Biogeosciences Discussions

Temperature characteristics of bacterial sulfate reduction in continental shelf and slope sediments

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Abstract

The temperature responses of sulfate-reducing microbial communities were used as fingerprints for their in situ temperature adaptation, their origin, and dispersal in the deep-sea. Sediments were collected from a suite of coastal, continental shelf, and
5 slope sediments from the southwest and southeast Atlantic and permanently cold Arctic fjords from water depths ranging from the intertidal zone to 4327 m. In situ temperatures ranged from 8 °C on the shelf to 1 °C on the lower slope and in the Arctic. Temperature characteristics of the active sulfate-reducing community were determined in short-term incubations with ^{35}S-sulfate in a temperature gradient block spanning
10 a temperature range from 0 to 40 °C. An optimum temperature (T_{opt}) between 27 °C and 30 °C for the South Atlantic shelf sediments and for the intertidal flat sediment from Svalbard was indicative of a psychrotolerant/mesophilic sulfate-reducing community, whereas $T_{opt} \leq 20$ °C in South Atlantic slope and Arctic shelf sediments suggested a predominantly psychrophilic community. High sulfate reduction rates (20–50 %) at
15 in-situ temperatures compared to those at T_{opt} further support this interpretation, and point to the importance of the ambient temperature regime for regulating the short-term temperature response of sulfate-reducing communities. A number of cold (<4 °C) continental slope sediments showed broad temperature optima reaching as high as 30 °C suggesting the additional presence of apparently mesophilic sulfate-reducing bacteria.
20 Since the temperature characteristics of these mesophiles do not fit with the permanently cold deep-sea environment, we suggest that these mesophilic microorganisms are of allochthonous origin and transported to this site. It is likely that they were deposited along with the mass-flow movement of warmer shelf-derived sediment. These data therefore suggest that temperature response profiles of bacterial carbon mineral-
25 ization processes can be used as fingerprints to infer mixing of bacterial communities of different geographic origins.

1 Introduction

About 95 % of the seafloor is permanently cold with in situ temperatures below 4 °C (Levitus and Boyer, 1994). Bacteria carrying out carbon mineralization in the cold sea-bed must be adapted to operate effectively under such low temperatures. Hence, psychrophilic bacteria with a suitable fluidity of the cell membrane and cold-adapted enzymes are particularly abundant in the deep sea (Margesin and Miteva, 2011). As a result of such microbial adaptation to low temperature, the rate and efficiency of organic carbon mineralization in the cold may be as high as in temperate and warm habitats (Kostka et al., 1998). However, bacteria were also isolated from the cold deep-sea floor that function at temperatures extending into the mesophilic range and that do not show cold adaptations (Rüger et al., 1989; Finster and Bak, 1992; Chen et al., 2003; Aono et al., 2010).

Thermal adaptation and flexibility of microorganisms to function effectively at different temperature regimes is related to underlying molecular mechanisms, e.g. to the presence of a large number of genes induced at low temperatures and cold-adapted proteins (Ting et al., 2010; Casanueva et al., 2010). Phenotypically these molecular adaptations are expressed as different cardinal temperatures of growth or respiration, i.e. temperature minimum (T_{min}), maximum (T_{max}) and optimum (T_{opt}), the T_{opt} indicating the temperature of the highest rate. By definition, psychrophilic bacteria have temperature minimum <0 °C, optimum ≤15 °C, and maximum ≤20 °C. Psychrotolerant bacteria have minimum ≤0 °C, optimum ≤25 °C, and maximum ≤35 °C. Mesophilic bacteria have minimum >0 °C, optimum 25–40 °C, and maximum 35–40 °C (after Morita, 1975).

Bacterial sulfate reduction is the predominant anaerobic carbon mineralization pathway in most continental shelf and slope sediments (Jørgensen and Kasten, 2006) and is also detected in sediments of the continental rise and the abyssal plains (Ferdelman et al., 1999; D'Hondt et al., 2003; Lee et al., 2008). Sulfate reduction rates can be quantified with high sensitity and precision by incubating sediment with ^{35}S-sulfate and measuring the rate of ^{35}S-sulfide formation (Fossing, 1995; Kallmeyer et al., 2004).

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This technique is one of the few that links the quantification of organic carbon mineralization rates to a physiologically defined group of microorganisms (Leloup et al., 2007; Lee et al., 2008).

