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Bacterial chemoautotrophic reoxidation in sub-Arctic sediments: a seasonal study in Kobbefjord, Greenland

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ABSTRACT: Anoxic mineralization of organic matter releases dissolved inorganic carbon and produces reduced mineralization products. The reoxidation of these reduced compounds is essential for biogeochemical cycling in sediments and is mainly performed by chemoautotrophic microbes, which synthesize new organic carbon by dark CO_2 fixation. At present however, the biogeochemical importance of chemoautotrophy in high-latitude sediments is largely unknown. Here, we determine the seasonal variation in sedimentary chemoautotrophic production in Kobbefjord (SW Greenland). Intact sediment cores from the fjord were incubated, and dark CO_2 fixation was quantified by combining bacterial phospholipid-derived fatty acid analysis with ^{13}C stable isotope probing (PLFA-SIP). Our results reveal a distinct seasonal cycle in chemoautotrophic activity, which increases after the spring bloom and shows lowest activity in the late winter when the fjord is covered by sea ice. The depth distribution of chemoautotrophic activity also varied seasonally, likely due to seasonal variation in the bioturbation activity of sediment infauna. Although chemoautotrophy rates (0.4 ± 0.2 mmol C m^{-2} d^{-1}) were in the low range for coastal sediments, they are comparable to those from intertidal sandflats and brackish tropical lagoons, and scale with the sulfide production through sulfate reduction in the fjord. Chemoautotrophic production in these fjord sediments thus appears to be mainly driven by sulfide oxidation and can re-fix 4 % of the CO_2 produced by mineralization.

KEY WORDS: Dark carbon fixation · Chemolithoautotrophy · Fatty acids · Stable isotope labeling · PLFA-SIP

INTRODUCTION

Reduced intermediates are formed during anaerobic mineralization of organic matter, and their reoxidation comprises a key process in the biogeochemistry of coastal sediments (Soetaert et al. 1996, Jørgensen & Nelson 2004). Oxygen is typically the terminal oxidant in this process, but intermediate reoxidation steps with nitrate or metal oxides can also be important (Jørgensen & Nelson 2004). Many of the microorganisms involved in these pathways are chemoautotrophs, which fix inorganic carbon using the chemical energy derived from the reoxidation reactions (dark carbon fixation). The oxidation of reduced sulfur compounds (dissolved free sulfide, thiosulfate, elemental sulfur, iron monosulfides and pyrite) forms

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the most important pathway sustaining chemoautotrophy in coastal sediments (Howarth 1984, Jørgensen & Nelson 2004, Boschker et al. 2014, Lipsewers et al. 2017). Although reoxidation is estimated to account for up to 70% of the oxygen consumption in coastal sediments (Soetaert et al. 1996), chemoautotrophy is typically not quantified in biogeochemical studies.

Studies on Arctic climate change foresee a substantial increase in primary productivity and sedimentary mineralization rates in fjords, as a consequence of the decrease in sea-ice cover in coming decades (Rysgaard & Glud 2007). Such increase in sedimentary organic matter turnover will likely affect the pools of reduced compounds in sediments and thus reoxidation processes. However, it is still unknown how chemoautotrophic production will respond to this forcing. A recent biogeochemical study by Sørensen et al. (2015) has described the seasonal carbon cycling in Kobbefjord, a fjord in SW Greenland. Clear seasonal changes were observed in the pelagic productivity in the fjord, but the benthic biogeochemistry did not respond accordingly, showing less variation throughout the year.

The main objective of this research was, for the first time, to investigate the seasonal changes in sedimentary chemoautotrophic reoxidation in a sub-Arctic coastal system. To this end, a seasonal sampling campaign was set up between June 2011 and May 2012 at Kobbefjord in SW Greenland. A combination of biomarker analysis and stable isotope probing (SIP) was used to evaluate the chemoautotrophic activity and its depth distribution in fjord sediments. This approach allowed us to resolve the monthly variations related to bioturbation and the potential biogeochemical role of chemoautotrophy in sub-Arctic sediments.

