# Sulfate reduction in surface sediments of the southeast Atlantic continental margin between 15°38′S and 27°57′S (Angola and Namibia)

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*Abstract*

   Sulfate reduction rates in the surface sediments from 17 stations from an along-slope transect (1,300 m) and from a cross-slope transect (855–4,766 m) were determined in the continental margin sediments of the Benguela Upwelling system. Profiles at all sites in the upwelling area showed increasing sulfate reduction rates from near zero at the surface to a peak at 2–5 cm (up to 29 nmol cm$^{-3}$ d$^{-1}$) and then decreasing exponentially with depth to near background rates at 10–20 cm depth (<2 nmol cm$^{-3}$ d$^{-1}$). Depth-integrated sulfate reduction rates were greatest at 1,300 m and decreased exponentially with water depth. Along the transect following the 1,300-m isobath, depth-integrated sulfate reduction rates were highest in the north Cape Basin (1.16 ± 0.23 mmol m$^{-2}$ d$^{-1}$), decreased over the Walvis Ridge (0.67 ± 0.02 mmol m$^{-2}$ d$^{-1}$), and were lowest in the south Angola Basin (0.31 ± 0.23 mmol m$^{-2}$ d$^{-1}$). Depth-integrated sulfate reduction rates were consistent with the known pattern of coastal upwelling intensities and were also strongly correlated with surface organic carbon concentrations. Sulfate reduction rates, both as a function of depth and in comparison with sediment trap data, indicated that lateral downslope transport of organic carbon occurs. Sulfate reduction was estimated to account for 20–90% of the published rates of total oxygen consumption for the sediments at 1,300 m depth and 3–16% of sediments from 2,000 to 3,000 m depth. Comparison of the sulfate reduction rate profiles with the published diffusive oxygen uptake rates showed that the kinetics of oxygen utilization in the surface sediments are much faster than those for anaerobic organic carbon remineralization, although the underlying cause of the difference was not clear.

The benthic remineralization of organic carbon exerts an important influence on the flux and distribution of carbon and nutrients throughout the ocean, especially along continental margins (Jahnke et al. 1990; Hensen et al. 1998; Wollast 1998). The distribution of bottom-water oxygen, dissolved inorganic and organic carbon fluxes, nutrient fluxes, and the balance between water-column particulate organic carbon flux and burial of organic carbon in the sediments is determined by the rate and perhaps the pathway of organic carbon remineralization. In the deep ocean, dissolved O$_2$ fluxes into the sediment account for the sum total of benthic remineralization processes (Cai and Reimers 1995; Jahnke 1996); however, anaerobic processes begin to play a quantitatively important role in organic carbon remineralization in continental margin sediments, where organic carbon is buried or becomes mixed beyond the zone where dissolved oxygen is present. Jahnke (1996) has suggested that continental margin regions account for ~40% of the particulate organic carbon flux to the deep ocean (sediments at >1,000 m of water depth); thus, anaerobic remineralization of organic carbon may have a significant impact on the fluxes of carbon and associated nutrient elements in these continental margin sites.

The oxidation of organic carbon by dissimilatory sulfate-reducing bacteria is thought to be the principal terminal process of anaerobic respiration in many continental margin sediments (Jørgensen 1982; Canfield et al. 1993; Thamdrup and Canfield 1996). Fortunately, and in contrast to the measurement of most other respiratory processes in marine sediments, a robust and relatively simple method for the determination of dissimilatory sulfate reduction exists with the application of the $^{35}$SO$_4^{2-}$ tracer method to undisturbed whole cores of sediment (Jørgensen 1978; Fossing and Jørgensen 1989). Yet, despite its relative ease of measurement and its importance to anaerobic organic carbon degradation, the number of continental slope and rise sites below 200 m water depth where sulfate reduction rates have been directly measured by the $^{35}$S tracer method are few: i.e., northeast Atlantic Porcupine Abyssal Plain (Battersby et al. 1985), Gulf of Maine (Christensen 1989), Peru Upwelling (Fossing 1990), east Australian Slope (Heggie et al. 1990), Gulf of Mexico (Lin and Morse 1991), Norwegian Trench (Canfield et al. 1993), Washington State Continental Margin (Devol and Christensen 1993), three sites on the continental slope of the

Benguela Upwelling (Pimenov et al. 1993), central Chile (Thamdrup and Canfield 1996; Ferdelman et al. 1997), and Cape Hatteras Slope (Martens et al. 1998). Here, we report on sulfate reduction rates from the continental margin of southwest Africa that form part of the Benguela Upwelling system. These data make up, to our knowledge, one of the most extensive data sets of sulfate reduction rates yet determined for any continental slope and rise.

The slope and shelf waters of the southwest African continental margin are distinguished by upwelling-induced primary productivity. An estimated shelf-edge productivity of 175–240 mmol C m$^{-2}$ d$^{-1}$ (Summerhayes et al. 1995) leads to the formation of organic-rich sediments on the shelf and slope (Calvert and Price 1983). The occurrence of sulfate reduction activity in surface sediments at three continental slope and rise sites within the Benguela Upwelling region (490, 560, and 4,165 m) using the $^{35}SO_4^{2-}$ tracer method has been previously demonstrated (Pimenov et al. 1993). Nevertheless, we wanted to explore quantitatively the extent and spatial variability of sulfate reduction throughout the entire upwelling area using the whole-core $^{35}SO_4^{2-}$ tracer method (Jørgensen 1978) in surface sediments (0–20 cm depth). We were particularly interested in examining both the distribution of sulfate reduction rate activity over sediment depth and the total areal rate of sulfate reduction as a function of (1) along-slope (N–S axis) upwelling intensity, (2) water depth (across-slope axis), and (3) intrastation variability.

Study area

The sediments on the continental slope of the southwest African continental margin consist of an organic-rich, marine, diatomaceous ooze, little diluted with terrigenous materials, because the adjacent coastal land mass is desert with no significant riverine input (Calvert and Price 1983). The area is directly influenced by the Benguela Current, which flows toward the equator and bifurcates into two distinct strands in the vicinity of Walvis Ridge (see Fig. 1A). Deflecting northwestward is the well-known Benguela Ocean Current, which forms the eastern boundary of the South Atlantic Ocean gyre. Of greater importance to this study is the northeastward-flowing branch or the Benguela Coastal Current, which transports cold water from the wind-dominated coastal area northward along the continental margin into the southern Angola Basin (Shannon and Nelson 1996). Between 14° and 17°S, the Benguela Coastal Current converges with the southward-flowing Angola Current to form the Angola–Benguela Front. The Angola–Benguela Front, a permanent feature that typically lies WNE–ENE and is most intense within 250 km of the coast, divides the Benguela coastal upwelling system from the Angola oceanic upwelling region (Schneider et al. 1996; Shannon and Nelson 1996).

