I n t r o d u c t i o n

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For some time, two concepts have been appreciated concerning methane seeps: (i) At any single point location on the seafloor, seepage is an ephemeral process bound to eventual dormancy, and (ii) carbonate pavements precipitated at methane seeps have high potential to enter the geological record as an archive of historic seepage. For the first time, this thesis applies *in situ*, time-resolved experiments with parallel biomarkers to begin addressing the fundamental question connecting points (i) and (ii):

> To what extent does the taphonomy of microorganisms in seep carbonates represent those species present during active seepage vs those last present before incorporation into the rock record?

While each chapter contains its own standalone introduction, the following section is intended to familiarize the reader with some of the general geological, geochemical, and geobiological aspects of methane seeps, as well as to motivate the overarching research questions addressed herein. At the end of this introduction, a brief summary of the principle questions addressed in each chapter is provided.

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Methane seeps, first discovered in the Gulf of Mexico in 1984 (Paull et al. 1984), are globally distributed geologic features in which reduced fluids, including methane, are advected upward from below the seafloor and meet the oxidized bottom waters of Earth's oceans. Methane seeps are located on both passive and active continental margins, with a variety of geologic processes (e.g., subduction, subseafloor salinity-driven density overturning) creating conduits for reduced fluids to move upwards (Judd 2003; Tunnicliffe et al. 2003; German et al. 2011). Worldwide, the most exhaustively studied methane seeps are those located in the Black Sea (Michaelis et al. 2002), the Mediterranean (Aloisi et al. 2002), and "Hydrate Ridge", a north-south promontory at 700-800 meters water depth off the coast of Oregon on the Cascadia margin (Boetius and Suess 2004).

Methane in seeps is generally sourced from decomposition of buried organic matter (originally produced photosynthetically). Methane production can be either thermogenic or biogenic, with the two processes yielding characteristically different $\delta^{13}C_{methane}$ values (Schoell 1980). At Hydrate Ridge, the seep most intensively studied in this thesis, the methane is highly depleted (approximately -65‰), indicating a mostly biogenic origin (Kastner et al. 1998; Suess et al. 1999; Boetius and Suess 2004). Once produced, depending on temperature and pressure conditions as well as the methane concentration itself, methane will either remain in the dissolved phase, become locked in methane hydrates, or bubble out of the seafloor as free methane gas. The dissolved component of subseafloor methane is oxidized predominantly in the subsurface by the microbially-mediated, sulfate-coupled anaerobic oxidation of methane (AOM):

$$CH_4 + SO_4^= \rightleftarrows HCO_3^- + HS^- + H_2O \qquad \text{(Eq. 1)}$$
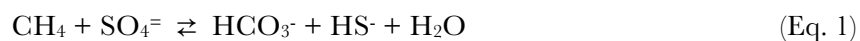
It is well established that consortia of anaerobic methane oxidizing archaea (ANME) and sulfate-reducing bacteria (SRB) work symbiotically to achieve AOM (Hinrichs et al. 1999; Boetius et al. 2000; Orphan et al. 2001b), although the mechanistic details of the process remain an active

area of investigation (Milucka et al. 2012; McGlynn et al. 2015; Scheller et al. 2016). AOM can also be accomplished with other electron acceptors including iron (Beal et al. 2009), manganese (Beal et al. 2009), nitrite (Ettwig et al. 2010), and nitrate (Haroon et al. 2013), but sulfate-coupled AOM is the dominant process in most seep environments. ANME archaea are subdivided into three clades: ANME-1, ANME-2, and ANME-3 (Orphan et al. 2001a; 2002; Knittel et al. 2005; Niemann et al. 2006). These ANME often live in tight consortia with deltaprotebacterial SRB of the *Desulfosarcina*, *Desulfococcus*, and *Desulfobulbus* genera (Orphan et al. 2002; Knittel et al. 2005; Lösekann et al. 2007; Schreiber et al. 2010; Green-Saxena et al. 2014), although reports also exist of ANME-1 and ANME-2 living as single cells or monospecies aggregates (Orphan et al. 2001b; 2002).

AOM in methane seeps oxidizes ~96% to ~100% of dissolved methane before it can escape to ocean bottom waters (Sommer et al. 2006). In cases where methane concentrations are high enough to nucleate ebullition, more methane escapes and the biological AOM filter is reduced to ~66% to 83% efficiency (Sommer et al. 2006). Nonetheless, methane seeps are estimated to consume ~78 Tg CH_4/year globally (and when including AOM in non-seep continental shelf sediments, estimates suggest global consumption of >350 Tg CH_4/year, implying also a high annual rate of subseafloor methane production; Hinrichs and Boetius 2000; Reeburgh 2007). Estimates suggest Earth's current (including anthropogenic influences) gross production and consumption of methane to be on the order of 500-600 Tg CH_4/year (Kirschke et al. 2013). As such AOM, including AOM in methane seeps, is a significant contributor to global methane cycling, and a small change in cycling efficiency at methane seeps might have a large impact on global budgets. Moreover, the contribution of methane seeps is likely to be higher than estimated, considering that the occurrence of seeps, which has been largely unknown, now appears to be extremely high: a recent study located seeps every 4 km along the continental slope off Nicaragua, Costa Rica, and Panama (Sahling et al. 2008).

Seeps may have played one or more important roles during Earth history. This could include, of course, a similar role as today, with AOM in seeps cycling a large amount of methane. Such a role has been proposed based on evidence of strongly ^{13}C-depleted kerogens from as old as 2.7 Ga (Hinrichs 2002) as well as ^{13}C-depleted carbonate deposits in the Proterozoic and Phanerozoic (Schrag et al. 2013). However, other mechanisms have also been invoked to explain ^{13}C signals in the ancient sedimentary record, including alternative microbial metabolisms and/or secondary alternation of carbonate minerals following burial (Grotzinger et al. 2011; Slotznick and Fischer 2016). Other contributions of subseafloor methane to Earth history have also been proposed. Perhaps the most catastrophic is the hypothesis that rapid and self-reinforcing destabilization of methane hydrates may have led to and/or been a result of dramatic climate warming during the Paleocene-Eocene Thermal Maximum (Katz et al. 1999), and during post-glacial hot house periods following snowball Earth events in the Proterozoic (Jiang et al. 2003).