MATERIALS AND METHODS

Study site and sediment sampling

To examine chemoautotrophy in a high-latitude depositional area, a site in the central area of Kobbefjord was selected (64° 10′ 48″ N, 51° 31′ 27″ W; SW Greenland near the capital city of Nuuk, Fig. 1). Kobbefjord has a complex bathymetry with numerous basins and sills and a maximum water depth of 140 m. The fjord receives freshwater inputs from a few rivers fed by snowmelt and glacier remnants (Sørensen et al. 2015). The sampling site was located in the central basin at a water depth of 110 m, and was sampled on 4 occasions: June 2011 at the beginning of summer, September 2011 during autumn, December 2011 in mid-winter, and in May 2012 (Table 1). During the sampling period, the field site was covered by sea ice from late winter (February 2012) to spring (late April 2012), corresponding to ~65 d of ice coverage.

Sediment cores were retrieved in Plexiglas liners (6 cm outer diameter and 50 cm in length) using a Kajak sampler (KC Denmark). Cores (n = 3) were subsampled in the laboratory with polycarbonate core liners (4 cm outer diameter and 20 cm in length) for chemoautotrophy incubations. A separate set of cores was used to perform parallel measurements of CO_2 and O_2 benthic fluxes, O_2 microsensor depth profiles, and sulfate reduction rates as described in Sørensen et al. (2015).

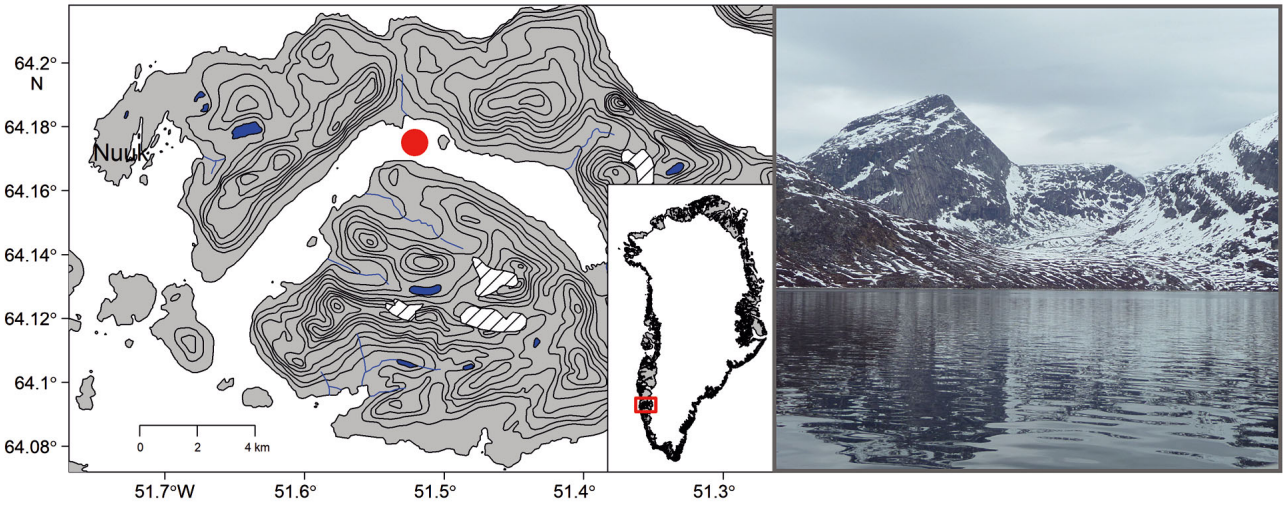

Fig. 1. Location of the study site in Kobbefjord (red circle) near the city of Nuuk, SW Greenland (inset map, red square). Blue areas indicate water, and white dashed areas indicate areas with permanent snow. Photo of Kobbefjord (facing south) taken at the sampling station during the June 2011 campaign

Table 1. Seasonal characteristics and activity measurements for Kobbefjord sediments. Chemoautotrophy rates (integrated over top 8 cm), sulfate reduction rates (SRR), benthic respiratory quotient (RQ), total (TOU) and dissolved oxygen uptake (DOU), and benthos mediated uptake (BMU = TOU − DOU). Mean ± SD. *T*: *in situ* temperature; ϕ: porosity

