Ecological Applications, 21(7), 2011, pp. 2664–2677

Effect of temperature on biogeochemistry of marine organic-enriched systems: implications in a global warming scenario

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Abstract. Coastal biogeochemical cycles are expected to be affected by global warming. By means of a mesocosm experiment, the effect of increased water temperature on the biogeochemical cycles of coastal sediments affected by organic-matter enrichment was tested, focusing on the carbon, sulfur, and iron cycles. *Nereis diversicolor* was used as a model species to simulate macrofaunal bioirrigation activity in natural sediments. Although bioirrigation rates of *N. diversicolor* were not temperature dependent, temperature did have a major effect on the sediment metabolism. Under organic-enrichment conditions, the increase in sediment metabolism was greater than expected and occurred through the enhancement of anaerobic metabolic pathway rates, mainly sulfate reduction. There was a twofold increase in sediment metabolism and the accumulation of reduced sulfur. The increase in the benthic metabolism was maintained by the supply of electron acceptors through bioirrigation and as a result of the availability of iron in the sediment. As long as the sediment buffering capacity toward sulfides is not surpassed, an increase in temperature might promote the recovery of organic-enriched sediments by decreasing the time for mineralization of excess organic matter.

Key words: benthic fluxes; bioirrigation; carbon mineralization; climate change; Nereis diversicolor; *Odense Fjord, Denmark; organic enrichment; sediment metabolism.*

Introduction

Warming of the climate is unequivocal, and is evident from observations of increased global air and ocean temperatures. The sea surface temperature (SST) is expected to rise 1–3°C in the next 100 years (IPCC 2007), although the temperature increase may be even higher in shallow and enclosed areas (Massa et al. 2009). For example, in the Baltic Sea, the SST has increased by three to more than seven times the global rate, leading to an increase of 1°C per decade in recent years (Mackenzie and Schiedek 2007, Belkin 2009) with similar increases of temperature (~1°C per decade) predicted in forthcoming decades (Doscher and Meier 2004). Accordingly, there are major concerns that many ecosystems will be unable to adapt naturally to such a rapid rise in temperature (IPCC 2007).

Coastal water bodies support critical processes that may be impacted by climate change (IPCC 2001). Many of these processes are important at a global scale. For instance, even though coastal sediments comprise only 7.5% of the total area of the sea bottom, ~55% of the organic matter (OM) turnover in the oceans occur in these sediments (Middelburg et al. 1997). Since degradation processes are temperature dependent, global warming may affect the global balances of carbon (C) and nutrients (Paerl et al. 2002), which may have consequences for biological productivity and food web processes (Hyun et al. 2009).

OM enrichment is one of the main types of pollution worldwide (Islam and Tanaka 2004). In marine sediments, OM is degraded by microbial processes that convert OM into inorganic carbon (CO_2) and nutrients (e.g., Valdemarsen and Kristensen 2010). The total amount of OM reaching the seabed controls rates of metabolism and benthic fluxes (Emerson and Hedges 2003). In coastal areas, most of the OM reaching the sediment is mineralized in the top layer (Serpa et al. 2007). O_2 penetration in coastal marine sediments is generally low (approximately a few millimeters) and depends on temperature, since higher temperature leads to decreased O_2 solubility and stimulates chemical and biological O_2 consumption (Kristensen 2000). Thus, higher temperatures promote the degradation of OM by microbial anaerobic processes, such as sulfate reduction. (Soetaert et al. 1996, Weston and Joye 2005, Glud 2008).

The rates of sulfate reduction, i.e., the microbially mediated reduction of sulfate to sulfide, depends on temperature and the availability of reactive organic substrates and sulfate (Rusch et al. 1998, Bottcher et al. 2004, Al-Raei et al. 2009). All of these controlling factors typically have an interactive effect on sulfate reduction rates (Westrich and Berner 1988, Pomeroy and Wiebe 2001). The fact that sulfate reduction rates show an exponential increase within the temperature regime typically found in coastal sediments (0–35°C) has

Manuscript received 17 November 2010; revised 15 April 2011; accepted 25 April 2011. Corresponding Editor: N. B. Weston.

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been verified in seasonal field studies (e.g., Kristensen et al. 2000, Bottcher et al. 2004), as well as in laboratory experiments (e.g., Finke and Jorgensen 2008, Robador et al. 2009). Similarly, sulfate reduction rates are greatly stimulated by the quality and quantity of deposited OM (Hansen et al. 1993, Holmer and Kristensen 1996).

High sulfate reduction rates may have negative environmental impacts, since accumulation of toxic hydrogen sulfide is detrimental for benthic communities (Hargrave et al. 2008). However, several processes mitigate hydrogen sulfide accumulation in sediments, the most important being spontaneous or microbially mediated sulfide reoxidation to sulfate with O_2 or Fe- and Mn-oxides (Schippers and Jorgensen 2002). Hydrogen sulfide can also precipitate with iron to form insoluble Fe-S compounds (Berner 1989, Canfield 1989, de Wit et al. 2001). The reoxidation of these compounds is stimulated by infauna and resuspension events, enhancing O_2 penetration into the sediments, whereby the sediments renew this buffering capacity toward sulfides (Heijs and van Gemerden 2000).

The functioning of coastal marine ecosystems is greatly influenced by infauna that stimulate benthic–pelagic coupling by enhancing microbial C oxidation and nutrient fluxes (Lohrer et al. 2004, Holmer et al. 2005) due to their engineering activities (bioturbation and bioirrigation). By means of bioturbation (sediment reworking) and bioirrigation (flushing of solutes), macrofauna increases the electron acceptor supply from the water column to the sediment, which deepens oxic boundaries and enhances aerobic metabolism and sulfate reduction, and results in increased metabolic capacity of sediments (Aller and Aller 1998, Meysman et al. 2006). *Nereis diversicolor* is a model species widely distributed in shallow sediments along Northern European coasts, and is frequently used in bioturbation experiments (e.g., Banta et al. 1999, Kristensen 2000). *N. diversicolor* lives in a semipermanent network gallery of burrows in the sediment (Mermillod-Blondin and Rosenberg 2006) and can stimulate benthic metabolism considerably when compared to defaunated sediments (Kristensen and Holmer 2001).

Coastal ecosystems are highly influenced by different anthropogenic activities, which lead to organic enrichment (Islam and Tanaka 2004), but the effect of global warming on biogeochemical cycles in organically enriched marine sediments has received little attention. The effects of a rise in temperature may be even more pronounced in densely populated coastal areas, where sediments are concurrently enriched with OM due to high discharges of sewage, nutrients, and industrial wastes (Sanz-Lázaro and Marin 2009). Understanding the response of OM-enriched sediments to increased temperature is critical for forecasting changes in biogeochemical cycling in coastal marine environments in a climate change scenario (Hyun et al. 2009).

The aim of this work was to simulate the effect of global warming on coastal sediments affected by OM enrichment and to assess alterations in biogeochemical cycling. We hypothesized that, under OM-enrichment conditions, temperature will increase sediment metabolism at a higher rate than expected if the two variables (temperature and OM enrichment) had occurred separately. By means of a mesocosm experiment, we tested the effect of increased water temperature on the biogeochemical cycles of coastal sediments affected by OM enrichment, focusing on C, S, and Fe dynamics.

Materials and Methods

Sampling of sediment and N. diversicolor

Well sorted, organically poor, Fe-rich sand (0.4% POC [particulate organic C]), 125 μmol/cm^3 of Fe and 220-μm average grain size) was collected in Fænø Sund, Denmark, in August 2008 (see details in Valdemarsen et al. 2009). Approximately 40 L of surface sediment from 0 to 10 cm depth in the sediment was collected from shallow water (<1 m water depth) with a shovel and sieved though a 1-mm mesh to remove macrofauna.

