



Distribution of oxygen, sulfides and optimum temperature for sulfate reduction in Antarctic marine sediments

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Abstract: Measurements were made of sediment characteristics, benthic microbial activity and optimum temperature for sulfate reduction at Signy Island, South Orkney Islands, Antarctica. There was little evidence to support any seasonal variation in oxygen penetration of surface sediments. Oxygen penetrated to only 1.5 to 3 mm throughout the year, despite bioturbation from a dense amphipod population. The distribution of acid volatile sulfides increased with depth below 1 cm and above this, surface sediments were lighter in colour and contained fewer sulfides. The rates of sulfate reduction increased during winter under sea-ice cover, and remained high after ice break up. Seasonal water temperature was relatively constant between -1.8 and 0.5°C . Optimum temperature for anaerobic sediment respiration was investigated using different substrates and was found to be in the range 17 – 27°C , suggesting that sulfate reducing bacteria are psychrotolerant as they were inhibited by low temperatures.

Key words: Antarctica, Signy Island, coastal sediments, oxygen penetration, sulfides, temperature, sulfate reduction.

Introduction

Despite their permanently low temperatures, around 0°C , the Antarctic seas have been considered to be one of the most productive marine regions of the world (El-Sayed 1984; Priddle *et al.* 1986). The seasonal cycle of sea-ice formation and break-up produces a distinct seasonal pattern of phytoplankton productivity (Heywood and Whitaker 1984). Primary production at Signy Island varies between, 86 – 289 $\text{g C m}^{-2} \text{y}^{-1}$ (Whitaker 1982), with sea-ice algae and microphytobenthic communities contributing significantly to that production (Gilbert 1991a, b). High sedimentation rates occur following a spring bloom of ice-edge algae (Palmisano and Sullivan 1983; Grossi *et al.* 1987) and as much as 50–80% of phytoplankton stock may sink to the bottom (McConville *et al.* 1985; Wassmann 1991). Bottom sediments in marine ecosystems are important sites of mineralization and nutrient

recycling, where high productivity causes rapid input of organic carbon to the sediment (Jørgensen, 1983). In the near-shore marine environment of the Antarctic, primary production is balanced by mineralization of organic carbon derived from primary production by benthic communities (Nedwell *et al.* 1993). Organic mineralization in these sediments is brought about by the activity of aerobic bacteria, together with sulfate reducing bacteria in the anoxic regions of the sediment below the surface aerobic layer (Sørensen *et al.* 1979). The contribution of sulfate reduction to aerobic mineralization is proportionally greater in coastal sediments where there is commonly only a shallow surface aerobic layer (Jørgensen 1982; Rysgaard *et al.* 1996), and declines in deeper water where diminished detrital deposition results in more oxidised sediments (Jørgensen 1983). Nedwell *et al.* (1993) found that annually, about 32% of benthic organic matter mineralization was anoxic at Signy Island, but the proportion of anoxic compared with oxic mineralization increased during the winter as organic matter was increasingly buried by the amphipod infauna.

Antarctic environments support large active populations of micro-organisms (Tanner and Herbert 1982; Palmisano *et al.* 1985; Wynn-Williams 1990). Heterotrophic bacteria rely on primary production for their energy supply (Fiala and Delille 1992) and these bacteria contribute significantly to energy transfer in the Antarctic (Delille and Perret 1991; Delille 1992). In marine sediments sulfate reduction and glucose mineralization coincides with psychrophilic growth temperatures, suggesting the presence of a psychrophilic community (Bowman *et al.* 2003), although, only a few truly psychrophilic anaerobic bacteria have been isolated (Purdy *et al.* 2003). Among the anaerobic bacteria, psychrotrophic communities appear to be predominant (Herbert 1986; Isaksen and Jørgensen 1996; Knoblauch *et al.* 1999). The highest temperature optimum for sulfate reduction, 21°C, was reported by Nedwell (1989) for an Antarctic sediment. Measurements to examine benthic microbial activity were made previously over a short summer period at Signy Island (Nedwell 1989) and then subsequently over an annual cycle (Nedwell *et al.* 1993; Nedwell and Walker 1995). Rates of microbial activity in these studies were found to be comparable to rates in temperate regions at much higher temperatures (Senior *et al.* 1982). This study was undertaken to examine the vertical distribution of oxygen and concentration of sulfides, alongside an investigation into the optimum temperature for sulfate reduction during the winter in sediments at Signy Island, over an annual cycle.

