Journal of Marine Research, *53*, 799–819, 1995

Carbon cycling in mesohaline Chesapeake Bay sediments 1: POC deposition rates and mineralization pathways

by Eric E. Roden[1,2], Jon H. Tuttle[1], Walter R. Boynton[1] and W. Michael Kemp[3]

ABSTRACT

Organic carbon cycling in sediments at two locations in the mesohaline Chesapeake Bay was analyzed using available data on sediment sulfate reduction, sediment oxygen consumption, and particulate organic carbon (POC) deposition and burial. Estimates of POC deposition based on the sum of integrated sediment metabolism and POC burial compared well with direct estimates derived from chlorophyll-*a* collection rates in mid-water column sediment traps. The range of POC deposition estimates (15–31 mol C m^{-2} yr^{-1}) accounted for a large fraction (36–74%) of average annual net primary production in the mesohaline Bay. The difference between rates of POC deposition and permanent burial indicated that 70–85% of deposited carbon is mineralized on the time scale of a year. Carbon mineralization through sulfate reduction accounted for 30–35% of average net primary production, and was likely responsible for 60–80% of total sediment carbon metabolism. Oxidation of reduced sulfur accounted for a large but quantitatively uncertain portion of SOC in mid-Bay sediments. Our results highlight the quantitative significance of organic carbon sedimentation and attendant anaerobic sediment metabolism in the carbon cycle of a shallow, highly productive estuary.

1. Introduction

Sediment trap studies indicate that a considerable fraction (10–50%) of total primary production in shallow (< 200 m deep) coastal ecosystems is deposited to the sediments (Suess, 1980). At water depths ≤ 20 m, this ratio often exceeds 40% (Hargrave and Taguchi, 1978; Smetacek, 1980; Taguchi, 1982). Similar conclusions have been drawn from organic deposition estimates based on rates of sediment carbon metabolism and burial (Jørgensen, 1977; Joiris *et al.,* 1982; Oviatt *et al.,* 1986b; Jørgensen and Revsbech, 1989). High rates of organic deposition typically lead to a predominance of anaerobic pathways of coastal sediment metabolism (Jørgensen, 1983; Nedwell, 1984; Capone and Kiene, 1988). Bacterial sulfate reduction (SR) is the principle carbon mineralization process in anoxic, sulfate-containing

---

[1] University of Maryland, Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, Solomons, Maryland, 20688, U.S.A.

[2] Present address: Department of Biological Sciences, The University of Alabama, Box 870344, Tuscaloosa, Alabama, 35487-0344, U.S.A.

[3] University of Maryland, Center for Environmental and Estuarine Studies, Horn Point Environmental Laboratories, Cambridge, Maryland, 21613, U.S.A.

coastal sediments (Martens and Berner, 1974; Oremland and Taylor, 1978; Senior *et al.*, 1982). Where carbon input to sediments is high, at least 50% of sediment carbon respiration and oxygen consumption (SOC) have been found to be coupled to sulfur cycling (Jørgensen, 1982; Howarth, 1984).

In shallow, highly productive estuarine environments such as Chesapeake Bay, organic matter sedimentation and mineralization are likely to constitute a major fraction of total carbon cycled within the system. In turn, high rates of organic sedimentation should favor anaerobic pathways of sediment carbon mineralization. In this paper we examine these hypotheses quantitatively by combining recent measurements of sediment organic carbon metabolism (SOC and SR) with independent estimates of organic carbon deposition and burial at two sites in the mesohaline Chesapeake Bay. By adding estimates of integrated sediment carbon mineralization to those of organic carbon burial we constrain a range of organic carbon sedimentation rates that can be compared directly with sediment-trap estimates of carbon deposition. These comparisons permit an evaluation of the accuracy of the sediment trap data, as well as a first-order estimate of the relative contribution of SR to total sediment carbon metabolism.

2. Materials and methods

a. Station locations and description. We consider two sites in the mesohaline region of Chesapeake Bay. Station R64 (38° 33′N, 76° 27′W; 16 m depth) is located on the western slope of the central channel, where overlying waters are hypoxic or anoxic during May–September. Station DB (38° 34′N, 76° 30′W; 10 m depth) is located on the western flank of the mid-Bay, where overlying waters are typically well-oxygenated. Sediments at both stations are fine-grained silt-clay, having porosities of 0.89–0.94 and 0.83–0.92 for the upper 12 cm sediment of R64 and DB sediments, respectively. Central channel sediments are temporarily colonized during the spring by small bivalves and polychaetes, which disappear with the onset of anoxia/hypoxia in the summer (Holland, 1988; Kemp *et al.*, 1990). A community of these organisms inhabits sediments at station DB year-round, although large seasonal changes in macrofaunal biomass occur (Kemp *et al.*, 1990). Bottom water temperatures at the two sites vary sinusoidally from a maximum of 25–26°C in August to a minimum of 1–2°C in February.

b. Sediment oxygen consumption. Measurements of SOC in the vicinity of station R64 for the years 1986–1989 were compiled from Boynton *et al.* (1990), Kemp *et al.* (1992), and from the unpublished data of W. R. Boynton and W. M. Kemp. SOC measurements at station DB were taken from Kemp *et al.* (1992) and from the unpublished data of W. M. Kemp. Most of the SOC measurements were made by ship-board incubation of triplicate box cores (Kemp *et al.*, 1992). On three occasions at station DB. SOC was measured under *in situ* benthic chambers in parallel with box core incubations as described by Kemp *et al.* (1992).

c. Sulfate reduction. SR rates were determined using the radiotracer methods of Jørgensen (1978) as described by Roden and Tuttle (1993). In brief, intact subcores (2.5 cm ID) collected from box cores were injected (through silicon-sealed ports in the core tubes) with 1–5 μCi of carrier-free $^{35}SO_4^{2-}$ (ICN Radiochemicals Co., Irvine, CA) at 2 cm intervals from 1 to 11 cm prior to incubation for 4–8 hours in a water bath at *in situ* temperature. Activity was terminated by freezing the cores. Reduced ^{35}S was released either by separate acid (6N HCl) and reduced chromium (Zhabina and Volkov, 1978) distillations, or by a single reduced chromium distillation. The H_2S evolved during the distillations was carried by an O_2-free N_2 stream into traps containing 20 ml (acid distillation) or 100 ml (reduced chromium distillation) of 10% zinc-acetate. Portions (2 ml) of the trap contents were mixed with 7 ml of Instagel (Packard Instrument Co., Downers Grove, IL) scintillation cocktail, and radioactivity determined with a liquid scintillation spectrometer (Packard Model 4330) operated in the DPM mode with quench correction by the external standards, channels-ratio method.

SR rates were calculated as the product of the fraction of added radioactivity recovered as reduced ^{35}S per unit time and the sulfate concentration at the corresponding depth in the sediment. Pore fluid samples for sulfate determination were obtained by sectioning intact cores at 1–3 cm intervals, loading the sediment sections into N_2-gassed 50 ml plastic centrifuge tubes, and centrifuging for 20–40 minutes at 2000 g. After centrifugation, the supernatant was removed with an N_2-gassed 10 ml syringe and filtered through an N_2-gassed in-line GF/C filter (Whatman) into a pre-weighed vial containing 0.5 ml of 10% zinc acetate. After analysis of ZnS content, the remaining pore fluid was filtered through a GF/C filter and stored at 4°C for subsequent sulfate analysis. Sulfate concentrations in appropriately diluted portions of pore fluid were determined with a Dionex (Sunnyvale, CA) Model 2020i ion chromatograph.

d. Sediment trap deployments. Sediment trap data were compiled from Boynton *et al.* (1990). At station R64, duplicate cylindrical tubes (76 cm × 7.6 cm ID) were suspended at ≈5 and 10 m depth for 1–2 week intervals between March and November 1986–1989. At station DB, duplicate traps were suspended at ≈3 and 6 m depth over one annual interval (August 1985–June 1986). The traps were not poisoned. Material collected in the traps was filtered onto pre-combusted GF/C filters and analyzed for total dry matter, POC, and Chlorophyll-*a* (Chl-*a*) content. When traps were deployed and retrieved, water samples collected by submersible pump from depths local to the traps were analyzed for total seston, POC, and Chl-*a* content. Parallel samples of surficial sediment (0–1 cm) were obtained from Van Veen grab samples

(1986) or Bouma box cores (1987–89) and analyzed for POC and Chl-*a* content. POC was determined with a CHN analyzer (Control Equipment Co. Model 240XA). Chl-*a* was determined by the method of Strickland and Parsons (1972).