N. diversicolor was collected from Fællesstrand in the outer part of Odense Fjord, Denmark (Kristensen 1993) in August 2008. Surface sediment from 0 to 10 cm depth was sieved through a 1-mm mesh, and healthy looking *N. diversicolor* were transferred to buckets with fresh seawater. Roughly 150 *N. diversicolor* of similar size (~5–6 cm length) were brought to the laboratory and maintained for a few days in 16°C aerated seawater before use.

Experimental setup

In the laboratory, the sampled sediment was divided into two 20-L portions, which served as control (−OM) or organically enriched sediment (+OM). The +OM sediment was enriched with 92 g labile OM in the form of finely ground fish feed (Ecolife, Dansk Ørredfoder [BioMar Limited, Grangemouth, UK], 49.4% particulate organic C [POC], and 8.1% particulate organic N [PON]). Sulfate (1 mol/L Na_2SO_4) was added to both −OM and +OM sediment to increase pore water sulfate to 49–52 mmol/L and to prevent sulfate depletion during subsequent sediment incubation. After enrichment, the −OM and +OM sediments were carefully homogenized by hand. The organic enrichment in +OM cores was ~0.1 mmol POC/cm^3 sediment, a level that has proved optimal for the stimulation of microbial metabolism in previous enrichment studies (Valdemarsen et al. 2009, 2010). For comparison, the enrichment of +OM sediment is equivalent to 26 mol POC/m^2, which is similar to the annual OM deposition close to fish farms or mussel farms (Morrisey et al. 2000, Callier et al. 2006, Holmer et al. 2007, Sanz-Lázaro et al. 2011).

From each portion of sediment (−OM and +OM), three cores with a 5 cm internal diameter (ID) and 36 cores with 8 cm ID were prepared in 35 cm long acrylic core liners. The core liners were closed at the bottom with rubber stoppers and ~20 cm sediment was added, leaving a 10–12 cm headspace above the sediment. The 5 cm ID cores were sectioned immediately to determine

initial sediment conditions. The remaining 8 cm ID cores were split into three groups, each containing 6 −OM and 6 +OM cores. Each group of cores was maintained at 16°, 22°, or 26°C in separate tanks containing 65 L GF/F-filtered seawater from Fænø Sund with a salinity of 17‰. The temperature in each tank was maintained constant by aquarium heaters and monitored every 5 min by underwater temperature loggers (HOBO, Pocasset, Massachusetts, USA). Temperatures were chosen on the basis of published literature in temperate areas similar to the study site (Kristensen 1993, Holmer and Kristensen 1996, Kristensen et al. 2000) and in accordance with the forecasted rise in temperature due to global warming (IPCC 2007). The water in each tank was vigorously stirred by air pumps, and in addition, the headspace in the sediment cores was stirred by 4 cm long magnetic bars placed a few centimeters above the sediment surface and driven by an external rotating magnet (~60 rpm). The cores were kept submerged and in darkness throughout the experiment (25–39 days). Roughly one-third of the water in each tank was exchanged with fresh seawater every week to prevent the accumulation or depletion of metabolites in the water column.

The 8 cm ID cores were left to acclimatize at the different temperatures for one day after preparation. Afterward, three healthy *N. diversicolor* were added to each core (~600 individuals/m^2) to simulate the natural density reported from estuarine habitats (Heip and Herman 1979, Vedel and Riisgard 1993). The time when polychaetes were added is hereafter referred to as $t = 0$.

TCO_2 efflux and sediment O_2 uptake

Total CO_2 (TCO_2) and sediment oxygen uptake (SOU) fluxes between sediment and water were determined every 2–4 days during the first two weeks and every week during the rest of the experiment. During the flux measurements, the water column of each sediment core was sampled and cores were closed with rubber stoppers. After 3–5 h (−OM) or 1–2 h (+OM), incubations were terminated and the water was sampled once more. Samples for TCO_2 were analyzed by flow injection analysis (Hall and Aller 1992). Samples for O_2 were analyzed according to the Winkler technique (APHA 1975). The flux of TCO_2 and SOU was calculated for the two levels of organic enrichment and for every temperature and reported in millimoles per square meter per day. During flux experiments O_2 was never depleted below 60% saturation to avoid experimental artifacts (Glud 2008).

Determination of bioirrigation rates

The irrigation activity of *N. diversicolor* was estimated according to Heilskov et al. (2006). One day prior to the final sectioning of cores, the water in each core was enriched with bromine (Br^-) to a final concentration of ~8 mmol/L. After incubating for ~24 h in Br^--rich water, cores were sectioned and the Br^- in pore water was determined. Irrigation activity was calculated from the depth-integrated Br^- inventory and corrected for the effect of passive diffusion.

Sectioning of cores

Three sediment cores with each sediment type (−OM and +OM) were sectioned initially ($t = 0$; henceforth, initial cores), and the remaining six −OM and +OM cores from every temperature treatment were sectioned at the end of the experiment (henceforth, final cores). Since temperature has a strong stimulatory effect on microbial reaction rates (2–4 fold increase for every 10°C increase in temperature [Westrich and Berner 1988, Finke and Jorgensen 2008]), the accumulation of inhibitory metabolites and depletion of sulfate might lead to biased rate estimates. Thus, the duration of individual temperature experiments varied, and final core sectioning of the sediments at 16°, 22°, and 26°C was performed after 39, 32, and 25 days, respectively. Despite these precautions, sulfate was depleted in +OM cores below 8 cm sediment depth (see *Results: Pore water solutes*). During every sectioning, cores were sliced into 1-cm sections to a depth of 2 cm and into 2-cm sections down to 16 cm depth. Every sediment slice was homogenized and sampled for dissolved and solid-phase parameters. Sediment subsamples (5–6 g) were preserved in 10 mL of 0.5 mol/L zinc acetate (ZnAc) for the determination of acid-volatile sulfides (AVS) and chromium-reducible sulfides (CRS). Pore water was extracted from another subsample by centrifugation (10 minutes, 1500 rpm [~3000 m/s^2]) and GF/F-filtration, and was analyzed for TCO_2, dissolved iron (Fe^{2+}), total dissolved sulfides (TH_2S), Br^-, and sulfate. Finally, the remaining sediment from every slice was used to determine sediment characteristics (density, water content, and POC).

Analysis

Sediment pools of AVS and CRS were determined using the two-step distillation technique of Fossing and Jørgensen (1989) modified according to Valdemarsen et al. (2009). The sediment content of total reducible inorganic sulfides (TRIS) was calculated as AVS + CRS.

TCO_2 in pore water was analyzed according to the procedures previously described. Pore water for the determination of Fe^{2+} was preserved with 0.5 mol/L HCl (0.1 mL per 0.4-mL sample) and analyzed by the ferrozine method (Stookey 1970) after reduction with hydroxylamine (Lovley and Phillips 1987). TH_2S in pore water was determined by colorimetric analysis (Cline 1969) of samples preserved with ZnAc (0.1 mL of 1 mol/L ZnAc per 0.9-mL sample). Samples for Br^- and sulfate were stored frozen (−18°C) until analysis by HPLC on a Dionex ICS-2000 system (Thermo Fisher Scientific, Waltham, Massachusetts, USA). Sediment density was determined gravimetrically by weighing a known volume of sediment using cut-off syringes. The water content was determined as loss in mass after drying (105°C, >12 h). POC was

determined in a Carlo Erba CHN EA1108 elemental analyzer (Carlo Erba, Milan, Italy) according to Kristensen and Andersen (1987).

