# Does macrofaunal nutrition vary among habitats at the Håkon Mosby mud volcano?

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**Abstract:** The Håkon Mosby mud volcano (HMMV) is one of the most studied cold-seep sites in Europe. Its exceptional fluid expulsion activity and large geochemical gradients from the centre to the periphery support dense biological communities and induce spatial heterogeneity in microbial activity and faunal zonation. At this site, the macrofauna has been little studied and the variability in its macrobenthic nutrition has not yet been investigated. In this study, based on the analysis of the stable isotopes of carbon and nitrogen, we determined nutritional patterns for macrofauna communities in three different habitats (microbial mats, sediment adjacent to the mat and Siboglinidae polychaete fields). $\delta^{13}C$ values of macrofaunal tissues varied among two habitats (microbial mats and Siboglinid fields), with lighter mean signatures on microbial mats (-46.9‰) than in Siboglinidae fields (-27.0‰). However, no small-scale variability was revealed between mats and adjacent sediment. The dominant carbon source in macrofaunal nutrition was chemosynthetically fixed and the bulk of organic carbon was derived from sulphur-oxidizing bacteria. However, the variability of $\delta^{13}C$ and $\delta^{15}N$ signatures of macrofauna within this habitat suggests the co-occurrence of two food chains on mats, one based on sulphur-oxidation and the other based on aerobic or anaerobic methanotrophy.

*Keywords:* Cold seep ● Håkon Mosby ● Macrofaunal nutrition ● Stable isotope analysis

## Introduction

In great contrast to the surrounding, sparsely inhabited background environment, cold-seep areas are generally characterized by high biomass (Sibuet & Olu-Le Roy, 2002). Seep communities are dominated by large, symbiont-bearing invertebrates (siboglinid polychaete tubeworms, mytilids, vesicomyid bivalves) that are considered to be "ecosystem engineers" and, together with microbial mats, constitute diverse habitats (Levin, 2005). Located within sediment and on carbonate crusts, the tubes or shells of these invertebrates support many macro- and meiofaunal taxa. Symbiont-bearing invertebrates thus contribute to habitat heterogeneity and thereby increase local species diversity (Cordes et al., 2009).

Nutrition of the associated, non-symbiont-bearing species may be based on local seep production, either by feeding on free chemoautotrophic micro-organisms or

through bacteria-invertebrate symbiotic relationships. Associated taxa may also rely on external inputs of photosynthesis-derived material. Stable isotope analyses in chemosynthetic-based ecosystems are performed to assess the contribution of chemosynthetic versus photosynthetic food sources and trophic relationships among faunal compartments (Peterson & Fry, 1987; Conway et al., 1994). Previous studies have highlighted the importance of the microbial compartment in the nutrition of non-symbiont-bearing fauna (Levin et al., 2000). Most studies showed that at bathyal or abyssal cold seeps, most species derive the bulk of their nutrition from chemoautolithotrophic sources (e.g. MacAvoy et al., 2005). However, these studies have also demonstrated that the contribution of chemosynthesis to faunal diets varies according to habitat (Levin & Michener, 2002; Levin & Mendoza, 2007; Olu et al., 2009).

Methane-seep communities were discovered 15 years ago at 1250 m depth along the Norwegian margin at a site called the Håkon Mosby mud volcano (72°N, 14°44'E) (Vogt et al., 1997) (Fig. 1). This is one of the most active mud volcanoes described thus far, showing exceptionally active mud, fluid, and gas emissions, with thermal and fluid flow gradients from the centre to the periphery (Milkov et al., 2004; Sauter et al., 2006; Feseker et al., 2008). This circular (1 to 1.5 km in diameter) geological formation is characterized by a zonation of microbial activity and sediment geochemistry (sulphide and oxygen gradients) (De Beer et al., 2006; Niemann et al., 2006). Chemosynthetic habitats are distributed along these activity gradients with a central zone apparently devoid of fauna, an intermediate zone covered by microbial mats and an outer zone colonised by two species of symbiont-bearing siboglinid polychaetes (Gebruk et al., 2003; Jerosch et al., 2007). According to the first video surveys, Siboglinidae fields appear to be dominated by *Sclerolinum contortum* Smirnov, 2000 (Monilifera), whereas *Oligobrachia haakonmosiensis* Smirnov, 2000 (Frenulata) has a more patchy distribution. Although the carbon isotopic signature of *O. haakonmobiensis* is consistent with methanotrophy (Gebruk et al., 2003), only sulphide-oxidizing symbionts have been revealed in either species (Lösekann et al., 2008). The widespread white microbial mats are dominated by giant sulphur-oxidizing filamentous bacteria from the genus *Beggiatoa* (Niemann et al., 2006; Lösekann et al., 2007). The meiofauna (32-500 μm) is clearly structured by habitat (Soltwedel et al., 2005; Van Gaever et al., 2006), as are the macro- and megafauna (Gebruk et al., 2003; Decker et al., in prep.) with a few, highly specialized taxa in the microbial mats and a more diversified fauna in siboglinid fields.