Materials and methods

The work was carried out at Signy Island (60°42' S, 45°36' W) in the South Orkney Islands, situated in the maritime Antarctic shown in Fig. 1. The sampling site was located in Factory Cove, a shallow embayment with a maximum depth of 9 m

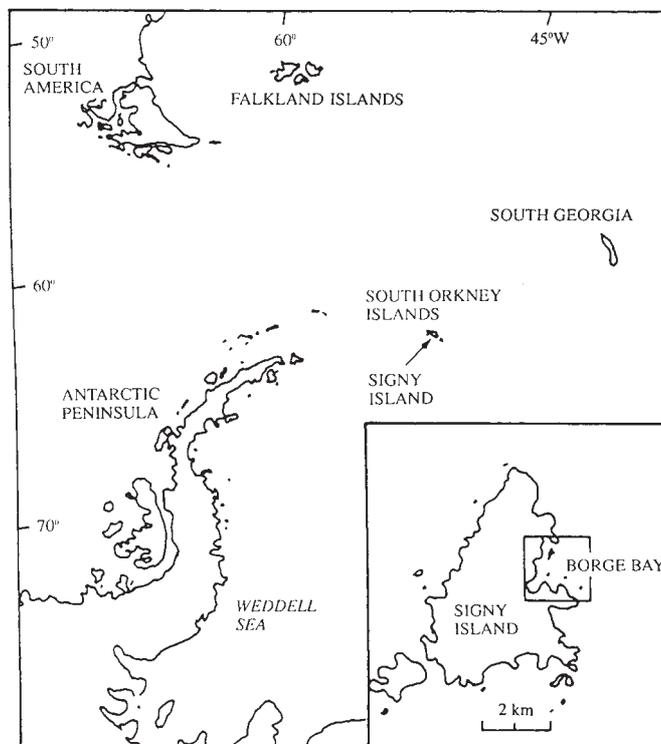


Fig. 1. The location of the South Orkney Islands and the detail of Borge Bay on the east coast of Signy Island.

within Borge Bay. The site has been described previously (Walker 2005). Factory Cove has fast-ice up to 1 m thick for between 70 and 241 days, and monthly mean seawater temperature small, ranging from -1.8°C to $+0.5^{\circ}\text{C}$ (Clarke *et al.* 1988). The site consisted of glacially eroded quartz-mica schist (Hall 1986), and the sediment was blackened below a light brown surface layer approximately 1 cm thick and supported a variety of invertebrates. The amphipods *Pontogenea rotundifrons* and *Tryphosa kergueleni* are common infaunal burrowers as is the bivalve *Yoldia eightsi*, and they are found in high densities. All cores of sediment for analysis were taken by SCUBA divers, and in all cases samples were returned to the laboratory within 10 min.

Vertical cores of sediment were taken using perspex tubes (50 cm \times 8 cm diameter) and frozen at -20°C . Frozen sediment was then extruded in 1 cm slices down to 25 cm and sectioned using a fine saw. The volume of each slice is known (from the dimensions of the core) and the wet weight of each slice was determined, and then dried to constant weight over 3 d at 80°C to determine the water content. From these data the porosity could be determined by taking the sediment wet weight and subtracting the sediment dry weight and then dividing this value by the sediment wet

weight. Density was calculated dividing the sediment wet weight by the volume of the slice. The sediment was frozen, so values for porosity are over estimates, whilst density was underestimated. Particle size measurements were made on sediment samples down to 10 cm, dried to constant weight and placed in a sieve shaker with Endecott sieves of mesh sizes of 2000 μm , 500 μm , 250 μm , 125 μm and 63 μm or 45 μm respectively. The sediment was shaken for 30 min. and each tray was reweighed to determine the particle size fractions of the sediment at each site. Granulometry was also used to determine whether there was any seasonal change in sediment type. Results of dry sediment retained by each sieve size were expressed as % of total dry mass. Five silver plated metal rods were deployed vertically in the sediment down to known depth for 3 d and retrieved on subsequent dives. The rods turned black as a result of chemical reduction of the silver plating forming silver sulphide in the anoxic region. The sub-oxic (chemically oxidised) layer remains unaffected and was determined by measuring the depth at which the blackening occurs from the surface of the sediment. The depth of the sub-oxic layer was also confirmed by observation of the light brown layer at the sediment surface. The pH profiles in cores of fresh sediment were taken using a pH meter and electrode (Corning, UK). Depth intervals of 200 μm down to 2 cm were achieved by using a micromanipulator to control the electrode. A layer of seawater was maintained above the sediment surface to allow a pH measurement at the beginning of the profile. The electrodes were standardised in buffers of pH 7.0 and pH 9.0.

