

Community electron transport of procaryotes in euryoxic estuarine sediment

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ABSTRACT: Rates of both tetrazolium and oxygen reduction were obtained seasonally from the top 8 cm of euryoxic estuarine sediment in southeastern New England, USA, over an *in situ* temperature range of 0 to 20 °C. Anoxic tetrazolium reduction was highest in the 3 to 5 cm layers at 15 °C (up to 860 nmol 2e⁻ cm⁻³ h⁻¹). Changes in the chemistry of deeper pore-waters (20 to 60 cm) occurring over 90 d indicated that metabolic rates (ca 42 nmol 2e⁻ cm⁻³ h⁻¹) were about an order of magnitude lower than those in the surface sediments. Parallel simultaneous estimates of O₂ reduction (reduced sediment preincubated in O₂-saturated ambient waters ± 10 mM NaN₃) averaged 4 times greater than tetrazolium reduction. The postulated occurrence of a mixed metabolic community consisting of facultatively anaerobic heterotrophs and chemolithotrophs agrees with the field data. The community is spread out vertically through watery sediment of a quiescent, highly depositional cove. Soft-bodied infauna may help maintain the Eh potential at ca - 200 mV from 1 to 60 cm; the sediment is not sufficiently cohesive to be strongly poised.

INTRODUCTION

Very high rates of microbial activity have been found in subsurface layers of coastal sediments near the redox discontinuity layer ('reductocline') (Novitsky & Kepkay 1981, Graf 1986, Novitsky & Karl 1986, Peroni & Rossi 1986). A strongly poised reductocline can be maintained by cohesive sediment and by abundant supplies of Fe that sequester reduced S. This transition zone contains a variety of oxidized and reduced organic and inorganic materials that sequentially and alternately function as electron donors and acceptors under a regime of advection, diffusion, and rapid recycling. A diverse assemblage of hetero-, mixo-, and auto-trophic microorganisms maintains this electrochemical gradient.

Here we present tetrazolium and oxygen reduction data from euryoxic and anoxic estuarine muds and find subsurface maxima in anoxic activity within the top 8 cm that decrease about 10-fold at depths of 50 to 60 cm. However, in contrast with studies cited above, the maxima occur in an electrochemically homogenous milieu. We attribute these higher rates to the existence of a quiescent depositional regime that promotes the

accumulation of watery muds and the subsequent extension of a poorly poised reductocline down to at least 60 cm in the sediment. Sediment has accumulated at this site up to the critical wave mixing depth (ca 1 m at MHW) so that no new net sedimentation occurs. In this regime, the sediment column is being metabolized from the bottom up, with both methanogens and sulfate-reducers occupying the same levels in top 10 cm muds (Hines & Buck 1982).

MATERIALS AND METHODS

Study area. Quiambog Cove (average depth = 1 m; area = 29 ha) is a submerged valley located near Stonington, Connecticut (41° 25' N, 71° 57' W) in southeastern New England, USA, that contains glacial till and alluvium. The mouth of the estuary is constricted by a railroad bridge constructed about a century ago. Consequently, the cove has rapidly filled with fine sediment to a level where no net sediment accumulation can occur because of turbulence. Similar construction activities have affected many of the drowned stream valleys throughout New England. The flow ratio (13 h river flow/tidal prism volume) for this cove ranges between 0.006 and 0.9, but remains less than 0.1 during 8 mo of the year. Average tidal flushing times range

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between 1.9 and 3.4 d (Foerster 1973). The sediment can be described as muddy clay that only rarely has salinities below 10‰. About 20% of the cove is covered with *Zostera marina*, and the remainder has various seasonal assemblages of *Gracillaria*, *Lomentaria*, *Enteromorpha*, and *Fucus*. Annual organic carbon (OC) supply to these sediments ranges from 70 to 170 mol m⁻² and averages 120, which includes 45 mol from terrestrial runoff (Matson 1982).