We estimated Net POC deposition rates by multiplying measured rates of Chl-*a* collection by the C:Chl-*a* ratio of material suspended in the water column adjacent to the traps (the average C:Chl-*a* ratio of material collected at the time of deployment and retrieval was used for these calculations). The rational for using this approach is discussed below. The C:Chl-*a* ratio of suspended seston averaged 99 ± 41 at station R64, with 90% of the values falling in the range of 50 to 200. At station DB, C:Chl-*a* ratios ranged from 55 to 155 with an average of 102 ± 29. These averages exceed those reported for marine phytoplankton assemblages (25–60, Parsons and Takahashi, 1984; 50–70 (Long Island Sound), Tantichodok, 1989 cited in Sun *et al.,* 1991), suggesting that some of the organic material collected in the water column and sediment traps was partially degraded rather than fresh phytoplankton material.

3. Results

a. Sediment oxygen consumption. Spring rates of oxygen consumption by central channel sediments (Fig. 1a) were about half those at flank station DB (Fig. 1b). With the onset of bottom water hypoxia/anoxia in the summer, SOC at station R64 approached zero. An autumn SOC peak occurred in central channel sediments, due at least in part to oxidation of accumulated sulfides when bottom waters were reaerated during fall turnover. The three very high summer SOC rates at R64 (Fig. 1a) resulted from measurements made when the oxygen concentration of water overlying sediment cores was accidentally elevated (to >1 mg liter^{-1}). These "outliers" indicate the potential for intense SOC during transient bottom water reaeration events which occur even in years of sustained anoxia (Malone *et al.,* 1986). However, because reliable data on the frequency of these events with concurrent SOC measurements are unavailable, the outliers were not included in our estimates of annual integrated rates of SOC (Table 1). Likewise, oxidation of H_2S (produced in the sediment) at or below the pycnocline during summer anoxia was also excluded from the sediment oxygen budget for station R64.

In contrast to station R64, August SOC rates at station DB were similar to spring rates (Fig. 1b). Benthic dome incubations yielded SOC rates similar to those determined from box core incubations. November SOC measurements at both stations suggested that rates declined during the autumn (Fig. 1). March–August integrated SOC at DB (Table 1) was calculated by allowing the average rate of 42 ± 6 ($n = 13$) mmol O_2 m^{-2} d^{-1} to apply for the entire period. August–November SOC at DB was calculated by allowing the March–August average rate to decrease linearly to 18 mmol O_2 m^{-2} d^{-1} from the end of August to the middle of November. Estimates of SOC during the winter at both stations (hatched areas in Fig. 1) were made by connecting the last fall and earliest spring SOC values by a straight line. Annual SOC

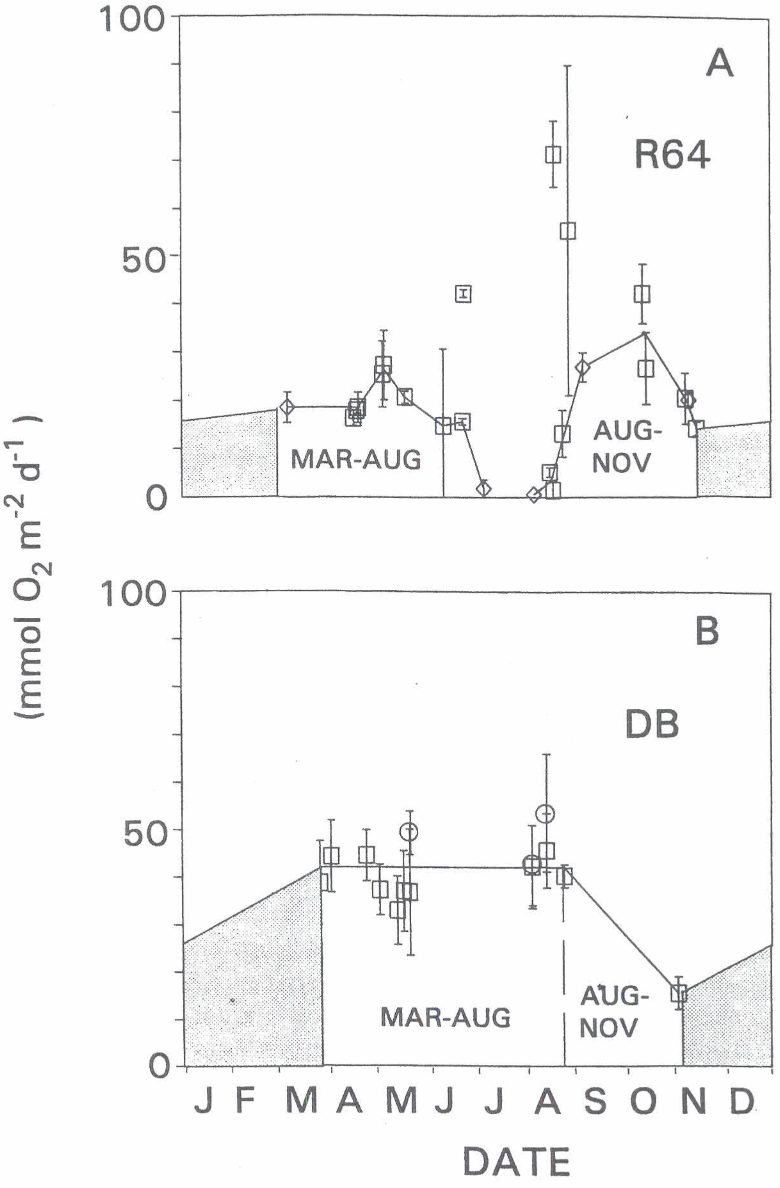

Figure 1. Mean SOC rates at stations R64 (A) and DB (B). Error bars indicate ±1 SD (n = 2–3). R64 data for the years 1984–1988 are pooled from Boynton *et al.* (1990), Kemp *et al.*, (1992), W. R. Boynton unpubl data, and W. M. Kemp, unpubl data. All measurements at R64 were made by box core incubation. DB data are from Kemp *et al.* (1992) and W. M. Kemp, unpubl data. DB measurements were obtained from box core (□) or benthic chamber (○) incubations. Area under the solid line was integrated trapezoidally to yield annual SOC rates (Table 1).

Table 1. Sediment sulfur and oxygen budgets for stations R64 and DB. Values are expressed in reduced S equivalents.

Station	Process	Process rate (mol m^{-2} time interval^{-1})			Annual total
		Mar–Aug[a]	Aug–Nov[b]	Dec–Feb[c]	
R64	S storage[d]	+0.65	+0.44	−1.09	0
	S burial[e]	0.23	0.17	0.16	0.56
	S reduction[f]	4.14	2.13	0	6.27
	S reoxid[g]	3.26	1.11	1.34	5.71
	SOC calc[h]	6.52	2.22	2.68	11.42
	SOC meas[i]	1.41	2.21	2.68	6.30
DB	S storage[d]	+0.61	−0.25	−0.36	0
	S burial[e]	0.54	0.39	0.36	1.29
	S reduction[f]	4.48	2.84	0	7.32
	S reoxid[g]	3.33	2.70	0	6.03
	SOC calc[h]	6.44	5.40	0	12.06
	SOC meas[i]	4.32	2.86	5.34	12.52

[a] Time interval = julian date 70–220; [b] time interval = julian date 220–330; [c] time interval = julian date 330–70.

[d] Temporary storage of solid-phase reduced sulfur was calculated from seasonal changes in reduced sulfur concentration in the upper 4–8 cm of sediment (data from Roden and Tuttle, 1993).