The vertical oxygen concentration profiles in cores of sediment were determined using oxygen electrodes (Revsbech *et al.* 1980) of the design by H. Van Gemerden (University of Gronigen) in conjunction with a calomel reference electrode (Corning, UK). The electrodes were connected to an oxygen meter (Strathkelvin Instruments Ltd, Scotland). The microelectrodes were calibrated for each oxygen profile using air-saturated seawater maintained at *in situ* temperature for the 100% value and in seawater saturated with sodium sulfite for the zero reading. The surface of the sediment was positioned to within 2 cm of the core rim to establish a steady water flow across the sediment surface. Cores of sediment were incubated in a water bath under circulating, air-saturated seawater from the sample site maintained at *in situ* temperature to maintain redox gradients. Cores were maintained under these conditions, before and during the measurements. Oxygen concentrations were determined at 100 m intervals using a micromanipulator to control the microelectrode. The electrode tip was placed above the sediment water interface and readings taken in the water column until the needle tip penetrated the sediment surface. Triplicate profiles of oxygen were then measured at different points on the surface of the sediment core. Oxygen concentration was expressed as percentage saturation of dissolved oxygen.

Duplicate large vertical cores were taken with perspex core tubes and horizontal sub samples (5 mL) were taken at depths over the 0–15 cm depth horizons with cut off hypodermic syringes as the sediment was extruded under a stream of OFN. In all

cases sediment cores were maintained at *in situ* temperature in a constant temperature laboratory while sub samples were taken. Each sediment sample was injected with 25 μL sodium ^{35}S -sulfate solution (50 μCi [1.85 MBq] mL^{-1} ; Specific activity 1275 Ci [47.2 Tbq]. mmol^{-1} ; Amersham International., UK) and incubated at *in situ* temperature for 24 h. At the end of the incubation the sediment samples were frozen to -80°C , to terminate further sulfate reduction (Howes *et al.* 1984). Samples were digested with tin (Skyring 1987) and acidic tin chloride solution as reducing agent under a stream of OFN to recover the radiotracer of both acid-volatile sulfide (AVS) and tin-reducible sulfide (TRS) (Skyring 1987; Nedwell 1989). Sulfide was trapped in zinc acetate solution (1% w/v) and at the end of the digestion sub samples were removed from the traps into scintillation cocktail (Instagel, Packard Instruments Ltd., UK) and radioactivity measured in a scintillation counter (Rackbeta, LKB Ltd, Bromma, Sweden) with an external standard to correct for quenching. Replicate samples of sediment from each depth layer were taken for determination of the sulfate concentration in the sediment pore water by ion chromatography (Dionex Sp 2000). Sediment pore water was recovered by centrifuging a sample of sediment at $6000 \times g$. The pore water was passed through a GF/C filter and frozen at -20°C until analysis. Further sediment samples were used to measure sediment porosity. The residue from each of the 40 mL zinc acetate traps were titrated with sodium thiosulfate solution to determine the concentrations of AVS and TRS present in each sediment sample (American Public Health Association, 1975).

Sediment taken from the 0–4 cm depth horizon was made up into slurries (50% v/v) in deoxygenated seawater and prepared as described by Nedwell (1989). Hungate technique was used to exclude oxygen from the slurry, all transfers and manipulations being carried out under a stream of OFN. Aliquots (16 mL) of the slurry was dispensed into 30 mL screw-capped universals, which were placed along an aluminium block incubator and allowed to equilibrate to temperature for 1 h. The aluminium block incubator was heated at one end and cooled at the other by thermo circulators (Biorad Ltd., UK). Experiments were carried out over temperature ranges between $8\text{--}33^{\circ}\text{C}$. Sodium lactate solution (100 μL to give 25 μM final concentration) was injected into each universal, followed immediately by 20 μL of ^{35}S -sulfate solution. The lactate was used to provide a supply of electron donor for sulfate reducers. In another experiment different substrates were used (100 μL each of sodium acetate and sodium propionate [2M solutions]). With 14 positions along the gradient, this created a 1.5°C temperature difference between adjacent universals. The temperature at each point along the gradient was checked by using a thermometer immersed in water in universals along the gradient, and was found to be linear. Universals were shaken thoroughly and placed back in the gradient block for 15 h to incubate. After incubation the universals of sediment slurry were frozen down to -80°C to stop further activity and to “fix” the sulfide until further treatment. Each sample was subsequently acidified, and the radioactivity in only the AVS portion determined, as described previously.