Sediment and pore-water chemistry. Sixteen pore-water samplers (Soil Moisture Samplers®) were cleaned, installed in the sediments to depths of 20 to 60 cm at 8 sites in the cove in early March, allowed to leach and equilibrate for 1 mo, and sampled in April (at 5 °C) and July (at 20 °C). Waters were removed *in situ* by displacing sampler contents with N₂ into a 50 cm³ syringe. The waters were immediately analyzed for redox potential (Eh) and pH (Corning electrodes), and NH₄⁺ (phenol/hypochlorite); preserved samples were later analyzed for Cl⁻ (Buchler-Cotlove Cl titrator), SO₄²⁻ (BaCl₂), alkalinity (titration), dissolved organic carbon (DOC; thermal combustion, IR detection), and carbohydrates (Gerchakov & Hatcher 1972). Box cores of the upper 10 to 15 cm were taken irregularly and were processed the same day for chemical constituents as above.

Tetrazolium and oxygen reduction. Solutions of INT (2-*p*-iodophenyl-3-*p*-nitrophenyl-5-phenyl 2H tetrazolium chloride; Sigma, Grade I) were made up at ca 25 mM in ethyl alcohol (EtOH), stored in acid-cleaned glass vials with Polyseal® caps to prevent evaporation of EtOH and wrapped with black tape to avoid photo-reduction. The EtOH solvent did not affect the activity of the samples tested at concentrations less than 10%, and in no case was the final EtOH concentration >2%. Standard curves were constructed with N₂-sparged solutions of either ascorbic acid or S²⁻ (as Na₂S·9H₂O; both Fisher Reagent Grade) as reductants. Molar absorptivities (17 400 l⁻¹ mol⁻¹ cm⁻¹, ± 2% at 465 nm) were identical to those reported by Altman (1976), and all INT added was completely reduced (Matson 1982).

Samples of surface mud were obtained with ordinary manual coring procedures that protected the integrity of the sediment-water interface. All muds were sectioned, subsampled, and processed under N₂ in a glove bag and slurried with filtered waters obtained from the coring site. Controls for chemical tetrazolium reduction were immediately autoclaved at 15 psi (= 10⁵ Pa) for 30 min in a gas-tight clamp device used to sterilize tubed media for methanogens (Hines & Buck 1982). Total acid-volatile sulfides (TS²⁻ = HS⁻ + H₂S + FeS) were measured colorimetrically with either methylene blue (Cline 1969) or INT (Matson 1985). Under N₂, 60 μl of 25 mM INT were added to 3 ml mud slurries to obtain a final optimum concentration of 0.5 mM INT (Matson

1982). Subsamples were incubated at *in situ* temperatures and were sacrificed after variable periods of up to 300 min depending upon (a) ambient temperature and (b) visual evidence of formazan production.

Reduction of INT in time-series incubations was stopped by filtration and resuspension of the sediment in several volumes of acetone, which extracts the INT-formazan. This extract also provided a blank for photosynthetic pigments (rarely >10% of absorbance at 465 nm). Acetone extraction of clastic sediments takes 0.5 to 2 h, sometimes requires clarification by filtration or centrifugation prior to spectrophotometry, and the extract is stable for at least 1 mo in the dark. Among 5 sets of duplicates slurried up to 5-fold, relative precision was 10 to 15% (Matson 1982, 1985).

INT reduction requires 2e⁻, and data are expressed as mol 2e⁻ equivalents per unit weight or volume of sediment per unit time. The time units and net biochemical reduction rates were calculated by 2 methods: (1) by subtraction of the 5, 10 or 20 min incubation data (which are mostly due to chemical INT reduction; Matson 1982, 1985, Peroni & Rossi 1986) from the 30 min, 60 min, or longer term incubations (depending on ambient temperature); and (2) by subtraction of autoclaved chemical controls from total tetrazolium reduction.

RESULTS

Sediment and pore-water chemistry

The Eh of the top 60 cm of sediment remained at about -200 mV in almost all samples between April and July (Table 1, Fig. 1). Pore-water Eh was greater than -200 mV in only 5 of 16 pore-water samplers in April, and in 1 of 15 in July. Sediment (Fig. 1) and pore-water (Table 1) pH varied slightly, remaining between 6.6 and 7.8. Both surface sediment and deeper pore waters showed evidence of freshwater intrusion, especially at sites nearer the head of the estuary (Stns QC7 to 9). SO₄²⁻ was slightly enriched in the warmed surface sediments in early June (Fig. 1), and was depleted by up to 100% in the pore-water samplers. In April, DOC and ammonium levels were quite high, and by July, when the sediments had warmed to 20 °C, alkalinities increased substantially with a corresponding decrease in DOC. DOC values ranged from a low of 1.5 mM in July to a high of 30 mM in April. Total carbohydrates were a minor fraction of the total DOC pool, and ranged from 0.008 to 0.056 mM.