Nearshore upwelling cells associated with topographic irregularities are a typical feature of the southwest African coastline. Trade winds, blowing southeast to northwest and principally during the summer months, induce upwelling of nutrient-rich South Atlantic central water near the coast. Westerlies, which occur more frequently in the winter months, tend to inhibit upwelling. The coastal upwelling is
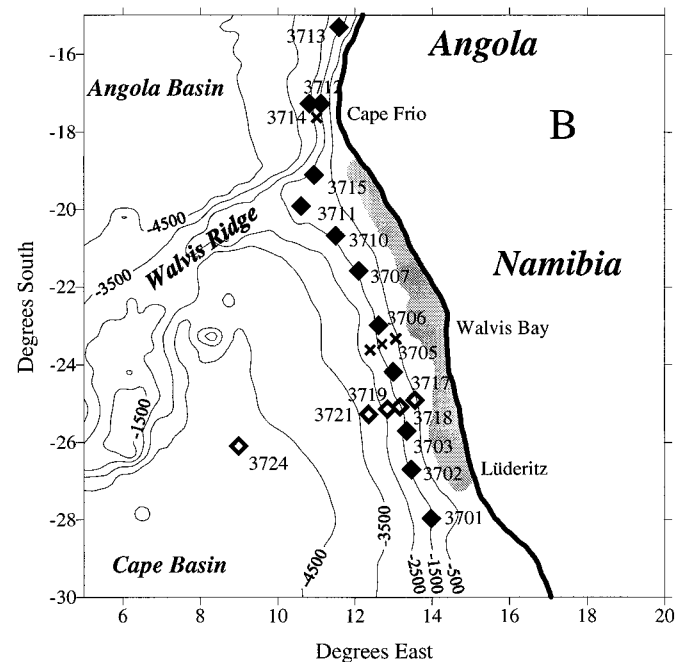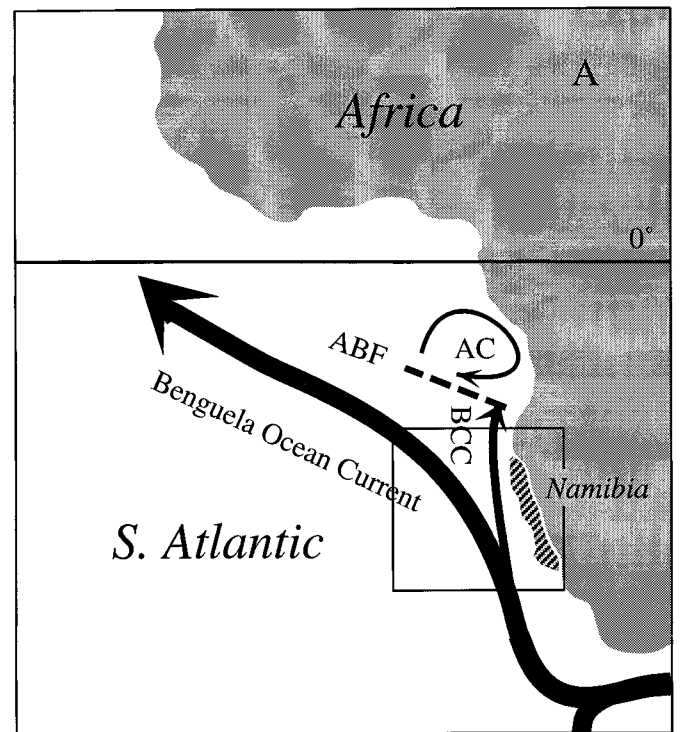




Fig. 1.   (A) Location of the sampling area (box) in the southeast Atlantic. Also indicated are circulation features of interest (drawn after Schneider et al. 1996), including the Angola Current (AC), the Benguela Coastal Current (BCC), the Angola–Benguela Front, and the Benguela coastal upwelling zone (hatched area). (B) Map showing station sites. Shown are the along-slope (~1,300 m) transect A (♦) and the cross-slope transect B (◇); X's mark relevant sites from Glud et al. (1994). The coastal upwelling area is shown by the gray stippled area. (Bathymetric data obtained from the National Geographical Data Center 1988.)

Table 1. Station locations, water depths, and sulfate reduction rates. The peak depth is the depth interval at which peak sulfate reduction rate was observed. The areal sulfate reduction rates represent the measured sulfate reduction rate integrated numerically over the upper 20 cm of sediment. Rates in parentheses are averages for the given oceanographic region.

| Station | (Latitude) | (Longitude) | Water depth (m) | Peak rate (nmol cm$^{-3}$ d$^{-1}$) | Sulfate reduction rate peak depth (cm) | Areal rate (mmol m$^{-2}$ d$^{-1}$) |
|---|---|---|---|---|---|---|
| Along-slope transect A | | | | | | |
| 3701 | 27°57.1′S | 14°00.3′E | 1,488 | 2.0 | 8–10 | 0.05 |
| North Cape Basin | | | | | | (1.16±0.23) |
| 3702 | 26°46.5′S | 13°27.3′E | 1,311 | 11.1 | 3–5 | 1.12 |
| 3703 | 25°31.0′S | 13°14.0′E | 1,372 | 16.0 | 4–5 | 1.35±0.42 |
| 3705 | 24°18.2′S | 12°59.8′E | 1,308 | 24.5 | 2–3 | 0.93 |
| 3706 | 22°43.2′S | 12°36.1′E | 1,313 | 28.9 | 2–3 | 1.75 |
| Walvis Ridge | | | | | | (0.67±0.02) |
| 3707 | 21°37.5′S | 12°11.6′E | 1,352 | 8.6 | 3–4 | 0.67±0.14 |
| 3710 | 20°33.7′S | 11°24.2′E | 1,312 | 12.6 | 3–4 | 0.61 |
| 3711 | 19°50.1′S | 10°46.3′E | 1,214 | 10.5 | 2–3 | 0.59 |
| 3715 | 18°57.3′S | 11°03.4′E | 1,203 | 6.8 | 2–3 | 0.85 |
| South Angola Basin | | | | | | (0.31±0.02) |
| 3712 | 17°11.2′S | 11°07.6′E | 1,243 | 3.6 | 4–5 | 0.18 |
| 3713 | 15°37.7′S | 11°00.3′E | 1,330 | 9.0 | 2–3 | 0.29 |
| 3714 | 17°09.6′S | 10°59.9′E | 2,060 | 5.5 | 2–3 | 0.37±0.18 |
| Cross-slope transect B | | | | | | |
| 3717 | 24°50.0′S | 13°21.0′E | 855 | 13.4 | 2–3 | 0.97±0.30 |
| 3718 | 25°53.7′S | 13°09.6′E | 1,317 | 19.9 | 4–5 | 1.39±0.33 |
| 3719 | 24°59.7′S | 12°52.3′E | 1,955 | 4.9 | 2–3 | 0.40±0.17 |
| 3721 | 25°09.1′S | 12°23.9′E | 3,013 | 3.3 | 2–3 | 0.14±0.04 |
| 3724 | 26°08.2′S | 08°55.6′E | 4,766 | 1.1 | 8–10 | 0–0.023 |

most continuous and intense at latitudes of 25–26°S with a semipermanent cell located between Lüderitz and Walvis Bays but decreases sharply in the northerly direction to Cape Frio, where seasonality plays a stronger role (Brongersma-Sanders 1983; Shannon and Nelson 1996). The typical westward extent of upwelling from these cells from the coast is 150–175 km. However, upwelling filaments, in the form of dipole eddies, often extend 200 km westward of Lüderitz and can reach distances of up to 1,000 km in extreme cases (Shannon and Nelson 1996). Variations in upwelling intensity can be observed in the intraannual variability of particle fluxes through the water column, as measured in sediment traps placed near Walvis Ridge (Wefer and Fischer 1993).