Results

The density of the sediment ranged from 1.6 g mL^{-1} at the sediment surface to 2.6 g mL^{-1} at 22 cm (Fig. 2a). Thus, the density of the sediment increases with depth due to compaction. Water content decreased with increase in depth of sediment from 42% at the top cm to 21% at 23 cm. Particle-size analysis for Factory Cove (data not shown) yielded little difference in composition during the seasonal cycle and consisted of 70–90% of the particles in the fine sand and very fine sand fractions (0.063–0.25 mm diameter). The mean depth of the sub-oxic layer during two summer deployments varied between 1.0 cm (SE = 0.15, $n = 5$) and 1.38 cm (SE = 0.26, $n = 5$). A pH profile is illustrated in Fig. 2b, and show a decrease in pH with increase in depth from pH 7.7 at the sediment surface to pH 7.2 at 2 mm depth. The presence of sea-ice in Factory Cove during the 1991 winter lasted for approximately 8 months, and was continuous between mid May to the end of December. Measurements of vertical profiles of dissolved oxygen in the sediments are illustrated in Fig. 3, and show oxygen disappearing below 1.5 to 3 mm depth. There was no obvious seasonal change in the depth of oxygen penetration, despite bioturbation from a dense amphipod population.

The rates of sulfate reduction determined in the cores from Factory Cove were first converted from rates on a sediment weight basis to equivalent rates per mL of sediment by multiplying by the measured specific gravity of the sediment at each depth. These rates were then integrated with depth over 0–15 cm depth by summa-

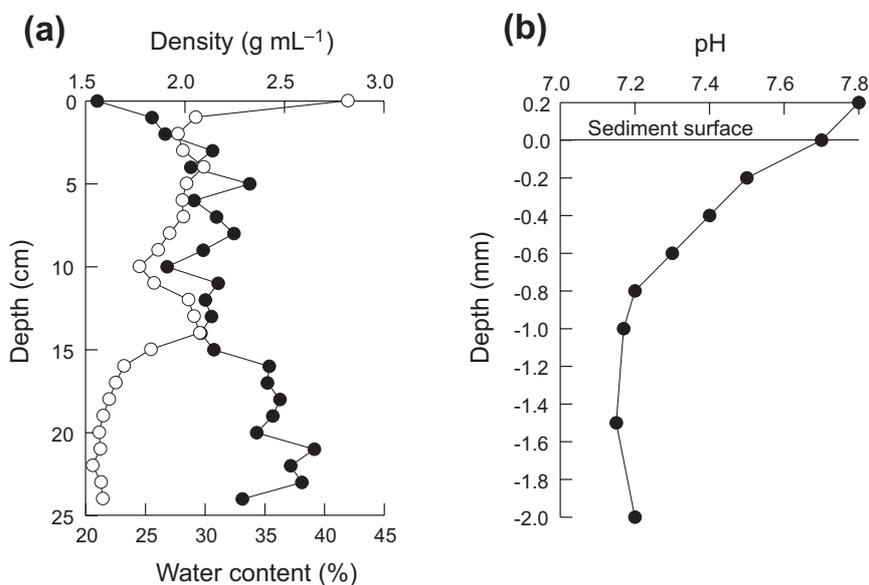


Fig. 2. Profiles showing sediment characteristics in Factory Cove: (a) density – ●; water content – ○, and (b) pH of sediment.