Besides ANME and SRB, methane seeps host a broad diversity of microorganisms. Studies have most intensively focused on methane seep sediments, finding that microbial assemblages in seep sediments are distinct from other marine sedimentary environments as assessed by 16S rRNA gene surveys (Pop Ristova et al. 2015; Ruff et al. 2015). Seeps are typified from other settings by high relative abundances of *Methanomicrobia* and *Deltaproteobacteria* classes (containing ANME and SRB, respectively), as well as bacterial candidate divisions Hyd24-12 and JS1 (Ruff et al. 2015). Targeted metagenomics have recently shown members of candidate division Hyd24-12 to contain genes consistent with fermentative metabolisms of simple sugars and the potential ability to reduce elemental sulfur to sulfide (Kirkegaard et al. 2016). Using single cell genomics, candidate division JS1 has recently been placed within the candidate phylum *Atribacteria*, and likely represents heterotrophic, strictly anaerobic microorganisms participating in fermentation of organic acids such as propionate and acetate (Nobu et al. 2016). Sulfur-cycling microorganisms, in particular putative sulfide-oxidizing members of the *Epsilonproteobacteria* and *Gammaproteobacteria*, are also common and abundant in seep sediments and are often manifested by

dense orange, pink, and/or white mats covering the seafloor (Nunoura et al. 2012; Niemann et al. 2013; Marlow et al. 2014b; Ruff et al. 2015).

The ANME, SRB, and other microbial species inhabiting methane seeps form the base of a complex food web of organisms which includes fish, bivalves (mussels and clams), tube worms, polychaetes, nematodes, and crabs (Levin 2005). The microbial and megafaunal inhabitants of methane seeps are one of the most recognizable seafloor features of methane seepage (in addition to a carbonate-strewn landscape and, occasionally, methane ebullition), helping researchers identify seep locales during seafloor exploration. Moreover, the distribution of biological organisms often mirrors the delivery of reduced fluids from below, effectively allowing biology to be used as a rough visual "map" of contemporary seepage (Barry et al. 1997; Treude et al. 2003; Orphan et al. 2004; Levin 2005).

This is useful and important because methane seepage is a spatially and temporally heterogeneous process. Lateral and vertical microbiological and geochemical heterogeneity is observed on the scale of meters or less (Sahling et al. 2002; Levin et al. 2003; Treude et al. 2003; Orphan et al. 2004; Pop Ristova et al. 2015). In general, microbial mats are observed to dominate high-flux areas, often ringed in a "bulls-eye" manner by bivalves on the periphery of seepage (Barry et al. 1997; Orphan et al. 2004). If methane ebullition is present, it is usually strong enough to disrupt any colonization by seep organisms in its direct (cm- to m-scale) proximity.

Temporal variation in seepage is one of the primary drivers of spatial heterogeneity of seep-dependent taxa and geochemistry. Seepage can vary on timescales from days (tidal forcing of the hydraulic head, fault blockage by hydrates or carbonates; Torres et al. 2002; Tryon et al. 2002) to hundreds of years (subduction thrust earthquake cycle in the Cascadia Margin; Tryon et al. 2002) to tens or hundreds of thousands of years (glacial/interglacial sea level forcing of the hydraulic head; Teichert et al. 2003; Watanabe et al. 2008). These timescales are reflected in age measurements of carbonate precipitates at methane seeps, which form inorganically (i.e., authigenically) within the sediment column as a result of the production of two units of alkalinity

(Alk) per one unit of dissolved inorganic carbon (DIC) from sulfate-coupled AOM (Eq. 1; Berner 1980; Ritger et al. 1987). Histograms of carbonate age measured by U-Th frequently indicate discontinuous precipitation on glacial/interglacial timescales (Aharon et al. 1997; Teichert et al. 2003; Kutterolf et al. 2008; Watanabe et al. 2008; Kiel 2009; Liebetrau et al. 2010; Feng et al. 2010). This presumably tracks discontinuous magnitudes of seepage flux and AOM driven by changes in methane hydrate stability as a function of sea level controlling the hydraulic head overlying seep systems. Such timescales would be compatible with other measurements which indicate approximately continuous precipitation, but not on the scale of greater than thousands of years (Naehr et al. 2000; Bayon et al. 2009).

Previous sampling efforts have shown seep carbonates to consist of a variety of morphologies including aragonite, calcite, dolomite, and mixtures thereof (Ritger et al. 1987; Kulm and Suess 1990; Bohrmann et al. 1998; Naehr et al. 2000; Greinert et al. 2001). The factors most often invoked to explain the precipitation of specific carbonate mineralogies have included Alk concentration (Ritger et al. 1987; Greinert et al. 2001; Luff and Wallmann 2003), Ca^{2+} and Mg^{2+} ion concentration (Ritger et al. 1987; Greinert et al. 2001), temperature (Naehr et al. 2000; Greinert et al. 2001), degree of calcium carbonate supersaturation (Naehr et al. 2000), and, more than any other factor, pore water sulfate concentration (Ritger et al. 1987; Burton 1993; Greinert et al. 2001; Peckmann et al. 2001; Aloisi et al. 2002; Reitner et al. 2005a). Based on empirical observations of the distribution of different calcium carbonate morphologies, thermodynamic and kinetic modeling, and carbon and oxygen isotope ratios of seep carbonates, the working hypothesis is that aragonites, which are more soluble than calcite and high-Mg calcite phases, precipitate at or near the sediment-water interface in a zone where alkalinity and carbonate supersaturation is quite high, but sulfate concentrations from the overlying bottom water remain high enough to inhibit calcite precipitation (Ritger et al. 1987; Aloisi et al. 2002; Gieskes et al. 2005). Calcites, accordingly, are hypothesized to form slightly deeper in the sediment column, perhaps near the zone of maximum AOM, where alkalinity is high and sulfate is depleted to zero

concentration. Dolomites, based primarily on carbon and oxygen isotope evidence, are predicted to form well below AOM zones, in horizons of microbial methanogenesis (Greinert et al. 2001; Gieskes et al. 2005).

At many methane seeps, including Hydrate Ridge, carbonate blocks and pavements are ubiquitous features of the seafloor landscape, covering hundreds of square meters on the seafloor (Kulm and Suess 1990; Boetius and Suess 2004) and extending vertically into the water column in special cases of euxinia such as the Black Sea (Michaelis et al. 2002). As such, seep carbonates provide an important hard habitat substrate for biological colonization. In addition to their lateral extent, subseafloor acoustic data shows that carbonates also extend vertically to meters or tens of meters below the sediment-water interface (Klaucke et al. 2008; 2012). Carbonates, therefore, represent a volumetrically significant (perhaps dominant) habitat substrate in methane seep benthic and subseafloor ecosystems (Marlow et al. 2014a). Despite this, investigations of carbonate-associated microbial and megafaunal ecology have been limited, in part due to unrecognized importance of seep carbonates as distinct habitats from seep sediments and in part due to their difficult sampling nature on the seafloor. With the exception of one early report (Jensen et al. 1992), studies of seep carbonate-associated megafaunal diversity have only recently begun to enter the literature (Ritt et al. 2010; 2011; Grupe et al. 2015; Levin et al. 2015).