## Methods

Sediments were obtained from the continental margin off Namibia and southern Angola and from the Cape Basin during F/S *Meteor* cruise 34-2 (29 January–18 February 1996). Locations of the sampling sites are shown in Fig. 1B and described in Table 1. Sediments were sampled along two axes. Transect A ran roughly longitudinally along the 1,300- to 1,400-m isobath parallel to the African coast from 27°57′S across Walvis Ridge to 14°38′S, and transect B extended normally from the continental shelf from a depth of 855 m (24°50′S, 13°21′E) into the Cape Basin at a depth of 4,800 m (26°08′S, 08°56′E). Dissolved $O_2$ concentrations in the

overlying water at all stations were between 150 and 200 $\mu$M (Schulz et al. 1996).

A multicorer was used to retrieve undisturbed sediment cores, which were immediately subsampled for porosity/density, sulfate concentration, and sulfate reduction measurements. Subcores (26 mm in diameter, ~30 cm long) for sulfate reduction measurements made in triplicate were taken from separate multicore casts. Subcores for total organic carbon, porosity, and sediment density determination were sectioned and refrigerated for later analysis on shore. Subcores for sulfate were sectioned and frozen for later analysis on shore. Sulfate concentrations (in pore waters separated by centrifugation and filtration through a 0.40-$\mu$m syringe filter) were measured by unsuppressed anion chromatography using a Waters 510 high-performance liquid chromatography pump, Waters WISP 712 autosampler (100 $\mu$l injection volume), Waters IC-Pak anion exchange column (50 × 4.6 mm), and a Waters 430 conductivity detector and 1 mM isophthalate buffer as eluant (in 10% methanol with pH adjusted to 4.5) with a flow rate of 1 ml min$^{-1}$. Porosity and density were determined on subsamples that were dried at 60°C. The percentage of organic carbon was determined in surface (0–1 cm) sediments at all stations on dried porosity/density subsamples that had been subsequently decarbonated by washing with 1M HCl. In contrast to sediment trap material, washing of sediment leads to an underestimation of <3% of the organic carbon content (Hedges and Stern
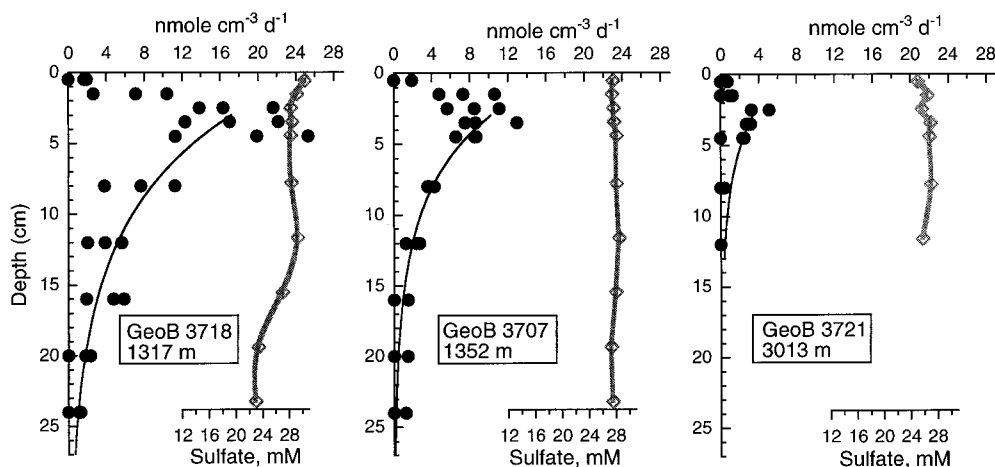
Fig. 2.   Sulfate reduction rates and pore-water sulfate concentrations from three stations: 3718, 3721, and 3707. The bold line through the sulfate reduction data shows the exponential fit of the data below the peak rate.

1984). The decarbonated samples were analyzed for carbon concentration using a Fisons 1500 NCS elemental analyzer.

The subcores for sulfate reduction rate measurements were immediately incubated in the dark at temperatures, but not pressures, reflecting in situ conditions (*see Discussion for further discussion on the effects of decompression on rate measurements*). To avoid stagnation over the sediment surface and thus more closely approximate the natural diffusive oxygen penetration into surface sediments, overlying water was removed from the top of the core until just a thin film remained. Both macrobenthic (i.e., pumping and the consequent injection of oxygen into greater depths) and meiobenthic activities may be inhibited by this treatment. At present, coring and subcoring may negatively affect pumping by temporarily decreasing the flux of $O_2$ into burrows, thus allowing sulfate reduction to proceed. However, it is difficult to gauge the effects, if any, that such treatment might have on the sulfate reduction rates at depth. Only when sulfate reduction rate measurements can be performed in situ by implementing disturbance-free incubations (i.e., direct injection of tracer into seabed without simultaneous coring) will we be able to evaluate the effects of the macrobenthos on sulfate reduction rates. Meiobenthic activities may also be perturbed as the meiobenthos respond to sharp chemical gradients near the sediment–water interface (i.e., oxygen gradients; Woodin et al. 1998). However, this effect should be restricted to within the first centimeter of sediment, where sulfate reduction rates are lowest. Such an error is likely to be far less significant than allowing the surface sediment to go anoxic, which would lead to a large overestimation of the surface sulfate reduction rate.

Sulfate reduction rate measurements were determined using the whole-core $^{35}SO_4^{2-}$ method (Jørgensen 1978). Subcores were injected at 1-cm intervals with ~5 μl of 80 kBq ml$^{-1}$ $^{35}SO_4^{2-}$ carrier-free tracer (Amersham). After 8–12 h, the bacterial activity was halted by slicing the cores at 1-cm intervals into an equal volume of 20% (w/v) zinc acetate solution and freezing. $^{35}S$ incorporation into total reducible inorganic sulfur (TRIS) was determined using the one-step

acidic Cr-II method (Fossing and Jørgensen 1989). Counting of the $^{35}SO_4^{2-}$ and ZnS from the Cr-II distillation was performed using a Canberra-Packard 2400 TR liquid scintillation counter (with Packard Ultima Gold XR as the scintillation mixture). Sulfate reduction rate blanks were determined by slicing cores into zinc acetate as described above and then adding 5 μl of tracer 30 min after sediment preservation. Further processing proceeded as for the normal samples. Blanks were determined at the surface (0–2 cm), from near the middle and from the lower part of subcores from eight stations representing the spatial extent of our sampling net. No systematic trend with depth, sample locality, or amount of tracer added was observed in the blank values. The mean blank value and standard deviation ($1\sigma$) was determined to be 136 ± 60 counts per minute (cpm) per distillation. We defined the detection limit as when $cpm_{TRIS} - cpm_{Blank} > 2\sigma_{Blank}$ (which for these samples became $cpm_{TRIS} - 136 > 120$).

## Results

*Depth distribution of sulfate reduction*—Figure 2 shows sulfate reduction rate profiles from three representative stations: GeoB 3718 (transect A/B, 1,317 m), showing the high sulfate reduction rate activity typical of the center of the upwelling zone; GeoB 3707 (transect A, 1,352 m), showing the lower rates typical of the rates north of the main upwelling; and GeoB 3721 (transect B, 3,013 m), a site from the upper continental rise. The shapes of the sulfate reduction profiles over the upper 20 cm were qualitatively the same at all but two sites. Only the intensity of sulfate reduction varied from one station to the next. Sulfate concentrations decreased only slightly from seawater values of 26–28 mM over the upper 30 cm at all sites, and Sta. GeoB 3718 exhibited the largest depletion, with values of 22–23 mM at 28 cm depth (Fig. 2). At stations where three replicate subcores were incubated and processed (GeoB 3703, 3707, 3714, 3717, 3718, 3719, and 3721), the profiles were indis-

tinguishable from one another (Fig. 2). Overall variability of sulfate reduction, as measured as total depth-integrated sulfate reduction over the uppermost 20 cm between cores from the same station ($1\sigma$/mean, $N = 3$), ranged from 21 to 49%. Sulfate reduction rates increased exponentially from near zero at the surface to a peak at depths between 2 and 5 cm. Below this peak, the rates decreased exponentially with depth as shown by the exponential fit of the data in Fig. 2. The peak sulfate reduction rate and the depths of peak sulfate reduction are given in Table 1. The two exceptions to the general pattern of sulfate reduction activity with depth were Sta. GeoB 3701 (southernmost, carbonaceous ooze) and Sta. GeoB 3724 (abyssal plain). No detectable sulfate reduction was observed within any of these cores except a single point in one of the replicate cores from each station.