[e] Burial of solid-phase reduced sulfur, calculated as the product of (1) the mass sedimentation rate (g dry sed m^{-2} d^{-1}) determined from ^{210}Pb and ^{239,240}Pu data (Officer *et al.*, 1984; see Table 3), and (2) the average dry weight reduced sulfur content of particles at depth (10–12 cm) in the sediment (mol S/g dry sed; Roden and Tuttle, 1993), and (3) the corresponding time interval (days).

[f] Integrated rates of sulfate reduction in the upper 12 cm of sediment, calculated from the area under the solid line in Fig. 2. Zeros were assigned for the Dec–Feb interval because rate measurements for this period are lacking and because this time interval was ignored in calculating annual rates of sulfate reduction.

[g] Estimated magnitude of reduced sulfur reoxidation, calculated as the difference between total sulfide production and reduced sulfur accumulation *plus* reduced sulfur burial (i.e. S reoxid = S reduction − S storage − S burial).

[h] Estimated magnitude of sediment oxygen consumption (SOC) associated with reduced sulfur reoxidation, assuming a 2:1 atomic ratio of oxygen consumption to reduced sulfur reoxidation (Jørgensen, 1977).

[i] Measured rate of SOC, integrated trapezoidally (Fig. 1) over the following time intervals: Apr–Aug = julian date 110–218 for R64, 115–218 for DB; Aug–Nov = julian date 219–314 for R64, 219–308 for DB; Nov–Apr = julian date 315–109 for R64, 309–114 for DB.

rates (Table 2) were determined from the area under the solid lines (hatched plus unhatched) in Figure 1. Unfortunately, these must be viewed as rather crude estimates, owing to the exclusion of summertime sulfide oxidation at station R64, and to the paucity of data over an annual cycle at station DB. With regard to the latter, for example, the averaging (direct interpolation) of spring and August SOC rates

Table 2. POC deposition rates at stations R64 and DB, derived from rates of Chl-*a* collection in mid-water column sediment traps as described in the text. S.D. refers to standard deviation of the mean.

Station	Year	Warm season interval (Julian date)	ΔT (days)	Warm season POC deposition[a] (mol C m^{-2})	Weighted average POC deposition[b] (mmol C m^{-2} d^{-1})
R64	1986	58–318	260	18.5	71.2
	1987	57–352	295	21.1	71.5
	1988	40–327	287	16.8	58.5
	1989	39–334	295	17.7	60.0
	Mean:			18.5	65.3
	S.D.:			1.9	6.1
DB	1985–1986	65–281	216	24.8	115

[a] Calculated by trapezoidal integration of area under the lines in Fig. 3.
[b] Warm Season POC deposition $x\ \Delta T^{-1}$.

may fail to account for what could arguably be the most active time of the year in DB sediments, i.e. June and July, when temperatures are near their annual maximum and labile carbon from the spring diatom deposition may still be present in surface sediments (see Roden and Tuttle, 1995). Also, it is likely that winter SOC minima at both stations are significantly lower than the Oct/Nov and Mar/Apr end-members used for interpolation of winter SOC rates, leading to an overestimation of SOC (which may or may not balance possible underestimation during the summer months).

b. Sediment sulfate reduction. Rates of SR (expressed in carbon units assuming a 2:1 stoichiometry for organic carbon oxidation coupled to SO_4^{2-} reduction) in central channel and western flank sediments increased from 10 and 20 mmol C m^{-2} d^{-1} in April to summer maxima of 120 and 150 mmol C m^{-2} d^{-1}, respectively (Fig. 2). By November, rates at the two stations decreased to 15–35 mmol C m^{-2} d^{-1}. Integrated rates of carbon flow through SR were calculated by graphical integration (see Table 3). The lines in Figure 2 were drawn on a visual basis to account for seasonal rate variations and variability among summer rates. Upper and lower limits on annual SR were set by substituting the upper and lower dashed lines, respectively, for the solid lines when integrating. The difference between upper and lower limit annual SR rate estimates amounted to 22 and 33% of the best estimate rates for stations R64 and DB, respectively. The integrated SR rates reported here are somewhat higher ($\leq 35\%$) than estimates based on Arrhenius and time/temperature relationships (Roden and Tuttle, 1993) owing to the fact that the graphical procedure accounted for early summer SR rate maxima which could not be reproduced by the Arrhenius equation.

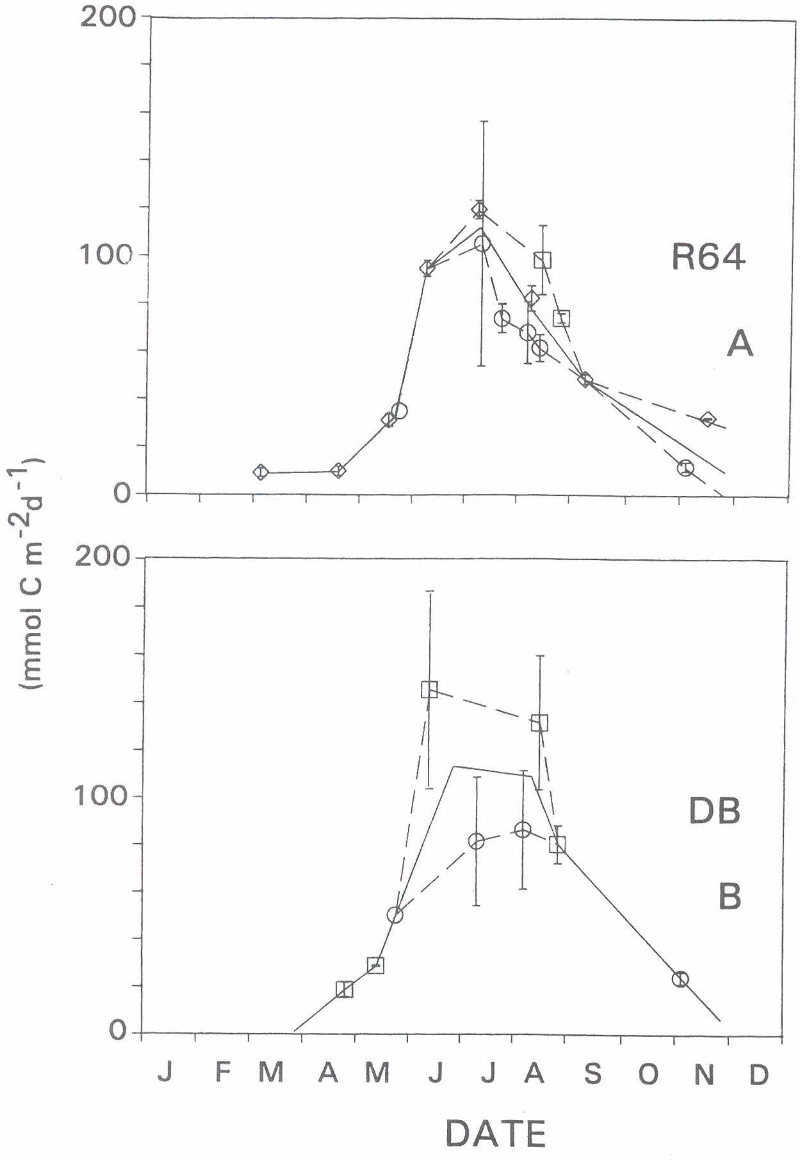

Figure 2. Mean areal SR rates (open symbols), expressed in carbon equivalents (1S = 2C). Error bars indicate ± 1 SD (n = 2–6). (A): R64 data from 1986 (□), 1987 (○), and 1989 (◇); 1989 rates are the unpubl data of and M. Marvin and D. Capone. (B): DB data from 1986 (□) and 1987 (○). The data were integrated graphically (area under the solid lines) to estimate annual SR rates (Table 3). The dashed lines are drawn to constrain upper and lower limit annual SR rates.

c. Sediment trap estimates of POC deposition. In many aquatic systems, especially coastal marine environments, resuspension of bottom sediments complicates interpretation of sediment trap collection rates (Steele and Baird, 1972; Oviatt and Nixon, 1975; Taguchi, 1982). In the present study we estimated net POC deposition rates by multiplying measured rates of Chl-*a* collection by the C:Chl-*a* ratio of material suspended in the water column local to the traps. We adopted this approach under the supposition that Chl-*a* deposition better reflects the input of newly produced organic material to sediments than do direct measurements of POC deposition, because resuspension effects are probably minimal in the case of Chl-*a*. The dry weight Chl-*a* content of suspended seston in mid-Bay waters is 10–100 fold higher than that of surficial (0–5 mm) bottom sediments (Boynton *et al.*, 1990), owing to the rapid decomposition (10–30% per day; Sun *et al.*, 1993) of Chl-*a* once it reaches the bottom. Resuspension contributions to the Chl-*a* collected in traps are thus likely to be negligible.