Date	*T* (°C)	ϕ	Chemoautotrophy (mmol C m^{-2} d^{-1})	SRR[a] (mmol C m^{-2} d^{-1})	RQ[a]	TOU[a] (mmol O_2 m^{-2} d^{-1})	DOU[a] (mmol O_2 m^{-2} d^{-1})	BMU (mmol O_2 m^{-2} d^{-1})
Jun 11	2	0.78 ± 0.06	0.5 ± 0.07	6.0 ± 1.6	0.7	11 ± 1.8	5 ± 3.3	6
Sep 11	3	0.75 ± 0.05	0.6 ± 0.04	12.2 ± 1.3	0.6	12 ± 0.6	6 ± 1.3	6
Dec 11	1	0.79 ± 0.04	0.4 ± 0.2	7.4 ± 1.3[b]	0.6	7 ± 1.7	7 ± 1.2	0
May 12	0	0.79 ± 0.05	0.08 ± 0.05	7.0 ± 1.8	1.3	7 ± 1.3	5 ± 0.9	2

[a]Sørensen et al. (2015); [b]rate was calculated as the average value from November 2011 and January 2012 since the measurement from December 2011 was not available

Stable isotope incubations

Using the line injection method, ^{13}C bicarbonate was added to the pore water of each sediment core through vertically aligned side ports in the core liners (0.5 cm apart; 100 µl of label per hole) up to 10 cm deep. A 20 mM stock solution of labeled $NaHCO_3$ (99% ^{13}C; Cambridge Isotope Laboratories) was prepared in calcium- and magnesium-free artificial seawater to prevent carbonate precipitation. The stock solution was bubbled with N_2 shortly before injections to remove oxygen (thus preventing spurious reoxidation on introduction of the label in anoxic pore water). Labeled cores were incubated for 24 h in June. As a low activity level was found in June, the incubation period was increased to ~48 h in the following 3 campaigns. Cores were incubated in seawater tanks at *in situ* temperatures, in the dark (to exclude photosynthetic carbon fixation), and the overlying water was continuously bubbled with air to maintain oxic conditions above the sediment as described in Vasquez-Cardenas et al. (2015).

At the end of the incubation period, sediment cores were sectioned at 0.5, 1, 2, 4, 6, and 8 cm depth. Sediment layers were collected in centrifuge tubes (50 ml), pore water was obtained by centrifugation (4500 rpm, 3400 × *g* for 5 min), and sediments were lyophilized for further analysis. Porosity was determined from water content and bulk sediment density. Water content was determined by weight loss after 24 h of lyophilization.

Phospholipid-derived fatty acid analysis

To determine the chemoautotrophic activity, we extracted bacterial phospholipid-derived fatty acids (PLFA) from sediment as described in Boschker (2004). Incorporation of ^{13}C into PLFA was analyzed by gas chromatography–isotope ratio mass spectrometry (GC-IRMS, Thermo) on an apolar analytical column (ZB5-MS Phenomenex). Two additional cores without the ^{13}C label were used as controls and were treated in the same manner as described above.

Incorporation rates of ^{13}C into individual PLFA (expressed in µmol PLFA C per g of dry sediment per day) were calculated for each sediment layer as the product of individual bacterial fatty acid concentrations (µmol PLFA C g^{-1}) and the ^{13}C fraction of these PLFA corrected for background values, and divided by the incubation time. Incorporation rates of ^{13}C bicarbonate were summed over all bacterial PLFAs between 12:0 and 20:0 and converted to carbon biomass using a conversion factor of 55 mole biomass C per mole of PLFA C (Boschker et al. 2014). To arrive at volumetric dark CO_2 fixation rates (i.e. µmol biomass C per cm^{-3} of bulk sediment per day), incorporation rates were multiplied with the conversion factor $\rho(1 - \phi)$, where ϕ is porosity and ρ is the solid sediment density; ρ was set equal to 2.60 g cm^{-3} for cohesive sediment. Incorporation rates were corrected for ^{13}C-labeling levels in pore water dissolved inorganic carbon (DIC). Background isotopic values in pore water DIC were analyzed in 2 cores without substrate addition. Pore water was obtained by centrifugation (4500 rpm, 3400 × *g* for 5 min) and ^{13}C DIC was measured by the head space technique with an elemental analyzer-IRMS equipped with a gas injection port C (Boschker et al. 2014). For a detailed description of the PLFA-SIP analysis and calculations refer to Boschker & Middelburg (2002) and Boschker (2004).