Data analysis

Significant differences between the initial and final concentrations of pore water solutes and solid-phase measurements were tested by pairwise *t* tests for −OM and +OM, respectively. The Mann-Whitney test was used to test differences for nonparametric data. The effect of temperature on individual parameters was tested by one-way ANOVA and subsequent ranking by Tukey's post hoc analysis for −OM and +OM individually. The Kruskal-Wallis test was used to detect the effect of temperature on nonparametric data. When significant differences were found in this test, the nonparametric multiple comparison Dunn test was applied to identify treatment differences (Dunn 1964). The combined effect of temperature and organic enrichment was tested by two-way factorial ANOVA for the bioirrigation rates, TCO_2 production, SOU, AVS, and CRS production and POC consumption. The temperature dependence of the same parameters was compared in −OM and +OM treatments by analysis of covariance, ANCOVA (Zar 1984). All data were reported as mean ± standard error (SE) and statistical tests were conducted with a significance level of $\alpha = 0.05$.

Results

Visual observations

Immediately after homogenization both −OM and +OM sediments were blackish gray. However, the cores quickly developed a red-brown surface layer, indicative of oxidized Fe. Furthermore, when *N. diversicolor* was observed near the core perimeter, burrow linings were easily distinguished by a similar ~1–3 mm thick red-brown oxidized sediment layer (Appendix A: Fig. A1). Based on visual observations, −OM and +OM cores developed differently. With the exception of oxidized surfaces, −OM cores kept their original blackish-gray color throughout the experiment, while +OM cores gradually blackened with time and were finally pitch black just beneath the oxidized surface layer. Furthermore, gas formation (probably CH_4) was observed in deep sediment in +OM cores (deeper than 8–10 cm), resulting in an accumulation of gas bubbles around the core perimeter (Appendix A: Fig. A1). This accumulation was more evident in the 26°C +OM cores.

Bioirrigation rates and recovery of N. diversicolor

There were no significant effects of temperature or of organic enrichment on bioirrigation rates. By the end of the incubations, Br^- decreased in all the cores from ~8 mmol/L at 0.5 cm depth to <2 mmol/L at 8–9 cm depth (Fig. 1), and depth-integrated Br^- inventories were markedly higher than predicted from passive diffusion (e.g., Valdemarsen et al. 2010). Br^- inventories showed that bioirrigation rates were 19 ± 4, 21 ± 2, and 24 ± 7 $L \cdot m^{-2} \cdot d^{-1}$ in −OM cores at 16°, 22°, and 26°C, respectively, and 13 ± 2, 18 ± 2, and 22 ± 4 $L \cdot m^{-2} \cdot d^{-1}$ in +OM cores at 16°, 22°, and 26°C, respectively.

Not all added *N. diversicolor* were recovered at the end of the experiment. On average, 2.3, 1.7, and 1.7 *N. diversicolor* were recovered from 16°, 22°, and 26°C −OM cores, respectively, and 1.3, 2, and 3 *N. diversicolor* were recovered from 16°, 22°, and 26°C +OM cores, respectively. The remaining *N. diversicolor* were presumed to have died. The potential OM enrichment resulting from dead *N. diversicolor* was assumed insignificant compared to total C mineralization in all treatments.

POC

Particulate organic carbon (POC) in the initial cores did not change with depth and was 0.60 ± 0.04 and 0.71 ± 0.02 $mmol/cm^3$ in −OM and +OM cores, respectively (Table 1), meaning that both types of sediment were well mixed. The +OM sediment showed a significantly higher POC content (~0.1 $mmol/cm^3$) than in −OM cores. In −OM cores there were no significant differences between initial and final POC. In the +OM cores, however, final POC was lower in the top 8 cm (significantly so for cores at 16° and 22°C), corresponding to 93%, 95%, and 49% mineralization of the added POC at 16°, 22°, and 26°C, respectively (Table 1). Below 8 cm depth, POC depletion was less pronounced and corresponded to 23%, 77%, and 54% mineralization of the added POC at 16°, 22°, and 26°C, respectively.

SOU and TCO_2 fluxes

The dynamics of TCO_2 fluxes and SOU were similar in all the temperature treatments and are shown for the 16°C treatment (Appendix B: Fig. B1). At this temperature, the SOU in −OM cores ranged between 18 and 45 $mmol \cdot m^{-2} \cdot d^{-1}$ and showed no significant change with time. In contrast, SOU in +OM cores was higher initially (144 ± 19 $mmol \cdot m^{-2} \cdot d^{-1}$) and decreased gradually to 82 ± 3 $mmol \cdot m^{-2} \cdot d^{-1}$ toward the end (Appendix B: Fig. B1). Similar trends were observed for SOU at higher temperatures. SOU in −OM cores varied little (27–58 and 34–80 $mmol \cdot m^{-2} \cdot d^{-1}$ at 22° and 26°C, respectively), whereas SOU in +OM cores was higher and showed a decreasing trend with time (SOU in +OM cores ranged from 101 to 204 and 110 to 157 $mmol \cdot m^{-2} \cdot d^{-1}$ at 22° and 26°C, respectively). The dynamics of TCO_2 fluxes were markedly different from those of SOU (Appendix B: Fig. B1). At 16°C, TCO_2 fluxes in −OM cores were more variable (10–100 $mmol \cdot m^{-2} \cdot d^{-1}$) than the SOU fluxes. Furthermore, TCO_2 fluxes in +OM cores were characterized by an initial increase, from 69 ± 44 to 624 ± 44 $mmol \cdot m^{-2} \cdot d^{-1}$ from day 4 to 11, and a subsequent gradual decrease to 137 ± 14 $mmol \cdot m^{-2} \cdot d^{-1}$ on day 34. Similar patterns were found for TCO_2 fluxes at higher temperatures. In −OM cores, TCO_2 fluxes varied from 46 to 217 and from 80 to 255 $mmol \cdot m^{-2} \cdot d^{-1}$ at 22° and 26°C, respectively. TCO_2 fluxes in +OM cores were always stimulated compared to −OM

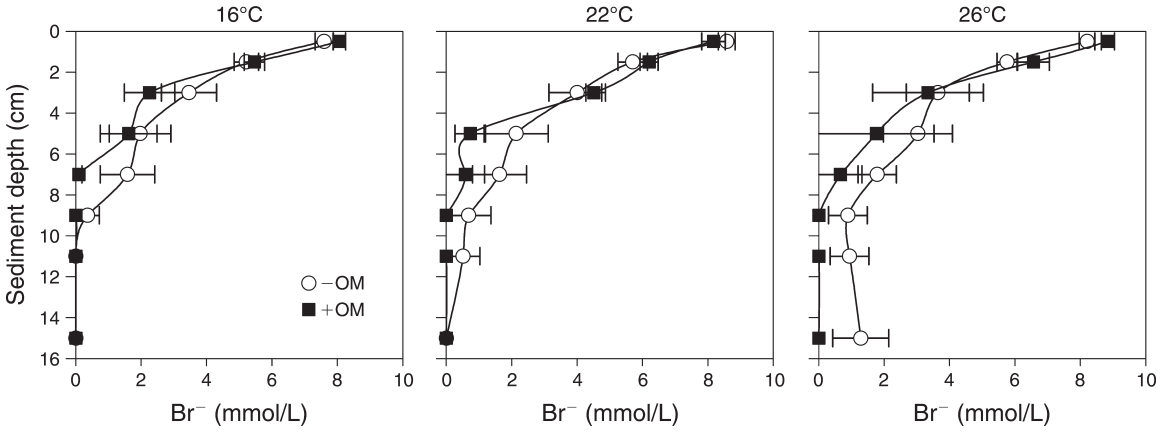

FIG. 1. Bromine (Br^-) concentrations by depth in pore water of final control sediment (−OM) and organic-enriched sediment (+OM) cores collected from Odense Fjord, Denmark, for the different temperature treatments (mean ± SE, $n = 6$). The 16°C treatment corresponds to the monthly average sea surface temperature (SST) in Danish coastal habitats; the 22° and 26°C treatments were chosen to reflect scenarios ~60 and 100 years in the future, respectively, based on the 1°C SST temperature rise observed during the last decades and future expected increases (~1°C per decade).

cores (range of 246–492 and 595–894 mmol·m^{-2}·d^{-1} at 22° and 26°C) and showed a strong temporal variation similar to that at 16°C.