In contrast, the POC content of suspended seston is only ≈ 5-fold higher than that of surficial bottom sediments. Because a large portion (70–80%) of the POC in mid-Bay surface sediments is unreactive (see Roden and Tuttle, 1995), entry of this material into sediment traps via resuspension can seriously bias estimates of the deposition of newly produced, labile organic carbon. For example, gross POC deposition rates were only ≈ 10% higher than Chl-*a*-derived POC deposition rates for R64 sediment traps (deployed 10 m above the bottom), whereas for station DB traps (deployed 4 m above the bottom) gross POC deposition exceeded Chl-*a*-derived POC deposition by 50%. These results suggest that traps deployed closer to the bottom are subject to greater inputs of resuspended surface sediment or sediment transported laterally from the more shallow flanks of the estuary. Correction factors are thus required to estimate net POC deposition rates from gross POC collection rates in situations where these processes are significant (Boynton *et al.*, 1991). However, the validity of applying such corrections is uncertain because they require several assumptions which are difficult to confirm. Given that Chl-*a*-derived POC deposition rates do not require correction factors, they probably represent the least ambiguous estimate of POC deposition rates. A detailed evaluation of the relative merit of various treatments of sediment trap data, as well as consideration of the seasonal dynamics of Chesapeake Bay sediment trap collections and their relationship to other water column processes (e.g. hydrography, primary production, grazing, etc) is beyond the scope of this paper. Rather, our intent is to use the available data to compare with other independent estimates of organic carbon input to mid-Bay sediments.

As noted previously for a portion of this data set (Garber, 1987), mid-water POC deposition rates at both stations were relatively constant on a time scale of months throughout the warm season (Fig. 3), although a high level of week-to-week variability (averaging ≈ 100% of the weighted average) was evident. Weighted

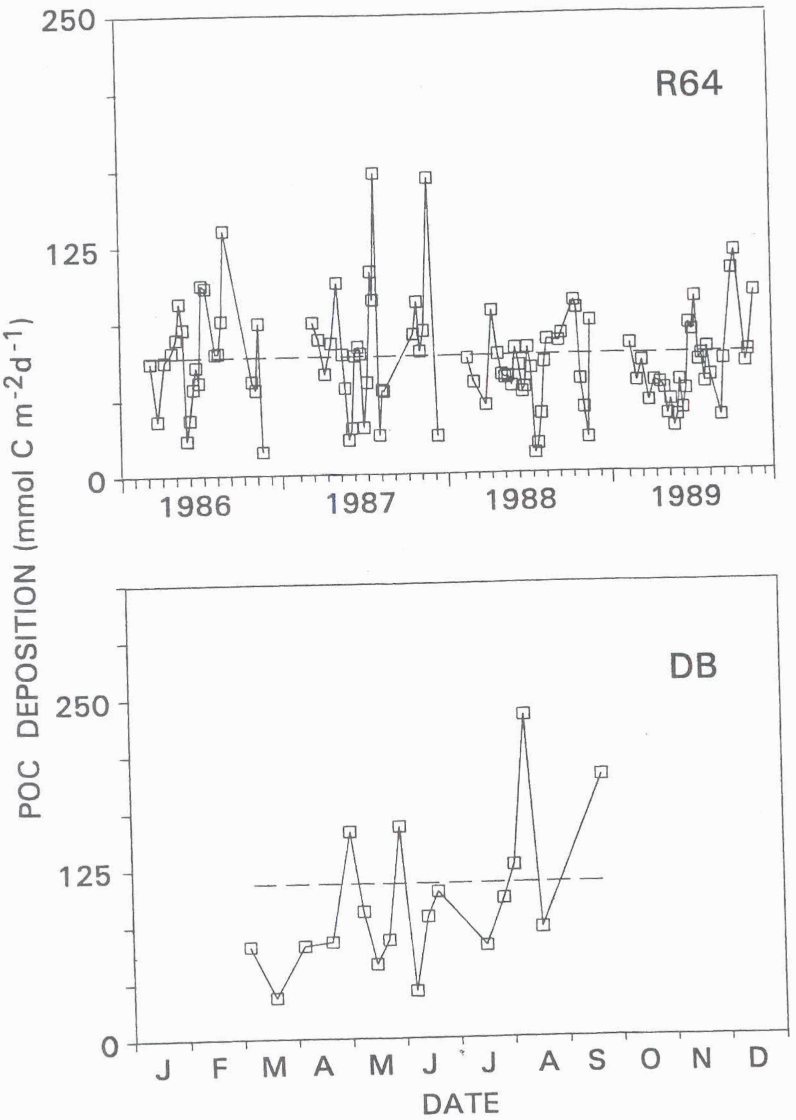

Figure 3. Rates of POC deposition at stations R64 and DB, derived from rates of Chl-*a* collection in mid-water column sediment traps. The dashed lines represent weighted average rates for the March–November warm season interval (Table 2).

average mid-water column Chl-*a* collection rates and the corresponding POC deposition rates were generally 50–100% higher than surface water column collection rates (data not shown). Collection rates of materials in the mid water column probably give a better representation of organic matter input to deep waters and sediments than collection rates in surface waters (Steele and Baird, 1972; Taguchi,

Table 3. Sediment carbon flux estimates for stations R64 and DB, expressed in mol C-equiv m^{-2} yr^{-1} (POC deposition and sediment SR rates refer to warm season (Mar–Nov) only). Dry mass sedimentation is expressed in units g cm^{-2} yr^{-1}. Note that column C under Aerobic Respiration refers to a ratio rather than a flux.

Station	Dry mass sedimentation	POC burial[c]	ΣSR[d]	Burial + ΣSR	Sediment trap POC deposition[e]	ΣSOC[f]	Aerobic resp. A[g]	B[h]	C[i]
R64	0.13[a]	2.5	12.6	15.1	17.6	6.3	−5.3	2.5	0.17
DB	0.30[b]	6.6	14.6	21.2	31.0	12.5	0.5	9.8	0.40

[a] Average of rates from ^{210}Pb and ^{239,240}Pu data at station 18 in Officer *et al.* (1984).

[b] From ^{210}Pb data at station 834G (12 m depth) in Officer *et al.* (1984).

[c] Calculated as $w_{dm} \cdot G_{nr}$, where w_{dm} = annual dry mass sedimentation rate, and G_{nr} = dry weight concentration POC at depth in the sediment (23.8 and 26.4 mg C g dry sed^{-1} for R64 and DB, respectively; Roden and Tuttle, 1993).

[d] Area under the solid lines in Fig. 2.

[e] Weighted average POC deposition rates from Table 2 multiplied by 270 to account for deposition during the March–November warm season interval.

[f] Area under the solid lines in Fig. 1.

[g] $A = \Sigma\mathrm{SOC} - (\Sigma\mathrm{SR} - 2J_S)$, where J_S = annual reduced sulfur burial (Table 1).

[h] B = Sediment Trap POC Deposition − (ΣSR + POC Burial).

[i] $C = B \cdot$ (Sediment Trap POC Deposition − POC Burial)$^{-1}$.

1982). The weighted average (daily basis) POC deposition rate (Table 2) was 76% higher at station DB than at R64. The weighted average deposition rates were multiplied by 270 to calculate 9-month, warm season integrated organic carbon input rates of 17.6 and 31.0 mol C m^{-2} for the two stations (Table 3).

d. POC burial. Dry mass sedimentation rates for sites very close to those sampled in this study are available from geochronological studies (Officer *et al.*, 1984). We have estimated permanent POC burial at stations R64 and DB by multiplying these rates by the average dry weight POC concentration at depth in the sediment (below which no significant change in POC concentration is observed) (Table 3). As with the sediment trap estimates of POC deposition, rates of dry mass sedimentation and POC burial at the shallow flank station DB were significantly higher than at channel station R64.