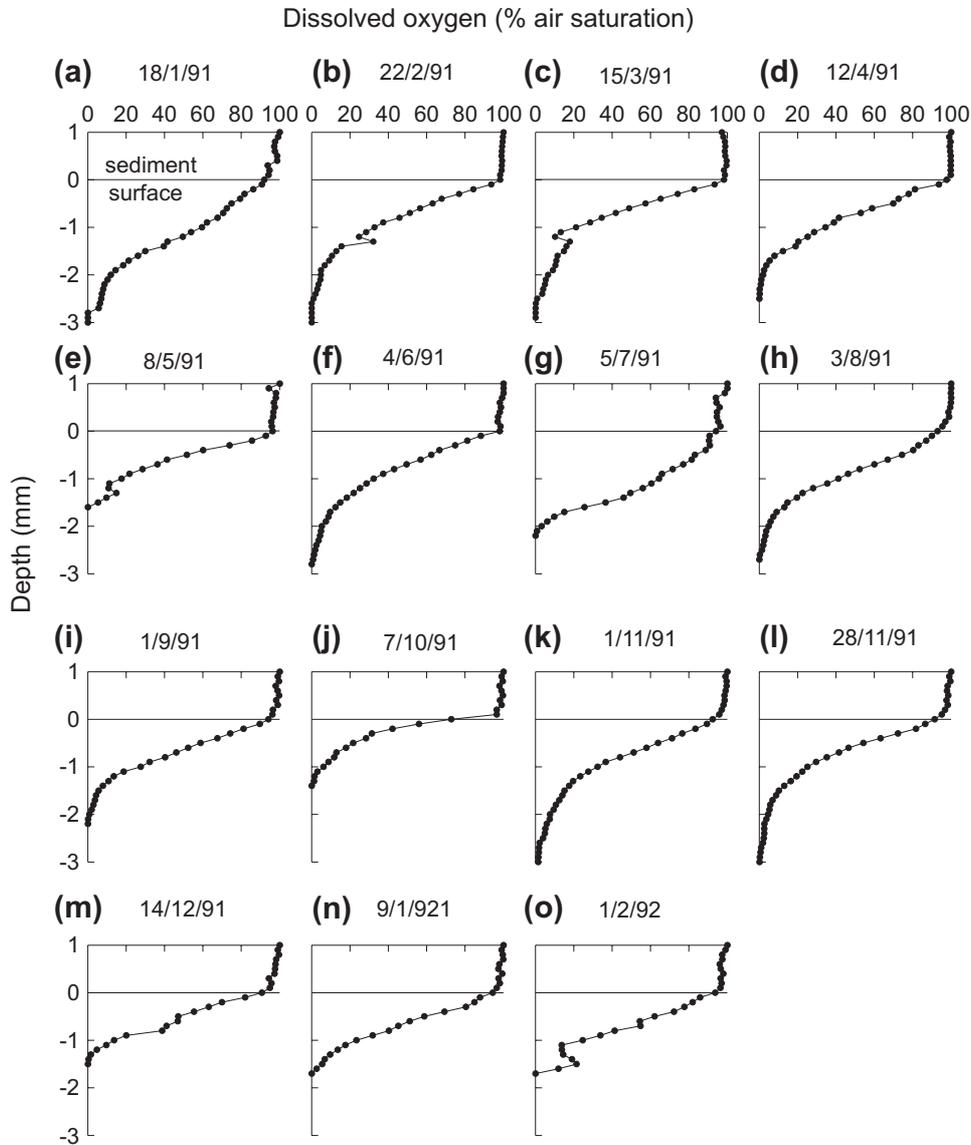


Fig. 3. Vertical profiles of oxygen penetration (% air saturation) in the surface sediment. Values represent means from triplicate profiles.

tion of adjacent 1 cm slices, and by using linear interpolation and a simple trapezium method to determine integrated sulfate reduction rates between measured horizons. The rates of sulfate reduction were initially low between January to March (Fig. 4), and then increased during winter after ice formation indicating increasing sulfate reduction activity through the winter. When the monthly samples were integrated over the 0–5 cm horizon over 1 year the results from the horizontal hypo-