In the main Benguela Upwelling sediments, as represented by Sta. GeoB 3703 (1,372 m), sulfate reduction integrated over the upper 20 cm represents >90% of the total cumulative sulfate-reducing activity observed within the sulfate-containing zone above the methane–sulfate transition (Fossing et al. in prep.). For the purpose of this report, we define ''areal sulfate reduction'' as the rate of sulfate reduction integrated over the upper 20 cm of sediment. However, as a cautionary aside to the interpretation of these and other ''depth-integrated'' sulfate reduction rates, significant rates of sulfate-reducing activity may extend to the depths of meters or more (Parkes et al. 1994). For example, north of Walvis Ridge, at Sta. GeoB 3714 (2,060 m), sulfate reduction rates below 20 cm are lower than at Sta. GeoB 3703, but because of greater sulfate penetration and distinct peaks of sulfate reduction rates at depths of >2 m, the surface 0–20 cm of sulfate reduction accounts for only 34% of the cumulative areal sulfate reduction rate (Fossing et al. in prep.). Thus, areal sulfate reduction rates, which are discussed below, are minimal estimates.

*Spatial distribution of depth-integrated sulfate reduction rates*—The sulfate reduction rates integrated over a depth of 0–20 cm tracked the expected spatial distribution of coastal upwelling intensity. The depth-integrated rates were enhanced in the main upwelling region, centered at 25–26°S, and declined northward across Walvis Ridge toward the Angola Front (Fig. 3, Table 2). Sta. GeoB 3718, at the intersection of transects A and B, exhibited the highest sulfate reduction activity in both the along-shore and cross-slope axes. This conjunction was not coincidental, because the 1,300-m isobath was chosen for study on the basis of geochemical and echo-sounder data from earlier *Meteor* expeditions (M-6 in 1988 and M-20 in 1993). The placement of transect B was chosen on the basis of on-board oxygen penetration rates made during study of transect A. In the along-shore transect A (Fig. 3A), depth-integrated sulfate reduction rates showed an abrupt change between Sta. GeoB 3701 and Sta. GeoB 3702; these changes were correlated with the transition from a relatively organic-poor carbonaceous ooze to an organic-rich, diatomaceous ooze characteristic of the upwelling zone. The highest sulfate reduction rates, from 0.9 to 1.92 mmol m$^{-2}$ d$^{-1}$, were observed between latitudes 25°31′S (GeoB 3703) and 22°43′S (GeoB 3706). Three subregions of sulfate reduction were clearly delineated along the

south–north transect of the Benguela Upwelling, as shown in Table 2: the Cape Basin Upwelling, which had the highest rates (1.16 ± 0.23 mmol m$^{-2}$ d$^{-1}$); Walvis Ridge, where areal sulfate reduction rates dropped by approximately one-half; and to the north along the rim of Angola Basin, where areal sulfate reduction rates were halved again. These three subregions differed significantly from one another, as confirmed by an analysis of variance in the areal sulfate reduction rates versus subregion ($P < 0.002$ that the null hypothesis is correct; confidence interval = 0.95). With increasing water column depth, sulfate reduction rates generally exhibited an exponential decrease, as shown in transect B (Fig. 3B). The only exception to this trend is that higher depth-integrated sulfate reduction rates were found at 1,300 m water depth (GeoB 3718) than at 855 m (GeoB 3717). Overall, depth-integrated sulfate reduction rates were strongly correlated with the percentage of organic carbon in the surface centimeter of sediment ($r^2 = 0.84$ for a linear fit; Fig. 4).

