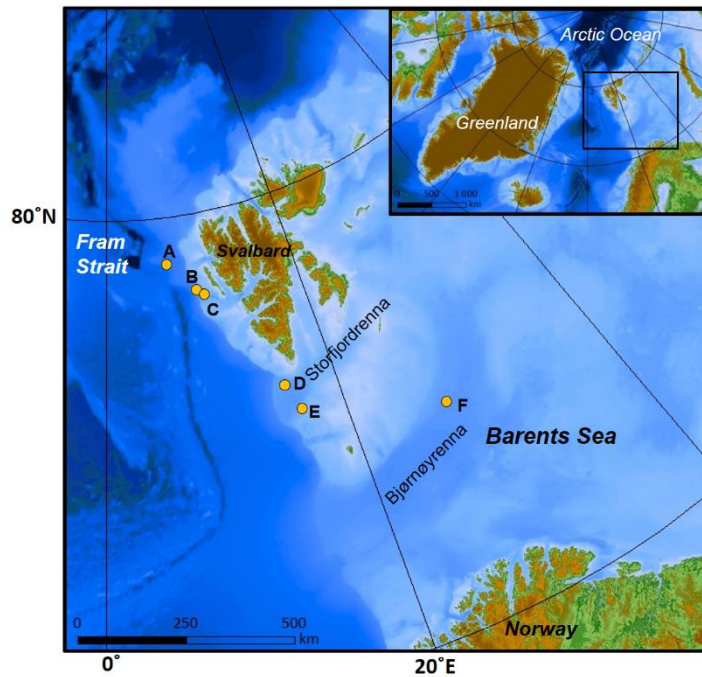
Figure 1: Methane seep locations (85-1200 m water depth) identified offshore western Svalbard and in the Barents Sea targeted and for biological and ecological surveys during 2014-2016 for this doctoral project. A – Vestnesa Ridge (VR) 1200 m deep, B - Prins Karls Forland (PKF 1) 240 m, C – Prins Karls Forland (PKF 5) 85 m, D – Storfjordrenna Gas Hydrate Mounds (GHM) 380 m, E – Storfjordrenna seep (SR) 350 m, F – Bjørnøyrenna Crater Area (BR) 335 m. Bathymetry from IBACO v. 3 Jakobsson et al. (2012).

1.2 Arctic Marine Ecosystems

Marine environments in the high Arctic are characterized by pulsed and intense seasonality in terms of light regime, sea ice cover and productivity. Temperatures are typically low, and fjords and deep basins can be exposed to sub-zero temperatures in bottom waters. These environmental characteristics are all strong drivers of benthic communities in Svalbard and the Barents Sea (e.g. Wlodarska-Kowalczuk et al. 2004; Berge et al. 2005, 2015, Carroll et al. 2008, 2011; Cochrane et al. 2012; Hunt et al. 2013; Kędra et al. 2013). Sea ice cover and seasonal variations create a strong link between primary productivity and processes in the pelagic realm and the export of organic material to the seabed (pelagic-benthic coupling) (Grebmeier and Barry 1991; Renaud et al. 2008; Wassmann and Reigstad 2011; Søreide et al. 2013). The Arctic shelves are productive regions and the Barents Sea is considered to be an ecological hotspot for the circumpolar Arctic and also an economically important region, with one of the richest fisheries in the world (Wassmann et al. 2006; Kjesbu et al. 2014; Haug et al. 2017). The interplay between cold Arctic waters and the input of warm Atlantic water, seasonal sea-ice cover and interactions in pelagic-benthic coupling, creates a

highly productive shelf region (Sakshaug 2004; Tamelander et al. 2006; Ingvaldsen and Loeng 2009; Degen et al. 2016).

Climate change is already evident in Arctic ecosystems. For the future, the Arctic is projected to undergo extensive environmental changes including reduced sea-ice cover, altered oceanographic patterns and increased ocean acidification (Włodarska-Kowalczuk and Weslawski 2001; Weslawski et al. 2011; Haug et al. 2017; Onarheim and Årthun 2017). Furthermore, it is predicted that such environmental changes will have large implications for the entire ecosystem including carbon cycling, biological productivity and biodiversity, and modified biogeographical bounderies (Fossheim et al. 2015; Renaud et al. 2015; Haug et al. 2017; Frainer et al. 2017).

1.3 Cold Seeps and Chemosynthetic Environments

Locations where emissions of methane, sulphide, or other reduced chemicals occur at the seafloor are known as cold seeps, and such places are documented from both deep sea and shallower ocean shelves worldwide (Foucher et al. 2007; Vanreusel et al. 2009; Olu et al. 2010; Levin et al. 2016). Cold seeps typically support distinct faunal communities, different from the surrounding area, and organisms living at seeps can rely directly or indirectly on anaerobic oxidation of methane (AOM) and sulphate reduction as an alternative energy source (Levin and Michener 2002; Boetius and Suess 2004; Niemann et al. 2006; Thurber et al. 2013). This process is known as chemosynthesis and can be an important energy source, especially in the deep sea, in addition to photosynthesis that takes place in the upper part of the world's oceans (Levin 2005; Levin et al. 2016). In this way, cold seeps are similar to hydrothermal vents where chemosynthetic biological communities can establish and thrive where hot fluids are emitted from the seabed. However, hydrothermal vents are linked to geothermal activity at the seafloor and are concentrated along the Earth's mid - ocean ridges and spreading zones, whereas cold seeps typically originate from gas reservoirs or hydrocarbon fluids in the sub-seabed, usually along continental margins and shelves (Van Dover 2000; Vanreusel et al. 2009; Levin et al. 2016).

Gases emitted at cold seeps can originate from dissociating clathrates or gas hydrates stored in sub-seabed reservoirs. Gas hydrates are ice-crystals that enclose natural gases such as methane, and these are stable in the seabed at high pressure and low temperatures. If the pressure decreases or the temperature increases, the gas hydrate stability zone (GHSZ) (the zone where the gas hydrates are stable in the ground) will change. This may lead to dissociation of gas hydrates, where the enclosed gas can be released into the seabed and eventually also to the water column (MacDonald 1990; Ferré

et al. 2012; Hunter et al. 2013). Dissociating hydrates and hydrocarbon emissions influence ocean chemistry (Hunter et al. 2013, Myhre 2016), and in shallow regions, gas can escape through the water column with the potential to reach the atmosphere (Ferré et al. 2012, Berndt et al. 2014, Sahling et al. 2014).

At cold seeps, long-term methane seepage can generate carbonate outcrop formations known as methane derived authigenic carbonates (MDAC). The precipitation of MDAC at cold seeps is the result of AOM and sulphate reduction through a consortium of various microbes (Hovland et al. 1987; Ritger et al. 1987; Bohrmann et al. 1998). Furthermore, cold seeps are also regularly associated with other distinctive seafloor features like pockmarks, craters, mounds or underwater pingos (Dando 1991; Long et al. 1998; Hovland and Svensen 2006; Ritt et al. 2012; Zeppilli et al. 2012). Large topographical structures at the seafloor add habitat-space complexity and heterogeneity, which can be particularly important in structuring deep-sea environments where relatively homogenous and featureless soft bottom plains are predominant (Rex 1981). In addition, such 3D features can attract vagrant fauna from surrounding habitats and increase local megafaunal diversity (Sellanes et al. 2008; Meyer et al. 2014).

Cold seeps are inhabited by various types of animal guilds including chemosymbiotic organisms (i.e. organisms dependent on mutualistic microbial synergies providing them with energy), microbial grazers or heterotrophic animals that exploit resources provided by the seep environment (Decker and Olu 2012; Thurber et al. 2013; Becker et al. 2013; Zapata-Hernández et al. 2014). Chemosymbiotic vesicomyid clams and bathymodiolin mussels (supported by microbial symbionts) are typical cold seep bivalves that are able to form large assemblages at the sea floor (Levin et al. 2003; Sahling et al. 2003; Cordes et al. 2010). Furthermore, chemosymbiotic siboglinid worms such as vestimentiferan tubeworms, can form large bush-like associations at cold seeps (Levin 2005; Olu et al. 2009; Carlier et al. 2010). These particular taxa are characteristically found at cold seeps and can all be recognized as 'ecosystem engineers', modifying and structuring their surrounding habitat in terms of influencing sediment chemistry by burrowing or re-working sediment or providing substrate for other organisms (Bergquist et al. 2005; Levin 2005; Olu et al. 2017). Ecosystem engineers enhance habitat availability for other animals and can in this way increase local biodiversity on different spatial scales (Jones et al. 1994; Levin 2005; Guillon et al. 2017).