Incubation of sediments or of pure cultures in a temperature gradient has been used to determine the cardinal temperatures for growth or respiration of microbial communities (Battley, 1964). Such incubations have shown that temperate sediments and permanently cold Arctic or Antarctic sediments host bacteria with widely different temperature adaptations (Isaksen and Jørgensen, 1996; Knoblauch and Jørgensen, 1998; Sahm et al., 1999; Brüchert et al., 2001; Hubert et al., 2009). Rates of metabolism at in situ temperatures relative to the rates at T_{opt} indicate how well bacteria perform under ambient low temperatures (Knoblauch and Jørgensen, 1998). The Arrhenius plot can be used for a graphical representation of the temperature dependence of bacterial metabolism (Arrhenius, 1908). Thereby, the logarithm of the rate of bacterial respiration or growth versus the inverse absolute temperature yields a linear relationship in the temperature range where the bacteria are well adapted, whereas deviations from linear slope at the upper or lower extreme express the inability of SRB to maintain a well-controlled metabolic activity and may indicate decoupled electron flow from ATP formation. The slope of the correlation can be used to calculate the apparent activation energy, E_a, where the E_a can be defined as the minimum energy required for initiating a chemical reaction. A reduction of the E_a value may therefore result in an increase of the reaction rate. Apparent E_a values are not activation energies in the strict chemical sense, because sulfate reduction occurs through a series of enzymatic reactions and calculated E_a values therefore measure an ecological response of the whole SRB community to temperature changes rather than the cooperative process between structural elements of an enzyme or a rate-limiting chemical step. From the energy of activation in a given temperature interval the Q_{10} value is calculated, i.e. the factor by which the rate of a reaction increases by a temperature increase of 10 °C (Arrhenius, 1908).

In the present study we analyzed the temperature dependence of sulfate reduction in shelf and slope sediments from the southwest and southeast Atlantic and compared

these data to permanently cold shelf sediments off Svalbard in the Arctic Ocean. We wanted to assess to which extent the temperature response of the microbial communities reflect the ambient temperature and whether their cardinal temperatures are the result of a narrow adaptation to ambient temperature or the consequence of mixed
5   communities of different temperature groups.

2   Material and methods

Sediments from the South Atlantic were collected in 2008 and 2009 at six stations located on the shelf and slope off central Namibia and off Uruguay and Argentina, respectively. Sediments from four stations in the Arctic were collected in 1998, 1999
10 and 2007 from fjords and an intertidal flat on the west coast of Svalbard. Samples were taken from the sediment zone of highest sulfate reduction rate, which was typically in the depth range of 3–10 cm (Jørgensen, 1982). Sediments were stored in gas-tight plastic bags at 4 °C until further processing in the laboratory within a few days. For measurements in whole sediment cores, sediment cores of 26 mm diameter and ca.
15 15 cm length were taken, sealed at both ends with rubber stoppers leaving air in the headspace, and stored at 4 °C. Coordinates for the study sites, in situ temperatures, and water depths at which sediments were collected are given in Table 1.

2.1   Oceanography and sedimentary setting

Namibian shelf and slope. The Benguela upwelling system has extremely high primary
20 productivity of 767–1051 g C m^{-2} yr^{-1} and is the most productive coastal upwelling area on Earth (Carr, 2002 Deep-Sea Research). The bottom water temperatures of Namibian shelf vary annually between 7 and 10 °C on the shelf and between 1 and 4 °C on the slope (Lass and Mohrholz, 2005). The shelf and slope system is characterized by seaward and downslope particle transport that maintains local high sedimentation
25 rates in a depo-center at 1000–1500 m water depth (Inthorn et al., 2005). Sediments

were collected from two stations during the R/V *Meteor* cruise M76/1 (Zabel and Ferdelman, 2008), one on the shelf in 130 m water depth and one on the continental slope in 2000 m water depth. Sediments from the shelf and from the slope have high concentrations of organic carbon content of up to 20 % dry weight that decrease to about 7–8 % in the depocenter on the continental slope (Inthorn et al., 2005). This decrease corresponds well with the decrease in sulfate reduction rates (SRR) with increasing water depth (Table 2, Brüchert et al., 2003).

SW Atlantic margin and basin. The region off Uruguay and Argentina has dynamic oceanographic conditions due to the confluence of two different water masses that cause high primary productivity and high deposition of organic matter (e.g. Behrenfeld and Falkowski, 1997). Sediments from the SW Atlantic were collected during the R/V *Meteor* cruise M78/3a/b on the continental shelf off Uruguay and on the slope off Argentina (Krastel, 2009; Wefer, 2009). Shelf bottom water temperatures vary between 7 and 10 °C and continental slope bottom water temperature are between 1° and 4 °C (Hansen et al., 2003; Ortega et al., 2007). This region is characterized by high sedimentation rates, gravity mass flows due to major turbidities and slides, and strong surface currents (Riedinger et al., 2005). The sediments in the study area are characterized by low carbonate concentrations and high concentrations of organic carbon and iron oxides (Hensen et al., 2003). SRR and TOC content are of the same magnitude as in shelf sediments off Namibia (Table 2). The TOC content of Argentine slope sediments decreased with water depth from 5 % to 1 %.

