Depth distribution of short-chain organic acid turnover in Cape Lookout Bight sediments

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Abstract—The midsummer depth distribution of acetate, propionate, butyrate, isobutyrate, lactate, and pyruvate turnover rates was measured in Cape Lookout Bight, North Carolina sediments. Acetate and pyruvate turnover rates were the highest measured; the range of rates measured were 170-420 μmole L⁻¹ h⁻¹ for acetate, and 160-670 μmole L⁻¹ h⁻¹ for pyruvate. Lactate, propionate, butyrate, and iso-butyrate together were precursors of less than 25% of the acetate metabolized, suggesting that most of the acetate was produced from the direct fermentation of larger organics, with pyruvate as a possible important intracellular intermediate. In general, surface sediments displayed high turnover rates and low concentrations; in deeper sediments turnover rates were roughly proportional to the corresponding concentrations.

INTRODUCTION

RECENT RESEARCH with a variety of anaerobic aquatic sediments has demonstrated the importance of short-chain organic acids (SCOAs) in the terminal steps of anaerobic organic matter oxidation. SCOAs are released as end-products of specific oxidations catalyzed by different anaerobic species; SCOAs released by one species are used by other species as substrates for further oxidation (e.g., SANSONE and MARTENS, 1982). Thus, a large percentage of the degraded organic carbon flows through SCOA intermediates (e.g., LOVLEY and KLUG, 1982), and the pathways followed are dependent upon the biogeochemical conditions which may favor one group of microorganisms over another.

SANSONE and MARTENS (1982) have proposed a model for the terminal steps of anaerobic organic matter oxidation in the presence and absence of sulfate. In this scheme acetate plays a key role in the degradation of complex organic compounds. The model thus suggests that acetate turnover rates are potential indicators for the overall rate of organic matter decomposition in anaerobic sediments, and may also indicate the absolute rate of organic matter mineralization (and by inference, the rates of deposition of labile organic matter) in such environments.

Only a few SCOAs turnover rates, however, have been reported for aquatic sediments (see Results and Discussion, below), and most measurements have been made for surface sediments only. Simultaneous measurements of SCOAs turnover rates vs. depth have been limited to at most three different SCOAs (e.g., BALBA and NEDWELL, 1982), and thus the relative importance of all the possible acetate precursors has not been determined. Specifically, it is not known which SCOAs are the major immediate precursors of acetate in these systems.

This paper reports turnover rates at various depths in the surface sediments from Cape Lookout Bight, North Carolina for acetate and five possible acetate precursors: propionate, butyrate, iso-butyrate, lactate, and pyruvate (Fig. 1). These data are used to deduce the carbon pathways and relative transformation rates of these SCOAs intermediates as a function of depth. This information allows a comparison of organic decomposition processes occurring in shallow sulfate-containing sediment, deeper sulfate-depleted sediment, and the transition zone in-between.

The data indicate that propionate, butyrate, iso-butyrate, and lactate are relatively minor components of the anaerobic decomposition of organic matter in Cape Lookout sediments. It is likely that the remaining acetate is produced directly from the fermentation of carbohydrates or other complex organics, with pyruvate acting as an important intracellular (or, perhaps, extracellular) intermediate. Turnover is very fast in the surface sediment although whole-sediment pools of SCOAs are very low; in deeper sediments the turnover rates are roughly proportional to concentration.

MATERIALS AND METHODS

Field site and sample collection

Sediment samples were collected from station A-I in Cape Lookout Bight, North Carolina (see map in MARTENS and KLUMP, 1980). This coastal basin contains organic-rich sediments which are bioturbated only during winter months (BARTLETT, 1981) and which contain 3-4% organic carbon by weight (MARTENS and KLUMP, 1980). The sedimentation rate is 8-12 cm y⁻¹ (CHANTON, 1979).

During mid-summer sulfate is depleted at approximately 10 cm, which is also the depth of maximum net methane production (Fig. 2). The sediment surface is suboxic at this time, as evidenced by its black color and the presence of an overlying Beggiatoa mat. SANSONE and MARTENS (1982) have reported the seasonal variation of SCOAs concentrations in the top 40 cm of these sediments, as well as seasonal changes in the rate of acetate and propionate turnover in the upper 5 cm of the sulfate-containing and sulfate-depleted zones.