The first detailed descriptions of microorganisms specifically associated with seep carbonates were a series of reports of microbial mats covering large carbonate chimneys extending meters above the seafloor in the anoxic bottom waters of the Black Sea (Pimenov et al. 1997; Thiel et al. 2001; Peckmann et al. 2001). These included microscopic observations of microbial filaments and lipid profile characterizations, and *in vitro* experiments showed the organisms to be capable of metabolic activity (Michaelis et al. 2002). Subsequent lipid and 16S rRNA gene analyses further characterized the chemotaxonomic and phylogenetic diversity of microorganisms inhabiting Black Sea seep carbonates (Tourova et al. 2002; Blumenberg et al. 2004; Reitner et al. 2005b). Around the same time, lipid and 16S rRNA gene surveys were

reported from several benthic seep carbonates in the Mediterranean Sea, unambiguously demonstrating the presence of ANME and SRB as well as other phylogeneticaly diverse microorganisms, including archaeal Marine Group I and bacterial alpha-, beta-, and gamma-proteobacteria, among others (Pancost et al. 2001; Aloisi et al. 2002; Heijs et al. 2006). Meanwhile, parallel analysis of four carbonate samples with five sediment samples from ~2,000 meters deep in the Black Sea yielded a higher concentration of microbial biomarkers and a distinct community of Archaea in the carbonates as compared to the sediments (Stadnitskaia et al. 2005). Not until 2014 was as systematic survey undertaken to compare microbial communities inhabiting seep carbonates vs seep sediments. Though limited in sample number, investigation at Hydrate Ridge revealed bacterial and archaeal 16S rRNA gene profiles to be differentiated by habitat substrate and seep activity, respectively (Marlow et al. 2014b). In the same year, seep carbonates were demonstrated to host metabolically active endolithic anaerobic methanotrophs, greatly expanding the potential contribution of AOM to subseafloor methane cycling (Marlow et al. 2014a).

The application of microbial biomarker analyses has not been limited to modern, actively venting methane seeps. Extraction and characterization of lipid biomarkers has been used in conjunction with isotopic and megafaunal fossil evidence to link geologic outcrops to historic methane seepage from as young as the Pleistocene to as old as the Carboniferous (Peckmann et al. 1999; Thiel et al. 1999; Peckmann et al. 2002; Goedert et al. 2003; Birgel et al. 2006b; a; Birgel et al. 2008b; a; Kiel et al. 2013; Natalicchio et al. 2015; Little et al. 2015). Besides just ancient seep identification, lipids have been used at sites wordwide to infer paleo-seepage flux (Stadnitskaia et al. 2008; Leefmann et al. 2008; Gontharet et al. 2009; Peckmann et al. 2009; Birgel et al. 2011; Hagemann et al. 2012) or ancient ANME-1 vs ANME-2 ratios (Niemann and Elvert 2008; Peckmann et al. 2009; Birgel et al. 2011; Natalicchio et al. 2015).

Paleo-seep studies rely on assumptions regarding both the fidelity with which biomarkers record methane seep microbial assemblages (chemotaxonomy) and the longevity of biomarkers

over time. Chemotaxomic understanding within methane seeps systems has grown as a result of extensive study and methodological development over the last ~15 years (Hinrichs et al. 2000; Rütters et al. 2001; Elvert et al. 2003; Sturt et al. 2004; Blumenberg et al. 2004; Rossel et al. 2008; Niemann and Elvert 2008; Schubotz et al. 2011; Yoshinaga et al. 2011; 2015), but the longevity (i.e., degradation rate) of biomarkers remains poorly constrained. Historically, intact polar lipids (IPLs) were assumed to be excellent recorders of live biomass due to rapid degradation after cell death of the bond between polar head group and glycerol backbone (White et al. 1979; 1997; Zink et al. 2003; Sturt et al. 2004). The core lipid, that which remains after loss of the polar head group, is assumed to be stable over geologic timescales and indeed core lipids have been recovered from seep carbonates in the sedimentary record as old as 300 million years (Birgel et al. 2008b). Recent evidence, however, has indicated IPLs may have high enough longevity to record more than just living microbial communities. In anoxic laboratory microcosm experiments of marine sediment, ester-based IPLs (in this case artificially spiked in from dead eukaryotic *Saccharomyces cerevisiae* cells, but also the dominant bond type found in bacterial lipids) degraded to <10% of original concentration within 100 days, but archaeal ether-based IPLs demonstrated no measurable degradation in the same time frame (Logemann et al. 2011). A more sensitive ^{14}C-labeling experiment, run for 300 days but only analyzing archaeal ether-linked IPLs, indicated such slow IPL degradation rates in anoxic marine sediment microcosms that the half-life of archaeal IPLs in subseafloor environments was extrapolated to be 10^3-10^5 years (Xie et al. 2013).

This begs the question posed on page 1 of this thesis: how do microorganisms respond to changes in seepage flux, and how is the microbial response recorded in carbonate-associated biomarkers?

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This thesis concerns the ecology of microorganism associated with seep carbonates from basic questions of inter-habitat diversity to novel, *in situ*, multi-biomarker, time-resolved seafloor experiments. Some basic questions addressed are:

Chapter One

• Does microbial diversity differ between subseafloor protolithic carbonate "nodules" and their adjacent sediments?
• To what extent do subseafloor geochemical parameters inform the capture of sediment-hosted microbial assemblages into solid habitat substrates?

Chapter Two

• Do fully lithified seep carbonates host distinct microorganisms from seep sediments, nodules, and bottom waters?
• How sensitive are carbonate-associated microbial assemblages to seepage activation or quiescence on 13-month timescales?
• Which microorganisms colonize sterile hard substrates placed at methane seeps, and is colonization substrate- or seepage-dependent?

Chapter Three

• In parallel analysis of DNA and IPL biomarkers, are similar or different sensitivities observed to seepage flux (and changes in seepage flux)?
• Are microbial biomarkers preferentially associated with particular morphologies of calcium carbonate?
• Given, for the first time, observed microbial responses to 13 months of *in situ* imposed seep quiescence, can future biomarker response to continued seep quiescence be quantitatively estimated?
• Are some microbial species' associated biomarkers particularly suited to be applied as proxies for "active" or "low activity" seep conditions recorded in ancient seep carbonates?

These three chapters represent the primary contribution of this thesis to the scientific community's understanding of seep carbonate-associated microbial ecology (Chapters One and Two were published in 2015, while Chapter Three is in manuscript form). Chapter Four concerns methods development for next-generation sequencing of the 16S rRNA gene, the most commonly employed microbial diversity assay in the literature and in this thesis, including extensive post-processing tests to ensure robust data interpretation. An appendix describes microbiological and geochemical results from a high-pressure incubation of methane seep sediments recovered from the Joetsu Knoll, Japan.