1.4 Using Stable Isotope in Ecological Analysis

Stable isotope analyses of $\delta^{13}C$ and $\delta^{15}N$ are used to trace carbon sources of animal tissue and to elucidate nitrogen sources and trophic levels in targeted organisms by comparing the ratio of naturally occurring stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) (Peterson et al. 1987; Hobson and Welch 1992; Søreide et al. 2006). Carbon isotopes obtains a specific ratio depending on the carbon fixation pathway, and can vary largely among carbon sources, producing a distinct imprint of the surrounding environment (Childress et al. 1986; Fry and Sherr 1989). Because of these varying carbon fixation pathways and isotopic fractionation, carbon assimilated from hydrocarbon resources can have a particularly depleted signal ($\delta^{13}C$ typically < -30 ‰), distinct from carbon originating from marine phytoplankton primary production ($\delta^{13}C$ ~ typically around -20‰ to -25‰) (Childress et al. 1986; Hobson and Welch 1992; Dando and Hovland 1992; Levin and Michener 2002; Levin et al. 2016). During the lifetime of an organism, carbon is incorporated into its tissue, however, the ratios change little with trophic transfers (Peterson et al. 1987; Fry and Sherr 1989; Layman et al. 2012). Depending on the overriding carbon source in an organism's habitat, stable isotope analysis of $\delta^{13}C$ can provide an indication of original sources of dietary carbon.

Nitrogen and the ratio between ($^{15}N/^{14}N$) is a useful tool to reveal trophic interactions among organism where the ratios of nitrogen isotopes, $\delta^{15}N$, relative to atmospheric nitrogen, is enriched in organisms at each trophic transfer (i.e. primary producers, first consumers 'grazers', secondary consumers 'predators') (Layman et al. 2012). Each trophic level is enriched typically by 3.4‰ to 3.8‰, leading to high enrichment of $\delta^{15}N$ in top predators (Fry 1988; Hobson and Welch 1992; Søreide et al. 2006; Layman et al. 2012). Isotopic fractionation occurs as a result of mass-balance and kinetic dynamics in natural environments, where the lighter isotopes are more mobile in a system relative to heavier isotopes (Peterson et al. 1987; Robinson et al. 2012).

In the Arctic and Barents Sea, offshore of coastal areas, we find two main marine carbon sources and primary producers; phytoplankton and ice algae (characteristic of $\delta^{13}C$ ~ -23‰ to -25‰ and -19‰ to -21‰ respectively) (Hobson et al. 1995; Tamelander et al. 2006; Søreide et al. 2006). Nitrogen values for phytoplankton and ice-algae are typically around $\delta^{15}N$ 4-6 ‰ and slightly higher for re-mineralized or decomposed sedimentary organic matter (Schubert and Calvert 2001; Søreide et al. 2006; Bergmann et al. 2009). In reduced environments, such as cold seeps, fauna hosting chemoautotrophic symbionts can exhibit particularly light $\delta^{15}N$ signals, sometimes also negative, since assimilation or fixation of inorganic nitrogen is possible (Lee and Childress 1994; Robinson

et al. 2012; Becker et al. 2013; Portail et al. 2016). By combining analyses of stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to assess energy sources and trophic structure, it is possible to study ecosystem food web dynamics and generate new insights on faunal interactions.

1.5 Arctic Cold Seeps

Cold seeps are recognized in all world oceans including polar regions (Domack et al. 2005; Paull et al. 2015; Åström et al. 2016; Demina and Galkin 2018). The hydrocarbon emissions recognized offshore Svalbard are believed to be caused by pressure and temperature changes linked to the most recent glacial period and the last glacial maximum (LGM) (Patton et al. 2015; Portnov et al. 2016; Wallmann et al. 2018). During this period of time, a large part of the Arctic and Northern Europe was covered by an extensive glacial ice sheet (the Eurasian Ice Sheet) (Ingólfsson and Landvik 2013; Patton et al. 2015, 2017; Łącka et al. 2015). Around Svalbard, a marine-based ice sheet, the Barents Sea Ice Sheet (BSIS), influenced the pressure and temperature boundaries in the seabed and gas hydrates remained stable (Portnov et al. 2016; Winsborrow et al. 2016; Wallmann et al. 2018). When deglaciation of the BSIS was initiated at the Barents Sea shelf-break, approximately 20 000 years ago this was followed by decreased pressure and increased temperature that changed the GHSZ (Rasmussen et al. 2007; Winsborrow et al. 2016; Serov et al. 2017; Wallmann et al. 2018). The changing pressure phase boundaries and rising temperatures triggered gas hydrate disassociation and allowed gas to escape through the seabed (Portnov et al. 2016; Andreassen et al. 2017; Wallmann et al. 2018).

The widespread gas seepages in Svalbard and the Barents Sea indicates that such seabed emissions can be a strong environmental driver influencing the biosphere and local seafloor conditions, including community structure and ecosystem function. The primary aim has been to describe the current seep-associated communities and habitats located on the shelf of western Svalbard and in the Barents Sea. This included determining the ecological structure and diversity of macrofaunal assemblages at high-Arctic cold seeps, describing how they compare with conventional, non-seep communities and examining the interaction between seep and non-seep communities where they co-occur. By combining results of analyses from different benthic habitats, this doctoral research project provides new insights into Arctic faunal community patterns at high-latitude cold seeps.

1.6 Objectives

The overall objective has been to examine the benthic community structure, diversity and trophic relationships at high-Arctic cold seeps.

- What are the faunal characteristics at methane cold seeps around Svalbard?
- How do seabed methane emissions influence the structure of benthic communities?
- To what extent do benthic macrofauna use chemosynthesis-derived carbon as a potential energy source?
- What are the basic food webs and trophic relationships at Arctic cold seeps?

The areas of focus in this study have been the western and central Barents Sea and the continental margin and shelf west of Svalbard (75˚-79˚ N). Svalbard has relatively mild climate considering its high-Arctic location. This is a result of the North Atlantic Current (NAC) system, which transports warm and saline water from the Atlantic Ocean along the west coast of Svalbard (Orvik and Niiler 2002, Rudels et al. 2005) (Figure 2). The western continental shelf areas west of Svalbard are typically influenced by Atlantic source water (>35 psu and >3°C) (Svendsen et al. 2002, Cottier et al. 2005, Nilsen et al. 2008). At the Barents Sea shelf, cold Arctic water (< 34.8 psu and <0°C) encounters the warmer Atlantic water in a mixing zone known as the 'Polar Front'. The mixing of Arctic and Atlantic influenced water masses and the Polar Front generate high productivity and strong linkages between ice-ecosystems and pelagic-benthic coupling at the shelf (Wassmann and Reigstad 2011; Søreide et al. 2013).
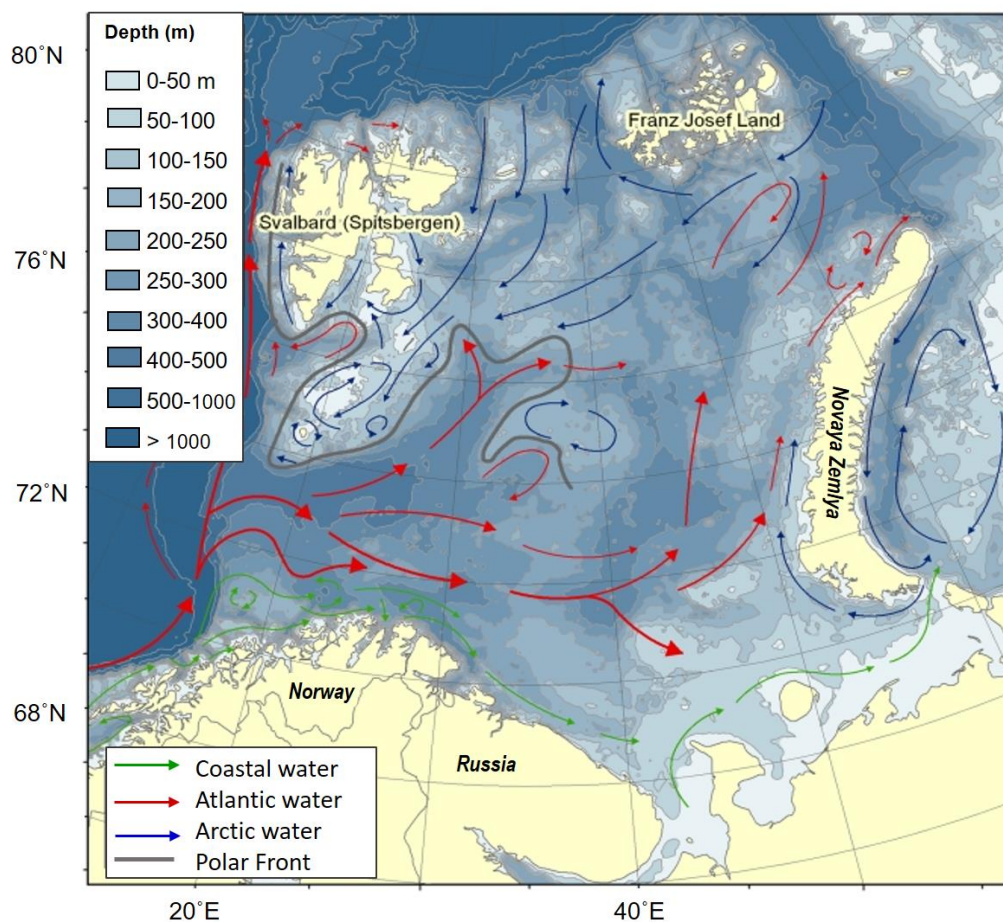