The first stable isotope analyses performed on macrofauna taxa from HMMV showed that carbon isotope signatures greatly vary, with a high contribution of methane-derived carbon (Gebruk et al., 2003). Dominant nematodes on microbial mats are assumed to mainly rely on chemosynthetic production from the sulphur-oxidizing *Beggiatoa* sp. (Van Gaever et al., 2006).

In this study, we sampled macro- and megafauna in three different habitats along the mud volcano. We aimed to test the influence of habitat on the isotope signatures of associated fauna and to investigate possible differences in food chains among or within habitats.

## Materials and Methods

Macro- and megafauna were sampled on the Håkon Mosby mud volcano (HMMV) during the Vicking cruise (May-June 2006) using the ROV *Victor 6000*. Three different habitats were sampled on HMMV: (1) white microbial mats (dominated by white filamentous bacteria), (2) sediment adjacent to the white microbial mats on the eastern border of the mud-flow area and (3) Sibogilinidae polychaete fields dominated by *Sclerolinum contortum* on the north-western border of the volcano (Fig. 1).

Macro- and megafauna taxa were sampled using a suction sampler manipulated by the ROV. Three replicates in each habitat were taken over a surface of 0.04 m² delineated by four laser beams. Zoarcid fishes were sampled individually using the suction sampler. For carbon and nitrogen isotope measurements, we selected 15 macro- or megafauna taxa, chosen for their dominance in samples and identified on board at the family taxonomic level or higher. These taxa represented 98%, 92% and 83% of the total associated macrofauna in the triplicate samples from microbial mats, adjacent sediment, and siboglinid fields, respectively. One to 20 individuals from each taxon were immediately fixed in liquid nitrogen. Macrofauna were not dissected; in ophiurids and fishes, muscle tissue was dissected for cryopreservation.

In the lab, organisms with carbonate skeletons were acidified with 4.75 M HCl and dried at 60°C for 72 h. Non-acidified organisms were freeze-dried for 48 h. After homogenisation, about $1.0 \pm 0.5$ mg of material (precision: 0.001 mg) were weighed in tin capsules. For small taxa in which the amount of dry material was insufficient, samples of individuals were pooled or alcohol-preserved individuals were used (Table 1). For bivalves and tanaids preserved in alcohol, isotope signatures were corrected based on the comparison of alcohol- and liquid nitrogen-preserved individuals.

$\delta^{13}C$ and $\delta^{15}N$ were analysed in duplicate samples using continuous-flow isotope-ratio mass-spectrometry (CF-IRMS) with a SerCon 20-20 stable isotope analyser (0.2‰ precision).