RESULTS AND DISCUSSION

Seasonal variations of chemoautotrophy

Our results show minor changes in PLFA patterns between the seasons and sediment depths (data not

shown). On average, highest values of fatty acid biosynthesis were found in 16:1ω7c (34 ± 8%), 18:1ω7c (18 ± 7%), 16:0 (17 ± 3%), 16:1ω5 (7 ± 7%), ai15:0 (4 ± 3%), 18:1ω9c (3 ± 3%), and 14:0 (3 ± 2%) fatty acids throughout the year and sediment depths. Such fatty acid patterns are typically found in chemoautotrophic sulfur-oxidizing and nitrifying bacteria (Lipski et al. 2001, Knief et al. 2003, Inagaki et al. 2004). In contrast, negligible incorporation of ^{13}C bicarbonate (less than 1%), as well as low concentrations (less than 0.1% of the total fatty acid concentrations per sample), were observed in fatty acids associated with microalgae (18:3ω3, Boschker & Middelburg 2002) or eukaryotes (18:2ω6, Glaubitz et al. 2009) indicating no direct or indirect ^{13}C uptake by these organisms during the incubation period. The fatty acid 20:5ω3, which is also used as a biomarker for microalgae, had higher relative concentrations (3 ± 3%) in sediments, but no ^{13}C bicarbonate was incorporated in this fatty acid confirming the absence of light-dependent ^{13}C fixation during the experiment.

The majority of dark carbon fixation measurements in the literature originate from coastal sediments in temperate areas (Enoksson & Samuelsson 1987, Bauer et al. 1988, Lenk et al. 2011, Boschker et al. 2014, Vasquez-Cardenas et al. 2015, Dyksma et al. 2016, Lipsewers et al. 2017) and only 1 study reports rates from tropical brackish lagoons (Santoro et al. 2013). Among these studies, 2 have evaluated seasonal changes in chemoautotrophic activity. One study examined a coastal hydrocarbon seep where chemoautotrophic activity increased in winter (Bauer et al. 1988), whereas the second study quantified chemoautotrophy in a marine lake, where the activity decreased in response to the summer hypoxia (Lipsewers et al. 2017). Our study is therefore the first to investigate the temporal and sediment-depth changes in chemoautotrophic activity in a high-latitude area.

Our seasonal evaluation of the benthic chemoautotrophic activity in Kobbefjord shows steady rates from summer to winter (0.4–0.6 mmol C m^{-2} d^{-1}) with a sharp decrease at the beginning of spring (0.08 mmol C m^{-2} d^{-1}, Table 1). Our results thus indicate a continuous availability of reduced compounds, most probably sulfur compounds (FeS, H_2S, S^0), from summer to winter, which are necessary for chemoautotrophic growth. These compounds are mostly produced through mineralization of organic matter via sulfate reduction (Howarth 1984). The decrease in chemoautotrophy in early spring hence suggests a limited production of sulfide at this time. However, this was not the case since the measured rates of sulfate reduction did not show a strong seasonal pattern (Table 1). Instead, the ratio of the benthic CO_2 production and O_2 consumption, or the benthic respiratory quotient (RQ) increased from 0.6 in autumn to 1.3 in spring (Table 1, Sørensen et al. 2015). This high RQ value in spring indicates an accumulation of reduced compounds in the sediment and therefore a decrease in aerobic reoxidation, which translates into lower chemoautotrophy.