Figure 2: Surface current regime around Svalbard and in the Barents Sea. Modified after Loeng (1991) and Johannesen et al. (2012).

2.1 Environmental Settings of the Western Svalbard Shelf

The island Prins Karls Forland (PKF) is located along the continental shelf and western Svalbard margin (Figure 1). At the PKF shelf, numerous places of seabed seepage have been reported within the depth range of 80-400 (Westbrook et al. 2009; Sahling et al. 2014) and moreover, elevated concentrations of methane have been measured in the water column (Graves et al. 2015; Steinle et al. 2015). This area is strongly influenced by warm Atlantic water masses originating from the NAC, strong currents and typically little or no ice cover throughout the year. The sediment at Prins Karls Forland margin is mainly composed of silty hemi-pelagic mud covered by a heterogeneous coarse mix of gravel, sand and ice rafted debris (IRD) (Åström et al. 2016).

2.2 The deep Vestnesa and Svyatogor Ridges

Vestnesa Ridge is a sediment drift ridge at 1200 m water depth, located in the Fram Strait at 79˚ N, along the northeast North Atlantic continental margin (Figure 1). The Fram Strait plays an important role in the large-scale circulation and is the main passage where deep-water and intermediate-water exchange occurs between the Arctic and the Atlantic Seas (Rudels et al. 2000). Vestnesa Ridge stretches over approximately 100 km, north of the Molloy transform fault in a southeast-northwest direction and a large part of the ridge is characterized by circular depressions described as pockmarks (Büenz et al. 2012; Plaza-Faverola et al. 2015). Pockmarks are features formed in near surface sediments where upward seepage of gas causes a sediment collapse (Cathles et al. 2010). High concentrations of methane have been detected both in the sediment and water column at Vestnesa pockmarks, together with gas hydrate recovery (Figure 3) (Hong et al. 2016; Åström et al. 2017a). A few 10's of kilometers southwest of Vestnesa lies Svyatogor Ridge, located at the northwestern tip of Knipovich Ridge. There is no active sign of methane gas venting from sediments nor escaping into the water column at Svyatogor; however, seismic profiles indicate paleo-seep features including pockmarks, chimneys (acoustic blanking) and subsurface gas deposits.

2.3 Western Barents Sea – Storfjordrenna and Gas Hydrate Mounds

Southeast of Svalbard is the Barents Sea shelf located with average water depth of ~230 m. The Barents Sea was largely covered by glacial ice during the LGM peaking around 23 000 years before present (BP) and started to deglaciate approximately 20 000 years BP (Rasmussen et al. 2007; Ingólfsson and Landvik 2013; Patton et al. 2015). Shallow banks and deep troughs characterize the

Barents Sea and the sea floor holds many postglacial features including megascale glacial lineations, grounding zones, wedges, and ice berg plough marks (Andreassen and Winsborrow 2009; Dowdeswell et al. 2010; Patton et al. 2015; Esteves et al. 2017). In the Barents Sea, cold Arctic and warmer Atlantic water masses meet in the 'Polar Front' (Johannessen and Foster 1978, Harris et al. 1998). This oceanic front delineates a northerly and southerly Barents Sea region, each displaying different ecosystem characteristics and productivity (Fossheim et al. 2015; Frainer et al. 2017).

In the western Barents Sea, along the Svalbard shelf margin there are several methane seeps aligned with the Hornsund Fault zone complex. These seeps occur near the predicted upper depth limit of the gas hydrate stability-zone in the mouth of the trough Storfjordrenna. The southernmost location is known as Storfjordrenna (SR) seep field (Figure 1) and this site is characterized as a predominant soft bottom plain where smaller carbonate outcrops, chemosymbiotic worms and microbial mats have been observed (Åström et al. 2016). A few tens of kilometers north of SR is a recently discovered field of topographic features, recognized as underwater gas hydrate mounds (GHM's) or pingo-like features (PLF) (Figure 1), referred to as PLF's in article IV, Åström et al. (2017b), (Serov et al. 2017; Hong et al. 2017). These rounded mounds are a few hundred meters long and rise approximately 8-10 meters from the seabed at water depths of around 380 m. Several of these mounds are active, emitting free gas, and gas hydrates in near surface sediments have been recorded. Moreover, elevated concentrations of methane have been detected in both sediment and bottom waters (Serov et al. 2017 Hong et al. 2017). Mounds have shown varying flaring activity where some seems to be in a "post-active stage", indicating different successional phases (Hong et al. 2018; Sen et al. 2018).

2.4 Bjørnøyrenna Craters

At the northwestern flank of the trough Bjørnøyrenna is a large area (~440 km^2) with up to 100's of craters and crater-mound complexes located (Solheim and Elverhøi 1993) (Figure 1). The size of the craters varies from a few hundred meters up to 1 km in diameter and 30 m deep while mounds rise up to 20 m above the seafloor. Gas flares have been detected with acoustic signals and primary emitted gas is recognized as methane (Åström et al. 2016; Andreassen et al. 2017). These craters are believed to have been formed approximately 15 000 years ago as a result of the deglaciation of the BSIS (Andreassen et al. 2017).

3.1 Benthic Sampling

There is a wide range of approaches to conducting offshore benthic sampling in marine environments for ecosystems surveys, habitat characterization and community analysis. Cross-disciplinary surveys and sampling can increase our knowledge of environmental changes. Furthermore, we can get an even more comprehensive understanding of an ecosystem by combining various types of equipment and methods, using both coring, grabs and trawls together with visual documentation such as underwater cameras and video (Beuchel et al. 2006; MacDonald et al. 2010; Bergmann et al. 2011; Jørgensen et al. 2011).

In order to sample the seabed and to collect information about the cold seep areas of focus in this study, multiple research cruises within CAGE have been carried out at targeted locations (Figure 1). Several different types of benthic samplers were used to collect benthic fauna such as van Veen grabs, multi-, and box corer and triangle dredges. In a few cold seep locations, there were possibilities to use an underwater camera for visualization of the seafloor prior sampling (Tow-Cam). Moreover, both video, sea floor images and benthic sampling were carried out using a remotely operating vehicle ROV during a Barents Sea cruise in 2016 (Figure 3).

Figure 3: From upper left A) Tow-Cam, multicore and CTD (CAGE-MISO) used during CAGE 15-2 cruise. B) ROV K30 (NTNU) used for the cold seeps in the Barents Sea during CAGE 16-5. C) van Veen grab in open mode. D) Gas hydrates recovered in a gravity core. E) Ice crystals in the shape of gas hydrates. F) Burning methane gas from disassociating gas hydrates as it is recovered from the sampled cores.