## Discussion

*Measurement of sulfate reduction in deep-sea sediments*—Shipboard handling and incubation of deep-sea sediments raises concerns about the effects of decompression on the accuracy of the sulfate reduction rate measurements. Despite the measurement of sulfate reduction rates using intact sediment cores, sediment samples are decompressed and temporarily warmed as they are brought to the ocean surface. The problem of pressure effects on deep-sea microbial processes remains unresolved, although a considerable body of literature that goes back to the pioneering work of Zobell (Zobell and Johnson 1949; Zobell 1952) exists. Difficulties in obtaining and handling sediment samples at pressures of 10 MPa (100 atm or ~1,000 m water depth), as well as unraveling the simultaneous effects of sample warming and decompression on bacterial communities, whose individual members may exhibit barotolerance, barophilicity, or baroinhibition (in the case of allocthonous bacteria arriving from the surface on sedimenting particles), have not led to any clear indication of how respiration rate measurements performed at earth surface atmospheric pressure may vary from their in situ rates. A variety of barophilic and barotolerant bacteria have been isolated from deep-sea sediments (Jannasch and Taylor 1984; Yayanos 1995), including anaerobic species, such as denitrifiers (Tamegai et al. 1997) and sulfate reducers (Parkes et al. 1995). These species also grow at surface temperature, which suggests that many of the barotolerant or barophilic species would not suffer because of decompression. However, deep-sea, autochthonous bacterial populations are strictly temperature adapted, and present-day isolation techniques may lead to underrepresentation of species that are sensitive to both warming and decompression (Yayanos 1995). Jannasch and Taylor (1984) describe a series of experiments in which substrate metabolism of acetate and glutamate increased in samples that were taken from 2,000 and 6,000 m and decompressed. The investigators argue that it is difficult to determine whether they were observing a true effect on substrate-specific transport, irrespective of organism, or simply enrichment for bacteria with
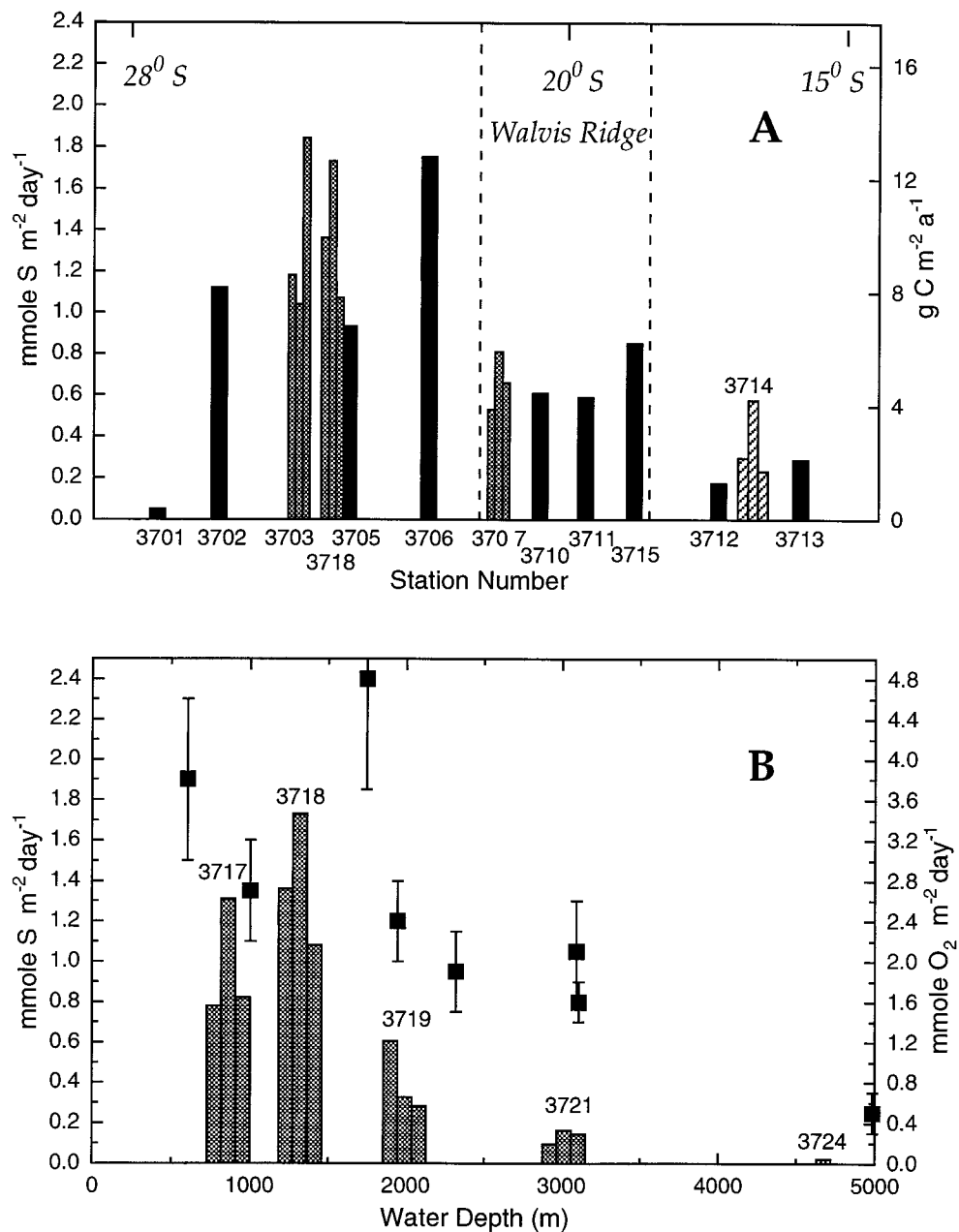
Fig. 3. (A) Depth-integrated (0–20 cm) sulfate reduction rates along a north–south transect at the 1,300-m isobath (except for GeoB 3714 at 2,060 m). Each bar represents the areal sulfate reduction rate from one whole-core measurement. Stations where sulfate reduction was measured in more than one core are shown in gray. (B) Depth-integrated (0–20 cm) sulfate reduction rates along a transect normal to the coast, extending from the upper continental slope to Cape Basin. Also plotted for comparison are the DOU rates from fig. 4 in Glud et al. (1994). Note that the scales for the sulfate reduction rates and DOU rates are scaled so that the data can be directly compared in equivalent amounts of carbon consumed (Eqs. 1, 2).

higher affinities at low barometric pressure. In contrast, Bianchi and Garcia (1993) have observed, in samples taken from the 1,000-m water column of the Mediterranean Sea, that decompression resulted in lower activities of $^{14}$C-glucose uptake than that for in situ uptake. Likewise, Rowe and Deming (1985) observed higher rates of $^{14}$C-labeled gluta-mate uptake in surface sediments of the abyssal North At-

lantic in sediments incubated at pressures corresponding to in situ conditions

A number of studies have demonstrated that shipboard measurements lead to steeper $O_2$ gradients and shallower penetration depths (Smith and Hinga 1983; Reimers et al. 1986; Glud et al. 1994). Glud et al. (1994) ascribe the dis-crepancies between shipboard and in situ oxygen measure-

Table 2. Estimates of the fraction of TOU consumed by reduced compounds resulting from sulfate reduction (SR) for the main upwelling area, continental rise, and a site north of Walvis Ridge. Estimates of the buried sulfur content were obtained from total sulfur concentrations from the 50- to 100-cm depth of gravity cores at Sta. GeoB 3703 and GeoB 3714 (Fossing et al. in prep.).

| Region | Stations | Sediment burial rate (cm ky$^{-1}$) | Sulfur, buried ($\mu$mol cm$^{-3}$) | Sulfur burial rate (mmol m$^{-2}$ d$^{-1}$) | Depth-integrated SR, 0–20 cm (mmol m$^{-2}$ d$^{-1}$) | SR, buried (%) | TOU (mmol m$^{-2}$ d$^{-1}$) | TOU as SR (%) |
|---|---|---|---|---|---|---|---|---|
| North Cape Basin (855–1,372 m) | 3702, 3703 3705, 3717, 3718, 3706 | 10* | 70–100 | 0.019–0.027 | 1.25±0.31 | 1.2–2.9 | 3.2–9.2§‖ | 20–96 |
| Continental rise (3,013 m) | 3721 | 1–3† | 70–100 | 0.005–0.008 | 0.14±0.04 | 2.7–8.0 | 2.3§ | 9–16 |
| South Angola Basin (2,060 m) | 3,714 | 30‡ | 70–100 | 0.05–0.08 | 0.31±0.02 | 15–28 | 3.2§–15.5‖ | 3–10 |

* Core PGPC12 as reported in Summerhayes et al. (1995).
† Core 532 as reported in Summerhayes et al. (1995).
‡ Schneider et al. (1992).
§ Holby and Riess (pers. comm.).
‖ Glud et al. (1994).

ments in the southeast Atlantic continental margin to a combination of pore-water expulsion (due to decompression of the core), decompression, and warming effects on the microbial community. Preliminary studies of the effect of pressure on sulfate reduction rate measurements have not, as yet, shown any evidence for such discrepancies. For instance, Martens et al. (1998) report that in situ incubations using $^{35}SO_4^{2-}$ (using with a benthic landing system) and concurrent shipboard incubations of sediments from 750 m off the continental slope of North Carolina gave similar results. Sulfate



Fig. 4. Depth-integrated (0–20 cm) sulfate reduction rates versus the percentage of organic carbon (%$C_{org}$) in the 0- to 1-cm depths of each station. The straight line represents a linear regression, where depth-integrated (0–20 cm) sulfate reduction rate = $0.26(\%C_{org}) - 0.099$. $r^2 = 0.84$.

reduction rates from a 3,500-m site in the Arabian Sea also show no significant differences between shipboard, nonpressurized sediment incubations and sediment that has been recompressed and incubated under pressures reflecting in situ conditions (Boetius and Ferdelman, unpubl. data). Moreover, unlike shipboard measurements of oxygen penetration depths and fluxes, we observed coherent variations in the spatial distribution of depth-integrated rates, which suggests that if there is an effect of decompression on sulfate reduction rates, the effect is proportional across all sites. Finally, macrofauna observed in cores from 1,300 m were still viable, and macrofauna from as deep as 2,000 m (GeoB 3714) were intact. Thus, is unlikely that dead, disintegrating macrofauna could contribute to high sulfate reduction. Therefore, despite the caveat that these sulfate reduction experiments were neither performed in situ nor performed at pressures reflecting in situ conditions, we conclude that the sulfate reduction rate data reported here accurately represent the in situ rates.