4. Discussion

a. Comparison of sediment POC loading estimates. One means of constraining rates of POC loading to mid-Bay sediments is to add estimates of permanent POC burial to those of total sediment carbon mineralization. To begin the calculation of total sediment carbon mineralization, we have made the assumption that aerobic respiration and SR are the predominant pathways of carbon metabolism in mid-Bay sediments, i.e. we ignored other possible anaerobic respiratory pathways such as denitrification, iron and manganese oxide reduction, and methanogenesis. Denitrification in the sediments at stations R64 and DB (Kemp *et al.,* 1990) accounts for oxidation of <0.5 mol C $m^{-2}\ yr^{-1}$, equal to $<4\%$ of the carbon flux through SR in these sediments. Although a recent study suggested that metal oxide reduction can play a significant role in coastal marine sediment carbon mineralization (Canfield *et al.,* 1993), recent experiments with mesohaline Bay sediments (Lustwerk and Burdige, 1993) indicate that iron and manganese diagenesis is dominated by interaction with the large quantities of sulfide produced by SR. Relatively high rates of SR are found in mid-Bay surface sediments (Roden and Tuttle, 1993), even during the spring and autumn when such sediments appear to be oxidized based on their brown coloration and positive redox potential (Kemp *et al.,* 1990). Moreover, during the summer when rates of carbon mineralization are maximal, mid-Bay surface sediments contain millimolar levels of sulfide (Roden and Tuttle, 1993), and thus metal reduction must be dominated by interaction with sulfide. Finally, estimates of methanogenesis in mid-Bay channel sediments based on pore water methane distributions (M. Marvin and D. Capone, unpubl data) amount to $<5\%$ of depth-integrated SR rates. Based on these considerations we feel justified in ignoring denitrification, metal oxide reduction, and methanogenesis in our calculations of total sediment metabolism.

The SR rate determinations reported here, although subject to *in situ* variability, are probably reliable estimates of anaerobic carbon mineralization because they are based on direct measurements (consideration of possible sources of error in these measurements suggests that if anything they represent *conservative,* i.e. lower-limit estimates of anaerobic carbon metabolism; Roden and Tuttle, 1993). In contrast, estimation of aerobic carbon respiration rates from SOC measurements in coastal sediments is complicated by the oxidation of reduced sulfur compounds by oxygen at or near the sediment-water interface (Jørgensen, 1977; 1983). Comparison of annually-integrated SR rates with estimates of reduced sulfur burial (Table 1) indicates that only a small fraction ($<20\%$) of the sulfide produced is retained in the sediments, the remainder of which is oxidized through processes that ultimately consume oxygen.

To assess the contribution of reduced sulfur oxidation to SOC we constructed budgets for sulfur and oxygen over March–August, August–November, and November–March time intervals (Table 1). Estimates of SOC attributable to sulfide oxidation in central channel sediments greatly exceeded measured SOC rates during the March–August interval. With respect to an annual cycle, the difference between total SR and permanent reduced sulfur burial exceeded (in carbon equivalents) total SOC by 80%. A large quantity of reducing equivalents was undoubtedly lost from central channel sediments via dissolved sulfide release to anoxic bottom waters during the summer (Roden and Tuttle, 1992; Kemp *et al.,* 1992), or via oxidation during transient bottom water reaeration events. Dissolved sulfide release from R64 sediments during anoxia corresponds to a potential oxygen demand of 1–2 g O_2 m^{-2} d^{-1} (Roden and Tuttle, 1992). This rate, integrated over a 90-d summer interval, would increase the annual SOC estimate by 44–88% (2.8–5.6 mol O_2 m^{-2} yr^{-1}). This calculation emphasizes the importance of summertime sulfur cycling in the annual oxygen budget of central channel deep waters.

Direct estimates of SOC at station DB during the March–August and August–November intervals (Fig. 1b) were lower than those predicted from estimates of reduced sulfur oxidation, and annual budget calculations (which include wintertime estimates of SOC) suggested that annual reduced sulfur oxidation approximated total SOC by DB sediments (Table 1). We interpret these results with caution, given the limited temporal coverage of the SOC measurements. In addition, with regard to the March–August and August–November intervals it is possible that we underestimated temporary reduced sulfur storage, the magnitude of which is subject to large uncertainties (Roden and Tuttle, 1993). This problem may have been particularly significant during the March–August interval, because some aerobic respiration undoubtedly occurred in DB sediments during spring macrofaunal recruitment. Despite uncertainties in the oxygen/sulfur budgets, sulfur cycling clearly plays a major role in controlling the ratio of carbon mineralization to SOC (i.e. the respiratory quotient) in DB sediments, particularly during the summer when maximum rates of SR occur very close to the sediment-water interface (see also Roden and Tuttle, 1993). Similar conclusions were drawn from recent studies of Narragansett Bay mesocosm sediments exhibiting metabolic rates comparable to those in the mid-Bay (Sampou and Oviatt, 1991a,b).

Given the difficulty in estimating aerobic respiration from measured SOC rates, we have chosen to use the measured SR rates to set a lower limit on the total rate of carbon mineralization in mid-Bay sediments. These rates can then be added to estimates of permanent POC burial to constrain the total rate of POC input (Table 3). The POC input rates calculated in this manner compare reasonably well with sediment trap-derived estimates of POC deposition, the latter being ≈20% and 40% higher at stations R64 and DB, respectively. The agreement between these values suggests that the sediment traps provide a robust estimate of the input of organic carbon to mid-Bay sediments. Verification of this suggestion awaits an accurate evaluation of the other potentially major pathways of carbon oxidation in mid-Bay sediments, i.e. aerobic respiration, which in turn will require detailed, simultaneous measurements of SOC and reduced sulfur formation, storage, and reoxidation over an entire annual cycle.

b. Role of POC deposition and sediment SR in the mid-Bay carbon cycle. Estimates of POC deposition to mid-Bay sediments derived from sediment traps and metabolism-plus-burial data range from 15.1 to 31.0 mol C m^{-2} (181 and 372 g C m^{-2}) (Table 3). Annual net primary production (NPP) in the mid-Bay region typically range from

25–50 mol C m^{-2} yr^{-1} (300–600 g C m^{-2}), although values as high as 65 mol C m^{-2} yr^{-1} have been reported (Flemer, 1970; Taft *et al.*, 1980; Boynton *et al.*, 1982; Malone *et al.*, 1988). At an average annual NPP rate of 42 mol C m^{-2} yr^{-1} (500 gC m^{-2}), total net POC deposition at stations R64 and DB accounts for 36–74% of total carbon production. A similarly large fraction of NPP is deposited to the sediments in other shallow coastal systems (Hargrave and Taguchi, 1978; Smetacek, 1980; Taguchi, 1982; Jørgensen, 1977; Joiris *et al.*, 1982; Oviatt *et al.*, 1986b; Jørgensen and Revsbech, 1989). As noted by Garber (1987), the mid-Bay seasonal pattern of sustained productivity and deposition throughout the warm season is in contrast to the predominance of the spring bloom in other coastal systems (Hargrave and Taguchi, 1978; Smetacek, 1980; Peinert *et al.*, 1982).