Samples were obtained with a diver-operated 13 cm diameter acrylic corer, and were kept in the dark at approximately in situ temperature (24-26°C) during the 2-4 h period.
between collection and processing. Use of sediment within 2 cm of the outer surface of the cores was avoided in order to minimize contamination.

Apparent turnover rate measurements

The methodology used for these measurements has been described in detail (Sansone and Martens, 1981, 1982). Whole-sediment (methanol-extractable) SCOAs concentrations (µmole l⁻¹) and corresponding reaction rate-constants (h⁻¹) were measured in 5-6 cm sediment depth intervals, and these parameters multiplied to obtain apparent turnover rates (µmole l⁻¹ h⁻¹), where l is the wet-sediment volume in liters.

The term "apparent" is used for two reasons. First, it is unknown what fraction of the whole-sediment concentration is available for use by sediment microorganisms (Sansone and Martens, 1982) since it is not known if solid-phase adsorption may increase or decrease SCOAs bioavailability. However, recent studies have shown that less than 20% of the whole-sediment acetate and butyrate pools, and approximately 5% of the lactate pool are adsorbed to the solid phase of Cape Lookout Bight sediments (Sansone, 1982; Sansone et al., in preparation). Second, the use of whole-sediment extractions result in concentration measurements that combine inter- and intracellular SCOAs pools, whereas the radiolabeled tracer used in the rate-constant measurements (see below) may not completely equilibrate between these pools during the course of the experiments. However, the very high rate-constants measured for acetate and pyruvate (see Results and Discussion) support the assumption that this equilibration is very fast for at least these two SCOAs.

Samples for SCOAs concentration measurements were freeze-dried and extracted with methanol, the extract evaporated, and the extracted SCOAs derivatized with methanolic HCl (Supelco, Bellefonte, PA) to form their methyl esters. Samples collected during 1982 were analyzed by gas chromatography (GC) using a 50 m, 0.20 mm i.d. SE-54 fused silica capillary column (J&W Scientific, Rancho Cordova, CA) with splitless injection; other samples were analyzed using the two-dimensional packed GC column described previously (Sansone and Martens, 1981).

SCOAs turnover rate-constants were measured by adding tracer quantities (<50 nCi) of ¹⁴C-labeled SCOAs to sediment slurries (sediment:dilutant = 3:1), incubating anaerobically at in situ temperatures for 5-30 min, killing the sediment biota with acid-formalin injections, and then recovering the label metabolized to ¹⁴CO₂ or ¹⁴CH₄. Incubations were conducted in sterile 15 ml Vacutainer tubes that were kept anaerobic via a Hungate-style nitrogen or argon gassing system (Hugate, 1969). Abiotic controls, which were killed just before the addition of labeled substrate, were used to correct for non-biological phenomena. Previous studies with acetate and propionate have shown that 85-90% of the added label can be recovered at the end of each experiment when using this type of apparatus (Sansone and Martens, 1981). The following labeled compounds were used: 1,2-¹⁴C-sodium acetate, 53.5 mCi/mmol (New England Nuclear (NEN), Boston, MA); 1-¹⁴C-sodium propionate, 56.7 µCi/mmol (ICN, Irvine, CA); 1-¹⁴C-sodium iso-butyrate, 56 µCi/mmol (ICN); 1-¹³C-sodium butyrate, 14.0 µCi/mmol (NEN); 1-¹³C-sodium pyruvate, 13.1 µCi/mmol (NEN); 1-²³C-sodium lactate, 137 µCi/mmol (NEN).

The use of slurries in these sediments is supported by the observation of Crill and Martens (in preparation) that Cape Lookout sediment which had been stirred and packed into 50 ml centrifuge tubes exhibited the same sulfate reduction rates as did samples in unstimred subcores, presumably due to the very homogeneous nature of these fine-grained sediments. In addition, King and Klug (1982) found that glucose uptake rates measured in organic-rich lake sediments using direct injection techniques were virtually identical to rates measured using sediment slurries.