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REFERENCES

Aharon, P., H. P. Schwarcz, and H. H. Roberts. 1997. Radiometric dating of submarine hydrocarbon seeps in the Gulf of Mexico. Geological Society of America Bulletin **109**: 568–579.

Aloisi, G., I. Bouloubassi, S. K. Heijs, R. D. Pancost, C. Pierre, J. S. Sinninghe Damsté, J. C. Gottschal, L. J. Forney, and J.-M. Rouchy. 2002. CH4-consuming microorganisms and the formation of carbonate crusts at cold seeps. Earth and Planetary Science Letters **203**: 195–203.

Barry, J. P., R. E. Kochevar, and C. H. Baxter. 1997. The influence of pore-water chemistry and physiology on the distribution of vesicomyid clams at cold seeps in Monterey Bay: Implications for patterns of chemosynthetic community organization. Limnology and Oceanography **42**: 318–328.

Bayon, G., G. M. Henderson, and M. Bohn. 2009. U–Th stratigraphy of a cold seep carbonate crust. Chemical Geology **260**: 47–56.

Beal, E., C. House, and V. Orphan. 2009. Manganese-and iron-dependent marine methane oxidation. Science **325**: 184–187.

Berner, R. A. 1980. Earth Diagenesis, Princeton University Press.

Birgel, D., D. Feng, H. H. Roberts, and J. Peckmann. 2011. Changing redox conditions at cold seeps as revealed by authigenic carbonates from Alaminos Canyon, northern Gulf of Mexico. Chemical Geology **285**: 82–96.

Birgel, D., J. Peckmann, S. Klautzsch, V. Thiel, and J. Reitner. 2006a. Anaerobic and Aerobic Oxidation of Methane at Late Cretaceous Seeps in the Western Interior Seaway, USA. Geomicrobiology Journal **23**: 565-577.

Birgel, D., M. Elvert, X. Han, and J. Peckmann. 2008a. ^{13}C-depleted biphytanic diacids as tracers of past anaerobic oxidation of methane. Organic geochemistry **39**: 152–156.

Birgel, D., T. Himmler, A. Freiwald, and J. Peckmann. 2008b. A new constraint on the antiquity of anaerobic oxidation of methane: Late Pennsylvanian seep limestones from southern Namibia. Geology **36**: 543–546.

Birgel, D., V. Thiel, Hinrichs, M. Elvert, K. A. Campbell, J. Reitner, J. D. Farmer, and J. Peckmann. 2006b. Lipid biomarker patterns of methane-seep microbialites from the Mesozoic convergent margin of California. Organic geochemistry **37**: 1289–1302.

Blumenberg, M., R. Seifert, J. Reitner, T. Pape, and W. Michaelis. 2004. Membrane lipid patterns typify distinct anaerobic methanotrophic consortia. Proceedings of the National Academy of Sciences **101**: 11111–11116.

Boetius, A., and E. Suess. 2004. Hydrate Ridge: a natural laboratory for the study of microbial life fueled by methane from near-surface gas hydrates. Chemical Geology **205**: 291–310.

Boetius, A., K. Ravenschlag, C. J. Schubert, D. Rickert, F. Widdel, A. Gieseke, R. Amann, B. B. Jørgensen, U. Witte, and O. Pfannkuche. 2000. A marine microbial consortium apparently mediating anaerobic oxidation of methane. Nature **407**: 623–626.

Bohrmann, G., J. Greinert, E. Suess, and M. Torres. 1998. Authigenic carbonates from the Cascadia subduction zone and their relation to gas hydrate stability. Geology **26**: 647.

Burton, E. A. 1993. Controls on marine carbonate cement mineralogy: review and reassessment. Chemical Geology **105**: 163–179.

Elvert, M., A. Boetius, K. Knittel, and B. B. Jørgensen. 2003. Characterization of Specific Membrane Fatty Acids as Chemotaxonomic Markers for Sulfate-Reducing Bacteria Involved in Anaerobic Oxidation of Methane. Geomicrobiology Journal **20**: 403–419.

Ettwig, K., M. Butler, D. Le Paslier, and E. Pelletier. 2010. Nitrite-driven anaerobic methane oxidation by oxygenic bacteria. Nature **464**: 543-548

Feng, D., H. H. Roberts, H. Cheng, J. Peckmann, G. Bohrmann, R. Lawrence Edwards, and D. Chen. 2010. U/Th dating of cold-seep carbonates: An initial comparison. Deep Sea Research Part II: Topical Studies in Oceanography **57**: 2055–2060.

German, C. R., E. Ramirez-Llodra, M. C. Baker, P. A. Tyler, and A. T. C. S. S. Committee. 2011. Deep-Water Chemosynthetic Ecosystem Research during the Census of Marine Life Decade and

Beyond: A Proposed Deep-Ocean Road Map. PLoS ONE **6**: e23259.

Gieskes, J., C. Mahn, S. Day, J. Martin, J. Greinert, T. Rathburn, and B. McAdoo. 2005. A study of the chemistry of pore fluids and authigenic carbonates in methane seep environments: Kodiak Trench, Hydrate Ridge, Monterey Bay, and Eel River Basin. Chemical Geology **220**: 329–345.

Goedert, J. L., V. Thiel, O. Schmale, W. W. Rau, W. Michaelis, and J. Peckmann. 2003. The Late Eocene "Whiskey Creek" methane-seep deposit (western Washington State). Facies **48**: 223–239.

Gontharet, S., A. Stadnitskaia, I. Bouloubassi, C. Pierre, and J. S. Damsté. 2009. Palaeo methane-seepage history traced by biomarker patterns in a carbonate crust, Nile deep-sea fan (Eastern Mediterranean Sea). Marine Geology **261**: 105–113.

Green-Saxena, A., A. E. Dekas, N. F. Dalleska, and V. J. Orphan. 2014. Nitrate-based niche differentiation by distinct sulfate-reducing bacteria involved in the anaerobic oxidation of methane. The ISME Journal **8**: 150–163.

Greinert, J., G. Bohrmann, and E. Suess. 2001. Gas Hydrate-Associated Carbonates and Methane-Venting at Hydrate Ridge: Classification, Distribution, and Origin of Authigenic Lithologies, p. 99–113. *In* C.K. Paull and W.P. Dillon [eds.], Natural Gas Hydrates. American Geophysical Union.

Grotzinger, J. P., D. A. Fike, and W. W. Fischer. 2011. Enigmatic origin of the largest-known carbon isotope excursion in Earth's history. Nature Geoscience **4**: 285–292.