Again assuming an annual NPP rate of 42 mol C m^{-2} yr^{-1} for the mid-Bay region, our estimates of carbon flow through SR amount to 30–35% of total carbon production in the mid-Bay system. If our results at R64 and DB are reflective of the contribution of SR to carbon mineralization in mid-Bay sediments underlying ≥ 10 m water depth, which account for $\approx 50\%$ of the bottom area of the estuary in the vicinity of our lateral transect, the importance of SR in the overall carbon cycle in this region of the Bay is obviously quite significant. However, a potentially important factor that complicates quantitative interpretation of the role of sediment SR in the overall mid-Bay carbon cycle needs to be considered. Resuspension and transport of surface sediment out of shallow areas along the flanks of the estuary may concentrate the deposition of organic carbon produced throughout the water column to sediments in more quiescent areas, e.g. within the deeper flank and central channel regions. This suggestion is supported by the fact that sediments underlying shallow waters (<5 m depth) in the mid-Bay region are typically sandy with relatively low concentrations of both organic matter ($<2\%$ dry wt) and silt/clays, whereas those found at ≥ 10 m depth are predominantly fine-grained with considerably higher organic matter concentrations ($\geq 5\%$ dry wt) (Hill, 1988). The phenomenon of deep-water sediment focusing, which has been well-documented in lake systems (Wetzel, 1983), may result in the sediments at stations R64 and DB receiving more than their m^2 share of organic carbon deposition derived from primary production in overlying waters. Thus our budgetary estimates of the contribution of sediment SR to total mid-Bay carbon metabolism must be tentatively interpreted as maximum values until accurate estimates of the degree of sediment focusing and/or systematic quantification of SR rates in shallow versus deeper water sediments become available.

Keeping the above caveat in mind, we can compare our results with those from other open water, plankton-dominated coastal systems for which both SR and NPP data are available (Table 4). During eutrophication experiments in the Narragansett Bay MERL mesocosms, sediment SR accounted for a very large fraction (46–74%) of annual NPP. In contrast, SR rates measured in the Baltic Sea-North Sea transition

Table 4. Fraction of net primary production (NPP) in plankton-dominated coastal ecosystems accounted for by depth-integrated sediment sulfate reduction (ΣSR). Values are expressed in units of mol C m^{-2} yr^{-1}.

Location	Water depth (m)	ΣSR	NPP	ΣSR/NPP	Reference
Chesapeake Bay					
R64	16	12.6 ± 3.0	42	0.30	this study
DB	10	14.7 ± 4.8	42	0.35	
MERL mesocosms					
Control	5.5	14.6	20.7	0.71	Sampou and Oviatt, 1991a (ΣSR), Frithsen *et al.*, 1985 (NPP)[a]
4X		17.4	23.5	0.74	
8X		19.8	42.4	0.47	
16X		18.2	29.9	0.61	
32X		24.0	52.7	0.46	
Baltic Sea-North Sea transition	17–200	3.6 ± 1.4	12.5	0.29	Jørgensen *et al.*, 1990
Peru upwelling zone	135–502	14.6 ± 7.9	76.1	0.19	Fossing, 1990

[a] Estimated by trapezoidally integrating weekly (Sept. 1982–Sept. 1983) measurements of dawn-dusk O_2 production minus dusk-dawn O_2 consumption, and adding back annual sediment O_2 consumption for the same time period (SOC data from Sampou and Oviatt, 1991a).

and the Peru upwelling zone accounted for a more modest 20–30% of annual NPP, in the same range as our estimates for the mid-Chesapeake Bay. These comparisons show that our results are not out of line relative to those from other productive coastal systems, and taken together they demonstrate that in addition to being a major contributor to total sediment metabolism, SR can be a potentially important component of the overall carbon cycle in such systems. As emphasized by Sampou and Oviatt (1991b), an important implication of this is that because only a small fraction of the sulfide produced by SR is typically retained in coastal sediments, reduced sulfur reoxidation plays a major role in the oxygen and energy dynamics of these systems.

c. Fate of POC deposition to mid-Bay sediments. The POC burial rate estimates for stations R64 and DB (2.5 and 6.6 mol C m^{-2} yr^{-1}, respectively) account for 17–31% of POC input as estimated by the sum of integrated SR and POC burial (Table 3). These burial estimates correspond to 14–21% of net POC deposition estimated from the sediment trap data (Table 2). Similarly high degrees of remineralization have been reported for other coastal sediments (Jørgensen, 1977; Joiris *et al.*, 1982; Jørgensen *et al.*, 1990; Sampou and Oviatt, 1991a; McNichol *et al.*, 1988), whereas in other sediments a much greater fraction ($\geq 50\%$) of carbon input is permanently buried (Martens and Klump, 1984; Taguchi, 1982; Jørgensen *et al.*, 1990). A trend

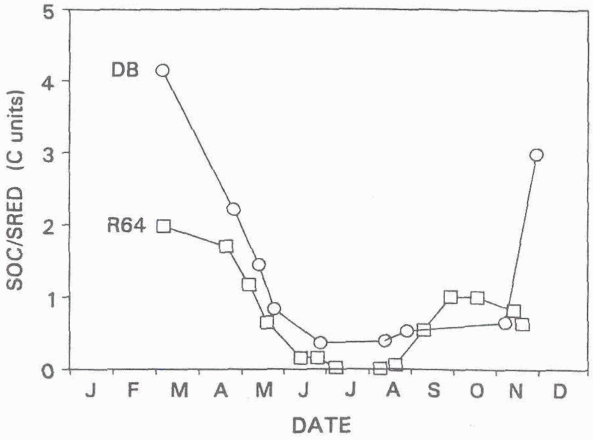

Figure 4. Ratio of SOC to depth-integrated (0–12 cm) SR rate (in carbon equivalents) at stations R64 (☐) and DB (○) over a warm season cycle. Ratios were calculated from SOC rates interpolated from the lines in Figure 1, and SR rates for the corresponding julian dates interpolated from the solid lines in Figure 2.

toward lower mineralization efficiency with higher carbon input is evident in these data, but the relationship is not a simple linear one. In this regard the source of POC input (e.g. phytoplankton versus terrestrial or marine macrophyte detritus) probably has a strong influence on the degree of organic carbon preservation. It is likely that most organic sedimentation in the open waters of the mid-Chesapeake Bay is linked to phytoplankton production, because particulate input from the Susquehanna River is largely confined to areas well north (≈ 50 km) of R64 and DB (Biggs and Flemer, 1972). Given the relative lability of phytoplankton-derived material, a high organic carbon mineralization efficiency in mid-Bay sediments is not unexpected. This situation differs, for example, from that in Cape Lookout Bight, where macrophyte detritus constitutes a large portion of total POC input, about 70% of which is preserved in the sediment (Martens and Klump, 1984).

Large seasonal variations in the ratio of SOC to depth-integrated SR (expressed in C equivalents) occurred in mid-Bay sediments (Fig. 4). SOC:SR ratios decreased from ≥ 3 in March to <1 by the end of May, approached zero in central channel sediments during summer anoxia, and were less than 0.5 at station DB during August. This pattern indicates a distinct shift from aerobic to anaerobic carbon mineralization during the early summer, even in sediments not overlain by anoxic bottom waters. Part of this dramatic shift may be linked to the onset of degradation of POC stored in surface sediments during the spring when temperatures are much lower (see Roden and Tuttle, 1995).

As discussed above, the available SOC data do not permit direct calculation of the contribution of aerobic respiration to sediment carbon mineralization. However, we can make a first approximation of this contribution by comparing sediment trap-derived POC collection rates and rates of carbon flow through SR. From the data in Table 3 (column C) we estimate that aerobic respiration may be responsible for 17 and 40% of carbon mineralization in sediments at stations R64 and DB, respectively. A higher value is expected for station DB sediments, which do not typically experience anoxia during the summer and which support an active macrofaunal community, at least during the spring and early summer (Kemp *et al.*, 1990). The data for DB must be interpreted with caution, however, because only one year of sediment trap measurements are available for this station. Moreover, the results of sediment trap deployments in shallow-water coastal environments must in general be interpreted cautiously because of the potential biasing influence of resuspension and deep-water sediment focusing. As with calculations of the contribution of sediment SR to total system carbon metabolism, these potential sources of error cast doubt on the accuracy of our estimates of the relative contribution of SR versus aerobic respiration to total mid-Bay sediment carbon metabolism. Nevertheless, we feel that our POC deposition and sediment SR rate estimates are sufficiently well-constrained so as to support at least *qualitatively* the suggestion of Mackin and Swider (1989) that an equal division of carbon flow through aerobic respiration and SR, thought to be typical of shallow (<20 m) subtidal coastal sediments (Jørgensen, 1982), does not hold for all situations. In fact, the available data indicate that R64 and DB sediments are analogous to those of Cape Lookout Bight (Chanton *et al.*, 1987) and Flax pond marsh (Mackin and Swider, 1989) in terms of the predominance of sulfur cycling in early diagenesis—a finding not unexpected given the high rate of organic matter sedimentation in the mid-Bay.