Benthic samples for community structure analysis have been processed according to the ISO 16665:2014 standard fieldwork protocols to ensure consistency and quality control of benthic faunal surveys. A standard van Veen grab station is typically comprised of 5 replicate samples á 0.1 m^{-2}. The standardized process involves sieving of the samples on board the research vessel (mesh size used in this study = 500 µm) and material retained on the sieve is fixed in formaldehyde (4 %), mixed with rose-bengal for staining living tissues and furthermore buffered with borax (sodium tetra-borate decahydrate). In the laboratory, samples have been sorted and identified to the lowest possible taxonomic level and stored in 80% ethanol. Organisms were separated into main phyletic groups where each individual was counted and weighed (aggregated wet weight in phyletic groups).

3.2 Sediment and Water Column Sampling

Sediment samples were collected to measure benthic chlorophyll *a* (Chl *a*) and phaeopigments (PhP), as indicators of photosynthetically based organic material deposited on the sea floor. Sediment Chl *a* indicates the relatively recently produced material, whereas phaeopigments are a degradation product of Chl *a*. Surface sediment pigment concentrations (upper 0-2 cm) from grab samples and push cores were analyzed by fluorometery in accordance with Holm-Hansen et al., (1965).

Porosity of sediment samples was determined by using a wet–dry method where pre-weighed vials of known volume were filled with sediment, re-weighed and later dried at 60° C until all water evaporated. The density of the sediment was calculated by using the basis from the wet weight of sediment and water combined (Zaborska et al. 2008).

Sediment grain size (fraction of pelite <0.63 µm) and total organic carbon (TOC) were determined by subsampling surface (0-2 cm), sediments (minimum 50 g) from grab samples. Grain size was determined according to Bale and Kenny (2005). The TOC samples were analyzed with a Shimadzu SSM TOC 5000 and Elementar Vario TOC Cube.

For compositional analyses of methane in water and sediments, a conventional head-space sampling preparation technique was applied. This involves analysis of bulk sediments collected from sediment cores, where sediment was transferred into headspace glass vials and mixed with a NaOH solution.

Vertical CTD (Conductivity, Temperature, Depth; SBE 9 plus sensor) profiles of seawater hydrography were taken prior sampling at selected locations. Niskin bottles mounted on the CTD were used to collected water samples from the chlorophyll maximum peak in the upper surface

waters in order to determine the Chl *a* concentration and photosynthetic organic matter in the water column. Seawater for bottom water methane concentration was collected using bottles mounted on the CTD. Immediately after recovery, seawater was mixed with pure nitrogen gas as conventional headspace to allow the headspace nitrogen to equilibrate with the dissolved methane in the water sample. Methane and other hydrocarbon concentrations were determined with a gas chromatograph (GC).

3.3 Stable Isotopes

Organisms used for the analysis of $\delta^{13}C$ and $\delta^{15}N$ stable isotope composition of were collected mainly from qualitative core and grab samples from both cold seep and non-seep locations. In addition, triangle dredges were used primarily in the Barents Sea and furthermore, pinpoint-targeted sampling was conducted using the ROV. Animals were sorted and identified immediately after collection and kept frozen prior analyses. Smaller organisms were processed whole whereas tissues from larger individuals were separated (e.g. muscle, tail, intestine, foot) depending on taxa. Sediment for stable isotope analysis was frozen immediately after collection. Water samples for analyses the stable isotopic signal of photosynthetic primary production, particulate organic matter (POM) from surface waters were collected with 1.2 L Niskin bottles mounted on a CTD. Samples were taken at the chlorophyll maximum peak in the water column.

To prepare the samples for stable isotope analysis, they were freeze-dried, homogenized and weighed into tin capsules. Final pretreatment and isotopic analysis were conducted at the Stable Isotope Laboratory, Department of Environmental Sciences, University of Basel, Switzerland. Trophic levels were calculated using fractionation values for each position according to Søreide et al. (2006), (3.4‰ for nitrogen and 0.6 ‰ for carbon) using the formula:

(1) $TL = ((\delta^{15}N_{cons.} - \delta^{15}N_{source}) / 3.4) + 1$

Where $\delta^{15}N_{cons}$ corresponds to the nitrogen value of the targeted organism (i.e. consumer) and $\delta^{15}N_{source}$ is the identified baseline nitrogen value of primary baseline resources in the system. Furthermore, a two-component mixing equation was used to calculate the fraction between two known carbon sources, based on the $\delta^{13}C$ values from individual organisms using the equation:

(2) $X_{fraction} = (C_{ind.} - C_1)/(C_2 - C_1)$

Here, C_{ind} is the $\delta^{13}C$ value of the targeted organism, C_1 represents one baseline carbon source and C_2 represents the other targeted carbon source.

Article I: Arctic Cold Seeps in Marine methane hydrate environments: impacts on shelf

macrobenthic community structure offshore Svalbard

Åström EKL, Carroll ML, Ambrose WG Jr and Carroll J.

Marine Ecology Progress Series doi: 10.3354/meps11773

The main goal with this article was to conduct a focused biological study on cold seep ecology in the high Arctic. Macro-benthic cold seep ecology in the Arctic was a poorly explored topic at the time of the first study. The aim was to describe the faunal communities in designated seep stations located on the western Svalbard shelf, Prins Karls Forland (PKF), and in the western and central Barents Sea; Storfjordrenna (SR) and Bjørnøyrenna (BR) to see if and how they differed from paired control (non-seepage) locations.

This study demonstrated that cold seeps have a strong localized impact on Arctic benthos, with small-scale heterogeneity in the surrounding adjacent seep habitat. In a few clearly methane seep-influenced (MSI) samples, the community pattern was consistent with that of a disturbed habitat, possessing low diversity, high abundance and high biomass.

Furthermore, we documented that the large-scale environmental differences were overriding any seep influence on the overall regional level (Figure 4). PKF shallow and deeper locations (85-240 m) were significantly different from the stations in the Barents Sea (SR+BR) with respect to species richness (S) and diversity (H'). Total faunal biomass was always higher at designated seep stations compared to non-seep controls, and we found high densities of chemosymbiotic worms in a few clearly seep influenced samples. The large scale environmental patters (water masses, temperature, sediment composition and depth) separating the PKF and Barents Sea region were apparent in structuring the overall benthic communities for the entire study region.

The Arctic seeps in this study show similarities with other cold methane seeps at lower latitudes possessing high habitat heterogeneity within small spatial scales by the formation of methane derived authigenic carbonates and biological seabed features such as chemosymbiotic worm tufts and microbial mats. This work was the first dedicated macrofaunal community study on High-Arctic methane seeps and provides key baseline results for future studies in a changing Arctic.
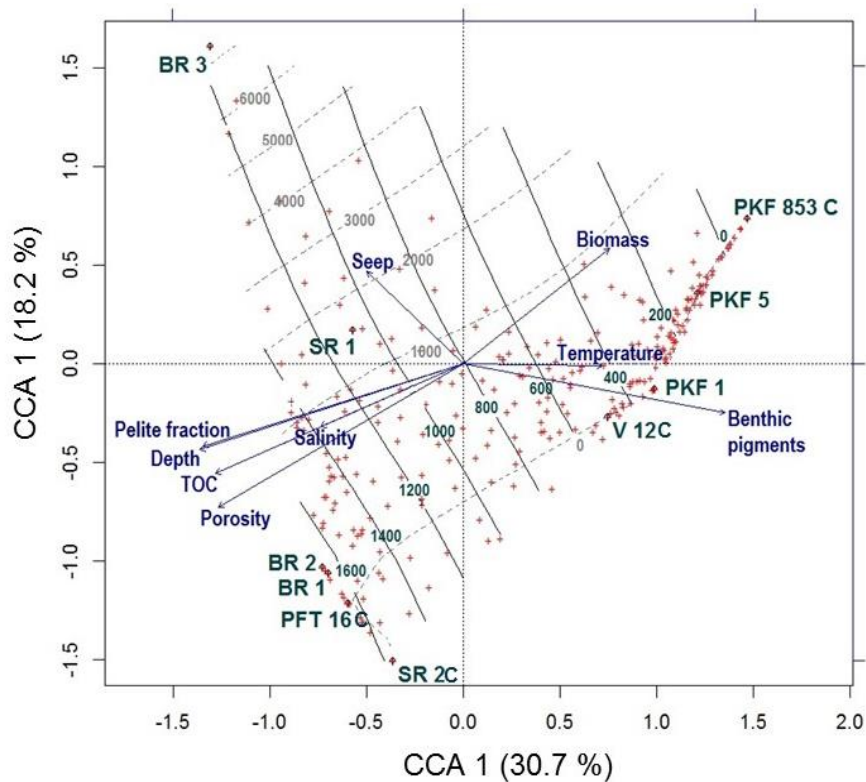
Figure 4: Canonical correspondence analysis (CCA) based on station abundances of taxa ordinated with standardized environmental variables: temperature, depth, salinity, pelite fraction, total organic carbon, porosity, benthic pigments and the categorical variable 'seep' in combination with aggregated station biomass.