In April, when the sediments were still cold from winter, these metabolites were strongly related, with linear regression coefficients >0.82 (Fig. 2). Later in July, the data were not as well related. Alkalinity

Table 1. Quiambog Cove pore-water chemistry. Z: depth; T.A.: titration alkalinity; sulfate data are percent depletion from seawater stoichiometry expected at *in situ* Cl^- ; CH_2O is glucose equivalents. * Samplers left undisturbed and resampled in July. Station numbers decrease towards the mouth of the estuary, and stations QCZ are located between Stns 4 and 7

Station	Z (cm)	Eh (mV)	pH	Cl^- (mM)	T.A. (meq l^{-1})	% SO_4^{2-}	DOC (mM)	NH_4^+ (mM)	CH_2O (mM)
April, 5° C									
QC-2S	26	-210	7.3	460	6.6	17	8.1	0.24	0.022
QC-3S	26	-220	7.5	470	9.1	50	22	0.50	0.031
QC4-S1	29	-220	7.8	460	12	54	22	1.5	0.014
QC4-S2	29	-220	7.7	450	-	58	24	0.70	0.021
QCZ-1S	26	-220	7.4	400	11	38	17	0.45	0.039
QCZ-2S	29	-160	7.5	360	4.8	47	15	0.60	0.008
QC7-S	17	-200	7.8	360	6.8	50	16	0.35	0.056
QC8-S1	9	+ 60	7.4	150	2.9	98	5.1	0.20	0.014
QC8-S2	27	-110	7.3	330	4.2	29	5.0	0.16	0.012
QC9-S	30	+ 60	7.1	260	4.3	42	5.4	0.15	0.005
QC2-L	50	-100	7.4	460	9.0	29	8.5	0.28	0.016
QC3-L	57	-220	7.7	480	22	75	30	1.0	0.005
QCZ-L1	57	-220	7.6	320	12	98	28	0.90	0.047
QCZ-L2	51	-220	7.8	310	16	86	20	0.90	0.017
QC7-L	51	-220	7.8	260	10	96	20	0.50	0.010
QC9-L	55	+ 90	7.4	110	4.2	91	4.9	0.26	-
July, 20° C									
*QC4-S1	29	-210	7.4	470	23	45	3.3	No July data	
QC5-S	27	-210	7.3	510	39	80	3.8		
*QC7-S	17	-210	6.9	370	24	55	3.3		
QC8-S1	27	-210	6.9	340	64	29	3.0		
*QC8-S2	27	-210	7.0	370	72	16	2.0		
QC9-S	30	-210	7.0	270	84	32	2.5		
*QCZ-S1	26	-210	7.5	420	22	57	3.4		
*QCZ-S2	29	-210	7.3	390	32	55	3.1		
QCZ-S3	30	-210	7.2	450	20	44	4.1		
QC6-L	55	-150	6.7	480	3.7	16	1.5		
QC8-L	55	-210	7.4	170	47	74	1.5		
*QC9-L	55	-210	6.6	120	40	49	3.1		
*QCZ-L1	57	-210	7.3	340	28	100	4.8		
*QCZ-L2	50	-210	7.2	320	18	67	2.9		
QCZ-L3	55	-210	7.4	450	83	80	7.5		

values increased dramatically to as high as 84 meq l^{-1} , while DOC values decreased ca 1 order of magnitude. In contrast, sulfate depletions (normalized to seawater

Cl^- stoichiometry) changed very little during this 90 d period.

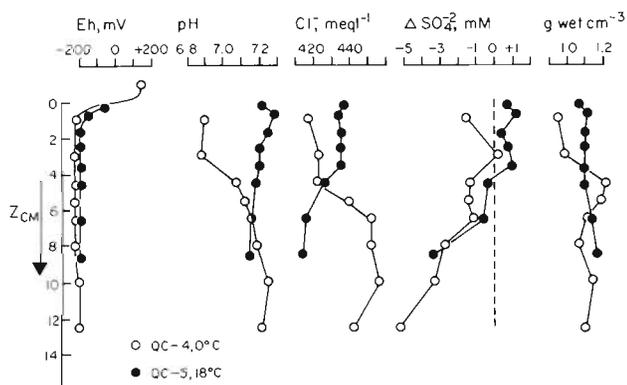


Fig. 1. Quiambog Cove surface sediment chemistry. Redox potential (Eh) and pH by direct insertion of electrodes into sectioned sediment under N_2 ; change in SO_4^{2-} concentrations from seawater Cl^- stoichiometry, and bulk sediment density