*Sulfate reduction as a reflection of $C_{org}$ supply in the Benguela upwelling sediments*—We observed a downslope maximum in sulfate reduction at 1,300 m, followed by a quasi-exponential decrease of sulfate reduction rates with increasing water depth. This distribution of areal sulfate reduction activity conforms to expected trends of benthic organic matter decomposition rates along continental margins. Sulfate reduction itself is directly linked to the remineralization of organic carbon, as shown in Eq. 1:

$$2CH_2O + SO_4^{2-} \rightarrow 2HCO^- + H_2S \qquad (1)$$

(For a discussion of the 2:1 stoichiometry between sulfate and carbon, *see* Thamdrup and Canfield 1996.) Generally, in systems where sedimentation is wholly derived from vertical settling of biogenic debris, it would be expected that the amount of organic material reaching the sediment should decrease with increasing water depth and thus result in correspondingly lower benthic remineralization rates (Suess 1980; Jahnke 1996). However, Jahnke et al. (1990) and Reimers et al. (1992) have demonstrated that the supply of or-
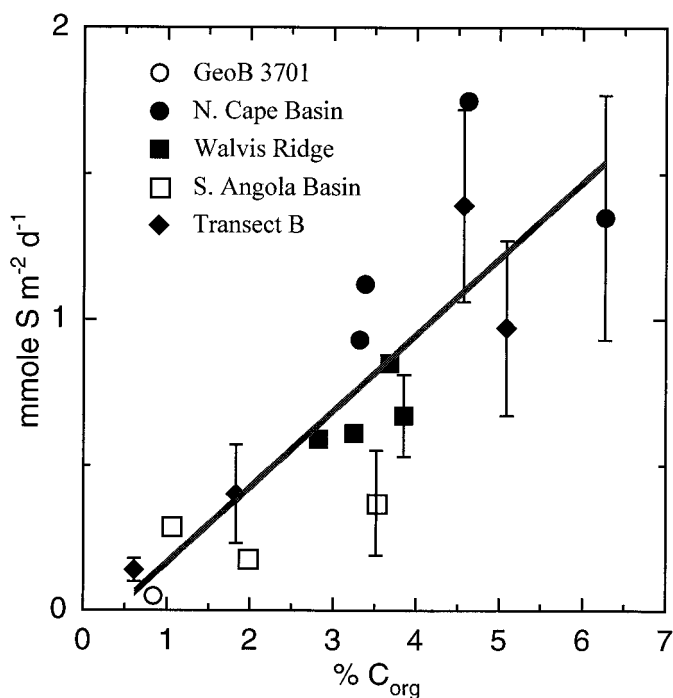
ganic carbon to the sediments of continental margins is independent of water depth. In central California continental margin sediments, the peak in benthic mineralization is at the foot of the continental slope (Jahnke et al. 1990). Anderson et al. (1994) have also observed an enhancement of organic matter deposition midway down the slope (~1,000 m) of the northwest Atlantic continental margin. Because of various aspects of the flow regime and sediment topography, these mid- and lower-slope sites trap organic-rich material transported downslope as well as vertically sinking debris (Jahnke et al. 1990). A midslope (1,743 m) peak in diffusive oxygen uptake (DOU) for the north Cape Basin continental margin can also be seen in the data from Glud et al. (1994), as shown in Fig. 3. Together with the maximum sulfate reduction rates observed at 1,300 m along transect B, the data suggest that the main depot of organic material on the north Cape Basin continental slope is to be found between 1,100 and 1,800 m depth.

It is also instructive to compare the areal rates of sulfate reduction activity to sediment trap studies from the same region. Sediment traps placed at 1,640 m water depth in the Walvis Ridge area to measure export fluxes of organic carbon from the surface waters gave annual organic carbon fluxes of 0.87–1.42 mmol C m$^{-2}$ d$^{-1}$ (Wefer and Fischer 1993). Sulfate reduction processes (0.68 ± 0.15) in this zone (Sta. GeoB 3710, 3711, and 3715) account for 1.36 mmol C m$^{-2}$ d$^{-1}$, assuming a stoichiometry of 2C:1S, as indicated by Eq. 1. This is equivalent to the total vertical flux of organic carbon measured in the nearby sediment traps. DOU rates for the same area lie between 1.9 and 2.9 mmol C m$^{-2}$ d$^{-1}$ (Glud et al. 1994; Ries and Holby unpubl. data). In addition, burial of organic carbon takes place in these sediments at a minimum rate of 0.5 mmol C m$^{-2}$ d$^{-1}$ given a sedimentation rate of 10 cm ky$^{-1}$ (Summerhayes et al. 1995) and an organic carbon content of 2 wt%. Taken together, the organic carbon burial rates and rates of organic carbon degradation based on sulfate reduction rates alone exceed the sediment trap fluxes and suggest that a considerable lateral export of shelf-derived organic carbon to the slope sediments must be occurring.

Areal sulfate reduction rates within the study area reflect organic carbon supply, as indicated by correlation of areal sulfate reduction rates with the spatial distribution of upwelling intensity and with surface-sediment organic carbon content. They are also independent of bottom-water oxygen concentrations for this area. As opposed to sediment trap studies or oxygen uptake measurements, sulfate reduction rate measurements integrate over long time spans. Given a sedimentation rate of 20 cm ky$^{-1}$, the average age of the uppermost 10 cm of a well-bioturbated sediment is 500 yr. In addition, we expect that the determined sulfate reduction rate values will not vary seasonally because the temperature of the overlying water is a nearly constant 4°C. Thus, depth-integrated sulfate reduction rate measurements provide an excellent tool for mapping the intensity of anaerobic processes within continental margin sediments.

*Comparison to other upwelling areas*—A cogent relationship between upwelling intensity and areal sulfate reduction exists when comparing the Benguela Upwelling system with other upwelling systems in which sulfate reduction has been measured. Table 3 shows a comparison of depth-integrated sulfate reduction rates and their corresponding rates of primary productivity. Upwelling intensities, as reflected by rates of primary productivity, are greatest along the eastern margin of South America (Peru and Chile), as are the depth-integrated rates of sulfate reduction (2.4–25.5 mmol S m$^{-2}$ d$^{-1}$). In comparison, sediments along the continental slope of eastern Australia, an area of only sporadic and weak upwelling with primary productivity in the range of 0.8–8 mmol C m$^{-2}$ d$^{-1}$ (Jitts 1965 in Heggie et al. 1990) exhibit much lower rates of sulfate reduction (0.007–0.56 mmol m$^{-2}$ d$^{-1}$). Both the rates of primary productivity and the depth-integrated rates of sulfate reduction in the continental slope sediments of the Benguela Upwelling system fall in the middle range between these two extremes and are very similar to the rates of primary productivity and sulfate reduction from the upwelling region of the northeast Pacific continental margin (Devol and Christensen 1993).