In sediments, the availability of electron acceptors (oxygen and nitrate) and donors (sulfide, metal oxides, and ammonium) throughout the sediment depends on the mechanism of pore water transport (Glud 2008). Sediments in Kobbefjord are cohesive (porosity: 0.78) and consequently the transport of solutes is determined by molecular diffusion. Molecular diffusion may limit the chemoautotrophic activity to the top centimeter of the sediment where electron donors and acceptors overlap (Boschker et al. 2014, Vasquez-Cardenas et al. 2015, Lipsewers et al. 2017). However, bioturbating fauna can enhance the transport of solutes through bio-irrigation by injecting electron acceptors in to deeper sediment layers, while bio-mixing of sediment particles promotes iron cycling (Kristensen & Kostka 2005, van de Velde & Meysman 2016). Through bio-mixing, iron sulfides are transported from deeper layers to the surface where they react with oxygen forming iron oxides and generating elemental sulfur that can be used by chemoautotrophs (Jørgensen & Nelson 2004). Bioturbation can thus increase reoxidation processes by chemoautotrophic microbes in both, deeper sediment layers and along burrow structures (Reichardt 1988, Kristensen & Kostka 2005, Vasquez-Cardenas et al. 2016). Biological mixing by fauna takes place on the top 5 cm of Kobbefjord sediments (Sørensen et al. 2015). Therefore, a possibility is that the intensity of bioturbation decreased towards spring, resulting in a reduced upward transport of iron sulfide into the oxic zone, which thus reduced reoxidation and the activity of the chemoautotrophic community. Although the benthic community was not studied in detail, and bioturbation intensities were not explicitly quantified, the benthic faunal activity can be estimated by considering the benthic mediated oxygen uptake (BMU). The BMU is defined as the difference between the total oxygen uptake (TOU) and the diffusive oxygen uptake (DOU) of the sediment (Glud 2008). In Kobbefjord, the BMU was strongly reduced in winter and early spring indicating a temporal decrease in faunal benthic activity similar to the seasonal decrease in dark carbon fixation (Table 1). The depth distribution of chemoautotrophic activity in

Kobbefjord sediments also showed a marked seasonality (Fig. 2). In summer (June 2011) and autumn (September 2011), activity was distributed equally in the top 8 cm of the sediment, while in winter (December 2011), the chemoautotrophic activity decreased below 2 cm depth, and by the beginning of spring (May 2012), all activity was strongly reduced throughout the whole sediment. These seasonal changes of the depth distribution of chemoautotrophy in Kobbefjord can likely also be attributed to seasonality in sediment bio-mixing. Injection of electron acceptors in deeper sediment and active redox cycling of iron compounds by bioturbation would explain the even distribution of chemoautotrophy in June and September 2011 up to 8 cm deep (Fig. 2). However, the decrease of chemoautotrophic activity below 2 cm in December suggests a reduction in bioturbation intensity in winter, when sea-ice cover starts to build up in Kobbefjord. A detailed study on the seasonal variations in bioturbation intensity and macrofaunal composition in combination with an assessment of the microbial population dynamics could help to further clarify the seasonal changes of chemoautotrophy in these sediments.

Biogeochemical importance of chemoautotrophy

Chemoautotrophs use reduced compounds (e.g. FeS, H_2S, S^0, NH_4) to re-fix CO_2 respired by heterotrophic organisms and thus serve as a source of renewed carbon in highly reduced environments such as hydrothermal vents and pelagic redoxclines (Wirsen et al. 1993, Glaubitz et al. 2009). Nonetheless, the biogeochemical importance of chemoautotrophy in coastal sediments is rarely assessed, and unknown in fjord systems. As such, this study is the first to report direct measurements of dark carbon fixation in high-latitude coastal sediments to determine the contribution of chemoautotrophy to the cycling of carbon.

The mean yearly depth-integrated chemoautotrophy rate obtained in Kobbefjord (0.4 ± 0.2 mmol C m^{-2} d^{-1}) is at the lower end of the range for coastal sediments and is comparable to activity found at different water depths and temperatures (Table 2). The chemoautotrophy rates from Kobbefjord compare well with a coastal hydrocarbon seep (0.02–1.0 mmol C m^{-2} d^{-1}, Bauer et al. 1988), a marine lake during hypoxia (0.2–1.1 mmol C m^{-2} d^{-1}, Lipsewers et al. 2017), and with surface rates (top 1 cm of sediment) from a tropical brackish lagoon (0.8 mmol C m^{-2} d^{-1}, Santoro et al. 2013) and intertidal sandflats in France (0.38–0.5 mmol C m^{-2} d^{-1}, Dyksma et al. 2016). The environmental mechanisms that control the rate of chemoautotrophy are still largely unknown. Reduced sulfur compounds, ammonium, and metal oxides all serve as electron donors for chemoautotrophs, but in coastal sediments, reduced sulfur species are likely the most important, being produced through sulfate reduction. Sulfate reduction rates from Kobbefjord range from 6 to 12 mmol C m^{-2} d^{-1} (Table 1), which are comparable to both Arctic sediments in Svalbard