Abundances of the two most common taxa are presented as isolines. Solid black lines: *Mendicula* cf. *pygmaea* (bivalve); dashed grey lines: Siboglinidae (polychaetes). Stations marked with a 'C' indicate non-seeping control stations (Modified from Åström et al. (2016)).

Article II: Methane Cold Seeps as Biological Oases in the High-Arctic Deep Sea

Åström EKL, Carroll ML, Ambrose WG Jr, Sen A, Silyakova, A and Carroll J

Limnolgy & Oceanography pp. 1-23. doi: 10.1002/lno.10732

This study focused on the high-Arctic deep sea and a methane seeping-gas hydrate sediment ridge; Vestnesa Ridge. Benthic macrofaunal deep-sea systems can differ substantially in terms of biomass, diversity and abundance from shallower shelf communities because of key environmental drivers such as depth, temperatures and seabed substrate. Another important limitation at the deep Arctic seafloor is food availability and the seasonal and spatial amount of particulate organic matter (POM) reaching the sea floor.

Infaunal samples were collected at two methane seeping pockmarks along the Vestnesa Ridge (VR) and were compared with infaunal core samples collected from an inactive non-seeping location, Svyatogor Ridge (SvR). The infaunal community was clearly different at these two locations and Vestnesa had both higher abundance, biomass, species richness and diversity (Figure 5).
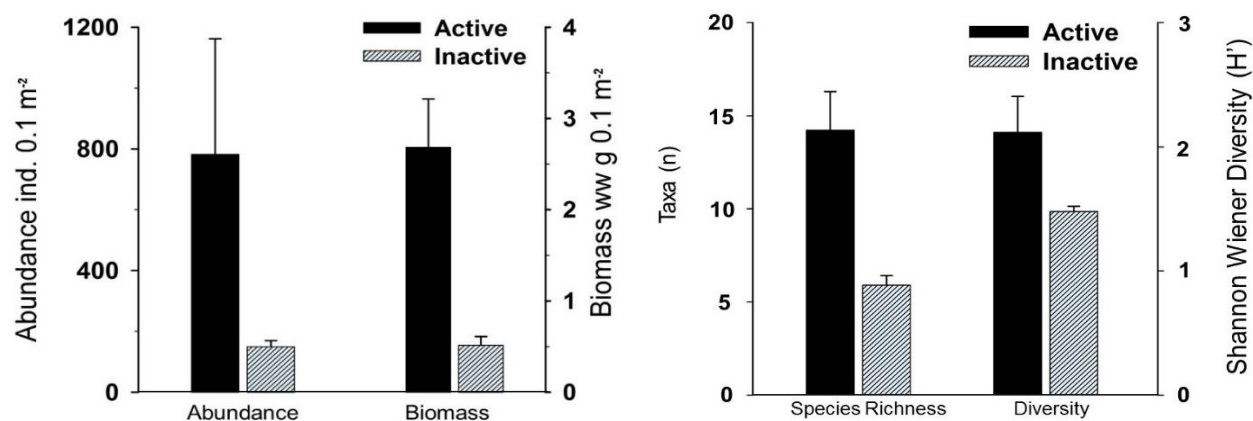

Figure 5: Infanual community parameters at active Vestnesa Ridge and inactive Svyatogor Ridge sites. a) Mean infaunal abundance and biomass, and b) mean Species Richness and Shannon Wiener diversity (H'). Faunal parameters were all significantly higher ($p < 0.05$) at Vestnesa Ridge. Error bars indicate ±SE. (From Åström et al. (2017a)).

In addition to the infaunal samples, sea floor photo-transects were conducted from the outside of the pockmark towards the inside in order to compare the habitat structure and asses megafaunal taxon richness based on presence/absence. There were large habitat differences between three designated locations ('Inside', 'Edge', 'Outside') along the transect into the pockmarks. 'Outside', the overriding substrate was soft bottom plains, sporadically interrupted by drop stones. The most common megafaunal taxa was brittle stars and occasionally, other larger megafauna were observed. At the 'Edge', the overriding seabed substrate remained as soft bottom, but here, no brittle stars were present and instead patches of microbial mats and chemosymbiotic worm tufts appeared on the seafloor. We could also note other megafauna such as sea spiders and eelpouts adjacent to these biological features. There were a significantly higher species richness inside the pockmark compared to outside. Inside the pockmarks, the habitat changed dramatically and large carbonate crust formations were observed at the seabed. Various different megafaunal taxa were seen associated with the carbonate formations and the habitat heterogeneity allowed both soft bottom dominated organisms and fauna associated to hard substrates to co-occur. In addition to the carbonate formations seen inside the pockmarks, microbial mats and worms tufts were also observed.
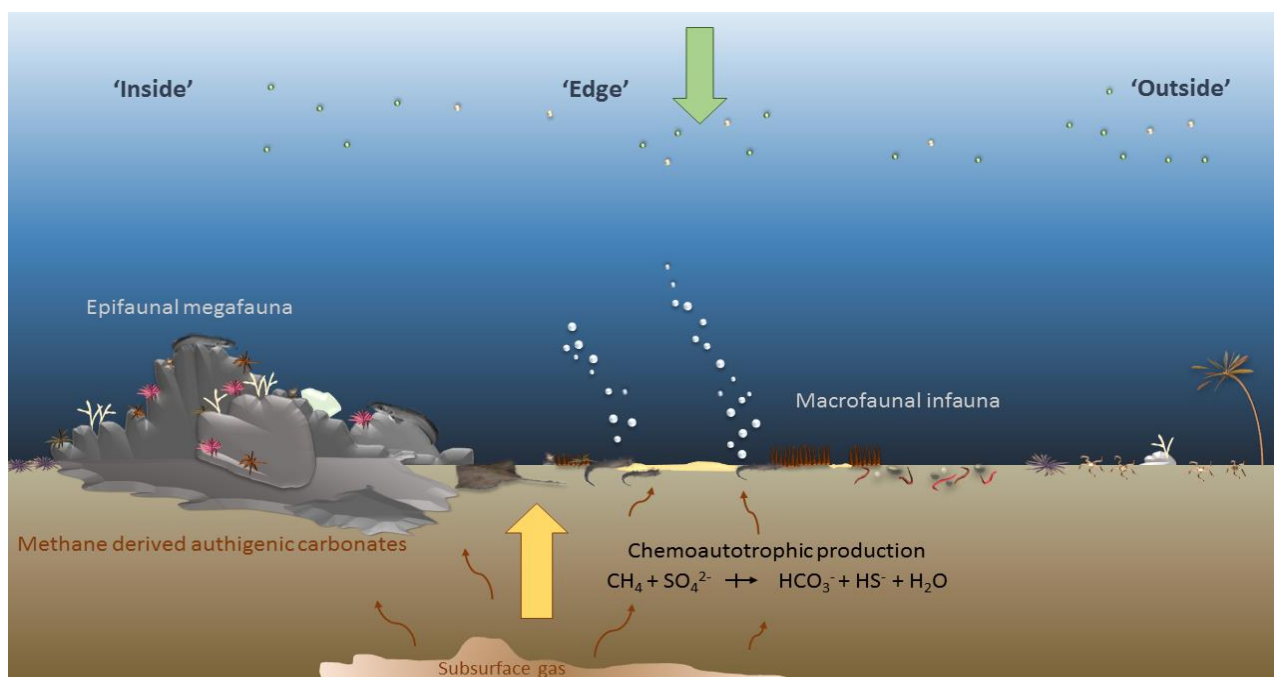
Figure 6: Schematic representation of the key habitat structures and processes occurring at the high-Arctic cold seep Vestnesa. An autochthonous (local) chemosynthetic energy source (yellow arrow) in addition to the photosynthetically derived detrital matter (green arrow) from the water column, in combination with hard substrate provided by the carbonate outcrops enhances both communities of infaunal macrofauna and epifaunal aggregation of megafauna at this site. (From Åström et al. (2017a))

We attributed the observed aggregation of megafaunal taxa inside the pockmarks to the increased habitat heterogeneity and 3D structure provided by carbonate formations, adding complexity to the deep-sea environment (Figure 6). Furthermore, the rich infaunal community seen at Vestnesa Ridge, was suggested to be supported from an additional energy source, i.e. the chemoautotrophic production coupled to the presence of hydrocarbons in the sediment (Figure 6). Vestnesa and Svyatogor Ridge possessed similar deep-sea characteristics in salinity, temperature, oxygen, sediment characteristics and there were no differences in photsynthtically derived chlorophyll content (phaeopigments and Chl a) in the sediment, indicating photosyntehtically produced food. The observed patterns suggest that methane is a key environmental driver at Vestnesa. Its utilization in the biosphere influences the benthic community creating a high-Arctic oasis contrasting to the deep-sea surroundings.