Grupe, B. M., M. L. Krach, A. L. Pasulka, and J. M. Maloney. 2015. Methane seep ecosystem functions and services from a recently discovered southern California seep. Marine Ecology **36**: 91-108

Hagemann, A., T. Leefmann, J. Peckmann, V.-E. Hoffmann, and V. Thiel. 2012. Biomarkers from individual carbonate phases of an Oligocene cold-seep deposit, Washington State, USA. Lethaia **46**: 7–18.

Haroon, M. F., S. Hu, Y. Shi, M. Imelfort, J. Keller, P. Hugenholtz, Z. Yuan, and G. W. Tyson. 2013. Anaerobic oxidation of methane coupled to nitrate reduction in a novel archaeal lineage. Nature, doi:10.1038/nature12375

Heijs, S. K., G. Aloisi, I. Bouloubassi, R. D. Pancost, C. Pierre, J. S. Sinninghe Damsté, J. C. Gottschal, J. D. Elsas, and L. J. Forney. 2006. Microbial Community Structure in Three Deep-Sea Carbonate Crusts. Microbial Ecology **52**: 451–462.

Hinrichs. 2002. Microbial fixation of methane carbon at 2.7 Ga: Was an anaerobic mechanism possible? Geochemistry Geophysics Geosystems **3**: 1042.

Hinrichs, and A. Boetius. 2000. The Anaerobic Oxidation of Methane, p. 457–477. *In* G. Wefer, D. Billett, D. Hebbeln, B.B. Jørgensen, M. Schluter, and T. Van Weering [eds.], Ocean Margin Systems. Springer Netherlands.

Hinrichs, J. M. Hayes, S. P. Sylva, P. G. Brewer, and E. F. DeLong. 1999. Methane-consuming archaebacteria in marine sediments. Nature **398**: 802–805.

Hinrichs, R. E. Summons, V. Orphan, S. P. Sylva, and J. M. Hayes. 2000. Molecular and isotopic analysis of anaerobic methane-oxidizing communities in marine sediments. Organic Geochemistry **31**: 1685–1701.

Jensen, P., I. Aagaard, R. A. Burke Jr, P. R. Dando, N. O. Jørgensen, A. Kuijpers, T. Laier, S. OHara, and R. Schmaljohann. 1992. "Bubbling reefs" in the Kattegat: submarine landscapes of carbonate-cemented rocks support a diverse ecosystem at methane seeps. Marine Ecology Progress Series **83**: 103–112.

Jiang, G., M. J. Kennedy, and N. Christie-Blick. 2003. Stable isotopic evidence for methane seeps in Neoproterozoic postglacial cap carbonates. Nature **426**: 822–826.

Judd, A. 2003. The global importance and context of methane escape from the seabed. Geo-Marine Letters **23**: 147-154

Kastner, M., K. A. Kvenvolden, and T. D. Lorenson. 1998. Chemistry, isotopic composition, and origin of a methane-hydrogen sulfide hydrate at the Cascadia subduction zone. Earth and Planetary Science Letters **156**: 173–183.

Katz, M. E., D. K. Pak, G. R. Dickens, and K. G. Miller. 1999. The Source and Fate of Massive Carbon Input During the Latest Paleocene Thermal Maximum. Science **286**: 1531–1533.

Kiel, S. 2009. Global hydrocarbon seep-carbonate precipitation correlates with deep-water temperatures and eustatic sea-level fluctuations since the Late Jurassic. Terra Nova **21**: 279–284.

Kiel, S., D. Birgel, K. A. Campbell, J. S. Crampton, P. Schiøler, and J. Peckmann. 2013. Cretaceous methane-seep deposits from New Zealand and their fauna. Palaeogeography, Palaeoclimatology, Palaeoecology **390**: 17–34.

Kirkegaard, R. H., M. S. Dueholm, S. J. McIlroy, M. Nierychlo, S. M. Karst, M. Albertsen, and P. H. Nielsen. 2016. Genomic insights into members of the candidate phylum Hyd24-12 common in mesophilic anaerobic digesters. The ISME Journal, doi:10.1038/ismej.2016.43

Kirschke, S., P. Bousquet, P. Ciais, M. Saunois, J. G. Canadell, E. J. Dlugokencky, P. Bergamaschi, D. Bergmann, D. R. Blake, L. Bruhwiler, P. Cameron-Smith, S. Castaldi, F. Chevallier, L. Feng, A. Fraser, M. Heimann, E. L. Hodson, S. Houweling, B. Josse, P. J. Fraser, P. B. Krummel, J.-F. Lamarque, R. L. Langenfelds, C. Le Quéré, V. Naik, S. O'Doherty, P. I. Palmer, I. Pison, D. Plummer, B. Poulter, R. G. Prinn, M. Rigby, B. Ringeval, M. Santini, M. Schmidt, D. T. Shindell, I. J. Simpson, R. Spahni, L. P. Steele, S. A. Strode, K. Sudo, S. Szopa, G. R. van der Werf, A. Voulgarakis, M. van Weele, R. F. Weiss, J. E. Williams, and G. Zeng. 2013. Three decades of global methane sources and sinks. Nature Geoscience **6**: 813–823.

Klaucke, I., D. G. Masson, C. J. Petersen, W. Weinrebe, and C. R. Ranero. 2008. Multifrequency geoacoustic imaging of fluid escape structures offshore Costa Rica: Implications for the quantification of seep processes. Geochemistry Geophysics Geosystems **9**, doi:10.1029/2007GC001708

Klaucke, I., W. Weinrebe, P. Linke, D. Kläschen, and J. Bialas. 2012. Sidescan sonar imagery of widespread fossil and active cold seeps along the central Chilean continental margin. Geo-Marine Letters **32**: 489–499.

Knittel, K., T. Lösekann, A. Boetius, R. Kort, and R. Amann. 2005. Diversity and Distribution of Methanotrophic Archaea at Cold Seeps. Applied and Environmental Microbiology **71**: 467–479.

Kulm, L. D., and E. Suess. 1990. Relationship between carbonate deposits and fluid venting: Oregon Accretionary Prism. Journal of Geophysical Research: Solid Earth **95**: 8899–8915.

Kutterolf, S., V. Liebetrau, T. Mörz, A. Freundt, T. Hammerich, and D. Garbe-Schönberg. 2008. Lifetime and cyclicity of fluid venting at forearc mound structures determined by tephrostratigraphy and radiometric dating of authigenic carbonates. Geology **36**: 707–710.

Leefmann, T., J. Bauermeister, A. Kronz, V. Liebetrau, J. Reitner, and V. Thiel. 2008. Miniaturized biosignature analysis reveals implications for the formation of cold seep carbonates at Hydrate Ridge (off Oregon, USA). Biogeosciences **5**: 731–738.

Levin, L. A. 2005. Ecology of cold seep sediments: Interactions of fauna with flow, chemistry, and microbes. Oceanography and Marine Biology: An Annual Review **43**: 1–46.