Tetrazolium and oxygen reduction

Over the entire range of *in situ* temperatures tested, anoxic INT reduction ranged from 0 to 860 $\text{nmol } 2e^-$ (0 to 430 nmol O_2 equivalents) $\text{cm}^{-3} \text{h}^{-1}$ (Table 2). Subsurface peaks in anoxic INT reduction occurred at all 4 temperatures. Maximum average activity was at 15 °C, and the highest depth average was at ca 5 cm. Biochemical oxygen reduction (distinguished from chemical oxygen demand [COD] with 10 mM NaN_3) at 15 and 20 °C ranged from 480 to 2100. At 15 °C, a minimum in O_2 reduction coincided with a maximum in INT reduction, while at 20 °C, the 2 rates showed similar trends. The average INT/ O_2 reduction rate ratios were 0.67 and 0.22 $\text{nmol } 2e^- \text{ cm}^{-3} \text{ h}^{-1}$ at 15 and 20 °C, respectively.

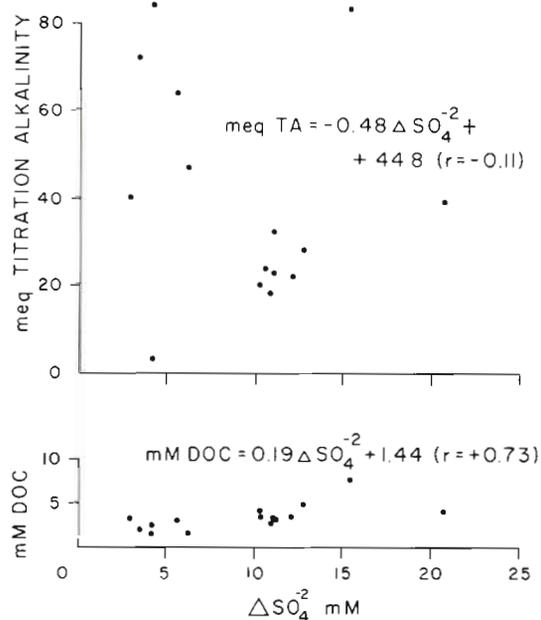
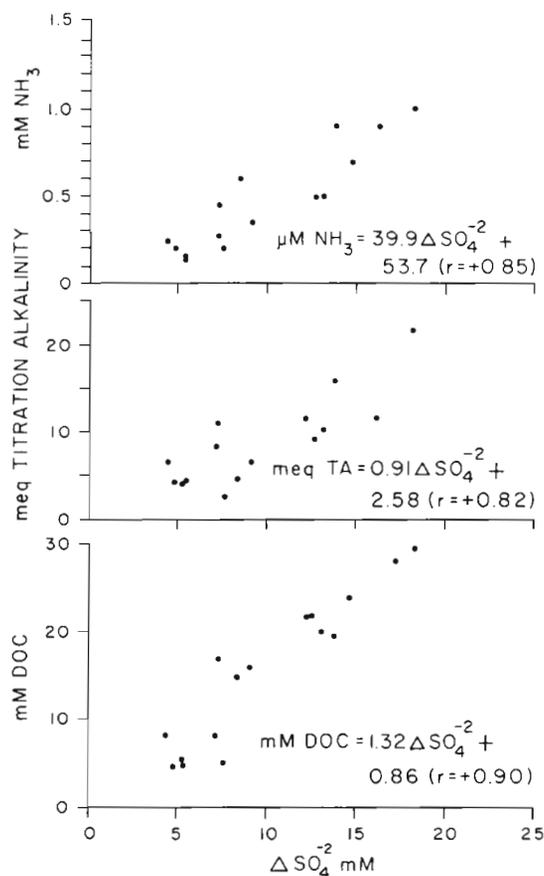


Fig. 2. Quiabog Cove pore-water chemistry. Relations plotted from data in Table 1 from April (left) and July (above)