West coast of Svalbard. Along the west coast of Svalbard primary productivity is controlled by light availability and ice coverage, and the influence of the West Spitsbergen current, which transports relatively warm water (0.5 to 2 °C) from the North Atantic to this latitude (Carmack et al., 2006). The Arctic sediments on the seafloor have very constant temperatures throughout the year ranging from −1 °C to +2 °C. Intertidal mud flats on the west coast of Svalbard have summer temperatures as high as 6 °C, but drop to −20 °C during the winter (Nørdli, 2005). The mean annual primary production along the west coast is around 120 g C m^{-2} y^{-1} (Sakshaug, 2004). SRR are also

relatively high and comparable to rates of many temperate shelf areas (Sagemann et al., 1998). Sediment was collected from four stations along the west coast of the main island of the Svalbard archipelago, Spitsbergen. Three stations were located centrally in fjords while the fourth was on an intertidal mud flat. The fjord sediments were taken in July 1998 and July 1999 with a Haps corer while the intertidal flat was sampled in August 2008 from the shore.

2.1.1 Sulfate reduction rate measurements

Sulfate reduction rates, SRR, were measured in two parallel sediment cores using the whole core incubation method (Jørgensen, 1978). These data are henceforth termed in situ SRR. 5 µl of carrier-free $^{35}SO_4^{2-}$ tracer solution in 4 % NaCl (~100 kBq per injection) was injected at 1 cm intervals to a depth of 16 cm. Incubation time was 8 h at in situ temperature. All samples were analyzed using the low-blank cold chromium distillation method described by Kallmeyer et al. (2004). Briefly, centrifuged sediment was diluted with 10 ml dimethylformamide and placed in a distillation flask. Total reduced inorganic sulfide (TRIS) was acid-distilled under nitrogen at room temperature after adding 12 ml 6N HCL and 12 ml 1M chromium chloride. The TRIS was recovered as zinc sulfide in traps containing 7 ml of 5 % w/v zinc acetate solution and ^{35}S was counted in a liquid scintillation counter (Packard, Tricarb 2500 TR). The scintillation cocktail was Lumasafe Plus (Lumac BV, Groningen, The Netherlands) mixed 2:1 (v/v) with the ZnS suspension.

2.1.2 Temperature dependence of SRR

The temperature dependence of SRR was determined in temperature gradient incubation experiments using a thermostated aluminum block (Isaksen and Jorgensen, 1996). The temperature in the gradient block ranged from −5 °C to +40 °C with a temperature increment between each sample of 1.5 °C. Sediment slurries were prepared by 1:2 (w/v) dilution with anoxic artificial seawater (Widdel and Bak, 1992). Sediment

slurries were made anoxic by bubbling with N_2, and 5 ml of slurry was transferred to each Hungate tube. Hungate tubes were flushed with N_2 (Bryant, 1972) and sealed with butyl rubber stoppers. The Hungate tubes were immediately placed in the temperature gradient block and pre-incubated to allow the sediments to reach thermal equilibrium. Then ^{35}S-labeled carrier-free sulfate (100 kBq final activity) was injected and the slurries were incubated with radiotracer. Incubations were stopped by transferring the sediment to 50 ml polyethylene centrifuge tubes with 20 ml 20 % zinc acetate to stop bacterial activity and to fix sulfides. Samples were kept frozen until further analysis. Subsequent processing followed procedures described in Kallmeyer et al. (2004). South Atlantic sediments were pre-incubated for 12 h, then radiotracer was injected and incubation continued for 24 h i.e. incubations lasted 36 h. Sediments from three Arctic seafloor stations (Kongsfjorden, Krossfjorden and Smeerenburgfjorden) were preincubated for an hour and incubations with the radiotracer lasted 12 h for Kongsfjorden and Krossfjorden and 8 h for Smeerenburgfjorden sediment.

2.1.3 Arrhenius plot and Q_{10}

Activation energies were calculated from the linear range of Arrhenius curves of the ^{35}S-sulfate reduction rates, k, as a function of temperature versus the inverse temperature $(1/T)$:

$$\ln(k) = \ln(A) + \left(\frac{-E_a}{R} \cdot \frac{1}{T} \right) \tag{1}$$

where E_a is the activation energy $(J\,mol^{-1})$, k is the rate of sulfate reduction $(nmol\,cm^{-3}\,day^{-1})$. A is a constant, R is the molecular gas constant $(8.314\,J\,K^{-1}\,mol^{-1})$, and T is the absolute temperature (K).