The average rates of SOU and TCO_2 fluxes were compared between treatments. Average SOU in −OM cores were 35 ± 4, 48 ± 7, and 55 ± 12 mmol·m^{-2}·d^{-1} at 16°, 22°, and 26°C, respectively, which was consistently lower than in +OM cores (98 ± 8, 125 ± 11, and 157 ± 36 mmol·m^{-2}·d^{-1} at 16°, 22°, and 26°C, respectively; Fig. 2). There were no significant differences between average SOU values at the different temperatures in −OM or +OM. The two-way ANOVA pointed to no significant differences in the interaction between temperature and OM enrichment, indicating an absence of synergistic and antagonistic effects between both factors. Furthermore, the ANCOVA showed that slopes of SOU vs. temperature were not significantly different in −OM and +OM cores (Fig. 2).

Average TCO_2 fluxes in −OM cores were 85 ± 7, 138 ± 15, and 257 ± 24 mmol·m^{-2}·d^{-1} at 16°, 22°, and 26°C, respectively (Fig. 2). In the +OM cores average TCO_2 fluxes were much higher (355 ± 21, 486 ± 43 and 775 ± 43 mmol·m^{-2}·d^{-1} for 16°, 22°, and 26°C, respectively). Temperature had a strong effect on TCO_2 efflux, since rates at 26°C were significantly stimulated more than twofold for both −OM and +OM cores when compared to TCO_2 efflux at 16°C. This was confirmed by the ANCOVA, which showed that the slopes of the regressions of TCO_2 efflux vs. temperature were significantly different in −OM and +OM cores. Furthermore, the two-way ANOVA showed significant interaction between temperature and OM enrichment (Fig. 2).

Total C mineralization was estimated as time-integrated TCO_2 efflux over the duration of the experiments, as in Valdemarsen et al. (2009). Carbon mineralization was stimulated by temperature in −OM cores: 3.3 ± 0.1, 4.4 ± 0.2, and 6.7 ± 0.3 mol/m^2 at 16°, 22°, and 26°C,

TABLE 1. POC (particulate organic carbon) concentration (mean ± SE) for initial ($n = 3$) and final ($n = 6$) −OM and +OM cores, respectively.

OM enrichment and depth (cm)	Initial concentration (mmol/cm^3)	Final concentration (mmol/cm^3), by temperature		
		16°C	22°C	26°C
−OM				
0–8	0.59 ± 0.05	0.60 ± 0.03	0.55 ± 0.01	0.59 ± 0.01
8–16	0.62 ± 0.04	0.59 ± 0.03	0.59 ± 0.01	0.59 ± 0.02
+OM				
0–8	0.71 ± 0.02	0.60 ± 0.02*	0.60 ± 0.02*	0.65 ± 0.05
8–16	0.72 ± 0.03	0.70 ± 0.02	0.64 ± 0.01*	0.67 ± 0.03*

Notes: POC concentration in final cores is presented for 0–8 cm depth and 8–16 cm depth, to reflect the changes observed in irrigated (0–8 cm) and nonirrigated (8–16 cm) sediment. The 16°C treatment corresponds to the monthly average sea surface temperature (SST) in Danish coastal habitats; the 22° and 26°C treatments were chosen to reflect scenarios ~60 and 100 years in the future, respectively, based on the 1°C SST temperature rise observed during the last decades and future expected increases (~1°C per decade). The sediment in the cores was collected in Fænø Sund, Denmark. The final cores were maintained at 16°, 22°, or 26°C in separate tanks containing filtered seawater from Fænø Sund.

* Differences between final and initial values significant at $P < 0.05$.

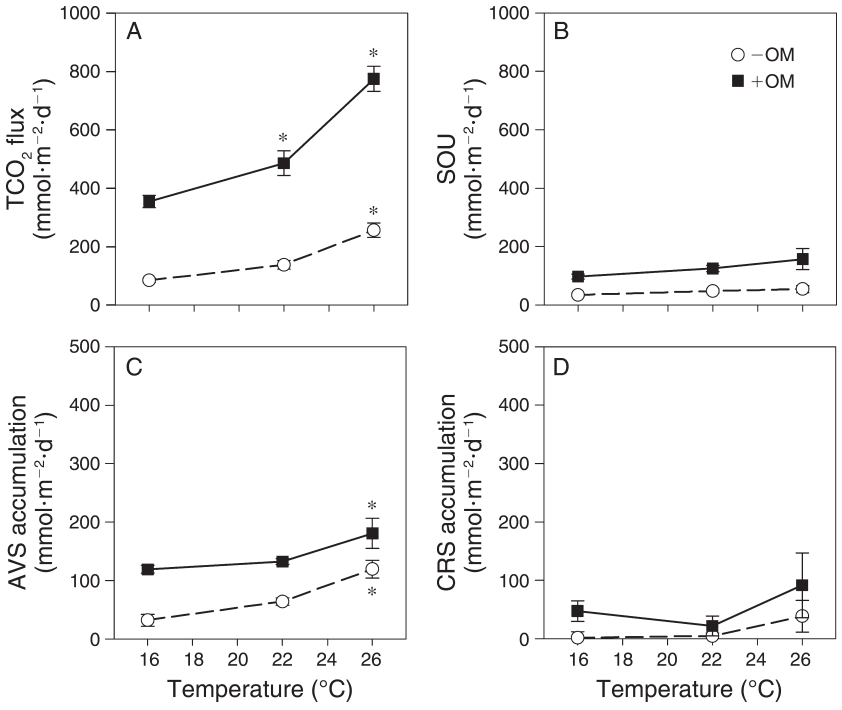

FIG. 2. Rates of (A) total CO_2 (TCO_2) fluxes and (B) sediment oxygen uptake (SOU), (C) acid-volatile sulfides (AVS), and (D) chromium-reducible sulfides (CRS) accumulation in response to temperature (mean ± SE, $n = 6$) in control sediment (−OM) and organic-enriched sediment (+OM). Rates were calculated as average exchange between sediment and water (TCO_2 and SOU) or depth-integrated accumulation (AVS and CRS) normalized to the duration of the different temperature treatments.

* Significant differences (ANOVA, $P < 0.05$) between rates at 16°C and rates at 22° or 26°C for –OM and +OM cores, respectively.

respectively. The same increasing tendency was observed in +OM cores, where C mineralization was 14 ± 0.3, 15 ± 0.6, and 19 ± 0.6 mol/m^2. Thus based on the difference between +OM and −OM cores, it appeared that 81%, 91%, and 113% of added POC was mineralized and released as TCO_2 at 16°, 22°, and 26°C, respectively.