*Importance of sulfate reduction as an organic carbon degradation pathway in Benguela Upwelling sediments*—Oxygen is the ultimate terminal oxidant for organic carbon remineralization in marine sediments, either in its dissolved, diatomic form or fixed as an oxidized Mn, Fe, N, S, or C compound. Hence, total oxygen uptake (TOU) by sediments can be taken to represent the total rate of sedimentary organic carbon remineralization. Therefore, we assume that the consumption of oxygen in the sediments represents the total oxidation of organic carbon to $CO_2$ according to the following equation:

$$CH_2O + O_2 \rightarrow CO_2 + H_2O \qquad (2)$$
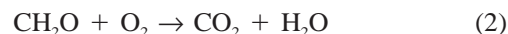
Moreover, TOU represents not only aerobic degradation processes, as indicated in Eq. 1, but the ultimate oxidation of reduced compounds arising from anaerobic respiratory processes, including, for instance, the oxidation of sulfide arising from sulfate reduction:

$$H_2S + 2O_2 \rightarrow SO_4^{2-} + 2H^+ \qquad (3)$$
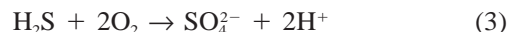
Thus, TOU represents the sum of aerobic and anaerobic processes, the latter of which is dominated in most coastal marine sediments by sulfate reduction (Jørgensen 1982; Canfield et al. 1993; Thamdrup and Canfield 1996). Depth-integrated rates of sulfate reduction can be directly compared to measured TOU rates, and, thus, we are able to estimate the contribution of anaerobic respiration, as represented by sulfate reduction, to the total sedimentary remineralization in Benguela Upwelling sediments. Fortunately, in situ measurements of both TOU and DOU rates are available for the Namibian continental margin sediments (Glud et al. 1994; Holby and Riess unpubl. data).

We can estimate the fraction of TOU, or total respiration, that is accounted for by sulfate reduction, assuming that reduced sulfur that is not permanently buried in the sediments becomes oxidized to sulfate, ultimately through the consumption of oxygen (Eq. 2). Table 2 shows estimates for the burial of sulfur and the consumption of oxygen attributable to sulfide oxidation. The rates of sulfur burial, although somewhat poorly constrained due to the paucity of sediment

Table 3. Comparison of depth-integrated sulfate reduction rates within the Benguela Upwelling system to primary productivity and bottom-water oxygen concentration in other selected continental margins.

| | Bottom-water $O_2$ concentration ($\mu$M) | Sulfate reduction (mmol S $m^{-2}$ $d^{-1}$) | Primary productivity (mmol C $m^{-2}$ $d^{-1}$) |
|---|---|---|---|
| Benguela Upwelling* | 150–200† | (Integrated over 20 cm) | 175–240‡ |
|   Cape Basin slope | | 1.16±0.23 | |
|   Walvis Ridge slope | | 0.67±0.02 | |
|   Angola Basin slope | | 0.31±0.02 | |
|   Cape Basin rise | | 0.135±0.04 | |
| Central Chile Upwelling§‖ | >100 | (Integrated over 8–10 cm) | 800¶ |
|   1,000–2,000 m | | 2.4¶–4.9# | |
| Peru Upwelling¶ | | (Integrated over 20 cm) | 83–830 |
|   502 m | 5 | 25.5 | |
|   2,650 m | >200 | 5.2 | |
| Washington State continental slope#** | | (Integrated over 30 cm) | 170 |
|   465 m | 47 | 1.3 | |
|   630 | 38 | 0.65 | |
| Gulf of Maine†† | | (Integrated over 30 cm) | 57 |
|   250–296 m | | 0.36–2.7 | |
| Gulf of Mexico continental slope‡‡ | | (Integrated over 5 cm) | |
|   1,086–2,008 m | | 0.038–2.45 | |
| East Australia continental slope | | | |
|   431–1,484 m | 200–300 | 0.007–0.56§§ | 0.8–8.3‖‖ |

* This study.
† Schulz et al. (1996).
‡ Summerhayes et al. (1995).
§ Ferdelman et al. (1997).
‖ Fossing (1990).
¶ Fossing et al. (1995).
# Thamdrup and Canfield (1996).
** Devol and Christensen (1993).
†† Christensen (1989).
‡‡ Lin and Morse (1991).
§§ Heggie et al. (1990).
‖‖ Jitts (1965) in Heggie et al. (1990).

accumulation rate data, are insignificant in comparison to the areal sulfate reduction rates. When comparing the areal sulfate reduction rates to the TOU measurements made in situ, sulfate reduction accounts for 20–96% of total oxygen consumption in the main upwelling sediments of the Cape Basin slope. At 3,013 m (along the continental rise) and at 2,060 m north of Walvis Ridge, the percentage of TOU as sulfate reduction falls to 9–16% and 3–10%, respectively. Overall, the percentage of organic carbon remineralization anaerobically mediated via sulfate reduction increases with decreasing depth in the upwelling-affected sediments south of Walvis Ridge. This trend may also be observed in Fig. 3B, in which both areal sulfate reduction rates and DOU rates taken from Glud et al. (1994) as a function of depth are shown (although DOU represents only that fraction of TOU that diffuses across the sediment–water interface). When compared to DOU measurements, areal rates of organic carbon remineralization due to sulfate reduction range between 0.5 and 1.2 times the DOU rates at a depth of 1300 m. With

increasing water depth, DOU rates are fivefold or more greater than the areal rates of sulfate reduction.

The sulfate reduction rate profiles themselves also provide further insight into the relationship between oxygen distributions, oxygen utilization, and sulfate reduction. In all but two of the sulfate reduction rate profiles, we observed a sharp increase in sulfate reduction rate from the sediment–water interface to a peak value lying between a depth of 2.5 and 4.5 cm that was then followed by an exponential decrease to nearly nondetectable rates between depths of 10 and 20 cm. The shape of these profiles below the sulfate reduction rate peak can be used to extrapolate back to rates of total organic carbon remineralization at the sediment surface. We assume that the sulfate reduction rates below the peak in the sulfate reduction rates accurately reflect the total rate of organic carbon remineralization (double the sulfate reduction rates). Canfield et al. (1993) and Thamdrup and Canfield (1996) have shown for other continental slope sediments (Skagerrak and Chile, respectively) that sulfate re-
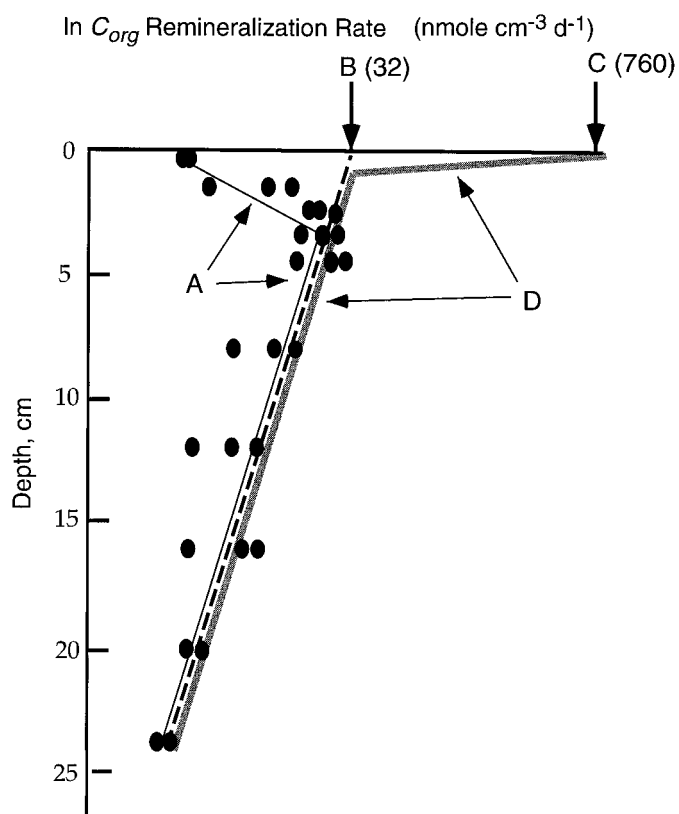
Fig. 5.   Idealization of natural log distribution of rates of organic carbon remineralization versus depth. Superimposed on sulfate reduction rate data (○) from Sta. GeoB 3718 are (A) the fit of the sulfate reduction rate data (solid black line), (B) the extrapolation of the fitted data to a surface organic carbon remineralization rate (dashed line), (C) a typical rate of oxygen utilization based on DOU measurements by Glud et al. (1994), and (D) the total combined rates of oxygen utilization (upper portion of thick, gray line) and anaerobic organic carbon remineralization (lower portion of thick, gray line). The area between lines A and B represents anaerobic organic carbon remineralization below 1 cm due to processes other than sulfate reduction.