Turnover rate-constants were calculated in two different manners depending upon the type of reaction being modeled. Reactions in which the labeled carbon of the substrate was released as ¹⁴CO₂ or ¹⁴CH₄ directly from the intact substrate were calculated using the equation defining a single-step first-order reaction:

\[
\frac{\text{db}}{\text{dt}} = \frac{N_k (a_0 - b)}{N_t}
\]

where:
- \(a_0\) = activity of added labeled substrate
- \(b\) = instantaneous activity of product
- \(b_i\) = activity of product \(\text{¹⁴CO}_2\) or \(\text{¹⁴CH}_4\) recovered at the end of the experiment
- \(k\) = turnover rate-constant (h⁻¹)
- \(N\) = number of labeled carbon positions in the labeled substrate
- \(t\) = incubation time.

In the two reactions modeled that did not meet the single-step criterion (butyrate cleavage to two acetates, and lactate oxidation to pyruvate) it was necessary to derive a system of first-order differential equations describing the reaction sequence, including the step(s) producing the \(\text{¹⁴CO}_2\) and \(\text{¹⁴CH}_4\) recovered, as a series of consecutive first-order irreversible reactions (e.g., Benson, 1960; Capellos and Bielski, 1972).

Errata: In eqn (1) the final term should be \(b/N\), not \(b\)

In eqn (2) the final term should be \(br/N\), not \(b\)
These equations were solved simultaneously using previously-determined rate-constants for acetate and/or pyruvate decarboxylation (using Eq. (2)). The root of the resulting equation was computed numerically with a programmable calculator to yield the value of the rate-constant for the initial step of the reaction (i.e., the step in which the added substrate is actually degraded, as opposed to the step(s) in which the recovered $^{14}$CO$_2$ or $^{14}$CH$_4$ is produced). Karl (1982) and King and Klug (1982) have stressed the importance of considering the intermediate labeled pools of substrate when studying multi-step reactions such as these.

In the case of lactate oxidation, it was necessary to model the data as a multi-step process because of the use of a uniformly-labeled tracer (1,2,3-$^{14}$C-sodium lactate) which releases $^{14}$CO$_2$ or $^{14}$CH$_4$ at several points in the degradation pathway (as opposed to the single point of $^{14}$CO$_2$ production possible from a singly-labeled compound such as 1-$^{14}$C-propionate).

RESULTS AND DISCUSSION

Figure 3 shows the mid-summer concentration and turnover rate-constant data obtained for the six SCOAs studied, along with the computed apparent turnover rates. The rates were calculated using rate-constants from various years from 1979 to 1982, and concentrations from 1982. The year-to-year consistency of Cape Lookout sediments (e.g., Klump and Martens, 1981) suggests that calculations using data from the same time period of different years will produce reasonable values. The present section will include discussions of the possible pathways of the SCOAs in the Cape Lookout sediment, the reasons for choosing the pathways used to model the data, and the possible errors resulting from such choices.

Acetate

Acetate can be formed from a variety of precursors in anaerobic systems; these include hexoses, fatty acids, amino acids, and alcohols (e.g., Thauer et al., 1977; Pfennig and Widdel, 1981). However, the relative importance of these possible precursors in sediments have not been determined. In general, the fermentations producing acetate require very low H$_2$ concentrations, and thus require the presence of either hydrogen-consuming sulfate-reducing bacteria (SRB) or methanogenic bacteria (MB) (e.g., Bryant, 1979; Mcinerney et al., 1979; Nedwell, 1982).

Acetate can be a major anabolic precursor for a variety of cellular constituents. However, in Cape Lookout sediments the anabolic uptake of acetate averaged less than 9% of the total acetate turnover during summer months (Sansone, 1980), and thus will not be considered in the present discussion.

Acetate has been observed to be the key organic intermediate in environments of anaerobic organic matter decomposition (e.g., Lovley and Klug, 1982; Wolin and Miller, 1982). This is because, in an efficient anaerobic decomposition system (i.e., one in which H$_2$ levels are very low), most of the carbohydrate and other organic matter utilized is fermented via acetate, CO$_2$ and H$_2$ (Bryant, 1979; Wolin and Miller, 1982). For example, King and Klug (1982) determined that acetate comprised 71% of the SCOAs (not including pyruvate) produced from added glucose after 1 h in a surface freshwater sediment. Thus, the rate of acetate turnover should be a good indicator of the overall rate of anaerobic decomposition. It may be particularly useful in comparing overall rates among anaerobic environments containing differing amounts of sulfate, since the role of acetate as the final organic component in the decomposition is independent of the sulfate concentration.