Pore water solutes

Sulfate was initially constant with depth in both −OM and +OM cores (49 ± 1.7 and 52 ± 1.5 mmol/L, respectively), indicating that initial sulfate addition was similar in both sediments. In final cores, sulfate levels were lower due to microbial sulfate reduction. In final −OM cores, sulfate was depleted to an average of 27 ± 2.6, 24 ± 2.0, and 20 ± 0.8 mmol/L, for 16°, 22°, and 26°C, respectively, and showed a constant distribution with depth. In final +OM cores, sulfate in the upper 6 cm was on average 5.5 ± 2.6, 6.4 ± 2.8, and 4.8 ± 2.7 mmol/L, for 16°, 22°, and 26°C, respectively, and fell to below the detection limit (<0.2 mmol/L) below 6–8 cm depth in all three temperature treatments (Fig. 3). Despite the high sulfate reduction rates, TH_2S in pore water was always close to the detection limit, generally <5 μmol/L, in both −OM and +OM cores.

Pore water TCO_2 was initially constant with depth in −OM and +OM sediments (11 ± 0.7 and 11 ± 0.3 mmol/L, respectively). In final cores, TCO_2 had accumulated to an average of 14 ± 3.5, 17 ± 4.1, and 15 ± 3.3 mmol/L in 16°, 22°, and 26°C −OM cores, respectively, and to 35 ± 7.9, 28 ± 6.3, and 22 ± 4.4 mmol/L in 16°, 22°, and 26°C +OM cores, respectively (Fig. 3). The distribution of TCO_2 in final cores was characterized by a gradual increase from the sediment surface to 6–8 cm depth and a constant distribution below. Below 6–8 cm depth, TCO_2 reached 26–32 mmol/L in −OM cores and 35–60 mmol/L in +OM cores (Fig. 3).

Fe^{2+} in pore water at the beginning of the experiment was homogeneously distributed with depth in −OM and +OM cores (0.06 ± 0.02 and 0.05 ± 0.01 mmol/L, respectively). The distribution of Fe^{2+} in pore water was similar in all treatments with the exception of +OM cores at 26°C, where Fe^{2+} was uniformly distributed (0.03 ± 0.01 mmol/L). Fe^{2+} distribution in all other treatments was characterized by a subsurface peak located at 0–2 cm depth and a uniform distribution below. While there was some variation in the magnitude of the subsurface peak, the Fe^{2+} concentration in deep sediment (below 2 cm depth) was similar in all treatments (0–0.2 mmol/L). In −OM cores the subsurface peak was 0.62, 0.56, and 0.27 mmol/L for 16°, 22°, and 26°C, respectively, and in +OM cores the subsurface

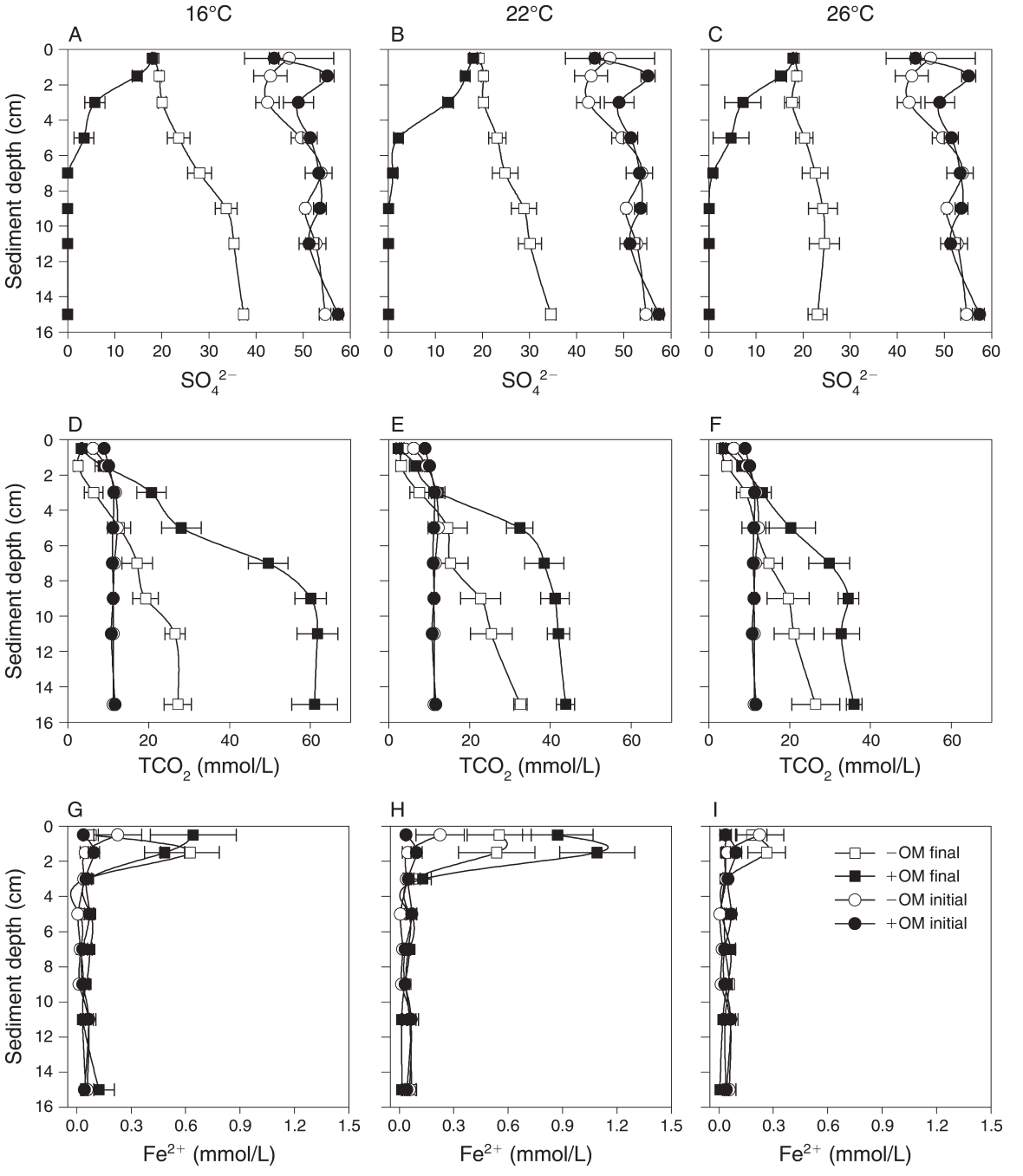

FIG. 3. Concentration (mean ± SE) of (A–C) SO_4^{2-}, (D–F) TCO_2, and (G–I) Fe^{2+} in pore water of initial control sediment (−OM) and organic-enriched sediment (+OM) cores ($n = 3$) and final −OM and +OM cores ($n = 6$).

peak was 0.64 and 1.10 mmol/L at 16° and 22°C, respectively (Fig. 3).