Levin, L. A., G. F. Mendoza, B. M. Grupe, J. P. Gonzalez, B. Jellison, G. W. Rouse, A. R. Thurber, and A. Waren. 2015. Biodiversity on the Rocks: Macrofauna Inhabiting Authigenic Carbonate at Costa Rica Methane Seeps. PLoS ONE 1–31.

Levin, L. A., W. Ziebis, G. F. Mendoza, V. Growney, M. D. Tryon, K. M. Brown, C. Mahn, J. M. Gieskes, and A. E. Rathburn. 2003. Spatial heterogeneity of macrofauna at northern California methane seeps: influence of sulfide concentration and fluid flow. Marine Ecology Progress Series **265**: 123–139.

Liebetrau, V., A. Eisenhauer, and P. Linke. 2010. Cold seep carbonates and associated cold-water corals at the Hikurangi Margin, New Zealand: New insights into fluid pathways, growth structures and geochronology. Marine Geology **272**: 307–318.

Little, C. T. S., D. Birgel, A. J. Boyce, J. A. Crame, J. E. Francis, S. Kiel, J. Peckmann, D. Pirrie, G. K. Rollinson, and J. D. Witts. 2015. Late Cretaceous (Maastrichtian) shallow water hydrocarbon seeps from Snow Hill and Seymour Islands, James Ross Basin, Antarctica. Palaeogeography, Palaeoclimatology, Palaeoecology **418**: 213–228.

Logemann, J., J. Graue, J. Köster, B. Engelen, J. Rullkötter, and H. Cypionka. 2011. A laboratory experiment of intact polar lipid degradation in sandy sediments. Biogeosciences **8**: 2547–2560.

Lösekann, T., K. Knittel, T. Nadalig, B. Fuchs, H. Niemann, A. Boetius, and R. Amann. 2007. Diversity and Abundance of Aerobic and Anaerobic Methane Oxidizers at the Haakon Mosby

Mud Volcano, Barents Sea. Applied and Environmental Microbiology **73**: 3348-3362.

Luff, R., and K. Wallmann. 2003. Fluid flow, methane fluxes, carbonate precipitation and biogeochemical turnover in gas hydrate-bearing sediments at Hydrate Ridge, Cascadia Margin: numerical modeling and mass balances. Geochimica et Cosmochimica Acta **67**: 3403–3421.

Marlow, J. J., J. A. Steele, W. Ziebis, A. R. Thurber, L. A. Levin, and V. J. Orphan. 2014a. Carbonate-hosted methanotrophy represents an unrecognized methane sink in the deep sea. Nature Communications **5**: 1–12.

Marlow, J., J. A. Steele, D. Case, S. A. Connon, L. A. Levin, and V. J. Orphan. 2014b. Microbial abundance and diversity patterns associated with sediments and carbonates from the methane seep environments of Hydrate Ridge, OR. Frontiers in Marine Science **1**: 1–16.

McGlynn, S. E., G. L. Chadwick, C. P. Kempes, and V. J. Orphan. 2015. Single cell activity reveals direct electron transfer in methanotrophic consortia. Nature 1–14.

Michaelis, W., R. Seifert, K. Nauhaus, T. Treude, V. Thiel, M. Blumenberg, K. Knittel, A. Gieseke, K. Peterknecht, T. Pape, A. Boetius, R. Amann, B. B. Jørgensen, F. Widdel, J. Peckmann, N. V. Pimenov, and M. B. Gulin. 2002. Microbial Reefs in the Black Sea Fueled by Anaerobic Oxidation of Methane. Science **297**: 1013–1015.

Milucka, J., T. G. Ferdelman, L. Polerecky, D. Franzke, G. Wegener, M. Schmid, I. Lieberwirth, M. Wagner, F. Widdel, and M. M. M. Kuypers. 2012. Zero-valent sulphur is a key intermediate in marine methane oxidation. Nature 1–10.

Naehr, T. H., N. M. Rodriguez, G. Bohrmann, C. K. Paull, and R. Botz. 2000. Methane-derived authigenic carbonates associated with gas hydrate decomposition and fluid venting above the Blake Ridge Diapir. Proceedings of the Proceedings of the Ocean Drilling Program **164**: 285-300.

Natalicchio, M., J. Peckmann, D. Birgel, and S. Kiel. 2015. Seep deposits from northern Istria, Croatia: a first glimpse into the Eocene seep fauna of the Tethys region. Geol. Mag. **152**: 444–459.

Niemann, H., and M. Elvert. 2008. Diagnostic lipid biomarker and stable carbon isotope signatures of microbial communities mediating the anaerobic oxidation of methane with sulphate. Organic geochemistry **39**: 1668–1677.

Niemann, H., P. Linke, K. Knittel, E. MacPherson, A. Boetius, W. Brückmann, G. Larvik, K. Wallmann, U. Schacht, E. Omoregie, D. Hilton, K. Brown, and G. Rehder. 2013. Methane-Carbon Flow into the Benthic Food Web at Cold Seeps – A Case Study from the Costa Rica Subduction Zone. PLoS ONE **8**: e74894.

Niemann, H., T. Lösekann, D. de Beer, M. Elvert, T. Nadalig, K. Knittel, R. Amann, E. J. Sauter, M. Schlüter, M. Klages, J. P. Foucher, and A. Boetius. 2006. Novel microbial communities of the Haakon Mosby mud volcano and their role as a methane sink. Nature **443**: 854–858.

Nobu, M. K., J. A. Dodsworth, S. K. Murugapiran, C. Rinke, E. A. Gies, G. Webster, P. Schwientek, P. Kille, R. J. Parkes, H. Sass, B. B. Jørgensen, A. J. Weightman, W.-T. Liu, S. J. Hallam, G. Tsiamis, T. Woyke, and B. P. Hedlund. 2016. Phylogeny and physiology of candidate phylum 'Atribacteria' (OP9/JS1) inferred from cultivation-independent genomics. The ISME Journal **10**: 273–286.

Nunoura, T., Y. Takaki, H. Kazama, M. Hirai, J. Ashi, H. Imachi, and K. Takai. 2012. Microbial Diversity in Deep-sea Methane Seep Sediments Presented by SSU rRNA Gene Tag Sequencing. Microbes and Environments **27**: 382–390.

Orphan, V. J., Hinrichs, W. Ussler, C. K. Paull, L. T. Taylor, S. P. Sylva, J. M. Hayes, and E. F. Delong. 2001a. Comparative Analysis of Methane-Oxidizing Archaea and Sulfate-Reducing Bacteria in Anoxic Marine Sediments. Applied and Environmental Microbiology **67**: 1922–1934.