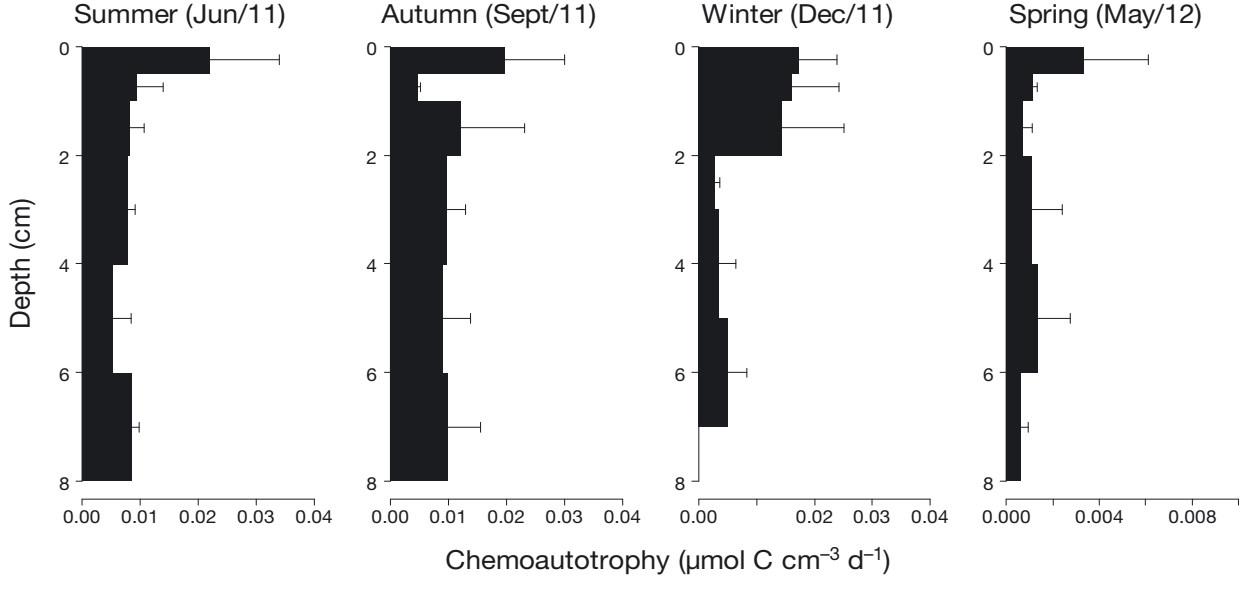

Fig. 2. Seasonal depth distribution of chemoautotrophic activity in Kobbefjord sediments. Bars indicate standard deviation (n = 3). Note change in scale for spring (May/12) panel

Table 2. Intact chemoautotrophy rates from diverse coastal marine sediments. Average rates and standard deviation are reported. mbsl: metres below sea level