Q_{10} values between 0 °C and 10 °C were calculated according to:

$$Q_{10} = \exp\left[\frac{E_a \cdot 10}{RT(T+10)} \right] \tag{2}$$

2.1.4 Solid phase analyses

Freeze-dried and homogenized sediment was analyzed for total carbon (TC) and total nitrogen (TN) with a Fisons NA 1500 (Series 2) Elemental Analyzer. Total inorganic carbon (TIC) was measured with a CM 5240 Orbis BV coulometer. Total organic carbon (TOC) was calculated by subtracting TIC from TC.

2.1.5 Sulfate measurements

Pore water sulfate concentrations were determined after centrifugation of sediment at 3500 rpm in capped centrifuge tubes with nitrogen headspace at 4 °C for 15 min. Supernatant pore water (1 ml) was preserved with 200 µl 1 % (w/v) Zn-acetate solution and stored frozen at −20 °C. Sulfate concentrations were measured by suppressed ion chromatography at 1:100 dilution with deionized water on a Metrohm 761 compact IC. Sulfate standards were prepared from Na_2SO_4, with concentrations ranging from 5 to 400 µM using an eight point calibration curve. Quality control samples, treated as unknowns were prepared from calibrated seawater (IAPSO) and analyzed at the start and end of every sample run.

3 Results

3.1 Characterization of study sites

The organic carbon and nitrogen content, expressed as % dry weight and molar C:N ratio are listed in Table 2. The highest organic carbon content was measured in Namibia (4.4 % TOC) and Uruguay (5.0 % TOC) shelf sediments and Namibia (6.5 % TOC) slope sediment. In the other sediments, TOC ranged from 1.2 % to 2.3 % TOC. The total nitrogen concentration (TN) ranged from 0.1 % to 0.9 %. Except for the Arctic intertidal flat sediments, where the molar C:N ratio was 16, C:N ratios calculated for other sediments ranged between 8 and 10. C:N ratios of ca. 10 determined for South Atlantic sediments

are typical for sediments with high TOC content deposited under highly productive marine systems with associated high organic matter fluxes (Meyers, 1994). C:N ratios of <10 generally characterize labile organic matter easily accessible to microorganisms.

Mean rates of in situ SRR in the zone of highest sulfate reduction (top 3 to 9 cm) are presented in Table 2. Highest rates were found in the Namibia shelf sediment, 65.8 nmol cm^{-3} d^{-1} and Uruguay shelf sediment, 43.6 nmol cm^{-3} d^{-1}. The lowest SRR, 6 nmol cm^{-3} d^{-1}, was found in Argentine sediment from 3300 m water depth, in the Arctic fjord sediment from Krossfjorden, 4.29 nmol cm^{-3} d^{-1}, and in Namibian slope sediment from 2000 m water depth, 3.59 nmol cm^{-3} d^{-1}.

3.2 Temperature dependence of SRR, South Atlantic

SRR measured in slurried sediments in the temperature gradient block are not representative of in situ rates, yet they are clearly related to ambient temperatures, water depth, and the availability of organic matter. In situ temperatures of Namibian and Uruguayan shelf sediments define a temperate environment conducive for mesophilic to psychrotolerant microorganisms. This is confirmed by the temperature curves of sulfate reduction in the shelf sediments (Fig. 1a, b), and the three cardinal temperatures, T_{min}, T_{opt}, and T_{max} (Table 3). In both shelf sediments T_{opt} were between 25 and 30 °C. SRR in Namibia slope sediments were 7 nmol cm^{-3} d^{-1} at the in situ temperature and increased to 72 nmol cm^{-3} d^{-1} at T_{opt}. In Uruguay sediment SRR at the in situ temperature were 3 nmol cm^{-3} d^{-1} and increased to 16 nmol cm^{-3} d^{-1} at T_{opt}.

In situ temperatures in the Namibian and Argentinian slope sediments range annually between 1 and 4 °C (Siedler, 1996). In these sediments the T_{opt} of sulfate reduction was distinctly lower than in the corresponding shelf sediments. The highest SRR were found at 22 °C and 20 °C, respectively (Fig. 1c, d, f), and the T_{max} was near 30 °C. A T_{opt} of only 12 °C was found in one of the sediments from the Argentine slope in 3400 m water depth (Fig. 1e). This sediment showed a broad temperature profile between 0 and 15 °C, but above 20 °C SRR dropped below the detection limit.