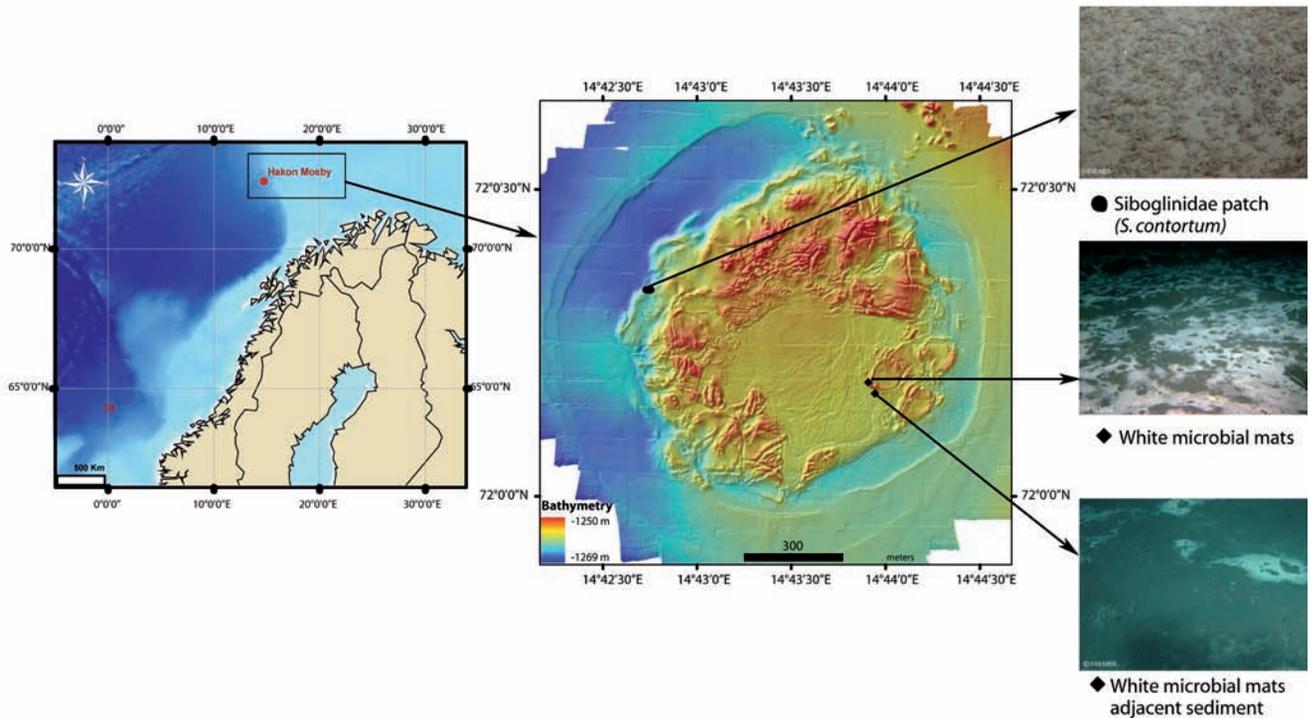Differences in $\delta^{13}C$ or $\delta^{15}N$ signatures among taxa or

**Figure 1.** Location of the Håkon Mosby mud volcano (HMMV) and the habitats sampled on the volcano. Microbathymetry of HMMV as determined from [high-]resolution multibeam echosounder mounted on the ROV *Victor 6000* (Jerosch et al., 2007).

**Figure 1.** Localisation de Håkon Mosby mud volcano (HMMV) et des habitats échantillonnés sur le volcan. Microbathymétrie du site déterminée à partir de l'échosondeur multifaisceau [haute] résolution du ROV *Victor 6000* (Jerosch et al., 2007).

habitats were tested using non-parametric methods (Kruskal-Wallis test, non-parametric multiple comparisons). All analyses were performed using the free open-source R software (R Development Core Team, 2008). The npmc library was used for non-parametric multiple comparisons (Helms & Munzel, 2008).

Trophic relationships were interpreted using both carbon and nitrogen signatures, based on the generally accepted enrichment rates of 1‰ in $\delta^{13}C$ and 3-4 ‰ in $\delta^{15}N$ between two successive trophic levels (Conway et al., 1994).

## Results and Discussion

The $\delta^{13}C$ signatures of the macro- and megafauna sampled in the different habitats on HMMV ranged from -51 to -20‰ (Table 1 & Fig. 2). According to these carbon isotope signatures (mean = -36.2‰, s.d. = 10.5‰), the fauna primarily depends on organic matter produced locally by chemoautrophic micro-organisms. A few taxa sampled in the outer-most habitat of the active seep area, i.e. the siboglinid field, may nevertheless rely primarily on external inputs of phytoplankton-derived carbon.

Comparison of habitats showed that microbial mats and siboglinid fields differed significantly in their macrofaunal $\delta^{13}C$ signature (Kruskal-Wallis: p = 0.001) (Fig. 2). Accordingly, the macrofauna associated with *S. contortum* had heavier mean $\delta^{13}C$ values (-27.0 ± 5.7‰) than macrofauna sampled on white microbial mats or in adjacent sediment (46.9 ± 1.4‰ and 47.0 ± 4.0‰, respectively). The carbon and nitrogen signatures of the macrofauna from sediment adjacent to microbial mats did not differ significantly from that for macrofauna on the mats $\delta^{13}C$ signature (npmc: p = 0.970). This result corroborates the fact that macrofaunal species composition in sediments adjacent to bacterial mats is generally similar to that on the mats.