Site	Coordinates	Depth (mbsl)	*T* (°C)	Chemoautotrophy (mmol m^{-2} d^{-1})	Sediment depths (cm)	Reference
Kobbefjord	64° 10′ 48″ N, 51° 31′ 27″ W	104	0–3	0.4 ± 0.2	0–6	This study
Marine lake	51° 44′ 49″ N, 3° 53′ 24″ E	7–34	5	2.1 ± 0.9 (oxic)	0–5	Lipsewers et al. (2017)
Grevelingen			18	0.7 ± 0.5 (hypoxic)	0–5	
Courseulles-sur-Mer	49° 20′ 22″ N, 0° 28′ 10″ E	0	19	0.38	0–1	Dyksma et al. (2016)
Calais	50° 59′ 49″ N, 1° 58′ 56″ E	0	21	0.50	0–1	
Janssand	53° 44′ 12″ N, 7° 41′ 56″ E	0	13	1.1	0–1	
Rattekaai	51° 20′ 4″ N, 4° 10′ 11″ E	0	14–17	21 ± 18	0–5	Boschker et al. (2014)
Zandkreek	51° 32′ 41″ N, 3° 53′ 22″ E	0	13–14	2.5 ± 0.5	0–5	
Carapebus	22° 15′ S, 41° 35′ W	2	25	1.0 ± 0.4	0–1	Santoro et al. (2013)
Visgueiro	22° 11′ S, 41° 24′ W	1.8		1.4 ± 2.6	0–1	
Pires	22° 10′ S, 41° 22′ W	1.8		0.8 ± 0.2	0–1	
Janssand	51° 43′ N, 7° 41′ E	0	6	3	0–3	Lenk et al. (2011)
Isla Vista,	34° 23′ 47″ N, 119° 51′ 39″ W	16	13	0.05 ± 0.04 (July)	0–5	Bauer et al. (1988)
(hydrocarbon seep)			17.5	0.58 ± 0.39 (December)		
Gullmar Fjord	58° 15′ 3″ N, 11° 27′ 3″ E	30	Not reported	4.8	0–4	Enoksson & Samuelsson (1987)

and temperate coastal sediments in northern Europe (Sagemann et al. 1998 and references therein). The yearly rate of sulfate reduction at Kobbefjord accounts for 70% (2.2 mol C m^{-2} yr^{-1}) of the total organic carbon mineralization (3.2 mol C m^{-2} yr^{-1}; Sørensen et al. 2015). Sulfate reduction hence produces 1.1 mol m^{-2} yr^{-1} of free sulfide ($2HCO_3$:$1H_2S$), which is equivalent to an electron transfer of 8.8 mol electrons m^{-2} yr^{-1}. Annually integrated chemoautotrophic production from our study amounted to 0.15 mol C m^{-2} yr^{-1}, which requires a total electron transfer of 0.60 mol electrons m^{-2} yr^{-1}. Assuming a limited accretion of sulfur in these sediments, chemoautotrophs would therefore only use 7% of the total electrons available from the oxidation of sulfur to fix CO_2 for biomass synthesis. This value scales well with the estimation of 4% to 8% energy efficiency for sulfur-oxidizing bacteria (Klatt & Polerecky 2015). Thus, the sedimentary chemoautotrophy at Kobbefjord can be sustained solely by sulfur oxidation. Moreover, our estimates suggest that the chemoautotrophic bacteria do not have decreased energy efficiency due to the low temperatures, and may be adapted to the year-round low temperatures as seen for sulfate reducers in Arctic sediments (Sagemann et al. 1998, Knoblauch et al. 1999)

To assess the contribution of chemoautotrophy to the carbon cycling in sediments, dark carbon fixation rates can be compared with the benthic mineralization rate. When the latter is lacking, the TOU of the sediment can be used as a proxy for the organic matter mineralization (Boschker et al. 2014). The handful of studies on coastal sediments that have addressed this issue indicate a contribution of chemoautotrophy to the carbon cycling ranging from 1% in brackish lagoons (Santoro et al. 2013) to 32% in temperate salt marsh sediments (Boschker et al. 2014). At Kobbefjord, the yearly mineralization rate for 2011–2012 was 3.2 mol C m^{-2} yr^{-1} (Sørensen et al. 2015), and the average yearly dark carbon fixation rate estimated here is 0.15 mol C m^{-2} yr^{-1}. This indicates that chemoautotrophic production at Kobbefjord can refix 4% of the total carbon respired in these sediments. Previous estimates based on the production rate of reduced sulfur species, burial rate of reduced compounds, and physiological efficiency of chemoautotrophs suggest that the average contribution of chemoautotrophy via H_2S to the recycling of carbon in coastal sediments is 7% on average (Jørgensen & Nelson 2004). The contribution of chemoautotrophy to the total mineralization at Kobbefjord is hence slightly lower than expected. With the predicted increase in global temperature that is estimated to reduce the ice coverage and substantially increase mineralization rates, chemoautotrophic reoxidation may play a more important role in carbon cycling than at present.

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