Article III: Trophic relationships and community structure at cold seeps in the
Barents Sea

Emmelie K.L. Åström-Hammenstig, Arunima Sen, Michael L. Carroll, Helge Niemann,
William G. Ambrose Jr., Moritz F. Lehman, JoLynn Carroll
(Manuscript)

For this manuscript (in preparation), the focus has been to use stable isotope composition of carbon (δ^{13}C) and nitrogen (δ^{15}N) in order to elucidate the utilization of carbon resources and identify trophic interactions of among organisms inhabiting cold seeps in the Barents Sea. By collecting animals from both cold seeps and non-seep locations, we aimed to test whether chemosynthesis derived carbon could be detected using bulk stable isotope analysis of δ^{13}C. In addition to the stable isotope analysis, a summary of the cold seep faunal community structure at Barents Sea cold seeps was provided including both new investigations and previously published samples from Åström et al. (2016).

Chemosymbitic siboglinid worms (Frenulata) were highly depleted in δ^{13}C (-38.2‰ and -47.1‰) (Figure 7), demonstrating their chemosynthesis based nutrition at the cold seeps. However, the most intriguing results demonstrated depleted signals of δ^{13}C (-26.1‰ to -31.4‰) in three different species of conventional (i.e. non-chemosymbiotic) worms; *Nepthys* sp., *Ophelina acuminata* and *Scoletoma fragilis*, signaling partial input of methane derived carbon in their diets and showing that methane based (i.e. chemosynthetic) carbon is incorporated into the conventional food web structure of the Barents Sea. A 2-source mixing model indicated that up to 28-41% of the diet of these high trophic level polychaetes was comprised of methane-derived carbon.

We detected large intra-specific variation among individuals in δ^{13}C values collected at the same location (Figure 7). Nepthids from BR crater-area exhibited a difference of 14.7‰ (-31.8 vs. -17.1 ‰) and Nepthids from SR differed 8.7 ‰, (-25.5‰ vs -16.8 ‰). Likewise, lumbrinerids, *S. fragilis*, collected at the GHM seeps varied almost 10‰, ranging between -29.1‰ to -18.9 ‰. No other such large variations were observed among any other taxa and these results suggested that they feed on distinctly different carbon sources.

The Barents Sea cold seeps examined in this study share similar faunal patterns such as high faunal abundance and biomass compared to non-seep locations, and support high densities of chemosymbiotic frenulates and thyasirid bivalves (~7000 ind.m^{-2} and 2500 ind. m^{-2} respectively).

Focused, localized methane emissions drive strong community-level effects over small spatial scales and frenulate worms function as benthic engineers, adding small-scale habitat heterogeneity.

Aggregations of macrofaunal species and commercially important fishes and crustaceans were seen associated with seep features such as microbial mats, carbonate outcrops, and chemosymbiotic worm tufts. The high biomass and the aggregation of fauna indicate that seep habitats can be of high ecological importance where carbonate rocks provide complexity and 3D structure providing shelter and substrate, and where hydrocarbon emissions and chemoautotrophy add a supplementary energy source into the Barents Sea shelf ecosystem. The cold seeps assessed in the Barents Sea are shallower (less than 400 m) than many other investigated cold seep systems worldwide and this is likely another important factors explaining why there is a high subset of conventional 'background species' represented at the these cold seeps.
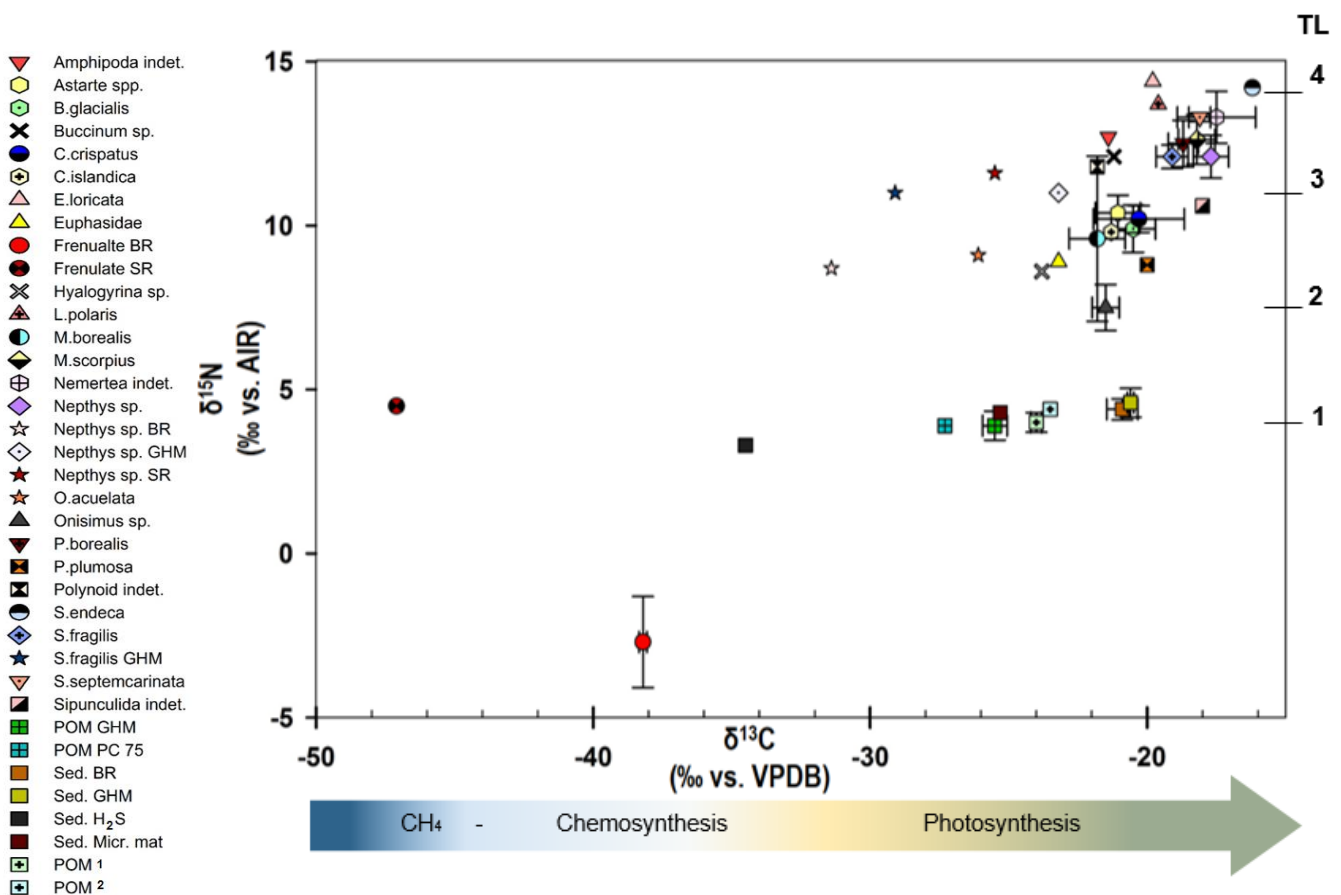

Figure 7: Bi-plot of $\delta^{13}C$ and $\delta^{14}N$ values of collected organisms, sediments and POM in the Barents Sea. Vertical and horizontal error bars represent standard deviation (±SD). POM [1] Søreide et. al. from (2006) and POM [2] from Søreide et. al. (2008). Horizontal arrow at the bottom of the graph show gradual input (from left to right) of methane-derived, chemosynthetic sources moving towards overriding photosynthetic sources. Vertical scale to the right indicate calculated trophic levels (TL) from Table 5 in article III.