Fe-sulfide accumulation

CRS was initially the dominant form of reduced sulfur, with on average 30 ± 0.4 and 27 ± 0.4 μmol/cm^3 in −OM and +OM sediment, respectively. In final −OM cores, CRS had only slightly accumulated to an average of 29 ± 0.8, 31 ± 0.5, and 35 ± 0.7 μmol/cm^3 at 16°, 22°, and 26°C, respectively. Greater CRS accumulation was observed in +OM cores, where final CRS levels were 39 ± 1.2, 32 ± 0.5, and 42 ± 1.7 μmol/cm^3 at 16°, 22°, and 26°C, respectively (Fig. 4). When integrated to 16 cm depth, the accumulation of CRS varied between 0.05 and 1.0 and between 0.7 and 2.3 mol/m^2 in −OM and +OM cores, respectively (Table 2). AVS, on the other

hand, accumulated to a much greater extent. In −OM cores, average AVS increased from 9 ± 0.3 to 16 ± 0.4, 21 ± 0.6, and 27 ± 0.8 μmol/cm^3 at 16°, 22°, and 26°C, respectively. In +OM cores, AVS accumulation was even greater (from an initial 11 ± 0.3 μmol/cm^3 to a final 43 ± 1.5, 38 ± 0.9, and 41 ± 1.1 μmol/cm^3 at 16°, 22°, and 26°C, respectively; Fig. 4). AVS accumulation in +OM cores was most intense in the upper 0–6 or 0–8 cm (reaching 120 μmol/cm^3 at 16°C), but was also significant below 6 cm depth (>65 μmol/cm^3). When integrated to 16 cm depth, AVS accumulation in −OM cores was 1.2–3.1 mol/m^2, which was low compared to the values obtained for the +OM cores (4.2–4.6 mol/m^2; Table 2). Hence, AVS was quantitatively the most important form of Fe-sulfide in both sediment types (contributing 76–96% and 66–86% to TRIS accumulation in −OM and +OM cores, respectively).

The average rates of AVS and CRS accumulation were obtained by normalizing depth-integrated accumulation (Table 2) for the duration of the incubations. There were no significant differences between CRS accumulation rates with temperature in the −OM cores (2 ± 10, 4 ± 5, and 39 ± 27 mmol·m^{-2}·d^{-1} at 16°, 22°, and 26°C, respectively) or in +OM cores (47 ± 18, 22 ± 17, and 91 ± 56 mmol·m^{-2}·d^{-1} at 16°, 22°, and 26°C, respectively; Fig. 2). The ANCOVA showed that the slopes of the regressions of CRS accumulation rates with temperature were not significantly different between −OM and +OM cores. The two-way ANOVA showed significant interaction between temperature and OM enrichment. Similarly, AVS accumulation rates at 16° or 22°C (32 ± 10 and 64 ± 7 mmol·m^{-2}·d^{-1} in −OM cores and 119 ± 7 and 132 ± 5 mmol·m^{-2}·d^{-1} in +OM cores) were not significantly different for −OM or for +OM cores, but showed an increasing trend with temperature (Fig. 2). At 26°C, however, the rates of AVS accumulation (119 ± 15 and 181 ± 26 mmol·m^{-2}·d^{-1} for −OM and +OM cores, respectively) showed significant stimulation for both −OM and +OM cores compared with the rates at 16°C (Fig. 2). As for CRS accumulation rates, the ANCOVA showed that the slopes of AVS accumulation vs. temperature were not significant in −OM or +OM cores. Additionally, two-way ANOVA showed significant interaction of temperature and OM enrichment.

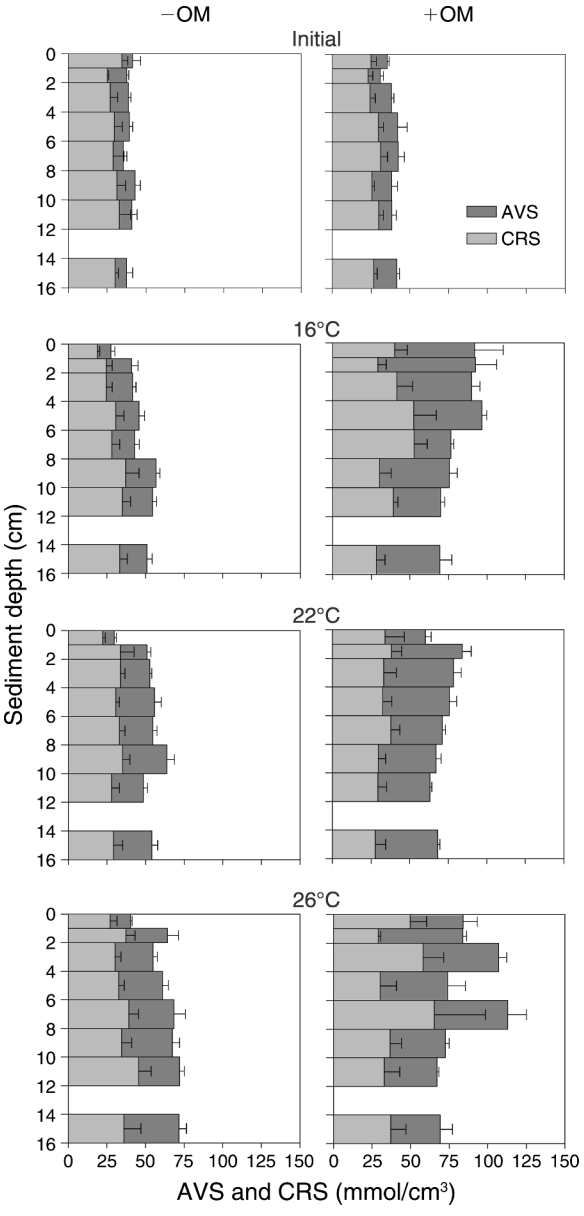

FIG. 4. Pools (mean + SE) of chromium-reducible sulfur (CRS, light-gray bars) and acid-volatile sulfides (AVS, dark-gray bars) with depth for initial cores ($n = 3$) and final cores ($n = 6$) in the different temperature treatments.

DISCUSSION

C and S cycling in organic-enriched sediment

C consumption in +OM cores was 3–6 fold higher than in −OM cores, indicating that added OM had a strong stimulatory effect on C mineralization. At the end of the experiment, POC concentrations in +OM cores were close to POC in −OM cores. Thus, the sediment mineralization capacity was remarkable considering that the OM added was equivalent to the annual OM deposition close to fish farms or mussel farms (Morrisey et al. 2000, Callier et al. 2006, Holmer et al. 2007, Sanz-Lazaro et al. 2011). The TCO_2 fluxes followed a trend found in other OM enrichment studies, where yeast and macroalgal detritus was used as the source of OM enrichment (Hansen and Kristensen 1998, Banta et al. 1999), except that the maximums in this study were four times higher than in these studies. This was probably due to the high lability of fish feed (Kristensen and Holmer 2001, Valdemarsen et al. 2009). TCO_2 fluxes were similar to those measured in a mesocosm experiment where fish feed was added to the sediment surface (Valdemarsen et al. 2010) and comparable to fluxes measured beneath temperate and tropical fish farms (Holmer and Kristensen 1992, Holmer et al. 2002, Holmer et al. 2003).

TABLE 2. Initial ($n = 3$) depth-integrated (0–16 cm) pools of CRS and AVS and total depth-integrated sulfide accumulation (ΔS) during the whole experiment based on the difference between final and initial cores.

OM enrichment and pool	Initial pool (mol/m^2)	ΔS (mol/m^2), by temperature		
		16°C	22°C	26°C
−OM				
CRS	4.84 ± 0.68	0.05 ± 0.42	0.13 ± 0.17	1 ± 0.7
AVS	1.45 ± 0.14	1.23 ± 0.39	2.05 ± 0.2*	3.1 ± 0.39*
+OM				
CRS	4.41 ± 0.18	1.85 ± 0.68	0.69 ± 0.54	2.29 ± 1.39
AVS	1.9 ± 0.15	4.65 ± 0.26*	4.24 ± 0.15*	4.52 ± 0.65*

* Differences between final and initial sulfide content significant at $P < 0.05$.