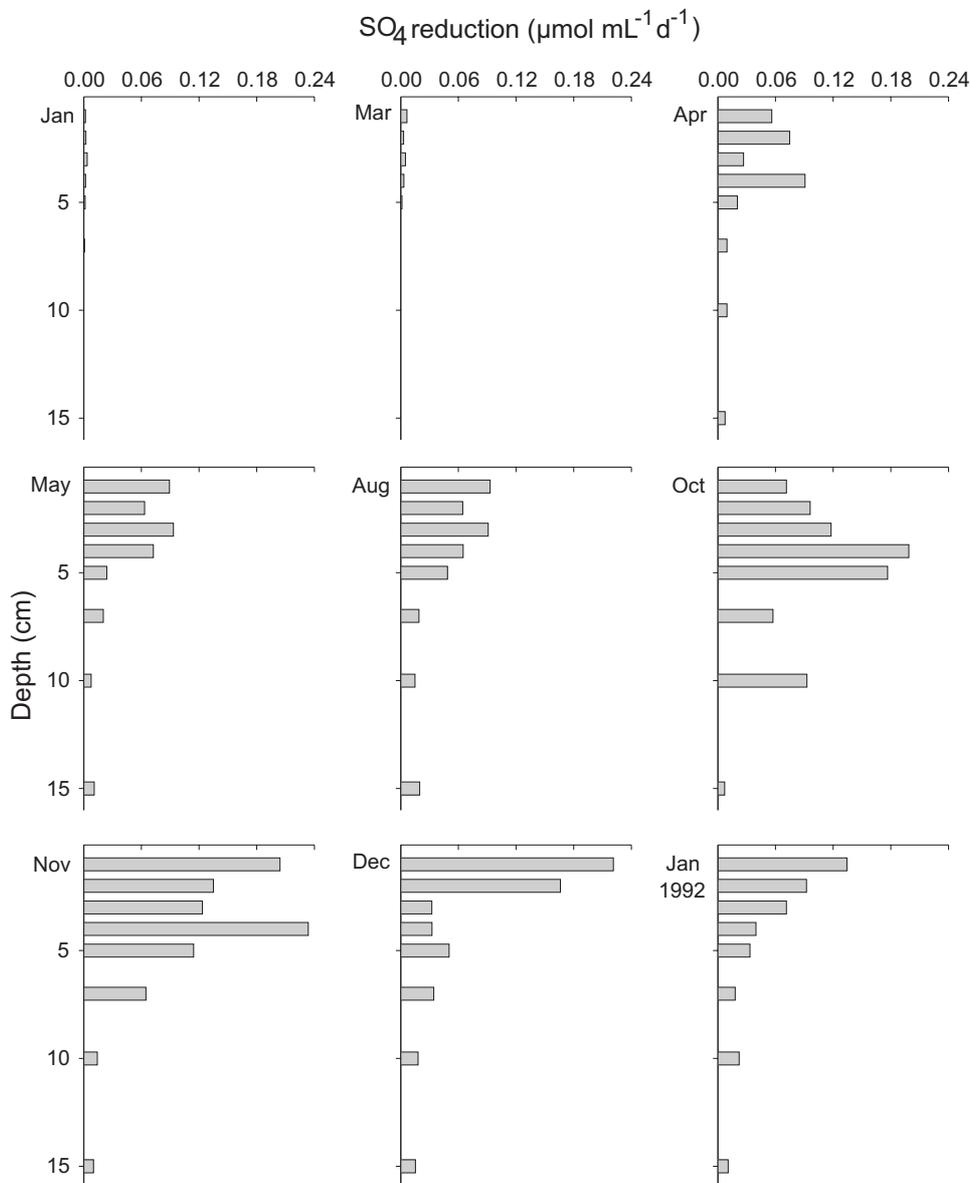


Fig. 4. Mean monthly profiles of rates of sulfate reduction for sediment over the 0–15 cm depth horizons using duplicate cores.

dermic samples was $1.31 \text{ moles SO}_4 \text{ m}^{-2} \text{ y}^{-1}$. In comparison, integration of the data over the 0–15 cm depth horizon, yielded a value of $2.01 \text{ moles SO}_4 \text{ m}^{-2} \text{ y}^{-1}$, equivalent to $3.98 \text{ moles C m}^{-2} \text{ y}^{-1}$, indicating that 32% of the total organic mineralization occurred anoxically by sulfate reduction (see Nedwell *et al.* 1993). The monthly sulfate reduction rates over the 0–15 cm depth horizon are illustrated in Fig. 4. The

Table 1
Some estimates of optimal microbial metabolic rates in bottom sediments.

Location	Microbial parameter	Optimum temperature (°C)	Reference
Mariager fjord, Denmark (29 m)	sulfate reduction	30–35	Isaksen and Jørgensen (1996)
Continental shelf, Eastern Antarctica (700–900 m)	growth rate	15	Bowmann <i>et al.</i> (2003)
Weddell Sea, Antarctica (>400 m)	sulfate reduction growth rate	28 18	Isaksen and Jørgensen (1996)
Signy Island, Antarctica (9 m)	sulfate reduction	21	Nedwell (1989)
Antarctica	growth rate	20–24	Nedwell and Rutter (1994)

Nedwell (1989). Sodium lactate gave an optimum temperature for sulfate reduction of 27°C at the end of summer and 17°C during the winter. Sodium acetate and sodium propionate had optimum temperatures for sulfate reduction of 25°C and 18°C respectively. Table 1 shows some estimates of optimal microbial metabolic rates in bottom sediments from other low temperature sites.

Discussion

The inshore marine environment around Signy Island is characterised by a distinct seasonal cycle of primary production (Clarke *et al.* 1988) and this in turn produces a distinct seasonal pattern of organic inputs to the bottom sediments (Walker 2005). The organic carbon budget in Factory Cove is broadly balanced between inputs and mineralization, which comprised mainly of aerobic sediment respiration and sulfate reduction (Nedwell *et al.* 1993). The rates of sulfate reduction increased throughout the winter under the sea-ice, presumably due to organic matter depletion at the sediment surface, and in turn reduced bioavailability of the organic carbon (Walker 2005). The sediment in this investigation was heavily bioturbated over the top 1 cm horizon, and several authors have examined infaunal densities in Factory Cove (Bone 1972; White 1984). This reworking of sediment and the introduction of detritus deeper down actively encourages increased microbial activity and accounted for up to 50% of the sediment respiration (Nedwell and Walker 1995). Benthic invertebrates may significantly increase the transport rate of oxygen into the surface layers of sediment above that due to diffusion alone both by irrigation of the sediment resulting from respiratory currents of water pumped through their burrows and bioturbation of the surface layer by their feeding and burrowing activities (Hylleberg and Henriksen 1980; Fry 1982). The many burrows of the infauna offers more surface area through which oxygen can penetrate.