Table 4.   Rates of areal organic carbon ($C_{org}$) remineralization due to sulfate reduction (SR), total anaerobic $C_{org}$ remineralization based on the extrapolated fit of the SR rate data, and model-predicted surface $C_{org}$ remineralization rates from stations at which triplicate cores were made. The number of SR rate measurements used for the exponential fit is given by *N*. Oxygen consumption rates are derived from the data of Glud et al. (1994) and are listed next to the nearest station from this study (Fig. 1B shows station locations).

| Station | N | Areal $C_{org}$ degradation (mmol C m$^{-2}$ d$^{-1}$) | | | Surface $C_{org}$ remineralization rate (nmol C cm$^{-3}$ d$^{-1}$) | |
|---|---|---|---|---|---|---|
| | | SR | Total anaerobic modeled | Anaerobic as SR (%) | Predicted | Oxygen consumption |
| 3703 | 28 | 2.70 | 2.93 | 92.2 | 31.0 | |
| 3707 | 12 | 1.34 | 1.56 | 85.9 | 35.3 | |
| 3715 | 9 | 1.70 | 1.69 | 100.1 | 15.5 | |
| 3714 | 20 | 0.58 | 0.79 | 73.4 | 10.7 | 533 |
| 3717 | 21 | 1.94 | 2.12 | 91.5 | 31.1 | 267 |
| 3718 | 18 | 2.78 | 3.10 | 89.7 | 51.6 | 757 |
| 3719 | 12 | 0.80 | 0.57 | 140 | 12.9 | 633 |
| 3721 | 9 | 0.28 | 0.37 | 75.7 | 13.2 | |

tion generally represents 70–90% of the total areal rate of anaerobic remineralization (Table 4). Volumetric rates of organic carbon remineralization extrapolated to the surface fall within the range of 10–75 nmol C cm$^{-3}$ d$^{-1}$ for Benguela Upwelling sediments. When these estimated organic carbon remineralization rates are compared to surface rates of oxygen consumption derived from the DOU data of Glud et al. (1994) for the same area, striking differences arise (Table 4). Rates, which are based on modeling of in situ oxygen profiles (Glud et al. 1994), reach >1,000 nmol C cm$^{-3}$ d$^{-1}$ for the surface 5–10 mm. More conservative estimates based on dividing the diffusive oxygen flux by the oxygen penetration depth also give rates in the range of 223–528 nmol C cm$^{-3}$ d$^{-1}$. These values are significantly higher (by roughly one order of magnitude) than the projected rates based solely on rates of anaerobic organic carbon remineralization. Gross differences between the kinetics of oxygen utilization and anaerobic organic carbon remineralization thus exist within these sediments.

Here it is useful to distinguish between the rates of oxygen utilization that have been directly observed in DOU measurements (Glud et al. 1994); the rates of anaerobic organic carbon remineralization, which are extrapolated from the rates of sulfate reduction as described above; and the rates of aerobic organic carbon remineralization, about which we can only speculate. Oxygen utilization includes both oxygen consumption due to aerobic organic carbon remineralization (Eq. 2) and oxidation of reduced inorganic compounds such as sulfide (Eq. 3). For instance, the high volumetric rate of oxygen utilization might represent the oxidation of newly settled material at the sediment–water interface, whereas sulfate reduction rates would reflect the slower remineralization of buried compounds that are more refractory in nature. Conversely, high rates of oxygen consumption may reflect the greater reactivity and abundance of reduced products, in par-

duction accounts for the majority of anaerobic organic carbon remineralization below the peak in sulfate reduction.

A second important assumption is that the exponential decrease in organic carbon decomposition below the peak SRR is simply an extension of the overall exponential decrease in organic carbon decomposition rates that begins at the surface. The decay of organic carbon in sediments is generally thought to follow first-order kinetics with respect to labile organic carbon concentration and, therefore, should exhibit an exponential decrease with depth (Boudreau 1992). This idealized relationship between sulfate reduction and organic decomposition versus sediment depth is presented in Fig. 5.

By fitting the organic carbon remineralization rates below the peak in sulfate reduction and extrapolating to the surface, we can now evaluate the total anaerobic decomposition rate, assuming also that aerobic decomposition occurs only in the uppermost 1 cm of sediment (Fig. 5). Comparison of the depth-integrated anaerobic organic carbon remineralization rates to that of sulfate reduction indicates that sulfate reduc-

ticular sulfur compounds, that have been mixed toward the surface through bioturbation.

For a contrasting example, we can loosely constrain the role that surface oxidation of reduced sulfur plays in the overall consumption of the DOU flux. In sediments typified by the data presented in Fig. 5 (GeoB 3718), we have already shown that oxidation of sulfide may account for 20–96% of TOU. Given that TOU rates measured in situ may exceed DOU fluxes by a factor of 1.2 to 4.2, depending on the density of fauna in the sediment (Glud et al. 1994), the proportion of the DOU flux consumed by the oxidation of reduced sulfide is likely to be upward of 50% to near 100%. If all the sulfide produced from sulfate reduction at Sta. GeoB 3718 were oxidized to sulfate within the first centimeter of sediment, an oxygen consumption rate of 280 nmol $cm^{-3}$ $d^{-1}$ would ensue. This is within the range of volumetric oxygen consumption rates determined from DOU measurements. Thus, the high volumetric rates of oxygen consumption at the sediment–water interface might better reflect the kinetics of sulfide oxidation than aerobic respiration.

At present, our sulfate reduction data allow us only to speculate on but not estimate the relative rates of oxygen consumption due to sulfide oxidation and aerobic organic carbon remineralization at the sediment–water interface. However, this is a critical point. Canfield (1994) has argued that the kinetics of aerobic organic carbon remineralization are inherently faster than for anaerobic processes because of the ability of oxygen-respiring organisms to enzymatically generate and use reactive oxygen radicals. Hartnett et al. (1998) have suggested that it is the exposure time of organic carbon to dissolved oxygen that controls the extent to which organic carbon is remineralized versus preserved in sediments from the continental margins of Washington State and Mexico. Thus, sulfide oxidation at the expense of aerobic remineralization will have implications for the remineralization and preservation of organic carbon in these sediments because less oxygen will be available for the aerobic remineralization of sediment organic carbon. We have demonstrated that sulfate reduction plays a major role in the remineralization of organic carbon in the surface sediments of the Benguela Upwelling area. Determining where and how the sulfide produced through sulfate reduction is oxidized back to sulfate and whether this plays a role in suppressing aerobic remineralization of organic carbon remains to be answered.

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