TCO_2 efflux was generally higher than SOU, and ratios between TCO_2 efflux and SOU were always >1, and increased with temperature (2.6, 3.1, and 5.6 in −OM cores and 3.7, 4.0, and 5.3 in +OM cores at 16°, 22°, and 26°C, respectively). The low ratios (1–2) between TCO_2 efflux and SOU are similar to those observed in other experiments (e.g., Heilskov et al. 2006, Valdemarsen et al. 2009), and higher ratios (>2) are typically associated with Fe-rich sediments (Valdemarsen et al. 2009). Ratios between TCO_2 fluxes and SOU close to 1 indicate a balanced biogeochemical cycling, where electron acceptors produced during anaerobic degradation are reoxidized at oxidized surfaces by consumption of O_2. High ratios (>1), on the other hand, indicate that a proportion of reduced electron acceptors (e.g., the sulfide produced during sulfate reduction) is buried as Fe-sulfides (i.e., AVS and CRS) (Canfield 1989, 1994). The high accumulation of reduced Fe-S compounds (especially AVS) and the stoichiometric ratio between TCO_2 efflux and SOU >> 2 confirmed this trend. Observations beneath fish farms also suggest that AVS is the main form of sulfide accumulation in organically enriched sediments (Holmer and Kristensen 1992, Holmer and Frederiksen 2007).

In this experiment the electron budget seemed to be in balance, when all important processes, TCO_2 efflux, SOU, and the TRIS accumulation, were considered (Fig. 2). Thus, minimum sulfate reductions rates could be estimated by adding TRIS accumulation to SOU, after taking into account the 2:1 stoichiometric ratio between O_2 and sulfide during sulfide oxidation (Jorgensen 1982, Thamdrup et al. 1994). It was assumed that all SOU was due to TRIS oxidizing processes, and macrofauna respiration was ignored since it typically only constitutes a minor fraction of SOU (Banta et al. 1999, Heilskov et al. 2006). Minimum sulfate reduction rates were 16, 45, and 131 $mmol \cdot m^{-2} \cdot d^{-1}$ for −OM cores, and 118, 91, and 193 $mmol \cdot m^{-2} \cdot d^{-1}$ for +OM cores at 16°, 22°, and 26°C, respectively (Fig. 2). Thus, OM enrichment stimulated sulfate reduction rates 7.2, 2.0, and 1.5 times at 16°, 22°, and 26°C, respectively, which is consistent with comparisons between fish farm sediments and nonimpacted reference sites (Holmer and Kristensen 1996, Holmer et al. 2003) and confirms the stimulatory effect of organic enrichment on sulfate reduction.

By comparing estimated sulfate reduction with time-integrated TCO_2 efflux, the relative importance of sulfate reduction for total sediment metabolism was determined. Assuming a 2:1 stoichiometric ratio between TCO_2 and sulfide production (Jorgensen 1982, Thamdrup et al. 1994), sulfate reduction in −OM cores accounted for 22%, 65%, and 105% of total benthic metabolism at 16°, 22°, and 26°C, respectively. In +OM cores the importance of sulfate reduction was 71%, 35%, and 50% for 16°, 22°, and 26°C, respectively. In −OM cores, the low degree of sulfate reduction observed at 16°C suggested that most of the organic matter was mineralized by degradation pathways other than sulfate reduction, such as aerobic respiration, denitrification, and metaloxide reduction, which are important metabolic pathways in nonenriched sediments (Canfield et al. 1993). At higher temperatures, the importance of sulfate reduction in −OM cores increased to 65–100%, which suggests that temperature has an overall stimulatory effect on sulfate reduction (Finke and Jorgensen 2008, Robador et al. 2009).

In +OM cores, benthic metabolism, evidenced from CO_2 effluxes, was also stimulated by labile organic matter, which suggested very high sulfate reduction rates comparable to those found in organic-enriched sediments (Holmer and Kristensen 1994, Holmer et al. 2002, Valdemarsen et al. 2010). TRIS accumulation, however, appeared to stagnate in +OM cores when temperature increased from 22° to 26°C, which may be due to hampered TRIS precipitation at high sulfate reduction rates, as suggested in previous enrichment experiments (Valdemarsen et al. 2010).

The impact of bioirrigation on C and S cycling

Irrigation rates were low compared with ventilation estimates of nonsuspension feeding *N. diversicolor* (580–720 $L \cdot m^{-2} \cdot d^{-1}$, 600 individuals/$m^2$) (Kristensen 2001), but are in the same range as estimates (5–13 $L \cdot m^{-2} \cdot d^{-1}$) of mixed macrofauna community irrigation (Valdemarsen et al. 2010). Thus *N. diversicolor* was a good proxy for simulating the bioirrigation activity of a natural macrofauna community. Neither bioirrigation rates nor the depths reached by *N. diversicolor* were influenced by temperature or organic enrichment, and all cores were bioirrigated to 6–8 cm depth (as indicated

by the depth of bromide and sulfate penetration; Figs. 1 and 3). This contradicts other studies where organic enrichment and temperature affected bioirrigation rates and/or depth (Kristensen and Kostka 2005, Heilskov et al. 2006, Przeslawski et al. 2009), which can be due to the fact that more sensitive species were used in previous studies. The lack of effect of OM enrichment and temperature on bioirrigation was not due to experimental artifacts, since depletion of Br^- in overlying water was minor and incubation times were long enough to account for differences in burrow flushing frequency (Quintana et al. 2011).

Thus bioirrigation by *N. diversicolor* facilitated a steady supply of electron acceptors (e.g., sulfate) to the upper 6–8 cm of sediment, which allowed for continuously high sulfate reduction rates. In the deeper nonirrigated sediment, sulfate reduction was hampered due to sulfate depletion. The effect of *N. diversicolor* was particularly evident from POC depletion in +OM cores, which was much more intense in the top 8 cm compared with deeper sediment, where microbial degradation was probably hampered due to sulfate depletion (Table 1, Fig. 3). Furthermore, the zone of POC depletion corresponded to the zone with highest TRIS accumulation, indicating that increased O_2 supply due to *N. diversicolor* ventilation was not enough to reoxidize all the sulfide produced. However, some sulfide reoxidation might have occurred by this process. The main impact of *N. diversicolor* in this study was therefore to maintain high levels of electron acceptors, which facilitated continuously high rates of C-mineralization by sulfate reduction.

Dissolved sulfide in pore water was always close to the detection limit (generally <5 μmol/L) in all the treatments, which was due to high Fe content and efficient sulfide buffering in the sediment (Valdemarsen et al. 2009, 2010). Such low levels of dissolved sulfide are unlikely to have a toxic effect on *N. diversicolor* (Miron and Kristensen 1993), and might explain why *N. diversicolor* did not show a stress response (i.e., increased bioirrigation) to high sulfate reduction and temperature in this study.

Temperature dependence of fluxes and S precipitation

The low-temperature treatment (16°C) corresponds to the monthly average SST in Danish coastal habitats (Holmer and Kristensen 1996). The 22° and 26°C temperature treatments were chosen to reflect temperature scenarios ~60 and 100 years into the future, respectively, based on the 1°C SST temperature rise observed during the last decades (Mackenzie and Schiedek 2007, Belkin 2009) and future expected increases (Doscher and Meier 2004; ~1°C per decade).

In this experiment, increased temperature enhanced sediment metabolism, as reflected by significantly stimulated TCO_2 efflux in both −OM and +OM cores. Temperature had a much lower impact on SOU than on TCO_2 efflux, possibly due to three reasons: (1) the bioirrigation of *N. diversicolor* did not depend on temperature, so there was no increase in SOU due to faunal activity; (2) the reoxidation of sulfides and hence O_2 consumption was limited due to the high Fe content of the sediment; and (3) O_2 diffusion, and thus SOU, was restricted by the experimental setup.