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3.3 Temperature dependence of SRR, Arctic

In the Arctic fjord sediments, the highest rates were measured in Smeerenburgfjorden (Fig. 1j). In this fjord, the SRR was 53 nmol cm^{-3} d^{-1} at the in situ temperature and increased to 200 nmol cm^{-3} d^{-1} at the T_{opt}. In the Arctic intertidal mud flat (Ymerbukta) and in Kongsfjorden sediment, SRR were about 40 % lower than at the T_{opt} (Fig. 1g, i). In Ymerbukta sediment, rates increased from 4 to 120 nmol cm^{-3} d^{-1} at T_{opt} and in Kongsfjorden sediment, they increased from 27 to 141 nmol cm^{-3} d^{-1}. In the other Arctic fjord sediments, rates increased from 4 to 44 nmol cm^{-3} d^{-1} at T_{opt} (Fig. 1h).

The temperature profile of SRR in Ymerbukta increased in the temperature range from −4 °C to 30 °C and dropped to near-zero at a T_{max} of 35 °C (Fig. 1g). In Smeerenburgfjorden and Krossfjorden sediment the temperature response curve was broad and increased from −4 °C to 27 °C and 23 °C with a T_{max} at 40 and 34 °C, respectively (Fig. 1g, h). Likewise, in Kongsfjorden sediment, SRR showed a psychrotolerant response as activity increased from −4 °C to a maximum at 18 °C, but was barely detectable above 34 °C.

3.4 Arrhenius plots and Q_{10}

The metabolic rates at in situ temperatures compared to T_{opt} were between 9 and 50 % for all the stations (Table 3, Fig. 2). The activation energies calculated from the Arrhenius plots ranged from from 25 to 55 kJ mol^{-1} while the Q_{10} factors were in the range of 2 to 3 (Table 3). In Namibia sediments activation energies ranged from 33 to 55 kJ mol^{-1} and in Argentine sediments from 26 to 55 kJ mol^{-1}.

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4   Discussion

4.1   Temperature response of SRR depends on the in situ $T\,^\circ$C and on the water depth

Our results support the basic notion that the ambient temperature regime of marine environments selects for microbial populations with the best-suited physiology for the respective environment. The permanently cold fjord sediments of the Arctic reflected predominant psychrophilic to psychrotolerant populations while the SRR temperature profile in temperate sediments reflected more mesophilic populations (cf. Isaksen et al., 1994; Sagemann et al., 1998; Isaksen and Jørgensen, 1996). Likewise, the bottom water temperatures of the Uruguayan and Namibian shelf of 7–10 °C as much as the relatively high summer temperatures in the arctic intertidal mud flat of Ymerbukta on Svalbard of 9 °C are consistent with relatively high T_{opt} of 25 to 30 °C and therefore likely indicate a greater abundance of mesophilic populations in these sediments (Fig. 1a, b and j).

A conspicuous property of the temperature-activity diagrams are broad temperature optima with relatively high T_{opt} and T_{max} values. For example, in our study with Smeerenburgfjorden sediment, a broad temperature profile with a T_{opt} at 27 °C was observed after 8 h incubation (Fig. 1j). Broad temperature optima have also been reported for other Arctic sediments (Arnosti et al., 1998; Sagemann et al., 1998). A temperature optimum near 30 °C in permanently cold sediment of 2 °C would at first appear inconsistent with the hypothesis that environmental temperatures select for specific microbial populations. However, this observation is consistent with pure culture temperature regulation studies. For example, in cold environments, the T_{opt} for anaerobic respiration of psychrophilic isolates was up to 10 °C higher than the T_{opt} for growth (Knoblauch and Jørgensen, 1999). This difference was explained by the fact that, in contrast to growth, the temperature response of respiration depends only on a selected part of the enzymatic machinery of a cell (Hamamoto et al., 1994; Feller et al., 1995). Our incubations were conducted over a sufficiently short time interval to allow microbial

populations to grow. Thus, the SRR reflect the short-term enzymatic capabilities of the in-situ sulfate-reducing community. Prolonged incubations in similar experiments have shown that the temperature optimum decreases over time (Brüchert et al., 2001; Finke and Jørgensen, 2008). It is apparent that sulfate-reducing microorganisms from these cold sediments maintain high activity at the highest temperatures only for a limited time. The temperature-activity diagrams shown in our study should therefore not be misunderstood as indicators of the true temperature optimum of the sulfate-reducing community, but should instead be regarded as typical activity fingerprints of the existing populations. These fingerprints allow comparisons with populations in other sediments and permit conclusions on the origins of these populations and their temperature characteristics.