Orphan, V., C. House, and Hinrichs. 2002. Multiple archaeal groups mediate methane oxidation in anoxic cold seep sediments. Proceedings of the Proceedings of the National Academy of Sciences **99**: 7663–7668.

Orphan, V., C. House, Hinrichs, K. McKeegan, and E. DeLong. 2001b. Methane-Consuming Archaea Revealed by Directly Coupled Isotopic and Phylogenetic Analysis. Science **293**: 484–487.

Orphan, V., W. Ussler, T. H. Naehr, C. H. House, Hinrichs, and C. K. Paull. 2004. Geological,

geochemical, and microbiological heterogeneity of the seafloor around methane vents in the Eel River Basin, offshore California. Chemical Geology **205**: 265–289.

Pancost, R. D., I. Bouloubassi, G. Aloisi, J. S. Sinninghe Damsté, and T. M. S. Scientific Party. 2001. Three series of non-isoprenoidal dialkyl glycerol diethers in cold-seep carbonate crusts. Organic geochemistry **32**: 695–707.

Paull, C. K., B. Hecker, R. Commeau, R. P. Freeman-Lynde, C. Neumann, W. P. Corso, S. Golubic, J. E. Hook, E. Sikes, and J. Curray. 1984. Biological Communities at the Florida Escarpment Resemble Hydrothermal Vent Taxa. Science **226**: 965–967.

Peckmann, J., A. Reimer, C. Luth, C. Luth, B. T. Hansen, C. Heinicke, J. Hoefs, and J. Reitner. 2001. Methane-derived carbonates and authigenic pyrite from the northwestern Black Sea. Marine Geology **177**: 129–150.

Peckmann, J., D. Birgel, and S. Kiel. 2009. Molecular fossils reveal fluid composition and flow intensity at a Cretaceous seep. Geology **37**: 847–850.

Peckmann, J., J. L. Goedert, V. Thiel, W. Michaelis, and J. Reitner. 2002. A comprehensive approach to the study of methane-seep deposits from the Lincoln Creek Formation, western Washington State, USA. Sedimentology **49**: 855–873.

Peckmann, J., V. Thiel, W. Michaelis, P. Clari, C. Gaillard, L. Martire, and J. Reitner. 1999. Cold seep deposits of Beauvoisin (Oxfordian; southeastern France) and Marmorito (Miocene; northern Italy): microbially induced authigenic carbonates. Int J Earth Sci (Geol Rundsch) **88**: 60–75.

Pimenov, N. V., I. I. Rusanov, M. N. Poglazova, L. L. Mityushina, D. Y. Sorokin, V. N. Khmelenina, and Y. A. Trotsenko. 1997. Bacterial mats on coral-like structures at methane seeps in the Black Sea. Microbiology **66**: 354-360.

Pop Ristova, P., F. Wenzhöfer, A. Ramette, J. Felden, and A. Boetius. 2015. Spatial scales of bacterial community diversity at cold seeps (Eastern Mediterranean Sea). The ISME Journal **9**: 1306–1318.

Reeburgh, W. S. 2007. Oceanic Methane Biogeochemistry. Chemical Reviews **107**: 486–513.

Reitner, J., J. Peckmann, A. Reimer, G. Schumann, and V. Thiel. 2005a. Methane-derived carbonate build-ups and associated microbial communities at cold seeps on the lower Crimean shelf (Black Sea). Facies **51**: 66–79.

Reitner, J., J. Peckmann, M. Blumenberg, W. Michaelis, A. Reimer, and V. Thiel. 2005b. Concretionary methane-seep carbonates and associated microbial communities in Black Sea sediments. Palaeogeography, Palaeoclimatology, Palaeoecology **227**: 18–30.

Ritger, S., B. Carson, and E. Suess. 1987. Methane-derived authigenic carbonates formed by subduction-induced pore-water expulsion along the Oregon/Washington margin. Geological Society of America Bulletin **98**: 147–156.

Ritt, B., C. Pierre, O. Gauthier, F. Wenzhöfer, A. Boetius, and J. Sarrazin. 2011. Diversity and distribution of cold-seep fauna associated with different geological and environmental settings at mud volcanoes and pockmarks of the Nile Deep-Sea Fan. Mar Biol **158**: 1187–1210.

Ritt, B., J. Sarrazin, J.-C. Caprais, P. Noël, O. Gauthier, C. Pierre, P. Henry, and D. Desbruyères. 2010. First insights into the structure and environmental setting of cold-seep communities in the Marmara Sea. Deep Sea Research Part I: Oceanographic Research Papers **57**: 1120–1136.

Rossel, P. E., J. S. Lipp, H. F. Fredricks, J. Arnds, A. Boetius, M. Elvert, and Hinrichs. 2008. Intact polar lipids of anaerobic methanotrophic archaea and associated bacteria. Organic geochemistry **39**: 992–999.

Ruff, S. E., J. F. Biddle, A. P. Teske, K. Knittel, A. Boetius, and A. Ramette. 2015. Global dispersion and local diversification of the methane seep microbiome. Proceedings of the National Academy of Sciences 1–6.

Rütters, H., H. Sass, H. Cypionka, and J. Rullkötter. 2001. Monoalkylether phospholipids in the sulfate-reducing bacteria Desulfosarcina variabilis and Desulforhabdus amnigenus. Archives of microbiology **176**: 435–442.

Sahling, H., D. G. Masson, C. R. Ranero, V. Hühnerbach, W. Weinrebe, I. Klaucke, D. Bürk, W. Brückmann, and E. Suess. 2008. Fluid seepage at the continental margin offshore Costa Rica and southern Nicaragua. Geochemistry Geophysics Geosystems **9**: 1–22.

Sahling, H., D. Rickert, R. W. Lee, P. Linke, and E. Suess. 2002. Macrofaunal community structure and sulfide flux at gas hydrate deposits from the Cascadia convergent margin, NE Pacific. Marine Ecology Progress Series **231**: 121–138.

Scheller, S., H. Yu, G. L. Chadwick, S. E. McGlynn, and V. J. Orphan. 2016. Artificial electron acceptors decouple archaeal methane oxidation from sulfate reduction. Science **351**: 703–707.

Schoell, M. 1980. The hydrogen and carbon isotopic composition of methane from natural gases of various origins. Geochimica et Cosmochimica Acta **44**: 649–661.

Schrag, D. P., J. A. Higgins, F. A. Macdonald, and D. T. Johnston. 2013. Authigenic Carbonate and the History of the Global Carbon Cycle. Science **339**: 540–543.

Schreiber, L., T. Holler, K. Knittel, A. Meyerdierks, and R. Amann. 2010. Identification of the dominant sulfate-reducing bacterial partner of anaerobic methanotrophs of the ANME-2 clade. Environmental microbiology **12**: 2327–2340.