Mid-Bay sediments also resemble those of Flax Pond and many other nearshore environments in having a high carbon remineralization efficiency and a low degree of reduced sulfur retention. Thus our data support the conclusion of Nixon (1987) that changes in nutrient input, productivity, and organic sedimentation should impact Chesapeake Bay sediments on a time scale of a year or less, due to the lability of the deposited organic carbon and to the tendency of reduced sulfur end products to be efficiently oxidized at or above the sediment-water interface.

d. Conclusions and further questions. Two independent lines of evidence (i.e. measurements of benthic carbon mineralization and burial, and sediment trap deployments) suggest that sediment POC deposition is a major pathway in the carbon cycle of the mid-Chesapeake Bay. It also appears that SR mediates a large fraction (60–80%) of sediment carbon mineralization in sediments at ≥ 10 m depth, and that this process may recycle a substantial portion of NPP in mid-Bay waters. In addition, reoxidation of reduced sulfur formed by SR is responsible for much of sediment oxygen consumption in mid-Bay sediments. An important consequence of the latter phenomenon is that aerobic processes such as macrofaunal activity and nitrification are severely depressed during times of peak metabolism in the summer, even in sediments underlying well-oxygenated waters (Kemp *et al.*, 1990). A shift in sediment N-cycling from coupled nitrification/denitrification to enhanced NH_4^+ release (Kemp *et al.*, 1990) has major implications, given that primary production is thought to be N-limited during the summer (D'Elia *et al.*, 1986). Input of nutrients released from subpycnocline sediments to surface waters during mixing events is known to influence summer algal productivity (Malone *et al.*, 1986; 1988; Tuttle *et al.*, 1987).

An important unanswered question is the nature of carbon and nutrient cycling processes across the wide range of mid-Bay sediments at depths above the pycnocline (i.e. < 10 m). Recent studies indicate that depth-integrated primary production in the shallow waters of the mid-Bay is at least as high as that in the deeper regions (Malone *et al.*, 1986; 1988). It is not yet known whether high rates of sediment organic matter deposition occur beneath these productive shallow waters (see above discussion of sediment focusing), nor whether increased organic deposition linked to eutrophication would cause a shift toward anaerobic processes in shallow water sediments. This question deserves attention because nutrients released from such sediments are probably returned to the euphotic zone on a shorter time scale (i.e. more consistently) than those released from sediments below the pycnocline.

Acknowledgments. This work was supported by NSF grant OCE 82-08032 and NOAA Sea Grant project R/DO-9 (awarded to J. H. Tuttle), NSF grant BSR 88-14272 (awarded to W. M. Kemp, W. R. Boynton, D. G. Capone, and others), NOAA Seagrant project R/P-20 (awarded to W. M. Kemp and W. R. Boynton), and Maryland Dept. of the Environment project 3-C-MDE-XX (awarded to W. R. Boynton and W. M. Kemp). We are indebted to P. Sampou and J. .M. Barnes for assistance in the field, and we gratefully acknowledge M. Marvin and D. Capone for permission to present unpublished data. We also thank P. Sampou for very helpful comments on the manuscript. Contribution No. 2654 from the Center for Environmental and Estuarine Studies, University of Maryland.

REFERENCES

Biggs, R. 1970. Sources and distribution of suspended sediment in northern Chesapeake Bay. Mar. Geol., *9,* 187–201.

Biggs, R. B. and D. A. Flemer. 1972. The flux of particulate carbon in an estuary. Mar. Biol., 12, 11–17.

Boynton, W. R., W. M. Kemp, J. Garber, J. M. Barnes, L. L. Matteson, J. L. Watts, S. Stammerjohn and F. M. Rohland. 1990. Chesapeake Bay Water Quality Monitoring Program, Ecosystem Processes Component, Level 1 Report No. 7, Part 2: Data Tables. UMCEES Ref. No. 90-062CBL, Univ. of MD, Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, Solomons, MD.

Boynton, W. R., W. M. Kemp, J. M. Barnes, L. L. Matteson, J. L. Watts, S. Stammerjohn and F. M. Rohland. 1991. Chesapeake Bay Water Quality Monitoring Program, Ecosystem Processes Component, Level 1 Report No. 8, Part 1: Interpretive Report. UMCEES Ref. No. 91-110CBL, Univ. of MD, Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, Solomons, MD.

Boynton, W. R., W. M. Kemp and C. Keefe. 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production, *in* Estuarine Comparisons, V. S. Kennedy, ed., Academic Press, New York, 69–90.

Boynton, W. R., W. M. Kemp, C. Osborne, K. Kaumeyer and M. Jenkins. 1981. Influence of water circulation rate on *in situ* measurements of benthic community respiration. Mar. Biol., *65,* 185–190.

Canfield, D. E., B. Thamdrup and J. W. Hansen. 1993. The anaerobic degradation of organic matter in Danish coastal sediments: iron reduction, manganese reduction, and sulfate reduction. Geochim. Cosmochim. Acta, *57,* 3867–3883.

Capone, D. G. and R. P. Kiene. 1988. Comparison of microbial dynamics in freshwater and marine environments: Contrasts in anaerobic carbon catabolism. Limnol. Oceanogr., *33,* 725–749.

Chanton, J., C. Martens and M. Goldhaber. 1987. Biogeochemical cycling in an organic-rich coastal marine basin. 7. Sulfur mass balance, oxygen uptake, and sulfide retention. Geochim. Cosmochim. Acta, *51,* 1187–1199.

Christensen, J. P. 1989. Sulfate reduction and carbon oxidation rates in continental shelf sediments, an examination of offshelf carbon transport. Cont. Shelf Res., *9,* 223–246.

D'Elia, C., J. Sanders and W. Boynton. 1986. Nutrient enrichment studies in a coastal plain estuary: phytoplankton growth in large-scale, continuous cultures. Can. J. Fish Aquat. Sci., *43,* 397–406.

Flemer, D. 1970. Primary production in the Chesapeake Bay. Chesapeake Sci., *11,* 117–129.

Fossing, H. 1990. Sulfate reduction in shelf sediments in the upwelling region of Central Peru. Cont. Shelf. Res., *10,* 355–367.

Frithsen, J. B., A. A. Keller and M. E. Q. Pilson. 1985. Effects of inorganic nutrient additions in coastal areas: A mesocosm experiment data report. Volume 1. MERL Series, Report No. 3, The University of Rhode Island, Kingston, RI.

Garber, J. 1987. Benthic-Pelagic Coupling in the Chesapeake Bay, *in* Perspectives on the Chesapeake Bay: Recent Advances in Estuarine Sciences, M. P. Lynch and E. C. Krome, eds., Chesapeake Research Consortium Publication No. 127, Glouchester Pt., VA, 11–34.

Hargrave, B. and S. Taguchi. 1978. Origin of deposited material sedimented in a marine bay. J. Fish. Res. Board Can., *35,* 1604–1613.

Hill, J. M. 1988. Physiographic distribution of interstitial waters in Chesapeake Bay. Report of Investigations No. 49. Maryland Geological Survey. Annapolis, MD.

Holland, A. 1988. Long-term variation of macrobenthos in a mesohaline region of Chesapeake Bay. Estuaries, *8,* 93–113.

Howarth, R. W. 1984. The ecological significance of sulfur in the energy dynamics of salt marsh and coastal marine sediments. Biogeochemistry., *1,* 5–27.

Joiris, C., G. Billen, C. Lancelot and J. Hecq. 1982. A budget of carbon cycling in the Belgian coastal zone: relative roles of zooplankton, bacterioplankton, and benthos in the utilization of primary production. Neth. Jour. Sea Res., *16,* 260–275.

Jørgensen, B. B. 1977. The sulfur cycle of a coastal marine sediment (Limfjorden, Denmark). Limnol. Oceanogr., *28,* 814–822.

—— 1978. A comparison of methods for the quantification of bacterial sulfate reduction in coastal marine sediments I. Measurement with radiotracer techniques. Geomicrobiol. Jour., *1,* 11–28.