These patterns can be seen in the depth profiles shown in Fig. 3A. The very high surface turnover rate is associated with a high surface turnover rate-constant and a depleted surface concentration. This phenomenon is observed with most of the SCOAs studied in Cape Lookout. Deeper sediments show high turnover rates associated with low rate-constants and elevated concentrations. The acetate concentration maximum observed at the depth of sulfate depletion may be a result of MB preference for H$_2$ rather than acetate as a source of energy (Mcinerney and Bryant, 1981). Detailed studies, however, are needed to determine the factors producing this feature.

The acetate turnover rate profile in Fig. 3A is similar to those reported for the top 10 cm of Danish coastal sediments (20–300 µM h$^{-1}$ (expressed per volume of interstitial water); Christensen and Blackburn, 1982), and for the top 10 cm of Wintergreen Lake sediments (110–500 µM h$^{-1}$; Lovley and Klug, 1982). Other reported acetate turnover values are lower, presumably reflecting lower levels of organic input to the sediments studied: 0.3–1.7 µM h$^{-1}$ for the top 5 cm of Lake Vechten sediment (Cappenberg and Jongejan, 1977), 1–12 µM h$^{-1}$ in the top 10 cm of Limfjorden (high sulfate) sediments (Ansbæk and Blackburn, 1980), 0–7.8 µM h$^{-1}$ for the top 22 cm of a saltmarsh (Balba and Nedwell, 1982), and 1.9–27 µmole l$^{-1}$ h$^{-1}$ for surface intertidal sediments (King et al., 1983).

Propionate

Propionate is anaerobically oxidized to acetate and CO$_2$, with the latter derived from the propionate carboxyl group (Sorensen et al., 1981; Pfennig and Widdel, 1981; Koch et al., 1983); I am unaware of any reports of complete propionate oxidation directly to CO$_2$, except in pure culture (Pfennig and Widdel, 1981). Propionate-oxidizing activity has been reported in both freshwater and marine sediments (Laanbroek and Pfennig, 1981; Sansone and Martens, 1981, 1982; Balba and Nedwell, 1982; Banat and Nedwell, 1983).

Propionate oxidation during midsummer is most rapid in the surface of Cape Lookout sediments, but slows to low rates at a point above 8 cm depth (Fig. 3B). This rate distribution is largely due to the shape of the rate-constant profile rather than that of the concentration profile, in agreement with the other SCOAs studied. The occurrence of the maximum concentration and very low turnover rates near the level of sulfate
Fig. 3. SCOA turnover rate-constants, whole-sediment concentrations, and computed turnover rates in Cape Lookout Bight sediments. Rates were calculated using 1982 concentration measurements, and rate-constants from the indicated dates. Horizontal lines through rate-constant data points are standard deviations of triplicate analyses; standard deviations are not shown when smaller than data symbols. Vertical lines indicate the depth intervals of samples.
depletion suggests that propionate oxidation may be less favorable under low sulfate conditions, and that higher substrate levels are needed to ensure a net energy yield for the reaction.

The low rates of propionate turnover indicate that propionate is not a major precursor for acetate in these sediments. The propionate turnover produces no more than 2% of the acetate utilized at any depth. BALBA and NEDWELL (1982) determined propionate turnover in the top 4 cm of saltmarsh sediment to be 0.3 µM h⁻¹; they concluded that at most 6% of the sediment acetate was derived from propionate. LOVLEY and KLUG (1982) measured propionate turnover in freshwater surface sediment to be 20 µM h⁻¹, or 13% of the acetate turnover. Experiments using coastal lagoonal sediment in which sulfate reduction was inhibited by molybdate (CHRISTENSEN, 1984) indicated that approximately 22% of the acetate was produced from propionate. Further measurements will be needed in other environments to determine if these variations represent fundamental differences among sediment types.

Butyrate

Since the pathway(s) for butyrate degradation in sediments have not been determined, the butyrate decarboxylation data presented here are calculated twice, with different pathways assumed in each case: a) direct oxidation to acetate and two CO₂ (Fig. 3C), and b) β-oxidation to form two acetates, with subsequent oxidation of the acetate to CO₂/CH₄ (Fig. 3D). It is possible, however, that both pathways are actually in operation simultaneously.

The two models resulted in significantly different profiles of turnover rate-constants and, hence, turnover rates. The direct oxidation rate-constant profile (Fig. 3C) is more consistent with those seen for the other SCOA's, in that there is a prominent surface maximum. In contrast, the β-oxidation profile (Fig. 3D) displays a maximum at the depth of sulfate depletion.