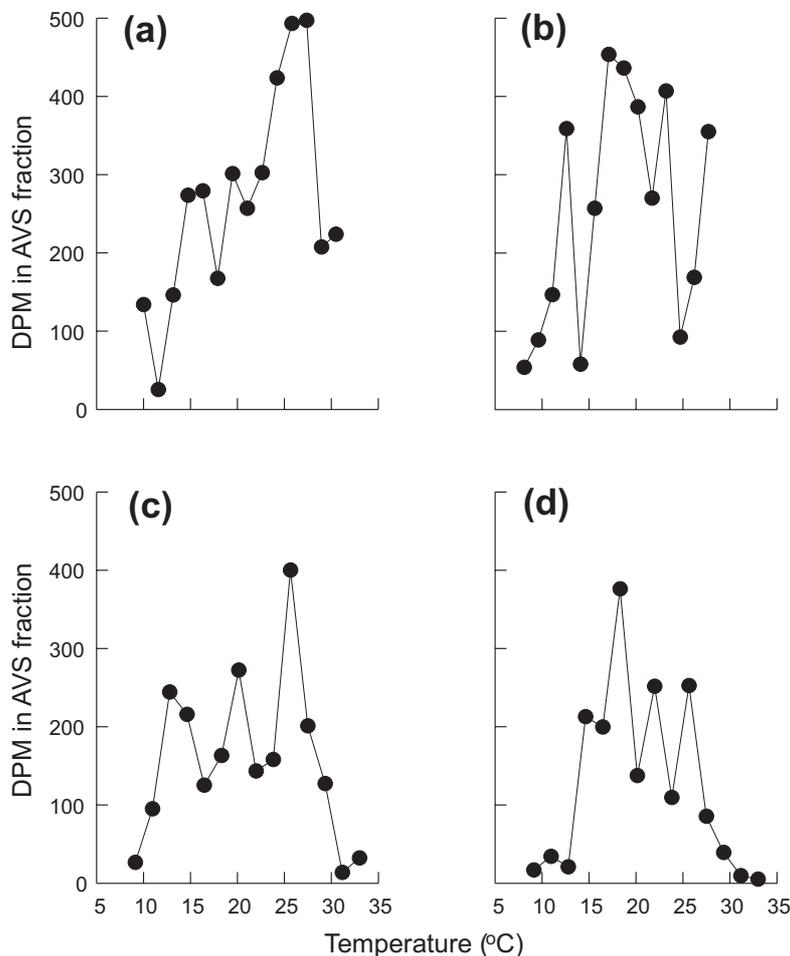


Fig. 6. Optimum temperature for sulfate reduction using sediment slurries with different radio labelled carbon sources: (a) sodium lactate in March before ice formation and (b) sodium lactate, (c) sodium acetate and (d) sodium propionate in August under ice during winter.

The density and water content of the sediment affects its porosity and thus the amount of pore water available for microbial activity. There was no seasonal trend observed in the depth to which oxygen penetrated the sediment, despite seasonal fluxes in organic matter deposited at the surface of the sediment. The fine particle sizes like those found at the Factory Cove site tend to limit the penetration of oxygen to just a few mm (Nedwell 1984; 1989; Revsbech and Ward 1984), as one possible explanation, but so does the presence of an active sulfate reducing bacterial population. The sub-oxic layer of the sediment was observed from cores, as the light brown layer which exists in the top 1 cm of the sediment, and oxygen was thought to penetrate down to this layer. However, with the use of microelectrodes the depth of dissolved oxygen penetration is now known to be considerably less

than those at which the sediment becomes chemically reduced (Revsbech *et al.* 1980; Revsbech and Jørgensen 1986). The formation of silver sulfide silver plated rods deployed in Factory Cove confirm the depth of the sub-oxic layer to be similar to those observed by eye. The pH range found in Factory Cove sediments compares with those found by Presley and Trefry (1980). The profiles of oxygen concentration in the sediments of Signy Island are not unlike inshore marine sediments found elsewhere. Oxygen concentrations decreased rapidly only a short distance from the surface of sub-Antarctic sediments (Platt 1979). Gundersen and Jørgensen (1990) found that oxygen was consumed only in the top 2.2 to 2.5 mm of sediment from Aarhus Bay.

Aerobic oxidation of organic detritus is confined to a very thin surface layer of sediment, and oxygen diffusing into this layer is rapidly consumed despite the permanently low temperature (Nedwell *et al.* 1993). Dissolved oxygen concentrations will decrease more or less rapidly with increased sedimentary depth, depending on the balance between oxygen influx from the sediment surface and its removal within the sediment. The aerobic layer may vary from many meters of depth in the sediments of the deep ocean, where both organic content and temperature are low, to only a few mm of depth in highly organic coastal marine sediments during the summer (Revsbech *et al.* 1980).