—— 1982. Mineralization of organic matter in the sea bed—the role of sulfate reduction. Nature, *296,* 643–645.

—— 1983. Processes at the sediment water interface, *in* The Major Biogeochemical Cycles and Their Interactions, B. Bolin and R. B. Cook, eds., Wiley and Sons, New York, 477–509.

Jørgensen, B. B. and N. P. Revsbech. 1989. Oxygen uptake, bacterial distribution, and carbon-nitrogen-sulfur cycling in sediments from the Baltic-North Sea transition. Ophelia, *31,* 29–49.

Jørgensen, B. B., M. Bang and T. H. Blackburn. 1990. Anaerobic mineralization in marine sediments from the Baltic Sea-North Sea transition. Mar. Ecol. Prog. Ser., *59,* 55–61.

Kemp, W. M., P. Sampou, J. Caffrey, M. Mayer, K. Henriksen and W. R. Boynton. 1990. Ammonium recycling versus denitrification in Chesapeake Bay sediments. Limnol. Oceanogr., *35,* 1545–1563.

Kemp, W. M., P. Sampou, J. Garber, J. Tuttle and W. R. Boynton. 1992. Seasonal depletion of oxygen from bottom waters of Chesapeake Bay: roles of benthic and planktonic respiration and physical exchange processes. Mar. Ecol. Prog. Ser., *85,* 137–152.

Lustwerk, R. L. and D. J. Burdige. 1993. Iron and manganese reduction in Chesapeake Bay sediments. EOS, Trans. Am. Geophys. Union., *74,* 326.

Mackin, J. and K. Swider. 1989. Organic matter decomposition pathways and oxygen consumption in coastal marine sediments. J. Mar. Res., *47,* 681– 716.

Malone, T., L. Crocker, S. Pike and B. Wendler. 1988. Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. Mar. Ecol. Prog. Ser., *48,* 235–249.

Malone, T., W. Kemp, H. Ducklow, W. Boynton, J. Tuttle and R. Jonas. 1986. Lateral variation in the production and fate of phytoplankton in a partially stratified estuary. Mar. Ecol. Prog. Ser., *32,* 149–160.

Martens, C. S. and R. A. Berner. 1974. Methane production in the interstitial water of sulfate depleted marine sediments. Science, *185,* 1167–1169.

Martens, C. S. and J. V. Klump. 1984. Biogeochemical cycling in an organic-rich coastal marine basin 4. An organic carbon budget for sediments dominated by sulfate reduction and methanogenesis. Geochim. Cosmochim. Acta, *48,* 1987–2004.

McNichol, A., C. Lee and E. Druffel. 1988. Carbon cycling in coastal sediments: 1. A quantitative estimate of the remineralization of organic carbon in the sediments of Buzzards Bay, MA. Geochim. Cosmochim. Acta, *52,* 1531–1543.

Nedwell, D. 1984. The input and mineralization of organic carbon in anaerobic aquatic sediments, *in* Advances in Microbial Ecology, Vol. 7, K. C. Marshall ed., Plenum Press, New York, 93–101.

Nixon, S. W. 1987. Chesapeake Bay nutrient budgets—a reassessment. Biogeochemistry, *4,* 77–90.

Officer, C., D. R. Lynch, G. H. Setlock and G. R. Helz. 1984. Recent sedimentation rates in Chesapeake Bay, *in* The Estuary as a Filter, V. S. Kennedy ed., Academic Press, New York, 131–158.

Oremland, R. S. and B. F. Taylor. 1978. Sulfate reduction and methanogenesis in marine sediments. Geochim. Cosmochim. Acta, *42,* 209–214.

Oviatt, C. A. and S. W. Nixon. 1975. Sediment resuspension and deposition in Narragansett Bay. Est. Coast. Mar. Sci., *3,* 201–217.

Oviatt, C. A., A. A. Keller, P. A. Sampou and L. L. Beatty. 1986a. Patterns of productivity during eutrophication: a mesocosm experiment. Mar. Ecol. Prog. Ser., *28,* 69–80.

Oviatt, C. A., D. Rudnick, A. A. Keller, P. Sampou and G. Almquist. 1986b. A comparison of system (O_2 and CO_2) and C-14 measurements of metabolism in estuarine mesocosms. Mar. Ecol. Prog. Ser., *28,* 57–67.

Parsons, T. R. and M. Takahashi. 1984. Biological Oceanographic Processes. Pergamon Press, Oxford.

Peinert, R., A. Saure, P. Stegmann, C. Stienen and H. Haardt. 1982. Dynamics of primary production and sedimentation in a coastal ecosystem. Neth. Jour. Sea Res., *16,* 276–289.

Roden, E. E. and J. H. Tuttle. 1992. Sulfide release from estuarine sediments underlying anoxic bottom water. Limnol. Oceanogr., *37,* 725–737.

—— 1993. Inorganic sulfur cycling in mid- and lower Chesapeake Bay sediments. Mar. Ecol. Prog. Ser., *93,* 101–118.

—— 1995. Organic carbon cycling in mesohaline Chesapeake Bay sediments 2: Kinetics of particulate and dissolved organic carbon turnover. J. Mar. Res., (submitted).

Sampou, P. and C. A. Oviatt. 1991. Seasonal patterns of sedimentary carbon and anaerobic respiration along a simulated eutrophication gradient. Mar. Ecol. Prog. Ser., *72,* 271–282.

Sampou, P. and C. A. Oviatt. 1991. A carbon budget for a eutrophic marine ecosystem and the role of sulfur metabolism in sedimentary carbon, oxygen, and energy dynamics. J. Mar. Res., *49,* 825–844.

Senior, E., E. Lindstrom, I. Banat and D. Nedwell. 1982. Sulfate reduction and methanogenesis in the sediment of a salt marsh on the east coast of the United Kingdom. Appl. Environ. Microbiol., *43,* 987–996.

Smetacek, V. 1980. Annual cycle of sedimentation in relation to plankton ecology in western Kiel Bight. Ophelia, Suppl. *1,* 65–76.

Steele, J. and I. E. Baird. 1972. Sedimentation of organic matter in Scottish Sea loch. Mem. Ist. Ital. Idrobial., *29* Suppl, 73–88.

Strickland, J. D. H. and T. R. Parsons. 1972. A practical methods of seawater analysis. Fish. Res. Bd. Can., Bull. 167, Second Edition.

Suess, E. 1980. Particulate organic carbon flux in the oceans—surface productivity and oxygen utilization. Science, *288,* 260–263.

Sun, M., R. C. Aller and C. Lee. 1991. Early diagenesis of chlorophyll-*a* in Long Island Sound sediments: a measure of carbon flux and particle reworking. J. Mar. Res., *49,* 379–401.

Sun, M. C. Lee, and R. C. Aller. 1993. Laboratory studies of oxic and anoxic degradation of chlorophyll-*a* in Long Island Sound sediments. Geochim. Cosmochim. Acta, *57,* 147–157.

Taft, J., W. Taylor, E. Harwig, and R. Loftus. 1980. Seasonal oxygen depletion in Chesapeake Bay. Estuaries, *3,* 242–247.

Taguchi, S. 1982. Sedimentation of newly produced particulate organic matter in a subtropical inlet, Kaneohe Bay, Hawaii. Est. Coast. Shelf Sci., *14,* 533–544.

Tuttle, J., R. Jonas, and T. Malone. 1987. Origin, development and significance of Chesapeake Bay anoxia, *in* Contaminant Problems and Management of Living Chesapeake Bay Resources, S. K. Majumdar, L. W. Hall Jr. and M. A. Herbert, eds., Pennsylvania Academy of Sciences, Phillipsburg, 442–472.

Wetzel, R. G. 1983. Limnology, Second Edition, Sunders College Publishing.

Zhabina, N. and I. Volkov. 1978. A method of determination of various sulfur compounds in sea sediment and rocks, *in* Environmental Biogeochemistry and Geomicrobiology, Vol. 3., W. E. Krumbein, ed., Ann Arbor Sci. Publ., Ann Arbor, MI, 735–746.

Received: *8 October, 1993;* revised: *4 May, 1995.*