Table 2. Biochemical INT and O₂ reduction rates (nmol 2e⁻ cm⁻³ h⁻¹; $\bar{X} \pm 1$ SD) from cores of Quiabog Cove muds obtained and incubated at *in situ* temperatures of 0, 10, 15, and 20° C. Calculated by subtracting the 5 min (at 15 and 20° C) or 20 min (at 0 and 10° C) reduction data. O₂ data from simultaneous, parallel incubations of proportional slurries in 300 ml biochemical oxygen demand (BOD) bottles \pm 10 mM NaN₃

Sediment depth (cm)	0° C INT	10° C INT	15° C INT	15° C O ₂	20° C INT	20° C O ₂	Depth mean* INT (SD)
0-1	0	80	240	1300	300	2100	160 (88)
1-2	90	330	770	1400	200	1700	350 (86)
2-4	180	140	860	480	85	930	320 (113)
4-6	43	140	810	1300	520	1000	380 (92)
6-8	0	380	320	1600	200	810	230 (74)
Temperature							
Mean	52	210	600	1200	260	1300	
SD	72	130	300	380	160	500	

* Averages based on 2 significant digits

The highest rates of anoxic INT reduction occurred in the mid-sections of each of the 10 cm cores. Averages for the 1 to 2 and 4 to 6 cm layers were about twice those for the surface sediments. However, the 0 to 1 cm sediments had rates of O₂ reduction as high as 2100 nmol cm⁻³ h⁻¹ at 20° C (7 times the surface layer INT rate) and 1300 nmol O₂ (5 times the INT rate) at 15° C. Also, at 15° C, biochemical O₂ reduction in the 4 to 8 cm

layers was as great as or greater than the rates in the surface sediments.

Net community catabolic rates for the deeper sediments were calculated from the changes in the pore-water samplers left undisturbed between April and July. After correction for diffusional fluxes (Berner 1980, Matson & Brinson 1985), net rates were 20 to 50 nmol SO₄²⁻, 11 to 35 nmol DOC, and 10 to 73 nmol CO₂

(all units of $2e^- \text{ cm}^{-3} \text{ h}^{-1}$). The latter 2 estimates assume the occurrence of organic carbon at oxidation state 0 (i.e. carbohydrate). The median of the CO_2 rates, $42 \text{ nmol } 2e^- \text{ cm}^{-3} \text{ h}^{-1}$, is (1) the same as the average 0°C INT rates, and (2) about 9-fold lower than the average for the 1 to 5 cm layer, regardless of temperature.

DISCUSSION

Total microbial community activity in many sediments is difficult to measure because a variety of electron donors and acceptors is metabolized simultaneously. Adjacent microniches of heterotrophic and autotrophic activity commonly occur and produce a spatially and temporally variable redox regime (Vanderborght & Billen 1975, Grundmanis & Murray 1977, Jorgensen 1977, Oremland & Taylor 1978, Hines & Buck 1982, Jorgensen & Revsbech 1985). To overcome this logistical problem and to study community metabolism from a common enzymic basis, variations of the electron transport system (ETS) method reported by Packard (1971) have been applied to both oxic and anoxic sediments (Weiser & Zech 1975, Zimmerman 1975, Olanczuk-Neyman & Vosjan 1977, Liu & Strachan 1981, Matson 1982, 1985, Graf 1986, Peroni & Rossi 1986). Although different alternate electron acceptors have been used (e.g. resazurin, several tetrazolium salts), all these techniques are conceptually similar to the methylene blue reduction indices used for decades in the health sciences to grade milk (Jay 1978). Tetrazolium salts interrupt electron transport by effectively competing with cytochromes (and not directly with the terminal electron acceptor) for electron pairs at sites specific for the particular tetrazolium salt, regardless of the character of the terminal electron acceptor (Altman 1976). They do not compete for $2e^-$ pairs with the terminal electron acceptor, but with the enzymes within the ETS that facilitate $2e^-$ flow. Various aspects of tetrazolium reduction have been described previously (Kopper 1952, Eidus et al. 1959, Tengerdy et al. 1967, Kalina & Palmer 1960, Saito & Iwaizumi 1969, Anderson & Hoyer 1974, Reichardt 1979, Smith & Pugh 1979, Baker & Mills 1982, Tabor & Niehof 1982, Vosjan 1982).