The in situ temperature of the south Atlantic sediments from greater water depths was lower than on the shelf and, accordingly, T_{opt} and T_{max} of sulfate reducing process decreased with increasing water depth (Fig. 1b, c, d, f). Temperature-activity profiles from the deep-water stations therefore indicate the predominance of psychrotolerant and even psychrophilic bacteria. The most extreme demonstration of this effect is seen in the Argentine sediment from 3400 m depth, where we measured a T_{opt} of only 12 °C after 36 h of incubation (Fig. 1e). A similarly low T_{opt} of 12.5 °C for sulfate reduction was observed in sediment from Antarctica in the Weddell Sea (Isaksen and Jørgensen, 1996). The authors reasoned that the temperature profile resembled the response of psychrophilic isolates and therefore likely reflected the growth rate optimum of a predominantly psychrophilic community (Isaksen and Jørgensen, 1996). In accordance with this, we found a low T_{opt} of 18 °C in Kongsfjorden sediment after only 12 h of incubation (Fig. 1i). This T_{opt} is comparable to the optima reported for growth of psychrophilic isolates of sulfate-reducing bacteria from Svalbard fjords (Knoblauch and Jørgensen, 1998).

4.2 SRR in shelf and slope sediments fall into three temperature groups

In the south Atlantic sediments, the spatial distribution of distinct thermal groups were related to the in situ temperature of the sediment and, consequently, to water depth. In south Atlantic, but also in Arctic sediments, broad temperature characteristics of SRR imply the presence of mixed SRB communities composed of mesophilic, psychrotolerant, and psychrophilic members (Arnosti et al., 1998; Rysgaard et al., 2004; Sahm et al., 1999). Thus, high T_{opt} of SRR on the shelf indicate a predominance of mesophilic and/or psychrotolerant SRB, whereas low T_{opt} in the deeper sediments imply the presence of SRB adapted to permanently cold conditions typical for psychrotolerant and psychrophilic microorganisms. The predominant temperature responses of SRR in south Atlantic incubations were psychrotolerant, which is consistent with earlier reports that psychrophiles are not dominant in these permanently cold sediments (Nedwell and Rutter, 1989). A relationship between the T_{opt} of sulfate-reducing populations and water depth was not observed in the Arctic fjord sediments, likely because the bottom water of the Svalbard fjords is permanently near 0 °C at all water depths throughout the year.

The SRR at in situ temperatures in the Argentine and Arctic sediments were 20 % to 50 % lower than the rates measured at T_{opt} in the temperature gradient block (Table 3). These values are comparable to those reported for cold-adapted Arctic SRB (Robador et al., 2009) and are consistent with relative growth rates determined for psychrophilic strains isolated from Arctic sediments (Knoblauch and Jørgensen, 1999). In Namibian shelf and slope sediments, the in situ rates were less <10 % of the rates at T_{opt} (Table 3), but E_a values of 38 and 55 kJ mol^{-1} for Namibian sediments suggested that SRB were well adapted to the ambient temperature. The corresponding Q_{10} values for SRR in South Atlantic sediments were around 2, which is typical for experimental studies from many marine environments (Kirchman et al., 2009). E_a values reported for permanently cold sediments vary in the range of 25–31 kJ mol^{-1}, depending on whether the community is more psychrotolerant or psychrophilic. The E_a values were similar to

those measured for sulfate reduction, denitrification and anammox in Arctic sediments (Fig. 2, Table 3) (Rysgaard et al., 1998; Gihring et al., 2010). These low Q_{10} values were found repeatedly for metabolic processes in Arctic and Antarctic sediments and imply a microbial community well adapted to ambient temperature.

4.3 Sediment transport effects on experimentally-determined temperature-activity relationships

In the upper and lower slope sediments off Argentina, SRR showed a psychrotolerant to psychrophilic signature (Fig. 1d, e, f), whereas in the cold slope sediments off Namibia the temperature activity response indicated a significant population of mesophilic SRB (Fig. 1c). Resuspension and dispersion of sub-optimally adapted organisms may inherit a mesophilic signature of a shelf SRB community to these deep-sea sediments. Organic matter from the Benguela upwelling system over the Namibia shelf undergoes continuous suspension and re-deposition leading to a net down-slope transport. The shelf material accumulates in depo-centers at 1000–1500 m water depth where the sediment is rich in organic matter (Inthorn et al., 2005, 2006). The slope sediments off Uruguay and Argentina are also characterized by dynamic depositional conditions with generally high sedimentation rates, gravity mass flows due to turbidies and slides, and strong surface currents and are also partially seeded by sediment originating from the continental shelf (Riedinger et al., 2005). The broad temperature response observed in these sediments may likewise reflect the downslope dispersion of mesophilic microorganisms.