Temperature modulates the microbial metabolism rate, and consequently, sediment respiration (Westrich and Berner 1988) . Thus, sulfate reduction rates are also temperature dependent in surface sediments (Bottcher et al. 2004, Al-Raei et al. 2009). Sulfate-reducing bacteria usually have a respiration optimum 10–20°C above their natural temperature regime (Isaksen and Jorgensen 1996, Knoblauch and Jorgensen 1999), so temperature is often a potentially limiting factor for sulfate-reducing bacteria (Pomeroy and Wiebe 2001).

In this experiment, the increase in temperature facilitated a shift toward increased anaerobic metabolism in both −OM and +OM cores (Jorgensen and Sorensen 1985), and benthic metabolism followed a nonlinear, almost exponential, stimulation as temperature increased. This trend can be expected for temperate sediments in this temperature range, since sulfate reduction rates in temperate sediments show an exponential increase up to a temperature threshold of ~35°C (Robador et al. 2009). In −OM cores the estimated sulfate reduction rates followed a trend similar to other studies from temperate regions (Arnosti et al. 1998, Robador et al. 2009), and a temperature increase of 10°C above the natural average summer SST stimulated sulphate reduction by a factor of 2 for both −OM and +OM cores, which agrees with Westrich and Berner (1988).

Implications

Coastal water bodies support critical processes that may be impacted by climate change (IPCC 2001), many of which are relevant at a global scale. Furthermore, coastal areas are increasingly affected by anthropogenic activities, such as sewage discharges and fish-farming effluents, which lead to organically enriched sediments (Islam and Tanaka 2004). The present study shows that OM enrichment and temperature enhance benthic metabolism. Sulfate reduction rates depend on temperature but also on the availability of reactive OM (Rusch et al. 1998, Bottcher et al. 2004, Al-Raei et al. 2009). When both temperature and labile OM are increased above the natural regime, sulfate reduction rates increase substantially (Koch et al. 2007). In this experiment, the combination of OM enrichment and increased temperature resulted in higher rates of sediment metabolism than either treatment alone (Fig. 2). In areas affected by OM enrichment (e.g., sediments impacted by fish farming), sediment metabolism can be expected to be limited by temperature since OM is, to some extent, not limiting, compared with nonenriched areas. In a global-warming scenario it can therefore be expected that sediment respiration will increase dramatically if the temperature increase is substantial.

Increased rates of sediment metabolism under higher temperatures and with OM enrichment may be ecologically beneficial. Areas affected by sources of OM enrichment, such as fish farming, have OM sedimentation rates that are normally above the threshold of the metabolic capacity of the sediment at current temperatures, and so the OM tends to accumulate in the seabed (Valdemarsen et al. 2009). Thus the increase of sediment metabolism as a result of temperature observed in this study can be interpreted as an increase in the metabolic capacity of the sediment. It must be stated, however, that an increase in sediment metabolism would also lead to higher buildup of toxic metabolic by-products, such as sulfides, and contribute to sediment anoxia. Also, the release of nutrients into the water column would be enhanced, and this may stimulate phytoplankton blooms (Bertuzzi et al. 1997).

In this experiment, Fe-rich sediment was used and sulfide produced by sulfate reduction precipitated with Fe and accumulated in the sediment, which resulted in a low concentration of dissolved sulfides. Due to the high sediment Fe content, dissolved sulfide never reached toxic levels and *N. diversicolor* survived despite high sulfate reduction rates. The high accumulation of TRIS, coupled to *N. diversicolor* irrigation, represents an oxygen debt. The reoxidation of the sulfides bound to Fe are needed to renew Fe buffering capacity of the sediment. Therefore, the combined effect of increasing sediment metabolism due to both OM enrichment and temperature can only be maintained as long as the Fe buffering capacity of sediments is not exceeded.

Any extrapolation of these results must be made carefully. First, mesocosm studies are always simplifications of natural ecosystems, although the dynamics of sediment metabolism in this study are comparable with data from field investigations. Second, we used a model species with specific bioturbating traits that could differ from those of other infaunal engineering species, although in this experiment, *N. diversicolor* was seen to bioirrigate with rates similar to those measured in other mesocosm experiments using natural macrofaunal assemblages (Valdemarsen et al. 2010). Third, OM enrichment was carried out homogeneously in the sediment, while in benthic ecosystems affected by OM enrichment, OM largely accumulates at the sediment surface and the concentration of OM decreases with depth in the sediment. Fourth, the Fe concentration in coastal sediments varies greatly, and so does the sediment buffering capacity toward sulfides. Finally, the OM used to simulate organic enrichment was highly labile (fish feed), and different results might have been obtained if more recalcitrant/refractory OM had been used.

Despite the above considerations, small-scale experiments using "model organisms" in mesocosms can be considered a useful approach for modeling apparently intractable global problems, such as ecosystem responses to climate change (Benton et al. 2007). Therefore, even though we acknowledge the limitations of a mesocosm to simulate real scenarios, the similarities observed between the results and the data from other experiments suggest that the present study could well be taken as a reflection of future scenarios.

Conclusions

Temperature increase due to climate warming would increase sediment metabolism. In this experiment, the increase in sediment metabolism was greater when temperature was increased and labile OM was added than with either treatment separately. Such an increase in sediment metabolism occurs through the enhancement of anaerobic metabolic pathways, mainly sulfate reduction. However, as long as the sediment buffering capacity toward sulfides is not surpassed, an increase in the temperature could limit OM accumulation in organic-enriched sediments.

Acknowledgments

The authors are grateful to Birthe Christensen, Katrine Clement Kirkegaard, and Kim Wendelboe for their help in the laboratory. We also appreciate the comments of two anonymous reviewers, which have improved the manuscript. M. Holmer was supported by FNU 09-071369, C. Sanz-Lázaro was supported by a predoctoral grant from the Ministerio de Educación y Ciencia of Spain, and T. Valdemarsen was supported by EU-project Thresholds (Contract No. 003933).

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APPENDIX A

A figure showing sediment cores with −OM and +OM treatments at the end of the experiment (day 25) (*Ecological Archives* A021-118-A1).

APPENDIX B

A figure showing fluxes of total CO_2 (TCO_2) and sediment oxygen uptake (SOU) in control sediment and organic-enriched sediment during the experiment at 16°C (*Ecological Archives* A021-118-A2).

ERRATA

Sanz-Lázaro et al. have discovered errors in two of the figures included in their article ("Effect of temperature on biogeochemistry of marine organic-enriched systems: implications in a global warming scenario"), published in the October 2011 issue (*Ecological Applications* 21:2664–2677). The top row of panels in Fig. 3 lacked units for SO_4^{2-} in the published version; the units should have been specified as mmol/L for all three temperatures. Also, the units for the horizontal axis in Fig. 4 were incorrectly given as mmol/cm^3; the correct units for AVS and CRS are μmol/cm^3. These errors were apparently introduced by our Graphics Department during preparation of figures for publication. We apologize to the authors and to our readers.

Brown et al. have discovered errors in Table 2 of their paper ("How long can fisheries management delay action in response to ecosystem and climate change?") in the January 2012 issue (*Ecological Applications* 22:298–310). Two entries in Table 2 may be incorrectly interpreted. The cause under the third row ("North Pacific Minke whales") should read "scientific uncertainty led to a long process to develop a management scheme, during which catch limits for commercial whaling were zero".

In addition, the cause in the fourth row ("Whales") should read "time period required between reviews of management strategy by the International Whaling Commission; this time period was selected using simulations and shown to be adequate".