Under anoxia, the 'in vivo' INT reduction technique used here measures all of SO_4^{2-} and Fe^{3+} reduction and a variable fraction of reduction of the other acceptors between SO_4^{2-} and O_2 in the electrochemical gradient. During electron transport directed towards the reduction of sulfate or iron, any of the paired electrons that do not reduce a tetrazolium ion continue to the end of the respiratory chain and produce either S^{2-} or Fe^{2+} , both of which reduce INT within seconds to minutes (Matson 1985). For all transport chains, the proportion

of electron pairs that reduce an INT molecule (rather than the next enzyme in the transport chain) depends upon (1) the relative concentration of INT (a cation) bound to the procaryotic membranes, and (2) the rate of $2e^-$ flow through the pool of community ETS chains.

Under low concentrations of naturally occurring terminal electron acceptors (TEAs), the ETS is generally quite sensitive to both changes in TEA concentration (Doelle 1975, Mitchell 1979) and to potentially toxic chemicals such as INT (Fahmy & Walsh 1952, Eidus et al. 1959, May et al. 1960, Slater et al. 1963, Clark et al. 1965). For example, with O_2 , INT begins to inhibit total electron flow (i.e. the reduction of both O_2 and INT) only when the INT/ O_2 ratio is greater than 0.3 (in units of $2e^-$; i.e. $100 \mu\text{M}$ INT and $320 \mu\text{M}$ O_2 ; Matson 1982, 1985). This TEA stoichiometry should also apply to other TEAs such as NO_3^- , NO_2^- , and Mn^{4+} . However, the reduced forms of these other TEAs (e.g. NO_2^- , NH_4^+ , and Mn^{2+}) do not reduce INT (as is the case for S and Fe), and, under N_2 , reoxidation and subsequent recycling is precluded.

Further, in a few experiments with yeasts, fungi, diatoms, and nematodes, we observed INT reduction only after many hours to days, while active procaryotes reduce INT within minutes, depending upon temperature. This is apparently due to the extended length of time (at least hours) required for the tetrazolia to penetrate intact cells and to become exposed to fermentation dehydrogenases and to the mitochondria of eucaryotes (both of which, in contrast to the membrane-bound respiratory enzymes of procaryotes, are found in the cytoplasm; Haddock & Jones 1977, Thauer et al. 1977). From this we tentatively conclude that the activity of fermenters (which may be important in the production of electron donors for sulfate-reducers; Sorensen et al. 1981, Howarth 1984) and of eucaryotes is not measured in this 'in vivo' INT assay. Also, no tetrazolia have been described that can be reduced at the *pe* of methanogenesis. These organisms may be quite numerous and active in some surface sediments (Oremland & Taylor 1978, Hines & Buck 1982). More importantly, the cytochrome chains of actively aerobic organisms collapse immediately (within seconds) and do not reduce INT when O_2 is removed with N_2 , as in this assay (Matson 1985). For these reasons, the community catabolic data presented here are largely restricted to the activity of procaryotes that are actively respiring under N_2 and in a regime of limited recycling of electron acceptors/donors, and therefore are underestimates.

A summary of cumulative oxic and anoxic community catabolism to 7 cm is given in Fig. 3. The total for INT reduction only is $207 \text{ mol } 2e^- \text{ m}^{-2} \text{ yr}^{-1}$, or 86 % of estimated total annual supply of OC to Quiambog Cove. If the O_2 reduction data are used for the surface

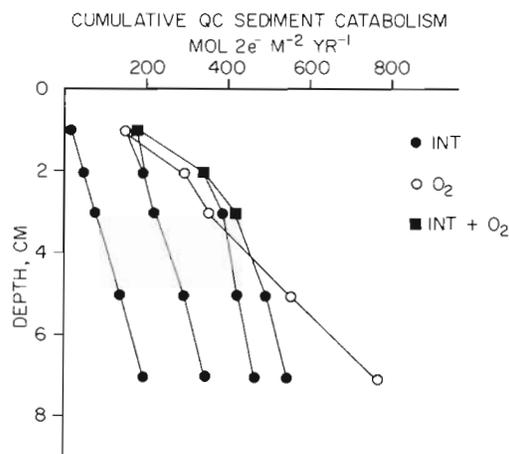


Fig. 3. Cumulative Quiamog Cove sediment catabolism. Depth averages for data in Table 2 integrated over the 7 cm sediment and extrapolated to annual rates

1 cm and added to the 1 to 7 cm INT data, then the total is $308 \text{ mol } 2e^- \text{ m}^{-2} \text{ yr}^{-1}$ or 1.3 times total OC supply. Organic matter contents of the subsurface muds to a depth of 7 cm average 5.5% or ca $320 \text{ mol OC m}^{-2}$ ($640 \text{ mol } 2e^-$ if it hypothetically exists as CH_2O , which it does not; Table 1) (Matson 1982). Therefore, in spite of the occurrence of anoxic catabolic rates that are approximately equivalent to total organic carbon supply, a substantial amount of OC persists in these sediments.