We suggest that the down-slope transport of sediment material from the warmer continental shelf to permanently cold, continental slope may seed deep-water sediments with mesophilic organisms. Anaerobic sulphate-reducing bacteria face the problem of toxic exposure to oxygenated water during transport. However, a number of SRB have been shown to develop molecular strategies to remove oxygen or to use oxygen temporarily for respiration to reduce its toxicity (Cypionka, 2000; Dolla et al., 2006).

Mesophilic and psychrotolerant SRB deposited in the cold slope sediments would appear less competitive compared to their autochthonous psychrophilic counterparts (Knoblauch and Jørgensen, 1999; Robador et al., 2009). For long-term survival and success, rate of growth and growth yield are true measures of microbial adaptation to environmental temperatures. Environmental conditions in organic matter-limited deep-sea sediment impose nutritional constrains that can impede microbial growth. It is conceivable that psychrotolerant bacteria transported down-slope have adaptive mechanisms to maximize and maintain a high growth yield at low temperature (Baker-mans and Nealson, 2004), but it is not clear how allochthonous, mesophilic SRB derived from the shelf may proliferate when relocated to greater depths. It is noteworthy, however, that in laboratory studies both psychrophilic and mesophilic sulphate reducing bacteria have shown comparable growth rates when grown on lactate (Knoblauch and Jørgensen, 1999; Sass et al., 1998) suggesting that proliferation of mesophiles in permanently cold environments is conceivable. The hypothesis that allochthonous mesophilic SRB are transported from the shelf and remain viable in permanently cold sediment is also supported by sulfate reduction rates measured in intertidal temperate sediment that showed a characteristic mesophilic temperature response even when the sediment was stored for two years at 0 °C, not changing the temperature response very much over this period of time (Robador et al., 2009). Clearly, despite the low ambient temperatures, the mesophilic sulfate-reducing community proliferated (Robador et al., 2009).

5 Conclusions

T_{min}, T_{max}, and T_{opt} temperatures for SRR in various continental shelf and slope sediments from the Atlantic and Arctic Ocean indicate the coexistence of different thermal groups of SRB. This observation has implications for predicting the likely outcome of long-term temperature changes of marine sediments in Arctic shelf and deep-sea habitats. The seeding of permanently cold deep-sea habitats with mesophilic

microorganisms must affect growth rates of the bacterial community at changed bottom water temperatures and can thus potentially affect the efficiency of organic carbon mineralization rates. The existing evidence from this study and from previous comparisons of carbon mineralization in permanently cold and temperate habitats point to the availability of reactive organic matter as the overriding limiting factor for long-term carbon mineralization in marine sediment (Kostka et al., 1998). The incubation experiments of SRR over two years (Robador et al., 2009) and recent experimental studies from lake sediment (Gudasz et al., 2010), suggest, however a more prominent role of temperature limitation. These different observations can be reconciled if one considers that an apparent temperature limitation effect may be temporary and is alleviated by community replacement with better temperature adaptations. The regional comparison indicates that over longer time scales, bacteria with the best physiological adaptation to exploit the available conserved energy in the respective environment will likely prevail. In the future it will be important to explore of what time scale such a community change to the best adapted community occurs.

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Interactive Discussion

Table 1. Sampling sites description.

Station	Coordinates	Water depth (m)	in situ T ˚C
Namibian shelf	25°0′ S 14°23′ E	130	8
Uruguay shelf	36°08′ S 53°16′ W	244	8
Namibian slope	25°45′ S 13°3′ E	2000	2
Argentine Basin	38°12′ S 54°56′ W	627	4
Argentine Basin	37°57′ S 53°50′ W	3400	2
Argentine Basin	39°28′ S 53°42′ W	4327	1
Arctic intertidial flat	78°16′ N 14°02′ E	0	6
Krossfjord	79°08′ N 11°39′ E	80	0
Kongsfjord	79°00′ N 11°40′ E	110	−1
Smeerenburgfjord	79°42′ N 11°05′ E	215	2

Table 2. Bulk geochemical analysis, carbon and nitrogen concentrations determined, for Namibian, Uruguayan, Argentine and Arctic sediments.