Article IV: A new genus and two new species of Thyasiridae associated with methane seeps off Svalbard, Arctic Ocean

After finding thyasirid bivalve shells from methane seeping areas offshore Svalbard, distinct from any other previously known mollusks' species, one genus and two new species were described in this article. The shells were recognized and identified to the family of Thyasiridae because of the characteristic furrow on the shell. The article describe the two species and how they are different from other known thyasirids around the world.

Thaysira capitanea sp.nov. is a large species compared to the majority of species described within the genera *Conochele, Ascetoaxinus* and *Channelaxinus*. The species has an equilateral shell and demarcated zones on the median and anterior parts as well as a distinct posterior sulcus which makes *T. capitanea* different to Atlantic thyasirids associated with cold seeps and other reduced environments and also separates it from the above-mentioned genera (Figure 8).
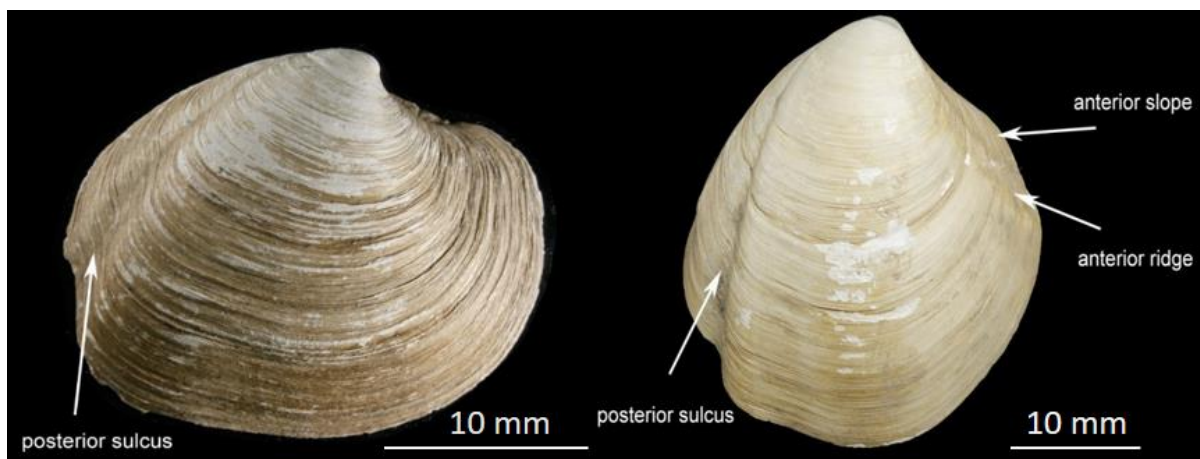

Figure 8: *Racothyas kolgae* sp. nov (left) and *Thyasira capitanea* sp. nov (right) from Svalbard cold seeps. (Photo: G. Oliver National Museum of Wales).

Rachotyhyas kolgae sp. nov is characteristically distinct from previously described thyasirids and by the time of the discovery, it could not be assigned to any of today's existing genera. Regarding *Racothyas* gen. nov. and *Racothyas kolgae* sp. nov, it is rare to describe a novel genus and taxa with such little material available, however, these shells are unique among other thyasirid bivalves in its characteristic outline, sunken lunule, lack of submarginal sulcus and wrinkled surface (Figure 8).

In addition to the taxonomic descriptions, the article includes an overview of dispersal of chemosynthetic fauna in the Svalbard - Barents Sea region related to the deglaciation of the Barents Sea Ice Sheet (BSIS). The environment where these bivalves were found is geologically young and the deglaciation of the BSIS started approximately 20 000 years ago. Favorable conditions to settle and a continuous supply of hydrocarbons in the sediment over a persistent period of time were probably fundamental in order to developed a macrofaunal chemosynthetic community. We suggested, based on the historical records of deglaciation in the region and the onset of sub-seabed hydrocarbon emissions, that the earliest chemosynthetic macrofaunal communities could have been formed around ~12 000-14 000 years ago. This time frame is short in terms of evolving chemosynthetic fauna *in situ* and therefore it is likely that chemosynthetic organisms have spread from nearby chemosynthetic communities in the North – Atlantic region and colonized cold seeps in the Svalbard-Barents Sea region.

Arctic colds seeps are still an underexplored research theme with respect to ecology and biology, however, the outcome of this thesis has surely pushed the forefront of Arctic cold seep ecology research forward. The relativity easy access to study areas to conduct sampling at the gas seeping shelves offshore Svalbard, and the access to research facilities and collaborators through CAGE, UiT – The Arctic University of Norway has made it possible to conduct interdisciplinary studies of cold seep ecology of these high-Arctic systems. Arctic cold seeps share many characteristic features with cold seeps at lower latitudes icluding the habitat heterogeneity over small spatial scales caused by microbial mats, chemosynthesizing worms and methane derived authighenic carbonates. It is also clear that methane seepage has a high impact on structuring faunal communities in these systems. The formation of carbonates indicates long-term seepage of hydrocarbon sources, making the cold seeps considerably more long-lived and stable in comparison to hydrothermal vents that tend to be more ephemeral systems. The carbonate reef-like structures add important hard bottom substrate in overriding soft bottom environments, and irregular carbonate formations create a heterogeneous habitat for macrofauna, both large motile and epibenthic organisms (**Article II, III**). The Arctic cold seeps appear as productive systems and interacts with 'background', non-seeping environments over various spatial scales. The cold seeps host organisms representative of the overall region and there is a high subset of conventional 'background' fauna inhabiting the seeps, co-existing with chemosymbiotic fauna (**Article I, II,** and **III**).

The frenulates are the most dominant and characteristic taxa at many of the investigated cold seep sites in this study (**Article I, II** and **III**). Even though they are small, thin worms, they occur in high abundances of thousands of individuals per square meter, forming large tufts on the seabed. Through ROV video and underwater camera photography, fields of these chemosymbiotic worms have been documented and oftentimes, conventional megafauna such as sea spiders, snails, shrimps and eelpouts occupy these tufts. Attached to the frenulate tubes, filamentous bacteria, epibenthic foraminifera, caprellids and other meiofauna are observed, suggesting that the frenulates also provide an important 3D structure and shelter for smaller organisms inhabiting the seep environment (**Article III**). It is still not resolved if higher trophic level organisms prey upon the frenulates directly or if they are feeding on animals occupying the worm tufts, although it has been suggested that frenulates could be incorporated in the diet of eelpouts (Gebruk et al. 2003). Nevertheless, extensive tufts of these worms, and its associated fauna, create a heterogeneous habitat and compose a rich food source for organisms.

In addition to chemosymbiotic worms, the bivalve *Mendicula* c.f. *pygmaea* was highly abundant in samples, particularly from the Barents Sea (**Article I, III**). This is a small (mm-large) thyasirid bivalve, prominent at stations both where active seepage was documented and at non-seep locations. Thyasirids are common from reduced environments such as vents, seeps and also where large organic falls occur (e.g. whale falls) (Duperron et al. 2013). The family of thyasirids includes heterotrophic species as well as mixotrophic and chemosymbiotic taxa. Throughout this study of Arctic cold seeps, there has not been any records of currently living typical cold seep bivalves such as the large vesicomyids or bathymodiolin mussels, as seen at cold seeps at lower latitudes. Chemosymbiotic bivalves have only been recorded in fossil samples both from the deeper cold seeps at Vestnesa (Ambrose et al. 2015; Hansen et al. 2017) and from shallower seeps in the Barents Sea, (GHM and SR) (Åström et al. 2017b). There are however records and dates of collected thyasirid shells the GHM and SR seeps which include more modern records, indicating that these bivalves supposedly could be found alive (**Article IV**), (Carroll et al. 2016).