In either case the butyrate turnover is only a small fraction (0.04-9%) of the acetate turnover in midsummer Cape Lookout sediments. In comparison, a butyrate turnover rate of 0.19 µM h⁻¹ (8% of the acetate turnover) was measured in the top 4 cm of saltmarsh sediment (BALBA and NEDWELL, 1982). In Wintergreen Lake surface sediment only 4% of added labeled glucose was fermented to butyrate in 1 h (KING and KLUG, 1982), and butyrate turnover was only 2% of acetate turnover (LOVLEY and KLUG, 1982). In contrast, SORENSEN et al. (1981) reported that 5-20% of the sulfate reduction in a coastal marine sediment was associated with butyrate oxidation.

Iso-butyrate

Iso-butyrate oxidation to succinyl CoA is well known, with the latter either used in the tricarboxylic acid cycle or oxidized to CO₂. Conversely, it is also possible that iso-butyrate may be oxidized directly to acetate. Because succinate oxidation data are not available for Cape Lookout Bight sediments, it is assumed that iso-butyrate is oxidized directly to acetate. The depth distributions show patterns similar to those exhibited by most of the other SCOA's (Fig. 3E), but the very low turnover rates indicate that iso-butyrate is not important in the flow of carbon in these sediments. Sulfate reduction inhibition experiments by CHRISTENSEN (1984) with coastal sediments indicated that approximately 9% of the acetate was produced from iso-butyrate.

Lactate

Lactate decomposition data presented here have been modeled assuming lactate oxidation to pyruvate with subsequent decarboxylation to acetate and CO₂/CH₄ (THAUER et al., 1977). The low rate of propionate turnover in these sediments (Fig. 3B) indicate that the other likely routes for anaerobic lactate decomposition are not of major importance: lactate oxidation to pyruvate with subsequent propionate production (succinate-propionate pathway) (GOTTSCHALK, 1979), and lactate fermentation to propionate, acetate, and CO₂ via the acrylate pathway (BRYANT, 1979; GOTTSCHALK, 1979).

Lactate turnover (Fig. 3F) in midsummer Cape Lookout sediment exhibits depth distributions similar to those of most of the other SCOA's studied. However, lactate turnover can account for only 4-15% of the acetate consumed at any given depth. In comparison, LOVLEY and KLUG (1982) reported lactate turnover in a surface freshwater sediment to be 2% of the acetate turnover. SRB were determined to be important in lactate degradation even in this low-sulfate environment since inhibition of sulfate reduction by Na₂MoO₄ addition resulted in a 58% decrease in lactate mineralization (SMITH and KLUG, 1981). KING and KLUG (1982) found that only 9% of labeled glucose added to freshwater sediment was converted to lactate after 1 h, suggesting that most of the carbon flow in such environments bypasses the lactate pool. NOVITSKY and KEPKAY (1981) found that less than 5% of the lactate utilized in aerobic and anaerobic Halifax Harbor sediment was incorporated into cellular material.

Pyruvate

Like acetate, pyruvate is an important intermediate for microbial intracellular metabolism. Unlike acetate, however, pyruvate is not believed to function as an extracellular intermediate (e.g., BRYANT, 1979), although pyruvate has been reported to be excreted by four strains of Desulfovibrio grown on lactate in batch culture (LEWIS and MILLER, 1975).

A variety of SRB have been observed in culture to utilize pyruvate as a sole carbon and energy source (e.g., POSTGATE, 1979; BRYANT et al., 1977; LAANBROEK and PFENNIG, 1981; WIDDEL et al., 1983).
However, in natural systems it is likely that much, if not most, of the pyruvate is involved exclusively with intracellular reactions, and thus measurements of its turnover by added-label tracer techniques must assume the existence of a mechanism for rapid transport into the cells. The extremely high pyruvate turnover rate-constants measured here (see below) suggest that pyruvate uptake kinetics are indeed very fast. Although this experiment is not strictly "natural," it is useful in demonstrating that pyruvate oxidation has the potential to produce a major share of the acetate being degraded in Cape Lookout Bight sediments.