Station	Organic carbon (wt %)	Nitrogen (wt %)	C/N	SRR nmol cm^{-3} d^{-1} (SR zone mean)
Namibia 130 m	4.4	0.5	10.5	65.8
Namibia 2000 m	6.5	0.9	10.4	3.59
Uruguay 244 m	5.0	0.6	10.0	43.6
Argentina 627 m	2.3	0.3	10.3	nd
Argentina 3400 m	1.3	0.2	9	nd
Argentina 4327 m	nd	nd	nd	6
Arctic 0 m	1.4	0.1	16	11
Krossfjord 80 m	nd	nd	nd	4.29
Kongsfjord 110 m	nd	nd	nd	12.6
Smeerenburgfjord 215 m	1.2	0.2	8.8	19.4

Table 3. Sulfate reduction activities and Arrhenius parameters determined in the temperature-gradient incubation experiments for Namibian, Uruguayan, Argentine and Arctic sediments.

Station	T_{opt} (°C)	SRR nmol cm^{-1} d^{-1} at in situ T	at T_{opt}	% SRR	E_a kJ mol^{-1}	Q_{10}
Namibia 130 m	25	7	72	9	55	2.8
Namibia 2000 m	22	2	29	7	38	2
Uruguay 244 m	27	3	16	20	32	2.9
Argentina 627 m	20	0.15	0.7	21	30	2.8
Argentina 3400 m	12	0.1	0.2	50	52	2.7
Argentina 4327 m	20	1.2	4.3	28	26	2.7
Arctic 0 m	30	8	120	15	25	2.7
Krossfjord 80 m	25	9.1	44	20	27	2.3
Kongsfjord 110 m	18	27	141	19	31	2.1
Smeerenburgsfjord 215 m	27	41	213	19	25	2
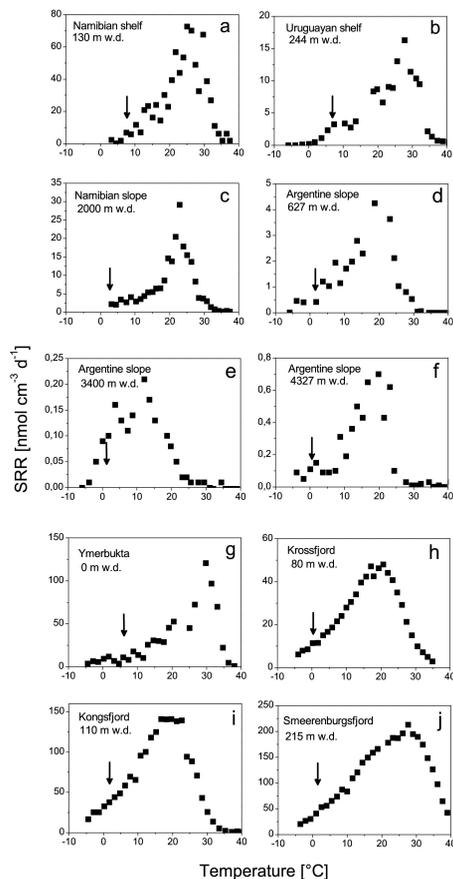
Fig. 1. SRR measured in temperature-gradient incubation experiments of sediment slurries from the different sampling sites. Arrows indicate in situ temperatures of sediments. "w.d." stands for water depth.
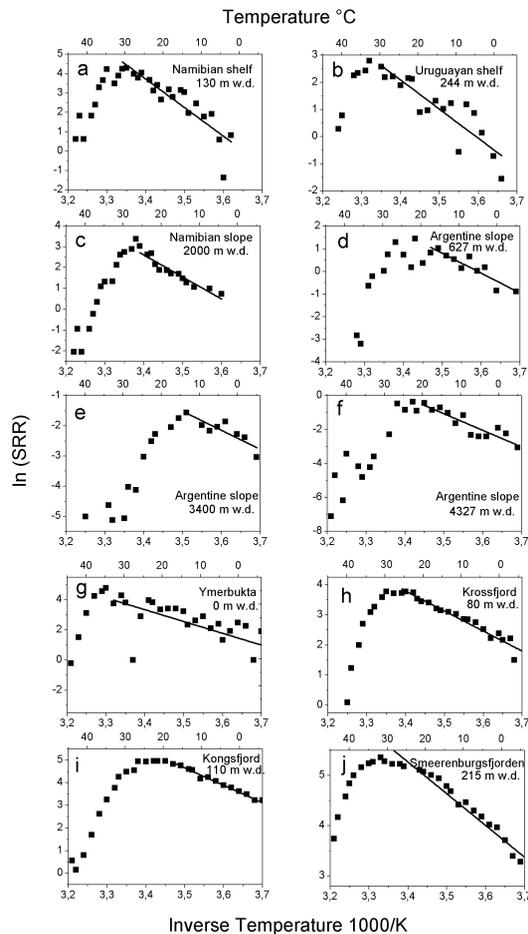
Fig. 2. Arrhenius plots of data in Fig. 1.