In the microbial mat habitat surrounding the active volcano centre and on adjacent sediment, the carbon signatures of all sampled mega- and macrofauna taxa were highly $^{13}C$-depleted. These habitats support a few species that are highly adapted to sulphide-rich and oxygen-depleted environments. The macrofauna may develop trophic specialisations, as shown in the dominant nematode on bacterial mats (Van Gaever et al., 2006). The Capitellidae polychaetes that dominate the macrofaunal
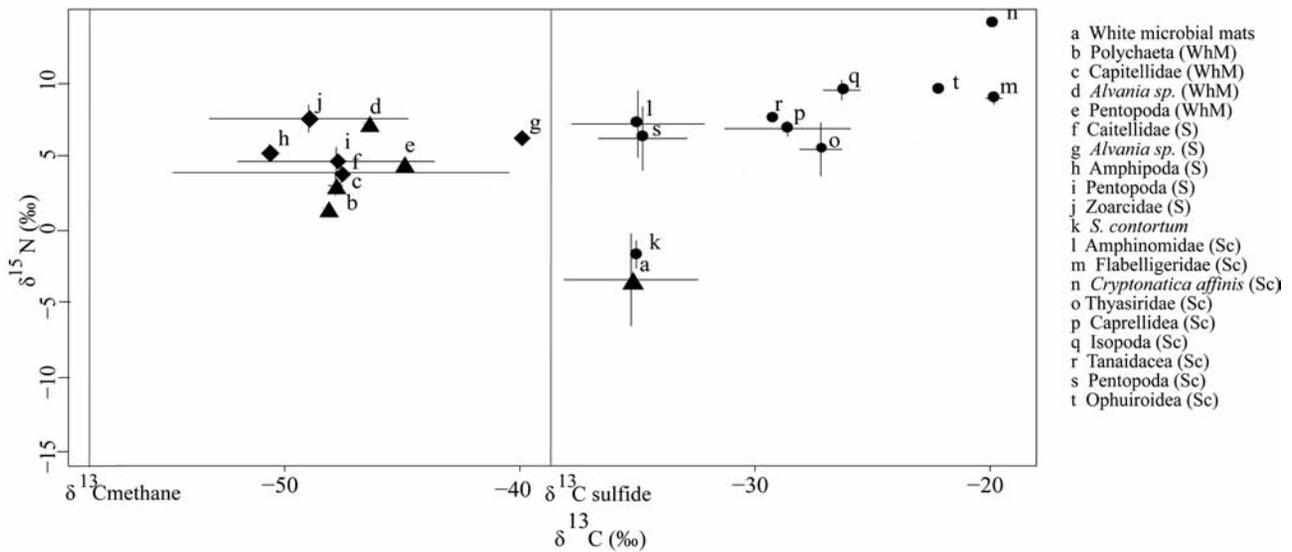
**Figure 2.** Isotope signatures of different taxa sampled on Håkon Mosby mud volcano (▲: in white microbial mats (WhM), ◆: in sediment adjacent to the microbial mats (S), ●: in Siboglinidae fields (Sc)).

**Figure 2.** Signature isotopique des différents taxons échantillonnés à Håkon Mosby mud volcano (▲: sur des biofilms microbiens blancs (WhM), ◆: dans le sédiment adjacent (S), ●: au sein des colonies de Siboglinidae (Sc)).

compartment on mats and in adjacent sediment showed similar carbon and nitrogen signatures in both habitats, as did the pygnogonids (Pentapoda), suggesting that these species employ opportunistic nutrition strategies. In contrast, Rissoidae gastropods *Alvania* sp. sampled on mats were more depleted in carbon than those sampled from adjacent sediment, with a difference of 6‰. This suggests that filamentous bacteria make up part of the gastropod diet. Similarly, it has been suggested that nematodes living on white microbial mats rely on sulphur-oxidizing *Beggiatoa*, as $\delta^{13}C$ values of -41.6 ± 0.4‰ and -42.7± 0.2 ‰ have been reported for mats (Van Gaever et al., 2006). In this study, microbial mats showed a less depleted $\delta^{13}C$ signature (-35.2 ± 2.8 ‰); however, this value is in the range of those reported at other seep sites (Levin & Michener, 2002; Levin & Mendoza, 2007).