The pyruvate turnover data presented here have been computed by assuming that pyruvate is decarboxylated in Cape Lookout sediments directly to acetyl-CoA (acetate) and CO₂. This assumption is based on the following considerations:

1. The low turnover rates of lactate and butyrate indicate that butyrate and mixed-acid fermentations (which produce butyrate, lactate, and ethanol from pyruvate) together are responsible for at most 10% of the acetate turnover in Cape Lookout Bight sediments.
2. Acetate fermentation, in which half of the pyruvate utilized is reacted with a carrier-bound methyl group in a transcarboxylase reaction to produce two acetates (e.g., GOTTSCHALK, 1979), will cause underestimates in the pyruvate turnover rate-constant if it is operating in Cape Lookout sediments. This result is due to the delay in 14CO₂ production after 14C-pyruvate degradation, resulting from the labeled carboxyl carbon passing through the acetate pool. If all of the pyruvate in Cape Lookout sediments were degraded via acetate fermentation the resultant underestimate of the pyruvate turnover rate-constant reported here would be approximately 50%.
3. Pyruvate anabolism associated with carbohydrate and amino acid synthesis during the turnover rate-constant experiments may deplete the pool of added pyruvate tracer, and thus may result in underestimates that would be significant if the rate of anabolic uptake of pyruvate were to exceed the turnover by a large amount. Unfortunately, data are not available to evaluate the significance of this possible source of error.

Despite the possible sources of underestimation mentioned above, the pyruvate rate-constants measured in Cape Lookout sediments were extremely high at all the depths studied (Fig. 3G); the measured pyruvate concentrations were also large but were nevertheless only one-tenth of the corresponding acetate levels. The computed apparent pyruvate turnover rates were thus approximately equal to that of acetate, except for the surface sample. This contrasts with previous investigations with other SCOAs that have been unable to account for more than a small fraction of the acetate observed to be degraded.

The suboxic-anoxic interface

The suboxic-anoxic interface, which exists in the upper parts of the 0–5 cm sample interval, along with the relatively high degradability of the available organic matter, may cause the very rapid turnover rates of SCOA in this interval. This hypothesis is consistent with the observations of NOVITSKY and KEPKAY (1981) that in Halifax Harbor sediments the metabolism of lactate, glutamate, and glucose was greatest in the transition from aerobic to anaerobic sediments. Suboxic oxidation, with its possible lack of interspecies SCO transfer, may also be the cause of the observed association of high surface SCO turnover rates with low SCO concentrations. Conversely, this association may be due to more efficient uptake and oxidation of SCOA by SRB due to high local sulfate concentrations. The comparatively slow surface pyruvate turnover rate indicates that pyruvate may not be the major acetate precursor in this interval. This contrast with deeper sediments suggests that a different type of organic matter oxidation is operating in surface sediment; at least part of the organics may be oxidized directly to CO₂ without passage through a pyruvate intermediate, perhaps in a coupling with oxygen and/or nitrate reduction.

The high turnover rates measured in the 0–5 cm depth interval likely reflect disproportionately high rates in the layer immediately adjacent to the sediment-water interface. This hypothesis is supported by a comparison of turnover rate-constants for acetate and propionate in the 0–5 and 2–7 cm depth intervals (Fig. 3A, B). The inclusion of the 0–2 cm interval in the 0–5 cm samples results in rate-constant measurements that are 6.9 and 3.1 times higher for acetate and propionate, respectively, than in the 2–7 cm samples.

CONCLUSIONS

The data presented here indicate that acetate and pyruvate dominate SCO turnover cycling in Cape Lookout sediments. Propionate, butyrate, and iso-butyrate appear to be of minor significance in this system, and lactate can supply less than 15% of the acetate metabolized at any depth measured. With the exception of the surface sediment, pyruvate decarboxylation is more than adequate to supply acetate for the measured acetate turnover. This contrasts with previous experiments which have been unable to identify the major SCO precursor(s) of acetate in anoxic sediments. It appears likely that most of the acetate is produced directly from the fermentation of carbohydrates or other complex organics, with pyruvate as an important intra-, or possibly extra-cellular intermediate.

In contrast to the surface sediment rates, apparent turnover rates in deeper sediments covaried with the associated SCO concentrations. If this relationship is shown to be generally true in other anaerobic sediments, measurements of SCO concentrations may provide a convenient approximate indication of the SCO turnover rates in non-surface sediments.

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