The investigated Arctic cold seeps in this project share the characteristics of high abundances, high biomasses and, to some extent, also high diversity, especially for infauna and megafauna (Åström et al. 2017a; Sen et al. 2018). In the deep sea, the cold seep community appears particularly prosperous and diverse compared to conventional Arctic deep-sea systems, and there are large contrasts in infaunal community structure (**Article II**). Megafauna aggregates around the typical seep features such as the carbonate outcrops, worm tufts and microbial mats and the cold seep appears as an oasis compared to the surrounding soft bottom deep-sea plains (**Article II**). Likewise, the same pattern is documented at the shallower shelves in the Barents Sea where larger organisms aggregate around specific seep features. Because of the habitat complexity and heterogeneity that we document at the seeps, this suggests that cold seeps in the Arctic are focal areas colonized by various types of organisms. The cold seeps could possibly function as refuge and biological hotspots for local productivity, where hydrocarbon emissions and chemoautotrophy add a supplementary energy source for high-Arctic ecosystems. So far, the conventional paradigm of the origin of marine productivity in the Arctic is based on the concept that energy sources originate solely from photosynthetic processes and carbon recycling. Chemoautotrophic production, in addition to photosyntetically-derived matter from surface waters seems, however, to have a boosting effect on the benthic faunal community at cold seeps (**Article I**, **II**). This additional carbon source, decoupled from the typical seasonal Arctic productivity-cycle driven by photosynthesis could play an important role in Arctic carbon cycling. It is still unknown, however, whether methane carbon contributes substantially to Arctic marine environments although the results from this study identify a local effect at individual seeps (**Article III**.) Nevertheless, it is likely that there are many yet unexplored

cold seeps and reduced environments in the Arctic since a large part of the Arctic consists of shelves that have been covered by glacial ice and potentially share a similar geological history and evolution as the shelves around Svalbard (Paull et al. 2015; Stranne et al. 2016; Demina and Galkin 2018). Is it possible that chemosynthesis and methane carbon sources play a larger role in the Arctic than previously thought? New insights in Arctic ecology and productivity challenge the current concepts of Arctic marine productivity and ecosystem processes with respect to both carbon sources, light regime and changing climate aspects (**Article II, III,** Berge et al. 2015; Degen et al. 2016; Frainer et al. 2017). The typical view of Arctic biological productivity is likely about to change.

There is also little knowledge about connectivity between the Arctic cold seeps and what perhaps restricts an eventual colonization of fauna from cold seeps at lower latitudes. Why are there no lamellibrachian tubeworms or large-bodied chemosymbiotic bivalves yet found? Are there limits in environmental variables such as temperature or chemical properties, or is it rather a question of limitations in a species' physiology, dispersal and spreading? (**Article IV**). Apparently, they have been colonizing the Arctic during Holocene since shells of chemosymbiotic clams are recorded (Ambrose et al. 2015; Carroll et al. 2016; Sztybor and Rasmussen 2016; Åström et al. 2017b). Could temperature be a limiting factor? Deep-sea environments, however, where many cold seeps are located, are typically exposed to cold bottom water temperatures (2-4˚C). Is it then sub-zero temperatures that possess the critical level?

The Arctic is a region undoubtedly affected by climate change and is undergoing rapid environmental changes. This connects to ecological implications where changes in oceanographic circulation patterns and reduction sea-ice cover and thickness are expected consequences in a warming Arctic, which could lead to changes in carbon cycling, biological productivity and trophic interactions. How climate change will affect Arctic cold seeps is also an unknown topic. Gas hydrates that destabilize from the seafloor because of increasing temperatures, and where methane is released into the water column, potentially reaching the atmosphere is supposedly only applicable on shallow Arctic shelves (Shakhova et al. 2010; Portnov et al. 2013, 2016; Myhre et al. 2016; Hong et al. 2017).

As stated in the first sentence in this chapter: Cold seeps in the Arctic are still an underexplored field in terms of what we know about the biology and the ecological interactions. This doctoral project has contributed to novel insights on Arctic cold seep communities and provided new information on methane and its utilization in the biosphere within the high-Arctic regime.

One of the most important statements in science that endlessly push us forward is that: "*We cannot value what we don't know*". This means that we cannot evaluate or conclude about things that we do not have understanding of or know about. This aspect is highly relevant for many fields in biology and ecology where the precautionary principle is applicable.

Even though we do not know exactly each and all purposes for our research, many of the largest breakthroughs' in sciences have been discovered through the study of something else. By chance, new findings have changed our understanding of the world and a great example of this is the first documentations of the hydrothermal vents (Ballard 1977; Grassle 1985). Vents were believed to be hostile, unlivable environments, but these unique ecosystems completely changed human perspective of life on Earth.
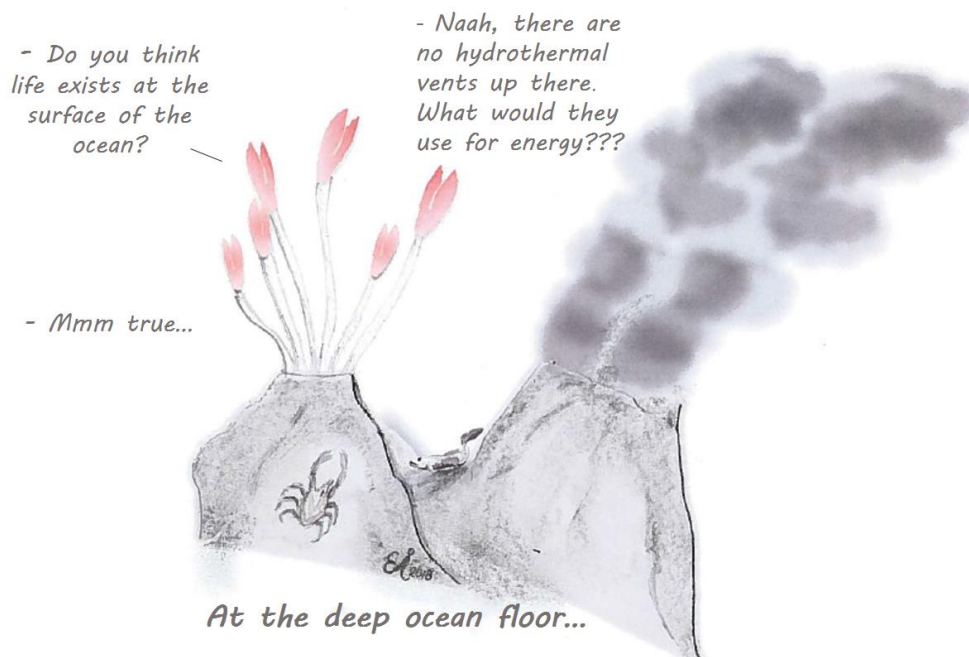
Modified after *"Beatrice the Biologist" www.beatricebiologist.com*

6

In summary, the Arctic cold seeps examined in this study share similar faunal patterns such as high faunal abundance and biomass compared to cold seeps at lower latitudes. The largest differences between the Arctic seeps and other seep environments are the faunal composition and the absence of specialized cold seep fauna in addition to the frenulate worms. The focused and localized methane emissions drive strong community-level effects over small spatial scales, however, the influence of methane seeps are not strong enough to override large-scale environmental drivers between regions.

Key findings from the study are:

I)   Cold seeps have a strong, localized effect over small spatial scales, supporting dense communities of small chemosymbiotic worms that play a fundamental role in structuring the seabed animal community

II)   Cold seeps are identified as focal areas for the biosphere, providing heterogeneous substrates and additional food resources independent of photosynthetic sources from the surface ocean, resulting in animal aggregations at these habitats.

III)   Methane-derived carbon is incorporated into the food web of the Barents Sea ecosystem.

IV)   Two new species of methane-associated bivalves were discovered at Svalbard cold seeps.

Cold seeps in the Arctic are of high ecological importance, especially in the deep-sea environments where soft bottom plains are the overriding habitat. Furthermore, aggregations of larger motile megafauna and many commercially important species are observed around the cold seeps. Characteristic seep features such as microbial mats, frenulate worm tufts and carbonate outcrops add complexity and 3D structure providing shelter and substrate for both sessile and motile fauna, and where hydrocarbon emissions and chemoautotrophy add a supplementary energy source into the Arctic ecosystem.

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Article I

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The art and science of asking questions
is the source of all knowledge

- Thomas Berger

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Biology is the science. Evolution is the
concept that makes biology unique

- Jared Diamond

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Trophic interactions and community structure at Barents Sea cold seeps

(manuscript)

The important thing in science is not
so much to obtain new facts as to discover
new ways of thinking about them

- Sir William Lawrence Bragg

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Nothing in biology make sense
except in the light of evolution

- Theodosius Dobzhansky

Life is like the ocean.
It can be calm or still, and rough or rigid
but in the end, it is always beautiful.

In the loving memory of my grandparents