The macro- and megafauna sampled on mats and in sediment adjacent to mats revealed much more depleted $\delta^{13}C$ signatures (-46.9 ± 1.4‰ and -47.0 ± 4.0‰, respectively) than the mat itself, with a difference of 10 to 13‰. These taxa, whose $\delta^{13}C$ signatures are in the range of invertebrates associated with methane-oxidizing symbionts (Conway et al., 1994), may be nutritionally linked to methanotrophic microbes. Aerobic methanotrophic bacteria may indeed occur in the top centimetre of sediment, along with single-cell anaerobic methanotrophic archaea (ANMA) (Lösekann et al., 2007). The isotopic signature of these microbial populations is unknown, but the methane

signature of -59.2‰ (Lein et al., 1999) is consistent with macro- and megafauna feeding on methanotrophic microbes. The Dorvilleidae and Capitellidae polychaetes, which are both sub-surface deposit feeders (Fauchald & Jumars, 1979), have low $\delta^{15}N$ values and are probably also primary consumers of methanotrophic microbes. Methanotrophic-derived nutrition has also been proposed for microbial mats on the Oregon margin where Dorvilleidae polychaetes may consume methane-oxidizing archaea (Levin & Michener, 2002). Dominant in the central mud area of HMMV, copepods are also assumed to rely on methanotrophic biomass, in light of their fatty acid and stable isotopic compositions (Van Gaever et al., 2009).

Pycnogonids and amphipods, which are both surface-deposit feeders (Iken et al., 2001), probably consume recycled organic matter. Zoarcidae fishes observed both on the microbial mats and in the adjacent sediment may be secondary consumers of small crustaceans and polychaetes. However, the variability of their carbon signature (-49.0 ± 7.5‰) suggests that they have a diversified diet, as observed in the Gulf of Guinea seeps (Olu et al., 2009). The specimen previously analysed by Gebruk et al. (2003) with a $\delta^{13}C$ value of -17.7‰ may rely on another carbon source, as do the fishes observed in Siboglinidae fields. Two food chains seem therefore to co-occur in the white microbial mat habitat: one based on sulphur-oxidation and the other based on aerobic or anaerobic methanotrophy.

In Siboglinidae fields, *S. contortum* had the lightest $\delta^{13}C$

**Table 1.** Isotope signatures (δ13C, δ15N) of major taxa sampled on different habitats on the Håkon Mosby mud volcano. (N: number of individuals or pooled samples; (n) is the total number of individuals sampled before pooling). % of M (M: macrofauna), proportion of the taxon in the total macrofauna sample from the habitat in question (siboglinids are not included in the *S. contortum* field habitat); zoarcids are not included in the macrofauna, but largely dominated the megafauna. Gastropods were identified by A. Warén.

**Tableau 1.** Signatures isotopiques (δ13C, δ15N) des principaux taxons récoltés dans les différents habitats de Håkon Mosby mud volcano. (N: nombre d'individus ou d'échantillons regroupés ; (n) est le nombre total d'individus récoltés avant le regroupement. % of M (M : macrofaune), part du taxon dans la macrofaune totale de l'échantillon pour chaque habitat (les siboglinidés ne sont pas pris en compte dans l'habitat des colonies de *S. contortum*) ; les zoarcidés ne sont pas pris en compte dans la macrofaune mais ils dominaient fortement la mégafaune. Les gastéropodes ont été identifiés par A. Warén.

| Taxon | White Microbial Mats | | | | Adjacent sediment | | | | *S. contortum* fields | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N (n) | % of M | δ 13C | δ 15N | N (n) | % of M | δ 13C | δ 15N | N (n) | % of M | δ 13C | δ 15N |
| White microbial mats | 5 | | -35.2 | -3.4 | | | | | | | | |
| Polychaeta | | 94 | | | | | | | | | | |
|   *S. contortum* | | | | | | | | | 4(20) | | -35.0 | -1.7 |
|   Amphinomidae | | | | | | | | | 3(9) | 11.8 | -34.9 | 7.1 |
|   Capitellidae | 2(15) | 91 | -47.8 | 2.9 | 8(15) | 47.9 | -47.6 | 3.8 | | | | |
|   Dorvilleidae | 1(10) | 1 | -48.3 | 1.4 | | | | | | | | |
|   Flabelligeridae | | | | | | | | | 9 | 1.7 | -19.8 | 8.8 |
| Bivalvia | | | | | | | | | | | | |
|   Thyasiridae | | | | | | | | | 5(20) | 33.7 | -27.2 | 5.4 |
| Gastropoda | | | | | | | | | | 1.2 | | |
|   *Cryptonatica affinis* | | | | | | | | | 1(2) | 0.06 | -20.0 | 13.7 |
|   *Alvania sp.* | 1(20) | 5.9 | -46.6 | 7.2 | 1(10) | 8.4 | -40.2 | 6.1 | | | | |
| Amphipoda | | | | | 3(9) | 17 | -50.6 | 5.2 | | | | |
|   Caprellidae | | | | | | | | | 3 | 4.9 | -28.6 | 6.8 |
| Isopoda | | | | | | | | | 4(8) | 17.7 | -26.3 | 9. 4o |
| Tanaidacea | | | | | | | | | 1(3) | 3.6 | -29.3 | 7.3 |
| Pentopoda | 1 | 0.2 | -45.1 | 4.6 | 8 | 6.7 | -47.8 | 4.6 | 6 | 6.5 | -34.8 | 6.1 |
| Ophiuroidea | | | | | | | | | 1 | 1.9 | -22.2 | 9.3 |
| Zoarcidae | | | | | 4 | | -49.0 | 7.5 | | | | |
| **Mean signature of macrofauna** | | | **-46.9** | **4.0** | | | **-47.0** | **5.4** | | | **-27.0** | **8.1** |