Integration of the rates of sulfate reduction, gave an annual sulfate reduction over the 0–15 cm horizon of $2.01 \text{ moles SO}_4 \text{ m}^{-2} \text{ y}^{-1}$, which indicated that 32% of the total organic mineralization occurred anoxically by sulfate reduction (see Nedwell *et al.* 1993). This data contrasts with other data available for sulfate reduction in the Antarctic (Franzmann *et al.* 1988) as the rates are much higher. This is possibly due to the very high primary productivity around Signy Island (Whitaker 1982; Clarke *et al.* 1988). An increasing rate of sulfate reduction and a corresponding decreasing rate of aerobic respiration during the winter suggests that the proportion of the organic mineralization which was driven by sulfate reduction increased throughout the winter, during the period when the overall rates of organic mineralization were decreasing. During winter the relative importance of the respiratory processes changed and sulfate reduction accounted for an increased fraction of the total respiration (Nedwell *et al.* 1993). This probably reflected the progressive burial of available organic matter by amphipod bioturbation from the sediment surface down into the anoxic sediment below 2 to 3 mm depth. The lack of further organic input during winter depleted the amount of available organic carbon in the surface sediment and hence diminished the relative significance of aerobic metabolism during this period. The highest mean sulfate reduction rates were observed in the 0–5 cm horizons. This confirms previous Antarctic sulfate reduction rates of Nedwell (1989). Other workers have reported high sulfate reduction over the 0–5 cm horizon (Senior *et al.* 1980; Skyring 1987).

A significant portion of reduced sulfate is converted to TRS, which may be pyrite, sulphur or organic sulphur. The total amount of sulfate which was reduced to

TRS ranged from 60% to 66% over the entire study period, with the rest reduced to AVS in the 34% to 40% range at all depths down to 25 cm. Nedwell and Takii (1988) found that AVS comprised similar proportions (about 40%) in the top 0–5 cm layer. If the rapid formation of pyrite is ignored, the rates of sulfate reduction and ecosystem respiration may be grossly underestimated (Howarth, 1979). In most marine sediments, soluble sulfides (H_2S) and iron monosulfides (FeS) are the only major short-term end products of sulfate reduction, and pyrite is believed to form only very slowly through the gradual reaction of iron monosulfides with elemental sulphur (Berner 1970).

The majority of Antarctic bacteria are considered to be psychrotrophic and not true psychrophiles (Herbert 1986; Upton and Nedwell 1989; Delille 1990; Delille and Cachet 1991; Isaksen and Jørgensen 1996; Knoblauch *et al.* 1999; Bowman *et al.* 2003; Purdy *et al.* 2003). Indeed, this is supported by results from many optimal growth studies, which found temperature optima between 25°C and 30°C in Antarctic marine bacteria (Baker 1974; Herbert and Tanner 1977; Reichardt 1987; Delille and Perret 1989). These temperatures are far in excess of those experienced in their natural habitat. Sulfate reduction in these Antarctic waters is significant in magnitude even when compared to sediments which exhibit much higher temperatures, but where sulfate reduction is greatly inhibited by low temperatures during winter. The SRB have an optimum temperature for sulfate reduction between 17–27°C, which is greatly above the temperature of the environment. As with temperate sediments (Abdollahi and Nedwell 1979) no seasonal trend of optimum temperature for sulfate reduction was found in the sediments of Signy Island. However in the sediments of Factory Cove where there was no significant seasonal temperature change, the seasonality of sulfate reduction was governed by organic inputs (Nedwell 1989; Nedwell *et al.* 1993). Delille (1990) also noted that nutrient supply rather than the temperature is the limiting factor determining microbial activity in sub-Antarctic coastal waters. These results demonstrate that the sulfate reducing bacteria (SRB) have optimum temperatures for sulfate reduction far greater than those experienced in the environment. The SRB metabolised the substrates provided in these experiments (sodium lactate, sodium acetate and sodium propionate), and thus were not carbon limited. Different substrates were used to determine if different temperature optima could be observed as it is well known that SRB are capable of acetate oxidation (Banat *et al.* 1981; Purdy *et al.* 2003) and can metabolise a range of short-chain organic molecules, including lactate (Posgate 1979). Other substrates for sulfate reduction may include volatile fatty acids (Mueller-Harvey and Parkes 1987). It is interesting to note therefore, that although the SRB seem well adapted to their low temperature environment, the optimum temperature for sulfate reduction (17–27°C) was nevertheless greatly above the temperature of the environment. The present data therefore gives little evidence of obligatory psychrophilic adaptation by the sulfate reducing bacteria in these Antarctic sediments.

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