Schubotz, F., J. S. Lipp, M. Elvert, and Hinrichs. 2011. Stable carbon isotopic compositions of intact polar lipids reveal complex carbon flow patterns among hydrocarbon degrading microbial communities at the Chapopote asphalt volcano. Geochimica et Cosmochimica Acta **75**: 4399–4415.

Slotznick, S.P., and W.W. Fischer. 2016. Examining Archean methanotrophy. Earth and Planetary Science Letters **344**: 52-59. doi:10.1016/j.epsl.2016.02.013.

Sommer, S., O. Pfannkuche, P. Linke, R. Luff, J. Greinert, M. Drews, S. Gubsch, M. Pieper, M. Poser, and T. Viergutz. 2006. Efficiency of the benthic filter: Biological control of the emission of dissolved methane from sediments containing shallow gas hydrates at Hydrate Ridge. Global Biogeochemical Cycles **20**: 1-14.

Stadnitskaia, A., D. Nadezhkin, B. Abbas, V. Blinova, M. K. Ivanov, and J. S. Sinninghe Damsté. 2008. Carbonate formation by anaerobic oxidation of methane: Evidence from lipid biomarker and fossil 16S rDNA. Geochimica et Cosmochimica Acta **72**: 1824–1836.

Stadnitskaia, A., G. Muyzer, B. Abbas, M. J. L. Coolen, E. C. Hopmans, M. Baas, T. C. E. van Weering, M. K. Ivanov, E. Poludetkina, and J. S. Sinninghe Damsté. 2005. Biomarker and 16S rDNA evidence for anaerobic oxidation of methane and related carbonate precipitation in deep-sea mud volcanoes of the Sorokin Trough, Black Sea. Marine Geology **217**: 67–96.

Sturt, H. F., R. E. Summons, K. Smith, M. Elvert, and Hinrichs. 2004. Intact polar membrane lipids in prokaryotes and sediments deciphered by high-performance liquid chromatography/electrospray ionization multistage mass spectrometry—new biomarkers for biogeochemistry and microbial ecology. Rapid Commun. Mass Spectrom. **18**: 617–628.

Suess, E., M. E. Torres, G. Bohrmann, R. W. Collier, J. Greinert, P. Linke, G. Rehder, A. Trehu, K. Wallmann, G. Winckler, and E. Zuleger. 1999. Gas hydrate destabilization: enhanced dewatering, benthic material turnover and large methane plumes at the Cascadia convergent margin. Earth and Planetary Science Letters **170**: 1–15.

Teichert, B., A. Eisenhauer, G. Bohrmann, A. Haase-Schramm, B. Bock, and P. Linke. 2003. U/Th systematics and ages of authigenic carbonates from Hydrate Ridge, Cascadia Margin: Recorders of fluid flow variations. Geochimica et Cosmochimica Acta **67**: 3845–3857.

Thiel, V., J. Peckmann, H. H. Richnow, U. Luth, J. Reitner, and W. Michaelis. 2001. Molecular signals for anaerobic methane oxidation in Black Sea seep carbonates and a microbial mat. Marine Chemistry **73**: 97–112.

Thiel, V., J. Peckmann, R. Seifert, P. Wehrung, J. Reitner, and W. Michaelis. 1999. Highly isotopically depleted isoprenoids: molecular markers for ancient methane venting. Geochimica et Cosmochimica Acta **63**: 3959–3966.

Torres, M., J. McManus, D. Hammond, M. De Angelis, K. U. Heeschen, S. L. Colbert, M. D. Tryon, K. M. Brown, and E. Suess. 2002. Fluid and chemical fluxes in and out of sediments hosting methane hydrate deposits on Hydrate Ridge, OR, I: Hydrological provinces. **201**: 525–540.

Tourova, T. P., T. V. Kolganova, B. B. Kuznetsov, and N. V. Pimenov. 2002. Phylogenetic Diversity of the Archaeal Component in Microbial Mats on Coral-like Structures Associated with Methane Seeps in the Black Sea. Microbiology **71**: 196–201.

Treude, T., A. Boetius, K. Knittel, K. Wallmann, and B. B. Jørgensen. 2003. Anaerobic oxidation of

methane above gas hydrates at Hydrate Ridge, NE Pacific Ocean. Marine Ecology Progress Series **264**: 1–14.

Tryon, M. D., K. M. Brown, and M. E. Torres. 2002. Fluid and chemical flux in and out of sediments hosting methane hydrate deposits on Hydrate Ridge, OR, II: Hydrological processes. Earth and Planetary Science Letters **201**: 541–557.

Tunnicliffe, V., S. K. Juniper, and M. Sibuet. 2003. Reducing environments of the deep-sea floor, p. 81–110. *In* Ecosystems of the World. Elsevier Press.

Watanabe, Y., S. Nakai, A. Hiruta, R. Matsumoto, and K. Yoshida. 2008. U–Th dating of carbonate nodules from methane seeps off Joetsu, Eastern Margin of Japan Sea. Earth and Planetary Science Letters **272**: 89–96.

White, D., D. B. Ringelberg, S. J. Macnaughton, S. Alugupalli, and D. Schram. 1997. Signature Lipid Biomarker Analysis for Quantitative Assessment In Situ of Environmental Microbial Ecology, p. 22–34. *In* R.P. Eganhouse [ed.], Molecular Markers in Environmental Geochemistry. American Chemical Society.

White, D., W. Davis, J. Nickels, J. King, and R. Bobbie. 1979. Determination of the sedimentary microbial biomass by extractible lipid phosphate. Oecologia **40**: 51–62.

Xie, S., J. S. Lipp, G. Wegener, T. G. Ferdelman, and Hinrichs. 2013. Turnover of microbial lipids in the deep biosphere and growth of benthic archaeal populations. Proceedings of the National Academy of Sciences **110**: 6010–6014.

Yoshinaga, M. Y., C. S. Lazar, M. Elvert, Y.-S. Lin, C. Zhu, V. B. Heuer, A. Teske, and Hinrichs. 2015. Possible roles of uncultured archaea in carbon cycling in methane-seep sediments. Geochimica et Cosmochimica Acta **164**: 35–52.

Yoshinaga, M. Y., M. Y. Kellermann, P. E. Rossel, F. Schubotz, J. S. Lipp, and Hinrichs. 2011. Systematic fragmentation patterns of archaeal intact polar lipids by high-performance liquid chromatography/electrospray ionization ion-trap mass spectrometry. Rapid Commun. Mass Spectrom. **25**: 3563–3574.

Zink, K.-G., H. Wilkes, U. Disko, M. Elvert, and B. Horsfield. 2003. Intact phospholipids—microbial "life markers" in marine deep subsurface sediments. Organic geochemistry **34**: 755–769.