(-35.0‰) and δ15N (-1.7‰) signatures, which are in agreement with their association with symbiotic bacteria. The diversified associated fauna corresponded to different levels of consumers (δ15N from 5.4 to 13.7‰), with the Naticidae gastropod *Cryptonatica affinis*, which showed the most 15N-enriched signature, at the top of the food web. Polychaete δ15N signatures varied by taxonomic family, revealing different trophic levels. Crustaceans had variable δ13C signatures, although their δ15N values were quite uniform (average +6.7‰), except for isopods. Isopods showed a heavier δ15N signature (+9.4‰), and are therefore positioned higher in the trophic chain. Thyasiridae bivalves generally have symbionts, but their high δ15N signature may indicate that the local species on HMMV are devoid of symbionts, as observed for few species (Southward, 1986; Dando & Spiro, 1993), or are mixotrophic, with a partial contribution of photosynthesis-derived carbon.

Given the δ13C signature of each associated taxon in comparison with that of *S. contortum*, which depends exclusively on sulphide oxidation, and the δ13C value of particulate organic carbon of -21‰ (Fry & Sherr, 1984), we can infer the degree of use of chemosynthesis- versus photosynthesis-based production. The nine associated macrofauna taxa sampled in the siboglinid field varied in their dependence on chemosynthesis. The Amphinomidae polychaetes and the pygnogonids with signatures similar to that of *S. contortum* (around -35‰) probably have an entirely chemosynthesis-derived diet. At the other end of the gradient, the Flabelligeridae polychaetes, the gastropod *Cryptonatica affinis* and ophiurids, with signatures around -20‰, mainly rely on off-seep organic inputs and only very weakly on local chemosynthetic production. Showing intermediate δ13C values, from -26 to -29‰, Thyasiridae bivalves, Caprellidae amphipods, isopods and tanaids derive part of their nutrition from local chemosynthesis, but also benefit from external inputs of photosynthesis-derived sources. The signature of *Thyasira* cf *dunbari* confirms that this species may not be in symbiosis or may have a mixotrophic diet.

The occurrence of background species, which are either vagrants that do not exploit seep production or are colonists that partially assimilate seep production, is probably related

to interface geochemistry, which is very different from the mat habitat (De Beer et al., 2006). With low sulphide concentrations and high penetration depth of oxygen, these conditions, intermediate to those found on seeps and normal sediment, allow vagrant species to emigrate from the background environment.

In conclusion, this study demonstrated variability in the carbon signature between two habitats of the Håkon Mosby mud volcano: the siboglinid *S. contortum* fields and the white microbial mats. Compared to the habitats near the active centre, the contribution of chemosynthetic production to the nutrition of seep fauna decreases in the outer siboglinid fields. However, no small-scale variability, tested between mats and adjacent sediment a few metres apart, was revealed. The nutrition gradient observed here is attributed to fluid flow and geochemical gradients that occur concentrically around the volcano. In addition, we showed that trophic chains are well separated among two habitats (white mats and siboglinid fields) and two different food chains seem to co-occur on microbial mats. The food web and the relative contribution of local seep production to macrofauna nutrition will be investigated in a future study and will be compared with other seep communities recently studied along the Norwegian margin.

## Acknowledgements

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