Recently, Graf (1986) and Novitsky & Karl (1986) mentioned the occurrence of high per-cell levels of subsurface microbial activity. These were considered anomalous in light of many reports of highest activity in the surface layer, either within or directly above the redoxcline (Graf 1986). We suggest that the higher subsurface rates reported here for both O_2 and INT are due to several factors. First, it is not surprising that anoxic INT reduction rates were higher below the redoxcline. The incubation conditions under N_2 inhibit the activity of obligate aerobes that may be a major component of the surface community. The higher O_2 reduction rates in the 0 to 2 cm layers in comparison with anoxic INT rates support this conclusion. Also, more organic matter occurs in the top 1 cm (9.5% OC) than in the next 8 cm (5.5% OC). Thus it remains that facultatively anaerobic bacteria, some of which can simultaneously reduce NO_3^- and Fe^{3+} (Thauer et al. 1977), are the active components of the subsurface community. These organisms, along with facultatively autotrophic chemolithotrophs, which may be responsible for the enrichments in SO_4^{2-} , and which migrate in response to diel and seasonal redox regimes, probably dominate the prokaryotic community structure. Further, anaerobes need to turn over more substrate than do aerobes in order to generate adenosine (ATP) triphosphate with their shorter electron transport

chains. Indeed, the ratio of TEA reduced/ATP generated is substantially lower for anaerobes. With these considerations, it is easy to imagine situations in which a low bacterial biomass (and low rates of anabolism) could have very high rates of (catabolic) activity 'per-cell'. That anaerobes are 'inefficient' depends upon perspective.

Second, these phenomena are probably mediated by the hydrologic regime of Quiamog Cove. Presently, net sedimentation does not occur due to rapid historical accumulation within the cove up to the critical wave resuspension depth. The sediments can be described as soupy mud which are heavily bioturbated by soft-bodied infauna (especially holothurians such as *Thyone* spp.) and which are intermittently resuspended during storms (Matson 1982). Resulting episodic oxygenation, together with sufficient rates of anoxic metabolism that recharge the sediment with both methane and S^{2-} (and both occur within the top few cm; Hines & Buck 1982) may maintain a 'euryoxic' milieu at this intermediate Eh (Bouleague & Michaud 1979, Lord & Church 1983). Periodic oxygenation may then resupply the sediment with oxidized TEAs (via either chemical or biochemical reoxidation) for facultatively anaerobic bacteria. After reduction, these reduced TEAs then become electron donors for chemolithotrophs and add to the recycled oxygen demand with electrons originally released during the decomposition of organic matter under anoxia. They also provide chemolithotrophs with the energy required to reduce respiratory pore-water CO_2 back to organic matter. In this way, both carbon and energy are conserved under anoxia.

Perhaps this is why 'microbial cells in the environment may exhibit unbalanced growth, i.e., they may be capable of certain types of metabolism [catabolism] without a concomitant increase in biomass [anabolism].' (Novitsky & Karl 1986, p. 34, contents of parentheses added). Biomass may remain relatively constant under a regime of switched community metabolism between heterotrophy (when labile OC is abundant) and chemolithotrophy, when both O_2 and the end-products of anoxic heterotrophy (reduced TEAs and CO_2) are abundant. The occurrence of prolific populations of chemolithotrophic bacteria, especially in winter and spring (Sorensen et al. 1979, Matson & Brinson 1985, Graf 1986), may compound this paradox by adding organic matter to sediments via recycled CO_2 and reduced TEAs. This 'coupled heterotrophy and autotrophy' (Kepkay & Novitsky 1980) may also help explain why coastal systems apparently consume more than they produce. This coupling may also help explain the post-depositional persistence of organic matter in coastal sediments (e.g. Kepkay et al. 1979, Rowe & Howarth 1985).

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